Local adaptive pigmentation in Asellus aquaticus -effects of UV-radiation and predation regime.

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LOCAL ADAPTIVE PIGMENTATION IN *ASELLUS AQUATICUS*
– EFFECTS OF UV-RADIATION AND PREDATION REGIME

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JONAS JOHANSSON

Dissertation
Lund 2005

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I Hargeby, A., Johansson, J. and Ahnesjö, J. 2004. Habitat-specific pigmentation in a freshwater isopod: adaptive evolution over a small spatiotemporal scale. – Evolution 58: 81–94. 29

II Johansson, J., Hargeby, A., Marklund, O. and Hertonsson, P. Effects of individual pigmentation on survival and behavior of *Asellus aquaticus* L. exposed to UV-radiation. – Submitted. 45

III Johansson, J. Predator-prey interactions between a damselfly larvae and a freshwater isopod. – Manuscript. 55

IV Johansson, J. and Hargeby, A. Predatory effects of perch (*Perca fluviatilis*) on size structure, activity and pigmentation of the freshwater isopod *Asellus aquaticus*. – Manuscript. 67

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LOCAL ADAPTIVE PIGMENTATION IN *ASELLUS AQUATICUS* – EFFECTS OF UV-RADIATION AND PREDATOR REGIME

INTRODUCTION

One of the objectives of this thesis was to explore contemporary evolution of locally adaptive pigmentation in a freshwater isopod, and the mechanisms behind the adaptation. Isopods are known to vary considerably in pigmentation between habitats (Steiner at al. 1977, Henry et al. 1996, Turk et al. 1996, Hargeby et al. 2005), and studies of contemporary evolution are valuable because they provide opportunity to observe ecological conditions that influence natural selection. The adaptive pigmentation in the studied isopod could be a response to a natural habitat alteration, in terms of e.g. food and selection pressure, since the adaptation occurred following a colonisation of a newly established habitat. Factors behind the adaptive change such as the genetic base of pigmentation, habitat choice, and selective predation were accounted for. Moreover, predation is a strong selective force on freshwater invertebrate prey traits and behaviour (Wellborn et al. 1996). Thus, effects of two common predators on isopod size dependent anti-predator traits and behaviour, survivor, and the effect of structural complexity on predation efficiency, were also explored. Finally, I examined the effect of an abiotic factor, UV-radiation, on *Asellus* behaviour and tolerance.

STUDY ORGANISM

Asellus aquaticus is a very common invertebrate in Swedish freshwaters and can be found in various habitats such as small ponds, eutrophic lakes and caves. In dense stands of vegetation *Asellus* densities can exceed 10,000 individuals per square meter (Hargeby 1990). Generally *Asellus* is regarded as a detritivore (Adcock 1982, Smock and Harlow 1983), feeding on dead organic matter and the bacteria and fungi associated with the material. However, *Asellus* can also be a grazer, feeding on plant tissue and periphyton (Marcus et al. 1978, Arakelova 2001). Invertebrate predators as well as waterfowl, and fish (Berglund 1968, Rask and Hiisivuori 1985) can prey upon *Asellus*.

SPATIAL AND TEMPORAL VARIATION IN PIGMENTATION

Lake Krankesjön and Lake Tåkern are two shallow Swedish lakes with historical records of structural shifts between periods with clear water and abundant submerged vegetation and periods with dominance of phytoplankton and turbid water (Blindow 1992). The two alternative states, with either macrophyte or phytoplankton dominance, are stabilized by biotic and abiotic feedback mechanisms, resulting in episodic shifts over a few years when the submerged vegetation expands or disappears (Scheffer et al. 1993). In Lake Krankesjön and Lake Tåkern each state tends to last for several years (Blindow et al. 1993). For benthic invertebrates, including *Asellus*, the expansion of submerged vegetation during a shift from phytoplankton to macrophyte dominance is likely to change the light climate, food-source (periphyton vs. detritus) as well as predation regime (Scheffer 1998; Jeppesen et al. 1998 and references therein). *Asellus* is highly exposed to predation from fish in unvegetated areas (Petridis 1990), and during the periods without submerged vegetation *Asellus* were most likely restricted to the reed belts surrounding the two lakes. However, when the submerged vegetation, mainly different stonewort species (*Chara* spp.), expanded *Asellus* colonised the re-established vegetation. In Lake Krankesjön, *Chara* started to recolonise the lake bottom in the mid 1980s and samples from 1987 showed that *Asellus* from *Chara* beds exhibited similar pigmentation as those found in nearby reed stands (Paper I; Figure 1). By contrast, in 2000 *Asellus* in *Chara* beds were significantly lighter pigmented than *Asellus* from nearby reed stands. Thus, there had been a reduction in pigmentation after the expansion of *Chara* beds. A similar pattern of differences in pigmentation was also found in Lake Tåkern (Paper I). Moreover, in Lake Tåkern samples taken at a reed islet situated in-between the *Chara* and the reed belt showed intermediate pigmentation of *Asellus* (Paper I). The variability in pigmentation was also higher at the islet compared to the other sites. It should be mentioned that there were not only light pigmented *Asellus* in the *Chara* and dark pigmented in the reed. In both habitats there were a continuous scale of pigmentation, but the average pigmentation was lighter in *Chara* compared to reed.

The change in *Asellus* pigmentation that occurred in the *Chara* habitat over the 13-year period could be an example of local adaptive evolution. Many studies have documented local adaptive evolution (Merilä et al. 2001) although the underlying time scale is often unknown. The change also corresponds with previous observations of contemporary adaptive evolution in other natural populations. Contemporary adaptation tends to fall into two general categories (I) colonization of new environments, and (II) local adaptations in heterogeneous environments and metapopulation structure (Reznick and Ghalambor 2001). The ecological processes associated with the re-colonization of *Chara* include exposure to new food source, a new biophysical environment, and new sets of predators and competitors. In contrast to several of the case studies of contemporary evolution, the environmental change in the present system was not associated with recent anthropogenic causes. The mechanisms behind the structural shifts in the lakes vary, and may be multi-causal, and not necessarily driven by anthropogenic disturbances (Scheffer 1998). Therefore, the change in *Asellus* pigmentation could be an adaptive response to a natural habitat change.

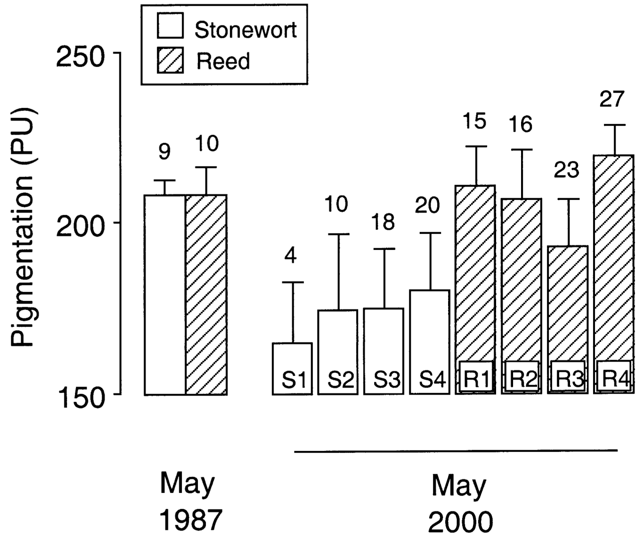

FIG. 1. Pigmentation (means+s.d.) in gravid females of *Asellus* from a *Chara* site and an adjacent reed site in Lake Krankesjön in May 1987, and from four *Chara* (S1–S4), and four reed sites (R1–R4) in May 2000. Numerals denote sample size.

POSSIBLE SELECTIVE FORCES BEHIND THE DIFFERENCES IN PIGMENTATION

Below I will discuss possible explanations for the change in *Asellus* pigmentation that occurred in the *Chara*. In order to assess what factors that drove the change in pigmentation of *Asellus* it was necessary to first determine whether pigmentation was a heritable or plastic trait. If pigmentation in *Asellus* was plastic, then factors like differences in food and pigment adjustment could have been involved. However, if pigmentation was heritable then factors like selective predation in combination with mechanisms that maintain the differences such as assortative mating could have been more important. Moreover, pigmentation and behaviour might be subjected to correlational selection (Forsman and Appelqvist 1998). Thus, independent of whether *Asellus* pigmentation was plastic or heritable, geno- or phenotype specific habitat choice could be part of the explanation.

Pigment adjustment and food source

There was no indication of pigment adjustment due to background matching or differences in diet as explanations to the differences in *Asellus* pigmentation between the habitats. Rearing of dark and light pigmented *Asellus,* on shoots of *Chara* or decaying leaves from the reed, did not result in any changes in pigmentation (Paper I). Hence, plasticity, as in the chameleon, appeared to have little effect on *Asellus* pigmentation. It could be argued that the results from the short (14 days) duration of the rearing microcosm experiment did not exclude the possibility that diet could have an effect on pigmentation over longer periods. However, we analysed differences in *Asellus* diet between light and dark pigmented *Asellus* collected in the *Chara* in Lake Krankesjön, using stable isotope technique, and found no difference between dark and light pigmented *Asellus*. Thus, it was not likely that pigmentation was explained by differences in diet (Paper I), as the dark and light pigmented *Asellus* appeared to feed on the same food source.

Genetic base of pigmentation

To analyse the genetic component of pigmentation we performed a common environment/garden, experiment in which we crossed different combinations of dark and light pigmented *Asellus*. The results indicated a genetic base for *Asellus* pigmentation. Two dark pigmented parents produced a darker offspring than two light pigmented parents (Paper I; Figure 2). Offspring from the combinations with one dark and one light pigmented parent did not differ from each other but from the dark-dark and light-light combinations of parents, and were intermediate of those (Paper I; Figure 2). These findings are consistent with previous work on *Asellus* populations that also showed a genetic base for *Asellus* pigmentation (Kosswig and Kosswig 1940).

Assortative mating

After confirmed that *Asellus* pigmentation was heritable, assortative mating with respect to pigmentation and size was examined. One could expect that assortative mating, i.e. mating with an individual that resembles yourself, could help maintain the difference in *Asellus* pigmentation between the habitats. *Asellus* form pre-mating pairs; the male grabs a female and carry her around before the mating can take place, because the female is only susceptible to fertilization in connection with moulting. This mate-guarding behaviour makes it easy to relate male and female pigmentation from pairs collected in the field. Pigmentation of *Asellus* pairs collected in *Chara* beds in Lake Krankesjön and in Lake Tåkern showed no correlation between male and female pigmentation, and thus mating appeared random with respect to pigmentation (Paper I). On the other hand, mating appeared to be assortative for size both in both lakes (Paper I). The observations from the *Chara* are purely correlative, and provide no evidence for behavioral mate preferences affecting the genetic variance with regards to pigmentation (Lynch and Walsh 1998). However, on a whole-lake scale, mating was likely to be assortative as a result of the differences in *Asellus* pigmentation between the habitats.

Substrate choice

If there was an active substrate choice connected to *Asellus* pigmentation the differences in pigmentation could be explained by *Asellus* pheno-

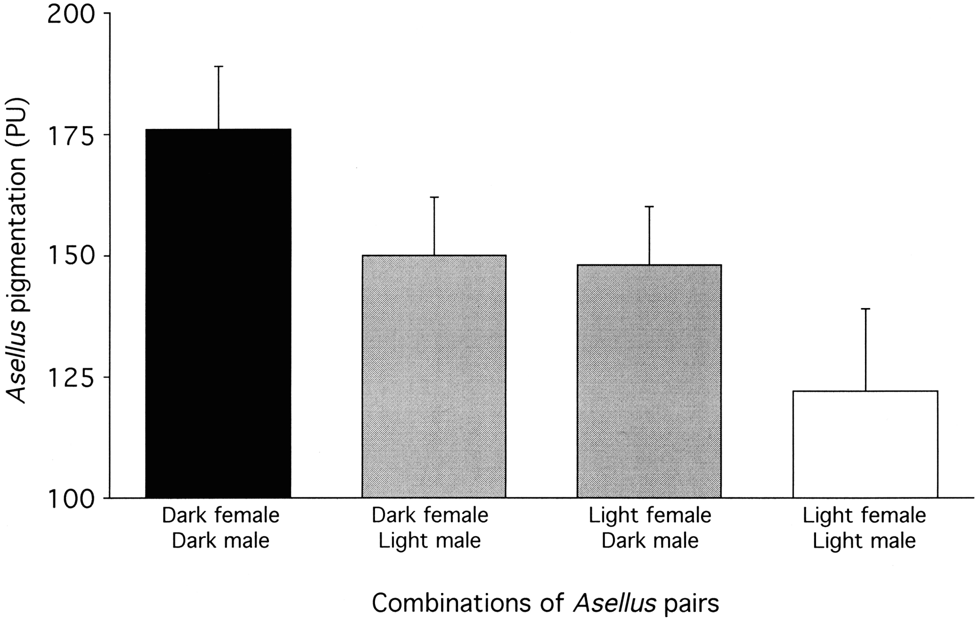

FIG. 2. Pigmentation (means+s.d.) in pooled *Asellus* F_1 offspring from a common environment/garden experiment in which pairs were combined from dark and light pigmented parents.

or genotype specific habitat choice. Colour specific habitat choice has been shown in aquatic snails (Byers 1983, Negovetic and Jokela 2000), and different habitat use between the sexes has been demonstrated in the marine isopod *Idotea baltica* (Jormalainen and Tuomi 1989, Merilaita and Jormalainen 2000). However, there were no indications that light pigmented *Asellus* preferred *Chara* shots to decaying leaves from the reed, when given the opportunity to choose. In an microcosm experiment, lasting 24 hours, where *Asellus* could choose substrate, both dark and light pigmented *Asellus* preferred leaves from the reed to shoots of *Chara* (Paper I).

Pigmentation selective predation

Predation is one of the strongest evolutionary forces shaping life history characteristics and morphological adaptations among aquatic invertebrate prey (Wellborn et al. 1996), and the foraging characteristics of the predators can determine which adaptations that reduce predation risk. In the presence of visual predators, cryptic colouration (Endler 1986, Merilaita 2001) and small body size might be important, whereas moderate activity is favourable if the predator uses more tactile cues (Wellborn et al. 1996). In environments where predation is a strong selective force, background colour matching (i.e. crypsis) is an adaptation in prey organisms (Endler 1978, 1986). Thus, local variation in prey colour may indicate adaptation to the visual characteristics of the background or predation pressure (Storfer et al. 1999). The *Chara* appears as a light habitat with a light green colour of the stems, and full access to the water surface for the sun. The reed on the other hand, makes a dark habitat as decaying parts of the reed are almost black and culms and leaves reduce incoming solar irradiance. If *Asellus* in the *Chara* were exposed to selective predation, i.e. higher predation rate on the most conspicuous *Asellus*, then it could be an advantage for the *Asellus* to be lighter pigmented in the *Chara* compared to the reed habitat, and this could explain the differences in pigmentation.

There are a number of differences between invertebrate and fish predators regarding their foraging behaviour. Invertebrate predators often rely on non-visual, mechanical and/or tactile cues, whereas fish in general are actively searching and depend more on visual cues when foraging (Wellborn et al. 1996). In the beds of *Chara* in Lake Krankesjön there are both fish and invertebrate predators (personal observation). Fish predators consist of e.g. perch, which is known to feed on *Asellus* (Rask and Hiisivuori 1985), and perch is also considered to be efficient in feeding in structurally complex habitats (Diehl 1988). Among invertebrate predators the damselfly *Enallagma cyathigerum* is one of the most abundant (personal observation). Pigmentation selective predation from these two common predators was examined as explanations for the differences in *Asellus* pigmentation. My results showed that light pigmentation was likely to increase *Asellus* fitness in an environment with a light background. Perch fed more on dark than on light pigmented *Asellus* against a light background in a laboratory experiment (Paper I; Figure 3). This is in accordance with other studies that also have shown that predation efficiency of fish feeding on isopods was affected by isopod pigmentation (Maskell et al. 1977, Brattey 1983, Merilaita 2001, Zimmer et al. 2002), and with studies showing that predation affect prey coloration (Endler 1986, Merilaita et al. 2001, Bond and Kamil 2002). In two similar laboratory experiments the damselfly *E. cyathigerum* was given the opportunity to feed on *Asellus* with different pigmentation. As expected, the damselfly did not show any preference for the least cryptic *Asellus* (Paper III), which indicated that visual cues were of little importance for feeding in *E. cyathigerum*. These findings was further supported by the fact that *E. cyathigerum* did not reduce feeding in darkness (Paper III). Similar results were also found for other damselfly larvae, e.g. *Erythromma najas*, which were feeding on chironomids with the same success both during day and night (Koperski 1998), and for *Coenagrion hastulatum* that did not reduce feeding in darkness (Johansson 1993). Thus, the importance of *Asellus* cryptic pigmentation when exposed to predation from *E. cyathigerum* appeared to be minor. In concert, my experiments indicated that selective predation from perch, but not from *E. cyathigerum*, might have been a force behind the development towards lighter pigmented *Asellus* in the *Chara* stands.

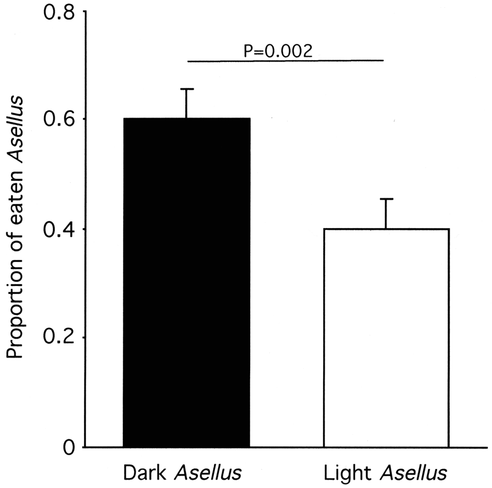

FIG. 3. Proportions of eaten dark and light pigmented *Asellus* in a predation experiment using perch as predator, and light sand as background. Error bars denote 95% CI (after arcsine-square root transformation). Line indicates significant difference with Wilcoxon signed rank test.

The differentiation between *Asellus* in the reed and the *Chara* habitats in Lake Krankesjön and Lake Tåkern was not restricted to pigmentation, but also included size at reproduction. Egg-carrying females in the reed were larger than females in the *Chara* (Paper I). In addition, pigmentation generally increased with *Asellus* size in the reed, whereas there was no relationship between pigmentation and size in *Chara* habitats (Paper I). The absence of a correlation in *Chara* supports the theory of differences in predation regime between the habitats, with dominance of invertebrate predators in the reed and fish predators in the *Chara* habitat, although this remains to be shown. An increased importance of visually oriented fish could drive the evolution towards smaller and lighter pigmented *Asellus* in recently established *Chara* stands, as a result of correlational selection for small body size and light pigmentation.

SIZE DEPENDENT PREDATION RISK

Invertebrate predators are often assumed to be prey size limited (Wellborn 1994b), i.e. they are limited by the size of their mouth or their ability to capture and handle the prey. In contrast, invertebrate feeding fish are rarely gape limited, and often prefer to feed on large prey (Mittelbach 1981, Dixon and Baker 1988, Wellborn 1994b). Given that an invertebrate predator is gape- or handling limited, there is a potential for a differential predation pressure on invertebrate prey during the ontogeny. This means that prey that reach a size refuge from invertebrate predation as adults may be highly exposed to predation as juveniles (Wissinger 1988, Wellborn 1994b). A laboratory experiment showed that *E. cyathigerum* fed on smaller size classes of *Asellus* but did not feed on the largest size class (Paper III; Figure 4), most likely due to physical constrains. Similarly, the isopod *Lirceus fontinalis* was exposed to predation from a streamside salamander as juveniles but reached a size refuge as adults (Sparkes 1996). Invertebrate predators are in general not known to be size selective, but feed non-selectively on available prey (Wellborn et al. 1996). Further, I tested size dependent predation by perch. The perch preferred large (7–8 mm) over smaller (3–4 mm) *Asellus* when given the opportunity to feed on both size classes (Paper IV). These results are in line with studies suggesting that littoral invertebrate feeding fish can be size selective (Holomuzki and Short 1990, Wellborn 1994). However, other studies have suggested that littoral invertebrate feeding fish are not size selective (e.g. Mittelbach 1981, Werner et al. 1983, Persson and Greenberg 1990). In conclusion, my experiments suggest that large *Asellus* were most vulnerable to predation from fish and small *Asellus* were most vulnerable to predation from damselfly larvae. However, one should keep in mind that small *Asellus* were still vulnerable to predation from perch even though the perch preferred larger *Asellus*, in contrast to predation from *E. cyathigerum*, where the largest *Asellus* were in a size refuge. This could have implications for anti-predator behaviour.

ANTI-PREDATOR BEHAVIOUR AND TRAITS

Activity

When an organism is exposed to predation risk it is obviously important to be able to adapt behaviourally to the risk. Reduced activity in benthic invertebrates is a common anti-predator response to the presence of fish (e.g. Williams and Moore 1985, Andersson et al. 1986, Åbjörnsson et al. 1997, Åbjörnsson et al. 2000). The cost of lowered activity is often reduced time to be spent on activities such as feeding and reproduction (reviewed by Lima and Dill 1990). Moreover, prey species are often treated as one group, and size dependent predation risk is not often taken into account (e.g. Williams and Moore 1985, Andersson et al. 1986, Main 1987, Holomuzki and Short 1988, Åbjörnsson et al. 1997, Åbjörnsson et al. 2000). However, size dependent predation

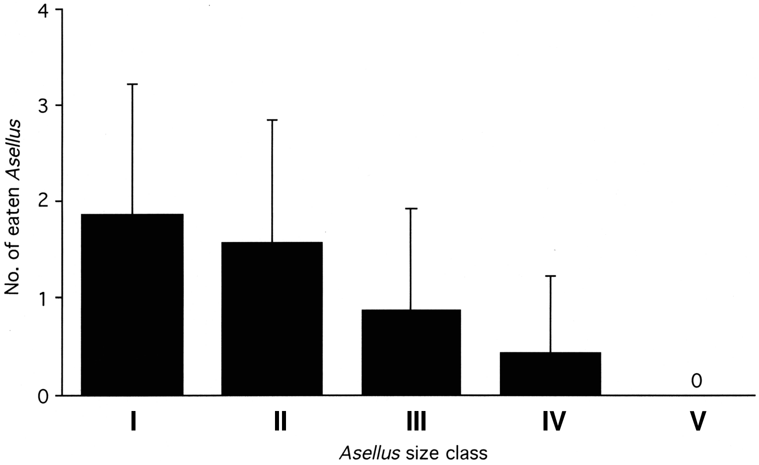

FIG. 4. Damselfly larvae *E. cyathigerum* predation on five size classes of *Asellus*. Means+s.d., n=7 for each size class. The size of the *Asellus* in size class 1 was 3.6±0.5 mm (mean±s.d.) and 9.9±0.7 mm for size class 5.

risk in benthic invertebrate species has been demonstrated in frog larvae exposed to predation from a dragonfly (Peacor and Werner 2000), and in small *E. cyathigerum* that responded more strongly than larger individuals to chemical cues from the predatory bug *Notonecta glauca* (Koperski 1997), indicating higher predation risk for the small larvae. Further more, juvenile freshwater snails (*Pomacea paludosa*) reacted to cues from a predatory turtle, whereas the reactivity declined, and finally disappeared as the snails became larger (Snyder and Snyder 1971).

My results indicated that *Asellus* could assess the prevailing predation risk and adapt behaviourally. In a three-week mesocosm experiment (150 L), with natural *Chara* vegetation, large *Asellus* reduced their activity in the presence of perch (Paper IV), a result that was in line with the fact that large *Asellus* suffered most from predation to perch in the laboratory experiment (Paper IV). However, the small *Asellus* were vulnerable to predation from perch even though the perch preferred larger *Asellus*. This could explain why both small and large *Asellus* lowered their activity when exposed to perch cues in a short-term (<1 hour) laboratory experiment (Paper IV). It is reasonable that in the short term, both small and large *Asellus* have to lower their activity as a response to perch predation risk. It has been suggested that fish chemical cues are important only in short-term (less than three days) anti-predatory behaviours by isopods (Holomuzki and Hatchett 1994). However, my results suggest that in a perspective of weeks or longer it is still important for large *Asellus* to reduce activity.

Since *E. cyathigerum* were not able to feed on the largest *Asellus* (Paper III), the predation risk from *E. cyathigerum* and fish should change during *Asellus* ontogeny. To test this I examined if predator avoidance differed between large and small *Asellus*. In two laboratory microcosm experiments I found that small *Asellus* (3–4 mm) decreased their activity and feeding when exposed to chemical cues from *E. cyathigerum*, whereas large *Asellus* (8–9 mm) did not (Paper III). The same difference in behaviour between large and small *Asellus* were found in both a short-term (< 1 hour) activity experiment (Paper III; Figure 5) and in an experiment where secondary effects on periphyton were observed over three days. Small *Asellus* exposed to *E. cyathigerum* cues grazed less periphyton than *Asellus* in controls (Paper III).

In conclusion my results suggest that lowered activity was an anti-predator response both for large and small *Asellus*, and that the behavioural response differed with varying predation regimes. The reduced activity in *Asellus* suggests that *Asellus* can assess the prevailing predation risk and adapt behaviourally. The ability to assess predation risk should be beneficial for prey organisms so that they do not overestimate the predation risk and stay too long in refuge with non-optimal food resources. The results from the periphyton experiment showed that the small *Asellus*, exposed

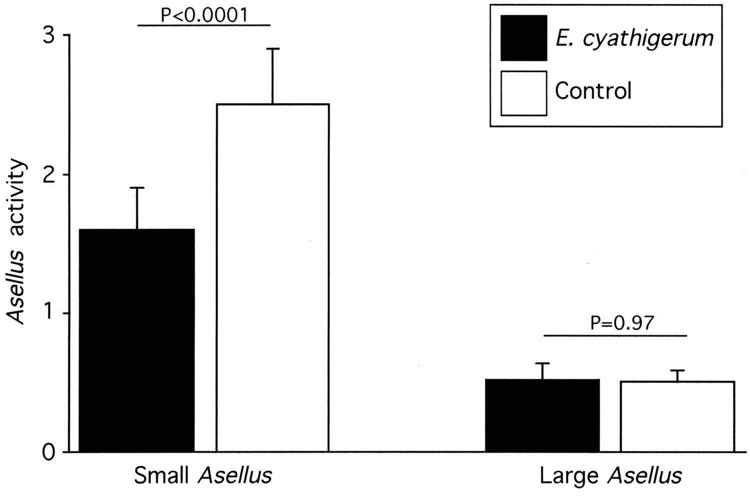

FIG. 5. *Asellus* activity (numbers of moving *Asellus*) in the presence (*E. cyathigerum*) and absence (Control) of chemical cues from *E. cyathigerum*. Means+s.d., maximum numbers of moving *Asellus* were 5 for small and 1 for large *Asellus*, $n_{small}=9$ and $n_{large}=10$ for each treatment. Lines indicate significant, and non-significant differences with t-test.

to cues from *E. cyathigerum*, fed less on the periphyton and thus probably spent more time in refuge.

Aggregation

In the mesocosm experiment where I examined the effects of perch presence on *Asellus* behaviour and survival I found that the variance in samples of *Asellus* density increased a week after the perch were introduced (Paper IV; Figure 6). The increased variance may be explained by an aggregative response in *Asellus* when exposed to perch. Patchiness of benthic invertebrates has been observed in the bug *Anisops wakefieldi* (Gilbert et al. 1999), in freshwater mussels (Fukuhara and Nagata 1995), in snails (Brown and DeVries 1985), but also in *Daphnia* zooplankton (Pijanowska and Kowalczewski 1997), and may be seen as an anti-predator response. Prey that sense the presence of a predator often aggregate at safe sites where food may be scarce, and food limitation might thus reduce growth (Scheffer 1997). Patchiness of benthic invertebrates can also have consequences for density dependent interactions, such as competition (Smith et al. 2003).

Cryptic pigmentation

A recent study showed that *Asellus* pigmentation can be cryptic over a wide range of habitats and lakes (Hargeby et al. 2005), and even though *Asellus* pigmentation was not plastic, it could be an anti-predator trait. It is possible that a number of different levels of *Asellus* pigmentation simultaneously could be cryptic in *Chara* beds because *Chara* stems make the light climate variable.

In natural conditions the viewing angle of a prey may be crucial for visual detection (Johnsen 2002). Because *Asellus* are present at all levels in the *Chara* stands (Marklund et al. 2001), they may be spotted by predators from different angels. From below, with the overlying water column as part of the background, a situation that may select for transparency (Johnsen 2001), or from above with the sediment and deeper layers of the vegetation as background. Thus, light or intermediate pigmented *Asellus* may be more cryptic than dark *Asellus* in the upper vegetation layers, whereas dark pigmentation may be cryptic against the sediment or deeper vegetation layers. This scenario might also be an explanation for the larger variance in *Asellus* pigmentation in samples from the *Chara* compared to the more homogeneous environment in the reed stands (Paper I).

STRUCTURAL COMPLEXITY

Despite a high density of perch in the experimental mesocosms, with natural densities of *Chara* vegetation, there was no effect of predation on *Asellus* survival (Paper IV; Figure 6). This result was somewhat surprising since perch is considered to be an efficient predator on invertebrates in structurally complex environments (Diehl 1988, Persson and Eklöv 1995). A possible explanation could be reduced efficiency of predation, which is likely in very dense stands of vegetation (Diehl

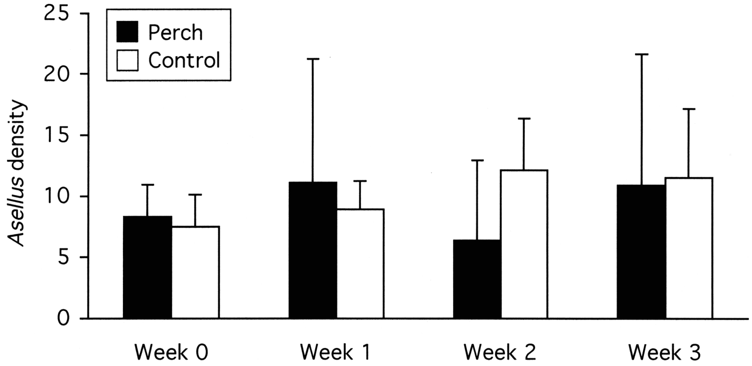

FIG. 6. *Asellus* density (means+s.d.) expressed as numbers of *Asellus* per g DM of *Chara* during each of the three weeks of the mesocosm experiment.

1988, Diehl 1992). Further, it has been suggested that perch shift diet from benthic invertebrates to micro-crustaceans if the habitat becomes too complex (Diehl 1992), which could have been the case here. *Asellus* cryptic pigmentation (Paper I, Hargeby et al. 2005), aggregation, and reduced activity might also be parts of the explanation.

In a laboratory experiment with three levels of plant biomass, overall foraging of *E. cyathigerum* decreased with increasing complexity (Paper III). This result was probably attributed to reduced encounter rate between predator and prey with increasing complexity. However, there was no difference in foraging efficiency between the control and low biomass treatment, which indicated that *E. cyathigerum* could be an efficient predator also in complex habitats, i.e. increased complexity do not necessarily lower feeding rates. In line with the lack of difference between the control and the low biomass treatment, no difference in survival of small fishes was recorded between a simple and a complex habitat when exposed to predation from dragonfly *Anax junius* larvae (Jordan and McCreary 1996). High predation efficiency in complex habitats might be important for the performance of *E. cyathigerum*, because complex habitats can provide a refuge against fish predation (Crowder and Cooper 1982), and often sustain high densities of potential prey organisms (Gillinsky 1984, Hargeby 1990, Diehl and Kornijów 1998). Moreover, the foraging efficiency of fish can be reduced in complex habitats (Diehl 1988, Diehl 1992), and thus damselflies might be important as predators in dense submerged vegetation.

PIGMENTATION AND UV-RADIATION

UV-radiation is attenuated rapidly with depth in most freshwaters and thus it has been suggested that harmful effects of UV-radiation on littoral food webs are restricted to extreme environments, such as alpine, polar, and anthropogenically acidified ponds and shallow lakes (Vinebrook and Leavitt 1999). The stands of *Chara* in shallow Lake Krankesjön can reach the water surface during the summer and UV-radiation might therefore be a factor to consider for the behaviour and distribution of *Asellus* within the *Chara*. The pigment in *Asellus* is a melanin (Needham and Brunet 1957), and has been shown to protect *Daphnia* zooplankton from harmful UV-radiation (Hebert and Emery 1990).

To my knowledge, differences in behaviour and tolerance to UV-radiation within a benthic invertebrate species have not been addressed before. The pigmentation in *Asellus* made it possible to look for differences between individuals with different pigmentation when exposed to UV-radiation. I examined if there were any differences in how dark and light pigmented *Asellus* tolerated, and behaved when exposed to natural levels of UV-radiation. In a laboratory microcosm experiment I tested the protective importance of the pigment in *Asellus*, and found that dark pigmented *Asellus* survived exposure to UV-radiation longer than light pigmented individuals (Paper II). In two other microcosm experiments, both in the laboratory and outdoors, *Asellus* avoided UV-radiation, and the avoidance behaviour was independent of *Asellus* pigmentation (Paper II; Figure 7). In line with these results, there were lower densities of *Asellus* at sites with natural levels of UV-radiation compared to sites where the UV-radiation was attenuated by Plexiglas filters in a field experiment (Paper II).

Stronger avoidance behaviour has been reported in unpigmentated *Daphnia pulex* than in pigmented individuals when exposed to UV-radiation (Rhode et al. 2001), indicating a connection between pigmentation and behaviour not seen in *Asellus*. Comparisons between phenotypes within a species may provide information on UV-radiation as a selective agent on pigmentation, and behaviour and pigmentation are likely to co-vary if correlational selection is acting (Sinervo and Svensson 2002). The lack of correlation between pigmentation and behaviour in *Asellus* indicate, either an absence of correlational selection on these traits in *Asellus*, or that any such selection is counter-balanced by other selective forces e.g. predation.

UV-radiation avoidance is widespread among aquatic organisms and has been found in e.g. mayflies (Johansson and Nyström 2004), amphibians (Langhelle et al. 1995, Adams et al. 2001), diptera larvae (Donahue and Schindler 1998, Kelly et al. 2001), caddisflies (Kiffney et al. 1997a), and fish (Kelly and Bothwell 2002). The high frequency of UV-radiation avoidance among

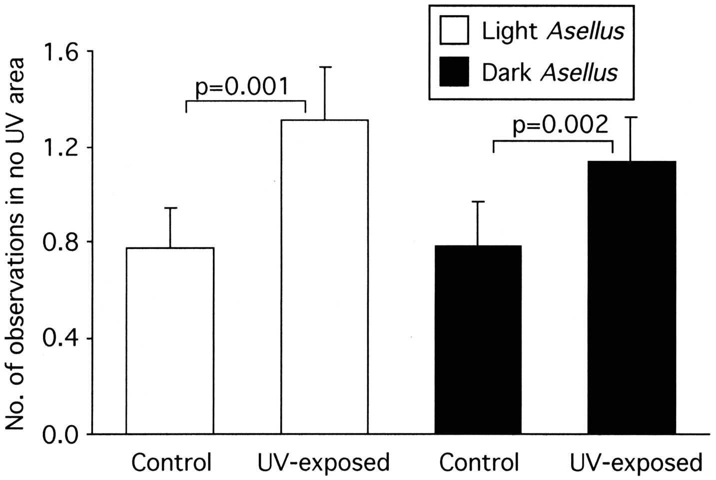

FIG. 7. Numbers of observed light and dark pigmented *Asellus* (means+s.d.) in the protected part (No UV radiation) of the experimental containers in the behavioral UV-radiation experiment. Lines indicate significant differences with Tukey/ Kramer post-hoc test. In control containers both parts of the experimental containers were not exposed to UV-radiation.

different taxa of freshwater organisms indicates that UV-radiation could have been a selective force also in a historical perspective. This theory is supported by analysis of sediments from mountain lakes suggesting that UV-radiation penetration has been higher during periods in the past than during the present period of anthropogenic ozone depletion (Leavitt et al. 1997). The interest in UV-radiation effects on aquatic ecosystems has received increased interest as a result of concerns about the thinning of the ozone layer. This increased interest has lead to insights on the general importance of UV-radiation effects in aquatic ecosystems (e.g. Bothwell et al. 1994, Hansson 2000, Rhode et al. 2001). In addition, my results show that also in lowland lakes ambient levels of UV-radiation could induce avoidance responses in the benthic community.

CONCLUDING REMARKS AND FUTURE PERSPECTIVES

In this thesis I have shown an alteration in a phenotypic trait with a genetic basis, and thus also a change in the genetic composition of the population. The alteration could be an adaptive response to natural habitat change not associated with anthropogenic causes. The relatively fast adaptive change in *Asellus* pigmentation occurred during conditions that favour rapid evolution, population growth, and a new environment in terms of i.e. predators, food, and physical environment. Moreover, my results suggested that both predators and abiotic factors such as UV-radiation might induce behavioural changes in a benthic invertebrate. *Asellus* can reach high population densities (Hargeby 1990) within submerged vegetation and a behavioural change in *Asellus* might therefore have implications for food web dynamics via effects on periphyton. Thus, the effect of *Asellus* grazing on periphyton and secondary effects on *Chara* could be an interesting road for future studies.

Most often co-existing organisms are well adapted to each others presence and invertebrate prey that naturally co-occur with fish are likely to possess anti-predator traits that reduce predation risk (Wellborn and Robinson 1991). This could be one reason why there were no large differences between the trials with, and without perch, in my mesocosm experiment. I.e. *Asellus* were used to the presence of perch and displayed a number of anti-predator traits that reduced predation risk. However, I believe that it is somewhat unnatural to compare between two extremes, e.g. no predator and predator. It is not very likely that the perch or the damselfly would be wiped out from Lake Krankesjön, or that the UV-radiation would disappear completely, as in the treatment with no UV-radiation in the UV-experiment. Still, I believe these experiments are useful in providing information of the mechanisms that explain the pattern that is seen in nature.

In the thesis I have presented results from field samplings, and field-, mesocosm- and laboratory microcosm experiments. The field sampling in Lake Kranksjön and Lake Tåkern revealed an interesting pattern concerning the differences in *Asellus* pigmentation and size between adjacent habitats. The pattern seen in the field samplings was the result of a number of mechanisms affecting *Asellus*, and its biotic and abiotic environment. Therefore, in my laboratory experiments I reduced the complexity to study single mechanisms related to *Asellus* pigmentation, and effects of size dependent predation. Among the mechanisms that I have explored could e.g. selective predation from perch contribute to the differences in *Asellus* pigmentation. Moreover, avoidance of UV-radiation and predation risk could be factors behind the low numbers of *Asellus* that generally are found in the upper part of the *Chara* vegetation. To assess what mechanisms that are most important could be complex, since the importance of a mechanism might shift over the year, but also on a short-term basis, over the day, or between one minute and another. However, studies of the importance of different mechanisms in multi factorial experiments, including multiple predator treatments could also be a perspective for coming research.

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SVENSK SAMMANFATTNING

Vattengråsuggan *Asellus aquaticus* är ett väldigt vanligt ryggradslöst djur i många typer av svenska vatten. Den kan bli över 10 mm stor och äter allt från dött organiskt material till levande alger och växter. Färgen hos gråsuggan kan variera mycket mellan olika miljöer. Den är oftast mörk men kan även vara nästan vit, t. ex. i underjordiska grottpopulationer. Jag har studerat hur pigmenteringen hos vattengråsuggan varierade mellan två olika livsmiljöer, habitat, i Krankesjön i Skåne och i Tåkern i Östergötland. Men jag har även undersökt hur vattengråsuggan på olika sätt undviker att bli uppäten och hur den påverkas av solens UV-strålning.

Både Krankesjön och Tåkern skiftar naturligt mellan stadier med tät undervattensvegetation och relativt bra siktdjup, och stadier som i stället domineras av algblomningar, orsakade av fytoplankton, och dåligt siktdjup. I båda sjöarna varierade pigmenteringen hos gråsuggorna kraftigt. De ljusaste djuren var nästan helt vita medan de mörkaste var så gott som svarta. Dessutom skiljde sig medelpigmenteringen, alltså den vanligaste färgtypen, åt mellan de två olika typer av habitat som jag studerade. Gråsuggorna hade ljusare pigmentering i bestånd av undervattensvegetation (oftast bestående av olika arter av kransalger), än i närliggande bestånd av vass.

Där bestånd av kransalger var nyetablerade, efter ett skifte från stadiet med algblomningar till stadiet som domineras av undervattensvegetation, blev gråsuggornas pigmentering ljusare från år till år. Till en början var gråsuggorna i de nyetablerade bestånden av kransalger lika mörka som gråsuggorna i vassarna.

Korsningar av ljusa och mörka gråsuggor visade att pigmenteringen var genetisk och nedärvdes till avkomman. Ljusa föräldrar fick ljus avkomma och mörka föräldrar fick mörk avkomma. Födan och anpassning av pigmenteringen hos en enskild gråsugga till bakgrundsfärgen hade däremot ingen inverkan på pigmenteringen. Gråsuggorna rörde sig inte heller mellan vassen och kransalgerna beroende på vilken färg de hade. De kunde alltså inte medvetet utnyttja sin färg som kamouflage och välja det habitat där de syntes minst. Valet av partner att para sig med verkade också ske oberoende av pigmenteringen.

Vilka krafter låg då bakom skillnaden i gråsuggornas pigmentering mellan kransalger och vass? En möjlig förklaring kan ha varit selektiv predation, från vanliga rovdjur såsom abborrar och flicksländelarver, på de minst kamouflerade mörka gråsuggorna i kransalgerna. Solstrålningen och den ljusgröna färgen gör att kransalgerna kan betraktas som ett ljust habitat, och den nästan svarta botten och den minskade solstrålningen att vassen blir ett mörkt habitat. I ett experiment visade det sig också predation från abborre kunde vara en del av förklaringen till förändringen i pigmentering. Abborrarna, som jagar m.h.a. synen, åt fler mörka än ljusa gråsuggor mot en ljus bakgrund. Däremot hade gråsuggornas grad av kamouflerad pigmentering ingen betydelse för deras risk att bli uppätna av flicksländelarver, som främst jagar med hjälp av känsel.

Den förändrade pigmenteringen hos gråsuggorna i kransalgerna var troligen en evolutionär anpassning till skillnader i naturliga urvalsprocesser mellan de två habitaten, t.ex. predation. Förändringen i pigmentering skedde i ett nytt habitat med en växande populationsstorlek vilket är förhållanden som gynnar snabb evolution.

Flicksländelarver, som placerades tillsammans med stora och små gråsuggor, åt av de små gråsuggorna, men det visade sig vara fysiskt omöjligt för dem att äta upp de största. Detta skulle kunna förklara varför små gråsuggor minskade sin aktivitet och betning av påväxtalger när de utsattes för lukt från flicksländor, medan stora gråsuggor inte gjorde det. Både stora och små gråsuggor minskade sin aktivitet när de utsattes för lukt från abborrar under en kort period. Men i ett mer storskaligt experiment, som varade i tre veckor, minskade stora gråsuggor sin aktivitet mest. Resultaten visade att gråsuggorna kan känna av vilka rovdjur som finns i omgivningen och anpassa sitt beteende därefter. I det storskaliga experimentet, med naturliga mängder kransalger, hade abborrar ingen effekt på antalet gråsuggor, trots att tätheten av abborrar var hög. Variationen i prov på tätheten av gråsuggor var däremot högre i närvaro av abborre jämfört med i kontrollerna utan abborre, vilket tyder på att gråsuggorna klumpade ihop sig. Det visade sig att flicksländor kan jaga effektivt även där vegetationen är tät. Detta kan göra dem till viktigare rovdjur än fiskar som verkar vara begränsade av vegetation i sitt födosökande. Tillsammans visar mina resultat att egenskaper som kamouflage, minskad aktivitet och samling i större grupper kan minska risken för en gråsugga att bli uppäten av abborrar i tät vegetation.

Gråsuggornas pigment har visat sig skydda djurplankton från skadlig UV-strålning och eftersom kransalgerna kan nå ända upp till vattenytan under sommaren kan gråsuggorna bli utsatta för solens UV-strålning. Mörka gråsuggor överlevde längre än ljusa när de exponerades för naturliga nivåer av UV-strålning i ett försök, något som inte visats hos bottenlevande ryggradslösa djur tidigare. I ett annat laboratorieförsök så undvek både ljusa och mörka gråsuggor UV-strålning om de hade möjlighet att göra det. Resultaten styrktes av ett fältexperiment i Krankesjön där fler gråsuggor samlades på platser där UV-strålningen var avskärmad med plexiglasfilter jämfört med platser med naturlig strålning.

De anpassningar i beteende hos gråsuggor som jag har presenterat här tyder på att UV-strålning och rovdjur kan ge beteenderesponser hos betande bytesdjur och därigenom också ha effekter på påväxtalger. Resultaten pekar också på att naturliga förändringar i miljön, såsom ett skifte från ett stadium med dominans av fytoplankton till ett med dominans av undervattensvegetation, kan leda till att den genetiska uppsättningen i en population förändras.

TACK M.M.

INTRODUKTION

Ser man på, den här delen av avhandlingen fångade din uppmärksamhet. Men du har väl åtminstone också läst sammanfattningen? Om du ännu inte hunnit göra det så kommer här en extra mycket populärvetenskaplig sammanfattning på svenska. Jag ger även några bra tips på fraser som du kan använda för att bryta isen vid middagsbordet på disputationsfesten. Dessutom gör jag några reflektioner över tiden som doktorand, påminner om en del ovetenskapliga händelser, och tackar en del personer för goda insatser under åren.

POPULÄRVETENSKAPLIG SAMMANFATTNING

Jag har alltså jobbat med att bl.a. scanna färgen på vattengråsuggor i nästan fem år (tro det eller ej). Min och mina medförfattares forskning visar att gråsuggornas färg kan vara anpassad till färgen på miljön där de lever, ett slags kamouflage. Det kan bero på att abborrar äter upp de gråsuggor som är dåligt kamouflerade. Flicksländelarver föredrar att äta små gråsuggor och abborrar föredrar stora gråsuggor. Abborrar jagar m.h.a. synen och flicksländor med känsel och därför är kamouflage troligen viktigast för stora suggor. Gråsuggorna verkar dessutom kunna känna av om det finns farliga djur i omgivningen och ta det lite lugnare då så att dom minskar risken att bli uppätna. Precis som hos människor så klarar mörka gråsuggor av att vara i solen längre än ljusa människor, men generellt sett tycker inte några gråsuggor, oavsett färg, om UV-strålning.

REPLIKER

Här följer nu några exempel på repliker som kan användas för att få igång samtalet vid middagsbordet under disputationsfesten. Om ni inte lyckas plugga någon av replikerna går det säkert bra att använda den gamla klassikern ”Och hur känner Du Jonas?”.

Exempel 1 – Visst är det fantastiskt att gråsuggorna kan känna av UV-strålning och undvika den.
– Jaa verkligen
– Det kan ju betyda att UV-strålning har varit en selektiv kraft på bentiska evertebrater också i ett historiskt perspektiv, och inte bara i dessa tider med ett förtunnat ozonlager, fascinerande.

Exempel 2 – Hörde du att dom stora gråsuggorna inte reagerar på lukten från *Enallagma cyathigerum*, och att det troligen beror det på att dom är i en storleksrefug.
– Jaaa-a
– Det kan ju medföra att predationstrycket från olika typer av predatorer varierar under gråsuggornas utveckling.

Exempel 3 – Jag tycker att förändringen i gråsuggornas pigmentering i kransalgerna i Krankesjön är ett utmärkt exempel på nutida evolution.
– Ohh jaaaa
– Och det visar att evolution inte alltid sker i väldigt långa tidsperspektiv som man ofta tror.

REFLEKTIONER

Tiden som doktorand har jag upplevt som både positiv och negativ. Det positiva har varit den stimulerande arbetsmiljön, människorna på Limnologen, resorna och som jag kallar det, den ”totala flextiden”, vilket har varit ovärderligt särskilt sedan Agnes och Viktor föddes. Det negativa var till en början lönen, inte ens 1999 var 12 500 kr i månaden, utan sociala förmåner, en värdig lön för en doktorand. Jag tycker att man ska höja statusen på doktorerandet genom att ta in färre doktorander och ge dem bättre villkor från början.

OVETENSKAPLIG SAMMANFATTNING

Åren som gått sedan jag började som doktorand i december 1999 har utan tvekan varit de mest händelserika åren i mitt liv. Det började redan mellan jul och nyår 1999 när jag och Sanna parkerade vår ”nya” fina SAAB för gott, i vägräcket på E4 an mellan Nyköping och Södertälje. Sedan, i juni 2000 flyttade vi till huset i Stångby där vi till en början hade hur mycket plats som helst. I november 2000 åkte vi doktorander på en oförglömlig resa till Brasilien där jag bl.a. fick uppleva fotboll på Maracana stadion i Rio och en massa capybaras och caipirinhas. I januari 2001 åkte jag till SIL konferensen i Melbourne och på vägen dit hälsade jag på Nils med familj under en mycket minnesvärd vecka i Thailand. På ”vägen hem” passade jag även på att ta en tur till Tasmanien. Sedan var det ganska lugnt tills sommaren 2002. På kvällen den 11 juli hade Limnologen grillfest på terrassen i Stångby. När alla hade åkt hem gick jag och la mig medan Sanna satt uppe och räknade tiden mellan värkarna. Agnes föddes på förmiddagen dagen därpå. I januari 2003 åkte jag tillsammans med ett litet gäng till Nya Zeeland. Agnes var bara sju månader gammal och jag längtade hem redan innan tåget hade lämnat Lernacken och kört ut på bron. Hemlängtan blev inte mindre av att jag en stor del av tiden bodde ensam på en forskningsstation uppe i bergen. Agnes kände inte igen mig när jag kom hem. I december 2003 kom Viktor och huset i Stångby blev plötsligt ganska litet. De sista åren av mitt doktorerande blev väldigt fragmentariska p.g.a. föräldraledighet för både Agnes och Viktor. Men jag och Anders hann i alla fall med en minnesvärd tur till Gotland och de vita grå(?)suggorna i Lummelundagrottorna. När jag började jobba igen efter att ha varit hemma med Viktor var det knappt två månader tills avhandlingen skulle vara klar och här är vi nu, våren 2005.

TACK

Avhandling

Först vill jag tacka dem som har haft en aktiv del i tillkomsten av den här avhandlingen. Det gäller i första hand min eminente handledare Anders, som är en mycket ödmjuk och vänlig man med stort kunnande och tålamod. Utan Anders engagemang och mjuka handledarstil hade det inte blivit någon avhandling. Stort tack Anders!

Sedan vill jag tacka övriga medförfattare Jonas A., Ola och Pia för gott samarbete.

Efter det vill jag tacka alla de som har bidragit med goda råd och/eller någon gång läst och kommenterat avhandlingens manus och/eller sammanfattning. Särskilt tack till min biträdande handledare Christer, men även till Patrik, Per, Emma, Lars-Anders, Håkan, Sanna och Lasse.

Slutligen tack till Håkan och Jacob för bidrag med fisk och till Balint och Peder för lån av utrustning till en del av experimenten och till Gunilla för layoutarbetet med själva avhandlingen.

Arbetskamrater

Men det finns ju naturligtvis också andra personer som har gjort min tid på Limnologiska avdelningen mer eller mindre uthärdlig. Jag vill därför skicka ett stort tack till…

Patrik, min kompetente och omtänksamme rumskamrat som aldrig frivilligt skulle berätta något om sig själv. Tack för att du alltid intresserat dig för mina knepiga frågor och idéer om saker och ting under årens lopp, rörande allt ifrån hur man bygger trappor och bullermurar, till filosofiska frågeställningar om kräftdjursforskning, och för att du får mitt fotbollsintresse att framstå som ljumt i förhållande till ditt fiskeintresse.

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Håkan, för alla pingismatcher i källaren, jag har för mig att du vann en match till slut, och för givande diskussioner i samband med olika fester och litteraturinläsning

Jag vill även tacka…

Emma för alla pratstunder.

Kerstin för hjälp med det praktiska.

Anders K. för hjälp de gånger datorn har strulat.

Marie för att du alltid är så glad och vänlig.

Karin R. för att du kom som en frisk fläkt och rörde om i gubbgrytan på Limnologen.

Alla ni som gjorde Brasilienresan oförglömlig, speciellt tack till min stjärtolycksbroder och rumskamrat Mikael.

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Vänner utanför jobbet

Jag vill även nämna några som gjort och gör livet utanför jobbet roligare: Markus, Liselott och Leo, Tommy, Mattias och Magnus med familjer, grannarna i Stångby och Jens och Lisa med barn. Rosas bör även det s.k. ”Soppgänget” vars trevliga tillställningar har blivit allt färre med åren, troligen p.g.a. de dynamiska liv som medlemmarna idag lever (Holmqvist 2005). Antalet tillställningar verkar vara starkt negativt korrelerat till antalet barn som gängets medlemmar lagt sig till med, men även andra faktorer har troligen betydelse.

Familj

Sist och därför mest vill jag tacka min älskade familj. Utan er hade avhandlingen säkert blivit både längre och bättre, men jag har ju mycket hellre tillbringat tid med er än med gråsuggorna (vilken komplimang). Ni betyder mycket mer än ni tror för mig även om jag inte alltid visar det på lämpligt sätt. Kanske har ni inte heller alltid förstått vad jag sysslat med under de här åren. Jag hoppas det har blivit lite klarare på den punkten nu när ni har läst eller precis ska till att läsa min avhandling (gäller ej Agnes och Viktor ännu)……

Tack

Helena, för all hjälp med barnpassning.

Annika och Lasse, bl.a. för att ni flyttade till Blentarp. Det har gjort Sannas och mitt liv lättare.

Anna, för att du (nästan) alltid finns där när det behövs

Mor och Far, för att ni alltid stöttat mig

Agnes och Viktor, för att ni lägger till en dimension i livet som inte går att beskriva, för dem som inte har egna barn, utan som måste upplevas.

Sanna, för att du vill leva och står ut med mig. Jag älskar dig innerligt, även om det inte alltid framgår så tydligt!

Slutligen

Om det nu är någon som känner sig förbigången så beror det enbart på min välkända oförmåga att komma ihåg. Tveka inte att upp problemet med mig i så fall. Gärna efter middagen på festen, eller så fort Ni har fått tag på avhandlingen och upptäckt att just Ni var bortglömd, så ska jag försöka gottgöra Er på något sätt.