

NOTE

Preferred Temperatures of Juvenile Lake Whitefish

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ABSTRACT. Lake whitefish (*Coregonus clupeaformis*) supported valuable commercial fisheries in all of the Great Lakes until the 1950s to 1960s when their populations collapsed due to overfishing, pollution, and predation by the exotic sea lamprey (*Petromyzon marinus*). Reduction of these population stresses has permitted significant recovery of the lake whitefish in the upper three Great Lakes since the 1980s, and limited but encouraging recovery is now apparent in Lakes Erie and Ontario. In the present study the thermal preferences of age-0 and age-1 lake whitefish were measured in the laboratory to provide a basis for determining thermal habitat use by juvenile lake whitefish and thermal niche overlap with exotic fishes that might prey on them. Final thermal preferenda of young lake whitefish varied inversely with fish size ranging from 16.8°C for fish averaging 1.9 g to 15.6°C for age-1 fish averaging 3.9 g. Final thermal preferenda were in agreement with the limited published information on temperature selection of juvenile lake whitefish in the laboratory and on thermal habitat use by wild, free-ranging populations in the Great Lakes.

INDEX WORDS: Great Lakes, lake whitefish, temperature selection, thermal habitat.

INTRODUCTION

The lake whitefish (*Coregonus clupeaformis*) historically supported valuable commercial fisheries in all of the Great Lakes (Baldwin *et al.* 1979). However, most Great Lakes lake whitefish populations collapsed by the 1950s to 1960s because of overfishing, pollution, and predation by the sea lamprey (*Petromyzon marinus*). Sea lamprey control efforts, improvements in water quality, and the imposition of more effective controls on the commercial fishery have resulted in limited but encouraging recovery of the lake whitefish in Lakes Erie (Great Lakes Fishery Commission 1995) and Ontario (Ontario Ministry of Natural Resources and New York State Department of Environmental Conservation 1994) and significant recoveries in portions of Lakes Superior (Hansen 1994), Michigan (Schneeberger 1995, Lychwick *et al.* 1995), and Huron (Ebener *et*

al. 1995). These recoveries demonstrate that with proper management this resource can probably be restored to productive levels in most of the habitat it formerly occupied in the Great Lakes. The remaining major impediment to restoration is posed by recent introductions of exotic species that can prey on lake whitefish (DeSorcie and Edsall 1995, Jude *et al.* 1995). A simple, direct approach for evaluating the potential effect of these introductions is to compare the fundamental thermal niches, FTN, (Magnuson *et al.* 1979, Christie and Regier 1988) of the native and exotic species of interest to see if they can be expected to co-occur in space and time (Edsall *et al.* 1993). In the present study the preferred (selected) temperatures of age-0 and age-1 lake whitefish were measured in the laboratory and used to determine the final preferendum, which is the point at which the acclimation and selected temperatures are identical (Fry 1947). This information was then used to describe the FTN and probable thermal habitat use of wild, free-ranging populations of juvenile lake whitefish and their potential

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thermal niche overlap with introduced fishes that might prey on them.

METHODS

The lake whitefish used in this study were reared from two groups of eggs taken in consecutive years from spawning fish in northern Lake Michigan and Lake Huron. The eggs were fertilized in the field and incubated through hatching at the Great Lakes Science Center at temperatures mimicking nearshore overwinter water temperatures in northern Lake Michigan. The fish were then held at 8 to 11°C until they were acclimated for testing in this study.

Fish were placed in 190-L test tanks at about 10°C and the temperature was increased or decreased 1°C/day until the desired temperature (5, 10, 15, 20, or 25°C) was reached in each tank. The fish were then held at those temperatures for an additional 1 to 3 weeks before they were tested. Fish from the first group of eggs (group-1 fish) were tested at age 0 and age 1; those from the second group of eggs (group-2 fish) were tested only at age 0.

The preferred temperature tests were conducted in a vertical temperature gradient that was created in a circular 760-L fiberglass tank, 1.2 m in diameter and 0.8 m deep (Fig. 1). A heating element constructed of 23 m of 20-gauge, 1-cm-diameter aluminum tubing was positioned inside the tank against the side and rear walls of the tank. Hot tap water (about 73°C) flowed down through the loops of tubing to the bottom of the tank, then up through a vertical insulated section of tubing on the right side of the tank that extended over the rim of the tank and discharged into a floor drain. Well water chilled to about 2°C was supplied to the tank through a vertical, insulated section of 1-cm-diameter aluminum tubing on the right side of the tank. The tubing was connected to a closed loop of perforated aluminum tubing that lay on the bottom of the tank and slowly released the well water into the tank around the perimeter of the tank bottom. This water was slowly displaced upward and exited the tank at the surface through a standpipe at the center of the tank. Tap water and well water flow rates were monitored and regulated with valved flowmeters on the inlet lines to the tank. By regulating the flow rates of the tap water and well water, a linear, vertical temperature gradient could be established and maintained indefinitely in the tank.

Water temperature in the tank was measured with

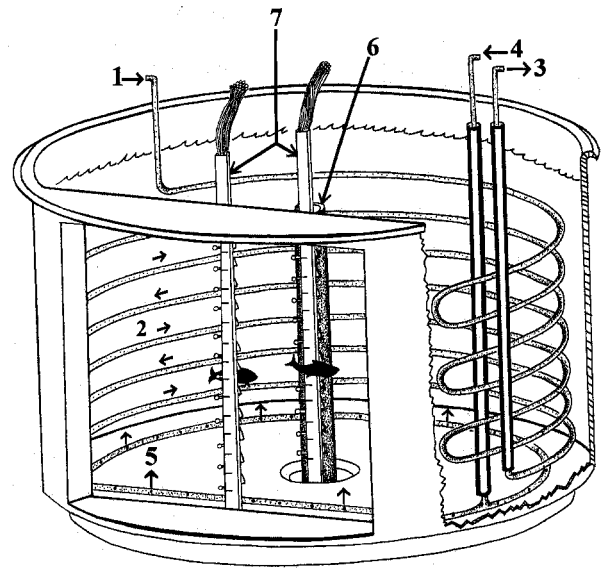


FIG. 1. Vertical thermal gradient tank showing (1) hot tap water inlet to heating coil, (2) arrows indicating direction of tap water flow in heating coil, (3) heating coil discharge, (4) well water inlet to tank, (5) loop of perforated tubing on tank bottom releasing well water into the tank, (6) well water outlet at tank surface via overflow standpipe, and (7) meter sticks each with 12 thermistors.

24 thermistors attached at 6-cm intervals to two plastic meter sticks (12 thermistors/meter stick) positioned vertically in the tank, one about 1 cm in front of the standpipe and the other about 1 cm behind the plate glass window. Temperature was recorded for each thermistor to the nearest 0.1°C at the rate of about 1 thermistor/sec.

Fish were not fed on the day they were tested. The test fish were removed from the acclimation tank with a dip net, placed in a beaker with water, and poured quickly through a 4-cm-diameter acrylic tube into the gradient tank. The lower end of the acrylic tube was submerged in the gradient tank to the depth where the water temperature was about the same as that in the acclimation tank from which the fish were taken. This procedure minimized the risk of heat shock posed by the acutely lethal temperatures at the surface in the gradient tank and helped the fish adjust quickly to conditions in the tank. Seven age-0 fish were tested at a time in the gradient tank because that was the minimum number that would school readily and swim continuously around the perimeter of the tank. The larger

age-1 fish were tested in groups of six because a group of that size performed well and because larger groups tended to disturb the temperature gradient.

Testing began when the fish were schooling and swimming continuously around the tank perimeter in an undisturbed manner; this usually occurred within 1 h after they were placed in the tank. An observer with a tape recorder vocally recorded the height (nearest 1.0 cm) above the tank bottom of the snout of each fish as the fish passed between the meter sticks and completed a circuit of the tank. Water temperature was also recorded on all 24 thermistors each time the school completed a circuit of the tank. Each group of fish was observed continuously for about 1 h until 100 selected temperature observations were recorded. The fish were then netted from the gradient tank, anaesthetized, and weighed as a group to the nearest 0.1 g. The temperature gradient was then allowed at least 12 h to reestablish before the next group of fish was placed in the tank.

RESULTS AND DISCUSSION

A few fish selected the highest or lowest temperature available to them, but all avoided temperatures higher than 26°C (Table 1), which borders the ultimate upper lethal temperature for the species (26.7°C; Edsall and Rottiers 1976). The modal temperatures for the 13 groups of fish shown in Table 1 varied from 9 to 23°C and were similar to (0.3°C higher to 1.6°C lower) the corresponding mean selected temperatures.

A plot of modal selected temperature against acclimation temperature for the fish acclimated to 15 and 20°C (Fig. 2) revealed that the final preferendum was highest for the age-0, group-2 fish (16.8°C), followed by the age-0, group-1 fish (15.9°C), and the age-1, group-1 fish (15.6°C). If the final preferendum is used as a surrogate for the optimum temperature for growth (Jobling 1981), then the FTN (optimum for growth +1°C, -3°C; Christie and Regier 1988) is 13.8 to 17.8°C for the age-0, group-2 fish; 12.9 to 16.9°C for the age-0, group-1 fish; and 12.6 to 16.6°C for the age-1, group-1 fish.

The one other published laboratory study of temperature selection by juvenile lake whitefish (Opuszynski 1974) tested age-0 fish (mean weight 1.1 to 1.7 g) and reported that their modal selected temperature was 17 to 18°C. These fish were held in an acclimation tank in which the temperature in-

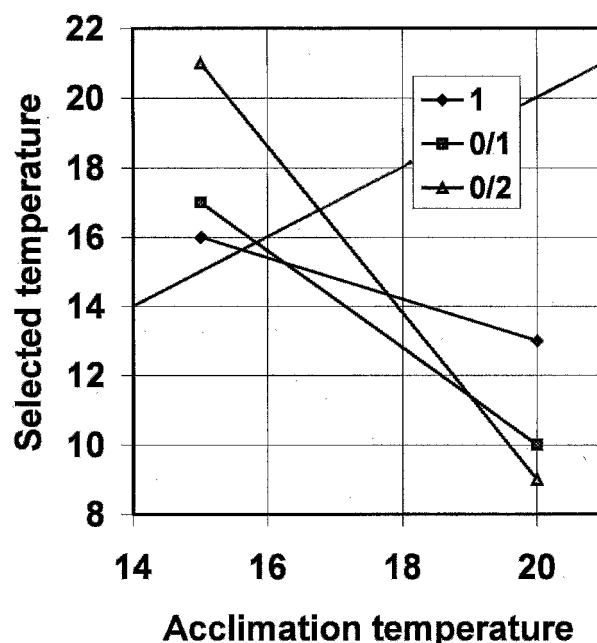


FIG. 2. Final thermal preferenda of age-0, group-2 (0/2), age-0, group-1 (0/1), and age 1, group-1 (1/1) lake whitefish tested in this study. The final preferendum for each of these three test groups is the point at which the modal selected temperature equals the acclimation temperature; this occurs at the intersection of the line of equality (shown passing through points 14,14 and 21,21) with the line connecting the modal selected temperatures for fish acclimated to 15 and 20°C in each of the three test groups.

creased gradually but irregularly from about 4°C in March to 16.1 to 16.4°C in early August when testing was done. Modal selected temperatures varied from 17 to 18°C, which was about 1 to 2 °C higher than their acclimation temperature. This suggests that the acclimation temperature at the time of testing was approaching the final preferendum. However, the absence of temperature selection data for groups of fish acclimated to temperatures several degrees higher and lower than 16°C precludes assignment of a final preferendum as in the present study (Fig. 2).

Opuszynski (1974) also tested age-1 lake whitefish (mean weight 5.7 g) and reported a final preferendum of 10°C. However, he expressed concern that this value was biased low because the test fish preferred to be associated with the tank bottom and exhibited a reluctance to move upward in the water column when the gradient in the tank was manipu-

TABLE 1. Selected temperatures of age-0 and age-1 lake whitefish. Frequency distribution modes shown in bold. All temperatures in °C. Age-0, group-2 fish were tested on 31 July–19 September; age-0, group-1 fish on 12 June–10 July; and age-1, group-1 fish on 10 March–25 April.

Selected temperature	Acclimation temperature by age and group												
	Age 0 (group 2)			Age 0 (group 1)					Age 1 (group 1)				
	10	15	20	5	10	15	20	25	5	10	15	20	25
26													
25	1	13			1	3							
24	59	16			7	5							
23	155	45		2	8	8			2	1			
22	66	49		15	38	20			7	8			
21	7	67		51	81	25			25	21			
20	12	50		70	83	38			40	64	2		1
19		30		99	63	46			83	97	10		1
18		15	1	38	4	44	4		89	7	19	4	1
17		6		20	1	48	11		36	2	43	2	2
16		2	3	3	3	39	6		12		53	11	3
15		1	2			12	26	2	6		39	12	1
14		1	7			7	28	4			17	46	3
13			17		1	1	33	3			6	71	2
12			25		1		36	14			10	32	2
11			51		2	2	42	39			1	17	3
10			56				46	88				3	3
9			139			1	33	60				1	172
8			1		6	1	33	57				1	6
7					2		2	34					
Range in gradient	27.7–6.9	26.0–7.6	25.2–7.8	27.6–6.3	26.9–6.3	28.0–6.7	28.8–26.9	28.2–6.4	26.8–7.2	26.9–7.1	26.9–7.5	26.7–7.7	25.9–8.2
Number of fish tested	21	21	21	21	21	21	21	21	18	12	12	12	12
Number of observations	300	299	302	298	301	300	300	301	300	200	200	200	200
Mean selected temperature	22.7	21.1	10.1	19.4	20	18.4	11.6	9.4	18.7	19.6	15.9	13.3	9.2

lated to move the isotherm they were occupying toward the tank surface. No such reluctance was seen in the present study as evidenced by the distributions in Table 1, which show that fish were at the tank bottom for only 38 of 3,501 observations.

The final preferenda for age-0 fish (Table 2) are in good agreement with each other and with that of the 3.9 g, age-1 fish, suggesting a final preferendum near 16 to 17°C (present study) or 17 to 18°C (Opuszynski 1974). In contrast, the final preferenda for the two groups of age-1 fish differed by almost 6°C. As noted above, this difference may reflect a final preferendum for Opuszynski's (1974) age-1 fish that is biased low because these fish exhibited

an affinity for the tank bottom. However, when the data are ordered by fish size, as in Table 2, they suggest strongly that the final preferendum is not a single fixed value for the species, but one that varies inversely with fish size (Table 2). The relation between fish size and final preferendum from Table 2 is described by;

$$\text{Final preferendum} = 20.212 - 1.614 \text{ fish size}, \quad (1)$$

where $r = 0.938$, $p = 0.05$, and $n = 3$).

The final preferenda determined in the present study for age-0 lake whitefish are in general agreement with the thermal habitat use information pub-

TABLE 2. Final preferenda of young lake whitefish^a.

Age (yrs)	Fish Group	Size (g)	Final preferendum (°C)	Test period	Source
0		1.1–1.7	17–18 ^b	5–7 Aug	Opuszynski (1974)
0	2	1.9	16.8	31 Jul–19 Aug	Present study
0	1	2.8	15.9	12 Jun–10 Jul	Present study
1	1	3.9	15.6	10 Mar–25 Apr	Present study
1		5.7	10	18–28 Mar	Opuszynski (1974)

^a Final preferendum after Fry (1947).

^b Estimated by inspection by source author.

lished for conspecifics of similar age in the Great Lakes. Newly hatched lake whitefish were pelagic and found near the shoreline in shallow water in the spring and early summer (Hart 1930, Faber 1970, Reckahn 1970, Hogman 1971). In South Bay, Lake Huron, when the temperature in the shoreline waters exceeded 17°C, young lake whitefish gradually moved to deeper offshore waters and became more strongly associated with the bottom (Reckahn 1970). Age-0 lake whitefish in South Bay occurred at the bottom at the 17°C isotherm in early July and August, moving gradually from a depth of about 12 m in early July to about 17 m in late August, as the thermocline was depressed by solar warming (Reckahn 1970). Published information on the thermal habitat use by age-1 fish is lacking but Table 2 suggests they select temperatures between 16 and 10°C.

Evidence of predation by exotic fishes on young lake whitefish in the Great Lakes is largely inferential. Introduced fishes, including the rainbow smelt (*Osmerus mordax*), alewife (*Alosa pseudoharengus*), and blueback herring (*Alosa aestivalis*) are piscivorous. Hogman (1971) found that adult alewives in the laboratory fed eagerly on lake whitefish larvae smaller than 17 to 18 mm, but ignored larger larvae and juveniles. Reckahn (1970) showed that in July and August juvenile lake whitefish in South Bay, Lake Huron occupied the metalimnion where alewife and rainbow smelt were in low abundance and posed little threat as competitors or predators.

The ruffe (*Gymnocephalus cernuus*), an exotic predator that is implicated in major declines in native coregonine populations in Europe (Pokrovskii 1961, Adams and Tippet 1991) and Russia (Pavlovsky and Sterligova 1987) was recently reported in northwestern Lake Huron where lake whitefish are abundant. The FTN of age-0 ruffe (18

to 22°C; Edsall *et al.* 1993) overlaps slightly with that of age-0 lake whitefish of about 1 g or smaller, indicating there is potential for ruffe to prey on them. The FTN of age-1 and older ruffe is unmeasured but probably is lower than that of the age-0 ruffe, suggesting the older ruffe could be expected to prey on age-0 lake whitefish until they grew to a size too large to be easily ingested by the ruffe.

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REFERENCES

- Adams, C.E., and Tippet, R. 1991. Powan, *Coregonus lavaretus* (L.), ova predation by newly introduced ruffe, *Gymnocephalus cernuus* (L.) in Loch Lomond, Scotland. *Aquacult. Fish.* 22:239–246.
- Baldwin, N.S., Saalfeld, R.W., Ross, M.A., and Buetner, H.J. 1979. *Commercial fish production in the Great Lakes*. Tech. Rep. 3, Great Lakes Fishery Commission, Ann Arbor, MI.
- Christie, G.C., and Regier, H.A. 1988. Measures of optimal thermal habitat and their relations to yields of four commercial fish species. *Can. J. Fish. Aquat. Sci.* 45:301–314.
- DeSorcie, T.J., and Edsall, T.A. 1995. Feeding rate of young-of-the-year ruffe on eggs of lake whitefish. *J. Freshwat. Ecol.* 10:225–229.
- Ebener, M.P., Johnson, J.E., Reid, D.M., Payne, N.P., Argyle, R.A., Wright, G.M., Krueger, K., Baker, J.P., and Weise, J. 1995. In *Status and future of Lake Huron fish communities*. In *The Lake Huron ecosystem: ecology, fisheries, and management*, eds. M. Munawar, T. Edsall, and J. Leach, pp. 125–169. Eco-

- vision World Monograph Series, S.P.B. Academic Publishing, The Netherlands.
- Edsall, T.A., and Rottiers, D.V. 1976. Temperature tolerance of young-of-the-year lake whitefish, *Coregonus clupeaformis*. *J. Fish. Res. Board Can.* 33:177–180.
- . Selgeby, J.H., DeSorcie, T.J., and French, J.R.P. III. 1993. Growth-temperature relation of young-of-the-year ruffe. *J. Great Lakes Res.* 19:630–633.
- Faber, D.J. 1970. Ecological observations on newly hatched lake whitefish in South Bay, Lake Huron. In *Biology of Coregonid Fishes*, eds. C.C. Lindsey and C.S. Woods, pp. 481–500. University of Manitoba Press, Winnipeg.
- Fry, F.E.J. 1947. *Effects of the environment on animal activity*. University of Toronto Studies, Biological Series 55, Publication of the Ontario Fisheries Research Laboratory 68.
- Great Lakes Fishery Commission. 1995. *Report of the Coldwater Task Group to the Lake Erie Committee, 22 March 1995*. Great Lakes Fishery Commission, Ann Arbor, MI.
- Hansen, M.J. 1994. *The state of Lake Superior in 1992*. Special Publication 94-1, Great Lakes Fishery Commission, Ann Arbor, MI.
- Hart, J.L. 1930. The spawning and early life history of the whitefish, *Coregonus clupeaformis* (Mitchill), on the Bay of Quinte, Lake Ontario. *Contrib. Can. Biol. Fish. (N.S.)* 6:165–214.
- Hogman, W.J. 1971. *The larvae of lake whitefish (Coregonus clupeaformis (Mitchell)) of Green Bay, Lake Michigan*. Doctoral dissertation. The University of Wisconsin, Madison.
- Jobling, M. 1981. Temperature tolerance and the final preferendum—rapid methods for the assessment of optimum growth temperatures. *J. Fish Biol.* 19:439–455.
- Jude, D.J., Janssen, J.J., and Crawford, G. 1995. Ecology, distribution, and impact of the newly introduced round and tubenose gobies on the biota of the St. Clair and Detroit Rivers. In *The Lake Huron ecosystem: ecology, fisheries, and management*, eds. M. Munawar, T. Edsall, and J. Leach, pp. 477–460. Eco-vision World Monograph Series, S.P.B. Academic Publishing, The Netherlands.
- Lychwick, T., Keniry, M., Belonger, B., Kroeff, T., Toneys, M. Peeters, P., Hogler, S., Rost, R., Eggold, B., and Surendonk, S. 1995. *Lake Michigan Management Reports*. Great Lakes Fishery Commission, Ann Arbor, MI.
- Magnuson, J.J., Crowder, L.B., and Medvick, P.A. 1979. Temperature as an ecological resource. *Amer. Zool.* 19:331–343.
- Ontario Ministry of Natural Resources and New York State Department of Environmental Conservation. 1994. *Ecosystem watch: status of the Lake Ontario ecosystem*. Ontario Ministry of Natural Resources, Napanee, and New York State Department of Environmental Conservation, Albany.
- Opuszynski, K. 1974. Selected temperatures of whitefish, *Coregonus clupeaformis* (Mitchill), in the vertical gradient tank. *Rocz. Nauk Roln., Seria H-Rybactwo*. 96:63–70.
- Pavlovsky, S.L., and Sterligova, O.P. 1987. Predation of ruffe, *Gymnocephalus cernuus*, and benthic invertebrates on the eggs of Lake Syam whitefish, *Coregonus lavaretus palassi*. *Vopr. Ikhtiol.* 5:765–770.
- Pokrovskii, V.V. 1961. Basic environmental factors determining the abundance of whitefish. *Trudy Soveshchaniy* 13:228–234 [Eng. Trans.]
- Reckahn, J.H. 1970. Ecology of young lake whitefish (*Coregonus clupeaformis*) in South Bay, Manitoulin Island, Lake Huron. In *Biology of Coregonid Fishes*, eds. C.C. Lindsey and C.S. Woods, pp. 437–460. University of Manitoba Press, Winnipeg.
- Schneeberger, P.J. 1995. *Status of Coregonines in Lake Michigan—1994*. Great Lakes Fishery Commission, Ann Arbor, MI.

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