

Evolution of sex differences in microhabitat choice and colour polymorphism in *Idotea baltica*

SAMI MERILAITA* & VEIJO JORMALAINEN†

*Department of Zoology, Uppsala University

†Department of Biology, Laboratory of Ecological Zoology, University of Turku

(Received 1 March 1996; initial acceptance 12 June 1996;

final acceptance 14 October 1996; MS. number: 5175)

Abstract. We studied microhabitat choice of colour morphs, causes of sex differences in microhabitat use and colour polymorphism in *Idotea baltica*, a marine isopod living mainly on the brown alga *Fucus vesiculosus*. The colour morphs differ in frequencies between the sexes and appear to be cryptic on the visually heterogeneous *Fucus*. In this study, no colour-morph-dependent preference for visually matching microhabitats was found. However, in all three experiments conducted, females were found more often on the lower parts of the *Fucus* than males. The microhabitat choice of the sexes was directed by some character of *Fucus* itself, not by preferred height within the plant. However, the sexes did not choose differently between upper and lower parts of *Fucus* as food. The food choice and substrate choice correlated in males but not in females, implying that microhabitat and feeding preferences are more tightly associated in males. We propose that the stronger preference for the less exposed lower parts of *Fucus* as microhabitat and the lack of correlation between microhabitat and substrate choice in females can be explained in terms of a greater investment in anti-predator protection in females than in males. Thus, the sexual difference in microhabitat choice would ultimately result from different strategies maximizing reproductive success in males and females. We suggest that the sexual differences in coloration and colour morph frequency in *I. baltica* are explained as an adaptation to sex differences in patterns of habitat use.

© 1997 The Association for the Study of Animal Behaviour

Patterns of microhabitat use are generally considered to result from predation risk and resource distribution among the microhabitats (Dill 1987; Lima & Dill 1990). An animal can reduce its risk of detection by a visually searching predator by preferring the microhabitat that either most resembles its coloration or offers the most protection (Edmunds 1974). Because crypsis depends on the visual resemblance between the animal's colour pattern and its background (Endler 1978) the evolution of cryptic coloration must be tightly linked to the evolution of microhabitat choice.

In colour polymorphic animals the phenotypes could, in some cases, attain the best crypsis by choosing different microhabitats (Edmunds 1974). Microhabitat choice can also differ between males

and females because of sex differences in resources needed for successful reproduction (Slatkin 1984). Both colour-morph-dependent microhabitat choice (Garcia-Dorado 1986; De Meeüs et al. 1993) and sex-dependent microhabitat choice (Hedrick 1993) can in theory enhance the maintenance of polymorphism under some conditions. Colour-morph-dependent (Schoener & Schoener 1976; Kettlewell & Conn 1977; Gillis 1982; Reinert 1984; Morey 1990; Sandoval 1994) and sex-dependent microhabitat choice (Jormalainen & Tuomi 1989; Forsman & Shine 1995) have also been found in some natural populations of colour polymorphic species.

Idotea baltica (Isopoda) is a widespread marine crustacean with genetically determined colour polymorphism (Tinturier-Hamelin 1963). In the northeastern Baltic it lives mainly on the bladder wrack *Fucus vesiculosus* which, with its epiphytes, is also the adults' main source of food (Salemaa 1979). *Fucus vesiculosus* is a brown alga with apical growth, the apices branching dichotomously

Correspondence: S. Merilaita, Department of Zoology, Uppsala University, Villavägen 9, S-752 36 Uppsala, Sweden (email: sami.merilaita@zoologi.uu.se). V. Jormalainen is at the Department of Biology, Laboratory of Animal Ecology and Systematics, University of Turku, FIN-20014 Turku, Finland.

once a year (e.g. Khailov et al. 1978; Carlson 1991). It constitutes a visually highly heterogeneous habitat (Salemaa 1978). The greenish yellow of the young tips changes gradually to the dark brown and black of the older mid and lower parts. The old parts may be encrusted by the bryozoan *Electra crustulenta* and the barnacle *Balanus improvisus*, and thus appear white-spotted. The younger parts are practically always free from epizoids. In addition the thallus may be a heterogeneous food source as a result of variation in the contents of secondary compounds and nutrients (Hay & Fenical 1988; Ilvessalo & Tuomi 1989; Yates & Peckol 1993) and in the structure of the tissue (Salemaa 1987) between the different parts of the thallus.

Idotea baltica has four main colour morphs which appear to be cryptic, and the degree of polymorphism varies between populations with the coverage of *E. crustulenta* on *Fucus* (Salemaa 1978). In polymorphic populations the sexes differ in morph frequencies so that the morph diversity is higher in the females (Salemaa 1978; Jormalainen et al. 1995). Among the males in a typical population, the most common morph, unicoloured *uniformis*, clearly outnumbers the second most common morph, white-spotted *albufusca*. In females, by contrast, the frequencies of *uniformis* and *albufusca* are roughly equal. The rest of the main morphs and the combinations of the main morphs are clearly less frequent (Salemaa 1978; Jormalainen et al. 1995). *Uniformis* appears to match visually on clean parts of *Fucus* and *albufusca* on parts encrusted by *Electra* and *Balanus*. The ground colour of the females on average is darker than that of the males (Jormalainen & Tuomi 1989). *Idotea baltica* is a frequent prey of several visually searching fish species, for example perch, *Perca fluviatilis*, and eelpout, *Zoarces viviparus* (Salemaa 1978; Jormalainen et al. 1995).

In colour polymorphic animals, habitat choice is of special interest, because the crypsis of each colour morph varies between visually different microhabitats in different ways. In other words, habitat choice is a central question in the evolutionary exploration of colour polymorphism. Earlier studies in *I. baltica* have indicated that microhabitat choice differs between the sexes (Jormalainen & Tuomi 1989), and there have also been some indications of colour-morph-dependent microhabitat choice (Salemaa 1986;

Jormalainen & Tuomi 1989). Here we present an experimental analysis of microhabitat choice in *I. baltica*. We specifically wanted to find out if the colour morphs choose visually matching microhabitats and whether the choice of height or the preference of different parts of *Fucus* as food could explain the sex differences in microhabitat choice.

METHODS

We carried out the experiments in the Archipelago Research Institute of the University of Turku in the Archipelago Sea, southwestern Finland (60°14'N, 21°60'E). Both isopods and algae used in the experiments were taken from the vicinity of the institute. We obtained the isopods by collecting *Fucus* and shaking them out from the thalli. We housed the isopods in 20-litre aerated aquaria with *Fucus* provided as food and habitat, and temperature and photoperiod following natural conditions. After the experiments the isopods were returned to sea.

Microhabitat Choice by Colour Morph and Sex

In May 1994 we carried out an experiment to study the effects of colour morph and sex on microhabitat choice. It was done in six successive subsets (i.e. series of replicates), the proportions of each morph and sex being equal in all of them. We used 10-litre cylinder-shaped aquaria with a semi-natural habitat with sand on the bottom, two stones to which two small *Fucus* thalli were fixed, and an additional stone. These experimental thalli were prepared from selected pieces of *Fucus* so that one had no epizoids, while the other consisted of pieces with barnacles and *Electra* on the lower parts. All the pieces were complete in the sense that they consisted of both young and old (i.e. more than 3 years old) parts. The two thalli in each aquarium were always from the same site in order to reduce variation from environmental differences. In each aquarium we introduced one *Idotea*, either a male *uniformis* ($N=30$) or *albufusca* ($N=27$), or a female *uniformis* ($N=29$) or *albufusca* ($N=29$). We recorded the location of each isopod 11–12 times with at least 2-h intervals during 3 days. The six microhabitat categories were young and old parts of the epizoid-free *Fucus*, young and old parts of the *Fucus* with

epizoites, bottom and open water (i.e. swimming). As young parts we defined the yellow and light brown parts, which were usually the last three branchings of the dichotomous thalli.

Height Choice

In May and the beginning of June 1995 we conducted an experiment to determine whether the isopods might choose their microhabitat by height or some property of the *Fucus* thallus itself. We placed a *Fucus* and an *I. baltica* of either sex in 2.5-litre jars. In half of the replicates the thallus was placed upright in a natural position ($N_{\text{males}}=16$, $N_{\text{females}}=13$), and in the other half the thallus was inverted with the basal part up and the apices down touching the bottom ($N_{\text{males}}=14$, $N_{\text{females}}=14$). The thalli reached from the bottom of the jar up to the water surface and were complete in the sense that they included both young and old parts. We observed the isopods 23–24 times with at least 1-h intervals during 3 days and recorded whether they were positioned in the old or the young part of the thallus. The division between old and young parts was made by the same criterion as in the first experiment.

Food Choice

In May and early June 1995 we conducted two sets of food-choice experiments using 1-litre plastic pots with a bottom area of 9×20 cm. In each pot we put one *Idotea* of either sex and on the bottom two pieces of *Fucus*, each larger than the isopods. The isopods were starved for 24 h before the experiment. To quantify food consumption we weighed the *Fucus* pieces to the nearest 1 mg before the experiment, and again after 120 h when the experiment was finished. Before weighing the alga pieces we carefully dried them with tissue paper. During the light hours of the experiment we recorded on which of the pieces the isopods were sitting 19–25 times with at least 1-h intervals. In the first series of replicates the isopods ($N_{\text{males}}=43$, $N_{\text{females}}=30$) were given a choice between an apical piece and a piece from an old part of *Fucus*. The young and old pieces in each pot always originated from the same *Fucus* thallus. In the second series of replicates the isopods ($N_{\text{males}}=44$, $N_{\text{females}}=25$) were offered a choice between apical pieces from a *Fucus* with and without epizoites. This was done to test

whether the existence of epizoites on the *Fucus* plant correlate with some characters of the thallus affecting food choice. Because the epizoites are mainly found on the lower parts of the thalli the two kinds of pieces did not differ in appearance and the possibility of vision-based choice was excluded. To tell the two kinds of pieces apart we cut them into different shapes. The tissue of the apical pieces was less than 2 years old. The algae were collected from the same site.

General Procedures and Analysis

The water temperature in the experiments ranged from 7.0 to 10.3°C following natural conditions. The photoperiod was 17:7 h light:dark. All the observations of the isopods were made during light hours when a behavioural response against visual predators could be expected.

When analysing the data, we used the relative frequency of observations in each microhabitat category. Because the distribution of these variables was not normal, a non-parametric two-factor analysis of variance based on an extension of the Kruskal–Wallis test was used for the factorial analyses (Zar 1984). We applied the method to the appropriate 2×2 factorial design (Seaman et al. 1994). When a common null hypothesis was tested with multiple tests and significances were found we applied a sequential Bonferroni test (Rice 1989) to control type I error rate over the group of tests.

RESULTS

Microhabitat Choice by Colour Morph and Sex

Microhabitat choice did not differ between the colour morphs *uniformis* and *albafusca* in either sex (Fig. 1a, Table I). The males were observed significantly more often on the young part of the epizoite-free thallus than the females (Fig. 1b, Table I). When contrasting young and old parts of *Fucus* in general, males were found more often on the young parts than females, while, conversely, the females were found more often on the old parts than males (Fig. 1b, Table I). When the epizoite-free thallus was contrasted with the thallus with epizoites, there were no differences between the sexes (Fig. 1b, Table I). There was a general preference for the thalli with epizoites

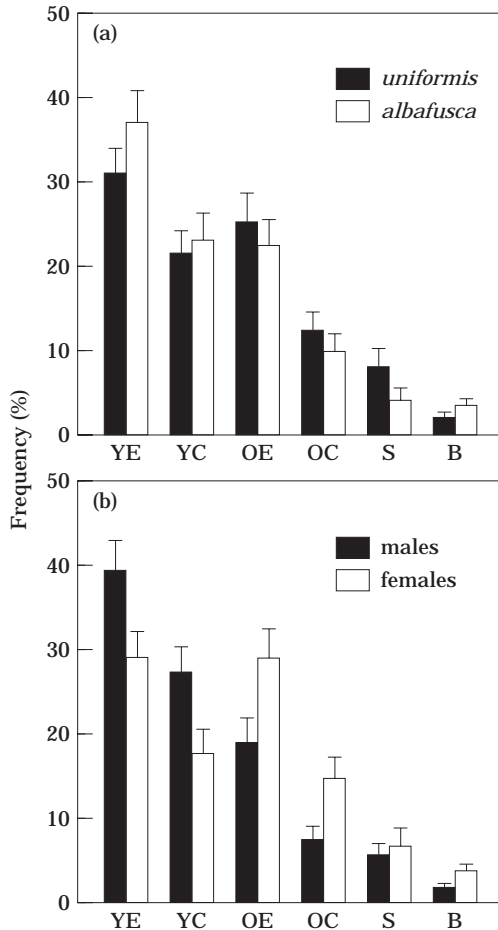


Figure 1. Microhabitat choice as percentages of observations ($\bar{X} \pm \text{SE}$) by (a) colour morph and (b) sex. The microhabitat categories are young (YC) and old (OC) parts of epizoite-free *Fucus*, and young (YE) and old (OE) parts of *Fucus* with epizoites, swimming (S) and bottom and stones (B). Note that there are epizoites only in OE.

(Wilcoxon signed-ranks test: $T=1518$, $N=115$, $P<0.001$; Fig. 1).

Height Choice

In the second experiment the microhabitat choice within *Fucus* was not affected by the position of the thallus (Fig. 2, Table II). Thus the microhabitat choice is directed by a preference for some specific part of *Fucus* and not by a preference for a certain height within the thallus. In this

experiment too, the females used the old parts of the *Fucus* more than did the males (Fig. 2, Table II), and in general the isopods were now more often on the old parts than in the first experiment. There were no differences between the sexes with respect to frequencies of swimming (Fig. 2, Table II).

Food Choice

In the first part of the food-choice experiment where the isopods were offered a choice between old and young parts of *Fucus*, both males (Wilcoxon signed-ranks test: $T=60.5$, $N=43$, $P<0.001$) and females ($T=7.5$, $N=30$, $P<0.001$) preferred the old part as substrate, and females significantly more so than males (Mann-Whitney U -test: $U=399$, $N_{\text{males}}=43$, $N_{\text{females}}=30$, $P<0.01$; Fig. 3a), which corresponds to the results of the microhabitat-choice experiment. On the other hand, there was a non-significant trend for males to be present on the young piece of *Fucus* more than females ($U=490.5$, $N_{\text{males}}=43$, $N_{\text{females}}=30$, $P<0.1$). The preference of males and females for the old part, and the stronger preference of females than males for the old part, were still significant after applying a sequential Bonferroni test to this group of four tests. In addition, males were found swimming more often than females ($U=476.5$, $N_{\text{males}}=43$, $N_{\text{females}}=30$, $P<0.05$). Females also ate more old than young *Fucus* (old: $\bar{X} \pm \text{SE}=36.1 \pm 5.2$ mg; young: $\bar{X} \pm \text{SE}=22.9 \pm 5.5$ mg; paired t -test: $t_{29}=-2.08$, $P<0.05$), while males ate similar amounts of the two pieces (old: $\bar{X} \pm \text{SE}=37.1 \pm 4.7$ mg; young: $\bar{X} \pm \text{SE}=38.3 \pm 5.9$ mg; paired t -test: $t_{42}=0.16$, NS). The difference between the consumption of the old and the young parts did not differ between the sexes (Mann-Whitney U -test: $U=538.5$, $N_{\text{males}}=43$, $N_{\text{females}}=30$, NS). However, none of these three tests of food consumption was significant after application of a sequential Bonferroni test. Interestingly, while the observations of the substrate choice during the light hours correlated with food choice in the males (Spearman's rank correlation coefficient: $r_s=0.36$, $N=43$, $P<0.05$; Fig. 4a), this was not the case in the females ($r_s=-0.27$, $N=30$, NS).

In the second part of the food-choice experiment both sexes were observed equally often on the apices of epizoite-free *Fucus* (Mann-Whitney U -test: $U=511.5$, $N_{\text{males}}=44$, $N_{\text{females}}=25$, NS;

Table I. Tests of colour morph and sex differences in microhabitat choice for the six microhabitat categories and pooled categories in *Fucus*

Microhabitat	Source of variation					
	Morph		Sex		Interaction	
	<i>H</i>	<i>P</i>	<i>H</i>	<i>P</i>	<i>H</i>	<i>P</i>
Epizoite-free <i>Fucus</i> , young	0.13	NS	8.95	<0.01*	0.77	NS
Epizoite-free <i>Fucus</i> , old	0.98	NS	5.85	<0.05	1.69	NS
<i>Fucus</i> with epizoites, young	1.41	NS	4.56	<0.05	0.45	NS
<i>Fucus</i> with epizoites, old	0.08	NS	3.14	<0.1	0.89	NS
Bottom	2.11	NS	2.90	<0.1	0.009	NS
Swimming	3.08	<0.1	0.58	NS	2.39	NS
Young parts	2.43	NS	15.1	<0.001**	0.15	NS
Old parts	0.87	NS	9.70	<0.01*	0.004	NS
Epizoite-free <i>Fucus</i>	0.029	NS	0.37	NS	0.011	NS
<i>Fucus</i> with epizoites	0.37	NS	0.0004	NS	0.013	NS

Non-parametric two-factor analysis of variance based on extension of Kruskal–Wallis test. In each test $df=1$. Significance levels after a sequential Bonferroni adjustment are indicated by asterisks (* $P<0.05$; ** $P<0.01$).

Fig. 3b), on the apices of *Fucus* with epizoites ($U=524.5$, $N_{\text{males}}=44$, $N_{\text{females}}=25$, NS), and swimming ($U=513.5$, $N_{\text{males}}=44$, $N_{\text{females}}=25$, NS). There was no difference in the amount eaten from the two apices in males (epizoite-free *Fucus*: $\bar{X} \pm \text{SE} = 45.8 \pm 7.2$ mg; *Fucus* with epizoites: $\bar{X} \pm \text{SE} = 43.2 \pm 4.9$ mg; paired t -test with logarithmic transformation: $t_{43}=0.48$, NS) or in females (epizoite-free: $\bar{X} \pm \text{SE} = 39.3 \pm 7.5$ mg, with epizoites: $\bar{X} \pm \text{SE} = 57.9 \pm 8.4$ mg; paired t -test: $t_{23} = -1.49$, NS). Neither did the difference between the consumption of the apices of epizoite-free *Fucus* and the apices of *Fucus* with epizoites respectively differ significantly between the sexes (Mann–Whitney U -test: $U=383.5$, $N_{\text{males}}=44$, $N_{\text{females}}=24$, $P<0.1$). Again substrate choice correlated significantly with food choice in males ($r_S=0.32$, $N=44$, $P<0.05$; Fig. 4b) but not in females ($r_S=0.32$, $N=24$, NS).

DISCUSSION

Colour morphs in polymorphic species with cryptic coloration might be expected to prefer visually matching backgrounds if this minimized the risk of detection by predators. However, the *albusca* individuals of *I. baltica* did not prefer the white-spotted parts of *Fucus*, nor did the *uniformis* individuals prefer the parts free from epizoites. On

the other hand, there was a difference in microhabitat choice between the sexes. The lack of colour-morph-specific microhabitat choice is what we should expect (1) if the resource use is approximately the same across the colour morphs, as seems to be the case in *I. baltica* (Salemaa 1979), and (2) if the benefit of decreased predation risk accruing as a consequence of morph-specific microhabitat choice was outweighed by its costs, for example, in terms of decreased opportunity for optimal foraging. There may also be genetic constraints preventing the linkage of colour morphs with matching microhabitat preferences.

A sexual difference in microhabitat use during the day was demonstrated in all our experiments. Throughout, females were observed more frequently on the old parts of *Fucus* than males. A sexual difference in the microhabitat choice in *I. baltica* was observed by Jormalainen & Tuomi (1989) with males preferring young parts of *Fucus*, but, instead of old parts of *Fucus*, females preferred the bottom. This difference may be due to the presentation of shorter pieces of *Fucus* in their experiment, so that both the young and old parts in their experimental set-up would be classified as young parts using the criteria applied in the present study. Moreover, the reproductive status of the females differed between the two studies: in the former, mature, mainly ovigerous females were used, whereas ours were immature and at the

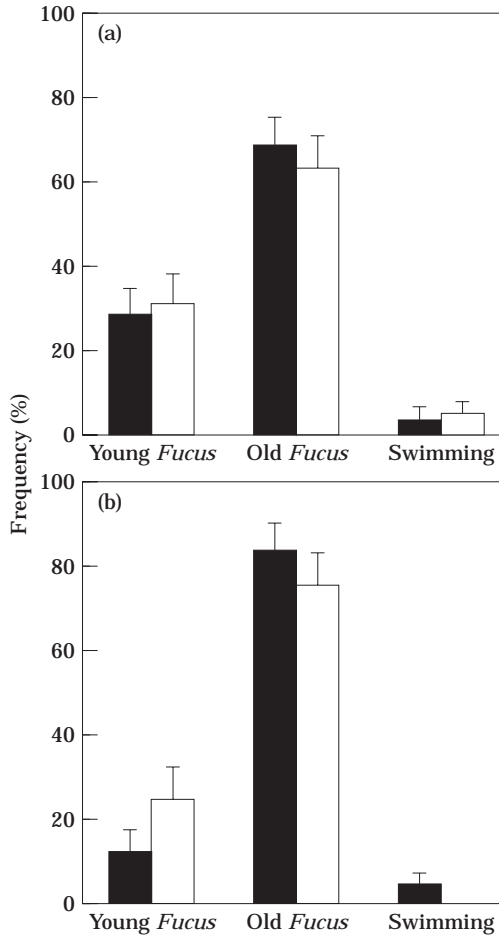


Figure 2. The microhabitat choice of males (a) and females (b) when the *Fucus* thalli stood upright (■) or were inverted (□) as percentages of observations ($\bar{X} \pm SE$).

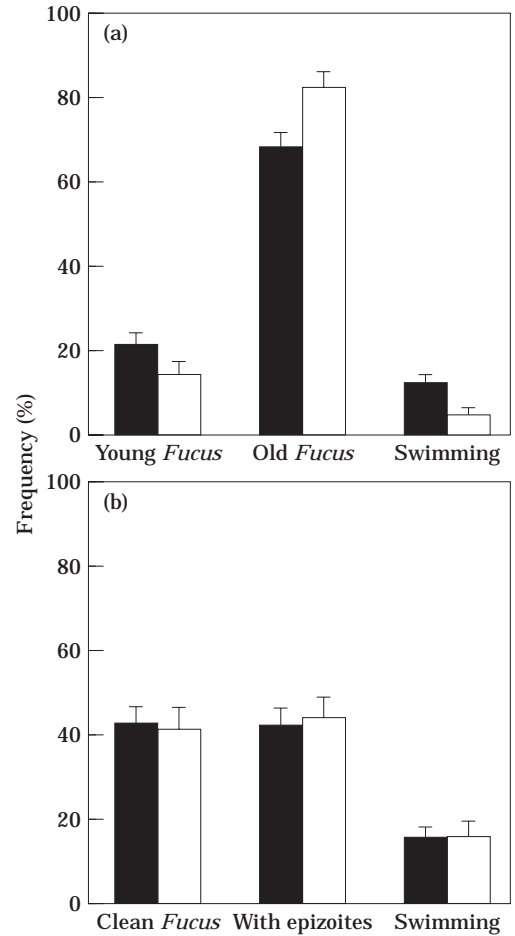


Figure 3. The observations on substrate choice as percentages ($\bar{X} \pm SE$) in males (■) and females (□) in the food-choice experiments between the young and old parts of *Fucus* (a) and between young apices of *Fucus* with and without epizoids (b).

Table II. Tests of the effect of the position of the *Fucus* thallus (upright or inverted) and sex on microhabitat choice

Microhabitat	Source of variation					
	Position of thallus		Sex		Interaction	
	<i>H</i>	<i>P</i>	<i>H</i>	<i>P</i>	<i>H</i>	<i>P</i>
Young part	1.70	NS	5.07	<0.05*	0.63	NS
Old part	1.21	NS	6.00	<0.05*	0.10	NS
Swimming	0.0006	NS	3.25	<0.01	2.50	NS

Non-parametric two-factor analysis of variance based on extension of Kruskal–Wallis test. In each test $df=1$. Significance levels after a sequential Bonferroni adjustment are indicated by asterisks (* $P<0.05$).

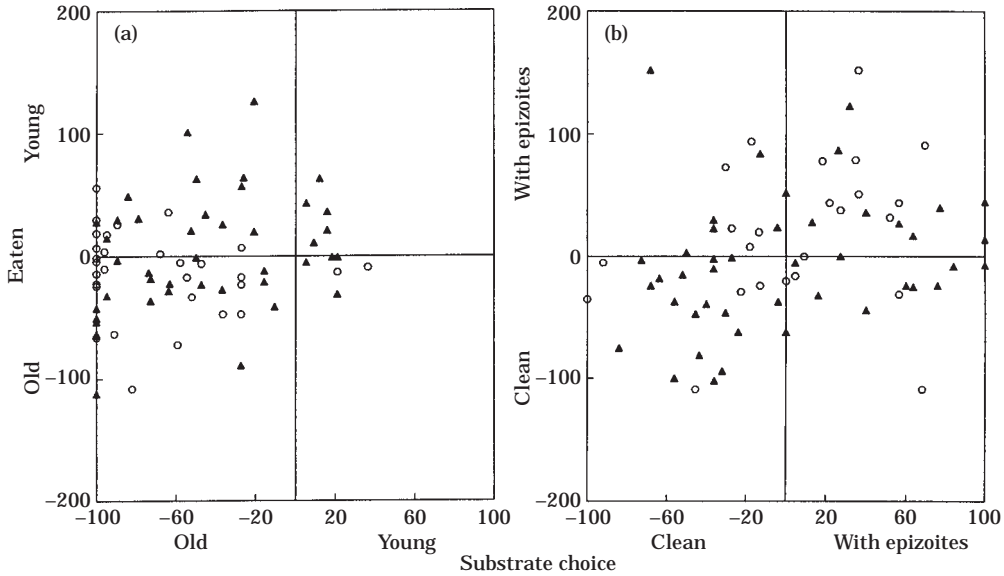


Figure 4. Substrate choice (percentages of observations) versus food choice (mg eaten/5 days) in males (\blacktriangle) and females (\circ). Substrate choice and food choice are expressed as the old *Fucus* subtracted from young *Fucus* (a), and as the apices of *Fucus* without epizoites subtracted from the apices of *Fucus* with epizoites (b).

stage when they accumulate resources for ovary development (Tuomi & Jormalainen 1988). The different size of thalli between the experiments in our study may also explain the variation in the strength of the preference between the old and the young parts. The thalli were larger and higher and thus had more old parts in the second experiment where both sexes were observed more often in the old parts than in the first experiment.

The isopods preferred certain parts of the thallus but not a certain height. Furthermore, the sex-dependent pattern of microhabitat choice was still present even after the three-dimensional habitat structure had been reduced to two pieces of *Fucus*, as in the food-choice experiment. Thus the sex-specific microhabitat use is directed by the characteristics of the different parts of the *Fucus* thallus.

The preference for the thallus with epizoites over the epizoite-free thallus, as was observed in the first experiment, was not supported by the food-choice experiment in which the apices of *Fucus* with epizoites were not preferred either as food or as substrate. In the first experiment we attempted to make the thalli with epizoites extreme by choosing the most spotted branches from several thalli and binding some of them

together to form the experimental thalli. As a consequence the thalli with epizoites were on average somewhat denser than the epizoite-free thalli. Therefore, the preference for the thalli with epizoites in the first experiment may have been a response to their larger size, as in several amphipod species (Stoner 1980; Leber 1985) or simply an area effect.

The evolution of sexual differences in microhabitat choice may be explicable in terms of competition between the sexes for a limiting resource or in terms of differences between the sexes in resources needed for successful reproduction (Slatkin 1984). Inter-sexual competition for food does not seem to be a plausible hypothesis in this case because of the abundance of food in the habitat, so the second hypothesis seems much more likely. This assumes that the trade-off between feeding and predator avoidance has different optima for males and females, respectively. It has been suggested that the reproductive success of female *I. baltica* depends mainly on their survival from the onset of breeding over the relatively long time of incubation to the release of the juveniles, while for the males it is more important to attain a large body size which promotes mate acquisition (Tuomi et al. 1988a, b). This

suggestion is supported by several facts. First, in males, which are the larger sex in this species, food consumption during maturation is higher than in females (Strong & Daborn 1979; Tuomi et al. 1988a), producing a large body size. Second, large body size in males is crucial both for obtaining a female (Jormalainen & Merilaita 1995) and for resisting attempts by other males to take her during amplexus (Jormalainen et al. 1994). Third, both predation experiments (Jormalainen et al. 1995) and observations of the sex ratios of cohorts in natural populations becoming female-biased with time (Salemaa 1979; Jormalainen & Tuomi 1989) support the notion that predation risk is lower in females than in males.

Predation risk decreases with increasing algal biomass and complexity, that is, with increasing cover (Nelson 1979; Stoner 1982; Leber 1985). The old parts, which are located within the *Fucus*, can therefore be expected to provide a better refuge from predators than the more exposed young parts in the outer sphere of the thallus. That the females are more often found on the old parts of *Fucus* than are the males may imply a greater investment in anti-predator protection in the females. The cost of this strategy may be a lower intake of food because of the restricted use of the habitat, which males cannot afford.

Furthermore, in contrast to males, the substrate choice of the females did not correlate with their food choice. This indicates that the females were spending less time where they were eating, and therefore probably also less time eating, than did the males. In general *I. baltica* is more active by night than by day, but in males the daytime activity is higher than in females and increases to the level of night-time activity during the breeding period (Hørlyck 1973; Jormalainen & Tuomi 1989). Bearing in mind that the substrate choice recordings were made only during the day, when visual predation is most intense, it seems probable that the females spent more time on the old parts during the day, while at night they must have been feeding on the young parts too.

A sexual difference in the quality of food needed for successful reproduction could also lead to a difference in microhabitat choice. However, food choice did not differ between males and females (see also Salemaa 1987). Furthermore, a difference in the nutritional needs between sexes is likely to result in dissimilar consumption of two completely different food sources rather than

various parts of *Fucus*, which was not tested in this study.

In *I. baltica* the frequency of the spotted *albafusca* morph is always higher in females than in males, and varies between populations in parallel with the amount of epizoites, especially *Electra*, on *Fucus* (Salemaa 1978). Conversely, the unicoloured *uniformis* is always in excess in males. The epizoites are concentrated on the old parts of the *Fucus*, and, as we have shown, females use the old parts more than do males. Males, in turn, use the young parts of *Fucus*, which are usually free from epizoites, more than females. Thus it seems that the coloration has evolved to match the prevalent background according to the sex-specific microhabitat use in *I. baltica*. Also the darker average coloration in females (Jormalainen & Tuomi 1989), which spend relatively more time on dark parts of *Fucus*, is in agreement with this hypothesis.

Why then is *I. baltica* polymorphic and not simply sexually dimorphic in coloration? First, the colour polymorphism is indeed partially sex-linked in *I. baltica*, the colour morphs, exclusive of *uniformis*, being genetically linked to the female sex chromosome. Females are the heterogametic sex, but the sex-determination mechanism involves minor sex-determination factors in addition to sex chromosomes (Tinturier-Hamelin 1963; Legrand et al. 1987). These minor sex-determination factors can turn a chromosomal male into a female and vice versa and thus prevent the complete sex-linkage of the colour morphs. Second, in exposed areas, where the epizoites on *Fucus* are absent or very scarce, the *albafusca* morph is likely to appear conspicuous in females compared with *uniformis*, and therefore the fitness of the colour morphs may differ between sites. Third, the other morphs, which exist only at low frequencies in our study area, are probably adaptations evolved in response to other kinds of habitats. In general, the complex polymorphism in this species may therefore be due to gene flow between populations inhabiting visually differing habitats. Predator-induced mechanisms leading to frequency-dependent selection may also be involved (Jormalainen et al. 1995).

To summarize, we found no colour-morph-dependent microhabitat choice in *I. baltica*. Instead, the microhabitat use differed between the sexes so that the females were observed more frequently on the old parts of *Fucus* than the

males during the day. We think that this reduces the predation risk from visually searching fish in females, in which survival over breeding is crucial. On the other hand, males are more prone to take risks to increase feeding and growth because of the importance of body size to their mating success. The colours and patterns seem to be adapted to the sex-specific patterns of microhabitat use that are ultimately determined by male and female reproductive strategies.

ACKNOWLEDGMENTS

We are grateful to the Archipelago Research Institute of the University of Turku for providing research facilities. We thank A. Berglund, A. Forsman and S. Ulfstrand for valuable comments on the manuscript and T.-P. Juvonen and P. Peura for assistance with field and laboratory work. Financial support to S.M. was provided by NorFA, the Royal Swedish Academy of Sciences and Inez Johansson foundation and to V.J. by the Academy of Finland.

REFERENCES

- Carlson, L. 1991. Seasonal variation in growth, reproduction and nitrogen content of *Fucus vesiculosus* L. in the Öresund, southern Sweden. *Bot. Mar.*, **34**, 447–453.
- Dill, L. M. 1987. Animal decision making and its ecological consequences: the future of aquatic ecology and behaviour. *Can. J. Zool.*, **65**, 803–811.
- Edmunds, M. 1974. *Defence in Animals: A Survey of Anti-predator Defences*. Harlow: Longman.
- Endler, J. A. 1978. A predator's view of animal color patterns. *Evol. Biol.*, **11**, 319–364.
- Forsman, A. & Shine, R. 1995. The adaptive significance of colour pattern polymorphism in the Australian scincid lizard *Lampropholis delicata*. *Biol. J. Linn. Soc.*, **55**, 273–291.
- García-Dorado, A. 1986. The effect of niche preference on polymorphism protection in a heterogeneous environment. *Evolution*, **40**, 936–945.
- Gillis, J. E. 1982. Substrate colour-matching cues in the cryptic grasshopper *Cirotettix rabula rabula* (Rehn & Hebard). *Anim. Behav.*, **30**, 113–116.
- Hay, M. E. & Fenical, M. 1988. Marine plant–herbivore interactions: the ecology of chemical defence. *A. Rev. Ecol. Syst.*, **19**, 111–145.
- Hedrick, P. H. 1993. Sex-dependent habitat selection and genetic polymorphism. *Am. Nat.*, **141**, 491–500.
- Hørlyck, V. 1973. Seasonal and diel variation in the rhythmicity of *Idotea baltica* (Pallas) and *Idotea granulosa* Rathke. *Ophelia*, **12**, 117–127.
- Ivessalo, H. & Tuomi, J. 1989. Nutrient availability and accumulation of phenolic compounds in the brown alga *Fucus vesiculosus*. *Mar. Biol.*, **101**, 115–119.
- Jormalainen, V. & Merilaita, S. 1995. Female resistance and duration of mate-guarding in three aquatic peracarids (Crustacea). *Behav. Ecol. Sociobiol.*, **36**, 43–48.
- Jormalainen, V. & Tuomi, J. 1989. Sexual differences in habitat selection and activity of the colour polymorphic isopod *Idotea baltica*. *Anim. Behav.*, **38**, 576–585.
- Jormalainen, V., Merilaita, S. & Tuomi, J. 1994. Male choice and male–male competition in *Idotea baltica* (Crustacea, Isopoda). *Ethology*, **96**, 46–57.
- Jormalainen, V., Merilaita, S. & Tuomi, J. 1995. Differential predation on sexes affects colour polymorphism of the isopod *Idotea baltica* (Pallas). *Biol. J. Linn. Soc.*, **55**, 45–68.
- Kettlewell, H. B. D. & Conn, D. L. T. 1977. Further background-choice experiments on cryptic Lepidoptera. *J. Zool., Lond.*, **181**, 371–376.
- Khailov, K. M., Kholodov, V. I., Firsov, Yu. K. & Prazukin, A. V. 1978. Thalli of *Fucus vesiculosus* in ontogenesis: changes in morpho-physiological parameters. *Bot. Mar.*, **21**, 289–311.
- Leber, K. M. 1985. The influence of predatory decapods, refuge, and microhabitat selection on seagrass communities. *Ecology*, **66**, 1951–1964.
- Légrand, J. J., Légrand-Hamelin, E. & Juchault, P. 1987. Sex determination in Crustacea. *Biol. Rev.*, **62**, 439–470.
- Lima, S. L. & Dill, L. M. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Can. J. Zool.*, **68**, 619–640.
- De Meeûs, T., Michalakis, Y., Renaud, F. & Olivieri, I. 1993. Polymorphism in heterogeneous environments, evolution of habitat selection and sympatric speciation: soft and hard selection models. *Evol. Ecol.*, **7**, 175–198.
- Morey, S. R. 1990. Microhabitat selection and predation in the Pacific treefrog, *Pseudacris regilla*. *J. Herpetol.*, **24**, 292–296.
- Nelson, W. G. 1979. Experimental studies of selective predation on amphipods: consequences for amphipod distribution and abundance. *J. exp. mar. Biol. Ecol.*, **38**, 225–245.
- Reinert, H. K. 1984. Habitat variation within sympatric snake populations. *Ecology*, **65**, 1673–1682.
- Rice, W. R. 1989. Analyzing tables of statistical tests. *Evolution*, **43**, 223–225.
- Salemaa, H. 1978. Geographical variability 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. 1986. Ecological and genetic adaptations of *Idotea* spp. (Isopoda, Crustacea). Ph.D. thesis, University of Helsinki.
- Salemaa, H. 1987. Herbivory and microhabitat preferences of *Idotea* spp. (Isopoda) in the Northern Baltic Sea. *Ophelia*, **27**, 1–15.
- Sandoval, C. P. 1994. Differential visual predation on morphs of *Timema cristinae* (Phasmatoidea):

- Timemidae) and its consequences for host range. *Biol. J. Linn. Soc.*, **52**, 341–356.
- Schoener, T. W. & Schoener, A. 1976. The ecological context of female pattern polymorphism in the lizard *Anolis sagrei*. *Evolution*, **30**, 650–658.
- Seaman, Jr, J. W., Walls, S. C., Wise, S. E. & Jaeger, R. G. 1994. Caveat emptor: rank transform methods and interaction. *Trends Ecol. Evol.*, **9**, 261–263.
- Slatkin, M. 1984. Ecological causes of sexual dimorphism. *Evolution*, **38**, 622–630.
- Stoner, A. W. 1980. Perception and choice of substratum by epifaunal amphipods associated with seagrasses. *Mar. Ecol. Prog. Ser.*, **3**, 105–111.
- Stoner, A. W. 1982. The influence of benthic macrophytes on the foraging behaviour of pinfish, *Lagodon rhomboides* (Linnaeus). *J. exp. mar. Biol. Ecol.*, **58**, 271–284.
- Strong, K. W. & Daborn, G. R. 1979. Growth and energy utilisation of the intertidal isopod *Idotea baltica* (Pallas) (Crustacea: Isopoda). *J. exp. mar. Biol. Ecol.*, **41**, 101–123.
- Tinturier-Hamelin, E. 1963. Polychromatisme et détermination génétique du sexe chez l'espèce polytypique *Idotea balthica* (Pallas) (Isopode Valvifère). *Cah. Biol. mar.*, **4**, 473–591.
- Tuomi, J. & Jormalainen, V. 1988. Components of reproductive effort in the aquatic isopod *Idotea baltica*. *Oikos*, **52**, 250–254.
- Tuomi, J., Jormalainen, V. & Ilvessalo, H. 1988a. Growth, food consumption and reproductive tactics of the aquatic isopod *Idotea baltica*. *Annls Zool. Fenn.*, **25**, 145–151.
- Tuomi, J., Jormalainen, V. & Ilvessalo, H. 1988b. Does the aquatic isopod *Idotea baltica* minimize the survival costs of reproduction? *Oikos*, **52**, 245–249.
- Zar, J. H. 1984. *Biostatistical Analysis*. 2nd edn. Englewood Cliffs, New Jersey: Prentice-Hall.
- Yates, J. L. & Peckol, P. 1993. Effects of nutrient availability and herbivory on polyphenolics in the seaweed *Fucus vesiculosus*. *Ecology*, **74**, 1757–1766.