

## Impacts of predation and intracohort cannibalism in the water strider *Gerris buenoi* (Heteroptera: Gerridae)

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Despite the growing appreciation of intraguild predation as a factor in the population dynamics of predatory invertebrates, few empirical studies exist, especially for cannibalism among individuals of the same age. We evaluate the relative role of such processes for the water strider *Gerris buenoi* with a field experiment. Field enclosures were used to rear water striders from the first instar to the adult stage. Each enclosure had compartments for three treatments: group rearing with free access for predators, group rearing under predator exclusion, and individual rearing under predator exclusion. Overall survival was similar in the group and individual rearings under predator exclusion, but was substantially lower where predators were present, indicating that predation by non-gerrids influences juvenile survival more than intracohort cannibalism. Regular censuses showed that most mortality occurred in the first instar. Moreover, survival in group rearings was lower than in individual rearings during this period, indicating that intracohort cannibalism is a relevant factor in the first few days of larval life. The bugs from individual rearings had the lowest average adult weight and longest development time, whereas the fastest-maturing and heaviest adults were those from group rearings under predator exclusion. This indicates that factors other than competition for food are responsible for variation in growth performance.

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Predation is a central topic in population ecology, and recently cannibalism and intraguild predation have been recognized as important factors shaping community structure and the evolution of life histories, especially among predatory invertebrates (reviewed by Fox 1975a, Polis 1981, Polis et al. 1989). Assessing the relative impacts of these mortality factors is therefore a prerequisite for understanding the dynamics of natural populations and how they affect communities and their component species.

The relative sizes of predator and prey are crucial in these interactions (e.g., Jamieson and Scudder 1979). In most cases it is older and larger individuals that cannibalize younger ones (Polis 1981), and most experimen-

tal studies have measured cannibalism by comparing the survival of smaller individuals in the presence and absence of larger conspecifics (Fox 1975b, Spence 1986, Spence and Cárcamo 1991, Van Buskirk 1992, Anholt 1994). Nevertheless, cannibalism among equally sized individuals has been reported (e.g., Fox 1975b, Polis 1980, Duelli 1981), and even among individuals of equal age, variation in instar duration can create considerable size differences and thus facilitate intracohort cannibalism (Matthey 1976). Experiments to study intracohort cannibalism normally have to be done in the laboratory (e.g., Fox 1975b, Duelli 1981), because rearing isolated individuals under field conditions is not practical for most species.

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Most experiments have studied survivorship at one of two time scales: either through the entire period of growth to the adult stage (Duelli 1981, Spence 1986, Spence and Cárcamo 1991, Anholt 1994) or over an interval much shorter than the life cycle (e.g., 10–15 d in a dragonfly with a 3-yr cycle, Van Buskirk 1992). While work at both time scales can reveal important information, susceptibility to cannibalism and predation may change during the larval period, and the results of the two types of studies may thus differ drastically.

In water striders, cannibalism and intraguild predation have long been known. Based mainly on casual observations, some authors have suggested that cannibalism is the dominant factor for the regulation of gerrid populations (Brinkhurst 1966, Matthey 1976). Intraguild predation among gerrids is a determinant for habitat partitioning among species (Spence 1983), whereas interference, including cannibalism, by older bugs can lead to habitat segregation among instars (Matthey 1976, Vepsäläinen and Nummelin 1986). Results of field experiments on cannibalism, however, have differed dramatically depending on the species examined: whereas young larvae of *Gerris buenoi* Kirkaldy had only slightly reduced survival rates in the presence of older conspecifics (Spence 1986), a similar experiment with *G. pingreensis* Drake and Hottes produced a severalfold drop in survivorship of younger larvae (Spence and Cárcamo 1991). Although Spence (1986) suggested a possible role for intracohort cannibalism in *G. buenoi*, there are no data about the relative role of this process.

Contrary to earlier reports that dismissed predation on gerrids by other animals as relatively unimportant (Brinkhurst 1966, Matthey 1976), field experiments have shown that predation by other arthropods is a major determinant of survival in *G. buenoi* (Spence 1986). Gerrids are regularly consumed by fishing spiders (Zimmermann and Spence 1989) and dragonfly larvae (Van Buskirk 1992); moreover, they are at least occasionally attacked by fish (Cooper 1984), birds and frogs (summarized by Callahan 1974).

In this paper we assess the relative impacts of intracohort cannibalism and predation on larval mortality in the water strider *Gerris buenoi*. We report the results of an experiment using field enclosures that extends the work of Spence (1986) and Spence and Cárcamo (1991). We estimated the impact of intracohort cannibalism from the reduction in the survival of bugs reared in groups relative to that of isolated bugs, and to assess predation by non-gerrids we compared survival in predator access and exclusion treatments. Besides overall survivorship, data from regular censuses also allow us to consider the temporal pattern of mortality under the experimental regimes. At this higher resolution, we examine if mortality causes varied throughout the larval period.

## Materials and methods

### Field experiment

We carried out our study on Experiment Pond at the George Lake Field Site near Edmonton, in central Alberta, Canada. The same site had been used for an earlier experiment by Spence (1986), who also provided a detailed description of the pond.

The water striders used in our experiment were offspring of direct-breeding adults collected in early and mid-July of 1992 on two neighboring ponds. Adults were kept as a mass culture in the laboratory for mating, and were provided with Styrofoam strips as oviposition substrates and with ample food (frozen flesh flies, *Neobelliera bullata* [Parker]). On 21 July we started the field experiment with first instar larvae from this mass culture. This date ensured that all offspring were in diapause condition, and that all but two were macropterous (for details, see Spence 1989). Groups of 50 hatchling larvae were counted into containers containing a moist paper towel; these were taken to the field site, and randomly allocated to treatments and enclosures. We replaced any larvae that had died during transport with larvae from the same mass culture. This procedure ensured that larvae were in the experimental enclosures within 48 h of hatching.

The enclosures were constructed of wooden frames (2 × 1 × 1 m), each divided into four compartments. The sides of the enclosures and the partitions between compartments were made of saran fabric (0.97 mm mesh size). In each enclosure, compartments were allocated to the three treatments haphazardly, but we tried to vary their arrangement relative to each other. One compartment was left open at the bottom and the top to give access to predators. Another compartment was covered at both the top and the bottom with mosquito screen (mesh size ca 1.4 mm) to exclude predators; any predators (mostly fishing spiders [*Dolomedes triton*], backswimmers [*Notonecta* sp.], and larvae of diving beetles [Dytiscidae] and damselflies) found within these compartments during daily checks were removed immediately. The remaining two compartments were used for individual rearings; they were screened and treated as for predator exclusion, but the larvae were reared individually in bottomless plastic containers (diameter ca 10 cm, rim ca 6 cm above water) that were kept afloat on the water surface by a strip of plastic foam glued around the outside. For each of the three treatments, replicated in six field enclosures, we used 50 larvae, giving a total sample size of 900 bugs. The larvae in all treatments were fed daily ad libitum (at least approximately the larva's own volume in individual rearings, corresponding amounts for group rearings) with insects caught in a nearby light trap, and presumably similar to the natural food fall on the pond.

At intervals of three to eight d, we censused the larvae in the predator access and exclusion treatments. During these censuses, we scooped up the larvae with a tea strainer, but avoided all other manipulations. The larvae reared individually were checked daily throughout the experiment. Within 24 h after the final molt, all adults were killed and dried at 60°C before weighing (resolution 1 µg).

### Statistical analyses

We used logit models for comparisons of survival in different treatments (e.g., Jobson 1992: 82–86). Logit models extend the framework of analysis of variance to categorical data (e.g., survival vs death) by using the logarithm of the odds as the response variable, i.e., in this study  $\ln[\text{survival} / (1-\text{survival})]$ . Model parameters were estimated by maximum likelihood methods, and tests use a  $\chi^2$  statistic. We used the CATMOD procedure of SAS for our analyses (SAS Institute 1990).

In addition to the analysis of overall survival from first instar to adult stage, the census data allowed us to analyze at which time the mortality occurs and when it differs between treatments. We defined mortality for each census period as the proportion of larvae alive at a census that died between then and the next census (as in conventional life table analysis; Carey 1993). Therefore, the first of these mortality estimates is for 21 July and is the proportion of the initial 50 bugs in each compartment that had died by the census on 23 July. We included individuals that molted to adults during a census period into the number initially present. The last census (i.e., the end of the census period beginning 1 September) was on 10 September. Because mortalities differed dramatically over time, we did not attempt to adjust for the varying length of census intervals (i.e., compute mortality rates). Comparisons were done by a separate logit analysis for each census period.

We used conventional analysis of variance to assess the effects of the three treatments on adult weight and development time. The model used treatment, sex, and enclosure as fixed effects; *F*-tests were based on type III sums of squares (SAS Institute, 1990). After preliminary analyses, only the treatment × enclosure interaction was retained, as all other interaction effects were nonsignificant. For pairwise comparisons between treatments, we controlled the experimentwise error rate using the Tukey-Kramer method (Sokal and Rohlf 1981).

Spence (1986) observed that development time was less variable in Gerrids exposed to predators than in those reared under predator exclusion. To assess this in our experiment, we compared the variances of development time in each enclosure and treatment, and additionally the differences of the minima, maxima, 10%, and 90% quantiles from the mean development time in

each treatment and enclosure. These values were analyzed in a one-way analysis of variance with treatment as the only factor. We performed pairwise comparisons with Tukey-Kramer tests.

## Results

### Overall survival

Survival to adulthood was variable among both treatments and enclosures (Fig. 1). With an overall average of 65%, individual rearings had high and relatively consistent survival. Group rearings with predators excluded were more variable in survival, but had a similar

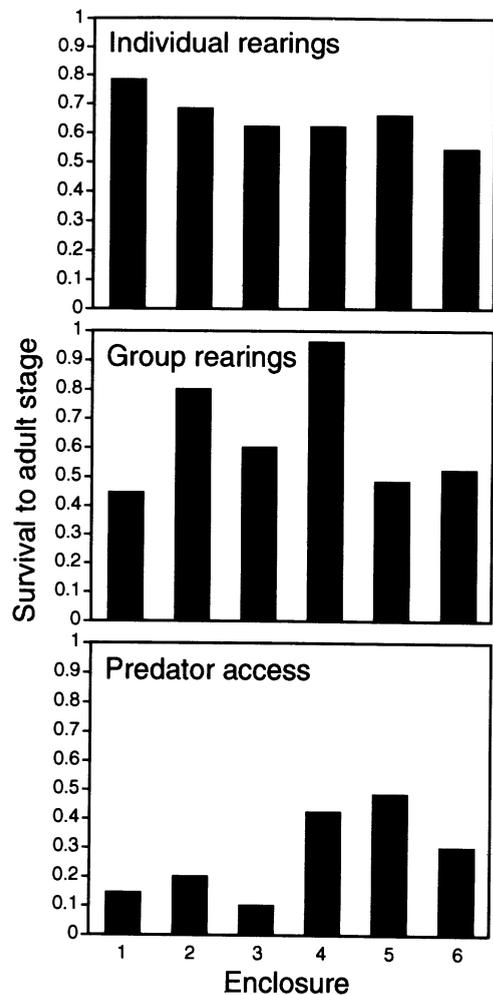


Fig. 1. Proportion of water striders surviving from first instar to adult stage. The experiment was started with 50 larvae for each treatment in each of the six enclosures. Predators were excluded from the individual and group rearing treatments, and the larvae in the predator access treatment were reared in groups.

average of 63.3%. In contrast, the average survival of 27.3% in compartments with predator access showed that predation had a substantial effect on the gerrids.

The logit analysis confirmed these patterns. The effects of the treatment ( $\chi^2 = 104.56$ ;  $df = 2$ ;  $P < 0.0001$ ), enclosure ( $\chi^2 = 26.36$ ;  $df = 5$ ;  $P = 0.0001$ ), and their interaction ( $\chi^2 = 52.76$ ;  $df = 10$ ;  $P < 0.0001$ ) were all highly significant. This is hardly surprising, because the analysis responds to relatively subtle effects due to the large total sample size ( $N = 900$ ). The range of variation in survival was greater between treatments (see above) than among enclosures (44–66.7%), and the variability among single replicates (corresponding to the treatment  $\times$  enclosure interaction) is at least as important as any systematic enclosure effects (Fig. 1). Therefore, we attribute most variation among replicates to random fluctuations of mortality factors, such as predators entering the compartments.

As this study was planned to address specific hypotheses, we used contrasts among the treatments explicitly designed to examine the relative roles of cannibalism and predation (SAS Institute 1990: 417 ff.). For assessing cannibalism, the main-effect parameters of the individual and group rearing treatments were compared. This contrast was not significant ( $\chi^2 = 0.54$ ;  $df = 1$ ;  $P = 0.46$ ), and thus indicates that cannibalism among gerrids of equal age is not a factor influencing survival over the entire larval period. Conversely, the test of predation, which opposed the predator access treatment to the other two, was highly significant ( $\chi^2 = 103.74$ ;  $df = 1$ ;  $P < 0.0001$ ), and thus firmly establishes the crucial role of predation as a determinant of survival.

### Temporal pattern of mortality factors

Mortality patterns differ clearly between treatments: not only the overall magnitude, but also the timing of major mortality episodes (Fig. 2). The results should be interpreted with some caution, especially in later census periods, as the numbers of larvae dwindle due to deaths and because of final molts, making estimates of survival probability increasingly inaccurate. Only in the first census period was there some mortality in each compartment, making it possible to estimate the full model; in the later periods, the models therefore contained some restricted parameter values.

During the first interval, i.e., from setup of the experiment to the first census, mortality was low in the individual rearings, but was at its highest level for both other treatments (Fig. 2). This low mortality under the individual rearing regime was confirmed by a test of the linear contrast between individual rearing and predator-free group rearing treatments ( $\chi^2 = 20.88$ ;  $df = 1$ ;  $P < 0.0001$ ); it shows that the higher mortalities in the two group rearing treatments could not be the effects of

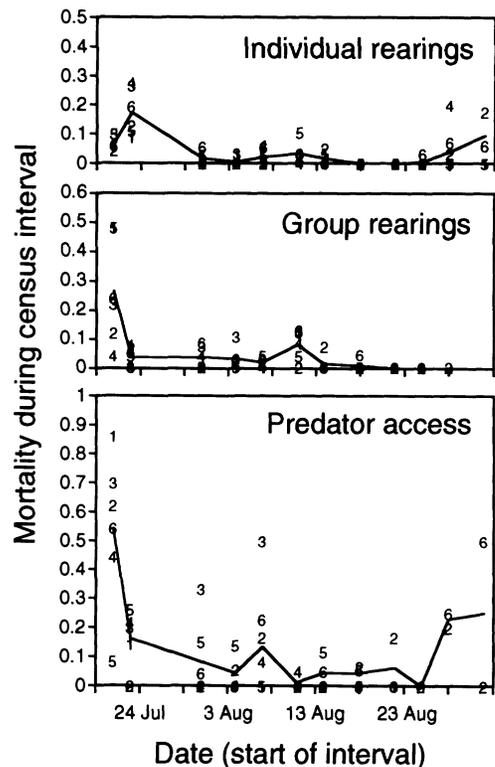


Fig. 2. Mortality during the intervals between successive censuses. Mortality values for single enclosures are indicated by their numbers, and the lines indicate mortality for all bugs within a treatment class (summed across enclosures). The values are plotted at the beginning of the respective census period, e.g., the values on 21 July refer to the period 21–23 July. Predators were excluded from the individual and group rearing treatments, and the larvae in the predator access treatment were reared in groups.

handling as the bugs were brought to the field, and it suggests that considerable cannibalism occurred among these young larvae. Despite substantial variation between enclosures (Fig. 2), the contrast between the predator access treatment and the other two treatments was statistically significant ( $\chi^2 = 98.76$ ;  $df = 1$ ;  $P < 0.0001$ ). This result and the magnitude of mortality under predator access (Fig. 2) indicate that predation is the major mortality cause in this period.

Differences among treatments are relatively small in the census periods starting on 31 July, 4 August, and 7 August, especially if one takes the variation among enclosures into account, and the linear contrasts for assessing both cannibalism and predation are not statistically significant. Due to diminishing sample sizes in the later periods, either the relevant parameters could not be estimated or the linear contrasts were not statistically significant. The lack of evidence for treatment effects after the second census suggests that the risks of cannibalism and predation for water strider larvae are concentrated mainly in the first few days of life.

Table 1. Analyses of variance for final weight and development time.

Source	df	Mean square	F	P
<b>Dry weight:</b>				
Treatment	2	2.47	27.72	0.0001
Enclosure	5	0.40	4.51	0.0005
Sex	1	9.94	111.68	0.0001
Treatment × enclosure	10	0.35	3.98	0.0001
Residual	347	0.089		
<b>Development time:</b>				
Treatment	2	2382.4	187.17	0.0001
Enclosure	5	712.5	55.98	0.0001
Sex	1	0.12	0.01	0.92
Treatment × enclosure	10	161.8	12.71	0.0001
Residual	411	12.7		

### Growth

Analyses of variance showed clear effects of the treatments on growth (Table 1). For weight, however, sexual dimorphism has a much larger influence than any of the experimental factors. Mean squares for treatment are substantially larger than those for enclosures or the treatment × enclosure interaction; we will therefore concentrate on treatment effects. Yet the statistically significant terms for enclosure and the treatment × enclosure interaction indicate that the analyses should be interpreted cautiously, especially when the aim is to generalize the results.

Individually reared adults were lighter than those reared in groups, but for the latter, weights did not differ significantly ( $P > 0.05$ ) between the predator access and predator exclusion treatments (Fig. 3A). Development time varied among treatments in the opposite order, and all differences are statistically significant ( $P < 0.05$ ): individually reared water striders had longer development times than group-reared ones,

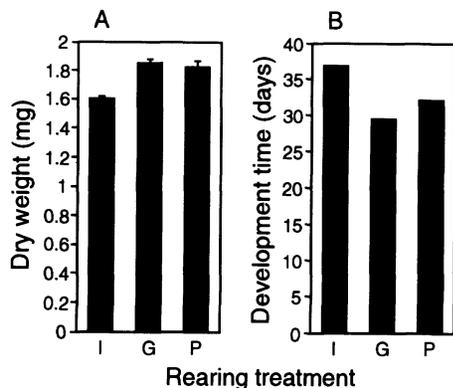


Fig. 3. Growth of water striders in different rearing conditions: dry weight of teneral adults (A) and development time from first instar to the final molt (B). The values are least-squares means, and therefore correct for sexual size dimorphism; error bars indicate their standard errors (error bars in B are too short to be seen; values are 0.27 for individual rearings, 0.28 for group rearings, and 0.49 for predator access). The treatments are individual rearing (I), group rearing under predator exclusion (G), and group rearing with predator access (P).

and those reared with predators excluded developed somewhat faster than those exposed to predators (Fig. 3B).

The variances in development time did not differ significantly among treatments ( $F = 2.88$ ;  $df = 2,15$ ;  $P = 0.09$ ). The other measures of variation only differed among treatments for the left-hand tail of the distribution of development time (from minimum to mean,  $F = 16.06$ ;  $df = 2,15$ ;  $P = 0.0002$ ; from 10% quantile to mean,  $F = 4.38$ ;  $df = 2,15$ ;  $P = 0.03$ ). With 8.2 d between the shortest and mean development time (averaged over enclosures), the individual rearings were more variable than the two other treatments (3.8 d for predator access and 3.2 d for predator exclusion). For the time between the 10% quantile and the mean development time, the only statistically significant difference was between individual rearings (5.1 d) and group rearings with predators excluded (2.6 d), whereas the predator access treatment was intermediate (3.3 d). Altogether, the distribution of development times has a longer left tail for individual rearings than for the group rearings with either predator access or predator exclusion, which do not differ significantly from each other.

### Discussion

In our study predation was the most important factor determining survival, reducing it by more than half relative to predator exclusion treatments. This result is consistent with an earlier study on the same pond (Spence 1986), but survival rates were generally higher in the present study (27% vs 10% with predator access, and 63% vs 35% with predator exclusion). The survival rate under predator access is also higher than that estimated for free-living larvae of *Gerris lacustris* by repeated quadrat sampling (11–17%; Zimmermann et al. 1982). This latter difference could reflect predation by gerrids from other size classes, which can be a major mortality factor in some situations (Spence 1983, Spence and Cárcamo 1991) but was relatively unimportant in a previous study of *G. buenoi* (Spence 1986).

It is not clear what caused the consistently higher survival in our experiment compared to those reported by Spence (1986), but we envision two possible explanations. (1) It is possible that the enclosures, which were higher than those used by Spence (1986; 60–80 cm above water vs 25–35 cm), reduced predation by fishing spiders (*Dolomedes triton*). Nevertheless, predators were able to enter, as we had to remove fishing spiders and aquatic predators from the screened compartments on numerous occasions. (2) Spence's (1986) experiment started about a month earlier than ours, and this difference in timing may have been sufficient to expose the larvae to a completely different community of predators in the two experiments. Such an explanation is especially plausible for aquatic predators such as early-instar larvae of damselflies and diving beetles, which prey on first instar gerrids (pers. obs.), and which are small enough to pass through the bottom screen of the enclosures, thus also affecting the "predator-exclusion" treatments. In central Alberta, most of these predators are univoltine and pass through the early instars before mid-July.

The impact of predation was most pervasive in the first few days of larval life: more than half the larvae of our experiment disappeared within the two days of the first census period (Fig. 2), whereas in later periods mortality was substantially lower. We doubt that the drop in mortality was due to the lack of predators preying on older larvae, as potential predators (especially fishing spiders) were present in the enclosures throughout the experiment. This temporal pattern contrasts with the estimates of instar-specific survival in *Gerris lacustris*, which are only slightly lower in the first instar than in the second to fourth instars (Zimmermann et al. 1982). Moreover, Zimmermann et al. found higher mortalities in the final instar, for which our data are inconclusive due to the small sample size. Such differences in timing of mortality may have important implications for population dynamics and influence life history evolution. Thus, generalizations about details of life history evolution may be unwarranted even across species that are otherwise fairly similar ecologically and closely related phylogenetically (Andersen 1993).

Intracohort cannibalism had little influence on overall mortality in our experiment (Fig. 1), as the average survival differed by less than 2% between the group and individual rearings under predator exclusion. Therefore, in combination with the study of Spence (1986), our results show that in this population cannibalism is unimportant as a mortality factor relative to predation. Yet at the higher resolution provided by our repeated censuses, intracohort cannibalism did appear to elevate mortality during the first few days of larval life. Due to variable mortality in later stages, however, this does not affect survival to adulthood noticeably. It is even possible that early and later mortality are somewhat compensatory: some larvae may be susceptible to cannibals

of the same age because they are of poor general condition (e.g., reflected by longer instar duration; Matthey 1976), but would otherwise most likely die from other causes, such as molting failure or disease.

Teneral adults from individual rearings had a substantially lower weight than those from the two group rearing treatments, but the predator exclusion and predator access treatments did not differ significantly (Fig. 3A). In contrast, Spence (1986) found that final weights were clearly higher for individuals reared under ambient predation levels than those of the predator exclusion treatment. He attributed this in part to higher natural food levels in the open compartments, as screened compartments may have excluded not only predators, but also emerging insects normally eaten by gerrids. In this experiment, however, food limitation and competition are ruled out as determining factors because the individual rearings resulted in a significantly lower mean weight despite food provided ad libitum.

Variation in growth performance among the three treatments is even more apparent for development time (Fig. 3B), where all pairwise comparisons were statistically significant. Again, there is no evidence for effects of competition, which would have produced the reverse order of treatments. In contrast, Spence (1986) found that predator access had little effect on the mean, but clearly narrowed the range of development times by reducing both tails of the distribution. In this experiment, the distributions of development time only differed among treatments in their left tails, but not in their right tails, where one would expect the effects of cannibalism by faster-growing larvae on slower-growing ones (e.g., Matthey 1976).

There was a negative association between development time and final weights, both within and between treatments. Such negative correlations have been found repeatedly in our study population, as well as in other gerrids (Blanckenhorn and Fairbairn 1995), and may be due to the physiological mechanisms underlying molting control (C. P. Klingenberg and J. R. Spence, unpubl.). Individually reared bugs had the poorest growth performance, whereas those from the treatment with the highest larval density, group rearings with predators excluded, showed the most vigorous growth. This is in agreement with casual observations in the laboratory, where growth and survival often are better in mass cultures than in individual rearings. The mechanisms underlying this phenomenon are unclear but worthy of investigation.

Altogether, our study clearly confirmed that predation is the dominant factor determining survival to the adult stage in this water strider population. In addition, intracohort cannibalism contributes substantially to mortality in the first few days of larval life. Most importantly, this study identifies poorly understood aspects of processes affecting mortality patterns. For

example, there are substantial differences from related species in the relative roles of cannibalism and predation (cf. *Gerris pingreensis*: Spence and Cárcamo 1991) and in the temporal pattern of mortality (*G. lacustris*: Zimmermann et al. 1982). Furthermore, it appears that slight changes in experimental conditions and timing generated striking differences in survival and growth performance from a similar study (Spence 1986). Thus, seasonal variation in action of mortality factors deserves further attention. The physiological basis of growth and its links to both competitive and synergistic interactions among larvae remain largely unclear, but seem to have a large impact on patterns of mortality. Future studies will need to address these problems to understand the processes determining survival of invertebrate predators in natural communities.

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