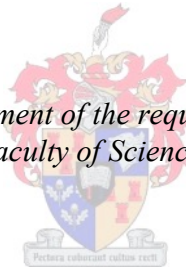


**Interactions between the invasive barnacle  
*Balanus glandula* and indigenous barnacles  
along the South African coast: the role of  
temperature and the implications of climate  
change**

by  
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*Thesis presented in fulfilment of the requirements for the degree of  
Master of Science in the Faculty of Science at Stellenbosch University*



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March 2015

## Declaration

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Haley R. Pope

Haley R. Pope

February 24, 2015

Date

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## ABSTRACT

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As marine invasions become increasingly prevalent, it is important to understand how climate change may moderate invasive species' spread and their interactions with native communities. *Balanus glandula*, an dominant intertidal barnacle, is one of few widely spread marine invasive species recognized along the South African coast. Since its introduction, *B. glandula* has become the dominant intertidal barnacle on the West Coast. Yet, as we understand little about the physiological tolerance of the invading population or how this species interacts with the native community, it is unclear whether this species will spread further along the coast and what impacts it may have. Therefore, I firstly determined the distribution and abundance of *B. glandula* in relation to native barnacle species in its current invaded range along the West Coast of South Africa. Abundances of *B. glandula* and native barnacles were monitored in the austral winter of 2012 and 2013 providing a first assessment of the species since it was recognized in 2007. Importantly, I found that *B. glandula* has spread around Cape Point, a well-known biogeographic break, and into False Bay. This suggests an ability to survive under the warmer conditions of the South Coast. Significant, yet non-systematic differences in the abundance of *B. glandula* among sites and years suggest fluctuations in recruitment intensity and variations in larval supply that typify barnacle populations. A decrease in the number of native barnacle species recorded along the West Coast may suggest that *B. glandula* is outcompeting native species. This chapter clearly illustrates the importance of long-term monitoring of marine invasive species.

In light of the movement of *B. glandula* onto the warmer South Coast and predicted climate warming in this region, I aimed to assess the impact of substratum temperature on the early life-history processes of *B. glandula* and the native barnacle, *Chthamalus dentatus*. From the results of my first chapter, there are concerns that this native species may have been displaced by *B. glandula* from the West Coast. Substratum temperature was manipulated using black, grey, white and clear PVC plates that were secured onto the substratum in the mid-shore. These were contrasted with bare rock at two sites on the West and South Coasts each. *B. glandula* recruited only on the West Coast and *C. dentatus* only on the South Coast. Although this prevented direct comparisons between species, their relative responses to substratum temperature were assessed. Unexpectedly, changing substratum temperature had no systematic effects on settlement, mortality, recruitment or growth of either species. While regional differences between the coasts must be acknowledged, the fact that settlement and recruitment of *B. glandula* were higher, mortality was lower and growth was greater on natural rock than that of *C. dentatus* is

notable. This suggests that a competitive advantage held by *B. glandula* may be more important in determining its future impacts on the South Coast than climate related changes in substratum temperature.

As intertidal organisms are affected not only by rock temperature during low tide, but also by water temperatures during high tide, I assessed the effect of water temperature on the relative food resource utilization and feeding behavior of *B. glandula* and the native, *Notomegabalanus algicola*. In order to simulate West and South Coast conditions, experiments were conducted at 13 and 20°C (the mean temperatures of the West and South Coasts, respectively) and at high ( $32 \times 10^6$  algal cells.ml<sup>-1</sup>) and low ( $1 \times 10^6$  algal cells.ml<sup>-1</sup>) food concentrations, representing the high and low primary productivity of the two coasts. Barnacles were allowed to feed for one hour after which remaining algal cells were quantified using flow cytometry. To assess feeding behavior, individuals of the two species were filmed and the percentage of feeding individuals, the time spent feeding, cirral beat rates and feeding types displayed were quantified. Under thermal and productivity profiles similar to both the West (i.e. 13°C and high productivity) and South Coasts (i.e. 20°C and low productivity), *B. glandula* demonstrated higher resource use than did *N. algicola*. Unexpectedly, *B. glandula* exhibited highest filtration under conditions representative of the South Coast. Temperature also affected the feeding behavior of both species. Under warmer South Coast conditions, *B. glandula* showed faster cirral beat rates than the native, yet no differences in the number of feeding barnacles or the time spent feeding were recorded. This result suggests that enhanced algal uptake by this species is likely a reflection of behavioral differences: more *B. glandula* barnacles fed and did so for longer with a faster beat rate under warmer temperatures than under cooler temperatures. These results suggest that (1) *B. glandula* displays heightened food resource utilization when compared to *N. algicola* regardless of water temperature or food concentration, (2) this likely reflects different feeding behaviors displayed by the two species, and (3) *B. glandula*'s feeding appears enhanced under warm conditions, assuming *B. glandula* can continue to meet its metabolic demands. Depending on the thermal tolerance of this species in terms of other physiological processes (e.g. reproduction), this barnacle may not be limited by warm South Coast conditions. Despite its temperate origin, future routine monitoring of this species will be vital in order to detect changes in its distributions and any impacts it may have on native species.

Overall, the findings from this study indicate that *B. glandula* has spread onto the South Coast and that warmer temperatures may not exert a direct regulating effect on the early life-history processes of *B. glandula*, but may illicit an increase in filtration and cirral beat rate, promoting higher resource utilization of *B. glandula* than native barnacles. It is thus predicted that neither regional temperature differences nor climate-induced changes in temperature are likely to represent a barrier for the further spread of this species.

## CHAPTER 1

### General Introduction

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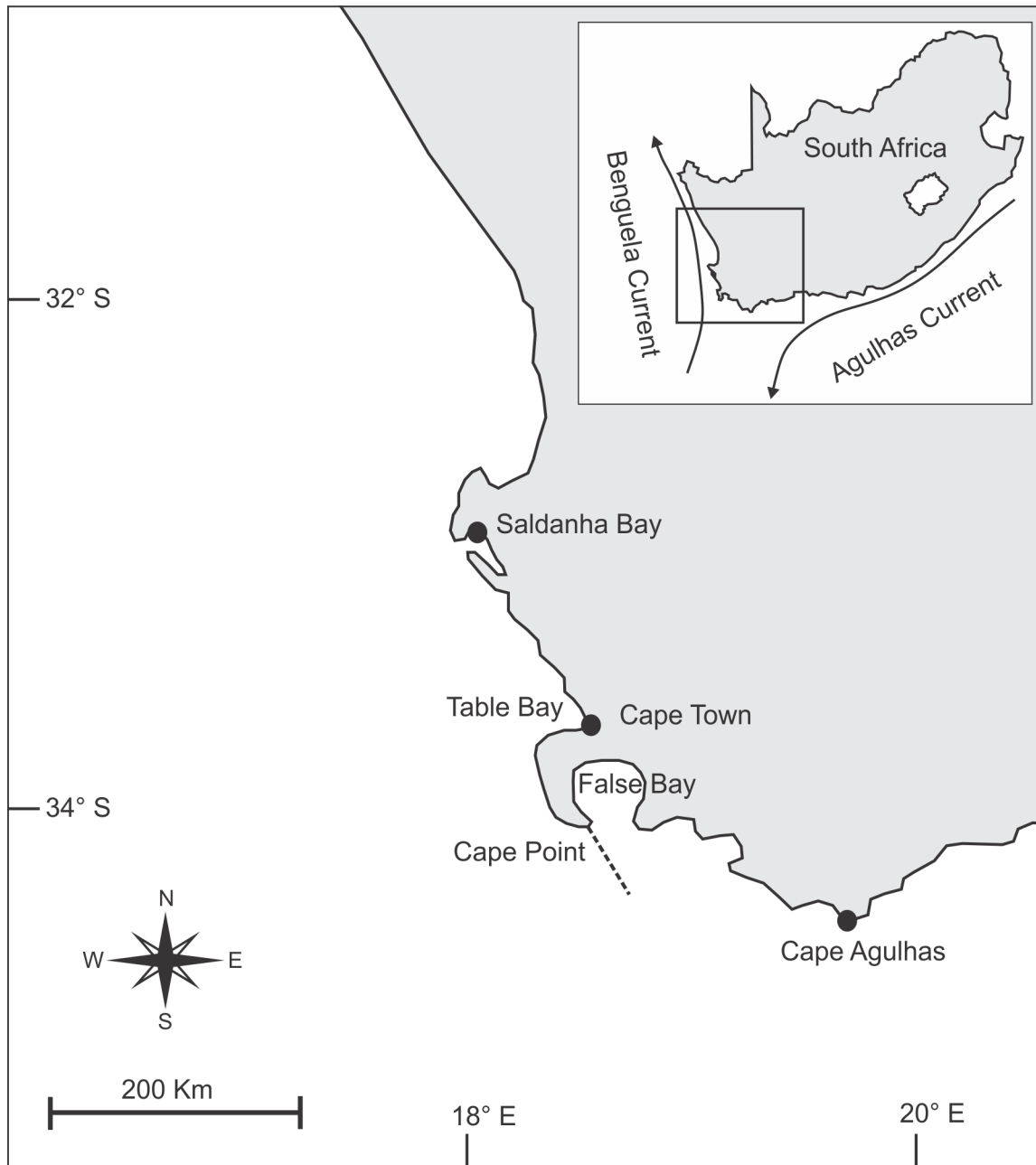
It is widely accepted that invasive species pose one of the largest threats to biodiversity (Carlton and Geller 1993; Parker et al. 1999; Ruiz et al. 1999; Grosholz 2002), especially in marine systems (Harley et al. 2006; Molnar et al. 2008; Sorte et al. 2010a). Invasive species are defined as aliens that are able to establish viable populations outside their native geographic ranges, spread within the invaded region (Perdereau et al. 2011), and have negative impacts on native communities (Branch and Steffani 2004; Harley et al. 2006; Molnar et al. 2008; Ricciardi and Cohen 2007). Marine invasions have been taking place globally since the beginning of sea-faring days both intentionally and accidentally, although accidental introductions outnumber the former (Ruiz et al. 1997). Historically, the main vectors of marine invasive species were wooden vessels carrying wood boring fouling organisms and dry ballast (Griffiths et al. 2009). In contrast, modern vectors include external fouling, ballast water, marine aquaculture, the aquarium trade, intentional releases and recreation (Carlton and Geller 1993; Ruiz et al. 1997). Still, the most common modes of marine species introduction are through external fouling and ballast water (Bax et al. 2003; Lewis et al. 2003). Introductions have increased over time as a result of human activities and globalization, which itself is predicted to increase and with it the potential number of invasive species (Mead et al. 2011a). As of 2012, approximately 90% of the world's trade was transported via ships (International Maritime Organization 2012) giving an indication of the strength of this pathway.

A commonly noted impact of invasive species is their potential for altering recipient communities (Hoffman and Sgrò 2011; Perdereau et al. 2011; Whitney and Gabler 2008). A commonly applied framework for categorizing invader's impacts was developed by Parker et al. (1999) and recognizes five different levels of impact: 1) genetic effects (i.e. changes in gene flow between populations and hybridization); 2) individual effects (i.e. growth, mortality, and behavioral changes of native biota); 3) changes in population dynamics (i.e. in species abundance, distributions, and extinctions); 4) community effects (i.e. changes in species composition, richness, evenness, and diversity); and 5) ecosystem impacts (i.e. depletion of resource supplies and changes in resource utilization and disturbance regimes). In each of these instances, just as the invasive species may react differently depending upon the community they are introduced into, so may native species and communities respond differently to new species entering the habitat (Parker et al. 1999). This makes it not only difficult to predict specific impacts of an invader, but also to manage them in appropriate and effective ways (Grosholz and Ruiz 1996; Parker et al. 1999; Harley et al. 2006).

### 1.1 History and trends in South African marine invasions

Bioinvasions were overlooked in South Africa for many years partly due to lack of scientific attention and partly due to lack of pre-invasion data documenting native biota. Although it can be assumed that marine invasions have taken place since the arrival of European vessels to South Africa, there is no formal data specifically addressing this (Mead et al. 2011a). In recent years, increasing numbers of modern marine invasions have been recognized and historical invasions have been resolved (Robinson et al. 2005; Griffiths et al. 2009; Mead et al. 2011b). Currently, 86 marine and estuarine alien and 39 cryptogenic species are recognized across 17 taxonomic groups in South Africa (Mead et al. 2011b). Of these alien and cryptogenic species, approximately 55 were recorded along the cool-temperate West Coast. Of the identified 86 alien species, 94% have been introduced unintentionally through ship fouling and ballast water (Mead et al. 2011a). Although currently low in number, introductions via mariculture are predicted to increase as it becomes a more prominent industry in South Africa (Mead et al. 2011a).

Despite the increasing numbers of marine invasive species recorded in South Africa, the only marine invasive species to date with quantified ecological impacts are *Mytilus galloprovincialis* (see Branch et al. 2008 for a review) and *Semimytilus algosus* (Greef et al. 2013). As *Balanus glandula*, an intertidal acorn barnacle, is the only other widely spread invasive species along the South African coast (Mead et al. 2011b), it is an important species in need of consideration. Additionally, documented impacts of this invader in Argentina (Elías and Vallarino 2001; Schwindt 2007) and Japan (Kado 2003; Geller et al. 2008) further justify studying this species in a South African context.



**Figure 1.** A map of the West and South Coasts of South Africa.

### 1.2 Invasion history of *Balanus glandula*

The invasion of barnacles has been a global problem for some time; so much so that today barnacles are considered one of the most common harbor-invading marine species (Elías and Vallarino 2001; Simon-Blecher et al. 2008). *B. glandula* is an invasive barnacle found in several locations around the world. Originally a native of the rocky shores of west coast North America (Newman and Abbot 1980), it ranges from the subarctic Aleutian Islands to the warm temperate Baja, California (Kado 2003). *B. glandula* has since invaded

cool temperate habitats in Argentina (Elías and Vallarino 2001; Schwindt 2007), Japan (Kado 2003) and most recently, South Africa (Simon-Blecher et al. 2008). In all three countries, *B. glandula* has been a successful invader and competitor (Elías and Vallarino 2001; Kado 2003; Laird and Griffiths 2008).

*B. glandula* first invaded the Argentinian coast in the early 1970s (Elías and Vallarino 2001). Once introduced, it spread along the coast rapidly (Schwindt 2007). Here, *B. glandula* settles in the beginning of winter before other barnacle species and supports highest cover on wave-exposed shores in the upper mid-intertidal (Elías and Vallarino 2001). Since there are no natural predators of *B. glandula* in Argentina, this invader was able to spread unchecked displacing at least two native barnacle species to lower in the subtidal zone (Elías and Vallarino 2001). As a result of this, native community composition and structure has changed in invaded areas (Schwindt 2007). *B. glandula*'s success as an invader has been attributed to its ability to colonize shorelines quickly, achieving high abundances (Schwindt 2007). After only 40 years since its introduction, *B. glandula* extends the length of Argentina, covering some 2900km of rocky shores across 10 degrees of latitude (Schwindt 2007).

The invasion of Japan occurred 20 - 40 years ago (Kado 2003). *B. glandula* was only found and recognized as an invasive species in 2000, having been overlooked because of its close resemblance to a native barnacle (*Semibalanus cariosus*) (Kado 2003). By the time it was officially recognized, *B. glandula* had become the dominant species in the intertidal zone in a number of harbors along the Japanese coast (Kado 2003). The species exhibited higher abundances than native barnacles and was thought to be displacing native barnacles as there has been a reduction in their abundances where *B. glandula* is present (Kado 2003). In areas where *B. glandula* was absent, native species were dominant (Kado 2003). This correlates with findings from Argentina and gives further support to the idea that *B. glandula* is a dominant invader with highly competitive characteristics. As in Argentina, the species' competitive edge is attributed earlier reproduction and settlement than native barnacles, thus enabling its establishment on open rock preemptively (Kado 2003).

Following the introductions to Argentina and Japan, *B. glandula* was recorded and described as an invasive species in South Africa in 2007 (Simon-Blecher et al. 2008). It has been estimated, based on photographic evidence, that *B. glandula* has been present in South Africa since at least 1992 (Laird and Griffiths 2008). This discrepancy in dates was due to *B. glandula* being misidentified as the native barnacle species, *Chthamalus dentatus* (Griffiths et al. 2009). Since the introduction of *B. glandula*, it has been suggested that *C. dentatus* has been outcompeted by *B. glandula* along the West Coast (Simon-Blecher et al. 2008). The alien barnacle was likely introduced to South Africa via hull fouling or ballast water (Griffiths et al. 2009) from the northwest coast of North America (Simon-Blecher et al. 2008). It is believed that the site of initial introduction was Table Bay or Saldanha Bay

(Figure 1), as these are major commercial ports within the invaded range (Griffiths et al. 2009).

High abundances, rapid population growth, wide physiological tolerances, and high competitive abilities are characteristics associated with many invasive species (Whitney and Gabler 2008). Invasive species that exhibit these traits can establish themselves in high densities and as a result sometimes exclude native species (Ricciardi and Cohen 2007). *B. glandula*'s competitiveness for space in both native (Crisp 1960) and introduced ranges (Elías and Vallarino 2001; Kado 2003; Schwindt 2007) makes it difficult for other barnacle species to successfully co-exist. For instance, in high population densities *B. glandula* has been shown to overgrow, crush, and pry other barnacles off rocks leaving them inhabiting areas outside *B. glandula*'s preferred zone (Gaines and Roughgarden 1985). Overall, *B. glandula* seems able to adapt to a variety of environments. Yet, as a variety of parameters determine whether or not an invader will be able to establish and persist, it is yet to be seen if this trend will carry across to the more newly invaded regions in South Africa under changing environmental conditions.

### *1.3 Potential effects of climate change on invasions*

As climate change drives alterations in air and water temperature and changes in biotic communities, invasive species ranges are likely to shift to include previously unreached locations (Whitney and Gabler 2008; Sorte et al. 2010a; Zerebecki and Sorte 2011). Species that are geographically widespread often have great genetic diversity and possess wide physiological tolerances, which enables them to adapt readily to changing conditions (Hoffmann and Sgrò 2011; Zerebecki and Sorte 2011). Evidence has shown that invasive species often have wide environmental tolerances (Whitney and Gabler 2008; Sorte et al. 2010a; Zerebecki and Sorte 2011). This valuable trait could enable some, like *B. glandula*, to survive at wide latitudinal ranges (Schwindt 2007). Changes in temperature could also have disproportional impacts on native species that may be more sensitive to changes in temperature than those of invasive species (Sorte et al. 2010a; Zerebecki and Sorte 2011). It has thus been suggested that exposure to changing temperatures may facilitate the expansion and dominance of invasive species (Sorte et al. 2010a).

Invaded communities as a whole are also likely to be impacted by temperature changes if certain species, life stages, or interactions are sensitive to temperature regimes (Sanford 2002; Harley et al. 2006; Herbert et al. 2007). Such changes in communities can precipitate shifts in species distributions, biodiversity, and biological processes (Sanford 2002; Harley et al. 2006). For instance, water temperature triggers the onset of oviposition in the intertidal whelk, *Thais lapillus*, whereas temperatures not within its preferred range inhibit oviposition (Largen 1967). In the long term, this could result in detrimental impacts on the affected populations or even the entire species, as spawning would not likely take



place (Largen 1967). This could have consequences for other species, such as those preyed upon by the whelk. Understanding how variations in climate changes and temperature influence interspecific interactions may help predict how those species will respond to such environmental changes (Bertness et al. 1999; Sanford 2002; Hoffman and Sgrò 2011).

#### 1.4 Thermal thresholds and physiological responses in the intertidal

Each species has a unique physiological tolerance that reflects their adaptive abilities in a thermally changing environment (Szathmary et al. 2009; Dong et al. 2011; Spinuzzi et al. 2013) and can determine which species survive (Somero 2010). For instance, in many cases intertidal species exposed to the same ambient temperature conditions will respond differently based on unique physiological tolerances (Helmuth et al. 2010; Wong et al. 2014). Physiological tolerances not only vary from species to species (Buckley et al. 2001; Szathmary et al. 2009), but also can change temporally and spatially in response to selective environmental pressures (Hutchison and Maness 1979; Buckley et al. 2001; O'Connor et al. 2007; Helmuth et al. 2010).

In the marine intertidal, ambient temperature conditions vary for sessile organisms due to differences in shore and rock orientation, tidal elevations, crevices, and shaded regions (Helmuth et al. 2010). Because both air and water temperatures directly affect an organisms' internal body temperature (Helmuth et al. 2006; Szathmary et al. 2009), survival and developmental rates can be greatly affected (O'Connor et al. 2007; Dong et al. 2011). For instance, ocean temperature can directly impact larval development rate for many species with planktonic larvae, affecting their survival and dispersal (O'Connor et al. 2007). Yet, many ectotherms are able to adjust their internal thermal tolerances behaviorally, allowing them to withstand higher than optimal ambient temperatures (Hutchison and Maness 1979; Miller and Denny 2011). An example of this is the acclimation of *Littorina* snail species to different temperature regimes that vary between geographic regions in the USA (Sorte et al. 2011). While this may not be specifically the case for ectotherms in the intertidal, it is likely that intertidal organisms do have an ability to adjust or acclimate to different thermal conditions outside their thermal optimums considering they are exposed to large daily temperature fluctuations (Helmuth et al. 2010). Metabolic rates can also be impacted by changing ambient temperatures (O'Connor et al. 2007; Dong et al. 2011). When temperatures reach an organisms' thermal threshold metabolic rates are reduced and the heat-shock protein (Hsp) response is induced (Dong et al. 2011). Hsp responses allow for a degree of thermal plasticity as marine organisms respond to changing thermal environments (Buckley et al. 2001; Berger and Emlet 2007). A study by Berger and Emlet (2007) found that *B. glandula* could survive at experimental temperatures ranging from 11°C to 34°C without evidence of any permanent protein damage. They found that at 23°C, a Hsp response was induced indicating that the barnacles were preparing for exposure to high temperatures and thermal stress that is routinely



experienced during low tide (Berger and Emlet 2007). Given this wide thermal range that *B. glandula* is able to survive under, it could indicate that the species is well adapted to living close to its thermal limit and therefore, could be well adapted to habitats in South Africa that experience ambient temperatures to its upper thermal limit. However, since there is currently no knowledge detailing the optimal temperature ranges for *B. glandula* in South Africa, it is unclear how the species will respond to environmental temperature changes that may occur as a result of climate change or if the species continues to spread along the South African coast where water temperatures increase.

### *1.5 Predicted climate change along the South African coast*

Climate change in South Africa is anticipated to alter oceanic and atmospheric variables, including sea surface temperature (SST), upwelling intensity, wind patterns, and wave action (Rouault et al. 2010). Large-scale assessments of SST have revealed temperature changes have occurred since the early 1980s (Rouault et al. 2010; Mead et al. 2013). Along the West Coast where upwelling is increasing in intensity, there has been a cooling trend of 0.5°C per decade (Rouault et al. 2010). In contrast, the East Coast, which is characterized by the warm Agulhas current, has shown a warming trend of 0.5°C per decade (Rouault et al. 2010). Falling between these extremes lies the South Coast. A region of transition between the temperate West Coast and the warmer conditions to the east (Shannon 1985), near-shore temperature increases from west to east (Smit et al. 2013). The area between Cape Point and Cape Agulhas is regarded as an oceanographically complex region, experiencing warm water intrusions by anti-cyclonic eddies pinched off from the warm Agulhas current (Lutjeharms and Van Ballegooyen 1988), as well as wind induced upwelling (Shannon and Nelson 1996). In this region lies False Bay, where water temperature variability is influenced by the Benguela upwelling system along the West Coast (Dufois and Rouault 2012). Fluctuations in water temperature as a result of intensification of upwelling events may impact the temporal variations in SST within the bay (Dufois and Rouault 2012). Due to this complexity explicit predictions of near-shore temperatures have not been made for this area.

### *1.6 Problems with generalized predictions*

Variations in environmental changes and species responses as detailed above, suggest that generalized predictions about the impacts of invasive species or of changes in biodiversity may not be appropriate or accurate. There is much variability and complexity accompanying predictions of environmental change (Mrowicki et al. 2014) as well predictions regarding to what extent they may affect a species geographic range, biotic interactions, or the recipient community (Whitney and Gabler 2008; Szathmary et al. 2009). At a species level, the effects of climate change are extremely variable and may only be revealed under certain conditions (i.e. at temperature extremes or during a particularly

vulnerable life-history stage) and may vary between species (Stachowicz et al. 2002). For instance, while some barnacle species are able to survive under extremely hot air temperatures for a long period of time (Crisp 1960), high temperatures have been associated with high mortality of juvenile barnacles (Lathlean and Minchinton 2012). At a community level, recipient communities as well as invasive species can respond to selective pressures and adapt to either become more or less receptive or more or less competitive (Whitney and Gabler 2008). Some native species and pre-existing invaders may facilitate the emergence and success of new invaders (Bruno et al. 2003; Wonham et al. 2005), while other native species may counteract initial impacts over time and reclaim dominance within the community or change environmental conditions that make the invader's persistence unlikely (Whitney and Gabler 2008). Thus, this is where possible invasion-specific research is needed.

### 1.7 Overall aims

Evidence suggests that climate change and associated environmental stressors can alter species interactions (Hellmann et al. 2008; Firth and Hawkins 2011). Furthermore, little research has quantified the spread and impact of South Africa's 86 marine and estuarine alien species and no research has assessed how temperature changes affect their interactions. Thus, it will be important to clarify how temperature changes may affect invasive species ranges, their biological processes, and how those in turn may affect interactions with native species along the South African coast.

To address this, my thesis has three overarching aims: (1) to assess the current distribution and abundance of *B. glandula* in relation to native barnacle species along the coast of South Africa; (2) to elucidate the effects of substratum temperature on the early life-history processes of *B. glandula* and the native barnacle, *C. dentatus*; and (3) to compare the effects of water temperature and food concentration on filtration and feeding behavior of *B. glandula* and the native barnacle, *Notomegabalanus algicola*. The information gained will provide insight into potential outcomes of the southeastward spread of *B. glandula* into warmer waters and will provide a better understanding for how biological processes of these species may be altered by climate induced changes in temperature.

## CHAPTER 2

### The status of the invasive barnacle *Balanus glandula* along the coast of South Africa

#### 1. Introduction

Each species has unique characteristics that influence its ability to spread and adapt to novel locales and conditions (Whitney and Gabler 2008; Blackburn et al. 2011). The ability of an alien species to establish and spread or have an impact within its introduced range is what distinguishes an invasive alien species from a non-invasive alien (Kolar and Lodge 2001; Blackburn et al. 2011). If a species' initial invasion is not hindered by biological constraints or environmental conditions they may spread from points of introduction into new habitats (Arim et al. 2006; Johnson et al. 2006). In such cases, species will continue to spread until environmental conditions limit suitable habitats (Blackburn et al. 2011), population dynamics hinder further spread (Arim et al. 2006), or biological interactions prevent further range extension (DeRivera et al. 2005; Dumont et al. 2011). Selective pressures may also encourage changes in behavior (Zabin et al. 2007) or morphology (Grosholz and Ruiz 2003; Torchin et al. 2003) enabling invasive species to successfully adapt to new environments (Grosholz and Ruiz 2003; Zabin et al. 2007). Characteristics of the recipient community can also encourage or discourage a species' spread (DeRivera et al. 2005; Whitney and Gabler 2008). While the absence of predators or competitors can enable invasive species to establish and spread, biotic resistance by native communities can hinder such progression (DeRivera et al. 2005; Dumont et al. 2011).

Abiotic factors often play a role in determining an invasive species' distribution, range or invasion success (Kelley et al. 2013). For example, temperature, salinity and wave exposure are known to influence the invasive crab, *Carcinus maenas* (Compton et al. 2010). Just as changes in sea temperature can influence marine species' ranges and abundances (Southward et al. 1995; Kelley et al. 2013), temperatures outside a species' optimal thermal range can increase mortality (O'Riordan et al. 2010; Lathlean and Minchinton 2012), and both temperature and salinity can have impacts on embryo and larval development and growth (Thiyagarajan and Qian 2003).

#### 1.1 Current distributions of barnacles along the South African coast

In South Africa, the native barnacle species that have historically occurred intertidally along the West Coast include: *Tetraclita serrata*, *Octomeris angulosa*, *Chthamalus dentatus*, *Austromegabalanus cylindricus*, *Notomegabalanus algicola*, and

*Amphibalanus amphitrite* (Branch et al. 2010). All of these barnacles extend from the northern most part of the West Coast, around Cape Point, and along the South Coast towards the Eastern Cape (Branch et al. 2010).

Currently, only one invasive barnacle species has been recognized along the South African West Coast, i.e. *Balanus glandula*. Since being recognized in 2007 (Simon-Blecher et al. 2008), *B. glandula* has successfully spread along the West Coast completely overlapping in geographic distribution with all six native barnacle species (Laird and Griffiths 2008). As of 2007, *B. glandula*'s distribution comprised approximately 400km of the West Coast from Eland's Bay to Misty Cliffs (Laird and Griffiths 2008) (Figure 1 & Table 1). At this time, *B. glandula* was most abundant at semi-exposed sites where it was abundant in all shore zones making it the dominant intertidal barnacle in its range (Laird and Griffiths 2008). Notably, *B. glandula* was absent along the South Coast where the native barnacles, *T. serrata*, *O. angulosa*, and *C. dentatus*, were the most abundant (Laird and Griffiths 2008). After this initial assessment, Laird and Griffiths (2008) suggested that the biogeographic break of Cape Point would limit the eastward spread of this invader.

The most recent distribution assessment was made seven years ago (Laird and Griffiths 2008). Considering that this is a recognized coastal invader, an updated distribution and abundance assessment is needed. It is against this backdrop that this chapter aims to assess the current distribution and abundance of *B. glandula* in relation to native barnacle species. In light of current knowledge, I hypothesize that,

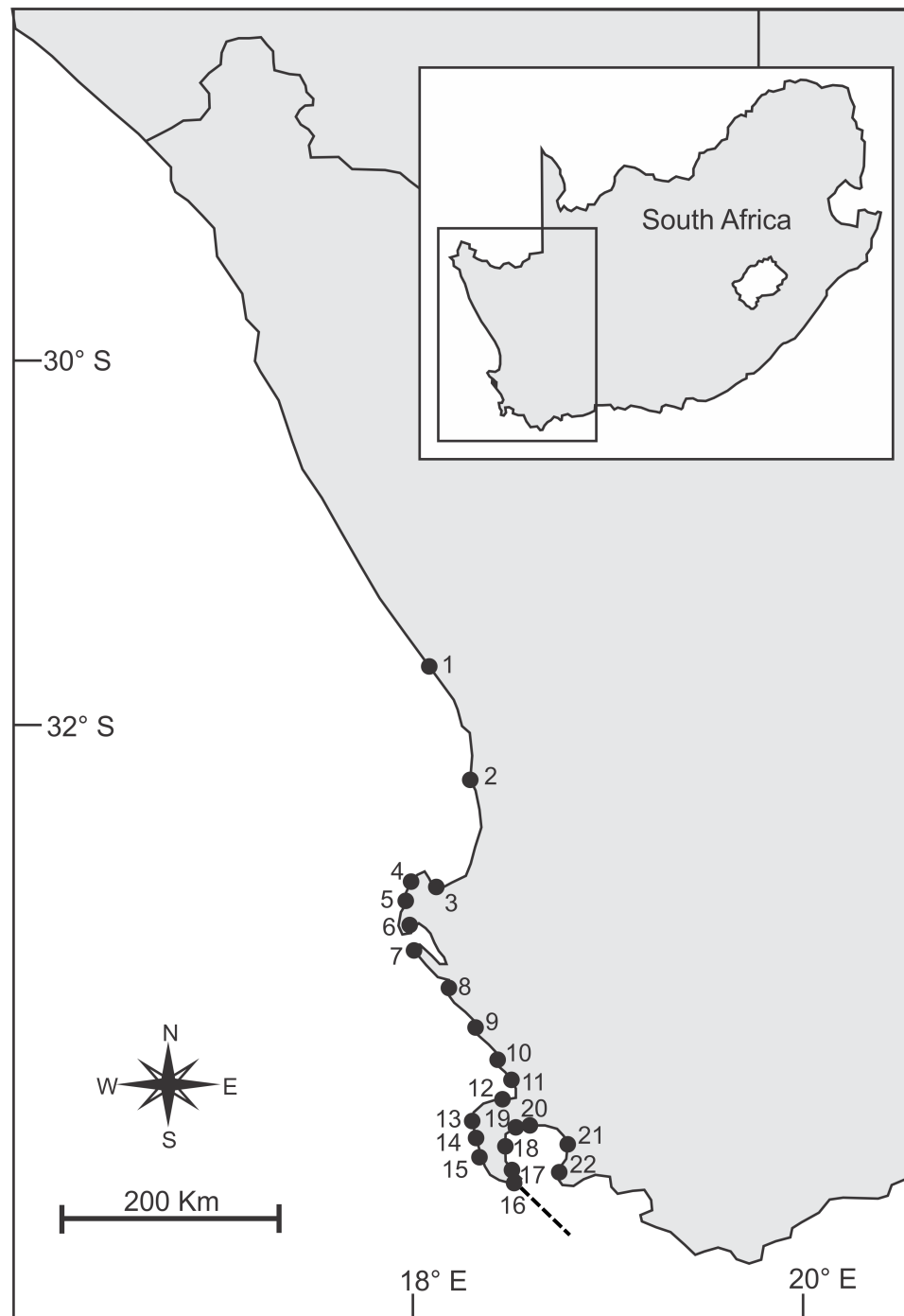
**H<sub>1</sub>:** *B. glandula* will have spread north up the West Coast and south only as far as Cape Point.

**H<sub>2</sub>:** *B. glandula* will have achieved higher abundances than native barnacle species at sites where it is currently present.

## 2. Methods

The distribution and abundance of *Balanus glandula* was surveyed in the austral winter of 2012 and 2013. Sites previously visited in 2007 were re-surveyed to update distribution and abundance information. A total of 22 sites were sampled (Figure 1 & Table 1) stretching along the South African coast. Due to the high density of barnacles at each site, 10 x 10cm quadrats were used to sufficiently determine abundance ( $.m^{-2}$ ). Ten quadrats were randomly placed within the high-, mid-, and low-shore zones at least 2m apart and the number of *B. glandula* and co-occurring native barnacle individuals were counted. Tidal

zones at each site were delineated using biological indicators following Blamey and Branch 2008.



**Figure 1.** Map of the 22 sites sampled along the West and South Coasts. Numbers refer to the site numbers listed in Table 1. Dashed line represents the biogeographic break of Cape Point.

**Table 1.** GPS coordinates and site descriptions of the sites surveyed along the West and South Coasts. Dashed line represents the biogeographic break of Cape Point. Sampled areas at each site were all wave-exposed.

<b>Number</b>	<b>Sites</b>	<b>GPS Coordinates</b>	<b>Site Description</b>
1	Lambert's Bay	32°05.442' S, 18°18.023' E	West-ward facing with tall rocky outcrops
2	Eland's Bay	32°19.076' S, 18°18.856' E	West-ward facing with tall rocky outcrops
3	St. Helena Bay	32°46.367' S, 18°02.863' E	West-ward facing
4	Paternoster	32°48.084' S, 17°55.140' E	West-ward facing with rocky outcrops and sand shores on either side
5	Cape Columbine	32°49.520' S, 17°50.792' E	West-ward facing with tall rocky outcrops
6	Marcus Island	33°02.019' S, 17°56.127' E	West-ward facing with large boulders and rocky outcrops
7	Tsaarsbank	33°08.892' S, 17°59.923' E	West-ward facing with tall rocky outcrops and sand shores
8	Yzerfontein	33°20.408' S, 18°09.211' E	West-ward facing with low rock cover and sandy shores
9	Ganzekraal	33°31.094' S, 18°19.257' E	West-ward facing with low rock cover and sandy shores
10	Melkbosstrand	33°44.002' S, 18°25.558' E	West-ward facing with rocky outcrops
11	Blouberstrand	33°48.135' S, 18°27.545' E	West facing with rocky outcrops and sandy shores on either side
12	Moulie Point	33°53.969' S, 18°24.274' E	West-ward facing with low rocky cover
13	Hout Bay	34°02.902' S, 18°21.650' E	Southwest facing with tall rocks surrounded by sand
14	Kommetjie	34°08.271' S, 18°19.198' E	Southwest facing with low rocky cover
15	Misty Cliffs	34°11.025' S, 18°21.601' E	Southwest facing with low rock cover surrounded by sand
16	Scarborough	34°11.982' S, 18°22.536' E	South-ward facing with large rocky outcrops
17	Cape Point	34°20.126' S, 18°25.520' E	South-ward facing with large rocky outcrops
18	Seaforth	34°12.004' S, 18°27.222' E	Southwest facing with large boulders and sandy shores
19	Dalebrook	34°07.436' S, 18°27.154' E	Southwest facing with low rocky cover
20	St. James	34°06.597' S, 18°27.420' E	Southwest facing with low rocky cover
21	Gordon's Bay	34°09.480' S, 18°51.438' E	Southwest facing with large boulders and rocky outcrops
22	Rooiels	34°18.298' S, 18°48.530' E	Southwest facing with tall rocky outcrops

Barnacle abundances were analyzed separately for each shore zone. All statistical analyses were performed in R (v.3.0.1). In order to meet the assumption of the analysis,

raw data for the mid-shore were log transformed due to extreme variations in abundances among sites. The abundances of *B. glandula* were then assessed among sites and years (i.e. 2012 and 2013) using a generalized least squares (GLS) model.

### 3. Results

#### 3.1 Species composition

The barnacle species recorded differed among years. The native species *Tetraclita serrata*, *Octomeris angulosa*, *Chthamalus dentatus*, and *Notomegabalanus algicola* were present in all years, although the latter two species were not consistently recorded (Table 2). Through time, fewer numbers of native species have been recorded on the West Coast. *Balanus glandula* was recorded on the South Coast for the first time in 2012 and then again in 2013 (Table 2).

**Table 2.** Barnacle species recorded along the West and South Coasts in 2007, 2012, and 2013. (✓) represents presence and (-) absence. Note: 2007 data were extracted from Laird and Griffiths (2008).

	2007		2012		2013	
	West	South	West	South	West	South
<i>B. glandula</i>	✓	-	✓	✓	✓	✓
<i>T. serrata</i>	✓	✓	✓	✓	✓	✓
<i>O. angulosa</i>	✓	✓	✓	✓	✓	✓
<i>C. dentatus</i>	✓	✓	-	-	-	✓
<i>N. algicola</i>	✓	-	✓	-	✓	-
<i>A. amphitrite</i>	-	✓	-	-	-	-

#### 3.2 Distribution

In 2012, *B. glandula*'s distribution ranged from Lambert's Bay to Dalebrook, False Bay (Table 3). Most notable, however, was the spread around the biogeographic break at Cape Point and its presence in False Bay. In 2013, *B. glandula*'s range had retracted to Eland's Bay on the West Coast, but had extended further into False Bay until St. James.

**Table 3.** The range occupied by *B. glandula* along the coast of South Africa in 2007 (extracted from Laird and Griffith 2008), 2012 and 2013. Dashed line represents the biogeographic break of Cape Point.

Site	2007	2012	2013
Lambert's Bay		I	
Eland's Bay			I
St. Helena Bay			
Paternoster			I
Cape Columbine			
Marcus Island			
Tsaarsbank			
Yzerfontein			
Ganzekraal			
Melkbosstrand			
Bloubergstrand			
Moulie Point			
Hout Bay			
Kommetjie			
Misty Cliffs			
Scarborough			
Cape Point			
Seaforth			I
Dalebrook		I	
St. James			I
Gordon's Bay			
Rooiels			

### 3.3 Abundance

*B. glandula* represented 100% of barnacles found at seven of 16 sites on the West Coast (i.e. Elands Bay, Paternoster, Cape Columbine, Marcus Island, Tsaarsbank, Yzerfontein, and Hout Bay) in both 2012 and 2013. In contrast, this species supported lowest abundances at the newest invaded site of St. James. Notably, the invader was more abundant than native barnacles at both Cape Point and Seaforth. Overall, native barnacles supported low abundances, especially on the West Coast when compared to *B. glandula*.



**Table 4.** Average abundances (number.m<sup>-2</sup>) of *B. glandula* and native barnacle species recorded in 2012 and 2013. (X) represents sites where the species was absent from all tidal zones in a particular year. (-) represent sites that were not sampled in 2012. Dashed line represents the biogeographic break of Cape Point.

Site	<i>B. glandula</i>						<i>T. serrata</i>						<i>O. angulosa</i>					
	High		Mid		Low		High		Mid		Low		High		Mid		Low	
Year	2012	2013	2012	2013	2012	2013	2012	2013	2012	2013	2012	2013	2012	2013	2012	2013	2012	2013
Lambert's Bay	90	X	290	X	40	X	X	X	X	X	X	X	X	X	X	X	X	X
Elands Bay	3380	348	2740	843	20	629	X	X	X	X	X	X	X	X	X	X	X	X
St Helena Bay	0	X	0	0	0	0	X	X	X	X	X	X	X	X	X	X	X	X
Paternoster	320	343	1640	504	0	21	X	X	X	X	X	X	X	X	X	X	X	X
Cape																		
Columbine	320	27	1640	851	0	261	0	X	0	X	10	X	0	X	50	X	0	X
Marcus Island	0	583	8240	359	0	1	X	X	X	X	X	X	X	X	X	X	X	X
Tsaarsbank	-	150	-	470	-	79	-	X	-	X	-	X	-	X	-	X	-	X
Yzerfontein	3590	244	2930	2088	1100	152	0	X	10	X	0	X	X	X	X	X	X	X
Ganzekraal	0	324	270	2	0	0	X	6	X	3	X	0	X	0	X	9	X	0
Melkbosstrand	0	52	6200	764	40	2	0	0	110	0	0	2	X	X	X	X	X	X
Blouberstrand	420	370	22610	1977	0	5	X	0	X	0	X	8	0	X	10	X	0	X
Moulie Point	190	203	1520	0	0	0	0	0	90	34	50	10	X	0	X	2	X	20
Hout Bay	180	1075	91500	2701	1420	1463	X	X	X	X	X	X	X	X	X	X	X	X
Kommetjie	0	2	100	0	80	0	0	3	0	0	150	0	X	X	X	X	X	X
Misty Cliff	1130	251	8310	373	2460	0	0	X	0	X	580	X	X	0	X	9	X	0
Scarborough	1610	87	3840	452	1620	58	X	0	X	0	60	10	X	X	X	X	X	X
Cape Point	50	0	110	113	10	7	0	0	0	1	70	4	0	X	0	X	20	X
Seaforth	0	52	0	0	0	0	X	0	X	34	X	0	X	X	690	0	180	X
Dalebrook	50	X	30	X	0	X	0	72	70	108	140	1	0	43	840	79	940	133
St James	-	18	-	7	-	0	-	0	-	147	-	0	-	0	-	64	-	12
Gordon's Bay	-	X	-	X	-	X	-	0	-	108	-	0	-	0	-	2	-	0
Rooiels	-	X	-	X	-	X	-	23	-	86	-	0	-	1	-	37	-	21

Site	<i>C. dentatus</i>						<i>N. algicola</i>					
	High		Mid		Low		High		Mid		Low	
	2012	2013	2012	2013	2012	2013	2012	2013	2012	2013	2012	2013
Lambert's Bay	×	×	×	×	×	×	0	0	0	0	10	7
Elands Bay	×	×	×	×	×	×	0	0	70	4	40	45
St Helena Bay	×	×	×	×	×	×	×	×	×	×	×	×
Paternoster	×	×	×	×	×	×	0	×	0	×	1500	×
Cape Columbine	×	×	×	×	×	×	0	0	0	0	1800	3
Marcus Island	×	×	×	×	×	×	0	0	0	0	80	5
Tsaarsbank	-	×	-	×	-	×	-	×	-	×	-	×
Yzerfontein	×	×	×	×	×	×	0	0	40	35	10	6
Ganzekraal	×	×	×	×	×	×	×	×	×	×	×	×
Melkbosstrand	×	×	×	×	×	×	0	0	0	35	360	285
Bloubergstrand	×	×	×	×	×	×	×	0	×	180	10530	890
Moulie Point	×	×	×	×	×	×	×	×	×	×	×	×
Hout Bay	×	×	×	×	×	×	×	×	×	×	×	×
Kommetjie	×	×	×	×	×	×	×	×	×	×	×	×
Misty Cliff	×	×	×	×	×	×	0	×	0	×	20	×
Scarborough	×	×	×	×	×	×	×	×	×	×	×	×
Cape Point	×	×	×	×	×	×	×	×	×	×	×	×
Seaforth	×	×	×	×	×	×	×	×	×	×	×	×
Dalebrook	×	×	×	×	×	×	×	×	×	×	×	×
St James	-	×	-	×	-	×	-	×	-	×	-	×
Gordon's Bay	-	79	-	0	-	0	-	×	-	×	-	×
Rooiels	-	4	-	3	-	0	-	×	-	×	-	×

On the West Coast, *B. glandula* occurred most abundantly in the mid-shore with average densities of  $711.5.m^{-2}$  ( $\pm 36.0$  SE) across all sites, while mean densities reached  $253.6.m^{-2}$  ( $\pm 13.8$  SE) and  $166.9.m^{-2}$  ( $\pm 17.9$  SE) in the high- and low-shore, respectively. On the South Coast, densities were more similar among tidal height, yet still showed highest abundances occurring in the mid-shore. Abundances reached  $11.6.m^{-2}$  ( $\pm 1.5$  SE),  $20.m^{-2}$  ( $\pm 1.6$  SE), and  $1.1.m^{-2}$  ( $\pm 0.2$  SE) in the high-, mid- and low-shore, respectively.

Within the high-shore, Yzerfontein supported the highest abundance of *B. glandula* in 2012 ( $359.m^{-2} \pm 67.97$  SE), while Hout Bay had the highest abundances in 2013 ( $1075.m^{-2} \pm 22.17$  SE) (Figure 2a). Abundances of this invader differed significantly among sites and between years in this zone (Table 5a). In the mid-shore, Hout Bay supported highest abundances of all sites with densities of  $9150.m^{-2}$  and  $2701.m^{-2}$  recorded in 2012 and 2013, respectively (Figure 2b). Within this zone, “site” and “year” significantly affected the abundance of *B. glandula* (Table 5b). Across all sites, fewer *B. glandula* were recorded in 2013 in the mid-shore than in 2012 (GLS,  $t=-5.3$ ;  $p<0.05$ ). In the low-shore, only “site” had a significant effect on *B. glandula* abundances (Table 5c). Misty Cliffs supported the highest abundances ( $105.m^{-2} \pm 43.37$  SE) in 2012, while in 2013 the highest densities were recorded in Hout Bay ( $1463.m^{-2} \pm 41.94$  SE) (Figure 2c).

**Table 5.** ANOVA results for the effect of site and year on the abundance of *B. glandula* for the a) high-shore, b) mid-shore, and c) low-shore. ns = non-significant.

ANOVA	Factor	df Effect	F-ratio	p-value
<b>a) High-shore</b>	Site	18	3.32	<0.05
	Year	1	9.92	<0.05
<b>b) Mid-shore</b>	Site	18	47.74	<0.05
	Year	1	27.23	<0.05
<b>c) Low-shore</b>	Site	18	2.81	<0.05
	Year	1	0.81	ns

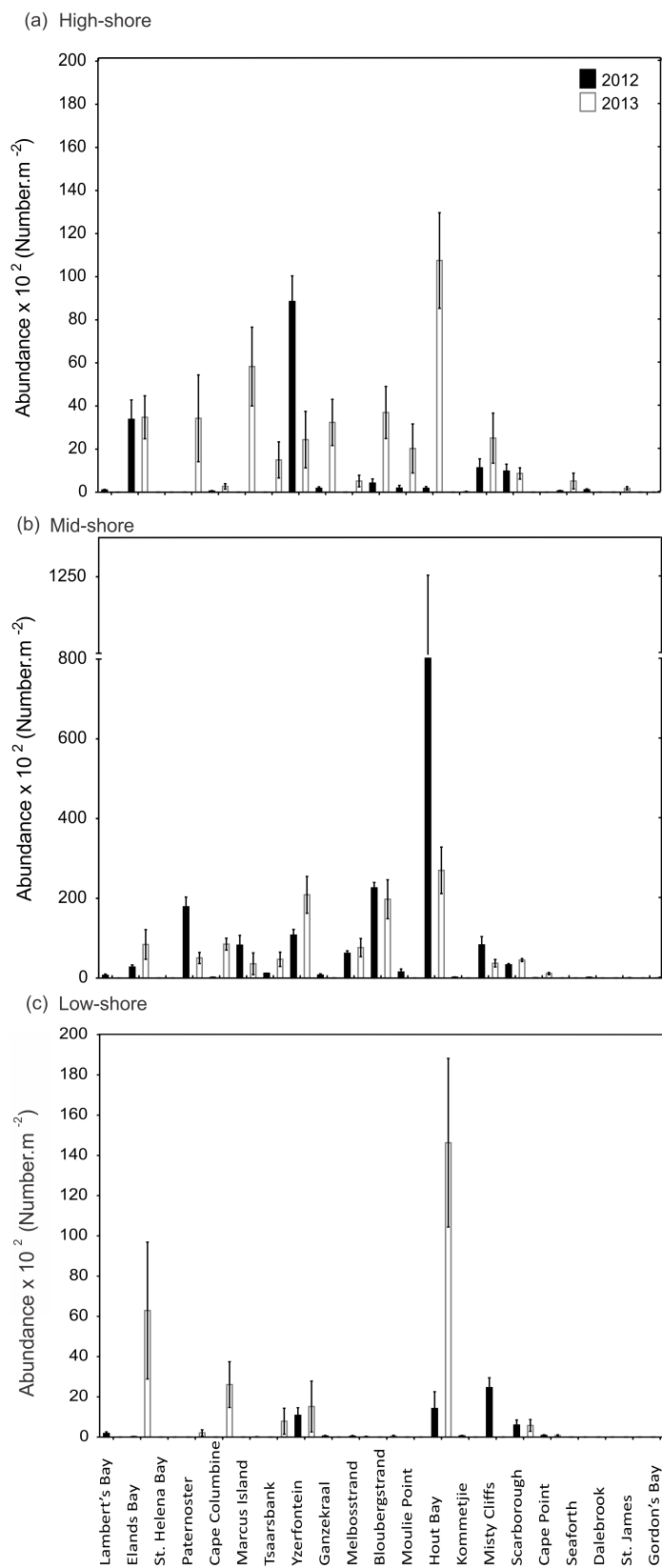


Figure 2. Mean ( $\pm$ SE) abundance of *B. glandula* in the a) high- b) mid- and c) low-shore in 2012 and 2013.

## 4. Discussion

*Balanus glandula* is an invasive acorn barnacle that has an invasion history in a number of locations (Kado 2003; Schwindt 2007; Simon-Blecher et al. 2008). As the distribution and abundance of this barnacle was last assessed along the South African coast when it was first recognized in 2007 (Laird and Griffiths 2008), updated information on the status of this invader was required. This chapter sought to assess this gap in knowledge.

### 4.1 Species composition

My results revealed that the number of native barnacle species has declined on the West Coast through time. However, this does not necessarily represent a loss of these species and may be reflective of the well-documented stochastic nature of barnacle settlement and recruitment (Zacherl et al. 2003; Hoffman et al. 2012) and larval supply (Bertness et al. 1996). However, since *B. glandula* has successfully outcompeted some native barnacle species (i.e. *B. amphitrite*) and mussel species in Argentina (Elías and Vallarino 2001) and possibly in Japan (Kado 2003), a decrease in the number of recorded native barnacle species along the South African West Coast is cause for concern. It is important to note however, that this study surveyed discrete sites so as to align with previous work (i.e. Laird and Griffiths 2008) and thus, the absence of *Chthamalus dentatus* from the West Coast in 2012 and 2013 does not necessarily represent extinction from the region. In the same way, the absence of *Amphibalanus amphitrite* from 2012 and 2013 data should not be taken to mean that the species is totally absent from the coast, but should highlight the need for long-term monitoring.

In contrast to *C. dentatus* and *A. amphitrite*, *Tetraclita serrata*, *Octomeris angulosa* continue to co-occur with *B. glandula* on both the West and South Coasts. Contrary to the results of this study, in 1996 *T. serrata* and *O. angulosa* were the most abundant intertidal barnacles in this region (Boland 1997). Both are slow growing barnacle species taking years to achieve full adult sizes (Boland 1997). These species tend to inhabit separate zones in the intertidal, the former preferring the high zone with lower wave action, while the latter prefers the low zone with higher wave action (Boland 1997). Both species therefore, only overlap in the mid-shore (Boland 1997). As *B. glandula* typically exhibits highest growth rates and occupies predominantly in the mid-shore (Wethey 1983; Laird and Griffiths 2008; Hoffman et al. 2012), this partitioning of the intertidal zone could explain why these native species continue to coexist even in the presence of *B. glandula*.

## 4.2 Distribution

Most notably, my results show a southern range expansion of *B. glandula* past the biogeographic break of Cape Point into False Bay. Conditions to the west of Cape Point appear optimal for *B. glandula* as they most closely match its native range on the west coast of North America (Simon-Blecher et al. 2008). While the West Coast of South Africa is characterized by cold water temperatures (i.e. mean 13°C) (Smit et al. 2013) and high primary productivity (Bustamante et al. 1995), conditions to the east of Cape Point are distinctly different as the cold Benguela ecosystem is replaced by the warmer Agulhas ecosystem (Dufois and Rouault 2012). Along this coast, average water temperatures are warm (i.e. mean 20°C) (Smit et al. 2013) with low primary productivity (Bustamante et al. 1995). The finding that *B. glandula* has breached Cape Point may suggest that this species is able to adapt to different conditions, as many invaders are (Grosholz and Ruiz 2003), or that conditions along the South Coast are within its thermal tolerance range. Support for the latter has been seen in Japan, where it was observed that *B. glandula* has spread along shores that experience higher air and water temperatures than occur in its native range (Geller et al. 2008). Recent work on near-shore water temperature along the South African coast has demonstrated that coastal waters on the South Coast are more similar to those on the West Coast than was previously thought (Smit et al. 2013). Regardless of the enabling mechanism, my results indicate that *B. glandula* may continue spreading along the South Coast.

The current distribution of *B. glandula* ranges from Eland's Bay to St. James in False Bay on the South Coast. Contrary to my prediction, *B. glandula* has not extended further north since 2007. However, as fluctuations in propagule pressure and recruitment are typical of barnacle invasion fronts (Alam et al. 2013), it is possible that the northern range contraction recorded in this study is temporary and that the species could continue to spread north in the future. Since sessile marine organisms most heavily rely on larval dispersal (Alam et al. 2013), propagule pressure is often an important determinant for how successful an invader will be at establishing itself at new sites (Zacherl et al. 2003; Lockwood et al. 2005).

## 4.3 Abundance

Barnacle recruitment often shows temporal and spatial variability (Pfaff et al. 2011). The non-systematic differences in abundance of *B. glandula* among sites and years within all shore zones are likely due to variability in recruitment intensity (Alam et al. 2013), variations in larval supply (Hoffman et al. 2012) and lag times between initial recruitment

and permanent establishment at the invasion front (Alam et al. 2013). Sites with previously established populations showed fluctuations in abundance, but did not exhibit local extinctions. Newly invaded sites, however, showed larger fluctuations in abundance or local extinctions (e.g. Dalebrook and Lambert's Bay). Elsewhere, recruitment intensity has shown to be the most important determinant of the invasion dynamics of *B. glandula* with several years of random fluctuations in abundance preceding permanent establishment (Alam et al. 2013). For invasive species, it can be expected that as recruitment density increases over time, lag times between settlement and establishment will shorten, as will the rate of local extinctions (Alam et al. 2013). It is probable that lag times described above are a likely explanation for the lower numbers of *B. glandula* in comparison to native barnacles at newly invaded South Coast sites. Only at Cape Point and Seaforth did *B. glandula* outnumber the native species, indicating that it has firmly established itself past the biogeographic break over time through numerous recruitment periods. At sites further into False Bay, *B. glandula* was not usually the dominant species.

Predation can also influence barnacle abundances (Fairweather 1988; Gaines and Roughgarden 1985; Hunt and Scheibling 1997). In South Africa, it was found that native whelk species consistently consumed the native barnacle, *N. algicola*, over *B. glandula* despite higher densities of the latter in some shore zones (Robinson et al. in press). Reduced predation of *B. glandula* may be an additional explanation for the invader's continual rise in abundance at previously established sites, seemingly at the expense of native barnacles. However, predation of *B. glandula* in general should not be ruled out and therefore, it may also explain the species low abundance and local extinctions at newly invaded South Coast sites.

## 5. Conclusion

Most notably, *Balanus glandula* has extended its range southward breaching the biogeographic break of Cape Point and spreading into False Bay. Although, *B. glandula*'s distribution retreated from Lambert's Bay to Eland's Bay in 2013, it is possible that the species could continue spreading north and south as the invasion front continues to move forward over time. This invader is also the dominant barnacle in the intertidal zone along the West Coast and may have displaced native barnacle species that have supported higher densities in the past. Despite the low current abundances of *B. glandula* in relation to native species along the South Coast, increases are expected to occur as it becomes permanently established over time. Considering these points, it is suggested that continued monitoring

of *B. glandula*'s populations dynamics and spread along the South African coast be prioritized. This will give a better indication of whether *B. glandula* continues to spread and what its impacts are on the native communities. In order to gain an understanding of the competitive nature of *B. glandula* and potential future impacts on native barnacles, my following chapter will assess the impacts of changing substrate temperature on the early life-history processes of *B. glandula* and the native barnacle, *Chthamalus dentatus*.

**Note:**

This work forms part of a publication currently in press (Robinson, T. B., Pope, H. R., Hawkin, L., Binneman, C. (in press). Predation-driven biotic resistance fails to regulate a sessile rocky shore invader. *Marine Ecology Progress Series*. DOI: 10.3354/meps11167).



## CHAPTER 3

### **The impact of changing substratum temperature on the settlement, mortality, recruitment and growth of *Balanus glandula* and its native comparator *Chthamalus dentatus***

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#### **1. Introduction**

Many impacts of climate change in marine systems are linked to changes in temperature (Bindoff et al. 2007; Doney et al. 2012). These changing temperatures can precipitate rising sea levels as well as changes in oxygen concentration (Keeling et al. 2010), nutrient availability (Doney et al. 2012), ocean circulation (Roemmich et al. 2007) and ocean acidification (Findlay et al. 2010). In turn, these physical and chemical factors can impact organismal physiological stress, prompting changes in recruitment (Shanks 2009; Lamb et al. 2014), mortality (Bertness 1989; Findlay et al. 2010), and growth rates (Sorte et al. 2010a; Lamb et al. 2014). On a larger scale, changes in species distribution and abundance (Brander 2010; Kordas et al. 2011; Moloney et al. 2013), species diversity (Barry et al. 1995; Harley et al. 2006), species interactions (Harley et al. 2006; Kordas et al. 2011; Doney et al. 2012) and community structure (Field et al. 2006; Doney et al. 2012) have also been recorded.

In light of climate change, there is a need to understand the environmental determinants of species distributional limits, yet these are often unclear due to different influences at multiple spatial scales (Helmuth et al. 2010; Lathlean et al. 2011; Hidas et al. 2013). Studies have shown how temperatures within the intertidal vary dramatically across spatial scales (Meager et al. 2011; Lathlean et al. 2011; Lathlean et al. 2013). These organisms are impacted by both air and water temperatures and thus it is necessary to consider both when characterizing the thermal intertidal environment (Lathlean et al. 2011). Often, the thermal stress of intertidal organisms is dictated by small-scale local conditions (Somero 2002; Helmuth et al. 2006; Helmuth et al. 2010). As such, species occupying habitats exposed to greater natural temperature variations (Somero 2010; Morley et al. 2014) and those with wide physiological tolerances (Zerebecki and Sorte 2011; Doney et al. 2012) may be less sensitive to changes in temperature than those exposed to low thermal variability or that have narrow physiological tolerances.

Changes in temperature could mean higher energy expenditure (Pörtner and Knust 2007; Doney et al. 2012), decreased productivity (Brander et al. 2010; Moloney et al. 2013) reproduction, growth or survival (Farrell et al. 2008; Doney et al. 2012). Intensification of climate variables like UV radiation, water temperature, and salinity can precipitate changes in the larval development of rocky shore invertebrates (Przeslawski et al. 2005). Due to the

nature of the intertidal, organisms inhabiting this zone routinely experience temperature variability being exposed at low tide, yet submerged at high tide. As such, it has been suggested that many live close to their thermal limits (Helmuth et al. 2010). As a result of changing climatic conditions and temperatures, species may disperse beyond their traditional range limit to new localities where conditions are within their physiological tolerances, which in turn can result in novel suites of species (Hillyer and Silman 2010; Somero 2012).

### *1.1 Synergistic effects between climate change and invasive species*

At a community level, climate change is predicted to influence the spread (Hellmann et al. 2008; Walther et al. 2009; Sorte et al. 2010b), abundance (Barry et al. 1995; Southward et al. 1995; Cockrell and Sorte 2013) and the potential impact of invasive species (Dukes and Mooney 1999; Walther et al. 2009) by altering the physical environment of recipient habitats and creating open niches. As temperatures change and invasive species distributions shift, they are placed in contact with new species (Hellman et al. 2008; Doney et al. 2012), resulting in novel competitive interactions (Byers 2002; Shinen and Morgan 2009) and changes in predator-prey relationships (DeRivera et al. 2005; Van der Putten et al. 2010). As many invasive species are generalists and able to tolerate a broad range of environmental conditions (Kolar and Lodge 2001; Sorte et al. 2010a; Cockrell and Sorte 2013), there is a concern that climate changes may favor invasive species, placing further pressure on native fauna (Byers 2002). Should marine invaders demonstrate rapid adaptive evolution such that has commonly been documented of terrestrial invaders (Huey et al. 2005; Rando and Verstrepen 2007; Dlugosch and Parker 2008; Carlsson et al. 2009), they may be further advantaged under conditions of environmental change. It is due to these synergisms between climate change and invasive species that it has been suggested that coming years are likely to see the reorganization of biological communities (Walther et al. 2009) and greater homogeneity between and within systems (Doney et al. 2012, Sadchethswaran et al. in review).

### *1.2 Thermal tolerances of *Balanus glandula* and *Chthamalus dentatus**

*Chthamalus dentatus* has historically occurred along the whole South African coastline (Branch et al. 2010). In contrast, *B. glandula* occurs predominantly along the cool West Coast and has recently been found to have successfully spread past the biogeographic break of Cape Point occurring within False Bay (see Chapter 2). It is not clear how far along the warmer South Coast this invader will spread. Initial surveys of *B. glandula* detected low abundances of *C. dentatus* within the invaded range (Laird and Griffith 2008), but this species was not recorded during subsequent surveys (see Chapter 2). While no dedicated survey has been conducted since, *C. dentatus* has not been recorded during routine

intertidal monitoring at five West Coast sites that began in 2012 (*Robinson pers comm*). It has been suggested that the dominance of *B. glandula* and concurrent reduction of *C. dentatus* is due to competition between the two species (Simon-Blecher et al. 2008). This raises questions about the nature of potential competition between these barnacles, how this may be altered under the warmer conditions of the South Coast, and how future changes in temperature may affect this interaction.

Currently, there is little knowledge regarding the thermal tolerances of either *B. glandula* or *C. dentatus*. However, the native and invaded ranges of *B. glandula* suggest it to be a cool temperate species (Newman and Abbott 1980; Rico and Gappa 2006, Schwindt 2007). In contrast, the fact that *C. dentatus* has historically occurred along the cool West Coast, along the warm South African East Coast and the tropical Mozambique coast (Branch et al. 2010) suggests it to be a warm temperate species.

Within this context, this chapter aimed to elucidate the effects of varying substratum temperature on the settlement, mortality, recruitment and growth of *B. glandula* and *C. dentatus*. This will (1) provide insight into potential outcomes of the eastward spread of *B. glandula* into warmer waters and (2) provide better understanding for how early life-history processes of these species may be altered by climate induced changes in temperature. In addressing these aims, I tested the following hypotheses:

**H<sub>1</sub>:** Barnacle settlement, mortality, recruitment and growth will differ between temperature treatments (i.e. black, white, grey and clear plates, and bare rock). Based on previous findings (Lathlean and Minchinton 2012), white plates are expected to exhibit highest settlement and recruitment rates, black plates to show the highest mortality and bare rock to have the highest growth rates. Clear plates are expected to reveal similar patterns as bare rock. These expectations can be summarized as follows:

Settlement: black < grey < transparent < rock < white

Mortality: rock < transparent < white < grey < black

Recruitment: black < grey < transparent < rock < white

Growth: black < white < grey < transparent < rock

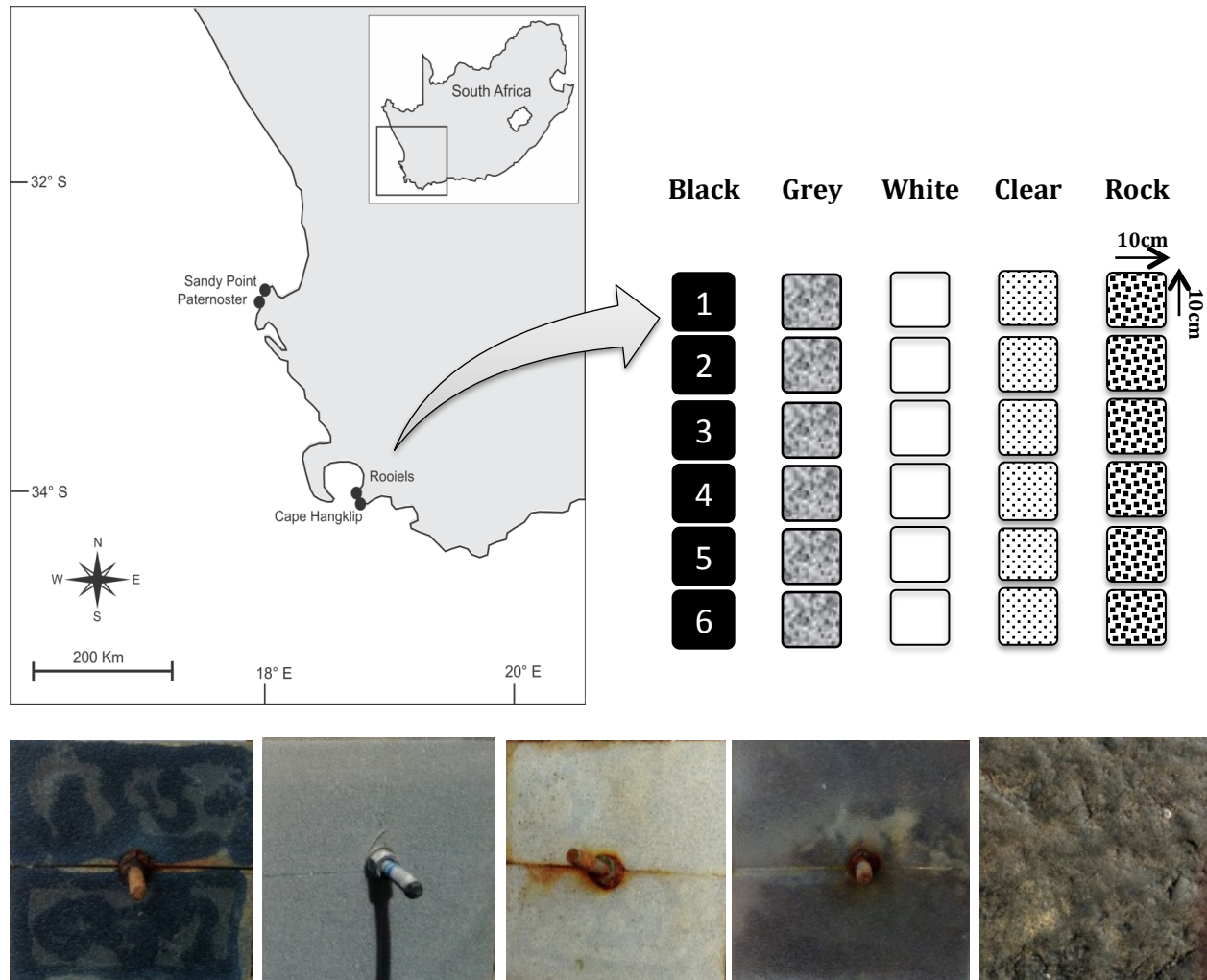
**H<sub>2</sub>:** *B. glandula* will show higher rates of settlement, recruitment and growth and lower rates of mortality compared to *C. dentatus*. These expectations are based on the current relative abundances of these species along the South African West Coast.

## 2. Methods

To validate differences in temperature among treatments (i.e. black, grey, white and clear plates and bare rock), a digital infrared (IR) thermometer (Omega OS561) was used. To minimize the effect of reflectance on readings, plates were shaded and all readings were taken 50cm away from each plate at 55° degree angles. The thermal resolution of the IR thermometer was 0.1°C and by recalibrating between measurements accuracy was  $\pm 1^\circ\text{C}$ . Emissivity ( $\epsilon$ ) was set at 0.95 as rocky substrata and invertebrates in the intertidal zone often vary between 0.95 and 1.0 (Denny and Harley 2006). Readings were taken on two different days: the first was clear and sunny with a mean ambient air temperature of 27.1°C during the time of sampling, while the second day was cloudy with a mean ambient air temperature of 21.2°C. Fifteen replicate readings were taken between 11h00 and 13h00 for each of the six treatments on each day.

Sites where *Balanus glandula* and *Chthamalus dentatus* co-occurred could not be found, as they do not currently overlap in their geographic ranges. As upwelling is known to influence barnacle recruitment (Pfaff et al. 2011), two West Coast sites within the Cape Columbine upwelling cell (i.e. Paternoster and Sandy Point) and two South Coast sites clustered within the Cape Hangklip upwelling cell (i.e. Rooiels and Cape Hangklip) were chosen (Figure 1). All sites experienced moderate wave exposure.

At each site, four treatments were used to manipulate rock temperature. Black, grey, white and clear granulated non-slip HW Aquac tape was glued onto clear 0.5mm PVC plates using clear ©Bostick marine glue (Figure 1). As not all colored tape was available with the same surface texture, clear tape was overlaid on all colors to standardize texture. This is important as barnacles are sensitive to texture when settling (Savoya and Schwindt 2010; Lathlean and Minchinton 2012). While black, grey and white plates were experimental treatments, clear plates acted as treatment controls (since they were a similar color to the rock once overlaid), and natural rock quadrats acted as experimental controls. While it has been shown that some fouling organisms, like algae and polychaetes, are sensitive to anti-fouling paint color and may have greater settlement on certain colors (Swain et al. 2006), no such studies have showed that barnacles are similarly affected by substrate color. Six 10 x 10cm plates of each treatment were randomly drilled into flat rock surfaces within the mid-shore zone, so as to give them maximum contact with the rock. Additionally, six 10 x 10cm natural rock quadrats were delineated at each site. All plates and quadrats faced northwest and were placed on surfaces orientated between 145° and 180°.



**Figure 1.** The experimental set-up of treatments used. Sites shown on the West Coast fall within the Cape Columbine upwelling cell, while those on the South Coast are located in the Cape Hangklip cell. Photographs of plates are depicted to illustrate differences in colors (i.e. black, grey, white, clear, and rock).

Photographs were taken of each plate every two weeks at low tide for 18 weeks from August to December 2013. These photographs were used to document settlement, mortality, recruitment and growth of each species. Individual barnacles that settled on plates were numbered based on their positions and were tracked through time. Settlement was documented up to week 18 by counting newly settled barnacles every two weeks. Mortality was documented up to week 18 by recording the loss of barnacles that had previously been present. Recruitment was defined as the number of barnacles still alive after week 10. As high mortality prevented using an age-class cohort approach, post-settlement growth was assessed for individual barnacles that settled by week 2 and had survived until week 6. As such, growth through time was taken as the change in basal area ( $\text{mm}^2$ ) measured every two weeks until week 6, and total growth as the basal area ( $\text{mm}^2$ ) of barnacles at week 6. Basal area was measured from photographs using ImageJ Software.

Barnacles measured were not touching and thus, there were no density-dependent growth effects.

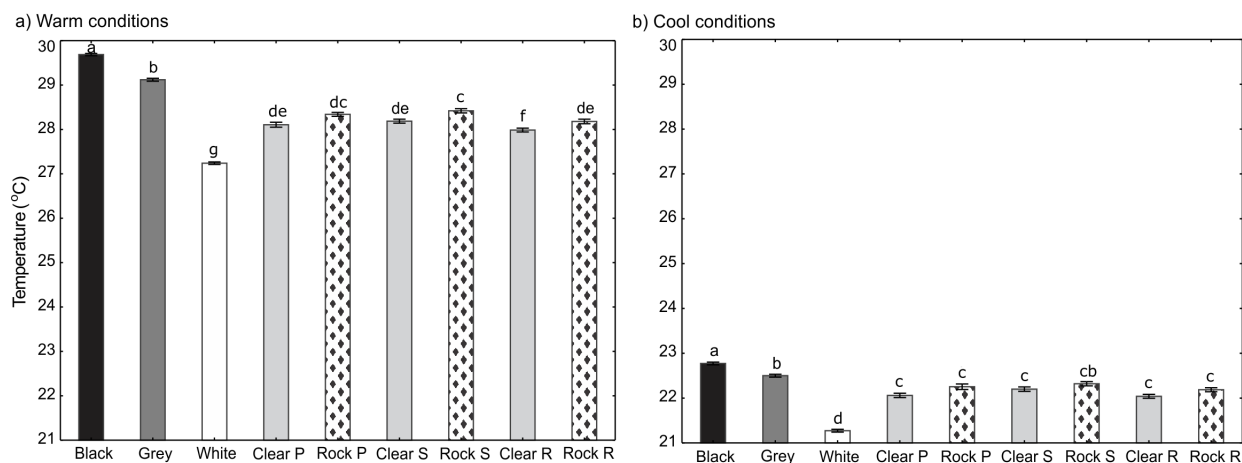
STATISTICA 12 was used to perform all analyses unless stated otherwise. ANOVAs and corresponding Tukey HSD tests were used to compare temperatures among treatments under warm and cool conditions. Because the color of the rock differed at each site and therefore, the clear plates also differed in color, temperature measurements for these treatments were analyzed separately per site.

As the two barnacle species did not co-settle they were analyzed separately. Cape Hangklip was unavoidably excluded from all analyses due to extremely low settlement (i.e. only nine barnacles settled on experimental plates in total). For all analyses of settlement, mortality and recruitment sites were grouped, where  $n=12$  plates for *B. glandula* (i.e. Sandy Point and Paternoster combined) and  $n=6$  plates for *C. dentatus* (i.e. only Rooiels) unless otherwise stated. For the analysis of growth, the level of replication was the number of individual barnacles pooled from all plates within a treatment. This approach was necessary to ensure sufficient replication throughout the six-week period for robust statistical analyses. Due to a severe storm that prevented me reaching Rooiels in week 16, no data was collected for this site at this time point. The loss of a large number of white plates at both West Coast sites in winter storms in week 11 resulted in this treatment only being included for statistical analyses that assessed settlement and growth of *B. glandula* through time and for total recruitment and growth that were quantified using data pre-week 11.

Kruskal-Wallis tests and multiple comparisons were used to compare settlement and mortality among treatments after 18 weeks, recruitment among treatments after ten weeks and growth among treatments after six weeks. Differences in the weeks analyzed per variable were strictly dependent upon the number of barnacles remaining on the plates. Barnacle settlement and mortality was pooled from all 18 weeks, however, recruitment was analyzed at week 10 as few barnacles survived all the way until week 18. Week 10 coincided with the last peak of settlement. Growth was calculated at week 6 as the same individual barnacles had to be present from week 2. After week 6 the number of individual barnacles still remaining steeply declined. As no statistical differences were found between Sandy Point and Paternoster data were combined ( $p>0.05$ ). When considering the effect of time and treatment on settlement, mortality, recruitment, and growth repeated-measures ANOVAs were conducted in R (v.3.0.1) followed by pairwise comparisons using adjusted Bonferroni p-values calculated by the single step method.

### 3. Results

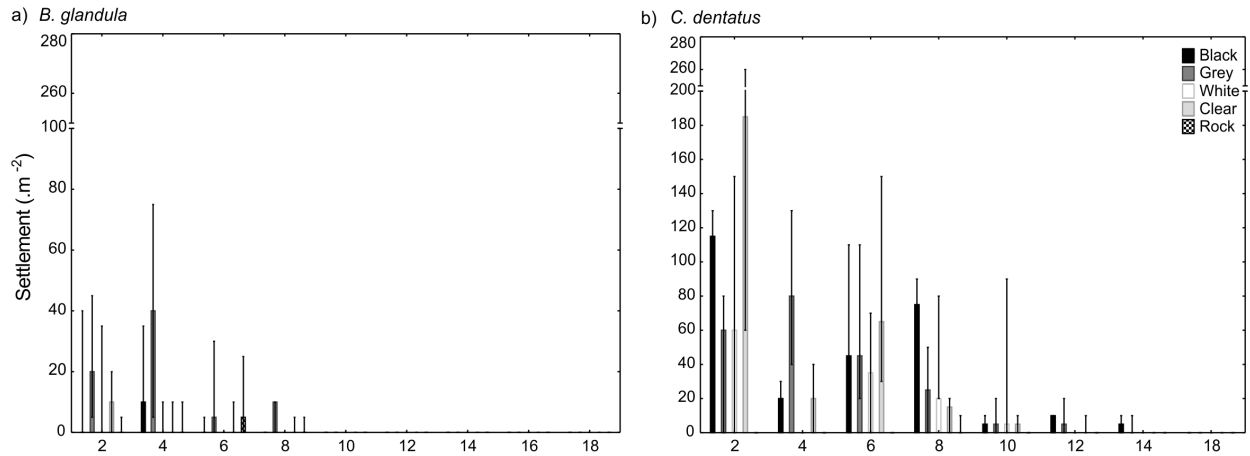
Regardless of weather conditions, a significant effect of treatment on the temperature of experimental plates was evident (ANOVA,  $p < 0.05$  in both cases) with black plates being hotter than grey, which in turn were hotter than white plates (Tukey HSD,  $p < 0.05$  in all cases) (Figure 2). Under warm conditions, rock temperatures were higher than those of clear plates at all sites (Tukey HSD,  $p < 0.05$  in all cases). While this trend was still evident under cool conditions, differences were not statistically significant ( $p > 0.05$ ).



**Figure 2.** Mean ( $\pm$ SE) temperature ( $^{\circ}$ C) of treatment plates on a) warm (air temperature= $27.1^{\circ}$ C) and b) cool (air temperature= $21.2^{\circ}$ C) conditions.  $n=15$  for all treatments. P= Paternoster, S=Sandy Point and R=Rooiels. Shared letters indicate no statistical difference ( $p > 0.05$ ).

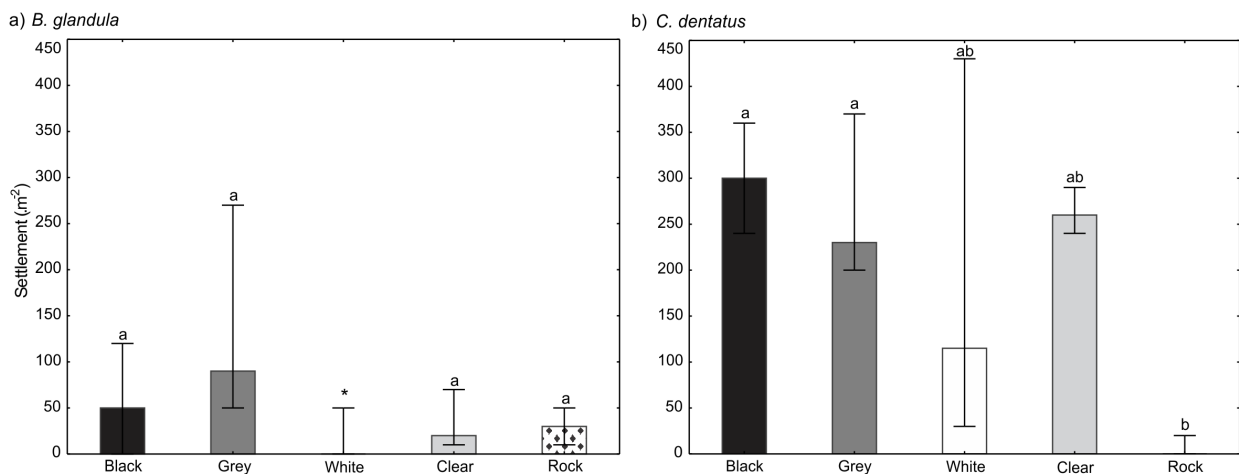
At both West Coast sites settlement of *B. glandula* through time showed a significant effect of sampling week (ANOVA,  $F_{5,11}=6.18$ ;  $p < 0.05$ ) and treatment (ANOVA,  $F_{5,11}=2.64$ ;  $p < 0.05$ ). Post-hoc analyses revealed that at Sandy Point black and white plates supported significantly lower settlement than grey plates (Multiple comparisons,  $p < 0.05$  in all cases), while no pairwise differences between treatments were evident at Paternoster. Settlement on all treatments peaked at week 4 and then decreased significantly (T-test,  $p < 0.05$  in all cases). At both sites, no *B. glandula* settlement was recorded after week 10 (Figure 3a). *C. dentatus* settled in higher numbers than *B. glandula* and over a longer period of time (Figure 3b). In contrast to *B. glandula*, *C. dentatus* settlement through time showed a significant effect of week (Repeated-measures ANOVA,  $F_{5,5}=14.37$ ;  $p < 0.05$ ), but no effect of treatment (Repeated-measured ANOVA,  $F_{5,5}=2.35$ ;  $p > 0.05$ ). Settlement on all treatments peaked between week 2 and 8 and then decreased significantly (T-test,  $p < 0.05$  in all cases), halting after week 14.





**Figure 3.** Median (25<sup>th</sup>, 75<sup>th</sup> percentiles) settlement (barnacles.m<sup>-2</sup>) through time of a) *B. glandula* (n=12) and b) *C. dentatus* (n=6).

While no significant differences in total settlement were recorded among treatments for *B. glandula* (Kruskal-Wallis,  $H_{3,40}=6.46$ ;  $p>0.05$ ) (Figure 4a), significant differences were detected for *C. dentatus* (Kruskal-Wallis,  $H_{4,28}=13.09$ ;  $p<0.05$ ). For the native barnacle, black and grey treatments supported significantly greater settlement than did natural rock (Multiple comparisons,  $p<0.05$  in all cases) (Figure 4b). It is notable that settlement on rock for *C. dentatus* was more than 100 times lower than on any of the treatment plates.

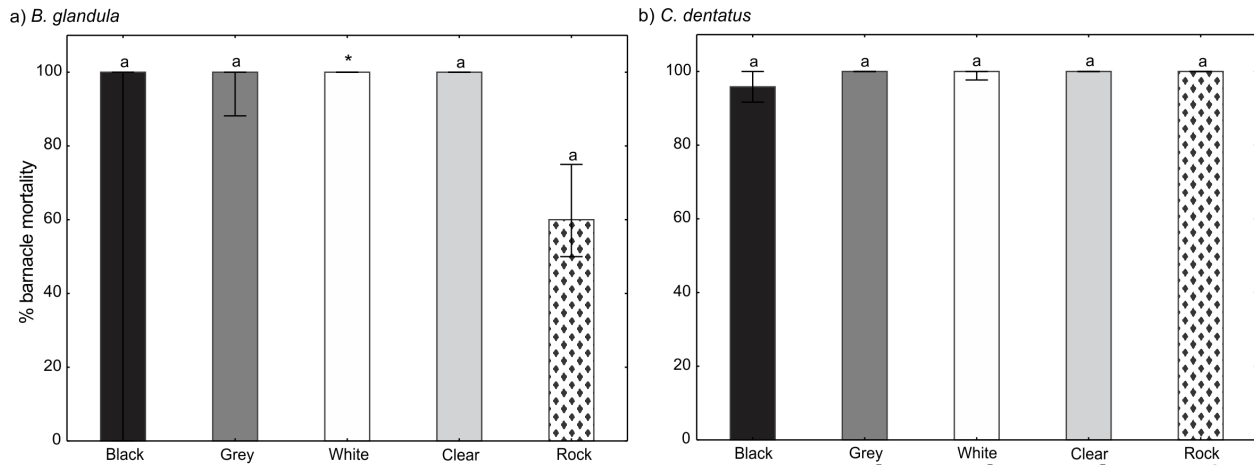


**Figure 4.** Median (25<sup>th</sup>, 75<sup>th</sup> percentiles) total settlement (barnacle.m<sup>-2</sup>) of (a) *B. glandula* and (b) *C. dentatus* recorded over 18 weeks. \*indicates exclusion from statistical analyses due to loss of experimental plates. Shared letters indicate no statistical difference ( $p>0.05$ ).

Significant differences in mortality of *B. glandula* were detected among treatments (Kruskal-Wallis,  $H_{3,34}=10.27$ ;  $p<0.05$ ) with mortality being lowest on rock. However, pairwise comparisons found no significant differences between treatments (Multiple

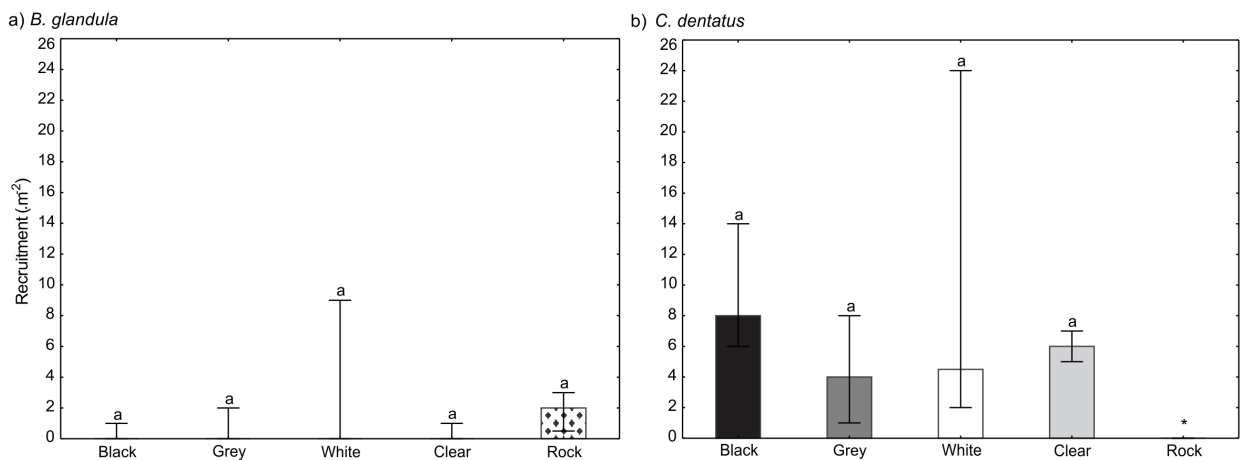


comparisons,  $p > 0.05$  in all cases) (Figure 5a). In contrast to *B. glandula*, *C. dentatus* showed no differences in mortality among treatments (Kruskal-Wallis,  $H_{4,23} = 7.12$ ;  $p > 0.05$ ) (Figure 5b).



**Figure 5.** Median (25<sup>th</sup>, 75<sup>th</sup> percentiles) percent barnacle mortality of (a) *B. glandula* and (b) *C. dentatus*. \*indicates exclusion from statistical analyses due to loss of experimental plates. Shared letters indicate no statistical difference ( $p > 0.05$ ).

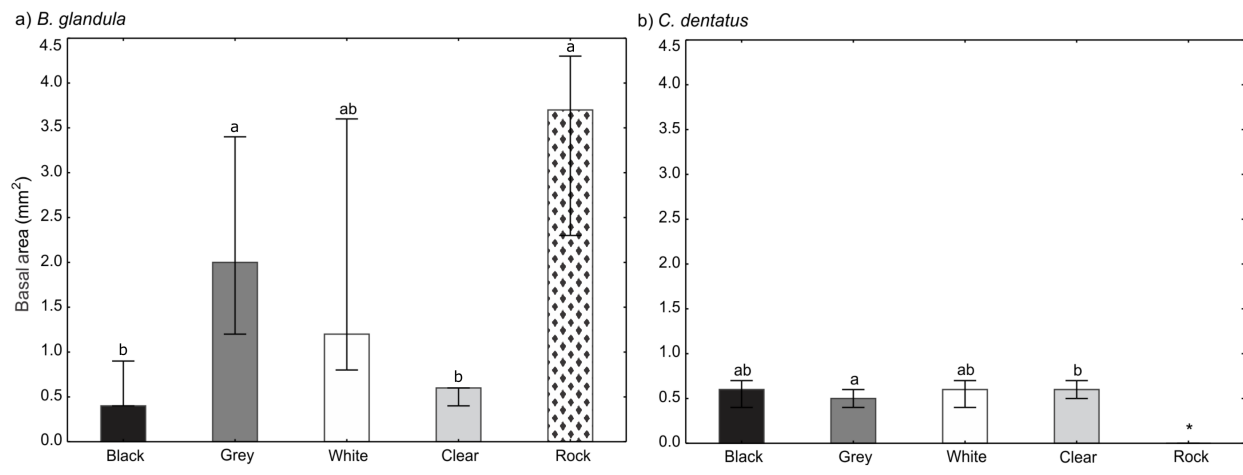
Recruitment of *B. glandula* was very low on all treatments and while higher on rock this was not statistically significant (Kruskal-Wallis,  $H_{4,43} = 6.84$ ;  $p > 0.05$ ) (Figure 6a). Recruitment of *C. dentatus* showed a different pattern with a significant effect of treatment (Kruskal-Wallis,  $H_{4,29} = 12.87$ ;  $p < 0.05$ ). Yet, pairwise comparisons revealed no differences in recruitment among treatments (Multiple comparisons,  $p > 0.05$  in all cases) (Figure 6b).



**Figure 6.** Median (25<sup>th</sup>, 75<sup>th</sup> percentiles) recruitment (barnacle.m<sup>-2</sup>) of (a) *B. glandula* and (b) *C. dentatus*. \*indicates exclusion from statistical analyses. Shared letters indicate no statistical difference ( $p > 0.05$ ).

An assessment of growth found that both *B. glandula* (ANOVA,  $F_{2,92} = 6.18$ ;  $p < 0.05$ ) and *C. dentatus* (ANOVA,  $F_{2,316} = 3.25$ ;  $p < 0.05$ ) grew slowest in the first two weeks following

settlement (Multiple comparisons,  $p < 0.05$  in all cases). Consideration of *B. glandula* growth over 6 weeks found non-systematic differences among treatments (Kruskal-Wallis,  $H_{4,216} = 50.02$ ;  $p < 0.05$ ). Largest barnacles occurred on rock, grey and white plates (Multiple comparisons,  $p < 0.05$  in all cases) (Figure 7a). *C. dentatus* growth over 6 weeks could only be assessed on experimental treatments as all barnacles that settled directly on rock died within the first four weeks after settling. The size reached by this species was less variable among treatments than that of *B. glandula* and once again non-systematic differences in growth were detected (Kruskal-Wallis,  $H_{3,626} = 26.56$ ;  $p < 0.05$ ). For *C. dentatus*, individuals on grey plates were smaller than clear plates (Multiple comparisons,  $p < 0.05$ ) (Figure 7b).



**Figure 7.** Median (25<sup>th</sup>, 75<sup>th</sup> percentiles) basal area (mm<sup>2</sup>) of (a) *B. glandula* and (b) *C. dentatus* after 6 weeks. \*indicates exclusion from statistical analyses. Shared letters indicate no statistical difference ( $p > 0.05$ ).

#### 4. Discussion

As a result of climate change, invasive species' distributions are expected to shift and expand into new habitats, facilitating contact with previously unencountered native species (Hellman et al. 2008; Doney et al. 2012). This is expected to alter species interactions in recipient regions (Byers 2002; Helmuth et al. 2006; Shinen and Morgan 2009). While climate-driven temperature changes will act at the level of individuals by increasing physiological stress, impacts will also manifest at the population level due to knock-on impacts on recruitment (Shanks 2009; Lamb et al. 2014), mortality (Bertness 1989; Findlay et al. 2010) and growth rates (Findlay et al. 2010; Sorte et al. 2010a; Lamb et al. 2014). In turn, these changes are likely to alter biotic interactions between invasive and native species (Byers 2002). It has been suggested that competition between the dominant invasive barnacle, *Balanus glandula*, and the native barnacle, *Chthamalus dentatus*, has caused a reduction in the numbers of the latter along the West Coast of South Africa (Simon-Blecher et al. 2008). Within this context this chapter aimed to elucidate the effects

of changing substratum temperature on the early life-history processes of these species to provide insight into potential outcomes of the eastward spread of *B. glandula*.

#### 4.1 Thermal manipulation of artificial substrata in the intertidal

The settlement of many marine organisms is influenced by substratum texture (Skinner and Coutinho 2005; Menge et al. 2010; Savoya and Schwindt 2010) and temperature (Shanks 2009; Lathlean et al. 2013). Many studies that have manipulated environmental variables in the intertidal have also employed the use of artificial settlement plates to account for surface texture successfully (Shanks 2009; Lathlean and Minchinton 2012). While these studies found that artificial substrata encouraged barnacle settlement and recruitment (see Menge et al. 2010 and Lathlean and Minchinton 2012) and increased mortality (Shanks 2009), my results do not concur. My results did not reveal systematic differences in settlement, mortality, recruitment or growth between treatment plates and rock. This could either indicate that settlement plates with textured tape appropriately accounted for substratum texture or that barnacle survival rates in this particular year were very low in general. Furthermore, possible differences in species responses could be at play and therefore, this study demonstrates the importance of also considering species-specific responses to experimental manipulations.

#### 4.2 Effect of temperature on early life-history processes

Temperature has been documented to have multiple impacts on intertidal organisms influencing not only population distributions (Somero 2002; Gilman 2006; Herbert et al. 2007; Jones et al. 2010), but also early life-history stages (Gosselin and Qian 1997; Hunt and Scheibling 1997; Lathlean et al. 2013; Rognstad and Hilbish 2014). For instance, body temperature (Harley and Lopez 2003) and mortality for barnacles (Harley and Helmuth 2003) and limpets (Denny and Harley 2006) is tightly correlated with rock temperature. Despite this, in my study temperature differences among treatments were not associated with differences in early life-history processes for either study species. This suggests that either settlement plate temperatures did not exceed thermal limits and that both species may have wide thermal tolerances, or that the temperature experienced on plates was sufficiently stressful that almost all barnacles died regardless of treatment.

*B. glandula* is native to the cool-temperate west coast of North America (Geller et al. 2008) where average water temperatures range from 2.2 to 21.1°C (Geller et al. 2008; Crawford 2014). Studies conducted along the west coast of the USA (Berger and Emler 2007) and invaded coastal areas of Argentina (Schwindt 2007) and Japan (Geller et al. 2008) have shown *B. glandula* is able to survive under a wide range of temperatures. In fact, in both Argentina and Japan *B. glandula* experiences wider temperature ranges than within its native range (Geller et al. 2008). While in its native range the upper distributional limits of *B. glandula* are negatively correlated with increasing temperature

(Harley 2011), the species has shown to tolerate substrate temperatures up to 46.5°C (Harley and Lopez 2003). In contrast, *C. dentatus*' historical presence along the entire South African coast (Branch et al. 2010) suggests it is a warm temperate species tolerant of a wide thermal range. This is particularly evident when considering that the average monthly water temperatures range from 11 to 26°C when moving from west to east along the South African coast (Smit et al. 2013). Thus, although temperature has shown to affect early life-history processes of some barnacle species (Shanks 2009; Findlay et al. 2010; Sorte et al. 2010a; Lamb et al. 2014), it is possible that temperature alone may not exert a direct regulating effect on these biological processes for either *B. glandula* or *C. dentatus*. A similar finding has been made for *Semibalanus balanoides* and *Elminius modestus* (Findlay et al. 2010). It is thus suggested that differences in early life-history processes between *B. glandula* and *C. dentatus* may be evidence of a competitive advantage held by *B. glandula* that may be more important in determining its future distribution and impacts on the South Africa coast than regional or climate related changes in substratum temperature.

#### 4.3 The role of competition in early life history processes

Interspecific competition is known to affect the settlement (Connell 1961a, 1961b; Kado 2003), mortality (Connell 1961a, Gaines and Roughgarden 1985; Hunt and Scheibling 1997), recruitment (Connell 1985; Menge 2000), and growth of barnacles (Menge 2000; Elías and Vallarino 2001; Leslie 2005). It has been suggested that *B. glandula* outcompeted native barnacles along the Japanese coastline by breeding at small sizes and settling in high densities before native barnacles, thereby disrupting their ability to settle and recruit (Kado 2003). The fact that *B. glandula* and *C. dentatus* do not co-occur in South Africa precludes direct assessments of competition, but my results may suggest that *B. glandula* shows relatively higher settlement than *C. dentatus* on natural rock. This relative higher settlement of *B. glandula* could be attributed to high fecundity rates (Newman and Abbott 1980) or its tendency to establish in high densities (Kado 2003; Geller et al. 2008). These traits could provide adaptive advantages in invaded regions and likely play a role in determining its settlement success in South Africa.

Mortality of newly settled invertebrates can be influenced by abiotic factors as well as competition and predation (Hunt and Scheibling 1997; Menge 2000). My results revealed that mortality rates for both species were very high – almost 100 percent in many cases. This aligns with numerous studies that have found newly settled invertebrates to be extremely susceptible to mortality (Gaines and Roughgarden 1985; Gosselin and Qian 1997; Menge 2000). While crowding can increase mortality of settled and growing barnacles (Connell 1985; Gaines and Roughgarden 1985), this was not evident in this study, as barnacles never touched. Some studies have found that mortality was significantly higher on artificial plates than on the natural rock due to heightened temperatures (Shanks 2009). While black and grey plates in my study did represent higher temperatures than

bare rock, white plates were significantly cooler. Mortality was also not significantly higher on artificial plates than on rock, suggesting that temperatures experienced on artificial plates in this study, did not represent lethal temperatures for either species. Although *B. glandula* and *C. dentatus* do not currently coexist, the lower relative mortality of *B. glandula* on rock recorded by this study is notable. Should this trend persist when the species are exposed to the same biotic and abiotic conditions, this pattern may reflect a competitive advantage held by *B. glandula*.

A species with high settlement and low mortality will experience high recruitment into the adult population. As barnacle life-history parameters are affected by temperature (Lathlean and Minchinton 2012, Lathlean et al. 2013; Alam et al. 2013), regional temperature differences and changing climate can be expected to affect population sizes. The fact that my results suggest higher relative recruitment of *B. glandula* than *C. dentatus* could be a reflection of *B. glandula*'s higher relative settlement and lower relative mortality on rock. While temperature played a direct role in influencing the recruitment of barnacles along the southeast coast of Australia (Lathlean and Minchinton 2012), my study did not find that to be the case in South Africa. Despite several differences between the two study designs, different time scales might explain these different outcomes. Since my study assessed not just early life-history, but also the effect of temperature over a long period of time (i.e. five months), my results are likely to be a good reflection of the relevance of temperature to these species at an ecological relevant scale along the coast of South Africa. However, it is also possible that temperature appears not to effect barnacle mortality and recruitment due to differential early post-settlement mortality on treatments that occurred between sampling intervals and thus, went undetected. Furthermore, because recruitment of both *B. glandula* and *C. dentatus* was so low and variable in this study, it's possible that the power to detect any significant differences among treatments was low.

In South Africa, the invasive intertidal mussel, *Mytilus galloprovincialis*, is known to exhibit high growth rates in comparison to native mussels (Steffani and Branch 2003), which is believed to give them a competitive advantage (Griffiths et al. 1992). My results provide evidence that *B. glandula* possesses such an advantage over *C. dentatus*. As individuals in the analyses were of the same age and both species reach similar adult sizes (5 – 10mm), *B. glandula*'s greater relative size after six weeks is indicative of a higher growth rate. This high growth is well documented in the literature (Connell 1961a, 1970; Leslie 2005). In low initial densities, *B. glandula* exhibits highest growth rates and thus is able to achieve large sizes quickly (Leslie 2005). In its native range, *B. glandula* achieves higher percent cover than the native barnacle *Chthamalus dalli* despite low initial densities (Menge 2000). These examples suggest that not only is a high growth rate competitively advantageous, but also that native species could be negatively impacted by the high growth rates of invasive species.

## 5. Conclusion

Results from this chapter revealed that there were no systematic effects of temperature on the early life-history processes of either species. However, the fact that settlement and recruitment of *Balanus glandula* were relatively higher, mortality was relatively lower, and growth was relatively greater on rock than that of *Chthamalus dentatus* is notable. In light of this, it is possible that a broad thermal tolerance coupled with a competitive nature could enable *B. glandula* to spread further north and southeastward along the South African coast despite climate-related changes. This study has revealed the importance of assessing the potential impacts of climate change on invasive species at a local scale and how they may moderate interactions between invasive and native species.

## CHAPTER 4

### **The effect of water temperature and food concentration on the filtration and feeding behavior of the invasive barnacle *Balanus glandula* and the indigenous barnacle *Notomegabalanus algicola***

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#### **1. Introduction**

Currently, limited methodologies exist to effectively assess and predict impacts of invasive species on native biota (Parker et al. 1999; Bollache et al. 2008). Recently, however, a novel methodology that compares resource utilization between invasive and native species has been developed to address this need (Dick et al. 2014). If found to be effective in a variety systems, this methodology could help predict a species' potential for becoming invasive and provide insight into possible ecological impacts (Bollache et al. 2008; Dick et al. 2013; Dick et al. 2014). To date, it has been shown that invasive species are generally more efficient at utilizing resources than native comparators, which is often mirrored in impacts detected in the field (Bollache et al. 2008; Johnson et al. 2008; Weis 2010; Dick et al. 2013). It follows that the higher the resource use of an invader in comparison to native biota, the greater threat it may represent to the receiving environment and the biotic communities (Dick et al. 2013). High resource use can be driven by a number of factors, such as differences in size or fecundity rates between invasive and native species (Bollache et al. 2008).

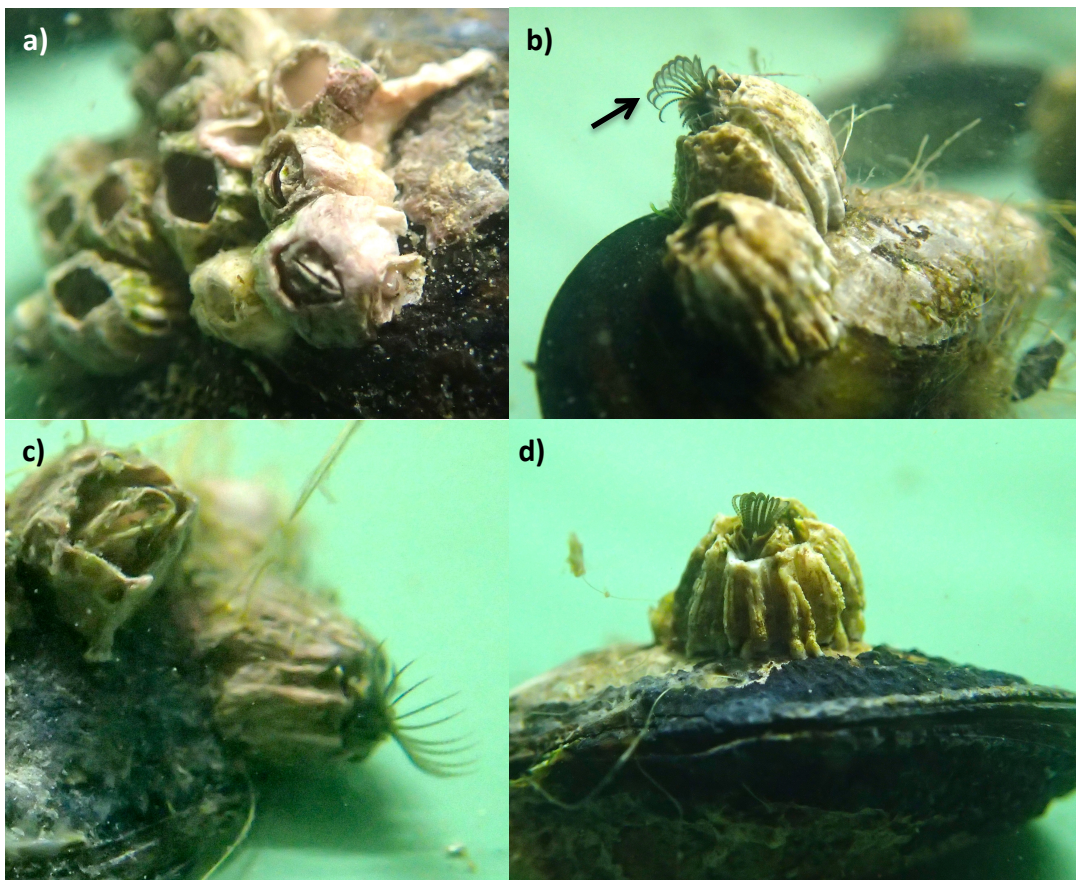
Comparisons of resource use between invasive and native species have already been undertaken in several biological systems. These include studies on plants (Funk and Vitousek 2007), marine amphipods (Bollache et al. 2008), freshwater amphipods (Dick et al. 2010; MacNeil et al. 2013), freshwater crayfish (Twardochleb et al. 2012), freshwater mysid crustaceans (Barrios-O'Neill et al. 2013) and freshwater fish (Alexander et al. 2014). In these investigations, resource use of the alien species was systematically higher than the native comparator. In some cases, this methodology may be helpful in quantifying the level of biotic resistance of a native community to invaders (Twardochleb et al. 2012; MacNeil et al. 2013) or how predator-prey relationships may be altered by invaders' resource use (Barrios-O'Neill et al. 2013). Although this methodology has been tested in a range of taxa, filter feeders have not been considered.

#### *1.1 Barnacle feeding structures and behavior*

Cyprid larvae are the free moving, non-feeding stage of the barnacle's life-history. Once attached to a substratum, they metamorphose into feeding juveniles (Gaines and Roughgarden 1985) and are then capable of both active and passive feeding (Geierman and Emler 2009). Barnacle feeding structures are called cirri, which are thin feather-like



appendages that are either swept through the water to create a current that carries particles to the barnacle, or are extended into the current to passively capture particles (Sanford et al. 1994; Geierman and Emlet 2009). Barnacles display four main feeding types: “inactive”, “active”, “passive”, and “pumping” (Geierman 2007 (Figure 1). Which feeding mode is employed is based in part on water flow (Crisp and Southward 1961; Lewis 1981; Geierman 2007). In higher currents, barnacles are typically passive feeders, maximizing their consumption rates while minimizing energy expenditure (Crisp and Southward 1961; Sanford et al. 1994; Geierman and Emlet 2009). In slower currents they often switch to active feeding (Crisp and Southward 1961; Trager et al. 1990; Sanford et al. 1994). Regardless of water flow juveniles often spend more time feeding than do adults (Sanford et al. 1994; Geierman and Emlet 2009).



**Figure 1.** Barnacle feeding types showing the movement of the cirri (indicated by the arrow) during a) inactive, b) active, c) passive and d) pumping feeding types.

Water temperature can affect the feeding rates of marine organisms, including barnacles (Sanford et al. 1994; Nishizaki and Carrington 2014). Barnacle cirral beat rates, and thus filtration rates, increase with temperature up to a threshold (Lewis 1981; Sanford et al. 1994; Geierman 2007). For some barnacle species, high temperatures are associated with slower feeding rates, which have been attributed to elevated metabolic rates and



increased energy expenditure during feeding (Sanford et al. 1994). *Balanus glandula* routinely experiences wide temperature ranges in its native range (Newman and Abbot 1980), which would likely influence its feeding rates. While an optimum thermal feeding range has been recorded at 10 – 15°C for this species in Washington, USA (Nishizaki and Carrington 2014), *B. glandula* also spans the coast down to the warmer waters of southern California, USA (Newman and Abbot 1980). Barnacles in this geographic region could have a higher optimum temperature for feeding, although a specific optimal range has not been documented here.

The presence of food can also influence barnacles feeding activity (Lewis 1981). When food is offered to barnacles, cirral beat rates often increase (Crisp and Southward 1961) and consumption rates increase proportionally with the concentration of food given (Crisp and Southward 1961; Sanford et al. 1994). At highest food concentrations, however, filtration rates decrease presumably because of greater acquisition of food particles during feeding (Crisp and Southward 1961). Particle size may also affect the feeding type employed (Crisp and Southward 1961) with barnacles unable to feed outside their particle handling range (Crisp and Southward 1961).

Despite comparisons of resource utilization having been carried out between invasive and native species in various systems, this methodology has not been tested for filter feeders. In this chapter, I aim to provide the first direct comparison of resource utilization between invasive and native barnacles. Specifically, I assess how water temperature and food concentration affect food filtration and feeding behavior of *B. glandula* and the native *Notomegabalanus algalicola*. Average temperatures experienced by these species along the West (13°C) and South (20°C) Coasts of South Africa were selected from the literature (Smit et al. 2013). These two coasts are also characterized by high and low primary productivity, respectively (Bustamante et al. 1995). By combining these variables, I aimed to test the effect of water temperature and food concentration on the food resource use of both species to gain an indication of how *B. glandula* might respond if (1) the species continues to spread southeast into warmer waters with lower productivity or (2) water temperatures increase as a result of climate change. This chapter thus tests the following hypotheses:

**H<sub>1</sub>:** Temperature will have an effect on the filtration of both species. It is anticipated that *B. glandula* will have higher filtration under cool West Coast conditions (13°C), while *N. algalicola* will have higher filtration under warmer South Coast conditions (20°C).

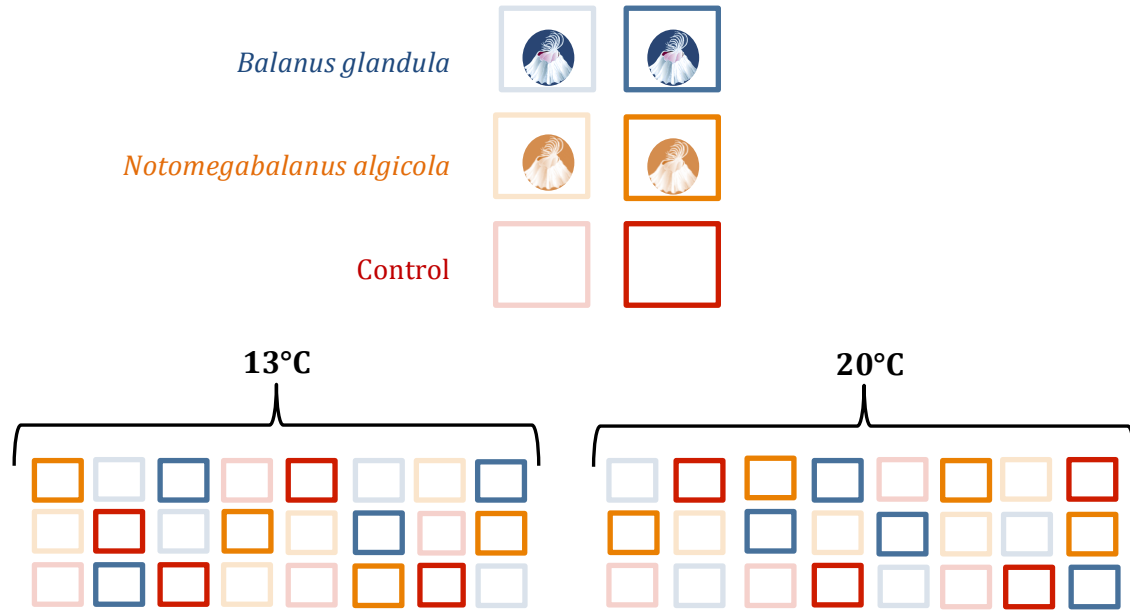
**H<sub>2</sub>:** Temperature will have an effect on the feeding behavior of both species. It is anticipated that more *B. glandula* will feed under cool West Coast conditions (13°C) and that they will feed for longer while exhibiting faster cirral beat rates. The opposite is expected for the native *N. algalicola*.

## 2. Methodology

*Balanus glandula* and *Notomegabalanus algalicola* were collected from Bloubergstrand along the West Coast of South Africa. To facilitate collection, only barnacles that had settled on mussel shells were selected. After collection, mussel shells were pried open and all flesh was removed. Barnacles were placed in tanks of artificial seawater and acclimated to lab conditions for at least 48 hours prior to experiments. Barnacles were fed a commercially produced algal feed comprised of *Isochrysis sp.* and *Pavlova sp.* ranging from 4-10 $\mu$ m in size (Brightwell Aquatics PhytōGold-S). As individuals of equivalent sizes could not be found on the shore, size was accounted for during all experiments by standardizing biomass among species: Fifty *B. glandula* barnacles and fifty *N. algalicola* barnacles were weighed using a scale and the average weight of each barnacle per species was determined. A fixed biomass of each species was selected for use in the experiments (i.e. it was determined that for every 20 barnacles of *B. glandula* weighing 9.74g, 30 barnacles of *N. algalicola* would be needed to achieve equal biomass).

### 2.1 Filtration trials

Barnacles were placed into tanks with 500ml artificial seawater with a salinity of 34ppt and starved for 48 hours to standardize hunger. Groups of each species weighing 4.87g were randomly allocated to (1) a high concentration treatment ( $32 \times 10^6$  algal cells.ml<sup>-1</sup>) or (2) a low concentration treatment ( $1 \times 10^6$  algal cells.ml<sup>-1</sup>). The high concentration was made by placing 0.042666ml of the algal solution in a tank with 499.957ml of seawater, whereas the low concentration was made by placing 0.00666ml of the algal solution in a tank with 499.993ml of seawater. This was done to maintain equal volumes in each tank. Algae used in this experiment were the same upon which the barnacles were maintained. Controls for each concentration were treated in the same way as experimental treatments, but no barnacles were added. All treatments were replicated four times (Figure 2). These filtration trials were run at 13 and 20°C. During the experiment, water flow was maintained by aerating tanks continuously. Flow cytometry was used to count the number of algal cells remaining after one hour. Algal cells were of similar size to beads used by the flow cytometer. Thus, the LIVE/DEAD® BacLight™ Bacterial Variability Counting Kit (L34856) was used to stain algal cells, making them clearly differentiable from the beads. Experimental temperatures were maintained using a digitally controlled chiller and did not vary by more than 0.05°C.



**Figure 2.** Experimental set-up run at 13 and 20°C. The color gradation represents algal cell concentrations from low (light) to high (dark). There were four replicates of each treatment.

## 2.2 Feeding behavior trials

In order to assess feeding behavior of *B. glandula* and *N. algicola* equal biomasses of each species (i.e. 9.74g) were placed in separate tanks with 3l of artificial seawater and supplied with  $375 \times 10^6$  algae cells.ml<sup>-1</sup>. Cameras mounted above tanks were used to film barnacles for ten minutes. From each video, the percentage of barnacles that fed was quantified. Of those barnacles that fed, five were randomly chosen and the following information recorded: (1) the length of feeding time, (2) cirral beat rate per minute and (3) feeding types displayed (i.e. inactive, active, passive, and pumping). Barnacles were recorded as “inactive” if they had closed opercula valves and were not feeding for at least 3 seconds; “active” if barnacles were extending and contracting their cirri in sweeping motions continually; “passive” if barnacles keep their cirri extended in the water column longer than one second while feeding; and were recorded as “pumping” if the opercula valves were open and cirri were folded together pumping up and down. Four replicates groups per species were run at each temperature.

## 2.3 Statistics

As there were no significant decreases in the number of algal cells in the experimental control tanks, we were able to assume that any decrease in the number of algal cells in the treatment tanks was due to barnacle consumption. Therefore, the controls were dropped from further statistical analyses and associated graphs, and resource utilization between species was compared.

As not all barnacles fed during the filtration experiments, the percentage of feeding barnacles per species was used as a correction factor during filtration analyses to standardize feeding effort (e.g. correcting for a 30% difference in the number of barnacles that fed between species). Generalized linear models (GLM) were conducted in R (v.3.0.1) to assess differences in algal cells remaining among species at the different temperatures. These were run separately under conditions of low and high algae concentrations. Post-hoc pairwise t-tests were then conducted using a Bonferroni p-value adjustment model.

When analyzing feeding behavior the percentage of feeding barnacles and the percentage time spent feeding by each species at 13 and 20°C were Arcsine transformed. The percentage of feeding barnacles, the time spent feeding, and the cirral beat rates were evaluated using a GLM in R to determine differences among species and temperature. Post-hoc pairwise t-tests were conducted using Bonferroni p-value adjustment models. Chi-squared tests were used to assess differences in the frequency of feeding types (i.e. active, inactive, passive and pumping) displayed by 20 barnacles of each species at each temperature.

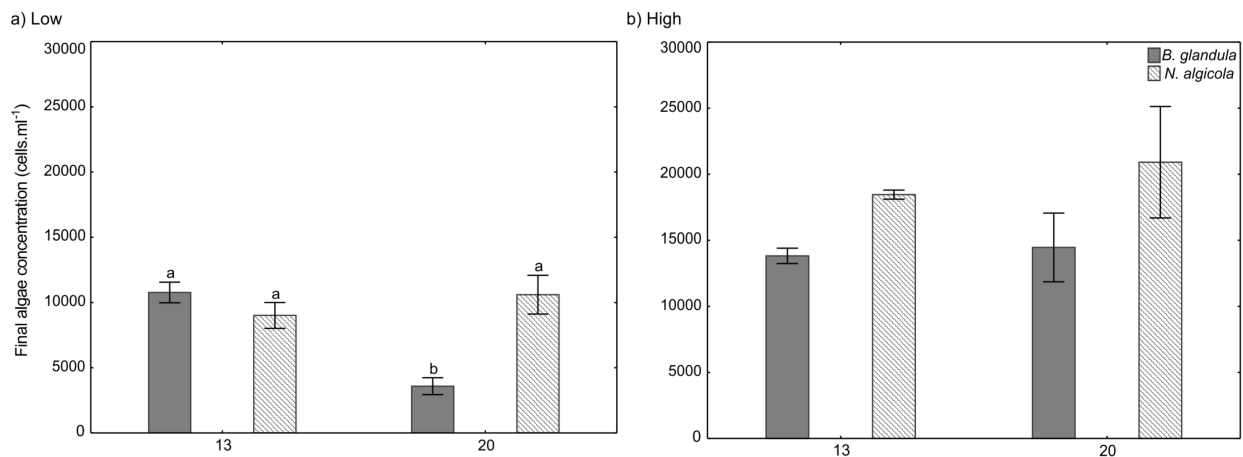
### 3. Results

#### 3.1 Filtration trials

Under experimental conditions simulating the South Coast (i.e. low algal concentration and warm water temperatures), species identity and temperature significantly affected the number algal cells remaining after one hour of barnacle filtration (Table 1). *B. glandula* removed significantly more algal cells under warmer temperatures associated with the South Coast than did the native species (Figure 3a). Under West Coast conditions (i.e. high algal concentration and cold water temperatures) only species identity significantly affected the number of remaining algal cells (Table 1). *B. glandula* removed more algal cells under cooler temperatures associated with the West Coast than did the native species (Figure 3b).

**Table 1.** a) GLM results of the effects of species and temperature on the number of algal cells remaining at low and high food concentrations after one hour of filtration. b) Results of post-hoc t-tests analyzing the effects of the low concentration on the number of remaining algal cells. B = *B. glandula*, N = *N. algicola*, 13 = 13°C, 20 = 20°C. ns = non-significant.

a) GLM	Factor	df	Effect	Null deviance	F-ratio	p-value
Low	Species	1		1908.2	4.02	ns
	Temperature	1		2568.6	5.42	p<0.05
	Species x Temp	1		10537.2	22.22	p<0.05
High	Species	1		5772.2	8.09	p<0.05
	Temperature	1		485.9	0.68	ns
	Species x Temp	1		77.7	0.10	ns
b) T-tests			B13	N13	B20	N20
Low	B13					
	N13		ns			
	B20		p<0.01	p<0.01		
	N20		ns	ns	p<0.01	



**Figure 3.** Mean ( $\pm$ SE) remaining algal cells (cells.ml<sup>-1</sup>) among species and temperature (13 and 20°C) at a) low and b) high concentrations, reflective of the South and West Coast, respectively. Shared letters indicate no statistical difference ( $p>0.05$ ).

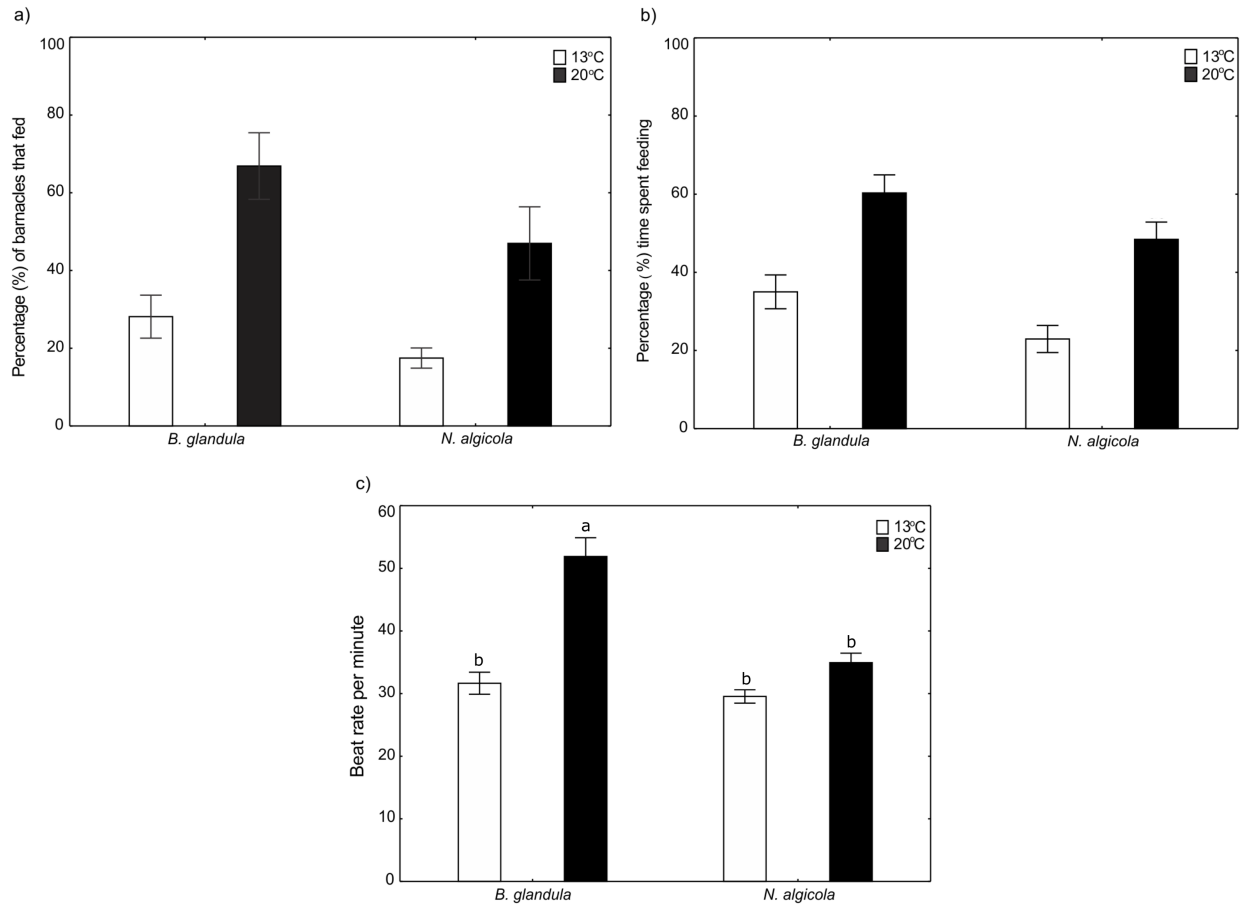
### 3.2 Feeding behavior trials

The percentage of barnacles that fed, the time spent feeding, and the cirral beat rate differed between *B. glandula* and *N. algicola* and was affected by temperature (Table 2). While the numbers of feeding barnacles did not differ among species within each temperature, more *B. glandula* fed at 20°C than did at 13°C (Figure 4). Both species spent a longer time feeding at 20°C than at 13°C (Figure 4b). Cirral beat rates were significantly affected by species identity and temperature (Table 2). *B. glandula*'s beat rate was

significantly faster at 20°C than at 13°C and also faster than the beat rate of *N. algalicola* at 20°C (Figure 4c).

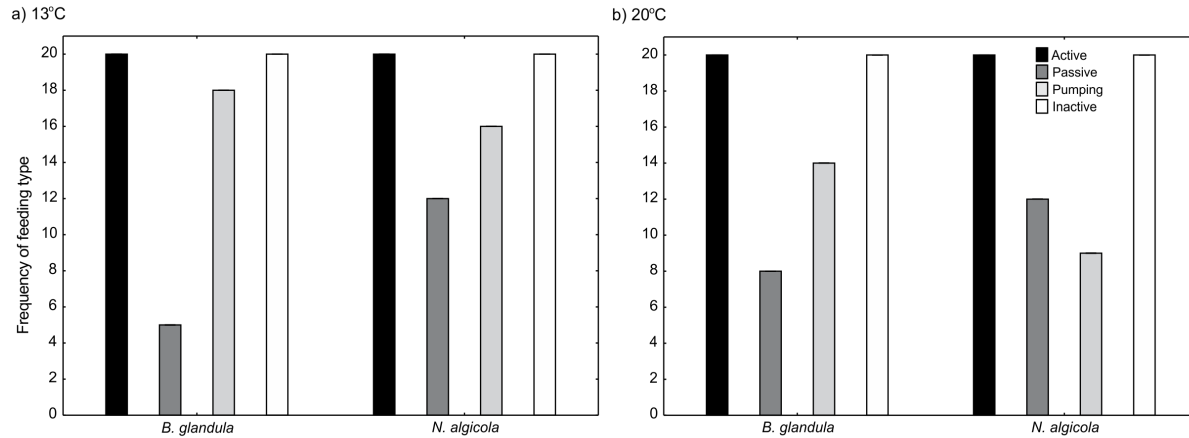
**Table 2.** a) Results from a GLM of the effects of species and temperature on the percentage of barnacles that fed, feeding time, and cirral beat rates. b) Results of post-hoc t-tests analyzing the effect of above variables on cirral beat rate. B = *B. glandula*, N = *N. algalicola*, 13 = 13°C, and 20 = 20°C. ns = not significant.

a) GLM	Factor	df	Effect	Null deviance	F-ratio	p-value
% Feeding	Species	1		17.89	5.30	p<0.05
	Temperature	1		86.73	25.71	p<0.01
	Species x Temp	1		0.106	0.03	ns
Feeding Time	Species	1		43.79	7.02	p<0.05
	Temperature	1		210.57	33.75	p<0.01
	Species x Temp	1		5.38	0.86	ns
Cirral Beat Rate	Species	1		49.16	26.23	p<0.01
	Temperature	1		89.33	47.77	p<0.01
	Species x Temp	1		18.87	10.09	p<0.01
b) T- tests			B13	N13	B20	N20
Cirral Beat Rate	B13					
	N13		ns			
	B20		p<0.01	p<0.01		
	N20		ns	p<0.01	p<0.01	



**Figure 4.** Mean ( $\pm$ SE) difference among species and temperature in a) percentage of feeding barnacles, b) percentage of time spent feeding, and c) cirral beat rate per minute. Shared letters indicate no statistical difference ( $p > 0.05$ ).

Neither species nor temperature had an effect on the frequency of feeding types displayed ( $X^2_{4, 8} = 6.01$ ,  $p > 0.05$ ) (Figure 5). There was, however, a trend of passive feeding being recorded more frequently for *N. algalicola* and pumping more frequently for *B. glandula* at both temperatures.



**Figure 5.** The frequency of feeding types displayed by 20 individuals of *B. glandula* and *N. algalicola* at a) 13°C and at b) 20°C, n = 20. All barnacles exhibit the active and inactive feeding types as only barnacles that were feeding were selected for analysis and at some point all barnacles were not feeding. There were no statistical differences between feeding types ( $X^2_{4,8} = 6.01, p > 0.05$ ).

## 4. Discussion

Comparisons of resource utilization between invasive and native species have shown promise in assessment and prediction of the impacts of invasive species on native biota (Bollache et al. 2008; Dick et al. 2014). To date, it has been shown that invasive species often exhibit a greater and more efficient use of food resources (Johnson et al. 2008; Weis 2010; Dick et al. 2013) and that the higher the resource utilization of an invader over the native species, the greater potential threat it represents for native communities (Dick et al. 2013). While these comparisons have been made in several biological systems (Twardochleb et al. 2012; Barrios-O'Neill et al. 2013; MacNeil et al. 2013; Alexander et al. 2014), this is the first application of the methodology in marine filter feeders. Climate change and associated temperature changes are likely to alter species and community interactions in marine systems (Pörtner and Knust 2007; Morley et al. 2014) and invasions will likely compound these changes (Brook et al. 2008; Sorte et al. 2010a). Thus, this study intended to assess how the combined changes in water temperatures and food concentration affect the filtration and feeding behaviors of the invasive barnacle, *Balanus glandula*, and the native, *Notomegabalanus algalicola*, along the coast of South Africa.

### 4.1 The effect of temperature and algae concentration on barnacle filtration

Studies have shown that both temperature (Sanford et al. 1994; Geierman 2007) and food concentration (Sanford et al. 1994) can influence barnacle feeding behavior. This work found that feeding is often greater at intermediate temperatures than at high temperatures, likely reflecting an increase in metabolic demand or an increase in thermal stress (Sanford et al. 1994; Nishizaki and Carrington 2014). In the presence of food



barnacles also tend to exhibit an increase in cirral beat rates (Crisp and Southward 1961) and thus consumption (Sanford et al. 1994).

The West Coast of South Africa is dominated by cool waters and high productivity (Bustamante et al. 1995). While my results revealed that filtration of *B. glandula* did not differ among temperatures, under conditions similar to the West Coast (i.e. 13°C and high algal concentrations), *B. glandula* demonstrated higher resource use than the native. This finding aligns with high abundances of *B. glandula* along the West Coast (see Chapter 2). In contrast, the South Coast is warmer and less productive (Brown et al. 1991). My results suggest that under these conditions *B. glandula* retains superior resource efficiency over *N. algicola*. This aligns with previous studies that have shown invasive species exhibit more efficient use of food resources than native comparators (Strayer et al. 1999; Johnson et al. 2008; Weis 2010). Overall, *B. glandula* displayed highest filtration under the warmer temperature than under cooler temperatures, which was contrary to what was predicted. Previous research supports this finding whereby the barnacle *Semibalanus balanoides* similarly displayed higher feeding rates at increasing temperatures (Sanford et al. 1994). A different pattern was observed for *N. algicola*, which showed no differences in filtration between West and South Coast conditions. Since this species has a range extending from west to east (Branch et al. 2010) its feeding optimum spans the thermal range of these coasts, which could account for this.

#### 4.2 Effect of temperature on barnacle feeding behavior

Changes in temperature can lead to changes in energy requirements and thus, behaviors may change to account for these alterations (Doney et al. 2012). These behavioral responses to changing temperature are known to occur in barnacles (Sanford et al. 1994; Geierman 2007; Nishizaki and Carrington 2014). My results revealed that the feeding behaviors of both species were affected by temperature. Although optimal thermal tolerance ranges for both *B. glandula* and *N. algicola* are unknown, both species successfully displayed feeding behaviors at both temperatures. This indicates that experimental temperatures are unlikely to have been outside either species thermal tolerance.

It is notable that more *B. glandula* barnacles were observed feeding for a longer time with a faster beat rate under warm South Coast conditions, than under cool West Coast conditions. These variables were also higher than those of *N. algicola* further indicating that this invader displays greater resource use than the native. Counter to my predictions, these findings suggest that *B. glandula* is not only able to filter at the higher temperatures, but is more active under warmer temperatures. This was unexpected as *B. glandula* is a cool temperate water species (Newman and Abbot 1980; Geller et al. 2008) and it was previously assumed that the species would not do well under the warm South Coast of

South Africa (Laird and Griffiths 2008). The results of several other studies taken together suggest a wide physiological tolerance of this species: *B. glandula* occurs in areas that experience cold water temperatures of around 2°C (Geller et al. 2008), while they feed optimally at intermediate temperatures of around 15°C (Nishizaki and Carrington 2014). *B. glandula* has also survived at temperatures up to 34°C, suggesting that the species may be adapted to thermally stressful environments (Berger and Emlet 2007) as well as cool temperate environments. If my findings hold true in the natural environment, heightened activity of *B. glandula* under warm South Coast conditions could be due to a wide physiological tolerance present in the South African population. For instance, if the native barnacle populations in North America have a broad physiological tolerance, but are not exposed to the extremes of this range, then the invading populations could successfully invade a variety of environments. Conversely, if the native populations have a narrow physiological tolerance, then a wide tolerance may be selected for in the invading population. Considering the wide temperature differences experienced along the entire west coast of North America and seasonal fluctuations (Crawford 2014), it is most likely that temperatures experienced by *B. glandula* along South African coast are within its physiological tolerance, but which may not be routinely experienced in its native range. This idea was suggested of *B. glandula* invading Japan (Geller et al. 2008).

It is important to note that while higher temperatures may not negatively affect filtration of adult barnacles, they may impact other biological processes or life stages, like reproduction or larvae development. Such evidence is seen in the barnacle, *Tesseropora rosea*, where warm temperatures result in reduced growth and survival (Lathlean et al. 2012). Similarly, while higher temperatures negatively impact the number of embryos and the survival of *Semibalanus balanoides* larvae (Rognstad and Hilbish 2014), temperature does not affect the species' rate of post-larvae growth (Findlay et al. 2010). Such differential thermal thresholds are known for other marine taxa as well (Rius et al. 2014).

While some barnacle species tend to display passive feeding more than others, many species of *Balanoides* tend not to exhibit this feeding type at all (Crisp and Southward 1961). My results suggest a higher frequency of the passive feeding type displayed by *N. algicola* and a higher frequency of pumping by *B. glandula* at both temperatures. Passive feeding is generally employed under intermediate water currents, while barnacles display active feeding under slower the water movement (Crisp and Southward 1961; Sanford et al. 1994; Nishizaki and Carrington 2014). Since the water flow speed was kept constant throughout the feeding behavior trials, differences in the feeding types displayed are not linked to water flow, but more likely reflect temperature driven or species-specific differences. These results have obviously implications for its presence here in South Africa and its recent spread around Cape Point (see Chapter 2). As 20°C represents an average water temperature along the South Coast (Smit et al. 2013), it possible that this

temperature does not represent a barrier for the species, but may actually represent a condition under which the species operates effectively.

## 5. Conclusion

This study represents the first attempt at applying a comparative resource use methodology to invasive marine filter feeders. This assessment has shown that *Balanus glandula* has the potential of invading the both the West and South Coasts of South Africa despite differences in temperature and productivity between the two. These results suggest 1) the invasive, *B. glandula*, exhibits a more efficient use of food resources than the native, 2) this is a reflection of differing feeding behaviors to temperature and food concentration by the two species, and 3) that the warmer South Coast conditions may not pose a barrier to the further spread and establishment of *B. glandula* in South Africa, assuming that *B. glandula* can meet its metabolic demand.

## SYNTHESIS

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Despite the fact that 86 marine alien species are recognized in South Africa, there is a general poor state of knowledge concerning the range and impacts of these species. To date, the impacts of only two invasive species have been quantified (see Mead et al. 2013 and Greef et al. 2013 for details). As climate change is an important driving force behind community changes and invasive species ranges are predicted to change (Whitney and Gabler 2008; Zerebecki and Sorte 2011), it is vital to quantify species' ranges and impacts to understand what changes may be induced by future climate change. To provide insight into potential outcomes of the eastward spread of *B. glandula* into warmer waters and provide better understanding for how biological processes of these species may be altered by climate induced changes in temperature, my thesis had three overarching aims: (1) to assess the current distribution and abundance of *Balanus glandula* in relation to native barnacle species along the West Coast of South Africa; (2) to elucidate the effects of varying substratum temperature on the settlement, mortality, recruitment and growth of *B. glandula* and the native *Chthamalus dentatus*; and (3) to assess the effect of water temperature and food concentration on the filtration and feeding behavior between *B. glandula* and the native *Notomegabalanus algicola*.

### CHAPTER 2: Status of *Balanus glandula*

*Balanus glandula*, an dominant intertidal invader, is one of few widely spread marine invasive species recognized along the South African coast (Mead et al. 2013). The aim of this study was to provide an up-to-date survey of the status of *B. glandula* in comparison to native barnacles, assessing (1) the distribution of *B. glandula* along the coast of South Africa to determine if the species was spreading and (2) the abundance of *B. glandula* and native barnacle species. Most notably, and despite previous expectations, it was found that *B. glandula* has extended its coast-wide range by 70km, breaching the biogeographic break of Cape Point and occurring in False Bay. While this well-known biogeographic break separates the cool temperate Benguela ecoregion from the warm temperate Agulhas ecoregion (Sink et al. 2011), Smit et al. (2013) showed that near-shore water temperatures along the South Coast up until Cape Agulhas experience similar temperatures to the West Coast for much of the year. Thus, it is possible that temperature may not be a restraining factor for the spread of *B. glandula* southward. Although, *B. glandula*'s distribution retreated from Lambert's Bay to Eland's Bay in 2013 and advanced back to Lambert's Bay in 2014 (Robinson et al. in press) this type of oscillation at invasion fronts is typical of barnacle populations (Suarez et al. 2006; O'Connor 2014). Given this, it is expected that the species will continue to spread further north as there is no known boundary to its spread in this direction.

While *B. glandula* showed consistently highest abundances in the mid-shore on the West and South Coasts, non-systematic differences in abundance of barnacles among sites and years suggest fluctuations in recruitment intensity and variations in larval supply that typify barnacle populations. *B. glandula* was the dominant barnacle in the intertidal zone along the West Coast, representing 100 percent of barnacles found at seven West Coast sites. A decrease in the number of native barnacle species recorded along the West Coast could suggest that *B. glandula* is outcompeting native species. However, the absence of these natives in this study does not demonstrate total exclusion from this coastline, but is cause for concern. Along the South Coast, native barnacles were most abundant. It is anticipated that increases in abundances of *B. glandula* are likely to occur as this species becomes more established at these newly invaded sites. This could have important consequences for the native communities along the South Coast, as those on either side of the biogeographic break of Cape Point are distinctly different (Emanuel et al. 1992; Sink et al. 2012). As such, this study clearly illustrates the importance of long-term monitoring and suggests that continued annual surveys are necessary to track future range changes of *B. glandula*, especially on the South Coast.

### **CHAPTER 3: Impact of substratum temperature on early life-history processes**

As marine invasions become increasingly prevalent, it is important to understand how climate change may moderate their spread and interactions with native communities. In light of the recent movement of *Balanus glandula* onto the warmer South Coast and predicted climate warming in this region, I aimed to determine the effect of changing substratum temperature at a local level on the early life history processes of *B. glandula* and its native comparator, *Chthamalus dentatus*. Using settlement plates of different colors, I manipulated substratum temperature to assess settlement, mortality, recruitment and growth of the two species. Settlement plates located at two sites on each coast were repeatedly photographed over the course of five months to track barnacles through time and quantify the effects on early life-history processes.

Although *B. glandula* recruited only on the West Coast and *C. dentatus* only on the South Coast preventing direct comparisons, their relative responses to substratum temperature were assessed. Unexpectedly, different substratum temperature had no systematic effects on settlement, mortality, recruitment or growth of either species. It was notable that the relative settlement of *B. glandula* on natural rock was higher than that of *C. dentatus*. This may be attributed to high fecundity rates of *B. glandula* (Newman and Abbott 1980) or a tendency to establish in high densities (Kado 2003; Geller et al. 2008). In addition, *B. glandula* showed relatively lower mortality on rock than the native. This pattern translated into higher recruitment of the invader on rock than was recorded for *C. dentatus*. If these trends persist should the species coexist, it may reflect a competitive advantage held by *B. glandula*. Growth for both species was slowest just after settlement,

but overall, *B. glandula* exhibited a faster growth rate than *C. dentatus* individuals. While regional differences between West and South Coasts must be acknowledged, the fact that settlement and recruitment of *B. glandula* were relatively higher, mortality was relatively lower and growth was relatively greater on rock than that of *C. dentatus* is notable. The findings from this chapter suggest that a competitive advantage held by *B. glandula* may be more important in determining its future spread and impacts on the South African coast than climate related changes in substratum temperature.

#### **CHAPTER 4: Effect of water temperature and food concentration on barnacle filtration and feeding behavior**

Evidence from multiple biological systems has suggested that invasive species exhibit heightened food resource utilization than native species (Dick et al. 2013). As climate change will likely further impact the interactions between invasive and native species, an assessment of how temperature moderates a species' resource utilization could help predict how those species will respond under new environmental conditions. This chapter aimed to determine the effect of water temperature and food concentration on the filtration and feeding behavior of *B. glandula* and the native barnacle, *N. algicola*. To mimic conditions along the West and South Coasts, barnacles were fed either a high ( $32 \times 10^6$  algal cells.ml<sup>-1</sup>) or low ( $1 \times 10^6$  algal cells.ml<sup>-1</sup>) algal concentration at 13 and 20°C. Remaining algae cells were counted using flow cytometry. To resolve differences in feeding between species, video footage was used to quantify the percentage of feeding barnacles, time spent feeding, cirral beat rates, and feeding types displayed.

Notably, both water temperature and food concentration played a role in influencing barnacle filtration and feeding behavior. While temperature did not affect the filtration of *N. algicola*, it did for *B. glandula*. Counter to our predictions, *B. glandula* exhibited greater filtration under warmer temperatures and lower algal concentrations similar to those of the South Coast. Under all thermal and productivity regimes, *B. glandula* demonstrated higher resource use than did *N. algicola*. Temperature affected the feeding behavior of both species. More *B. glandula* barnacles fed and fed for longer with a faster beat rate under warmer temperatures than under cooler temperatures. These variables were also greater than those of *N. algicola* under cooler temperatures. *B. glandula* was not only able to function at the higher temperatures, but also that the species was more active under warmer temperatures. This is notable considering that *B. glandula* was not anticipated to do well under the warmer South Coast (Laird and Griffith 2008). However, as the west coast of North American experiences broad temperature differences from north to south (Crawford 2014), it is therefore likely that the South African population of *B. glandula* has a broad thermal tolerance that may enable it to withstand wide thermal ranges. These results suggest that (1) the invasive, *B. glandula*, exhibits greater consumption of food resources than the native regardless of temperature or food

concentration, (2) this likely reflects the different feeding behaviors displayed by the two species, and (3) *B. glandula*'s feeding appears enhanced under warm conditions.

In conclusion, results from this project show that *B. glandula* has spread onto the South Coast and that warmer temperatures might not exert a direct regulating effect on the early life history processes of *B. glandula*. Warmer temperatures did illicit an increase in filtration and cirral beat rate, suggesting that if the metabolic demands of *B. glandula* are continually met under South Coast conditions, the species may display higher resource use than under cold West Coast conditions in the field. These results may be indicative of a competitive advantage held by *B. glandula* coupled with a broad thermal tolerance. Thus, it is predicted that neither regional temperature differences nor climate-induced changes in temperature are likely to represent a barrier for the further spread of this species.



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