Tail spine length in the *Daphnia galeata* complex: costs and benefits of induction by fish

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Abstract

We studied the combined effect of fish kairomones and food conditions on the relative tail spine length (RTL) of five *Daphnia* taxa, and the interaction of these factors with the vertical distribution of the daphnids. The experiment was done in two large-scale indoor containers, the so-called plankton towers in Plön, Germany. We conducted a competition experiment in which food level and the presence of fish chemicals and later fish were varied. A strong response of RTL to fish kairomones (e.g., longer tail spines), significant differences in RTL between species, but no differences in RTL with water depth were found. Further, we observed that these *Daphnia* taxa produced a higher RTL only under high food conditions. This suggests that there is a cost related to the production of longer tail spines.

In a preliminary study in lake Plußsee, we found that *Daphnia* had longer average RTL than in the towers. Further, we noted significant differences in RTL between the two sampling dates, which may be related to a lower food level. We also detected a strong inverse correlation between RTL and depth. We discuss the implications of these findings for the co-existence of co-occurring *Daphnia* species and their hybrids.

Introduction

An important factor influencing community structure and the evolution of life-history characteristics in aquatic systems is predation (e.g., Lynch, 1980; Zaret, 1980; Kerfoot & Sih, 1987). In planktonic foodwebs, for example, invertebrate predators, such as cyclopoid copepods, predaceous cladocerans like *Leptodora kindtii*, and larvae of the phantom midge, *Chaoborus* spp., generally are negatively size selective predators on daphnids, and these prey taxa are expected to favour early growth to an invulnerable size, at the expense of delayed reproduction (Lynch, 1980). In contrast, most fish species predate in a positive size-selectively fashion on most zooplankters, and hence clones of *Daphnia* adapted to fish predation are predicted to mature early and at a smaller size. Several studies (for review see Larsson & Dodson, 1993) have indicated that even the mere presence of chemicals released by predators (kairomones) can induce these life-history shifts

in cladocerans in the direction predicted by theoretical models (Taylor & Gabriel, 1992).

Besides changes in the life-history, planktonic animals can reduce predation risk through changes in morphological structures (e.g., tail spine, neck teeth and helmet) (Zaret, 1980; Dodson, 1989; Tollrian, 1995b). Several authors have shown that in zooplankton, especially in *Daphnia*, neck teeth and increases in helmet length can be induced by the presence of invertebrate predators (for review see Larsson & Dodson, 1993). It was demonstrated that the presence of the morphological defence structures provide a selective advantage compared to individuals without these structures (Havel & Dodson, 1984; Tollrian, 1995a).

Recently it was shown that also kairomones excreted by fish can cause (tail) spine length to increase in *Daphnia magna* (Spaak, Boersma & De Meester, unpublished results) and *Odonata* larvae (Johansson & Samuelsson, 1994). This could be caused by very unspecific reactions to predator kairomones, but this

does not seem very likely, as Stibor & Lüning (1994) showed that the reaction of daphnids to different predators is rather specific. Most likely, the increase in tailspine as caused by fish kairomones is also an adaptive response. Barnhisel (1991), Swaffar & O'Brien (1996) demonstrated that longer tail spines reduce predation by fish.

Most researchers studying the reaction of multiple traits to chemicals exuded by predators have assumed that morphological changes, such as the induction of helmets, neck teeth and spines, should have costs (Jacobs, 1967; Parejko & Dodson, 1991) and show changes in life history traits as a result of these costs. However, several independent studies (Spitze, 1992; Black, 1993; Lüning, 1994; Tollrian, 1995b) have observed a poor association between the degree of neck teeth induction and differences in life-history characteristics. This was interpreted by most of the above mentioned authors as evidence that neck teeth formation is low in costs. However, this lack of association could be caused by independent reactions of different traits, i.e. the presence of morphological defences making life-history changes unnecessary (De Meester, 1996; De Meester & Pijanowska, 1997). Results of the few studies that involved two different traits indeed indicated that induced responses in different traits can be at least partly uncoupled (Spitze, 1992; Lüning, 1994; De Meester & Pijanowska, 1997). Anecdotal evidence, however, suggests (Boersma unpublished) that spine formation does have a cost; under low food conditions spines of *Daphnia magna* tend to be shorter than when food is not limiting. Hence, in this study, we will investigate whether tail spine induction by fish in several *Daphnia* taxa differs under different food levels.

Besides morphological defences, *Daphnia* also shows changes in behaviour in response to fish and fish kairomones. From the reported behavioural responses e.g. swarming (Young et al., 1994; Mitchell et al., 1995), escape behaviour (De Meester & Pijanowska, 1997), and vertical migration (Ringelberg, 1980), diel vertical migration (DVM) has been most extensively studied (Ringelberg, 1964, 1991, 1995; Stich & Lampert, 1981; Ringelberg et al., 1991a,b; Ringelberg & Flik, 1994; De Meester et al., 1995; Ringelberg & Van Gool, 1995). Because fish feed primarily in the upper part of the water column and cause a heterogeneous depth distribution in zooplankton, we hypothesise a positive relationship between spine length and the vertical distribution of *Daphnia*. We expect

longer spined individuals in the upper part of the water column.

Within the *Daphnia galeata – cucullata – hyalina* species complex, taxon specific life history features have been shown to mediate hybrid maintenance. For example, the combination of a relative high intrinsic rate of increase (*r*) and small body size may give the *D. cucullata × galeata* hybrid a selective advantage over either parental species in a lake with moderate fish predation (Spaak & Hoekstra, 1995). Differences in spine production were found among *Daphnia* taxa (Swaffar & O'Brien, 1996), thus we also expect different reactions in these taxa to fish chemicals. Indeed Spaak, Boersma & De Meester (unpublished results) found clonal variation for spine length in response to fish kairomones.

In the present study, we report on the variation in spine length among *Daphnia* taxa that occur in the Plußsee, a small eutrophic lake in Northern Germany. The *Daphnia* community from this lake was used as a model system to investigate the co-existence among hybrid and parental *Daphnia* taxa. To determine how fish kairomones, fish, and food level influence the depth distribution and competition among taxa, an experiment was done in the plankton towers of the Max Planck Institute for Limnology in Plön. Here we concentrate on interspecific differences in tail spine length in relation to fish, food, and depth.

Material and methods

Field study

Plußsee is a small (1429 ha) funnel-shaped lake surrounded by trees. It is stratified for a large part of the year with an anoxic zone that starts between 6 and 8 m (Table 1). Mean depth of this eutrophic lake is 9.4 m. and the maximum depth is 27 m. The *Daphnia* community of the lake consists of *D. galeata*, *D. cucullata* and the hybrids *D. cucullata × galeata*, *D. cucullata × hyalina* and *D. galeata × hyalina* (Wolf & Mort, 1986; Spaak, 1995b). The fish fauna of Plußsee consists of 13 species; roach (*Rutilus rutilus*) and perch (*Perca fluviatilis*) comprise about 70% of the standing stock (Krambeck et al., 1994).

We sampled the lake on 30 May 1996 and 11 June 1996 around noon and mid-night. We collected plankton at 1 m depth intervals using a 23 l Schindler water sampler. The water samples were taken directly to the laboratory. If present, thirty adult daphnids from each

Table 1. Some physical parameters of the Plußsee on both sampling dates, 30 May and 10 June 1996

Depth (m)	30 May 1996			10 June 1996		
	Chlorophyll (μg l^{-1})	Temp. ($^\circ$C)	O$_2$ (mg l^{-1})	Chlorophyll (μg l^{-1})	Temp. ($^\circ$C)	O$_2$ (mg l^{-1})
0–1	53.9	15.6	13.7	13.8	21.7	15.1
2–3	33.9	13.8	11.2	26.2	15.6	12.2
4–5	11.1	8.4	5.6	12.3	8.7	4.4
6–7	20.3	5.1	0.6	20.3	5.5	0.4
>7	8.9	4.2	0.6	8.9	4.2	0.4

sample were randomly selected. Body length, the distance between the top of the eye and the base of the tailspine, and the length of the tail spine were measured. Individual daphnids were frozen at –80 $^\circ$C in microtiter plates for later electrophoretic analysis which enables taxonomic determination (Spaak, 1996). The rest of each sample was preserved in 4% formaldehyde and counted later to determine densities.

Experimental set-up

A large-scale competition experiment was conducted in the plankton towers (Lampert & Loose, 1992) using twenty clones (four clones of each taxon) collected from the Plußsee in autumn 1995. Clones were selected based on their electrophoretical genotype. In order to ensure replication, and for statistical analysis both towers received the same treatment. The effect of different treatments was tested sequentially. The towers were filled with filtered (10 μm) water from nearby lake Schöhsee. We changed food levels during the experiment from 0.8 mg C l^{-1} (high) to 0.3 mg C l^{-1} (low). Because the towers become unstable after roughly fifty days, they were emptied and cleaned before the second phase of the experiment. Food levels during the second part of the experiment were 0.8 mg C l^{-1} (see Figure 1). Food levels were established once a day during the high food treatment and twice a day during the low food treatment. Two algal species (*Scenedesmus acutus* and *Rhodomonas* were used as food in a 9:1 mixture. Both towers had a thermocline (20 $^\circ$C/8 $^\circ$C) at a depth of eight meters. Under the thermocline an anoxic zone was created to mimic Plußsee conditions (summarised in Table 1). The entire experiment was completed under long day light conditions (16 h light, 8 h dark).

Each tower was stocked with 300 adult daphnids per clone in the first part of the experiment and 200 per clone in the second. The clones were grown in 12 l buckets and acclimated to the experimental temperature, light and food conditions. Samples were usually taken at night, but we also took additional day samples to examine diurnal vertical migration (not reported in this study). Sampling was done at ten depths (0.6, 2, 3, 4, 5, 6, 7, 8, 9, 10 and 11 m) in both towers simultaneously using pumps and flow through traps (Lampert & Loose, 1992). Per port, sixty randomly chosen adult individuals (if available) were analysed electrophoretically for taxon determination. These animals were measured the same way as the field samples, with the rest of the sample fixed in 4% formaldehyde and counted later.

After 37 days a fish factor treatment was established in both towers. Next to each tower a sixty l tub was placed containing fifty individuals of *Leuciscus idus* (mean length six cm). Water was pumped from the towers at a depth of six m into the tubs, and then returned to the towers. After fifty days, the first part of the experiment was stopped and the system returned to initial conditions (Figure 1). The second part of the experiment was done at a food level of 0.8 mg C l^{-1}, and fish chemicals were added continuously as described above. On day 109 we introduced two fish into each tower, two more fish were added on day 116 and day 120.

Data analysis

Relative tail spine lengths (RTL) were calculated for all measured individuals of the towers ($n = 18164$) and the Plußsee ($n = 2072$) as: tail spine length/body length. Body length of *Daphnia* is known to be affected by fish chemicals and food level (Stibor, 1992; Spaak & Hoekstra, 1995). Changes in RTL could therefore be a result of changes in body length alone. Moreover, larger *Daphnia* tend to have a relatively shorter tail spine
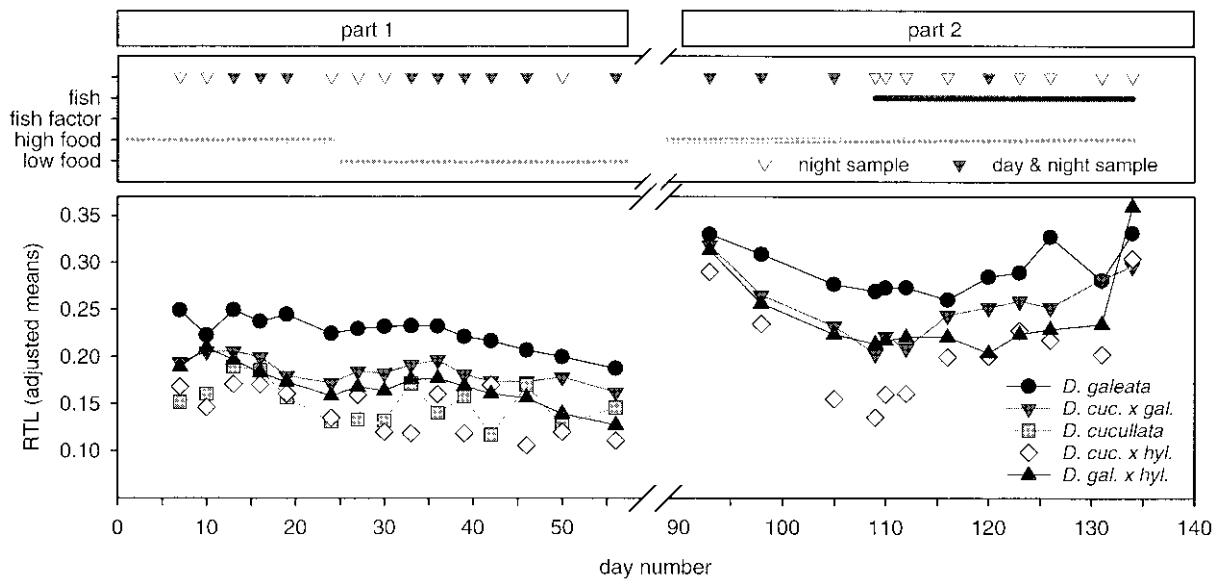
Figure 1. Upper panel: experimental design of the tower experiment. The first part of the experiment started on 14 February 1996 (day 1), the second part on 8 May (day 84); lower panel: RTLs, plotted as adjusted means of the 5 *Daphnia* taxa during the experiment.

(Lampert & Wolf, 1986; Pijanowska, 1990). Hence to correct differences in body length in our analyses we used body length as a covariate in ANOVAs, and calculated adjusted means in this way correcting for difference of RTL associated with body length.

For the analysis of the tower experiment, we used the following subsets of the data: parthenogenetic females, sampling depths from 0.6–7 m, and night samples. During the second phase of the experiment, *D. cucullata* rapidly disappeared from the towers. It was therefore excluded in the analysis of the high food–fish treatment. In all analyses we combined the data from both replicate towers. ANCOVAs were used to test for significant differences among taxa during specific treatments (food: high–low: fish factor: yes–no; fish: yes–no) using all these treatments as fixed effects, and body length as covariate. As plots of adjusted means are less informative, and more difficult to compare with data collected in other studies than plots of real means, real means are shown in the figures. These interaction plots for the mean reaction of taxa on the treatments were constructed with 95% confidence limits.

Results

Plußsee

Total densities of the *Daphnia* taxa found in the Plußsee differed between the two sampling dates of 58 ind 1^{-1} on 30 May and 191 ind 1^{-1} on 11 June. *D. galeata* and *D. cucullata* had the highest densities, whereas *D. hyalina* × *cucullata* was absent. Because day and night distributions were not different on both sampling dates, therefore they were combined. RTL was different for the four *Daphnia* taxa found in the Plußsee. Average RTL decreased significantly between the two sampling dates (Figure 2). *D. galeata* had the highest RTL, *D. cucullata* and *D. cuc.* × *gal.* intermediate, whereas the hybrid *D. gal.* × *hyl.* showed the strongest decrease between sampling dates. RTL were also significantly different among depths (Figure 3, Table 2) with smaller tail spines at greater depths. This decrease was the strongest for *D. galeata* and *D. gal.* × *hyl.*, whereas *D. cucullata* and *D. cuc.* × *gal.* showed only a small decrease in tail spine length with depth.

Towers

During the tower experiment we observed significant differences in RTL between the taxa. Overall, RTL were smaller in the tower experiment than those in the

Table 2. Results of two-way ANCOVAs for relative tail spine length in the Plußsee. Body length was used as a co-variate. The first ANOVA tested for taxon and date effects, the second for taxon and depth

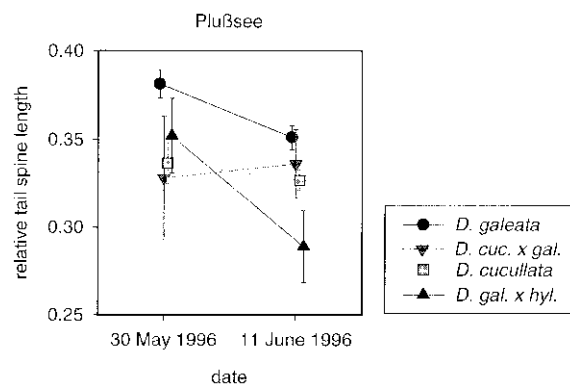| Source	df	MS	F
Taxon	3	0.4646	67.10***
Date	1	0.0656	9.47**
Taxon × date	3	0.0147	2.13
Error	2063	0.0069	
Taxon	3	0.2791	43.84***
Depth	9	0.0213	3.34***
Taxon × Depth	27	0.0141	2.22***
Error	1710	0.0064	

$**p < 0.01, *** p < 0.001.$

Figure 2. Interaction plot of mean relative tail spine length (RTL) in the Plußsee with 95% confidence limits for both sampling dates. RTL was plotted for the 4 most abundant taxa. *D. cucullata × hyalina* was found on 11 June only at very low frequencies, and therefore not plotted.

Plußsee. With high levels of food present, we observed a significant increase of RTL in the presence of fish factor (Figure 4A). When the fish factor treatment is compared to the treatment with fish, RTL of *D. cuc. × gal.*, *D. galeata* and *D. gal. × hyl* increased even more (Figure 4B). In both situations, there also was a significant interaction between taxon and fish(factor) (Table 3).

Under low food conditions, RTL were smaller and no reaction or even a negative reaction to fish factor was observed (Figure 4C). The differences among the taxa were comparable with those at high food levels and also significant (Table 3). When the response of the five taxa to food is plotted under fish factor conditions (Figure 4D) it is clear that the *Daphnia galeata* complex only reacted to fish factor with a higher RTL when

Table 3. Results of two-way ANCOVAs on taxon, fish factor, fish and food effects on relative tail spine length under different circumstances in the plankton towers. 4A: fish factor under high food; 4B fish under high food; 4C fish factor under low food; and 4D food level under the presence of fish factor. Body length was used as a co-variate. The numbers correspond with the interaction plots of Figure 4

Figure	Source	df	MS	F
4A	Taxon	4	0.5104	79.06***
	Fish Factor	1	0.5490	85.05***
	Taxon × Fish Factor	4	0.0207	4.22**
	Error	3779	0.0065	
4B	Taxon	3	1.3844	229.79***
	Fish	1	0.1412	23.44***
	Taxon × Fish	3	0.0140	2.32
	Error	5430	0.0065	
4C	Taxon	4	0.5858	138.10***
	Fish Factor	1	0.0363	8.56**
	Taxon × Fish Factor	4	0.0091	2.14
	Error	5109	0.0042	
4D	Taxon	4	0.5061	107.93***
	Food level	1	1.1753	250.62***
	Taxon × Food level	4	0.0117	2.50*
	Error	4406	0.0047	

$*p < 0.05, ** p < 0.01, *** p < 0.001.$

Table 4. Results of a three-way ANCOVA for the relative tail spine length in the plankton towers. Body length was used as a co-variate. This analysis was done using night data from the high food level period (see text)

Source	df	MS	F
Fish factor	1	0.4506	71.87
Taxon	4	1.0606	169.15
Depth	6	0.0151	2.41
Fish factor × taxon	4	0.0654	10.44
Fish factor × depth	6	0.0098	1.58
Taxon × depth	24	0.0074	1.19
Fish factor × taxon × depth	24	0.0113	1.80
Error	7474	0.0063	

$*p < 0.05, ** p < 0.01, *** p < 0.001.$

food is high. Three taxa (*D. cuc. × gal.*, *D. galeata* and *D. gal. × hyl*) showed parallel reaction norms to different food levels, whereas the reaction of *D. cucullata* and *D. cuc. × hyl.* was significantly stronger to an increase in food (Figure 4D).

In contrast to what was found in the Plußsee, the change of RTL with depth was not as clear in the
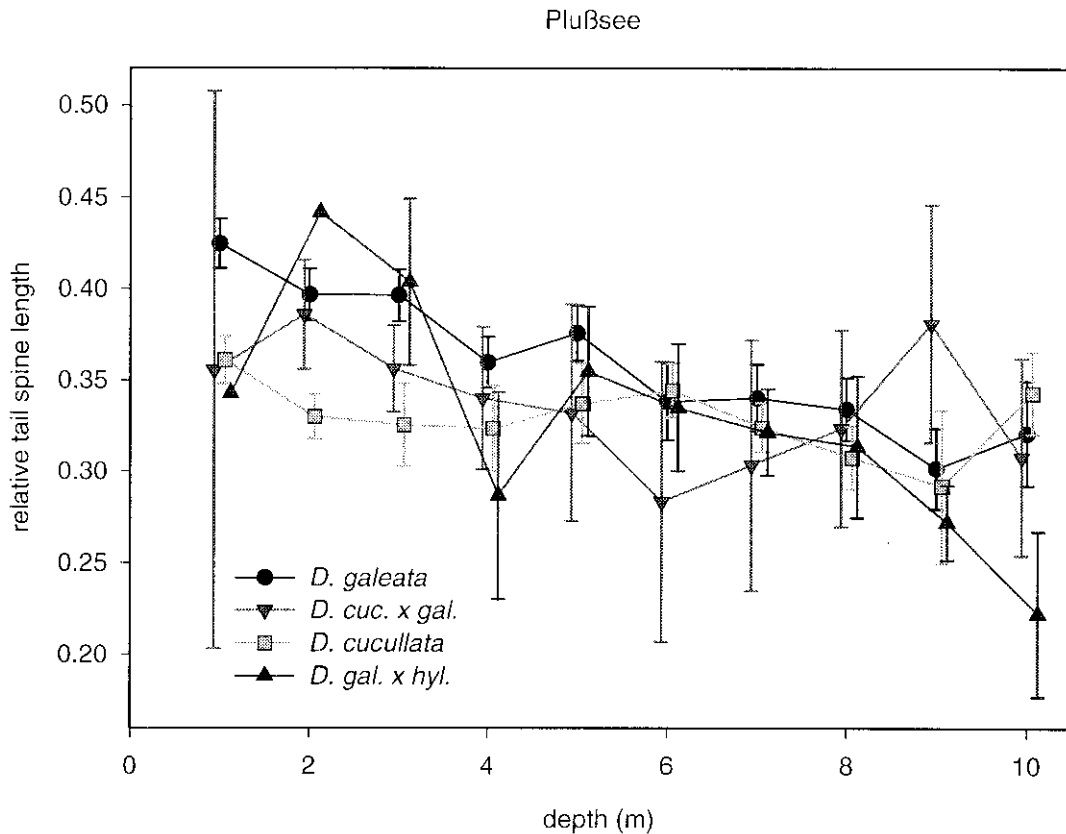
Plußsee

Figure 3. Mean RTLs with 95% confidence limits of 4 *Daphnia* taxa in the Plußsee plotted against depth. Data from both sampling dates and sampling times were pooled.

towers. The effect of depth on RTL was only significant at the 0.05 level, although also in the towers animals found at greater depths had lower values for RTL. When plotted against depth (Figure 5) the reaction to fish factor was evident.

Discussion

Our study clearly shows that relative tail spine length (RTL) of *Daphnia* is a plastic trait, the size of which can be influenced by kairomones excreted by fish. (Figures 4 and 5). Although many life history, behavioural and morphological shifts of *Daphnia* in the presence of fish kairomones have been reported (Ringelberg, 1991; Stibor, 1992; Hanazato, 1995; Macháček, 1995; Reede, 1995; Reede & Ringelberg, 1995; De Meester, 1996), an increase in RTL has not been reported in response to fish chemicals. All studies that investigated the induction of morphological defences in *Daph-*

nia were done with invertebrate predators (for review see Larsson & Dodson, 1993), and only one of them (Lüning, 1995) reported longer tail spines in *Daphnia pulex*, induced by *Chaoborus* kairomones.

RTL, being a relative trait, depends both on body size and tail spine length. Therefore it must be made sure that not indirectly the effect of fish on body size is studied, since it is well known that fish chemicals reduce the body size of *Daphnia* (see references above). We analysed the data with ANCOVAs using body length as a covariate. Although significant effects of body size on RTL were found, the main effects (fish factor, food, taxon) remained significant, which indicates that even when changes in body length are corrected for relative spine length of animals from both the field and the laboratory were still very variable, and responsive to different treatments, which is also illustrated by the pattern of the adjusted means of RTL plotted against time Figure 1).
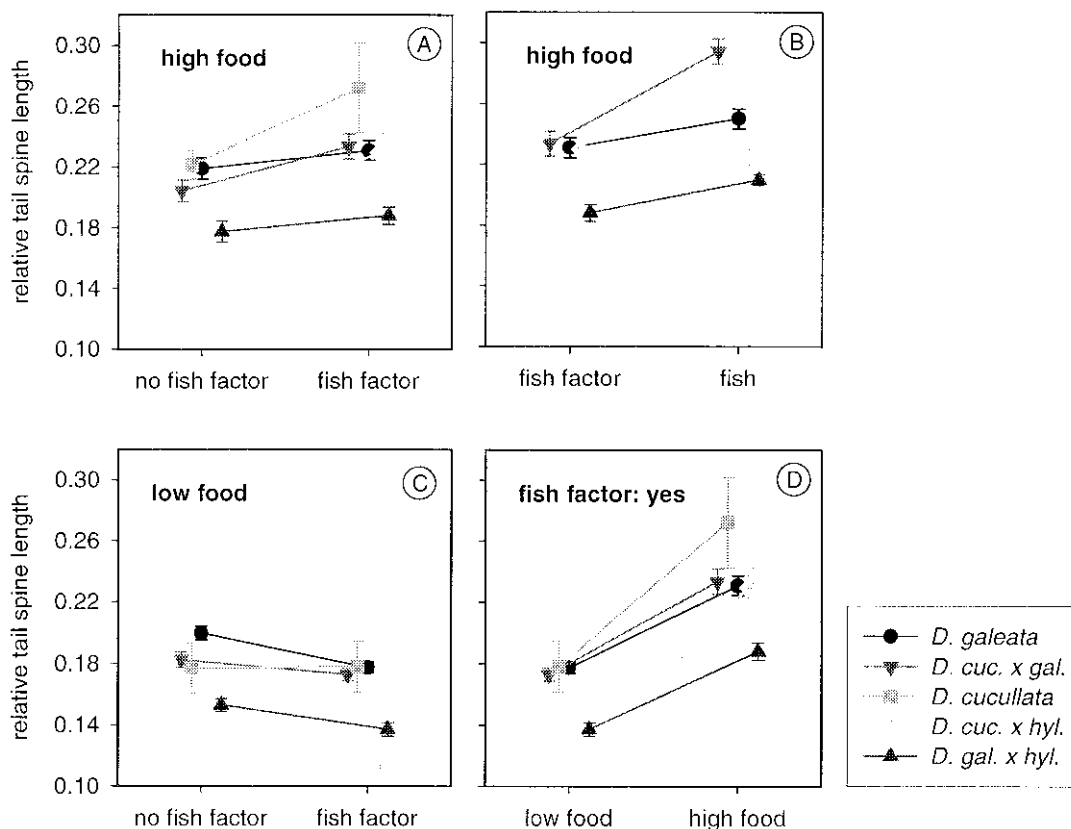
Figure 4. Interaction plots of mean RTLs in the plankton towers with 95% confidence limits of different *Daphnia* taxa against fish factor and fish under high food conditions (A, B) against fish factor under low food conditions (C) and against food level under the presence of fish factor (D). Data from both towers were combined.

The main question that remains to be answered is about adaptiveness, or do longer tail spines in the presence of fish really give daphnids a selective advantage over individuals with smaller tail spines? Although we did not specifically investigate selective predation, the differences in RTL between the period with only fish factor compared with fish present in the towers (Figure 4B) suggests that daphnids with a shorter RTL were selectively removed from the towers. Moreover, some recent studies show that longer tail spines reduced predation risk of *Daphnia* to fish. Swaffar & O'Brien (1996) found the small bluegill (20–35 mm) prefer *D. magna* with short tail spines over *D. lumholzi* of similar size with long tail spines. Moreover, they also observed that the longer tail spines of *D. lumholzi* caused greater ingestion difficulties to the small bluegills. In a study on another cladoceran species (*Bythotrephes cederstroemi*), it was also shown that longer tail spines were an effective protection against predation by small (50–60 mm) perch (Barnhisel, 1991).

Most studies on the link between predator-induced changes in life-history characteristics and morphology have focused on costs of the induced changes in morphology (e.g., Black, 1993; Tollrian, 1995b). The inability to find correlations between the degree of morphological change and changes in life-history characteristics was interpreted as evidence for the low cost of these morphological defences in daphnids. However, our observation that fish only induced longer tail spines at high food levels indicates that there are in fact cost involved with the development of longer tail spines. Recently Van Gool & Ringelberg (1995) found the same phenomenon for phototactic behaviour of *Daphnia.* They showed that *D. galeata* × *hyalina* exhibits a stronger phototactic behaviour to fish kairomones in the presence of food than in the absence of food.

RTL under natural conditions (Plußsee) were found to be larger compared to the towers (Figures 2 and 4). Such a difference between natural and culture con-
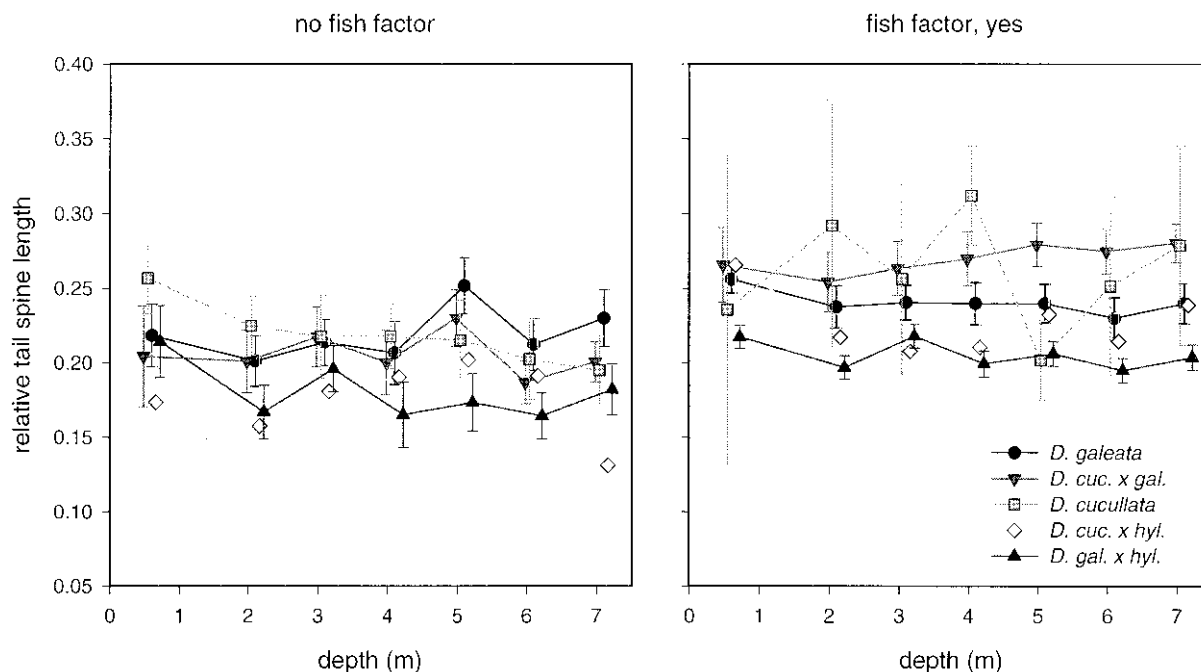
no fish factor

fish factor, yes

Figure 5. Mean RTLs with 95% confidence limits of 5 *Daphnia* taxa in the plankton towers, plotted against depth for the fish factor and non fish factor treatment. Only high food conditions are plotted.

ditions has also been found before (Jacobs, 1961; Hanazato & Ooi, 1992). Traditionally this has been explained by differences in light- and turbulence regimes between the laboratory and the field (Jacobs, 1961), but more recently different kairomone levels have been used to explain these differences (Tollrian, 1990). However, most likely the fish-kairomone concentrations in the towers were much higher, as the fish biomass was around thirty times higher in the towers compared with that in Plußsee (ca. 3000 kg ha^{-1} *versus* 100 kg ha^{-1} (Kremser, 1995). A complicating factor, however, is the presence of the invertebrate predator *Chaoborus flavicans* in the Plußsee. The effect on RTL of kairomones of this predator are similar to the ones observed in this study (cf., Lüning, 1995), which might explain the longer tail spines found in the Plußsee. Our hypothesis that relative tailspine length should decrease with depth was supported by our Plußsee data (Figure 3), and to a lesser extent by the data from the plankton towers. This phenomenon was not observed before. At shallow depths, where predation risk by visual predators is highest, we found the largest RTL, thus compensating for the more risky vertical migration behaviour. We were surprised that this pattern was only found to a small extent in the tower experiment. One explanation is that in our experimental set up, with

a mixing strategy to keep oxygen levels in the epilimnion of the towers saturated, no gradient in kairomone concentrations was present. The fact that RTL become less between two sampling dates might be caused be a reduced food availability in the lake. *Daphnia* densities increased from 30 May to 11 June and chorophyl concentrations decreased (Table 1). Another sign for food shortage is the significant reduction of the mean clutch, from 3.5 to 2.8 eggs per female.

Although the reaction to fish in the plankton towers was comparable for all five investigated taxa (Figures 4 and 5), we still observed remarkable differences among the taxa. On high food, *D. cucullata* (the smallest taxa), showed the highest RTL reaction to fish chemicals. The strong reaction of the *D. cucullata × galeata* hybrid to the presence of fish is remarkable (Figure 4B). This is in accordance to earlier studies (Spaak, 1995a; Spaak & Hoekstra, 1995) that showed that *D. cucullata × galeata* hybrids exhibit specific combinations of traits that might give them a relative advantage over parental species against fish and invertebrate predation. In our study taxa with *D. hyalina* 'blood' showed the smallest RTL. It is likely that because *D. hyalina* has more extreme DVM behaviour than *D. galeata* (Stich & Lampert, 1981), it developed fewer other defence strategies. Indeed, we found during our tower experi-

ment the strongest DVM behaviour for the *D. galeata* × *hyalina* and *D. cucullata* × *hyalina* hybrids.

In summary, the relative spine length in daphnids is a very plastic trait, which is influenced by both food conditions, and the presence of predator kairomones. Different taxa have different RTL, and react differently to environmental conditions. Our observation, that the kairomones excreted by fish influence the length of the spine in daphnids suggests that spines might also be a morphological defence structure against predation by these predators.

Acknowledgements

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