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ARTICLE

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Abstract
Introduced landlocked Rainbow Smelt *Osmerus mordax* are hypothesized to be a major factor in the decline of Lake Whitefish *Coregonus clupeaformis* populations in many lakes. We sought to identify the size of Lake Whitefish preyed upon by adult Rainbow Smelt and how the efficiency of Rainbow Smelt predation changes Lake Whitefish ontogeny. In a laboratory setting, we exposed larval Lake Whitefish of increasing sizes to groups of seven Rainbow Smelt (>100 mm) for a 1-h period and observed predation behaviors and efficiencies. In each trial, the group of Rainbow Smelt consumed at least one larval Lake Whitefish, which were up to 45 mm in length (up to 89% of Rainbow Smelt gape width). Predation efficiency, the total number of Lake Whitefish consumed by Rainbow Smelt during trials, was 100% after Lake Whitefish hatching and followed a decreasing sigmoidal response to increasing lengths of Lake Whitefish. The apparent predatory window of Rainbow Smelt on Lake Whitefish is from Lake Whitefish size at hatch (~12 mm) to approximately 34 mm. Rainbow Smelt generally required multiple attacks to capture a single Lake Whitefish. The capture efficiencies of Rainbow Smelt decreased from 30% as Lake Whitefish length increased and were highly variable within each Lake Whitefish size-group. The overall impact that Rainbow Smelt predation will have on Lake Whitefish populations is dependent on the growth rate of Lake Whitefish, environmental conditions that cause the Lake Whitefish hatching period to coincide with Rainbow Smelt spawning events, and the degree of overlap in habitat use between spawning Rainbow Smelt, nonspawning subadult Rainbow Smelt, and hatching Lake Whitefish.

Populations of smelts of the genus *Osmerus* have been identified as major larval predators in freshwater lakes of both North America and Eurasia (Foltz and Norden 1977; Sterligova 1979; Loftus and Hulsman 1986; Myers et al. 2009). In inland lakes throughout North America, Rainbow Smelt *O. mordax* populations are often nonnative as a result of both legal and illegal stocking and subsequent expansions (Evans and Waring 1987). These introduced populations are often implicated in the decline of native fish populations (Anderson and Smith 1971; Loftus and Hulsman 1986; Evans and Waring 1987; Evans et al. 1988; Myers et al. 2009). In both the Laurentian Great Lakes and smaller inland lakes, Rainbow Smelt can affect recruitment of native coregonids, specifically Cisco *Coregonus artedi* and Lake Whitefish *C. clupeaformis* (O'Gorman 1974; Loftus and Hulsman 1986; Hrabik et al. 1998; Myers et al. 2009). Although Rainbow Smelt predation has been implicated in causing recruitment declines for Lake Whitefish and Ciscoes in the Great Lakes, other factors certainly have contributed, such as overfishing, habitat alteration, invasive species, and changes in the lower food webs (Hartman 1973; Christie 1974; Hoff 2004).

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In order to be efficient predators of larval fish Rainbow Smelt predation on larval coregonids is gape-limited at a threshold size of greater than 100 mm (Selgeby et al. 1978; Loftus and Hulsman 1986; Haakana and Huuskonen 2009; Myers et al. 2009). Loftus and Hulsman (1986) found strong evidence of Rainbow Smelt predation on Lake Herring (i.e., Cisco) and Lake Whitefish, where Rainbow Smelt ranged from 85 to 215 mm. MacCrimmon and Pugsley (1979) found fish remains in Rainbow Smelt over 160 mm, and Stedman and Argyle (1985) found coregonid remains in Rainbow Smelt over 100 mm. This size translates to age-2 and older Rainbow Smelt in the Great Lakes and similar or older fish for other lakes with these species present.

The emergence of Cisco and Lake Whitefish larvae from spawning substrates coincides temporally with Rainbow Smelt spawning in the early spring, closely following ice-out. Spawning locations for these coregonids vary from lake inlets and streams to windswept shores, but commonly comprise clean, rocky substrate with sufficient interstitial spaces for egg incubation (Hart 1931; Nester and Poe 1984; Bégout Anras et al. 1999). Eggs are incubated over the winter and hatch when water temperatures approach 10°C (Faber 1969; Nester and Poe 1984; Bégout Anras et al. 1999). Similarly, Rainbow Smelt tend to use windswept shores, shoals, and streams for spawning. After spawning, adult Rainbow Smelt are voracious feeders, as feeding is often suspended during spawning and followed by intense feeding behaviors (MacCrimmon and Pugsley 1979; Loftus and Hulsman 1986). If larval coregonid spawning and nursery habitat occurs in proximity to Rainbow Smelt spawning areas, Rainbow Smelt predation could have devastating effects on coregonid recruitment.

Applying the hypothesis that predation by adult Rainbow Smelt may lower recruitment of Lake Whitefish, we sought to characterize the predation efficiency of adult Rainbow Smelt on larval Lake Whitefish in a laboratory setting and in so doing establish how and when predation may be responsible for low recruitment rates of coregonids in general. We hypothesized that overall Rainbow Smelt predation rates and predation efficiency would decrease as larval Lake Whitefish length increases, up to a point where Rainbow Smelt are no longer efficient predators on Lake Whitefish larvae. Our objective was to determine the length range of larval Lake Whitefish that are susceptible to Rainbow Smelt predation, which is an important component of assessing risk from spatiotemporal overlap with predatory Rainbow Smelt.

METHODS

Study species.—Sexually mature Lake Whitefish were collected during spawning periods using 1.5-m-deep trap nets with 30.5-m leads. Trap nets were set in 1–2 m of water along known spawning movement corridors in Clear Lake (township T10 R11 WELS, Piscataquis County, Maine; 46°31′16.02″N, 69°7′33.97″W). Trap nets were checked twice a week starting October 15 until ice restricted access to the nets, which typically occurred by the third week of November. Fish were removed from the trap nets and transported to shore for processing. Eggs were manually expelled and fertilized. They were then water-hardened at Clear Lake and transported to the Enfield State Fish Hatchery, Enfield, Maine, where they were incubated in McDonald jars. Before hatch, eggs were transported to the Aquaculture Research Center located at the University of Maine, Orono. The eggs remained in McDonald jars until hatching. After hatching, Lake Whitefish larvae were held in dark blue, cylindrical, plastic tanks measuring 30 cm in diameter and 60 cm tall. Lake Whitefish began consuming 2-d-old *Artemia* nauplii (Great Salt Lake strain, ~450 μm; Brine Shrimp Direct, Ogden, Utah) at 2 d posthatch. Water temperature was maintained at 10°C in each tank using a flow-through system with a water bath, and overhead fluorescent lights provided light at a 12 h light : 12 h dark cycle at a level of 350 lx.

Larval whitefish were separated into 20 size-groups of 15 fish each, and group mean fork lengths ranged from 9.5 to 44.5 mm (Table 1). These groups were each placed in 37-L glass aquaria, the sides of which were blackened. Water temperature was maintained at 10°C and 50% water exchanges were performed daily. Fish were fed 600 *Artemia*/L, which were rinsed with freshwater, five times a day throughout the experiment. Adult landlocked Rainbow Smelt were obtained after spawning from bait dealers who legally collected them through the ice from local systems. All Rainbow Smelt were of sexual maturity and therefore considered adult. Twenty-one Rainbow Smelt, 113–128 mm TL, were used in this experiment (Table 2). Seven adult Rainbow Smelt were placed in each of three tanks containing 100 L of flow-through freshwater at ~10°C. Rainbow Smelt were not fed outside the actual predation trials and were acclimated for 3 d before the first trial.

Predation trials.—Before each predation trial, digital images were taken of larval Lake Whitefish, grouped by tank, for size measurements. All larvae in a single trial were anesthetized using 5 mL of tricaine methanesulfonate (MS-222; 100 mg/L, buffered with 0.20 mM $NaCO_3$, pH = 7.0) in 250 mL of water. All larvae were photographed together on a 20–mm-grid petri dish using a digital camera (Canon Powershot S3 IS, 6.0 mp) mounted 30 cm above the petri dish. Size measurements were determined using digital imaging techniques and ImageJ software (D. Gorsky and J. Zydlewski, unpublished; Rasband, ImageJ: http://rsb.info.nih.gov/ij/). Larval fish were revived in aerated freshwater and then allowed to recover for an hour before experimentation. Photographic measurements of Rainbow Smelt were again taken at the conclusion of all of the predation trials.

Every 4 d, three predation trials were performed using each group of Rainbow Smelt once for a total of 20 trials taking place on seven separate days between June 26 and July 13, 2009. We used the same three groups of Rainbow Smelt for each set of predation trials without exchanging individuals. Trials were performed in the same tanks that the Rainbow Smelt were held in. These tanks were circular white tanks, 1 m across

TABLE 1. Mean Lake Whitefish length and measurements of documented predation behaviors for predation trials using Rainbow Smelt. Predicted body height of larval fish was calculated using the regression of length to body height.

Mean larval length (mm)	Predicted body height (mm)	Larval whitefish used (*n*)	Pursuits	Attacks	Captures	Trial efficiency (Captures/fish)	Capture efficiency (Captures/Attack)	Predator behavior (Attacks/Pursuit)
9.5	2.1	15				1.00		
12.8	2.5	15				1.00		
26.7	4.4	15	26	90	13	0.87	0.14	3.46
28.9	4.6	15	33	60	10	0.67	0.17	1.82
29.5	4.7	15	33	56	8	0.53	0.14	1.70
30.0	4.8	15	36	66	13	0.87	0.20	1.83
30.2	4.8	15	33	62	9	0.60	0.15	1.88
30.5	4.9	14	87	124	8	0.57	0.06	1.43
30.6	4.9	15	17	37	10	0.67	0.27	2.18
31.3	5.0	15	43	63	4	0.27	0.06	1.47
33.2	5.2	15	57	58	6	0.40	0.10	1.02
33.6	5.3	13	24	16	3	0.23	0.19	0.67
35.3	5.5	15	26	21	3	0.20	0.14	0.81
35.5	5.5	15	30	6	1	0.07	0.17	0.20
35.7	5.5	15	38	54	4	0.27	0.07	1.42
37.1	5.7	17	26	48	5	0.29	0.10	1.85
38.9	5.9	14	17	13	3	0.21	0.23	0.76
39.4	6.0	15	36	12	1	0.07	0.08	0.33
42.8	6.5	14	41	33	3	0.21	0.09	0.80
44.5	6.7	15	32	27	2	0.13	0.07	0.84

and 1.5 m deep. During predation trials, the water level was lowered to improve visibility from the surface to approximately 25 cm depth. For every set of predation trials, we rotated the tanks of Rainbow Smelt that would receive the smallest Lake Whitefish group. Trials were performed at 1000 hours. A total of 15 Lake Whitefish larvae were introduced to each tank of Rainbow Smelt. Two Lake Whitefish larvae were introduced at a time at 2-min intervals using a PVC tube that placed the fish at the side of the tank. The final individual larva was introduced singly.

Predation trials were videotaped for 60 min using a high-definition, digital, video recorder and wide-angle lens (Canon Vixia HV30) fixed to a frame at a distance of 1 m from the water surface, directly over the tank. Videos were transferred to a computer and reviewed using Microsoft Media Player (Microsoft, Redmond, Washington). During video review, we documented "pursuits," "attacks," "captures," and, at the end of each trial, the number of actively swimming larval fish remaining. We identified "pursuits" as movements consisting of multiple thrusts and sudden direction change towards larvae. "Attacks"

TABLE 2. Total length (TL), weight, and gape measurements of adult Rainbow Smelt for each tank used in predation trials.

	Predation trial		
Measurement	A	B	C
Length range (mm)	113–125	119–128	118–128
Mean length (mm) ± SE	119.7 ± 1.8	122.3 ± 1.5	121.9 ± 1.7
Weight range (g)	7.4–10.4	8.3–11.8	8.4–12.4
Mean weight (g) ± SE	8.9 ± 0.4	9.8 ± 0.5	9.7 ± 0.5
Gape height range (mm)	11.7–15.2	10.8–12.8	11.5–13.7
Mean gape height (mm) ± SE	13.3 ± 0.5	11.7 ± 0.3	12.7 ± 0.3
Gape width range (mm)	6.6–8.3	7.3–8.0	7.5–8.2
Mean gape width (mm) ± SE	7.3 ± 0.2	7.5 ± 0.1	7.8 ± 0.1

were aggressive pursuits sometimes involving a C-start type of attack, where an individual curls its body followed by a quick flex back to straight to provide high burst-swimming movement. "Pursuits" differed from "attacks" in that Rainbow Smelt broke off the pursuits before larvae were in striking distance. Finally "captures" included attacks that caused larval Lake Whitefish mortality either by injury or consumption. The first two predation trials were performed in a square tank without video review so only the trial efficiency was measured. To determine whether Rainbow Smelt were gape-limited during any predation trial performed, we compared the limiting dimensions of each species, gape width for Rainbow Smelt, and head height of Lake Whitefish. Gape measurements for Rainbow Smelt were performed using a caliper, and Lake Whitefish head height was measured using the same procedure as measuring the fish's TL.

Data analysis.—Three summary statistics of predation were analyzed across all size trials: (1) overall predation rates, (2) capture efficiency, and (3) pursuits per attack. Overall predation rates were measured based on the total number of prey captured relative to the total number of larval fish introduced during the 60-min period. Variation in predation rates relative to fish size was modeled using a logistic functional response model in which Lake Whitefish larval length was used as the independent variable and overall Rainbow Smelt predation rate was used as the dependent variable. Capture efficiency was calculated by observing the frequency of attacks resulting in successful capture during the trial period. The capture efficiency was then regressed against larval length using linear regression. Finally, the number of pursuits per attack was determined to identify predatory behavior changes across larval lengths. These data were likewise analyzed using linear regression. All regressions and coefficients were tested using an α-value of 0.05.

RESULTS

Predation by adult Rainbow Smelt on larval Lake Whitefish occurred in every trial performed (Figure 1). During the first two trials, when larvae were less than 15 mm, all larval Lake Whitefish were consumed by adult Rainbow Smelt. Predation rates were high (>50%) for larval Lake Whitefish with lengths less than 30 mm (Figure 1). Overall predation dropped quickly from approximately 50% to below 10% as larval Lake Whitefish lengths increased from 25 to 40 mm. Once larval fish lengths exceeded 40 mm, predation was low; typically only one larval Lake Whitefish was consumed per trial. The change in predation rates followed a logistic functional response with larval size as follows:

$$\pi(y) = \frac{e^{(6.4-0.2x)}}{1 + e^{(6.4-0.2x)}},$$

where x is the mean length of the larval lake whitefish and $\pi(y)$ is the predation rate ($G^2 = 37.2$, df = 19, $P < 0.001$).

Adult Rainbow Smelt generally required multiple attacks to capture larval Lake Whitefish (Figure 2). The relationship between the number of attacks needed for capture and larval Lake Whitefish length was not significant ($F_{1,16} = 1.68$, $P = 0.214$). Variation in capture efficiency tended to vary with larval size, and the highest variability in capture success occurred at smaller lengths. Adult Rainbow Smelt were never able to consume larval fish with high capture efficiencies (>30% capture efficiency). For larval fish with lengths less than 35 mm, Rainbow Smelt capture efficiency ranged between 6% and 31%, while efficiencies for larvae above 35 mm ranged between 7% and 23%. Across size-groups, the maximum capture efficiency generally decreased as larval lengths increased (Figure 2).

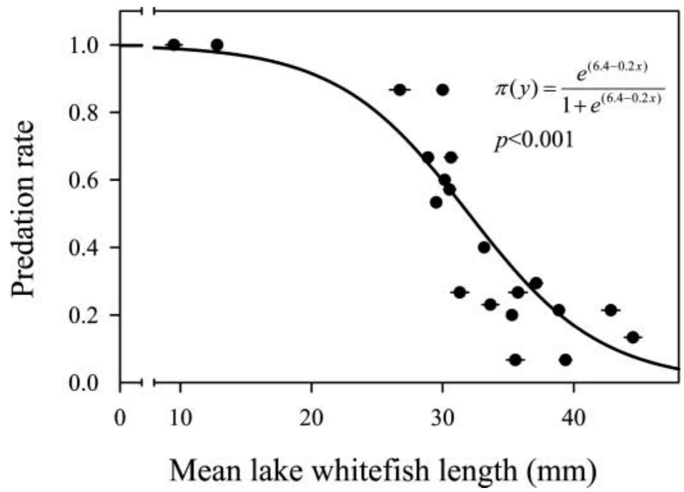

FIGURE 1. Overall predation rate of adult Rainbow Smelt preying on larval Lake Whitefish of increasing mean total lengths. Predation rate represents the number of captured prey per total number of prey introduced. Error bars represent the SE in larval lengths used in each predation trial.

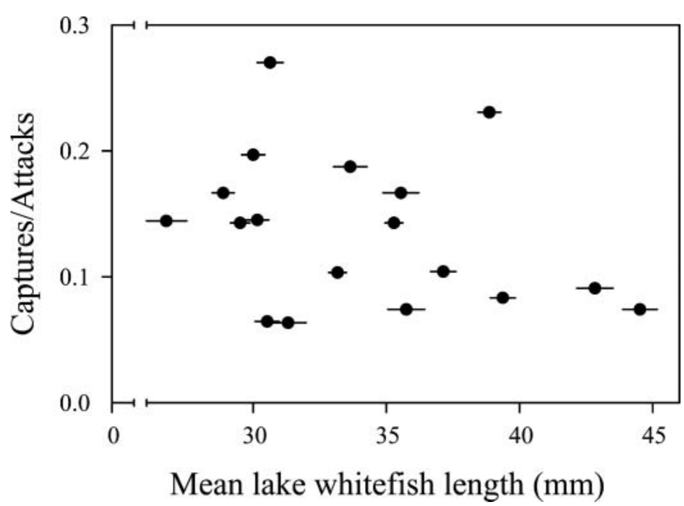

FIGURE 2. Capture efficiency in individual tanks of Rainbow Smelt on larval Lake Whitefish of different mean total lengths. Capture efficiency represents the number of attacks made per capture. Linear regression of data was not significant.

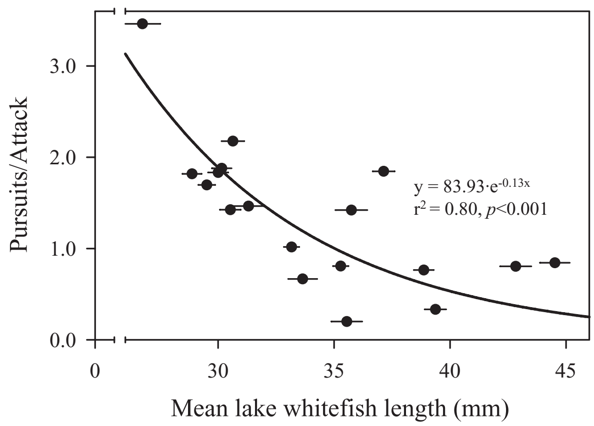

FIGURE 3. Observed attacks per pursuits of Rainbow Smelt on larval Lake Whitefish of increasing mean total lengths. Error bars represent the SE in larval lengths used in each predation trial. Linear regression of data are significant following the equation: $y = -0.11x + 5.05$, with $r^2 = 0.47$ and $P = 0.002$.

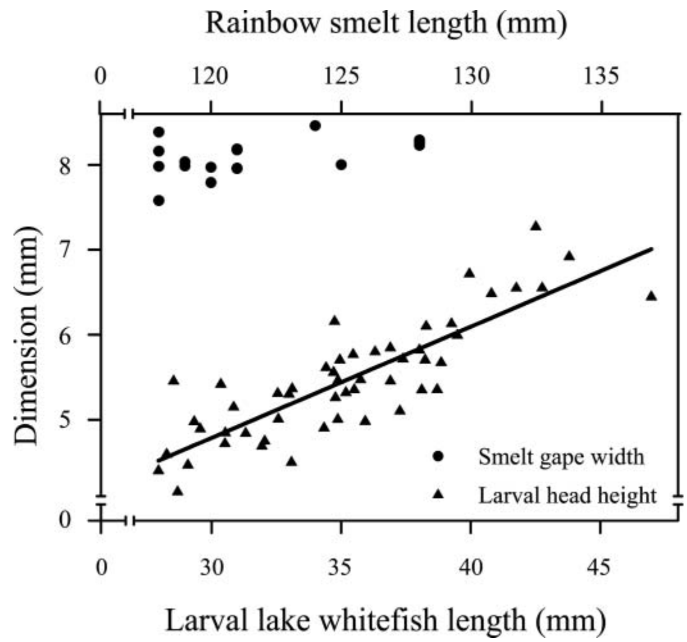

FIGURE 4. Rainbow Smelt gape width and Lake Whitefish head height in relation to the fork length (FL) of both species. Circles represent the gape width of the 21 Rainbow Smelt used in predation trials in relation to FL. Triangles represent the head height of Lake Whitefish in relation to FL. Length and head height of Lake Whitefish follow a significant linear regression: $y = 0.13x - 0.86$, with $r^2 = 0.71$ and $P < 0.001$.

Rainbow Smelt predatory behavior changed as larval Lake Whitefish lengths increased (Figure 3). The ratio of pursuits to attacks followed a negative-sloped linear function ($r^2 = 0.80$, $F_{1,16} = 27.5, P < 0.001$). When larval fish were small (<35 mm) adult Rainbow Smelt were more likely to proceed from pursuit to actual attack once a pursuit was initiated, as opposed to making numerous pursuits before actually attacking larger larval fish (>35 mm).

At the conclusion of the study Rainbow Smelt had fork lengths between 113 and 128 mm and gape widths between 6.6 and 8.3 mm and had an overall mean of 7.6 mm (Table 2). Larval Lake Whitefish head height increased with length and followed a significant linear relationship ($r^2 = 0.71$, $F_{1,50} = 121.6$, $P < 0.001$; Figure 4). The largest measured head height was 7.3 mm or 96% of the mean gape width of Rainbow Smelt and larger than three of the smallest Rainbow Smelt's gape width. Larval fish over 40 mm had a mean head height of 6.7 mm, which was 89% of the mean gape width of Rainbow Smelt. Larval Lake Whitefish less than 40 mm in length had a mean head height of 5.3 mm or 70% of mean Rainbow Smelt gape width.

DISCUSSION

Rainbow Smelt interactions with Cisco and Lake Whitefish have been extensively studied (Anderson and Smith 1971; Loftus and Hulsman 1986; Evans and Waring 1987; Evans et al. 1988; Hrabik et al. 1998; Myers et al. 2009). The results from these studies have documented predatory ability by Rainbow Smelt on Lake Whitefish. This predation has been suggested to be the cause for observed declines in whitefish recruitment (Loftus and Hulsman 1986; Myers et al. 2009). Although our experiment tested Rainbow Smelt predation on Lake Whitefish in a laboratory setting, the results of our study demonstrateed the size-dependent relationship between Lake Whitefish prey and Rainbow Smelt predation. In our experiment, the predatory window for Rainbow Smelt of 113–128 mm TL that consumed larval Lake Whitefish was from 12 mm, the typical size at hatch, to 43 mm, the approximate length when overall predation rate was below 10%. However, in systems like the Great Lakes where smelt have been observed to feed on fish after reaching lengths of 130 mm (MacCrimmon and Pugsley 1979; Evans and Waring 1987) and where age-3 and older adult Rainbow Smelt exceed 150 mm TL (Gorman 2007), the limit of the predatory window for Lake Whitefish may exceed 43 mm. As Lake Whitefish larvae grew, Rainbow Smelt became less efficient at capturing Lake Whitefish and behaviorally were more likely to pursue fish rather than attack them. The decline in trial and capture efficiencies as Lake Whitefish length increased suggests that predator avoidance behaviors by Lake Whitefish and gape limitation of Rainbow Smelt contributes to lower predation rates. Some of the larger Lake Whitefish groups reached head heights near the limit of the Rainbow Smelt gape width, and it is possible some Rainbow Smelt were gape-limited and could not prey on the larger Lake Whitefish. Before reaching this size, avoidance behavior by Lake Whitefish may have already been driving predation efficiency down. Behaviors such as schooling, swimming deeper, and burst swimming may reduce predation (Eklöv and Diehl 1994); all of these behaviors, including swimming along the bottom, were observed in our study. Christensen (1996) suggested gape limitation often may not be realized since avoidance behaviors alone can control the maximum size of prey ingested. In nature, any of the observed avoidance behaviors in our experiment would most probably increase survival sharply, but in the confines of our experimental tanks, one or two avoidance maneuvers did not sufficiently remove the individual from the threat of predation, and thus our predation estimates are most probably high. Natural environments would allow larvae to escape and evade the fish beyond the limits imposed by our 1-m-diameter experimental tanks.

The effectiveness of Rainbow Smelt predation on the smaller larvae suggests that in lakes that contain both species, the highest potential impact of predation by Rainbow Smelt may occur soon after Lake Whitefish larvae hatch and are occupying surface waters near spawning areas. After hatching, larval Lake Whitefish occupy shallow surface waters for the first 3 weeks (Hart 1931). The sharp reduction in predation efficiency by Rainbow Smelt on Lake Whitefish between 24 and 36 mm indicates that it is essential for Lake Whitefish to grow quickly through this critical period to avoid predation. Growth rates of Lake Whitefish are variable and depend on temperature and prey availability. Laboratory studies of larval Lake Whitefish growth rates show that in typical spring temperatures (∼10°C) and with abundant prey availability (>600 zooplanton/L), larval Lake Whitefish may take over 74 d from time of hatch to pass through the defined predatory window (Gorsky and Zydlewski, unpublished). As demonstrated by Myers et al. (2009), increases in the length of time that larval fish are exposed to predation will lead to larval mortality approaching 100%. For higher survival in the face of Rainbow Smelt predation pressure, coregonid populations will require abundant prey and appropriate temperatures to allow for faster growth, but additionally larval fish will also have to use predatory avoidance techniques to ensure survival.

To fully understand the magnitude of predation pressure of Rainbow Smelt on Lake Whitefish populations, information about individual populations and spawning habitat use in each lake will be required. Past studies have been inconsistent in documenting the influence of Rainbow Smelt predation on Lake Whitefish or Cisco in general (Selgeby et al. 1978). Rainbow Smelt are considered opportunistic feeders, so high densities and habitat overlap may be required for this interaction to take place. Specific examples show that when spawning habitats overlap, the effect of predation can be extremely high (Loftus and Hulsman 1986; Myers et al. 2009). Additionally, when there are high densities of Rainbow Smelt, few prey items consumed per individual can still have major effects on recruitment. In Lake Ontario, cyclical patterns in recruitment were observed for Rainbow Smelt due to cannibalism in which low numbers of prey items per individual were documented (Lantry and Stewart 2000). This suggests that even when low numbers of prey items per predator are observed, the effect of high predator density will cause the predatory influence to be more substantial. Past observations of low predation levels by Rainbow Smelt on larval fish suggest there is a weak effect due to predation. This may be an underrepresentation of the predatory impact simply because of the high numbers of Rainbow Smelt that are able to prey on the individuals.

At a majority of the sizes tested in this study, Rainbow Smelt never had high capture efficiencies, but were nonetheless eventually successful in consuming a proportion of the larvae presented to them within the 1-h trial. Laboratory studies of predation have shown similar or higher capture efficiencies for their respective prey compared with our observations of Rainbow Smelt predation on Lake Whitefish (Christensen 1996; Brooking et al. 1998). Some of these studies showed capture efficiencies of above 50% for the smallest prey items. It is possible that Rainbow Smelt capture efficiencies of larval Lake Whitefish may be higher when Lake Whitefish are closer to the size at which they hatch. The first two trials of our study were performed using a slightly different design, and we were not able to quantify capture efficiency when larval lengths were less than 20 mm. The larvae of the size we tested may have already begun to perform behaviors that limited predation efficiency. Brooking et al. (1998) first observed avoidance behavior in Walleye *Sander vitreus* larvae after 24 d posthatch at lengths of 16.3 mm. This early observation of avoidance behaviors may be occurring with Lake Whitefish. The fact that Rainbow Smelt capture efficiencies were always low may be an indication that the Lake Whitefish larvae used in our experiments could already perform some level of predator avoidance.

In conclusion, this study showed that if Rainbow Smelt greater than 100 mm have high overlap in habitat use with Lake Whitefish larvae, they can be predators within a critical size window, which could lead to larval whitefish recruitment failure. We determined that for Rainbow Smelt of 113–128 mm TL, the predatory window for Lake Whitefish occurs from size at hatch to about 43 mm. In systems such as the Great Lakes where adult Rainbow Smelt reach sizes >150 mm TL, the limit of the predatory window for Lake Whitefish is probably greater. Larvae may be able to increase survival if temperature and food conditions allow for higher growth, and if larvae use predator avoidance behaviors to minimize predation. In order to effectively assess the impact of Rainbow Smelt predation on Lake Whitefish recruitment, knowledge about the abundance and size structure of the Rainbow Smelt population, and timing and habitat use by spawning and larval fish for both species in the lake or area of the lake of interest is required.

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