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Does trimethylamine induce life-history reactions in *Daphnia*?

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Abstract

Laboratory experiments were carried out to investigate life-history reactions of *Daphnia* to trimethylamine (TMA), a substance, which has recently been found to induce a similar phototactic reaction in *Daphnia* as fish kairomones. The effects of different treatments (control, fish kairomone and TMA) on the life-history traits of five clones of *D. magna* and one clone of *D. galeata* and *D. hyalina*, respectively, were studied. Only *D. magna* exhibited significant reactions to TMA and to fish kairomone. *D. galeata* showed no significant responses to either TMA or to fish kairomone. *D. hyalina* reacted to the fish treatment with two traits (size and number of eggs at maturity). The comparison of the reaction norms to TMA and fish kairomone demonstrated that the directions of some responses to both factors were similar but were different for others such as for size at maturity. TMA resulted in a larger size at maturity in *D. magna*, whereas fish kairomone had no significant influence on this trait. We, therefore, conclude that trimethylamine is not the primary causative chemical agent in fish induced life-history adaptations in *Daphnia*.

Introduction

Predation has a major impact on freshwater community structure (e.g. Kerfoot & Sih, 1987; Carpenter & Kitchell, 1993). The effect of zooplankton population predators, selecting for large-sized prey, such as fish, has been well-documented (Gliwicz & Pijanowska, 1989; Lampert, 1993a). Fish do not only directly affect population dynamics of zooplankters, they also exude substances which are perceived by their prey. Zooplankters, especially members of the genus *Daphnia*, react to the presence of these fish-substances with behavioural adaptations (Ringelberg, 1991; De Meester, 1993; Lampert, 1993b), life-history traits (Stibor, 1992; Stibor & Lüning, 1994), as well as changes in their morphology (Tollrian, 1994; Spaak & Boersma, 1997). These substances are defined as kairomones, as they are produced by a sender and evoke a reaction in the recipient favourable only to the recipient (Dicke & Sabelis, 1992). It is assumed that the substance produced is specific to fish, since *Daphnia* show specific adaptive responses to fish water when compared to reactions evoked by kairomones from invertebrate predators. It is notable, however, that Ringelberg & Van Gool (1998) have shown that bacteria are involved in the production of the fish kairomone.

To date, the fish kairomone has neither been isolated nor have its chemical characteristics fully been characterised (Loose et al., 1993; Von Elert & Loose, 1996; Ringelberg & Van Gool, 1998; Von Elert & Pohnert, 2000). It is not known whether the fish kairomone is just one reactive substance or a mixture of several chemicals. The identification of this/these infochemicals is of major importance to further research in this field (see Larsson & Dodson, 1993; Stibor & Lampert, 2000). It would not only allow experiments with well-defined kairomone concentrations but it would also allow the quantification of the kairomone in natural systems.

Boriss et al. (1999) showed that trimethylamine (TMA), a major component of the typical fish smell, resulting from bacterial degradation of the osmolyte trimethylamineoxide (TMAO), induced an enhanced phototactic downward reaction in *Daphnia*. The same behavioural response is observed when

daphnids are exposed to water that previously contained fish (Ringelberg, 1991; Van Gool & Ringelberg, 1995). This reaction is adaptive since it triggers Diel Vertical Migration (DVM) of *Daphnia*, a behavioural strategy reducing predation risk by fish (Lampert, 1989; Lampert, 1993b). Recently, there has been considerable debate as to whether TMA is indeed the (or one of the substances making up the) kairomone exuded by fish (Sakwińska, 2000; Pohnert & Von Elert, 2000). Both studies argued that this is not likely to be the case, mainly because of concentration problems (Pohnert & von Elert, 2000), or of differences between the reactions to TMA and fish (Sakwińska, 2000). We, therefore, set out to answer the question whether TMA induces life-history reactions in different *Daphnia* taxa, whether these responses are similar to those observed for fish kairomones, and if TMA could be used as a substance to mimic fish in laboratory experiments.

Materials and methods

We investigated the life-history reactions in the presence of TMA in three experiments. In the first experiment, we tested five *Daphnia magna* clones under fish incubation water, control, and TMA (5 μM) conditions. In the second experiment, we investigated whether smaller species of *Daphnia* were also susceptible to TMA and fish kairomones, and in the third experiment, we tested if the life-history responses depend on the TMA concentrations in the five *D. magna* clones.

In the first experiment, five *D. magna* clones, four of which (clone 1–4) originated from a lowland lake (Großer Binnensee, Northern Germany) and one (clone 5) from a pond in Frankfurt (Germany), were tested. For the preparation of the media, water from mesotrophic Schöhsee in Plön was filtered, and chemostat-grown *Scenedesmus obliquus* were added to a final food concentration of 1 mg C l^{-1}. The light:dark cycle was 16:8 h. The experiment was conducted in 200 ml glass vessels which were gas tight in order to keep the TMA concentrations constant. Each of the experimental vessels was stocked with two third-brood neonates (<12 h old) and the media was exchanged on a daily basis. The animals were subjected to the following treatments: (i) control; (ii) fish incubation water deriving from an aquarium containing two ides (*Leuciscus idus*) of about 10 cm length in 20 l for 23 h; and (iii) TMA in a concentration of 5 μM. The experiment was carried out with five replicates for every treatment×clone combination. Both animals were kept in each vessel and means of the measurements on both individuals were used.

In the second experiment, we tested two species, a *D. galeata* clone originating from an alpine lake (Aroser Obersee, Switzerland) and a *D. hyalina* clone taken from a pre-alpine lake (Lake Constance, Germany). The latter clone was the same used by Boriss et al. (1999) in their experiments on the TMA-induced changes in phototactic behaviour. The animals were grown at 20 °C in filtered (0.45 μm) and aerated lake water from eutrophic Greifensee, Switzerland. The mothers of the experimental animals were kept individually in glass vessels at a 12:12 h light cycle, and water was changed daily. Chemostat-grown algae (*S. obliquus*) were added as food to a final carbon concentration of 1 mg l^{-1}. The experiment was conducted in a flow-through set-up in which daphnids were kept individually in 150 ml Perspex cylinders closed with plankton gauze (mesh size 150 μm), with an exchange rate of 3.5 d^{-1}. The media in the reservoir bottles were stirred continuously, and renewed daily. Each of the experimental vessels was stocked with two third-brood neonates (<13 hold), one of which was removed from the vessels on the fourth day of the experiment which were subjected to the following treatments: (i) control; (ii) fish incubation water deriving from an aquarium containing two adult bitterlings (*Rhodeus sericeus amarus*) of about 5 cm in 10 l of unfiltered lake water for 21 h; (iii) TMA in a concentration of 5 μM. The experiment was carried out with three replicates for every treatment×clone combination.

In the third experiment, we used the same clones and the same experimental set-up as in experiment one. We cultured the five clones under 0, 5 (same animals as in experiment 1), 30 and 75 μM TMA.

In all three experiments, we measured life-history parameters, which are influenced by fish kairomones (e.g. Stibor, 1992; Boersma et al., 1998): size, age and number of eggs at maturity. Moreover, we estimated the intrinsic rate of population growth rate, *r*, iteratively using the Euler-Lotka equation (e.g. Stearns, 1992) for adult instars one to three. Two-way ANOVAs with treatment (fixed effect) and clone (random effect) or species (fixed effect) were carried out, followed by post-hoc comparisons to asses the significance of the reactions to fish and TMA for each clone/species separately.

Table 1. (a) Results of the two-way ANOVAs for experiment 1 with five *D. magna* clones. Clones were random, and treatment fixed factors; (b) Homogeneous groups after post-hoc tests (Duncan multiple range test). Different characters indicate a significant difference at the 5% level (F=Fish treatment; C=Control; T=TMA 5 μM)

(a) Trait	Source	df	MS	*F*	*P*
Size at Maturity	Clone	4	0.0545	5.6575	**0.0006**
	Treatment	2	0.2302	34.8826	**0.0001**
	Clone×treat.	8	0.0066	0.6845	0.7032
	Error	58	0.0096		
Age at maturity	Clone	4	2.7365	4.0162	**0.0060**
	Treatment	2	23.5713	20.0177	**0.0016**
	Clone×treat.	8	1.1775	1.7282	0.1107
	Error	59	0.6814		
No. of eggs at maturity	Clone	4	1.1377	0.2199	0.9262
	Treatment	2	39.7605	12.0458	**0.0038**
	Clone×treat.	8	3.3008	0.6379	0.7424
	Error	55	5.1741		
r	Clone	4	0.0038	5.0229	**0.0016**
	Treatment	2	0.0170	7.6107	**0.0141**
	Clone×treat.	8	0.0022	2.9124	**0.0089**
	Error	54	0.0008		

(b) Clone:	1			2			3			4			5		
	F	C	T	F	C	T	F	C	T	F	C	T	F	C	T
Size at maturity	A	A,B	B	A	A	B	A	A,B	B	A	A	B	A	A,B	B
Age at maturity	A	B	A	A	B	B	A	A	A	A	B	A	A	B	A
Number of eggs	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A
r	A	B	A	A	B	A	A	B	B	A	A	B	A	B	A

Results

In the first experiment, we observed a significant treatment effect in all of the four life-history traits (Table 1a). However, the post-hoc test showed that significant differences between treatments for single clones were only found for size and age at maturity and *r* (Table 1b). We also found significant differences between the TMA and fish treatment for some of the traits and some clones (Table 1b). In all except for one case, the direction of the response to both treatments was the same (Figs 1, 3 and 4). For size at maturity, we observed qualitative differences between the TMA and the fish treatments for all of the clones under study (Table 1b). In the presence of TMA size at maturity increased significantly compared to the control in two of the five clones, whereas no significant effect to the fish treatment could be found (Table 1b, Fig. 4).

In the second experiment, we found a significant species effect for three of the four investigated traits (Table 2a). Only the age at maturity did not differ between the *D. galeata* and the *D. hyalina* clone. The size at maturity decreased significantly in the presence of fish kairomones (Fig. 4) caused only by the reaction of *D. hyalina* (Table 2b). Furthermore, *D. hyalina* produced significantly more eggs in the presence of fish incubation water compared to the control treatment (Table 2b, Fig. 2). No significant effect of the TMA treatments on any life-history trait was found in experiment 2.

In experiment 3, significant effects of the TMA concentrations were found for size at maturity and the intrinsic rate of population increase *r* (Table 3). The *D. magna* clones were generally smaller with increasing TMA concentration but still larger than in the control (Fig. 5). The intrinsic rate of population in-

Table 2. (a) Results of the two-way ANOVAs for experiment 2 with *D. galeata* and *D. hyalina*. Both factors were fixed; (b) Homogeneous groups after post-hoc tests (Duncan multiple range test). Different characters indicate a significant difference at the 5% level (*F*=Fish treatment; C=Control; T=TMA 5 μM)

(a) Trait	Source	df	MS	*F*	*P*
Size at maturity	Species	1	0.7289	878.3450	<**0.0001**
	Treatment	2	0.0113	13.5922	**0.0011**
	Species×treat.	2	0.0022	2.6576	0.1144
	Error	11	0.0008		
Age at maturity	Species	1	0.2222	1.0000	0.3370
	Treatment	2	0.3889	1.7500	0.2153
	Species×treat.	2	0.3889	1.7500	0.2153
	Error	12	0.2222		
No. of eggs at maturity	Species	1	53.3889	56.5294	<**0.0001**
	Treatment	2	0.7222	0.7647	0.4869
	Species×treat.	2	2.7222	2.8824	0.0950
	Error	12	0.9444		
r	Species	1	0.0337	58.3027	<**0.0001**
	Treatment	2	0.0003	0.5105	0.6127
	Species×treat.	2	0.0011	1.8765	0.1954
	Error	12	0.0006		

(b)	*D. galeata*			*D. hyalina*		
	F	C	T	F	C	T
Size at maturity	A	A	A	A	B	B
Age at maturity	A	A	A	A	A	A
Number of eggs	A	A	A	A	B	A,B
r	A	A	A	A	A	A

crease *r* decreased with increasing TMA concentration (Fig. 5).

Discussion

The results of the first experiment clearly demonstrate that TMA induced life-history reactions in *Daphnia magna* (Table 1), whereas in the second experiment, no statistically significant responses to TMA were found nor for *D. galeata* neither for *D. hyalina*. *D. galeata* did also not exhibit significant reactions to fish incubation water and therefore might not be sensitive to fish kairomones. Besides, the *D. galeata* clone we used was considerably smaller than the *D. hyalina* clone (Fig. 1). In a recent study, Spaak et al. (2000) found that smaller *Daphnia* taxa were less reactive to fish kairomones than larger ones and that only the largest taxa significantly reduced their size at maturity in fish incubation water. However, in both experiments, a significant reaction to fish kairomones was found for at least one of the four investigated traits and for at least one clone (Tables 1 and 2). *D. hyalina* showed a significant reduction in its size at maturity and an increased number of eggs at first reproduction in the presence of fish kairomone, whereas four of the five *D. magna* clones exhibited a reduction in age at maturity in fish incubation water. It is important to mention that the TMA concentrations used in all our experiments were based on the concentrations used by Boriss et al. (1999). However, a recent study showed that these concentrations were much higher than TMA concentrations found in fish incubation water (Pohnert & Von Elert, 2000). Even so, the *D. hyalina* clone did not show any reaction to TMA, although it was shown to be sensitive to fish kairomone.

Table 3. Results of the two-way ANOVAs for experiment 3 with the five *D. magna* clones as random and the three different TMA concentrations as fixed factors

Trait	Source	df	MS	*F*	*P*
Size at maturity	Clone	4	0.0268	2.7856	**0.0344**
	TMA conc.	2	0.0532	4.6895	**0.0449**
	Clone×conc.	8	0.0113	1.1789	0.3269
	error	60	0.0096		
Age at maturity	Clone	4	3.5133	3.9924	**0.0062**
	TMA conc.	2	3.2133	3.7220	0.0720
	Clone×conc.	8	0.8633	0.9811	0.4597
	error	60	0.8800		
No. of eggs at maturity	Clone	4	2.8633	0.5246	0.7180
	TMA conc.	2	20.4100	2.5939	0.1354
	Clone×conc.	8	7.8683	1.4415	0.1983
	error	60	5.4583		
r	Clone	4	0.0040	3.8839	**0.0072**
	TMA conc.	2	0.0024	7.7181	**0.0136**
	Clone×conc.	8	0.0003	0.5849	0.7863
	error	60	0.0005		

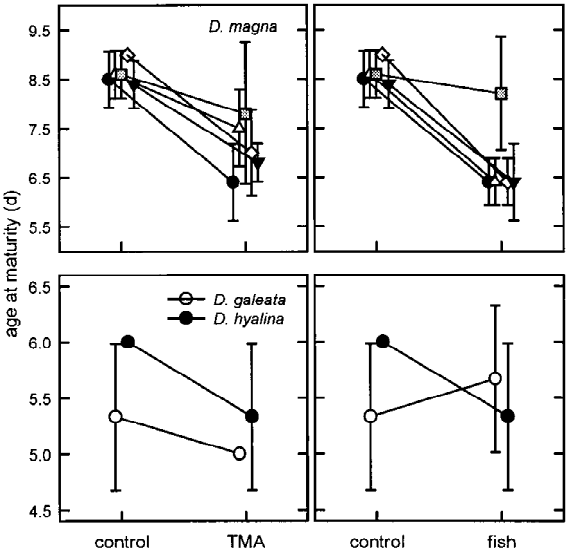

Figure 1. Age at maturity-comparison of reaction norms to TMA and to fish infochemicals in two life-history experiments with different *Daphnia* clones and species. Error bars indicate 95% confidence limits.

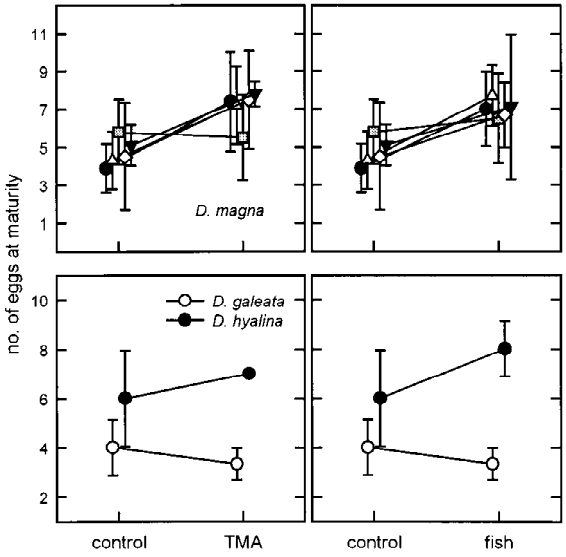

Figure 2. Size of the first clutch-comparison of reaction norms to TMA and to fish infochemicals in two life-history experiments with different *Daphnia* clones and species. Error bars indicate 95% confidence limits.

The comparison of the reaction norms to fish kairomone with those to TMA shows that the reactions to both treatments had the same direction in some traits. In experiment 1, the direction of the reactions was the same for age at maturity and for *r*, which increased in the presence of TMA and fish incubation water. How-

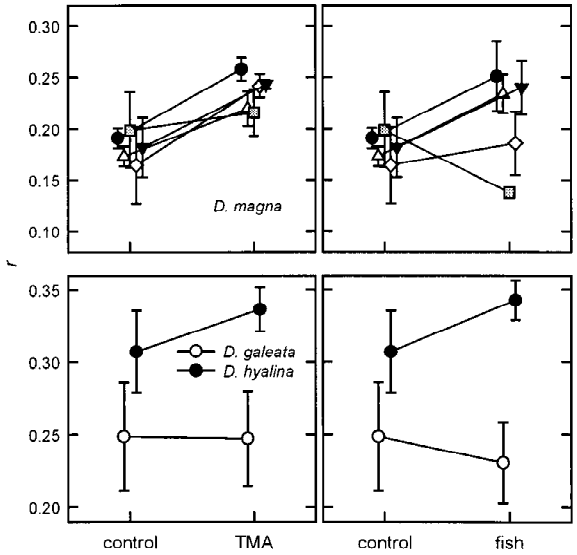

Figure 3. Intrinsic rate of population increase *r*-comparison of reaction norms to TMA and to fish infochemicals in two life-history experiments with different *Daphnia* clones and species. Error bars indicate 95% confidence limits.

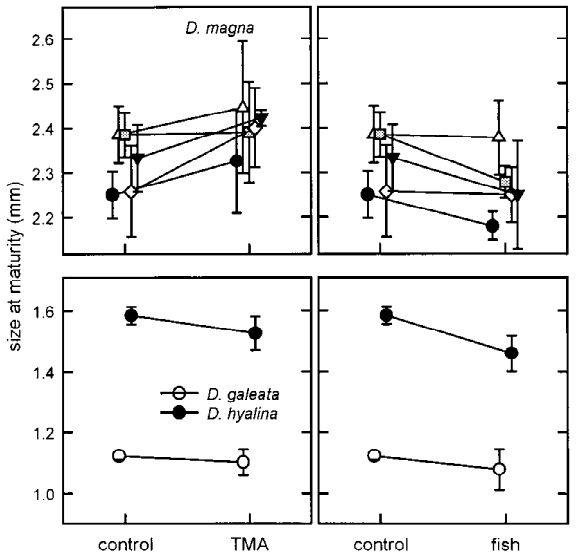

Figure 4. Size at maturity-comparison of reaction norms to TMA and to fish infochemicals in two life-history experiments with different *Daphnia* clones and species. Error bars indicate 95% confidence limits.

ever, the direction of the reaction to TMA was not always the same as to fish kairomones. In *D. magna* and *D. hyalina*, the size at maturity decreased significantly in fish incubation water, whereas it showed no significant change in the presence of TMA. Several studies have shown that especially the size at maturity is strongly affected by kairomones from size-selective

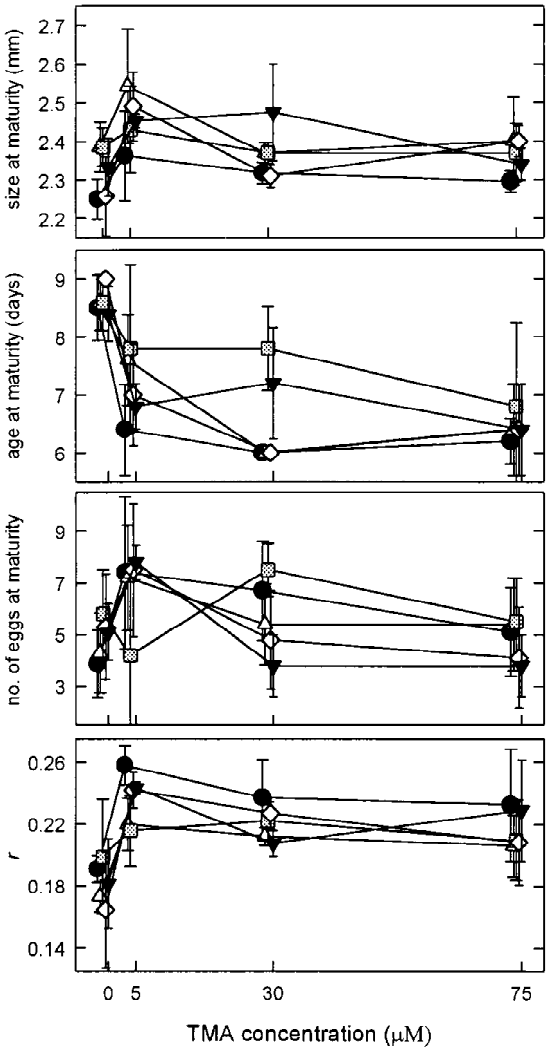

Figure 5. Life-history reactions of five *D. magna* clones to different concentrations of TMA. Error bars indicate 95% confidence limits.

predators (Stibor, 1992; Weider & Pijanowska, 1993; Stibor & Lüning, 1994; Boersma et al., 1998). In the presence of predators selecting for large-sized prey daphnids typically remain smaller, thus increasing the chance of successful reproduction before being eaten.

Results of experiments on the effect of TMA seem to be highly variable. In contrast to our results, Sakwińska (2000) found that TMA and fish water affected size-related traits similarly and that the size at maturity was decreased in both treatments. She further reported a discrepancy of TMA and fish kairomone effects in fitness-related traits. Fitness (quantified as fecundity and age at maturity) was increased in the presence of fish kairomone whereas it decreased in the TMA

treatments (Sakwińska, 2000). Those results again are in contrast to ours which show an increased intrinsic rate of population increase in the fish and also in the TMA treatments. These different findings might result from the fact that we worked with lower TMA concentrations in our first two experiments than Sakwińska. Our third experiment demonstrates that the size at maturity and the intrinsic rate of population increase decrease significantly with increasing TMA concentration. However, our first two experiments demonstrated that TMA indeed induces life-history changes in *Daphnia*, but that these are different from those responses to fish kairomones.

One could speculate that these differences in the reaction to TMA and fish kairomone might result from different concentrations of the triggering chemical in fish water and in TMA solution. Our third experiment showed significant differences for two life-history reactions to different TMA concentrations of the five *D. magna* clones (Table 3). The lowest TMA concentration generally induced the strongest reaction (Fig. 5). Other studies have shown that increasing levels of fish kairomone induce a gradual decrease in size at maturity (Reede, 1995; Stibor, 1995), and vertical displacement behaviour (Pohnert & Von Elert, 2000). Reede (1995) also observed a stronger reduction in size at maturity at the lowest kairomone level, whereas Stibor (1995) found a decreasing size at maturity with increasing fish kairomone levels. In our third experiment, the size at maturity decreased with increasing TMA concentrations as was expected but the animals were still larger in the TMA treatments than in the controls which is different from the reaction to fish kairomones (Fig. 4).

In this study, we are not able to answer the question if TMA is the fish kairomone or one component of it. Several chemical substances, not necessarily originating from predators but even environmental contaminants and pesticides, are known to induce life-history and morphological changes (Hanazato, 1991; Barry, 1999b) as well as behavioural reactions in *Daphnia* (Michels et al., 1999). *D. magna* clones showed the same negative phototactic behaviour in the presence of the pollutants copper and pentachlorophenol, as in the presence of fish kairomones (Michels et al., 1999). Hanazato (1999) found that *Daphnia* develop the same morphological structures in the presence of two pesticides as in the presence of kairomones from the invertebrate predator *Chaoborus*. These chemicals, mostly of anthropogenic origin, seem to mimic the effects of natural infochemicals (Barry, 1999a), or disturb the chemical communication within a natural community (Hanazato, 1999). In their recent study, Pohnert & Von Elert (2000) showed that fish incubation water still induces vertical displacement reactions in *Daphnia* after TMA and other volatile tertiary amines had been removed which implies that TMA is not part of the fish kairomone.

The results of our study show that the reactions of *Daphnia* to TMA are qualitatively the same as those to fish kairomones for some traits, but not for all. Hence, our results confirm the findings of Sakwińska (2000) who also demonstrated differences in the responses of *Daphnia* to TMA and to fish kairomones, leading her to conclude that TMA does not trigger anti-predatory life-history shifts. Hence, we conclude that TMA cannot be used in laboratory experiments as a substance mimicking fish kairomones. Moreover, based on the evidence from our study, and that of the study of Pohnert & Von Elert (2000), we must at this moment also conclude that TMA is most likely not the kairomone inducing anti predator changes in *Daphnia*.

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