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What Determines Prey Size Selectivity in Piscivorous Fishes?

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Abstract. A survey of studies examining prey size selectivities of piscivorous fishes showed a consistent pattern of selection for small-sized prey. This pattern was independent of predator and prey type as well as predator size. I argue that despite the ontogenetic increase in mean prey size ingested by many piscivores, the consistent inclusion and selection of small prey sizes in their diets indicate that observed prey size selection may be a passive process mediated by differential size-based capture success rather than active preferences.

Introduction

As predators grow they tend to broaden their diet to include larger prey (Wilson 1975; Peters 1983; Polis 1988; Shine 1991). This result is common in fish feeding studies and is generally attributed to ontogenetic increases in predator mouth gape and swimming speed (Ivlev 1961; Keast and Webb 1966; Werner 1979; Houde and Schekter 1980; Blaxter 1986; Osenberg and Mittelbach 1989; Persson 1990; Malmquist et al. 1992). It is not clear whether such patterns in prey selection are a consequence of prey vulnerability to predation (O'Brien et al. 1976, 1989; Greene 1983, 1985) or a result of active predator choice (Mittelbach 1981; Werner et al. 1983). Ivlev (1961) first quantified fish diet preferences by using an electivity index that compared prey ingested with prey availability. He predicted that piscivorous predators should prefer the largest prey they are able to ingest. Similarly, Harper and Blake (1988), using an energetic model that combined fish swimming mechanics and feeding behavior, also predicted that the largest prey size available should maximize piscivorous feeding efficiencies.

In this chapter, I review those studies in which quantitative measures of prey size selectivity were collected for piscivorous fishes. I then determine how the observed patterns in prey size selectivity may be a consequence of differential prey vulnerability. I also compare predictions of optimal prey sizes based on energy maximization to the observed preferred prey sizes, and suggest ways in which including predator success rates can produce more accurate predictions.

Methods

In this study I use the terms 'selectivity' and 'preference' interchangeably as many of the studies reviewed here do. However, prey selectivity (or electivity) is often defined as any difference between

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distributions of prey sizes (or types) in the environment (availability) and the composition of the predator's diet (Ivlev 1961; Eggers 1977), whereas preference usually refers to prey selectivity when all food types are equally available, or more precisely, active selection (Johnson 1980; Greene 1983). Thus, prey items can be selected but not preferred (Juanes 1992).

Tables 1 and 2 summarize the 32 studies from the piscivorous fish predation literature that contained quantitative measures of prey size preference, defined as the rank order of choices. From each of these studies I extracted the following ranges: predator sizes used, prey sizes offered (or available), prey sizes selected when given a choice, and if available, optimal prey sizes (as predicted using energy maximization models). In seven of the studies, authors determined prey size preferences from the observed number of individuals eaten in each size category without testing the results statistically. In the other 25 studies, size preferences were analyzed statistically by either testing whether (1) the observed numbers consumed per size category differed from random expectation (e.g. Chi-squared test), (2) the mean number of prey consumed differed among prey size categories (e.g. ANOVA), or (3) the frequency distributions differed between prey sizes available and eaten (e.g. Kolmogorov-Smirnov test). Six studies contained predictions of optimal sizes based on maximizing energy intake rate. Thirteen studies were conducted in the field (Table 1) whereas the remainder (studies 14-32) were based in the laboratory (Table 2). Two studies (#4 and 18, Tonn et al. 1991; #8 and 28, Juanes 1992) contained both field and laboratory components, which are considered separately.

Potential trends in the location of preferred prey size ranges relative to offered prey size ranges and predicted optimal size ranges (as listed in Tables 1 and 2) were tested by comparing their midpoints. Thus, the midpoint of the preferred size range could be either 'smaller', 'equal,' or 'larger' than the midpoint of the offered or the optimal size range. The overall counts were analyzed using a chi-square test to detect differences from a random choice.

RESULTS

The data depicting those studies conducted in the field and in the lab are shown in Figs. 1 and 2 respectively. Clearly, the trend of prey size selectivity is towards the lower part of the range offered (in 92.5% of the treatments, smaller-than-average prey were selected; see Table 3). In each of these studies, all of the offered prey sizes were available to the predator. That is, they were capable of ingesting individuals over the whole range and frequently took prey from the upper part of the range offered (i.e., none of the sizes offered were gape-limiting to the particular predator being tested). Nevertheless, the lower part of the range was ingested preferentially (Table 3).

The exceptions to this pattern show either no size selection, preferences for intermediate-sized prey, or selection of the largest prey available. Mauck and Coble (1971–study 20), using pike (*Esox lucius* Linnaeus) as the predator and the bigmouth buffalo (*Ictiobus cyprinellus* [Valenciennes]) as prey, and East and Magnan (1991–study 26), using large (250–380 mm TL) brook trout (*Salvelinus fontinalis* [Mitchill]) as the predator and creek chub (*Semotilus atromaculatus* [Mitchill]) as the prey, found no evidence of prey size selectivity. Wolfert (1965-study 1), using walleye (*Stizostedion vitreum* [Mitchill]) as the predator and the emerald shiner (*Notropis atherinoides* Rafinesque) as the prey, and Hoyle and Keast (1987-study 7), using the largemouth bass (*Micropterus salmoides* [Lacepede]) as the predator and pumpkinseed (*Lepomis gibbosus* [Linnaeus]) as prey, found preferences for

Table 1. Summary of prey size selection studies conducted in the field. FL, TL, and SL are fork, total and standard lengths, respectively. ?L indicates those studies where the length measure was not specified. Numbers in parentheses are mean values. NP signifies that no optimal predictions were made. Statistical tests are as follows: NT: no test, SI = Shorygin's index, ZT = Z test, ANC = ANOVA and Chesson's alpha, MWU = Mann-Whitney U-test, WTS = Wilcoxon two-sample test, MT = Median test, AN = ANOVA, VSE = Vanderploeg and Scavia E*, and MH = Mantel-Haenszel test. An asterisk represents those studies where field enclosures were used. All measurements are in mm.

Study	Predators			Prey						
no.	Species	Common name	Size	Species	Common name	Sizes avail.	Sizes selected	Optimal size	Test	Source
1	*Stizostedion vitreum*	walleye	(108) TL	*Alosa pseudoharengus*	Alewife	33-69 (48)	33-47 (42)	NP	NT	Wolfert 1965
			(157)			52-102 (89)	52-60 (56)			
			(157)	*Notropis atherinoides*	Emerald shiner	38-61 (51)	45-54 (49)			
			(226)			48-86 (69)	48-65 (55)			
			(108)	*Dorosoma cepedianum*	Gizzard shad	35-76 (56)	35-50 (46)			
			(157)			49-130 (102)	49-64 (55)			
			(108)	*Perca flavescens*	Yellow perch	33-74 (53)	33-42(36)			
			(157)			53-76 (63)	(53)			
2	*Stizostedion vitreum*	walleye	136-363 SL	*Gasterosteus aculeatus*	Threespine stickleback	10-70 (38)	10-45 (32)	NP	MWU	Banbura et al. 1989
3	*Stizostedion vitreum*	walleye	61-221 TL	various		20-80	20-50	NP	VSE	Knight et al. 1984
						20-80	20-40			
			217-385			30-110	30-70			
						15-90	15-50			
						20-100	20-60			
						30-120	30-85			
						30-120	30-55			
			350-583			40-120	40-90			
	Perca flavescens	yellow perch	152-242			20-120	40-70			
						20-120	20-40			

	Predators			Prey						
Study no.	Species	Common name	Size	Species	Common name	Sizes avail.	Sizes selected	Optimal size	Test	Source
4*	*Perca fluviatilis*	Eurasian perch	165-198 TL	*Carassius carassius*	Crucian carp	50-119	50-59	NP	MH	Tonn et al. 1991
5	*Esox masquinongy* x *E. lucius*	Tiger muskellunge	120-150 TL 160-200	*Pimephales promelas*	Fathead minnow	30-70 30-80	30-50 30-60	30-50 50-80	NT	Gillen et al. 1981
			120-150 160-200	*Lepomis macrochirus*	Bluegill sunfish	20-50 20-60	20-30 20-30	40-50 50-70		
6	*Alosa pseudoharengus*	Alewife	149-182 TL	*Perca flavescens*	Yellow perch	7-10 (8.3)	7-8.5 (7.4)	NP	WTS	Brandt et al. 1987
7	*Micropterus salmoides*	Largemouth bass	70-285 FL	*Lepomis gibbosus*	Pumpkinseed	25-140 30-150 30-160	25-35 65-85 95-105	55-65 85-115 105-115	NT	Hoyle and Keast 1987
				Perca flavescens	Yellow perch	35-180	35-55	75-85		
8	*Pomatomus saltatrix*	Bluefish	(70) TL (103) (76) (107) (108)	*Menidia menidia*	Atlantic silverside	15-50 (31) 15-50 (33) 15-50 (33) 15-60 (34) 15-70 (42)	15-30 (22) 15-40 (29) 15-30 (21) 15-40 (28) 15-55 (36)	40-50 40-50 40-50 50-60 60-70	MT	Juanes 1992
			(70) (107) (84) (108) (114) (134) (129)	*Anchoa mitchilli*	Bay anchovy	20-45 (40) 25-65 (47) 15-60 (37) 15-35 (27) 15-35 (26) 15-45 (32) 15-40 (30)	20-30 (23) 25-55 (38) 15-40 (29) 15-30 (23) 15-30 (25) 15-35 (29) 15-35 (27)			

Table 1—cont.

	Predators			Prey						
Study no.	Species	Common name	Size	Species	Common name	Sizes avail.	Sizes selected	Optimal size	Test	Source
9*	*Oncorhynchus kisutch*	Coho salmon	110-120 FL	*O. keta*	Chum salmon	43-63	43-52	NP	ZT	Hargreaves and LeBrasseur 1986
10	*Oncorhynchus kisutch*	Coho salmon	70-150 FL	*O. nerka*	Sockeye salmon	28-34	28-29	NP	ANC	Ruggerone 1989
11*	*Oncorhynchus kisutch*	Coho salmon	105-120 FL	*O. nerka*	Sockeye salmon	29-44	29-34	NP	AN	Ruggerone 1992
12*	*Gasterosteus aculeatus*	Threespine stickleback	(38) SL	*Mallotus villosus*	Capelin	(5.1)	(5.3)	NP	AN	Litvak and Leggett 1992
13	*Zeus faber*		141-510 TL	*Cepola macrophthalma*		40-600	40-300	NP	SI	Stergiou and Fourtouni 1991

Table 2. Summary of prey size selection studies conducted in the lab. FL, TL, and SL are fork, total, and standard lengths, respectively. ?L indicates those studies where the length measure was not specified. Numbers in parentheses are mean values. NP signifies that no optimal predictions were made. Statistical tests are: NT = no test, BT = binomial test, GT = G test, MA = Manly-Chesson preference index and ANOVA, MH = Mantel-Haenszel test, ZT = Z test, KS = Kolmogorov-Smirnov test, VSE = Vanderploeg and Scavia E*, TT = t test, HT = H test, AN = ANOVA, CS = Chi square test, MR = multiple regression, and MWU = Mann-Whitney U-test. All measurements are in mm.

	Predators			Prey						
Study no.	Species	Common name	Size	Species	Common name	Sizes offered	Sizes selected	Optimal size	Test	Source
14	*Stizostedion vitreum*	walleye	35-100 FL	*Pimephales promelas*	fathead minnow	20-55 26-40	20-30 26-30	NP	VSE	Vandenbyllaardt et al. 1991
15	*Perca flavescens*	yellow perch	121-180 TL	*Umbra limi*	mudminnow	60-100	60-76	NP	MH	Tonn and Paszkowski 1986
16	*Perca flavescens*	yellow perch	232-268 TL	*P. flavescens*	yellow perch	52-73	52-59	NP	BT	Post and Evans 1989
17	*Perca fluviatilus*	Eurasian perch	55-95 SL	*Pungitius pungitius*	10-spine stickleback	13-24 (21)	(20)	NP	TT	Nelson and Bonsdorff 1990
18	*Perca fluviatilis*	Eurasian perch	170-210 TL 170-210 140-180 140-180	*Carassius carassius*	crucian carp	50-119 80-119 30-109 60-89	50-69 80-99 30-60 60-69	NP	MH	Tonn et al. 1991
19	*Esox lucius*	pike	178-305 TL 330-584	*Lepomis gibbosus*	pumpkinseed	(41)-(79) (63)-(140)	(41) (63)	NP	NT	Beyerle and Williams 1968
20	*Esox lucius*	pike	111-126 ?L 147-164	*Pimephales promelas*	fathead minnow	30-90 30-90	30-50 30-50	NP	NT	Mauck Coble 1971
			224-303 250-316	*Cyprinus carpio*	carp	30-130 40-130	30-60 40-70			
			224-316 455-503	*Notemigonus crysoleucas*	golden shiner	30-130 50-160	30-110 50-140			

Table 2—cont.

	Predators			Prey						
Study no.	Species	Common name	Size	Species	Common name	Sizes offered	Sizes selected	Optimal size	Test	Source
			224-316	*Ictiobus cyprinellus*	bigmouth buffalo	30-80	30-80			
			224-316 422-446	*Lepomis macrochirus*	bluegill	50-90 30-110	50-80 30-80			
21	*Esox lucius*	pike	230-245 ?L	*Phoxinus phoxinus*	minnow	37-79	37-45	67-79	MWU	Hart and Connelan 1984
22	*Esox lucius*	pike	210-288 ?L	*Scardinius erythrophthalmus*	rudd	60-110	60-90	NP	GT	Hart and Hamrin 1988
23	*Esox lucius*	pike	223-248 ?L	*Scardinius erythrophthalmus*	rudd	73-106	73-86	73-106	HT	Hart and Hamrin 1990
24	*Micropterus salmoides*	largemouth bass	225-275 SL 315-365	*Dorosoma cepedianum*	gizzard shad	75-175 75-175	75-100 75-100	NP	ZT	Wright 1970
25	*Micropterus salmoides*	largemouth bass	113-140 SL 213-219 273-279	*Pimephales promelas*	fathead minnow	20-70 30-60 30-60	20-50 40-60 30-60	NP	MA	Hambright 1991
			113-140 213-219 273-279	*Lepomis gibbosus*	pumpkinseed	20-70 30-80 40-90	20-40 30-50 40-60			
26	*Salvelinus fontinalis*	brook trout	150-250 TL 250-380	*Semotilus atromaculatus*	creek chub	40-170 40-170	40-60 40-170	NP	AN	East and Magnan 1991
27	*Lepomis macrochirus*	bluegill	40-51 SL	*Morone americana*	white perch	3-15	3-7	NP	NT	Margulies 1990

Table 2—cont.

Study no.	Predators Species	Predators Common name	Predators Size	Prey Species	Prey Common name	Sizes offered	Sizes selected	Optimal size	Test	Source
28	*Pomatomus saltatrix*	bluefish	50-80 TL	*Menidia menidia*	Atlantic silverside	20-70	20-40	50-70	CS	Juanes 1992
			90-120			20-70	20-40	50-70		
			130-160			50-100	50-70	80-100		
						20-100	20-40	80-100		
						20-70	20-40	50-70		
			170-200			50-100	50-70	80-100		
						20-100	20-40	80-100		
						20-100	20-100	80-100		
29	*Oncorhynchus kisutch*	coho salmon	90-150 FL	*O. gorbuscha* *O. keta*	pink salmon chum salmon	20-90 20-90	20-50 20-50	NP	NT	Parker 1971
30	*Cynoscion nebulosus*	spotted seatrout	170-212 TL	*Leiostomus xanthurus*	spot	60-94	60-80	NP	KS	Minello and Zimmerman 1984
31	*Gasterosteus aculeatus*	threespine stickleback	35-60 SL	*Mallotus villosus*	capelin	3.9-6.7	5-6.7	NP	KS	Pepin et al. 1992
32	*Scomber scombrus*	Atlantic mackerel	(35) ?L	various		2-9	5-9	NP	MR	Pepin et al. 1987

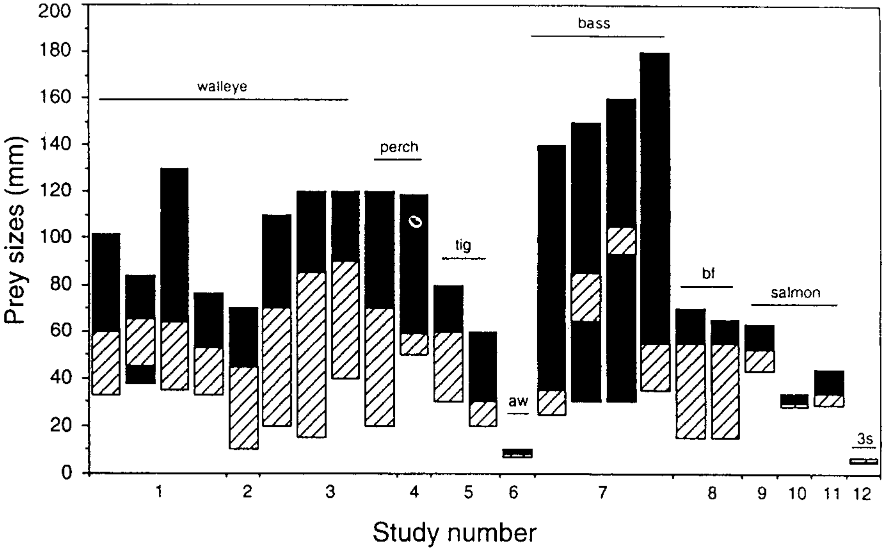

Figure 1. Prey sizes available and selected for those studies conducted in the field. Each histogram represents the range of prey sizes available (i.e., solid plus hatched). The hatched region represents the range of prey sizes that were selected by the predator (thus the solid region represents the 'less preferred' prey sizes). Within a study each histogram represents the results for each prey species used except for studies 3 and 7 where the results are also summarized for each predator size class (#3) and field site (#7), respectively. The Stergiou and Fourtouni (1991, #13) study is not included because of its large size ranges. Data are taken from Table 1. The lines above the histograms connect studies using the same predators: perch = yellow perch (study 3) and Eurasian perch (study 4), tig = tiger muskellunge, aw = alewife, bass = largemouth bass, bf = bluefish, salmon = coho salmon, and 3s = threespine stickleback.

intermediate prey sizes (although in Wolfert's study the mean prey size consumed was smaller than the average prey size available). In five studies (6, 12, 27, 31, 32), prey <10 mm were used. In three of these studies (12, 31, and 32), preferences were found for larger prey.

Among those studies using optimal diet models, nearly all predicted optimal prey size ranges which tended to be larger than those selected by the predator (Fig. 3, Table 3). The exception was small (120-150 mm TL) tiger muskellunge (*Esox masquinongy* Mitchill x *Esox lucius* Linnaeus) feeding on fathead minnows (*Pimephales promelas* [Rafinesque]) (Gillen et al. 1981, study 5), where the prediction matched the observed selected prey size range.

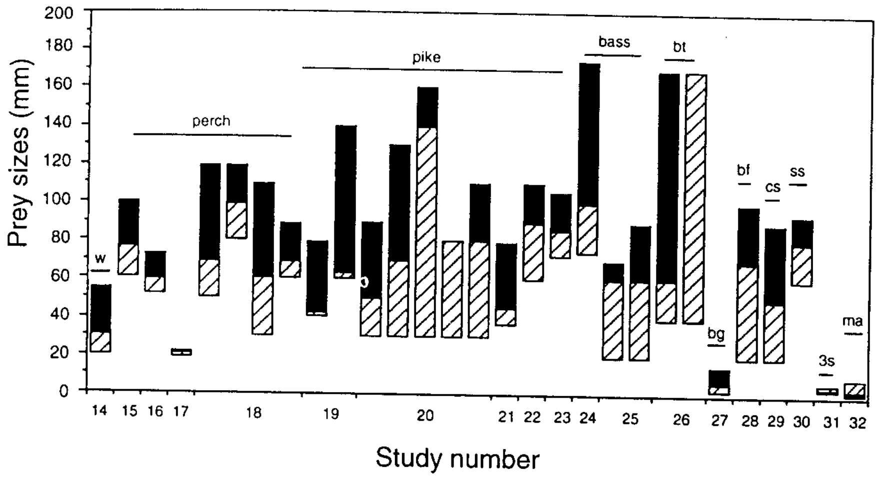

Figure 2. Prey sizes available and selected for those studies conducted in the laboratory. Histograms represented as in Figure 1. Within a study each histogram represents the results for each prey species used except for studies 18 (where all experiments are included) and 26 (where each bar represents a different predator size range). Data are taken from Table 2. The lines above the histograms connect studies using the same predators: w = walleye, perch = yellow perch (studies 15 and 16) and Eurasian perch (studies 17 and 18), bass = largemouth bass, bt = brook trout, bg = bluegill, bf = bluefish, cs = coho salmon, ss = spotted seatrout, 3s = threespine stickleback, and ma = Atlantic mackerel.

Table 3. A comparison of the preferred vs. offered or optimal prey size ranges. The midpoints of the preferred size ranges were either smaller, larger, or equal to the offered or optimal size ranges. Data were taken from Tables 1 and 2. χ^2 is the chi-square value. The asterisk represents significant chi-squared values ($p < 0.05$).

	Comparison			
	Smaller	Larger	Equal	χ^2
Offered vs. preferred				
All data	86	5	2	148.29*
Field studies	44	2	0	65.21*
Lab studies	42	3	2	66.41*
Optimal vs. preferred				
All data	18	1	0	26.00*

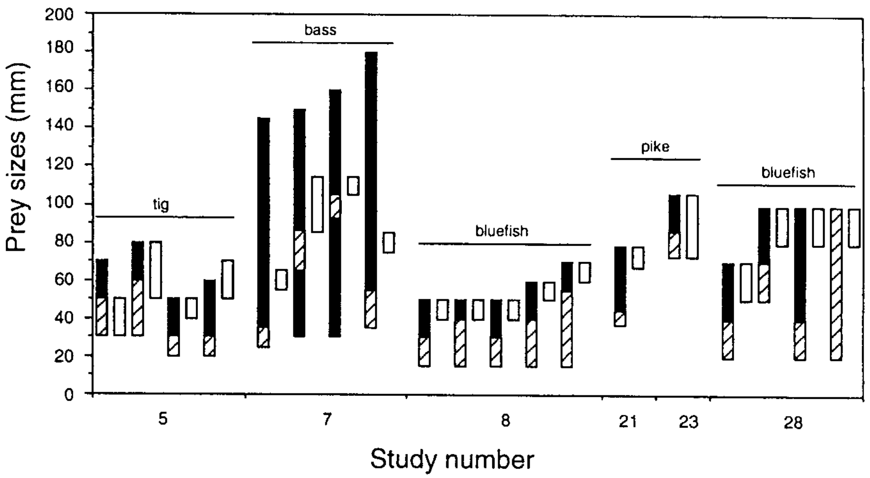

Figure 3. A comparison of prey sizes selected and optimal prey sizes predicted from energy maximization models. Each treatment comparison is represented by two bars. The open bar on the right represents the range of optimal prey sizes predicted. The bar on the left represents the range of prey sizes available (solid plus hatched) and the portion of those selected (hatched region). Data and study numbers are taken from Tables 1 and 2. The terms above the histograms represent the predators used in each study: tig = tiger muskellunge, bass = largemouth bass.

DISCUSSION

The results of the studies surveyed here show a consistent pattern of preference for small-sized prey by a variety of piscivorous fishes (Tables 1 and 2, Figs. 1 and 2). This pattern is independent of predator and prey type as well as predator size. Although fish may show preferences for particular prey species (Mauck and Coble 1971; Gillen et al. 1981; Eklov and Hamrin 1989), they consistently select smaller prey when given a choice.

Preference for large prey was found only in three (studies 12, 31, 32) of the five studies where very small prey sizes (<10 mm) were used. These exceptions may be due to lowered encounter rates with very small prey. For example, while Brownell (1985) and Folkvord and Hunter (1986) have shown that larvae of Cape anchovy (*Engraulis capensis* Gilchrist) and northern anchovy (*E. mordax* Girard) <8 mm in length were subject to lower ingestion rates, it was because their small size and lack of pigmentation made them less visible and thus less easily detectable than larger larvae.

WHAT DETERMINES PREY SIZE SELECTIVITY?

Research on foraging theory has focused mainly on the role of predator habitat and diet choice while the factors affecting encounter and capture probabilities have received comparatively less attention (Stephens and Krebs 1986; Persson and Diehl 1990). Sih and Moore (1990) have suggested that in many cases prey behavior may be as important as predator choice in determining predator diets. They argue that optimal diet theory makes predictions about active predator choice (i.e., attack probabilities), which is only one component of preference. Encounter rates and capture success can also be important components in determining predator feeding preference and can by themselves generate preferences in the absence of active predator choice. Sih and Moore (1990) concluded that, in general, predictions derived from optimal diet theory were more accurate when prey were less mobile. They further showed that, at least for invertebrate predators, prey behaviors that influence encounter rates and relative capture success were the main determinant of preference in that group.

Prey vulnerability to a particular predator can be viewed as the product of its encounter rate with the predator and the capture success of that predator (Pastorok 1981; Greene 1983, 1986; Litvak and Leggett 1992). Because encounter rate is generally assumed to be a positive function of prey size while capture success is assumed to be negatively related to prey size, the resulting vulnerability curve is typically a convex parabola. The prey size at which vulnerability is maximized will thus depend on the shapes of the component functions (Fig. 4). Greene (1983, 1986) has argued that the interaction of differential encounter and susceptibility (capture success) rates can lead to perceived predator preference without any active predator choice. Various authors have shown that such a 'passive' foraging tactic can often explain patterns in prey size selectivity as well as optimal foraging models that assume active prey selection (Pastorok 1981; Dunbrack and Dill 1983; Greene 1983; Scott and Murdoch 1983; Osenberg and Mittelbach 1989). The importance of these interactions in predicting observed diets also appears to be a function of predator foraging tactics (e.g., ambush vs. pursuit predators), and prey mobility and escape behaviors. Thus, prey selection is shifted towards larger conspicuous prey for visual particulate feeders, whereas prey selection in filter feeders may be shifted towards smaller, less evasive prey (Confer and Blades 1975; Drenner et al. 1978; Greene and Landry 1985; Greene 1985, 1986).

In reviewing their work on pike, Hart and Hamrin (1990) suggest that although small fish prey (rudd and minnows) are usually less profitable (in terms of energy/handling time) they are selectively ingested because they are 'easier to catch' (although no attack success data are reported). If 'passive' prey selection rather than active predator choice determines the observed selectivity of piscivorous fishes for small prey sizes, the vulnerability curve should be skewed to the left (Fig. 4). Peak vulnerabilities at small prey sizes imply that, in contrast to planktivores, piscivore capture success rates are strongly size-dependent or encounter rates are relatively independent of prey size, or both.

CAPTURE SUCCESS IN PISCIVORES

Prey size/predator size ratios for piscivores are generally large compared with planktivorous fishes (Werner 1979). Piscivores can ingest prey up to 50% of their length, and tend to ingest prey that average 20–30% of their length (Hoogland et al. 1956; Lawrence 1958; Gillen et al. 1981; Hoyle and Keast 1987; Hambright 1991). In comparison, planktivores ingest much smaller (and higher numbers of) prey. Small prey sizes combined with relatively low mobilities result in relatively high capture success rates for planktivores feeding on 'optimally sized' prey (usually >70%, Confer and Blades 1975; Werner 1977; Greene 1983; Godin 1990). Piscivores tend to have comparatively lower success rates than planktivores (usually <70%, Werner 1977; Major 1978; Webb and Skadsen 1980; Webb 1982;

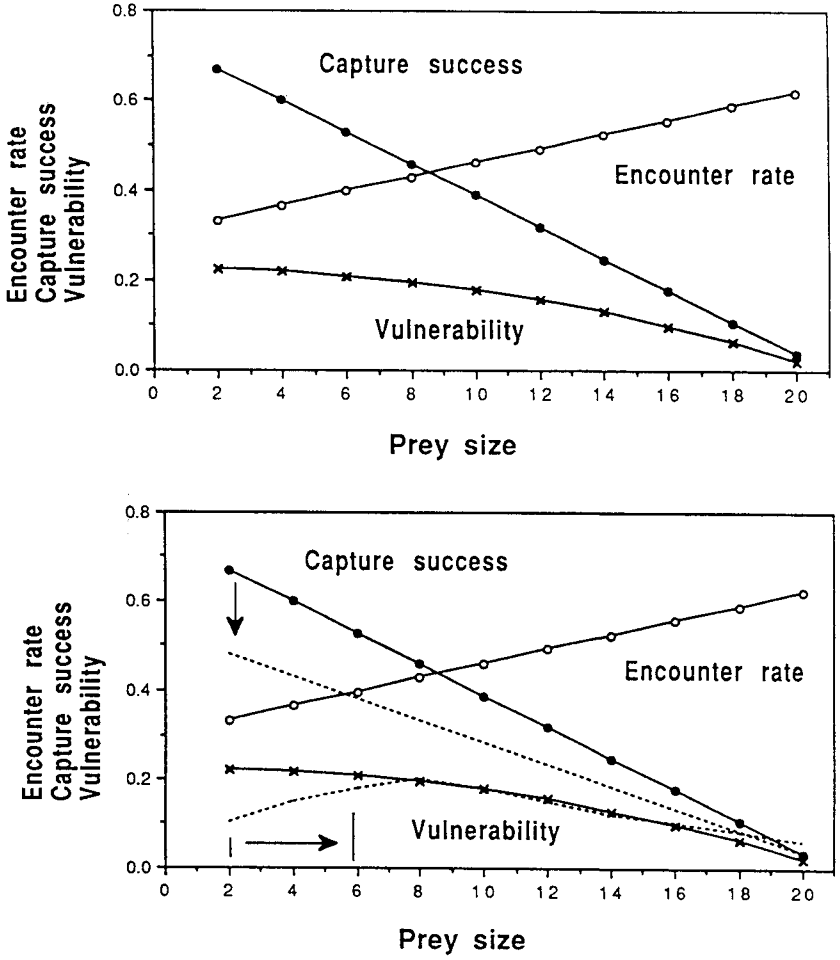

Figure 4. Prey vulnerability (x—x) as a function of prey size. Vulnerability is the resulting product of encounter rate (o—o) with a predator and the capture success (•—•) of that predator. Capture success is assumed to be negatively related to prey size, whereas encounter rate is assumed to be positively related to prey size. Top: Vulnerability peaks at small prey sizes, exemplifying the pattern observed for piscivores. Bottom: Decreasing the slope of capture success vs. prey size leads to a shift in the vulnerability peak towards larger prey, exemplifying the pattern observed for planktivores. A similar result would be obtained by increasing the slope of the encounter rate curve.

Howick and O'Brien 1983; Wahl and Stein 1988; Juanes 1992). Because fish prey can rapidly develop effective escape behaviors, piscivore capture success is often a strong function of prey size and development stage (Folkvord and Hunter 1986; Butler and Pickett 1988; Blaxter and Fuiman 1990; Reimchen 1991; Juanes 1992). The influence of prey size on capture success is likely to be most important for small predator-prey size ratios (i.e., when prey are a large proportion of predator size), where a small change in prey size can result in a large change in capture success (Miller et al. 1988).

ENCOUNTER RATE VS. PREY SIZE

Encounter rates are rarely measured in studies of piscivore foraging. In those studies where foraging models were developed, either encounter rates were controlled (by offering only one prey; Gillen et al. 1981; Hoyle and Keast 1987), search times were assumed to be independent of prey size but a function of prey density (Hart and Connellan 1984; Hart and Hamrin 1990) or only attack rates were measured and assumed to be similar to encounter rates (i.e., attack upon encounter) (Anderson 1984; Juanes 1992). Therefore, very little information is available on the potential relationship between encounter rate and prey size. Since most of the prey used in piscivore foraging studies tend to be schooling fishes, and most fish schools contain similarly sized individuals (Nursall 1973; Major 1977, 1978; Keenleyside 1979; Pitcher et al. 1985, Theodorakis 1989), encounter with a school would mean having to make a choice between many prey of similar size. Encounters with schools might thus result in a flexible foraging tactic (Dill 1983) that precludes the need for active prey selection. Thus encounter rates of piscivores and their prey are more likely to be determined by the size and density of schools (Eggers 1977) rather than prey size.

The independence of encounter rate and prey size, along with the strong size-dependence of capture success, suggests that prey vulnerability for piscivores may be more strongly determined by prey susceptibility than for planktivores, thus skewing the peak of the vulnerability curve farther to the left (Fig. 4; Wilson 1975; Greene 1983, 1986). Juanes (1992) showed that age-0 bluefish (*Pomatomus saltatrix* [Linnaeus]) attacked different-sized fish prey at similar rates, which was consistent for a range of bluefish sizes. Since bluefish appeared to ingest more small prey than predicted by chance, Juanes (1992) concluded that attack occurred upon encounter, and that selectivity was thus determined primarily by size-dependent prey vulnerability. Hart and Hamrin (1988, 1990) proposed a similar form of passive selection for pike feeding on goldfish (*Carrassium auratus* [Linnaeus]) and rudd (*Scardinius erythrophthalmus* [Linnaeus]).

FORAGING MODELS AND PISCIVORES

Foraging theory has provided relatively simple models that can predict prey size preferences for generalized predator-prey combinations (Stephens and Krebs 1986). Six of the studies surveyed here used foraging theory to predict optimal prey sizes for piscivores (Tables 1 and 2, Fig. 3). In most cases, optimal prey sizes were overestimated; that is, the model predicted larger optimal prey sizes than the animal actually ingested. Juanes (1992) showed that incorporating predator success rate into the profitability argument could provide more accurate predictions of the observed prey size for bluefish feeding on Atlantic silversides than when they were ignored. Incorporating relative success rates into the calculation of prey value may thus result in more accurate predictions of prey size. Harper and Blake's (1988) energetic model for a generalized piscivorous predator-prey interaction also predicted that large prey sizes should maximize feeding efficiency. However, their model assumed that the predator was always successful (i.e., capture success = 100%), handling time was zero and that the prey was still, alone, and fully exposed. These assumptions ignore potential prey behavior and may have led to their inaccurate predictions.

Sequential encounter (i.e., prey items are encountered one after the other) is a basic assumption of the optimal diet breadth model (Stephens and Krebs 1986). However, piscivores feeding on schooling fish are more likely to experience simultaneous encounter with a variety of prey, suggesting that use of the optimal diet model would be incorrect (Eggers 1977; Stephens and Krebs 1986). The use of the 'flock-encounter' model is perhaps more appropriate in this situation because it assumes simultaneous encounter with a group of prey, although only one prey item can be attacked at each group encounter since an attack generally results in the breakup of the group (Stephens et al. 1986). Hart and Hamrin (1990) used this model to predict the critical search time required for pike to switch from smaller (less profitable) to larger (more profitable) rudd. The results of their experiments showed that the model could not successfully predict the switch in prey size since small prey were always preferred over large prey independent of search time. The authors concluded that one of the major errors in their model was the assumption that capture success was independent of prey size. Differential sized-based capture success (Reimchen 1991; Juanes 1992) would result in the devaluation of small prey sizes (since larger prey will have a lower capture success than smaller prey) such that they would become more (or equally) profitable than large prey sizes (Fig. 5).

PREDATOR-PREY RELATIONSHIPS

What is perhaps most surprising about the results presented here is that preferred prey sizes do not appear to increase with predator size (except in Hoyle and Keast 1987, Table 1) as Ivlev (1961) originally predicted. Perhaps the commonly observed ontogenetic increase in the range and mean size of prey ingested by piscivores has led to the assumption of ontogenetic increases in preferred prey sizes (Popova 1967, 1978; Nielsen 1980; Knight et al. 1984; Webb 1986; Polis 1988; Persson 1990). However, mean prey size ingested may increase because the maximum prey size ingested increases while minimum prey sizes remain constant (Wilson 1975; Werner 1979; Hunter 1980; Polis 1988). Popova (1978) and Popova and Sytina (1977) have shown that such a pattern may be a general one for piscivorous fish. Their results show that for five freshwater species of piscivorous fishes (pike, sheatfish [*Silurus glanis* Linnaeus], perch [*Perca fluviatilis* Linnaeus], zander [*Stizostedion lucioperca* (Linnaeus)], and asp [*Aspius aspius* (Linnaeus)]), mean prey size ingested tended to be closer to the minimum prey size. Relative prey sizes (percent of predator length) were large at the transition to piscivory (≈50%), but tended to decline dramatically as predator size increased, eventually stabilizing at about 10%. Popova (1978) further claimed that these relationships also apply to marine piscivores, particularly cod (*Gadus morhua* Linnaeus). Similar patterns showing larger increases in maximum prey sizes compared with minimum prey sizes in relation to predator growth have been noted for juvenile coho (*Oncorhynchus kisutch* [Walbaum]) and chinook (*O. tshawytscha* [Walbaum]) salmon (Ruggerone 1989; Brodeur 1991), walleyes (Nielsen 1980), tigerfish (*Hydrocynus* spp.)

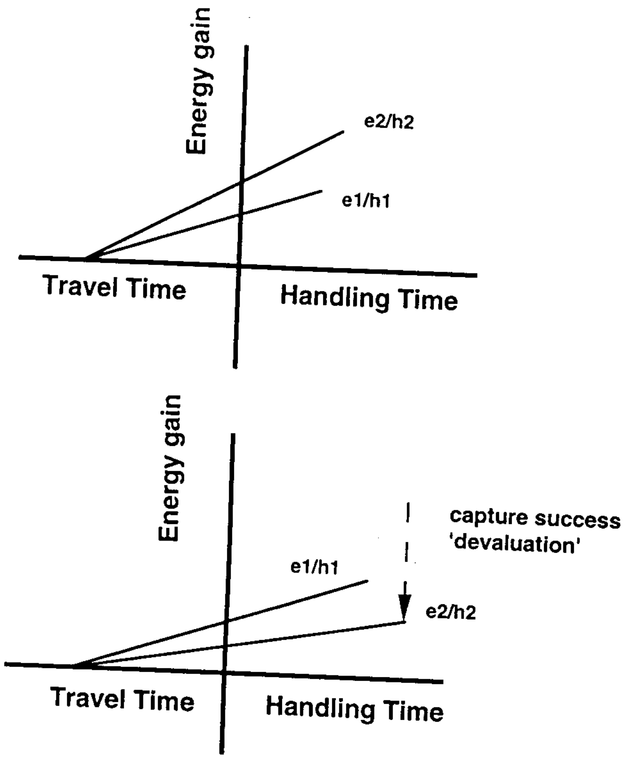

Figure 5. Using the marginal value theorem (simultaneous or 'flock-encounter' model, Stephens et al. 1986) to predict optimal prey choice when encountering a school of prey. Top: Each prey item is defined by its energy content (e1 and e2) and handling time (h1 and h2). The slope of the line connecting the travel time between schools and each prey item defines that item's profitability (calculated as e/h). Thus, because of the steeper slope, prey item 2 is the optimal choice for that search time. Bottom: Incorporating size-based capture success devalues the profitability of prey item 2 more than that of prey item 1, so that prey item 1 is now the optimal choice.

(Jackson 1961; Lewis 1974), and for oceanic and estuarine age-0 bluefish (Juanes 1992; Juanes et al. 1993; Marks and Conover 1993). Similarly, many other studies have also demonstrated that piscivorous fishes tend to ingest prey much smaller than the possible maximum (as measured by mouth gape) (Lawrence 1958; Gillen et al. 1981; Hoyle and Keast 1987; Hambright 1991; Juanes 1992). These common patterns in predator-prey sizes are likely due to an ontogenetic increase in relative predation success rates (Nursall 1973; Werner 1977; Hoyle and Keast 1987; East and Magnan 1991; Juanes 1992). Thus, as fish grow, successively larger prey are included in the diet because of their increased vulnerability. However, smaller prey are never excluded from the diet because their relative vulnerability stays high.

Wilson (1975) has proposed that such an asymmetry in resource use (i.e., overlapping prey size ranges of both small and large predators resulting in a competitive advantage to larger predators) may apply to most particulate feeders. The consistent inclusion and selection of small prey sizes in the diet of most piscivorous fishes suggest that the predatory impact on small-sized forage fishes may be even greater than is already assumed (Miller et al. 1988) and could have significant effects on community structure (Hackney 1979; Crowder et al. 1987; Hambright et al. 1991; He and Wright 1992; Tonn et al. 1992) and prey morphology (Brönmark and Miner 1992).

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Literature Cited

Anderson, O. 1984. Optimal foraging by largemouth bass in structured environments. *Ecology* 65: 851-861.

Banbura, J., M. Przybylski, and P. Frankiewicz. 1989. Selective predation of the pike *Esox lucius*: comparison of lateral plates and some metric features of the three-spined stickleback *Gasterosteus aculeatus*. *Zoologica Scripta* 18: 303-309.

Beyerle, G.B. and J.E. Williams. 1968. Some observations of food selectivity by northern pike in aquaria. *Transactions of the American Fisheries Society* 97: 28-31.

Blaxter, J.H.S. 1986. Development of sense organs and behaviour of teleost larvae with special reference to feeding and predator avoidance. *Transactions of the American Fisheries Society* 115: 98-114.

Blaxter, J.H.S. and L.A. Fuiman. 1990. The role of the sensory systems of herring larvae in evading predatory fishes. *Journal of the Marine Biological Association of the U.K.* 70: 413-427.

Brandt, S.B., D.M. Mason, D.B. MacNeill, T. Coates, and J.E. Gannon. 1987. Predation by alewives on larvae of yellow perch in Lake Ontario. *Transactions of the American Fisheries Society* 116: 641-645.

Brodeur, R.D. 1991. Ontogenetic variations in the type and size of prey consumed by juvenile coho, *Oncorhynchus kisutch*, and chinook, *O. tshawytscha*, salmon. *Environmental Biology of Fishes* 30: 303-315.

Brönmark, C. and J.G. Miner. 1992. Predator-induced phenotypical change in body morphology in crucian carp. *Science* 258: 1348-1350.

Brownell, C.L. 1985. Laboratory analysis of cannibalism by larvae of the Cape anchovy *Engraulis capensis*. *Transactions of the American Fisheries Society* 114: 512-518.

Butler, J.L. and D. Pickett. 1988. Age-specific vulnerability of Pacific sardine, *Sardinops sagax*, larvae to predation by Northern anchovy *Engraulis mordax*. *Fishery Bulletin* 86: 163-167.

Confer, J.L. and P.I. Blades. 1975. Omnivorous zooplankton and planktivorous fish. *Limnology and Oceanography* 20: 571-579.

Crowder, L.B., M.E. McDonald, and J.A. Rice. 1987. Understanding recruitment of Lake Michigan fishes: the importance of size-based interactions between fish and zooplankton. *Canadian Journal of Fisheries and Aquatic Sciences* 44 (Suppl. 2): 141-147.

Dill, L.M. 1983. Adaptive flexibility in the foraging behavior of fishes. *Canadian Journal of Fisheries and Aquatic Sciences* 40: 398-408.

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. *Journal of the Fisheries Research Board of Canada* 35: 1370-1373.

Dunbrack, R.L. and L.M. Dill. 1983. A model of size dependent surface feeding in a stream dwelling salmonid. *Environmental Biology of Fishes* 8: 41-54.

East, P. and P. Magnan. 1991. Some factors regulating piscivory of brook trout, *Salvelinus fontinalis*, in lakes of the Laurentian Shield. *Canadian Journal of Fisheries and Aquatic Sciences* 48: 1735-1743.

Eggers, D.M. 1977. The nature of prey selection by planktivorous fish. *Ecology* 58: 46-59.

Eklov, P. and S.F. Hamrin. 1989. Predatory efficiency and prey selection: interactions between pike *Esox lucius*, perch *Perca fluviatilis* and rudd *Scardinus erythrophthalmus*. *Oikos* 56: 149-156.

Folkvord, A. and J.R. Hunter. 1986. Size-specific vulnerability of northern anchovy, *Engraulis mordax*, larvae to predation by fishes. *Fishery Bulletin* 84: 859-869.

Gillen, A.L., R.A. Stein and R.F. Carline. 1981. Predation by pellet-reared tiger muskellunge on minnows and bluegills in experimental systems. *Transactions of the American Fisheries Society* 110: 197-209.

Godin, J.G.J. 1990. Diet selection under the risk of predation, p. 739-770. *In* R.N. Hughes (ed.), Behavioural Mechanisms of Food Selection. NATO ASI Series, G20. Springer-Verlag, Berlin.

Greene, C.H. 1983. Selective predation in freshwater zooplankton communities. *Internationale Revue der gesamten Hydrobiologie* 68: 297-315.

Greene, C.H. 1985. Planktivore functional groups and patterns of prey selection in pelagic communities. *Journal of Plankton Research* 7: 35-40.

Greene, C.H. 1986. Patterns of prey selection: implications of predator foraging tactics. *American Naturalist* 128: 824-839.

Greene, C.H. and M.R. Landry. 1985. Patterns of prey selection in the cruising calanoid predator *Euchaeta elongata*. *Ecology* 66: 1408-1415.

Hackney, P.A. 1979. Influence of piscivorous fish on fish community structure in ponds, p. 111-121. *In* H. Clepper (eds.), Predator-Prey Systems in Fisheries Management. Sport Fishing Institute, Washington, D.C.

Hambright, K.D. 1991. Experimental analysis of prey selection by largemouth bass: role of predator mouth width and prey body depth. *Transactions of the American Fisheries Society* 120: 500-508.

Hambright, K.D., R.W. Drenner, S.R. McComas, and J.N.G. Hairston. 1991. Gape-limited piscivores, planktivore size refuges, and the trophic cascade hypothesis. *Archiv fur Hydrobiologie* 121: 389-404.

Hargreaves, N.B. and R.J. LeBrasseur. 1986. Size selectivity of coho (*Oncorhynchus kisutch*) preying on juvenile chum salmon (*O. keta*). *Canadian Journal of Fisheries and Aquatic Sciences* 43: 581-586.

Harper, D.G. and R.W. Blake. 1988. Energetics of piscivorous predator-prey interactions. *Journal of Theoretical Biology* 134: 59-76.

Hart, P.J.B. and B. Connellan. 1984. Cost of prey capture, growth rate and ration size in pike, *Esox lucius* L., as functions of prey weight. *Journal of Fish Biology* 25: 279-292.

Hart, P. and S.F. Hamrin. 1988. Pike as a selective predator. Effects of prey size, availability, cover and pike jaw dimensions. *Oikos* 51: 220-226.

Hart, P.J.B. and S.F. Hamrin. 1990. The role of behaviour and morphology in the selection of prey by pike, p. 235-253. *In* R.N. Hughes (ed.), Behavioural Mechanisms of Food Selection. NATO ASI Series, G 20. Springer-Verlag, Berlin.

He, X. and R.A. Wright. 1992. An experimental study of piscivore-planktivore interactions: population and community responses to predation. *Canadian Journal of Fisheries and Aquatic Sciences* 49: 1176-1183.

Hoogland, R., D. Morris, and N. Tinbergen. 1956. The spines of sticklebacks (*Gasterosteus* and *Pygosteus*) as means of defence against predators (*Perca* and *Esox*). *Behaviour* 10: 205-236.

Houde, E.D. and R.C. Schekter. 1980. Feeding by marine fish larvae: developmental and functional responses. *Environmental Biology of Fishes* 5: 315-334.

Howick, G.L. and W.J. O'Brien. 1983. Piscivorous feeding behaviour of largemouth bass: an experimental analysis. *Transactions of the American Fisheries Society* 112: 508-516.

Hoyle, J.A. and A. Keast. 1987. The effect of prey morphology and size on handling time in a piscivore, the largemouth bass (*Micropterus salmoides*). *Canadian Journal of Zoology* 65: 1972-1977.

Hunter, J.R. 1980. Feeding ecology and predation of marine larvae, p. 34-77. *In* R. Lasker (ed.), Marine Fish Larvae: Morphology, Ecology and Relation to Fisheries. University of Washington Press, Seattle, Washington.

Ivlev, V.S. 1961. Experimental Ecology of the Feeding of Fishes. Yale University Press, New Haven, Connecticut.

Jackson, P.B.N. 1961. The impact of predation, especially by the tiger-fish (*Hydrocyon vittatus* Cast.) on African freshwater fishes. *Proceedings of the Zoological Society of London* 136:603-622.

Johnson, D.H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61: 65-71.

Juanes, F. 1992. The advantages of advection: recruitment, piscivory, growth, and consumption of young-of-the-year bluefish (*Pomatomus saltatrix*). Ph.D. Dissertation. Marine Sciences Research Center, State University of New York, Stony Brook, New York.

Juanes, F., R.E. Marks, K.A. McKown, and D.O. Conover. 1993. Predation by age-0 bluefish on age-0 anadromous fishes in the Hudson River estuary. *Transactions of the American Fisheries Society* 122: 348-356.

Keast, A. and D. Webb. 1966. Mouth and body form relative to feeding ecology in the fish fauna of a small lake, Lake Opinicon, Ontario. *Journal of the Fisheries Research Board of Canada* 23: 1845-1874.

Keenleyside, M.H.A. 1979. Diversity and Adaptation in Fish Behaviour. Springer-Verlag, New York.

Knight, R.L., F.J. Margraf, and R.F. Carline. 1984. Piscivory by walleyes and yellow perch in western Lake Erie. *Transactions of the American Fisheries Society* 113: 677-693.

Lawrence, J.M. 1958. Estimated sizes of various forage fishes largemouth bass can swallow. *Proceedings of the Annual Conference of Southeastern Fish and Wildlife Commissioners* 11: 220-225.

Lewis, D.S.C. 1974. The food and feeding habits of *Hydrocynus forkahlii* Cuvier and *Hydrocynus brevis* Gunther in Lake Kainji, Nigeria. *Journal of Fish Biology* 6: 349-363.

Litvak, M.K. and W.C. Leggett. 1992. Age and size-selective predation on larval fishes: the bigger-is-better hypothesis revisited. *Marine Ecology Progress Series* 81: 13-24.

Major, P.F. 1977. Predator-prey interactions in schooling fishes during periods of twilight: a study of the silverside *Pranesus insularum* in Hawaii. *Fishery Bulletin* 75: 415-426.

Major, P.F. 1978. Predator-prey interactions in two schooling fishes, *Caranx ignobilis* and *Stolephorus purpureus*. *Animal Behaviour* 26: 760-777.

Malmquist, H.J., S.S. Snorrason, S. Skulason, B. Jonsson, O.T. Sandlund, and P.M. Jonasson. 1992. Diet differentiation in polymorphic Arctic charr in Thingvallavatn, Iceland. *Journal of Animal Ecology* 61: 21-35.

Marks, R.E. and D.O. Conover. 1993. Ontogenetic shift in the diet of young-of-year bluefish *Pomatomus saltatrix* during the oceanic phase of the early life history. *Fishery Bulletin* 91: 97-106.

Mauck, W.L. and D.W. Coble. 1971. Vulnerability of some fishes to northern pike (*Esox lucius*) predation. *Journal of the Fisheries Research Board of Canada* 28: 957-969.

Miller, T.J., L.B. Crowder, J.A. Rice, and E.A. Marschall. 1988. Larval size and recruitment mechanisms in fishes: toward a conceptual framework. *Canadian Journal of Fisheries and Aquatic Sciences* 45: 1657-1670.

Minello, T.J. and R.J. Zimmerman. 1984. Selection for brown shrimp, *Penaeus aztecus*, as prey by the spotted seatrout, *Cynoscion nebulosus*. *Contributions in Marine Science* 27: 159-167.

Mittlebach, G.G. 1981. Foraging efficiency and body size: a study of optimal diet and habitat use by bluegills. *Ecology* 62: 1370-1386.

Nelson, W.G. and E. Bonsdorff. 1990. Fish predation and habitat complexity: are complexity thresholds real? *Journal of Experimental Marine Biology and Ecology* 141: 183-194.

Nielsen, L.A. 1980. Effect of walleye (*Stizostedion vitreum vitreum*) predation on juvenile mortality and recruitment of yellow perch (*Perca flavescens*) in Oneida Lake, New York. *Canadian Journal of Fisheries and Aquatic Sciences* 37: 11-19.

Nursall, J.R. 1973. Some behavioral interactions of spottail shiners (*Notropis hudsonius*), yellow perch (*Perca flavescens*), and northern pike (*Esox lucius*). *Journal of the Fisheries Research Board of Canada* 30: 1161-1178.

O'Brien, W.J., N.A. Slade, and G.L. Vinyard. 1976. Apparent size as the determinant of prey selection by bluegill sunfish (*Lepomis macrochirus*). *Ecology* 57: 1304-1310.

O'Brien, W.J., B.I. Evans, and H.I. Browman. 1989. Flexible search tactics and efficient foraging in saltatory searching animals. *Oecologia* 80: 100-110.

Osenberg, C.W. and G.G. Mittelbach. 1989. Effects of body size on the predator-prey interaction between pumpkinseed sunfish and gastropods. *Ecological Monographs* 59: 405-432.

Parker, R.R. 1971. Size selective predation among juvenile salmonid fishes in a British Columbia inlet. *Journal of the Fisheries Research Board of Canada* 28: 1503-1510.

Pastorok, R.A. 1981. Prey vulnerability and size selection by *Chaoborus* larvae. *Ecology* 62: 1311-1324.

Pepin, P., S. Pearre, and J.A. Koslow. 1987. Predation on larval fish by Atlantic mackerel, *Scomber scombrus*, with a comparison of predation by zooplankton. *Canadian Journal of Fisheries and Aquatic Sciences* 44: 2012-2018.

Pepin, P., T.H. Shears, and Y. de Lafontaine. 1992. Significance of body size to the interaction between a larval fish (*Mallotus villosus*) and a vertebrate predator (*Gasterosteus aculeatus*). *Marine Ecology Progress Series* 81: 1-12.

Persson, L. 1990. Predicting ontogenetic niche shifts in the field: What can be gained by foraging theory?, p. 303-321. *In* R.N. Hughes (ed.), Behavioural Mechanisms of Food Selection. NATO ASI, G20. Springer-Verlag, Berlin.

Persson, L. and S. Diehl. 1990. Mechanistic individual-based approaches in the population/community ecology of fish. *Annales Zoologie Fennici* 27: 165-182.

Peters, R.H. 1983. The Ecological Implications of Body Size. Cambridge University Press, Cambridge.

Pitcher, T.J., A.E. Magurran, and J.I. Edwards. 1985. Schooling mackerel and herring choose neighbours of similar size. *Marine Biology* 86: 319-322.

Polis, G. 1988. Exploitation competition and the evolution of interference, cannibalism, and intraguild predation in age/size structured populations, p. 185-202. *In* B. Ebenman and L. Persson (eds.), Size-Structured Populations. Springer-Verlag, New York.

Popova, O.A. 1967. The 'predator-prey' relationship among fish, p. 359-376. *In* S.D. Gerking (ed.), The Biological Basis of Freshwater Fish Production. Blackwell Scientific Publications, Oxford.

Popova, O.A. 1978. The role of predaceous fish in ecosystems, p. 215-249. *In* S.D. Gerking (ed.), Ecology of Freshwater Fish Production. John Wiley & Sons, New York.

Popova, O.A. and L.A. Sytina. 1977. Food and feeding relations of Eurasian perch (*Perca fluviatilis*) and pikeperch (*Stizostedion lucioperca*) in various waters of the USSR. *Journal of the Fisheries Research Board of Canada* 34: 1559-1570.

Post, J.R. and D.O. Evans. 1989. Experimental evidence of size-dependent predation mortality in juvenile yellow perch. *Canadian Journal of Zoology* 67: 521-523.

Reimchen, T.E. 1991. Trout foraging failures and the evolution of body size in stickleback. *Copeia* 1991: 1098-1104.

Ruggerone, G.T. 1989. Coho salmon predation on juvenile sockeye salmon in the Chignik lakes, Alaska. Ph.D. Dissertation. School of Fisheries, University of Washington, Seattle, Washington.

Ruggerone, G.T. 1992. Threespine stickleback aggregations create a potential predation refuge for sockeye salmon fry. *Canadian Journal of Zoology* 70: 1052-1056.

Scott, M.A. and W.W. Murdoch. 1983. Selective predation by the backswimmer, *Notonecta*. *Limnology and Oceanography* 28: 352-366.

Shine, R. 1991. Why do larger snakes eat larger prey items? *Functional Ecology* 5: 493-502.

Sih, A. and R.D. Moore. 1990. Interacting effects of predator and prey behavior in determining diets, p. 771-796. *In* R.N. Hughes (ed.), Behavioural Mechanisms of Food Selection. NATO ASI, G20. Springer-Verlag, Berlin.

Stephens, D.W. and J.R. Krebs. 1986. Foraging Theory. Princeton University Press, Princeton, New Jersey.

Stephens, D.W., J.F. Lynch, A.E. Sorensen, and C. Gordon. 1986. Preference and profitability: theory and experiment. *American Naturalist* 127: 533-553.

Stergiou, K.I. and H. Fourtouni. 1991. Food habits, ontogenetic diet shift and selectivity in *Zeus faber* Linnaeus, 1758. *Journal of Fish Biology* 39: 589-603.

Theodorakis, C.W. 1989. Size segregation and the effects of oddity on predation risk in minnow schools. *Animal Behaviour* 38: 496-502.

Tonn, W.M. and C.A. Paszkowski. 1986. Size-limited predation, winterkill, and the organization of *Umbra-Perca* fish assemblages. *Canadian Journal of Fisheries and Aquatic Sciences* 43: 194-202.

Tonn, W.M., C.A. Paszkowski, and I.J. Holopainen. 1991. Selective piscivory by perch: effects of predator size, prey size, and prey species. *Proceedings of the International Association of Theoretical and Applied Limnology* 24: 2406-2411.

Tonn, W.M., C.A. Paszkowski, and I.J. Holopainen. 1992. Piscivory and recruitment: mechanisms structuring prey populations in small lakes. *Ecology* 73: 951-958.

Vandenbyllaardt, L., F.J. Ward, C.R. Braekevelt, and D.B. McIntyre. 1991. Relationships between turbidity, piscivory, and development of the retina in juvenile walleyes. *Transactions of the American Fisheries Society* 120: 382-390.

Wahl, D.H. and R.A. Stein. 1988. Selective predation by three esocids: the role of prey behavior and morphology. *Transactions of the American Fisheries Society* 117: 142-151.

Webb, P.W. 1982. Avoidance responses of fathead minnow to strikes by four teleost predators. *Journal of Comparative Physiology A* 147: 371-378.

Webb, P.W. 1986. Locomotion and predator-prey relationships, p. 24-41. *In* M.E. Feder and G.V. Lauder (eds.), Predator-Prey Relationships: Perspectives and Approaches from the Study of Lower Vertebrates. University of Chicago Press, Chicago, Illinois.

Webb, P.W. and J.M. Skadsen. 1980. Strike tactics of *Esox. Canadian Journal of Zoology* 58: 1462-1469.

Werner, E.E. 1977. Species packing and niche complementarity in three sunfishes. *American Naturalist* 111: 553-578.

Werner, E.E. 1979. Niche partioning by food size in fish communities, p. 311-322. *In* H. Clepper (ed.), Predator-Prey Systems in Fisheries Management. Sport Fishing Institute, Washington, D.C..

Werner, E.E., G.G. Mittelbach, D.J. Hall, and J.F. Gilliam. 1983. Experimental tests of optimal habitat use in fish: the role of relative habitat profitability. *Ecology* 64: 1525-1539.

Wilson, D.S. 1975. The adequacy of body size as a niche difference. *American Naturalist* 109: 769-784.

Wolfert, D.R. 1965. Food of young-of-the-year walleyes in Lake Erie. *Fishery Bulletin* 65: 489-494.

Wright, L.D. 1970. Forage size preference of the largemouth bass. *Progressive Fish Culturist* 32: 39-42.