

Depth selection behavior, fish kairomones, and the life histories of *Daphnia hyalina* × *galeata* hybrid clones

Luc De Meester

Max-Planck-Institut für Limnologie, Postfach 165, 24302 Plön, Germany; Laboratory of Aquatic Ecology, Katholieke Universiteit Leuven, De Beriotstraat 32, 3000 Leuven, Belgium

Lawrence J. Weider¹

Max-Planck-Institut für Limnologie, Postfach 165, 24302 Plön, Germany

Abstract

We studied life-history characteristics of 22 genetically distinct *Daphnia hyalina* × *galeata* clonal lineages isolated from samples taken at different depths in the Schöhsee Lake (Germany) in the presence and absence of fish kairomones. Substantial genetic variability was observed for all traits investigated. The presence of fish kairomones had a significant effect on all traits except relative length of the tail spine and age at maturity. All genotypes (clones) had a significantly smaller size at maturity and produced smaller offspring in the presence of fish kairomones, an observation that is consistent with the hypothesis of an adaptive response. Overall, reproductive output was less for fish-induced animals, but the effect was relatively small for the size of the first clutch and for the intrinsic rate of increase compared to the differences observed for size of the second and subsequent clutches. Adult body size was related to habitat selection behavior. Clones established from animals that were caught in the epilimnion during the day and early in the evening (termed “risk-tolerant” [RT] depth selection behavior) were found to be smaller, both in the absence and presence of fish kairomones, than clones isolated from the hypolimnion (termed “risk-averse” [RA] depth selection behavior). This relationship suggests a coadaptation between size-related life-history traits and habitat selection (depth selection) in zooplankton. There were no significant differences in the shifts in life-history characteristics between clones exhibiting RT and RA depth selection behavior in response to the presence of fish kairomones.

Habitat selection has been identified as a potentially important force in maintaining genetic variation in natural populations (Jaenike and Grimaldi 1983; Rausher 1984; Hedrick 1986; Jaenike and Holt 1991). Zooplankton, particularly the cladoceran microcrustacean, *Daphnia*, have proven to be very useful model organisms in the study of the relationship between habitat selection and ecologically important traits. A number of studies have reported inter- or intrapopulational genetic variation in a multitude of ecologically relevant traits in *Daphnia* (reviewed by Carvalho 1994; De Meester 1996b). Several recent studies have provided important contributions to our knowledge of genetic variation in life-history traits in zooplankton (e.g., Ebert et al. 1993a,b; Spaak and Hoekstra 1995). Furthermore, habitat selection in zooplankton can be realized along temporal (King 1972, 1980)

and spatial (diel vertical migration: De Meester 1994b; Leibold et al. 1994; De Meester et al. 1995; Geedey et al. 1996) axes. Both Pace et al. (1984) and Carvalho (1987) found evidence for temporal habitat selection in natural *Daphnia* populations, with clones isolated in different seasons differing in life-history characteristics such that summer clones have their highest relative fitness at higher temperatures than winter clones and vice versa. Carvalho and Crisp (1987) observed that “generalist” clones (i.e., those remaining relatively common throughout the year) coexisted with “seasonal” clones (i.e., those showing clear-cut seasonal density peaks) and “opportunistic” clones (i.e., those having a more erratic occurrence).

In addition to temporal habitat selection, spatial habitat selection, especially vertically, is also important in zooplankton. Genotypes may differ in daytime depth preference, as has been shown by field studies using electrophoretic markers (e.g., Weider 1984, 1985; Müller and Seitz 1993), by in situ enclosure experiments (Leibold et al. 1994), and by the observation of heritable variation in phototactic behavior in *Daphnia* (De Meester 1991, 1993a, 1996a), which has been shown to be closely related to day depth in outdoor containers (De Meester 1993b). De Meester (1994a) suggested that there might be a coadaptation between day-depth selection and life-history traits in *Daphnia*, with smaller animals remaining in shallower water during the day, when compared with larger animals (see also De Meester 1995; De Meester et al. 1995; Reede and Ringelberg 1995, 1998).

Diel vertical migration (DVM) of zooplankton is generally believed to be a visual predator avoidance behavior (Lampert

¹ Present address: The University of Oklahoma Biological Station, HC 71, Box 205, Kingston, Oklahoma 73439.

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1993). All else being equal, smaller zooplankton individuals are less vulnerable to visual predators when compared to larger individuals. This implies that smaller individuals can remain higher in the water column during the day and still not have a higher risk of being preyed upon. However, large-bodied *Daphnia* are able to grow and reproduce at lower food concentrations than small-bodied ones (Gliwicz 1990) and are therefore better adapted to remain in marginal habitats (i.e., at greater depths, which are often characterized by poor food quality and quantity) during a significant part of the day. The observation that small zooplankters often remain higher in the water column during the day than large ones is evident from interspecific comparisons (Hutchinson 1967; Pijanowska and Dawidowicz 1987; Hays et al. 1994), as well as from intraspecific studies of ontogenetic stages (Huntley and Brooks 1982; Johnsen and Jakobsen 1987). Recently, evidence has shown that this pattern may also hold for different-sized genotypes of the same species. Leibold and Tessier (1991) observed that body size of *Daphnia pulicaria* clones isolated from populations that remained in the hypolimnion during the day tended to be larger when raised in a common environment than clones isolated from migrating populations. Further, De Meester (1994a) compared the life-history characteristics of nine *Daphnia magna* clones, which exhibited different phototactic behaviors, and observed that clones with different DVM behaviors differ in their life histories. Positively phototactic animals, which remain in near-surface waters during the day, achieve a high intrinsic rate of increase (r) at a small adult body size through rapid development, at a cost of producing smaller neonates. Intermediately phototactic animals, which reside in deeper water during the day, achieve a similarly high intrinsic rate of increase but through the production of larger clutches. They mature at a larger body size and produce larger neonates that are more starvation resistant than positively phototactic animals. Reede and Ringelberg (1995) compared life-history features of two *D. hyalina* × *galeata* clones (one migrating and one nonmigrating) isolated from Lake Maarsveen (The Netherlands) and reported differences in adult body size and offspring size similar to those reported by De Meester (1994a) for positively and intermediately phototactic clones of *D. magna*. Although the patterns reported by these studies are concordant with expectations, the study by De Meester (1994a) involved laboratory stocks derived from different populations, whereas Reede and Ringelberg (1995) studied only one clone for each type of depth selection behavior, which implies that their results offer only circumstantial evidence of a relationship between genetic variation in life-history traits and depth selection behavior in natural populations. Recently, Reede and Ringelberg (1998) confirmed their previous observations in a study involving six migrating and six nonmigrating *D. hyalina* × *galeata* clones isolated from Lake Maarsveen, thereby adding to the data supporting the hypothesis of a link between diel vertical migration behavior and life-history variation in *Daphnia*.

In the present paper, we present evidence for genotype-dependent depth selection behavior in the *D. hyalina* × *galeata* hybrid population of a small glacial lake in northern Germany (Schöhsee) and report on the life-history charac-

teristics of 22 genetically distinct clonal lineages isolated from this population. We compare and contrast the life histories of lineages that were derived from females isolated from a depth at which predation pressure by fish is expected to be high (e.g., epilimnion), with those of lineages isolated from deeper water layers. A previous field study by Guisande et al. (1991) on the same population indicated that smaller adults remain in the epilimnion during the day. Although this is in agreement with the hypothesis formulated by De Meester (1994a), the study by Guisande et al. (1991) did not differentiate between genetic and environmentally induced variation in body and clutch sizes between epilimnetic and hypolimnetic animals. The goals of the present paper were (1) to determine whether this population, which shows a very clear-cut DVM pattern during summer, harbors genetic variation for depth selection behavior and DVM, (2) to determine whether there is intrapopulation genetic variation in life-history characteristics of the *D. hyalina* × *galeata* hybrid population of the Schöhsee, (3) to test the hypothesis that this genetic variation is linked with depth selection (DVM) behavior, (4) to verify whether there is genetic variation in the response to fish kairomones with respect to life-history traits in this population, (5) to check whether the relationship between life-history characteristics and depth distribution also holds for animals that have been induced by fish kairomones, and (6) to investigate whether clones with RT depth distributions have a tendency to respond differentially to fish kairomones when compared with clones that exhibit RA depth selection behavior. We will explain these terms below.

Materials and methods

Study site and sampling—The Schöhsee is a small (approximately 0.8 km wide × 1.5 km long) mesotrophic glacial lake located in Plön, Germany. The vertical distribution of the *D. hyalina* × *galeata* hybrid population inhabiting this lake, as well as its associated size distribution, has been previously studied by Guisande et al. (1991). On 5–6 July 1994, we carried out three independent sampling series in which 31-liter Schindler–Patalas trap samples were taken at 5-, 15-, and 21-m depths both during the day (1200 h) and at night (2400 h). One sample series (two replicate samples taken at each depth) was fixed with 4% formaldehyde to determine the population densities in the different depth strata. From each of these samples, adult and juvenile daphnids were counted, and the body lengths (millimeters) of 20 adults (if present) were measured from each depth. The animals from a second sampling series were frozen at -80°C for later electrophoretic analysis, and a third set of samples was taken to establish clonal cultures. These live samples were taken from 5, 15, and 21 m during the day but only from the 21-m depth at night. There were very few adults residing in the epilimnion (0–10 m) during the day, so additional samples were taken with a plankton net (255- μm mesh) to ensure that we had enough adults to establish cultures in the laboratory and to determine the genetic structure using allozyme electrophoresis. In addition, live animals were collected around 2300 h at a depth of 5 m. Between

2210 h (around sunset) and 2330 h, we took a 31-liter sample from the 5-m depth every 10 min and monitored in this way the upward migration of adult *Daphnia*. At 2210 h, there were hardly any adults in the near-surface sample. By 2300 h, there was a substantial increase in the number of adults at 5 m, though the number was still relatively low. At 2330 h, a large portion of the *Daphnia* population had migrated to the epilimnion. We isolated adult females from the 5-m depth sample taken at 2300 h and considered them to be "early migrators." Similar to animals residing in the epilimnion during the day, animals migrating to the epilimnion early in the evening have, at least with respect to visual predators, a more risky behavior (RT) than animals that migrate to the epilimnion later at night or remain in the hypolimnion (RA).

Electrophoretic analysis—A total of 429 adult females were analyzed for allelic variation at five enzyme loci (PGI, AO, PGM, MDH, and sAAT) using cellulose acetate electrophoresis (see Hebert and Beaton 1989 for a description of each of the enzymes). Sample sizes varied from 79 to 98 individuals per depth, except for the epilimnetic sample taken during the day (plankton net towed through upper 9 m of the lake, $n = 36$) and the sample taken at 21-m depth during the night ($n = 45$). Protocols for electrophoresis were as described by Hebert and Beaton (1989), except that samples for MDH and sAAT were run on a 0.05-M Tris-maleate buffer (pH 7.8; Richardson et al. 1986), which improved resolution. The sAAT locus is diagnostic for differentiating between *D. hyalina* × *galeata* hybrids and the parental species in northern Germany (Wolf and Mort 1986; Schwenk and Spaak 1995). The remaining four loci were used to differentiate between multilocus allozyme genotypes (MLAGs). MLAGs should be considered clonal groups, because they harbor additional genetic variation (see also further). We used the MLAGs as markers to detect genetic differences in depth selection behavior and DVM patterns. We tested for heterogeneity in allele frequencies among samples taken from different depths using the contingency chi-square analysis of BIOSYS-1 (Swofford and Selander 1981). The null hypothesis is that there are no differences in vertical distribution and MLAGs.

Clonal lineages—Eleven to thirteen clonal lineages were established from each of the day samples taken at 5-, 15-, and 21-m depths and from the night sample taken at 21-m depth. An additional five lineages were established from the early-night sample (2300 h) taken at 5-m depth (Table 1). These clonal lineages were assayed for their MLAGs at PGI, AO, PGM, MDH, and sAAT using cellulose acetate electrophoresis. Given that the *D. hyalina* × *galeata* population of the Schöhsee was characterized by a few abundant MLAGs and a large number of rarer ones (see further), some MLAGs were represented among the clonal lineages established from several samples (Table 1). A total of 12 MLAGs were represented in the 54 clonal lineages (clones) established in the laboratory. Twenty-two clones representing the 12 MLAGs were chosen for further analysis, with the more abundant MLAGs being represented by multiple lineages isolated from different depths (Table 1). Our intent was to maximize

Table 1. Clonal lineages (clones) used in the life-table experiment. Number of lineages and MLAGs in the live samples taken at different depths in the Schöhsee, 5 July 1994, based on a total of 54 isolated lineages. Lineage: number of lineages isolated from the sample (in parentheses: number of different lineages used in the experiment); MLAGs—represented among the lineages, as revealed by cellulose acetate electrophoresis at four loci: AO, MDH, PGI, and PGM (in parentheses: number of different MLAGs represented in the experiment).

Sample	Sample label	Lineage (exp.)	MLAGs (exp.)
Day, 5 m	D5*	11 (5)	3 (3)
Day, 15 m	D15	13 (3)	5 (2)
Day 21 m	D21	13 (3)	4 (1)
Evening (2300 h), 5 m	E5*	5 (4)	4 (2)
Night (2400 h), 21 m	N21	12 (7)	8 (4)
Total		54 (22)	12 (12)

* Lineages isolated from D5 and E5 samples are considered to be representative of clones with RT depth selection behavior.

the number of genetically distinct clones in our analysis to examine the full range of potential depth selection behaviors. By using the allozyme markers to distinguish among these clonal lineages, we ensured that we would not end up with an experiment that essentially involved only one (generalist) clone. In hindsight, this approach appeared to be unnecessary. Twenty of the 22 clones were a posteriori screened for variation at two random amplified polymorphic DNA (RAPD) loci (OPB-04 and OPB-15, Operon Technologies; unfortunately, 2 of the 22 clones had gone extinct in our culture collection before they could be analyzed). All 20 clones, including those showing identical MLAGs, were genetically distinct for the RAPD markers. Quite surprisingly, there was no significant (or only marginally significant) association between allozyme-based and RAPD-based genetic similarities among lineages (Mantel test: $z = 0.17514$, $t = 1.577$, $P = 0.074$; see also Fig. 1). These results have a number of important implications. First, they clearly indicate that MLAGs on our four allozyme markers harbor additional genetic variation (i.e., they represent a large number of distinct clones) and therefore, really represent clonal groups. Second, the lack of a significant association between allozyme and RAPD markers and the high genetic diversity within MLAGs also indicate that our choice of lineages was essentially random. Therefore, we can treat our samples from the different depths as being random samples of genetically distinct lineages. In the remainder of this paper, we will use the terms "clone," "genotype," "clonal lineage," and "lineage" synonymously.

A distinction was made between clones with RT and RA depth selection behavior. Clones were categorized as RT if they were isolated from samples taken from the epilimnion during the day or relatively early in the evening (2300 h). Considering the importance of visual predation as an ultimate cause of DVM in zooplankton (Lampert 1993), whether or not an individual ventures into the epilimnion during the day or early in the evening (early migrators) will greatly influence its survival probability. By remaining in the epilimnion during the day or migrating into the epilimnion early

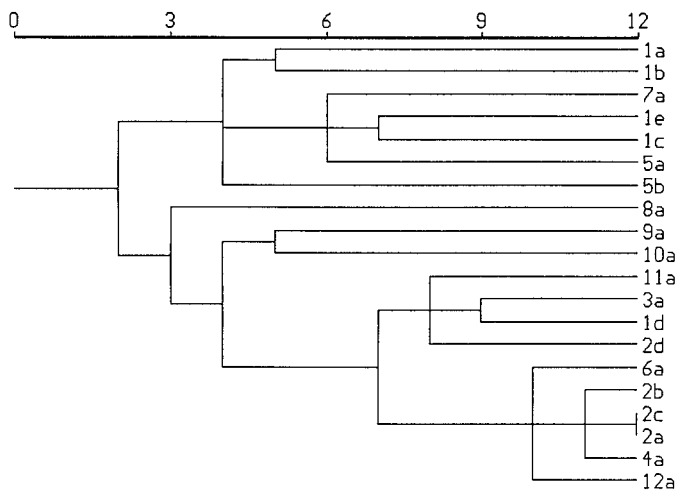


Fig. 1. Tree showing the genetic similarity among MLAGs detected by allozyme electrophoresis. Numbers refer to MLAGs; characters refer to different lineages of the same MLAG as detected by allozymes. The tree was constructed using the cladistic mode of the TREE subroutine in NTSYS (Rohlf 1990). Presence and absence of specific RAPD bands for primers OPB-04 and OPB-15 were coded as binary (0, 1) characters, and a simple matching coefficient (SIMQUAL subroutine) was calculated for each pair of MLAGs. The data were standardized using the DCENTER subroutine and were imported into the NJOIN (neighbor-joining) subroutine of NTSYS using midpoint rooting. Only one tree was detected.

in the evening, an individual is able to exploit better conditions but at a higher predation risk. Therefore, we reasoned that only clones with certain characteristics (e.g., small body size) could exploit this option successfully. In our analysis of the effect of habitat selection on life-history characteristics, we therefore compared the overall means of all clones that were found in the samples taken at 5 m during the day or early in the evening (i.e., RT behavior) with those of all clones that were exclusively found in the hypolimnion (15–21 m, day or night; RA behavior). Based on this dichotomy, 9 and 13 of the 22 clones studied were classified as RT and RA clones, respectively.

Our differentiation between RT and RA clones is based on the presence of these clones in an albeit limited set of samples taken from different water depths. The fact that we did not assess the differences in behavior of all clones used in the present experiments with independent experiments may weaken our claim that we are dealing with a true habitat selection behavior. However, the data of De Meester et al. (1995) show that at least three clones (1, 6, and 20) used in the present study show differences in habitat selection behavior that are in accordance with our distinction between RT and RA behavior. Clone 20, the largest of the three, resided deeper in the water column during mesocosm experiments, both in the absence and presence of fish kairomones and in the presence of fish (De Meester et al. 1995).

Life-table experiment—Animals were cultured individually in 100-ml jars, filled with 0.45-mm filtered Schöhsee water. Culture conditions mimicked summer conditions in the epilimnion, i.e., long-day photoperiod (14:10 light:

dark), high food concentration (chemostatically cultured *Scenedesmus acutus*; adjusted daily to a concentration of 1 mg C liter⁻¹), and high temperature (20°C). Medium and food were refreshed daily. There were two treatments: absence and presence of fish kairomones. In the fish-kairomone treatment, Schöhsee water was conditioned by the presence of fish (*Leuciscus idus*, two fish approximately 5 cm long in a 40-liter aquarium) for 24 h, after which the medium was filtered through a 0.45-mm filter. In the treatment without fish kairomones, lake water was also aged for 24 h but was not conditioned by the presence of fish.

For the life-table experiment (Table 1), we had four replicates for each of the 22 clones. The experiment started with the inoculation of second clutch neonates <12 h old. Their mothers had been cultured for one generation on treatment conditions. All individuals had been cultured independently for at least two generations. The great-grandmother generation was started by isolating young adults as individuals under standard conditions (high food, high temperature, and absence of fish kairomone). Two randomly chosen offspring from the second clutch of each of these animals were inoculated as replicate grandmaternal lines and cultured under standard conditions. One offspring from the second clutch of these grandmothers was inoculated at the start of the maternal generation, with one of the two replicate grandmaternal lines per clone being randomly assigned to the fish-kairomone treatment. All lines were therefore cultured for one (grand maternal) generation under standard conditions (absence of fish kairomones) and, subsequently, for one (maternal) generation under treatment conditions (absence or presence of fish kairomone) before the start of the experiment.

The animals in the life-table experiment were monitored every 12 h until the release of the third clutch. Body size was measured for every adult instar (SIZE(1)–(4)), from the top of the eye to the base of the tail spine. The body size of the neonates was determined by averaging the size of four randomly chosen neonates from each individual for each of the three clutches (SIZENEO(1)–(3)). Length of the tail spine was measured in animals carrying their first clutch. To correct for differences in body size, the relative length of the tail spine (RELTAIL(1)) was calculated as the length of the tail spine (in millimeters) divided by the size at maturity (in millimeters). Age at maturity (AGE(1)) and age at release of the first, second, and third clutches (AGE(2)–(4)) were determined to the nearest 12 h. Clutch size was determined for the first four clutches (BR(1)–(4)). The number of offspring in the first three clutches was determined by the number of neonates produced; size of the fourth clutch was determined by counting the number of eggs in the brood pouch (dissected when necessary to obtain a precise count). The difference between both approaches lies in the number of degenerating eggs not being taken into account when the number of eggs in the brood pouch rather than the number of neonates produced is counted (Threlkeld 1987). In our experiment, however, this difference was expected to be small because of the high food concentration. Total number of offspring was calculated by summing the clutch sizes of all four broods. From developmental times and clutch sizes (survival was 100%), the intrinsic rate of increase (r) was

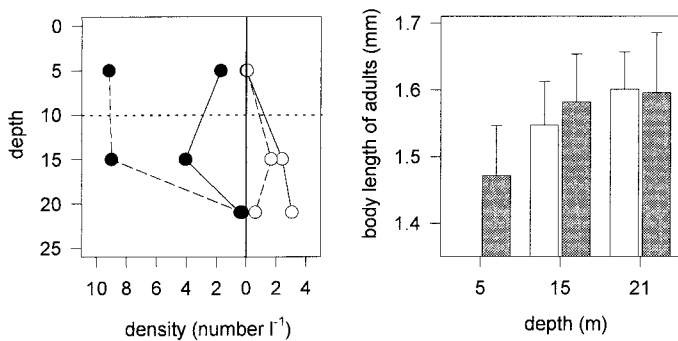


Fig. 2. Left panel: vertical distribution of adults (solid line) and juveniles (hatched line) during the night (solid symbols, left side) and during the day (empty symbols, right side) as revealed by two replicate 31-liter samples taken at 5-, 15-, and 21-m depths. The dotted line indicates the thermocline situated at 9–10 m. Right panel: average ± 2 SE of the body length (top of the eye to base of the tail spine, in millimeters) of adult *Daphnia* caught at different depths during the day (empty bars; no adults found at 5 m) and during the night (shaded bars).

estimated by solving iteratively the Euler–Lotka equation (Stearns 1992).

The effects of fish treatment and clone were tested by two-way analyses of variance (ANOVAs), with both clone and fish conditioning as fixed factors. Clone is considered a fixed factor because we selected particular depths and times to take our samples. The traits analyzed as dependent variables were size at maturity ((SIZE(1)), size of the neonates of the first clutch (SIZENEO(1)), relative length of the tail spine at maturity (RELTAIL), age at maturity (AGEMAT), size of the first clutch (BR(1)), total number of neonates (eggs) produced in four broods (TOTBR), and the intrinsic rate of natural increase (r).

To check whether RT and RA clones differed in life-history characteristics, we carried out a two-way ANOVA using clonal means as input data and testing for the effect of behavior and the presence of fish kairomones. A significant effect of behavior would indicate that these two groups of clones differ in life-history characteristics, whereas a significant behavior by treatment interaction would indicate that RT clones exhibit a response to the presence of fish kairomones different from that of RA clones.

Results

Vertical distribution and genetic structure—Figure 2 shows the vertical distribution of juvenile and adult *Daphnia* during the day and night, as well as the average body length of adults in the different samples. There is a tendency for adults to be larger at greater depth, but the differences are not statistically significant (one-way ANOVA, $P = 0.108$). During the day, the population density of *Daphnia* in the epilimnion (5-m depth) was so low that only one juvenile and no adults were found in the samples (total of 62 liters). At night, almost all animals were found in the upper 15 m.

Using variation at sAAT as a diagnostic trait, most of the *Daphnia* of the Schöhsee were found to be *D. hyalina* \times *galeata* hybrids. Eight out of 429 adults (1.86%) belonged

to *D. galeata*. No *D. hyalina* spp. were found in our samples, but an analysis of 994 adults collected on different sampling days during July 1994 yielded one adult of *D. hyalina* (0.1%; De Meester and Weider unpubl. data), suggesting that both parental species cooccur at very low frequencies with their hybrid in this lake. Within the population of hybrids (421 individuals analyzed from the sampling series of 6 July 1994), a total of 35 MLAGs could be detected (based on electrophoretic variation at PGI, PGM, AO, and MDH). The population was characterized by a few abundant and many rare MLAGs. Approximately 48.3% of the animals sampled belonged to MLAG A, and only two other MLAGs were relatively abundant: 5.4% of the animals belonged to MLAG B, and 9.6% belonged to MLAG C. Most of the other MLAGs, however, represented $<2\%$ of the population.

There were highly significant differences in allele frequencies among samples taken at different depths both during the day ($P < 0.0001$ for all loci except MDH) and at night ($P < 0.0001$ for all loci except MDH). Figure 3 plots the vertical day- and nighttime distributions of the three most abundant MLAGs found in the lake. At night, MLAG A tends to be higher in the water column than MLAG B and C, whereas during the day, both the relative abundance at the two hypolimnetic depths and the relative abundance in the epilimnetic sample (of unknown volume) differ among MLAGs.

Life-history characteristics—The results of the life-table experiment are plotted in Figs. 4, 5. Results of the two-way ANOVAs (Table 2) indicate a highly significant overall effect of clone and fish conditioning on all life-history characteristics examined for the *D. hyalina* \times *galeata* population in the Schöhsee, except for age at maturity and relative length of the tail spine (no significant effect of fish kairomone). There is a significant clone \times treatment interaction effect for all traits studied, except for relative length of the tail spine. The highly significant effect of clone indicates that there is genetic variation present in the population for all traits studied. A comparison of RT and RA clones indicates that the two groups of clones differ significantly in the mean value of size at maturity (Table 3). Figures 4 and 5 indeed show that RT clones tend to mature at a smaller size than RA clones. None of the four lineages with an adult body size of >1.45 mm in the absence of fish kairomones was found in the epilimnion during the day or among the early migrators. In the presence of fish kairomones, the difference in body size between RT and RA clones remained. There is no difference in the size of the first clutch between the two groups of clones (Fig. 5), and there is a tendency for RT clones to have smaller total clutch sizes than RA clones when raised in the presence of fish kairomones (Fig. 5), but this difference is not statistically significant. We did not detect a significant behavior \times treatment interaction for any of the traits observed (Table 3), thus indicating that there are no significant differences between the two groups of clones in their response to the presence of fish chemicals.

Fish conditioning had a highly significant effect on all traits studied, except for the relative tail-spine length and age at maturity (Table 2). The presence of fish chemicals resulted in a smaller size at maturity in all clones studied,

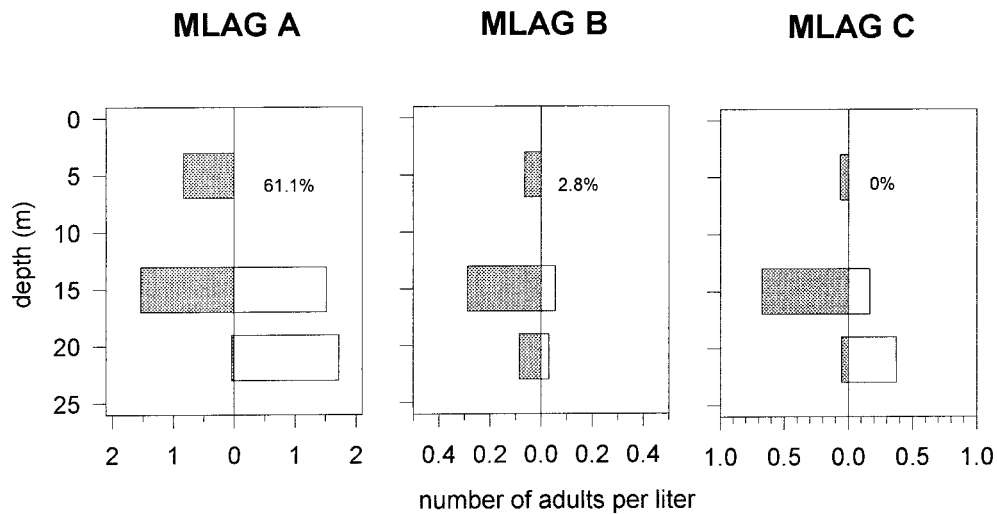


Fig. 3. The vertical distribution of the three most abundant *D. hyalina* × *galeata* MLAGs (MLAG A: 48.3% of the population; MLAG B: 5.36%; and MLAG C: 9.6%) observed in the Schöhsee on 6 July 1994. Shaded: night; open: day. The vertical distributions were reconstructed from the relative frequencies of MLAGs in samples taken from different depths (total sample size = 421 adult females) and data on the abundance of adult *D. hyalina* × *galeata* at those depths (see Fig. 1). In the epilimnion during the day, the population density of *Daphnia* was so low that it could not be determined from samples with a 31-liter Schindler–Patalas. For this sample, the relative abundance (percent of total sample) of each of the three MLAGs is indicated on the graph.

and most clones produced smaller and fewer offspring, resulting in a lower intrinsic rate of increase (Fig. 4). The average difference between the size of the first clutch of animals cultured in the presence and absence of fish was approximately one offspring.

Most clones exhibited an average r between 0.28 and 0.32. In the presence of fish kairomones, some small-bodied clones had a lower value (0.24–0.26), whereas some intermediate-sized clones showed, on average, relatively high values for r (0.33–0.35). Because differences in developmental time are relatively small, except for some of the small-bodied clones in the presence of fish, differences in r largely reflect differences in fecundity (Fig. 5).

Discussion

The results shown in Fig. 2 are in good agreement with the observations by Guisande et al. (1991). The *Daphnia* population of the Schöhsee exhibits a clear-cut DVM, and there is a tendency for animals caught at greater depths to be larger than animals caught in the epilimnion. Because of the large variation in body length within samples and the relatively low number of animals measured, this pattern was not significant in our study. Even though no adults were caught in epilimnetic samples during the day by routine sampling, we were able to collect adults from the epilimnion by screening larger volumes of water with a plankton net.

Even though almost 50% of the *Daphnia* population of the Schöhsee belongs to the same MLAG (as revealed by allozyme electrophoresis at four loci), the lack of a significant association between genetic variation at the allozyme loci and the RAPD markers indicates that genetic diversity is extremely high in this population and that each MLAG

actually represents many different genetically distinct clonal lineages. Under such circumstances, it may be impossible to use allozymes as markers to detect genetic differences between subpopulations, merely because of lack of resolution. Yet we observed highly significant differences in allele frequencies among *Daphnia* samples taken at different depths in the Schöhsee, indicating that, even in this population in which almost all animals engage in a clear-cut DVM, there is genetic differentiation in depth selection behavior. This has been confirmed experimentally in plankton tower experiments (De Meester et al. 1995), using three clones that were examined in the present life-table experiment (lineages 1, 6, and 20). The vertical distributions of MLAGs A and C, of which lineages 1 and 6 are clonal representatives in the Schöhsee, as documented in the present study (Fig. 3), are, in fact, in reasonably good agreement with the behavior observed for clonal lineages of these MLAGs in the plankton towers (labeled genotypes 1 and 2 in De Meester et al. 1995).

The *D. hyalina* × *galeata* hybrid population of the Schöhsee contains substantial genetic variation with respect to life-history traits. Although we sampled only on 1 d in summer (5 July 1994), the results of our life-table experiment indicate a potential for microevolutionary responses in every trait studied. With respect to size at maturity, genetic variability was associated with differences in habitat selection behavior (RT vs. RA depth selection behavior). On average, genotypes with an RT depth selection behavior (DVM) are smaller than genotypes with a habitat selection behavior that makes them less vulnerable to visual predation (i.e., RA). Large-bodied clones were caught only in the hypolimnion; none were detected in the samples taken in the epilimnion

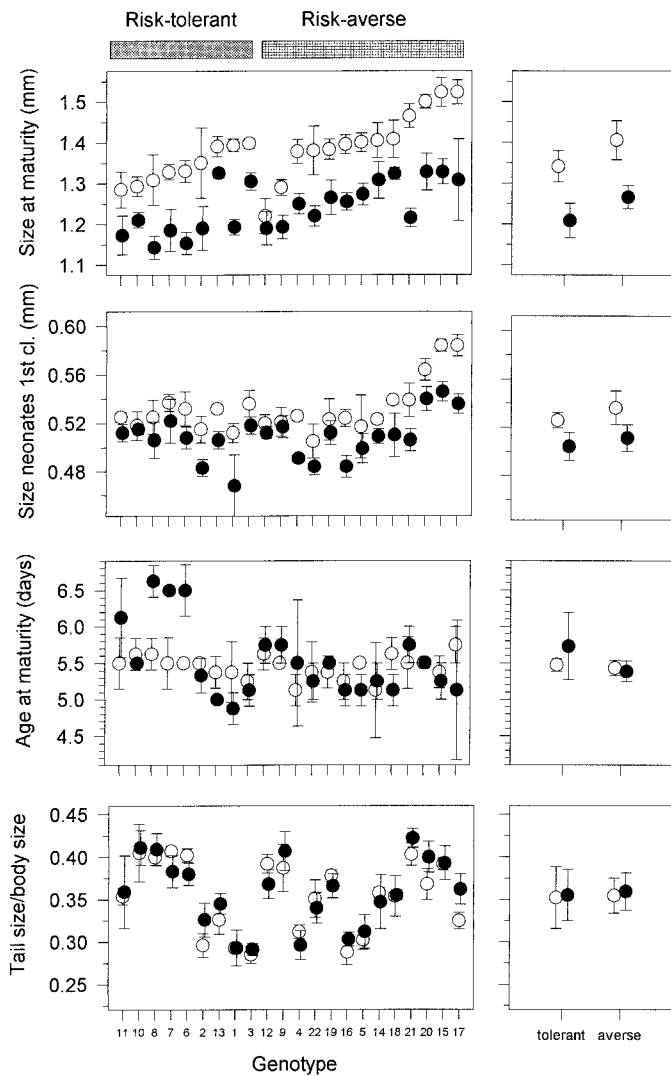


Fig. 4. Left panels: clonal averages (± 2 SE) of size at maturity, average size of the neonates of the first clutch, age at maturity, and relative tail-spine length for 22 clonal lineages (clones) isolated from different depths in the Schöhsee (July 1994). Empty symbols: absence of fish kairomones; filled symbols: presence of fish kairomones. Clones 1–9 were isolated from the epilimnion during the day or early in the evening and are defined as clones with an RT depth selection behavior. Within each group of RT and RA depth selection behaviors, the clones are ordered according to size at maturity. Right panels: average (± 2 SE) size of the neonates of the first clutch, age at maturity, and relative tail-spine length of clones with RT and RA depth selection behaviors, based on clonal averages.

during the day or early in the evening (no epilimnetic samples were taken at night).

The difference between RT and RA depth selection behavior should not be equated with nonmigrating and migrating behavior. In zooplankton populations such as the *Daphnia* population inhabiting the Schöhsee, most of the animals appear to migrate to some extent. Rather, the difference between RT and RA depth selection behavior is re-

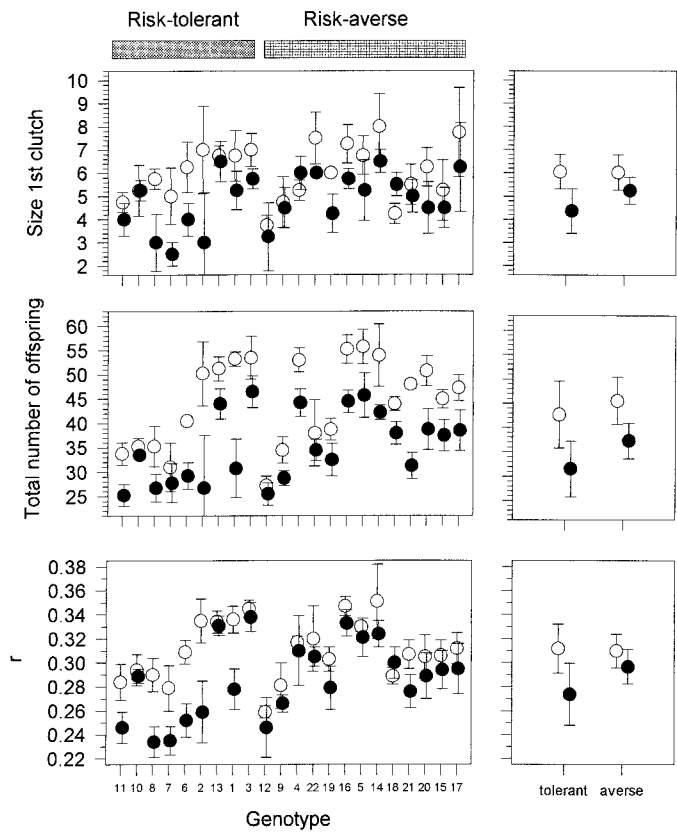


Fig. 5. Left panels: clonal averages (± 2 SE) of size of the first clutch, total number of offspring produced in the first four clutches, and intrinsic rate of increase, r , for 22 clonal lineages (clones) isolated from different depths in the Schöhsee (July 1994). For symbols and organization of the graphs, see legend of Fig. 3. Right panels: average (± 2 SE) size of the first clutch, total number of offspring produced in the first four clutches, and intrinsic rate of increase, r , of clones with RT and RA depth selection behaviors, based on clonal averages.

lated to the amplitude of migration (Fig. 3) and the timing of migration (i.e., early migrants).

The observation that small-bodied genotypes remain higher in the water column during the day or migrate earlier at dusk than large-bodied ones is consistent with an adaptive response, given the importance of visual predation in structuring *Daphnia* populations in lakes (Lampert 1987). Small-bodied genotypes realize a relatively high intrinsic rate of increase at a smaller body size than large-bodied genotypes but at a cost of producing smaller (and thus less starvation resistant) offspring (see De Meester 1994a). They can afford to do so, because their habitat selection entails relatively good habitat quality. This results in two alternative strategies that may have equal fitnesses. In fact, two of the clones used in the present study (clones 1 and 20) were shown to have an equal fitness in a mesocosm experiment, both in the absence and presence of predation pressure by fish (De Meester et al. 1995). The tendency of some of the small-bodied clones to have a smaller r than the large-bodied clones in the present common garden experiment (Fig. 4) is likely to be compensated for in the field, because animals staying

Table 2. Results of two-way ANOVAs testing for the effect of clone and treatment (absence or presence of fish kairomone) on life-history characteristics of 22 *D. hyalina* × *galeata* hybrid clones isolated from the Schöhsee, July 1994; ns, not significant.

		df effect	MS effect	df error	F	
SIZE (1)	Clone	21	0.0336	132	17.228	<0.000001***
	Fish	1	0.8181	132	419.336	<0.000001***
	L × F	21	0.0056	132	2.881	0.00013***
SIZENEO (1)	Clone	21	0.0029	132	17.323	<0.000001***
	Fish	1	0.0243	132	147.172	<0.000001***
	L × F	21	0.0003	132	1.941	0.013*
RELTAIL (1)	Clone	21	0.0213	132	34.808	<0.000001***
	Fish	1	0.0011	132	1.845	0.177 ns
	L × F	21	0.0010	132	1.585	0.062 ns
AGEMAT	Clone	21	0.6724	132	4.914	<0.000001***
	Fish	1	0.2401	132	1.754	0.187 ns
	L × F	21	0.4663	132	3.407	0.000009***
BR (1)	Clone	21	8.4015	132	6.337	<0.000001***
	Fish	1	61.4545	132	46.354	<0.000001***
	L × F	21	2.5974	132	1.959	0.012*
TOTBR	Clone	21	457.149	132	25.299	<0.000001***
	Fish	1	3718.642	132	205.790	<0.000001***
	L × F	21	63.023	132	3.488	0.000006***
r	Clone	21	0.0057	132	17.911	<0.000001***
	Fish	1	0.0251	132	79.574	<0.000001***
	L × F	21	0.0009	132	2.856	0.00015***

*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$ after correction for multiple testing (seven ANOVAs) by sequential Bonferroni (Rice 1989).

Table 3. Results of two-way ANOVAs testing for the effect of behavior (RT vs. RA depth selection behavior) and treatment (absence or presence of fish kairomone) on life-history characteristics of 22 *D. hyalina* × *galeata* hybrid clones isolated from the Schöhsee (July 1994), using overall clonal group means as input data. Nine RT and 13 RA clones were categorized; ns, not significant.

		df effect	MS effect	df error	F	
SIZE (1)	Behavior	1	0.039	40	9.227	0.0042*
	Fish	1	0.198	40	47.035	<0.000001***
	B × F	1	0.0001	40	0.028	0.866 ns
SIZENEO (1)	Behavior	1	0.00081	40	2.063	0.1586 ns
	Fish	1	0.0056	40	14.429	<0.00049**
	B × F	1	0.000027	40	0.069	0.794 ns
RELTAIL	Behavior	1	0.000101	40	0.0584	0.810 ns
	Fish	1	0.000180	40	0.0963	0.758 ns
	B × F	1	0.000002	40	0.0009	0.976 ns
AGEMAT	Behavior	1	0.397	40	3.0013	0.091 ns
	Fish	1	0.119	40	0.8965	0.349 ns
	B × F	1	0.251	40	1.8988	0.176 ns
BR (1)	Behavior	1	1.600	40	1.162	0.287 ns
	Fish	1	17.163	40	12.462	0.001**
	B × F	1	1.913	40	1.389	0.245 ns
BRTOT	Behavior	1	186.844	40	2.775	0.104 ns
	Fish	1	1017.556	40	15.115	0.000372**
	B × F	1	19.612	40	0.291	0.592 ns
r	Behavior	1	0.0011	40	1.312	0.259 ns
	Fish	1	0.0074	40	9.171	0.0043*
	B × F	1	0.0015	40	1.856	0.181 ns

*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$ after correction for multiple testing (seven ANOVAs) by sequential Bonferroni.

higher in the water column will experience higher temperatures. The results of the present life-table experiment and the one carried out by De Meester (1994a) thus suggest that coadaptation between depth selection behavior and life-history strategies can be found in both pond- and lake-dwelling *Daphnia* species. The results of Reede and Ringelberg (1995, 1998) are also qualitatively in agreement with ours and provide additional support for coadaptation of life-history traits and depth selection behavior. Although small-bodied lineages are present in the hypolimnion of the Schöhsee, the *D. hyalina* × *galeata* hypolimnetic subpopulation is numerically dominated by intermediate- and large-bodied genotypes. This is presumably the result of the advantages provided by a larger body size in daphnids with respect to starvation resistance and competition under suboptimal conditions (Gliwicz 1990; De Meester 1994a, 1995; Boersma 1995). Moreover, we have shown elsewhere in plankton tower experiments (De Meester et al. 1995) that the relationship between body size and depth selection behavior not only exists at the among-genotype level but also at the within-genotype level. Using the aforesaid subset of clones (1, 6, and 20) studied in the present experiment, we observed that adults of the large-bodied clone 20 had a deeper day depth than adults of clones 1 and 6 (De Meester et al. 1995). We also observed that the adults of clones 1 and 20 that remained in the epilimnion during the day were smaller than the adults of the same clones that migrated into the hypolimnion. This suggests that the relationship between body size and depth selection behavior of adult *Daphnia* reported by field studies (e.g., in the Schöhsee: Guisande et al. 1991 and present study) is the result of both a within-genotype (large vs. small adults of a given clone) and a between-genotype (large-bodied vs. small-bodied clone) component.

As has been shown by several other studies (e.g., Stibor 1992; Reede and Ringelberg 1995, 1998), the presence of fish-mediated chemicals induces strong shifts in life-history characteristics in species of the *Daphnia longispina* species complex. There was a significant effect of fish kairomones on all traits, except for the relative length of the tail spine and age at maturity. The direction of the response to fish kairomones toward smaller adult body sizes is the same for all clones analyzed and is consistent with an adaptive interpretation: in the presence of kairomones of a visual predator, *Daphnia* spp. mature at a smaller size and produce smaller offspring, which results in a lower vulnerability to visual predation. With respect to all traits except relative length of the tail spine, the response to the presence of fish kairomones is clone dependent. Irrespective of this genetic variability in the response to fish kairomones, there is no significant difference in the response induced by the presence of fish kairomones between clones with an RT and RA habitat selection behavior for any of the traits studied. Genotypes with different depth selection behaviors thus differ strongly in the mean value of adult body size, but they do not differ in the magnitude of the change in these traits in response to the presence of predator kairomones. This is in agreement with data from Boersma et al. (1999), who observed that four *D. magna* populations were genetically differentiated from each other with respect to the mean value of life-history traits but did not differ in the response to fish kairomones. Data on

phototactic behavior, however, indicate that local adaptation is primarily exhibited at the level of the response to predator kairomones (De Meester 1996a). As has been suggested by De Meester and Cousyn (1997) and Boersma et al. (1999), this difference in pattern of genetic differentiation may be related to the fact that the time lag for the induction of an efficient defense is much lower for behavioral than for life-history traits (Padilla and Adolph 1996).

From our data, it can be concluded that the shift to a smaller adult body size observed in the presence of fish kairomones would result in a lower fitness in the absence of visual predation. Clutch sizes are reduced, and the neonates produced are smaller and thus of lower quality, at least in terms of starvation resistance (Tessier and Consolatti 1989). Contrary to previous work, we also found a fitness cost in terms of the intrinsic rate of increase. Several previous studies have reported a greater relative allocation (similar absolute allocation) to reproduction in fish-kairomone-induced *Daphnia* compared to noninduced animals (Stibor 1992; Weider and Pijanowska 1993; Stibor and Lüning 1994), as well as a shift to earlier reproduction (Stibor 1992; Reede and Ringelberg 1995). These results indicate that fish-kairomone-induced animals may often have a higher intrinsic rate of increase than noninduced animals (e.g., Reede and Ringelberg 1995). In our experiment, however, the average value of r of induced animals was lower than that of noninduced animals for most clones, and the reduction in r was significant for seven clones (contrast analysis after two-way ANOVA, $P < 0.05$). There was a substantial reduction in the total number of offspring produced during the first four adult instars. Contrary to previous reports, we found no effect of induction on age at maturity or on average adult instar duration (data not shown). Although the resolution with which we measured time-related traits was limited to 12 h and may therefore have been insufficient to detect subtle effects, this resolution is as good as or better than that of previous studies (24 h in Weider and Pijanowska 1993; Reede and Ringelberg 1995; 12 h in Stibor and Lüning 1994). In our experiment, however, the induced lines were preadapted for one generation to the presence of fish kairomones, because we studied the second generation of induced animals (i.e., animals born from mothers that were already cultured in the presence of fish chemicals), whereas other studies considered the first generation of induced animals (Weider and Pijanowska 1993; Stibor and Lüning 1994; Reede and Ringelberg 1995). (Stibor [1992] also considered the second generation but only reported size at maturity for this generation.) This different approach may explain the discrepancy between our results and previous studies. It is indeed conceivable that the first generation of induced animals has a reduced age at maturity, because relatively large neonates grow to relatively small (induced) adults. In the second generation, however, the neonates produced are also small (due to induction), and no reduced developmental time would be expected when compared to animals cultured in the absence of fish kairomones. If this pattern is verified with additional data, the observation of an increased intrinsic rate of increase in the first generation of induced animals reported by previous studies needs to be placed in the proper context: it only holds for the first generation.

Another point to be addressed deals with the amount of genetic variation observed in the present study, which may have been influenced by the fact that we worked with clones of a taxon of hybrid origin rather than with clones of one of the parental species. Crosses between parental species may yield genotypes with a wide array of life-history characteristics (e.g., F_1 hybrid characters are, on average, intermediate to those of parental species; Weider 1993), especially given the possible inclusion in our study of F_2 hybrids and backcrosses. There is indeed an indication that some of the clones used in this study may be backcrosses. Wolf and Mort (1986) reported that *D. galeata* is fixed for the *f* allele at AO, whereas *D. hyalina* is fixed for the *s* allele (see also review by Schwenk and Spaak 1995). If so, clone 16 (*sf* for sAAT and *ss* for AO) might represent a backcross between *D. hyalina* × *galeata* hybrids and *D. hyalina*, whereas our clone 18 (*sf* for sAAT and *ff* for AO) might represent a backcross between *D. hyalina* × *galeata* and *D. galeata*. Although backcrosses may have been included in our study, the removal of clones 16 and 18 from our analysis would not change our conclusions. It should also be mentioned that, if the large genetic variation observed in the present study is attributed in part to the hybrid origin of the clones, then this aspect does change the interpretation of the origin of the genetic diversity but does not change our view on the mechanism(s) enabling these clones to coexist. Our conclusion on the relationship between depth selection behavior and life-history traits remains robust.

In summary, we conclude that the *D. hyalina* × *galeata* population in the Schöhsee (1) harbors genetic variation for depth selection behavior and DVM, and (2) harbors substantial genetic variation with respect to several key life-history traits. We also observed that (3) genetic variation in adult body size is associated with differences in depth selection (DVM) behavior (i.e., RT vs. RA depth selection behavior). In addition, we observed that (4) there is genetic variation in response to fish kairomone with respect to life-history traits in this population. We also observed, however, that (5) genotypes with RT depth distributions did not on average differ in their response to fish kairomones when compared to genotypes with RA depth selection behavior. Combined with the results of De Meester et al. (1995), the results of the present study corroborate the notion that coadaptation of life-history traits with traits influencing habitat selection may be important in maintaining genetic polymorphism for habitat selection in natural populations—more specifically, depth selection behavior and DVM patterns in zooplankton populations.

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