Why does herbivore sex matter? Sexual differences in utilization of *Fucus vesiculosus* by the isopod *Idotea baltica*

Veijo Jormalainen, Tuija Honkanen, Anita Mäkinen, Anne Hemmi and Outi Vesakoski

Optimal feeding is often constrained by predation avoidance, which may direct feeding to take place on more sheltered, but less profitable, parts of the habitat. Though constrained, feeding preferences and/or digestive capabilities should co-evolve with the energetic and nutritional needs of the animal. These needs, as well as risk taking for these goals, may differ between the sexes. We studied sexual differences in the utilization of the brown alga *Fucus vesiculosus* by the marine isopod *Idotea baltica*. In a feeding preference test with small pieces of alga both sexes prefer the apical, newly grown parts to the basal parts. However, males show stronger preference than females. When isopods are reared on the apical or basal part of the alga alone, sexes grow differently on these parts. Females gain weight equally well and their intermolt duration is the same on both parts of the alga, while males perform clearly worse on the basal than on the apical part. Despite the better quality of the apical parts of the alga, in a grazing experiment in a “semi-natural” environment with whole bushes of *F. vesiculosus* also the basal parts are consumed, and even preferred over apical parts by females. We suggest that feeding preferences are subordinate to microhabitat choice, and therefore predation avoidance constrains optimal feeding. We hypothesize that the better ability of females than that of males to utilize the basal parts of the alga for growth is a co-adaptation to their risk-averse general reproductive strategy. We discuss the sexual differences in host plant utilization in the context of reproductive strategies of the sexes, especially different risk sensitivity of foraging, and its potential consequences on plant-herbivore interaction.

Natural selection is expected to optimize feeding behavior of a herbivore. Food preferences, both between plant species and between different plant parts of varying quality, are part of this optimization. However, fitness of a herbivore is not only a function of quality and quantity of the ingested food, but includes also the components of survival and mating success. In other words, optimal feeding may be commonly constrained, e.g. by predation risk or time trade-offs with reproductive activities (e.g. Duffy and Hay 1991, McNamara et al. 1991, Bednekoff 1996).

A striking feature of sexual reproduction is that the fitness maximization strategies of the sexes typically differ (Trivers 1972, Clutton-Brock and Parker 1992, Arnold and Duvall 1994). Due to anisogamy and consequent differences in the potential reproductive rates of the sexes, male fitness is, in general, more sensitive to the number of mates than female fitness. Female fitness, in turn, is much more responsive to fecundity of each reproductive bout. Due to this basic asymmetry, various traits may have slightly different optimum values for the sexes, which generate niche separation and selects for sexual dimorphism (Slatkin 1984). These differences may often be further enhanced and complemented by sexual selection (Andersson 1994).
Different fitness maximizing strategies of the sexes can be expected to influence their feeding ecology. Especially a difference in the energetic demands of reproduction may be an important factor affecting energy intake and feeding preferences. For example, males and females often show dimorphism in the structures related to feeding, such as mouthparts, indicating differences in diets (Shine 1989). Furthermore, direct differences between sexes in food consumption (references in Slansky 1993), feeding preferences (Sandlin and Willig 1993), digestion rate (Gross et al. 1996) or growth rate (Strong and Daborn 1979, Rossiter et al. 1988) show that feeding strategies of the sexes may differ. Despite this relatively straightforward expectation there are no detailed analyses on such effects and their causes or consequences to plant-herbivore interactions (Slansky 1993).

Here, we analyze feeding preferences and growth of both sexes of *Idotea baltica* (Pallas; Crustacea, Isopoda) between parts of the perennial brown alga, *Fucus vesiculosus* (L.; Fucales). This alga forms a highly variable food source for its herbivores because its thallus consists of parts differing in age and chemical contents (Tuomi et al. 1989). Contents of both nutrients and secondary compounds also show high temporal variation, covarying largely with growth rate (Ilvessalo and Tuomi 1989, Carlson 1991, Peckol et al. 1996). Growth rate peaks in May–June coinciding with the amount of irradiance and ambient seawater nutrients, and growth continues throughout the year excluding only the midwinter period (Strömberg 1986). We compare the quality of newly grown vegetative apices and more than one year old basal parts for the fitness of males and females of this herbivore. During autumn, at the time of our experiment, new vegetative fronds contain more nitrogen than basal parts (Carlson 1991). Newly grown parts are also softer than old thalli (Tuomi et al. 1989). Actively growing plant parts usually contain more soluble carbohydrates (Westermeyer and Gomez 1996) which are digested more effectively by crustacean herbivores than structural carbohydrates, common in aged parts (Arrontes 1989). Phlorotannins, secondary compounds that often deter herbivore feeding (Hay and Fenical 1988, Targett and Arnold 1998), are found in greater concentration in old than in apical parts, but their concentration in apices increases towards autumn (Rönningberg and Ruokolaiti 1986, Ilvessalo and Tuomi 1989, Tuomi et al. 1989). Consequently, from all these variations between apical and basal parts of *F. vesiculosus* we predicted apical parts to be more profitable food for *I. baltica*.

Seaweeds, in addition to food, provide habitat and shelter for their small-sized herbivores, so called meso-herbivores, against visually oriented predators (Nicotri 1980, Hay 1992). *F. vesiculosus* forms a visually heterogeneous habitat: basal parts are blackish or dark brown, turning gradually to yellowish or light green towards the apices (Salemaa 1978). Basal parts reflect less light, are less exposed and more shaded than the apices. Experiments on microhabitat choice of *I. baltica* show that these animals are generally more frequently found on basal parts of the alga (Merilaita and Jormalainen 1997, 2000). Consequently, we expect basal parts to offer better shelter against numerous visually searching fish predators feeding on *Idotea*.

Because grazing on high quality food on the apices is likely to be risky, we hypothesized that *I. baltica* may have to trade-off food quality and predator avoidance. If the fitness components of resource accumulation, survival and mating success are differently important for males and females, we can expect different solutions to this trade-off. Sexes may adapt different utilization strategies of the host plant. In this paper, we specifically 1) test feeding preferences of *I. baltica* between basal and apical pieces of the alga in a laboratory experiment and measure the amount of consumption towards apical and basal parts of whole bushes of the *F. vesiculosus* in a “semi-natural” environment, 2) evaluate the quality of these parts of the alga for *I. baltica* by measuring growth performance when reared separately on either part, and 3) we do this separately for both sexes to test whether sexes show divergent preferences and whether the quality of different parts of the alga is different for males and females. We interpret the sexual differences in food utilization patterns in the context of reproductive strategies of the sexes and risk sensitive foraging, and discuss some potential consequences of such differences for plant-herbivore interactions.

**Material and methods**

**Study organisms**

*Idotea baltica* is a generalist feeder, feeding mainly on *F. vesiculosus* (Salemaa 1987, Schaffelke et al. 1995) but also on its epiphytic algae (Ravanko 1969). It is a color polymorphic species with all the common morphs being cryptic against the thallus of *F. vesiculosus* (Salemaa 1978). In the northern Baltic *I. baltica* juveniles are born in July. For their first months juveniles feed on filamentous algae, mainly *Cladophora glomerata* and move on to *F. vesiculosus* within three months after birth spending the rest, about 11–14 months, of their life there.

*Fucus vesiculosus* is a dominant, belt-forming brown alga of the littoral community in our study area in the Archipelago Sea, SW Finland. It is a perennial species reaching the age of five to seven years (Knight and Parke 1950). The thallus grows by branching dichotomously; it consists of both vegetative apices and, during the reproductive period, generative apices.
Animals for the laboratory experiments were collected from the vicinity of the Archipelago Research Institute of the University of Turku (60°14’N, 21°40’E) during September 1998. They were of the generation born during the summer, and had started to feed on F. vesiculosus, from which they were collected. At this age, sexual size-dimorphism develops and sexes can be separated on the basis of external genitalia, but the animals are still immature until next summer when reproduction takes place (Tuomi et al. 1988). In the laboratory, the sexes were maintained together until the start of the experiments. The experiments were performed in 1-L containers with aeration, a stone as a habitat, and under light:dark rhythm of 14 h:10 h at 12°C.

Feeding preference tests

We studied feeding preferences of male and female I. baltica between apical and basal parts of F. vesiculosus in two separate tests. The main difference between these experiments was that the first one was conducted in the laboratory in small containers (1-L) with tiny pieces of algae, the second one in large, “semi-natural” pools with whole bushes of algae. We assumed that food quality as such plays the major role in food choices of the first experiment, while habitat selection by Idotea may strongly modify feeding in the second experiment.

In the first experiment, we gave each animal (30 males, 30 females) two pieces, about 0.3 g (fresh weight) in size, from the same individual alga for food. The apical piece was cut from the tip of a vegetative frond, including the apical meristem and extending less than two cm downwards. The basal piece was from the oldest part of the alga where thallus around the midrib was still present. We used ten freshly collected individual algae; each of them was offered to three males and three females. Animals were randomly assigned to individual containers on 19 October. They were starved for one day before being fed the pieces of the alga. The experiment lasted for six days. Algae were weighed (to the nearest 1 mg) before and after the experiment by drying them first between paper tissues for 5 s. Control containers without a herbivore were run in the same conditions in order to control for autogenous change in the weight of the algal species. Although the autogenous change was negligible (see below), we corrected for it following the method presented by Roa (1992): food consumption was calculated as the loss of fresh weight of the pieces when a herbivore was present minus the weight change of a randomly chosen control piece.

The second feeding experiment was conducted in 60-L through-flow pools in order to study patterns of grazing by males and females on different parts of whole bushes of F. vesiculosus. Pools were located outside under natural light. The experiment was started on 24 September. In each pool, we put two to three F. vesiculosus bushes of natural size, and 30 male (3 pools) or female (2 pools) Idotea. Each bush was constructed by binding four randomly chosen, freshly collected and digitally photographed pieces of thallus together. The average height of these pieces was 29 ± 5.3 cm (N = 54), and the number of dichotomous branching points varied between 5 and 12. Idotea were allowed to feed for 10 d, after which the bushes were taken apart and the blades photographed. By comparing the photographs before and after feeding, area of consumed thallus was determined by an image analysis program (Optimas 6.5). The amount of grazing was measured for each bush, separately for the most recent one to two dichotomous branches (hereafter “apical”), and for the third or older dichotomous branches (hereafter “basal”).

Herbivore performance test

We studied growth and intermolt duration of male and female I. baltica fed with either apical or basal parts of F. vesiculosus. Before the experiment, we maintained individuals (32 males, 30 females) in 1-L containers. These were fed with a large piece of alga, having both apical and basal parts, and a pellet of high protein aquarium food, and monitored daily for detecting the occurrence of molt. As soon as an individual molted, the experiment was started. The first replicate was started on 24 September, and thereafter on successive days until all animals molted.

At the start, each animal was weighed (to the nearest 0.1 mg) after drying the animal quickly between paper tissues. This was repeated and the mean of two weighings was used in order to reduce measurement error. A weighed, either apical or basal, piece of alga was given to animals and it was replaced with a fresh one every 5 d. The consumed pieces were dried and weighed (to the nearest 0.01 mg, after 24 h in 60°C). Animals were checked daily for the occurrence of molt. The experiment lasted the entire intermolt until the next molt, after which the animals were reweighed. From the data we calculated food consumption during the intermolt, growth, growth rate (growth/intermolt duration), and production efficiency (percentage of weight increment of the total food consumption in terms of dry weights).

In order to control autogenous change in the weight of the alga, we ran control containers during the whole duration of the experiment without a herbivore in exactly the same conditions. Based on a large control data set there was no autogenous change in the weight of the basal piece (pairwise t-test, t426 = 1.91, NS), and a slight decrease of 2.7%, on average, of the initial weight of the apical piece (pairwise t-test, t382 = 9.78, P < 0.001), during a 5-d feeding period. Although this change was small compared to the mean consumption...
(21% in the performance test, 24% in the preference test), we corrected the consumption of the apical piece. This correction was calculated as a mean of autogenous changes, calculated proportionally from both initial and final weights. Thus, the actual food consumption was assumed to take place continuously during the whole feeding period, and the amount of biomass consumed affected the quantity of correction.

Statistical analyses

Data were analyzed by repeated measures ANOVA, and standard ANOVA and ANCOVA (GLM procedure in SAS 6.12 package; SAS Institute 1990). The assumptions of homoscedasticity and normally distributed error variances were tested by Levene’s test and Kolmogorov-Smirnov test statistics on the distribution of residual variance, respectively.

Feeding preferences in the laboratory experiment were analyzed as a paired design by treating consumption of apical and basal pieces as repeated measures and sex (fixed factor) of *I. baltica* and individual algae (random factor) as grouping factors. Similarly, food consumption, in terms of area consumed, in the “semi-natural” pool experiment was analyzed by treating the consumption of apical and basal parts of each *F. vesiculosus* bush as repeated measures and the sex of *I. baltica* as a fixed factor.

Differences in performance between sexes and between apical and basal parts were tested by two-way ANOVA. Initial size of the animal was used as a covariate in order to decrease variance and to remove the effect of size difference between sexes. The assumption of homogenous regression slopes between different treatment groups is critical for performing ANCOVA; the fulfillment of this assumption was tested before proceeding to analysis. A priori comparisons for testing differences in performance between apical and basal parts separately in males and females were done on the covariate-adjusted means by using contrasts.

Results

In the food preference test between basal and apical pieces of the alga males ate more than females (Fig. 1a, Table 1), and the total consumption varied significantly between individual algae (Table 1). There was a general preference for the apical part over the basal one (Fig. 1a). However, this preference was dependent on sex and varied between individual algae (Table 1). Interestingly, the preference of the apical part was much stronger in males than in females (Fig. 1). On some individual algae the preference for apical parts was weaker than on others, or even reversed (Table 1). The degree of the preference for apical parts did not correlate significantly with total food consumption (females: \( r = 0.55, \ P = 0.10, \ N = 10 \); males: \( r = 0.38, \ P = 0.27, \ N = 10 \), suggesting that variation in within-alga differences between apical and basal parts, not the overall quality of individual algae, explain the variability of preferences.

Sexes of *I. baltica* showed different grazing patterns towards apical and basal parts also in the pool experiment with whole bushes of the *F. vesiculosus* (Fig. 1b). Females consumed more of the basal parts of the bushes, while males preferred the apical parts (Fig. 1b), as revealed by the significant preference × sex interaction (Table 2).

In the experiment in which *I. baltica* were fed with either apical or basal part, we used the initial size of the animal as a covariate in the analysis of food consumption and performance. Sexual size-dimorphism was evident already at the start of the experiment males (wet weight; mean ± SD, \( N: 47.0 \pm 15.1 \) mg, 32) being clearly larger than females (26.7 ± 5.2 mg, 30). The effect of this size difference is removed from the adjusted means shown in Fig. 2.

![Fig. 1.](image-url)
When animals had no choice, both sexes still consumed more of the apical than of the basal part (Fig. 2a, Table 3; a priori comparison of adjusted consumption between apical and basal parts: females $t = 2.85$, $P < 0.01$; males $t = 6.05$, $P < 0.001$). As in the feeding preference test, the difference between the consumption of the two parts was higher in males than in females as revealed by the significant sex $\times$ part interaction (Table 3). The total consumption was higher in males (wet weight; mean $\pm$ SD, $N$: apical: 0.52 $\pm$ 0.18 g, 18; basal: 0.33 $\pm$ 0.13 g, 14) than in females (apical: 0.34 $\pm$ 0.14 g, 15; basal: 0.20 $\pm$ 0.07 g, 15). This difference was due to their larger size because controlling for initial size removed the sex difference in total consumption (Table 3).

Consistently with the feeding preference and consumption rate, *I. baltica* grew better when fed on the apical part (Fig. 2b, Table 3). Moreover, sexes differed in their ability to utilize the different parts of the alga for their growth; males did not grow in weight at all and intermolt duration was longer on the basal part, while females performed equally well on both parts (Fig. 2b, c; a priori comparison of adjusted growth while females performed equally on both parts and intermolt duration was longer on the basal part, for their growth; males did not grow in weight at all in their ability to utilize the different parts of the alga apical part (Fig. 2b, Table 3). Moreover, sexes differed in their larger size because controlling for initial size removed the sex difference in total consumption (Table 3).

When growth was analyzed in terms of length increment, we found no significant main effects but a significant sex $\times$ part interaction ($F_{1,55} = 4.38$, $P < 0.05$): females gained length equally well on apical (mm; mean $\pm$ SD, $N$: 0.68 $\pm$ 0.18, 15) and basal parts (0.82 $\pm$ 0.20, 14) while males grew clearly better on apical (1.05 $\pm$ 0.17, 17) than on basal parts (0.49 $\pm$ 0.21, 12). The growth rate (weight gain during intermolt/intermolt duration) was generally better on the apical part, but the ability to utilize the basal part varied between the sexes as revealed by the significant sex $\times$ part interaction (Fig. 2d, Table 3).

Production efficiency, i.e. the ability of animals to convert consumed dry biomass to dry biomass of their own, was better on the apical part (Fig. 2e, Table 3). Production efficiency of males tended to be lower than that of females, but it was equally so on both parts as there was no significant sex $\times$ part interaction (Table 3).

### Discussion

Both the feeding preference test between pieces of alga and the growth performance test indicated that apical parts of *F. vesiculosus* are better quality food for *I. baltica* than basal parts. Food consumption, when animals had no choice, matched the consumption of algal parts in the preference test. Thus, the preference test between the pieces of alga revealed the true quality of the part. *I. baltica*, especially males, do not compensate for the lower quality of basal parts by increasing consumption suggesting that the low quality may result from harmful compounds.

There are no earlier studies on the growth performance of mesoherbivores on different parts of seaweeds or between the sexes of herbivores. In the few existing within-plant feeding-preference tests in brown algae a preference of apical parts over the basal ones (Cronin and Hay 1996) or a preference of newly grown parts (Poore 1994, Pavia et al. 1999) by crustacean mesoherbivores has been found. Within-plant variation, especially in concentrations of secondary metabolites, has often been suggested to explain such preferences (Steinberg 1984, Poore 1994, Cronin and Hay 1996), but physical characteristics and distribution of carbohydrates, lipids and amino acids in the thallus may be equally important (Hay and Fenical 1988). However, within-plant variation in food quality alone cannot explain the preferences in *I. baltica* because both the degree of preference and growth performance between the parts were sex specific. Males showed stronger preference for the apical parts than females, and accordingly, their performance was good on the apical but poor on the basal part. Females performed equally well on both parts.

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**Table 1.** Test statistics of the repeated measures ANOVA for food consumption in the feeding preference test. Effects of "sex" and "alga" test for differences between sexes and individual alga, and "preference" tests for the difference between consumption of the apical and basal piece. Data shown in Fig. 1a.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>MS ($\times 10^{-4}$)</th>
<th>df</th>
<th>$F$</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Between subjects</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sex</td>
<td>245.1</td>
<td>1</td>
<td>17.9</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Alga</td>
<td>33.7</td>
<td>9</td>
<td>2.46</td>
<td>&lt;0.05</td>
</tr>
<tr>
<td>Sex $\times$ Alga</td>
<td>10.6</td>
<td>9</td>
<td>0.77</td>
<td>0.64</td>
</tr>
<tr>
<td><strong>Within subjects</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Preference</td>
<td>693.1</td>
<td>1</td>
<td>43.7</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Preference $\times$ Sex</td>
<td>197.8</td>
<td>1</td>
<td>12.5</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Preference $\times$ Alga</td>
<td>72.0</td>
<td>9</td>
<td>4.5</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Preference $\times$ Sex $\times$ Alga</td>
<td>24.8</td>
<td>9</td>
<td>1.57</td>
<td>0.16</td>
</tr>
<tr>
<td>Error</td>
<td>15.8</td>
<td>39</td>
<td></td>
<td></td>
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</tbody>
</table>

**Table 2.** Test statistics of the repeated measures ANOVA for food consumption (in terms of consumed area) of apical vs basal parts for males and females in the experiment in pools with a "semi-natural" environment. Data shown in Fig. 1b.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>MS</th>
<th>df</th>
<th>$F$</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Between subjects</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sex</td>
<td>498</td>
<td>1</td>
<td>9.49</td>
<td>&lt;0.1</td>
</tr>
<tr>
<td>Error (Pool)</td>
<td>52.5</td>
<td>3</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Within subjects</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Preference</td>
<td>25.8</td>
<td>1</td>
<td>0.35</td>
<td>NS</td>
</tr>
<tr>
<td>Preference $\times$ Sex</td>
<td>575</td>
<td>1</td>
<td>7.89</td>
<td>&lt;0.05</td>
</tr>
<tr>
<td>Preference $\times$ Pool</td>
<td>149</td>
<td>3</td>
<td>2.04</td>
<td>0.18</td>
</tr>
<tr>
<td>Error (Part)</td>
<td>72.8</td>
<td>9</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Different physiological demands

Why do the sexes perform differently on apical and basal parts of the alga? A straightforward physiological explanation would be that sexes differ in their qualitative nutritional needs and that apical and basal parts differ in nutritional quality. The sexes of *I. baltica* differ at least in two respects that are likely to be important for nutritive requirements and energy allocation. Firstly, size dimorphism develops during autumn, at the time of our experiments (Strong and Daborn 1979, Tuomi et al. 1988). Thus, the growth rate of males is higher than that of females. Secondly, ovary development of *Idotea* females starts at instars several stages before oviposition. In a closely related species, *I. pelagica*, which has a similar life-cycle, ovary development starts within two months after the birth in July and one fifth of the final oocyte diameter develops by the end of the year (Sheader 1977). Thus, females in our experiment were most probably provisioning resources for the developing ovaries. Crustacean ovaries contain lots of lipids (e.g. Clarke et al. 1985) suggesting that females either allocate the energy content of the assimilated food differently than males or have a dissimilar diet, or both.

Different nutritional needs for growth and reproduction of the sexes may explain their different performance on apical and basal parts if critical nutrients are unevenly distributed within the alga. It is possible that basal parts contain some nutrients that females can readily use for their needs but which males do not need or cannot utilize. However, our data implicate that physiological demands alone may not explain the feeding patterns of the sexes in variable conditions.

Ecological constraints on optimal feeding

The evolution of feeding preferences and assimilation efficiency of a certain type of food is complicated by constraints on optimal feeding. For a marine mesograzer the most obvious is predation risk (e.g. Petraitis 1987, Hay et al. 1989, Duffy and Hay 1991, 1994, Trowbridge 1994, Stachowicz and Hay 1999). When predation mortality is a major fitness component, host and diet selection may be subordinate to habitat selec-
tion, even at a cost to foraging (e.g. Nicotri 1980, Bednekoff 1996, Arrontes 1999). Such risk-sensitive feeding behavior is commonly found in empirical studies; under increased predation risk feeding may be suppressed (Angradi 1992, Bishop and Brown 1992, Vadas et al. 1994) or a habitat shift to safer habitats may occur (Pierce 1988, Horat and Semlitsch 1994, Turner 1997).

In *I. baltica*, different physiological demands cannot sufficiently explain why the pattern of food consumption in the experiment with whole bushes, i.e. with the natural habitat, differed from that of the feeding preference test with small pieces of algae in the laboratory. In the experiment with whole bushes, females consumed more basal part than in the preference test suggesting that habitat selection dominated feeding preferences. In earlier experiments where *I. baltica* females were found to prefer old thallus as food, the food preference was suggested to be similarly subordinate to habitat choices (Merilaita and Jormalainen 2000).

*I. baltica* is preyed on by numerous species of visually orienting fishes (Salemaa 1978) and its population density may be strongly regulated by predation. The importance of predation risk on microhabitat choice behavior of this species is obvious: there is a general preference of old, dark, basal parts of *Fucus* as a substrate (Merilaita and Jormalainen 1997). This preference for dark substrates remains even on artificial backgrounds, and it is stronger during daylight than during the dark hours further emphasizing the adaptive function of habitat choice against predation risk from visually searching predators (Merilaita and Jormalainen 2000). Consequently, habitat preference for basal parts is in clear contrast with the apical part being better food. In our grazing experiment with whole bushes, we found that basal parts were readily consumed and that females even preferred those to apical parts. Furthermore, in the field the basal parts of *F. vesiculosus* are commonly found much more heavily grazed than the apical fronds (Salemaa 1987). This suggests that the feeding pattern of *I. baltica*, in general, is suboptimal and that these animals are adapted to trade off growth for predation avoidance by feeding on basal parts of the alga. Actual presence of predators in the field may further hinder utilization of apical tips if *Idotea* can behaviorally adjust to ambient predator presence.

The sexes of *I. baltica* differ in their microhabitat preferences (Jormalainen and Tuomi 1989, Merilaita and Jormalainen 1997, 2000). In addition to the general preference for old parts as microhabitat, females prefer the old parts more strongly than males. Accordingly, females are found on apical parts more often than males. Merilaita and Jormalainen (1997, 2000) suggested that the sexual difference in microhabitat choice results from the different reproductive strategies of the sexes: Males have a more risk-prone feeding strategy than females because size is crucial for their mating

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>df</th>
<th>Food consumption</th>
<th>Growth rate</th>
<th>Growth</th>
<th>Intermolt duration</th>
<th>Production efficiency</th>
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<tbody>
<tr>
<td>Sex</td>
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<td>0.562</td>
<td>0.05</td>
<td>0.82</td>
<td>3.545</td>
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<tr>
<td>Part</td>
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<td>439.5</td>
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<td>8.65</td>
<td>15.78</td>
<td>2.38</td>
</tr>
<tr>
<td>Sex × Part</td>
<td>0</td>
<td>53.31</td>
<td>4.84</td>
<td>4.58</td>
<td>5.136</td>
<td>2.04</td>
</tr>
<tr>
<td>Error</td>
<td>11</td>
<td>1,100</td>
<td>1.435</td>
<td>1.62</td>
<td>1.423</td>
<td>0.49</td>
</tr>
</tbody>
</table>

Table 3. Test statistics of the ANCOVA for differences between sexes and between groups reared on different parts (apical or basal) of the alga. Initial weight of an animal was used as a covariate. Data shown in Fig. 3.
success. Females, on the other hand, may do best by decreasing predation risk by choosing less exposed microhabitats and decreasing mobility. Although their fecundity increases with size, size, as such, may be less important for the fitness of females than for males. A small male may end up with no matings at all, while all females probably get their eggs fertilized.

Our data support the hypothesis that food utilization patterns of the sexes are co-adapted with the general differences in reproductive strategies. Females may have adapted to utilize the parts of Fucus that offer good protection better than males; this would demand an enhanced capability of the digestive system to handle harmful compounds, like phlorotannins, concentrations of which are higher in basal parts of F. vesiculosus (Tuomi et al. 1989, unpublished data by the authors). Males, in turn, may be unable to handle phlorotannins and keep a high growth rate simultaneously.

**Evolution of host plant utilization patterns**

An interesting evolutionary question is whether feeding preferences and the capabilities of the digestive system of a herbivore evolve purely within the plant-herbivore interaction, or, can upper trophic levels act as a selective agent modifying these traits? Environmental constraints on optimal feeding may be important factors especially in those plant-herbivore systems in which predation has a prominent role in regulating herbivore populations. For example, natural enemies may be a major selective agent for specialization (Bernays and Graham 1988). In small-sized marine herbivores habitat and food are closely tied. Their specialization to feeding on chemically well-defended species of algae, which at the same time offer protection against fish predation, has been attributed to selection from upper trophic levels (Hay et al. 1989, 1990, Duffy and Hay 1991).

In our case, the basal parts of the alga are generally lower quality food for I. baltica. However, predation risk may force them to use the basal, more sheltered parts of F. vesiculosus as a habitat, and also as a food resource. Thus, predation may regulate population dynamics of I. baltica not only by direct removal of individuals but also by decreasing growth rate of the survivors by directing grazing to less profitable parts. In general, risk sensitivity of foraging may spread grazing pressure away from the exposed, apical parts to the more sheltered parts. Within-plant grazing patterns, in turn, are supposed to act as selective agents for allocation of defenses between plant parts (Rhoades 1979, Steinberg 1984).

Sexual segregation of feeding preferences and differences in the capability to utilize various plant parts further complicate plant-herbivore coevolution. If the sexes specialize to feed on different parts of the plant the situation for the plant mimics multiple herbivore species feeding on the same host (e.g. Hougen-Eitzman and Rausher 1994, Pilson 1996). Specific counter-adaptations of the plant are less likely to arise because they are less efficient in decreasing grazing. The strongest allocation to defense should evolve against the sex having the more harmful effect on plant fitness, but it may be inefficient against the other sex. Therefore, feeding differences between sexes of a herbivore favor more general defenses, and shift the coevolutionary relationship between the plant and animal, if such exists, from a specific to diffuse one (cf. Janzen 1980, Futuyma 1998).

Current theory of plant-herbivore interactions, apart from coevolutionary considerations and optimal defense models, focuses mainly on physiological responses of plants to environmental variation and consequent direct effects on herbivore fitness. A more comprehensive herbivore perspective has been much less emphasized. No general theory formalizing the mechanisms how feeding behavior and ingested plant biomass translate to herbivore fitness exists. Within- and between-plant utilization patterns, risk sensitivity of foraging, and sexual differences in reproductive allocation and resource acquisition of herbivores are crucial components of such a theory.

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