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Feeding preferences for juvenile and adult algae depend on algal stage and herbivore species

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ABSTRACT: Juvenile marine organisms are physically and chemically different from adults. Consequently, the ecology of juveniles, particularly their interactions with other organisms, may change as they age. Yet, they are often considered to function as 'miniature adults'. To explore how ecological interactions change as juvenile seaweeds mature, we investigated among-species food preferences of 4 species of grazers for 8 species of common intertidal and subtidal macroalgae in laboratory multiple-choice feeding-preference experiments. Grazers were offered either juvenile tissues or adult tissues of 8 species of macroalgae. Food preferences of grazers among both juvenile and adult brown algae differed among herbivore species. Within herbivore species, the relative grazing rates on juveniles of a given species were not significantly correlated with grazing rates on adult tissues of that species. Thus, food preferences of herbivores among species of macroalgae are dependent upon the age of the algal tissue and the species of herbivore being considered. Stage-specific differences in preferences between juveniles and adults are likely a result of chemical and morphological changes occurring during algal development. Further work is needed to characterize these changes and further determine their impacts on the ecological characteristics of juvenile marine macroalgae.

KEY WORDS: Brown algae · Development · Food preferences · Herbivory · Juveniles

INTRODUCTION

Herbivory is important in determining the final structure of many marine benthic communities (Lubchenco 1978, 1983, Lubchenco & Menge 1978, Duggins 1980, Hay 1981, 1985, Lubchenco & Gaines 1981, Hawkins & Hartnoll 1983, Steneck 1983, 1986, 1988, Duggins & Dethier 1985, Carpenter 1986, Lewis 1986, Schiel & Foster 1986, Witman 1987). Grazers often exert their influence on community dynamics by consuming the sporeling or juvenile stages of algae (Lubchenco 1978, 1983, Robles & Cubit 1981, Dayton 1985, Dean et al. 1989, Asano et al. 1990, Paine 1992). Macroalgae that survive through the early sporeling stages of their life-history tend to persist because they become too large to be removed by most herbivores and 'escape in size' (Lubchenco & Gaines 1981).

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Herbivore food preferences, as demonstrated in laboratory feeding experiments, are helpful in predicting which species are most likely to be consumed in the field and consequently which species are likely to persist in the community. However, most food preference studies are conducted with adult algae, which may be physically and chemically different from juveniles. Juvenile stages of algae are thinner and puncture more easily than adults (K. Van Alstyne et al. unpubl.). Phlorotannins, or polyphenolic compounds, which are thought to function as chemical defenses towards some species of herbivores (Geiselman & McConnell 1981, Steinberg 1984, 1985, 1988, Ragan & Glombitza 1986, Van Alstyne & Paul 1990, Targett & Arnold 1998), occur in different concentrations in juveniles and adults (Denton et al. 1990, Van Alstyne et al. unpubl.). Therefore, it is probable that food preferences of herbivores among species of adult macroalgae may differ from herbivore preferences for juveniles.

In this study, we examine food preferences of 4 common intertidal and subtidal invertebrate herbivores for juvenile and adult stages of some common species of kelps and fucoid brown algae. We conducted laboratory multiple-choice feeding-preference assays to determine the relative preferences of herbivores among species of seaweeds. We then compared preferences for juveniles versus adults to determine if the preferences were stage-specific.

MATERIALS AND METHODS

Collection sites. Purple sea urchins (*Strongylocentrotus purpuratus*), snails (*Lacuna porrecta* and *Tegula funebralis*), and isopods (*Idotea wosnesenskii*) were collected from low to mid intertidal pools at Boiler Bay, OR, USA, ~5 km north of the town of Depoe Bay, OR. All animals were kept in flow-through seawater tables at the Hatfield Marine Science Center (HMSC) in Newport, OR, and fed a mixture of macrophytes that included species used in feeding experiments. Juvenile and adult individuals of 6 species of kelps, *Alaria marginata*, *Costaria costata*, *Egregia menziesii*, *Hedophyllum sessile*, *Lessoniopsis littoralis*, and *Nereocystis luetkeana*, and 2 species of fucoid brown algae, *Fucus gardneri* and *Fucus spiralis*, were also collected from Boiler Bay. Within 2 to 3 h of collection, algae were transported on ice to HMSC where they were immediately used in feeding-preference experiments. Juveniles were the smallest recognizable individuals we could find for each species; most were 2 to 10 cm long. Adult algae were the same size as reproductive individuals of a given species, although individuals used in these experiments were not always in reproductive condition.

Feeding preference assays. In each experiment, consumers (either *Strongylocentrotus purpuratus*, *Tegula funebralis*, *Idotea wosnesenskii* or *Lacuna porrecta*) were offered similar sized pieces of juvenile and adult algae. The pieces given to urchins had a mass of ~0.5 g; *T. funebralis* were given ~0.25 g pieces and *L. porrecta* and *I. wosnesenskii* were given pieces of ~0.15g. Experiments with all herbivores except *L. porrecta* were conducted in 5 cm diameter plastic Rubbermaid™ containers that had been modified by removing 3 cm diameter pieces from the bottoms and lids and replacing them with 1 mm mesh fiberglass screening to allow water flow through the containers. Experiments with *L. porrecta* were performed in 40 mm diameter plastic Petri dishes that had been modified by cutting 25 mm diameter holes in both parts of the dish and covering them with 1 mm mesh fiberglass screening. All experiments took place in outdoor flow-through seawater tables at HMSC. Animals were starved for 2 to 4 d prior to conducting feeding-preference experiments so they would consume the algae before it started deteriorating. Cronin & Hay (1996) found that starving the sea urchins *Arbacia punctulata* caused them to be less selective when offered choices of artificial diets with and without secondary metabolites in them; it is not known whether all herbivores respond to starvation in this way or if starvation affects preferences for intact algae.

Multiple-choice feeding-preference experiments were conducted to assess preferences among species of macroalgae. In each experiment, herbivores were simultaneously offered choices of 8 foods, either pieces of adult *Alaria marginata*, *Costaria costata*, *Egregia menziesii*, *Fucus gardneri*, *F. spiralis*, *Hedophyllum sessile*, *Lessoniopsis littoralis*, and *Nereocystis luetkeana*, or pieces of juvenile plants of the same species (N = 5 to 11). An equal number of control arenas in each experiment contained algae without herbivores and were used to assess autogenic changes in the algae that occurred during the course of the experiments.

Algal pieces were blotted dry and weighed prior to the start of the experiments. Containers were checked periodically and herbivores were removed when at least half the algae in the container had been consumed. At the conclusion of the experiment, experimental and control algae were again blotted dry and reweighed to determine mass changes. Data from experimental replicates in which less than 25% or greater than 75% of the algae was consumed were discarded.

A Yao's *R* test was used to determine whether food preferences among species differed significantly in each experiment. Yao's *R* is a multivariate method that is appropriate for data from multiple-choice feeding-preference experiments in which consumption rates are not independent within arenas (Manly 1993).

For each of the 8 algal species, an overall mass change was calculated separately for juveniles and adults by subtracting the mean mass changes (final masses minus initial masses) in the control arenas from the mean mass changes in the experimental arenas. Correlation analyses were conducted between the overall mass change of adult tissues versus the overall mass change of juvenile tissues to determine if among-species preferences for juveniles and adults were correlated within each herbivore species.

RESULTS

Herbivores exhibited significant preferences (α = 0.05 in Yao's *R* tests) among algal species in most of the feeding experiments (Figs. 1 to 4). The preferences differed among the species of herbivores and between juveniles and adult algae within species of herbivores.

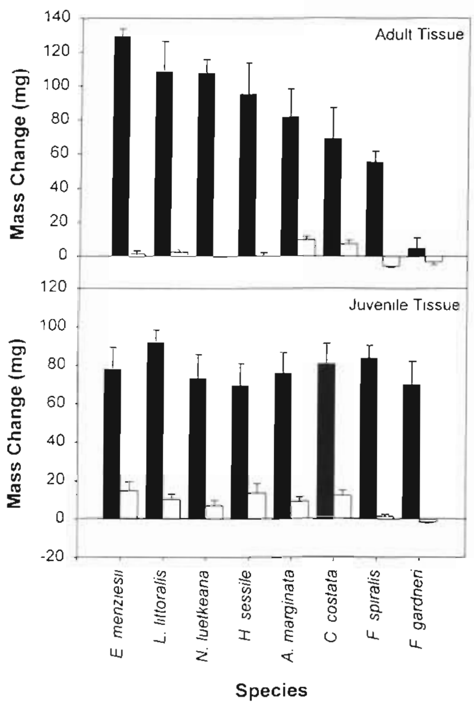

Fig. 1. Consumption rates of juvenile (N = 11) and adult (N = 10) brown algal tissues by *Strongylocentrotus purpuratus*. Urchins were offered tissues from all 8 species simultaneously. Black bars represent mean mass changes of algal tissues ± 1 SE in experimental arenas with herbivores. White bars represent mean mass changes of algal tissues ± 1 SE in control arenas without herbivores. Consumption rates of adult tissues, but not juvenile tissues, differed significantly among species (adults: p = 0.0016 from Yao's *R* test; juveniles: p = 0.8244 from Yao's *R* test)

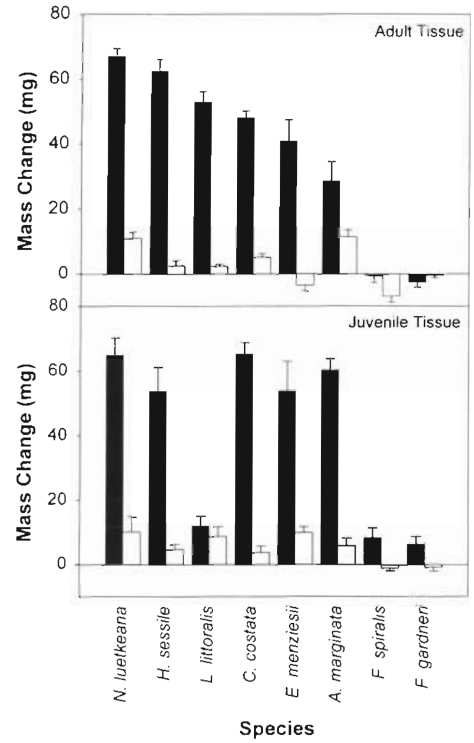

Fig. 2. Consumption rates of juvenile (N = 8) and adult (N = 5) brown algal tissues by *Tegula funebralis*. Symbols as in Fig. 1. Consumption rates of adult and juvenile tissues differed significantly among species (adults: p = 0.0001 from Yao's *R* test; juveniles: p < 0.001 from Yao's *R* test)

In experiments with adult tissues, sea urchins consumed larger amounts of kelp than fucoid brown algae (Fig. 1). However, no significant preference (p > 0.05 in Yao's *R* tests) was displayed by the urchins among species of juveniles. *Tegula funebralis* and *Lacuna porrecta* also preferred adult kelps to adult fucoid brown algae (Figs. 2 & 3). When offered juvenile tissues, they showed significant preferences among species (*T. funebralis*: p = 0.001, *L. porrecta*: p < 0.001 in Yao's *R* tests), but these preferences were different than preferences for adults. In experiments with *T. funebralis*, this was especially notable for *Lessoniopsis littoralis*, which was preferred as adults, but not as juveniles, and *Alaria marginata* which was a low preference food as an adult but a high preference food as a juvenile (Fig. 2). Similarly, *Costaria costata* juveniles were highly preferred by *L. porrecta*, but adults were only an intermediate preference food (Fig. 3). Food preferences among adult tissues by *Idotea wosnesenskii* were different from preferences of other herbivores (Fig. 4). *I. wosnesenskii* exhibited the highest preference for both adult and juvenile *Alaria marginata* and intermediate preferences for adult *Fucus spiralis*, a low preference food for the other 3 herbivores (Figs. 1 to 3). Preferences for juveniles tracked preferences for adults more closely in the *I. wosnesenskii* preference experiments than for the other herbivores (Fig. 4).

There were no significant correlations between preferences for adult and juvenile tissues (Fig. 5; *Strongylocentrotus purpuratus*: Pearson correlation coefficient = 0.224, p > 0.05, *Tegula funebralis*: Pearson correlation coefficient = 0.494, p > 0.05, *Lacuna porrecta*: Pearson correlation coefficient = 0.167, p > 0.05, *Idotea wosnesenskii*: Pearson correlation coefficient = 0.625, p > 0.05).

DISCUSSION

Changes in morphology, chemistry, behavior, and mortality accompany the transition from juvenile to adult stages in marine organisms (Bernard 1967, Werner & Gilliam 1984, Hooker & Morse 1985, Zann et al. 1987, Rowley 1990, Keesing & Halford 1992, Gosselin & Chia 1994, 1995a,b, 1996, Lindquist & Hay 1996, Gosselin 1997). In a survey of survival in recently

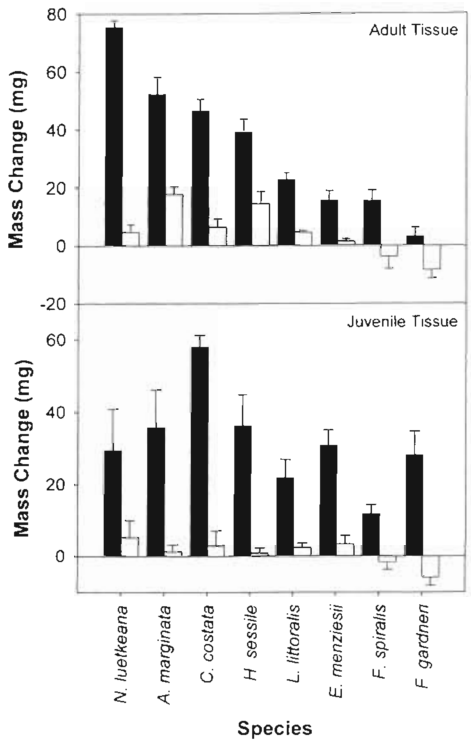

Fig. 3. Consumption rates of juvenile (N = 7) and adult (N = 9) brown algal tissues by *Lacuna porrecta*. Symbols as in Fig. 1. Consumption rates of adult and juvenile tissues differed significantly among species (adults: p = 0.0118 from Yao's *R* test; juveniles: p = 0.0333 from Yao's *R* test)

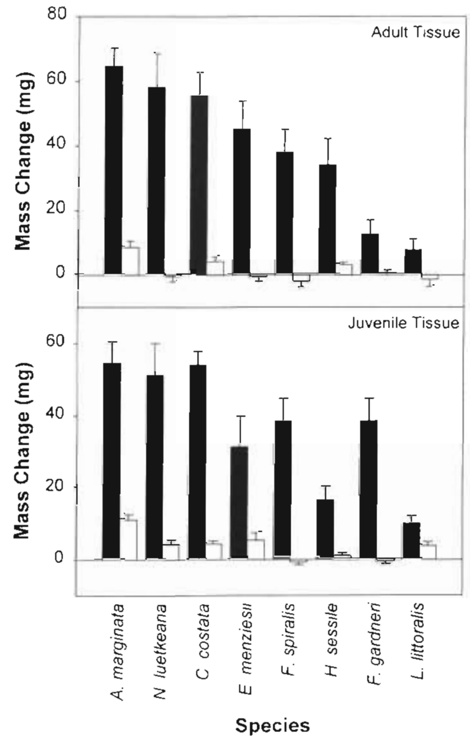

Fig. 4. Consumption rates of juvenile (N = 7) and adult (N = 7) brown algal tissues by *Idotea wosnesenskii*. Symbols as in Fig. 1. Consumption rates of adult and juvenile tissues differed significantly among species (adults: p = 0.0003 from Yao's *R* test; juveniles: p < 0.001 from Yao's *R* test)

settled marine invertebrates, Gosselin & Quan (1997) found that mortality rates of juveniles were generally highest the first day after settlement and strongly declined thereafter. Changes in mortality during development were often a result of decreases in the susceptibility of juveniles to predation and desiccation as they aged.

Much less is known about differences between the physical properties, chemical properties, and ecology of juvenile and adult macroalgae. Juvenile survival rates of macroalgae are thought to be affected by temperature and desiccation stresses (Brawley & Johnson 1991), herbivory (Lubchenco 1983, Brawley & Johnson 1991, Worm & Chapman 1998), freezing (Bird & McLachlan 1974), competition with other algal species (Reed 1990, Worm & Chapman, 1998), and wave action (Vadas et al. 1990). However, little data are available comparing the effects of these stresses on survival at different life-history stages.

Our study showed that a change in food preferences by herbivores occurs as plants age; a species that is a preferred food as a juvenile is not necessarily a preferred food as an adult. Juvenile algae differ from adults in a number of physical and chemical properties that may affect herbivore food preferences. Juveniles are generally smaller, thinner, and can be punctured more readily than adults (Van Alstyne et al. unpubl.). They can have higher tissue nitrogen concentrations and lower C:N ratios (Van Alstyne et al. unpubl.) which may influence food choice because many herbivores are thought to be nitrogen limited (Mattson 1980). Concentrations of phlorotannins have been shown to decrease with increasing thallus length in *Alaria marginata* (Van Alstyne et al. unpubl.). However, in the northwest Atlantic, phlorotannin concentrations were lower in juveniles than adults of *Fucus vesiculosus* and *F. evanescens*, and similar in juveniles and adults of *F. spiralis* (Denton et al. 1990).

Food preferences for macroalgal species also differed markedly among the 4 herbivore species. Urchins and snails generally preferred adult kelps to adult fucoid brown algae; however, this was not the case for isopods. Differences in preferences may reflect differences in the feeding apparatuses, nutritional requirements, or tolerances to chemical defense levels of the herbivores. Of the 4 herbivore species used in this study, urchins have the largest mouthparts relative to the size of their food. Feeding rates of

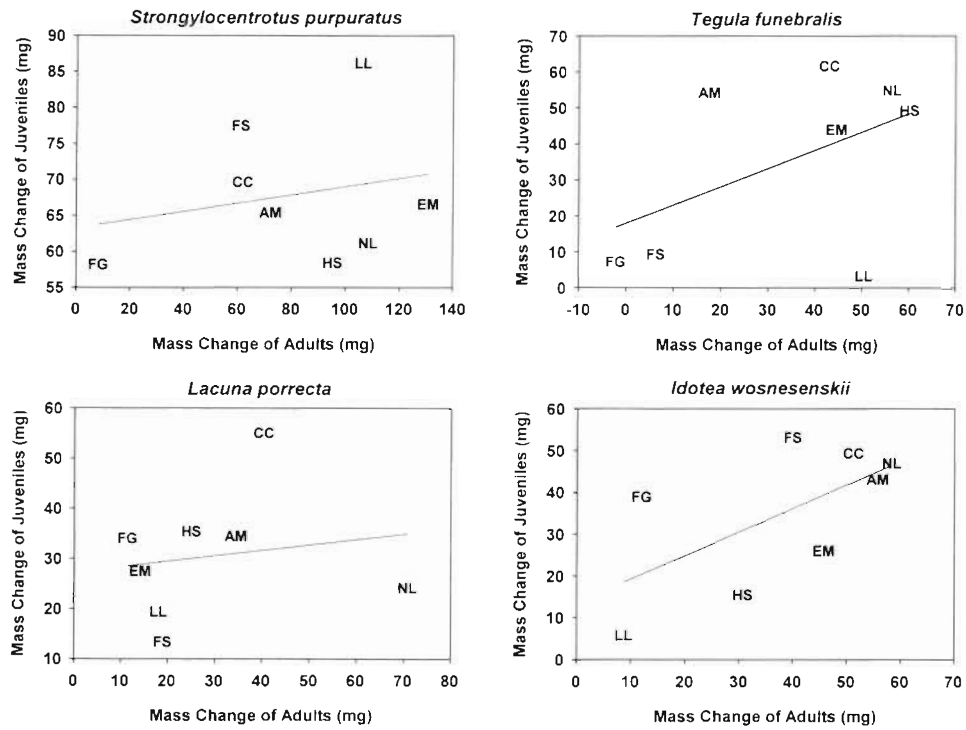

Fig. 5. Plots of consumption of adult versus juvenile tissues for each species (AM: *Alaria marginata*, CC: *Costaria costata*, EM: *Egregia menziesii*, FG: *Fucus gardneri*, FS: *Fucus spiralis*, HS: *Hedophyllum sessile*, LL: *Lessoniopsis littoralis*, NL: *Nereocystis luetkeana*). Rates were calculated as the mean mass change in experimental arenas with grazers minus the mean mass change in the control arenas without grazers. Lines represent the best fit linear regression to the data. In all cases, there was no significant correlation between mass consumption of adult and juvenile tissues by herbivores (Pearson correlation coefficient, $p > 0.05$)

urchins and *Tegula funebralis* from the eastern Pacific region are known to be affected by concentrations of phlorotannins in their diets (Steinberg 1988, Steinberg et al. 1995), whereas mesograzers, small herbivores that often use algae as habitats as well as a food source, are often tolerant of chemical defenses (Hay et al. 1989a,b, 1990a,b). Small grazers such as *Idotea* and *Lacuna porrecta* may be less affected by the high concentrations of phenolic compounds in the fucoid brown algae and more responsive to differences in algal morphological features.

As pointed out by Gosselin (1997) in a study of ontogenetic changes in benthic intertidal snails, juveniles are not simply 'miniature adults' (Gibbs 1984). Our laboratory feeding experiments demonstrate that changes accompanying the development of seaweeds have the potential to affect interactions between species in the field.

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