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ABSTRACT

Water mites (Hydracarina) are not consumed by some fish because of their distastefulness or toxicity. We obtained evidence that some individual largemouth bass (*Micropterus salmoides*) specifically targeted mites as prey in a small unproductive and unexploited lake in Michigan's Upper Peninsula, USA. Bass stomachs that contained water mites tended to have high numbers of mites, with up to 780 mites in individual stomachs. Stronger evidence for foraging specialization was provided by repeated examination of stomach contents from recaptured bass; many bass contained water mites more often than would be expected by chance (one-sample t-test [$H_0=0$], $t = 3.54$, $P < 0.0001$). Also, there was no correlation between bass density and the percentage of bass consuming mites ($r = 0.0183$) further suggesting that foraging on mites was an individual response rather than a population strategy.

INTRODUCTION

Diet data sets that extend over many years provide unique opportunities to examine foraging behaviors. As such, we have amassed >4,000 individually-tagged largemouth bass (*Micropterus salmoides*) gut samples spanning 23 years from a single lake (Paul Lake) in Michigan's Upper Peninsula, USA (Hodgson et al. 2006, Hodgson and Hodgson 2000, Hodgson et al. 1993 and Hodgson and Kitchell 1987) as a corollary data set of a larger ecosystem project (Carpenter et al. 2001 and Carpenter et al. 1987). The diets of individual largemouth in this study were diverse with a wide breadth of prey species including zooplankton, water mites, benthic macroinvertebrates, terrestrial insects, fishes, amphibians, and small mammals (Hodgson and Kitchell 1987, Hodgson et al. 1993, Hodgson and Hansen 2005). Also, the foraging behavior of largemouth bass was relatively plastic, varying with prey availability, foraging experience (Colgan et al. 1986), and foraging specializations (Schindler et al. 1997).

Foraging specialization by individual predators on particular prey types is especially interesting when the prey possess chemical defenses made conspicuous with aposematic coloration. Such a prey species is the bright red water mite (various species of the Order Hydracarina) that has long been considered unpalatable to a variety of fishes, including fingerling largemouth bass (Kerfoot et al. 1980). It has been shown that largemouth bass are capable of avoiding noxious prey advertised with warning coloration (Brown 1937). However, because of prey resource limitations in Paul Lake, with bass densities often exceeding $250\text{-}300\text{-ha}^{-1}$, individual bass may have developed foraging specializations on normally unexploited prey resource, including a *Chaoborus* specialization (Rick 2007). Since adult bass in Paul Lake forage on a wide array of prey species, it would not be unexpected to find adult bass in the population specifically targeting water mites as prey.

This study examined the foraging behavior of largemouth bass on water mites in Paul Lake, which is a small, oligotrophic and seepage lake (1.7 ha, $z_m = 15$ m; mean epilimnion chlorophyll = $4.2\text{ g}\cdot\text{L}^{-1}$) in the Upper Peninsula of Michigan, USA ($46^{\circ}15'N$, $89^{\circ}30'W$). Paul Lake has not experienced any angling exploitation for decades,

subsequently providing a unique opportunity to examine a predatory interaction where trophic interaction has had sufficient time to fully develop free from human manipulation. Additionally, largemouth bass has been the only fish species in Paul Lake since 1976 (Leavitt et al. 1989).

METHODS AND MATERIALS

Fish used for diet analysis were collected in the littoral zone by angling and electrofishing; however, pelagic fish were collected in 2001 and 2006 as part of a study of bass predation on *Chaoborus* (Rick 2007). Schnabel methodology (Ricker 1975) was used to estimate population densities.

We restricted our analysis to individually tagged adult fish (≥ 150 mm total length) because we could not individually tag smaller fish and they also contributed $< 20\%$ to the bass biomass (Schindler et al. 1997). Our diet analysis included 4,367 individual fish collected from 1984 to 2006. Fish were sampled six-seven times in most years. During 2001 and 2006, sampling events nearly doubled due to collection of pelagic fish for the *Chaoborus* study. Mean annual sample size was 189.9 (SE = 14.2). From these fish, we collected 201 total diet samples in which 305,508 diet items were chronicled.

Stomach contents were removed with gastric lavage (Hodgson et al. 1993). Twenty-two diet categories were compressed into five for this study, which were enumerated within the following prey categories: water mites, zooplankton (*Daphnia* spp. and *Chaoborus* spp.), benthic macroinvertebrates and terrestrial insects, fish and terrestrial vertebrates. Prey items were enumerated and expressed as relative abundance (percentage of total number of prey items in each bass stomach).

RESULTS AND DISCUSSION

Largemouth bass have been described as specialists (Keast 1979), as generalist feeders (Winemiller and Taylor 1987) and as opportunistic/optimal foragers (Hodgson and Kitchell 1987, Schindler et al. 1997, Hodgson and Hodgson 2000). In this study, the adult largemouth bass population exhibited a broad diet breadth ranging from zooplankton to small mammals. Water mites were also consumed.

While water mites were a component of the aggregate diet, they comprised only a small proportion of the total diet items (Table 1). With the exception of 1993, mites were present in all sample periods. The multi-year mean relative abundance of mites was 6.4% (SE = 1.1); the annual mean ranged from 0.1% in 1993 to 19.8% in 2004. The total multiple-year sample mean was 4.0 mites per bass (of all bass sampled), with the mean number of mites per bass in bass that contained mites ranging from 1.0 in 1993 to 88.9 in 1984. The percent of bass with mites ranged from 1.8% in 2000 to 23.1% in 1989; overall, 12.9% of bass stomachs sampled contained mites.

Some evidence for target foraging by individual bass upon water mites was provided by examination of feeding histories from multiple-recaptured bass. There were 45 individual bass that contained > 100 mites (maximum 780; Table 2). Collectively, 566 (13.0% of the total diet analyses) bass diets contained 16,487 mites. Furthermore, these

Table 1. Mean relative abundance (%), with standard errors in parentheses, of five prey categories of largemouth bass in Paul Lake from 1984-2006.

| Prey item | Relative Abundance |
|--|--------------------|
| Water mites | 6.4 (1.1) |
| Zooplankton (<i>Daphnia</i> spp. and <i>Chaoborus</i> spp.) | 67.3 (3.24) |
| Benthos including terrestrial insects | 24.9 (3.94) |
| Fish | 1.4 (0.37) |
| Terrestrial vertebrates | 0.04 (0.01) |

data demonstrated that those bass stomachs containing water mites had them in greater frequency than would be expected by chance alone (one-sample t-test [$H_0=0$], $t = 3.54$, $P < 0.0001$).

The mean number (all years) of mites per bass stomach (of those stomachs with mites) was 29.1 with considerable interannual variability. Therefore, those sample dates that averaged more than 29.1 mites per stomach (essentially positive z-scores) may provide further evidence for foraging behavior that targeted mites. As such, twenty-eight dates (13.9%) within our data may suggest active targeting of mites as prey (Fig. 1).

The 23-year adult bass density averaged 175.4 ha^{-1} . Although adult bass population densities varied from $>300 \text{ ha}^{-1}$ in 1985, to $<60 \text{ ha}^{-1}$ in 1993, there was no correlation between the percentage of bass with water mites in their diet and bass population density ($r = 0.0183$), suggesting that predation on mites was more an individual foraging targeting behavior than a population functional response driven by mite density.

Water mites that are bright red in color, such as those species considered in the present study, have long been thought to represent a complex of unpalatable Müllerian mimics (Elton 1923). Kerfoot et al. (1980) showed that red water mites are unpalatable to a variety of fishes, including fingerling largemouth bass. They also concluded that fish actively learn to avoid distasteful water mites, but that avoidance apparently depends on continued exposure (see also Kerfoot 1982). It would also appear from the results of these studies, and those of Eriksson et al. (1980), that fish generally are more likely to resort to water mites as a regular food item when the availability of alternative food items is proportionally low. Schindler et al. (1997) have shown that Paul Lake bass are capable of adjusting their foraging strategies relative to prey availability in that individual bass become more specialized when prey availability decreases. We have shown that some individual largemouth bass consumed water mites disproportionately with respect to other members of their population, suggesting that these bass they may have become active mite predators.

Although water mites were never an important component of the overall diet, they were regularly observed in the diets of all size cohorts of adult bass in Paul Lake. Water mites were preyed upon throughout the growing season. Variability among samples in intensity of water mite consumption generally increased in mid-season (Fig. 1), reflecting the occurrence of samples during that period that contained either above-average numbers of mites or above-average proportions of bass that specialized on mites. Kerfoot (1982) suggested that seasonal patterns in consumption of aposematic prey might reflect changes in the densities of palatable and unpalatable aposematic prey. However, because our *post-hoc*, corollary mite analysis originated from a larger ecosystem study design (Carpenter et al. 2001 and Carpenter et al. 1987), we regrettably have no data on water mite densities. Despite this, we are confident that the well-documented foraging plasticity of largemouth bass has allowed some members of the Paul Lake population to utilize an unconventional prey resource.

Table 2. Number of multiple-recaptured fish with water mites in their gut from Paul Lake, 1984-2006.

| Number of recaptures | Number of fish | Mean number mites per gut (range) |
|----------------------|----------------|-----------------------------------|
| 6 | 1 | 261.5 (2-780) |
| 5 | 2 | 13.4 (1-101) |
| 4 | 3 | 40.0 (1-153) |
| 3 | 13 | 177.4 (1-766) |
| 2 | 57 | 53.9 (1-490) |

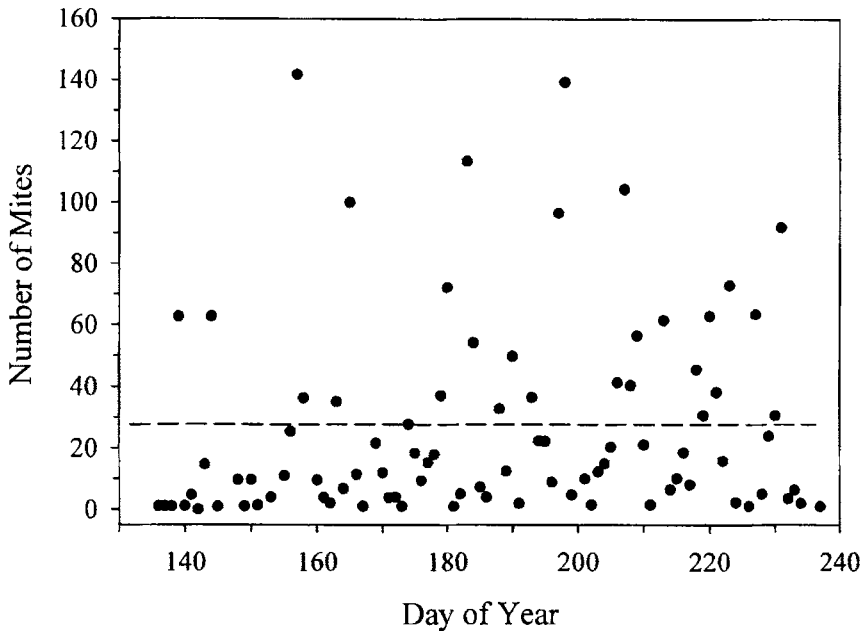


Figure 1. Number of water mites in bass stomachs (of those stomachs with mites) in Paul Lake from 1984 to 2006. Each data point represents the mean number of mites in bass collected on a particular day. The dashed line represents the 23-year average of number of mites (29.1) in bass (of those that contain mites).

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