



## 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  $\cdot \text{ml}^{-1}$ ) or low ( $1 \times 10^6$  algal cells  $\cdot \text{ml}^{-1}$ ) 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

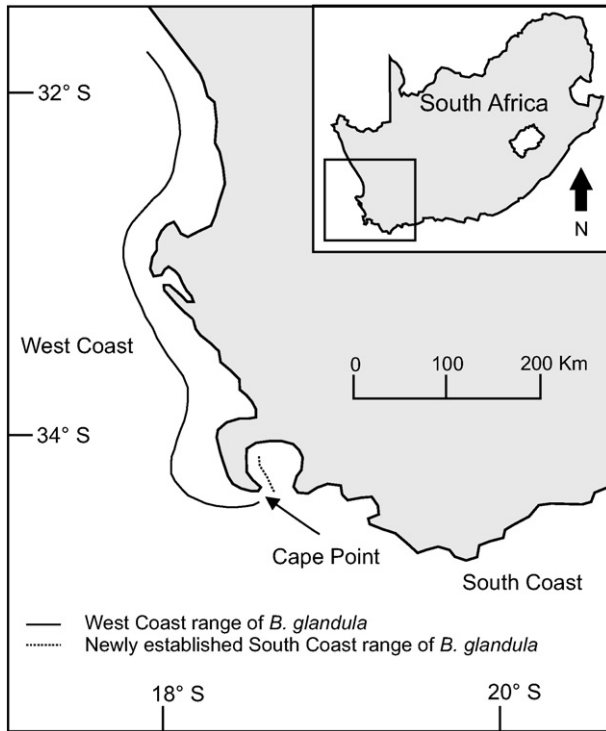
has altered intertidal community structure (Schwindt, 2007) and displaced native barnacle species (Elías and Vallarino, 2001; Kado, 2003), becoming the dominant barnacle along invaded regions (Kado, 2003; Schwindt, 2007).

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  $\cdot \text{m}^2$  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

Bonferroni adjusted *p*-values. Data from each algal concentration were analysed independently as they represent spatially distinct environmental conditions, rendering direct comparisons of little practical value.

## 2.2. Feeding behaviour trials

In order to assess feeding behaviour of *B. glandula* and *N. algicola*, four replicate groups per species comprised of a standardized biomass of  $9 \pm 0.26$  g were placed in separate tanks with 3 l of aerated artificial seawater at both 13 °C and 20 °C and then supplied with  $1.0 \times 10^6$  cells·ml<sup>-1</sup>. Cameras mounted above tanks were used to film the barnacles for 10 min after the addition of the algae. 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 time spent feeding, (2) cirral beat rate per minute and (3) the feeding types displayed. To gain a detailed measure of feeding behaviour, barnacles were recorded as “inactive” if they had closed opercula valves and were not feeding for at least 3 s; “active” if cirri were continuously extended into the water column and retracted in sweeping motions; “passive” if cirri were extended in the water column for longer than 1 s without a sweeping motion; and “pumping” if the opercula valves were open and cirri were pulsing up and down repetitively without being fully extended into the water column. This is based upon the methods used by Crisp and Southward (1961) and Geierman and Emler (2009).

When analysing feeding behaviour, 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 cirral beat rates were evaluated using a two-factor GLM to consider differences among species (2 levels; *B. glandula* and *N. algicola*) and temperature (2 levels; 13 and 20 °C). Post-hoc pairwise *t*-tests were then conducted using Bonferroni adjusted *p*-values. A Chi-squared test was used to assess differences in the frequency of feeding types (i.e. inactive, active, passive and pumping) displayed by each species at the two temperatures. All analyses were carried out in R v. 2.15.1 (R Development Core Team, 2012).

## 3. Results

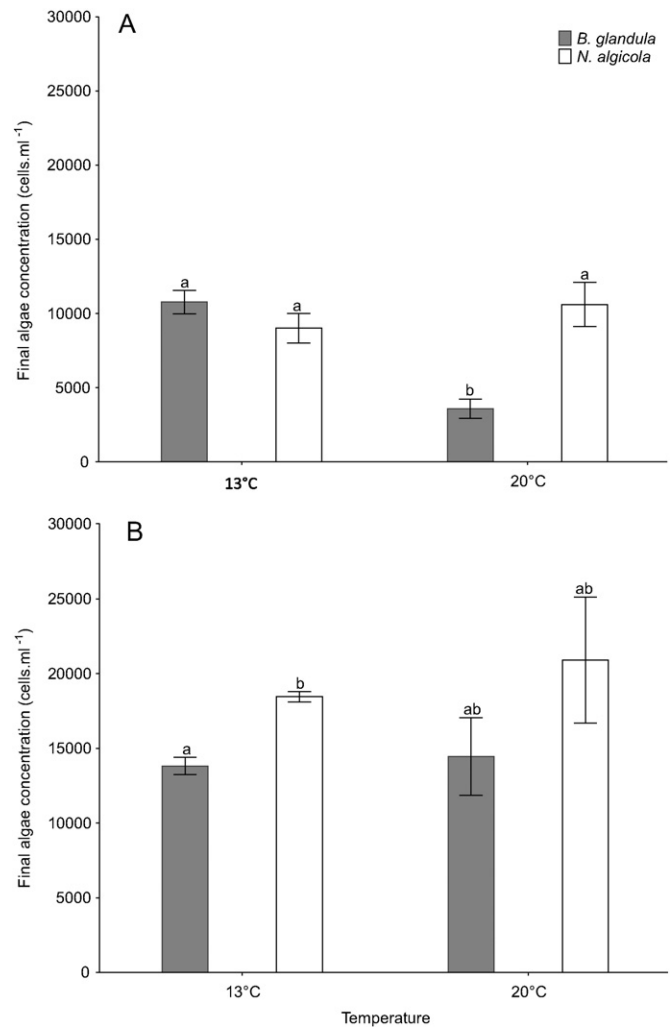
### 3.1. Filtration trials

Under experimental conditions simulating the South Coast (i.e. low algal concentration and warm water temperature), species identity and temperature significantly affected the number of algal cells remaining (Table 1). Here, *B. glandula* removed significantly more algal cells than did the native species (Fig. 2a). Under West Coast conditions

**Table 1**

Effect of temperature and food availability on algal concentration. a) GLM results of the effects of species and temperature on the number of algal cells remaining at low and high food concentrations after 1 h of filtration; b) results of post-hoc *t*-tests analysing 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	<i>p</i> -Value
Low	Species	1		1908.2	4.02	ns
	Temperature	1		2568.6	5.42	<i>p</i> < 0.05
	Species × Temp	1		10,537.2	22.22	<i>p</i> < 0.05
High	Species	1		5772.2	8.09	<i>p</i> < 0.05
	Temperature	1		485.9	0.68	ns
	Species × Temp	1		77.7	0.10	ns
b) T-tests			B13	N13	B20	N20
Low	B13					
	N13	ns				
	B20	<i>p</i> < 0.01	<i>p</i> < 0.01			
	N20	ns	ns		<i>p</i> < 0.01	



**Fig. 2.** Remaining algal concentrations. Mean ( $\pm$  SE) algal cells remaining after 1 h of filtration by *Balanus glandula* and *Notomegabalanus algicola* at 13 and 20 °C under conditions of a) low and b) high algal concentrations. Shared letters indicate no statistical difference (*p* > 0.05).

(i.e. high algal concentration and cold water temperature) only species identity affected the number of remaining algal cells (Table 1), with *B. glandula* once again removing more algal cells than *N. algicola* (Fig. 2b).

### 3.2. Feeding behaviour 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). More *B. glandula* individuals fed at 20 °C than did at 13 °C (Fig. 3a), while individuals of both species spent longer feeding at 20 °C than at 13 °C (Fig. 3b). Cirral beat rates were significantly affected by both species identity and temperature (Table 2). The beat rate displayed by *B. glandula* was significantly faster at 20 °C than at 13 °C and also faster than the beat rate of *N. algicola* at 20 °C (Fig. 3c). The frequency of feeding types displayed did not differ between species or temperatures ( $X^2_{4,8} = 6.01$ , *p* > 0.05) (Fig. 4).

## 4. Discussion

Evidence from multiple biological systems has shown that damaging invasive species tend to exhibit heightened food resource utilization in comparison to native species (Dick et al., 2014, 2013). It is also evident that such resource use can be dependent on a range of abiotic factors

**Table 2**

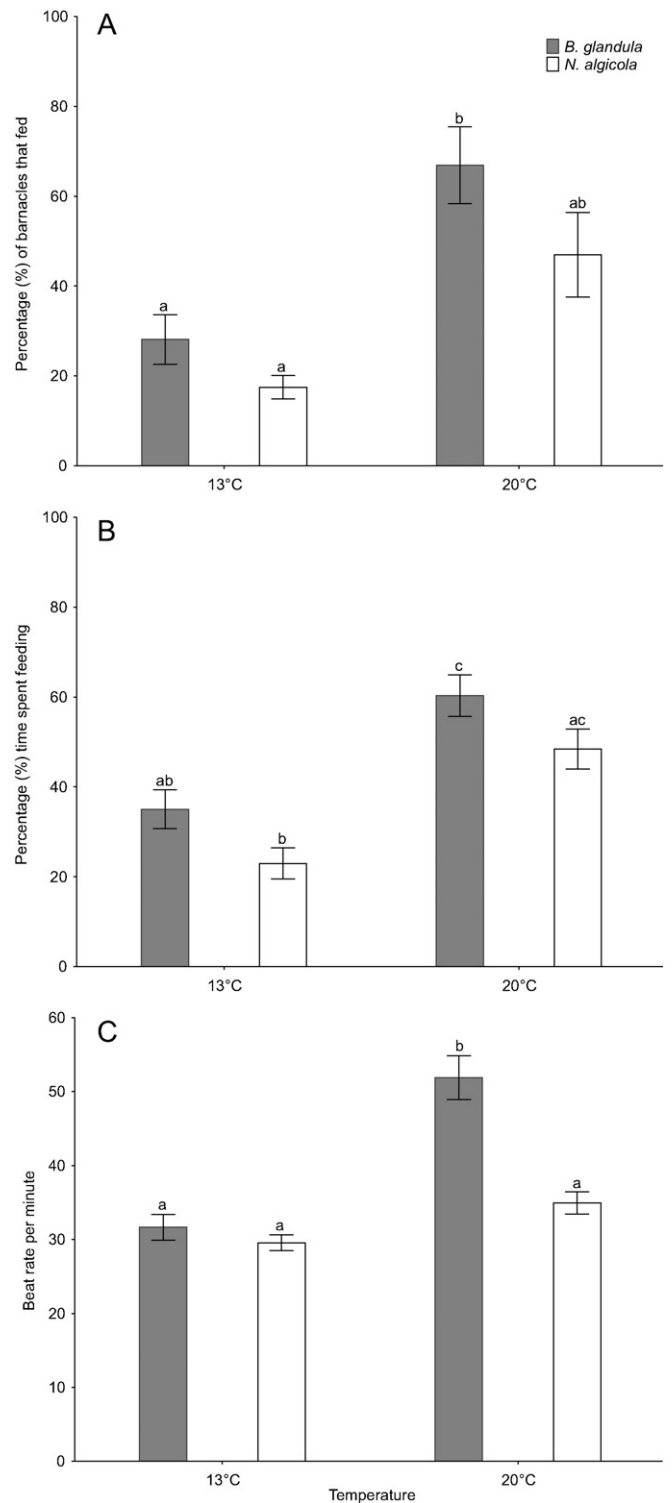
Effect of temperature on barnacle behaviour. Results from a) a GLM of the effects of species and temperature on the percentage of barnacles that fed, feeding time, and cirral beat rates; b) post-hoc t-tests analysing the effect of above variables on cirral beat rate. B = *B. glandula*, N = *N. algicola*, 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 × 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 × 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 × 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		

that relate to habitat (Laverty et al., 2015; de Mérona et al., 2003). As such, an assessment of how temperature moderates an invader's resource use could help predict how it will respond to new environments and under different temperature regimes. Thus, this study compared the resource use and feeding behaviour of the invasive barnacle *B. glandula* and the native *N. algicola* under different temperature and productivity regimes reflecting the South African coastline. Most notably, *B. glandula* demonstrated higher resource use than the native, regardless of the thermal or productivity regime. This finding corroborates the dominance of *B. glandula* along the South African West Coast (Laird and Griffiths, 2008) and suggests that this invader could maintain its dominance along the newly invaded South Coast despite the warmer less productive conditions.

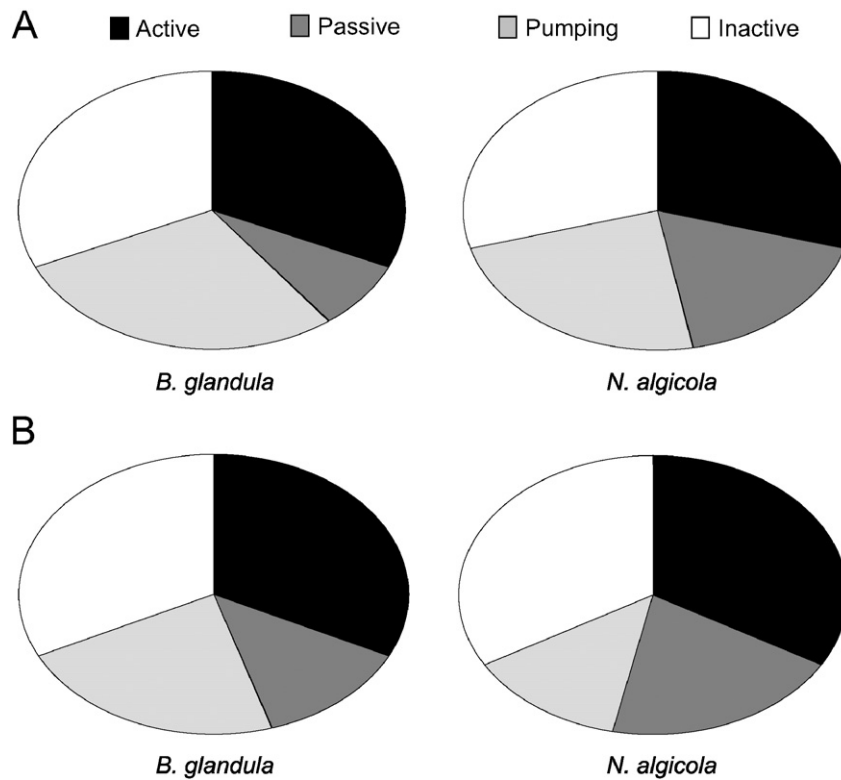
Barnacle consumption and feeding behaviour are known to be affected by temperature and food concentration (Crisp and Southward, 1961; Geierman, 2007; Sanford et al., 1994). Thus, differences in the uptake of algae by both species were anticipated due to changes in these environmental conditions. It was predicted that *B. glandula* would be most efficient at filtering under conditions similar to the West Coast (i.e. 13 °C and high algal concentrations), as this species is known to support high abundances in the region (Robinson et al., 2015); has only been reported as invasive to cool temperate regions (Alam et al., 2013; Elías and Vallarino, 2001; Kado, 2003); and has demonstrated optimal feeding at 10–15 °C in its native range (Nishizaki and Carrington, 2014). In addition, it was predicted that *B. glandula* would be more efficient at consuming algae than *N. algicola* under these conditions, while the native species was predicted to be more proficient at warmer temperature under low algal concentrations.

The first prediction was not upheld as the invader was most efficient at filtering under South Coast conditions (i.e. 20 °C and low algae concentration). The second prediction was only partially supported as *B. glandula* displayed superior resource use over *N. algicola* under all conditions considered. There were also no differences in filtration between coastal conditions for the native species. These findings are likely explained by the fact that *B. glandula* has a large native range that predominantly spans temperate waters, but also extends into warm southern California (Kado, 2003). Therefore, while some populations of this barnacle feed optimally under cool conditions (Nishizaki and Carrington, 2014), the species may have a broad thermal range for efficient feeding. In addition, invasive populations may have a large capacity for phenotypic plasticity, a trait often associated with successful alien species (Smith, 2009). Indeed, broad latitudinal ranges, tolerance to environmental variability and phenotypic plasticity have been highlighted as common traits of introduced species in aquatic systems (Bates et al., 2013; Roman and Darling, 2007).



**Fig. 3.** Barnacle feeding behaviour trials. Mean (±SE) a) percentage of feeding barnacles, b) percentage of time spent feeding, and c) cirral beat rate per minute among species and temperature. Shared letters indicate no statistical difference ( $p > 0.05$ ).

While numerous studies have correlated elevated resource use of high-impact invaders over native comparators with impacts in the field (Alexander et al., 2014; Barrios-O'Neill et al., 2014; Bollache et al., 2008; Dick et al., 2013), few have considered the mechanisms behind this pattern. In this study however, it was found that behaviour differed between species and was affected by temperature. Notably, more *B. glandula* fed for longer, and exhibited faster cirral beat rates than *N. algicola*. This pattern was accentuated at high temperature. While



**Fig. 4.** Barnacle feeding types. The frequency of feeding types displayed by *B. glandula* and *N. algicola* at a) 13 °C and at b) 20 °C. There were no statistical differences between feeding types ( $\chi^2_{4,8} = 6.01, p > 0.05$ ).

such responses in feeding behaviour to these variables have been recorded in barnacles before (Geierman, 2007; Nishizaki and Carrington, 2014; Sanford et al., 1994), the importance of the current findings lies in that they demonstrate behavioural differences in resource acquisition are driving the apparent advantage *B. glandula* has over *N. algicola* and are conserved under different temperatures.

Should the *B. glandula* invasion follow the pattern for invasive mussels in this region (Alexander et al., 2015), where elevated resource uptake is mirrored by dominance in the field, these results suggest that this invasive barnacle could spread along the South African South Coast and become dominant as it has on the West Coast. It is important to note, however, that while warmer temperatures may not negatively affect the filtration of adult *B. glandula*, they may impact other thermally sensitive biological processes, like reproduction or larvae development (Lathlean et al., 2012; Rognstad and Hilbish, 2014), which could ultimately regulate *B. glandula* in this region. In addition, the role of biotic interactions in limiting the South Coast range of this barnacle remains unexplored. Some insight may be gained from the West Coast though, as in this region native whelk predators are known to avoid feeding on *B. glandula* (Robinson et al., 2015), although the response of South Coast whelks to this novel food source will only become clear if the invasion continues to spread.

## 5. Conclusion

While comparative resource use has been proposed as a predictive methodology for forecasting impacts of alien species (Dick et al., 2014) and numerous studies have retrospectively provided support for its predictive capacity (Alexander et al., 2014; Dick et al., 2014, 2013; Laverty et al., 2015), this approach is still to be utilized to its full predictive potential. The present study tested this approach on the invasive barnacle, *B. glandula*, in a region where it is well established as the dominant barnacle (Laird and Griffiths, 2008) with known impacts (Sadchatheeswaran et al., 2015). Notably, this study applied the concept

predictively to a newly invaded biogeographic region. These results add strength to the growing body of evidence that invasive species tend to have greater resource use capabilities than do native comparators and suggest in this instance that behavioural differences underpin differential filtration efficiency. Notably, these findings suggest that *B. glandula* could continue to spread along the South Coast and become a dominant intertidal barnacle as it has along the West Coast of South Africa.

## Disclosures

Author contributions: TBR and MEA conceived this study. While all authors contributed to all stages of this work, HRP lead the laboratory and field work; MEA guided the statistical analyses; HRP and TBR lead the manuscript preparation. All three authors have approved the final version of this submission.

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