

## Assessing feeding competition between lake whitefish *Coregonus clupeaformis* and round whitefish *Prosopium cylindraceum*

Andrew MACPHERSON<sup>1,2</sup>, John A. HOLMES<sup>1,3</sup>, Andrew M. MUIR<sup>1,4</sup>,  
David L. G. NOAKES<sup>1,5\*</sup>

<sup>1</sup> Axelrod Institute of Ichthyology and Department of Zoology, University of Guelph, Guelph, Ontario, N1G 2W1, Canada

<sup>2</sup> Faculty of Architecture, Landscape and Design, University of Toronto, 230 College Street, Toronto, M5T 1R2, Canada

<sup>3</sup> Pacific Biological Station, Fisheries and Oceans Canada, Nanaimo, British Columbia V9T 6N7, Canada

<sup>4</sup> Golder Associates, Yellowknife, NWT, A1C 1T0, Canada

<sup>5</sup> Fisheries and Wildlife Department and Oregon Hatchery Research Center, Oregon State University, Corvallis, Oregon 97331-3803 USA

**Abstract** We collected lake whitefish *Coregonus clupeaformis* and round whitefish *Prosopium cylindraceum* from the main basin of Lake Huron and Georgian Bay in the Laurentian Great Lakes of North America to investigate details of diet and feeding tactics of these species in different seasons. Lake whitefish supports important commercial fisheries in Lake Huron and both species make use of habitats near the Bruce Nuclear Power Development, on the eastern shore of Lake Huron. Most fish of both species showed generalist feeding behavior, but some lake whitefish appeared to show specialist prey selection. The invasive spiny water flea *Bythotrephes longimanus* was an important component of the diet of both species. There was considerable dietary overlap between the whitefish species, but the ecological implications of these dietary overlaps are mitigated by the fact that dominant prey species differed in most seasons. We conclude that the potential for ecologically significant interactions between lake whitefish and round whitefish resulting from competition for similar benthic food resources in the main basin of Lake Huron is probably low [*Current Zoology* 56 (1): 109–117 2010].

**Key words** Lake Huron, Diet, Feeding tactics, Seasonal variation, Invasive species

Lake whitefish *Coregonus clupeaformis* and round whitefish *Prosopium cylindraceum* are important members of a related Holarctic species complex found in northern post-glacial lakes, rivers, and brackish waters. These species are sympatric in many large North American lakes. Lake whitefish attain larger maximum body sizes, are longer-lived and are most common at depths ranging from 18 to 90 meters (Reighard, 1910; Rawson, 1951; Qadri, 1961; Cucin and Regier, 1966). Round whitefish are smaller and occupy a moderate range of depths between 6 and 36 meters (Rawson, 1951; Bailey, 1963). Both species are benthivores. Diet studies have demonstrated that amphipods (e.g., *Diporeia* spp.), gastropods and aquatic insects, especially chironomid larvae and pupae, are common prey items in their diets (Rawson, 1951; Qadri, 1961; Watson, 1963; Normandeau, 1969; Armstrong et al., 1977; Pothoven and Nalepa, 2006). The majority of these studies have con-

cluded that both species are opportunistic feeders since the relative importance of the major prey and other taxa in the diet tend to differ among populations and species. Although there is overlap in the depth ranges preferred by these whitefish species and diet studies demonstrate that adult diets may overlap in sympatric situations, at least in terms of the major prey taxa consumed, the potential for significant ecological interactions is not known.

Lake whitefish support commercial and aboriginal fisheries in most of the large North American lakes that they inhabit. Historically this species has been the dominant species in fisheries in the Laurentian Great Lakes (Fleischer, 1992). Lake whitefish harvests in lakes Ontario, Michigan and especially Huron now dominate fisheries in the Great Lakes. At present more than 90% of the whitefish harvest in Lake Huron is in the main basin. While lake whitefish populations in

---

Received Jan. 05, 2010; accepted Jan. 31, 2009

\* Corresponding author. E-mail: David.Noakes@oregonstate.edu

© 2010 *Current Zoology*

Lake Huron remain abundant, populations in Lake Ontario have declined dramatically in recent years, apparently as a result of changes in their prey base (Bernard et al., 2009). Round whitefish has been of some commercial importance in the upper Great Lakes (e.g., Bailey, 1963), but production was low relative to lake whitefish and currently there are no fisheries targeting round whitefish.

The effects of invasive non-native species on food webs and fisheries in the Great Lakes are increasing, and are of increasing concern. Recent declines in the abundance of lake whitefish in eastern Lake Ontario have been linked to dreissenid mussel colonization of the lake (Hoyle et al., 1999), through hypothesized adverse effects on *Diporeia* spp. in the lake (Dermott, 2001; Bernard et al., 2009). *Diporeia* spp. are the preferred prey species of both whitefish species, and there is widespread evidence of catastrophic declines in those prey populations (Dermott, 2001; Watkins et al., 2007). Colonization of dreissenid mussels has also been implicated in declines of *Diporeia* spp. in Lake Michigan since 1993 (Landrum et al., 2000), and concomitant declines in lake whitefish body condition and growth (Pothoven et al., 2001). If the linkages in these food webs are as tight as hypothesized, then the recent invasion of the non-native amphipod *Echinogammarus ischnus* and the non-native spiny water flea *Bythotrephes longimanus* in lakes Michigan and Huron (Dermott et al., 1998; Nalepa et al., 2001) may contribute to continued reductions in lake whitefish productivity in these lakes. However, alternative hypotheses, such as density-dependence responses in whitefish populations have not yet been tested as causal mechanisms for the declines in whitefish populations since the early 1990's.

Lake whitefish and round whitefish occur sympatrically in Lake Huron (Scott and Crossman, 1973), and they are found together in the waters around Douglas Point, on the eastern shore of the main basin (Fig. 1). In this study we examined the diets of both these species at this location by identifying stomach contents from fish collected at different seasons over the course of one year. We used those data to investigate seasonal variation in diet in each species, to describe foraging tactics of the two species, and to estimate the dietary overlap between species across seasons. Testing of the hypothesis of dietary overlap and trophic competition is critical, in light of invasive non-native species, changes in prey species, potential impacts of industrial development and the importance of whitefish to aboriginal and commercial

harvests in the Great Lakes.

## 1 Materials and Methods

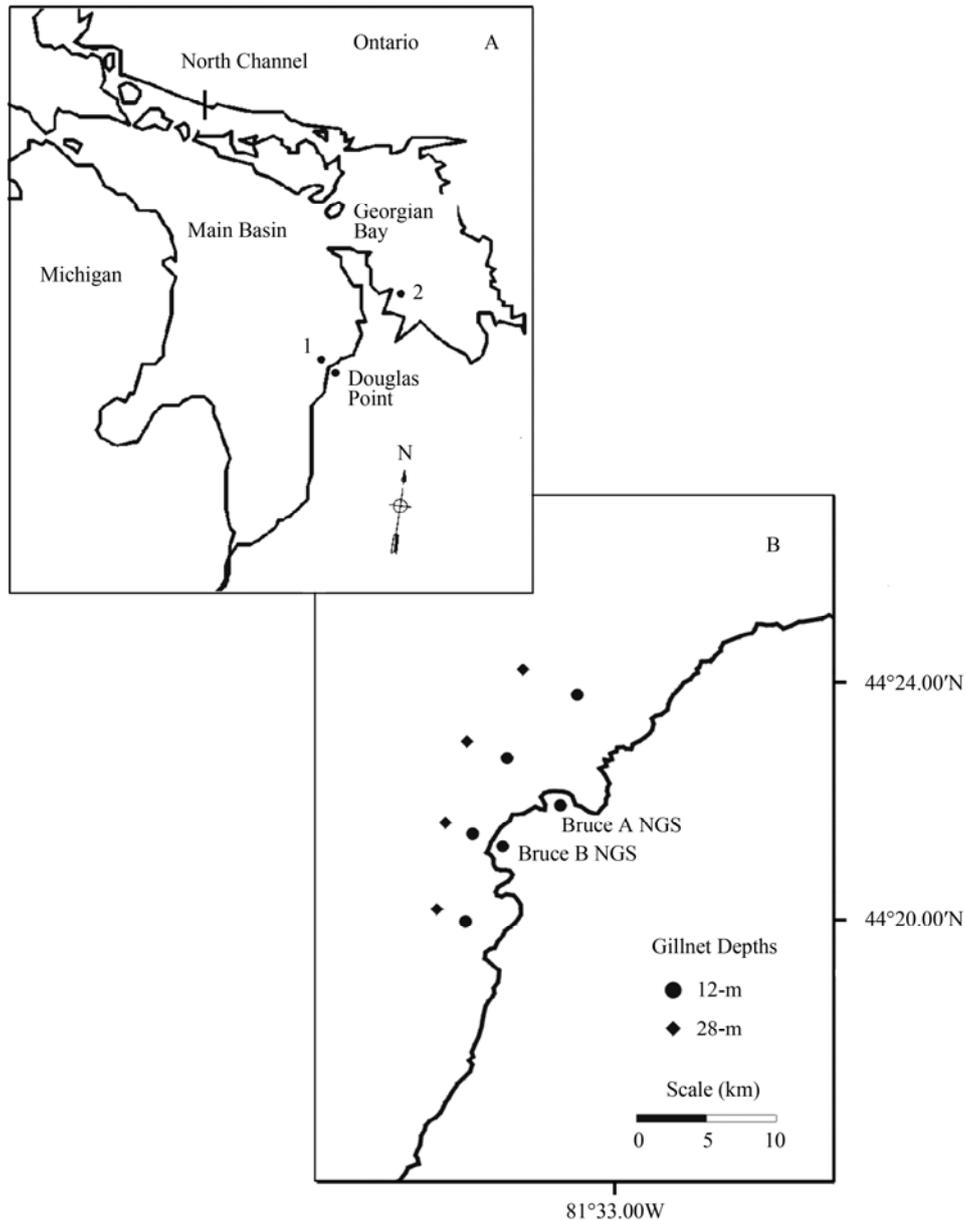
We collected lake whitefish and round whitefish in May and November 2000 from eight sites around Douglas Point (Fig. 1) with 274 m long gillnets. Each net consisted of a 91.5 m panel of 6.67 or 6.83 mm mesh and a 183 m panel of 11.4 or 12.1 mm mesh (all mesh sizes are stretched measurements). The larger mesh panels are standard commercial gear for harvesting lake whitefish in Lake Huron and the smaller mesh panel is used commercially to harvest chubs (*Coregonus* spp.) and yellow perch *Perca flavescens* but is effective in catching round whitefish as by-catch. The nets were set overnight at 12 and 28 m water depths to validate fish species and size composition for hydroacoustic surveys conducted as part of a study on the impacts of the Bruce Nuclear Power Development on whitefish in Lake Huron. An additional sample of lake whitefish was collected from Georgian Bay, a different basin of Lake Huron, on 17 October 2000 at two locations (44° 55.00'N, 81° 07.07'W and 44° 55.81'N, 81° 05.65'W) to provide a spatial contrast for diet and feeding tactics.

Fish were sexed by macroscopic examination of gonads and the fork length ( $\pm 1$  mm) and wet mass ( $\pm 1$  g) of each fish were measured and recorded prior to preservation. Fish captured in May were preserved in 10% buffered formalin for 3 months prior to removing digestive tracts (from the esophagus to the anus) in August 2000. Individual intestinal tracts were stored in 70% ethanol until we examined the contents. The November collection of fish were fixed in 10% formalin for one week and then transferred to 70% ethanol prior to study of stomach contents. Fish captured in October 2000 were frozen ( $-20^{\circ}\text{C}$ ) until we removed the digestive tracts and examined stomach contents. Fulton's condition index was calculated based on the fresh lengths of weights of each fish using the formula

$$K = W/L^3 \times 10^5,$$

where  $W$  is wet mass (g) and  $L$  is fork length (mm). Length and weight data are expressed as mean  $\pm$  SE.

The esophagus and stomach of each fish were detached from the intestine immediately anterior to the pyloric caecae and the contents were flushed with distilled water into pre-weighed aluminum trays and dried at  $60^{\circ}\text{C}$  for 48 hours. Dried prey items were sorted and counted with binocular dissecting microscopes (50 $\times$  magnification) and were identified to the lowest possible taxonomic level using keys in Pennak (1978) and Merritt and Cummins (1996). Prey were subsampled



**Fig. 1** Map of Lake Huron showing (A) sample sites in the main basin at Douglas Point (1) and in Georgian Bay (2), and (B) gillnet locations at Douglas Point

volumetrically for enumeration if large numbers of a particular prey item were observed and subsample counts were expanded to the total volume of the sample. Recognizable morphological features, such as head capsules of chironomids or caudal spines of *Bythotrephes longimanus* were used to identify and enumerate partially digested or fragmented prey items.

We used frequency of occurrence and prey-specific volume to describe the diets of the two species of whitefish. Frequency of occurrence records the proportion of fish with food in their digestive tracts that had eaten a particular prey item (Amundsen et al., 1996).

Prey-specific volume refers to the proportion of the total digestive tract volume that a prey taxon comprises in those fish in which that prey occurs (Amundsen et al., 1996). These diet metrics provide qualitative indications of the presence/absence of a prey type in the diet and a representative measure of bulk applicable to all prey taxa (Hyslop, 1980), respectively.

Estimates of prey-specific volume were standardized with a point system (Wilhelm et al., 1999) to remove bias associated with spatial and temporal variations in fish body size. For each fish with food in its digestive tract the contents were assigned a total of 10 points.

Each prey taxon in the gut contents of a fish was assigned a value from 1 to 10 points, depending on its contribution to the total volume of food, regardless of the size of the digestive tract or total volume of the contents. The points for each food category in a sample of  $N$  fish are summed and expressed as a percentage of the total points ( $N \times 10$ ) for the sample. Wilhelm et al. (1999) reported that this method produced reliable prey volume data for bull trout *Salvelinus confluentus* when compared to direct measurements of prey volume consumed. Prey-specific volume was then calculated as

$$P_i = (\sum S_i / \sum S_{ii}) \times 100$$

where  $P_i$  is prey-specific volume of prey  $i$ ,  $S_i$  is the volume of the digestive tract contents (in points) comprised of prey  $i$  in an individual fish, and  $S_{ii}$  is the total digestive tract content in those fish with prey  $i$  in their digestive tract at time  $t$ .

We used a graphical analysis to assess feeding strategies and the importance of prey in the diet of each species (Amundsen et al., 1996). Prey-specific volume is plotted against frequency of occurrence and information on the importance of prey taxa in the diet and feeding tactic is provided by the distribution of points along the axes and diagonals. The importance of prey in the diet increases along the diagonal from lower left (the origin) to upper right, with rare prey items plotted in the lower left corner and dominant prey items located in the upper right corner. The feeding strategy is inferred by the distribution of points along the vertical axis. Prey points in the upper half of the plot are indicative of specialization, whereas those points in the lower half of the plot indicate generalized feeding.

Dietary overlap between lake whitefish and round whitefish was estimated using Schoener's (1970) similarity index (a),

$$a = 1 - 0.5 (\sum |P_{xi} - P_{yi}|),$$

where  $P_{xi}$  and  $P_{yi}$  are the points proportions of food category  $i$ , in the diets of lake whitefish  $x$  and round whitefish  $y$ . A value of  $a = 0$  is interpreted as no overlap, versus  $a = 1$  which means the diets overlap completely. Overlap values of  $a = 0.6$  or greater are considered to be biologically significant in terms of prey items consumed by groups  $x$  and  $y$  (Wallace, 1981). We used the Schoener index because it is one of the few diet overlap indices that performs adequately when information on prey availability to a species is not available (Wallace, 1981), as is the case in our study.

## 2 Results

A total of 66 lake whitefish and 55 round whitefish

were collected for this study. Round whitefish were not collected at the Georgian Bay site in October and only a small sample ( $n = 5$ ) of lake whitefish was obtained at Douglas Point in May. Lake whitefish collected from Georgian Bay in October were significantly longer [fork length (FL):  $526.4 \pm 11.35$  mm, Analysis of Variance,  $F_{1,58} = 9.735$ ,  $P = 0.003$ ] and heavier ( $2011 \pm 186.71$  g; Analysis of variance  $F_{1,58} = 10.04$ ,  $P = 0.003$ ) than lake whitefish collected at Douglas Point in November (FL:  $486.6 \pm 5.89$  mm;  $1454.4 \pm 50.75$  g), although fish from these sites were in similar condition (Georgian Bay median = 1.325, range 1.13 – 1.88; Douglas Point median = 1.30, range 0.90 – 1.47). Round whitefish collected in May were significantly smaller (FL:  $352.6 \pm 5.05$  mm; Analysis of Variance,  $F_{1,55} = 13.08$ ,  $P = 0.0007$ ) and lighter ( $488.7 \pm 21.12$  g; Analysis of Variance,  $F_{1,55} = 19.58$ ,  $P = 0.00005$ ) than fish sampled in November (FL -  $375.5 \pm 4.83$  mm;  $607.5 \pm 24.03$ g), but the condition of fish in May (median 1.10, range 0.88 – 1.40) did not differ substantially from the condition of fish in November (median 1.11, range 0.86 – 1.73). Lake whitefish collected in May ( $n = 5$ ) averaged  $484.0 \pm 8.05$  mm (FL) and  $1546.3 \pm 150.22$  g in weight. Neither whitefish species exhibited sexual dimorphism in fork length (lake whitefish,  $F_{2,58} = 1.18$ ,  $P = 0.31$ ; round whitefish,  $F_{1,55} = 0.63$ ,  $P = 0.43$ ), or mass (lake whitefish,  $F_{2,58} = 2.48$ ,  $P = 0.09$ ; round whitefish,  $F_{1,55} = 1.71$ ,  $P = 0.19$ ).

The diets of 80 fish with food in their stomachs ( $n = 41$  fish with empty stomachs; Table 1) were analyzed. The proportion of whitefish with empty stomachs in May was low (13% of round whitefish) but increased to 29% of round whitefish and 53% of lake whitefish sampled in November (Table 1). Sex ratios of captured fish did not differ significantly from unity with the exception of the round whitefish sample in May, which was skewed strongly in favor of females (0.194 male: 0.806 female). Our sampling protocol did not differ substantially between months, so bias favoring the collection of females in May is unlikely.

The diets of lake whitefish and round whitefish sampled in the early spring and late fall of 2000 consisted of 14 prey groups (Table 1). The stomachs of both lake whitefish and round whitefish at Douglas Point contained mainly gastropods (Physidae and Lymnaeidae) and the isopod *Ascellus racovitzai* in May and the spiny water flea *Bythotrephes longimanus* in November. Spiny water flea accounted for 32.9% and 90.6% of the food volume in non-empty stomachs of lake whitefish and round whitefish in November, respectively (Table

**Table 1** Mean prey volumes (in points) in the stomachs of Lake whitefish and Round whitefish with food collected in the main basin of Lake Huron and Georgian Bay in May, October, and November 2000. A blank space indicates that the prey item was absent in the fishes examined. *n* is the number of stomachs containing food

	Lake whitefish			Round whitefish	
	May <sup>A</sup>	Oct <sup>B</sup>	Nov <sup>A</sup>	May <sup>A</sup>	Nov <sup>A</sup>
Total number of stomachs examined, <i>N</i>	5	22	36	31	24
Total number with food, <i>n</i>	5	14	17	27	17
Amphipoda		0.7			
<i>B. longimanus</i>		41.4	14.7		42.4
<i>B. longimanus</i> embryos		38.6	18.2		48.2
Cambaridae		0.7	5.9	2.2	1.8
Isopoda- <i>Ascellus racovitzai</i>	28.0		4.1	29.6	
Chironomidae (midges)			5.9		
Ephemeroptera (mayflies)			4.1		1.2
Hymenoptera		7.1	1.8	27.4	4.7
Lymnaeidae (pond snails)				9.6	
Physidae (pouch snails)	8.0		7.1	2.2	
Unidentified Gastropoda (snails)	36.0		8.8	25.3	0.6
Pelecypoda (clams, mussels)	4.0		7.6		
Hirudinia (leeches)	24.0				
Fish		8.6	21.8		0.6

A: Collected at Douglas Point, main basin of Lake Huron. B: Collected in Georgian Bay, Lake Huron.

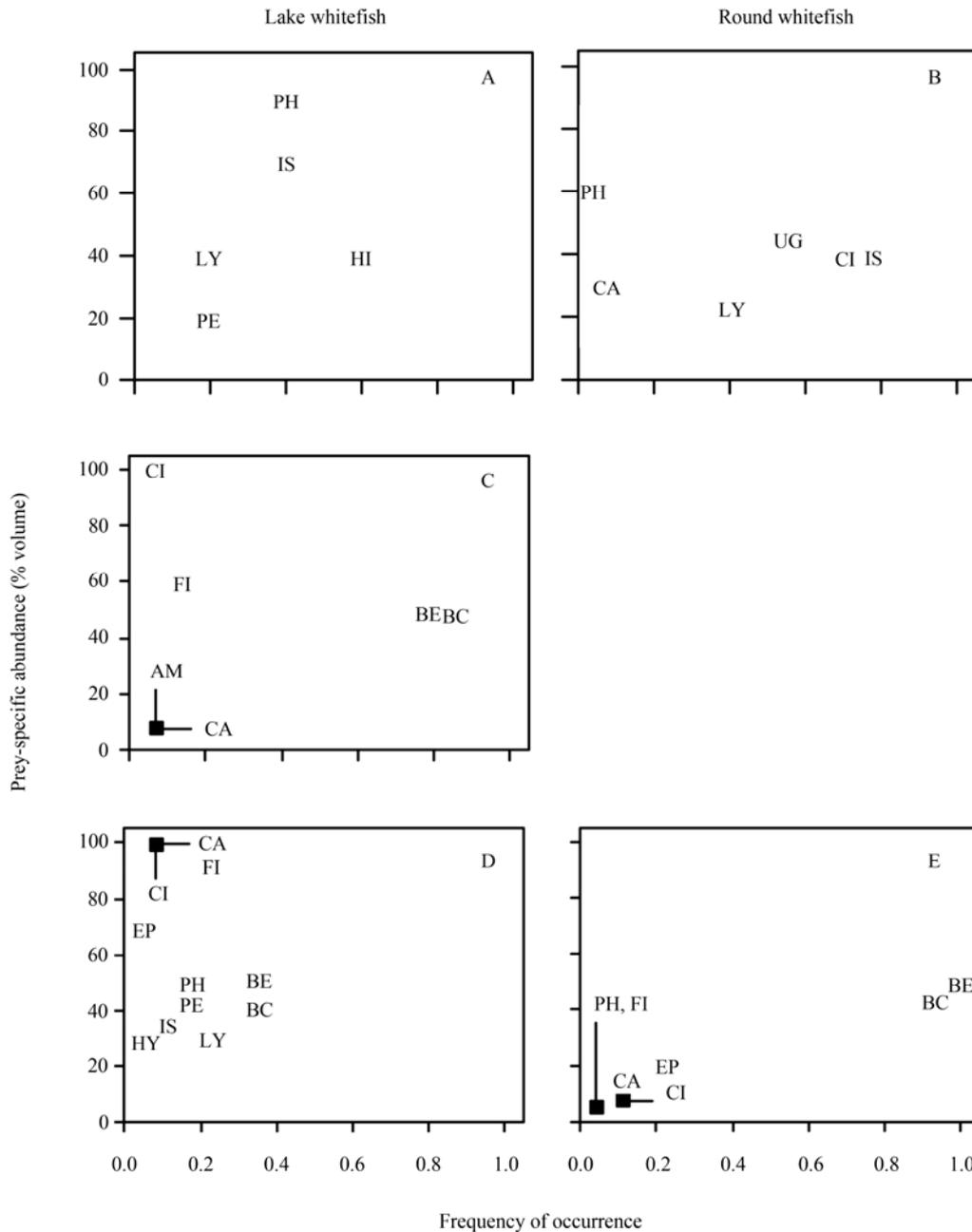
1). Leeches were found in 60% of the lake whitefish stomachs with food, accounting for 24.0% of the volume in May whereas chironomid larvae, although a common prey item (70% of stomachs with food), constituted only 5.9% of the volume of gut contents in round whitefish in May. Amphipods were not enumerated in the diet of either species at Douglas Point in May or November and were only a minor component of the diet of lake whitefish in October (0.7% of the volume). Lake whitefish collected in October from Georgian Bay had fed more heavily on spiny water fleas (80% of the food volume in stomachs with food) and had a narrower range of prey items in their stomachs compared to lake whitefish collected in November from Douglas Point (Table 1).

Both lake whitefish and round whitefish exhibited generalized patterns of feeding on most prey groups in May 2000 based on plots of prey-specific volume and frequency of occurrence (Fig. 2). Although some lake whitefish appear to be specialized on pond snails and isopods in May (Fig. 2A), these results are probably sensitive to the small sample size ( $n = 5$ ). Round whitefish had generalized feeding patterns in November (Fig. 2E), although spiny water fleas were consumed by all fish and accounted for 45% – 48% of the gut contents in November 2000. The remaining prey groups in the No-

vember diet never accounted for more than 20% of prey abundance, and were never found in fewer than 20% of the non-empty guts (Fig. 2E). Although spiny water fleas were also the most frequent prey in lake whitefish diets in November (Fig. 2D), feeding patterns varied from specialization on chironomids, crayfish, fish and mayflies by some individuals to generalized feeding on pond snails, pouch snails, clams, isopods and Hymenoptera larvae.

Spiny water fleas were a predominant component in the diet of Georgian Bay lake whitefish (Fig. 2C), but not in the November diet of lake whitefish from Douglas Point (Fig. 2D). However, lake whitefish from both localities exhibited generalized feeding behavior on spiny water fleas and other prey items. Some fish from Georgian Bay specialized on chironomid larvae and fish, which is consistent with the November sample from Douglas Point. Diet diversity was narrower in the Georgian Bay fish in October, compared to the Douglas Point fish in November.

Schoener's similarity index (*a*) values were 0.401 in May and 0.415 in November, corresponding to a diet overlap of about 40% in each month. The November similarity value is likely more reliable than the May value, which may be biased by the small lake whitefish sample ( $n = 5$ ). These index values show that both



**Fig. 2** Plots of prey-specific volume against frequency of occurrence of prey items in the stomachs of lake whitefish and round whitefish in May (A, B), October (C), and November (D, E) 2000

Prey items identified are: AM – Amphipoda (scuds); BC – *Bythotrephes longimanus* (Cladocera); BE – *B. longimanus* embryos; CA – Cambaridae (crayfish); CI – chironomids (Diptera); EP – Ephemeroptera (mayflies); FI – fishes; HI – Hirudinia; HY – Hymenoptera; IS – Isopoda (*Ascellus racovitzai*); LY – Lymnaeidae (pond snails); PE – Pelycypoda (clams); PH – Physidae (pouch snails); UG – unidentified gastropods (snails).

species fed on a similar range of prey, but the dominant prey taxa in their diets differed (Table 2).

Both lake whitefish and round whitefish showed seasonal variation in diet at Douglas Point. Lake whitefish switched from a diet of mollusks, isopods and leeches to a broader range of prey in November, but no clearly dominant prey species was evident. In contrast, the diet of round whitefish was dominated by chironomids, iso-

pods and gastropods in May, and even more heavily dominated by spiny water flea in November.

A small number ( $n = 7$ ) of lake whitefish collected in November 2000 showed specialized feeding on mayflies, fish, crayfish and chironomid larvae (Fig. 2D). The majority of these individuals ( $n = 4$ ) specialized on small fish that on average constituted 92.5% of stomach volumes.

### 3 Discussion

Stomach contents analysis provides evidence of the most recent, short-term feeding activities and prey preferences of fishes (Winemiller, 2007). Our study demonstrates plasticity in the feeding behavior of lake whitefish sampled at Douglas Point. While the majority of whitefish exhibited a generalized feeding strategy on a range of prey, a small number collected in November 2000 showed specialized feeding patterns, particularly on small fish. Lake whitefish are neither obligate generalists nor specialists, but may be able to alter their feeding tactics depending upon prey availability. Similar feeding plasticity has been reported in salmonine fishes (Bryan and Larkin, 1972) and European whitefish (Amundsen et al., 2004) that are capable of concentrating on specific prey when local concentrations of prey are discovered by individual fish. In contrast to the mixture of strategies exhibited by lake whitefish, round whitefish were predominately generalized feeders since most of the prey points on the feeding tactic plots (Fig. 2) are in the lower parts of these plots, i.e., most prey represent <50% of the volume of stomach contents. Other studies of whitefish diets in North America have concluded that both these whitefish species are opportunistic feeders, consuming prey species in proportion to their availability (density) in lacustrine environments, rather than selecting specific organisms (Hart, 1931; Qadri, 1961; Watson, 1963; Normandeau, 1969; Bidgood, 1973; Armstrong et al., 1977). However, most of these diet studies (including the present study) document only what was consumed by the fish captured, they do not provide data on food availability, i.e., water column and benthic organisms were not sampled concurrently with the fish. In most cases these studies are in large lakes, where it would be logistically very difficult, if not impossible, to adequately sample potential benthic and planktonic prey organisms.

The proportion of lake whitefish and round whitefish at Douglas Point with empty stomachs increased from May to November as expected because spawning occurs in the November-December period and both species are reported to cease feeding during spawning (Scott and Crossman, 1973). The finding that approximately 50% of the stomachs from the November lake whitefish sample contained food was higher than we expected at this time (Table 1). We believe that these fish were still staging prior to spawning, and thus they continued to feed during this period. Hart (1931) reported the same observation in his study of lake whitefish in the Bay of

Quinte, Lake Ontario. The relatively low number of empty stomachs in round whitefish in November may be a result of the fact that this species spawns later than lake whitefish (Scott and Crossman, 1973) and so reproductive staging was probably not as far advanced as in lake whitefish.

Amphipods were not a large component of the diet of either lake whitefish or round whitefish caught near Douglas Point in May or November. This finding contrasts with previous whitefish diet studies (Rawson, 1951; Qadri, 1961; Watson, 1963; Normandeau, 1969; Armstrong et al., 1977) in which amphipods such as *Diporeia* spp. typically comprised more than 40% of the prey items consumed by either species when that prey was available in the deep waters inhabited by whitefish during the summer (June – September). Historically, *Diporeia* spp. were the dominant species in offshore benthic communities in the Great Lakes (e.g., Nalepa, 1989), and provided a link between pelagic production and upper trophic levels (Nalepa et al., 2000). The absence of amphipods in the diets of the lake whitefish and round whitefish we sampled could be consistent with declines in *Diporeia* spp. abundance observed elsewhere in the Great Lakes (e.g., Landrum et al., 2000; Dermott, 2001; Pothoven et al., 2001) or, alternatively, since *Diporeia* spp. inhabit the deep waters of the Great Lakes, their absence in the fish we collected near Douglas Point is consistent with the normal seasonal variation in diet associated with migratory movements of these species into shallower waters in the fall. We cannot definitively interpret the absence of amphipods at present because we did not sample fish in the summer months and because we did not sample benthic macro-invertebrates independently so we do not have prey density data from which to establish availability to fish.

We sampled in the spring and fall of 2000 because we expected that we would find both species inshore at these times. Knowledge of the movement patterns of populations of both species, and how those movements would influence diet is not available for either species. The inshore movement of lake whitefish in the spring is hypothesized to be related to feeding in Great Lakes populations (Reighard, 1910; Koelz, 1929; Hart, 1931). Similar spring movements of lake whitefish populations have not been reported in other large lakes (e.g., Great Slave Lake, Rawson, 1951) nor small inland lakes (e.g., Lake Simcoe, Semple, 1968) either because this behavior does not occur or because the appropriate studies have not been conducted. Our small sample of lake whitefish in May ( $n = 5$ ) may be related either to limited

onshore movement in the main basin of Lake Huron during the spring or our sampling occurred after lake whitefish returned offshore. The inshore movement of both whitefish species in the fall is related to spawning activity (Scott and Crossman, 1973). Sex ratios of our samples did not provide any evidence of sex-specific behavior in either species in the fall, but the dominance of female round whitefish in the spring sample may indicate sexual differences in foraging behavior near Douglas Point.

We found that diet overlap between lake whitefish and round whitefish at Douglas Point was about 40%, based on Schoener's similarity index (Schoener, 1970). This value is less than 0.60, which is considered a threshold for the development of significant ecological interactions between species (Schoener, 1970). Although our diet analyses show that a similar range of prey species is consumed by each whitefish species, dominant prey in the diet of lake whitefish and round whitefish differ in May and especially in November, lessening the impact, if any, of each species on the other. These prey differences may be related to the habitats used by each species. Round whitefish were more common than lake whitefish in nets set at 12 m depths, whereas lake whitefish were more common than round whitefish in nets set at 28 m depths. The bottom at 12 m depths around Douglas Point is dominated by boulders and cobble whereas at 28 m depth the bottom is smoother with patches of sand and depositional areas between pockets of boulders and cobble (Carey, 1984; Balesic and Martin, 1987). We conclude that the potential for inter-specific competition among populations of lake whitefish and round whitefish in the main basin of Lake Huron at the beginning (spring) and end (fall) of the main growing season (summer – not sampled) is low.

**Acknowledgements** This study is part of a large, collaborative project (Whitefish Interactions with Nuclear Generating Stations, WINGS) involving the Chippewas of Nawash First Nation, the University of Guelph, Bruce Power, Inc. and Ontario Power Generation. We thank Nawash Fisheries Assessment personnel Jay Jones, Frank Soloman Jr. and Jim Ashkewe for their assistance in collecting, measuring and removing fish stomachs. Gillnet tug and gear were subcontracted from McLay Marine Enterprise, Ltd. and Jim and Frank McLay, Southampton, Ontario. We thank Steve Crawford and Don Wismer for constructive comments on earlier drafts of this manuscript, and in various aspects of data preparation and analyses. We dedicate this manuscript to Bev Scott, a pioneer in the study of whitefish biology, still active in fish biology in his 92<sup>nd</sup> year.

## References

- Amundsen PA, Gabler HM, Staldvik FJ, 1996. A new approach to graphical analysis of feeding strategy from stomach contents data: Modification of the Costello (1990) method. *J. Fish Biol.* 48: 607–614.
- Amundsen PA, Knudsen R, Klemetsen A, Kristoffersen R, 2004. Resource competition and interactive segregation between sympatric whitefish morphs. *Annal. Zool. Fenn.* 41: 301–307.
- Armstrong JW, Liston CR, Tack PI, Anderson RC, 1977. Age, growth, maturity, and seasonal food habits of round whitefish *Prosopium cylindraceum* in Lake Michigan near Luddington, Michigan. *Trans Am. Fish. Soc.* 106: 151–155.
- Bailey MM, 1963. Age, growth and maturity of round whitefish of the Apostle Islands and Isle Royale regions, Lake Superior. *U. S. Fish Wild. Serv. Fish. Bull.* 63: 63–75.
- Balesic H, Martin ID, 1987. Bruce GS 'B' preoperational biological study summary, 1979 to 1983. *Ont. Hydro Res. Div., Toronto, Ontario. Rep 87-185-K.*
- Bernard A, Ferguson MM, Noakes DLG, Morrison BJ, Wilson CC, 2009. How different is different? Defining units for management and conservation in a problematic exploited species. *Can. J. Fish. Aquat. Sci.* 66: 1617–1630.
- Bidgood BF, 1973. Divergent growth in two lake whitefish *Coregonus clupeaformis* populations. *J. Fish. Res. Board Can.* 30: 1683–1696.
- Bryan JE, Larkin PA, 1972. Food specialization by individual trout. *J. Fish. Res. Board Can.* 29: 1615–1624.
- Carey WE, 1984. Bruce Nuclear Power Development (BNPD) post-operational aquatic studies summary 1979 to 1981. *Ont. Hydro Res. Div., Toronto, Ontario. Rep. 84-47-K.*
- Cucin D, Regier HA, 1966. Dynamics and exploitation of lake whitefish in southern Georgian Bay. *J. Fish. Res. Board Can.* 23: 221–274.
- Dermott R, 2001. Sudden disappearance of the amphipod *Diporeia* from eastern Lake Ontario, 1993-1995. *J. Great Lakes Res.* 27: 423–433.
- Dermott R, Witt J, Um YM, and Gonzalez M, 1998. Distribution of the Ponto-Caspian amphipod *Echinogammarus ischnus* in the Great Lakes and replacement of native *Gammarus fasciatus*. *J. Great Lakes Res.* 24: 442–452.
- Fleischer GW, 1992. Status of coregonine fishes in the Laurentian Great Lakes. *Pol. Arch. Hydrobiol.* 39: 247–259.
- Hart JL, 1931. The growth of the whitefish *Coregonus clupeaformis* (Mitchill). *Contrib. Can. Fish. Biol.* 17: 411–429.
- Hoyle JA, Schaner T, Casselman JM, Dermott R, 1999. Changes in lake whitefish *Coregonus clupeaformis* stocks in eastern Lake Ontario following *Dreissena* mussel invasion. *Great Lakes Res. Rev.* 4: 5–10.
- Hyslop EJ, 1980. Stomach content analysis: A review of methods and their application. *J. Fish Biol.* 17: 411–429.
- Koelz W, 1929. Coregonid fishes of the Great Lakes. *U. S. Bur. Fish. Bull.* 43: 297–643.
- Landrum PF, Gossiaux DC, Nalepa TF, Fanslow DL, 2000. Evaluation of Lake Michigan sediment for causes of the disappearance of *Diporeia* spp. in southern Lake Michigan. *J. Great Lakes Res.* 26: 402–407.
- Merritt RW, Cummins KW, 1996. *An Introduction to the Aquatic Insects of North America*. 3<sup>rd</sup> Edition. Dubuque, Iowa: Kendall/Hunt Publ.
- Nalepa TF, 1989. Estimates of macroinvertebrate biomass in Lake

- Michigan. *J. Great Lakes Res.* 15: 437–443.
- Nalepa TF, Hartson DJ, Buchanan J, Cavaletto JF, Lang GA et al., 2000. Spatial variation in density, mean size and physiological condition of the Holarctic amphipod *Diporeia* spp. in Lake Michigan. *Fresh. Biol.* 43: 107–119.
- Nalepa TF, Schlosser DW, Hondrop SA, Fanslow DL, Tuchman ML et al., 2001. First finding of the amphipod *Echinogammarus ischnus* and the mussel *Dreissena bugensis* in Lake Michigan. *J. Great Lakes Res.* 27: 384–391.
- Normandeau DA, 1969. Life history and ecology of the round whitefish *Prosopium cylindraceum* (Pallas), of Newfound Lake, Bristol, New Hampshire. *Trans. Am. Fish. Soc.* 98: 7–13.
- Pennak RW, 1978. Fresh-water invertebrates of the United States. 2<sup>nd</sup> Edition. New York: Wiley and Sons.
- Pothoven SA, Nalepa TF, 2006. Feeding ecology of lake whitefish in Lake Huron. *J. Great Lakes Res.* 32: 489–501.
- Pothoven SA, Nalepa TF, Schneeberger PJ, Brandt SB, 2001. Changes in diet and body condition of lake whitefish in southern Lake Michigan associated with changes in benthos. *N. Am. J. Fish. Manage.* 21: 876–883.
- Qadri SU, 1961. Food and distribution of lake whitefish in Lac la Ronge, Saskatchewan. *Trans. Am. Fish. Soc.* 90: 303–307.
- Rawson DS, 1951. Studies of the fish of Great Slave Lake. *J. Fish. Res. Board Can.* 8: 207–240.
- Reighard P, 1910. A plan for promoting the whitefish production of the Great Lakes. *Bull. Bur. Fish.* 28 (Part 1): 643–695.
- Schoener TW, 1970. Non-synchronous spatial overlap of lizards in patchy habitats. *Ecology* 51: 408–418.
- Scott WB, Crossman EJ, 1973. Freshwater fishes of Canada. Ottawa, Ontario: Fish. Res. Board Can. Bulletin 184.
- Semple JR, 1968. Taxonomic and ecological characteristics of lake whitefish *Coregonus clupeaformis* (Mitchill) in Lake Simcoe. M. Sc. thesis, Univ. Guelph, Guelph, Ontario, Canada.
- Wallace RK Jr, 1981. An assessment of diet-overlap indices. *Trans. Am. Fish. Soc.* 110: 72–76.
- Watkins JM, Dermott R, Lozano SJ, Mills EL, Rudstam LG, et al., 2007. Evidence for remote effects of dreissenid mussels on the amphipod *Diporeia*: Analysis of Lake Ontario benthic surveys, 1972–2003. *J. Great Lakes Res.* 33: 642–657.
- Watson NHF, 1963. Summer food of lake whitefish *Coregonus clupeaformis* Michill from Heming Lake, Manitoba. *J. Fish. Res. Board Can.* 20: 279–286.
- Wilhelm FM, Parker BR, Schindler DW, Donald DB, 1999. Seasonal food habits of bull trout from a small alpine lake in the Canadian Rocky Mountains. *Trans. Am. Fish. Soc.* 128: 1176–1192.
- Winemiller KO, 2007. Interplay between scale, resolution, life history and food web properties. In: Rooney N, McCann KS, Noakes DLG ed. *From Energetics to Ecosystems: the Dynamics and Structure of Ecological Systems*. Dordrecht: Springer Academic Publishers, 101–126.