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Immediate and delayed life-history responses of *Daphnia ambigua* to conspecific cues

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Studies of planktonic organisms have shown that various life-history traits, and consequently population growth rate, can be affected by chemical cues released by high densities of conspecifics. In this work we test for potential delays in population responses to conspecific cues in the cladoceran Daphnia ambigua through: (i) evaluating the influence of maternal environment on life-history traits of their daughters, and (ii) identifying the developmental stages that need to be exposed to conspecific cues to observe significant changes in life-history attributes. Our results revealed that exposure to conspecific cues decreased population growth rate of D. ambigua, mainly due to reduced offspring number and delayed maturation. Growth rate reduction was also dependent on the mother's environment, and interaction effects arose between current generation and past-generation environments. The observed variations in maturity and fertility were triggered by exposure to conspecific cues during early development. We hypothesize that conspecific cues are able to induce delayed life-history effects and therefore delayed density dependence at the population level.

INTRODUCTION

Planktonic organisms such as crustaceans, rotifers and microalgae have been shown to develop a variety of phenotypic responses to chemical signals released by other organisms, and particularly by natural enemies such as predators and competitors. The reported responses include changes in behavioral, morphological, as well as life-history traits (Tollrian and Harvell, 1999; Lass and Spaak, 2003).

The understanding of causes and consequences of these individual-level responses to the biotic environment is particularly relevant from an ecological point of view since their effects propagate to the population level via their consequences on population growth, and to the community level by driving trait-mediated indirect effects (Wootton, 1994; Morin, 1999; Dambacher and Ramos-Jiliberto, 2007).

Although the study of chemically mediated phenotypic plasticity in aquatic organisms has received increasing attention during the last two decades (see Tollrian and Harvell, 1999 and references therein), most research has focused on non-lethal effects induced by predators. Examples include colony formation by algae (Hebert and Grewe, 1985; Larsson and Dodson, 1993; Lass and Spaak, 2003; Rhode *et al*., 2004; Verschoor *et al*., 2004; Ceh *et al*., 2005), neck, teeth and helmet development by cladocerans (Dodson, 1989, Jeschke and Tollrian, 2000, Riessen and Young, 2005), and elongation of spines and appendices in rotifers (Gilbert, 1966; Stemberger and Gilbert, 1987). Predators also induce behavioral avoidance responses in their zooplankton prey (Lampert, 1989; Ramos-Jiliberto and Zúñiga, 2001; Ramos-Jiliberto *et al*., 2004), as well as shifts in life-history traits (Burns, 2000; Lürling *et al*.,

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2003; Mikulski *et al*., 2004; Ślusarczyk and Rygielska, 2004). In contrast, less effort has been devoted toward assessing whether or not conspecific competitors can also induce phenotypic responses comparable with those driven by heterospecific enemies. Nonetheless, there is evidence that high densities of conspecifics alter some fitness components in zooplankton, and that chemical cues are able to transmit such effects (Kirk, 1998; Burns, 2000; Lürling *et al*., 2003).

In this work we analyze the consequences of life-history changes, induced by high densities of conspecifics, on the population growth rate of a clone of *Daphnia ambigua*. We test for potential delays in population responses to conspecific cues by means of evaluating the influence of the maternal environment on the offspring's traits, and identifying the developmental stages that need to be exposed to conspecific cues in order to observe relevant changes in their life-histories.

METHODS

Test organisms

The experimental individuals were isolated from a clone of *D. ambigua* collected from Lake El Plateado (33°04′S 71°39′W, Valparaíso, Chile). Several adult daphniids were reared in the laboratory in individual beakers prior to the experiments. From them, we discarded the less healthy ones and then one of the remaining clones was randomly selected for experimentation. Lake El Plateado is a small, warm-monomictic and eutrophic lake with a strong stratification phase during the warm season (Ramos-Jiliberto *et al*., 1997; 2004). *D. ambigua* is the most abundant *Daphnia* species in lakes of central Chile.

Daphniids were individually maintained in beakers with aerated filtered lake water (0.45 μm), hereafter C-medium. Temperature was kept at 20 ± 0.2°C in a water bath, with photoperiod 12:12 L:D. *Daphnia* were fed daily with the green alga *Chlorella vulgaris*, at non-limiting concentration (near 10^6 cells·mL^{-1}). Daphniids used in the experiments came from the third clutch of a single parthenogenetic grandmother.

The experimental medium (D-medium) with conspecific cues was obtained from four stock cultures containing 150 adult *D. ambigua* in 1 L of C-medium. The organisms in these cultures were transferred every 2 days into clean beakers with 1 L of C-medium, and fed daily. Two of the cultures were renewed on even days and two on odd days, in order to maintain chemical homogeneity of the experimental media. Neonates were excluded and dead adults were replaced every 2 days in order to keep the adult density nearly constant. The density of *Daphnia* used in our D-medium falls below maximal field reports (Davies, 1985; Jürgens *et al*., 1994; see also Burns, 2000). Before use, D-medium was filtered (0.45 μm) and aerated for 6 h.

Life-history experiments

Twenty neonates (<12 h old) obtained from a single grandmother reared individually in 60 mL of medium, were transferred individually into 100 mL beakers containing 60 mL of either C-medium (control) or D-medium (treatment) with 10 replicates each. The beakers were kept at 20 ± 0.2°C and pH was controlled throughout the experiment (average pH = 8.1 for both C- and D-medium). Every 24 h all individuals were transferred to fresh medium with fresh food and checked for survival and number of neonates released by each animal.

The experiment concluded when all females released their third brood. We tested for differences in age at first reproduction (AFR) and brood size by means of Kruskal−Wallis ANOVA (analysis of variance) by ranks. From the third brood of one experimental *Daphnia* exposed to D-medium, we took 20 neonates, half of which were exposed back to C-medium (DC treatment) and half in D-medium (DD treatment). For these treatments we recorded life-table data as detailed previously. The intrinsic population growth rate (*r*) was estimated from the Euler−Lotka equation.

Developmental window for responsiveness to cues

In this experiment we recorded AFR and first brood size. The developmental period of *D. ambigua*, from early egg to first reproduction, was split into four development phases (age classes) with duration of 3 days each (Fig. 1).

One hundred neonates were randomly obtained from the third brood of 15 sister mothers (belonging to the third brood of a single grandmother). These 15 mothers were reared in single glasses with 60 mL of C- or D-medium at 18 ± 0.2°C in a water bath with a 12:12 L:D photoperiod and fed daily with *C. vulgaris* (10^6 cells mL^{-1}). Seven mothers were exposed individually to D-medium just after they released their second brood. From the third brood of these mothers we took 40 newborns for the treatments requiring embryonic exposure to D-medium. From the eight mothers kept in C-medium we took 60 newborns for the treatment requiring post-embryonic exposure to D-medium and for the controls CC. The neonates were placed

Treatment	Developmental stages											
	E			J_1			J_2			J_3		
CC												
E	■	■	■									
J_1				■	■	■						
J_2							■	■	■			
J_3										■	■	■
From E to J_1	■	■	■	■	■	■						
From E to J_2	■	■	■	■	■	■	■	■	■			
From J_1 to J_3				■	■	■	■	■	■	■	■	■
From J_2 to J_3							■	■	■	■	■	■
CD	■	■	■	■	■	■	■	■	■	■	■	■

Fig. 1. Experimental design for testing sensitive stages to conspecific cues (see text for further details). Each cell represents an age interval of 1 day. Black cells indicate the developmental phases of *D. ambigua* that were exposed to D-medium. E, egg/embryonic stage; J_1–J_3, first to third juvenile stages, 3 days duration each at 18 ± 0.2°C.

individually into 100 mL beakers containing 50 mL of medium. Each experimental treatment was performed in 10 replicates. In this experiment we exposed the animals to conspecific cues during a given phase of their development, according to the design shown in Fig. 1. In this way we estimated which of the development phases were more sensitive to the exposure to cues. In this experiment two treatments were considered as controls: CC, where *Daphnia* were exposed to C-medium from egg until the end of the experiment; and CD, where *Daphnia* were exposed to D-medium from egg until the end of the experiment. We used a test of multiple comparisons by ranks for detecting significant differences among treatments, after verifying significant differences by Kruskal–Wallis ANOVA.

RESULTS

Life-history experiments

The results summarized in Fig. 2 show that AFR of females exposed to CD, DC and DD treatments was significantly delayed, relative to the control CC. This means that AFR was delayed when either *Daphnia* were exposed to D-medium directly, or when their mothers were exposed to D-medium independent of the current exposure.

Figure 3 reveals that first brood size of females exposed to CD treatment was significantly smaller than under treatments CC and DD. The second brood of *D. ambigua* exposed to the CD treatment was significantly smaller than under treatments CC and DC, whereas the second and third brood size under the DC treatment was also significantly higher than DD.

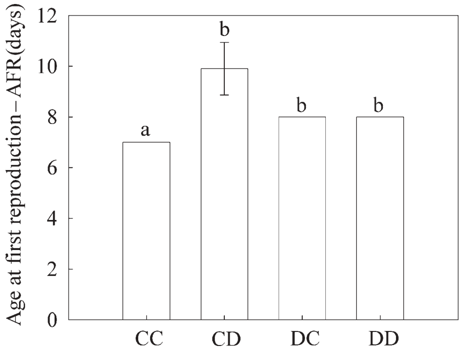

Fig. 2. AFR of: *Daphnia* exposed to C-medium (CC); *Daphnia* from C mothers exposed to D-medium from birth to the end of experiment (CD); *Daphnia* exposed to C-medium, born from mothers exposed to D-medium (DC) and *Daphnia* exposed to D-medium, born from mothers exposed to D-medium (DD). Different letters indicate significant differences among treatments ($P < 0.001$, multiple comparisons by ranks). Error bars show 95% confidence intervals.

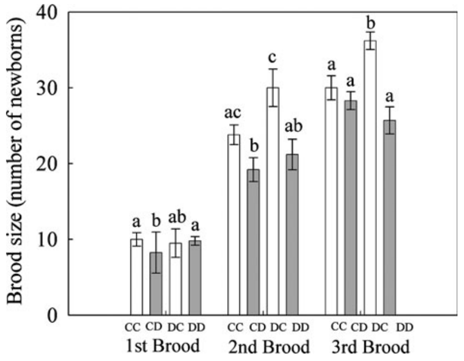

Fig. 3. Brood size for the three first broods of: *Daphnia* exposed to C-medium (CC); *Daphnia* from C mothers exposed to D-medium from birth to the end of the experiment (CD); *Daphnia* exposed to C-medium, born from mothers exposed to D-medium (DC) and *Daphnia* exposed to D-medium, born from mothers exposed to D-medium (DD). Different letters indicate significant differences among treatments ($P < 0.001$, multiple comparisons by ranks) for each brood. Gray bars indicate exposure to D-medium. Error bars show 95% confidence intervals.

Figure 4 shows the intrinsic population growth rate (r) of *D. ambigua* exposed to the different treatments. Both treatment CC and DC, where experimental *Daphnia* were reared in control medium, exhibited a significantly higher r relative to all other treatments ($P < 0.05$). Note that animals under treatment CD exhibited the lowest growth rate, and intermediate values of r were obtained from treatments DD.

Results from two-way ANOVA reveal that experimental environment exert a significant effect on r ($F_{1,36} = 98.78$; $P < 0.001$), but that the mother's environment did not ($F_{1,36} = 2.83$; $P > 0.05$). Nevertheless, there are significant interaction effects between maternal environment and experimental environment ($F_{1,36} = 16.96$; $P < 0.001$), i.e. the effect of direct exposure to cues depends

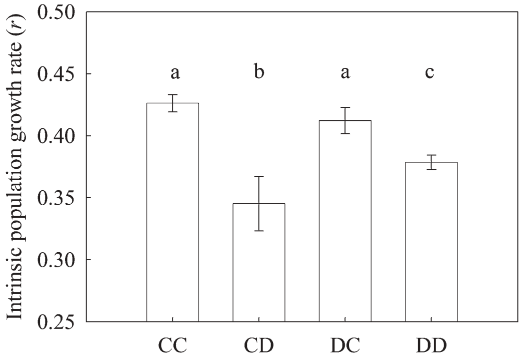

Fig. 4. Intrinsic population growth rate (*r*) of: *Daphnia* exposed to C-medium (CC); *Daphnia* from C mothers exposed to D-medium from birth to the end of experiment (CD); *Daphnia* exposed to C-medium, born from mothers exposed to D-medium (DC) and *Daphnia* exposed to D-medium, born from mothers exposed to D-medium (DD). Different letters indicate significant differences among treatments ($P < 0.05$, Tukey *post-hoc* test). Error bars show 95% confidence intervals.

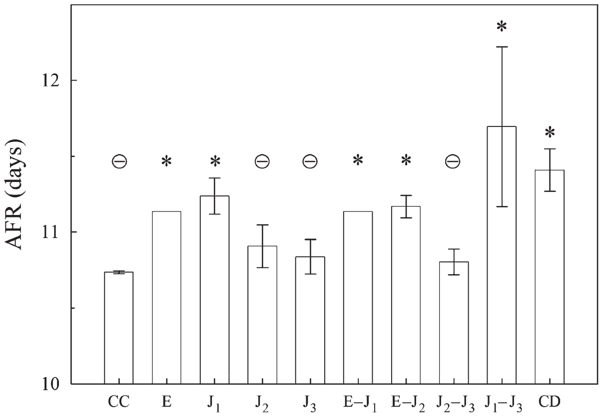

Fig. 5. AFR of *D. ambigua* exposed to conspecific cues during different developmental periods. CC, C-medium during the entire experiment; CD, D-medium during the entire experiment; E, D-medium during egg phase. Other treatments are exposure to D-medium during the corresponding juvenile phases. Asterisks show significant differences ($P < 0.05$, multiple comparison by ranks) relative to CC control, whereas symbol ⊖ shows significant differences relative to CD control. Error bars show 95% confidence intervals.

on the maternal experience (Fig. 4). *Daphnia* directly exposed to D-medium exhibit lower *r* than those exposed to control medium, but this difference is less pronounced if their mothers have been previously exposed to D-medium. Therefore, there was a positive effect of maternal exposure on *r* of the offspring.

Developmental window for responsiveness to cues

The results of this experiment showed that shifts in AFR and first brood size were induced by exposure to conspecific cues only at early development stages (Figs 5 and 6).

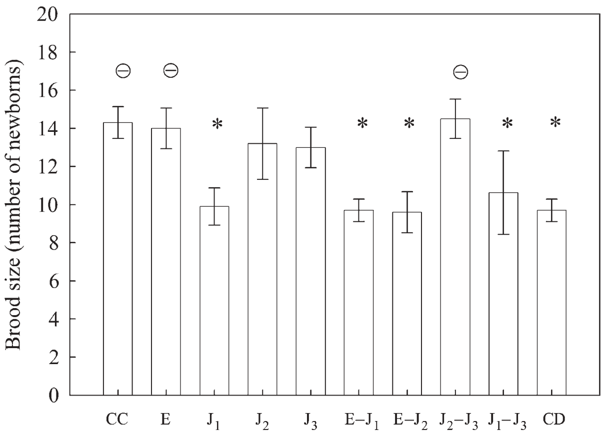

Fig. 6. First brood size of *D. ambigua* exposed to conspecific cues during different developmental periods. CC, C-medium during the entire experiment; CD, D-medium during the entire experiment; E, D-medium during egg phase. Other treatments are exposure to D-medium during the corresponding juvenile phases. Asterisks show significant differences ($P < 0.05$, multiple comparison by ranks) relative to control CC, whereas symbol ⊖ shows significant differences relative to control CD. Error bars show 95% confidence intervals.

Our results showed that AFR of daphniids is significantly higher after induction during E or J_1.

Figure 6 shows that brood size at first reproduction is significantly lower after induction at stages where J_1 is included.

DISCUSSION

Carmona *et al.* (Carmona *et al.*, 1993) found that either high densities of conspecifics or their cues induced mixis in the rotifer *Brachionus plicatilis*. Likewise, Kirk (Kirk 1998) showed that population growth rate of the rotifer *Synchaeta pectinata* decreased with autotoxin concentration, leading to direct density-dependence. Yoshinaga *et al.* (Yoshinaga *et al.*, 1999) observed that under media conditioned with high densities of *Brachionus*, the time to maturity and duration of embryonic development were shorter as compared with fresh medium. Later on, Burns (Burns 2000) demonstrated that soluble substances released by high densities of *Daphnia* decreased the growth rate and reproduction of both conspecific and heterospecific *Daphnia*. More recently, Lürling *et al.* (Lürling *et al.*, 2003) found that conspecific cues induced a delayed age at maturity and a reduced body size at maturity in *Daphnia pulex*, as well as a reduced brood size in both *D. pulex* and *Daphnia cucullata*. Our results reveal that *D. ambigua* exposed to conspecific cues decrease their population growth rate, and that this response is mainly due to reduced offspring number and delayed maturation.

These results are in agreement with those of Cleuvers *et al*. (Cleuvers *et al*., 1997), who reported for *D. magna* a maturation delay of similar magnitude to that which we observed as an effect of high density. Our results also indicated that the contributions of fertility to changes in growth rates were strongly dependent on the specific treatment. Whenever both mothers and daughters lived in either D- or C-medium, fertility was not affected. Conversely, fertility was reduced in *Daphnia* living in D-medium whose mothers lived in C-medium, and increased in *Daphnia* living in C-medium whose mothers lived in D-medium. On the other hand, exposing either mothers or daughters to conspecific cues always delayed maturation.

Furthermore, we observed that life-history shifts were also dependent on maternal environment, since an interaction effect exists between current-generation and past-generation exposure to cues. Maternal exposure to conspecific cues enhances average population growth rates of *Daphnia* that are exposed to high densities of conspecifics, mainly through increased fertility. These results agree with those of Cleuvers *et al*. (Cleuvers *et al*., 1997), although these authors focused on changes in offspring quality.

To our knowledge, maternal effects of conspecific cues on life-history traits have not been reported previously for *Daphnia* or other cladocerans. Nevertheless, conspecific cues via maternal effects have been shown to modify diverse phenotypic traits in other taxa, such as sex ratio in gypsy moth (Myers *et al*., 1998), offspring body size in damselfish (McCormick, 2006), and offspring development in desert locust (Simpson and Miller, 2007).

Our experiments also showed that exposure to conspecific cues during early development drove the observed life-history changes. This is also a new result in the frame of *Daphnia* responses to conspecific cues, although previous work demonstrated that exposure to predator-released cues during early stages is needed for triggering phenotypic responses in cladocerans (Krueger and Dodson, 1981; Hanazato, 1990; Machácek, 1995; Mikulski *et al*., 2005) and other taxa (Hoverman and Relyea, 2007). Nevertheless, the specific stage that is more sensitive to chemical cues differs among the study systems and traits measured. Embryonic exposure, for example, was not considered by Mikulski *et al*. (Mikulski *et al*., 2005) and gave negative results in the work of Hanazato (Hanazato, 1990), which suggests that the responses to crowding could be clone specific. In this work we observed that delayed AFR can be induced by exposure to conspecific cues during stages E and J_1 only. Therefore, embryonic induction could explain the delayed AFR on both DC and DD treatments shown in Fig. 2. On the other hand, juvenile (J_1) but not embryonic exposure to conspecific cues explained the significant reduction observed in first brood size. Since embryonic and juvenile exposure to conspecific cues triggered life-history changes in mature individuals of *D. ambigua*, particularly delayed AFR and decreased first brood size, our study organisms are able to present the kind of delayed responses called ‘cohort effects’ (Lindström and Kokko, 2002). Of course, we cannot rule out that other traits could be induced to change during later phases in the life cycle.

This work did not evaluate interclonal variability of the reported responses of *D. ambigua* to conspecific cues. Although this goal goes beyond the scope of the present work, it constitutes a limitation that should be considered for future work. We expect to find quantitative differences in life-history traits among clones (Boersma *et al*., 1999), but more interesting should be to clarify whether or not the qualitative trends reported here are consistent among populations.

Our results support the conclusion that high densities of conspecifics promote life-history variation within as well as between generations, and that the phenotypic changes are induced at early developmental phases by chemical cues. Therefore, conspecific cues are able to induce delayed life-history effects through both maternal and cohort effects. As a consequence, life-history shifts in *D. ambigua* associated with conspecific cues have the potential to promote delayed negative feedback at the population level, which in theory could exert strong effects on the dynamics and stability of populations (Ginzburg and Taneyhill, 1994; Beckerman *et al*., 2002; Lindström and Kokko, 2002). Future work should clarify whether the life-history plasticity and transgenerational effects reported here constitute true adaptive responses or simple inhibitory effects. Likewise, studies of zooplankton ecology should consider the potential effect of these sources of density dependence on population and community dynamics of aquatic systems.

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