

Predator-mediated genotypic shifts in a prey population: experimental evidence

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Abstract. We demonstrate the effect of fish predation on genotype frequencies in a laboratory population composed of two *Daphnia magna* clones, with historically contrasting exposures to fish predation. The two clones differed in their responsiveness to predation via differential avoidance/escape behavior. The clone which coexists with fish in nature is more responsive to the presence of a fish predator, while the clone not exposed to fish predation does not exhibit the defensive reaction. Fish caused a rapid (within 18 h) and significant shift in *Daphnia* clonal composition, from 1:1 to 8:1, in favor of the responsive clone. Genotype-specific defensive abilities (*modus defendi*) can contribute greatly to the phenomenon of genotype replacement under selective predation.

Key words: *Daphnia* – Vertical migration – Predator-induced behavior – Clonal replacement

As a major source of mortality in many natural populations (Elton 1927), predation can be a potent selective factor shaping avoidance and escape behavioral responses in prey populations (e.g., Sih 1987; Lima and Dill 1990). Differences among genotypes with respect to their responsiveness to predation can enhance differences in their short-term survival probabilities within a prey population. The effects of natural selection in the wild have been demonstrated for numerous traits among a wide variety of plants and animals (Endler 1986). Though predation has been invoked as a selective agent in causing evolutionary changes in many cases, direct selection for behavioral traits has only occasionally been reported in natural populations (but see Fawcett 1984; Dickman 1992).

In this study, we investigated the effect of predation on microevolutionary changes within a prey population, based on behavioral traits. We demonstrate the effect of fish predation on genotype frequencies in a laboratory population of the freshwater parthenogenetic cladoceran *Daphnia magna* Straus. We non-randomly selected two genetically distinct, but morphologically indistinguishable clones that differed in their past exposure to fish predation. One of them originates from a fishless shallow pond near Warsaw (Poland) and for the past 12 years has not been exposed to any predation in the laboratory (clone W). The second (clone B) originates from the Großer Binnensee (Schleswig-Holstein, Germany), a shallow brackish lake inhabited by fish. It has been recently reported that clones of another cladoceran, *Daphnia pulex*, isolated from ponds inhabited by invertebrate predators showed significantly greater morphological response to the presence of predators than clones from predator-free ponds (Parejko and Dodson 1991). It therefore seemed plausible that clone B, which shared its recent evolutionary history with predators, would be more efficient in terms of anti-predator behavioral defence and, as a consequence, would be exterminated at a slower rate. Various defensive behavioral responses to fish predation (e.g. vertical and horizontal distribution patterns, direct escape abilities) have recently been examined in these two clones (Pijanowska et al., unpubl. data), and the predicted differences in their behavior were indeed found.

Among a broad variety of defensive responses by planktonic animals, avoiding surface waters in daytime is recognized as an efficient mechanism that can reduce the risk of predation by visual predators, by using a spatial refuge in deep water during the day (for recent reviews see Lampert 1989, 1993). There is growing empirical evidence that this behavior can be induced by chemical compounds released into the environment by a potential predator, without accompanying selection/mortality (for review see Pijanowska 1993). The comparison of vertical distribution patterns between the two clones in a system of single, 1-m-long plexiglas tubes

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illuminated from above (Dawidowicz 1993), under standardized conditions in fish-free water and water containing fish exudates (Loose et al. 1992) revealed that these two clones differed remarkably in their behavioral reactions to the chemical presence of a predator (Pijanowska and Dawidowicz, unpubl. data). In fish water, *Daphnia* from clone B showed a clear tendency to stay deeper during the day, while *Daphnia* from clone W remained permanently at the surface: mean day depth of clone B animals (42.5 ± 8.9 cm; mean ± 1 SD), differed from the mean day depth of clone W (3.7 ± 1.2 cm) at $P < 0.0001$ (Mann-Whitney *U*-test). It was shown elsewhere (Dawidowicz and Loose 1993; Loose et al. 1992) that in the same experimental system *Daphnia magna* from the Binnensee can migrate even deeper, reaching the bottom of the tubes. Mean day depths in fish-free water were 3.8 ± 0.8 cm and 2.2 ± 0.5 cm for clones B and W, respectively, and did not differ significantly (Pijanowska and Dawidowicz, unpubl. data). Though these clones do not coexist in the wild, they offer a suitable target for short-term selection by a fish predator since they express two distinct clone-specific behaviors.

Methods

Six cylindrical plastic containers (75 cm high, 50 cm upper diameter, 150 l capacity) were filled with lake water filtered through a 10- μ m filter. Water temperature was $18.1 \pm 0.2^\circ$ C (mean ± 1 SD), and light at the surface ranged from 0.16 to 0.18 μ E $m^{-2} s^{-1}$. A plastic mesh-screen (4 mm mesh size) was installed at mid-depth in each container; *Daphnia* could easily swim through the screen. By restricting the movement of fish to the upper layer, we created a bottom refuge for those *Daphnia* that could avoid predation at the surface by downward migration. In three of the six containers, three fish (sunbleaks, *Leucaspis delineatus* L., of 6.5 ± 0.9 cm mean total length) per container were allowed to swim freely for 48 h. They were transferred daily for about 1 h to glass aquaria, and fed with approximately 100 *Daphnia* per fish. After 48 h, fish were removed and 600 *Daphnia* (1:1 mixture of clones B and W, mean individual size at the beginning of the experiment 1.32 ± 0.22 mm and 1.31 ± 0.21 mm, mean ± 1 SD, respectively) were introduced to each of the six containers, and for the next 48 h, they were allowed to distribute in the water column. *Daphnia* were fed with a suspension of the green alga *Scenedesmus acutus* at a concentration of 1 mg C l^{-1} , adjusted daily in each of the six containers. After 48 h, a single fish was introduced to each of those three containers which had previously held fish; they were allowed to feed for 18 h (6L:6D:6L). The three control populations were exposed neither to the fish cue nor to predatory pressure, to compare *Daphnia* distributions with and without fish and to provide an estimate of background mortality not caused by predation.

All survivors (at the end of the experiment, mean *Daphnia* size was 1.56 ± 0.02 mm in clone B, and 1.47 ± 0.07 mm in clone W, means ± 1 SD) in each of the six containers were harvested from above the screen and then counted. After removing the screen, the remaining animals were harvested from below. Final clonal frequencies were obtained using cellulose acetate gel electrophoresis (Hebert and Beaton 1989). The glutamate-oxaloacetate transferase (GOT, EC.2.6.1.1) locus served as a diagnostic marker. All survivors in the fish containers and 96 animals per control container from above and from below the screen were assayed separately.

In addition to the spatial distribution patterns, we examined the direct escape capability of *Daphnia* from both clones assuming that a predator would less frequently attack the more evasive prey. *Daphnia* of each clone (mean size of animals was 1.33 ± 0.02 mm in clone B, and 1.42 ± 0.16 for clone W) were exposed for 24 h to water

that for the previous 24 h had contained two fish per 10 l, fed with 100 *Daphnia* each. *Daphnia* were fed with a *Scenedesmus acutus* suspension, at a concentration of 1 mg C l^{-1} . One hundred individuals of each clone were offered to a single fish (sunbleak, 6.0–7.0 cm total length) in a 4.5-l glass jar (three replicates per clone). To minimize the inter-individual variation in feeding behavior, all six fish were starved for 24 h and then, before the experiment, fed with 100 *Daphnia* each. The number of successful attacks was noted during the first 10 min of feeding trials, starting with the first successful attack. The number of survivors was counted after 30 min.

Results and discussion

Fish-mediated mortality ranged from 56.2 to 83.7% ($72.4 \pm 14.3\%$ on average, mean ± 1 SD). Regardless of the strength of predatory impact, the relative survival rate of clone B was up to 8 times more than that of clone W (Fig. 1). Fish caused a rapid (within 18 h) and significant shift in *Daphnia* clonal composition. Thus, the final clonal proportion (8B:1W) differed significantly from initial proportion (1B:1W) at $P < 0.001$, (χ^2 goodness of fit).

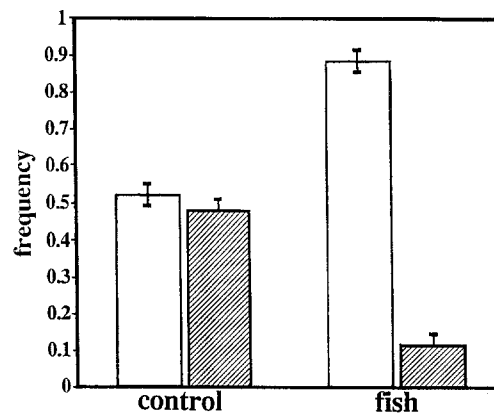


Fig. 1. The effect of 18 h fish predation on the proportions of two *Daphnia* clones offered in the same initial numbers at the start of the experiment (means $\pm 95\%$ CI). Open bars: *Daphnia* clone B from a lake with fish (Binnensee); shaded bars: *Daphnia* clone W, which had not been exposed to predation for at least 12 years

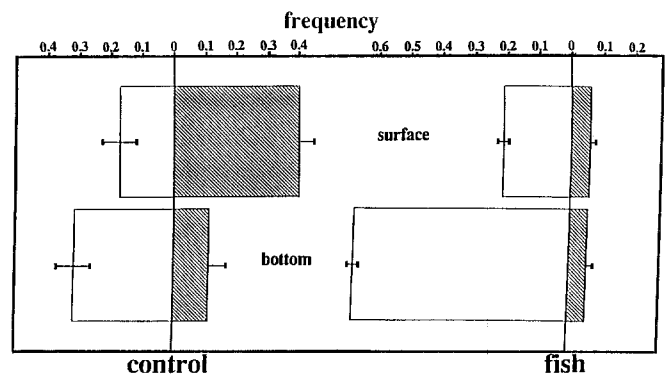


Fig. 2. Final vertical distributions of two *Daphnia* clones after 18 h of fish feeding, shown as surface (above the screen) and bottom (below the screen) fractions of total *Daphnia* densities in the control and fish treatments (means $\pm 95\%$ CI). Open bars: clone B; shaded bars: clone W

Clone-specific behavior must have affected predator choice [average value of Manly's α preference index (Manly 1974) for clone B, $\alpha_B = 0.284 \pm 0.116$, differed from $\alpha_W = 0.718 \pm 0.114$ at $P < 0.0098$, two-sample t -test].

The greater survivorship of *Daphnia* from clone B can be ascribed to their strong tendency to remain deeper (below the screen) in the water column (Fig. 2), which was enhanced in the presence of fish.

Experimentally tested short-term survivorship also differed significantly between the two clones ($14 \pm 5\%$ survivors after 30 min of fish feeding in clone B compared to $5 \pm 1\%$ in clone W, means ± 1 SD, $P < 0.05$, two-sample t -test, after correction for unequal variances). *Daphnia* from clone B showed significantly greater evasiveness when exposed to fish than animals from the same size range from clone W (mean ± 1 SD number of successful attacks within the first 10 min of fish feeding trials was 22 ± 4 for clone B, which differed from 47 ± 7 for clone W at $P < 0.01$, two-sample t -test). When a predator is foraging on clone B animals, it takes it more than twice as long to successfully complete an attack sequence. Thus both, vertical distribution patterns and direct escape capability can confer resistance to fish predators and promote greater survivorship of clone B animals.

The inter-clonal differences in responsiveness to predation via differential avoidance/escape behavior are most probably related to the clones' contrasting experience of predation in the wild; i.e., *Daphnia* from clone B which coexist with fish in nature are more responsive to the presence of fish than animals from clone W. Gliwicz (1986) suggested that there should be a high probability of extinction of non-responsive genotypes when they are exposed to a predator. In the absence of simultaneous disruptive selection on other characters, natural selection will then result in the reduction of genetic variance within populations (Endler 1986; Spitze 1991). However, the outcome of selection can be reversed within a few generations when high metabolic costs are associated with predator avoidance. In our study, we measured one important fitness component, i.e., "viability fitness". The energetic costs of defense can strongly influence the second constituent of individual fitness, "reproductive fitness" (Janzen 1981). In the wild, where the coexistence of responsive and non-responsive ethotypes/genotypes has been shown to occur in *Daphnia* populations (Weider 1984, 1985; de Meester 1990), genotype-specific defensive abilities (*modus defendi*) and genotype-specific costs of defence can contribute greatly to the phenomenon of genotype replacement under selective predation. The maintenance of genetic variation in prey populations may be to a large extent attributed to differential viability and reproductive fitness of different ethotypes under changing predation regimes. An obvious next step to further understanding of the phenomenon of genotypic replacement under selective predation would be to study the effect of predatory pressure on a mixture of behaviorally distinct genotypes isolated from the same

population, and estimate inter-genotype differences in fitness components.

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