
Commentary on Effects of Anthropogenic and Natural Organic Chemicals on Development, Swimming Behavior, and Reproduction of *Daphnia*, a Key Member of Aquatic Ecosystems

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Because of their trophodynamic role, small invertebrates are often critical components of ecosystems. An especially important group of freshwater invertebrates is the water fleas of the genus *Daphnia*. These animals are often the dominant herbivores in lakes and ponds. They play a key role in determining water clarity (by grazing on algae) and they are an important part of the diet of fish. Natural chemical signals (kairomones) produced by predators affect the development, life history strategy, and behavior of zooplankton. Laboratory studies of anthropogenic chemicals that have biological activity (xenobiotics), such as the insecticide carbaryl, have demonstrated effects of concentrations in the 1 to 5 ppb range on *Daphnia* development, growth rate, and swimming behavior in our laboratory experiments. Low concentrations of carbaryl inhibit growth and reproduction and delay maturation, whereas survivorship was not effected. These sublethal exposures to carbaryl reduced *Daphnia* population growth rate (productivity) by about 15% (at 5 ppb), enough to have significant ecological effects on the rest of the lake community. The insecticide carbaryl showed synergistic interactions with natural chemicals associated with predators (kairomones) that modify *Daphnia* development and life history characteristics. In addition, there were complex synergisms between carbaryl, the predator odors, and oxygen concentration (low oxygen concentration can be either a natural environmental stress or an anthropogenic stress). *Daphnia* produce males facultatively, usually in late fall; at other times, reproduction is asexual. There is some evidence from long-term field studies that the maximum frequency of males has declined since the 1940s, when estrogen-mimicking xenobiotics first appeared in lakes. A decrease in sexual recombination will result in maladapted *Daphnia* relative to their constantly changing environment. — Environ Health Perspect 103(Suppl 4):7–11 (1995)

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Introduction

The larger species of wildlife, such as eagles, alligators, and pumas, interact with and depend on an ecological support structure in which the major players are invertebrates. Although individually small and inconspicuous, invertebrates play major roles in the transfer of energy from autotrophs to the tips of the food web.

The long-term goal of our research is to understand how planktonic communities work in terms of population dynamics of the individual member species, energy flow among species, and patterns of species diversity and phenology. A current and fundamental question concerns the influence of natural and anthropogenic chemicals in inducing changes in the development, life history strategy, and behavior of zooplankton (1–4).

Results of studies of zooplankton have shown that many species depend on chemical signals, in natural situations, for optimal development. For example, the phenomenon of cyclomorphosis (an annual change in morphology seen from generation to generation, in which some species have long spines and helmets during the summer) is cued by a combination of physical conditions and natural chemical signals (kairomones) produced by predacious fish and invertebrates (5). Zooplankton also modify their life history and reproductive strategies (e.g., rate of maturation, size and number of eggs) in response to kairomones. Similarly, zooplankton swimming behavior, especially diel vertical

migration (during which zooplankton populations move deeper in the lake during the day, and rise at night), depends on the presence of kairomones (6,7).

Anthropogenic chemicals can induce changes that mimic the effects of natural kairomones (8–10). For example, xenobiotics and natural chemical signals show both direct and synergistic effects on zooplankton development (11,12). The purpose of our current research is to understand how natural and anthropogenic chemicals interact in lakes to induce changes in the development, behavior, and ultimately the community ecology of zooplankton.

To study zooplankton development and behavior, we have focused on laboratory cultures of the Cladoceran (water flea) *Daphnia*. *Daphnia* are ideal representatives of the zooplankton partly because of the ease with which they are cultured in the laboratory and partly because of their key position in aquatic food webs (Figure 1). *Daphnia* species (along with their smaller cousins *Ceriodaphnia*) are often used in laboratory bioassays of kairomones (13) or potentially toxic chemicals (14–16).

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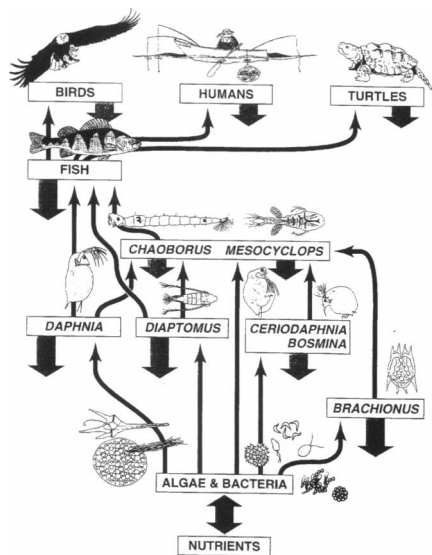


Figure 1. An idealized food web for a freshwater lake showing the position of *Daphnia* as a herbivore that affects both algae and fish abundances.

Daphnia occupy a key position in aquatic food webs because they are often the most significant herbivore (17) by determining water quality through their selective consumption of algae (18) and providing a major dietary component for several fish species (19), and because of their large size, high rate of reproduction, and lack of an effective escape response.

Daphnia in lakes, like other zooplankton and unlike larger animals higher in the food web, typically contain (bioaccumulate) only low levels of toxic xenobiotics. For example, *Daphnia* in Lake Ontario contained only about 1 ppb PCB and 10 ppb DDT in the 1980s (20). These levels do not even approach levels of acute toxicity (14,21). However, *Daphnia* ecology can be modified significantly by low to moderate sublethal concentrations of toxic xenobiotics (22,23). The nonlethal effects we have studied can be divided into three general categories: a) development and life history, b) swimming behavior, and c) reproductive effects.

Developmental and Life History Effects

Daphnia morphology determines much of their life-history strategy (2). For example, smaller body size tends to reduce feeding rate, reduce mortality from fish, and increase the chance of being eaten by invertebrate predators such as *Chaoborus*. The typical *Daphnia* response to either kairomone or the insecticide carbaryl (Table 1) is a reduction in body length,

Table 1. Examples of morphological change induced by 10 ppb carbaryl.^a

Species	Body length	Head length	Tail length
<i>Daphnia galeata mendotae</i>	-11	+17	NS
<i>Daphnia lumholtzi</i>	NS	+24	+10
<i>Daphnia pulex</i>	-2	NS	ND
<i>Daphnia retrocurva</i>	-7	NS	NS

Abbreviations: NS, no significant difference; ND, no data. ^aChanges are expressed as percent of the control average. Average values are given for statistically significant differences (ANOVA, $p < 0.05$). Data are from Hanazato and Dodson (10,11).

longer developmental time to maturity, and at high levels of pesticides, induction of morphological defenses such as higher helmets, longer tail spines, or neck teeth.

We have found several synergistic interactions between carbaryl and the *Chaoborus* kairomone. Carbaryl and kairomone typically interact to further reduce adult body size and juvenile growth rate (Table 2). When oxygen stress is combined with carbaryl and kairomone (Table 3), there are further synergistic reductions in body size and growth rate (12). Another stress factor, pH, may have a similar synergistic interaction with the natural and anthropogenic chemicals (24).

Swimming Behavior

Zooplankton (especially copepods, but including cladocerans such as *Daphnia*) show

complex swimming behavior that is necessary for proper nutrition and to avoid predators. On a small scale, many zooplankton have a fast swimming escape response used to avoid predators (25), and zooplankton may have the ability to maintain their position in food patches (26). At a large scale, zooplankton often show diel vertical migration, in which they sink lower in the lake during the day to avoid fish and rise at night to take advantage of the warmer water near the surface (2). Results from laboratory studies of individual swimming behavior show that swimming behaviors can be modified by exposing the zooplankton to various predators or by exposure to toxic xenobiotics.

Our lab uses a video system to record and digitize the three-dimensional swimming track of individual zooplanktonic animals (4,27). This system can be used to

Table 2. Effects of carbaryl (5 and 10 ppb) and presence or absence of *Chaoborus* kairomone on three population growth rate factors.

	DF	P	Significant effects
Time to maturity			
Carbaryl	2	NS	
Kairomone	1	NS	
Interaction	2	.	59% longer (5 ppb carbaryl, kairomone)
Clutch size			
Carbaryl	2	NS	
Kairomone	1	***	38% fewer eggs per female
Interaction	2	NS	
Size at maturity			
Carbaryl	2	NS	
Kairomone	1	.	4% shorter
Interaction	2	**	11% shorter (5 ppb carbaryl, kairomone)

Abbreviations: DF, degrees of freedom; P, probability of finding the observed effect if the null hypothesis (of no effect) is true; NS, not significant (probability is greater than 0.05). * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$. Data from Hanazato and Dodson (10).

Table 3. Synergistic effects of carbaryl (C), *Chaoborus* kairomone (K), and oxygen concentration (O). C was at 5 ppb, K was present or absent, and O was 2 or 9 ppm.

	Necktooth induction in first instar	Necktooth induction in second instar	Neonate length	Adult length	Growth rate	Time to mature	Size of first clutch
C*K*O	.	-	-	**	-	.	-
C*K	-	***	***	-	***	-	***
C*O	-	***	-	-	-	-	.
K*O	-	-	-	***	-	-	-

Significant interactions are marked *= $p < 0.05$, **= $p < 0.01$, ***= $p < 0.001$. Based on results of Hanazato and Dodson (12).

study behavior of zooplankton from field populations or in laboratory experiments and behavioral bioassays. For example, Dodson et al. (4) report at least three different swimming behaviors as responses to *Chaoborus* kairomone or carbaryl. Using different recording techniques, Dawidowicz et al. (6) and Loose et al. (7) have shown that diel vertical migration of *Daphnia* is a response to fish smell (kairomone), and therefore this large-scale behavior is also potentially modified by xenobiotics. Also, *Daphnia* spatial orientation (28) is changed, and phototactic response (29,30) appears abnormal in sublethal concentrations of toxic xenobiotics.

Reproductive Effects

Many pesticides, other toxic xenobiotics (such as PCBs and dioxins), and common industrial chemicals (such as nonylphenol and phthalates) are estrogen mimics (31,32). These mimics are implicated as agents that interfere with male development in wildlife populations, including Florida alligators (33), turtles (34), and panthers (35); Texas turtles (36); southern California sea gulls (37); Great Lakes salmon (38); and English trout (39). This interference is of interest because of the potentially devastating effects on both wildlife and human reproductive biology (40,41).

Many zooplankton (cladocerans and rotifers) have a reproductive strategy based on facultative parthenogenesis (virgin birth) (42). Females produce daughters during most of the summer growing season. When environmental conditions deteriorate (crowding, cooler temperatures, low food), females produce males and haploid eggs. The number of males produced in a population depends on the genetics of the population and the intensity of the environmental signals. The sex ratio is not set at 50%, but usually is some smaller percent of males.

Growth and molting in crustaceans is regulated by a variety of hormones, including juvenile hormone and ecdysteroids (43). It is probable that development of Cladoceran males (genetically identical to their mothers) is also under hormonal control, as in vertebrates. Thus, it is possible that Cladoceran sex ratio may be influenced by some of the same xenobiotics that interfere with vertebrate sexual maturation.

We hypothesize that the flexible Cladoceran sex ratio might be more easily influenced by hormonelike xenobiotics, than would obligate sexual species (such as copepods) that typically are genetically

locked into a 1:1 sex ratio. We predict that the maximum *Daphnia* sex ratio observed during a year will be higher before 1945 than after. A test of this hypothesis would be to examine historical records of *Daphnia* sex ratios in lakes from before and after the advent of anthropogenic toxic organics in the middle 1940s. Surprisingly few historical zooplankton samples or reports of cladoceran sex ratios exist. The only example currently known to us is for Lake Mendota, Wisconsin (Table 4), for which we have estimates of the maximum sex ratio observed in 1895, 1975, and 1991. The data for Lake Mendota show a dramatic decrease in the maximum frequency of males for two *Daphnia* species and no change in the already low frequency for the third species. These data are consistent with the hypothesis that anthropogenic compounds are affecting *Daphnia* reproductive strategy in a lake, but more data (e.g., from European lakes for which there are long series of historical samples) is needed before we can conclude that the lower sex ratio in *Daphnia* is a general phenomenon.

Ecological Consequences

Morphology and Life History

In natural predator-prey systems, the induction of morphological predator defenses (such as high helmets or long tail spines) by kairomones is often (although not always) associated with a reduction in biological fitness, measured as the population growth rate of a clone (1,18,44-47). The reduction in fitness, when it occurs, is usually due to a longer developmental time (from neonate to adult); in some cases there is also a decrease in the number of eggs per clutch. A similar reduction in fitness is seen in *Daphnia* exposed to carbaryl (Table 5). The synergistic effect of both the kairomone and carbaryl (Table 4) reduced the population growth to half or less of that predicted from the separate effects of the two factors. Such a large reduction is particularly important to *Daphnia*, which typically requires a high rate of population growth to persist through periods of high mortality from predators (18,23,48-50). Thus, synergistic effects among environmental factors, kairomones, and anthropogenic toxic compounds are likely to result in depression or extirpation of *Daphnia* populations in contaminated water bodies.

Swimming Behavior

Swimming behaviors also have ecological consequences. Abnormal behaviors caused

Table 4. Temporal variation in *Daphnia* sex ratio in Lake Mendota, Wisconsin.

	Maximum percent males		
	1895	1975	1991
<i>D. retrocurva</i>	50	<0.2	1.6
<i>D. pulicaria</i>	33	2.3	2.2
<i>D. galeata</i>	4	3.1	0.2

*The 1895 data are from Birge (60); the more recent data are from samples taken by Dodson.

by toxic xenobiotics may result in higher mortality due to both vertebrate and invertebrate predators. For example, an increase in swimming velocity will increase encounter rate with predators and therefore increase the rate of mortality (51).

Given the intense mortality often experienced by zooplankton such as *Daphnia* (18), even a small increase in the mortality rate may result in the disappearance of the population from a lake.

In addition to affecting swimming behavior, it is probable that xenobiotics affect other behaviors such as feeding and mating. Reduction in feeding activity at sublethal levels of xenobiotics has been well documented (23).

Synergisms

Natural stress factors such as low pH, low oxygen concentration, high temperature (52), presence of kairomones, and low food density (53), tend to reduce *Daphnia* growth rate. Some, or perhaps all, of these stress factors interact synergistically with toxic xenobiotics. Thus, *Daphnia*, and by implication zooplankton in general, may be especially susceptible to low levels of toxic organic compounds when the population is also responding to several natural stress factors.

Reproductive Effects

Male *Daphnia* are seldom ecologically (trophically) significant in a direct way.

Table 5. Estimated population growth rate (r) for *Daphnia pulex* exposed to various combinations of *Chaoborus* kairomone and the insecticide carbaryl.^a

Carbaryl, $\mu\text{g l}^{-1}$	Control medium	<i>Chaoborus</i> kairomone
0	0.231	0.147
5	0.213	0.115
10	0.146	0.062

^aData from Hanazato and Dodson (11). The r values are unreplicated so we cannot test for statistical significance of differences. However, estimates of the variables used to estimate r values were replicated, and we found significant effects on growth reproduction rates and a significant interaction between carbaryl and kairomone (11).

However, the ecological and evolutionary role of male *Daphnia* is to allow for sexual recombination in the population to produce offspring that are different from the parents, therefore holding the possibility of being adapted to changing environmental conditions. Without sexual reproduction, it is possible that clones of asexually reproducing *Daphnia* would be at a serious disadvantage in those years in which environmental conditions do not match the requirements of the particular clones. Competition in sub-optimal years could result in the reduction or disappearance of *Daphnia* populations. For some *Daphnia* genotypes, fertilization of haploid eggs is required for the production of the resting eggs used to survive inhospitable environmental conditions such as freezing, anoxia, or drying (54). For these genotypes, suppression of males would result in immediate extirpation.

Daphnia are often important components of planktonic communities. *Daphnia* biology is affected by a wide range of toxic xenobiotics and appears to be particularly vulnerable to carbaryl and other toxic xenobiotics (55). *Daphnia* are replaced by smaller and less efficient herbivores in

experimental ponds treated with doses as low as 10 ppm carbaryl (56). Because of the important grazing role of *Daphnia* (57–59), loss of *Daphnia* from a lake can reduce water quality and reduce the efficiency of energy transfer from phytoplankton to fish (24). Reduction or removal of *Daphnia* from a lake food web may result in a greener lake that produces fewer fish and has a greater tendency toward winter kill. Thus, subtle effects on *Daphnia* caused by sublethal concentrations of toxic organics can have significant and readily apparent consequences to lakes.

Summary

- *Daphnia* is a key member of the lake community. It occupies a central position in the food chain and affects both water quality and fish production.
- Smaller *Daphnia*, induced by low concentrations of carbaryl and other xenobiotics, are less efficient herbivores. The lower efficiency is potentially reflected as a reduction in water quality as algae become more abundant.
- Lower reproductive rates, associated with nonlethal concentrations of xenobiotics,

result in a reduced ability of *Daphnia* to outproduce their predators. If the *Daphnia* reproductive rate is insufficient to match the losses to predators, the *Daphnia* population will decline or disappear.

- Out-of-context induction of developmental, behavioral, or reproductive changes by xenobiotics reduces *Daphnia* competitive ability relative to other zooplankton species. The reduced competitive ability is the result of energy allocated to changes that have no biological benefit.
- Abnormal swimming induced by xenobiotics reduces *Daphnia* survival if it increases predation rate. This can lead to reduction or disappearance of the *Daphnia* population.
- Loss of sexual reproduction, if caused by hormonelike activity of xenobiotics, will decrease *Daphnia* adaptability to changing environments. If sexual reproduction is necessary to produce resting stages that produce the next generation, then suppression of males can lead to rapid extirpation of the *Daphnia* population.

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