

'Co-consumption' and 'protective coating': two new proposed effects of epiphytes on their macroalgal hosts in mesograzer-epiphyte-host interactions

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ABSTRACT: Multiple-choice feeding experiments were performed with the isopod *Idotea granulosa* and the amphipod *Gammarus locusta* as consumers. In a first experiment, 2 different types of tissues of the brown seaweed *Fucus vesiculosus* and its main macroepiphytes, *Ulva lactuca* and *Elachista fucicola*, were offered. *I. granulosa* rejected apices of *F. vesiculosus* and preferred *E. fucicola*, while *G. locusta* clearly preferred *F. vesiculosus* tissue, especially the meristematic apices. In a second experiment, *F. vesiculosus* tissue with and without *E. fucicola* was offered together. For *I. granulosa*, the consumption of *F. vesiculosus* was enhanced by the presence of the epiphyte, while for *G. locusta* there was no difference in consumed *F. vesiculosus* mass. *G. locusta*, however, showed behavioural rejection of *E. fucicola*, and thus, the epiphyte acted as 'protective coating'. We conclude that host (*F. vesiculosus*) tissue could be 'co-consumed' by mesograzers (*I. granulosa*) that were attracted by the presence of epiphytes and that these epiphytes therefore may have a 2-fold negative effect on the host (i.e. competition for light, nutrients etc. and attraction of consumers). 'Co-consumption' and 'protective coating' add 2 more facets to the very variable and case-dependent interrelationships of mesograzer-epiphyte-host systems; their relevance in nature, however, remains to be demonstrated.

KEY WORDS: Herbivory · Feeding preference · *Fucus* · Crustacean grazers · Macroepiphytes · Multiple choice

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INTRODUCTION

The interactions between mesograzers (sensu Hay et al. 1987, Brawley 1992) and marine vegetation have received considerable attention during the last 2 decades (see e.g. reviews by Jernakoff et al. 1996, Arrontes 1999 and references therein). Grazing can be a major organizing force for littoral seaweed communities (e.g. Southward & Southward 1978, Lubchenco 1982, 1983, Petraitis 1987, Williams 1990a, Worm & Chapman 1998), but interaction patterns can be complicated by epiphytic macroalgae growing on host seaweeds (D'Antonio 1985, Pavia et al. 1999) or seagrasses

(Williams & Ruckelshaus 1993, reviews, e.g., by Orth & van Montfrans 1984, Mazzalla et al. 1992, Jernakoff et al. 1996). Macroepiphytes have increased in abundance on many marine shores due to anthropogenic eutrophication (Rönnberg et al. 1992, Philippart 1995, Wear et al. 1999). Epiphytes are mainly believed to have a detrimental influence on the host's fitness because of competition for light (Neckles et al. 1993, Short et al. 1995, Cebrian et al. 1999) and for CO₂ (Sand-Jensen 1977, Sand-Jensen et al. 1985) or by enhancing drag (D'Antonio 1985) and decreasing the reproductive output of the host (Orth & van Montfrans 1984, D'Antonio 1985). While hosts are commonly thick, slow-growing and long-lived perennial macrophytes with a low surface:volume ratio, macroepiphytes generally have a finer structure, higher surface:

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volume ratio, faster growth (Nielsen & Sand-Jensen 1990) and higher nutrient uptake (Hein et al. 1995, Pedersen & Borum 1997).

Although most mesograzers can live on a whole array of marine algae, many reveal clear preferences when offered a choice of food types (Nicotri 1980, Watson & Norton 1985, Schaffelke et al. 1995, Pavia et al. 1999, van Alstyne et al. 1999). No uniform patterns have, however, emerged concerning large algal groups as food (e.g. browns, reds, greens) or taxonomic units of mesograzers (e.g. isopods, amphipods, snails). Even mesograzers of the same genus may have very different preferences (Salemaa 1987, Norton et al. 1990, Williams 1990b). Macroepiphytes are often preferred as food over the host plants, and mesograzing has therefore been assessed as being beneficial to the latter (Brawley & Adey 1981, D'Antonio 1985, Brawley & Fei 1987, Philippart 1995), but also the host itself may be consumed (Salemaa 1987, Poore 1994, Viejo 1999). Different mesograzers may affect their food algae synergistically (Viejo & Arrontes 1992). When fucoids are the basibiont, phlorotannins may act as chemical defense to grazing, but the concentrations of phlorotannins seem to be very variable among fucoid species (Denton & Chapman 1991), among different age classes (Denton et al. 1990), and among seaweed tissues (Steinberg 1984, Poore 1994) of the same species. Moreover chemical defense in seaweeds may be induced by previous grazing (van Alstyne 1988, Yates & Peckol 1993, Peckol et al. 1996). The food choice of many mesograzers seems to be a combination of food and habitat preferences (Nicotri 1980, Buschmann 1990, Boström & Mattila 1999). Macroepiphytes often increase the substrate complexity (Hacker & Steneck 1990, Martin-Smith 1993, Gee & Warwick 1994) and, thus, may host a more diverse array of grazer species (Gunnill 1982, Jacobi & Langevin 1996), providing them with shelter from wave action (Salemaa 1986), desiccation and predation (Stoner 1985, Boström & Mattila 1999).

In another study that focussed on the influence of nutrient level on epiphytes of *Fucus vesiculosus* and the shading effects of the epiphytes on the host, we noticed that overgrown *F. vesiculosus* plants, accessible only to swimming animals, displayed more bite marks than initially clean plants (Engelbert unpubl. data). This observation initiated the present study that aims to test whether the most abundant swimming mesograzers, the isopod *Idotea granulosa* and the amphipod *Gammarus locusta*, consume *F. vesiculosus* tissue preferentially when overgrown by its most abundant macroepiphytes. This would imply that epiphytes, in addition to their known detrimental effects, further negatively influence the host by attracting its consumers.

MATERIALS AND METHODS

Preference between *Fucus vesiculosus* and its main epiphytes. Experiments were performed during July 1999 at the field station of the Norwegian Institute for Water Research (NIVA) near Drøbak, Norway, located near the Drøbak Sound of the Oslo Fjord (59° 38' N, 10° 40' E). Since no constant-temperature chambers were available, experiments were carried out inside a laboratory. A light:dark cycle of 16:8 h with constant low light of the ceiling lighting ($4 \mu\text{mol m}^{-2} \text{s}^{-1}$) was used. Temperature ranged from 24°C (day) to 21°C (night). Small aquaria (11 × 17 × 11 cm) were filled with 300 ml of filtered seawater. Specimens of *Idotea granulosa* were sampled from *Fucus vesiculosus* in the Oslo Fjord, while *Gammarus locusta* was sampled from mesocosm basins (basic mesocosm design described in Bakke 1990 and in Bokn et al. 1993). To avoid stress and mortality of the grazers, they were not weighed before the experiments, but we tried to obtain a representative assortment of the size classes that predominated in the Fjord and in the mesocosms (ca 10 mm for both species), respectively, excluding very big and very small individuals. Pieces of macroalgae were used as food items. Several items of 1 type were offered per aquarium. We attempted to offer similar masses of all food types, which led to different numbers of items for different species in the first experiment. Macroalgal pieces were blotted between several layers of paper towels and their initial fresh weight was measured to the nearest 0.1 mg.

In the first experiment, 6 tips of *Fucus vesiculosus*, 7 mid parts of *F. vesiculosus*, 20 tufts of *Elachista fucicola* (obtained as epiphyte from *F. vesiculosus*) and 12 pieces of 1 to 2 cm² of *Ulva lactuca* were offered together to 20 individuals of *Gammarus locusta* (mean blotted fresh weight = 0.31 ± 0.04 g) or to 15 individuals of *Idotea granulosa* (0.30 ± 0.03 g), respectively, or kept without grazers as controls. The mid parts of *F. vesiculosus* were 1 cm sections of whole branches taken between 5 and 10 cm from the distal end (including midrib, but avoiding bladders). Care was taken to offer *F. vesiculosus* without any visible epiphytes. Of each algal food type, ca 0.2 g blotted fresh weight were offered per aquarium. Algal units were randomly distributed in the aquaria before the grazers were added. Aquaria were then arranged randomly, and after 1 d were randomly re-arranged. We used 6 aquaria with *I. granulosa*, 6 with *G. locusta*, and 6 without any grazers as control for autogenic changes. From 08:00 h to midnight, aquaria were checked at least every second hour for dead grazers that were replaced by new ones of similar size. The experiment was started at 16:00 h and terminated after 32 h at 08:00 h when *G. locusta* obviously had eaten half of the mass of *F. vesiculosus*

tips in 1 container. Since the control served for both grazer species, the whole experiment was terminated. Grazers were sampled from the basins, and their numbers and total (per aquarium) fresh weight was measured after letting them crawl over paper towels. Food items were separated by type and their final blotted fresh weight was measured.

Preference among *Fucus vesiculosus* with and without *Elachista fucicola*. The second experiment was performed with the same aquaria under the same conditions as described above. Here, 8 discs, each with a diameter of 1 cm and obtained from the mid part of *Fucus vesiculosus* (including midrib, but avoiding bladders) on which *Elachista fucicola* tufts grew, were offered together with 8 discs of the same thallus area but without visible epiphytes to *Idotea granulosa* or *Gammarus locusta*, respectively, or held under the same conditions as controls for autogenic changes. Starting numbers for *I. granulosa* and *G. locusta* were 19 (mean blotted freshweight 0.25 ± 0.03 g) and 15 (0.36 ± 0.02 g) individuals, respectively. Eight units per food type were used to obtain an even distribution of items in the containers and equal starting amounts of both *F. vesiculosus* types. We used discs instead of whole thalli to exclude habitat-choice effects from food preference. Furthermore, the initial mass of overgrown *F. vesiculosus* discs can only be estimated with uniform units (see below). This experiment was started at 13:00 h and terminated after 44 h at 09:00 h. At the termination of the experiment, for the *G. locusta* treatments *E. fucicola* was still distinctly visible on all discs that initially had *E. fucicola* as epiphyte, and separation of food types was therefore straightforward. In 3 aquaria of the *I. granulosa* treatments, *E. fucicola* had been grazed down completely from a few discs (≤ 3 out of 8 discs) that initially had epiphytes. In these cases, the respective number of discs was drawn randomly from the discs found without *E. fucicola* to obtain again 8 '*E. fucicola*' discs and 8 discs without *E. fucicola*. From *F. vesiculosus* discs with *E. fucicola*, the final blotted fresh weight was measured in union. Afterwards, *E. fucicola* tufts were carefully removed with pointed forceps and their fresh weight measured separately from that of the respective *F. vesiculosus* discs.

For clarity, hereafter *FONLY* will denote *Fucus vesiculosus* discs that were offered without *Elachista fucicola*, *FUC* will be the *F. vesiculosus* portion of the *F. vesiculosus* discs with *E. fucicola*, while *ELA* will indicate the *E. fucicola* portion. (*FUC+ELA*) will be the *F. vesiculosus* disc with its epiphyte *E. fucicola* weighed together, while *FUC+ELA* will be the sum of both portions weighed separately. These abbreviations will denote their total amount of fresh weight per experimental container, i.e. 8 discs in case of *FONLY* and *FUC*.

It is impossible to know the genuine initial masses of the separate components when *Fucus vesiculosus* overgrown by *E. fucicola* (*FUC+ELA*) is offered. The initial amount of *FUC* is, however, a necessary parameter if one wants to estimate the amount eaten for a comparison with *FONLY*. Although the true values for the consumption of *FUC* and *ELA* must remain unknown, and especially the initial amount of *ELA* was not controlled, for initial *FUC* an estimate exists, assuming that autogenic changes were as insignificant (see 'Results') in *FUC* as in *FONLY*, and that 8 discs of *FONLY* did initially not differ systematically from 8 discs of *FUC*. Assuming that autogenic changes can be neglected during experimental time for *Fucus* disc (see 'Results'), the best estimate for initial *FUC* is the average of all initial *FONLY* discs (0.4702 ± 0.0287 g) having similar areas. For each consumer container, the final amount of *FUC* was subtracted from this average to obtain an estimate of the eaten amount for *FUC*-discs ($FUC_{\text{eaten}} = FONLY_{\text{initial, average}} - FUC$). The eaten amount of *ELA*-tufts was then calculated by subtracting eaten *FUC* from eaten (*FUC+ELA*): $ELA_{\text{eaten}} = [(FUC+ELA)_{\text{initial}} - (FUC+ELA)_{\text{final}}] - FUC_{\text{eaten}}$.

Statistical analysis. Simultaneously offered food types are not statistically independent, and therefore univariate methods like ANOVA cannot be used to analyse this type of experiment (Hay et al. 1988, Peterson & Renaud 1989). However, in a succession of papers (Roa 1992, Manly 1993, Lockwood 1998), several multivariate methods have been developed in order to solve this problem. When controls for autogenic changes are necessary, as in the present study, the Yao method presented by Manly (1993) seems to be the best choice for the analysis of multiple-choice feeding preference experiments. As shown by Lockwood (1998), this method is, however, flawed by the variation in the total amount eaten among experimental containers, because absolute amounts consumed are used as data for the analysis. The method proposed by Lockwood to overcome this drawback, however, does not include controls for autogenic changes. Since autogenic changes could not be neglected in the first experiment with 4 food types, we offset the amounts eaten of each food type with the amounts of change in control containers in a random 'container by container' arrangement (as proposed by Manly 1993) before we applied Lockwood's test. Since the statistic T^2 is then dependent on the special random pairing, 4 different random pairings were used to get an idea of the variation in the results concerning the significance. Lockwood's method also provides significances for all pairwise comparisons of the proportional amount eaten of all food types. In addition, we applied Yao's test (Manly 1993) to confirm the results from the extended method after Lockwood (1998)

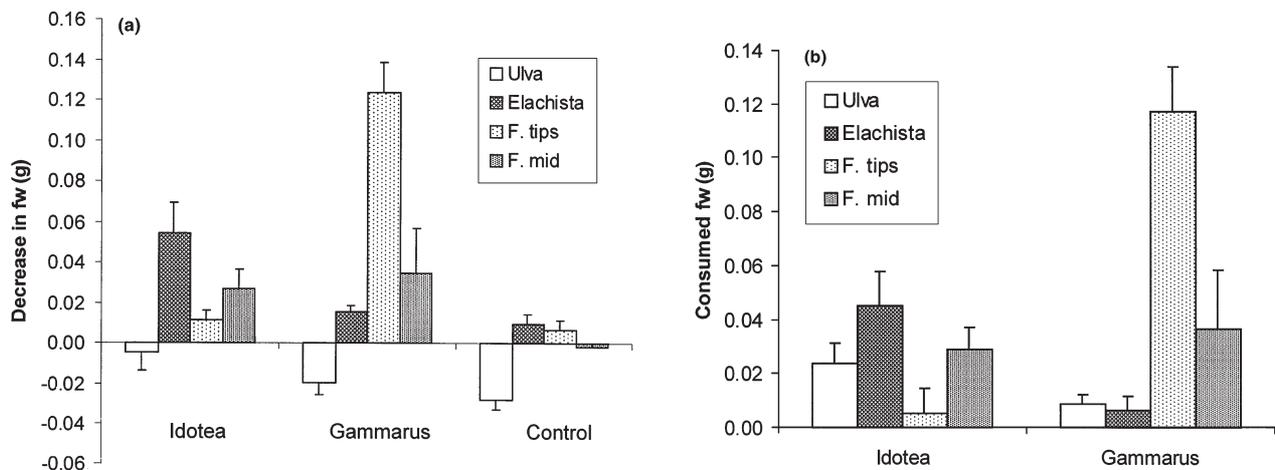


Fig. 1. *Ulva lactuca*, *Elachista fucicola*, *Fucus vesiculosus* apices and *F. vesiculosus* mid parts. (a) Decrease (means \pm SD, $n = 6$) in fresh weight (fw) of pieces offered in multiple-choice experiments to *Idotea granulosa* and *Gammarus locusta*, or held without grazers as controls for autogenic changes; negative values indicate growth. (b) Consumed fresh weight after grazer treatment data were offset with controls in random pairing

concerning the null hypothesis of equal consumption of all food types.

In the second experiment, the amount eaten from *Fucus vesiculosus* discs without *Elachista fucicola* (FONLY) was tested against the amount eaten from *Fucus* with *E. fucicola* in combination (FUC+ELA). Since there were only 2 food types and controls could be neglected (see 'Results'), a simple paired Student's *t*-test could be employed following recommendations of Peterson & Renaud (1989).

RESULTS

Preference among *Fucus vesiculosus* and its main epiphytes

In general, *Elachista fucicola* and *Fucus vesiculosus* were reduced in weight when exposed to grazers (Fig. 1a), while the mass of *Ulva lactuca* increased during the course of the experiment (negative values in Fig. 1a). Except for mid parts of *F. vesiculosus*, considerable autogenic changes occurred. The loss in *E. fucicola* control (and treatment) containers was partly due to disintegration of tufts from handling, but there was no such obvious reason for *F. vesiculosus* tips.

When data from the grazing treatments were offset with controls in random-container pairing, it became obvious that *Idotea granulosa* ate most of *Elachista fucicola*, but also consumed *Ulva lactuca* and mid parts of *Fucus vesiculosus* to some extent, while *F. vesiculosus* tips were hardly eaten (Fig. 1b). *Gammarus locusta*, in contrast, clearly preferred *F. vesiculosus*, especially the apices. It

should be noted that the error bars showing the standard deviation in Fig. 1b are those resulting from only one of $6! = 720$ possible ways to offset controls with treatments. When data were tested for validity of the null hypothesis (H_0) of equal consumption of all food types, both methods of analysis resulted in a highly significant ($p < 0.001$) rejection of this general H_0 , regardless of the random pairing with Lockwood's (1998) method (Table 1). The resulting T^2 , however, revealed considerable variation (i.e. in some cases $p \ll 0.001$). When all pairwise comparisons were performed, the pattern of significances was quite consistent among the 4 random pairings for *G. locusta*; *U. lactuca*, *E. fucicola* and *F. vesiculosus* mid parts were consumed significantly less than *F. vesiculosus* tips, while no significant differences could be detected among consumption of *U. lactuca*, *E. fucicola* and *F. vesiculosus* mid parts (Table 1b, cf. Fig. 1b). For *I. granulosa*, the significance of pairwise comparisons was more dependent on the special random pairing of treatments with controls. In 3 of 4 cases, *E. fucicola* was grazed significantly more than *F. vesiculosus* tips (i.e. comparison of the highest with the lowest mean amount eaten), in 2 of 4 cases, *F. vesiculosus* mid parts were grazed significantly more than *F. vesiculosus* tips, and in 1 of 4 pairings, *U. lactuca* was consumed significantly more than *F. vesiculosus* tips.

Preference among *Fucus vesiculosus* with and without *Elachista fucicola*

None of the food types was grazed to an extent where it became unavailable for the consumers. *Idotea*

granulosa removed a maximum of 8.8% of *FONLY* and 19.1% of (*FUC+ELA*) in single containers, while *Gammarus locusta* consumed a maximum of 29.9% of *FONLY* and of 19.7% of (*FUC+ELA*). Values for the other (5) replicates were mostly considerably below these maxima (Fig. 2a). The changes in biomass in the controls were negligible (<1% for each food type and in all containers) and controls were only used for estimations of *FUC* and *ELA* (see 'Materials and methods'). *I. granulosa* grazed significantly more (*FUC+ELA*) than *FONLY*, while *G. locusta* consumed a similar amount of *FUC+ELA* and *FONLY* (Fig. 2a, paired *t*-test: *I. granulosa*: $t = 4.08$, $p < 0.01$; *G. locusta*: $t = 1.14$, $p < 0.5$, control: $t = 1.71$, $p < 0.2$; $df = 5$). So far, however, it remains unclear whether the *FUC* or the *ELA* portion of (*FUC+ELA*) was consumed by the grazers. By using an average for the initial *FUC*, the variation of initial amounts is excluded from the data. Therefore, and because data are based on assumptions that are difficult to test, no effort was made to test differences statistically. The estimation of initial values of *FUC* and *ELA* is further complicated by a loss due to

Table 1. *Idotea granulosa* and *Gammarus locusta*. Analyses of multiple-choice feeding-preference experiments. Grazers were offered choice of *Ulva lactuca* (*Ulva*), *Elachista fucicola* (*Elach.*), *Fucus vesiculosus* tips (*F. tips*) and *F. vesiculosus* mid parts (*F. mid*). Null-hypothesis of equal consumption was tested with (a) Yao's test (Manly 1993), and (b) Hotelling's T^2 test on proportion data (Lockwood 1998). Analysis in (b) depends on random pairing of treatment containers with control containers. To evaluate this dependency, analyses were done with 4 different random pairings. T^2 is shown in the upper left corner together with p for general H_0 . Subtables show results of pairwise tests for significant differences after Lockwood (1998). These also differ with random pairing (ns = not significant; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$). For further explanations see 'Materials and methods'

(a)	R	f	F	df	p
<i>Idotea</i>	155.19	9.46	40.79	3, 7	***
<i>Gammarus</i>	432.73	6.10	96.93	3, 4	***

(b)	<i>Idotea</i>				<i>Gammarus</i>			
	<i>Ulva</i>	<i>Elach.</i>	<i>F. tips</i>		<i>Ulva</i>	<i>Elach.</i>	<i>F. tips</i>	
67.3 ***				535.9 ***				
<i>Elach.</i>	ns			<i>Elach.</i>	ns			
<i>F. tips</i>	ns	*		<i>F. tips</i>	***	***		
<i>F. mid</i>	ns	ns	ns	<i>F. mid</i>	ns	ns	*	
198.4 ***				3291.8 ***				
<i>Elach.</i>	ns			<i>Elach.</i>	ns			
<i>F. tips</i>	ns	ns		<i>F. tips</i>	***	**		
<i>F. mid</i>	ns	ns	**	<i>F. mid</i>	ns	ns	*	
119.1 ***				2182.2 ***				
<i>Elach.</i>	ns			<i>Elach.</i>	ns			
<i>F. tips</i>	ns	**		<i>F. tips</i>	***	***		
<i>F. mid</i>	ns	ns	ns	<i>F. mid</i>	ns	ns	*	
181.0 ***				653.8 ***				
<i>Elach.</i>	ns			<i>Elach.</i>	ns			
<i>F. tips</i>	*	**		<i>F. tips</i>	***	***		
<i>F. mid</i>	ns	ns	*	<i>F. mid</i>	ns	ns	*	

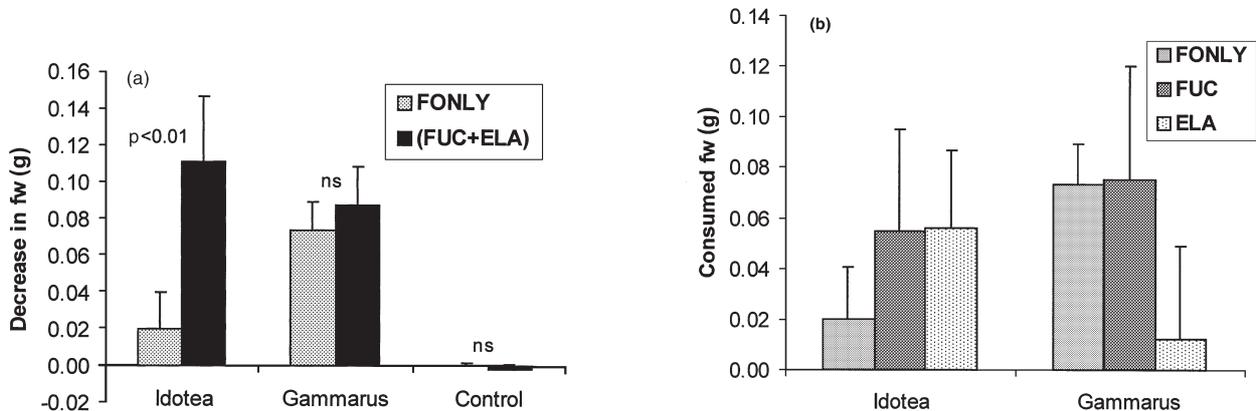


Fig. 2. *Fucus vesiculosus*. (a) Decrease (means \pm SD, $n = 6$) in fresh weight (fw) of *F. vesiculosus* discs with (*FUC+ELA*) or without (*FONLY*) *Elachista fucicola* as an epiphyte that had been offered in multiple choice to *Idotea granulosa* and *Gammarus locusta*, or that had been held without grazers as controls for autogenic changes; negative values indicate growth; results of paired Student's *t*-tests for differences between *FONLY* and (*FUC+ELA*) are shown. (b) Consumed fresh weight of *F. vesiculosus* discs with (*FUC*) or without (*FONLY*) *E. fucicola* as an epiphyte, and of the epiphyte (*ELA*)

evaporation during the separating procedure. On average, 3% of fresh weight biomass were lost. It has to be assumed that the *ELA* component contributed relatively more to this loss because of its higher surface:volume ratio, while it may have contributed absolutely less than *FUC* because of its lower absolute mass (final ratio *ELA:FUC* in controls = 1: 4.93). For all these reasons, data have to be taken as rough estimates. Estimates for *FUC* and *ELA* and measured values of *FONLY* in Fig. 2b show that *I. granulosa* ate more than twice as much *F. vesiculosus* with *Elachista fucicola* epiphytes (*FUC* compared with *FONLY*) and consumed about the same amount *E. fucicola* (*FUC* compared with *ELA*). For *G. locusta*, no difference could be seen between *F. vesiculosus* discs with (*FUC*) and without (*FONLY*) *E. fucicola*, and the epiphyte was only consumed to a very low extent.

DISCUSSION

Several studies have shown that mesograzers may have a beneficial effect on seagrasses (Howard 1986, Neckles et al. 1993, Williams & Ruckelshaus 1993, Philippart 1995, Nelson 1997) and on marine macroalgae (D'Antonio 1985, Duffy 1990) by removing epiphytes. In some studies, the epiphytes (sensu Wahl 1989) were the preferred food for the mesograzers (Brawley & Fei 1987), but in other cases the host itself was preferably consumed (Poore 1994). Another possibility is that mesograzers prefer the macroepiphytes, but switch to the host when the epiphytes have been eaten (Kangas et al. 1982) or when the mesograzers grew from juveniles to adults (Salemaa 1987). It is, however, also imaginable that, even under stable conditions of epiphyte supply, mesograzers that have been attracted by the epiphytes also consume the host when it is palatable, although to a lesser degree. The vicinity to the host leads therefore to its co-consumption.

In our first experiment, *Idotea granulosa* displayed a preference for the epiphytes and for older parts of *Fucus vesiculosus* over meristematic *F. vesiculosus* tissue. In the second experiment, *I. granulosa* significantly consumed more of *F. vesiculosus* and *Elachista fucicola* offered as a host-epiphyte system than of a clean host (*F. vesiculosus*). Estimates of the consumed mass of the components of the host-epiphyte system indicate that the consumption of *F. vesiculosus* tissue is considerably enhanced by the presence of the epiphyte. We propose to term this pattern 'co-consumption' and would like to emphasize that it is different from 'accidental' consumption when the host is eaten because the grazer cannot differentiate its grazing between epiphyte and host as, e.g., in case of the periwinkle *Littorina mariae* browsing the microflora from

F. serratus and ingesting also epidermal tissue of the host (Norton et al. 1990, Williams 1990a). D'Antonio (1985) also suggested that amphipods may damage the host while preying on the epiphytes.

Gammarus locusta distinctly preferred *Fucus vesiculosus* over the epiphytes in the first experiment. *G. locusta* should therefore have a potential deleterious effect on *F. vesiculosus*, and its effect could even be stronger at the population level, since the meristematic tissue was distinctly preferred to older tissue (see Poore 1994 for a similar case). In the second experiment, only the second most preferred food, older *F. vesiculosus* mid parts, was offered with or without the least-preferred *Elachista fucicola*. The hypothesis for the second experiment was, therefore, that discs with *E. fucicola* would be consumed to the same extent as discs without epiphytes or would even be rejected. This hypothesis was corroborated in 2 ways: both types of *F. vesiculosus* discs were eaten in similar amounts, and, in addition, *G. locusta* showed a distinct rejective feeding behaviour by consuming *F. vesiculosus* tissue only around the locations where *E. fucicola* tufts were attached. Thus, *E. fucicola* seems to act as protection from *G. locusta* grazing, at least as long as other *F. vesiculosus* tissue (not overgrown by *E. fucicola*) is available, as was the case in our experiment. It still remains to be tested whether the positive effect (defense against grazing) or the negative effects (competition for light and nutrients) of *E. fucicola* are more important in natural environments. *E. fucicola* can potentially settle on most thallus parts of *F. vesiculosus* (Russell 1988) and can cover its host quite densely (Karez pers. obs.). Thus, more generally, 'protective coating' may be another function of epiphytes for its host. Although we have added 2 additional facets (i.e. 'co-consumption' and 'protective coating') to the assortment of interrelations between epiphytes-hosts-mesograzers (e.g. Brawley 1992, Arrontes 1999), it must be remembered that our results were obtained from laboratory experiments which have to be interpreted cautiously when used to explain mechanisms in nature (Brawley 1992). By using pieces of algae rather than whole plants we tried, however, to exclude habitat-selection mechanisms that are often shown to act concomitantly with feeding preference of mesograzers (e.g. Nicotri 1980). Mesograzers seem to have deleterious effects on seaweed populations only when grazer densities are unnaturally high (Fralick et al. 1974, Kangas et al. 1982, Arrontes 1999), and normally *F. vesiculosus* populations can cope with grazing (Salemaa 1987). It remains therefore to be shown that the mechanism of co-consumption has relevance in nature and whether it was the underlying mechanism for the trend observed in our experiments where clean *F. vesiculosus* was obviously grazed less than *F. vesiculosus* with epiphytes. Perennial hosts, such as *F. vesiculosus*, suffer

increasingly from shading by phytoplankton and epiphytes on many anthropogenically eutrophicated coasts (Rönnerberg et al. 1992). Grazing may act as a counterbalance to increased growth of ephemeral algae (Neckles et al. 1993, Lotze et al. 1999, Worm et al. 1999). However, our results suggest that certain mesograzers may also enhance deleterious effects of epiphytes by co-consumption.

Our results show that generalizations for epiphyte-host-mesograzer interactions are hard to formulate (Nicotri 1980, Arrontes 1999). Although most mesograzers display significant preferences for certain algal species, they seem able to feed on several food types (e.g. Lubchenco 1978). The preference for different algae implies that the presence or absence of certain species of macroepiphytes will influence the choices and consumption of several or all mesograzers and, moreover, may influence them differently. Thus, the interaction pattern not only depends on the mesograzer considered, but also on the host and the specific set of macroepiphytes (e.g. van Alstyne et al. 1999). This is highlighted by the different preferences and potential influences on the host by the 2 mesoherbivore species in the present study, but becomes even more clear when our results are compared with those of Pavia et al. (1999). Pavia et al. conducted a very similar experiment on the western coast of Sweden, in which pieces of the 2 main macroepiphytes (*Ceramium nodulosum* and *Pilayella littoralis*) and meristematic and old tissues of a furoid host (*Ascophyllum nodosum*) were offered as multiple choice to the same grazer species as in our study. Pavia et al. also found a difference among the mesograzer preferences, but those, however, were the opposite to those in our study: large individuals of *Gammarus locusta* preferred macroepiphytes, while large *Idotea granulosa* preferred meristematic tips of *A. nodosum*. In concordance with our findings, 3 species of *I. granulosa* preferred older tissue over apices of *Fucus vesiculosus* in the study of Salemaa (1987), although this was least pronounced for *I. granulosa*. In neither Pavia et al.'s study nor the present study were the nutritional value or the content of deterring polyphenols in the tissues offered in the respective experiments measured, so no assessment can be made in this respect.

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