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The influence of a fish exudate on two clones of the hybrid *Daphnia galeata* × *hyalina*

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Key words: *Daphnia*, fish-exudate, intrinsic rate of increase, life-history

Abstract

Two *Daphnia* clones were isolated from different day depths during the period of diel vertical migration and were tested for their life-history responses to a fish exudate released by juvenile perch. Animals were exposed to fish exudate every 24 or 48 h. Both clones responded to the exudate by exhibiting earlier maturation and larger sizes of first clutches, which resulted in higher rates of population increase. Also, neonates were smaller in the presence of the exudate. It was found that the clone isolated from a deeper day depth ('migrating clone') was less sensitive to the exudate than the clone isolated from the surface waters, which was presumed to be non-migrating. The non-migrating clone responded by having smaller neonate sizes and smaller sizes at maturity than the migrating clone. The non-migrating clone responded to the fish chemical when it was exposed to it every 24 or 48 h, whereas the migrating clone only responded to the exudate if exposed to it every 24 h.

Introduction

The adaptive value of diel vertical migration (DVM) is generally believed to be a decrease in mortality due to visual predators (see Lampert, 1989, 1993 for reviews). In Lake Maarsseveen, *Daphnia galeata* × *hyalina* performs a DVM for some weeks when 0+ perch (*Perca fluviatilis*) are present in the open water, and are preying on daphnids. During the first few weeks, average population day depth increases. The *Daphnia* population consists of many genetically distinct clones (Spaak & Hoekstra, 1993). One possible explanation for the increasing day depth is that clones exhibit differential migration, and combined with predation, some clones react less to relative changes in light intensity and/or fish exudates, which enhance reactivity (Ringelberg, 1991 *et al.* and submitted). As a result, at the height of the migration period, daphnids are no longer found in the epilimnion during daytime.

Migrating and non-migrating clones, the two extreme types, are subject to different environmental conditions during the period of migration and therefore their life history traits should be different (Stich & Lampert, 1984) if we deal with the two extreme strate-

gies. Some of these characteristics will be genetically determined and others phenotypically induced. Several examples of the latter can be found in the literature. For instance, Machacek (1991) reported larger clutch sizes and smaller eggs in *D. galeata* treated with fish exudates and Stibor (1992) found similar effects in *D. hyalina*. A chemical, released by *Chaoborus*, has been shown to cause delayed maturation and fewer but larger offspring in *D. pulex* (Luning, 1992). The effect of fish exudates on behavioural traits varies in different clones of *D. magna* (De Meester, 1993) and Weider & Pijanowska (1993) have shown that clones, isolated from different ponds, do have different life history responses to chemical cues released by predators such as age and size at maturation.

Whether it is advantageous to migrate or not, depends on the extent of predation pressure, food concentration and on the vertical temperature gradient. Also of importance is to what extent phenotypic changes and genotypical differences occur in pertinent life history traits? Therefore, we argue that exudates of juvenile perch might have a different effect on these traits in migrating and non-migrating clones from Lake

Table 1. Summary of experimental conditions, all of which were performed in the absence and presence of fish exudate

Treatment	1	2	3	4
Temperature	20 °C	20 °C	20 °C	20 °C
Average algal concentration (mg C/l)	0.57	0.57	1.14	1.14
Media refreshed every	24 h	48 h	24 h	48 h
Experiments carried out with clone	M3/O2	M3/O2	M3	M3
Number of animals	10/10	7/7	10	10

Fig. 1. Schematic representation of one unit of the flow through system.

Maarsseveen. Here, we report on the results of experiments to test this hypothesis.

Material and methods

Several individuals of the hybrid *Daphnia hyalina* × *galeata* were collected from Lake Maarsseveen I, at the beginning of the period of diel vertical migration in June 1992. Some were caught at a day depth of 0–7 m (non-migrating animals) and others at a day depth of 15–25 m (migrating animals). From these animals, clones were cultured and maintained in the laboratory under controlled conditions for several generations before the life-history experiments were started. Clones were kept in transparent glass jars filled with 1.0 l of filtered lake water. They were fed a surplus

of log-phase cells of *Scenedesmus acuminatus* three times a week and the water in the vessels was renewed weekly. *Scenedesmus* was grown in Woods Hole MBL in continuous culture (Guillard, 1975).

In the experiments, two genetically distinct clones (K. Schwenk, pers. comm.) were used, a migrating one (hereafter referred to as clone M3) and a non-migrating one (hereafter referred to as clone O2). Neonates (< 12 hours old) were used in the experiments as shown in Table 1.

In Fig. 1, one unit of the culturing set-up is shown.

Individual animals were grown in tubes (9) in which the bottom consisted of a gauze (mesh-size 150 µm) through which algae can pass freely, but neonates cannot. Seven tubes were placed in a cuvette (8) and the latter was placed in a controlled-temperature waterbath (3). Algae (*Scenedesmus acuminatus*) were grown in reservoir bottles (7) which were illuminated by fluorescent lamps (10). The Skinner valves (2a and b) and the peristaltic pump (1) were connected to a timer. At certain times, Skinner valve 2a would open and the cuvette would empty into the beaker (4) (a small amount of medium remains behind for the animals to swim in). Then valve 2b would open and the cuvette (8) (and thus the tubes – 9) would be refilled with a fresh amount of algal suspension from the reservoir bottle. Lastly, the algal suspension in the beaker (4) would be pumped back into the reservoir bottle. In this way, the tubes were refreshed every six hours with medium from the bottles and the food concentration was kept as constant as possible throughout the experiments. The amount of algal suspension fed to the daphnids was checked regularly. Culture medium in the reservoir bottles was refreshed each day or every other day (Table 1) with log-phase cells of *Scenedesmus acuminatus* grown in continuous culture. The light/dark cycle was 16/8 hours.

The experiments were conducted with water from the hypolimnion (no young perch present) of Lake Maarsseveen, which was continuously filtered through a sandfilter at 20 °C. Water containing fish-exudate was obtained from an aquarium containing about 20 liters of lake-water and 10 individuals of perch (*Perca fluviatilis*) of approximately 3 cm length. Half the water in the aquarium was refreshed every day and feces were removed simultaneously. The 'fish-water' used in the experiments was filtered through a 0.2 µm mesh filter.

Neonates in the tubes were counted and removed daily. Also size and age at maturity (i.e. the day on

Fig. 2. Intrinsic rate of increase calculated for each age class in different clones of *D. galeata* $\times$ *hyalina*. Dotted lines represent fish treatments, solid lines represent the controls. Confidence limits are presented in Table 2. a. Clone O2. Food level: 0.57 mg C/l; fish exudate added every 48 hours; b. Clone O2 (open circles) and clone M3 (crosses). Food level: 0.57 mg C/l; fish exudate added every 24 hours; c. Clone M3. Two food levels: Top lines 1.14 mg C/l, bottom lines 0.57 mg C/l; fish exudate added every 48 hours; d. Clone M3. Food level: 1.14 mg C/l; fish exudate added every 24 hours.

which the first clutch of eggs was deposited in the brood pouch) were determined. The experiments were continued until the calculated intrinsic rate of increase (r) reached an approximately constant value. This usually took 14–18 days.

The daphnids treated with fish exudate, were kept in 1/3 fish-water and 2/3 hypolimnion water. Control animals were kept in 100% hypolimnion water.

Population growth rates, ages and sizes at maturity and offspring sizes were determined. A Student's *t*-test was used to calculate differences between treatments and clones.

Population growth rate calculations

Population growth rates were calculated according to the Euler equation:

Table 2. Intrinsic rates of increase with 95%-confidence limits calculated on the fifteenth day of the experiments, as depicted in Fig. 2

Inset	Clone	Treatment	Food	r-value
A	O2	Control	0.57	0.225 ± 0.017
A	O2	Fish	0.57	0.272 ± 0.046
B	O2	Control	0.57	0.121 ± 0.047
B	O2	Fish	0.57	0.253 ± 0.025
B	M3	Control	0.57	0.120 ± 0.048
B	M3	Fish	0.57	0.251 ± 0.020
C	M3	Control	0.57	0.262 ± 0.059
C	M3	Fish	0.57	0.259 ± 0.047
C	M3	Control	1.14	0.344 ± 0.011
C	M3	Fish	1.14	0.341 ± 0.009
D	M3	Control	1.14	0.239 ± 0.077
D	M3	Fish	1.14	0.301 ± 0.041

$$1 = \sum e^{-rx} l_x m_x, \quad (1)$$

where r = intrinsic rate of increase for the population, x = age class in days, l_x = probability of surviving to age x , and m_x = age specific fecundity.

Since r cannot be isolated on one side of the equation, iterative calculations must be performed. However, this will leave us with only one value for r per data set from which the variance cannot be calculated. A variance was generated by applying the Jackknife method as described by Meyer *et al.* (1986).

Results

Population growth rates

Figure 2a shows that population growth rates of clone O2 were higher if fish exudate was added to the culture medium. The difference was significant up to an age of about 13 days if the medium was refreshed every 48 h ($t = 12$: $p < 0.03$, $df = 12$ / $t = 13$: $p = 0.34$, $df = 12$). If the medium was refreshed every 24 h, the difference was more pronounced and remained significant throughout the experiment. This was the same for both clones (Fig. 2b, clone O2: $p < 0.001$, $df = 15$. Clone M3: $p < 0.001$, $df = 18$). If the medium was refreshed every 48 h, no differences in population growth rates were found for clone M3 (Fig. 2c). This held for both food concentrations. Differences in growth rates due to different food levels however, were significant ($p < 0.01$, $df = 18$). Figure 2b also shows that with fish exudate administered every 24 h, no difference in population growth rate patterns between the two clones, was present.

If the medium was refreshed every 24 h, clone M3 also showed differences in growth rates although this difference was not significant at the highest food level (Fig. 2d. $p = 0.12$, $df = 18$). At the lowest food concentration, the difference was significant during the course of the entire experiment (Fig. 2b. $p < 0.001$, $df = 18$).

Age and size at maturity

Across all treatments, animals from clone M3 did not differ significantly in size (Fig. 3). Daphnids from clone O2 were smaller if fish exudate was present. The difference was significant if the media were refreshed every other day (Fig. 3. $p < 0.001$, $df = 12$). Howev-

Fig. 3. Size at maturity for experimental conditions 1–4, as described in Table 1. C – control, F – fish treatment. Vertical bars represent 95% confidence limits.

Fig. 4. Age at maturity for experimental conditions 1–4, as described in Table 1. C – control, F – fish treatment. Vertical bars represent 95% confidence limits.

er, animals from clone O2 were always significantly smaller than those from clone M3 ($p < 0.001$, $df = 12$).

Clone O2 reproduced significantly earlier if fish exudate was added every 24 or every 48 hours ($p < 0.001$, $df = 12$). With a daily administered dose of fish exudate, this also held true for clone M3 ($p < 0.001$, $df = 18$) and no significant clonal differences were observed (Fig. 4).

Offspring size

In Figs 5a and b, neonates from first clutches for both clones were significantly smaller in the presence of fish exudate ($p < 0.001$, $df = 48$ for both clones). Also, O2 neonates were significantly smaller than those of M3 under similar conditions ($p < 0.001$, $df = 48$). Although juveniles tended to become larger with increasing age of the mothers, neonates of O2 fish-treated animals were always significantly smaller than those of the control group ($p < 0.001$, $df = 48$). This difference disappeared in clone M3 as the mothers grew older.

Discussion

The population of *Daphnia* in Lake Maarsseveen in summer consists of *D. galeata* and the hybrid *D. galeata* $\times$ *hyalina*. Allozyme analysis has revealed that both taxa are composed of different clonal groups, in which the relative abundances change from year to year and within a single season (Spaak & Hoekstra, 1993). Of the specimens collected in the lake during the diel vertical migration period of 1992, clone O2 probably did not migrate since it was taken from the upper water layers during daytime. Clone M3 probably migrated because the parent animal was collected at a greater depth during daytime. Our experimental cultures revealed that differences in life histories between these two clones exist and that several traits changed differentially in the presence of exudates from juvenile perch. These perch are visual predators and larger *Daphnia* will be more vulnerable to predation than smaller ones. Therefore, a smaller size and an additional reduction in size in the presence of fish exudate, as exhibited by clone O2, will diminish predation risk. Animals from the migrating clone were larger and no corresponding decrease in size was observed.

The non-migrating daphnids from clone O2 produce more offspring in the early period of reproduction if exudates of perch are present. Thus, this clone increases its chances of successful reproduction before it is eaten. In addition, clone O2 produces smaller juveniles, which stand a better chance of evading visual predators. It is possible that subsequent generations, i.e. granddaughters of the experimental mothers, are even more reduced in size than the first generation, as was found for *Daphnia hyalina* by Stibor (1992).

The migrating clone M3 showed no reduction in body length, but clutch size increased in the presence of perch exudates. Since DVM decreases the risk of predation by fish, a reduction in size could be advantageous because invertebrate predation is reduced (Lynch, 1980). However, the risk of predation by fish is not reduced completely in migrating animals since at the height of the migration period, *Daphnia* are still found in the gut of young perch. Therefore, the production of large clutches as early as possible must be advantageous for the migrating animals as well. Since clone M3 does not reduce body length, while clutches increase in size in the presence of fish exudate, no trade-off between somatic growth and number of offspring seems to be present, at least not under the experimental conditions used in this study.

Another difference between the clones seems to be a higher sensitivity to fish exudate for clone O2. This clone responded to the less frequent addition of the exudate, while clone M3 did not. At low predator densities in the lake and probably at low concentrations of the kairomone, animals from clone O2 might already be able to shift their life history traits, while the migrating clone would not respond. Kairomone concentration effects exist as was demonstrated by Loose (1993) with respect to the extent of migration in large experimental plankton towers.

Both clones O2 and M3 have higher population growth rates if perch exudate is present. Differences between the fish and the control groups were significant at the beginning of the reproductive period, but such differences were not always significant later in the life cycle. This is the result of a larger clutch size earlier in life. Neonates hatching from eggs from smaller clutches are larger and have higher survival rates (Tessier & Consolatti, 1989). Therefore it is not always advantageous to have larger clutches in the absence of predatory fish. At the higher food level, clone M3 no longer showed any difference in population growth rate between the fish and control treatments. This might indicate a food-fish exudate interaction. Or, perhaps the population growth rate had reached a maximum and could not increase further. Another possibility is that if a higher amount of algae was added, this also means that the amount of bacteria introduced in the media was also higher. Since the fish exudate is probably degraded by bacteria, this could cause faster decomposition and hence a weaker response. This is a point for further study.

Two strategies of population survival, migration or superior life history traits, were described by Stich & Lampert (1984) for *D. hyalina* and *D. galeata*, respectively, in Lake Constance. The present study indicates that both strategies can be present within one hybrid population complex. Moreover, it is not simply an additional strategy, since in the migrating clone, the expression of some life-history traits also changed in the presence of fish exudates. The *Daphnia* population in Lake Maarsseveen may consist of several genotypes with different potentials to migrate in addition to different potentials for shifting life-history characters (Weider, 1984, 1985). At one end of the spectrum, strongly migrating animals were found with no life-history adaptations, while the other end may be represented by non-migrating animals with phenotypic plasticity in life-history traits. When juvenile fish predators appear in the lake, this would lead to partial and dif-

Fig. 5. Offspring sizes for both clones. Food concentration: 0.57 mg C/l, fish exudate added every 24 hours. a. means for the first two clutches; b. means for the last two clutches of the culture period. Vertical bars represent 95% confidence limits.

ferential migrations and shifts in relative clonal dominance, the extent of such clonal shifts would depend on food conditions and predation pressure. Changes both in amplitude of diel vertical migration (Ringelberg & Flik, submitted) and in clonal composition (Spaak & Hoekstra, 1993) were observed for different years in Lake Maarsseveen. However, more research has to be done before it is clear whether there is a dynamic genotypic shift related to vertical migration strategies.

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