

Effects of infochemicals released by gape-limited fish on life history traits of *Daphnia*: a maladaptive response?

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Life history shifts in daphnids in response to fish infochemicals are generally interpreted as an adaptive response to positive size-selective predation. This interpretation does, however, not hold for larval and small juvenile planktivorous fish, which due to gape limitation, feed on small and medium sized prey. In a life table experiment we show that daphnids exposed to infochemicals excreted by small gape-limited perch and larger perch changed their life history in the same direction, irrespective of the contrasting size-selection of the fish. However, responses to fish infochemicals were strongly influenced by food conditions for daphnids. In the high food treatments size at maturity was decreased in the presence of fish infochemicals, whereas age at maturity remained unchanged. Under low food conditions, size at maturity was generally smaller compared with the high food situation, but unaffected by fish infochemicals. By contrast, age at maturity, which was increased at low food levels, was significantly lower in fish treatments compared with the control. We conclude that life history responses of daphnids to gape-limited fish can indeed be maladaptive, but only in situations of high food availability. This combination of factors is, however, rather unlikely because gape-limited fish usually occur in late spring during the clear water phase when daphnids are severely food limited. We thus hypothesize that the costs of this maladaptive response under negative size-selective predation will be low under field conditions and the selective advantage under positive size-selective predation later in the season will outweigh these costs.

INTRODUCTION

Phenotypic plasticity of *Daphnia* in response to predator-released infochemicals is one of the best-studied examples of inducible defences (Tollrian and Dodson, 1999). Daphnids are able to adapt their behaviour (e.g. diel vertical migration), their morphology (e.g. neckspines) or their life history (e.g. size and age at maturity) in specific ways depending on the kind of predator they perceive via infochemicals. A distinct dichotomy in the life history response of *Daphnia* to predators with different patterns of prey selection has been shown (Riessen, 1999a). The most clearly affected traits were size and age at maturity, which were decreased in the presence of (different) fish and the invertebrate predator *Notonecta* whereas in the presence of *Chaoborus* reproduction was delayed and size at maturity tended to be increased.

Since both fish and *Notonecta* preferably feed on large prey (O'Brien, 1979; Scott and Murdoch, 1983) the observed life history shifts in response to these predators appear to be clearly adaptive.

However, the 'normal' strategy to decrease size at maturity in the presence of fish should be counteractive and even increase vulnerability if planktivorous fish, due to gape-limitation, feed on small or medium-sized prey and additionally select egg-carrying individuals. In temperate regions this scenario can be expected for young of the year (YOY) fish in early summer. It has clearly been shown for yellow perch [*Perca flavescens* (Hansen and Wahl, 1981)] and Eurasian perch [*Perca fluviatilis* (Mehner *et al.*, 1998)] that they feed mainly on small size classes of *Daphnia* (and other small crustaceans, but not on large daphnids) during their first weeks of life. The period of gape-limitation is

offset (at least for *Daphnia galeata* and *Daphnia pulex*) when YOY perch reach a total length (TL) of 25–30 mm ~4–6 weeks after hatching. At that size, the difference in modal *Daphnia* length between those found in fish stomachs and those present in the lake becomes positive (Mehner *et al.*, 1998). Consequently, during the period of gape-limitation a decrease in size should actually increase the vulnerability of *Daphnia*. From their study of gape size-dependent feeding of YOY perch on *D. galeata*, Mehner *et al.* (Mehner *et al.*, 1998) indeed concluded that the population was more vulnerable to gape-limited perch in a year when size at maturity was strongly decreased in early summer compared with a year when the size at maturity remained higher. Although many studies have emphasized the importance of YOY fish predation for *Daphnia* population dynamics (Mills and Forney, 1983; Cryer *et al.*, 1986) and for the induction of phenotypic responses, e.g. behavioural reactions (Ringelberg *et al.*, 1997; Van Gool and Ringelberg, 2002), the aspect of ontogenetic changes in size-selective feeding was usually not considered. To our knowledge no study exists, where the timing of these changes was related to the timing of life history shifts in their daphnid prey.

Newly hatched perch larvae were found to influence *Daphnia* swimming behaviour (Van Gool and Ringelberg, 2002), but it has never been shown that gape-limited fish do induce life history shifts in daphnids. The smallest fish used to produce infochemicals for life table experiments were YOY Eurasian perch of 30 mm length (Reede and Ringelberg, 1995; Reede, 1997). At that size gape-limitation is offset (Hansen and Wahl, 1981; Mehner *et al.*, 1998). Although the infochemicals excreted by fish seem to contain rather unspecific substances related to fish physiology (Loose *et al.*, 1993; von Elert and Pohnert, 2000), the possibility cannot be excluded that fish only start producing them, or that their inductive effects on *Daphnia* life history traits change, after reaching a size at which gape-limitation is offset.

A number of life history traits are known to respond to food shortage in an opposite manner to adaptations induced by infochemicals (Lynch, 1989; Boersma and Vijverberg, 1994). Thus, a strong interaction of food limitation and fish infochemicals could be expected since the occurrence of YOY fish usually coincides with a period of low food conditions during the spring clear-water phase (Tessier, 1986; Wu and Culver, 1994). Only a few studies have addressed the question of effects of fish infochemicals under limiting food conditions, some finding no interaction effect of food and infochemicals on life history responses of daphnids (Macháček, 1991; Doksaeter and Vijverberg, 2001), whereas others found a strong interaction of both factors on *Daphnia* reaction norms (Weber, 2001; Weetman and Atkinson, 2002).

The following questions were addressed in this study: (i) do infochemicals excreted by gape-limited YOY fish induce life history shifts in *Daphnia* or not? (ii) If they do, are these life history shifts different from those induced by infochemicals released by larger fish? (iii) How do food conditions modify the effects of fish infochemicals? We discuss these findings from an evolutionary perspective by asking ourselves whether the effects of infochemicals released by gape-limited YOY fish on life history traits of *Daphnia* are likely to be adaptive under field conditions.

METHOD

Life table experiments were performed in a flow-through system similarly used in earlier experiments (Doksaeter and Vijverberg, 2001). Transparent experimental vessels (140 mL) were placed in a thermostatically controlled water bath with a constant temperature of 18°C and exposed to a 16:8 h light:dark regime. Peristaltic multi-channel pumps provided a constant dilution rate of the media of 3.6 day⁻¹.

The experimental animals belonged to one clone of the hybrid *Daphnia hyalina* × *galeata* from Lake Maarsseveen, the Netherlands. This clone was known to be responsive to fish infochemicals (Doksaeter and Vijverberg, 2001) and, according to allozyme electrophoresis, represented a clonal group which is very abundant in Lake Maarsseveen in spring (M. Brehm, NIOO-KNAW, personal communication). From a stock culture, which was raised under laboratory conditions for several generations, some adult females were isolated. Neonates born during a 12 h interval were placed into 1 L beakers with membrane-filtered lake water and *Scenedesmus obliquus* (see below) added to achieve a food concentration of 1 mg particulate organic carbon L⁻¹. The media were replaced every day. Light and temperature conditions were the same as in the experiment. Offspring from the second brood were isolated and reared under the same conditions. Neonates from the second brood of these animals were used in the experiment. All experimental animals were born during a 12 h time interval. Their initial size was 0.73 ± 0.03 mm ($n = 9$). Every culture vessel was stocked with five animals in order to account for any loss or mortality. Each treatment consisted of six replicates.

The water for the fish treatments was prepared in the following way. For the treatment with large fish two perch (*Perca fluviatilis*) of 9 cm TL were kept in an aquaria of 20 L capacity. YOY perch (*Perca fluviatilis*) were raised from eggs collected in the field (Saidenbach Reservoir, Germany) and fed with rotifers and newly hatched nauplii of *Artemia salina* until they had reached a TL of ~17 mm. At that size they are definitely able to feed on small daphnids, but still clearly gape-limited (Hansen and Wahl, 1981; Mehner *et al.*, 1998). YOY perch were placed in two aquaria of

10 L capacity at a density of 10 per L. Until the end of the experiment (after two weeks) some individuals had grown to 22 mm TL, a size at which they are still gape-limited. Growth in size (and individual biomass) was compensated by a decreasing density in the aquaria (from 10 to 8 ind. L⁻¹), to keep the total fish biomass per volume approximately constant.

When expressed on a fresh weight per volume basis, the biomass of YOY perch ($\sim 0.3 \text{ g L}^{-1}$) was about equal to the biomass of the larger perch [calculated on the basis of length-wet weight regressions given by (Mehner *et al.*, 1995) and H. Dörner, personal communication] and similar to fish densities used in earlier experiments (Loose *et al.*, 1993; Reede, 1995; Dokseter and Vijverberg, 2001). Since the actual infochemical concentration could not be controlled, this was the only way to ensure that its concentration in the treatments with YOY fish was at least equally high as in the treatments with larger fish. It is likely though that the actual infochemical concentration was higher in the aquaria with YOY perch, because their weight-specific metabolic activity should be higher compared with larger fish. As a check whether the effective infochemical concentration was indeed in the same order of magnitude in both fish treatments, the 'YOY fish water' was additionally applied in a lower concentration (see below).

Large perch were fed *D. pulex* collected daily from a nearby pond. Gape-limited YOY perch were fed on a mixture of *Artemia* nauplii, *D. hyalina* \times *galeata* from a batch culture and small *D. pulex* (derived by sieving field-caught animals with a 600 μm mesh). About 2 h after feeding the fish were transferred to clean aquaria, thereby removing remaining food items and faeces and replacing two-thirds of the medium with sand-filtered lake water. After 12 h of incubation half of the water was removed from the aquaria, membrane-filtered (0.45 μm) and used in the experiments.

Lake water was collected twice per week from Lake Maarsveen and circulated over a sandfilter for 2–3 days to ensure complete biodegradation of naturally occurring kairomones (Van Gool and Ringelberg, 2002). Prior to use, the water was membrane-filtered (0.45 μm). Algae (*Scenedesmus obliquus*) were cultured at high nutrient levels on a modified WC medium (Guillard and Lorenzen, 1972) in a continuous culture with a growth rate of 1.25 per day. They were harvested every day, gently centrifuged and re-suspended in membrane-filtered lake water before being added to the experimental media in densities equivalent to 1 mg C L⁻¹ or 0.1 mg C L⁻¹, respectively. For both food densities the following fish treatments were prepared: 0% fish water (control), 60% water obtained from large perch (L60), 60% water obtained from gape-limited YOY perch (YOY60) and 10% water obtained from gape-limited YOY perch (YOY10). Media were renewed daily, the storage vessels were permanently stirred.

The culture vessels were checked once per day for surviving daphnids and one randomly selected animal from each replicate was measured carefully (base of the tail spine to the anterior margin of the head) and subsequently put back into the culture vessel. The age and size at maturity was determined from the day when the first eggs were observed in the brood pouch. Clutch size was determined for the first three clutches. The number of offspring was determined from the number of neonates released. Newborns from the second brood (four randomly chosen neonates from each replicate) were also measured. The experiment was terminated when daphnids had reached the third adult instar (i.e. had released neonates from their first two broods). As a measure of fitness, the intrinsic rate of increase (r) was estimated by solving the Euler–Lotka equation (Stearns, 1992) iteratively. Based on laboratory findings this parameter mainly reflects age-specific fecundity and additionally includes some background mortality which mainly occurred in the low food treatments. Calculated this way, r , of course, cannot be compared with population growth rates as determined from field samples, thus including predatory mortality and consequently, it is a rather simplified measure of fitness (see Discussion).

Effects of fish treatment and food level on life history traits were tested by two-way analysis of variance (ANOVAs) and differences between means were analysed with a Tukey HSD multiple comparison test. The relation between body and clutch size in different treatments was analysed separately for high and low food levels by analysis of covariance (ANCOVA).

RESULTS

At high food conditions all fish treatments had a significant effect on size at maturity of *Daphnia* (Figure 1, Table I), whereas no difference between different fish treatments could be detected (Table II). Age at maturity did not significantly differ in any fish treatment compared with the control at high food (Tukey HSD, $P > 0.1$). Under low food conditions the effects were reversed (Figure 1). Size at maturity was generally low but unaffected by fish treatments (Tukey HSD, $P > 0.1$), whereas age at maturity was significantly decreased in fish treatments compared with the control (Tukey HSD, $P < 0.001$). The latter effect was more pronounced in the YOY60 treatment compared with the other fish treatments.

At high food concentrations there was a clear relation between body and clutch size (Figure 2). After testing for homogeneity of slopes ($F_{3,90} = 0.488$, $P = 0.692$) a clear treatment effect could be shown ($F_{3,93} = 18.785$, $P > 0.001$) which could not be explained by differences among fish treatments ($F_{2,73} = 1.363$, $P = 0.262$). Only very

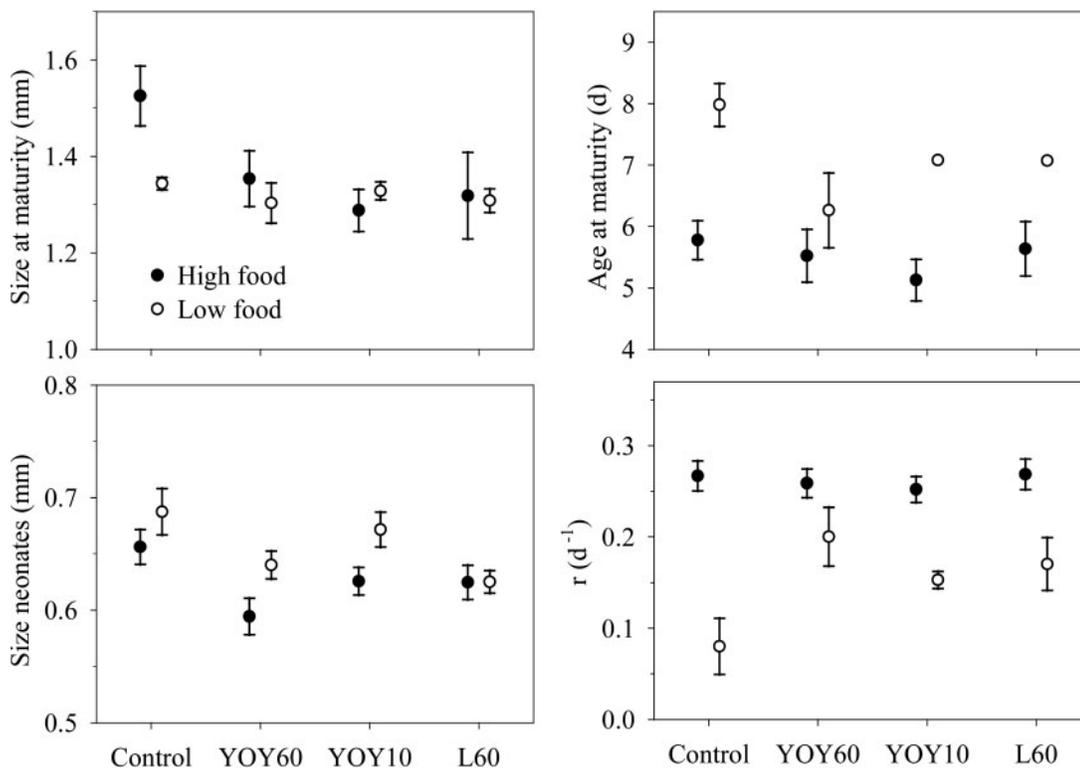


Fig. 1. Characteristics (means \pm 2 SE) of several life history traits (size at maturity, age at maturity, size of neonates of the second brood and intrinsic rate of increase, r) of one clone of *D. hyalina* \times *galeata* in treatments with different applications of fish infochemicals and at two food levels. Control = no fish infochemical; YOY60 and YOY10 = application of 60 and 10%, respectively, of water inhabited for 12 h by gape-limited juvenile perch in the culture medium; L60 = application of 60% of water inhabited for 12 h by larger perch in the culture medium.

Table I: Results of two-way ANOVA testing for the effect of food (high-low) and infochemical treatment (control, 60% YOY water, 10% YOY water, 60% water conditioned by larger fish) on life history characteristics of one clone of D. hyalina \times galeata

	df effect	MS effect	df error	F	P
SFR					
Food	1	0.03061	40	8.20	0.006649
Fish	3	0.04255	40	11.39	0.000015
Food \times Fish	3	0.02714	40	7.27	0.000529
AFR					
Food	1	30.066	40	147.161	0.000000
Fish	3	2.169	40	10.617	0.000029
Food \times Fish	3	1.255	40	6.144	0.001547
Offspring size					
Food	1	0.02593	104	33.53	0.000000
Fish	3	0.01598	104	20.67	0.000000
Food \times Fish	3	0.00323	104	4.18	0.007717
r					
Food	1	0.146869	40	201.429	0.000000
Fish	3	0.007209	40	9.888	0.000052
Food \times Fish	3	0.008794	40	12.061	0.000009

The investigated traits were size at first reproduction (SFR), age at first reproduction (AFR), offspring size (second brood), and intrinsic rate of increase (r).

Table II: Results of two-way ANOVA testing for differences between infochemical treatments (60% YOY water, 10% YOY water, 60% water conditioned by larger fish) at two food levels (high-low) on life history characteristics of one clone of *D. hyalina* × *galeata*

	df effect	MS effect	df error	F	P
SFR					
Food	1	0.00041	30	0.10	0.750994
Fish	2	0.00133	30	0.33	0.719151
Food × Fish	2	0.00622	30	1.56	0.225866
AFR					
Food	1	17.041	30	78.634	0.000000
Fish	2	0.638	30	2.942	0.068124
Food × Fish	2	1.113	30	5.135	0.012080
Offspring size					
Food	1	0.02037	82	27.86	0.000001
Fish	2	0.00765	82	10.47	0.000089
Food × Fish	2	0.00485	82	6.64	0.002133
<i>r</i>					
Food	1	0.065446	30	97.581	0.000000
Fish	2	0.002241	30	3.342	0.048955
Food × Fish	2	0.001619	30	2.415	0.106583

The investigated traits were size at first reproduction (SFR), age at first reproduction (AFR), offspring size (second brood), and intrinsic rate of increase (*r*).

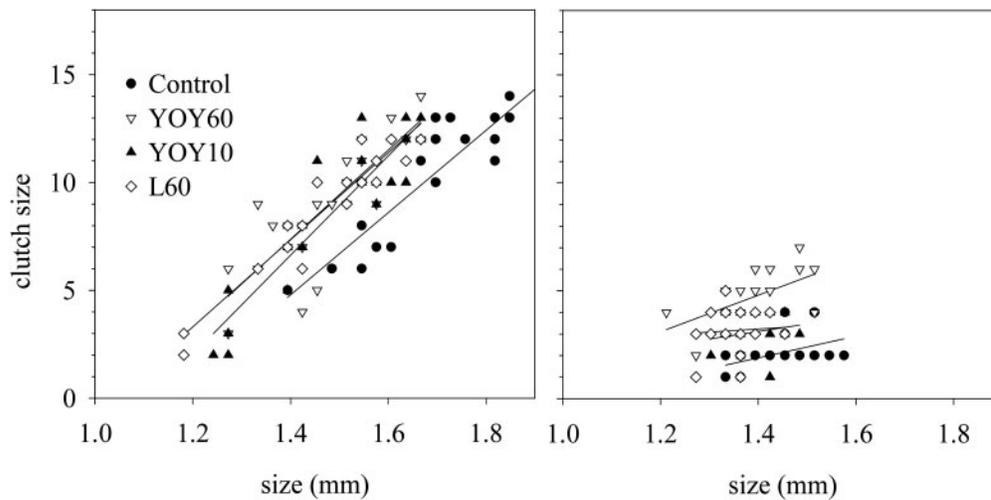


Fig. 2. Clutch size (first three clutches) in relation to body size of one clone of *D. hyalina* × *galeata* exposed to different treatments with fish infochemicals at high (left) and low (right) food levels. Control = no fish infochemical; YOY60 and YOY10 = application of 60 and 10%, respectively, of water inhabited for 12 h by gape-limited juvenile perch in the culture medium; L60 = application of 60% of water inhabited for 12 h by larger perch in the culture medium.

few eggs were produced at low food concentrations, but values tended to be higher in fish treatments (Figure 2). The relation with body size differed significantly between treatments ($F_{3,89} = 42.817$, $P < 0.001$), but the slopes were homogenous (ANCOVA $F_{3,86} = 0.645$, $P = 0.588$). However, contrary to the results in the high

food treatments, we also found significant differences between fish treatments ($F_{2,63} = 18.149$, $P < 0.001$).

The offspring size (second brood) was decreased in the presence of fish infochemicals at high food conditions, regardless of the size of the fish (Figure 1). The overall effect of low food concentrations was an increase in

offspring size. A significant decrease of offspring size occurred only in treatments YOY60 and L60 (Tukey HSD, $P = 0.00206$ and $P = 0.00013$, respectively), but not in YOY10 at low food (Tukey HSD, $P = 0.88$). Due to these inconsistent responses, offspring size was the only life history trait with highly significant differences between fish treatments (Table II).

The intrinsic rate of increase (r) was strongly affected by food conditions (Figure 1, Table I). The overall effect of fish infochemicals was significant (Table I), but this was due to a strong increase at low food conditions only (Figure 1). At high food concentrations r did not differ among treatments.

DISCUSSION

This study shows that when studying adaptive life history shifts in response to fish infochemicals, one needs to consider possible ontogenetic changes in predator foraging behaviour and the interacting effects of additional factors. While life history shifts in response to gape-limited fish seem to be maladaptive at first sight, we suggest that food-mediated phenotypic plasticity will generally result in an increase in fitness of daphnids exposed to fish predation under field conditions.

The life history shifts found in this study in response to fish infochemicals at high food conditions in general confirm findings from earlier experiments which were usually also performed at non-limiting food conditions. Size at maturity was found to be the most clearly affected trait in a meta-analysis including 10 studies of fish-induced life history shifts in daphnids (Riessen, 1999a). Age at maturity was affected to a lesser extent at high food conditions, consistent with our results and some more recent studies (Boersma *et al.*, 1999; De Meester and Weider, 1999; Doksæter and Vijverberg, 2001; Weetman and Atkinson, 2002). Fish infochemicals also often induced a smaller offspring size (Reede and Ringelberg, 1995; Spaak *et al.*, 2000). A large clonal variability with respect to the traits for which clones show a response to fish infochemicals has been shown though (Boersma *et al.*, 1998). Specific life history traits of single clones may even respond in an opposite manner to the 'normal' direction of fish-induced shifts (De Meester and Weider, 1999; Spaak *et al.*, 2000). In general, however, fish-induced life history changes reported in the literature fit into the general view that they represent adaptive responses to positive size-selective predation. Here we argue that this interpretation might not be of general ecological relevance because (i) YOY fish, often representing the most important vertebrate zooplanktivores in lakes, show a negative size-selective feeding mode during a critical period in early summer and (ii) effects of fish infochemicals may depend on food conditions.

Interactive effects of food availability and infochemicals

In response to low food conditions the direction of changes in single life history traits (with the exception of size at maturity) was opposite to changes induced by fish infochemicals when high food concentrations are considered as standard condition (Orcutt and Porter, 1984; Lynch, 1989). Consequently, we found a strong interaction of food and infochemicals on life history traits, confirming results by Weber (Weber, 2001) and Weetman and Atkinson (Weetman and Atkinson, 2002), but contrasting with results obtained in other studies (Macháček, 1991; Reede and Ringelberg, 1995; Reede, 1997; Doksæter and Vijverberg, 2001). The food effects in our study were clearly different from gradual differences in life history responses between different fish treatments, which can be explained by different concentrations of the fish infochemical (Reede, 1995).

Conflicting results with regard to the interaction of food limitation and fish infochemicals can in most cases be explained by differences in culture conditions of experimental animals. In some of those studies which did not find strong food effects, 'low' food levels were likely still too high to be limiting [0.25 and 0.57 mg C L⁻¹ in Reede (Reede, 1997) and Reede and Ringelberg (Reede and Ringelberg, 1995), respectively]; ~ 0.5 mg C L⁻¹ in Macháček (Macháček, 1991) assuming a conversion factor of 50 to relate chlorophyll *a* to carbon content (Strickland, 1960). Since strong non-linear effects of resource depression on *Daphnia* life history can be expected at food concentrations < 0.3 – 0.5 mg C L⁻¹ (Orcutt and Porter, 1984; Lynch, 1989; Boersma and Vijverberg, 1994), even small differences in food and (pre-) culture conditions may explain large discrepancies in observed life history responses between different studies.

When comparing studies on *Daphnia* life history under limiting food conditions attention has to be paid both to the pre-culturing history of the animals and the feeding regime (static set-up with pulsed feeding versus flow-through systems with continuous food supply). Especially low food conditions have proven difficult to control in a static set-up (Porter and Orcutt, 1980) and the frequency of food supply has implications for experimental results (MacIsaac and Gilbert, 1991). Within the constraints of available knowledge we conclude that life history effects of infochemicals depend strongly on food availability (Weber, 2001; Weetman and Atkinson, 2002).

Adaptive significance of life history shifts

Since we showed here that the response to fish infochemicals does not relate to the actual feeding behaviour of the predator [confirming results of e.g. (Loose *et al.*, 1993)],

it seems that daphnids are constrained in their use of predator-released information and that a response to fish infochemicals may even be detrimental to the daphnids. Indeed, one might argue that YOY fish have an advantage in producing the infochemical because they would earlier be able to feed on egg-carrying prey. Feeding on egg-carrying daphnids should be more profitable than feeding on equally-sized prey without eggs (Culver *et al.*, 1985) and there is some evidence that fish indeed select egg-carrying cladocerans over non-egg carrying specimens (Koufopanou and Bell, 1984; Gliwicz, 1994). In that case the infochemical released by gape-limited fish should actually be categorized as being an allomone instead of a kairomone (Brown *et al.*, 1970).

From a *Daphnia* perspective it should indeed be more beneficial not to respond in the 'usual' way to fish infochemicals as long as the fish are gape-limited. However, since fish obviously smell the same to *Daphnia*, irrespective of size or ontogenetic stage (this study), species and food (Loose *et al.*, 1993; von Elert and Pohnert, 2000), daphnids only have the 'choice' between responding and not responding. Daphnids collected at different times of the season in the field were found to differ in responsiveness in life history parameters to fish infochemicals (Stibor and Lampert, 2000). If non-responsive clones should dominate the population during the clear-water phase and these clones are eventually replaced by responsive clones in summer there would be no 'dilemma' in the response of the daphnids. However, Stibor and Lampert (Stibor and Lampert, 2000) provide no evidence for this assumption, because they only studied the period between July and December and even in these samples, genetic markers did not reflect the change in life history properties. The (very responsive) clone of *D. hyalina* × *galeata* we used in our experiment was collected in spring before YOY fish were present and represents a clonal group which dominated the population in Lake Maarsseveen also during summer (M. Brehm, NIOO-KNAW, personal communication). Although this fact does not preclude the possibility of clonal succession, we can at least conclude from our results that the dominance of YOY fish will not initiate a replacement of clones which are sensitive to fish infochemicals if the time of low food for *Daphnia* and gape-limited feeding of YOY fish coincide.

Assuming that life history shifts in response to fish infochemicals are beneficial during most of the season, an increase in vulnerability for a rather short period of gape-limited feeding of YOY fish in early summer can be seen as a cost the daphnids have to pay for being protected later in summer and autumn. Indeed, theoretical studies suggest that life history plasticity 'is adapted to the long-term variation in predation schedules', but that 'its effectiveness would have limits' (Taylor and Gabriel, 1993). In addition, it has to be kept in mind that YOY fish never occur alone,

although their numerical density may predominate over larger planktivorous fish by several orders of magnitude (Wagner *et al.*, 2004). The cost of a maladaptive response to small gape-limited fish might be low, however, due to the interaction of the infochemical effect with effects of food limitation on *Daphnia* life history. Gape-limited juvenile fish usually occur during the spring clear-water phase when daphnids are severely food limited (Tessier, 1986; Wu and Culver, 1994). Even in highly productive systems which lack a clear-water phase, daphnids can be expected to become food limited during periods of high abundance in early summer (Boersma *et al.*, 1996). We found that life history shifts in response to fish infochemicals under low food conditions differ remarkably from responses at high food, confirming results by Weber (Weber, 2001). While size at maturity was not decreased in fish treatments compared with the control under low food conditions, age at maturity was significantly lower in fish treatments. This trait is much more important for general fitness in terms of population growth rate r than size at maturity. Thus, a decreased age at maturity [at least in the first induced generation (De Meester and Weider, 1999)] should also be a 'useful' strategy at high predation risk, irrespective of the size-selection of the predator. While this argument remains speculative at this point, it can at least be concluded that at low food conditions daphnids do not increase their vulnerability to gape-limited fish by further decreasing size at maturity in response to fish infochemicals. Our study suggests that life history responses to fish infochemicals will change when food conditions for daphnids increase later in summer as can be expected in temperate lakes (Sommer *et al.*, 1986). At that time YOY fish are no longer gape-limited and under these conditions (with increasing food levels inducing a low age at maturity but increasing size) a decrease of the size at maturity may indeed allow the daphnids to coexist with YOY (and other zooplanktivorous) fish.

It should be noted, however, that any adaptive argument with regard to life history shifts in response to predators remains highly speculative. It has, for example, never been conclusively shown that a decrease in size at maturity of ~0.2 mm (as found in most laboratory studies of fish-induced life history shifts) indeed decreases vulnerability to fish predation. By contrast, the effectiveness of behavioural responses to fish cues is much easier to demonstrate (Vos *et al.*, 2002). Those few modelling approaches which suggest an adaptive significance of a smaller size at maturity under threat of fish predation worked with rather arbitrarily chosen parameters for the size-selection of the fish (Taylor and Gabriel, 1992; Spaak *et al.*, 2000). They also assumed that fish feed in a strictly size-selective manner, whereas there is strong evidence that prey visibility (determined, in case of daphnids, mainly

by the presence of eggs) is at least as important (Vuorinen *et al.*, 1983; Tucker and Woolpy, 1984; Hessen, 1985).

Generally, the use of r (calculated from laboratory data, thus excluding predation) as fitness parameter seems inappropriate, but modelling approaches including predation thus far remain highly speculative due to the complex feeding behaviour of fish. What is really needed are experimental data proving (or not) the adaptive significance of fish-induced life history reactions. Also our argument stated above that food limitation during the clear-water phase mitigates the maladaptive response to gape-limited fish needs to be confirmed in future studies. Since food levels were also found to interact with temperature effects (Neill, 1981; Giebelhausen and Lampert, 2001) three-way interactions are possible as well (Weetman and Atkinson, 2002). A demographic modelling approach, based on detailed field observations of patterns of food limitation and fish predation and on laboratory experiments, may provide the necessary information to analyse the complex predator-prey relationship between *Daphnia* and juvenile fish and its evolutionary implications in more detail (Riessen, 1999b).

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REFERENCES

- Boersma, M. and Vijverberg, J. (1994) Resource depression in *Daphnia galeata*, *Daphnia cucullata* and their interspecific hybrid: life history consequences. *J. Plankton Res.*, **16**, 1741–1758.
- Boersma, M., Van Tongeren, O. F. R. and Mooij, W. M. (1996) Seasonal patterns in the mortality of *Daphnia* species in a shallow lake. *Can. J. Fish. Aquat. Sci.*, **53**, 18–28.
- Boersma, M., Spaak, P. and De Meester, L. (1998) Predator-mediated plasticity in morphology, life history, and behavior of *Daphnia*: the uncoupling of responses. *Am. Nat.*, **152**, 237–248.
- Boersma, M., De Meester, L. and Spaak, P. (1999) Environmental stress and local adaptation in *Daphnia magna*. *Limnol. Oceanogr.*, **44**, 393–402.
- Brown, W. L. J., Eisner, T. and Whittaker, R. H. (1970) Allomones and kairomones: transspecific chemical messengers. *BioScience*, **20**, 21–22.
- Cryer, M., Peirson, G. and Townsend, C. R. (1986) Reciprocal interactions between roach, *Rutilus rutilus*, and zooplankton in a small lake: prey dynamics and fish growth and recruitment. *Limnol. Oceanogr.*, **31**, 1022–1038.
- Culver, D. A., Boucherle, M. M., Bean, D. J. and Fletcher, J. W. (1985) Biomass of freshwater crustacean zooplankton from length-weight regressions. *Can. J. Fish. Aquat. Sci.*, **42**, 1380–1390.
- De Meester, L. and Weider, L. J. (1999) Depth selection behavior, fish kairomones, and the life histories of *Daphnia hyalina* × *galeata* clones. *Limnol. Oceanogr.*, **44**, 1248–1258.
- Doksæter, A. and Vijverberg, J. (2001) The effects of different food and temperature regimes on life-history responses to fish kairomones in *Daphnia hyalina* × *galeata*. *Hydrobiologia*, **442**, 207–214.
- Giebelhausen, B. and Lampert, W. (2001) Temperature reaction norms of *Daphnia magna*: the effect of food concentration. *Freshwater Biol.*, **46**, 281–289.
- Gliwicz, Z. M. (1994) Relative significance of direct and indirect effects of predation by planktivorous fish on zooplankton. *Hydrobiologia*, **272**, 201–210.
- Guillard, R. R. L. and Lorenzen, C. J. (1972) Yellow-green algae with chlorophyllide-c. *J. Phycol.*, **8**, 10–14.
- Hansen, M. J. and Wahl, D. H. (1981) Selection of small *Daphnia pulex* by yellow perch fry in Oneida Lake, New York. *Trans. Am. Fish. Soc.*, **110**, 64–71.
- Hessen, D. O. (1985) Selective zooplankton predation by pre-adult roach (*Rutilus rutilus*): the size-selective hypothesis versus the visibility-selective hypothesis. *Hydrobiologia*, **124**, 73–79.
- Koufopanou, V. and Bell, G. (1984) Measuring the cost of reproduction IV. Predation experiments with *Daphnia pulex*. *Oecologia*, **64**, 81–86.
- Loose, C. J., von Elert, E. and Dawidowicz, P. (1993) Chemically-induced diel vertical migration in *Daphnia*: a new bioassay for kairomones exuded by fish. *Arch. Hydrobiol.*, **126**, 329–337.
- Lynch, M. (1989) The life history consequences of resource depression in *Daphnia pulex*. *Ecology*, **70**, 246–256.
- Macháček, J. (1991) Indirect effects of planktivorous fish on the growth and reproduction of *Daphnia galeata*. *Hydrobiologia*, **225**, 193–197.
- MacIsaac, H. J. and Gilbert, J. J. (1991) Competition between *Keratella cochlearis* and *Daphnia ambigua*: effects of temporal patterns of food supply. *Freshwater Biol.*, **25**, 189–198.
- Mehner, T., Schultz, H. and Herbst, R. (1995) Interaction of zooplankton dynamics and diet of 0+ perch (*Perca fluviatilis* L.) in the top-down manipulated Bautzen reservoir (Saxony, Germany) during summer. *Limnologica*, **25**, 1–9.
- Mehner, T., Plewa, M., Hülsmann, S. and Worischka, S. (1998) Gape-size dependent feeding of age-0 perch (*Perca fluviatilis*) and age-0 zander (*Stizostedion lucioperca*) on *Daphnia galeata*. *Arch. Hydrobiol.*, **142**, 191–207.
- Mills, E. L. and Forney, J. L. (1983) Impact on *Daphnia pulex* of predation by young yellow perch in Oneida Lake, New York. *Trans. Am. Fish. Soc.*, **112**, 151–161.
- Neill, W. E. (1981) Developmental responses of juvenile *Daphnia rosea* to experimental alteration of temperature and natural seston concentration. *Can. J. Fish. Aquat. Sci.*, **38**, 1357–1362.
- O'Brien, W. J. (1979) The predator-prey interaction of planktivorous fish and zooplankton. *Am. Sci.*, **67**, 572–581.
- Orcutt, J. D. J. and Porter, K. G. (1984) The synergistic effects of temperature and food concentration on life history parameters of *Daphnia*. *Oecologia*, **63**, 300–306.

- Porter, K. G. and Orcutt, J. D. J. (1980) Nutritional adequacy, manageability, and toxicity as factors that determine the food quality of green and blue-green algae as food for *Daphnia*. In Kerfoot, W. C. (ed.), *Evolution and Ecology of Zooplankton Communities*. University Press of New England, Hanover, New Hampshire, pp. 268–281.
- Reede, T. (1995) Life history shifts in response to different levels of fish kairomones in *Daphnia*. *J. Plankton Res.*, **17**, 1661–1667.
- Reede, T. (1997) Effects of neonate size and food concentration on the life history responses of a clone of the hybrid *Daphnia hyalina* × *galeata* to fish kairomones. *Freshwater Biol.*, **37**, 389–396.
- Reede, T. and Ringelberg, J. (1995) The influence of a fish exudate on two clones of the hybrid *Daphnia galeata* × *hyalina*. *Hydrobiologia*, **307**, 207–212.
- Riessen, H. P. (1999a) Predator-induced life history shifts in *Daphnia*: a synthesis of studies using meta-analysis. *Can. J. Fish. Aquat. Sci.*, **56**, 2487–2494.
- Riessen, H. P. (1999b) *Chaoborus* predation and delayed reproduction in *Daphnia*: a demographic modeling approach. *Evol. Ecol.*, **13**, 339–363.
- Ringelberg, J., Flik, B. J. G., Aanen, D. and Van Gool, E. (1997) Amplitude of diel vertical migration (DVM) is a function of fish biomass, a hypothesis. *Arch. Hydrobiol. Spec. Issues Adv. Limnol.*, **49**, 71–78.
- Scott, M. A. and Murdoch, W. W. (1983) Selective predation by the backswimmer, *Notonecta*. *Limnol. Oceanogr.*, **28**, 352–366.
- Sommer, U., Gliwicz, Z. M., Lampert, W. and Duncan, A. (1986) The PEG-model of seasonal succession of planktonic events in fresh waters. *Arch. Hydrobiol.*, **106**, 433–471.
- Spaak, P., Vanoverbeke, J. and Boersma, M. (2000) Predator-induced life history changes and the coexistence of five taxa in a *Daphnia* species complex. *Oikos*, **89**, 164–174.
- Stearns, S. C. (1992) *The Evolution of Life Histories*. Oxford University Press, Oxford, 249 pp.
- Stibor, H. and Lampert, W. (2000) Components of additive variance in life history traits of *Daphnia hyalina*: seasonal differences in the response to predator signals. *Oikos*, **88**, 129–138.
- Strickland, J. D. H. (1960) Measuring the production of marine phytoplankton. *Bull. Fish. Res. Bd. Canada*, **122**, 1–172.
- Taylor, B. E. and Gabriel, W. (1992) To grow or not to grow: optimal resource allocation for *Daphnia*. *Am. Nat.*, **139**, 248–266.
- Taylor, B. E. and Gabriel, W. (1993) Optimal adult growth of *Daphnia* in a seasonal environment. *Funct. Ecol.*, **7**, 513–521.
- Tessier, A. J. (1986) Comparative population regulation of two planktonic cladocera (*Holopedium gibberum* and *Daphnia catawba*). *Ecology*, **67**, 285–302.
- Tollrian, R. and Dodson, S. I. (1999) Inducible defenses in cladocera: constraints, costs, and multipredator environments. In Tollrian, R. and Harvell, C. D. (eds), *The Ecology and Evolution of Inducible Defenses*. Princeton University Press, Princeton, New Jersey, pp. 177–202.
- Tucker, R. P. and Woolpy, S. P. (1984) The effect of parthenogenetic eggs in *Daphnia magna* on prey location by the bluegill sunfish (*Lepomis macrochirus*). *Hydrobiologia*, **109**, 215–217.
- Van Gool, E. and Ringelberg, J. (2002) Relationship between fish kairomone concentration in a lake and phototactic swimming by *Daphnia*. *J. Plankton Res.*, **24**, 713–721.
- von Elert, E. and Pohnert, G. (2000) Predator specificity of kairomones in diel vertical migration of *Daphnia*: a chemical approach. *Oikos*, **88**, 119–128.
- Vos, M., Flik, B. J. G., Vijverberg, J., Ringelberg, J. and Mooij, W. M. (2002) From inducible defence to population dynamics: modelling refuge use and life history changes in *Daphnia*. *Oikos*, **99**, 386–396.
- Vuorinen, I., Rajasilta, M. and Salo, J. (1983) Selective predation and habitat shift in a copepod species – support for the predation hypothesis. *Oecologia*, **59**, 62–64.
- Wagner, A., Hülsmann, S., Dörner, H., Janssen, M., Kahl, U., Mehner, T. and Benndorf, J. (2004) Initiation of the midsummer decline of *Daphnia galeata* in the biomanipulated Bautzen Reservoir as related to predation, non-consumptive mortality and recruitment: a balance. *Arch. Hydrobiol.*, in press.
- Weber, A. (2001) Interactions between predator kairomone and food level complicate the ecological interpretation of *Daphnia* laboratory results. *J. Plankton Res.*, **23**, 41–46.
- Weetman, D. and Atkinson, D. (2002) Antipredator reaction norms for life history traits in *Daphnia pulex*: dependence on temperature and food. *Oikos*, **98**, 299–307.
- Wu, L. and Culver, D. A. (1994) *Daphnia* population dynamics in Western Lake Erie: regulation by food limitation and yellow perch predation. *J. Great Lakes Res.*, **20**, 537–545.

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