

## Impacts of Predation by the Copepod, *Mesocyclops pehpeiensis*, on Life Table Demographics and Population Dynamics of Four Cladoceran Species: a Comparative Laboratory Study

Jiang-Shiou Hwang<sup>1,\*</sup>, Ram Kumar<sup>2</sup>, and Chung-Su Kuo<sup>1</sup>

<sup>1</sup>Institute of Marine Biology, National Taiwan Ocean University, Keelung 202, Taiwan

<sup>2</sup>Ecosystem Research Lab, Acharya Narendra Dev College (University of Delhi), Govindpuri, Kalkaji, New Delhi 110 019, India

(Accepted March 17, 2009)

**Jiang-Shiou Hwang, Ram Kumar, and Chung-Su Kuo (2009)** Impacts of predation by the copepod, *Mesocyclops pehpeiensis*, on life table demographics and population dynamics of four cladoceran species: a comparative laboratory study. *Zoological Studies* 48(6): 738-752. Predation is a major source of prey mortality in which the goal of the predator is to maximize the efficiency with which it can ingest its prey while that of the prey is to develop strategies to minimize mortality due to predation. Copepods are dominant invertebrate predators in tropical freshwater ecosystems. The evolutionary responses to copepod predation pressures are not known in tropical systems. The predatory copepod, *Mesocyclops pehpeiensis*, is numerically abundant and exerts major predation pressures on different cladoceran species in tropical and subtropical freshwater systems. We investigated in the laboratory the responses of 4 cladoceran species: *Scapholeberis kingii*, *Ceriodaphnia cornuta*, *Moina macrocopa*, and *Daphnia similoides* to the copepod *Mes. pehpeiensis*. Two experiments were conducted: (a) life table demographics in a control and in water preconditioned by the copepod, and (b) population dynamics in a control, in the presence of the copepod, and in water preconditioned by the copepod. With the exception of *S. kingii*, average reproductive rates in the other 3 cladocerans were significantly higher in copepod-conditioned water than in the control. Furthermore, *D. similoides* showed a higher increase in reproductive rates in copepod-conditioned water than did the other 3 cladoceran species. The presence of the copepod severely suppressed the population growth trajectories of all 4 cladoceran species tested. The copepod-imposed reduction in population growth rates was significantly higher for *Moi. macrocopa* and *S. kingii*. With the exception of *S. kingii*, the other 3 cladocerans reproduced earlier in the copepod treatment. The neonate size at hatching and maximum body sizes reached by the 3 cladocerans (except *S. kingii*) in treatments were larger than those in the controls. <http://zoolstud.sinica.edu.tw/Journals/48.6/738.pdf>

**Key words:** Cyclopoida, Predation, Cladocera, Conditioned water, Life table.

Both vertebrate and invertebrate predators in aquatic ecosystems affect the life history and morphology of prey populations directly by preying on them and indirectly by releasing infochemicals or semiochemicals (Lüning 1992, Stibor and Lüning 1994, Chang and Hanazato 2005). Various environmental factors, like predation and competition, and physical factors, like temperature and constancy of ecosystem parameters, are known to influence the life history of organisms

and hence alter the community composition in aquatic ecosystems (Chang and Hanazato 2005, Castilho-Noll and Arcifa 2007). Of all these selection pressures, predation is the primary mechanism influencing the evolution of cladoceran life histories (Kerfoot and Sih 1987, Chang and Hanazato 2002 2003, Kumar 2003). Apart from directly influencing prey (i.e., mortality, Kerfoot 1977), predation also causes indirect effects on the prey (i.e., by releasing chemicals or kairomones)

\*To whom correspondence and reprint requests should be addressed. E-mail: Jshwang@mail.ntou.edu.tw

into the medium which may cause a phenotypic response (Boersma et al. 1998) in some prey characters, including morphological (Tollrian 1990), genetic (Pijanowska et al. 1993) behavioral (De Meester 1996, Pijanowska 1993 1994, Reede and Ringelberg 1995) and life history traits (Macháček 1991, Spitze 1992, Weider and Pijanowska 1993, Kumar 2003, Kumar and Hwang 2008). Since a prey species experiences a fluctuating predator regime throughout its lifespan, this phenotypic plasticity is assumed to be adaptive either by increasing the chances of the prey remaining alive (by escape behavior like vertical migration; De Meester et al. 1995) or by shifting prey life histories to maximize fitness (Spitze 1992, Stibor 1992). For example, a single clone of the cladoceran *Daphnia hyalina* shows shifts in its life history depending upon which predator (vertebrate and/or invertebrate) releases kairomones (Stibor 1992). In fish-conditioned water, *Daphnia* reproduced earlier and at a smaller size, and exhibited greater reproductive investment compared to the controls, while *Daphnia* raised in *Chaoborus*-conditioned water showed delayed reproduction at a larger size (Stibor 1992, Engelmayer 1995).

Invertebrate planktivorous predators also indirectly influence their prey by causing temporal and spatial differences in their life history parameters (Lampert and Sommer 1997). Among invertebrate predators, cyclopoid copepods are numerically dominant in pelagic food webs of tropical and subtropical eutrophic fresh waters. They exert large impacts on the structure and dynamics of planktonic communities (Kerfoot and Sih 1987, Kumar and Rao 2001, Kumar 2003, Chang and Hanazato 2005, Devetter and Seďa 2006), by selectively predating on various zooplankton (Williamson 1983, Rao and Kumar 2002, Kumar and Rao 2003, Chang and Hanazato 2005). They play important roles as pelagic invertebrate predators and should be considered, along with fish, as determinants of the abundance and community structure of zooplankton (Karabin 1978, Matsumura-Tundisi et al. 1990). Although the direct lethal impacts of predation are obvious in many cases, indirect effects are not conclusively known (Spaak and Hoekstra 1997, Riessen and Young 2005). Convincing evidence for the direct and indirect impacts of copepod predation comes from predator exclusion and introduction experiments using enclosures in field and laboratory experiments (Vanni 1986 1988, Roche 1990, Paul et al. 1995). Some cyclopoids, for example the genera

*Mesocyclops* (Williamson 1983, Rao and Kumar 2002), *Diacyclops* (Stemberger 1985), etc., may exert strong selection pressures on cladocera by preferentially preying on many cladoceran species (Kumar and Rao 1999a b, Chang and Hanazato 2002 2003 2005, Rao and Kumar 2002). In response to cyclopoid predation pressure, many cladocerans may change their morphology and/or life history patterns, depending on the intensity and type of predator (reviewed by Lynch 1980, Stibor 1992, Riessen 1999a b). For instance, cyclomorphosis, seasonality, and its role in the fitness of daphnids in response to predation were widely studied (Weider and Pijanowska 1993, Spaak 1995). Defense mechanisms in prey species as a strategy to reduce predation are generally assumed to impose costs (Riessen and Sprules 1990, Riessen 1992, Barry 1994, Spaak and Boersma 1997). Daphnids' responses to fish kairomones include relatively early maturation, a shorter age, a smaller size at 1st reproduction, higher fecundity, and changes in behavioral parameters (Macháček 1991, Reede 1997, Mikulski et al. 2004). Predatory copepods, through chemical secretions, cause growth retardation in some species (Larsson and Dodson 1993, Gliwicz 1994) and spinal elongation in others (Havel 1987, Havel and Dodson 1984).

Among various cyclopoid species, *Mesocyclops pehpeiensis* is a common and at times numerically dominant cyclopoid copepod found in shallow lakes, ponds, and wetlands in many tropical and subtropical freshwater ecosystems (Hwang et al. 2009). Not much is known about the impacts of predation on cladoceran species co-occurring with this cyclopoid (Kumar and Rao 1999a, Rao and Kumar 2002, Chang and Hanazato 2003 2005, Kumar 2003). Furthermore, most information related to cladoceran responses to copepod predation comes from work conducted with *Daphnia*. Compared to the large body of published information on predator-induced defenses in *Daphnia*, there is surprisingly little information on non-daphnid cladoceran species. Rao and Kumar (2002) reported that smaller or intermediate-sized non-daphnid cladocerans are preferably selected against *Daphnia* by the similarly sized cyclopoid *Mes. thermocycloides*, and are more vulnerable to copepod predation (Kumar 2003, Chang and Hanazato 2005). Therefore, in the present study, we evaluated the direct and indirect effects of the cyclopoid copepod *Mes. pehpeiensis* on life history attributes and population dynamics of 4 cladoceran

species commonly found in the natural habitats of the copepod which represent a wider size range (body lengths of 580 to 2134  $\mu\text{m}$ ).

## MATERIALS AND METHODS

Representative cladocerans commonly found in nature which co-occur with the copepod *Mes. pehpeiensis* were chosen for laboratory tests (author's unpubl. data). The cladoceran species chosen were *Daphnia similoides*, *Moina macrocopa*, *Ceriodaphnia cornuta*, and *Scapholeberis kingii* (Table 1). All experimental animals used in the present study were cultured in the laboratory and maintained continuously for at least 2 months before being used in the experiments. Starter cultures of the copepods were collected from an aquaculture pond and maintained in the laboratory on a mixed diet of rotifers, cladocerans, and the unicellular alga *Chlorella vulgaris*. Stock cultures were maintained in 1000 ml beakers and kept in a temperature gradient incubator at a temperature of  $25 \pm 1.5^\circ\text{C}$ , but were expanded when necessary to 10 L glass aquaria and kept at ambient temperature. Only adult (5-8 d old), non-ovigerous females were used in the tests. Cultures of cladocerans were established in each case from field-collected individuals and maintained in autoclaved tap water, using the green alga *C. vulgaris* as food at densities of (2 and  $3.5 \times 10^6/\text{ml}$ ). All experiments, with 4 or 5 replicates for each treatment, were conducted in 250 ml glass beakers containing 200 ml of autoclaved tap water.

The unicellular alga, *C. vulgaris*, was used as an exclusive food for routine cladoceran cultures with food levels ranging (2-3)  $\times 10^6$  cells/ml. The alga, *C. vulgaris*, was mass cultured in 2.5 L borosilicate solution bottles using vitamin-enriched

Kuhl and Lorenzen's nutrient medium (Kuhl and Lorenzen 1964). When used in the experiments, the alga was always harvested in the log phase.

Copepod preconditioning was carried out by incubating 20 copepods in 500 ml of autoclaved water for 24 h at a set temperature of  $25 \pm 1.5^\circ\text{C}$  in an incubator. The cyclopoids were removed, and the water was filtered through a  $0.45 \mu\text{m}$  Sartorius membrane filter (Tisch Environmental Inc. Miami, US) before being used in the experiments. The experimental design included (i) copepod-conditioned water with *C. vulgaris* as food, and (2) a control (200 ml autoclaved water with *C. vulgaris* as food). In the population dynamics experiment, in addition to the copepod-conditioned water and control, we used an additional copepod treatment (2 adult female cyclopoids in 200 ml of autoclaved water with *C. vulgaris* as food). The experiment was conducted in 250 ml glass beakers with 4 replicates for each treatment. Each beaker contained 200 ml of medium of either copepod-conditioned water or autoclaved tap water with *C. vulgaris*, at a concentration of  $2.5 \times 10^6$  cells/ml. The total number of beakers was 32 for the life table experiment (4 replicates  $\times$  2 conditions  $\times$  4 species) and 48 (4 replicates  $\times$  3 conditions  $\times$  4 species) for the population dynamics experiment. Ten neonate cohorts (~6 h old) of each of the 4 cladoceran species were introduced into respective beakers, and in the population dynamics experiment, 2 adult cyclopoid females were introduced in the copepod treatments for each of the 4 cladoceran species. Observations were taken using a stereozoom microscope at  $24 \pm 2$  h intervals to record the number of individuals of the original cohorts which remained alive and the number of offspring produced. Body sizes of the offspring were measured for each species at each treatment. The surviving individuals of the original cohorts were then

**Table 1.** Length, width, and dry weight of the experimental animals. Values are given as the mean  $\pm$  SE ( $n = 20$ )

Group	Species	Length ( $\mu\text{m}$ )		Width ( $\mu\text{m}$ )		Dry mass ( $\mu\text{g}$ )
		Adult	Neonate	Adult	Neonate	
Cladocera	<i>Ceriodaphnia cornuta</i>	580 $\pm$ 20	320 $\pm$ 8.6	363 $\pm$ 8.3	210 $\pm$ 6.8	3.0
	<i>Moina macrocopa</i>	1560 $\pm$ 40	648 $\pm$ 18.6	456 $\pm$ 16.9	226 $\pm$ 9.6	4.60
	<i>Daphnia similoides</i>	2134 $\pm$ 62.5	870 $\pm$ 40	1004 $\pm$ 38.8	588 $\pm$ 22.5	27.2
	<i>Scapholeberis kingii</i>	656 $\pm$ 20.5	360 $\pm$ 28	428 $\pm$ 14.34	254 $\pm$ 20.5	-
Copepoda	<i>Mesocyclops pehpeiensis</i>	933 $\pm$ 48.6 (length of the prosome)	-	-	-	0.24

transferred to a fresh beaker containing appropriate medium. Ovigerous copepods recorded in the experimental beakers were replaced by nonovigerous females. In the population dynamics experiment, daily observations were continued until the respective populations became stable. In each experiment, the morphology and body sizes of these cladocerans introduced into the copepod culture were compared to those without copepods. To investigate the effect of predators on morphological attributes (body size, size of the posterior spine, and helmet formation), cladocerans present in the copepod treatment and conditioned waters were observed under a stereozoom microscope, and body sizes were measured.

### Behavioral study

One individual *Mesocyclops* female (aged 6-8 d), deprived of food during the preceding 3 h, was offered 3 d old neonates (with body sizes as shown in table 1) of each of the cladoceran species at densities similar to those used in the life table study, and was continually observed. Using a high-speed video camera (1024 × 1024 pixels with a frame rate of 500 fps and shutter at 8 μs (Fastcam system: Photron, Fastcam-ultima 1024, USA) mounted on a stereomicroscope (Olympus SZX12, Tokyo, Japan) and following the methodology given in Strickler and Hwang (1999), Hwang et al. (1993), Hwang and Strickler (2001), and Dahms and Hwang (2009), we frame-by-frame recorded the predation behavior of *Mesocyclops* preying upon cladoceran species used in this study. The prey handling time (time lapsed between an attack of the prey by the copepod and its resumption of movement after ingestion; Tsai 2007) was recorded to the nearest 0.1 s with a stopwatch. For all cladoceran prey used in the present study, consumption was partial; therefore, the release of the partially consumed prey by the copepod was taken as the endpoint. For each prey species, 8-10 individual observations were made to obtain an average handling time.

### Data analyses

Age-specific life expectancy ( $e_x$ ), longevity ( $l_x$ ), and fecundity ( $m_x$ ) were calculated for each species in each treatment, using standard life-table methods (Pianka 1988) with the following formulae:

life expectancy

$$e_x = \sum_{t=1}^{\infty} tP_x = \sum_{t=0}^{\infty} tP_x q_x + t,$$

net reproductive rate (NRR)

$$R_0 = \sum_{r=0}^{\infty} l_x m_x, \text{ and}$$

generation time

$$T = \left( \sum_{r=0}^{\infty} l_x m_x x \right) / R_0;$$

where  $tP_x$  is the probability that the number of individuals of  $x$  age group will survive for  $t$  more days, i.e., live up to at least age  $x + t$ ,

$$tP_x = \frac{l_x + t}{l_x},$$

and  $q_x$  is the probability of individuals of age group  $x$  (i.e., between the ages of  $x$  and  $x + 1$ ) dying,

$$q_x = \frac{l_x - l_{x+1}}{l_x}.$$

The life expectancy at birth ( $e_0$ ) and NRRs were used for the statistical analyses.

The population growth rate ( $r$ ) was calculated from the exponential phase of population growth using the formula

$$r = \frac{\ln Nt + \ln N_0}{t};$$

where  $N_0$  is initial population density and  $Nt$  is the population density after time  $t$ . Statistical significance among treatments was tested with 1-way analysis of variance (ANOVA). A posteriori (post hoc) multiple comparisons among means were made using the least significant difference (LSD) test. Correlation coefficients were also determined where required. Two group comparisons in cases where the parametric distribution of the data was not certain were made using Mann-Whitney U-tests (Mann and Whitney 1947).

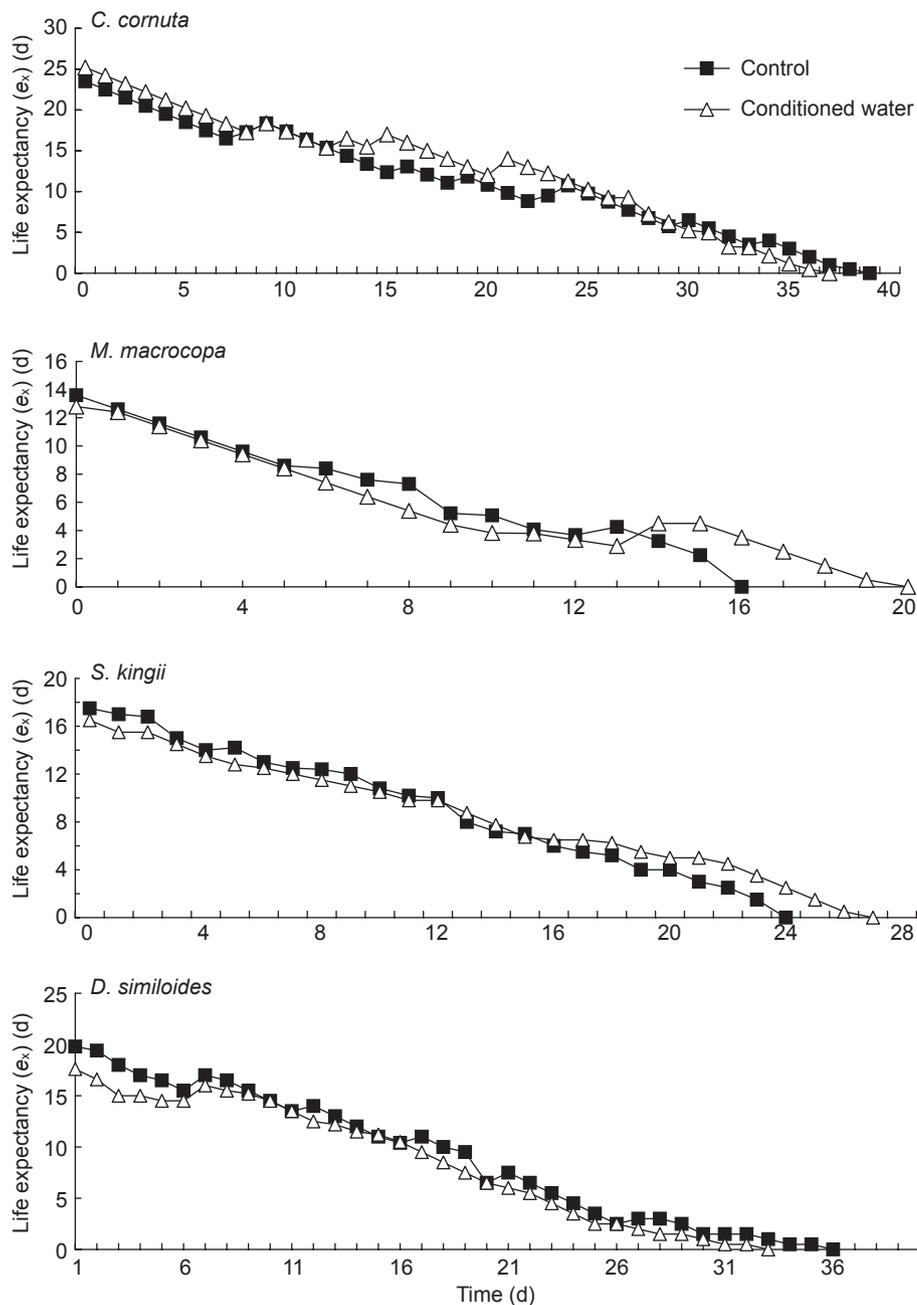
## RESULTS

For all 4 cladoceran species, life expectancy at birth between the controls and those in copepod-conditioned water did not significantly differ (Fig. 1). The highest life expectancy in all 4 cladoceran species tested was not generally at birth ( $e_0$ ) (Fig. 1); this suggests that neonates were more vulnerable to copepod predation. The percent

differences in life expectancy at birth between controls and cladocerans raised in copepod-treated water were significantly higher in *Moi. macrocopa* and *S. kingii* than that in *C. cornuta* ( $p < 0.3$ , Mann-Whitney U-test).

The effects of preconditioning medium with the copepod were more prominent on reproduction (Fig. 2). With the exception of *S. kingii*, the

average net reproductive rates in the other 3 cladocerans were significantly higher in copepod-conditioned water than in the controls (Fig. 2). Furthermore, the preconditioning-induced percent increase in the NRR was significantly higher for *D. similoides* than for the other 3 cladocerans ( $p < 0.05$ , 1-way ANOVA followed by the SNK test). With the exception of *S. kingii*, the other 3

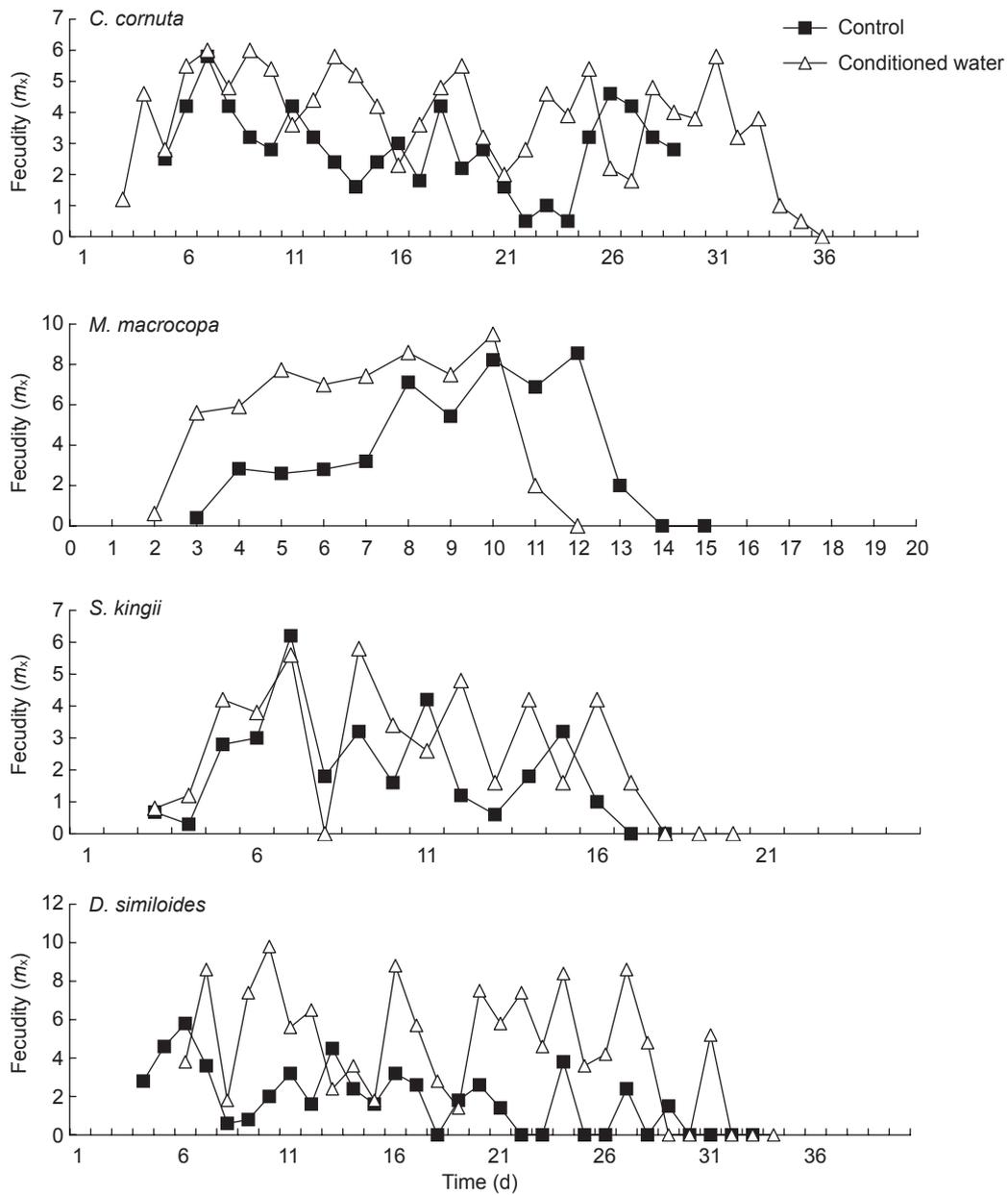


**Fig. 1.** Age ( $x$ )-specific life expectancy ( $e_x$ ) of *Ceriodaphnia cornuta*, *Moina macrocopa*, *Daphnia similoides*, and *Scapholeberis kingii* in copepod-conditioned water and the control. The values shown are the mean of 4 replicate cohorts, each with an initial sample size of 10 (error bars were omitted to avoid clutter).

cladoceran species exhibited a higher population growth in copepod-conditioned water than either in the control or in the presence of the copepods (Fig. 3). Population growth rates of *S. kingii* in copepod-conditioned water did not significantly differ ( $p = 1.24$ , 1-way ANOVA) from that in the control; however in the other 3 cladoceran species, population growth rates were significantly higher in copepod-conditioned water (Fig. 4). In all 4 cladoceran species, the rates of population

increase were significantly lower in the presence of copepods (Fig. 4). The copepod-imposed percent decrease in the population growth rate was significantly higher in *C. cornuta* followed by *S. kingii*, *D. similoides*, and *Moi. macrocopa*. Therefore in terms of percent decreases in the population growth rate, vulnerabilities of the cladocerans were in following order: *C. cornuta* > *S. kingii* > *D. similoides* > *Moi. macrocopa*.

The time taken to produce the 1st clutch

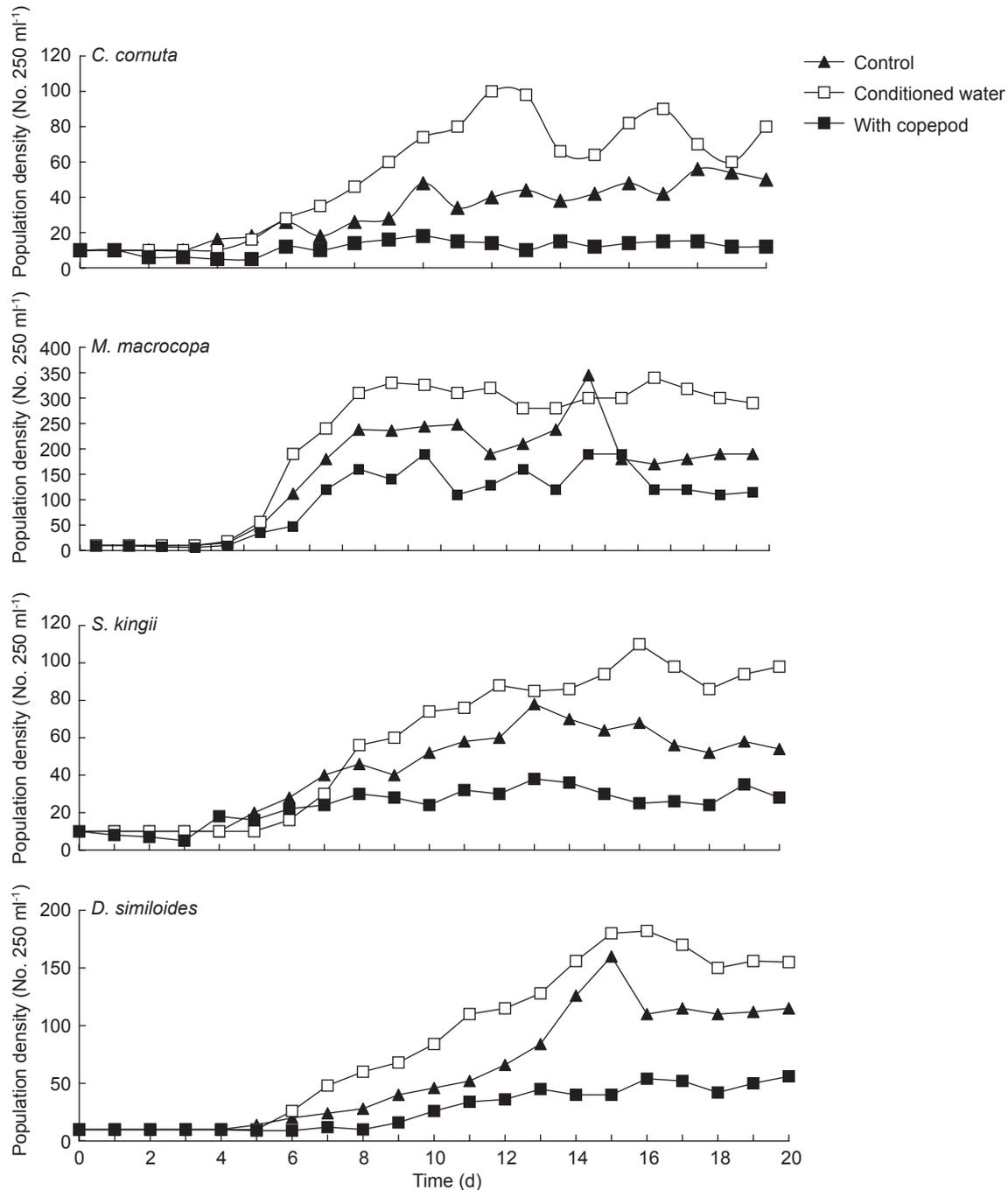


**Fig. 2.** Age (x)-specific fertility ( $m_x$ ) of *Ceriodaphnia cornuta*, *Moina macrocopa*, *Daphnia similoides*, and *Scapholeberis kingii* in copepod-conditioned water and the control. The values shown are the mean of 4 replicate cohorts, each with an initial sample size of 10 (error bars were omitted to avoid clutter).

for *M. macrocopa*, *C. cornuta*, and *D. similoides* in the copepod treatment was significantly lower than that in the control (Fig. 4,  $p < 0.05$  SNK test). For *Moi. macrocopa*, the time taken to produce the 1st clutch was significantly lower in copepod-conditioned water ( $p < 0.05$ ; 1-way ANOVA followed by the SNK test), which was not

significant in the other 3 cladocerans (Fig. 4).

*Moina macrocopa* and *D. similoides* produced larger neonates in copepod-conditioned water than that in the control (Fig. 5;  $p < 0.01$ ; 1-way ANOVA). The maximum body sizes attained by the cladocerans did not significantly differ among treatments (SNK test, Fig. 5). The larger

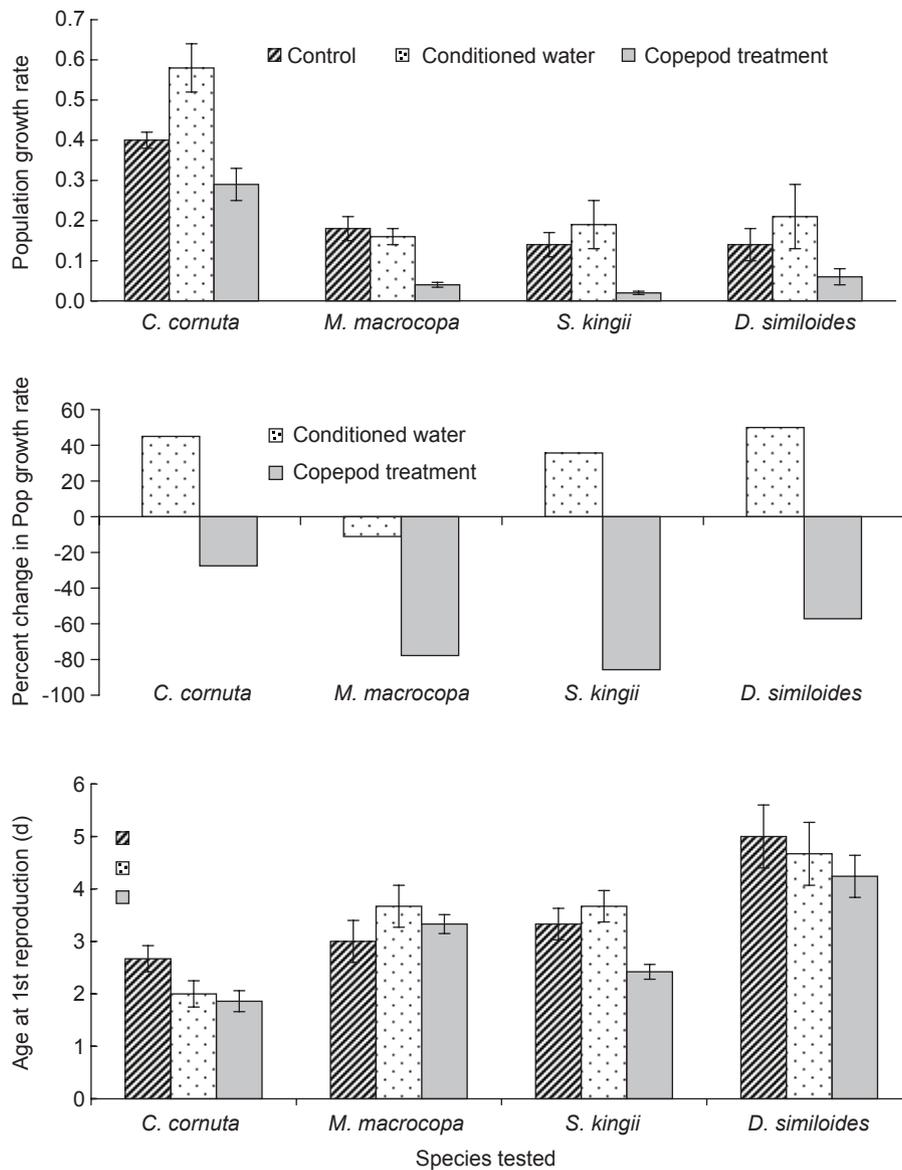


**Fig. 3.** Population growth trajectories of *Ceriodaphnia cornuta*, *Moina macrocopa*, *Daphnia similoides*, and *Scapholeberis kingii* in copepod-conditioned water, in the presence of copepods, and in the control. The values shown are the mean of 4 replicate cohorts, each with an initial sample size of 10 (error bars were omitted to avoid clutter).

cladoceran, *Daphnia*, kept in the copepod culture beaker showed a detectable morphological response, whereas the other 3 cladocerans showed no detectable morphological differences from those in the controls. More than 70% of *Daphnia* developed a helmet and neck teeth in the copepod culture beaker but not in the control. Furthermore, the average size of the posterior spine of the *Daphnia* population kept in the copepod culture beaker was significantly longer than those in the control (without copepods).

**Behavioral observations**

We cinematographically observed that the copepod was able to successfully subdue and capture all 4 cladoceran species used in our study. The prey handling times and vulnerabilities (percent change in *r* value; Table 2) were not significantly correlated. The handling time was maximal for the larger cladocera, *D. similoides*, followed by *C. cornuta* and *Moi. macrocopa*, and was minimal for the littoral cladocera, *S. kingii*. Figure 6 illustrates



**Fig. 4.** Population growth rates (*r*) (mean ± SD; *n* = 4), copepod-imposed percent change in the population growth rates, and the age at 1st reproduction (mean ± SD; *n* = 4) of *Ceriodaphnia cornuta*, *Moina macrocopa*, *Daphnia similoides*, and *Scapholeberis kingii* in copepod-conditioned water, in the presence of copepods, and in the control.

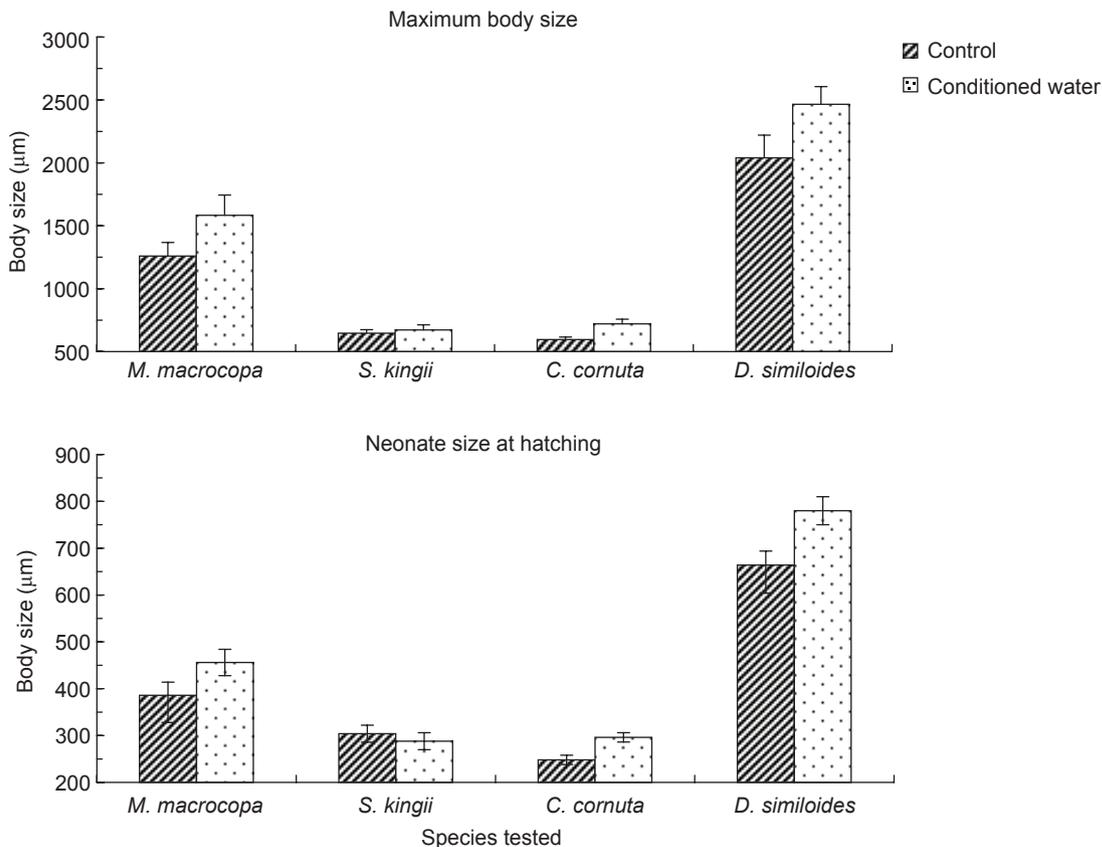
steps of prey capture mechanisms exhibited by the copepod in capturing the cladoceran *C. cornuta*.

## DISCUSSION

The higher survival and reproduction in copepod-conditioned water indicates that the direct negative impact of copepod predation is, to some extent, offset by the indirect positive impacts on life history attributes. Our observations indicate that when subjected to copepod predation, non-daphnid cladocerans used in these studies evolved no detectable morphological changes to deter predation. However, they evolved avoidance by changing some of their life-history attributes. The percent reduction in life expectancy at birth and population growth rates in the presence of a copepod indicate that the intermediate-sized cladoceran *Moi. macrocopa* and the smaller cladoceran littoral species *S. kingii* are more vulnerable to copepod predation than either *D. similoides* or *C. cornuta*.

A shorter age at 1st reproduction, a larger neonate size, and a higher fertility in copepod-conditioned water shows that *Moina* is able to respond more quickly and adjust its life history attributes to deter predation, but that the smaller-sized *S. kingii* is defenseless as it showed no life history or morphological responses to copepod predation. Furthermore, in *D. similoides*, the negative impact of predation on the growth rate was almost comparable to the positive impact in conditioned water.

The differential impact of copepod predation on cladocerans is supported by an earlier study in which given a 3 species choice (*C. cornuta*, *Moi. macrocopa*, and *D. similoides*), *Mesocyclops* selected the intermediate-sized *Moina* regardless of the relative abundances of the other 2 species (Rao and Kumar 2002). There was a negative selection for *Daphnia* at all proportions. *Moina* has a relatively thin carapace and lacks a posterior spine which *Daphnia* has, and hence it exhibits increased vulnerability to *Mesocyclops* predation even in the presence of alternate prey



**Fig. 5.** Body sizes (mean  $\pm$  SD;  $n = 4$ ) of neonates at hatching and maximum body sizes attained by *Ceriodaphnia cornuta*, *Moina macrocopa*, *Daphnia similoides*, and *Scapholeberis kingii* in copepod-conditioned water and the control.

(Kumar and Rao 2003). Furthermore, *Moina* exhibits higher fecundity than other cladoceran prey (Kumar and Rao 1999a). Matsumura-Tundisi et al. (1990) showed that the thick cuticle reduces the predation risk in *Ceriodaphnia*, which otherwise should be highly vulnerable because of its smaller size. Williamson (1980) made similar observations with *Mes. edax* which selected the soft-bodied *Diaphanosoma* and avoided the hard-carapaced *Bosmina*. Adults of relatively large-sized cladocerans might be less vulnerable, but their early instars (Gliwicz and Umana 1994) and sometimes eggs developing in a brood chamber (Gliwicz and Stibor 1993) are subjected to heavy predation pressures, with consequences for population growth. Some cladocerans have evolved spines and other processes to reduce egg predation by copepods (Hanazato and Dodson 1995, Weber and Declerck 1997).

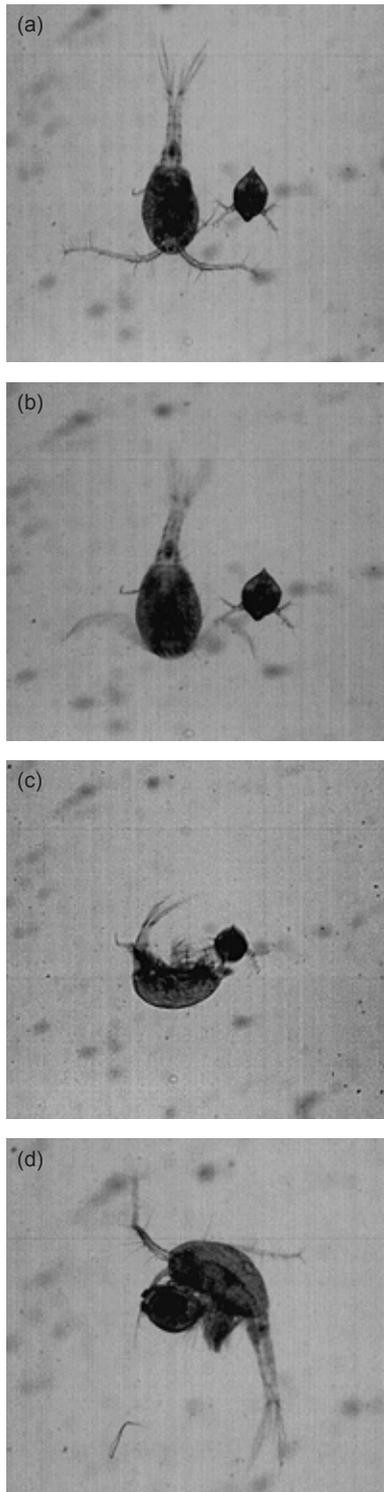
The body size of an organism is a very important life history parameter predicting the fitness of individuals or populations. There is an optimal body size for any species in a specific environment (Lynch 1997). In general, vertebrate planktivores selectively feed on the largest prey and invertebrate predators on relatively smaller prey. Therefore, zooplankton species tend to evolve smaller body sizes under vertebrate predation pressure and larger body sizes when invertebrate predation pressure is the major evolutionary force (Kumar 2003). We recorded a larger maximum body size and neonate size at hatching for 3 cladocera species, but *S. kingii* showed no significant change in either the maximum body size or the size of the neonate at hatching. Migrating and non-migrating clones of a *D. galeata* × *hyalina* hybrid also showed differences in body size due to the presence of fish kairomones (Reede and Ringelberg 1995), i.e., non-migrating clones were smaller while migrating clones did not significantly differ in size. According to Reede and Ringelberg (1998), daphnids not only

mature earlier and hence attain a smaller size, but also grow at a slower rate compared to those not exposed to fish kairomones. Macháček (1991) and Stibor (1992) suggested that reduced growth rates in the presence of fish kairomones could favor greater reproductive efforts (i.e., a larger clutch size). However, Weider and Pijanowska (1993) did not observe such a shift in *D. magna*. They stated that a reduced growth rate (i.e., as exhibited by a reduction in  $r$ ) might be costly. The maternal body size is also very important in determining the size and number of offspring produced (Lynch 1980, Lampert 1993). The generally accepted notion is that larger females produce larger clutches and larger offspring. Invertebrate predators like copepods select small-sized prey, and therefore prey should grow to a larger body size in the presence of such predators. Spitze (1991), Tollrian (1995), and Weber and Declerck (1997) observed that populations of *D. pulex* did evolve towards a larger body size. The high somatic growth rate in young instars of *D. galeata* did not result in reduced reproductive output (Weber and Declerck 1997). The animals had a high intrinsic rate of increase and produced more and larger neonates in the presence of *Chaoborus* than in the controls. In contrast, Lüning (1992) observed the opposite – a reduced rate of body growth in *D. pulex*. This divergence in results may have been due to differences in their strategies in response to the presence of a predator (Weber and Declerck 1997).

Variation in offspring size is a common phenomenon in many organisms (Stearns 1977 1992), and the fitness of the offspring depends upon the amount of maternal investment per offspring (Smith and Fretwell 1974, Alekseev and Lampert 2001). Possible participation of maternal effects in cladoceran functional responses was earlier elucidated. In changing environments, the presence of a predator and other environmental variability was experimentally shown to be sensed

**Table 2.** Cladoceran species-specific handling times (mean ± SE,  $n = 16-20$ ) by the copepod *Mesocyclops pehpeiensis*

Cladoceran species	Handling time ( $n = 16-20$ ) (s)	Copepod-imposed vulnerability (% change in the $r$ value)
<i>Ceriodaphnia cornuta</i>	282 ± 46.4	-85.7
<i>Scapholeberis kingii</i>	112.8 ± 28.2	-77.8
<i>Moina macrocopa</i>	196.8 ± 56.8	-27.5
<i>Daphnia similoides</i>	447.6 ± 108.74	-57.1



**Fig. 6.** Sequence of video film (high-speed video camera at  $1024 \times 1024$  pixels with a frame rate of 500 fps, a shutter speed of  $8 \mu\text{s}$ , and storage memory of 1536 frames) showing piece-by-piece predation mechanism of the copepod capturing the cladoceran prey *Ceriodaphnia cornuta*: (a) the distance at which the cladocera is detected, (b) the copepod initiating an attack response, (c) attacking the prey, and (d) the copepod handling and capturing *Ceriodaphnia*.

by mothers, which passed on the information to their offspring (Mousseaux and Fox 1998). Such maternal effects are mechanisms for adaptive phenotypic responses to the environment (Alekseev and Lampert 2001 2004, LaMontagne and McCauley 2001). *Daphnia* mothers are capable of assessing the environmental conditions (e.g., food level, Urabe and Sterner 2001) and using this information to adjust the size and number of offspring (Gliwicz and Guisande 1992, Stibor 1992). Furthermore, a tradeoff between the size and number of offspring was observed in many cladocerans (Ebert 1992). In general, a reduction in neonate size is observed when fish predation is high, an observation consistent with results obtained in all studies using fish kairomones. Small offspring size was reported by Reede (1995 1998), Reede and Ringelberg (1995), Weber and Declerck (1997), and Sakwinska (1998). Weber and Declerck (1997) observed a large neonate size and a lower age at maturity compared to the controls in *D. galeata* in the presence of a *Chaoborus* extract. It is disadvantageous for cladocerans to produce smaller neonates when copepod cues are present, because individuals resulting from small eggs would be small and hence more vulnerable to starvation and size-selective predation. Lynch (1980) proposed 3 alternatives for size at 1st reproduction depending upon the type of predation: (a) under fish predation, a small neonate with a small size at maturity should be favored; (b) under invertebrate predation, large sizes at birth and maturity should be favored; and (c) a large neonate size and small adult size should be simultaneously favored when cladocerans are subjected to both invertebrate and vertebrate predation.

Quite often in some cladocerans, there may be a minimum body size which must be achieved before the 1st clutch can form, but the time taken to reach that critical size might vary depending on different environmental conditions. Consequently, the body size and the age at 1st reproduction are most likely to be affected by predation pressures. The age at maturity is another life history parameter that is known to vary in response to different predation regimes. In the presence of fish kairomones, *D. galeata* (Macháček 1991), *D. hyalina* (Stibor 1992), *D. magna* (Weider and Pijanowska 1993), and a *D. galeata*  $\times$  *hyalina* hybrid (Reede 1995) matured at earlier ages. However, Sakwinska (1998) observe no effect of kairomones on the age at 1st reproduction in *D. magna*. Reede (1995), who observed a logarithmic

decrease in age at maturity with increasing fish kairomone levels, considered such a response to be a beneficial strategy because the daphnid gets a chance to reproduce before a predator eats it. *Daphnia hyalina* in fish and *Notonecta* treatments showed a significant reduction in the age at 1st reproduction (~5 d) when compared to the controls (6 d), but a delayed age at 1st reproduction (7 d) in *Chaoborus* treatment (Black 1993, Stibor and Lüning 1994). Pijanowska and Kowalczewski (1997) showed that *D. magna* subjected to cyclopoid copepod predation pressure released its 1st clutch significantly earlier (~16 h) than those in the controls as also found in the present study. A higher fecundity may also be due to a larger body size of the mother which is a consequence of the presence of a *Chaoborus* extract (Scheiner and Berrigan 1998), since fecundity increases with body size (Lampert 1993). However, Lynch (1980) predicted a larger body size but a smaller clutch size in the presence of invertebrate predators. In some studies, fecundity showed no difference at all or it was even lower (Havel and Dodson 1984, Walls and Ketola 1989, Lüning 1992). It was suggested that the lower reproductive effort under *Chaoborus* predation may be due to the costs associated with defensive structures (Havel and Dodson 1984, Walls and Ketola 1989). In the presence of cyclopoid copepod cues, *D. magna* matured earlier, achieved a larger body size, and produced a larger number of offspring than did control animals (Pijanowska and Kowalczewski 1997), as was also found in the present study.

The spiny morph of *Daphnia* was attacked but not captured by the copepod in our 30 min of observations, whereas the smaller cladocera *C. cornuta* (length  $320 \pm 8.6$  mm; width  $210 \pm 6.8$  mm;  $n = 10$ ) was attacked and captured in < 1 min. A predator induced crest formation in *Daphnia* was earlier observed (Grant and Bayly 1981, Riessen 1994). Figure 6 elucidates the mechanism of prey capture in copepods on cladoceran prey. However, detailed mechanisms will be elaborated elsewhere (under preparation). *Ceriodaphnia*, which otherwise should be more vulnerable because of its small size, faces less predation risk from the cyclopoid because it has a thicker cuticle (Matsumura-Tundisi et al. 1990) and hence requires more handling time ( $282 \pm 45.6$  s) than *Moina* ( $197 \pm 23.4$  s). *Mesocyclops pehpeiensis* spent more than twice the amount of time handling *Daphnia* than it did for *Moina*, making net profitability (biomass gained by the predator/handling time) to the copepod nearly

the same (0.018 and 0.016) for both prey species (Table 2).

Invertebrate predators, being numerically abundant, constitute the major predation pressure on a wide variety of zooplanktonic species (Zaret 1980, Dodson and Havel 1988, Parejko and Dodson 1991) and consequently have a significant impact on population growth trajectories of zooplankton. In eutrophic water bodies, cyclopoid copepods are dominant pelagic invertebrate predators (Irvine and Waya 1993, Maier 1996, Kumar and Rao 1998). They exert differential predation pressure based on the intrinsic rate of natural increase, morphology, size, and behavior of the prey (Stemberger 1985, Roche 1990, Hanazato and Dodson 1995, Kumar and Rao 1999a 2001, Rao and Kumar 2002). *Mesocyclops pehpeiensis* is an abundant (40 to 60 individuals/L), medium-sized omnivorous cyclopoid species, perennially occurring in ponds, pools, shallow ditches, rice paddy fields, and littoral zones of lakes and ponds in Taiwan (author's field observations). Like many other cyclopoid copepods (Kumar and Rao 1999a b, Rao and Kumar 2002, Kumar et al. 2008), it selectively preys upon a wide range of prey types (Chang and Hanazato 2005).

**Acknowledgments:** Financial support provided by the Department of Science and Technology, Government of India under the young scientist scheme (SR/OY/LS-09/2001) and subsequently by the National Science Council, Taiwan for a postdoctoral fellowship (0940020949Dt 2005/03/10) to the 2nd author and research funding (NSC 97-2621-B-019-001, NSC97-2611-M-019-004, and NSC97-2621-B-019-004) to the 1st author is gratefully acknowledged. Acharya Narendra Dev College, University of Delhi is acknowledged for allowing the 2nd author to use his earned leave. We thank 2 anonymous reviewers for their comments and suggestions.

## REFERENCES

- Alekseev VR, W Lampert. 2001. Maternal control of resting-egg production in *Daphnia*. *Nature* **414**: 899-901.
- Alekseev VR, W Lampert. 2004. Maternal effects of photoperiod and food level on life history characteristics of the cladoceran *Daphnia pulicaria* Forbes. *Hydrobiologia* **526**: 225-230.
- Barry MJ. 1994. The costs of crest induction for *Daphnia carinata*. *Oecologia* **97**: 578-288.
- Black AR. 1993. Predator induced phenotypic plasticity in *Daphnia pulex*: life history and morphological responses

- to *Notonecta* and *Chaoborus*. *Limnol. Oceanogr.* **38**: 986-996.
- Boersma M, P Spaak, L De Meester. 1998. Predator-mediated plasticity in morphology, life history, and behaviour of *Daphnia*: the uncoupling of responses. *Am. Nat.* **152**: 237-248.
- Castilho-Noll MSM, MS Arcifa. 2007. Mesocosm experiment on the impact of invertebrate predation on zooplankton of a tropical lake. *Aquat. Ecol.* **41**: 587-598.
- Chang KH, T Hanazato. 2002. Morphological defense of *Bosmina fatalis* against invertebrate predators in Lake Suwa. *Verh. Int. Ver. Limnol.* **28**: 1279-1283.
- Chang KH, T Hanazato. 2003. Vulnerability of cladoceran species to predation by the copepod *Mesocyclops leuckarti*: laboratory observations on the behavioral interaction between predator and prey. *Freshwater Biol.* **48**: 476-484.
- Chang KH, T Hanazato. 2005. Impact of selective predation by *Mesocyclops pehpeiensis* on a zooplankton community: experimental analysis using mesocosms. *Ecol. Res.* **20**: 726-732.
- Dahms HU, JS Hwang. 2009. Perspectives of underwater optics in biological oceanography and plankton ecology studies. *J. Mar. Sci. Technol.* (accepted).
- De Meester L. 1996. Local genetic differentiation and adaptation in freshwater zooplankton population: patterns and processes. *Ecoscience* **3**: 385-399.
- De Meester L, LJ Weider, R Tollrian. 1995. Alternative antipredator defences and genetic polymorphism in a pelagic predator-prey system. *Nature* **378**: 483-485.
- Devetter M, J Seďa. 2006. Regulation of rotifer community by predation of *Cyclops vicinus* (Copepoda) in the Řimov Reservoir in spring. *Int. Rev. Hydrobiol.* **91**: 101-112.
- Dodson SI, JE Havel. 1988. Indirect prey effects: some morphological and life history responses of *Daphnia pulex* exposed to *Notonecta undulata*. *Limnol. Oceanogr.* **33**: 1274-1285.
- Ebert D. 1992. A food-independent maturation threshold and size at maturity in *Daphnia magna*. *Limnol. Oceanogr.* **37**: 878-881.
- Engelmayer A. 1995. Effects of predator-released chemicals on some life history parameters of *Daphnia pulex*. *Hydrobiologia* **307**: 203-206.
- Gliwicz ZM. 1994. Relative significance of direct and indirect effects of predation by planktivorous fish on zooplankton. *Hydrobiologia* **272**: 201-210.
- Gliwicz ZM, C Guisande. 1992. Family planning in *Daphnia*: resistance to starvation in offspring born to mothers grown at different food levels. *Oecologia* **91**: 461-467.
- Gliwicz ZM, H Stibor. 1993. Egg predation by copepods in *Daphnia* brood cavities. *Oecologia* **95**: 295-298.
- Gliwicz ZM, G Umana. 1994. Cladoceran body size and vulnerability to copepod predation. *Limnol. Oceanogr.* **39**: 419-424.
- Grant JWG, IAE Bayly. 1981. Predator induction of crests in morphs of the *Daphnia carinata* King complex. *Limnol. Oceanogr.* **26**: 201-218.
- Hanazato T, SI Dodson. 1995. Morphological defenses of *Daphnia* against copepod predation on eggs. *Arch. Hydrobiol.* **133**: 49-59.
- Havel JE. 1987. Predator-induced defenses: a review. In WC Kerfoot, A Sih, eds. Predation, direct and indirect impact on aquatic communities. Hanover, NH: Univ. Press of New England, pp. 263-278.
- Havel JE, SI Dodson. 1984. *Chaoborus* predation on typical and spined morphs of *Daphnia pulex*: behavioral observations. *Limnol. Oceanogr.* **29**: 487-497.
- Hwang JS, R Kumar, CW Hsieh, AY Kuo, S Souissi, MH Hsu, JT Wu, WC Liu, CF Wang, QC Chen. 2009. Patterns of zooplankton distribution along the marine, estuarine and riverine portions of the Danshuei ecosystem in northern Taiwan. *Zool. Stud.* (in press)
- Hwang JS, JR Strickler. 2001. Can copepods differentiate prey from predator hydromechanically? *Zool. Stud.* **40**: 1-6.
- Hwang JS, JT Turner, JH Costello, DJ Coughlin, JR Strickler. 1993. A cinematographic comparison of behavior by the calanoid copepod *Centropages hamatus*: tethered versus free-swimming animals. *J. Exp. Mar. Biol. Ecol.* **167**: 277-288.
- Irvine K, R Waya. 1993. Predatory behaviour of the cyclopoid copepod *Mesocyclops aequatorialis aequatorialis* in Lake Malawi, a deep tropical lake. *Verh. Int. Ver. Limnol.* **25**: 877-881.
- Karabin A. 1978. The pressure of pelagic predators of the genus *Mesocyclops* (Copepoda, Crustacea) on small zooplankton. *Ekol. Pol.* **26**: 241-257.
- Kerfoot WC. 1977. Implications of copepod predation. *Limnol. Oceanogr.* **22**: 316-325.
- Kerfoot WC, A Sih. 1987. Predation: direct and indirect impacts on aquatic communities. Hanover, NH: Univ. Press of New England, 386 pp.
- Kuhl A, H Lorenzen. 1964. Handling and culturing of *Chlorella*. In DM Prescott, ed. *Methods in cell physiology*, vol. 1. New York and London, pp. 152-187.
- Kumar R. 2003. Effect of *Mesocyclops thermocyclopoides* (Copepoda, Cyclopoida) predation on population dynamics of different prey: a laboratory study. *J. Freshwater Ecol.* **18**: 383-393.
- Kumar R, JS Hwang. 2008. Ontogenetic shifts in the ability of the cladoceran, *Moina macrocopa* Straus and *Ceriodaphnia cornuta* Sars to utilize ciliated protists as food source. *Int. Rev. Hydrobiol.* **93**: 284-296.
- Kumar R, P Prasad, HU Dahms, LC Tseng, JS Hwang. 2008. Potential of three aquatic predators to control mosquitoes in the presence of alternative prey: a comparative experimental assessment. *Mar. Freshwater Res.* **59**: 817-835.
- Kumar R, TR Rao. 1998. Postembryonic developmental rates as a function of food type in the cyclopoid copepods *Mesocyclops thermocyclopoides* Harada. *J. Plankton Res.* **20**: 271-287.
- Kumar R, TR Rao. 1999a. Demographic responses of adult *Mesocyclops thermocyclopoides* (Copepoda, Cyclopoida) to different plant and animal diets. *Freshwater Biol.* **42**: 487-501.
- Kumar R, TR Rao. 1999b. Effect of algal food on animal prey consumption rates in the omnivorous copepod, *Mesocyclops thermocyclopoides*. *Int. Rev. Hydrobiol.* **84**: 419-426.
- Kumar R, TR Rao. 2001. Effect of the cyclopoid copepod *Mesocyclops thermocyclopoides* on the interactions between the predatory rotifer *Asplanchna intermedia* and its prey *Brachionus calyciflorus* and *B. angularis*. *Hydrobiologia* **453/454**: 261-268.
- Kumar R, TR Rao. 2003. Predation on mosquito (*Anopheles stephensi* and *Culex quinquefasciatus*) larvae by *Mesocyclops thermocyclopoides* (Copepoda; Cyclopoida) in the presence of alternate prey. *Int. Rev. Hydrobiol.* **88**:

- 570-581.
- LaMontagne JM, E McCauley. 2001. Maternal effects in *Daphnia*: what mothers are telling their offspring and do they listen. *Ecol. Lett.* **4**: 64-71.
- Lampert W. 1993. Phenotypic plasticity of the size at first reproduction in *Daphnia*: the importance of maternal size. *Ecology* **74**: 1455-1466.
- Lampert W, U Sommer. 1997. *Limnoecology: the ecology of lakes and streams*. New York and Oxford, UK: Oxford Univ. Press, 382 pp.
- Larsson P, S Dodson. 1993. Chemical communication in planktonic animals. *Arch. Hydrobiol.* **129**: 129-155.
- Lüning J. 1992. Phenotypic plasticity of *Daphnia pulex* in the presence of invertebrate predators: morphological and life history responses. *Oecologia* **92**: 383-390.
- Lynch M. 1980. The evolution of cladoceran life histories. *Q. Rev. Biol.* **55**: 23-42.
- Lynch M. 1997. Fitness and optimal body size in zooplankton populations. *Ecology* **58**: 763-774.
- Macháček J. 1991. Indirect effect of planktivorous fish on the growth and reproduction of *Daphnia galeata*. *Hydrobiologia* **225**: 193-197.
- Maier G. 1996. Copepod communities in lakes of varying trophic degree. *Arch. Hydrobiol.* **136**: 455-465.
- Mann HB, DR Whitney. 1947. On a test of whether one or two random variables is stochastically larger than the other. *Ann. Math. Stat.* **18**: 50-60.
- Matsumura-Tundisi T, AC Rietzler, ELG Espindola, JG Tundisi, O Rocha. 1990. Predation on *Ceriodaphnia cornuta* and *Brachonius calyciflorus* by two *Mesocyclops* species coexisting in Barra Bonita reservoir (SP, Brazil). *Hydrobiologia* **198**: 141-151.
- Mikulski A, D Lipowska, J Pijanowska. 2004. Ontogenetic changes in *Daphnia* responsiveness to fish kairomone. *Hydrobiologia* **526**: 219-224.
- Mousseau TA, CW Fox. 1998. The adaptive significance of maternal effects. *Trends Ecol. Evol.* **13**: 403-407.
- Parejko K, SI Dodson. 1991. The evolutionary ecology of an antipredator reaction norm: *Daphnia pulex* and *Chaoborus americanus*. *Evolution* **45**: 1665-1674.
- Paul AG, PR Leavitt, DW Schindler, AK Hardlie. 1995. Direct and indirect effects of predation by a calanoid copepod (subgenus: *Hesperodiptomus*) and of nutrients in a fishless alpine lake. *Can. J. Aquat. Sci.* **52**: 2628-2638.
- Pianka ER. 1988. *Evolutionary ecology*, 4th ed. New York: Harper and Row, 468 pp.
- Pijanowska J. 1993. Diel vertical migration in zooplankton: fixed or inducible behaviour? *Arch. Hydrobiol. Beih. Erg. Limnol.* **39**: 89-97.
- Pijanowska J. 1994. Fish-enhanced patchiness in *Daphnia* distribution. *Verh. Int. Verein. Limnol.* **25**: 2366-2368.
- Pijanowska J, A Kowalczewski. 1997. Cues from injured *Daphnia* and from cycloids feeding on *Daphnia* can modify life histories of conspecifics. *Hydrobiologia* **350**: 99-103.
- Pijanowska J, LJ Weider, W Lampert. 1993. Predator-mediated genotypic shifts in a prey population: experimental evidence. *Oecologia* **96**: 40-42.
- Rao TR, R Kumar. 2002. Patterns of prey selectivity in the cyclopoid copepod, *Mesocyclops thermocyclopoidea* Harada. *Aquat. Ecol.* **36**: 411-424.
- Reede T. 1995. Life history shifts in response to different levels of fish kairomones in *Daphnia*. *J. Plankton Res.* **17**: 1661-1667.
- Reede T. 1997. Effects of neonate size and food concentration on the life history responses of a clones of the hybrid *Daphnia galeata* and *Daphnia hyaline* to fish kairomones. *Freshwater Biol.* **37**: 389-396.
- Reede T, J Ringelber. 1995. The influence of a fish exudates on two clones of the hybrid *Daphnia galeata*, *Daphnia hyalina*. *Hydrobiologia* **307**: 207-212.
- Reede T, J Ringelber. 1998. Differential life history responses of several pelagic *Daphnia* clones differing in migratory behaviour. *Aquat. Ecol.* **32**: 245-253.
- Riessen HP. 1992. Cost-benefit model for the induction of an antipredator defense. *Am. Nat.* **140**: 349-362.
- Riessen HP. 1994. Morphological response of *Daphnia* to *Chaoborus* predation. *Ver. Int. Verein Limnol.* **25**: 2382-2386.
- Riessen HP. 1999a. *Chaoborus* predation and delayed reproduction in *Daphnia*: a demographic modeling approach. *Evol. Ecol.* **13**: 339-363.
- Riessen HP. 1999b. Predator induced life history shift in *Daphnia*: a synthesis of studies using meta-analysis. *Can. J. Fish. Aquat. Sci.* **56**: 2487-2494.
- Riessen HP, WG Sprules. 1990. Demographic costs of anti predator defenses in *Daphnia pulex*. *Ecology* **71**: 1536-1546.
- Riessen HP, JD Young. 2005. *Daphnia* defense strategies in fishless lakes and ponds: one size does not fit all. *J. Plankton Res.* **27**: 531-544.
- Roche KF. 1990. Some aspects of vulnerability to cyclopoid predation of zooplankton prey individuals. *Hydrobiologia* **198**: 152-162.
- Sakwinska O. 1998. Plasticity of *Daphnia magna* life history traits in response to temperature and information about a predator. *Freshwater Biol.* **39**: 681-687.
- Scheiner SM, D Berrigan. 1998. The genetics of phenotypic plasticity. The cost of plasticity in *Daphnia pulex*. *Evolution* **52**: 368-378.
- Smith CC, SD Fretwell. 1974. The optimal balance between size and number of offspring. *Am. Nat.* **108**: 499-506.
- Spaak P. 1995. Cyclomorphosis facilitates the maintenance of a *Daphnia* hybrid among its parental species. *Hydrobiologia* **307**: 283-289.
- Spaak P, M Boersma. 1997. Tail spine length in the *Daphnia galeata* complex: costs and benefits of induction by fish. *Aquat. Ecol.* **31**: 89-98.
- Spaak P, JR Hoekstra. 1997. Fish predation on a *Daphnia* hybrid species complex: a factor explaining species coexistence? *Limnol. Oceanogr.* **42**: 753-762.
- Spitze K. 1991. *Chaoborus* predation and life history evolution in *Daphnia pulex*: temporal pattern of population diversity, fitness and mean life history. *Evolution* **45**: 82-92.
- Spitze K. 1992. Predator-mediated plasticity of prey life history and morphology: *Chaoborus americanus* predation on *Daphnia pulex*. *Am. Nat.* **139**: 229-247.
- Stearns SC. 1977. The evolution of life history traits: a critique of the theory and a review of the data. *Ann. Rev. Ecol. Syst.* **8**: 145-171.
- Stearns SC. 1992. *The evolution of life histories*. Oxford, UK: Oxford Univ. Press.
- Stemberger RS. 1985. Prey selection by the copepod *Diacyclops thomasi*. *Oecologia* **65**: 492-497.
- Stibor H. 1992. Predator induced life-history shifts in a freshwater cladoceran. *Oecologia* **92**: 162-165.
- Stibor H, J Lüning. 1994. Predator induced phenotypic variation in the pattern of growth and reproduction in

- Daphnia hyalina* (Crustacean; Cladocera). *Funct. Ecol.* **8**: 97-101.
- Strickler JR, JS Hwang. 1999. Matched spatial filters in long working distance microscopy of phase objects. *In* PC Cheng, PP Hwang, JL Wu, G Wang, H Kim, eds. *Focus on multidimensional microscopy*. Singapore: World Scientific Publishing, **2**: 217-239.
- Tollrian R. 1990. Predator induced helmet formation in *Daphnia cucullata* (Sars). *Arch. Hydrobiol.* **119**: 191-196.
- Tollrian R. 1995. Predator-induced morphological defenses: cost, life history shifts, and maternal effects in *Daphnia pulex*. *Ecology* **76**: 1691-1705.
- Tsai TS. 2007. When prey acts as a lever: prey handling behavior of the Chinese green tree viper, *Trimeresurus stejnegeri* (Viperidae: Crotallinae). *Zool. Stud.* **46**: 631-637.
- Urabe J, RW Sterner. 2001. Contrasting effects of different types of resource depletion on life-history traits in *Daphnia*. *Funct. Ecol.* **15**: 165-174.
- Vanni MJ. 1986. Fish predation and zooplankton demography: indirect effects. *Ecology* **67**: 337-354.
- Vanni MJ. 1988. Freshwater zooplankton community structure: introduction of large invertebrate predators and large herbivores to a small-species community. *Can. J. Fish. Aquat. Sci.* **45**: 1758-1770.
- Walls M, M Ketola. 1989. Effects of predator induced spines on individual fitness in *Daphnia pulex*. *Limnol. Oceanogr.* **34**: 390-396.
- Weber A, S Declerck. 1997. Phenotypic plasticity of *Daphnia* life history traits in response to predator kairomones: genetic variability and evolutionary potential. *Hydrobiologia* **360**: 89-99.
- Weider LJ, J Pijanowska. 1993. Plasticity of *Daphnia* life histories in response to chemical cues from predators. *Oikos* **67**: 385-392.
- Williamson CE. 1980. The predatory behavior of *Mesocyclops edax*: predator preferences, prey defenses and starvation induced changes. *Limnol. Oceanogr.* **25**: 903-909.
- Williamson CE. 1983. Behavioral interactions between a cyclopoid copepod and its prey. *J. Plankton Res.* **5**: 701-711.
- Zaret TM. 1980. *Predation and freshwater communities*. New Haven, CT: Yale Univ. Press.