



Morphological and life-history shifts of the exotic cladoceran *Daphnia exilis* in response to predation risk and food availability

Mauricio J. Carter^{a,*}, Patricia Silva-Flores^{b,c}, J. Pablo Oyanedel^b, Rodrigo Ramos-Jiliberto^d

^a Center for Ecology & Conservation, College of Life & Environmental Sciences, University of Exeter, Campus Cornwall, Penryn TR10 9EZ, United Kingdom

^b Facultad de Ciencias, Universidad de Chile, Las Palmeras, 3425 Ñuñoa, Santiago, Chile

^c Department Biology I, Organismic Biology: Mycology, Ludwig-Maximilians-University München, Menzinger Str. 67, D-80638 München, Germany

^d Centro Nacional del Medio Ambiente, Fundación de la Universidad de Chile, Av. Larraín 9975, La Reina, Santiago, Chile

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ABSTRACT

The zooplankter *Daphnia exilis* was found recently in reservoirs of central Chile. This species has been described as being tolerant to osmotic stress and chemical pollution, although the available information about its ecological properties is limited. Motivated by likelihood of being witnesses to a biological invasion, in this study we contribute to expand the knowledge of this exotic species through evaluating its ability to respond phenotypically to two major ecological factors: predation risk and food availability. Specifically, we analysed shifts in life-history and morphological traits of *D. exilis* in response to fish-released infochemicals, at different food densities. Our results revealed that the organisms were affected in their temporal trajectories of body size and shape, as well as in maturation time and fertility, in response to both predator cues and food availability. The presence of fish kairomones led to a decrease of age at maturity, and an increase of reproduction size and fecundity, especially at lower levels of resources. Our analyses indicated that asymptotic body size was affected only by food level, but the rate of increase in body size was sensitive to both fish kairomones and food level. The relative length of the tail spine decreased during early ontogenetic states, reaching a minimum around the age at maturity. This pattern was significantly enhanced in the presence of fish kairomones. However, our results did not match completely the typical responses of daphnids to fish kairomones.

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Introduction

Recently, a new invertebrate species has been detected inhabiting a set of lakes and ponds associated with the copper mining industry in Chile. The cladoceran *Daphnia exilis* Herrick, 1895 was found in and around the reservoir Huechún (33°4'0"S; 70°47'0"W) in the central zone of Chile (Heine-Fuster et al. 2010). Previous records on the plankton of Chilean brackish and freshwater systems showed the absence of this species (see reviews in Ruiz and Bahamonde 1989; Oyanedel et al. 2008; Marquez-García et al. 2009). This species was limited to south western United States and north eastern Mexico, typically inhabiting ponds affected by pollutants (Hairston et al. 1999) and exhibiting a high tolerance to salinity (Brendonck and De Meester 2003; Heine-Fuster et al. 2010). In this context, the study of the ecology of this species in its new habitat could provide valuable information for assessing its potential

of establishment and the likely consequences on the structure and functioning of host ecosystems.

Native predators able to attack introduced species are typically viewed as a strong component of biotic resistance to invasion (Elton 1958; Levine et al. 2004). In this vein, many species of *Daphnia* are known to change their phenotype in response to environmental cues informing about predation risk by fish (Lass and Spaak 2003). This kind of phenotypic plasticity, when exhibited by exotic species, is known to comprise a strategy that could favour establishment in new environments (Engel and Tollrian 2009). This is especially relevant in aquatic ecosystems, where predation is considered to be a main structuring force of plankton communities (Black and Hairston 1988; Abrams 2000). Plastic predator-driven phenotypic responses of prey (hereafter “defences”) are known to be a suitable strategy for reducing mortality in environments with variable predation risk, provided that the expression of defences involves a fitness cost (Benard 2004). A wide range of phenotypic traits may be involved in a defensive response, including several life history, behavioural, and morphological traits (Agrawal 2001). Costs of shifting the values of defensive traits are often related to reduction of energy intake (Lima 1998) and to energy reallocation to defence development and maintenance (Stibor and Luning 1994; Hanazato

* Corresponding author at: Centre for Ecology & Conservation, University of Exeter, Cornwall Campus, Penryn, Cornwall TR10 9EZ, United Kingdom.
Tel.: +44 0 114 2220117; fax: +44 0 114 2220002.

E-mail address: M.J.Carter-Montecinos@exeter.ac.uk (M.J. Carter).

et al. 2001; Pijanowska et al. 2006; Beckerman et al. 2007). In *Daphnia*, these shifts in energy use may affect fitness components such as growth rate, fertility or age and size at maturity (Boersma et al. 1998; Benard 2004; Dawidowicz and Wielanier 2004). Hence, constraints of predator-induced responses may be determined by food availability (Noonburg and Nisbet 2005; Pauwels et al. 2010; Rabus and Laforsch 2011).

In this study we evaluate the ability of the alien species *D. exilis* to develop plastic responses to cues released by native fish predators. More specifically, we analysed potential predator-induced morphological and life-history shifts under different food availabilities. We found that traits related to patterns of body growth and shape, as well as development and reproduction, exhibited significant plasticity in response to predation risk and food level. Nevertheless, the observed phenotypic responses only partially matched prey responses against visual predators reported in previous studies.

Materials and methods

Study organisms

The experiment was carried out with a clone of *D. exilis* isolated from Ovejería reservoir, a copper tailing located 3 km north of Huechun reservoir and 45 km northwest of Santiago, Chile. This miner dam was completed in 2002, being part of the same watershed (Huechun valley) that Huechun reservoir (García 2007). Predator kairomones was obtained from the fish *Cheirodon interruptus* (Jenyns, 1842), which is a common pelagic fish present throughout freshwater systems in central Chile (Zunino et al. 2009). *C. interruptus* has been characterized as a generalist fish, having to microcrustacean as main item in its diet (Escalante 1987). *Chlorella vulgaris* (10^6 cel mL⁻¹) was used as food resource for *D. exilis*. These species inhabit lakes and ponds of the central zone of Chile (Oyanedel et al. 2008; Heine-Fuster et al. 2010).

Experimental design

The experiments were conducted in a climate chamber at a temperature of 22 °C (± 1.5) and long day photoperiod of 16:8 L:D, white fluorescent light with 400–800 lux at water surface (EPA *Daphnia* Culture Standards). Cladocerans and fish were reared in a medium composed of 1/3 of lake water and 2/3 of aged tap water (Carter et al. 2008). The organisms were obtained as follows. To reduce maternal and grand-maternal effects we used individuals from the third brood of a single mother. Twelve individuals of *D. exilis* were reared individually in 50 mL bakers containing 40 mL of medium. This volume was previously proved to be sufficient for maintain *D. exilis* with high survival and reproduction rates. Just after releasing their second brood, six *Daphnia* were transferred to control medium (K–) and the remaining six were changed to kairomones medium (K+). In this way, the focal generation of *Daphnia* (daughter from the third brood) was exposed to the experimental media during their entire ontogenesis. From the third brood of the six K– mothers, 30 randomly chosen daughters were taken as experimental organisms. The same was made from the six K+ mothers. Thus, 10 *Daphnia* were allocated to each of the six treatments consisting of three levels of food density crossed with two treatments of kairomones. The food levels were 1×10^5 cel mL⁻¹ (High), 5×10^4 cel mL⁻¹ (Medium) and 1×10^4 cel mL⁻¹ (Low). To obtain kairomones, the standard procedure of fish-conditioned medium was used (Dzialowski et al. 2003; Bernot et al. 2006). For simplicity, hereafter the entire mixing of dissolved chemicals released by fish and potential conspecific alarm signals will be called “kairomones”. The kairomones medium was obtained placing two fishes of similar sizes (5.5–6 cm length each) into 3 L of medium (0.67 ind L⁻¹) with 20 individuals of *D. exilis*

as food, for 24 h. Daily, the fish medium was renewed and the obtained fish-conditioned medium was filtered through 0.45 μ m prior to use. This way, we avoided the presence of bacteria, faeces from predator and surviving *Daphnia* in our experimental medium (Declerck and Weber 2003; Slusarczyk and Rygielska 2004).

Response variables

We evaluated morphological and life-history traits as response variables. As morphological traits, we measured total length (from the top of the head to the tip of the tail spine), body length (from the top of the head to the base of the tail spine), and length of the tail spine (from the base to the tip). These measurements were made at every *instar*, from digital images using UTHSCSA IMAGE-TOOL for windows, version 3.0 (Wilcox et al. 2002). For each experimental individual, data of total length and body length versus developmental stage (*instar*) were fitted to the following sigmoid curve by means of least squares non-linear regression:

$$L(i) = \frac{L_{\max} - L_{\min}}{1 + (h/i)^a} + L_{\min},$$

where $L(i)$ = body length at *instar* i , L_{\max} = asymptotic body length (projected length at infinite age), L_{\min} = starting body length, h = *instar* at which half of L_{\max} is reached, and a = shape parameter (abruptness) of the curve (this parameter was not considered for final analyses). This function was chosen because is flexible enough as to fit standard growth curves, which was verified with our data before its use.

To analyse the growth of the tail spine, we considered the ratio of tail spine length to body length, standardized to a zero to one scale. The data of relative tail spine length versus *instar* were fitted to the quadratic function:

$$S(i) = \alpha - \beta i + \gamma i^2,$$

where $S(i)$ is the standardized tail spine/body length ratio at *instar* i . The following biologically relevant parameters were used for analysis: β = (initial) rate of change of S , $I = \beta/2\gamma$ = *instar* at which occurs the minimal S , and $S_{\min} = \alpha - \beta^2/4\gamma$ = minimal value of S .

As life-history traits, we recorded age at first reproduction (AFR), body size at first reproduction (SFR), and number of eggs in the first clutch. Due to that at low food treatment the animals did not lay eggs, only high and medium food treatment were used in the final analyses of life histories traits. Data were analysed by means of two-way randomization ANOVA, using the software RT 2.1 (Manly 1997).

Results

Morphological traits

Independently of predation risk and food availabilities, both total length and body length showed sigmoid growth pattern (Fig. 1). The relative length of spine S followed a parabolic pattern of growing, where S decreased during the juvenile stages and then increased during adulthood (Fig. 1). For each experimental individual, raw data of morphological measures through the ontogeny were fitted to a statistical model in order to compare the value of its parameters (see “Section Materials and methods”). All fits were highly significant ($P < 0.001$, F -test).

For total length, parameter L_{\max} was significantly affected only by food availability (Table 1), exhibiting larger values at higher food levels (Fig. 2A). In addition, parameter h was affected by kairomones, food availability as well as their interaction (Table 1). Parameter h decreased with increasing food, but the effect size vanished with the addition of the kairomones (Fig. 2B).

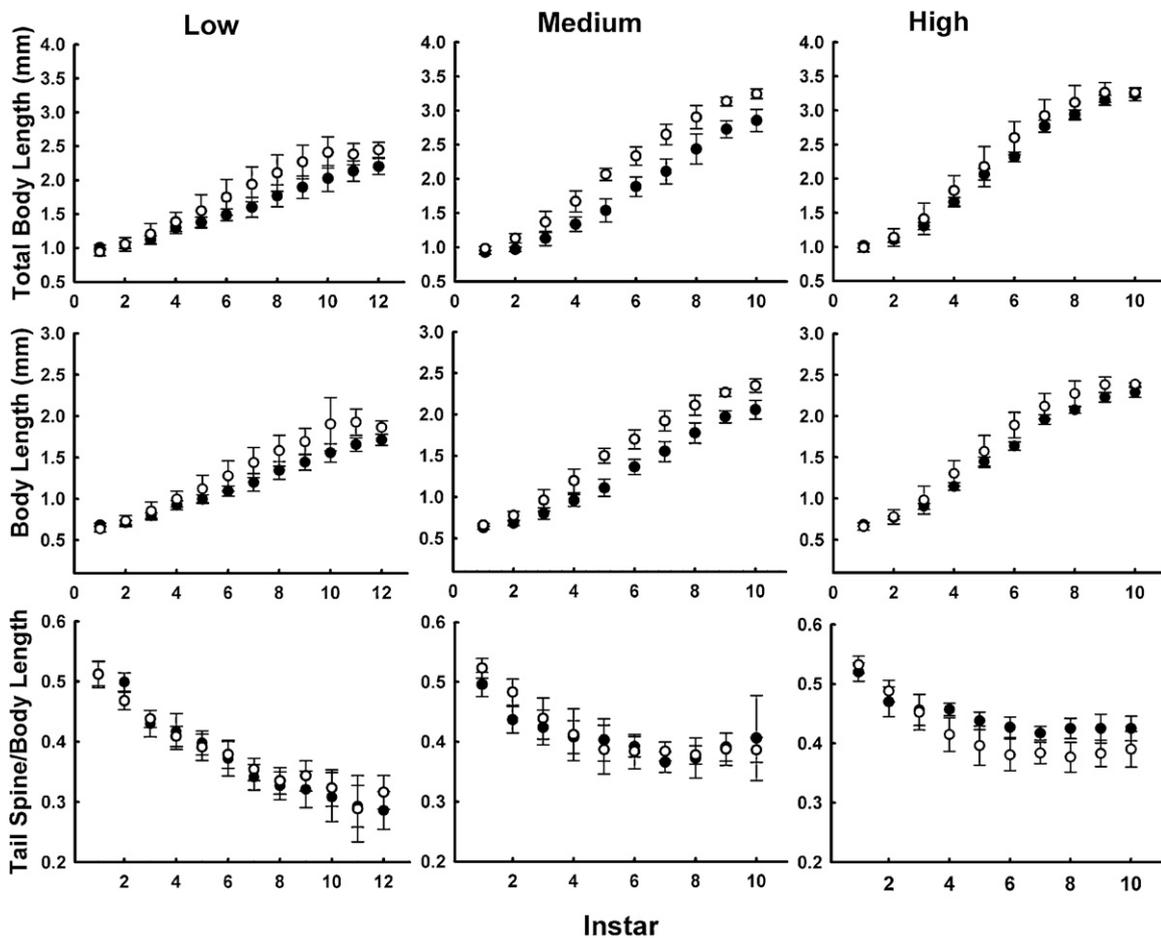


Fig. 1. Growing pattern of total body length, body length (without spine) and relative spine length in *D. exilis*, in presence (open circles) and absence (solid circles) of predator cues at three different food availabilities; 1×10^5 cel \times L⁻¹ (High), 5×10^4 cel \times L⁻¹ (Medium) and 1×10^5 cel \times L⁻¹ (Low).

For body length, parameter L_{max} was not affected by kairomones, food availability, or their interaction (Table 1). Similar to total length, parameter h for body length was affected by the three sources of variation (Fig. 2C and D), kairomones, food availability and their interaction (Table 1).

Regarding the change of the relative length of the tail spine, parameter β was affected by both kairomones level and the interaction between food availability and kairomones (Table 1). Parameter β , which represents the rate of change of tail spine/body length

ratio, increased in the presence of the kairomones but this effect vanished at lower food levels, which explains the significance of the interaction term (Fig. 3A). Parameter i , which represents the stage at which S stops its decreasing phase, was only affected by food treatments (Table 1), where i was delayed at the lowest food level (Fig. 3B). Finally, parameter S_{min} was affected by all sources of variation, kairomones, and their interaction (Table 1). The addition of kairomones exerted an effect on S_{min} that moved from positive to negative as the food level increased (Fig. 3C).

Table 1

Result of the randomization factorial ANOVA testing for the effects of food and kairomones on morphological and life history traits of *Daphnia exilis*. Statistical test were performed with the parameters that describe shape of growth rate of total length, body length and tail spine/body length respectively (see "Section Materials and methods").

	Kairomone	Food	Kairomone \times food
Total length			
L_{max} (mm)	$F_{1,54} = 1.59$	$F_{2,54} = 7.43^{**}$	$F_{2,54} = 2.12$
h (instar)	$F_{1,54} = 4.24^*$	$F_{1,54} = 8.53^{***}$	$F_{2,54} = 3.77^*$
Body length			
L_{max} (mm)	$F_{1,54} = 0.13$	$F_{2,54} = 3.07$	$F_{2,54} = 1.06$
h (instar)	$F_{1,54} = 9.82^{**}$	$F_{2,54} = 24.3^{***}$	$F_{2,54} = 4.14^*$
Tail spine/body length			
β (mm instar ⁻¹)	$F_{1,54} = 13.07^{**}$	$F_{2,54} = 1.05$	$F_{2,54} = 3.11^*$
i (instar)	$F_{1,54} = 2.76$	$F_{2,54} = 21.6^{**}$	$F_{2,54} = 1.29$
S_{min}	$F_{1,54} = 4.61^*$	$F_{2,54} = 37.4^{***}$	$F_{2,54} = 5.74^{***}$
Life history traits			
SFR (mm)	$F_{1,36} = 8.66^*$	$F_{2,36} = 57.2^{***}$	$F_{2,36} = 0.21$
AFR (instar)	$F_{1,36} = 42.19^{***}$	$F_{2,36} = 5.73^*$	$F_{2,36} = 0.12$
Clutch size (counts)	$F_{1,36} = 7.11^*$	$F_{2,36} = 48.1^{***}$	$F_{2,36} = 12.2^{***}$

* $P < 0.05$ indicates statistical significance.

** $P < 0.01$ indicates statistical significance.

*** $P < 0.001$ indicates statistical significance.

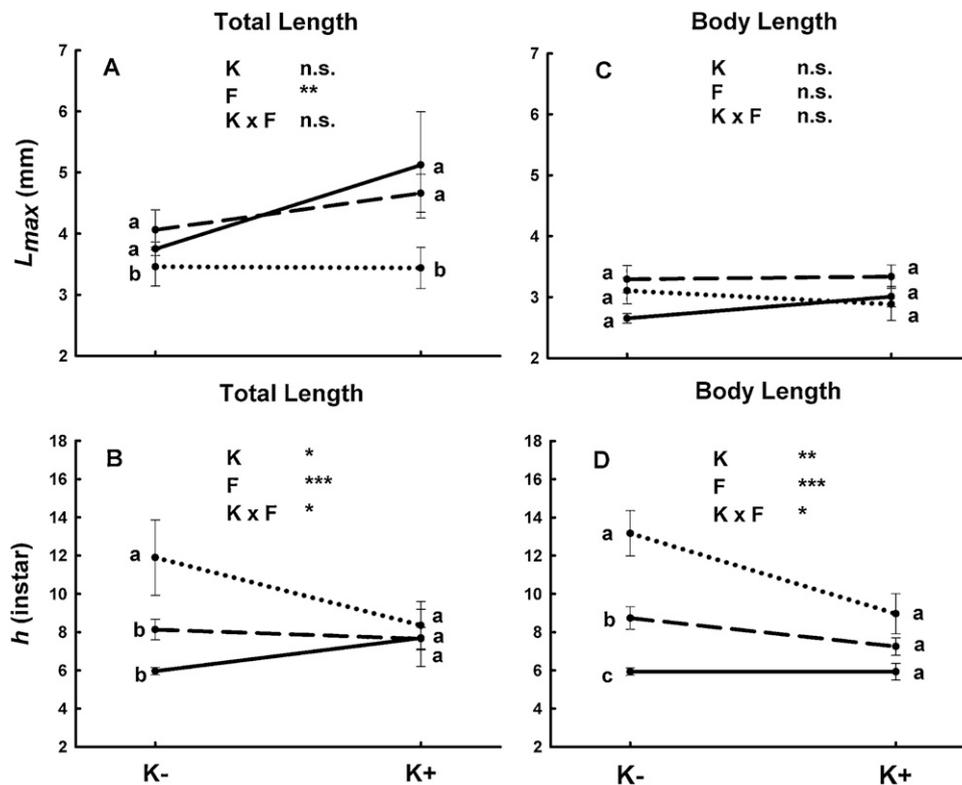


Fig. 2. Means and SE of parameters fitted to growth of total length and body length in *D. exilis*. Food levels are indicated by: High (continuous lines), Medium (dashed lines), and Low (dotted lines). A and C shows asymptotic body length (L_{max}) parameter of the fitted sigmoid curve (see “Section Materials and methods”); C and D shows the *instar* at which half of the maximal length is reached (h). Statistical significance is indicated for kairomone (K), food (F), and interaction between factors (K x F) as: $P < 0.05$ (*), $P < 0.01$ (**), $P < 0.001$ (***). Common alphabetic superscripts indicate no significant difference between means within kairomone treatment but across food experimental levels (Tukey’s test).

Life history traits

Our results indicate additive effects of kairomones and food availability on the size at first reproduction, so that adulthood was reached at higher body sizes when food availability and kairomones levels were higher (Fig. 4A and Table 1). Our results also indicate that the first reproduction of *D. exilis* occurred at an earlier age when the food availability was higher or kairomones were present (Fig. 4B and Table 1). Finally, the three sources of variation exerted a significant effect on clutch size, kairomones, food availability, and their interaction (Table 1). At high food concentration, smaller clutches were laid with the addition of the kairomones, whereas the opposite was obtained at a lower level of food (Fig. 4C).

Discussion

Our results revealed that the phenotype of *D. exilis* responded to both predator cues and food availability. These factors affected temporal trajectories of body size and shape as well as maturation and fertility. In particular, predator kairomones triggered earlier maturation, increased size at first reproduction and promoted higher fecundity at lower levels of resources. These changes partially match the expected responses of daphnids to fish kairomones, where early maturation is correlated with small size at first reproduction, and fitness costs are expected to be found as a result of allocation trade-offs (Tollrian and Harvell 1999; Lass and Spaak 2003; Beckerman et al. 2007). However, current empirical evidence about the form of life-history responses of zooplankton to fish kairomones is not conclusive (Doksaeter and Vijverberg 2001; Weetman and Atkinson 2002; Hulsmann et al. 2004; Gliwicz and

Maszczyk 2007; Pauwels et al. 2010), being apparently species-specific.

Previous experimental results indicate that body size of cladocerans is a critical trait associated with vulnerability to fish predation (Tollrian and Harvell 1999; Laforsch and Tollrian 2004; Iglesias et al. 2011). Fishes are size-selective predators that exhibit preference for prey items of larger sizes. Therefore, under fish risk, daphnids commonly respond by decreasing their adult body size, which allow them to be less visible and less vulnerable to fish predators (Black and Hairston 1988). Also, the experimental evidence has indicated that at low food levels *Daphnia* exhibits a lower body growth rate in presence of fish kairomones, a pattern that is buffered at high food availability (Gliwicz and Maszczyk 2007; Pauwels et al. 2010). Our results showed that the asymptotic body size (L_{max}) of *D. exilis* did not respond to fish kairomones, as it did body growth (h), size and age (*instar*) at which the animals reached maturity as well as the size of their first clutch. This scenario suggests that a possible strategy of *D. exilis* when facing fish is to grow faster during juvenile stages, develop soon and invest in high reproductive effort once mature. Thus, instead maximizing survival, as most previous research found, *Daphnia* could react to fish risk through maximizing reproduction. These fish-induced developmental shifts were more evident at lower food availability, possibly due to that at saturating food level body growth and reproduction cannot be increased further. Nevertheless, vulnerability to fish predation could be increased by a larger size at first reproduction, which can be interpreted as an ecologic cost (community trade-off (Garay-Narvaez and Ramos-Jiliberto 2009)) of the defensive reaction, deviating from the classical prediction of decreased body size as a response to risk of fish predation (Tollrian and Harvell 1999; Lass and Spaak 2003).

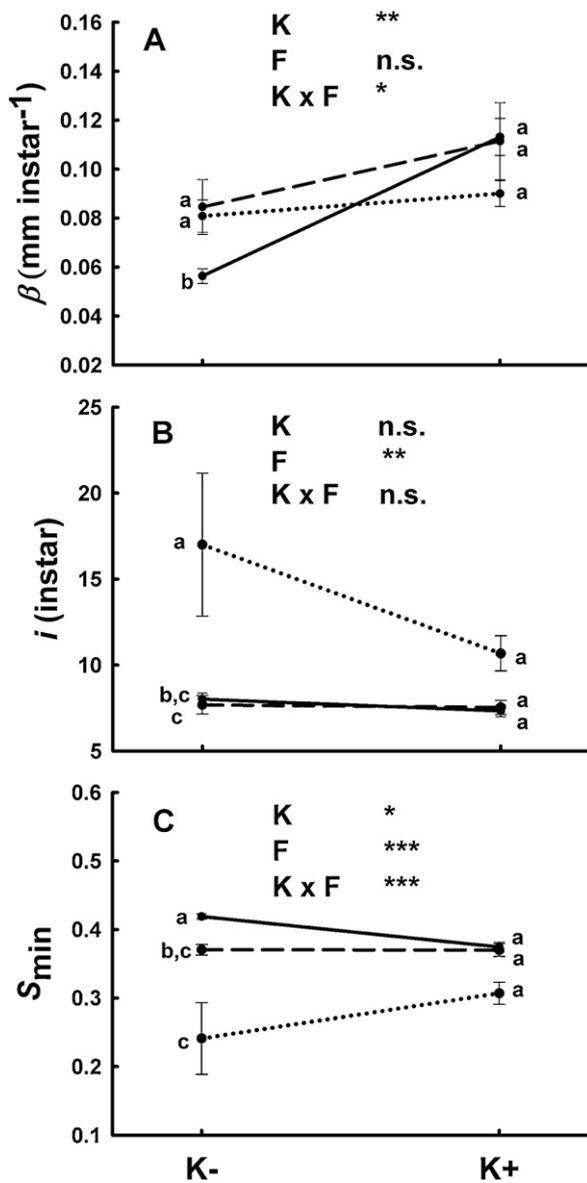


Fig. 3. Means and SE of parameters fitted to temporal changes of the tail spine/body length ratio in *D. exilis*. Food levels are indicated by: High (continuous lines), Medium (dashed lines), and Low (dotted lines). (A) Shows the rate of change of the tail spine/body length ratio (β) in the quadratic function (see “Section Materials and methods”). (B) Shows the instar at which occurs the minimal tail spine/body length ratio (i). (C) Shows the minimal value of tail spine/body length ratio (S_{min}). Statistical significance is indicated for kairomone (K), food (F), and interaction between factors (K \times F) as: $P < 0.05$ (*), $P < 0.01$ (**), $P < 0.001$ (***). Common alphabetic superscripts indicate no significant difference between means within kairomone treatment but across food experimental levels (Tukey's test).

Despite the acceptance that tail spine length represents an evident trait that leads to difficult prey handling by gape-limited predators, it has scarcely been studied. In general its responsiveness when faced with different kinds of predation cues is unknown (Havel and Dodson 1984; Caramujo and Boavida 2000; Carter et al. 2008). Our results indicated that *D. exilis* reduced the relative length of its tail spine during development, until it reached maturity (see Fig. 1, bottom row), a pattern that was modified by exposure to fish infochemicals and food level (Fig. 3B and C). We suggest two alternative explanations to this morphological pattern. First, the tail spine is a constitutive morphological defence in *D. exilis*, and its presence during early developmental states constitutes a defence against invertebrate predators. The presence of

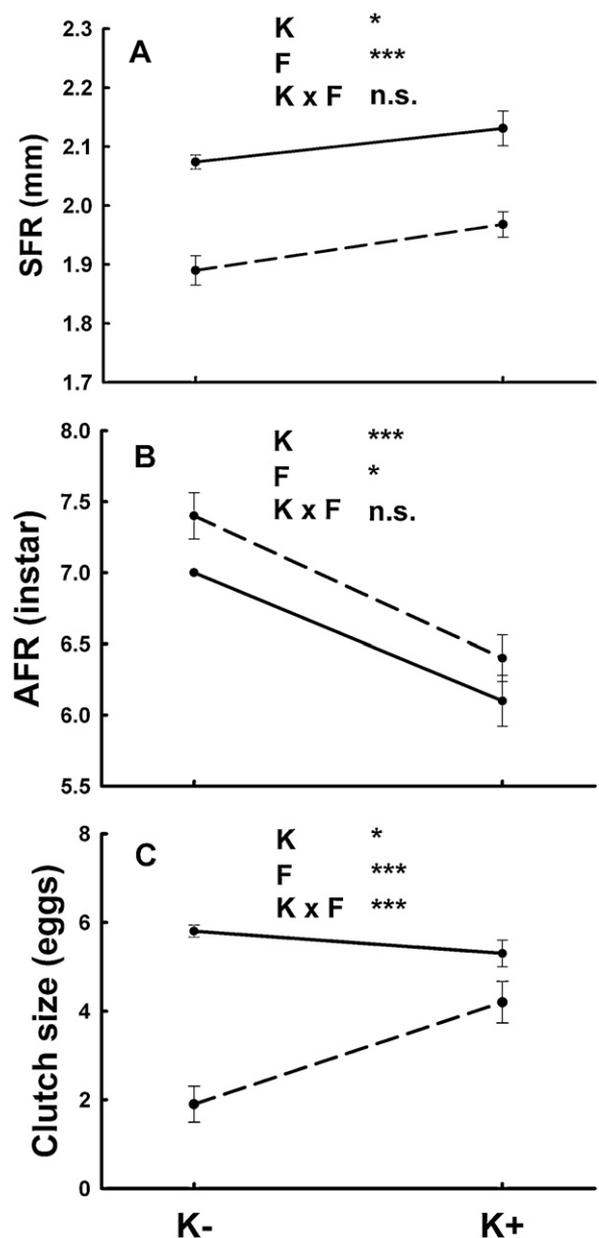


Fig. 4. Means and SE of life history traits evaluated in *D. exilis*. Food levels are indicated by: High (continuous lines), Medium (dashed lines), and Low (dotted lines). (A) Shows the size at first reproduction (SFR). (B) Shows the age at first reproduction (AFR). (C) Shows the clutch size. Statistical significance is indicated for kairomone (K), food (F), and interaction between factors (K \times F) as: $P < 0.05$ (*), $P < 0.01$ (**), $P < 0.001$ (***).

morphological defences in the first instar is typical of daphnids that inhabit environments with invertebrate predators, which exploit small individual prey (Tollrian and Harvell 1999; Dzialowski et al. 2003). However, planktivorous predators in lakes and reservoirs of central Chile are dominated by introduced and native pelagic fish at their firsts developmental states (Zunino et al. 2009). Invertebrate predators able to eat *Daphnia* are not conspicuous in this region, except for water mites of the genus *Piona* (Carter et al. 2008) that have been found in some eutrophic water bodies. Thus, morphological defences observed in *D. exilis* could be an adaptation to native environments where invertebrate predators are important. Our preferred hypothesis nevertheless is that the tail spine is a constitutive structure and its faster decrease in relative length in presence of fish cues is a consequence of energetic allocation to maximizing juvenile growth, development and earlier

reproduction. This explanation is consistent with our findings on life history shifts discussed above. In this vein, a shorter spine length could also lead to an ecological cost of reaction to fish if invertebrate predators inhabited the environment.

We did not find evidences of energetic trade-offs associated to fish induced morphological and life history shifts. Nevertheless, we find some evidence pointing towards the occurrence of ecological costs, which could be crucial for the abundance of the focal species. On the other hand, the fact that increased food level and addition of fish cues drove similar changes in the measured traits, could suggest that fish cues acted as a food supplement that improves fitness. This was reported previously (Pauwels et al. 2010). In practice it is difficult to distinguishing whether the observed traits shifts were a response to perceiving kairomone information or a result of food improvement. Although particulate matter was experimentally removed, dissolved compounds might eventually enhance algal quality and thus improve nutritional condition of daphnids. We found that some morphological and life history responses were affected by kairomone and food in a non-additive way, which suggest that those two factors are not completely interchangeable. Nevertheless, future studies should consider empirical validation of kairomone effects, via using control strains with known responses to kairomones, chemical controls (e.g. added nutrients) or physico-chemical inactivation of the kairomone.

The invasive potential of *D. exilis* has been highlighted previously for Ondaga Lake (Hairston et al. 1999), where this species was reported to invade the system during a temporal pollution window. Coincidentally, *D. exilis* was recently found in a system of reservoirs and ponds associated with the mining industry in Chile, an activity known to exert chemical disruption in freshwaters. Studying sediment record from Onondaga Lake in USA Hairston and co-workers found that *D. exilis* replaced native cladoceran species, during the lake exhibited higher levels of industrial pollution. However, when the pollution going down and the lake began to recover *D. exilis* disappeared from the record (Hairston et al. 1999; Hairston et al. 2005), which probably was a consequence between less competitive abilities and predation vulnerability of *D. exilis* in absence of pollution. Although these evidence from field works suggest the pollution resistance capabilities of *D. exilis*, few experimental work have been developed thereon. For instance, assessment about the toxic effect of chromium pollutant has been tested on *D. exilis* in lab conditions (Martinez-Jeronimo et al. 2008). In this vein, Heine-Fuster et al. (2010) showed *D. exilis* to exhibit a broad tolerance to osmotic stress and to behave as an osmoconformer, which was believed to confer it a comparative advantage over other competing and predator species.

This study helps to expand our knowledge about the ecological properties of this exotic species. Nevertheless, an interclonal comparison is highly desirable to perform in future studies. The confinement of this species to a rather narrow geographical distribution, together with its presumably high invasive potential, makes the present demographic process of *D. exilis* in Chile an interesting model for ecological, biogeographical and evolutionary research.

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