

NUTRIENT ENHANCEMENT INCREASES PERFORMANCE OF A MARINE HERBIVORE VIA QUALITY OF ITS FOOD ALGA

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Abstract. Herbivore performance and reproductive output are expected to covary with qualitative changes in the host plant. The availability of nutrients may be especially important for the quality of algae as food through its effect on both primary and secondary metabolism and within-plant variation. We evaluated the effect of the nutrient enrichment of the brown alga *Fucus vesiculosus* on the fecundity, mass gain, intermolt duration, and food consumption of females of the herbivorous isopod *Idotea baltica*. We reared the isopods on algae grown either under enhanced nutrient conditions or as controls for the entire duration of the intermolt preceding mating and oviposition. The herbivores fed on nutrient-treated algae achieved higher growth rates, consumed more food, and laid more and larger eggs than the controls. The nutrient treatment increased the amount of insoluble sugars and reduced both the total carbon content in the alga and the physical toughness of the thallus. On the other hand, the treatment had no effect on the amount of total nitrogen or phlorotannins in the algal tissue. This implies that the clear increase in herbivore performance and fecundity may be due to quantitative changes in the carbohydrate metabolism rather than to the lower content of feeding deterrents in the tissue of *F. vesiculosus*. We suggest that eutrophication may potentially improve the quality of *F. vesiculosus* for herbivores. The reproductive success, growth, and food consumption of *I. baltica* increase on algae maintained in a nutrient-rich environment; this is likely to be reflected in herbivore density and grazing pressure. This in turn may have potential ecological consequences for the maintenance of viable *F. vesiculosus* belts, thereby contributing to the structure of littoral algal assemblages in marine ecosystems.

Key words: brown algae; eutrophication; *Fucus vesiculosus*; herbivore fecundity; herbivory; *Idotea baltica*; isopod growth; isopods; marine herbivore; nutrients; performance; plant quality.

INTRODUCTION

Plants are capable of responding plastically to changing environmental conditions by changes in their nutrient intake, photosynthesis, and secondary metabolism (Bryant et al. 1983, Grime et al. 1986). The availability of nutrient resources, for instance, is reflected in the growth, nutrient contents, and defensive chemistry of plants (Herms and Mattson 1992). In addition to this environmental plasticity, both the primary and the secondary chemical composition of a plant changes with the growth-differentiation status of the tissues, causing within-plant variation in the quality of the plant for consumers (Tuomi et al. 1989, Denton et al. 1990, Herms and Mattson 1992, Cronin and Hay 1996a).

The amounts of nutrients, proteins, and energy compounds in the diet are often highly critical for the growth and reproductive success of herbivores (Boyd and Goodyear 1971, Pyke et al. 1977, Hughes 1980, Mattson 1980). Furthermore, an herbivore may have to cope with harmful feeding deterrents, which may be toxic or may reduce digestive efficiency (Stern et al. 1996). Thus the quality of the available plant material may play multiple roles in determining the growth and reproductive success of an herbivore. Variation in host

plant quality has been suggested to potentially affect the population dynamics of herbivores (Haukioja 1980, Rhoades 1985, Berryman 1996).

The resource-based plant-herbivore hypotheses, the carbon-nutrient balance hypothesis, and the growth differentiation hypothesis (Bryant et al. 1983, Herms and Mattson 1992, Tuomi 1992) predict that carbon-based plant defenses will be high under nutrient deficiency and will decrease with improving nutrient resources. This is because nutrient limitation depresses growth; photosynthetic carbon can then be allocated to carbon-based secondary compounds at low or no cost. These compounds include polyphenolics, which are often considered defensive against herbivores in both terrestrial and marine environments (e.g., Geiselman and McConnell 1981, Steinberg 1988, Steinberg and Van Altena 1992, Yates and Peckol 1993, Targett and Arnold 1998). In addition to changes in secondary chemistry, active plant growth due to improved nutrient resources is expected to increase its nutritive value for herbivores (Cockfield 1988, Price 1991, Cronin and Hay 1996a), which is also empirically confirmed in several terrestrial plants and their insect herbivores (Ruohomäki et al. 1996, Mutikainen et al. 2000 and references therein).

The eutrophication of coastal waters enhances nutrient resources for littoral algae. Therefore, if algal quality reflects the abundance of resources, eutrophication

cation may increase the nutritive value of algae for herbivores in terms of either reduced feeding-deterrent compounds or enhanced amounts of primary chemistry products such as carbohydrates and proteins. Many studies have shown that nutrient availability has the potential to affect algal quality. In most cases, an abundance of resources has reduced the amount of defensive secondary compounds of the plant (e.g., Coley et al. 1985, Ilvessalo and Tuomi 1989, Yates and Peckol 1993, Arnold et al. 1995, Cronin and Hay 1996b, Peckol et al. 1996).

The quality of algae as a food source for herbivores has usually been studied by feeding-preference tests (e.g., Nicotri 1980, Geiselman and McConnell 1981, Steinberg 1985, 1988, Van Alstyne 1988, Arrontes 1990, Renaud et al. 1990, Denton and Chapman 1991, Duffy and Hay 1991, Rosenthal and Berenbaum 1992, Fleury et al. 1994, Hay 1996, Pavia et al. 1997). Although feeding preferences and performance may covary in some generalist herbivores and their hosts (Poore and Steinberg 1999), plain preference tests do not generally allow conclusions as to the effect of quality variation on herbivore fitness. There have been only a few studies of the relationship between food quality and the performance and reproductive output of herbivores in marine communities (Duffy and Hay 1991, Winter and Estes 1992, Kennish 1997, Poore and Steinberg 1999, Cruz-Rivera and Hay 2000a, b). These studies show that variations in between-species algal quality may potentially affect the population parameters of the herbivores. Yet there have been no earlier studies examining the effect of environmentally induced plasticity in within-species algal quality on herbivore fitness. Such information would be valuable when (1) evaluating the effects of eutrophication on consumer trophic levels and consequent changes in grazing pressure and (2) assessing the importance of bottom-up vs. top-down mechanisms controlling mesoherbivore populations.

In this study, we experimentally test the effects of nutrient increment on the quality of *Fucus vesiculosus* L. (bladder wrack) for a crustacean mesograzer *Idotea baltica* Pallas. We focus on the following questions: First, does nutrient increment affect the quality of *F. vesiculosus* in terms of chemical characteristics? Second, do these environmentally induced changes in algal quality affect the growth and fecundity of its major herbivore? We discuss the potential bottom-up influence of eutrophication on the population dynamics and abundance of the herbivore *I. baltica* and its ecological consequences on the littoral community of the shallow marine environment.

MATERIAL AND METHODS

Study organisms

Idotea baltica is a widely distributed herbivorous isopod crustacean occurring in the littoral zone of the

brackish Baltic Sea. As an adult it feeds mainly on *Fucus vesiculosus* (Salemaa 1987, Schaffelke et al. 1995, Jormalainen et al. 2001a). Grazing pressure on *F. vesiculosus* by this herbivore is generally high, as judged by grazing marks (Salemaa 1987; A. Hemmi and V. Jormalainen, *personal observations*). The breeding period of *I. baltica* starts in late May to early June, when females are fertilized during their parturial molt. After fertilization, the females lay their eggs in a ventral marsupium, where embryos are hatched until the release of juveniles in July (Haahtela 1978, Strong and Daborn 1979). Most of the animals die during the autumn after their first reproductive period, thus reaching an age in the northern Baltic of ~13–15 mo (Salemaa 1979).

F. vesiculosus (Phaeophyceae, Fucales) is distributed along the western and eastern sides of the Atlantic Ocean (Lüning 1990). In our study area in the Archipelago Sea, southwest Finland, it is a dominant large rockweed of the littoral community. The young, growing apical thallus is light in color and less tough than the older part of the thallus, which is darker and often covered with epiphytes and epifauna. Apical tissues are also better in their nutritive value and contain less phlorotannins compared to the basal parts (Ilvessalo and Tuomi 1989, Tuomi et al. 1989, Jormalainen et al. 2001b). Therefore, within-plant differences are expected in the quality of food for herbivores (Jormalainen et al. 2001b) and in the capability of a plant to respond to changes in resource availability. Some of the apical tips of the alga develop into reproductive organs, receptacles, which mature during spring and early summer. The reproductive fronds decay during late summer; in this experiment we therefore used only vegetative fronds.

Herbivore performance on algae of varying quality

Manipulation of F. vesiculosus.—The algal bushes received nutrient treatment for 7–13 d before pieces were cut and given to the herbivores. Fresh algae for the treatment were collected weekly throughout the experiment from the same growing site in the vicinity of the Archipelago Research Institute of the University of Turku (60°14' N, 21°40' E) in late April 1999. In order to lessen possible variation in algal quality between different genotypes, individual bushes of *F. vesiculosus* were divided in half; the halves were placed in 27-L tanks, four each for nutrient treatment and for controls. Thus both treatments contained algae of the same four genotypes, from which the pieces were haphazardly cut for the feeding assays. The tanks were situated outdoors in natural light conditions and were cooled with continuous water flow-through outside the tank wall. The water was changed and fresh inorganic nutrients (40 µg/L nitrate NO₃-N, 120 µg/L ammonia NH₄-N, and 30 µg/L phosphate PO₄-P), in a form readily available to algae (Hanisak 1983, Hurd and Dring 1990), were added at 3-d intervals.

TABLE 1. (A) Nutrient concentration in water (in micrograms per liter) taken at three distinct times during the treatment of *Fucus vesiculosus* and (B) statistics from one-way ANOVA of differences between nutrient-enhanced (Nutrient +) and control water.

A) Mean nutrient concentrations			
Nutrient	Treatment	Means \pm 1 SD	
Total nitrogen	Control	347 \pm 25	
	Nutrient +	473 \pm 85	
NO ₂ -N, NO ₃ -N	Control	22.5 \pm 11.5	
	Nutrient +	65.0 \pm 6.0	
NH ₄ -N	Control	9.6 \pm 7.6	
	Nutrient +	97 \pm 3.1	
PO ₄ -P	Control	5.6 \pm 1.2	
	Nutrient +	48 \pm 1.2	
B) ANOVA			
Source	df	F	P
Total nitrogen	Treatment	6.12	0.07
	Error		
NO ₂ -N, NO ₃ -N	Treatment	31.4	<0.01
	Error		
NH ₄ -N	Treatment	336	<0.001
	Error		
PH ₄ -P	Treatment	1985	<0.01
	Error		

Note: For all means, $n = 3$.

Water samples from the tanks were taken (randomly in relation to nutrient addition) on three separate occasions during the experiment to verify the ambient nutrient levels during the manipulation period. Seawater was taken for all the experiments from the pelagic area, outside the direct influence of land-originating nutrients, from a depth of 6 m. Nutrients were analyzed by the standardized methods used by the Finnish National Board of Waters (Koroleff 1976, 1979). The nutrient concentrations and one-way ANOVAs are shown in Table 1. The nutrient levels in the nutrient increment treatment were generally well within the limits occurring naturally in eutrophicated areas in the study area. Nitrate-N and phosphate-P in the control water source may periodically reach the values measured in the increment treatment, while the level of ammonium-N remains at a lower level.

Determination of intermolt duration, growth, and fecundity of I. baltica.—Animals for the laboratory experiments were collected from the same growing site as the algae. Until the beginning of the experiment they were maintained individually in 1-L containers with continuous aeration, with a stone as a habitat and under a light : dark rhythm of 17 h : 7 h at 12–13°C. They were fed with both apical and basal parts of *F. vesiculosus*. The animals were checked daily to detect the occurrence of molt. After an animal had molted, its intermolt stage was determined from the development stage of the mar-

supial plates (cf. Haahtela 1978). We used only females of *I. baltica* (1) because we were especially interested in the effects of food quality on the fecundity of this herbivore and (2) because the life history stage, in terms of intermolt rank, could be determined and synchronized at the beginning of the experiment.

Right after a female had completed the molt preceding the intermolt stage before the parturial molt, it was weighed (to the nearest 1 mg) before beginning the experimental procedures. In the standardized weighing procedure, the animal was gently dried between two paper tissues for 5 s, weighed, put back in water for ~10 s, dried, and reweighed. The mean of these two weighings was used in the analyses. The initial fresh mass of the females was 58.5 \pm 14.4 mg and their length 15.3 \pm 1.5 mm (mean \pm 1 SD, $n = 84$). The first replicate started on 12 May, and the measurements were repeated thereafter on successive days until all the animals had molted.

The animals were randomly assigned to four different feeding groups in a 2 \times 2 factorial experiment for their entire intermolt: they were fed with either the apical or the basal part of *F. vesiculosus*, which were premanipulated either in nutrient-treated or control tanks. The apical part consisted of the most recent 2 cm of the vegetative tip; the basal part of corresponding size was cut from a location ~6–7 cm downward from the tip of the thallus. The initial fresh mass of the algal pieces was 252 \pm 43 mg (mean \pm 1 SD, $n = 82$). The test tanks used were 1-L containers; water and algae were changed at 7-d intervals. The test containers were kept at 12–13°C, under a 17 h : 7 h light : dark rhythm. Illumination was supplied by four 400-W sodium vapor lamps (Sylvania, Danvers, Massachusetts, USA) to provide photosynthetic light throughout the course of the experiment. In the nutrient increment group, the test tank always received nutrient-enhanced water, at a concentration half of that used in the prior manipulation of algae, to prevent the algal pieces from changing in quality during the 7-d experiment interval.

Food consumption was measured as the loss of fresh mass of the algal pieces. We corrected this for the autogenic change in fresh mass (see Table 5), which was obtained from control containers run simultaneously and under equivalent conditions but without herbivores. The corrected consumption was calculated as the loss of fresh mass in the treatment piece of the alga (E) minus the change (increase) in fresh mass of a randomly chosen control piece (C) of a corresponding part and nutrient treatment (Roa 1992):

$$(E_{\text{initial}} - E_{\text{final}}) - (C_{\text{initial}} - C_{\text{final}}) = \text{food consumption.}$$

Food consumption, in terms of dry masses, was calculated using regression coefficients obtained from both fresh mass (FM) and dry mass (DM; 24 h in 60°C) of algae in control containers. The DM/FM ratio differed between the apical and the basal parts of the alga, but was not affected by nutrient treatment (see Table

5). The regression equation for the apical part was $DM = 0.0030 + 0.1738 \times FM$ ($df = 45$, $R^2 = 0.74$, $F = 129$, $P < 0.001$) and for the basal part $DM = -0.0066 + 0.3054 \times FM$ ($df = 45$, $R^2 = 0.88$, $F = 344$, $P < 0.001$).

The toughness of the algal tissue was measured using an apparatus (Mecmesin portable force indicator; Mecmesin, Slinfold, West Sussex, UK) that measures the force (in Newtons) needed to punch a rod 3 mm in diameter through the thallus.

The experiment was terminated when the parturial molt had been detected, after which the animal was weighed again the same way as in the beginning and returned to its container. One randomly chosen male *I. baltica* was given to each female to provide fertilization of eggs and induce egg laying (Borowsky 1987). The animals copulated within a few hours and the females laid their eggs within 12 h after copulation. To measure the fecundity of the females, their eggs were carefully removed by injecting distilled water into the marsupium. The eggs were gently soaked with distilled water to remove the salty seawater; they were then counted and the total mass of eggs was dry-weighed in a pre-weighed test tube (24 h at 60°C). After egg removal, the animal was dry-weighed (24 h in 60°C). The initial dry mass of the animal (DM_a) was calculated using a regression coefficient obtained from the final fresh mass (FM_a) and dry mass (animal mass + egg mass): $DM_a = 0.2018 \times FM_a$ ($df = 63$, $R^2 = 0.98$, $F = 3685$, $P < 0.001$). The rate of mass gain per day was calculated as the increase in dry mass divided by the intermolt duration. Production efficiency was calculated as the percentage of dry mass gain of the algal dry material consumed during the intermolt.

Testing the direct effect of water-borne nutrients on *I. baltica*

To rule out the possibility that water-borne nutrients would, instead of modifying the quality of the food alga, directly affect the performance of *I. baltica*, we ran an experiment testing the effect of nutrient-enriched water on herbivores in similar conditions as the previous experiment. The animals were reared in either nutrient enriched or control water and fed artificial food made of freeze-dried and finely ground *F. vesiculosus* and aquarium fish food (Wardley's Shrimp Pellets, Hartz Mountain Corporation, Secaucus, New Jersey, USA) in a ratio of 3 : 2, incorporated into agar disks in the dry mass/fresh mass ratio equal to *F. vesiculosus* apices (see Table 5). Artificial food was used to prevent changes in the quality of food during the 7-d interval.

First, a prospective power analysis (Thomas and Krebs 1997) was conducted to calculate the required number of replicates to detect a difference in the magnitude observed in the experiment with natural algae in intermolt duration between means of nutrient treated and control animals with the observed error variance and at the power of 87%. As a result, the experiment

TABLE 2. (A) Mean values of three performance indicators of *Idotea baltica* and (B) statistics from one-way ANCOVA to test the direct effects of enhanced nutrient levels (Nutrient +) on performance of *I. baltica*.

A) Mean values			
Variable	Treatment	Mean \pm 1 SE	
Intermolt duration (d)	Control	31.8 \pm 1.4	
	Nutrient +	32.2 \pm 1.4	
Mass gain (mg)	Control	3.74 \pm 0.23	
	Nutrient +	3.18 \pm 0.23	
Mass gain rate (mg/d)	Control	0.13 \pm 0.01	
	Nutrient +	0.10 \pm 0.01	
B) ANCOVA			
Source	df	F	P
Intermolt duration			
Treatment	1	0.04	0.85
Initial mass	1	0.02	0.90
Error	77		
Mass gain			
Treatment	1	1.82	0.18
Initial mass	1	11.65	0.001
Error	77		
Mass gain rate			
Treatment	1	2.71	0.10
Initial mass	1	5.6	0.02
Error	77		

Note: For all means, $n = 40$.

was performed with 40 animals at $\alpha = 0.05$ level in each treatment. Results were analyzed by a one-way ANCOVA, with nutrient increment as a fixed factor and the initial size of an herbivore as a covariate. Water-borne nutrients had no direct effect on intermolt duration, mass gain, or growth rate (Table 2). Because of the high statistical power of the test, we can conclude that nutrients in the water do not directly affect performance of *I. baltica* and that any differences found between animals reared on nutrient treated or control algae must be mediated by the algal quality.

Chemical analyses

The total content of phenolics (hereafter called phlorotannins; Van Alstyne 1995) in the algae was measured by the Folin-Ciocalteu technique (modified by Nurmi et al. 1996). Phloroglucinol was used as a standard. Total contents of nitrogen and carbon were determined as a percentage of dry material by a LECO CHN-900 carbon-hydrogen-nitrogen analyzer (LECO, St. Joseph, Michigan, USA). The amounts of soluble and insoluble sugars (in terms of absorbencies) in the algal tissue after the initial nutrient treatment were analyzed by the phenol sulphuric acid method of carbohydrate determination (Dubois et al. 1956), with a slight modification involving the separation of soluble and insoluble sugars (Arrontes 1989).

All the chemical analyses were run on freeze-dried and finely ground algal material, stored at -20°C until determination.

Statistical analyses

Differences between nutrient treatments and parts of the alga in the intermolt duration, mass gain, mass gain rate, production efficiency, and egg number and egg mass of the herbivores were analyzed by two-way ANCOVA, using the initial mass of an animal as a covariate. Food consumption was tested by two-way ANOVA, since the regression slopes for initial mass showed heterogeneity between the algal parts.

The relationship between intermolt duration and dry-mass gain was studied by calculating the Pearson correlation coefficient between the residuals with the effects of the treatments removed. The similarity of this relationship among the treatments was tested by two-way ANCOVA using mass gain as the dependent variable and intermolt duration as a covariate. There was no difference between the four treatment combinations, as shown by nonsignificant intermolt duration \times treatment factor interactions.

Differences between treatment and part in total contents of nitrogen and phlorotannins, carbon content, and tissue toughness were analyzed by two-way ANOVA. The amounts of soluble and insoluble sugars, in terms of absorbencies, were analyzed by two-way ANCOVA, using the concentration of the algal mass in the liquid as a covariate. To ensure that the assumptions for ANOVA and ANCOVA were fulfilled, Levene's test was used to test for homogeneity of variances, and the Kolmogorov-Smirnov test was used to test for the normality of distribution. Furthermore, to allow the use of the covariate, tests were conducted to ascertain the homogeneity of regression slopes among treatments. This was assured by the nonsignificant covariate \times treatment factor interactions effect obtained for every treatment combination. All statistical analyses were performed using general linear models in SAS 6.12 (GLM procedure in SAS 6.12 package; SAS Institute 1990).

RESULTS

Herbivore performance

During the whole intermolt period, *I. baltica* females consumed significantly more apical than basal parts and tended to consume slightly more nutrient-treated than control algae. Consumption of the basal parts was almost equally low in both treatment and control groups, but the treated apical parts of *F. vesiculosus* were the most highly consumed (Fig. 1a, Table 3). When the initial mass of an animal was included in the model as a covariate, the regression slopes showed clear heterogeneity between the parts of the alga (part \times covariate interaction: $F_{1,65} = 4.42$, $P < 0.05$). The difference in food consumption between the algal parts was greatest among the smallest animals (Fig. 2; regression analysis of food consumption with initial mass; apical parts, $df = 37$, $R^2 = 0.65$, $b = 12.4$, $P < 0.001$; basal parts, $df = 31$, $R^2 = 0.15$, $b = 24.2$, $P < 0.05$).

The animals reared on nutrient-treated algae had a sig-

nificantly shorter intermolt duration than those fed on control algae (Fig. 1b, Table 3). There was no difference between apical and basal parts (Fig. 1b, Table 3).

We observed a similar pattern in the mass gain of *I. baltica*: they gained more total mass and at a higher rate when reared on fertilized apical tips (Fig. 1c, d, Table 3). The treatment with extra nutrients increased isopod mass gain most in the actively growing apical tips, as indicated by the marginally significant treatment \times part interaction. Mass gain was especially low among the animals that were offered the apical parts of the control algae (Fig. 1c, d, Table 3). Similarly, the production efficiency of the herbivores, in terms of algal dry biomass converted to isopod dry biomass, was significantly higher for the nutrient treated parts and again tended to be even more so for the treated apical parts (Fig. 1e, Table 3). Daily food consumption was significantly higher in the nutrient-treated group (Fig. 1f, Table 3). The treatment \times part interaction was significant, indicating the greatest increase in consumption in the treated apical parts.

The responses of both our growth measures, mass gain and the speed of the molt cycle, were in the same direction. The animals that grew most also did it most rapidly, as shown by the negative correlation between mass gain and intermolt duration ($r = -0.28$, $P < 0.05$, $n = 62$, tested after removing treatment effects by using residuals).

In parallel with the growth and productivity indicators, all three measures of fecundity of *I. baltica* females increased in the nutrient-treated groups. The egg number, total egg mass, and single egg mass, produced by an individual, were significantly higher in the nutrient-treated groups (Fig. 3a-c, Table 4). In the numbers of eggs there was a marginally significant interaction of part and nutrient treatment: in the control group females produced more eggs when feeding on the basal part, while in the nutrient-treated algae this association was reversed (Fig. 3a, Table 4).

In order to analyze in detail the performance of isopods on different parts of the alga, we conducted a priori contrasts between the parts in the control treatment. Although there was a general tendency for better performance on the basal parts, none of these contrasts were statistically significant (Figs. 1, 3; intermolt duration, $F_{1,77} = 0.21$, $P = 0.65$; mass gain, $F_{1,57} = 2.90$, $P = 0.09$; mass gain rate, $F_{1,57} = 2.28$, $P = 0.14$; production efficiency, $F_{1,51} = 2.36$, $P = 0.13$; egg production, $F_{1,60} = 1.99$, $P = 0.16$).

Chemical quality of the algae

Neither total nitrogen and phlorotannins concentrations nor the dry mass/fresh mass ratios of algal tissue were affected by the treatment (Table 5). There was a significant difference between the parts of the algae, apical parts containing more nitrogen and fewer phlorotannins and showing a lower DM/FM ratio than the basal parts (Table 5). However, we found some changes

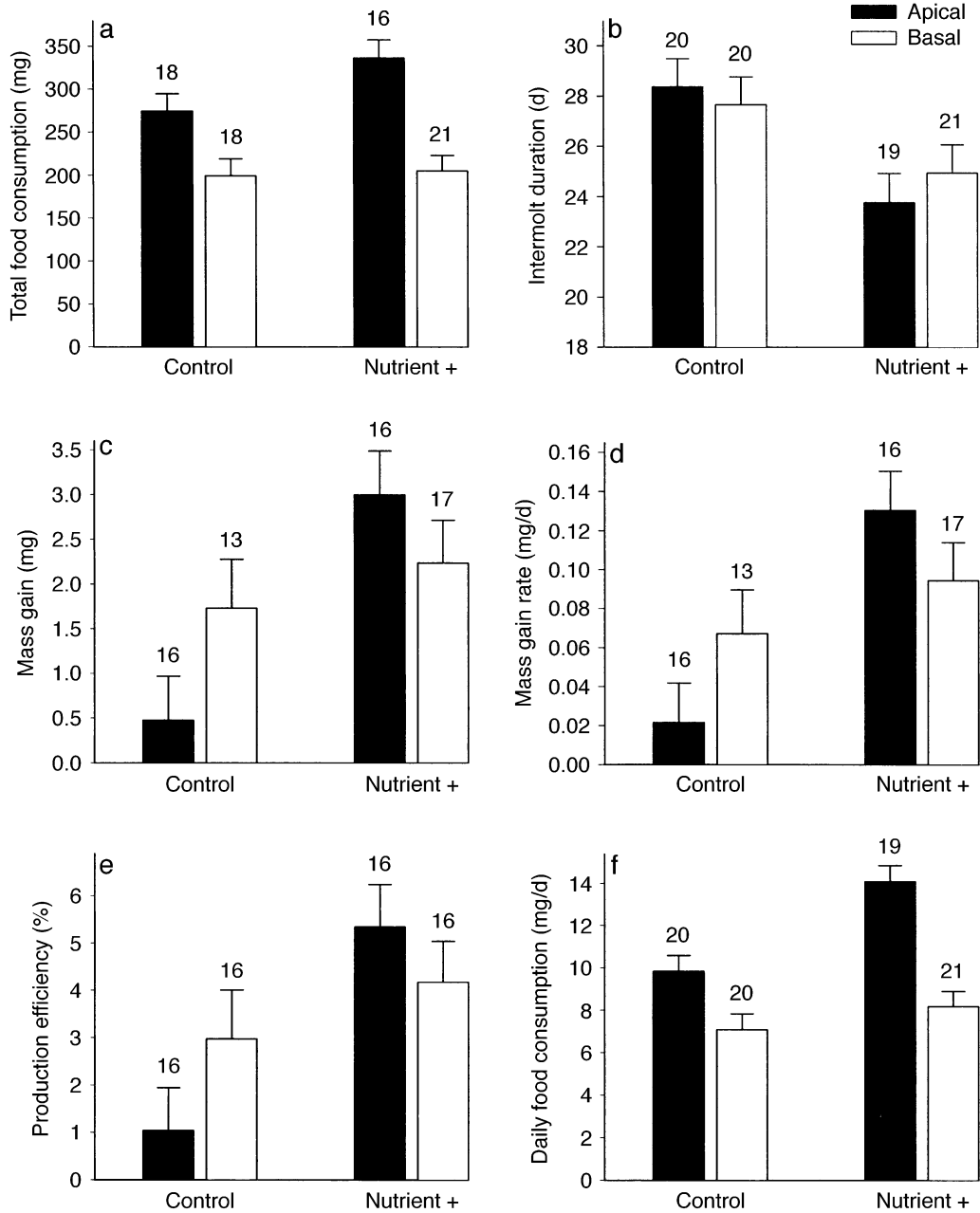


FIG. 1. (a) Food consumption (fresh mass), (b) intermolt duration, (c) mass gain (dry mass), (d) mass gain rate (dry mass), (e) production efficiency, and (f) daily food consumption (fresh mass) of *Idotea baltica* females reared on either nutrient-treated (Nutrient +) or control *Fucus vesiculosus* and on apical or basal parts of algae during the intermolt period (means + 1 SE, n above bars), adjusted for initial mass of animal, except for (a) and (f).

in chemical quality related to the nutrient treatment of the algae. First of all, the amounts of insoluble sugars increased significantly in both the apical and basal parts. Basal parts also tended to contain slightly more insoluble sugars. The amounts of soluble sugars did not respond to treatment (Table 5). Total carbon concentration decreased significantly in the nutrient-treated algae (Table 5). Secondly, the nutrient treatment significantly affected the physical toughness of algal

tissue. Generally, older parts of *F. vesiculosus* were tougher than young, apical parts, and nutrient increment significantly reduced the toughness of both the apical and basal parts (Table 5).

DISCUSSION

Performance of I. baltica

The herbivores performed clearly better when reared on algae maintained in a nutrient-rich environment, as

TABLE 3. Statistical test results for effects of nutrient treatment of algae and algal part consumed (Part) on various performance indicators of *Idotea baltica* females.

Source	Total food consumption (fresh mass)			Intermolt duration			Mass gain		
	df	F	P	df	F	P	df	F	P
Treatment	1	13.42	0.09	1	10.52	<0.01	1	9.07	<0.01
Part	1	14.69	<0.001	1	0.04	0.84	1	0.54	0.63
Treatment × Part	1	0.28	0.16	1	0.72	0.40	1	4.01	0.05
Mass	1	2.05	0.16	1	0.45	0.50
Error	68			77			57		

Notes: Test statistics are shown for ANOVA on food consumption and for ANCOVA for others, with initial mass of animal used as the covariate. Data are shown in Fig. 1.

revealed by both growth indicators: rate of mass gain and intermolt duration. Moreover, all the measures of fecundity showed a parallel improvement: the animals laid more and bigger eggs when consuming nutrient-treated algae. Since a large part of ovary development in *Idotea* takes place during the intermolt preceding the sexual molt, the mass gain includes both somatic growth and reproductive allocation (Sheader 1977, Jormalainen and Tuomi 1989). The magnitude of the total difference in egg mass between the nutrient treatments equaled the corresponding difference in mass gain. This implies that the higher mass gain on the nutrient-treated algae is explained by increased resource accumulation in the ovaries. It has been suggested that the reproduction of *I. baltica* is based predominantly on accumulated resources, with no somatic costs (Tuomi and Jormalainen 1988, Tuomi et al. 1988). However, the reduced duration of the intermolt means that high-quality food also speeds up the molting cycle.

We also found a negative phenotypic correlation within the treatment groups between mass gain and the duration of the intermolt. Thus, those individuals that gained mass efficiently also came to their reproductive molt quicker, and feeding with nutrient-treated algae shifted this relationship toward the direction of a higher rate of mass gain. As the mass gain seemed to consist mainly of reproductive investment, the duration of the intermolt may be determined by the maturation of eggs, after which oviposition becomes possible.

The part of the alga had no effect on reproductive output or on the growth indicators of the herbivore as such when feeding on nutrient-treated alga; however, apical parts supported the animals better than basal parts. When feeding on control algae, on the other hand, both fecundity and growth indicators tended to be better on basal parts, although this difference was not statistically significant in any of the measurements. Female *I. baltica* may have adapted to utilizing the basal parts equally well or even better than the apical tips when preparing to reproduce. Jormalainen et al. (2001b) have shown that the females of immature *I. baltica* can sustain growth almost equally well on apical and basal parts of *F. vesiculosus*, whereas males perform clearly worse on basal than on apical parts. They suggest that avoidance of predation is more important for female

fitness and that females are therefore better adapted to a utilization of the basal parts. Under natural conditions, females tend to inhabit and consume the lower parts of the algal bushes. If eutrophication most enhances the quality of the apical parts, thus changing the relative profitability of apical and basal parts, it may pay for females to shift towards a more risk-prone strategy and consume the more profitable upper parts.

Both production efficiency and food consumption per day were higher in the nutrient-treated group, especially when fed on apical parts. Total consumption of the different parts of the alga depended on the size of the animal: consumption in general increased with size, but small individuals were not equally capable of consuming the tougher basal parts, which also contain more phlorotannins than apical parts. Hence, as the individual gets larger, it becomes more capable of consuming equal amounts of apical and basal parts in terms of fresh mass; due to the higher dry-mass content of the basal parts, it thus gains more organic material in terms of dry mass from the basal parts. The size of an individual may therefore contribute to its ability to adjust its food consumption of lower quality plant material, either through the developmental stage of the mouth parts or through incomplete acclimation of the digestive system to handle substances that deter feeding.

In contrast to observations on certain species of marine amphipods (Cruz-Rivera and Hay 2000a), *I. baltica* seems to be unable to compensate for the lower quality of algal food by increasing its food consumption. This could be due to higher concentrations of harmful substances in the control alga; thus the animal may not be capable of increasing consumption over some given limit. The daily consumption rate of nutrient-treated apical tips was also significantly higher than that of control tips. It is thus possible that some decrease in defensive mechanisms against grazing in *F. vesiculosus* had occurred due to nutrient enhancement, although we could not trace it using the crude chemical characterization of the alga (see Changes in quality of *F. vesiculosus*). However, the physical toughness of the alga, which may be viewed as a mechanical defense, declined as a response to treatment. From the point of view of the alga, eutrophication may thus ac-

TABLE 3. Extended.

Mass gain rate			Production efficiency			Food consumption/d		
df	F	P	df	F	P	df	F	P
1	10.90	<0.01	1	5.58	<0.05	1	13.04	<0.001
1	0.05	0.82	1	0.38	0.54	1	34.25	<0.001
1	3.90	0.05	1	2.81	0.10	1	4.52	<0.05
1	0.91	0.34	1	1.82	0.18
57			51			76		

celerate grazing by *I. baltica*, rather than diminish the loss of tissue, which would be plausible if compensatory feeding occurred.

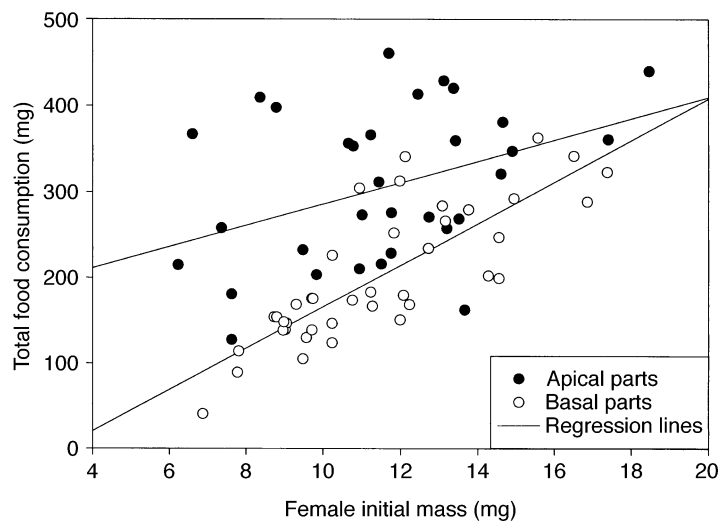
Changes in quality of F. vesiculosus

Nutrient treatment had no effect on the concentrations of total nitrogen or phlorotannins in the alga. Thus, we found no direct evidence that the resource-based hypotheses on the responses of secondary chemistry to nutrient resources might predict the allocation of resources in *F. vesiculosus* when excess nutrients are available. This finding is partly supported by previous studies by Yates and Peckol (1993) and Peckol et al. (1996), where nutrient enrichment decreased the polyphenolic concentration of *F. vesiculosus* only in nitrogen-poor sites, indicating the importance of ambient nutrient levels. In this study, nutrient concentrations in control water were relatively high and phlorotannin concentrations in general considerably higher compared to levels in a study by Yates and Peckol (1993). However, phlorotannins may still play a role in explaining the herbivore performance on *F. vesiculosus*. For example, brown-algal phlorotannins are labile compounds, molecular size being important in determining the potential defensive capacity against marine herbivores (Steinberg and Van Alstena 1992, Boettcher and Targett 1993, Arnold and Targett 1998,

Targett and Arnold 1998). It is thus possible that qualitative changes in phlorotannin composition had occurred as a response to the nutrient manipulation.

The concentration of polyphenolics can be relatively high in the brown algae in general. In this study, the phlorotannin concentration varied between 8 and 10% of the dry matter. Suggested ecological functions of phlorotannins include acting as a UV screen (Pavia et al. 1997), as antimicrobial, antipathogenic, or antifouling substances (Pawlik 1992, Schmitt et al. 1995, Targett and Arnold 1998), and, most commonly, as feeding deterrents against herbivores. Phlorotannins (or polyphenols) have been found to deter feeding by various marine herbivores, in particular by a number of amphipods (Denton and Chapman 1991, Poore 1994, Pereira and Yoneshigue-Valentin 1999), gastropods (Geiselman and McConnell 1981, Steinberg 1985, Winter and Estes 1992, Yates and Peckol 1993), and fishes (Boettcher and Targett 1993). In some cases, however, crustacean mesoherbivores have turned out to be unaffected (Cronin and Hay 1996b, c, Pavia et al. 1997). This has led to suggestions that mesograzers responses to phlorotannins are species specific (Hay et al. 1989; see Targett and Arnold 1998 for review). If this is true of *I. baltica*, factors other than phlorotannins may be more crucial for the performance and reproduction of this herbivore. Furthermore, several co-oc-

FIG. 2. Food consumption (fresh mass) during the intermolt period in relation to initial dry mass of the animal.



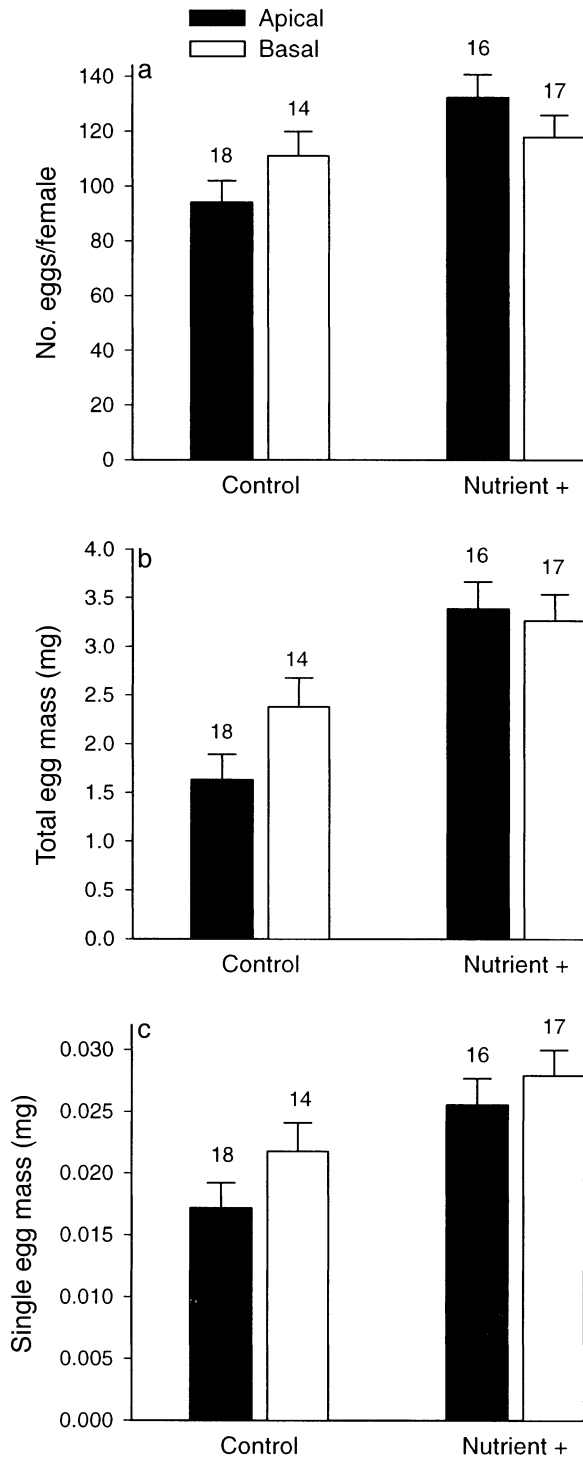


FIG. 3. (a) Number of eggs, (b) total mass of eggs, and (c) mass of single egg per individual reared on either nutrient-treated (Nutrient +) or control *Fucus vesiculosus* and on apical or basal parts of algae during the intermolt period (mean \pm 1 SE, n above bars), adjusted for initial mass of the animal.

curing compounds and their interactions, rather than just a single compound, may affect digestive and metabolic efficiency of the animals. The results of the sugar analyses indicate that the clear increase in herbivore fecundity and performance may be due to quantitative (or qualitative) changes in carbohydrate metabolism. *F. vesiculosus* may have allocated part of the excess resources to storage compounds rather than utilizing them for more rigorous growth. For example, the most important storage product of photosynthesis in the order Fucales, chrysolaminaran, is a polysaccharide (e.g., McCandless 1981, van den Hoek et al. 1995; for biosynthesis see Roessler 1987). The decrease in total carbon content as a response to nutrient treatment further hints at changes in carbon allocation. However, a better understanding of the whole complexity of primary and secondary metabolisms is required if we want to determine the precise chemical basis of algal quality for herbivores.

Ecological consequences

Geographical variation in the breeding periods of *I. baltica* suggests that life history traits show a great deal of plasticity when environmental conditions change. Under oceanic conditions, *I. baltica* is capable of breeding throughout the year and producing several cohorts per year (Naylor 1972, Salemaa 1979). In our study area, on the other hand, the breeding period is largely restricted to the early summer, partly due to harsh temperature conditions in the winter. However, Kangas et al. (1982) assumed that in the northern Baltic some females born in the summer would be able to breed already in the following fall. Small, ovigerous *I. baltica* were also observed in the field in late fall in 1999, although at very low frequencies (A. Hemmi and V. Jormalainen, *personal observation*).

Improvement in food quality may lead to quicker maturation due to an increased growth rate and shorter intermolt duration. This has the potential to shorten the life history of *I. baltica* and may enable the production of at least a partial second cohort. Furthermore, the increased growth rate of the female before maturity may result in enlarged body size, which as such is known to increase reproductive output. An increase in individual fecundity will in turn lead to an accelerated rate of population growth. High population densities of the herbivores, finally, may well cause severe overgrazing of *F. vesiculosus* at least locally, as has been suggested to have occurred in the late 1970s in the northern Baltic (Kangas et al. 1982, Haahtela 1984, Hällfors et al. 1984). Intense aquaculture in the form of fish farming has caused locally enhanced concentrations of nitrogen and phosphorus in coastal areas (Gowen and Bradbury 1987, Rönnberg et al. 1992). It is thus reasonable to assume that the magnitude of the nutrient treatment in this study corresponds to the ambient situation and that the consequent effects on herbivore success can be generalized to natural conditions.

TABLE 4. Test statistics from ANCOVA on effects of nutrient treatment of algae and algal part consumed on fecundity of *Idotea baltica* females.

Source	Number of eggs laid			Total mass of eggs		Mass of a single egg	
	df	F	P	F	P	F	P
Treatment	1	7.41	<0.01	22.87	<0.001	11.55	<0.01
Part	1	0.02	0.89	1.28	0.26	2.65	0.11
Treatment × Part	1	3.56	0.06	2.46	0.12	0.27	0.61
Mass	1	18.11	<0.001	11.16	<0.01	0.25	0.62
Error	62						

Notes: Initial mass of animal was used as the covariate. Data are shown in Fig. 3.

TABLE 5. (A) Algal characteristics of apical and basal parts (adjusted means ± 1 SE with *n* in parentheses) and (B) statistics of ANOVA or ANCOVA.

Characteristic	A) Adjusted means			B) ANOVA or ANCOVA			
	Treatment	Apical	Basal	Source	df	F	P
Phlorotannins (percentage of DM)	Control	8.19 ± 0.21 (6)	9.54 ± 0.21 (6)	Treatment	1	0.08	0.77
	Nutrient +	8.13 ± 0.21 (6)	9.72 ± 0.21 (6)	Part	1	50.46	<0.001
				Treatment × Part	1	0.37	0.55
				Part			
				Error	20		
Total nitrogen (percentage of DM)	Control	2.01 ± 0.04 (6)	1.32 ± 0.04 (6)	Treatment	1	4.75	0.50
	Nutrient +	2.06 ± 0.04 (6)	1.33 ± 0.04 (6)	Part	1	0.33	<0.001
				Treatment × Part	1	0.29	0.58
				Part			
				Error	20		
Insoluble sugars (absorbance)	Control	0.314 ± 0.024 (6)	0.363 ± 0.024 (6)	Treatment	1	5.38	<0.05
	Nutrient +	0.380 ± 0.025 (6)	0.411 ± 0.024 (6)	Part	1	2.76	0.11
				Treatment × Part	1	0.14	0.71
				Concentration	1	31.75	<0.001
				Error	19		
Soluble sugars (absorbance)	Control	0.042 ± 0.006 (6)	0.052 ± 0.006 (6)	Treatment	1	0.85	0.37
	Nutrient +	0.040 ± 0.006 (6)	0.044 ± 0.006 (6)	Part	1	1.49	0.24
				Treatment × Part	1	0.29	0.60
				Concentration	1	10.45	<0.01
				Error	19		
Total carbon (percentage of DM)	Control	36.25 ± 0.20 (6)	37.33 ± 0.20 (6)	Treatment	1	11.19	<0.01
	Nutrient +	35.93 ± 0.20 (6)	36.31 ± 0.20 (6)	Part	1	13.35	<0.01
				Treatment × Part	1	3.03	0.10
				Part			
				Error	20		
Toughness	Control	0.496 ± 0.04 (45)	0.858 ± 0.04 (46)	Treatment	1	23.63	<0.001
	Nutrient +	0.280 ± 0.04 (45)	0.674 ± 0.04 (45)	Part	1	83.91	<0.001
				Treatment × Part	1	0.15	0.70
				Part			
				Error	177		
Autogenic change of control algae (FM, mg/7 d)	Control	0.025 ± 0.002 (24)	0.008 ± 0.002 (24)	Treatment	1	0.99	0.32
	Nutrient +	0.028 ± 0.002 (23)	0.009 ± 0.002 (23)	Part	1	100.87	<0.001
				Treatment × Part	1	0.28	0.60
				Part			
				Initial mass	1	15.03	<0.01
DM/FM ratio of control algae	Control	0.192 ± 0.005 (24)	0.275 ± 0.005 (24)	Treatment	1	0.88	0.35
	Nutrient +	0.180 ± 0.005 (23)	0.278 ± 0.005 (23)	Part	1	333.1	<0.001
				Treatment × Part	1	2.34	0.13
				Part			
				Error	90		

Notes: In sugar analyses, liquid concentration was used as the covariate. In growth of control algae, initial fresh mass of piece of algae was used as the covariate. DM = dry mass; FM = fresh mass.

However, direct generalizations may be confounded by the responses of other species of the community. The role of epiphytes in the nutrient uptake efficiency of the bladder wrack may be of great importance in diminishing the amount of genuinely available nutrients and light for *F. vesiculosus* in the field. In addition, although we have here shown the potential bottom-up control mechanism of *I. baltica* populations through food quality, these populations may also be top-down controlled by predatory fishes, which may suppress the population-level consequences of enhanced individual performance of the herbivores by environmentally induced improvements in food quality.

Recent studies on the regulation of marine algal assemblages have found that mesograzers may strongly modify the benthic community structure by selective grazing and by suppressing macroalgal blooms (Duffy and Hay 2000, Lotze et al. 2000, Worm et al. 2000). However, the regulation of mesograzer populations themselves is generally less well understood. There exists some evidence that mesograzer densities may be limited by food quantity (Edgar and Aoki 1993), but, on the other hand, several studies (e.g., Van Dolah 1978, Heck et al. 2000) have reported considerable top-down effects of fishes in reducing the numbers of mesograzers. Our results show that the key life history parameters of a mesograzer may be strongly affected by the quality of the major food plant, thus highlighting the importance of bottom-up control of grazers via quality, not quantity of their food. In dense *F. vesiculosus* belts, food quantity hardly limits *I. baltica* populations, but food quality may well do so. Also, *I. baltica* is heavily preyed by several abundant fish species (Salemaa 1978), but currently there is no data to reveal the relative importance of these two potential controlling mechanisms in natural conditions.

In conclusion, eutrophication has the potential to improve the quality of *F. vesiculosus* for herbivores. The reproductive success and growth rate of *I. baltica* increase on algae maintained in a nutrient-rich environment; this is likely to be reflected in herbivore density and to increase the grazing pressure on the alga. This in turn may have potential ecological consequences for the maintenance of viable bladder wrack belts and may have partly contributed to the recent changes in perennial macroalgal communities.

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LITERATURE CITED

- Arnold, T. M., C. E. Tanner, and W. I. Hatch. 1995. Phenotypic variation in polyphenolic content of the tropical brown alga *Lobophora variegata* as a function of nitrogen availability. *Marine Ecology Progress Series* **123**:177–183.
- Arnold, T. M., and N. M. Targett. 1998. Quantifying *in situ* rates of phlorotannin synthesis and polymerization in marine brown algae. *Journal of Chemical Ecology* **24**:577–595.
- Arrontes, J. 1989. A new method for estimating digestive efficiency in herbivorous crustaceans. *Comparative Biochemistry and Physiology* **94A**:133–136.
- Arrontes, J. 1990. Diet, food preference and digestive efficiency in intertidal isopods inhabiting macroalgae. *Journal of Marine Biology and Ecology* **139**:231–249.
- Berryman, A. A. 1996. What causes population cycles of forest Lepidoptera? *Trends in Ecology and Evolution* **11**:28–32.
- Boettcher, A. A., and N. M. Targett. 1993. Role of polyphenolic molecular size in reduction of assimilation efficiency in *Xiphister mucosus*. *Ecology* **74**:891–903.
- Borowsky, B. 1987. Laboratory studies of the pattern of reproduction of the Isopod Crustacean *Idotea baltica*. *Fishery Bulletin* **85**:377–380.
- Boyd, C. E., and C. P. Goodyear. 1971. Nutritive quality of food in ecological systems. *Archiv für Hydrobiologie* **69**:256–270.
- Bryant, J. P., F. S. Chapin, III, and D. R. Klein. 1983. Carbon/nutrient balance of boreal plants in relation to vertebrate herbivory. *Oecologia* **86**:202–209.
- Cockfield, S. D. 1988. Relative availability of nitrogen in host plants of invertebrate herbivores: three possible nutritional and physiological definitions. *Oecologia* **77**:91–94.
- Coley, P. D., J. P. Bryant, and F. S. Chapin, III. 1985. Resource availability and plant antiherbivore defense. *Science* **230**:895–899.
- Cronin, G., and M. E. Hay. 1996a. Within-plant variation in seaweed palatability and chemical defenses: optimal defense theory versus the growth-differentiation balance hypothesis. *Oecologia* **105**:361–368.
- Cronin, G., and M. E. Hay. 1996b. Effects of light and nutrient availability on the growth, secondary chemistry, and resistance to herbivory of two brown seaweeds. *Oikos* **77**:93–106.
- Cronin, G., and M. E. Hay. 1996c. Susceptibility to herbivores depends on recent history of both the plant and the animal. *Ecology* **77**:1531–1543.
- Cruz-Rivera, E., and M. E. Hay. 2000a. Can quantity replace quality? Food choice, compensatory feeding, and fitness of marine mesograzers. *Ecology* **81**:201–219.
- Cruz-Rivera, E., and M. E. Hay. 2000b. The effects of diet mixing on consumer fitness: macroalgae, epiphytes, and animal matter as food for marine amphipods. *Oecologia* **123**:252–264.
- Denton, A. B., and A. R. O. Chapman. 1991. Feeding preferences of gammarid amphipods among four species of *Fucus*. *Marine Biology* **109**:503–506.
- Denton, A., A. R. O. Chapman, and J. Markham. 1990. Size-specific concentrations of phlorotannins (anti-herbivore compounds) in three species of *Fucus*. *Marine Ecology Progress Series* **65**:103–104.
- Dubois, M., K. A. Gilles, J. K. Hamilton, P. A. Rebers, and F. Smith. 1956. Colorimetric method for determination of sugars and related substances. *Analytical Chemistry* **28**:350–356.
- Duffy, J. E., and M. E. Hay. 1991. Food and shelter as de-

- terminants of food choice by an herbivorous marine amphipod. *Ecology* **72**:1286–1298.
- Duffy, J. E., and M. E. Hay. 2000. Strong impacts of grazing amphipods on the organization of the benthic community. *Ecological Monographs* **70**:237–263.
- Edgar, G. J., and M. Aoki. 1993. Resource limitation and fish predation: their importance to mobile epifauna associated with Japanese *Sargassum*. *Oecologia* **95**:122–133.
- Fleury, B. G., A. Kelecom, R. C. Pereira, and V. L. Teixeira. 1994. Polyphenols, terpenes and sterols in Brazilian Dictyotales and Fucales (Phaeophyta). *Botanica Marina* **37**:457–462.
- Geiselman, J. A., and O. J. McConnell. 1981. Polyphenols in brown algae *Fucus vesiculosus* and *Ascophyllum nodosum*: chemical defenses against the marine herbivorous snail *Littorina littorea*. *Journal of Chemical Ecology* **7**:1115–1133.
- Gowen, R. J., and N. B. Bradbury. 1987. The ecological impact of salmonid farming in coastal waters: a review. *Oceanography and Marine Biology: An Annual Review* **25**:563–575.
- Grime, J. P., J. C. Crick, and J. E. Rincon. 1986. The ecological significance of plasticity. Pages 5–29 in D. H. Jennings and A. J. Trewavas, editors. *Plasticity in plants*. Company of Biologists Limited, Cambridge, UK.
- Haahtela, I. 1978. Morphology as evidence of maturity in isopod Crustacea, as exemplified by *Mesidotia entomon* (L.). *Annales Zoologici Fennici* **15**:186–190.
- Haahtela, I. 1984. A hypothesis of the decline of the bladder wrack (*Fucus vesiculosus* L.) in SW Finland in 1975–1981. *Limnologia* **15**:345–350.
- Hällfors, G., P. Kangas, and Å. Niemi. 1984. Recent changes in the phytal at the south coast of Finland. *Ophelia* **3**(Supplement):51–59.
- Hanisak, M. D. 1983. The nitrogen relationships of marine macroalgae. Pages 699–730 in E. J. Carpenter and D. G. Capone, editors. *Nitrogen in the marine environment*. Academic Press, New York, New York, USA.
- Haukioja, E. 1980. On the role of plant defenses in the fluctuation of herbivore populations. *Oikos* **35**:202–213.
- Hay, M. E. 1996. Marine chemical ecology: what's known and what's next? *Journal of Experimental Marine Biology and Ecology* **200**:103–134.
- Hay, M. E., J. E. Pawlik, J. E. Duffy, and W. Fenical. 1989. Seaweed–herbivore–predator interactions: host plant specialization reduces predation of small herbivores. *Oecologia* **81**:418–427.
- Heck, K. L., Jr., J. R. Pennock, J. F. Valentine, L. D. Coen, and S. A. Sklenar. 2000. Effects of nutrient enrichment and small predator density on seagrass ecosystems: an experimental assessment. *Limnology and Oceanography* **45**:1041–1057.
- Hermes, D. A., and W. J. Mattson. 1992. The dilemma of plants: to grow or defend. *Quarterly Review of Biology* **67**:283–335.
- Hughes, R. N. 1980. Optimal foraging theory in the marine context. *Oceanography and Marine Biology: An Annual Review* **18**:423–481.
- Hurd, C. L., and M. J. Dring. 1990. Phosphate uptake by intertidal furoid algae in relation to zonation and season. *Marine Biology* **107**:281–289.
- Ivessalo, H., and J. Tuomi. 1989. Nutrient availability and accumulation of phenolic compounds in the brown alga *Fucus vesiculosus*. *Marine Biology* **101**:115–119.
- Jormalainen, V., T. Honkanen, and N. Heikkilä. 2001a. Feeding preferences and performance of a marine isopod on seaweed hosts—cost of habitat selection. *Marine Ecology Progress Series* **220**:219–230.
- Jormalainen, V., T. Honkanen, A. Mäkinen, A. Hemmi, and O. Vesakoski. 2001b. Why does herbivore sex matter? Sexual differences in utilization of *Fucus vesiculosus* by the isopod *Idotea baltica*. *Oikos* **93**:77–86.
- Jormalainen, V., and J. Tuomi. 1989. Reproductive ecology of the isopod *Idotea baltica* (Pallas) in the northern Baltic. *Ophelia* **30**:213–223.
- Kangas, P., H. Autio, G. Hällfors, H. Luther, Å. Niemi, and H. Salemaa. 1982. A general model of the decline of *Fucus vesiculosus* at Tvärminne, south coast of Finland in 1977–81. *Acta Botanica Fennica* **118**:1–27.
- Kennish, R. 1997. Seasonal patterns of food availability: influences on the reproductive output and body condition of the herbivorous crab *Grapsus albolineatus*. *Oecologia* **109**:209–218.
- Koroleff, F. 1976. Determination of nutrients. Pages 117–133 in G. Grasshof, editor. *Methods of seawater analysis*. Verlag Chemie, Weinheim, New York, New York, USA.
- Koroleff, F. 1979. The general chemical analysis methods of seawater. Meri, Number 7. Finnish Institute of Marine Research, Helsinki, Finland.
- Lotze, H. K., B. Worm, and U. Sommer. 2000. Propagule banks, herbivory and nutrient supply control population development and dominance patterns in macroalgal blooms. *Oikos* **89**:46–58.
- Lüning, K. 1990. Seaweeds—their environment, biogeography and ecophysiology. John Wiley and Sons, New York, New York, USA.
- Mattson, W., Jr. 1980. Herbivory in relation to plant nitrogen content. *Annual Review of Ecology and Systematics* **11**:119–161.
- McCandless, E. L. 1981. Polysaccharides of seaweeds. Pages 559–588 in C. S. Lobban and M. J. Wynne, editors. *The biology of seaweeds*. Blackwell, Oxford, UK.
- Mutikainen, P., M. Walls, J. Ovaska, M. Keinänen, R. Julkunen-Tiitto, and E. Vapaavuori. 2000. Herbivore resistance in *Betula pendula*: effect of fertilization, defoliation, and plant genotype. *Ecology* **81**:49–65.
- Naylor, E. 1972. British marine isopods. *Synopses British Fauna* **3**:1–86.
- Nicotri, M. E. 1980. Factors involved in herbivore food preference. *Journal of Experimental Marine Biology and Ecology* **42**:13–26.
- Nurmi, K., V. Ossipov, E. Haukioja, and K. Pihlaja. 1996. Variation of total phenolic content. *Journal of Chemical Ecology* **22**:2023–2040.
- Pavia, H., G. Cervin, A. Lindgren, and P. Åberg. 1997. Effects of UV-B radiation and simulated herbivory on phlorotannins in the brown alga *Ascophyllum nodosum*. *Marine Ecology Progress Series* **157**:139–146.
- Pawlik, J. R. 1992. Chemical ecology of the settlement of benthic marine invertebrates. *Oceanography and Marine Biology: An Annual Review* **30**:273–335.
- Peckol, P., J. M. Krane, and J. L. Yates. 1996. Interactive effects of inducible defense and resource availability on phlorotannins in the north Atlantic brown alga *Fucus vesiculosus*. *Marine Ecology Progress Series* **138**:209–217.
- Pereira, R. C., and Y. Yoneshigue-Valentin. 1999. The role of polyphenols from the tropical brown alga *Sargassum furcatum* on the feeding by amphipod herbivore. *Botanica Marina* **42**:441–448.
- Poore, A. G. B. 1994. Selective herbivory by amphipods inhabiting the brown alga *Zonaria angustata*. *Marine Ecology Progress Series* **107**:113–123.
- Poore, A. G. B., and P. D. Steinberg. 1999. Preference–performance relationships and effects of host plant choice in an herbivorous marine amphipod. *Ecological Monographs* **69**:443–464.
- Price, P. W. 1991. The plant vigor hypothesis and herbivore attack. *Oikos* **62**:244–251.
- Pyke, G. H., H. R. Pulliam, and E. L. Charnov. 1977. Optimal

- foraging: a selective review of theory and tests. *Quarterly Review of Biology* **52**:137–154.
- Renaud, P. E., M. E. Hay, and T. M. Schmitt. 1990. Interactions of plant stress and herbivory: intraspecific variation in the susceptibility of a palatable versus an unpalatable seaweed to sea urchin grazing. *Oecologia* **82**:217–226.
- Rhoades, D. F. 1985. Offensive–defensive interactions between herbivores and plants: their relevance in herbivore population dynamics and ecological theory. *American Naturalist* **125**:205–238.
- Roa, R. 1992. Design and analysis of multiple-choice feeding-preference experiments. *Oecologia* **89**:509–514.
- Roessler, P. G. 1987. UDP glucose pyrophosphorylase activity in the diatom *Cyclotella cryptica*: pathway of chrysolaminarin biosynthesis. *Journal of Phycology* **23**:494–498.
- Rönnberg, O., K. Ådjers, C. Ruokolampi, and M. Bondestam. 1992. Effects of fish farming on growth, epiphytes and nutrient content of *Fucus vesiculosus* L. in the Åland Archipelago, northern Baltic Sea. *Aquatic Botany* **42**:109–120.
- Rosenthal, G. A., and M. R. Berenbaum, editors. 1992. Herbivores: their interactions with secondary plant metabolites. Volume II. Ecological and evolutionary processes. Academic Press, San Diego, California, USA.
- Ruohomäki, K., F. S. Chapin, III, E. Haukioja, S. Neuvonen, and J. Suomela. 1996. Delayed inducible resistance in mountain birch in response to fertilization and shade. *Ecology* **77**:2302–2311.
- Salemaa, H. 1978. Geographical variety in the colour polymorphism of *Idotea baltica* (Isopoda) in the northern Baltic. *Hereditas* **88**:165–182.
- Salemaa, H. 1979. Ecology of *Idotea* spp. (Isopoda) in the northern Baltic. *Ophelia* **18**:133–150.
- Salemaa, H. 1987. Herbivory and microhabitat preferences of *Idotea* spp. (Isopoda) in the northern Baltic Sea. *Ophelia* **27**:1–15.
- SAS Institute. 1990. SAS/STAT user's guide: statistics, version 6. Fourth edition. Volume 2. SAS Institute, Cary, North Carolina, USA.
- Schaffelke, B., D. Evers, and A. Walhorn. 1995. Selective grazing of the isopod *Idotea baltica* between *Fucus evanescens* and *F. vesiculosus* from Kiel Fjord (western Baltic). *Marine Biology* **124**:215–218.
- Schmitt, T. M., M. E. Hay, and N. Lindqvist. 1995. Constraints on chemically mediated coevolution: multiple functions of seaweed secondary metabolites. *Ecology* **6**:107–113.
- Shearer, M. 1977. The breeding biology of *Idotea pelagica* (Isopoda: Valvifera) with notes on the occurrence and biology of its parasite *Clypeoniscus hanseni* (Isopoda: Epicaridea). *Journal of the Marine Biological Association of United Kingdom* **57**:659–674.
- Steinberg, P. D. 1985. Feeding preferences of *Tegula funebris* and chemical defenses of marine brown algae. *Ecological Monographs* **55**:333–349.
- Steinberg, P. D. 1988. Effects of quantitative and qualitative variation in phenolic compounds on feeding in three species of marine invertebrate herbivores. *Journal of Experimental Marine Biology and Ecology* **120**:221–237.
- Steinberg, P. D., and I. Van Alena. 1992. Tolerance of marine invertebrate herbivores to brown algal phlorotannins in temperate Australasia. *Ecological Monographs* **62**:189–222.
- Stern, J. L., A. E. Hagerman, P. D. Steinberg, and P. K. Mason. 1996. Phlorotannin–protein interactions. *Journal of Chemical Ecology* **22**:1877–1899.
- Strong, K. W., and G. R. Daborn. 1979. Growth and energy utilization of the intertidal isopod *Idotea baltica* (Pallas) (Crustacea: Isopoda). *Journal of Experimental Marine Biology and Ecology* **41**:101–123.
- Targett, N. M., and T. M. Arnold. 1998. Predicting the effects of brown algal phlorotannins on marine herbivores in tropical and temperate oceans. *Journal of Phycology* **34**:195–205.
- Thomas, L., and C. J. Krebs. 1997. A review of statistical power analysis software. *Bulletin of the Ecological Society of America* **78**:126–139.
- Tuomi, J. 1992. Toward integration of plant defense theories. *Trends in Ecology and Evolution* **7**:365–367.
- Tuomi, J., H. Ilvessalo, P. Niemelä, S. Sirén, and V. Jormalainen. 1989. Within-plant variation in phenolic content and toughness of the brown alga *Fucus vesiculosus* L. *Botanica Marina* **32**:505–509.
- Tuomi, J., and V. Jormalainen. 1988. Components of reproductive effort in the aquatic isopod *Idotea baltica*. *Oikos* **52**:250–254.
- Tuomi, J., V. Jormalainen, and H. Ilvessalo. 1988. Growth, food consumption and reproductive tactics of the aquatic isopod *Idotea baltica*. *Annales Zoologici Fennici* **25**:145–151.
- Van Alstyne, K. L. 1988. Herbivore grazing increases polyphenolic defenses in the intertidal brown alga *Fucus distichus*. *Ecology* **69**:655–663.
- Van Alstyne, K. L. 1995. The comparison of three methods for quantifying brown algal polyphenolic compounds. *Journal of Chemical Ecology* **21**:45–58.
- van den Hoek, C., D. G. Mann, and H. M. Jahns, editors. 1995. *Algae: an introduction to phycology*. Cambridge University Press, Cambridge, UK.
- Van Dolah, R. F. 1978. Factors regulating the distribution and population dynamics of the amphipod *Gammarus palustris* in an intertidal salt marsh community. *Ecological Monographs* **48**:191–217.
- Winter, F. C., and J. A. Estes. 1992. Experimental evidence for the effects of polyphenolic compounds from *Dictyonium californicum* Ruprecht (Phaeophyta: Laminariales) on feeding rate and growth in the red abalone *Haliotis rufescens* Swainson. *Journal of Experimental Marine Biology and Ecology* **155**:263–277.
- Worm, B., H. K. Lotze, and U. Sommer. 2000. Coastal food web structure, carbon storage, and nitrogen retention regulated by consumer pressure and nutrient loading. *Limnology and Oceanography* **45**:339–349.
- Yates, J. L., and P. Peckol. 1993. Effects of nutrient availability and herbivory on polyphenolics in the seaweed *Fucus vesiculosus*. *Ecology* **74**:1757–1766.