The thermal biology of *Carcinus maenas* as a tool for conservation, mitigation, and invasion predictions

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Abstract

Carcinus maenas is a thermally tolerant invasive species that have successfully colonized every continent except Antarctica. Invasive species negatively impact native species, and *C. maenas*, in particular, has been implicated in the local losses of several ecologically important species. Anthropogenic activities are primarily to blame for species invasions, and climate change will exacerbate their dominance over native species. In this thesis, I explore the thermal ecology of *C. maenas* by mapping their thermal niche, modeling changes in abundance and temperature, and synthesizing thermal limits. Using mixed modeling of global abundance data, I show that the green crab abundance is not changing globally and that their abundance is related to temperature variability. By reviewing the literature, I show that green crabs have life-stage and region-specific tolerances. Juvenile green crabs appear to be the most vulnerable stage and may be responsible for driving changes in green crab abundance. I also review knowledge gaps and recommendations for future research, including standardizing methods and resolving unknown adult thermal limits. This thesis presents *Carcinus maenas* as an incredibly robust species with vast thermal tolerances promoting their global invasion.

General Summary

The European green crab (*Carcinus maenas*) is transported by shipping and trade. By developing populations and taking over food and habitats, green crabs threaten natives and are referred to as invasive. Native species are threatened by global temperature rise (climate change), while invasives have higher tolerances. Here, I explore how air and sea temperature impacts green crabs. I examine how green crab abundance has changed over the last 100 years and whether abundance changes relate to temperature change or variability. I show that abundance is not increasing through time and that temperature variability can predict changes in green crab abundance. I also review the literature on green crab thermal ecology and discuss gaps and recommendations for future research. My review points to life stage tolerance differences and suggests that juveniles are threatened by extreme heat or cold.

Co-Authorship Statement

All primary intellectual and practical contributions reported in this thesis were completed by Brandy S. Biggar and Amanda E. Bates.

Chapter 2

- I, Brandy Biggar, identified research questions, accumulated and analyzed the data, created the figures and tables, and wrote the chapter
- Cynthia McKenzie and Iain McGaw helped refine the objectives
- Alan Young, Brady Quinn, Christopher Bloch, Cynthia McKenzie, Emily Grason, Jennifer Yakamishyn, Markus Frederich, Michael Burrows, Ron Thresher, and Sylvia Yamada contributed data
- Amanda E. Bates helped design the conceptual framework, shared and edited code, and revised all aspects

Chapter 3

- I, Brandy Biggar, set up the research objectives, completed the review, analyzed the data, created figures and tables, and wrote the chapter
- Cynthia McKenzie and Iain McGaw helped conceptualize this chapter based on my findings from Chapter 2
- Amanda E. Bates helped refine the key messages and revised all my work

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Chapter 1

An introduction to green crab invasion history and biology

An introduction to green crab invasion history and biology

Introduction

Temperature consistently emerges as a dominant driver of species' behaviors and life-history processes, including growth (Cunningham and Read, 2003; McElhaney and Souza, 1976; Watanabe and Okada, 1967), reproduction (Hoegh-Guldberg and Pearse, 1995; Newell and Branch, 1980), and population dynamics (Angilletta, 2009; Magnuson et al., 1979; Pilot et al., 2006). Having a thermal dependence forces species to remain within their physiologically optimal environmental conditions; therefore, rising temperatures force thermally dependent species to shift their distributions higher (in elevation and/or latitude; Engelhard et al., 2014; Perry et al., 2005; Thomas, 2010) to compensate. Predicting changes to species distributions is an essential step in conservation and ecosystem management (Brown and Yoder, 2015; Elith et al., 2010; Reside et al., 2019). However, temperature changes are not geographically uniform, nor do they affect organisms equally (Angilletta, 2009; Berner et al., 2020; Brambilla et al., 2019), thereby making accurate predictions difficult. Species with a wide thermal tolerance breadth, a characteristic common in invasive species (Zerebecki and Sorte, 2011), may fare better with rising temperatures. Broad physiological tolerances, generalist diet, high transport potential, and sizeable reproductive output all contribute to the ability of invasive species to colonize unfamiliar habitats. This combination of traits strongly contributes to the prediction that invasive species will excel with global warming (Bellard et al., 2013; Dukes and Mooney, 1999; Sorte et al., 2013).

Species introductions occur as a result of human activity, either directly (e.g., pet trade, biological control; Early et al., 2016; Lockwood et al., 2019; Myers and Cory, 2017; Simberloff and Stiling, 1996), or indirectly (e.g., shipping and trade; Fernandez, 2007; O'Brien et al., 2017). However, not every species introduction results in an invasion (Figure 1.1; Sakai et al., 2001). Following transportation to a new location, species must survive in the new environmental conditions, which may require adaptations (Pergl et al., 2017; Sakai et al., 2001). After successful colonization, species must establish a self-sustaining population before spreading (Pergl et al., 2017; Sakai et al., 2001). The colonization and establishment of non-native species often has a cost to native species (e.g., competition, predation; Gallardo et al., 2015) and ecosystems (e.g., direct damages, eutrophication; Marbuah et al., 2014, Gallardo et al., 2015). These adverse effects are the final step for a species to be classified as invasive (IUCN, 2016; Simberloff, 2005).

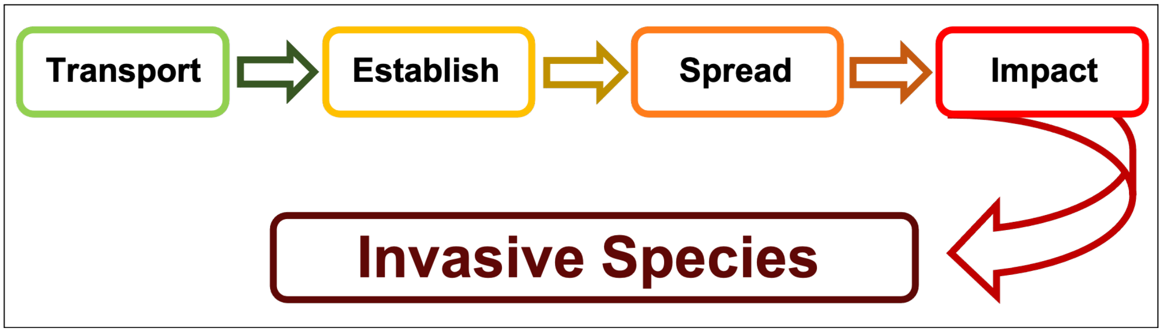

Figure 1.1 Invasion pathway. The steps a newly introduced species undergoes before classification as 'invasive'. Transport is the physical movement to a new habitat; establish is the species surviving new local conditions; spread is when they successfully reproduce and grow in numbers; impact is the last step in which introduced species must cause harm before being classified as 'invasive'. Based on Sakai et al., 2001.

Studying invasion dynamics benefits many fields, including conservation ecology (Davis, 2006; Hobbs and Huenneke, 1992), evolutionary ecology (Vermeij, 1996; Zenni et al., 2013), and macroecology (Kondoh, 2006; Tepolt and Palumbi, 2020). Isolated populations of the same species can develop genetically unique tolerances (microevolution), offering insights into genetic drift and phenotypic variation (Baker et al., 1990; Clegg et al., 2002; Tepolt and Somero, 2014). Due to multiple global invasions, several reproductively isolated groups are available for comparison, making *Carcinus maenas* an excellent model species for studying ecological theory (Carlton and Cohen, 2003; Klassen and Locke, 2007).

Invasion History

Carcinus maenas (Linnaeus, 1758) is a small green shore crab and highly invasive species that has, since the 1800s, traveled the globe to every continent except Antarctica (Carlton and Cohen, 2003; Cohen et al., 1995; Klassen and Locke, 2007). The common name for this species is the European green crab, whereby the "European" distinction differentiates *C. maenas* from *Carcinus aestuarii*, the Mediterranean green crab (Carlton and Cohen, 2003; Furota et al., 1999). The European green crab (hereafter, green crab) is native to Europe and North Africa (Carlton and Cohen, 2003; Cohen et al., 1995; Klassen and Locke, 2007), with a home range encompassing the area surrounded by Iceland, Norway, the Baltic and Mediterranean Seas, Mauritania, and Morocco (Roman and Palumbi, 2004; Tepolt and Palumbi, 2020).

The first and most well-known green crab invasion was in eastern America in the 1800s (Say, 1817). Despite confusion and debate about this initial invasion, *C. maenas* is generally agreed to have first colonized the eastern seaboard between Rhode Island and New York (NY) (Carlton and Cohen, 2003; Cohen et al., 1995; Klassen and Locke, 2007). By 1872, the green crab spread north to Cape Cod and then to Maine by the 1890s (Figure 1.2). *C. maenas* was first reported in Canada in July 1951 on the Digdeguash River, New Brunswick (NB) (Klassen and Locke, 2007). Throughout the 1950s, *C. maenas* expanded to St. Mary's Bay and Minas Basin, Nova Scotia (NS) (Cohen et al., 1995; Klassen and Locke, 2007). Meanwhile, in the 1960s, the green crab appeared to have reached its northern limit around Halifax, NS, when spreading halted for several decades (Leim, 1951; Roman, 2006). It was not until the 1990s that green crabs were discovered farther north in Cape Breton and Bras d'Or Lake, NS, and Georgetown, Prince Edward Island (PEI) (Carlton and Cohen, 2003; Klassen and Locke, 2007; Roman, 2006). The dispersal of the green crab through the Northumberland Strait (between PEI and mainland NS and NB) was the most rapid expansion on record, reaching dispersal speeds up to 100 km per year (Klassen and Locke, 2007). Green crabs were officially recorded in Placentia Bay, Newfoundland and Labrador (NL) in 2007 but had been observed several years earlier by fisherpersons (Best et al., 2017; Blakeslee et al., 2010; Jeffery et al., 2017). Over a decade later, the Placentia Bay green crabs have become well-established and spread westward into nearby Fortune Bay, a vital Lobster fishery (Fisheries and Oceans Canada (DFO), 2018). A second Newfoundland invasion, first detected in Stephenville, occurred on the island's west coast in 2008 (DFO, 2018). Additionally, the crabs spread north to Bonne Bay by 2010 and now reach Port Saunders on the northwest edge of the island (DFO, 2018). Green crabs have not been identified along the northeast coast of Newfoundland or anywhere in Labrador (Figure 1.2). This Atlantic group has persisted for over 200 years.

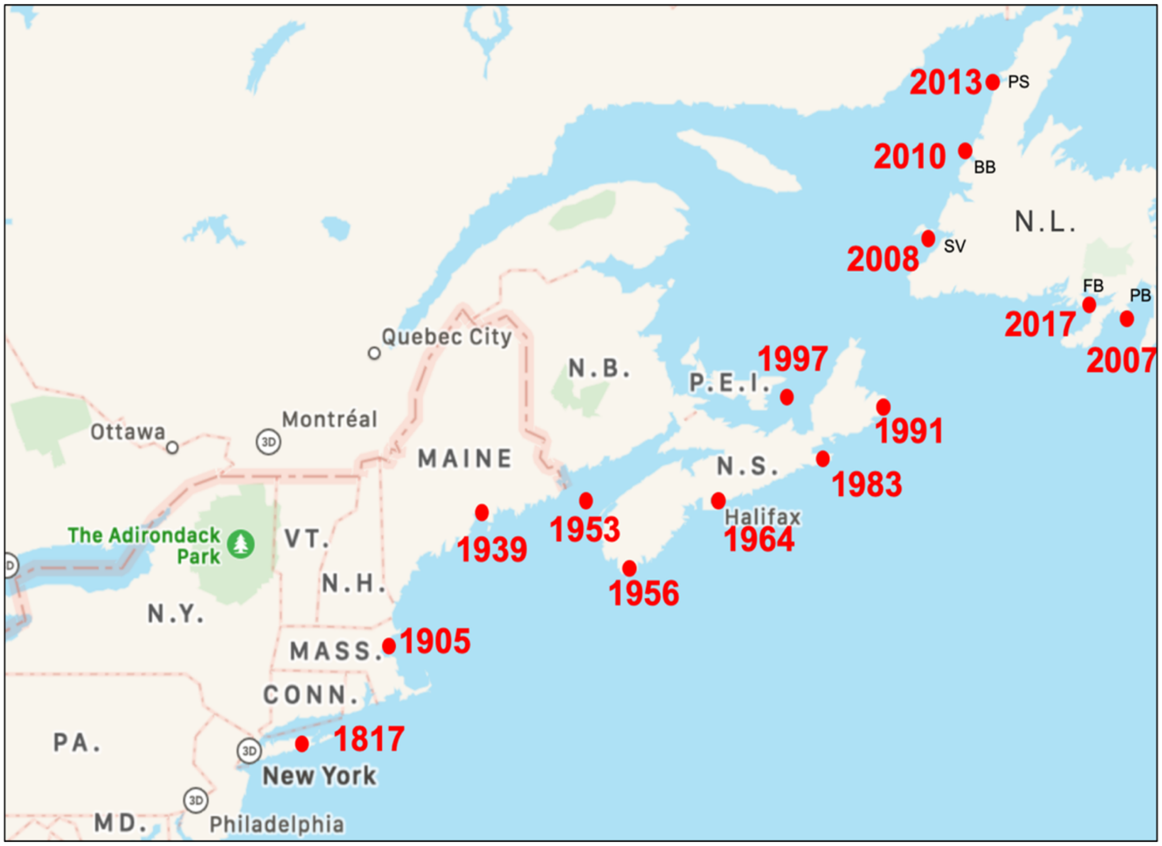

Figure 1.2 Map of eastern North American *Carcinus maenas* invasion. The North American invasion of the Atlantic coast began in the south in 1817 and rapidly spread north. Abbreviations clockwise around Newfoundland starting from the earliest date: PB: Placentia Bay, FB: Fortune Bay, SV: Stephenville, BB: Bonne Bay, PS: Port Saunders. Invasion dates primarily based on Carlton and Cohen, 2003; Cohen et al., 1995; Klassen and Locke, 2007.

Around the time green crabs were gaining a strong foothold in northern NS (1990's), they were also beginning to invade the western Pacific coast of North America. The first west American green crab was reported in San Francisco Bay, California (CA) (Cohen et al., 1995; Figure 1.3). By 1994, they spread north to Bodega Harbor, CA, and south to Monterey Bay, CA (Carlton and Cohen, 2003; Grosholz and Ruiz, 1995). In 1997, green crabs were reported in Oregon and Washington (Carlton and Cohen, 2003; Yamada et al., 2015). Meanwhile, in 1999, they made landfall in Canada, with reports in Barkley Sound and Esquimalt Harbour, British Columbia (BC) (Klassen and Locke, 2007). At the same time that green crabs were invading Newfoundland on the east coast (2007), they reached Quatsino Sound, BC, northern Vancouver Island (DFO, 2018). The Strait of Juan de Fuca was invaded in 2012, and San Juan Island in 2016 (Brasseale et al., 2019; Figure 1.3).

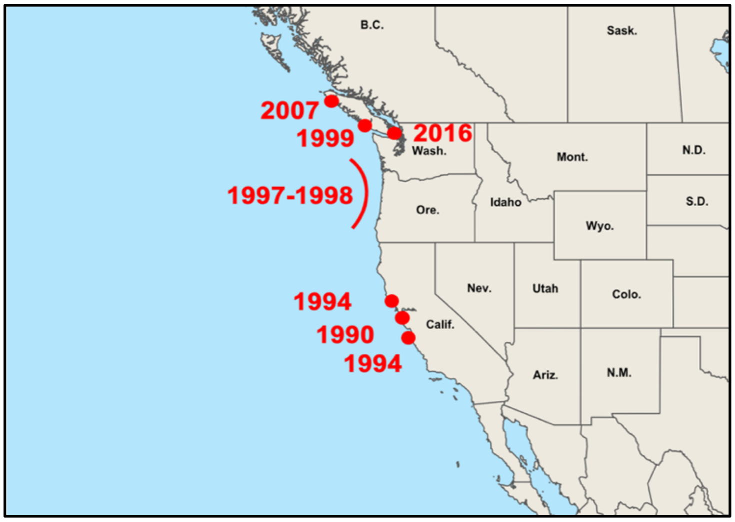

Figure 1.3 Map of western North American *Carcinus maenas* invasion. Beginning in California, 1994, the Pacific invasion spread north up the coast to British Columbia. Invasion dates, Carlton and Cohen, 2003; Cohen et al., 1995; Klassen and Locke, 2007.

The third well-documented and well-established *Carcinus maenas* invasion is in Australia. *C. maenas* was first reported in Port Phillip, Victoria, in 1900 (Carlton and Cohen, 2003; Figure 1.4A). While in 1993, the green crab made it to northern Tasmania, and in 1995 there was a report of a single male in Perth (Carlton and Cohen, 2003). Tanner (2007) reports that green crabs are abundant along Australia's coasts. However, Thresher et al. (2003) conducted a trapping study around Australia and found green crabs in Victoria, southern New South Wales, and northern Tasmania. Overall, there are fewer recorded observations for the invasive west Pacific green crabs than the other invasions.

The last well-established invasive group of *Carcinus maenas* is South Africa; this group is not well documented. In 1983, green crabs reportedly inhabited Table Bay Docks, South Africa (Carlton and Cohen, 2003). In 1990, Le Roux et al. (1990) reported that the crab had spread to nearby sites. However, nearly 20 years later, Mabin et al. (2017) found green crab abundance decreasing in South Africa; the only reproducing crabs remaining were at Table Bay and Hout Bay harbors (Figure 1.4B). Unlike the North American green crabs, this group does not appear to be thriving. Mabin et al. (2017) suggest that the South African wave action is too intense for the crab to prosper. Green crabs have persisted at sheltered artificial harbors (Mabin et al., 2017), suggesting that anthropogenic changes may benefit green crabs in some scenarios. Due to the inadequate data available, this invasive group is not discussed further in this thesis.

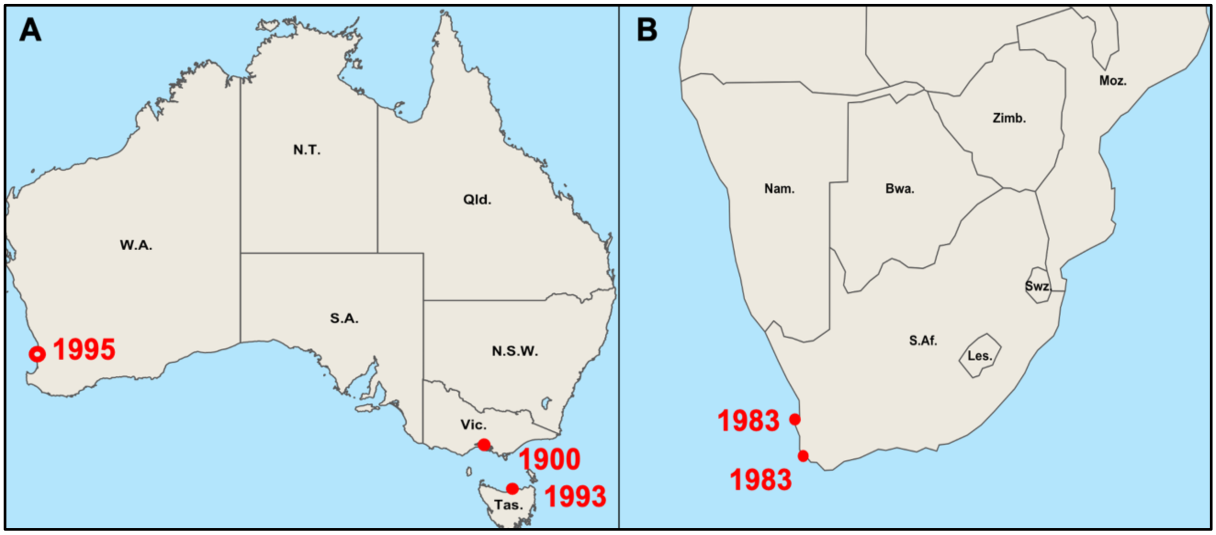

Figure 1.4 Map of Southern Hemisphere *Carcinus maenas* invasions. A) The southwest Pacific invasion was first documented in Victoria, Australia. A single report was recorded in 1995 from Perth. B) The South African group persists only in Table Bay and Hout Bay harbors. Invasion dates, Carlton and Cohen, 2003 and Mabin et al., 2017.

There are only four well-established invasions of *C. maenas*, but many other regions have reported single sightings (Carlton and Cohen, 2003; Cohen et al., 1995; Klassen and Locke, 2007; Figure 1.5). Individuals have been reported from Rio de Janeiro (1857), Panama (1866), Sri Lanka (1867), Hawaii (1873), Madagascar (1922), Myanmar (1933), Pakistan (1971), and Japan (1984). Some papers suggest that the Japan sightings were the closely related species *Carcinus aestuarii* (Thresher et al., 2003). However, both *Carcinus* species have been confirmed (molecularly) in Tokyo (Carlton and Cohen, 2003; Geller et al., 2003).

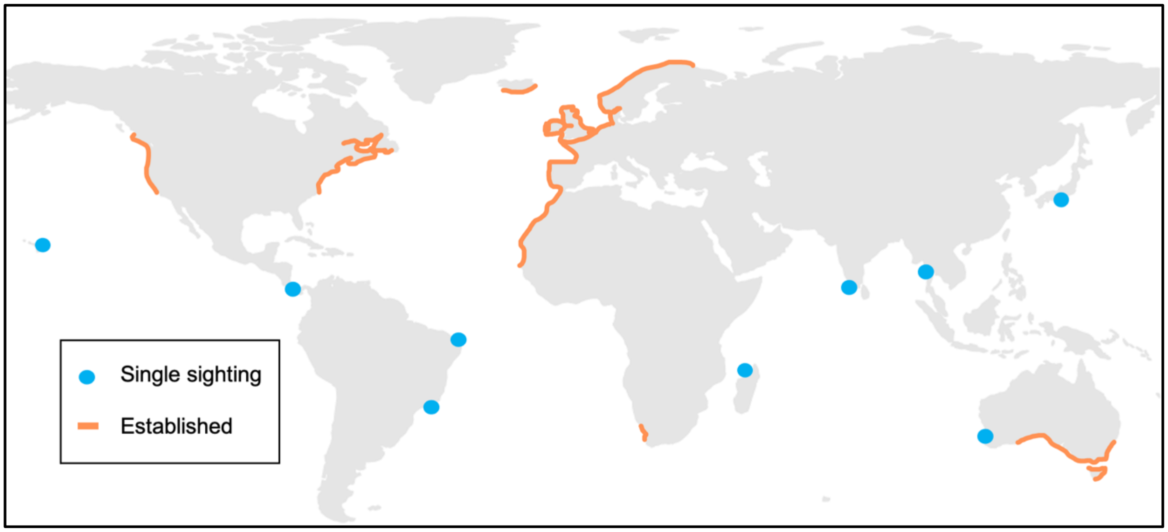

Figure 1.5 Map of established *Carcinus maenas* ranges. Established green crabs (orange) and single sightings (blue). Invasion dates, Carlton and Cohen, 2003; Cohen et al., 1995; Klassen and Locke, 2007.

When the invasive west Atlantic green crabs stopped expanding their distribution north (Halifax, Nova Scotia (NS), 1960's), they were believed to be limited by the colder Canadian climate (Roman, 2006). Therefore, when they rapidly expanded their distribution and abundance in the Northumberland Strait, the warming global temperatures were implicated (Roman, 2006). In 2006, Roman conducted a genetic analysis on crabs from New York to Prince Edward Island; he found that at least five new lineages had been introduced to NS, bringing much higher genetic diversity to the newly invaded region (Roman, 2006). Studies also compare invasive west Atlantic genetic data with native Atlantic genetics and found that the "second wave" into eastern North America was consistent with crabs from northern Europe (Jeffery et al., 2017; Tepolt and Palumbi, 2020). The northern European crabs are better adapted to cold, which may have aided their invasion into Newfoundland (NL) (Coyle et al., 2019; Tepolt and Palumbi, 2020). Contact between crabs from the two invasions occurred around NS, resulting in a hybrid group (Lehnert et al., 2018). The hybrid crabs were the first to invade and establish in NL (Tepolt and Palumbi, 2020), leading to reports that hybrids are even more cold-hardy than the northern crabs. When *C. maenas* invaded NL a second time (west coast), it was by the northern European crabs (Jeffery et al., 2017). These groups currently remain separated within Newfoundland (Fisheries and Ocean Canada (DFO), 2018); however, warming temperatures and increased global trade may favor the expansion of their distributions.

Green crab biology

The green crab has several characteristics that promote transport and establishment in new locations where it is a fierce competitor to native species with significant ecosystem impacts (Boudreau et al., 2013; McDonald et al., 2001; Walton et al., 2002). Thus, the green crab ranks amongst the 100 worst invasive species (IUCN, 2016). In Atlantic Canada*, Carcinus maenas* overlaps in habitat and diet with the most commercially important decapod species, the American lobster (*Homarus americanus*), which generates 1.6 billion dollars per year in the Canadian Atlantic regions (DFO, 2019). Beginning in 2007, *H. americanus* landings in Atlantic Canada decreased (for several years in a row), coinciding with the introduction of *C. maenas* (Rayner and McGaw, 2016; DFO, 2007); however, they have since recovered (since 2011; DFO, 2011). In previous laboratory experiments in the invasive west Atlantic range, green crabs have out-competed juvenile lobsters for food and shelter; one study even found that *C. maenas* consumed juvenile lobster (League-Pike and Shulman, 2009; Lord and Dalvano, 2015; Rayner and McGaw, 2016; Rossong et al., 2006). Globally, studies have linked green crabs to negative impacts on shellfish (Floyd and Williams, 2004; Grosholz et al., 2011; Miron et al., 2005), other crabs (Jensen et al., 2002; MacDonald et al., 2007; McDonald et al., 2001), and commercial fisheries (Kern et al., 2002; Walton et al., 2002). Perhaps the greatest threat of all is the green crab's decimation of the common eelgrass (*Zostera marina*). *Zostera marina* is an essential foundation species that provide nursery grounds for commercially important species, including Atlantic cod (*Gadus morhua*) and American lobster (Heck et al., 1995; Matheson et al., 2016). Numerous studies have attributed eelgrass loss to the green crab, which digs for prey in the substrate, cuts shoots, and decreases sunlight by sediment accumulation (Davis et al., 1998; Garbary et al., 2014; Malyshev and Quijón, 2011; Matheson et al., 2016; Neckles, 2015).

Carcinus maenas is a high-impact invasive species with high phenotypic plasticity, generalist diet, and large temperature and salinity tolerances (Cohen et al., 1995; Tepolt and Somero, 2014). In agreement with the plasticity-invasion hypothesis (i.e., high phenotypic plasticity aids in invasion success), Edgell and Hollader (2011) credit the green crabs' invasion success to their ability to rapidly adjust physiology, behavior, and morphology (i.e., phenotypic plasticity). Green crabs can also rapidly adjust their behavioral and morphological predation response (Battini and Bravo, 2020; Edgell and Hollander, 2011). For example, feeding type (e.g., shell crushing versus aperture-probing) and large claw size have been correlated with gastropod shell-type (Edgell and Hollander, 2011). Although *C. maenas* primarily feed on bivalves and gastropods, gut content analyses and feeding experiments show that they consume at least 158 different genera (Cohen, 1995; Cohen et al., 1995; Kelley, 2013), including neurotoxic sea slugs (Battini and Bravo, 2020). Furthermore, green crabs are opportunistic feeders with a wide range of feeding styles, including cannibalism (Klassen and Locke, 2007; Pardal et al., 2006), nutrient absorption across the gill membrane (Blewett and Goss, 2017), kleptoparasitism of con- and heterospecifics (Boudreau et al., 2013; Quinn et al., 2011), and even surviving starvation for three or more months (Edgell and Hollander, 2011). As a eurythermal (34 to -1 ºC; Ahsanullah and Newell, 1977; Cohen, 1995; Kelley, 2013) and euryhaline (54 to 1.4‰ S; Broekhuysen, 1936; Cohen, 1995) ectotherm, *C. maenas* live in various habitats, commonly found from the inter- to subtidal to a depth of six meters (but occasionally down to 60 m; Cohen, 1995; Crothers, 1968). Habitats include rocky coasts, sand, mud, *Zostera marina* beds, and marshes (Cohen, 1995; Kelley, 2013).

Carcinus maenas further facilitate their invasion success with a broad breeding potential (high fecundity), variable time-to-maturation, and specialized reproductive morphology (Klassen and Locke, 2007). Females spawn one to two times per year, laying up to 185,000 eggs at a time (Berrill, 1982; Klassen and Locke, 2007). *Carcinus maenas* eggs hatch and metamorphose through three zoeae and one megalopa stage (all planktonic) before settling on the benthos as juvenile crabs (Berrill, 1982; DiBacco and Therriault, 2015). Female green crabs reach reproductive size after one to three years (Berrill, 1982; Klassen and Locke, 2007). Maturation age is reached earlier in the Pacific than in the east or west Atlantic (Berrill, 1982). When a female is ready to mate, she emits a pheromone, and her chosen mate takes up guard duty until she molts; mating occurs while the female is soft-shelled (Berrill and Arsenault, 1982; Christy, 1987; Klassen and Locke, 2007). Male green crabs can improve their reproductive standings by remaining in the intermoult stage; increased intermoult makes the carapace larger and thicker, especially the master claw (McGaw et al., 1992; Reid et al., 1997; Styrishave et al., 2004). Lengthened intermoult also causes color morphs in green crabs, with longer intermoult resulting in a red-pigmented carapace (McGaw et al., 1992; McGaw et al., 2011; Reid et al., 1997; Styrishave et al., 2004). However, prolonged intermoult comes at a trade-off, including lowered tolerance, competitive disadvantage, and compromised physiology (Himes et al., 2017; McGaw and Naylor, 1992; Styrishave et al., 2004). Green crabs typically live up to seven years and reach a maximum size of 10 cm (carapace width; Klassen and Locke, 2007). *C. maenas* is highly studied and often referred to as a model species (Leignel et al., 2014; Rodrigues and Pardal, 2014).

Thesis objectives

The overall objective of this thesis is to explore the distribution and thermal ecology of *Carcinus maenas*. In Chapter 2, the objectives were to explore the distributions of the native and invasive green crabs and the changes in temperature and abundance through time. I use two-stage linear mixed effect models of year-to-year temperature and abundance changes to make informed predictions regarding the potential impacts of hotter and colder than average air and sea surface temperatures. I also compare the impact of extreme weather events on *C. maenas*. In Chapter 3, the main objectives were to review and summarize the *C. maenas* thermal ecology literature and synthesize quantitative thermal limits of the green crab. I summarize the knowledge gaps and make recommendations for future research.

Significance

In 2008, a multi-departmental (Fisheries and Ocean Canada, Department of Fisheries and Aquaculture, and Memorial University of Newfoundland) crab harvest removed over 25,000 lbs (~350,000 individuals) of green crab from Newfoundland in 20 days (Blakeslee et al., 2010). Despite these mitigation attempts (and others like them), the invasive green crab continues to expand its range throughout Atlantic Canada (Blakeslee et al., 2010). This attempt suggests that, as temperatures continue to rise and global trade increases, green crabs will contunie to expand and increase their detrimental effects.. Therefore, it is imperative to improve our understanding of the abiotic factors impacting green crab distribution.

Chapter 2

Temperature variability predicts abundance change in invasive and native European green crabs, *Carcinus maenas*

Temperature variability predicts abundance change in invasive and native European green crabs, *Carcinus maenas*

Abstract

Climate change and global trade are accelerating the transport and subsequent spread of species outside their native regions. Characteristics that elevate the likelihood of species transport and establishment are the same attributes that give them an advantage over native species, including broad geographic extent, high environmental tolerances, and generalist diet. Using time-series abundance data from four unique geographical locations, I show that green crab abundances are increasing in the warm and warming regions of the native and invasive Atlantic ranges. Furthermore, thermal variability from one year to the next predicts fluctuations in *C. maenas* abundance. Moreover, I show that invasive crabs are located in regions with air and sea surface temperatures more extreme than what they experience in their native range. These findings implicate that *C. maenas* live in diverse thermal environments that differ from their native range, are sensitive to environmental variability, and may prosper under winter warming.

Introduction

Globalization has increased transport networks and inadvertently escalated introductions of species to geographic locations outside their native range (Bates et al., 2013; McNeely, 2000; Molnar et al., 2008). While some new species introductions have minimal or even positive impacts (King et al., 2006; Matheson and Gagnon, 2012; Rodriguez, 2006; Rodriguez-Cabal et al., 2012), others spread rapidly and have wide-ranging direct and indirect negative impacts (Molnar et al., 2008; Pimentel et al., 2005; Vila et al., 2011). Introduced species that negatively impact the ecosystem are referred to as invasive and can cause biodiversity loss (Butchart et al., 2010; Doherty et al., 2016; Orth et al., 2006), regime shifts (Gaertner et al., 2014; Shackleton et al., 2018), and species extinctions (Blackburn et al., 2004; Buckton, 2001; Burbidge and Manly, 2002), all of which impact natural resources and economic activities (Holmes et al., 2009; Pimentel et al., 2005; Sakai et al., 2001; Xu et al., 2006). Species invasions are rapidly increasing in distribution and abundance with no sign of slowing (Hulme, 2009; Miller et al., 2021).

Research suggests that invasive species fare better than natives under climate change (Bates et al., 2013; Bellard et al., 2013; Sorte et al., 2013), as species with larger thermal tolerances are physiologically better prepared for temperature change and variability. Invasiveness (capacity to invade; Higgins and Richardson, 2014) is related to traits that increase survival in heterogeneous environments such as high fecundity (Labrie et al., 2006; Moravcová et al., 2010), extreme environmental tolerance (e.g., salinity, temperature, oxygen; Fenollosa and Munné-Bosch, 2020; Zerebecki and Sorte, 2011), and generalism (e.g., diet, habitat; Crowder and Snyder, 2010; Gallagher et al., 2015). Moreover, generalists often inhabit broad geographic regions and have a greater probability of transportation to new locations (Bates et al., 2013; Devictor et al., 2008, Edgell and Hollader, 2011; Higgins and Richardson, 2014, Zerebecki and Sorte, 2011). Therefore, high invasiveness increases the capacity to survive, establish (Clavel et al., 2011; Hellmann et al., 2008), and out-compete natives (Solter et al., 2013; Weis, 2010).

Niche conservatism theory suggests that introduced species are most likely to establish in environments similar to their native habitat (Broennimann et al., 2007; Peterson, 2003). Therefore, species distribution models make invasion predictions based on the native niche (Broennimann et al., 2007; Elith et al., 2010; Peterson, 2003); where niche refers to the combined set of biotic and abiotic factors defining a species habitat (Brown, 1984; Hutchinson, 1957). However, species and ecosystems are spatially and temporally dynamic; therefore, despite expectations (niche conservatism; Broennimann et al., 2007; Robertson et al., 2008), invasive and native environmental conditions do not always match (niche mismatch; Broennimann et al., 2007; Early and Sax, 2014; Petitpierre et al., 2012; Tingley et al., 2014). Several studies have provided evidence for shifts in species geographic ranges (Nania et al., 2020), thermal niches (Gallagher et al., 2010; Srivastava et al., 2020), and even temporal niches (Harrington et al., 2009). Niche shifts occur by evolution (e.g., new traits expand habitable area) or release from constraining factors (e.g., reduction in competition; Broennimann et al., 2007). By nature of their high adaptability, invasive species occasionally undergo niche shifts (Tingley et al., 2014), suggesting that species distribution models based on climate matching may not always be accurate (Early and Sax, 2014).

Although many abiotic factors can successfully predict species' geographic patterns, temperature often emerges as one of the strongest predictors (Angilletta, 2009; Bykova et al., 2012; Frenne et al., 2013). Therefore, despite the potential for niche mismatch discussed above, temperature is a strong determinate of species distributions due to its correlation with processes from the cellular level (e.g., metabolic theory, Valladares et al., 2014; temperature-size rule, Angilletta and Dunham, 2003) to communities and macroecological patterns (e.g., latitudinal diversity gradient, Hillebrand, 2004; Pianka, 1966; Roy et al., 1998). In fact, Magnuson et al. (1979) proposed that temperature be considered a resource that individuals both rely on and compete for (e.g., habitats in optimal thermal zones). Therefore, the rise of global mean temperatures (0.18 ºC per year since 1981; NOAA, 2020) is expected to cause wide-ranging impacts to species health and geographic distributions (Easterling et al., 2000; Parmesan, 2006; Parmesan and Yohe, 2003; Walther et al., 2002). For instance, species niches are expected to shift poleward (broadening on their cold edge and shortening on their warm edge; Chen et al., 2011; Easterling et al., 2000; Hampe and Petit, 2005) to counteract the adverse physiological effects of warming (Baldanzi et al., 2015; Methorst et al., 2017; Sunday et al., 2012). Hence, environmental temperatures that characterize a species' niche underpin predictions of future invasions. Key research areas include understanding how temperature relates to abundance change, correlates with other abiotic factors, and predicts distribution shifts.

Despite documented niche mismatches, general patterns commonly emerge in how temperature structures species distributions along environmental gradients. In particular, abundances are often highest near the center of species distributions (e.g., geographic distribution) and decrease towards the edges (Brown, 1984; Sagarin and Gaines, 2002; Waldock et al., 2019). This bell-shaped distribution pattern occurs from the geographic alignment of environmental gradients, whereby optimal conditions occur mid-range (Sagarin and Gaines, 2002; Vye et al., 2020). Furthermore, thermal and geographic niches are (negatively) correlated (i.e., latitude-temperature gradient; Chaudhary et al., 2017; Jurgens and Gaylord, 2018; Zhang et al., 2019); thus, the poleward edge of species distributions are typically the coldest, while the equatorward edges are the warmest (Greiser et al., 2020). In response to warming temperatures, species distributions may shift poleward to reduce physiological stress at the warm edge and take advantage of new habitat space that emerges with warming (Parmesan and Yohe, 2003; VanDerWal et al., 2013; Walther et al., 2002).

Species with broad geographic ranges (typical in invasive species) present a compelling opportunity to examine fundamental theories of invasion success in novel spaces and test predictions of macroecological patterns. *Carcinus maenas*, the European green crab, is a model species with several widespread and geographically distinct ranges, which may be compared in a macroecology framework to test ecological theory. Furthermore, because green crabs are extensively monitored with several publicly available time-series databases (e.g., Biodiversity Information Serving Our Nation, BISON; INaturalist; BioTime), this species an ideal model to examine responses in difference geographic regions which have distinctive temperature regimes.

Here, my overarching objective is to characterize the thermal range of *Carcinus maenas* on different continents and test how changes in air and sea surface temperatures influence abundance trends. I first quantify the thermal niche of the green crab in its native (northwest Atlantic) and invasive (northeast Atlantic, northeast Pacific, and southwest Pacific) regions. Based on niche conservatism theory (Broennimann et al., 2007;

Peterson, 2003), I expect thermal niche matching between the GEOGRAPHIC? ranges (although see discussion above). Next, I use a meta-analytic framework to relate changes in green crab abundance to changes in remotely-sensed air and sea surface temperatures through time. Based on *C. maenas'* suite of invasive traits and successful invasion history, I predict that green crab abundances in the four study regions have increased through time, especially where air and sea surface temperatures are warming. Finally, I test whether green crabs living on the edge of their distribution will be more sensitive to year-to-year variability in summer and winter air and sea surface temperatures (abundant-center hypothesis, Brown, 1984). Thus, I predict that green crab abundances relate to air and sea surface temperature variability, especially at the GEOGRAPHIC? range edge.

Methods

Distribution data. To identify and map the global distribution of *Carcinus maenas* and determine its thermal limits, I collected occurrence datasets from the following online databases: Global Biodiversity Information Facility (GBIF, gbif.org), Ocean Biodiversity Information System (OBIS, obis.org), iNaturalist (inaturalist.org), and Biodiversity Information Serving Our Nation (Bison, bison.usgs.gov). All geolocated occurrence observations matching "*Carcinus maenas*" were included (i.e., *Carcinus sp.* and *Carcinus aestuarii* were excluded).

Abundance data. I compiled twenty-six abundance datasets from eight countries and fourteen states or provinces to quantify changes in *C. maenas* abundance (Supplementary Table S1.1). I acquired *Carcinus maenas* abundance data from the online databases

BioTime (Dornelas et al., 2018) and the Department of Fisheries and Oceans community aquatic monitoring program (DFO CAMP). Next, I searched the Web of Science (Clarivate Analytics, 2021) abundance data collected at the same site through time (minimum four years) using the keywords ("green crab" OR "*Carcinus maenas*") *AND* (abundance OR time-series). The authors were contacted to request collaboration and data access. If collaboration was not an option, data were extracted from the paper using Web Plot Digitizer (apps.automeris.io/wpd) or Tabula (tabula.technology, Harrington et al., 2009). The datasets were divided into those that targeted entire species assemblages, and those that targeted the green crab specifically—ten assemblage-level survey studies (collected with trawls, grabs, and seins) and sixteen targeted-sampling surveys (quadrats, transects, and traps) were obtained. For community datasets, site-by-species matrices were computed to represent all date-site combinations, thereby including sampling units where *C. maenas* was absent.

Temperature data. Two satellite temperature datasets, air temperature (AirT) and sea surface temperature (SST), were selected to quantify changes in temperature at each study location and time. Air temperature data were obtained from the Natural Environment Research Council's data repository for atmospheric science and earth observation (CRU-TS3.26, Harris et al., 2020). These data are gridded at a 0.5º spatial resolution and collected monthly, spanning 1901 to 2017. Sea temperatures were downloaded from the Met Office Hadley Centre's satellite sea ice and sea surface temperature (SST) data set (HadISST; Willmott and Matsuura, 2001). HadISST data are in a 1º grid format, spanning from 1870 to present. Both temperature data sets were downloaded as NetCDF files, and the package "RNetCDF" was used to view and manipulate the data (Michna and Woods, 2017). These temperature data were chosen for their long records dating back to the start of the green crab data. It was essential to match abundance and temperature data temporally to quantify relative thermal change.

Temperature data were matched to corresponding *C. maenas* occurrence records to calculate the thermal range of each region (native Atlantic, invasive Atlantic, invasive east Pacific, and invasive southwest Pacific). AirTs and SSTs were matched to abundance observations by date and geolocation based on Euclidean distance to identify trends through time. I took the minimum and maximum AirT and SST of the previous year for each date and location, resulting in four temperature variables: max AirT, min AirT, max SST, and min SST (Code S2.1). Minimum and maximum temperatures were selected to represent the maximum hot and minimum cold temperatures (SST) at each site. To examine trends in the warm and cold edges of the GEOGRAPHIC? range, I took the mean SST of the previous decade to represent the climatology. The climatology variable assumed that a long-term (10-year) temperature average would be representative of the location within each range (i.e., the northern cold edge, warm center, or southern hot edge).

Statistical analyses. Analyses were completed using RStudio Version 1.1.456 (R Core Team, 2018). Modeling began with a global model incorporating all predictors (maximum air temperature, minimum air temperature, maximum sea surface temperature, minimum sea surface temperature climatology) and covariates (site, study, region). I then used a combination of backward selection and Akaike Information Criterion (AIC) to determine the best fit. I scaled the predictor and covariate variables to improve model stability and allow direct effect size comparisons (Harrison et al., 2018). Model assumptions were checked by examining residuals and Q-Q plots.

Five-year temperature and abundance were modeled using a two-stage approach to determine if *C. maenas* abundance has increased in regions with warming. In the first stage, generalized linear models estimate changes in abundance and temperature over five years (glm, package: MASS; Venables and Ripley, 2002). Studies with more than seven years of sampling were split into ca. five year (4-7) blocks to standardize study duration and reduce heterogeneity in the slope estimates due to study duration (i.e., an eight year study was split into two four year studies). Longer studies have shallower slope estimates. A follow-up analysis with only studies of ≥10 years was conducted to ensure the data set splitting did not influence the interpretation of results. The four different temperature variables and abundance were modeled separately for each site (5 models were run for 639 sites) and the slope represents the site-level change over the ~ five years. The slopes of abundance and temperature parameters were extracted for inclusion in the second modeling stage (hereafter abundance slopes and temperature slopes). Slopes were plotted to visualize how many sites had positive versus negative trends (i.e., increase/decrease through time). Intercept models of each abundance and temperature variable were modeled to determine the expected mean, as another indication of whether the five-year change was positive or negative.

In the second modeling stage, the abundance slopes were modeled as the response to each temperature slope (from stage one) for each region (4 models for 639 sites). Models were visually inspected to ensure goodness of fit. I used linear mixed-effects models (lme, package: nlme; Pinheiro et al., 2019) for the stage two modeling process to consider the data's inherent nested structure (site within study) as a random effect. I also used the fixed variance option to account for residual variability.

To measure variability between years (hereafter distinguished as "year-to-year variability"), the residuals from each first stage slope model (abundance and temperatures) were extracted. Linear mixed-effects modeling was used to analyze the response of year-to-year abundance to year-to-year temperature differences (lme, package: nlme; Pinheiro et al., 2019).

Results

Distribution. *Carcinus maenas* is a globally distributed and widely monitored species. Based on publicly available observations (GBIF; Figure 2.1A), I show that the green crab has been observed on every continent except Antarctica. However, there are four persistent established regions of green crabs. The native range encompasses northern Africa up to northern Norway and has the most considerable latitudinal extent (34.5º; 36º N to 70.5º N). The eastern coast of North America is the most geographically restricted (latitudinally) invasive range (12º; 38º to 50º N), with the longest-standing presence in eastern North America (1817 to 2021; Say, 1817). The invasive east Pacific crabs had the second-largest latitudinal extent (32º; 20.5º to 52.5º N), from the Gulf of California to

Haida Gwaii, BC. The fourth group stretches around Australia's south and east coasts from southern Tasmania to Gladstone, Queensland (20º; 23.5º to 43.5º S). The native and invasive Atlantic crabs had the heaviest sampling over the longest time, and the northern hemisphere had the most observations (80,000 versus 250).

The mean air temperature over the study period (1900 to 2020) was coolest in the invasive Atlantic range, with the other invasive regions tending to lie on the warmer edges of the native climate niche (mean air temperatures: 12.7 ºC east Pacific, 14.8 ºC southwest Pacific, 9.4 ºC native, 7.9 ºC west Atlantic). The invasive Atlantic range experienced more extreme air and sea surface temperatures than the native Atlantic crabs (Figure 2.1B,C). The invasive Atlantic air temperatures were cooler (minimum) and warmer (maximum) than the native's thermal niche. The invasive Atlantic's minimum winter air temperature was 4 ºC colder than the native Atlantic's, while the summer air maximum was 2 ºC warmer. The invasive east and southwest Pacific crabs had summer and winter sea surface and air temperatures within the native Atlantic's thermal niche, but mainly on the warmer end (Figure 2.1B,C).

Abundance and temperature trends. I used a generalized linear modeling approach to quantify changes in abundance and temperature (winter AirT, summer AirT, winter SST, summer SST) over five years. I plotted the slopes for each site to visualize overall trends (Figure 2.2), then added the mean of the slopes and the expected mean from the intercept models (Table S2.3) to clarify the overall trend. From these plots and the intercept models, green crab abundances did not systematically increase or decrease over the time spans present in the data, based on the five-year blocks the time was split into. All regions had sites with increasing and decreasing *C. maenas* abundance (the distribution of the slopes fall ca. symmetrically above and below zero). Temperature trends did not show any systematic change over the periods of study. Due to insufficient data, I could not run first-stage models for the invasive southwest Pacific crabs, so I plotted the raw data to visualize any emergent trends (Figure 2.3).

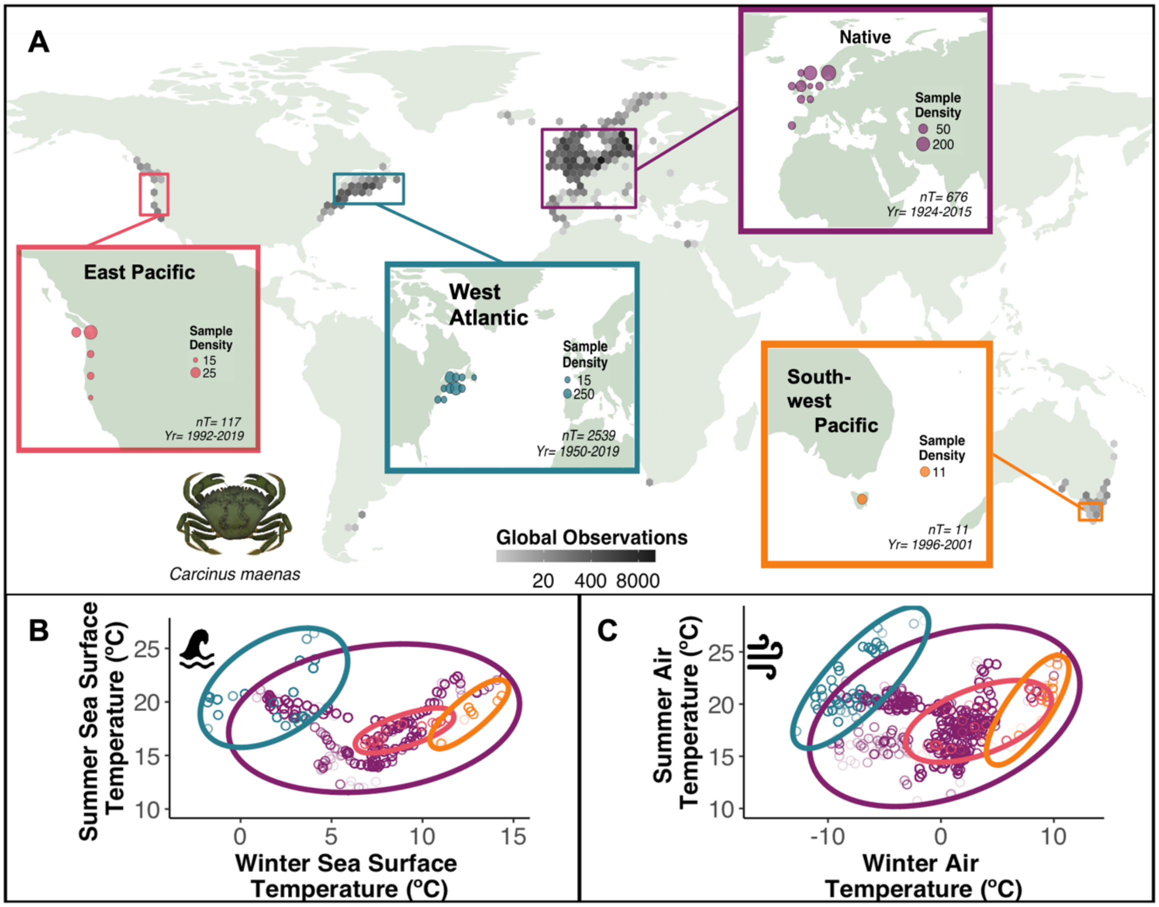

Figure 2.1 The distribution of *Carcinus maenas*. A) Globally recorded observations from online databases (grey; 1900 to 2020). Regions of study (colored squares) along with relative sampling density, total number of observations (nT), and years sampled (Yr). Thermal ranges of the four studied ranges based on B) warmest and coldest sea surface temperatures and C) warmest and coldest air temperatures of the previous year for the entire colonized region. Dot, ellipse, and line colors correspond with colored squares in A to represent region (pink = invasive east Pacific, teal = invasive Atlantic, purple = native Atlantic, orange = invasive southwest Pacific). Crab sketch by Richards, C., 2020.

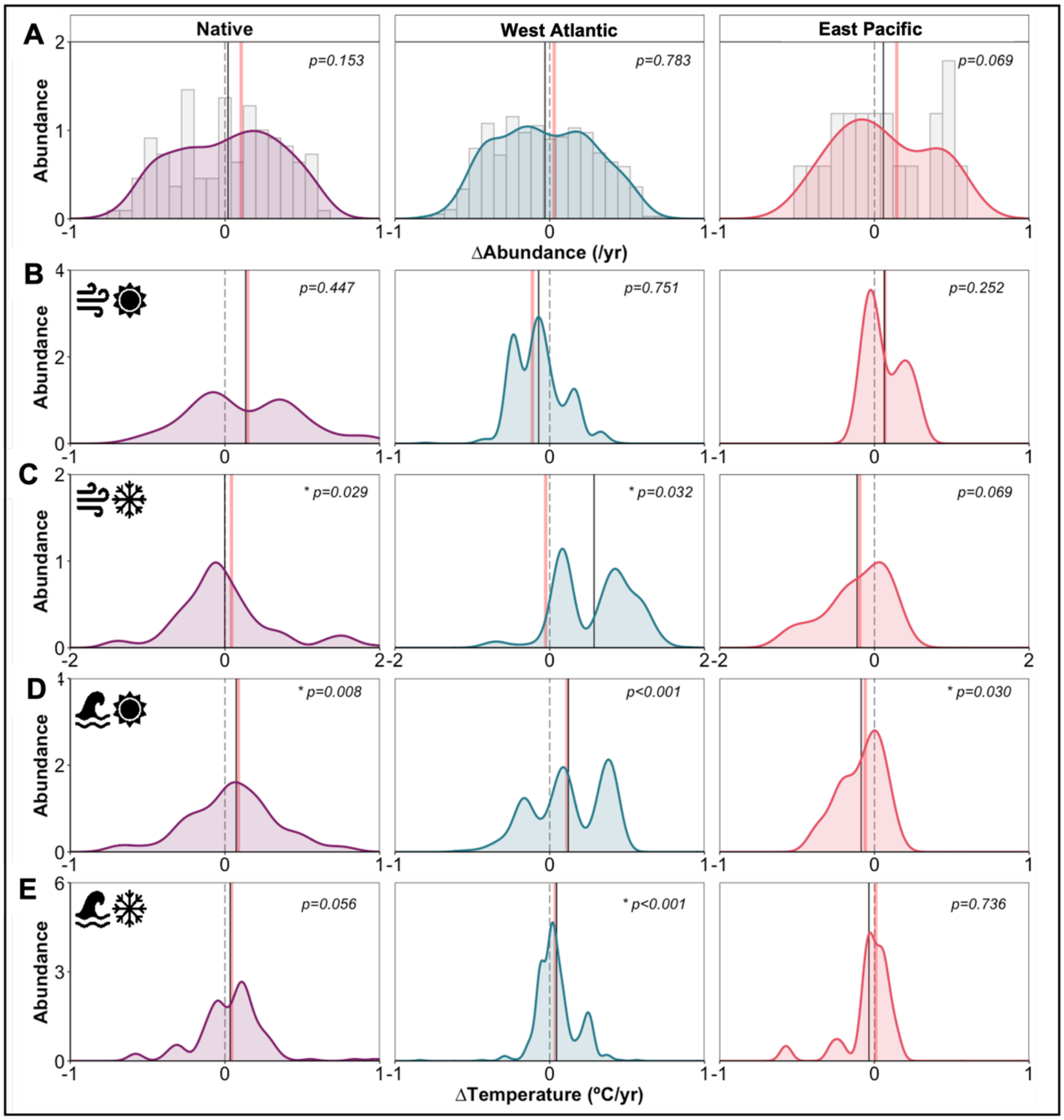

Figure 2.2 Intercept models. Distribution of generalized least-squares linear model slopes for each variable (rows) modeled against time (year). Time is based on each region's abundance data. Changes in A) abundance; B) summer and C) winter air temperatures; D) summer and E) winter sea surface temperatures per year per site. Dashed vertical lines represent zero, solid black lines represent mean. Red lines and *p*-values correspond to the expected mean from intercept models. The last column represents the invasive east Pacific.

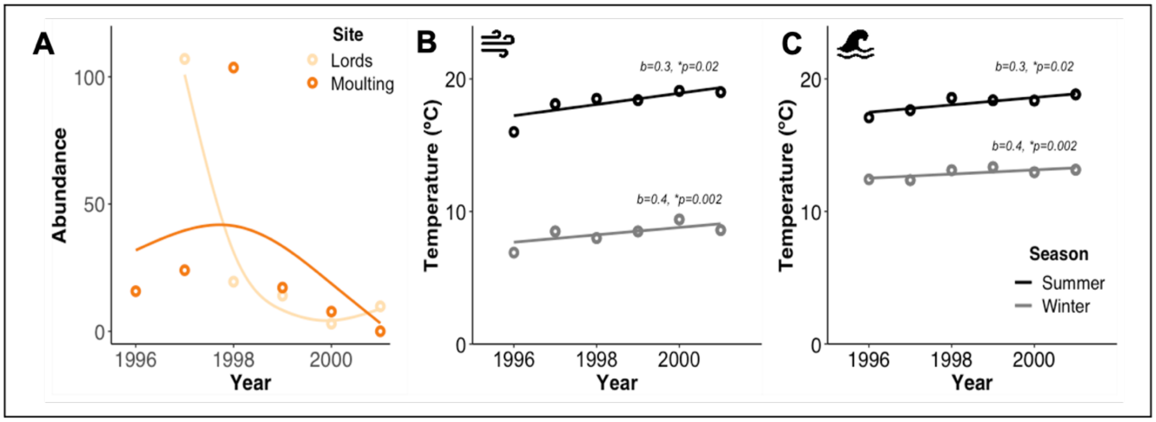

Figure 2.3 Southeast Pacific *C. maenas* abundance and temperature changes. A) *C. maenas* abundance through time at two sites (Lords and Moulting) in Tasmania, AUS. Trend lines are from a 75th percentile q-gam. Seasonal ocean B) air and C) sea surface temperatures in two seasons, with linear model fitted lines.

Five-year analyses. I quantified the relationship between five-year abundance change (i.e., the abundance slope) and five-year temperature change (i.e., the temperature slope) for each of the four temperature metrics (i.e., winter AirT, summer AirT, winter SST, summer SST). Data was sparse from the invasive east and southwest Pacific ranges; thus, these regions were excluded from the formal analysis. I found a strong positive relationship between abundance change and climatology (climatology being the mean SST of the previous decade). All temperature variables had positive coefficients regarding climatology, native Atlantic (summer air temperature (SummAirT) 0.061, winter air temperature (WinAirT) 0.059, summer sea surface temperature (SummSST) 0.076, WinSST 0.070), invasive Atlantic (SummAirT 0.033, WinAirT 0.043, SummSST 0.039, WinSST 0.059), and global models (SummAirT 0.32, WinAirT 0.041, SummSST

0.035, WinSST 0.055) suggesting that abundance increased at warmer sites (Figure 2.4, Supplementary Tables S2.4-S2.6).

There was a positive relationship between five-year abundance and temperature changes (for three out of four temperature variables) in the global (SummAirT 0.024, WinAirT 0.055, WinSST 0.037) and invasive Atlantic (SummAirT 0.045, WinAirT 0.075, WinSST 0.036) models. Similarly, the climatology and five-year temperature change interaction showed a positive relationship with five-year abundance change in the invasive Atlantic (SummAirT 0.032, WinAirT 0.022, WinSST 0.020) and global models (SummAirT 0.056, WinAirT 0.030, WinSST 0.030; Figure 2.4, Supplementary Tables S2.4-S2.6). The positive relationship between five-year abundance and temperature changes with climatology, indicated by the interaction coefficient, suggests that abundance increased at warmer sites where warming occurred.

Year-to-Year analyses.

The residuals from first stage models (abundance and temperatures) were analyzed using linear mixed-effects models to determine the relationship between year-to-year abundance and temperature variabilities. The global year-to-year models showed a strong positive relationship between year-to-year abundance variability and year-to-year temperature variability with all four temperature variables (SummAirT, 0.072, $p < 0.001$; WinAirT, 0.027, $p = 0.001$; SummSST, 0.077, $p = 0.001$; WinSST, 0.076, $p = 0.017$; Figure 2.5, Supplementary Table S2.8). Thus, years with increases or decreases in abundance tended to relate to years with increasing or decreasing temperature. Regional year-to-year analyses did not reveal significant trends (Tables S2.8-S2.12).

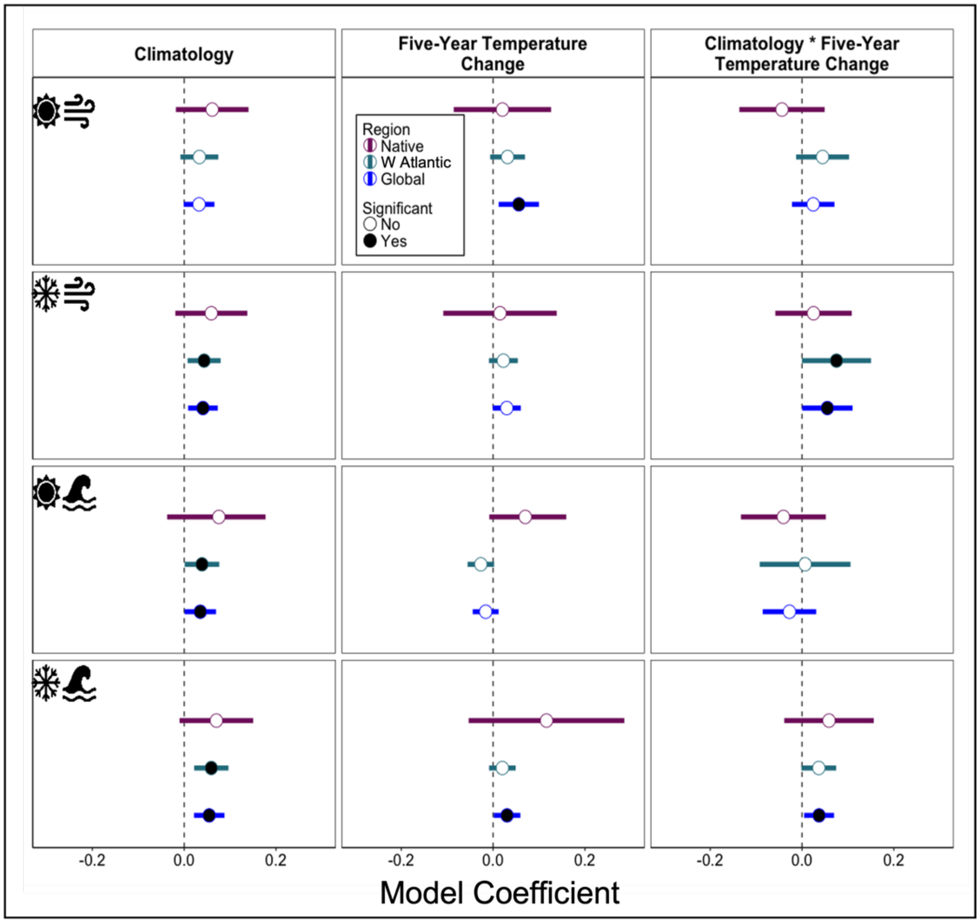

Figure 2.4 Five-year *Carcinus maenas* abundance and temperature change. Model coefficients (dots) and standard deviations (lines) from linear mixed-effects models of the change in five-year abundance relative to the change in five-year temperature. Each region (colors) and each temperature (rows) were modeled separately as well as globally. Significance determined by confidence interval not crossing 0 and *p*-value < 0.05 (black infilled dots). Icons from the top row down: summer AirT, winter AirT, summer SST, winter SST. Climatology is the site-specific mean SST of the past decade.

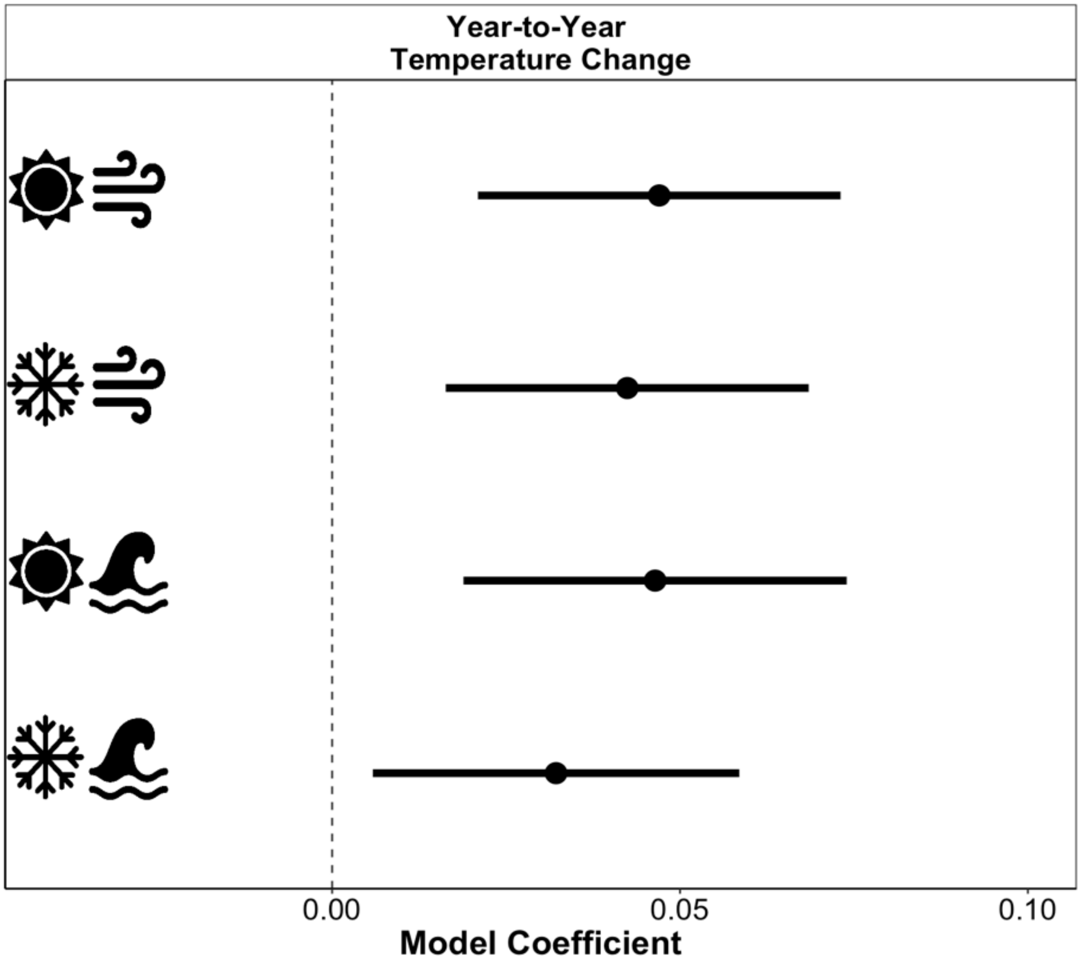

Figure 2.5 Year-to-year *Carcinus maenas* abundance and temperature variability. Model coefficients (dots) and standard deviations (lines) of linear mixed-effects models of year-to-year variability in abundance and temperature. Temperature variables (y-axis; summer AirT, winter AirT, summer SST, winter SST) were modeled separately. Significant effects are shown by a filled dot and determined by confidence intervals that do not cross zero and *p*-value < 0.05.

Discussion

Here, I report a mismatch in the thermal niches of native and invasive geographic ranges of green crabs using publicly available occurrence data from four regions. I found that despite significant warming of air and sea surface temperatures, the overall green crab abundance changes over the study period split into ~5-year chunks (1924 to 2020) did not show a consistent increase or decrease across all studies. Even so, there was a strong positive relationship between abundance and temperature change (Bowler et al., 2017; Rohde, 1992; Waldock et al., 2019; Willig et al., 2003), with different responses depending on the climatology (mean SST of last ten years per site), particularly in the invasive Atlantic range. In addition, year-to-year green crab abundance was positively related to temperature variation. Thus, remotely sensed air and sea surface temperatures predict increases and decreases in abundance in green crabs when regressed over five years, and when quantified from one year to the next.

Invasive species are expected to successfully colonize regions similar to their native habitat (niche conservatism; Broennimann et al., 2007; Peterson, 2003). Indeed, this was the case for the invasive east and southwest Pacific green crabs; however, the invasive Atlantic green crabs showed niche-mismatch. Specifically, the invasive Atlantic crabs were reported in both hotter and colder regions (than crabs from the native geographic range), suggesting a niche shift. This result is not entirely surprising simply because green crabs have lived in the east Atlantic for over 200 years (Say, 1817), and there is evidence of multiple invasion events AND ADAPTATION? (Tepolt and Palumbi, 2015, 2020). Evolutionary mechanisms (e.g., selection, genetic drift) commonly drive niche-shifts (Broennimann et al., 2007) and may help explain the spread of the invasive Atlantic range further north, where temperature extremes are both colder and hotter than the native range (Tepolt and Palumbi, 2015, 2020). These results suggest that we may expect to see continued expansion of current green crab ranges and new colonizations in areas where they were unsuccessful in the past.

Time-series abundance data from three regions showed that global green crab abundances averaged no net change. However, mean abundance changes in all three regions were positive; thus, more sites were increasing in abundance than decreasing. By contrast, the southwest Pacific crabs decreased in abundance, but the data was severely limited. A key question is why net abundance change is so stable, given what we know about the species. First, mitigation efforts in the invasive range may play a role. Both the invasive Atlantic and east Pacific regions have made continuous efforts to detect and mitigate green crabs (Fisheries and Oceans Canada (DFO), 2018; Grason et al., 2018; Vercaemer et al., 2015). In Nova Scotia, for example, 15,000 crabs were caught over 24 days (Cohen, 1995), while another 157 tonnes were removed in mitigation experiments from 2011 to 2015 (Vercaemer et al., 2015). A further 1,000 crabs per day were removed in Maine and Connecticut in 1960 and more than 25,000 lbs from Newfoundland in 2008 (Blakeslee et al., 2010; Cohen, 1995).

Green crab abundances are increasing on the warm edge of their thermal niche in the native and invasive Atlantic regions, providing evidence of an invasive species succeeding with climate warming and supporting the ‘poised to prosper’ hypothesis (Mainka and Howard, 2010; Rahel and Olden, 2008; Sorte et al., 2013). However, this is not the case in Australia, where the crabs experience temperatures much warmer than the other regions (based on remotely sensed temperature data). Thus, while elevated (warmer than average) temperatures do seem to pose a limit to the green crab, there are several mechanisms (which follow) that might underpin their success and present compelling directions for future research. For instance, warming ocean temperatures, particularly in the winter and spring, might favor the success of juvenile stages, which are less cold tolerant than adults (Dawirs, 1985; Klassen and Locke, 2007). Warming might also favor green crabs by decreasing the health and subsequent competitive ability of other species. For example, Lauchlan et al. (2019) reported that increasing temperatures cause behavioral homogenization between competitors, reducing dominance; hence, rising temperatures may reduce competing forces. For instance, green crabs are restricted in the southern end of their invasive Atlantic range by blue crabs (*Callinectes sapidus*). However, the competitive interaction diminishes in elevated (warmer-than-average) waters (Rogers et al., 2018). Furthermore, warmer temperatures correlate with increased juvenile prey quality and, therefore, increased year-class strength of green crab juveniles (Yamada et al., 2015). These findings suggest that climate change favors green crabs and may promote further spread to new regions.

The year-to-year variability analysis results provide strong evidence that temperature fluctuations, independent of the long-term trend, can predict green crab abundance changes. These results are expected, as large temperature fluctuations can incur energetic debt and drive high mortality rates (Ottersen and Stenseth, 2001; Parsons, 1994). Moreover, green crab larvae have reduced development and survival in colder- and warmer-than-average temperatures (Berrill, 1982; Cohen et al., 1995; Torres and Giménez, 2020). Furthermore, temperature appears to influence green crab abundances at different time scales as both 1) temperature variability between years and 2) 5-year warming trends were positively related to green crab abundances.

While these analyses implicate the importance of temperature as a predictor for abundance changes in this species. Indeed, large-scale climate patterns are expected to predict abundance patterns in both space and time because regional temperature trends reflect climate patterns (e.g., ENSO, atmospheric circulation cells; Plaut and Simmonet, 2001), which in turn affect biotic (e.g., productivity; Grace, 1988; Jonas et al., 2015) and abiotic factors (e.g., wind, precipitation; Seino et al., 2018). However, coarse geographic-scale satellite temperature data (1º) coupled with fine geographic-scale (0.1º) abundance data ignores fine-scale processes that impact local-scale factors (Bates et al., 2018; Trenberth and Hurrell, 1997). Furthermore, sea surface temperatures were used, but adult green crabs are benthic organisms; therefore, SST is not accurate for the diverse thermal conditions experienced (Gaudin et al., 2018; Smale and Wernberg, 2009). Thus understanding the importance of local-scale processes in impacting macro-ecological trends is a key direction for future research.

Few abundance records outside the native and invasive Atlantic regions impeded the analyses in this study. Despite aiming to model green crab abundances from three invasive regions, abundance data was insufficient to model changes in the invasive east and southwest Pacific crabs. Thus, a critical future direction will be implementing green crab time-series monitoring in regions with low data availability (e.g., Australia and Africa).

Conclusion

Here, I combine global green crab occurrence data with satellite-derived sea surface and air temperature data to show a thermal niche-mismatch between the native and invasive Atlantic crabs. Despite the species' apparent success, analyses with green crab abundance data showed no evidence of systematic abundance changes through time. Even so, green crab abundances increased on the southern (warm) edge of their Atlantic ranges (both the invasive and native???), particularly at sites where the temperature is increasing. I also find that year-to-year abundance corresponds to short-term temperature variability. Thus, my findings implicate a role for both SST and Air Temp???? in predicting green crab abundance patterns. Overall, ocean temperature will likely play a crucial role in the future success of the green crab at annual and longer time scales, a vital consideration for predicting the distribution and impact of this species with ongoing climate change..

Chapter 3

A review of the thermal biology of the European green crab, *Carcinus maenas*

A review of the thermal biology of the European green crab, *Carcinus maenas*

Abstract

Carcinus maenas is a well-studied species that has invaded nearly every continent, impacting numerous ecologically and economically important habitats and species. In the context of climate change and habitat modification, predicting where species invasions will occur is relevant and essential to conservation. Here, I review and synthesize the current literature regarding the thermal biology of *Carcinus maenas* to assist in conservation efforts (e.g., invasion predictions, risk mitigation) based on the crab's thermal tolerance. From the literature review, I find that thermal biology is explicitely addressed in 2% of all *C. maenas* papers (105 of 4,539 papers). Using a gap analysis, I reveal several apparent knowledge gaps, including the interaction of distribution and abundance with temperature-dependent survival and comparisons of thermal biology across life-stages. After comparing thermal tolerance values across studies, I find that juveniles are more physiologically sensitive to warmer- and colder-than-average temperatures than adults. Meanwhile, based on experimentally derived thermal tolerance values, adults have short-term tolerance of a wide range of temperatures (≤ –1 to ≥ 38 °C) and low vulnerability to marine heatwaves and cold spells. I conclude with recommendations for increased thermal tolerance studies with standardized methods.

Background

Invasive species are one of the greatest threats to global biodiversity, representing a significant challenge for conservation and land management groups (Gallien et al., 2010;

Liang et al., 2014). Invasive species tend to have a common set of characteristics (e.g., generalist, wide tolerance, high fecundity) that improve their relative success in new habitats (Layman and Allgeier, 2012; Sorte, 2016; Stigall, 2012). However, these characteristics also increase the threat that invasive species can impose on natives by facilitating competitive exclusion (Didham et al., 2007; Huxel, 1999; Molnar et al., 2008). Therefore, it is imperative to improve early detection and successful mitigation of invasive species to conserve natural biodiversity (Gallien et al., 2010; Liang et al., 2014).

Species invasions have rapidly increased since the establishment of global trade (Mooney and Cleland, 2001; Sardain et al., 2019) and continue to escalate with climate change—due, in part, to their large geographic ranges and broad thermal tolerances (Mainka and Howard, 2010; Sorte et al., 2013; Stigall, 2012). Adaptation to heterogeneous environmental factors is predicted to improve survival (with temperature change) over long timescales, thus benefiting those species under a climate change scenario. However, short-term changes (e.g., heatwaves and cold spells) are less predictable and often more extreme (i.e., extreme weather events; Añel et al., 2017; Egondi et al., 2015; Frölicher et al., 2018). Extreme weather events receive less attention than global warming but are arguably just as important, posing more significant short-term risks and substantially impacting ecosystems by driving species redistribution and mass mortality events (Frölicher et al., 2018; Frölicher and Laufkötter, 2018; Kron et al., 2019; Oliver et al., 2021; Stott, 2016).

A species thermal tolerance indicates the range of temperatures they have adapted to (Pörtner, 2010). However, thermal resistance processes impose metabolic costs, which result in short-timescale limitations for extreme temperature changes or longer-timescale limitations for smaller temperature changes (Pörtner, 2010). Oxygen demands restrict organisms to a range of temperatures known as the thermal window (also tolerance range or tolerance window), which includes the optimal performance temperature range, as well as the thresholds where performance declines (Frederich and Pörtner, 2000; Giomi and Poertner, 2013; Jost et al., 2012; Pörtner, 2010). The optimal range represents temperatures that maximize performance and is bounded by an upper and lower threshold (pejus temperatures; Frederich and Pörtner, 2000). Beyond the pejus temperature (T_P) is the pejus range—the range of temperatures at which reduced aerobic scope leads to decreasing performance (Frederich and Pörtner, 2000). Pejus temperatures are defined by changes in physiological characteristics such as reaction time and accumulation of AMP-activated protein kinase (AMPK) or heat shock proteins (HSP; Jost et al., 2012). The last thresholds in the thermal window are the upper and lower critical temperatures (T_C), defined by physiological characteristics such as maximum or minimum heart rate, onset of anaerobic metabolism, or death (also referred to as critical thermal maximum or minimum (CTmax, CTmin); Frederich and Pörtner, 2000; Jost et al., 2012). The temperature ranges past this threshold are called the pessimum ranges, indicating death is imminent unless acclimation occurs (Frederich and Pörtner, 2000; Jost et al., 2012). Within the pessimum range, organisms exploit short-term survival mechanisms associated with high energy expenditures (Pörtner, 2010). Therefore, the range of temperatures an organism inhabits (their thermal niche) corresponds with their thermal window.

To explore the importance of temperature-related research on a widespread invasive species, I synthesize published papers in the field of thermal biology. As a model species (Davies et al., 2020; Rodrigues and Pardal, 2014), studies focusing on *C. maenas* cover a broad range of topics and have interdisciplinary and inter-regional value, making a holistic synthesis of green crab thermal niche characteristics and limits widely beneficial. I filter the 4,539 *"Carcinus maenas"* papers on the Web of Science (Clarivate Analytics, 2021) and thoroughly review those that match the search terms (n = 252) and were deemed relevant (n = 105) to identify various ways temperature affects green crabs. In doing so, I reveal trends in the types of questions addressed by research to date, and identify gaps in our understanding of the thermal biology of this species. Combining all of the reported quantitative thermal limits (T_P and T_C, as described above) for the species, I present a comparison and synthesis of life-stage specific thermal limits. Furthermore, I compare thermal tolerance values with local satellite-captured air and sea surface temperatures to predict green crab responses to extreme weather events.

Methods

Literature search. To characterize studies focussing on the thermal biology of *Carcinus maenas*, I conducted a literature search using the Web of Science core collection literature database (Clarivate Analytics, 2021). Search operators were used along with the following keywords: (*Carcinus* OR *maenas* OR green crab) AND (thermal OR temperature OR heat OR tolerance). Terms were entered in the 'topic' field, which searches through paper titles, abstracts, keywords, and Keywords Plus®. The keyword search returned 252 papers, which required further screening. Titles and abstracts were reviewed to determine whether the studies fit the inclusion criteria (i.e., inclusion in the literature review was any relationship between temperature and the biology of green crabs). From the screening process, 105 papers were selected for the review. New papers were included up to May 2021. The literature search process is shown in Figure 1.

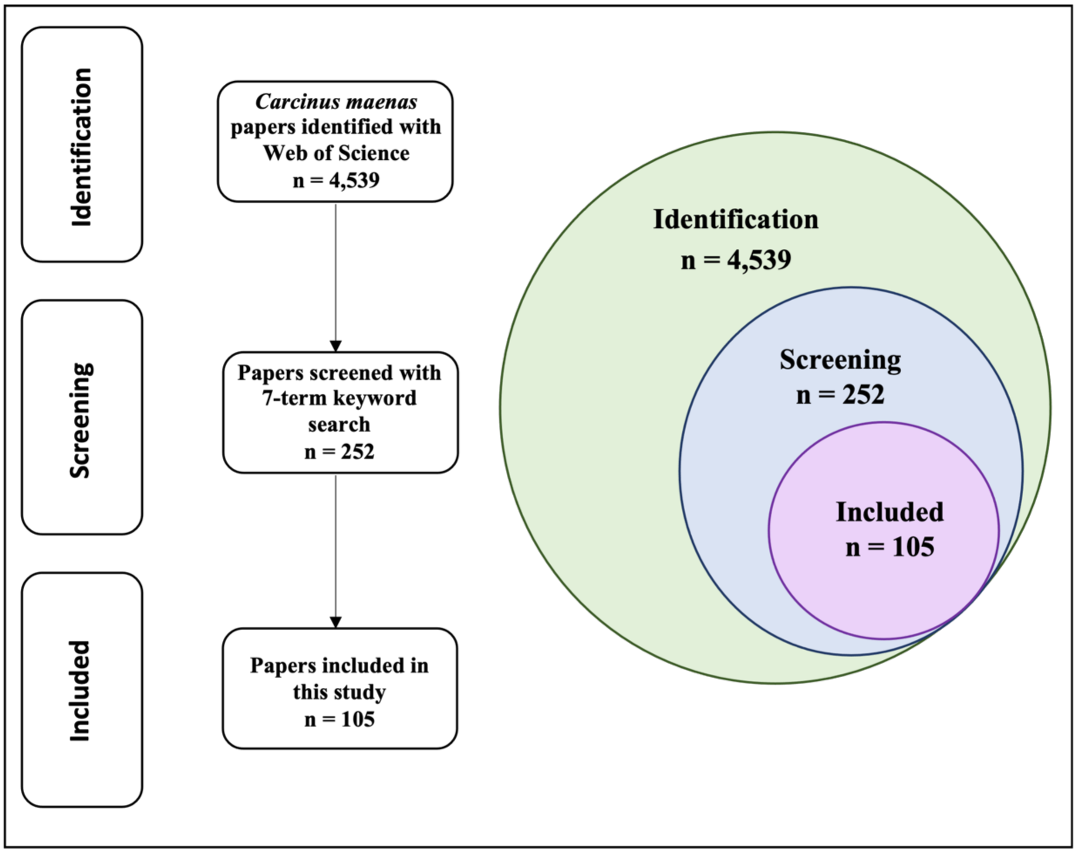

Figure 3.1 Literature search outline. The initial search for '*Carcinus maenas* ' returned 4,539 papers. The 7-term keyword search returned 252 papers, and the screening process resulted in 105 papers being included in the study.

Gap analysis. Following the methods proposed in Research to Action (see below; Wallis and Wright, 2020), I conducted a gap analysis to detect areas where further research is needed. Using a web structure, I plotted the key concepts (randomly in page-space) from every paper, then drew causal connections (existing research) between concepts. The arrows were drawn in the direction of impact (i.e., independent variable to dependent variable), and in some cases, arrows were drawn in both directions. I mapped the most relevant categories for grouping data based on the concepts with the most connections. According to Wallis and Wright (2020), exploitable gaps for future research exist where categories are not connected, which are identified with red connections in Figure 3.2.

Literature analysis. To describe the *C. maenas* thermal biology literature, I first grouped papers into five category levels based on their key concept (the single most dominant idea), as determined in the gap analysis. The key concepts were determined to be those which had more than four linkages.

For Category A (concept, n = 5), papers were grouped into five concepts: species patterns, populations, behavior, development, and performance. The species patterns concept was based on the geographical presence (spatial occurances) of green crabs; the population concept identified genetics papers where green crabs were collected from a specific location or region; the behavior concept focused on whole-organism activities, movements and behaviours; crab growth and metamorphosis distinguished the development concept; and the performance concept identified papers examining abiotic factors influencing aerobic processes.

I repeated the process of identifying the most dominant concept of the paper (secondary to the key concept) to create a sub-grouping, Category B. Category B (specialty, n = 15) included the following (which are described next): distribution, occurrence, abundance, inter-specific, intra-specific, genetics, feeding, competition, movement, growth, larvae, morphology, salinity, molecules, and physiology. The specialties (sub-categories) within the patterns concept (distribution, occurrence, and abundance) all explored the relationship between temperature and species geographic pattern (i.e., realized temperature limits). The population concept included the inter-specific, intra-specific, and genetics specialties (sub-categories). Similar to the patterns concept, these papers also compared temperature and geography, but they had a stronger focus on *comparing* populations. Inter-specific and intra-specific papers explored thermal biology differences between and within green crab regions. At the same time, the genetics specialty was focused on comparing green crab genetics (which may be inter- or intra-specific but had a greater genetics focus). Behavior included experiments and observations that focused on the relationship between temperature and feeding, competition, or movement. Development encompassed studies that explored the fundamental relationship between temperature and growth (e.g., molt stages), larvae (e.g., development through the larval stages), and morphology (e.g., temperature-size rule). Finally, salinity, molecules, and physiology included the specialties within the survival concept. The salinity papers (n = 2) exclusively referred to the thermal mitigation of low salinity (i.e., temperature tolerance is negatively correlated with salinity; Broekhuysen, 1937). Molecular papers focused on molecules produced by green crabs to aid in thermal tolerance (e.g., heat shock protein, sphingomyelin). Lastly, the physiology papers exclusively looked at the minimum and maximum critical thermal tolerance (CTMin, CTMax).

Category C (biological level, n = 4) described the biological level of organization the study focused on (i.e., cellular, individual, population, community). The cellular level was commonly associated with molecular studies as they involved processes in and between cells. Individual-level studies tended to represent laboratory experiments (e.g., CTMax) because they focused on the individual, whole organisms. Population described papers that looked at a regional group of individuals. Community described inter-species studies where green crabs were compared with other species (e.g., the impact of temperature on competition).

Finally, Category D described the region green crabs originated from (region, n = 5). This category followed the four geographic groups described previously: native Atlantic, and invasive Atlantic, east Pacific, and southwest Pacific. However, there was also a grouping named 'other' for studies that compared multiple regions or focused on the green crab species as a whole (i.e., global). To display the frequency of papers per concept and region (Cat. A, C), I plotted them as bar graphs (Figure 3.3, Supplementary Table S3.1).

Data synthesis. To empirically describe green crab thermal biology, I collected and compared the quantitative thermal limits found in the literature and defined the thermal window with pejus and critical temperatures. I then plotted the thermal limits identifying thresholds (minimum and maximum temperatures) to growth, feeding, and tolerance. Tolerance limits represented the critical minimum and maximum temperature (CTMin and CTMax) at which individuals lost their righting responses or died (Allen et al., 2016; Kingsolver and Umbanhowar, 2018). Tolerance limit endpoints across studies are reported in Supplementary Table S3.2 and plotted by life stage (Figure 3.5A, Supplementary Table S3.2). CTMax values were the most frequent response metric in the papers and were plotted separately by geographic region (Figure 3.6B-D).

To inform predictions regarding green crab response to extreme weather events, green crab quantitative thermal tolerance limits were compared with two satellite-derived temperature datasets—air and sea surface. Air temperature data was sourced from the Natural Environment Research Council's data repository (Climate Research Unit Time Series Version 3.26 (CRU-TS3.26), Harris et al., 2020). These data were gridded at a 0.5º spatial resolution and collected monthly, spanning 1901 to 2017. Sea surface temperatures (SSTs) were downloaded from the Met Office Hadley Centre's satellite sea ice and sea surface temperature (SST) dataset (Hadley Centre Global Sea Ice and Sea Surface Temperature (HadISST), Willmott and Matsuura, 2001). The HadISST data are in a 1º grid format, spanning from 1870 to the present. Both temperature datasets were downloaded as NetCDF files, and the package "RNetCDF" was used to view and manipulate the data (Michna and Woods, 2017). To determine apparent green crab risk (based on regional satellite temperatures), adult maximum thermal tolerances (CTMax) were plotted with the maximum temperatures over the last ten years (Figure 3.6, Supplementary Table S3.3). Minimum temperatures were not included in this analysis because the adult CTMin is functionally absent (specifically unknown) and, as such, does not present a severe short-term risk. Finally, to explore the potential risk of extreme weather events to juvenile green crabs, minimum thermal tolerance was plotted against the minimum and mean sea surface temperatures since cold weather events appear to be the factor most restricting to juveniles. Here, air temperatures were not included because the larval and egg stages are exclusively marine (water column, not intertidal or terrestrial; Figure 3.7).

Results

Literature search. The literature keyword search yielded 252 papers; not all were relevant, and 105 were selected for inclusion based on the abovementioned methods. The selected papers had 84 unique lead authors, and publication dates spanned 1937 to 2020.

Gap analysis. From the gap analysis, eight dominant concepts with more than four linkages each (depicting existing research) were identified, i.e., ocean conditions, color morph, patterns, behavior, life stage, survival, minimum, and maximum thermal tolerance (CTMin, CTMax). Several gaps were found between the eight main categories (Figure 3.2), with the most gap-lines connected to CTMin. There were also several gaps between inter-and intra-regional, life stage, and survival.

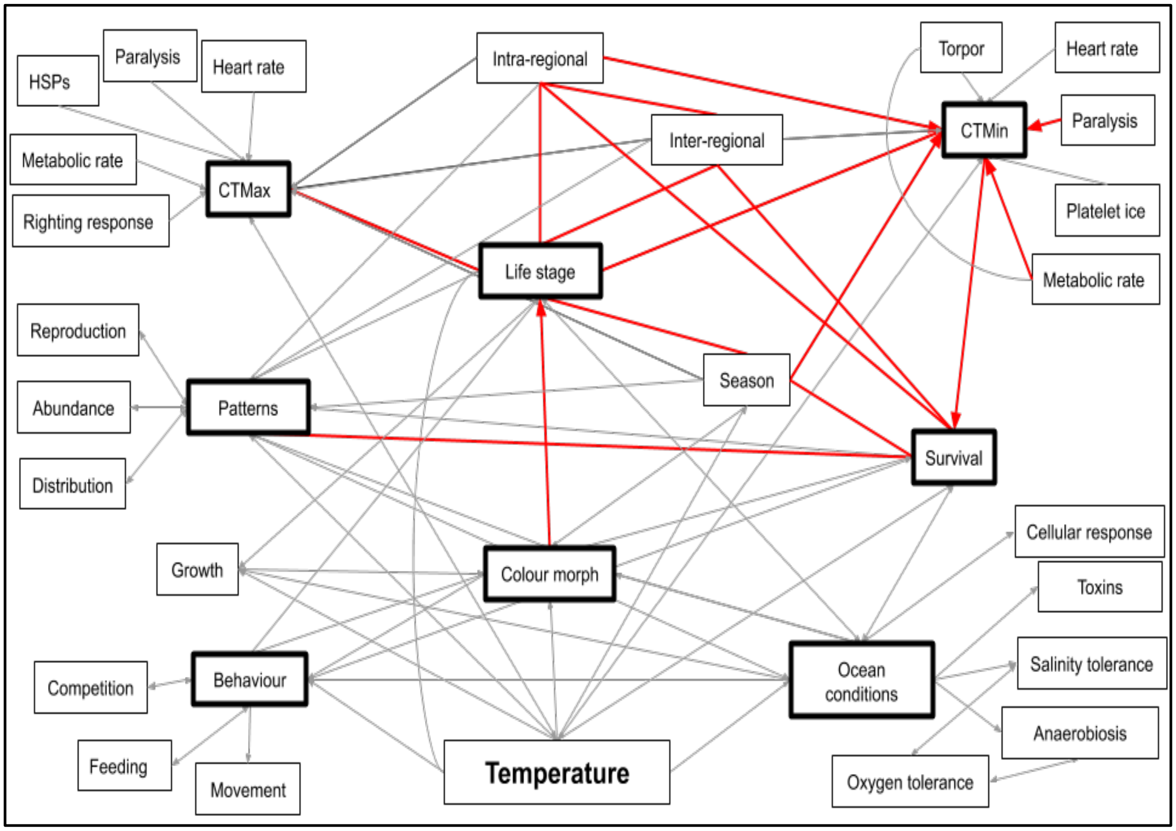

Figure 3.2 Gap analysis of *Carcinus maenas* thermal biology literature. Boxes are the key concepts found within the literature search. Grey arrows between concepts show reported relationships for different studies. Thick boxes highlight the most researched concepts (more than four existing study links). Red arrows were added between concepts with missing linkages to highlight research gaps.

Literature analysis. Of the 105 selected thermal biology papers (Table S3.1), 63% of concepts focused on survival (33%) and development (30%). Larvae-related papers were the most abundant specialty (24% of all papers), and physiology was the next largest with 23% of all papers. Species patterns and population were the least researched green crab thermal biology concepts, with seven papers each. The division of concepts into specialties is shown in Figure 3.3; concepts and specialties are listed in Table S3.1.

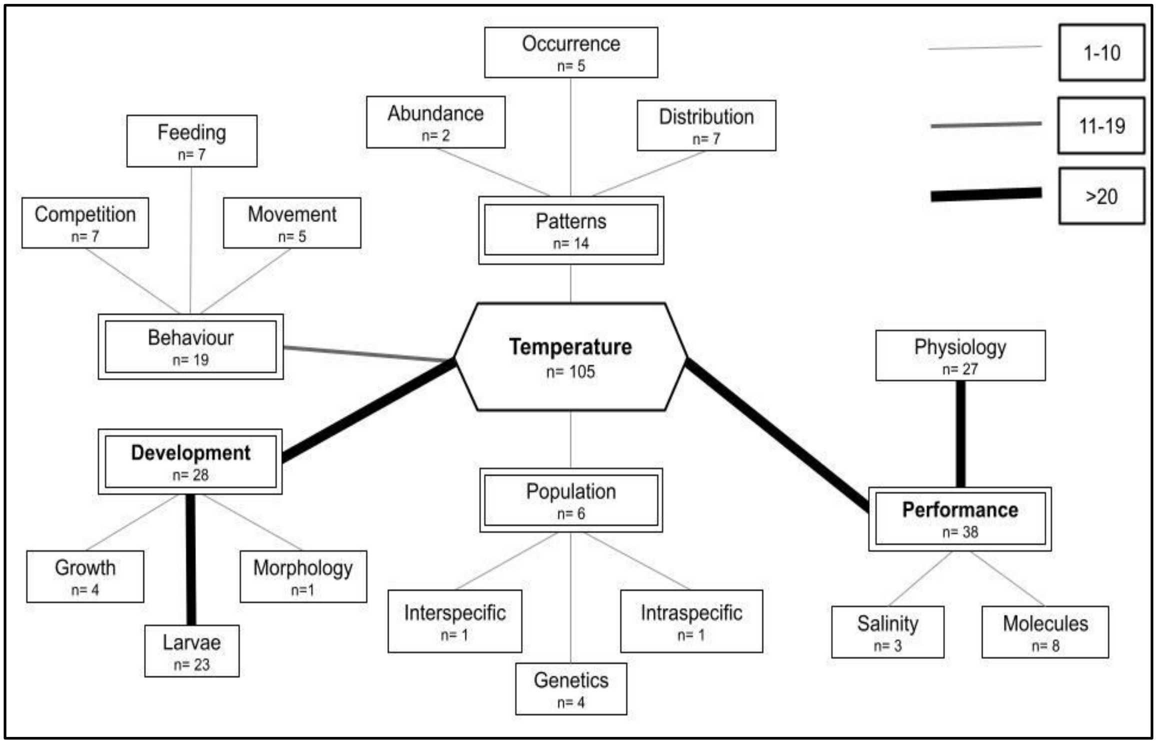

Figure 3.3 Grouped *Carcinus maenas* thermal biology research. Line size and shade denote the number of papers in each group; thickest and darkest correspond to the most considerable quantity. Double-lined boxes are used for concepts (Cat A), single-lined for specialties (Cat B). Numbers under group titles represent the total number of *C. maenas* thermal biology papers focusing on the given category (out of 105).

On a per-region basis, the thermal biology studies dominantly regarded the native crabs (51%) relative to the other regions in this review. The next most studied region was the invasive Atlantic (26% of reviewed papers). The invasive east and southwest Pacific regions made up only 11 and 1% of the reviewed literature, respectively. The individual and population levels of the biological organization category were most common (52 and 29%, respectively; Figure 3.4). Overall, the publishing rate of green crab thermal biology literature has increased through time. Native green crab thermal biology literature has been published at a relatively constant rate (Figure 3.4C). In the invasive Atlantic, *C. maenas* thermal biology research increased around 2000. From 1990 to 2000, the east Pacific had a peak in research, with a more significant rise in the early 2000s.

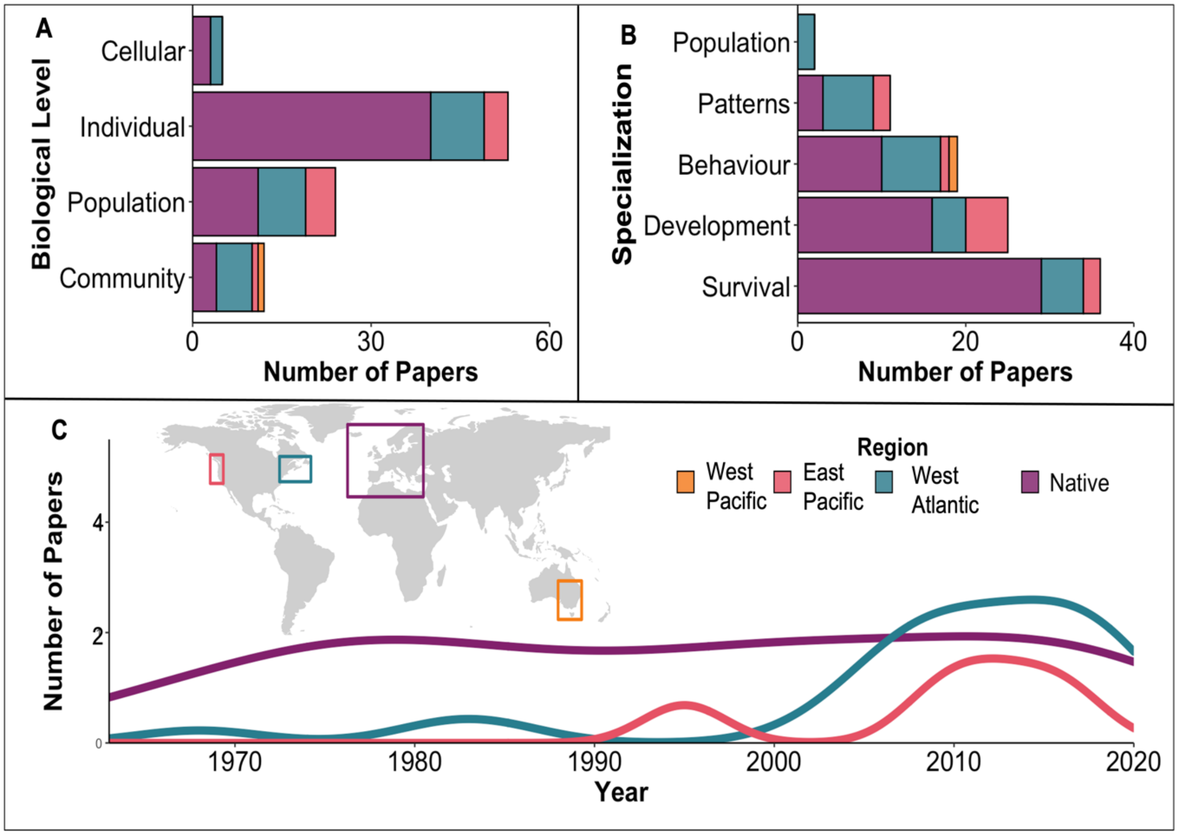

Figure 3.4 ***Carcinus maenas*** **thermal biology literature**. Papers sorted by region (colors) and A) biological level, B) specialty, and C) year published. Map inset represents the geographical location of the four regions and their associated color. The invasive southwest Pacific ocean region did not have enough papers to include on the timeline.

Data analyses. From the literature search, I found 56 quantitative thermal limit values for *Carcinus maenas*. However, pejus temperature studies were virtually non-existent. Jost et al. (2012) suggest that green crabs do not have a pejus temperature or that the pejus and pessimum have merged. Therefore, theoretically, the species would abruptly switch from optimum to pessimum, with death thereafter (Figure 3.5; Jost et al., 2012). However, Taylor and Wheatly (1979) found a T_P of 28 ºC when crabs emigrated out of progressively warmed water (in laboratory). The behavior exhibited by Taylor and Wheatly's (1979) crabs show uncomfortable conditions at 28 ºC (i.e., not optimum) followed by avoidance behavior (i.e., pessimum, due to ability to respond and avoid).

The majority of values overall were adult-stage critical thermal maximum (CTMax) values (31/56). The CTMax values range from 29.7 ºC (Tepolt and Somero, 2014) to 38.3 ºC (Jørgensen et al., 2017). I was unable to find a critical thermal minimum (CTMin) for adult-stage *C. maenas;* however, Kelley et al. (2014) and Tepolt and Somero (2014) both found over 90% survival of crabs subjected to ≤ –1 ºC in three regions (native Atlantic, invasive Atlantic, invasive east Pacific). Adult *C. maenas* have reported minimum feeding limits of 3 to 10 ºC (Audet et al., 2008; Baldridge and Smith, 2008; Bélair and Miron, 2009; Berrill, 1982; Dawirs and Dietrich, 1986; Eriksson and Edlund, 1977) and a minimum growth limit of 10 ºC (with native and invasive Atlantic crabs; Berrill, 1982; Eriksson and Edlund, 1977). There was a relatively large variance in the adult-stage minimum thermal feeding limit (3 to 10 ºC). However, only two of the minimum feeding temperature limits were experimental (Baldridge and Smith, 2008; Bélair and Miron, 2009), but both were pre-determined and static (not ramped); the other three minimum feeding limits were observational (Audet et al., 2008; Berrill, 1982; Eriksson and Edlund, 1977). Quantitative thermal limit values are presented in Figure 3.6.

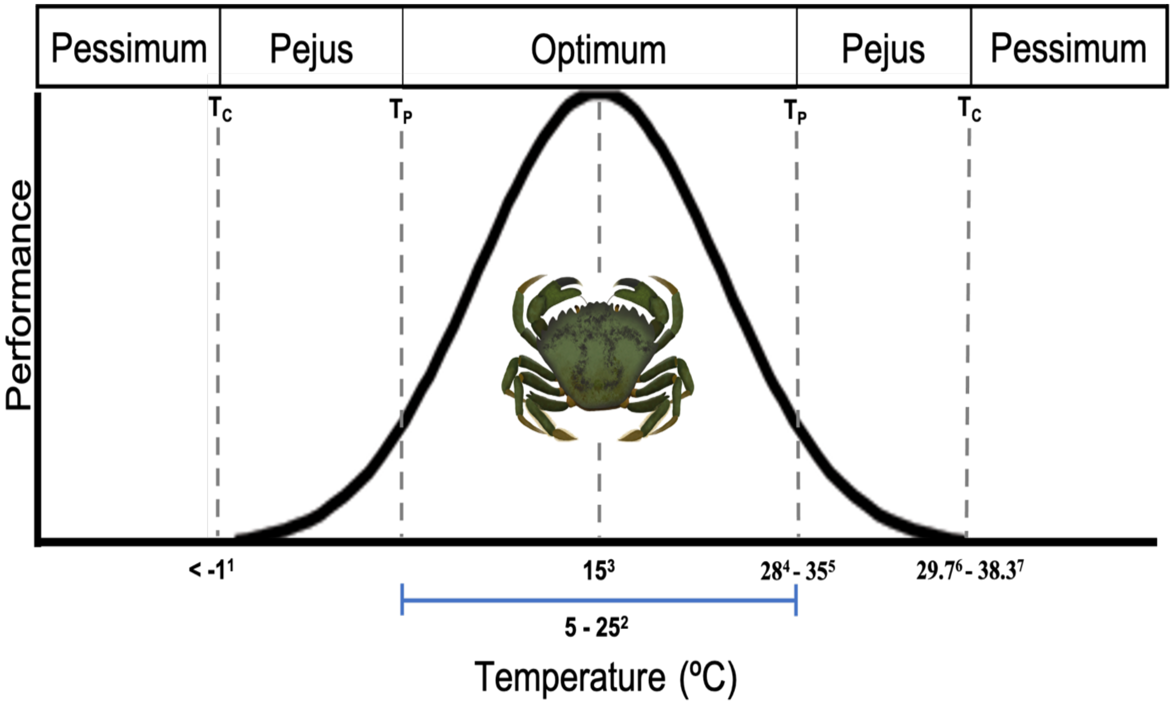

Figure 3.5 ***Carcinus maenas*** **thermal window.** Proposed temperatures defining the thermal window of *C. maenas*. Top boxes represent thermal ranges, separated by a grey dashed line representing threshold temperatures. The middle threshold line represents optimal temperature, T_P is pejus temperature, T_C is critical temperature, the blue line below the axis represents the optimum range, subscripts correspond with citations. Black performance curve is hypothetical. Superscripts correspond to the following: 1. Kelley et al., 2014; Tepolt and Somero, 2014; 2. McGaw and Whiteley, 2012; 3. Robertson et al., 2002; 4. Taylor and Wheatly, 1979; 5. Jost et al., 2012 *listed as combined pejus-pessimum threshold; 6. Tepolt and Somero, 2014; 7. Jørgensen et al., 2017.

Only two quantitative thermal limits were found for *Carcinus maenas* eggs: minimum thermal limit for survival (Crothers, 1967) and minimum thermal limit for growth (Dawirs, 1985); both were reported as 10 ºC. Larvae had the most diverse thermal limit types reported in the literature, but most (6 of 10 thermal limit values) report minimum and maximum thermal limits to growth. The lower thermal limits to larval growth ranged from 7 to 10 ºC, whereby two were experimentally derived (Dawirs, 1985; Nagaraj, 1992), and a third was observational based on green crab occurrence (Compton et al., 2010). Three papers reported that the upper larval thermal limit is 25 ºC, one was cited (Crothers, 1967), one was observed (Sprung, 2001), and one was experimental (Nagaraj, 1993; Table S3.2). No minimum temperature was reported for larval feeding, but the maximum temperature reported was 18 ºC (Dawirs and Dietrich, 1986). Growth and feeding limit experiments all used pre-determined, static temperatures. The minimum and maximum thermal tolerance values reported for larvae were experimentally derived, CTMin values 10 and 12 ºC (Dawirs, 1985; deRivera et al., 2007), CTMax value 22.5 ºC (deRivera et al., 2007). All quantitative thermal limits are plotted in Figure 3.6 and reported in Table S3.2, along with relevant experiment information.

The green crabs used in the CTMax experiments were collected in different seasons in the native Atlantic region (summer-winter) relative to the invasive Atlantic and east Pacific (spring-summer) regions. The highest CTMax values were found in the warmest seasons (summer-fall). The invasive Atlantic only reported CTMax in summer, while the invasive east Pacific CTMax was only studied in spring and summer. Invasive Atlantic green crabs had the highest mean reported CTMax (35.7 ºC), the native Atlantic and invasive east Pacific crabs had similar reported mean values: 34.4 and 34.3 ºC, respectively. The arithmetic mean of the reported adult *C. maenas* CTMax across studies was 33.9 ºC. Across these results, I found correlations between CTMax and acclimation temperature, acclimation time, ramp speed, and sample size. Methodology was also highly variable, for instance, crabs were acclimated at temperatures ranging from 6 to 25 ºC at time spans ranging from 1 to 4 weeks. Experimental sample sizes ranged from 4 to 12 individuals; ramping rates ranged from 1 to 12 ºC per hour (Table S3.2).

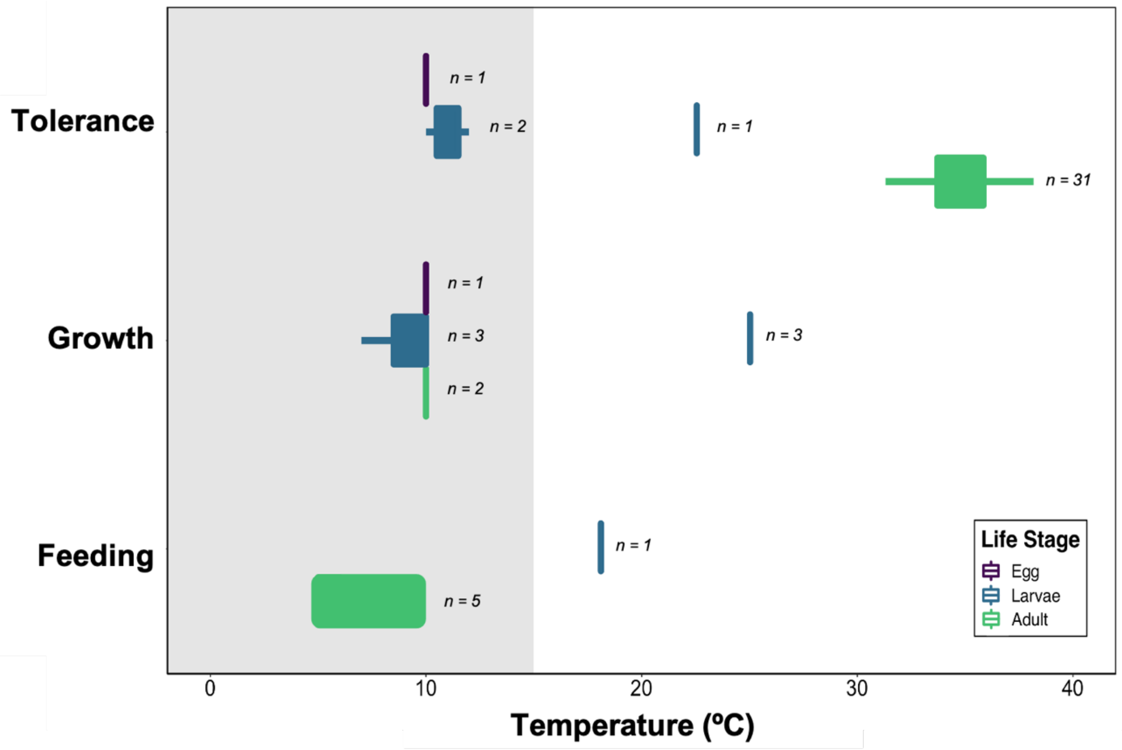

Figure 3.6 *Carcinus maenas* thermal limits reported in literature. Quantitative thermal limits color-coded by life stage with darkest corresponding to egg and lightest to adult. Single vertical lines represent one or more values of the same temperature. Whiskers represent 1.5 times interquartile range. Values within the grey box are the lower limits; values outside the grey box are upper limits.

I compared the adult *C. maenas* thermal tolerance values with satellite-derived temperature data to explore the impact extreme weather events may have on green crabs. I found no overlap between sea surface temperature and CTMax (Figure 3.7A). However, I did find maximum recorded satellite air temperatures cross into reported adult CTMax limits (Figure 3.7B). I also compared regional temperatures to early life stage *C. maenas* limits to see if extreme weather events appear to be a threat to juvenile green crabs. The minimum SST was frequently below both the larval and egg CTMin values in all seasons and all regions (Figure 3.8).

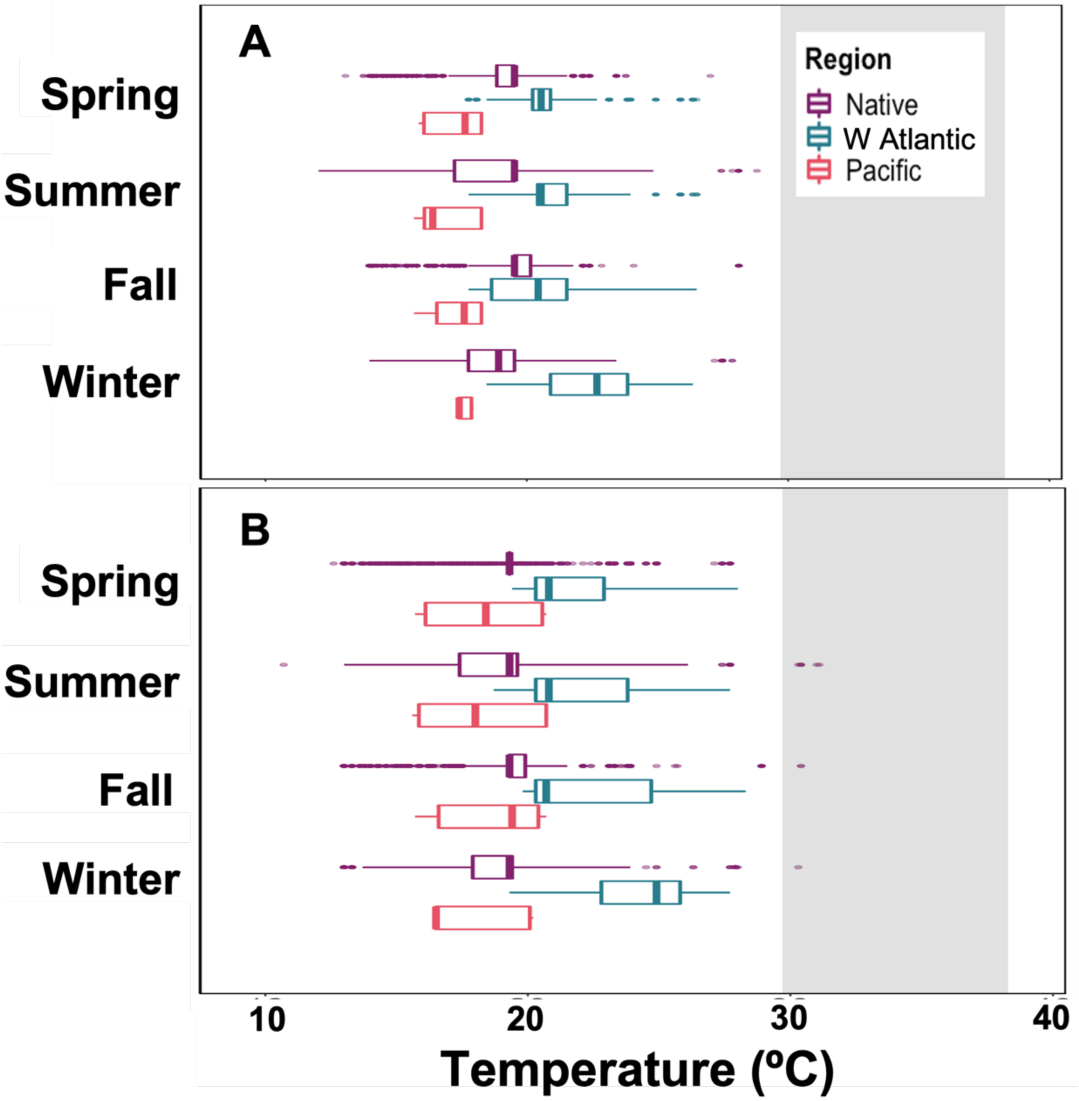

Figure 3.7 Maximum seasonal regional temperatures. Boxplots of the maximum A) sea surface and B) air temperatures over the last ten years from satellites. Whiskers are three times the interquartile range, dots are outliers. Grey boxes represent the range of adult *C. maenas* critical thermal maximum limits reported in the literature (i.e., CTMax; n = 31). Colors represent region. Pacific refers to the invasive east Pacific crabs.

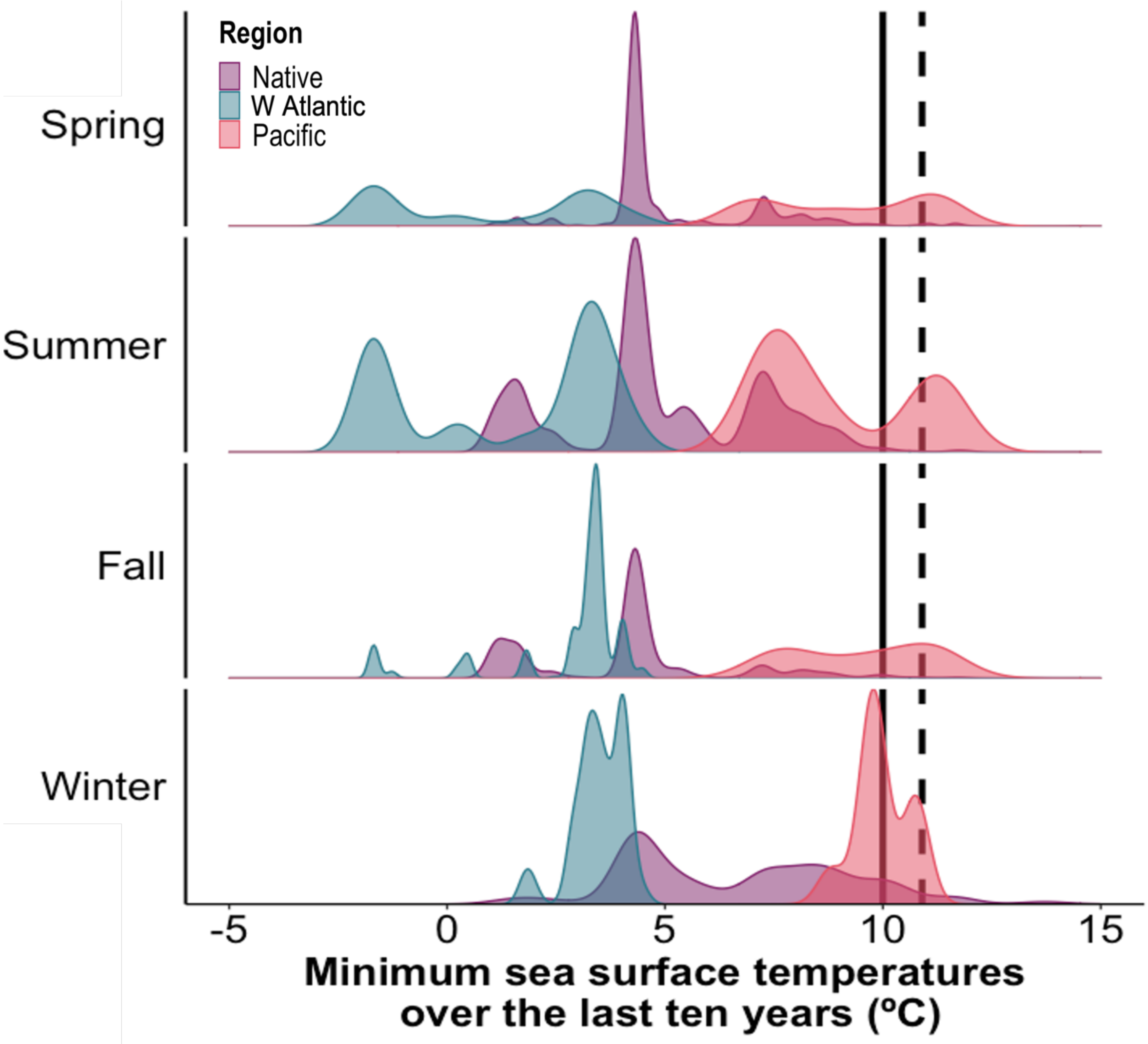

Figure 3.8 Minimum sea surface temperatures. Distribution of minimum sea surface temperatures over the last ten years for three regions of *Carcinus maenas*. Solid lines represent the critical thermal minimum for *C. maenas* eggs (n =1), dashed lines represent the mean critical thermal minimum for larvae (n = 2). Colors correspond to regions. Pacific refers to the invasive east Pacific crabs.

Discussion

This review of the *Carcinus maenas* thermal biology literature suggests several knowledge gaps, few quantitative studies, and no methodological standardization in previous experiments that assess thermal physiology to support broad-scale comparisons and macroecological questions. Several critical knowledge gaps were pinpointed, such as studies that compare thermal responses in different sexes, life-stages, and regions. Furthermore, there is a lack of quantitative evidence of green crab thermal limits despite the importance of these values for invasion prediction models. Despite being studied separately and having different study designs, evidence suggests that green crab adults and larvae have unique thermal tolerances and that larvae may represent the limiting stage to survival in terms of thermal exposure.

Carcinus maenas is a highly studied model species and is the focus of over 4,000 studies (at least); however, only 105 of these studies specifically include temperature effects (according to this review). With environmental temperatures being such an essential factor in defining species environmental niches (Angilletta, 2009), performance (Pörtner, 2002), and fitness (Gilchrist, 1995), I expected a greater number of papers in my review. One significant gap in the green crab literature lies in the differences between life-stage studies. The effects of warm temperatures are the primary focus in adult studies, with experiments measuring metabolic rate, muscle spasm, righting response, and death. Furthermore, adult thermal limit studies are more commonly dynamic, with ramped temperatures rather than set treatments. Meanwhile, larval thermal limit experiments primarily explore cold temperatures on development and survival with pre-determined static temperatures. Gaps were also found between the patterns, survival, and inter- and intra-regional concepts, any combinations of which would present valuable novel research. Lastly, no studies examined thermal limits in more than one life stage, and few include genetic or sex variability (Kelley et al., 2011; Tepolt and Palumbi, 2020). Future research should study these gaps (life-stage, sex, region) to make specific conclusive statements regarding green crab thermal vulnerabilities. This review suggests that high temperatures are a more significant threat to adults, while low temperatures are a more significant threat to juveniles; however, the evidence remains inconclusive without balanced, reproducible studies.

I also highlight a need for greater focus on study design to make results ecologically relevant (realistic natural conditions), comparable (standardized), and broadly representative. I found little evidence of consistency in thermal values or pejus and pessimum ranges despite the abundance of green crab research. The majority of values in this review are critical maximum temperatures (CTMax), although other values in the thermal window (particularly the optimal range) are arguably more informative and valuable. CTMax has been the focus of thermal biology research, but studies are highly context-specific, as seen in the wide range of reported values. Furthermore, many thermal limit studies are observational (unimpeded observation in the natural environment without manipulation). These observational studies do not control outside factors; therefore, causality must be inferred (Brennan and Croft, 1994). Furthermore, observational studies introduce several forms of unintentional bias, including selection bias (e.g., not observing difficult-to-access sites), information bias (Hammer et al., 2009), and observer bias (e.g., over or underestimation; Zvereva and Kozlov, 2021), due to the opportunistic and time-dependent nature of these studies (Lin et al., 2017).

Experimental results are highly dependent on study design, and the green crab thermal biology studies herein used a large variety of designs. Different ramping rates, acclimation lengths and temperatures, sample sizes, and endpoint measures make these studies virtually incomparable. Studies with faster ramping rates often result in higher CTMax values (Bates and Morley, 2020; Chown et al., 2009; Rezende et al., 2014). Indeed, the highest CTMax reported here (38.3 ºC) was returned using the fastest ramping rate (15 ºC hr^{-1}; Jørgensen et al., 2017). In fact, several studies used ramping rates which may not be ecologically relevant (i.e., 12 to 15 ºC hr^{-1}; such rapid changes in temperature occur in limited areas, such as the intertidal) and make it difficult to extrapolate the results to real-world scenarios. Furthermore, several studies have linked acclimation time and temperature to thermal limit results (Chanthy et al., 2012; McGaw and Whiteley, 2012; Moyano et al., 2017; Padilla-Ramírez et al., 2015; Xia et al., 2017). Meanwhile, sample size has been shown (mathematically) to impact results by changing the probability that an event occurs by chance (Button et al., 2013; Ioannidis, 2005). Lastly, the endpoint measure impacts experimental results because the processes selected to characterize experimental endpoints often occur at different temperatures (e.g., paralysis versus death).

Adult green crabs have remarkable physiological flexibility, environmental variability resistance, and the ability to withstand short-term exposure to extreme temperatures (≤ -1

to 38 ºC). Adult males are the primary focus in the green crab thermal biology literature; the effects of high temperature have been studied in numerous ways, including behavior (competition, feeding, movement), performance (metabolic rate, death, CTMin, CTMax), and growth patterns (sexual maturation, molting, polymorphisms). These studies suggest that a small, slow increase to mean temperatures may benefit green crabs. For example, feeding (Matheson and Gagnon, 2012a, 2012b), movement (Rayner and McGaw, 2016), and competition (Matheson and Gagnon, 2012a, 2012b) were all correlated with temperature in experimental studies. Furthermore, environmental temperatures mitigate the physiological stress of unfavorable salinities (Broekhuysen, 1937; Spitzner et al., 2019; Torres and Giménez, 2020). In fact, CTMax studies have shown that adult green crabs can tolerate short-term exposure to temperatures up to 38.3 ºC (dependent on the experimental methods, as discussed above; Jørgensen et al., 2017; Tepolt and Somero, 2014; Table S3.3). Meanwhile, CTMin studies found 90% survival down to ≤ –1 ºC (Kelley, 2014; Tepolt and Somero, 2014). Together, these results suggest that green crabs have, at least, short-term resilience against extreme temperatures.

This review highlights the wide range of values proposed to define the thermal window of *Carcinus maenas*. Robertson et al. (2002) proposed 15 ºC as the optimal temperature for performance, while McGaw and Whiteley (2012) propose 5 to 25 ºC as the optimal range. Various other studies agree with these approximate values (Cohen et al., 1995; Robertson et al., 2002; Taylor et al., 1977a); however, when we look at the thresholds beyond the optimal range, things are less clear. Jost et al. (2012) could not ascertain any pejus temperature, as all of their parameters (AMPK, HSP, heart rate, lactate, righting response) remained unchanged up to the critical temperature. It is, therefore, possible that *C. maenas* has a pejus temperature very close to the critical temperature or that the species has eliminated the pejus temperature (Jost et al., 2012). However, Taylor and Wheatly (1979) found a pejus temperature of 28 ºC when crabs exhibited avoidance behavior in response to slowly heated water. Furthermore, CTMax studies reported significant variance between values (29.7 to 38.3 ºC). Thus, it seems that green crab thermal studies are highly dependent on the individual (e.g., age, sex, region) and experimental methods (e.g., acclimation time, ramping speed). The lack of clear information on *C. maenas* pejus thresholds and ranges provides a seemingly essential and exciting area for future research.

Defining the optimal range is further complicated by the lack of evidence on the cold end of the species' tolerance. Two studies attempted to measure the CTMin (Kelley, 2014; Tepolt and Somero, 2014) but could only cool the water to –1 ºC. Spaargaren (1984), however, measured hemolymph (i.e., crab "blood") separated from the animal to determine its freezing point and found that crystallization occurs far below the freezing point of seawater (–9 to –15 ºC). While it is challenging to test animals below the freezing point of seawater, the few studies that have attempted, provide compelling evidence that *C. maenas* will not freeze in seawater, and therefore, has the potential to expand its distribution to colder regions (Kelley, 2014; Spaargaren 1984; Tepolt and Somero, 2014). Furthermore, several authors (Cohen et al., 1995; Naylor, 1962; Robertson et al., 2002) describe an off-shore ocean migration, whereby crabs avoid cooling surface temperatures in the winter months by moving to deeper waters. However, Naylor (1962) found no evidence of a complete off-shore migration and suggested that even in the coldest month, crabs still migrate up-shore with high tide, where they may become stranded. Other authors have presented evidence of *C. maenas* stranding's lasting several days (Edwards, 1958; Robertson et al., 2002). Previous studies have found that intertidal invertebrates can have a body temperature that varies up to 20 ºC in one tidal cycle (Jost et al., 2012). Therefore, rapidly falling temperatures may cause such a metabolic depression in green crabs that they are left motionless and unable to retreat (Broekhuysen, 1937). Furthermore, following a particularly cold European winter, many species (including *C. maenas*) were found dead in dredges (Crisp 1964; Waugh, 1964). Interestingly, the smaller individuals (of several different species, including *C. maenas*) had higher survival, which the authors surmised was due to higher movement than adults, where those who succumb to lethargy, torpor, and stranding are at greater risk of predation (Crisp 1964; Waugh, 1964). Therefore, it seems that the most significant risk that cold poses to *C. maenas* is not the temperature itself but rather the temperature-induced side-effects.

Although *settled* juvenile green crabs appear to be at lower risk than adults, this work provides strong evidence that *pre-settled* larvae are the most thermally sensitive life stage, with cold temperatures posing the most significant risk. Larval growth occurs within the temperature range of 7 to 25 ºC (Dawirs and Dietrich, 1986; de Rivera et al., 2007), while thermal tolerance levels are reportedly within 10 to 22 ºC (de Rivera et al., 2007). This difference may be due to experimental differences (e.g., ramping rate, experiment endpoint, season collected) or regional differences. Less research has been conducted on the effects of warm temperatures (than cold temperatures) on green crab larvae. What is known, with reasonable certainty, is that lower temperatures increase development time, which may reduce the juvenile's ability to complete development, resulting in lower overall survivorship (Banas et al., 2009). Delayed development requires more energy (and therefore more nutrients) while potentially causing predator-prey mismatch (Sprung, 2001; Strasser and Günther, 2001). For example, if plankton bloom and die before *C. maenas* hatch, there will be lower nutrient availability, which may cause developmental failure (Sprung, 2001). Studies on the number of days required for development at a given temperature (phenological window) show that green crab larvae have thermal-temporal requirements (Giménez et al., 2020). For example, at 12.5 ºC, de Rivera (2007) found a phenological window of 59 days; in other words, at 12.5 ºC, 59 days would be required for successful larval development. Therefore, if the water column does not reach 12.5 ºC by an early enough time of year (that it will remain ≥ 12.5 ºC for 59 days), *C. maenas* larvae would not develop successfully. By quantifying thermal-temporal larval requirements, we can predict the success of a reproducing group based on past and projected future climates. The phenological window of development (i.e., thermal-temporal relationship) should be considered in future studies, distribution models, and conservation efforts because larvae appear to be the most vulnerable *C. maenas* life-stage (though see above discussion on study balance).

The results of this study are dependent on the comprehensiveness of the review. While this study aims to be thorough (and included filtering 4,539 papers, e-mail notifications, and multiple search methods), I may have overlooked some studies. First of all, the results are almost entirely dependent on papers being available on the Web of Science (the search engine chosen). The only way papers outside of the Web of Science were included was by reviewing the references. However, it is fair to assume that any highly relevant studies would be cited within the references (of the papers) read. Secondly, the search terms may have missed relevant papers due to the search string itself or the way it was used. The search terms were entered into the 'topic' field in Web of Science, which searches the title, abstract, keywords, and Keywords Plus®. Therefore, any relevant papers not including the specific search terms in those fields may have been missed. Furthermore, two papers found from references were unavailable despite trying several search engines and library inter-loans: Hart, 1955; MacPhail and Lord, 1954. Lastly, the species has gone by several other names not accounted for in this study (i.e., I did not include *Carcinides sp., Cancer sp., Cancer granulatus, Cancer pygmeus,* or *Cancer granarius* in my searches; WoRMS Editorial Board, 2021).

Conclusions

This review provides evidence regarding the need for methodological standardization using ecologically relevant and repeatable methods in green crab thermal biology studies. I also suggest that future studies be designed to compare life stages, sexes, and regions to reduce the adult male bias of current studies. Furthermore, I show that adult green crabs are physiologically robust and can withstand short-term exposure to sea temperatures up to 30 ºC and down to –1 ºC. Finally, I present evidence suggesting that larvae are more thermally sensitive than adults, have reduced survivorship following colder-than-average breedings seasons, and do not receive the warranted modeling and projection focus.

Chapter 4

Final conclusions on a thermal biology green crab thesis

Final conclusions on a thermal biology green crab thesis

Summary

Species and ecosystems are under increasing threat from anthropogenic stressors (Derraik, 2002; Fischer and Lindenmayer, 2007; Jetz et al., 2007; Walther et al., 2002). Two of the leading threats to biodiversity are climate change and invasive species (Gallardo and Aldridge, 2013; Mainka and Howard, 2010). Climate change forces species to adapt, move, or die (Corlett and Westcott, 2013; Habary et al., 2017), while invasive species are out-competing and killing natives (Mooney and Cleland, 2001; Vilcinskas, 2015). Conservation groups and government organizations monitor invasive species to protect native ecosystems, but increased knowledge is essential to mitigate and manage these impacts (Mooney and Cleland, 2001; Vilcinskas, 2015).

Throughout this thesis, I take a macroecological approach to studying a globally abundant and highly impactful species, *Carcinus maenas*. Chapter (Ch.) 2 explores regional characteristics, changes through time, and the relationship between temperature change and abundance using worldwide occurrence and abundance records and satellite-derived temperature data. I further examine the effects of temperature on *C. maenas* by reviewing the thermal biology literature and synthesizing the research topics and quantitative thermal limits in Ch. 3. My overarching objectives were:

1. Define *C. maenas* thermal distribution based on geographic occurrences (Ch. 2);
2. Calculate abundance and temperature changes through time (Ch. 2);
3. Examine the correlation between abundance and temperature variability (Ch. 2);

4. Determine focal points and gaps in *C. maenas* thermal ecology literature (Ch. 3);
5. Compile and synthesize all reported *C. maenas* thermal limits (Ch. 3);
6. Compare reported thermal limits to regional satellite temperature metrics (Ch. 3).

Summary of results

This thesis presents several new directions of understanding regarding the thermal biology of *Carcinus maenas*. My review (Ch. 3) highlights several knowledge gaps by synthesizing and categorizing the thermal biology literature. For instance, few studies have examined the optimal window or pejus temperatures, with most thermal tolerance studies focusing on critical temperatures. Furthermore, adult thermal tolerance is most commonly studied regarding high temperatures, while studies on juveniles focus on cold temperatures (Figure 3.6, Table S3.2). Chapter 3 compares green crab quantitative thermal limits across different life stages (Figure 3.6, Table S3.2) and finds life-stage specific tolerances (i.e., adults cope with a broader range of temperatures than juveniles; Klassen and Locke, 2007). A narrow thermal tolerance makes juvenile green crabs more sensitive to longer- or colder-than-average winters resulting in developmental failure. The extreme weather sensitivity of juvenile green crabs, and the subsequent decline in adult abundance (after one to three years), align with my Ch.2 results showing that year-to-year temperature variability and abundance are correlated. This thesis implicates the role of winter warming (and cooling) in promoting (and limiting) the future success of this species, likely due to the sensitivity of juvenile stages. Furthermore, Chapter 3 showed region-specific tolerances, whereby northern European and hybrid crabs have greater cold adaptation (Tepolt and Palumbi, 2015, 2020), also aligning with the Chapter 2 results (i.e., the invasive Atlantic crabs colonized regions more extreme than natives). Finally, these results demonstrate that green crabs may perform well with warming winters.

Implications

This thesis highlights the unique qualities of *Carcinus maenas*. For example, invasive Atlantic crabs have a thermal niche encompassing more extreme high and low temperatures than the native Atlantic crabs. Regional differences are not surprising since the initial invasion was over 200 years ago (Say, 1817), eventually resulting in three genetically unique west Atlantic groups (Tepolt and Palumbi, 2015, 2020; Figure 4.1). The northern invasive Atlantic crabs (from Norway) are more cold-adapted than the southerners (from Portugal), while the hybrids are even more cold-hardy (Coyle et al., 2019; Tepolt and Palumbi, 2020). The invasion of crabs with greater thermal tolerances may have facilitated the eastern American colonization further north into Newfoundland (Tepolt and Palumbi, 2020) and may contribute to the thermal niche mismatch found in Chapter 2 (Figure 4.1). These findings are significant for species distribution models, which often rely on native geographical ranges (Guisan and Thuiller, 2005; Rödder et al., 2009); thus, potentially underestimating the survivable range. Therefore, I advocate for the inclusion of population dynamics, dispersal potential (Guisan and Thuiller, 2005), geographical or thermal distributions, and failed colonization attempts to increase model accuracy.

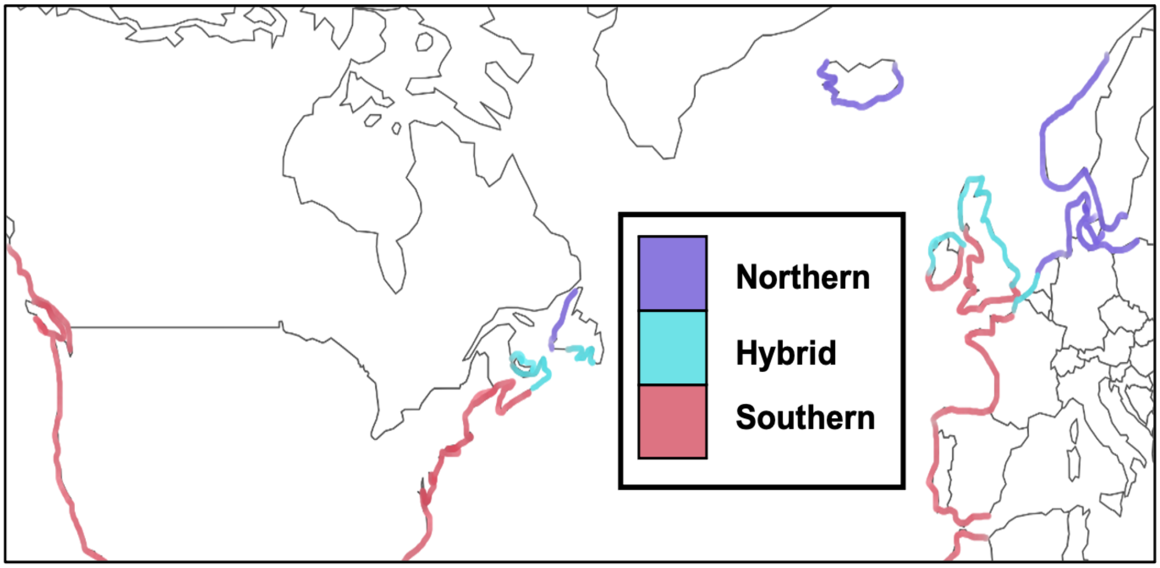

Figure 4.1 ***Carcinus maenas*** **genetic population and geographic regions.** Map of native green crabs (northern, hybrid, southern) and their North American invasions, with approximate geolocations.

I provide evidence, throughout this thesis, that green crabs are thermally robust, yet changes in abundance are inherently linked to temperature. Specifically, I found that green crabs can colonize regions more thermally extreme than their home-range (Figure 2.1), tolerate sub-zero seawater, and survive acute extreme warm-weather events. However, despite wide thermal tolerances, I also show that year-to-year temperature variability influences and predicts green crab abundance changes (Figure 2.5) and that extreme weather events impact juvenile development and recruitment. I propose the following mechanism to explain this contradiction: 1) extreme weather event, 2) above-average juvenile mortality, 3) low recruitment, and 4) subsequent adult abundance decline (within 1–3 years; Figure 4.2). In other words, adult green crabs are thermally resistant, but juveniles are not, and therefore, juveniles represent the bottleneck to population growth and survival.

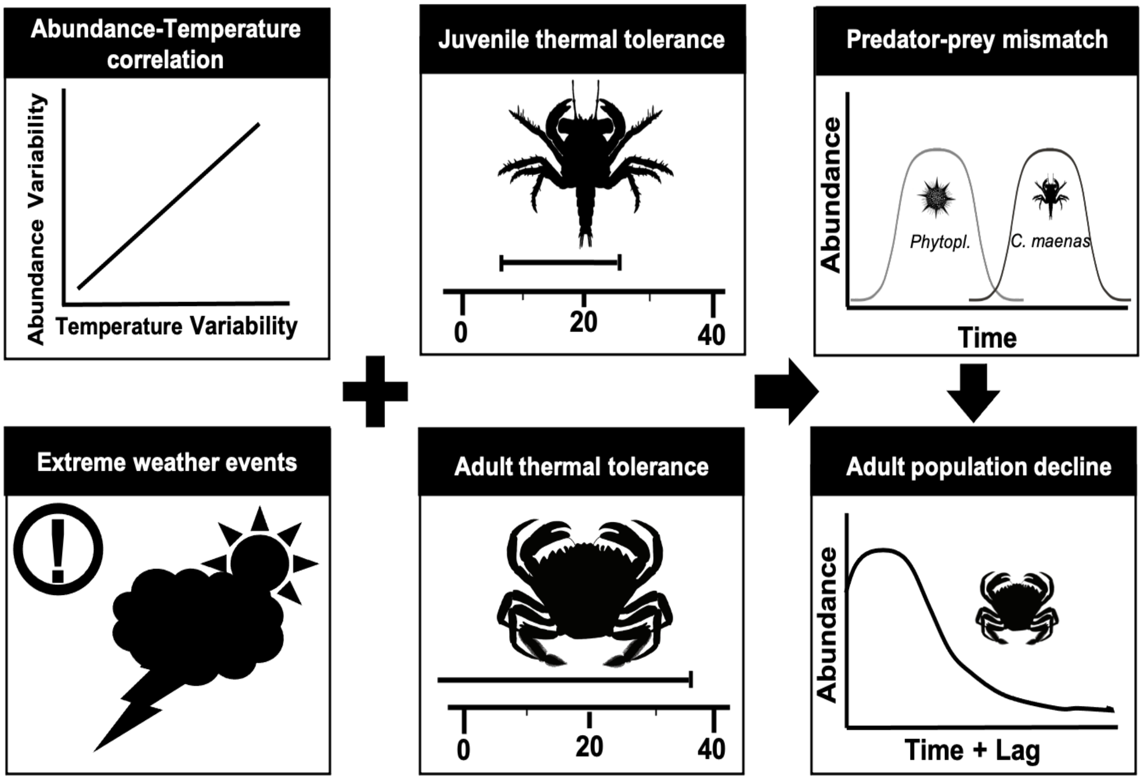

Figure 4.2 Extreme weather events decrease green crab abundances. Conceptual figure showing that green crab abundance and temperature variability are related, and extreme weather events exert physiological stress on juveniles. Extreme weather events can delay juveniles from hatching, leading to predator-prey mismatch, decreased juvenile survival, and reduced adult abundance following a lag while crabs mature.

Future Work

I recommend that *Carcinus maenas* monitoring programs be implemented in and around Australia and South Africa. This recommendation is based on the invasion history (Ch. 1) and low quantity of data in these regions (Ch. 2). Perhaps, monitoring is of lower concern to South Africa, as a recent survey (Mabin et al., 2017) found that abundances are declining and restricted to two small human-made harbors. Australia, however, appears to have low certainty on the location and abundance of green crabs currently in the region. I propose that environmental groups follow the lead of Grason et al. (2018), who created a successful citizen-science-based monitoring and removal program that educates and learns from the public and local Indigenous communities.

Species distribution models are commonly based on the native range and use presence-only or presence-absence data (Guisan and Thuiller, 2005; Rödder et al., 2009). Niche-based models are helpful in projecting the native niche into geographic space; however, these models do not always find the full potential range (Rödder et al., 2009). This concept is demonstrated in Chapter 2, where the green crabs' native and invasive Atlantic distributions did not match (thermal niche mismatch). Furthermore, Chapter 3 shows that green crabs have both life-stage and region-specific tolerance levels. If models only consider native adult needs, they may provide inaccurate predictions. Therefore, I recommend that future distribution models include species-specific information. Rödder et al. (2009), for example, propose that niche-based models remain a starting point while more specific information (e.g., natural history, genotype, migration processes) be used to enhance the model. Adding species-specific information to distribution models will improve accuracy and allow for planning and preparation.

I also propose that future studies further explore the role temperature plays in green crab success. This thesis shows that satellite-derived air and sea surface temperature variability is strongly related to year-to-year green crab abundance variability. Using broad-scale temperature data is a common strategy in macroecology due to high accessibility; however, broad-scale averaged data can miss out on fine-scale local differences (Bates et al., 2018; Trenberth and Hurrell, 1997). The data used here were collected monthly on a one-degree grid, thereby missing potentially significant temporal (hourly, daily) and spatial (meters to kilometers) fluctuations that organisms respond to. Therefore, I recommend that future studies utilize fine-scale temperature data as a more ecologically relevant measure of species impact. It would also be beneficial to include other factors that affect green crab distribution, such as habit type and shore energy (Cohen et al., 1995; McGaw and Whiteley, 2012). Furthermore, this thesis implies that green crabs are not currently limited by temperature in the warm end of their ranges, but ranges are also not spreading on this end. Therefore, future studies should examine other mechanisms that may limit green crab expansion.

Finally, I advocate for the repetition, standardization, and pre-conception of *C. maenas* thermal tolerance study methods. I found 24 papers reporting quantitative thermal limits, one on the pejus range, none with the same methods (e.g., ramping speed), and few using ecologically appropriate methods (most used a 12 to 15 ºC temperature increase per hour). None of the adult critical thermal maximum studies used the same methods, which is necessary for making comparisons between a changing variable; however, experimental context must also be pre-determined to reflect this decision. Repetition and expansion of previous thermal tolerance studies can help confirm results, clarify confusion about the thermal window and pejus temperatures, and make appropriate inter-regional comparisons. As the weak link, juvenile stages need more research with standardized, repeatable, and ecologically relevant methods. This thesis shows that juvenile *C. maenas* are at risk from extreme weather events due to the pressures of unfavorable temperatures and food shortages. Furthermore, Yamada et al. (2015, 2017) show that extreme weather events impact recruitment and retention, imposing additional risk to this already sensitive life stage. Most juvenile studies are laboratory experiments on metamorphosis and development; the literature could use observational and modeling studies examining extreme weather on *C. maenas* juveniles.

Final Conclusions

In conclusion, this thesis supports the hypothesis that *Carcinus maenas* will prosper with climate change (Bellard et al., 2013; Sorte et al., 2013). This conclusion is based on 1) the species' broad thermal tolerances, 2) colonization of regions more thermally extreme than the native niche and, 3) increasing abundance in areas with warming. I further conclude that the results in this thesis can help improve the accuracy of species distribution models based on 1) niche-mismatch, 2) life-stage-specific tolerances, and 3) region-specific tolerances (Figure 4.1). Lastly, I conclude that these results can aid green crab mitigation efforts based on 1) year-to-year variability predicting green crab abundance and 2) juvenile green crab sensitivity to extreme weather events. This thesis accomplished my objectives, composed constructive conclusions, and formulated recommendations for future *Carcinus maenas* research.

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Appendix 1

Chapter 2

Supplementary Material

Supplementary Contents

Tables

Code

TABLES

Table S2.1 Study data information summary. Symbol ¥ denotes data acquired from the literature; § indicates data obtained from online databases; all others were provided directly by listed contact. Obs. is the number of observations in study. State is the province or state, two-letters except PEI; three-letter bold abbreviations are countries.

Data Source	Contact info	Dates	Obs.	Site	State
Brady Quinn	bk.quinn@unb.ca	2008-2017	68	1	NB
Jennifer Yakimishyn	jennifer.yakimishyn@canada.ca	2014-2018	221	45	BC
Michael Burrows	michael.burrows@sams.ac.uk	2001-2010	233	25	**SCT**
Sylvia Yamada	yamadas@science.oregonstate.edu	2002-2019	85	5	OR
Christopher Bloch	cbloch@bridgew.edu	2003-2017	15	1	MA
Sorte et al., 2017 ¥	csorte@uci.edu	1972-2014	4374	20	ME
BioTime 110 § Ostler, 2012	steve.wilkinson@jncc.gov.uk	1954-2000	4042	174	**SCT**
BioTime 191 § NEFSC, 2012	steven.fromm@noaa.gov	1900-1975	4919	44	ME
BioTime 196 § Moore and Howson, 2013	rja4@st-andrews.ac.uk	1976-2012	763	37	**SCT**
BioTime Study ID 428 § Barceló et al., 2009 Olsen et al., 2009 Rogers et al., 2011 Stenseth 1999	halvor.knutsen@imr.no	1919-2015	9847	11	NOR
Welch, 1968 ¥	n/a	1953-1966	142	5	ME

Grosholz et al., 2005 ¥	tedgrosholz@ucdavis.edu	1992-2002	11	1	CA
de Rivera et al., 2011 ¥	derivera@pdx.edu	1992-2006	14	1	CA
Vercaemer and Sephton, 2016 ¥	Benedikte.Vercaemer@dfo-mpo.gc.ca	2008-2015	405	94	NB
Beukema, 1991 ¥	jan.beukema@nioz.nl	1969-1990	43	1	**DMK**
Ron Thresher	Ron.Thresher@csiro.au	1996-2001	61	3	**TAS**
Markus Frederich	mfrederich@une.edu	2012-2019	81	1	ME
O'Connor, 2014 O'Connor, 2018 ¥	noconnor@umassd.edu	1999-2016	44	2	MA
Mathieson and Berry, 1997 ¥	—	1985-1994	10	1	**SCT**
Langhamer et al., 2016 ¥	olanghamer@gmail.com	2002-2012	27	3	**SWD**
Poirier et al., 2017 ¥	pquijon@upei.ca	2000-2013	106	13	PE
Alan M. Young	ayoung@salemstate.edu	2013-2016	31	1	MA
DFO; CAMP §	Monica.boudreau@dfo-mpo.gc.ca	2004-2019	9707	214	NB
Bessa et al., 2010 ¥	afbessa@student.zoo.uc.pt	2003-2007	167	4	PT
Cynthia McKenzie	Cynthia.mckenzie@dfo-mpo.gc.ca	2010-2017	40	1	NL
Emily Grason	egrason@uw.edu	2001-2019	44	6	WA

Table S2.2 Latitudinal range and temperature characteristics. Location and temperature descriptors of the four study regions, native Atlantic (Europe), invasive Atlantic (east North America), invasive east Pacific (west North America), invasive west Pacific (Australia). Temperature measures correspond to the years the studies were present over.

Region Characteristic		**Native**	**West Atlantic**	**East Pacific**	**West Pacific**
Latitude (ºN)	Min	36.2	38.1	36.6	-43.5
	Max	70.5	52.8	52.5	-23.5
	Range	15.9	14.7	34.3	20
Study Duration (years)	Min	1924	1950	1992	1996
	Max	2015	2019	2019	2001
	Total	92	38	28	6
Minimum AirT (ºC)	Min	-12	-15.1	14.4	6.9
	Max	11.1	1.7	20.6	9.4
Maximum AirT (ºC)	Min	11	13.7	14.4	16
	Max	23.5	25.2	20.6	19.1
Minimum SST (ºC)	Min	1.53	-1.8	7.54	17.1
	Max	14.4	14.4	13.0	18.8
Maximum SST (ºC)	Min	11.7	13.8	13.9	16
	Max	20.9	23.1	17.4	19.1

Table S2.3 Five-year intercept models. Parameter estimates for linear mixed-effects intercept models testing five-year variability in *C. maenas* abundance, summer air, winter air, summer sea surface, and winter sea surface temperatures relative to time (year). Separate models for each region, including all together (global).

Response ~ 1, random = ~ 1 | Study / Region, weights = varFixed (~Abundance sd)

Region	**Response**	**Coefficient**	**Standard error**	**p-value**
Global	ΔAbundance	0.0531	0.0384	0.167
	ΔSummer AirT	0.0439	0.0394	0.265
	ΔWinter AirT	0.0284	0.0840	0.736
	ΔSummer SST	0.0319	0.0344	0.355
	ΔWinter SST	0.0124	0.0309	0.689
Native	ΔAbundance	0.0216	0.0387	0.579
	ΔSummer AirT	0.132	0.0295	< 0.001
	ΔWinter AirT	0.00661	0.0649	0.919
	ΔSummer SST	0.0864	0.0317	0.00790
	ΔWinter SST	0.0426	0.0220	0.0561
West Atlantic	ΔAbundance	0.0365	0.0747	0.625
	ΔSummer AirT	-0.101	0.0530	0.0572
	ΔWinter AirT	-0.0370	0.150	0.806
	ΔSummer SST	0.00293	0.0407	0.943
	ΔWinter SST	-0.0277	0.0560	0.622
East Pacific	ΔAbundance	0.0820	0.118	0.497
	ΔSummer AirT	0.0891	0.0474	0.0812
	ΔWinter AirT	-0.0755	0.108	0.497
	ΔSummer SST	-0.0451	0.0368	0.241
	ΔWinter SST	-0.00190	0.0377	0.961

Table S2.4 Five-year change in global *C. maenas* abundance and temperatures. Parameter estimates for global linear mixed-effects models testing the change in *C. maenas* abundances through time relative to changes in temperature.

ΔAbundance ~ ΔTemperature * climatology, random = ~ 1 | Site / Study

Temperature	Fixed effect	Coefficient	Std. error	p-value
Summer AirT	Intercept	0.0337	0.0388	0.385
	ΔTemperature	0.0243	0.0236	0.303
	Climatology	0.324	0.0170	0.0571
	ΔTemperature * Climatology	0.0560	0.0223	0.0124
Winter AirT	Intercept	0.0851	0.0425	0.0460
	ΔTemperature	0.0551	0.0279	0.0487
	Climatology	0.0409	0.0164	0.0131
	ΔTemperature * Climatology	0.0298	0.0156	0.0561
Summer SST	Intercept	0.0269	0.0408	0.510
	ΔTemperature	-0.0274	0.0296	0.356
	Climatology	0.0352	0.0174	0.0437
	ΔTemperature * Climatology	-0.0162	0.0144	0.260
Winter SST	Intercept	0.0447	0.0376	0.235
	ΔTemperature	0.0371	0.0166	0.0260
	Climatology	0.0545	0.0169	0.00130
	ΔTemperature * Climatology	0.0304	0.0147	0.0390

Table S2.5 Five-year change in native *C. maenas* abundance. Parameter estimates for native linear mixed-effects models testing the change in *C. maenas* abundances through time relative to changes in temperature.

ΔAbundance ~ ΔTemperature * climatology, random = ~ 1 | Site / Study

Temperature	Fixed effect	Coefficient	Std. error	p-value
Summer AirT	Intercept	0.0617	0.0506	0.226
	ΔTemperature	-0.0437	0.0468	0.353
	Climatology	0.0610	0.0399	0.129
	ΔTemperature * Climatology	0.0203	0.0534	0.705
Winter AirT	Intercept	0.0619	0.0496	0.215
	ΔTemperature	0.0250	0.0419	0.552
	Climatology	0.0591	0.0395	0.138
	ΔTemperature * Climatology	0.0150	0.0622	0.810
Summer SST	Intercept	0.0665	0.0502	0.188
	ΔTemperature	-0.0406	0.0466	0.385
	Climatology	0.0755	0.0422	0.0770
	ΔTemperature * Climatology	0.0701	0.0540	0.197
Winter SST	Intercept	0.0640	0.0498	0.202
	ΔTemperature	0.0587	0.0491	0.235
	Climatology	0.0702	0.0404	0.0854
	ΔTemperature * Climatology	0.116	0.0854	0.177

Table S2.6 Five-year change in west Atlantic *C. maenas* abundance. Parameter estimates for linear mixed-effects models testing the change in *C. maenas* abundances through time relative to changes in temperature.

ΔAbundance ~ ΔTemperature * climatology, random = ~ 1 | Site / Study

Temperature	Fixed effect	Coefficient	Std. error	p-value
Summer AirT	Intercept	0.00548	0.0745	0.942
	ΔTemperature	0.0448	0.0293	0.128
	Climatology	0.0331	0.0209	0.115
	ΔTemperature * Climatology	0.0315	0.0193	0.103
Winter AirT	Intercept	0.103	0.0853	0.228
	ΔTemperature	0.0751	0.0383	0.0505
	Climatology	0.0434	0.0183	0.0183
	ΔTemperature * Climatology	0.0224	0.0160	0.162
Summer SST	Intercept	-0.0243	0.0847	0.775
	ΔTemperature	0.00666	0.0503	0.895
	Climatology	0.0388	0.0191	0.0433
	ΔTemperature * Climatology	-0.0268	0.0147	0.0688
Winter SST	Intercept	0.00873	0.0745	0.907
	ΔTemperature	0.0364	0.0192	0.0585
	Climatology	0.0591	0.0190	0.00200
	ΔTemperature * Climatology	0.0201	0.0147	0.171

Table S2.7 Five-year change in east Pacific *C. maenas* abundance. Parameter estimates for Pacific linear mixed-effects models testing the change in *C. maenas* abundances through time relative to changes in temperature.

ΔAbundance ~ ΔTemperature * climatology, random = ~ 1 | Site / Study

Temperature	Fixed effect	Coefficient	Std. error	p-value
Summer AirT	Intercept	0.0519	0.126	0.687
	ΔTemperature	0.0686	0.0970	0.494
	Climatology	-0.103	0.0963	0.309
	ΔTemperature * Climatology	0.0922	0.132	0.499
Winter AirT	Intercept	0.103	0.132	0.450
	ΔTemperature	-0.00749	0.0924	0.937
	Climatology	-0.0676	0.0761	0.394
	ΔTemperature * Climatology	-0.125	0.154	0.434
Summer SST	Intercept	0.707	0.0902	0.450
	ΔTemperature	0.0166	0.0700	0.817
	Climatology	0.144	0.106	0.199
	ΔTemperature * Climatology	-0.272	0.107	0.0268
Winter SST	Intercept	0.0842	0.133	0.540
	ΔTemperature	-0.00804	0.0770	0.919
	Climatology	-0.0634	0.0918	0.504
	ΔTemperature * Climatology	-0.0436	0.170	0.803

Table S2.8 Year-to-year variability in global *C. maenas* abundance. Parameter estimates for linear mixed-effects models testing year-to-year variability in global *C. maenas* abundances relative to year-to-year variability in summer air, winter air, summer sea surface, and winter sea surface temperatures.

Abundance residual ~ Temperature residual * climatology, random = ~ 1 | Site / Study

Variable	Fixed effect	Coefficient	Std. error	p-value
Summer AirT	Intercept	< 0.001	0.0133	0.995
	Temperature	0.0718	0.0203	< 0.001
	Climatology	-0.00261	0.0133	0.844
	Temperature * Climatology	-0.0376	0.0201	0.0618
Winter AirT	Intercept	< 0.001	0.0133	0.994
	Temperature	0.0273	0.00827	0.00100
	Climatology	-0.00258	0.0133	0.846
	Temperature * Climatology	0.0248	0.0105	0.0179
Summer SST	Intercept	< 0.001	0.0133	0.999
	Temperature	0.0769	0.0241	0.00140
	Climatology	-0.00267	0.0133	0.841
	Temperature * Climatology	-0.00789	0.0154	0.756
Winter SST	Intercept	< 0.001	0.0133	0.999
	Temperature	0.0760	0.0317	0.0167
	Climatology	-0.00256	0.0133	0.847
	Temperature * Climatology	0.0365	0.0194	0.215

Table S2.9 Year-to-year variability in native *C. maenas* abundance. Parameter estimates for linear mixed-effects models testing year-to-year variability in native *C. maenas* abundances relative to year-to-year variability in summer air, winter air, summer sea surface, and winter sea surface temperatures.

Abundance residual ~ Temperature residual * climatology, random = ~ 1 | Site / Study

Variable	Fixed effect	Coefficient	Std. error	p-value
Summer AirT	Intercept	< 0.001	0.0292	0.975
	Temperature	0.0205	0.0403	0.610
	Climatology	0.00774	0.0292	0.791
	Temperature * Climatology	-0.0816	0.0442	0.0654
Winter AirT	Intercept	< 0.001	0.0291	0.996
	Temperature	0.0652	0.0234	0.00560
	Climatology	0.00702	0.0291	0.809
	Temperature * Climatology	0.0382	0.0360	0.289
Summer SST	Intercept	< 0.001	0.0292	0.990
	Temperature	0.0574	0.0564	0.309
	Climatology	0.00697	0.0292	0.811
	Temperature * Climatology	-0.0731	0.0671	0.277
Winter SST	Intercept	< 0.001	0.0292	0.997
	Temperature	0.114	0.0643	0.0759
	Climatology	0.00628	0.0292	0.830
	Temperature * Climatology	0.0770	0.0860	0.371

Table S2.11 Year-to-year variability in west Atlantic *C. maenas* abundance. Parameter estimates for linear mixed-effects models testing year-to-year variability in *C. maenas* abundances relative to year-to-year variability in summer air, winter air, summer sea surface, and winter sea surface temperatures.

Abundance residual ~ Temperature residual * climatology, random = ~ 1 | Site / Study

Variable	Fixed effect	Coefficient	Std. error	p-value
Summer AirT	Intercept	< 0.001	0.0153	0.999
	Temperature	0.0849	0.0238	< 0.001
	Climatology	-0.00961	0.0153	0.530
	Temperature * Climatology	-0.0197	0.0201	0.329
Winter AirT	Intercept	< 0.001	0.0153	0.992
	Temperature	0.0162	0.00841	0.0540
	Climatology	- 0.00970	0.0153	0.527
	Temperature * Climatology	0.0122	0.00984	0.217
Summer SST	Intercept	< 0.001	0.0153	0.999
	Temperature	0.0819	0.0273	0.00270
	Climatology	-0.00880	0.0153	0.566
	Temperature * Climatology	0.0118	0.0268	0.659
Winter SST	Intercept	< 0.001	0.0153	0.999
	Temperature	0.0672	0.0378	0.0757
	Climatology	-0.00910	0.0153	0.553
	Temperature * Climatology	0.0381	0.0301	0.206

Table S2.12 Year-to-year variability in east Pacific *C. maenas* abundance. Parameter estimates for linear mixed-effects models testing year-to-year variability in Pacific *C. maenas* abundances relative to year-to-year variability in summer air, winter air, summer sea surface, and winter sea surface temperatures.

Abundance residual ~ Temperature residual * climatology, random = ~ 1 | Site / Study

Variable	Fixed effect	Coefficient	Std. error	p-value
Summer AirT	Intercept	-0.00352	0.128	0.978
	Temperature	0.104	0.166	0.531
	Climatology	-0.00487	0.0895	0.957
	Temperature * Climatology	0.0480	0.149	0.749
Winter AirT	Intercept	< 0.001	0.131	0.995
	Temperature	0.00516	0.0663	0.938
	Climatology	< 0.001	0.0900	0.999
	Temperature * Climatology	0.0442	0.0711	0.535
Summer SST	Intercept	-0.00297	0.129	0.982
	Temperature	-0.0254	0.133	0.849
	Climatology	<0.001	0.0897	0.999
	Temperature * Climatology	0.0842	0.119	0.482
Winter SST	Intercept	-0.00253	0.137	0.985
	Temperature	-0.0188	0.131	0.887
	Climatology	< 0.001	0.0907	0.994
	Temperature * Climatology	0.117	0.140	0.403

Code

Code S2.1 Matching and extracting temperature data

Packages and Data

```
library(RNetCDF)
library(abind)
library(sp)
library(raster)
library(dplyr)
```

(Amanda E. Bates et al., 2018)
This link is where I got my SST data from, I use CDF format in this code.
Open and read the temperature file. You can see the variables in this CDF file and what units they are recorded in, pay close attention to the time units (e.g. days since 1870-1-1).

```
setwd("/Users/brandybiggar/Documents/Masters/Crabs_R/Temp.data/")
weekly_sst<-open.nc("HadISST_sst.nc")
print.nc(weekly_sst)
sst<-read.nc(weekly_sst,unpack=T)
head(sst)
```

Create a vector of each variable to match up below for site and time.
Make a grid of all possible latitude and longitude combinations.
Combine multidimensional arrays into a single SST array.

```
long<-data.frame(sst[4])
lat<-data.frame(sst[3])
time<-data.frame(sst[1])

all.lat.long1<-expand.grid(long[,1],lat[,1])
all.lat.long<-all.lat.long1

sst.array<-abind(sst[5])
```

Temporal aspects

Load dataset with observations to be matched to temperature.
Convert Day, Month, Year into Julian day with start time 1870-01-01.
Calculate number of days since the start of the temperature dataset for each observation.

```
CRAB<-read.csv("egc_working_data_35.csv")
CRAB$DaySince0 <- ceiling(
  julian(strptime(CRAB$date, format = "%d/%m/%Y"), origin = as.Date("1870-01-01")))
CRAB$Time1 <- as.numeric(CRAB$DaySince0)
```

Create an empty matrix to store the values in once we extract them.

```
temp.matrix<-as.data.frame(matrix(0,dim(CRAB),5))

colnames(temp.matrix)<-
c("HADiSST.Match","HADiSST.Mean","HADiSST.Min","HADiSST.Max","MinDist")
```

Run a loop to extract temperature for each observation.

```
for (i in 1:dim(CRAB)[1]){
  diff.times<-abs(syears$Time1[i]-time[,1])
  time.point<-which(diff.times==min(diff.times)[1])
  diff.times2<-abs(syears$Time2[i]-time[,1])
  end.point<- which(diff.times2==min(diff.times2)[1])
  #### EUCLIDEAN DISTANCE ####
values<-sqrt(((syears[i,]$long)-(all.lat.long[,1]))^2+((syears[i,]$lat)-
(all.lat.long[,2]))^2)
  lat.long<-all.lat.long[which(values<=min(values))+2,]
  lat1<-which(lat==lat.long[,2][1])
  long1<-which(long==lat.long[,1][1])
  temp.matrix[i,1]<-mean(sst.array[long1,lat1,time.point:end.point[1]],
na.rm=T)
  temp.matrix[i,2]<-min(sst.array[long1,lat1,time.point:end.point[1]],
na.rm=T)
  temp.matrix[i,3]<-max(sst.array[long1,lat1,time.point:end.point[1]],
na.rm=T) }
```

Bind to original observation data and save.

```
CRABTemps<-cbind(CRAB,temp.matrix)
setwd("/Users/brandybiggar/Desktop/")
write.csv(CRABTemps, "CRABTempsDate.csv")
```

Code S2.2 Green crab multi-stage meta-analysis code

Packages and Data

```
library(MASS)
library(nlme)
library(dplyr)
library(plyr)
setwd("/Users/brandybiggar/Desktop/")
CRAB<-read.csv("egc_dat_35.2.csv")
```

Stage 1

Subset the data by 5 year study/site. Create a dataframe to store results from loop. Label the dataframe columns. Check to make sure no sites are all zeroes. Run the models in a loop to get all the slopes for stage 2.

```
sname=data.frame(unique(CRAB$X5YrSiteName));rownames(sname)<-sname[,1]
mat<-as.data.frame(matrix(0,dim(sname)[1],9))
colnames(mat)<- c("AbunSlope", "AbunSD","X5YrSiteName","Source","Site",
                "SiteLong","SiteLat","reg","natinv")
a<-CRAB %>% group_by(X5YrSiteName) %>%
dplyr::summarise (min = min(MeanRawAbun), max=max(MeanRawAbun))

for (i in 1:dim(sname)[1]){
  dat<-subset(CRAB,X5YrSiteName==rownames(sname)[i])
  m2<-gls(data=dat, scale(MeanRawAbun) ~ ScaleYR)
  mat[i,1:2]<-
c(summary(m2)$coefficients[2],as.data.frame(summary(m2)$tTable)[2,2])
  mat[i,3:6]<- c(rownames(sname)[i], dat$Source[1], dat$Site[1],
dat$SiteLong[1])
  mat[i,7:9]<-c(dat$SiteLat[1], dat$reg[1], dat$natinvas[1]) }
```

Then get the residuals from the model for hypothesis 3.

```
getabundanceTrends<-list()
for (i in 1:dim(sname)[1]) {
  dat<-subset(CRAB,X5YrSiteName==rownames(sname)[i])
  m1<-gls(data=dat, scale(MeanRawAbun) ~ ScaleYR)
  getabundanceTrends[[i]] <- as.data.frame(residuals(m1)) }
getabundanceTrendsOUT<- do.call("rbind.fill", getabundanceTrends)
```

Check the model fits

Run a loop to produce a plot of the model fit for each site.

```
{ pdf(width = 15, useDingbats=FALSE,height = 25, bg="white",
file="glmqqnormJun6.pdf")
  par(mfrow=c(10,5))
  par(oma=c(5,1,1,1))
  par(mar=c(5,5,0,1))
```

```
  for (i in 1:dim(sname)[1]) {
    dat<-subset(CRAB,X5YrSiteName==rownames(sname)[i])
    m1<-glm(data=dat, round(MeanRawAbun)~ ScaleYR, family=poisson)
    qqnorm(residuals(m1))
    title(sname[i,], line = -2)}}
```

Stage 1 part two - temperature slopes

Run a loop to extract model slopes for four different temperature variables at each site.

```
mat<-as.data.frame(matrix(0,dim(sname)[1],9))
colnames(mat)<- c("X5YrSiteName","SumSSTSlope", "SumSSTSD","WinSSTSlope",
"WinSSTSD",                    "SumAirSlope",
"SumAirSD","WinAirSlope","WinAirSD")

for (i in 1:dim(sname)[1]) {
  dat<-subset(CRAB, X5YrSiteName==rownames(sname)[i])
  m1<-glm(data=dat, MaxSST~ScaleYR)
  m2<-glm(data=dat, MinSST~ScaleYR)
  m3<-glm(data=dat, MaxAir~ScaleYR)
  m4<-glm(data=dat, MinAir~ScaleYR)
  mat[i,1]<- rownames(sname)[i]
  mat[i,2:3]<-
c(summary(m1)$coefficients[2],as.data.frame(summary(m1)$tTable)[2,2])
  mat[i,4:5]<-
c(summary(m2)$coefficients[2],as.data.frame(summary(m2)$tTable)[2,2])
  mat[i,6:7]<-
c(summary(m3)$coefficients[2],as.data.frame(summary(m3)$tTable)[2,2])
  mat[i,8:9]<-
c(summary(m4)$coefficients[2],as.data.frame(summary(m4)$tTable)[2,2])}
```

Put temperature slopes together with abundance slopes and save file.

```
slopes<-left_join(crabslopes,mat, by="X5YrSiteName")
write.csv(slopes, "FINALSlopesJul5.csv")
```

Again, extract and save residuals to use for hypothesis 3.

```
getabundanceTrends<-list()
for (i in 1:dim(sname)[1]) {
  dat<-subset(CRAB,X5YrSiteName==rownames(sname)[i])
  m1<-glm(data=dat, MaxAir~year)
  getabundanceTrends[[i]] <- as.data.frame(residuals(m1)) }
getabundanceTrendsOUT<- do.call("rbind.fill", getabundanceTrends)

tempresids1<-getabundanceTrendsOUT #WinAir
tempresids2<-getabundanceTrendsOUT #SumAir
tempresids3<-getabundanceTrendsOUT #WinSST
tempresids4<-getabundanceTrendsOUT #SumSST
resids<-cbind(crabresids,tempresids1,tempresids2,tempresids3,tempresids4)

colnames(resids)<-c("AbunResid","WinAirResids","SumAirResids",
```

```
"WinSSTResids","SumSSTResids")

resids2<-cbind(CRAB,resids)
write.csv(resids2, "FINALResidsJul5.csv")
```

Stage 2

Subset data by region to run models separately.

```
natslope<-filter(slopes, reg == "Native")
atlslope<-filter(slopes, reg == "Naturalized")
pacslope<-filter(slopes, reg == "Pacific")
ausslope<-filter(slopes, reg == "Indian")

m1<-lme(data= natslope, AbunSlope ~ scale(SumSSTSlope)*scale(MeanSSTLastTen),
        random=~1|Study, weights= varFixed(~AbunSD))

m2<-lme(data= atlslope, AbunSlope ~ scale(SumSSTSlope)*scale(MeanSSTLastTen),
        random=~1|Study, weights= varFixed(~AbunSD))

m3<-lme(data= pacslope, AbunSlope ~ scale(SumSSTSlope)*scale(MeanSSTLastTen),
        random=~1|Study, weights= varFixed(~AbunSD))

m4<-lme(data= ausslope, AbunSlope ~ scale(SumSSTSlope)*scale(MeanSSTLastTen),
        random=~1|Study, weights= varFixed(~AbunSD))
```

Check model summary and model fit. Extract intervals to plot.

```
summary(m1)
qqnorm(m1)
intervals(m1)
```

Hypothesis 3

Subset residual data by region to run models separately. Australia models did not converge so we do not proceed with them here.

```
natresids<-filter(resid, reg=="Native")
atlresids<-filter(resid, reg=="Atlantic")
pacresids<-filter(resid, reg=="Pacific")

m1<-lme(data=natresids, AbunResid~WinSSTResids*scale(MinSSTLastTen),
        random=~1|x5YrStudyNum)

m2<-lme(data=atlresids, AbunResid~WinSSTResids*scale(MinSSTLastTen),
        random=~1|x5YrStudyNum)

m3<-lme(data=pacresids, AbunResid~WinSSTResids*scale(MinSSTLastTen),
        random=~1|x5YrStudyNum)
```

Check model summary and model fit. Extract intervals to plot.

```
summary(m1)
qqnorm(residuals(m1))
intervals(m1, which = "fixed")
```

Appendix II

Chapter 3
Supplementary Material

Supplementary Contents

Tables

TABLES

Table S3.1 Literature search results. All 92 papers that were included in the *Carcinus maenas* thermal ecology review, along with the four categories they were grouped into. Category A is the main concept of the paper. Category B is a specialty of the concept. Category C is the biological level of organization focused on in the paper, and Category D is the region of focus or sampling.

Reference	A. Concept	B. Specialty	C. Bio. level	D. Region
(Aagaard, 1996)	Survival	Physiology	Individual	Native
(Ahsanullah and Newell, 1977)	Survival	Physiology	Individual	Native
(Aldrich, 1981)	Survival	Physiology	Individual	Native
(Atrill et al., 1999)	Behavior	Movement	Population	Native
(Audet et al., 2008)	Development	Growth	Population	W Atlantic
(Baldridge and Smith, 2008)	Development	Growth	Individual	W Atlantic
(Banas et al., 2009)	Development	Larvae	Population	E Pacific
(Bélair and Miron, 2009a)	Behavior	Competition	Community	W Atlantic
(Bélair and Miron, 2009b)	Behavior	Feeding	Community	W Atlantic
(Berrill, 1982)	Development	Larvae	Population	W Atlantic
(Best et al., 2014)	Survival	Physiology	Individual	W Atlantic
(Beukema, 1991)	Development	Larvae	Population	Native
(Broekhuysen, 1937)	Development	Juvenile	Community	Native
(Camus et al., 2004)	Survival	Physiology	Individual	Native
(Carlton and Cohen, 2003)	Patterns	Distribution	Population	Other
(Carter and Fraser, 1991)	Behavior	Movement	Community	Native
(Chapelle, 1978)	Survival	Molecules	Cellular	Native
(Cohen and Carlton, 1995)	Patterns	Occurrence	Community	E Pacific
(Cohen et al., 1995)	Development	Larvae	Individual	E Pacific
(Compton et al., 2010)	Patterns	Distribution	Population	Other
(Coyle et al., 2019)	Population	Genetics	Population	W Atlantic
(Crisp, 1964)	Patterns	Occurrence	Population	Native

(Crothers, 1967)	Development	Growth	Individual	Native
(Cuculescu et al., 1998)	Survival	Physiology	Population	Native
(Cuculescu et al., 1999)	Survival	Molecules	Cellular	Native
(Dawirs and Deidrich, 1986)	Development	Larvae	Individual	Native
(Dawirs et al., 1986)	Development	Larvae	Individual	Native
(Dawirs, 1985)	Development	Larvae	Individual	Native
(Derivera et al., 2007)	Development	Larvae	Individual	W Atlantic
(Edwards, 1958)	Patterns	Distribution	Population	Native
(El Babili et al., 1997)	Survival	Molecules	Cellular	Native
(Elner, 1979)	Behavior	Feeding	Individual	Native
(Erikkson and Edlund, 1977)	Development	Larvae	Population	Native
(Freitas et al., 2007)	Behavior	Competition	Community	Native
(Giménez et al., 2020)	Development	Larvae	Individual	Native
(Giomi and Poertner, 2013)	Survival	Physiology	Individual	Native
(Hidalgo et al., 2005)	Patterns	Occurrence	Population	Other
(Himes et al., 2017)	Survival	Salinity	Individual	W Atlantic
(Hopkin et al., 2006)	Survival	Physiology	Individual	Native
(Hyde et al., 2012)	Survival	Physiology	Individual	Native
(Hyde et al., 2015)	Survival	Physiology	Individual	Native
(Jeffery et al., 2018)	Population	Genetics	Cellular	W Atlantic
(Jørgensen et al., 2017)	Survival	Physiology	Individual	Native
(Jost et al., 2012)	Survival	Physiology	Individual	W Atlantic
(Jungblut et al., 2018)	Survival	Molecules	Individual	Native
(Kelley et al., 2011)	Survival	Physiology	Individual	E Pacific
(Kelley et al., 2013)	Survival	Physiology	Individual	E Pacific
(Kelley et al., 2015)	Development	Morphology	Population	Other
(Kelley, 2014)	Population	Genetics	Population	Other
(Klassen and Loche, 2007)	Patterns	Distribution	Population	W Atlantic
(Klein Breteler, 1975)	Survival	Physiology	Individual	Native
(Lauchlan et al., 2019)	Behavior	Competition	Community	W Pacific
(Leignel et al., 2014)	Survival	Physiology	Individual	Other
(Lowen et al., 2016)	Patterns	Distribution	Population	E Pacific
(Madeira et al., 2012)	Survival	Physiology	Community	Native

(Madeira et al., 2014)	Survival	Molecules	Community	Native
(Matassa and Trussell, 2015)	Behavior	Feeding	Population	W Atlantic
(Matheson and Gagnon, 2012)	Behavior	Competition	Community	W Atlantic
(Matheson and McKenzie, 2014)	Behavior	Feeding	Individual	W Atlantic
(McGaw and Nancollas, 2018)	Survival	Physiology	Individual	W Atlantic
(McGaw and Whiteley, 2012)	Behavior	Feeding	Individual	E Pacific
(Mcnaught and Norden, 2011)	Patterns	Distribution	Community	W Atlantic
(Mohamedeen and Hartnoll, 1989)	Development	Larvae	Individual	Native
(Murray and Seed, 2010)	Behavior	Feeding	Individual	Native
(Nagaraj, 1993)	Development	Larvae	Individual	Native
(Naylor, 1962)	Behavior	Movement	Population	Native
(Naylor, 1963)	Behavior	Movement	Individual	Native
(Newell et al., 1972)	Survival	Physiology	Individual	Native
(Quinn, 2018)	Patterns	Abundance	Population	W Atlantic
(Rayner and McGaw, 2019)	Behavior	Competition	Individual	W Atlantic
(Rey et al., 2019)	Development	Larvae	Population	Native
(Robertson et al., 2002)	Survival	Physiology	Individual	Native
(Rodrigues et al., 2015)	Survival	Molecules	Individual	Native
(Roff et al., 1984)	Patterns	Distribution	Population	W Atlantic
(Rogers et al., 2018)	Behavior	Competition	Community	W Atlantic
(Roman, 2006)	Population	Genetics	Cellular	W Atlantic
(Spaargaren, 1974)	Survival	Salinity	Individual	Native
(Spaargaren, 1984)	Survival	Physiology	Individual	Native
(Sanchez-Salazar et al., 1987)	Behavior	Feeding	Individual	Native
(See and Feist, 2009)	Development	Larvae	Population	E Pacific
(Sharp et al., 2003)	Patterns	Occurrence	Community	W Atlantic
(Simonik and Henry, 2014)	Survival	Physiology	Individual	W Atlantic
(Souza et al., 2019)	Behavior	Competition	Individual	Native
(Spitzner et al., 2018)	Development	Growth	Cellular	Other
(Spitzner et al., 2019)	Development	Larvae	Individual	Native
(Sprung, 2001)	Development	Larvae	Population	Native
(Strasser and Günther, 2001)	Development	Larvae	Population	Native
(Styrishave et al., 1999)	Survival	Physiology	Individual	Native

(Taylor and Wheatly, 1979)	Survival	Physiology	Individual	Native
(Taylor et al., 1977a)	Survival	Physiology	Individual	Native
(Taylor et al., 1977b)	Survival	Salinity	Individual	Native
(Tepolt and Palumbi, 2015)	Population	Interspecific	Population	Other
(Tepolt and Palumbi, 2020)	Population	Intraspecific	Population	Other
(Tepolt and Somero, 2014)	Survival	Physiology	Individual	Other
(Torres et al., 2020a)	Development	Larvae	Individual	Native
(Torres et al., 2020b)	Development	Larvae	Individual	Native
(Truchot, 1973)	Survival	Molecules	Individual	Native
(Wallace, 1973)	Survival	Physiology	Individual	Native
(Waugh, 1964)	Patterns	Occurrence	Population	Native
(Weber et al., 2008)	Survival	Molecules	Individual	Native
(Welch, 1968)	Patterns	Abundance	Population	W Atlantic
(Williams, 1967)	Development	Larvae	Individual	Native
(Yamada et al., 2015)	Development	Larvae	Population	E Pacific
(Yamada et al., 2017)	Development	Larvae	Population	E Pacific
(Young et al., 2006)	Behavior	Movement	Individual	Native

Table S3.2 *Carcinus maenas* thermal limits reported in literature. *Carcinus maenas* thermal limits for feeding, growth, and tolerance in the three life stages: egg, larvae, and adult. Method refers to how the thermal limit was derived. Abbreviations: Obs., observed; Exp., experiment; Cit., citation; Mod., modeled.

Reference	Region	Life stage	Temp. (ºC)	Limit	Method
(Audet et al., 2008)	W Atlantic	Adult	6.0	Feeding	Obs
(Baldridge and Smith, 2008)	W Atlantic	Adult	10.0	Feeding	Exp
(Belair and Miron, 2009)	W Atlantic	Adult	5.0	Feeding	Exp
(Berrill, 1982)	W Atlantic	Adult	10.0	Growth	Obs
(Berrill, 1982)	W Atlantic	Adult	5.0	Feeding	Obs
(Compton et al., 2010)	Native	Larvae	10.0	Growth	Obs
(Crothers, 1967)	Native	Egg	10.0	Tolerance	Cit
(Crothers, 1967)	Native	Larvae	25.0	Growth	Cit
(Cuculescu et al., 1998)	Native	Adult	31.3	Tolerance	Exp
(Cuculescu et al., 1998)	Native	Adult	31.8	Tolerance	Exp
(Cuculescu et al., 1998)	Native	Adult	32.5	Tolerance	Exp
(Cuculescu et al., 1998)	Native	Adult	33.5	Tolerance	Exp
(Cuculescu et al., 1998)	Native	Adult	34.2	Tolerance	Exp
(Cuculescu et al., 1998)	Native	Adult	35.4	Tolerance	Exp
(Cuculescu et al., 1998)	Native	Adult	35.8	Tolerance	Exp
(Dawirs and Deidrich, 1986)	Native	Larvae	18.0	Feeding	Exp
(Dawirs, 1985)	Native	Egg	10.0	Growth	Exp
(Dawirs, 1985)	Native	Larvae	7.0	Growth	Exp
(Dawirs, 1985)	Native	Larvae	12.0	Tolerance	Exp
(de Rivera et al., 2007)	W Atlantic	Larvae	10.0	Tolerance	Exp
(de Rivera et al., 2007)	W Atlantic	Larvae	22.5	Tolerance	Exp
(Erikkson and Edlund, 1977)	Native	Adult	10.0	Growth	Mod
(Erikkson and Edlund, 1977)	Native	Adult	3.0	Feeding	Mod
(Hopkin et al., 2006)	Native	Adult	31.9	Tolerance	Exp
(Hopkin et al., 2006)	Native	Adult	34.1	Tolerance	Exp
(Hyde et al., 2012)	Native	Adult	33.0	Tolerance	Exp
(Jørgensen et al., 2017)	Native	Adult	38.3	Tolerance	Exp
(Jost et al., 2012)	W Atlantic	Adult	35.0	Tolerance	Exp

(Kelley et al., 2011)	E Pacific	Adult	31.7	Tolerance	Exp
(Kelley et al., 2011)	E Pacific	Adult	34.7	Tolerance	Exp
(Kelley et al., 2011)	E Pacific	Adult	35.5	Tolerance	Exp
(Kelley et al., 2011)	E Pacific	Adult	36.2	Tolerance	Exp
(Madeira et al., 2012)	Native	Adult	35.0	Tolerance	Exp
(Nagaraj, 1993)	Native	Larvae	10.0	Growth	Exp
(Nagaraj, 1993)	Native	Larvae	25.0	Growth	Exp
(Sprung, 2001)	Native	Larvae	25.0	Growth	Obs
(Tepolt and Somero, 2014)	E Pacific	Adult	29.7	Tolerance	Exp
(Tepolt and Somero, 2014)	W Atlantic	Adult	34.1	Tolerance	Exp
(Tepolt and Somero, 2014)	Native	Adult	34.2	Tolerance	Exp
(Tepolt and Somero, 2014)	E Pacific	Adult	34.9	Tolerance	Exp
(Tepolt and Somero, 2014)	W Atlantic	Adult	35.1	Tolerance	Exp
(Tepolt and Somero, 2014)	Native	Adult	35.5	Tolerance	Exp
(Tepolt and Somero, 2014)	E Pacific	Adult	35.5	Tolerance	Exp
(Tepolt and Somero, 2014)	W Atlantic	Adult	35.8	Tolerance	Exp
(Tepolt and Somero, 2014)	Native	Adult	36.1	Tolerance	Exp
(Tepolt and Somero, 2014)	W Atlantic	Adult	36.3	Tolerance	Exp
(Tepolt and Somero, 2014)	Pacific	Adult	36.4	Tolerance	Exp
(Tepolt and Somero, 2014)	W Atlantic	Adult	36.5	Tolerance	Exp
(Tepolt and Somero, 2014)	W Atlantic	Adult	37.0	Tolerance	Exp
(Tepolt and Somero, 2014)	Native	Adult	37.3	Tolerance	Exp
Additional unverified limits and the papers they are cited in					
(Klassen and Loche, 2007)	W Atlantic	Adult	10.0	Growth	Cit
(Klassen and Loche, 2007)	W Atlantic	Adult	7.0	Feeding	Cit
(Klassen and Loche, 2007)	W Atlantic	Larvae	18.0	Growth	Cit
(Strasser and Gunther, 2001)	Native	Larvae	25.0	Growth	Cit
(Welch, 1981)	W Atlantic	Adult	10.0	Growth	Cit
(Yamada et al., 2015)	E Pacific	Egg	10.0	Tolerance	Cit

Table S3.3 Upper critical thermal limits reported in the literature. The method is how the authors measured CTMax; the ability to right themselves (RR), or heart failure (Death). Ramping is how quickly temperature is raised during experiments in ºC per hour. Abbreviations USA: United States, POR: Portugal, ENG: England, SCT: Scotland, CAD: Canada, DMK: Denmark, NOR: Norway, RR: righting response. Pacific referes to the invasive east Pacific, Atlantic refers to the invasive west Atlantic.

Region	**Country**	**Season**	**Method**	**CTMax (ºC)**	**Std Er (ºC)**	**Ramp (ºC hr $^{-1}$)**	**Acclim. temp (ºC)**	**Acclim. time (weeks)**	**Sample size**	**Reference**
Native	ENG	RR	Sum	31.8	0.27	12	8	3	9	(Cuculescu et al 1998)
Native	ENG	RR	Win	32.5	0.2	12	15	3	5	(Cuculescu et al 1998)
Native	ENG	RR	Fall	33.5	0.5	12	8	3	4	(Cuculescu et al 1998)
Native	ENG	RR	Fall	34.2	0.12	12	15	3	5	(Cuculescu et al 1998)
Native	ENG	RR	Sum	35.4	0.26	12	22	3	12	(Cuculescu et al 1998)
Native	ENG	RR	Fall	35.8	0.11	12	22	3	6	(Cuculescu et al 1998)
Native	UK	RR	Win	31.94	0.72	12	9	2-3	8	(Hopkin et al. 2006)
Native	UK	RR	Sum	34.08	0.41	12	14-17	2-3	9	(Hopkin et al. 2006)
Native	UK	RR	NA	33.04	0.2	12	8	3	8	(Hyde et al. 2012)
Native	DMK	DT	Fall	38.3	0.2	15	12	2-3	10	(Jørgensen et al., 2017)
Atlantic	USA	RR	Sum	34-36	NA	6	12-15	1	5	(Jost et al., 2012)
Pacific	CAD	DT	NA	31.7	NA	4	6	6	15	(Kelley et al., 2011)
Pacific	USA	DT	NA	34.7	NA	4	6	6	15	(Kelley et al., 2011)
Pacific	CAD	DT	NA	35.5	NA	4	23	6	15	(Kelley et al., 2011)
Pacific	USA	DT	NA	36.2	NA	4	23	6	15	(Kelley et al., 2011)
Native	POR	RR	Sum	35	NA	1	24	2	NA	(Madeira et al., 2012)

Pacific	USA	DT	Spr	29.7	1	5	5	4	6	(Tepolt and Somero 2014)
Atlantic	CAD	DT	Sum	34.1	0.3	5	5	4	12	(Tepolt and Somero 2014)
Native	NOR	DT	Sum	34.2	0.4	5	5	4	8	(Tepolt and Somero 2014)
Pacific	CAD	DT	Sum	34.9	0.5	5	5	4	6	(Tepolt and Somero 2014)
Atlantic	USA	DT	Sum	35.1	0.3	5	5	4	10	(Tepolt and Somero 2014)
Pacific	CAD	DT	Sum	35.5	0.5	5	25	4	10	(Tepolt and Somero 2014)
Native	POR	DT	Sum	35.5	0.5	5	5	4	12	(Tepolt and Somero 2014)
Atlantic	USA	DT	Sum	35.8	0.5	5	5	4	12	(Tepolt and Somero 2014)
Native	NOR	DT	Sum	36.1	0.3	5	25	4	10	(Tepolt and Somero 2014)
Atlantic	USA	DT	Sum	36.3	0.6	5	25	4	7	(Tepolt and Somero 2014)
Pacific	USA	DT	Spr	36.4	0.2	5	25	4	5	(Tepolt and Somero 2014)
Atlantic	CAD	DT	Sum	36.5	0.2	5	25	4	10	(Tepolt and Somero 2014)
Atlantic	USA	DT	Sum	37	0	5	25	4	8	(Tepolt and Somero 2014)
Native	POR	DT	Sum	37.3	0.2	5	25	4	11	(Tepolt and Somero 2014)

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