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By

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ABSTRACT

A STUDY OF THE EFFECTS OF THREE MACROINVERTEBRATE PREDATORS ON FISH AND NOTONECTIDS

By

Michael Paul Rondinelli

In freshwater systems lacking large fish predators, much of the predation experienced by smaller fish and invertebrates may be attributable to macroinvertebrates. I examined the predation effects of three macroinvertebrate species on the survivorship and behavior of fish and backswimmers (Insecta: Notonectidae). Field experiments which subjected prey to predators in experimental enclosures showed that macroinvertebrates can impose significant mortality on fish and insect prey. Results from experiments involving two predator species provided no evidence of interactive effects on fish survivorship. Laboratory behavioral experiments showed conclusively that fish reacted differently in microhabitat choice and general activity to different insect predators. Laboratory predation experiments run under two different lighting conditions demonstrated that macroinvertebrates can prey as effectively in darkness as in the light, suggesting tactile, hydrodynamic, or chemical prey detection by these insects.

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Introduction

One of the driving forces regulating the structure of freshwater communities is predation. Many studies have documented the impact of predatory fish in structuring the distribution, abundance, and behavior of fish (Hall and Werner 1977, Milinski and Heller 1978, Werner et al. 1983, Mittelbach 1984, Power et al. 1985, Gilliam and Fraser 1987) and invertebrates (Brooks and Dodson 1965, Macan 1966, Hall et al. 1970, Stein and Magnuson 1976, Gliwicz 1986). Previous work which examined the impacts of invertebrate predators on fish populations, however, is almost entirely anecdotal (Cockerell 1919, Langlois 1932, Kingsbury 1936, Wright 1946, Pennak 1978, Foster and Ploch 1990), but see Crowl and Alexander (1989) for a noteworthy exception. There is considerable evidence that invertebrate densities are largely restricted by fish predation (Macan 1966, Hall et al. 1970, Bendell 1986). Fish predators tend to forage size-selectively, preying preferentially on and cropping off larger species as opposed to smaller species (Brooks and Dodson 1965, Crowder and Cooper 1982). In fishless ponds or ponds containing small fish species that are unable, because of gape-limitation, to feed on large invertebrates, insect predators may grow and reproduce very efficiently due to a lack of appreciable predation pressure, enabling them to achieve considerable densities and become potentially important sources of mortality for many aquatic species. Predation on fish and invertebrates in these systems may be induced solely or primarily by large aquatic hemipterans or larval odonates. It has been suggested that certain predatory macroinvertebrates such as the larva of the dragonfly, Anax junius, have the capacity to be the dominant predators in aquatic food chains when fish are absent (Robinson and Wellborn 1987). If populations of voracious insects such as A. junius can attain considerable sizes, studies investigating potential impacts by such predators are certainly worthwhile and perhaps necessary to the understanding of predator-prey dynamics and community structure in fishless ponds or systems devoid of large fish.

Much research has been devoted to the effects of odonate larvae on prey communities, in particular larval anurans (Woodward 1983, VanBuskirk 1988, Skelly and Werner 1990) but also cladocerans and benthic invertebrates (Thorp and Cothran 1984, Robinson and Wellborn 1987). Larval odonates feed on a variety of prey species and have been classified as generalist predators by many (e.g. Pritchard 1964, Folsom and Collins 1984, Thorp and Cothran 1984, Wallace et al. 1987). If such plasticity in diet exists and there is an abundant supply of small fish in addition to invertebrate prey, odonates would be expected to exert some predation pressure on fish species. Problems with rearing young fish in holding ponds resulting from odonate predation have been previously reported (Wilson 1917, Wright 1946). Kingsbury (1936) concluded that survivorship of fish in rearing ponds invaded by Anax junius larvae can easily be reduced by 50% or more. In addition to odonate larvae, other invertebrates, in particular hemipterans, have the capacity to impose considerable mortality in fish populations. Langlois (1932) found that large populations of Notonecta undulata in three Ohio ponds consumed all introduced largemouth bass fry within a very short time. Giant water bugs (Belostomatidae) are also highly predaceous on vertebrates such as fishes, tadpoles, and even snakes (Wilson 1958, Pennak 1978).

In the present study, I investigate the effects of predation by three macroinvertebrate species, larvae of the dragonfly Anax junius (Odonata: Aeshnidae), the backswimmer Notonecta (Hemiptera: Notonectidae), and the giant water bug Belostoma (Hemiptera: Belostomatidae), on populations of juvenile fathead minnows (Pimephales promelas) and notonectids. This was accomplished in part by field experiments, in which predator and prey densities were manipulated in experimental enclosures. I hypothesized that, based on the generalist foraging mode of each predator and their abilities to capture and consume fish, survivorship of fishes in enclosures containing any of the three predators would decrease. The extent of predation is, of course, dependent upon the success of individual predators, which in turn is contingent on a multitude of factors including density of prey (Blois-Heulin 1990), prey size (Werner et al. 1983), hunger level (Cloarec 1989), and structural complexity of the habitat (Crowder and Cooper 1982, Folsom and Collins 1984).

Efficiency of predation generally declines with increasing habitat complexity (Crowder and Cooper 1982). In manipulating the amount of vegetation in enclosures, therefore, I suspected that prey survivorship would be lower in low density-vegetation enclosures than in high density-vegetation enclosures due to the decreased availability of refuges (see Folsom and Collins 1984). The presence of heterospecific predators can also influence predator success by interactive facilitation, interference, or predation among the predators (VanBuskirk 1988). Notonectids are significantly smaller in size (≤ 14 mm) than late-instar aeshnids (≤ 80 mm) and belostomatids (≤ 26 mm), which are both known to capture and consume notonectids in the laboratory (M. Rondinelli, *personal observation*). Since size is so often an important determinant in dictating the extent of predator/prey interactions (Mittelbach 1981, Werner et al. 1983) as are the abilities to capture and handle prey, I predicted that these considerably larger species would interact with notonectids through predation, thus mitigating somewhat the direct effects imposed by Anax and Belostoma on fathead minnow mortality. By controlling or reducing the potential effects of some of these factors influencing foraging rates while manipulating others, it may be possible to obtain a view of the potential predation events occurring naturally in the marsh.

Additionally, one may be interested in examining possible diel variations in feeding rates. Restriction of feeding to certain times of the day has characteristically been viewed as a mechanism to reduce competition over shared resources or to lessen the risks of predation (Streams 1982). Through laboratory experiments, I examine the basis for foraging periodicity in the three invertebrate predators by manipulating lighting conditions. Knowledge of potential diel foraging patterns may indeed provide evidence for a reduction in competition or predation risk; however, this was beyond the scope of the present study and I was concerned simply with the abilities of predators to feed with and without light. If a species forages as efficiently during nighttime hours as it does during the day, we are provided clues as to possible prey detection mechanisms other than visual means (Streams 1982). Such adaptive flexibility in foraging behavior may be a potential mechanism allowing for coexistence of species. In addition to investigating potential alterations in foraging mode in the laboratory, I examined rates of predation within lighting treatments to corroborate field results and to make comparisons between foraging efficiencies of the three predator species.

Lastly, I explored predator and prey behavior in a series of laboratory experiments to not only document specific interactions between individuals but also to determine methods of predator avoidance and escape, if any, utilized by prey species. Variations in antipredator morphology and behavior can have profound implications on the success and distribution of prey species (Tonn and Magnuson 1982, Robinson 1988). The presence of armor, spines, or chitinous exoskeletons may be effective deterrents to predation. However, when predators are able to overcome such obstacles or if prey lack protective morphology, prey must rely on maneuverability, schooling, and spatial avoidance mechanisms to escape capture (Wahl and Stein 1988). Here, I examine and compare spatial patterns and general activity of fathead minnows and notonectids with and without the threat of predation and also escape tactics of both prey species when exposed to odonate and belostomatid predators.

Materials and Methods

Study site description

The study site is Foggy Bottom Marsh, a 0.9 ha rectangular-shaped wetland approximately 42 km southeast of Michigan State University in Bunker Hill township, southcentral Michigan (Figure 1). Water levels generally achieve a maximum depth of 1.1 m in late autumn through early spring while minimum levels vary from year to year, depending primarily on the amount of summer rainfall. In 1990 water levels dropped to 15 cm by late August and in October 1991, the marsh dried up completely except for a deep ditch which runs along the entire western periphery. There is no permanent inlet or outlet. The marsh is boardered by trees on three sides, and on the fourth side by dense rows of rye grass and cattails. Riparian vegetation consists primarily of the grass Leersia oryzoides and the cattail Typha latifolia. Thick mats of submergent vegetation dominated by Potamogeton and Polygonum are present in spring and summer. Much of the water surface of the marsh is blanketed at this time by Lemna minor and Wolffia punctata. The water basin is composed of clay and marl sediments overlain by decaying plant matter and fine humic material. Water color was observed to be green-brown and clarity poor in spring and summer due to the suspension of fine particles and to the rapid increase of

Figure 1. Location of Foggy Bottom Marsh, Bunker Hill Township, MI.

algal populations. Since water levels are relatively shallow, wind action is probably an important component contributing to the turbidity of the marsh.

ANIMAL FAUNA

It is likely that harsh environmental conditions in winter and summer are important in determining the diversity of fish species in the marsh. Only those species able to withstand extreme diurnal and seasonal fluctuations in dissolved oxygen and temperature are capable of inhabiting such a system. The central mudminnow, Umbra limi, brook stickleback, Culaea inconstans, and fathead minnow, Pimephales promelas, the only fish species found at Foggy Bottom, are typical of Umbra-cyprinid systems (sensu Tonn and Magnuson 1982) characterized by low D.O. levels and low connectedness. Each species has a unique oxygen-sequestering mechanism that allows it to survive and thrive in systems where other fish species could not. Mudminnows breathe air or use air bubbles trapped at the water surface, stickleback utilize oxygenated microlayers of water, and fathead minnows are efficient in extracting oxygen from water at very low concentrations (Klinger et al. 1982).

While the number of central mudminnows remained almost negligible in both 1990 and 1991, the relative densities of the much more populous brook stickleback and fathead minnow varied dramatically. Brook stickleback dominated the fish community in 1990. Extensive sampling in a variety of microhabitats with steel mesh funnel traps and a hand seine indicated that the ratio of brook stickleback to fathead minnow was approximately 50:1. After a harsh event in mid-May 1991 when water temperatures exceeded 35 deg C for more than 8 days, the ratio approximated 1:300 (based on the sampling regime described above). It is unknown whether the recently produced offspring of brook stickleback were unable to survive this period or the adult brook stickleback succumbed before offspring were produced. The latter is likely, since prime spawning times for brook stickleback are in late May and early June and large numbers of dead adults were found floating on the water surface while very few dead juveniles were observed.

Many invertebrate taxa are well represented in the spring and summer. The benthic community is comprised primarily of dipterans, mainly Chironomidae, with Ceratopogonidae and Ephydridae fairly common over brief intervals. Perhaps the greatest diversity of the invertebrate fauna is represented by vegetation dwelling species, in particular aeshnid odonates, Zygoptera, Corixidae, Notonectidae, Dytiscidae, Nepidae, Naucoridae, and Belostomatidae. The most abundant predatory invertebrates in the marsh are the aeshnids, (in particular larvae of _Anax_), notonectids (_Notonecta_), and belostomatids (_Belostoma_).

Vertebrates associated with the marsh area include several species of waterfowl, the most numerous being the mallard duck, blue-winged teal, and wood duck, and predatory birds such as the great blue heron, green heron, pied-billed grebe, and belted kingfisher. Northern leopard frogs and green frogs were numerous within and along the banks of the marsh. Few taxa of mammals were observed in or near the study area.

Field experiments

I conducted a series of field experiments in order to examine predation patterns and intensities of the invertebrate predators Anax junius, Belostoma flumineum, and Notonecta on juvenile fathead minnows and, in some cases, on each other. The fathead minnow population in the marsh is comprised predominantly of this juvenile size class throughout the spring and summer as adults of this species breed continuously and proficiently during these seasons. Experiments were conducted in 12 1.11 m^2 (1.22 x 0.91 m) enclosures arrayed linearly along the western periphery of the marsh. Frames were constructed of polyvinylchloride piping filled with sand, which grounded cages in the event of strong winds. Nitex netting (620 u) was secured on four sides by Goop plumbers glue and monofilament fishing line; the cage bottom was composed of coarser mosquito netting. Two strips of mosquito netting were stapled to the topside of each enclosure to deter escape by experimental invertebrates or entrance by birds and mammals. Water depth in enclosures approximated 0.35 m. From 16 July 1991 to 30 August 1991, I conducted seven experiments.

The design for each experiment varied (see Table 1). Experiments 1 and 2 were conducted to explore the effect of adult Belostoma and Notonecta on the density of juvenile fathead minnows and Notonecta; each experiment used different densities of the two predator species. Similarly experiments 3 and 4 were designed to examine the influence of Anax larvae and Notonecta on the numbers of fish and Notonecta. Experiments 1-4 each had one treatment with two predator types (enclosures 1-3 in each) to determine if any significant interactions existed between predator species which might affect the respective fathead minnow populations. Trials 5 and 6 were set up to again determine the impact of dragonfly larvae and notonectids on the fathead minnow sample population, but also to determine if the amount of vegetation (1, 3, and 6 clumps/enclosure) plays a role in affecting the efficiency of predation by these invertebrates. In these experiments, I used an intermediate number of vegetation clumps (4) in control cages with the assumption that the amount of vegetation has no effect on fathead minnow survivorship in no-predator cages (controls). Finally, experiment 7 explores predation in cages with fixed densities of Anax and varying densities of fish. Only 5 Anax larvae/enclosure were used in this experiment due to the scarcity of this size class in the marsh at that time; all other experiments involving Anax used 10 individuals/enclosure. Fathead minnow densities were fixed in all experiments except experiment 7. The range of minnow

TABLE 1. Experimental design for field experiments. Type and quantity of organisms are shown for 8-12 enclosures over 7 experimental trials, as well as dates of each experiment. F=Fathead minnow, N=*Notonecta*, A=*Anax junius*, B=*Belostoma*. Treatments were randomized across enclosures.

	Experiment						
	16-20 July	23-27 July	1-5 Aug	6-10 Aug	14-18 Aug	19-23 Aug	26-30 Aug
Treatment Type	1	2	3	4	5[*][!]	6[*][?]	7
1	60F,6B,10N	120F,12B,27N	120F,10A,27N	240F,10A,27N	240F,10A	240F,10A	120F,5A
2	60F,6B,10N	120F,12B,27N	120F,10A,27N	240F,10A,27N	240F,10A	240F,10A	120F,5A
3	60F,6B,10N	120F,12B,27N	120F,10A,27N	240F,10A,27N	240F,10A	240F,10A	120F,5A
4	60F,6B	120F,12B	120F,10A	240F,10A	240F,10A	240F,10A	240F,5A
5	60F,6B	120F,12B	120F,10A	240F,10A	240F,10A	240F,10A	240F,5A
6	60F,6B	120F,12B	120F,10A	240F,10A	240F,10A	240F,10A	240F,5A
7	60F,10N	120F,27N	120F,27N	240F,27N	240F	240F,27N	480F,5A
8	60F,10N	120F,27N	120F,27N	240F,27N	240F	240F,27N	480F,5A
9	60F,10N	120F,27N	120F,27N	240F,27N	--	240F,27N	480F,5A
10	60F	120F	120F	240F	--	240F,27N	480F
11	60F	120F	120F	240F	--	240F	480F
12	60F	120F	120F	240F	--	240F	480F

[*] Vegetation clump density within these experiments varied.

[!] Cages 1 and 2 contained 1 clump each; cages 3 and 4 contained 3 clumps each; cages 5 and 6 contained 6 clumps each; cages 7 and 8 contained 4 clumps each

[?] Cages 1, 2, 7, and 8 contained 1 clump each; cages 3 and 4 contained 3 clumps each; cages 5, 6, 9, and 10 contained 6 clumps each; cages 11 and 12 contained 4 clumps each densities used in enclosures was comparable to that found in similar-sized areas in the marsh proper, however natural populations were observed to be extremely patchy. In all experiments, treatments were randomly assigned across enclosures. All fathead minnows used in experimental field trials ranged from 12-15 mm standard length. Due to the large number of individuals used and the likelihood of high handling mortality, lengths of fathead minnows were estimated by eye. Samples of juvenile fish which I predicted were in the range of 12-15 mm SL were taken every two weeks and standard lengths measured in the laboratory. These lengths almost always fell within the experimental range. Surprisingly, individuals of this size range were readily available throughout the summer, suggesting continuous breeding by adults or poor growth of existing juveniles. Fish were captured with a dip net and immediately transferred to cages by creating a small pool of water in my hand and gently placing the fish (within the pool of water) in the cage. In contrast to a direct transfer (by net) of fish to enclosures, this method yielded low handling mortality and allowed more convenient size estimation of captured fish. Each enclosure was inspected every 30 min for 2 hr and any dead or dying fish were removed and replaced. Individuals of similar-sized adult Belostoma and Notonecta were collected by seining primarily through beds of Polygonum but also open water areas and promptly distributed via dip net to cages. Three species of notonectids were observed in the marsh (N. undulata, N. borealis, and N. lunata) but only N.

undulata and, rarely, N. borealis were used in these experiments. Lengths of experimental individuals were estimated visually. If individuals appeared to be more than 2 mm smaller or larger than the target size for Belostoma (22 mm) and more than 1 mm smaller or larger for Notonecta (12 mm) then they were not used. Some individuals of what I estimated to be the appropriate experimental size for each species were preserved and later measured in the lab. Lengths of all these individuals fell within the desired size range for experiments. Any captured female belostomatid carrying eggs either had the egg mass removed before being placed in a cage or was not used in the experiments. Anax larvae were obtained by seining dense areas of Polygonum and sweeping against submerged Leersia stems and leaves with a small dip net. Recently molted nymphs were not used in field experiments since these larvae do not feed at such a developmental stage and would likely be easy prey for other A. junius larvae (see Ross 1971). All experimental dragonfly larvae were similar-sized late-instar nymphs (50-52 mm). Lengths of all experimental larvae were measured immediately after capture. None used differed by more than 2 mm. Larvae that differed slightly in size (± 2 mm maximum difference) showed no disparities in their abilities to capture and handle fish and invertebrates of the size used in the present study (M. Rondinelli, *personal observation*).

The ratio of invertebrate densities in cages involving two predator types roughly corresponded with natural ratios in the marsh; these estimates were based on sweep net and seine samples taken from habitats in which the three experimental predator types are known to coexist (e.g. beds of Polygonum, borders of submerged Leersia). Both sweep and seine samples covered approximately the area of an experimental cage. It is probable, however, that the three invertebrate species are patchily distributed throughout the marsh. I inspected the emergent portion of each enclosure daily for exuviae of recently-emerged adult dragonflies; those larvae that had metamorphosed were replaced. Adults of Notonecta and Belostoma are largely aquatic but have the capability to leave the water (both are powerful fliers). Undetected escape by these species in cages was therefore much more likely than by dragonfly larvae. Vegetation for use in cages was arranged in clumps by grouping cut stems of Leersia and securing the cut ends with rubber bands. 28.4 g fishing sinkers were then suspended from the rubber bands to prevent bundles from drifting in enclosures during the course of an experiment. Fresh clumps were constructed and implemented every other trial. Clump density was varied in experiments 5 and 6 (Table 1) to determine if vegetation quantity influences rates of predation in cages. Clump density was held constant at 5 clumps/cage in experiments 1, 2, 3, 4, and 7.

Each field experiment was run for five days. Fresh individuals of Notonecta and Belostoma were used for each experimental trial whereas the same dragonfly larvae were used in two successive experiments. Measurements of water temperature and dissolved oxygen were recorded for each cage daily or every other day. At the termination of an experiment, each enclosure was hoisted on to a boat and remaining organisms gathered by hand and counted. Treatment means (of number of missing organisms) were used as response variables in statistical analyses within experimental trials. One-way and two-way analysis of variance (ANOVA) were used to compare missing fathead minnow densities between treatments. Individual pairwise comparisons of means were tested using Fisher's method of Least Significant Difference. Comparisons of numbers of missing invertebrates between treatments was accomplished through independent t-tests.

Laboratory experiments

Laboratory experiments were designed largely for the purpose of describing and quantifying specific behaviors, spatial distributions, and escape tactics of prey (e.g. fathead minnow, Notonecta) with and without the threat of predation. In addition, I wanted to determine if differences exist in foraging rates of predators (Anax, Notonecta, Belostoma) in light and in darkness. If predators are as effective or more effective in capturing and consuming prey in darkness than they are in the light, the results may reflect a shift in foraging mode (visual vs. alternate methods). Results of such tests would be especially useful in describing events likely occurring in the field that are not easily witnessed.

For all experiments, Anax larvae, adult Belostoma, and adult Notonecta (of the sizes used in field experiments) were collected periodically from Foggy Bottom and held separately in 110 L glass aquaria. Invertebrates across all treatments were fed cultured midge larvae, Chironomus tentans, and mosquito larvae, *ad libitum*. Juvenile fathead minnows (12-14 mm standard length) from Foggy Bottom were similarly maintained and fed coarsely ground Wardley's Fish Flakes. Experiments were conducted in aerated glass aquaria (24.1 x 14.7 x 17.3 cm) filled with 2.5 L of conditioned tap water and furnished with a sand bottom, into which was rooted a small sprig of false (plastic) vegetation on one side. This vegetation was similar to Leersia used in field experiments, having long thin leaf blades durable enough to withstand the weight of a clinging dragonfly larva. Aquarium water was changed after every third experimental trial, regardless of treatment.

BEHAVIORAL EXPERIMENTS

A total of 24 experimental trials were conducted to document and quantify behaviors of the predators and prey used in the present field study. The experimental design across trials varied (Table 2) but the general protocol for each was similar. For aquaria designated as predator treatments, I introduced individual predators that had been starved for 24 hr. If the predator used was Anax, I temporarily employed the

TABLE 2. Experimental design for behavioral experiments. Type and quantity of organisms used are shown for each of 24 experimental trials. Each trial consisted of 25 10-sec observation bouts (staggered by 60 sec intervals) of spatial distributions of all individuals*. Activity was observed continuously and recorded for all individuals in each trial. F=Fathead minnow, N=_Notonecta_, A=_Anax junius_, B=_Belostoma_.

Trial	Organisms used (treatment)
1	5F
2	5F
3	5F
4	5F
5	3N
6	3N
7	5F,1A
8	5F,1A
9	5F,1A
10	5F,3N
11	5F,3N
12	5F,3N
13	3N,1A
14	3N,1A
15	3N,1A
16	3N,1B
17	3N,1B
18	3N,1B
19	5F,1B
20	5F,1B
21	5F,1B
22	5F,3N,1A
23	5F,3N,1A
24	5F,3N,1A

* Spatial distribution scores were not recorded for treatments involving _Belostoma_ or all three _Anax junius_, _Notonecta_, and fathead minnow (trials 16-24). Only observations of general activity were recorded.

use of a mesh divider to separate the larva from prey organisms until the experiment commenced. Ten minutes were allocated prior to the start of an experiment to allow for acclimation of organisms to aquaria. I then positioned myself approximately 1.5 m from the aquaria and observed and recorded behavior of predators (if present) and prey. Specifically I recorded the activities of individuals and, in most trials, the spatial distributions of prey relative to the predator. An "X" was recorded if any of the prey organisms were within 4 cm of an individual predator. An "O" was recorded if all prey organisms were greater than 4 cm from an individual predator. Distance was estimated visually (if the apparent distance was close to 4 cm, a "O" score was recorded). In no-predator experiments, an "X" or "O" scoring was based on the distance of a prey individual to the vegetation sprig since all three predator types used are known to cling to submerged structures. Although activity was recorded continuously, records of spatial distribution were based on 10 sec observational intervals staggered by 60 sec "rest" intervals. Only activity was recorded for treatments involving belostomatids or treatments including all three Anax, Notonecta, and fathead minnow. Any prey item consumed during an experiment was replaced immediately with a fresh individual. Means of spatial distribution scores (e.g. mean number of "X" scores for a given treatment group) were compared statistically by one-way ANOVA to determine any significant differences between responses of prey organisms to varying predator treatments. Tukey's test was used to compare individual means.

LIGHT\DARK PREDATION EXPERIMENTS

To examine if prey capture success by predators is influenced by a possible shift in foraging mode and to "reinforce" field study results, I conducted a series of short-term experiments in which predators and prey together were subjected to treatments of 10 hr continuous light exposure or 10 hr continuous dark exposure. Species used were the same as those used in behavioral experiments (but with new individuals). As in the behavioral experiments, the general protocol for each trial was identical but participants across trials varied (Table 3). Dark experiments were conducted by wrapping aquaria entirely with 4-ply dark plastic, which served to inhibit any light penetration. I postulated that individual predators could no longer search visually for food items in the dark and must rely on alternate means for capturing prey (if predators feed at all in darkness). The format for light experiments was identical to that for dark experiments except that no plastic wrap was employed. After 10 hr, the type and number of organisms remaining were counted and recorded. Statistically, I compared prey mortality between light and dark-treated groups with independent t-tests to examine the basis for diel foraging behavior in predators. Additionally, one-way ANOVA was used to determine if there

TABLE 3. Experimental design for light\dark predation experiments. Type and quantity of organisms are shown for each experimental trial. 29 trials each of the format indicated below were run under two different environmental conditions: 10 hr continuous light exposure and 10 hr continuous dark exposure. F=Fathead minnow, N=*Notonecta*, A=*Anax junius*, B=*Belostoma*.

Trial	Organisms used
1	5F,1A
2	5F,1A
3	5F,1A
4	5F,1A
5	5F,1A
6	10F,1A
7	5F,3N
8	5F,3N
9	5F,3N
10	5F,3N
11	5F,3N
12	5F,3N
13	5F,3N
14	5F,3N
15	5F,1B
16	5F,1B
17	5F,1B
18	5F,1B
19	5F,1B
20	3N,1B
21	3N,1B
22	3N,1B
23	3N,1B
24	3N,1B
25	5F,3N,1A
26	5F,3N,1A
27	5F,3N,1A
28	5F,3N,1A
29	5F,3N,1A

were significant differences in minnow survivorship within lighting treatments. Means of missing notonectids within light treatments were compared through independent t-tests.

Results

Field experiments

FATHEAD MINNOW SURVIVORSHIP:

A normality test of ordered residuals of the numbers of missing fish in field experiments indicated that these data are normally distributed (Table 4). Box's small sample variance test (Dixon and Massey 1969) indicated that variances of numbers of missing fish in all treatment groups within each experiment were homogeneous (Table 5). These tests were conducted to ensure the appropriateness of parametric tests for statistically analyzing fathead minnow mortality data obtained from field experiments. Since experiments 1-4 contained treatments involving simultaneous inclusions of two predator types, two-factor ANOVA was utilized to discern the direct effects of each predator type as well as any interactive effects between them which may have influenced survivorship of fathead minnows.

Belostoma significantly reduced the number of fathead minnows in enclosures at both minnow densities (Tables 6 and 7, Exps. 1, 2). This predator was apparently adept at escaping from enclosures, however, as only 17 of the initial 36 individuals were accounted for at the conclusion of Experiment 1, and 34 of the initial 72 were present at the conclusion of Experiment 2. Of those Belostoma remaining at

TABLE 4. Shapiro-Wilk normality test for numbers of missing fathead minnows in field experiments. Calculated w values less than the critical w value provide evidence of non-normally distributed data (Gill 1978a).

Experiment	n	w	P
1	12	0.982	> 0.9
2	12	0.914	0.1 < P < 0.5
3	12	0.919	0.1 < P < 0.5
4	12	0.906	0.1 < P < 0.5
5	8	*	
6	12	0.951	0.5 < P < 0.9
7	12	0.926	0.1 < P < 0.5

* Values for coefficients of ordered differences tabulated only for n ≥ 11 (see Gill 1978b), therefore test not performed

TABLE 5. Tests for homogeneity of variance of all treatment groups in field experiments 1-7 with numbers of missing fish as the response variable. Box's small sample F-approximation (Dixon and Massey 1969) was used since less than 10 replicates per treatment were implemented in each and every experiment.

Exp	Approximate F	df	P
1	1.578	3, 115	0.199
2	0.294	3, 115	0.830
3	0.336	3, 115	0.799
4	0.048	3, 115	0.986
5	0.302	3, 28	0.823
6*	0.160	4, 37	0.957
7	0.657	3, 115	0.569

* One treatment group (control) had no variance; this group was therefore excluded from the analysis

TABLE 6. Means of numbers of missing fathead minnows for each treatment type in field experiments 1-4. Entries in the table give means ± SD. Percent mortality ± SD is also indicated for each treatment condition.

Exp	Treatment Type	Mean	Percent mortality
1	Bel	8.3 ± 4.5	13.8 ± 7.5
	Not	5.7 ± 0.6	9.5 ± 0.1
	Bel and Not	11.7 ± 3.2	19.5 ± 5.3
	No predators	6.0 ± 2.6	10.0 ± 4.3
2	Bel	11.3 ± 4.2	9.4 ± 3.5
	Not	19.7 ± 2.9	16.4 ± 2.4
	Bel and Not	26.7 ± 2.5	22.3 ± 2.1
	No predators	1.7 ± 2.1	1.4 ± 1.8
3	Anax	28.3 ± 4.5	23.6 ± 3.8
	Not	16.7 ± 3.2	13.9 ± 2.7
	Anax and Not	33.0 ± 7.0	27.5 ± 5.8
	No predators	7.0 ± 4.6	5.8 ± 3.8
4	Anax	51.7 ± 5.1	21.5 ± 2.1
	Not	30.3 ± 6.8	12.6 ± 2.8
	Anax and Not	68.3 ± 6.0	28.5 ± 2.5
	No predators	12.0 ± 5.6	5.0 ± 2.3

TABLE 7. Two-factor ANOVA table for field experiments 1-4 with numbers of missing fathead minnows as the response variable. An '*' indicates a significant treatment effect.

Exp	Source	Sum of squares	df	Mean square	F-ratio	P
1	Bel	52.083	1	52.083	5.482	0.047^*
	Not	6.750	1	6.750	0.711	0.424
	Bel*Not	10.083	1	10.083	1.061	0.333
	Error	76.000	8	9.500		
2	Bel	208.333	1	208.333	22.936	0.001^*
	Not	833.333	1	833.333	91.743	$< 0.001^*$
	Bel*Not	5.333	1	5.333	0.587	0.466
	Error	72.667	8	9.083		
3	Anax	1064.083	1	1064.083	42.281	$< 0.001^*$
	Not	154.083	1	154.083	6.123	0.038^*
	Anax*Not	18.750	1	18.750	0.745	0.413
	Error	201.333	8	25.167		
4	Anax	4524.083	1	4524.083	129.260	$< 0.001^*$
	Not	918.750	1	918.750	26.250	0.001^*
	Anax*Not	2.083	1	2.083	0.060	0.813
	Error	280.000	8	35.000		

the end of these experiments, 4 were dead. *Notonecta* had a significant mortality effect in Experiment 2 but not in Experiment 1. There was no evidence of a significant interaction between *Belostoma* and *Notonecta* in either experiment. *Anax junius* strongly depressed fathead minnow populations in Experiments 3 and 4 (Tables 6 and 7, Exps. 3, 4). Direct effects on fathead minnows imposed by *Notonecta* were also significant in each experiment. In neither experiment was the *Anax* x *Notonecta* interaction term significant. Two larvae from one enclosure and one larva from another enclosure were unaccounted for at the termination of Experiment 4. Significant differences in the mortality of fathead minnows between treatment types was evident in Experiments 5-7 (Table 8), as shown by one-way ANOVA (Table 9). For these tests, Fisher's Least Significant Difference method was used to distinguish which means differed because this test provides high power for nonorthogonal planned pairwise comparisons (Day and Quinn 1989). In Experiment 5, survivorship of fathead minnows was significantly lower in the three vegetation-manipulated *A. junius* treatments (1 clump: $P < 0.009$, 3 clumps: $P < 0.007$, 6 clumps: $P < 0.008$) when compared to the treatment with no *A. junius*, but survivorship did not differ among the *Anax* treatments. The amount of vegetation therefore, which varied in these predator treatments, had no effect on the number of minnows consumed. One dragonfly larva was missing from each of two cages in this experiment.

TABLE 8. Means of numbers of missing fathead minnows for each treatment type in field experiments 5-7. Entries in the table give mean ± SD. Percent mortality ± SD is also included for each treatment condition.

Exp	Treatment type	Mean	Percent mortality
5	Anax/1 veg clump	50.5 ± 3.5	21.0 ± 1.5
	Anax/3 veg clump	53.5 ± 5.0	22.3 ± 2.1
	Anax/6 veg clump	51.5 ± 10.6	21.5 ± 4.4
	No Anax (control)	17.0 ± 5.7	7.1 ± 2.4
6	Anax/1 veg clump	63.5 ± 6.4	26.5 ± 2.7
	Anax/3 veg clump	58.0 ± 8.5	24.2 ± 3.5
	Anax/6 veg clump	53.0 ± 4.2	22.1 ± 1.8
	Not/1 veg clump	17.5 ± 3.5	7.3 ± 1.5
	Not/6 veg clump	18.0 ± 0.0	7.5 ± 0.0
	Control	12.5 ± 5.0	5.2 ± 2.1
7	Anax/120 minnows	21.0 ± 2.6	17.5 ± 2.2
	Anax/240 minnows	43.0 ± 5.6	17.9 ± 2.3
	Anax/480 minnows	48.3 ± 7.6	10.1 ± 1.6
	No Anax/480 minnows	21.3 ± 3.5	4.4 ± 0.7

TABLE 9. One-way ANOVA table for field experiments 5-7 with numbers of missing fish as the response variable.

Exp	Source	Sum of squares	df	Mean square	F-ratio	P
5	Treatment	1829.375	3	609.792	13.439	0.015
	Error	181.500	4	45.375		
6	Treatment	5481.417	5	1096.283	39.270	< 0.001
	Error	167.500	6	27.917		
7	Treatment	1843.583	3	614.528	22.831	< 0.001
	Error	215.333	8	26.917		

Minnow mortality was again significantly greater in each of the three Anax treatments versus the control in Experiment 6 (1 clump: $P < 0.001$, 3 clumps: $P < 0.001$, 6 clumps: $P < 0.001$), but these means did not differ amongst one another, again suggesting that vegetation quantity played little or no role in determining fathead minnow survivorship. All dragonfly larvae were accounted for at the end of the experiment, however one dead nymph was found. Notonecta did not influence survivorship as neither mean from the two Notonecta treatments (1 clump and 6 clumps) differed from that of the control or one another.

In experiment 7, Anax treatments which utilized 240 minnows and 480 minnows were both significantly different from the control ($P < 0.002$ and $P < 0.001$, respectively), but the Anax treatment with 120 minnows was not. Means from treatments with the two higher minnow densities, therefore, differed from that of the lower density treatment ($P < 0.002$ and $P < 0.001$), but they did not differ from each other. All dragonfly nymphs were present at the conclusion of the experiment.

NOTONECTA SURVIVORSHIP:

Variances in the number of missing Notonecta between treatment groups in Experiments 1-4 were homogeneous (Table 10). Escape by Notonecta from cages was not apparent as only 12 individuals out of the 273 total possible were unaccounted for in no-Belostoma or no-Anax treatments. Natural mortality

TABLE 10. Tests for homogeneity of variance of treatment groups in field experiments 1-4 with numbers of missing *Notonecta* as the response variable. Box's small sample F-approximation was used since less than 10 replicates per treatment were implemented in each experiment.

Exp	Approximate F	df	P
1	0.460	1, 48	0.501
2	1.674	1, 48	0.202
3	0.278	1, 48	0.601
4	0.000	1, 48	1.000

was very low in these treatments: only 3 dead individuals were found among the remaining 265 Notonecta.

Belostoma imposed significant mortality on Notonecta in both Experiment 1 and Experiment 2 (Table 11, Exps. 1 and 2). Evidence that Belostoma was indeed preying on Notonecta was provided by the fact that a number of dead notonectids were observed on cage bottoms at the end of the experiments; in particular Experiment 2, where 13 exoskeletons were collected from the three cages comprising the Belostoma treatment. Belostoma is a sucking predator and does not macerate its prey but instead sucks the body fluids from its victims, leaving behind their outer integuments.

Survivorship of notonectids was also significantly depressed by A. junius (Table 11, Exps. 3 and 4). In neither experiment were any dead Notonecta observed in treatments with Anax. Such an absence of exoskeletons is not unexpected, since Anax nymphs tear apart their victims and ingest most or all of their contents.

WATER TEMPERATURE/DISSOLVED OXYGEN:

Levels of dissolved oxygen (D.O.) rarely differed between cages by more than 2 mg/L at any one measurement. Although readings were generally taken only once or twice a day, substantial diurnal fluctuations in dissolved oxygen were evident within the experimental cages (Figure 2). On sunny days, levels generally reached a maximum at 1100 hr and continued until aproximately 1800 hr, after which they dropped

TABLE 11. Independent t-tests for field experiments 1-4. Means of the number of missing Notonecta were compared between groups.

Exp	Groups tested	n	Mean	t	P
1	Fathead + Not + Bel	3	4.667		
	Fathead + Not	3	1.000	5.500	0.005
2	Fathead + Not + Bel	3	9.000		
	Fathead + Not	3	1.667	6.957	0.002
3	Fathead + Not + Anax	3	8.333		
	Fathead + Not	3	2.000	6.008	0.004
4	Fathead + Not + Anax	3	5.667		
	Fathead + Not	3	0.333	11.314	< 0.001

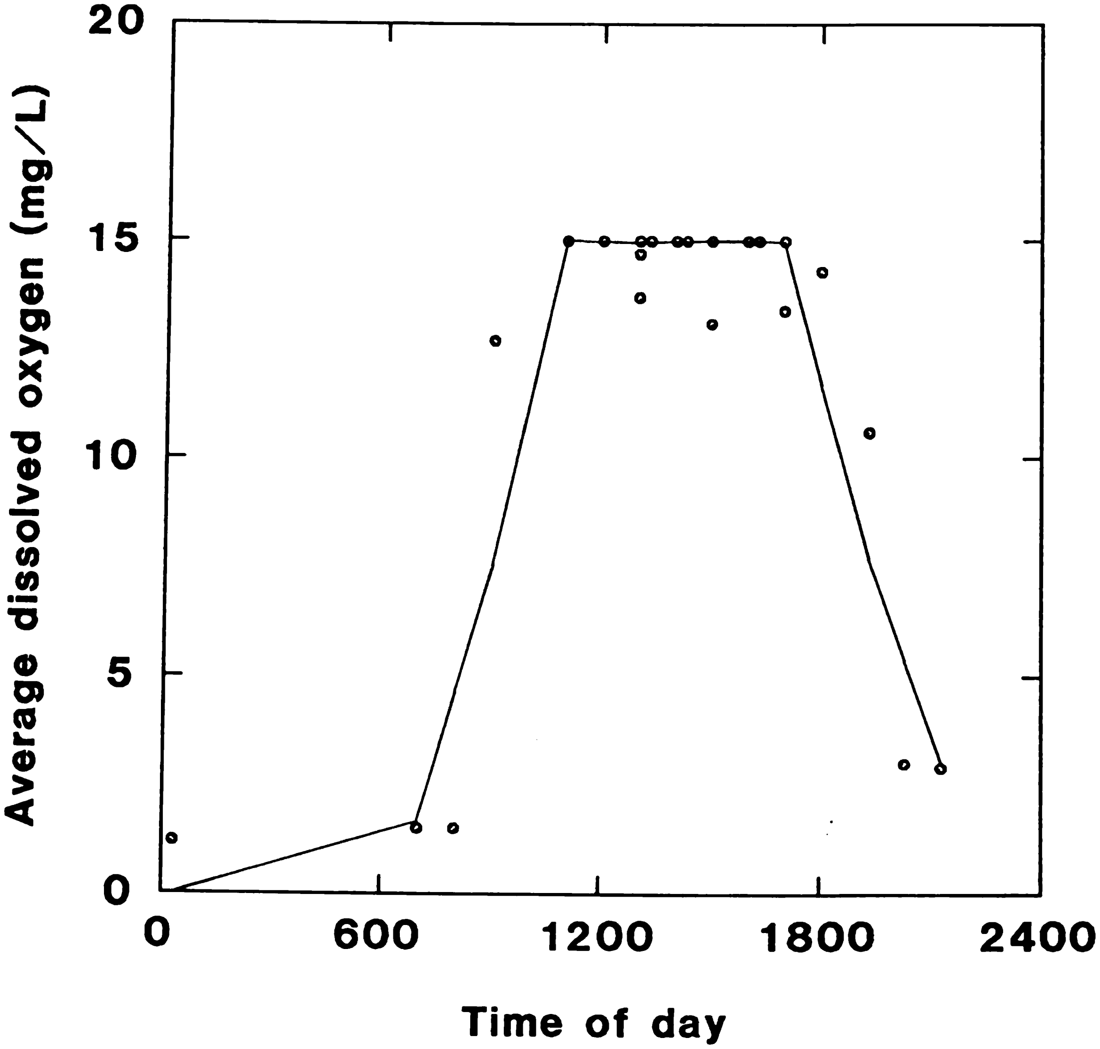

Figure 2. Average dissolved oxygen of experimental field enclosures as a function of time of day on sunny days. Measurements were taken across experiments (from 16 July to 30 August). The maximum D.O. level which could be measured was 15.0 mg/l. The line was fitted by a smoothing method (LOWESS) described by Cleveland (1981).

off steeply and appeared to stabilize at a minimum of 1 to 2 mg/L. On the two days (8 August and 19 August) in which it rained, the D.O. content averaged 2.2 mg/l and 2.4 mg/l in cages at 10:00 am and 10:30 am, respectively. No readings were taken on any day between 1:00 am and 6:00 am, but it is reasonable to assume that oxygen content in the water was reduced during this time. In addition to the low variability of oxygen content among cages on a given day, D.O. levels varied little across experiments (at identical times of the day). Periodic measurements of dissolved oxygen in the marsh proper were very similar to those recorded for cages, indicating little or no cage effects on oxygen levels. No clear relationship exists between water temperature and time of day (for sunny days), (Figure 3). The range of temperatures was considerable for certain hours of the day, particularly afternoon hours. Generally, water temperature was highest during the afternoon, however some of the afternoon measurements were as low as those in the evening. As with dissolved oxygen, water temperature within cages was nearly the same as that in the marsh.

Laboratory experiments

SPATIAL PATTERNS OF FATHEAD MINNOWS:

Fathead minnows from three groups were tested for differences in their relative spatial positioning in aquaria. Variances from the three treatment groups were homogeneous

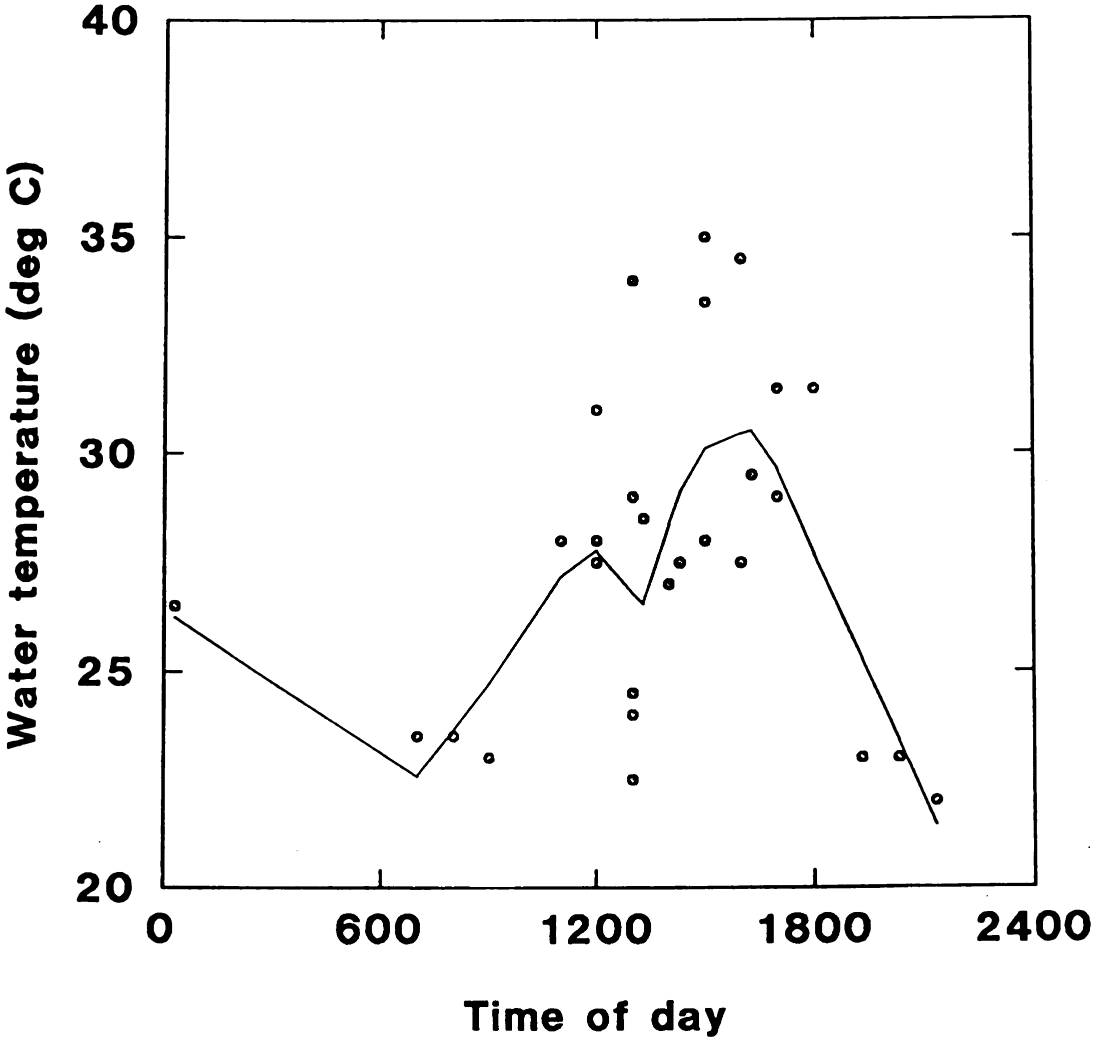

Figure 3. Water temperature in experimental field enclosures. Measurements were taken across experiments (from 16 July to 30 August). Each data point actually represents an average of 12 enclosures although there was no variability in water temperature between enclosures at any one reading. The line was fitted by the LOWESS smoothing method (Cleveland 1981).

(Table 12). Spatial distribution patterns, however, differed between treatments (Table 13). Tukey's test was used to determine which means differed since it has high power for testing unplanned pairwise comparisons of means (Day and Quinn 1989). Since predators in these experiments (*Anax* and *Notonecta*) were often attached to the artificial vegetation sprig on one side of the aquarium, it was appropriate to use the sprig stem as a reference point for which to compare spatial positioning in no-predator (control) experiments with that in predator experiments. Minnows spent more time away from the stem when it was occupied by *Anax* than when it was unoccupied in the control ($P < 0.002$). Commonly all 5 fish would aggregate and quickly relocate to the far (non-vegetated) side of the tank after movement by the nymph, where they remained in a school. In the only spatial distribution experiment in which a nymph ventured off the stem and on to the sand bottom, minnows actively avoided the larva by swimming behind the vegetation and inhabiting that particular portion of the tank.

Minnows avoided the *Notonecta*-occupied vegetation compared to the unoccupied control, but the difference was not significant ($P > 0.175$). Fish were often observed swimming directly in front of a notonectid and only when an individual notonectid lurched suddenly off the vegetation would the minnows take refuge at the far end of the aquarium. If a sudden swimming bout by a notonectid occurred early in the experiment, the minnows would again, after a time, swim freely

TABLE 12. Test for homogeneity of variance of treatment groups in spatial distribution laboratory experiments with numbers of "X" scores (within 4 cm of predator) of fathead minnows as the response variable. Box's small sample F-approximation was used since less than 10 replicates per treatment were implemented in each experiment.

Treatment groups	Approximate F	df	P
Fathead (control) Fathead + Not Fathead + Anax	0.177	2, 101	0.838

TABLE 13. One-way ANOVA table for spatial distribution laboratory experiments with numbers of "X" scores (within 4 cm of predator) of fathead minnows as the response variable. Treatment groups were "Fathead (control)", "Fathead + Not", and "Fathead + Anax".

Source	Sum of squares	df	Mean square	F-ratio	P
Treatment	503.333	2	251.717	21.315	0.001
Error	82.667	7	11.810		

in the vicinity of one or more predators, seemingly unconcerned by their presence. Minnows avoided the Anax-inhabitated vegetation more frequently than the Notonecta-inhabited vegetation ($P < 0.011$).

SPATIAL PATTERNS OF NOTONECTA:

Due to the lack of variance in one of the two treatment groups (Notonecta group), no statistical analysis was conducted. In comparing the control (3 Notonecta) with the Anax treatment (3 Notonecta + 1 Anax larva), however, it is obvious that there was little difference in the spatial use of Notonecta between treatments. In both control replicates, notonectids occupied the vegetation or the surface water above the vegetation throughout the entire course (25 min) of the experiments; this explains the zero variance in this group. In the three replicates in which Anax was present, notonectids occupied these areas for 25, 21, and 25 minutes of the 25 minute trial. Even after being struck at by a nymph, individuals would usually swim back toward the vegetation. This suggests that Notonecta does not appear to spatially avoid vegetation-dwelling odonate predators and may rely on other antipredator mechanisms for survival.

GENERAL ACTIVITY PATTERNS:

The following largely qualitative activity patterns of predators and prey were also recorded from aquarium observations. The range of behavioral responses of A. junius larvae to surrounding prey varied substantially, but appeared to depend largely on prey type present. When exposed only to 5 fathead minnows, nymphs would often remain motionless on the vegetation during the majority of the experiment. When a minnow would eventually venture near, the nymph would very slowly reposition itself (if necessary) on the stem, orient its head toward the fish, and extend the anterior part of its body away from the vegetation in order to get close enough for a labial strike. Minnows appeared to be sensitive even to such deliberate movements by the predator, and usually would quickly swim away. Often the larva would visually follow the movements of the minnow school, swivelling and orienting its head in the direction of activity. Minnows clearly did not swim as much in the presence of Anax. Capture of a fathead minnow by Anax always occurred when clinging to vegetation or while thrusting upward off the aquarium bottom at a passing fish. Escape by a captured minnow was never observed; those captured were always consumed. Consumption of minnows lasted from 20 sec to 50 sec and generally occurred while on the vegetation, although in one instance a larva consumed a minnow while on the aquarium bottom, away from the vegetation stem.

Activity of A. junius nymphs was considerably greater when subjected to 3 adult Notonecta as prey items. Notonectids did not frighten as easily as fathead minnows and almost always occupied areas on the vegetation in close proximity to the dragonfly larva, often allowing the predator to approach it. Instead of relying on a sit-and-wait mode of predation as evidenced with fathead minnows, larvae would generally actively crawl around and pursue individuals on the vegetation. Even after larvae would lunge and strike at them on the vegetation, notonectids would almost always return, sometimes to the same location. Invariably a Notonecta that had escaped a larva would depart from the stem or leaf, return, and perch on the dorsal portion of the larva's abdomen. The frequency of attacks was greater with notonectids than with fathead minnows. In one experiment, a dragonfly larva made 8 unsuccessful lunges at prey individuals, while in another experiment, 4 unsuccessful attempts were made. This increase in attack frequency is likely due to the persistence of Notonecta in inhabiting areas adjacent to or in close proximity to the dragonfly larva. Success of capturing and then consuming notonectids by A. junius was poor. In one experiment with Anax and Notonecta, only 18% of captures (n=11 captures) resulted in consumption of prey individuals. In another experiment, not one notonectid was consumed even though one or more of the individuals were captured a total of 10 times. Captured Notonecta were typically observed vigorously moving their legs in an attempt to escape their captor. Time taken to escape was generally 1-5 sec and escapees were usually uninjured. The time it took to manipulate and ingest a notonectid was much greater than for a fathead minnow, the longest consumption period lasting 220 sec.

Dragonfly larvae also foraged actively when both prey types were present and seemed to pursue whatever prey type was in the vicinity of capture. In one experiment, an Anax made 6 unsuccessful lunges at minnows and 6 failing attempts at notonectids. In two of the three experiments, one prey type of each was consumed while in the third only a fathead minnow was eaten. Behavior of nymphs appeared to be similar to that observed when exposed to notonectids, except that nymphs were even more motile in pursuing prey individuals. Such enhanced locomotor activity could be a result of the greater number of prey individuals available for capture and/or to increased activity among prey organisms. For example, fathead minnows appeared confused by the movements of one or more predators (usually the haphazard motions of a swimming notonectid but also deliberate movements by Anax) and thus spent more time swimming than when exposed to only one predator type, possibly increasing their vulnerability. In one experiment, a disoriented minnow swam directly in front of and was captured by a larva after having been encountered by a Notonecta that had lurched suddenly off a leaf blade. Only once during the three experiments was a notonectid observed to strike (unsuccessfully) at a minnow. The lunge occurred from the water surface.

Except for a few moments of swimming, notonectids, when alone with fathead minnows, were content to perch motionless on the vegetation or, infrequently, at the water surface or side of the aquarium. Only 4 attempts were made to capture minnows in the three experiments, 2 from the surface, 1 from the vegetation, and 1 from the aquarium wall. All attempts failed.

Belostomatids were extremely inactive when subjected to either fathead minnows or Notonecta. When with minnows, Belostoma clung to the vegetation stem, inverted, the entire duration of each experiment. Movement by a belostomatid was observed in only one trial, and this involved a very subtle repositioning of itself on the stem. Minnows avoided the vegetation for approximately the first half of the experiment, then freely swam in and near the vegetated area.

Belostoma were successful in capturing a notonectid in two of the three experiments. Both strikes occurred when a notonectid departed from a vegetation leaf and, upon returning, attempted to occupy an area on the stem directly in front of the belostomatid. Each victim was quickly grasped, manipulated, and slowly drained of its body fluids. As when in isolation with minnows, belostomatids never abandoned the vegetation stem and, aside from the two incidences of capture, remained stationary throughout the course of the experiments.

LIGHT/DARK PREDATION EXPERIMENTS:

Light vs. dark comparisons: Variances of numbers of missing fish between treatment groups exposed to 10 hr light and 10 hr darkness were homogeneous (Table 14). Two treatment groups ("Fathead + Bel" light-exposed group and "Fathead + Not" dark-exposed group) had no variance thus preventing statistical light vs. dark comparisons between these treatments. There

TABLE 14. Homogeneity of variance test of treatment groups compared under 10 hr continuous light exposure and 10 hr continuous dark exposure with number of missing fish as the response variable. Box's small sample F-approximation was used since less than 10 replicates per treatment were implemented in each experiment.

Treatment group	Approximate F	df	P
Fathead + Anax	1.498	1, 299	0.222
Fathead + Anax + Not	1.770	1, 192	0.185
Fathead + Bel	*		
Fathead + Not	**		

* There was zero variance in the number of missing fish in light experiments (variance test not performed)

** There was zero variance in the number of missing fish in dark experiments (variance test not performed) was no significant difference in the number of fathead minnows consumed between light and dark treatments with only Anax as the predator (Table 15). Nymphs in dark-treated aquaria actually ate slightly more minnows than those in lit aquaria. Nymphs also ate more minnows in the dark when notonectids were present, but again the difference was not significant (Table 15). Both sets of experiments suggest that larvae of A. junius forage as successfully in darkness as they do in the light. In both light and dark experiments, notonectids were able to capture only one minnow (this occurred in a light experiment). Belostomatids were similarly unsuccessful, capturing but one minnow in all trials; the capture occurred in darkness.

Variances in the numbers of missing Notonecta did not differ among treatment groups (Table 16). Dark-treated Anax ate slightly more notonectids than did light-treated larvae, but this difference was not significant (Table 17). Belostoma also foraged as effectively on notonectids in the dark as in the light, although once again no statistically significant difference was observed (Table 17).

Within treatment comparisons: Variances of fathead minnows consumed between groups were homogeneous in both light-treated (Table 18) and dark-treated (Table 19) groups. Only three groups were compared in an analysis of variance within each lighting regime since one group in each had no variance. The ANOVA showed that groups within lighting conditions strongly

TABLE 15. Independent t-tests comparing numbers of missing fathead minnows from treatment groups containing identical numbers of predators but different lighting regimes (10 hr continuous light vs. 10 hr continuous darkness).

Treatment	Groups tested	n	Mean	t	P
Light	Fathead + Anax	6	4.000		
Dark	Fathead + Anax	6	4.500	0.542	0.599
Light	Fathead + Anax + Not	5	2.400		
Dark	Fathead + Anax + Not	5	3.400	1.768	0.115
Light	Fathead + Bel	5	0.000		
Dark	Fathead + Bel	5	0.200	*	
Light	Fathead + Not	8	0.125		
Dark	Fathead + Not	8	0.000	**	

* t-test not performed since light treatment group had no variance

** t-test not performed since dark treatment group had no variance

TABLE 16. Homogeneity of variance test of treatment groups compared under 10 hr continuous light exposure and 10 hr continuous dark exposure with numbers of missing Notonecta as the response variable. Box's small sample F-approximation was used since less than 10 replicates per treatment were implemented in each experiment.

Treatment group	Approximate F	df	P
Fathead + Not + Anax	0.100	1, 192	0.752
Not + Bel	0.000	1, 192	1.000

TABLE 17. Independent t-tests of numbers of missing Notonecta from treatment groups exposed to 10 hr continuous light and 10 hr continuous darkness.

Treatment	Groups tested	n	Mean	t	P
Light	Fathead + Not + Anax	5	1.800		
Dark	Fathead + Not + Anax	5	2.000	0.408	0.694
Light	Not + Bel	5	1.400		
Dark	Not + Bel	5	1.600	0.577	0.580

TABLE 18. Homogeneity of variance test for treatment groups subjected to 10 hr continuous light with numbers of missing fathead minnows as the response variable. Box's small sample F-approximation was used since less than 10 replicates per treatment were implemented for each experiment.

Groups tested	Approximate F	df	P
Fathead + Anax Fathead + Not Fathead + Not + Anax	0.620	2, 433	0.538*

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* The "Fathead + Bel" group had no variance and was thus excluded from this analysis

TABLE 19. Homogeneity of variance test for treatment groups subjected to 10 hr continuous darkness with numbers of missing fathead minnows as the response variable. Box's small sample F-approximation was used since less than 10 replicates per treatment were implemented for each experiment.

Groups tested	Approximate F	df	P
Fathead + Anax Fathead + Bel Fathead + Not + Anax	1.534	2, 324	0.217*

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* The "Fathead + Not" group had no variance and was thus excluded from this analysis

TABLE 20. One-way ANOVA table for 10 hr continuous light predation experiments with numbers of missing fathead minnows as the response variable. Treatment groups were "Fathead + Anax", "Fathead + Not", and "Fathead + Not + Anax".

Source	Sum of squares	df	Mean square	F-ratio	P
Treatment	51.942	3	17.314	100.448	< 0.001
Error	3.275	19	0.172		

TABLE 21. One-way ANOVA table for 10 hr continuous darkness predation experiments with numbers of missing fathead minnows as the response variable. Treatment groups were "Fathead + Anax", "Fathead + Bel", and "Fathead + Not + Anax".

Source	Sum of squares	df	Mean square	F-ratio	P
Treatment	70.618	3	23.559	41.447	< 0.001
Error	10.800	19	0.568		

TABLE 22. Homogeneity of variance test of treatment groups in light and dark laboratory experiments with numbers of missing Notonecta as the response variable. Box's small sample F-approximation was used since less than 10 replicates per treatment were implemented in each experiment.

Treatment	Groups tested	Approximate F	df	P
Light	Not + Bel Fathead + Not + Anax	0.619	1, 192	0.432
Dark	Not + Bel Fathead + Not + Anax	0.229	1, 192	0.633

TABLE 23. Independent t-tests of numbers of missing Notonecta from treatment groups subjected to either 10 hr continuous light or 10 hr continuous darkness.

Treatment	Groups tested	n	Mean	t	P
Light	Not + Bel	5	1.400		
	Fathead + Not + Anax	5	1.800	0.394	0.397
Dark	Not + Bel	5	1.600		
	Fathead + Not + Anax	5	2.000	1.000	0.347

differed in predation intensity (Tables 20, 21). *Anax* nymphs ate significantly more minnows in the light when exposed to minnows alone compared to nymphs offered both minnows and *Notonecta* (Tukey's test, $P < 0.002$). There was no significant difference, however, between these groups in darkness ($P > 0.834$). This indicates that larvae may have concentrated a greater portion of their foraging effort on *Notonecta* or were distracted more by notonectids in light experiments than in dark experiments, perhaps alleviating somewhat the predation pressure on minnows. Both *Anax* treatment groups had significantly greater mortality of minnows than the "*Notonecta* + fathead" group in the light ($P < 0.001$ for both comparisons). Mortality was obviously lower for minnows exposed to *Belostoma* when compared to minnows subjected to either *Anax* treatment since belostomatids failed to consume a single fish in any light experiments ($P < 0.001$ for both). Both dark-treated *Anax* groups had much lower minnow survivorship than the *Belostoma* group ($P < 0.001$ for both comparisons) and the *Notonecta* group ($P < 0.001$ for both).

Variances in notonectid mortality were not significantly different in groups in either lighting scheme (Table 22). In both light and dark treatments, *A. junius* larvae ate more notonectids than *Belostoma*, but the differences were not significant (Table 23).

Discussion

Anax junius larvae had significant direct effects on fathead minnow mortality in field experiments. Mortality was as high as 28.3% and as low as 18.3% in enclosures containing 10 Anax + minnows (field experiments 3-6), while the highest measure of mortality in enclosures containing no predators in these experiments was 9.2%. Similar predator success was observed in laboratory experiments. Anax junius can be a major source of predation on larval anurans (Heyer et al. 1975, Wilbur and Fauth 1990), but little experimental evidence exists for its effects on fishes. The results presented here suggest that, in ponds lacking large fish or with small gape-limited fish, large aeshnid odonates could cause considerable reductions in the densities of small fish. Large fishes, when present, tend to remove Anax in lakes and ponds, presumably due to its large size and high activity (Robinson and Wellborn 1987). In a system such as Foggy Bottom Marsh, which contains no fish predators, Anax larvae can complete their larval development relatively unencumbered. Furthermore, there is no evidence that the two insectivorous fish species present (brook stickleback and central mudminnow) feed on early instars of Anax since extensive gut sampling data from both species (n=388 guts examined) failed to reveal a single odonate larvae eaten (M. Rondinelli, *unpublished data*). It is logical to assume that for this reason, primarily, larvae are able to achieve considerable densities in Foggy Bottom Marsh. It is unknown, however, what Anax larvae feed on naturally in the marsh. Many authors conclude that they are opportunistic foragers, consuming a wide range of invertebrate and vertebrate taxa and that there does not appear to be strong preferences involved in prey selection (Pritchard 1964, Folsom and Collins 1984, Blois 1985), although there is at least one experimental study which provides evidence that Anax preferentially pursue and, consequently, capture the more abundant of two prey types (i.e. switching) in the laboratory (Bergelson 1985). If larvae do indeed feed on prey species according to their proportion in the environment, minnows would likely comprise a significant portion of their diet since they are abundant in the marsh. The presence of refugia (and prey activity), however, are often more important than prey density in dictating natural predation rates on prey species (Folsom and Collins 1984, Cloarec 1990). In the present study, survivorship of fathead minnows did not differ in low (1 clump), medium (3 clumps), or high (6 clumps) vegetation enclosures, indicating that vegetation did not influence the number of minnows consumed in enclosures. Studies have suggested or demonstrated a positive correlation between increasing structure or macrophyte density and reduced predation risk (Macan 1966, Crowder and Cooper 1982, Streams 1986). These studies, however, have all involved predation by fish on invertebrates; it is possible that the advantage accrued to a fish or invertebrate in inhabiting an area of increased weed density may be offset if a high density of predatory invertebrates are found within this habitat. Moving to an area of dense vegetation to avoid predation by fish may increase susceptibility to macroinvertebrate predators such as odonates, nepids, and belostomatids (Bennett and Streams 1986). Additionally, Folsom and Collins (1984) found that Anax predation on Hyalella was significantly reduced only at a very high density of Elodea stems. In the present study, the lack of a significant difference in the number of fish consumed at varying clump densities indicates that vegetation was of little use to minnows in harboring protection from odonate larvae. Areas of dense vegetation in the natural marsh community may actually be the regions of greater risk for minnows since most macroinvertebrate predators are found there and there are no large cruising predators (i.e. piscivorous fish) in open-water areas. From the standpoint of predation only (and hence disregarding habitat-specific resource levels), fathead minnows should occupy open-water areas where there are fewer predators. Unfortunately, no tests of natural microhabitat choice were carried out, but large numbers of minnows were typically observed in regions of open water as well as in areas of low and high densities of macrophytes. Open water regions were relatively uncommon, however, during the time of field experimentation, due to the rapid proliferation and spread of Polygonum and Potamogeton.

Anax larvae and Notonecta did not interact to affect the survivorship of fathead minnows. This is contrary to my hypothesis that dragonfly larvae would prey on notonectids to the extent that minnows would benefit from the shared predation (e.g. "spreading the risk", Wilbur and Fauth 1990). Anax did indeed consume notonectids (Table 9, experiments 3 and 4) but further inspection of minnow survivorship showed that survival was actually slightly lower (yet not significantly so) with both predators present than with each predator present individually, suggesting a slight additive mortality effect by the predator species. Ultimately, these findings indicate that Anax and Notonecta had independent effects on fathead minnow mortality: the separate effects of each macroinvertebrate predator were significant in reducing minnow densities but the reductions were not influenced in any way by the presence of the other predator. VanBuskirk (1988) found a similar survival response by 4 species of larval anurans subjected to the odonates, Anax junius and Tramea carolina. Interactive effects of these predators were non-significant in altering anuran guild composition. Additionally, Wilbur and Fauth (1990) discovered additive effects (non-significant interactions) by A. junius larvae and Notopthalmus newts on Bufo and Rana tadpole survival and size in experimental ponds. The reason there were no strong additive effects in the present study is presumably due to Anax dampening the direct effects of Notonecta on minnows by preying partially on notonectids. An alternative explanation for the lack of significant additive effects in enclosures with both predators is that Anax is simply displacing some of its hunger on alternate prey (Notonecta). This is unlikely, however, since comparatively few notonectids were eaten. Furthermore, Notonecta had significant direct effects on minnow survival in these experiments; by consuming a small portion of notonectids, Anax presumably lessened slightly the impact of these direct effects. Relatively speaking, therefore, notonectids were more agents of predation than of prey.

Notonectids, however, had no significant effects on fathead minnow survivorship in Experiment 1 (minnow density= 60/enclosure, Notonecta density = 10/enclosure) or Experiment 6 (minnow density = 240/enclosure, Notonecta density = 27/enclosure). Since minnow density was relatively low in Experiment 1, notonectids did not encounter minnows as frequently as in Experiments 2, 3, and 4 (27 Notonecta/enclosure and 120, 120, and 240 minnows/enclosure, respectively). Encounter rate is often directly correlated with predator and prey densities (Bailey 1988), and it is probable that notonectids did not have an impact on the minnow population simply because there were few individuals of both predators and prey. Starting notonectid and minnow densities in Experiment 6 were the same as those in Experiment 4, in which minnow survival was significantly reduced by notonectids. Although the range of minnow sizes was equivalent in all field experiments (12-15 mm standard length), it is possible that the majority of minnows used in Experiment 6 were slightly larger than those used in

Experiment 4 (Experiment 6 was initiated 13 days after the start of Experiment 4, so minnows probably grew slightly during this time); if these minnows exceeded some "critical size" within the 12-15 mm SL range above which 12 mm notonectids are unable to capture and consume fish, they would be immune to predation. Cronin and Travis (1986) found diminished predation rates by *N*. *indica* and *N*. *undulata* as the size of *Rana* tadpoles increased and mention that notonectids generally have a narrower range of sizes of tadpoles which can be captured compared to other insect predators. The same trend may apply for fish prey.

Adult belostomatids apparently were successful in escaping from experimental enclosures. Nonetheless, they preyed effectively on minnows in both Experiment 1 and Experiment 2. Belostomatids consumed more minnows in Experiment 1 than notonectids, but notonectids were slightly more successful in Experiment 2 (the result in Experiment 2 is misleading, however, since many *Belostoma* had escaped from enclosures). Although no solid comparative conclusions can be drawn from these results, *Belostoma* may have an advantage over *Notonecta* because of increased encounter probability and a greater ability to handle large prey. For example, Victor and Ugwoke (1987) report that the giant water bug *Sphaerodema nepoides* (length=15 mm) was successful in capturing and consuming zygopteran nymphs and larval anurans up to 15 mm. The experiments of Crowl and Alexander (1989) showed that 19-22 mm *Belostoma flumineum* fed voraciously on 20-27 mm mosquitofish (*Gambusia*). The large size of experimental *Belostoma* is thus an advantage since sizable prey can be captured and handled more easily. Powerful raptorial forelegs aid *Belostoma* in grasping and holding large struggling prey. In addition, larger predators generally have greater visual resolution than smaller predators, thus allowing for increased prey detection and, consequently, enhanced prey encounter rates (Li et al. 1985). Like *Anax*, *Belostoma* did not interact with notonectids to affect minnow survival. Belostomatids consumed significant numbers of notonectids in enclosures containing both predators, and hence could have mitigated any direct mortality imposed by notonectids on fathead minnows, particularly in Experiment 2, in which *Notonecta* significantly decreased minnow survivorship.

Both *Anax* and *Belostoma* fed on notonectids at roughly the same rate in enclosures, but such a conclusion is not robust since a high percentage of belostomatids escaped from enclosures. In addition, percent mortality inflicted by *Anax* on minnows and on notonectids was approximately the same, which suggests that *Anax* feeds in proportion to relative abundances of various prey types, a conclusion reached by others (Pritchard 1964, Blois-Heulin 1990). Both predators have different anatomical features which enable them to overcome the chitinous exterior of *Notonecta*. *Belostoma* has a sturdy rostrum capable of penetrating hard-bodied prey, while *Anax* relies on its powerful labium, which contains sharp palps effective in piercing large prey (Pritchard 1965).

Pritchard (1964) noted, however, that notonectids were common in habitats studied but conspicuously absent from the fecal pellets of dragonfly larvae, attributing the absence to the protective features (large size and hard external morphology) of notonectids. There is some evidence that size may not be as important as hardness. Folsom and Collins (1984) proposed that small pleids were eaten less frequently by A. junius larvae compared to larger species due to their hard elytra, which rendered it difficult for dragonfly larvae to hold them in their labial palps. Nevertheless, dragonfly larvae in the present field study consumed proportionally as many notonectids as fathead minnows.

Water temperature may have a subtle effect on predation rates in enclosures. Metabolic rate may increase under higher temperatures, leading to increased predator hunger level and thus augmented rates of predation. Increased temperature might also indirectly lead to enhanced predation. Higher temperatures caused an increase in swimming behavior of the backswimmer Anisops deanei and hence increased its encounter rate with sit-and-wait predators (Bailey 1988). In the present study, there should have been no disparity in the number of prey eaten due to variable temperatures within experiments since temperatures were always identical in enclosures. Dissolved oxygen effects should also have been minimal; D.O. levels did not vary from enclosure to enclosure significantly. In addition, natural mortality was low for all three predator species and for fathead minnows, suggesting

that abiotic factors did not contribute greatly to mortality.

Fathead minnows spatially avoided Anax larvae in laboratory experiments, spending as much as 96% of the experimental period at least 4 cm away from the predator. Skelly and Werner (1990) found that larval American toads (Bufo americanus), in the presence of Anax junius larvae, inhabited the unoccupied portion of a container 70.2% of the time compared with only 56.2% in its absence. Moody et al. (1983) showed that fathead minnow schools occupied the corners of tanks rather than open water after the introduction of tiger muskellunge. Active movement to and occupancy of an area containing no predators would appear to be a simple mechanism reducing mortality risk. Notonectids, on the other hand, almost exclusively occupied the vegetated portion of aquaria containing Anax larvae. Only when struck at did notonectids move off the vegetation, but they would almost always return after a few seconds. The size of the experimental units (aquaria), of course, may have limited the distance travelled by notonectids following a strike, but it is clear that they did not employ spatial avoidance as an antipredator strategy, at least within the confines of aquaria used. The presence of potential prey (fathead minnows) also did not appear to affect the spatial distribution of notonectids. These results are contrary to the findings of Sih (1982), who found that vulnerable early instars of N. hoffmanni avoided the central portions of natural stream pools and experimental tubs, areas in which cannibalistic conspecifics are known to forage. Notonectids are typically associated with vegetation (Bennett and Streams 1986) and prefer these areas as perching sites to ambush prey. Their reliance on vegetation for perching sites, even in the absence of prey, involves a high risk of mortality in the present study since almost all strikes and captures by dragonfly larvae occurred on or near vegetation. It is possible that notonectids were not cued by the slow stalking movements of Anax, had an innate preference for vegetation, or simply depended on their chitinous exterior for protection. Anax larvae clearly had difficulty grasping and holding on to notonectids with their palps. If notonectids do depend on large size, hard external morphology, and vigorous escape response as antipredator mechanisms, this would agree with the conclusions reached by Pritchard (1964) concerning the absence of notonectids in the diet of larval dragonflies.

Fathead minnows did not spatially avoid Notonecta and did not appear to avoid Belostoma. This may be a result of the almost complete absence of movement by these predators, a component typical of a sit-and-wait foraging strategy. Unexpectedly, few strikes by Notonecta and no attacks by Belostoma on minnows were observed in laboratory experiments. In addition, only one minnow was consumed by each species in all laboratory predation experiments, however belostomatids did strike at, capture, and consume notonectids. It is possible that both species may necessitate a higher level of crypticity (i.e. more vegetation) to successfully ambush and capture swimming prey or may have a shorter maximum strike distance than dragonfly larvae. In either case, laboratory experiments involving notonectid or belostomatid predation on minnows did not support results obtained in field experiments.

Prey activity is obviously a critical factor influencing predator capture success (Folsom and Collins 1984). Due to their fusiform shape, fathead minnows have limited maneuverability and thus rely mostly on schooling to escape predators (Wahl and Stein 1988). In studies testing esocid predation on a variety of prey fish species, fathead minnows consistently demonstrated the lowest survivorship (Moody et al. 1983, Robinson 1988, Wahl and Stein 1988). In addition, fathead minnows have no spines or hard rays to interfere with mouthparts of predators. Lack of maneuverability and soft external morphology undoubtedly contributed to their susceptibility in this study. Minnows were never observed to escape from Anax larvae once captured (in sharp contrast to Notonecta) and most captures occurred when a solitary minnow wandered from a school and ventured near the vegetation. Minnows did school but swam noticeably less in the presence of Anax. Absence of movement is regarded as an effective antipredator strategy (Woodward 1983, Heads 1985, Streams 1986, Skelly and Werner 1990), particularly in response to sit-and-wait predators as a means to reduce encounter rates (Cooper et al. 1985). Notonectids, except when attacked, usually remained motionless on vegetation in close proximity to Anax. According to Cooper et al. (1985), sit-and-wait predators encounter and capture swimming prey significantly more often than sedentary prey. In light of this, fathead minnows should have been more susceptible to *Anax*, which is normally classified as a sit-and-wait predator (Pritchard 1964, 1965) than notonectids, but both were eaten at roughly the same rate in both field and laboratory experiments. This suggests that *Anax* has the flexibility to forage by mobile means or by ambush. Indeed, *Anax* utilized a sit-and-wait mode of predation with mobile prey (fathead minnows) but actively stalked sedentary prey (notonectids). It is probable that such flexibility contributes to *Anax*'s success in foraging on a wide variety of natural prey types. *Belostoma* and *Notonecta* are true ambush predators and should be capable of preying effectively on fathead minnows. For the most part, these predators consumed large numbers of minnows in field experiments but, as mentioned previously, did not do so in laboratory experiments, perhaps due to an extraneous variable contributing to predator success (e.g. specific vegetation density) that was present in the field but lacking in the laboratory. *Belostoma* was successful in capturing and consuming sedentary prey (*Notonecta*) in both field and laboratory experiments, probably due to the penchant of *Notonecta* to occupy vegetation, even in close proximity to predators.

Anax larvae were as successful in capturing minnows and notonectids in darkness as they were in the light. The ability to detect, capture, and consume prey in darkness as well as in light unquestionably serves to accentuate Anax's potential as an important predator in systems lacking large fish. Foraging patterns of some predators are probably entirely determined by the presence or absence of light and are not under any exogenous control (Streams 1982). The results obtained in this study demonstrate that Anax foraging is light-independent. With visual detection of prey being virtually eliminated by covering experimental aquaria, the implication is that larvae were forced to employ other means of obtaining prey. Libellulids fed on various prey items in darkness, but no such response was observed in Aeshna larvae (Pritchard 1965). Pritchard proposed that the large setae on the legs of libellulids enabled them to receive tactile stimuli better than aeshnids. Baetis mayflies have receptors on their cerci to detect hydrodynamic cues created by stonefly predators (Peckarsky and Penton 1989). Furthermore, Ischnura larvae most likely detect notonectid predators by hydrodynamic cues (Heads 1985). Most species of Notonecta have mechanoreceptors on their legs and abdomen which aid in the detection and location of surface prey (Streams 1982). It is possible, therefore, that Anax larvae have sensory structures capable of detecting pressure wave differences or possibly chemical stimuli that allow it to locate and capture prey at night. Prey capture may also occur as a result of direct tactile stimulation: one must keep in mind that prey are also prevented from visual detection of predators, and may literally swim into a predator and thus be captured.

Belostoma also preyed successfully on notonectids in darkness, indicating that it too may possess a system of sensory detection other than a visual one for locating prey. The consumption rates of similar-sized, late-instar Belostoma flumineum preying on snails under 24 hr continuous light and 24 hr continuous darkness did not differ significantly (Kesler and Munns 1989). The authors conclude that light was not a critical component to prey location and that, in all likelihood, Belostoma uses a variety of cues in detecting prey. In addition, prey capture by the belostomatid Sphaerodema was unaffected after havings its eyes painted over with waterproof paint (Victor and Ugwoke 1987). In conclusion, both Anax and Belostoma apparently possess structures or sensory sytems enabling them to capture prey in darkness, a mechanism which presumably allows them to forage at all times of the day or night. Inferential evidence for diel foraging periodicity in these predators, therefore, is weak.

In summary, my results have shown that larvae of the dragonfly Anax junius have the potential to inflict significant mortality on populations of small fish. Effects imposed may also be non-lethal, as fish exposed to Anax in the laboratory exhibited schooling behavior, swam less, and behaviorally shifted to areas vacant of predators. The potential for Anax to be a dominant predator in systems void of large fish is apparently due to many factors, including its large size, voraciousness, and ability to strike quickly.

Anax also appears able to switch its mode of foraging from a sit-and-wait manner to a cruising manner, thus enabling it to feed effectively on mobile or sedentary prey. This along with its generalist feeding tendency may help explain its cosmopolitan distribution in the United States. Additionally, Anax appears able to forage in darkness on mobile or stationary prey, providing further evidence for its potency as a predator. There is some evidence that Anax predation may be size-limited (Pritchard 1965, Heyer et al. 1975), hence Anax may be an important agent of selection for increased growth rates in fish, tadpoles, and invertebrates.

The efficacy of Belostoma and Notonecta on fish populations is unclear since laboratory experiments failed to substantiate findings in the field. An extrinsic factor in the field which was not present in experimental laboratory aquaria may explain this discordance. Prey size is probably a more important feature limiting notonectid predation than either dragonfly or belostomatid predation and may in part explain this predator's non-significant mortality effects in later field experiments. Since they are prey size-limited (Cronin and Travis 1986), notonectids may also induce selection for enhanced growth in potential prey species. Belostoma readily consumed notonectids in the field and under both light and dark conditions in the laboratory, suggesting its potential as an important predator on hard-bodied invertebrates.

Further work is necessary to substantiate the relative importance of macroinvertebrate predators on natural prey populations. Dragonfly larvae, notonectids, and belostomatids all prey on a wide variety of aquatic organisms. It would be advantageous in future experiments, therefore, to supply field enclosures with ambient densities of alternate prey in order to determine the relative trends in prey selection by these macroinvertebrate predators. In addition, individual predators captured across a range of natural microhabitats could be subjected to gut analyses to further elucidate their "normal" diets. By examining predation effects in these ways, it will be possible to gain a clearer understanding of natural patterns of predation in freshwater systems dominated by invertebrate predators rather than by fish predators.

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