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BIOENERGETICS AND TROPHIC DYNAMICS

Changes in Lake Whitefish Diet in Lake Michigan, 1998-2001

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Abstract

Lake whitefish (*Coregonus clupeaformis*) were collected for diet analysis from Michigan's waters of Lake Michigan during 1998-2001. When the benthic amphipod *Diporeia* spp. was available, it was an important item in the diets of small (<430 mm) and large (>430 mm) lake whitefish. In southern Lake Michigan, the most-common prey consumed in the absence of *Diporeia* spp. included zebra mussels (*Dreissena polymorpha*), gastropods, chironomids, and *Mysis relicta*. In northern regions of the lake, alternative prey included chironomids, isopods, *Bythotrephes*, and fish. Following the decline of *Diporeia* spp. in southeastern Lake Michigan between 1998 and 2001, their contribution to the diet of small lake whitefish fell from 57% to 1% (dry weight). The contribution of *Diporeia* spp. to the diet was similar for small fish captured in nearshore (9-30 m) and offshore (31-46 m) waters. *Mysis* were more common in the diets of fish collected at offshore stations whereas

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chironomids and zebra mussels were more common in fish from nearshore stations.

Introduction

Recent declines in condition and growth of lake whitefish (*Coregonus clupeaformis*, hereafter, whitefish) in the Great Lakes have been attributed to a number of factors (Hoyle et al. 1999; Pothoven et al. 2001), including declines in the abundance of their benthic prey *Diporeia* spp. (hereafter, diporeia as a common name), increased consumption of zebra mussels (*Dreissena polymorpha*), and density-dependent factors.

There is little information on the diet of whitefish even though the species has long been a mainstay of the commercial fishery. Available information indicates that the diet of whitefish in the Great Lakes historically consisted of amphipods, chironomids, gastropods, and *Mysis* (Ihssen et al. 1981; Jude et al. 1981). More-recent data indicate that the decline of diporeia and the proliferation of zebra mussels may have resulted in changes in the diet of whitefish (Hoyle et al. 1999; Pothoven et al. 2001).

The objective of this study was to evaluate the diet of whitefish in Lake Michigan and to determine future research needs.

Methods

Whitefish were collected from 13 stations located in seven of ten Lake Michigan whitefish management zones (WFM) (Fig. 1). Whitefish were collected in water 9- to 46-m deep using monofilament gillnets (6.4- to 17.8-cm stretched mesh) and a 7.6-m semi-balloon, 4-seam bottom trawl (13-mm stretched-mesh cod-liner). Sampling took place during April-October 1999-2001, but most fish (73%) were collected in the spring (April-June). Whitefish were also collected during 1998 from WFM-08. No fish were collected for diet analysis from either WFM-00, WFM-01, or WFM-03.

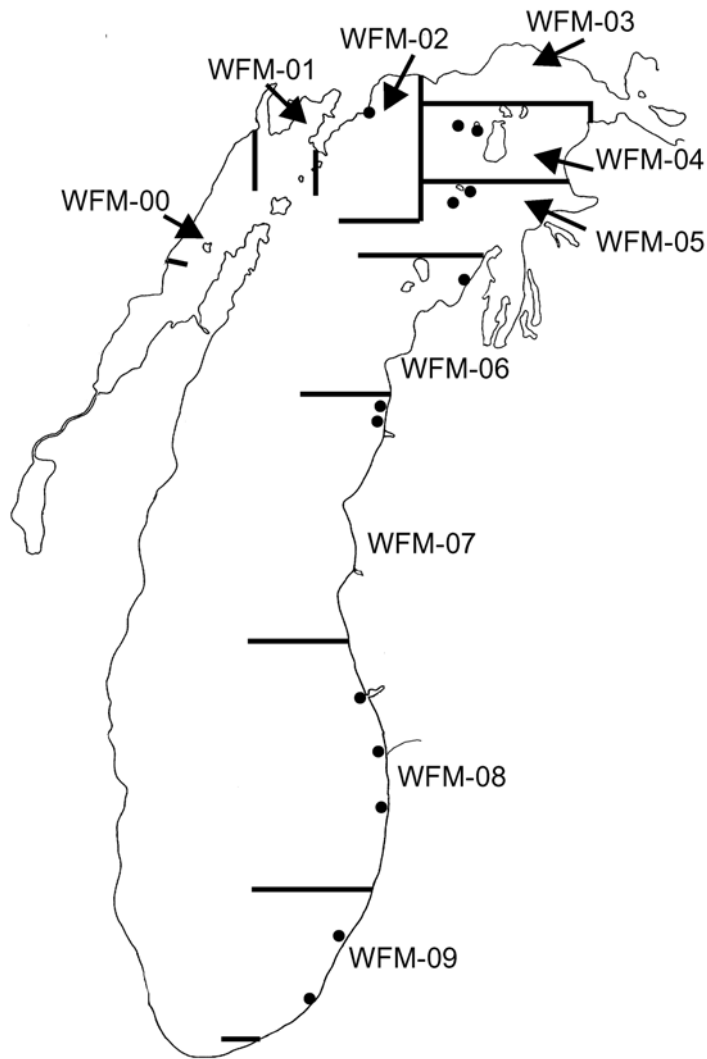


Fig. 1. Location of stations (•) and whitefish management zones (WFM) where whitefish were collected for diet analyses, 1998-2001.

All fish were weighed and measured, and stomachs (esophagus to pyloric caeca) were removed and frozen. In the laboratory, stomachs were dissected and prey items were identified and counted. Approximately 25% of stomachs were empty and were not included in subsequent analyses. Lengths of whole prey were measured using a computer image-analysis system. Length-weight regressions from the literature were used to compute the mean individual weight for each prey type (Johnson and Brinkhurst 1971; Nalepa and Quigley 1980; Smock 1980; Shea and Makarewicz 1989; Makarewicz and Jones 1990; Prejs et al. 1990; T. Nalepa, Great Lakes Environmental Research Laboratory, 2205 Commonwealth Blvd., Ann Arbor, MI, 48105, personal communication). Dry weights of partially digested prey were assumed to be equal to the mean weight of measured prey of the same species. Microzooplankton (Copepoda, Cladocera) were added to a known volume of water and subsampled with a Hensen-Stemple pipette. For species that were not measured, total counts were multiplied by representative dry weights (Hawkins and Evans 1979; Nalepa and Quigley 1980) and summed to obtain biomass.

Diets were shown as the percent of the total calculated stomach-content dry weight for fish from each management zone, year, or depth zone. Diet composition was determined separately for small (<430 mm) and large (>430 mm) whitefish. These size-classes were chosen based on the legal size limit for whitefish in the commercial fishery. Results were summarized for each management zone to detect regional differences. Stomach-content data from WFM-02, WFM-04, and WFM-05 were combined because of the small sample sizes in these northern zones. Fish from WFM-08 were used to examine temporal changes in diet during 1998-2001. Diets were also compared for fish collected from nearshore (9-30 m) stations vs. offshore (31-46 m) stations.

Results and Discussion

Based on data collected during 1998-2001, the diets of whitefish were variable throughout Lake Michigan. In some areas, the regional differences in diet reflected regional differences in the density of diporeia. The diet of large whitefish consisted mainly (95%) of age-0 alewife (*Alosa pseudoharengus*) in the northernmost zones (WFM-02, WFM-04, and WFM-05) of Lake Michigan (Table 1). The invertebrates *Bythotrephes* (3%) and diporeia (1%) were also found but were at very low levels. In WFM-06, the diet of large whitefish consisted of isopods (61%) and chironomids (37%) (Table 1). No diporeia were found in whitefish stomachs in WFM-06. The density of diporeia in the lake was relatively low ($<1,000\cdot\text{m}^{-2}$) in WFM-02, WFM-04, WFM-05, and WFM-06 during this study (T. Nalepa, Great Lakes Environmental Research Laboratory, 2205 Commonwealth Blvd., Ann Arbor, MI, 48105, personal communication).

Table 1. Percent of total dry weight for diet items of small (<430-mm TL) and large (>430-mm TL) whitefish collected from WFMs in Lake Michigan, 1999-2001 (WFM-08, 1998-2001). *N* = number of whitefish used for analyses. Length = mean length (mm TL) of fish used for analyses.

Diet item	Small fish			Large fish				
	WFM -07	WFM-08	WFM-09	WFM-02, 04, 05	WFM-06	WFM-07	WFM-08	WFM-09
Diporeia	53	38	0	1	0	84	19	0
Chironomidae	9	31	38	<1	37	6	6	10
<i>Dreissena polymorpha</i>	1	6	17	<1	<1	<1	23	35
<i>Mysis relicta</i>	20	9	0	0	0	5	26	<1
Sphaeriidae	1	6	8	<1	<1	2	5	5
Gastropoda	0	4	31	<1	1	<1	13	48
Isopoda	2	<1	0	<1	61	1	<1	0
<i>Bythotrephes</i>	0	1	0	3	0	0	1	0
Fish	14	1	0	95	0	2	0	0
Other	<1	5	6	0	1	1	6	1
<i>N</i>	20	215	28	29	14	41	90	32
Length	376	349	367	629	495	492	467	455

Diporeia accounted for 53% and 84% of the diet of small and large whitefish, respectively, in WFM-07 (Table 1). Whitefish were only collected from the northern portion of WFM-07 where the density of diporeia was 2,000-3,000·m⁻² in 2000. The density of diporeia in WFM-07 had not been particularly high (3,000-4,000·m⁻²) relative to other regions in the lake in 1994-1995 (Nalepa et al. 2000). Zebra mussels were not an important component of the diet of whitefish in either the northern or central management zones.

In WFM-08, the diet of whitefish consisted of several prey items including diporeia, chironomids, *Mysis*, zebra mussels, and gastropods (Table 1). Drastic declines of diporeia occurred in WFM-08 during 1998-99, although the species persisted at densities of 5,500·m⁻² in the northern portion of this management zone (Pothoven et al. 2001). Sufficient numbers of whitefish were caught in WFM-08 to examine temporal changes in diet relative to the declines of diporeia between 1998 and 2001. By 2000, the densities of diporeia ranged from near zero to 1,000·m⁻² (Pothoven et al. 2001). In 1998, the diet of small whitefish in WFM-08 consisted mainly of diporeia (57%) and chironomids (20%) (Table 2). Following the decline of diporeia in 1999, the diet of small whitefish consisted mainly of chironomids (66%). The percentage of diporeia in the diet increased from 7% in 1999 to 33% in 2000. The contribution of *Mysis* increased from 0-3% to 30% between 1998-99 and 2000. Diporeia had declined to very low densities in WFM-08 in 2001. In that year, chironomids (34%) and *Mysis* (35%) were the main prey consumed by small whitefish, while diporeia comprised 1% of the diet.

Table 2. Percent of total dry weight for diet items of small (<430-mm TL) and large (>430-mm TL) whitefish collected from WFM-08 in Lake Michigan, 1998-2001. *N* = number of whitefish used for analyses.

Diet item	Small fish				Large fish	
	1998	1999	2000	2001	2000	2001
Diporeia	57	7	33	1	31	<1
Chironomidae	20	66	15	34	5	3
<i>Dreissena polymorpha</i>	9	2	1	3	5	47
<i>Mysis relicta</i>	3	0	30	35	42	1
Sphaeriidae	4	2	12	13	7	1
Gastropoda	3	7	<1	7	<1	39
Ostracoda	0	6	<1	<1	<1	<1
<i>Bythotrephes</i>	<1	0	6	0	2	0
Zooplankton	<1	8	<1	0	0	<1
Other	2	1	3	5	6	9
<i>N</i>	78	62	42	33	45	38
Mean length	355	290	397	387	465	471

Information on the diet of large whitefish in WFM-08 was available only for 2000-2001. In 2000, the diet of large whitefish was similar to that of small whitefish and comprised mainly diporeia (31%) and *Mysis* (42%) (Table 2). In 2001, the diet of large whitefish consisted mostly of zebra mussels (47%) and gastropods (39%).

The increases in diporeia and *Mysis* in the diet in 2000 in WFM-08 could reflect differences in sampling depths among years. In 2000, 42% of the fish in WFM-08 were collected from a 45-m depth, whereas fish were collected from shallower depths (<35 m) in other years. Diporeia and *Mysis* are generally more abundant offshore (Nalepa et al. 2000; Pothoven et al. 2000). *Mysis*, however, were found in stomachs of fish collected from water as shallow as 15 m in April 2000. *Mysis* continued to be an important prey for small whitefish in 2001.

In the southernmost management zone (WFM-09), diets consisted mainly of gastropods and chironomids (for small fish) and zebra mussels and gastropods (for large fish) (Table 1). Diporeia began to decline in WFM-09 in 1992 and were virtually absent by 1997 (Nalepa et al. 2005).

Whitefish may be adapted to consume hard-shelled prey items such as zebra mussels because they historically have consumed molluscs such as gastropods. In the absence of a high-energy prey source (for example, diporeia), however, the consumption of mainly hard-shelled prey could have detrimental bioenergetic consequences for whitefish (Ihssen et al. 1981; French and Bur 1996; Pothoven et al. 2001). Additionally, alternative prey (for example, chironomids) may not be sufficiently abundant to sustain whitefish (Pothoven et al. 2001).

One could expect that the diet of whitefish in northern Lake Michigan will become similar to that in southern regions as diporeia continues to decline and zebra and quagga (*D. bugensis*) mussels increase throughout the lake. On the other hand, diet patterns in the northern regions may not become similar to those observed in the southern regions if prey other than zebra mussels are available. For example, in this study, large whitefish were observed to become piscivorous and/or consume isopods in northern regions of the lake where diporeia were already scarce.

Diets of whitefish collected from nearshore (<30 m) and offshore (31-46 m) areas differed (Table 3). The contribution of diporeia was generally similar between depth zones for small whitefish. Chironomids and zebra mussels were more common in the diets of whitefish from nearshore stations relative to offshore stations, while the contribution of *Mysis* to the diet was much higher offshore. Studies of whitefish diets need to account for differences in depth distribution. Seasonal movements of whitefish between nearshore and offshore areas further complicate such analyses. Additionally, whitefish may be moving farther offshore in the Great Lakes. Although diporeia and other large prey such as *Mysis* are more abundant offshore, bioenergetic costs associated with feeding in deeper, colder water may be high (O’Gorman et al. 2000).

Table 3. Percent of total dry weight for diet items of small (<430-mm TL) and large (>430-mm TL) whitefish collected from nearshore (<30 m) and offshore (31-46 m) zones in Lake Michigan, 1998-2001. *N* = number of lake whitefish used for analyses.

Diet item	Small fish		Large fish	
	Nearshore	Offshore	Nearshore	Offshore
Diporeia	38	35	5	35
Chironomidae	34	9	16	1
<i>Dreissena polymorpha</i>	8	<1	22	<1
<i>Mysis relicta</i>	4	29	<1	58
Sphaeriidae	4	7	2	3
Gastropoda	4	0	4	<1
<i>Bythotrephes</i>	<1	4	<1	2
Fish	0	14	46	0
Other	7	2	4	<1
<i>N</i>	165	39	35	25

There was little correlation between the length of whitefish and the lengths of diporeia ($r^2 = 0.02$) and zebra mussels ($r^2 = 0.10$) that were consumed. The modal length of diporeia in the diet of whitefish was 6-8 mm, indicating that whitefish consumed mostly adults. In contrast, the modal length of zebra mussels (2-4 mm) in the diet of whitefish indicated that the smallest zebra mussels were consumed.

Our data indicate that if diporeia are available, they are an important prey item for both small and large whitefish. *Diporeia* were already beginning to decline at the start of this study (1998), so the species historically may have been an even more important prey. On the other hand, the importance of diporeia in this study could also be somewhat inflated because most fish were collected in the spring. Other fish (for example, bloater (*Coregonus hoyi*) and alewife) are also dependent upon diporeia as a food source during the spring (Rand et al. 1995).

Future research is needed in several areas to understand how changes in the food web of the Great Lakes might affect the diet of whitefish. First, researchers need to have a better understanding of the age-specific and seasonal patterns in diets. Second, researchers need to conduct bioenergetics analyses to understand how the ration of whitefish could be changing. Studies on feeding behavior are needed to understand how prey type, density, and predator size affect foraging patterns and success. Information on diets of whitefish from areas where diporeia remain abundant would provide better insight into the importance of this species as a prey resource.

Acknowledgements

Funding and field support were provided by the Great Lakes Environmental Research Laboratory, National Oceanic and Atmospheric Administration; Michigan Department of Natural Resources; and the Great Lakes Fishery Trust. Contribution 1261 of the Great Lakes Environmental Research Laboratory, NOAA, Ann Arbor, MI, 48105.

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