RESEARCH ARTICLE

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Herbivory in the gammarid amphipod *Aora typica*: relationships between consumption rates, performance and abundance across ten seaweed species

Abstract This paper reveals a substantial capacity for herbivory of seaweeds in the gammarid amphipod *Aora typica*, adults eating seven of ten taxonomically and morphologically diverse seaweed species offered to them in a no-choice assay. The green algae *Ulva spathulata* and *Enteromorpha intestinalis* were consumed at the highest rates in both no-choice (2.3–2.5 mg blotted weight individual^{-1} day^{-1}) and multiple-choice assays (0.5–1.3 mg blotted weight individual^{-1} day^{-1}). Adult *A. typica* collected from two different species of brown seaweeds had very similar feeding preferences to each other. Juvenile *A. typica* grew to reproductive maturity on the green algae *E. intestinalis* and *U. spathulata*, and the brown algae *Carpophyllum maschalocarpum* and *Ecklonia radiata*. In common with previous studies on members of other amphipod families, survivorship of juvenile amphipods was positively correlated with feeding preferences of adults across seaweed species ($r^2 = 0.43$, $P = 0.04$). However, densities of *A. typica* on seaweeds in the field (excluding the intertidal *E. intestinalis* and *U. spathulata*) were not significantly correlated with feeding preferences of adults ($r^2 = 0.07$, $P = 0.5$) or survivorship of juveniles ($r^2 = 0.17$, $P = 0.31$). This suggests that either host seaweeds are not a major dietary component of these amphipods in nature, or that the host's value as a food source is overridden by other properties such as the degree of shelter it affords from larger consumers. This study provides the first demonstration that a member of the cosmopolitan amphipod family Aoridae is capable of consuming a diverse range of seaweeds.

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Introduction

Herbivorous amphipods are often abundant on seaweeds (Brawley 1992; Conlan 1994), but the factors determining host plant use by these small crustaceans are not yet well understood (Arrontes 1999). Host use by herbivorous amphipods is often presented as a trade-off between the potentially conflicting needs of the amphipods for both an adequate food source and a refuge from larger consumers (Hay et al. 1987; Hay 1992). This trade-off can cause amphipods to be rare on plants they favour in feeding assays, and abundant on low-preference species (Duffy and Hay 1991). Young amphipods are released directly on to their mother's host seaweed as well-developed juveniles and remain there for some time regardless of host quality (Poore and Steinberg 1999), so the mother's choice of host plant will have a direct impact on the performance (survival, growth, reproduction) of her offspring (Duffy and Hay 1991; Poore and Steinberg 1999; Cruz-Rivera and Hay 2001). In order to understand and generalise about factors affecting amphipod host plant use we need fundamental data on relationships between feeding preferences, performance and field densities for a variety of amphipod species, but very little such information exists at present.

Our current knowledge of herbivory in marine amphipods is largely restricted to just two families, the Ampithoidae (Hay et al. 1987; Tegner and Dayton 1987; Poore and Steinberg 1999) and the Hyalidae (McBane and Croker 1983; Buschmann 1990; Poore 1994), although recent reviews list a number of other families known to contain members capable of consuming marine plants (Brawley 1992; Conlan 1994). The cosmopolitan family Aoridae is missing from these lists, presumably because its members are often regarded as opportunistic suspension and deposit feeders (Goodhart 1939; Enequist 1950; Zimmerman et al. 1979). However, the aorid *Microdeutopus gryllotalpa* is also capable of consuming a variety of red and green seaweeds (Borowsky 1980; Galán Jiménez et al. 1996; Heckscher et al. 1996), and

Aora gracilis, *A. spinicornis* and *Lembos websteri* will eat filamentous or finely chopped algae (Shillaker and Moore [1987](#); Dixon and Moore [1997](#)). The aorid genus *Aora* is common on seaweeds in temperate Australasia (Barnard [1972](#); Edgar [1983](#); Taylor and Cole [1994](#)). *A. typica* Krøyer, 1845, is particularly abundant on subtidal seaweeds at Goat Island in northeastern New Zealand, and it also occurs in adjacent land-based seawater systems where it destructively grazes the green seaweed *Ulva* sp. growing in outdoor culture (N. Barr and R. Taylor, personal observation).

The purpose of this study is to evaluate the capacity of *A. typica* to eat a variety of seaweeds, and to describe relationships between feeding preferences, performance and abundance of the amphipod across those seaweed species. To this end we ran no-choice assays to determine which of ten seaweeds *A. typica* would eat when it had no alternative food available, and multiple-choice assays to evaluate relative preferences for the different seaweed species. Separate multiple-choice assays were run using amphipods collected from two different seaweed species to test whether feeding choices were affected by recent experience. To determine which seaweeds could support the development of *A. typica* to reproductive maturity, we monitored the survivorship, growth and time to first ovulation of newly released juveniles cultured on each species. Finally, we quantified densities of *A. typica* on seaweeds in the field.

Materials and methods

Study sites and organisms

Organisms were collected from rocky reefs near the University of Auckland's Leigh Marine Laboratory at Goat Island, in northeastern New Zealand (36° 16′S, 174° 48′E). *A. typica* were identified following Myers and Moore ([1983](#)). Ten common seaweeds were investigated as a habitat and food source for *A. typica*: the green algae *Enteromorpha intestinalis* and *Ulva spathulata* (O. Ulvales); the brown algae *Zonaria turneriana* (O. Dictyotales), *Carpophyllum maschalocarpum*, *Cystophora torulosa* and *Sargassum sinclairii* (O. Fucales) and *Ecklonia radiata* (O. Laminariales); and the red algae *Osmundaria colensoi* (O. Ceramiales), *Amphiroa anceps* (O. Corallinales) and *Pterocladia lucida* (O. Gelidiales). These seaweeds were chosen because of their taxonomic and structural diversity, and their availability at collection sites near our laboratory. All were inhabited by *A. typica* in the field, except for the intertidal species *E. intestinalis* and *U. spathulata*. *U. spathulata* was included because *A. typica* was observed to graze *Ulva* spp. in culture and inhabits subtidal *U. pertusa* at the nearby Mokohinau Islands (R. B. Taylor and P. J. Brown, personal observation), while *E. intestinalis* was included because its high palatability to larger grazers may result in its exclusion from the subtidal where it

would otherwise be available for colonisation by *A. typica* (Taylor and Steinberg [2005](#)). All seaweeds were collected from 1 to 4 m below low water at Pennys Reef and Waterfall Gutter at Goat Island, except for *E. intestinalis* and *U. spathulata*, which were collected from intertidal platforms at Pennys Reef and the eastern end of Pakiri Beach, respectively. Seaweeds were identified following Adams ([1994](#)) and Phillips and Nelson ([1998](#)), and maintained in the Leigh Marine Laboratory's flow-through seawater system until used for assays within 1–2 days.

Feeding assays

Aora typica used in feeding assays were collected from subtidal seaweeds. Several individual seaweeds were placed in a plastic bag by a diver, and amphipods were later removed by dipping their host seaweed in freshwater for 5–10 s. This freshwater dip was necessary to encourage the amphipods to leave their tubes. A larger volume of seawater was then immediately added to the freshwater, and all *A. typica* individuals observed were transferred into full-strength seawater. Those that recovered from this treatment were used in feeding assays within a day. They were not fed during this holding period.

Herbivory was quantified using multiple-choice and no-choice assays. In the multiple-choice assays all seaweed species were simultaneously presented to the amphipods, with the results indicating relative preferences for the various seaweeds. In the no-choice assay the amphipods were presented with a single seaweed species.

Feeding assays were run indoors in December 2002 using plastic containers holding ∼300 ml of seawater. Containers were kept at ∼22°C under Philips TLD 58 W/840 cool white fluorescent lighting on a 12:12 light–dark cycle. Ten replicate containers were used for all assays. Rates at which amphipods fed were quantified by offering the amphipods pre-weighed pieces of fresh seaweed, and measuring the change in weight of this seaweed over the following 2–3 days, relative to the change in weight of an ungrazed control piece of tissue from the same individual seaweed. A different individual seaweed was used for each replicate. For each seaweed species two pieces of apical tissue free of macroscopic fouling organisms were blotted dry with paper towels and weighed (± 1 mg). Tissue pieces were added directly to containers, except for *E. intestinalis* fronds, which had to be cable-tied together to prevent their floating to the surface. At the end of the trial, remaining seaweed tissues plus their paired controls were blotted dry and re-weighed. The amount of each seaweed species consumed in each replicate was calculated as: $(H_i \times C_f / C_i) - H_f$, where H_i and H_f were pre-assay and post-assay blotted weights of tissue exposed to the grazer, and C_i and C_f were pre-assay and post-assay blotted weights of paired controls for autogenic changes in weight.

A no-choice assay was run using *A. typica* collected from *Sargassum sinclairii*. A ∼30 mg piece of seaweed tissue and two amphipods were added to each replicate container. Any amphipods that died were replaced with live ones. To confirm that reductions in seaweed tissue weight were due to amphipod grazing, we noted whether frass piles were present in each replicate at the end of the experiment (78 h).

Multiple-choice assays were run using *A. typica* from both *Sargassum sinclairii* and *Zonaria turneriana*, to determine whether preferences differed for amphipods taken from different host seaweeds. A ∼100 mg piece of tissue from each seaweed species and 12–13 amphipods were added to each replicate container. Dead amphipods were not replaced, but the number of live amphipods in each replicate at the end of the assay (56 h) was recorded and used to calculate per capita rates of consumption.

Performance

The ability of *A. typica* to survive and grow to reproductive maturity on the seaweeds used in the feeding assays was assessed by culturing newly released juveniles on each species. Amphipods are brooders and release well-developed juveniles, making it possible to measure the effects of different diets on their fitness from an early age (Robertson and Lucas 1983; Duffy and Hay 1991). To acquire newly released juveniles, gravid *A. typica* females were taken from outdoor *Ulva* sp. cultures and kept for 4–7 days in separate 60-mm diameter petri dishes containing seawater and a small piece of *Ulva* sp. The petri dishes were kept at ∼20°C under Philips TLD 58 W/840 cool white fluorescent lighting on a 12:12 light–dark cycle. On 20 October 2003, when most females had released numerous juveniles from their marsupia, juveniles were carefully pipetted into petri dishes containing seawater with 5×10^6 MW polyethylene oxide added at 5 nM to reduce entrapment in the surface tension (Sandifer et al. 1975). Eleven juveniles were taken from each female, with each juvenile added to a petri dish containing a small piece of tissue from one of the ten seaweed species used in the feeding assays or a no-food control containing only a small piece of fibreglass windowscreen for the amphipod to cling to (Chapelle and Peck 1995). Twenty replicates were run. Culture dishes were kept at ∼20°C under Philips TLD 58 W/840 cool white fluorescent lighting on a 12:12 light–dark cycle. Seawater was replaced ∼weekly, and seaweed tissue ∼fortnightly. Water in many of the dishes containing *Carpophyllum maschalocarpum* and *Ecklonia radiata* was changed more frequently as freshly cut tissues of these seaweeds often exuded a brown liquid (probably phlorotannins). All amphipods were checked every 2 days until the first ovulating female was observed, after which they were all checked daily. At each observation, deaths and ovulating females were recorded, and algal tissue or fibreglass windowscreen were moved back next to any amphipods that had lost physical contact with them. At the end of the experiment on day 45, surviving amphipods were preserved in 70% ethanol and their lengths measured from the tip of the rostrum to the rear of the fifth pereonite. Differences among survivorship curves were analysed by the Wilcoxon test using the SAS procedure LIFETEST (SAS Institute Inc. 1990), with post hoc pairwise comparisons made following Fox (1993). The ability of the analysis to distinguish among individual survivorship curves was low due to alpha adjustment for the large number of pairwise comparisons involved.

Field densities

Natural densities of *A. typica* were measured on all of the seaweed species used in the feeding and performance assays. Most seaweeds for this survey were collected in April and May 2001 from the same sites given earlier, as part of another study (Taylor and Steinberg 2005), except for *U. spathulata*, *Sargassum sinclairii*, and *Amphiroa anceps*, which were collected in December 2002, January 2003, and February 2004, respectively.

Small clumps of *Amphiroa anceps* and *E. intestinalis*, and individuals of the other seaweed species were enclosed in plastic bags after being cut off ∼10 mm above the holdfast ($n = 10$), and were later shaken vigorously in freshwater until all mobile animals were dislodged. The effectiveness of this method was visually confirmed for a subset of seaweeds of each species. Animals were trapped on a 0.2-mm mesh sieve, except for *Ecklonia radiata*, where slime exudation necessitated use of 0.5-mm mesh. Seaweeds were dried in a salad spinner (ten rotations of the handle) and weighed (± 0.1 g). Samples were preserved in 5% formaldehyde w/v and washed on a 1-mm mesh sieve prior to enumeration.

Results

Feeding

In the no-choice assay *A. typica* consumed seven of the ten seaweeds offered, at average rates ranging from 0.6 to 2.5 mg blotted weight individual^{-1} day^{-1} (Fig. 1). The amphipods did not consume the red algae *Amphiroa anceps* and *Pterocladia lucida*, or the brown alga *Cystophora torulosa*. Faecal matter was observed in all replicate containers except those containing these latter three seaweeds. *Ulva spathulata* and *E. intestinalis*, green algae of the order Ulvales, were eaten at the highest rates (averages of 2.5 and 2.3 mg blotted weight individual^{-1} day^{-1}, respectively).

Ulva spathulata and *E. intestinalis* were also the seaweeds consumed at the highest rates in the multiple-choice assays (averages of 1.1–1.3 and 0.5–0.9 mg blotted weight individual^{-1} day^{-1}, respectively), with consumption rates of the other species being very low (Fig. 2). Either *U. spathulata* or *E. intestinalis* was the most eaten seaweed in 19 out of 20 replicates. Host plant origin had little effect on feeding preferences for *A. typica* collected
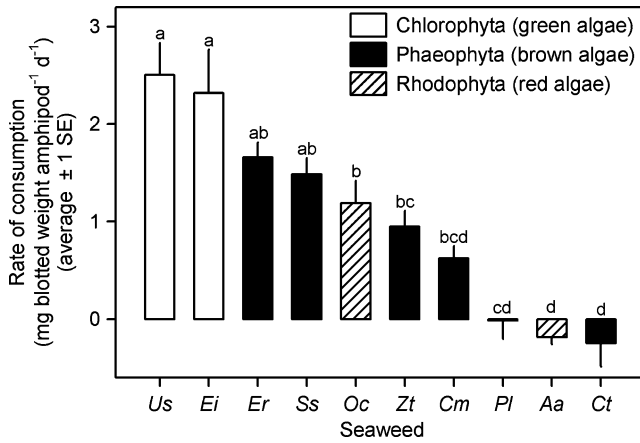
Fig. 1 Consumption of seaweeds by the gammarid amphipod *Aora typica* in a no-choice assay. One-way ANOVA: $F = 17.8$, $P < 0.0001$, $n = 9$–10. *Bars labelled with the same lower case letter do not differ significantly* ($P > 0.05$) *according to Tukey's HSD. See Table 1 for full seaweed species names*

from *Sargassum sinclairii* (Fig. 2a) and *Zonaria turneriana* (Fig. 2b), with negligible amounts of the host seaweed eaten in either case.

Performance

Survival of *A. typica* was highest on the brown seaweed *Carpophyllum maschalocarpum*, where 17 out of 20 individuals were still alive when the fitness experiment was terminated on day 45, and none died after day 5 (Fig. 3a). On the other seaweeds, mortality occurred throughout the experiment and far fewer individuals survived to the end. After *Carpophyllum maschalocarpum*, survivorship was highest on the green algae *E. intestinalis* (9 out of 20 alive at day 45) and *U. spathulata* (8 out of 20). On the brown algae *Ecklonia radiata* and *Sargassum sinclairii* 4 out of 19 *A. typica* survived to day 45, and 2 out of 19 on the brown alga *Cystophora torulosa*. On the other seaweeds all individuals were dead by day 31. All seaweeds supported better survivorship than the controls, which contained only a square of fibreglass windowscreen.

Of the *A. typica* that survived to day 45, individuals on *U. spathulata* and *Enteromorpha intestinalis* were largest (mean lengths from the tip of the rostrum to the rear of the fifth pereonite were $2.8 \pm \text{SE } 0.1$ mm and 2.7 ± 0.1 mm, respectively), while individuals on the other seaweeds averaged 1.5–2.2 mm in length (Fig. 3b).

Amphipods ovulated on four of the seaweeds: the green algae *E. intestinalis* and *U. spathulata*, and the brown algae *Carpophyllum maschalocarpum* and *Ecklonia radiata*. Time to first ovulation varied little among host seaweeds, averaging 37–41 days (Fig. 3c). The proportion of individuals that ovulated at least once also varied little. Of the amphipods alive at day 45, ovulation was observed at least once in 9 out of 17 individuals on *Carpophyllum maschalocarpum*, 4 out of
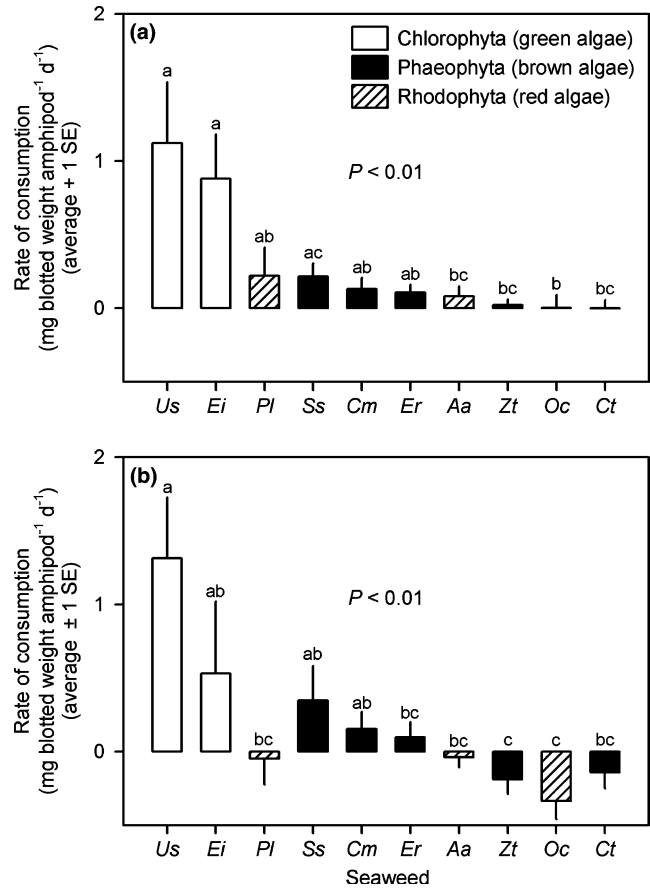

Fig. 2 Consumption of seaweeds by the gammarid amphipod *Aora typica* in multiple-choice assays, for amphipods collected from (**a**) *Sargassum sinclairii* and (**b**) *Zonaria turneriana*. Statistics are for Friedman nonparametric test of ranks (Conover 1980). *Bars labelled with the same lower case letter do not differ significantly* ($P > 0.05$) *according to Friedman test. See Table 1 for full seaweed species names*

9 on *E. intestinalis*, 1 out of 3 on *Ecklonia radiata*, and 4 out of 8 on *U. spathulata*.

Field densities

Aora typica was not found on intertidal *E. intestinalis* or *U. spathulata* (Table 1), the two seaweeds consumed at highest rates in the feeding assays. Highest mean densities were found on *Sargassum sinclairii* (197 individuals 100 g seaweed blotted weight^{-1}), intermediate mean densities on *Zonaria turneriana* and *Pterocladia lucida* (16–17 individuals 100 g seaweed blotted weight^{-1}) and low mean densities (< 5 individuals 100 g seaweed blotted weight^{-1}) on the other seaweed species.

Relationships between feeding preferences, performance and field densities

Rank of feeding preference for seaweeds was positively correlated with rank of survivorship on those seaweeds

Fig. 3 Survival (**a**), length (from the tip of the rostrum to the rear of the fifth pereonite) (**b**), and time to first ovulation (**c**) of newly released juveniles of the gammarid amphipod *Aora typica* raised on seaweeds. Controls were given no food. See Table 1 for full seaweed names. *Lines or bars labelled with the same lower case letter* do not differ significantly ($P > 0.05$) according to test of Fox (1993) (**a** *subscripted beside species initials*) or Tukey's HSD (**b**, **c**). Replicates in which amphipods could not be relocated alive or dead ($n = 5$ across all seaweeds) were removed from plots and analyses. Initial $n = 20$ amphipods per seaweed
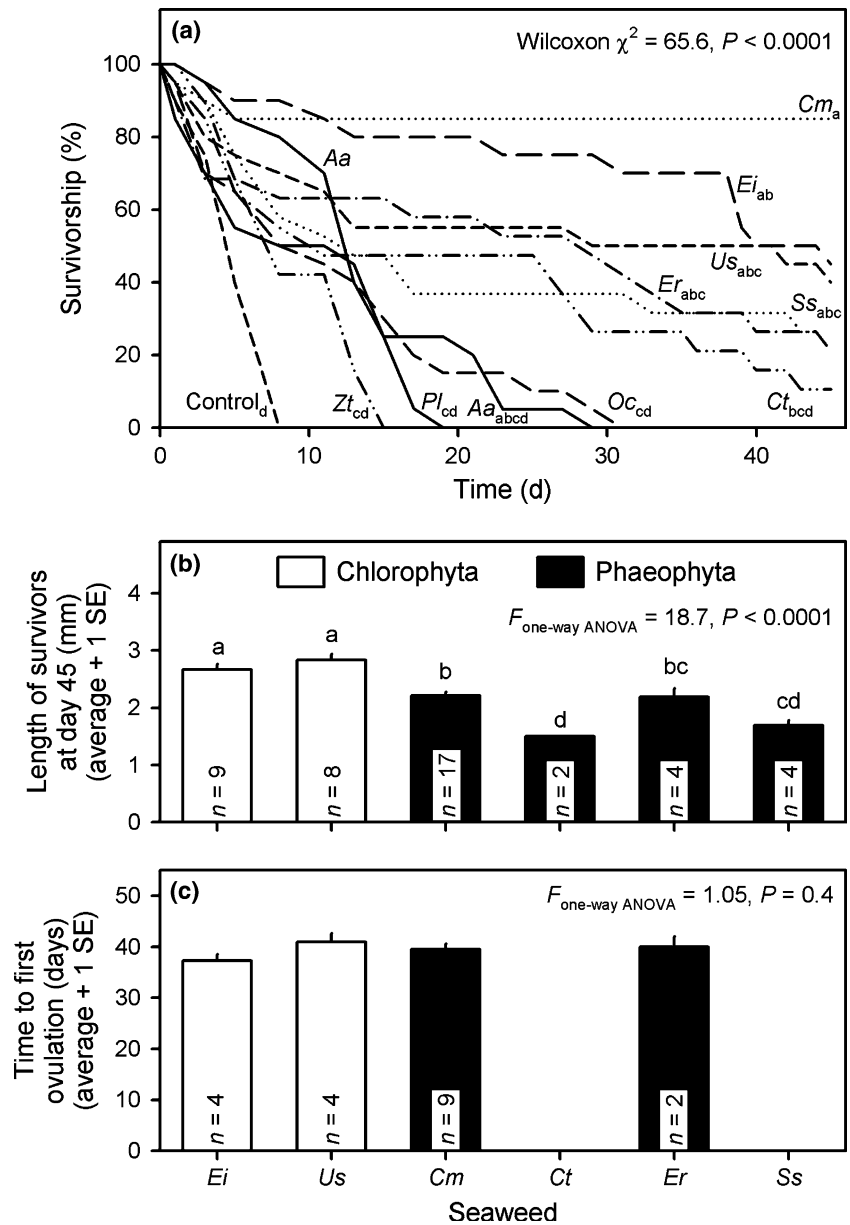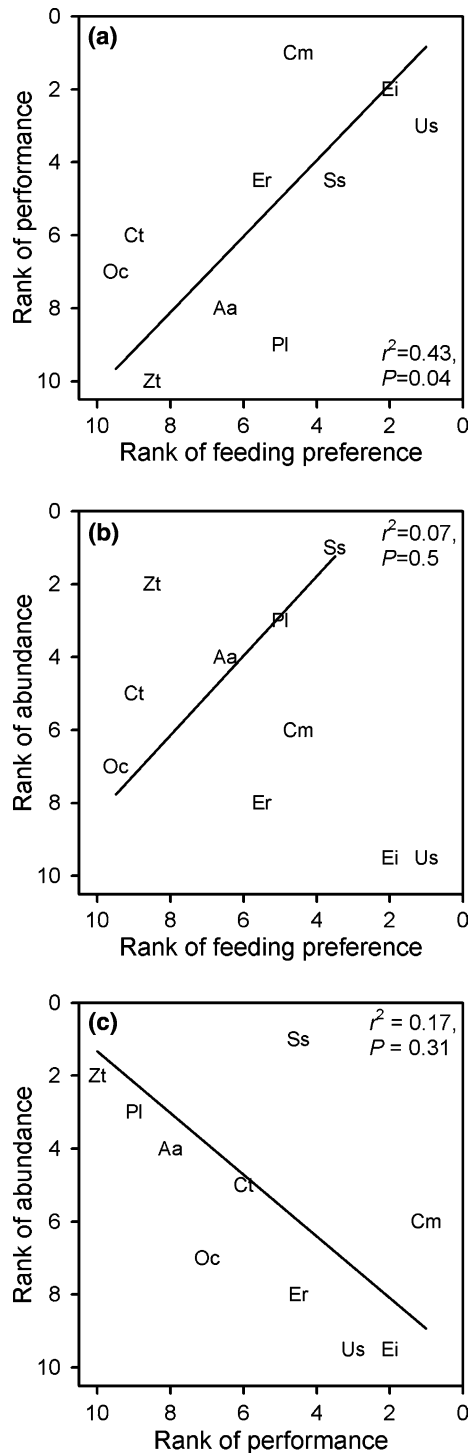

($r^2 = 0.43$, $P = 0.04$; Fig. 4a). However, rank of abundance on seaweeds in the field did not show a statistically significant correlation with feeding preference ($r^2 = 0.07$, $P = 0.5$; Fig. 4b) nor a statistically significant correlation with performance ($r^2 = 0.17$, $P = 0.31$; Fig. 4c). Abundance data for the two intertidal seaweeds sampled (*E. intestinalis* and *U. spathulata*) were excluded from these analyses because *A. typica* appears to be rare on intertidal seaweeds in New Zealand (see Appendix IV in Barnard 1972 where it is listed as *Aora* sp.; Myers and Moore 1983).

Discussion

Aora typica consumed a taxonomically, structurally and chemically diverse range of seaweed species in no-choice assays, eating seven out of ten species offered. The Aoridae can now be added to existing lists of amphipod families known to contain members capable of grazing seaweeds (Brawley 1992; Conlan 1994). The lack of dietary specialisation shown by *A. typica* is typical for herbivorous amphipods (Hay and Steinberg 1992; Arrontes 1999). Multiple-choice assays revealed a clear preference for *U. spathulata* and *E. intestinalis*, two members of the green algal order Ulvales. This preference is shared by a diverse range of other grazers (Littler and Littler 1980; Hay et al. 1988; Barry and Ehret 1993). *Ulva* and *Enteromorpha* are soft, nutritionally rich (Cruz-Rivera and Hay 2001; Taylor and Steinberg 2005), and generally are considered free of chemical defences (e.g., Lubchenco 1978, but see Borowsky and Borowsky 1990; Van Alstyne et al. 2001).

Fig. 4 Relationships among feeding preferences of the gammarid amphipod *Aora typica* for seaweeds, performance of *A. typica* when grown on those seaweeds, and densities of *A. typica* on the seaweeds in the field. Ranks of feeding preference were calculated as the average rank of feeding rates from the two choice assays (Fig. 2a, b). Ranks of performance were taken from survivorship data by ordering seaweeds clockwise from the *top right* of Fig. 3a (the seaweed supporting the most surviving amphipods at the end of the experiment) towards the *bottom right* (the seaweed with the lowest non-zero number of survivors at the end) then towards the *bottom left* (the seaweed on which all amphipods died most rapidly). Ranks of densities on seaweeds were taken from Table 1. A ranking of one indicates the most preferred food, highest survival, or highest abundance. Note that the axes for all plots are reversed so that survival etc. increases as one reads from *left to right*, or from *bottom to top*. See Table 1 for full seaweed names. *Lines* are for reduced major axis regressions (McArdle 1988), and P values are for tests of H_o: slope=0. *Lines and statistics* for abundance plots exclude data for the intertidal algae *Enteromorpha intestinalis* and *Ulva spathulata* (see results for explanation)

and Steinberg 1999). Relationships between feeding preference for different seaweeds (as measured using multiple-choice assays) and juvenile performance have also been described for the ampithoid *Ampithoe longimana* (Duffy and Hay 1991; Cruz-Rivera and Hay 2001). Although both these studies concluded that adult feeding preferences were not good predictors of juvenile performance, plots of their data nevertheless reveal positive correlations between rank of feeding preference and rank of survivorship (determined as for Fig. 4a of our study), with the relationship strong ($r^2=0.81$, $P=0.037$, $n=5$) for data from Duffy and Hay (1991, their Figs. 2A and 4), and fairly weak ($r^2=0.22$, $P=0.24$, $n=8$) for data from Cruz-Rivera and Hay (2001, their Figs. 2a and 4a). In the ampithoids *Ampithoe valida* (Nicotri 1980) and *Peramphithoe parmerong* (Poore and Steinberg 1999) habitat choice of adults was positively correlated with performance of juveniles across seaweeds. Habitat choice as measured by association of amphipods with particular seaweed species in multiple-choice assays is likely to be related to feeding preference in small relatively immobile herbivores, but this correspondence cannot be confirmed for these two studies as consumption rates were not quantified by Nicotri (1980), and Poore and Steinberg (1999) only ran no-choice assays in which high consumption rates may indicate either high preference or compensatory feeding on less preferred nutritionally-poor species (Poore and Steinberg 1999; Cruz-Rivera and Hay 2000, 2001). The hyalellid *Allorchestes compressa* also exhibited a positive relationship between feeding preferences of adults and performance of juveniles, although this was driven mainly by decaying *Ecklonia radiata* (Robertson and Lucas 1983), as opposed to the fresh seaweeds examined in the present study and other aforementioned studies. In summary, food or habitat preference is positively correlated, to varying strengths, with juvenile performance in all the relevant studies that we could locate on herbivorous marine amphipods.

Densities of *A. typica* on seaweeds in the field were not strongly positively correlated with feeding prefer-

Feeding preferences of adult *A. typica* were positively correlated with survivorship of juveniles across seaweeds, as would be expected if adults prefer foods that also maximise the fitness of their offspring. Young amphipods are likely to consume the food plant selected by their mother because they are released as juveniles directly onto her individual host seaweed, where most of them remain for at least 2 weeks (in the case of the ampithoid *Peramphithoe parmerong*; Poore

ence or performance of juveniles. This was true even when we removed data for the highly-preferred intertidal seaweeds *U. spathulata* and *E. intestinalis*, which may have had low densities of *A. typica* due to the harsh physical environment of the intertidal sites that these plants inhabit locally, as *A. typica* are abundant on *Ulva* spp. kept submersed in outdoor tanks at the Leigh Marine Laboratory and on subtidal *U. pertusa* at the nearby Mokohinau Islands (R. B. Taylor and P.J. Brown, personal observation). In other studies field abundances of amphipods have shown inconsistent relationships with feeding preferences and performance. Densities of *Ampithoe longimana* in late summer (but not earlier in the season) broadly reflected feeding preferences and performance (Duffy and Hay 1991), and densities of *Peramphithoe parmerong* were also positively correlated with juvenile performance across seaweeds (Poore and Steinberg 1999). However, the hyalellid *Allorchestes compressa* was most common on branching red algae but preferentially fed and grew best on decaying *Ecklonia radiata* (Robertson and Lucas 1983), and the hyalids *Hyale hirtipalma* and *Hyale media* were found on a range of seaweeds but not their most preferred food species, the red alga *Iridaea laminarioides* (Buschmann 1990). It was suggested that the seaweeds inhabited by *Allorchestes compressa* and the *Hyale* spp. afforded greater protection from predatory fishes than the seaweeds they preferred to eat, which these highly mobile non-tubiculous amphipods were able to gather as particles (Robertson and Lucas 1983) or move on to at night to feed from (Buschmann 1990). More sedentary tube-dwelling amphipods (such as the ampithoids and aorids) are thought to be under strong selective pressure to inhabit lower quality seaweeds in order to avoid direct or incidental consumption by larger consumers (Hay 1992, 1997; Duffy and Hay 1994). This may explain why field densities were not correlated with feeding preferences or performance in *A. typica*. Alternatively, it is possible that host seaweeds are not a major component of the diet of *A. typica* in the field, but instead influence amphipod abundances via other properties, such as their value as a surface from which to graze detritus or epiphytic algae, or as a structure from which to resist wave action or avoid predation (Taylor and Cole 1994).

Although *A. typica* clearly are capable of consuming tissue of many seaweed species and have been observed to destructively graze living *Ulva* spp. in outdoor cultures at the Leigh Marine Laboratory, the extent to which the amphipod grazes its host seaweeds in nature is uncertain. It is probable that *A. typica* also consume material other than their host seaweed in the field, given that the amphipod occurred on several seaweeds that it refused to eat in a no-choice assay and on which it performed poorly in culture (the red algae *Amphiroa anceps* and *Pterocladia lucida*, and the brown alga *Cystophora torulosa*). Moreover, *A. typica* is common on plastic surfaces in the Leigh Marine Laboratory's flow-through seawater system, where it presumably feeds upon suspended and/or deposited material. *Aora* collected from Norwegian soft sediments were observed in aquaria to sieve detrital material from a suspension of surface sediments that the amphipod induced via pleopod movement (Enequist 1950). Note that Enequist's identification of his specimens as *A. typica* was probably incorrect (Myers and Costello 1984). *A. gracilis* and *A. spinicornis* collected from *Laminaria* holdfasts in the United Kingdom similarly filter-fed on a range of particulate matter in aquaria, as well as eating live and dead crustaceans, and small (1 mm) pieces of the red alga *Ceramium* (Dixon and Moore 1997). Our attempts to determine the natural diet of *A. typica* living on seaweeds in the field by examining gut contents were unsuccessful, and as for most of the other amphipods

Table 1 Densities of the gammarid amphipod *Aora typica* (individuals retained on 1-mm mesh) on seaweeds from northeastern New Zealand

Seaweed	Density of *Aora typica* (individuals 100 g seaweed blotted weight^{-1}) (average $\pm$ 1 SE)	Source
Chlorophyta		
Enteromorpha intestinalis	0 ± 0	Taylor and Steinberg (2005)
Ulva spathulata	0 ± 0	Present study
Phaeophyta		
Carpophyllum maschalocarpum	0.4 ± 0.3	Taylor and Steinberg (2005)
Cystophora torulosa	3.6 ± 2.0	Taylor and Steinberg (2005)
Ecklonia radiata	0.1 ± 0.1	Taylor and Steinberg (2005)
Sargassum sinclairii	197.2 ± 57.3	Present study
Zonaria turneriana	17.0 ± 5.1	Taylor and Steinberg (2005)
Rhodophyta		
Amphiroa anceps	4.7 ± 3.1	Present study
Osmundaria colensoi	0.3 ± 0.3	Taylor and Steinberg (2005)
Pterocladia lucida	16.2 ± 5.5	Taylor and Steinberg (2005)

See text for collection sites and dates. $n = 10$

that consume seaweeds in laboratory assays (Bell 1991) there is an urgent need to develop practical methods for assessing the importance of seaweeds as a food source in nature.

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