



# Despite prolonged association in closed populations, an intertidal predator does not prefer abundant local prey to novel prey

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The diets of predators should reflect interactions between their behavioural and anatomical constraints and the availability and accessibility of prey, although feeding preferences may also reflect adaptation to locally abundant prey, particularly in closed populations. On the south-east coast of Australia, the whelk *Haustrum vinosum* (Lamarck, 1822) and its prey communities provide a model system in which to test the effect of variation in prey availability on diet and dietary preferences. *Haustrum vinosum* is a direct developing species, forming effectively closed populations, with the potential for local adaptation at local and regional scales. Here we show that populations of whelks east and west of a biogeographical barrier encounter different prey assemblages, and have different feeding patterns and apparent prey preferences. We then use a prey choice experiment to test for evidence that *H. vinosum* from three populations west of the barrier display an inherent preference for its most frequently encountered western prey species, the mussel *Brachidontes rostratus* (Dunker, 1857), over a novel prey, the barnacle *Tesseropora rosea* (Krauss, 1848). We detected no prey preference within any population, suggesting past association with *B. rostratus* did not influence prey selection. Our data support the hypothesis that predators with limited dispersal and high population differentiation are able to maintain flexible generalist foraging patterns, even when they encounter novel prey. © 2013 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2013, 108, 812–820.

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## INTRODUCTION

Optimal foraging theory predicts that if predators have prolonged association with the same communities of prey then selection should favour specialization and preference for high-quality and locally abundant prey (Futuyma & Moreno, 1988). Alternatively, if predators encounter variable environments and a range of potential prey species with differing defences, selection should favour flexible, generalists (Bell, 1990; Krebs & Davies, 1993). Such flexibility may be especially favoured in the marine intertidal environment, where prolonged predator–prey associations are unlikely, and indeed localized adaptation or

site-specific selection in general is expected to be strongly opposed by both temporal variability in demographic processes and biological interactions, and by high levels of gene flow associated with planktonic larval dispersal (Johnson & Black, 1984; Ayre, 1985; Marshall *et al.*, 2010; Sanford & Kelly, 2011).

The degree of flexibility that might be expected of an important class of intertidal predators, the whelks, is unclear. Some whelks, despite widespread distributions, are direct developers without planktonic life stages, and therefore rely upon rafting for episodic dispersal, which may allow long-distance, albeit infrequent, colonization of different habitats (Thiel & Gutow, 2005). Consequently, such species can form largely closed and highly genetically subdivided populations that typically experience very low levels of interpopulation gene flow (e.g. Hoskin, 1997; Ayre,

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Minchinton & Perrin, 2009). Moreover, they should display considerable capacity for localized adaptation, but we predict that the extent to which these whelks display specialization upon locally abundant prey species will depend on both the inherent flexibility of the predatory behaviour and current and historical patterns of variation in prey availability. Although many feeding studies of these important predators have typically labelled them as generalists (e.g. Hughes & Dunkin, 1984a), the strength of their prey preferences and capacity to handle novel prey has rarely been rigorously evaluated.

Recently, Sanford & Worth (2009) demonstrated that the direct-developing predatory whelk *Nucella canaliculata* (Duclos, 1832) displays striking adaptation to the occurrence of a prey species, the mussel *Mytilus californianus* Conrad, 1837, at a regional scale. Southern populations of *N. canaliculata* that co-occur with *M. californianus* prey readily upon this mussel, whereas northern populations, where *M. californianus* is absent, lack the capacity to overcome the novel defence provided by its relatively thick shell. Sanford & Worth (2009) found that this behavioural dichotomy is heritable, which implies that their capacity to consume particular prey species may be shaped by selection, at least for whelks that are poor dispersers. Nevertheless, it is unclear whether this study system is a rare case mediated by an extreme defensive adaptation or whether the predatory behaviour of whelks is generally limited by their evolved preferences for locally abundant prey, or their inability to consume novel prey.

Despite extensive reports of the feeding ecology of whelks it is difficult to assess the evidence for dietary specialization because many earlier studies assume that the feeding preference of whelks can be inferred from simple observations of feeding in the field (e.g. Paine, 1969; Underwood, Chapman & Crowe, 2004). Field surveys have inherent biases because the duration and frequency of the observations, and the handling time and accessibility of prey that are being consumed by the predator may distort the estimates of the number of each prey type consumed (Fairweather & Underwood, 1983). Moreover, field studies also typically do not relate diet to prey availability (Paine, 1966; Dayton, 1971; Menge, 1976), although some have acknowledged these biases (Fairweather & Underwood, 1983; Yamamoto, 2004). Laboratory studies of preference can reduce confounding effects such as the variation in size, quality, and encounter rates of prey that are found in field studies (e.g. Underwood & Clarke, 2005; Peharda & Morton, 2006; Taplin, 2007). To examine prey preference in whelks we therefore need to examine consumption in the field in relation to prey availability, and then test whether these apparent preferences are consistent when

whelks are offered a choice of prey (of the same size, quality, quantity, and with the same handling constraints).

Along the south-east coast of Australia the distribution of the direct-developing whelk *Haustrum vinosum* (Lamarck, 1822) spans a major biogeographical barrier, the south-east Australian biogeographical barrier, or SABB (Fig. 1), that limits the distribution of many rocky intertidal prey species (Knox, 1963; O'Hara & Poore, 2000; Hidas *et al.*, 2007). At locations west of the barrier the mussel *Brachidontes rostratus* (Dunker, 1857) is the most abundant prey species in the intertidal community, whereas further east of the barrier several species of barnacle, including *Tesseropora rosea* (Krauss, 1848), which has a southern range limit east of the SABB (Poore, 2004; Hidas *et al.*, 2007; Lathlean *et al.*, 2010), are the most abundant prey. Based on observations in several parts of its range *H. vinosum* is considered a generalist predator (Synnot, 1980), but there is also experimental evidence that it exhibits preferences for locally abundant prey species (Bayliss, 1982). As expected for a direct developer, genetic studies have shown that local populations (i.e. those on isolated headlands) are highly differentiated (Triantafillos, Donnellan & Butler, 1998; Ayre *et al.*, 2009). *Haustrum vinosum* and its associated native and novel prey communities thus provide a model system to test the generality of the ideas presented by Sanford & Worth (2009).

To test whether *H. vinosum* consumed prey in proportion to their availability we firstly quantified the composition of the prey community, the abundance of prey species, and the observed feeding patterns of *H. vinosum* at two locations to the east and three to the west of the SABB (Fig. 1). We predicted that, because local populations of *H. vinosum* are highly differentiated and prey communities either side of the barrier are strikingly different, feeding patterns of *H. vinosum* will also differ significantly among regions, and it will consume a disproportionate amount of the locally abundant prey species. We then conducted a laboratory feeding experiment with three populations of *H. vinosum* from west of the SABB to examine their relative preference for the locally abundant species, the mussel *B. rostratus*, versus a novel prey species, the barnacle *T. rosea*. *Tesseropora rosea* is a novel prey for the western populations of *H. vinosum* because its distribution is limited to locations ~300 km to the east, beyond the biogeographic barrier (Poore, 2004; Hidas *et al.*, 2007; Lathlean *et al.*, 2010), and it is morphologically dissimilar (being larger and having a thicker test) to other abundant barnacle species within the western region (Anderson & Anderson, 1985). Unfortunately, prey species of comparable novelty and in sufficient abundance were not avail-

able to allow similar testing of the preferences of *H. vinosum* within eastern populations. We predicted that if feeding preferences reflect localized adaptation to prey then *H. vinosum* from the western region will prefer the mussel *B. rostratus* over *T. rosea* (because *B. rostratus* is both the dominant prey in the western region and has a long history of association with *H. vinosum*, Triantafillos *et al.*, 1998; Ayre *et al.*, 2009). At the same time we acknowledge that optimal foraging theory predicts that prey abundance is not the only factor that influences prey choice, and, of course, differences in prey abundance and composition among headlands can influence feeding preferences.

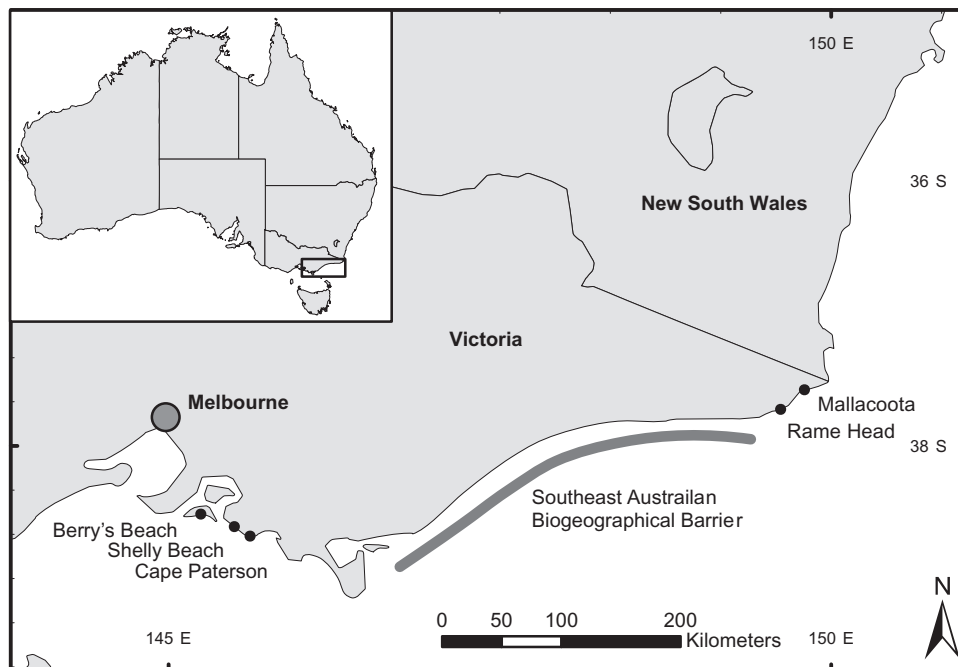
## MATERIAL AND METHODS

### GEOGRAPHICAL VARIATION IN AVAILABLE PREY AND OBSERVED DIET

We measured the availability of potential prey and the feeding patterns of *H. vinosum* in November 2009 on five rocky intertidal shores, spanning approximately 400 km of coastline, including locations within the western and eastern regions on either side of the SABB (Fig. 1). At each rocky shore location we selected two replicate sites (separated by 20 m) that extended 5 m up the shore from the mean low water mark and 30 m alongshore. Because of the small area of rocky shore at Rame Head, only one site could be established. At each site, 30 (1 m × 1 m) quadrats

were haphazardly selected and densities of adult *H. vinosum* were recorded. Prey availability was then estimated by photographing two of the possible four 0.25-m<sup>2</sup> (50 cm × 50 cm) subquadrats from the 1-m<sup>2</sup> quadrat used for estimating whelk abundance (giving a total of 60 photo quadrats per site). The abundance of potential prey in each photo quadrat was assessed as percentage cover with the point of intersection method, using CORAL POINT COUNT with EXCEL EXTENSION 4.1 (Kohler & Gill, 2006). The availability (percentage cover) of individual prey species was calculated as a proportion of all available prey species (percentage cover). To assess if the observed diet (*sensu* Fairweather & Underwood, 1983) of *H. vinosum* varied along the coast in response to prey availability, the frequency of predation and the identity of prey was recorded for all *H. vinosum* encountered within the 30 1-m<sup>2</sup> quadrats. Predation was scored by removing the whelks from prey and checking for signs of feeding, such as an extended proboscis or signs of drilling. At each location, we gathered data from more than 100 feeding individuals.

Two-factor nested ANOVA, with rocky shore locations on either side of the SABB ( $N = 3$  in the western region and  $N = 2$  in the eastern region), was used to test for significant differences in the percentage cover of available prey within and between regions using JMP 9 (SAS Institute Inc., 1989–2007). Location was considered a random factor and region a fixed factor. Randomly removing locations from the western



**Figure 1.** Map showing rocky shore locations on the western (Berry's Beach, Shelly Beach, and Cape Paterson) and eastern (Rame Head and Mallacoota) sides of the south-east Australian biogeographical barrier (solid curved line).

region to balance the design did not alter statistical outcomes (see Results). We used Cochran's test to detect heterogeneity of variances, and data were transformed to  $\log(x + 1)$  if appropriate (Winer, 1971). To determine whether *H. vinosum* showed evidence of differing patterns of prey consumption at different locations, we compared the proportions of available prey and the proportions consumed by *H. vinosum*.

#### PREY PREFERENCES OF *HAUSTRUM VINOSUM*

To determine whether *H. vinosum* from populations located west of the SABB preferentially consumed the abundant prey, the mussel *B. rostratus*, in preference to the novel prey, the barnacle *T. rosea*, we conducted laboratory feeding preference trials using the methods of Taplin (2007). *Haustrum vinosum* was collected at the same three western locations that we used to estimate prey availability and diet (Fig. 1). Because populations of *H. vinosum* are effectively closed to migration (Triantafillos *et al.*, 1998; Ayre *et al.*, 2009), these three locations represent three independent tests of the hypothesis that foraging behaviour is shaped by localized adaptation. Within each western location, we haphazardly selected thirty individual *H. vinosum* of similar size ( $7.3 \pm 0.10$  mm aperture length), together with a set of intermediate-sized *B. rostratus* ( $20.9 \pm 0.30$  mm shell length), to be used as a locally specific abundant prey. As the novel prey, we used *T. rosea* of similar size,  $3.9 \pm 0.03$  mm aperture length, collected from rocky intertidal shores near Wollongong, New South Wales. To ensure that *T. rosea* was presented intact we used specimens that were attached to the shells of the large limpet *Cellana tramoserica* (Holten, 1802). Each individual barnacle that was offered as a prey item was attached to a separate fragment of *C. tramoserica* shell. During the course of the feeding trial neither the barnacles nor mussels aggregated, eliminating possible density-dependent feeding biases. Each whelk was held in a separate submerged 650-mL aquarium that was randomly positioned within water tables. The water tables were part of a recirculating seawater system that was refreshed every week by exchanging one-third of the volume of water in the system. Over the duration of the experiment, the water temperature was held constant at  $21 \pm 1$  °C under a 12-hour dark/12-h light cycle.

The feeding trials involved offering each whelk a choice of five *B. rostratus* and five *T. rosea* that were randomly positioned. The small size of the individual aquaria and the random positioning of prey were designed to reduce the potential influence of encounter rate on results. Each aquarium was inspected daily to quantify prey consumption. A prey item was considered eaten when there were obvious signs of

drilling through a shell or if the shell was empty. There was no natural mortality of barnacles or mussels in control aquaria without whelks. There was no evidence that daily inspections disturbed the feeding process of *H. vinosum*.

The calculation of prey preference using Taplin's (2007) method assumes that the order in which prey is consumed discloses information about preference, with the more preferred prey being consumed first. This design follows the standard definition of preference in preferential voting, whereby each individual selects their most preferred candidate first, and continues until all candidates have been voted for; therefore, the first prey eaten is the most preferred and the last prey eaten is the least preferred (Taplin, 2007). The resultant null hypothesis would be that prey consumption is random. Therefore, the first prey that is eaten is assigned the first rank (1), the second the second rank (2), and so on, until all prey have been assigned a rank, with the last prey item being assigned a rank of 10. As handling time and digestion rates can influence feeding rate, actual times to consume a prey are not used. When not all prey items are consumed, as was the case here, remaining prey items are assigned the average of the remaining preference scores: that is, they are considered 'tied for last' (Taplin, 2007). Importantly, the ranking of these prey items occurs at an individual level and this allows individuals (and groups of individuals) to be considered independent tests of the hypothesis being tested.

To test for potential effects of recent feeding experience on prey choice (learning), we randomly assigned groups of ten whelks per location to each of three acclimation diets for 14 days prior to the assessment of feeding preference: (1) ad libitum diet of exclusively *B. rostratus*; (2) ad libitum diet of exclusively *T. rosea*; or (3) starvation. By feeding diets of only mussels or only barnacles, we predicted that this exposure and hence experience might increase the preference for each of these prey. By starving whelks we aimed to reduce the effect of earlier feeding experience on their local shores (Hughes & Dunkin, 1984a; Wieters & Navarrete, 1998). After the acclimation period, and immediately before the feeding trial began, all individuals were starved for 7 days to ensure that none of the whelks were satiated (Jackson & Underwood, 2007).

Individual preference scores were calculated for two orthogonal factors: acclimation diet (mussel, barnacle, or starvation) and rocky shore location (BB, Berry's Beach; SB, Shelly Beach; or CP, Cape Paterson), and there were ten replicate trials per acclimation diet at each location, giving 90 separate trials to determine prey preference. Differences in average preference scores were analysed with two-factor ANOVA using JMP 9 (SAS Institute Inc., 1989–2007), with location

as a random factor and acclimation as a fixed factor. Ultimately, there was no significant effect of acclimation ( $F_{2,4} = 2.345$ ,  $P = 0.212$ ) or the interaction of acclimation by location ( $F_{4,81} = 1.091$ ,  $P = 0.366$ ) on prey preference, and therefore data were pooled across the three acclimation treatments to increase power of tests of prey preference at each location.

Importantly, according to Taplin's (2007) method, in this study an average preference score of  $> 5.5$  indicated a preference for *B. rostratus* and a score  $< 5.5$  indicated a preference for *T. rosea*. We therefore used a one-tailed, one sample Student's *t*-test at each location to provide three independent tests of our hypothesis that *H. vinosum* should prefer the abundant mussel *B. rostratus* over the novel barnacle *T. rosea*.

## RESULTS

### GEOGRAPHICAL VARIATION IN AVAILABLE PREY AND OBSERVED DIET

The percentage cover of potential prey varied greatly within and between regions. At locations within the western region (BB, SB, and CP), the mussel *B. rostratus* was the most abundant prey, with an average of 15% cover. There was a dramatic and significant decrease in the abundance of *B. rostratus* east of the break [region,  $F_{1,4} = 82.67$ ,  $P < 0.001$ ; location (region),  $F_{4,354} = 6.09$ ,  $P < 0.001$ ; Fig. 2A], where on average it was found to give  $< 1\%$  cover. At eastern locations, where *B. rostratus* was rare, the small honeycomb barnacle *Chamaesipho tasmanica* (Foster & Anderson, 1986) was the most abundant prey species, with 6% cover (Fig. 2C). The percentage cover of *C. tasmanica* did not vary significantly within regions, and *C. tasmanica* was present at all locations at similar low abundances [region,  $F_{1,4} = 2.69$ ,  $P = 0.176$ ; location (region),  $F_{4,354} = 17.31$ ,  $P < 0.001$ ; Fig. 2C]. The southern range limit of *T. rosea* occurs within the eastern region and, consequently, *T. rosea* was not discovered within the western region. Therefore, *T. rosea* is a novel prey for populations of *H. vinosum* west of the SABB. At the southern range limit within the eastern locations, *T. rosea* occupied  $< 1\%$  cover (Fig. 2G).

We recorded four other potential prey species: the barnacles *Tetraclitella purpurascens* (Wood, 1815), *Chthamalus antennatus* (Darwin, 1854), and *Catomerus polymerus* (Darwin, 1854), and the tube-worm *Galeolaria caespitosa* (Lamarck, 1818). When the percentage cover of all barnacle species was combined, no significant differences in cover were detected among regions [region,  $F_{1,4} = 0.01$ ,  $P = 0.925$ ; location (region),  $F_{4,354} = 31.07$ ,  $P < 0.001$ ; Fig. 2E).

Differences in available prey communities were accompanied by differences in the observed diet of *H. vinosum*. In the western region the diet of *H. vino-*

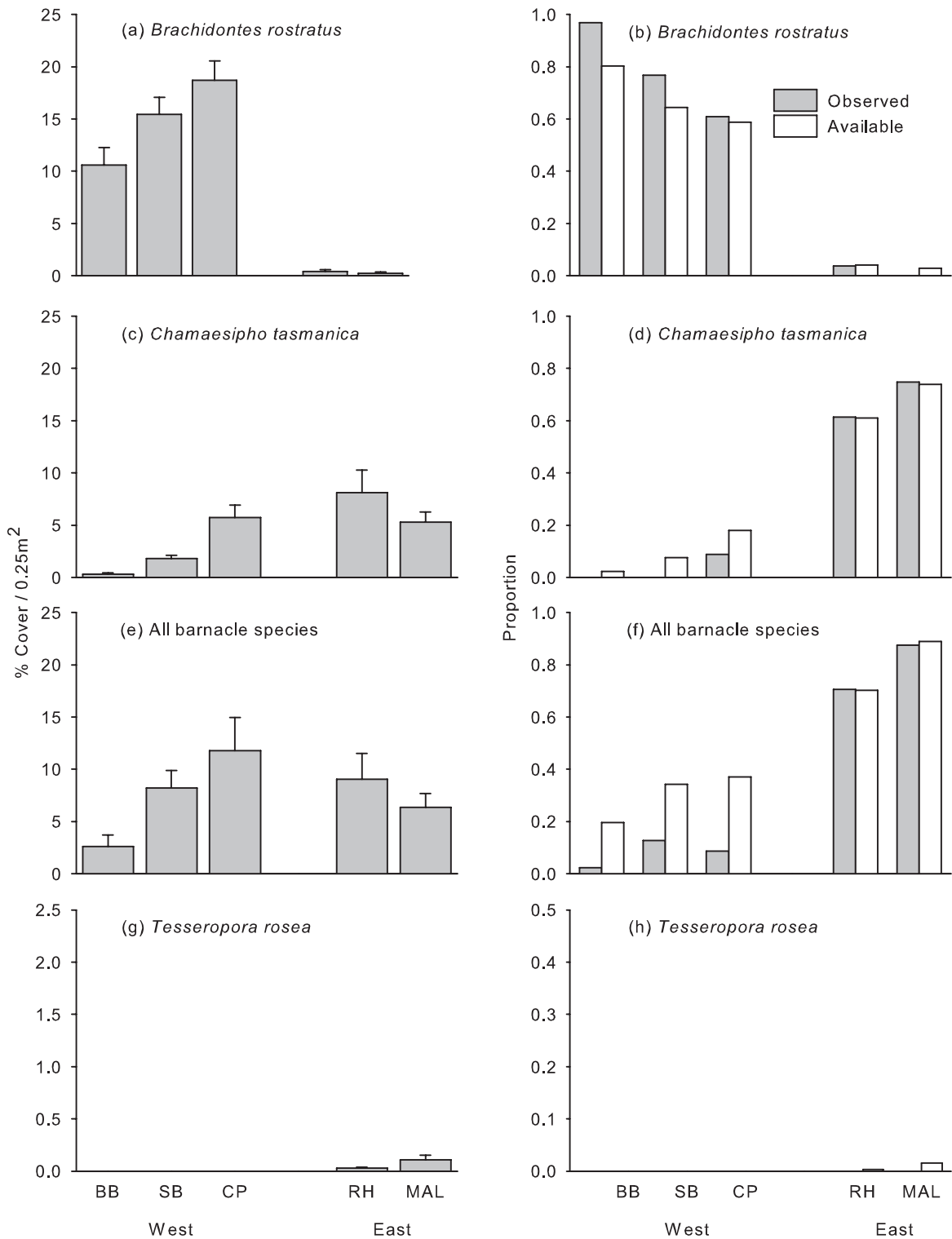
*sum* was dominated by the mussel *B. rostratus*: on average, *B. rostratus* accounted for up to 97% of the prey consumed at BB (Fig. 2B). At these western locations, *H. vinosum* consumed mussels up to 20% more frequently than would be predicted by their abundance. This suggests that whelks at western locations preferentially consume this prey species (Fig. 2B). Interestingly, as the density of *B. rostratus* increased (CP  $>$  SB  $>$  BB) its availability actually decreased because the prey community diversified (Fig. 2); despite this reduction in availability, *B. rostratus* remained the most commonly consumed prey type. The importance of *B. rostratus* as a prey species decreased dramatically within the eastern region, where the diet of *H. vinosum* was typically more varied, but was composed primarily of barnacles (Fig. 2F). Within eastern locations, the consumption of prey species appeared to be proportional to their availability: for example, *H. vinosum* at Mallacoota and Rame Head consumed *C. tasmanica* in proportion to their availability (Fig. 2D). *Haustrum vinosum* was observed eating *T. rosea* at Mallacoota and Rame Head (R. A. McWilliam, pers. observ.), although this was not detected within our quantitative sampling.

### PREY PREFERENCES OF *HAUSTRUM VINOSUM*

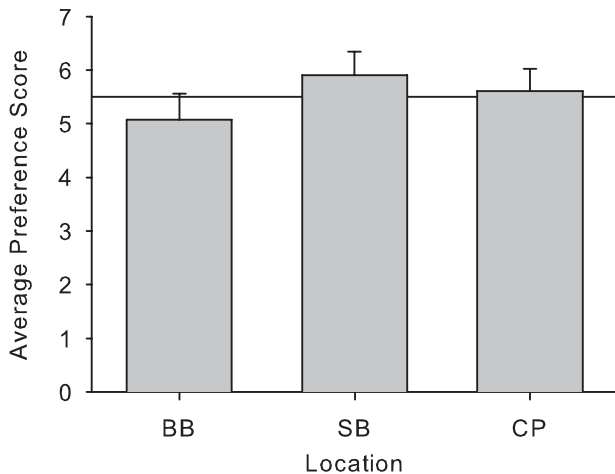
The feeding trial was conducted for 68 days, during which 66% (301) of mussels and 56% (255) of barnacles were consumed. There was no difference in either the time to first attack ( $t_{88} = 1.43$ ,  $P = 0.156$ ) or which prey species was consumed first ( $\chi^2_2 = 0.74$ ,  $P = 0.863$ ) across locations. This pattern persisted until the end of the feeding trial, when it was shown that there was no significant difference in preference scores among the locations ( $F_{2,87} = 0.086$ ,  $P = 0.918$ ). Furthermore, one-sample Student *t*-tests of preference scores for each location failed to detect any significant variation from the null hypothesis of 5.5 (BB,  $t_{29} = 0.81$ ,  $P = 0.491$ ; SB,  $t_{29} = 1.02$ ,  $P = 0.158$ ; CP,  $t_{29} = 0.52$ ,  $P = 0.303$ ; Fig. 3). Consequently, in the region west of the SABB, where we had expected a strong preference for *B. rostratus*, three independent tests with different populations revealed no evidence of prey preference for either prey type (Fig. 3).

## DISCUSSION

Our field surveys of prey consumption and availability on either side of the SABB provide clear evidence that the whelk *H. vinosum* is an important generalist predator throughout its south-eastern Australian range. Moreover, despite a life history that features direct development and consequent extreme inter-population genetic subdivision for neutral markers (Ayre *et al.*, 2009), together with variation in prey



**Figure 2.** Graphs on the left are mean ( $\pm$ SE) percentage cover of abundant potential prey species at locations to the west (BB, Berry's Beach; SB, Shelly Beach; CP, Cape Paterson) and east (RH, Rame Head; MAL, Mallacoota) of the south-east Australian biogeographical barrier. Right-hand graphs indicate the proportion of each species in the diet of *Haustrum vinosum* in comparison with availability.



**Figure 3.** Mean ( $\pm$ SE) preference scores across the three western locations. The reference line indicates a null hypothesis of no preference (i.e. a preference score of 5.5).

availability and consumption, we found no evidence that whelks within each of the three populations of *H. vinosum* were unable to eat novel prey, namely the barnacle *T. rosea*. Nor did these western populations display a consistent preference for the regionally dominant prey, the mussel *B. rostratus*. Indeed, although our surveys of prey availability and predation revealed substantial within- and among-region variation in prey availability and consumption, our feeding trials revealed no variation in prey preference in the western populations examined. This was somewhat surprising as *T. rosea* occurs only within the eastern region, and should be novel to each of the three populations of *H. vinosum* that were tested. In contrast, *B. rostratus* is consistently the numerically dominant prey species for the western populations and the most commonly eaten species within those populations. These results contrast sharply with those of Sanford & Worth (2009, 2010), who found that *N. canaliculata* (from populations that occurred in a bioregion rich in the preferred mussel prey *Mytilus trossulus* Gould, 1850) were unable to consume the novel prey *M. californianus*. It seems probable that the situation presented by Sanford & Worth (2009, 2010) will prove to be unusual, and that whelks such as *H. vinosum* that have evolved as generalist foragers will rarely show such striking localized adaptation to locally abundant prey.

This is the first study to quantify the abundance of the dominant sessile mid-intertidal prey organisms across the SABB, supporting earlier less detailed work by Hidas *et al.* (2007) and Coulson *et al.* (2011). Importantly, we were able to demonstrate that the mussel *B. rostratus* was the numerically dominant

sessile macroinvertebrate on the rocky shore within the western region. It is also clear from our field surveys that *T. rosea* is a truly novel prey species within western populations of *H. vinosum*, and hence these populations have had no prior experience with this species. The high abundance of *B. rostratus* across western locations, together with our finding that within this western region *B. rostratus* was consumed more frequently than predicted from its relative abundance, suggests that if selection favours specialization rather than dietary flexibility, then an innate preference for this mussel over the barnacle *T. rosea* should exist in these populations. Estimating dietary preference using field observations can be difficult because observations of prey consumption can only be performed in 'snapshots' (Fairweather & Underwood, 1983), and in this case, of necessity, we assumed that percentage cover accurately reflects the relative availability of prey. At the minimum, however, it is clear that within western populations *H. vinosum* do eat large quantities of *B. rostratus*, and that each of these populations has had a long association with this prey (Bennett & Pope, 1953; Knox, 1963).

Contrary to our prediction, we found, in three independent tests using whelks from isolated rocky shore headlands, no evidence that western populations of *H. vinosum* preferred the locally abundant *B. rostratus* to the novel prey species *T. rosea*. Moreover, *H. vinosum* displayed an equal preference for both prey types, irrespective of recent acclimation treatment. The design and analysis of this feeding trial ensured that all whelks had equal access to similar-sized prey, and that any biases that could be introduced through handling times and encounter rates were minimized (Taplin, 2007). The ease with which *H. vinosum* consumes the novel *T. rosea*, together with the broad range of prey consumed within local populations, suggests that the predicted range expansions of macroinvertebrates within this region will not be accompanied by an escape from predation (Wernberg *et al.*, 2011). Our findings are similar to those reported by Carroll & Wethey (1990), where the whelk *Nucella lamellosa* (Gmelin, 1791), which is also a directly developing species, added the barnacle *Semibalanus balanoides* (Linnaeus, 1758) to its diet without any prior experience in the field. Moreover, Morton (2008) reported that in simple trials *H. vinosum* was able to attack and consume mussel species from beyond its natural range, although he did not attempt to test for prey preference. Strikingly, in our study *H. vinosum* was shown to be capable of consuming a novel species that has distinctly different morphology to the most commonly consumed and locally abundant mussel prey, but it is unclear, despite obvious visual differences in shell shape, whether

*T. rosea* possess defences that are significantly different from the local barnacle species that western populations encounter.

In conclusion, our study strongly supports the prediction that selection favours a flexible foraging strategy, despite limited dispersal and high differentiation, in temporally and spatially heterogeneous prey communities (Futuyma & Moreno, 1988). Our data support earlier claims (Bayliss, 1982; Morton, 2008) that *H. vinosum*, like other species of whelks (Hughes & Dunkin, 1984b; Fairweather, 1988), is a generalist predator, and for the first time the feeding preference of *H. vinosum* was able to be inferred from observational field data. Interestingly, we have a system in which localized adaptation should be possible because each population is effectively closed to migration. Nevertheless, although our field survey implied that *H. vinosum* might prefer its locally abundant prey, this prediction was not supported by rigorous laboratory trials. We predict that selection is favouring a generalist foraging strategy because these prey populations are ephemeral and community compositions can change rapidly within locations (Underwood & Chapman, 2000).

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