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Density-dependent changes in individual foraging specialization of largemouth bass

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Abstract Individual foraging specializations are an important source of intraspecific variability in feeding strategies, but little is known about what ecological factors affect their intensity or development. We evaluated stomach contents in marked individual largemouth bass (*Micropterus salmoides*) and tested the hypothesis that diet specialization is most pronounced during periods with high conspecific densities. We collected diet data over 10 years from an unexploited population of largemouth bass that displayed a greater than threefold variation in density. Although diet composition of the aggregate bass population did not change during the study, bass body condition was inversely correlated with population size. Individual marked bass exhibited high diet consistency (diet overlap between successive captures) during years with high population densities. Diet overlap between randomly assigned pairs of bass was not correlated with population size. We did not detect the expected positive relationship between diet breadth and population size. Our analyses demonstrate that population responses to density changes may represent the sum of many unique individual foraging responses and would be obscured by pooled sampling programs. Behavioral flexibility of individuals may contribute to the ability of largemouth bass to function as a keystone predator in many aquatic communities.

Key words Density dependence · Diet consistency · Intraspecific variability · Keystone predator · Largemouth bass

Introduction

Among the basic tenets of modern biology is that individuals are unique entities whose characteristics are determined by their genetic makeup, physiology and behavior (Lomnicki 1988). Behavioral and morphological variation among individuals of a species can have important effects on intra- and interspecific interactions in ecological communities (Lomnicki 1988; DeAngelis and Gross 1992). Much of the intraspecific variation among individuals in foraging behavior, habitat selection, and migration patterns is attributable to differences in age (reviewed by Polis 1984), sex (e.g., Selander 1966; Schoener 1967; Keast 1977; Mushinsky et al. 1982) and body size (Keast 1977; Mushinsky et al. 1982; Polis 1984; Werner and Gilliam 1984; Ebenman and Persson 1988). Fishes provide extreme examples of intraspecific ecological variation because of their enormous changes in body size during their lifetime (Werner and Gilliam 1984).

Foraging behaviors of fishes often exhibit considerable intraspecific variation that cannot be accounted for by size, age, or sex of individuals. Although this level of intraspecific variation is often treated as statistical noise (Ringler 1983), much of the observed variation in foraging tactics can be explained by foraging specializations of individuals (Ringler 1983; Magurran 1986). Some foraging specializations are associated with trophic polymorphisms (Robinson and Wilson 1994). Other individual foraging specializations not associated with trophic polymorphisms can be quite pronounced and sustained over relatively long periods (Bryan and Larkin 1972; Ringler 1983; Magurran 1986).

Despite the importance of intraspecific variation to population dynamics (Lomnicki 1988), foraging models (Werner et al. 1981) and evolutionary models of speciation (Van Valen 1965, Maynard Smith 1966), little is known of how intraspecific variation in foraging tactics among individuals changes as a density-dependent process. Individual differences or specialization in foraging tactics may be especially important during times of in-

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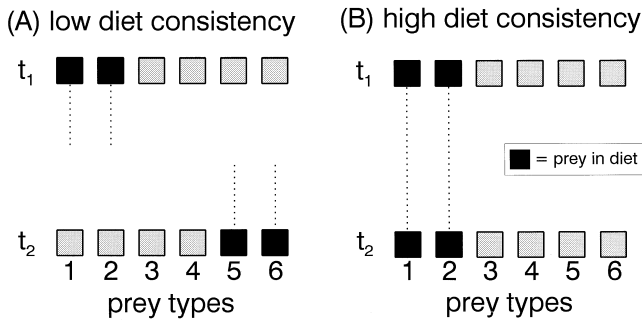


Fig. 1 A, B Illustration of two levels of diet consistency for a predator foraging from a community with six potential prey types. In both examples the predator chooses two of six available prey types. In **A** the forager exhibits low diet consistency as there is no overlap in diet choice between the two sampling periods t_1 and t_2 . In **B** the predator exhibits high diet consistency as both prey types are included in equal proportions in both sampling periods

tense intraspecific competition when prey become scarce (Magurran 1986). However, it remains unclear whether individual specializations are adaptive, and what ecological factors are important in the development of individual foraging specializations (Ehlinger 1990).

Analyses of foraging specializations are usually concerned with *diet breadth*, the number or evenness of prey types included in the diet of a predator (Levins 1968). An alternative form of individual specialization is the tendency of individuals to demonstrate selection for the same prey type(s) through time. We refer to this as *diet consistency*, which can be evaluated only by knowing the identity of individual predators (Fig. 1). We differentiate these two terms to indicate that diet breadth and diet consistency are two complementary components of foraging specializations by predators. Despite the importance of diet consistency in characterizing foraging specializations, studies of diet consistency in free-ranging predators are exceedingly rare (but see Bryan and Larkin 1972).

The largemouth bass (*Micropterus salmoides*) is a relatively large and typically piscivorous predator common to water bodies throughout the continental United States and southern Canada (MacCrimmon and Robbins 1975). Largemouth bass often occur in relatively high densities where they are present (Heidinger 1975) and can be viewed as keystone predators in many aquatic communities (Keast 1985; Carpenter et al. 1987; Carpenter and Kitchell 1993; Mittelbach et al. 1995). The diets of largemouth bass are diverse with prey ranging from fishes and amphibians to benthic invertebrates and zooplankton (Keast 1985; Hodgson and Kitchell 1987). Largemouth bass foraging is also relatively plastic, changing with prey availability (Hodgson and Kitchell 1987), habitat complexity (Anderson 1984), body size (Keast 1985; Olson 1996) and foraging experience (Colgan et al. 1986).

We studied the diet dynamics of an unexploited population of adult largemouth bass for 10 years while the population experienced a greater than threefold density

change. Because we could uniquely mark and recapture individual bass, we were able to quantify feeding histories of individual predators in the field and estimate their degree of diet consistency. We tested the hypothesis that individual diet consistency is most pronounced during periods with high conspecific densities. We also compared our results with predictions from optimal foraging models for expected changes in diet breadth during periods of intense intraspecific competition (Pyke et al. 1977). Specifically, we expected that largemouth bass diet breadth would increase during periods of high conspecific densities. Here we describe the tendency of individuals to specialize on certain groups of prey during periods of high bass densities. We demonstrate that diet consistency is an individual-specific foraging response to high conspecific densities that is not necessarily associated with changes in diet breadth of individuals or of the whole population. The behavior of individual fish appears to be an adaptive response to increased intraspecific competition, even though this relationship is obscured at the population level.

Methods

Study site

Data were collected during 1984–1993 from Paul Lake, a small (1.5 ha), deep (maximum depth 15 m) kettle lake located at the University of Notre Dame Environmental Research Center near Land o' Lakes, Wisconsin (89°32'W, 46°13'N). Paul Lake is located on a private reserve and is an unexploited, unmanipulated system that has served as a long-term reference lake for several whole-lake manipulations conducted during the last decade (Carpenter and Kitchell 1993).

Largemouth bass have been the only piscivorous fish species in Paul Lake since around 1976 (Leavitt et al. 1989). We restricted our analyses to adult bass (≥ 150 mm total length) that were marked as individuals. We did not include individuals < 150 mm total length because we were unable to uniquely mark them, and they contribute only a small fraction of the population biomass (mean 19%, SE=6).

Bass population estimates

Populations were estimated in mid-May and mid-August each year. Angling and boomshocker electrofishing techniques were used to establish a marked population of fish for Petersen mark-and-recapture estimates (Ricker 1975). All fish were marked with numbered Floy tags for identification. Electroshocking was used to recapture individuals 1–2 days after the marked population was established in each census. On each mark-and-recapture census, we electroshocked the entire shoreline of the lake and sampled all fish that were caught. Each fish was measured (total length, nearest 1 mm) and weighed (nearest 1 g) either on an electronic balance or using a spring scale. Annual average population densities were calculated as the mean of the May and August surveys in each year.

Diet data collection and analyses

Angling and electroshocking in the littoral zone were used to collect bass for diet analyses generally between 0800 and 1200 hours and 1600 and 2000 hours, once monthly during May through August. Within 60 min of capture, the stomach of each fish was

Table 1 Nineteen diet categories considered in the study of largemouth bass foraging in Paul Lake, Minnesota

Prey category
Small zooplankton ^a
Large zooplankton ^b
Ephemeroptera larvae
<i>Chaoborus</i> spp. (larvae)
Hydracarina
Chironomid pupae
Coleopteran larvae
Odonate naiads
Odonate adults
Trichopteran nymphs
<i>Notonecta</i>
Mollusca
Hirudinea
Redbelly and finescale dace
(young-of-year) largemouth bass
Juvenile (>1 year) largemouth bass
Crayfish
Other vertebrates ^c
Amphipods

^a *Polyphemus pediculus* and copepods

^b *Daphnia* spp. and *Holopedium gibberum*

^c Frogs, snakes, voles, shrews, mice, and birds

flushed into a 0.29-mm Nitex mesh concentrator with a modified hand-pumped pressurized backpack sprayer (Seaburg 1957). Items too large to pass through the efferent tube of the pump were removed using a blunt forceps. Samples were backwashed into individual vials and preserved in 95% ethyl alcohol for later enumeration.

Stomach contents of 1006 individuals were analysed. The mean number of fish sampled on any given sampling date was 25 (SE=2), and in any year was 101 (SE=9). Individuals with empty stomachs (19 out of 1006) were excluded from statistical analyses. Stomach contents were identified according to Hilsenhoff (1975), Pennak (1978), and Balcer et al. (1984), and grouped into 19 prey categories previously assessed for Paul Lake organisms (Hodgson et al. 1993) (Table 1). A total of 81,615 individual prey items were enumerated. An average of 83 individual prey items was found in each bass stomach sampled throughout the study.

Data analyses

As an indicator of bass body condition we used the residual between the observed mass of an individual fish and the mass predicted from the long-term length-mass regression for all individuals in this study:

$$\ln(Mass) = -11.4 + 3.021 * \ln(Length) \quad (1)$$

($r^2=0.97$, $P < 0.001$, $n=1006$). The standard error of the intercept was 0.093, and of the slope was 0.017. A positive residual indicated that an individual was heavier than the average for that length while a negative residual indicated the opposite. Examination of the residuals around this length-mass regression showed no association between the length of bass and body condition.

We used the measure B (Levins 1968) to indicate diet breadth of largemouth bass:

$$B = \frac{1}{\sum p_i^2} \quad (2)$$

where p_i is the fraction of total diet mass represented by item i . This index is minimized at 1.0 when only one prey type is found in the diet, and is maximized at n , where n is the total number of prey types, each representing an equal proportion of the diet. We calculated Levins' measure in three ways to represent the diet

breadth of (1) the average individual in the population on each sampling date, (2) the aggregate diet of the population on each sampling date, and (3) the aggregate population in each year. Diet breadth of individuals was calculated from the proportion by mass of each diet category found in individual stomach contents on each sampling date. Diet breadth of the population was determined by first calculating the aggregate diet composition by summing the amount of each diet category encountered in the stomach contents across the entire population of individuals sampled on each date or in each year, and then applying Eq. 2.

We assessed intra-annual diet consistency from marked individuals sampled at least twice in the same year. An average of 16 individuals (SE=2) was recaptured in each year. Diet consistency was calculated as the percent overlap of an individual's diet between at least two successive sampling dates as:

$$P(x)_{t_1 t_2} = \left[\sum^n (\text{minimum } p_{i t_1}, p_{i t_2}) \right] 100 \quad (3)$$

where $p_{i t_1}$ and $p_{i t_2}$ are the proportions of diet category i at times t_1 and t_2 representing two successive captures of individual x in the same year. This index estimates the propensity of individual fishes to select specific prey types consistently through time. A value of 0 indicates no diet overlap between successive samples, and a value of 100 indicates perfect diet overlap between successive samples. To determine whether individual diet consistency differed from diet overlap among individuals in the population, we also computed the percent overlap between 1000 randomly assigned pairs of individuals (that were not sampled on the same date) drawn from the pool of all fish sampled for stomach contents in a given year.

Relationships between variables were determined using either simple correlation or linear least squares regression. We treated the annual means as independent data points ($n=10$) in all cases, except in a comparison of diet consistency and diet breadth for all individuals recaptured in the study ($n=162$). Residuals around regressions were checked for normality and serial correlation (Drapper and Smith 1981).

To evaluate whether diet consistency in largemouth bass changed with increases in the length of time between samplings, we blocked the data into two time periods: a high bass density period from 1984 to 1988 and a low bass density period from 1989 to 1993. We used two-way ANOVA to determine whether the length of the time interval between successive captures affected the diet consistency of individuals, and whether bass density altered the effect of time on diet consistency.

Results

Bass population dynamics and changes in body condition

Over 10 years the estimated population size of adult largemouth bass ranged from 97 to 316 individuals (Fig. 2). Although bass size distributions differed among years, bass length did not vary systematically with bass population size (Fig. 3). Bass body condition was significantly and negatively correlated ($r = -0.78$, $n=10$, $P < 0.01$) with population size (Fig. 4).

Changes in diet composition and breadth with bass density

Diet composition of the average adult largemouth bass in Paul Lake did not change despite greater than threefold changes in bass density. The percentage contributions

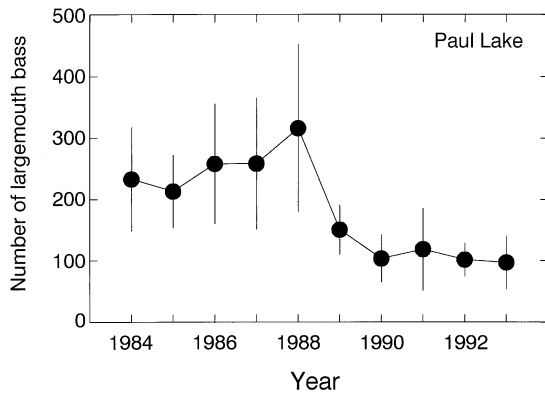


Fig. 2 Changes in population size of adult largemouth bass in Paul Lake between 1984 and 1993. Each data point represents the mean of a spring and fall mark-recapture estimate. Error bars represent standard errors associated with Petersen mark-and-recapture population estimates

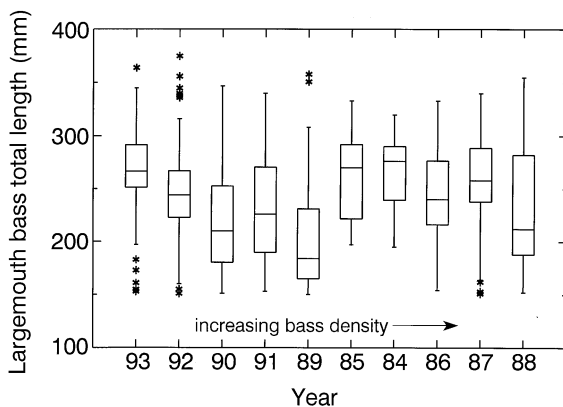


Fig. 3 Boxplots of lengths of largemouth bass >150 mm in Paul Lake by year of the study. Years have been arranged in order of increasing bass population size. The median is denoted by the central horizontal line. The upper and lower hinges of the boxes denote the interquartile range (H). The whiskers denote the range of values that fall within $1.5 \times H$ of the hinges. Values outside the whiskers are denoted by asterisks

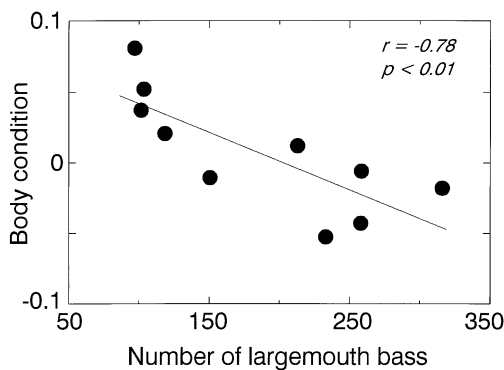


Fig. 4 Relationship between body condition and population size in adult largemouth bass in Paul Lake between 1984 and 1993 ($r = -0.78$, $n = 10$, $P < 0.01$). Each data point represents the mean of all observations taken in each year

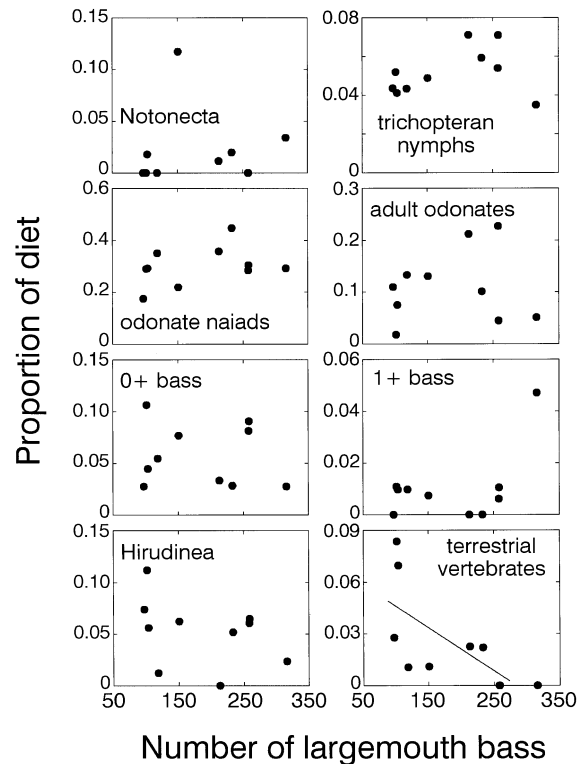


Fig. 5 Contributions of eight most profitable diet categories (based on prey body size, i.e., largest prey) to diets of largemouth bass versus bass population size in Paul Lake for each of the 10 years in the study. Only the proportion of terrestrial vertebrates in diets is significantly correlated ($r = -0.68$, $n = 10$, $P < 0.02$) with bass density. Proportional contributions of all other 18 diet categories were not significantly correlated with populations size ($P > 0.2$)

from 18 of the 19 prey categories were not correlated with bass population density during the study ($P > 0.10$, $n = 10$, Fig. 5). Only the proportion of terrestrial vertebrates in bass diets was significantly correlated with bass density ($r = -0.68$, $n = 10$, $P < 0.05$, Fig. 5, bottom right).

Diet breadth of the bass population was not related to population size on any sampling date ($r = -0.20$, $n = 10$, $P > 0.5$) or any year ($r = -0.37$, $n = 10$, $P > 0.15$), or for the average individual ($r = -0.14$, $n = 10$, $P > 0.5$, Fig. 6). The aggregate diet breadth of the population in any year (mean = 6.71, SE = 0.53) was approximately 4 times the diet breadth of individuals (mean = 1.62, SE = 0.07) within any year. Aggregate diet breadth of the population on any sampling date (mean = 4.72, SE = 0.13) was approximately 3 times the mean diet breadth of individuals.

Changes in individual diet consistency with bass density

Mean annual diet consistency of marked individuals was positively related to bass population size (Fig. 7, $F_{1,8} = 6.02$, $P < 0.04$). Individuals tended to have higher diet consistency at high bass densities than at low densities. There was no significant relationship between percent diet overlap in randomly paired individuals and population size ($F_{1,8} = 0.07$, $P > 0.75$). Therefore, trends in

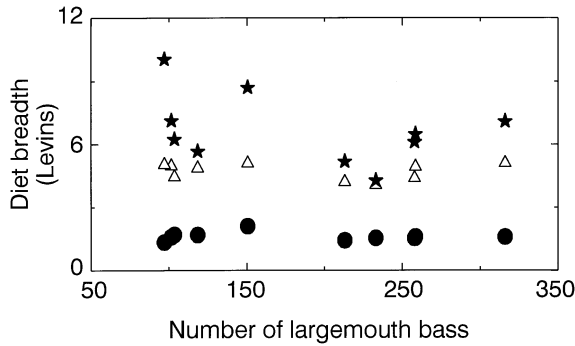


Fig. 6 Relationship between population size and mean annual diet breadth calculated for the average individual on any sampling date (filled circles), the aggregate population on any sampling date (open triangles), and for the aggregate population over the entire summer (stars)

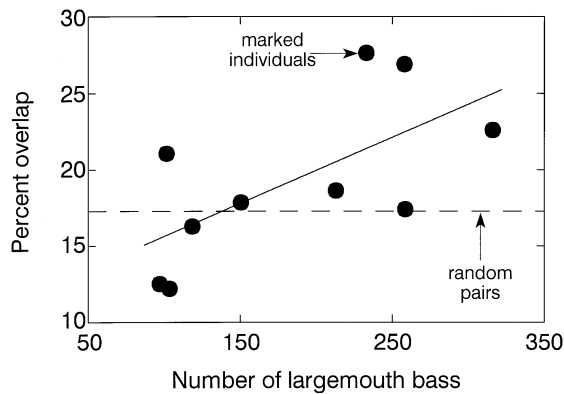


Fig. 7 Individual diet consistency (measured as the average percent overlap between two successive samplings of marked individuals) as a function of bass density. Least squares regression to describe this relationship is: [percent overlap = $11.3 + (0.043 \times \text{bass density})$; $P < 0.04$, $r^2 = 0.43$]. The mean percent overlap (17.3%) from randomly paired individuals is shown for comparison (dashed line). Percent diet overlap between randomly paired individuals was not significantly related to bass density

individual diet consistency were not confounded by changes in diet choice within the population as a whole. The average (intra-annual) percent overlap in diets of randomly paired individuals was 17.3% (SE=1.0).

The length of time between recaptures of individual bass had no significant effect on the diet consistency for that time period (Fig. 8, $F_{2,156} = 0.246$, $P > 0.75$). Although there was some indication that diet consistency decreased with increased time interval between samplings at low bass densities but not at high bass densities (Fig. 8B), the effect was not significant in a two-way ANOVA ($F_{2,156} = 0.113$, $P > 0.85$).

To determine whether individual diet consistency was related to diet breadth, we compared values of individual diet consistency to the mean diet breadth from the two samples used to calculate diet consistency for all individuals recaptured during the study. Individual diet consistency was not related to diet breadth of individuals

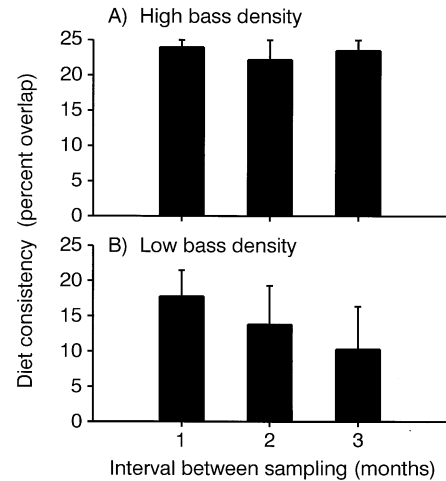


Fig. 8 A, B Effect of length of time interval between successive samplings on estimated diet consistency of marked individuals. Data were blocked into **A** high bass density years, 1984–1988, and **B** low bass density years, 1989–1993. Length of time interval between sampling events had no effect on diet consistency during either period ($P > 0.75$)

($r = 0.08$, $P > 0.3$, $n = 162$). Therefore, individuals that demonstrated high diet consistency did not show decreased diet breadth that could indicate foraging specialization.

Discussion

The negative relationship between largemouth bass body condition and population size (Fig. 4), suggests that resource availability was diminished during periods with high conspecific densities. Although diet breadth did not change with population size (Fig. 6), individual diet choice was more consistent during years with high bass densities (Fig. 7). Bass foraging responses to changes in population size were observed for individuals, but not at the population level. Therefore, population level predation responses to density changes result largely from the sum of many unique individual foraging responses.

Mechanisms leading to individual diet consistency

Individual largemouth bass tended to have more consistent diets during periods with high conspecific densities (Fig. 7). This change in diet consistency cannot be attributed to changes in the size structure of the bass population, as population size was independent of the size distribution of individuals (Fig. 3). Although we are unable to identify the mechanisms that lead to changes in bass diet consistency, we propose two hypotheses that might explain the development of this foraging response.

The first hypothesis is related to bass territoriality. It is possible that individual bass are territorial with the size of home ranges inversely related to population density. Therefore, when conspecific densities increase,

home range size should decrease. If prey are patchily distributed at a scale approximately the same grain as bass territory size, increases in bass density would decrease the number of prey types available to the average predator. As a result, predators would be expected to become more consistent in diet during times of high conspecific densities because restricted home range size allows encounters with fewer prey types. Our data do not support this hypothesis. If it were correct, we should also expect that diet breadth would decrease as diet consistency increased. This was not the case for adult largemouth bass in Paul Lake where diet consistency was independent of diet breadth.

Bryan and Larkin (1972) showed that highly mobile individual trout maintained as much diet consistency as individuals that were repeatedly caught in the same stream location. Therefore, diet consistency did not appear to result from territoriality in streams. Results from Bryan and Larkin (1972) and our study suggest that diet consistency in some fishes is the result of active selection for certain prey types rather than associated with prey encounter due simply to patch choice by the predator.

Learning and experience are dynamic components of the foraging strategies of largemouth bass (Colgan et al. 1986) and other fishes (Ware 1971; Godin 1978; Werner et al. 1981; Dill 1983; Ehlinger 1989; Kieffer and Colgan 1991). Foraging experience for certain prey types generally increases predator efficiency on those prey. Presumably gaining experience involves an active learning process with associated costs. These costs might include lost foraging time or lowered feeding efficiency as a predator learns to detect, capture, and handle new prey types (Werner et al. 1981; Ehlinger 1989). The costs associated with learning to feed on a new prey type should reinforce the established foraging regime (Dukas and Clark 1995). Therefore, if resource levels influence foraging strategies, it is possible that at high population densities (when presumably high-quality prey become scarce), the benefits of maintaining an established foraging regime outweigh the costs associated with learning to consume all prey types encountered. At low predator densities, prey may be sufficiently abundant that selecting prey as they are encountered is a more appropriate foraging strategy than maintaining a consistent diet.

We evaluated diet consistency across time intervals with a minimum duration of 1 month. Therefore, if development of search images (Curio 1976) or specific foraging skills were important in maintaining diet consistency of individuals, these skills must be maintained over relatively long periods. At time scales of days and hours, diet consistency is probably reinforced by diurnal shifts in prey availability and patch choice by the predator. Bryan and Larkin (1972) showed that diet consistency was highest over short periods but was partially maintained over periods up to about half a year. Our data suggest that diet consistency in largemouth bass is maintained for up to several months, especially during times with high conspecific densities (Fig. 8). How individual

foraging specializations are reinforced and maintained over different time scales, and whether intraspecific competition changes the degree to which diet consistency of individuals is maintained, remains unresolved.

Application to optimal foraging models

The strong negative relationship between density and body condition probably reflects intraspecific competition. However, bass diets did not respond as might be expected by traditional views of intraspecific competition and optimal foraging. Optimal foraging theory predicts that when preferred prey become scarce (for instance when intraspecific competitive interactions are intense) diet breadth should increase as lower-quality prey are included in the suite of prey consumed by a predator (Pyke et al. 1977; Krebs 1978). We expected that increases in diet breadth would mirror decreases in body condition of largemouth bass. Instead, foraging responses at the level of individual predators appeared to be the most sensitive to changes in bass densities. Flexibility of individual foragers' behavior led to greater consistency within individual diets but did not lead to expected changes in diet breadth at the population level.

There are several reasons why diet breadth might not have changed as predicted by optimal foraging theory. Most importantly, foraging theory assumes that prey selection by a predator is a function of prey availability (Stephens and Krebs 1986). We do not know whether prey availability changed during our study but can only infer that availability decreased when bass densities were high, as reflected in decreased bass body condition. However, our data demonstrate that diet composition of bass generally did not vary with changes in bass density. If the bass population in Paul Lake had fallen to low enough densities to allow prey fishes to flourish, we probably would have observed a focusing of bass predation on fishes (Hodgson et al. 1993), thus leading to the expected narrowing of diet breadth.

Alternative explanations for the insensitivity of diet breadth to bass density include inappropriate temporal scale of analysis, interactions between the predator functional response, and prey growth rates (Hansson 1995), inappropriate classification scheme of prey categories (Krebs 1989), and that bass do not perceive the environment in a fine-grained manner as foraging models often assume (Schluter 1981). Predators such as largemouth bass live in patchy environments. Models that do not account for predator behavior in spatially and temporally heterogeneous environments may oversimplify this foraging system. In heterogeneous environments, high intraspecific variation in foraging mode may be adaptive just as intraspecific variation in morphology is adaptive (Van Valen 1965) and as a result may be a relatively common phenomenon. Differential responses by individuals to changes in conspecific densities may obscure expected trends in the "average" fish or the population as a whole. In the case of largemouth bass foraging in Paul

Lake, it appears that foraging flexibility allows individuals to become selective on subsets of the entire suite of prey types available to the population. Therefore, bass population impacts on prey resources appear to be more complex than simply the sum of the average individual impact.

Largemouth bass as a keystone predator

The largemouth bass is a keystone predator whose population dynamics often precipitate changes throughout entire communities and ecosystems (Keast 1985; Carpenter et al. 1987; Carpenter and Kitchell 1993; Mittelbach et al. 1995). The specific features of largemouth bass that make them more effective predators than many other large piscivores are not well understood (Mittelbach et al. 1995). The ability of largemouth bass populations to achieve numerical dominance in many of the systems where they occur (Heidinger 1975), and maintain high population densities through time (Carpenter and Kitchell 1993), probably contribute to their role as keystone predators in many aquatic communities. We believe that the foraging plasticity among individuals of a population demonstrated by largemouth bass is an important attribute of this powerful effect.

A recent effort to characterize keystone species suggests that keystones have effects on communities that are disproportionately large compared to their abundance (Power et al. 1996). Thus, numerically dominant species are precluded from this definition of keystones. The ability of largemouth bass to have large impacts on aquatic communities at low densities (i.e., keystone effects; Carpenter and Kitchell 1993; Mittelbach et al. 1995) is reinforced by their ability to achieve numerical dominance in many systems. The role of largemouth bass in structuring aquatic communities must, therefore, be viewed as a dynamic process that includes important interactions at both high and low population densities.

Predator versatility (Curio 1976) refers to the ability of individuals to specialize on a subset of prey types, or in a subset of foraging strategies that are included in the entire repertoire of the species. Our data provide two examples of such predator versatility in largemouth bass. First, diet breadth of the average individual is much less than that of the entire population (Fig. 6). Second, our analysis of the diets of individuals demonstrates that individual bass adopt unique foraging patterns that are maintained through relatively long time periods (i.e. at least a month) when conspecific densities are high.

In an environment where prey supply is unpredictable, a generalist foraging strategy is the most appropriate for energy maximization (Dill 1983). Despite their morphological adaptation to foraging on relatively large-bodied prey (Werner 1979; Hoyle and Keast 1988), largemouth bass are generally opportunistic and successfully forage on prey spanning several orders of magnitude in size, and many taxonomic categories (Hodgson and Kitchell 1987). We have demonstrated that large-

mouth bass develop individual-specific foraging regimes that are maintained through time. This phenomenon is analogous to the 'training effect' that can bias predator diet selection towards prey types it has previously consumed (Oaten and Murdoch 1975). Stability of predator-prey systems is often enhanced by the addition of alternate prey (Inouye 1980; Powell 1980; but see Abrams 1987) and by "training effects" on predator functional responses (Oaten and Murdoch 1975). A generalist foraging strategy combined with versatility probably stabilizes largemouth bass population dynamics and those of many its prey. However, because bass can effectively forage on alternate prey (i.e., benthic insects), they are capable of reducing their preferred prey (e.g., planktivorous fishes) to very low densities, or even causing local extirpation (Murdoch and Bence 1987).

In our analysis of largemouth bass diets in Paul Lake we observed only 9 incidents of bass predation on prey fish species in more than 1000 diet samples. Paul Lake bass populations are sustained at high biomass primarily through predation on benthic resources. Opportunistic switching to predation on fishes when they are sporadically available (Hodgson and Kitchell 1987) can lead to virtual elimination of planktivorous fishes from the community. Development of increased individual foraging consistency may enable bass to effectively use alternate resources (i.e., benthos) during periods with intense intraspecific competition and, therefore, sustain high population densities when their preferred prey are absent. Whether the degree of foraging plasticity we have observed in largemouth bass is unique to this species is unknown.

Identifying keystone interactions remains an important but difficult goal of community ecology (Mills et al. 1993; Menge et al. 1994; Brown 1995). In the case of largemouth bass, opportunistic foraging ability (Stroud and Clepper 1975; Hodgson and Kitchell 1987) and behavioral flexibility at the level of individual predators, such as that we have described, probably combine to make largemouth bass a powerful keystone predator in many aquatic communities.

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