The ecological role of chemical stimuli for the zooplankton: predator-induced morphology in *Daphnia*

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Summary. Numerous adaptive predator-induced responses occurred when eight clones representing seven *Daphnia* (Crustacea: Cladocera) species were tested against three common predators: fourth instar larval phantom midge *Chaoborus americanus*, adult backswimmer *Notonecta undulata*, and small sunfish *Lepomis macrochirus*. The predators were confined within small mesh bags, suggesting that the signal for induction is chemical. The induced responses included longer tail spines, longer heads, smaller bodies, increased egg clutches, and decreased lipid reserves. Each *Daphnia* species responded to each of the three predators in a unique manner. Induced responses in the above characters showed no significant association. The induced morphological changes are generally consistent with current theories of what is an adaptive response for the various sizes of *Daphnia* exposed to tactile and visual predators. The abundance of induced responses in these experiments suggests that predator-induced responses are a widespread and ecologically important phenomenon of the freshwater zooplankton.

Key words: *Chaoborus* – *Daphnia* – *Lepomis* – *Notonecta* – Predator-induction

Zooplankton are paradigms of phenotypic plasticity: Woltereck (1909) first coined the term "reaction norm" in reference to the temporal cyclic morphological changes that occur within *Daphnia* populations. A number of studies on *Daphnia* and other zooplankton populations show that this phenotypic plasticity, within a single clone, can be a function of a number of physical factors, such as temperature, photoperiod, turbulence, and food supply (Hrbaček 1959; Jacobs 1962; Lampert and Wolf 1986).

Havel (1987) and Stemberger and Gilbert (1987) summarize a number of studies showing changes in morphology and life history characteristics can be induced in herbivorous zooplankton by the presence of chemical signals produced by co-existing predators. For North American *Daphnia*, there are a number of examples. Krueger and Dodson (1981) showed that some clones of *Daphnia pulex* Leydig develop neck teeth as juveniles, when in the presence of the predator *Chaoborus americanus* (Johanssen). Havel and Dodson (1987) subsequently showed that the presence of the neck teeth was associated with an increased juvenile development, and perhaps a lower reproductive rate, rate

factors that may be disadvantageous to these r-specialists under predator-free conditions. Dodson (1988a) found that elongated helmets observed in *Daphnia galeata mendotae* and *D. retrocurva* can be induced by the presence of the common predators *Notonecta* (back swimmers) and *Chaoborus* (phantom midge larvae). Hebert and Grewe (1985) reported that the pointed helmets of adult *Daphnia ambigua* were lost in culture, but could be induced by growing the animals in the presence of *Chaoborus*. Dodson and Havel (1988) found that *D. pulex* shows a number of responses to the predator *Notonecta*, including a reduction in neonate and adult body size and lowered lipid stores. It is beginning to appear that many species of *Daphnia* respond developmentally and morphologically to the presence of predators.

The present study was designed to test for induced morphological responses in a representative array of clones of the genus *Daphnia*. I chose eight clones representing seven species, from the small *D. parvula* to the large *D. pulex*. The clones were collected from a range of water bodies, from small ponds to large lakes. Specifically, (1) How common are these morphological responses among *Daphnia*?, (2) For neonates and primiparous adults, are there induced changes in tail spine length, head length, body length, lipid index, and clutch size? Do clones respond differently to different predators and do different clones respond differently to the same predators? (3) Are there patterns, such as correlations or mutual exclusions in the expression of the various anti-predator morphologies? That is, are the induced responses predator-specific, as suggested by Gilbert (1980), and (4) Do the responses appear to be adaptive, according to the scheme of Dodson (1974).

Methods

The 8 *Daphnia* clones used separately in these experiments are the same as those described in Dodson (1988, 1989). The culture methods were the same, and the animals were fed the same concentrations of algae. The *Daphnia* were fed a mixture of green algae dominated by *Scenedesmus* (about 6.7×3.4 μm) and *Chlorella* (about 6.7 μm diameter). Food concentrations are given as wet weights, estimated from volume and abundance of algal cells (see Table 9 for an example). The algae were grown in a 120 L aquarium and food concentrations were monitored spectrophotometrically, using the method described in Dodson and Havel (1988).

The experiments were in 4 L jars of algal suspension, initially adjusted to 8–11 mg Wet Weight L^{-1}. The jars were stirred once a day. As in earlier studies using the same algae (Dodson and Havel 1988), the algal concentration dropped overnight before being restirred, because of settlement, by as much as 33%. The daily average algal concentration was calculated using the pre and post-stirring concentrations.

In general, the *Daphnia* were given only the initial feeding, and the daily average algal concentration decreased by less than 10% over the course of the 7 day experiment. This food level was found to be optimal for the expression of induced responses by Dodson and Havel (1988) and Dodson (1988). In a few cases optical density of a jar drifted 2% higher or lower than the others during the course of an experiment, indicating a change in algal wet weight concentration of about 25%. The concentration was then adjusted back to the median value of the other jars with aged tap water or concentrated algal solution.

About 25 ovigerous *Daphnia* were introduced into each jar at the beginning of an experiment. A 163 μm mesh bag (approximately 1 L volume) was placed in each jar, keeping the *Daphnia* on the outside of the bag. About 25 additional *Daphnia* were put into the water in the bag. The same clone was always used inside the bag as outside the bag. To the bags were added either no predator (the predator control treatment), four fourth instar *Chaoborus americanus* (phantom midge) larvae, two adult *Notonecta undulata* (backswimmers), or one *Lepomis macrochirus* (bluegill sunfish) about 2.5 cm in length.

These experiments (one for each clone) were designed to detect the presence or absence of an induced response. Since I had no way of knowing the amount of signal produced by each predator, I chose predator densities that were higher than found in nature, and likely to produce a strong induction, if the prey clone was responsive. Quantitative comparisons of the strength of signals from different predators await the identification of the signal, presumably one or more specific chemicals (Dodson and Havel 1988).

For each experiment, there were 12 jars, including three controls and three for each predator treatment. These jars were kept at room temperature (19–21° C) and at ambient photoperiod in a room with northern exposure (no direct sunlight) producing up to 1200 lux (113 foot candles). The temperature and light level were within the ranges indicated by Jacobs (1962) as optimal for helmet development. The jars were kept on a table, and the arrangement of jars was changed each day to reduce the possibility of position effects.

At the end of 7 days, approximately one *Daphnia* generation, the *Daphnia* were removed from the jars by filtration and measured live, as in Dodson (1988). Ten neonates and ten primiparous adults were selected haphazardly (the first ten) and measured from outside the bag in each jar. The parameters were core body length (BL), head length (HL), tail spine (shell spine) length (TL), lipid index (LI, as described by Tessier and Goulden 1982) and for the adults, the number of eggs or embryos carried in the brood chamber (E/F). Because HL, TL, and E/F are known to be a function of body length, I also calculated the ratios HL/BL, TL/BL, and (E/F)/BL, to test for changes proportional to changes in body length, in case head length, body length, or clutch size were linearly related to body length. Thus, there were six parameters for neonates and eight for

adults. A mean value was calculated for each parameter in each jar.

For each parameter in each experiment, the mean values for replicate jars of the predator treatments were compared to those of the control treatments, using Sokal and Rohlf's (1981) method for planned comparisons of means in a single classification Model I anova.

As the experiments were run, I noticed that several of the clones showed an increased clutch size in the presence of bluegill sunfish. To test whether the increase was due to an increase in food level, I counted, using a hemocytometer cell, the dominant algae in control and bluegill-treatment jars of the *D. ambigua* clone AW1 experiment. This clone showed the largest increase in clutch size in the presence of bluegill.

A 2×2 Contingency Table method (Grieg-Smith 1983) was used to test (with 1 degree of freedom) for pair-wise associations between induced responses, for the three predators combined, for the combined adults of the eight clones. Significance was tested using a Fisher Exact Probability test. Associations can be either positive or negative. Clones were pooled and responses were recorded as present or absent. A responses was scored as "present" if it was statistically significant. For example, in a comparison of instances of significant responses in head length and tail length for adults, there were, of the twenty-four pairs, 7 instances of both significant head and tail responses, three instances of significant head alone, and ten of significant tail alone, giving a non-significant probability of association.

Results and analysis

Treatment averages are given in Tables 1–8. An elongated tail spine (tail spine length divided by body length) was the most frequent response to the predators. For adults, Tables 1–8 show 17 (of a possible 24) instances of a tail spine significantly longer than the control spine. Each of the eight clones showed at least one example of an elongated adult spine. Neonates were less responsive than adults: neonates often showed no response when the adults did, but in no case was the opposite true. There was no example of an induced shorter tail spine. Most adult responses were to the *Notonecta* and *Lepomis*: 8 and 7, respectively, compared to 2 for *Chaoborus*.

There were 7 instances of induced changes of head length in adults: 3 for *Chaoborus*, 3 for *Notonecta*, and 1 for *Lepomis*. These were all elongations, except for *D. ambigua* adults exposed to *Lepomis*, which had shorter heads. In no case did *Lepomis* induce a longer adult head. The responses of two strongly cyclomorphic clones (*D. galeata mendotae* DGA and *D. retrocurva* R1) are discussed in detail in Dodson (1988a). There are several discrepancies in head length response between neonates and adults. *D. ambigua* neonates exposed to *Chaoborus* had significantly longer heads (all had a sharp-pointed head), while the adults showed no response (all had a rounded head). Note that this is the opposite pattern reported by Hebert and Grewe (1985), who found that adults but not neonates grew pointed helmets for *Chaoborus*. *D. ambigua* adults exposed to *Lepomis* had shortened heads, while the neonates did not. Neonates of *D. g. mendotae* had significantly shorter heads in the presence of *Lepomis*. Otherwise, the neonates tended to lack elongated heads when the adults did respond in this manner.

Table 1. Average values for *Daphnia ambigua*, clone AW1. Parameter abbreviations are BL = body length, HL = head length, and TL = tail length: as in Figure 1. Also, LI = Lipid Index, E/F = primiparous clutch size. Statistical significance is based on the within-group mean square estimate from a single classification anova of the three jar means of each of the four treatments

Stage	Parameter	Treatment mean			
		Control	Chaoborus	Notonecta	Lepomis
Neonate	BL (mm)	0.477	0.491	0.457	0.429*
	LI	2.97	2.97	1.93**	0.85***
	HL/BL	0.043	0.062**	0.056	0.052
	TL/BL	0.451	0.473	0.472	0.468
Adult	BL (mm)	1.032	1.056	0.926**	1.060
	LI	1.17	1.06	0.18**	0.52*
	E/F	1.50	1.77	1.47	5.89***
	HL/BL	0.036	0.031	0.040	0.027**
	TL/BL	0.041	0.041	0.055*	0.053*
	(E/F)/BL	1.46	1.69	1.58	5.61***

Significance levels: $* < 0.05$, $** < 0.01$, $*** < 0.001$, F ratio with 1,8 df

Table 2. Average values for *Daphnia galeata mendotae*, clone DGA. Parameter abbreviations and statistical significance codes as in Table 1. These data are taken from Table 1, Dodson (1988a), with permission of the editor

Stage	Parameter	Treatment mean			
		Control	Chaoborus	Notonecta	Lepomis
Neonate	BL (mm)	0.621	0.618	0.635	0.616
	LI	3.00	3.00	2.90	2.97
	HL/BL	0.173	0.183?	0.184*	0.158*
	TL/BL	0.800	0.802	0.789*	0.792*
Adult	BL (mm)	1.616	1.627	1.595	1.469***
	LI	2.92	2.94	2.93	2.70**
	E/F	5.20	5.06	4.73	4.37
	HL/BL	0.129	0.159**	0.175***	0.125
	TL/BL	0.441	0.435	0.470**	0.462*
	(E/F)/BL	3.22	3.11	2.97	2.97

Table 3. Average values for *Daphnia obtusa*, clone G5A. Parameter abbreviations and statistical significance codes as in Table 1

Stage	Parameter	Treatment mean			
		Control	Chaoborus	Notonecta	Lepomis
Neonate	BL (mm)	0.521	0.515	0.457***	0.522
	LI	2.93	2.80	2.63	2.60*
	HL/BL	0.090	0.038	0.041	0.036
	TL/BL	0.386	0.392	0.408	0.392
Adult	BL (mm)	1.431	1.419	1.220***	1.407
	LI	2.93	2.93	2.87	2.70**
	E/F	6.37	6.20	6.10	8.00*
	HL/BL	0.021	0.020	0.021	0.021
	TL/BL	0.158	0.167	0.200***	0.173*
	(E/F)/BL	4.45	4.37	5.01	5.69*

Table 4. Average values for *Daphnia parvula*, clone TO1. Abbreviations and statistical significance codes as in Table 1

Stage	Parameter	Treatment mean			
		Control	Chaoborus	Notonecta	Lepomis
Neonate	BL (mm)	0.485	0.485	0.442***	0.425***
	LI	3.00	2.93	3.00	2.90
	HL/BL	0.085	0.084	0.084	0.079
	TL/BL	0.495	0.501	0.484	0.490
Adult	BL (mm)	0.994	0.997	0.944**	0.982
	LI	2.67	2.58	2.85	1.60***
	E/F	2.35	2.03	2.17	3.97***
	HL/BL	0.048	0.055	0.047	0.044
	TL/BL	0.188	0.217***	0.208**	0.210**
	(E/F)/BL	2.37	2.04	2.29	4.05***

Table 5. Average values for *Daphnia pulex*, clone SBL. Parameter abbreviations and statistical significance codes as in Table 1

Stage	Parameter	Treatment mean			
		Control	Chaoborus	Notonecta	Lepomis
Neonate	BL (mm)	0.663	0.623	0.577**	0.607*
	LI	3.00	3.00	2.80*	3.00
	HL/BL	0.040	0.047	0.037	0.034
	TL/BL	0.447	0.470	0.482*	0.468
Adult	BL (mm)	1.938	1.824	1.548**	1.551**
	LI	3.00	2.87	1.53***	1.63***
	E/F	4.67	5.24	4.12	4.93
	HL/BL	0.025	0.024	0.028	0.023
	TL/BL	0.232	0.288	0.321**	0.310*
	(E/F)/BL	2.41	2.88	2.66	3.20*

Table 6. Average values for *Daphnia pulicaria*, clone PM1. Abbreviations and statistical significance codes as in Table 1

Stage	Parameter	Treatment mean			
		Control	Chaoborus	Notonecta	Lepomis
Neonate	BL (mm)	0.656	0.652	0.645	0.631
	LI	2.83	3.00	2.30*	2.27*
	HL/BL	0.041	0.038	0.037	0.041
	TL/BL	0.540	0.581*	0.600**	0.564
Adult	BL (mm)	1.675	1.668	1.645	1.503***
	LI	1.88	1.55**	1.47***	1.57**
	E/F	4.66	4.63	4.70	4.67
	HL/BL	0.026	0.028	0.026	0.027
	TL/BL	0.365	0.439**	0.470***	0.469***
	(E/F)/BL	2.78	2.78	2.86	3.10

Body length decreased in adults in 9 instances, and in neonates decreased in 7 instances and increased in one (*Chaoborus*, Table 8). Adult body length decreased in *D. pulex* SBL in the presence of both *Lepomis* and *Notonecta*. Each of the other clones showed reduced adult body length for *Lepomis* or *Notonecta*, but not both.

Clutch size was influenced by the kind of predator present. Four of the eight clones had a statistically significant

Table 7. Average values for *Daphnia retrocurva*, clone R1. Abbreviations and statistical significance codes as in Table 1. These data are taken from Table 2, Dodson (1988a), with permission of the editor

Stage	Parameter	Treatment mean			
		Control	*Chaoborus*	*Notonecta*	*Lepomis*
Neonate	BL (mm)	0.477	0.472	0.460	0.443**
	LI	2.80	2.93	2.53	2.57
	HL/BL	0.444	0.451	0.480*	0.433
	TL/BL	0.828	0.845	0.860*	0.860*
Adult	BL (mm)	1.158	1.173	1.164	1.116**
	LI	2.30	2.07	1.98	1.78
	E/F	3.67	4.43	4.28	4.73*
	HL/BL	0.337	0.387*	0.533***	0.373
	TL/BL	0.454	0.463	0.518**	0.505*
	(E/F)/BL	3.17	3.78	3.68	4.24**

Table 8. Average values for *Daphnia retrocurva*, clone R3. Abbreviations and statistical significance codes as in Table 1

Stage	Parameter	Treatment mean			
		Control	*Chaoborus*	*Notonecta*	*Lepomis*
Neonate	BL (mm)	0.444	0.460***	0.439	0.437
	LI	2.97	2.63	2.47	2.80
	HL/BL	0.437	0.449	0.466**	0.432
	TL/BL	0.852	0.846	0.883	0.867
Adult	BL (mm)	1.167	1.177	1.143	1.115*
	LI	2.03	1.37**	1.35**	1.13***
	E/F	5.43	5.33	4.73	5.93
	HL/BL	0.321	0.365*	0.528***	0.351
	TL/BL	0.479	0.499	0.551*	0.507
	(E/F)/BL	4.65	4.53	4.14	5.32*

larger absolute average clutch size. When the clutch size was standardized by dividing by body length, six clones had a statistically significant larger clutch size. All increases were in the presence of *Lepomis*. Only *D. galeata mendotae* and *D. pulicaria* showed no response to *Lepomis*. There were no instances of a significant decrease in clutch size.

Algal counts were done to test for undesirable food effects within experiments, which might be causing the reduced clutch sizes. The *D. ambigua* control and bluegill treatments were analyzed using a nested anova with 6 samples per jar, three jars per treatment, and two treatments (Table 9). The anova found no significant differences in cells/ml or cell volume/ml between algal concentrations of the two treatments, for any of the five classifications of phytoplankton.

Lipid Index was reduced in neonates in six instances, and in adults in 13 instances. All clones but *D. retrocurva* R3 showed at least one significant lipid reduction. As adults, two clones responded to *Chaoborus*, 4 to *Notonecta*, and 7 to *Lepomis*.

Of the ten possible pair-wise comparisons of the five characters measured on adults, none showed a statistically significant association.

Table 9. A comparison of the number and volume of phytoplankton cells/ml for the Control and Bluegill treatments in the *Daphnia ambigua* AW1 clone experiment. Phytoplankton data are from the last day of the experiment, after stirring. "STD" is the overall standard deviation calculated from the total mean squares of a nested anova with 6 samples per jar, three jars per treatment, and two treatments

Taxon	10^5 Cells/ml			μm^3 Cell volume	10^6 μm^3/ml Total volume	
	Averages		STD			
	Control	Bluegill			Control	Bluegill
Scenedesmus sp A	7.52	8.33	0.58	33.6	25.3	28.0
large *Chlorella*	1.75	1.30	0.68	156.0	27.3	20.3
Scenedesmus sp B	0.87	0.51	0.12	63.4	5.5	3.2
small *Chlorella*	0.48	0.43	0.06	8.2	3.9	3.5
Ankistrodesmus spp	0.28	0.20	0.04	57.6	1.6	1.5
Total volume:					63.6	56.5

Discussion

Frequency of induction

Morphological responses appear to be abundant, even in typically "non-cyclomorphic" species such as *D. pulex*. Each of the eight clones responded to at least two of the three predators (Tables 1–8). Multiple responses were the rule. Each of the eight clones showed 3 or 4 responses. The observed changes are not a complete description of morphological changes, since many aspects of the morphology were not measured. For example, Dodson and Egger (1980) found that carapace thickness shows variation between forms of *Daphnia pulex*. I conclude that induced morphological responses are a common aspect of the biology of *Daphnia*. Based on the partial results already available for other species (Havel 1987; Stemberger and Gilbert 1987; Dodson 1988a), it seems reasonable to expect the same pattern of abundant examples of morphological induction in other ecologically similar genera such as *Bosmina, Ceriodaphnia, Diaphanosoma,* and *Holopedium,* and perhaps also the planktonic copepods and rotifers.

Patterns of induced responses can be compared to predictions of Dodson (1974). These predictions were based on arguments concerning what would be the most advantageous morphological response for different classes of predators. In these experiments, *Chaoborus* is a tactile non-visual predator specializing on the smaller end of the *Daphnia* size scale. *Lepomis* and *Notonecta* are visual predators, specializing on the larger *Daphnia* (Dodson 1974, 1988). Effective defenses against *Chaoborus* would be large body size or elongated heads and spines. Defenses against *Lepomis* would be small body size and transparency; elongated parts might be neutral, or effective against larval fish. Defenses against *Notonecta* are similar to those of fish, except that *Notonecta* has a narrower range and perhaps a smaller modal preferred prey size.

Tail spine length

The argument of Dodson (1974) would lead to the prediction that an elongated tail spine should be a response to

Chaoborus, and not necessarily the other two species. Just the opposite was observed. Perhaps this is because a longer tail spine does protect against larval fish (Balcer 1988), and because the longer tail spine has no disadvantage in the face of larger fish. (However, more experimentation is needed here. With ingenuity, almost any induced response can be argued to be adaptive. What is needed for a better understanding of the role of induced responses is a theory that predicts adaptations less ambiguously.)

Head length

Head length responded to the three predators as predicted by Dodson (1974). The three clones that showed a longer head responded to *Chaoborus* and *Notonecta*, but not to *Lepomis*. Thus, the elongated heads of two species of the most extreme cyclomorphic *Daphnia* can be induced by the presence of predators, as well as environmental factors such as temperature, turbulence, and abundant food (Dodson 1988a).

Except for *D. pulicaria*'s shorter head in the presence of *Lepomis*, there was no example of shorter heads or tail spines in the presence of any of the predators.

Body length

Although not as obvious as an increase in head length or tail spine length, changes in body length are a frequent component of cyclomorphosis (Hutchinson 1967). In three cases, significantly smaller neonates were not associated with smaller adults. This suggests that the life history consequences of induced changes may not all be apparent by the end of one generation.

The observed instances of smaller bodies are probably adaptive responses. In Tables 1–8 there is no example of a clone producing a larger body size in response to *Notonecta* or *Lepomis*. Reduction is induced by the two predators that prefer larger-sized *Daphnia*. The two smallest species which may be too small for significant fish predation show no decrease in body size in the presence of *Lepomis*. However, in the presence of *Notonecta*, which probably has a lower minimum size preference, the two smallest species show a significant reduction in body length.

Clutch size

Of the six clones with larger clutches, all but *D. obtusa* also had significantly smaller neonates, suggesting that the total egg mass is conserved, being divided up into smaller packets. The relationship is not exact. If egg mass is conserved, and if neonate body length is a good measure of egg size, then an increase in clutch size by a factor of k would be accompanied by a decrease in neonatal length by the reciprocal of the cube root of k. *D. ambigua*, with the largest increase in eggs (by a factor of 3.84) should have had neonates smaller by a factor of 0.64. Since the smaller neonates were about 0.90 as long as the controls, the total egg mass probably also increased. The other four species have smaller increases in clutch size and more or less matching decreases in the neonate body length.

It is a matter of faith among limnologists that herbivorous zooplankton produce as many offspring as they are able to, depending on food abundance. Thus, is the increase in clutch size induced by bluegill due to a change in the quantity or quality of algae in the bluegill treatments? In general, in none of these experiments were algal concentrations of a jar allowed to drift more than about 10% from the others, and no trend was noticed of higher food in the bluegill treatments. A careful analysis of algae in the most extreme case, a comparison of the control and bluegill treatments of *D. ambigua*, showed (Table 9) no significant difference between concentrations of any of the 5 most abundant algal taxa, nor for total algal concentration. There was a trend toward more algae in the control jars, just the opposite of what would be expected if food level were controlling clutch size. Thus, I conclude that the clutch increase is not due to an increase in food concentration in the bluegill jars, but is a response to the bluegill, and is at the expense of some other part of the *Daphnia*'s energy budget. More research is indicated for this potentially important response.

The two species whose clutches do not increase in the presence of bluegill are large species from lakes. Clutch size reduction in the presence of large size-selective predators may be a general pattern, related to the higher predator diversity found in larger bodies of water, as suggested by Gilbert (1980). For example, in the case of large *Daphnia* species, a larger clutch of smaller offspring will increase r if only fish-like predators are present, but would be a strong disadvantage if predators specializing on small *Daphnia*, such as *Chaoborus*, were also present. On the other hand, the smaller species seem to produce the smaller offspring, when bluegill are present, perhaps because they are already small enough to be vulnerable to *Chaoborus*.

Increased clutch size, and the associated decreased neonate size, was never a response to the small-prey-preferring *Chaoborus*. Of the three predators, *Chaoborus* is the specialist on prey the size of neonatal *Daphnia*. Once again, it appears that *Daphnia* respond in an adaptive manner to a specific predator.

Lipid index

Although changes in lipid index have not been considered a typical response to predators, this was one of the most common responses observed in these experiments. Thus, the mere presence of a predator may be enough to reduce the energy stores, and therefore the pattern of energy allocation and competitive ability of a *Daphnia* species. Since different *Daphnia* respond differently to each predator, it is possible that strategies for competition involve tradeoffs with predator defense. The existence of such energy budget restrictions could make disadvantageous a too early, intense, or extended induced response.

Reproducibility of induction

This survey was not designed to test for variation of induced responses over the year. Such an experiment would best de done when the purified chemical signal or signals are available. However, the results for *Notonecta* induction of small body size in *Daphnia pulex* clone SBL, done in October of 1986 and January of 1987 (Dodson 1988b) agree substantially with the results in Table 5, done in February, 1987. Also, the results of the two clones of *D. retrocurva*, done in December 1986 and April 1987 (Tables 7 and 8) are substantially the same.

Table 10. A comparison of the predators to which *Daphnia* clones react with an induced morphological response, and the predators with which they co-occur. Morphological responses include all significant changes seen in Tables 1–8. ? = The predator is scarce or occurs in the littoral zone only. The predator occurrence data are taken from Table 2 of Dodson (1988b)

Daphnia species and clone	Responds to	Co-occurs with
D. ambigua AW1	*Lepomis* *Notonecta*	*Lepomis* *Notonecta*
D. galeata mendotae DGA	*Chaoborus* *Lepomis* *Notonecta*	*Chaoborus* *Lepomis* *Notonecta*?
D. obtusa G5A	*Lepomis* *Notonecta*	*Notonecta*
D. parvula TO1	*Chaoborus* *Lepomis* *Notonecta*	*Lepomis*? *Notonecta*?
D. pulex SBL	*Lepomis* *Notonecta*	*Chaoborus* *Notonecta*
D. pulicaria PM1	*Chaoborus* *Lepomis* *Notonecta*	*Chaoborus* *Lepomis* *Notonecta*?
D. retrocurva R1	*Chaoborus* *Lepomis* *Notonecta*	*Lepomis* *Notonecta*?
D. retrocurva R3	*Chaoborus* *Lepomis* *Notonecta*	*Chaoborus*? *Lepomis* *Notonecta*?

Interactions between responses

If *Daphnia* had a simple developmental program, then we might expect several of the morphological responses to be positively associated. For example, if the head gets longer, the tail also gets longer. If *Daphnia* had a limited energy budget, and limited options to respond to predators, then we would expect responses to be negatively associated. For example, if the head gets longer, the tail shows no response. What we see for the eight clones in this study are neither positive nor negative associations: induced responses occurred independently of one another. These results imply developmental flexibility on the part of *Daphnia* in their ability to respond to predation. Thus, while it is fairly certain that the *Daphnia* are energy limited, it is not possible to predict the disadvantage associated with any particular induced predation defense: the energy needed for the defense can potentially be routed from one or more of a large number of sources with the total budget.

Behavioral and morphological responses

Dodson (1989) found that clones tended to respond behaviorally only to naturally co-occurring predators. The pattern shown by morphological responses is less clear (Table 10). Clones tend to respond morphologically to their natural predators. Even *D. pulex* SBL, which does not respond to *Chaoborus* in the characters observed in this study

(Table 10), does produce neck teeth in response to *Chaoborus*. The clones also respond to predators with which they probably do not co-occur. For example, all clones except *D. galeata mendotae* DGA, had a smaller body size in the presence of Bluegill, even though *D. obtusa* lives in fishless rock pools, and *D. pulex* SBL does not co-occur with Bluegill.

Lipid stores may be diverted, *via* induction, to either morphological or behavioral predator defenses. The pattern of reductions in Lipid Index roughly matches behavioral responses to predators. In both cases, few clones responded to *Chaoborus*, but most responded to *Notonecta* and *Lepomis*. However, only one of the clones, *D. pulicaria* PM1, responded to *Chaoborus* both behaviorally and with a lowered Lipid Index.

In summary, these experiments with a few clones of *Daphnia* and three of their predators imply that predator-induced morphological defenses to predators are a widespread phenomenon. These responses are varied and often well suited for a certain class of predators. The induced responses confer advantages on the prey species and may be paid for in a number of ways that will modify the prey's susceptibility in other predators and competitors. The hypotheses developed from laboratory experiments on a few species need to be expanded to more genera and need to be tested in natural habitats. Predator-induced responses promise to be an important aspect of the population and even community ecology of freshwater zooplankton.

References

Balcer MD (1988) Ecology of the crustacean zooplankton and young-of-the-year rainbow smelt populations of western Lake Superior. Chapter 3: Observations on the feeding behavior of young rainbow smelt. Ph.D. thesis. University of Wisconsin, Madison, Wisconsin, USA, p 83

Dodson SI (1974) Adaptive change in plankton morphology in response to size-selective predation: A new hypothesis of cyclomorphosis. Limnol Oceanogr 19:721–729

Dodson SI (1988a) Cyclomorphosis in *Daphnia galeata mendotae* Birge and *D. retrocurva* Forbes as a predator-induced response. Freshwat Biol 19:109–114

Dodson SI (1988b) The ecological role of chemical stimuli for the zooplankton: Predator-avoidance behavior in *Daphnia*. Limnol Oceanogr 34 (in press)

Dodson SI, Egger DL (1980) Selective feeding of red phalaropes on zooplankton of arctic ponds. Ecology 61:755–763

Dodson SI, Havel JE (1988) Indirect prey effects: Some morphological and life history responses of *Daphnia pulex* exposed to *Notonecta undulata*. Limnol Oceanogr vol. 33, W.T. Edmondson special celebratory issue. (in press)

Gilbert JJ (1980) Further observations on developmental polymorphism and its evolution in the rotifer *Brachionus calyciflorus*. Freshwat Biol 10:281–294

Green J (1960) Seasonal polymorphism in *Scapholeberis mucronata* (O.F. Muller) (Crustacea: Cladocera). J Anim Ecol 32:425–539

Havel JE (1987) Predator-induced defenses: A review. In Predation: Direct and indirect impacts on aquatic communities. Kerfoot WC, Sih A (eds) New England Press. Hanover, New Hampshire, pp 263–278

Havel JE, Dodson SI (1987) Reproductive costs of *Chaoborus*-induced polymorphism in *Daphnia pulex*. Hydrobiology 150:273–281

Hebert PDN, Grewe PM (1985) *Chaoborus*-induced shifts in the morphology of *Daphnia ambigua*. Limnol Oceanogr 30:1291–1296

Hrbacek J (1959) Circulation of water as a main factor influincing the development of helmets in *Daphnia cucullata* Sars. Hydrobiologia 13:170–185

Hutchinson GE (1967) A treatise on limnology. Volume 2. Wiley, New York, p 1115

Jacobs J (1962) Light and turbulence as co-determinants of relative growth rates in cyclomorphic *Daphnia*. Int Rev Ges Hydrobiol 47:146–156

Krueger DA, Dodson SI (1981) Embryological induction and predation ecology in *Daphnia pulex*. Limnol Oceanogr 23:219–223

Lampert W, Wolf HG (1986) Cyclomorphosis in *Daphnia cucullata*: morphometric and population genetic analysis. Journal of Plankteon Research 8:289–303

Sokal RS, Rohlf EJ (1981) Biometry. second edition. Freeman and Company, San Francisco, California, p 776

Tessier AJ, Goulden CE (1982) Estimating food limitation in cladoceran populations. Limnol Oceanogr 27:707–717

Woltereck R (1909) Weitere experimentelle Untersuchungen über Artwanderung, speziell über das Wesen quantitativer Artunterschiede bei Daphniden. Ver Deutsch Zool Gesell 1909:110–172