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# Predator pressure determining pigmentation and morphology in *Asellus aquaticus*



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## Abstract

The predator-prey interaction between fish and *Asellus aquaticus* phenotype have been discussed in many articles. Predators have been suspected to be an evolutionary selective force in different habitats with *Asellus aquaticus*, even though it is unclear how the selection works. A study was therefore conducted in Lake Erken, Uppsala County, Sweden. Nine sites and two contrasting habitats, (inner littoral & outer littoral zone) with large differences in substrate composition and colouration were investigated.

This study implies that the differences in *Asellus aquaticus* phenotypic characters are results of predator density, with a trade-off between prey that is easy to find (fits predators search image) and the abundance of specific prey phenotype. There is a strong correlation between predator abundance and prey pigmentation, where predators most likely select for either conspicuous prey or for more frequently common cryptic prey, a phenomenon known as apostatic selection. Biometrical measures (morphology) of *Asellus aquaticus* are most likely influenced by both predator abundances and intraspecific competition.

## Introduction

Benthic animals of the littoral zone do have a great importance for the total ecosystems, even though it is generally poorly understood (EC, 2006) (Wetzel, 2001) Benthic fauna constitutes a large fraction of the total food resource for fish (Vander Zanden and Vadeboncoeur, 2002). Among benthic fauna is *Asellus aquaticus* very abundant, with monthly average numbers that sometimes exceeds 10000 individuals/m<sup>2</sup> in lake Erken (Andersson, 1969).

Different kinds of predators use a large variety of methods to find benthic animals and gain energy from them, and many predators are visual feeders. Several adaptations have been made to keep the balance between predator and prey such as in the prey cryptic appearance to blend in to an environment, thereby avoiding detection and being preyed upon (Johnsson and Kjällman-Eriksson, 2008).

In environments with high predation rate a common adaption in prey is an anti-predator appearance, like prey crypsis (Endler 1978, 1986). Several studies have investigated prey crypsis, such as for the freshwater Isopod *Asellus aquaticus* adaptation to the environment and predators (Hargeby et al 2004, Hargeby et al 2005, Eroukmanoff et al, 2009). There is a pigmentation difference in *A. aquaticus* phenotype that is likely to be a result of differences between the inner and outer littoral habitat (Hargeby, 2005). There is also evidence for prey crypsis in several other species (Bond & Kamil, 1998; Ruxton et al, 2004; Johnsson and Kjällman-Eriksson, 2008).

Difference in phenotypic appearance has a great impact on individual fitness, but the main factor for different adaptations may shift.

In phenotypic evolution, two general measurements are crucial, pigmentation and morphology (general composition of body measurements).

In lakes it is likely to find two ecotypes (Figure 1) of *A. aquaticus* in inner and outer littoral zone (Eroukhmanoff et al, 2009), even though it is unclear what drives the differences between ecotypes (Eroukhmanoff & Svensson, 2009).



Figure 1. Dark and light morph of *A. aquaticus*.

In this study I investigated the influence of predation pressure on morphological and pigmentation differences in *A. aquaticus* occupying two contrasting habitats. I used field observations and measured morphology and pigmentation of *A. aquaticus* at different sites that vary in predator abundance.

I hypothesized that if predation is important for habitat divergence in *A. aquaticus*, then the differences between the habitats might increase with increasing predator abundance.

## Materials and methods

The hypothesis was investigated (27-06-2008 - 28-08-2008) in Lake Erken by sampling both benthic animals and fish at nine sites (shown in appendix), with two adjacent benthic habitats at each site. The sites were chosen to be as similar as possible, according to emerged and submerged vegetation. The inner littoral habitats were chosen to be in the reed belt, at 0.5 - 1 m depth. The outer littoral habitats were situated outside the reedbelt, at 2 - 3 m depth. The inner littoral zone consisted of a dense reed belt, which contributes to a shaded environment with large amounts of dark degrading detritus. The overall lighter substrate in the outer littoral zone was characterised by green submerged plants and some patches of detritus. *Asellus aquaticus* was sampled qualitatively in the inner littoral zone using a benthic fauna net with mesh size of 0.5 mm. Quantitative sampling of littoral fauna in the inner littoral zone were performed with a tube sampler, 100 mm in diameter; 5 tube samples at each site. Benthic fauna in the submerged vegetation (closely outside the reed belt) were sampled qualitatively with an Ekman-grabber; 5 samples at each site. The benthic fauna was separated from the sediment and detritus by sieving and cleaning the samples with a water beam and a sieve (0.5 mm mesh size).

Fishing was performed by using Nordic multimesh gillnets, two littoral nets at each site. The nets were put out for one full day (24 hours). All fishes that were collected from the gillnets were identified to species and measured for length and weight. Fishes with size from ca 10 cm and longer were caught during the survey, the fish abundances were used as a measure of predation. Fish abundance (as opposite to fish biomass) is an adequate measure of predator activity as small fish are more dependent on benthic fauna as a food resource, and that small fish are searching more actively (Bull et al 1996, Johnsson and Bohlin 2006, Johnsson & Kjällman-Eriksson 2008) due to intraspecific competition and for reaching reproductive state. When fish are searching more actively they also use more energy and consume more biomass from prey. To use the fish biomass as a measurement of predation rate would therefore bias the main purpose of the investigation, by favouring body mass more than number of hunters.

## Photography

About 30 living individuals of *Asellus aquaticus* were randomly selected from each sampled habitat. Within the same day as *A. aquaticus* were collected, they were photographed during fixed light conditions (flourescent lamps) on a white background and together with a fixed greyscale, with a camera (Canon PowerShot G9) mounted on a small tripod. *A. aquaticus* were kept alive and each of the photographed individuals was then put in to an eppendorf tube, to be stored in a freezer ( $< -20^{\circ}\text{C}$ ) to preserve the samples for further analysis.

## Pigmentation and morphological analysis

Photographs of 688 individuals were analysed in Adobe Photoshop 7.0.1 for body length (mm) and pigmentation. In pigment analysis the dorsal body was measured, excluding extremities. The pigment analysis yields values between 0-255, where 0 is dark and 255 is bright. The values from body length and pigment analysis were then compared with the white square of the greyscale (Figure 2), which has a fixed length, colour and area.

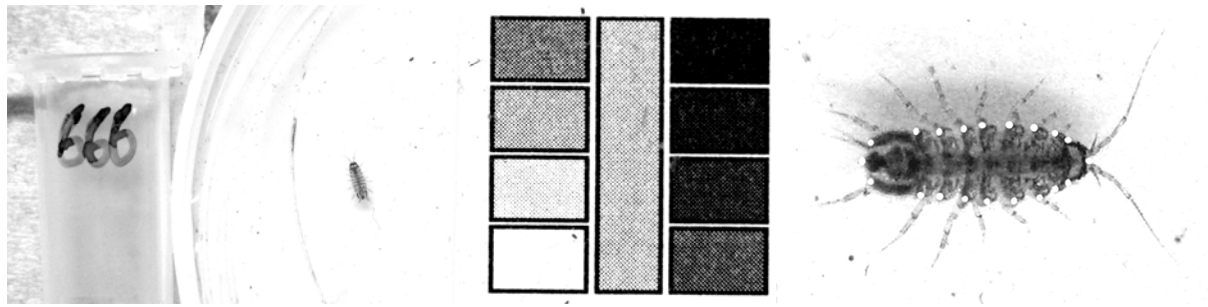


Figure 2. Photograph of *Asellus aquaticus* and grey scale (to the left), close up picture of *A. aquaticus* dorsal view with 20 white landmarks (to the right).

The pigment value was transformed ( $1 - (A. \textit{aquaticus} \textit{ pigmentation} / \textit{ pigmentation} \textit{ of the white square in the greyscale})$ ).

The transformation were executed to compensate for possible differences in light conditions, the pigmentation values had a span from 0 to 1, where 0 is light and 1 is dark pigmented individuals.

It is known from previous studies that there is a correlation between length of *A. aquaticus* and pigmentation, where longer individuals often are darker pigmented (Hargeby, 2005). This correlation between length and colouration of *A. aquaticus* was also present in this study, length where therefore set as a covariate to the mean pigmentation calculation, for the population at each habitat. The average length of *A. aquaticus* was 4.5 mm in this study.

Morphological measures of 500 individuals were analysed, 20 landmarks on the dorsal side of each individual were digitized (Figure 2).

I used multivariate geometric shape analysis to achieve a morphological index concerning body shape for each individual. In order to make each landmark in an individual comparable with other individuals, independent of size, I used the analysis program TPSRW (thin-plate spline relative warp).

The advantages of using this method for examination of morphology lies in its flexibility and accuracy to make predictions of shape variations in and between populations (Bookstein 1991, Marcus et al. 1996).

TPSRW was used to calculate uniform scores and partial warps for each individual, TPSRW is not dependent of body length in the measured structure. Relative uniform scores parameterize the studied animals by taking in to consideration all the similarities they have, concerning overall shape.

The partial warps calculate all differences in particular regions of the measured geometry and make it possible to see local extensions/contractions on the body

shape (Bookstein 1991, 1996). All partial warps and uniform scores from individuals sampled from the same habitat were then pooled and a DFA (Discriminant Function Analysis) was calculated based on the discrimination between the two habitats. By using DFA, a morphological index is formed for each individual. The program TPSREGR (Rohlf 1993 b) was used to display the original coordinates and shape changes linked to the morphological index.

The comparison of coloration and morphological differences of the *A. aquaticus* population at each habitat and between habitats at each site, were analysed by using ANOVA analysis.

### **Stable isotope analysis**

The stable isotopes were analysed since they are an important part in many investigations that handle differences between habitats as well as food web compositions and migratory patterns. There is a connection between the proportions of rare stable isotopes in plants, bacteria or algae and the place they grow in the lake. The organisms living and eating/degrading the same food resource get the same nitrogen isotope signal. When *A. aquaticus* stay within the same habitat and degrading same food resource it results in a difference between *A. aquaticus* in outer littoral zone and inner littoral zone. Migratory patterns is therefore suspected to be seen.

A selection of samples was made, depending on size and morphological characters; large animals were preferably chosen. The selected individuals were then dried in an oven for 24 hours at 60 °C, each individual of sufficient weight (0.8-1.2 mg) was placed in a thin-cup that was closed up to a compact spherical structure. Individuals of less than 0.8 mg of weight were pooled with other individuals to make a weight >0.8 mg. The selection of *A. aquaticus* was sent to UC Davis Stable Isotope Facility, for analysis of stable isotope ratio in the samples. During statistical analysis of stable isotope analysis differences between sites and habitats or site\*habitat interactions were looked for.

### **Statistics and statistical programs used in the investigation**

Data were handled and sorted in Excel. Statistical calculations such as: multivariate analysis, ANOVA, ANCOVA and regression analysis, were executed in Minitab and SPSS.

## Results

A total of 1130 fishes were caught in the Nordic littoral multimesh gillnets during the survey. The total number of fish caught at each littoral habitat was used to determine predator density.

There were 9 species of fish caught during the study; bleak (*Alburnus alburnus*), bream (*Abramis brama*), perch (*Perca fluviatilis*), pike (*Esox lucius*), roach (*Rutilus rutilus*), rudd (*Carassius carassius*), ruffe (*Gymnocephalus cernuus*), tench (*Tinca tinca*) and white bream (*Abramis bjoerkna*).

Out of the species that were caught, bleak is the only species that is not known to predate on *Asellus aquaticus*, even though bleak prey on food resources that are shared among the other fish species.

### Pigmentation analysis

There was a difference in pigmentation (one-way ANOVA analysis of sites and colour). There were pigmentation differences between the sites and habitats, as well as a significant interaction between habitat and site according to crossed factor General Linear Model (GLM) ANOVA analysis on 562 individuals divided on 9 sites with 2 habitats at each site (Table 1).

Table 1. Statistics for pigmentation analysis, where only photos of the best quality were chosen to be analysed. The table shows highly significant difference in tested parameters.

	DF	Mean Square	F	P
Size	1	37018.2	318.69	0.000
Site	8	2973.8	25.6	0.000
Habitat	1	1411.2	12.15	0.001
Site*Habitat	8	1562.9	13.45	0.000
Std. Error	535	116.2		

The pigmentation difference within sites versus fish abundance (Figure 3) followed a quadratic curve, which indicates a shift in the predators prey preference (Figure 4 & 5). Few predators lead to a low degree of pigment adaptation in *A. aquaticus* (Figure 3) and high abundance of predators gave the same response.

Pigmentation in figure 3 and 4 was highly correlated to fish abundance with R-square values of 66% and 86%, compared to the inner littoral habitat (Figure 5) where fish abundance did not seem to correlate to *A. aquaticus* coloration.

Figure 4 and 5 indicate that the *A. aquaticus* is light coloured when fish abundance/ predator density is at an intermediate level, ca 120 fishes per site and catch. Darker coloured individuals were sampled at intermediate predator level, compared to when fish abundance were high or low.



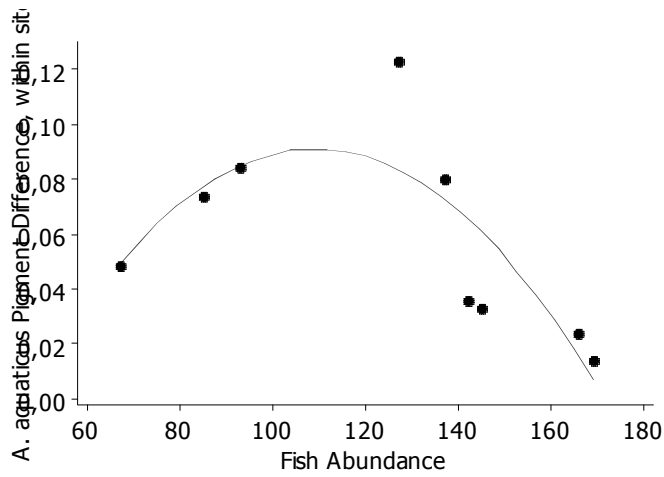


Figure 3. Fitted line plot describing the influence of fish density (x-axis) on *A. aquaticus* absolute pigmentation difference between inner littoral habitat and outer littoral habitat (Y-axis).  $R^2 = 0.66$ .

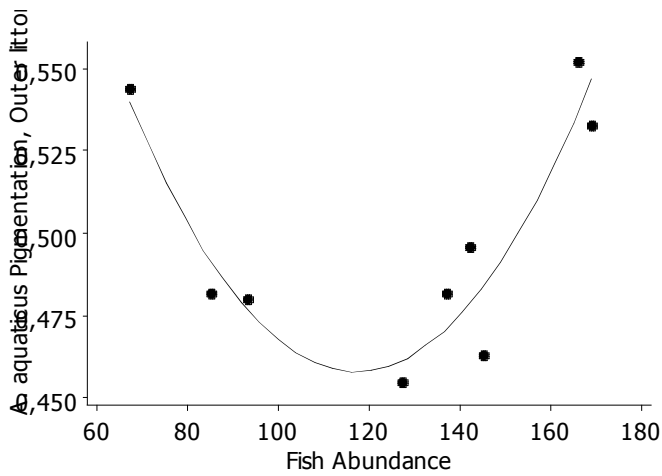


Figure 4. Fitted line plot describing *A. aquaticus* pigmentation in outer littoral habitats versus total number of predators (fish abundance).  $R^2 = 0.86$ .

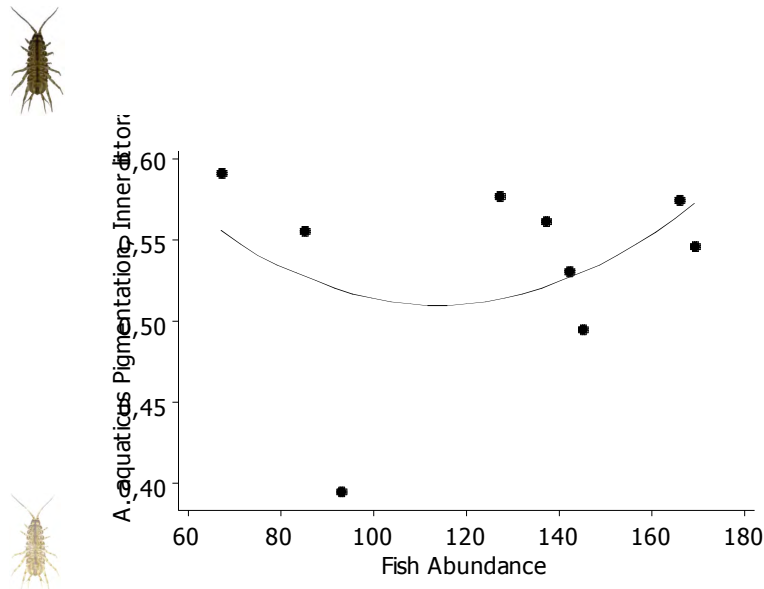


Figure 5. Fitted line plot describing pigmentation of *A. aquaticus* in inner littoral habitats (y-axis) versus fish abundance (x-axis). Outlier belongs to habitat 3, the inner littoral habitat 3 is much lighter, compared to the other habitats in this investigation.  $R^2 = 0.13$ .

### Morphological analysis

The morphological differences between *A. aquaticus* from inner and outer littoral habitats were not correlated to fish abundance (Figure 6). The morphology in the inner littoral zone were not correlated to fish abundance ( $R^2$  (adj) = 0.0), whereas the morphology in the outer littoral habitats was correlated to fish abundance (Figure 7).

In general were 66% of the *A. aquaticus* correctly classified to the habitat, according to the typical appearance and a typical morphologic index value of an *A. aquaticus* found either in the inner littoral zone or in the outer littoral zone. 65% of the inner littoral *A. aquaticus* were classified to the right group, 67% of the outer littoral *A. aquaticus* were classified to the right habitat.

The difference between habitats (inner & outer littoral) was highly significant ( $P < 0.000$ ). In inner littoral habitat the *A. aquaticus* bodyshape was in general broader and given a more positive morphologic value than in the outer littoral zone. Table 2 shows that site\*habitat interaction was not significant ( $P = 0.078$ ).

There was a significant morphological difference ( $P=0.001$ ) between the 9 different sites. 500 individuals were morphologically examined, divided between 9 sites with 2 habitats at each site.

Table 2. Table of statistics for morphological analysis, where only photos of the best quality were chosen to be analysed. The table shows highly significant difference in tested parameters concerning site, habitat and close to significant difference in site\*habitat interaction.

	DF	Mean Square	F	P
Site	8	3.2889	3.44	0.001
Habitat	1	75.8411	79.43	0.000
Site*Habitat	8	1.7034	1.78	0.078
Std. Error	482	0.9548		

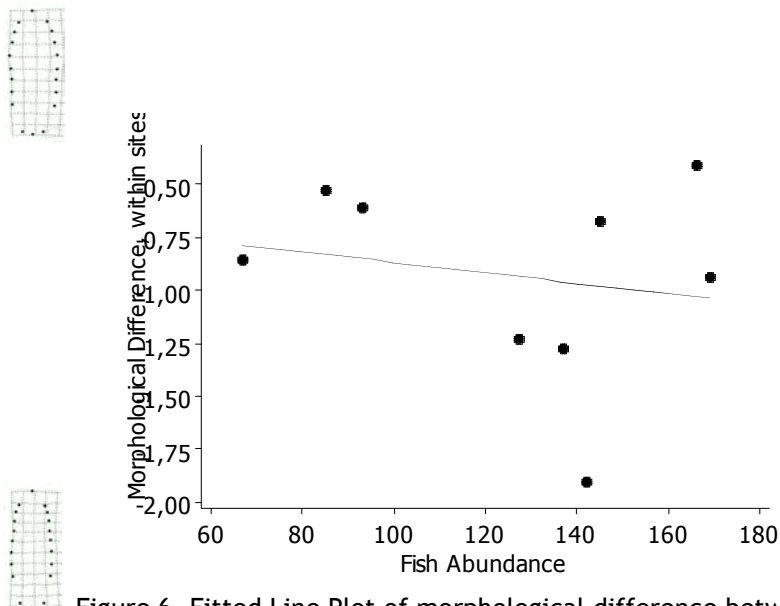


Figure 6. Fitted Line Plot of morphological difference between inner and outer littoral zone, (mean values of: outer littoral - inner littoral) versus fish abundance. A more positive value in this morphometric index leads to a generally broader body shape.  $R^2=0.04$ .

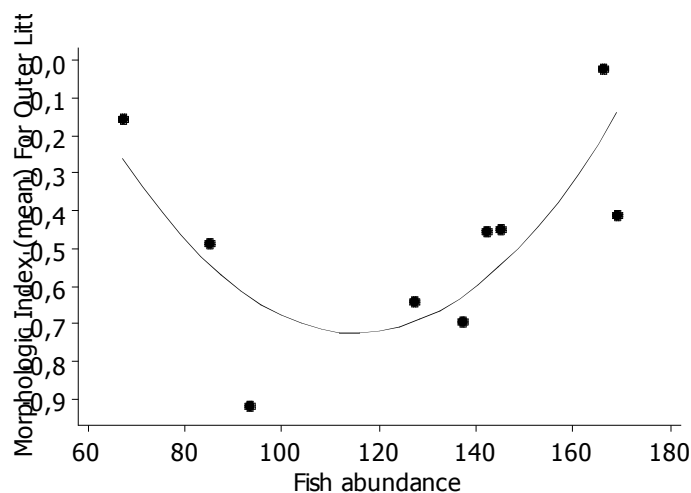


Figure 7. Fitted line plot of morphological differences in outer littoral zone depending on fish abundance.  $R^2 = 0.60$ .

### Isotope analysis

There was a significant habitat difference between inner and outer littoral, in isotopes  $\delta^{13}C$  ( $P= 0.025$ ) and  $\delta^{15}N$  ( $P= 0.011$ ).

### Discussion

In this study I found that predator abundance was related to patterns in *A. aquaticus* pigmentation and less correlated to morphology. Pigmentation of *A. aquaticus* is likely to depend on predation pressure (Figure 3, 4 & table 1), whereas morphology is possibly more linked to the environmental structure or other factors (Figure 6 and 7). The stable isotope analysis showed a significant difference in  $\delta^{13}C$  and  $\delta^{15}N$  signals in *A. aquaticus* between habitats, which implies that individuals feed in a fixed environment during long time periods and that they probably do not move between habitats.

Predators have different methods to become successful hunters, find prey, process prey and gain a positive value of net energy from prey. One important factor is how predators select prey. When fish abundance is low the fishes seems to catch easily detected preys that are less cryptic to the background. With higher fish abundance the cryptic prey become more abundant. When fish abundance is moderately high, a shift in pigmentation towards darker coloured individuals of *A. aquaticus* seems to appear (Figure 3, 4 & 5). When predator abundance exceeds moderate levels the abundance of cryptic prey decreases. This might reflect a shift in search image and feeding strategy in fish predators, towards the most abundant morph of *A. aquaticus*. The difference in pigmentation among *A. aquaticus* (Figure 3) in this investigation is suggested to be a cause of that abundance of cryptic prey raises till intermediate predator abundance is reached. When there is more well adapted cryptic prey left in a habitat, the expected predator response is to change search picture and forage on the most abundant prey morph. With high abundance of predators follows possibly a higher predation on well adapted *A. aquaticus* morphs.

This phenomenon of altering search image is known in apostatic selection. Apostatic selection is a common response of predators, where they rely on a trade-off between preys that are easy to find (which fits the search image) and the abundance of specific morphs. The fish search efficiency in this investigation may follow the same apostatic selection pattern as was shown in Bond & Kamil's (1998) study of predator efficiency in blue jays. This study implies that experimental predator search efficiency studies of for example blue jays fit field study results of a predator/anti-predator response in *A. aquaticus*.

The shift was much more distinct and correlated in the outer littoral zone (Figure 4). The stronger pigmentation shift in the outer littoral zone (Figure 4) compared to the inner littoral zone (Figure 5), may be explained by that visually active hunting predators are more likely to find prey outside dense shelters (Mattila, 1992) like aquatic plants or reed belts. In the inner littoral zone, benthic invertebrates (e.g. *Odonata* larvae) are the main predators upon benthic fauna, (Rask & Hiisivuori, 1985) while more visually hunting predators, like fish, are less common. In the outer littoral zone fish is more common and *Odonata* larvae are less common (Wagner & Hansson, 1998). Different predator structure in the inner and outer littoral zone is also a good reason why *A. aquaticus* pigmentation difference and predator abundance correlate less in the outer littoral zone (Figure 5).

Slower or less movement in prey is thought to be favourable to avoid detection in habitats with visually hunting fish. A correlation between narrow body shape and slower movement have been found by Eroukmanoff & Svensson (2009) as well as a narrow morphologic shape in *A. aquaticus* in the outer littoral zone was observed in this study. Morphological differences in *A. aquaticus* were, compared to difference in pigmentation, not as influential (Figure 6 and 7), even though *A. aquaticus* morphology in outer and inner littoral differed significantly.

It is likely that the morphological differences between habitats in this study are driven by more factors than predation. Fish abundance had no relation to morphological difference between habitats (Figure 6), as well as less correlation in the outer littoral (Figure 7) compared to pigmentation (Figure 4).

It has been shown in perch (*Perca fluviatilis*) that having a broader/deeper body shape is favourable to forage in the more vegetated littoral zone (Svanbäck & Eklöv, 2003). The broad body shape in *A. aquaticus* is likely to be an effect of that mobility is favourable in dense habitats with predators like *odonata* larvae. *Odonata* larvae have low resolution compound eyes that are useful in short range pursue (Hemmi & Zeil, 2003) where the larvae often sit and wait for the prey (Mikolajewski et al, 2006). *A. aquaticus* in the inner littoral is therefore likely to react faster and outrun a predatory threat, compared to the less active individuals in the outer littoral zone that possibly are more adapted to predators like fish, that possess superior speed endurance (Eroukmanoff et al, 2009; Eroukmanoff & Svensson, 2009). The morphology seems to be dependent on fish abundance in the outer littoral zones (Figure 7). In the inner littoral zone, fish predation does not appear to be a selective force upon the morphology of *A. aquaticus*. However, which other factors that drives the differences in morphological status between inner and outer littoral ecotypes of *A. aquaticus* is not clearly understood. Leaves of the submerged plant *Elodea sp.* resemble the shape and size of *A. aquaticus* that

is living in the outer littoral and where environment adaptation is a likely explanation. The evolution of one strict phenotype might depend on multiple factors. In this study intraspecific competition may contribute to the lower morphological correlation to predator density. The phenotypic differentiation and even possibly evolution in *A. aquaticus* is probably a part in a top-down regulated system, where predation is the most likely agent (Hargeby et al. 2004, Hargeby et al. 2005, Eroukmanoff & Svensson 2009). If predation pressure and the number of predators are constant during long time within a habitat, it is likely that species of *A. aquaticus* can evolve, with predation as a selective agent.

Prey phenotypic evolution is less influenced by predator density (and thereby predation pressure) if the number of predators is changing much.

If predator abundance goes in cycles, with alternating search pictures among many predatory fish species this will possibly not lead to a rapid evolution of *A. aquaticus* in well established environments.

The correlation between *A. aquaticus* cryptic appearance and number of predators found in this investigation is striking, even though replicated studies are needed to confirm the resembled apostatic selection relationship between predator and prey.

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## References

Andersson, E. (1969). Life cycle and growth of *Asellus aquaticus* (L.) with special reference to the effects of temperature Institute of Freshwater Research. Drottningholm. Rep. No. 49, pp. 5-26.

Angelo, G. Solimini . Free, G. Donohue, I. Irvine, K. Pusch, M. Rossaro, B. Sandin, L. Cardoso, A C. (2006). Using Benthic Macroinvertebrates to Assess Ecological Status of Lakes Current Knowledge and Way Forward to Support WFD Implementation. European Commission Directorate-General Joint Research Centre Institute for Environment and Sustainability. Institute for Environment and Sustainability.

Bertine, Angéline. David, Bruno. Cézilly, Frank. Alibert, Paul .(2002). Quantification of sexual dimorphism in *Asellus aquaticus* (crustacea: Isopoda) using outline approaches: *Biological Journal of the Linnean Society*, 77, 523-533

Bull, CD. Metcalfe, NB. Mangel, M. (1996). Seasonal matching of foraging to anticipated energy requirement in anorexic juvenile salmon. *Proc R Soc Lond B* 263:13 -18

Bond, Alan B. Kamil. Alan, C. (1998). Apostatic selection by blue jays produces balanced polymorphism in virtual prey. *Nature*, VOL 395, 8 OCTOBER 1998.

Bookstein, F L. (1991). *Morphometric tools for landmark data: geometry and biology*. - Cambridge Univ. Press.

Bookstein, F L. (1996). A standard formula for the uniform shape component in landmark data. - In: Marcus, L. F., Corti, M., Loy, A. et al. (eds), *Advances in morphometrics*. Plenum Press, pp. 153-168.

EC (2006). European commission, Institute for environment and sustainability. Using benthic macroinvertebrates to assess ecological status of lakes current knowledge and way forward to support WFD implementation. EUR 22347 EN Luxembourg: Office for official publications of the european communities. ISSN 1018-5593.

Endler, J A. (1978). A predator´s view of animal color patterns. *Evol. Biol.* 11:319 - 364.

Endler, J A. *Natural selection in the wild*. (1986). Princeton Univ. Press, Princeton, NJ.

Eroukmanoff, F. Svensson, E I. (2009). Contemporary parallel diversification, antipredator adaptations and phenotypic integration. *PLoS ONE* 4:e6173. doi:10.1371/journal.pone.0006173.

Eroukmanoff, F. Hargeby, A. Arnberg, N N. Hellgren O. Bensch S. Svensson E I. (2009). Parallelism and historical contingency during rapid ecotype divergence in an isopod *J. Evol. Biol.* 22. 1098-1110 (European society for evolutionary biology).

Hargeby, A. Johansson, J. Ahnesjö, J. (2004). Habitat-specific pigmentation in a freshwater isopod: Adaptive evolution over a small spatiotemporal scale. *Evolution* 58: 81-94.)

Hargeby, A. Stoltz, J. Johansson, J. (2005). Locally differentiated cryptic pigmentation in the freshwater isopod *Asellus aquaticus*. *Journal of Evolutionary Biology* 18, 713-721.

Hemmi, J M. Zeil, J. (2003). Robust judgement of inter-object distance by an arthropod. *Nature* 421: 160-163.

Johansson, J I. Bohlin, T. (2006). The cost of catching up: increased winter mortality following structural growth compensation in the wild. *Proc R Soc Lond B* 273: 1281–1286

Johansson, J I. Kjällman-Eriksson, K. (2008). Cryptic prey colouration increases search time in trout (*salmo trutta*): effects of learning and body size *Behavioral Ecology and Sociobiology* Volume 62, Number 10, 1613-1620,

Marcus, L F. Corti, M. Loy, A. Et al. (1996). *Advances in morphometrics*. - Plenum Press.

Mattila, J. (1992). The effect of habitat complexity on predation efficiency of perch *Perca fluviatilis* L. and ruffe *Gymnocephalus cernuus* (L.) *Journal of experimental marine biology and ecology*. Volume 157, Issue 1 Pages 55-67

Mikolajewski, DJ. Johansson F, Wohlfahrt B, Stoks R (2006) Invertebrate predation selects for the loss of a morphological antipredator trait. *Evolution* 60: 1306-1310.

Rask, M. and Hiisivuori. (1985). The predation on *Asellus aquaticus* by perch *Perca fluviatilis* in a small forest lake. *Hydrobiologica* 121, 27–34.

Rohlf, F J. (1993) a. TPSRW: thin-plate spline relative warp analysis. - Dept. of Ecology and Evolution, State Univ. of New York, NY.

Rohlf, F J. (1993) b. Relative warp analysis and an example of its application to mosquito wings. - In: Marcus L. F, Bello, E. and Garcia-Valdescasas, A. (eds), *Contributions to morphometrics*. Monografias del Museo Nacional de Ciencias Naturales, Madrid, Spain, pp. 131-159.

Ruxton, G D. Sherratt T. N., Speed M. P. (2004). *Avoiding attack: the evolutionary ecology of crypsis, warning signals and mimicry*. Oxford, UK: Oxford University Press.

Svanbäck, R. Eklöv, P. (2003). Morphology dependent foraging efficiency in perch: a trade-off for ecological specialization? - *Oikos* 102: 273-284.

Vander Zanden, M J. Vadeboncoeur, Y. (2002). Fishes as integrators of benthic and pelagic food webs in lakes. *Ecology* 83: 2152-2161.

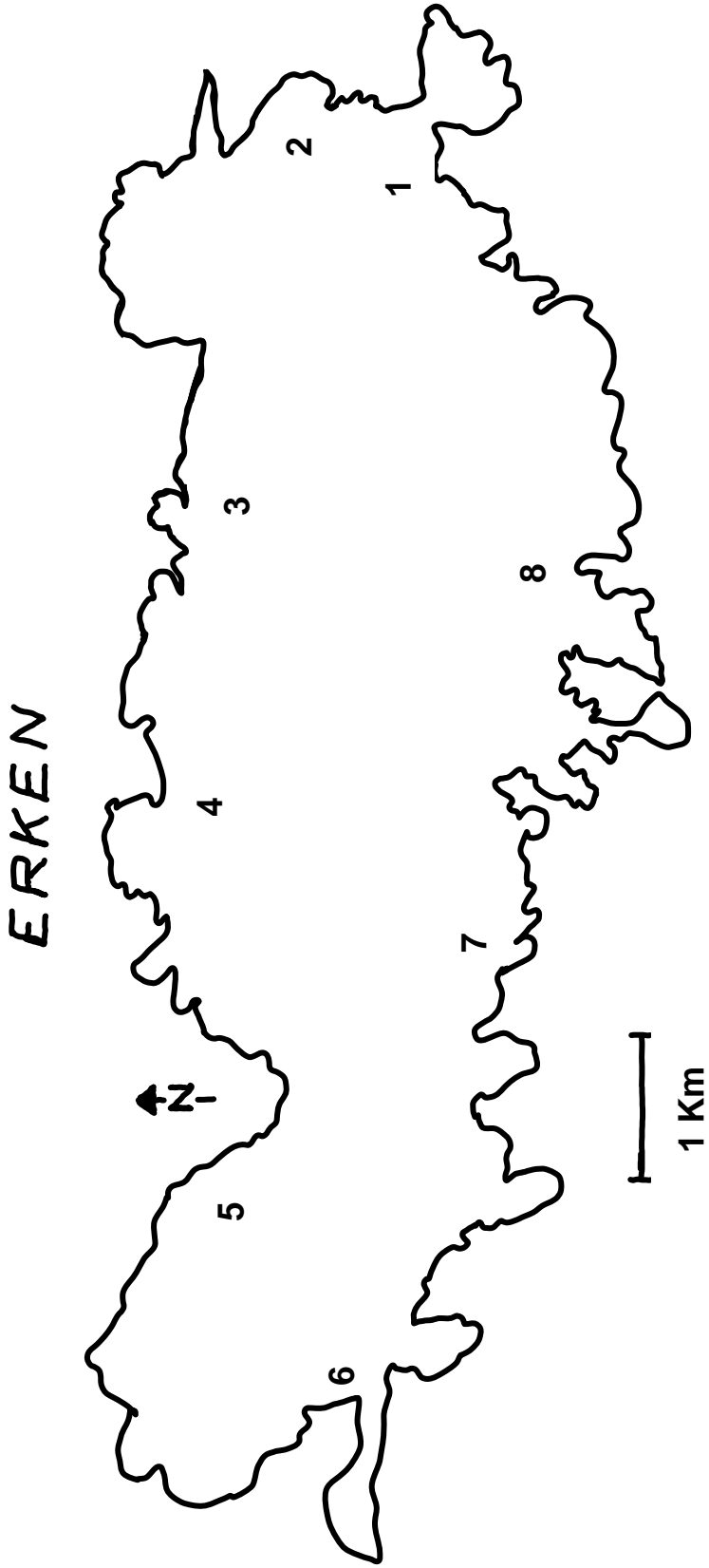


Wagner, B M. and Hansson, L A. (1998). Food competition and niche separation between fish and Red-necked Grebe *Podiceps grisegena* (boddaert1783). *Hydrobiologica* 368, 75–81.

Wetzel, R G. (2001). S - 665. Limnology- Lake and river ecosystems, Third edition, San Diego: Academic Press, San Diego, California.

Appendix

Map and coordinates of investigated habitats in Lake Erken.



## Coordinates

Site & Habitat	North	East
1 Littoral	59 50.397	018 38.536
1 Pelagic	59 50.576	018 38.290
2 Littoral	59 50.999	018 38.846
2 Pelagic	59 50.905	018 38.436
3 Littoral	59 51.286	018 36.411
3 Pelagic	59 51.146	018 36.335
4 Littoral	59 51.420	018 34.156
4 Pelagic	59 51.217	018 34.209
5 Littoral	59 51.121	018 31.185
5 Pelagic	59 51.067	018 30.716
6 Littoral	59 51.036	018 29.086
6 Pelagic	59 51.167	018 29.346
7 Littoral	59 50.156	018 32.559
7 Pelagic	59 50.302	018 32.683
8 Littoral	59 49.750	018 35.613
8 Pelagic	59 49.917	018 35.785
9 Littoral	59 50.146	018 37.714
9 Pelagic	59 50.290	018 37.578