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Geographic covariation of chemical quality of the host alga *Fucus vesiculosus* with fitness of the herbivorous isopod *Idotea baltica*

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Abstract Environmental and/or genetic among-site variation in plant quality may influence growth and fecundity of specialized herbivores inhabiting a particular site. Such variation is important as it generates spatial variation in selection for traits related to plant–herbivore interaction. Littoral macroalgae are known to respond plastically to environmental variation by modifying their chemistry or morphology. We studied geographic variation in phlorotannin, nitrogen, protein, and sugar (fucose, mannitol, and melibiose) concentrations of the brown alga *Fucus vesiculosus* at 12 sites separated by 0.5 to 40 km in the naturally fragmented Archipelago Sea in the northern Baltic Sea. By this regional variation in algal chemistry we attempted to explain among-population variation in size and fecundity of the crustacean herbivore *Idotea baltica*. We observed high spatial variation in all the measured chemical characteristics of *F. vesiculosus*, as well as in female size and the number of eggs produced by the herbivores. Spatial variation in nitrogen or protein contents of the alga did not explain the variation of herbivore traits. However, egg size positively covaried with spatial variation in the concentration of mannitol, the major storage carbohydrate of the alga. Such a positive relationship may arise if *I. baltica* can utilize the nutritive value of a mannitol-rich diet thereby being better able to provision the developing eggs with energy-rich metabolites. Unexpectedly, the concentration of phlorotannins, secondary metabolites having a putative role in defense against herbivory, positively covaried with the size of the herbivore. Among-population variation in host plant chemistry and covariation of that with herbivore growth and reproduction imply that herbivores respond to the local quality of their host plants, and that geographical

structuring of populations has to be taken into account in studies of plant–herbivore interactions.

Introduction

Geographical or biological dispersal barriers in a fragmented environment may generate variation in plant–herbivore interactions within a relatively small scale through variation in selection pressures among populations. If environmentally or genetically induced spatial variation in host plant quality affects fitness of herbivores, it may consequently modify the plant–herbivore interaction among the different localities. Spatial variation in host algal quality may thus be seen in the fitness of the consumers as shown in a few previous studies by Poore and Steinberg (2001), Honkanen et al. (2002) and Taylor et al. (2003). Sotka and Hay (2002) suggested that different herbivore populations may have adapted, possibly genetically, to utilize the host species differently. Geographical structuring of populations may be important in modifying the species interactions, thereby affecting also the coevolutionary dynamics of the interacting species (Thompson 1999a).

Perennial macroalgae inhabiting marine littoral habitats show lots of spatial variation in their characteristics and are therefore appealing objects for studies on geographic variation in food plant quality. For example, perennial brown algae show spatial variation in their morphology (Rice et al. 1985; Kalvas and Kautsky 1993; Ruuskanen 2000), contents of storage compounds such as nitrogen or sugars (Chapman and Graigie 1978; Kornfeldt 1982; Gómez et al. 1998; Lehvo et al. 2001), and in production of phlorotannins (e.g. Van Alstyne et al. 1999, 2001), polyphenolic secondary metabolites specific to brown algae. While morphology and nutritive quality of host plants are important for herbivores (reviewed in Mattson 1980 and Lucas et al. 2000), secondary metabolites may affect herbivore nutrition both directly and indirectly by interacting with digestibility of

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nutrients (reviewed by Paul et al. 2001). Phlorotannins are especially interesting with respect to herbivores' performance as they may act as feeding deterrents (Steinberg 1988; Steinberg and Van Alstena 1992; Winter and Estes 1992; Targett and Arnold 1998) and may have an injurious impact on herbivores' digestive efficiency (reviewed by Targett and Arnold 1998; 2001).

Production of phlorotannins shows phenotypic plasticity with respect to several environmental factors, which contribute to spatial heterogeneity of the growing environment. High ambient nutrient level, for example, usually lowers production of phlorotannins (e.g. Ilvessalo and Tuomi 1989; Yates and Peckol 1993; Arnold et al. 1995; Cronin and Hay 1996a; Pavia and Toth 2000a). In addition, the amount of phlorotannins is modified by UV radiation (Pavia et al. 1997; Swanson and Druehl 2002), light availability (Pavia and Toth 2000a), wave exposure (Ilvessalo and Tuomi 1989; but see Van Alstyne et al. 1999), and, in some but not all cases, by the degree of herbivory or simulated grazing (Van Alstyne 1988; Cronin and Hay 1996b, Yates and Peckol 1993; Peckol et al. 1996; Hammerström et al. 1998; Pavia and Toth 2000b). Such plasticity implies that phlorotannins may have multiple functional roles in algae, ranging from structural compounds of the cell wall to mediators in interspecific interactions (Arnold and Targett 2003).

Among-species differences in phlorotannins over large geographical scales have been examined by Steinberg (1989), Van Alstyne and Paul (1990), and Targett et al. (1992, 1995). On the other hand, intra-specific spatial variation in algal chemical composition has been studied much less. In several fucooid species, considerable variation in phlorotannins over a range of spatial scales, including among separate growing sites quite close to each other (~ 1 km), has been found (Ilvessalo and Tuomi 1989; Targett et al. 1992; Pavia and Åberg 1996; Van Alstyne et al. 1999; Pavia et al. 2003). While among-species differences and interspecific differences among the different areas are likely to represent genetic variation, the contributions of genetic and environmental components of variation are not known for small-scale spatial variation in phlorotannins for any species, mainly due to lack of knowledge on the genetic structure of algal populations. A study on genetic differentiation of *Fucus serratus* populations suggests that detectable genetic differentiation may occur at spatial scales of over 2 km (Coyer et al. 2003).

The Archipelago Sea in the northern Baltic Sea consists of thousands of islands separated by pelagic areas, thus forming a naturally fragmented geographic mosaic. In this mosaic landscape, littoral habitats confront highly variable environmental conditions such as different wave exposure, bottom topography, ambient nutrient availability, and temperature regime, and these habitats are geographically more or less isolated from each other. Such an environment provides potential for spatial variation in littoral plant–herbivore interactions. Here we focus on spatial variation in the chemical

composition of the perennial brown alga *Fucus vesiculosus* (L.) and in reproductive characteristics of the isopod *Idotea baltica* (Pallas) that inhabits and consumes *F. vesiculosus*. Laboratory studies have shown that variation in food quality is a crucial determinant of the performance of *I. baltica* (Jormalainen et al. 2001; Hemmi and Jormalainen 2002; Hemmi and Jormalainen 2004). For example, enhanced nutrient availability improves quality in *F. vesiculosus* for herbivores by increasing the total amount of sugars, which results in remarkable improvement in growth and fecundity of the herbivore *I. baltica* (Hemmi and Jormalainen 2002). However, it is not known to what extent natural variation in chemistry of *F. vesiculosus* may affect performance of *I. baltica* in the field, where there is always a range of other potential food sources available. Therefore, we took advantage of the geographic structuring of the plant and herbivore populations to study the possible covariation of herbivore performance with algal chemistry. To our knowledge, this is the first attempt to link among-population variation in marine algal chemistry and fecundity of the herbivore population inhabiting and consuming the alga.

In this study, we specifically measured variation among the local populations of the brown alga *F. vesiculosus* in the amount of nitrogen, the primary metabolites fucose, mannitol, melibiose, and proteins, and the secondary metabolite phlorotannin. We further measured fecundity and body size of the respective local populations of the isopod herbivore *I. baltica*. We asked the following questions: (1) is there spatial intra-specific variation in chemical quality of *F. vesiculosus* among the populations? (2) If so, to what extent do the among-population variation in nutritive value and/or algal secondary metabolites explain variation in fecundity and body size of *I. baltica*?

Materials and methods

Study species and biological analyses

Idotea baltica (Pallas) is a herbivorous isopod crustacean that is widespread in the northern part of the Atlantic Ocean, including the Baltic Sea. The breeding period starts in May and is highly synchronized due to strong seasonality. Females are fertilized during the parturial molt, after which they lay eggs into the ventral marsupium (brood pouch). Juveniles are released after an incubation period of about 40 days. Juveniles eat mainly *Cladophora glomerata* until September when they switch to the adult diet of *Fucus vesiculosus* (Salemaa 1979; Jormalainen et al. 2001). In our study area in the Archipelago Sea, northern Baltic Sea, populations of *I. baltica* live in close association with the host plant *F. vesiculosus*, which covers the rocky littoral shores. These sites are patchily distributed in the fragmented archipelago environment. Because *I. baltica* does not have a planktonic dispersal stage, and mobility increases

the risk of predation (Jormalainen et al. 1995), dispersal among the local populations, commonly separated by pelagic zones, is likely to be relatively restricted. Therefore, potential for genetic differentiation among local populations exists.

F. vesiculosus (L.) (Phaeophyceae) is a widespread, perennial brown macroalga, which forms dense belts on shallow, rocky shores. As a key species of littoral vegetation it provides habitat for a wide variety of other plants and animals. It is a delicious plant with relatively large and sinking female gametes. Though male spores are mobile, the zygotes of *F. vesiculosus* are assumed to fall within a few meters from the mother, and thus the dispersal ability of fucoid propagules is very low (Chapman 1995). Thus, large-scale dispersal of *Fucus* may be relatively rare and probably occurs mainly via detached, fertile fronds driven by wind and currents.

We chose a total of 12 *F. vesiculosus* populations from the Archipelago Sea (Fig. 1). The sites are located in a naturally fragmented archipelago, 500 m to kilometers apart from each other, and separated by islands and deeper, pelagic waters that form dispersal barriers for both *Fucus* and *Idotea* populations. We sampled 8 of the sites on 20–23 June 2000 and the rest (Fig. 1; Pargas, Päiväluoto, Högholm South, and Högländet) on 23–24 June 2001. The two sampling years did not differ with respect to algal chemistry or herbivore fecundity. We sampled randomly ten *F. vesiculosus* individuals from each site and cut ten apical tips (extending 3–4 cm from the tip) from each individual for chemical analyses. The algae were transported to the laboratory, freeze-dried, and subsequently stored at -20°C until the chemical analyses of phlorotannins, nitrogen, proteins, and sugars.

We simultaneously collected 18–53 ovigerous *I. baltica* females from *F. vesiculosus*. The animals were stored in 70% alcohol until their eggs were removed from the marsupium, counted, and dry-weighted. The animals were dry-weighted after egg removal to obtain individual size. Body mass is strongly correlated with body length

in *I. baltica* (regression of log body length to log body weight from unpublished data on three populations: $R^2=0.91, F_{1,251}=2474, P<0.0001$). Egg size, in terms of average mass of a single egg, was calculated by dividing the total egg mass by the number of eggs. We used females because their intermolt stage can be determined morphologically (Haahtela 1978) and hence we could exclude size variation due to age differences by choosing females in the same intermolt stage. Because of the highly synchronized egg-laying period, we were able to schedule the collection dates so that the eggs were all in a very early stage of development. Therefore, we could exclude possible variation in number of eggs and egg size due to differences in developmental stage of the eggs.

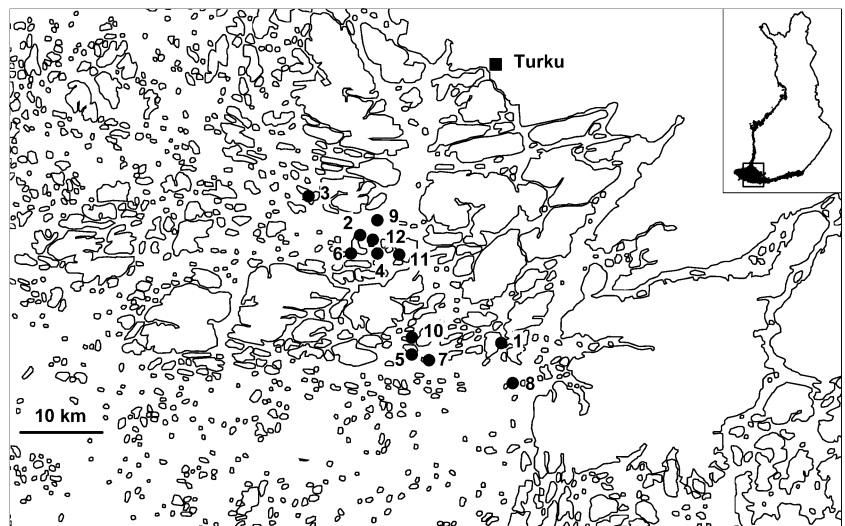
Chemical analyses

We measured the content of total soluble phenolics by a modification of the Folin–Ciocalteu method (Waterman and Mole 1994). Dry phloroglucinol (ICN Biomedicals Inc.) was used as the reference compound. The Folin–Ciocalteu assay also quantifies non-phenolic hydroxylated aromatic compounds, but these make up $<5\%$ of the total Folin–Ciocalteu-reactive compounds (Van Alstyne 1995). In the following, we use the term “phlorotannins” for these total phenolics, since brown algae are not known to contain other polyphenolics (Ragan and Glombitza 1986).

Protein analyses were conducted on algae collected from the eight sites sampled in 2000. We quantified the total amount of proteins using the spectrophotometric Bradford assay (Bradford 1976; Davis 1988) at the wavelength 595 nm with bovine serum album as a standard agent.

The concentrations of individual sugars were measured from 70% acetate soluble fraction extracted from freeze-dried and pulverized algae, using a gas chromatographic method modified from Suomela et al.

Fig. 1 Locations of the 12 study sites in the Archipelago Sea, northern Baltic (1 Pargas, 2 Päiväluoto, 3 Korpinkarit, 4 Högholm South, 5 Svinö, 6 Katava, 7 Gulskär, 8 Högländ, 9 Orhis, 10 Peno, 11 Haverö, 12 Högholm)



(1995). The gas chromatogram was equipped with flame ionization detector and a capillary column PE-5MS (30 m×0.25 mm ID). The oven temperature was increased from 70° to 290°C over 51 min (70°C, 2 min; 70–250°C, 6°C min⁻¹; 250–290°C, 20°C min⁻¹; 290°C, 17 min). The detector and injector temperatures were 280°C. Nitrogen was used as carrier gas (flow rate 1 ml min⁻¹) and inositol as an internal standard. The three sugars, fucose, mannitol, and melibiose, were chosen because they gave clearly separable and repeatable signals in gas chromatography analysis and were relatively abundant in all samples.

Statistical analyses

We tested differences in plant chemistry (concentrations of phlorotannins, nitrogen, protein, and sugars) and in size of *I. baltica* females among local populations by one-way analysis of variance (ANOVA). To characterize the amount of among-population variation in algal chemistry, we calculated the proportion of variance due to population. Differences among local populations in the number of eggs, total egg mass, and egg size were analyzed by one-way analysis of covariance (ANCOVA), using the mass of the females after egg removal as a covariate. When significant differences were obtained, pairwise comparisons between all sites (Tukey's studentized range test) were conducted. The assumptions of ANOVA and ANCOVA were checked and fulfilled.

We calculated Pearson correlation coefficients between phlorotannin, nitrogen, protein, and sugar concentrations both from the pooled data over all sites and by using site-specific average concentrations. We analyzed the spatial covariation of plant chemistry with size and reproduction of *I. baltica* using stepwise multiple regression analyses, where size and reproductive traits of *I. baltica*, one at the time, were used as dependent variables and plant chemistry as independent variables. Also in these analyses, site-specific means were used. When analyzing the number of eggs, total egg mass and egg size, female size without eggs was forced in the model as an independent variable before plant chemistry. All the statistical analyses were run by SAS 8.01 (Procedures GLM, MIXED and REG; SAS Institute 1990).

Results

The algal populations differed significantly in the concentrations of phlorotannins, nitrogen, and proteins (Table 1; Fig. 2a–c), as well as the sugars fucose, mannitol, and melibiose (Table 1; Fig. 2d–f). The proportion of the among-population variance of the total variance was highest in proteins, and lowest in the sugar concentrations (Table 1).

The number of eggs, total egg mass, and egg size of *I. baltica* differed between the populations as well (Fig. 3;

Table 1 Results of ANOVA testing the differences between the sites in chemical characteristics of *Fucus vesiculosus*. The first column indicates the proportion of among-population variance of the total variance [among-population variance component/(among-population variance component + residual variance)*100]. *NDF* numerator degrees of freedom; *DDF* denominator degrees of freedom

Source	Among-population variance of total variance	NDF, DDF	<i>F</i>	<i>P</i>
Phlorotannin concentration	17.03%	11, 106	3.02	0.0015
Nitrogen concentration	25.65%	11, 106	4.32	<0.0001
Protein concentration	67.40%	7, 70	7.68	<0.0001
Fucose concentration	9.24%	11, 106	2.00	0.0353
Mannitol concentration	9.11%	11, 106	1.99	0.0367
Melibiose concentration	15.28%	11, 106	2.77	0.0034

Table 2). ANCOVAs (Table 2) showed a strong dependency of fecundity on female size, larger females producing not just more (Fig. 3a), but also bigger (Fig. 3c) eggs. There were no population by female size interactions in egg numbers or egg sizes (all *Ps* > 0.15) implying that although the size-specific egg production varied among the populations, female size influenced egg production similarly in all the populations (Fig. 3a–c).

Phlorotannin concentration in *F. vesiculosus* correlated negatively with nitrogen concentration, but that was due to negative relationships within rather than among populations (Table 3). Mannitol concentration correlated positively with melibiose as well as fucose concentrations; the latter correlation was significant also when using site-specific means, implying that the relationship was due to both larger-scale spatial and smaller-scale within-population covariation (Table 3). Protein concentration did not correlate with either nitrogen or phlorotannin concentration, but the site-specific mean protein concentration correlated positively with melibiose concentration (Table 3). Within-site negative correlations were observed between nitrogen and both mannitol and melibiose, and within-site positive correlations between phlorotannins and both mannitol and melibiose (Table 3).

Stepwise multiple regression analysis on the spatial dependency of size and reproductive traits of *I. baltica* on algal chemistry showed that size of females was positively affected by the phlorotannin concentration in *F. vesiculosus* (Fig. 4a; $R^2 = 0.502$; $F_{1,11} = 10.09$, $P < 0.01$). None of the other factors reached a significance level of $P < 0.15$. The number of eggs was strongly determined by female size ($R^2 = 0.884$, $F_{1,11} = 76.19$, $P < 0.0001$). After controlling for female size, none of the remaining factors significantly explained the number of eggs. Total egg mass was also positively affected by female size ($R^2 = 0.706$, $F_{1,11} = 24.03$, $P < 0.001$), but the mean mannitol concentration of the algal population explained the significant 17% of the residual variation ($R^2 = 0.168$; $F_{1,11} = 11.93$, $P < 0.01$). The mean egg size in the

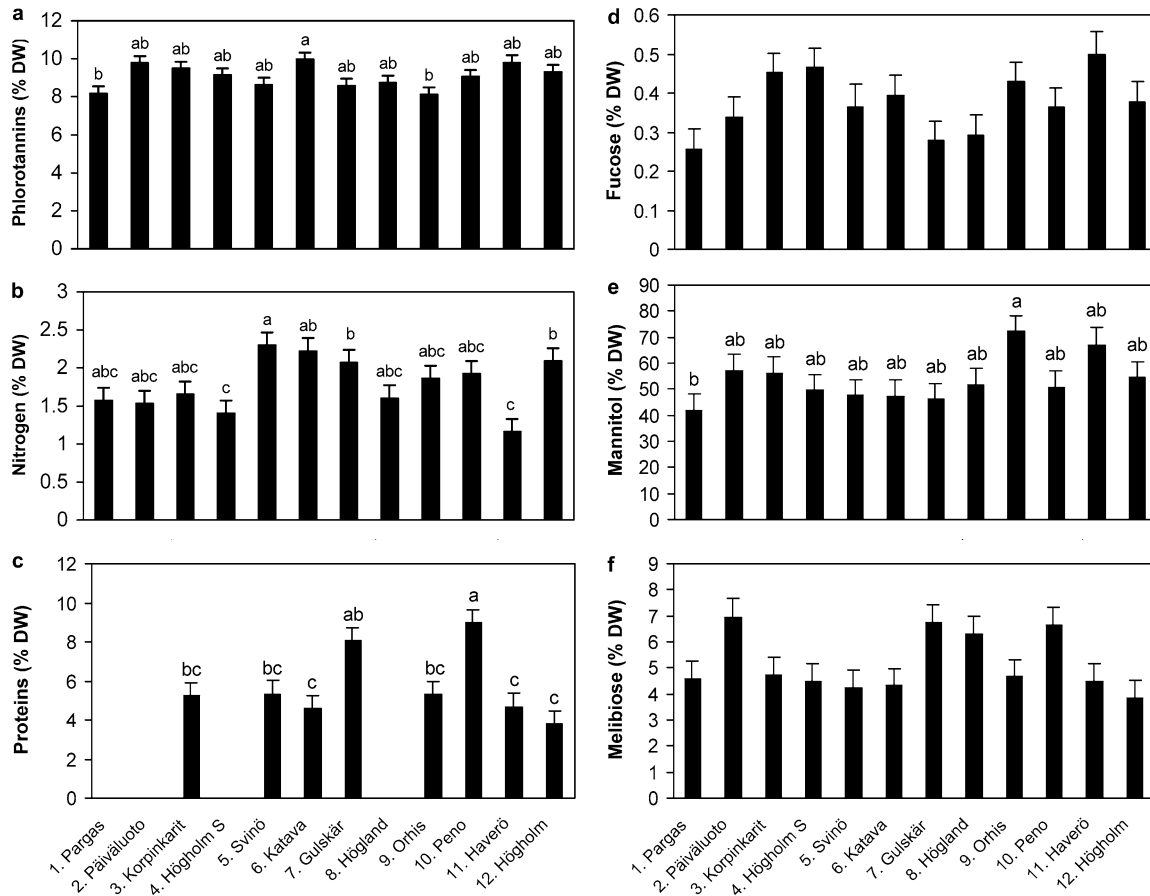


Fig. 2a–f Chemical characteristics of the food alga *Fucus vesiculosus* from each site (mean \pm SE). **a** phlorotannins, **b** nitrogen, **c** proteins, **d** fucose, **e** mannitol, and **f** melibiose. Different letters above the bars indicate significant differences at the $P < 0.05$ level according to Tukey's a posteriori comparisons. In **d** and **f** there were no significant pairwise differences after controlling for multiple comparisons. The sites are ordered from left to right according to the ascending number of eggs per female in each population. Values were measured from only eight sites in c

population was to some extent (26%) explained by female size ($R^2 = 0.263$; $F_{1,11} = 3.57$, $P = 0.088$), and after removal of the size effect, a significant 32% of the residual variation was explained by mannitol concentration of the algal population (Fig. 4b; $R^2 = 0.316$; $F_{1,11} = 6.74$, $P = 0.003$).

Discussion

We observed among-population variation in phlorotannin, nitrogen, protein, and sugar concentrations of *F. vesiculosus*. Variation was moderate to high, depending on the trait. This is consistent with the previous studies examining relatively small-scale spatial intraspecific variation in fucoid chemistry (e.g., Ilvessalo and Tuomi 1989 and Honkanen et al. 2001: phlorotannins and nitrogen; Pavia and Åberg 1996 and Pavia et al. 2003: phlorotannins; Zvyagintseva et al. 2003: sugars). There was also some spatial covariation in the chemical quality of algae as the contents of mannitol positively correlated

with that of fucose and the contents of melibiose with that of proteins. Thus, the quality of algae as food differed among the sites often in several chemical characteristics. In the current study, we were not focusing on the effects of within-site differences in algal quality on herbivore performance, but the within-site variation in food quality is potentially important for feeding preferences of herbivores. We found positive within-site covariation of all the sugars, positive covariation of phlorotannin with mannitol and melibiose, and negative covariation of nitrogen with phlorotannins, mannitol, and melibiose. Because of such covariation in chemistry, interpretations from correlative studies where feeding preferences or performance are related to a concentration of just one chemical trait have to be very cautious.

There is very little data on the effect of spatial interspecific variation in algal chemistry on herbivore fitness, but the existing data suggest that it may strongly modify fitness of herbivorous crustaceans (Cronin and Hay 1996b; Cole and Haggitt 2001; Taylor et al. 2003). Body size of *I. baltica* females showed remarkable spatial variation as well. Because the number of eggs and, to a lesser extent the egg size, increased with body size, the variation in body size should translate into spatial variation in fitness. Body size covaried with the phlorotannin concentration in *F. vesiculosus* population of the site: the higher the phlorotannin concentration, the larger were the females of *I. baltica*. This was an

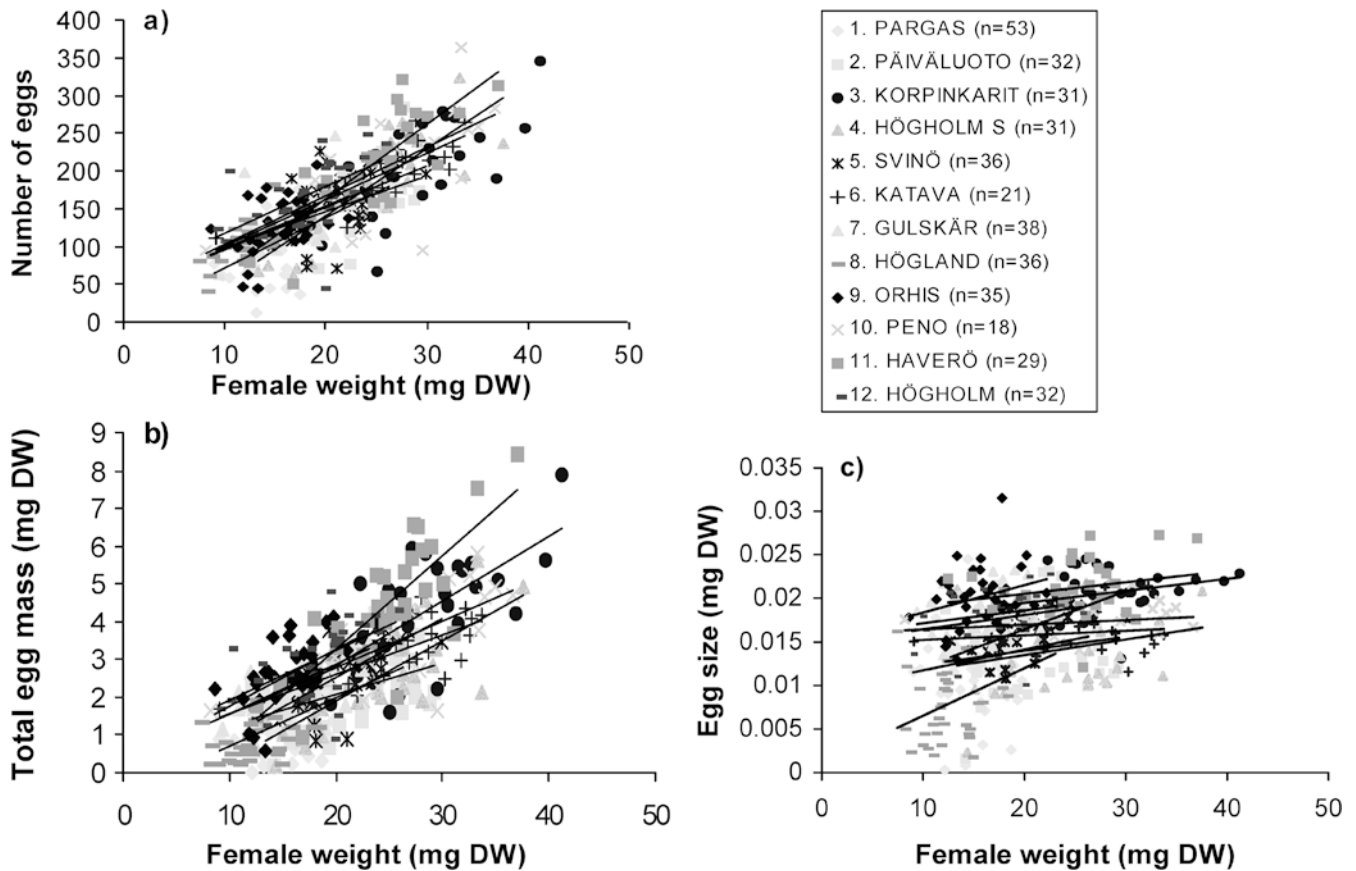


Fig. 3 The relationship between female size and **a** the number of eggs, **b** total egg mass, and **c** egg size in the 12 local populations

unexpected result since phlorotannins are usually assumed to have a detrimental rather than beneficial influence on the assimilation efficiency of herbivores (Stern et al. 1996; reviewed in Targett and Arnold 1998). However, not all herbivores are negatively affected by phlorotannins (reviewed in Targett and Arnold 2001) suggesting that adaptations to utilize phlorotannin-rich algae for food have evolved among marine herbivores.

We suggest three possible explanations for this observation: first, *I. baltica* may have adapted to utilize phlorotannins as an energy source. Phloroglucinol, the basic monomer unit of the phlorotannin polymers, can possibly be utilized to yield energy and/or carbon (M. Nikinmaa, personal communication). Degradation of such compounds can take place either by aerobic, enzymatic reactions or by fermenting microbes (Schink et al. 2000; Gibson and Harwood 2002). Microbes have been found in the hepatopancreas and hindgut of

terrestrial and semiterrestrial isopods, in which they have been shown to enhance digestive processes (Zimmer et al. 2001; 2002; Zimmer 2002). However, very little is known about intestinal microbes in marine isopods; in the only existing study, Zimmer et al. (2001) did not find endosymbionts in *I. wosnesenskii*, but nevertheless their results suggest that this species has an ability to digest phenolics. Jormalainen et al. (2001) found that *I. baltica* prefers the phlorotannin-rich brown algal species for food, which gives further circumstantial support for the possibility of an ability to utilize phlorotannins in one way or another. However, minor amounts of non-phlorotannin contaminants that can not be distinguished by the Folin–Ciocalteu assay (less than 5%; Van Alstyne 1995) may account for the bigger size of the herbivores, but we do not find this explanation very plausible.

Second, the herbivores may have chosen more of algal species other than *F. vesiculosus* in their diet in those populations where phlorotannins in *F. vesiculosus* were relatively high and, thus, phlorotannins could have

Table 2 Results of ANCOVA testing the differences between the sites in number of eggs, total egg mass, and egg size of *Idotea baltica* females. Dry weight of the female without eggs was used as a covariate

Source	Number of eggs			Egg mass			Egg size		
	df	F	P	df	F	P	df	F	P
Population	11	4.39	< 0.0001	11	7.37	< 0.0001	11	11.31	< 0.0001
Female weight	1	295.78	< 0.0001	1	140.57	< 0.0001	1	14.19	0.0002
Error	376			376			376		

Table 3 Correlations between the chemical characteristics of *F. vesiculosus*. Mean of site-specific correlation coefficients \pm SE, n , are shown below the diagonal (*asterisk* indicates significant deviation from zero at $P < 0.05$, calculated as $1.96 \cdot \text{SE}$). Regional correlations, based on site-specific means (r , P , n), are shown above the diagonal

	Proteins	Nitrogen	Phlorotannins	Fucose	Mannitol	Melibiose
Proteins	–	0.106	–0.383	–0.575	–0.403	0.783
	–	0.803	0.349	0.136	0.323	0.022
	–	8	8	8	8	8
Nitrogen	0.074 \pm 0.156	–	–0.179	–0.319	–0.135	0.382
	–	–	0.578	0.313	0.676	0.221
	8	–	12	12	12	12
Phlorotannins	0.127 \pm 0.131	–0.308 \pm 0.096	–	0.484	–0.057	–0.438
	–	*	–	0.111	0.861	0.155
	8	12	–	12	12	12
Fucose	0.202 \pm 0.165	–0.146 \pm 0.096	0.098 \pm 0.099	–	0.660	–0.431
	–	–	–	–	0.019	0.162
	8	12	12	–	12	12
Mannitol	0.033 \pm 0.142	–0.217 \pm 0.054	0.141 \pm 0.059	0.523 \pm 0.104	–	–0.117
	–	*	*	*	–	0.718
	8	12	12	12	–	12
Melibiose	–0.024 \pm 0.079	–0.322 \pm 0.091	0.282 \pm 0.082	0.191 \pm 0.096	0.572 \pm 0.057	–
	–	*	*	*	*	–
	8	12	12	12	12	–

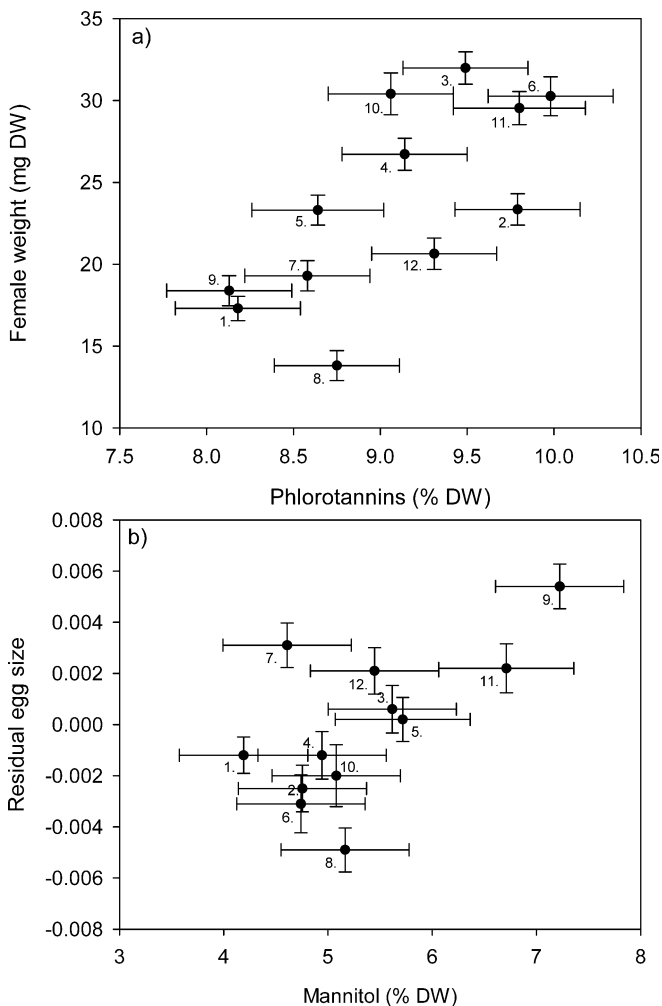


Fig. 4 Relationships between **a** site-specific mean phlorotannin concentration and female size, and **b** site-specific mean mannitol concentration and residual egg size (after effect of female size removed; means \pm SE, *site number* adjacent to each dot)

deterred them toward the lower-phenolic plants. Several other common algal species in the community have been shown to be less preferred but nevertheless to provide higher growth rate to *I. balticathan* *F. vesiculosus* alone (Jormalainen et al. 2001; Hemmi and Jormalainen 2004). The apparent inconsistency in the food preference and utilization efficiency has been explained by habitat preference for the persistent and complex habitat that gives shelter against predation (Jormalainen et al. 2001). Thus the lower mortality within *Fucus* habitat could then counterbalance the cost due to lower nutritional quality, but the optimal feeding strategy may depend on the local concentration of phlorotannins in *F. vesiculosus*.

Third, abiotic factors may have modified simultaneously both the algal chemistry and life-history traits of the herbivores. For example, the observed among-population variation may have been influenced by factors such as local temperature variation or variation in light availability. In sites with turbid water, water temperature rises faster in spring and the algal individuals reach closer to the surface. High water temperature increases the growth rate of crustaceans up to the optimum temperature, after which the growth rate may decrease (Hartnoll 2001; Shuster and Guthrie 1999; Panov and McQueen 1998). High phlorotannin concentration of the alga in the same sites may arise as a response to exposure to high UV radiation near the surface, as found in several brown algae, including *F. vesiculosus* (Pavia et al. 1997; Jormalainen and Honkanen 2001; Swanson and Druehl 2002). Other compounds that were not identified in this study may have an important role in modifying consumption patterns and herbivore traits as well (Deal et al. 2003; Hemmi et al. 2004). On the basis of recent studies (Poore and Steinberg 2001; Honkanen et al. 2002; Sotka and Hay 2002; Taylor et al. 2003), there is most probably a causal relationship between the host algal quality and fitness of the herbivores among populations instead of some third external factor affecting the plants and herbivores.

The number of eggs as well as the total egg mass showed substantial variation among sites as well. Body size of the mother was the most important determinant of both these fitness components. Egg number and size are typically maternal characters, and thus factors affecting female size directly modify reproductive output. After removing the effect of the body size of the mother, spatial variation in algal chemistry did not covary with the number of eggs, but the mannitol concentration of the food alga population positively covaried with egg size. Large egg size is known to be crucial in promoting forthcoming growth and survival of the offspring (Roff 1992; Einum and Fleming 2000). *F. vesiculosus* in the northern Baltic contains maximum amounts of mannitol in April–May (Lehvo et al. 2001). It uses mannitol as a storage compound to support growth during periods of low light in autumn and winter (Jensen 1956; Lüning et al. 1973; Gómez et al. 1998). The main period of ovarian development of *I. baltica* matches the time of maximum mannitol concentrations. Therefore, mannitol content of the alga may be especially important during the period of egg provisioning as it may provide energy-rich nutrition for the developing oocytes. This further highlights the important role of the sugar content of food in modifying reproductive performance of the isopods, as suggested by laboratory experiments (Hemmi and Jormalainen 2002). Mannitol concentration also correlated positively with other sugars, especially with fucose, which may indicate a similar functional role of these carbohydrates in the alga. Alternative explanations of the positive spatial covariation of phlorotannins with the fitness of the herbivore and mannitol with egg size in this plant–herbivore interaction remain ad hoc hypotheses until further experimentation.

Spatial variation in host-plant chemical quality among local populations and covariation of that with both the body size and egg size of the herbivore imply that herbivore fitness responds to plant chemistry. This emphasizes that a geographical mosaic has to be taken into account when studying plant–herbivore interactions. In fragmented environments, plant–herbivore interactions may form a geographic mosaic where the traits of the parties may evolve differently depending on the local selective environment (Thompson 1999b, Kingsolver et al. 2002). Some populations of herbivores may then be better adapted to utilize their host plants and, vice versa, local plant populations may vary in the level of their resistance. Though this study does not provide evidence for coevolutionary mosaics, among-site variation in plant chemistry and regional covariation of that with herbivore performance are prerequisites for the geographic mosaic of coevolution to occur. While confirmation of coevolutionary mosaic would demand evidence on genetic structuring of interacting populations, gene flow and local adaptations, we hypothesize that the interaction between *Idotea* and *Fucus* in a naturally fragmented archipelago may be a potential case of such a mosaic.

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