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Research article

Habitat heterogeneity, predation and gene flow: colour polymorphism in the isopod, *Idotea baltica*

SAMI MERILAITA*
Department of Animal Ecology, Evolutionary Biology Centre, Uppsala University, Norbyvägen 18 D, SE-752 36 Uppsala, Sweden
**Present address: Department of Ecology, Evolution and Marine Biology, University of California, Santa Barbara, CA 93106-9610, USA, tel.: +1-805-893-8249; fax: +1-805-893-4724; e-mail: merilait@lifesci.ucsb.edu*

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Abstract. The colour polymorphic isopod *Idotea baltica* inhabits the brown alga *Fucus vesiculosus* which is often colonised by the white epizoite *Electra crustulenta* (Bryozoa). In an experiment the predation risk for the different colour morphs of *I. baltica* was highly dependent on background colouration. Morph frequencies and *Electra* density varied substantially among 10 collecting sites but correlated poorly with each other, suggesting that local selection for cryptic colouration may be counteracted by gene flow. Indeed, estimates based on four polymorphic allozymes suggested rate of gene flow to be high. These results support the hypothesis that locally varying selection for cryptic colouration counteracted by gene flow contributes to the maintenance of colour polymorphism in *I. baltica*. The visual differences between the microhabitats and the differential microhabitat use between males and females seem to result in different patterns of selection on males and females for cryptic colouration. Also this is likely to play an important role for the polymorphism.

Key words: camouflage, colour polymorphism, divergent selection, gene flow, predation

Introduction

Colour polymorphism is an intriguing evolutionary phenomenon. What are the mechanisms responsible for the maintenance of several variants of a selected trait in one and the same populations? One possible answer is diverging selection pressures between localities counteracted by gene flow. Natural selection favouring local adaptations in a heterogeneous environment can lead to genetic differentiation among geographically separated populations (Endler, 1977). Gene flow may promote adaptation by making genetic novelties available throughout the species range, but can also restrict differentiation among local populations (Slatkin, 1987, 1994). In concert, natural selection for local adaptations and gene flow between populations can maintain genetic variation

in populations (Felsenstein, 1976; Hedrick *et al*., 1976; Jones *et al*., 1977; Sandoval, 1994a; King and Lawson, 1995).

In particular when polymorphism of cryptic colouration is considered, selection will obviously be closely associated with local conditions. Optimal colouration will be determined by the visual characteristics of the local habitat and in heterogeneous habitats also by microhabitat choice and microhabitat proportions within the habitat (Endler, 1978; Merilaita *et al*., 1999). Therefore, not only the visual differences in habitat between localities but also visual differences within a habitat together with microhabitat choice may influence on colour polymorphism. Given that the resource needs differ between males and females of a species, leading to differing habitat use patterns, this might result in divergent selection on male and female colouration and, eventually, introduce new cryptic morphs (c.f. Slatkin, 1984; Hedrick, 1993).

Here, I present a study about the significance of these factors affecting the colour polymorphism in the isopod *Idotea baltica* (Pallas). In this species the frequencies of the cryptic colour morphs as well as the visual characteristics of the habitat differ between localities (Salemaa, 1978). If the variation of the visual characteristics among locations is substantial the role of gene flow might be important for the polymorphism. Further, males and females differ in their microhabitat choice (Merilaita and Jormalainen, 1997, 2000). If the microhabitats differ visually, there may be divergent selection for cryptic colouration between males and females. Also this would obviously be of significance for the colour polymorphism. Specifically, I studied (I) predation risk of colour morphs of *I. baltica* on visually different backgrounds, (II) variation in morph frequencies among localities, (III) variation in visual characteristics of background among localities and between microhabitats within localities, and (IV) rate of gene flow based on indirect estimates from allozymes.

Methods

I. baltica and its habitat

In the Baltic Sea *I. baltica* (subspecies *baltica*) has five genetically determined colour morphs (Tinturier-Hamelin, 1963; Salemaa, 1978). At the south-western coast of Finland, where this study was carried out (Fig. 1), the uniform-coloured *uniformis* is the most frequent morph followed by the white-spotted *albafusca*. The three other morphs, the marbled *maculata* and the white-striped *bilineata* and *bilineata-lineata*, as well as combinations of the patterned morphs, are rare in this region (Salemaa, 1978; Jormalainen *et al*., 1995). The ground colour of *I. baltica* ranges from greenish yellow to brown and black, and an individual can to some extent change it through chromatophore

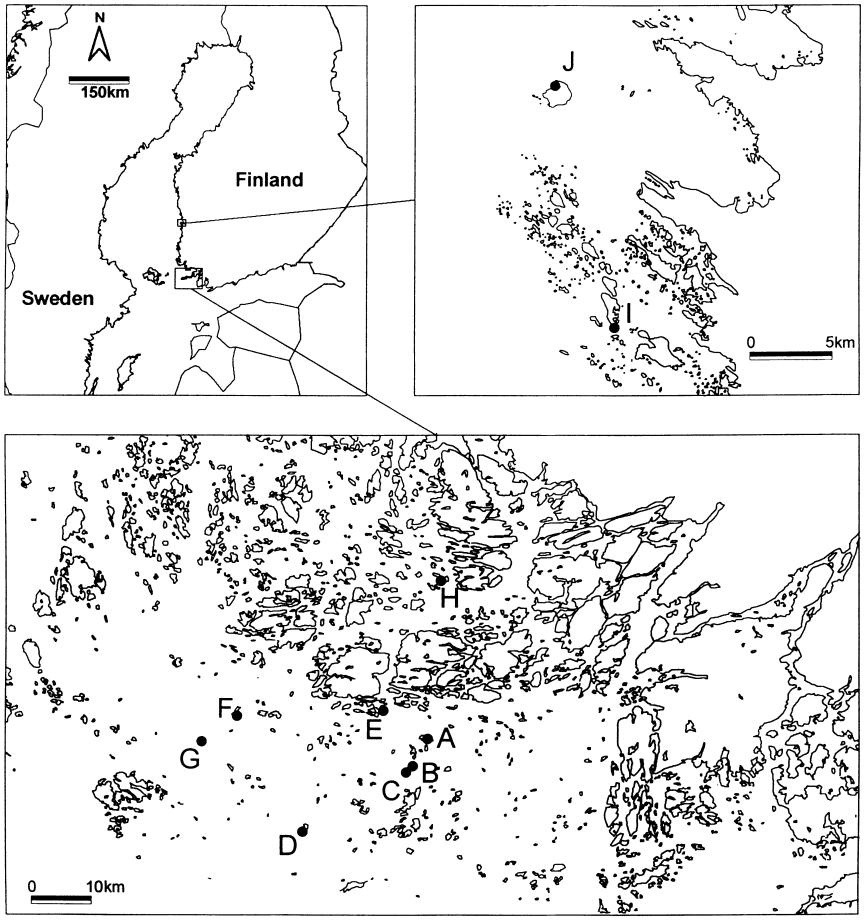

Figure 1. Geographic location of the 10 sampling sites.

responses to improve background matching (Tinturier-Hamelin, 1963). However, the white areas of the patterned morphs always remain unchanged.

In *I. baltica*, females are the heterogametic sex. Based on crossing experiments, it has been proposed that the genes for the four patterned morphs are located in the female chromosome, but that these morphs are also found in males because the sex-linkage is not perfect (Tinturier-Hamelin, 1963; Legrand-Hamelin and Legrand, 1982a,b). This would also provide a mechanistic explanation for the lower frequency of the patterned morphs in males than in females (c.f. Salemaa, 1978; Jormalainen *et al.*, 1995).

In the northern Baltic, *I. baltica* primarily inhabits *Fucus vesiculosus* (L.), which is the only brown alga in the area. The white bryozoan epizoite *Electra crustulenta* (Pallas) is often found growing on the alga. In this habitat the

morphs *uniformis* and *albafusca* appear cryptic (Salemaa, 1978; Merilaita, 1998). However, colour morph frequencies vary geographically between populations, and this variation seems to be related to how sheltered the habitat is, such that high exposure to wave action decreases the biotic diversity of the littoral community, including the diversity of *I. baltica* morphs and the density of white epizoites on *F. vesiculosus* (Salemaa, 1978). This has been suggested to decrease the proportion of the *albafusca* morph in areas with high exposure to waves through visual predation by fish (Salemaa, 1978). Accordingly, the proportion of the *albafusca* in relation to *uniformis* is expected to be higher around the islands of the inner archipelago than around the islands of the outer archipelago (Salemaa, 1978).

In *I. baltica* there is no colour-morph-dependent microhabitat choice, but instead males and females use the habitat differently (Merilaita and Jormalainen, 1997, 2000). Males are found more often than females in the apical parts of *F. vesiculosus*. Also mate choice in *I. baltica* is independent of colour morph (Jormalainen *et al*., 1992).

Predation experiment

Idotea baltica is preyed on by visually searching fishes, such as perch (*Perca fluviatilis* L.) (Salemaa, 1978; Jormalainen *et al*., 1995). I therefore used perch as predator in an experiment to examine the relative susceptibility of *albafusca* and *uniformis* phenotypes to predation in two visually different backgrounds. The fish were caught with a net (25 mm mesh size) and then habituated in 100 or 300 l aquaria, 6–12 fish in each, for 19–43 days on a diet of gammarids and commercial fish food. Two days before the experiment I moved a single fish to a 27 l aquarium with gravel and stones on the bottom. During the day preceding the experiment no food was provided. The experimental aquaria (27 l) were provided with either black gravel or with a mixture of black (90%) and white (10%) gravel imitating clean *F. vesiculosus* and *F. vesiculosus* with white epizoites, respectively. I used such two-dimensional habitat in order to prevent the isopods from hiding such that they only could use body colouration to conceal themselves. I released two isopods, one *uniformis* and one *albafusca* with a distinct pattern, in the aquarium 20 min before the perch was introduced. This allowed them to adjust the darkness of their ground colour to the background (Jormalainen and Tuomi, 1989). Note that there is no difference between the colour morphs in their preference for visually different parts of habitat (Merilaita and Jormalainen, 1997). Each pair was matched with respect to body length (to the nearest 0.5 mm), sex and reproductive status. The isopod which the perch ate or attacked first was considered as less cryptic on the current background. I rejected a replicate if there was an obvious difference in activity between the isopods, if a predation attempt was made when an isopod

was swimming so that the perch did not see it against the bottom, or if a predation attempt did not take place within 60 min. Each perch was used once on each of the two backgrounds in random order. Each isopod was used in only one replicate. After the experiment the fish were released back to the sea.

Sampling

I sampled *I. baltica* by collecting *F. vesiculosus* and shaking them out from the seaweed thalli. Collections were done around 10 islands in the archipelago in south-western Finland (Fig. 1) on June 26–29, 1996 (localities A–D) and on June 25–July 1, 1997 (E–J). I chose the sampling sites so that they would fall on three transects across the gradient of exposure from the inner to the outer archipelago (A–G and I, J; see Fig. 1). The purpose was to obtain variation in visual characteristics of the habitats within the three groups of sampling site as a result of variation in the density of *E. crustulenta* on *F. vesiculosus*. A separate sample from the inner archipelago was also taken (H). Consequently, the samples came from four groups of sampling sites. Thus there are three levels of population hierarchy: (1) local population, referring to the isopods at a sampling site, (2) local populations within a group of sampling sites, and (3) total population, which includes all 10 sampling sites. For each sample I classified the isopods according to sex and colouration and stored them in a freezer (−70 °C) for electrophoresis. Because the colour pattern of *albafusca* morph is highly variable (e.g. Merilaita, 1998) I used a four digit code (0 = no white spots, 1 = some small white spots, 2 = some large white spots, and 3 = considerable proportion of the surface is white) to classify it, in addition to record its presence or absence. In order to compare the visual characteristics of the habitat of *I. baltica* between the sites, I also collected 10–19 randomly chosen *F. vesiculosus* thalli from each sampling site. From each plant *E. crustulenta* colonies were measured along a randomly selected branch from the base to the apex of the plant. I calculated *E. crustulenta* density as the proportion of the length of the branches covered.

Electrophoresis analyses

In order to estimate gene flow, I used electrophoresis to study allozyme variation among the local *I. baltica* populations. I chose for the analysis the four allozyme loci which Bulnheim and Fava (1982) found to be polymorphic out of 12 studied loci in *I. baltica* in the northern Baltic. These four loci were phosphoglucose isomerase (PGI; EC 5.3.1.9), phosphoglucomutase (PGM; EC 5.4.2.2), gluconate pyruvate transaminase (GPT; EC 2.6.1.2.) and mannose-6-phosphate isomerase (MPI; EC 5.3.1.8). They were examined for allozyme frequencies by electrophoresis on cellulose acetate plates (Titan III, Helena

Laboratories, Beaumont, Texas) according to the methods outlined in Hebert and Beaton (1989). From each animal 2–4 legs or pleopods were homogenised in 10–15 μl Tris–HCl (100 mM, pH 8.0) and then centrifuged for 5 min at 12,000 × *g*. The resulting supernatants were applied on cellulose acetate plates and run for 25 min (PGI, PGM and MPI) or 45 min (GPT). PGI, PGM and MPI were stained as described in Hebert and Beaton (1989). GPT was visualised using the defluorecent method (e.g. Allendorf *et al*., 1977) adapted for the same agar overlay technique used with the other allozymes. For all allozymes individuals were rerun to cross-check scorings between plates and to resolve unclear bands. The alleles in each locus were numbered ascending from the one with the fastest electrophoretic mobility to the slowest one. The visualisation of MPI did not work consistently in the analysis of the samples from 1996 (populations A–D), but was unproblematic later. Therefore, MPI was excluded from the analysis of population structure when all the local populations were included.

I analysed the allozyme frequencies using Arlequin software (Schneider *et al*., 1997). Departure from the Hardy–Weinberg equilibrium was tested following a procedure using a modified version of Markov chain random walk algorithm described by Guo and Thompson (1992). The number of Markov chain steps was set to 100,000 preceded by 1000 dememorisation steps. I used Wright's F_{ST}-statistics to indirectly estimate gene flow (Slatkin, 1985). The parameter F_{ST} measures the extent of population subdivision by comparing the average heterozygosity of local populations to the average heterozygosity of the total population expected under random mating (Wright, 1978). Low values of F_{ST} can be interpreted to indicate a high level of gene flow (Avise, 1994). F_{ST} ranges from 0 to 1, but its estimates can yield even slightly negative values in which case they should be interpreted as zeros (Long, 1986). I calculated pairwise F_{ST} estimates between each pair of sampling sites. I also used a hierarchical analysis of molecular variance (AMOVA). AMOVA is based on a hierarchical analysis of variance framework and enables investigation of population structure by testing *F*-statistics at different levels of spatial hierarchy, that is within the local populations (F_{ST}), among local populations within the groups of sampling sites (F_{SC}) and among the groups of sampling sites (F_{CT}). Tests of statistical significance of the pairwise F_{ST} estimates and the AMOVA were based on non-parametric permutation procedures (see Schneider *et al*., 1997). For the pairwise F_{ST} estimates 1000 permutations and for the AMOVA 16,000 permutations were made.

To test if the differences in colour morph frequencies are coupled with the allozyme divergence among the local populations, I used Mantel matrix randomization test (Manly, 1997). The test was done on the pairwise F_{ST} estimates and pairwise differences in colour morph frequencies separately for males and females. Significance testing was based on 5000 permutations.

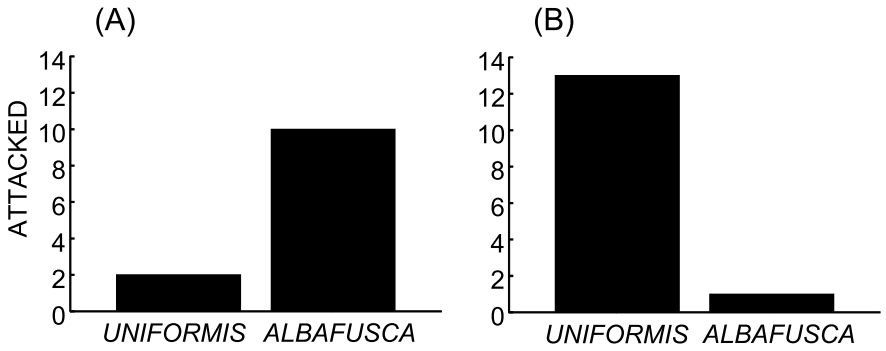

Figure 2. Number of the replicates in which *uniformis* or *albafusca* was first attacked (A) on uniform dark background and (B) on white-spotted background by perch.

Results

Predation experiment

In the predation experiment the colour morph resembling the background more closely was significantly less susceptible to predation on both backgrounds (Fig. 2). On the uniform black background ($n = 12$), *albafusca* was attacked more often than *uniformis* ($\chi^2 = 5.33$, df = 1, $p < 0.05$), while on the white-spotted background ($n = 14$) *uniformis* was attacked more often than *albafusca* ($\chi^2 = 10.29$, df = 1, $p < 0.01$).

Variation in colour morph frequencies

Colour morph frequencies varied significantly among the sampling sites (males: $\chi^2 = 33.7$, df = 9, $p < 0.001$; females: $\chi^2 = 92.1$, df = 9, $p < 0.001$; Table 1). Both the presence of *albafusca* trait ($\chi^2 = 48.5$, df = 1, $p < 0.001$) and the strength of its expression ($\chi^2 = 68.3$, df = 3, $p < 0.001$) depended on sex. The *albafusca* morph in general, and especially the *albafusca* of scores 2 and 3, were overrepresented in females and underrepresented in males when compared to expected frequencies. However, the proportion of *albafusca* individuals at the sampling sites correlated positively between males and females ($r_s = 0.90$, $n = 10$, $p < 0.001$). Also, the mean *albafusca* score correlated between males and females ($r_s = 0.85$, $n = 10$, $p = 0.0018$).

The density of *E. crustulenta* on *F. vesiculosus* varied significantly among the sampling sites (Kruskal–Wallis test: H = 118.3, df = 9, $p < 0.001$; Table 1). In several locations (C, D, F and G; Table 1) there were no or only few *E. crustulenta* but still the frequency of the *albafusca* morph was substantial. Consequently, *E. crustulenta* density did not correlate significantly with the

Table 1. The number of *I. baltica* males and females and the relative frequency of *uniformis* and *albafusca* morphs in the samples, and the density of *E. crustulenta* on *F. vesiculosus* for each sampling site

	A	B	C	D	E	F	G	H	I	J
Males	35	28	31	43	37	36	30	46	43	27
uniformis	0.629	0.714	0.807	0.651	0.676	0.833	0.867	0.674	0.977	1.000
albafusca	0.371	0.286	0.193	0.349	0.324	0.167	0.133	0.326	0.023	0.000
1	0.229	0.179	0.129	0.209	0.243	0.167	0.133	0.304	0.000	0.000
2	0.114	0.071	0.032	0.093	0.054	0.000	0.000	0.000	0.023	0.000
3	0.029	0.036	0.032	0.047	0.027	0.000	0.000	0.022	0.000	0.000
Females	56	32	32	21	93	32	62	45	70	70
uniformis	0.393	0.406	0.625	0.381	0.409	0.563	0.516	0.356	0.757	0.986
albafusca	0.607	0.594	0.375	0.619	0.591	0.437	0.484	0.644	0.243	0.014
1	0.196	0.281	0.156	0.238	0.280	0.125	0.226	0.244	0.171	0.014
2	0.179	0.125	0.031	0.048	0.237	0.187	0.145	0.200	0.014	0.000
3	0.232	0.187	0.187	0.333	0.075	0.125	0.113	0.200	0.057	0.000
E. crustulenta density (%)	18.9	1.4	0	0	14.3	0.3	0	40.3	2.2	0.1

For *albafusca* the relative frequency of each phenotypic class is also presented.

relative frequency of *albafusca* males ($r_s = 0.39$, $n = 10$, $p = 0.27$) or females ($r_s = 0.40$, $n = 10$, $p = 0.25$) across the sampling sites. In the localities with mean density >1%, on average 31.1% (range: 22.0–44.9%) of the height of alga down from the apical tips was completely free from *E. crustulenta*. This indicates a visual contrast between the apical and basal part of the alga in localities where *E. crustulenta* is present.

Electrophoresis analyses

Electrophoresis revealed five alleles in PGI, seven in PGM, four in GPT and five in MPI (Table 2). Compared to the starch gel electrophoresis for some Baltic *I. baltica* populations made by Bulnheim and Fava (1982) this is one rare allele more for both PGM (allele 7; Table 2) and GPT (allele 1). For the PGI locus I did not observe the rare fastest allele of Bulnheim and Fava (1982), but instead two rare ones more in the slow end (alleles 4 and 5).

None of the three allozyme loci PGI, PGM and GPT deviated significantly from the Hardy–Weinberg expectation for neutral alleles in any of the samples ($p > 0.05$ in all tests). Pairwise F_{ST} estimates between the sampling sites were generally very low, the highest being $F_{ST} = 0.014$ (Table 3). Consequently, the allelic frequencies can be considered to be highly similar among the populations.

The AMOVA revealed that variation within local populations accounted for most of the allozyme variation (Table 4). Variation among local populations

Table 2. Sample sizes and allele frequencies for the four loci in the 10 sampling sites

	A	B	C	D	E	F	G	H	I	J
PGI										
n	88	59	63	64	79	66	92	66	113	97
1	0.023	0.008	0.032	0.016	0.013	0.030	0.027	0.030	0.022	0.010
2	0.903	0.949	0.929	0.922	0.930	0.939	0.929	0.886	0.938	0.969
3	0.068	0.042	0.032	0.063	0.057	0.030	0.043	0.076	0.040	0.021
4	0.006	0.000	0.000	0.000	0.000	0.000	0.000	0.008	0.000	0.000
5	0.000	0.000	0.008	0.000	0.000	0.000	0.000	0.000	0.000	0.000
PGM										
n	87	59	60	63	78	65	92	66	111	96
1	0.006	0.017	0.025	0.008	0.013	0.008	0.000	0.030	0.014	0.010
2	0.178	0.161	0.150	0.111	0.174	0.154	0.136	0.098	0.158	0.182
3	0.460	0.475	0.450	0.476	0.445	0.508	0.478	0.545	0.416	0.417
4	0.264	0.220	0.283	0.310	0.284	0.277	0.304	0.227	0.330	0.302
5	0.086	0.076	0.083	0.087	0.071	0.054	0.065	0.083	0.063	0.073
6	0.006	0.034	0.017	0.000	0.013	0.000	0.016	0.008	0.018	0.016
7	0.000	0.017	0.000	0.008	0.000	0.000	0.000	0.008	0.000	0.000
GPT										
n	88	59	63	64	79	66	92	66	113	97
1	0.000	0.000	0.000	0.000	0.006	0.000	0.000	0.000	0.000	0.000
2	0.244	0.288	0.349	0.305	0.272	0.288	0.310	0.204	0.252	0.278
3	0.750	0.712	0.651	0.680	0.715	0.712	0.679	0.795	0.747	0.716
4	0.006	0.000	0.000	0.016	0.006	0.000	0.011	0.000	0.000	0.005
MPI										
n	–	–	–	–	78	64	87	66	111	96
1					0.032	0.008	0.023	0.023	0.005	0.000
2					0.523	0.602	0.644	0.629	0.613	0.628
3					0.348	0.320	0.270	0.273	0.279	0.304
4					0.071	0.063	0.057	0.053	0.081	0.063
5					0.026	0.008	0.006	0.023	0.023	0.005

within groups of sampling sites was very low and non-significant. However, variation among groups of local populations was significant, even though it accounted for less than 1% of the variation (Table 4). The fixation indices were low at all hierarchical levels of population, suggesting a high degree of gene flow within and among the groups of sampling sites.

The results were very similar, when all four loci from the localities E–J were used in the analysis. None of the four loci in any of these samples differed significantly from the Hardy–Weinberg expectation for neutral alleles. The pairwise F_{ST} estimates between the sampling sites were again very low, the highest being $F_{ST} = 0.009$. The population structure revealed by AMOVA was practically identical to the one based on three loci from 10 locations (Table 4).

Differences in colour morph frequencies among local populations did not increase with allozymic differences (Mantel matrix randomization test based on

Table 3. Pairwise F_{ST} estimates between the 10 local populations based on PGI, PGM and GPT loci, and, in parentheses, distances between the sampling sites in kilometers

	A	B	C	D	E	F	G	H	I	
B	−0.00304									
	(5)									
C	0.00315	−0.00301								
	(6)	(2)								
D	−0.00035	−0.00254	−0.00440							
	(25)	(21)	(20)							
E	−0.00441	−0.00483	−0.00232	−0.00359						
	(9)	(10)	(11)	(24)						
F	−0.00244	−0.00550	−0.00178	−0.00434	−0.00431					
	(31)	(30)	(29)	(22)	(24)					
G	0.00056	−0.00244	−0.00437	−0.00586	−0.00320	−0.00490				
	(37)	(35)	(34)	(22)	(30)	(7)				
H	0.00068	0.00353	0.01706	0.00734	0.00596	0.00342	0.00962			
	(26)	(31)	(32)	(47)	(23)	(40)	(47)			
I	−0.00115	0.00133	0.00312	0.00045	−0.00320	0.00016	0.00081	0.01005		
	(147)	(152)	(153)	(162)	(142)	(143)	(148)	(122)		
J	0.00015	−0.00171	−0.00114	−0.00022	−0.00409	−0.00148	−0.00062	0.01442	−0.00290	
	(161)	(165)	(166)	(175)	(156)	(156)	(161)	(136)	(14)	

Table 4. Results of AMOVA for three loci from all 10 local populations and, in parentheses, for four loci from six local populations (see text for details)

Source of variation	df	Percentage of variation	Fixation index	*p*
Among groups of local populations	3 (2)	0.31 (0.40)	0.0031 (F_{CT}) (0.0040)	0.018 (0.015)
Among local populations within groups	6 (3)	−0.26 (−0.24)	−0.0026 (F_{SC}) (−0.0024)	0.89 (0.90)
Within local populations	1564 (1020)	99.95 (99.84)	0.0005 (F_{ST}) (0.0016)	0.47 (0.38)
Total	1573 (1025)			

10 populations and 45 pairwise comparisons for males: $r = -0.19$, $p = 0.069$; for females: $r = 0.023$, $p = 0.38$). This indicates that the variation in coloration is uncoupled from the allozymic variation.

Discussion

The predation experiment showed that the predation risk for both the *uniformis* and the *albafusca* morphs was strongly dependent on the visual background. *Albafusca* suffered lower predation than *uniformis* on the white-spotted

background, suggesting that it could be adapted to habitats where *F. vesiculosus* frequently carries white epizoites. Likewise, *uniformis* was significantly less susceptible to predation than *albafusca* on the monochrome background, suggesting an adaptation to *F. vesiculosus* free of white epizoites. In general, there is a wealth of examples showing that predation can select for prey colouration that resembles the visual background (Cott, 1940; Edmunds, 1974; Sandoval, 1994b).

The density of the epizoite *E. crustulenta* on *F. vesiculosus* varied significantly among the islands in the archipelago. Consequently, the direction of selection for cryptic colouration is likely to differ among local populations. However, the relative colour morph frequencies of the local *Idotea* populations poorly corresponded to the density of *E. crustulenta*. This is in accordance with the hypothesis that gene flow can interfere with local adaptations (Slatkin, 1985, 1987; Storfer *et al*., 1999).

Although it is impossible from this study to predict exactly when, in terms of density of *E. crustulenta*, selection should favour *albafusca* or *uniformis*, obviously we should expect *uniformis* to be favoured in habitats with no or few *E. crustulenta*. However, local populations in such habitats (except population J) were highly polymorphic. The unexpectedly high frequency of *albafusca* morph in these islands of the outer archipelago could be explained by gene flow from the inner archipelago interfering with local selection for cryptic coloration. As the islands, and thus also the local populations of *I. baltica* around them are much bigger in the inner archipelago, it seems likely that gene flow would mainly be from the inner to the outer archipelago. Because the islands of the outer archipelago are smaller and more isolated, there is also a possibility that the density of predators may be low there, which might result in somewhat lower intensity of selection for cryptic coloration in these local populations.

Both pairwise F_{ST} estimates and AMOVA suggested a high rate of gene flow to occur among local *I. baltica* populations on the geographic scale of this study. The pairwise F_{ST} estimates and the fixation indices from the AMOVA were very low. Furthermore, based on the AMOVA, practically no genetic differentiation was observed between local populations within the groups of sampling sites. The groups of local populations were slightly but significantly subdivided. These regional differences indicate a negative effect of distance on gene flow because the distances between regions were on average higher than the distances between the local populations within regions. These results are supported by the study by Bulnheim and Fava (1982) which shows a highly uniform isozyme composition in *I. baltica* between sampling sites in the southern Baltic Sea.

This genetic similarity among the local populations conceivably might reflect common ancestry rather than ongoing gene flow. This would require that all the local populations encompassed in the present study would be representative

and undifferentiated samples of a common ancestral population, which invaded the Baltic Sea after the last ice age. However, such a static explanation is incompatible with the island dynamics of the Finnish archipelago. Post-glacial land lifting, which currently is 4.1–6.4 mm/year in the study area (Kakkuri, 1990), continually creates new islands, at the same time as old islands merge to the mainland. Consequently, littoral organisms are slowly colonising new areas and abandoning old ones. I consider it unlikely that such a continuous subsampling of the highly polymorphic allozymes of *I. baltica* would have resulted in the high genetic homogeneity observed here, unless the rate of gene flow has been high.

The high rate of gene flow in *I. baltica* is probably due to animals drifting with uprooted seaweed, or swimming or drifting by themselves (Tully and Céidigh, 1986; Fava *et al.*, 1992). Newly born juveniles probably are especially likely to be washed away from their substrate by wave action.

The apical parts of *F. vesiculosus* were free from epizoites even in those habitats where the lower parts were densely covered by them. Because *I. baltica* males more often than females reside on the apical parts of the alga (Merilaita and Jormalainen, 1997, 2000), *albafusca* is likely to suffer a higher predation risk in males than in females. This conclusion is also supported by an earlier predation experiment (Jormalainen *et al.*, 1995) where *albafusca* had lower predation risk in females than males, and females in general had lower predation risk than males. Thus, sex-dependent predation susceptibility of the morphs may provide an adaptive explanation for the higher proportion of *albafusca* in females than in males. This divergent selection between sexes can especially be expected to take place in the inner archipelago where the density of *E. crustulenta* is high, resulting often in a strong visual contrast between the apical and the lower parts of *F. vesiculosus*. It may have facilitated the initial evolution of the colour morphs and may provide an additional mechanism for the maintenance of the polymorphism in *I. baltica*.

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