Exploring Life History Characteristics of Naturalized Versus Stocked Chinook

Research Final Report to the Great Lakes Fishery Trust

Grant 2011.1198

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PROJECT ABSTRACT

Grant #: 2011.1198

Title: Exploring Life History Characteristics of Naturalized Versus Stocked Chinook

Abstract body:

Purpose:

Naturalization of stocked populations can result in divergence of life-history traits from domestic stocks. Lake Michigan supports popular Chinook (*Oncorhynchus tshawytscha*) Salmon fisheries that have been sustained by stocking since the late 1960s. Natural recruitment of Chinook Salmon in Lake Michigan has increased in the last few decades and currently contributes over 50% of Chinook Salmon recruits. Samples collected as part of a lakewide mass-marking of Lake Michigan Chinook Salmon, starting with the 2006 year class, indicated hatchery fish average 30-mm longer and 130 grams heavier than naturalized fish at age-1. We hypothesized that selective forces differ for naturalized and hatchery populations resulting in divergent life-history characteristics with implications for Chinook Salmon population production and the Lake Michigan fishery. Specific life-history metrics of interest include: age- and size- at maturity, spawning run timing, fecundity, and sex ratio.

Objectives:

We evaluated life history characteristics between naturally recruited and stocked Chinook Salmon in Lake Michigan to help discern potential changes resulting from naturalization and implications for fisheries.

A. Conduct an analysis of historical data to determine if life-history parameters changed through time as the Chinook Salmon population became increasingly naturalized.
B. Conduct a two-year field study of naturalized and hatchery stocked Chinook Salmon spawning populations to quantify differences in life-history metrics of adults.
C. Determine if reproductive potential differs between naturalized and hatchery stocked Chinook salmon by measuring egg thiamine levels.

Methods:

A. We evaluated 23 years of biological data collected by the Michigan Department of Natural Resources (MDNR) to determine if average life-history parameters changed through time. Specific metrics included: age-at-maturity, size-at-maturity, and sex ratio. We also evaluated the relationship between adult female weight (i.e., an index of fecundity) and potential environmental influences that included prey biomass estimates and historic stocking densities. Statistical tests relied upon general linear models including analysis of variance and, in some cases, analysis of covariance to test for significant interaction terms.
B. We collected biological samples from adult Chinook Salmon spawning populations during two years (2012 and 2013). Study sites were selected to target a hatchery-stocked spawning population (at Medusa Creek), a naturalized spawning population (at the Betsie River), and a spawning population comprised of naturalized and hatchery-stocked adults, whose origins could not be discerned (at the Little Manistee River) in northwest Michigan. Samples were collected during creel surveys and at MDNR weirs. Creel survey sampling periods were two weeks and the entire survey period began in early fall and continued through October. We evaluated age- and size-at-maturity, aspects of reproductive investment (i.e., fecundity and egg size), and spawning run timing. Size at maturity was measured from harvested fish measured during the creel survey or fish harvested at MDNR weirs. Age was estimated using scale samples from harvested fish and in the second year we also collected fin rays to estimate ages, as they have been reported to be more accurate for Chinook salmon in Idaho rivers. Fecundity was measured from sampling ovaries of females harvested in the fishery and weirs. Fecundity was estimated by enumerating eggs in a subsample of the ovary and extrapolating to total ovary weight. Egg diameter and egg weights were measured from scanned images of egg samples using digital imaging software. Statistical tests relied upon general linear models including analysis of variance and, in some cases, analysis of covariance to test for significant interaction terms.
C. We submitted Chinook egg subsamples for laboratory analysis of total thiamine concentration to determine if egg and larvae survivability may differ between naturalized, hatchery-stocked, and a mixed spawning population. Samples were submitted for the naturalized and mixed populations in 2012, and all three population types in 2013. In response to a request from MDNR biologists, we also submitted Coho salmon eggs for total thiamine analysis in 2013. We tested for significant differences in total egg thiamine concentrations among populations using analysis of variance.

Results:

A. We found weak evidence of changes in life-history demographics through time and that environmental effects may be more influential than population-specific characteristics. Maturity at age did not change, size-at-maturity varied through time with a weak declining trend in weight through time (Figure 1) but a trend was not detected for adult total length though time. We did identify a decrease in the male:female ratio through time (Figure 2). Mean annual weights of adult females exhibited an asymptotic relationship with prey biomass (Figure 3) and a positive linear relationship with annual Chinook Salmon stocking rates.
B. Angler effort peaked at similar times in both the naturalized and hatchery-stocked fisheries and diminished at the end of October, which indicated that the spawning runs occurred about the same time regardless of origin (Figure 4). Age- and size- at maturity revealed no differences among spawning populations. We also found no differences in mean fecundity between spawning populations, however we did find that the largest and heaviest eggs were from the mixed population, smallest from the naturalized population, and intermediate sized from the hatchery-stocked population (Figure 5).
C. Egg thiamine concentrations differed between naturalized and mixed population females in 2012 (Table 1). In 2013, we again found those differences, but results from hatchery-stocked fish indicated they did not differ from either naturalized or the mixed population (Table 1). On average, Chinook salmon egg thiamine concentrations were above the ED50 (concentrations below the ED50 are associated with 50% larval mortality). Coho salmon samples from the Platte River were, on average, below the ED50 and significantly lower than Chinook salmon levels.

Conclusions:

In general, our results did not indicate significant life-history divergence between naturalized and hatchery-stocked Chinook salmon populations in Lake Michigan. We found weak evidence of changes in spawner demographics in a historical analysis (objective A) and few significant differences from a field study that sampled naturalized, mixed, and hatchery-stocked populations (objective B). We did find significant differences in egg thiamine concentrations between mixed and naturalized Chinook salmon spawning populations, but the hatchery-stocked population did not differ from the other types (objective C).

In contrast to salmon hatchery supplementation programs in the Pacific northwest, where divergence between hatchery and natural populations is commonly a concern from a conservation genetics perspective, divergence in the Great Lakes is principally a concern relative to angler satisfaction and fishery sustainability. Mature Chinook Salmon in Lake Michigan did not show strong differences in life-history traits between hatchery and naturalized fish. Run timing, trends in angler effort, timing of maturation (i.e., age or length), and fecundity were similar between hatchery and naturalized spawning runs, however small differences were observed in egg size metrics.

Egg thiamine concentrations in Lake Michigan Chinook Salmon were above the ED50 threshold (concentrations below the ED50 are associated with 50% larval mortality), but those for Coho Salmon were below the ED50 level. Comparatively, egg thiamine concentrations in the Chinook Salmon we examined were higher, on average, than those previously reported for several Great Lakes including Lake Michigan and did not indicate high occurrence of thiamine deficiency. The increase for Chinook Salmon is specifically noteworthy, and somewhat unexpected, given Lake Michigan's Chinook Salmon now have increased consumption of Alewives, which are the primary source of thiamine deficiency in Great Lakes salmonids. Future research will be required to determine what mechanism could be underlying increased egg thiamine levels in Chinook salmon, but our data suggested that effects of early mortality syndrome on recruitment may be less severe now than in recent history.

The future demographics of Lake Michigan's Chinook Salmon spawning population cannot be fully discerned from our analyses and field study, but for now there appears to be relative stability with environmental variability. Stability through time supports the hypothesis that there is not large genetic divergence among populations. A recent genetics evaluation reported that Lake Michigan Chinook Salmon are a single, panmictic population based on samples from 18 spawning sub-populations. However, a lack of detectable genetic divergence among spawning sub-populations does not rule out the potential for divergent phenotypic expression in life-history traits between hatchery and naturalized fish. Currently, the natural resource agencies working within the Lake Michigan Technical Committee coordinate the tagging of all Chinook salmon stocked into Lake Michigan with microwire tags. As the tagged hatchery and untagged naturalized fish are recovered from fisheries and weir harvests, further comparisons of life-history characteristics between hatchery and naturalized Chinook Salmon will become achievable.

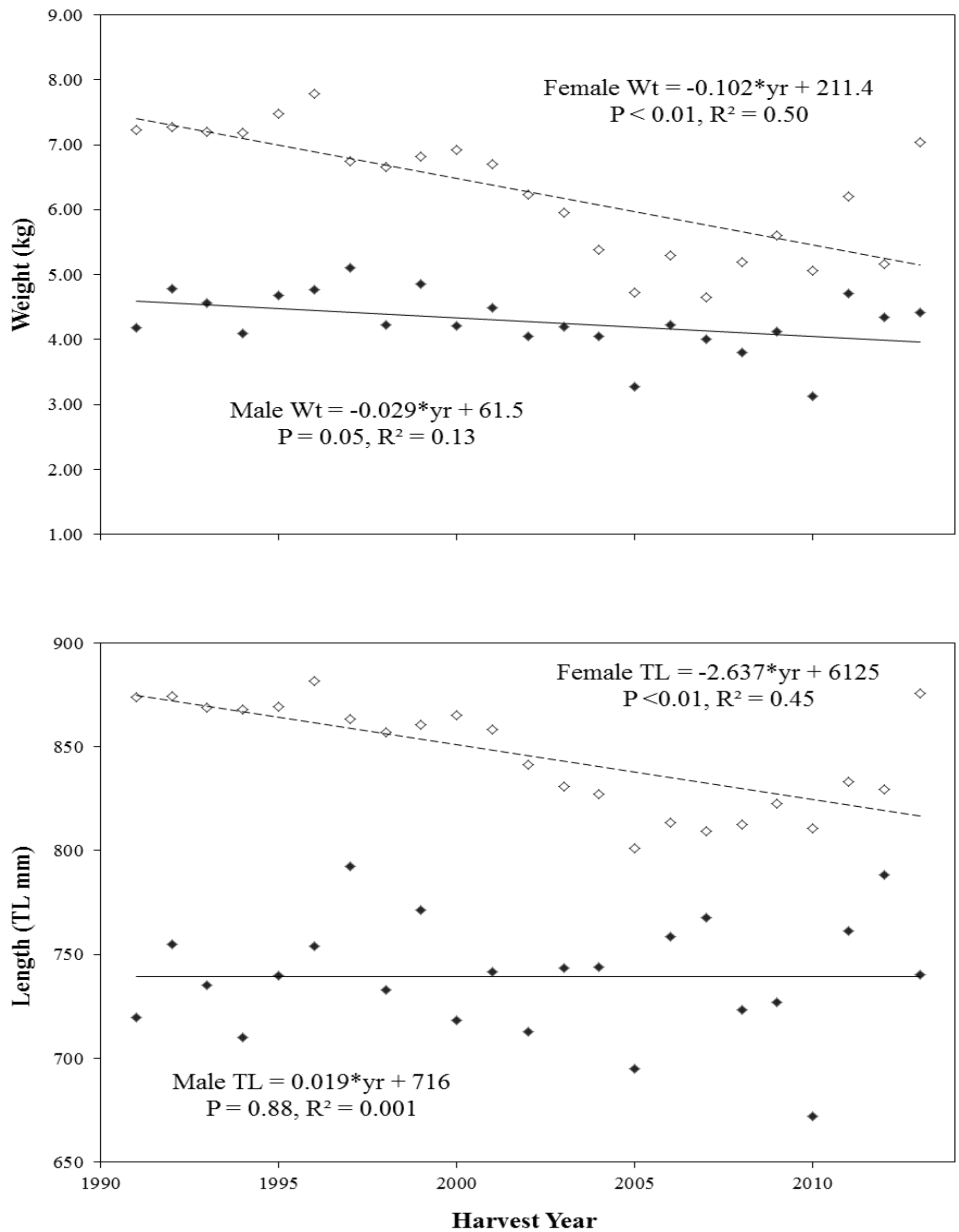

Figure 1. Mean weight (top) and total length (bottom) at maturity of Lake Michigan Chinook Salmon collected from Michigan Department of Natural Resources weirs during the fall migration. Fish collected from the weirs were a mixture of naturalized and hatchery produced fish. Female are represented by open diamonds and a dashed line. Males are depicted with solid diamonds and a solid line. Data are for all age classes harvested from 1991 through 2012.

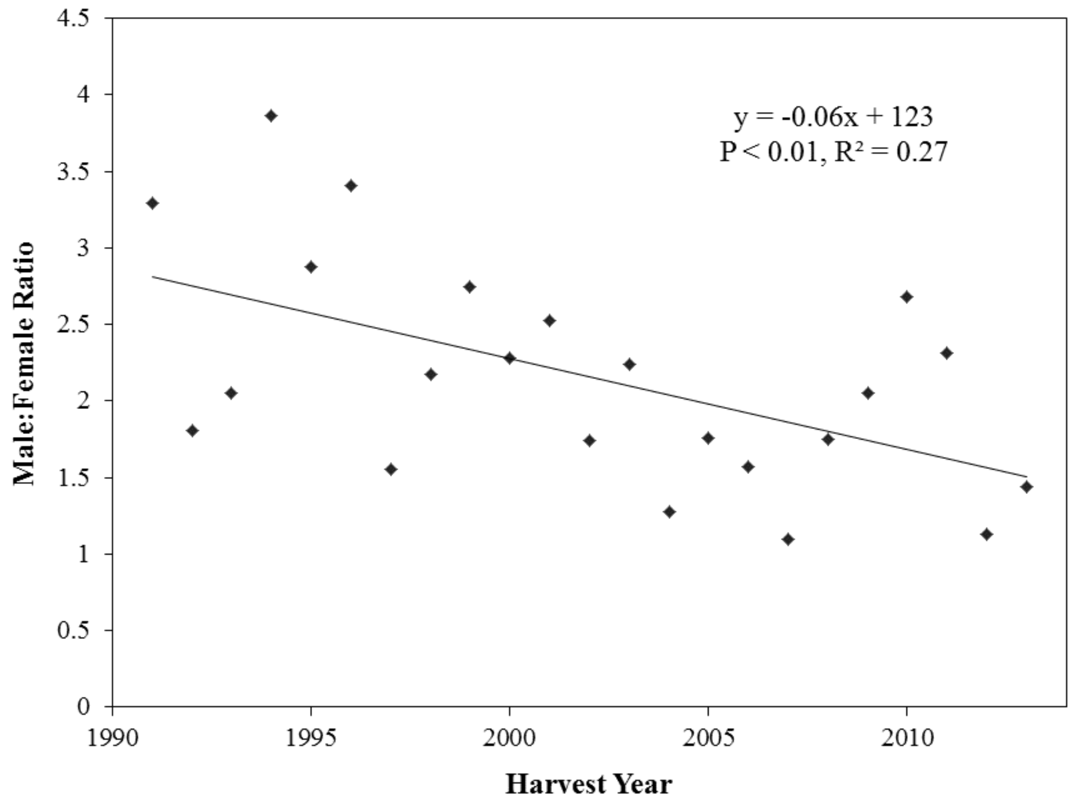

Figure 2. Ratios of male to female Lake Michigan Chinook Salmon harvested during the fall migration from Michigan Department of Natural Resources weirs through time. Fish collected from the weirs were a mixture of naturalized and hatchery produced fish. Data are for all age classes harvested from 1991 through 2013.

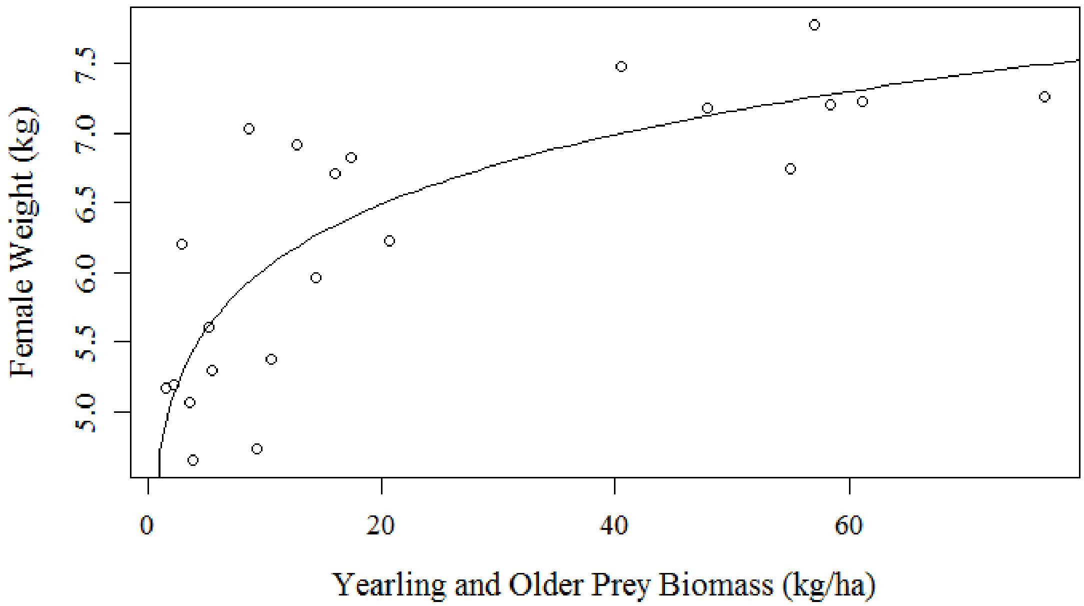

Figure 3. Relationship between mean female weight of Chinook Salmon harvested from weirs to prey biomass. Chinook Salmon harvest data were collected from weirs between 1991 and 2013. Prey biomass estimates were from USGS trawl data collected from 1991 through 2013, excluding 1998.

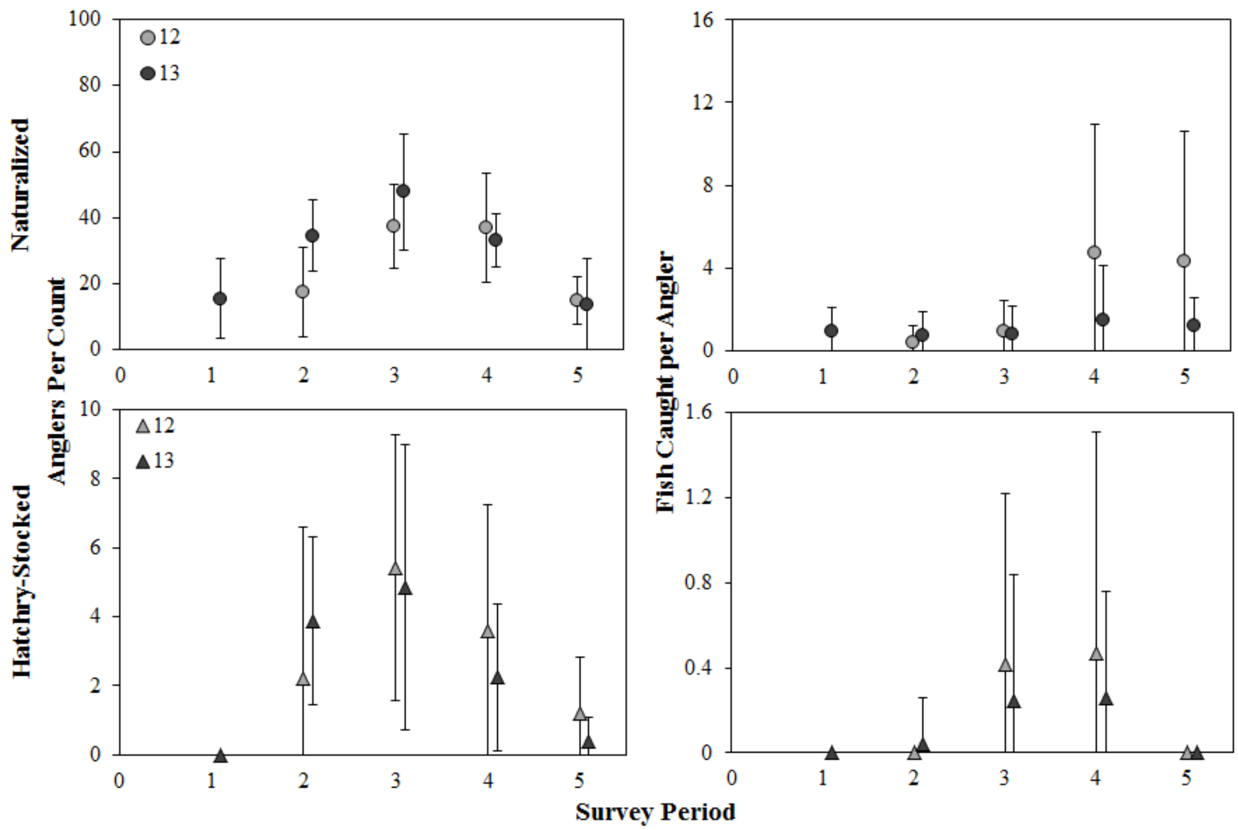

Figure 4. Average (±SD) angler count per survey and catch success of Chinook Salmon during the fall 2012 (grey) and 2013 (black) sampling seasons. The naturalized population (circles, top row) data presented in is from the Homestead Dam location on the Betsie River. The stocked population (triangles, bottom row) data presented was collected from Medusa Creek. The scale of the y-axis differs between the top and bottom row to allow temporal comparisons to be made between populations (12=2012, 13=2013).

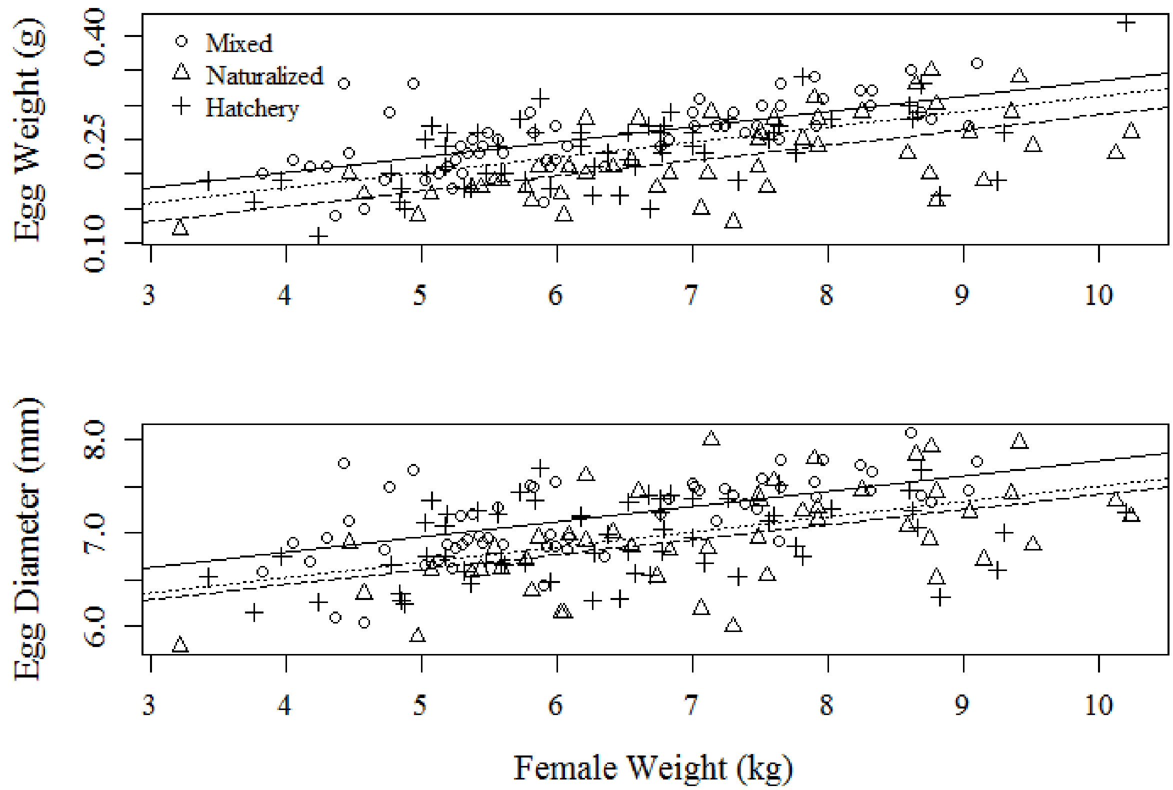

Figure 5. Egg size (i.e., weight and diameter) to female weight relationship of Chinook Salmon collected during the fall migration from naturalized, hatchery-stocked, and mixed (partially naturalize and hatchery-stocked) populations of fish occurring within Lake Michigan. Samples were collected from Michigan Department of Natural Resources weirs and a roving-access creel survey. Lines depict the linear relationship of the naturalized (dashed), hatchery-stocked (dotted), and mixed (solid) mixed population of salmon.

Table 1. Sample size (n), mean concentrations (nmol/g), and standard deviations (SD) of total thiamine in the eggs of Chinook and Coho Salmon from naturalized, mixed, and hatchery-stocked populations in Lake Michigan. 2012 and 2013 data were analyzed separately due to imbalance in samples sizes; an outlier of 21.9 nmol/g from the 2012 naturalized population was removed. Mean values not followed by a common superscript significantly differ ($p < 0.05$).

		2012			2013		
Species	Population	n	Mean	SD	n	Mean	SD
Chinook	Naturalized	11	5.25[a]	1.4	27	4.20[a]	1.1
	Mixed	10	3.99[b]	0.9	20	3.40[b]	0.8
	Hatchery-stocked	-	-	-	24	3.87[ab]	1.5
Coho	Hatchery-stocked	-	-	-	32	2.27[c]	0.6

FINAL NARRATIVE REPORT

Grant: 2011.1198

Project Title: Exploring Life History Characteristics of Naturalized Versus Stocked Chinook

Grantee Organization: U.S. Geological Survey - Great Lakes Science Center

Project Team: Mark W. Rogers, Janice A. Kerns, David B. Bunnell, Randy M. Claramunt, and Paris D. Collingsworth

Contact Person: Mark W. Rogers, U.S. Geological Survey, Great Lakes Science Center, Lake Erie Biological Station, mwrogers@usgs.gov.

Grant Amount: $256,107.00

Start and End Dates: 12/31.2011 – 10/30/2014

Key Search Words: Chinook salmon, life-history, spawning, population dynamics

Background/Overview

1. **Briefly summarize the project description as outlined in the original proposal.**

   Naturalization of stocked populations can result in divergence of life-history traits from those exhibited by domestic stocks. Divergence between naturalized (i.e., feral) and hatchery fish may be exacerbated if traits are heritable and either 1) naturalized populations are reproductively isolated from hatchery populations or 2) hatchery practices invoke differing selection factors than those experienced by naturalized fish. Although separating genetic and environmental effects on phenotypic trait expression is challenging, many fish life history traits have been experimentally shown to be heritable (e.g., Conover et al. 2005). Divergences in heritable traits via selection processes have implications for both population sustainability and fishery performance. For example, critical population production parameters (e.g., reproductive characteristics, Einum and Flemming 1999) and fishery parameters (vulnerability to angling, Philipp et al. 2009) are heritable in some species, and thus, divergence can result in a changes in fitness and fishery contributions between naturalized and stocked populations (Araki et al. 2008). Concerns for divergence between wild and hatchery fish have been especially noted for Pacific northwest salmonines due to high heritability in life-history traits and extensive stocking.

Pacific salmonine introductions into the Laurentian Great Lakes increased in the late 1960s when managers sought a way to reduce ecological effects of invasive Alewives *Alosa pseudoharengus* (Krueger et al. 1995) and develop valuable fisheries (Tanner and Tody 2002). Lake Michigan supports popular Chinook Salmon *Oncorhynchus tshawytscha* fisheries that have been sustained by stocking (Claramunt et al. 2013). The Michigan Department of Natural Resources (MDNR) annually collects data focused on open-lake fishery creel surveys at Michigan ports, returning fish to hatchery imprint ponds (e.g., Medusa Creek), and Chinook Salmon returns to MDNR weirs. Evaluations to date have focused on percent contribution of naturalized fish to the population, collection of scales for estimating ages, and length and weight data. From this information, biologists have been able to determine that natural recruitment of Chinook Salmon in Lake Michigan has increased in the last few decades and currently contributes over 50% of Chinook Salmon recruits (Claramunt et al. 2008; Jonas et al. 2008; Claramunt et al. 2013). Tagged fish have also allowed for initial evaluations between hatchery and naturalized fish. For example, Williams (2012) reported that hatchery fish were, on average, 30 mm longer and 130 g heavier at age-1 than naturalized fish. The increasing contribution of naturalized Chinook Salmon to the Lake Michigan population has raised concerns whether potential life-history differences could have implications for fisheries management and harvests. For example, if naturalized Chinook Salmon were found to have spawning runs later than stocked fish, then these fish may be less vulnerable to angler harvest as the weather worsens in late autumn.

We sought to evaluate life history characteristics between naturalized and stocked Chinook Salmon in Lake Michigan to help discern potential changes resulting from naturalization and implications for fisheries. Specific life-history metrics of interest included: age- and size- at maturity, aspects of female reproductive investment (i.e., female weight, fecundity, egg size), and spawning run timing. We also evaluated the implications of spawning run timing on angler effort and catches. Our project used 23 years of historical data collected from multiple MDNR sampling locations (Figure 1) and a two-year field project in northwest Michigan (Figure 2) for biological data collection to support these investigations. We also evaluated potential differences in population reproductive potential by measuring total egg thiamine concentrations.

Pacific salmon fisheries in the Great Lakes are estimated to have a multi-billion dollar economic impact (Tanner and Tody 2002). Fish Community Objectives set for Lake Michigan that were developed to address A Joint Strategic Plan for Management of Great Lake Fisheries (GLFC 2007) recognizes the prominent role Pacific Salmon have played and will play in the future. By exploring population-specific characteristics, we can develop expectations as shifts from a hatchery supported to a naturalized, self-sustaining Chinook Salmon population occur in Lake Michigan and what these potential changes mean to fisheries management strategies.

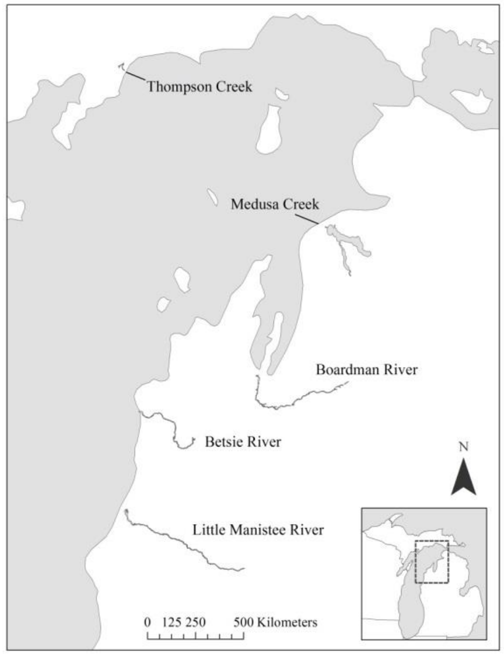

Figure 1. Map of rivers and creeks where Chinook Salmon samples were collected for historical analyses.

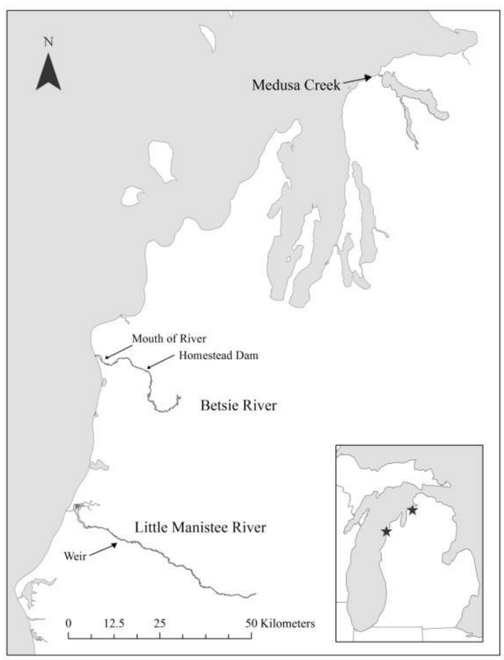

Figure 2. Map of field study areas and creel survey locations for Lake Michigan salmon life history conducted during the fall of 2012 and 2013. Stars in smaller inset map indicate approximate locations of areas 1 (Medusa Creek, a hatchery population) and 2 (Betsie River, a naturalized population; and Little Manistee River, a mixed population).

2. Briefly summarize any significant changes to the work performed in comparison to the plan of work originally proposed and funded. If changes were made, describe how they affected your ability to achieve the intended outcomes for the work.

   We had to adapt our field study due to an unexpected fishery closure at the Betsie River mouth sampling site. Due to extremely low water levels in 2012 that resulted in minimal fish passage, the Michigan Department of Natural Resources imposed a fishery closure that went into effect during our sampling season and will remain in-place for five years (Figure 2). The fishery remained open further up-stream, and thus, we were able to continue collecting biological samples and angler effort data from this naturalized spawning population. However, we expect the magnitude of creel survey metrics (e.g., angler counts) increased due to the increasing concentration of anglers.

   In January 2013, we gave a project briefing at the Lake Michigan Technical Committee meeting where we were asked if egg thiamine comparisons among spawning population types was a component of our study. It was not in the original proposal, but we felt this information would be of value to the management community and added a third objective (objective C above). This added objective addressed the question of “do naturalized fish have higher egg thiamine levels?” which could facilitate reproduction and self-sustainability. We feel this addition made a beneficial contribution to our study, will be of interest to fisheries managers, and will result in a peer-reviewed publication.

Figure 2. Low water levels at the Betsie River’s mouth resulted in a highly braided river with minimal fish passage. The MDNR ordered a fishery closure.

Outcomes

3. **To what extent and how (if at all) did this research project advance scientific knowledge of the issue?**

   Given the desire of the Lake Michigan fisheries management community to attain self-sustaining stocks that support sustainable harvests (Eshenroder et al. 1995), an implicit objective is that naturalized salmonine populations will exhibit life-history characteristics that are just as amenable to fisheries harvest as hatchery populations. Our study was the first to evaluate multiple life-history hypotheses regarding Lake Michigan's naturalized and hatchery stocked Chinook Salmon population as well as conduct a field study to directly test some of these assumptions.

   We hypothesized that multiple life-history parameters would differ between naturalized and hatchery stocked fish based on literature from the Pacific northwest and discussions with Lake Michigan fisheries biologists. For example, we hypothesized that hatchery fish would return to spawn at younger ages and there would be an increasing frequency of jacks (i.e., males in spawning condition at ages 1 or 2) relative to naturalized spawning populations. An increased number of jacks could have multiple fishery implications such as lower average weights of angler harvested fish from hatchery spawning populations. We also hypothesized that naturalized populations would have spawning runs that occurred later in the year, which could make them less accessible to anglers due to weather conditions in late fall.

   Our evaluation of adult size, timing of spawning runs, and fecundity revealed that there were few detectable differences between naturalized and hatchery-stocked fish at this time. Timing of spawning runs, and associated angler effort, were similar among spawning population types and did not support the concern than spawning timing was later for naturalized fish. Size and weight metrics also did not support the concern that angler harvested fish would likely be smaller in hatchery supported spawning populations. In general, our results did not support that life-history characteristics of naturalized fish would have large influences on fisheries dynamics. Important to note though that our study was limited to Lake Michigan tributaries primarily in northwestern Michigan. Thus, our sampling does not incorporate the potential variability among tributaries distributed around the lake.

   By examining historic Chinook Salmon weir harvest data coupled with our field study at Lake Michigan tributaries, we provided base-line spawner life-history demographics that can help inform population trends as they become naturalized. The future demographics of Lake Michigan's Chinook Salmon spawning population cannot be fully discerned from our retrospective analysis and field study, but for now there appears to be relative stability and comparability that are shaped by environmental variability (e.g., forage fish biomass). Our work also highlights one of the values of the mass marking program by allowing for distinction of hatchery versus naturalized Chinook salmon and how the program can facilitate stock-specific investigations.

4. To what extent and how (if at all) did this project contribute to the education and advancement of graduate or undergraduate students focused on Great Lakes fishery issues?

This project contributed to the career of Janice Kerns, a Ph.D. student during the study, who largely led the field data collection, data analysis, and much of the report writing. This project provided an opportunity to improve her leadership skills and roles in project management, which will be essential to her career. Janice had previously mostly worked on large rivers and temperate inland lakes, and thus, working on Lake Michigan greatly contributed to her diversity and gave her a larger appreciation of our valuable Great Lakes fisheries. The project is expected to result in three peer-reviewed publications and Janice will likely be lead author on several.

5. To what extent and how (if at all) did this work help you or others on your team build new relationships with others in the research or management communities?

This project resulted in a stronger relationship between U.S. Geological Survey (Great Lakes Science Center) and the Michigan Department of Natural Resources (Charlevoix Fisheries Research Station) and the Illinois-Indiana Sea Grant. For several parties on the project, it was their first time working with each other on a research project. By reaching out to Chinook salmon research biologists with Idaho Fish and Game for Chinook age estimation methods, we were able to introduce them to the importance of Pacific salmon fisheries in the Great Lakes. This project resulted in working together on project design, sampling at weirs, and assigning age estimates of fish with multiple MDNR biologists that are now new colleagues.

6. To what extent and how (if at all) do the findings have action implications for fishery managers?

The few significant differences we found indicate that hatchery selection processes likely have not induced directional selection that would facilitate divergences between hatchery-stocked and naturalized Chinook salmon. If results had been strongly contrasting, as has occurred in the Pacific Northwest, then considerations for improved brood stock selection or genetics management may have been encouraged. Outcomes of our research will be shared with the Lake Michigan fisheries managers at an upcoming Lake Michigan Technical Committee Meeting and action implications could be forthcoming.

7. **Considering the above or other factors not listed, what do you consider to be the most important benefits or outcomes of the project?**

   We were able to empirically and experimentally address a management concern previously expressed by Lake Michigan management agencies related to potential effects of increased naturalization on Chinook salmon fisheries. Although somewhat limited in scope (e.g., spawning populations, geographically, tributaries only) we were able to test several hypotheses related to demographics of spawning populations that support important seasonal fisheries.

Related Efforts

8. **Was this project a standalone effort, or was there a broader effort beyond the part funded by the GLFT? Have other funders been involved, either during the time of your GLFT grant or subsequently?**

   This project was a standalone effort with no additional funding sources.

9. **Has there been any spin-off work or follow-up work related to this project? Did this work inspire subsequent, related research involving you or others?**

   As described above, we added a third objective during the duration of this project (i.e., egg thiamine concentration analysis). By identifying some differences among species and spawning population types and then comparing to historical published values, it is plausible that more regular monitoring of Pacific salmon egg thiamine concentrations may be desired.

Communication/Publication of Findings

10. **List publications, presentations, websites, and other forms of formal dissemination of the project deliverables, tools, or results, including those that are *planned* or *in process*.**

We expect three publications from this project to be submitted to peer-reviewed journals within the next year:

Trends in Adult Spawner Characteristics as Lake Michigan's Stocked Chinook Salmon Became Increasingly Naturalized

Comparison of Life-History Characteristics Between Naturalized and Stocked Chinook Salmon in Lake Michigan

Egg Thiamine Status and Population Comparisons of Lake Michigan Pacific Salmon

11. **Please, characterize your efforts to share the findings of the research with state, federal, Tribal, and interjurisdictional (e.g., Great Lakes Fishery Commission) agencies charged with management responsibilities for the Great Lakes fishery.**

    We have provided two briefings at Lake Michigan Technical Committee meetings, a committee of the Great Lakes Fishery Commission, with representatives from all management agencies that oversee Lake Michigan fishery resources. We will make publications and final report materials available to that group.

12. **Please identify technical reports and materials attached to this report by name and indicate whether you are requesting that GLFT restrict access to the materials while you seek publication.**

    There are no technical reports or other materials for which we request restricted access.

13. **Manuscripts. Grantees submitting one or more publications or pending publications in lieu of a stand alone technical report must submit a cover memo that confirms that all aspects of the funded research are incorporated in the published work, and in cases of multiple publications, identifies or crosswalks the grant-funded objectives to the published article containing results.**

    All aspects of this research will be incorporated into the publications that are in preparation.

Discussion

Despite advances in hatchery technology and practices to minimize differences between hatchery and wild fish, hatcheries cannot produce fish identical to wild born fish (Knudsen et al. 2006). Salmonids have been among the most studied species for comparing life-history differences between hatchery stocked and wild-borne fish. Life-history traits that have been found to differ between hatchery and wild individuals include relative fitness, maturation timing, timing of spawning, fecundity, and growth rates (Olson et al. 1995; Jonsson et al. 1996; Hoffnagle et al. 2008; Williamson et al. 2010; Williams 2012). All of these factors have implications for population production and population sustainability.

In our retrospective analyses, stable age at maturity argued against significant hatchery induced genetic or phenotypic changes. Age-at-maturity has been reported as a heritable trait in Chinook Salmon (Hankin et al. 1993; Kinnison et al. 2011) and a trend through time could result from non-random brood stock selection. In contrast, hatchery innovations (e.g., improved feed quality) could induce faster growth through time and facilitate earlier maturation that could be propagated because size-at-age is a heritable trait (Kinnison et al. 2011). Johnson and Friesen (2013) also reported no changes in hatchery Chinook Salmon age-at-maturity using 17 years of data from the Pacific Northwest.

We observed a declining trend in adult weight through time. This decline occurred during a time of declining prey fish biomass, however there are other factors that could contribute to declining weight at maturity for female and male Chinook Salmon. Within Lake Michigan, declines in prey energy density could be exacerbated by declines in overall prey fish biomass and could also underlie decreased size-at-maturity. After dreissenid mussels invaded Lake Michigan, Madenjian et al. (2006) reported 23% lower energy density in adult Alewives. Madenjian et al. (2006) used bioenergetics models to estimate that lower prey energy density would necessitate a 22.1% increase in Alewife consumption, relative to pre-invasion consumption rates, to weigh 8 kg at age 4, and this may not have been possible given declines in Alewife biomass. Furthermore, numerous size trend studies have been conducted within the salmon fisheries of the Pacific Northwest and have associated the declines with trends in ocean currents, evolutionary trends driven by selective fisheries, changes in growing conditions, broad-scale environmental conditions, and density-dependent competition (e.g., Bigler et al. 1996; Kendall and Quinn 2011; Johnson and Friesen 2013). Thus, any potential divergence due to hatchery selection processes or alternative life-history strategies could be masked by environmental changes.

Our hypothesis that a more balanced sex ratio would occur as naturalized fish increasingly contributed to the spawning population was supported, although it may not have occurred by the mechanism we expected. Knudsen et al. (2006) described how an imbalanced sex ratio could result from an increasing proportion of younger hatchery fish. In our study we found no trend in age at maturity which suggests the age at return of males or females may not be influencing the change in sex ratio. Another possible explanation could be the decline in mature female size that we observed between 1991 and 2011. Holtby and Healey (1990) assessed 31 populations of Coho Salmon from California to Alaska and found changes in sex ratios to be directly related to female/male size ratios. For the Coho Salmon populations examined there were two types of populations, one where males out number females and females are larger at maturity, whereas in the other population type the sexes are equally abundant and equal in size at maturity (Holtby and Healey 1990). However, Holtby and Healey (1990) concluded that foraging strategies and foraging success could impose sex-specific constraints on growth that could influence maturation and alter sex ratios. Further research would be required to determine if an interaction between sex-specific foraging strategies during a time of declining prey biomass could have resulted in the decrease in male:female sex ratio for Lake Michigan Chinook Salmon.

To explain the decline in size of females, we looked at how Chinook Salmon stocking rates and prey biomass influenced the size of mature female Chinook Salmon. The female size to prey biomass relationship was explained by an intuitive asymptotic relationship where increased prey biomass resulted in increased female weight until a saturation point was met. The stocking rate relationship on the other hand appeared less intuitive and contrary to expectations with a direct positive relationship with female size. Our expectation was that higher stocking rates would lead to higher Chinook Salmon densities and result in increased intra-specific competition. If there are unlimited resources, fish should remain at their largest attainable size. Tsehaye et al. (2014) also examined changes in the salmonine community of Lake Michigan and found that age-3 Chinook Salmon growth was inversely related to the stocking rate in the previous year. The difference between our study and Tsehaye et al. (2014) could be explained by the fact that they included data during initial stocking of salmon into Lake Michigan when weights of fish were at their highest, Alewife biomass was high, and Chinook Salmon densities were low. During this initial period, the weights of fish may have been independent of density-dependent interactions due to unlimited prey (i.e., Alewife abundance) availability compared to more recent times. An alternative explanation is that Lake Michigan fisheries management agencies adjust Chinook Salmon stocking rates based on growth and forage biomass estimates, and thus, stocking levels are higher when conditions for growth are higher.

Our field experiment was designed to determine if life-histories differed between stocked and naturalized Chinook Salmon in Lake Michigan. In contrast to salmon hatchery supplementation programs in the Pacific northwest where divergence between hatchery fish and natural populations is commonly a great concern from a conservation genetics perspective (e.g., Berejikian and Ford 2004; Ford et al. 2006), divergence in the Great Lakes is of concern relative to angler satisfaction and fishery sustainability. Mature Chinook Salmon in Lake Michigan did not show strong differences in life-history traits between hatchery released and naturalized fish. Run timing, trends in angler effort, timing of maturation (i.e., age or length), and fecundity were similar between hatchery and naturalized spawning runs, however small differences were observed in egg size.

Creel surveys indicated no differences in run time of migrating fish. The results of this exploration revealed no clear seasonal trend differences in angler counts, however estimates of mean fish caught per angler or catch success estimates were difficult to interpret given unusual water level effects. In the first year of the study, low lake levels on Lake Michigan caused changes in the access and flow to the Betsie River. During this time, the water was so low the mouth of the river was largely inaccessible and hundreds of fish were stranded on mudflats before they had a chance to swim upstream. In response to the extremely low water and concern over their vulnerability to anglers, the MDNR closed the fishery at the mouth of the river half way through the first study season to allow fish access to the spawning grounds. We believe that this action caused an atypical change in catch success further up river where our data was collected. This trend can be compared to the second year of the study when catch success remained constant as the mouth of the river remained closed to angling throughout the entire second season. Given the disparity in the characteristics within the fishery between years, it is hard to decipher what type of trend would occur in a typical year. With the consistency in access to the fishery in the second year, we believe that the second year more closely resembles the catch success trend for a typical year when there are no access restrictions. If this is true, the resulting flat trend would be in opposition to our initial hypothesis: that hatchery origin fish should have earlier run times than those of naturalized origin.

We also found little to no differences in life history characteristics between hatchery-stocked, naturalized, and mixed spawning stocks of Chinook Salmon in Lake Michigan. Age, size, fecundity, and timing of seasonal return of mature fish were similar across all populations examined. Our results differ from findings by Williams (2012) who found age-1 hatchery Chinook Salmon to be significantly larger than their naturalized counter parts, but we only evaluated adults. For our study, we compared the size of mature returning fish and it is possible that any size advantage hatchery fish had as juveniles faded with maturity. The one area that we did find statistical difference occurred within the size of female eggs, but it is difficult to discern whether the magnitude of the difference is of biological significance given the differences in the intercepts between the largest (mixed) and smallest (naturalized) eggs was only 0.4mm and 0.5g. Theoretically, increased egg size should lead to increased survival and growth that could be carried through into adulthood (Einum and Fleming 1999). Although we did not evaluate differences in survival within this study, we found no differences in mean length between spawning stocks. This suggests that any biological advantage of large egg size may not be realized through the growth of fish into maturity.

Age and size at maturity can vary within and among populations based on individual differences in metabolic rates, availability of food, and environmental conditions. Our data suggested that female Chinook Salmon mature at similar sizes no matter which population they came from within Lake Michigan. In a review paper, Jonsson and Jonsson (1993) describe that within a cohort faster growing individuals are constrained by food limitation sooner than their slowing growing counterparts. The primary diet item of Chinook Salmon in Lake Michigan are Alewives (Warner et al. 2008; Jacobs et al. 2013), and their abundance declined dramatically between the early 1960s and early 1980s (Madenjian et al. 2005), then remained at somewhat low levels through 2004. Since 2004, however, the Alewife population has, on average, been at even lower densities (Madenjian et al. 2014). Hence, we speculate that the faster growing Chinook Salmon within a cohort will lose their competitive size advantage after the first year or two of life given that they do not undergo another ontogenetic shift to an alternative feeding niche. Thus, when fish size is constrained by the feeding opportunities, the best option for fast growers will be to mature at the growth inflection. For Lake Michigan Chinook Salmon, female size has been shown to have an asymptotic relationship with prey availability (see above), therefore it is possible that once faster growing fish have reached this growth limit, they mature, and return to spawn.

In contrast to previous studies, we found ages generated from fin rays and scales were not different. Copeland et al. (2007) reported that fin rays not only had superior precision but also were more accurate than scales (99% versus 82%, respectively) for Chinook Salmon in the Pacific coast. One reason for this disparity may be due to differences in environmental conditions experienced by each population. Copeland et al. (2007) considered only ages from the oceanic stage of the fish sampled and noted that the slight decrease in accuracy observed by Chilton and Bilton (1986) was due in part to estimating total ages which include the combined freshwater and ocean ages. Copeland et al. (2007) also concluded that salmon that experience extended freshwater phases, harsh weather, or long juvenile migrations have increased likelihood of growth checks or false annuli, thus making age estimation more challenging. Environmental variables experienced by the Chinook Salmon in Lake Michigan are far different than their Pacific relatives with shorter migration times and distinct weather extremes in the Great Lakes. These differences would lead to seasonal disparities in growth rates affecting how annuli are formed and therefore, affect the ease of age estimation.

Egg thiamine concentrations in Lake Michigan Chinook Salmon were above the ED50 threshold, but those for Coho Salmon were below the ED50 level. Coho Salmon egg thiamine concentrations were within the range of previously cited concentrations from Lake Michigan (Fitzsimons et al. 2007; Wolgamood et al. 2005). Egg thiamine concentrations in the Chinook Salmon were higher, on average, than those found previously in Lakes Ontario, Michigan, and Huron where averages ranged from 1.4 to 2.1, 0.75 to 2.69, and 0.58 to 3.72 nmol/g, respectively (Fitzsimons et al. 2007; Wolgamood et al. 2005). Increased thiamine levels, relative to previously reported levels, suggested recruitment may be less affected by thiamine deficiency that results in early mortality syndrome. Similarly, Claramunt et al. (2012) showed an increasing trend in egg thiamine levels for Lake Trout in Lake Michigan since the late 2000s, which also indicated decreased thiamine deficiency. The increase for Chinook Salmon is specifically noteworthy, and somewhat unexpected, given Lake Michigan's Chinook Salmon now have increased diet contributions from Alewives, particularly smaller-sized Alewives (Jacobs et al. 2013). Recent analysis of Lake Michigan Chinook Salmon diets suggest Alewives currently comprise over 90% of their diet compared to the mid-1990s when their diet was more diverse and Alewives comprised a smaller relative portion (Jacobs et al. 2013). Furthermore, Madenjian et al. (2006) reported a reduction in Alewife energy density which would require salmonines to consume approximately 20% more Alewife biomass to maintain historically observed growth rates. Taken together, one would predict that thiamine egg levels in Lake Michigan salmonids would currently be lower than historical measures. Future research will be required to determine what mechanism could be underlying increased egg thiamine levels in Chinook Salmon, but our data suggest that effects of early mortality syndrome on recruitment may be less severe now than in recent history.

Similar to other published studies, we found thiamine levels were related to fish size. For all spawning populations of Chinook and Coho Salmon, we found decreasing egg thiamine levels with increasing female weight. Other studies have reported a negative relationship between egg thiamine levels and female weight in Atlantic Salmon *Salmo salar* (Werner et al. 2006), between liver thiamine levels and Chinook Salmon length (Honeyfield et al. 2008) and between muscle thiamine levels and Chinook Salmon length (e.g., Fitzsimons et al. 2012). Decreasing thiamine levels with increasing fish size has been attributed to the increasing proportion of Alewife in the diets as Chinook and Coho Salmon grow to larger sizes.

Egg thiamine concentrations of Pacific salmonid species within Lake Michigan varied among population of different origins, and possibly between years within a population. Thus, given the limited spatial scale of our study (northeastern Lake Michigan), our results may not necessarily reflect lake-wide trends in egg thiamine concentrations. In 2012, egg thiamine from a naturalized Chinook Salmon population exceeded that of a mixed population, and this pattern was repeated in 2013. In 2013, however, we also failed to detect a difference in egg thiamine concentrations between a pure hatchery population and either naturalized or mixed populations. One possible explanation is that population-specific differences in diet led to the observed differences in egg thiamine. An alternative hypothesis for future research is that naturalized populations have evolved some physiological capability to ameliorate the negative effects of thiaminase derived from Alewife, and that this adaption could be contributing to the increasing proportion of naturalized recruits in Lake Michigan over the past decade or so.

Coho Salmon were analyzed only in 2013 and only from a hatchery stock, yet our results revealed egg thiamine concentrations that could be impacting egg survival. Coho Salmon egg thiamine concentrations were significantly lower than all Chinook Salmon populations we evaluated with an average value that fell between the ED20 and ED50, but was above the range (0.66 to 1.15 nmol/g) reported by Wolgamood et al. (2005) that resulted in EMS in offspring in the Platte River, Michigan. Interestingly, Wolgamood et al. (2005) proposed that an entire spawning population of Coho Salmon in Thompson Creek, a tributary to Lake Michigan, could have experienced complete recruitment failure due to low thiamine induced EMS.

Our results suggest that management agencies could benefit from implementation of an egg thiamine monitoring program for species beyond Lake Trout. First, the ability for naturalized spawners to produce viable recruits to the fishery relies upon the ability to produce viable offspring. Having sustainable naturalized populations of desired Pacific salmon is a management goal in Lake Michigan (Eshenroder et al. 1995). Secondly, the harvest of eggs for hatchery propagation to support salmon stockings assumes that eggs will be viable for fingerling production. Of particular importance to our study, we included eggs harvested at the Little Manistee weir which is critical to Lake Michigan salmon propagation. In fact, Lake Michigan management agencies that desire stocking of Chinook and Coho Salmon primarily use eggs harvested at the Little Manistee weir in Michigan. Lastly, changes in the prey fish community in Lake Michigan could influence egg thiamine levels. As described above, changes in the abundance of Alewives and diets of Chinook Salmon may alter egg thiamine levels through time. Depending on retention rates of thiaminase, increased consumption of Alewives by Chinook Salmon could enhance accumulation rates and potentially cause increased thiamine deficiency at younger ages. As the Lake Michigan food web continues to be modified by species invasions and changing nutrient dynamics, the implications of thiamine concentrations on Pacific salmon recruitment may continue to change.

Stocked and naturalized Chinook Salmon in Lake Michigan have relatively short lives (maximum age of about five) that are influenced by environmental conditions and fluctuate with changing prey conditions (Warner et al. 2008). For the near future, the limited differences among Chinook Salmon populations we investigated suggested that fisheries managers and salmon anglers should expect similar trends in population characteristics. This is not to say that divergence in the future is not possible. Pacific salmon populations stocked in to New Zealand waters in the 1900s have seen divergence from their original stocked population, but this divergence occurred over a much longer time period compared to the residence time of Chinook Salmon in Lake Michigan (Kinnison et al. 2011). Therefore, it will be important to monitor for possible difference in the populations through subsequent generations and continue the current multi-agency mass marking program that allows delineation between hatchery and naturalized fish.

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