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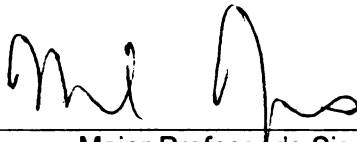
A RE-ASSESSMENT OF RAINBOW SMELT (OSMERUS
MORDAX) PREDATION ON CISCO (COREGONUS ARTEDI)
IN LAKE SUPERIOR

presented by

JARED T. MYERS

has been accepted towards fulfillment
of the requirements for the

M.S. degree in Fisheries & Wildlife



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A RE-ASSESSMENT OF RAINBOW SMELT
PREDATION ON CISCO

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PREDATION ON CISCO (*COREGONUS ARTEDI*) IN LAKE SUPERIOR

By

The work reported in this thesis by Jared T. Myers

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comparing several sampling strategies for estimating larval cisco abundance

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stage is necessary to allow for a more comprehensive understanding of

investigating hypotheses about the role of rainbow smelt in the Lake Superior

to assess larval cisco populations. This study contributes to the understanding of

and large-scale research in Lake Superior. This study contributes to the understanding of

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show that incidental predation by rainbow smelt on larval cisco is not a significant

mortality for larval cisco. Our results suggest that rainbow smelt predation on

have played an important role in the decline of larval cisco populations in Lake

rainbow smelt predation may not be a significant factor in the decline of

recruitment of cisco but highlights the need for further research on the

the occasional successful predation events by rainbow smelt on larval cisco.

Department of Fisheries and Wildlife

2008

ABSTRACT

A RE-ASSESSMENT OF RAINBOW SMELT (*OSMERUS MORDAX*) PREDATION ON CISCO (*COREGONUS ARTEDI*) IN LAKE SUPERIOR

By

Jared T. Myers

The work reported in my thesis addresses two fundamental issues for understanding larval cisco dynamics. In the first chapter I report on our study comparing several sampling strategies for estimating the abundance of larval cisco. Development of a sampling program that effectively captures the larval stage is necessary to allow estimation of important population metrics and for investigating hypotheses concerning recruitment. Our work improved our ability to assess larval cisco populations, which will facilitate interagency coordination and large-scale research initiatives. In the second chapter we examine the influence of rainbow smelt predation on the survival of larval cisco in two large Lake Superior embayments. Past research attempting to understand the role of rainbow smelt in determining cisco recruitment has led to varying results. We show that incidental predation by rainbow smelt can be a substantial source of mortality for larval cisco. Our evidence also suggests that rainbow smelt may have played an important role in the historic collapse of cisco. We recognize that rainbow smelt predation may not be the only mechanism inhibiting the recruitment of cisco but believe that this added mortality could be detrimental to the occasional successful cisco year class.

ACKNOWLEDGEMENTS

I am indebted to my mentors, Jason Stockwell, Mike Jones, and Dan Yule for their guidance and support. I am also thankful for the efforts of Ken Cullis, Casey Frantz, Allison Gamble, Jeff Black, and Jon Chicone. As always, I am grateful to my friends and colleagues at the MSU-Quantitative Fisheries Center, USGS-GLSC–Lake Superior Biological Station, and OMNR–Upper Great Lakes Management Unit. Jason Stockwell, Dan Yule, Mike Jones, Jean Adams, David “Bo” Bunnell, Tom Hrabik, Sture Hansson, and Jon Deroba have provided constructive comments throughout the writing process.

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piscivores (Dryer and Bell 1984, Brown et al. 1999). At the turn of the 20th century, cisco supported major commercial fisheries throughout the Great Lakes. However, cisco stocks collapsed by 1928 in Lake Erie (Hartman 1973), 1955 in lakes Ontario and Huron (Christie 1973, Berst and Spangler 1973), and 1960 in Lake Michigan (Wells and McCain 1973). Populations of cisco reached a low in Lake Superior by 1976, but these stocks were not decimated to the same degree as stocks in the lower lakes (Jason Stockwell, United States Geological Survey, personal communication). Lake Superior cisco populations have recovered to support commercial fisheries, yet highly variable recruitment (Bronte et al. 2003) has led to the perception that the stocks are unstable.

Restoration of native coregonids in the lower lakes has recently received increased attention (Fitzsimons and D'Ignazio 2006). The Great Lakes Fishery Commission (GLFC) recognizes the economic value and desirability of striving towards stable, native fish communities in all the Great Lakes, as evidenced by the GLFC Strategic Vision for Healthy Great Lakes Fisheries:

"The commission shall encourage the development and the restoration of healthy aquatic ecosystems in the Great Lakes and shall support the development of...

society, contain predominantly **INTRODUCTION** communities, and support

fisheries with increasing contributions of naturally reproducing fish. Conserving

biolog Historically, cisco *Coregonus artedii* were found throughout the Great Lakes (Scott and Crossman 1998) and played a key role in the food web by serving as a trophic linkage between zooplankton resources and native

piscivores (Dryer and Beil 1964, Brown et al. 1999). At the turn of the 20th century, cisco supported major commercial fisheries throughout the Great Lakes. However, cisco stocks collapsed by 1928 in Lake Erie (Hartman 1973), 1955 in lakes Ontario and Huron (Christie 1973, Berst and Spangler 1973), and 1960 in Lake Michigan (Wells and McClain 1973). Populations of cisco reached a low in Lake Superior by 1976, but these stocks were not decimated to the same degree as stocks in the lower lakes (Jason Stockwell, United States Geological Survey, personal communication). Lake Superior cisco populations have recovered to support commercial fisheries, yet highly variable recruitment (Bronte et al. 2003) has led to the perception that the stocks are unstable.

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"The commission shall encourage the rehabilitation and conservation of healthy aquatic ecosystems in the Great Lakes that provide sustainable benefits to

society, contain predominantly self regulating fish communities, and support fisheries with increasing contributions of naturally reproducing fish. Conserving biological diversity through rehabilitation of native fish populations, species, communities, and their habitat has a high priority." Lakes. In sum, restoration of

cisco in the lower Great Lakes appears to be an opportunity to achieve fish

comm It is largely understood that a forage base composed of predominately native species is desirable in each of the Great Lakes. Fisheries managers recognize cisco as a central species in the native fish communities of the Great Lakes coldwater systems (DesJardine et al. 1995, Eshenroder et al. 1995, Stewart et al. 1999, Ryan et al. 2003, Horns et al. 2003). Statements made by each of the respective lake committees call for the re-establishment of self-sustaining cisco populations in each of the lower lakes.

success There are several reasons why the functioning of the lower lakes' ecosystems would benefit from the recovery of cisco. Cisco are not subject to the large-scale die-offs characteristic of alewife *Alosa pseudoharengus* (O'Gorman and Schneider 1986), which will help stabilize prey fish abundances in the lower lakes. Cisco may facilitate the restoration of native piscivores by reducing the occurrence of Early Mortality Syndrome (EMS), a condition linked to thiamine deficiency and believed to be impeding recovery of native piscivores (Fitzsimons et al. 1999). Rainbow smelt *Osmerus mordax* and alewife are high in thiaminase and lake trout that rely on these non-native prey produce thiamine-deficient eggs, preventing successful reproduction in the lower lakes. Researchers have shown that size of prey relative to predator size may be an important factor influencing

predator growth rates (Werner 1974, Mittlebach 1981). Restoring a larger bodied prey fish, such as cisco, could improve both growth and fecundity of native lake trout populations. Self-sustaining populations of cisco may also provide additional opportunities for commercial fisheries in the Great Lakes. In sum, restoration of cisco in the lower Great Lakes appears to be an opportunity to achieve fish community objectives and improve ecosystem health.

Reaching the goal of self-sustaining cisco stocks will be challenging.

Decisions on numbers and/or appropriate life stages to stock will be difficult because of limited information on early life stage mortality rates and mechanisms that control recruitment. To make informed decisions it is important to understand how cisco function within their environment. *A priori* knowledge of mechanisms important to population dynamics will increase the probability of restoration success. Despite decades of research and management our understanding of cisco dynamics is still vague.

A group of researchers interested in the rehabilitation of cisco convened in 2004 to discuss the status, research, and restoration needs of cisco in each of the respective Great Lakes (Fitzsimons and O'Gorman 2006). After a period of thought and additional research, many members of the 2004 group met again in the spring of 2006. The opinions from these experts were that the larval stage was critical for understanding cisco population dynamics and impediments to their rehabilitation. Along with stressing the importance of the larval stage, researchers hypothesized that multiple biotic and abiotic mechanisms may determine the success of a given year class.

Lake Superior cisco stocks are believed to be near historic levels of abundance, providing an environment for examining hypothesized bottlenecks in cisco life history. The work reported in my thesis, which was conducted in collaboration with the United States Geological Survey – Great Lakes Science Center and the Ontario Ministry of Natural Resources – Upper Great Lakes Management Unit, addresses two fundamental issues for understanding larval cisco dynamics. In the first chapter I report on our study comparing several sampling strategies for estimating the abundance of larval cisco. Development of a sampling program that effectively captures the larval stage is necessary to allow estimation of important population metrics and investigating hypotheses concerning recruitment (Sammons and Bettoli 1998, Castro and Hernandez 2000, Karjalainen et al. 2000). Our work improved our ability to assess larval cisco populations, which will facilitate interagency coordination and large-scale research initiatives. In the second chapter we examine the influence of rainbow smelt predation on the survival of larval cisco in two large Lake Superior embayments. Past research attempting to understand the role of rainbow smelt in determining cisco recruitment has led to varying results. We show that incidental predation by rainbow smelt can be a substantial source of mortality for larval cisco. Our evidence also suggests that rainbow smelt may have played an important role in the historic collapse of cisco. We recognize that rainbow smelt predation may not be the only mechanism inhibiting the recruitment of cisco but believe that this added mortality could be detrimental to the occasional successful cisco year class.

CHAPTER I:
EVALUATING SAMPLING STRATEGIES FOR
LARVAL CISCO (*COREGONUS ARTEDI*)

Abstract. To improve our ability to assess larval cisco *Coregonus artedii* populations in Lake Superior, we conducted a study to compare several sampling strategies. First, we compared density estimates of larval cisco concurrently captured in surface waters with a 2 x 1-m paired neuston net and a 0.5-m (diameter) conical net. Density estimates obtained from the two gear types were not significantly different, suggesting that the conical net is a reasonable alternative to the more cumbersome and costly neuston net. Next, we assessed the effect of tow pattern (sinusoidal versus straight tows) to examine if propeller wash affected larval density. We found no effect of propeller wash on the catchability of larval cisco. Given the availability of global positioning systems, we recommend sampling larval cisco using straight tows to simplify protocols and facilitate straightforward measurements of volume filtered. Finally, we investigated potential trends in larval cisco density estimates by sampling four time periods during the light period of a day at individual sites. Our results indicate no significant trends in larval density estimates during the day. We conclude estimates of larval cisco density across space are not confounded by time at a daily timescale. Well-designed, cost effective surveys of larval cisco abundance will help to further our understanding of this important Great Lakes forage species.

Introduction

The larval stage of cisco *Coregonus artedii* development is characterized by a pelagic existence (Anderson and Smith 1971, Selgeby et al. 1978, Hatch and Underhill 1988, Oyadomari and Auer 2004), where a host of physical and biotic influences may act to limit recruitment (Roughgarden et al. 1988, Heath 1992). Research has shown that erratic fluctuations in adult abundance of many fish species, like those observed for Lake Superior cisco (Yule et al. 2008a), are often the result of extremely high mortality rates and variable survivorship during the larval phase (Ricker 1954, Houde 1987). Many mechanisms have been proposed to explain variations in recruitment, but the relative importance of alternative mechanisms remains poorly understood (Cushing 1996).

Development of a sampling program that effectively captures the larval stage is a promising avenue for estimating important population metrics and investigating hypotheses concerning recruitment (Sammons and Bettoli 1998, Castro and Hernandez 2000, Karjalainen et al. 2000).

Reliable assessment techniques are critical so that attempts to understand complex ecological processes are not undermined by poor survey design. Net avoidance is a serious consideration when attempting to measure the abundance of agile planktonic organisms (Barkley 1972). If cisco larvae exhibit an escape response, nets with a smaller effective sampling area would be subject to conservative estimates of density compared to more encompassing gears. Also, it would be expected that smaller nets would be more sensitive to the patchiness

of larval cisco (Oyadomari and Auer 2004) while larger framed nets would reduce variability caused by fine-scale patchiness. Recent studies have suggested that larval fish may react to the turbulence induced by a vessel's propeller (Claramunt et al. 2005, Overton and Rulifson 2007). This creates a potential for differences in estimated density due to the pattern in which the gear is towed and the time spent directly in the boat wash. An added consideration is that samples within a survey are confounded by the inherent limitation of sampling over both space and time simultaneously (Levin 1992). Researchers have found that coregonid larvae in Finnish lakes are aggregated near the surface during daytime, with maximum catches occurring at approximately 1100-1400 hours (Viljanen et al. 1995). In Lake Superior it has been demonstrated that larval cisco density is generally highest in the surface stratum (Selgeby et al. 1978, Hatch and Underhill 1988) during daytime (Oyadomari and Auer 2004), yet no study has investigated the repeatability of estimates through this period.

In this study we compare the performance of two gears for estimating larval cisco abundance and make recommendations for survey tactics for this important Great Lakes species. The present work was part of a larger study to investigate the impact of rainbow smelt predation on larval cisco in Thunder Bay and Black Bay, Ontario. Sampling of both bays in a timely fashion required us to collect larval cisco using two vessels equipped with different gears. We assessed the performance of the two gear types (a 2 x 1-m paired neuston net and a 0.5-m [diameter] conical net) to determine whether density and mean length estimates from the smaller conical net were comparable to those estimated from the

neuston net. We also investigated whether propeller wash influenced density and mean length estimates by comparing samples collected off the stern of vessels using sinusoidal and straight tow patterns. Finally, we examined potential trends in density estimates from early morning to late afternoon to examine if time of day could be ignored when generating mean density estimates across sites within a day.

Methods

Data for this study were collected in Thunder Bay and Black Bay, Ontario (Figure 1) during 2-25 May 2006. Two vessels were used to collect samples. The first vessel was a 7.9-m Bertram with twin, 3.6 liter, stern-driven, Mercruiser engines and was equipped with a hydraulic winch. Larval fishes were sampled from this vessel with a 2 x 1-m paired neuston net (hereafter referred to as "neuston net") towed in the surface stratum. The second vessel was a 6-m Boston Whaler with twin 150 horse power Evinrude E-TEC outboard motors. Larval fishes were sampled with a 0.5-m (diameter) conical net (hereafter referred to as "conical net") towed in the upper 1 m of the water column from this vessel. Both gears were equipped with 500- μ m mesh nets.

A single sample consisted of a 5-min tow in the 0-1 m stratum. Nets were deployed behind each vessel with approximately 30 m of warp line out. During sampling, each vessel weaved in a sinusoidal pattern to minimize towing time in the respective vessels' wash. The exception to this protocol was when testing for

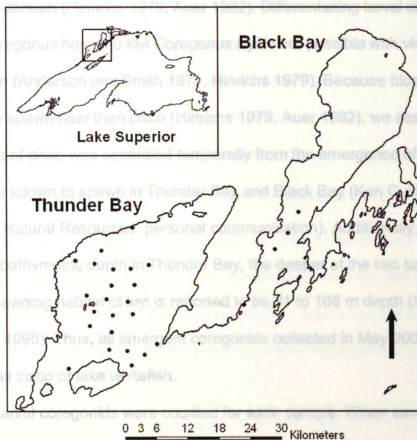


Figure 1. Stations used to evaluate sampling strategies for larval cisco.

the effects of propeller wash, in which one sample was towed in a sinusoidal manner while the other paired sample (e.g. from the same vessel) was collected using a straight pull. To maintain consistency, all tows were pulled with the wind on the stern at a speed of 3.2 to 3.9 km/hr. The volume of water filtered was determined using General Oceanics model 2030 flowmeters. Both collections from the paired neuston net were pooled for a single sample. All specimens were preserved in 95% ethyl alcohol.

Larval lake whitefish *Coregonus clupeaformis* were distinguishable from other larval coregonids based on size (Hinrichs 1979) and melanophore patterns

across the dorsum (Hinrichs 1979, Auer 1982). Differentiating larval cisco from bloater *Coregonus hoyi* and kiyi *Coregonus kiyi* is not possible with visual observation (Anderson and Smith 1971, Hinrichs 1979). Because bloater are believed to spawn later than cisco (Hinrichs 1979, Auer 1982), we assumed that emergence of cisco was separated temporally from the emergence of bloater. Kiyi are not known to spawn in Thunder Bay and Black Bay (Ken Cullis, Ontario Ministry of Natural Resources, personal communication). Additionally, the maximum bathymetric depth in Thunder Bay, the deeper of the two bays, is 91 m and the spawning habitat of kiyi is reported to be 91 to 168 m depth (Scott and Crossman 1998). Thus, all emergent coregonids collected in May 2006 were identified as cisco or lake whitefish.

All larval coregonids were counted for each sample. When samples contained ≤ 100 larval fish all specimens were identified as cisco or lake whitefish and photographed using a Leica S6D dissecting scope equipped with a Panasonic digital camera. When samples contained > 100 individuals a random sample of 50 specimens were identified as cisco or lake whitefish and photographed. Photographs were used to digitally measure total length of each fish to the nearest 0.1 mm. Density of larval cisco ($\# / 1,000 \text{ m}^3$ of water) in each sample was calculated by dividing number caught by volume of water filtered. We assumed net efficiency was 100%. All statistical tests were performed using the statistical software SAS (SAS Institute Inc. 2003). Our significance level for all analyses was $\alpha = 0.05$.

Gear Comparison the one zero observation (Johnson and Rauser 1971).

Mostly To compare density estimates and length measurements between the two gears, we collected samples using side-by-side tows with the two vessels. The vessels were separated by approximately 50 m. Coordination by way of VHF radio allowed for synchrony in gear deployment and tow duration. To satisfy the assumption of normally distributed errors, density estimates were $\log_{10}$ -transformed prior to analysis. A paired *t*-test was used to test the null hypothesis that there was no difference between density estimates from the two gears. For length comparisons we used a Kolmogorov-Smirnov test to test the null hypothesis that there was no difference between the distributions of preserved lengths from the two gears.

To investigate potential patterns in fish density estimates during

Tow Pattern we sampled a site during two hours of the day

(approx To examine the effect of turbulence caused by the propellers on density estimates and average preserved length, paired samples were collected successively at various sites. One sample of each pair was collected using a sinusoidal pattern and the other sample was collected using a straight pull. A single gear was used for sampling a specific site yet both vessels (and the respective gears of each vessel) were used within this analysis. The sequence of collections at a specific site was determined randomly. Both tows began at approximately the same starting position yet the respective transects were not overlapped. Collection of both samples took approximately 25 minutes. To satisfy assumptions of normality we applied a $\log_{10}$ -transformation, with a small

constant added to the one zero observation (Johnson and Rausser 1971). Mosteller and Tukey (1977) recommended adding a constant that is $1/6$ the minimum observable value, leading us to use a constant of 3 (i.e. with a single larvae captured by the conical net the minimum density estimate was $18 \text{ larval cisco} / 1,000 \text{ m}^3$). A paired t -test was used to assess the null hypothesis of no differences between density estimates derived from sinusoidal and straight tow patterns. A Kolmogorov-Smirnov test was used to test for differences in the length frequency distributions resulting from the pattern in which the net was towed.

Daytime Trends

To investigate potential patterns in larval cisco density estimates during light hours, we sampled a site during four time periods over the course of a day (approximately 0600, 1000, 1400, 1800). Within each time period, three consecutive samples were collected using the neuston net. This strategy was replicated for a total of six days (six different sites) throughout the study period. A $\log_{10}$ -transformation was applied to the density estimates prior to analysis to stabilize variances and better meet assumptions of normality. A repeated measures ANOVA was used to test the null hypothesis that there were no temporal trends within the light period of an individual day. Because the model is incapable of handling missing data we performed the analysis twice. In the first analysis we used only the days in which a complete set of 12 samples were collected ($n = 3$). In the second analysis we used only the first sample from each

time period, thereby increasing the sample size ($n = 5$). On May 5, 2006 rough seas prevented the collection of all late afternoon samples, causing us to exclude this day from both analyses.

Results

A total of 162 ichthyoplankton samples were collected to meet the objectives of this study. We collected 114 samples using the neuston net and 48 samples using the conical net. We captured 31,246 and 1,331 cisco larvae with the neuston and conical nets, respectively. Very few lake whitefish larvae were identified during the study. Rainbow smelt larvae were observed in the samples but were not counted. The number of samples collected and coregonid larvae counted for the three respective analyses are summarized in Table 1.

Table 1. The number of samples collected, number of coregonid larvae captured, and the mean density ($\# / 1,000 \text{ m}^3$) of cisco larvae sampled for the evaluation of sampling strategies in Thunder Bay and Black Bay, Ontario during 2-25 May 2006.

Tow Pattern	Gear Comparison		Tow Pattern		Daytime Trends
	Neuston	Conical	Sine	Straight	Neuston
No. Samples	28	28	20	20	66
No. Whitefish Larvae	2	0	5	0	17
No. Cisco Larvae	8,088	1,089	5,145	242	18,013
Mean Cisco Density ($\pm \text{SE}$)	474 (98)	672 (212)	299 (75)	331 (110)	453 (69)

Gear Comparison

A total of 28 side-by-side tows were made with the two gears. Density estimates ranged between 50 and 2,317 larvae/1,000 m³ for the neuston net and 33 and 4,651 larvae/1,000 m³ for the conical net. Density estimates were not significantly different between the two gears (t -value = -0.473, P = 0.64, DF = 27; Figure 2A). Given the observed variance for the 28 paired collections we would have been able to detect an effect size of 1.46 with 80% power (Lenth 2006). Because we are ultimately interested in mechanisms that cause orders of magnitude differences in abundance, we feel that a difference between gears of less than 50% is not meaningful for larval cisco assessments and our sampling effort was appropriate for the objectives of this investigation. Cisco larvae caught using the neuston net had a mean length of 10.85 mm (SE = 0.026, n = 1,389) and those caught by the conical net had a mean length of 10.73 mm (SE = 0.042, n = 548). The distribution of larval cisco lengths were significantly different between the two respective gears (K-S test: D = 0.094, P < 0.005) although the differences in lengths captured were very small (Figure 2B).

Tow Pattern

We collected 10 paired samples using each respective net for a total of 20 comparisons. Because we found no difference between the two gears we combined data from both nets for one analysis examining the effect of propeller wash. We found no significant difference in density estimates based on tow pattern (t -value = 1.715, P = 0.104, DF = 19; Figure 2C). Cisco larvae captured

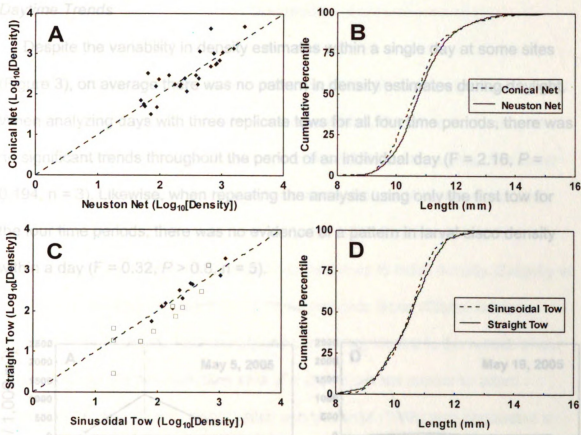
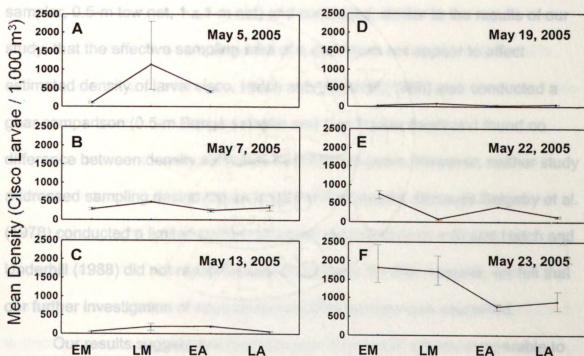


Figure 2. (A) Log₁₀-transformed larval cisco density (#/1,000 m³) estimates and (B) cumulative length frequency distributions of larval cisco collected with side-by-side tows using a 2 x 1-m paired neuston net and a 0.5-m (diameter) conical net. (C) Log₁₀-transformed larval cisco density (#/1,000 m³) and (D) the cumulative length frequency distributions of larval cisco collected using sinusoidal and straight tow patterns with either a 2 x 1-m neuston net (◆) or a 0.5-m (diameter) conical net (□). The dashed lines (A and C) are 1:1 lines.

using the sinusoidal tow pattern had a mean length of 10.45 mm (SE = 0.031, n = 688) and those caught using a straight tow pattern had a mean length of 10.50 mm (SE = 0.035, n = 677). The Kolmogorov-Smirnov test revealed a significant difference between the length frequency distributions resulting from the alternative tow patterns ($D = 0.078$, $P < 0.05$), despite the fact that the cumulative length frequency distributions were remarkably similar (Figure 2D).

Daytime Trends

Despite the variability in density estimates within a single day at some sites (Figure 3), on average there was no pattern in density estimates during daylight. When analyzing days with three replicate tows for all four time periods, there was no significant trends throughout the period of an individual day ($F = 2.16$, $P = 0.194$, $n = 3$). Likewise, when repeating the analysis using only the first tow for the four time periods, there was no evidence of a pattern in larval cisco density within a day ($F = 0.32$, $P > 0.8$, $n = 5$).



Sampling Period

Figure 3. Average larval cisco density ($\# / 1,000 \text{ m}^3$) as a function of time of day. Sampling events occurred in the early morning (EM), late morning (LM), early afternoon (EA), and late afternoon (LA) for six individual days at different sites. Error bars represent the range of estimated densities for each sampling event.

Discussion

Several studies have examined the dynamics of cisco early life history by attempting to estimate abundance of swim-up larvae. Evidence from many of these studies has shown emergent cisco to be distributed throughout the water column but concentrated primarily in the surface stratum (Anderson and Smith 1971, Selgeby et al. 1978, Hatch and Underhill 1988, Oyadomari and Auer 2004), leading us to use only surface horizontal tows to index density. Selgeby et al. (1978) evaluated the performance of several gear types (Clarke-Bumpus sampler, 0.5-m tow net, 1 x 1-m net) and concluded, similar to the results of our study, that the effective sampling area of a gear does not appear to affect estimated density of larval cisco. Hatch and Underhill (1988) also conducted a gear comparison (0.5-m Bongo sampler and 1-m Tucker trawl) and found no difference between density estimates from the two gears. However, neither study addressed sampling design issues in light of their results. Because Selgeby et al. (1978) conducted a limited number of paired comparisons ($n = 5$) and Hatch and Underhill (1988) did not report detailed diagnostics for their analysis, we felt that our further investigation of appropriate sampling devices was warranted. Our results suggest that samples from the conical net are comparable to those from the much larger neuston net. Because conical nets are affordable, can be deployed from any small vessel without special requirements (e.g., hydraulic winch), and result in smaller catches (equating to less laboratory processing time), we recommend the conical net for future surveys of larval

cisco. We note that smaller sample volumes and the patchiness of local distributions may cause surveys using conical nets to be vulnerable to greater variation in density estimates. To some extent this can be offset by increasing the number of tows conducted. Depending on the objectives of future studies this may be an important consideration when choosing a gear to deploy. The length frequency distributions of larvae captured by the two gears were significantly different, with the neuston net capturing slightly larger individuals (Figure 2B). We consider this difference, while significant according to the K-S test, is small enough to be unimportant from a practical viewpoint. Both nets captured a limited range of larval cisco sizes, possibly due to the emigration of larger age-0 cisco from the surface waters or gear avoidance by larger larvae. We feel alternate sampling strategies and gears would be needed to assess age-0 cisco once they reach larger sizes, a goal beyond the scope of the present study.

A recent study showed bow-mounted push nets had an increased efficiency for sampling of larval sunfish *Lepomis* spp. but not for gizzard shad *Dorosoma cepedianum*, suggesting that vessel interference may influence larval fish catchability for certain species (Claramunt et al. 2005). Because of the sea conditions encountered in Lake Superior and the rigid mounting apparatus used to deploy this gear type, its use was not considered as it would often rise above the waters surface with the rise and fall of the vessels bow. Instead, we tested for effects of vessel interference within our sinusoidal tow versus straight tow analysis. Despite the concerns, we did not observe an effect on estimated density caused by tow pattern. The difference in length frequency distributions for

the two tow patterns, while statistically significant, were very small (Figure 2D) and are very unlikely to represent differences that would influence the biological interpretation of survey results. Given the availability of global positioning systems, we recommend sampling larval cisco using straight tows to simplify protocols and facilitate straightforward measurements of volume filtered (distance x net mouth area). We do not however suggest abandoning the use of flowmeters, as their use may serve as an added measure of distance.

Finally, our investigation showed no trends in density over the light period of a day, which indicates density estimates across space within a given day are comparable and can be used to estimate mean density for the sampled region. Recent efforts to measure spawner and recruit abundance are based on statistical grids (10' latitude by 10' longitude) because this scale is of interest to managers within Lake Superior. Assessments of larval cisco will be of more utility when they are executed to the same scale. Collectively, our results suggest that multiple vessels/agencies can be used to conduct larval cisco surveys of major geographic regions within Lake Superior, facilitating large-scale research initiatives.

When designing sampling programs, it is imperative to understand the biases associated with different gears and strategies. Studies targeting the larval phase of cisco should employ gears known to efficiently capture the demographics of this life stage. However, it is also important to make effective use of time and resources. Developing protocols that balance these conditions will ensure that surveys achieve a rigorous estimate of abundance across the

widest possible spatial range. Using a coordinated effort to advance the level of understanding of cisco early life history in Lake Superior will facilitate research initiatives and ultimately provide a greater understanding of cisco population dynamics.

IN LAKE SUPERIOR

Abstract. Evidence from small lakes suggests that predation on larval cisco (*Coregonus artedii*) by non-native rainbow smelt (*Osmerus mordax*) can lead to cisco suppression or extirpation. However, research on larger lakes has led to equivocal conclusions. In this study, we examine the potential predation effects of rainbow smelt in two adjacent but contrasting environments on Lake Superior. We sampled ichthyoplankton, pelagic fish communities, and diet composition of rainbow smelt and used a bioenergetics model to estimate the proportion of cisco larvae consumed by rainbow smelt in each bay. Our results suggest predation by rainbow smelt can account for up to 100% mortality of larval cisco. We summarized density estimates of predators and prey at different spatial scales and found predation impact decreased as smelt abundance increased. Finally, we examined the sensitivity of past estimates of estimates of rainbow smelt abundance derived from bottom trawl surveys and extrapolations of temporal overlap between rainbow smelt and larval cisco. After adjusting these parameters to reflect current understanding, we found previous estimates may have been conservative. We conclude rainbow smelt may have been an important contributor to the decline in cisco populations in Lake Superior.

CHAPTER II:

AN EMPIRICAL RE-ASSESSMENT OF THE PREDATORY EFFECTS OF RAINBOW SMELT (*OSMERUS MORDAX*) ON CISCO (*COREGONUS ARTEDI*)

IN LAKE SUPERIOR

Abstract. Evidence from small lakes suggests that predation on larval cisco *Coregonus artedii* by non-native rainbow smelt *Osmerus mordax* can lead to cisco suppression or extirpation. However, research on larger lakes has led to equivocal conclusions. In this study, we examine the potential predation effects of rainbow smelt in two adjacent but contrasting embayments on Lake Superior. We sampled ichthyoplankton, pelagic fish communities, and diet composition of rainbow smelt and used a bioenergetics model to estimate the proportion of cisco larvae consumed by rainbow smelt in each bay. Our results suggest predation by rainbow smelt can account for up to 100% mortality of larval cisco. We summarized density estimates of predators and prey at different spatial scales and found predation impact decreased as spatial resolution increased. Finally, we examined the sensitivity of past conclusions to estimates of rainbow smelt abundance derived from bottom trawl samples and assumptions of temporal overlap between rainbow smelt and larval cisco. After adjusting these parameters to reflect current understanding, we found previous predation estimates may have been conservative. We conclude rainbow smelt may have been an important contributor to the demise and slow recovery of cisco in Lake Superior.

Hrabik et al. (1998) showed that Introduction

of cisco in Sparkling Lake, Wisconsin

first do Exotic species introductions threaten ecosystem integrity worldwide (Mack et al. 2000; Mooney and Hobbs 2000). Freshwater systems are especially vulnerable to biological invasions (Sala et al. 2000; Lodge 2001). The loss of diversity, as a consequence of species invasions, appears to be greater in freshwater systems compared to terrestrial systems (Ricciardi and Rasmussen 1999; Mooney and Cleland 2001). A successful invasion event often features a rapid increase in the invading species followed by declines of previously abundant native species (Capelli 1982; Worthington and Lowe-McConnell 1994; Ricciardi et al 1998). Despite the practical importance of understanding the relationship between exotic and native species, the mechanisms by which exotic species impact native species are often poorly understood (Mercado-Silva 2007).

concl After intentional introduction to Crystal Lake, Michigan, in 1912, rainbow smelt *Osmerus mordax* escaped into Lake Michigan by 1923 and subsequently spread throughout the Great Lakes (Van Oosten 1937). Within small lake systems, the effect of exotic rainbow smelt on native cisco *Coregonus artedii* populations has been well documented. Evans and Loftus (1987) reported the negative impact of rainbow smelt invasions in Ontario Lakes, noting the substantial change in food web interactions and displacement of native species such as cisco. Loftus and Hulsman (1986) combined empirical evidence with modeling to show that rainbow smelt predation on coregonid larvae was the primary cause for recruitment failure in Twelve Mile Lake, Ontario. Similarly,

Hrabik et al. (1998) showed that predation by rainbow smelt led to the extirpation of cisco in Sparkling Lake, Wisconsin, only eight years after rainbow smelt were first detected. Further, restoration of walleye *Sander vitreus* populations in northern Wisconsin lakes has increased predation pressure on rainbow smelt, leading to cisco recovery (Krueger and Hrabik 2005). However, inferences drawn from these small-lake studies may not be applicable to the much larger Great Lakes because ecosystem size could lead to differences in spatial and temporal overlap of predator and prey (Peterson et al. 1999).

Biological invasions have had many effects on native fish communities within the Great Lakes (Mills et al. 1993; Ricciardi 2001; Madenjian et al. 2008). However, investigators have reached different conclusions about the affect of rainbow smelt on cisco in Lake Superior. Anderson and Smith (1971) and Christie (1974) found negative correlations between rainbow smelt and cisco and concluded that rainbow smelt were responsible for the collapse of cisco stocks. Anderson and Smith (1971) suggested competition was the mechanism that caused cisco to decline. Swenson (1978) suggested that turbidity contributed indirectly to the decline of cisco by concentrating larval cisco and predatory rainbow smelt in surface waters. Further, Cox and Kitchell (2004) developed an ecosystem simulation model to evaluate hypotheses concerning recruitment failure of Lake Superior cisco and found that their “strong rainbow smelt predation” hypothesis best fit the time series data (1929-1998).

In contrast, neither predation (Selgeby et al. 1978) nor competition (Selgeby et al. 1994) by rainbow smelt were identified as important factors

contributing to the decline of Lake Superior cisco in the Apostle Island region, Wisconsin, and Black Bay, Ontario. Selgeby (1982) examined commercial catch and effort statistics for the Wisconsin cisco fishery spanning 1936 to 1978 and concluded overfishing was the likely cause of stock collapse. Bronte et al. (2003) added that if rainbow smelt were depressing cisco abundance prior to the late 1970s, then the 90% reduction in rainbow smelt biomass during 1978-1981 should have resulted in immediate strong recruitment of cisco, which did not occur until the 1984 year class (MacCallum and Selgeby 1987).

In this study, we performed a comparative assessment of the influence of rainbow smelt predation on larval cisco populations in Thunder and Black Bays, Ontario. Despite their close proximity, these bays exhibit contrasting physical and biological characteristics. Thunder Bay (74,000 ha) is oligotrophic with moderate densities of rainbow smelt while Black Bay (51,000 ha) is more productive and currently supports higher densities of rainbow smelt. Historically, both bays supported large commercial fisheries for cisco (Jacobson et al. 1987), but these fisheries declined throughout the 1980s. The Thunder Bay cisco stock is presently composed of several year classes and the stock appears strong (Yule et al. 2008a), but the Black Bay cisco stock is likely well below historic levels. We used a bioenergetics model to estimate consumption of larval cisco by rainbow smelt and compared this to estimates of total larval cisco abundance for each bay. We also examined the effect of spatial averaging of density estimates on our conclusions. Specifically, we compared estimates when we assumed each bay had homogenous densities of rainbow smelt and larval cisco with estimates

obtained using the observed spatial variation in predator and prey densities. Finally, we re-estimated predation rates from the data of Selgeby et al. (1978), using the WI bioenergetics model and more recent information on several key assumptions, including duration of predator prey overlap and availability of rainbow smelt to bottom trawl gear.

Methods

Larval cisco survey

We conducted two synoptic surveys of both Thunder and Black Bays in 2006. Thunder Bay sampling occurred between 2-7 May and 21-25 May, while sampling of Black Bay occurred on 13 May and 19-20 May. A systematic sampling design (Figure 4) was employed after pilot data suggested 1 site/1,000 ha would result in standard errors that were 20-30% of the mean density (U.S. Geological Survey, *unpublished data*). Two vessels were used during the survey. A 2 x 1-m paired neuston net ("neuston net") was deployed from one vessel and a 0.5-m (diameter) conical net ("conical net") was deployed from the second vessel. Both nets had 500- μ m mesh. A single sample consisted of a 5-min tow in the 0-1 m depth stratum. Nets were towed 30 m behind each vessel. To maintain consistency, all tows were pulled with the wind on the stern with vessel speed ranging from 3.2 to 3.9 km/hr. The volume of water filtered was determined using General Oceanics (Miami, Florida) model 2030 flowmeters. The two net samples from the paired neuston net were pooled into a single sample for each tow. Cisco

larvae were present in the surface stratum throughout the study period and all collected specimens were preserved in 95% ethyl alcohol. Previous analyses demonstrated the two gears provide comparable larval cisco density estimates and repeated sampling at several sites showed estimates did not vary over daylight hours (Myers et al. In Press).

Previous studies have demonstrated that larval cisco are generally concentrated near the surface (Selgeby et al. 1978, Hatch and Underhill 1988, Oyadomari and Auer 2004). We estimated abundance of larval cisco in each bay during each synoptic survey by multiplying mean densities by the volume of water in the uppermost 1 m of the water column of each bay. An analysis of

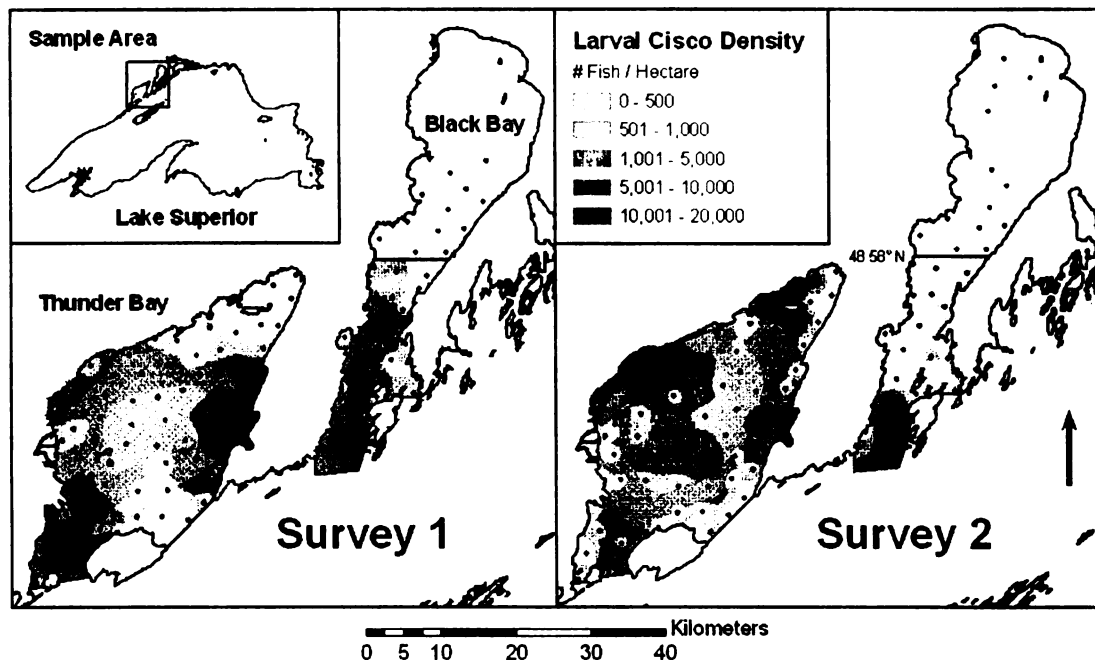


Figure 4. Map of larval cisco sampling locations and density estimates in Thunder and Black Bays, Lake Superior. Two synoptic surveys of each bay were completed between 2-25 May 2006. Interpolated surfaces were created using inverse distance weighting.

larvae length-frequency distributions showed that fish collected during the second synoptic survey of both bays were likely new emergers, so we opted to estimate total larval abundance by summing the two estimates for each bay.

Visual identification of larval coregonids is inexact. Lake whitefish *Coregonus clupeaformis* larvae are distinguishable from other larval coregonids based on larger size (Hinrichs 1979) and melanophore patterns across the dorsum (Hinrichs 1979, Auer 1982). Differentiating larval cisco from other coregonids like bloater *Coregonus hoyi* and kiyi *Coregonus kiyi* is difficult (Anderson and Smith 1971, Hinrichs 1979). Because bloater are believed to spawn later than cisco (Hinrichs 1979, Auer 1982), we assumed that emergence of cisco was separated temporally from the emergence of bloater. Kiyi are not known to spawn in Thunder Bay and Black Bay. We therefore identified larval coregonids as cisco or lake whitefish.

All larval fish in each sample were counted. When samples contained ≤ 100 larval fish all specimens were identified and photographed using a Leica S6D dissecting scope equipped with a Panasonic digital camera. When samples contained > 100 individuals a random sample of 50 specimens were selected to estimate proportions of cisco and lake whitefish. We measured total length (TL) of each photographed fish to the nearest 0.1 mm using SigmaScan Pro 5 software (SPSS, Inc., Chicago, IL). Density (larval cisco/ $1,000 \text{ m}^3$ of water) was calculated for each sample. Because the northernmost extent of the hydroacoustic survey in Black Bay was approximately 48.58° N latitude, average larval density values were calculated using only sites south of this latitude (Figure

4). It is unlikely that cisco spawn in the northern reaches of Black Bay as commercial fisherman have not been successful there (Ken Cullis, Ontario Ministry of Natural Resources, personal communication).

Hydroacoustics and trawling survey

Multiple gears were used to estimate densities of age-1 and older fish in Thunder and Black Bays between 13-22 May 2006. All samples were collected using the U.S. Geological Survey (USGS) research vessel *Kiyi*. Between 13-15 May, we collected four daytime bottom trawl samples in each bay at standardized sites sampled annually each spring (Stockwell et al. 2006a). We also collected a daytime midwater trawl sample (between 20-39 m depth) at a Black Bay site on 17 May where high densities of larval cisco had been collected on 16 May. We systematically surveyed each bay during the nighttime hours of 16-22 May using a series of parallel acoustic transects spaced at roughly 3 km intervals (Figure 5). Nighttime work commenced 30 minutes after the start of nautical twilight and ended 1-2 hours before nautical twilight ended. We collected night midwater trawl samples periodically along the acoustic survey path, with a total of 7 and 14 samples collected from Black and Thunder Bays, respectively. Bottom trawl samples were not collected at night because rainbow smelt (the species of main interest in this study) perform diel vertical migration in Lake Superior (Heist and Swenson 1983; Yule et al. 2007).

The depth distribution, acoustic size, and densities of fish were estimated using a DT-X digital echosounder (BioSonics, Inc., Seattle, Washington)

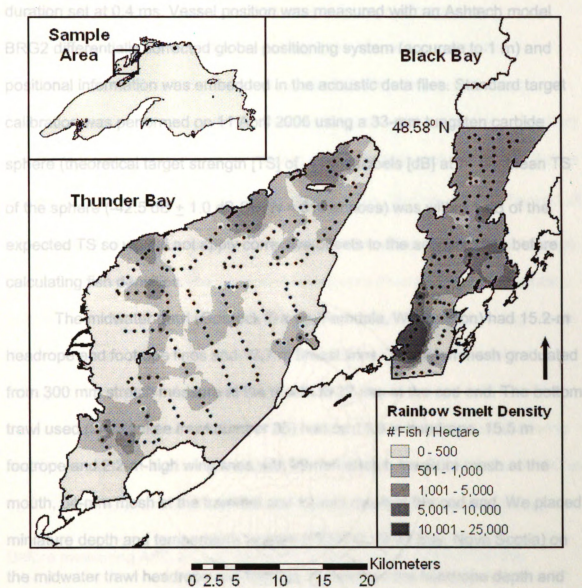


Figure 5. Map of acoustically-derived rainbow smelt density estimates collected in Thunder and Black Bays (Lake Superior), 17-22 May 2006. Acoustic densities were estimated for each 1 km of boat travel. Interpolated surfaces were created using inverse distance weighting.

equipped with a 120 kHz circular split-beam transducer with a half-power beam width of 6.7° . The transducer was mounted on a 1.2-m-long tow body and was deployed 1 m below the surface. The transducer emitted 3 pings/s with the pulse

duration set at 0.4 ms. Vessel position was measured with an Ashtech model BRG2 differentially corrected global positioning system (accurate to 1 m) and positional information was embedded in the acoustic data files. Standard target calibration was performed on 11 April 2006 using a 33-mm tungsten carbide sphere (theoretical target strength [TS] of -41.5 decibels [dB] at 7° C). Mean TS of the sphere (-42.5 dB $\pm$ 1.0 dB SD, N = 619 echoes) was within 1 dB of the expected TS so we did not apply corrective offsets to the acoustic data before calculating fish densities.

The midwater trawl (Gourock Trawls, Ferndale, Washington) had 15.2-m headrope and footrope lines and 13.7 m breast lines. The nylon mesh graduated from 300 mm stretch measure at the mouth to 12 mm at the cod end. The bottom trawl used (3/4 Yankee trawl number 35) had an 11.9 m headrope, 15.5 m footrope and 2.2-m-high wing lines with 89-mm stretch measure mesh at the mouth, 64-mm mesh at the trammel and 12-mm mesh at the cod end. We placed miniature depth and temperature loggers (VEMCO, Shad Bay, Nova Scotia) on the midwater trawl headrope and footrope to measure the headrope depth and trawl mouth height when fishing.

Trawl catches were sorted by species and weighed in aggregate to the nearest gram. For small catches (< 50 individuals per species) all fish were measured to the nearest mm total length. For larger catches at least 50 individuals per species were selected randomly and measured and the remaining fish were counted.

Fish density estimates and apportioning acoustic targets to species.

Acoustic data were processed using Echoview software version 3.25.55.06 (SonarData Ltd., Tasmania, Australia). Fish density estimates were developed using echo integration methods. We used a bottom tracking algorithm to establish a line 0.2 m above the bottom (i.e., “a bottom exclusion line”). Before measuring mean volume backscattering strength (i.e., S_v) we double-checked all echograms to ensure bottom echoes were properly excluded. A second line was added 3-5 m below the transducer of all echograms (“surface line”) to exclude echoes in the transducer near field and any air bubbles resulting from high seas. We used the embedded vessel position data to define 1,000 m intervals on echograms and each interval was further divided into 10-m-high cells from the surface line to the bottom exclusion line. We measured the area backscattering coefficient (ABC) in each cell. MacLennan and Fernandez (2000) defined ABC as $10^{(S_v/10)} \times T$, where T is the mean thickness of the cell (m) being integrated.

Before measuring ABC we applied a -65 dB S_v threshold to minimize the inclusion of backscattering from the macroinvertebrate *Mysis relicta*. We estimated the mean backscattering cross section (σ_{bs}) of the average size fish in each cell from mean target strength ($\sigma_{bs} = 10^{TS/10}$). We used identical criteria for single-target acceptance defined by Yule et al. (2006) except the minimum TS in the present study was set at -60 dB. This lower threshold was chosen to ensure that age-1 rainbow smelt were included in the calculation of mean TS. Parker Stetter et al. (2006) showed that yearling and older rainbow smelt consistently

had a TS larger than -60 dB in Lake Champlain (New York - Vermont, United States, and Quebec, Canada). Fish density (#/ha) by cell was calculated by dividing ABC by σ_{bs} and multiplying the resultant by 10,000 (i.e., $10,000 \text{ m}^2 = 1 \text{ ha}$). All 10-m-high cells in each 1000-m-long interval were summed to estimate total density in each interval.

To apportion acoustic targets to species we developed an approach for separating rainbow smelt from cisco based on differences in their acoustic sizes. Using a parallelogram drawing tool available in the Echoview software, we drew midwater trawl paths on echograms (all data were time tagged). We then exported single targets from each trawl path so that TS distribution data could be compared to length distributions in each trawl sample. We used TS distributions from nearly-pure catches of cisco and rainbow smelt to determine the relative proportions of these species at locations where trawl samples were not collected. Of the 21 night midwater trawl samples, two were nearly-pure cisco (> 97% by number) and two were nearly pure rainbow smelt (98%). The single targets from these trawl paths were used in a recursive partitioning platform available in JMP 5.1 (SAS Institute, Inc., Cary, NC) to determine the TS “cutting values” which most significantly separated the mean TS of these species. The recursive partitioning technique was applied to the four possible pair-wise comparisons to determine four cutting values that we then averaged.

We compared the efficacy of our mean “cutting value” approach for separating rainbow smelt and cisco acoustic targets by comparing predicted proportions of cisco and rainbow smelt (separated with the cutting value) to

observed proportions in each of the 16 night midwater trawl samples that were not used to develop the cutting values. We excluded one deepwater midwater trawl sample because the catches of both rainbow smelt and cisco were minimal. We used a *t*-test for independent samples to test the null hypothesis that hydroacoustics and midwater trawling achieve similar proportions of rainbow smelt and coregonids. We set $\alpha = 0.05$ for all statistical tests.

Rainbow smelt food habits

Rainbow smelt stomachs were collected to assess food habits. Upon capture, rainbow smelt were quickly sorted into 10-mm-wide length bins (i.e., < 50 mm, 50-59 mm,...,>150 mm) targeting up to 10 fish per bin per trawl sample and placed on ice to slow digestion. We then excised stomachs and combined them into one sample vial per length bin per trawl sample. Stomachs were preserved in alcohol, and vials were labeled with the trawl serial number and length bin so we could later determine where and when the stomachs were collected.

Consumption and predation mortality estimates

We used the Wisconsin bioenergetics model (Wisconsin SeaGrant, UW-Madison, Center for Limnology, Bioenergetics v 3.0 software) to estimate rainbow smelt predation on larval cisco populations. Because larval cisco and rainbow smelt were caught during the duration of our study (2-25 May 2006) we opted to model consumption of rainbow smelt for 30 days (i.e., 1-30 May). We

separated rainbow smelt into four size classes (≤ 60 mm, 61-90 mm, 91-120 mm, and >120 mm; Figure 6) to structure the bioenergetics analysis with respect to rainbow smelt size.

The bioenergetics model required several inputs, including average temperature experienced by rainbow smelt, rainbow smelt diet composition, and the caloric content of both rainbow smelt and their prey. Because Thunder Bay was isothermic at 4.7°C , we used this temperature in the Thunder Bay simulations. In Black Bay, water temperature near the surface was slightly warmer (5.8°C) than near the lakebed (4.9°C) so we used a value of 5.4°C . We examined rainbow smelt stomach contents under a dissecting microscope (Nikon SMZ-2B). Contents were separated into the following categories: *Mysis relicta*, *Diporeia spp.*, zooplankton, larval coregonids, or other items (terrestrial insects, benthic organisms, yearling and older fish, etc.). Because the larvae in the ichthyoplankton survey were identified predominately as cisco ($>99\%$), coregonid larvae in rainbow smelt were assumed to be cisco. Each respective diet item was placed in a drying oven for 24 hours at 60°C and weighed to the nearest 0.0001 gram using an analytical balance (Sartorius ED2245). We determined the average diet composition (as determined by dry weight) in each bay by pooling all stomachs in each rainbow smelt size class (Table 2). We used the estimates of rainbow smelt energy density reported by Lantry and Stewart (1993). A relationship provided by Elliot et al. (1996) was used to convert standard

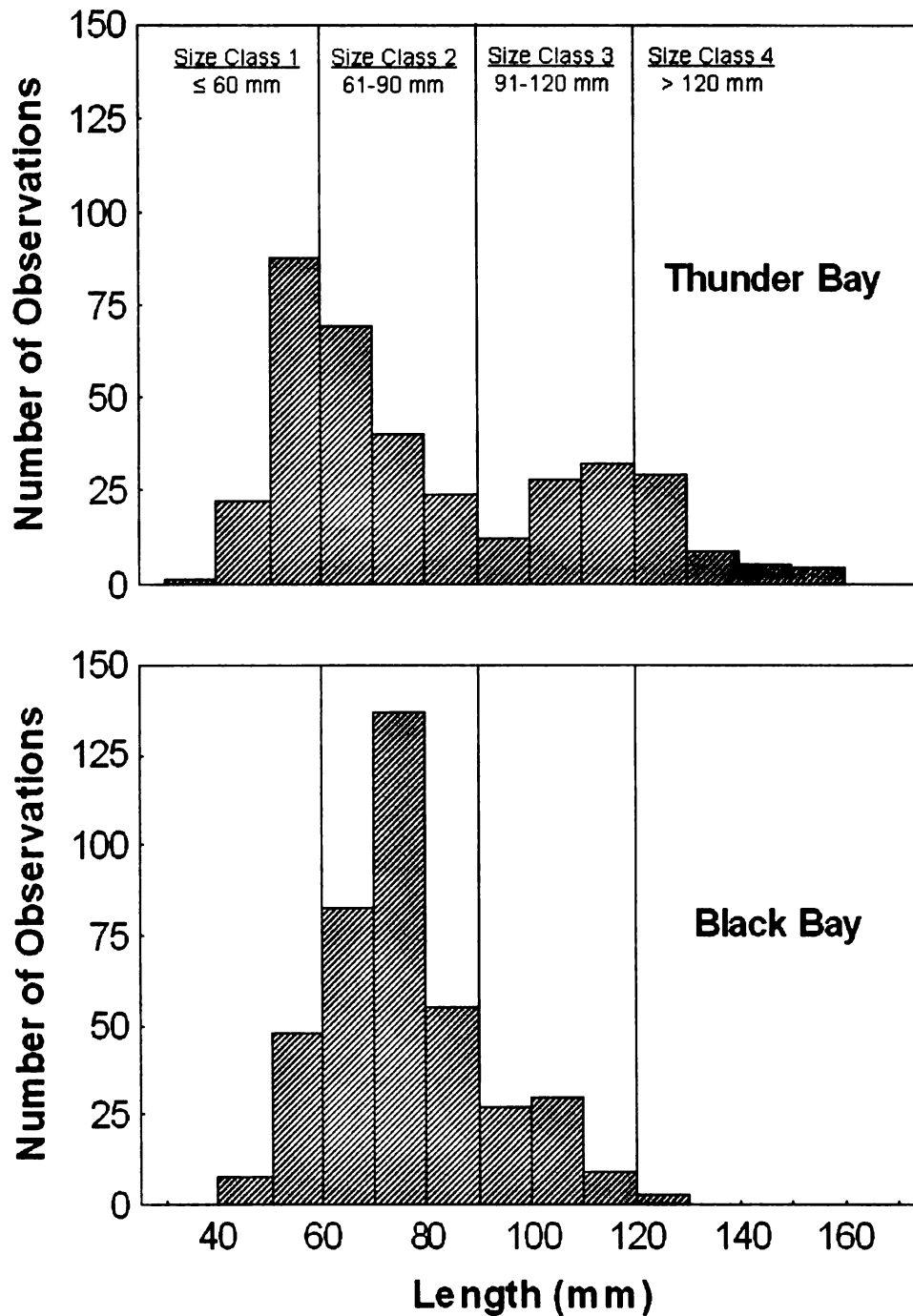


Figure 6. Length frequency distributions for Thunder Bay (363 measurements) and Black Bay (400 measurements) rainbow smelt and the four size classes (≤ 60 mm, 61-90 mm, 91-120 mm, > 120 mm) used to structure the bioenergetic analyses.

Table 2. Relative contribution of each prey item to the diet of rainbow smelt. Percentages are based on the dry weight of stomach contents.

	Length (mm)	Stomachs Examined	Stomachs w/ Food	Diet Item				
				Mysis	Diporeia	Plankton	Cisco Larvae	Other
Thunder Bay	≤60	171	44	18.9%	0.0%	78.8%	0.0%	2.3%
	61-90	268	151	43.3%	0.7%	54.1%	0.0%	1.9%
	91-120	165	101	58.2%	8.5%	30.0%	2.0%	1.3%
	>120	134	71	60.1%	15.9%	7.6%	0.1%	16.4%
Black Bay	≤60	107	53	0.5%	0.0%	99.5%	0.0%	0.0%
	61-90	342	306	5.8%	1.0%	91.5%	0.1%	1.8%
	91-120	266	240	3.4%	4.6%	88.1%	0.2%	3.6%
	>120	96	57	12.5%	8.5%	43.7%	0.1%	35.3%

length(SL) reported by Lantry and Stewart (1993) to an estimate of total length (TL). We calculated the average length of rainbow smelt in each size class in each bay and used a length-weight relationship for rainbow smelt in Lake Superior (Yule et al. 2007) to estimate the average individual weight in each size class (Table 3).

We used literature values to estimate energy densities of prey consumed by rainbow smelt (Table 4). Johnson et al. (1998) reported a linear relationship between energy density and weight of cisco up to 500 g. Because the weight of individual cisco larvae is negligible, we used the intercept (4,550 J/g) of the Johnson et al. (1998) relationship to estimate energy density of larval cisco (Table 4). This estimate of energy density falls within the range of values

Table 3. Model inputs for rainbow smelt energy density (J/g wet weight) in Thunder Bay and Black Bay. Simulation day 1 is May 1. Average length within each size class was determined using the information provided in Figure 6.

	Simulation	Rainbow Smelt Total Length			
	Day	≤60	61-90	91-120	>120
Thunder Bay		Average Length (mm) within Bin			
		54	72	108	132
		Average Weight (g)			
		0.5	1.4	5.7	11.2
		Energy Density (J/g)			
		3268	3526	4997	5205
Black Bay	1	3268	3526	4997	5205
	30	3372	3511	4425	4674
		Average Length (mm) within Bin			
		55	75	103	123
		Average Weight (g)			
		0.6	1.6	4.8	8.8
		Energy Density (J/g)			
	1	3268	3784	4954	5127
	30	3372	3650	4373	4581

Table 4. Energy density (J/g wet weight) of prey items found in the stomachs of rainbow smelt from Thunder and Black Bays in Lake Superior.

Prey	Energy Density (J/g)	Source
<i>Mysis relicta</i>	3,537	Johnson et al. (1993)
<i>Diporeia spp.</i>	4,386	Johnson et al. (1993)
Zooplankton	3,016	Johnson et al. (1993)
Larval Cisco	4,550	Johnson et al. (1993)
Other (Insects and Fish)	3,786	Lantry and Stewart (1993)

reported for other Great Lakes larval fishes (Hartman and Margraf 1992). Energy density was held constant throughout our 30-day model simulations.

Growth of rainbow smelt during our 30 day simulations was too small to estimate accurately from our data. Therefore, we used a range of P-values (proportion of maximum consumption) to estimate consumption. We modeled two scenarios: 1) the P-value needed for maintenance (i.e., start wt = end wt) for each size rainbow smelt size class (P-value = 0.18-0.22), and 2) a P-value of 0.5, which corresponds with the observed growth reported by Baily (1964). These P-values provided a range of realistic growth trajectories and thus predation intensities.

The bioenergetics model integrated all variables and predicted the biomass of each prey item consumed, given the rate of feeding. We multiplied the biomass consumed by our estimates of rainbow smelt abundance to estimate the total biomass of larval cisco consumed. The biomass of larval cisco consumed was divided by their average mass to estimate the total number consumed. Average mass of cisco larvae (0.003 g) was estimated by weighing 89 individuals (ranging from 9.5-12 mm) to the nearest 0.001 grams. After completing a model simulation for each size class we summed across size classes to estimate total numbers of cisco larvae consumed in each bay. We estimated the mortality attributable to rainbow smelt predation by dividing the number of cisco larvae consumed by the total abundance of cisco larvae in each bay. Predation mortality (PM) was calculated in following manner:

$$PM = (D * C * R) / L$$

where D is the duration of feeding (days in contact), C is the number of cisco larvae consumed per day (dependent on the daily ration), R is rainbow smelt abundance, and L is larval cisco abundance. We did not allow predation mortality to exceed 100%.

Effect of spatial scale on predation mortality

To examine the influence of spatial scale on our estimates of predation mortality, we analyzed the data at three different scales. In the first analysis we calculated the arithmetic mean densities of rainbow smelt in each bay using the 1,000 m acoustic intervals as sample units. We calculated the arithmetic mean density of larval cisco for each synoptic survey using all 5-minute larval tows. Abundance of rainbow smelt and cisco larvae was calculated by multiplying density estimates by the area of each respective bay. Total abundance of cisco larvae was calculated by adding estimates of abundance from the two synoptic surveys of each bay. In the second analysis, Thunder Bay was divided into quadrants, Black Bay was halved, and mean regional densities were calculated. We determined which samples were collected in each region and calculated mean regional densities. Abundance of each region was calculated by multiplying average density (#/ha) for the region by its area (ha). Total abundance of cisco larvae within a region was calculated by adding results from the two synoptic surveys. Total abundance of available cisco larvae was calculated by summing regional abundances for each bay. In the final analysis we divided both bays into grids measuring $\leq 1,000$ ha (i.e., a grid was less than 1,000 ha if the shoreline did

not permit for a complete grid). We used the Geostatistical Analyst Extension of ArcMap version 9.0 (ESRI, Redlands, CA) to create interpolated surfaces using inverse distance weighting. The number of pixels (1 ha) in each grid were counted to determine the area of each grid. We used the average of all pixels within a grid to estimate densities of rainbow smelt and cisco larvae during the first and second synoptic survey. We calculated abundance by multiplying the density estimates by the area of each respective grid. Total abundance of cisco larvae in each grid was determined by adding the abundance estimates from each synoptic survey. Total abundance of cisco larvae was calculated by summing the abundances from each respective grid.

Re-assessment of earlier findings

Selgeby et al. (1978) and Selgeby et al. (1994) examined the influence of rainbow smelt on the survival of larval cisco in Black Bay and the Apostle Islands in 1974. Because of similarities in the objectives and sampling location (Black Bay) of Selgeby et al. (1978) and our current study, we compared and contrasted assumptions of the two approaches. Selgeby et al. (1978) estimated rainbow smelt densities with day bottom trawls but Mason et al. (2005) later showed day bottom trawl samples provided lower estimates of rainbow smelt densities when compared to acoustic and midwater trawl (AC-MT) methods. Also, Selgeby et al. (1978) assumed that rainbow smelt consumed larval cisco during a 5-10 day period. However, results of our study suggest that both larval cisco and rainbow smelt overlap for a much longer period (≈ 30 days).

To determine the average number of cisco larvae consumed by rainbow smelt within a given day in May 1974, Selgeby et al. (1978) scaled the mean stomach content mass and the average number of cisco larvae present in the guts to project daily rations of 1.5% and 2.5% of their body weight. Using information provided by Selgeby et al. (1978) and Selgey et al. (1994) we developed a bioenergetics model to re-estimate the average number of cisco larvae consumed by rainbow smelt within a given day in May 1974. The proportion of diet items found in the stomachs of rainbow smelt in the spring of 1974 was reported in Selgeby et al. (1994). The value of rainbow smelt energy density, energy density of their prey, and temperature in Black Bay was assumed to be the same as our current study. We used daily rations of 1.5% and 2.5% (in lieu of P-values) to estimate the average number of cisco larvae consumed by rainbow smelt in each of the four rainbow smelt size classes (≤ 60 mm, 61-90 mm, 91-120 mm, and >120 mm). Predation mortality was calculated using the equation described previously. Abundance of rainbow smelt and larval cisco in May 1974 was reported in Selgeby et al. (1978).

Results

Larval cisco survey

Density ($\pm$ SE) of cisco larvae in Thunder Bay averaged $2,796 \pm 69.7$ fish/ha ($n = 63$) during the first synoptic survey (2-7 May) and $3,343 \pm 54.5$ fish/ha ($n = 74$) during the second survey (21-25 May). In Black Bay, density of

cisco larvae declined from an average of $1,850 \pm 208$ fish/ha ($n = 16$) during the first survey (13 May) to 471 ± 53 fish/ha ($n = 19$) during the second survey. Differences in larval distributions were apparent during the two surveys of both bays (Figure 4). With exception of the extreme northeast and southeast portions of the Thunder Bay, relatively high densities of larval cisco were found throughout the bay during both surveys. In Black Bay there appeared to be a north-to-south gradient in larval cisco density. Four larval samples were collected in the most northern waters of Black Bay (Figure 4) on 19 May 2006 but no cisco larvae were captured.

Hydroacoustics and trawling survey

During 17-22 May 2006 we collected 220 and 96 km of acoustic data in Thunder Bay and Black Bay, respectively (Figure 5). Cisco were predominant in Thunder Bay, representing 57.3% of 2,156 fish caught by night midwater trawl samples, followed by rainbow smelt (30.9%), kiyi (5.0%), and bloater (4.9%). Rainbow smelt were the principal species in Black Bay, representing 95.4% of the fish caught in night midwater trawl samples (4,701 total fish). The mean cutting-edge TS value for separating cisco and rainbow smelt was -44.59 dB. We calculated expected proportions of rainbow smelt and cisco in each of the 16 midwater trawl samples not used to develop this mean cutoff value. Expected proportions of rainbow smelt and coregonids did not vary significantly from the actual proportions captured in the 16 midwater trawl samples (rainbow smelt: t -

value = -0.335, $P > 0.7$, DF = 30, Figure 7A; coregonids: t -value = -0.934, $P > 0.3$, DF = 30, Figure 7B).

We concluded that the approach used to apportion acoustic targets to species was reasonable. Thus, when calculating species densities we assumed all targets smaller than -44.59 db were rainbow smelt, regardless of depth. This empirically derived cutting edge value (-44.59) is consistent with recent literature reporting acoustic versus real size relationships for rainbow smelt and coregonids. For example, an equation by Rudstam et al. (2003) predicts the TS of a 150 mm rainbow smelt to be -44.40 dB at 120 kHz, which is within 0.2 dB of our cutting value. Meanwhile, an equation by Mehner (2006) (developed for vendace *Coregonus albula*) predicts that a 150 mm coregonid has a TS of -40.91 dB, which is considerably larger than an equivalent size rainbow smelt. We were confident in our identification of rainbow smelt using acoustic TS because most captured rainbow smelt (98.9%) were less than 150 mm total length (TL) and most captured cisco exceeded 225 mm TL.

Acoustically derived estimates of rainbow smelt density were generally high in Black Bay ($3,435 \pm 460$ fish/ha; Table 5), with the greatest values along the southwest shore and the central east portions of the bay (Figure 5). The estimate of rainbow smelt density using acoustics at night was approximately three times higher than the value obtained from four day bottom trawl samples collected in Black Bay ($1,181 \pm 460$ fish/ha; Table 5). In Thunder Bay, there were small areas of moderate rainbow smelt abundance but densities were generally low across most of the bay (Figure 5). The estimated mean density of rainbow

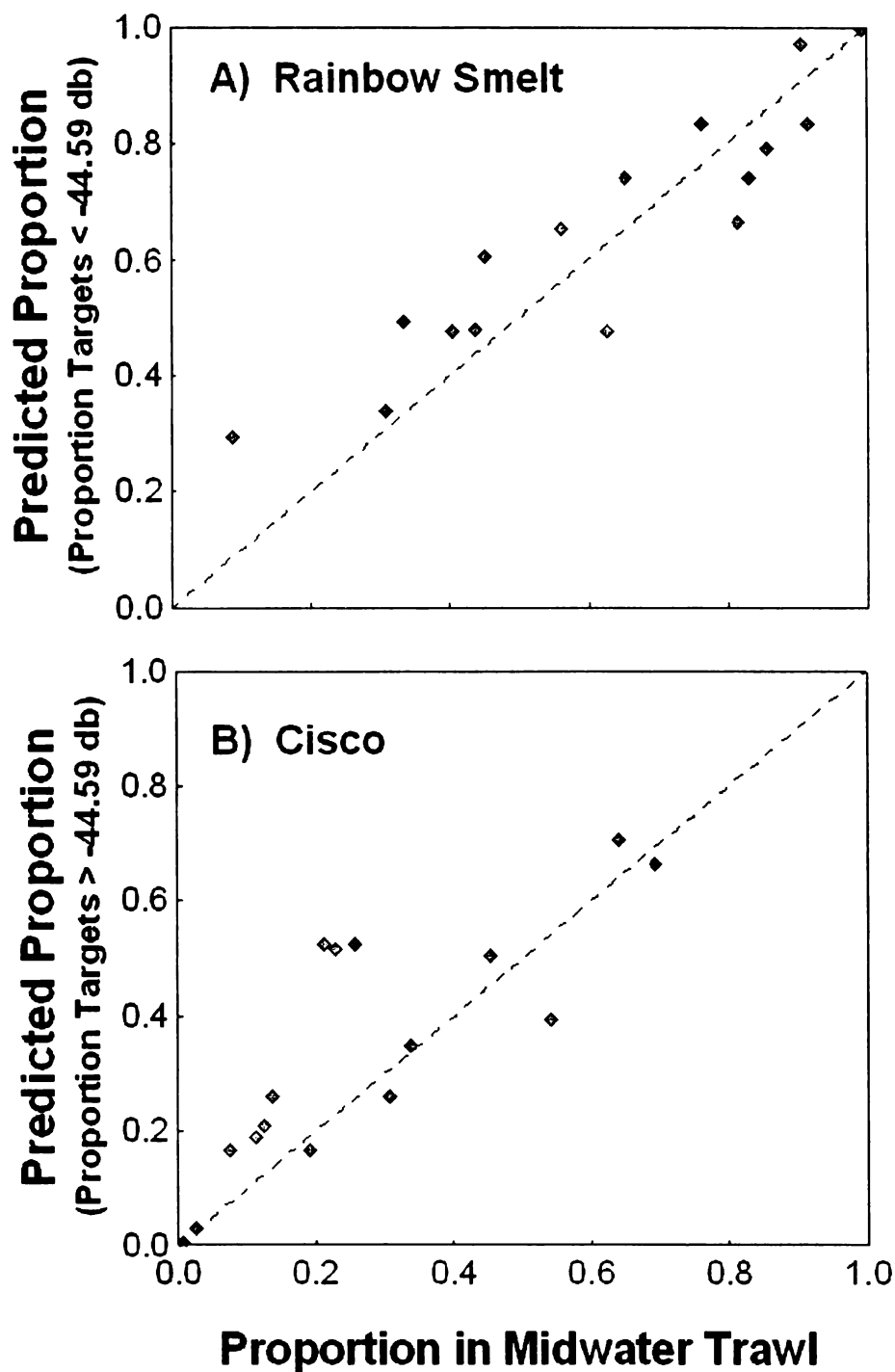


Figure 7. Observed proportions of rainbow smelt (A) and coregonids (B) captured in midwater trawls versus the predicted proportions from the TS distributions developed using the cutting-edge approach to apportion targets to species. The dashed line is the 1:1 line. A frequency distribution of the differences is located in the lower right corner.

Table 5. Rainbow smelt density estimates (rainbow smelt/ha [$\pm$ SE]) using night acoustics and midwater trawling (AC-MT) and day bottom trawls (BTR) in Thunder and Black Bays.

	<i>AC-MT</i>	<i>BTR</i>
Thunder Bay	530 (34)	932 (486)
Black Bay	3,435 (460)	1,181 (460)

smelt in Thunder Bay was 530 ± 34 fish/ha using night acoustics. Based on four day bottom trawls, the mean density of rainbow in Thunder Bay was 932 ± 486 fish/ha. Use of day bottom trawls to characterize the fish communities would lead to the inference that rainbow smelt densities were similar between Thunder and Black Bays (Table 5). However, evidence from acoustic coverage of both bays suggests that rainbow smelt densities were 6-7 times greater in Black Bay compared to Thunder Bay. The day midwater trawl collected in Black Bay caught XXXX rainbow smelt. Because of the concerns associated with using bottom trawls to target pelagic species, we only used acoustically-derived estimates of rainbow smelt density in our bioenergetic analyses.

Rainbow smelt size-structure, consumption, predation mortality, and the effect of spatial scale

A total of 386 and 400 rainbow smelt were randomly selected and measured for total length in Thunder and Black Bays, respectively. There were two prominent size classes in Thunder Bay while there was proportionally more yearling (fish < 100 mm) rainbow smelt in Black Bay (Figure 6). A total of 1,549 rainbow smelt stomachs were examined (Table 2). Fifty percent of the stomachs

from Thunder Bay contained food compared to 81% of the stomachs from Black Bay. As rainbow smelt increased in size their diet shifted from predominately zooplankton to larger prey (*Mysis relicta*, terrestrial insects, fish). The incidence of larval cisco in rainbow smelt guts was low in both Thunder and Black Bays (Table 2).

Using arithmetic mean density estimates of rainbow smelt and larval cisco for Thunder Bay, we estimated that rainbow smelt consumed 107-261 million cisco larvae (depending on the p-value), equivalent to a predation mortality of 24-58% (Figure 8). Similarly, dividing Thunder Bay into four regions resulted in a projected 104-254 million larvae consumed, which was 23-55% of the larval cisco population (Figure 8). When densities of predators and prey were estimated for each 1,000 ha grid cell in Thunder Bay, we projected that rainbow smelt consumed only 80-178 million larvae, or 17-38% of the estimated larval cisco population (Figure 8).

Using arithmetic mean density estimates of rainbow smelt and larval cisco for Black bay we projected that 23-48 million cisco larvae were consumed during May 2006, or 48-100% of the larval cisco population (Figure 8). Dividing Black Bay into a north and south region resulted in a projected 23-52 million larvae consumed (43-100% of the larval cisco population). When densities of predators and prey were estimated for each 1,000 ha grid cell we projected that rainbow smelt consumed only 22-31 million larvae, 38-53% of the larval cisco population (Figure 8).

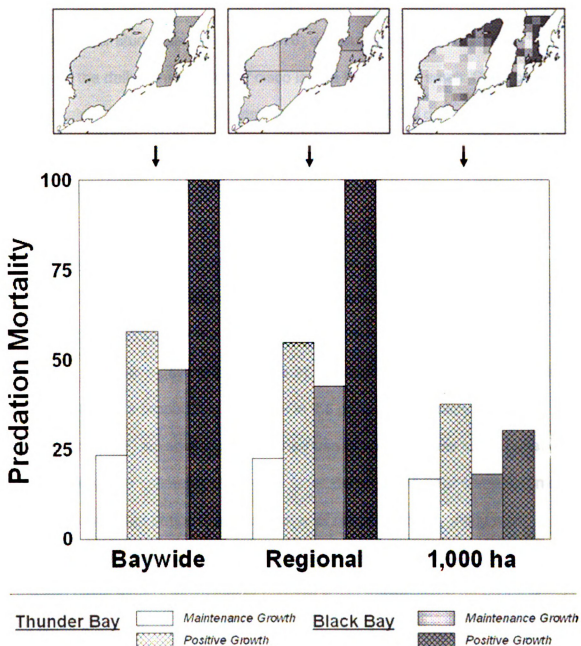


Figure 8. The estimated percentage of the larval cisco population consumed by rainbow smelt in both Thunder Bay and Black Bay. Two rates of feeding (maintenance growth: P -value ≈ 0.2 ; positive growth P -value ≈ 0.5) were used to encompass the probable growth of rainbow smelt through the 30-day simulations.

Re-assessment of earlier findings

The earlier study (Selgeby et al. 1978) and our study yielded similar estimates of the daily consumption of cisco larvae by rainbow smelt. Selgeby et al. (1978) calculated average consumption rates of 4.6 (1.5% daily ration) and 7.7 (2.5% daily ration) cisco larvae per day per rainbow smelt. The bioenergetics model gave consumption estimates of 6.0 (1.5% daily ration) and 10.9 (2.5% daily ration) cisco larvae per day in May 1974. Using the 1974 estimates of rainbow smelt and larval cisco densities (368/ha and 258,000/ha, respectively) reported by Selgeby et al. (1978), rainbow smelt were expected to consume 3.3-5.5% (Selgeby et al 1978) or 5.2-9.4% (bioenergetics model) of the larval cisco population during a five-day period (Figure 9). Increasing the period of overlap to 30 days resulted in a proportional increase in the predation mortality (Figure 9). Selgeby et al. (1978) acknowledged that their use of bottom trawls could have caused conservative estimates of rainbow smelt density. The gear comparison of this study showed that bottom trawl estimates of rainbow smelt density were conservative compared to AC-MT estimates for Black Bay but not Thunder Bay. For the two bays, AC-MT estimates of rainbow smelt density were on average 1.1.72 times greater than day bottom trawl estimates. Correcting rainbow smelt density estimates by a factor of 1.72, along with a 30 day period of overlap, resulted in predation mortality estimates approaching 100% (Figure 9).

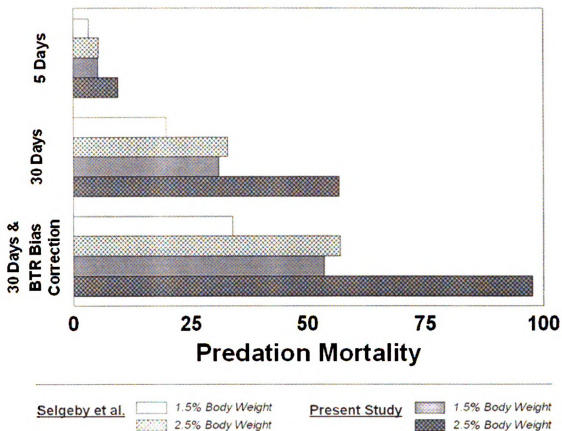


Figure 9. Approach of Selgeby et al. (1978) compared to our bioenergetics analysis and the sensitivity of results to assumptions of temporal overlap and bias due to sampling gear.

Discussion

We found that predation mortality by rainbow smelt could account for 16.9-57.8% and 37.8-100% of the mortality imposed on larval cisco populations in Thunder and Black Bays, respectively. Our consideration of different feeding rates and spatial scales led to the range in our estimates of predation mortality. Fisheries ecologists are recognizing more and more that fish distributions are patchy (Kolasa and Pickett 1991) and that the scale of an investigation influences

how we perceive ecological processes (Wiens 1989, Mason and Brandt 1999). The heterogeneity associated with spatial distributions can have fundamental effects on biological processes (Mason and Brandt 1996, Stockwell and Johnson), interactions amongst species (Tilman and Karevia 1997, Ault et al. 1999), and how natural resources are managed (Loehle 1991). Despite the concern about scaling effects, it is often still ignored in investigations of fish growth and production, predator-prey interactions, and sustainability of fisheries (Mason and Brandt 1999). Our study provides support for the claim that spatial scale of an investigation may affect the outcome of the research. If we had assumed that rainbow smelt and larval cisco were evenly distributed across the bays, we would have concluded that predation by rainbow smelt had a substantial effect on cisco. However, if we account for the spatial distributions of predator and prey by dividing the bays into 1,000 ha grids, the apparent impact of rainbow smelt decreases. It is difficult to recommend the appropriate spatial resolution for investigating these questions because we do not fully understand the movement of predators or prey through time. Multiple estimates of predator abundance throughout our simulation period would have improved our understanding of the degree of movement within a bay and the importance of spatiotemporal distributions.

Given our spatial coverage of each bay using hydroacoustics, we believe that density estimates based on acoustics and midwater trawls (AC-MT) represent the rainbow smelt populations of Thunder and Black Bays more accurately than our limited day bottom trawl sampling. Bottom trawls generally

provide conservative estimates of abundance, especially when the target species are above the trawl path or evade the approaching gear (Stockwell et al 2007, Yule et al. 2008b). Selgeby et al. (1978) only sampled rainbow smelt from Black Bay with bottom trawl samples because 41 day midwater trawl samples in the Apostle Islands caught zero rainbow smelt. During this study we captured rainbow smelt in the surface waters of Black Bay during daylight hours using a midwater trawl. This provided further evidence that day bottom trawl sampling provides conservative estimates of rainbow smelt density. In fact, the density estimate of rainbow smelt in Black Bay using AC-MT was six to seven times the estimate from bottom trawls (Table 5). However, bottom trawl sampling in Thunder Bay achieved a greater estimate of density compared to AC-MT. We believe that, by chance, the bottom trawl samples in Thunder Bay were collected in areas of high rainbow smelt density. The correction factor of 1.72, calculated using data from both bays, was an objective approach for recasting the bottom trawl derived rainbow smelt density estimates reported by Selgeby et al. (1978).

Selgeby et al. (1978) concluded that rainbow smelt predation was not affecting cisco populations because cisco stocks sustained a commercial operation at above average (historical) catch levels during the 1970s. However, Black Bay cisco stocks declined precipitously in the 1980s (Dextrase et al. 1986). Over a twenty-year period, Dextrase et al. (1986) observed increases in the length, age and growth of cisco in Black Bay, which was similar to what Selgeby (1982) reported for cisco populations that collapsed in U.S. waters of Lake Superior. Selgeby's (1982) analysis of the Wisconsin cisco fishery led him to

conclude that overfishing caused cisco stocks to collapse and later Dextrase et al. (1986) reached the same conclusions for the decline of cisco stocks in Black Bay. We believe the increases in length, age, and growth reported by Dextrase et al. (1986) were not the consequence of overfishing, but instead were linked to failed recruitment. Yule et al. (2008) provided evidence suggesting that cisco can live 20+ years and that variable recruitment is likely a natural characteristic of the species. Thus, we propose that Black Bay cisco stocks were adversely affected by rainbow smelt predation and that cisco stocks would have declined throughout the 1980s even in the absence of commercial fishing, albeit likely at a slower rate.

In support of Selgeby et al. (1978), Bronte et al. (2003) suggested that rainbow smelt were not impeding the recruitment of cisco because declines in rainbow smelt abundance in the late 1970s should have released cisco from this bottleneck. However, this inference relies on the assumption that large (>150 mm) rainbow smelt were the major source of cisco predation, because the decline in smelt densities during 1978-1981 was limited to large rainbow smelt (Gorman 2007). Despite an absence of large-bodied rainbow smelt in our samples, our modeling showed rainbow smelt can still have a significant effect on larval cisco. We believe that consumption of larval cisco by rainbow smelt, as reported by Selgeby et al (1994), may have played a pivotal role in the decline of cisco in Black Bay.

We recognize our estimates of consumption are sensitive to the suite of assumptions we made. For example, conservative estimates of larval cisco

abundance would inflate estimates of rainbow smelt predatory impact. We assumed larvae were concentrated in the surface stratum and that two synoptic surveys was adequate for estimating abundance. This assumption seems to be consistent with most studies (Anderson and Smith 1971, Selgeby et al. 1978, Hatch and Underhill 1988, Oyadomari and Auer 2004) yet it is important to mention that vertical movement patterns and ontogeny of age-0 cisco is poorly understood (Selgeby et al. 1978). It will be important that future larval cisco surveys be designed using an approach for estimating abundance throughout the water column.

Finally, we recognize that predation by rainbow smelt may not be the only mechanism contributing to low cisco recruitment events. Bronte et al. (2003) reported year class strength in different regions of Lake Superior was synchronized and Yule et al. (2008) suggested sporadic recruitment may be a natural characteristic of these populations. Together, these studies suggest large-scale physical processes are what determine the magnitude of cisco recruitment. Our findings suggest the added pressure of rainbow smelt predation is sufficient to dampen the magnitude of the occasional successful year class or eliminate annual hatches altogether.

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