Demographic costs of Chaoborus-induced defences in Daphnia pulex: a sensitivity analysis

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Summary. We examined the demographic costs of Chaoborus-induced defensive spine structures in Daphnia pulex. Our aim was to assess the role of resource limitation and the interaction effects of limiting food level and antipredator structures on fitness of D. pulex and to pinpoint those life stages that are most sensitive to changes in the defence regime. Chaoborus-induced and typical morphotypes of D. pulex were reared at high and low food concentrations. Instar-based matrix population models were used to quantify the effects of predator-induction, food and their interaction on fitness of D. pulex. Predator-induction caused a statistically significant reduction in fitness at low food levels, but not at high food levels. Sensitivity analyses revealed that the fitness effects were primarily due to changes in the growth rate in instars 1–5, and secondarily to small reductions in the fertility of instars 5–10. The interaction between Chaoborus exposure and low food concentration was negative, and mediated through growth and fertility components. Both these components were reduced more in the Chaoborus-exposed, low food treatment than would be expected in the absence of interaction.

Key words: Predator-prey interaction – Inducible defence – Population growth – Daphnia pulex – Chaoborus

Inducible defences that are triggered by cues from, or direct contact with a consumer, occur commonly in clonal invertebrates as well as in plants (reviewed by Havel 1987; Adler and Harvell 1990; Harvell 1990). In many organisms studied, inducible defences have been shown to be efficient in preventing predation (e.g. Gilbert and Stemberger 1984; Harvell 1984, 1986; Havel and Dodson 1984; Lively 1986; Schultz 1988). It has been suggested that inducible defences cost less than permanent defences (Coley et al. 1985; Gulmon and Mooney 1986; Harvell 1986; Havel and Dodson 1987; Simms and Rauscher 1987; Stemberger 1988; Black and Dodson 1990; Riessen and Sprules 1990). However, most known antipredator structural defences entail a cost (reviewed by Harvell 1990). The benefits of predator-induced defences are evident in unpredictable environments: a potential prey can respond fast to cues emitted by predators.

The consequences of metabolic or energetic costs for selection depend on their effects on individual life history parameters and thus on fitness. Experimental comparison of predator-induced and typical morphotypes of a species may reveal costs measured in terms of individual fitness. In animals, where induction in some cases can be triggered by chemical cues without actually damaging the target, measuring the possible costs of defence may be easier than in plants.

The invertebrate dipteran predator Chaoborus induces the formation of a neck spine in the embryo and first instar of Daphnia pulex (Cladocera) (Krueger and Dodson 1981; Vuorinen et al. 1989; Parejko and Dodson 1990). In addition to Chaoborus larvae, Notonecta and small sunfish have also been reported to trigger responses in different Daphnia species (Dodson 1989). Some D. pulex clones characteristically carry a spine always in the first instar, but not any further in the absence of Chaoborus-factor (Walls and Ketola 1989).

Induced neck spines in D. pulex have been shown to serve a defensive function (Havel and Dodson 1984). A few recent studies have shown that spine production in D. pulex carries a cost evident in the delayed timing of first reproduction (Walls and Ketola 1989; Black and Dodson 1990; Riessen and Sprules 1990) and in lower population growth rate (Havel and Dodson 1987; Black and Dodson 1990; Riessen and Sprules 1990). However, the relative impact of survival, growth, and fertility components on the overall effect of antipredator responses on prey population growth has not been studied intensively.

Our results go beyond recent studies (Walls and Ketola 1989; Black and Dodson 1990; Riessen and Sprules 1990) in several ways. We used instar-classified
rather than traditional age-classified demographic models, which allows us to measure effects on the more biologically meaningful parameters of instar-specific survival, growth, and reproduction. By manipulating food level as well as predator exposure, we can quantify the interaction of the costs of inducible defences with physiological stress. We predicted that the cost of induction would be greater under low food conditions (see also Black and Dodson 1990). Finally, by combining our demographic models with sensitivity analysis, we are able to determine the portions of the life cycle which contribute the most to the fitness costs of induction.

Methods

Experimental design

Animals used in the experiment were first instar female offspring from either the second or third clutch laid under experimental conditions by parthenogenetically reproducing *Daphnia pulex* Leydig females. These parent females belonged to a clone collected from a small pond in Turku, SW Finland (60° 27' N 22° 15' E), in 1985. *Chaoborus crystallinus* De Geer larvae were collected from a pond in Turola, SW Finland, during the winter 1987. We used *Daphnia magna* Straus, which is not inducible by the *Chaoborus* factor (but see Ketola and Vuorinen 1989), to control for the possible negative overall water quality changes due to the presence of *Chaoborus* larvae in the culture water. The *D. magna* clone was obtained from a pond in Turku in 1985. All stocks were maintained in the laboratory at 12 °C and were fed regularly.

We maintained the food alga *Scenedesmus* sp. in a log phase by culturing it in aerated liquid medium (Waris 1953) in three flasks under 16L:8D light cycle at room temperature. Each flask was harvested on two consecutive days: algae in a flask were sieved (40 μm mesh) after the second harvest and new culture medium (approximately 300 ml) was added to replace the harvested volume.

The experiment with *Daphnia pulex* was a 2 × 2 factorial design where the factors were the quality of culture water (sieved lake water or sieved, *Chaoborus*-treated water) and the food concentration (100,000 or 15,000 cells ml⁻¹). *D. magna* were reared only in the higher (100,000 cells ml⁻¹) food concentration both in sieved and *Chaoborus*-treated water because the lower food concentration selected for *D. pulex* would not have sustained growth and reproduction of *D. magna*.

We reared *D. pulex* and *D. magna* experimental animals solitarily in 20 ml polystyrene jars. The basic culture medium was sieved (25 μm Nylon mesh), aerated lake water supplemented with cultured *Scenedesmus* sp. alga. *Chaoborus* spp. do not occur in Lake Littoistenjärvi, Turku, where the water used in the experiment was taken. The culture medium was changed daily by transferring the animals with a pipette to a new jar provided with fresh culture medium.

*Chaoborus*-treated water was prepared by keeping three 4th instar *Chaoborus crystallinus* larvae in sieved lake water in a 1/3 litre jar (*Chaoborus* density 9 larvae litre⁻¹). Water taken from the *Chaoborus* jar was replaced by an equal volume of sieved lake water daily. The turnover time of *Chaoborus*-treated water was 1.5 days. We fed each *Chaoborus*-larva with approximately five newborn *D. pulex* every day. When some of the *Chaoborus*-larvae pupated during the experiment, we immediately replaced them by new 4th instar larvae. The experiment was run at a constant 20 °C from March to May, 1987.

Basic life table data were collected from cohorts of 12 individual *D. pulex* in each treatment combination and 8 individual *D. magna* in each of the two high food level treatments. One *D. pulex* individual was accidentally killed in the sieved lake water, high food level and one in *Chaoborus*-exposed water, low food level treatment, and were excluded from analysis. Each individual was examined daily, while being transferred to a new jar. Neck spines were counted, carapace length was measured as the longest distance along a straight line between the ventral base of the tail spine and the anterior edge of the shed carapace (40X and 100X magnification), and the offspring laid in each clutch were counted.

Demographic methods

Population projection matrices. In order to examine the demographic effects of the treatments, we used an instar-classified matrix population model. The population projection matrix A contains instar-specific fertility (Fᵢ) in the first row. On the main diagonal the probabilities (Pᵢ) of surviving and remaining in the same instar, and on the subdiagonal appear the probabilities (Gᵢ) of surviving and growing to the next instar. This is the "standard size-classified model" of Caswell (1988, 1989b). The projection interval was one day.

The coefficients Pᵢ and Gᵢ include both growth and survival; a simple parameterization (Caswell 1982) is to write Gᵢ = αᵢγᵢ and Pᵢ = αᵢ(1 - γᵢ), where αᵢ is the instar-specific survival probability and γᵢ is the instar-specific growth probability.

The parameters Pᵢ, αᵢ, and γᵢ are estimated from the life table data. The growth probability γᵢ is estimated as Tᵢ⁻¹, where Tᵢ is the mean duration of instar i. Tᵢ was estimated as the average duration of instar i among all animals that survived to instar i + 1. This estimate is slightly biased because it excludes the stage durations of the animals that die during the instar, and longer stage durations are disproportionately represented among these animals. The bias in this case is negligible because mortality rates are very low and instar durations short. The stage-specific mortality rate μᵢ is estimated by dividing the number of deaths occurring in instar i by the number of individual-days of exposure, given by the sum of the stage durations for all animals that survive to instar i + 1. (This estimate of exposure is also slightly biased because it ignores the partial exposure of animals that died during the instar.) The survival probability σᵢ = 1 - μᵢ. The stage-specific fertility rate Fᵢ is estimated by the total number of offspring produced during instar i, divided by the exposure.

The dominant eigenvalue λ of the projection matrix A gives the projected population growth rate (i.e. fitness; Charlesworth 1980; Lande 1982); the corresponding continuous time rate is r = ln λ. The corresponding right and left eigenvectors v and w give the stage distribution and reproductive value distribution, respectively. The sensitivity of λ to changes in the entries of A is δλ/δαᵢ = νᵢwᵢ, where the eigenvectors are assumed to be scaled so that the scalar product of v and w equals 1. The sensitivities of λ to changes in σᵢ and γᵢ are δλ/δσᵢ = γᵢνᵢwᵢ + (1 - γᵢ)νᵢwᵢ and δλ/δγᵢ = wᵢ(1 - νᵢ). See Caswell (1989b) for further details.

Statistical analysis. We used a jackknife resampling method (Meyer et al. 1986) to calculate confidence intervals around r for each treatment. These confidence intervals permit approximate tests of the significance of treatment effects on r, but a more rigorous approach is provided by randomization tests (Edgington 1987; Noreen 1989) while requiring no parametric assumptions.

To test the effect of *Chaoborus* exposure at low food levels, we note that the data consist of 11 or 12 individuals in each of two treatments, each individual characterized by its reproductive and survival history. Under the null hypothesis of no treatment effect, the measurements on each individual are independent of the treatment to which it was assigned. By randomly assigning individuals, with their measurements, to treatments, we generate a distribution of treatment effects on r. The probability of obtaining as large an effect as observed, given the null hypothesis, is simply the proportion of all permutations giving as large or larger an effect. Because of the large number of possible permutations, we used a random sampling procedure to estimate the significance level. For more details, see Caswell (in preparation).