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Effects of insecticides on interactions between the predator *Chaoborus* and its prey *Daphnia*

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INTRODUCTION

Predation and competition are important biotic factors controlling population dynamics of organisms and the structure and function of communities in lake ecosystems. If interactions between predators and prey and between competitors are affected by anthropogenic toxicants contaminating natural water bodies, their toxic effects should therefore influence both individual communities and whole ecosystems. Mesocosm experiments have shown that toxicants may influence some organic populations directly, but others indirectly through interactions. For example, contamination by chemicals often causes blooms of some species by reducing predators and competitors [1,2,3]. Understanding of such indirect effects is needed to evaluate the influence of chemicals on lake ecosystems.

It has been demonstrated in the near past that there are interactions between predators and prey mediated by natural organic chemicals [4]. Prey organisms change their morphology, behavior and life history characteristics in order to reduce their vulnerability to predators in response to chemicals released from the predators. The chemicals are termed kairomones, these being defined as substances giving benefit to the receivers rather than the releasers [5]. A well-studied species-species interaction mediated by kairomones is that between the predacious midge larva, *Chaoborus*, and its prey, the cladoceran *Daphnia*, which develops protuberant structure as an anti-predator device [6].

I have obtained experimental results suggesting that insecticides disturb such interactions. The present paper reviews the results and discusses the phenomenon.

INTERACTION BETWEEN *CHAOBORUS* AND *DAPHNIA* MEDIATED BY A KAIROMONE

The fact that *Chaoborus* larva releases a kairomone, which induces morphological changes in *Daphnia*, was reported for the first time by Krueger and Dodson in 1981 [7], who found that juveniles of *D. pulex* formed neckteeth, a toothed dorsal crest, in response to the natural organic chemical. Since then, many papers have reported that various *Daphnia* species (*D. ambigua, D. galeata, D. retrocurva, D. cucullata*) develop protuberant structures such as high helmets and long tail spines when exposed to the kairomone [8,9,10,11]. These structures are functioning as anti-predator devices, which reduce the vulnerability of *Daphnia* to predation [12,13]. The *Chaoborus* kairomone also induces escape behavior of *Daphnia* from the predator [14]. Thus, the kairomone is of benefit to *Daphnia*.

However, there is a trade-off in the kairomone-mediated *Chaoborus* - *Daphnia* interaction. The anti-predator response of *Daphnia* seems to have a cost because the prey animals show deterioration of some life history characteristics when exposed to the kairomone. They have a reduced mature size and clutch size, and an increased maturation time [15,16,17]. Consequently, their population growth rate is reduced. Furthermore, the tolerance of *Daphnia* to some environmental stresses such as high water temperature, food shortage and low oxygen concentration is decreased in the presence of the kairomone [18,19,20].

The chemical structure of the *Chaoborus* kairomone has not been identified yet. However, some physical and chemical features of the chemical have been elucidated [8,21,22].

COMBINED EFFECTS OF KAIROMONE AND INSECTICIDES ON *DAPHNIA* LIFE HISTORY CHARACTERISTICS

Pesticides are toxicants, which reduce rates of growth and reproduction of various kinds of

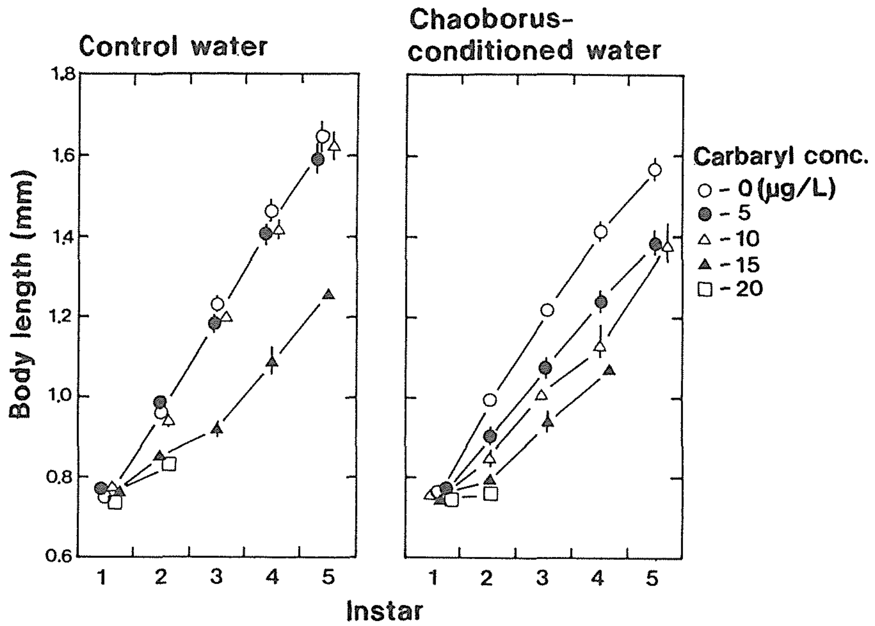

Fig. 1. Growth in body length (mm) of *Daphnia pulex* reared in the control water (without the *Chaoborus* kairomone) or the *Chaoborus*–conditioned water (with the kairomone) with carbaryl at 0, 5, 10, 15 and 20 μg l^{-1}. (redrawn from Hanazato and Dodson [17]).

animals including *Daphnia*. The *Chaoborus* kairomone has similar effects on *Daphnia* and becomes toxic at a high concentration [23]. Thus, these two kinds of chemicals are similar in their effects.

Hanazato and Dodson (1992,[17]) exposed *D. pulex* to the kairomone and an insecticide, carbaryl, simultaneously and analyzed the combined effects of the chemicals. Sublethal concentrations of carbaryl (5 and 10 μg/L) reduced the growth rate, mature size and increased the maturation time significantly in the medium with the kairomone, but did not without it (Fig. 1, Table 1). Consequently, the insecticide reduced the population growth rate of *Daphnia* more intensely in the presence of the kairomone than in its absence.

The kairomone induced neckteeth formation by *D. pulex* in instars 1–2 and prolonged the intermoulting period of the juveniles. *Daphnia* may become sensitive to toxicants soon after molting, and therefore the moulting of the spined morphs increases the risk of damage from the insecticide. The prolongation of the intermoulting period of juveniles may be another factor increasing the sensitivity of *Daphnia* to carbaryl in the presence of the kairomone. This results in an increased exposure period of juveniles to the insecticide, which are the life stage of *Daphnia* most sensitive to the insecticide [24].

Hanazato and Dodson (1992,[17]) found synergism in the combined effects of the kairomone and carbaryl. The results thus indicate that the *Chaoborus* kairomone reduces the tolerance of the *Daphnia* to carbaryl. In other words, *Daphnia* becomes more sensitive to the insecticide when it coexists with the predators.

COMBINED EFFECTS OF KAIROMONE AND INSECTICIDES ON *DAPHNIA* MORPHOLOGY

Hanazato (1992,[25]) found that *D. ambigua* developed marked spike–like helmets in juvenile stages when exposed to a harmful concentration of the insecticide carbaryl for a short time during the final embryonic stage to the first instar. Later, Hanazato (1991,[26]) confirmed that six kinds of insecticide (carbamate and organophosphorus insecticides) had the same effects on

Table 1. Maturation time and mature size of *Daphnia pulex* reared in the control water (without the *Chaoborus* kairomone) or the *Chaoborus*-conditioned water (with the kairomone) (from Hanazato and Dodson [17]).

Carbaryl concentration (μg l^{-1})		Control water			*Chaoborus*-conditioned water		
		0	5	10	0	5	10
Maturation time (days)							
	n	10	8	6	12	12	7
	Mean	5.2	5.1	5.3	6.3	8.25	7.7
	SE	0.13	0.13	0.2	0.13	0.39	0.92
	P[a]					**	*
Mature size (mm)							
	n	10	8	6	12	12	7
	Mean	1.67	1.63	1.63	1.56	1.49	1.49
	SE	0.039	0.037	0.040	0.014	0.018	0.014
	P[a]					**	**

[a]Significance in difference between individuals in each of the treatments with 5 or 10 μg carbaryl l^{-1} and the control (0 μg carbaryl l^{-1}). * = $p<0.05$; ** = $p<0.01$.

the morphology of the same species, whereas herbicides and a fungicide did not. Because the morphological changes were quite similar to the daphnid's response to the *Chaoborus* kairomone, it seemed that the anthropogenic chemicals switched on the formation of the helmets, an antipredator morphology, which originally evolved as a response to the kairomone. Furthermore, Hanazato and Dodson (1993,[27]) found that four species of cyclomorphic *Daphnia*, *D. pulex*, *D. galeata mendotae*, *D. retrocurva* and *D. lunholtzi*, also formed neckteeth or helmets when exposed to carbaryl. So, it may be suggested that insecticides, which contaminate various water bodies, could be a factor inducing morphological changes in *Daphnia* [25]. However, the conditions under which *Daphnia* develops the protuberant structure in response to insecticide exposure are restricted. The chemical concentration must be high enough to harm the animals and the exposure period must be short.

Hanazato and Dodson (1992,[17]) exposed *D. pulex* to sublethal concentrations of the insecticide carbaryl (5 and 10 μg l^{-1}) and the *Chaoborus* kairomone simultaneously, and found that some individuals maintained neckteeth for a longer period over several instars than the individuals exposed only to the kairomone. Hanazato (1995,[28]) again tested the combined effect of carbaryl and the kairomone on *Daphnia* morphology using *D. ambigua*, and found that continuous exposure to carbaryl at 1 μg l^{-1} enhanced helmet development of the *Daphnia* in the presence of the kairomone (Fig. 2). These results suggest that even sublethal concentrations of insecticides can affect morphology of *Daphnia* if the animals coexist with predators releasing kairomones.

GENERAL DISCUSSION

Carbaryl at 5 μg l^{-1} did not exert any marked effects on *D. pulex* if the animals were exposed to only carbaryl [17]. However, 5-μg l^{-1} carbaryl prolonged the period that *D. pulex* kept the neckteeth when the animals were exposed to both carbaryl and the kairomone simultaneously. This is also the case for *D. ambigua*. The development of helmets by *Daphnia* was enhanced by 1 μg l^{-1} carbaryl in the presence of the kairomone, while this carbaryl concentration was too low to do any damage to the *Daphnia* [24]. Hence it may be concluded that even quite low (sublethal) concentrations of insecticides can affect the morphology of *Daphnia* in the presence of the predator *Chaoborus*.

The neckteeth and helmets interfere with predation on *Daphnia* by *Chaoborus* [12,13]. This suggests that insecticides reduce the vulnerability of *Daphnia* to predators by inducing the devel-

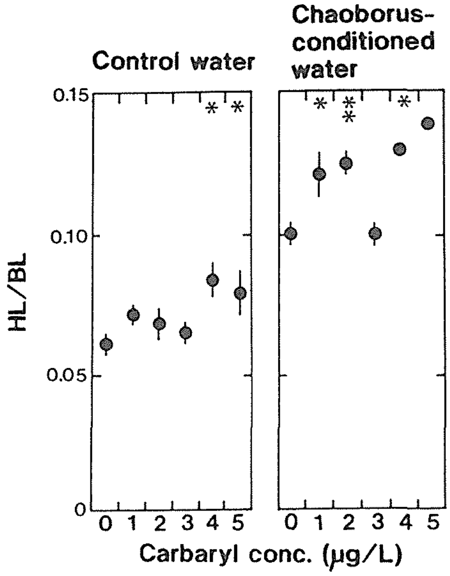

Fig. 2. Ratio of head length to body length (HL/BL) of the instar 2 of *Daphnia ambigua* exposed to six different concentrations of carbaryl (0, 1, 2, 3, 4, 5 µg l^{-1}) in the control water (without the *Chaoborus* kairomone) or the *Chaoborus*-conditioned water (with the kairomone). Vertical bars show 1SE. Statistical significance (ANOVA) in difference between individuals in each of the treatments with 1 - 5 µg l^{-1} carbaryl and the control (0 µg l^{-1} carbaryl) is shown at the top of the panels. *= $p<0.05$; **= $p<0.01$. (redrawn from Hanazato [28]).

opment of antipredator morphology, and therefore that *Daphnia* exposed to sublethal concentrations of insecticides may increase their survivorship in the presence of predators. However, it has been shown that sublethal concentrations of insecticides lead to deterioration of life history characteristics of *Daphnia* synergistically with the kairomone, and thus they reduce the growth rate of *Daphnia* populations. Furthermore, insecticides alter *Daphnia* behavior and may increase its vulnerability to predation by making the animals attract the attention of visual predators and increase their rate of encounter with ambush predators [29]. Consequently, the chemicals may reduce survivorship in the presence of predators. This is the opposite of the situation with insecticides, which increase survivorship of *Daphnia* by inducing formation of protuberant structures. Thus, the effects of insecticides on predator-prey interactions seem to be complicated.

This review has focused on the combined effects of insecticides and the kairomone from *Chaoborus*. However, it is known that kairomones, which affect *Daphnia* populations, are also released from other predators such as fish. The fish kairomones reduce the mature size, maturation time and offspring size of *Daphnia*, while increasing its clutch sizes [30,31]. These life history responses make it possible for *Daphnia* to start reproduction at a smaller size and produce more offspring, and therefore reduce the vulnerability of the *Daphnia* populations to fish, which prefer larger daphnids as prey. Therefore the responses of *Daphnia* have been considered to be adaptive. However, it is possible that the fish kairomone may reduce the tolerance of *Daphnia* to insecticide contamination because smaller neonates induced by the kairomone are more sensitive to stress than larger ones [32]. Thus, insecticides may affect *Daphnia* populations in the presence of various predators which release kairomones.

I have indicated the possibility that even sublethal concentrations of insecticides influence *Daphnia* populations through predator-prey interactions mediated by kairomones. *Daphnia* are key species in ecosystems of lakes and ponds because they are effective grazers on algae (primary producers) and are favorably preyed on by fish (top predators). Thus, insecticides contaminating the water bodies may affect the whole ecosystem by controlling the *Daphnia* populations. The effects of interactions among organisms need to be considered when evaluating the effects of anthropogenic chemicals on aquatic ecosystems.

Various freshwater organisms communicate with one another using chemical signals [4], and the chemical communication may play an important role in maintaining the freshwater ecosystems [33,34]. Anthropogenic chemicals such as insecticides seem to disturb the natural organic chemical communication in freshwater communities.

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