Predation-driven biotic resistance fails to restrict the spread of a sessile rocky shore invader

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ABSTRACT: The invasive barnacle *Balanus glandula* has progressively spread along the South African west coast. We used multiple approaches to assess the role of predation by indigenous whelks in regulating this expansion. *B. glandula* abundance and distribution were monitored annually while field observations and laboratory experiments assessed the relative predation pressure on *B. glandula* and the native barnacle *Notomegabalanus algicola*. In the mid-shore, the whelks *Trochia cingulata* and *Burnupena lagenaria* fed on *N. algicola* most often despite the alien *B. glandula* covering a mean of 86 % of the shore at this site. Lower on the shore, the same feeding pattern was evident, although *N. algicola* was spatially dominant. Feeding experiments revealed that small (mean ± SD shell length: 13.9 ± 0.3 mm) and large (19.6 ± 0.5 mm) *T. cingulata* consumed up to 70 % more *N. algicola* than *B. glandula*, displaying a significant avoidance of the alien. While small (15.5 ± 0.5 mm) *B. lagenaria* displayed the same pattern, large individuals (27.7 ± 0.4 mm) consumed equal numbers of the 2 barnacles. The avoidance of *B. glandula* may be explained by this species possessing thicker shell and opercular plates than *N. algicola*, while a narrow margin of vulnerable soft tissue around the circumference of the opercular plates makes the native an attractive prey choice. This study demonstrates that predation-driven biotic resistance has not contained the expansion of *B. glandula* along the South African coast.

KEY WORDS: *Balanus glandula* · Biological invasions · Marine invasive species · South Africa · Barnacle · Whelk · *Notomegabalanus algicola*

INTRODUCTION

The spread of alien species depends not only on the suitability of the abiotic environment (Schneider 2008, Sorte et al. 2010) but also on traits of the invader (Callaway & Ridenour 2004, Nyberg & Wallentinus 2005) and characteristics of the recipient community (Stachowicz et al. 2002). While measures of the physical environment are relatively easily made, species-specific tolerance ranges and the role of biological influences on the range extension of marine alien species can be subtle. Numerous theories have been proposed to explain the interaction between native biota and invaders (e.g. diversity-driven biotic resistance: Elton 1958, Stachowicz et al. 2002; evolution of increased competitive ability: Blossey & Notzold 1995; invasional meltdown: Simberloff & Von Holle 1999; enemy release: Keane & Crawley 2002; development of novel weapons: Callaway & Ridenour 2004), but while these theories differ mechanistically, they essentially describe the ability (or inability) of a native community to resist an invasion (Kimbro et al. 2013).

A recent review of biotic resistance in marine systems (Kimbro et al. 2013) highlighted that algae are commonly unable to resist invasions by other producers through competition unless recipient communities are diverse (e.g. Bando 2006, Cebrian et al. 2011), while regulation of invasive algae by native consumers is generally not effective (e.g. Vermeij et

al. 2009). Notably, most marine studies have considered invasive consumers, and these invasions appear more strongly resisted than invasions by producers (Kimbro et al. 2013). While recent studies have interrogated biotic resistance in aquaculture (Dumont et al. 2011) and harbour (Rius et al. 2014) environments, little is understood of biotic resistance to open coast invasions by biota that exert their impact primarily through the acquisition of non-food based resources such as space (but see Zabin & Altieri 2007). Examples of such species include sessile primary space occupiers on rocky shores that are often dominant in their native and/or invasive ranges (e.g. the mussel *Mytilus galloprovincialis*: Branch et al. 2008; the reef-building polychaete *Boccardia proboscidea*: Jaubet et al. 2011).

While research on biotic resistance in marine systems has focused on subtidal systems, we suggest that rocky intertidal habitats also offer a useful model system in which to test the hypothesis due to 3 inherent characteristics. Firstly, predator–prey interactions are easily observed and experimentally manipulated on the shore (Paine 1994). Secondly, the organisms involved are easily collected and maintained in the laboratory, enabling controlled laboratory assessments of interactions (Freeman et al. 2014). Thirdly, adult populations of intertidal species are constrained to linear ranges along the coast, enabling easy monitoring of their spread (Sagarin & Gaines 2002, Sanford & Swezey 2008). Importantly, these characteristics facilitate research in regions where subtidal studies may be logistically challenging. This is important if research is to be extended into historically understudied regions like Africa.

Balanus glandula is an intertidal barnacle native to the rocky shores of the west coast of North America (Carlton et al. 2011). Over the last 4 decades, this species has invaded the southwest Atlantic coast of Argentina (Vallarino & Elias 1997), the northwest Pacific coast of Japan (Kado 2003) and the southeast Atlantic coast of South Africa (Simon-Blecher et al. 2008). While this barnacle was first recognised along the South African west coast in 2007, photographic evidence suggests that it was introduced more than 20 yr ago (Laird & Griffiths 2008). By the time this invasion was recognised, *B. glandula* was already the dominant barnacle, accounting for 78.5% of all barnacles (Laird & Griffiths 2008). While its abundance was patchy at both meso- and macro-scales, this barnacle supported up to 28 455 ind. m^{-2} and had a range of 400 km stretching from Elands Bay to Misty Cliffs on the Cape Peninsula (Laird & Griffiths 2008). As predatory gastropods are commonly the dominant predators of intertidal barnacles (Barnes 1999), often regulating their distribution and abundance (Connell 1970, O'Riordan et al. 2010), it calls into question the role of native predatory whelks in mediating the expansive invasion of *B. glandula* along the South African coast.

We adopted 3 approaches to assess the role of predation-linked biotic resistance in regulating the spread of *B. glandula*. First, we monitored the abundance and distribution of this aggressive invader to quantify changes in population status and geographic range. Second, we undertook field observations to evaluate the hypothesis that *B. glandula* experiences less predation pressure than that of the most abundant native barnacle *Notomegabalanus algicola*. Last, we used laboratory experiments to assess the hypothesis that native whelks would show an avoidance of the alien barnacle. To help explain differences in predation we tested for differences in structural defences and palatability between the 2 barnacles.

MATERIALS AND METHODS

Abundance and range of *Balanus glandula*

The distribution and abundance of *B. glandula* was monitored annually in the winter months of 2012, 2013 and 2014. Selected sites surveyed by Laird & Griffiths (2008) were resurveyed (Fig. 1, Table 1) and new sites were added. The range of *B. glandula* was delimited once no individuals had been recorded along the coast for 30 km. At each site, the abundance of this invasive barnacle was recorded in 0.1 m^2 quadrats (n = 10) that were randomly placed both within the mid- and low-shore.

Field observations of feeding patterns

All predation studies were carried out at Bloubergstrand (Fig. 1). This site was chosen as it supports large populations of the indigenous whelks *Burnupena lagenaria* and *Trochia cingulata* (previously *Nucella cingulata*), as well as *B. glandula* and the indigenous barnacle *Notomegabalanus algicola*. At this site, the percentage cover of each barnacle species was scored in 15 randomly placed 0.25 m^2 quadrats in the mid- and low-shore during 2 sequential tidal series. Percentage cover was estimated by dividing the quadrat into 100 squares each representing 1% cover. The high-shore was not included,
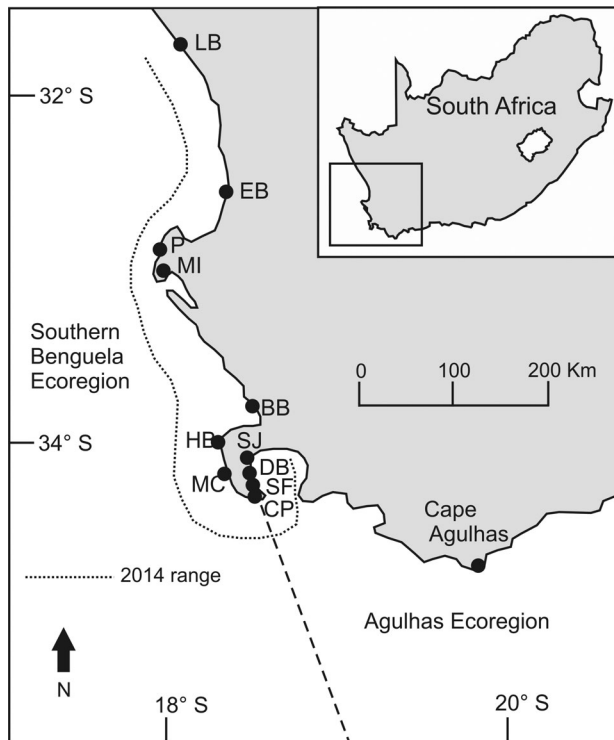
Fig. 1. Sampling sites along the west and south coasts of South Africa and places named in the text. Field observations were undertaken at Bloubergstrand (BB); site abbreviations as in Table 1

Table 1. Sites surveyed during monitoring of *Balanus glandula* along the South African coast

Site	GPS coordinates	
	S	E
LB: Lambert's Bay	32° 05.442′	18° 18.023′
EB: Elands Bay	32° 19.076′	18° 18.856′
P: Paternoster	32° 48.084′	17° 55.140′
MI: Marcus Island	33° 02.019′	17° 56.127′
BB: Bloubergstrand	33° 48.135′	18° 27.545′
HB: Hout Bay	34° 02.902′	18° 21.650′
MC: Misty Cliffs	34° 11.025′	18° 21.601
CP: Cape Point	34° 20.126′	18° 25.520′
SF: Seaforth	34° 12.004′	18° 27.222′
DB: Dalebrook	34° 07.436′	18° 27.154′
SJ: St. James	34° 06.597′	18° 27.420′

as it supported only *B. glandula*. These measurements were made during the evening low tide, and feeding activity of the 2 whelk species on the 2 barnacles was assessed in each quadrat. Based on observations of whelks maintained in the laboratory, individuals were considered to be feeding if they did not move from their original position for more than 30 s and were observed to be making small oscillating movements.

Prey-selection experiments

To complement our field observations and gain a measure of predation by *B. lagenaria* and *T. cingulata* on the 2 barnacle species over an extended period, we undertook 5 d laboratory feeding experiments. This approach also offered the opportunity to consider the effect of whelk size on the choice of barnacle prey species. Whelks and barnacles were collected from the mid- and low-shore at Bloubergstrand. As both barnacle species could be found on the shells of the mussel *Mytilus galloprovincialis*, barnacles were collected by collecting mussels that

contained more than 50 individual barnacles of either species. In the laboratory, the mussels were opened and cleaned of all flesh. The number of barnacles present on a mussel shell was then standardised to 20 individuals of either species. In the field, *B. glandula* and *N. algicola* supported only 1 size class each and therefore sizes unavoidably differed between species (*B. glandula* mean ± SD basal diameter of 5.5 ± 0.7 mm and *N. algicola* 4.5 ± 0.6 mm). In order to determine the effect of whelk size on predation, 2 size classes (based on shell length) of each whelk species were used, i.e. *B. lagenaria* large (27.7 ± 0.4 mm) and small (15.5 ± 0.5 mm) and *T. cingulata* large (19.6 ± 0.5 mm) and small (13.9 ± 0.3 mm). Animals were starved for 48 h prior the experiment to standardise hunger.

Individual 2 l tanks were set up containing 2 mussel shells: 1 with 20 *B. glandula* and 1 with 20 *N. algicola.* Control tanks contained no whelks while treatment tanks had either 1 small or 1 large whelk. Mussel shells were secured to the bottom of the tanks. Due to space constraints, only 10 control tanks, 10 tanks containing 1 small whelk each and 10 tanks containing 1 large whelk could be maintained at any time. Two such runs were completed for each whelk species. As *t*-tests showed no significant differences between runs for each treatment for each whelk species (p > 0.05), runs were combined to achieve a sample size of 20 replicates treatment^{-1} whelk^{-1}. All tanks were supplied with filtered and aerated sea water maintained at 15°C and were subject to a 12 h light cycle. Dead barnacles were not replaced during the experiment, as at no stage were all individuals of one species depleted. The numbers of empty barnacle tests were recorded after 5 d as a measure of predation.

Comparison of barnacle structural defences and palatability

In order to understand how morphological features may regulate differences in predation on the 2 barnacle species, shell wall plate thickness, opercular plate thickness, opercular length and opercular width were compared between 20 *B. glandula* and *N. algicola* individuals. In addition, wall plates of each were checked for the presence of external ribbing and the position of the opercular plates in relation to the opercular opening.

To assess how palatability may affect prey selection by *B. lagenaria* and *T. cingulata*, 10 whelks of each species were offered 5 *B. glandula* and 5 *N. algicola.* All barnacles were removed from their shells prior to being presented to the whelks. The numbers of barnacles of each species eaten within 30 min were recorded. Only individuals of the large size class of each whelk species were used in these trials. Prior to the experiment, whelks were starved for 48 h to standardise hunger.

Statistical analyses

Prior to all statistical tests, data were checked for normality using normal probability plots and homoscedasticity of variances using ratios of maximum to minimum variances (Zar 2010). Significance levels for all analyses were set at $\alpha = 0.05$. Unless stated otherwise, all analyses were conducted in STATISTICA 10.

The abundance of *B. glandula* was assessed among sites and years using a generalized least squares (GLS) model for each intertidal zone (i.e. with site and year as predictor variables and abundance as the outcome variable). The best model was chosen based on the lowest value of Akaike's information criterion. This analysis was done in R. Raw data for the midshore were log transformed as a result of extreme variation in abundances among sites.

Field observations of *B. lagenaria* and *T. cingulata* feeding on barnacles were analysed separately for the mid- and low-shore. As no significant effect of sampling occasion was found for % cover of the 2 barnacle species, the number of each whelk species present or predating on *B. glandula* and *N. algicola* (*t*-tests p > 0.05 in all cases), data from the 2 occasions were combined for all analyses. The % cover of the 2 barnacles was compared using a *t*-test while the numbers of each whelk species feeding on *B. glandula* and *N. algicola* were compared using a general-ized linear model (GLM) with a Poisson error distribution in R.

Barnacle mortality during predation experiments was compared among whelk species, barnacle species and between treatments using a multi-factorial ANOVA, followed by a Fisher LSD post hoc test. Data obtained from predation experiments were also used to calculate Ivlev's electivity index (*E*). The purpose of the index is to characterise the electivity (i.e. degree of selection) of a prey species by the predator. The relationship is defined as:

$$E = (r_i - p_i/r_i + p_i) \tag{1}$$

where *E* is the measure of electivity, calculated with data obtained after 5 d, r_i is the proportion of prey species *i* in the diet (i.e. number of prey species *i* consumed divided by the total number of barnacles consumed), and p_i is the proportion of prey species *i* available (Ivlev 1961). In this experiment, whelks were offered equal numbers of each prey species, so $p_i = 0.5$, and potential values of *E* ranged from 0.333 (exclusive diet) to 0 (equal preference for each species) to −1 (complete avoidance), with negative values indicating avoidance of the prey, 0 indicating random selection and positive values indicating active selection (Ivlev 1961). As selection of one barnacle species was not independent of the other species within a tank (Peterson & Renaud 1989, Roa 1992), *E* indices were compared using Friedman's ANOVA and Kendall's coefficient of concordance. This was followed by a multiple comparisons test for nonparametric randomised block analysis of variance following Zar (2010).

Morphological features of *B. glandula* and *N. algicola* and the numbers of individuals consumed per whelk species in palatability trials were compared using ANCOVA to account for the unavoidable differences in basal diameter between barnacle species. Prior to these analyses, the assumptions of normality of the error terms, homogeneity of variance, similar range of covariate values and homogeneity of the slopes and linearity (Quinn & Keough 2002) were considered.

RESULTS

Abundance and range of *Balanus glandula*

In 2012, *B. glandula* had expanded its known range in a northerly direction by more than 100 km, extending from Elands Bay to Lambert's Bay (Fig. 2). Notably, it had also extended its distribution in a
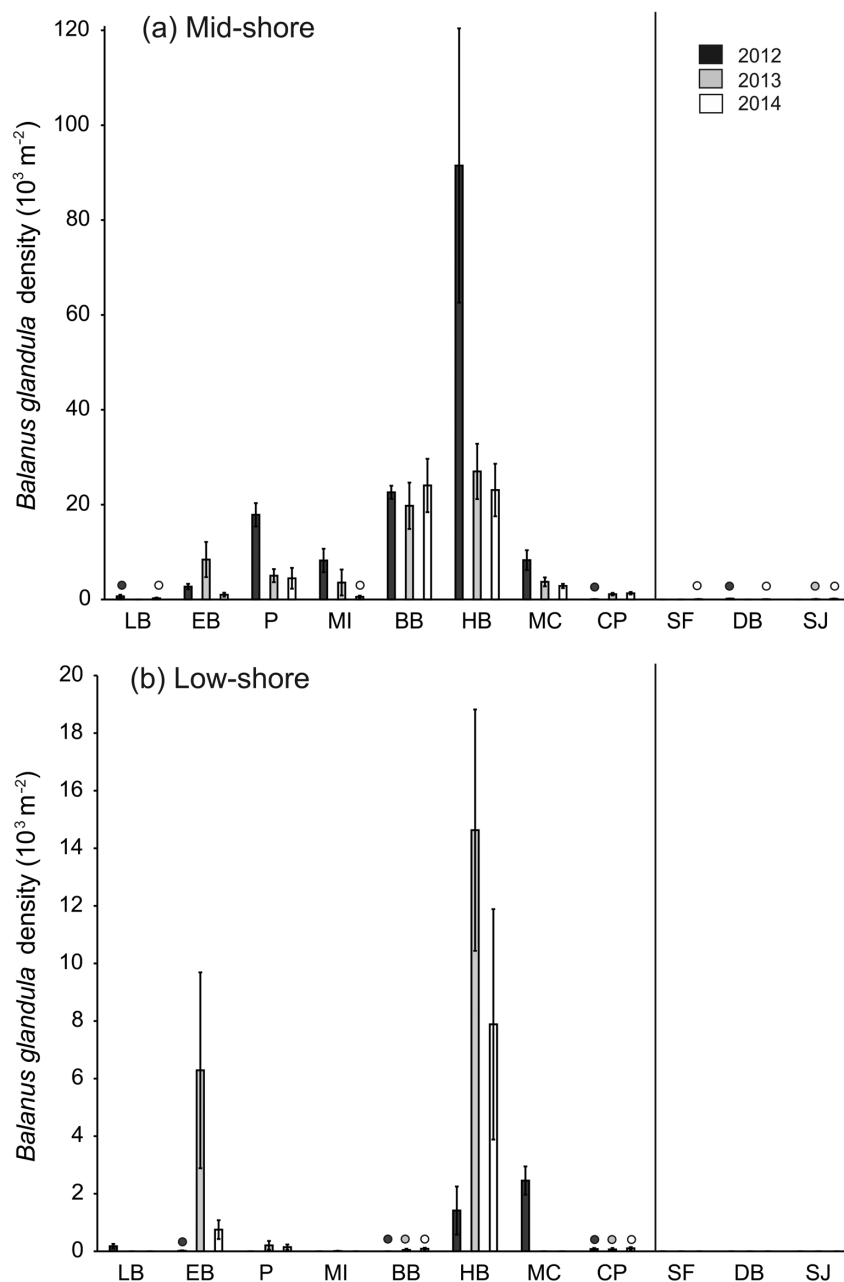
Fig. 2. Abundance ±SE of *Balanus glandula* at 11 sites monitored from 2012 to 2014. Circles indicate years when the barnacle was present but at densities below 700 ind. m^{-2}. The solid line represents the Cape Point biogeographic break. Site abbreviations as in Table 1

were observed at Seaforth every year. As of 2014, this species occurs from Lambert's Bay to St. James.

The alien barnacle accounted for 100% of barnacles recorded at Elands Bay, Paternoster, Marcus Island and Hout Bay in all years but varied in abundance (Fig. 2). In the mid-shore where *B. glandula* was most abundant, abundance varied with both site (ANOVA, F = 49.14, p = 0.0012) and year (ANOVA, F = 35.39, p = 0.00006), with lower densities being recorded in 2013 (GLS model, t = −5.361643, p = 0.00002). In the low-shore, densities of this barnacle did not differ significantly among years but varied among sites (GLS model, p = 0.0002 in both cases).

Field observations of feeding patterns

In the mid-shore, *B. glandula* was the more dominant of the 2 barnacle species, covering 86 ± 2.4% (SE) of the zone compared to less than 2 ± 0.9% covered by *Notomegabalanus algicola* (*t*-test, t = 38.1, p = 0.009; Fig. 3a). In this zone, *Burnupena lagenaria* and *Trochia cingulata* whelks occurred at densities of 3.9 ± 0.87 and 4.7 ± 0.71 ind. m^{-2}, respectively. A high proportion of both whelk species was observed feeding (83% of *B. lagenaria* and 73% of *T. cingulata*), with both species feeding on significantly more indigenous *N. algicola* than on *B. glandula* (Table 2) despite the low abundance of the former. Low on the shore, *N. algicola* was the dominant barnacle species, covering an average of 41 ± 0.7% of the shore in comparison to only 3 ± 0.8% covered by *B. glandula* (*t*-test, t = 11.2, p = 0.033). *B. lagenaria* was more common in this zone (7.1 ± 0.60 ind. m^{-2}) than in the mid-shore, with 88% of whelks observed feeding. In contrast, *T. cingulata* was less abundant than in the mid-shore (4.1 ± 0.82 ind. m^{-2}), but the proportion of feeding whelks increased to 79%. As in the mid-shore, both whelks fed on significantly more *N. algicola* than on alien barnacles (Table 2), although *B. lagenaria* consumed more barnacles of both species than did *T. cingulata* (Fig. 3b).
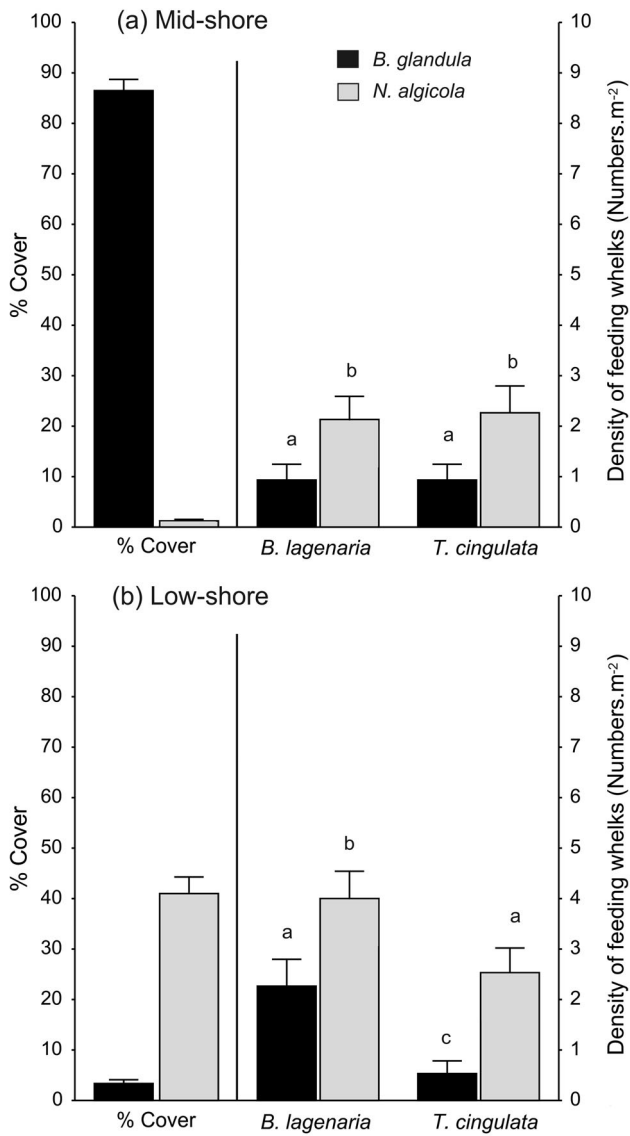
southerly direction by more than 50 km and breached the biogeographic break of Cape Point, spreading to Dalebrook. Over the next 2 yr, the northerly range limit of this alien oscillated between Lambert's Bay and Elands Bay. In 2013, the southerly limit extended from Dalebrook to St. James where it remained, although the species was not consistently present at Dalebrook. It is notable that new recruits

Fig. 3. Percentage cover of *Balanus glandula* and *Notomegabalanus algicola* and the mean (± SE) density of *Burnupena lagenaria* and *Trochia cingulata* whelks feeding on each of these barnacles in (a) the mid-shore and (b) the low-shore. The percentage cover of the 2 barnacles differed significantly in both zones (*t*-test, p < 0.05 in both cases). Shared letters indicate no significant differences in the number of barnacles consumed by the whelks (general linear model, p > 0.05)

Prey-selection experiments

Laboratory feeding experiments revealed that both whelk species consumed significantly more *N. algicola* than *B. glandula* (Fig. 4, Table 3), although this pattern was not exhibited by large *B. lagenaria* (Fisher LSD, p = 0.055). The significantly lower barnacle mortality in control treatments (Fisher LSD, p <

Table 2. Results of a general linear model analysing the number of *Burnupena lagenaria* and *Trochia cingulata* whelks feeding on the barnacles *Balanus glandula* (alien) and *Notomegabalanus algicola* (indigenous) in the field

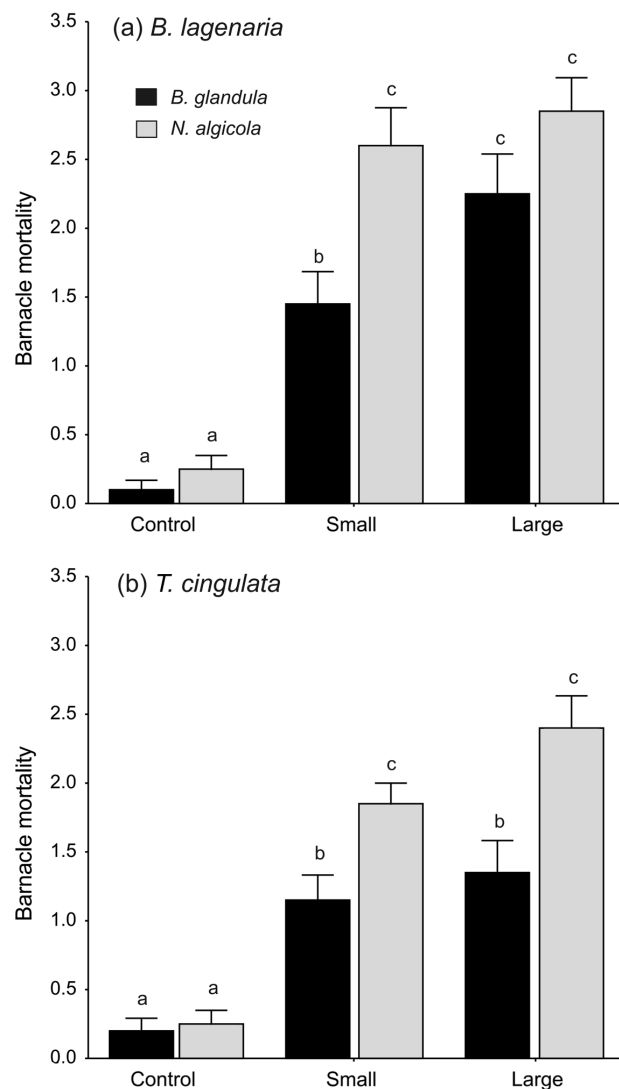| Shore zone	Effect	df	F	p
Mid-shore	Whelk sp.	1	0.09	0.771
	Barnacle sp.	1	31.6	0.0009
	Whelk sp. × Barnacle sp.	1	0.03	0.849
Low-shore	Whelk sp.	1	40.79	0.0008
	Barnacle sp.	1	40.80	0.0007
	Whelk sp. × Barnacle sp.	1	8.42	0.004

Fig. 4. Mean (± SE) mortality of *Balanus glandula* and *Notomegabalanus algicola* barnacles simultaneously offered to small and large (a) *Burnupena lagenaria* and (b) *Trochia cingulata* whelks after 5 d. Control treatments had no whelks

Table 3. Results of a factorial ANOVA analysing the number of dead *Balanus glandula* and *Notomegabalanus algicola* barnacles at the end of laboratory prey selection experiments. Treatments constitute controls (i.e. barnacles with no whelks) and exposure to small and large whelks

Whelk species	Effect	df	F	p
Burnupena lagenaria	Treatment	2	64.75	0.0001
	Barnacle sp.	1	12.56	0.0006
	Treatment × Barnacle sp.	2	2.61	0.078
Trochia cingulata	Treatment	2	49.16	0.0001
	Barnacle sp.	1	17.74	0.0002
	Treatment × Barnacle sp.	2	4.23	0.0169

0.05 for both species) is indicative of mortality in whelk treatments resulting from predation. Ivlev's electivity index showed both size classes of *B. lagenaria* consuming significantly more *N. algicola* and fewer *B. glandula* than would be expected if diet was proportional to abundance of prey (Fig. 5a, Table 4). Small individuals, however, showed a significantly greater avoidance of *B. glandula* and preference for *N. algicola* (p = 0.032) than did the large whelks. *T. cingulata* also demonstrated a preference for feeding on the indigenous barnacle while avoiding *B. glandula* (Fig. 5b, Table 4). However, no significant difference in preference for *N. algicola* (p = 0.068) or avoidance of *B. glandula* (p = 0.081) was observed between small and large individuals of this species.

Comparison of barnacle structural defences and palatability

The morphological characteristics of *B. glandula* and *N. algicola* show marked differences (Fig. 6). While both barnacles have 6 wall plates, the opercular plates of the native were more exposed than those of *B. glandula*, and a narrow ring of vulnerable soft

Table 4. Results of Friedman's ANOVAs and Kendall's coefficient of concordance comparing Ivlev's electivity (*E*) between barnacle species (*Balanus glandula* and *Notomegabalanus algicola*) and among size classes of the 2 indigenous whelk species

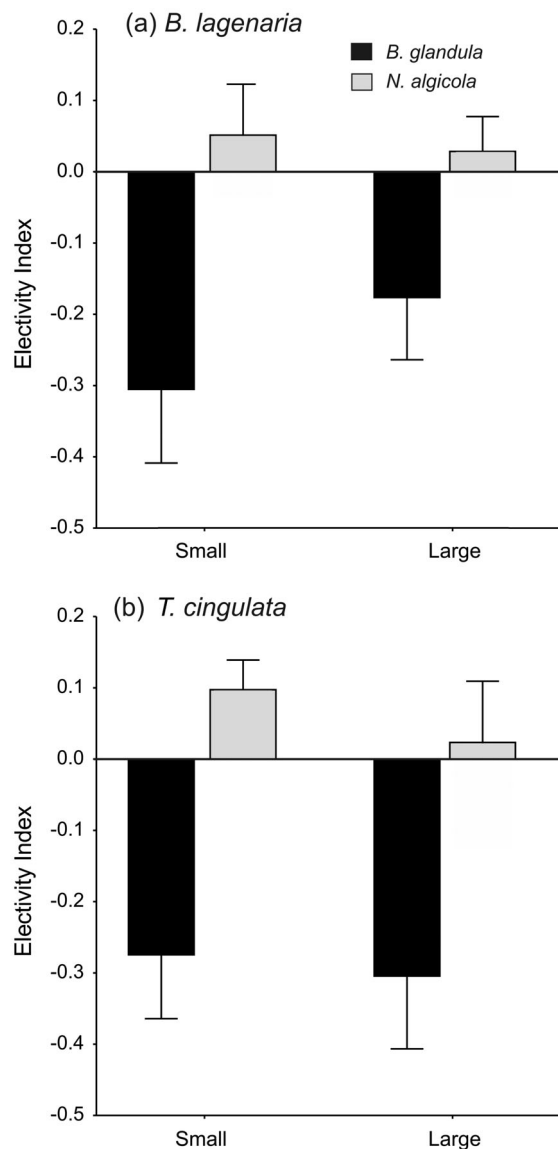| Whelk species	ANOVA χ^2 (n = 20, df = 3)	p	Kendall's coefficient of concordance
Burnupena lagenaria	14.05	0.009	0.23
Trochia cingulata	14.70	0.006	0.25

Fig. 5. Ivlev's electivity index (±SE) for (a) *Burnupena lagenaria* and (b) *Trochia cingulata* whelks offered the barnacles *Balanus glandula* and *Notomegabalanus algicola*. Small and large size class whelks were offered equal quantities of barnacles. In this case, Ivlev's index theoretically ranges from 0.333 (exclusive diet) to 0 (equal preference for each species) to −1 (complete avoidance). Positive values indicate active selection while negative values indicate prey avoidance

tissue was found around the opercular plates of *N. algicola*. External ribbings on wall plates were present in the alien but absent in the native barnacle. In addition, *B. glandula* had significantly thicker walls (ANCOVA, $F = 70.5$, p = 0.017) and opercular plates (ANCOVA, $F = 52.5$, p = 0.026) and significantly longer (ANCOVA, $F = 68$, p = 0.045) and wider opercula (ANCOVA, $F = 11.0$, p = 0.035) than *N. algicola*,
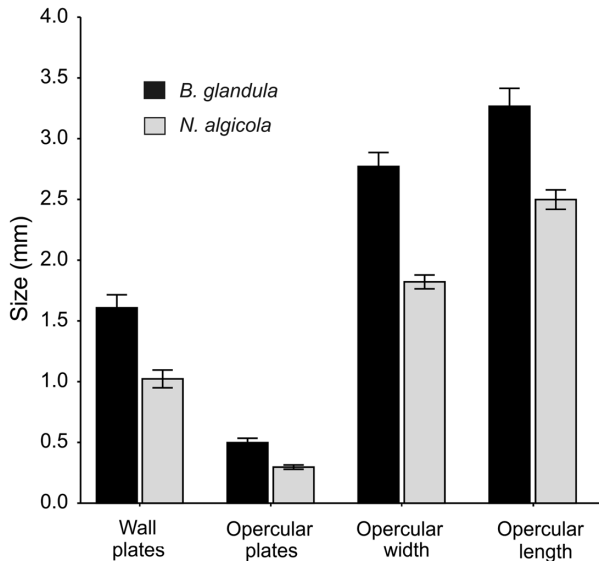
Fig. 6. Mean (± SE) wall plate thickness, opercular plate thickness, opercular width and opercular length of *Balanus glandula* and *Notomegabalanus algicola*. All 4 measures differed significantly between the 2 barnacle species (ANCOVA, p < 0.05 in all cases)
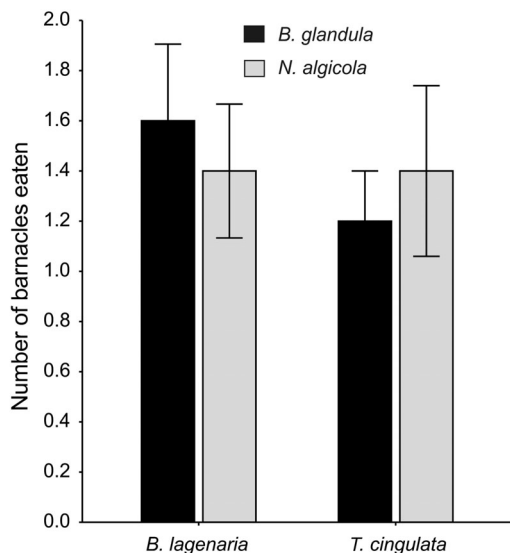

Fig. 7. Mean (± SE) number of shelled *Balanus glandula* and *Notomegabalanus algicola* consumed by *Burnupena lagenaria* and *Trochia cingulata* whelks when simultaneously offered 5 of each barnacle species. No significant differences were detected between the number of each barnacle species consumed by either whelk (ANCOVA, p > 0.05 in both cases)

even when the differences in size were accounted for.

No significant differences were recorded in the number of shelled *B. glandula* and *N. algicola* consumed by either whelk species (ANCOVA, p > 0.05 in both cases; Fig. 7).

DISCUSSION

While substantial research effort has focused on the anthropogenic drivers of marine invasions (for example, see Minchin 2007, Forrest et al. 2009, Mineur et al. 2012, Seebens et al. 2013), studies quantifying the regulators and inhibitors of the spread of these species are less common (Carlsson et al. 2009, Freestone et al. 2013). Of those studies that have considered biotic resistance to marine alien species, most have focused on resistance to invasive consumers and have recorded stronger resistance than studies considering invasive producers (Kimbro et al. 2013). However, little is understood about resistance to non-predatory invasive species that exert their impact through the acquisition of non-food based resources. We aimed to address this gap by considering predation-driven biotic resistance to the intertidal barnacle *Balanus glandula* along the South African coast.

This barnacle had a range of 400 km along the South African west coast when it was first recognised in 2007 (Laird & Griffiths 2008), but has now extended this by 150 km. Most notably, *B. glandula* has spread south and breached the biogeographic break of Cape Point, a well established boundary that delimits the cool temperate Southern Benguela Ecoregion to the west and the warmer Agulhas Ecoregion to the east (Sink et al. 2012), 2 regions that share <20% similarity in faunal composition (Emanuel et al. 1992). It was previously thought unlikely that *B. glandula* would spread past Cape Point (Laird & Griffiths 2008) for 2 reasons. Firstly, the temperatures of its native (Kado 2003) and other invasive ranges (Elias & Vallarino 2001, Kado 2003, Rico & López-Gappa 2006) match the cool temperate west coast, suggesting that the warmer waters of the south coast were outside the thermal range of this species. Secondly, prevailing currents move in a westerly direction (Harris 1978), making larval spread around the point in an easterly direction unlikely. While the mechanism of spread remains unclear, *B. glandula* has extended its range east past Cape Point. This may be explained by recent work that documented *in situ* nearshore water temperatures along the South African coast for the first time (Smit et al. 2013) and showed that mean temperatures remain below 18°C east of Cape Point until Cape Agulhas, although summer temperatures reach 20°C in some areas. It thus remains unclear how far this barnacle may spread along the south coast or whether warmer pockets along the coast will pose a barrier. The oscillating nature of the invasion front of this species up

the west coast is often observed in invasive species, as populations consolidate over time before continuing to spread (Suarez et al. 2006, O'Connor 2014). This pattern has been recorded for *B. glandula* in Japan (Alam et al. 2013), where local extinctions occurred at the invasion front but declined in frequency after 5 yr when recruitment increased (Alam et al. 2013). It is expected that *B. glandula* will continue to spread north up the South African west coast as there is currently no known barrier to its spread in that direction.

Unfortunately, qualitative consideration of the impact of the spread of *B. glandula* on indigenous barnacles is not possible, as no systematic historic monitoring of rocky shores has taken place in within the range of this aggressive invader. The only study that may have shed light on this aspect was undertaken on Marcus Island (Robinson et al. 2007), but there, native barnacles were spatially and temporally variable even before the invasion of *B. glandula*. Nonetheless, Simon-Blecher et al. (2008) suggested that the dominance of *B. glandula* and the concurrent coast-wide reduction of the native chthamaloid *Chthamalus dentatus* were driven by competition between these barnacles.

The fact that *B. glandula* has spread so prolifically raises questions about the role of predation as a regulator of this species, especially as it is controlled by whelk predators in its native range (Connell 1970). From our field observations of feeding patterns and laboratory prey-selection experiments, we accepted our hypotheses that (1) *B. glandula* experiences less predation pressure by native whelks than does the native barnacle *Notomegabalanus algicola* and (2) native whelks show an avoidance of this invader. A similar avoidance of a novel barnacle prey by predatory whelks was observed in northern California (USA), where the range expansion of the volcano barnacle *Tetraclita rubescens* was ascribed to recent warming and low predation pressure in its new range (Sanford & Swezey 2008). While small *Burnupena lagenaria* and all *Trochia cingulata* whelks avoided *B. glandula* in feeding trials, large *B. lagenaria* showed no avoidance. Taken together with the fact that large *B. lagenaria* are most abundant in the low-shore (T. B. Robinson pers. obs.), this suggests that while predation-driven biotic resistance may not be controlling the range extension of the invasive barnacle, predation by *B. lagenaria* may influence its downshore distribution, at least in areas where this whelk is abundant. This finding supports suggestions by Laird & Griffiths (2008) that predation may have a regulatory effect on low-shore *B. glandula* populations. This manifestation of biotic resistance potentially constraining an invasion (i.e. in its vertical extent) aligns with previous suggestions that biotic resistance is more likely to limit invasions rather than repel them (Levine et al. 2004, Carlsson et al. 2009). Nonetheless, at the scale of this invasion, the effect of predation by *B. lagenaria* is likely to be quite small, as this whelk occurs at highest densities on sheltered shores (Blamey & Branch 2009) where *B. glandula* is least abundant (Laird & Griffiths 2008). While biotic resistance to *B. glandula* has not been assessed in its other invaded ranges (i.e. Japan and Argentina), it would be interesting to determine whether predation plays a regulating role in these regions.

Low predation pressure on a novel prey may be explained by various factors, including (1) the absence of a co-evolutionary history (Dietl 2003); (2) behavioural mechanisms relating to lack of experience with handling the prey (Wieters & Navarrete 1998); (3) superior defences in comparison to other prey choices (Palmer 1982); and (4) low palatability (Nelson et al. 2011). It is unlikely that either the absence of co-evolution or handling inexperience explain the observed avoidance of *B. glandula*. As this barnacle has been present for at least 20 yr and its high abundance makes it the species most often encountered by whelks in the field, prey naivety should not have influenced our findings. However, assessments of morphological defences revealed that *N. algicola* is much more vulnerable to whelk predation than *B. glandula* is. As no drill holes were found in any of the barnacles used during laboratory experiments, it appears that whelks attacked through the opercular openings of the barnacles, or in the case of *N. algicola*, through the flesh around the opercular plates. The finding that *B. lagenaria* and *T. cingulata* did not differentiate between the alien and native barnacles when their shells were removed indicates that palatability does not differ between the 2 species. Instead, the differences in structural defences (like exposed soft tissue and thinner wall and opercular plates) are likely to explain the preference for *N. algicola* and the avoidance of *B. glandula* displayed by both whelks.

While the results from this study are reflective of the situation on the west coast, it is unclear what biotic resistance *B. glandula* may face east of Cape Point. Although *B. lagenaria* does occur on the south coast, *T. cingulata*, along with many intertidal predatory whelks, is confined to the Southern Benguela Ecoregion. Particularly between Cape Point and Cape Agulhas, most intertidal whelks are scavengers and will thus not affect the potential spread of this invasive barnacle. While large predators such as

crabs and starfish prey on *B. glandula* in its native range (Connell 1970), these are not expected to play a regulatory role along the south coast. Intertidal crabs in this region are either algal feeders or are restricted to the extreme low-shore, and no predatory starfish occur intertidally along this coast. It is thus suggested that for as long as abiotic conditions are within the tolerance range of *B. glandula*, this aggressive invader will continue to spread along the south coast of South Africa.

While some studies have recorded predation-driven biotic resistance on rocky shores (Reusch 1998, Shinen et al. 2009) or found evidence for such resistance developing after a lag phase (Carlsson et al. 2009), we recorded no predator resistance to the coast-wide spread of *B. glandula*, despite the species having been established for more than 20 yr. The avoidance of this very abundant source of potential prey by native intertidal whelks is likely a result of the superior structural defences of the barnacle. While low predation pressure is undoubtedly at play in this system, the role of other biotic interactions such as competition and facilitation should not be ignored. In particular, the role of competition between native barnacles and *B. glandula* in regulating the vertical range of the invader remains to be considered, as previous work in Hawaii has demonstrated how native grazers can facilitate the settlement of invasive barnacles (Zabin & Altieri 2007). Our study highlights the need to consider mainstream invasion hypotheses like biotic resistance in various systems and regions to assess how widely applicable they are. It is through rigorous testing of these ideas that we will gain a better understanding of the role of biological interactions in regulating the spread and impact of alien species.

LITERATURE CITED

Alam AKMR, Hagino T, Fukaya K, Okuda T, Nakaoka M, Noda T (2013) Early phase of the invasion of *Balanus glandula* along the coast of Eastern Hokkaido; changes in abundance, distribution, and recruitment. Biol Invasions 16:1699–1708

Bando KJ (2006) The roles of competition and disturbance in a marine invasion. Biol Invasions 8:755–763

Barnes M (1999) The mortality of intertidal cirripedes. Oceanogr Mar Biol Annu Rev 37:153–244

Blamey LK, Branch GM (2009) Habitat diversity relative to wave action on rocky shores: implications for the selection of marine protected areas. Aquat Conserv 19: 645–647.

Blossey B, Notzold R (1995) Evolution of increased competitive ability in invasive nonindigenous plants—a hypothesis. J Ecol 83:887–889

Branch GM, Odendaal F, Robinson TB (2008) Long-term monitoring of the arrival, expansion and effects of the alien mussel *Mytilus galloprovincialis* relative to wave action. Mar Ecol Prog Ser 370:171–183

Callaway RM, Ridenour WM (2004) Novel weapons: invasive success and the evolution of increased competitive ability. Front Ecol Environ 2:436–443

Carlsson NO, Sarnelle O, Strayer DL (2009) Native predators and exotic prey—an acquired taste? Front Ecol Environ 7:525–532

Carlton JT, Newman WA, Pitombo FB (2011) Barnacle invasions: introduced, cryptogenic, and range expanding Cirripedia of North and South America. In: Galil BS, Clark PF, Carlton JT (eds) In the wrong place—alien marine crustaceans: distribution, biology and impacts. Springer Verlag, Berlin, p 159–214

Cebrian E, Ballesteros E, Linares C, Tomas F (2011) Do native herbivores provide resistance to Mediterranean marine bioinvasions? A seaweed example. Biol Invasions 13:1397–1408

Connell JH (1970) A predator-prey system in the marine intertidal region. I. *Balanus glandula* and several predatory species of *Thais.* Ecol Monogr 40:49–78

Dietl GP (2003) Coevolution of a marine gastropod predator and its dangerous bivalve prey. Biol J Linn Soc 80: 409–436

Dumont CP, Gaymer CF, Thiel M (2011) Predation contributes to invasion resistance of benthic communities against the non-indigenous tunicate *Ciona intestinalis.* Biol Invasions 13:2023–2034

Elias R, Vallarino EA (2001) The introduced barnacle *Balanus glandula* (Darwin) in the Mar del Plata port as a structuring species in the intertidal community. Invest Mar 29:37–46

Elton CS (1958) The ecology of invasions by animals and plants. Methuen, London

Emanuel BP, Bustamante RH, Branch GM, Eekhout S, Odendaal FJ (1992) A zoogeographic and functional approach to the selection of marine reserves on the west coast of South Africa. S Afr J Mar Sci 12:341–354

Forrest BM, Gardener JPA, Taylor MD (2009) Internal borders for managing invasive species. J Appl Ecol 46:46–54

Freeman AS, Dernbach E, Marcos C, Koob E (2014) Biogeographic contrast of *Nucella lapillus* responses to *Carcinus maenas.* J Exp Mar Biol Ecol 452:1–8

Freestone AL, Ruiz GM, Torchin ME (2013) Stronger biotic resistance in tropics relative to temperate zone: effects of predation on marine invasion dynamics. Ecology 94: 1370–1377

Harris TFW (1978) Review of the coastal currents in southern African waters. South African National Scientific Programmes Report 30, Cape Town

Ivlev VS (1961) Experimental ecology of the feeding of fishes. Yale University Press, New Haven, CT

Jaubet ML, Sanchez MA, Rivero MS, Garaffo GV, Vallarino EA, Elias R (2011) Intertidal biogenic reefs built by the polychaete *Boccardia proboscidea* in sewage-impacted areas of Argentina, SW Atlantic. Mar Ecol 32:188–197

Kado R (2003) Invasion of Japanese shores by the NE Pacific barnacle *Balanus glandula* and its ecological and biogeographical impact. Mar Ecol Prog Ser 249:199–206

Keane RM, Crawley MJ (2002) Exotic plant invasions and the enemy release hypothesis. Trends Ecol Evol 17: 164–170

Kimbro DL, Cheng BS, Grosholz ED (2013) Biotic resistance in marine environments. Ecol Lett 16:821–833

Laird MC, Griffiths CL (2008) Present distribution and abundance of the introduced barnacle *Balanus glandula* in South Africa. S Afr J Mar Sci 30:93–100

Levine JM, Andler PB, Yelenik SG (2004) A meta-analysis of biotic resistance to exotic plant invasions. Ecol Lett 7: 975–989

Minchin D (2007) Aquaculture and transport in a changing environment: overlap and links in the spread of alien biota. Mar Pollut Bull 55:302–313

Mineur F, Cook EJ, Minchin D, Bohn K, MacCleod A, Maggs CA (2012) Changing coasts: marine aliens and artificial structures. Oceanogr Mar Biol Annu Rev 50:189–234

Nelson DWM, Crossland MR, Shine R (2011) Foraging responses of predators to novel toxic prey: effects of predator learning and relative prey abundance. Oikos 120:152–158

Nyberg CD, Wallentinus I (2005) Can species traits be used to predict marine macroalgal introductions? Biol Invasions 7:265–279

O'Connor NJ (2014) Invasion dynamics on a temperate rocky shore: from early invasion to establishment of a marine invader. Biol Invasions 16:73–87

O'Riordan RM, Power AM, Myers AA (2010) Factors, at different scales, affecting the distribution of species of the genus *Chthamalus* Ranzani (Cirripedia, Balanomorpha, Chthamaloidea). J Exp Mar Biol Ecol 392:46–64

Paine RT (1994) Marine rocky shores and community ecology: an experimentalist's perspective. In: Kinne O (ed) Excellence in ecology. Book 4. Ecology Institute, Oldendorf/Luhe

Palmer AR (1982) Predation and parallel evolution: recurrent parietal plate reduction in balanomorph barnacles. Paleobiology 8:31–44

Peterson CH, Renaud PE (1989) Analysis of feeding preference experiments. Oecologia 80:82–86

Quinn GP, Keough MJ (2002) Experimental design and data analysis for biologists. Cambridge University Press, Cambridge

Reusch TBH (1998) Native predators contribute to invasion resistance to the non-indigenous bivalve *Musculista senhousia* in southern California, USA. Mar Ecol Prog Ser 170:159–168

Rico A, López-Gappa JJ (2006) Intertidal and subtidal fouling assemblages in a Patagonian harbour (Argentina, Southwest Atlantic). Hydrobiologia 563:9–18

Rius M, Potter EE, Aguirre JD, Stachowicz JJ (2014) Mechanisms of biotic resistance across complex life cycles. J Anim Ecol 83:296–305

Roa R (1992) Design and analysis of multiple-choice feeding preference experiments. Oecologia 89:509–515

Robinson TB, Branch GM, Griffiths CL, Govender A, Hockey PAR (2007) Changes in South African rocky intertidal invertebrate community structure associated with the invasion of the mussel *Mytilus galloprovincialis*. Mar Ecol Prog Ser 340:163–171

Sagarin RD, Gaines SD (2002) Geographical abundance distributions of coastal invertebrates; using one-dimensional ranges to test biogeographic hypotheses. J Biogeogr 29:985–997

Sanford E, Swezey DS (2008) Response of predatory snails to a novel prey following the geographic range expansion of an intertidal barnacle. J Exp Mar Biol Ecol 354:220–230

Schneider KR (2008) Heat stress in the intertidal: comparing survival and growth of an invasive and native mussel under a variety of thermal conditions. Biol Bull (Woods Hole) 215:253–264

Seebens H, Gastner MT, Blasius B (2013) The risk of marine bioinvasion caused by global shipping. Ecol Lett 16: 782–790

Shinen JS, Morgan SG, Chan AL (2009) Invasion resistance on rocky shores: direct and indirect effects of three native predators on an exotic and a native prey species. Mar Ecol Prog Ser 378:47–54

Simberloff D, Von Holle B (1999) Positive interactions of non-native species: invasional meltdown? Biol Invasions 1:21–32

Simon-Blecher N, Granevitze Z, Achituv Y (2008) *Balanus glandula*: from North-West America to the west coast of South Africa. Afr J Mar Sci 30:85–92

Sink K, Holness S, Harries L, Majiedt P and others (2012) National Biodiversity Assessment 2011: technical report. Volume 4: Marine and coastal component. South African National Biodiversity Institute, Pretoria

Smit AJ, Roberts M, Anderson RJ, Dufois F and others (2013) A coastal seawater temperature dataset for biogeographical studies: large biases between *in situ* and remotely-sensed data sets around the coast of South Africa. PLoS ONE 8:e81944

Sorte CJB, Williams SL, Zerebecki RA (2010) Ocean warming increases threat of invasive species in a marine fouling community. Ecology 91:2198–2204

Stachowicz JJ, Fried H, Osman RW, Whitlatch RB (2002) Biodiversity, invasion resistance, and marine ecosystem function: reconciling pattern and process. Ecology 83: 2575–2590

Suarez ER, Fahey TJ, Groffman PM, Yavitt JB, Bohlen PJ (2006) Spatial and temporal dynamics of exotic earthworm communities along invasion fronts in a temperate hardwood forest in south-central New York (USA). Biol Invasions 8:553–564

Vallarino EA, Elias R (1997) The dynamics of an introduced *Balanus glandula* population in the southwestern Atlantic rocky shores. The consequences on the intertidal community. Mar Ecol 18:319–335

Vermeij MJ, Smith T, Dailer M, Smith C (2009) Release from native herbivores facilitates the persistence of invasive marine algae: a biogeographical comparison of the relative contribution of nutrients and herbivory to invasion success. Biol Invasions 11:1463–1474

Wieters EA, Navarrete SA (1998) Spatial variability in prey preference of the intertidal whelks *Nucella caniculata* and *Nucella emarginata*. J Exp Mar Biol Ecol 222: 133–148

Zabin CJ, Altieri A (2007) A Hawaiian limpet facilitates recruitment of a competitively dominant invasive barnacle. Mar Ecol Prog Ser 337:175–185

Zar JH (2010) Biostatistical analysis, 5th edn. Prentice-Hall, NJ