

The effect of a predatory leech, *Nephelopsis obscura*, on mortality, growth, and production of chironomid larvae in a small pond

J.B. Rasmussen

Dept. of Biology, University of Calgary Calgary, Alberta, Canada T2N 1N4

Summary. The effect of a predatory leech, *Nephelopsis obscura*, on survivorship, growth, and production of chironomid larvae was studied by enclosure experiments carried out in a small pond. The prey population was composed almost entirely of the tubiculous, microphagous chironomid larvae, *Chironomus riparius* and *Glyptotendipes paripes*. *Nephelopsis* significantly reduced chironomid survivorship within the enclosures, and accounted for most of the measured mortality of fourth instar larvae. The cropping by *Nephelopsis* was not significantly biased toward either prey species. In long-term experiments (66 d) chironomid biomass in enclosures without leeches reached much higher levels than in enclosures containing *Nephelopsis*. This increase in biomass was due to growth of surviving larvae, rather than recruitment, since emergence and oviposition were not going on during the course of the experiments. The enhanced survivorship of larvae within leech-free enclosures was eventually accompanied by reduced growth and specific production (daily production/biomass) for *C. riparius*, which made up about 90% of the larval population. Growth and specific production of *G. paripes* (10% of larval population) was not affected. Short-term experiments (25 d) involving manipulation of densities and species ratio (9:1 CR:GP and 1:9 CR:GP) of larvae revealed that growth of the majority species was strongly influenced by larval density, whereas growth of the minority species was not. The same pattern was observed both in the presence and in the absence of *Nephelopsis* and was a result of differences in resource utilization between the two species. In the short-term experiments, growth rates estimated for larvae exposed to leeches were significantly less than those for larvae in leech-free enclosures. This could be due either to size-biased consumption of larvae by *Nephelopsis*, or possibly a disturbance factor leading to reduced larval food intake and/or increased metabolic costs.

Key words: Predation – Manipulation – *Hirudinea* – *Chironomidae* – Growth

Composition and dynamics of freshwater zoobenthic communities can be markedly affected by predators (Hayne and Ball 1956; Hall et al. 1970; Crowder and Cooper 1982;

Morin 1984a, b). Most studies have involved fish predators, but some experimental work has been done with invertebrate predators (Hall et al. 1970; Benke 1975, 1978). Many leeches are predators on zoobenthos (Hilsenhoff 1963; Davies et al. 1978; Anholt 1986) but their impact on prey survivorship, growth, and species composition is unknown. Furthermore, Sih et al. (1985) found no predator manipulation studies involving non-arthropod carnivores in a freshwater system.

Prairie ponds in Alberta, Canada can support extremely high densities of leeches, mainly *Nephelopsis obscura* Verrill, which feed primarily on chironomid larvae (Davies et al. 1978). In Stephenson Pond (near Calgary, Alberta) *Nephelopsis* (750/m²) plus two prey species, *Chironomus riparius* Meigen and *Glyptotendipes paripes* (Edwards), made up most of the zoobenthic biomass. In this pond, enclosure experiments were carried out to answer the following questions: (1) Does *Nephelopsis* exert detectable effects on mortality and biomass of the chironomid larvae? (2) Does their presence affect the prey species ratio, either through biased consumption, or through effects on prey species interaction? (3) What are the effects of this predator on prey production and per capita growth rates of chironomid larvae?

Methods and materials

The study area

Stephenson Pond (2 m deep and area 2 ha), a hypereutrophic pond near Calgary, Alberta (114°16'W; 51°9'N), featured densities of *C. riparius* plus *G. paripes* in excess of 25,000/m². These two species plus the predatory leech, *Nephelopsis obscura* made up 98% of the zoobenthic biomass in the pond. Rasmussen (1984a) provided limnological information on the pond and described the life-cycles and production ecology of the chironomid larvae. Both species emerged in early May and had univoltine life-cycles; by August recruitment had completely ceased and the larval populations were made up solely of fourth instars. All of the experiments were carried out on fourth instars since earlier instars are of short duration and much more sensitive to sieving and manipulation. Although emergence did not take place during the experimental period (August–October, 1980 and 1981) the larvae were feeding actively and growing throughout this period (Rasmussen 1984a and b).

Experiments were carried out within 0.35 m² enclosures

Present address and address for offprint requests: Dept. of Biology, McGill University 1205 Ave. Docteur Penfield, Montreal Québec, Canada H3A 1B1

(Rasmussen 1985). Water and microplankton could circulate across the 0.25 mm mesh, but neither chironomid larvae nor leeches could enter or leave. The enclosures were placed at 1 m depth, with their bottoms pushed into the mud, and tops projecting about 10 cm out of the water. Sieved mud (10–15 cm) was added to the bottom of each enclosure and the desired animal community for each treatment was added and allowed to colonize the sediment. After the mud had settled, sufficient pond water was added to bring the inside concentration of *Aphanizomenon* colonies up to that of the ambient water. In order that the chironomid larvae would not have to be handled and enumerated individually, Ekman grabs from an area of previously determined larval density were sieved, leeches removed, and the sieve residue containing the chironomid larvae was added to the enclosure. Leech removal from sieve residue was estimated to be 98% effective for individual <20 mg; therefore, the few leeches that were inadvertently added to the enclosures designated "leech-free" were almost all <20 mg. Laboratory observations indicated that *Nepheleopsis* <20 mg were too small to capture fourth instars of these chironomid larvae. *Nepheleopsis* were then added at ambient density (0.075/cm²) to the appropriate enclosures by individual enumeration. These leeches ranged from 20–250 mg (wet wt) with means at the start of the experiments ranging from 61–70 mg.

The vertical profile of dissolved oxygen and chlorophyll concentrations of the water column inside the enclosures were compared to similar measurements from the ambient water. Dissolved oxygen was measured with a YSI DO probe, and chlorophyll *a* was measured by the SCOR/UNESCO spectrophotometric technique of Strickland and Parsons (1972).

Long-term (66 d) predator removal experiment

On August 10, 1980 the chironomid population at 1 m depth consisted of small fourth instars and had the composition outlined in Table 1. Four enclosures (that replicated this population) were established, with two containing *Nepheleopsis* at ambient density (0.075/cm²), and two without *Nepheleopsis*. Each enclosure was sampled at approximately 2–3 week intervals (till Oct. 15) by removing six 20 cm² cores at each sampling time. Mortality was estimated as the change in density over the course of the experiment since no recruitment was occurring. Production of chironomid larvae of both species was estimated by the Allen curve method (Winberg 1971) since larval cohorts were even-aged and non-overlapping.

$$P = \sum_t (\bar{W}_{t+1} - \bar{W}_t) \cdot \frac{(\bar{N}_{t+1} + \bar{N}_t)}{2}$$

where \bar{W} = mean weight, and \bar{N} = population density at time *t*, will yield an estimate that assumes a linear relationship between changes in \bar{N} and \bar{W} in the between sampling interval. Specific production (Zaika 1973) over a time interval is:

$$\frac{P_t}{\Delta t \cdot \frac{(\bar{B}_{t+1} + \bar{B}_t)}{2}}$$

where \bar{B} = the mean biomass of the species. The selectivity index of Chesson (1978) (α) was used in testing for a species bias in the consumption of prey by the leeches.

$$\alpha_i = \frac{r_i/p_i}{\sum_i r_i/p_i}$$

where r_i = the number of the *i*th prey species consumed by the predator, and p_i = the number present in the environment. Since the predation could not be directly observed, but must rather be inferred by decreases in density, r_i was estimated as the decline in density of the *i*th prey species over the course of the experiment.

Short-term (25 d) manipulations of predators, larval density, and larval species ratio

Chironomid larvae were established in enclosures at different initial densities half of these received *Nepheleopsis* (0.075/cm²), and half were leech-free. The treatments are outlined in Table 1. The experiments were carried out in September 1980 and 1981. Two different larval populations were tested, a 9:1 CR:GP mixture (1980) and a 1:9 CR:GP mixture (1981). These two species ratios were chosen because they were strongly contrasting ratios, and because larval populations featuring these ratios were available within the study area. The sites from which the experimental larvae were obtained were first sampled with cores (20 cm², *n* = 25) to determine densities of each species of chironomid, and then the number of Ekman grabs required to establish the treatment density for each enclosure was removed. The Ekman grabs were sieved, leeches and extraneous matter was removed, and the larvae were added to the enclosures as described previously. Although this technique did not permit as fine a control over larval densities as total counts, it did not require individual handling and enumeration of larvae which would have been impossible except on a much smaller spatial scale. All enclosures were allowed to stand undisturbed for three days prior to initial sampling; they were then sampled again 25 days later.

Calculations and statistical analyses

The growth rate of each chironomid species was estimated by subtracting initial mean weights (wet) from final mean weights, and dividing by the duration of the experiment (25 days). The treatment larval density (total CR + GP) was taken as the mean of the initial and final densities. Mean weight was determined for each species in each sample by collectively weighing the blotted larvae (nearest 0.01 mg) and dividing by the number present.

Within each experiment (Table 1) no significant between-enclosure differences in starting weights of larvae were detected; therefore, the initial weights of each species in each experiment were taken as the pooled mean over all the enclosures comprising the experiment. This greatly reduced the variance associated with starting weight estimates, and therefore, increased the precision of the growth estimates. At the termination of each experiment, one or two Ekman grabs were taken from each enclosure after the core samples had been removed. This provided a larger sample of larvae for weighing resulting in increased precision of the estimates of final larval weight. This was especially important in determining the growth increment of the least abundant species in the low density treatments.

The growth rate vs. density relationships obtained in the presence of *Nepheleopsis* were compared to those found in their absence. Model 1 (least squares linear) regression was used to establish the statistical significance of the

Table 1. Summary of the experiments reported in this paper, and their rationale (CR = *C. riparius* and GP = *G. paripes*)

Experiment	Purpose	Species-ratio	Duration	Density treatments <i>Nephelopsis</i> present	absent
No. 1 Table 2	Analysis of the effect of <i>Nephelopsis</i> on production and mortality of CR and GP	9:1 CR:GP	66 days	4.2 larvae/cm ² 2 enclosures	4.2 larvae/cm ² 2 enclosures
No. 2 Fig. 1a	Analysis of larval growth vs. larval density for <i>Nephelopsis</i> present vs. absent	1:9 CR:GP	25 days	0.2–2.4 larvae/cm ² 6 densities, 1 enclosure each	0.2–2.8 larvae/cm ² 7 densities, 1 enclosure each
No. 3 Fig. 1b	Analysis of larval growth vs. larval density for <i>Nephelopsis</i> present vs. absent	9:1 CR:GP	25 days	1.3–3.9 larvae/cm ² 7 densities, 1 enclosure each	1.0–4.2 larvae/cm ² 6 densities, 1 enclosure each

growth rate vs. density relationships, using the mean values estimated for each enclosure. The effect of *Nephelopsis* was statistically analysed by analysis of covariance (Zar 1974). Since two strongly contrasting larval populations (9:1 CR:GP and 1:9 CR:GP) were used in these experiments, intraspecific density effects could be compared to interspecific effects. For both species ratios, the effect of total larval density on the majority species will be predominantly intraspecific effects; whereas, interspecific density effects (if present) will be mainly seen as density effects on growth of the minority species.

Results

Long-term (66 d) predator removal experiment (Table 1)

The ambient chironomid population of Aug. 10, 1980 (4.2 larvae/cm²; 9:1 CR:GP; biomass 10.95 mg/cm²) was replicated in four enclosures two with *Nephelopsis* at ambient density and two without *Nephelopsis*. With the leeches present, larval density decreased by 2.72/cm² (64.7%), and the biomass decreased to 6.42 mg/cm² despite considerable production of biomass by the larvae (5.72 mg/cm²). Thus the biomass consumed by the leeches can be estimated to be 10.25 mg/cm² (136.6 mg/leech) which is 94% of the initial biomass.

In the leech-free enclosures the density change was negligible, and larval biomass rose to 18 mg/cm². Numerically, neither population departed from the 9:1 CR:GP starting ratio, and α (selectivity index of Chesson 1978) estimated for *Nephelopsis* feeding on both prey species was close to the null value (for the two prey case) of 0.5. *C. riparius* grew much faster in August than in September and October, in both sets of enclosures as well as in the ambient population (Rasmussen 1984a). From Aug. 10–Sept. 5 the total production, specific production, and per capita production for *C. riparius* was not significantly different between the two treatments (Table 2). However, from Sept. 5–Oct. 15 production of this species all but ceased in the leech-free enclosures where biomass had nearly doubled, and was significantly less for all three parameters than that recorded for the enclosures containing *Nephelopsis*. Throughout the experiment *G. paripes* grew at nearly a constant rate in both sets of enclosures and in the ambient population. None of the production parameters for this species was significantly affected by the presence or absence of leeches.

The mortality and growth of larvae in the enclosures

that contained *Nephelopsis* at ambient density closely tracked those described for the ambient population by Rasmussen (1984a). The total annual production for this 1980–81 larval cohort (ambient population at 1 m depth in Stephenson Pond) was 18.5 mg/cm², and the total production estimated for the Aug. 10–Oct. 15 experimental interval was 8.40 mg/cm². Thus nearly half of the total annual chironomid production occurred during the experimental interval although it was only 66 d long.

Short-term (25 d) manipulation of predators, larval density, and species ratio (Table 3; Fig. 1)

In all of the experiments outlined in Fig. 1 significant negative effects of chironomid density on growth of one or both chironomid species were recorded. In Fig. 1a (1:9 CR:GP) the effect of total larval density on growth of *G. paripes* was highly significant (Table 3). Furthermore, the slopes, both in the presence and absence of leeches, were significantly more negative than those recorded for *C. riparius* (Table 3). In Fig. 1b (9:1 CR:GP) the effect of density on the growth rate of *C. riparius* was highly significant (Table 3), and the slopes, both in the presence and absence of leeches, were significantly more negative than those recorded for *G. paripes*. Thus the majority species always experienced much stronger retardation of growth by elevated density than did the minority species, indicating that intraspecific density effects were much stronger than interspecific effects. In fact, in two of the four experiments the density effect on the minority species was not significant at $P < 0.05$.

In the short-term experiment, 11 of the 13 enclosures that contained *Nephelopsis* at ambient densities had final larval densities that were significantly lower (t -test $P < 0.05$) than initial larval densities. The two that did not, had the lowest larval densities tested (< 0.5 /cm²). None of the 13 leech-free enclosures had significant larval mortality during the 25 d period. Mortality estimates ($\Delta \bar{N}$) from the leech-containing enclosures increased significantly with initial larval density (\bar{N}_0) and the equation

$$\Delta \bar{N} (\#/\text{cm}^2) = 0.369 (\pm 0.085) + 0.188 (\pm 0.031) \bar{N}_0 (\#/\text{cm}^2)$$

$$r^2 = 0.80 \text{ S.E. of estimate} = 0.104$$

$$n = 13 \quad P < 0.0005$$

was fitted by linear regression. Mortality expressed as a fraction of initial density declined significantly, with increased initial density

Table 2. The effect of predator removal (*Nepheleopsis obscura*) on a series of chironomid population parameters (Aug. 10–Oct. 15, 1980)

	Enclosures with <i>N. obscura</i> (0.075/cm ²) (n = 2)	t-test (df = 2)	Enclosures without <i>N. obscura</i> (n = 2)
Estimated mortality (no/cm ² /66 d)	2.72	***	0.3
Final chironomid biomass (mg/cm ²)	6.42	**	18.0
<i>G. paripes</i> production Aug. 10–Oct. 15 mg/cm ²	1.30	n.s.	2.56
<i>C. riparius</i> production Aug. 10–Sept. 5 mg/cm ² Sept. 5–Oct. 15 mg/cm ²	3.46 0.96	n.s. ***	4.87 0.10
<i>G. paripes</i> specific production (mg/d/mg biomass) Aug. 10–Oct. 15	0.0190	n.s.	0.0155
<i>G. riparius</i> specific production (mg/d/mg biomass) Aug. 10–Sept. 5 Sept. 5–Oct. 15	0.0139 0.0037	n.s. **	0.0154 0.0002
<i>G. paripes</i> production per individual (mg/day) Aug. 10–Oct. 15	0.077	n.s.	0.088
<i>C. riparius</i> production per individual (mg/day) Aug. 10–Sept. 5 Sept. 5–Oct. 15	0.046 0.0097	n.s. ***	0.046 0.00026

* = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.005$

Table 3. Regression statistics for chironomid density manipulation experiments (Fig. 1)

		Regression Equation	df	$P <$	r^2
a 1:9 CR:GP	<i>G. paripes</i>	● $G = 74.2 (\pm 3.4) - 24.4 (\pm 1.74) N$	6	0.001	0.96
	<i>G. paripes</i>	○ $G = 44.9 (\pm 3.5) - 16.6 (\pm 1.05) N$	5	0.005	0.94
	<i>G. riparius</i>	● $G = 57.8 (\pm 3.5) - 8.28 (\pm 2.34) N$	6	0.05	0.71
	<i>G. riparius</i>	○ $G = 44.8 (\pm 3.9) - 7.89 (\pm 2.92) N$	5	0.10	0.61
		For ● Slope GP < Slope CR $t = 5.52$ df = 9 $P < 0.001$			
		For ○ Slope GP < Slope CR $t = 2.80$ df = 9 $P < 0.05$			
b 9:1 CR:GP	<i>G. paripes</i>	● $G = 112.0 (\pm 6.6) - 5.2 (\pm 1.70) N$	5	0.05	0.69
	<i>G. paripes</i>	○ $G = 65.3 (\pm 5.6) - 4.03 (\pm 1.55) N$	6	0.10	0.57
	<i>G. riparius</i>	● $G = 57.5 (\pm 5.3) - 13.6 (\pm 1.83) N$	5	0.005	0.93
	<i>G. riparius</i>	○ $G = 35.1 (\pm 3.9) - 8.9 (\pm 1.42) N$	6	0.005	0.89
		For ● Slope CR < Slope GP $t = 3.37$ df = 9 $P < 0.01$			
		For ○ Slope CR < Slope GP $t = 2.31$ df = 9 $P < 0.05$			

G growth rate expressed as $\mu\text{g/day}$; N density expressed as larvae/cm²;

● enclosures without leeches; ○ enclosures with ambient density of *Nepheleopsis*.

Units for the slope of the growth rate vs. larval density relationship are ($\mu\text{g/d}$)/(larvae/cm²)

$$\frac{\Delta \bar{N}}{\bar{N}_0} = 0.509 (\pm 0.030) - 0.060 (\pm 0.011) N_0 (\#/\text{cm}^2)$$

$$r^2 = 0.77 \quad \text{S.E. of estimate} = 0.037 \quad n = 13 \quad P < 0.0005$$

indicating predator satiation in the functional response. These two equations were obtained by combining the data obtained from the 9:1 CR:GP and the 1:9 CR:GP experiments. The chironomid mortality (25–46% of initial densities) was not significantly biased toward either species. For

C. riparius, Chesson's alpha averaged 0.62 ± 0.18 for the 9:1 CR:GP larval population and 0.55 ± 0.17 for the 1:9 CR:GP mixtures. These values are not significantly different from each other (indicating no frequency dependence) or from 0.5, the null value of the index for two food types. Larval density also had no effect on selectivity.

The growth rates estimated for both chironomid species in the presence of *Nepheleopsis* (Fig. 1) were significantly lower than those estimated from leech-free enclosures. In

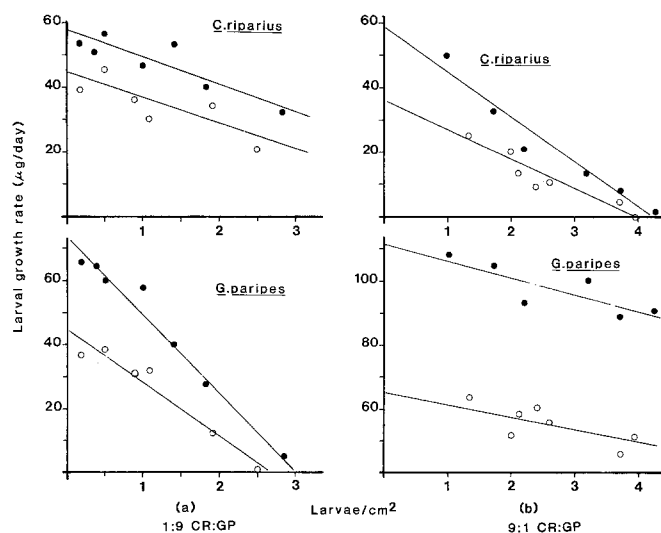


Fig. 1a, b. Effect of *Nephelopsis* on the growth of chironomid larvae at various densities for (a) 1:9 CR:GP and (b) 9:1 CR:GP. Lines were fitted by least squares linear regression (see Table 3). Closed circles leech-free, and open circles ambient leech density. Each point represents the mean larval growth rate and density estimated from a single enclosure

three of the four cases shown in Fig. 1, the difference was significant at all larval densities ($P < 0.05$ ANCOVA comparison of parallel regressions). In the remaining case (CR in the 9:1 CR:GP population) the effect was significant for larval densities $< 2.0/\text{cm}^2$.

The enclosure regime

Measurements of dissolved oxygen and chlorophyll *a* concentrations inside the enclosures did not reveal any major differences from those found in the ambient water. Furthermore, the vertical distribution of both chironomid species plus *Nephelopsis* within sediment cores taken from the enclosures, were indistinguishable from cores taken outside. Rasmussen (1983) also showed that the enclosure environment did not affect the growth rate of either *G. riparius* or *G. paripes*. These observations together with the fact that no significant density reduction was observed for either chironomid species in leech-free enclosures, indicate that the enclosure regime had little or no adverse effect on the experimental animals.

Discussion

The few studies that have been done on the effects of predator removal on freshwater benthic prey have produced highly variable and conflicting results, and thus few general patterns have emerged (Sih et al. 1980). This lack of agreement cannot be attributed solely to differences in the effects produced by different predators, since a wide range of outcomes have been observed in manipulation studies involving bluegill sunfish (Hall et al. 1970; Hayne and Ball 1956; Welch and Ball 1966; Crowder and Cooper 1982). Other studies of the effects of fish exclusion on benthos are those of Kajak (1972) and Morin (1984a and b). Similar experiments have been carried out with large invertebrate predators such as odonates (Hall et al. 1970; Benke 1976, 1978) and stoneflies (Peckarsky and Dobson 1980). No experiments of this kind

have been conducted on smaller benthic invertebrate predators (e.g. Tanypodinae or triclads).

Some studies revealed no (or barely detectable) effects on total prey biomass (Hall et al. 1970, both for bluegill and dragonfly manipulations; Benke 1978), whereas others found 2–5 fold increases in prey biomass in predator-free areas (Hayne and Ball 1956; Crowder and Cooper 1982; Kajak 1972). Most studies, regardless of effects on total prey biomass, do indicate that abundances of large prey such as *Hexagenia*, Odonata, amphipods, or *Chironomus* tend to be reduced by predators. Thus Hall et al. (1970) found that removal of large prey by predators, led to compensatory increases in the abundance of small, rapidly recruiting prey. Although these authors did not detect changes in overall prey biomass, they were able to demonstrate a significantly higher rate of insect emergence from ponds that had no fish. Had my study involved prey that had shorter life-cycles and recruited continually throughout the ice-free season, as many smaller chironomids do, it seems likely that *Nephelopsis* would have decreased both prey biomass and density much less, and would instead have affected emergence and turnover. Thus I am hypothesizing that where the prey community contains a substantial fraction of smaller, less easily located, rapidly recruiting species with short life cycles, effects on total prey biomass will be less dramatic (density should even increase), and predators would alternatively be expected to affect recruitment and turnover.

The results of my enclosure experiments, and the close correspondence between the *Nephelopsis*-containing enclosures and the ambient chironomid population (Rasmussen 1984a) with respect to survivorship and growth, indicate that *Nephelopsis* was the primary source of mortality for final instar chironomids in Stephenson Pond, and that these leeches have a great influence on the chironomid biomass. Fourth instar densities declined by more than one-half (Table 2) during August–September, and this survivorship was about the same as that experienced by second and third instar larvae during June–July (Rasmussen 1984a). Although I have observed *Nephelopsis* feeding on young instar chironomids, nothing is known of their impact on survivorship of these stages. First-third instar chironomid larvae are very sensitive to sieving and handling, and the techniques used in this study would likely have resulted in excessive larval mortality had experiments been attempted during June–July on young instars.

Although the presence of *Nephelopsis* substantially increased mortality of chironomid larvae (thinning the larvae enough to greatly reduce intraspecific density effects on chironomid growth and production) the leeches did not exert a significant influence on the relative abundance of the two chironomid species. No foraging bias or frequency dependent cropping was detected. Furthermore, the experiments that involved manipulation of larval densities and species ratios indicated that coexistence between the two chironomid species was likely to occur whether or not *Nephelopsis* was present since interspecific density effects were barely detectable both with and without the leeches (Fig. 1; Table 3). Rasmussen (1984b, 1985) showed that *C. riparius* and *G. paripes* had different modes of foraging, and therefore, would likely coexist even in the complete absence of leeches.

The apparent reduction of chironomid growth rate by *Nephelopsis* (Fig. 1; Table 3) may be an artifact introduced by size-biased cropping. If this was the case, the production

estimates made for the larval populations exposed to leech predation, (and in turn, the estimate of biomass consumed by the leeches) may be underestimating true values by up to 30%. On the other hand, it could have resulted from the leeches disturbing the larvae leading to reduced food intake and/or increased larval metabolic costs. Since *Nepheleopsis* is much larger and more active within the sediment than either of the chironomid species, and shares the same microhabitat, it is certainly possible that the leeches could exert a considerable disturbing effect on the larvae.

Conclusion

This is the first study of the impact of predatory leech on its prey community using field manipulative techniques. Cropping by *Nepheleopsis* was the major source of mortality for final instar chironomid larvae, and greatly reduced larval densities, biomass, and intraspecific density effects on chironomid growth. Since intraspecific density effects between the chironomid larvae were very weak even in the absence of *Nepheleopsis*, and the cropping by *Nepheleopsis* was not species biased with respect to chironomid larvae, no effects of the leeches on species composition of the prey community could be detected.

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References

- Anholt B (1986) Prey selection by the predatory leech *Nepheleopsis obscura* in relation to three alternative models of foraging. *Can J Zool* 64:649–655
- Benke AC (1976) Dragonfly production and prey turnover. *Ecology* 57:915–922
- Benke AC (1978) Interactions among coexisting predators – a field experiment with dragonfly larvae. *J Anim Ecol* 47:335–350
- Chesson J (1978) Measuring preference in selective predation. *Ecology* 59:211–215
- Crowder LB, Cooper WE (1982) Habitat structural complexity and interactions between bluegills and their prey. *Ecology* 63:1802–1913
- Davies RW, Wrona FJ, Everett RP (1978) A serological study of prey selection by *Nepheleopsis obscura* Verrill (Hirudinoidea). *Can J Zool* 56:587–591
- Hall DJ, Cooper WE, Werner EE (1970) An experimental approach to the production dynamics and structure of freshwater animal communities. *Limnol Oceanogr* 15:839–938
- Hayne DW, Ball RC (1956) Benthic productivity as influenced by fish predation. *Limnol Oceanogr* 1:162–175
- Hilsenhoff WL (1963) Predation by the leech *Helobdella stagnalis* on *Tendipes plumosus* (Diptera:Tendipedidae) larvae. *Ann Ent Soc. America* 56:252–261
- Kajak Z (1972) Analysis of the influence of fish on the benthos by the method of enclosures. pp 781–793 in Kajak Z, Hillbricht-Ilkowska A (eds) *Productivity Problems of Freshwaters*. Warsaw, PWN Polish Scientific Publishers
- Morin PJ (1984a) The impact to fish exclusion on the abundance and species composition of larval odonates: Results of short-term experiments in a North Carolina farm pond. *Ecology* 65:53–60
- Morin PJ (1984b) Odonate guild composition: experiments with colonization history and fish predation. *Ecology* 65:1866–1282
- Peckarsky BL, Dodson SI (1980) Do stonefly predators influence benthic distributions in streams? *Ecology* 61:1275–1282
- Rasmussen JB (1983) An experimental analysis of competition and predation, and their effects on growth and coexistence of chironomid larvae in a small pond. PhD thesis University of Calgary, Calgary, Alberta, p 220
- Rasmussen JB (1984a) The life-history, distribution and production of *Chironomus riparius* and *Glyptotendipes paripes* in a prairie pond. *Hydrobiologia* 119:65–72
- Rasmussen JB (1984b) Comparison of gut contents and assimilation efficiency of the fourth instar larvae of two coexisting benthic chironomidae, *Chironomus riparius* Meigen and *Glyptotendipes paripes* (Edwards). *Can J Zool* 62:1022–1026
- Rasmussen JB (1985) Effects of density and microdetritus enrichment on the growth of chironomid larvae in a small pond. *Can J Fish Aquat Sci* 42:1418–1422
- Sih A, Crowley P, McPeck M, Petranka J, Strohmeier K (1985) Predation, competition, and prey communities: a review of field experiments. *Ann Rev Ecol Syst* 16:269–311
- Strickland JDH, Parsons TR (1972) A manual of sea water analysis. *Bull Fish Res Bd Can* No 125, p 186
- Welch EB, Ball RC (1966) Food consumption and production of pond fish. *J Wildlife Mgmt* 30:527–536
- Winberg GC (1971) Methods for the estimation of production of aquatic animals. Duncan A (Transl) Academic Press, London
- Zaika VE (1973) Specific production of aquatic invertebrates. Wiley, New York/Israel Program of Scientific Translations. Jerusalem, Israel
- Zar JH (1974) Biostatistical analysis. Prentice-Hall, Toronto

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