UC Santa Barbara

UC Santa Barbara Previously Published Works

Title

Prey Selection by Freshwater Predators with Different Foraging Strategies

Permalink

https://escholarship.org/uc/item/4087k9cb

Journal

Canadian Journal of Fisheries and Aquatic Sciences, 42(11)

ISSN

0706-652X

Authors

Cooper, Scott D Smith, Daniel W Bence, James R

Publication Date

1985-11-01

DOI

10.1139/f85-216

Copyright Information

This work is made available under the terms of a Creative Commons Attribution License, available at https://creativecommons.org/licenses/by/4.0/

Peer reviewed

Prey Selection by Freshwater Predators with Different Foraging Strategies

Scott D. Cooper, Daniel W. Smith, and James R. Bence

Department of Biological Sciences, University of California, Santa Barbara, CA 93106, USA

Cooper, S. D., D. W. Smith, and J. R. Bence. 1985. Prey selection by freshwater predators with different foraging strategies. Can. J. Fish. Aquat. Sci. 42: 1720–1732.

We observed several freshwater predators, including the odonate larvae *Pachydiplax longipennis* and *Anax junius*, the hemipterans *Notonecta unifasciata* and *Buenoa scimitra*, the dytiscid larva *Acilius semi-sulcatus*, and juvenile *Gambusia affinis*, feeding on a variety of microcrustacean prey and determined the frequency of the component parts of predator–prey interactions (encounter, attack, capture, ingestion). Encounter rates were the most important determinant of predator selectivity when predators were presented with a variety of microcrustacean prey. When only copepod species were used as prey, however, both encounter rates and capture success were important in determining predator diets. We used our data to test hypotheses concerning relationships between predator foraging mode and patterns of prey selection: mobile predators exhibited stronger selection for sedentary prey than did sit-and-wait predators; our own and literature data also indicated that macroinvertebrate sit-and-wait predators are better able to capture, and have higher selectivity for evasive prey than do mobile predators. A predator's attack acceleration, however, may be a better predictor of its selectivity for evasive versus nonevasive prey than its mean swimming speed.

Les auteurs ont observé plusieurs prédateurs dulçaquicoles, y compris les larves d'Odonates Pachydiplax longipennis et Anax junius, les Hémiptères Notonecta unifasciata et Buenoa scimitra, la larve de Dyctiscidés Acilius semisulcatus et des juvéniles de Gambusia affinis, se nourrissant d'une variété de microcrustacés et ont déterminé la fréquence des composantes des interactions prédateur-proie (rencontre, attaque, capture, ingestion). Les taux de rencontre déterminaient principalement le choix des prédateurs quand ceux-ci étaient en présence d'une variété de proies. Toutefois, quand seulement des copépodes étaient utilisés comme proies, les taux de rencontre et le succès de capture déterminaient en grande partie le régime des prédateurs. Les auteurs ont utilisé leurs données pour vérifier des hypothèses sur les relations entre la méthode de recherche de la nourriture observée chez le prédateur et les systèmes de choix des proies : les prédateurs mobiles choisissaient plus souvent des proies sédentaires que ceux qui étaient à l'affût. De plus, leurs données et celles qui sont déjà publiées révèlent que les prédateurs macroinvertébrés à l'affût ont plus de succès pour la capture et montrent une sélectivité plus élevée des proies fuyantes que les prédateurs mobiles. La vitesse d'attaque de la part du prédateur peut toutefois donner une meilleure prévision de sa sélectivité pour les proies fuyantes par rapport aux proies sédentaires que la vitesse natatoire moyenne.

Received July 11, 1984 Accepted July 23, 1985 (J7866) Reçu le 11 juillet 1984 Accepté le 23 juillet 1985

n extensive literature is devoted to patterns of prey selection by planktivores (see reviews in Hall et al. 1976; Zaret 1980a; Hurlbert and Mulla 1981; Greene 1983). Much of this work, however, relies on inference and speculation from gut analyses and predation trials to explain patterns in predator diets. Dissection of a predation event into its component parts (encounter, attack, capture, and ingestion), on the other hand, provides direct information about the mechanisms underlying patterns of prey selection (Holling 1966; Swift and Fedorenko 1975; Pastorok 1981; Greene 1983; Riessen et al. 1984; Wright and O'Brien 1984). Specifically, observations of predator and prey behavior permit a better understanding of why and how predators select prey. In addition, direct observation contributes to the testing and refinement of general models of predation (O'Brien 1979; Greene 1983; Riessen et al. 1984; Wright and O'Brien 1984), and may identify the characteristics

of prey and predator that allow or preclude their coexistence in nature (Kerfoot 1982).

The specific goals of our work were twofold: (1) to determine the relative importances of various behavioral components (i.e. encounter, attack, capture, and ingestion) to the prey preferences shown by common freshwater predators; (2) to use these behavioral data to test two predictions: (a) Sedentary prey will compose a smaller proportion of the diets of sit-and-wait predators than of the diets of cruising predators. This prediction arises from considerations of the frequency of predator–prey encounter; sit-and-wait predators will only rarely contact and eat sedentary prey (Schoener 1971; Gerritsen and Strickler 1977; Pianka 1982; Greene 1983). (b) Evasive prey will compose a smaller proportion of the diets of active foragers than of the diets of sit-and-wait predators, because evasive prey should be able to detect the approach of a cruising predator and

Exp.	Predator	Predator starvation (d)	No. of prey types	No. ind./prey type	No. rep. trials	Volume (L)	Duration (min/rep.)	TE	ТІ
Series I									
1	Buenoa	0-1	14	10	9	2	45-170	294	109
2	Acilius	NR	13	10	2	2	80-105	192	40
3	Anax	1	11	10	8	1	23-65	105	64
4	Pachydiplax	5-6	10	10	10	0.5	15-60	158	100
5	Gambusia	1	4	10	10	2	1.5-7	220	107
6	Notonecta	1	5	10	6	1	60-120	143	47
7	Notonecta	47	3	20	9	0.5	25-66	100	64
Series II									
8	Gambusia	1	2	10	9	2	5	124	17
9	Pachydiplax	1	2	40	7	0.5	5-30	121	66
10	Buenoa	4	3	20	7	1	15-68	356	43
11	Gambusia	2	3	20	7	2	10-11	420	77
12	Pachydiplax	5	3	20	8	0.5	20-50	223	68

TABLE 1. Summary of predation experiments. "Predator starvation" is the amount of time predators were starved, and "volume" is the volume of water in which trials were run. TE is the total number of encounters observed and TI is the total number of ingestions observed. NR = not recorded.

take evasive action before or early in an attack. Ambush predators do not produce such early-warning signals and should, therefore, more successfully capture evasive prey.

We used several locally available microcrustacean prey in these predation trials, including Daphnia pulex, Ceriodaphnia reticulata, Sida crystallina, Simocephalus vetulus, Scapholeberis kingii, Pleuroxus denticulatus, Diaptomus pallidus, Diaptomus franciscanus, Cyclops vernalis, and ostracods. The predators studied were the larvae of the odonates Pachydiplax longipennis and Anax junius, the larvae of the beetle Acilius semisulcatus, the hemipterans Notonecta unifasciata and Buenoa scimitra, and the teleost Gambusia affinis.

Methods

Can. J. Fish. Aquat. Sci. Downloaded from www.nrcresearchpress.com by Santa Barbara (UCSB) on 01/20/14 For personal use only.

With the exception of Acilius larvae, predators and prey used in these experiments were collected from ponds and lakes in Santa Barbara County, California. Acilius larvae were collected from North Inyo Crater Pond in Mono County, California. Predation trials were conducted in the laboratory in small aquaria $(25.5 \times 6.4 \times 15.2 \text{ cm}, \text{ internal } l \times w \times h)$ under constant illumination from fluorescent light sources. Water temperatures ranged from 22 to 27°C. Other experimental conditions are listed in Table 1.

We introduced equal numbers of each of 2-14 prey types into aquaria containing filtered (52 µm) pond water. Container volumes and prey densities were manipulated so that we could observe a number of interactions in 1 h. Predators were added at the start of the experiment, and the behavior of the animals was watched for either a predetermined time (0.5-2h) or until a predetermined number of prey had been eaten (usually 10). We introduced a different predator individual for each replicate trial, and individual predators were never reused.

We noted the number of encounters (E), attacks (A), captures (C), and ingestions (I) and measured handling times (HT) for each prey type, and then calculated the number of predator-prey encounters per hour, attack probability (proportion of encounters resulting in attack = A/E, capture success (proportion of attacks resulting in capture = C/A), ingestion efficiency (proportion of captures resulting in ingestion = I/C, and α , a selectivity index (Chesson 1978, 1983). We could not, however, count both encounters and attacks for two predators, Pachydiplax and Gambusia. Pachydiplax showed no obvious behavioral responses to prey prior to attack, and in the Gambusia trials we could score only predator attacks on prey, but not encounters, because of the high rate of predator-prey interactions. In most trials, prey were replaced as they were eaten; however, in the Gambusia trials, prey were consumed too rapidly for replacement. In the Gambusia trials, we estimated prey preferences with formulae that take prey depletion into account (Chesson 1983).

Two sets of experiments were conducted. In the first series of predation trials, individuals of each of six predator species were presented with a prey assemblage composed of a variety of cladoceran, ostracod, and copepod species. In the second series of trials, a mixture of two or three copepod species was presented to individual predators. Three different predator species were used in these trials (Table 1).

Swimming speeds of prey were measured after experiments 1, 4, and 12 (Tables 1, 2) under the same conditions as used in those experiments (i.e. predators present). The back and bottom of the aquarium were marked with a grid composed of $1 \times 1 \text{ cm}$ cells, and two observers traced swimming paths on similarly gridded paper. Individual prey were watched for 1 min, swimming paths were monitored for at least five individuals of each prey type, and traced swimming paths were measured with a map wheel. With the exception of Acilius larvae, swimming or crawling speeds of predator individuals were determined, immediately after predation trials, using the techniques outlined above. Prey lengths (exclusive of the tail spine in Daphnia and the caudal furca in copepods) and predator head widths were measured with an ocular micrometer at $\times 6$ to $\times 25$, and lengths of predators were measured with a millimetre rule.

We used sign tests to determine if there were consistent differences in encounter rate, attack probability, capture success, ingestion efficiency, and α among prev types for each predator species (Conover 1982). Statistical analyses for trials using Acilius are not shown because there was insufficient replication in these trials for statistical testing. We used the Kruskal-Wallis test to determine if there were significant

TABLE 2. Characteristics of predators and prey used in predation trials. Numbers in parentheses under life history stages of some predators are predator head widths in millimetres. Prey swimming speeds (SS) measured after experiments 1, 4, and 12 are presented separately because prey speeds differed significantly among trials. Numbers in parentheses under prey and predator speeds are standard errors. For comparison, we have listed swimming speeds reported in the literature for these prey or similarly sized species in the same genus.

				Predators				
Species	Lif histo stag	e Tota ory lengt ge (mm	l h)	Foraging mode	I	Foraging speed (mm/s)	Microdistribution	Code
Pachydiplax longipennis	Lar	va 19	A	mbush		0	Rests on bottom	Р
Notonecta unifasciata Anax junius	(4.2 Adu Larv (4.9	2) ilt 10 va 25	Aı Sle	mbush ow stalk or ambush		0 0.9	Rests at surface On bottom	N An
Buenoa scimitra	Adu	ilt 7	Co	ontinuous swimming stroke – gl	 ide	4.9 (1.1)	Water column; does not forage at surface or bottom	В
Acilius semisulcatus	Larv (1.5	va 22 5)	Co	ontinuous swimming			Water column; sometimes at surface, not at bottom	Ac
Gambusia affinis	Juver	nile 24	Co	Continuous swimming		11.8 (2.6)	Throughout water column	G
				Prey				
Species	Size class	Length (mm)	SS ₁ (mm/s)	SS ₄ (mm/s)	SS ₁₂ (mm/s)	SS _{lit} (mm/s)	Microdistribution	Code
Ceriodaphnia reticulata	Large	0.70-0.78	0.4	1.5		0.8–1.5ª	Water column, but	Ce
C. reticulata	Small	0.38	(0.2)	(0.3)	—		Water column, but	Ce
Daphnia pulex	Large	2.1-2.3	1.3	4.9 (0.4)			Throughout water	Da
D. pulex	Medium	1.35-1.50	(0.2) 0.9 (0.2)	2.0		1.3-3.3 ^{c,d,e}	Throughout water	Da
D. pulex	Small	0.70-0.82	0.7	0.8		0.5-1.2 ^{a,c}	Throughout water	Da
Scapholeberis kingii	Large	0.60-0.69	0.07				Associated with	Sc
Pleuroxus denticulatus	Large	0.40-0.60	0.0	0.5 (0.2)			Attached to or crawling on sides or bottom,	Ch
Ostracod	Small	0.61-0.73	0.03	0.5		—	Moving slowly or	0
Sida crystallina	Large	1.22	0.0	(0.4)			Attached to sides or	Sd
Simocephalus vetulus	Large (l)	1.78-1.90	0.1 (0.1)	0.0			Attached to sides or bottom; swims into water column very	Sm
S. vetulus	Medium (m)	1.32	0.2 (0.2)				Attached to sides or bottom; swims into water column very	Sm
S. vetulus	Small (s)	0.65-0.82		0.8 (0.5)	_	_	Attached to sides or bottom; swimns into water column very	Sm
Cyclops vernalis	Large	0.96-1.60	0.0	0.9 (0.4)	9.2, 0.4 ^h (2.8, 0.2)	1.5-3.0 ^{a,b}	Usually resting, occasionally swimming on bottom; sometimes	Су

Can. J. Fish. Aquat. Sci., Vol. 42, 1985

on sides, occasionally in water column

Prey								
Species	Size class	Length (mm)	SS ₁ (mm/s)	SS₄ (mm/s)	SS ₁₂ (mm/s)	SS _{lit} (mm/s)	Microdistribution	Code
Diaptomus pallidus	Small	1.00-1.48	0.5	1.0	$1.1, 1.2^{h}$ (0.5, 0.1)	0.2-1.5 ^{a,c,d,f,g}	Throughout water	Di
Diaptomus franciscanus	Large	1.67-2.02	0.7 (0.1)		(0.5, 0.1) 1.9, 4.3 ^h (0.6, 0.6)	2.4–3.2 ^g	Throughout water column	Di

^aLi and Li 1979.

^bGerritsen 1978.

^cGerritsen 1980a. ^dGerritsen 1980b.

^ePastorok 1980b.

^fSwift and Fedorenko 1975.

^gGiguére et al. 1982.

^hValues for Experiment 12. The first value is mean swimming speed for the first five replicate trials and the second is mean swimming speed for the last three trials.

effects of predator species on the encounter probabilities, attack probabilities, capture successes, ingestion efficiencies, and α s for each prey type. If this test indicated significant differences among predator species for a given behavioral parameter for a given prey species, we applied the multiple comparisons procedure (Conover 1982). An encounter probability, p(E), for a given prey type is the encounter rate for that prey type divided by the total encounter rate for all prey types under consideration. For comparisons among predator species we only used data for the prey types common to all experiments, i.e. large Daphnia pulex, large Simocephalus vetulus, adult Diaptomus pallidus females, and adult Cyclops vernalis females in the series I trials and adult Diaptomus pallidus females, adult D. franciscanus females, and adult Cyclops vernalis females in the series II trials. Other statistical methods were taken from Conover (1982).

Results

Characteristics of Predators and Prey

The characteristics of predators and prey used in these experiments are summarized in Table 2. The predators can be ranked along a gradient of average speed as *Pachydiplax < Notonecta < Anax < Buenoa < Acilius < Gambusia*. Although *Pachydiplax* and *Notonecta* are both sit-and-wait predators, *Notonecta* changed its perch site more often than *Pachydiplax*. Anax larvae used a mixed strategy, alternately crawling and remaining motionless, while *Buenoa*, *Acilius*, and *Gambusia* moved more or less continuously. *Notonecta* and *Pachydiplax* generally respond only to very close prey, but the other predators responded to and stalked prey over distances of >2 cm.

The prey used in these predation trials display a variety of behavioral characteristics (Table 2). The pelagic zooplankton (*Daphnia*, *Ceriodaphnia*, and the calanoid copepods) swim continuously, and swimming speeds increase with increasing body size. The ostracods, littoral cladocerans (*Sida*, *Simocephalus*, *Scapholeberis*, *Pleuroxus*), and cyclopoid copepods are more sedentary. The copepods exhibit much more vigorous escape responses than the cladocerans or ostracods (Drenner et al. 1978). Prey Preferences and Behavioral Observations

In the first series of predation trials, we simultaneously exposed each predator to a variety of microcrustacean prey (Table 1). Encounter rate was, by far, the most important determinant of predator diets in these trials (Fig. 1, 2, 3, 4). For all predator species, there were significant positive correlations between encounter rate and selectivity (α) among prey types (Spearman rank correlation coefficients $(r_s) = +0.70$ to +0.98, P < 0.10 - 0.001). For the invertebrate predators, there were no significant differences in capture success among different sizes and species of ostracod or cladoceran prey (Table 3; Fig. 2-4). All predators ingested virtually all prey that they captured; consequently, there were also no significant differences in ingestion efficiency among different sizes and types of prey. Thus, patterns of prey selection among cladoceran and ostracod prey were determined almost entirely by encounter rates. All invertebrate predators preferred large over small Daphnia because encounter rates increased with increasing daphnid size (Fig. 1, 3). Encounter rates and selectivity indices were generally low for small littoral cladocerans (Sida, small Simocephalus, Pleuroxus, Scapholeberis) compared with large pelagic cladocerans (i.e. Daphnia, Fig. 1, 4). The low encounter rates for small littoral cladocerans can be attributed to at least three factors: (1) these prey were small and, consequently, inconspicuous to the large-size selective predators used in these experiments; (2) these prey moved slowly or infrequently, thereby reducing encounter rates with sedentary predators such as Pachydiplax; (3) these benthic or surface prey were microspatially segregated from predators which foraged in the water column. An exception to the latter pattern was *Notonecta*'s relatively high α for Scapholeberis, but Notonecta occurred in the surface stratum where Scapholeberis was found, and often encountered and ate this small cladoceran. For most predators, capture success for cladocerans was generally high, compared with copepods, and did not vary much among species or prey sizes (Table 3; Fig. 2, 3, 4). Capture successes for copepods, on the other hand, were often low and differed among copepod species (see below, Table 3; Fig. 2, 4, 5).

A second series of experiments (series II) was conducted to

Can. J. Fish. Aquat. Sci., Vol. 42, 1985





FIG. 1. Encounter rates (encounters per hour, stippled bars) and selectivity indices (α s, open bars) for prey types presented to each of four predator species. Numbers under each prey type are prey lengths in millimetres. Solid circles denote pelagic cladocerans, open circles denote littoral cladorcerans and ostracods, solid triangles signify cyclopoid copepods, and open triangles denote calanoid copepods. Prey code is presented in Table 2. The horizontal line represents the value if selection were random. Vertical bars = ± 1 se.

further study predation by Gambusia, Buenoa, and Pachydiplax on evasive, copepod prey. In these experiments, the relative importance of encounter rate and capture success in determining predation rates was dependent on the particular combination of predator and prey. When Gambusia was used as a predator (experiment 8), electivity indices for Diaptomus pallidus and similarly sized (1.25 mm) Cyclops vernalis were not significantly different ($\bar{X} \pm 1 \text{ se} = 0.43 \pm 0.15 \text{ vs}. 0.57 \pm 0.15$). In this experiment, higher encounter rates for Diaptomus were effectively balanced by higher capture success for Cyclops (Di A/h = 117.3 ± 36.9 , $C/A = 0.09 \pm 0.03$ vs. Cy $A/h = 48.0 \pm 12.5$, $C/A = 0.38 \pm 0.12$; P < 0.05, Wilcoxon signed ranks test). With *Pachydiplax* as the predator, encounter rates and α s for Cyclops were significantly higher than those for Diaptomus $(\bar{X} \pm 1 \text{ se} = 68.0 \pm 19.9 \text{ A/h}, \alpha = 0.72 \pm 0.09 \text{ for } Cyclops \text{ vs.}$ $24.7 \pm 7.3 \text{ A/h}, \alpha = 0.28 \pm 0.09 \text{ for Diaptomus}, P < 0.05,$ Wilcoxon signed ranks test). There were no differences in *Pachydiplax* capture success for these two prey species (Cy C/A $= 0.57 \pm 0.07$, Di C/A $= 0.53 \pm 0.13$, experiment 9). Thus, these results support the hypothesis that ambush predators can more efficiently capture evasive prey, such as Diaptomus, than can mobile predators (see below).

When presented with three copepod species (experiments 10-12), all three predators had low capture successes and electivity values for the large diaptomid (*Diaptomus franciscanus*) in spite of high encounter and attack rates for this prey type (Fig. 5). *Gambusia* preferred *Cyclops* over both diaptomids,

primarily because of the fish's higher capture success for cyclopoids (Table 3; Fig. 5). *Buenoa*, on the other hand, selected the smaller diaptomid, *Diaptomus pallidus* over the other two copepods, because this predator rarely encountered the sedentary, benthic cyclopoids and could not capture *Diaptomus franciscanus*.

In the Pachydiplax trials, there was an abrupt change in cyclopoid behavior between the fifth and sixth trials (Table 2). During the first five trials, cyclopoids were quite active, swimming at an average speed of 9.2 mm/s, while in the last three trials, the cyclopoids became more quiescent (average swimming speed of 0.4 mm/s). As a result, encounter rates and electivity indices for cyclopoids were much higher in the first five trials than in the last three (trials 1-5: Cy $A/h = 31.4 \pm 5.9$, $\alpha = 0.75 \pm 0.07$; trials 6-8: Cy A/h = 2.9 ± 1.0, $\alpha = 0.15 \pm$ 0.08, P < 0.05, Mann-Whitney U-test). Encounter rates and capture success for both species of Diaptomus, and capture success for Cyclops, did not significantly differ between the first five versus the last three trials. Because Cyclops became much rarer in the diet of *Pachydiplax* in the last three trials, electivity indices for Diaptomus pallidus increased (trials 1-5: $\alpha = 0.17 \pm 0.05$; trials 6-8: $\alpha = 0.72 \pm 0.17$; P < 0.05, Mann-Whitney U-test). These results emphasize the importance of prey activity and consequent encounter rates in determining the diets of ambush predators. In the series I and II trials, ingestion efficiency was similar for all prey types and did not influence patterns of predator selectivity.



FIG. 2. Attack probabilities (A/E, stippled bars) and capture successes (C/A, open bars) for prey types presented to each of four predator species. Other designations as in Fig. 1.



FIG. 3. Encounter probabilities (p(E)s), open triangles), capture successes (C/A), open circles), and selectivity indices (αs) , solid circles) for different sizes of *Daphnia pulex* presented to *Notonecta* (experiment 7). For comparison we included data on *Gambusia* size selectivity taken from Bence and Murdoch (1985). Vertical bars = ± 1 se.

Can. J. Fish. Aquat. Sci., Vol. 42, 1985

Can. J. Fish. Aquat. Sci. Downloaded from www.nrcresearchpress.com by Santa Barbara (UCSB) on 01/20/14 For personal use only.



FIG. 4. Left: encounter rates (encounters per hour, stippled bars) and selectivity indices (α s, open bars) for prey types presented to *Notonecta* and *Gambusia*. Right: attack probabilities (A/E, stippled bars) and capture successes (C/A, open bars) for prey types used in these trials. Other designations as in Fig. 1. Mean lengths of prey used in these trials were as follows: *Notonecta* trials: Da = 1.52 mm, Sm = 1.51 mm, Sc = 0.58 mm, Di = 1.21 mm, and Cy = 1.18 mm; *Gambusia* trials: Da = 1.68 mm, Sm = 1.69 mm, Di = 1.35 mm, and Cy = 1.37 mm.

Test of the Hypotheses

We first tested whether selection for sedentary prey is stronger by cruising than by ambush predators. To do this we examined selectivity for Simocephalus (sedentary prey) over similarly sized Daphnia (mobile prey) by using data for only these two prey types. The results support our hypothesis: there was a significant positive correlation between average predator foraging speed and the electivity index for Simocephalus (Spearman $r_s = +0.83$, P < 0.05). This result was the product of a positive correlation between encounter probability for Simocephalus and predator foraging speed (Spearman $r_s = +0.60, P < 0.10$). There was no relationship between predator foraging speed and capture success for Simocephalus (Spearman $r_s = -0.43$, P > 0.10). Encounter rates and electivity indices for large Simocephalus were generally low for Buenoa and the ambush predators (Notonecta, Pachydiplax), but were higher for visual cruising predators (Acilius, Gambusia, Anax) (Table 4; Fig. 1, 4). Although they sometimes adopted an ambush foraging mode, we classified Anax naiads as cruising predators because they were often observed stalking large Simocephalus over distances of several centimetres.

Second, we tested whether selection for evasive prey is stronger by ambush than by cruising predators. We did this by comparing our results for evasive prey (the copepod *Diaptomus*) with those obtained for comparably sized, nonevasive *Daphnia*. Adult copepods have much stronger escape responses than *Daphnia* (Drenner et al. 1978), while other important characteristics (microdistributions and swimming speeds of *Daphnia* and *Diaptomus*) were comparable in our experimental containers. Although all predators consumed more *Daphnia* than copepods, the relative rates at which these two prey types were eaten corresponded to our prediction. Among invertebrate

predators, there was a significant negative correlation between predator foraging speed and α for *Diaptomus* ($r_s = -0.93$, P < 0.01), and between predator foraging speed and capture success for Diaptomus ($r_s = -0.83$, P < 0.05). There was no relationship between predator foraging speed and encounter probability for Diaptomus ($r_s = -0.20$, P > 0.10). However, when the vertebrate predator, Gambusia, was included in the analyses, there were no significant correlations between predator foraging speed and α s, encounter probabilities, or capture successes for copepods ($r_s = -0.50$ for predator speed vs. C/A, $r_s = -0.39$ for predator speed vs. α). This change can be attributed to Gambusia's slightly higher capture success for copepods when compared with cruising invertebrate predators (see Discussion). With one exception, capture successes and electivity indices for copepods were significantly higher for our most sedentary predator, Pachydiplax, than for other predator species in the first series of trials (Fig. 1, 2, 4; Table 4). In the one exception, capture success for *Diaptomus* was not significantly different for Pachydiplax versus Anax. Capture success for Diaptomus was, however, generally low and variable in the Anax trials (Fig. 2).

There was a significant positive correlation between attack probability and capture success across prey types for *Buenoa* and *Anax* (*Buenoa* = +0.99, P < 0.001; *Anax* = +0.88, P < 0.05; Spearman rank correlation analysis). Although these correlations could be interpreted as active predator choice of nonevasive prey, our observations suggest that these correlations were a consequence of prey flight from approaching predators before an attack was launched.

To test the generality of our hypothesis regarding the relationship between the foraging mode of macroinvertebrate predators and selectivity for evasive prey, we combined our data with literature data. In our survey we examined results from laboraTABLE 3. Summary of significant differences in behavioral parameters among prey types for each predator species. Prey types connected by an underline are not significantly different (P > 0.05, sign test). Because of the limited number of replicates, we could not run statistical tests for the *Acilius* trials. Tests dealing with ingestion efficiency are not presented because ingestion efficiencies were not significantly different among prey types. Prey code and sizes are given in Table 2. The letters 1, m, and s after the prey code designates size classes large, medium, and small. IR = insufficient number of values for a statistical test; α = selectivity index, E = encounter rate, A/E = attack probability, and C/A = capture success.

Predator	Exp.	Parameter	High Lo)W
Buenoa	1	α Ε	Dal Dam <u>Das Ce Sml</u> Sc Sms Smm Sd Ch O Dil Dis G <u>Dal Dil</u> Dam Das Dis Sml Ce Smm Sc O Cy Sd Chy Sr	Cy ms
		A/E	Dal Dam Das Sml Dis Dil	
		C/A	Dal Dam Das Sml Dil	
Anax	3	α	Dam Dal Sml Sc Di Das O Ce Sms Chy Cy	
		Ε	Dam Dal Sml Sc Di O Cy Chy Ce Das Sms	
		A/E C/A	Dam Dal IR	
Pachydiplax	4	α	Dal Cy Dam Ce O Di Sml Chy Das Sms	
		E	also Cy > O, Di > Das Dal Di Cy Dam Ce Q Chy Das Sml Sms	
			also $Dam > Das$, $Cy > Ce$	
		C/A	<u>Dal Cy</u> Di	
Gambusia	5	α	Da <u>Sm Di</u> Cy	
		E C/A	Da <u>Sm Di Cy</u> Sm Da Cy Di	
Notonecta	6	a	Da Sc Sm Cv Di	
11010iieeiu	Ũ	е Е	Da Sc Cy Di Sm	
		A/E	Da Sc Sm Di Cy	
		C/A	<u>Sc Da Sm Cy</u> Di	
Buenoa	10	α	Dis <u>Cy Dil</u>	
		Ε	Dil Dis Cy	
		A/E	<u>Cy Dis Dil</u>	
		C/A	<u>Cy Dis</u> Dil	
Gambusia	11	α	Cy <u>Dil Dis</u>	
		Ε	<u>Dil Dis</u> Cy	
		C/A	Cy <u>Dil Dis</u>	
Pachydiplax	12	α	<u>Dis Cy</u> Dil	
		Ε	<u>Dil Cy Dis</u>	
		C/A	<u>Cy Dis</u> Dil	

tory or in situ studies where predators were exposed to copepods (usually *Diaptomus*), cladocerans (usually *Daphnia* of comparable size), or both together. In some studies, additional prey types were available. We also included the results from a few field diet studies where prey abundance had been quantified. We assumed that relative predation rates on copepods versus daphnids were not affected by whether copepods and daphnids were available alone, together, or with additional prey types. For the statistical analysis of these data, we followed the conservative procedure of treating each predator genus as a replicate. Ambush predators had significantly higher electivity indices for copepods (over cladocerans) than did cruising predators (Table 5).

Discussion

Our observations of predator-prey interactions illustrate several important points. First, except for copepods, prey were virtually defenseless against predators. Cladocera, especially, were attacked, captured, and eaten when encountered; thus, their coexistence with predators in nature must rely on mechanisms (temporal or spatial segregation, small size, or reduced visibility) that minimize the frequency of encounters with predators (Greene 1983). Copepods, on the other hand, were often able to evade capture (Drenner et al. 1978; Wright and O'Brien 1984). Second, we found that predators attacked nearly

Can. J. Fish. Aquat. Sci., Vol. 42, 1985



FIG. 5. As for Fig. 4 but for three copepod species presented to each of three predator species. Random selection of these three prey types would result in selectivity indices (α s) of 0.33. Prey code and lengths: Cy = Cyclops vernalis, 1.60 mm; Dis = Diaptomus pallidus, 1.48 mm; and Dil = D. franciscanus, 2.01 mm.

all prey that they encountered; the preferences demonstrated by these predators were largely a function of the prey's vulnerability to encounter and capture. Thus, many of the predators examined here did not appear to "choose" to attack prey. Although ingestion efficiency played little role in determining patterns of prey selection by predators in our experiments, ingestion efficiency can play a role in determining predation rates on hard-bodied (e.g. large ostracods) or bad-tasting prey (e.g. water mites) by some of these predators (Kerfoot et al. 1980; Kerfoot 1982; S. D. Cooper, D. W. Smith, and J. R. Bence unpubl. data).

We predicted that mobile predators would select sedentary prey more strongly than would ambush predators. This prediction stems from a consideration of predator-prey encounter frequencies: cruising predators should encounter sedentary prey at higher rates than do ambush predators (Gerritsen and Strickler 1977). Indeed, our results confirmed that ambush predators rarely encountered, and therefore rarely ate, sedentary prey. In contrast, sedentary prey were more vulnerable to active predators because of higher encounter rates with these predators. An exception to this trend was *Buenoa*, a cruising predator whose electivity index for sedentary prey (i.e. *Simocephalus*) was low; however, *Buenoa* rarely responded to, and did not attack, prey that were not actively swimming in the water column.

Data reported in the literature also support the above hypothesis. Active predators, including flatworms, cyclopoid copepods, and some water mites, feed at comparable rates on *Daphnia* and similarly sized *Simocephalus* (Paveljeva and Zankai 1971;

TABLE 4. Summary of significant differences in measured parameters among predator species for each prey type. Predator species connected by an underline are not significantly different (P > 0.05, Kruskal–Wallis test, multiple comparisons procedure). Tests dealing with ingestion efficiencies are not presented because ingestion efficiencies were not significantly different among predator species. Predator code as in Table 2; parameter codes as in Table 3.

Prey	Parameter	High Low
Series I		
Daphnia	α	<u>B Ac N</u> An P G
	p(E)	<u>B An N</u> P Ac G
	A/E	Ac B An N
	C/A	<u>An P B G N Ac</u>
Simocephalus	α	<u>Ac G An N B P</u>
	p(E)	<u>Ac G N An</u> B P
	A/E	B An N Ac
	C/A	<u>P An B G N Ac</u>
Diaptomus	α	P <u>GAnNBAc</u>
	p(E)	<u>PBGNAnAc</u>
	A/E	<u>N An Ac B</u>
	C/A	<u>P An</u> G N B Ac
Cyclops	α	P <u>GNAnBAc</u>
	p(E)	<u>PNGBAnAc</u>
	A/E	<u>N B An</u>
	C/A	P <u>BGNAn</u>
Series II		
Large Diaptomus	α	<u>GBP</u>
	p(E)	<u>GBP</u>
	C/A	<u>PBG</u>
Small Diaptomus	α	BPG
	p(E)	<u>B G P</u>
	C/A	<u>P B</u> G
Cyclops	α	<u>G P</u> B
	p(E)	<u>P G B</u>
	C/A	<u>G P B</u>

Brandl and Fernando 1975; Schwartz and Hebert 1982), and cruising fish and copepod predators feed heavily on stationary *Chaoborus* larvae (Stenson 1978, 1980; Williams 1980; Kerfoot 1982). Some damselfly naiads can apparently switch from an ambush to a cruising foraging mode resulting in increased selection for the sedentary *Simocephalus* relative to *Daphnia* (Akre and Johnson 1979; Johnson and Crowley 1980). We could find no examples of the relative selectivity on mobile versus sedentary prey by ambush predators, although one report (Smyly 1980) suggested that the sedentary habit of *Chydorus* effectively limits its losses to the ambush predator, *Chaoborus*.

Active predators preyed more equitably on sedentary and mobile prey than did ambush predators; however, in the field this pattern is complicated by at least two factors. First, many active predators are open-water forms and they rarely encounter sedentary prey that occur mainly in vegetation or on the bottoms of lakes. Even within our small experimental containers there was microspatial segregation of predators and prey. Second, some cruising predators (e.g. *Buenoa*) may respond to and attack only moving prey. This would be true both for tactile predators which respond only to hydrodynamic cues and to visual predators which respond only to prey motion (Pritchard 1965; Strickler 1975; Pastorok 1980a). In addition, moving prey are more conspicuous than nonmotile prey to those predators that do not require prey movement to stimulate attack (Confer and Blades 1975; O'Brien 1979; Zaret 1980b; Kerfoot 1982; Janssen 1982; Wright and O'Brien 1984). For these reasons, active predators may also take a preponderence of active versus sedentary prey, although the differential should not be as marked as that displayed by sedentary predators.

Our second prediction was that evasive prey would be more vulnerable to sedentary as opposed to mobile predators because capture success would be higher for ambush predators. Analyses of our own and literature data indicated that capture successes and electivity indices for copepods are very low for all macroinvertebrate cruising predators, whereas some ambush predators are relatively efficient at capturing copepods and, hence, have relatively high electivity indices for copepods.

Other, less direct, evidence also supports this conclusion. For example, some studies have reported the efficient capture of copepods by ambush predators, and copepods are often an important component of the diets of such ambush predators as zygopteran naiads, corixids, hydroids, and chaoborids (Fischer 1964; Lawton 1970; Griffiths 1973; Reynolds 1975; Thompson 1978; Kajak and Rybak 1979; Hairston 1979; Cuker and Mozley 1981). In contrast, cruising predators, such as water mites and freshwater jellyfish, have very low predation rates on evasive copepods compared with nonevasive prey (Ellis-Adam and Davids 1970; Dodson and Cooper 1983). Data on the selection of evasive (Diaphanasoma, helmeted Daphnia) versus nonevasive cladocerans (nonhelmeted Daphnia) by cruising (water mites, Buenoa, and related forms) and ambush predators (Chaoborus) also indicate that electivity indices for evasive prey will be higher for ambush than for active predators (O'Brien and Vinyard 1978; Winner and Greber 1980; Grant and Bayly 1981; Riessen 1982; Cooper and Smith 1982). Among freshwater predators, then, there is a general relationship between predator foraging mode and selectivity for evasive prey.

There are, however, two groups of cruising predators, the predatory copepods and particulate-feeding fish, which often have relatively high electivity values for evasive versus nonevasive prey. In the case of predatory copepods, other parts of the predator-prey interaction (e.g. ingestion efficiency) may override the importance of capture success in determining patterns of prey selection (Kerfoot 1977, 1978; Li and Li 1979; O'Brien et al. 1979, 1980; Williamson and Gilbert 1980; Williamson 1983; Dodson 1984). In the latter case, fish can counter the evasive responses of prey by modifying their attack behavior (Confer and Blades 1975; Vinyard 1980, 1982; Winfield et al. 1983). In fact, some fish switch from a continuous cruising mode to more of an ambush mode when attempting to catch copepods (J. R. Bence, unpubl. data). In contrast with other predators, both fish and copepods will often actively pursue and overtake escaping zooplankton prey (Jamieson 1980; Winfield et al. 1983).

Is there a better predictor than predator foraging speed of a predator's degree of selection for evasive versus nonevasive prey? Although our hypothesis is correct to some extent, it appears that the attack acceleration of predators may be more important than foraging speed in determining the success of predators in capturing evasive prey. Predators that are success-

TABLE 5. Summary of capture successes (C/A) and selectivity indices (α s, Chesson 1978, 1983) calculated for evasive versus nonevasive prey for a variety of ambush and active predators. Unless otherwise noted, comparisons are for *Diaptomus* (Di) versus comparably sized *Daphnia* (Da). Selectivity indices for *Diaptomus* were significantly higher for ambush than for cruising predators (P < 0.05, Mann–Whitney U-test).

Predator	Di a	Di C/A	Da C/A	Predator species and literature source	Notes
Ambush					
Chaoborus	0.58	0.30	0.44	 flavicans α: Swüste et al. 1973; Smyly 1980. C/A: Smyly 1980 americanus α: Vinyard and Menger 1980; Sprules 1972; von Ende and Dempsey 1981; Anderson and Raasveldt 1974; Lynch 1979; Melville and Maly 1981. C/A: Vinyard and Menger 1980; Swift 	Vinyard and Menger 1980: $\alpha = Di vs. Moina$
				and Fedorenko 1975; Riessen et al. 1984 <i>punctipennis</i> α: Winner and Greber 1980 sp. α: Lewis 1977	Lewis 1977 and Winner and Greber 1980: $\alpha = Di vs.$ Diaphanosoma
Notonecta	0.16	0.03	0.46	trivittatus C/A: Swift and Fedorenko 1975 undulata α : Lynch 1979 unifasciata α and C/A: this study	·
Pachydiplax	0.40	0.56	0.90	longipennis: this study	
X	0.39	0.30	0.60		
SE	0.13	0.15	0.15		
Cruising					
Mysis	0.09	0.20	0.73	relicta α: Grossnickle 1978; Cooper and Goldman 1980; Bowers and Vanderploeg 1982; Ramcharan et al. 1985, C/A: Ramcharan et al. 1985	Ramcharan et al. 1985: $\alpha = Cy vs. Da$
Neomysis	0.20			mercedis α : Murtaugh 1981	Murtaugh 1981: $\alpha = \bar{X}$ of field and lab data
Piona	0.02			<i>constricta</i> α: Riessen 1982 <i>limnetica</i> α: Gliwicz and Biesiadka 1975	
Acilius	0.00	0.00	0.42	semisulcatus: this study	
Buenoa	0.00	0.00	0.63	scimitra: this study	
Mesostoma	0.00			ehrenbergii: Maly et al. 1980	
Gammarus	0.04			lacustris: Anderson and Raasveldt 1974	
X	0.05	0.07	0.59		
SE	0.03	0.07	0.09		

ful in capturing agile prey often have rapid attack responses (e.g. odonates, chaoborids, copepods, particulate-feeding fish), whereas predators that are less successful at capturing evasive prey often have slower attacks (Pritchard 1965; Kerfoot 1977; Janssen 1978; Pastorok 1980a, 1980b; Vinyard 1980, 1982; Williamson 1983). In many cases, there appears to be a relationship between predator foraging speed and attack acceleration; i.e. cruising predators often show little acceleration when attacking prey, whereas ambush predators often have rapid strikes.

Acknowledgements

We thank N. Hemphill, E. McCauley, and J. C. Roff for reviewing this paper.

References

- AKRE, B. G., AND D. M. JOHNSON. 1979. Switching and sigmoid functional response by damselfly naiads with alternate prey available. J. Anim. Ecol. 48: 703-720.
- ANDERSON, R. S., AND L. G. RAASVELDT. 1974. Gammarus predation and the possible effects of Gammarus and Chaoborus feeding on the zooplankton composition in some small lakes and ponds in western Canada. Can. Wildl. Serv. Occas. Pap. 18: 1–23.
- BENCE, J. R., AND W. W. MURDOCH. 1985. Prey size selection and its relation to optimal diet theory. Ecology. (In press)

BOWERS, J. A., AND H. A. VANDERPLOEG. 1982. In situ predatory behavior of Mysis relicta in Lake Michigan. Hydrobiologia 93: 121-131.

- BRANDL, Z., AND C. H. FERNANDO. 1975. Food consumption and utilization in two freshwater cyclopoid copepods (*Mesocyclops edax* and *Cyclops* vicinus). Int. Rev. Gesamten Hydrobiol. 60: 471–494.
- CHESSON, J. 1978. Measuring preference in selective predation. Ecology 59: 211-215.
 - 1983. The estimation and analysis of preference and its relationship to foraging models. Ecology 64: 1297-1304.
- CONFER, J. L., AND P. I. BLADES. 1975. Omnivorous zooplankton and planktivorous fish. Limnol. Oceanogr. 20: 571-579.
- CONOVER, W. J. 1982. Practical nonparametric statistics. 2nd ed. John Wiley & Sons Inc., New York, NY. 462 p.
- COOPER, S. D., AND C. R. GOLDMAN. 1980. Opossum shrimp predation on zooplankton. Can. J. Fish. Aquat. Sci. 37: 909-919.
- COOPER, S. D., AND D. W. SMITH. 1982. Competition, predation, and the relative abundances of two species of *Daphnia*. J. Plankton Res. 4: 859-879.
- CUKER, B. E., AND S. C. MOZLEY. 1981. Summer population fluctuations, feeding, and growth of *Hydra* in an arctic lake. Limnol. Oceanogr. 26: 697-708.
- DODSON, S. I. 1984. Predation of *Heterocope septentrionalis* on two species of *Daphnia*: morphological defenses and their cost. Ecology 65: 1249–1257.
- DODSON, S. I., AND S. D. COOPER. 1983. Trophic relationships of the freshwater jellyfish Craspedacusta sowerbyi Lankester 1880. Limnol. Oceanogr. 28: 345-351.
- DRENNER, R. W., J. R. STRICKLER, AND W. J. O'BRIEN. 1978. Capture probability: the role of zooplankter escape in the selective feeding of planktivorous fish. J. Fish. Res. Board Can. 35: 1370-1373.
- ELLIS-ADAM, A. C., AND C. DAVIDS. 1970. Oviposition and post-embryonic

development of the watermite *Piona alpicola* (Neuman, 1880). Neth. J. Zool. 20: 122-137.

- FISCHER, Z. 1964. Some observations concerning the food consumption of the dragonfly larvae of *Erythrosoma najas* Hans and *Coenagrion hastulatum* Charp. Pol. Arch. Hydrobiol. 12: 253–264.
- GERRITSEN, J. 1978. Instar-specific swimming patterns and predation of planktonic copepods. Verh. Int. Ver. Limnol. 20: 2531-2536.

1980a. Adaptive responses to encounter problems, p. 52–62. In W. C. Kerfoot [ed.] Evolution and ecology of zooplankton communities. The University Press of New England, Hanover, NH.

1980b. Sex and parthenogenesis in sparse populations. Am. Nat. 115: 718–742.

- GERRITSEN, J., AND J. R. STRICKLER. 1977. Encounter probabilities and community structure in zooplankton: a mathematical model. J. Fish. Res. Board Can. 34: 73-82.
- GIGUÉRE, L. A., A. DELAGE, L. M. DILL, AND J. GERRITSEN. 1982. Predicting encounter rates for zooplankton: a model assuming a cylindrical encounter field. Can. J. Fish. Aquat. Sci. 39: 237–242.
- GLIWICZ, Z. M., AND E. BIESIADKA. 1975. Pelagic water mites (Hydracarina) and their effect on the plankton community in a neotropical man-made lake. Arch. Hydrobiol. 76: 65–88.
- GRANT, J. W. G., AND I. A. E. BAYLY. 1981. Predator induction of crests in morphs of the Daphnia carinata King complex. Limnol. Oceanogr. 26: 201-218.
- GREENE, C. H. 1983. Selective predation in freshwater zooplankton communities. Int. Rev. Gesamten Hydrobiol. 68: 297–315.
- GRIFFITHS, D. 1973. The food of animals in an acid woodland pond. J. Anim. Ecol. 42: 285-293.
- GROSSNICKLE, N. E. 1978. The herbivorous and predaceous habits of Mysis relicta in Lake Michigan. Ph.D. thesis, University of Wisconsin-Madison, Madison, WI. 107 p.
- HAIRSTON, N. G. JR. 1979. The adaptive significance of color polymorphism in two species of *Diaptomus* (Copepoda). Limnol. Oceanogr. 24: 15–37.
- HALL, D. J., S. T. THRELKELD, C. W. BURNS, AND P. H. CROWLEY. 1976. The size efficiency hypothesis and the size structure of zooplankton communities. Annu. Rev. Ecol. Syst. 7: 177-208.
- HOLLING, C. S. 1966. The functional response of invertebrate predators to prey density. Mem. Entomol. Soc. Can. 48: 1–86.
- HURLBERT, S. H., AND M. S. MULLA. 1981. Impacts of mosquitofish (Gambusia affinis) predation on plankton communities. Hydrobiologia 83: 125-151.
- JAMIESON, C. D. 1980. The predatory feeding of copepodid stages III to adult Mesocyclops leuckarti (Claus), p. 518–537. In W. C. Kerfoot [ed.] Evolution and ecology of zooplankton communities. The University Press of New England, Hanover, NH.
- JANSSEN, J. 1978. Feeding behavior repertoire of the alewife, Alosa pseudoharengus, and the ciscoes Coregonus hovi and C. artedii. J. Fish. Res. Board Can. 35: 249-253.

1982. Comparison of searching behavior for zooplankton in an obligate planktivore, blueback herring (*Alosa aestivalis*), and a facultative planktivore, bluegill (*Lepomis macrochirus*). Can. J. Fish. Aquat. Sci. 39: 1649–1654.

- JOHNSON, D. M., AND P. H. CROWLEY. 1980. Odonate "hide and seek": habitat-specific rules?, p. 569-579. In W. C. Kerfoot [ed.] Ecology and evolution of zooplankton communities. The University of New England Press, Hanover, NH.
- KAJAK, Z., AND J. RYBAK. 1979. The feeding of *Chaoborus flavicans* Meigen (Diptera, Chaoboridae) and its predation on lake zooplankton. Int. Rev. Gesamten Hydrobiol. 64: 361-378.
- KERFOOT, W. D. 1977. Implications of copepod predation. Limnol. Oceanogr. 22: 316–325.

1978. Combat between predatory copepods and their prey: Cyclops, Epischura and Bosmina. Limnol. Oceanogr. 23: 1089–1102.

- 1982. A question of taste: crypsis and warning coloration in freshwater zooplankton communities. Ecology 63: 538-554.
- KERFOOT, W. C., D. L. KELLOGG, JR., AND J. R. STRICKLER. 1980. Visual observations of live zooplankters: evasion, escape, and chemical defenses, p. 10-27. *In* W. C. Kerfoot [ed.] Evolution and ecology of zooplankton communities. The University Press of New England, Hanover, NH.
- LAWTON, J. H. 1970. Feeding and food energy assimilation in larvae of the damselfly *Pyrrhosoma nymphula* (Sulz.) (Odonata: Zygoptera). J. Anim. Ecol. 39: 669-689.
- LEWIS, W. M. JR. 1977. Feeding selectivity of a tropical *Chaoborus* population. Freshwater Biol. 7: 311-325.
- LI, J. L., AND H. W. LI. 1979. Species-specific factors affecting predator-prey interactions of the copepod Acanthocyclops vernalis with its natural prey, Limnol. Oceanogr. 24: 613–626.

Can. J. Fish. Aquat. Sci., Vol. 42, 1985

- LYNCH, M. 1979. Predation, competition, and zooplankton community structure: an experimental study. Limnol. Oceanogr. 24: 253-272.
- MALY, E. J., S. SCHOENHOLTZ, AND M. T. ARTS. 1980. The influence of flatworm predation on zooplankton inhabiting small ponds. Hydrobiologia 76: 233-240.
- MELVILLE, G. E., AND E. J. MALY. 1981. Vertical distributions and zooplankton predation in a small temperate pond. Can. J. Zool. 59: 1720-1725.
- MURTAUGH, P. A. 1981. Selective predation by Neomysis mercedis in Lake Washington. Limnol. Oceanogr. 26: 445-453.
- O'BRIEN, W. J. 1979. The predator-prey interaction of planktivorous fish and zooplankton. Am. Sci. 67: 572-581.
- O'BRIEN, W. J., C. BUCHANAN, AND J. F. HANEY. 1979. Helmets and invisible armor: structures reducing predation from tactile and visual planktivores. Ecology 60: 287-294.
- O'BRIEN, W. J., D. KETTLE, H. RIESSEN, D. SCHMIDT, AND D. WRIGHT. 1980. Dimorphic Daphnia longiremis: predation and competitive interactions between the two morphs, p. 497–505. In W. C. Kerfoot [ed.] Evolution and ecology of zooplankton communities. The University Press of New England, Hanover, NH.
- O'BRIEN, W. J., AND G. L. VINYARD. 1978. Polymorphism and predation: the effect of invertebrate predation on the distribution of two varieties of Daphnia carinata in South India ponds. Limnol. Oceanogr. 23: 452-460.
- PASTOROK, R. A. 1980a. Selection of prey by *Chaoborus* larvae: a review and new evidence for behavioral flexibility, p. 538-554. *In* W. C. Kerfoot [ed.] Evolution and ecology of zooplankton communities. The University Press of New England, Hanover, NH.
 - 1980b. The effects of predator hunger and food abundance on prey selection by *Chaoborus* larvae. Limnol. Oceanogr. 25: 910–921.
 - 1981. Prey vulnerability and size selection by Chaoborus larvae. Ecology 62: 1311-1324.
- PAVELJEVA, E., AND N. P. ZANKAI. 1971. Quantitative nutritional characteristics of some water mites species. Ann. Biol. Tihany 38: 177-181.
- PIANKA, E. R. 1982. Evolutionary ecology. 3rd ed. Harper and Row, New York, NY. 416 p.
- PRITCHARD, G. 1965. Prey capture by dragonfly larvae (Odonata: Anisoptera). Can. J. Zool. 43: 271–289.
- RAMCHARAN, C. W., W. G. SPRULES, AND R. W. NERO. 1985. Notes on the tactile feeding behaviour of *Mysis relicta* Lovén (Malacostraca: Mysidacea). Verh. Int. Ver. Limnol. 22: 3215–3219.
- REYNOLDS, J. D. 1975. Feeding in corixids (Heteroptera) of small alkaline lakes in central B.C. Verh. Int. Ver. Limnol. 19: 3073-3078.
- RIESSEN, H. P. 1982. Predatory behavior and prey selectivity of the pelagic water mite *Piona constricta*. Can. J. Fish. Aquat. Sci. 39: 1569–1579.
- RIESSEN, H. P., W. J. O'BRIEN, AND B. LOVELESS. 1984. An analysis of the components of *Chaoborus* predation on zooplankton and the calculation of relative prey vulnerabilities. Ecology 65: 514–522.
- SCHOENER, T. W. 1971. Theory of feeding strategies. Annu. Rev. Ecol. Syst. 2: 369–404.
- SCHWARTZ, S. S., AND P. D. N. HEBERT. 1982. A laboratory study of the feeding behavior of the rhabdocoel *Mesostoma ehrenbergii* on pond Cladocera. Can. J. Zool. 60: 1305-1307.
- SMYLY, W. J. P. 1980. Food and feeding of aquatic larvae of the midge Chaoborus flavicans (Meigen) (Diptera: Chaoboridae) in the laboratory. Hydrobiologia 70: 179-188.
- SPRULES, W. G. 1972. Effects of size-selective predation and food competition on high altitude zooplankton communities. Ecology 53: 375–386.
- STENSON, J. A. E. 1978. Differential predation by fish on two species of *Chaoborus* (Diptera, Chaoboridae). Oikos 31: 98-101.
 - 1980. Predation pressure from fish on two *Chaoborus* species as related to their visibility, p. 618–622. *In* W. C. Kerfoot [ed.] Evolution and ecology of zooplankton communities. The University Press of New England, Hanover, NH.
- STRICKLER, J. R. 1975. Swimming of planktonic Cyclops species (Copepoda, Crustacea): pattern, movements and their control. p. 599–613. In T. Y. T. Wu, C. J. Brokaw, and C. Brennen [ed.] Swimming and flying in nature. Plenum Press, New York, NY.
- SWIFT, M. C., AND A. Y. FEDORENKO. 1975. Some aspects of prey capture by Chaoborus larvae. Limnol. Oceanogr. 20: 418–425.
- SWÜSTE, H. F. J., R. CREMER, AND S. PARMA. 1973. Selective predation by larvae of *Chaoborus flavicans* (Diptera, Chaoboridae). Verh. Int. Ver. Limnol. 18: 1559–1563.
- THOMPSON, D. J. 1978. Prey size selection by larvae of the damselfly, *Ischnura elegans* (Odonata). J. Anim. Ecol. 47: 769-785.
- VINYARD, G. L. 1980. Differential prey vulnerability and predator selectivity: effects of evasive prey on bluegill (*Lepomis macrochirus*) and pumpkinseed (*L. gibbosus*) predation. Can. J. Fish. Aquat. Sci. 37: 2294–2299. 1982. Variable kinematics of Sacramento perch (*Archoplites inter-*

ruptus) capturing evasive and nonevasive prey. Can. J. Fish. Aquat. Sci. 39: 208-211.

- VINYARD, G. L., AND R. A. MENGER. 1980. Chaoborus americanus predation on various zooplankters; functional response and behavioral observations. Oecologia 45: 90-93.
- VON ENDE, C. N., AND D. O. DEMPSEY. 1981. Apparent exclusion of the cladoceran Bosmina longirostris by invertebrate predator Chaoborus americanus. Am. Midl. Nat. 105: 240-248.
- WILLIAMS, E. H. 1980. Disjunct distributions of two aquatic predators. Limnol. Oceanogr. 25: 999-1006.
- WILLIAMSON, C. E. 1983. Behavioral interactions between a cyclopoid predator and its prey. J. Plankton Res. 5: 701–711.
- WILLIAMSON, C. E., AND J. J. GILBERT. 1980. Variation among zooplankton predators: the potential of Asplanchna, Mescocyclops, and Cyclops to attack, capture, and eat various rotifer prey, p. 509-517. In W. C. Kerfoot [ed.] Evolution and ecology of zooplankton communities. The University Press of New England, Hanover, NH.
- WINFIELD, I. J., G. PEIRSON, M. CRYER, AND C. R. TOWNSEND. 1983. The behavioural basis of prey selection by underyearling bream (Abramis brama (L.)) and roach (Rutilus rutilus (L.)). Freshwater Biol. 13: 139-149.
- WINNER, R. W., AND J. S. GREBER. 1980. Prey selection by Chaoborus punctipennis under laboratory conditions. Hydrobiologia 68: 231-233.
- WRIGHT, D. I., AND W. J. O'BRIEN. 1984. The development and field test of a tactical model of the planktivorous feeding of white crappie (*Pomoxis* annularis). Ecol. Monogr. 54: 65-98.
- ZARET, T. M. 1980a. Predation and freshwater communities. Yale University Press, New Haven, CT. 187 p.

1980b. The effect of prey motion on planktivore choice, p. 594-603. In W. C. Kerfoot [ed.] Evolution and ecology of zooplankton communities. The University Press of New England, Hanover, NH.