Oecologia (2000) 123:252–264 © Springer-Verlag 2000

Edwin Cruz-Rivera · Mark E. Hay

The effects of diet mixing on consumer fitness: macroalgae, epiphytes, and animal matter as food for marine amphipods

Received: 14 September 1998 / Accepted: 22 October 1999

Abstract Herbivores are thought to achieve adequate nutrition by consuming numerous species of plants or by occasionally consuming animal tissue. Although active selection of diverse foods is common in nature, the relationship between diet mixing and consumer fitness is poorly understood, especially in marine environments. We studied the fitness-based consequences of dietary mixing in the sympatric amphipods *Ampithoe marcuzzii*, *A. valida*, *Cymadusa compta*, and *Gammarus mucronatus* by measuring survivorship, growth, and fecundity of these amphipods when they were offered single species of algae, a single animal food, a mixture of algal species, or a combination of algae and animal matter. For the more sedentary, tube-building amphipods *A. marcuzzii*, *A. valida*, and *C. compta*, fitness on mixed algal diets was matched by fitness on at least one of the monospecific algal diets, suggesting that they could benefit from preferential feeding on those algae in the field. The more mobile amphipod, *G. mucronatus*, survived and grew similarly on the mixed diets and on the filamentous brown alga *Ectocarpus siliculosus*. However, its fecundity was significantly higher when feeding on the algal and animal mixture than on *Ectocarpus* alone. Additionally, for *G. mucronatus*, fitness on mixed algae, mixed algae plus animal matter, and animal matter alone was equivalent, although female growth (but not gonad production) was slightly lower on animal matter alone than on the mixed algae combined with animal food. Thus the more mobile amphipod, *G. mucronatus*, was the only species able to perform well on animal food alone. In contrast, *A. valida* and *C. compta* experienced large negative effects when limited to consuming animal matter alone. For these two species, combining algae and animal matter did not enhance fitness over combining only algae. Fitness effects of specific algal diets showed some general similarities, but also considerable variance among the amphipods. For example, *E. siliculosus* was generally better food than other algae for all four amphipods, whereas *Sargassum filipendula* was generally poor. However, *A. marcuzzii* did not suffer negative effects of consuming only *Sargassum*. The red alga *Polysiphonia* sp. and the green alga *Enteromorpha flexuosa* decreased fitness in *A. marcuzzii*, *C. compta*, and *G. mucronatus*, but not *A. valida*, and the negative effects of *Polysiphonia* were considerably larger for *A. marcuzzii* than for the other amphipods. Our data show that nutritional requirements, even among related species (e.g., *A. marcuzzii* and *A. valida*), can be dramatically different. Diet mixing may benefit more mobile consumers like *Gammarus* that are better able to search for different foods, and may be less important for more sedentary herbivores like *Ampithoe* and *Cymadusa* that consume, and live in close association with, individual host plants.

Key words Amphipods · Dietary mixing · Fitness · Herbivores · Occasional carnivory

Introduction

Herbivore diets are lower in nutrients and higher in non-digestible structural materials than the body tissues that they must build from these diets (Mattson 1980; White 1993; Sterner and Hessen 1994; Gulati and DeMott 1997). To cope with these poor-quality foods, herbivores often feed selectively on plants or plant parts of higher quality, have digestive associations with microbial symbionts, synchronize their life cycles to coincide with seasonal bursts of higher-quality foliage, or show compensatory feeding when limited to lower-quality plants

---

E. Cruz-Rivera[1]
Institute of Marine Sciences,
University of North Carolina at Chapel Hill, 3431 Arendell Street,
Morehead City, NC 28557, USA

M.E. Hay (✉)
School of Biology, Georgia Institute of Technology,
Atlanta, GA 30332-0230, USA
e-mail: mark.hay@biology.gatech.edu
Tel.: +1-404-8948429, Fax: +1-404-894-0519

Present address:
[1] University of Guam Marine Laboratory, UOG Sation,
Mangilao, GU 96923, USA

(Mattson 1980; Martin 1987; Slansky and Rodriguez 1987; Simpson and Simpson 1990; Slansky 1993; White 1993; Van Soest 1994). Alternatively, herbivores may select a mix of complementary plants that balance their nutritional requirements (Pennings et al. 1993; Bernays et al. 1994), or may exhibit occasional carnivory to enhance their protein uptake (Mattson 1980; Dearing and Schall 1992; White 1993). Diet mixing can also benefit herbivores by diluting chemical defenses in particular foods (Freeland and Janzen 1974; Bernays et al. 1994).

Dietary mixing has been well documented for a variety of marine, freshwater, and terrestrial herbivores (Kitting 1980; Belovsky 1984; Bjorndal 1991; Speiser and Rowell-Rahier 1991; Dearing and Schall 1992; Pennings et al. 1993; Bernays et al. 1994; Sanders et al. 1996; Bernays and Minkenberg 1997; DeMott 1998), with marine herbivores commonly having very broad and generalized diets (Randall 1967; Hawkins and Hartnoll 1983; Hay 1992; Wahl and Hay 1995). Although mixing foods is generally assumed to be beneficial for consumer performance and is often treated as adaptive (White 1993), few studies experimentally document the relationship between dietary mixing and consumer fitness (Pennings et al. 1993). This is not surprising. The long life span or complex life cycles of many consumers often constrain efforts to measure dietary effects on fitness.

In terrestrial systems, dietary mixing occurs for animals ranging from insects to primates (White 1993), but there are few cases where the consequences of these feeding behaviors have been quantified. For example, both birds and spiders can experience increased growth when fed mixtures of insect prey (Greenstone 1979; Krebs and Avery 1984; but see Toft and Wise 1999). However, of the numerous examples showing mixing of plant diets or mixing of plant with animal foods, only a few demonstrate that consumers on mixed diets attain higher survivorship, growth, or reproduction than conspecifics on single natural foods (MacFarlane and Thorsteinson 1980; Johnson and Boyce 1990; Bernays et al. 1994; but see Bernays and Minkenberg 1997).

For marine systems, only a handful of studies have used natural foods to address the long-term effects of single versus mixed diets on consumer performance or fitness (Larson et al. 1980; Lobel and Ogden 1981; Watanabe 1984; McTigue and Zimmerman 1991; Steinberg and van Altena 1992; Pennings et al. 1993; Rogers et al. 1995; Kennish 1996; Schmidt and Jónasdóttir 1997). All but two of these studies (Watanabe 1984; McTigue and Zimmerman 1991) have concentrated on only one consumer, making it difficult to generalize about the importance of diverse feeding strategies for sympatric animals.

Amphipods have short generation times, carry their eggs in an external brood pouch, and can be cultured on diverse diets with relative ease. Amphipods, thus, offer an excellent opportunity for evaluating dietary effects on fitness because they can be grown from newly produced juveniles to egg-bearing adults in a few weeks and many reproductive parameters that are difficult to obtain for larger consumers can be measured (e.g., Robertson and Lucas 1983; Duffy and Hay 1991b; Graça et al. 1993; Kneib et al. 1997). Although the nutritional ecology of amphipods and other mesograzers is poorly understood (Brawley 1992), studies show that many amphipods consume a range of plant, animal, and detrital foods (Nelson 1979b; Zimmerman et al. 1979; Pederson and Capuzzo 1984; Agnew and Moore 1986; Bärlocher and Howatt 1986; Hay et al. 1987; DeLong et al. 1993), with a few species showing a strong preference for particular prey species or groups (Nicotri 1977, 1980; Nelson 1979b; Zimmerman et al. 1979; Robertson and Lucas 1983; Hay et al. 1987, 1988a, 1990; Duffy and Hay 1991b, 1994). Therefore, dietary mixing could be important for these consumers if less preferred foods are consumed as a way of achieving nutritional balance (Pennings et al. 1993; Bernays et al. 1994) or if they supplement their plant or detrital diets with periodic consumption of animal tissues (Mattson 1980; White 1993).

In this study, we compare the relative importance of dietary mixing and single foods for four phytal amphipods that are widely distributed in the western North Atlantic: *Ampithoe marcuzzii*, *A. valida*, *Cymadusa compta*, and *Gammarus mucronatus*. Our experiments assess the effects of various macroalgae, algal epiphytes, animal matter, and combinations of algae or algae and animal tissue on the fitness (survivorship, growth, and fecundity) of these consumers. By using four co-occurring mesograzers and including common seaweeds as well as animal matter in diets, we insured that fitness effects were measured across a range of available food and consumer types.

Materials and methods

Amphipods were obtained from algae collected near Morehead City, North Carolina, USA (34°42’ N, 76°41’ W). During the winter and spring, when these experiments were performed, both perennial and ephemeral algae were abundant, as were amphipods, due to the seasonal absence of most predatory fishes (Nelson 1979a, 1979b; Duffy 1990; Duffy and Hay 1991b). To obtain our mesograzers, we collected abundant seaweeds at our sites, including the green algae *Bryopsis plumosa*, and *Enteromorpha* spp., the red algae *Polysiphonia* spp., and *Spyridia hypnoides*, and the brown algae *Ectocarpus* spp., *Fucus vesiculosus*, and *Sargassum filipendula*, transported them to the laboratory, and carefully inspected each for phytal amphipods.

We studied the effects of various single diets, or dietary mixtures, on the fitness of four of the most abundant amphipod species collected: *A. marcuzzii*, *A. valida*, *C. compta*, and *G. mucronatus*. Natural diets of most amphipods are poorly known, but diets often appear to be broad, with some species consuming foods ranging from detritus through seaweeds to animal tissues. Although little is known about *A. marcuzzii*, this species associates with seaweeds, and prefers to feed on the brown macroalga *S. filipendula* (Duffy 1990). Its congener *A. valida* is a broadly distributed species (Pomeroy and Levings 1980; Alonso et al. 1995) which also associates with, and readily consumes, diverse macroalgae (Nicotri 1977, 1980; Duffy and Hay 1994; Alonso et al. 1995; Deal 1997). Gut contents of *C. compta* have revealed algae, detritus, and some vascular plant material (Nelson 1979b), and feeding on algae has been documented under both field (Hauxwell et al. 1998) and laboratory (Zimmerman et al. 1979) conditions. Similarly, gut contents and laboratory observations on *G. mucronatus* have suggested a generalized diet of detritus, macroalgae, and microalgae (Zimmerman et al. 1979; Bärlocher and Howatt 1986; Duffy and Hay 1994; see *Carinogammarus mucronotus* in Sanders et al. 1962). This amphipod is commonly associated with subtidal macroalgae and seagrasses (LaFrance and Ruber 1985; Fredette and Diaz 1986) in the North Atlantic. These dietary lists are crude and incomplete due to the relatively poor understanding of amphipod feeding and nutrition (Bell 1991; Duffy and Hay 1991a; Brawley 1992); however, it seems clear that these species are relatively generalized feeders.

Ampithoe and *Cymadusa* belong to the family Ampithoidae (Bousfield 1973; Barnard and Karaman 1991) and build mucous tubes on the plants they inhabit, thus somewhat limiting their foraging range or mobility (Duffy and Hay 1991b, 1994; Poore and Steinberg 1999). *G. mucronatus* does not build tubes, is more mobile (Duffy and Hay 1994), and belongs to the family Gammaridae (Bousfield 1973; Barnard and Karaman 1991). Ovigerous females from each species were individually placed in small petri dishes for 1 week, and allowed to hatch their offspring. During this time, females and newborns were allowed to feed on a mixture of algal species from which the females were collected. For all species, one sibling from each female was used in each treatment. Offspring from each female were assigned randomly to either one of the diets, or to a starvation control receiving no food. These amphipods were individually placed in small petri dishes and followed through time. To reduce the probability that small amphipods would get trapped in the surface tension, which can enhance mortality (Duffy and Hay 1991b; Cruz-Rivera and Hay, in press), we dusted the surface of the water with cetyl alcohol (Sigma). This compound breaks the surface tension and is not toxic to the animals.

Amphipods were not measured at the beginning of the experiments because in initial efforts we found that measuring these small and delicate juveniles increased mortality. However, after only 1 week and with a microscopic resolution of 20 µm, differences in size among siblings of *A. valida*, *C. compta*, and *G. mucronatus*, as well as among families within each species, are small (E. Cruz-Rivera, personal observation), suggesting that it is reasonable to assume all treatments started with juveniles of similar size. Additionally, because newborns were assigned randomly to each treatment, initial variance in size among siblings and families would contribute similarly to each of the experimental treatments. The number of siblings obtained per *A. marcuzzii* female was generally smaller than for the other amphipod species: only six treatments, rather than nine, were evaluated for this amphipod. We raised *A. marcuzzii* (n=22 per treatment) on four individual algae (*Enteromorpha flexuosa*, *Polysiphonia* sp., *Ectocarpus siliculosus*, *S. filipendula*), a combination of all four algae (=mixed algae), and a starvation treatment. The other three amphipod species (n=25 per treatment) were cultured on a starvation treatment, on one of five species of algae (*E. flexuosa*, *Polysiphonia* sp., *E. siliculosus*, *F. vesiculosus*, *S. filipendula*), on frozen brine shrimp alone (*Artemia salina*), on a mixture of all five algae (=mixed algae), and on a mixture of all five algae plus brine shrimp (=mixed algae+ *Artemia*), for a total of nine treatments. Thus, we raised amphipods on either single algal species, brine shrimp, mixtures of algae, or mixtures of algae and brine shrimp together. Starvation treatments provided information on baseline amphipod mortality in the absence of food. Although some females were collected from *B. plumosa* and *S. hypnoides*, these macroalgae were not tested because they could not be collected consistently throughout our assays.

Amphipods were monitored daily and foods were always available in excess. Algae for food were collected from the same sites where we originally obtained the amphipod females. *Ectocarpus* and *Polysiphonia* were always collected as epiphytes from *S. filipendula*. Care was taken to provide only one algal food to amphipods being raised on single-alga treatments. We did this by using algal pieces that were free of visible epibionts. Brine shrimp (*A. salina*) represented our animal-derived food and were purchased frozen. Before offering this food to the amphipods, brine shrimp were thawed in clean seawater. Food was replaced every 1–2 days, and water was changed every 2–3 days. Petri dishes were scrubbed every 2–3 days to eliminate fecal pellets and reduce the growth of microbes that could serve as alternative food sources or potential pathogens.

We measured survivorship, growth, and fecundity for each species. For species that ovulated, survivorship (in days) was measured as the number of individuals alive only until the first female became ovigerous in any of the treatments. This was necessary because females were killed at ovulation in order to quantify fecundity. For *G. mucronatus*, which does not ovulate when cultured using these methods (Cruz-Rivera and Hay, in press), survivorship was measured until the experiment was terminated on day 30. Survivorship data were analyzed, and post hoc comparisons among treatments were made, using chi-square analyses. Because survivorship of *G. mucronatus* was measured over a longer period than in any of the other species, we ran additional statistical analyses at day 15, comparable to the time at which all other species first became ovigerous.

Size at death was measured from the rostrum to the last large coxa under a dissecting microscope. Growth (in µm/day) was then calculated as size at death divided by the number of days lived in that treatment. For determining growth, we considered only amphipods that survived beyond the day the last amphipod in the starvation treatments died. This prevented us from using amphipods that may not have fed at all, and from using very small amphipods for which measurement errors could have been large. In a few cases, dead individuals could not be accurately measured because of microbial degradation. These were excluded from the analyses.

At ovulation, females were fixed in formalin, measured, and beheaded to extract the eggs from the brood pouch. For *A. marcuzzii*, *A. valida*, and *C. compta*, we measured female growth (µm/day), length at ovulation (µm), days to ovulation, clutch size, and we calculated individual egg volumes (in µl) by measuring the length and width of eggs, and applying the formula for the volume of a spheroid. Individual egg volumes were added to obtain total clutch volumes. We also recorded the number of females that failed to ovulate in the experiments with *Ampithoe* and *Cymadusa* (but not *Gammarus*, explained below) when they could be reliably sexed. Because few amphipods matured and expressed secondary sexual characters on some diets, we were unable to quantify the total number of females present. However, because amphipods were assigned at random, we considered those diets to be suppressing fecundity, rather than having no females. We present qualitative information for those treatments. For *G. mucronatus*, which did not produce eggs during our experiments, we approximated reproductive potential by calculating the area of the gonads visible on each side of the female body and dividing by 2 (µm^2/female side), upon termination of the assay. Experiments were ended when most discernible females had produced eggs (26–27 days for *Ampithoe* and *Cymadusa*), or when most individuals in our experimental populations had developed obvious adult characters (30 days for *Gammarus*). Upon termination of the experiments, all individuals remaining alive were killed and measured.

Growth and reproductive data were analyzed with one-way ANOVA. Homogeneity of variances was tested using $F_{\max}$ tests. Data were appropriately transformed when necessary. If variances were homogeneous, post hoc comparisons, were made using Tukey's HSD tests, adjusted for unequal sample sizes. If heterogeneity among variances could not be corrected through transformations, we used Welch's tests. Treatments in which only one individual survived or ovulated were not included in the ANOVA, but the data are presented in the results for comparison.

Results

Food type significantly affected survivorship for all four species of amphipods (P<0.001 for all species, chi-square

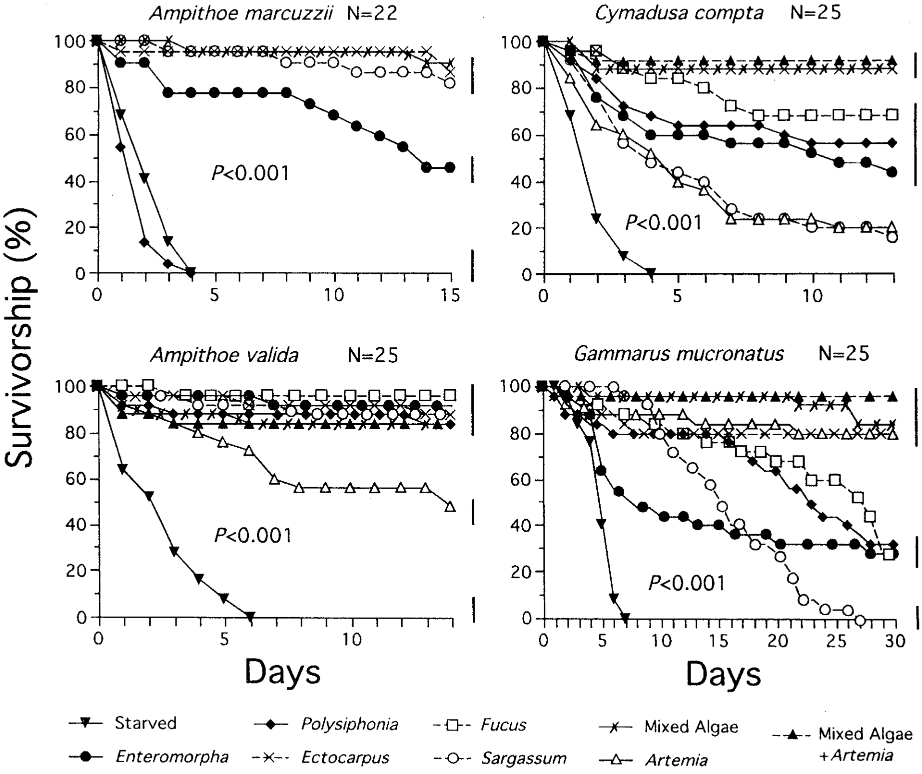

Fig. 1 Survivorship of four sympatric amphipods on single and mixed diets. The mixed algal treatment for *Ampithoe marcuzzii* contained fewer species than for the other amphipods (see Materials and methods). Animals were monitored daily, but some symbols are deleted from the graphs to enhance clarity of the figures. Significance values and groupings (shown by *vertical lines* to the right of the survivorship plots) are from chi-square analyses assessing survivorship on the last day plotted

tests; Fig. 1). At day 15, when the first *A. marcuzzii* female ovulated, survivorship was high (82–91%) and similar on *E. siliculosus*, *S. filipendula*, and mixed algae, intermediate (45%) on *E. flexuosa*, and very low (0%) on either *Polysiphonia* sp. or the starved treatment. In fact, *A. marcuzzii* confined with *Polysiphonia* sp. died as rapidly as those with no food. In contrast to *A. marcuzzii*, the congeneric *A. valida* survived well and similarly on all diets containing algae (84–96%). However, when fed on animal matter alone (*Artemia*), survivorship was significantly suppressed (48%; Fig. 1).

With one exception, *C. compta* and *G. mucronatus* showed generally similar patterns of survivorship among diets. For both species, survivorship was highest (Fig. 1) when fed mixed algae, mixed algae+*Artemia*, or *Ectocarpus* (80–96%), intermediate on *Enteromorpha*, *Polysiphonia*, and *Fucus* (28–68%), and lowest on *Sargassum* and the starvation treatment (0–16%). For *C. compta*, survivorship on *Artemia* alone was low and did not differ significantly from that on *Sargassum* or the starvation control (Fig. 1). In contrast, survivorship of *G. mucronatus* on *Artemia* was equivalent to survivorship values produced by the best diets (Fig. 1). Thus, *G. mucronatus* was the only species whose survivorship was not depressed by feeding on animal matter alone.

The females of *A. marcuzzii*, *A. valida*, and *C. compta* first became ovigerous on days 13–15 of the experiments. Because measuring egg number and size required killing these females, we analyzed survivorship on the different foods at those dates. In contrast, survivorship of *G. mucronatus* was analyzed after 30 days because these amphipods never ovulated. For more similar contrasts among species, we ran an additional analysis for *G. mucronatus* comparing all treatments at day 15 so that dietary effects could be compared among all species after similar times of exposure to the diets. For three of our treatments, patterns for *G. mucronatus* after 15 days differed to those after 30 days. At day 15, survivorship in all feeding treatments except *E. flexuosa* and *S. filipendula* was equivalent, but amphipods survived significantly better on any of the feeding treatments than they did in the starved treatment. These differences between 15 and 30 days for *G. mucronatus* indicate that the negative effects of *Polysiphonia*, *Fucus*, and *Sargassum* diets increased with time of exposure to those diets (Fig. 1).

Of the 807 amphipods we cultured, only 6 could not be measured due to microbial degradation following death. Growth of all species was significantly affected by diet ($P<0.001$, one-way ANOVA; Fig. 2), with patterns for growth generally paralleling patterns for survivorship (i.e., amphipods usually grew best on the diets that supported higher survivorship, but there were a few interesting exceptions). Similar to the patterns in survivorship (Fig. 1), *A. marcuzzii* growth was equivalent on *Ectocarpus*, *Sargassum*, and the mixed algal treatment, but growth was depressed significantly (≈30%) when confined to *Enteromorpha* ($P<0.001$, one-way ANOVA; Fig. 2), a diet which also caused lower survivorship (Fig. 1).

A. valida attained highest growth on mixed algae and mixed algae+*Artemia*, followed by *Ectocarpus*, *Entero-*

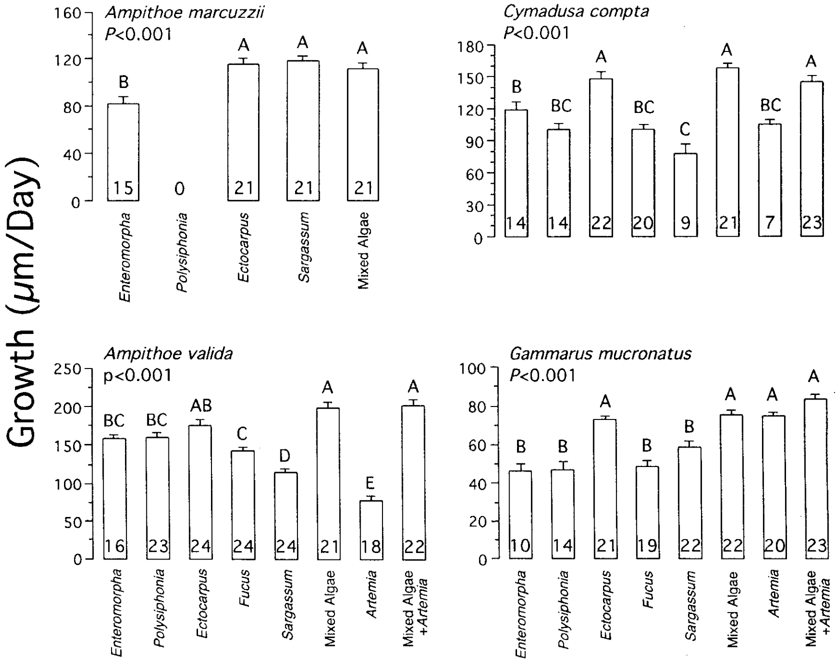

Fig. 2 Growth (mean+1 SE) of amphipods on single versus mixed diets. The mixed algal treatment had fewer algal species for *A. marcuzzii* than for the other three amphipods (see Materials and methods). *Numbers at the base of the bars* denote the number of individuals measured. Analyses are by one-way ANOVA followed by Tukey's HSD. *Similar letters above bars* indicate no significant differences among those treatments

morpha, and *Polysiphonia*. The two mixed-diet treatments, but not *Ectocarpus*, produced significantly larger individuals than *Enteromorpha* and *Polysiphonia* (Fig. 2), although survivorship had not differed among these treatments (Fig. 1). Although *A. valida* survived similarly on *F. vesiculosus* and *S. filipendula* as in all other treatments containing algae (Fig. 1), growth on *Sargassum* was suppressed significantly compared to all other treatments containing algal foods, and growth on *Fucus* was significantly suppressed compared to growth on *Ectocarpus*, mixed algae, or mixed algae+*Artemia* (P<0.05, Tukey's HSD, Fig. 2). Both *Fucus* and *Sargassum* are fucalean algae, but growth on *Fucus* was significantly higher than growth on *Sargassum*. Growth on *Artemia* was significantly lower than for any other fed treatment. *Artemia* was also the treatment producing the lowest survivorship for this species (among the fed treatments; Fig. 1). Growth on *Artemia* was only 30–60% of that on any of the other diets. Therefore, for *A. valida*, animal matter alone was a lower-quality food than algae.

C. compta grew significantly faster when feeding on *Ectocarpus* alone, mixed algae, or mixed algae+*Artemia*, than when feeding on any of the other treatments (P<0.05, Tukey's HSD). This paralleled our findings for survivorship (Fig. 1). *Enteromorpha*, *Polysiphonia*, *Fucus*, *Artemia*, and *Sargassum* yielded lower growth, with *Enteromorpha* producing significantly better growth than *Sargassum* (P<0.05, Tukey's HSD; Fig. 2). Thus, *C. compta* feeding on *Sargassum* grew 20–50% slower than when feeding on any of the other diets. Interestingly, *Artemia* caused high mortality in this species (only 20% survivorship, Fig. 1), but surviving individuals grew at rates comparable to four of the five monospecific algal diets (Fig. 2).

Growth of *G. mucronatus* paralleled our findings for survivorship (Fig. 1), with the possible exception of the *Sargassum* treatment. For this amphipod, all treatments fell into one of two significant groupings (Fig. 2). Growth was highest on the *Ectocarpus*, mixed algal, mixed algal+*Artemia*, and *Artemia*-alone treatments. *Sargassum*, *Enteromorpha*, *Polysiphonia*, and *Fucus* diets produced lower but similar growth. Although no individuals survived beyond 27 days on the *Sargassum* diet (Fig. 1), growth on this diet was equivalent (Fig. 2) to growth on diets sustaining significantly (≈30%) higher survivorship.

Dietary effects on fecundity and other fitness-related variables of the females showed that particular diets strongly suppressed reproductive potential in these amphipods. For *A. marcuzzii*, all females in the *Ectocarpus*, *Sargassum*, and mixed algal treatments became ovigerous. We could not quantify how many females were present in the *Enteromorpha* treatment because growth was suppressed (Fig. 2) and none of the amphipods matured to the stage where secondary sexual characters were clearly expressed (Table 1). However, because amphipods were assigned randomly to all treatments, and the treatments with high survivorship contained 30–50% females, it is unlikely that no female amphipods were present in the *Enteromorpha* diet (or the *Polysiphonia* treatment, where all individuals died). Females in the *Ectocarpus*, *Sargassum*, and mixed algal treatments grew at equivalent rates, ovulated at equivalent sizes and ages, had similar clutch sizes, produced eggs of similar volume, and had equivalent clutch volumes (Fig. 3). Thus, fitness in the *Polysiphonia* (which produced no survivors) and *Enteromorpha* treatments was zero, and lower than in any of the other three fed treatments (Figs. 1, 2, and 3).

Table 1 Totals and percentages (in parentheses) of females ovulating during the experiments, for the three amphipod species that produced eggs (see Materials and methods). No data are available for treatments in which most amphipods did not develop secondary sexual characters (sexes indistinguishable) or died early in the assays (no survivors)

Amphipod	Diet	Ovulating females	Remarks
Ampithoe marcuzzii	*Enteromorpha*	0 (0)	Sexes indistinguishable
	Polysiphonia	0 (0)	No survivors
	Ectocarpus	10 (100)	All individuals matured
	Sargassum	10 (100)	All individuals matured
	Mixed algae	6 (100)	All individuals matured
Ampithoe valida	*Enteromorpha*	13 (93)	All individuals matured
	Polysiphonia	10 (100)	All individuals matured
	Ectocarpus	7 (88)	All individuals matured
	Fucus	13 (100)	All individuals matured
	Sargassum	9 (100)	All individuals matured
	Mixed algae	12 (92)	All individuals matured
	Artemia	0 (0)	Sexes indistinguishable
	Mixed algae+*Artemia*	7 (100)	All individuals matured
Cymadusa compta	*Enteromorpha*	5 (100)	All individuals matured
	Polysiphonia	5 (83)	All individuals matured
	Ectocarpus	11 (100)	All individuals matured
	Fucus	6 (86)	All individuals matured
	Sargassum	0 (0)	Sexes indistinguishable
	Mixed algae	12 (92)	All individuals matured
	Artemia	0 (0)	Sexes indistinguishable
	Mixed algae+*Artemia*	7 (100)	All individuals matured

A. valida experienced complete suppression of ovulation in the *Artemia*-alone treatment. Of the 13 individuals that were alive at the end of the experiment, only 1 had developed clear secondary sexual characters (a female). In contrast, of the 7–13 recognizable females in the *Enteromorpha*, *Ectocarpus*, and mixed algal treatments, only one female in each failed to produce eggs (Table 1). All females produced eggs in the remaining treatments. Thus, *Artemia* greatly decreased survivorship (Fig. 1), growth (Fig. 2), and fecundity (Fig. 4) for this species. Similar to the patterns of growth for the entire experimental population (Fig. 2), growth of the females was significantly decreased on *Sargassum* and *Fucus* compared to most of the other diets ($P<0.001$, one-way ANOVA; Fig. 4), and growth tended to be highest on *Ectocarpus*, mixed algae, and mixed algae+*Artemia*. Although rigorous statistical groupings changed slightly when analyses of the entire population (Fig. 2) were compared to analyses of the females alone (Fig. 4), the overall patterns were very similar.

A. valida females tended to become ovigerous at a smaller size in the *Fucus* and *Sargassum* treatments ($P<0.001$, one-way ANOVA; Fig. 4). Females ovulating on *Fucus* were significantly smaller than those on the two mixed-diet treatments ($P<0.05$, Tukey's HSD), but were of equivalent size as those fed on any of the other algae offered alone ($P>0.05$, Tukey's HSD). In contrast, females on *Sargassum* ovulated at a significantly smaller size than in any of the other treatments, except for *Fucus*. Ovulation was delayed for females feeding on *Sargassum*, when compared to most other diets except *Fucus* and *Polysiphonia* ($P<0.001$, one-way ANOVA; Fig. 4). Although females in the two mixed-diet treatments and the *Ectocarpus* treatment tended to ovulate sooner than in other diets, the days to ovulation in those three treatments were not statistically different from the *Enteromorpha* and *Polysiphonia* treatments ($P>0.05$,

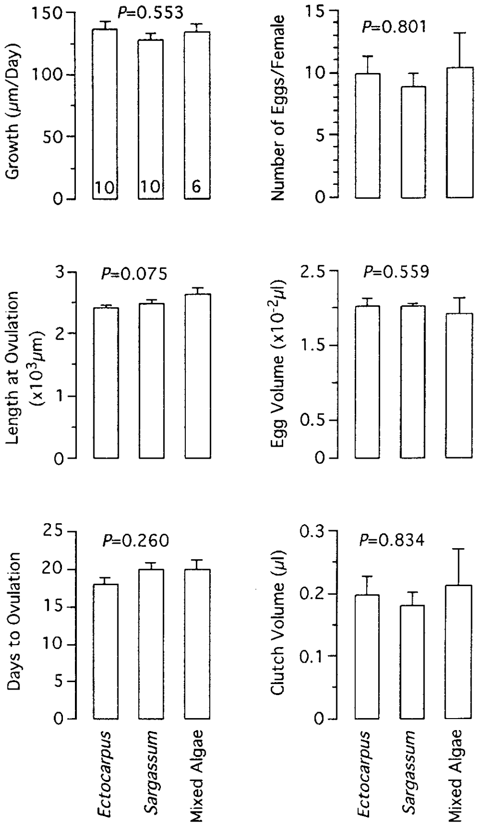

Fig. 3 Reproductive parameters measured for mature females of *A. marcuzzii*. Because all amphipods on *Polysiphonia* died, and those on *Enteromorpha* did not reach sexual maturity, only three treatments produced ovulating females (see Table 1). *Bars* represent means+1 SE and *numbers at the base of the bars* in the upper-left histogram indicate total number of females per treatment. Analyses are by one-way ANOVA

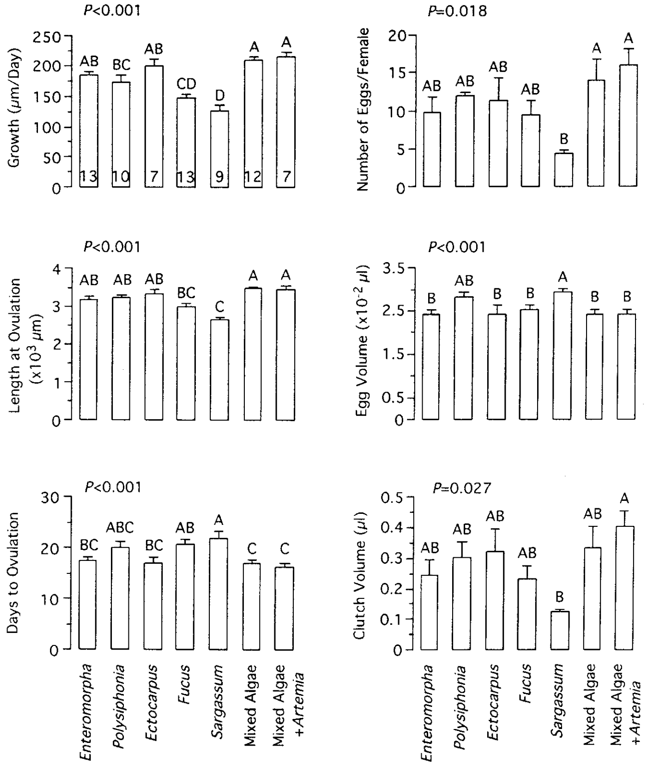

Fig. 4 Female reproductive parameters measured in *Ampithoe valida*. The *Artemia* treatment did not produce any reproductive females (Table 1). *Bars* represent means+1 SE and *numbers at the base of the bars* indicate total number of females per treatment. Analyses are by one-way ANOVA followed by Tukey's HSD or Welch's test for significant groupings. *Bars with the same letters* are not significantly different

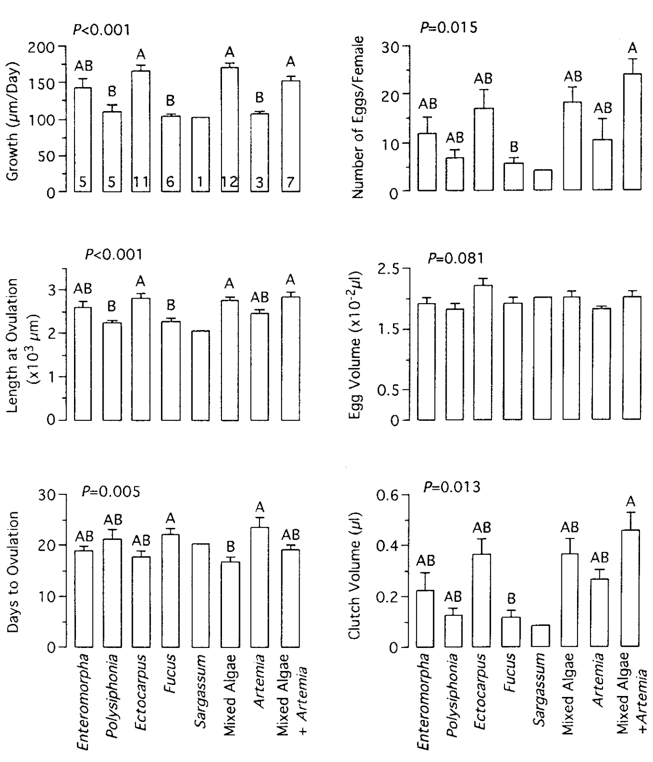

Fig. 5 Reproductive parameters measured in *Cymadusa compta* females. Because only one female ovulated on *Sargassum*, this treatment is excluded from the statistical analyses, but the data for this female are plotted for comparison. Symbols and analyses are as in Fig. 4

Welch's test; Fig. 4). Clutch size differed among diets (P=0.018, one-way ANOVA; Fig. 4), with *Sargassum* producing the lowest number of eggs per female (55–75% lower than other diets), and the two mixed-diet treatments producing the highest. Despite considerable differences in mean clutch size among treatments, the variance was often large and there were, thus, few significant differences among treatments in post hoc pairwise comparisons (as determined by Welch's tests; Fig. 4).

Diet influenced the volume of individual eggs in *A. valida* (P<0.001, one-way ANOVA; Fig. 4). *A. valida* females fed on a monospecific diet of *Sargassum* produced larger eggs, and this difference in egg volume was statistically significant compared to all treatments except *Polysiphonia*. Despite producing larger eggs, the total volume of the clutch was significantly smaller for females fed on *Sargassum* because they produced so few eggs (P=0.027, one-way ANOVA; Fig. 4). However, as with clutch size, clutch volume showed high variance among treatments and post hoc comparisons could only detect statistical differences between the mixed algae+*Artemia* diet and the *Sargassum* monospecific diet (P<0.05, Welch's test; Fig. 4).

For *C. compta*, of the 49 females developing secondary sexual characters, only 3 failed to ovulate (one in each of the *Fucus*, *Polysiphonia*, and mixed algal treatments). However, very few individuals in the *Sargassum* or *Artemia* treatments survived, and these were often too small at death to be sexed reliably (Table 1). Nevertheless, 1 female became ovigerous in the *Sargassum* treatment and 3 females ovulated in the *Artemia* treatment, so at least some individuals attained maturity on these two diets. Because including a treatment with one replicate would violate the assumptions of ANOVA, our analyses did not include the *Sargassum* treatment. In addition, the low number of replicates in several of the treatments constrained our statistical power, particularly during post hoc comparisons.

Growth of *C. compta* females (Fig. 5) mirrored the pattern for the entire experimental population (Fig. 2). Female growth was significantly higher on the *Ectocarpus*, mixed algal, and mixed algal+*Artemia* treatments than on the *Polysiphonia*, *Fucus*, or *Artemia* treatments. Female growth on *Enteromorpha* was intermediate and statistically indistinguishable from all other treatments. Similar to the patterns for growth, *C. compta* females ovulated at significantly larger sizes (P<0.001, one-way ANOVA; Fig. 5) in the *Ectocarpus*, mixed algal, and mixed algal+*Artemia* treatments, than on the *Polysiphonia* and *Fucus* treatments. Length at ovulation was intermediate in the *Enteromorpha* and *Artemia* treatments, which were not statistically different from any of the other diets (Fig. 5).

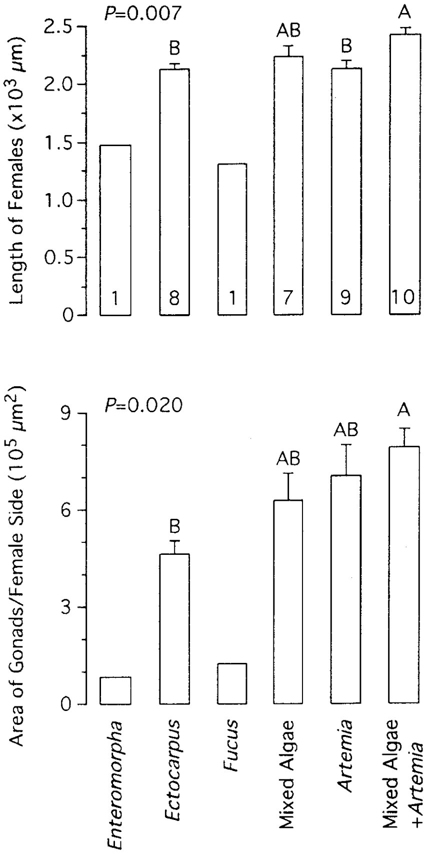

Fig. 6 Reproductive traits measured in *G. mucronatus* females. The *Enteromorpha* and *Fucus* treatments are not included in the analyses because only one female matured in each, but the data are shown for comparison. Other symbols and analyses are as in Fig. 4

Ovulation occurred significantly sooner (P=0.005, one-way ANOVA; Fig. 5) in the mixed algal treatment than in either the *Fucus* or *Artemia* treatments, but all other diets were intermediate and statistically indistinguishable from all other treatments. Variance in clutch sizes was high, but differences among treatments were significant (P=0.015, one-way ANOVA; Fig. 5). Females on *Fucus* produced significantly fewer eggs than those on the mixed algal+*Artemia* treatment (P<0.05, Welch's test), but none of the other treatments were statistically different from the rest despite large differences in mean egg output (Fig. 5). The patterns for clutch volume mirrored those for clutch size (P=0.013, one-way ANOVA; Fig. 5).

Because *G. mucronatus* did not produce eggs, we analyzed the size of the females and the area of the developing gonads after 30 days. The *Enteromorpha* and *Fucus* treatments produced only one female each, so these two treatments were excluded from the analyses. No females with gonads occurred in the *Polysiphonia* treatment. In fact, few matured to the point of expressing secondary sexual traits clearly, and only one female could be positively identified. Female size after 30 days (P=0.007, one-way ANOVA; Fig. 6) was significantly higher in the mixed algal+*Artemia* treatment than on *Artemia* alone or on *Ectocarpus*, but indistinguishable from the mixed algal diet. The mixed algal treatment did not differ from any treatment producing more than one female. Although differences in female size were significant, they were small (5–10%). In contrast, differences in gonadal size among some treatments were large (P=0.02, one-way ANOVA; Fig. 6). Gonads of females fed on *Ectocarpus* were 42% smaller than those of females fed on mixed algae+*Artemia* and this difference was significant (P<0.05, Tukey's HSD). However, gonadal area in the mixed algae, and the *Artemia* treatments were not statistically different from any of the other treatments, despite being considerably larger than on *Ectocarpus* (Fig. 5).

Discussion

Because plant tissue is nutritionally poor and feeding from one or a few plant species may not provide balanced nutrition, both mixing of food plants and occasional carnivory have been interpreted as strategies enhancing nutrient acquisition in herbivores (Mattson 1980; White 1993). The benefits of these feeding behaviors, however, are not always apparent because many studies demonstrating dietary mixing do not test the consequences of single versus mixed diets on consumer performance (e.g., Kitting 1980; Belovsky 1984; Speiser and Rowell-Rahier 1991; Dearing and Schall 1992; see also Pennings et al. 1993). Nevertheless, studies have shown that aquatic micrograzers may attain higher fitness by supplementing their algal diets with protozoa or cyanobacteria (Sanders et al. 1996; Schmidt and Jónasdóttir 1997; DeMott 1998). Supplementing natural plant diets with animal material enhances performance or fitness in some crustaceans (McTigue and Zimmerman 1991; Kennish 1996; Cruz-Rivera and Hay, in press), and has been suggested or demonstrated to enhance fitness for terrestrial herbivores (Johnson and Boyce 1990; White 1993). Bjorndal (1991) showed that freshwater turtles could increase digestibility of plant matter by also consuming insect larvae, thus demonstrating a possible mechanism through which dietary mixing could further enhance fitness by indirectly enhancing the assimilation of plant material. Similarly, mixing plant foods has positive effects on the performance of some gastropods (Watanabe 1984; Pennings et al. 1993), fish (Lobel and Ogden 1981), and insects (MacFarlane and Thorsteinson 1980; White 1993; Bernays et al. 1994; Bernays and Minkenberg 1997). However, mixed algal diets have not been demonstrated to be better than some single foods for certain sea urchins (Larson et al. 1980; Steinberg and van Altena 1992) or gastropods (Rogers et al. 1995; see also Pennings et al. 1993).

In our experiments, all amphipods survived, grew well, and attained high fecundity on mixed diets. In most instances, however, the fitness on mixed diets was matched on some single plant diets such as *Ectocarpus*. Only for *G. mucronatus* did we find that mixed diets enhanced fitness over all monospecific algal diets (Fig. 6).

Contrary to what one might expect from the generally held notion that plant-eating consumers are nitrogen limited (Mattson 1980; White 1993), adding animal tissue (*Artemia*) to the mixed seaweed diet did not significantly affect survivorship, growth, or fecundity of any of the consumers tested. Additionally, for *A. valida* and *C. compta*, limiting the consumers to *Artemia* suppressed survivorship and growth more than limiting them to some single algal diets. Given the number of studies showing, or suggesting, positive effects of occasional carnivory for herbivores and omnivores, our results for *A. valida* and *C. compta* appear unusual. They suggest that these amphipods may be more herbivorous than *G. mucronatus*, which performed relatively well on a diet of *Artemia* alone. Most overviews suggesting that herbivores are nitrogen or protein limited have focused primarily on interactions between terrestrial herbivores and higher plants (e.g., Mattson 1980; White 1993). Because seaweed thalli tend to be less refractory and more digestible than the foliage of terrestrial plants, it is possible that nitrogen acquisition may be less critical for marine than for terrestrial herbivores.

For all species, culturing amphipods on mixtures of algae generally resulted in similar survivorship, growth, and fecundity as feeding on *E. siliculosus* alone. This suggests that *A. valida* and *C. compta* were either feeding selectively on this alga or combining diets without any relative benefit over consuming only *Ectocarpus*. For *A. marcuzzii*, fitness on the mixed algal treatment was equivalent to that on either *Ectocarpus* or *Sargassum* alone (Figs. 1, 2, and 3), implying that this amphipod was selectively consuming either of those algae, or combining diets without enhancing its fitness over some monospecific diets. However, a previous investigation conducted in this same area demonstrated that *A. marcuzzii* strongly preferred *S. filipendula* over *E. siliculosus* when various sympatric seaweeds were offered simultaneously (Duffy 1990). Both algae are abundant during the times of the year when *A. marcuzzii* recruits. This suggests that feeding choices of this amphipod may not correlate closely with dietary consequences on fitness.

Disparities between feeding choices and fitness consequences of diet have been best studied in herbivorous insects for which predator escape, mate searching, low relative mobility, or constrained ability to "remember" food plants can strongly affect feeding preference and host plant choice (Price et al. 1980; Bernays and Graham 1988; Futuyma and Moreno 1988; Courtney and Kibota 1990; Hay and Steinberg 1992). Although survivorship and growth of *G. mucronatus* on *Ectocarpus* were similar to survivorship and growth on the two mixed diets (mixed algae and mixed algae+*Artemia*), gonad production was ≈40% less on the *Ectocarpus* diet than on the mixed diets. This difference, however, was only significant when *Ectocarpus* was compared to the mixed algae+*Artemia* treatment, but not the mixed algal treatment. Nevertheless, reproductive potential was suppressed when *G. mucronatus* fed only on *Ectocarpus*. For this amphipod, dietary mixing was clearly beneficial (Fig. 6).

The value of specific algae as foods showed interesting contrasts and similarities. In general, *E. siliculosus* as a single food source was a higher-quality food for all four amphipod species. However, for *A. marcuzzii*, *S. filipendula* was as beneficial as *Ectocarpus* (Table 1, Figs. 1, 2, and 3). In contrast, *Sargassum* was among the poorest, if not the poorest, of all monospecific algal diets for the other three amphipods (Table 1, Figs. 1, 2, 4, and 6). The relative food values of *E. flexuosa*, *Polysiphonia* sp., and *F. vesiculosus* also varied considerably among mesograzers. For example, *Enteromorpha* suppressed development in *A. marcuzzii*, but for the congeneric *A. valida*, amphipods fed on *Enteromorpha* and *Ectocarpus* had equivalent survivorship, growth, and fecundity (Table 1, Figs. 1, 2, and 4). For *C. compta*, *Enteromorpha* produced lower survivorship and growth compared to *Ectocarpus* and the two mixed-diet treatments (Figs. 1, 2). For this amphipod, we were unable to rigorously document suppressed reproduction in the *Enteromorpha* treatment compared to others (Fig. 5), but our power to detect statistical differences among diets was constrained by the low number of females maturing and ovulating on some diets.

Amphipods also differed considerably in their performance on the *Polysiphonia* diet. *A. marcuzzii* isolated with *Polysiphonia* sp. died at the same rate as in the starved treatment (Fig. 1), *Gammarus* and *Cymadusa* survived at intermediate rates on *Polysiphonia* (Fig. 1), but *A. valida* survived and produced eggs as well on *Polysiphonia* as on any of the diets (Table 1, Figs. 1, 2, and 4). Although both *Polysiphonia* sp. and *E. siliculosus* were collected as epiphytes of *S. filipendula*, these two algae were clearly different as food sources for these amphipods. Grazing by mesoherbivores on epiphytic algae can be beneficial to aquatic plants by reducing the negative effects of shading, drag, or competition for nutrients that epiphytes exert on their hosts (Orth and van Montfrans 1984; Jernakoff et al. 1996). Thus, mesograzer feeding on epiphytes is viewed as an important process in marine plant communities (Orth and van Montfrans 1984; D'Antonio 1985; Brawley 1992; Jernakoff et al. 1996; Jernakoff and Nielsen 1997; but see Mukai and Iijima 1995). However, Duffy (1990) demonstrated that the effects of amphipods on hosts versus epiphytic algae depended on the amphipods involved; some species selectively graze epiphytes while others focus on host tissue. Our data suggest that not only the mesograzer species, but also the identity of the epiphytes, will influence the potential for consumers to control fouling (Jernakoff et al. 1996; Jernakoff and Nielsen 1997). Some amphipods attained high fitness by feeding on some epiphytes (*E. siliculosus*), while dying rapidly if they fed on others (*Polysiphonia* sp.). Some of the species tested faired as well on large macrophytes as on filamentous algae. For sea urchins, which may feed on coarser spatial scales than amphipods, it has been demonstrated that the attractiveness of potential food plants can be dramatically altered by the epiphytic species fouling host algae (Wahl and Hay 1995). Variability in epiphyte community structure may therefore have complex indirect consequences for the dynamics of plant-herbivore interactions, even for herbivores foraging at different scales.

F. vesiculosus was generally a poor food for all the species against which it was tested (Figs. 1, 2, 4, 5, and 6). Nevertheless, *A. valida* occurs at high densities on *Fucus* (Deal 1997), and this alga seems to be a preferred host for *A. valida* in North Carolina (E. Cruz-Rivera, personal observation based on numerous field collections). Recent investigations have shown that this amphipod associates with *Fucus* in the field, feeds readily on *Fucus*, and remains in the tubes it constructs on this seaweed even at low tide when the plants are completely out of the water (Deal 1997; E. Cruz-Rivera, personal observation). This close association between *A. valida* and *Fucus* at some sites, despite the costs in performance it entails, could be explained if the amphipod gains protection from predators, or achieves other indirect advantages, by living on and consuming a suboptimal food. Interactions between predation pressure, habitat choice, and constraints on diet have been suggested, or shown, to be important for herbivores as diverse as sea urchins, crabs, polychaetes, gastropods, amphipods, insects, and desert rodents (Vance and Schmitt 1979; O'Dowd and Hay 1980; Price et al. 1980; Hay and Fuller 1981; Hay et al. 1987, 1988a, 1988b, 1990; Bernays and Graham 1988; Futuyma and Moreno 1988; Courtney and Kibota 1990; Duffy and Hay 1994; Stachowicz and Hay 1996, 1999; reviewed in Hay 1992, 1996; Hay and Steinberg 1992). Although we observed that feeding only on *Fucus* caused average decreases in fecundity, some individuals developed and ovulated at similar rates as those living on better diets. It is possible that genetic diversity or phenotypic plasticity accounts in part for the success of this amphipod in colonizing diverse habitats. *A. valida* is not a specialist, and it associates with brown, green, and red algae, as well as seagrasses, at different sites around the world (Nicotri 1977, 1980; Pomeroy and Levings 1980; Duffy and Hay 1994; Alonso et al. 1995; Deal 1997). If interactions among host plant choice, feeding, and fitness are important for this species, they could be context dependent or operate as local phenomena.

Interestingly, *A. valida* females feeding on *Sargassum* produced eggs that were significantly larger than eggs from females in all other treatments but *Polysiphonia*, even though the *Sargassum* diet strongly suppressed clutch size. Females on *Sargassum* also became ovigerous at a smaller size (Fig. 4). It appeared that *A. valida* feeding on *Sargassum* attempted to compensate for the low numbers of eggs by making larger eggs. In contrast, for *C. compta*, there was a non-significant trend towards larger eggs when that amphipod fed on nothing but *Ectocarpus* (Fig. 5), the monospecific diet producing the highest overall survivorship, growth, and fecundity. Egg size can be influenced by food quality or quantity in diverse animals (Helm et al. 1973; Bayne et al. 1978; Brody and Lawlor 1984; Leather 1994; Williams 1994) and this can have important consequences for their offspring (but see Karlsson and Wiklund 1984). For example, when food is limiting, larger eggs can produce larger newborns that are more resistant to food limitation or have increased ability for dispersal compared to smaller newborns (Capinera 1979; Brody and Lawlor 1984; Hutchings 1991; Leather 1994; Williams 1994; Smith and Bruun 1998). Bigger eggs may also produce larger offspring that are less susceptible to predation (Kaplan 1992). The costs and benefits of variable size in amphipod eggs remain to be studied.

Our findings that two of the three amphipods tested on *Artemia* alone show strong detrimental effects of consuming animal matter suggest that these species may be better adapted to algal than animal food. These findings relate well to published observations on the amphipod species studied here. For example, *A. marcuzzii* and *A. valida* both readily consume large seaweeds, and associate with macroalgae in the field (Nicotri 1977, 1980; Duffy 1990; Duffy and Hay 1994; Alonso et al. 1995; Deal 1997). *C. compta* associates with algae (Hauxwell et al. 1998; also see Materials and methods) but it is also abundant among seagrasses (Nelson 1979a, 1979b; Stoner 1979; Lewis 1984). Although *C. compta* can consume detritus, algae, and some vascular plant material (Nelson 1979b; Hauxwell et al. 1998), it apparently prefers macroalgae and epiphytes over detritus (Zimmerman et al. 1979; but see Nelson 1979b). Our data show that it can successfully live as a herbivore without supplementing its diet with animal matter or detritus (Figs. 1, 2, and 5).

In contrast to the other amphipods, *G. mucronatus* performed well on animal matter, algal mixtures, or a combination of animal and algal food, arguing for a more generalized, omnivorous diet as has been previously suggested (Zimmerman et al. 1979; LaFrance and Ruber 1985; Bärlocher and Howatt 1986; Fredette and Diaz 1986; Cruz-Rivera and Hay, in press). Although *G. mucronatus* is often assumed to be an omnivore feeding on plants, animals, and detritus, gut contents have not confirmed its use of animal matter (Bärlocher and Howatt 1986; *Carinogammarus mucronotus* in Sanders et al. 1962), and manipulative studies on food choice have not used animal material among the foods offered (Zimmerman et al. 1979; Duffy and Hay 1994). In our experiments, we often observed *G. mucronatus* grab pieces of *Artemia* and feed in a fashion described for other species of *Gammarus* (MacNeil et al. 1997), even though algal foods were abundant. This behavior was not observed for *A. valida* or *C. compta*. Thus, *Gammarus* is likely to be a more generalized feeder that exploits detrital, animal, and plant matter, although it is capable of surviving and maturing by feeding only on certain seaweeds (e.g., *Ectocarpus*), despite achieving lower fecundity than on a mixed diet or a diet of only animal matter (Fig. 6).

Lack of reliable information on the trophic ecology of marine mesograzers has often lead investigators to assume that most mesograzers exploit similar resources (reviewed in Brawley 1992). However, sympatric mesograzers may live in very close proximity while exploiting markedly different resources, thus having differential impacts on communities (Duffy 1990; Brawley 1992; Jernakoff and Nielsen 1997; Duffy and Hay, in press). In the case of the amphipods studied here, considerable variance in the effects of different foods suggests that nutritional requirements can be quite different even among congeners (e.g., *A. marcuzzii* and *A. valida*). The among-species patterns of food use also suggest that the variable ability of mesograzers to use alternative plant or animal resources will determine how populations will be affected when preferred foods become limiting (see also Pennings et al. 1993; Bernays and Minkenberg 1997).

The three species of amphipods that showed no net gains from mixing foods are all tube builders that spend considerable time in close association with their hosts. In contrast, the species showing enhanced fitness on a more diverse diet is a more mobile amphipod (Duffy and Hay 1994) that is likely better able to search for different foods. Links between mobility and diet have been noted before in both marine and terrestrial systems (Hay et al. 1987, 1988b; Bernays and Graham 1988; Courtney and Kibota 1990; Duffy and Hay 1994; Cruz-Rivera and Hay, in press), but the role of mobility in favoring or inhibiting dietary mixing has not been explicitly addressed (but see Bernays and Minkenberg 1997). Although dietary mixing is important for diverse animals, it may be less important for some small herbivores like *Ampithoe* and *Cymadusa*, whose lower mobility may restrict their ability to acquire diverse foods.

Acknowledgements We thank R. Taylor, D. Simberloff, and two anonymous reviewers for comments on earlier versions of this paper. Financial support was provided by NSF grant OCE 95-29784 to M.E. Hay.

References

Agnew DJ, Moore PG (1986) The feeding ecology of two littoral amphipods (Crustacea), *Echinogammarus pirtloti* (Sexton & Spooner) and *E. obtusatus* (Dahl). J Exp Mar Biol Ecol 103: 203–215

Alonso G, Tablado A, Lopez Gappa J, Magaldi N (1995) Seasonal changes in an intertidal population of the amphipod *Ampithoe valida* Smith, 1873. Oebalia 21:77–91

Bärlocher F, Howatt SL (1986) Digestion of carbohydrates and protein by *Gammarus mucronatus* Say (Amphipoda). J Exp Mar Biol Ecol 104:229–237

Barnard JL, Karaman GS (1991) The families and genera of marine gammaridean Amphipoda (except marine gammaroids). Rec Aust Mus [Suppl] 13

Bayne BL, Holland DL, Moore MN, Lowe DM, Widdows J (1978) Further studies on the effects of stress in the adult of the eggs of *Mytilus edulis*. J Mar Biol Assoc UK 53:673–684

Bell SS (1991) Amphipods as insect equivalents? An alternative view. Ecology 72:350–354

Belovsky GE (1984) Herbivore optimal foraging: a comparative test of three models. Am Nat 124:97–115

Bernays EA, Graham M (1988) On the evolution of host specificity in phytophagous arthropods. Ecology 69:886–892

Bernays EA, Minkenberg OPJM (1997) Insect herbivores: different reasons for being a generalist. Ecology 78:1157–1169

Bernays EA, Bright KL, Gonzalez N, Angel J (1994) Dietary mixing in a generalist herbivore: tests of two hypotheses. Ecology 75:1997–2006

Bjorndal KA (1991) Diet mixing: nonadditive interactions of diet items in an omnivorous freshwater turtle. Ecology 72:1234–1241

Bousfield EL (1973) Shallow water gammaridean Amphipoda of New England. Cornell University Press, Ithaca

Brawley SH (1992) Mesoherbivores. In: John DM, Hawkins SJ, Price J (eds) Plant-animal interactions in the marine benthos. Clarendon, Oxford, pp 235–263

Brody MS, Lawlor LR (1984) Adaptive variation in offspring size in the terrestrial isopod *Armadillium vulgare*. Oecologia 61: 55–59

Capinera JL (1979) Qualitative variation in plants and insects: effects of propagule size on ecological plasticity. Am Nat 114: 350–361

Courtney SP, Kibota TT (1990) Mother doesn't know best: selection of hosts by ovipositing insects. In: Bernays EA (ed) Plant-insect relationships, vol 2. CRC, Boca Raton, Fla, pp 161–188

Cruz-Rivera E, Hay ME (in press) Can quantity replace quality? Food choice, compensatory feeding, and fitness of marine mesograzers. Ecology

D'Antonio C (1985) Epiphytes on the rocky intertidal red alga *Rhodomela larix* (Turner) C. Agardh: negative effects on the host and food for herbivores. J Exp Mar Biol Ecol 86:197–218

Deal MS (1997) The causes and consequences of within-species variation in seaweed chemical defenses. PhD thesis, University of North Carolina at Chapel Hill, Chapel Hill, NC

Dearing MD, Schall JJ (1992) Testing models of optimal diet assembly by the generalist herbivorous lizard *Cnemidophorus murinus*. Ecology 73:845–858

DeLong MD, Summers RB, Thorp JH (1993) Influence of food type on the growth of a riverine amphipod, *Gammarus fasciatus*. Can J Fish Aquat Sci 50:1891–1896

DeMott WR (1998) Utilization of a cyanobacterium and a phosphorous-deficient green alga as complementary resources by daphnids. Ecology 79:2463–2481

Duffy JE (1990) Amphipods on seaweeds: partners or pests? Oecologia 83:267–276

Duffy JE, Hay ME (1991a) All amphipods are not all created equal: a reply to Bell. Ecology 72:354–358

Duffy JE, Hay ME (1991b) Food and shelter as determinants of food choice by an herbivorous marine amphipod. Ecology 72: 1286–1298

Duffy JE, Hay ME (1994) Herbivore resistance to seaweed chemical defense: the roles of mobility and predation risk. Ecology 75: 1304–1319

Duffy JE, Hay ME (in press) Strong impacts of grazing amphipods on the organization of a benthic community. Ecol Monogr

Fredette TJ, Diaz RJ (1986) Life history of *Gammarus mucronatus* Say (Amphipoda: Gammaridae) in warm temperate estuarine habitats, York River, Virginia. J Crust Biol 6:57–78

Freeland WJ, Janzen DH (1974) Strategies in herbivory by mammals: the role of plant secondary compounds. Am Nat 108: 269–289

Futuyma DJ, Moreno G (1988) The evolution of ecological specialization. Annu Rev Ecol Syst 19:207–233

Graça MAS, Maltby L, Calow P (1993) Importance of fungi in the diet of *Gammarus pulex* and *Asellus aquaticus*. Oecologia 96: 304–309

Greenstone MH (1979) Spider feeding behavior optimises dietary essential amino acids. Nature 282:501–503

Gulati RD, DeMott WR (1997) The role of food quality for zooplankton: remarks on the state-of-the-art, perspectives and priorities. Freshwater Biol 38:753–768

Hauxwell J, McClelland J, Behr PJ, Valiela I (1998) Relative importance of grazing and nutrient controls of macroalgal biomass in three temperate shallow estuaries. Estuaries 21:347–360

Hawkins SJ, Hartnoll RG (1983) Grazing of intertidal algae by marine invertebrates. Oceanogr Mar Biol Annu Rev 21:195–282

Hay ME (1992) The role of seaweed chemical defenses in the evolution of feeding specialization and in the mediation of complex interactions. In: Paul VJ (ed) Ecological roles of marine natural products. Cornell University Press, Ithaca, pp 93–118

Hay ME (1996) Marine chemical ecology: what is known and what is next? J Exp Mar Biol Ecol 200:103–134

Hay ME, Fuller PJ (1981) Seed escape from heteromyid rodents: the importance of microhabitat and seed preference. Ecology 62: 1395–1399

Hay ME, Steinberg PD (1992) The chemical ecology of plant-herbivore interactions in marine versus terrestrial communities. In: Rosenthal GA, Berenbaum MR (eds) Herbivores: their interactions with secondary plant metabolites, vol II. Ecological and evolutionary processes. Academic Press, San Diego, pp 372–408

Hay ME, Duffy JE, Pfister CA, Fenical W (1987) Chemical defense against different marine herbivores: are amphipods insect equivalents? Ecology 68:1567–1580

Hay ME, Duffy JE, Fenical W, Gustafson K (1988a) Chemical defense in the seaweed *Dictyopteris delicatula*: differential effects against reef fishes and amphipods. Mar Ecol Prog Ser 48:185–192

Hay ME, Renaud PE, Fenical W (1988b) Large mobile versus small sedentary herbivores and their resistance to seaweed chemical defenses. Oecologia 75:246–252

Hay ME, Duffy JE, Fenical W (1990) Host-plant specialization decreases predation on a marine amphipod: an herbivore in plant's clothing. Ecology 71:733–743

Helm MM, Holland DL, Stephenson RR (1973) The effect of supplementary algal feeding of a hatchery breeding stock of *Ostrea edulis* on larval vigor. J Mar Biol Assoc UK 53:673–684

Hutchings JA (1991) Fitness consequences of variation in egg size and food abundance in brook trout *Salvelinus fontinalis*. Evolution 45:1162–1168

Jernakoff P, Nielsen J (1997) The relative importance of amphipod and gastropod grazers in *Posidonia sinuosa* meadows. Aquat Bot 56:183–202

Jernakoff P, Brearley A, Nielsen J (1996) Factors affecting grazer-epiphyte interactions in temperate seagrass meadows. Oceanogr Mar Biol Annu Rev 34:109–162

Johnson RG, Boyce MS (1990) Feeding trials with insects in the diet of sage grouse chicks. J Wildl Manage 54:89–91

Kaplan RH (1992) Greater maternal investment can decrease offspring survival in the frog *Bombina orientalis*. Ecology 73: 280–288

Karlsson B, Wiklund C (1984) Egg weight variation and lack of correlation between egg weight and offspring fitness in the small brown butterfly *Lasiommata megera*. Oikos 43:376–385

Kennish R (1996) Diet composition influences the fitness of the herbivorous crab *Grapsus albolineatus*. Oecologia 105:22–29

Kitting CL (1980) Herbivore-plant interactions of individual limpets maintaining a mixed diet of intertidal marine algae. Ecol Monogr 50:527–550

Kneib RT, Newell SY, Hermeno ET (1997) Survival, growth and reproduction of the salt-marsh amphipod *Uhlorchestia spartinophila* reared on natural diets of senescent and dead *Spartina alterniflora* leaves. Mar Biol 128:423–431

Krebs JR, Avery MI (1984) Chick growth and prey quality in the European bee-eater (*Merops apiaster*). Oecologia 64:363–368

LaFrance K, Ruber E (1985) The life cycle and productivity of the amphipod *Gammarus mucronatus* on a northern Massachusetts salt marsh. Limnol Oceanogr 30:1067–1077

Larson BR, Vadas RL, Keser M (1980) Feeding and nutritional ecology of the sea urchin *Strongylocentrotus drobachiensis* in Maine, USA. Mar Biol 59:49–62

Leather SR (1994) Life history traits of insect herbivores in relation to host quality. In: Bernays EA (ed) Insect-plant interactions, vol 5. CRC, Boca Raton, Fla, pp 175–207

Lewis FG III (1984) Distribution of macrobenthic crustaceans associated with *Thalassia*, *Halodule*, and bare sand substrata. Mar Ecol Prog Ser 19:101–113

Lobel PS, Ogden JC (1981) Foraging by the herbivorous parrotfish *Sparisoma radians*. Mar Biol 64:173–183

MacFarlane JH, Thorsteinson AJ (1980) Development and survival of the twostriped grasshopper, *Melanoplus bivittatus* (Say) (Orthoptera: Acrididae), on various single and multiple plant diets. Acrida 9:63–76

MacNeil C, Dick JTA, Elwood RW (1997) The trophic ecology of freshwater *Gammarus* spp. (Crustacea: Amphipoda): problems and perspectives concerning the functional feeding group concept. Biol Rev 72:349–364

Martin MM (1987) Invertebrate-microbial interactions: ingested fungal enzymes in arthropod biology. Cornell University Press, Ithaca

Mattson WJ Jr (1980) Herbivory in relation to plant nitrogen content. Annu Rev Ecol Syst 11:119–161

McTigue TA, Zimmerman RJ (1991) Carnivory vs herbivory in juvenile *Penaeus setiferus* (Linnaeus) and *Penaeus aztecus* (Ives). J Exp Mar Biol Ecol 151:1–16

Mukai H, Iijima A (1995) Grazing effects of a gammaridean Amphipoda, *Ampithoe* sp., on the seagrass *Syringodium isoetifolium*, and epiphytes in a tropical seagrass bed of Fiji. Ecol Res 10:243–257

Nelson WG (1979a) Experimental studies of selective predation on amphipods: consequences for amphipod distribution and abundance. J Exp Mar Biol Ecol 38:225–245

Nelson WG (1979b) An analysis of structural pattern in an eelgrass (*Zostera marina* L.) amphipod community. J Exp Mar Biol Ecol 39:231–264

Nicotri ME (1977) The impact of crustacean herbivores on cultured seaweed populations. Aquaculture 12:127–136

Nicotri ME (1980) Factors involved in herbivore food preference. J Exp Mar Biol Ecol 42:13–26

O'Dowd, DJ, Hay ME (1980) Mutualism between harvester ants and a desert ephemeral: seed escape from desert rodents. Ecology 61:531–540

Orth RJ, Montfrans J van (1984) Epiphyte-seagrass relationships with an emphasis on the role of micrograzing: a review. Aquat Bot 18:43–69

Pederson JB, Capuzzo JM (1984) Energy budget of an omnivorous rocky shore amphipod, *Calliopius laeviusculus* (Krøyer). J Exp Mar Biol Ecol 76:277–291

Pennings SC, Masatomo TN, Paul VJ (1993) Selectivity and growth of the generalist herbivore *Dolabella auricularia* feeding upon complimentary resources. Ecology 74:879–890

Pomeroy WM, Levings CD (1980) Association and feeding relationships between *Eogammarus confervicolus* (Amphipoda, Gammaridae) and benthic algae on the Sturgeon and Roberts Banks, Fraser River Estuary. Can J Fish Aquat Sci 37:1–10

Poore AGB, Steinberg PD (1999) Preference-performance relationships and effects of host plant choice in a herbivorous marine amphipod. Ecol Monogr 69:443–464

Price PW, Bouton CE, Gross P, McPheron BA, Thompson JN, Weiss AE (1980) Interactions among three trophic levels: influence of plants on interactions between insect herbivores and natural enemies. Annu Rev Ecol Syst 11:41–65

Randall JE (1967) Food habits of reef fishes of the West Indies. Stud Trop Oceanogr 5:655–897

Robertson AI, Lucas JS (1983) Food choice, feeding rates, and the turnover of macrophyte biomass by a surf-zone inhabiting amphipod. J Exp Mar Biol Ecol 72:99–124

Rogers CN, Steinberg PD, Nys R de (1995) Factors associated with oligophagy in two species of sea hares (Mollusca: Anaspidea). J Exp Mar Biol Ecol 192:47–73

Sanders HL, Goudsmit EM, Mills EL, Hampson GE (1962) A study of the intertidal fauna of Barnstable Harbor, Massachusetts. Limnol Oceanogr 7:63–79

Sanders RW, Williamson, CE, Stutzman PL, Moeller RE, Goulden CE, Aoki-Goldsmith R (1996) Reproductive success of "herbivorous" zooplankton fed algal and nonalgal food resources. Limnol Oceanogr 41:1295–1305

Schmidt K, Jónasdóttir SH (1997) Nutritional quality of two cyanobacteria: how rich is 'poor' food? Mar Ecol Prog Ser 151: 1–10

Simpson SJ, Simpson CL (1990) The mechanisms of nutritional compensation by phytophagous insects. In: Bernays EA (ed) Insect-plant interactions, vol 2. CRC Press, Boca Raton, Fla, pp 111–160

Slansky F Jr (1993) Nutritional ecology: the fundamental quest for nutrients. In: Stamp NE, Casey TM (eds) Caterpillars: ecological and evolutionary constraints on foraging. Chapman & Hall, New York, pp 29–91

Slansky F Jr, Rodriguez JG (eds) (1987) Nutritional ecology of insects, mites, spiders, and related invertebrates. Wiley, New York

Smith HG, Bruun M (1998) The effects of egg size and habitat on starling nestling growth and survival. Oecologia 115:59–63

Speiser B, Rowell-Rahier M (1991) Effects of food availability, nutritional value, and alkaloids on food choice in the generalist herbivore *Arianta arbustorum* (Gastropoda: Helicidae). Oikos 62:306–318

Stachowicz JJ, Hay ME (1996) Facultative mutualism between an herbivorous crab and a coralline alga: advantages of eating noxious seaweeds. Oecologia 105:377–387

Stachowicz JJ, Hay ME (1999) Reducing predation through chemically-defended camouflage: indirect effects of plant defenses on herbivores. Ecology 80:495–509

Steinberg PD, Altena I van (1992) Tolerance of marine invertebrate herbivores to brown algal phlorotannins in temperate Australasia. Ecol Monogr 62:189–222

Sterner RW, Hessen DO (1994) Algal nutrient limitation and the nutrition of aquatic herbivores. Annu Rev Ecol Syst 25:1–29

Stoner AW (1979) Species specific predation on amphipod crustacea by the pinfish *Lagodon rhomboides*: mediation by macrophyte standing crop. Mar Biol 55:201–207

Toft S, Wise DH (1999) Growth, development, and survival of a generalist predator fed single and mixed-species diets of different quality. Oecologia 119:191–197

Vance RR, Schmitt RJ (1979) The effect of the predator-avoidance behavior of the sea urchin *Centrostephanus coronatus*, on the breadth of its diet. Oecologia 44:21–25

Van Soest P (1994) Nutritional ecology of the ruminant. Cornell University Press, Ithaca, NY

Wahl M, Hay ME (1995) Associational resistance and shared doom: effects of epibiosis on herbivory. Oecologia 102:329–340

Watanabe JM (1984) Food preference, food quality, and diets of three herbivorous gastropods (Trochidae: *Tegula*) in a temperate kelp forest habitat. Oecologia 62:47–52

White TCR (1993) The inadequate environment: nitrogen and the abundance of animals. Springer, Berlin Heidelberg New York

Williams TD (1994) Intraspecific variation in egg size and egg composition in birds: effects on offspring fitness. Biol Rev 68:35–59

Zimmerman R, Gibson R, Harrington J (1979) Herbivory and detritivory among gammaridean amphipods from a Florida seagrass community. Mar Biol 54:41–47