

## Life history strategy and depth selection behavior as alternative antipredator defenses among natural *Daphnia hyalina* populations

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### Abstract

We analyzed distribution patterns and life history traits in 14 natural *Daphnia hyalina* populations. The populations at shallower depths during the day began reproduction at a smaller size and showed higher reproductive effort. Since surface avoidance and small maturation size both reduce likelihood of fish predation, these data suggest that depth selection behavior and life history patterns are mutually adjusted alternative ways of coping with predation. Even though the relationship between residence depth and size at first reproduction was the same in partially anoxic and fully oxygenated lakes, the two types of lakes differed in how the two strategies were exhibited. In the partially anoxic lakes the behavioral defense was realized to the maximum possible extent, since the animals were found just above the boundary of the anoxic zone, and the life history strategy was adjusted to defensive behavior. In some of the fully oxygenated lakes some populations resided well above the lake bottom and exhibited correspondingly small size at first reproduction. Thus, the behavioral defense was not fully used, which demonstrates that in some circumstances life history modifications can be preferred over behavioral defense.

Predation is an important selective force that has been shown to drive evolution of a range of traits in prey organisms including behavior (e.g., Gliwicz 1986) and life history (e.g., Reznick et al. 1990). There is a continuously growing number of examples of induced defenses, in particular in aquatic organisms (reviewed in Tollrian and Harvell 1999; see also DeWitt 1998; Leonard et al. 1999). The ubiquitous occurrence of induced defenses suggests that antipredator traits are often costly. A wealth of studies has indeed shown that the costs of defenses can be substantial (e.g., Riessen and Sprules 1990; Tollrian and Dodson 1999; Van Buskirk 2000). Many prey species possess multiple defense traits. Although exhibiting the whole range of defenses can often provide maximum protection, it might not always be necessary, and, moreover, it might be too costly. If the defense strategies do not need to be exhibited to their maximal extent, different combinations of antipredator traits can be equally favored (e.g., Rundle and Brönmark 2001). Moreover, there are cases where only particular combinations of defense traits are effective (e.g., Brodie 1989). This can lead to coexistence of different strategies, which may help to maintain genetic variation for defense-related traits in prey populations. One can also hypothesize that, given their inducibility, existence of multiple defense traits allows fine tuning of antipredator strategy by employing the most effective or

the least costly defense in any given circumstances. Despite these interesting possibilities, studies considering the interplay among multiple defenses are relatively rare (but see De Meester et al. 1995; Sparkes 1996; Straile and Halbich 2000).

In *Daphnia*, both depth selection behavior, often manifest as diel vertical migration, and life history strategy constitute effective antipredator defenses. Residing at deep and dark water layers during the day reduces predation risk because hunting efficiency of planktivorous fish is limited by illumination (Stich and Lampert 1981; Lampert 1989). One life history strategy that offers protection against fish predation is early maturation at smaller size. This increases the chances of survival and reproduction in the presence of predators that select large-sized prey individuals (Brooks and Dodson 1965; Kerfoot and Sih 1987). Both behavioral and life history strategies entail substantial costs. Residing deep is associated with low temperatures, which bring about large decreases in growth rates (Dawidowicz and Loose 1992; Loose and Dawidowicz 1994), while small size at maturity is related to decreased competitive ability (Gliwicz 1990; Sakwińska unpubl. data). Both strategies were shown to be inducible by chemicals exuded by fish (kairomones) (reviewed in Larsson and Dodson 1993). Under exposure to fish exudates, animals have been shown to remain deeper during the day (Dodson 1988; Ringelberg 1991), mature smaller and at earlier age, and show higher reproductive effort (Macháček 1991; Stibor 1992). In the face of widely varying predation pressure, considerable and sometimes unnecessary costs make the accurate adjustment of the defense strategies to current predation risk, and factors that affect costs (such as food conditions), particularly important. The fact that the different sets of traits are inducible makes such adjustment potentially fast and feasible for individuals.

There is some evidence from laboratory studies that life history strategy and depth selection behavior comprise alternative antipredator defenses. It has been shown that clones of *Daphnia* found at shallower depths in the field (Tessier and Leibold 1997; De Meester and Weider 1999), or which ex-

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hibited positive phototactic responses in the laboratory trials (De Meester 1994), matured earlier and at smaller size when raised in the laboratory. In an experiment in large indoor enclosures, in the presence of fish, a large-sized, but deep dwelling clone coexisted with another one that was smaller and resided shallower (De Meester et al. 1995). Numerous studies considered the variation in residence depth in the field and its possible causes (e.g., Gliwicz and Pijanowska 1988; Leibold and Tessier 1991), and the same is true for life history patterns (e.g., Leibold and Tessier 1991; Gliwicz and Boavida 1996). Although it has been known that larger individuals migrate deeper (for review see Lampert 1989), no attempt was made to evaluate both depth selection behavior and size at first reproduction in the field to determine how these two traits covary under natural conditions.

The goal of this study was thus to establish how life history and behavioral defensive strategies are associated in natural *Daphnia hyalina* populations. We have studied a range of *D. hyalina* populations, the largest, and thus most vulnerable to fish predation, species occurring in the study lakes. The extent of defensive behavior was quantified as daytime residence depth. Although rarely attempted (Stibor and Lampert 1993; Boersma 1995; Gliwicz and Boavida 1996), it is also possible to extract information from field data on at least some life history traits relevant for vulnerability from predation: size at first reproduction and reproductive effort. Our main prediction was that *Daphnia* found at shallower depths mature at smaller size and show higher reproductive effort. In addition, we attempted to identify factors that might alter the profitability or feasibility of either strategy and control for potential confounding factors that are well known to affect *Daphnia* life history and distribution, mainly food conditions and temperature (e.g., Lampert et al. 2003).

## Methods

Fourteen lakes located within a radius of 100 km in North-eastern Poland were sampled once in July 1995. The lakes were all at least 19 m deep and thermally stratified in summer but varied in terms of water transparency and the thickness of hypolimnetic anoxia. The fish community composition is shown in Table 1. More information on the zooplankton communities can be found in Mlonek (1998). Water temperature and dissolved oxygen concentration were measured at 1-m intervals (with an YSI54A oxygen meter, YSI). Water transparency was quantified as Secchi depth at midday (1100–1300 h). To quantify the food concentration available for *Daphnia*, the particular organic carbon concentration was determined using a NC 2500 carbon analyzer (CE Instruments) in particles smaller than 40  $\mu\text{m}$  in epilimnion and hypolimnion water samples. The epilimnetic and hypolimnetic samples were taken with a 1-liter Patalas trap from the depths of 1 and 16 m, respectively. Water transparency, oxygen concentration, temperature, and carbon concentrations were measured at midday. The relative density of planktivorous fish was assessed with a Simrad echosounder EY-M (Simrad AS) along an arbitrary transect that cut through the deepest point of a lake, at 2200 h on the same day the *Daphnia* samples were obtained. Echograms were

Table 1. Some environmental characteristics of the studied lakes.

| Lake               | Lake name abbreviation | Dominant planktivorous fish* | Fish density (rank) | Thermocline depth (m) | Population temperature ( $^{\circ}\text{C}$ ) | Organic carbon concentration (mg carbon $\text{L}^{-1}$ ) |             |
|--------------------|------------------------|------------------------------|---------------------|-----------------------|---|---|-------------|
|                    |                        |                              |                     |                       |   | Epilimnion  | Hypolimnion |
| Dłużec             | DI                     | ream, roach, perch           | 13                  | 4                     | 21  | 2.57  | 1.53        |
| Białe Krutyńskie   | BK                     | ream, roach                  | 5                   | 4                     | 21  | 1.78  | 1.18        |
| Ublik Wielki North | UWN                    | ream, roach, whitefish       | missing             | 5                     | 12  | 1.04  | 0.54        |
| Dobskie West       | DoW                    | smelt, vendace               | 1                   | 5                     | 12  | 1.50  | 0.38        |
| Ublik Wielki South | UWS                    | ream, roach, whitefish       | 7                   | 4.5                   | 11  | 0.63  | 0.57        |
| Sedraneckie West   | SeW                    | smelt, vendace               | 3                   | 5                     | 9   | 4.18  | 1.61        |
| Ublik Mały         | UM                     | ream, perch, whitefish       | 8                   | 4.5                   | 10  | 0.87  | 0.84        |
| Czarne             | Cz                     | ream, perch, vendace         | 6                   | 4                     | 13  | 1.31  | 1.21        |
| Sedraneckie East   | SeE                    | smelt, vandace               | 4                   | 5                     | 9   | 1.50  | 0.43        |
| Boczne             | Bo                     | ream, roach                  | 11                  | 6                     | 8   | 1.20  | 0.65        |
| Dobskie East       | DoE                    | smelt, vendace               | 9                   | 4.5                   | 11  | 1.29  | 1.75        |
| Rospuda            | Ro                     | whitefish, vendace           | 10                  | 6                     | 8   | 0.58  | 1.58        |
| Piłakno            | Pi                     | ream, vendace                | 12                  | 5                     | 14  | 0.90  | 0.99        |
| Garbaś             | Ga                     | roach, perch, smelt          | 2                   | 6                     | 12  | 1.79  | 0.62        |

\* Source: Polish Angling Association. Bream, *Abramis brama*; perch, *Perca fluviatilis*; roach, *Rutilus rutilus*; smelt, *Osmerus eperlanus*; vendace, *Coregonus albus*; whitefish, *Coregonus lavaretus*.

scanned, and two image fragments per lake were analyzed. The joint surface of dark area, reflecting fish abundance, was determined using the software program Scion Image. To take into account the fact that fish were restricted to oxygenated layers, only the image fragments corresponding to the area above the oxygen-depleted zone were included (thus depth of analyzed fragments varied from 4.5 to 40 m). The length of each fragment corresponded to 500 m in the field.

The zooplankton samples were taken at midday (1100–1300 h) and midnight (2300–0100 h) in vertical hauls using a quantitative closing plankton net (mesh size 150  $\mu\text{m}$ ) from discrete 6-m layers as near as possible to the deepest point of the lake. The samples were immediately fixed with 4% formaldehyde and later analyzed with a dissecting microscope. Morphological criteria were used to distinguish *D. hyalina* from other *Daphnia* species (Šrámek-Hušek et al. 1962). To determine depth distributions and density of *D. hyalina* populations, the animals were counted, depending on their density, in 25% to 100% of the sample. Average nighttime and daytime *D. hyalina* population depths were calculated separately for adult and juvenile individuals. Body length of up to 140 individuals per sample (or, if not abundant enough, the whole sample) was measured and their maturation status was determined using a morphological criterion (Edmondson and Litt 1982) and the number of eggs carried by each measured female was counted. *Chaoborus flavicans* individuals were counted in all the samples taken during the night.

To estimate size at first reproduction in each population, we used logit regression (Proc Logistic, SAS Institute) where the body length is treated as the independent variable and the reproductive status as the response variable. The analysis yielded the value of the body length, corresponding to a probability of 0.5 of having matured. This body length is an estimate of the size at first reproduction in a given population (see also Boersma 1995). The analysis was first conducted on pooled data from all daytime samples for each lake. The minimum sample size in this analysis was 69, but more commonly around 200 data points were available. Whenever sample size permitted, separate estimates of size at first reproduction of animals found in different layers during the day were obtained. We estimated initial relative fecundity as the average fecundity (number of eggs per gravid female) of animals in the three smallest adult size categories divided by body size at first reproduction in a given population. We chose this measure as relatively unbiased by immediate phenotypic selection by size-selective predators that prefer larger prey with larger egg clutches.

## Results

The daytime depth of *D. hyalina* adult populations varied greatly among lakes (Fig. 1); in contrast, nighttime distributions were quite similar. In 7 out of 14 investigated lakes hypolimnetic anoxia was detected, which clearly limited the daytime distribution of the animals (Fig. 1). To explore the factors responsible for the variation in daytime distribution in our data set, we examined the correlations of daytime population depth with a range of potentially relevant habitat

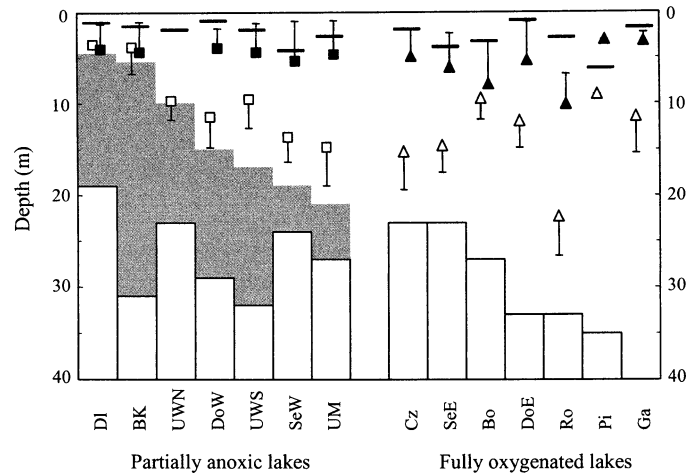


Fig. 1. Daytime (open symbols) and nighttime (filled symbols) *Daphnia hyalina* population depths of the adults (mean  $\pm$  standard deviation) in partially anoxic (squares) and fully oxygenated lakes (triangles). The zone that is inaccessible to *Daphnia* because of insufficient oxygen concentrations is indicated by a shaded area; white bars indicate maximal depth at the sampling stations. Secchi depth (measure of water transparency) is indicated by black horizontal bars. The abbreviated lake names are on the x-axis.

characteristics: fish density, water transparency, thickness of accessible zone, and food gradient between epilimnion and hypolimnion (see Table 1). The habitat suitable for *Daphnia* is considered to be limited by oxygen concentration (Wright and Shapiro 1990; Lass et al. 2000). We assumed that the zone accessible for *Daphnia* was limited by either the lake bottom at the sampling station (which was very close to the maximal depth of the lake) or the oxygen concentrations below 1  $\text{mg L}^{-1}$ . This was supported by the virtual lack of *Daphnia* in samples from layers with lower oxygen concentrations. The food concentration gradient was the difference between the epilimnetic and hypolimnetic organic carbon concentrations. Among the considered correlations (adult daytime residence depth vs. rank of fish density, thickness of accessible zone, food gradient, and water transparency) none proved to be significant for data on all lakes pooled (all  $p$  values larger than 0.1). The depth of thermocline was not considered among the potentially relevant habitat characteristics because it was virtually identical among all the study lakes (Table 1). In addition, most populations resided well below the thermocline during the day (Fig. 1). *C. flavicans* was either present at rather low densities (maximum 0.03 individuals  $\text{L}^{-1}$ ) or it was entirely absent.

Initial inspection of the data revealed that different factors might govern daytime distribution in partially anoxic and fully oxygenated lakes. In anoxic lakes *D. hyalina* populations always resided just above the anoxic layer (Fig. 1). In agreement with our assessment, when partially anoxic and oxygenated lakes were considered separately, a significant correlation between the depth of the oxygenated zone and daytime population depth was found among populations from partially anoxic lakes ( $r = 0.86$ ,  $n = 7$ ,  $p < 0.015$ ). No other correlation was significant (all  $p$  values larger than 0.2), and, in particular, there was no correlation between the

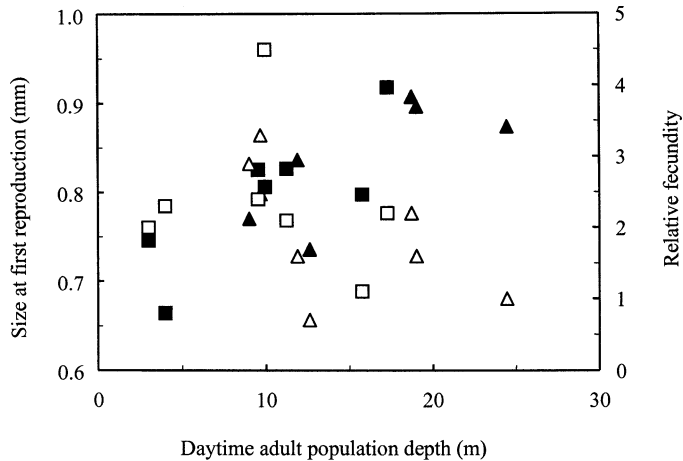


Fig. 2. The association between daytime residence depth and size at first reproduction (filled symbols) and relative fecundity (open symbols) among populations from fully oxygenated (triangles) and partially anoxic lakes (squares).

thickness of the accessible zone and daytime depth in populations inhabiting fully oxygenated lakes (Fig. 1).

To test our main hypothesis, we investigated the correlation between daytime residence depth and life history traits. Size at first reproduction was larger and relative initial fecundity lower for populations where the animals were found deeper during the day (size at first reproduction [SFR],  $r = 0.72$ ,  $n = 14$ ,  $p < 0.004$ ; Fecundity,  $r = -0.54$ ,  $n = 14$ ,  $p < 0.05$ ) (Fig. 2). However, it is well known that the temperature and food conditions strongly affect *Daphnia* life history. As the water temperature decreased with depth and the thermal stratification patterns were very uniform across the lakes (Table 1), the animals from populations residing deeper experienced colder temperatures that might have increased their size at maturity. On the other hand, the minimum food conditions in the studied populations were above the incipient limiting level for *Daphnia longispina* (Muck and Lampert 1980) (Table 1). We estimated the average food conditions experienced before maturation as the weighted average of epilimnetic and hypolimnetic conditions (assuming 16 and 8 h was spent in the hypolimnion and epilimnion,

respectively). As the *Daphnia* from lakes Białe Krutyńskie and Dłużec were always in epilimnion, hypolimnetic values were not taken into account for these populations. There was no correlation between size at first reproduction or relative initial fecundity and food conditions experienced before maturation (SFR,  $r = -0.08$ ,  $n = 14$ ,  $p = 0.78$ ; Fecundity,  $r = -0.44$ ,  $n = 14$ ,  $p = 0.12$ ). Temperature experienced before maturation was estimated on the basis of daytime and nighttime average depths of the immature individuals (assuming 16 and 8 h was spent in the hypolimnion and epilimnion, respectively). The populations that experienced lower temperatures before maturity had larger size at first reproduction ( $r = -0.58$ ,  $n = 14$ ,  $p < 0.03$ ), but there was no correlation with initial relative fecundity ( $r = 0.01$ ,  $n = 14$ ,  $p < 0.97$ ). Hence, it was possible that larger size at maturity of deeper residing populations could be explained by the colder temperatures they experienced (e.g., Boersma 1995).

To resolve that issue, we calculated partial correlations between daytime population depth and size at first reproduction and relative fecundity, with temperature and food conditions experienced before maturation held constant. Partial correlation indicated that larger size at first reproduction was correlated with daytime population depth even when variation in temperature and food concentrations was taken into account ( $r_p = 0.58$ ,  $n = 14$ ,  $p < 0.05$ ). It also confirmed that deeper residing populations had lower initial relative fecundity ( $r_p = -0.64$ ,  $n = 14$ ,  $p < 0.025$ ) (Fig. 2).

In eight lakes, the samples were large enough to permit estimation of size at first reproduction for groups of animals residing at different depths within the same lake (Table 2). In other lakes either all individuals were found residing at the same layer or the sample sizes were insufficient. The within-lake differences in size at first reproduction were much smaller than those among populations. We found no association between size at first reproduction and daytime depth within lakes.

## Discussion

We found that *Daphnia* from shallower residing populations started reproduction at smaller size. Taking into ac-

Table 2. Size at first reproduction (mm) and sample sizes (number of juveniles/reproducing animals) of *D. hyalina* found at different depths during the day estimated by logit regression. In the other lakes insufficient sample sizes or the presence of the animals at only one depth layer precluded this analysis.

| Depth | Lake            |                  |                 |                  |                  |                 |                 |                  |
|-------|-----------------|------------------|-----------------|------------------|------------------|-----------------|-----------------|------------------|
|       | DoW             | SeW              | UM              | Cz               | SeE              | DoE             | Ro              | Ga               |
| 3     |                 | 0.74<br>(47/5)   |                 |                  |                  |                 |                 | 0.72<br>(33/50)  |
| 9     | 0.82<br>(41/99) | 0.95<br>(118/22) | 0.82<br>(40/29) |                  |                  | 0.83<br>(39/70) |                 | 0.73<br>(116/42) |
| 15    | 0.84<br>(41/65) | 0.94<br>(70/69)  | 0.80<br>(30/38) | 0.91<br>(27/50)  | 0.91<br>(101/38) | 0.84<br>(8/11)  |                 | 0.74<br>(34/100) |
| 21    |                 | 0.90<br>(29/111) | 0.82<br>(19/48) | 0.89<br>(22/144) | 0.88<br>(42/95)  |                 | 0.86<br>(66/36) | 0.74<br>(15/47)  |
| 27    |                 |                  |                 |                  |                  |                 | 0.90<br>(29/34) |                  |

count variation in temperature experienced by animals remaining at different depths revealed that shallow-residing populations also had higher fecundity/body size ratio—a likely manifestation of increased reproductive effort. Both staying at deep and dark water layers during the day and life history with small size at first reproduction and high reproductive effort protect from fish predation. Thus, the extent of use of the two defense strategies was negatively associated among studied populations. These findings support the hypothesis that depth selection behavior and life history strategy are alternative antipredator strategies relevant for natural populations. To our knowledge, this is the first demonstration of such relationship for field populations. This finding agrees with within-population comparisons (Tessier and Leibold 1997; De Meester and Weider 1999) where the behavior inferred from field data and life history traits measured in the laboratory indicated that among genotypes sampled from the same population deeper residing ones are larger at maturity. Based on our results together with findings of other authors (De Meester et al. 1995; Tessier and Leibold 1997; De Meester and Weider 1999) we predict that negative association between these two major defense traits will be found if the investigated genotypes originate from habitats of similar predation pressure.

We did not find a correlation between residence depth and life history patterns within the populations. That such a relationship exists was suggested by several studies (De Meester 1994; Tessier and Leibold 1997; De Meester and Weider 1999). In our data set, the variation in size at first reproduction was much smaller among animals residing at different depths within a single population than variation among populations. Often, a great majority of animals was found in a single layer, and thus the variation in depth selection behavior was undetectable. For some of the lakes, the lack of a significant association might be due to smaller sample sizes available for within-population comparisons or the fact that the vertical sampling resolution was not sufficient. However, in some of the lakes, despite the good sample sizes and fairly even distribution of the animals throughout the water column, not even the trend in the expected direction was observed. Thus, the possibility of coexistence of different strategies appeared to be limited within a population but was readily maintained among populations. The factors that promote and limit the coexistence of the defense strategies certainly merit further investigation.

We could exclude with reasonable certainty the influence of several potentially important factors known to affect *Daphnia* distribution and life history. The food conditions in the study lakes were at least close to the incipient limiting concentration for *D. longispina* (Muck and Lampert 1980) and in most lakes surpassed this value. Thus, we did not expect to see strong effects of food concentrations either on *Daphnia* distribution or on life history, and our analyses confirmed this conjecture. Also temperature, which is known to affect *Daphnia* distribution (e.g., Marcogliese and Esch 1992), could not explain the variation we found not only because our study lakes were remarkably homogenous in terms of thermal stratification, but also because *Daphnia* seemingly “ignored” the thermocline. The effect of invertebrate predators was also not very likely, since the density

of the only predator species present, *C. flavicans*, was rather low. As in any comparative study, we could not account for all factors that might have potentially affected the traits we investigated. However, we think that it is highly unlikely that the association between life history and behavioral traits we have found arose spuriously. In fact, given the inherent variability of natural habitats, we find the strength of this association quite remarkable.

The mutual adjustment of behavioral and life history strategies raises the question whether any one strategy is more beneficial, and in what circumstances. This issue was addressed in two theoretical studies where Fiksen (1997) concluded that life history modifications should take precedence over behavioral defense while Vos et al. (2002) suggested that behavioral defense should be more effective. Our data highlight several points relevant to this topic. First, the choice between the strategies is not always feasible. In two lakes, Białe Krutyńskie and Dłużec, there was virtually no choice of residence depth. The life history with maturation at small size and high reproductive effort was the only viable one. Second, the partially anoxic and fully oxygenated lakes differ in how the two strategies are mutually adjusted. In the anoxic lakes the animals were found close to the boundary of the anoxic zone, a phenomenon that has been reported previously (e.g., Tessier and Leibold 1997). This implies that the behavioral defense was realized to the large extent, and suggests that life history strategy was adjusted to defensive behavior in concordance with the model developed by Vos et al. (2002). The situation appeared to be quite different in fully oxygenated lakes. Not only were some populations found well above the lake bottom, but many also resided even shallower than those from partially anoxic lakes. For example, *Daphnia* from lake Piłakno were found relatively shallow and accordingly started the reproduction at small size. This demonstrates that in some circumstances life history modifications could be preferred over behavioral defense as predicted by the model developed by Fiksen (1997). To summarize, we have found that either depth selection behavior or life history modifications can be a preferred defense strategy.

Here, we have described the association between behavioral and life history strategies without specifying whether the mutual adjustments happen through selection on a set of fixed (noninducible) strategies or via individual plasticity or induction. Our study cannot directly answer the question regarding which mechanism is responsible for the patterns we found. In principle, both are possible. Field (Gliwicz and Boavida 1996; Tessier and Leibold 1997) and laboratory studies (Leibold et al. 1994; De Meester 1996) have demonstrated that *Daphnia* populations are locally adapted in terms of behavioral and life history traits to the predation pressure in their habitats. However, both strategies are inducible and can be rapidly adjusted to chemically sensed predation pressure (Tollrian and Dodson 1999). The fact that the behavioral defense is not always feasible under natural conditions can make the inducibility of life history strategy particularly important.

## References

- BOERSMA, M. 1995. Competition in natural populations of *Daphnia*. *Oecologia* **103**: 309–318.

- BRODIE, E. D. 1989. Genetic correlations between morphology and antipredator behavior in natural populations of the garter snake *Thamnophis ordinoides*. *Nature* **342**: 542–543.
- BROOKS, J. L., AND S. I. DODSON. 1965. Predation, body size, and composition of plankton. *Science* **150**: 28–35.
- DAWIDOWICZ, P., AND C. J. LOOSE. 1992. Metabolic costs during predator-induced diel vertical migration of *Daphnia*. *Limnol. Oceanogr.* **37**: 1589–1595.
- DE MEESTER, L. 1994. Life histories and habitat selection in *Daphnia*: Divergent life histories of *D. magna* clones differing in phototactic behaviour. *Oecologia* **97**: 333–341.
- . 1996. Evolutionary potential and local genetic differentiation in a phenotypically plastic trait of a cyclical parthenogen, *Daphnia magna*. *Evolution* **50**: 1293–1298.
- , AND L. J. WEIDER. 1999. Depth selection behavior, fish kairomones, and the life histories of *Daphnia hyaline* × *galeata* hybrid clones. *Limnol. Oceanogr.* **44**: 1248–1258.
- , L. J. WEIDER, AND R. TOLLRIAN. 1995. Alternative antipredator defences and genetic polymorphism in a pelagic predator-prey system. *Nature* **378**: 483–485.
- DEWITT, T. J. 1998. Costs and limits of phenotypic plasticity: Tests with predator-induced morphology and life history in a freshwater snail. *J. Evol. Biol.* **11**: 465–480.
- DODSON, S. 1988. The ecological role of chemical stimuli for the zooplankton—predator-avoidance behavior in *Daphnia*. *Limnol. Oceanogr.* **33**: 1431–1439.
- EDMONDSON, W. T., AND A. H. LITT. 1982. *Daphnia* in Lake Washington. *Limnol. Oceanogr.* **27**: 272–293.
- FIKSEN, O. 1997. Allocation patterns and diel vertical migration: Modeling the optimal *Daphnia*. *Ecology* **78**: 1446–1456.
- GLIWICZ, M. Z. 1986. Predation and the evolution of vertical migration in zooplankton. *Nature* **320**: 746–748.
- . 1990. Food thresholds and body size in Cladocerans. *Nature* **343**: 638–640.
- , AND M. J. BOAVIDA. 1996. Clutch size and body size at first reproduction in *Daphnia pulicaria* at different levels of food and predation. *J. Plankton Res.* **18**: 863–880.
- , AND J. PIJANOWSKA. 1988. Effect of predation and resource depth distribution on vertical migration of zooplankton. *Bull. Mar. Sci.* **43**: 695–709.
- KERFOOT, W. C., AND A. SIH. 1987. Predation: Direct and indirect impacts on aquatic communities. New England Press.
- LAMPERT, W. 1989. The adaptive significance of diel vertical migration of zooplankton. *Funct. Ecol.* **3**: 21–27.
- , E. McCAULEY, AND B. F. J. MANLY. 2003. Trade-offs in the vertical distribution of zooplankton: Ideal free distribution with costs? *Proc. R. Soc. Lond. Ser. B Biol. Sci.* **270**: 765–773.
- LARSSON, P., AND S. DODSON. 1993. Chemical communication in planktonic animals. *Arch. Hydrobiol.* **129**: 129–155.
- LASS, S., M. BOERSMA, AND P. SPAAK. 2000. How do migrating daphnids cope with fish predation risk in the epilimnion under anoxic conditions in the hypolimnion? *J. Plankton Res.* **22**: 1411–1418.
- LEIBOLD, M., AND A. J. TESSIER. 1991. Contrasting patterns of body size for *Daphnia* species that segregate by habitat. *Oecologia* **86**: 342–348.
- , ———, AND C. T. WEST. 1994. Genetic, acclimatization, and ontogenic effects on habitat selection behavior in *Daphnia pulicaria*. *Evolution* **48**: 1324–1332.
- LEONARD, G. H., M. D. BERTNESS, AND P. O. YUND. 1999. Crab predation, waterborne cues, and inducible defenses in the blue mussel, *Mytilus edulis*. *Ecology* **80**: 1–14.
- LOOSE, C. J., AND P. DAWIDOWICZ. 1994. Trade-offs in diel vertical migration by zooplankton: The costs of predator avoidance. *Ecology* **75**: 2255–2263.
- MACHÁČEK, J. 1991. Indirect effect of planktivorous fish on the growth and reproduction of *Daphnia galeata*. *Hydrobiologia* **225**: 193–197.
- MARCOGLIESE, D. J., AND G. W. ESCH. 1992. Alterations of vertical distribution and migration of zooplankton in relation to temperature. *Am. Midl. Nat.* **128**: 139–155.
- MLONEK, A. 1998. Day- and night-time vertical distribution of planktonic crustaceans in several lakes in North-eastern Poland (in Polish). M.S. thesis, Univ. of Warsaw.
- MUCK, P., AND W. LAMPERT. 1980. Feeding of freshwater filter-feeders at very low food concentrations: Poor evidence for “threshold feeding” and “optimal foraging” in *Daphnia longispina* and *Eudiaptomus gracilis*. *J. Plankton Res.* **2**: 367–379.
- REZNICK, D. A., H. BRYGA, AND J. A. ENDLER. 1990. Experimentally induced life-history evolution in a natural population. *Nature* **346**: 357–359.
- RIESEN, H. P., AND W. G. SPRULES. 1990. Demographic costs of antipredator defenses in *Daphnia pulex*. *Ecology* **71**: 1536–1546.
- RINGELBERG, J. 1991. Enhancement of the phototactic reaction in *Daphnia hyalina* by a chemical mediated by juvenile perch (*Perca fluviatilis*). *J. Plankton Res.* **13**: 17–25.
- RUNDLE, S. D., AND C. BRÖNMARK. 2001. Inter- and intraspecific trait compensation of defence mechanisms in freshwater snails. *Proc. R. Soc. Lond. B Biol. Sci.* **268**: 1463–1468.
- SPARKES, T. C. 1996. The effects of size dependent predation risk on the interaction between behavioral and life history traits in a stream dwelling isopod. *Behav. Ecol. Sociobiol.* **39**: 411–417.
- ŠRÁMEK-HUŠEK, R., M. STRAŠKRABA, AND J. BRTEK. 1962. Fauna ČSSR 16. Lupenonožci—Branchiopoda [in Czech]. ČSAV.
- STIBOR, H. 1992. Predator induced life-history shifts in a freshwater cladoceran. *Oecologia* **92**: 162–165.
- , AND W. LAMPERT. 1993. Estimating the size at maturity in field populations of *Daphnia* (Cladocera). *Freshw. Biol.* **30**: 433–438.
- STICH, H. B., AND W. LAMPERT. 1981. Predator evasion as an explanation of diurnal vertical migration by zooplankton. *Nature* **293**: 396–398.
- STRAILE, D., AND A. HALBICH. 2000. Life history and multiple antipredator defenses of an invertebrate pelagic predator, *Bythotrephes longimanus*. *Ecology* **81**: 150–163.
- TESSIER, A. J., AND M. A. LEIBOLD. 1997. Habitat use and ecological specialization within lake *Daphnia* populations. *Oecologia* **109**: 561–570.
- TOLLRIAN, R., AND S. I. DODSON. 1999. Inducible defenses in Cladocera: Constraints, costs, and multipredator environments, p. 177–202. *In* R. Tollrian and C. D. Harvell [eds.], *The ecology and evolution of inducible defenses*. Princeton Univ. Press.
- , AND C. D. HARVELL. 1999. *The ecology and evolution of inducible defenses*. Princeton Univ. Press.
- VAN BUSKIRK, J. 2000. The costs of an inducible defense in anuran larvae. *Ecology* **81**: 2813–2821.
- VOS, M., B. J. G. FLIK, J. VIJVERBERG, J. RINGELBERG, AND W. M. MOOIJ. 2002. From inducible defences to population dynamics: Modelling refuge use and life history changes in *Daphnia*. *Oikos* **99**: 386–396.
- WRIGHT, D., AND J. SHAPIRO. 1990. Refuge availability—a key to understanding the summer disappearance of *Daphnia*. *Freshw. Biol.* **24**: 43–62.

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