

Demographic response of *Stratiodrilus aeglaphilus* (Anelida, Histiobdellidae) to organic enrichment: experimental assessment

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Abstract Demographic responses of a commensal annelid of freshwater crayfish, *Stratiodrilus aeglaphilus*, to a sublethal organic enrichment were tested. Censuses of the *S. aeglaphilus* population were performed every 3 days during a 27 days period. The demographic variables were estimated using a quadratic programming method. Population growth rate (λ) was 1.0230 in the control, and 0.9145 in the organic enrichment treatment, it was indicating positive growing and decrease, respectively. Decomposition analysis showed an antagonistic response of the demographic parameters to organic enrichment, with negative contributions from eggs and juveniles stasis and growing probabilities, and positive contributions from adults survival and fecundity. After the organic enrichment, the positive effect on adults could not compensate the adverse effect on the early stages, thus causing a reduction of the population density of *S. aeglaphilus*.

Keywords Epibiont · Eutrophication · Matrix populations · Quadratic programming · Decomposition analysis

Introduction

Environmental disturbances from natural and anthropogenic origins have diverse ecological effects at all levels of biological organization (Suter, 1993). In freshwater ecosystems population changes are mainly related to flow oscillations and eutrophication, due to agriculture practices and non-treated urban sewage (Haslam, 1995; Gasith & Resh, 1999). Such changes modify growth, reproduction and survival, thus influencing the population growth rate (λ) and, consequently, its abundance (Haslam, 1995; Mariapan et al., 1997). Nevertheless, the anthropogenic disturbances may affect the demographic parameters (i.e. fecundity, growth and survival) differentially. These effects, often subtle, cannot be evaluated solely assessing λ requiring more sophisticated approaches (Caswell, 2001).

Aegla laevis (Latreille, 1818) is an endemic decapod crustacean inhabiting well-oxygenated gravel bottom streams and rivers from Central Chile (Bahamonde et al., 1998), which may reach densities up to 250 ind m⁻² in the Maipo basin (33°46' S 70°54' W) (Bahamonde & López, 1961). However, the abundance of this species has recently diminished, presumably as a consequence of water quality

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deterioration due to organic enrichment (Bahamonde et al., 1998). Current repeated searches have not shown specimens in the main course of river Maipo, which suggest a possible local extinction. However, small populations are still found on stream affluents.

Aegla laevis hosts a complex epibiont community of protozoans, platyhelminthes and polychaetes. *Stratiodrilus aeglaphilus* Vila & Bahamonde, 1985 is a polychaete that inhabits the exterior carapace of *A. laevis* and completely develops its life cycle on its host (Steiner & Amaral, 1999), the genus *Stratiodrilus* is known as commensal of freshwater crayfish from Australia, Tasmania, Madagascar and South and Central America (Martin & Britayev, 1998). Each female of *S. aeglaphilus* deposit up to eight eggs in the branchial chamber of the host; inside the eggs, a cryptolarvae is developed; after 7 days, a juvenile emerges and moves to the branchial chamber. Finally, after 9 days, the adults move to the carapace, completing the life cycle in 16 days (Vila, 1962; Moyano et al., 1993).

In this study, we experimentally tested the effects of organic enrichment on the demography of *Stratiodrilus aeglaphilus*. The possible existence of such a relationship, together with its sense, may help to explain its local extinction in Maipo River, clarifying whether this process has been a consequence of the absence of hosts or of a *S. aeglaphilus* faster population negative response.

Materials and methods

Similar sized individuals of *Aegla laevis* (12.58 ± 0.49 mm; $\bar{x} \pm 2SE$), were selected from Aguas Claras stream ($33^{\circ}44' 27.4''$ S $70^{\circ}53' 59.7''$ W), a small spring affluent of Maipo river, 1 Km before the confluence with the main river. The selected specimens were kept at 15 ± 2 °C under darkness during 1 week, in an aquarium with 20 l of micro filtrated water (0.7- μ m filter) from the original stream.

To ensure the initial homogeneity, the populations of *Stratiodrilus aeglaphilus* present on 20 individuals of *Aegla laevis* were censused to analyze the abundance and frequency distribution of life cycle stages. After checking the initial conditions, 120 individuals of *A. laevis* were randomly assigned to two 40 l aquaria and maintained at similar conditions during an

acclimatization period of 1 week. The control aquarium was filled with 20 l of micro filtrated water from the Aguas Claras stream. The treatment aquarium was filled with 10 l of water from Aguas Claras stream and 10 l of eutrophic water from Maipo river, reaching comparable conditions to the '70s, when *A. laevis* was still present in this river (Bahamonde et al., 1998).

The physical and chemical variables of water were monitored according to standard methods (APHA, 1998).

Censuses of *Stratiodrilus aeglaphilus* population were performed every 3 days during a period of 27 days. For every census, four *A. laevis* from each aquarium were randomly collected and the total number of eggs, juveniles and adults of *S. aeglaphilus* were recorded, complementarily health of individuals was evaluated by the presence of abnormalities, such as colour, shape and size. The life cycle stages frequency distribution was ordered as matrix vector with the stages abundance in it, the procedure was performed for each census. In order to evaluate the effect of the organic enrichment on per-stage abundance, we performed a one-way repeated-measure ANOVA (Zar, 1996). The data sets satisfied the ANOVA assumptions of normality (Kolmogorov–Smirnov test) and homogeneity of variances (Levene test). All statistical analyses used Statistica 6.0 (StatSoft, Tulsa, USA).

Additionally, a projection matrix was estimated from the functional stages distribution vectors, for both control and treatment populations. Matrixes were estimated using quadratic programming method (Wood, 1994, 1997), constrained to the life cycle of this species (Fig. 1). This appears an adequate procedure to obtain demographic parameters, especially in species with complex life-cycles or cryptic stages, for which it is difficult to obtain these parameters using life tables. For each matrix, λ was calculated as the dominant eigenvalue, and confidence intervals were estimated using bootstrap method (Levin et al., 1996; Hansen et al., 1999). Accordingly, resampling was performed on four replicates of averaged census (same number as in the experiment). To obtain a temporal series of pseudo-vectors, this was used to estimate a projection matrix with the quadratic programming method. This procedure was repeated 10,000 times. For each matrix, λ was recorded; and the 95% confidence

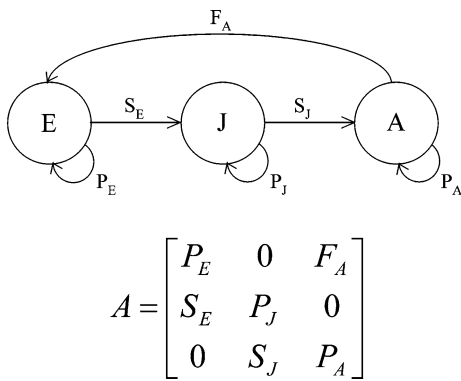


Fig. 1 *Stratiodrilus aeglaphilus* stage-classified life cycle. Top, graphic representation: E, eggs; J, Juveniles and A, adults. Bottom, demographic matrix based on this three life stage cycle: P_E eggs stasis probability, S_E growth probability from eggs to juvenile, P_J Juvenile stasis probability, S_J growth probability from juvenile to adult, P_A adults stasis probability and F_A adults fecundity

interval was obtained by the percentile method (Zar, 1996).

The demographic variables most contributing to changes in λ were evaluated by retrospective analysis using a life table response experiment (Caswell, 2001):

$$\lambda^{(k)} \approx \lambda^{(c)} + \sum_{ij} (a_{ij}^{(k)} - a_{ij}^{(c)}) \frac{\partial \lambda}{\partial a_{ij}} \Big|_{(A^{(k)}+A^{(c)})/2}$$

where $\lambda^{(k)}$ and $\lambda^{(c)}$ are the values of λ for treatment and control, respectively. Each term in the sum, is the contribution of the difference in the element a_{ij} to the overall effect of treatment on λ weighted by the sensibility of a mean matrix estimated from the experimental and control matrix (Levin et al., 1996).

Results

Initial conditions

Control and treatment aquaria presented similar temperature and dissolved oxygen values (Table 1). Nutrients showed notable differences, being higher in the treatment than control: total nitrogen was 2-fold higher, total phosphorous was almost 10-fold higher, turbidity was 13-fold higher in the treatment aquarium and pH diminished in nearly one unit (Table 1). These four variables are commonly related with organic enrichment (Lampert & Sommer, 1997).

Table 1 Physical and chemical variables values in control (stream Aguas Claras) and treatment (Mix 10:10, river Maipo: Aguas Claras)

	Control	Treatment
Oxygen	8.52 mg l ⁻¹	8.23 mg l ⁻¹
N (total)	204.00 mg l ⁻¹	432.00 mg l ⁻¹
P (total)	15.4 mg l ⁻¹	144.25 mg l ⁻¹
Turbidity	2.9 NTU	38.0 NTU
Temperature	15.4°C	15.3°C
pH	8.0	7.1

Population of *Stratiodrilus aeglaphilus* in each host showed no differences at the beginning of the experiment in abundance (ANOVA, $F_{19,38} = 1.17$, $P = 0.39$) nor in stage structure (Kolmogorov–Smirnov, $D = 0.33$ $P > 0.05$).

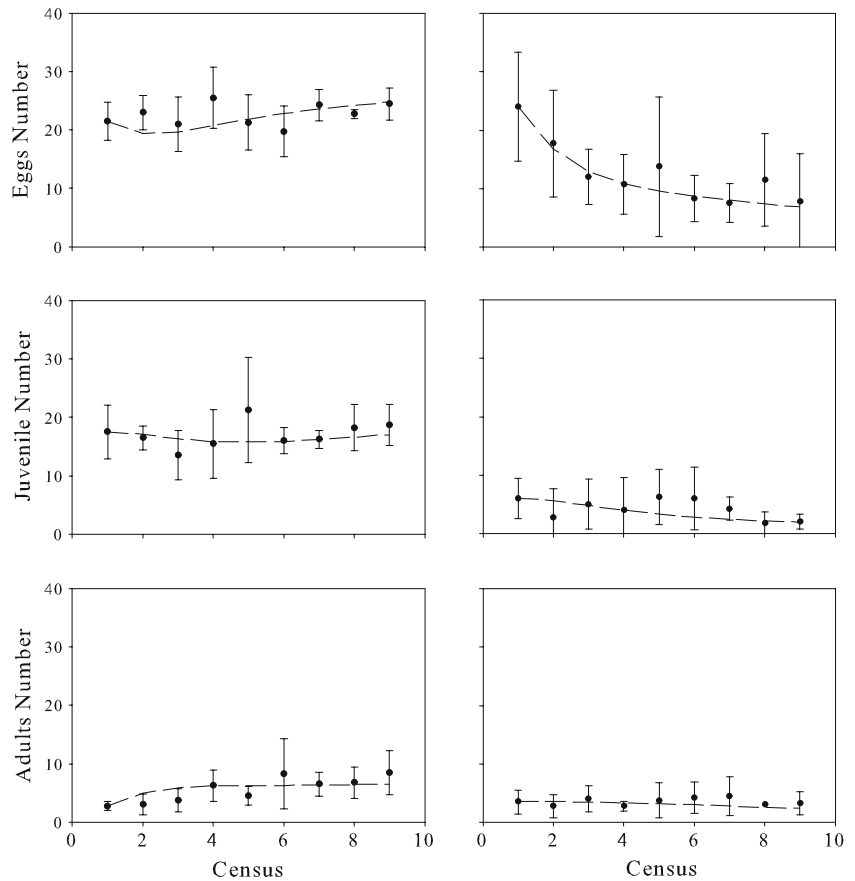
Demographic analysis

The organic enrichment decreased significantly the density of the three *Stratiodrilus aeglaphilus* life stages along the experimental period, particularly eggs and adults decreased significantly throughout time (Table 2; Fig. 2a, b). No abnormalities were found on *S. aeglaphilus* eggs, juveniles or adults

Table 2 Summary of repeated-measures ANOVA between control and organic enrichment treatment in three stages of life of *S. aeglaphilus*

Stage	Factor	Source variation	DF	F	P
Eggs	Between	Treatment	1	157.71	<<0.001
		Error	6		
	Within	Time	8	3.71	0.002
		Time* <i>Treatment</i>	8	5.21	<<0.001
		Error	48		
Juvenile	Between	Treatment	1	366.32	<<0.001
		Error	6		
	Within	Time	8	2.082	0.056
		Time* <i>Treatment</i>	8	2.207	0.043
		Error	48		
Adults	Between	Treatment	1	26.92	0.002
		Error	6		
	Within	Time	8	3.81	0.002
		Time* <i>Treatment</i>	8	3.08	0.007
		Error	48		

Fig. 2 Densities for the three stages of *Stratiodrillus aeglaphilus*. Comparison of observed (points) and predicted (dashed lines), predictions are based on demographic parameters estimated by quadratic programming. The observed values are means over four replicates; the error bars are two times the standard error of those mean. Left control and right organic enrichment treatment



under experimental treatment with organic matter and control treatment.

The control populations showed a high stasis probability for eggs and juveniles, and also a higher probability for growing from egg to juvenile and juvenile to adult than treatment aquaria (Table 3). The treatment populations showed a higher stasis probability at the adult stage with a higher fecundity than the control. The demographic parameters projected curves explained very well the dynamics of the three stages, both in experimental and control populations, remaining within the 95% confidence interval estimated from data (Fig. 2).

The value of λ , was higher in the control than in the treatment ($\lambda = 1.0230$; Confidence 95%: 0.9935–1.0852), indicating an increasing population growth. On the contrary, in treatment, λ was less than one ($\lambda = 0.9145$; Confidence 95%: 0.8209–0.9864) indicating a population decrease (Table 3).

The overall negative effect of organic enrichment on λ , was a consequence of negative contributions of

Table 3 Demographic parameters estimated using quadratic programming, for control and organic enrichment treatment. (P_E) eggs stasis probability, (S_E) growth probability from eggs to juvenile, (P_J) juvenile stasis probability, (S_J) growth probability from juvenile to adult, (P_A) adults stasis probability and (F_A) adults fecundity. Values in parenthesis represent two times the standard error of mean

	Treatment	Control
P_E	0.5346 (0.1870)	0.7867 (0.1357)
P_J	0.6078 (0.1841)	0.7141 (0.1801)
P_A	0.8444 (0.1416)	0.4885 (0.5115)
S_E	0.0814 (0.1749)	0.2133 (0.1861)
S_J	0.0888 (0.3707)	0.2038 (0.0923)
F_A	1.1312 (1.0879)	0.8973 (0.7802)
λ	0.9145 (0.0719)	1.0230 (0.0622)

eggs and juveniles stasis and growing probabilities to λ , but also of the positive contributions of adult survival and fecundity to λ (Fig. 3).

It is important to note that all *Stratiodrillus aeglaphilus* hosts (*Aegla laevis*) remained healthy

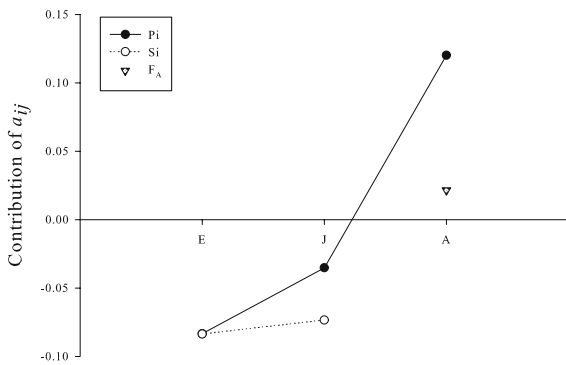


Fig. 3 Contributions of the effects of organic enrichment on λ *S. aeglaphilus*, (Si) stasis probability, (Pi) growth probability and (F_A) adults fecundity

and no mortality was observed during the experimentation period.

Discussion

The parameters estimated by the quadratic method accounted for the demographic mechanisms responsible for the changes in population structure, as the decrease of eggs and juveniles proved to be related to an increasing mortality, since factors such as migration and predation could not take place in early stages of *Stratiodrilus aeglaphilus*, due to the fact that eggs are fixed and larvae remain in the branchial chamber; also, no predators have been observed in all the experiment time. As reported for other taxa, the increase in eggs mortality is a frequent response of stressed species (Lienesch et al., 2000; Binelli et al., 2001). A special case is *Stratiodrilus aeglaphilus* eggs under experimental treatment with organic matter increment that did not show any sign of damage and evidence of dead eggs was not observed. This incongruence between estimated and observed mortality, together with the fact that in this matrix model, the emerging mortality was assigned to egg mortality and not to juvenile death, suggests that the decrease in egg number could be the result of a reduction in the duration of the stage instead of direct mortality of eggs. This phenomenon has been observed in estuarine polychaetes at sewage treatments, where the duration of one or more life stages decrease, therefore reducing the reproduction period and, thus, the chance of population permanence

(Levin et al., 1996). Early births tend to have positive impacts on population growth (Lewontin, 1965; Caswell & Hasting, 1980). In this case, the emerging juveniles are confronted to an adverse environment that promotes a higher mortality, this explaining the negative effect at a population level.

There were an adult increasing survival and fecundity, apparently as a consequence of the diminishing of population total abundance, which might imply the weakening of density-dependent pressure, and then *Stratiodrilus aeglaphilus* adults can increase growth and reproduction by the release of food and space resources (Sibly, 1996; Calow et al., 1997; Grant, 1998; Barata et al., 2002). However, these positive effects of organic enrichment on adult stages were not enough to counterbalance the detrimental effects suffered by eggs and juvenile stages of *S. aeglaphilus*.

In conclusion, the response of *Stratiodrilus aeglaphilus* population to organic enrichment was antagonistic between two stages, positive on adults and negative on the eggs. Moreover, according to our results, this response was faster than that of its host (*Aegla laevis*), which remained healthy during the experimental period. Therefore, the final outcome for the symbiont population density is a net negative effect that would explain *S. aeglaphilus* local extinction in Maipo River.

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