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Daphnid morphology deters fish predators

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Abstract Spine and helmet production in zooplankton are thought to provide protection from invertebrate rather than vertebrate predators. We examined selectivity for *Daphnia lumholtzi*, a species that exhibits extreme cyclomorphosis with a large helmet and long tail spine (total length can exceed 5 mm), by juvenile bluegill (15–80 mm) in the laboratory and field. Bluegill consumed more *D. pulex* than *D. lumholtzi* when the species were presented alone. When the daphnids were offered together in equal numbers, bluegill selected against *D. lumholtzi*. Bluegill foraging behavior helped explain the observed nonrandom feeding. Bluegill capture efficiency foraging on *D. pulex* was high (85–100%) and handling times were low (usually too short to detect), whereas efficiencies were lower (40–96%) and handling times were longer (1–3 s) when foraging on *D. lumholtzi*, particularly for fish < 50 mm. As they gained experience, bluegill < 50 mm that oriented towards *D. lumholtzi* rejected them more often than striking. In addition, more *D. lumholtzi* were rejected and expelled than were *D. pulex*. From these experiments, we conclude that larger bluegill (> 50 mm) are able to forage more successfully on *D. lumholtzi* than smaller fish. Selectivity by bluegill collected from a reservoir infested with *D. lumholtzi* verified our laboratory conclusions. Smaller bluegill selected against *D. lumholtzi*, whereas it was a preferred diet item for bluegill > 50 mm. These results show that the morphology of *D. lumholtzi* interferes with

predation by small planktivorous fish, posing foraging constraints for these fish more similar to those of piscivores, where handling time is important, than to those of planktivores, where prey density is of primary importance.

Key words *Daphnia lumholtzi* · Morphology · Predation · Predator avoidance · Selectivity

Introduction

Species that endure predation have evolved a myriad of physiological, behavioral, and morphological defense strategies, many of which are used in combination, to deter predators (see Endler 1986 for a complete discussion). Some species exhibit plastic life history traits in response to predation pressure, e.g., *Bosmina longirostris* matures at a smaller size in the presence of predators than in their absence (Vonder Brink and Vanni 1993). Others express phenotypic plasticity in the presence of predators to reduce their individual risk of predation, e.g., by the production of various types of spines to deter predators. Spines make prey difficult to handle by increasing the effective cross-sectional diameter of prey, thereby restricting gape-limited predators (Endler 1986). Consequently, spines also increase the probability that the prey will escape or be rejected (Gilbert 1966; Forbes 1989; Barnhisel 1991a).

Although many animals possess permanent structures to deter predation (e.g., porcupines, sea urchins, and sticklebacks), others develop spiny structures only in response to predator-related cues. Development of spines to deter predation appears primarily in aquatic taxa such as algae (Lampert et al. 1994), rotifers (Gilbert 1973), cladocerans (O'Brien and Vinyard 1978; Grant and Bayly 1981; Havel and Dodson 1985), marine bryozoans (Harvell 1984), and barnacles (Young 1986). Inducible spine production in dragonfly nymphs has also been suggested (Johansson and Samuelsson 1994). Spine and helmet production protect zooplankton from inverte-

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brate predators, making them difficult or impossible to swallow (Dodson 1974). While they provide direct protection from invertebrate predators, Dodson (1974) hypothesized that cyclomorphosis also protects zooplankton from vertebrate predators by decreasing core body size, making them less visible to vertebrate predators. Several authors suggest that the elongated heads of some zooplankton may deter fish predators (see Brooks 1965; Green 1967; Hebert 1978). The best evidence to date is offered by Jacobs (1967) who found crested *Daphnia* spp. less susceptible to guppy predation than uncrested individuals although he did not identify the mechanism determining this differential susceptibility.

Zooplankton endure tremendous predation pressure from planktivorous fish; consumption of zooplankton by larval fish can drastically reduce zooplankton abundance (Dettmers and Stein 1992; DeVries and Stein 1992). Likewise, sufficient zooplankton resources are important for successful recruitment of larval fish (Kashuba and Matthews 1984; Hart and Werner 1987; Welker et al. 1994). Most larval fish are constrained in the prey they can select by the size of their gape (Hansen and Wahl 1981; Breningan and Stein 1994) while juvenile and adult fish maximize consumption by selecting larger (Werner and Hall 1974) or seemingly larger (O'Brien et al. 1976) zooplankton taxa. Little time is required to consume zooplankton; growth of both larval (Welker et al. 1994) and juvenile (Prout et al. 1990; Breck 1993) planktivores often correlates positively with prey density. Therefore, encounter rate is often of primary importance for successful foraging by planktivorous fish (Gerking 1994; Juanes 1994). As fish attain larger sizes, handling time for zooplanktonic invertebrates decreases and rarely limits planktivory by adult fish. In contrast, handling time of prey is believed to be more limiting for fish feeding on macroinvertebrates (Mittelbach 1981) and for piscivorous fish (Juanes 1994). *Bythotrephes cederstroemi*, a zooplankton with a long caudal process, provides one notable exception, requiring eight times as long to handle than unspined daphnids (Barnhisel 1991b).

Deterrence of fish predation by zooplankton morphology has rarely been documented but may be the ultimate cause of spines in *Daphnia lumholtzi* (Green 1967; Tollrian 1994; Work and Gophen 1995). In support of this idea, Swaffar and O'Brien (1996) found that small bluegill (20–35 mm) consumed fewer and rejected more *D. lumholtzi* than *D. magna*. From this work, we know that small bluegill are limited in their ability to consume *D. lumholtzi*, but the mechanistic basis for this response remains unknown. Here, we further examine to what extent the extreme morphology of *D. lumholtzi* interferes with fish predation, and investigate the causal mechanism explaining observed nonrandom feeding. We test fish throughout the bluegill juvenile life history stage (15–80 mm), since fish length influences the size of prey a fish can consume (Breningan and Stein 1994; Mayer and Wahl 1997). Unlike Swaffar and O'Brien (1996), who controlled for equal total lengths between daphnid spe-

cies, we control for equal body lengths, since visually feeding fish select prey based on prey body length (Dodson 1974; O'Brien et al. 1976). We conducted two sets of laboratory experiments; the first examines the selectivity of young bluegill foraging on *D. lumholtzi* and *D. pulex* alone and in combination. In the second, we conducted behavioral foraging experiments to examine differential consumption of prey species. Lastly, we present diet selectivity for bluegill collected from an invaded reservoir to determine the extent of predation on *D. lumholtzi*.

Materials and methods

Laboratory experiments

We used late-larval and juvenile bluegill in our experiments since they constitute a large proportion of many fish populations, are more likely to be impacted by spines than adult fish, and because they overlap temporally with *D. lumholtzi* (Kolar et al. 1997). Bluegill (15–80 mm total length) seined from ponds at the Sam Parr Biological Station, Kinmundy, Ill., were held for 1 week in the laboratory prior to experiments on a natural zooplankton assemblage, and were then starved for 24 h before use in experiments. We collected *D. lumholtzi* from Lake Springfield, Ill. (39.7°N, 89.6°W, 1,582 ha, 9.1 m maximum depth, 4.0 m mean depth) by vertical tows from the bottom using a 0.5-m-diameter (500 µm mesh) conical ichthyoplankton net. They were transported in coolers, moved to 76-l aquaria and fed from algal cultures (mostly *Chlamydomonas* spp.). Since the helmet and tail spine length of *D. lumholtzi* decreases with time in culture (Sorensen and Sterner 1992; C. Kolar, personal observation), they were used within 4 days of collection. *D. pulex* collected from Lake Shelbyville, Ill., were cultured in the same manner as *D. lumholtzi*. All animals were held and tested at room temperature (20–23°C).

Daphnids were size-sorted to isolate individuals of each species with similar body sizes. To isolate *D. lumholtzi*, zooplankton were poured through a 1-mm plastic mesh screen. *D. lumholtzi* retained on the screen were used as test animals. To isolate juvenile *D. pulex* with similar body length as *D. lumholtzi*, we passed culture water through a 0.5-mm sieve; animals which passed through the screen were used in tests. We measured 20 individuals of each species from each test date using a dissecting microscope (×25) equipped with an ocular micrometer to compare daphnid lengths between treatments. We measured body and total length of both species similarly: body length (mid-eye to end of carapace) and total length (from tip of helmet to end of tail spine). The body length of *D. lumholtzi* (mean ± 1 SE, 0.76 ± 0.01 mm) used in experiments was similar to that of *D. pulex* (0.77 ± 0.01 mm; ANOVA, $F_{1,72} = 0.28$, $P = 0.60$), but the total length of *D. lumholtzi* (2.31 ± 0.03 mm) was longer than that of *D. pulex* (1.07 ± 0.01 mm; ANOVA, $F_{1,72} = 540.28$, $P < 0.01$). Selectivity experiments were conducted in 1994–1996; behavioral foraging experiments were conducted in 1995–1996.

Selectivity experiments

We examined the selectivity of bluegill foraging on *D. lumholtzi* alone, *D. pulex* alone, and a mixed-species treatment with equal numbers of the two species. Individual bluegill were placed into experimental chambers filled with aerated water 24 h prior to experiments. Because counting individual daphnids was labor intensive, we used an appropriate volume of water for the size of fish being tested (from 2 l for smaller bluegill to 10 l for the largest). We conducted pilot trials to determine an appropriate study volume based on bluegill length where bluegill foraging was not inhibited and daphnid numbers were not reduced excessively. A density of 75

daphnids/l was used in all treatments. Daphnids were size-sorted as described above and an appropriate number were hand-counted using a micropipette. After removing the airstone, daphnids were added to the experimental chamber. Bluegill were left to forage undisturbed for 1 h after which time the bluegill was removed and the remaining daphnids were collected and preserved in Lugol's solution. We then returned the bluegill to the chamber and it remained unfed until the next trial (24 h later). Each bluegill ($n = 36$) was used in each of the three treatments. The order in which treatments were conducted on each bluegill was chosen randomly.

Daphnids remaining in the chamber were identified, enumerated, and the body lengths of 20 individuals of each species were measured (to the nearest 0.01 mm) to compare the body length of the remaining daphnids to those of the initial assemblage. After completing the three treatments, bluegill were also weighed (to the nearest 0.01 g), measured (to the nearest mm), and preserved in 75% ethanol.

For data analysis, we divided bluegill into three nonoverlapping size categories with similar numbers of individuals: 15–27, 33–47, and 52–80 mm. Overall effects of fish length and prey species on the total number of *Daphnia* consumed were examined using a repeated-measures analysis of variance (RM-ANOVA) in which fish length category was the between-subject effect and treatment was the within-subject effect. We used a linear contrast to compare the number of daphnids eaten in the mixed-species treatment to the number eaten in the *D. pulex*-alone treatment. Mauchly's criterion was used to test for sphericity and the Huynh-Feldt correction was used in reporting the results of the within-subject effect in the analysis.

We compared the body lengths of *Daphnia* remaining after the experiment to those initially added using analysis of covariance (ANCOVA). Fish length was the covariate, mean *Daphnia* body length was the dependent variable and type (either initial culture or those remaining after the experiment) was the independent variable. A separate analysis was conducted on each treatment. All analyses were completed using either PROC GLM or PROC REG in SAS (SAS 1991). An α value of 0.05 was employed in all analyses.

Foraging behavior experiments

We also observed the behavior of bluegill foraging on either *D. lumholtzi* or *D. pulex*. Bluegill were acclimated for 24 h in individual experimental chambers. A density of 75 size-sorted daphnids/l was again used for these experiments. Bluegill foraging behavior was observed for 15 min and recorded on audio tape for later analysis. At the end of the experiment, the bluegill was removed, daphnids were collected and preserved, and the bluegill was returned to the chamber. Twenty-four hours later, the bluegill was given the other daphnid species in a similar trial. The initial species used for each fish was selected randomly. Again, bluegill used in trials ($n = 40$) were weighed, measured, and preserved in 75% ethanol after completing both treatments. The predation sequence was documented with the following nonoverlapping categories (Fig. 1): orient (moving into striking position near prey item), reject (not striking at prey after orienting), strike (attempting to capture prey), capture, handling (manipulating prey in mouth), expel (after attempting to swallow), and ingestion. The number of orients, rejects, strikes, misses, captures, expels, ingests and the time (s) spent handling prey were determined in 1-min increments for each trial. We defined handling time as the time from prey capture until the commencement of search (in the vein of Werner and Hall 1974; Mayer and Wahl 1997). Our definition differs from that originated in Holling (1966).

Overall effects of fish length and prey species on the total number of each behavior and total time handling prey were examined using two-factor ANOVA. Tukey's HSD was used to determine differences between bluegill length categories. Similar two-factor ANOVAs were conducted on behavioral probabilities in the predation sequence: strikes/orient, captures/strike, and ingestions/capture (similar to Holling 1966; Barnhisel 1991a). These

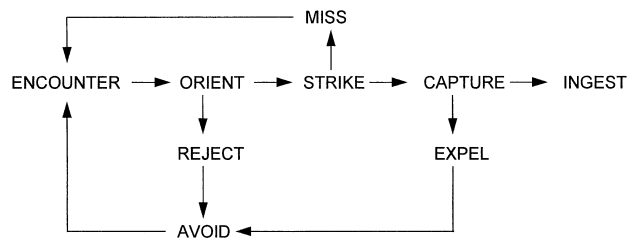


Fig. 1 Behavioral pathways from encounter through ingestion for late-larval and juvenile bluegill preying on *Daphnia lumholtzi*

data were first arcsine transformed. We also examined how each of the above behaviors and behavioral probabilities varied over the duration of the 15-min experiment using a two-factor RM-ANOVA. Because of zeros in the behavior data set, behavioral probability data were combined into three 5-min categories. All analyses were conducted using PROC GLM (SAS 1991) and an α value of 0.05.

Field selectivity

We collected fish and zooplankton from four stations in Lake Springfield, Ill., on 13 and 26 July 1994, and 11 July and 21 September 1995, during the times of peak abundance of *D. lumholtzi* (Kolar et al. 1997). Seine (6-mm round mesh, 6.4 m long \times 1.0 m deep) hauls were made about 50 m in length along the shore at a uniform depth of 1.0–1.25 m. We preserved all fish collected in 75% ethanol. Since few larger bluegill were collected by seine, we also electrofished for larger bluegill on 14 August 1997. Duplicate zooplankton samples were collected at each site by vertical tows using a 0.5-m diameter zooplankton net (64 μ m mesh) adjacent to each seine site. Samples were preserved in a sucrose-10% formalin solution to prevent carapace distortion (Haney and Hall 1973).

In the laboratory, bluegill were measured (to the nearest millimeter) and stomachs were analyzed until five in each 10-mm size increment that contained food had been examined. Food items were identified to the lowest practical taxonomic level (usually genus), counted, and weighed (nearest 0.001 g). Zooplankton biomass was estimated (using the same equation for all members of a genus) from equations found in Rosen (1981). Zooplankton samples were adjusted to 100 ml and subsampled by 1-ml aliquots. Crustacean zooplankton (nauplii, copepods, cladocerans, and ostracods) were enumerated and identified. Subsamples were examined until at least 200 of the most common taxa had been enumerated. Since we were interested only in selectivity for *D. lumholtzi*, we divided zooplankton into two groups: *D. lumholtzi* and all other crustacean zooplankton. We calculated Chesson's (1983) coefficient of selectivity to examine selectivity of *D. lumholtzi* over native crustacean zooplankton. The α values from individual fish were averaged within each 10-mm length category. Mean selectivity coefficients were compared to random feeding (1/number of prey types) using paired *t*-tests with a Bonferroni correction of the decision level (0.05/number of pairwise comparisons) to provide an overall error rate of 0.05 (Scheiner 1993). Data were arcsine transformed to meet the normality assumption.

Results

Laboratory experiments

Selectivity experiments

Overall, the number of prey eaten increased with bluegill length: 56.0 ± 4.8 daphnids for small bluegill,

116.0 ± 7.9 for medium, and 291.9 ± 18.9 for large fish (Table 1). There was also an effect of prey treatment, with more *D. pulex* being eaten alone (183.5 ± 20.3) than *D. lumholtzi* alone (128.5 ± 21.2); the mixed-species treatment was intermediate in numbers eaten (142.5 ± 18.1) and different from the other two treatments (Fig. 2). While there was no significant interaction between fish length and treatment (Table 1), the relative numbers of each species consumed became more similar as fish length increased (Fig. 2; small bluegill ate 3 times more *D. pulex* than *D. lumholtzi*, medium bluegill ate 1.5 times more, and large bluegill ate 1.05 times more). Since the number of prey eaten in the mixed-species treatment overall was lower than the number of *D. pulex* eaten in the *D. pulex*-only treatment (Fig. 2), the presence of *D. lumholtzi* interfered with bluegill foraging, resulting in an overall lower ingestion rate.

The same patterns of consumption were observed within the mixed-species treatment. The number of *Daphnia* eaten increased with bluegill length: 56.8 ± 4.6 for small bluegill, 102.5 ± 13.3 for medium, and 288.8 ± 31.4 for large fish (Fig. 2, two-way ANOVA, $F_{2,66} = 69.73$, $P < 0.0001$). The mean number of *D. pulex* eaten (90.0 ± 11.1) was greater than the mean number of *D. lumholtzi* eaten (57.0 ± 9.6; two-way ANOVA, $F_{1,66} = 16.10$, $P = 0.0002$). Across length categories, bluegill consumed similar relative numbers of each species (two-factor ANOVA, interaction term, $F_{2,66} = 0.59$, $P = 0.56$). Again, although the interaction between fish length category and species was not significant, as bluegill length increased, the number of *D. lumholtzi* eaten relative to the number of *D. pulex* eaten increased (Fig. 2).

The foraging of bluegill did not change the mean body length of *D. pulex* remaining in the chamber from the initial assemblage either in the *D. pulex*-alone treatment (two-factor ANCOVA, $F_{1,52} = 1.90$, $P = 0.17$) or in the mixed-species treatment ($F_{1,58} = 3.40$, $P = 0.07$). There was also no effect of bluegill length

on the body length of remaining *D. pulex* (*D. pulex*-alone treatment, $F_{1,52} = 1.51$, $P = 0.23$; mixed-species treatment, $F_{1,58} = 0.72$, $P = 0.40$). Thus predation by bluegill 15–80 mm on *D. pulex* was not size selective.

Bluegill did show size selectivity when foraging on *D. lumholtzi*, however. The body lengths of *D. lumholtzi* from the initial assemblage were smaller than those remaining after the experiment in the mixed-species treatment (two-factor ANCOVA, $F_{1,59} = 4.82$, $P = 0.03$). There was also a similar trend in the *D. lumholtzi*-alone treatment ($F_{1,61} = 3.09$, $P = 0.08$). Thus, bluegill selectively removed the smaller *D. lumholtzi*. In both the mixed-species ($F_{1,59} = 33.13$, $P < 0.0001$) and *D. lumholtzi*-only ($F_{1,61} = 30.73$, $P < 0.0001$) treatments, smaller bluegill selected smaller *D. lumholtzi* than did larger fish.

Foraging behavior experiments

Most predation on *D. pulex* occurred within the first few minutes of the experiment and was generally successful (Fig. 3): fish would orient, strike, capture, and ingest most prey. Bluegill foraged on *D. pulex* without difficulty and continued foraging until they appeared satiated (smaller bluegill) or continued to forage through

Table 1 Results of a repeated-measures ANOVA showing the effects of treatment (*Daphnia lumholtzi* alone, *D. pulex* alone, mixed species at 1:X), and bluegill length (15–27, 33–47, and 52–80 mm) on the number of daphnids eaten in 1 h. The Huynh-Feldt correction was used for reporting the within-subject effect

Effect	df	SS	F	P
Between subject				
Fish length	2	1,062,367	55.09	<0.0001
Linear contrast				
<i>D. pulex</i> vs mixed species	1	505,553	52.43	<0.0001
Error	33	318,190		
Within subject				
Treatment	2	60,048	17.55	<0.0001
Treatment*fish length	4	4,292	0.63	0.64
Error	66	112,936		

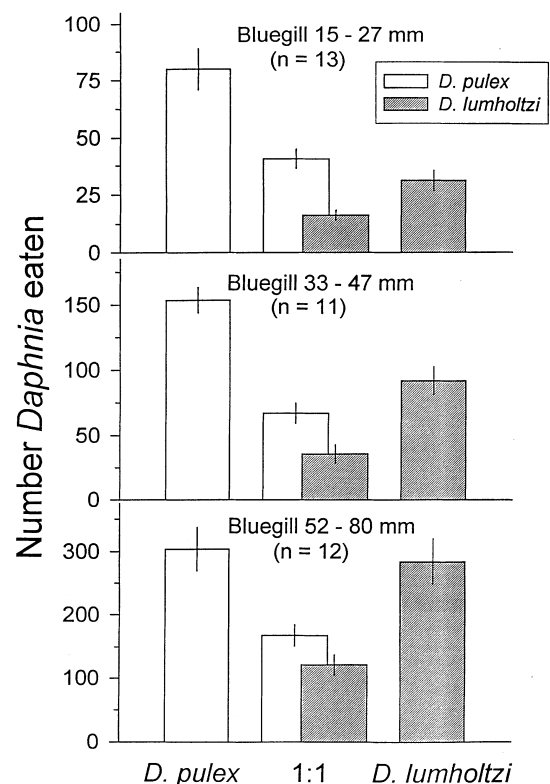


Fig. 2 Number of daphnids eaten in 1-h selectivity experiments by bluegill length categories in three treatments (*D. pulex* alone, *D. lumholtzi* alone, and a 1:1 mix of both species). Vertical error bars represent ± 1 SE; sample size is given in parentheses

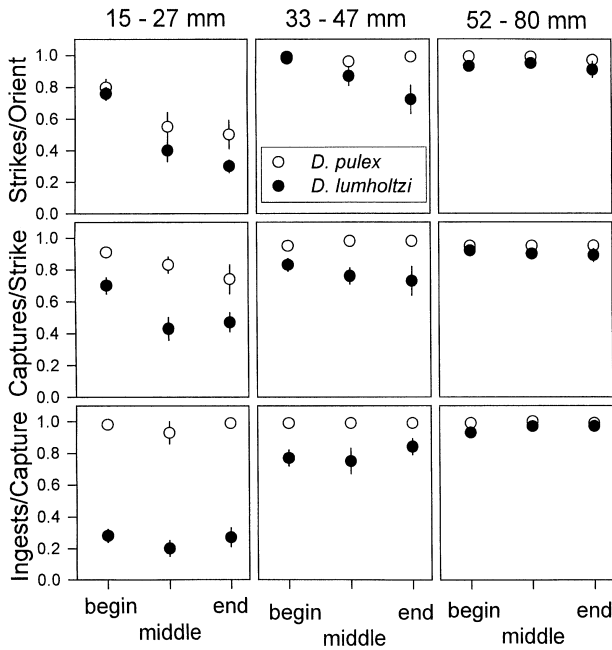


Fig. 3 Numbers of ingestions of either *D. pulex* or *D. lumholtzi* for three length categories of bluegill in foraging behavior experiments. Vertical error bars represent ± 1 SE

the experiment. While foraging on *D. lumholtzi*, however, bluegill encountered difficulty and consumed less prey than when foraging on *D. pulex* (Fig. 3). Failure to ingest *D. lumholtzi* could result from interruption at several places along the behavioral pathway of bluegill foraging (Table 2). Upon encounter, bluegill would orient toward *D. lumholtzi* and often reject it. If it tried to strike at the prey, it was often missed and captured *D. lumholtzi* were often expelled. Repeated orients that resulted in rejects and captures that resulted in expels contributed toward a lower ingestion rate of *D. lumholtzi* compared to that of *D. pulex*.

Most predation on *D. lumholtzi* also occurred toward the beginning of the experiment but less were eaten compared to foraging on *D. pulex* (Fig. 3). At first, small and medium bluegill would attack and ingest *D. lumholtzi* until one was captured such that the spines would lodge in the buccal cavity. Bluegill often flared their operculi and buccal cavity and shook their head in an attempt to dislodge the *D. lumholtzi* (similar to yellow perch, *Perca flavescens*, behavior foraging on *Bythotrephes*; Barnhisel 1991a). As fish gained experience with *D. lumholtzi*, strikes declined and bluegill < 50 mm began orienting and then rejecting prey with greater frequency (Fig. 3). Larger bluegill, however, continued to strike at *D. lumholtzi* at the same rate through the experiment (Fig. 3).

All lengths of bluegill oriented similarly toward *D. pulex* and *D. lumholtzi* (Table 2). Prey species was also not important in determining the number of strikes, although there was a trend toward more strikes at *D. pulex* than *D. lumholtzi* ($P = 0.08$, Table 2). From

Table 2 Means (± 1 SE) of the total number of various behaviors that occurred during each of the 15-min foraging behavior experiments. Also shown are resulting P -values from two-factor ANOVAs run on the totals using treatment and bluegill length category as independent variables. In each ANOVA, the degrees of freedom were partitioned as follows: treatment (1 df), length category (2 df), treatment by length interaction (2 df), and error (74 df)

Behavior	15-27 mm		33-47 mm		52-80 mm		P-values		
	<i>D. pulex</i>	<i>D. lumholtzi</i>	<i>D. pulex</i>	<i>D. lumholtzi</i>	<i>D. pulex</i>	<i>D. lumholtzi</i>	Treatment	Length	Treatment* length
Orients	98.9 (10.4)	157.5 (10.7)	153.2 (15.0)	149.6 (16.3)	178.6 (17.1)	135.5 (16.5)	0.74	0.09	0.002
Strikes	77.1 (11.2)	73.8 (8.7)	151.0 (14.8)	137.0 (16.4)	176.1 (16.1)	131.1 (16.7)	0.08	<0.001	0.28
Captures	76.7 (11.0)	47.9 (5.7)	144.3 (14.3)	105.0 (11.4)	169.1 (16.3)	118.0 (15.2)	0.001	<0.001	0.54
Ingests	70.9 (11.1)	11.8 (2.2)	143.8 (14.4)	82.9 (12.1)	170.8 (17.1)	111.9 (14.9)	<0.001	<0.001	0.99
Handle/prey	0.1 (0.04)	17.3 (5.2)	0.01 (0.003)	1.3 (0.5)	0.01 (0.01)	0.60 (0.20)	0.002	<0.001	<0.001
Handling	2.9 (1.2)	146.1 (36.2)	0.7 (0.3)	69.5 (16.7)	1.70 (1.40)	52.3 (16.8)	<0.001	0.03	0.03

this point in the predation sequence, however, there were large differences in the frequency of predation events between prey species. Captures and ingestions increased proportionately with fish size and were consistently higher for *D. pulex* than for *D. lumholtzi* (Table 2). Far more *D. lumholtzi* were rejected, missed, and expelled than *D. pulex*. Small bluegill rejected and expelled more prey than larger bluegill as indicated by the significant interaction term (Table 2).

There were also differences between prey species and fish length in the relative success rate of various aspects of the predation sequence (Fig. 3). Bluegill foraging on *D. lumholtzi* were less likely to strike after orienting than when foraging on *D. pulex* (RM-ANOVA, between-subject effect, $F_{1,74} = 6.03$, $P = 0.02$). Small fish were less likely to strike after orienting than larger ones. Strikes per orient for small bluegill showed a similar decline for both prey species over time (Fig. 3), though likely controlled by different mechanisms. Small bluegill ingested an average of 70.9 ± 11.1 *D. pulex* during the experiments and appeared satiated within a few minutes of foraging. The same fish consumed an average of only 11.8 ± 2.2 *D. lumholtzi* during the experiments – these fish, therefore, decreased their attack rate more than nearly satiated fish feeding on *D. pulex*.

Small and medium bluegill were more likely to capture *D. pulex* than *D. lumholtzi* after striking than large bluegill (RM-ANOVA, between-subject effect, $F_{2,74} = 21.30$, $P < 0.01$; Tukey's HSD, $P < 0.05$). Not only did bluegill capture more *D. pulex* than *D. lumholtzi*, but they ingested them with higher efficiency (Fig. 3). Bluegill of all lengths tested had between 85–100% ingestion efficiency (ingestion/capture) preying on *D. pulex* (Fig. 3). When foraging on *D. lumholtzi*, however, ingestion efficiency was lower, increasing with bluegill length. The importance of bluegill length for foraging successfully on *D. lumholtzi* is evident: the probability of successfully completing any given component of the predation sequence increased with bluegill length (Fig. 3). Overall, bluegill were far more successful in all aspects of predation while foraging on *D. pulex* than while foraging on *D. lumholtzi*.

The low ingestion efficiencies of bluegill foraging on *D. lumholtzi* may be explained largely by difficulties in handling, presumably due to its spines. Bluegill spent much more time handling *D. lumholtzi* (146.1 ± 36.2 s handling for small bluegill, 69.5 ± 16.7 s for medium bluegill, and 52.2 ± 16.8 s for large bluegill) than *D. pulex* (2.9 ± 1.2 s handling for small bluegill, 0.7 ± 0.3 s for medium, and 1.7 ± 1.4 s for large bluegill; Fig. 4). Because of the high handling time for *D. lumholtzi*, bluegill spent a substantial amount of time attempting to swallow prey over the course of the experiment. Small bluegill spent up to 30% of the time, particularly early in the experiment, handling *D. lumholtzi*. Medium fish spent up to 20% of the time handling prey, and even large bluegill spent 10% of the time handling *D. lumholtzi*.

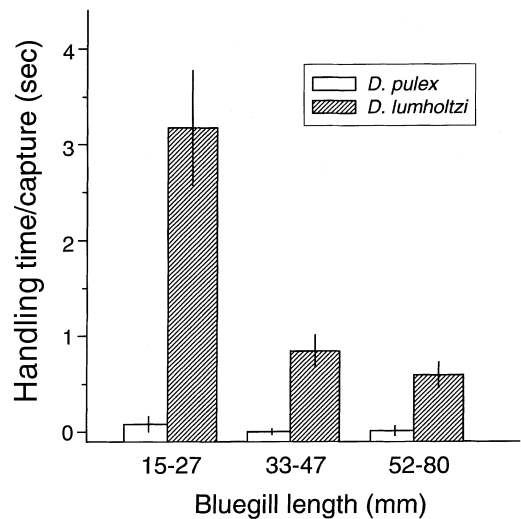


Fig. 4 Mean handling time per prey item for bluegill foraging on either *D. lumholtzi* or *D. pulex*. Handling times are higher for *D. lumholtzi* than *D. pulex* at all bluegill lengths. Vertical bars represent ± 1 SE

Field selectivity

We examined a total of 145 bluegill stomachs and found *D. lumholtzi* in 21% of them. We also found *D. lumholtzi* in stomachs of brook silverside (*Labidesthes sicculus*), emerald shiner (*Notropis atherinoides*), red shiner (*N. lutrensis*), golden shiner (*Notemigonus crysoleucas*), green sunfish (*Lepomis cyanellus*) and white bass (*Morone chrysops*). We found no *D. lumholtzi* in any of the bullhead minnow (*Pimephales vigilax*) or gizzard shad (*Dorosoma cepedianum*) examined.

In bluegill, zooplankton (including *D. lumholtzi*) constituted $16.8 \pm 2.5\%$ of stomach content weight. The remainder of the stomach content was dominated ($> 80\%$) by aquatic insects (primarily chironomid larvae and pupae). Seventy bluegill consumed zooplankton and we calculated selectivity coefficients for *D. lumholtzi* on these fish. Bluegill from smaller length categories (10–19 mm, 20–29 mm, 30–39 mm, 40–49 mm) selected against *D. lumholtzi* (t -test, all P -values < 0.05). In bluegill greater than 50 mm, *D. lumholtzi* were actually preferred zooplankton prey (Fig. 5; t -test, both P -values < 0.05).

Discussion

Our data show dramatic differences in bluegill foraging on *D. lumholtzi* compared to *D. pulex* for virtually every foraging behavior we measured and for every predation event we observed. When foraging on *D. pulex*, the predation sequence was linear: prey were encountered, the bluegill oriented, attacked, captured, and then ingested prey. Prey were consumed with 85–100% efficiency and handling times were usually too short to detect (similar to observations of Mittelbach 1981;

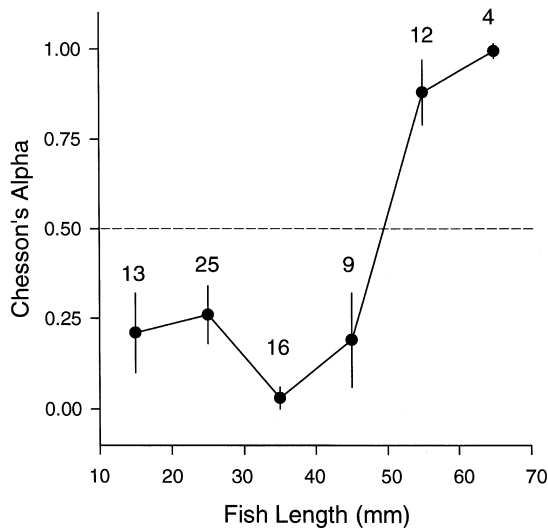


Fig. 5 Chesson's coefficient of selectivity for bluegill collected from Lake Springfield, Ill., 1994–1997. Vertical bars represent ± 1 SE. The dashed line represents neutral selection ($1/\text{number of prey categories}$). Sample sizes are given above the points

Bence and Murdoch 1986). Preying on *D. lumholtzi*, however, presented challenges for bluegill throughout the range of sizes tested. All sizes of bluegill had substantially higher handling times when foraging on *D. lumholtzi* than while foraging on *D. pulex*. Smaller bluegill had more difficulty capturing and ingesting *D. lumholtzi* and ingested fewer *D. lumholtzi* compared to *D. pulex* than larger fish. In addition, fish < 50 mm selected against *D. lumholtzi* in both the laboratory and field. Therefore, fish size is an important factor in determining success of foraging on *D. lumholtzi*.

We found that smaller bluegill (< 50 mm) altered their behavior foraging on *D. lumholtzi* within the time of our experiment. At the beginning, these bluegill attacked *D. lumholtzi* readily, but after unprofitable attempts, the bluegill would begin orienting and then rejecting prey more often than striking. Avoidance behavior is an example of operant conditioning where an animal 'learns' to associate one of its own behaviors with a reward or punishment and then either repeats or avoids the behavior, depending on whether the reinforcement was positive or negative (Campbell 1990). A similar scenario occurs in the development of aversion to *Bythotrephes* in yellow perch: fish first attacked *Bythotrephes* readily but as they gained experience, they ceased attacking it (Barnhisel 1991a). Similar to yellow perch feeding on *Bythotrephes*, aversion to *D. lumholtzi* by small gape-restricted bluegill is an efficient response to the spiny, but visually conspicuous *D. lumholtzi*. In our experiments, larger bluegill (52–80 mm) did not avoid *D. lumholtzi*, even though they had lower ingestion rates and longer handling times while foraging on *D. lumholtzi* than when foraging on *D. pulex*. Since larger bluegill are less restricted by gape (Bremigan and Stein 1994), they are better able to handle and consume *D. lumholtzi* and continued to attack.

Capturing, manipulating, and ingesting *D. lumholtzi* is challenging and energetically costly for smaller bluegill. We predicted, therefore, unless efficiency could be improved over time, that bluegill less than around 50 mm should avoid *D. lumholtzi*. These predictions were validated by our field selectivity results. In the field, bluegill < 50 mm selected against *D. lumholtzi*, whereas *D. lumholtzi* was a preferred diet item for larger bluegill. Our field data also show, however, that bluegill as small as 15 mm can consume *D. lumholtzi* (although they select against it). In these stomachs, a small number of *D. lumholtzi* (4.2 ± 1.2) corresponded to a high proportion of stomach content weight ($70 \pm 15\%$). While our data are limited, if stomach volumes of these small fish consuming *D. lumholtzi* remain low for extended periods of time, growth would be reduced.

We agree, therefore, with the predictions of Swaffar and O'Brien (1996) that small fish are more likely to be impacted by the invasion of *D. lumholtzi* than larger fish and further add that bluegill less than around 50 mm should avoid *D. lumholtzi*. In addition, the potential for *D. lumholtzi* to directly impact small obligate planktivores is limited by temporal segregation. Larval fish densities typically peak in May or June (Guest et al. 1990; Dettmers and Stein 1992; Welker et al. 1994) and predation pressure on zooplankton is highest when fish larvae are abundant. In midwestern waters, *D. lumholtzi* overwinters as resting eggs and does not appear until early summer, peaking in abundance in July (Kolar et al. 1997). So by summer, when *D. lumholtzi* becomes an abundant member of the zooplankton community, the diet breadth of most fish species is large enough so that they do not depend heavily on zooplankton. Thus, the potential for negative effects of *D. lumholtzi* on these species is low.

Exceptions, however, include the sunfish. Most sunfishes, with bluegill generally being the most important ecologically and economically, have protracted spawning periods that allow reproduction to occur during spring and summer months. Thus, late-larval and early juvenile bluegill are present into the summer and fall. These fish require zooplankton after native zooplankton peaks in the spring (Welker et al. 1994). Abundant *D. lumholtzi*, largely unavailable to small fish, may limit the foraging success of these sunfish. If competition for macroinvertebrates is high or these late-spawned bluegill are too small to switch from zooplankton, these fish would experience decreased growth. Slowed growth leads to a host of negative impacts, including sustained vulnerability to predation (Nielsen 1980). We also have recent evidence that later-spawned bluegill can be the major contributors of recruits into the population in geographic regions where overwinter mortality is low (D. Wahl, unpublished data). Later-spawned individuals avoid predation pressure experienced by their earlier cohorts and are too small to be preferred by most piscivores later in the season. So, while *D. lumholtzi* has limited potential to affect many species, it may impact a vulnerable life stage of an important species.

Spine production in zooplankton generally serves as protection against invertebrate predators by inhibiting the ability of predator mouthparts to engulf prey (Dodson 1974). Dodson also hypothesized that spine production serves to shunt growth into inconspicuous structures to decrease core body size, keeping zooplankters less visible to vertebrate predators. Production of these structures entails energetic costs such as longer developmental times (Riessen and Sprules 1990; Barry 1994) or smaller broods (Kerfoot 1977; Riessen 1984). Barry (1994) estimated that the energetic cost of crest production for *D. carinata* is 60 eggs over the lifetime of the individual. Given these high costs associated with spine production, why does *D. lumholtzi* produce such elaborate spines?

If visual planktivores select for zooplankton with a body length > 1 mm (Dodson 1974), *D. lumholtzi* (with a mean body length of 0.8 or 0.9 mm) would not be a preferred prey for fish. In addition to the helmet and tail spine, *D. lumholtzi* also has lateral fornices and is virtually transparent, both defenses that presumably act to deter fish predators. Given its relatively small size, these numerous antipredatory defenses seem extreme, but are likely related to high predation pressure in its native ecosystems. Evidence of fish predation on *D. lumholtzi* is contradictory from within its native range. Green (1967) found only nonhelmeted *D. lumholtzi* in the stomachs of *Alestes baremose*, a common planktivore in Lake Albert, East Africa, suggesting that the spines of *D. lumholtzi* effectively deter fish predators, but others credit grey mullets (*Acanthobrama terraesanctae*) and *Tilapia aurea* with the extinction of spined *D. lumholtzi* from Lake Kinneret, Israel, in the 1950s (Gophen 1979).

Since planktivores ingest many small prey with relatively low mobilities, they have higher capture success (usually >80%; Confer and Blades 1975; Mayer and Wahl 1997) than piscivores (usually <70%; Webb 1986; Wahl and Stein 1988). Similarly, planktivorous prey are small and relatively defenseless, so prey are pursued, captured, and ingested within a second or two (Mittelbach 1981; Gerking 1994; Wazenbock 1995) whereas handling times for individual prey by piscivores are considerably higher (3–6 min for esocids, Wahl and Stein 1988; 2–10 min for walleye, Einfalt and Wahl 1997). In general, because of the high capture success and short handling times of planktivores, search time (Gerking 1994) and prey density (Werner and Hall 1974; O'Brien et al. 1976) are of much greater importance to a particulate feeder than is capture success (Juanes 1994) or handling time (Gerking 1994).

Bluegill foraging on *D. lumholtzi* are exceptions to these generalities. We found that bluegill (15–80 mm) foraging on *D. lumholtzi* face foraging constraints more similar to piscivores than to those of planktivores. Bluegill < 50 mm had probabilities of capture and ingestion of *D. lumholtzi* more typical of piscivores than planktivores. Bluegill of all sizes tested also spent substantial amounts of time attempting to swallow *D. lumholtzi*: from 0.5 to 4 s/prey depending on bluegill

length (from 4 to 15 times longer attempting to swallow *D. lumholtzi* than *D. pulex*) and up to 30% of total time spent foraging. Even large bluegill spent 10% of the experiment attempting to swallow *D. lumholtzi*. Spending such large portions of time attempting to swallow prey that could be spent foraging may have negative energetic consequences for fish in the field. The antipredatory defenses of increasing handling time and decreasing capture success to deter predation by planktivores has also been found in fish foraging on *Bythotrephes* (Barnhisel 1991a, b). The tactic of frustrating planktivores with these defenses is thus far unique for these two species of zooplankton and demonstrates the ability of zooplankton morphology to deter fish predators.

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