

# Fish kairomones alter life cycle and growth of a calanoid copepod

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In this study, we evaluate the effects of chemical information present in exudates of the zooplanktivorous fish *Cnesterodon decemmaculatus* (Poeciliidae) on the life cycle and growth of the planktonic copepod *Notodiaptomus conifer*. Semi-static assays were carried out using five concentrations of fish water (FW; 0.41–3.3 fish L<sup>-1</sup>), and a control (without fish). Copepods responded to FW by faster development and earlier maturation at smaller body size which resulted in a decline in the number of eggs in the first clutch. The proportional duration of each larval stage was not modified in the presence of fish chemical information, indicating that *N. conifer* maintained an equi-proportional development according to the growth model proposed for copepods. Some parameters of the copepod life history changed depending on FW concentration, while other responses were induced merely by the presence of fish exudates, regardless of concentration. This study shows that calanoid copepods display as clear individual life history responses to kairomones as those that have been known for cladocerans, since 1980s. The observed responses are consistent with physiological mechanisms acting directly on development and constitute an example of the importance of predator–prey interactions as a selective force in aquatic environments.

## INTRODUCTION

In aquatic ecosystems, predator–prey interactions play a key role (Stearns, 1992; Lampert and Sommer, 1997), generating complex co-evolutionary processes capable of altering the spatial and temporal distribution of organisms, as well as determining the structure of populations and communities (Gliwicz, 2002). It is well known that the presence of a potential predator in the zooplankton community can cause certain phenotypic responses in prey organisms (Mort, 1986; Dodson, 1988, 1989; Gliwicz and Maszczyk, 2007), tending to increase the possibility of surviving (modifying their morphology or behaviour), and maximizing fitness (altering their life history) (Weider and Pijanowska, 1993).

Many studies have revealed that a great part of these responses are chemically induced by predator-derived kairomones (Macháček, 1991; Stibor, 1992; Larsson and Dodson, 1993; Macháček, 1993; Tollrian, 1994; de

Mester and Weider, 1999; Forward and Rittschof, 2000; Rose *et al.*, 2001). Nevertheless, most of the studies on life history responses have been carried out on the cladoceran genus *Daphnia*. For instance, many authors (Stearns, 1976, 1977, 1992; Lynch, 1980) have attempted to address the issue of trade-offs between two conflicting energy demands: either maximizing further growth and accumulation of materials for egg production or maximizing probability of survival until first reproduction. For example, the presence of chemicals produced by the fish *Leucaspis delineaatus* in the water can trigger a change in resource allocation pattern reflected in an alteration in the size of *D. magna* and the time of first fecundity during their life cycle (Weider and Pijanowska, 1993) (see Lass and Spaak, 2003 for review).

In spite of their importance, studies that demonstrate that calanoid copepods are as equally sensitive to fish kairomones as cladocerans are scarce. Current knowledge on their capacity of detection and response to chemical

information on predation risk are generally focused on behavioural parameters. For example, some copepods reduce their feeding activity in the presence of fish kairomones (Cieri and Stearns, 1999), which are capable of changing their behaviour (Ramcharan and Sprules, 1991), even their daily migratory cycles (Hansson *et al.*, 2007). Copepods, with complex life cycles, are suitable biological models to study the adjustments of their life history parameters as well as the effects of kairomones on the equiproportionality model proposed for free-living copepods (Corkett and McLaren, 1970; Landry, 1983; Corkett, 1984; Hart, 1990).

According to this model, each larval stage constitutes a fixed proportion of the total time of development independently of natural factors that influence metabolism (Hart, 1990, 1996, 1998). Numerous studies on growth and developmental models in copepods have been made to predict the effects of natural factors, such as temperature and food quality (Uye, 1988; Carlotti and Sciandra, 1989; Hart, 1994, 1996, 1998), or xenobiotic factors, such as pesticides (Brown *et al.*, 2002). Nevertheless, the possible stability of such models in relation to fish kairomones has not yet been well elucidated.

The objectives of this study were: (i) to evaluate whether chemical information on predation-risk present in exudates of the fish *Cnesterodon decemmaculatus* affects life history parameters and growth of the planktonic copepod *Notodiaptomus conifer*; (ii) to determine the minimum sensitivity threshold of any such apparent effect, and (iii) to evaluate the effects of fish kairomones on the equiproportionality model proposed for free-living copepods.

We hypothesize that chemical information on predation risk present in fish exudates can induce adjustments in copepods life history traits and cause alterations in their equiproportional development. A series of experimental semi-static assays were carried out using five fish water (FW) densities and the responses of copepods in relation to fish exudates were evaluated during their larval development and the first part of their adult life. Copepods may respond to fish kairomones by earlier maturation at smaller body size that causes decline in the number of eggs per clutch. This study highlights the importance of life-history modifications and addresses the plasticity capacity of copepods to make adjustments in their life cycle, when the risk assessed as chemical information on fish presence is increased.

## METHOD

### Selection and rearing of test organisms

*Notodiaptomus conifer* (Sars, 1901) is a diaptomid copepod, endemic to the Neotropical region (Ringuelet, 1958;

Dussart, 1984), frequent in the Paraná River alluvial plain. It was selected because it is representative of the zooplankton of the region and because of its availability for laboratory culture. The fish predator selected, *C. decemmaculatus* (Jenyns, 1842), is a small zooplanktophagous local native poeciliid fish (Oliveros, 1980; Escalante, 1983; Rossi, 1989), easily maintained in the laboratory and suitable for use in bioassays.

Copepods were collected from 1000 L tanks placed outside in the Instituto Nacional de Limnología (CONICET-UNL), Santa Fe, Argentina, using a 250- $\mu\text{m}$  plankton net. These tanks were several years ago inoculated with zooplankton from water bodies of the Paraná River alluvial plain. A laboratory stock culture was maintained under controlled conditions of photoperiod (16:8 h light–darkness) and temperature ( $20 \pm 2^\circ\text{C}$ ). Water from the same tanks, twice filtered with a 25- $\mu\text{m}$  mesh and aerated, was used as the culture medium with food added (see below). Fish were collected from a culture pond at the same Institute using a fishing net and transported to the laboratory for acclimation and size-selection.

### Control water and fish-conditioned water

Control water (tank water, TW) was collected from copepod culture tanks, filtered and oxygenated. Physico-chemical characteristics were measured according to the Standard Methods for the Examination of Water and Wastewater (in  $\text{mg L}^{-1}$ ): dissolved  $\text{O}_2$ , 6.415 ( $\pm 0.835$ ); nitrates,  $<0.1$ ; nitrites, 0.01; ammonium, 0.29; chlorides, 3.5; sulphates, 8.3; total alkalinity ( $\text{CaCO}_3$ ), 77; bicarbonates, 94; sodium, 7.7; magnesium, 6.8; calcium, 12.9; potassium, 1.8; OQD, 10;  $\text{O}_5\text{BD}$ , 0.08. Also pH 8.39 ( $\pm 0.24$ ) and conductivity 245.33 ( $\pm 28.18$ )  $\mu\text{S cm}^{-1}$  were measured.

To obtain FW, 20 adult *C. decemmaculatus* similar in size (length  $3.6 \pm 0.6$  cm) were placed in a fish tank (6 L) with TW. Five FW dilutions, made with TW immediately before copepod bioassay water exchange, resulting in concentrations of 100, 50, 25, 12.5 and 6.25% FW, corresponding to 3.3, 1.65, 0.82 and 0.41 fish  $\text{L}^{-1}$ , respectively, were used. Fish were not fed during the experiments to avoid altering FW chemical quality.

### Life history experiments

Ovigerous females from the stock culture of *N. conifer* were isolated to obtain nauplii ( $<24$  h after hatching) that were placed individually in 12 mL glass containers with 6 mL of culture medium. Larger copepodites were placed in the same glass containers with 12 mL of culture medium. Experiments were conducted with 25–40 replicates. During the assays, culture media were

renewed daily for the control and the FW treatments. The stock culture and the test individuals were fed *ad libitum* with a *Chlorella* sp. concentrate (density  $3.7 \times 10^3$  cells mL<sup>-1</sup>).

The following response traits were chosen as indicator of sensitivity to chemical signals: (a) total naupliar development time, (b) duration of each copepodite stage, (c) total development time to maturity, (d) percentage of ovigerous females, (e) time to formation of the first egg sac, (f) number of eggs on the total females present in the population (total females at each FW concentration) and (g) size of copepodite instar C1 to C6. The developmental stage reached by each individual was determined daily under a stereoscopic microscope. Life tables, designating as C1, C2, C3, C4 and C5 the successive copepodite larval stages, were carried out. As an indicator of growth for each copepodite stage, total length of moults was measured (from the tip of prosome to the end of caudal rami) using a Nikon 41 602 micrometric ocular lens. The mean ratio of measured adult was 47.7 and 52.3% to male and female respectively.

Once the adult stage was reached, females were isolated and placed in 20 mL glass containers with the respective medium together with five to eight males to induce fertilization. The observations continued for 15 more days to register the number of fertilized females, the time to production of the first egg sac and the number of eggs per female.

### Statistical analysis

To test the significance of each concentration of fish-conditioned water on life history (development time, growth, first reproduction time and fecundity) of *N. conifer*, a one-way ANOVA was used for each of the life history parameters followed by a *post hoc* Dunnett's test. Differences were considered to be significant at  $P < 0.05$ . Prior to ANOVA, normality and homogeneity of variances of the data were tested and confirmed using the Kolmogorov–Smirnov test.

The specific proportion of each copepodite stage to the copepodite developmental time was calculated. The  $\chi^2$  goodness-of-fit test was used to evaluate the effects of fish kairomones on the equiproportional model proposed for copepods.

Fish-conditioned water effects on length increment were examined by linear regression:

$$TL_{t+1}(\text{postmolt}) = a + b (TL)(\text{premolts})$$

where  $a$  is the intercept in  $TL_{t+1}$ , and  $b$  is the constant of growth.

To evaluate if fish-conditioned water effects are concentration dependent, the Pearson correlation

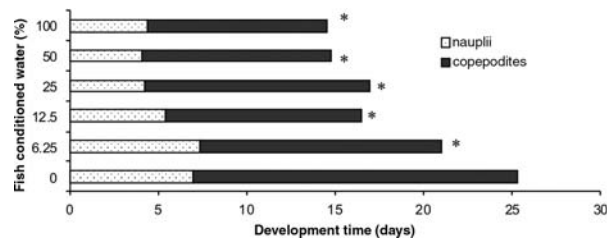


Fig. 1. Average development time of nauplii and copepodites. \* $P < 0.005$  to total development time.

coefficient was calculated between each parameter and all FW dilutions tested. All analyses were carried out using the statistical package GraphPad InStat (2004).

## RESULTS

### Mortality and development time

During the period of development of organisms, mean mortality at the end of the life cycle was 5 and 17.2% for nauplii and copepodites, respectively.

Figure 1 shows the mean time of development for nauplii and copepodites: nauplii showed significant differences (ANOVA,  $P < 0.005$ ;  $df = 141$ ) between the time of development in the control and the four higher concentration treatments, but not between the control and the 6.25% FW treatment (Dunnett,  $P > 0.05$ ). Total copepodite development time differed significantly between the control and the five FW treatments (ANOVA,  $P < 0.005$ ;  $F = 16.098$ ;  $df = 108$ ). In general, there was a tendency towards a more rapid total development in copepods exposed to fish-treated water (FW) (ANOVA,  $P < 0.05$ ;  $F = 26.087$ ;  $df = 105$ ) (Fig. 1).

The development time of each copepodite stage is illustrated in Fig. 2. In most stages, significant differences were evident in all FW treatments (ANOVA,  $P = 0.05$ ). In general, development time decreased significantly with rising FW concentration ( $r = -0.4505$ ;  $df = 108$ ;  $F = 27.252$ ;  $P < 0.0001$ ).

On the other hand, the analysis of the proportion of each copepodite stage showed that there were no significant differences between the control and the FW concentrations tested (Table I). This indicates that each copepodite larval stage maintained the proportion in relation to the total time of development for each treatment.

### Fecundity

The percentage of breeding (ovigerous) females correlated negatively with FW concentration ( $r = -0.8392$ ;  $df = 5$ ;  $P = 0.0367$ ). Moreover, very low fecundity was

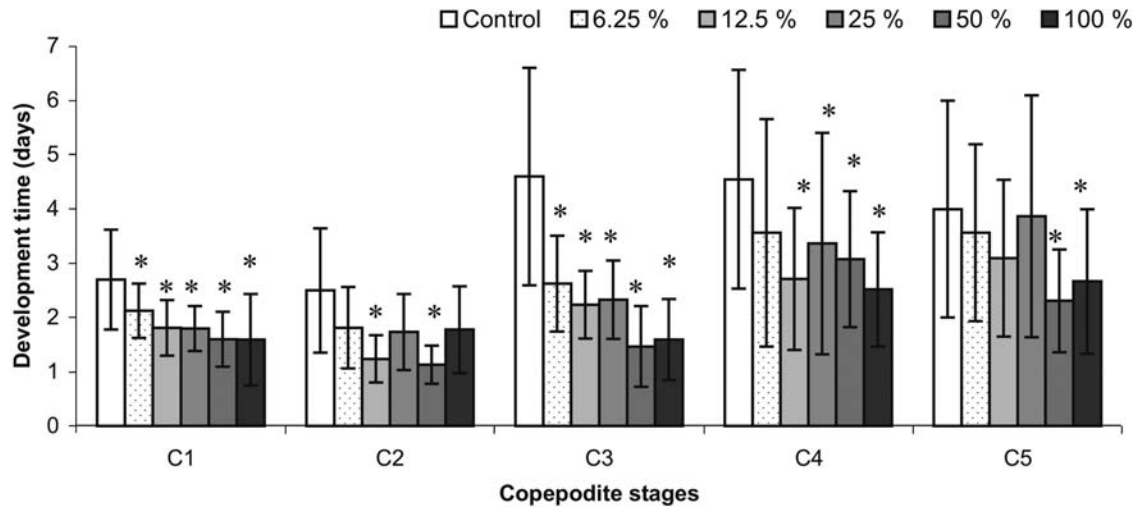


Fig. 2. Mean development time of each copepodite stage, control and test FW concentrations. \* $P < 0.005$ .

recorded at the highest concentrations (Table II). The average egg production for the total female population was significantly different between the highest FW concentration and the control (ANOVA,  $P < 0.005$ ;  $F = 2.665$ ;  $df = 62$ ), while average clutch size overall declined significantly with rising FW concentration ( $r = -0.4581$ ;  $df = 62$ ;  $P = 0.0002$ ) (Table II). The time to production of the first egg sac was also affected by the presence of fish exudates (Table II); however, this response was dose independent, and unrelated to FW concentration ( $r = -0.2116$ ;  $df = 38$ ;  $P = 0.1960$ ).

**Growth**

Copepods at the two highest FW concentrations were significantly smaller than control animals at the C4 stage [ANOVA,  $F = 2.78$  (at 50%) and  $F = 2.70$  (at

100%);  $df = 47$ ;  $P < 0.05$ ] and at maturity [ANOVA,  $F = 3.49$  (at 50%) and  $F = 3.77$  (at 100%);  $df = 62$ ;  $P < 0.05$ ] (Fig. 3). Analysis of the mean total body length of individuals at each copepodite stage reveals that individuals exposed to higher concentration of FW grew less than the control ones (Fig. 4).

Table III shows the correlation analysis between life history parameters and FW concentrations. Total development time, size at maturity, the proportion of ovigerous females and the number of eggs per female declined significantly with rising FW concentration (Fig. 5). Only time to egg-sac production did not differ significantly.

Table I: Mean proportion (%) of copepodite development spent in copepodite stages (C1 to C5) in control and different concentrations of FW, with associated statistics ( $\chi^2$  value and P-value)

Fish conditioned water (%)	Proportion of each copepodite stage (%)					$\chi^2$	P
	C1	C2	C3	C4	C5		
0	14.7	13.6	25.1	24.8	21.8		
100	15.7	17.5	15.7	24.8	26.3	5.6	0.2305 (ns)
50	15.0	10.6	13.7	28.8	21.6	6.44	0.1685 (ns)
25	14.4	13.8	18.6	23.3	30.8	5.527	0.2373 (ns)
12.5	16.3	11.2	20.2	24.5	27.9	3.288	0.5108 (ns)
6.25	15.5	13.2	19.2	26.0	26.0	2.3	0.6770 (ns)

**DISCUSSION**

The results of this study clearly indicate that copepods respond to fish-conditioned water from potential fish predators through significant changes in various critical life history parameters: namely, total development time, earlier sexual maturity and smaller body size. Moreover,

Table II: Proportion of ovigerous females, number of eggs per female and time to first egg sacs in control and all FW treatments

Fish conditioned water (%)	Ovigerous females (%)	Eggs per female (average)	Time to first egg sac (days)
100	30	2.00 ( $\pm 3.4$ )*	5.67 ( $\pm 0.5$ )*
50	37.5	3.13 ( $\pm 4.4$ )	6.67 ( $\pm 1.5$ )
25	44.4	4.08 ( $\pm 4.8$ )	5.5 ( $\pm 2.3$ )*
12.5	91.66	8.21 ( $\pm 2.6$ )	4.46 ( $\pm 2$ )
6.25	85.71	8.71 ( $\pm 4.5$ )	5.83 ( $\pm 2.2$ )*
0	83.3	6.42 ( $\pm 3.5$ )	9.9 ( $\pm 2.3$ )

\* $P < 0.005$ .

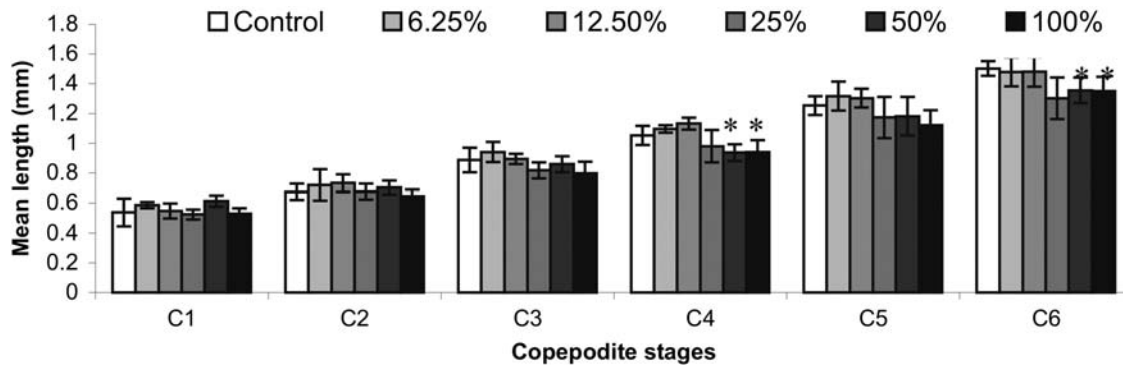


Fig. 3. Mean body length of each copepodite stage at different FW concentrations and control. \* $P < 0.005$ .

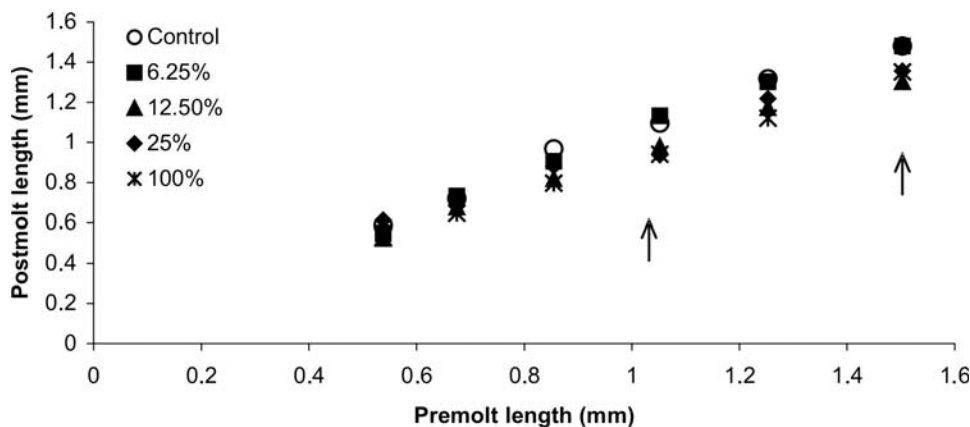


Fig. 4. Relation between premolt and postmolt length of copepodids (C1 to C6) in the control and all FW dilutions. Arrows indicate values significantly different to the control ( $P < 0.005$ ).

we have shown that copepods, as sensitive to the risk of visual predation as cladocerans, are susceptible to life-history modifications when the risk assessed as chemical information on fish presence is increased.

However, in spite of the observed changes in copepod life history, the proportion of each developmental stage in all FW concentrations was similar to that in the control, indicating that *N. conifer* did not deviate from its equiproportional development schedule as a result of the exposure to chemical information on predation risk present in fish exudates. While equiproportional development is independent of natural parameters that could affect metabolism, such as temperature or food quality (Hart, 1996, 1998; Van Den Bosch and Wilfried, 1994), this study shows for the first time that it is also independent of alarm chemicals. In this context, since kairomones are also natural components, normally acting as mediators in biological predator–prey interactions, it is reasonable to think that they would not modify the normal molting pattern, although inducing adaptive metabolic responses in organisms. On the other hand, there would be

a developmental constraint that makes the molting pattern so constant and inflexible.

The adjustments in the life cycle of *N. conifer* are consistent with changes expected in response to the presence of chemical information on predation risk. These results agree with those reported by other authors, who found a great phenotypic plasticity in cladocerans subjected to different fish chemical communicators (Štíbor, 1992; Engelmayer, 1995; Štíbor and Macháček, 1998). The reduction in the generation time and the decrease in size observed in *N. conifer* would constitute “positive responses” *sensu* Hanazato *et al.* (2001) and according to Beckerman *et al.* (Beckerman *et al.*, 2007) it would be the result of physiological mechanisms acting directly on development. These mechanisms reflect the feeding pattern of a vertebrate predator, such as *C. decemmaculatus*, feeding on an invertebrate (Hall *et al.*, 1976; Riessen, 1999; Reznick *et al.*, 2002) and would determine the distribution of energy available among conflicting demands, such as different activities and/or structures.

Nauplii as well as copepodites exposed to FW developed significantly faster. This chemically induced

Table III: Pearson correlation coefficients of *Notodiaptomus conifer* life history parameters in relation to different dilutions of fish conditioned water

Parameter	R	F	N	P
Development time	-0.5527	45.754	109	<0.0001 (s)
Adult size	-0.4347	14.215	68	0.0004 (s)
% fecund females	-0.8392	9.521	64	0.0367 (s)
No. of eggs per female	-0.4581	16.199	63	0.0002 (s)
Time of first egg sac	-0.2116	1.734	39	0.1960 (ns)

s, significant; ns, not significant.

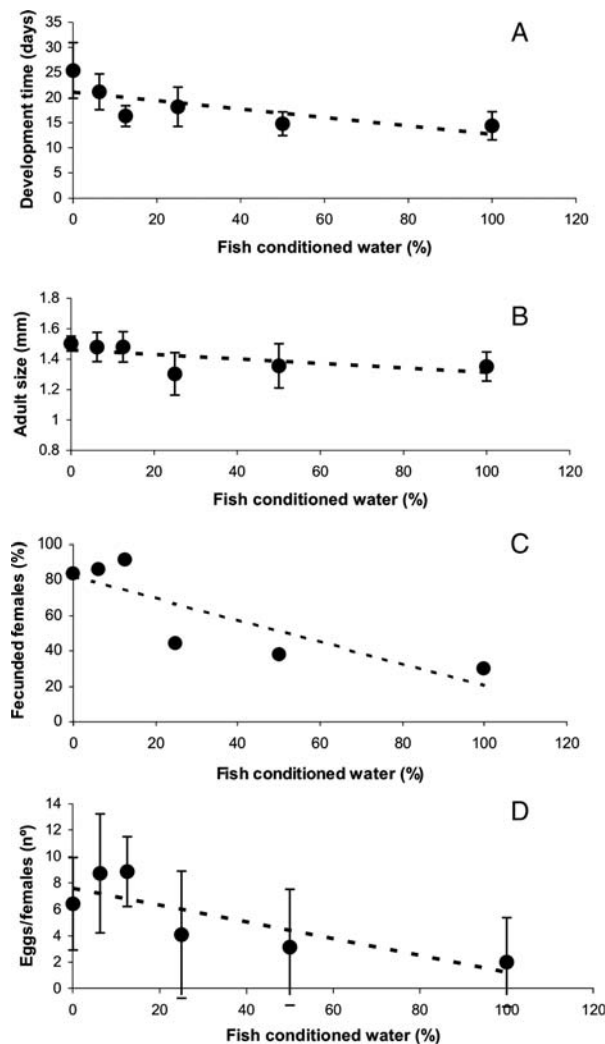


Fig. 5. Relation between (A) total development time; (B) adult size; (C) proportion of ovigerous females (no. of ovigerous females per female population) and (D) absolute mean fecundity (no. of eggs per females) and FW concentrations.

response represents an efficient strategy to reach the reproductive adult stage before being consumed by predators (Lynch, 1980). These results agree with those obtained by other investigators who studied the effects of fish chemical information on experimental populations of cladocerans (Stibor, 1992; Weider and Pijanowska, 1993; Riessen, 1999).

The smaller size at maturity of copepods raised in higher FW concentrations provides evidence of the need to reduce the time of development to mature as soon as possible and implies a modification of resource allocation during ontogenesis (Weider and Pijanowska, 1993). Moreover, other authors have demonstrated that the presence of chemicals indicating danger reduces the feeding activity of copepods (Cieri and Stearns, 1999) and cladocerans (Rose *et al.*, 2001). These authors consider that this strategy would reduce the risk of being consumed by predators because food in the intestine increases visibility or because movements used in feeding help the mechanical identification of the prey. However, considering that a lower feeding activity does not imply a lower efficiency in food assimilation (Beckerman *et al.*, 2007), smaller size could be a direct consequence of accelerated development to maturity and a higher reproductive success (Macháček, 1991; Stibor, 1992; Ball and Baker, 1996), and not necessarily a reduction in the quantity of carbon available (due to a lower intake or to a loss because of an increase in the respiratory rate). In this sense, the main adaptive mechanism of organisms in relation to chemical information on predation risk was a modification in energy allocation during the whole developmental cycle towards an early maturity. Additionally, smaller size at maturity would reduce the risk of detection and capture by visual predators, such as *C. decemmaculatus*.

In relation to survival itself, the results obtained agree with previous studies on cladocerans (Dodson *et al.*, 1995; Rose *et al.*, 2001), which show that kairomones did not alter survival *per se*.

Interestingly, the percentage of females fertilized at the two highest concentrations of FW (50 and 100%) was very low compared with that in the control. Recent studies have demonstrated that most copepods use chemical signals to recognize and locate their mates during reproduction (Yen *et al.*, 1991), especially in presence of predators, where an increase in the swimming activity would be very risky (Guerritsen and Strickler, 1977). However, the presence of other (natural or xenobiotic) chemicals in the medium could interact with these substances decreasing the effectiveness of chemical communication. To date, there are very few studies evaluating the effects of physico-chemical variations of the medium on pheromones (Steele *et al.*, 1992; Dodson

et al., 1995), but the presence of fish exudates would probably alter this chemical communication. Copulatory behaviour is a highly complex process that requires not only morphological but also ethological compatibility and is energetically costly (Blades and Youngbluth, 1980; Maier, 1995). For this reason, reproductive success should be studied in the context of interactions with ethological, mechanical and environmental aspects.

In common with the results obtained for *Daphnia longispina* by Castro et al. (Castro et al., 2007), the effects of FW on some life history parameters of *N. conifer* were concentration dependent, while others were binary responses, activated merely by the presence of fish. In this study, correlation analyses showed that development time, body size, the proportion of ovigerous females and the number of eggs per female were affected in a concentration-dependent manner. On the other hand, time to formation of the first egg sac seemed unrelated to FW concentration: fish presence alone was sufficient to induce a response, the magnitude of which did not vary with info-chemical dosage.

Based on total development time of organisms and time to formation of the first egg sac in fertilized females, our results indicate that a minimum threshold for detecting the presence of fish would be below 6.25% (0.41 fish L<sup>-1</sup>). Beckerman et al. (Beckerman et al., 2007) and Castro et al. (Castro et al., 2007) found responses in cladocerans exposed to chemical information of other poeciliid species of similar length at concentrations between 3 and 0.5 fish L<sup>-1</sup>. Changes in the life history of *N. conifer* at the minimum test concentration used in this study confirm that calanoid copepods are as equally sensitive to fish kairomones as cladocerans and susceptible to life-history modifications when the risk assessed as chemical information on fish presence is increased.

On the other hand, based on body size, or the number of eggs per female as isolated response parameters, significant differences from the controls were evident only at higher FW concentrations. These findings show that it is very important to analyse the complete life history of organisms, exposing the early larval stages, sensitive to environmental changes, to fish chemical information, to know their minimum levels of sensitivity, as proposed by Weider and Pijanowska (Weider and Pijanowska, 1993).

Finally, considering the changes in the demographic variables examined in this study at concentrations between 3.3 and 0.41 fish L<sup>-1</sup>, we conclude that chemical information on predation risk affects parameters of the life history and growth of calanoid copepods: the earlier time of first reproduction and the reduced number of eggs per clutch (egg sac) was simply an effect

of individual decision to increase the chance of egg production by doing this before the individual copepod is eventually captured by fish, hence in the time when the amount of maternal resources for eggs is still much lower than later at greater body size and more resources were accumulated for egg production.

Responses depended on fish density for most of the parameters analysed and physiological mechanisms induced as strategies to maximize fitness did not alter the proportion of each larval stage, demonstrating that *N. conifer* responds to the general model proposed by Hart (Hart, 1990) for free-living copepods (equiproportional development). Observed life history adjustments constitute adaptive responses to the presence of these size-selective predators and exemplify, on the one hand, the importance of predation as a selective force in natural environments and, on the other hand, the phenotypic plasticity of copepods. Owing to the scarcity of studies focusing on the adjustments in life history traits, there is a clear need for further analyses of the mechanism of action of kairomones, the responses of other species of copepods and the incidence of the effects combined with other (natural and/or xenobiotic) chemical compounds.

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## REFERENCES

- Ball, S. L. and Baker, R. L. (1996) Predator-induced life history changes: Antipredator behavior costs or facultative life history shifts? *Ecology*, **77**, 1116–1124.
- Beckerman, A. P., Kieski, K. and Baird, D. J. (2007) Behavioural versus physiological mediation of life history under predation risk. *Oecologia*, **152**, 335–343.
- Blades, P. I. and Youngbluth, M. J. (1980) Morphological, physiological, and behavioral aspects of mating in calanoid copepods. In Kerfoot, W. C. (ed), *Evolution and Ecology of Zooplankton Communities*. University Press of New England, NH, pp. 39–51.
- Brown, R. J., Rundle, S. D., Hutchinson, T. H. et al. (2002) A copepod life-cycle test and growth model for interpreting the effects of lindane. *Aquat. Toxicol.*, **63**, 1–11.
- Carloti, F. and Sciandra, A. (1989) Population dynamics model of *Euterpina acutifrons* (Copepoda: Harpacticoida) coupling individual growth and larval development. *Mar. Ecol. Prog. Ser.*, **56**, 225–242.

- Castro, B. B., Consciencia, S. and Goncalves, F. (2007) Life history responses of *Daphnia longispina* to mosquitofish (*Gambusia holbrooki*) and pumpkinseed (*Lepomis gibbosus*). *Hydrobiologia*, **594**, 165–174.
- Cieri, M. D. and Stearns, D. E. (1999) Reduction of grazing activity of two estuarine copepods in response to the exudate of a visual predator. *Mar. Ecol. Prog. Ser.*, **177**, 157–163.
- Corkett, C. J. (1984) Observations on development in copepods. *Crustaceana*, **7** (Suppl.), 150–153.
- Corkett, C. J. and McLaren, I. A. (1970) Relationships between development rate of eggs and older stages of copepods. *J. Mar. Biol. Assoc. UK*, **50**, 161–168.
- De Mester, L. and Weider, L. J. (1999) Depth selection behavior, fish kairomones and the life histories of *Daphnia hyalina* × *gelata* clones. *Limnol. Oceanogr.*, **44**, 1248–1258.
- Dodson, S. I. (1988) The ecological role of chemical stimuli for the zooplankton: predator-avoidance behavior in *Daphnia*. *Limnol. Oceanogr.*, **33**, 1431–1439.
- Dodson, S. I. (1989) The ecological role of chemical stimuli for the zooplankton: predator-induced morphology in *Daphnia*. *Oecologia*, **78**, 361–367.
- Dodson, S. I., Hanazato, T. and Gorski, P. R. (1995) Behavioral responses of *Daphnia pulex* exposed to carbaryl and *Chaoborus* kairomone. *Environ. Toxicol. Chem.*, **14**, 43–50.
- Dussart, B. H. (1984) Some Crustacea Copepoda from Venezuela. *Hydrobiologia*, **113**, 25–67.
- Engelmayer, A. (1995) Effects of predator-released chemicals on some life history parameters of *Daphnia pulex*. *Hydrobiologia*, **307**, 203–206.
- Escalante, A. (1983) Contribución al conocimiento de las relaciones tróficas de peces de agua dulce del área platense. III. Otras especies. *Limnobiós*, **2**, 453–463.
- Forward, R. B. and Rittschof, D. (2000) Brine shrimp larval phtoresponses evolved in diel vertical migration: activation by fish mucus and modified amino sugars. *Limnol. Oceanogr.*, **44**, 1904–1916.
- Gliwicz, Z. M. (2002) On the different nature of top-down and bottom-up effects in pelagic food webs. *Freshw. Biol.*, **47**, 2296–2312.
- Gliwicz, Z. M. and Maszczyk, P. (2007) *Daphnia* growth is hindered by chemical information on predation risk at high but not at low food levels. *Oecologia*, **150**, 706–715.
- GraphPad InStat (2004) Grupo Infostat, FCA. Universidad Nacional de Córdoba. Primera Edición, Editorial Brujas. Argentina.
- Guerritsen, J. and Strickler, J. R. (1977) Encounter probabilities and community structure in zooplankton: a mathematical model. *J. Fish Res. Board Canada*, **34**, 73–82.
- Hall, D. J., Threkelde, S. T., Burns, C. W. *et al.* (1976) The size efficiency hypothesis and the size structure of zooplankton communities. *Annu. Rev. Ecol. Syst.*, **7**, 177–208.
- Hansson, L. A., Nicolle, A., Brodersen, J., Romare, F., Nilsson, P. A., Brönmark, C. and Skov, C. (2007) Consequences of fish predation, migration, and juvenile ontogeny on zooplankton spring dynamics. *Limnol. Oceanogr.*, **52**, 696–706.
- Hanazato, T., Fueki, K. and Yoshimoto, M. (2001) Fish-induced life-history shifts in the cladocerans *Daphnia* and *Simocephalus*: are they positive or negative responses? *J. Plankton Res.*, **23**, 945–951.
- Hart, R. C. (1990) Copepod post-embryonic durations: pattern, conformity, and predictability. The realities of isochronal and equiproportional development, and trends in the copepodid-naupliar duration ratio. *Hydrobiologia*, **206**, 175–206.
- Hart, R. C. (1994) Equiproportional temperature-duration responses, and thermal influences on distribution and species switching in the copepods *Metadiaptomus meridianus* and *Tropodiaptomus spectabilis*. *Hydrobiologia*, **272**, 163–183.
- Hart, R. C. (1996) Naupliar and copepodite growth and survival of two freshwater calanoids at various food levels: demographic contrasts, similarities and food needs. *Limnol. Oceanogr.*, **41**, 648–658.
- Hart, R. C. (1998) Copepod equiproportional development: experimental confirmation of its independence of food supply level, and a conceptual model accounting for apparent exceptions. *Hydrobiologia*, **380**, 77–85.
- Lampert, W. and Sommer, U. (1997) *Limnoecology: the Ecology of Lakes and Streams*. Oxford University Press, New York, Oxford, 382p.
- Landry, M. R. (1983) The development of marine calanoid copepods with comments on the isochronal rule. *Limnol. Oceanogr.*, **28**, 614–624.
- Larsson, P. and Dodson, S. (1993) Chemical communication in planktonic animals. *Arch Hydrobiol.*, **129**, 129–155.
- Lass, S. and Spaak, P. (2003) Chemically induced anti-predator defences in plankton: a review. *Hydrobiologia*, **491**, 221–239.
- Lynch, M. (1980) The evolution of cladoceran life histories. *Q. Rev. Biol.*, **55**, 23–42.
- Macháček, J. (1991) Indirect effect of planktivorous fish on the growth and reproduction of *Daphnia galeata*. *Hydrobiologia*, **225**, 193–197.
- Macháček, J. (1993) Comparison of the response of *Daphnia galeata* and *Daphnia obtusa* to fish produced chemical substance. *Limnol. Oceanogr.*, **38**, 1544–1550.
- Maier, G. (1995) Mating frequency and interspecific matings in some freshwater cyclopoid copapods. *Oecologia*, **101**, 245–250.
- Mort, M. A. (1986) *Chaoborus* predation and the function of phenotypic variation in *Daphnia*. *Hydrobiologia*, **133**, 39–44.
- Oliveros, O. B. (1980) Campaña limnológica “*Keratella* I” en el Río Paraná Medio: Aspectos tróficos de peces de ambientes leníticos. *Ecología*, **4**, 115–126.
- Ramcharan, C. W. and Sprules, W. G. (1991) Predator-induced behavioral defense and its ecological consequences for two calanoid copepods. *Oecologia*, **86**, 276–286.
- Reznick, D., Bryant, M. J. and Bashey, F. (2002) r- and K-selection revisited: in the role of population regulation in life-history evolution. *Ecology*, **83**, 1509–1520.
- Riessen, H. P. (1999) Predator-induced life history shifts in *Daphnia*: a synthesis of studies using meta-analysis. *Can. J. Fish Aquat. Sci.*, **56**, 2487–2494.
- Ringuelet, R. A. (1958) Los crustáceos copépodos de las aguas continentales de la República Argentina. *Sin. Sistem.*, **1**, 1–126.
- Rose, R. M., Warne, M. and Lim, R. P. (2001) Factors associated with fish modify life history traits of the cladoceran *Ceriodaphnia cf. dubia*. *J. Plankton Res.*, **23**, 11–17.
- Rossi, L. (1989) Alimentación de larvas de *Salminus maxillosus* Val. 1840 (Pisces, Characidae). *Iheringia Ser. Zool.*, **69**, 49–59.
- Sübor, H. (1992) Predator induced life-history shifts in a freshwater cladoceran. *Oecologia*, **92**, 162–165.
- Stearns, S. C. (1976) Life-history tactics: a review of the ideas. *Q. Rev. Biol.*, **51**, 3–47.



- Stearns, S. C. (1977) The evolution of life history traits: a critique of the theory and a review of the data. *Annu. Rev. Ecol. Syst.*, **8**, 145–171.
- Stearns, S. C. (1992) *The Evolution of Life Histories*. Oxford University Press, Oxford, 249p.
- Stibor, H. and Machacek, J. (1998) The influence of fish-exuded chemical signals on the carbon budget of *Daphnia*. *Limnol. Oceanogr.*, **43**, 997–1000.
- Tollrian, R. (1994) Fish-kairomone induced morphological changes in *Daphnia lumholtzi* (SARS). *Arch. Hydrobiol.*, **130**, 69–75.
- Uye, S. (1988) Temperature-dependent development and growth of *Calanus sinicus* (Copepoda: Calanoida) in the laboratory. *Hydrobiologia*, **167/168**, 285–293.
- Van den Bosch, F. and Gabriel, W. (1994) A model of growth and development in copepods. *Limnol. Oceanogr.*, **39**, 1528–1542.
- Weider, L. J. and Pijanowska, J. (1993) Plasticity of *Daphnia* life histories in response to chemical cues from predators. *Oikos*, **67**, 385–392.
- Yen, J., Sanderson, B., Strickler, J. R. et al. (1991) Feeding currents and energy dissipation by *Euchaeta rimana*, a subtropical copepod. *Limnol. Oceanogr.*, **36**, 362–369.