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Selective predation on cladocerans by common pond insects

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A variety of common pond insects was presented with a mixture of different size classes of *Daphnia magna* or different sizes of *Daphnia pulex*, *Moina affinis*, and *Ceriodaphnia* sp. in predation trials. Juvenile *Belostoma flumineum* and most instars of *Notonecta undulata* and *Anax junius* fed at the highest rates on the largest available cladoceran prey, and late-instar *Buenoa confusa* fed at the highest rates on prey between 0.8 and 2.0 mm in length. Predation rates of instar IV *Chaoborus americanus* larvae were highest on *Daphnia* < 1 mm in length, and lowest on *Daphnia* > 2 mm in length. First-instar *Chaoborus* larvae did not eat cladocerans in these trials. The size-selective feeding patterns exhibited by *Notonecta* adults and late-instar *Anax* were similar in the light and dark, although overall feeding rates were depressed in the dark. *Buenoa*, on the other hand, only exhibited size-selective feeding in the light. The results indicate, however, that all of these insect predators can feed in the dark. Predation rates for late-instar *Chaoborus* larvae were unaffected by light conditions or the presence of filamentous algae. *Chaoborus* larvae were readily eaten by late-instar *Notonecta* and *Anax*.

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Des insectes d'étang ont été mis en présence de *Daphnia magna*, *Daphnia pulex*, *Moina affinis* et *Ceriodaphnia* sp. au cours d'expériences sur la prédation. Les jeunes *Belostoma flumineum* et la plupart des stades de *Notonecta undulata* et d'*Anax junius*registrent leur taux maximal de prédation en se nourrissant des plus gros cladocères disponibles et les *Buenoa confusa* de dernier stade préfèrent les proies entre 0,8 et 2,0 mm de longueur. Les larves de stade IV de *Chaoborus americanus* ont leur taux maximal de prédation lorsqu'elles se nourrissent de *Daphnia* < 1 mm et leur taux minimal, lorsqu'elles se nourrissent de *Daphnia* > 2 mm. Les larves de *Chaoborus* de premier stade n'ont pas mangé de cladocères durant les expériences. La sélection des proies en fonction de la taille chez les adultes de *Notonecta* et les derniers stades d'*Anax* est la même à la lumière et à l'obscurité, bien que les taux généraux de consommation de nourriture diminuent à l'obscurité. En revanche, *Buenoa* ne fait de la sélection de proies qu'à la lumière. Les résultats indiquent cependant que tous les prédateurs peuvent se nourrir à l'obscurité. Les taux de prédation chez les larves de *Chaoborus* de dernier stade ne sont affectés ni par les conditions de l'éclairage ni par la présence d'algues filamenteuses. Les larves de *Chaoborus* servent aussi de proies aux larves de derniers stades de *Notonecta* et d'*Anax*.

[Traduit par le journal]

Introduction

Although a number of studies have examined the prey preferences of fish, salamander larvae, copepods, and chaoborid larvae (reviewed in Zaret 1980; see also Pastorok 1981; Wong 1981; Li and Li 1979; Brambilla 1980), the prey preferences of many freshwater planktivores remain largely unknown. Until recently, information on prey selection by freshwater coelenterates, flatworms, water mites, mysids, amphipods, and a variety of predatory insects was largely nonexistent (Thompson 1975; Gittelmann 1978; Akre and Johnson 1979; Cooper and Goldman 1980; Dodson and Cooper 1983; Murtaugh 1981a, 1981b; Scott and Murdoch 1983; Riessen 1981). Many of these predators, however, are abundant in freshwater habitats, particularly fishless ponds and the littoral zone of lakes, and may exert a significant influence on zooplankton assemblages (Maly et al. 1980; Scott 1980; Arts et al. 1981; Cooper and Smith 1982). As part of a study examining the effects of predation on pond cladoceran populations (Cooper 1979), I investigated the selective feeding of common pond insects on cladocerans. The results of those investigations are presented here.

Methods

All insect predators and most cladoceran prey were collected from Bavarian Sausage Pond, a small pond on the outskirts of

Madison, Wisconsin (Smith and Cooper 1982). Some of the *Moina* used in these trials were collected from a small pond on the University of Wisconsin campus, and *Daphnia magna* was taken from laboratory cultures. Predation trials were conducted in the laboratory in jars filled to the 856-mL level with filtered (52 μ m) pond water. Temperature conditions were similar to surface summer water temperatures encountered in the field (20–23°C). A preliminary set of trials was designed to test the prey size preferences of three hemipteran predators (*Notonecta undulata*, *Belostoma flumineum*, *Buenoa confusa*), an odonate predator (*Anax junius*), and a dipteran predator (*Chaoborus americanus*). Ten individuals of each of two to three size classes of *Daphnia magna* were simultaneously offered to late instars of each predator species in jars placed under a 12 h light (L) : 12 h dark (D) photoperiod (= 23–35 total prey/L, experiment 1). In a second experiment (experiment 2) three *D. magna* size classes were offered to each of five *Notonecta undulata* instars (instars II to adult) under similar conditions. Subsequent prey-choice experiments offered one to three size classes of two or three cladoceran species (*Daphnia pulex*, *Ceriodaphnia* sp., *Moina affinis*) to each predator species. Equal numbers of each prey size class (10 to 20 per jar) were simultaneously offered to predators in these trials (= 46–69 total prey/L). For comparison, recorded densities of pelagic cladocerans in Bavarian Sausage Pond ranged from 0 to 1332/L (\bar{X} = 73) during the summer of 1978.

The effects of light on predation rates and prey selection were tested by concurrently conducting trials in complete darkness and constant, bright fluorescent light. In another set

of trials conducted in 258-mL volumes, *Chaoborus* predation rates were determined both in the light and in the dark, in the absence or presence of filamentous algae (0.05–0.49 g wet weight). In a final set of trials, instar III or IV *Chaoborus* larvae (10/258-mL jar) were fed to adult *Notonecta* or large *Anax* naiads.

Except for trials using *Chaoborus* larvae, one predator was added to each replicate jar. Two fourth-instar *Chaoborus* larvae or eight first-instar *Chaoborus* larvae were added to each replicate in which these predators were tested. Sizes of predators and prey, and the number of replicates in each experiment are presented in the Results section. Predators used in these experiments were either taken directly from the field or were starved for less than 24 h in the laboratory before experiments began.

In all experiments control and experimental jars were initially alike in all respects except for the addition of predator(s) to experimental jars. Numbers of living prey were counted in each jar at the end of each trial period. The difference between initial and final prey numbers in the experimental jars was corrected for control mortality (Healy 1952) and used as an estimate of the number of prey eaten during the trial period. Depending on the rate of prey disappearance, trial periods lasted from 2 to 69 h. From these data, predator clearance rate (k) values were calculated:

$$k = \frac{-\ln(P_f/P_o)}{XT}$$

where P_f and P_o are the final and initial prey densities (number per litre), X is the predator density (number per litre), and T is the length of the trial period in days; k has the dimensions "numbers of litres cleared of prey per predator per day" and is constant if the consumption rate (number of prey eaten per predator per day) is approximately a linear function of prey density (Frost 1972; Dodson 1975). Since initial densities of each prey type were equivalent, k can also be used as an index of predator selectivity. "Preference" and "selection" as used here mean that clearance rates for one prey type were consistently higher than those for another prey type. Prey length (exclusive of the tail spine in *Daphnia*), *Chaoborus* head lengths, and head widths of macroinvertebrate predators were measured with an ocular micrometer at $\times 6$ – $\times 25$. Statistical methods were taken from Conover (1971) and Wilcoxon and Wilcox (1964).

Results

In experiment 1 *Anax* naiads (head widths = 2.5–2.75 mm) and *Notonecta* adults exhibited a consistent preference for the largest *Daphnia*, *Chaoborus* IV larvae preferred the smallest *Daphnia*, and *Buenoa* subadults preferred the two smallest *Daphnia* size classes (sign test, $P < 0.05$; Fig. 1). While replication was not sufficient for statistical testing, additional trials involving *Buenoa* adults (head width = 1.3 mm) and *Belostoma* juveniles indicated that adult *Buenoa* preferred the intermediate *Daphnia* size class (1.9 mm) and juvenile *Belostoma* preferred the largest *Daphnia* size class (3.1 mm). In addition, a small *Anax* naiad (head width = 1.6 mm) gave k values of 0.48 for

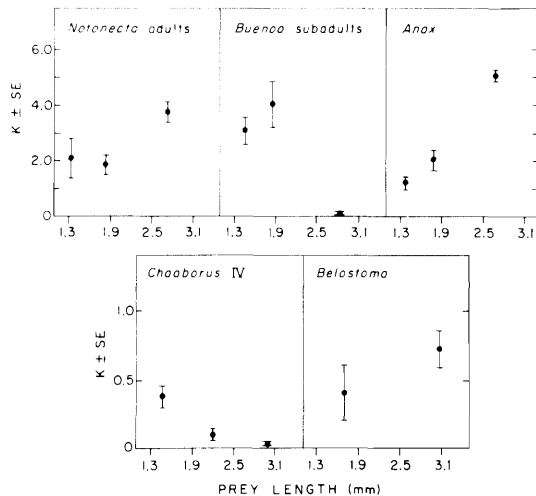


FIG. 1. Clearance rates of common Bavarian Sausage Pond predators on different sizes of *Daphnia magna*. There were five replicate trials for each predator species, except *Belostoma* juveniles where there were three. Mean head widths for each predator species were as follows: *Notonecta* adults = 2.7 mm, *Buenoa* subadults = 1.1 mm, *Anax* naiads = 2.6 mm, *Belostoma* juveniles = 2.2 mm. Mean head length of *Chaoborus* IV larvae was 1.4 mm.

both of the smallest prey sizes (1.5, 2.2 mm) and 0 for the largest prey size (3.0 mm)

In a series of 12 trials (experiment 2), five *Notonecta* instars were tested. Instar II *Notonecta* preferred the smallest available *Daphnia* size class (length = 1.3 mm) while larger instars (instars III to adult) preferred the two largest *Daphnia* size classes (length > 2 mm, Fig. 2). Instar IV *Notonecta* fed at higher rates on all *Daphnia* sizes than the other *Notonecta* instars ($P < 0.05$, Wilcoxon rank sum test). Instar V and adult *Notonecta* did not eat the smallest prey (length = 1.3 mm) in these trials.

In trials of predator preference for cladocerans collected from local ponds, *Chaoborus* IV larvae exhibited declining clearance rates with increasing *Daphnia pulex* size (k values for *Daphnia* 0.5–1 mm long > 1–2 mm *Daphnia* > 2–3 mm *Daphnia*, $P < 0.05$, median test). The k values for both juvenile and adult *Ceriodaphnia* and *Moina* were not significantly different. *Daphnia pulex* juveniles were eaten at significantly higher rates than *Ceriodaphnia* juveniles and *Ceriodaphnia* and *Moina* juveniles and adults were eaten at significantly higher rates than large *Daphnia* (> 2 mm) ($P < 0.05$, median test). Examination of the composite graph for both the *Daphnia magna* trials and the other prey-choice trials suggest that *Chaoborus* IV larvae may have an optimal prey size of 0.6–1.0 mm, although this trend is complicated by differences in k for different prey species (Fig. 3). *Chaoborus* I larvae

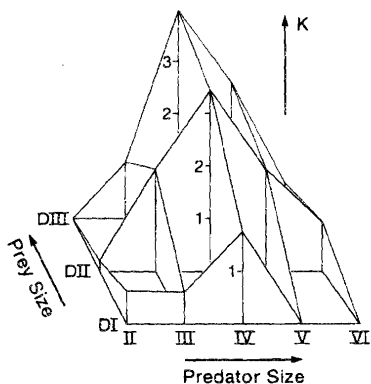


FIG. 2. Clearance rates of five *Notonecta undulata* instars feeding on three size classes of *Daphnia magna*. Head widths of each *Notonecta* instar were as follows: II = 1.4 mm, III = 1.6 mm, IV = 1.7 mm, V = 2.2 mm, VI = 2.6 mm. *Daphnia* lengths were as follows: I = 1.3 mm, II = 2.2 mm, III = 3.1 mm. There were three replicate trials for each of *Notonecta* instars IV to adult (VI), two for instar III, and one for instar II. Standard errors for nonzero k values (instars III–VI) were ca. 5% of their respective means.

TABLE 1. The effects of light and filamentous algae on clearance rates of *Chaoborus* IV larvae; $k_D = k$ value for *Daphnia*, $k_C = k$ value for *Ceriodaphnia* ($\bar{X} \pm S_x$, $n = 4$). Initially, there were 20 individuals of each prey species per 258-mL jar (= 155 cladocerans/L). There were no significant differences between k values obtained for any two treatments (median test, $P > 0.05$)

	Algae	No algae
Light	$k_D = 0.15 \pm 0.07$ $k_C = 0.06 \pm 0.02$	$k_D = 0.37 \pm 0.17$ $k_C = 0.18 \pm 0.09$
Dark	$k_D = 0.28 \pm 0.13$ $k_C = 0.06 \pm 0.01$	$k_D = 0.23 \pm 0.10$ $k_C = 0.12 \pm 0.12$

($P < 0.05$ for *Notonecta*, $P < 0.07$ for *Anax*, sign test; Figs. 4, 5). *Notonecta* exhibited the same feeding patterns in trials conducted in the dark, while *Anax* preferred large *Daphnia* (2.65 mm) over all other prey types in dark trials ($P < 0.05$ for *Notonecta*, $P < 0.07$ for *Anax*, sign test). *Anax* fed at significantly higher rates on both *Daphnia* size classes and *Moina* adults in the light as compared with the dark, and *Notonecta* fed at higher rates on 1.84 mm *Daphnia* and *Ceriodaphnia* adults in light as opposed to dark trials ($P < 0.05$, Wilcoxon rank sum test; the light vs. dark significance level for 2.65 mm *Daphnia* in the *Notonecta* trials was $P < 0.10$). In three additional trials, larger *Anax* naiads (mean head width = 7.7 mm) did not eat *Moina* or *Ceriodaphnia* and consistently preferred large *Daphnia* (2.65 mm) over smaller *Daphnia* (1.84 mm) despite the large variability in individual feeding rates (Fig. 5).

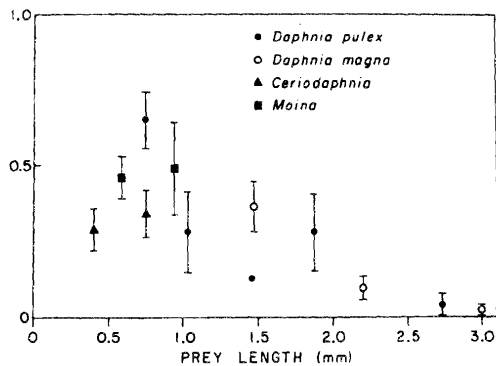


FIG. 3. Clearance rates of *Chaoborus* IV larvae on different sizes of different prey species. ●, *Daphnia pulex*; ○, *D. magna*; ■, *Moina*; ▲, *Ceriodaphnia*. Values represent means ± standard errors for 5–16 replicate trials.

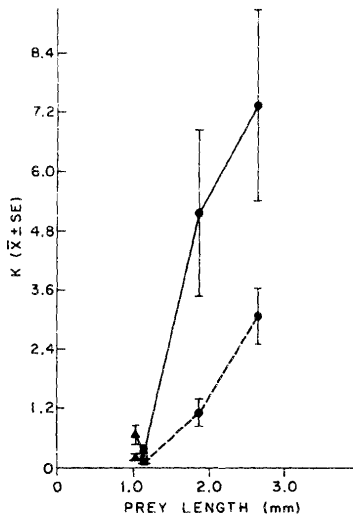


FIG. 4. Clearance rates of *Notonecta* adults on common cladoceran species. Solid line represents trials conducted in the light; the broken line represents trials conducted in complete darkness. Prey code as in Fig. 3. Values represent means ± standard errors for five replicate trials.

(mean head length = 0.34 mm) did not eat cladocerans in predation trials.

Chaoborus IV larvae fed as efficiently in the dark as in light, and the addition of filamentous algae to predation trials had no significant effect on *Chaoborus* clearance rates (Table 1). In this experiment *Daphnia* (mean length = 1.29 mm) was consistently preferred over *Ceriodaphnia* (mean length = 0.87 mm) regardless of light conditions and the abundance of filamentous algae ($P < 0.05$, sign test).

Both *Notonecta* adults and large *Anax* naiads (mean head width = 5.2 mm) showed a pronounced preference for large *Daphnia* (2.65 mm) over smaller *Daphnia* (1.84 mm) and for *Daphnia* adults over *Ceriodaphnia* and *Moina* adults in trials conducted under bright light

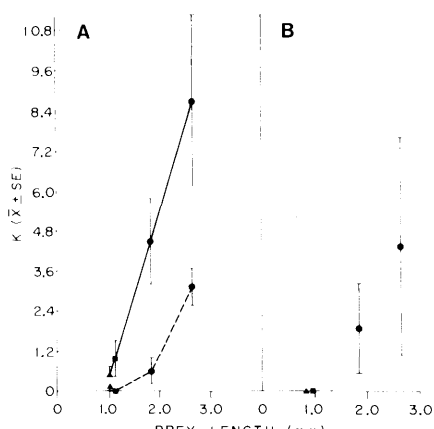


FIG. 5. Clearance rates of *Anax* naiads on common cladoceran species. The solid line represents trials conducted in the light; the broken line represents trials conducted in complete darkness. *Anax* in A had a mean head width of 5.5 mm, while *Anax* in B had a mean head width of 7.6 mm. Prey code as in Fig. 3. Values represent means \pm standard errors for four replicate trials in A, three trials in B.

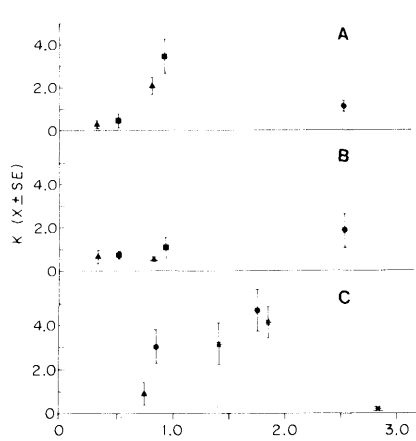


FIG. 6. Clearance rates of *Buenoa* adults on common cladoceran species. Trials in A were conducted under lighted conditions, trials in B were conducted in the dark, and trials in C were conducted under a 10 h L : 14 h D light cycle. Prey code as in Fig. 3, except asterisks denote *Daphnia magna*. There were five or six replicate trials for each of series A-C.

Buenoa adults exhibited higher k values on prey items between 0.8 and 2.0 mm long, as opposed to prey items that fell outside this size range, in trials conducted, at least partially, under bright light ($P < 0.05$, sign test, Figs. 6A and 6C). In addition, *Buenoa* preferred 1.78-mm *Daphnia* over 0.86-mm *Daphnia* in the set of trials conducted in a 10 h L : 14 h D photoperiod (Fig. 6C, $P < 0.05$, sign test). *Buenoa* showed no significant difference between k values obtained for any two prey classes under dark conditions (Fig. 6B). *Buenoa* fed at significantly higher rates on adult *Moina* and

Ceriodaphnia in the light as compared with the dark ($P < 0.05$, Wilcoxon rank sum test, Figs. 6A and 6B). *Buenoa* adults were size selective only under lighted conditions.

In a series of additional predation trials, late-instar *Chaoborus* larvae were fed to *Notonecta* adults or large *Anax* naiads (head width = 4.5–7.5 mm). Mean clearance rates for adult *Notonecta* were 0.30 L/predator per day ($n = 2$) for instar III *Chaoborus* and 0.6 L/predator per day ($s_{\bar{x}} = 0.02$, $n = 3$) for instar IV *Chaoborus*. Large *Anax* naiads exhibited mean clearance rates of 0.26 L/predator per day ($n = 2$) for instar III *Chaoborus* and 2.83 L/predator per day ($s_{\bar{x}} = 1.58$, $n = 4$) for instar IV *Chaoborus*. These results cannot be directly compared to the prey-choice trials because these *Chaoborus* trials were conducted in much smaller containers (258 mL). They indicate, however, that macroinvertebrates will prey on *Chaoborus* larvae when given the opportunity.

Discussion

Although some authors have characterized invertebrate planktivores as selective predators on small zooplankton (Hall et al. 1976; Dodson 1974), these and other results show that many invertebrate predators prey selectively on large zooplankton (see also Scott and Murdoch 1983; Cooper and Goldman 1980; Murtaugh 1981b). In these experiments most instars of *Notonecta* and *Anax* and juvenile *Belostoma* preyed selectively on the largest available zooplankton prey, whereas late-instar *Buenoa* preferred cladocerans between 0.8 and 2.0 mm in length. Although little data exists on the prey size preferences of these predators, results reported by Scott and Murdoch (1983) for *Notonecta hoffmanni* and by McArdle and Lawton (1979) for *Notonecta glauca* generally agree with those reported here for *Notonecta undulata*. Gittelman (1978) reported that *Notonecta undulata* adults, when presented with corixids ranging from 2 to 11 mm in length, fed at the highest rates on prey 4–5.5 mm long. In addition, Pritchard (1965) found that small *Aeshna interrupta lineata* naiads struck most frequently at discs 1 or 2 mm in diameter while smaller (0.5 mm) and larger (3–5 mm) discs were attacked at lower rates. My field observations indicate that late instars of *Notonecta* and *Anax* may primarily rely on terrestrial insects (for *Notonecta*) or dipteran larvae and oligochaetes (for *Anax*) as their principal food sources (see also Pritchard 1964; Streams 1974). Of the life history stages of *Notonecta*, instar IV nymphs consistently exhibit the highest predation rates on cladocerans (Scott and Murdoch 1983; McArdle and Lawton 1979; this study). Later instars of *Notonecta* and very large *Anax* naiads are probably more efficient at taking larger, nonplanktonic prey. All *Buenoa* instars, on the other hand, are primarily planktivorous.

Late instars of *Chaoborus americanus* exhibited the

highest clearance rates on the smallest *Daphnia* spp. available in these experiments, agreeing closely with size preferences reported by other investigators for this and similarly sized species (reviewed in Pastorok 1980; see also Brambilla 1980; Vinyard and Menger 1980). The larger *Chaoborus trivittatus* often selectively preys on larger *Daphnia* (optimal length ca. 1.5 mm (Pastorok 1981)). First-instar *Chaoborus* larvae did not eat small daphnids in predation trials, probably because small daphnids were too large for small chaoborids to capture and handle.

Although components of predator-prey interactions related to prey size appear to be major determinants of predator preference (discussed below), there were differences in predation rates on different prey species independent of prey size. *Chaoborus* IV larvae and *Buenoa* adults preyed at significantly higher rates on *Daphnia* juveniles than on similarly sized *Ceriodaphnia* adults (Figs. 3 and 6, but see Smyly (1980)). Scott and Murdoch (1983) obtained a similar result for *Notonecta* feeding on *Daphnia* and *Ceriodaphnia* of similar size. Furthermore, Scott and Murdoch (1983) found that *Notonecta* preferred *Moina* (length = 1.1 mm) over larger *Daphnia* (length = 1.9 mm), a result which contradicts my findings (Fig. 4). It is possible that this discrepancy is due to species-specific differences in behavior, since Scott and Murdoch (1983) used different species of *Notonecta* and *Moina* than I did. The design of some of the *Notonecta* and *Anax* trials precludes a clear delineation of species vs. size-specific prey selection, but recent studies using these or similar predators and a wider variety of *Daphnia pulex* sizes confirms the size-dependent feeding patterns reported here (S. D. Cooper, D. W. Smith, and J. R. Bence, in preparation).

The mechanisms for observed prey size preferences are probably related to the frequency of predator encounters with prey, the capture success of predators, and changes in predator response to prey. Predator-prey encounter frequencies increase with increasing prey size because prey swimming speeds and (or) predator reactive distances increase with increasing prey size (Pastorok 1981; O'Brien 1979). On the other hand, if prey are large relative to the predator, predators often have increasing difficulty with securing and handling prey as prey size increases (J. R. Bence and W. W. Murdoch, personal communication; Gittelmann 1978). These opposing behavioral trends may result in humped curves of selectivity vs. prey size, because selectivity will initially increase with increasing prey size owing to increasing predator-prey encounter frequencies, but will subsequently decline owing to the overriding importance of decreasing predator capture success (Pastorok 1981). Declines in *Chaoborus* clearance rates with increasing prey size and the upper prey size limits for small notonectids and aeshnids were probably

related to the low efficiency with which these predators captured and handled large prey (Vinyard and Menger 1980). Although capture success may be important in determining predation rates of notonectids and aeshnids feeding on some cladoceran species (O'Brien and Vinyard 1978; Cooper and Smith 1982), capture successes of large notonectids and aeshnids on the different sizes and species of prey used in these trials were often similar (S. D. Cooper, D. W. Smith, and J. R. Bence, in preparation). This is probably because the behaviors of these cladoceran species are not radically different and because these prey are small relative to these predators. The large prey size preferences of the large insect predators were probably the result of increased predator encounters with large prey. Furthermore, my observations indicated that the largest predators (e.g., *Notonecta*) often failed to respond to the smallest prey, and the smallest predators (e.g., *Chaoborus*) often avoided the largest prey (see also Scott and Murdoch 1983).

Chaoborus larvae fed at similar rates in the light and in the dark, which is not surprising since they use hydrodynamic cues to locate prey (Giguère and Dill 1979; Swift and Forward 1981). On the other hand, *Notonecta*, *Buenoa*, and *Anax* fed on some prey at higher rates in the light than in the dark (Figs. 4-6). Notonectids apparently use mechanical cues in the location and capture of prey, although sight may play a subsidiary role (Lang 1980; Murphey and Mendenhall 1973; Baerands 1950). Scott and Murdoch (1983) report that *Notonecta hoffmanni* feeds at slightly, but significantly, higher rates in the light than in the dark, and Giller and McNeill (1981) found that different *Notonecta* species exhibited different propensities for feeding in the dark vs. the light. Zalom (1978) reported no light-dark feeding differences for the eight notonectid species he tested, although his Fig. 3 suggests that *Notonecta kirbyi* ate significantly more at night while *N. lobata* fed at significantly higher rates during the day. *Notonecta undulata* fed at slightly, but not significantly, higher rates during the day, and *Buenoa* spp. showed little difference in light vs. dark feeding behavior (Zalom 1978; also see O'Brien and Vinyard 1978). A variety of evidence suggests that aeshnid naiads are primarily visual predators (Pritchard 1965; Oakley and Polka 1967; Sherk 1977). Richard (1960, cited in Pritchard (1965)), however, found that young aeshnid larvae may detect prey using mechanical cues, but that sight becomes increasingly important as the naiads grow. The results of these investigations suggest that the relative importance of mechanical vs. visual cues in prey detection by notonectids and aeshnids varies from species to species or from instar to instar.

The differences in feeding rates recorded from light vs. dark predation trials are difficult to interpret,

however, because light levels can affect the behavior of prey as well as predators. The size-selective patterns exhibited by *Notonecta* adults and late-instar *Anax* were similar in the light and dark, although overall feeding rates were depressed in the dark (Figs. 4 and 5). *Buenoa*, on the other hand, only exhibited size-selective feeding in the light, although this result may have been due to size-specific changes in prey behavior rather than changes in predator behavior (Fig. 6). Although Zalom (1978) and O'Brien and Vinyard (1978) could find no light vs. dark feeding differences for *Buenoa* or *Anisops*, these investigators presented their predators with large prey (brine shrimp or large *Daphnia*). My results for *Buenoa* also indicate that there were no significant differences in feeding rates on large *Daphnia* presented in the light or dark; however, there were significant light-dark feeding differences for smaller prey. In addition, dark feeding rates on at least some prey types were significantly different from zero for all predators, indicating that all have the capability to feed in the dark. Because notonectids can locate prey using vibrational signals, it is not surprising that notonectids exhibited significant predation rates in the dark. It is surprising, however, that large *Anax* naiads fed in the dark, because *Anax* has been characterized as a visual predator (Pritchard 1965). Additional experiments with large *Aeshna walkeri* naiads feeding on mayflies in complete darkness confirm that at least some aeshnids can capture prey in the absence of visual cues (S. D. Cooper, unpublished data). Although these insect predators may primarily use one type of cue in detecting prey, they apparently have the capability to capture prey using other sorts of cues.

What implications do these results have for the effect of these insect predators on cladoceran assemblages? Although the youngest instars of these predator species prefer smaller prey, the overall impact of these early instars on prey populations is limited owing to their short duration and their lower predation rates relative to later instars (Cooper 1979). In general, intensive predation by notonectids and aeshnids should favor the dominance of small cladoceran species, whereas intensive predation by *Chaoborus* larvae should favor the dominance of large cladoceran species. Field experiments examining the effects of these predators on zooplankton assemblages generally support this model (Hall et al. 1970; Scott 1980; Lynch 1979; von Ende and Dempsey 1981; Smith and Cooper 1982), although predation's effect may be obscured by increased prey fecundity resulting from (temporarily) reduced prey densities (Neill 1981). In addition, many predatory insects found in ponds and small lakes have minimal impact on cladoceran populations owing to the vertical and (or) horizontal segregation of predator and prey populations (Cooper 1979; Arts et al. 1981; Melville and

Maly 1981; Fedorenko 1975). For example, in Bavarian Sausage Pond hemipteran predators are found near or at the water's surface, while odonate naiads are found perching on vegetation. *Daphnia* and *Ceriodaphnia*, on the other hand, are most abundant in middepth water strata, and *Daphnia* is more abundant in open water than vegetated habitats (Cooper 1979; see also Cooper and Smith 1982). Although the mechanisms responsible for these distributional patterns are unclear, it is clear that prey and predator populations are often separated in space.

In addition to their direct effects on cladoceran populations, predators may indirectly affect prey populations through their interactions with other predator species. Direct observations indicate that all late-instar predators (*Buenoa*, *Notonecta*, *Anax*, *Chaoborus*) prey on younger conspecifics under crowded laboratory conditions (also see Fox 1975a, 1975b; von Ende 1979). In addition, late-instar *Notonecta* fed on almost all other insect predator species, *Anax* naiads fed on *Chaoborus* and *Ischnura* larvae, and *Buenoa* fed on *Chaoborus* larvae in laboratory aquaria. The predation trial results indicate the potential for macroinvertebrate predation on *Chaoborus* larvae in the field (see also Pritchard 1964). Hall et al. (1970) reported consistently lower *Chaoborus* densities in ponds where hemipteran and odonate predators were abundant than in ponds where these predators were rare. Cooper (1979) found that the relative abundance of *Chaoborus* late instars in littoral vs. open-water areas of a small pond was inversely correlated with *Notonecta*'s relative abundance in those habitats, although partial vertical segregation of these two predator species precluded the clear attribution of this pattern to direct interactions between them. If sufficiently intense, macroinvertebrate predation on zooplankton populations and macroinvertebrate predation on small-size selective invertebrate predators would contribute to the same result: the dominance of a zooplankton assemblage by a small zooplankton species.

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