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Opportunistic Foraging by Largemouth Bass (*Micropterus salmoides*)

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ABSTRACT: During 1980, adult largemouth bass diets in Peter and Paul lakes (Michigan's Upper Peninsula), included prey ranging in size from zooplankton (*e.g.*, *Daphnia*) to vertebrates (fishes, amphibians, reptiles and small mammals). A partial winterkill in 1980-1981 reduced bass populations in both lakes by as much as 50%. Given the observed reduction in adult bass density and presumed reduction in intra-specific competition for food in 1981, we anticipated dietary changes as a consequence of more food being available to each surviving bass.

Two approaches to foraging theory were compared in this study. Functional response models predict that density-dependent effects should be seen simply as increased numbers of each prey type eaten and that all prey will remain in the diet. By contrast, optimal foraging theory predicts that an increase in overall prey density will result in lower ranked prey items being dropped from the diet in an inverse order of ranking; the forager should become more specialized as net energy gain increases.

Our data demonstrate opportunism in bass foraging behavior but provide support for the general tenets of optimal foraging theory. Large prey in the size range of the cost-curve nadir of adult bass were more abundant in the 1981 stomach samples. Lowest-ranked prey (*e.g.*, *Daphnia*) became less important in 1981. Overall diet breadth of bass decreased. Growth rates of adult bass were greater in 1981 than 1980.

INTRODUCTION

Two somewhat different approaches to the study of diet selection have emerged in recent decades. One is based on experimental analysis of the functional components of the predation process (Ivlev, 1961; Holling, 1966). This approach is represented in reviews by Nilsson (1978), O'Brien (1979) and Dill (1983). In general, mechanistic analyses of the predator's perceptive capabilities, behavioral responses, mechanical capabilities and motivational state are combined in what are generally termed functional response models to yield predictions of predation rates on each of the available prey types. A second class of models is derived from extensions of experimental, mechanistic studies that emphasize optimization by the predator. The basic ideas of MacArthur and Pianka (1966) and Emlen (1966) have been expanded to include a theory of diet breadth or diversity (Schoener, 1971). Various published symposia and monographs include reviews of this perspective (Kamil and Sargent, 1981; Pyke, 1984) and its application to fishes (Stroud and Clepper, 1979).

Laboratory and field studies have demonstrated the applicability of the optimality approach to foraging by fishes (Werner and Hall, 1974; Vince *et al.*, 1976; Werner, 1979; Mittlebach, 1981; Stoner, 1982). Other models based simply on measures of reactive distance and the probability of successful capture (*i.e.*, functional response models) offer equally tenable correspondence between expected and observed results (reviewed by Dunbrack and Dill, 1983). More recently, evaluation of the constraints imposed on foraging behavior has been developed to assess the roles of predator avoidance (Werner and Gilliam, 1984) and the biomechanical components of prey perception (Li *et al.*, 1985). Although both optimality and functional components will probably

continue to prove imperfect, they do offer the merits of testable theory and can serve as the basis for generality in an otherwise confusing diversity of descriptive diet studies.

A major difficulty in studies of predator-prey interactions lies in making a realistic determination of prey availability and/or abundance. Laboratory studies based on simple choice trials cannot include the diversity, spatial heterogeneity and variability of natural prey assemblages. Although microcosm, mesocosm and pond studies offer the advantages of replication, they have shortcomings of unknown scale effects (Hurlbert, 1984; Carpenter and Kitchell, 1987). Field studies of natural prey assemblages must be based on sampling that adequately estimates prey distribution, abundance and availability as perceived by the predator. Where predation is intense, major reductions and even local extinctions of highly preferred prey can result. Intensive sampling programs may resolve those difficulties but can be extremely costly and, ultimately, of unknown accuracy and precision. An alternative approach is to develop contrasting expectations based on existing theory, then conduct tests that can reduce the possibilities to a smaller subset.

Although both types of foraging models allow predictions of selectivity or predator preferences, the major distinction between optimality models and the functional response-type models is that an optimizing predator should choose *not* to eat low-ranked prey when more highly preferred prey are readily available. By contrast, the diet of predators obeying functional response rules should simply reflect encounter frequencies and the modifiers of probability of successful capture until satiation occurs. These can be stated as hypotheses specific to the example developed herein:

Functional response hypothesis: Prey should appear in the diets of a predator in proportion to their rates of encounter. Diet breadth should remain unchanged or increase slightly as relative prey availability increases.

Optimal foraging hypothesis: The abundance of low-ranked prey in the diet should be inversely proportional to that of more highly ranked prey. Diet breadth should decrease as relative prey availability increases because the presence of low ranked prey in the diet depends on the relative abundance of more highly ranked prey. Diet breadth should decrease as relative prey availability increases.

The purposes of this paper are (1) to describe a method for summarizing diet data that allows a single graphic expression of predator preference and (2) to test hypotheses derived from theoretical constructs (optimal foraging theory and functional components analysis) that offer contrasting predictions of diet dynamics. We do this based on intra- and interannual studies of diets of largemouth bass (*Micropterus salmoides*) in two Michigan lakes.

METHODS

Study site.—Peter and Paul lakes are located within the University of Notre Dame Environmental Research Center (UNDERC) in the Upper Peninsula of Michigan (Gogebic Co.), and have been experimentally manipulated since 1951. The control lake (Paul) and the experimental lake (Peter) are as closely similar as field conditions permit in that a single lake has been effectively divided and maintained permanently in that state. The history of research studies in these lakes and current limnological data are reported in Kitchell and Kitchell (1980) and Elser *et al.* (1986).

Prior to 1950, both lakes had substantial populations of largemouth bass. In 1951 the lakes were treated with rotenone and stocked with rainbow trout (*Salmo gairdneri*) (Johnson and Hasler, 1954). Trout could not reproduce in these systems and after stocking ceased in the 1960s the property manager (O. J. Steward) introduced in 1975, 25 adult largemouth bass into Peter Lake. By 1978 adult bass had invaded Paul Lake. At the onset of the present study both lakes supported dense reproducing populations of bass with virtually no fishery exploitation (Table 1). We assume that food resources are

generally limiting to bass growth in these lakes. Growth rates in both lakes are similar and substantially below average rates for other lakes of the region (Snow, 1969).

Collection methods.—We selected angling as the most consistent and effective collection method for largemouth bass. We used a lure size that approximated prey sizes near the nadir of the cost curve of Werner (1977, 1979). All bass were collected from the littoral zone by casting toward the shore line between 0800 - 1000 and 1500 - 1800 hr. Each individual was measured (TL; nearest 1.0 mm), weighed (spring scale; nearest 1.0 g), and finclipped. Scales were sampled, and the stomach was flushed (Seaburg, 1957) before each fish was released. Stomach contents were washed into a 0.28 mm Nitex mesh concentrator and preserved in 95% ethyl alcohol. Flushing did not appear to injure the bass as repeatedly evidenced by several recaptures during the same day. Items too large to pass through the efferent tube of the pump (e.g., crayfish, frogs and rodents) were removed with a blunt forceps. Prey species were grouped by size (mg dry weight).

Stomach analysis.—Individual stomach analyses were done on a total of 637 bass from both lakes. Stomach contents were identified to the lowest possible taxon. Most food items were intact, permitting easy identification; however, occasional items in a fragmented state (e.g., insect wings, abdominal segments, beetle carapaces, etc.) were more difficult to identify. Fragments were counted as single individuals unless two or more fragments obviously came from different individuals; then these fragments were counted as separate individuals. Identification and taxonomy of macroinvertebrates generally followed Hilsenhoff (1975).

Data for each food type were analyzed in three ways: frequency of occurrence, the percent numbers of food items and percent total dry weight of all food items. Some weights were determined in the laboratory and others obtained from the literature (Cummins and Wuycheck, 1971; Wissing and Hasler, 1971; Driver *et al.*, 1974; Dumont *et al.*, 1975; Driver, 1981).

As a general representation of diet dynamics the Index of Relative Importance (IRI) for each particular food category was calculated according to George and Hadley (1979). The IRI is obtained by first summing % numbers (N), % weight (W) and frequency of occurrence (FO) of each food category in the diet which generates the index of absolute importance (IAI) for a particular dietary item, where:

$$IAI_a = \% N_a + \% W_a + FO_a$$

a summation of all IAI values is then used to calculate the index of relative importance (IRI) for each dietary item (a), or:

$$IRI_a = 100 IAI_a / \sum_{i=1}^n IAI_i$$

where n is the total number of food items. Thus, the range of IRI for any diet item is 0-100.

TABLE 1.—Population estimates (numbers of adult bass per hectare) based on Schnabel capture-recapture method (Overton and Davis, 1969) and catch per effort methods. Standard errors (SE) are in parentheses

Lake	Year	Population Estimate			
		N-ha ⁻¹	(SE)	N-h ⁻¹	% Recapture
Peter	1980	355	(145)	3.5	7.5
	1981	181*	(48)	2.5	10.5
Paul	1980	339	(108)	2.8	9.4
	1981	137**	(214)	1.9	23.8

* ($X^2 = 56.5$, $P < 0.01$)

** ($X^2 = 85.7$, $P < 0.01$)

Graphic presentation of IRI in this paper followed the methods of Hulberg and Oliver (1978) and was selected as an easy way to represent bass diet breadth. All three statistics necessary to calculate the IRI (%N, %W and FO) are used to graphically represent the IRI for each food item (*see* legend of Figure 3 for a more detailed description of IRI graphic presentation).

Prey preferences.—Given the difficulties of sampling highly preferred prey items, we emphasized sampling of abundant, low-ranked prey and their relative changes in predator diets as the basis for tests of the contrasting diet predictions.

A Schindler-Patalas plankton trap (202 μ m mesh) was used to assess zooplankton abundance. In 1980, samples consisted of day (1200 hr) and night (2400 hr) collections taken on each bass sampling date (N = 8). Samples were collected at 2-m intervals to a maximum depth of 14 m. In 1981, day samples were also collected on bass sampling dates (N = 5) at 0.5-m intervals to a maximum depth of 7 m, but night sampling was conducted on only 7 June and 1 August. Zooplankton were preserved in 95% alcohol. Daphnid length (top of eye to base of abdominal spine) was measured to the nearest 0.1 mm with a microprojector. Taxonomy followed Pennak (1978).

To create an expectation of preferred prey, 13 food types were plotted on Werner's (1979, his Fig. 6) cost-curve. By plotting prey species on Werner's cost-curve (Fig. 1), prey items of this study are assigned a cost-ranking. This ranking is then used to order the presentation which follows (*e.g.*, tabular data is presented with lowest ranked prey from top to bottom and on Figures 3 and 4 the ranking is from left to right). Largest prey, crayfish and terrestrial vertebrates, occupy bottom and righthand positions. The original curve was constructed for largemouth bass of 200 g, which is close to the mean bass weight of 190 g for both lakes over both sample seasons in the present study.

Age and growth.—Scale annuli were used to age the fish based on a method described by Jearld (1983). Scales were mounted on plastic slides and projected with a microprojector. Estimates of growth rates were made by measuring the distance from last annulus to edge of the scale (M_1) and the distance from the scale focus to outer edge of the scale (M_2). The $M_1:M_2$ ratio was expressed as a percentage for only 5-year-old bass of all bass aged since they represented the greatest proportion (72%) of fish aged. This method was selected to estimate interannual growth rate differences since the comparative widths of the last annulus would represent a valid index of current growth rate (Gulland, 1985). The use of percentage data also normalizes for differences in initial bass sizes. Time of capture was divided into four seasonal groupings (period I: early to mid-June; period II: early to mid-July; period III: late July to early August; and period IV: late August).

Statistical methods follow Zar (1984) and Snedecor and Cochran (1967).

RESULTS

Adult bass growth rates were greater in 1981 than 1980 as expected from the significant decline in bass densities in both lakes (Table 1), the slope of the regression of the weight-length relationship increased significantly in both lakes, and mean weights increased significantly between respective years (Table 2). Increases in the last scale annulus growth percentages were observed in each seasonal grouping between years and lakes (Table 3). Generally significant differences (Mann-Whitney U-test) were observed in interannual comparisons with the exception of the late July to August period in both lakes and early July period in Peter Lake.

Adult bass food habits varied monthly and yearly in Peter and Paul lakes. Diet breadth (number of different prey species in the diet) was greater than regularly reported in the literature for bass of similar sizes and age classes (*e.g.*, Lewis *et al.*, 1961, 1974; Lewis and Helms, 1964; Scalet, 1977; Paragamian, 1978; Keast, 1979). The most noticeable exception to published accounts of adult largemouth bass foraging activities was a regular and size-selective predation on large cladocerans (Fig. 2). In 1980 the mean size of ingested *Daphnia* (all sampling dates combined) was 2.30 mm and 2.27

mm in Peter and Paul lakes, respectively, whereas the average size of *Daphnia* of the water column was 1.52 mm and 1.09 mm. Similar results were obtained in 1981, where the mean size of ingested *Daphnia* was 2.46 mm and 2.20 mm, and those in the water column averaged 1.24 mm and 1.30 mm, in Peter and Paul lakes respectively.

Zooplankton (Cladocerans) mean seasonal densities (all sampling periods) varied between lakes and years. In Peter Lake, density increased nonsignificantly between 1980 ($5.6 \cdot 1^{-1}$) and 1981 ($7.8 \cdot 1^{-1}$). In Paul Lake, 1980 density ($13.2 \cdot 1^{-1}$) was significantly greater ($t = 2.31$, $P > 0.05$) than the 1981 density ($10.0 \cdot 1^{-1}$). The 1981 zooplankton density was significantly greater ($t = 2.86$, $P > 0.01$) than in Peter Lake. In 1980, many bass from both lakes consumed cladocerans. Frequencies of occurrence (individual sample periods) ranged from 0.10 to 0.90 in Peter Lake, and 0.11 to 0.72 in Paul Lake. Foraging on zooplankton decreased, especially in Paul Lake, during 1981. Fre-

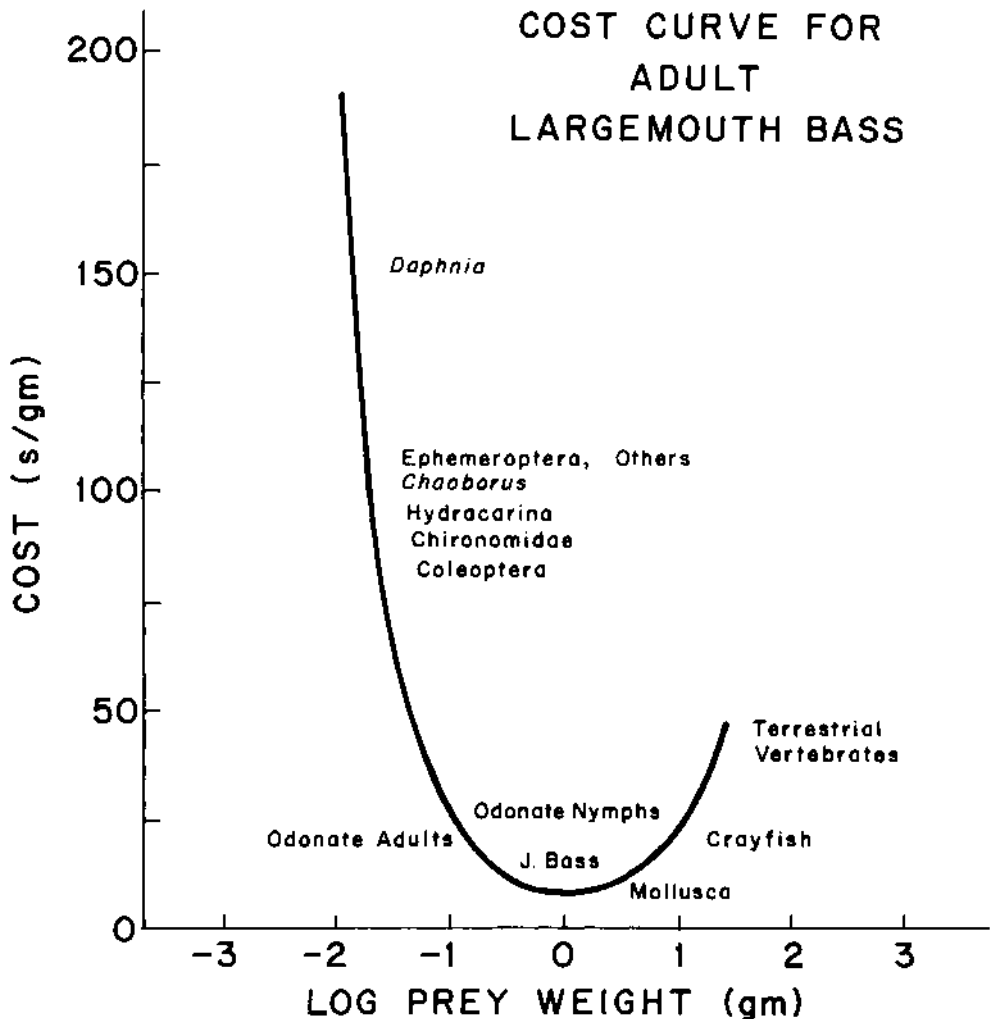


Fig. 1.—Cost curve for largemouth bass of 200 g. The curve is based on Werner (1979) and plots the 13 food groups seen in the Peter and Paul lake bass in 1980 and 1981

quency of occurrence ranged from 0.13 to 0.84, and 0.00 to 0.40 in Peter and Paul lakes in 1981, respectively. The mean yearly importance (IRI) of cladocerans as a forage item decreased between 1980 and 1981 (21.6 to 12.7 in Peter Lake, and 18.3 to 12.2 in Paul Lake; Figs. 3 and 4). This decline corresponded with an increased dietary importance of other prey items ranked nearer the nadir of the cost-curve (e.g., *Chaborus*, chironomids and odonate naiads; Fig. 1), which collectively increased in IRI from 29.2 to 35.2 and 28.1 to 40.0 in Peter and Paul lakes, respectively. In Peter Lake predation on bass juveniles and other vertebrate prey items was more important in 1981; IRI increased between years from 9.0 to 17.1. This trend was not observed in Paul Lake where IRI decreased from 16.9 to 15.6. Other diet items (coleopterans, ephemeropterans, etc.) basically remained the same between years in both lakes (Tables 4 and 5; Figs. 3 and 4).

Seasonal shifts in prey selectivity were demonstrated (IRI, Tables 4 and 5) in both lakes during both collection years. During warmer months (June-July) diet breadth increased with increased metabolic demands (mean seasonal epilimnetic temp. = 22.8 C), whereas diet breadth narrowed during the cooler periods of the season (mean seasonal

TABLE 2.—Mean length and weight data, sample size, and weight-length regressions for adult bass of Peter and Paul lakes in 1980 and 1981

Lake Year	N	\bar{x}	Weight (g) range	\bar{x}	Length (mm) range	Regression [log Y = a(log X) + b]		
						a	b	r ²
Peter (1980)	157	155	70-495	230	115-314	-3.98	2.61	0.85
(1981)	132	187*	72-368	248	205-312	-4.71	2.91*	0.90
Paul (1980)	141	204	90-478	256	180-329	-3.44	2.38	0.86
(1981)	101	213**	70-300	258	170-293	-3.65	2.47**	0.92

+ (t = 5.82, P < 0.01)

+ + (t = 4.69, P < 0.01)

* (F = 6.97, P < 0.01)

** (F = 3.54, P < 0.05)

TABLE 3.—Mean % scale growth (based on M_1/M_2) since last scale annulus formation for 5-year largemouth bass from Peter and Paul lakes in 1980 and 1981. Numbers in parenthesis equal 2 SE

Period	Mean % scale growth of last annulus			
	Peter Lake		Paul Lake	
	1980	1981	1980	1981
Early to mid-June	5.64(2.40)	10.34(1.53)*	6.14(1.64)	9.70(1.91)*
Early July	9.56(2.03)	10.32(1.51)	6.68(2.34)	11.05(1.86)**
Late July early August	7.56(2.92)	9.33(2.38)	8.58(1.75)	8.98(3.59)
Late August	11.18(1.82)	16.40(1.41)**	9.22(3.68)	11.78(3.70)***

* (U = 191.5, P < 0.01)

** (U = 69.2, P < 0.05)

+ (U = 88.2, P < 0.10)

+ + (U = 67.2, P < 0.05)

+ + + (U = 68.2, P < 0.10)

epilimnetic temp. = 12.9 C). For example, in May bass preyed minimally on *Daphnia* (mean IRI for both lakes and years = 4.4), but there was a substantial increase in zooplanktivory as water temperature increased in June and July (mean IRI = 21.7). This trend also continued into later samples in both lakes and was independent of seasonal changes in *Daphnia* density. Epilimnetic *Daphnia* were significantly more abundant in Peter Lake during the cooler parts of the sampling season (early-late season combined mean density = $11.0 \cdot 1^{-1}$; midseason combined mean density = $3.2 \cdot 1^{-1}$; $t = 3.68$, $P > 0.05$). *Daphnia* density remained relatively constant throughout the season in Paul Lake (early-late season mean density = $11.9 \cdot 1^{-1}$, and midseason mean density = $12.6 \cdot 1^{-1}$). Seasonal prey availability of other species also influenced the breadth of diet. Bass juveniles were consumed during periods of greatest availability (June-October), with consumption peaking during midsummer. Likewise, diets were supplemented appreciably with adult anurans when available (late summer) and with *Notonecta* (early autumn). Rodents and crayfish were rare but significantly augmented the dietary biomass. Odonates (Libellulidae, etc.) which have low energetic cost-benefit ratios and are highly preferred prey (Werner, 1979) remained as a seasonal staple to the diet.

Seasonal shifts in diet diversity were recorded. Numbers of zooplankton were not included in the calculation in an attempt to evaluate dietary selection of all other items as the bass reduced their consumption of zooplankton between respective years. With the exception of the June collection periods (both years), there is a general pattern of reduced diet diversity in 1981 compared to 1980 (Table 6).

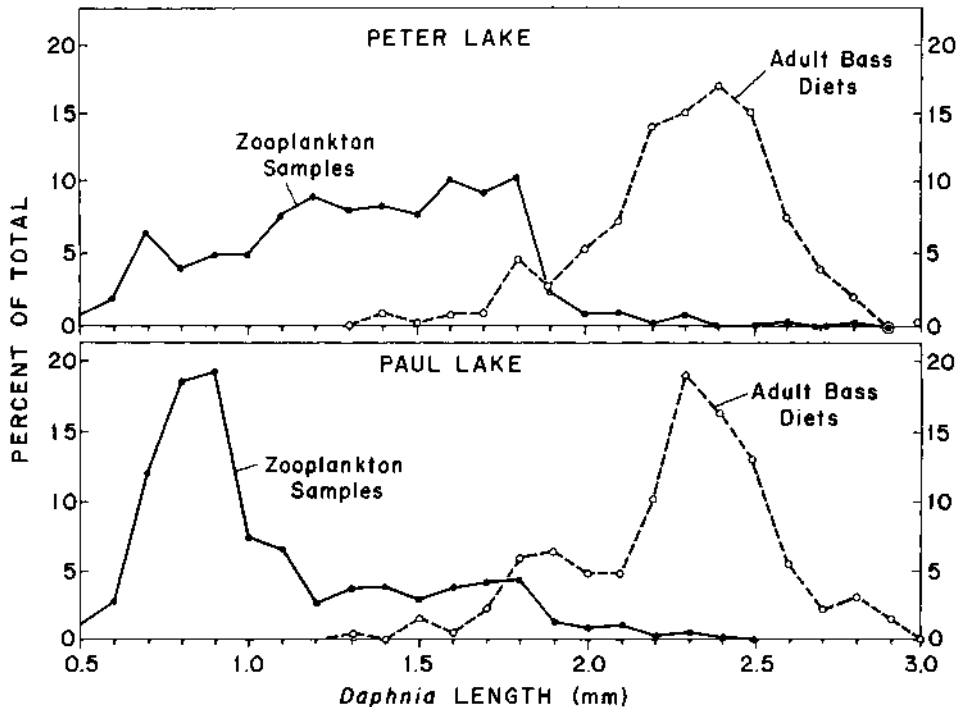


Fig. 2. — *Daphnia* size class distribution in the zooplankton and in the diets of adult largemouth bass for Peter and Paul lakes in 1980. Measurements (all sampling dates combined) are from top of eye to base of abdominal spine ("X"); to convert to a measurement from top of head to base of spine ("Y") the regression equation is $Y = 0.119 + 1.00X$; $r^2 = 0.99$

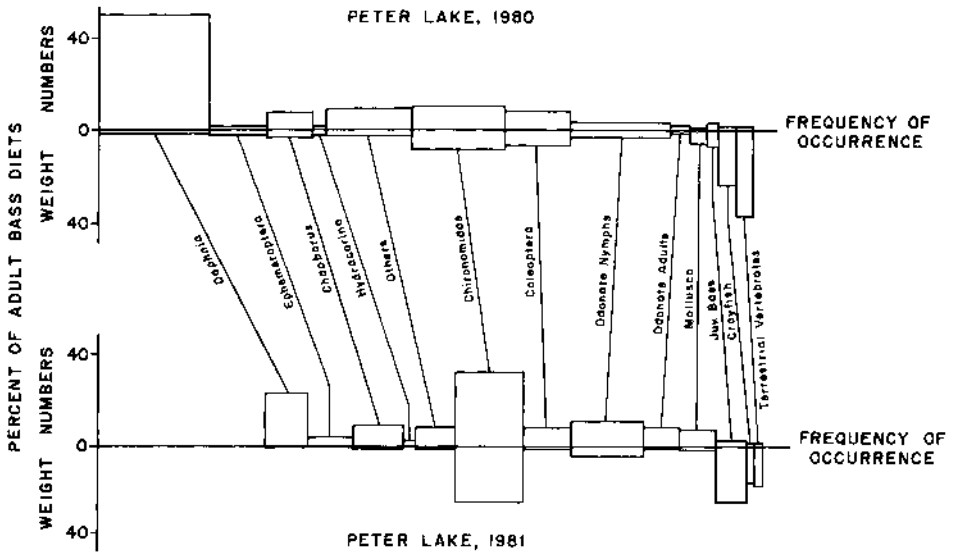


Fig. 3.—Relative importance of prey items in adult largemouth bass in Peter Lake for 1980 and 1981. All three statistics necessary to calculate an IRI (%N, %W, FO) are graphically represented here. The vertical axes above and below the horizontal axis represent annual mean %N and %W, respectively, for each diet category. The horizontal axis (drawn to the same scale as the vertical axes) measures annual mean FO for each diet category and collectively represents cumulative FO of all items. The rectangular areas that result (three axes) comparatively represent respective IRI of each prey group. Prey items near the nadir of the cost curve (Werner, 1979) are centered on the FO axis

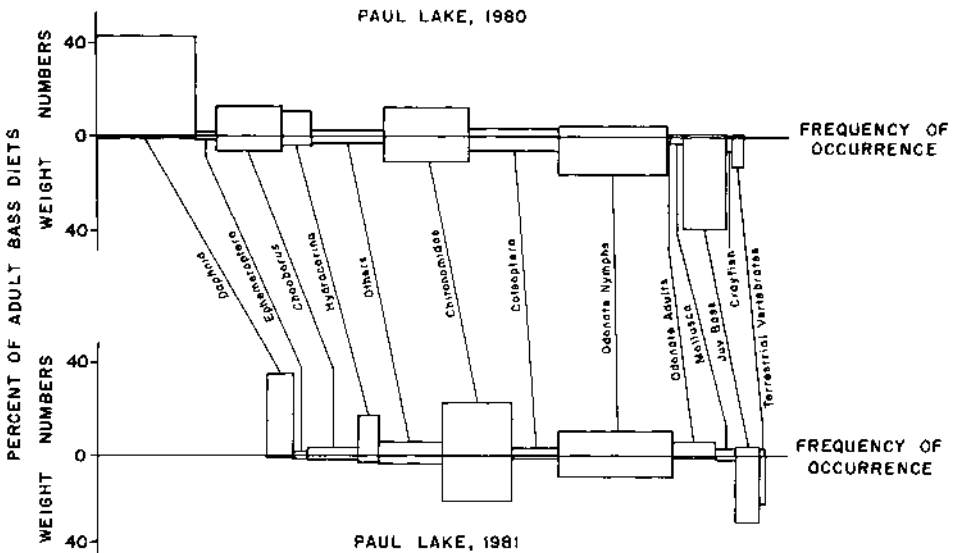


Fig. 4.—Relative importance of prey items in adult largemouth bass in Paul Lake for 1980 and 1981. See Figure 3 for description

TABLE 4. — Indices of relative importance (IRI) of the food items in the diet of adult largemouth bass in 1980 in Peter (PE) and Paul (PA) lakes

Food item	23 May		13 June		20 June		11 June		25 July		6 August		22 August		8 October	
	PA	PE	PA	PE	PA	PE	PA	PE	PA	PE	PA	PE	PA	PE	PA	PE
Zooplankton*	3.8	6.3	10.3	27.6	26.3	13.0	18.3	21.4	19.8	34.3	16.5	19.7	24.0	30.5	27.5	19.8
Ephemeroptera	0	0	3.1	7.9	4.4	10.2	0.7	7.8	1.0	2.7	1.8	8.6	1.9	0.8	0	3.7
Chaoborus	28.6	7.5	16.1	9.9	4.8	13.8	6.5	2.6	7.2	3.6	11.3	8.8	1.9	2.5	10.6	3.4
Hydracarina	0	0	6.4	0	3.3	1.2	1.5	0	12.3	0.7	11.9	7.2	11.9	0.8	0	0
Others**	7.1	16.0	5.0	1.4	4.4	6.8	6.2	7.5	2.5	2.7	0	4.4	12.4	8.9	26.8	36.9
Chironomids	13.1	42.0	28.4	7.7	12.0	10.6	8.1	4.3	12.8	14.3	19.3	12.8	7.2	9.0	0	0
Coleoptera	26.0	28.3	14.4	10.4	5.5	15.0	8.9	11.9	9.0	4.1	5.6	4.3	3.0	2.4	8.2	0
Odonata (naiads)	21.4	0	5.0	7.4	10.0	8.9	12.1	14.9	14.6	15.6	8.5	11.7	18.6	12.5	26.9	11.3
Odonata (adults)	0	0	0	1.4	1.1	5.4	3.4	5.2	0.7	0	0	0	0	0.8	0	0
Mollusks	0	0	0	0	7.1	0	0.8	11.6	0	4.2	4.5	1.9	0	4.3	0	0
Bass juveniles	0	0	11.9	15.3	14.6	0	3.0	1.6	11.4	1.8	5.9	0	19.2	2.2	0	0
Crayfish	0	0	0	11.0	6.6	15.1	0	0	0	11.8	0	0	0	10.3	0	0
Other vertebrates	0	0	0	0	0	0	3.5	11.4	7.9	4.3	14.7	20.5	0	15.0	0	24.6

*Cladocera: *Daphnia*, *Holopedium*, and chydorids

**Others: Macroinvertebrates

DISCUSSION

Diets of adult largemouth bass in Peter and Paul lakes were seasonally variable and selection of preferred prey increased after adult densities were reduced by a partial winterkill. Although bass diets reflect substantial opportunism, the results of this study are better forecast from an optimal foraging view than from functional response models. However, the strict tenets of optimal foraging models were not supported. Bass ate more highly ranked prey and less *Daphnia* in 1981 but did not exclude low-ranked prey from the diet. In terms of predator plasticity, can the optimal foraging models be used in a descriptive fashion when meaningful measures of availability of highly preferred and high-ranked prey larger items (e.g., odonate naiads and adults, frogs, crayfish, etc.) cannot be effectively made? One approach is to plot the respective prey sizes on a cost curve for the particular predator. With an array of potential prey types available to the predator on a cost-curve, the range of prey ranking can be estimated and the cause-effect relationships developed for diet dynamics. In this case, easily monitored but low-ranking prey items (e.g., *Daphnia*; Fig. 1) could serve as an index of diet selectivity and a measure of foraging optimization. The relative importance of *Daphnia* in the diet serves as an indirect indicator of the availability and abundance of high-ranked prey. A practical solution to the problems of estimating availabilities of highly preferred but rare prey may be to adopt the indirect evidence offered by predation on low-ranked prey.

Data resulting from this method suggest that largemouth bass in Peter and Paul lakes demonstrated unusual foraging behavior. In the presence of intense intraspecific competition and the absence of any significant interspecific competition, the bass have developed more generalized foraging habits than would be expected of largemouth bass of equal size and age. Keast (1979), in a study of Lake Opinicon, Ontario, where largemouth bass coexisted with 16 other species of fishes, reported a dietary diversity of 1.4

TABLE 5.—Indices of relative importance (IRI) of the food items in the diet of adult largemouth bass in 1981 in Peter (PE) and Paul (PA) lakes

Food item	22 May		6 June		4 July		31 July		21 August	
	PA	PE	PA	PE	PA	PE	PA	PE	PA	PE
Zooplankton*	0	7.4	0	12.6	1.4	3.7	26.6	6.8	32.9	23.7
Ephemeroptera	0	13.7	0	2.4	5.4	6.3	0	1.9	3.2	1.4
<i>Chaoborus</i>	11.2	17.8	8.4	4.4	0.9	7.6	4.0	2.0	3.2	2.8
Hydracarina	3.6	2.4	10.5	2.9	16.1	1.6	0	0	5.0	0
Others**	19.9	0.8	9.2	9.8	9.9	8.9	2.6	4.8	1.6	7.3
Chironomids	37.8	37.1	14.2	10.4	2.8	12.2	10.0	29.5	18.8	0
Coleoptera	13.7	6.4	2.5	4.6	3.7	13.5	5.3	5.8	3.2	4.2
Odonata (naiads)	8.2	3.3	23.7	9.5	17.1	19.4	17.6	13.6	22.0	6.7
Odonata (adults)	0	0	7.5	13.7	19.1	10.1	0	1.0	3.6	0
Mollusks	5.6	3.7	0	0	0	1.5	3.3	10.5	6.5	22.4
Bass juveniles	0	3.6	23.7	29.8	15.1	8.5	16.1	7.4	0	9.9
Crayfish	0	4.0	0	0	0	6.5	0	0	0	12.3
Other vertebrates	0	0	0	0	8.6	0	14.6	16.7	0	9.5

*Cladocera: *Daphnia* and *Holopedium* and chydorids

**Others: Macroinvertebrates

(Levins' index; Levins, 1968), whereas the largemouth bass in Peter and Paul lakes demonstrate a mean diet diversity of 4.7 (range of 2.3 to 10.1; Table 6).

Schoener (1969), in modeling energy/time relationships, suggested that several circumstances favor a generalist strategy. Of these, two apply here: (1) if food density is low and there is a premium on being able to take a large range of prey, and (2) when a predator has a relatively long period to gain energy in the absence of interspecific competition. Werner (1979) and O'Brien (1979) demonstrated that largemouth bass morphology would allow them to forage over a wide range of prey sizes. This would enable them to more efficiently use larger prey than would be possible for other centrarchids of similar size, but the largemouth bass buccal cavity morphology is not well-adapted for zooplanktivory (Alexander, 1970a, 1970b; Drenner *et al.*, 1978). Nevertheless, adult largemouth bass in Peter and Paul lakes regularly prey on zooplankton.

Two interesting questions arise. Does prey type availability promote the generalist habit of foraging behavior observed here, or is the population forced into zooplanktivory as a function of its own density-dependent effect on prey resources? In part, the latter alternative is suggested, in that with a reduction in intraspecific competition between years (partial winterkill) the diets of the bass shifted toward a more specialized mode of foraging. This shift in foraging behavior is evidenced in several ways: (1) a reduction of the lowest-ranked food items (*e.g.*, *Daphnia*). Collectively (both lakes), the mean annual number of *Daphnia* per gut decreased significantly from 30.7 to 15.2 ($t = 1.75$, $P < 0.05$) from 1980 to 1981. This was also demonstrated in a proportional decline in the relative importance index (Figs. 3 and 4) of *Daphnia* between years in both lakes. These changes would be more evident if it were not for a few smaller adults sampled late in 1981 which contained large numbers of cladocerans; (2) an increase in the occurrence and importance of the highly preferred, high-ranked prey items in the diet (larger macroinvertebrates) in 1981; (3) a decline in the cumulative frequency of occurrence of food items. Although the same food items are present in the diet during both years, the data suggest a comparative dietary specialization in 1981 because of the narrowing of the frequency of occurrence axis between respective years. In other words, narrowing the cumulative frequency of occurrence axis (Figs. 3 and 4) indicates that individual fish shifted toward a more specialized foraging behavior and diet breadth decreased as relative total prey availability increased. Collectively, this would be demonstrated by a shorter total frequency of occurrence axis; (4) and as postulated by optimal foraging theory, as individuals optimize their foraging behavior, there should be evidence of a concomitant increase in growth in the respective populations. These growth-rate increases are expected results, and are not exclusive to the optimal foraging model (*e.g.*, an expected outcome of an appropriate density-dependent response). One of our original objectives was to contrast the predictions of optimal foraging and functional response models. Neither proved wholly sufficient although the optimal foraging approach provided more nearly adequate forecasts of observed changes. The rules for prey choice by bass are more complex than those based on encounter frequency, yet not so rigorous as those based on prey switching and strict optimization.

TABLE 6. — Mean indices of diversity ($-\log H = \sum P_i \log P_i$; Levins, 1968) of diet with the exclusion of zooplankton based on mean number of items eaten in Peter and Paul lakes in 1980 and 1981

Lake (season)	May	June	July	August
Peter (1980)	3.6	4.5	5.7	7.9
(1981)	2.4	10.1	5.4	5.4
Paul (1980)	3.1	4.3	5.5	3.7
(1981)	2.7	6.6	3.6	3.7

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