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**LOCAL AND SEXUAL DIVERGENCE
IN HOST-USE TRAITS AND ANTI-PREDATOR
ADAPTATIONS IN THE MARINE HERBIVORE**
Idotea balthica

by

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*This thesis is dedicated to the memory of my beloved brother
Timo Valteri Vesakoski (1976-2001)*

LIST OF ORIGINAL PAPERS

This thesis is based on the following articles, which will be referred to in the text by their Roman numerals.

- I Jormalainen, V., Honkanen, T. and Vesakoski, O. 2008: Geographical divergence in host use ability of a marine herbivore in alga-grazer interaction. - *Evolutionary Ecology* **22**: 545-559
- II Vesakoski, O., Rautanen, J., Ramsay, T. and Jormalainen, V. Divergence in host use ability of a marine herbivore from two habitat types. – *Submitted manuscript*
- III Vesakoski, O., Haavisto, F. and Jormalainen, V. Local divergence in colour polymorphism: Anti-predator adaptations relative to habitat type - *Submitted manuscript*
- IV Vesakoski, O., Merilaita, S. and Jormalainen, V. 2008: Reckless males, rational females: Dynamic trade-off between food and shelter in the marine isopod *Idotea balthica*. - *Behavioural Processes* **79**: 175-181.
- V Vesakoski, O., Boström, C., Ramsay, T. and Jormalainen, V. Sexual and local divergence in host exploitation in the marine herbivore *Idotea baltica* (Isopoda). -*Journal of Experimental Marine Biology and Ecology* **367**: 118-126.

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1. INTRODUCTION

1.1. Host-herbivore interactions in a spatial context

A key element in studies on host-herbivore interactions is to understand the evolutionary change in the host exploitation patterns of herbivores (e.g. Ehrlich and Raven 1964, Poore et al. 2008). During the last decades, the evolution of host-herbivore interactions has been put in a spatial framework, as it has been acknowledged that without this particular aspect, “nothing would make sense in ecology” (Hanski 1999, Denno et al. 2005, Gripenberg and Roslin 2007). The spatial aspect is important because typically species within a population live in a heterogeneous resource environment with local differences in quality of the host, composition of host plant assemblage or presence and type of enemies (Fox and Morrow 1981, Schluter 2000, Reznick and Ghalambor 2001, Kawecki and Ebert 2004). This variation in the biotic and in the abiotic environment promotes spatially varying selective environments and is likely to lead to spatial divergence in host exploitation patterns (Endler 1977, Thompson 1994, 1999).

Spatial view of host-herbivore interactions provides an exciting approach to study the adaptive evolution of host exploitation patterns and host range (Travis 1996, Reznick and Ghalambor 2001). Examining evolutionary change in real time is often impossible if the species has longer generation time than that of fruit flies. One possible solution is to replace the temporal dimension with spatial one and focus on the geographic variation in traits in different selective environments instead of temporal change (Endler 1986). By substituting the temporal dimension for the spatial, one assumes that spatial variation in selective environments is comparable to temporal change in selection and that spatial variation allows an assessment of the different selective forces at work (Kawecki and Ebert 2004). Recently, spatial variation in host exploitation patterns has received an increasing amount of attention, both in studies of host-herbivore interactions (Boecklen and Mopper 1998, Sotka 2005, Thompson 2005, Greischar and Koskella 2007) and those targeting sympatric speciation (reviewed in Schluter 2001, Via 2001, Fitzpatrick et al. 2008).

1.2. Divergence of populations

1.2.1. Adaptive divergence

Spatial variation in selective pressures is likely to cause the adaptive divergence of populations (Mayr 1947, Endler 1986). This is an important phenomenon in biology because the differentiation of populations is the first step towards speciation (Via 2001, Nosil et al. 2009). Adaptive divergence refers to a change in characters through natural selection and is thus different from divergence through random processes, such as genetic drift or founder effects (Lande 1976, Gomulkiewicz et al. 2007). It is worth noting, however, that adaptive divergence is influenced not only by divergent natural selection,

but also by gene flow and phenotypic plasticity (Crispo 2008, Nosil 2008). These may either promote or constrain the adaptive divergence. In this thesis I have concentrated to study how natural selection promotes population divergence.

Unfortunately there is a confusing variety of terms used to describe the adaptive divergence of populations. Although they have been used synonymously to some extent, they do address somewhat different aspects of the phenomenon. In this thesis, I will consider the divergence of populations as **ecological divergence** (Fox and Morrow 1981, Schluter, 2001, Rundle and Nosil, 2005, Funk et al. 2006), because I study the impact of locally differing ecological conditions on the adaptations of populations. The ecological divergence of populations may lead to reproductive isolation and finally to **ecological speciation** (Muller 1942, Funk et al. 2006). This attribute “ecological” separates the phenomenon from other speciation processes such as allopatric speciation (the speciation of geographically distinct populations).

Populations may diverge by adapting to their local environment (Mayr 1947). **Local adaptation** means that a population has a “home site advantage”; it has a higher fitness in its sympatric environment than populations from allopatric environments (Williams 1966, Kawecki and Ebert 2004). Thompson (1994, 1999, 2005) combined the ideas of local adaptation and co-evolution between host and herbivore into his **geographic mosaic theory of coevolution**. This theory postulates that a spatially varying environment (biotic or abiotic) creates a **selective mosaic**, for instance for herbivore species. As selection pressures vary among locations, different populations are expected to adapt to their local environment. The outcome is an **adaptive mosaic**. It is worth noting however, that the mosaic theory does not assume that all populations will show local adaptations to their sympatric environment. As with the metapopulation theory (Hanski 1999), the mosaic theory takes into account both population dynamics as well as the local characteristics of populations (e.g. selective environment, gene flow, population size etc.) in the expected outcome of selection. The selective mosaic includes not only locations with strong selection (e.g. tight coevolution between host and herbivores), but also those with milder selective pressures and a potentially stronger gene flow. Moreover, maladaptations may occur if the gene flow from neighbouring populations introduces traits that are adaptations there but maladaptations in the new environment (Thompson 1994). In the former population type, but not in the latter ones, organisms are expected to adapt to the local environments. Thus, the adaptive mosaic includes populations with local adaptations, but also those without. In this thesis, the idea of a selective and adaptive mosaic is very much the central approach to understand the variation in herbivore-host exploitation patterns. This approach provides a holistic and mechanical view of population interactions not only for studies on co-evolutionary processes, but also for studies on population divergence in general.

The selective mosaic is not entirely random as some locations are more alike and therefore create more similar selective pressures than others. For example, within an herbivore host range, localities with a similar composition of host assemblages create **replicated ecological**

landscapes (Reimchen and Nosil 2006) or perhaps more accurately, replicated selective environments. Populations occupying similar selective environments are assumed to show **parallel divergence** and, resulting from these, **parallel adaptations**, which differ from those adaptations of other populations living in different selective environments (Jones et al. 1992). The parallel divergence of populations in replicated selective environments may ultimately result in **parallel speciation** (e.g. Reznick and Ghalambor 2001, Rundle and Nosil 2005 and references therein). Both parallel speciation and ecological speciation actually fall under **sympatric speciation**; the speciation of geographically overlapping populations (Diekmann and Doebeli 1999, Fitzpatrick et al. 2008, Nosil 2008).

1.2.2 Criteria for local adaptations

The concept of local adaptation has been increasingly exploited in studies on host-herbivore interactions (Van Zandt and Mopper 1998; Katz and Shykoff 1998, Lajeunesse and Forbes 2002). The two criteria of Kawecki and Ebert (2004) are widely used to detect local adaptations (Greishar and Koskella 2007). The first criterion, i.e. “Local vs. foreign”, is fulfilled when a population has higher fitness in its sympatric environment than does a population allopatric to this environment (Fig. 1 a, b). The second criterion, i.e. “Home vs. away”, is met when a population has a higher fitness with their sympatric environment than in an allopatric environment (Fig. 1 a, c). For herbivores, the host plant or host assemblage creates the sympatric environment. The first criterion alone, or together with the second would be enough to prove local adaptations. Fulfilment of the second criterion alone gives less determinate evidence for local adaptation. However, it indicates genetic differentiation of populations and that some populations are superior to others (Fig. 1c; Kawecki and Ebert 2004).

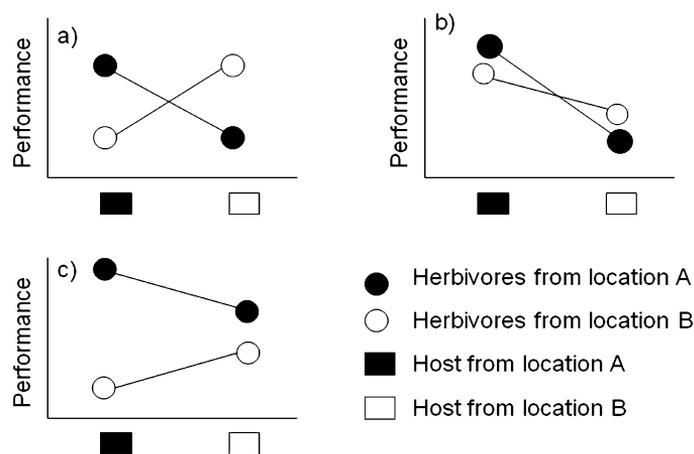


Figure 1. “Local vs. foreign” and “Home vs. away” criteria according to Kawecki and Ebert (2004). a) Both the “Local vs. foreign” and the “Home vs. away” criteria are fulfilled. b) Only the “Local vs. foreign” criterion is fulfilled; both populations have higher fitness in their sympatric environment than the allopatric populations. However, one of the environments is better for both populations. c) Only the “Home vs. away” criterion is fulfilled, because both populations have higher fitness in their sympatric environment than in an allopatric environment. However, population A outperforms B in both habitats.

1.3. Gene flow, phenotypic plasticity and maternal effects

Earlier, **gene flow** was expected to decrease the possibility of local adaptations (Holt and Gomulkiewicz 1997). However, the effect of gene flow seems to be more complicated and it has been suggested that a low or intermediate level of gene flow could actually enhance the possibility of local adaptation (Gandon et al. 1996, Lively 1999, Gandon 2002, Greishar and Koskella 2007, Räsänen and Hendry 2008). Although genetic diversity may simply be too limited to allow local adaptations in small populations (Leimu and Fisher 2008), gene flow may increase genetic diversity and thus the probability of local adaptations (Garant et al. 2007). One important variable in adaptive divergence is the ratio between the strength of gene flow and that of location-specific selection pressures. A strong variation in local selection pressures could override the intermixing effect of gene flow (Via 2001). Indeed, there are already examples showing the occurrence of adaptive genetic divergence of populations, in spite of on-going gene flow (reviewed in Funk et al. 2006, Leinonen et al. 2008, Niemiller et al. 2008).

Phenotypic plasticity and **maternal effects** alike must be considered in studies of local adaptation because they cause patterns similar to local adaptations, but confusingly, they may also be adaptive (Mousseau and Fox 1998, Thompson 2005, Nussey et al. 2007). Phenotypic plasticity has been considered as an alternative evolutionary outcome to adaptive divergence. Phenotypic plasticity is the ability of individuals to alter their phenotype in response to environmental conditions (Schlichting 1986). The relationship between phenotypic plasticity and adaptive divergence is under debate, as they are also viewed as raw material for adaptive divergence (West-Eberhard 1989, reviewed in Crispo 2008). Basically, there are two alternative ways to cope with a heterogeneous environment: Either the character in question is so plastic that phenotypic plasticity gives at least moderate fitness in most habitat types, or different populations adapt genetically to their sympatric environments (Crispo 2008). However, achieving and maintaining plasticity is also assumed to incur costs and constraints (Futuyama and Moreno 1988). Briefly, in an unpredictable environment, plasticity is beneficial compared to fixed adaptations, but in a stable environment specialised (or locally adapted) individuals would outperform the plastic ones (Westoby 1978, Berenbaum 1996, Bernays & Minkenberg 1997).

It has been suggested that phenotypic plasticity and adaptive divergence would not be contradictory outcomes after all, because plasticity may actually trigger adaptive genetic divergence (Crispo 2008). Plasticity allows animals to successfully settle to new habitats and survive and reproduce there (Agosto 2006). Second, plasticity ensures phenotypic variation in selective responses. Third, selection may act on most fitting phenotypes of a plastic population without the need to first develop a completely new trait through mutations. Finally, the degree of plasticity could diminish during the process of local adaptation. This is because in a stable environment the locally adapted individuals should have higher fitness compared to the plastic “jack-of-all-trades” individuals. In this sense, the relationship between phenotypic plasticity vs. local adaptation is connected to the

relationship between generalism *vs.* specialism of an herbivore. Consider the evolution of host exploitation patterns of a small-sized herbivore species: Phenotypic plasticity and its decline over the course of genetic local adaptation present patterns similar to the specialisation process of generalist herbivore. Generalism, as with plasticity, is adaptive in a heterogeneous environment but in homogeneous environments, specialism should be a better strategy because specialists are expected to have higher fitness on the host plant. In unpredictable environments, however, the cost of specialism outweighs its benefits because the host range of a specialist is narrower than that of a generalist (Trowbridge, 1991 and references therein; Fox and Morrow 1981, Futuyma and Moreno 1988, Jaenike 1990, Via 1991, Després et al. 2007). Thus, both these processes lead to similar predictions about the evolution of the host-use range of herbivores: The specialisation process of a generalist herbivore (or local adaptation of a plastic herbivore) would result in the narrowing of the host range. At the species level, this would be seen as among-population variation in the width of the host range.

In some cases, maternal effects may cause similar outcomes to genetic adaptations and phenotypic plasticity. A maternal effect in a trait means that its phenotype is influenced (partly) by the mother. This influence may be caused by the genotype, the phenotype or the behaviour of the mother (Wade 1998). For example, the host choice of an ovipositing butterfly determines the quality of the food the larvae will feed upon (Chew and Robbins 1984), while in marine isopods, the quality of the food the mother consumes may affect the size and survival of the offspring (Hemmi and Jormalainen 2004).

1.4. Expanding the theory of local adaptations

1.4.1 Local adaptations in replicated selective environment

Thus far, studies of local adaptations have often focused on how geographic variation in the host plant quality affects the herbivore host-use traits (Nosil and Crespi 2006). This research tradition probably comes from studies targeted to reveal whether there has been chemical co-evolution between the host and the herbivore, and indeed the theory of the geographic mosaic of co-evolution was first developed to explain variations in the results in such works (Thompson 1999). In this thesis, paper **I** follows this research tradition by focusing on the geographical variation of herbivore host-use traits with respect to variations in host chemistry. Studies of this type are effective in indicating whether there is among-population variation and whether this variation agrees with local adaptations according to the criteria of Kawecki and Ebert (2004). Further, as shown in paper **I**, the variation among herbivore populations can be connected to spatial variations in the host plant quality to identify those factors responsible for the divergence. However, as the number of traits examined in both the herbivore and host are often limited for practical reasons, it is possible that the variation of traits between these does not match. In this case, and if the data also fails to meet the criteria of local adaptations in some of the populations

(see also Chapter 3.6.1.), one is unable to tell whether the variation among herbivore populations is a result of random processes (Gomulkiewicz et al. 2007), or whether some other, unknown environmental character has caused the observed selective mosaic.

One solution to this drawback lies in studying herbivore populations that occur in replicated selective environments. With this approach, one concentrates on two or more distinct selective environments (e.g. habitat types) and examines whether the adaptations of the studied populations are parallel, either within or between replicated landscapes. Random processes alone would hardly result in parallel divergence in multiple populations within a habitat type. Thus, in papers **II**, **III** and **V**, I apply the above mentioned approach and study herbivore host exploitation traits and colour polymorphism in replicated selective environments.

1.4.2 Predation modifying local adaptations

As discussed earlier, the local variation in both the host quality and in the composition of host plant assemblages may create a selective mosaic for herbivore host-use traits, such as the performance on a given host or a preference order among hosts. In studies on this type of questions, it is assumed that the first trophic level, or more precisely, the quality of the host or composition of host plant assemblage, is responsible for the selective mosaic and that the evolving character of the herbivore is a host-use trait of some kind. This approach in studying local adaptations could be classified as a “bottom-up approach”, as it focuses on how the first trophic level influences the second trophic level. Instead, “top-down approach” is taken in studies focusing on the influence of third trophic level. This approach is applied in some studies of coevolution between host-parasite as they include not only plant-parasite, but also animal-parasite interactions (Hoeksema and Forbes 2008). Instead, there are only a handful of examples showing local adaptations in anti-predator traits of herbivores in respect to locally varying selection by the predators (Abrams 2001, Nosil and Crespi 2006, Nosil and Sandoval 2008). The complete paradigm of trophic interactions with simultaneous and interactive “top-down” and “bottom-up” influences is largely neglected in studies of local adaptations (Gripenberg and Roslin 2007).

Predators select for both the anti-predatory behaviour of herbivores (e.g. host and habitat choice), as well as prey morphology (Caro 2005). Cryptic coloration is an example of this (Endler 1978, Merilaita et al. 1999). If the selection pressure imposed by predators is spatially inconsistent, it may create spatially different anti-predator adaptations in herbivores (Abjornsson et al. 2004). Therefore, a selective mosaic could also be created by the local variation in predator species or their densities. Predators could also create the selective mosaic through interaction with the first trophic level: Locations may vary visually as a consequence of spatial variation in the composition of the host species assemblage or in the appearance of a single host species. The concealing effect of a cryptic coloration is not determined by the appearance of the prey alone,

but rather by the visual interaction between the appearance of the prey and its habitat (Merilaita 1999). Consequently, morphs differ in their degree of crypsis in different backgrounds (habitats) and accordingly, the predation pressure on morphs may depend on the background. Thus, the optimal morphology or colouration (or other anti-predator traits) may vary among populations or habitats. Predators or the interaction between predators (their perceptual mechanisms) and habitat may create a selective mosaic for herbivores, which themselves may have local adaptations in anti-predator traits. In paper **III**, I apply this predator-mediated approach for studying local adaptations.

There are studies showing intraspecific variation in cryptic colouration (reviewed for spiders in Oxford and Gillespie 1998, for anurans in Hoffman and Blouin 2000). However, much less is known about factors causing this variation (Nosil and Crespi 2006) and/or whether the intraspecific variation represents local adaptations. Examples of the latter include walking-stick insects (*Timema cristinae*), where two pattern morphs are associated with different host species (Sandoval 1994), and the freshwater isopod *Asellus aquaticus*, in which light and dark morphs occur in distinct host plant assemblages (Hargeby et al. 2004). If habitats differ according to their predator regimes (predator presence/absence), rather than their first trophic level, further examples may also include fish species, such as the three-spine stickleback, *Gasterosteus aculeatus* (Bell et al. 1982), the guppy, *Poecilia reticulata* (Endler 1987, 1988,) as well as amphibians, e.g. the streamside salamander, *Ambystoma barbouri* (Storfer et al. 1990).

1.4.3 Differences in local adaptations between males and females

In general, the host exploitation patterns of herbivores are assumed to represent a resolution of the trade-off between food and shelter (Sih 1980, Dill 1987, Lima and Dill 1990, Duffy and Hay 1991, Hay 1997, Brown and Kotler 2004). However, this resolution is not necessarily consistent among individuals. For example, males and females usually have different fitness maximising strategies with respect to both nutritional demands and anti-predator behaviour (Trivers 1972, Slatkin 1984, Lima and Dill 1990, Arnold and Duvall 1994). Also, in many species, the predation risk differs between males and females and this has a major overall effect on their foraging behaviour (Main 1987 and references therein; Caro 2005, Verdolin 2006). Although males are most often considered to be more risk-prone (Williams et al. 2001; Brown and Braithwaite 2005 and references therein), females have been reported to take higher risks in some species (e.g. Abrahams and Dill 1989, Rochette et al. 2001, Skals et al. 2003). Males and females have also been shown to differ in both foraging behaviour and habitat use (Huang and Sih 1990, Levri and Lively 1996, Merilaita and Jormalainen 1997, Forsman and Appelqvist 1999, Pardo and Johnson 2004, Ahnesjö and Forsman 2006, Post and Götmark 2006). Thus, sex-specific responses to the trade-off between risks and resources may be expected and in turn, they are likely to result in sex-specific host exploitation patterns. Indeed, sexually varying ecology, morphology and behaviour are likely to result in sexually

differing selective pressures. Thus, although males and females may co-occur in the same selective environment, they may show different adaptive responses (Slatkin 1984, Schluter 2001).

Populations within a replicated selective environment may exhibit parallel independent adaptations. While differences between the sexes may be population specific (Badyaev et al. 2000), they may be equal in populations within a particular selective environment: Sex-specific differences in the values of food and shelter result from the ecological dissimilarities of the sexes, which may cause sexually dissimilar adaptations in different selective environments. As far as I am aware, Hendry et al. (2006) were the first to combine adaptations in replicated landscapes with habitat-dependent sexual variation. They studied the sexual dimorphism in the size and morphology of populations of wild guppies living in different selective environments and found that the sexual dimorphism differed among population's from two selective environments. To summarise, the theory of local adaptations assumes that the host exploitation pattern of an herbivore species is not uniform within a species but varies among individuals from different populations. The hypothesis of sexually diverged adaptations in replicated landscapes further assumes that groups of individuals within a population, such as males and females, may vary in host exploitation patterns, but that this would be similar among populations within a particular habitat type. The variation in sexual dimorphism of morphological traits among distinct habitat types has been studied at least in lizards (Butler et al. 2000, Butler and Losos 2002), guppies (Hendry et al. 2006) and sticklebacks (Reimchen and Nosil 2006 and references therein). However, this type of variation has been ignored in studies of the evolution of herbivore host exploitation patterns, although it may result in a situation where a herbivore species has multiple fitness optima in host-use, rather than a single one.

1.5 Aims of the thesis

In this thesis, I studied spatial variation in herbivore adaptations by connecting the frameworks of ecological divergence, selective mosaic and parallel adaptations, using as my study species the marine crustacean grazer *Idotea balthica* and its host plants. In general, studies on ecological divergence (or local adaptations) have been biased towards the terrestrial environment, while empirical evidence of the ecologically-based divergence of populations in marine environments is scarce, relying on a few studies only (reviewed by Sotka 2005, Duran and Rützler 2006). It is probable that the opportunity for local adaptations in the marine environment has previously been considered unlikely because many marine herbivores have pelagic larvae, resulting in high rate of gene flow, which may prohibit the evolution of local adaptations (Sotka 2005; but see Kruse et al. 2004).

My first objective was to study whether the host-use traits or anti-predator adaptations of *Idotea balthica* diverged among populations. The second aim was to expand upon

this by examining whether the populations within a selective environment were more similar than those between the selective environments. This was done by applying both the “bottom-up” and “top-down” approaches. Papers **I**, **II** and **V** follow the research tradition of local adaptation, where the focus was on the interaction between the first and second trophic levels. In paper **III**, I used the “top-down” approach and studied whether predators caused ecological divergence in an anti-predator trait of *I. balthica*, namely, the colour morph frequencies of populations.

The third aim was to study whether the sexes show dissimilar adaptations in different selective environments (**V**). This was preceded by a set of experiments, which demonstrated sexual variation in microhabitat use and anti-predator adaptations (**IV**). More specifically, in the latter work I examined how food and shelter are valued by males and females, including individuals with distinct colour morphs and whether this was further influenced by temporal variations in predation risk. Although the questions addressed by the original papers are described in more detail in the material and methods section (Section 2), a short summary is presented here:

- 1) Are the *I. balthica* populations inhabiting one selective environment divergent in their host-use abilities and is this divergence consistent with the criteria for local adaptations? Does local variation in plant chemistry contribute to the selective mosaic for the host-use ability of *I. balthica*? (**I**)
- 2) Are the *I. balthica* populations inhabiting two kinds of selective environments divergent in their host-use abilities or colour morph frequencies? Is this divergence consistent with the criteria for local adaptations? (**II**, **III**)
- 3) Do the sexes of *I. balthica* differ in how they value risks and resources (**IV**)? Are the adaptations to local selective environments sex-specific (**V**)?

2. MATERIAL AND METHODS

2.1. Study species

2.1.1. *Idotea balthica*

Idotea balthica (Pallas; Isopoda) is an important grazer of littoral algal communities in the Baltic Sea (Salemaa 1979). It is a wide spread species occurring from the Atlantic coasts to Mediterranean Sea (Bulnheim and Fava 1982). In the Northern Baltic Sea, it occurs most frequently in zones of the bladder wrack, *Fucus vesiculosus* L., but it is also found in eelgrass meadows, *Zostera marina* L. (Salemaa 1979, Boström et al. 2006). *I. balthica* is a generalist herbivore of various algae and vascular plants (Salemaa 1978). In my study area, i.e. the Northern Baltic Sea, although *I. balthica* prefers *F. vesiculosus* over other studied hosts, it does not maximise their growth (Nicotri 1980, Jormalainen et al. 2001a). It can however, grow and reproduce solely on *F. vesiculosus* (Hemmi and Jormalainen 2002). In the Northern Baltic, the lifespan of *I. balthica* is 13-15 months (Salemaa 1979). They mature and have their reproductive period from June to July, with juveniles released from the females' brood pouch 3-4 weeks later (Jormalainen and Tuomi 1989). Very few of the adult animals survive until autumn and thus the generations are not overlapping.

Idotea balthica is a colour polymorphic species (Fig. 2). The most common morphs in the Northern Baltic are the monochromatic *uniformis* and the white-spotted *albafusca* (Salemaa 1978). Other morphs include the marbled *maculata* and striped morphs *bilineata* (with two longitudinal stripes) and *lineata-bilineata* (with three longitudinal stripes). Combinations of the patterns occur as well. In my studies, I have combined the striped morphs into one class, *lineata*. The function of the coloration of *I. balthica* is most likely concealment as predation pressure by visually-hunting fish is thought to be high (Salemaa 1978, Merilaita 1998, 2001). Interestingly, the sexes have different colour morph frequencies and slightly different behaviours also: The apical and basal parts of *Fucus vesiculosus* differ as food and shelter and male and female isopods use them differently, males occurring more often in the more exposed apical parts (Merilaita and Jormalainen 1997, 2000). The sexes are probably adapted to utilise different parts of *F. vesiculosus* as food, as males grow faster when fed with apical parts, whereas females grow equally well with both (Jormalainen et al. 2001b). Males' occurrence in the more exposed parts is probably one reason for the higher realised predation risk of males (Jormalainen et al. 1995).

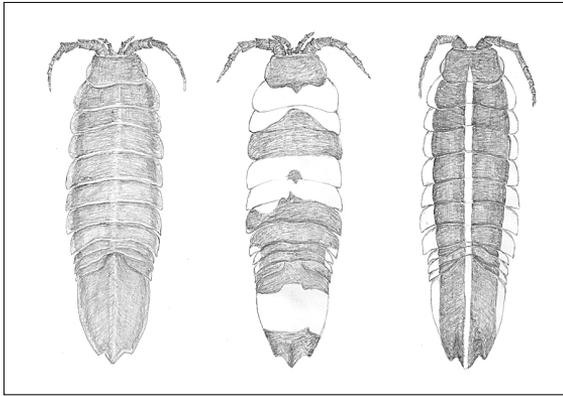


Figure 2. From left, monochromatic *uniformis*, spotted *albafusca* and striped *lineata* (*lineata-bilineata*). These morphs were used in the predation experiment in the paper **III**. Size of *I. balthica* differs between sexes, populations and host assemblages. In the populations in paper **III**, mean size of mature females in algal assemblages (see below) was 14.7 mm but in angiosperm assemblages 12.0 mm. Instead, mean size of mature males in algal assemblages was 18.6 mm but in angiosperm assemblages only 14.7 mm (see also paper **II**).

2.1.2. Study area and host assemblages

My studies were conducted in the archipelago of the Northern Baltic Sea. The sampled populations occurred in the littoral areas of the islands or the mainland. Each experiment included several populations and the precise locations are given in the original papers. Populations within a species may diverge when there is spatial variation in the biotic interactions and/or the species has a metapopulation structure (Boecken and Mopper 1998, Reznick and Ghalambor 2001). My study system meets these assumptions: the study area in the Northern Baltic Sea is naturally fragmented by thousands of islands (Granö et al. 1999, Merilaita 2001). The hosts provide a heterogeneous environment for the herbivore populations: the chemical quality of the main host plant, the brown alga, *Fucus vesiculosus* varies locally (Hemmi and Jormalainen 2004a, Koivikko et al. 2008), as does the composition of the potential host assemblages in general. *Idotea balthica* inhabits the littoral zones, and the pelagic areas between the locations may decrease the rate of gene flow among isopod populations. The isopod populations are diverged by their life-history traits (timing of reproduction, body size, reproductive output; Hemmi and Jormalainen 2004) and by their cryptic colouration (Salemaa 1978, Jormalainen et al. 1995, Merilaita 2001). Thus, I had reason to expect divergence of populations in host-use traits also.

Fucus vesiculosus L. is a perennial brown alga, forming dense belts along the shallow, rocky littoral shorelines of the Baltic Sea. Although *F. vesiculosus* is the only perennial, belt-forming macro-alga in my study area, other *Fucus* species are also found in the Southern Baltic Sea. In the Northern Baltic Sea, *F. vesiculosus* constitutes an important habitat for organisms in littoral ecosystems. Other algae commonly found in *F. vesiculosus*-dominated assemblages include the filamentous algae *Pilayella littoralis* L., *Dictyosiphon foeniculaceus* (Hudson), *Elachista fucicola* (Velley), *Cladophora glomerata* L., *Ulva intestinalis* L. (formerly *Enteromorpha intestinalis*); *Ceramium tenuicorne* (Kützing), *Stictyosiphon tortilis* (Ruprecht), *Ectocarpus siliculosus* (Dillwyn) and *Furcellaria lumbricalis* (Hudson). The relatively low performance of *Idotea balthica* on the highly preferred host *F. vesiculosus* is attributable, at least in part, to phlorotannins of the algae.

Phlorotannins are phenolic secondary metabolites present only in brown algae, and they can account for up to 15 % of the dry-mass of the alga (Arnold and Targett 1998). In my study area, the dry weight of *F. vesiculosus* constitutes on average 8 – 10 % phlorotannins (Hemmi and Jormalainen 2004a, Koivikko et al. 2005). One function of phlorotannins is to act as defensive compounds against herbivory (reviewed in Arnold & Targett 1998; meta-analysis in Jormalainen and Honkanen 2008). The performance of *I. balthica* is negatively correlated with the phlorotannin content possibly because they reduce the herbivore species ability to assimilate carbon and nitrogen (Jormalainen et al. 2005).

Zostera marina is a meadow-forming vascular plant inhabiting soft, sandy bottoms at depths of 2-4 m. The study area has low salinity of 4-6 ‰ allowing co-occurrence of marine and limnic species. Indeed, other typical species in angiosperm assemblages include *Potamogeton pectinatus* L., *Zannichellia palustris* L. and *Ruppia spiralis* L.

The spatial variation in the composition of host plant assemblages is one possible factor creating a selective mosaic for *Idotea balthica*. There is also among-population variation in the quality of a single host plant species, as populations of *Fucus vesiculosus* vary in their chemical content (Hemmi and Jormalainen 2004a) and in morphology (Ruuskanen and Bäck 1999). Trait variation is likely caused both by genetic substructuring of the population (Tatarenkov et al. 2007) and by plastic responses to abiotic and biotic environment, e.g. to nutrient supply (Koivikko et al. 2005). The dispersal of the host plants of *I. balthica* is partly inhibited by the geographic structure of the area and while pieces of adult *F. vesiculosus* may drift from one location to another, the dispersal of the eggs and sperm cells of *F. vesiculosus* are restricted to relatively close to parent individuals in the brackish water conditions (Coyer et al. 2003 and references therein). In the Baltic Sea, *Zostera marina* reproduces clonally and Reusch et al. (1999) showed that a whole eelgrass meadow may be dominated by a one genotype. Nevertheless, the chemical quality of *Z. marina* populations differs, as shown by the variation in the amount of total phenolic compounds (I). In practice, when considering the local adaptations from herbivore perspective, it is irrelevant whether the spatial variation in the quality of the host plant is phenotypic or genetic, as long as it is temporally stable.

I chose *Fucus vesiculosus* and *Zostera marina* as host species because they are both dominants in their habitats and create the typical structure of their respective assemblages (Fig. 3). These two assemblages (hereafter algal and angiosperm assemblages) provide very different visual backgrounds for the colour morphs, such that habitat-specific effects on their survival could be expected. Moreover, algae and seagrass are very dissimilar hosts qualitatively. The consumption and efficient utilisation of *F. vesiculosus* may require the ability to cope with phlorotannins and to use *Z. marina* as a host species may require ability to degrade cellulose. Thus, the same digestive processes are hardly suitable for the efficient exploitation of both host species. Specialisation to a chemically-defended host is assumed to incur costs, in terms of a decreased ability to utilise other possible hosts. *F. vesiculosus* is known to employ such chemical defences, phlorotannins. Thus,

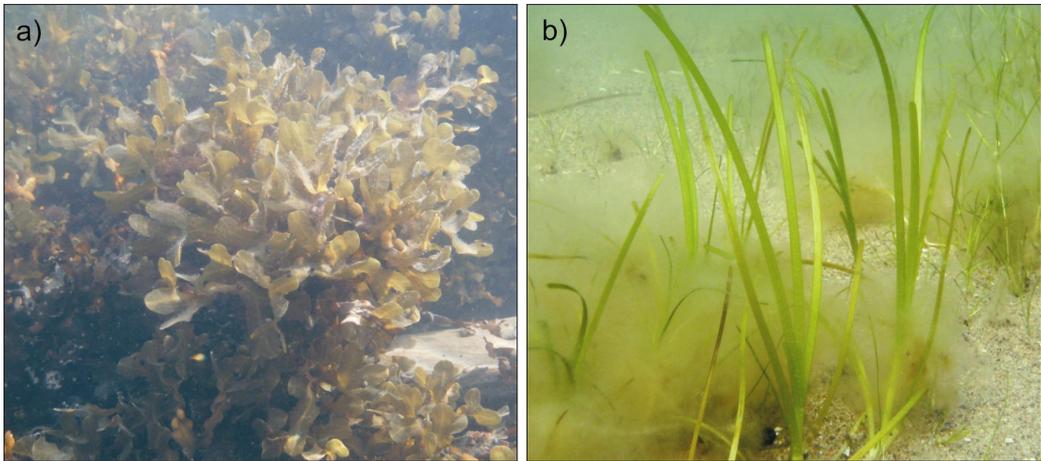


Figure 3. The studied host plant assemblages: a) algal assemblage dominated by *Fucus vesiculosus* and b) angiosperm assemblage dominated by *Zostera marina*. Photos by Samuli Korpinen (3a) and Outi Vesakoski (3b).

I assumed that adaptation to utilize *F. vesiculosus* may involve specialisation process. I further assumed that this could be seen as a narrower host range of *I. balthica* populations sympatric to algal assemblages compared to the host range of isopod populations living in angiosperm assemblages.

For papers **II**, **III** and **V**, I collected isopods from both algal as well as angiosperm assemblages, the former being selected based on the absence of the latter in the near vicinity. By comparison, in the angiosperm assemblages, there were typically some *Fucus vesiculosus* growing on solitary rocks and stones or on the shallow rocky edge of the otherwise sandy angiosperm meadows. These were rare, however, compared to the overall coverage of vascular plants. Therefore, these host plant assemblages were likely to comprise distinct selective environments for *I. balthica* populations.

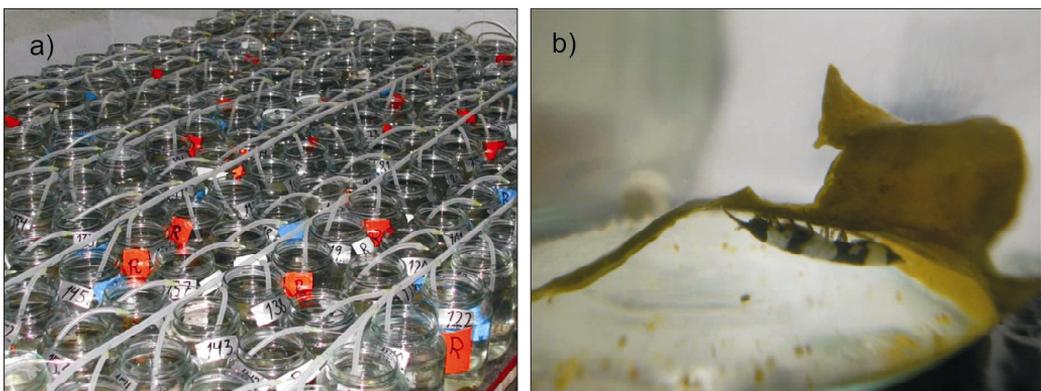


Figure 4. In the performance experiments, the isopods were a) kept in aerated 1-litre glass jars and b) fed with pieces of host plants (*alfafusca* female on a piece of *F. vesiculosus*). Photos by Veijo Jormalainen.

2.2. General methods

In the algal assemblages, I collected bushes of *Fucus vesiculosus*, manually or with a rake, either by wading along the shoreline or from a boat. I searched for *Fucus* bushes attached to stones with the aim of returning these intact to the sea after the isopods were removed. In the angiosperm assemblages the isopods were collected by scuba diving: divers collected fresh plant material in net bags and avoided harming the roots. In both cases, the isopods were then sought from within the collected plant material.

After field sampling, the animals were transported to the Archipelago Sea Research Institute, University of Turku (60°14'N, 21°60'E). Before the experiments, the isopods were kept in aerated tanks with their host plants. During the experiments, the isopods were maintained individually in glass jars (Fig. 4), in which the water was aerated and changed at minimum intervals of five days. In addition, these holding jars were aerated throughout most of the experiments. When using fresh food, the food plants were maintained in through-flow seawater pools under natural light conditions or besides the dock of the research station. Fresh food was provided at minimum intervals of five days or was replaced before the food had been consumed.

The sex of the isopods was determined based on their genitalia. The colour morphs were determined by one person based on instruction in Salemaa (1978). Individual's morph patterns are not plastic, but the overall darkness is as the isopods may change their colour to some extent from dark to light according to the background colour. Thus all colour determinations were conducted on specimens kept for ten minutes over a light background under natural or artificial light. In the performance experiments (**I**, **II**, **V**), I measured the growth and/or the reproductive output (number of eggs and total brood mass). When measuring reproduction, I ensured that all isopods entered the experiment at the same age. Isopods grow by moulting and the females may copulate and reproduce only in a parturial moult. The approach of the reproductive moult can be followed by studying the morphological change of the marsupial plates.

The data were analysed with the SAS statistical software package (SAS institute 1999). In general, the performance experiments were analysed with either fixed or mixed ANCOVA's (analysis of covariance) or ANOVA's (analysis of variance), and hierarchical models were used most often. In paper **IV**, the main statistical analysis involved a repeated ANOVA. By comparison, in paper **III**, I used generalised mixed models. The statistics, analyses and mean values are explained in more detail in the original papers.

2.3. Study questions and specific methods

2.3.1. Divergence in host-use traits

In paper **I**, I focused on the divergence of host-use ability of *Idotea balthica* populations sympatric to *Fucus vesiculosus* and studied whether the host-use ability varied

among populations. In total, 270 female isopods were collected from the three algal assemblages (90 from each). Simultaneously, algae were sampled from each assemblage for experimental food for the isopods. The study was a reciprocal feeding experiment, implying that each isopod from a given population was fed with sympatric algae (30 isopods), plus the two allopatric algae (30 + 30). The algae were maintained in both control and nutrient-enriched environments to expand the variation in host plant quality and to reveal those potentially important algal traits in host-use ability. The host-use ability of the isopods was measured in terms of growth and reproductive output. In addition, I examined whether divergence was due to adaptations to the sympatric host quality. Total sugars, phlorotannins and proteins were analysed from the host plants to investigate whether they were responsible for locally varying selection pressures.

Paper II focused on variation in host-use traits among isopods from different host assemblages. I knew from the paper I that there is variation among populations within a host plant assemblage. To reliably compare isopods from different host assemblages, replicate populations within distinct assemblage types were needed. Thus, isopods and host plants were collected from three algal and three angiosperm populations (60 females from each, totalling 360 individuals). I investigated whether there was divergence among populations, as well as among the host plant assemblages of algae and angiosperms. I performed again a reciprocal feeding experiment, providing either *Fucus vesiculosus* or *Zostera marina* from the different locations as food (six types of food). Ten isopods from each population were fed with one food type. However, my main interest lay in the difference between *Fucus* and *Zostera* diets, rather than any quality differences among the host populations. In an additional experiment, I studied the contribution of phenotypic plasticity to host-use ability by growing laboratory-born juveniles in a controlled environment and measured their growth on either sympatric or allopatric host species (*F. vesiculosus* or *Z. marina*). I measured the performance of the isopods in terms of reproductive output (first experiment) and growth (second experiment).

In paper V, I compared host exploitation patterns between the sexes: I tested the hypothesis of sexually divergent adaptations in replicated selective environments. I measured the performance (growth) of juvenile isopods on five diets: *Fucus vesiculosus*, *Zostera marina*, *Potamogeton pectinatus*, *Cladophora glomerata* and a mix of these. In addition to host-use ability, the host preference was studied in a dual-preference experiment. First, I studied the preference for the structural host (pieces of the natural hosts) and considered this as the natural host choice situation. However, when using pieces of natural host species, the host value in terms of food and shelter are intermixed, making it impossible to assess which factor caused the host choice. To separate these two factors, I removed the structural value of the host plants. This was achieved by drying and powdering the host species, combining the powder with agar-agar and moulding this into artificial food pellets. The isopods were then allowed to choose amongst the food pellets. In other words, the second preference experiment studied the nutritional host preference.

To summarise, by conducting both preference and performance studies it was possible to study different aspects of the herbivore host-use traits. Further, I was able to compare the results and determine whether the isopods selected their host according to its nutritive or protective value. Isopods were collected from six algal and six angiosperm assemblages: ten isopods from each population (five males, five females; totalling to 120 individuals) for the preference experiments and 30 isopods from each population (15 males, 15 females, totalling to 360 individuals) for the performance experiments. The hosts were collected from single locations. The total content of sugars, proteins and phenolic compounds of the host plants were quantified.

One aim of this thesis was to approach local adaptations from multiple angles employing several different approaches. In addition to preference and performance experiments, I also investigated whether the isopods from the two habitat types showed different degrees of specialisation to their sympatric hosts (**II**, **V**). *Fucus vesiculosus* contains high amounts of phlorotannins known to affect the performance of *Idotea balthica* (Jormalainen et al. 2005). Therefore, I expected that isopods sympatric to *F. vesiculosus* would be more specialised to the alga and would show also a more specialised pattern of host-use. Cost of specialisation might be expressed as a decreased ability to utilise the alternative hosts. In paper **II**, this cost was estimated by comparing differences in the performance of the populations between the two diets. A more specialised host-use ability would be manifested as a bigger difference in performance between the two diets. In paper **V**, the same was studied using a mixed diet treatment in performance experiment. I assumed that the lower performance on mixed diet would indicate more specialised host-use ability and higher performance more generalised host-use ability.

2.3.2. Divergence in anti-predator traits

When sampling isopods from the two assemblages for the paper **II**, I noted that in angiosperm assemblages there were more *lineata* isopods than ever seen in algal assemblages. This led to hypothesis that not only host use traits but also cryptic colouration may respond to locally varying selective pressures. In papers **I**, **II** and **IV**, I used the “bottom-up” approach and studied the effects of the first trophic level to the second. By contrast, in paper **III**, the “top-down” approach was used to measure predator-mediated anti-predator adaptations: I studied the divergence of colour morph frequencies among populations and between host plant assemblages. As the cryptic colouration of a prey species is a response to selection imposed by predator behaviour (Endler 1978, Merilaita et al. 1999, Caro 2005), the observed variation in the colour morph frequencies of *Idotea balthica* populations could be a response to locally varying predation pressures. I assumed first, that the host plant assemblages provide spatially varying visual backgrounds for the morphs. Second, the visual variation of backgrounds might affect the perception of the predators and alter the predation pressure that the morphs experience in these two assemblages.

Male and female isopods were collected from four algal and four angiosperm assemblages, with the aim of sampling 100 males and 100 females from each. The populations were sampled three times to study whether the frequencies would be temporarily stable. The adult population was first sampled in spring and the juvenile populations the following autumn to study whether the colour morph frequencies were stable among generations. In the subsequent spring, the juvenile populations were sampled (only six of eight) again to see whether the morphs survived equally during the winter.

I further studied the potential mechanism of habitat-specific colour morph variation, by examining if the perch (*Perca fluviatilis*) would prey selectively on the colour morphs (*uniformis*, *albafusca*, *lineata*; Fig. 2). In the same experiment, I studied also whether the habitat-specific colour morph frequencies could be considered local adaptations. For this I conducted the predation experiment in aquaria with either an algal or angiosperm habitat.

2.3.3. Divergence between sexes and colour morphs

Based on earlier findings on sexual differences in *Idotea balthica* (Salemaa 1978, Jormalainen & Tuomi 1989, Jormalainen et al. 1995, Merilaita and Jormalainen 1997, 2000, Merilaita 2001), I hypothesised that host exploitation patterns may vary between sexes within a population. In paper IV, I studied whether males and females value food and shelter differently and whether their microhabitat choice within *Fucus vesiculosus* could be explained by this variation. The value of food and shelter had not been studied previously by simultaneously manipulating both factors. This was achieved by removing the structure of the host and conducting the experiment in a simplified environment: The host (*F. vesiculosus*) was dried and powdered and moulded into artificial food pellets. The pellets were presented in 2.7 litre aquaria, of which half the bottom was half white and half black. The apical pieces of *F. vesiculosus* appear light green, whereas the basal parts are dark brown. Thus, within a *F. vesiculosus* bush, there is a strong separation in exposure among these microhabitats (basal-apical). I used the black and white halves of the aquaria as concealing and exposing backgrounds, mimicking the basal and apical parts of *F. vesiculosus* (see also Merilaita and Jormalainen 1997, 2000). The isopods microhabitat choice was first studied without food, then with food in one half only (concealing or exposing) and finally with food in both halves but of differing quality. In each experiment, I used different isopods. There were 80 replicates (i.e. 80 isopods) in experiment. Further, in a population, other distinct phenotypes such as colour morphs, may differ by their host exploitation traits. In paper (IV) I also studied whether individuals with different colour morphs would value food and shelter differently.

The sexual variation in host exploitation patterns was also studied in paper V, where the question was whether the sexes would have dissimilar adaptations to their sympatric host assemblage. Here, I studied the host-use traits of the isopods as explained earlier. In

paper **III**, I also studied sexual variation in adaptations to host plant assemblages, with respect to colour morph frequencies. For this purpose, the colour morph frequencies of both male and female isopods from the sampled populations were recorded. Further, in the predation experiment, different aquaria were established for males and females to control for sexual variation in predation pressure (**III**).

3. RESULTS AND DISCUSSION

3.1. Spatial divergence

3.1.1. Divergence in host-use traits

In paper I, I found that the populations of *Fucus vesiculosus* differed in their quality as food for *I. balthica*. This suggests that spatial variation in the quality of *F. vesiculosus* creates a selective mosaic for the host-use ability of the isopods. However, according to the two criteria by Kawecki and Ebert (2004), the isopods were not universally locally adapted to their sympatric hosts. One of the isopod populations performed best on its' sympatric host, but all of the other populations performed best on this algal population also. It is noteworthy that this particular algal population has been found to have exceptionally low level of phlorotannins (I, Koivikko et al. 2008). It is possible that isopods in this location have adapted to low level of phlorotannins, whereas the other isopod populations have adapted to the higher levels of phlorotannins of their sympatric algal populations. Consequently, the isopods from the low-phlorotannin-population were unable to efficiently utilise the high phlorotannin algae from the other locations thus fulfilling the 'Local vs. foreign' criterion. Conversely, isopods from populations with higher phlorotannin levels may perform even better upon an allopatric host with lower levels of chemical deterrent (see also chapter 3.6.). Furthermore, in two of the three isopod populations, the performance correlated negatively with the phlorotannin content of the host. This suggests that the phlorotannin content of *F. vesiculosus* is a selective factor affecting the evolution of host-use ability in *I. balthica*.

The isopod populations living in different host plant assemblages had divergent host-use abilities (II, V). In paper II, I found support for the 'Local vs. foreign' criterion (Fig. 1b; Kawecki and Ebert 2004). Populations originating from algal assemblages performed better on the *Fucus vesiculosus* diet than those from the angiosperm (*Zostera marina*) assemblage and *vice versa*. This pattern was similar for the reproductive outputs of adult, field-collected females and also for the growth of laboratory-raised juveniles. However, in the juveniles the pattern was weaker. Instead, the 'Home vs. away' criterion (Fig. 1; Kawecki and Ebert 2004) was not fulfilled: Isopods originating from both assemblages performed better on the *Fucus* than on *Zostera* diet, indicating that *F. vesiculosus* was clearly superior to *Z. marina* as food (see also chapter 3.6.).

3.1.2. Divergence in the degree of generalism

Results in paper II and V show that the degree of specialism or generalism may vary among *Idotea balthica* populations and between host plant assemblages also. The degree of specialism was measured as a relative difference in the ability to utilize two different hosts species (II) or difference in performance on a mixed diet consisting of all

four host species (V). The populations from the angiosperm assemblages showed less specialised host-use ability than those from the algal assemblages. This was shown by the populations from algal assemblages exhibiting greater performance differences between the two hosts (II). A similar variation in the degree of specialisation was found at the population level also: The *Idotea* population with the best performance on the *Fucus* diet showed the poorest performance on the *Zostera* diet. Moreover, the population with a slightly poorer performance on the *Fucus* diet, performed slightly better on the *Zostera* diet (II). A similar result was found in paper V, where the isopods from the angiosperm assemblage gained more weight on the mixed diet than those from the algal assemblage, indicating that the former expressed a more generalist host-use ability. These results give reason to assume that the ability to exploit *F. vesiculosus* constrains the capacity to utilise *Z. marina*. This supports the hypothesis that decreased ability to use other possible hosts could counteract the benefits of specialisation (Trowbridge 1991).

3.1.3. Divergence in colour morph frequencies

The colour morph frequencies also varied among *Idotea balthica* populations and host plant assemblages (III). It was shown that the colour morphs *lineata* and *albafusca* were more common in the angiosperm assemblages, while the monochromatic colour morph *uniformis* was more frequent in the algal assemblages. This result was repeated on three sampling occasions in six of the eight populations, i.e. in the adult isopods collected in subsequent years and in the juvenile isopods also. Thus, the colour morph frequencies were characteristic traits of populations. As the frequencies were partly habitat-specific showing parallel adaptations between the selective environments, I consider the results as evidence for spatially divergent natural selection caused by habitat-specific predation pressures. Interestingly, in a larger spatial scale the colour morph differences are even more drastic as the pattern morph with a single white stripe is common in the Southern Baltic Sea (Bulnheim and Fava 1982, pers. obs.) but there has not been a single individual in our samples.

Another example of variation in colouration that correlates with habitat type comes from the freshwater isopod, *Asellus aquaticus* (Hargeby et al. 2004). The darkness of the cuticula of *A. aquaticus* varies within two assemblages: populations associated with *Chara* spp. and those populations associated with *Phragmites australis*. The terrestrial walking-stick insect, *Timema cristinae* has also been shown to possess habitat-specific colour morph frequencies (Sandoval 1994, Nosil and Crespi 2006). Sandoval and Crespi (2008) further showed that the trait can develop independently among locations without the need for a common ancestral population: They found that the dorsal stripes in *Timema* species evolved independently five or six times within that clade, each time in association with hosts with needle-like leaves. Habitat-specific colour morphs may also be caused by habitat-specific sexual selection or interaction between natural and sexual selection,

such as in guppies *Poecilia reticulata* (e.g. Endler 1995). However, in *I. balthica* sexual selection has not been found to affect colouration (Jormalainen et al. 1995).

3.2. Sex-specific host exploitation

In paper IV, I present a set of experiments concerning sexual differences in the resolution of the trade-off between risks and resources. Males and females were found to value food and shelter differently. Firstly, if no food was available and the isopods only needed to choose between the concealing (dark) and the exposing (light) microhabitats, the females used the concealing microhabitat more often and showed more aversion to risky behaviour than the males did. In the second experiment, a food item was added to one side of the aquaria. Both sexes were more interested in the presence of food than in concealment, but the presence of food affected females more than males. In the third experiment, isopods were allowed to choose between combinations of high and low quality food as well as the concealment level of the background. Here, although the food quality outweighed the value of concealment in both sexes, it had an even stronger influence on female microhabitat choice. In sum, the results showed, somewhat controversially, that while the females were more interested in shelter, they were more willing than males to trade it for the higher quality food. Consequently, the microhabitat choice of males could be described as being more reckless - at least it was more independent on the studied factors, namely food and shelter.

In terms of mobility, males moved more between the microhabitats. Higher activity has been connected to higher predation risk (Jormalainen et al. 1995) and in this sense they were more risk-prone than females. This “reckless” habitat-use behaviour of males may be explained by mate-seeking behaviour, which also exists outside the breeding season (behavioural syndromes; Sih et al. 2004 a, b). A probable consequence of the more reckless behaviour was documented in the predation experiment, where the males were preyed on at a faster rate than the females (III).

Sexual divergence in the host-use abilities differed within the host plant assemblages (V). The performance experiment in paper V showed that the host exploitation pattern differed between the sexes and between populations from the two host plant assemblages. Although the sexual differences in performance on each host showed the same direction in both habitat types, the magnitude of these differences varied. In isopod populations from the algal assemblage, males grew better than females on *Cladophora glomerata*, while in those populations from the angiosperm assemblage, males grew better than females on *Potamogeton pectinatus*. These results are in accordance with my former studies showing that the host exploitation pattern of *Idotea balthica* is both sex-specific and spatially divergent. This habitat specific sexual difference also supports the hypothesis that sexual differences among populations are not random but may be connected to particular selective environment (Hendry et al. 2006). I know no other examples of this in host-use traits or in herbivores in general. Instead, a number of studies concerning

fish morphology show that while sexual size-dimorphism varies among populations, it may be parallel in populations within a selective environment (Butler and Losos 2002, Reimchen and Nosil 2006, Hendry et al. 2006).

Moreover, in the preference experiment in paper V, where isopods were allowed to choose between five different host plants, the populations differed according to their original host assemblages. All the isopods preferred *F. vesiculosus* as the structural host (see also Nicotri 1980, Jormalainen et al. 2001a, Orav-Kotta and Kotta 2004). However, those populations from the angiosperm assemblages showed an even greater preference for it. There were no differences between the sexes in this respect, while the preference for nutritional hosts did not vary among populations or sexes.

3.3. Which host-use trait to study?

I studied the different aspects of host exploitation of *Idotea balthica* by comparing their preferences for structural and nutritional aspects of the hosts and performance on the host plants (V). Interestingly, the interpretation of host-use patterns would have been very different if based on any single experiment alone: The most preferred structural host was *Fucus vesiculosus*, whereas all the vascular plants were more preferred as nutritional hosts. Finally, the best performance was provided by the filamentous green alga *Cladophora glomerata*. Because the structural host preference (influenced by both the structural and nutritional qualities of the host) differed completely from the nutritional host preference, the host plant preference was not dictated by the chemical characteristics of the plants. However, the structural host preference did not match the performance results either. As structural host preference did not correlate with performance, I conclude that *I. balthica* is not optimally adapted to utilise its favourite host as a single food source and that nutritional qualities do not solely determine the host choice. The absence of a correlation between the structural host preference and performance has previously also been found in this species in a comparison among six algal hosts (Jormalainen et al. 2001a). If the performance was linked solely to the chemical characters of the hosts, the nutritional host choice would co-vary with the performance (Via 1986, Thompson 1988). However, there was no such association either. This leads to conclusion that the structural characters of the host are important determinants in the host choice of *I. balthica* (Nicotri 1980, Jormalainen et al. 2001a, Mira and Bernays 2002, Orav-Kotta and Kotta 2004, for the importance of predation risk on foragers see also Boström and Mattila 1999, Lind and Cresswell 2005). Also a recent meta-analysis (Verdolin 2006) emphasised the importance of predation risk over food quality in determining host exploitation patterns.

To summarise, these findings lend support to the suggestion that *Idotea balthica* pays a cost in terms of decreased growth rate for choosing a host plant according to its value as shelter (see also Nicotri 1980, Jormalainen et al. 2001a): *Fucus vesiculosus* was highly preferred as a structural host, but did not provide good performance. In contrast,

although the performance on *Cladophora glomerata* was high, this host species had a low preference rank in the experiments with adult-sized isopods.

3.4. Colour polymorphism as a local anti-predator adaptation

In the predation experiment (III), I found that the predation imposed by the perch differed in strength between the colour morphs of *Idotea balthica*: *lineata* was eaten less than both *uniformis* and *albafusca*. However, the predation risk of the colour morphs was similar in both habitats and for males and females. Thus this experiment did not support the hypothesis that local variance in colour morph frequencies would be caused by varying predation pressure for the morphs in visually different host plant assemblage.

In general, this finding was somewhat unexpected, because according to this result, the *lineata* morph should have a higher survival than the other morphs in both assemblages. However, in the field data I found that this was the rarest morph in algal assemblage and was also rather rare in the angiosperm assemblage. One possible explanation may be that perch comprise only a small part of the predation pressure on *Idotea balthica* in nature, while mortality due to other predators may be more important. Salemaa (1986) listed more than ten species of predatory fish that feed on *I. balthica*. Secondly, the cognitive capabilities of predators may also play a role. Jormalainen et al. (1995) found a partial indication that perch may form a “search image” for the colour morph of *I. balthica* that occurred in their aquaria (a comparison between *albafusca* and *uniformis*). I consider it possible, that the perch in my experiment had a learned searching behaviour that facilitated them to find more easily the morphs common in their original habitat. The perch originated from the vicinity of Archipelago Research Institute from an area where *lineata* morph is very rare (I have found only one individual out of several hundreds). I aimed to remove any previously achieved biases in predator behaviour by maintaining the perches in the laboratory for at least two weeks and by feeding them with other food than in the experiment. They were also maintained in a different habitat than in the experiment. It is possible, however, that their former habits were maintained throughout the habituation period and experiment. If this is the case, the cognitive capabilities of this predator play an important role in the selection of prey (see e.g. Punzalan et al. 2005).

I consider anti-predator traits of an herbivore potentially useful approach for studying local adaptations. The criteria by Kawecki and Ebert (2004) could be actually applied here although I they did not fulfil in this study. The superior survival of the *lineata* morph in the angiosperm assemblage (in sympatric environment; environment where the morph is much more frequent) than in the algal habitat (allopatric environment; environment where the morph is vary rare) would have fulfilled the “Home vs. away” criterion for local adaptation (Kawecki and Ebert 2004). The “Local vs. foreign” criterion would also have been fulfilled if the survival of *lineata* would have been higher in the angiosperm habitat compared to *uniformis* morph, which was typical to algal assemblages. This type

of result was found in *Timema* spp., where the survival of the morphs was higher in the habitat where they were more frequent (Nosil and Crespi 2006).

Local adaptation in a marine environment has been studied only rarely (Sotka 2005). The present studies are to my knowledge among the only ones, where divergence in host exploitation patterns (II, V) and in anti-predator traits (V) has been demonstrated in a marine herbivore occupying distinct habitat types. There is some earlier support for the evolution of habitat-specific divergence in habitat preferences in marine amphipods. Stanhope et al. (1992) studied the host choice of the amphipod *Eogammarus confervicolus* and found that amphipods originating from three habitat types within the same area preferred the sympatric host as habitat, their preference being genetically determined. A comparison of the preference data and genetic analyses showed that a similar habitat shift had occurred independently in two spatially distinct estuaries (Stanhope et al. 1993). My results, with three (II), four (III) or six (V) replicate populations from each of the habitat types also provide evidence for parallel selective environments within plant assemblages.

Poore & Steinberg (2001) also studied local adaptations with respect to growth and survival in the marine amphipod *Peramphithoe parmerong* originating from two host patches within the same geographical locality. They found no signs of local adaptation at this smaller geographical scale. By comparison, Sotka & Hay (2002) and Sotka et al. (2003) chose a larger spatial scale and studied host preference and juvenile fertility in the marine amphipod *Ampithoe longimana*. They sampled populations that were sympatric and allopatric to a chemically defended host genus and found that the sympatric population had a higher preference for and fitness with the chemically defended host than the allopatric populations. They did not use reciprocal feeding experiments and thus, they did not test for the local adaptations criteria. They assumed that the difference was either due to the relaxed selection pressure for the chemically defended host in the allopatric populations, or as a result of genetic drift.

3.5. Local adaptation or something else?

I found multiple traits that were divergent among populations or between host plant assemblages: host-use abilities (II, V), host preference (V) and colour morphs frequencies (III). However, although the differences in performance were small between the habitat types and sexes, Boecklen and Mopper (1998) have pointed out that selection coefficients as small as 1-5 % may be enough to cause adaptive divergence. Further, variations in life-history traits, body size (II, III, V) and the timing of reproduction (II) among habitat types also points to an ecological divergence of populations (see also Fox and Morrow 1981, Schluter 2001, Rundle and Nosil 2005, Funk et al. 2006).

Random processes, phenotypic plasticity and maternal effects may also generate differences among population in host-use traits (Gomulkiewicz et al. 2007, Nussey et al. 2007), being thus potential alternative explanations for the divergence observed here.

I controlled for random processes, e.g. genetic drift and founder effects, by sampling multiple populations from each of the host plant assemblages, assuming that random processes would hardly result in a similar pattern from multiple locations. Populations within a habitat type were more similar than those between habitat types, showing that the divergence in host-use abilities was not due to random effects but rather caused by parallel selective pressures among locations within a given assemblage.

Phenotypic plasticity may allow organisms to acclimate to their local environment, and they may show better performance in their sympatric host because they are acclimated to consume this (Thompson 2005). I found a similar pattern in the host-use abilities among adult, field collected isopods, as well as among juveniles raised from birth under uniform laboratory conditions. Thus, plasticity, i.e. an acclimation to efficiently exploit the familiar host, cannot solely explain the divergence found here. This pattern was, however, weaker for juveniles, suggesting that the host-use ability of *Idotea balthica* also has a plastic component. The colour patterns of *I. balthica* are a trait without a plastic component (Tinturier-Hamerlin 1963). Instead, the colour morph frequencies of populations could be plastic and change according to fluctuation in predation pressure. However, the frequencies remained constant between the two generations, despite the strong winter mortality. This means that the frequencies were not “just” a plastic, year-to-year changing responses to winter mortality. Most importantly, the winter mortality did not alter the frequencies, which means that the selective environments remained constant between the generations. Further, the stability of the frequencies suggested that gene flow was not strong enough to alter them.

Maternal effects may also contribute to the juveniles' host-use ability. For example, if the host-use ability depends on endosymbiotic or gut microbes, the juveniles may get them from their mothers (Herre et al. 1999). To completely exclude maternal effects, one should maintain the species in laboratory conditions for generations to diminish the maternal variation caused by the natural environment. Finally, it is worth noting that both maternal effects and phenotypic plasticity have also been suggested to be adaptive and in some cases they may fuel the genetic divergence of populations: Among-population differences induced by phenotypic plasticity or maternal effects could trigger the divergence of populations, which in turn may lead to genetic sub-structuring of the species (Mousseau and Fox 1998, West-Eberhard 2003).

3.6. Theoretical considerations

3.6.1. Problems in detecting local adaptations

In the studies of local adaptations, the two criteria of Kawecki and Ebert (2004; Fig. 1; Chapter 1.2.2.) have been widely used (Greishar and Koskella 2007). These criteria, however, are rather restrictive for some conditions. First, when comparing two or more host species, the fulfilment of the “Home vs. away” criterion appears unlikely.

This is simply because the qualitative variation of two species may be so vast that local adaptations cannot override it. In my study, *Zostera marina* was clearly a lower quality food for the isopods and only the examination of the first criterion (“Local vs. foreign”) made sense. The situation is different in studies comparing populations within one host species. However, even in these cases it may also be that one of the studied plant populations is superior food for all the herbivore populations studied, such as the algal population in paper I, which recorded the lowest phlorotannin levels.

Second, judgement of occurrence of local adaptations by “Local vs. foreign” criterion may be simplified in some contexts. The fulfilment of this criterion may actually depend on which kind of adaptation and host trait are being considered. For example, in paper I, one host trait important for the herbivore host-use was the phlorotannin content. Adaptation to high levels of phlorotannins may or may not result to an in digestive capability demanding high levels of phlorotannins to function optimally. If it does, the fulfilment of the criterion could be assumed when comparing two herbivore populations sympatric to hosts with low (population A) and high (B) levels of phenolic compounds. However, the adaptation may also be e.g. an ability to tolerate high levels of phlorotannins. In this case, the population B would perform better on highly defended host compared to population A. Still, when compared the performance between host with high and low level of defense, both the herbivore populations may have higher fitness on the host with low level of defence. This would result to patterns where population B would have equal or even better performance on the allopatric host with low levels of phlorotannins (Fig. 5). In this example, both the populations would be locally adapted, but the “Local vs. foreign” criterion would fail to identify it.

Actually, the fulfilment of the “Local vs. foreign” criterion is more likely when comparing two host species than when comparing populations within a host species. This is because the costs of specialisation to a certain host species could be more easily seen as a decreased ability to utilise other host species (or a decrease in generalism

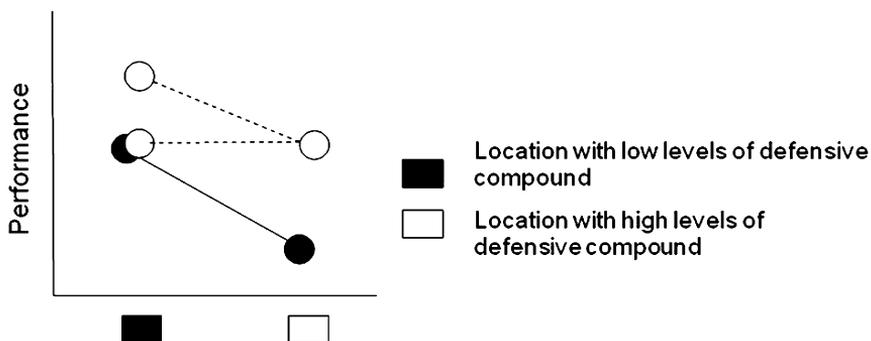


Figure 5. Two possible outcome of studies of local adaptations. The black population is adapted to a host with low levels of defensive compounds and can poorly utilize the host with high levels of defense. The white population is adapted to high levels of defensive compounds and can tolerate well the sympatric host. However, it would perform equally well or better on allopatric host with lower levels of defensive compound.

or in phenotypic plasticity). This effect was observed in paper **II**, where the elevated capacity to exploit *Fucus vesiculosus* was connected with a reduced ability to use *Zostera marina*.

Third, let us assume that the idea of an adaptive mosaic *sensu* Thompson (1994, 1999) is correct. Then, according to his theory, the expectation should not be that all populations would show local adaptations. Instead the adaptive mosaic should also include populations with maladaptations or with no adaptation (or, originally, with no ongoing co-evolution between the host and the herbivore). Consequently, in a sample of three populations, one could actually find anything, e.g. three populations with local adaptations, three with maladaptations or three with something between these. Alternatively, one could also find one population with local adaptations, one with maladaptations and one without any obvious pattern. This means that amount of populations in a study should be large. It also implies that one could interpret that a species possesses *a possibility* for local adaptations if some percentage of the populations show a home-site advantage. Clearly, a more precise expectation should be formulated when detecting an adaptive mosaic.

3.6.2. Impact of within-species variation in host-use traits

In paper **V**, I found sexual differences in response to the selective environments. This has interesting implications for the evolution of the host-use patterns of herbivores. First of all, the adaptations to local environments affect the evolutionary outcomes at the species level. Because the possible optimal host-use adaptations depend on the local selective environment (e.g. available hosts), there may not be a single fitness optimum at the species level. Instead, the trait optimum may differ among populations. Gene flow may further transmit adaptation among populations and a trait adaptive in one selective environment may appear as maladaptation in another environment.

Further, multiple alternative optima may also exist within a population, as different types of individuals (e.g. males and females) vary in their fitness maximising strategies. Sexual difference in the optimal value of a trait may hinder the local adaptation of a population if the genetic correlation between the sexes is very high, which is often the case, at least for morphological traits (Lande 1980, Badyaev et al. 2000). Actually, these aspects cast doubt upon the view that the mean trait value we see in a population would reflect the optimal adaptation to the environment. This is nonetheless often the presupposition when studying any morphological or behavioural traits. Instead, it could be useful to consider optimal adaptations in the context of different adaptive landscapes for populations, sexes and colour morphs (Bolnick et al. 2003, Poore and Hill 2006).

3.6.3. Two types of anti-predator traits

Cryptic colouration is one of the anti-predator adaptations of *Idotea balthica*. In addition, *I. balthica* has a compilation of anti-predator adaptations, such as low activity during the time of high predation risk (daytime; Jormalainen and Tuomi 1989, **IV**); a preference for *Fucus vesiculosus*, which provides good shelter but is low quality food (Nicotri

1980, Jormalainen et al. 2001a, V); and a preference for a dark (concealing) background (Merilaita and Jormalainen 1997, 2000, IV). Further, *I. balthica* is able to change its behaviour when sensing an olfactory cue from fish, rapidly hiding itself in vegetation (pers. obs.). Such anti-predator traits have fundamentally different characteristics and may be divided into two classes.

First, the herbivores have anti-predator adaptations that decrease the risk of encountering a predator. These are constantly employed, independent of whether the herbivore has detected a predator. They are actually analogous to constitutive defence chemicals in plants. Borrowing from this field, I propose calling these traits “constitutive anti-predator defences”. Conversely, herbivores also have adaptations that they only use under immediate threat when encountering a predator. These are analogous to inducible defences in plant and thus, they could be termed “inducible anti-predator defences”. This division becomes important when studying their evolution. “Constitutive anti-predator defences” can be studied without having predators present, whereas the actual threat is needed in the study of “inducible anti-predator adaptations”. Further, results from studies of *Idotea balthica* suggest that females may have stronger “constitutive anti-predator defences” than males. It would be interesting to study whether male *I. balthica* may have balanced this difference with stronger “inducible anti-predator defences”. To further understand the effect of sexual differences in host exploitation patterns of herbivores, it would also be of great interest to study whether these two strategies occur in different magnitude in males and females.

4. CONCLUSIONS

I studied ecological divergence in the marine environment in *Idotea balthica* occupying a naturally fragmented marine environment, by testing first whether the variation in quality of a host species was associated with divergence of host-use traits. Then I investigated the divergence of host-use traits and colour polymorphism with respect to the composition of the local host assemblage. Further, I tested the hypothesis that the host-use adaptations may be sex-specific and that this would further vary between selective environments, i.e. between host assemblages. I studied the ecological divergence as a result of both bottom-up forces (effects of plant quality or the host assemblage), as well as a result of selection arising from top-down regulation (predator-mediated selection). In conjunction with the latter, I examined whether predation by perch would be the discriminative selective agent between the host plant assemblages.

Idotea balthica populations differed in their host-use traits (**I**, **II**, **V**), in life history traits (size, sexual size-dimorphism, timing of reproduction; **II**, **III**) and in colour morph frequencies (**III**). These results, together with the variation of host populations in their chemical quality (**I**; see also Hemmi and Jormalainen 2004a, Koivikko et al. 2008) suggest that the studied *I. balthica* populations were diverged. The divergence was not likely caused by random processes, as the populations within a host plant assemblage type were more similar than the populations between the assemblage types. The differences between host plant assemblages were small, but they were repeated in different experiments and in very different traits: life-history traits (**II**), host-use ability and degree of generalism (**II**, **V**), host preference (**V**) and colour morph frequencies (**III**).

Sexual differences in fitness maximising strategies seem to affect both microhabitat use and anti-predator adaptations (**IV**), but also local adaptations of herbivores in general. My results suggest that although the variation in the composition of host assemblages drives the divergence of populations, the same selective environment is different for males and females. Because of the differences in fitness maximising strategies and the consequent morphological and behavioural adaptations, the sexes do not “experience” the selective pressures similarly. This suggests that the sexual variation in host exploitation patterns should be taken into account when studying the evolution of host-herbivore interactions.

My studies provide a glance to the subtlety of the selective pressures herbivores face in their environment. On one hand the pressures come from different directions (from bottom-up and top-down) and on the other hand, they affect the populations unevenly. Instead of expecting a uniform response in a species level, one can assume population-specific adaptations. My result suggest however, that the evolution of local adaptations could be suppressed by the antagonistic effect of gender-specific responses to selective environments.

It seems clear that *I. balthica* populations in the Northern Baltic Sea have reached the “first stage” of speciation, the population differentiation (Nosil et al. 2009), and that this have been caused by divergent ecological selection by the sympathic host plant assemblage. It remains unknown however, whether the ecological divergence has caused reproductive isolation among the populations. *I. balthica* has a wide geographical distribution, it occurs in multiple habitat types and has well-known ecology. This makes it a promising study species to further study the evolution of reproductive isolations and test other ecological rules in population divergence and in speciation.

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