

Direct and indirect effects of juvenile *Buenoa macrotibialis* (Hemiptera: Notonectidae) on the zooplankton of a shallow pond

Abstract—We investigated the effects of juvenile *Buenoa macrotibialis* on the small bodied (<500 μm) zooplankton assemblage with which it naturally occurs. By monitoring 37–46-liter enclosures with and without *Buenoa* over 9–12 d, we found that second and fourth instar *Buenoa* caused large declines in the copepod *Tropocyclops extensus* and the rotifer *Hexarthra mira*. Additionally, populations of several small rotifers increased in the presence of fourth instar *Buenoa*, probably because of release from *Tropocyclops* predation, competition, or both.

Notonectids are predaceous aquatic insects known to cause dramatic community changes (Murdoch et al. 1984; Geddes 1986; Arnér et al. 1998) as well as phenotypic and behavioral responses in their prey (Grant and Bayly 1981; Dodson and Havel 1988; Dodson 1988; Lüning 1992; Zagarese and Marinone 1992). However, their impact on smaller zooplankton (e.g., rotifers) has been mostly neglected, perhaps because notonectids typically prefer the largest available prey that they can ingest (Cooper 1983; Murdoch and Scott 1984). Although some prey may not be directly affected by predation, they may still experience positive or negative indirect effects of a predator's presence (reviews in Wootton 1994; Pace et al. 1999). Here we investigate direct and indirect effects of juvenile notonectids on the natural zooplankton assemblage of a permanent, shallow, fishless pond (Johnson Pond) in Vermont, U.S.A., paying particular attention to effects on small taxa which were abundant during our study period.

We were interested in the Johnson Pond system for several reasons. First, most studies of notonectid effects on zooplankton communities have been done in comparatively species-poor communities of temporary ponds and cattle tanks (Fox 1975; Murdoch et al. 1984; Blaustein 1998). Those sites certainly represent important habitat for notonectids, but notonectids also are common in permanent ponds worldwide. Second, the pelagic zooplankton community of Johnson Pond is dominated by small-bodied taxa (Gilbert and Hampton unpubl.) of a size range generally not included in notonectid studies (<0.5 mm body length). Third, juvenile notonectid diets are less well known than adult diets, and most juvenile diet descriptions are based on direct observations of predator–prey interactions (*but see* Giller 1986), a method naturally biased toward observation of large prey (Streams 1974). Fourth, the impact of juvenile notonectids on pelagic zooplankton in Johnson Pond was suspected to be dramatic because juveniles are abundant in the central, open water during the summer months and may be a dominant invertebrate planktivore. Several researchers have noted that *Buenoa* appears to be primarily an open-water forager (Hungerford 1933; Gittelman and Bergtrom 1977).

We used 37–46-liter enclosures in separate 9- and 12-d experiments to test the hypothesis that the presence of juvenile *Buenoa macrotibialis* would reduce population sizes

of some zooplankton species. We did not expect to see indirect effects of *Buenoa* on zooplankton populations over such short experimental periods, but were surprised to discover that these were pronounced.

Study site—Johnson Pond, located on privately owned land in Norwich, Vermont, U.S.A. (43°44'N 72°18'W), is small (0.1 \times 0.05 km), shallow (maximum depth 1.5 m), and fishless. Gilbert and Hampton (unpublished) sampled the zooplankton community during day and night intermittently from May to October 1998, and found it to consist primarily of small-bodied (<0.5 mm) cyclopoid copepods (*Tropocyclops extensus*) and rotifers (*Hexarthra mira*, *Keratella cochlearis*, *Anuraeopsis fissa*, *Polyarthra remata*, and *P. dolichoptera*). Many potential zooplanktivores are present, such as newts, notonectids, predaceous diving beetles, odonate larvae, *Chaoborus* larvae, and cyclopoid copepods. The most abundant open-water zooplanktivores during our study were red-spotted newts (*Notophthalmus viridescens*) and the small notonectid *B. macrotibialis*. Newts were often observed in the water column or perched among *Chara* and *Potamogeton* stands in the central part of the pond during the study period, and were regularly found in traps suspended near the water surface the following year (Hampton unpubl.).

Throughout the summer *Buenoa* is patchily distributed outside the littoral zone in approximately the upper third of the water column. *Buenoa* in Johnson Pond appears to overwinter as eggs, consistent with Rice's (1954) descriptions of *B. macrotibialis* and *B. limnocastoris* in Michigan. In Johnson Pond, juvenile *Buenoa* hatch in mid-May and become abundant by early June. Adults appear in late June, and a new juvenile cohort begins to develop in July. This later cohort is not as numerically large or temporally uniform in development as the first. Juveniles are mostly absent by mid-September, when adults exhibit a great deal of mating behavior. Adults persist in the pond until ice develops in November, but presumably die over the winter.

Enclosure experiments—Four rafts constructed of cedar and Styrofoam each supported two clear plastic bags open at the top and covered with 0.5 mm plastic mesh to exclude terrestrial detritus and insects. The rafts were anchored in open water near the littoral zone in water deep enough to allow the bags to hang freely from the rafts. The bags were closed at the bottom and were approximately 0.75 m deep and 0.4 m in diameter. In experiment 1 (with second instar *Buenoa*), we filled each of the bags with 37.9 liters of well-mixed whole pond water collected on the afternoon of 29 July 1998. From a boat, we scooped the water with buckets from the water surface in the middle of the pond, alternated pouring buckets into two large plastic containers (~150 liters) in the boat, and mixed the containers vigorously. Then we filled each enclosure with water from both containers,

alternating containers and enclosures during the process to improve the uniformity of zooplankton abundance and composition among the enclosures. We collected 40 second instar *Buenoa* (~1.7-mm body length) and placed 10 of them in each of the four experimental enclosures (0.26 individuals L^{-1}). Four enclosures without *Buenoa* served as controls. Our protocol for experiment 2 (with fourth instar *Buenoa*) was similar, with the following exceptions. As we discovered that zooplankton distribution changed vertically with time of day (Gilbert and Hampton unpubl.), we filled the enclosures with 45.4 liters of surface water collected both during the afternoon (22.7 liters) and night (22.7 liters) of 27 August 1998. During the day, we collected 20 fourth instar *Buenoa* (~3.6-mm body length). At night, after the enclosures were filled, we placed five of them in each of the four experimental enclosures (0.11 individuals L^{-1}). These experimental predator densities were comparable to juvenile *Buenoa* densities in the field that summer. On 2 July 1998, we estimated from haphazard daytime sweep net samples that the open water density of *Buenoa* instars 1–4 ranged from 0.018 individuals L^{-1} to 0.23 individuals L^{-1} . Because locations for our sweep net samples were blindly chosen, these field estimates do not represent the highest densities found in *Buenoa* patches.

Zooplankton were sampled in all enclosures on the start date and then periodically every 3 to 5 d. We used a 1-liter beaker and mixed the water in each enclosure from bottom to top six times and then scooped out 2 liters of water. We concentrated this sample through a 25- μm mesh and preserved the zooplankton with acid Lugol's solution. Water temperature in the enclosures was similar to that in the open water of the pond. After the last samples were taken, all remaining water from each enclosure was strained through a 0.5 mm mesh cloth. The mesh was then rinsed over a container, and all contents were preserved for enumeration of larger and rarer zooplankton. Mean *Buenoa* survival was 80% in experiment 1 and 85% in experiment 2.

We counted all zooplankton in each sample, without subsampling, at 50 \times magnification with a dissecting microscope. *Tropocyclops* copepodites and adults were summed together, and nauplii were counted separately. Nauplii were probably almost all *T. extensus*, but some may have been those of *Acanthocyclops vernalis*. All count data were log-transformed, which did not qualitatively change the results of the following model but did improve normality and homoscedasticity to meet model assumptions. We used a repeated measures ANOVA (JMP, SAS Institute) in MANOVA context to determine differences between control and experimental treatments for each zooplankton taxon that numerically comprised >1% of the zooplankton community on any given date during an experiment. Within each experiment, we used the Dunn-Šidák formula to adjust the acceptable *P*-value to allow for nonindependence of zooplankton taxa across analyses (experiment-wise *P* = 0.05).

Because prey body size has so often been shown to be important in notonectid predator-prey interactions (Gittelman 1978, Cooper 1983; Scott and Murdoch 1983; Arnér et al. 1998), we estimated the predator effect on each of the most common zooplankton taxa using a common metric and regressed it onto prey body length (Cooper 1983; Dodson

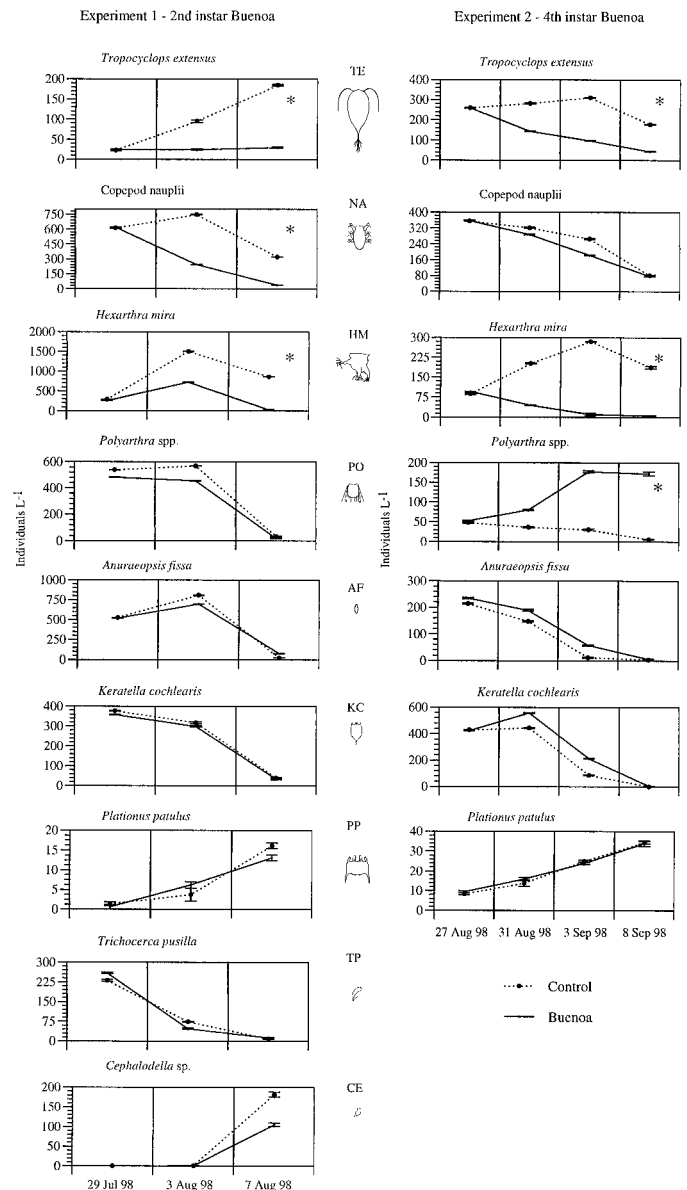


Fig. 1. Mean zooplankton concentration (± 1 SE) in enclosures with and without *Buenoa* predators, calculated from enumeration without subsampling of 2-liter zooplankton samples. * indicates significant differences between treatments (experiment-wise *P* < 0.05). Generalized body shapes of prey are shown next to the abbreviated prey name.

and Cooper 1983; Osenberg and Mittelbach 1996; Osenberg et al. 1997). Predator impact (PI) on the ninth day of each experiment was calculated as: $PI = \ln(N_E/N_C)/(tP)$, where N_E is the mean density of the prey populations in the predator treatments, N_C is the mean density of the prey populations without predators, t is the duration of the experiment, and P is the number of predators in each enclosure.

Our methods for evenly distributing zooplankton among enclosures were highly effective (Fig. 1). Densities of zooplankton taxa on the start dates, 29 July and 27 August, were remarkably similar in control and experimental treatments. We determined significance of a *Buenoa* effect mainly by

examining how this predator changed the trajectory of zooplankton populations through time (time \times treatment interaction terms). However, because the start-date densities were almost always the same, a significant treatment term also indicated a significant predator effect. Where initial zooplankton density was not the same, the treatment effect was not interpreted as *Buenoa* effect.

The effects of *Buenoa* on the zooplankton are shown in Fig. 1. The *P*-values reported here were compared to the Dunn-Šidák corrected *P*-values discussed above to determine significance ($P = 0.0057$ for experiment 1; $P = 0.0073$ for experiment 2). The second instar *Buenoa* in experiment 1 significantly depressed numbers of *T. extensus* nauplii (time \times treatment $P = 0.0319$, treatment $P = 0.0008$), copepodites and adults (time \times treatment $P < 0.0001$, treatment $P = 0.0009$), and the rotifer *H. mira* (time \times treatment $P = 0.0037$, treatment $P = 0.0003$). The larger *Buenoa* in experiment 2 also significantly reduced *Tropocyclops* copepodites and adults (time \times treatment $P = 0.0006$, treatment $P < 0.0001$) and *Hexarthra* (time \times treatment $P = 0.0007$, treatment $P < 0.0001$), but the decrease in nauplii was not significant (time \times treatment $P = 0.0264$, treatment $P = 0.0390$).

Several rotifer species increased in the treatments with fourth instar *Buenoa* (experiment 2), an effect not seen in the treatments with second instar *Buenoa* (experiment 1). *Polyarthra* spp. (mostly *P. remata*) increased dramatically (time \times treatment $P = 0.0071$, treatment $P = 0.0005$). Two other small species, *A. fissa* and *K. cochlearis*, also increased though not significantly (*Anuraeopsis*: time \times treatment $P = 0.0514$, treatment $P = 0.0148$; *Keratella*: time \times treatment $P = 0.3205$, treatment $P = 0.0216$). The treatment effect for *A. fissa* should be treated cautiously, because initial densities were somewhat different and trajectories in both treatments look similar (Fig. 1).

The effects of *Buenoa* presence on this small-bodied zooplankton community appeared to be related to prey body size (Fig. 2), although the regressions were not quite significant. The smallest taxa ($<150 \mu\text{m}$) were mostly unaffected, or positively affected, by *Buenoa*, whereas the largest of the common community members were negatively affected.

The large zooplankton retained by the coarse mesh at the end of the experiments were counted without subsampling, such that all animals larger than 0.5 mm in each enclosure were counted, excluding any that may have adhered to the bags after rinsing. These data were analyzed separately with Welch's one-way ANOVA. These mean numbers of taxa were not significantly different between treatments in either experiment (Table 1). The distributions showed little or no pattern, with two exceptions. In treatments with the second instar *Buenoa* (experiment 1), *Acanthocyclops vernalis* was slightly less abundant ($P = 0.06$). In treatments with the fourth instar *Buenoa* (experiment 2), the large cladoceran *Simoccephalus serrulatus* was somewhat less abundant ($P = 0.07$). No adjustments for non-independence were made of the *P*-values reported for these larger taxa.

Zooplankton population declines—We can infer from these results that small zooplankton were the primary *Buenoa* prey in our enclosures, and are likely an important re-

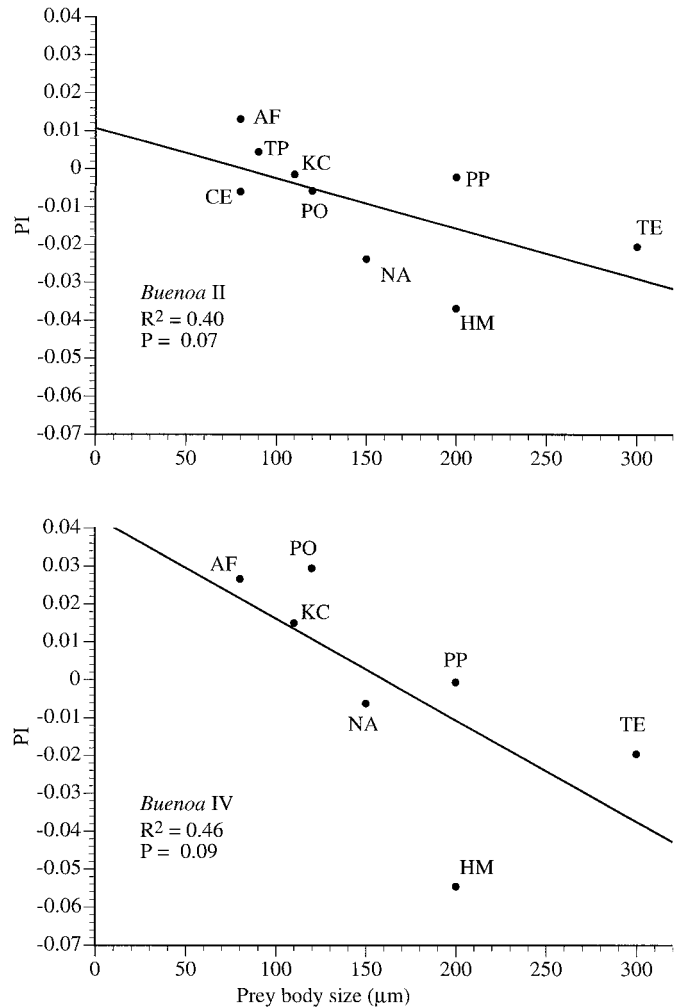


Fig. 2. Relationship between predator impact, $\ln(N_E/N_C)/(tP)$, and prey body length. See Fig. 1 for taxon abbreviations.

source during notonectid development in Johnson Pond. We observed throughout the experiments that juvenile *Buenoa* continued to grow and most molted once near the end of experiments. Thus, *Hexarthra* and *Tropocyclops* probably were the most important prey of both juvenile instars of *Buenoa*, a conclusion strongly supported by the large differences in prey abundance between control and predator treatments in both experiments (Fig. 1). We consider the prey in our enclosures to have been a fair representation of naturally occurring potential prey for *Buenoa* in Johnson Pond. As previously discussed, *Buenoa* is primarily found in open water, and thus is unlikely to frequently encounter littoral prey that were mostly excluded in our experiments. The lack of potential surface prey in the enclosures probably also was unimportant, since *Buenoa* seems to be exclusively zooplanktivorous (Hall et al. 1970; Gittelmann 1974) and probably does not commonly attack terrestrial prey trapped on the surface film as do some other notonectid genera (Gittelmann 1974, 1977; Cooper 1983; Cooper et al. 1985).

The decline of *Hexarthra* in the *Buenoa* treatments certainly is due to its ingestion by this notonectid and cannot

Table 1. Mean total number (± 1 SE) of large (>0.5 mm) animals found in each treatment at the end of enclosure experiments with second and fourth instar *Buenoa* predators. The initial volume of the second instar enclosures was 39.75 liters, and the end volume was 35.75 liters. The initial volume of fourth instar enclosures was 45.4 liters, and the end volume was 41.4 liters. There were 10 second instar *Buenoa* per enclosure, and five fourth instar *Buenoa* per enclosure. No treatment differences were significant using Welch's ANOVA. Boldface indicates that *F*-values were almost significant, as discussed in text.

Taxon	Experiment 1 Second instar <i>Buenoa</i>		Experiment 2 Fourth instar <i>Buenoa</i>	
	Control	Predator	Control	Predator
<i>Acanthocyclops</i>	17.5 (9.9)	3.7 (3.5)	1.5 (1.3)	1.8 (1.7)
<i>Chaoborus</i>	2.3 (3.2)	1 (1)	5.3 (2.6)	2.5 (3.8)
Juvenile pleids	1 (1.2)	0.3 (0.6)	0	0
Ostracods	9 (3.6)	9 (9.2)	2.3 (1.5)	3.8 (4.4)
Chironomids	3 (1.8)	1.3 (1.2)	1 (1.4)	1 (1.2)
<i>Simocephalus</i>	6.8 (5.4)	1.3 (1.5)	28.5 (13.5)	10.8 (4.2)
Mites	0.5 (0.6)	0	0	0
Mayfly larvae	1 (1.2)	1.3 (1.2)	1 (0.8)	0.8 (0.6)
Hydrophilid beetles	0	0.3 (0.6)	0	0
Dipteran larvae	2.3 (3.9)	0	0.3 (0.5)	0.3 (0.6)
<i>Sida</i>	0	0	20.5 (8.3)	14.3 (10.4)
<i>Ceriodaphnia</i>	0	0	15 (19.5)	1.8 (4.0)

be attributed to competition for shared resources. *Buenoa* is strictly predatory, and *Hexarthra* probably is primarily detritivorous (Pourriot 1965). In laboratory experiments, juvenile *Buenoa* readily eats *Hexarthra mira* (Hampton and Gilbert unpubl.).

The suppression of *Tropocyclops* may be the effect of *Buenoa* predation on nauplii, copepodites, or adults. Predation on any of these stages might produce the observed decreases in both experiments (Fig. 1). In laboratory experiments, *Buenoa* instars 2–6 can prey on *Tropocyclops* adults and copepodites (Diéguez and Gilbert unpubl.), but similar experiments with nauplii have not been done.

It is unlikely that *Buenoa* suppressed *Tropocyclops* through competition for limiting food resources. *Buenoa* is carnivorous, whereas *T. extensus* (formerly known as *T. prasinus mexicanus*) eats algae and probably only micro-zooplankton, including some rotifers (Stemberger and Gilbert 1984; DeMott and Watson 1991; Adrian and Frost 1993). Because many small rotifers were present in the enclosures with *Buenoa* for most of the experimental period (Fig. 1), predation by *Buenoa* on *Hexarthra* should not have appreciably affected the food available to *Tropocyclops*. In addition, *Hexarthra* may be too large for *Tropocyclops* to ingest.

Our observation that *Buenoa* suppressed *Tropocyclops* and *Hexarthra* is consistent with results from some previous studies. Notonectids are known to prey on copepods (Streams 1974; Cooper et al. 1985; Geddes 1986; Giller 1986; Gilbert and Burns 1999; Gilbert and Shiel unpubl.), although the copepod prey studied generally have been larger than *T. extensus* and less preferred than cladocerans and dipteran larvae. Ingestion of *Hexarthra* in our experiments is consistent with the finding of Gilbert and Burns (1999) that juveniles of the notonectid *Anisops wakefieldi* ate only relatively large (>0.15 mm) rotifers.

Of the common rotifer taxa that were not eaten in our experiments, most (*Keratella cochlearis*, *A. fissa*, *Polyarthra* spp., *Cephalodella* sp., and *Trichocerca pusilla*) probably were too small for *Buenoa* to exploit (Fig. 2). Gilbert and

Burns (1999) reported that juvenile *Anisops wakefieldi* significantly suppressed *P. dolichoptera*. This rotifer is larger (~ 150 μm) than *P. remata* (~ 120 μm), and hence perhaps more susceptible to notonectids. Also, perhaps the presence of more highly preferred prey in our enclosures may have reduced *Buenoa* predation on *Polyarthra* (see Jeffries 1988; Chesson 1989).

Prey body size appeared to be an important determinant of predator effect in this assemblage (Fig. 2). However, other factors clearly affect this relationship. For instance, *Hexarthra* was more negatively affected by *Buenoa* than was *Tropocyclops*, despite its smaller size, perhaps because *Hexarthra* was capable of much higher reproduction in the control treatments over these relatively short experimental periods. *Platyonus patulus* (formerly known as *Platylas patulus* and then *Brachionus patulus*) is approximately the same size as *Hexarthra*, but showed no response to *Buenoa* presence (Fig. 2). In laboratory experiments, *Platyonus* can be eaten by *Buenoa* (Hampton and Gilbert unpubl.). However, it was very rare in the enclosures (Fig. 1) and thus may not have been selected. Also, it is usually attached to substrata by a mucus strand, and thus may rarely have been encountered by *Buenoa*.

Zooplankton population increases—In the enclosures with larger *Buenoa* (experiment 2), the increase in *Polyarthra*, and that of *Keratella* and *Anuraeopsis* to a lesser extent, probably is due to the decline of *Tropocyclops*. Release from *Hexarthra* competition is unlikely. In both treatments of experiment 1, *Hexarthra*, *Polyarthra*, *Keratella*, and *Anuraeopsis* coexisted in greater abundance than they did in experiment 2 (Fig. 1). In addition, Pourriot (1965, 1977) reported no overlap in the diets of *Hexarthra* and *Polyarthra*. *H. mira* is probably a specialist on detritus, whereas *Polyarthra* eats a variety of algae (see also Bogdan and Gilbert 1984, 1987). Most *Keratella* species also eat various algae in addition to detritus (Pourriot 1965, 1977; Bogdan and Gilbert 1984, 1987). *Anuraeopsis* may compete with

Hexarthra for detritus. Detritus may have been in lower abundance in the control treatment of experiment 2 and thus limiting for *Anuraeopsis*. It is most likely that increases of small rotifer taxa in the *Buenoa* treatments of experiment 2 were caused by release from *T. extensus* predation, competition, or both. Because *T. extensus* is omnivorous, it is difficult to determine whether predation or competition is more important.

Hall et al. (1970) reported an increase in *K. cochlearis* in experimental pools with high densities of odonate and notonectid predators. This increase corresponded to decreases in large cladocerans, and so was likely due to release from exploitative and interference competition with cladocerans (see Gilbert 1988). The presence of *Craspedacusta sowerbyi*, a freshwater jellyfish, also led to increases of *K. cochlearis* and *Brachionus angularis* in short-term (28 h) laboratory experiments (Dodson and Cooper 1983). The authors speculated that these increases were caused by the removal of the predatory rotifer *Asplanchna* by jellyfish predation.

Differences between experiments—The most obvious difference between the two experiments is that the abundances of small rotifer taxa significantly increased only in experiment 2 with fourth instar *Buenoa*. This finding was surprising because the predator density was less than half of that in experiment 1 with the second instar predator. We suggest two explanations. First, inclusion of the nighttime surface water in experiment 2 greatly increased the initial density of copepods. Thus, *Tropocyclops* predation and competition in the control would have been much stronger, and *Tropocyclops* removal by *Buenoa* in the experimental treatments would have provided the opportunity for more resounding effects. Second, the fourth instar *Buenoa* in experiment 2 may have had higher per capita ingestion rates than the second instar *Buenoa* in experiment 1.

Conclusions—Juvenile *Buenoa* probably subsists on small cyclopoid copepods and large rotifers such as *Hexarthra* during its development in the open water of Johnson Pond. Because of its strong and direct suppression of the copepods, it indirectly releases small rotifers from predation by, or competition with, the copepods.

Direct effects of adult notonectids, particularly in the larger-sized genus *Notonecta*, probably are limited to larger prey. Researchers have consistently reported that average prey size increases with notonectid size (Ellis and Borden 1970; Streams 1974; Fox 1975; Murdoch and Scott 1984; Giller 1986). As notonectids grow larger, they increasingly ignore smaller prey (Cooper 1983; Scott and Murdoch 1983). Ellis and Borden (1970) suggest that larger notonectids may be morphologically ill-equipped to handle small prey. The indirect effects we report for small rotifer taxa should be expected for backswimmers of any size, given that notonectids are known to remove the largest available zooplankton prey, and thus probably the most effective zooplankton competitors and predators. Indirect effects of aquatic insect predation on zooplankton communities likely have been vastly underestimated in the past because of neglect of smaller (<0.5 mm) taxa. Overall, interactions between aquatic insects and small zooplankton have been rarely studied. Notable excep-

tions are the comprehensive work of Hall et al. (1970) in which notonectid and odonate predators were manipulated, and studies on *Chaoborus* which often report results for small zooplankton (e.g., Elser et al. 1987; Moore 1988a, 1988b; González 1998).

Several studies suggest that rotifer taxa may be more directly affected by insect predation than previously thought. A notonectid from the Southern Hemisphere, *Anisops deanei*, depleted populations of the rotifer *Brachionus calyciflorus* in laboratory experiments with naturally cooccurring prey assemblages (Gilbert and Shiel unpubl.). Zagarese and Marinone (1992) showed that *Keratella tropica* had shorter spines in the presence of *Buenoa*, an intriguing observation suggesting that a notonectid kairomone may induce a developmental response in the rotifer that reduces its susceptibility to notonectid predation. Walsh (1995) has demonstrated that the larval damselfly *Enallagma carunculata* can effectively prey on the common littoral rotifer *Euchlanis dilatata* in the laboratory, and several researchers report that unspecified rotifers are included in larval odonate diet (Lawton 1970; Pearlstone 1973). Direct and indirect effects of insect predators on rotifers may be particularly strong in fishless ponds where macroinvertebrate predators can proliferate (Macan 1965, 1966; Bennett and Streams 1986; Mittelbach 1988; Evans 1989).

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Ammonium excretion by Antarctic krill *Euphausia superba* at South Georgia

In Atkinson and Whitehouse (2000) the last two sentences of the paragraph ending at the top of the right column of p. 57 should read:

Samples were analyzed colorimetrically for dissolved nutrients using Technicon segmented flow analyzers (Mantoura and Woodward 1983; Whitehouse 1997). Previous intercalibration tests had shown that the methods used were comparable, with detection limits of 0.01–0.02 mmol m⁻³ and reproducibility (the percentage of significant difference of 10 replicates at 3.0 mmol m⁻³) of 0.4–1.0% (Mantoura and Woodward 1983; Whitehouse and Woodley 1987).

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Diffusive boundary layers of the colony-forming plankton alga, *Phaeocystis* sp.—implications for nutrient uptake and cellular growth

There is a printing error in Equation 10 of Ploug et al. (1999). This equation should read

$$Sh = 1.014 + 0.15x(Pe)^{1/2} \quad (10)$$

The correct constant (0.15) was used in the calculations. This printing error thus has no consequences for the conclusions of the paper.

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