



J. Plankton Res. (2014) 36(4): 1140–1145. First published online March 23, 2014 doi:10.1093/plankt/fbu023

SHORT COMMUNICATION

Morphological defences of invasive *Daphnia lumholtzi* protect against vertebrate and invertebrate predators

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Received September 23, 2013; accepted February 23, 2014

Corresponding editor: Beatrix E. Beisner

Daphnia lumholtzi invaded North American lakes and reservoirs. It forms prominent spines, which are inducible by fish kairomones. We tested the two hypotheses that the long spines protect against vertebrate (fishes) and invertebrate (*Chaoborus*) predators. Our experiments revealed that adults with longer spines survived significantly better under fish predation and juveniles with longer spines were additionally better protected under *Chaoborus* predation. Our study is the first direct proof that long spines effectively protect against both predators. Our results support the idea that the anti-predator devices may represent an important functional mechanism for the invasion success of *D. lumholtzi*.

KEYWORDS: biological invasion; *Chaoborus* predation; *Daphnia lumholtzi* fish predation; morphology; spines

Identifying invader's traits and their potential effects on resident native biota could improve our understanding of exotic species invasions. Defence morphologies of a species may offer protection against predators in an invaded habitat (e.g. Barnhisel, 1991a,b; Engel and Tollrian, 2009), and may therefore provide a benefit over resident prey species, contributing to its successful establishment in the new habitat.

Daphnia lumholtzi Sars, native to tropical and subtropical Africa, Asia and Australia (Benzie, 2005), invaded North American freshwaters most likely via introductions of exotic African fish species (Sorensen and Sterner, 1992; Havel and Hebert, 1993). After its first detection in Texas and Missouri in 1990 (Sorensen and Sterner, 1992; Havel and Hebert, 1993), *D. lumholtzi* rapidly colonized many other North American lakes, reservoirs and rivers (Havel and Shurin, 2004). *Daphnia lumholtzi* possesses a large pointed head spine (helmet) and a pronounced tail spine whose length can greatly exceed those observed in any North American *Daphnia* species (Havel and Hebert, 1993). In invaded North American waters, *D. lumholtzi* populations typically appear in late spring/early summer and remain in the water column until late autumn. Its helmet and tail spine are longest when fish predation is most intense (Sorensen and Sterner, 1992; Work and Gophen, 1995; Kolar et al., 1997). Long helmets and tail spines in *D. lumholtzi* are inducible by chemical cues released from fishes (fish kairomones; Tollrian, 1994; Dzialowski et al., 2003; Laforsch et al., 2006; Engel and Tollrian, 2009) or by high temperature (Yurista, 2000). Our previous work revealed that spined *D. lumholtzi* were superior competitors over North American *Daphnia pulex* under fish predation (Engel and Tollrian, 2009). The long spines of *D. lumholtzi* may thus provide effective defences against visually foraging planktivorous fish. However, a protective effect of the spiny morphology of *D. lumholtzi* against fish predators has not been shown directly so far. Prior studies examining a protective effect of its spines either examined selectivity of several fish species foraging on the exotic species in the field (Kolar and Wahl, 1998; Lienesch and Gophen, 2001, 2005; Lemke et al., 2003) or tested *D. lumholtzi* and a morphologically different North American *Daphnia* species in laboratory fish predation experiments (Swaffar and O'Brien, 1996; Kolar and Wahl, 1998; Engel and Tollrian, 2009). While these studies showed lower mortalities of *D. lumholtzi*, it is likely that different *Daphnia* species differ in more traits, including visibility or behaviour. Furthermore, the underlying mechanisms were not revealed.

Morphological defences such as helmets, tail spines, thicker carapaces and neck teeth protect *Daphnia* against invertebrate predators (e.g. Dodson, 1974; Tollrian, 1995;

Tollrian and Dodson, 1999; Laforsch and Tollrian, 2004; Rabus et al., 2013). Thus, the spines of *D. lumholtzi* might act as protective devices against invertebrates. *Daphnia lumholtzi* co-occurs with *Chaoborus* larvae in some invaded North American waters (Sorensen and Sterner, 1992; Çelik et al., 2002; Williams and Pederson, 2004). Dzialowski et al. (Dzialowski et al., 2003) showed that *D. lumholtzi* exhibits morphological and life history changes in response to kairomones released from *Chaoborus* larvae. Swaffar and O'Brien (Swaffar and O'Brien, 1996) suggested that *Chaoborus* larvae are unable to feed on *D. lumholtzi* of 2 mm or larger in total length. However, an advantage of the long spines of *D. lumholtzi* against *Chaoborus* predation has not yet been proven.

We tested two hypotheses: (i) the long helmets and tail spines of *D. lumholtzi* offer adults protection against vertebrate (fishes) and (ii) the long helmets and tail spines of *D. lumholtzi* offer juveniles protection against invertebrate (*Chaoborus*) predation. To address these hypotheses, we used a *D. lumholtzi* clone with permanently long spines and compared its vulnerability to these predators against an otherwise very similar *D. lumholtzi* clone with shorter spines.

The two *D. lumholtzi* clones (as in Engel and Tollrian, 2009) originated from two North American locations. Clone *D. lumholtzi* TE ("short-spined clone", "S clone") was isolated from Fairfield Reservoir, Texas. Adults from this (inducible) clone do not possess helmets in the absence of predators. However, the first juvenile instars of this clone exhibit small helmets, which gradually decrease in length until adulthood. Clone *D. lumholtzi* AR ("long-spined clone", "L clone") derived from Canyon Lake, Arizona. This long-spined (L) clone permanently possesses a large, pointed helmet and a very long tail spine. *Daphnia* were maintained in clonal cultures in artificial medium (Jeschke and Tollrian, 2000). They were fed daily with *Scenedesmus acutus* ($>1.0 \text{ mg C L}^{-1}$). Both predators used in our experiments are commonly found in North American lakes. Three-spined sticklebacks *Gasterosteus aculeatus* are widely distributed in European, North Asian and North American freshwater, brackish and marine systems (e.g. Paepke, 1996). Experimental sticklebacks (~1 year old; total length: 25–28 mm; mean total length: 26 mm) derived from two stream systems of the Sempt, Fehlbach and Strogen, Germany. Fishes were held in aerated artificial medium in a 150 L aquarium under continuous fluorescent light at 15°C, and were fed daily with chironomids. During the fish predation experiments, they additionally received a mixture of *Daphnia* spp., and were starved for 24 h prior to use in the trials. Fishes had been naive to both *D. lumholtzi* clones before the experiment. Fourth-instar larvae of the phantom midge *Chaoborus flavicans* were collected from Lake

Klostersee, Germany. *Chaoborus* larvae were stored in artificial medium (1.5 L glass beakers) at 14°C, and every second day received a mixture of *Daphnia* spp. Prior to the *Chaoborus* predation experiments, the larvae were starved for 24 h, and acclimated to 20°C.

The fish predation trials were carried out in the laboratory under fluorescent light at 20°C. Age-synchronized, non-gravid adult females were randomly chosen from each *D. lumholtzi* clone. To avoid potential fish kairomone-induced differences in body length (e.g. smaller body size) or behaviour (e.g. induced alertness), which may have an effect on fish predators' preference, we did not expose them to fish predator cues in our experiments. To ensure similar body-sized *Daphnia* prey for the fishes, we measured (prior to each experiment) morphological parameters with a digital image-analysis system (Soft Imaging System, Analysis Pro, Münster, Germany). We recorded helmet length (HL; from tip of helmet to top of eye), body length (BL; from top of eye to base of tail spine) and tail spine length (TL; from base of tail spine to tip of tail spine) and calculated the relative HL [(HL/BL) × 100] and the relative TL [(TL/BL) × 100]. The mean body length of adults of both clones used for our fish predation trials did not significantly differ [S clone: 1.25 mm, L clone: 1.31 mm; Mann–Whitney *U* tests (M–W *U*), $P > 0.05$]. However, both the mean relative helmet length (69%) and the mean relative tail spine length (92%) of the L clone were significantly longer than those of the S clone (14 and 61%, respectively; M–W *U*, both $P < 0.001$). One hour before each experiment, the fishes were acclimated to laboratory conditions. The predation trials were carried out in a 10 L black shielded glass beaker, containing 3 L aerated medium, into which a single stickleback was placed 5 min prior to each trial. The fish feeding period started with the addition of a 50 : 50 prey mixture, i.e. 10 individuals from each clone (20 *Daphnia* in total). By direct observation of the fish from above, the number of consumed *Daphnia* and discontinued attacks (i.e. attacks without prey consumption) was recorded. When half of the prey items were consumed, the predation trial was terminated by removing the fish. The elapsed time for the foraging period was noted. The remaining daphnids were preserved and the number of surviving *Daphnia* per clone was recorded. Prior to the next trial, the experimental equipment was cleaned. Each fish ($N = 10$) was used three times, i.e. in each of three predation experiments on consecutive days (30 trials in total) to test for short-term learning effects. Data were tested for normal distribution and homogeneity of variances. M–W *U* were used to analyse for morphological differences (relative HL, relative TL and BL) between both *D. lumholtzi* clones. A Wilcoxon signed ranks test was performed on each of the three fish predation experiments and another one on the entire data set (30 trials) to analyse for

differences in the number of surviving animals between both clones (two related samples). To analyse for short-term learning effects in the fishes, a Friedman test (for repeated measures) was carried out per clone to test for differences in the clonal survival among the three experiments. Another Friedman test was used to analyse for differences in the number of discontinued attacks by the fishes among the three experiments.

In *Chaoborus* predation trials, we tested first (neonate), second and third juvenile instars of both *D. lumholtzi* clones. Age-synchronized, non-induced animals from each *D. lumholtzi* clone were tested separately in 10 replicate trials per instar (except S clone: 13 replicates in first instar and 9 replicates in third instar). Each *Chaoborus* larva was only used in a single predation experiment. Again, prior to each trial, the morphological parameters of the juvenile *Daphnia* were measured (analogous to the fish predation experiments) to ensure that they were all of the same body size. The three juvenile instars of both prey clones used in our *Chaoborus* predation trials differed in the lengths of their morphological features. In each instar, the juveniles of the L clone had an almost similar body length (although in second and third instars significantly larger), and both significantly (except: tail spine length in first instar) longer helmet and tail spine lengths as well as significantly larger total lengths compared with the S clone (Table I). For each trial, 10 *D. lumholtzi* of the same instar and clone were placed in a 600 mL glass beaker, containing 200 mL of medium. Each predation trial started by adding a single, starved, fourth-instar larva of *C. flavicans* to each beaker. The predation trials were conducted over 5 h at 20°C in darkness. Preliminary investigations showed that a *C. flavicans* larva is able to consume about half of the 10 *Daphnia* provided (S clone) within this time (K. Engel, unpublished data). Thereafter, the number of remaining juvenile *Daphnia* was recorded. M–W *U* were used to analyse for morphological differences and differences in the number of surviving animals between both *D. lumholtzi* clones per instar.

In the fish predation experiments, we found a significantly lower mortality of the L clone compared with the S clone (Wilcoxon tests, first experiment: $P = 0.004$, second experiment: $P = 0.047$, third experiment: $P = 0.004$; all 30 fish predation trials, mean number of surviving animals ± SE, L clone: 6.10 ± 0.27 , S clone: 3.80 ± 0.17 , Wilcoxon test, $P < 0.001$; Fig. 1). There were no significant differences in the clonal survival among the three fish predation experiments (Friedman tests, per clone, both $P > 0.05$). The number of discontinued attacks by the fishes did not significantly differ among the three experiments (mean ± SE, first experiment: 3.20 ± 0.63 , second experiment: 3.80 ± 0.39 , third experiment: 3.70 ± 0.70 ; Friedman test, $P > 0.05$).

Table 1: Morphological parameters of the first three juvenile instars (1, 2 and 3) of the two Daphnia lumholtzi clones (long-spined (L) clone and short-spined (S) clone) used in the predation experiments with Chaoborus flavicans

Juvenile instar	Morphological parameter	Long-spined (L) clone			Short-spined (S) clone			P
		Mean	SE	N	Mean	SE	N	
1	HL (mm)	0.34	0.002	100	0.18	0.001	130	<0.001
	Relative HL (%)	61.20	0.380	100	32.04	0.25	130	<0.001
	TL (mm)	0.46	0.004	100	0.46	0.004	130	0.250
	Relative TL (%)	83.37	0.530	100	82.62	0.47	130	0.217
	BL (mm)	0.55	0.003	100	0.55	0.003	130	0.195
	Total length (mm)	1.35	0.007	100	1.18	0.007	130	<0.001
2	HL (mm)	0.51	0.003	100	0.19	0.002	100	<0.001
	Relative HL (%)	69.49	0.360	100	27.95	0.23	100	<0.001
	TL (mm)	0.59	0.004	100	0.53	0.003	100	<0.001
	Relative TL (%)	80.22	0.500	100	77.55	0.44	100	<0.001
	BL (mm)	0.74	0.003	100	0.68	0.002	100	<0.001
	Total length (mm)	1.84	0.007	100	1.40	0.005	100	<0.001
3	HL (mm)	0.65	0.004	100	0.19	0.003	90	<0.001
	Relative HL (%)	72.65	0.420	100	22.03	0.28	90	<0.001
	TL (mm)	0.76	0.005	100	0.59	0.007	90	<0.001
	Relative TL (%)	84.32	0.590	100	69.95	0.51	90	<0.001
	BL (mm)	0.90	0.004	100	0.85	0.007	90	<0.001
	Total length (mm)	2.31	0.010	100	1.63	0.015	90	<0.001

The morphological parameters (means \pm SE) recorded were both absolute (mm) and relative (%) helmet length (HL) and tail spine length (TL), absolute body length (BL; mm) and total length (total length; all trait lengths combined; mm). *N* indicates the number of individual juvenile *Daphnia* measured prior to use in the *Chaoborus* predation trials. Each juvenile instar was analysed for morphological differences between the two *D. lumholtzi* clones using Mann–Whitney *U* tests.

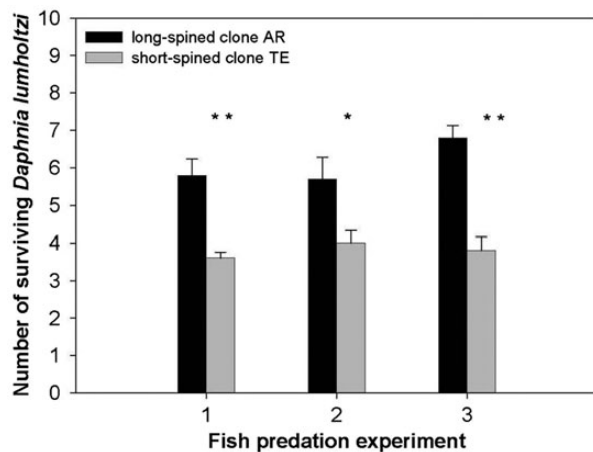


Fig. 1. The number of surviving animals in the predation experiments with *Gasterosteus aculeatus*. Means (\pm 1 SE) of adult animals of two different *Daphnia lumholtzi* clones (long-spined (L) clone and short-spined (S) clone) remaining after three (1, 2 and 3) fish predation experiments (with each 10 trials/fishes) are shown. Asterisks indicate significant differences (* P < 0.05, ** P < 0.01, *** P < 0.001).

In the *Chaoborus* predation experiments, in the first/ neonate instar, we found no significant difference in the survival rate between both *D. lumholtzi* clones under *Chaoborus* predation (M–W *U*, P > 0.05; Fig. 2). However, in the second and third instars, juveniles of the L clone survived *Chaoborus* predation significantly better (M–W *U*, P < 0.001 and P = 0.008; Fig. 2).

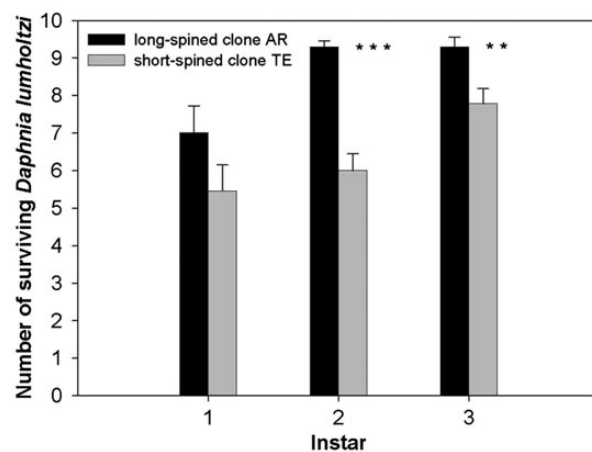


Fig. 2. The number of surviving animals in the predation experiments with *Chaoborus flavicans*. Means (\pm 1 SE) of juvenile animals (instars 1, 2 and 3) of two different *Daphnia lumholtzi* clones (long-spined (L) clone and short-spined (S) clone) remaining after 9–13 separate *Chaoborus* predation trials per instar and clone are shown. Asterisks indicate significant differences (* P < 0.05, ** P < 0.01, *** P < 0.001).

Our study revealed that the long helmets and tail spines of *D. lumholtzi* serve as multi-tools offering protection against predation by vertebrate fishes and invertebrate *Chaoborus* larvae. These results support the hypothesis that the anti-predator devices constitute an important functional mechanism for *D. lumholtzi*'s invasion success (Engel and Tollrian, 2009). Similarly, Barnhisel (Barnhisel, 1991a,b)

demonstrated for the invasive cladoceran *Bythotrephes* that its long caudal spine protects the invader against predation by young fishes. Thus, defence morphologies of an invading species may offer a selective advantage over resident prey species and may favour its successful establishment in the newly invaded communities.

Our fish predation experiments demonstrated a distinct advantageous effect of the long morphological features (helmets and tail spines) of adult *D. lumholtzi* against fish predators (Fig. 1). So far, only a few studies have shown protective effects against fish predators in other *Daphnia* species (e.g. Jacobs, 1967; Zaret, 1972). Green (Green, 1967) reported from Lake Albert, East Africa, that *Alestes baremose* foraged selectively on unhelmeted *D. lumholtzi*, and suggested an advantage of helmeted *D. lumholtzi* in the presence of fishes. Thus, our results provide evidence for Green's assumption (Green, 1967) and confirm prior studies with *D. lumholtzi*, which showed lower mortalities of the invasive species compared with native North American *Daphnia* species under fish predation (e.g. Swaffar and O'Brien, 1996; Kolar and Wahl, 1998; Engel and Tollrian, 2009).

Fishes select their prey according to visibility and body size (Brooks and Dodson, 1965; Dodson, 1974; Werner and Hall, 1974; O'Brien *et al.*, 1976; Zaret, 1980). Thus, differences in *Daphnia* prey morphology, such as in body size (e.g. body length), in pigmentation or in prey behaviour (e.g. alertness, swimming speed) can distinctly influence selectivity and fish foraging. Here, we used non-gravid, similar body-sized individuals from two *D. lumholtzi* clones without kairomones. We thus could exclude predator kairomone, species and body size-related differences that would have influenced prey selection and foraging behaviour of our predatory fishes. However, we cannot exclude potential differences in swimming speed or behaviour of these clones, as we did not examine such differences here.

Although our small fishes preferentially fed on the S clone, they were large enough (26 mm in length) and able to consume both *D. lumholtzi* clones. Thus, prevention of ingestion by the body enlargement cannot be the only defensive effect. While we found no indication for short-term learning in the fishes either to avoid or to handle the spiny prey, Kolar and Wahl (Kolar and Wahl, 1998) reported for juvenile bluegills (<50 mm) that they selectively avoided *D. lumholtzi* with gained experience. Thus, fish species may differ in their learning abilities or more experience is needed for learning.

Our *Chaoborus* predation experiments revealed that the long spines of the L clone in the second and third juvenile instars (in first instar just a trend) provide a distinct protection against *Chaoborus* predation (Fig. 2). Wilson and Hebert (Wilson and Hebert, 1993) observed differences in the susceptibility of two coexisting *Daphnia pulex* clones

to calanoid copepod predation due to differences in juvenile (second and third instars) body morphology, i.e. tail spine lengths. This implies that the differences in juvenile head and tail spine lengths of our two *D. lumholtzi* clones (Table I) were responsible for their different mortality under *Chaoborus* predation.

We did not observe a significant difference in the survival rate in the first/neonate instar of both *D. lumholtzi* clones. Most likely, the differences in helmet and tail spine length (not significantly different in first instar) in addition to the body length (Table I) were not sufficiently large enough to offer a "size refuge". Similarly, the first juvenile instar of *Chaoborus kairomone* induced *D. pulex* and *Daphnia cucullata* did not experience lower mortality, while the later instars of the induced morphs had an advantage under *Chaoborus* predation (Tollrian, 1995; Laforsch and Tollrian, 2004).

We have shown that long helmets and tail spines of adult *D. lumholtzi* are effective and beneficial features protecting against predation by vertebrate fishes. In addition, we demonstrated here for the first time that long spines of juvenile *D. lumholtzi* additionally provide protection against invertebrate predation by *Chaoborus* larvae. Advantages in the survival of *D. lumholtzi* under predation by fishes and by *Chaoborus* larvae may likely impose negative effects on North American zooplankton as well as on their vertebrate and invertebrate predators. These protective effects suggest that the anti-predator devices of *D. lumholtzi* may represent, possibly among other factors such as thermal tolerance (Lennon *et al.*, 2001; Fey and Cottingham, 2011, 2012; Engel and Tollrian, 2012), an important mechanism for its invasion success in North America.

ACKNOWLEDGEMENTS

We thank M. Kredler, E. Osipova and E. Hochmuth for their help during the experiments; C. Laforsch and W. Gabriel for discussions; J. Elser, K.H. Sorensen and R.W. Sterner for kindly providing the *D. lumholtzi* clones; and Associate Editor B.E. Beisner and two anonymous reviewers for valuable suggestions.

FUNDING

This work was partially supported by a PhD grant from the Hanns-Seidel-Foundation to K.E.

REFERENCES

Barnhisel, D. R. (1991a) Zooplankton spine induces aversion in small fish predators. *Oecologia*, **88**, 444–450.

- Barnhisel, D. R. (1991b) The caudal appendage of the cladoceran *Bythotrephes cederstroemi* as defence against young fish. *J. Plankton Res.*, **13**, 529–537.
- Benzie, J. A. H. (2005) *Cladocera: The genus Daphnia (including Daphniopsis) (Anomopoda: Daphniidae)*. Backhuys Publishers, Leiden, The Netherlands.
- Brooks, J. L. and Dodson, S. I. (1965) Predation, body size and composition of plankton. *Science*, **150**, 28–35.
- Çelik, K., Schindler, J. E., Foris, W. J. et al. (2002) Predator-mediated coexistence of exotic and native crustaceans in a freshwater lake? *Biol. Inv.*, **4**, 451–454.
- Dodson, S. I. (1974) Adaptive change in plankton morphology in response to size-selective predation: a new hypothesis of cyclomorphosis. *Limnol. Oceanogr.*, **19**, 721–729.
- Dzialowski, A. R., Lennon, J. T., O'Brien, W. J. et al. (2003) Predator-induced phenotypic plasticity in the exotic cladoceran *Daphnia lumholtzi*. *Freshwater Biol.*, **48**, 1593–1602.
- Engel, K. and Tollrian, R. (2009) Inducible defences as key adaptations for the successful invasion of *Daphnia lumholtzi* in North America?. *Proc. R. Soc. B*, **276**, 1865–1873.
- Engel, K. and Tollrian, R. (2012) Competitive ability, thermal tolerance and invasion success in exotic *Daphnia lumholtzi*. *J. Plankton Res.*, **34**, 92–97.
- Fey, S. B. and Cottingham, K. L. (2011) Linking biotic interactions and climate change to the success of exotic *Daphnia lumholtzi*. *Freshwater Biol.*, **56**, 2196–2209.
- Fey, S. B. and Cottingham, K. L. (2012) Thermal sensitivity predicts the establishment success of nonnative species in a mesocosm warming experiment. *Ecology*, **93**, 2313–2320.
- Green, J. (1967) The distribution and variation of *Daphnia lumholtzi* (Crustacea: Cladocera) in relation to fish predation in Lake Albert, East Africa. *J. Zool. Lond.*, **151**, 181–197.
- Havel, J. E. and Hebert, P. D. N. (1993) *Daphnia lumholtzi* in North America: another exotic zooplankton. *Limnol. Oceanogr.*, **38**, 1823–1827.
- Havel, J. E. and Shurin, J. B. (2004) Mechanisms, effects, and scales of dispersal in freshwater zooplankton. *Limnol. Oceanogr.*, **49**, 1229–1238.
- Jacobs, J. (1967) Untersuchungen zur Funktion und Evolution der Zyklomorphose bei *Daphnia*, mit besonderer Berücksichtigung der Selektion durch Fische. *Arch. Hydrobiol.*, **62**, 467–541.
- Jeschke, J. M. and Tollrian, R. (2000) Density-dependent effects of prey defences. *Oecologia*, **123**, 391–396.
- Kolar, C. S. and Wahl, D. H. (1998) Daphnid morphology deters fish predators. *Oecologia*, **116**, 556–564.
- Kolar, C. S., Boase, J. C., Clapp, D. F. et al. (1997) Potential effect of invasion by an exotic zooplankton, *Daphnia lumholtzi*. *J. Freshwater Ecol.*, **12**, 521–530.
- Laforsch, C., Beccara, L. and Tollrian, R. (2006) Inducible defenses: the relevance of chemical alarm cues in *Daphnia*. *Limnol. Oceanogr.*, **51**, 1466–1472.
- Laforsch, C. and Tollrian, R. (2004) Inducible defenses in multipredator environments: cyclomorphosis in *Daphnia cucullata*. *Ecology*, **85**, 2302–2311.
- Lenke, A. M., Stoeckel, J. A. and Pegg, M. A. (2003) Utilization of the exotic cladoceran *Daphnia lumholtzi* by juvenile fishes in an Illinois River floodplain lake. *J. Fish Biol.*, **62**, 938–954.
- Lennon, J. T., Smith, V. H. and Williams, K. (2001) Influence of temperature on exotic *Daphnia lumholtzi* and implications for invasion success. *J. Plankton Res.*, **23**, 425–434.
- Lienesch, P. W. and Gophen, M. (2001) Predation by inland silversides on an exotic cladoceran, *Daphnia lumholtzi*, in Lake Texoma, U.S.A. *J. Fish Biol.*, **59**, 1249–1257.
- Lienesch, P. W. and Gophen, M. (2005) Size-selective predation by inland silversides on an exotic cladoceran, *Daphnia lumholtzi*. *Southwest. Nat.*, **50**, 158–165.
- O'Brien, W. J., Slade, N. A. and Vinyard, G. L. (1976) Apparent size as the determinant of prey selection by bluegill sunfish (*Lepomis macrochirus*). *Ecology*, **57**, 1304–1310.
- Paepke, H. J. (1996) *Die Stichlinge. Gasterosteidae*. Westarp-Wissenschaften, Magdeburg, Germany.
- Rabus, M., Söllradl, T., Clausen-Schaumann, H. and Laforsch, C. (2013) Uncovering ultrastructural defences in *Daphnia magna* – an interdisciplinary approach to assess the predator-induced fortification of the carapace. *PLoS ONE*, **8**, e67856.
- Sorensen, K. H. and Sterner, R. W. (1992) Extreme cyclomorphosis in *Daphnia lumholtzi*. *Freshwater Biol.*, **28**, 257–262.
- Swaffar, S. M. and O'Brien, W. J. (1996) Spines of *Daphnia lumholtzi* create feeding difficulties for juvenile bluegill sunfish (*Lepomis macrochirus*). *J. Plankton Res.*, **18**, 1055–1061.
- Tollrian, R. (1994) Fish-kairomone induced morphological changes in *Daphnia lumholtzi* (Sars). *Arch. Hydrobiol.*, **130**, 69–75.
- Tollrian, R. (1995) *Chaoborus crystallinus* predation on *Daphnia pulex*: can induced morphological changes balance effects of body size on vulnerability?. *Oecologia*, **101**, 151–155.
- 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, NJ, USA, pp. 177–202.
- Werner, E. E. and Hall, D. J. (1974) Optimal foraging and the size selection of prey by the bluegill sunfish (*Lepomis macrochirus*). *Ecology*, **55**, 1042–1052.
- Williams, J. J. and Pederson, C. L. (2004) Diel vertical migration in *Daphnia lumholtzi* (Sars). *J. Freshwater Ecol.*, **19**, 305–311.
- Wilson, C. C. and Hebert, P. D. N. (1993) Impact of copepod predation on distribution patterns of *Daphnia pulex* clones. *Limnol. Oceanogr.*, **38**, 1304–1310.
- Work, K. and Gophen, M. (1995) The invasion of *Daphnia lumholtzi* (SARS) into Lake Texoma (USA). *Arch. Hydrobiol.*, **133**, 287–303.
- Yurista, P. M. (2000) Cyclomorphosis in *Daphnia lumholtzi* induced by temperature. *Freshwater Biol.*, **43**, 207–213.
- Zaret, T. M. (1972) Predator-prey interaction in a tropical lacustrine ecosystem. *Ecology*, **53**, 248–257.
- Zaret, T. M. (1980) *Predation and Freshwater Communities*. Yale University Press, New Haven, CT, USA.