Changes in Movements of Chinook Salmon Between Lakes Huron and Michigan After Alewife Population Collapse

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<A> Abstract

Alewives *Alosa pseudoharengus* are the preferred food of Chinook Salmon *Oncorhynchus tshawytscha* in the Laurentian Great Lakes. Alewife populations collapsed in Lake Huron in 2003, but remained comparatively abundant in Lake Michigan. We analyzed capture locations of coded-wire-tagged Chinook Salmon before, during, and after Alewife collapse (1993–2014). We contrasted the pattern of tag recoveries for salmon released at Swan River in northern Lake Huron and Medusa Creek in northern Lake Michigan. We examined patterns during April–July, when salmon were primarily occupied by feeding, and August–October, when salmon were primarily occupied by spawning. We found evidence that the Swan River salmon shifted their feeding location from Lake Huron to Lake Michigan after the collapse. Over years, proportions of Swan River salmon captured in Lake Michigan increased in correspondence with the decline in Alewives in Lake Huron. Mean proportions of Swan River salmon captured in Lake Michigan were 0.13 (SD, 0.14) before (1993–1997) and 0.82 (SD, 0.22) after (2008–2014) and were significantly different (Pairwise permutation test: Z=2.80, P=0.01). In contrast, proportions of Medusa Creek salmon captured in Lake Michigan did not change. Means were 0.98 (SD, 0.05) before and 0.99 (SD, 0.01) after. The mean distance to the center of the coastal distribution of Swan River salmon shifted 357 km (SD, 169) during April–July, from central Lake Huron before to central Lake Michigan after. The coastal distributions of salmon during August–October were centered on the respective sites of origin, which suggested that salmon returned to release sites to spawn regardless of their feeding locations. Regarding the impact on Alewife populations, this shift in inter-lake movement would be equivalent to increasing the stocking rate within Lake Michigan by 30%. The primary management implication is that inter-lake coordination of Chinook salmon stocking policies would be expected to benefit the recreational fishery.

<A> Introduction

Chinook Salmon *Oncorhynchus tshawytscha* were successfully introduced into lakes Michigan and Huron of the Laurentian Great Lakes in the 1960s to support recreational fisheries and to suppress overabundant Alewives *Alosa pseudoharengus*, a non-native planktivore (Tanner and Tody 2002; Claramunt et al. 2012). Populations of Lake Trout *Salvelinus namaycush*, the native apex piscivore, had collapsed during the mid-20th century from commercial fishing and predation by invasive Sea Lamprey *Petromyzon marinus* (Wells and McClain 1973). The loss of Lake Trout reduced fishing opportunities and enabled Alewives to reach extremely high abundances (Smith 1968; Wells and McClain 1973; Muir et al. 2012). Along with Chinook Salmon, other salmonine predators also were stocked to support fisheries and ecosystem rehabilitation, including Lake Trout, Rainbow Trout *Oncorhynchus mykiss*, Coho Salmon *Oncorhynchus kisutch*, and Brown Trout *Salmo trutta*. However, Chinook Salmon were arguably the most successful in terms of their popularity among recreational anglers and their performance as Alewife predators (Stewart and Ibarra 1991; Claramunt et al. 2012). Beginning in the 1980s, many Chinook Salmon were tagged with coded-wire tags (CWTs) to evaluate their survival and movements. Adlerstein et al. (2007; 2008) analyzed CWT recoveries to describe the seasonal movement patterns of Chinook Salmon during the 1990s and found that salmon traveled extensively within each lake but traveled little between lakes even though the connection between lakes, the Straits of Mackinaw, is a broad, deep channel with no apparent barriers to fish passage. These results supported the prevailing management structures which were designed to organize and coordinate Chinook Salmon management by individual lakes. For example, management within the state of Michigan was coordinated by Lake Basin Teams and international and interstate management across the lakes was coordinated by Lake Committees through the Great Lakes Fishery Commission (GLFC). Thus, Chinook Salmon fishing regulations and stocking policies were developed separately by lake, with minimal attention to inter-lake coordination.

More recently, however, assessment of catch-per-effort (*CPE*) in recreational fisheries showed that the distribution of Chinook Salmon in the two lakes changed after the 1990s (Clark et al. 2016). Clark et al. (2016) suggested that the change may have been driven at least in part by increases in inter-lake travels of Chinook Salmon from Lake Huron into Lake Michigan as a response to changes in the relative abundance of Alewives between lakes. Alewives are the preferred food of Great Lakes Chinook Salmon (Jacobs et al. 2013), and Alewife populations collapsed in Lake Huron in 2003 and have subsequently remained low (Riley et al. 2008; O'Gorman et al. 2012; Roseman et al. 2016). In contrast, Alewives have persisted in Lake Michigan despite a declining trend in recent years, and Chinook Salmon abundance is nearing an all-time high (Tsehaye et al. 2014; Clark et al. 2016; Madenjian et al. 2016). Fisheries managers have agreed to manage for a sustainable balance between Chinook Salmon and Alewives in Lake Michigan so as to maintain both at near present abundance levels and to avoid a collapse as occurred in Lake Huron (Lake Michigan Committee 2014).

In Lake Huron, abundance and body condition of Chinook Salmon declined sharply after the collapse of Alewives (Johnson et al. 2010; Brenden et al. 2012), but the severity of these declines varied regionally. The *CPE* of Chinook Salmon in the sport fishery declined over 90% from 2002 to 2010 in the main basin south of 45^{o} N latitude (Figure 1) (Clark et al. 2016), likely from starvation as evidenced by critically low body conditions measured in this region after the Alewife collapse (Johnson et al. 2007). In contrast, declines in abundance and body condition were less affected in the main basin north of 45^{o} N latitude and in Georgian Bay (Johnson and Gonder 2013; Clark et al. 2016). Chinook Salmon populations remain physically healthy and seasonally abundant in these regions. Our hypothesis is that these Chinook Salmon were able to persist at comparatively high levels because they changed their feeding locations from Lake Huron to Lake Michigan to take advantage of the more abundant Alewives in Lake Michigan. In this study we test our hypothesis by assessing the spatial distribution of captures of CWT Chinook Salmon over a series of years that include periods before, during, and after the collapse of Alewife populations in Lake Huron. We will attempt to relate any changes found to changes in the relative abundance of Alewives between lakes.

<A> Methods

We compared movement patterns of CWT Chinook Salmon released at index sites in each lake, Swan River in Lake Huron and Medusa Creek in Lake Michigan (Figure 1), over a period of 21 years (1993–2014). These sites provided the longest and most continuous set of tag-capture data for Chinook Salmon among the potential sites. Also, these sites had several other desirable characteristics. Both are small streams with little potential for Chinook Salmon natural reproduction; are the same distance (80 km) on opposite sides of the dividing line between the two lakes (middle of the Straits of Mackinaw); and are north of 45^{o} N latitude where the primary potential exists for the exchange of fish between lakes (Figure 1). From 1991–2014, tagged Chinook Salmon were released at both index sites in all but 5 years (1995– 1999), when none were tagged at Medusa Creek (Table 1). The fish released at both sites were reared from eggs and tagged at Platte River and Wolf Lake State Hatcheries in Michigan in the Lake Michigan watershed (Figure 1) and were transported by truck to the release sites. Production water for Platte River Hatchery was primarily from Brundage Creek and spring water from Brundage Spring. Production water for Wolf Lake Hatchery was predominately from wells. From 1991–1999 and 2007–2014, all tagged fish for both index sites came from Platte River Hatchery (Table 1).

We used preexisting datasets for our analysis that were produced and maintained by the Michigan Department of Natural Resources (MDNR), U.S. Fish and Wildlife Service (USFWS), and U.S. Geological Survey, Great Lakes Science Center (USGS, GLSC). These included data on: 1) tagging and recovery of CWT Chinook Salmon (MDNR and USFWS); 2) recreational fishing effort (MDNR); and 3) YAO Alewife abundance (USGS, GLSC). The tagging data included fish that were manually tagged with CWTs and fin-clipped through 2009, and fish that were tagged and fin-clipped using an automated system (AutoFish System™, Northwest Marine Technology, Shaw Island, WA) thereafter. Under both processes, CWTs were inserted into cartilaginous tissue in the snout, while adipose fins were clipped to provide an external identifier of tagged fish. Unique tag numbers were assigned to groups of fish to denote year classes and stocking locations. These tagging operations included making estimates of the amount of tagging error and loss and the effectiveness of fin clipping. The results provided estimates of the number of effectively tagged fish by lot and are hereafter referred to as the number of recoverable tags. During the study, the mean recoverable tags by lot was 95.6% (SD, 6.0%), and this mean value was applied to tag lots for which information on tagging error/retention at release was not available.

Free-ranging Chinook Salmon in the open-waters of the lakes were sampled for tags in catches of the recreational fishery, and we adjusted capture rates for differences in fishing effort by subregions within lakes. We used estimates of fishing effort that targeted trout and salmon from boats for the state of Michigan portion of both lakes as reported by Clark et al. (2016). Fishing effort was estimated through angler surveys using a stratified, random sampling design at all major salmon fishing access sites (Su and Clapp 2013). Troll fishing from boats was the most effective mode of capturing Chinook Salmon and regularly accounts for 85% of the harvest (Rakoczy and Svoboda 1997). Fishing effort was measured in angler hours, defined as the total number of anglers multiplied by the total hours of each completed fishing trip (Su and Clapp 2013).

We compared annual trends in opposite-lake capture rates for the index sites to trends in yearling and older (YAO) Alewife abundance. We defined opposite-lake captures as captures of fish released at Swan River in Lake Michigan and captures of fish released at Medusa Creek in Lake Huron. In addition, we compared Lake Michigan captures rates, finer-scale coastal distributions, and minimum distances and directions traveled for series of years before and after the Alewife collapsed in Lake Huron.

We used estimates of abundance of YAO Alewives derived from lake-wide, bottom trawl surveys to characterize trends in abundance of Alewives within the individual lakes (Madenjian et al. 2016; Roseman et al. 2016). These surveys have produced annual, lake-wide biomass estimates for YAO Alewives since 1973 by expanding the biomass caught in areas swept by trawls to the estimated amount of all similar habitats lake wide. However, while these estimates reflected the trends in abundance in each lake, they differed by lake in the proportion of area covered, seasonal timing, gear size, and towing methods (Gorman 2012). For example, in Lake Michigan, 11.9-m head rope, 20-m footrope, ¾ Yankee bottom trawls were towed along contour depths of 9 to 110 m for 10 minutes at several index transects each year. In Lake Huron, trawl sizes changed over the years: 11.9 m head rope trawls from 1973–1991 and 21-m head rope trawls from 1992–2014. We did not attempt to make direct comparisons of abundances between lakes, because such a comparison would have been dubious and was not necessary to test our hypothesis. The trend in abundance of Alewives in Lake Huron was the most important factor for testing our hypothesis, because it showed the timing of Alewife population collapse. The trend in abundance in Lake Michigan was sufficient to show Alewives persisted and were comparatively abundant there.

We divided captures of fish from each site into spatial and seasonal strata. We used two levels of spatial strata. Because our primary objective was to determine the extent of inter-lake movement, we first divided captures by lake. Then we used annual trends in the proportions of opposite-lake captures as a measure of the distribution of tagged fish between lakes when comparing to Alewife abundances. Second, because we wanted to describe finer-scale lake distributions and evaluate minimum distances and directions traveled, we organized captures into a regional grid system that was similar to methods used for evaluating movements of Chinook Salmon on the Pacific Coast of North America (e.g. Weitkamp 2010). We defined three regions in Lake Michigan as LM1, LM2, and LM3 and three regions in Lake Huron as LH1, LH2, and LH3 (Figure 1). We restricted our analysis to regions in state of Michigan waters because tag recovery effort was extensive and consistent there for our entire period of study. We assumed that captures in these regions would serve our primary purpose of identifying changes in inter-lake movements and would provide useful descriptions of coastal distributions and minimum distances and directions traveled from the stocking sites. These regions spanned the entire latitudinal gradient and covered about half the main basins of each lake. However, it should be recognized that the lakes are up to 160 km wide (east-west) and 500 km long (north-south), and the recreational fisheries, from which tagged fish were captured, primarily operated within 15 kilometers from shore. This meant that the movement patterns of Chinook Salmon we described herein were heavily weighted towards shoreline areas and should be considered as near-shore or coastal distributions.

We divided years into two seasonal strata, because we thought it was likely that Chinook Salmon would change their feeding locations but not their spawning locations. Chinook Salmon stocks in the Great Lakes are semelparous fall spawners. The hatchery fish used in this study were released near the mouths of Swan River or Medusa Creek in April–May. They entered the open lakes as fingerling-sized smolts (90–95 mm total length), fed and grew for one to four years until maturity, and then returned to the site of their release to attempt to spawn beginning in mid-August through October. Thus, to help isolate feeding and spawning behavior, we defined the months of April through July as the feeding season and the months of August through October as the spawning season. We realized our definitions of feeding and spawning seasons were only approximations; for example, Chinook Salmon do feed in August through October, and immature fish might not exhibit spawning behavior in fall. Nonetheless, dividing tag recovery data into these two seasons is reasonable based on life history considerations. Fishing effort and captures of salmon were very limited during the winter months of November through March because wind, cold, and ice cover reduced fishing effort to near zero, so this season was excluded from analysis.

We examined the correlation in timing of changes in movements between lakes to changes in Alewife abundance by comparing annual trends of the proportions of opposite-lake capture to annual trends in the abundance of YAO Alewives in the source lakes. We reasoned that the hypothesis would be supported if: 1) the trend in the proportion of opposite-lake captures for Swan River during the feeding season appeared to be inversely related to the trend in abundance of YAO Alewives in Lake Huron; and 2) the proportion of opposite-lake captures for Medusa Creek was comparatively low during the feeding season, or at least did not increase when the abundance of YAO Alewives in Lake Huron decreased.

We tested for significant ($\alpha = 0.05$) changes in the proportion of captures in Lake Michigan by site and season using nonparametric permutation tests that compared the annual proportions by site and season in periods before (1993–1997) and after (2008–2014) the Alewife collapse in Lake Huron. We organized captures as though the tagging of Chinook Salmon was initially designed to be a set of single-factor experiments to test the effects of reducing Alewife abundance in Lake Huron on the proportions of fish captured in Lake Michigan. Thus, our design can be viewed as though Medusa Creek (Lake Michigan) was an experimental control site where Alewives were present in both before and after periods and Swan River (Lake Huron) was the experimental treatment site where Alewives were present before, but were greatly reduced or absent after. We excluded 2009 and 2010 from the after period because we judged there were insufficient captures (<10 per year) during the feeding season for Swan River (Appendix Table A1). We did not include the 1998–2007 recovery data in these tests, because, based on the timing of the Alewife collapse in Lake Huron, we thought movement patterns during that period could be in a transitional state. Also, no tagged Chinook Salmon were released at Medusa Creek during 1995–1999 (Table 1) and, because of the relatively short life span of these fish, insufficient captures (<10 per year) were collected for Medusa fish from 1998–2001 (Appendix Tables A3 and A4). Applying these criteria resulted in a balanced, one-way comparison of before and after periods with a sample size of 5 years per period for the tests (i.e., 1993–1997 before and 2008, 2009, 2012–2014 after). Hereafter, we will refer to the after period simply as 2008–2012. In an initial analysis, we examined whether the groups defined by release site, season, and period differed in the proportion of salmon recovered from Lake Michigan (response variable) using a multifactorial permutation test (Manly 1998); the *lmp* function from the *LmPerm* package in *R*. This approach uses normalized sum of squares and type 3 tests (i.e., it evaluates an effect with all others in the model). Given this model would lead to significant (α = 0.05) interaction effects and an overall significant model (in comparison with a constant mean model), we planned to followed up with four specific before versus after period comparisons of interest: 1) Swan River salmon recovered in feeding season; 2) Medusa Creek salmon recovered in feeding season; 3) Swan River salmon recovered in spawning season; and 4) Medusa Creek salmon recovered in spawning season. These post hoc tests were based on pairwise permutation tests with Bonferroni-adjusted *P* values (α = 0.05) to correct for the family-wise error rate in the multiple-test comparisons. We used the *PairwisePermutationTest* function in the *rcompanion* package in *R* for these tests (Mangiafico 2016).

We described coastal distributions of Chinook Salmon for each release site by plotting the average annual proportions and standard errors of fish captured by lake region in each season. We compared plots of distributions for before (1993–1997) and after (2008–2014) periods. We assessed differences in lake distributions by visual comparisons of these plots. If our hypothesis was correct, we expected the coastal distribution of Swan River fish to shift into Lake Michigan during the feeding season in the after period, and the distributions for Medusa Creek fish not to change, or at least not to shift into Lake Huron.

We defined the displacement distance for each capture as the shortest swimming distance from its release site to the center of the lake region of capture. These displacement distances would represent the minimum distances travelled from the release site. Distances were measured with the Google Earth® ruler function. We calculated means (SDs) for displacement distances by age for captures aggregated for entire fishing seasons (April–October), feeding seasons (April–July), and spawning seasons (August– October). We also calculated coefficients of variation (CV = 100 · SD/mean) to compare the relative dispersion of captures by season. Our displacement distances for entire fishing seasons were comparable to methods used by Weitkamp (2010) to calculate the mean minimum distances traveled by age for 29 Chinook Salmon stocks along the Pacific Coast of North America and allowed us to compare age-specific distances traveled for stocks in lakes Huron and Michigan to stocks in their native range.

To help assess changes in directions traveled by Chinook Salmon, we standardized distributions of displacement distances so that they were centered on the release sites. That is, we assigned a negative sign (-) to distances for captures from lake regions to the west of the release site, a positive sign (+) to distances for captures from lake regions to the east of the release site, or a distance of 0 to captures from the lake region containing the release site. This approach causes the mean displacement distance for any sample of captures to be zero if fish moved equally to the west and the east of the release site, to be negative if more fish moved greater distances to the west, or to be positive if more fish moved greater distances to the east. Because of the geographic configuration of the lakes, these (-) and (+) directions would actually be southwest and southeast from the stocking sites (Figure 1), but we treated the continuous Lake Michigan-Lake Huron shoreline within the state of Michigan as a straight, east-west line for the analysis. The end result is essentially a linearized simplification of the two-dimensional map space, but it provided a practical assessment of potential changes in direction and mean minimum distances of movements. We defined the mean, standardized displacement distance as the net displacement distance and compared net displacement distances by site, season, and age group in before and after periods by plotting them on maps of the lakes.

We expected that spatial differences in fishing effort and temporal differences in numbers of tags released would bias the distribution of tag recoveries. We knew that fishing effort in Lake Huron was substantially lower than in Lake Michigan and that fishing effort had declined to a greater extent in Lake Huron over the period of study (Clark et al. 2016). Also, the number of recoverable tags stocked by year varied from 0–394 thousand (Table 1). In order to adjust for these biases, we weighted each individual capture by the fishing effort in the stratum (i.e., region, season, and year) of its capture and the number of recoverable tags released in the year it was stocked. Then, we used the sum of weighted captures in each stratum as an index of abundance of tagged fish in the stratum. In essence, our weighting adjustment was similar to assuming *CPE* is an index of abundance, but here we are assuming captures-per-effort-per-number-tagged is an index of abundance. Thus, the index of abundance of tagged fish *NR* in region *i*, season *j*, and year *k* from a given site was:

$$NR_{i,j,k} = \sum_{l=1}^{nr_{i,j,k}} WC_{i,j,k,l}$$

where $nr_{i,j,k}$ was the total number of captures in region *i*, season *j*, year *k* and $WC_{i,j,k,l}$ was the l^{th} weighted capture. Similarly, the index of abundance of tagged fish in an entire lake *NL* in region *i*, season *j*, year *k* from a given site was:

$$NL_{i,j,k} = \sum_{l=1}^{nl_{i,j,k}} WC_{i,j,k,l}$$

where $nl_{i,j,k}$ was the total number of captures in lake *i*, year *j*, year *k*, and $WC_{i,j,k,l}$ is the l^{th} weighted capture. Weighted captures *WC* were calculated as:

$$WC_{i,j,k,l} = (1/E_{i,j,k})/T_m$$

where $E_{i,j,k}$ was the fishing effort in region *i*, season *j*, and year *k* and T_m is the number of recoverable tags stocked at the given site in year *m*, which was the year the tagged fish was released.

Assessment of other potential biases. – We were aware of two other potential sources of bias in our analysis that we wanted to assess: 1) temporal and spatial differences in mortality; and 2) temporal and spatial differences in sampling effort for tagged fish. Concerning the first, we knew that proportional distributions of fish over space could change because movement patterns changed, mortality patterns changed, or both. For example, if the proportion of Swan River fish captured in Lake Michigan increased in the after period, it could be caused by increased fish movement from Lake Huron to Lake Michigan, by increased mortality of fish entering Lake Huron (e.g., from starvation), or a combination of both. To evaluate the potential effects of mortality bias on spatial distributions of Swan River-released fish, we calculated total capture rates (i.e., all captures from both lakes for a cohort divided by number of recoverable tags stocked for the cohort) by year in both the before and after periods. We used the total capture rates as surrogates for survival/mortality and tested for differences between periods with a pairwise permutation test ($\alpha = 0.05$) (Mangiafico 2016). We reasoned that if the spatial distributions of captures changed from Lake Huron to Lake Michigan in the after period because mortality increased in Lake Huron and not because movement patterns changed, it should be reflected as significantly lower total capture rates for after period cohorts. Alternatively, if the capture rate in the after period was equal to or greater than the before period, then it would be more likely that changes in movements were responsible for changes in spatial distributions.

Concerning the second potential bias, it should be recognized that overall recoveries of tags were obtained from numerous sources, and that each source had potential biases with respect to spatial distribution. We attempted to minimize biases by only using recoveries taken from the open-water recreational fishery by technicians who were trained to collect tagging data. This fishery generally targeted Chinook Salmon and consistently operated in both of our seasonal strata. Other captures, such as those from stream fisheries, weirs, research assessments, commercial fisheries, and volunteer anglers were not used because returns from these sources occurred only during spawning and not the feeding season (i.e., stream fisheries and weirs), Chinook Salmon were not targeted and bycatch was sporadic across strata (i.e., commercial fisheries and research assessments), or captures were not spatially or temporally consistent (i.e., voluntary returns from anglers). The technicians collecting data consisted of three primary types: angler survey clerks (i.e., technicians employed to collect data on fishing effort and catch), tag recovery technicians (i.e., technicians employed specifically to target tag recovery by sampling angler catches), and charter captains (professional anglers who serve as guides for others).

The temporal and spatial deployment of sampling effort and the efficiency of tag recovery per unit of effort was different for each type of technician (Adlerstein et al 2007), which potentially could have caused biases in describing the lake spatial distributions of Chinook Salmon. The majority of the CWT recoveries were from two sources, angler survey clerks (42%) and tag recovery technicians (48%). Sampling effort of angler survey clerks was the most temporally and spatially consistent over the entire period of study because these technicians were deployed in a stratified sampling design with a primary purpose of estimating the catches and fishing efforts for multiple species of fishes. They collected CWT Chinook Salmon only when they were observed in angler catches. On the other hand, tag recovery technicians targeted CWT trout and salmon. They sampled at times and places where the highest trout and salmon catches were expected, such as during fishing tournaments, and they were more efficient in obtaining tags per unit of sampling effort. Because fishing tournaments were not evenly distributed throughout the lakes, we were concerned that this type of target sampling could bias the spatial distribution of captures of CWT Chinook Salmon. We elected to use captures by tag recovery technicians in spite of this potential bias, because addition of these captures more than doubled the sample size, and we though the bias would have a minimal effect on the results. However, to assess the presence and degree of this potential bias, we ran one-way permutation tests of symmetry and post hoc pairwise permutation tests using data from each source of recovery separately (α = 0.05) to evaluate the proportions of Swan River salmon captured in Lake Michigan in before and after periods during the feeding season, the combination of greatest interest. We assumed that if results of tests were similar for both sources of recovery, then target sampling did not cause undue bias in the distributions.

<A> Results

Our analysis was based on a total of 2,327 recoveries (1,095 in feeding season and 1,232 in spawning season) of CWT Chinook Salmon released at Swan River, Lake Huron (Appendix Tables A1 and A2) and 2,718 recoveries (1,349 in feeding season and 1,369 in spawning season) of fish released at Medusa Creek, Lake Michigan (Appendix Tables A3 and A4). These captures all met our criteria of being collected by trained technicians from the open-water recreational fishery in state of Michigan waters, and were used in all the analyses after being adjusted for fishing effort and numbers stocked.

<B> Proportions of Captures by Lake Versus Alewife Abundance

The estimated percent of CWT Chinook Salmon released at Swan River, Lake Huron and captured in Lake Michigan during the feeding season showed an increasing trend over years, which appeared to be inversely related to the population density of YAO Alewives in Lake Huron (Figure 2 – top panel). The estimated percent captured in Lake Michigan increased sharply from 16% in 1999 to 58% in 2000, which was 4 years prior to the Alewife collapse in Lake Huron, but did correspond with the peak abundance of YAO Alewives in Lake Michigan (Figure 2 – bottom panel). On the other hand, the estimated percent of salmon released at Medusa Creek, Lake Michigan and captured in Lake Huron during the feeding season (Figure 2 – bottom panel), the estimated percent of Swan River salmon captured in Lake Michigan during the spawning season (Figure 3 – top panel), and the estimated percent of Medusa Creek salmon captured in Lake Huron during the spawning season (Figure 3 – bottom panel) were all consistently low and without apparent trend, and thus, did not appear to be related to the abundance of YAO Alewives in either lake.

We found a highly significant overall effect for the proportion captured in Lake Michigan for the groups defined by site of release, season, and period (Multifactorial permutation test; $P < 0.000001$). Given that all the interactions were highly significant, main effects were not interpreted, and we focused on our planned comparisons. Of the four planned comparisons, the only significant result was the before and after period comparison of Swan River salmon recovered in feeding season, where a higher proportion of fish were recovered in Lake Michigan after Alewife collapse than before (Table 2).

<B> Coastal Distributions Before and After Alewife Collapse

Graphical comparisons of coastal distributions before and after Alewife collapse also showed that the distribution of tagged fish released at Swan River shifted from Lake Huron to Lake Michigan during the feeding season (Figure 4 – top panel). In contrast, the majority of captures of salmon released at Medusa Creek were in Lake Michigan regions in both before and after periods (Figure 4 – bottom panel). During the spawning season, the greatest portion of captures occurred in the lake regions where fish were released (Figure 5).

<B> Displacement Distances

Mean displacement distances for all age groups were greater in the feeding season than the spawning season. They ranged from 127 km (SD, 125) to 274 km (SD, 160) in the feeding season and from 55 km (SD, 110) to107 km (SD, 110) in the spawning season (Table 3). On the other hand, CVs were greater in the spawning season than the feeding season for all ages. For example, CVs for age-1 fish for Swan River were 157% in the spawning period and 70% in the feeding season (Table 3). Mean displacement distances by age ranged from 85 km (SD, 116) to 177 km (SD, 177) for captures aggregated for entire fishing seasons (April–October)

<B> Net Displacement Directions Before and After Alewife Collapse

In the feeding season, the net displacement directions for salmon released at Swan River shifted from east of the stocking site, in the before period, to west of the stocking site in the after period. When these distances are repositioned onto maps of the lakes, it is clear that Swan River salmon of all ages shifted locations from Lake Huron to Lake Michigan (Figure 6). In the before period, net displacements were +7 km (SD, 231), +81 km (SD, 142), and +100 km (SD, 121) east of the stocking site in Lake Huron for ages 2, 3, and 4, respectively. Net displacement was -70 km (SD, 223) west of the stocking site for age 1, but still in Lake Huron (Figure 6 – top panel). In contrast, during the after period, net displacements were -293 km (SD, 132), -316 km (SD, 144), and -337 km (SD, 150) from the stocking site and well into Lake Michigan for ages 1, 2, and 3, respectively (Figure 6 – bottom panel). Therefore, the change in displacement location for Swan River fish from before to after was 223 km (SD, 178) at age 1, 323 km (SD, 187) at age 2, 418 km (SD, 146) at age 3, and 357 km (SD, 169) for all fish combined. No age 4 fish were captured during the after period.

For salmon released at Medusa Creek, net displacements in the feeding season were all west of the stocking site in both before and after periods, which means they were well into Lake Michigan (Figure 7). During the before period, net displacements were -245 km (SD, 118), -225 km (SD, 124), and -220 km (SD, 109) west of the stocking site in Lake Michigan for ages 1, 2, and 3, respectively (Figure 7 – top panel). During the after period, net displacements for all age groups were -209 km (SD, 101) east of the stocking site in Lake Michigan (Figure 7 – bottom panel).

During the spawning season, net displacements for fish released at Swan River in both before and after periods were relatively short distances east or west of the site, all within Lake Huron (Figure 8). The net displacements were +30 km (SD, 102) east of the stocking site for age-2-and-older fish and -40 km (SD, 168) west of the site for age-1 fish (Figure 8 – top panel). Net displacements for salmon of all ages were -34 km (SD, 104) to -64 km (SD, 133) west of the stocking site during the after period, but still within Lake Huron (Figure 8 – bottom panel). Net displacements for fish released at Medusa Creek were all relatively short distances west of the stocking site and all within Lake Michigan (Figure 9), varying from -198 km (SD, 127) for age-1 fish in the before period to -35 km (SD, 79) for age-3 fish in the after period.

<B> Assessment of Potential Bias

Potential biases from increased mortality in Lake Huron did not have a significant effect (α = 0.05) on the distribution of recoveries between lakes. Total capture rates for Swan River fish were not significantly different in before and after periods (Pairwise permutation test: Z = 1.47, P = 0.14).

Potential biases from target sampling did not have a significant effect (α = 0.05) on the distribution of recoveries between lakes. The distributions in before and after periods for salmon released at Swan River and captured in Lake Michigan were statistically significant for captures collected solely by spatially-consistent sampling (Pairwise permutation test: Z= 2.80, P = 0.02, P adjusted = 0.04) and for captures collected solely by target sampling (Pairwise permutation test: Z= 2.95, P = < 0.01, P adjusted = 0.01).

<A> Discussion

The multiple analyses of CWT Chinook Salmon we conducted all supported the hypothesis that the fish stocked into northern Lake Huron changed their feeding location from Lake Huron to Lake Michigan to take advantage of the more abundant Alewives in Lake Michigan. The proportion of Swan River salmon captured in Lake Michigan increased during the feeding season and the timing of the increase corresponded with the decline in YAO Alewife abundance in Lake Huron. Alewife abundance has remained low in Lake Huron for over 10 years and the proportion of Swan River salmon captured in Lake Michigan has remained high (Figure 2). The proportion captured in Lake Michigan was significantly greater (α = 0.05) in years after than before Alewife collapse (Table 2). Spatial assessment of capture locations within and between lakes showed that the coastal distributions of Swan River salmon shifted to Lake Michigan after collapse (Figure 4). And finally, the net displacement distances of Swan River salmon shifted 357 km from central Lake Huron to central Lake Michigan after collapse (Figure 6). We ruled out the potential effects of biases in these analyses caused by spatial differences in natural mortality and for different methods of sampling for tagged fish. In contrast, the same analyses applied to Medusa Creek salmon found that those fish tended to remain in Lake Michigan for the entire period of study. Thus, tag recoveries from these two stocking sites suggested that the shift in inter-lake movement was in one direction: Lake Huron to Lake Michigan.

The degree of change in movement patterns that we found were reasonable based on the expected feeding behavior and physical capabilities of Chinook Salmon. The shift in capture locations occurred only during April–July, a time of year when salmon were primarily feeding, and it has been established that Chinook Salmon in the Great Lakes preferred Alewives as prey, even when Alewife abundance was low and alternative prey were present (Jacobs et al. 2013). In addition, the minimum distances moved by Chinook Salmon in our study, including the distance from Swan River to central Lake Michigan (300 km), were comparable to distances of movement reported previously for the species in their native range (Quinn 2005; Weitkamp 2010). The grand average minimum distance traveled for 29 West Coast stocks was 152 km, 215 km, 297 km, and 314 km for ages 1, 2, 3, and 4, respectively (Weitkamp 2010), which could be compared directly to our “entire fishing season” distances in Table 3. Thus, minimum distances traveled by our Great Lakes stocks were about average for younger salmon (age 1) but below average for older salmon (ages 2–4).

The basic movement behavior of Chinook Salmon in lakes Huron and Michigan was similar to that observed in their native range on the West Coast of North America. That is, they imprinted on their stocking sites, traveled hundreds of kilometers in open-water to feed, and displayed a high degree of homing fidelity in returning to their stocking sites to attempt to spawn. Even the Swan River fish maintained a high degree of homing fidelity to their release site after changing their feeding location from Lake Huron to Lake Michigan. Their distribution during the spawning season remained centered on LH1, the lake region containing Swan River, for the entire 21-year study period (Figure 5). Fish released at Medusa Creek also displayed a high degree of homing fidelity (Figure 5).

However, major changes in coastal distributions like we found here have not been reported for Chinook Salmon in the Pacific Ocean. Studies there found that stocks from the same freshwater origin and genetic background maintained distinctive coastal distributions that were consistent over years despite considerable variability in ocean ecological factors, including periods of strong El Niño and La Niña events (Weitkamp 2010; Quinn et al. 2011; Chamberlin and Quinn 2014). In contrast, our Swan River Chinook Salmon were from the same freshwater origin, run type, and genetic background for our entire period of study (Weeder et al. 2005; Suk et al. 2012), yet they displayed a major, long-term change in their coastal distribution that was most likely driven by ecological factors (i.e., changes in forage distribution). While many unknowns remain regarding genetic versus ecological control of coastal distributions, our findings suggested that changes in ecological factors can lead to substantial changes in movement patterns and coastal distributions. Chinook Salmon are not native to the Great Lakes, and this fact could have confounded genetic control of feeding migrations here causing salmon to be more opportunistic. Also, the Pacific Ocean probably contains more numerous forage options for Chinook Salmon as compared to the Great Lakes where they rely heavily on Alewives and travel long distances to seek them out. In addition, our ability to detect the change in distribution of Swan River salmon was enhanced because we stratified our captures into seasonal periods. Had we not done so, the consistency of the homing behavior in August–October might have obscured the change in distribution that occurred only in April–July.

We found that Chinook Salmon in lakes Huron and Michigan were spatially more dispersed in the spawning season than the feeding season. For fish released at both sites and for all age groups, CVs for displacement distances in the spawning season were about double those for the feeding season (Table 3). We can only speculate that greater dispersion in the spawning season was caused by separation of mature and immature fish, with mature fish tending to return to release site and immature fish tending to remain in spring-summer feeding areas.

Although we focused our assessment on only two stocking sites, we think the results have broader management implications. First, Chinook Salmon tagged and released at other sites in region LH1 since 2011 have travelled into Lake Michigan at rates similar to salmon stocked at Swan River (authors' unpublished data), and the potential impact of all LH1-stocked salmon on the forage base of Lake Michigan is likely significant. An average of 0.7 million Chinook Salmon per year have been stocked in LH1 in recent years versus 1.8 million per year stocked directly into all of Lake Michigan. Therefore, even if only 80% of the LH1 fish fed in Lake Michigan, which would be reasonable based on our findings, then movements of LH1 salmon into Lake Michigan would have a similar impact on the forage base as directly increasing the annual stocking rate within Lake Michigan by 0.5 million Chinook Salmon, or by about 30%. Thus, consideration of Chinook Salmon stocked into region LH1 of Lake Huron when determining stocking policies for Lake Michigan would be expected to enhance effective management of the Lake Michigan recreational fishery, based on our analysis results. Also, because the shift in movement of Swan River salmon has persisted for over 10 years, it is unlikely to change in the future unless the relative abundance of Alewives in the two lakes also changes. Nevertheless, continuing to tag Chinook Salmon stocked into northern Lake Huron at a sufficiently high level would enable fishery managers to monitor possible future changes in inter-lake movement patterns.

The only other Chinook Salmon stocked into Lake Huron and potentially travelling to Lake Michigan were released in the Province of Ontario, where an average of 0.3 million fingerlings per year were stocked. Most of these fish were stocked into southern Georgian Bay about 400 km from Lake Michigan, but they have not been tagged in recent years, so we could not describe their movement dynamics. However, it seems likely that some of these fish have been feeding in Lake Michigan, because CPE of anglers in Georgian Bay did not decline after the Alewife collapse (Clark et al. 2016). Also, mean minimum recovery distances of over 700 km from tagging sites have been observed for Chinook Salmon in the Pacific Ocean (Weitkamp 2010), so Lake Michigan should be within range of Georgian Bay salmon. Tagging or marking Chinook Salmon stocked into Georgian Bay would broaden our understanding of inter-lake movement, which, in turn, would be expected to improve management of the Lake Michigan recreational fishery.

Wild, naturally-produced Chinook Salmon originating in tributaries of Lake Huron are also likely entering Lake Michigan. Tagged wild and hatchery Chinook Salmon of the same genetic background and originating from the same freshwater sites displayed similar marine distributions in the Pacific Ocean (Weitkamp 2010). In Lake Huron, Ontario tributaries in particular are known to produce substantial numbers of wild Chinook Salmon (Johnson et al. 2010; Johnson and Gonder 2013), and these wild fish are genetically similar to the tagged, hatchery fish released at Swan River (Suk et al. 2012). Furthermore, based on otolith microchemistry, Marklevitz et al. (2016) found that the recreational catch of Chinook Salmon in Lake Huron during 2010 was composed mostly of wild fish, of which, 55% originated from streams of southern Georgian Bay and 35% originated from streams in northern Lake Huron. The northern Lake Huron group included fish originating from the same freshwater region (LH1) as the Swan River fish, which indicated there must be substantial natural reproduction in streams entering LH1. If these LH1-wild fish behave as LH1-hatchery fish, then the majority are currently traveling to Lake Michigan in the feeding season. Additional work in the future examining otolith microchemistry of wild fish from Lake Michigan could help determine the proportion coming from Lake Huron tributaries.

Another important result from this study with management implications was that age-1 Chinook Salmon exhibited mean minimum travel distances of up to 300 km (Figure 6). The importance of this finding related to the way that managers have been estimating the amount of Chinook Salmon natural reproduction. Since the late-1990s, all hatchery-reared Chinook Salmon stocked into Lake Michigan were marked with either oxytetracycline (Williams 2012) or CWTs (Bronte et al. 2012). Managers used the proportion of unmarked age-1fish captured in the fishery to estimate wild recruitment rates (Williams 2012). We found that an average of 82% of tagged fish released at Swan River and captured during the feeding seasons of 2008–2014 were captured in Lake Michigan and that these fish were already present in Lake Michigan by age 1 (Figure 6). Prior to 2014, estimates of wild recruitment were made using the total number of fish stocked within each individual lake without any consideration of inter-lake movement. Tagged, age-1 salmon stocked into Lake Huron and moving into Lake Michigan would have biased these estimates of wild recruits. Therefore, based on our results, we suggested to fisheries managers to account for Chinook Salmon planted in region LH1 of Lake Huron when estimating the abundance of wild Chinook Salmon that will potentially feed in Lake Michigan, and our suggestion was implemented (Notes of winter meeting of the Lake Michigan Technical Committee in Zion, Illinois, January 28–29, 2015, B. Breidert, Indiana Department of Natural Resources, Chair).

One of the main limitations of our study was our assumption that state of Michigan waters were representative of the whole lakes, which was necessary to assemble the most temporally and spatially consistent recovery data. One possible violation of this assumption would be that tagged Chinook Salmon increased their movements during the feeding season into Ontario waters of Lake Huron, because if this happened, it would weaken our conclusion that Swan River fish shifted their feeding locations into Lake Michigan. However, we thought this was unlikely given that *CPE* of Chinook Salmon in Ontario waters declined or remained constant after the collapse of Alewives (Clark et al. 2016). On the other hand, *CPE* of Chinook Salmon increased more in Wisconsin waters of Lake Michigan than in Michigan waters after collapse

(Clark et al. 2016), which suggested that Swan River salmon could have moved into Wisconsin waters of Lake Michigan at a greater rate than into Michigan waters. If so, then our conclusion would be strengthened, because it would mean that more Swan River fish were in Lake Michigan than we estimated. The potential effects of these biases can be resolved more definitively in the future, because the CWT program for Chinook Salmon was expanded in 2011–2016, so that all hatchery-reared Chinook Salmon were tagged and the sampling for recoveries was expanded and made more consistent across state boundaries.

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Table 1. – Numbers (thousands) of Chinook Salmon tagged (recoverable CWTs) and released at Swan River (Lake Huron) and Medusa Creek (Lake Michigan) from 1991-2014. Total number and number from each source hatchery, Platte River (PR) and Wolf Lake (WL), are given below release site.

	Swan River, Lake Huron			Medusa Creek, Lake Michigan		
Year	PR	WL	Total	PR	WL	Total
1991	203	0	203	106	0	106
1992	187	0	187	100	0	100
1993	189	0	189	86	0	86
1994	186	0	186	85	0	85
1995	92	0	92	0	0	0
1996	86	0	86	0	0	0
1997	91	0	91	0	0	0
1998	86	0	86	0	0	0
1999	94	0	94	0	0	0
2000	88	0	88	82	0	82
2001	85	103	187	75	94	170
2002	95	84	180	97	100	197
2003	94	101	195	97	98	195
2004	89	87	175	97	85	182
2005	96	89	185	97	88	186
2006	63	93	157	80	89	169
2007	96	0	96	89	0	89
2008	88	0	88	97	0	97
2009	93	0	93	96	0	96
2010	98	0	98	215	0	215
2011	394	0	394	215	0	215
2012	336	0	336	190	0	190
2013	360	0	360	71	0	71
2014	348	0	348	68	0	68
Totals	3,637	556	4,193	2,043	556	2,599

Table 2. – Summary of pairwise permutation test results comparing the proportion of Chinook Salmon captured in Lake Michigan during before (1993–1997) and after (2008–2014) periods for groups based on sites of release and seasons of capture. Adjusted *P* was the Bonferroni adjustment for 4 test comparisons. The "*" indicates that before and after distributions were significantly different ($P < 0.05$). Means and SDs of the groups are also given for reference.

Release site, Period	Mean	SD	Z	*P*	Adjusted *P*	
			Feeding Season			
Swan River						
Before	0.13	0.14	2.80	0.01	0.04	*
After	0.82	0.21				
Medusa Creek						
Before	0.98	0.05	0.66	0.51	1.00	
After	0.99	0.01				
			Spawning Season			
Swan River						
Before	0.06	0.02	-0.36	0.71	1.00	
After	0.05	0.01				
Medusa Creek						
Before	0.97	0.04	-1.29	0.20	0.80	
After	0.91	0.07				

Table 3. – Mean displacement distances (km) (SDs) and coefficients of variation (CV = 100 · SD/mean) by site and age for Chinook Salmon captures aggregated by entire fishing season (April–October), feeding season (April–July), and spawning season (August–October). Means are for the entire period of study (1993–2014) and do not account for direction of travel.

		Age (years)			
Release site	Mean recoveries per age group	1	2	3	4
Entire fishing season					
Swan River	583	142 (163)	177 (177)	122 (155)	85 (116)
CV		114%	100%	127%	137%
Medusa Creek	694	141 (125)	171 (123)	141 (120)	141 (108)
CV		89%	72%	85%	77%
Feeding season					
Swan River	274	237 (167)	274 (160)	197 (164)	127 (125)
CV		70%	58%	83%	98%
Medusa Creek	340	201 (120)	226 (106)	208 (103)	200 (73)
CV		60%	47%	50%	36%
Spawning season					
Swan River	309	82 (128)	72 (127)	55 (110)	60 (103)
CV		157%	176%	198%	171%
Medusa Creek	354	93 (108)	107 (110)	88 (104)	102 (111)
CV		116%	103%	119%	109%

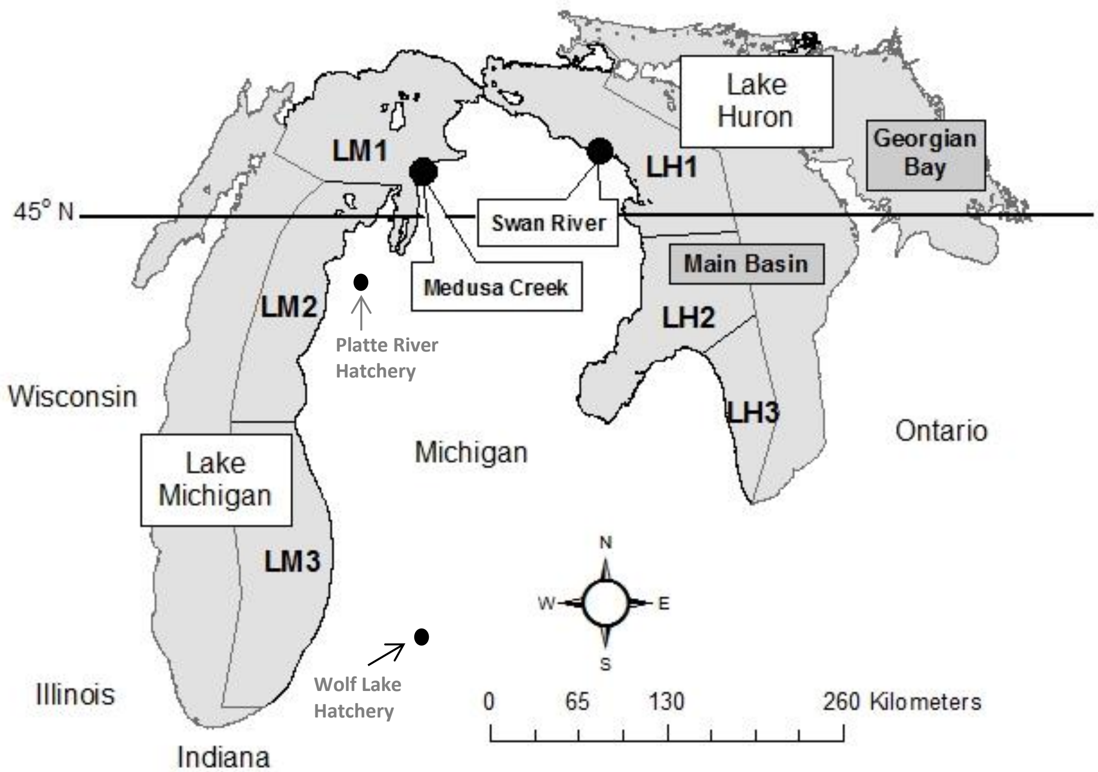

Figure 1. – Regions used to evaluate Chinook Salmon movements are delineated on this map as LM1, LM2, LM3 in Lake Michigan and LH1, LH2, and LH3 in Lake Huron. Locations of Medusa Creek and Swan River stocking sites and Platte River and Wolf Lake Hatcheries are also indicated on the map. Medusa Creek and Swan River are 80 km and 87 km, respectively, from the dividing line between lakes Michigan and Huron.

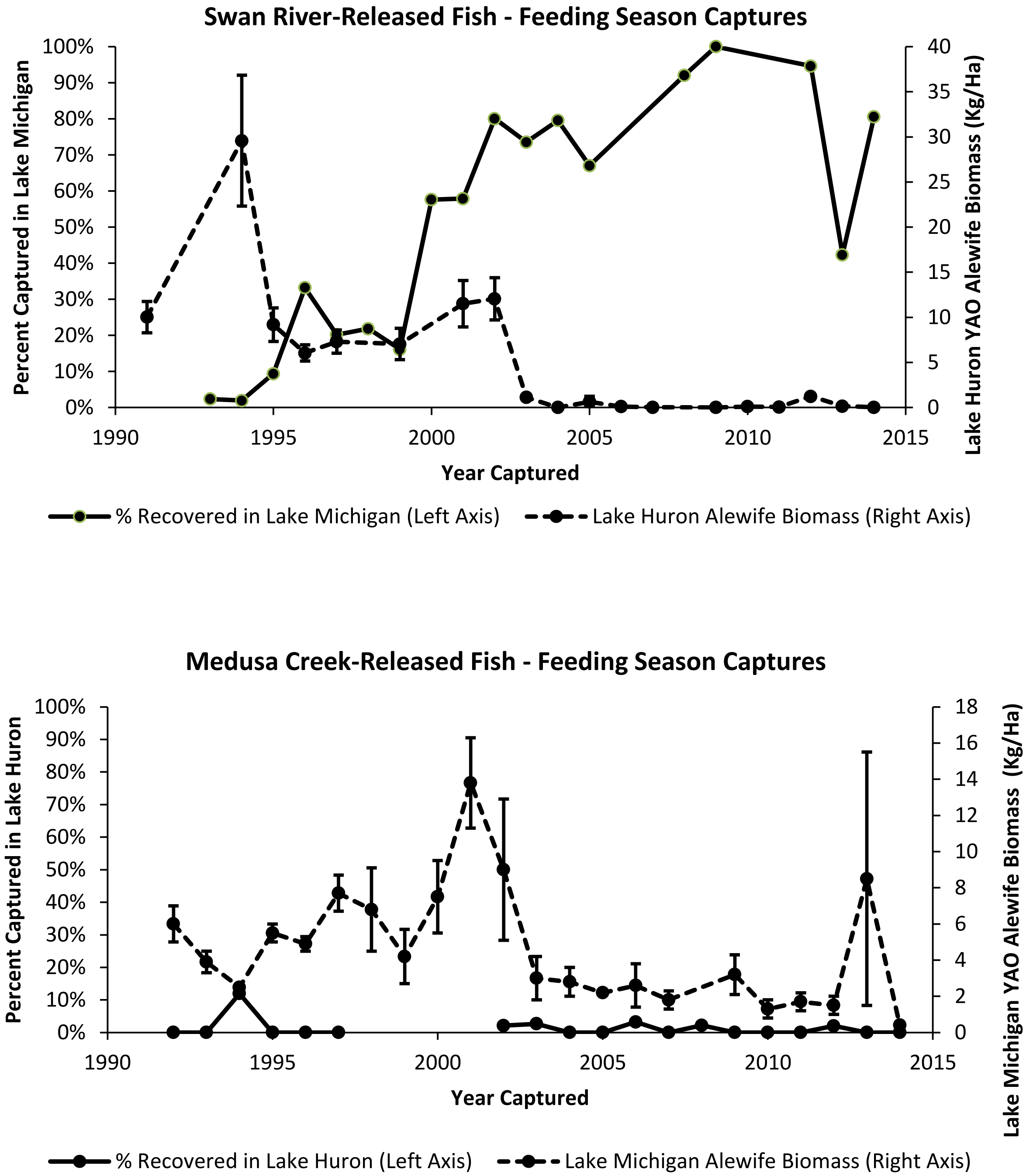

Figure 2. – For the April–July feeding season, the top panel shows the percent of Chinook Salmon released at Swan River in Lake Huron and captured in Lake Michigan (left axis) along with YAO Alewife biomass by year in Lake Huron (right axis). Also for the feeding season, the bottom panel shows the percent of Chinook Salmon released at Medusa Creek in Lake Michigan and captured in Lake Huron (left axis) along with YAO Alewife biomass by year for Lake Michigan (right axis). Error bars for YAO Alewife biomass are ± 1 standard error.

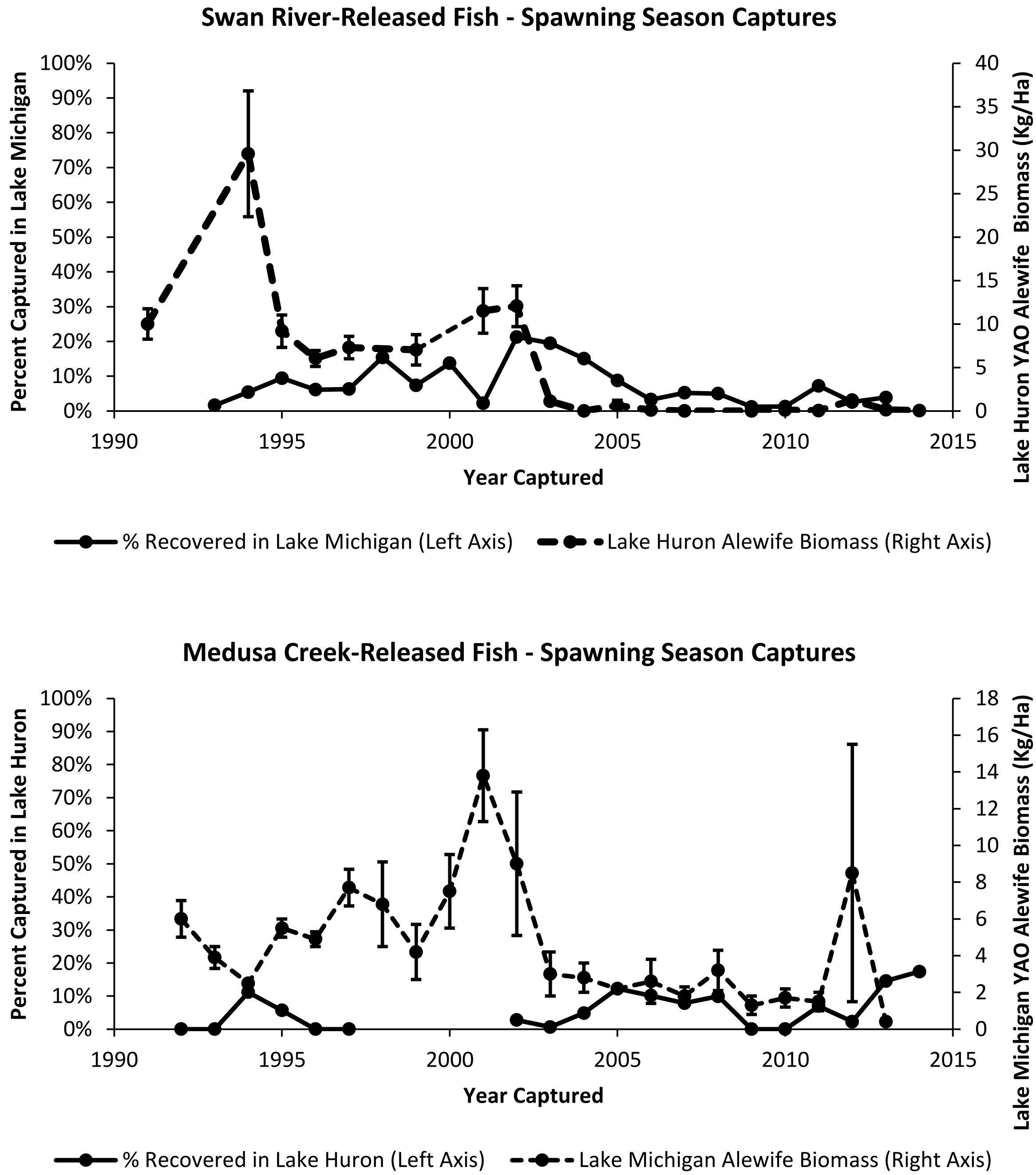

Figure 3. – For the August–October spawning season, the top panel shows the percent of Chinook Salmon released at Swan River in Lake Huron and captured in Lake Michigan (left axis) along with YAO Alewife biomass by year in Lake Huron (right axis). Also for the spawning season, the bottom panel shows the percent of Chinook Salmon released at Medusa Creek in Lake Michigan and captured in Lake Huron (left axis) along with YAO Alewife biomass by year for Lake Michigan (right axis). Error bars for YAO Alewife biomass are ± 1 standard error.

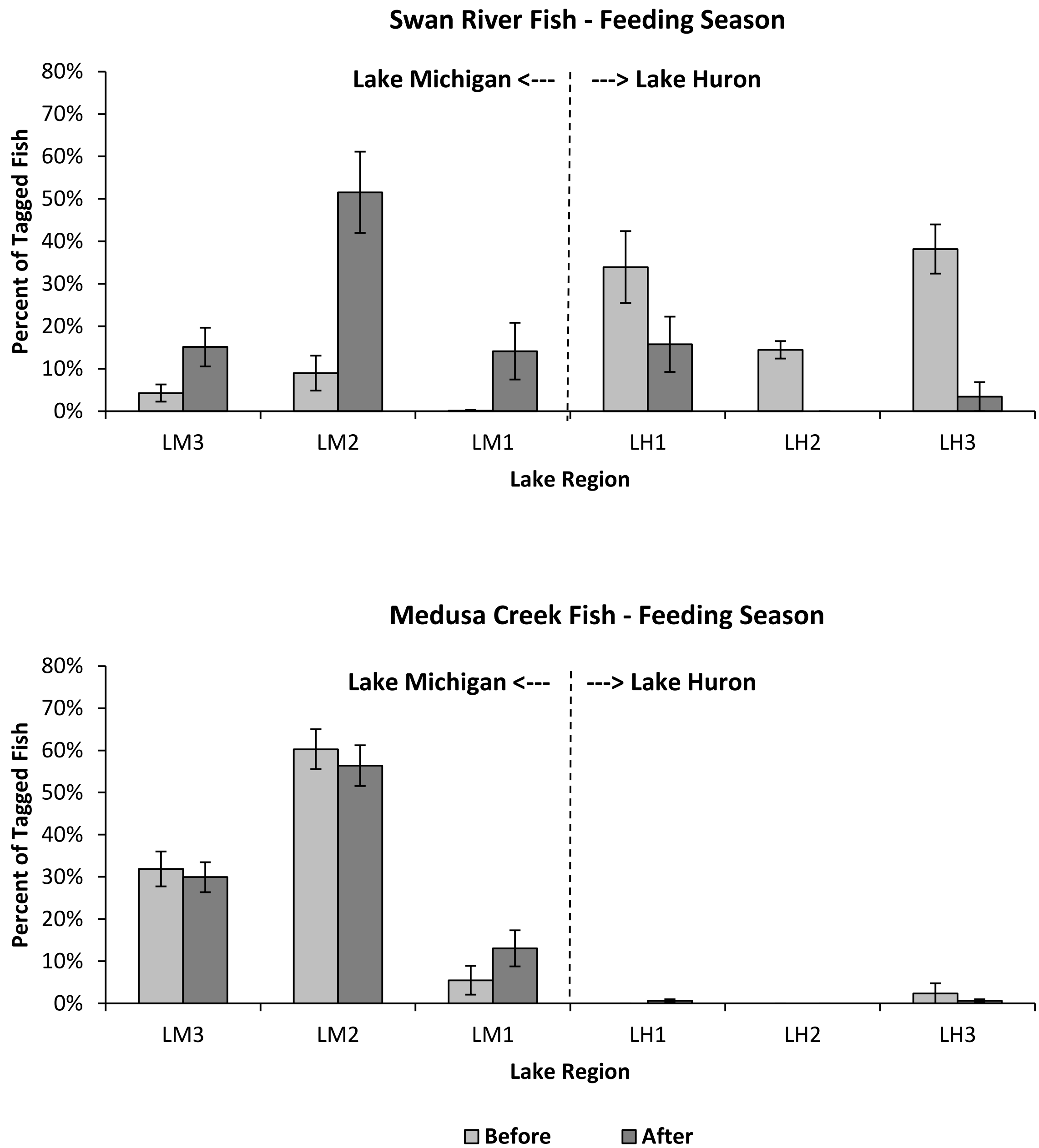

Figure 4. – Distributions of captured Chinook Salmon before (1993–1997) and after (2008–2014) the collapse of Alewives in Lake Huron during the feeding season. The top panel shows average annual percentages captured by region for fish released at Swan River, Lake Huron. The bottom panel shows average annual percentages captured by region for fish released at Medusa Creek, Lake Michigan. Error bars are ± 1 standard error of annual values.

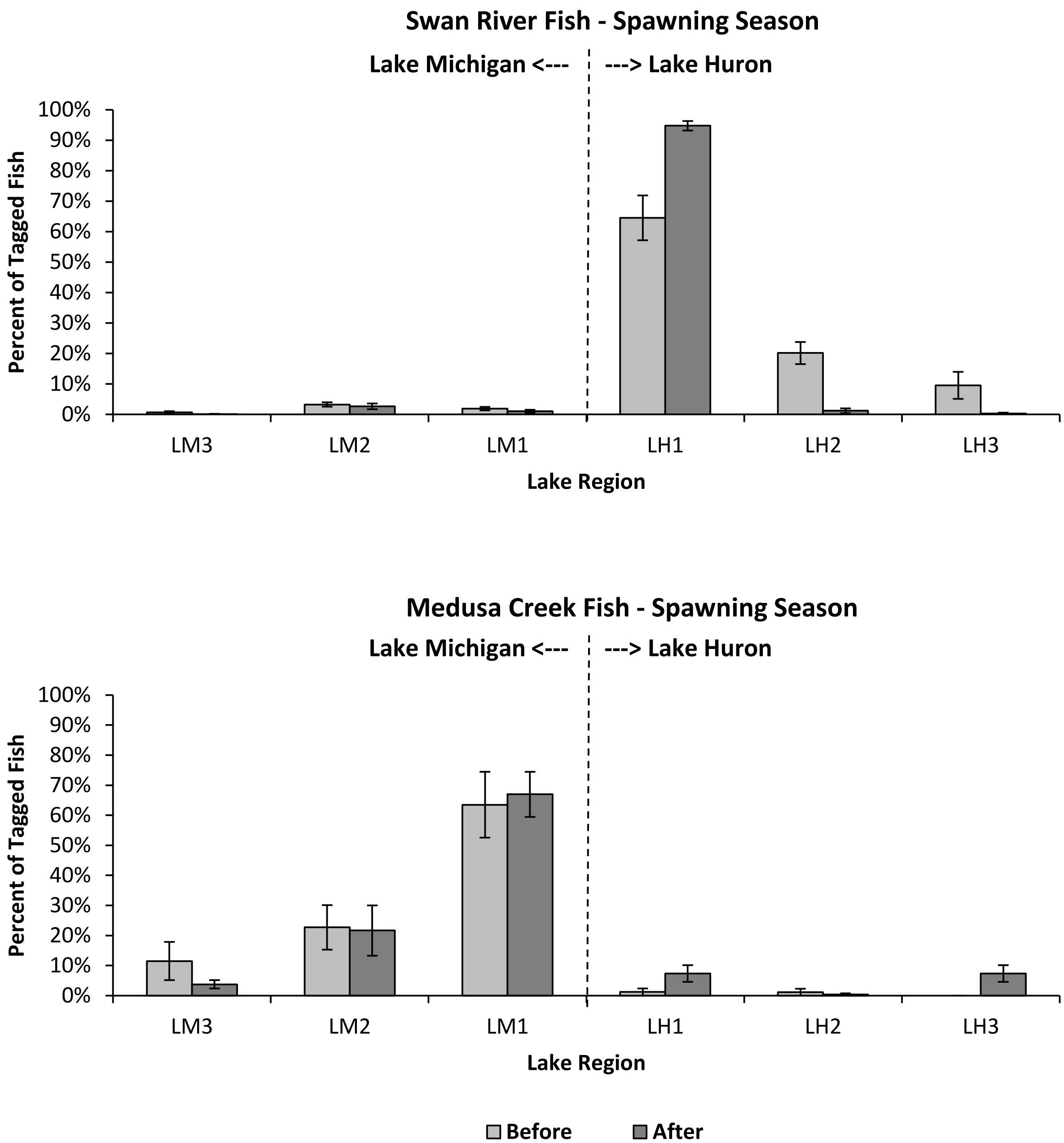

Figure 5. – Distributions of captured Chinook Salmon before (1993–1997) and after (2008–2014) the collapse of Alewives in Lake Huron during the spawning season. The top panel shows average annual percentages captured by region for fish released at Swan River, Lake Huron. The bottom panel shows average annual percentages captured by region for fish released at Medusa Creek, Lake Michigan. Error bars are ± 1 standard error of annual values.

Swan River – Feeding Season

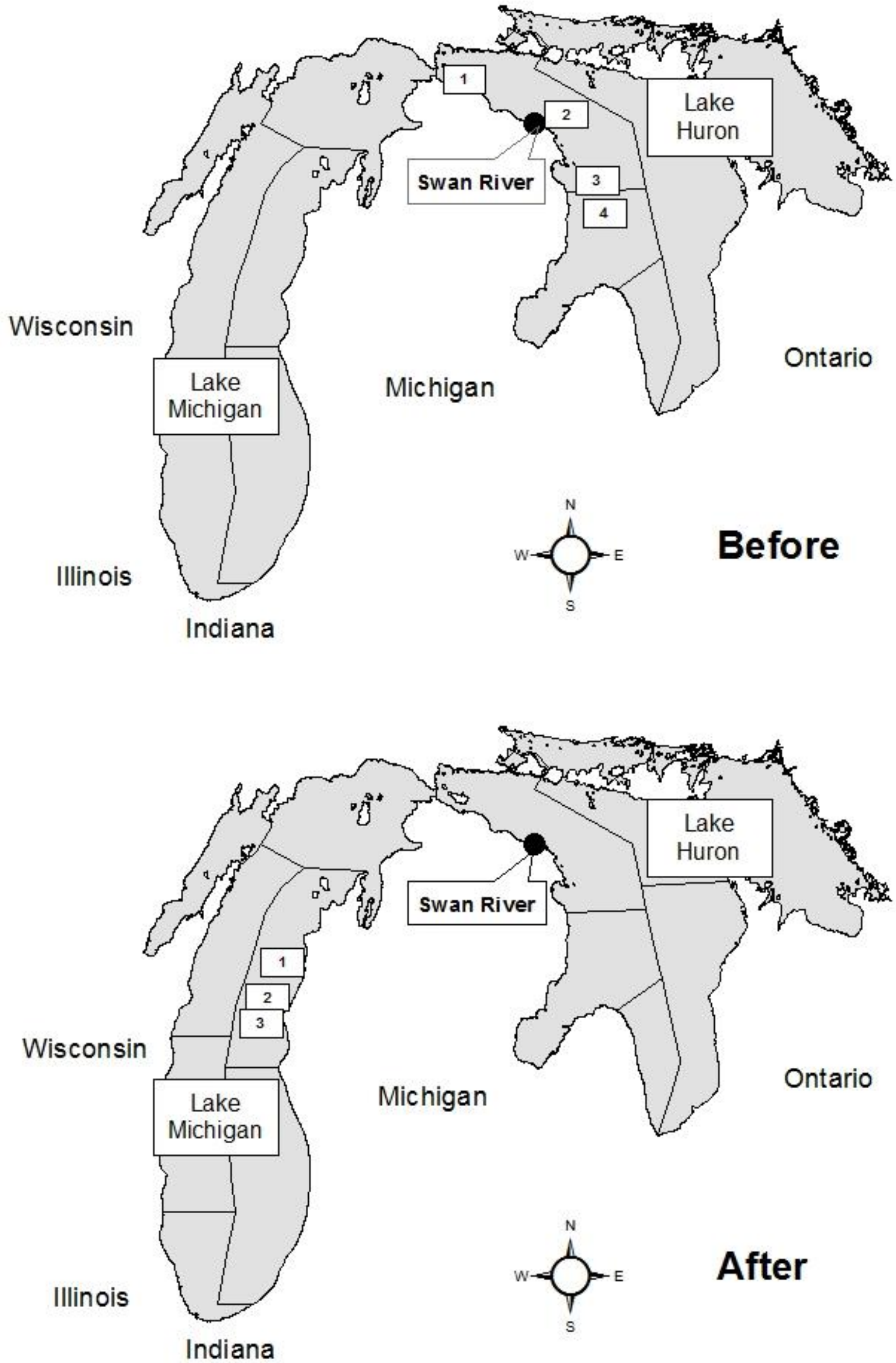

Figure 6. – Numbered boxes on maps represent age groups of tagged Chinook Salmon stocked at Swan River, Lake Huron. Locations of boxes show the approximate the net displacement directions from Swan River during the feeding season before (1993–1997 – top panel) and after (2008–2014 – bottom panel) the collapse of Alewife populations in Lake Huron.

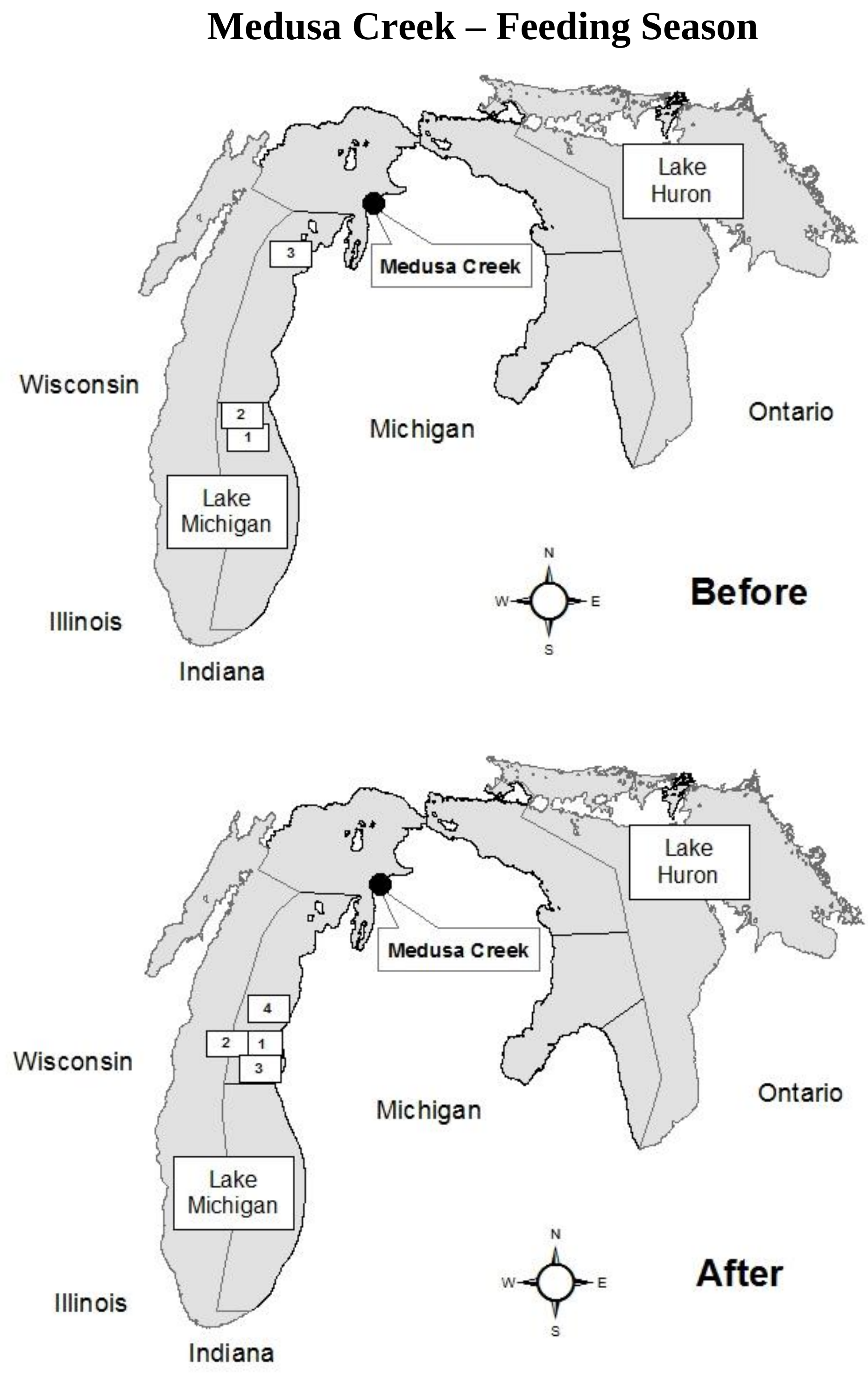

Figure 7. – Numbered boxes on maps represent age groups of tagged Chinook Salmon stocked at Medusa Creek, Lake Michigan. Locations of boxes show the approximate the net displacement directions from Medusa Creek during the feeding season before (1993–1997 – top panel) and after (2008–2014 – bottom panel) the collapse of Alewife populations in Lake Huron.

Swan River – Spawning Season

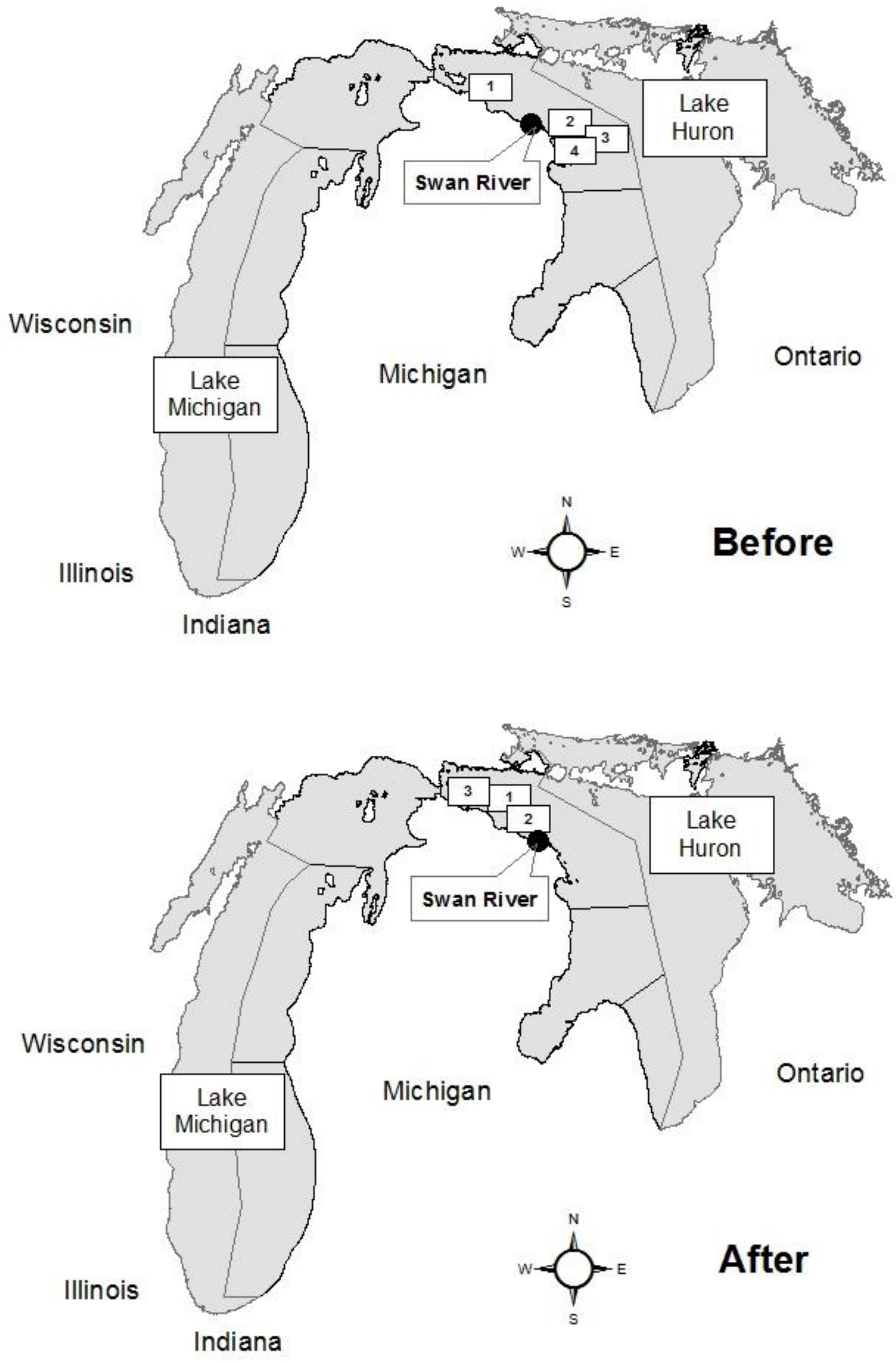

Figure 8. – Numbered boxes on maps represent age groups of tagged Chinook Salmon stocked at Swan River, Lake Huron. Locations of boxes show the approximate the net displacement directions from Swan River during the spawning season before (1993–1997 – top panel) and after (2008–2014 – bottom panel) the collapse of Alewife populations in Lake Huron.

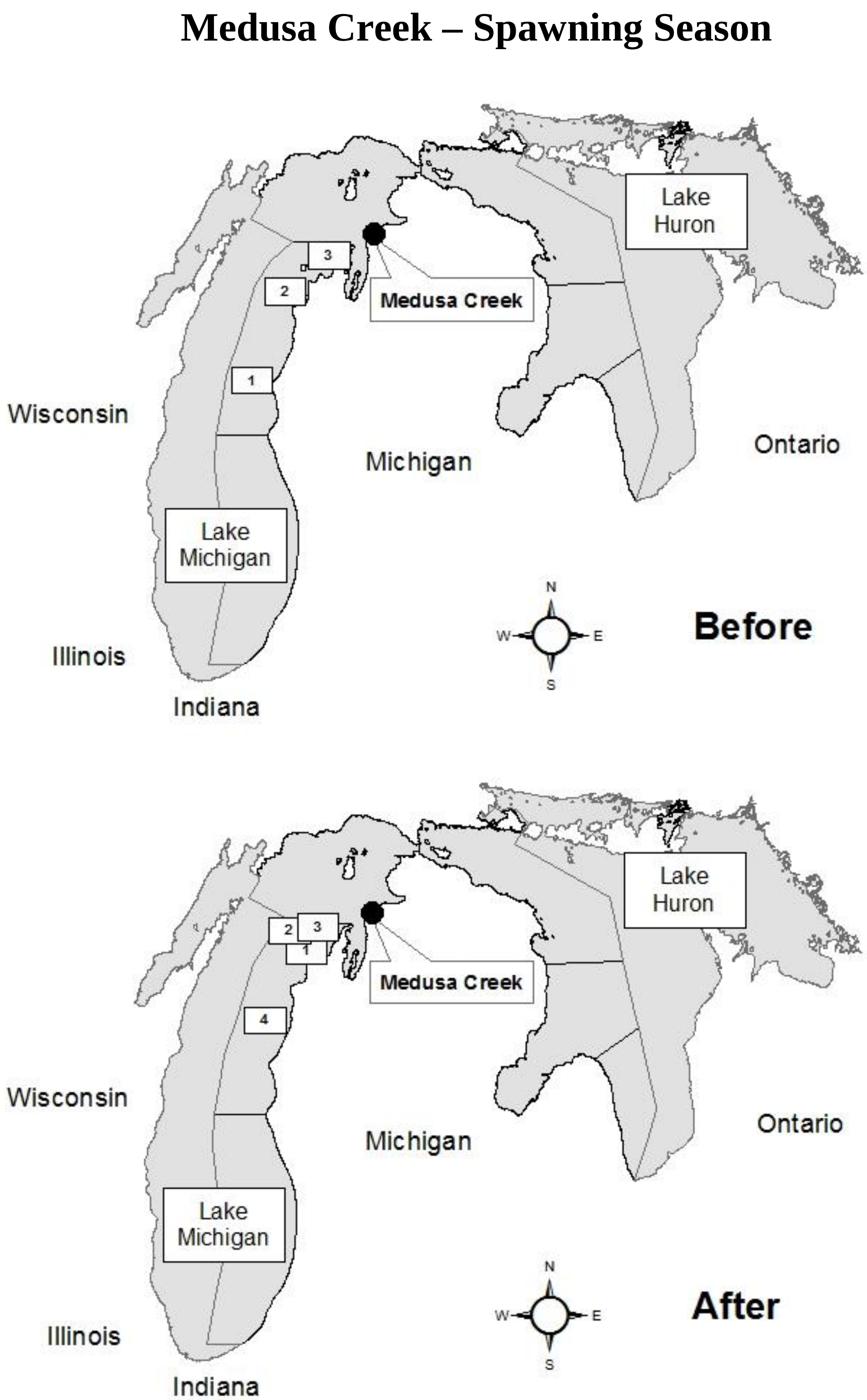

Figure 9. – Numbered boxes on maps represent age groups of tagged Chinook Salmon stocked at Medusa Creek, Lake Michigan. Locations of boxes show the approximate the net displacement directions from Medusa Creek during the spawning season before (1993–1997 – top panel) and after (2008–2014 – bottom panel) the collapse of Alewife populations in Lake Huron.

<A> Appendix: Number of individual captures for each release site by season, year, lake, and lake region.

Table A1. – Locations of feeding season (April–July) recoveries for Chinook Salmon released at Swan River Lake Huron.

	Lake and region of capture								
	Michigan				Huron				
Year	LM3	LM2	LM1	Lake total	LH1	LH2	LH3	Lake total	Grand total
1993	1	1	0	2	8	7	14	29	31
1994	4	1	0	5	43	21	44	108	113
1995	3	15	2	20	106	45	32	183	203
1996	6	16	0	22	7	14	14	35	57
1997	11	11	0	22	22	19	28	69	91
1998	8	18	0	26	16	21	12	49	75
1999	4	4	0	8	12	3	4	19	27
2000	13	15	0	28	6	1	1	8	36
2001	5	7	0	12	0	1	2	3	15
2002	10	15	2	27	1	2	1	4	31
2003	33	13	0	46	5	0	1	6	52
2004	23	16	10	49	6	2	0	8	57
2005	5	10	2	17	2	0	0	2	19
2006	1	1	0	2	2	0	0	2	4
2007	2	3	3	8	0	0	0	0	8
2008	5	10	8	23	1	0	0	1	24
2009	6	7	1	14	0	0	0	0	14
2010	0	4	0	4	0	0	0	0	4
2011	1	5	0	6	1	0	0	1	7
2012	7	27	6	40	2	0	0	2	42
2013	14	21	7	42	9	0	2	11	53
2014	45	75	3	123	9	0	0	9	132
Grand total	207	295	44	546	258	136	155	549	1095

Table A2. – Locations of spawning season (August–October) recoveries for Chinook Salmon released at Swan River Lake Huron.

	Lake and region of capture								
	Michigan				Huron				
Year	LM3	LM2	LM1	Lake total	LH1	LH2	LH3	Lake total	Grand total
1993	1	1	0	1	15	7	1	23	24
1994	0	2	0	5	69	13	0	82	87
1995	3	7	3	12	74	34	2	110	122
1996	2	3	0	4	31	22	4	57	61
1997	1	3	1	5	70	24	3	97	102
1998	1	8	3	11	25	22	0	47	58
1999	0	8	1	9	58	3	1	62	71
2000	0	0	1	4	31	4	0	35	39
2001	3	2	0	2	35	1	0	36	38
2002	0	4	2	10	27	8	4	39	49
2003	4	15	3	19	42	4	0	46	65
2004	1	10	5	16	33	4	0	37	53
2005	1	5	1	6	9	0	0	9	15
2006	0	2	0	2	4	0	0	4	6
2007	0	3	0	3	7	0	0	7	10
2008	0	7	0	7	24	0	0	24	31
2009	0	2	0	4	19	0	0	19	23
2010	2	1	0	1	19	0	0	19	20
2011	0	2	0	2	19	0	0	19	21
2012	0	9	0	9	28	2	0	30	39
2013	0	7	1	18	118	1	0	119	137
2014	10	16	6	29	130	1	1	132	161
Grand total	27	117	35	179	887	150	16	1053	1232

Table A3. – Locations of feeding season (April–July) recoveries for Chinook Salmon released at Medusa Creek Lake Michigan.

	Lake and region of capture								
	Michigan				Huron				
Year	LM3	LM2	LM1	Lake total	LH1	LH2	LH3	Lake total	Grand total
1993	10	9	0	19	0	0	0	0	19
1994	9	7	0	16	0	0	1	1	17
1995	14	11	3	28	0	0	0	0	28
1996	5	15	0	20	0	0	0	0	20
1997	4	5	1	10	0	0	0	0	10
1998	0	1	0	1	0	0	0	0	1
1999	0	0	0	0	0	0	0	0	0
2000	0	0	0	0	0	0	0	0	0
2001	0	1	0	1	0	0	0	0	1
2002	21	35	2	58	0	0	1	1	59
2003	89	40		129	0	2	0	2	131
2004	73	71	22	166	0	0	0	0	166
2005	40	77	23	140	0	0	0	0	140
2006	50	43	21	114	1	0	0	1	115
2007	28	60	22	110	0	0	0	0	110
2008	27	50	17	94	1	0	0	1	95
2009	17	59	1	77	0	0	0	0	77
2010	17	36	3	56	0	0	0	0	56
2011	19	27	2	48	0	0	0	0	48
2012	35	84	7	126	1	0	0	1	127
2013	20	19	4	43	0	0	0	0	43
2014	34	52	0	86	0	0	0	0	86
Grand total	512	702	128	1342	3	2	2	7	1349

Table A4. – Locations of spawning season (August–October) recoveries for Chinook Salmon released at Medusa Creek Lake Michigan.

	Lake and region of capture								
	Michigan				Huron				
Year	LM3	LM2	LM1	Lake total	LH1	LH2	LH3	Lake total	Grand total
1993	5	6	10	21	0	0	0	0	21
1994	6	8	6	20	2	0	0	2	22
1995	0	6	5	11	0	1	0	1	12
1996	3	5	25	33	0	0	0	0	33
1997	0	6	11	17	0	0	0	0	17
1998	0	0	2	2	0	0	0	0	2
1999	0	0	0	0	0	0	0	0	0
2000	0	0	0	0	0	0	0	0	0
2001	0	3	0	3	0	0	0	0	3
2002	3	10	23	36	2	0	0	2	38
2003	23	39	86	148	0	1	0	1	149
2004	19	32	84	135	6	0	0	6	141
2005	6	35	39	80	3	0	0	3	83
2006	14	93	62	169	4	0	0	4	173
2007	6	53	20	79	1	0	0	1	80
2008	5	56	17	78	3	0	0	3	81
2009	0	54	20	74	0	0	0	0	74
2010	1	29	39	69	0	0	0	0	69
2011	1	10	77	88	2	0	0	2	90
2012	4	39	60	103	1	0	0	1	104
2013	13	14	69	96	5	1	0	6	102
2014	9	32	30	71	4	0	0	4	75
Grand total	118	530	685	1333	33	3	0	36	1369