Habitat Connectivity and Quality Alter Population Growth and Community Structure of Marine Crustaceans

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Cover Image: Spatially structured seagrass habitats; Coobowie, South Australia

Photo credit: Katherine A. Heldt

Declaration

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Chapter 4

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Chapter 5

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Abstract

Communities are linked by dispersers that arrive from neighboring habitats and sustain emerging populations. Differences in recruitment establish dissimilarities in composition and diversity among communities and alter levels of connectivity. In heterogeneous habitats, source populations provide propagules to neighboring sinks, which rely on incoming recruits to sustain populations. However, recruitment is not static, and changing environmental conditions that alter habitats can shift population growth and community structure. In this thesis, I evaluate whether changing environmental conditions, such as habitat loss and future climate change, drive shifts in community assembly and population growth. Using marine peracarids as a model system, I examined the effects of isolation on community assemblage trajectories in seagrass beds and explored the effects of elevated temperature and CO_2 on population growth and quality of amphipods that inhabit temperate reef ecosystems.

Here, I show that the identity and abundance of recruits leads to local (α) and between-community (β) diversity differences and that the state of communities is dependent on incoming source recruits. Isolation from sources elicits different responses within and among species, which minimizes differences among communities and shifts species abundances. Furthermore, I show how environmental conditions (i.e. elevated temperature and CO_2), that enhance resource availability in sinks, can boost reproductive output and population growth of an amphipod species (*Cymadusa pemptos*). My test of the hypothesis that future climate conditions enhances sexual characters, reducing variation in mating success and boosting population growth, suggests that future climate might relax constraints on mechanisms of reproduction. As

future climate conditions drive population outbreaks, growing establishment of artificial structures that are increasingly used as habitats provide amphipods with alternative settlement space.

Together, these studies highlight the importance of examining population growth and community assembly in spatially structured systems. Sources and sinks that are undergoing shifts in abundance and quality of habitats drive change in the density and distribution of mobile species, and when favorable conditions align, such as greater resource availability and reduced competition and predation, populations can boom. However, the potential for population growth depends on how individuals distribute across spatially structured habitats. Since the identity and abundance of incoming recruits drives sink population growth and community structure, it is essential to understand the effect each species' dispersing stage (i.e. male, female and juvenile) and resource requirements have on sink development.

CHAPTER 1

Chapter Image: Teaching during Marine Ecology Camp at Coobowie, SA.

Photo credit: Nicole Mertens

Chapter 1

General Introduction

In spatially structured systems, dispersers can support population growth in neighboring habitats (Wilson 1992). The density and diversity of recruits can therefore drive population growth and community structure in heterogeneous habitats (Leibold *et al.* 2004). Source populations are net exporters sending recruits to neighboring sink habitats, and incoming recruits increase sink population growth (Pulliam 1988) and vary the structure of communities (Kneitel & Miller 2003). However, changing environmental conditions, such as habitat loss and future climate change (i.e. ocean warming and acidification), have the potential to decrease the quality and availability of habitats (Connell *et al.* 2013), which in turn, can reduce immigration and isolate communities (Jaquiéry *et al.* 2008; Munguia & Miller 2008).

Isolation from sources ultimately leads to population extinction in sinks and decreases diversity (Shmida & Wilson 1985). Yet species with mobile life-stages may be able to maintain connectivity among spatially structured habitats by altering abundance and distribution across habitats (Niebuhr *et al.* 2015). Here, recruitment to alternative habitats and use of less preferred, readily available resources can boost population growth (Cappuccino *et al.* 1995). This thesis investigates population growth and community structure in spatially structured marine habitats and examines source-sink theory as an underlying frame-work for which populations undergoing environmental change can persist. The general introduction that follows first establishes the ability of recruits to alter community structure in neighboring habitats. Then, the introduction details the flow of recruits between source-sink habitats and describes how future climate conditions can shift the population structure of sources and sinks. The last sections of the introduction touch base on the impact a recruit's traits and life-stage have on spatially structured populations and the influence of recruits, resource availability, and mating opportunities on crustacean population growth.

1.1 Recruits Alter Assembly of Neighboring Communities

Communities linked by recruits interact (Gilpin & Hanski 1991; Wilson 1992) with the identity and abundance of incoming recruits potentially driving community structure of neighboring habitats (Sutherland & Karlson 1977; Sams & Keough 2012). Differences in recruitment across similar habitats ultimately establish communities that are dissimilar in composition and diversity (Levin 1974; Law & Morton 1993; Forde & Raimondi 2004), and such community dissimilarities in local (α) and between-community (β) diversity can ultimately alter regional diveristy (γ; Loreau & Mouquet 1999; Amarasekare 2003). However, dispersal among spatially structured habitats can be biased such that the flow of recruits is primarily from well-established source communities to neighboring communities (MacArthur & Wilson 1967; Shmida & Wilson 1985), and increasing dispersal frequencies can reduce variance among communities (i.e. β diversity; Kneitel & Miller 2003).

Neighboring communities become isolated when habitat loss eliminates source communities that are net exporters of recruits (Pulliam 1988; Thompson *et al.* 2017). Isolation from sources shifts community structure of neighboring habitats as the abundance and distribution of species decreases across spatially structured habitats (Gonzalez *et al.* 1998; Munguia & Miller 2008; Mouquet *et al.* 2011). Yet, species with active dispersing life-stages can re-distribute during habitat loss, and such dispersers can rescue populations from extinction and maintain local diversity (Resasco *et al.* 1998).

Species with mobile life-stages can shape community patterns (Munguia 2004; Amarasekare 2010; Matias *et al.* 2013) and restore connectivity during habitat loss (Niebuhr *et al.* 2015). However, logistical constraints of empirical studies limit the number and range of field experiments evaluating the impacts of isolation on community structure (Logue *et al.* 2011). Currently, empirical studies range from small microcosms (e.g. 96 well plates, Venail *et al.* 2008) to large field experiments (e.g. fragmented forests; Davies *et al.* 2001), but a majority of studies test diversity and abundance responses of invertebrates, protists, and bacteria in artificial microcosms (Logue *et al.* 2011). Fewer constraints of computational studies has led to theory preceding experimentation (Agrawal *et al.* 2007), and there is a general need for more empirical studies that include natural stochastic processes (Jacobson & Peres-Neto 2010).

1.2 Source Recruits Increase Growth of Sink Populations

In spatially structured systems, population growth depends on the quality of habitats and incoming recruits (Ye *et al.* 2014). High quality habitats contain source populations that have greater birth than death rates and positive growth (Pulliam 1988). In contrast, sink populations have lower birth than death rates and often persist in low quality habitats, and given the greater reproductive output of source populations, the flow of recruits is primarily from sources to sinks (Pulliam 1988). Here, sink habitats can provide source recruits with alternative settlement space (Pulliam & Danielson 1991; Amarasekare 2004).

Recruits from high quality sources sustain population growth in neighboring habitats, and without emigrants, sink populations decline and become extinct (Pulliam 1988; Howe *et al.* 1991). Populations persist in low quality sinks because preferred habitats become crowded (i.e. ideal free distribution; Fretwell & Lucas 1969) and occupied by older, dominant individuals (i.e. ideal preemptive distribution; Brown 1964). Under the ideal free distribution, individuals distribute across habitats in a way that optimizes survival and reproductive success (Loehle 2012), and as crowding in high quality habitats decreases average fitness of populations, emigration increases to neighboring habitats (Denno & Roderick 1992). Similarly, under the ideal preemptive distribution, dominant individuals occupy high quality breeding sites (Pulliam & Danielson 1991), and subordinates disperse to habitats where more breeding sites are available but are of lower quality (Dias & Blondel 1996; Breininger & Carter 2003). These distribution theories suggest that populations are highly dynamic (Hanski & Gilpin 1991; Hanski 1998) with individuals dispersing as habitat quality declines (Ronce 2007).

Population growth of sources and sinks can match the spatial arrangement and quality of habitats; if source habitats are degraded, individuals can shift to sinks (Boughton 1999; Johnson 2004). Indeed, sinks can be ephemeral, and short-term studies can be used to identify such temporal sinks (Munguia 2015). However, sinks have the potential to become source populations in the future (Boughton 1999), and transgenerational studies are needed to further investigate spatially structured systems. Such studies across multiple generations are rare because it requires intensive tracking of populations (e.g. 2 years, Pavlacky *et al.* 2012; 12 years, Thomas *et al.* 1996) and communities (e.g. 3 years, Tonkin *et al.* 2016; 5 years, Stoffels *et al.* 2015). By studying species that produce multiple generations within a year (e.g. amphipods, Sainte-Marie 1991 and insects, Altermatt 2009), we can begin to examine, over shorter time-frames, how intergenerational changes in population growth and distribution alter source-sink dynamics.

1.3 Spatially Structured Populations under Future Climate Change

Under ocean warming and acidification, the level of heterogeniety among habitats may shift (Russell *et al.* 2009) as habitats become lost or degraded (Connell *et al.* 2013). Future climate change has gained considerable attention in the last few years (Harvey *et al.* 2013; Nagelkerken & Connell 2015; Calosi *et al.* 2016), and oceans are predicted to warm and acidify (Duarte *et al.* 2013), with global mean surface temperatures rising 4.8°C and CO_2 increasing 851 – 1370 ppm by 2100 (Representative Concentration Pathway 8.5; IPCC 2014). While some species adapt and thrive under future climate conditions, other species will decline (Kroeker *et al.* 2010; Kroeker *et al.* 2013; Poloczanska *et al.* 2013), and understanding how future climate conditions affect the structure of populations within heterogeneous habitats is key in evaluating a species' persistence (Bellard *et al.* 2012).

As future climate conditions redirect the flow and distribution of recruits (Harley *et al.* 2006), source populations can shift to sink populations. If sinks become sources, population growth can be maintained as the quality of sink habitats increases relative to sources, converting sinks to sources (Dias 1996). Alternatively, if less preferred, low quality habitats are readily available, individuals can increase reproductive output and population growth in sinks (Watkinson & Sutherland 1995; Jansen & Yoshimura 1998; Boughton 1999; Murphy 2001). Alternative habitats (e.g. turf; Connell *et al.* 2014) are increasingly present under elevated temperature and CO_2 conditions (Russell *et al.* 2009; Connell *et al.* 2013) and can provide consumers with valuable food and habitat resources (Brawley & Adey 1981; Falkenberg *et al.* 2014). Here, consumption of local habitats modifies habitat assemblages (Duffy & Hay 2000; McSkimming *et al.* 2015) in a way that boosts population growth (Connell *et al.* 2017).

1.4 Life-stage and Traits of Recruits Shift Population Structure

The ability to disperse at multiple life-stages (e.g. juvenile, sub-adult, and adult) facilitates movement during habitat loss events and climate change (Baguette *et al.* 2013). Species with mobile adult life-stages and traits that enable dispersal experience a greater number of habitats within a life-time than species that only disperse as juveniles (Pineda *et al.* 2007). Mobile dispersers drive change in population structure by shifting the distribution and abundance of juveniles and adults (Pulliam *et al.* 1992), and theory that focuses on settlement of passive dispersers (e.g. larval transport of sessile species) overlooks the impact adult recruits have on population structure (Palmer *et al.* 1996).

The life-stage in which individuals recruit will ultimately alter sink population growth and persistence (Pulliam *et al.* 1992). Female-biased dispersal increases mate availability and offspring production, which accelerates spread to new habitats (Miller & Inouye 2013). In addition, Munguia et al. (2015) shows that fewer females establish in sinks isolated from sources leading to male-biased populations with delayed population growth. Such dispersal differences among life-stages occur when movement is influenced by life experiences and resource requirements of individuals (Bowler &

Benton 2005), and natal habitats that shape the traits of adult dispersers may cause asymmetry in local adaption (Benard & McCauley 2008).

Sinks and sources that differ in population structure experience different selection pressures (Holt 1996; Urban & Skelly 2006). Selection in high quality sources is likely to produce individuals that have greater reproductive output (Kawecki 1995; Møller 1995), and a greater diversity of individuals dispersing from sources increases gene flow in alternative habitats (Roman 2006; Bay *et al.* 2008). In contrast, sink populations that are maladapted and have low fitness, often depend on immigration to increase the rate of adaptation (Holt *et al.* 2003). Greater fitness of source populations is particularly noticeable in territorial species, where subordinate individuals in sink habitats produce few offspring or forego reproduction (Breininger & Carter 2003). However, immigrants from sources can boost sink population size and fitness, which initially facilitates local adaptation and allows for population persistence in sinks (Holt *et al.* 2004).

1.5 Structure and Growth of Marine Crustacean Populations

Crustaceans consist of species groups (e.g. amphipods, isopods, and tanaids) that have different life-history (Borowsky 1983; Beermann & Purz 2013) and recruitment strategies (Tsai & Dai 2001; Munguia *et al.* 2007). Amphipod species are well-known for their traits of rapid development, relatively short generation times and ability to disperse and colonize habitats (Franz 1989; Sainte-Marie 1991; Munguia *et al.* 2007). Recruitment strategies of amphipod species can alter population dynamics; amphipods dispersing as adults (*Neomegamphopus hiatus* and *Melita nitida*) initially exhibit higher local population growth, while dispersing *Bemlos unicornis* juveniles, establish slowly and evenly across the region but dominate amphipod communities (Munguia *et al.* 2007). Furthermore, multiple dispersal events within an individual's life-span can boost local population growth when resources (Duffy & Harvilicz 2001) and mating opportunities (Franz & Mohamed 1989) are distributed unevenly across habitats.

Individuals that rapidly deplete local resources can temporarily increase reproductive output, resulting in population outbreaks (Abbott & Dwyer 2007; Stieha *et al.* 2016). Here, environmental conditions that increase access to resources boost local population growth, but the spread of outbreaks across the region is dependent on population density and selection for dispersal (Cappuccino *et al.* 1995). For example, as densities increase and crowding limits resources, spill-over to neighboring habitats and dispersal towards new resources can sustain booming populations (Yang *et al.* 2008). Yet the potential for population persistence depends on the quality of recruits, and when local source habitats provide high quality resources, trait variation and fitness increases (Cothran & Jeyasingh 2010; Cothran *et al.* 2011) within populations.

Local resources of high quality enhance populations by increasing survival, body size, and sexually selected traits of individuals (Cothran *et al.* 2014). In sexually dimorphic crustaceans, males develop enlarged characters (e.g. body, antennae, and claw size) that are used for female pairing and guarding during mating (Cothran *et al.* 2010). The influence male character size has on mating opportunities is relative to trait size of other individuals within the population, and when there is variation among individuals, large males have reproductive advantages (Shuster & Wade 2003; Cothran & Jeyasingh 2010). Here, the quality of individuals mating can play an important role in defining population structure because low quality females of smaller size will produce fewer offspring and reduce the rate of population growth (Glazier 2000).

1.6 Thesis Hypotheses and Outline

In this thesis, I evaluate the effects of habitat loss and the combination of elevated temperature and CO_2, on community structure and population growth, respectively. I use a model system of marine crustaceans inhabiting coastal habitats of South Australia (i.e. seagrass and temperate reef habitat) to test the following hypotheses:

1. Isolation from a source elicits species-specific responses that increase similarities among community assemblages (Chapter 2).
2. Original sinks switch to sources as changes in resources (i.e. nests, food, and habitat availability) under elevated temperature and CO_2 boost population quality of a temperate reef amphipod species (Chapter 3).
3. Future climate conditions of elevated temperature and CO_2 increases amphipod reproductive output and local population growth, and under such population outbreaks, amphipod sexual characters (i.e. body and claw size) are enhanced (Chapter 4).
4. Habitat use shifts under future climate conditions with amphipods increasing use of artificial habitats over natural (i.e. kelp and turf; Chapter 5).

1.6.1 Thesis outline

A brief outline of each data chapter and the general discussion is provided below.

Chapter 2. Communities in spatially structured habitats are connected by recruits. Incoming recruits from sources drive assembly in neighboring habitats, and the diversity and abundance of recruits governs community trajectories. In this chapter, I used crustacean communities in coastal seagrass beds to examine local (α) and between-community (β) diversity in habitats that were isolated from a local source and to determine whether two neighboring communities exposed to the same source consistently differed in α diversity, regardless of isolation and age. Additionally, I evaluated abundances of the 16 species in communities and tested for differences in abundance among life-stages of 5 species. If recruits from a local source drive assembly of neighboring communities, isolation will alter β diversity and negatively impacts a species' ability to recruit. However, if a species' ability to recruit is not influenced by isolation, abundances in neighboring communities will be maintained, and for some species, broader dispersal of juveniles over adults may further increase abundance across communities.

Chapter 3. High quality habitats contain source populations that support population growth of sinks. In sink habitats, populations rely on recruits from sources; however future climate conditions can degrade source habitats and reduce the abundance and quality of source recruits. In this chapter, I used experimental populations of amphipods (*Cymadusa pemptos*), inhabiting South Australian temperate reefs, to test whether ocean warming and acidification reverses the role of sources and sinks. If future climate conditions increase resource availability in sink habitats and boost reproductive quality and output of sink individuals, original sinks can convert to sources.

Chapter 4. Ocean warming and acidification are often considered stressful environmental conditions, leading to decreased abundances and population extinctions. However, if future climate conditions increase resource availability or reduce predation and competition, environments can become favorable and reproduction and population growth can increase. In this chapter, I test whether experimental amphipod populations (*C. pemptos*), across multiple generations, can boost population sizes by altering mating success under future climate conditions. Here, I examined whether increases in size and decreases in variation among male traits, such as body and claw size, were associated with greater female fecundity and egg production.

Chapter 5. Human modification to coastal habitats coupled with ocean warming and acidification will drive shifts in the abundance of natural marine habitats. Under future climate, kelp assemblages of South Australian temperate reefs will decline in abundance relative to turfs and urban structures. Kelp and turf provide amphipods (*C. pemptos*) with natural habitat and food resources. Yet, when available, amphipods also establish high densities on urban structures. In my final data chapter, I evaluate whether the role of artificial structures as marine habitats will increase relative to natural habitats.

Chapter 6. This chapter briefly reports the main findings of each data chapter and presents a cohesive discussion on how changing environmental conditions, such as habitat loss and climate change, drive asymmetrical shifts in community structure and switch source-sink habitats, enabling population growth. Furthermore, Chapter 6 contains a section that establishes the ecological importance of examining populations and communities in spatially structured habitats and a final section that discusses future research directions.

Thesis format. Each data chapter (2 - 5) has been written in the form of an individual scientific paper, following journal formatting, and can be read independently. This thesis is consistently formatted in American English since a majority of data chapters are under review in American Journals. At the start of each chapter, a statement of authorship lists co-authors and details their contributions to the paper. Chapter 4 is a published journal article, and the remaining chapters are under review in internationally recognized journals. Chapters 2 - 5 of this thesis form a coherent body of work, which is followed by a discussion (Chapter 6). Using the framework of source-sink theory, this thesis aims to further our understanding of how the identity and abundance of recruits can shift development of spatially structured populations and communities. Furthermore, this thesis provides insight into the impacts of habitat loss and future climate change on marine crustacean populations and communities.

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Chapter 2

Chapter Image: *Platynympha longicaudata* dispersing among habitats.

Photo credit: Katherine A. Heldt

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Chapter 2

Neighboring marine communities are not created equal: rich communities have greater responses to isolation than poor communities

2.1 Abstract

In spatially structured systems, the degree to which local dispersal influences development of neighboring communities depends on the density and diversity of incoming recruits. Yet, the identity (e.g. species and life-stage) of immigrants may be unequal across communities, and abundances of initial recruits from surrounding habitats (i.e. a local source) may drive different assembly trajectories and maintain dissimilarities in community composition. We tested whether communities isolated from their local source had fewer species' abundances, decreased local diversity (α), and greater between-community diversity (β) than connected communities that remained associated with their local source. We paired well established, source communities with two newly created habitats in South Australian seagrass beds and quantified abundance and diversity of crustaceans within each neighboring habitat. Furthermore, we examined differences between community trajectories and determined which life-stage(s) (i.e. male, female, and juvenile) is most abundant for each species. Between neighbouring communities, one was species-rich and the other was species-poor, and these differences in α diversity persisted after isolation and as communities aged. However, isolation temporarily increased β diversity among species-rich communities but not poor communities. Community trajectories shifted after isolation

with 11 species having greater abundance in one community over the other (e.g. rich vs. poor). In contrast, 4 species, such as *Paradexamine pacifica*, increased in abundance across communities while *Ianiropsis tridens* decreased. Three species relied on a specific life-stage to disperse (be juveniles or adults), and when a greater proportion of males recruit, as seen in *C. pemptos*, population growth in communities may be limited. The pathway by which neighboring communities differ in diversity is therefore governed by the identity and abundance of local recruits in spatially structured systems.

2.2 Introduction

Communities are linked by dispersers with local populations supplying propagules to neighboring habitats (Hanski and Gilpin 1991; Wilson 1992). Populations in newly created habitats rely on incoming propagules to maintain diversity (Hanski 1982; Loreau and Mouquet 1999) and reflect changes at local (α) and regional (γ) scales when less competitive, rare species recruit (Shmida and Wilson 1985; Wilson 1992; Amarasekare 2003). However, where immigration is unequal among communities (Drake et al. 1993), theory suggests that greater between-community diversity (β) will occur because dominant species prevail in some but not all communities (Law and Morton 1993; Mouquet and Loreau 2003).

Community structure, the identity and abundance of co-occurring species, can be highly dependent on external propagule supply (Shmida and Wilson 1985; Louette and De Meester 2007). The pathway that a particular habitat undergoes to assemble a localized community is therefore dependent on the sequence, density, and diversity of incoming species (Sutherland and Karlson 1977; Drake 1991; Munguia 2014). Hence, similar habitats can contain different species, communities may not follow highly predictable and deterministic succession (e.g. Odum 1969), and local sources that supply propagules have the potential to alter trajectories, defining how communities assemble through time.

In marine systems, assembly is not an orderly and directional process (Sutherland and Karlson 1977), and reductions in emigration and recruitment disrupt community assembly (Kneitel and Miller 2003; Loeuille and Leibold 2008). Fewer dispersers from local sources can limit connectivity between communities, decreasing α diversity (Loreau and Mouquet 1999; Cadotte and Fukami 2005). However, mobile species have the ability to maintain populations as non-random dispersal events shift community structure (Munguia 2004; Amarasekare 2010), and change in a species' distribution (Munguia 2014) and abundance (Munguia 2015) can modify assemblage and trajectory differences between neighboring communities.

Population growth and community assembly depend on whether individuals dispersing into habitats are ready to reproduce and dominate, or whether individuals require growth before reaching maturity and competitive status (Hillebrand et al. 2008; Sams and Keough 2012). Species with rapid immigration rates and fast developing offspring can dominate communities and prevent other species from establishing (Edwards and Stachowicz 2010). Furthermore, the life-stage in which species recruit (e.g. juvenile, female, male) alters trajectories such that fecund females, by releasing offspring, rapidly increase local population growth, while juvenile dispersers distribute more evenly across habitats and slowly increase population growth (Munguia et al. 2007). For example, greater mate availability aids amphipod population growth but when recruits are male-biased, local abundance is reduced (Munguia 2015), and population extinction of marine invertebrates has the potential to shift community structure (Munguia and Miller 2008).

Community trajectories may differ as immigrants with different life-history strategies (Munguia et al. 2007; Munguia 2015) and colonization abilities (Norderhaug et al. 2002; Valdivia et al. 2014) establish. We paired well established, local source communities with newly created habitats in South Australian seagrass beds to examine community dependency to the neighboring source. We first contrasted changes in local (α) and between- community (β) diversity between isolated communities that lost their source and connected communities that remained next to their source. If local sources drive assembly in neighboring habitats, we expect connected communities to have greater α and lower β diversity than isolated communities. We further expect that communities will be comprised of a subset of species that mirrors the local source and predict that communities isolated from local sources will undergo different trajectories. Finally, we determined species abundances in neighboring communities. If isolation does not affect a species' ability to colonize new habitats, then recruits will continue to maintain abundances in neighboring communities. Alternatively, if isolation negatively impacts a species' colonization, then fewer recruits will decrease abundances, and species not affected by source loss will dominate communities. However, broader dispersal of juveniles over adults can drive species colonization, and the life-stage in which individuals recruit may influence whether a species remains abundant in neighboring communities.

2.3 Materials and methods

2.3.1 Field methods

This study was conducted during October-November 2015 in the Gulf of St. Vincent near Coobowie, South Australia (35°03'18.6"S, 137°43'52.4"E), approximately 200 m off-shore, where the bay is composed of sandy sediment and seagrass (*Zostera muelleri*) patches intermixed with grapeweed (*Caulocystis uvifera*) assemblages. In South Australia, seagrass beds are inhabited by a variety of crustaceans including amphipods (e.g. *Cymadusa pemptos*, *Paradexamine pacifica*, *Caprellinoides mayeri*), isopods (e.g. *Platynympha longicaudata*, *Ianiropsis tridens*, *Paranthura microtis*, *Cerceis acuticaudata*), and tanaids (e.g. *Chondrochelia billambi* and *Chondrochelia occiporta*).

We placed settlement habitat of local source communities in the field 42 days prior to addition of new habitats (i.e. neighboring communities). New settlement habitats were placed in the field 20 mm from a source for 7d in a triangular fashion (Fig. S1), and at the beginning of the experiment (day 0), there were two new habitats associated with each source, 100 mm from each other. The 20 mm distance between a local source and each neighboring community allowed direct dispersal from one habitat to another to be estimated (Munguia 2015, Munguia unpubl. data), and at day 0, each neighboring community relied on external recruits, from local sources and the background environment, to increase population growth and diversity. A final set of habitats were placed in isolation (i.e. 3 m from the nearest source) to measure the level of background recruits independent of source influence.

The experiment consisted of 3 treatments: (a) removal of sources from the field, which isolated communities from their source; (b) connected communities that remained associated with their source; and (c) background habitats. Treatments were arranged in a triangular fashion (Fig. S1), 3 m apart, and placement of treatments within each triangle was randomized. Since habitats were destructively sampled, we replicated the experiment for each collection period, consisting of communities being 2d, 8d, and 18d old. The experimental setup consisted of 12 blocks (i.e. each block contained one each of isolated, connected, and background treatment per collection period; N = 36 total per age) 20 m apart, and time of collection was randomly pre-determined within each block.

Settlement habitat consisted of hard plastic, 25 mm mesh (100 mm by 75 mm) shaped into a cylinder and contained soft, 5 mm mesh (two pieces of 200 mm by 50 mm). This mesh setup is quickly colonized by crustaceans (García-Sanz et al. 2012) and also allows for tube dwelling crustaceans, such as *C. pemptos*, *C. billambi*, and *C. occiporta*, to establish colonies. Habitats were tethered to a 150 mm long PVC pipe that was attached to a brick anchor. Each habitat was suspended 30 mm above the substrate, but well within the seagrass canopy and remained submerged during periods of low tide. Following deployment, at 2, 8 or 18 days, we collected habitats by enclosing each cylinder within a Ziploc$^{©}$ bag, preventing animals from escaping (Munguia 2004; Munguia 2007). Samples were brought to the lab and rinsed with freshwater, and the freshwater solution containing invertebrates was filtered through a 0.05 mm mesh. Crustaceans were identified, counted, and the sex of each individual (i.e. male, female, juvenile) was determined under a dissecting microscope. Local diversity and species abundances in sources, neighboring communities, and backgrounds were calculated for each collection period.

2.3.2 Statistical analyses

First, we evaluated whether local (α) diversity was similar between neighboring communities. A paired t-test compared α diversity between communities associated to the same source for each age. Consistently, one community associated to each source had higher richness than the other, allowing us to identify species-rich and species-poor communities within each local system (see results). Second, a two-way MANOVA was used to determine whether the isolation treatment (connected vs. isolated) and age (2, 8, vs. 18d) influenced a change in α diversity between neighboring communities as dependent variables. This second analysis focused on the combined community response to treatments. Next, to assess β diversity, we examined similarities in community structure between isolated and connected communities using a Principal Coordinate Analysis (PCoA). The PCoA model was run with all species, except singletons (i.e., species with one individual), and for each age using Bray-Curtis dissimilarities. The resulting first two axes of the PCoA were then used to calculate the distance from each community to its treatment centroid (Anderson 2006a; Oksanen et al. 2016), as this reflects (dis)similarity in community structure among assemblages (Maloney et al. 2011) and allows for statistical comparisons between two or more treatments (Anderson 2006b). A two-way ANOVA tested the effects of age and isolation treatments on the centroid distances of rich communities, and a second two-way ANOVA tested for effects of age and isolation on centroid distances of poor communities.

Finally, we determined net abundance for each species (i.e. abundance in each neighboring community minus abundance in background communities). Further, for five species, we calculated the net abundance of adult males, adult females and juveniles in 18d old communities. We tested for differences among the three life-stages of each species with a Kruskal-Wallis test followed by a Dunn's test post-hoc analysis to correct for multiple comparisons, and ensured that non-parametric tests were used when data did not meet parametric assumptions. Analyses were conducted in JMP (v12, SAS Institute, Cary, NC; paired t-test and MANOVA) and R (v3.1-3, R Core Team 2015; ANOVA and non-parametric analyses, Dinno 2016).

2.4 Results

Consistently, in every experimental system, one community had significantly greater α diversity than the other (Fig. 1; Table 1), allowing us to define communities as either rich or poor. Differences between rich and poor communities occurred at 2 days and remained throughout the experimental period, regardless of isolation treatment (MANOVA, $F_{10,130} = 2.47$, $P = 0.01$; Table 2). Rich communities had greater α diversity and abundance than background communities while poor communities had lower α diversity than background communities (Fig. 1; Table S1). Furthermore, rich communities that were isolated from their source had greater β diversity than connected communities, and the greatest β diversity among rich communities occurred at 8 days ($F_{5,66} = 4.62$, $P < 0.01$; Fig. 2, Table 3; Fig. S2; Table S2). In contrast, β diversity among poor communities was not influenced by the isolation treatment or age ($F_{5,66} = 1.27$, $P = 0.29$; Fig. 2, Table 3).

In connected systems, 5 species had similar net abundance in poor and rich communities. Net abundance of the most dominant species, *Ianiropsis tridens* isopods (Fig. 3a), decreased with age, while three species increased with age (i.e. *Paradexamine pacifica* amphipods, Fig. 3b; *Cymadusa pemptos* amphipods, Fig. 3d; *Chondrochelia* *occiporta* tanaids, Fig. 3e). Each of these four species (*I. tridens* isopods, *P. pacifica* and *C. pemptos* amphipods, and *C. occiporta* tanaids) had similar positive net abundances among life-stages ($p > 0.05$; Table S4). The fifth species, *Gnathia mulieraria* isopods, had a net abundance of zero in rich and poor connected communities (Table S3).

Net abundance differed between connected rich and poor communities for 11 species. Overall, net abundance of *C. billambi* tanaids increased with age (Fig. 3c), and juvenile abundance was greater than males and females but only in poor communities (Rich communities: $p > 0.05$; Poor communities: $X^2 = 6.409$, df = 2, $p = 0.04$; J = 3.7 ± 2.4, M = 0.3 ± 0.8 SE, F = 0.2 ± 0.2 SE net abundance; Table S4). The remaining 10 species had greater net abundance in one community over the other in connected systems (Table S3).

In isolated systems, 5 species had similar net abundances between rich and poor communities. Positive net abundance of *P. pacifica* amphipods (Fig. 3g) and *C. billambi* tanaids (Fig. 3h) increased with age and did not differ among life-stages ($p > 0.05$; Table S4). Two other crustaceans had positive abundance (i.e. *Caprellinoides mayeri* amphipods and *Cerceis acuticaudata* isopods) and one species (*Platynympha longicaudata* isopods) had negative net abundance in isolated rich and poor communities (Table S3).

Net abundance differed between rich and poor communities in isolated systems for 11 species. *Ianiropsis tridens* isopods (Fig. 3f) decreased with age in isolated communities, yet had a greater proportion of juveniles relative to males and females in rich communities (X^2= 9.964, df = 2, p = 0.01; J = 13.2 ± 12.9 SE, M = 0.4 ± 0.6 SE, F = 0.6 ± 1.0 SE net abundance; Table S4), while in poor communities life-stages did not differ in abundance (p > 0.05; Table S4). In contrast, abundance of *C. pemptos* increased with age (Fig. 3i), with a greater proportion of juveniles and males in poor communities (X^2 = 7.404, df = 2, p = 0.02; J= 3.6 ± 2.6, M = 1.25 ± 0.7; F = 0.0 ± 0.5 net abundance; Table S4) and similar abundances across life-stages in rich communities (p > 0.05). Finally, abundance of *C. occiporta* tanaids increased in rich communities, while in poor communities net abundances decreased with age (Fig. 3j) regardless of life-stage (p > 0.05; Table S4). Net abundances of the 8 remaining species were greater in one community over the other in isolated systems (Table S3).

2.5 Discussion

Local sources do not support communities equally, and isolation causes communities to differ in β diversity because the identity and abundance of recruits varies from one habitat to the next. Community assemblages are therefore variable and differences are partially driven by the dispersing strategies of co-occurring species. Some species do not rely on a specific life-stage to recruit and show increases in abundance equally across communities. Yet other species rely on a specific life-stage to disperse (be juveniles or adults) or show greater abundance in one community relative to the neighboring community. This uneven distribution of individuals occurs in both connected and isolated communities. However isolation from a source during these early stages of community formation can also produce sharp declines in abundance across communities for species that occasionally rely on juveniles to disperse.

Experimental communities contained a subset of species from sources, and α diversity increased with community age. Within 2 days, rich communities contained twice as many species than background habitats, although many of these species had low abundances (e.g. *C. mayeri* amphipods and *C. acuticaudata* isopods with net abundance less than 1). Greater α diversity of communities over backgrounds reflects the increased potential for recruits of inferior competitors or rare species to establish in new habitats that may act as sinks (Wilson 1992; Amarasekare 2003). Yet poor communities had lower α diversity than backgrounds suggesting that not all communities can support a diverse assemblage. Consistent differences in α diversity may have established because initial dispersal rates (Loreau and Mouquet 1999) and species interactions of recruits (Wilson 1992; Law and Morton 1993) varied between communities.

Isolation elicits different responses among species, and when a species' ability to colonize a community decreases, population growth declines and assemblage trajectories shift. Isolation from a local source reduces immigration to neighboring communities and can shift community structure and diversity (Loreau and Mouquet 1999; Loeuille and Leibold 2008). While intermediate levels of immigration can maintain α diversity, a loss of local dispersers may increase the influence of local processes (e.g. predation and competition) on α diversity and increase β diversity (Kneitel and Miller 2003). In this study, trajectories of rich communities shifted under isolation, with 11 out of 16 species exhibiting different abundances between rich and poor communities. In contrast, 4 species, including *P. pacifica* amphipods, were broadly abundant across rich and poor communities after isolation, while one species, *P. longicaudata* isopods, was not present in isolated communities. Broadly abundant species, that are able to colonize new habitats, will dominate isolated communities and maintain abundances independent of source recruits, and with increasing dispersal rates, regional (γ) diversity may increase while β diversity decreases (Kneitel and Miller 2003).

Dispersal abilities differ among species, and by understanding each species' habitat specialization (Pandit et al. 2009), dispersing stage (Munguia et al. 2007), and population turnover (Drake 1990), we can better predict the extent to which shifts in the diversity and abundance of source recruits will alter community trajectories. Habitat specialization can limit a species' presence in communities and increase movement in and out of communities (Pandit and Kolasa 2012). However, a species' distribution across habitats depends on the dispersing life-stage (e.g. *I. tridens* tanaids, *C. billambi* tanaids, and *C. pemptos* amphipods), such that juveniles are more likely to colonize a greater number of habitats and have lower initial abundances than adults, which rapidly colonize few habitats (Munguia et al. 2007). Furthermore, life-stages settling in new habitats may experience different selection pressures than in local sources (Pulliam and Danielson 1991; Bowler and Benton 2005; Munguia 2015), and the number and identity of immigrants recruiting to neighboring habitats will ultimately determine population turnover and growth (Winker et al. 1995; Gaggiotti and Smouse 1996).

Both rich and poor communities are strongly influenced by local sources, and when connected to a source, communities show rapid increases in abundance. Initial recruits arriving to a community have a competitive advantage over other species (Sutherland and Karlson 1977). Yet, further development of a community strongly depends on the identity of incoming species and their interacting strengths, as proposed by theory (Law and Morton 1993). Isolation from a source does not affect species equally in communities, and some species can rapidly generate self-sustaining populations and reduce temporal effects in new habitats (Munguia 2015). In sexually reproducing species like amphipods and isopods, sex ratios can be sharply affected by isolation, and a greater proportion of males over females, as seen in amphipods (*C. pemptos*), can limit population growth in communities. Differences in community trajectories are therefore governed by the identity and abundance of local source recruits that increase diversity of one community over the other, and by accounting for innate differences among assemblages, we can better evaluate the potential for species to persist in isolated systems.

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2.7 Tables

Table 1. Difference in α diversity between the two communities for each age. Statistical differences were obtained with a paired t-test where each experimental system was considered one unit (n = 24).

	Rich vs. poor communities			
Community Age (d)	df	Mean difference	T-ratio	*P*
2	23	1.21	-5.80	**<0.01**
8	23	1.33	-6.22	**<0.01**
18	23	1.54	-5.23	**<0.01**

Table 2. MANOVA results showing the response of α diversity to age (A; 2, 8, and 18d) and the isolation treatment (I; connected and isolated) in neighboring communities. η^2 is the proportion of variance explained by age (N = 24 community pairs for each age).

	F	*P*	η^2
Age (A)	4.41	0.002	0.77
Isolation (I)	0.77	0.468	
A x I	1.36	0.251	0.92

Table 3. Two-way ANOVAs testing the effect of age (A; 2, 8, and 18d) and isolation treatment (I; connected and isolated) on β diversity for species-rich and species-poor communities.

	df	MS	F	*P*
Rich				
Age (A)	2	0.057	5.95	**<0.01**
Isolation (I)	1	0.066	6.83	**0.01**
A x I	2	0.021	2.18	0.12
Residual	66	0.009		
Poor				
Age (A)	2	<0.001	0.06	0.94
Isolation (I)	1	0.004	0.17	0.68
A x I	2	0.079	3.03	0.06
Residual	66	0.026		

2.8 Figures

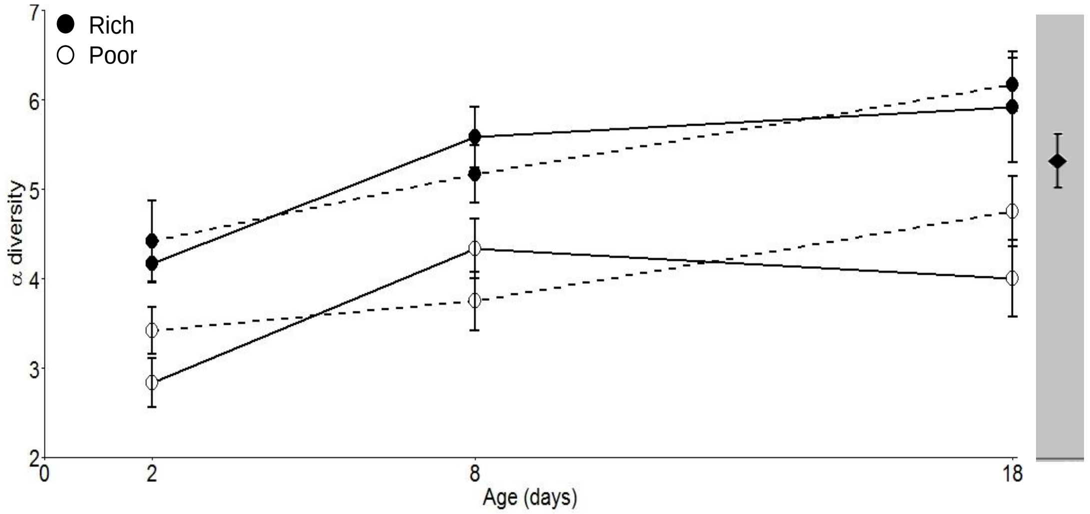

Figure 1. Differences in mean α diversity ± SE between communities associated to the same source. Regardless of being connected (solid line) and isolated (dashed line), one community was species-rich (black circle) while the other was species-poor (open circle). Background richness (black diamond), in 18d old communities, is displayed within the gray box.

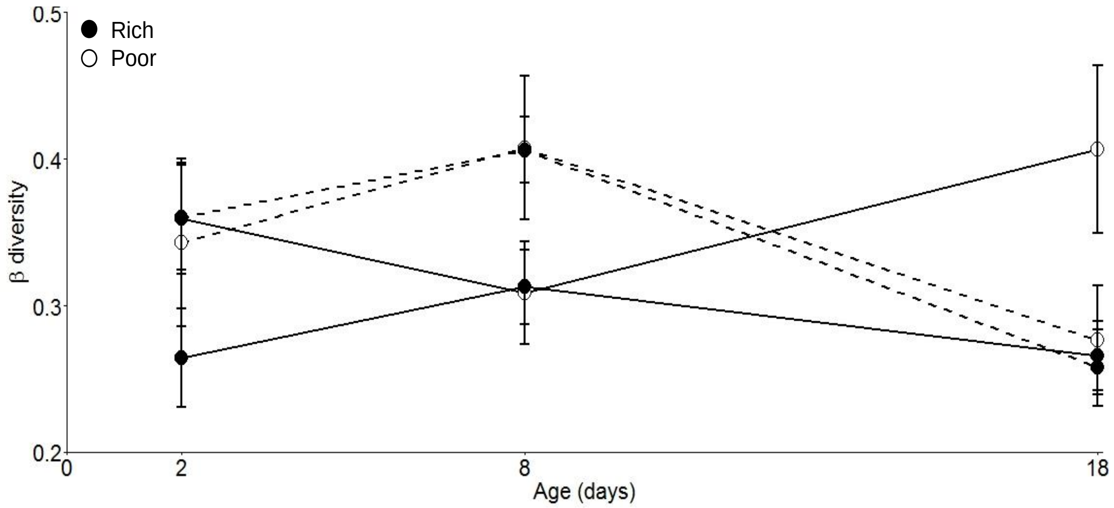

Figure 2. β diversity showing that isolation shifted structure of species-rich communities (black circle) but not species-poor communities (white circle). A larger mean β diversity± SE measure represents greater dissimilarity among communities that were connected (solid line) or isolated (dashed line).

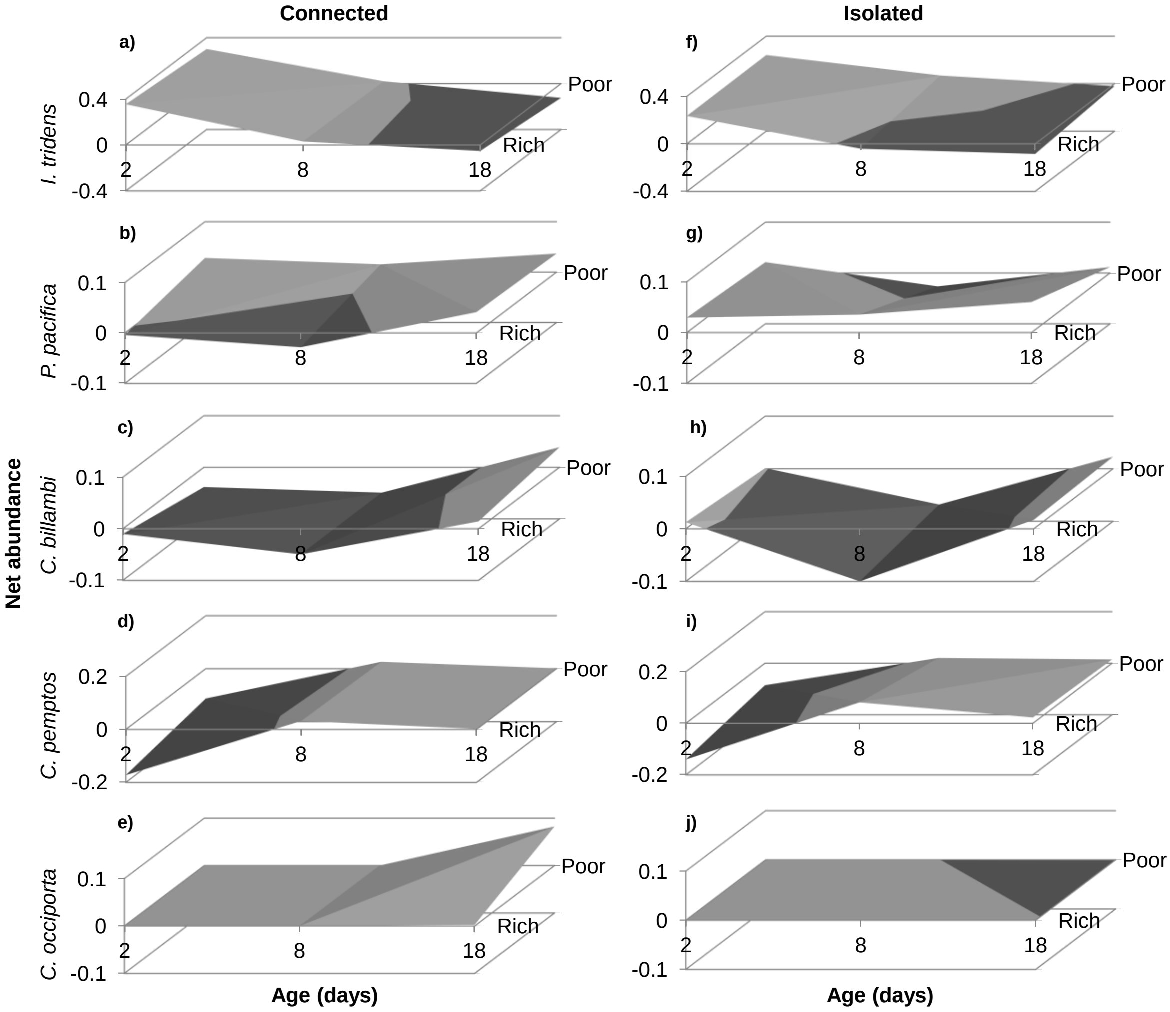

Figure 3. Species-specific abundances in communities. Mean differences in relative abundance between communities and backgrounds were calculated for 5 species (i.e. *I. tridens* isopods, *P. pacifica* amphipods, *C. billambi* tanaids, *C. pemptos* amphipods, and *C. occiporta* tanaids) in 2, 8, and 18d old rich and poor communities that were connected (a-e) or isolated (f-j). Positive values (light gray) reflect species that have greater abundance in communities than backgrounds, while negative values (dark gray) represent species that are locally restricted in communities.

2.9 Supplementary Materials

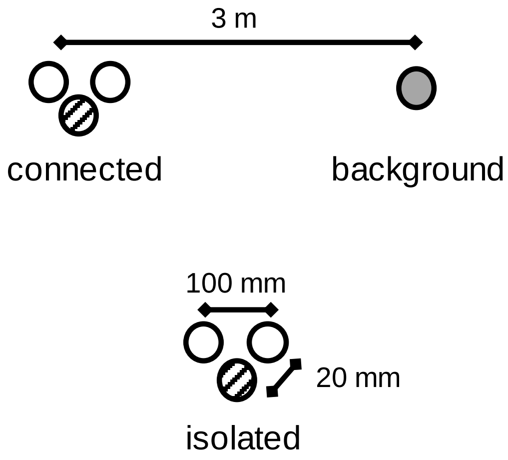

Figure S1. The experimental set-up was in a triangular fashion with two new habitats (i.e. communities, white circles) paired to a single local source (pattern circles). New habitats were 100mm from each other and 20mm from a source. The three treatments (a) connected, (b) isolated, and (c) background habitats (gray circles) were 3m apart.

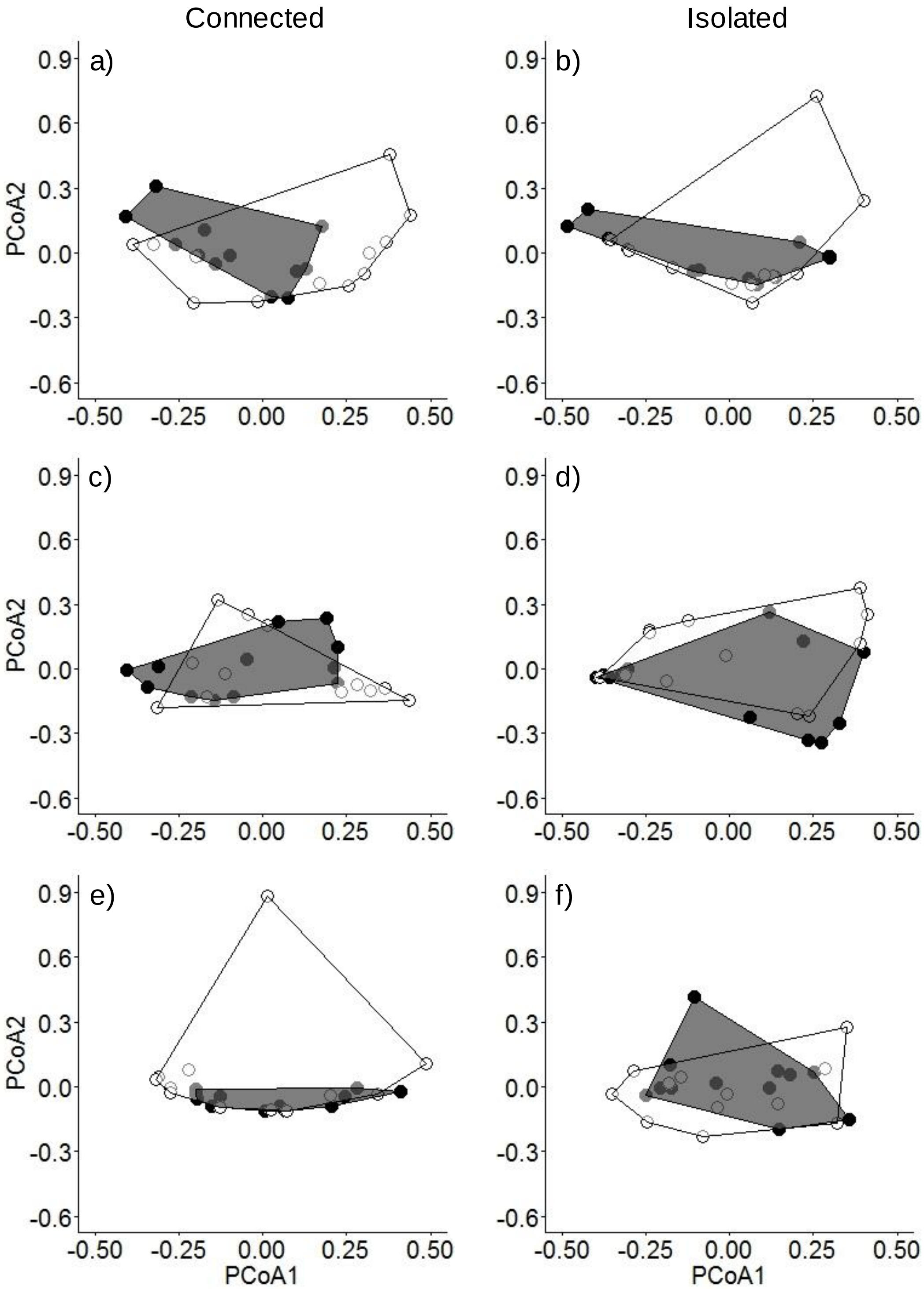

Figure S2. PCoA plot of rich (black circle) and poor (white circle) community assemblages that were a,b) 2d; c,d) 8d; or e,f) 18d of age and were connected or isolated. Distances were calculated using Bray-Curtis dissimilarity. Convex hulls reflect spread of species-rich (dark gray polygon) and species-poor (white polygon) communities in multivariate space.

Table S1. Average α diversity and abundance ± SE as a function of age (days) for sources, communities, and backgrounds. Communities were connected to a source or isolated, and one community was species-rich while the other was species-poor.

	α			Abundance		
Age (d)	2	8	18	2	8	18
Connected community						
Rich	4.2 ± 0.2	5.6 ± 0.3	5.9 ± 0.6	38 ± 6	56 ± 11	88 ± 12
Poor	2.8 ± 0.3	4.3 ± 0.3	4 ± 0.4	21 ± 4	43 ± 7	78 ± 18
Isolated community						
Rich	4.5 ± 0.5	5.2 ± 0.3	6.0 ± 0.4	37 ± 9	46 ± 9	105 ± 11
Poor	3.4 ± 0.3	3.8 ± 0.3	4.8 ± 0.4	27 ± 5	40 ± 13	94 ± 19
Source	5.5 ± 0.6	5.8 ± 0.3	6.0 ± 0.3	111 ± 20	126 ± 21	126 ± 15
Background	1.9 ± 0.4	3.4 ± 0.4	5.2 ± 0.5	5 ± 1	22 ± 4	65 ± 8

Table S2. Percent variation explained by the first two PCoA axes for connected and isolated communities that were 2, 8, and 18 days old.

	PCoA1 (%)			PCoA2 (%)		
Age (d)	2	8	18	2	8	18
Connected	54.7	53.7	38.6	22.3	19.3	26.1
Isolated	44.0	47.2	55.2	24.1	19.9	23.6

Table S3. Average net abundance ± 95% CI of crustaceans in 18d old communities after subtracting background abundances. Species with positive values are more abundant in communities than backgrounds, while species with negative values are less abundant in communities than backgrounds. In the table, species are ordered by net abundance of connected rich communities, with the largest positive value at the top and the largest negative value at the bottom.

Species	Crustacean type	Connected		Isolated	
		Rich	Poor	Rich	Poor
Ianiropsis tridens	Isopod	10.3 ± 21.9	6.8 ± 38.3	20.8 ± 21.0	13.8 ± 22.9
Paradexamine pacifica	Amphipod	6.3 ± 3.4	4.4 ± 3.4	8.3 ± 4.4	3.6 ± 3.1
Chondrochelia billambi	Tanaid	3.4 ± 3.7	4.7 ± 6.8	5.9 ± 7.5	8.8 ± 14.4
Cymadusa pemptos	Amphipod	1.7 ± 3.1	0.3 ± 3.1	4.9 ± 3.9	4.9 ± 7.1
Platynympha longicaudata	Isopod	1.3 ± 3.2	-0.4 ± 0.4	-0.3 ± 0.4	-0.1 ± 0.3
Caprellinoides mayeri	Amphipod	0.3 ± 0.4	0.0 ± 0.0	0.1 ± 0.2	0.3 ± 0.5
Serolina acaste	Isopod	0.3 ± 0.4	0.0 ± 0.0	0.2 ± 0.2	0.0 ± 0.0
Cerceis acuticaudata	Isopod	0.2 ± 0.2	0.0 ± 0.0	0.3 ± 0.4	0.1 ± 0.2
Amphilochus ruperti	Amphipod	0.1 ± 0.3	-0.1 ± 0.2	0.1 ± 0.2	-0.1 ± 0.2
Victoriopisa australiensis	Amphipod	0.1 ± 0.2	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.2
Ampithoe boiana	Amphipod	0.1 ± 0.5	-0.3 ± 0.3	0.0 ± 0.5	-0.1 ± 0.4
Chondrochelia occiporta	Tanaid	0.1 ± 0.3	0.0 ± 0.2	0.0 ±0.2	-0.1 ± 0.2
Paranthura microtis	Isopod	0.0 ± 1.2	-1.1 ± 1.0	0.3 ± 0.8	-0.8 ± 0.7
Caprella scaura	Amphipod	0.0 ± 0.0	0.1 ± 0.2	0.1 ±0.2	0.0 ± 0.0
Gnathia mulieraria	Isopod	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.2	0.0 ± 0.0
Paramoera willsi	Amphipod	-0.1 ± 0.5	0.1 ± 0.7	-0.3 ± 0.4	0.0 ± 0.8

Table S4. Kruskal-Wallis followed by a Dunn's test post-hoc analysis testing for abundance differences among males (M), females (F), and juveniles (J) of each species in 18d old communities.

Communities	Species	df	X^2	*P*-value
Connected Rich	*I. tridens*	2	4.916	0.086
	P. pacifica	2	0.223	0.895
	C. billambi	2	2.445	0.295
	C.pemptos	2	1.067	0.587
	C. occiporta	2	1.031	0.597
Connected Poor	*I. tridens*	2	5.624	0.060
	P. pacifica	2	2.441	0.295
	C. billambi	2	6.409	0.041[1]
	C.pemptos	2	1.905	0.386
	C. occiporta	2	-	-
Isolated Rich	*I. tridens*	2	9.964	0.007[2]
	P. pacifica	2	2.116	0.347
	C. billambi	2	3.228	0.199
	C.pemptos	2	3.781	0.151
	C. occiporta	2	2.000	0.368
Isolated Poor	*I. tridens*	2	2.350	0.309
	P. pacifica	2	0.631	0.729
	C. billambi	2	1.225	0.542
	C.pemptos	2	7.404	0.025[3]
	C. occiporta	2	-	-

[1] *C. billambi* Dunn's test: M vs. F (z = 0.17, p = 1.00); M vs. J (z = 2.27, p = 0.03); F vs. J (z = -2.10, p = 0.05)

[2] *I. tridens* Dunn's test: M vs. F (z = 0.39, p = 1.00); M vs. J (z = -2.52, p = 0.02); F vs. J (z = 2.91, p = 0.01)

[3] *C.pemptos* Dunn's test: M vs. F (z = -2.15, p = 0.05); M vs. J (z = 0.36, p = 1.00); F vs. J (z = -2.52, p = 0.02)

Chapter 3

Chapter Image: *Cymadusa pemptos* fecund female.

Photo credit: Katherine A. Heldt

Statement of Authorship

Title of Paper	Sinks become sources as changing climate boosts reproductive output and quality of populations
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Principal Author

Name of Principal Author (Candidate)	Katherine A. Heldt		
Contribution to the Paper	Led the conception and design of the project. Conducted the study, collected, and analyzed the data and drafted and revised the manuscript.		
Overall percentage (%)	85		
Certification	This paper reports on original research I conducted during the period of my Higher Degree by Research candidature and is not subject to any obligations or contractual agreements with a third party that would constrain its inclusion in this thesis. I am the primary author of this paper.		
Signature		Date	10/03/2017

Co-Author Contributions

By signing the Statement of Authorship, each author certifies that:

i. the candidate's stated contribution to the publication is accurate (as detailed above);

ii. permission is granted for the candidate in include the publication in the thesis; and

iii. the sum of all co-author contributions is equal to 100% less the candidate's stated contribution.

Name of Co-Author	Sean D. Connell		
Contribution to the Paper	Contributed to the conception and design of the project and provided suggestions, comments and feedback on the manuscript. Provided funding.		
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Contribution to the Paper	Contributed to the conception and design of the project and provided suggestions, comments and feedback on the manuscript.		
Signature		Date	10/03/2017

Chapter 3

Sinks become sources as changing climate boosts reproductive output and quality of populations

3.1 Abstract

Source populations in high quality habitats produce individuals that establish and maintain low quality sink populations; yet environmental change can reduce reproductive capacity in source habitats. We tested whether ocean warming and acidification reverses the roles of source and sink populations and determined whether changes in resource availability under future climate increase reproductive quality and output of sink individuals to cause switching of the original sinks to sources. We used large mesocosms containing herbivorous amphipods that consume and build nests in highly productive turf source habitats, but also build nests and seek refuge in unpalatable kelp. Under future climate, resource availability declined in source habitats (i.e. turfs) causing a shift in preference to kelp where nest building increased. The original sinks (i.e. kelps) became sources as individuals increased in quality (i.e. body size, egg size, and fecundity) which boosted population growth. When environmental change degrades source habitats and boosts sink habitats, their roles can reverse, and resulting increases in population growth can enable sinks to become the suppliers of high quality individuals that increase reproductive output and maintain population connectivity; hence switching original sinks to sources.

3.2 Introduction

Heterogeneous habitats vary in environmental conditions with species thriving in local patches that best fit their fundamental niche (Chase and Leibold 2003). Source habitats have positive population growth, while individuals residing in less suitable sink habitats have high mortality and low reproductive output which can result in population extinction (Pulliam 1988). Yet populations can persist in sink habitats when propagules arrive from a prosperous source (e.g. mass effects, Shmida and Wilson 1985; Pulliam 1988). However, as changing environments modify spatially structured habitats (Connell et al. 2013, Munguia et al. 2011), population persistence will not only be dependent on habitat quality (Jaquiéry et al. 2008, Stieha et al. 2016) but also on reproductive capacity of individuals dispersing (Caudill 2003, Bowler and Benton 2005).

Changing environmental conditions often alter the spatial arrangement of populations and reduce the quality of sources and sinks (Bender et al. 1998, Airoldi et al. 2008). Loss of high quality habitats negatively impacts reproduction and population growth in sources (Haynes and Cronin 2003, Mouquet et al. 2011). The result of declining source quality is fewer propagules supporting sink population growth and a decline in sink population quality (Pulliam 1988). However, in some cases, loss of high quality habitats can lead to greater use of less suitable habitats, and greater adult survival in less suitable habitats can help switch sinks to sources and prevent population decline (Murphy 2001).

Spatially structured habitats can therefore sustain source-sink populations facing changes in habitat quality (Mouquet and Loreau 2002). However, reversing the role of original sinks to sources is dependent on the quality and abundance of individuals recruiting (Stearns and Sage 1980, Holt et al. 2003), such that emigration of a few reproductive adults will have greater consequences on local population growth than many juveniles (Munguia et al. 2007, Munguia 2015). Furthermore, segregation of life-stages, where high quality adults reproduce within and defend source habitats and less competitive juveniles inhabit sinks (Møller 1995) leads to greater increases in population growth of sources, but not sinks. Similarly, females that are dispersal limited may exhibit minimal movement from sources to sinks, which establishes male-biased sink populations with reduced fecundity and growth (Kawecki 2003, Munguia 2015). Low quality individuals without the traits needed to obtain suitable habitat and mates (e.g. larger body size) will ultimately reduce reproductive output in sinks (Holmes et al. 1996), while high quality individuals from sources have the potential to increase sink population growth and switch original sinks to sources.

Mobile species will experience a number of habitats across landscapes, and by inhabiting high quality habitats, individuals can increase reproductive success (Pulliam and Danielson 1991, Kawecki 1995). Marine amphipods often exhibit habitat preferences (Hay et al. 1990, Poore and Steinberg 1999) and are closely associated with algal habitats that provide both food and shelter (Duffy and Hay 1991). In addition, amphipods disperse at multiple life-stages (e.g. juvenile, sub-adult, and adult) and have high population turn-over rates (months; Sainte-Marie 1991). Such life-history traits allow individuals to respond to environmental changes (Munday et al. 2013, Heldt et al. 2016), and it is likely that amphipod source populations can fuel establishment of sinks and stabilize regional population growth (Munguia 2015).

Changing environmental conditions, such as ocean warming and acidification, affect spatially structured habitats and can lead to population explosion or extinction (Cappuccino et al. 1995, Heldt et al. 2016). These environmental changes provide an opportunity to understand the influence of habitat quality and availability on population growth (Duarte et al. 2012, Cockrell and Sorte 2013). We used a model system of herbivorous amphipods that consume and build nests in highly productive turf source habitats, but can also build nests and seek refuge in unpalatable kelp. In this study, we tested whether elevated temperature and CO_2 would switch kelp sink habitats to source habitats, having a positive impact on kelp amphipod populations. We considered turfs as source habitat in current climate conditions because turf amphipod quality is enhanced via larger body sizes that have greater reproductive output and population growth, while kelp is considered a sink habitat containing amphipods of lower quality (i.e. small body sizes, lower reproductive output and population growth). However, we propose that modification to resource availability, for grazing or nest building, can cause amphipods to shift habitat occupancy and affect life history traits. If the increasing presence of turf source habitats under future climate conditions (Connell and Russell 2010, Connell et al. 2013, Falkenberg et al. 2015) meets grazer metabolic demands (Savage et al. 2004, Stieha et al. 2016), but not nest-building requirements (e.g. building materials and substrate surface; Christie et al. 2009, McDonald and Bingham 2010), amphipod body size, fecundity and density will increase in low quality sink habitats (i.e. kelp). As consumption of high quality turfs (i.e. source habitats) increases under future climate (Anderson et al. in review), kelp (i.e. sink habitats) may provide amphipods with essential refuge habitat and allow amphipod populations to persist. Here, we suggest that changes in the quality of spatially structured habitats will switch original sinks to sources and increase reproductive capacity of original sink populations.

3.3 Materials and methods

3.3.1 Study system

South Australian temperate reefs, composed of large kelp beds (*Ecklonia radiata*), are inhabited by a diverse array of benthic organisms. In recent years, temperate reefs adjacent to the Adelaide Metropolitan area have experienced habitat loss and an associated increase in the presence of turf algae (mat-forming, mixed assemblages; Connell et al. 2014). Although turf provides herbivores with valuable food resources (Brawley and Adey 1981, Falkenberg et al. 2014), turf may be a less suitable habitat for benthic organisms due to its decreased structural complexity (Christie et al. 2009).

Marine amphipods inhabiting macroalgae rely on their mobility to disperse among habitats (Christie et al. 2009) and exhibit host-plant preferences that influence adult survival and offspring performance (Poore and Steinberg 1999). In open branched algae, nest-building amphipod host-plant preferences are affected by competition and predation (Edgar 1983) with amphipod microhabitat preferences influencing species co-occurrences (Beermann and Franke 2012). *Cymadusa pemptos* is a common territorial ampithoid found in temperate coastal waters of South Australia, and similar to other *Cymadusa* sp. (Sainte-Marie 1991; Cruz-Rivera and Hay 2000; Appadoo and Myers 2003), is estimated to reach maturity in 4-6 weeks with populations undergoing 2-3 generations in only a few months. This species is a voracious consumer of turf and builds nests on turf if within close proximity of kelp (KAH personal observation).

C. pemptos uses both kelp and turf habitats; however amphipod densities are greater in turf (80 m^{-2}) than kelp (12 m^{-2}). Furthermore, amphipods in turf are larger with females producing more eggs per female (Turf = 19.06; Kelp = 10.67) and bigger eggs (Turf = 0.16 mm^2; Kelp = 0.06 mm^2) than amphipods inhabiting kelp. Here, palatable turfs may provide important food resources that kelp does not, enhancing the quality of turf source populations.

3.3.2 Source-sink populations in mesocosms

Six experimental tanks (2,000 L) were established at the South Australian Research and Development Institute (SARDI) facilities (West Beach, South Australia; 34.9453 ˚S, 138.5038 ˚E) in September 2013. Briefly, the experimental set-up is described below, and further details on design, operation, and water chemistry are described by Falkenberg et al. (2016). To be within forecasted conditions, we elevated temperatures by 2.5°C and pCO_2 by 250 ppm (IPCC 2007). Tanks were randomly assigned climate treatments and independently maintained as current climate (n = 3 tanks ambient temperature, ~15˚C, and ambient CO_2, pCO_2 ~400 ppm and ~8.15 pH units) and future climate (n = 3 tanks elevated temperature, ambient + 2.5˚C, and elevated CO_2, ambient pCO_2 + 250 ppm and ambient - 0.15 pH units). Kelp (n = 5 holdfasts and fronds at 1.2 kg per tank), turf (n = 5 tiles per tank; 10cm x 10cm seeded fiber-board), and amphipods (100 individuals per tank) collected from Adelaide Metropolitan temperate reefs were placed into tanks. Kelp were weighted to the bottom of tanks by attaching holdfasts to plastic trellis that was tied to bricks. Amphipods were collected in the field by enclosing entire kelp plants in a plastic bag to ensure experimental densities reflected natural densities, and densities were homogenized across tanks. Turf tiles were placed on the bottom of each tank to seed tanks; turf was growing on the sides of tanks within one month.

For each tank, temperature and pH were measured at different times of the day every day, and measurements at noon were representative of tank environmental conditions for that day (Falkenberg et al. 2016). Water chemistry differed between current and future climate tanks with treatments achieving target environmental conditions. In current conditions, average temperature was 15.4 ˚C ± 0.1 SE and average pH was 8.16 ± 0.01 SE, while in future conditions, average temperature was 17.9 ˚C ± 0.3 SE and average pH was 7.99 ± <0.01 SE. Average pCO_2 in current conditions was 381 µatm ± 38 SE and in future conditions was 663 µatm ± 80 SE. In current conditions, average alkalinity in tanks was 2,563 µmol kg^{-1} ± 3 SE, and in future conditions average alkalinity was 2,547 µmol kg^{-1} ± 2 SE.

Amphipods were collected from turf and kelp habitats within each tank in December 2013, after experiencing 3 months of treatment conditions. A subsample of turf populations was collected by scraping turf off of tank walls directly into containers. Entire kelp populations were collected by dipping kelp fronds in freshwater, gently wiping each blade, and filtering the freshwater containing amphipods through a 0.5 mm mesh. Amphipods were preserved in 100% ethanol and counted with the aid of a dissecting microscope. Juveniles were highly abundant; therefore, after removing adults we re-suspended samples in 500 mL ethanol and subsampled all individuals within 50 mL. The surface area of kelp fronds and area of turf sampled was measured (m^2), and amphipod density for each tank was calculated as the sum of adults and subsampled juveniles per m^2. Females were inspected under a dissecting microscope, and the number of eggs per female was counted. Adults and eggs from each tank were photographed and body length (rostrum to third uropod) and egg size (mm^2) was measured using imageJ (Schneider *et al.* 2012). Algal biomass was quantified in December 2013; kelp in each tank was re-weighed and 0.2 m^2 of turf was scraped from each tank and placed in a drying oven (60˚C).

To evaluate habitat quality, we quantified nest building (nests per cm^2), feeding (grams algae consumed), and resource availability in kelp (i.e. fronds) and turf habitats experiencing current and future climate conditions. We counted the number of nests built per amphipod in three 72 cm^2 samples per tank in each of kelp and turf habitat and weighed three 0.5 g samples of kelp and turf per tank at day 0 and after 3 days to evaluate amphipod feeding. We assumed that resource availability was a function of per capita nest building (number of nests per amphipod) and algal biomass (grams of algae) such that $\Delta_y / \Delta_z = \left(\frac{\bar{y}_f - \bar{y}_c}{SE_{\bar{y}_c}}\right) \Big/ \left(\frac{\bar{z}_f - \bar{z}_c}{SE_{\bar{z}_c}}\right)$,

Where glass's delta (Δ) uses the standardized difference between two means (future treatment = $\bar{x}_1$, $n_1 = 3$ and control treatment = $\bar{x}_2$, $n_2 = 3$) and the standard error of the control treatment (SE_2) to determine effect size for samples with unequal variances (Cohen 1988, Ferguson 2009), and provides the magnitude of treatment effects without pooling variances (Grissom and Kim 2005). Therefore, Δ_y is the mean difference in per capita nest building between future (f) and current (c) climate standardized by the standard error of per capita nest building under current climate, and Δ_z is the mean difference in algal biomass between future and current climate standardized by the standard error of algal biomass under current climate. Standard deviations were calculated from the control group to avoid effect sizes changing under equal means and different variances. Nest building, feeding, resource availability, and amphipod density and body size under current and future climate conditions were also compared by calculating effect sizes using Glass's delta (Δ).

3.3.3 Statistical analyses

Two-way ANOVAs examined the impact of climate and habitat on amphipod fecundity (i.e. proportion of fecund females per tank, number of eggs/female, and egg size). Egg size was log transformed, and female body size was used as a covariate in an ANCOVA that examined the impact of climate and habitat on differences in egg number per female. In cases with significant two-way interactions, we explored the effects of climate on female fecundity for each habitat using a one-way ANOVA. All analyses were completed in JMP (v10, SAS Institute, Cary, NC).

3.4 Results

Elevated future climate conditions negatively affected source habitat quality (Fig. 1a-c; Table 1) and shifted amphipod life history traits in source-sink habitats (Fig. 1d-f; Table 1). Nest building declines in turf under elevated temperature and CO_2, while feeding of turf escalates (Fig. 1a,b). Depletion of turf resources under future climate (Fig. 1c) was associated with shifts in body size under future climate with males growing larger in kelp and females becoming smaller in turf (Fig. 1e,f; Table 1).

A greater proportion of females were brooding eggs (Fig. 2a; 2-way ANOVA $F_{3,4} = 13.70$, P = 0.01; Table 2) under future climate, and there was a significant increase in the proportion of fecund females in kelp, but not turf (Table 3). Female egg production increased with body size but was not influenced by habitat type or climate treatments (Fig. 2b, 2-way ANCOVA $F_{4,132} = 15.48$, $P < 0.01$; Table 2). Yet under future climate, egg size increased in kelp and decreased in turf (Fig. 2c; 2-way ANOVA $F_{3,988} = 183.33$, $P < 0.01$). Furthermore, sex ratios of kelp and turf amphipods were female-biased under future climate, and the ratio of adults to juveniles was lower in turf than kelp (Table 1).

3.5 Discussion

As changing climate modifies preferred habitats that are readily occupied, spatially structured populations need to adjust. In marine temperate habitats, the kelp-turf mosaic can sustain populations experiencing changing environmental conditions that shift habitat quality. Highly palatable turfs are sought by *C. pemptos* as important food and habitat resources. The higher productivity of turf (i.e. source habitats) over kelp (i.e. sink habitats) is reflected in turf amphipods having larger bodies, bigger eggs, and greater densities than kelp amphipods. Yet under future climate, kelp residents have greater density and body size, with increases in fecundity and egg size. Amphipod densities increase under future climate, and resource availability of sources declines with amphipods shifting habitat utilization and having greater settlement in kelp relative to the palatable turf. Reductions in source habitat quality were associated with decreases in turf amphipod body and egg size under future climate. For mobile species experiencing future climate conditions, small adjustments in resource use can shift original sink habitats to sources where large, fecund individuals bolster population growth.

Herbivory reduces living space when food and habitat resources are the same source. Consumption of local habitats can have consequences on population growth as preferred source habitats are lost (Duffy 1990, Duffy and Hay 1991, Abbott and Dwyer 2007) shifting algal assemblages (Duffy and Hay 2000). In this kelp-turf system, consumption of turf increases under future climate, and while turf is favorable nest-building habitat it is readily consumed because reduced phlorotannin and high nutrient concentration increases palatability (Falkenberg et al. 2013, Anderson et al. in review). Yet turf habitats alone cannot support growing populations under future climate, and individuals shift to neighboring sink habitats.

Flexibility in resource use reduces stress on habitats with partitioning of feeding and living-space resulting in positive population growth. However, exploitation of habitats is risky because the costs associated with dispersal can have negative consequences on population growth (Travis and Dytham 1999, Munguia et al. 2007). Under future climate, individuals shifted to neighboring sink habitats with amphipods achieving high densities. Greater C:N ratio and phlorotannin concentration most likely prevents kelp consumption (Norderhaug et al. 2006, Anderson et al. in review), but kelp is structurally complex providing a greater number of females with shelter required for mating (Borowsky 1980). Female preferences for favorable reproductive resources that can enhance fertility (i.e. larger eggs and greater fecundity; Hemmi and Jormalainen 2002) and large males seeking mates (Vesakoski et al. 2008) can shift population structure in original sinks (Munguia 2015). Furthermore, future climate can exacerbate population growth in sinks as enhanced primary productivity (Connell and Russell 2010) meets higher metabolic demands (Alenius and Munguia 2012, Ghedini et al. 2015) and reduced dispersal risk maximizes exploitation of habitats (Pistevos et al. 2015).

The consequences of degraded source habitats on marine and terrestrial populations will be dependent on propagule production under future climate. Sink habitats shifting to sources will allow populations to persist (Pulliam 1988), and selection forces related to the quality of source individuals will shape sink population growth (Dale 2001, Munguia 2015). Here, increased egg sizes under future climate can enhance the quality of sink populations leading to larger individuals and greater fecundity; however, maternal effects can also interact with environmental conditions to play an important role in the quality and quantity of eggs produced (Dick et al. 1998, Einum and Fleming 2000). High quality source individuals can therefore increase growth and genetic diversity of sink populations (Holt et al. 2004) and reduce sink founder effects (Bay et al. 2008). Given the expected rate of environmental change, sink habitats transitioning to sources may be able to sustain population growth (Grear and Burns 2007) and aid in repopulation of neighboring habitats (Breininger and Carter 2003).

Population growth is regulated by shifts in the quality of spatially structured habitats under future climate. Consumption of favorable habitats by mobile species will alter resource use and shift populations to less suitable habitats. Original sinks will transition to sources as heightened use of low quality habitats provides large, reproductive adults with refuge, increasing mating opportunity and female fertility. Greater propagule production in sinks, a reflection of increasing sink quality under future climate, will drive population growth. Ultimately, the population consequences of original sinks shifting to sources will be dependent on selection forces related to the quality of individuals with high quality individuals in sinks sustaining regional populations. The potential for spatially structured habitats to support population outbreaks under future climate will therefore be contingent upon source-sink systems maintaining population connectivity and exchanging high quality propagules.

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3.7 Tables

Table 1. Amphipod characteristics showing that four of the six values switch, and as climate changes, decreases in turf habitats are matched by increases in kelp habitats. Means ± 1 standard error.

	Turf		Kelp	
	Current	Future	Current	Future
Nest building (cm^{-2})	2.00 ± 0.69	0.44 ± 0.29	2.00 ± 1.02	3.00 ± 0.67
Male body size (mm)	10.34 ± 0.43	9.36 ± 0.73	7.46 ± 0.57	8.87 ± 0.24
Female body size (mm)	10.41 ± 0.22	9.73 ± 0.50	8.08 ± 0.33	8.61 ± 0.20
Adult:Juvenile ratio	3.68 ± 2.24	1.89 ± 0.29	8.14 ± 4.13	12.41 ± 3.06
M:F sex ratio	0.38 ± 0.20	0.57 ± 0.07	0.20 ± 0.10	0.43 ± 0.05
Feeding (g)	0.12 ± 0.03	0.30 ± 0.15	0.01 ± 0.00	0.02 ± 0.01

Table 2. Model results for female fertility from experimental tanks. Fixed factors were habitat type (H; turf and kelp) and climate (C; current and future). Dependent variables for female fertility were the proportion of fecund females, number of eggs/female, and egg size (mm^2). The model for number of eggs per female included female body size as a covariate.

Main effects	df	F	P
Proportion fecund			
Habitat	1	1.03	0.37
Climate	1	31.72	**<0.01**
H x C	1	8.35	**0.04**
No. eggs/female			
Habitat	1	0.69	0.41
Climate	1	0.40	0.53
H x C	1	<0.01	0.96
Log body size		46.59	**<0.001**
Egg size (mm^2)			
Habitat	1	0.41	0.52
Climate	1	72.22	**<0.001**
H x C	1	477.69	**<0.001**

Table 3. One-way ANOVAs testing the effect of climate on female fertility within each habitat. The dependent variables for ANOVAs were proportion of fecund females and egg size (mm^2).

	Turf			Kelp		
Dependent variables	df	F	P	df	F	P
Proportion fecund	1, 2	2.00	0.29	1, 2	312.51	**<0.01**
Egg size (mm^2)	1,437	67.20	**<0.001**	1,551	867.10	**<0.001**

3.8 Figures

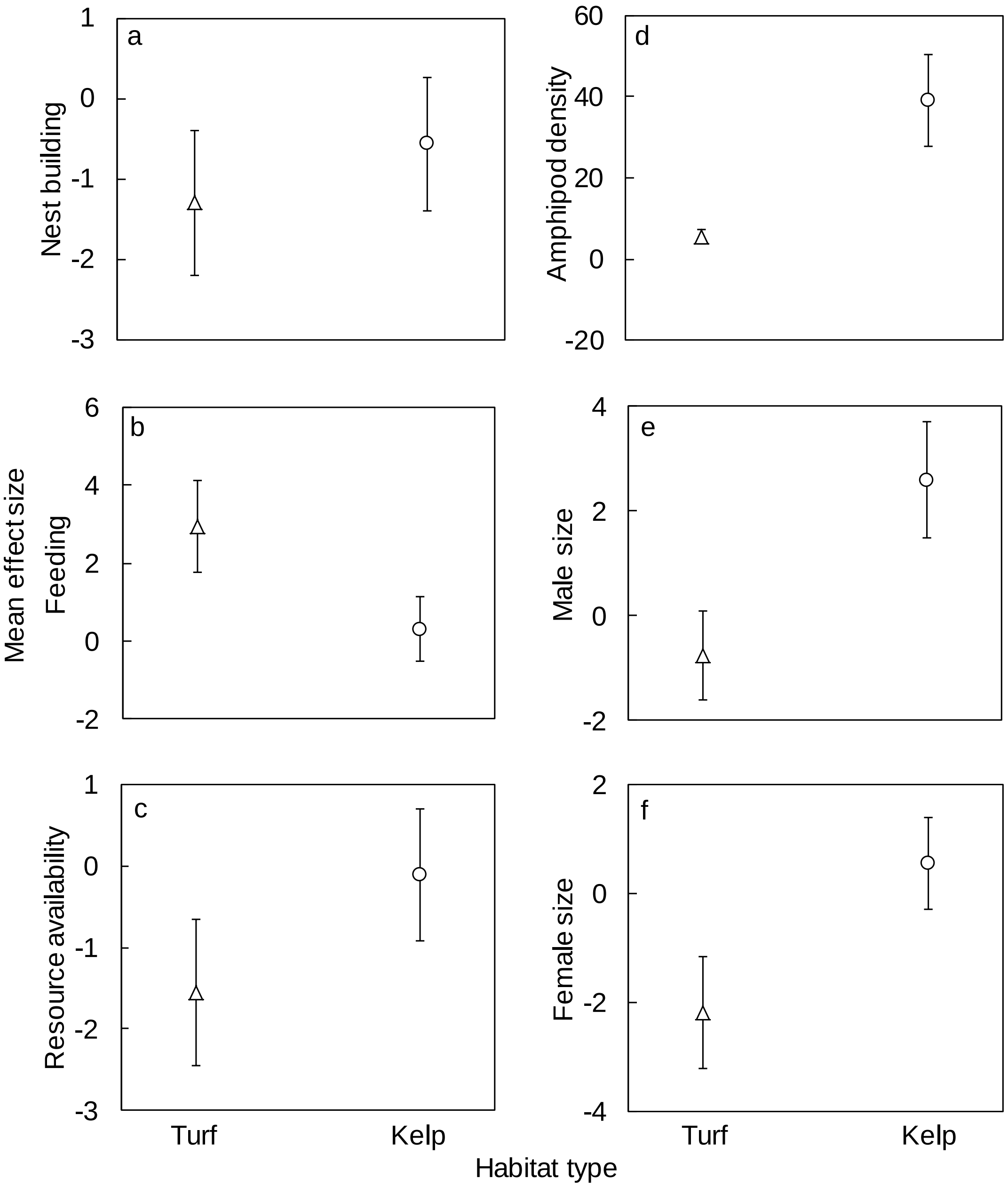

Figure 1. Roles of sources and sinks reverse under future climate. Switches between kelp (circle) and turf (triangle) as climate changes effect sizes of a) nest building b) feeding, c) resource availability, d) amphipod density, e) male body size, and f) female body size. Effect sizes were calculated using Glass's delta ± SD, where positive values on the y-axis represent increases under future climate, and negative values on the y-axis represent decreases under future climate.

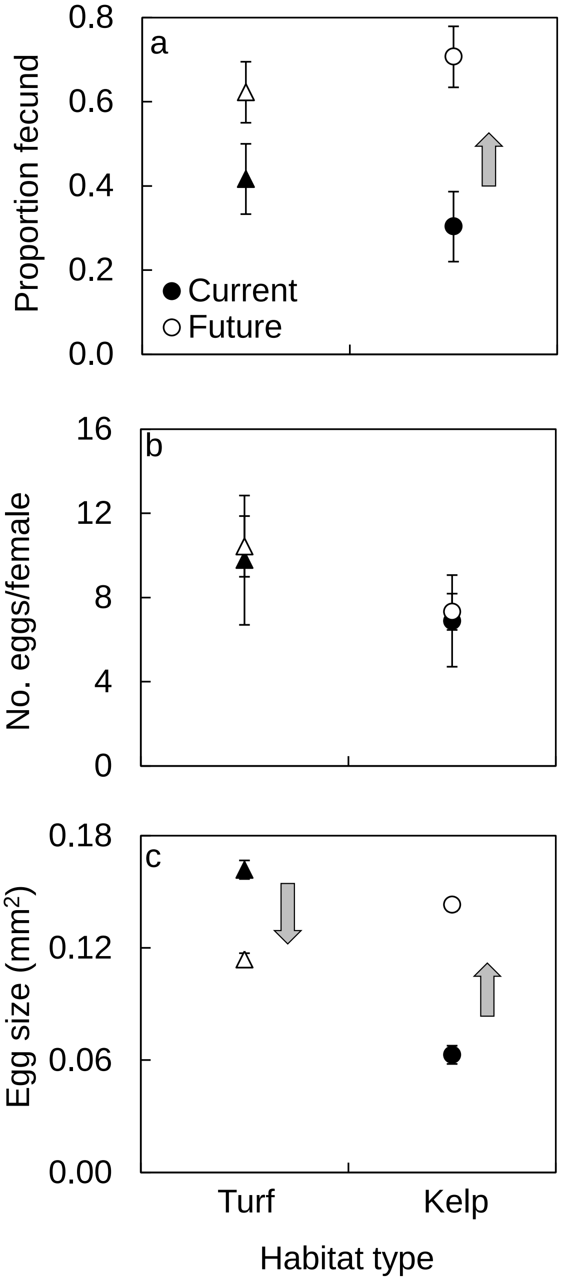

Figure 2. Increasing female fertility in original sinks under future climate, including mean ± SE a) proportion of fecund females, b) number of eggs per female, and c) egg size (mm^2). Fertility of females is shown in turf (triangle) and kelp (circle) habitats under current (black) and future (white) climate. Gray arrows represent significant increases or decreases in fertility under future climate.

Chapter 4

Chapter Image: *Cymadusa pemptos* male with enlarged claw.

Photo credit: Katherine A. Heldt

Statement of Authorship

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Name of Principal Author (Candidate)	Katherine A. Heldt		
Contribution to the Paper	Contributed to the conception and design of the project. Conducted the study, collected, and analyzed the data and drafted and revised the manuscript.		
Overall percentage (%)	80		
Certification	This paper reports on original research I conducted during the period of my Higher Degree by Research candidature and is not subject to any obligations or contractual agreements with a third party that would constrain its inclusion in this thesis. I am the primary author of this paper.		
Signature		Date	10/02/2017

Co-Author Contributions

By signing the Statement of Authorship, each author certifies that:

i. the candidate's stated contribution to the publication is accurate (as detailed above);
ii. permission is granted for the candidate in include the publication in the thesis; and
iii. the sum of all co-author contributions is equal to 100% less the candidate's stated contribution.

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Contribution to the Paper	Contributed to the conception and design of the project and assisted with data analysis and the development and revision of the manuscript.		
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Chapter 4

4.1 Published Manuscript

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Future climate stimulates population out-breaks by relaxing constraints on reproduction

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When conditions are stressful, reproduction and population growth are reduced, but when favourable, reproduction and population size can boom. Theory suggests climate change is an increasingly stressful environment, predicting extinctions or decreased abundances. However, if favourable conditions align, such as an increase in resources or release from competition and predation, future climate can fuel population growth. Tests of such population growth models and the mechanisms by which they are enabled are rare. We tested whether intergenerational increases in population size might be facilitated by adjustments in reproductive success to favourable environmental conditions in a large-scale mesocosm experiment. Herbivorous amphipod populations responded to future climate by increasing 20 fold, suggesting that future climate might relax environmental constraints on fecundity. We then assessed whether future climate reduces variation in mating success, boosting population fecundity and size. The proportion of gravid females doubled, and variance in phenotypic variation of male secondary sexual characters (i.e. gnathopods) was significantly reduced. While future climate can enhance individual growth and survival, it may also reduce constraints on mechanisms of reproduction such that enhanced intra-generational productivity and reproductive success transfers to subsequent generations. Where both intra and intergenerational production is enhanced, population sizes might boom.

When environmental conditions are stressful, reproduction and population growth are delayed[1], but when favourable, reproduction and population size can boom[2]. The effects of future climate on animal populations are often considered within the context of strong negative effects while strong positive effects are less considered. Ocean warming and acidification are considered stressors[3,4] through increasing metabolic costs of individuals[5–7]. Nonetheless, elevated temperature can have positive effects through an increase in metabolism[8] enabling population growth[9] when elevated resources brought by carbon enrichment[10] meet metabolic demands. It is possible that future climate may not only relax constraints on population growth, but also enable some populations to boom.

Herbivore populations appear particularly sensitive to future climate as meta-analyses suggest a general decrease in population size[11,12]. Yet, while unusual, there is evidence for population growth in herbivores[12], which could be through the relaxation of abiotic and biotic constraints on reproductive output. Indeed, elevated CO_2 and temperature can enhance food intake as a function of increasing per capita herbivory[13,14]. Such conditions may not only enhance reproductive success, but over successive generations they may also yield substantive increases in population sizes. While future conditions enhance foraging resources[13] and survival amongst predators[15], little is known about the contribution of reproductive success to population growth. Where reproductive success adjusts to favourable environmental conditions, the relaxation of competitive restriction to mates becomes a critical mechanism[16–18].

Intensifying intraspecific interactions buffer runaway reproductive success as populations become increasingly dense[19]. Increasing competition for mates reduces male access to mates, and less competitive males are unable to reproduce[20]. Females play a particularly strong role in determining male mating success across a broad spectrum of

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taxa (e.g. territorial birds[21], fish[22], and crustaceans[23]). Females can increase reproductive output when mating with high quality males[24] or reduce the intensity of male-male competition to increase overall reproductive success[16].

As a test of this enhanced reproduction mechanism, we propose that the relaxation of abiotic constraints imposes strong directional selection on male ornaments which increase access to mates as male sexually selected traits become more exaggerated and homogenized[25,26]. Access to mates is gained when individuals deploy an array of successful mating strategies arising from sexual selection often producing dissimilar phenotypes[18,27,28]. Phenotypic traits are costly to maintain in stressful environments[29–31], and males with the most appealing traits will monopolize females[18,28]. We consider, therefore, that as environmental constraints are relaxed, a higher proportion of males can maintain costly traits, predicting reduced variation in sexually selected characters[32] and an increase reproductive success[33] that together results in population growth[18,34].

The development of theory on future climate as a facilitator of population growth lags behind that of climate as a stressor causing population decline. While the idea that future climate need not constrain population size is well known[12], there are few tests of hypotheses that predict population growth, particularly the mechanisms enabling growth via enhanced reproductive potential. We tested whether elevated temperature and carbon dioxide could increase population growth of a herbivorous amphipod (*Cymadusa pemptos*), and to account for this population increase we observed reproductive potential by testing the prediction that phenotypic variation in male secondary sexual characters is reduced while females fecundity is enhanced.

Results

Populations exhibited changes after 3 months with increases in size occurring under the combination of elevated temperature and CO_2 (i.e. future climate). Population sizes under future climate increased by at least 2500% relative to contemporary climate (Fig. 1a; Table S1; $X^2_{3,7} = 8.22$, $P = 0.042$). The proportion of fecund females increased under future climate (Fig. 1b; Table S1, $F_{3,7} = 4.63$, $P = 0.044$), and there were fewer fecund females per male under future climate (Fig. 1c). However, the OSR did not differ between current and future climate (Table S1; $F_{3,6} = 1.48$, $P = 0.31$). Size frequency distributions in current and future climate had unimodal distributions at the end of the experiment (Fig. S1), reflecting overlapping generations driving population growth[35].

Males and females responded differently to elevated temperature and CO_2 (Fig. 2). Male amphipods were larger under future climate relative to current conditions (Fig. 2a), driven by the effect of elevated temperature (Fig. S2, Table S2; $F_{3,643} = 23.24$, $P < 0.0001$). In contrast, female body size did not differ among treatments (Fig. 2a; Fig. S2; Table S2; $F_{3,411} = 1.22$, $P = 0.30$). Male gnathopods dramatically increased in size under future climate compared to female gnathopods (Fig. 2b). Increases in male gnathopod size (Fig. S2; Table S3; $F_{7,639} = 180.60$, $P < 0.0001$) was driven by a synergistic effect of temperature and CO_2 (Table S3; Current temperature: $F_{3,204} = 119.99$, $P < 0.0001$ and Elevated temperature: $F_{3,435} = 241.52$, $P < 0.0001$). Female gnathopod size decreased under elevated temperatures (Fig. S2; Table S3; $F_{7,407} = 25.29$, $P < 0.0001$). At a population level, male gnathopod variance was reduced (Fig. 2c) primarily due to elevated CO_2 (Table S4; $F_{3,643} = 3.08$, $P = 0.03$) while variance in female gnathopod size (Fig. 2c) did not differ among treatments (Table S3; $F_{3,408} = 0.41$, $P = 0.74$).

The number of eggs produced (Table S5) did not differ among the treatments in our study. Egg number was a function of female body size (Table S5; $F_{7,232} = 8.72$, $P < 0.0001$), but female size did not consistently predict egg number across treatments (Table 1). In ambient conditions, egg number was independent of female size (Table 1), while temperature caused a disproportionate effect of female size on egg number. In contrast, elevated CO_2 caused a linear increase in egg number with female size. When both elevated temperature and CO_2 were present, female size had a significant non-linear effect on eggs produced (Table 1). Females experiencing elevated temperatures exponentially increased egg production, optimizing reproductive output (Table 1; Fig. S3) rather than increasing body size (Fig. 2a).

Discussion

Treatments that created future climate conditions (i.e. the combination of elevated temperature and CO_2) not only enhanced fecundity, but the apparent increase in reproductive success translated into greater population size over successive generations (Fig. S4). Increases in male body and gnathopod size were associated with an increase in the proportion of fecund females. As predicted from our model of sexual selection acting to buffer population growth, we observed wide variance in male gnathopod size in contemporary conditions, suggesting intense competition among individuals[19,36], and a narrowing of this variance by future climate. Such reductions in variance of sexually selected traits reduce the intensity of male-male competition that is associated with decreased mate guarding and increased mating opportunities[18,36]. In addition, females shifted resource investment to egg production under elevated temperatures rather than enhancing size; life-history strategies were altered to optimize the number of eggs brooded under future climate, increasing population size. The relaxation of constraints on reproductive output was associated with enhanced food productivity in the same experiment (i.e. filamentous turfs[37]) and the associated reduction in predation[15] could only have assisted in translating reproductive success into population growth over successive generations.

To assess whether future climate may boost intergenerational population growth, we need to understand how reproductive potential translates enhanced productivity to the next generation. Energy flows from producer to consumer will depend on both metabolic effects on the consumer[38,39] and effects on the abundance and food quality of the producer recognizing variation among producer species[40,41]. For populations to grow, reproductive success needs to contribute and build upon both enhanced survivorship (i.e. reduced predation[15]) and individual growth; of which the latter is underpinned by greater metabolic demand[6,42,43] and met by greater foraging activity[13] of elevated primary productivity[39]. Population explosion under future climate is likely to be underpinned by the positive influence of elevated temperature on metabolic rate[7], where requirements for greater food are met by the effect of carbon enrichment on algal resources[43]. Algal productivity can be supercharged by elevated temperature and carbon dioxide, particularly on fine, filamentous algae that herbivorous amphipods consume, but under

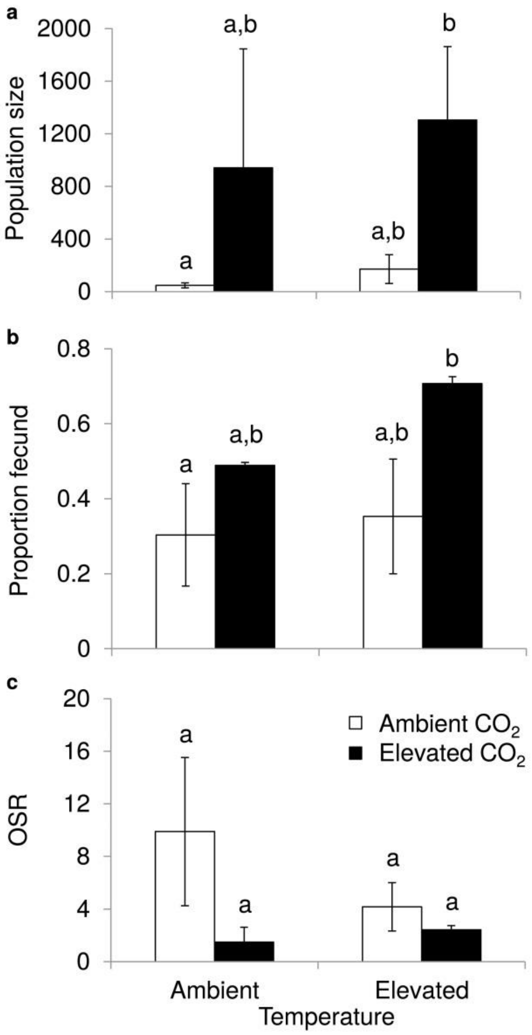

Figure 1. Effect of elevated temperature, elevated CO_2, and the combination of elevated temperature and CO_2 on population size and reproduction. Ambient and elevated temperature is on the x-axis with white bars representing ambient CO_2 and black bars representing elevated CO_2. (**a**) Average population size (±SEM; $n = 12$). (**b**) Average proportion of fecund females (±SEM; $n = 12$). Females with offspring within the brood pouch were considered fecund. (**c**) Average operational sex ratio (OSR, the ratio of fecund females to males) (±SEM; $n = 12$). Different letters represent statistically different ($P < 0.05$) means.

current climate are normally ephemeral and sparse[10]. While there is recognition that temperature and carbon dioxide can ramp up primary productivity[44], there has been less recognition of how this primary productivity may translate into an increase in secondary productivity. The lack of research that makes these connections between trophic levels has left some serious gaps in understanding for the stability of future food webs[12]. Here, we consider a critical mechanism that would allow for flexibility in mating strategy so individuals can adjust their reproductive investment[32] when the concomitant increase in metabolic demand and population size is not constrained by resources or predators.

Future climate provides conditions that relax the drivers of variance in male traits. Strong selection on male sexually selected traits such as the amphipod's gnathopod is affected by per capita resource availability[45], such that reduced availability causes stress that widens variance in gnathopod size[32]. Widened variation among male gnathopod size within a population leads to disproportional mate guarding and competition, which has been shown to affect reproductive success in related species[36]. Female choice often selects for male sexually-selected traits[46], and when females are less choosy, male trait variance decreases[47]. When females are less choosy, a higher

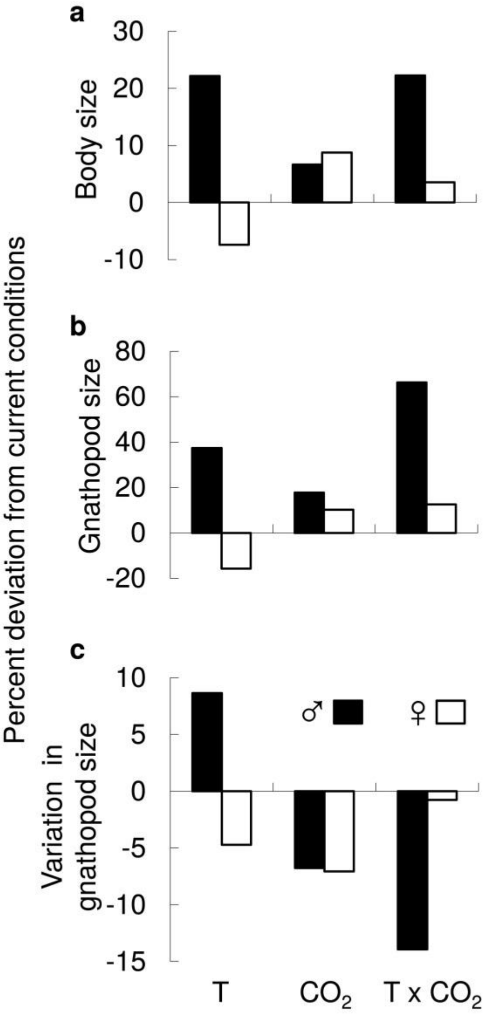

Figure 2. Selection on male and female traits under elevated temperature (T), carbon dioxide (CO_2), and a combination of elevated temperature and carbon dioxide (T × CO_2). Percent deviation from current conditions (control treatment) of (**a**) body size, (**b**) gnathopod size, and (**c**) variation in gnathopod size for males (black bars; $n = 647$) and females (white bars; $n = 415$). Deviation represents the treatment effect size (T, CO_2 and T × CO_2) relative to ambient; positive values represent an increase and negative values represent a decrease in average traits. Variation in gnathopod size is obtained by averaging the absolute value of studentized residuals from the gnathopod to body size regression.

Treatment	Intercept	Body (x)	Body^2 (x^2)
Ambient	0.318 (0.933)	0.745 (0.667)	5.554 (0.623)
Elevated Temperature	−0.942 (0.394)	**1.428 (0.006)**	**3.043 (0.036)**
Elevated CO_2	**−2.420 (0.017)**	**2.131 (<0.0001)**	0.931 (0.449)
CO_2 × Temperature	**−1.512 (0.022)**	**1.638 (<0.0001)**	**3.019 (0.009)**

Table 1. Polynomial regressions of the number of eggs produced per female against female body size for each of the four treatment conditions. Data were log-transformed before analysis. Numbers in parentheses are the *P*-values testing for similarities against an intercept = 0 or slope = 0.

proportion of females could become gravid[48]. Females are also likely to reach maturation more quickly under future climate, further boosting the effect of reduced choosiness on reproductive output. These results provide insight into short-term studies that demonstrate the ability of amphipods to quickly adapt to elevated CO_2[49] and temperature[50], and naturally occur in greater abundance at CO_2 seeps[12]. However, future studies should tease apart the effect of variation in male secondary characters driving fecundity under future climate conditions.

In conclusion, we suggest that intergenerational increases in population size might be facilitated by adjustments in reproductive success to favourable environmental conditions. For some consumers, therefore, future climate may not only increase individual growth and survival, but this added production ought to carry over to subsequent generations through increased reproductive success. Such population growth is normally buffered by mechanisms that govern reproductive success and its translation through survival to successive generations, but for many species we argue that the indirect effects of climate via resource provisioning and trophic control may reduce this buffering capacity. While the effects of future climate as a stressor has dominated research effort to date, we are only beginning to realise that it may also favour reproduction and population growth of some species which can also boom under these same conditions.

Methods

Cymadusa pemptos is a common Ampithoid herbivore in temperate kelp forests of South Australia with preferred feeding on benthic turfs (Heldt *unpub.*). Males have larger gnathopods than females and both sexes build and inhabit nests among subtidal algae, such as seagrass (0.6–0.8 m depth[51]) and kelp beds (3–5 m depth). *Cymadusa pemptos* reaches maturity in an estimated 4–6 weeks, and females produce between 10 and 19 eggs (Heldt *unpub.*), similar to other *Cymadusa* species where females can live for up to 4 weeks after releasing brood[52–54]. To test responses of herbivorous *C. pemptos* populations to future climate, we designed an experiment using mesocosms with a crossed design of elevated temperature and CO_2. We refer to future climate conditions as the combined effects of elevated temperature and elevated CO_2.

Flow-through mesocosm tanks (2,000 L, $n = 12$) were established at the South Australian Research and Development Institute, in West Beach, South Australia (34.9453 °S, 138.5038 °E) in September 2013. An incoming flow rate (4 L min^{-1}) of filtered natural seawater (salinity ~40 ppt) was used to maintain water quality, and all mesocosms experienced natural spring and summer daylight cycles for South Australia. Temperature and CO_2 were manipulated to reflect ambient conditions of the sites in which organisms were sourced (i.e., current temperature and atmospheric CO_2 concentrations[44]), and treatments of future climate were set using predictions in the 2007 IPCC report[55]. Each mesocosm was maintained as an independent replicate. Within each replicate mesocosm, individual heater/chiller units and independent adjustments to CO_2 input maintained target temperature and CO_2 conditions. Heater/chiller units (TC-60 Aquarium Chillers, TECO Refrigeration Technologies, Ravenna, Italy), CO_2 generated by gas mixers (Pegas 4000 MF, Columbus Instruments, Columbus Ohio USA), and water flow were independently manipulated for each mesocosm[56].

Each mesocosm was stocked with a local community of primary producers (five kelp holdfasts and fronds at 1.2 kg [*Ecklonia radiata*] and five seeded fibre-board tiles (10 cm × 10 cm) containing a mixed assemblage of filamentous algae[37]), herbivores (five sea urchins [*Heliocidaris erythrogramma*], fifteen marine gastropods [*Turbo undulatus*], and *Cymadusa pemptos* amphipods). Predators were also present, one crab (*Ozius truncatus*), three sharks (*Heterodontus portusjacksoni*[15], and one spiny lobster (*Jasus edwardsii*). To ensure that experimental densities reflected natural densities, we seeded mesocosms with kelp habitat harboring natural *C. pemptos* populations. To collect amphipods with kelp, each kelp was entirely enclosed with a plastic bag in the field with the holdfast removed intact, thus sealing in natural amphipod densities[57–59]. Amphipod abundances were homogenized across tanks as all kelp fronds were kept in holding tanks prior to placement in each of the mesocosms with an estimated 100 amphipods and OSR of 6:1. The multi-trophic level mesocosms lasted multiple generations of amphipods. Use of vertebrates in these experiments, described in previously published work[15], were approved by the University of Adelaide animal ethics committee (permit: S-2013-095) and in accordance to the University's animal ethics guidelines. Shark collections were carried out with permission of the South Australian Government Department of Primary Industry and Regions SA (permit: 990295).

Temperature and pH were measured at different times of the day every day for each tank[56]; this sampling revealed that noon measurements were representative of the environmental conditions of the tank for that day. Total alkalinity (T_A) was measured weekly for each tank and used for pCO_2 calculations. Temperature and pH differed between ambient and elevated conditions and followed natural daily fluctuations throughout the entire experiment[56]. The average temperature and pH for current conditions (C; ambient temperature and CO_2) were 15.4 °C ± 0.1 SE and 8.16 ± 0.01 SE respectively. In contrast, future conditions (T × CO_2; elevated temperature and CO_2) had a temperature of 17.9 °C ± 0.3 SE and pH 7.99 ± <0.01 SE. The elevated temperature treatment (T, elevated temperature and ambient CO_2), had a temperature of 18.1 °C ± 0.2 SE and pH 8.15 ± 0.01 SE. Finally, in the elevated CO_2 treatment (CO_2; ambient temperature and elevated CO_2) the average temperature was 15.4 °C ± 0.1 SE and the average pH was 8.01 ± 0.01 SE. For all treatments, pH was calculated from back-transformed hydrogen ion concentrations. Total alkalinity was measured using a potentiometric titrator (888 Titrando, Metrohom, USA) and pCO_2 was determined using CO_2SYS program for Excel[56,60]. Average alkalinity and pCO_2 measures differed among C ($T_A = 2563\,\mu mol\ kg^{-1} \pm 3$, $pCO_2 = 381\,\mu atm \pm 38$), T ($T_A = 2562\,\mu mol\ kg^{-1} \pm 10$, $pCO_2 = 427\,\mu atm \pm 42$), CO_2 ($T_A = 2555\,\mu mol\ kg^{-1} \pm 5$, $pCO_2 = 607\,\mu atm \pm 52$) and T × CO_2 ($T_A = 2547\,\mu mol\ kg^{-1} \pm 2$, $pCO_2 = 663\,\mu atm \pm 80$) treatments.

In December 2013, 13 weeks after stocking mesocosms, kelp fronds from each mesocosm were removed, dipped into freshwater, and gently wiped; this allowed us to collect amphipods that had undergone 2–3 generations in experimental conditions. The freshwater containing amphipods was filtered through a 0.5 mm mesh and amphipods were preserved in 100% ethanol. All adults were accounted for and photographed; juveniles were subsampled by stirring and removing 10% of the solution and collected individuals were separated for photographic analysis. Photographs were taken using a Canon G10 camera fitted with a high definition 10x macro lens, and body size (mm length) for all individuals and gnathopod size (i.e. the second appendage, mm length from the tip of the dactyl to the base of the propod when the chelae were closed) for adults were measured using ImageJ[61].

We first analysed population-level responses to elevated temperature and elevated CO_2 treatments. Amphipod population size was compared among treatments using a generalized linear model with a normal error distribution and two levels of CO_2 and temperature treatments (i.e. ambient and elevated). The proportion of fecund females and operational sex ratio (OSR) were compared among treatments using two-way ANOVAs. The proportion of fecund females was arcsin transformed, and OSR was calculated as the number of fecund females relative to the number of males in a given population and log transformed.

Next, we analysed individual-level responses to the experimental treatments. Body size, gnathopod size, and the number of eggs per female were log transformed. Changes in body size between treatments were tested for each sex using a two-way ANOVA. Differences in gnathopod size were compared using a two-way ANOVA with body size as a covariate. Significant 3-way interactions between the two treatments and the covariate were further analysed for each level of temperature treatment (i.e. current and elevated) using an ANCOVA with CO_2 as a fixed effect and body size as a covariate. To explore population-level variation in gnathopod size between treatments, we obtained studentized residuals from a gnathopod to body size regression of each treatment and sex and used the absolute value of studentized residuals to calculate mean residual variation (i.e., reflecting variation in gnathopod size independent of body size). Variation in gnathopod size was square root transformed, and a two-way ANOVA tested for treatment effects. To represent changes under future climate relative to current conditions, we calculated the difference between future and current condition means (e.g., either body size, gnathopod size and gnathopod variation) standardized by the current mean. Finally, the number of eggs produced by females was compared across treatments with a two-way ANOVA using female body size as a covariate. Relationships between body size and egg production were non-linear, and to further analyse relationships, we regressed the number of eggs per female against female body size for each of the treatment using second-order polynomial regressions with log-transformed data. We ensured data met parametric assumptions and set alpha = 0.05; analyses were carried out in JMP (SAS Institute, Cary, NC).

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Author Contributions

P.M. conceived the project. S.D.C. and B.D.R. coordinated and conceived the mesocosm program. K.A. and K.A.H. collected data. K.A.H. and P.M. analyzed the data.

Additional Information

Supplementary information accompanies this paper at http://www.nature.com/srep

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4.2 Supplementary Materials

Figure S1

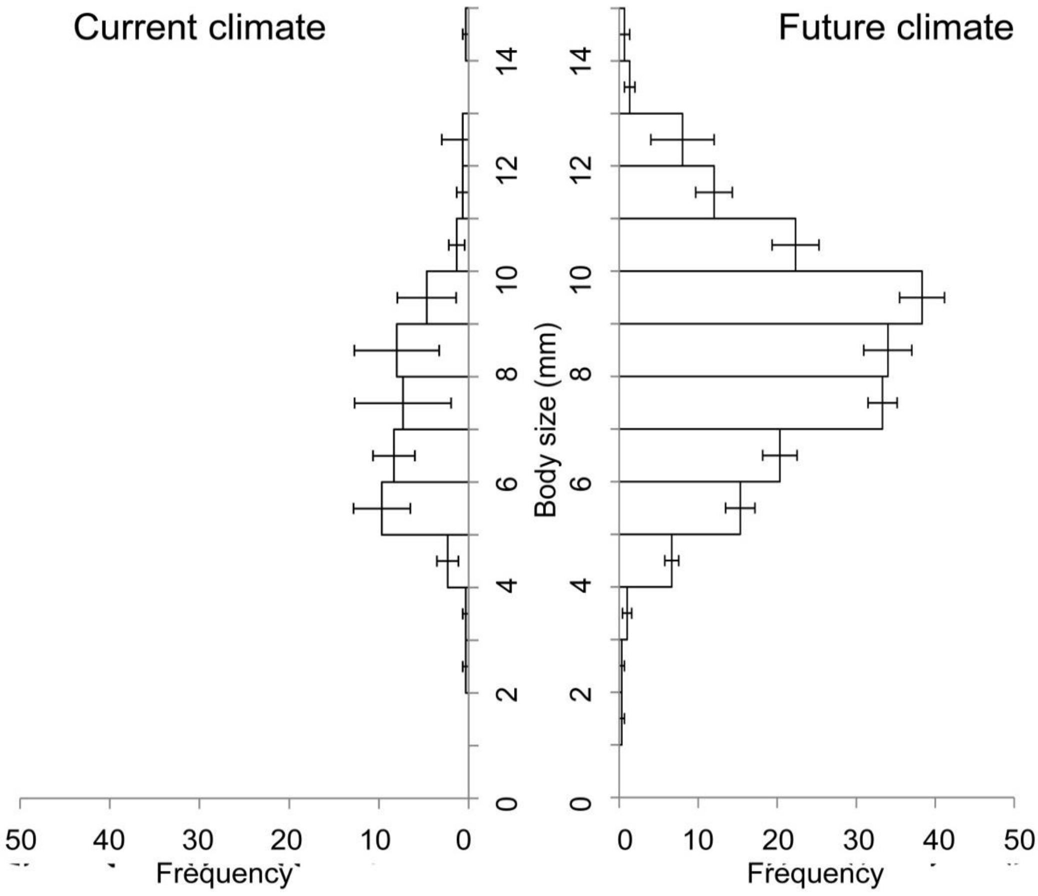

Figure S1 Body size (mm length) frequency distributions of *C. pemptos* populations under current (left panel) and future climate conditions (right panel) (Means ± SEM for each size class). Average body size in current climate conditions was 7.5 ± 0.3 and in future climate conditions was 8.5 ± 0.1.

Figure S2

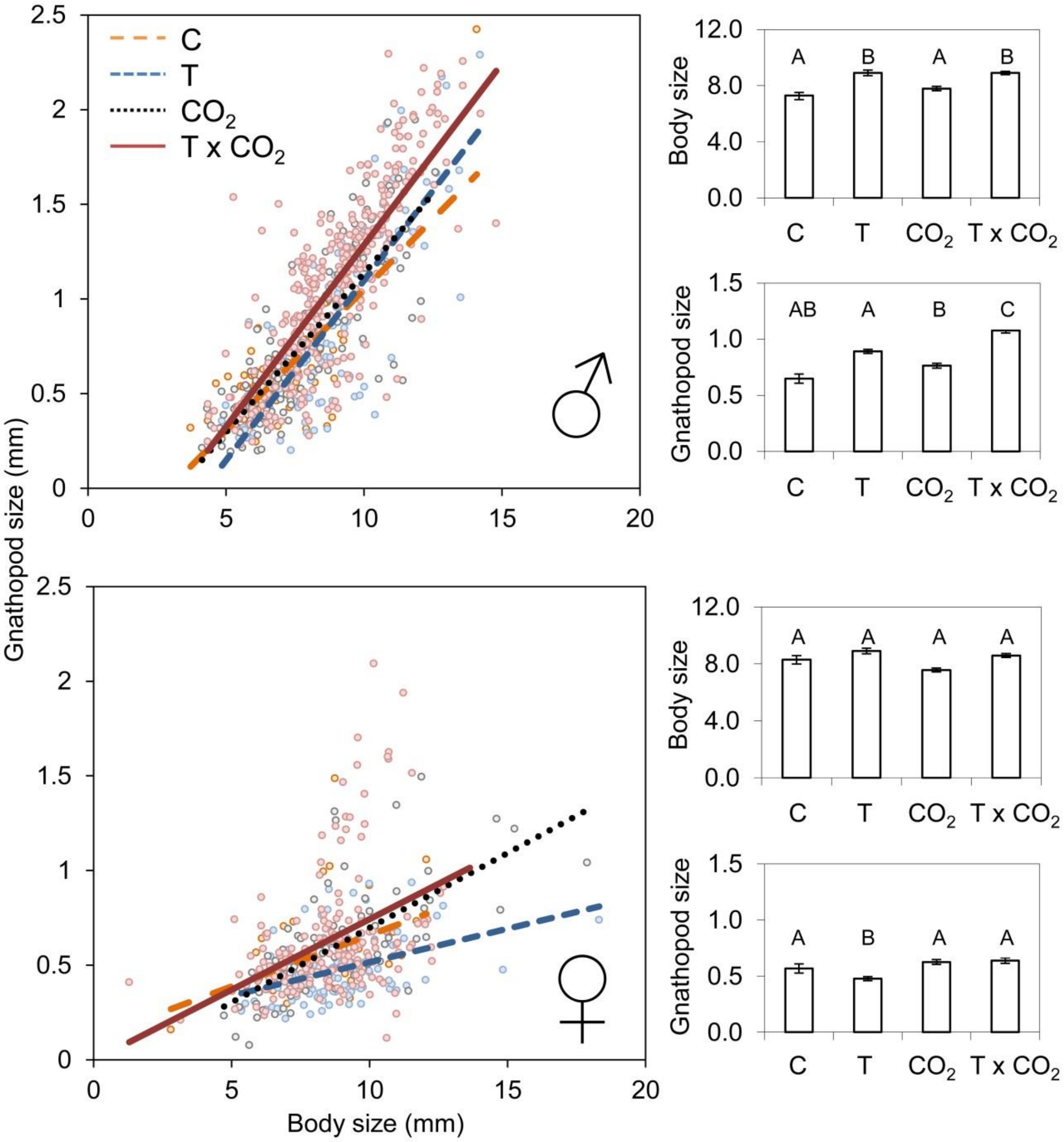

Figure S2 Gnathopod size to body size (mm length) regressions and average body and gnathopod sizes under ambient temperature and CO_2 (C; orange line, long dashes), elevated temperature (T; blue line, short dashes), elevated CO_2 (CO_2; black line, dotted), and elevated temperature and CO_2 (T x CO_2; red line, solid) conditions. Different letters represent statistically different ($P < 0.05$) means. ***Top*** Males, ***bottom*** Females.

Figure S3

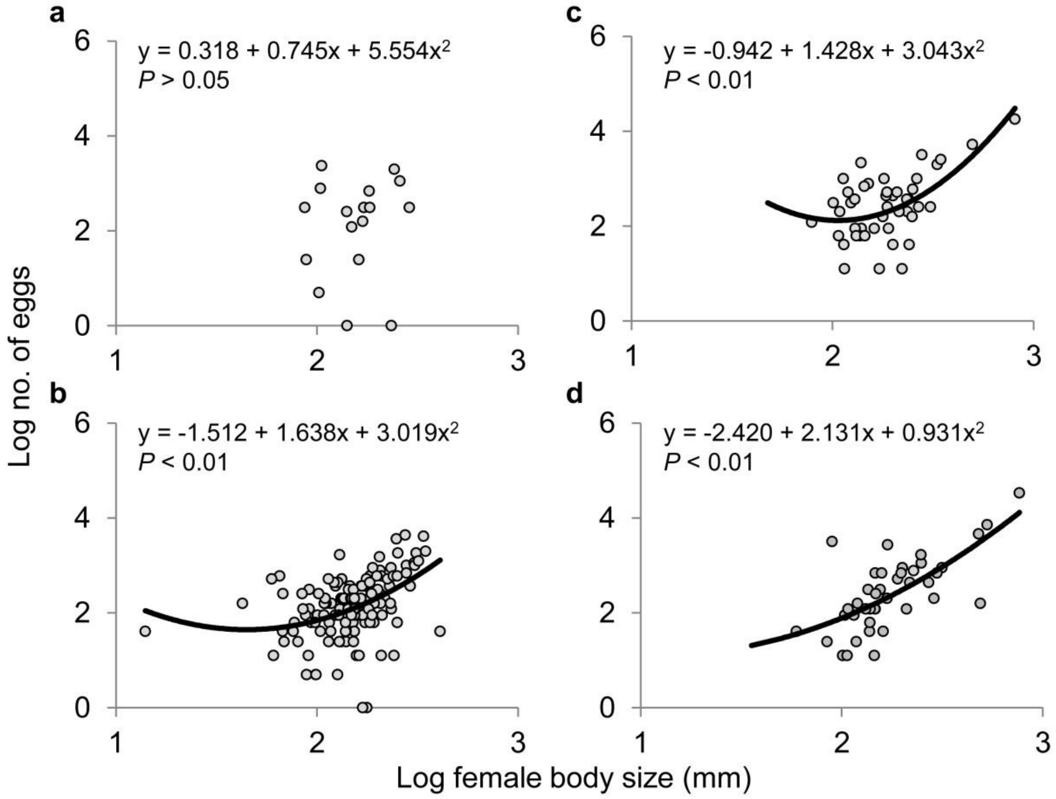

Figure S3 Polynomial regressions of the number of eggs produced per female to female body size (mm length) under a) current climate (ambient temperature and ambient CO_2), b) future climate (elevated temperature and elevated CO_2), c) elevated temperature and ambient CO_2, and d) ambient temperature and elevated CO_2. Note the log scale on the x and y-axis.

Figure S4

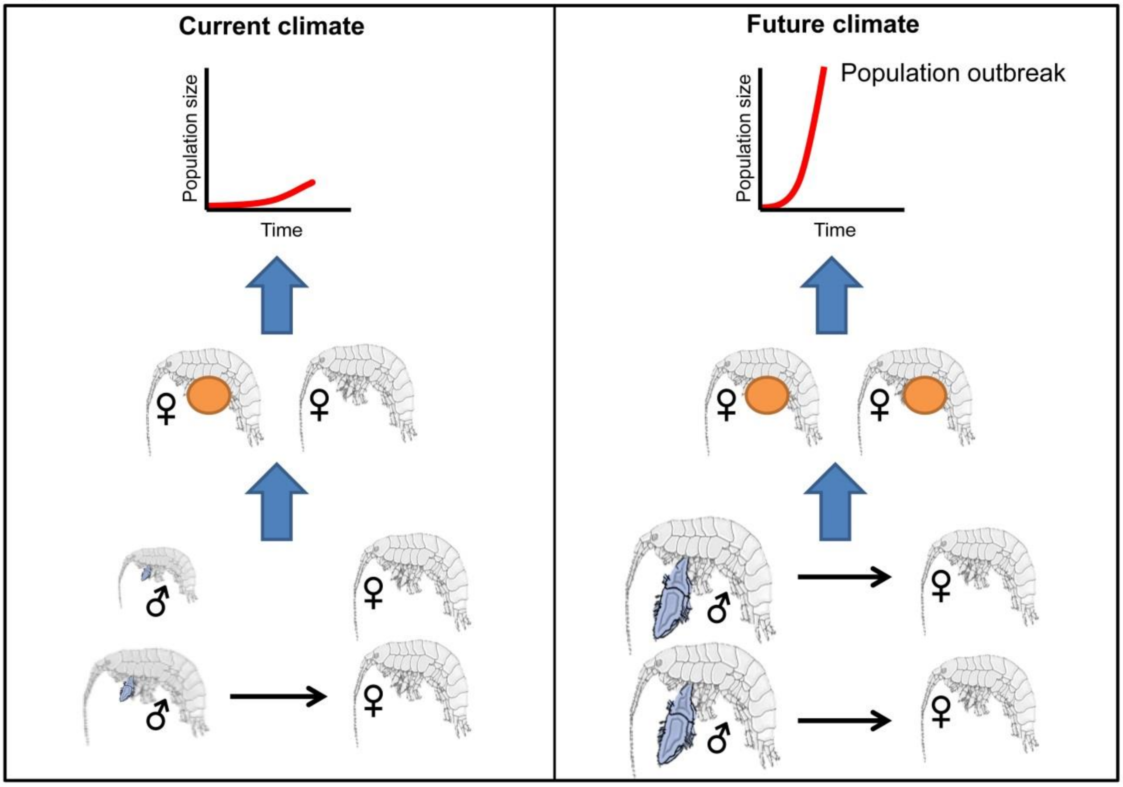

Figure S4 Population outbreaks of *Cymadusa pemptos* under current and future climates. Relative to current climate, the proportion of gravid females doubled and variance in phenotypic variation of male secondary sexual characters (i.e. gnathopods; highlighted in blue) was significantly reduced under future climate. Black arrows represent mating success with fecund females brooding eggs (orange circles). Amphipod image modified from Peart 2007.

Table S1. Results from a generalized linear model testing the effect of CO_2 and temperature on population size, and a two-way ANOVA testing these treatments on the proportion of fecund females and operational sex ratio (OSR).

	Population Size			Proportion Fecund			OSR		
Full Model	**df**	**X^2**	**p-value***	**df**	**F-value**	**p-value***	**df**	**F-value**	**p-value***
	3,7	8.22	**0.0415**	3, 7	4.63	**0.0435**	3, 6	1.48	0.3118
Main Effects		X^2	p-value*		F-value	p-value*		F-value	p-value*
CO_2 (C)		**5.19**	**0.0228**		2.55	0.1543		0.07	0.7977
Temp (T)		0.81	0.3680		**9.15**	**0.0192**		3.19	0.1245
C x T		0.03	0.8669		1.24	0.3025		0.85	0.3932

*significant effects and interactions, *P*<0.05, are in bold

Table S2. Two-way ANOVAs testing the effect of CO_2 and temperature on male and female body size (mm length).

	Male Body Size			Female Body Size		
Full Model	**df**	**F-value**	**p-value***	**df**	**F-value**	**p-value***
	3, 643	23.14	**<0.0001**	3, 411	1.22	0.30
Main Effects		F-value	p-value*		F-value	p-value*
CO_2 (C)		1.95	0.1631		0.06	0.8117
Temp (T)		62.49	**<0.0001**		2.29	0.1313
C x T		1.74	0.1871		1.69	0.1937

*significant effects and interactions, *P*<0.05, are in bold

Table S3. Two-way ANOVAs testing the effect of CO_2 and temperature on male and female gnathopod size (mm length) using body size as a covariate. Because of a significant 3-way interaction, we then performed an ANCOVA for each temperature treatment testing differences between CO_2 treatments with body size as a covariate. P-values <0.05 are in bold.

	Male Gnathopod Size			Female Gnathopod Size		
Full Model	**df**	**F-value**	**p-value***	**df**	**F-value**	**p-value***
	7, 639	180.60	**<0.0001**	7, 407	25.29	**<0.0001**
Main Effects		F-value	p-value*		F-value	p-value*
CO_2 (C)		26.04	**<0.0001**		10.21	**0.0015**
Temp (T)		3.02	0.0829		2.54	0.1116
C x T		5.04	**0.0251**		11.97	**0.0007**
Log Body (B)		697.80	**<0.0001**		122.70	**<0.0001**
C x B		1.85	0.1742		1.93	0.3343
T x B		4.63	**0.0319**		2.10	**0.0215**
C x T x B		7.83	**0.0053**		0.61	0.0966

ANCOVAs for each temperature treatment.

Ambient temperature	Male Gnathopod Size			Female Gnathopod Size		
Full Model	**df**	**F-value**	**p-value***	**df**	**F-value**	**p-value***
	3, 204	119.99	**<0.0001**	3,122	34.38	**<0.0001**
Main Effects		F-value	p-value*		F-value	p-value*
CO_2 (C)		0.59	0.4426		0.08	0.78
Log Body (B)		242.94	**<0.0001**		70.77	**<0.0001**
C x B		7.13	**0.0082**		3.09	0.08
Elevated temperature	Male Gnathopod Size			Female Gnathopod Size		
Full Model	**df**	**F-value**	**p-value***	**df**	**F-value**	**p-value***
	3, 435	241.52	**<0.0001**	3,285	26.96	**<0.0001**
Main Effects		F-value	p-value*		F-value	p-value*
CO_2 (C)		42.45	**<0.0001**		35.45	**<0.0001**
Log Body (B)		544.50	**<0.0001**		40.69	**<0.0001**
C x B		1.38	0.2410		0.31	0.58

*significant effects and interactions, $P<0.05$, are in bold

Table S4. Two-way ANOVAs testing the effect of CO2 and temperature on variance in male and female gnathopod size (mm length).

	Male Gnathopod Variance			Female Gnathopod Variance		
Full Model	**df**	**F-value**	**p-value***	**df**	**F-value**	**p-value***
	3, 643	3.08	**0.0269**	3, 408	0.41	0.7447
Main Effects		F-value	p-value*		F-value	p-value*
CO_2 (C)		26.04	**0.0225**		0.97	0.3262
Temp (T)		3.02	0.2467		0.07	0.7873
C x T		5.04	0.8246		0.24	0.6268

*significant effects and interactions, $P<0.05$, are in bold

Table S5. Two-way ANOVA testing the effect of CO_2 and temperature on the number of eggs per female using body size as a covariate.

	Number of Eggs		
Full Model	**df**	**F-value**	**p-value***
	7, 232	8.72	**<0.0001**
Main Effects		F-value	p-value*
CO_2 (C)		0.24	0.6222
Temp (T)		0.06	0.8035
C x T		1.71	0.1925
Log Body (B)		**21.23**	**<0.0001**
C x B		0.08	0.7771
T x B		0.09	0.7588
C x T x B		**5.08**	**0.0251**

*significant effects and interactions, *P*<0.05, are in bold

Chapter 5

Chapter Image: *Cymadusa pemptos* within nests.

Photo credit: Katherine A. Heldt

Statement of Authorship

Title of Paper	Increasing use of human dominated habitats as CO_2 emissions warm and acidify oceans
Publication Status	☐ Published ☐ Accepted for Publication ☑ Submitted for Publication ☐ Unpublished and Unsubmitted work written in manuscript style
Publication Details	Currently under review in Estuaries and Coasts

Principal Author

Name of Principal Author (Candidate)	Katherine A. Heldt		
Contribution to the Paper	Led the conception and design of the project. Conducted the study, collected, and analyzed the data and drafted and revised the manuscript.		
Overall percentage (%)	85		
Certification	This paper reports on original research I conducted during the period of my Higher Degree by Research candidature and is not subject to any obligations or contractual agreements with a third party that would constrain its inclusion in this thesis. I am the primary author of this paper.		
Signature		Date	05/03/2017

Co-Author Contributions

By signing the Statement of Authorship, each author certifies that:

- i. the candidate's stated contribution to the publication is accurate (as detailed above);
- ii. permission is granted for the candidate in include the publication in the thesis; and
- iii. the sum of all co-author contributions is equal to 100% less the candidate's stated contribution.

Name of Co-Author	Sean D. Connell		
Contribution to the Paper	Contributed to the conception and design of the project and provided suggestions, comments and feedback on the manuscript. Provided funding.		
Signature		Date	05/03/2017

Name of Co-Author	Pablo Munguia		
Contribution to the Paper	Contributed to the conception and design of the project and provided suggestions, comments and feedback on the manuscript.		
Signature		Date	05/03/2017

Chapter 5

Increasing use of human dominated habitats as CO_2 emissions warm and acidify oceans

5.1 Abstract

Urban and artificial structures are increasingly added to the world's coasts during a time, in which changing climate is forecast to drive shifts in naturally occurring habitats. We ask whether the role of artificial structures as marine habitats will increase in importance relative to their natural counterparts, particularly as natural habitats are negatively affected by ocean warming and acidification. To evaluate this model, we contrasted use of natural (kelp forest and turfing algae) and artificial habitat (plastic pier-piling) by a nest-building amphipod (*Cymadusa pemptos*) under current and future climate conditions of CO_2 and temperature. Under future conditions, amphipod populations in mesocosms increased, but this did not lead to greater proportional colonization of kelp and turf. Instead, colonization doubled in artificial habitats, and there was increasing production and occupation of nests on artificial habitats relative to natural habitats. In an age when human modification of natural substrata is increasingly cited as an agent of wildlife decline, understanding the future role of artificial habitats as replacement dwellings for natural habitats is critical. We provide an understanding of the future role of natural and artificial habitats, identifying the possibility that use of urban structures as marine habitats may increase.

5.2 Introduction

In a world of increasing human population growth and urbanization where shifts in natural habitats are induced by rapidly changing environmental conditions, urban and artificial structures have the potential to provide refuge for displaced species. Global alteration of ocean ecosystem functioning, due to increasing human CO_2 emissions favors shifts towards novel communities (Nagelkerken and Connell 2015), but almost no investigations have considered how these future changes will affect human dominated habitats. Furthermore, it is unknown as to whether use of urban structures as habitat will strengthen or diminish under changing abiotic conditions that drive loss of natural habitats.

In marine environments, coastal urban structures provide novel habitats for a diverse array of organisms (Glasby and Connell 1999). Assemblages on urban structures (e.g. marinas, jetties, seawalls, and oil rigs) are distinct from surrounding natural habitats (Connell and Glasby 1999; Dafforn et al. 2009; Dafforn et al. 2015). Artificial structures support fewer rare species (Chapman 2003), and the increasing presence of human dominated habitats promotes colonization of marine invaders (Mineur et al. 2012). Changing climate and transformations of natural environments (e.g. displacement of kelps by turfs, Connell et al. 2013) may increase use of urban structures, particularly for mobile species that relocate to less populated habitats (Norderhaug et al. 2002, Munguia 2004, Munguia 2014) or rapidly establish new environments (Valdivia et al. 2014). The possibility that change to natural habitats may combine with global change to increase use of urban structures as habitats has not been explored.

Urban structures may act as alternative habitats along coastlines for which natural environments are degraded by local human activity (e.g. local nutrient and sediment pollution), particularly under changing climate. Ocean warming and acidification drives change to the abundance of invertebrates (Sorte et al. 2010; Garrard et al. 2014) altering population growth and habitat use. Furthermore, concomitant shifts in the quality and availability of natural habitats (Scheffer et al. 2001; Brodie et al. 2014) that favor or hinder population growth (Flather et al. 2002) may affect whether urban structures are used as habitats. We propose that there is the potential for change in habitat use by invertebrates under future climate as a consequence of a reduction of preferred habitat and emergence of artificial structures.

If populations change as a function of future climate, changes to community structure are predicted as the abundances of species reorganize around available habitat (Sorte and Stachowicz 2011; Doney et al. 2012). Mobile marine amphipods are highly responsive to changing environmental conditions (Dick et al 1998; Hauton et al. 2009), where abundance increases drive a greater degree of nest building and change in the habitats they occupy (Brawley et al. 1981; Kitting et al. 1984; Duffy 1990). The ability of amphipods to disperse among algal habitats (Poore 2005) and to increasingly occupy urban structures by building nests on surfaces (Franz 1989; Greene et al. 2007) suggests that stasis in their relative abundance among environments is unlikely as natural habitat and climate changes. Indeed, these highly competitive taxa, whose plasticity to changing environmental conditions is renown (Hauton et al. 2009; Cothran and Jeyasingh 2010; Cothran et al. 2011), may rapidly adjust to novel environmental conditions as their populations grow (Heldt et al. 2016).

In this study, we evaluate whether the role of artificial structures as habitats might increase under future climate predictions. Specifically, we determined effects of future climate on population density and examined the importance of artificial habitats relative to natural habitats for a nest-building amphipod. Amphipods are competitive colonizers; females brood offspring and give birth to fully-developed juveniles that can immediately build nests and consume algae (Borowsky 1983; Dixon and Moore 1997). This life history trait allowed us to test whether shifts in nest production (i.e. number of nests built per capita) and occupation (i.e. number of amphipods per nest) drives colonization from natural to artificial habitats under ocean warming and acidification. Our experimental approach quantified relative habitat use proportional to habitat availability in response to climate change.

5.3 Materials and methods

We tested whether habitat use shifts from natural to artificial habitats under ocean warming and acidification by observing colonization rates of a marine amphipod, *Cymadusa pemptos*, which is a nest building Ampithoid species common to southern Australia. *C. pemptos* primarily builds nests on available substrate surfaces, similar to other species of Ampithoids (Skutch 1926; Appadoo and Myers 2003). To test use of artificial habitats by *C. pemptos*, we used unnatural materials (e.g. smooth, rigid vertically suspended plastic surfaces) that are commonly used to construct urban structures (Bulleri and Chapman 2010). We focused on this temperate species because their environments are predicted to undergo shifts in habitats from productive kelp canopies (*Ecklonia radiata*) to turf-forming algae (mixed turf assemblages; Connell et al. 2014) under future climate (Gorman and Connell 2009).

5.3.1 Acclimation tanks

We established amphipod populations under treatments of current and future climate in acclimation tanks consisting of kelp canopies and turf, two natural habitats present along the rocky coasts of temperate Australia. Amphipods were placed into tank mesocosms (2,000 L; diameter = 1.7 m; height = 1.4 m) and allowed to pass through multiple generations (i.e. approximately 3 generations) before their abundances were quantified on kelp (*n* = 5 kelp plants, 1.2kg/tank). To ensure that experimental densities (100 amphipods/tank) reflected natural densities, we seeded mesocosms with kelp habitat harboring natural *C. pemptos* populations (Heldt et al. 2016). To establish turf habitat, seeded fiber-board tiles were placed on the bottom of tanks (n = 5 tiles of 10 cm × 10 cm/tank). The design, operation and water chemistry of the acclimation tanks are described in detail by Falkenberg et al. (2016) for which we elevated temperature by 2.5^{o}C and pCO_2 by 250 ppm to be within forecasted conditions (IPCC 2007). In summary, a total of six independently maintained tanks were randomly assigned climate treatments (*n* = 3 tanks ambient temperature, ~15˚C, and ambient CO_2, pCO_2 ~400 ppm and ~8.15 pH units, and *n* = 3 tanks elevated temperature, ambient + 2.5˚C, and elevated CO_2, ambient pCO_2 + 250 ppm and ambient - 0.15 pH units). Every day for each tank, we measured temperature and pH at different times of the day (Falkenberg et al. 2016), and noon measurements were representative of environmental conditions of the tank for that day. In addition, we calculated pCO_2 of each tank using weekly measurements of total alkalinity (T_A).

Climate treatments achieved target environmental conditions of current (ambient temperature and CO_2) and future climate (elevated temperature and CO_2). Water chemistry differed between current and future climate tanks (Falkenberg et al. 2016).

Current climate tanks had an average temperature and pH of 15.4 ˚C ± 0.1 SE and 8.16 ± 0.01 SE respectively. In contrast, future climate tanks had an average temperature of 17.9 ˚C ± 0.3 SE and pH 7.99 ± <0.01 SE. Average $p\text{CO}_2$ measures differed between current climate tanks (381 µatm ± 38 SE) and future climate tanks (663 µatm ± 80 SE), and tanks had an average alkalinity of 2,563 µmol kg^{-1} ± 3 SE in current climate and 2,547 µmol kg^{-1} ± 2 SE in future climate.

5.3.2 Colonization experiments

To test for shifts in colonization between natural and artificial habitat, we experimentally quantified the rate of nest building and occupancy among kelp (i.e. rough, flexible algae), turf (i.e. soft, filamentous algae), and plastic surfaces (i.e. smooth, rigid BPA-free plastic suspended vertically) in current and future climate conditions. Three habitats (kelp fronds, turfs, and plastic wall) of standard area (18 × 4 cm) were placed within each 160 mL transparent cylindrical container (i.e. n = 18 microcosms; 3 microcosms per 2,000 L tank × 6 tanks). Habitats recovered in flowing seawater for several hours (Poore and Steinberg 1999) prior to the addition of amphipods, which were collected from kelp fronds. Kelp, turf, and amphipods experienced at least 11 weeks of treatment conditions (i.e. current or future climate) prior to placement in microcosms and were collected from within the tank in which the microcosm was suspended. We stocked microcosms with amphipod abundances that were proportional to densities of their assigned acclimation tank, reflecting expected amphipod densities under current and future climate. Microcosms were sealed (0.5mm mesh, 9 cm diameter) and submerged (0.25 m depth) to allow exchange of water, but prevent amphipods and habitats from exiting microcosms. After three days, microcosms were removed from tanks and water was quickly poured across the seal.

Amphipods in nests were not disturbed by immediate removal of water and remained within their nest (KAH personal observation). Finally, the seal was removed, and using tweezers, nests and residents within nests were removed from each habitat and counted. To obtain a representative sample size, we repeated the experiment, completing three trials over three consecutive weeks (total N = 54 microcosms).

5.3.3 Data analysis

First, to test the effect of future climate on tank population density by ANOVA, data were log-transformed. Second, nest production (i.e. number of nests built per capita) and occupation (i.e. number of amphipods per nest) of amphipods was quantified among the three habitats after sufficient time for dispersal and nest building within microcosms (i.e. 3 days; Munguia et al. 2007; Munguia 2015). To illustrate climate driven differences in nest production (i.e. number of nests built per capita) and occupation (i.e. number of amphipods per nest), we subtracted mean responses under current climate from future climate and calculated standard error from pooled effect sizes. Ultimately, nest building and occupation will lead to colonization and population establishment in a given habitat area. Proportional colonization was estimated as the number of amphipods within nests, within each habitat, relative to the total number of nests across all three habitats per unit area; such that, for each treatment, the sum of proportional colonization per cm^2 in kelp, turf and artificial habitats is equal to one if all amphipods colonized. Proportional colonization data were square root transformed to meet parametric assumptions and analyzed using a linear mixed model with climate, habitat type, and the interaction of climate and habitat type as fixed factors and trial and tank as random factors. Analysis of proportional colonization was further split by habitat type to understand the effect of climate for each habitat. This resulted in a linear mixed model with climate as a fixed factor and trial and tank as random factors. These models tested for effects of habitat and climate by analyzing the variance not explained by population size reflected in each tank. Analyses were done using JMP (v10, SAS Institute, Cary, NC).

5.4 Results

Future climate conditions caused populations to more than triple in density (m^{-2}) within mesocosms ($F_{1,4}$ = 12.57, P = 0.02), and nest production and occupancy in each of the three habitats shifted under future climate (Fig.1). There was a strong positive effect of future climate conditions on per capita nest building and the number of amphipods occupying each nest on artificial surfaces (Fig. 1). In contrast, there was a negative effect of future climate on per capita nest production and occupancy per nest on turfs, while per capita nest building decreased on kelp despite increased occupation per nest under future climate (Fig. 1). As a consequence of shifts in nest production and occupancy, proportional colonization differed among habitat type and climate treatments (Fig. 2). Colonization of artificial habitats under future climate conditions was at least 3 times greater, yet was unchanged on kelps and turfs (Fig. 2; Table 1).

5.5 Discussion

Research into future climate tends to focus on ocean change as a stressor, yet for some species, the environmental conditions of future climate can favour population growth. By relaxing constraints on population growth, some populations may even boom, transferring reproductive success to successive generations (Cappuccino et al. 1995; Heldt et al. 2016). Such generational increases in population size may be accelerated by favorable environmental conditions and the ability to exploit novel environments. We observed that ocean warming and acidification drives population growth of amphipods; a group that is well known for their traits of rapid development, relatively short generation times and active recruitment and colonization (Franz 1989; Sainte-Marie 1991; Munguia et al. 2007). Indeed, future population growth was experimentally associated with greater colonization of artificial habitats relative to natural habitats, suggesting greater use of urban structures under ocean change.

Construction of urban structures tends to be concentrated around relatively sheltered harbors; the same localities in which land derived pollution drives replacement of kelp forests by low-lying turfs (Gorman and Connell 2009). The probability of displacement of kelp forests by turf-forming algae only increases with ocean warming and acidification (Connell and Russell 2010; Connell et al. 2013), particularly when combined with local pollution (Russell et al. 2009; Falkenberg et al. 2013). This directional shift in which expanding turfs displace kelp forests whilst novel habitats increase in the form of urban structures represents substantial habitat change for amphipods. We demonstrate that such expansion of turfs would only exacerbate amphipod crowding because they dwell in turfs less under future conditions. Consequently, amphipods appear to increasingly use urban structures as nest production and occupancy escalates, suggesting that they will become more reliant on urban structures as populations grow and kelp habitat either remains static or declines. Such condition-dependent dispersal to alternative habitats is common among mobile taxa, having notable effects on population dynamics (e.g. reproductive potential, Denno and Roderick 1992; mate competition, Munguia 2015), including our observation showing increased use of artificial habitats.

We hypothesize three potential mechanisms by which amphipods increasingly use artificial habitats under future climate. First, under future human expansion it is predicted that natural habitats will be increasingly lost (Connell and Russell 2010) and replaced by urban structures (Glasby and Connell 1999; Munguia et al. 2011). If natural nest-building habitats decline in abundance, amphipods may either seek alternative habitats or remain in limited habitats that reduce carrying capacity (Ronce 2007). Second, under future climate, amphipods experience large increases in abundance (Heldt et al. 2016), suggesting that carrying capacity has increased. Such population explosions can lead to overcrowding (Lloyd 1967) and colonization of alternative habitats (e.g., artificial structures). Finally, the need for alternative habitats may be facilitated by the predicted reduction of sensory ability making amphipods less choosy when colonizing habitats (Nagelkerken and Munday 2015). In which case, individuals may colonize habitats without preference, reflecting an increase of nests on artificial habitats that become increasingly available.

Our results highlight the potential for urban structures to have a strengthened role as marine habitats under future climate conditions. The observation that ocean warming and acidification drives an overall increase in population growth and colonization of artificial habitats suggests that future climate may well facilitate population expansion of many highly dispersive invertebrate species with flexible life histories. Urban structures may provide alternative habitats as natural environments are crowded and competition for space increases. Unlike natural habitats, the homogeneity of design and construction materials of urban structures provides opportunities for establishment of a few species that could potentially dominate urban coasts (Dafforn et al. 2015) and reduce species diversity relative to surrounding natural environments (Bulleri and Chapman 2010). We build a first step towards establishing the role of urban structures under future climate conditions, emphasizing that it is not only shifts in the availability of natural habitats that may drive changes in habitat use, but also the increasing reliance of taxa on artificial habitats. This more holistic approach to recognizing marine habitats may assist ecologists anticipate the future role of natural and urban habitats; identifying the possibility that the role of urban structures as marine habitats may only increase.

5.6 References

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5.7 Tables

Table 1 Analysis of proportional colonization from a linear mixed effects model where climate (C) and habitat type (H) were fixed factors and trial number and tank were random factors. Trial and tank effects accounted for 1.4% and 0% of the variance, respectively. Given the 2-way interaction between habitat type and climate, a second mixed model explored the effect of climate on nest occupancy for each habitat keeping trial and tank as random effects. Trial accounted for 6.3% of the variance for kelp, 0.5% for turf, and 0.0% for artificial habitats, while tank accounted for 18.9% of the variance for kelp, 13.9% for turf, and 10.2% for artificial habitats

Model for all habitats (kelp, turf, and artificial)			
Source	*df*	*F-ratio*	*p-value**
Climate (C)	1	1.20	0.24
Habitat (H)	2	11.50	**<0.01**
C x H	2	6.42	**<0.01**
Model for Kelp Habitat			
Climate (C)	1	0.09	0.78
Model for Turf Habitats			
Climate (C)	1	3.91	0.32
Model for Artificial Habitat			
Climate (C)	1	16.56	**0.03**

*significant effects and interactions are in bold $P < 0.05$

5.8 Figures

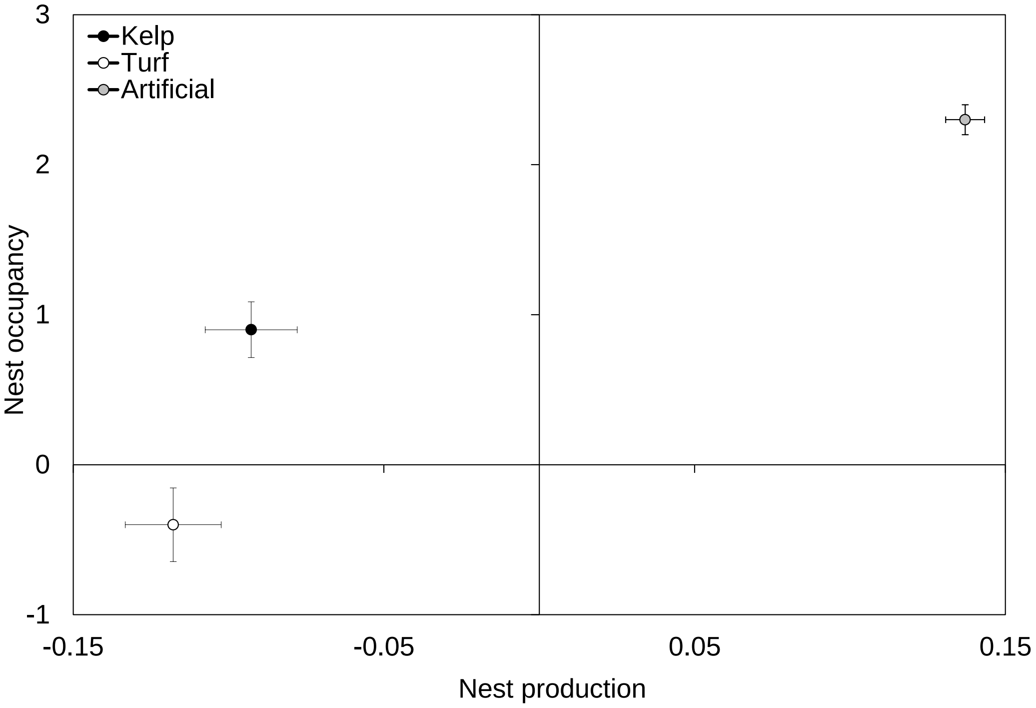

Fig. 1 The influence of future climate on increasing use of artificial structures via establishment leading to crowding. Nest production (i.e. number of nests built per capita) and occupancy (i.e. number of amphipods per nest) can lead to crowding and represents amphipod establishment. Kelp (black circle), turf (open circle), and artificial habitats (gray circle) ± SEM pooled effect size. Values represent the treatment effect size (i.e. future climate) relative to current climate; positive values represent increasing production and occupancy (e.g. artificial surfaces) and negative values represent declining production and occupancy (e.g. turfs)

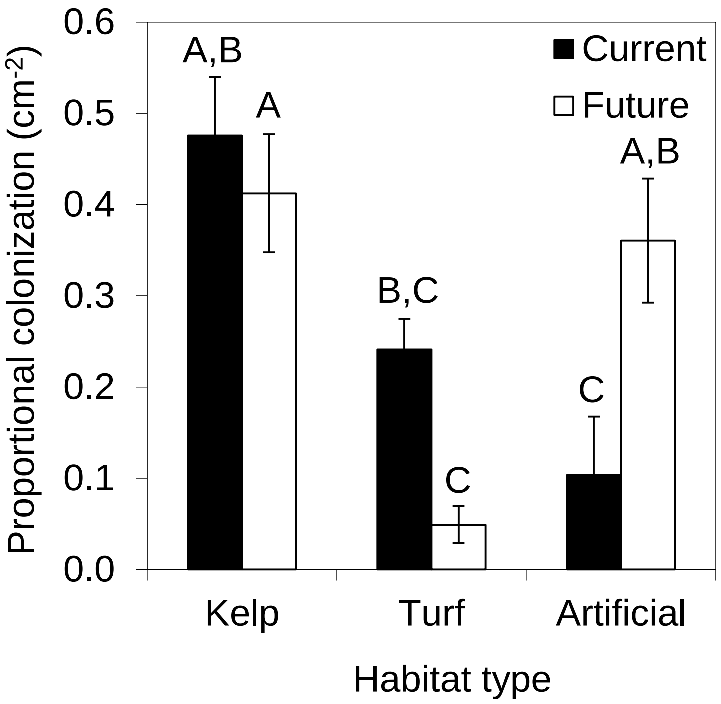

Fig. 2 Proportional habitat colonization under current and future climate. Amphipods within nests per cm^2 ± SEM under current (black bars; ambient temperature and CO_2) and future climate conditions (open bars; elevated temperature and CO_2). Different letters represent statistically different means ($P < 0.05$)

Chapter 6

Chapter Image: Sun setting over the Coobowie Marine Station, SA.

Photo credit: Katherine A. Heldt

Chapter 6

General discussion

Human modification of coastal habitats has become an increasingly important driver of population growth and community structure in marine systems (Dafforn *et al.* 2015; Nagelkerken & Connell 2015). By exposing spatially structured populations and communities to changing environmental conditions (e.g. habitat loss and future climate change), we can begin to understand how dispersal of juvenile and adult life-stages enable species' persistence. In this thesis, I evaluated population and community responses to habitat loss and future climate conditions in spatially structured systems, where decreases in the availability and condition of habitats are predicted to limit the flow of recruits from sources and lead to population extinction in sinks (Pulliam 1988). However, when mobile individuals offset source loss by dispersing to surrounding habitats, population persistence is possible (Boughton 1999).

Ultimately, the abundance and diversity of species emigrating from sources will alter assembly and species co-existence (Munguia 2004; Munguia 2014) in neighboring habitats. Chapter 2 of this thesis revealed that crustacean recruits from local source habitats drive community structure in neighboring habitats; in coastal seagrass beds, communities connected to a source had different assemblages than communities isolated from a source. Furthermore, recruits were distributed unequally across similar habitats, and neighboring sinks differed in α diversity, such that one community was species rich and the other was species poor. Overall, isolation increased β diversity of rich communities, and while a few species were equally abundant across sinks with juvenile recruits driving abundances, a majority of species had greater abundance in one sink over the other.

Changes in the quality and abundance of spatially structured habitats under future climate conditions (Connell & Russell 2010; Connell *et al.* 2013) alter the distribution and density of individuals (Harley *et al.* 2006). In South Australian temperate reefs, turf source habitats provide valuable food and nest-building resources, and amphipods (*Cymadusa pemptos*) inhabiting turf have larger body sizes, bigger eggs, and greater densities (Chapter 3). However, under combined elevated temperature and CO_2, greater consumption and reduced resource availability of turf was associated with a decrease in the quality of turf amphipods. In contrast, amphipods in kelp sink habitats increased in quality (e.g. larger body and egg size and higher fecundity) under future climate conditions. Chapter 3 demonstrated that original sinks can convert to sources when switches in the quality of habitats and individuals boost reproductive output and population growth. Intergenerational increases in population size were facilitated by adjustments in reproductive success to favourable environmental conditions (Chapter 4). As discussed in Chapter 4, decreased variation among male enhanced characters (e.g. body and claw size) reduced constraints on mechanisms of reproduction, and the proportion of fecund females doubled in kelp, leading to population outbreaks. Such intergenerational growth can spill-over to neighboring habitats, and the role of artificial structures as marine habitats may increase in importance relative to their natural counterparts, kelp and turf. Here, urban structures, which are increasingly built in coastal environments, provided amphipods with alternative settlement space, as shown by greater colonization of artificial habitats (Chapter 5). These results suggest that, by shifting recruitment and resource use, species with traits of rapid development, relatively short generation times, and active recruitment and colonization (Franz 1989; Sainte-Marie 1991; Munguia, Mackie & Levitan 2007) can flourish in oceans as they warm and acidify. Hence, a better understanding of species' traits that enable change in abundance and distribution across habitats is key in evaluating population growth and community assembly. Below, Chapter 6 provides further discussion on key findings from each data chapter and briefly addresses ecological importance and future research directions.

6.1 Asymmetrical Shifts in Sink Community Structure after Isolation

If we consider sinks to be homogenous, we may well underestimate the ability of species to persist in sinks after source habitats become lost or degraded. Recruits that link spatially structured habitats increase population growth and diversity of communities (Shmida & Wilson 1985). Source-sink theory posits that source populations are net exporters, sustaining population growth of sinks (Pulliam 1988) and new habitats, but differences in the identity and abundance of recruits alter abundances and community patterns (Chapter 2). Source recruits distribute unequally across similar habitats and establish different trajectories between neighboring communities (i.e. species rich and poor communities; Chapter 2), and isolation only increases β diversity of species rich communities (Chapter 2). This result suggests that communities connected to the same local source will have innate assemblage differences, and it is unlikely that co-occurring species will have similar responses to isolation. By understanding the natural history of a system (Osman *et al.* 2010) and increasing our understanding of how trait variation of dispersers alters ecological processes in heterogeneous habitats (Bolnick *et al.* 2011), community patterns may be more predictable through time.

6.2 Source-Sink Switches Enable Population Outbreaks under Future Climate

Indeed, species can prevail under changing environmental conditions, even when future climate conditions reduce the quality and availability of source habitats. As source habitats decline, dispersal to alternative, sink habitats can maintain population growth (Boughton 1999). Under future climate conditions, mobile amphipods alter resource and habitat use, and when an individual's metabolic and reproductive demands are met, populations boom (Chapter 3 and 4). Reproductive output increases as consumption of food resources enhances the quality of individuals (i.e. larger body size and fecundity) and as individuals gain access to mating resources (i.e. settlement space and nest-building materials). Here, reduced variation among male traits associated with greater female fecundity boosts population growth (Chapter 4), and high quality individuals that maintain population links and increase use of neighboring habitats switch sinks to sources.

6.3 Ecological Importance

Understanding how shifts in the spatial arrangement and connectivity of habitats influence a species' abundance and distribution is key in evaluating community assembly under habitat loss scenarios and future climate change (Holyoak & Heath 2016). Forecasts of future climate predict that environmental variability will increase (IPCC 2014), and such variation, when correlated with population shifts, has the potential to drive population outbreaks (Gonzalez & Holt 2002). Mechanisms that underpin source-sink theory consider the importance of natural, stochastic processes on the direction and flow of propagules (Gonzalez & Holt 2002). However, more in-situ experimental studies need to examine the impact of natural processes on variation among communities in heterogeneous habitats (Chapter 2).

By knowing a species' abundance and distribution across spatially structured habitats, we can better manage and conserve populations that can aid in repopulation of neighboring habitats (Breininger & Carter 2003). Preservation of heterogeneous habitats enhances population growth (Chapter 3), and conservation efforts are often focused on preserving pristine, source habitats. However, if we ignore conservation of neighboring habitats that are new or of lower quality, degradation and loss of heterogeneous habitats can drive species extinctions (Hanski 2011). While artificial habitats provide species with essential habitat as their natural counterparts decline (Chapter 5), homogeneity of urban structures should be minimized in order to diversify communities (Chapman & Blockley 2009).

Finally, in order to predict whether a species can adapt to future climate conditions, we must understand the reproductive mechanism(s) by which population growth occurs (Candolin & Heuschele 2008). Under future climate conditions, constraints on reproduction are relaxed and populations boom (Chapter 4). Greater availability of resources (Connell *et al.* 2013) and reduced predation (Pistevos *et al.* 2015) under elevated temperature and CO_2 can aid enhancement of male characters, and reduced variation among male traits has the potential to increase mating success and the proportion of fecund females (Chapter 4). This study highlights the ecological importance of examining how mating strategies can mediate population outbreaks while also considering that the state of each trophic level will ultimately play a role in intergenerational growth.

6.4 Future Research Directions

Immigration plays an important role in shaping communities, but the effects of external recruits on a species' distribution and abundance must be decoupled from demographic population growth (Ehrlén & Morris 2015). Population growth increases when dispersers survive and reproduce after immigration (Burgess *et al.* 2012), and measures of disperser' traits (e.g. age, life-stage, individual attributes), combined with genetic methods, can establish the degree to which immigrants increase population growth (Matter *et al.* 2009). Since the cost of dispersal varies among individuals (Benard & McCauley 2008; Hall *et al.* 2009), future studies, should use holistic approaches (e.g. measure recruit traits, demographic parameters, and genetic components) to evaluate mechanisms underlying population growth in spatially structured habitats (Peery *et al.* 2008; Lowe & Allendorf 2010).

Furthermore, holistic approaches should be used to determine which reproductive mechanisms underlie population growth under future climate (Candolin & Heuschele 2008; Cornwallis & Uller 2010). While decreased variation among male sexually selected characters is associated with greater female fecundity and population outbreaks (Chapter 4), it is important to tease apart the effect of variation in male secondary characters on female fecundity. Reproductive success is affected by the ability of males to compete and guard mates (Iribarne, Fernandez & Armstrong 1995) and by female choice (Cothran 2008), and when there is little variation among male traits and females are less choosy, a higher proportion of females can become fecund (Kvarnemo & Ahnesjo 1996). Further evaluation of mating strategies under current and future climate conditions should include male-male competition and mate choice tests, where the reproductive outcome is measured in heterogeneous habitats and from parental to F2 generations (Bussière *et al.* 2007).

Given that mobile crustaceans can live in high densities (e.g. greater than 10,000 tanaids m^{-2}, Delille *et al*. 1985 and 800,000 amphipods m^{-2}, Beermann & Purz 2013) and undergo population outbreaks, studies should further evaluate the extent to which these species groups (e.g. amphipods, isopods, and tanaids) can dominate urban structures (Greene & Grizzle 2007; Beermann 2014). Population outbreaks of amphipods may be a management concern because individuals can alter habitat assemblages on artificial habitats (Franz 1989) and because greater availability and use of urban structures under future climate conditions (Dafforn *et al.* 2015) may increase the opportunity for transfer across oceans in ballast waters or fouled boat hulls (Mineur *et al.* 2012). Here, it is important to track crustaceans in order to determine potential transport vectors and evaluate the potential for initial recruits to establish populations in new habitats.

Innovative tracking methods should be used to advance the number of empirical studies completed in the field. Tracking of smaller individuals (e.g. < 300 g) is challenging (Wikelski *et al.* 2007); however, novel tagging techniques, such as dietary fatty acid profiles (Bayes *et al.* 2014), can enable tracking of invertebrate movement between source-sink populations. If tagging is not possible, stable isotope analyses may provide an alternative method for determining dispersal patterns (Macneale, Peckarsky & Likens 2005; Williamson, Jones & Thorrold 2009). By using novel methods, there is increased potential for continuous tracking of populations across multiple generations in the field and for tracking of communities across a wider range of habitats.

6.5 Conclusion

This thesis first shows that the identity and abundance of local source recruits drives community structure in neighboring habitats. Isolation influences the abundance of co-occurring species, and communities exposed to the same source differ in α diversity. Yet few studies have examined whether such innate differences in richness can cause unequal changes in community structure after isolation. In order to mitigate the negative impacts of habitat loss on spatially structured communities, we must better understand the natural history of marine systems and have a better grasp on how the life-stage of dispersers influences a species' abundance and distribution. Second, this thesis provides insight into mechanisms that drive growth of spatially structured populations under future climate change. Shifts in the quality and abundance of habitats converts sinks to sources, but this shift is dependent on high quality individuals recruiting to sinks. Greater use of sink habitats coupled with high quality food from sources, relaxes constraints on reproduction and boosts population growth. Such population growth can lead to overcrowding of artificial habitats, and greater prevalence of urban structures along our coasts will only facilitate use of artificial habitats as natural habitats become degraded. At a time when habitat loss and future climate change are increasingly modifying coastal habitats, this thesis recognizes the importance of examining population growth and community assembly in association with habitat heterogeneity and furthers our understanding of how the identity and abundance of recruits can shift development of spatially structured populations and communities.

6.6 References

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