



## Filtration, feeding behaviour and their implications for future spread: A comparison of an invasive and native barnacle in South Africa



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### ABSTRACT

The intertidal barnacle, *Balanus glandula* (Darwin), has invaded the South African coast within the past few decades. This species is currently the dominant barnacle on the cool and productive West Coast and has recently spread east past the biogeographic break of Cape Point. To understand if this invader is likely to establish dominance in these warmer, less productive waters, the effect of water temperature and food availability on the relative food resource use and feeding behaviour of *B. glandula* was investigated in comparison to the native barnacle, *Notomegabalanus algicola* (Pilsbry). To mimic conditions along the two coasts, barnacles were fed either a high ( $32 \times 10^6$  algal cells  $\cdot$  ml<sup>-1</sup>) or low ( $1 \times 10^6$  algal cells  $\cdot$  ml<sup>-1</sup>) algal concentration, representing the high and low primary productivity of the coasts respectively, at 13 and 20 °C. After an hour of filtration, the remaining cells were quantified using flow cytometry. To further resolve differences in feeding among species, video footage was used to quantify feeding behaviour. Notably, both water temperature and food concentration influenced barnacle filtration. However, regardless of thermal and productivity profiles, *B. glandula* demonstrated higher resource use than *N. algicola*. Unexpectedly, *B. glandula* exhibited highest filtration under conditions representative of the South Coast, not under cooler conditions that are typical of its native range and its initial invaded range along South African West Coast. Under these warmer, less productive conditions, *B. glandula* showed faster cirral beat rates than the native barnacle, although no differences in the number of feeding barnacles or the time spent feeding were recorded. Results suggest that (1) *B. glandula* displays heightened food resource use when compared to *N. algicola* regardless of water temperature or food concentration, (2) this likely reflects different feeding behaviours of the two species, and (3) feeding by *B. glandula* is enhanced under warmer water conditions. This work implies that the invasive barnacle may hold an advantage under South Coast conditions that could facilitate its spread in this newly invaded region.

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### 1. Introduction

The introduction of marine species into novel areas is occurring around the world at an increasing rate (Rilov and Galil, 2009; Wonham and Carlton, 2005). Coastal marine systems are particularly at risk from biological invasions and experience high levels of introductions of non-native species (Ruiz et al., 1997; Sorte et al., 2010). An example of one such introduced species is *Balanus glandula*, an acorn barnacle that is invasive in several locations around the world. Originally a native of the west coast of North America, ranging from the subarctic Aleutian Islands to the warm temperate Baja, California (Kado, 2003), *B. glandula* has invaded cool temperate habitats in Argentina (Elías and Vallarino, 2001) and Japan (Kado, 2003). In these invaded ranges, *B. glandula* has spread rapidly from initial points of introduction and

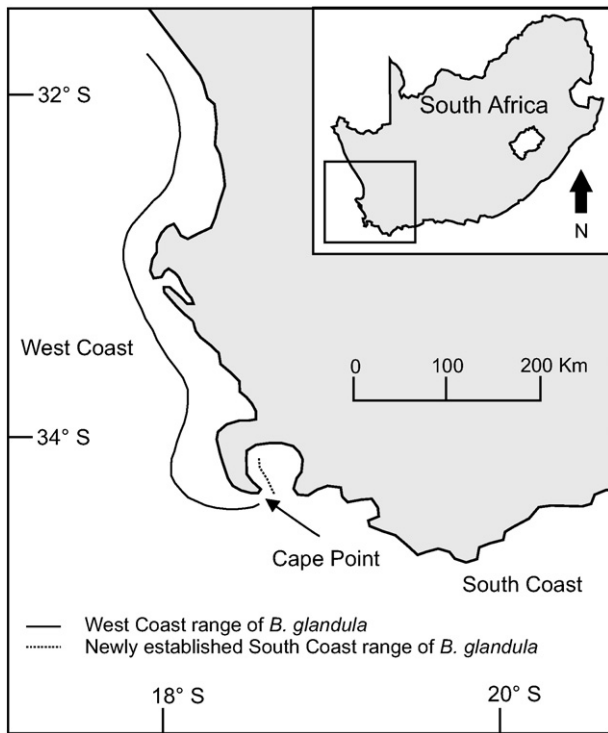
has altered intertidal community structure (Schwindt, 2007) and displaced native barnacle species (Elías and Vallarino, 2001; Kado, 2003), becoming the dominant barnacle along invaded regions (Kado, 2003; Schwindt, 2007).

This barnacle has also successfully invaded South Africa and is commonly found along the open coast (Laird and Griffiths, 2008). Since its introduction, it has become the dominant intertidal barnacle on the West Coast (Robinson et al., 2015), overlapping in geographic distribution with all six native barnacle species including *Notomegabalanus algicola* (Laird and Griffiths, 2008). In this region, it has altered community structure through the reduction of habitat complexity where it has replaced the invasive mussel, *Mytilus galloprovincialis*, in the upper mid-shore (Sadchatheeswaran et al., 2015). Notably, the abundance of a littorinid snail, *Afrolittorina knysnaensis*, has been positively correlated with the cover of this barnacle demonstrating a 20-fold increase in abundance following the establishment of *B. glandula* (Sadchatheeswaran et al., 2015). While *B. glandula* has supported densities above 15,000 individuals  $\cdot$  m<sup>2</sup> at West Coast sites since at least 2012 (Robinson et al., 2015), it has only recently spread east past the biogeographic break of Cape Point (Fig. 1) along South Africa's South Coast. In

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**Fig. 1.** The established range of *Balanus glandula* along the West Coast of South Africa and the recent spread onto the South Coast.

this newly invaded region it has a patchy distribution on the western shores of False Bay where densities remain below 700 individuals·m<sup>2</sup> in invaded pockets of shoreline (Robinson et al., 2015). Along the recently invaded South Coast, water temperatures are warmer than the established range on the West Coast and it is unknown how this range expansion will progress under these conditions. The invasion history of *B. glandula* has, however, raised concerns about its potential spread and impact along this coastline (Geller et al., 2008; Schwindt, 2007; Sachatheeswaran et al., 2015).

Previous attempts to effectively assess and predict impacts of invasive species on native biota have had limited success (Parker et al., 1999; Sakai et al., 2001; van Kleunen et al., 2010). However, an emerging approach that has shown promise has focused on resource use comparisons between invasive and native species (Dick et al., 2014). Multiple studies have shown that invasive species are generally more efficient at utilizing resources than native comparators, with findings corroborated by associated negative impacts in the field. These impacts include alterations in native community structure leading to a reduction in species richness (Alexander et al., 2014; Bollache et al., 2008) and declines in prey populations (Dick et al., 2014; Laverty et al., 2015). Most recently, this approach has been applied to mussels along the South African coast where it was found that invasive mussels are more efficient filter feeders than are trophically analogous native species and that these differences reflect abundances on the shore (Alexander et al., 2015). It follows that the higher the resource use of an invader in comparison to native biota, the greater the threat it may represent to the recipient communities (Dick et al., 2014), and this is especially true if increased resource use translates to greater abundances, spread and subsequent impact. Therefore, this study attempted to address this concept of comparative resource use in the invasive–native barnacle system in South Africa.

Barnacles display three main feeding types (Geierman, 2007): in an “active” mode, cirri are actively extended and retracted repetitively and continuously (Crisp and Southward, 1961; Geierman and Emler, 2009); in a “passive” mode cirri are extended and held into the water column collecting food particles before being retracted (Crisp and Southward,

1961); and “pumping” is implemented by pulsing cirri up and down without ever being fully extended into the water column (Crisp and Southward, 1961; Geierman and Emler, 2009). Water temperature is known to affect the feeding rates of barnacles with cirral beat rates and thus, filtration rates, increasing with temperature up to a threshold (Geierman, 2007; Nishizaki and Carrington, 2014; Sanford et al., 1994). This threshold is likely driven by elevated metabolic rates (Sanford et al., 1994). The presence of food can also influence feeding activity with consumption rates increasing proportionally with food concentration (Crisp and Southward, 1961; Sanford et al., 1994). At high food concentrations, however, filtration can decrease presumably because of feeding saturation (Crisp and Southward, 1961). As such, it was predicted that temperature would influence the feeding of both barnacle species, and that based on observed heightened resource use capabilities in invasive species (Dick et al., 2014), *B. glandula* individuals would remove more algae in comparison with the native.

In this study, resource use was compared between the invasive acorn barnacle *B. glandula* and the native barnacle *N. algicola*. Specifically, the effect of water temperature and food concentration on algal consumption of these two species was investigated under laboratory conditions that were representative of the cooler productive West Coast and the warmer, less productive South Coast. Water temperature effects on the feeding behaviours of the invasive and native species were also examined. Lastly, these results were interpreted in terms of current patterns of establishment to infer on how the range expansion of *B. glandula* along the South Coast may progress.

## 2. Methods

Both *B. glandula* and *N. algicola* were collected from Bloubergstrand (−33.796767°S, 18.462082°E) and immediately transported back to the laboratory. Barnacles were placed into tanks with continuously aerated artificial seawater at a salinity of 28–32 ppt and allowed to acclimate for at least 48 h. Barnacles were maintained ad libitum on a commercially produced algal feed comprised of *Isochrysis* sp. and *Pavlova* sp. ranging from 4 to 10 μm in size (Brightwell Aquatics PhytōGold-S).

### 2.1. Filtration trials

As individuals of equivalent sizes could not be found on the shore, size was accounted for during all experiments by standardizing biomass. This was achieved by allocating a biomass of  $4 \pm 0.13$  g of barnacles as a replicate. To avoid comparing adults and settlers, only individuals from cohorts more than 6 months old were used. Prior to filtration trials, barnacles were starved for 48 h to standardize hunger. Replicate groups of each species were placed in 500 ml circular tanks and randomly allocated as 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 treatment. Thus, four replicates were performed for each treatment. The algal resource provided to the barnacles was the same as that which had been fed to barnacles prior to experimentation. Algal filtration trials were run at two temperatures representing South Africa’s west (13 °C) and south coasts (20 °C) (Smit et al., 2013). Experimental temperatures were maintained by a digitally controlled chiller and did not vary by more than 0.05 °C. Flow cytometry using the LIVE/DEAD® BacLight™ Bacterial Viability Counting Kit (L34856) was used to count the number of algal cells collected in triplicate 1 ml water samples from each tank after 1 h.

As a greater proportion of *B. glandula* individuals fed during experiments than did native barnacles, the percentage of feeding barnacles per species was used as a correction factor to standardize feeding effort when analysing the number of algal cells remaining at the end of the filtration experiment. Final algal concentrations were examined with respect to species (2 levels; *B. glandula* and *N. algicola*) and temperature (2 levels; 13 and 20 °C) using a two-factor GLM, with quasipoisson error distribution. Post-hoc pairwise t-tests were then conducted using

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