

Alistair G. B. Poore · Nicole A. Hill

## Sources of variation in herbivore preference: among-individual and past diet effects on amphipod host choice

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**Abstract** Understanding which factors affect the feeding preferences of herbivores is essential for predicting the effects of herbivores on plant assemblages and the evolution of plant–herbivore interactions. Most studies of marine herbivory have focussed on the plant traits that determine preferences (especially secondary metabolites), while few studies have considered how preferences may vary among individual herbivores due to genetic or environmental sources of variation. Such intraspecific variation is essential for evolutionary change in preference behaviour and may alter the outcome of plant–herbivore interactions. In an abundant marine herbivore, we determined the relative importance of among-individual and environmental effects on preferences for three host algae of varying quality. Repeated preference assays were conducted with the amphipod *Peramphithoe parmerong* and three of its brown algal hosts: *Sargassum linearifolium*, *S. vestitum* and *Padina crassa*. We found no evidence that preference varied among individuals, thus constraining the ability of natural selection to promote increased specialisation on high-quality *S. linearifolium*. Most of the variation in preference occurred within individuals, with amphipod preferences strongly influenced by past diet. The increased tendency for amphipods to select alternate hosts to that on which they had been recently feeding indicates that amphipods are actively seeking mixed diets. Such a feeding strategy provides an explanation for the persistence of this herbivore on hosts in the field that support poor growth and survival if consumed alone. The effects of past diet indicate that herbivore preferences are a function of herbivore history in addition to plant traits and

are likely to vary with the availability of algae in space and time.

### Introduction

Most herbivores display strong preferences among the plant species available in their local environment. Understanding the factors that affect this selective behaviour is crucial for predicting the effects of herbivores on plant assemblages and the evolution of herbivore behaviour. Consequently, plant selection by herbivores has been a major focus of ecological, evolutionary and applied research into plant–herbivore interactions (Futuyma and Moreno 1988; Jaenike 1990).

Research into the preferences of marine herbivores has predominantly focussed on the importance of plant traits in determining how herbivores rank the available plant resources. Numerous studies have shown that preference among plant parts, individuals or species may be explained by the concentration and composition of secondary metabolites (reviewed in Paul et al. 2001), nutritional value (e.g. Cruz-Rivera and Hay 2000a) or toughness (e.g. Pennings and Paul 1992). Few studies, however, have considered how preferences may vary among individual herbivores, and how this intraspecific variation may alter plant–herbivore interactions. Heritable variation in host use among individuals is a prerequisite for evolutionary change in herbivore behaviour—via selection on differences in performance across hosts. Such selection should promote preferences for high-performance hosts and lead to a correlation between preference and performance (Via 1986; Thompson 1988).

While there is evidence of heritable variation in the performance (i.e. growth and survival) of some marine herbivores (Duffy and Hay 1991; Poore and Steinberg 1999; Hemmi and Jormalainen 2004), the relative influence of genetic and environmental variation on preferences is largely unknown (Sotka 2003). Genetically determined variation in preference has been documented

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A. G. B. Poore (✉) · N. A. Hill  
School of Biological, Earth and Environmental Sciences,  
University of New South Wales, NSW, 2052 Sydney, Australia  
E-mail: a.poore@unsw.edu.au  
Tel.: +61-2-93852154  
Fax: +61-2-93851558

for very few marine herbivores, especially in contrast to the well-documented examples available for terrestrial insect herbivores (Futuyma and Peterson 1985). Within populations, preference for algal hosts has been shown to vary among genotypes of the salt marsh amphipod *Gammarus palustris* (Guarna and Borowsky 1993), among individuals of the sea slug *Placida dendritica* (Trowbridge 1991) and between the sexes of the isopod *Idotea baltica* (Jormalainen et al. 2001). On larger spatial scales, populations of the amphipod *Ampithoe longimana* display heritable variation in their ability to consume the chemically defended brown alga, *Dictyota menstrualis* (Sotka and Hay 2002; Sotka 2003).

Variation in herbivore size, reproductive status (Agnew and Singer 2000), dietary experience (Szentesi and Jermy 1990) and condition may also strongly affect herbivore behaviour and thus contribute to variation in preferences among individuals. Some marine herbivores are known to change host use with size (e.g. the sea hare *Aplysia californica*, Pennings 1990b; and the echinoid *Holopneustes purpurascens*, Williamson et al. 2004), but the influence of herbivore size and age on preferences is largely unknown. Similarly, few studies have considered how the feeding history of individuals (past diet or starvation) may contribute to intraspecific variation in preferences. Periods of starvation have been shown to increase the likelihood of urchins consuming chemically deterrent algae (Cronin and Hay 1996) and of fish consuming artificial diets containing deterrent metabolites (Thacker et al. 1997). The few studies to examine how recent diet may alter preferences have shown either no effects (the isopod *Dynamene bidentata*, Morán and Arrontes 1994) or relatively minor effects (the isopod *Ligia pallasii*, Pennings et al. 2000).

Given the limited understanding of intraspecific variation in the preferences of marine herbivores, we aim to test whether preferences of the herbivorous amphipod *Peramphithoe parmerong* vary among individuals and the degree to which preferences are altered by recent feeding history. This herbivore displays strong preferences among available algal species, with the host most highly preferred (the brown alga *Sargassum linearifolium*) supporting much higher growth and survival than the less preferred species (Poore and Steinberg 1999). Differences in performance among hosts and the presence of variance among families in performance indicate that selection by algae has the potential to alter host use (Poore and Steinberg 2001). Such selection should result in increased specialisation on high-preference algae if there is heritable variation in preference—currently unknown for this species. The presence of *P. parmerong* on low-quality hosts in the field (Poore and Steinberg 1999; Poore 2004) could result from some individuals displaying increased preference for these species, rather than all individuals having a certain likelihood of selecting these hosts. The strong consequences of releasing juveniles on a poor-quality host could lead to differences in the selectivity of brooding females from that of other life history stages.

We asked the following specific questions: (1) What is the amount of among-individual variation in the preferences of *P. parmerong* among three species of brown algae that differ in their quality for amphipod growth and survival? (2) Do preferences vary among male, female (brooding and non-brooding) and juvenile amphipods? (3) Are preferences altered by recent feeding history? (4) Are preferences affected by a brief period of starvation?

## Methods

### Study organisms and site

*Peramphithoe parmerong* Poore and Lowry is an herbivorous amphipod (Crustacea, Amphipoda, Ampithoidae), abundant in the shallow subtidal algal beds around Sydney, Australia. It is found exclusively on brown macroalgae which it uses as both food and habitat. All individuals build open-ended nests from adjacent algal fronds, attaching fronds together with a silk-like substance (Poore and Lowry 1997). In this study, we consider among-individual variation in preferences among three algal species which vary strongly in their suitability for amphipod growth and survival (Poore and Steinberg 1999). *S. linearifolium* (Turner) C. Agardh is the most highly preferred alga and supports the highest growth and survival. *Padina crassa* Yamada is the least preferred and a poor-quality host with survival as low as 14% of that on *S. linearifolium* (Poore and Steinberg 2001). *S. vestitum* (R. Brown ex Turner) C. Agardh has an intermediate ranking for both preference and performance of *P. parmerong*. All three species live in close proximity, with distances among algal individuals well within the range of dispersing amphipods (Poore 2005).

Collections of *P. parmerong* and macroalgae were taken from Shark Bay, Port Jackson, NSW, Australia (33°51'9" S, 151°16'0" E). At this site, each of the algal species is abundant on a shallow (0.5–3 m) sandstone platform.

### Among-individual variation in preference

We tested whether individual *P. parmerong* vary in their preference for *S. linearifolium*, *S. vestitum* and *P. crassa* by repeated preference trials among these algal species. By taking multiple measurements on each individual amphipod, phenotypic variance can be partitioned into that among individuals and that within individuals. The degree of individual specialisation was quantified by Roughgarden's (1979) index,  $WIC_s/TNW_s$ , for discrete data where  $WIC_s$  is the within-individual component of variation in resource use and  $TNW_s$  the total niche width of the population (as described in Bolnik et al. 2002). Values close to one indicate a population of individual generalists, while values close to zero indicate individual specialisation.

Eighty individuals (20 each of males, brooding females, non-brooding females and juveniles) were

offered a choice among pieces of *S. linearifolium*, *S. vestitum* or *P. crassa* on each of five consecutive nights. Algal pieces free of visible epiphytes were cut into equal surface areas to equalise the probability of encounter by amphipods (approximately 5.3 cm<sup>2</sup>, determined from wet weight-surface area regressions for each species (Poore and Steinberg 1999). Algae were left in seawater for 1 h and placed in a circular array held between two plastic rings within experimental containers (6.5×5×4 cm<sup>3</sup>) separated from larger tanks of seawater by 300 µm mesh. Individual amphipods were added to each container, and the algal piece on which they formed a nest was recorded after one night. This trial was then repeated four times with fresh pieces of algae offered each day. The tanks were kept in a 20°C constant temperature room with a 12 h dark:12 h light cycle.

The number of amphipods selecting each alga on each day was contrasted against the expectation of equal numbers (i.e. no preference) using a one-way  $\chi^2$  analysis. The frequency of choosing each alga and of making no choice, from each individual, was then used to calculate the index of individual specialisation,  $WIC_s/TNW_s$ . The probability that the observed value was obtained from a population of generalists was calculated from bootstrap re-sampling of 1,000 populations (i.e. tests against a null model of no individual specialisation, Bolnik et al. 2002).

A two-way contingency analysis was performed to test whether preferences varied among amphipods of different status (male, brooding female, non-brooding female and juvenile) (a 4×4 exact test, status vs. host choice). The analysis was done separately on each day of the trial to ensure independence of data points (i.e. only one value from each individual per analysis).

#### Effects of past diet and condition on preference

Given the large differences in amphipod performance on these three algal hosts (Poore and Steinberg 1999), we expected that feeding history may influence subsequent preferences. To test the effects of past diet on preferences among *S. linearifolium*, *S. vestitum* and *P. crassa*, we fed 40 individual *P. parmerong* on each of these diets for 3 days. On the fourth day, amphipods were subjected to the preference assay among these three species of algae (as described above) and their choice of host recorded after the following night. The dependence of host choice on past diet was tested using a two-way contingency analysis (three past diets vs. three current choices). The magnitude of any deviations from the expected counts on each alga was examined by standardised residuals following the contingency analysis (Agresti 1996).

Preference among available hosts may be altered by animal condition, with previous studies showing that marine herbivores can become less discriminating after periods of starvation (Cronin and Hay 1996). We tested whether starvation affected *P. parmerong* preferences among algal hosts by contrasting 40 amphipods that had been starved for 2 days with 40 amphipods that had fed on *S. linearifolium* for the same period. After the initial

period of 2 days, amphipods were subjected to a preference assay among *S. linearifolium*, *S. vestitum* or *P. crassa* (as described above). The number that selected each alga was recorded after one night and analysed with a two-way contingency analysis (starved/non-starved vs. alga chosen).

#### Statistical analyses

The software IndSpec1 was used to calculate the index,  $WIC_s/TNW_s$ , and the associated probabilities from bootstrap re-sampling (Bolnik et al. 2002, available from Ecological Archive E083-056-S1). Contingency analyses were carried out using SYSTAT (Version 10, SPSS Inc.). The 4×4 exact test was performed with the online calculator available at <http://www.physics.csbsju.edu/stats/>. The significance level was taken as  $P < 0.05$ .

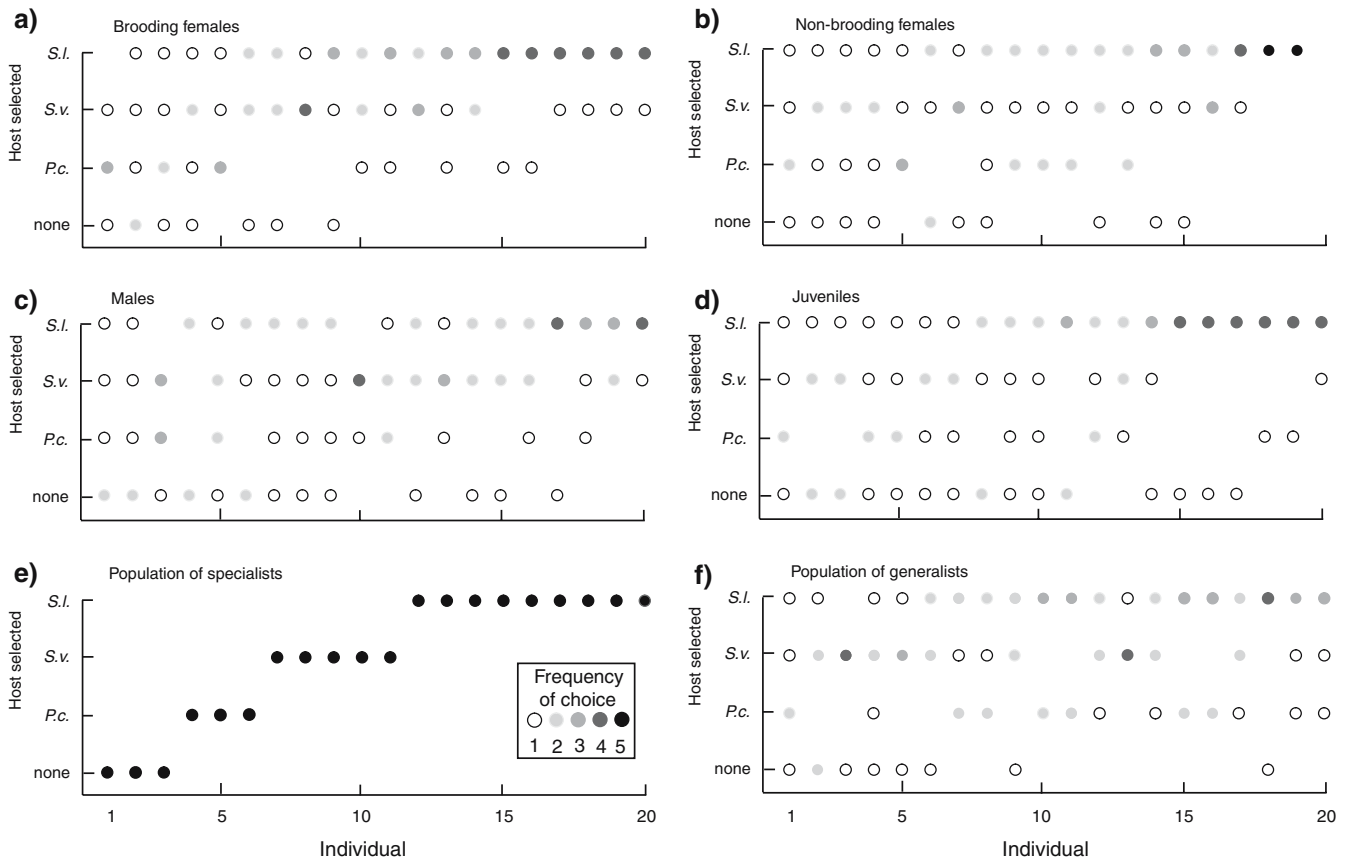
## Results

### Among-individual variation in preference

*Peramphithoe parmerong* displayed strong preferences among the three algal hosts ( $\chi^2 > 12.5$ ,  $df = 3$ ,  $P < 0.006$  for each of the 5 days). *S. linearifolium* was the most highly preferred (selected in 44% of all trials, pooling days and individuals), followed by *S. vestitum* (26% of trials) and then *P. crassa* (14% of trials). We detected no significant among-individual variation in *P. parmerong* preferences among *S. linearifolium*, *S. vestitum* and *P. crassa* (Fig. 1). Roughgarden's (1979) index of among-individual specialisation indicated a population of generalised individuals ( $WIC_s/TNW_s = 0.74$ ). This value was higher than 79% of the 1,000 re-sampled populations that represent a null model of generalised individuals. The index was similarly non-significant if the cases in which amphipods did not select an alga were removed ( $WIC_s/TNW_s = 0.73$ ,  $P = 0.57$ ). The sex and reproductive status of the amphipods did not affect their algal preferences (Fig. 1, exact tests for all 5 days,  $P > 0.41$ ).

### Effects of past diet and condition on preference

The preferences of *P. parmerong* among the three species of algae were dependent on their recent feeding history ( $\chi^2 = 9.92$ ,  $df = 4$ ,  $P = 0.04$ ). The largest deviations from the expected counts (in decreasing order of magnitude of the standardised residuals, Fig. 2) were: (1) an increased tendency to select *P. crassa* if previously fed on *S. linearifolium*; (2) a decreased tendency to select *S. linearifolium* if previously fed on *S. linearifolium*; (3) a decreased tendency to select *P. crassa* if individuals had fed on *P. crassa* or *S. vestitum*; and (4) an increased tendency to select *S. linearifolium* if previously fed on the poor-quality *P. crassa*. The first of these is the likely cause of interaction between past diet and present choices, given that adjusted residuals greater than two indicate a lack of fit of the null hypothesis in that cell (Agresti 1996).



**Fig. 1** Variation in preferences among individuals of *P. parmerong* selecting among three species of algae: *S. linearifolium*, *S. vestitum* and *P. crassa*. Data are the frequency of each algal choice and of making no choice, from five repeated preference trials of 20 individuals of brooding females (a), non-brooding females (b), males (c) and juveniles (d) (total of 80 individuals). The lower two panels present simulated distributions of preferences from a population of specialised individuals (e) and a population of generalists (f). The specialised individuals have the observed host choices of the population distributed

among the individuals to maximise among-individual variance. The generalised population is a simulation where the probability of each individual selecting a given host is in proportion to choices made by the entire population. Hosts are ranked in order of host quality (where *S. linearifolium* is the highest). Individual amphipods are sorted according to the mean host ranking (where 1 = *S. linearifolium*; 2 = *S. vestitum*; 3 = *P. crassa*; and 4 = no choice) across five trials such that those selecting the poorest combination of diets appear on the left while those selecting the highest combination appear on the right

Amphipod preferences among the three species of algae were unaffected by a period of 2 days of starvation prior to the preference assay (Fig. 3). Amphipods that had been feeding did not differ in their preferences from those that had been starved, with both groups maintaining their high preference for *S. linearifolium* ( $\chi^2=6.29$ ,  $df=3$ ,  $P=0.10$ ). The absence of any effect of starvation remains if the analysis is repeated with the removal of those animals that did not make a choice ( $\chi^2=0.76$ ,  $df=2$ ,  $P=0.68$ )

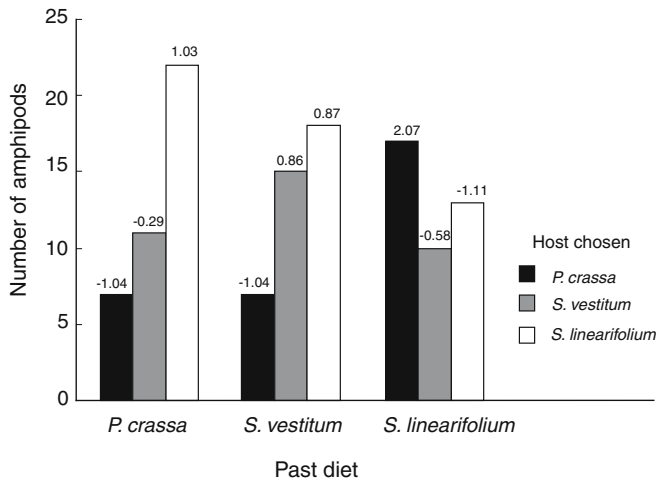
**Discussion**

Among-individual variation in preference

Most marine herbivores are generalists, consuming algae from many families and often all three divisions of macroalgae (Hay and Steinberg 1992). This host range

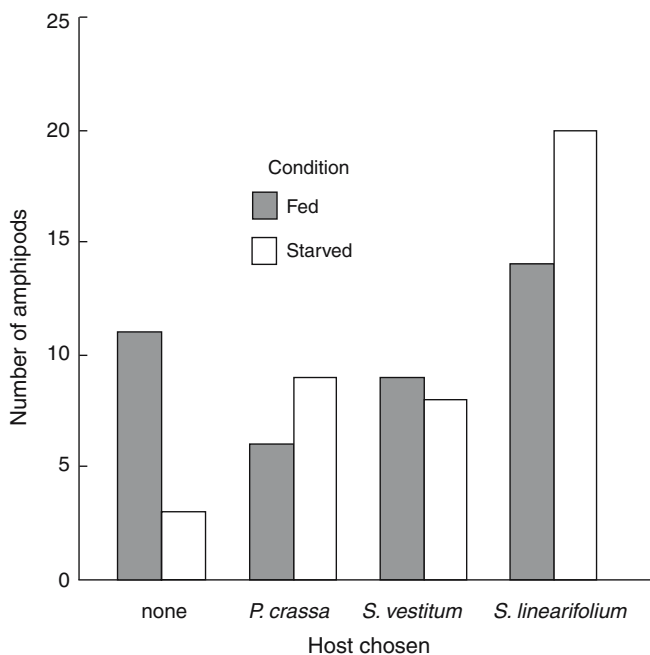
contrasts strongly with that of insect herbivores on land, 75% of which are restricted to feeding from only one family of plants (Bernays and Chapman 1994). Population and species level estimates of diet breadth in marine herbivores, however, may mask important variation in diet among individual herbivores. The diet breadth of individual herbivores in terrestrial ecosystems is commonly narrower than that recorded for the species (Fox and Morrow 1981). More generally, individual variation in resource use often comprises a majority of variation within a population and has been commonly overlooked in ecological studies (Bolnik et al. 2003). Despite intra-specific variation in preferences being an important predictor of the effects of herbivores on plants and a prerequisite for evolutionary change in host use, the degree to which host range is a property of individuals or populations is poorly understood for marine herbivores.

We found no evidence to suggest that individuals of an abundant marine herbivore, the amphipod *P. parmerong*, were specialised to certain hosts among those



**Fig. 2** The effects of past diet on preferences of *P. parmerong* among three species of algae: *S. linearifolium*, *S. vestitum* and *P. crassa*. Data are counts of amphipods selecting each alga in a three-way preference assay. Numbers above the bars are the standardised residuals from the contingency analysis of past diet versus host selected. Negative residuals indicate reduced tendency to select that alga, while positive residuals indicate an increased tendency to select that alga

available to this species. Most of the variation in preferences expressed among three host species that varied strongly in their quality for amphipod performance occurred within individuals. The population thus consists of many generalised individuals, rather than subsets of individuals with a more restricted diet than the



**Fig. 3** The effects of a short period of starvation on preferences of *P. parmerong* among three species of algae: *S. linearifolium*, *S. vestitum* and *P. crassa*. Data are the counts of amphipods selecting each alga and of making no choice, in a three-way preference assay

population as a whole. A similar lack of variation among individuals was found for the limpet *Acmaea scutum* in which each individual maintained a mixed diet (Kitting 1980). While individual specialisation has been documented for some marine herbivores (e.g. the sea slug *P. dendritica*, Trowbridge 1991) and a few other marine consumers (e.g. the predatory whelk *Nucella emarginata*, West 1986), the paucity of studies to date makes it difficult to assess the degree of individual specialisation likely among marine herbivores. Even fewer studies have demonstrated that any such variation in preferences has a genetic basis. We are familiar with only two species for which preferences have been shown to have a genetic basis—the amphipods *G. palustris* (Guarna and Borowsky 1993) and *A. longimana* (Sotka and Hay 2002; Sotka 2003).

Intraspecific variation in preferences provides a target for natural selection, but evolutionary change in these preferences will only occur if that variation is heritable (Via 1990). If feeding on individual hosts, *P. parmerong* is subjected to strong selection via differential performance on available hosts, with growth and survival on the poor-quality *P. crassa* being very low in contrast to the high-quality *S. linearifolium* (Poore and Steinberg 1999, 2001). A simple adaptive model suggests that such selection should result in a population of herbivores specialised to *S. linearifolium*, which is also the most abundant host in the field. The continued presence of *P. parmerong* on poor-quality hosts in the field, however, indicates that measuring the performance on single species diets is inappropriate (see below) or that the evolution of such specialisation has been constrained by ecological or genetic factors. Ecological constraints include herbivore mobility, plant availability (explored for *P. parmerong* in Poore 2004), natural enemies and the history of association between plant and herbivore (Thompson 1988). Genetic constraints include the heritability of traits responsible for host choice and the genetic relationship among such traits (Futuyma and Peterson 1985; Via 1990). The performance of *P. parmerong* on *S. linearifolium* and *P. crassa* has been shown to be heritable and may thus respond to selection (Poore and Steinberg 2001). Selection on preferences, however, will only lead to increased specialisation if they too are heritable. Given that the consistency of repeated behaviours within an individual (repeatability) is considered an upper limit on heritability (Falconer and Mackay 1996), the lack of individual specialisation demonstrated here may constrain the evolution of increased specialisation and provide an explanation for the occurrence of this species on poor-quality hosts.

While most of the variance in preference occurs within individuals of the population sampled at Shark Bay, it is possible that there is evolutionarily important variation among individuals at spatial scales larger than tested here. Heritable variation in preferences among populations of herbivorous amphipods has been demonstrated for *A. longimana* (Sotka and Hay 2002). In that species, populations that lived within the geographic

range of the chemically defended brown alga *D. menstrualis* had increased preferences for this alga in comparison to populations that lived outside its range. The degree to which preferences of *P. parmerong* may vary on these scales is currently unknown, although no differences have been found among populations in the Sydney region (separated by 2–15 km) in their ability to survive and grow on *S. linearifolium* and *P. crassa* (Poore and Steinberg 2001). It is also possible that heritable variation in preferences would be detected using other methods to assess among-individual variation. While the repeatability of behaviours is routinely used in the behavioural literature to quantify phenotypic variation among individuals (e.g. Brooks 1996; Howard and Young 1998), more direct measures of heritability (e.g. half-sib families, parent–offspring regressions) or experiments with greater statistical power may be successful in detecting heritable variation.

#### Effect of past diet and condition on preference

The preferences of *P. parmerong* were dependent on the identity of the alga recently consumed, indicating strong environmental influences on host plant selection in this herbivore. Past diet may affect future herbivore choices through learning (Szentesi and Jermy 1990), responses to novel food types (Bernays and Raubenheimer 1991) or changes to herbivore condition that can alter the expression of preferences (Cronin and Hay 1996). More generally, the identity of past habitats experienced is thought to be an important source of variation on future habitat choices in a wide range of animals (Davis and Stamps 2004).

*Peramphithoe parmerong* displayed an increased preference for the poor-quality *P. crassa* after having fed on *S. linearifolium*. Given that long periods of feeding on *P. crassa* are associated with greatly reduced survival (Poore and Steinberg 2001), this result is inconsistent with an optimal choice model of individual hosts and suggests that *P. parmerong* are actively seeking a mixed diet. The available hosts cannot be simply ranked without regard for the prior experience of herbivores. Similar dependence on past diets has been shown for several marine herbivores (the sea hare *Dolabella auricularia*, Pennings et al. 1993; the sea slug *P. dendritica*, Trowbridge 1991; the isopod *L. pallasi*, Pennings et al. 2000) and other marine consumers (the nudibranch *Aoelidia papillosa*, Hall et al. 1982). Such results have obvious implications for the conduct and interpretation of laboratory feeding and preference assays (Cronin and Hay 1996).

Many generalist herbivores perform better when feeding on mixed diets (e.g. Dearing et al. 2000; Behmer et al. 2002), thus promoting diet breadth rather than specialisation on highly ranking hosts. Few marine herbivores have been examined in this regard, but increased performance on mixed diets has been recorded for amphipods (Cruz-Rivera and Hay 2000b), isopods (Hemmi and Jormalainen 2004) and sea slugs (Pennings et al. 1993).

The mobility of *P. parmerong* among hosts in the field (Poore 2005) and the diet breadth displayed here by individuals suggest that measures of the performance of *P. parmerong* on mixed diets, currently unknown, may greatly assist in understanding the host choice in this herbivore. Traditional arguments for the maintenance of mixed diets in generalist herbivores involve the acquisition of complementary nutrients from alternative hosts and the minimisation of secondary compound intake (Freeland and Janzen 1974). Simple measures of nutritional value do not differ among the three algal hosts tested (percent nitrogen, Poore and Steinberg 1999), but the detailed nutritional requirements of *P. parmerong*, as with most marine herbivores, are poorly understood. The preferences of *P. parmerong* are strongly affected by the presence of non-polar secondary metabolites in brown algae, but each of the hosts considered here lack such compounds (Poore and Steinberg 1999). The potential exists for *P. parmerong* to select diets based on the content or composition of phenolic compounds (phlorotannins) as the two species of *Sargassum* contain highly variable concentrations, with *S. vestitum* containing approximately 2.5 times that of *S. linearifolium* (Steinberg and van Altena 1992). There are no published data on the phenolic content of *P. crassa*, but other species in this genus have relatively low concentrations, similar to that of *S. linearifolium* (Steinberg 1991).

The altered preferences after consuming the poor-quality host *P. crassa* are unlikely to be due simply to reduced feeding on this alga during the initial phase of the past diet experiment, as a similar period of starvation had no such effects. Host rankings among *S. linearifolium*, *S. vestitum* and *P. crassa* were unaffected by starvation, and there was no evidence for reduced discrimination among the hosts due to food deprivation. Periods of starvation have been shown to increase the likelihood of echinoids consuming chemically deterrent algae (Cronin and Hay 1996) and the levels of discrimination among herbivorous fish consuming artificial foods with deterrent metabolites (Thacker et al. 1997). Other herbivores show similar patterns to *P. parmerong*, with preferences unaffected by short periods of starvation (e.g. the gastropod *Littorina littorea*, Imrie et al. 1990; the sea slug *P. dendritica*, Trowbridge 1991).

Additional factors that may contribute to intraspecific variation in preferences include herbivore age, size, sex and reproductive status (e.g. ovigerous females being more selective, Agnew and Singer 2000). These factors are largely unexplored for marine herbivores with some evidence of variation among herbivores of different size (Pennings 1990a) and sex (Jormalainen et al. 2001). We found no evidence that the preferences of juvenile *P. parmerong* differed from those expressed by adult individuals, despite few juveniles inhabiting *P. crassa* in the field (Poore 2004). Similarly, the sex and reproductive status of adults did not affect the preferences despite the expectation that brooding females would be more selective given the strong consequences of releasing juveniles on a poor-quality host.

## Conclusions

The effects of past diet on preference and the absence of any detectable variation among individuals indicate that the diet breadth of *P. parmerong* is displayed at the level of the individual. Past diet affected future feeding choices, with the preferential selection of algal species which have not been recently consumed indicating that amphipods were actively seeking mixed diets. Such feeding behaviour provides a mechanism for the persistence of this species on hosts that support poor performance when consumed alone. An understanding of the degree of intraspecific variation in preferences will aid our ability to predict how herbivores affect algal assemblages and the way in which variation in plant quality may select for herbivore specificity. If preferences commonly vary with past diet, the likely impacts of herbivores on algal assemblages will also vary in space and time with changes in the local availability of plants.

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