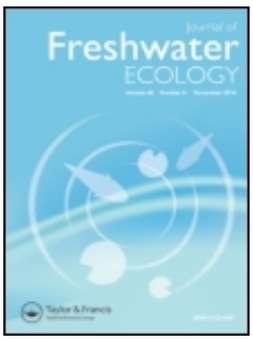

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NOTE

Foraging specialization by the opportunistic largemouth bass (*Micropterus salmoides*)

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The opportunistic foraging nature of largemouth bass (*Micropterus salmoides*) is thought to preclude it from specialization when prey resources are in abundance. Here, we describe largemouth bass foraging specialization on *Chaoborus* spp. *Chaoborus* spp. specialization was unexpected because largemouth bass is a diurnal littoral visual predator, whereas *Chaoborus* spp. occupy the surface waters of the pelagic zone at night and are energetically unfavorable. Largemouth bass foraging in the pelagic zone, determined by core body temperature, had significantly ($p < 0.001$) more *Chaoborus* spp. per gut (249.3) than littoral foragers (68.4). Individual largemouth bass diet consistency over time was greater than the diet consistency of random pairings, indicating that pelagically oriented largemouth bass specialize in *Chaoborus* spp. predation. This unusual individual foraging behavior is likely caused by heavy intraspecific competition, which leads some fish to acquire new prey search images due to prey resource limitation.

Keywords: largemouth bass (*Micropterus salmoides*); foraging specialization; *Chaoborus* spp.; foraging strategy

Introduction

In dense monospecific populations, intra-specific competition may cause generalist species to develop specialized foraging habits. For example, during periods of heavy intra-specific competition, the generalist rock bass (*Ambloplites rupestris*) and smallmouth bass (*Micropterus dolomieu*) can exhibit specialist planktivore diets normally thought to be energetically unfavorable (Clady 1974; Fischer and Frost 1997). Largemouth bass (*Micropterus salmoides*), a keystone predator in many small temperate lakes, does not typically display this specialist behavior (Clady 1974; Hodgson and Kitchell 1987; Hodgson et al. 1993). Largemouth bass is an opportunistic forager that consumes a wide variety of prey items including fish, aquatic insects, terrestrial mammals, and birds (Bryan and Larkin 1972; Hodgson and Kitchell 1987; Hodgson et al. 1993, 2006, 2008; Schindler et al. 1997; Hodgson and Hodgson 2000). This opportunistic nature is thought to preclude it from developing a specialist diet.

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We examined foraging by largemouth bass on the phantom midge (*Chaoborus* spp.) in a small temperate lake. *Chaoborus* spp. are characteristic of the pelagic zone. In order to forage on *Chaoborus* spp., largemouth bass must leave its preferred habitat in the littoral zone and forage in the open water (Soranno et al. 1993). We compared the diet composition of littoral and pelagically oriented largemouth bass, as determined by core body temperature, to evaluate largemouth bass specialization on *Chaoborus* spp.

Materials and methods

Largemouth bass were sampled from the littoral and pelagic zones once weekly from late May to August 2006 in Paul Lake, Michigan (46.252719°N, 86.504085°W). Paul Lake is a small (2.2 ha), deep (maximum depth = 19 m, mean depth = 6 m) kettle lake that has remained unexploited by angling since 1971 (Carpenter et al. 1987). Paul Lake contains a small population of pumpkinseed (*Lepomis gibbosus*) but largemouth bass is the dominant fish species present and has a historic population density between 307.8 and 412.4 fish ha^{-1}; in 2006, the largemouth bass density was 353.5 fish ha^{-1}. The littoral zone was sampled by angling near the shoreline at depths <2 m. The pelagic zone was sampled in the metalimnion (depth = 5–6 m) by angling with weighted lines. Over half of the fish were captured in the pelagic zone.

In total, 107 individual largemouth bass >150 mm total length (TL) were captured; largemouth bass <150 mm TL were not included in this study. There were 283 recaptures. The fish were individually floy-tagged so that recaptured fish could be identified. Core body temperature (T_B; to the nearest 0.1°C) was determined by inserting an electronic thermometer probe into the stomach of each fish immediately upon capture. The T_B of each fish was used to determine whether it had been foraging in the deep or shallow waters prior to capture.

Stomach contents from individual largemouth bass were collected by gastric lavage shortly after capture and preserved in 95% ethyl alcohol. Diet items were identified to the lowest relevant taxon following the taxonomy of Hilsenhoff (1975) and then separated into 19 categories according to Schindler et al. (1997). We calculated the percentage of each food type of the total number of food items by all fish in the sample (% number), and percentage of wet mass (% mass) following Hodgson et al. (1993).

Diet consistency is a statistical measure of similarity between the diets of an individual fish (identified by floy tags) caught on different sample dates. The diet consistency was calculated as

$$P(x)_{t1t2} = \left[\sum (\text{minimum } p_{i\,t1}, p_{i\,t2})\right] 100,$$

where $p_{i\,t1}$ and $p_{i\,t2}$ are the proportions of diet category i in the diet at times t_1 and t_2, respectively, for individual x (Schindler et al. 1997). Diet consistency was calculated for every consecutive capture of each individual fish, as well as for 1000 random pairs of separate fish caught on different sample dates. A high level of diet consistency reflects two very similar diets and therefore similar foraging strategies (Schindler et al. 1997). If the observed diet consistency is greater than the random pairings, there is an indication that some individuals have developed a specialized diet and foraging strategy. We tested for difference in mean number of *Chaoborus* spp. per gut of pelagic- and littoral-oriented largemouth bass using a two sample *t*-test.

Results and discussion

Overall, *Chaoborus* spp. were abundant in largemouth bass diets but make up a small proportion of diets by weight (Table 1). The number of *Chaoborus* spp. in the diets of largemouth bass with T_B between 17°C and 20°C varied between a mean of 180.5 (SE = 51.0) per diet at $T_B = 18$°C to a mean of 418.3 (SE = 72.3) per diet at $T_B = 17$°C (Figure 1). Largemouth bass with T_B between 21°C and 29°C averaged <100 *Chaoborus* spp. per diet. Pelagic foragers had significantly ($p < 0.001$) more phantom midges per gut (mean = 249.3) than littoral foragers (mean = 68.4). Diet consistency among recaptured fish (42.6%; SE = 2.4) during the summer of 2006 was greater than the diet consistency among randomly chosen pairs of fish (35.6%; SE = 0.1). This result indicates that individual fish were consistently foraging on the same diet items. This high diet consistency supports the hypothesis of specialization through the development of new prey search images (Schindler et al. 1997). In largemouth bass, this is consistent with behavioral changes due to intraspecific competition from Paul Lake's high population density (Schindler et al. 1997). Taken together, these results suggest that largemouth bass specialize in Paul Lake and that pelagic-oriented individuals specialize on *Chaoborus* spp.

Table 1. Diet composition of largemouth bass by percentage of numbers and percentage of weight.

Diet item	Number (%)	Weight (%)
Pelagic invertebrates	29.06	0.77
Chaoborus spp.	62.27	6.02
Benthic invertebrates	7.78	25.25
Fish	0.82	57.77
Other	0.06	10.18

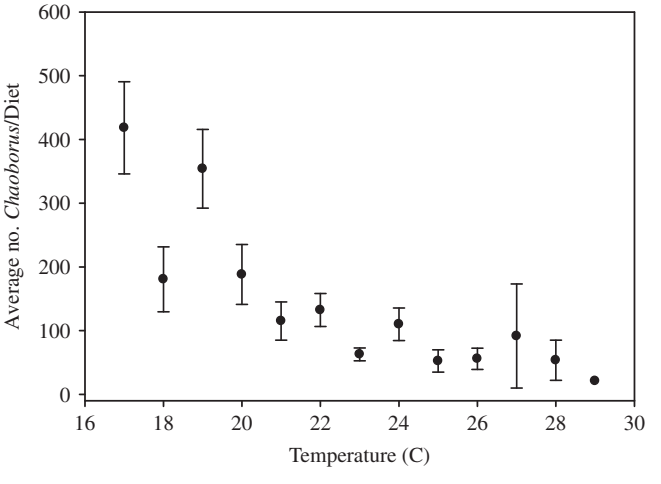

Figure 1. Average number of *Chaoborus* spp. in the diet of largemouth bass at various T_B intervals (to the nearest 0.1°C).

Schindler et al. (1997) found that the average diet consistency between random pairs of fish in Paul Lake was 17.3% (SE = 1.0) over the 10-year period from 1984 to 1993, much lower than the diet consistency we observed between random pairs in 2006. The observed (not random pairs) diet consistency values for the 10-year period were all less than the random pair value for 2006. This discrepancy is likely because Schindler et al. (1997) only sampled fish from the littoral zone. Pelagically oriented plankton specialists would not be included in their sample as they were in our study. Thus, the values reported by Schindler et al. (1997) may not be representative of the whole-lake population of largemouth bass and may underestimate the degree of foraging specialization in the whole population by excluding *Chaoborus* spp. specialists. Similarly, Hodgson et al. (1993) found that *Chaoborus* spp. are relatively unimportant in the diet of largemouth bass as judged by a small index of relative importance value compared to other diet items. However, the fish sampled by Hodgson et al. (1993) also came only from littoral sampling and thus their index of relative importance values may not adequately represent the importance of *Chaoborus* spp. to pelagically oriented largemouth bass. By purposely including fish foraging in the pelagic zone, the same place where the largemouth bass specializing on *Chaoborus* spp. forage, our study captured more specialists than Schindler et al. (1997) and Hodgson et al. (1993). These specialist largemouth bass had very similar diets due to their similar foraging patterns, and consequently a greater diet consistency was reflected throughout the entire sample.

In Paul Lake, we observed that >50% of bass were consistently feeding in the pelagic zone on *Chaoborus* spp., which supports our hypothesis that Paul Lake contains largemouth bass that are *Chaoborus* spp. specialists. These largemouth bass had higher than average numbers of *Chaoborus* spp. per diet each time they were sampled and a more consistent diet composition than expected without specialization. Paul Lake largemouth bass were specializing on a lower cost-benefit prey item due to the extremely high population density, which creates a scarcity of high cost-benefit prey items.

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