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Habitat heterogeneity, body size and phenotypic diversity in *Idotea granulosa* (Isopoda) on the north-east coast of England

S.L. Hull*, L.J. Winter and G.W. Scott

University of Hull, Scarborough Centre for Coastal Studies, Filey Road, Scarborough, YO11 3AZ
*Corresponding author, e-mail: S.Hull@biosci.hull.ac.uk

Samples were collected from six pools in order to examine the distribution, body length, base colour and phenotypic diversity (chromatophore pattern) of *Idotea granulosa* populations on five different species of algae (*Ceramium*, *Corallina*, *Chondrus*, *Fucus* and *Enteromorpha*), on each of two shores. Holbeck (HOL) pools had significantly higher habitat heterogeneity in terms of algal species diversity than did those on the more exposed Filey Brigg (FB). *Idotea* densities were significantly higher and mean body size significantly smaller on *Corallina* than the other algal species. Isopods were significantly larger on *Fucus*. There was no significant difference in base colour frequencies between shores but there was a positive association between the brown base colour and *Corallina* and the green colour and *Fucus*.

The commonest chromatophore pattern morph was the *granulosa-maculata* that occurred in 44% of the isopods sampled and five out of ten chromatophore patterns accounted for <10% of the population. The *uniformis* morph was rare on both shores. There was no significant difference in chromatophore pattern frequency between the sexes. The *lineata-maculata* morph and *maculata* morphs showed a positive association with *Corallina* and *Fucus* respectively. There was a significant difference in chromatophore pattern frequency between adults and juveniles. The *uniformis* and *maculata* patterns occurred in higher frequencies than expected in the adult population whereas the reverse was true of the *granulosa-maculata* and *lineata-maculata* morphs.

A total of 85 different phenotypes were recorded from both shores, with 51 of these being exclusively found in HOL pools. Holbeck pools had a significantly higher isopod phenotypic diversity than did those from FB. There was no significant difference in phenotypic diversity between adult and juvenile *Idotea* at HOL, however juveniles had a significantly higher phenotypic diversity than did adults at FB. Overall, there was a significant positive correlation between rockpool algal diversity and isopod phenotypic diversity.

INTRODUCTION

Habitat structure has primarily been expressed as either habitat complexity (relating to small-scale physical attributes of the habitat such as algal physiognomy), or as habitat heterogeneity that refers to the 'patchiness' of the larger-scale environment (Hicks, 1985). The effects of both habitat complexity and heterogeneity have been the focus for recent studies in the marine environment. Habitat complexity has been shown to affect both the abundance and diversity of assemblages, with algal species with more complex physiognomic structure supporting greater individual species abundance and higher diversity than those with a more simple structure (e.g. epifaunal species (Gee & Warwick, 1994), ostracods (Hull, 1997)). In a study of intertidal rocky shore habitat heterogeneity, Archambault & Bourget (1996) showed that small-scale substrate heterogeneity accounted for much of the variance in species abundance whereas larger scales (km) accounted for much of the variance in species richness. Such variation in habitat structure not only increases the number of niches available for colonization (Hicks, 1985), but may also increase refuges from predation (Coull & Wells, 1983) or reduce the effects of predation by altering the foraging efficiency and encounter rates of predators with their prey (Diehl, 1992).

Predators alter not only the abundance, distribution and size–frequency structure of their prey populations (see references in Diehl, 1992), but also the frequency of colour morphs within the population. Firstly, the evolution of cryptic coloration, in which prey items match the background colour of the habitat, is thought to be closely linked with the evolution of habitat selection (De Meeus et al., 1993). Cryptic morphs reduce the risk of detection of a prey species from visually searching predators and hence increase in frequency within the population. Secondly, predators relying on visual detection to locate cryptically coloured prey may ignore highly coloured conspicuous individuals leading to high frequencies of such morphs within a population (Endler, 1978). This apostatic selection is a form of frequency-dependent selection and is thought to be one of the main factors maintaining colour morph frequencies within heterogeneous environments (Cook & Kenyon, 1991).

Intertidal isopods are important constituents of the algal fauna on rocky shores predominantly feeding upon the algae and detritus (Salemaa & Ranta, 1991) and many idoteid isopods show conspicuous colour polymorphism (Arrontes, 1991). In the genus *Idotea*, the background coloration is derived from the algal pigments in the diet (Lee, 1966) and does change when animals have been reared upon different algal species (Salemaa & Ranta, 1991). In *Idotea baltica* Pallas, background coloration has been shown to vary in intensity with background colour (Jormalainen & Tuomi, 1989). In *I. baltica* structural coloration has been shown to be genetically determined (Tinturier-Hamelin, 1963) with the alleles determining the chromatophore patterns being located upon the heterochromosomes. In the Baltic and Mediterranean Seas, colour polymorphism in *I. baltica* has been shown to change with substrate composition (Guarino et al., 1993), differential predation (Jormalainen et al., 1995) and differences in microhabitat use between the sexes (Jormalainen & Tuomi, 1989; Merilaita & Jormalainen, 1997). All authors suggest that the structural coloration reduces predation risk. Whilst *I. baltica* is the dominant species found in the Baltic, on the shores of north-east England *Idotea granulosa* (Ranke) is the most abundant isopod.

The aims of the current study were, firstly to examine the size class distribution and density of *I. granulosa* upon five different species of algae collected from rockpools on two shores with differing degrees of habitat heterogeneity (where habitat heterogeneity refers to the diversity of algae within pools). Secondly, to determine if base colour and chromatophore pattern frequencies varied between the sexes, between adults and juveniles, between the different species of algae and between shores. Finally, the null hypothesis that there was no significant difference in phenotypic diversity between shores with different habitat heterogeneity was tested.

MATERIALS AND METHODS

Sample collection and processing

Samples of algae were collected from two rocky shores along the north-east coast of England, Holbeck (54°16′N 0°25′W) and the exposed shore on Filey Brigg (54°14′N 0°24′W). The samples were collected from six mid-shore pools during March 2000. Holbeck beach (HOL) is a heterogeneous moderately exposed rocky shore where clumps of fucoid algae are interspersed with rockpools and barnacle and mussel beds. The exposed shore at Filey Brigg (FB) is more homogeneous being predominantly covered in barnacle beds with large coralline algal pools. In order to estimate algal species diversity (i.e. habitat heterogeneity) the percentage cover of each algal species was recorded from each of the six pools sampled. Pools of similar size (approximately length 1.5 m, breadth 1 m, depth 0.5 m) containing *Ceramium nodulosum* (Lightfoot) Ducluzeau (Rhodophyceae), *Corallina officinalis* (L.) (Rhodophyceae), *Chondrus crispus* Stackhouse (Rhodophyceae), *Enteromorpha* spp. (Chlorophyceae) and *Fucus vesiculosus* L. (Phaeophyceae) were chosen for sampling; the algae were chosen due to their abundance and differences in colour and structural complexity. Hereafter the algae will be referred to by genus only. A polythene bag was placed around a monospecific clump of algae and the algae scraped into the bag to prevent the loss of isopods. *Idotea granulosa* were removed from the algae and for each individual the body length (in mm), sex (male, female or juvenile), base colour and chromatophore/leuocophore pattern was recorded. All recording of colour and pattern was undertaken on a standard white surface immediately after removal from the algae using a binocular microscope. Sex was determined using the morphological features described by Naylor (1955) and animals of <5 mm in length were classified as juveniles (Salemaa & Ranta, 1991). Base colour was assigned to four categories (red, brown, green and yellow). Using the classification system developed by Salemaa & Ranta (1991), ten different chromatophore/leucophore patterns were recorded; *uniformis* (even colour no pattern), *granulosa* (highly variable white patches along dorsal line of segments), *maculata* (highly variable mottled or marbled pattern), *lineata* (dorsal stripe extending from head to telson), *granulosa-lineata*, *granulosa-maculata*, *granulosa-lineata-maculata*, *granulosa-albafusca*, *granulosa-maculata-albafusca* and *granulosa-lineata-albafusca* (for full description of the patterns and illustration see Salemma & Ranta (1991)). The phenotype was described by recording the occurrence of the each segment on which the coloration appeared.

Isopod densities are expressed as number of individuals per 20 g^{-1} dry weight of algae.

Data analysis

In order to examine within pool habitat heterogeneity, Shannon–Wiener diversity (H′) was calculated for each pool using the algal percentage cover data (Magurran, 1988). In order to test the null hypothesis that there was no significant difference in algal species diversity or algal species richness (S=number of species) within the pools between the shores, a Shannon–Wiener *t*-test was applied to the H′ data (Magurran, 1988) and a Mann–Whitney *U*-test to the species richness data (Fowler et al., 1998).

Isopod density and size data both followed a normal distribution (Kolmogorov–Smirnov test, $P>0.05$ in both cases) and there was no significant heterogeneity between the variances (in all cases, Levene's test, $P>0.05$), two-way ANOVA was used to test the null hypothesis that there was no significant difference in isopod density or body size between the different species of algae and between shores (Fowler et al., 1998). The individual body length measurements were assigned to 2 mm size-classes in order to construct size frequency histograms for each algal species on each shore.

In order to determine if there was any difference in base colour diversity between the different algal species within shores or between shores, Shannon–Wiener diversity (H′) was calculated for each sample (Magurran, 1988). The H′ values conformed to a normal distribution (Kolmogorov–Smirnov test, $P>0.05$) and there was no significant heterogeneity between the variances (Levene's test, $P>0.05$), therefore a two-way ANOVA was used to test the null hypothesis that there was no significant difference base colour diversity between the different species of algae and between shores (Magurran, 1988). The same procedure was applied to the phenotype data, where each individual had been scored for occurrence of leucophores/chromatophores on each segment. A Shannon–Weiner *t*-test was used to determine if there was a significant difference in phenotypic diversity between adults and juveniles within a shore (Magurran, 1988).

The base colour data was then pooled by algal species within shore. Chi-square-tests were used to determine if there was homogeneity in base colour frequency between shores and between the sexes (Fowler et al., 1998). Contingency tables were used to determine if there was an association between base colour and algal species. Where expected values were less than five, the frequencies for rare colours were pooled prior to calculation (Fowler et al., 1998). The same procedure was applied to chromatophore pattern data.

RESULTS

Habitat heterogeneity

The number of isopods recovered from the samples at HOL and FB was 627 and 538 respectively. There was a significant difference in both algal species diversity and species richness within the pools from the two shores. In terms of species richness, HOL pools contained significantly more algal species (median=8 species) than did those from FB (median=5.5 species) (Mann–Whitney U-test, W=56.5, $P=0.0065$). Algal diversity was also significantly higher in the pools from HOL (mean $H'=1.74\pm0.087$) than those from FB (mean $H'=1.53\pm0.11$) (Shannon–Wiener t-test, $t=6.23$, df=9, $P<0.001$). Filey Brigg pools were dominated by red algae, especially *Corallina*. Mean percentage cover of *Corallina* in FB pools was 68.5% (±4.1%) compared to a mean of 55% (±3.7%) for the pools at HOL. Therefore with respect to algal species, HOL pools had higher habitat heterogeneity than did those at FB.

Isopod density and size

There was a significant difference in *Idotea* density both between the two shores and between the different algal species (Table 1). Isopod densities were significantly higher in HOL pools than those at FB (HOL mean density=41.8 ±6.96, FB mean density=32.2 ±4.19). On both shores, *Corallina* supported significantly higher numbers of isopods than were found on the other species of algae (*Corallina* mean density=80.8 ±27.9 isopods g^{-1} dry weight) and isopods occurred in significantly lower densities on *Enteromorpha* than the other algal species (*Enteromorpha* mean density=3.3 ±2.8; *Chondrus* mean density=36.5 ±5.5; *Fucus* mean density=37.7 ±5.8; *Ceramium* mean density=27.2 ±2.3; Tukey $P=0.05$). The significant interaction term in the two-way ANOVA (Table 1) suggested isopod density on each algal species varied between shores.

There was no significant difference in mean isopod size between the two shores (Table 2). However, there was a significant difference in isopod size between the different algal species. On both shores, mean body size of *Idotea* was significantly larger on *Fucus* than on the other algal species (mean body length=9.07 ±3.47 mm) and the mean body size of isopods found on *Corallina* (mean body length=3.56 2.4 mm) was significantly smaller than on the other algal species (Tukey $P=0.05$). In order of magnitude, mean *Idotea* body size followed the pattern *Fucus* > *Enteromorpha* > *Chondrus* > *Ceramium* > *Corallina*.

Table 1. *Summary of the results of the two-way ANOVA tests for the effect of shore and algal species upon the density of* Idotea granulosa.

Source	df	Adj MS	F	P
Shore	1	1016.8	18.95	<0.001
Algae	4	8939.5	116.58	<0.001
Shore*Algae	4	1053.3	19.63	<0.001
Error	50	53.7		

Table 2. *Summary of the results of the two-way ANOVA tests for the effect of shore and algal species upon the body size of* Idotea granulosa.

Source	df	Adj MS	F	P
Shore	1	6.02	0.63	0.428
Algae	4	1165.39	121.67	<0.001
Shore*Algae	4	265.15	27.68	<0.001
Error	1155	9.58		

Figure 1 reflects the differences in isopod size distribution and proportion of each size class allotted to each base colour for the five species of algae. The population found on both *Corallina* and *Ceramium* was dominated by small juvenile isopods. Only 9.7% of the population found on *Ceramium* (Figure 1A) was greater than mm in length and the dominant size class (3–5 mm) accounted for 43.3% of the population. On *Corallina* (Figure 1B), the 1–3 mm size class accounted for 59.8% of the population, whereas only 8.7% of the individuals found on *Fucus* (Figure 1C) were found within this class and 51.6% of the population were between 5–9 mm. On *Fucus*, 23.7% of the isopods were greater than mm in length. The 3–5 mm size class accounted for 34.5% of the population found on *Chondrus* (Figure 1D), however there is a more even distribution of size across the other classes up to 1 mm. *Enteromorpha* supported low densities of juvenile isopods and few large individuals (Figure 1E).

Isopod base colour and chromatophore/leucophore pattern

There was no significant difference in base colour frequencies between shores or between the sexes (χ^2, $P>0.05$ in all cases). The base colour data from both shores was pooled in order to examine the association between the different colours and the different algal species and to examine the homogeneity of frequencies between the sexes and adults and juveniles found upon the five species of algae. Figure 1(A–E) also reflects the base colour frequency found upon the different algal species. There was a significant association between isopod base colour frequency and algal species ($\chi^2=590.5$, df=12, $P<0.01$). In the following paragraph figures in brackets denote the percentage each base colour accounts for in the total population. On *Ceramium* (Figure 1A) there was a positive association with the red (57.9%) and a negative association with the green isopods (only 4.3%). Brown isopods (63.1%) had a strong positive association with *Corallina* (Figure 1B) whereas the green occurred in lower frequencies than expected (14.4%). Green isopods (57%) showed a strong positive association with *Fucus* (Figure 1D) whereas red (6.4%) showed a strong negative

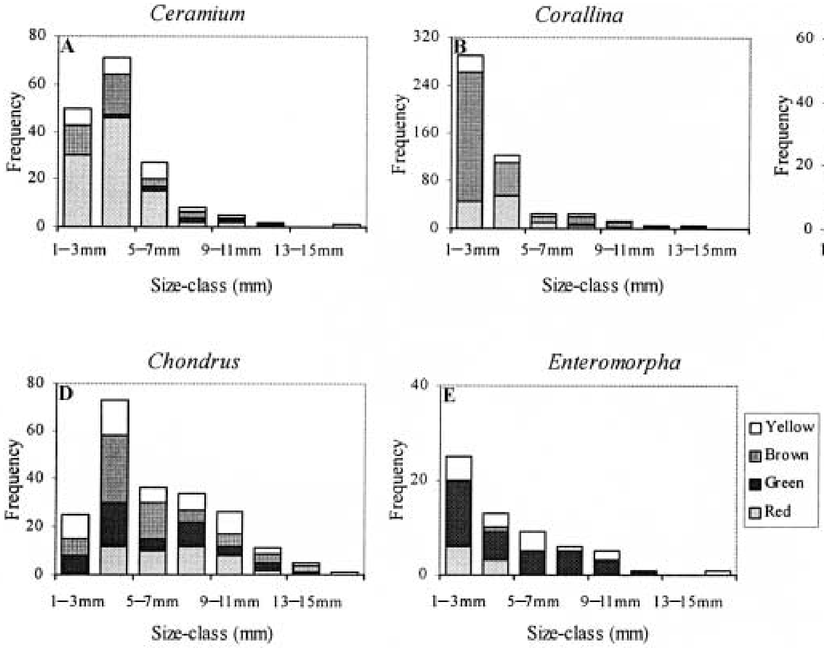

Figure 1. *Idotea granulosa* size–frequency and the proportion of each size-class corresponding to each of the four base colours for five species of intertidal rockpool algae.

association with this species. The pattern was not as marked on *Chondrus* (Figure 1C) but the yellow colour (31.7%) occurred in higher frequencies than was expected. Despite low frequencies, the green colour (56.7%) showed a positive association with *Enteromorpha* (Figure 1E). There was no significant difference in the base colour frequency between the sexes upon each algae, however there was a significant difference in the base colour frequency between adult and juvenile isopods (χ^2=212.3, df=3, $P<0.01$). The brown isopods occurred in lower frequencies and the green in higher frequencies than was expected in the adults, whereas the reverse was true for the juveniles.

Overall, five chromatophore patterns accounted for <10% of the total isopods sampled (*uniformis*, *granulosa-lineata*, *granulosa-albafusca*, *maculata-granulosa-albafusca* and *granulosa-lineata-albafusca*). The most common pattern morph was the *granulosa-maculata* (44% of the isopods sampled), followed by the *maculata* (22.2%), the *granulosa* (18.4%) and the *lineata-maculata* morphs (5.7%). There was no significant difference in chromatophore pattern frequencies between between the sexes on each algal species (χ^2, $P>0.1$ in all cases), but there was a significant difference in chromatophore pattern between the shores (χ^2=55.8, df=5, $P<0.01$). In HOL pools, the *lineata-maculata* morph occurred in higher frequencies and the *maculata* pattern in lower frequencies than expected. Whereas at FB, both the *lineata-maculata* and *granulosa* morph occurred in lower frequencies and the *maculata* morph in higher frequencies than were expected. The chromatophore pattern data from both shores was pooled in order to examine the association between the pattern and the different algal species. There was a significant association between isopod chromatophore pattern frequency and algal species (χ^2=246.2, df=15, $P<0.01$). The *granulosa-maculata* pattern had a strong positive association with both *Ceramium* and *Fucus*, whereas the *maculata* pattern had a strong negative association with *Ceramium*, *Corallina* and *Chondrus* but a strong positive association with *Fucus*. The *lineata-maculata* pattern showed a strong positive association with *Corallina* whereas *granulosa* also showed a strong positive association with *Chondrus*. There was a significant difference in pattern frequency between adult and juvenile isopods (χ^2=76.6, df=8, $P<0.01$). The *uniformis* and *maculata* patterns occurred in higher frequencies in the adult population but lower in the juveniles. The reverse was true of the *granulosa-maculata* and *lineata-maculata* patterns, both were at higher frequencies than expected in the juveniles.

Each individual isopod was scored for phenotypic diversity (the occurrence of chromatophores and leucophores on each segment). A total of 85 different phenotypes was recorded from both shores, with 51 of these being exclusively found in HOL pools and 18 in FB pools. Most occurred in very low frequencies, one or two individuals per phenotype. This data was used to test the null hypothesis there was no significant difference in isopod phenotypic diversity between shores or algal species. There was a significant difference in phenotype diversity both between shores and algal species (Table 3). Pools at HOL contained a significantly higher phenotype diversity (mean H′=1.79 ±0.316) than did those at FB (mean H′=1.39 ±0.299). Holbeck samples (median number of phenotypes=8.5) contained a higher number of phenotypes than did FB (median number of phenotypes=5.0) (Mann–Whitney *U*-test, W=814, $P<0.001$). Samples from *Ceramium* contained a lower morph diversity than did those from *Chondrus* and *Fucus* (Tukey P=0.05). The interaction term in the ANOVA was also significant, indicating that phenotype diversity on the algae varied between the two shores. A Shannon–Weiner *t*-test showed that there was no significant difference in phenotype diversity between adults and juveniles at HOL (Shannon–Weiner *t*-test, t=0.98, df=16, $P>0.05$) whereas juveniles showed a significantly higher phenotypic diversity than

Table 3. *Summary of the results of the two-way ANOVA tests for the effect of shore and algal species upon* Idotea granulosa *phenotype diversity.*

Source	df	Adj MS	*F*	*P*
Shore	1	1.8790	40.48	<0.001
Algae	3	0.6969	15.01	<0.001
Shore*Algae	3	0.1410	3.04	0.040
Error	40	0.0464		

adults on FB (Shannon–Weiner *t*-test, $t=3.94$, df=116, $P<0.001$). Overall, there was a significant positive relationship between phenotypic diversity and habitat heterogeneity within pools (Spearman rank correlation coefficient, $r_s=0.774$, $P=0.003$).

DISCUSSION

In terms of algal species, the rockpools at HOL presented a more heterogeneous environment that those at FB as they contained a greater number of more equally distributed species. The HOL pools had a higher isopod phenotypic diversity and greater number of phenotypes than the FB pools. Colour polymorphism in isopods has been strongly linked to associated algal communities and the encrusting epifauna associated with macroalgae. Interestingly, the algae on both shores sampled during the current study was devoid of epiphytes and encrusting epifauna, both of which are thought to provide added substrates for cryptically coloured isopods to hide upon (Merilaita, 1998). Salemaa (1978) noted that phenotypic diversity decreased with degree of exposure in the northern Baltic and suggested that this correlated to the biotic composition of the algal community. The FB study area is markedly more exposed than that at HOL and supports a lower algal diversity which in turn presents lower substrate heterogeneity hence isopod phenotypic diversity.

Idoteid isopods are known to forage on a wide variety of algal types, but are often found to have unequal distributions on the different algal species within a shore (Salemaa & Ranta, 1991). In the current study, on both shores, *Idotea* population densities were significantly higher, and the mean body size significantly lower on *Corallina* than the remaining four species of algae (see Figure 1B). Coralline algae are thought to provide a refuge from fish predation as many fish predators find it difficult to forage for prey within the dense, inflexible fronds (Coull & Wells, 1983). Previous workers have noted that juvenile isopods occur in higher densities on filamentous algae (such as *Ceramium* and *Cladophora* in *Idotea baltica*, (Jansson, 1970)) and that they move from the filamentous algae to the richer food resources on the fucoids as they mature (Salemaa & Ranta, 1991). Juveniles may also be constrained by the physical toughness of *Fucus* as a potential food source. The mean body size of the *Idotea granulosa* populations on fucoid algae were significantly larger than those found on the other algal species (Figure 1C) and animals of intermediate size were found upon *Chondrus*. This apparent shift in microhabitat with body size was accompanied by a change in base colour frequency (predominantly brown on *Corallina* and green on *Fucus*) reflecting the incorporation of the pigments from the algal food plant into the carapace (Lee, 1966). In laboratory experiments, Salemaa & Ranta (1991) noted that base colour changed within four weeks to that of the algal substrate. Therefore, the differential distribution of sizes observed during the current study could be the result of differential microhabitat choice with size for both shelter from visual predators and changes in dietary preferences with maturity.

There was no significant difference in phenotypic diversity between adult and juvenile isopods in pools at HOL, but there was a higher phenotypic diversity in juvenile isopods than adults at FB. Salemaa (1978) noted that a minimum of 18 fish species preyed upon a related species, *I. baltica*, in the fucoid algae belt in the Baltic, and one explanation for the observed change in phenotypic diversity in the current study could be that conspicuous juveniles were removed by predation. This would result in the lower phenotypic diversity observed in adults at FB. Due to the differences in exposure between the two shores, different predators with different search images may predate upon the isopods. A second explanation could be that the same predators exist on both shores (they are only 10 km away from each other) but the increased heterogeneity found at HOL provides additional substrate upon which the phenotypes could remain cryptic. However, the findings suggest that different selection pressures operate on juvenile isopods on the two shores and this is currently under investigation.

There were strong positive and negative associations between some chromatophore patterns and the different algal species. For example the *maculata* pattern had a strong negative association with *Ceramium*, *Corallina* and *Chondrus* but a strong positive association with *Fucus*. Such associations may reflect habitat choice (Merilaita & Jormalainen, 1997) or merely be the consequences of predator-mediated selection for conspicuous phenotypes resulting in an apparent association between phenotype and algal species. Selection would not solely operate upon phenotypic variation, the correct behaviour would also be important in ensuring that an individual was not detected by a visually searching predator. The resulting associations found during the current study may reflect not only the degree of crypsis of the morph upon an algal substrate, but also the animal using the correct behaviour choosing the area in which its coloration would be the most cryptic and orientating itself to maximize the effect.

Cryptic morphs reduce the risk of detection of a prey species from visually searching predators leading to high frequencies of such morphs within a population (Endler, 1978). In the current study, the *uniformis* pattern morph was rare (less than 5% of the population) and the most abundant pattern was the *granulosa*-*maculata* (44% of all the isopods sampled), followed by the *maculata* (22.2%) and the *granulosa* (18.4%) pattern. On both shores, most isopods sampled had some degree of structural coloration. Therefore it appears that such coloration may confer some protection from visually searching predators. However, on the Isle of Man, *uniformis* was the commonest morph within the populations sampled (52.7% of all the isopods) and the *granulosa* morph accounted for a further 41.2% of the population (Salemaa & Ranta, 1991). This may be an artefact of sampling, as the current study looked at the spatial variation in phenotype whereas that of Salemaa & Ranta (1991) also considered temporal variation.

Salemaa & Ranta (1991) also observed during laboratory experiments that some juvenile isopods tended to lose their chromatophore patterns as they moulted; however the loss of pattern appeared to be related to food quality and body size. Over 70% of the 3 mm isopods fed on *Fucus serratus* lost their pattern during the four week experiment, at 4 mm only 48% changed and no change in pattern was observed at 6 mm. When the data from the current study was re-examined looking only at those animals greater than 6 mm in length, the same pattern was still apparent; *uniformis* only accounted for 7.7% of the adult population whereas the *maculata* and *granulosa-maculata* accounted for 38.9% and 31.1% of the adult population respectively. Therefore there are marked frequency differences in phenotype of adult isopods between the current study and those reported for the Isle of Man. This could be a combination of differential selection for specific phenotypes by different predators between the different geographical areas, differences in habitat heterogeneity hence substrate on which the isopods can be cryptic and genetic differences between the populations.

In a related species, *I. baltica*, chromatophore pattern is thought to be genetically determined (Tinturier-Hamelin, 1963) therefore the differences in chromatophore pattern observed between the current study and previous ones could reflect genetic differences between populations. This was reflected in the observed differences in phenotypic diversity between shores. Marked microgeographic allozyme differentiation (even between populations less than 10 m apart) within shores has been demonstrated in the isopod *Jaera albifrons*, Piertney & Carvalho (1995). This has been attributed to localized population extinction and recolonization due to the instability of the boulder microhabitat and the patchiness of suitable microhabitats on the shore. Also in some isopod species (e.g. *Paracerceis sculpta*, Shuster & Levy (1999)) cuticular pattern has been demonstrated to be sex-linked, however as there was no significant difference in chromatophore pattern between the sexes this does not appear to be the case in *I. granulosa*. The genetic structure of *I. granulosa* populations is currently under investigation.

In summary, the current study has demonstrated that phenotypic diversity in *I. granulosa* is higher in more heterogeneous environments. This may be a reflection of the interactions between the genetic composition of the populations, predation and the availability of contrasting microhabitats in terms of algal diversity.

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