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International Council for the Exploration of the Sea

Integration of individual based information into fishery and environmental management applications

ICES CM 2009/J:13

Seasonal migration of salmonids in the Great Lakes interpreted from coded-wire-tag recoveries

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Abstract
In the Laurentian Great Lakes, introduced Pacific salmonids are dominant pelagic predators and support valuable recreational fisheries. General declines in stocks during the 1980s prompted mass-tagging programs to investigate movements, and to inform assessments and stocking. Millions of smolts implanted with coded-wire-tags (CWTs) were released and recovered from fisheries, surveys, and weirs. In this paper, we consolidate and refine our previous analysis of Chinook salmon movements in lakes Michigan and Huron where we investigated feasibility of using CWT recoveries from different sources to study movements and analyzed seasonal movements in lakes Huron and Michigan. We based our study on recoveries from recreational fisheries and used Generalized Linear Models, and used recoveries from all sources to complement the analysis. We modeled recoveries by fishing trips to estimate spatially and temporally explicit abundance indices, and accounted for efficiency among recovery sources (charterboat reports, creel-clerk interviews, and dedicated-tag collections). Results show the feasibility of using recovery data from recreational fisheries to study movement. Since variation in recovery levels among recovery sources was significant, and larger than temporal or spatial variation, studies based on CWT recoveries need to consider efficiency to avoid biases. Distribution of tagged fish indicated displacements from southern areas towards the north from spring through summer, from inshore to offshore areas during summer, and back to near original stocking sites in the fall as spawning season approached. Movement patterns coincided with favorable water temperatures and prey distributions, and there were similarities with the published accounts of movement patterns exhibited by Chinook salmon in the Pacific Ocean from which Great Lakes populations originated. Seasonal changes in Chinook salmon distribution influence recreational fisheries, and stocking strategies should consider influences of movement patterns on fishing opportunities. Thus, our results have implications for fisheries management and also for tagging study design in the region and other large-scale systems.

Introduction

Chinook salmon (*Oncorhynchus tshawytscha*) were introduced to the Great Lakes in 1967 to help control exotic forage fishes, particularly alewife *Alosa pseudoharengus* and rainbow smelt *Osmerus mordax,* that had reached nuisance levels during the 1960s, and to create a sport fishery (Tody and Tanner 1966). Both objectives were realized as salmon stocking increased into the 1980s and the sport fishery contributed billions of dollars to the economy of the region (Keller et al. 1990). Currently, the species plays a key role in Great Lake ecosystems as a top predator and still supports profitable sport fisheries, although controlling abundance of nuisance prey is a feedback affecting Chinook salmon abundance because of growth effects on fecundity, age at maturity and recruitment (Riley et al. 2008, Adlerstein et al. 2008)

In the late 1980s, because of growing concerns about exceeding carrying capacity for salmonid predators in lakes Michigan and Huron (Kitchell and Crowder 1986), U.S. state resource agencies initiated a mass-marking and recovery program to estimate Chinook salmon natural reproduction and post-stocking survival, and to track fish movements. Since then, in Lake Michigan about 9,000,000 smolts implanted with coded-wire-tags (CWT) were stocked. As part of the marking program, about 4,000,000 smolts implanted with CWTs were stocked in Michigan waters of Lake Michigan from 1990-1994 (Table 1, Figure 1), and about 30,000 to 50,000 were released annually in Wisconsin waters. Most tagged fish in Lake Michigan were released in the central-east region (Figure 1) and the majority of recoveries from these stocking events were made by 1999. In Lake Huron, over 4,000,000 CWT marked smolts were released between 1991 and 2000 mostly in northern and central management areas on the west side of the lake ((Table 1, Figure 1). Marked fish constituted about 15% of the total numbers of Chinook salmon stocked per year in each lake.

Several recovery programs were set in place to complement the CWT-mass tagging efforts. Tagged fish were caught and recovered from multiple sources with different efficiencies. Fish were caught by commercial fisheries, assessment operations, by chartered and non-chartered recreational fisheries, as well as from fishing at piers, ice shanties and shore. Tags were recovered by creel clerks, CWT collection specialists and volunteers, by resource agency personnel at weirs on spawning grounds, and also were reported by charter boat captains.

Information on Chinook salmon movement is indispensable for assessment and management. Reliable information on distribution and movements is needed to guide management decisions, particularly on stocking strategies (Johnson et al. 2005). Nevertheless, studies that describe the movements of Chinook salmon in the Great Lakes are scarce. In Lake Michigan, few studies available based on catch rates in recreational fisheries (Keller et al., 1990, Benjamin and Bence 2003), and tag recoveries from marked fish (Lake Huron Technical Committee and Lake Michigan Salmonid Working Group 2005, Johnson et al. 2005) have indicated that seasonal movements of Chinook salmon were significant and mostly associated with changes in relative abundance of prey fish (Keller et al. 1990). Based on the few studies available, Chinook salmon stocks in lakes Michigan and Huron are currently treated as a single management unit or stock (Johnson et al. 2005). For Lake Michigan, justification for the single stock approach was based on movement information that had been derived from studies of Chinook salmon diet (Elliott, 1993). Although management does not explicitly account for movement, it is based on implicit views regarding mixing and movements of fish stocked in different locations.

In this study, we summarize information about the Chinook salmon CWT-marking program, and select results from two studies we performed on movement using CWT data. These studies investigated the feasibility of using CWT data from different recovery sources to describe and model seasonal movements of Chinook salmon within lakes Huron and Michigan (Adlerstein et al. 2007a, b). Our modelling studies of fish spatial and temporal distributions were based on Chinook salmon marked with CWTs, released and recovered in coastal waters of lakes Michigan and Huron along the Lower Peninsula of the State of Michigan. Data for the analysis were recovery rates of CWT tagged fish from recreational fisheries. We also used absolute recoveries of CWT tagged fish from all sources of recovery to complement the modelling.

MATERIAL AND METHODS

Analysis of CWT recoveries

General approach

We used a regression approach and modeled CWT recovery numbers and recovery effort to develop spatially and temporally-explicit abundance indices. The efficiency to recover CWT from recreational fisheries, assessment surveys, and operations at weirs varied, and tag-recovery data from these sources cannot be combined and standardized because effort is in different units. Thus, we selected data from the recreational fisheries. Because we used fishing trips as unit of effort we selected recreational fisheries conducting fishing trips, which excludes fishing from piers, ice shanties and shore, for which the unit of effort is not a fishing trip. We analyzed the species composition of the catch to select only those trips that have a chance of fishing Chinook salmon. Further, there are two kinds of recreational fisheries conducting fishing trips (chartered and non-chartered) and three sources of CWT recoveries (clerk interviews, headhunters collections and captain reports), and thus the analysis requires consideration of the effort and efficiency in recovering tags. To that effect, we modeled CWT recoveries by trip using Generalized Linear Models (GLM) (McCullagh and Nelder 1989) and included the fishery-source of recovery as a predictor variable. We inferred seasonal movements under the assumptions that monthly variations in distribution are mainly due to movements where: 1) general decreases in catch rates in all study areas along the east shores of Lake Michigan and the west coast of Lake Huron (State of Michigan waters) are caused by movements offshore, thus in direction away from coastal areas of release, and 2) changes in the relative levels of recoveries by trips among areas along each coast where decreases in some areas co-occurred with increases in others are caused by latitudinal movements.

Data for the analysis

Data for our regression analysis represented recoveries of CWT fish from recreational fisheries in Michigan waters of Lake Michigan and Lake Huron (Figure 1).

We analyzed movement from fish released along the east coast of Lake Michigan and west coast of Lake Huron by selecting CWT recoveries of fish that were released in those areas. We used CWT data from the Michigan Department of Natural Resources (MDNR) CWT database, and fishery catch and effort data from the MDNR Creel, Charterboat and Headhunter Fishery databases. CWT recoveries were reported to or collected by the MDNR. Recoveries from the non-charter fishery were made by clerks during creel interviews and by headhunters. Recoveries from the charter fishery were reported by charterboat captains and also sampled by headhunters. Headhunters are CWT collection specialists employed by the MDNR to monitor the recreational salmonid fishery and inspect anglers' catch for Chinook salmon and other salmonids. Headhunters search exclusively for specimens with missing adipose fins, indicative of presence of CWT tags, and collect the fish snout/head and record recovery data. In contrast, creel clerks only occasionally collect tagged fish, instead concentrating on counts and interviews to measure recreational fishing effort and harvest.

Data from all sources of CWT recoveries were obtained from fish tagged and released as smolts. The CWT is an engraved piece of wire, 0.25-mm in diameter, and inserted in the snout of the fish prior to release. Tag loss was assumed to be negligible (Hale and Gray 1998). During tagging, the adipose fins were removed to allow external recognition of fish bearing CWT. Following tagging, each lot of stocked fish was evaluated for CWT retention and fin clip quality. Fish recovered were inspected for fin clips, and snouts were removed from those with missing adipose fins and transferred to laboratories for further processing, tag removal and code identification. Recovered fish have the snout removed for tag extraction and interpretation. The code is then read under a microscope, and the data are entered into the CWT database. Tagging and tag recovery procedures are described in detail in the MDNR web page (www.michigan.gov/dnr/0,1607,7-153-10364_10951_11301-97831--,00.html). CWT recovery programs and processing of tags were carried out through collaborative efforts of the U.S. Geological Survey-Great Lakes Science Center, MDNR, Chippewa-Ottawa Resource Authority, Ontario Ministry of Natural Resources, the U.S. Fish and Wildlife Service, and various fishing groups.

To analyze movement of fish released in Lake Michigan, we evaluated data from 1,987 CWT Chinook salmon recovered in Michigan waters of Lake Michigan in statistical districts MM4 to MM8 (Table 2) (Figure 1). Most recoveries were made in the central-east region and by charterboat captains (Table 2). Data were from 1993, when the Headhunter program started, until 1999 when most CWT from fish stocked in 1990-1994 had been recovered. To analyze movement of fish released in Lake Huron, we evaluated data from 3,366 CWT Chinook salmon recovered from all management areas in U.S. waters of Lake Huron (Table 2). Data were collected from 1993 until 2001. We complemented the analysis with data from absolute number of CWT recoveries from 10,049 CWT fish released in U.S. waters and recovered in U.S. and Canadian waters, and from 389 CWT fish released in Canadian waters and recovered in U.S. waters. These data were from all recovery sources, including modes of recreational fishing (volunteer returns) and non-recreational sources that were not included in the regression analysis (above). Data from fish that were released and recovered in Canada were not available for analysis.

Fishery data to estimate fishing effort consisted of catch information in the charterboat and non-charterboat fishery by fishing trip, date, fishing location, and site of the interview. To select fishing trips that had the potential to catch Chinook salmon we analyzed the species composition as the recreational fisheries in both lakes target multiple species and the chances of catching a particular species varies with the species targeted. We identified that Chinook salmon were practically absent in catches from the Michigan recreational fisheries when yellow perch were present both in chartered and non-chartered trips. Thus, we excluded trips with yellow perch. Based on this definition, we identified that the number of fishing trips that had the potential to catch Chinook salmon in each lake was about 15,000 trips per year

To pair CWT recoveries with the recovery effort, we aggregated the data on CWT recoveries and trips conducted in both recreational fisheries effort by month, statistical district of recovery, and type of fishery, and we matched the number of CWT fish with the corresponding effort for each source of recovery.

Analysis

For the GLM analysis of recovery data we used the following model:

$$g(\mu_{ymdg}) = \alpha + \delta_y + \phi_m + \lambda_d + \tau_g \quad (1)$$

where g () is a link function, μ is the expected number of CWT recovered by the corresponding number of trips, δ is the year, Ø is the month, λ the statistical district, and τ the source of tag recovery. The recovery source variable with four corresponding levels accounts for differences in efficiency among recovery sources. The models incorporated a binomial distribution to describe the probability of obtaining a given number of tags with the associated number of trips. Each trip was treated as a Bernoulli trial with the expected catch of CWT fish constrained between 1 and 0 (multiple recoveries occur but seldom because few fish are marked and daily fishing are limited to five salmonids, no more than three of which could be Chinook salmon (Rutherford 1997). We selected the best performing logit function, the canonical link for the binomial family. We investigated first-order interactions investigated but did not test for higher-order interactions. We tested significance of explanatory variables by analysis of deviance and examined model residuals and estimation of the dispersion parameter of the binomial models to check validity of the model assumptions. All tests were performed at the 95% confidence level. GLMs were run with routines contained in the S-Plus programming environment (Becker et al. 1988).

To complement the GLM analysis and expand the spatial distribution of CWT recoveries, we examined fish displacement using absolute CWT numbers of fish released and recovered in Lake Michigan in Michigan and Wisconsin waters and in Lake Huron in Michigan and Ontario waters.

RESULTS

An average of 15 and 20 coded-wire-tagged Chinook salmon was recovered from the catch of 1,000 trips in the recreational fisheries in Michigan waters of lakes Michigan and Huron respectively. The main effect GLM incorporating statistical district, month, year and source of recovery explained 60% of the variability in tag recoveries by trip in Lake Michigan and 50% in Lake Huron (Table 3). In both regions, CWT recovery rates varied significantly among recovery sources, and by month, year and area. The difference among recovery sources was similar between lakes with highest rates for headhunters sampling chartered trips and lowest among creel clerks sampling non-chartered trips (Table 3). In Lake Michigan, the largest source of variation in recovery rate was among years, since CWTs were released up to 1994 and recoveries made up to 5 years later were very low. In Lake Huron, releases continued for several years and the difference in rates among recovery sources was more important (Table 3).

Main effects models guided our interpretation of longitudinal movements while interactions between month and statistical districts informed us about latitudinal movements. For Lake Michigan the main effect model indicated that recovery levels decreased from May to August and increased in September (Figure 2), suggesting that fish moved away from Michigan districts during spring and summer and back during September approaching the spawning season. Rates also were highest in central areas and among headhunters sampling charterboat fishing trips, and decreased after 1996 (Figure 2). The relative recovery levels among statistical districts varied significantly with month (district - month interaction: probability of Chi < 0.0001) suggesting latitudinal movements. The pattern observed was that rates in the most southern area in May were similar to those in neighboring areas to the north and decreased during June through August as levels in northern areas became relatively higher (Figure 3). By September the distribution among areas was similar to that in May (Figure 3). Based on these patterns, Chinook salmon presumably concentrated along the southeast coast of Lake Michigan in winter, and moved towards the central coast region in June and July. In Lake Huron, rates increased towards the end of the season in September and October, suggesting that fish moved away from Michigan districts before the fishing season started in spring and returned from regions outside of the study areas as spawning time approached. Also, rates were highest in central-northern areas and among headhunters sampling charter and non-charterboat fishing trips, and decreased after 1999 (Figure 3). Significant interaction between area and month (probability of Chi < 0.04) indicated that CWT recoveries by trip did not vary in synchrony across statistical districts. The pattern observed was an increase in rates from south to north as the season progressed from May to August (Figure 3), suggesting fish movement in a northerly direction.

GLMs of marked fish released in one statistical area of Lake Michigan and Lake Huron

GLM results indicate that in Lake Michigan marked fish released in MM7 were recovered in all areas indicating movement from the release areas to other areas, although recoveries by trip were highest in the area of release (MM7). In particular in MM6 rates were not significantly different to those in MM7 (Figure 4). Similarly in Lake Huron, recoveries by trip were highest in the area of release MH3 but were recovered in all areas also indicating movement (Figure 4). In Lake Michigan, recovery rates decreased from May to July and increased to higher levels in September in all areas suggesting that Chinook salmon made seasonal movements to the west in spring and back. In Lake Huron, recovery levels in all areas increased from May to August suggesting that Chinook salmon also made seasonal movements to the west into near shore waters (Figure 4). In both cases, highest recovery levels occurred in fall. Further, interactions between month and area were significant in both lakes and indicate an increase in recoveries by trip from south towards the north as the season progressed. A similar pattern was shown by GLMs of recoveries from all release areas as shown in Figure 3.

Maps of the GLM-standardized CWT distribution presented in Figures 5 and 6 show changes in densities of Chinook salmon in both lakes in all areas and from south to north as the study season progressed. We interpreted these changes to be the result of movements westward and northward during the study season. These figures show that despite seasonal movements, most fish remained in, or returned to the release area where they concentrated to spawn.

Absolute number of CWT recoveries to further assess longitudinal movements

Absolute numbers of CWT recoveries from available datasets indicate movement of Chinook salmon between the east and west coast of Lake Michigan and west and east coast of Lake Huron. These numbers give further support to patterns found from the

GLM analysis. In Lake Michigan, 356 CWT Chinook salmon released in Michigan waters were recovered in Wisconsin in statistical districts WM1 to WM6, and 492 CWT released in Wisconsin waters of Lake Michigan were recovered in Michigan waters in statistical areas MM2 to MM8 (Table 4). In Lake Huron, about 400 fish released in Canadian waters were recovered in U.S. waters in statistical districts MH1 to MH6, and over 100 fish released in U.S. waters were recovered in Canada (Table 4). Also, 610 CWT Chinook salmon released in Lake Huron, mostly in MH1 were recovered in Lake Michigan (Table 4). Highest recoveries of Wisconsin tagged fish in Michigan were during July and August as well as those recoveries of Michigan tagged fish in Wisconsin. The Canadian tagged fish were recovered in U.S. waters in increasing numbers from April to July, then in decreasing numbers through October. Most of the fish tagged in the U.S. and recovered in Canada were found in November and April. These numbers indicate that regardless of region of origin (east or west shoreline), fish moved offshore, and probably became mixed as the summer progressed. If our GLM analysis would have been implemented without identifying the origin of the fish, seasonal movement could have been obscured by the longitudinal movement of fish in both lakes.

DISCUSSION

Our results showed that recoveries by trip of CWT Chinook salmon in recreational fisheries of the Lake Huron and Lake Michigan varied significantly among recovery sources and that this variation was larger than seasonal or spatial fluctuations. The magnitude of the variation, fairly similar in fisheries in both lakes, indicates that population studies based on unadjusted tag recoveries combined from several sources will be biased without accounting for differences in efficiency of the recovery source. The GLM coefficients derived in this study can be used to correct for this problem, where those for charterboat and headhunter recoveries were highest. Higher catches per trip in charter operations occurred because the numbers of anglers per boat were, on average, double that in non-charter operations, trips tended to be longer, number of rods per angler was higher and captains had greater experience in catching fish than non-charter anglers. Headhunters recovered tagged fish more efficiently than creel clerks and charterboat captains since the program was specifically implemented to sample CWT fish, nevertheless the magnitude of the difference was previously unknown.

Results of our Chinook salmon movement studies are consistent with few available reports for the study region. Seasonal longitudinal movements of fish released in Lake Michigan and in Michigan waters derived from our GLM analysis are consistent with information from other related studies, although northwards movements have not been described. Our results show fluctuations in recoveries indicative of Chinook salmon movements away from the east coast during July and August and back in the fall and from southern areas towards the north from May through summer. For Lake Huron, there are no previous studies to compare our findings on Chinook salmon seasonal distribution. Based on CWT recovery rates, we found that Chinook salmon released along the west coast of the lake moved near shore during early spring and north during summer, returned mostly to areas near stocking locations in summer and fall, and moved east to deep over-winter areas. Results are consistent with observations on latitudinal seasonal changes in Chinook salmon distribution by Diana (1990). Diana (1990) did not investigate movement but attempted to collect sufficient Chinook salmon specimens for diet analysis along the western shore of Lake Huron and found that Chinook salmon were available only from near Port Huron in the south during May and from northern areas in July. Diana (1990) concluded that salmon migrated in a northerly direction in western Lake Huron during summer. We propose that Chinook salmon stocked along the western shore of Lake Huron over-winter in deep waters of Lake Huron and return towards the west coast in summer (where some fish return to stocking rivers to spawn in the fall**).** Evaluation of absolute number of CWT recoveries reinforced GLM results on movements away from the east coast of Lake Michigan during summer by indicating movement of fish released from Michigan waters into Wisconsin waters, and of fish released in Lake Huron from Michigan waters into Canadian waters. Finally, results on longitudinal and latitude movement are consistent with auxiliary analysis based on catch rates of Chinook salmon in gill net surveys by Adlerstein et al. (2007b) not reported here. Results showed catch rate fluctuations of all fish caught in these surveys indicative of Chinook salmon movement towards the north in starting in spring, away from Michigan waters towards the west in late spring and summer, as well as within Michigan waters towards offshore deeper areas.

Chinook salmon movements found in this study can be related to environmental cues including warming water temperatures, thermocline development, and prey distribution, and also may be genetically influenced. The few previous studies of Chinook salmon movement in the Great Lakes suggest high mobility and seasonal migrations, and indicate that the most important drivers of their distribution are temperature and prey (Keller et al. 1990; Elliot 1993; Benjamin and Bence 2003). Both alleged drivers of salmon distribution experience seasonality (Brandt et al 1991), and are consistent with Chinook salmon movements away from nearshore areas in spring and towards nearshore areas in fall, and with northwards movements in spring to summer. Fish released in the west moved towards the east at the same time that fish released in the east moved west, suggesting that the described patterns resulted from movements away from nearshore areas in response to similar biological or environmental cues occurring along both coasts. Distributions of salmonines in the Great Lakes, as well as in the Pacific Ocean, are influenced by water temperature (Haynes and Keleher 1986; Haynes et al. 1986; Nettles et al. 1987; Olson et al. 1988; Aultman and Haynes 1993; Höök et al. 2004). Although Chinook salmon are most often found at temperatures around 10-12^{o}C (Stewart and Ibarra 1991; Walker et al. 2000; Hinke et al. 2005), during summer individuals can inhabit much warmer waters at temperatures up to 20^{o}C (Olson et al. 1988; Wurster et al. 2005). These higher temperatures are within the preference range of alewife prey (Brandt et al. 1991). During spring in the extreme south-eastern area of Lake Michigan where higher Chinook salmon densities were found, surface waters of around 8.5 - 16.5^{o}C are approximately 4 - 6^{o}C warmer than in the north and 2 - 4^{o}C warmer than in the west (Brandt et al. 1991). However, during summer when the thermocline is more pronounced, surface waters can exceed 20^{o}C. Thus, Chinook salmon likely moved offshore and deeper in the water column in response to these temperature changes.

In addition to water temperature, environmental cues for Chinook salmon movement likely include prey distribution. Alewives and rainbow smelt undergo seasonal lakewide migrations in the Great Lakes and are the major components of salmonines' diets (Madenjian et al. 2002; Rybicki and Clapp 1996) and Lake Huron (Diana 1990;

Dobiesz et al. 2003). Alewife move from deep wintering areas towards shallow waters in spring as water temperatures increase, and to deeper waters in the fall (Brown 1972; Argyle 1982; Brandt et al. 1991). Thus, decreasing catch rates of Chinook salmon nearshore found in this study could be explained by movements of prey offshore, where studies have reported higher densities of alewives during mid to late summer (Brandt et al. 1991; Warner et al. 2006). The northwards movement trend not only can be related to environmental cues but also is consistent with the hypothesis of genetic influence on movement of Chinook salmon. Chinook salmon populations in the northeast Pacific Ocean exhibit movement patterns that have been interpreted as being heritable (Myers et al. 2005). After ocean entry, Chinook salmon from the Green River, WA population, the original source of eggs for salmon stocked in Lake Michigan and Lake Huron, remain in coastal waters and move primarily northwards during spring and summer. Movement patterns found in our study also were similar to those movements of individuals from the Green River population.

In summary, our results describing distribution and movements increase our understanding of Chinook salmon populations and provide valuable information on recreational fisheries. We believe that Chinook salmon tend to be located high in the water column and in areas during spring because of warmer water temperatures that coincidently have a higher concentration of prey. From May to July, fish in the nearshore move north following the warming of surface water. During July and August, fish start to move away from the coast into deeper waters as nearshore and surface waters warm and prey distribution changes. The results suggest that minor changes in weather conditions can have an impact on the recreational fisheries by altering the distribution of Chinook salmon. Assuming Chinook salmon distributions respond to lake conditions, a rapid warming of a specific area of the lake is likely to precipitate a rapid decline in fishery catch rates as fish move offshore and become less densely aggregated in the water column.

Insights from this study have management implications relative to stocking locations and the fishing opportunities that they provide. Since Chinook salmon distribution seems determined by movements that can be affected by temperature and forage conditions, the number of fish released in a stocking area will mainly contribute to the seasonal fall fishery in the same area when fish return to spawn. Because the lake-wide fishery is not directly linked to site-specific stocking rates, but more likely to the movement patterns described herein, managers should consider survival of smolts associated with stocking sites as the most important criteria for stocking strategies. Also, if Chinook salmon distributions are determined by forage conditions, as abundance of alewives is declining (Riley et al. 2008), it is possible that a shift in the prey base could result in changes in population distribution becoming less available for the recreational fisheries. This suggests that it is important for management to focus more effort in studying prey fish populations. Further, our results of extensive Chinook salmon movements in lakes Michigan and Huron support management based on a single-stock hypothesis; although further work is needed to determine population structure and gene flow of wild salmon and also to refine our study of movements.

Table 1 . Total number of recoverable Chinook salmon marked with coded-wire tags (adjusted by tag retention, MDNR unpublished data) by statistical district in Michigan waters of Lake Michigan and Lake Huron (Michigan Department of Natural Resources Coded-Wire Tag Database). No fish were marked after 1994 in Lake Michigan.

Year	**Statistical districts**					
			Lake Michigan			
	MM3	**MM4**	**MM6**	**MM7**	**MM8**	**Total**
1990	98,393		295,361	187,724		581,478
1991	105,647	95,487	288,107	295,436	99,555	884,592
1992	100,302	97,458	288,583	279,027	97,266	862,636
1993	86,102	81,724	282,625	283,871	82,392	816,714
1994	84,577	90,756	256,390	274,030	98,281	804,034
Total	475,021	365,425	1,411,066	1,320,088	377,494	3,953,278
			Lake Huron			
	MH1	**MH3**	**MH4**	**MH5**	**MH6**	**Total**
1991	215,617	246,842				462,459
1992	208,052	150,910				358,956
1993	200,100	201,640		100,000		501,740
1994	200,128	200,130		100,080		500,338
1995	102,000	205,805		207,943		515,748
1996	103,140	196,356		205,877		505,373
1997	102,354	203,990		206,242		512,586
1998	101,287		176,391	204,143		481,821
1999	102,277		167,367			269,644
2000	101,731	104,339	225,940		162,800	594,810
Total	1,436,686	1,510,012	569,698	1,024,295	162,800	4,703,481

Table 2. Numbers of Chinook salmon marked with coded-wire tags, recovered by selected recovery sources in the recreational fishery along management areas of State of Michigan waters and between May and October. Tagged fish were released and recovered in Michigan waters of Lake Michigan between 1993 and 1999 and recovered in Lake Huron between 1993 and 2001. Sources selected for the analysis include CBT (reported by charter captains), CCK (creel clerk interviews), HHB (headhunter sampled from charter fisheries), and HHR (headhunter sampled from non-charter fisheries).

	Source of recovery			
Statistical district	CBT	CCK	HHB	HHR
Lake Michigan				
MM4	4	37	0	0
MM5	17	41	9	11
MM6	318	119	63	144
MM7	512	90	167	144
MM8	28	109	68	106
May	139	54	112	90
June	116	52	83	92
July	140	79	42	87
August	266	106	59	73
September	176	154	11	23
Lake Huron				
MH1	18	136	1	330
MH2	32	263	17	507
MH3	146	515	12	292
MH4	140	86	58	178
MH5	84	89	7	173
MH6	16	43	3	218
May	33	36	11	259
June	49	100	15	185
July	108	225	35	574
August	124	330	34	509
September	109	332	2	126
October	10	94	0	6

Table 3. Analysis of Deviance for main effects GLM of tag recovery rates of Chinook salmon in recreational fisheries of Michigan waters of lakes Michigan and Huron, and coefficients for source of recovery. Recoveries are from May to September 1993 to 1999 and statistical districts MM-4 to MM-8 for Lake Michigan, and from May to October 1993 to 2001 and from statistical districts MH-1 to MH-6 for Lake Huron. Source of recovery coefficients are in logit link scale and estimated using a contrast treatment matrix with charterboat captains reporting tags as reference level.

Terms	df	Deviance	Residual Deviance	Pr(Chi)
Lake Michigan				
NULL	532	4050.7		
Source of recovery	3	669.5	3381	<0.0001
Year	6	875.8	2505	<0.0001
Statistical district	4	674.6	1831	<0.0001
Month	4	137.1	1694	<0.0001
Lake Huron				
NULL	898	6341		
Source of recovery	3	1732	4608	<0.0001
Year	8	764	3843	<0.0001
Statistical District	5	235	3608	<0.0001
Month	5	242	3366	<0.0001

Coefficients	Value (logit scale)	Standard Error	t-value
Lake Michigan			
Charter self-reported	-3.867	0.059	-18.5187
Non-charter creel	-0.431	0.073	-5.8399
Charter headhunter	1.611	0.076	20.9503
Non-charter headhunter	0.473	0.070	6.7338
Lake Huron			
Charter self-reported	-5.770	0.141	-40.8673
Non-charter creel	-0.395	0.059	-6.6570
Charter headhunter	1.884	0.128	14.7673
Non-charter headhunter	1.421	0.056	25.2789

Table 4. Location of release and recovery of coded-wire tag recoveries from Chinook salmon released and recovered in Michigan and Wisconsin waters of Lake Michigan and in Lake Huron for all years in the study from all recovery sources (recreational fishing including pier, shore, volunteer returns, and non-recreational sources). ONT corresponds to Canadian districts OH-1 to OH-5 in Figure 1.

Recovered	**Released in Lake Michigan**							
	Michigan waters					**Wisconsin waters**		
	MM3	**MM4**	**MM6**	**MM7**	**MM8**	**WM3**	**WM4**	**Total**
In Michigan waters								
MM1	9	8	3	4	4	0	0	28
MM2	10	2	0	0	0	23	2	37
MM3	697	33	5	6	2	4	1	748
MM4	173	453	13	8	3	4	4	658
MM5	612	145	65	24	8	52	9	915
MM6	267	131	2417	267	73	164	21	3,340
MM7	154	86	199	469	75	106	19	1,108
MM8	66	23	86	87	124	69	14	469
In Wisconsin waters								
WM1	17	23	13	26	8	-	-	87
WM2	8	6	4	10	6	-	-	34
WM3	33	15	28	25	11	-	-	112
WM5	22	14	13	40	17	-	-	106
WM6	2	3	3	7	2	-	-	17
In Lake Huron								
All areas	77	103	35	30	11	49	4	309
Total	2,147	1045	2,884	1003	344	471	74	7,968

Recovered	**Released in Lake Huron**					
	Michigan waters				**Ontario waters**	
	MH1	MH3	MH4	MH5	MH6	ONT	Total
In Lake Huron Michigan waters							
MH1	3,160	293	34	88	15	64	3,654
MH2	619	404	24	106	9	121	1,283
MH3	423	1,597	54	162	12	63	2,311
MH4	181	244	107	110	16	44	702
MH5	172	202	21	678	16	36	1,125
MH6	165	197	30	149	28	59	628
In Lake Huron Canadian waters							
Ontario	67	48	0	10	0	-	125
In Lake Michigan							
All areas	462	100	15	25	6	2	610

Total	5,250	3,085	285	1,328	102		389	10,438

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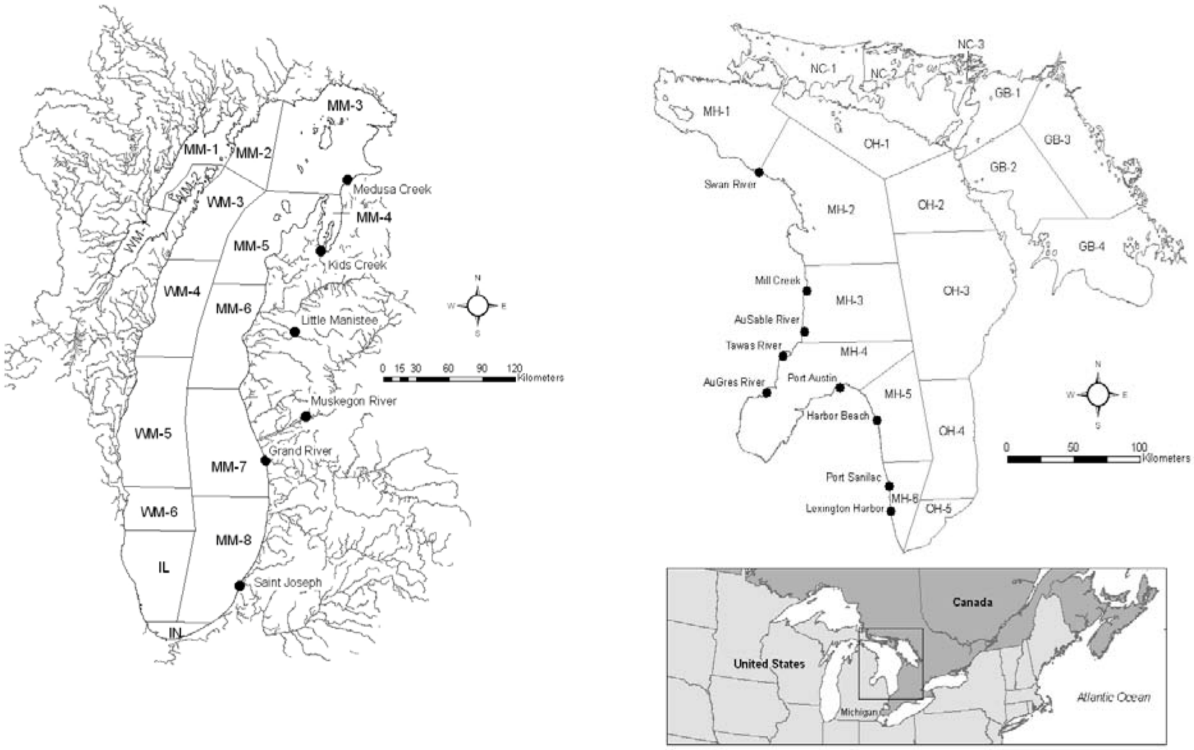

Figure 1. Maps of Lake Michigan and Lake Huron showing statistical districts and Chinook salmon release locations. In Lake Huron, statistical districts MH-1 to MH-6 are located within U.S. waters and other districts are in Canadian waters.

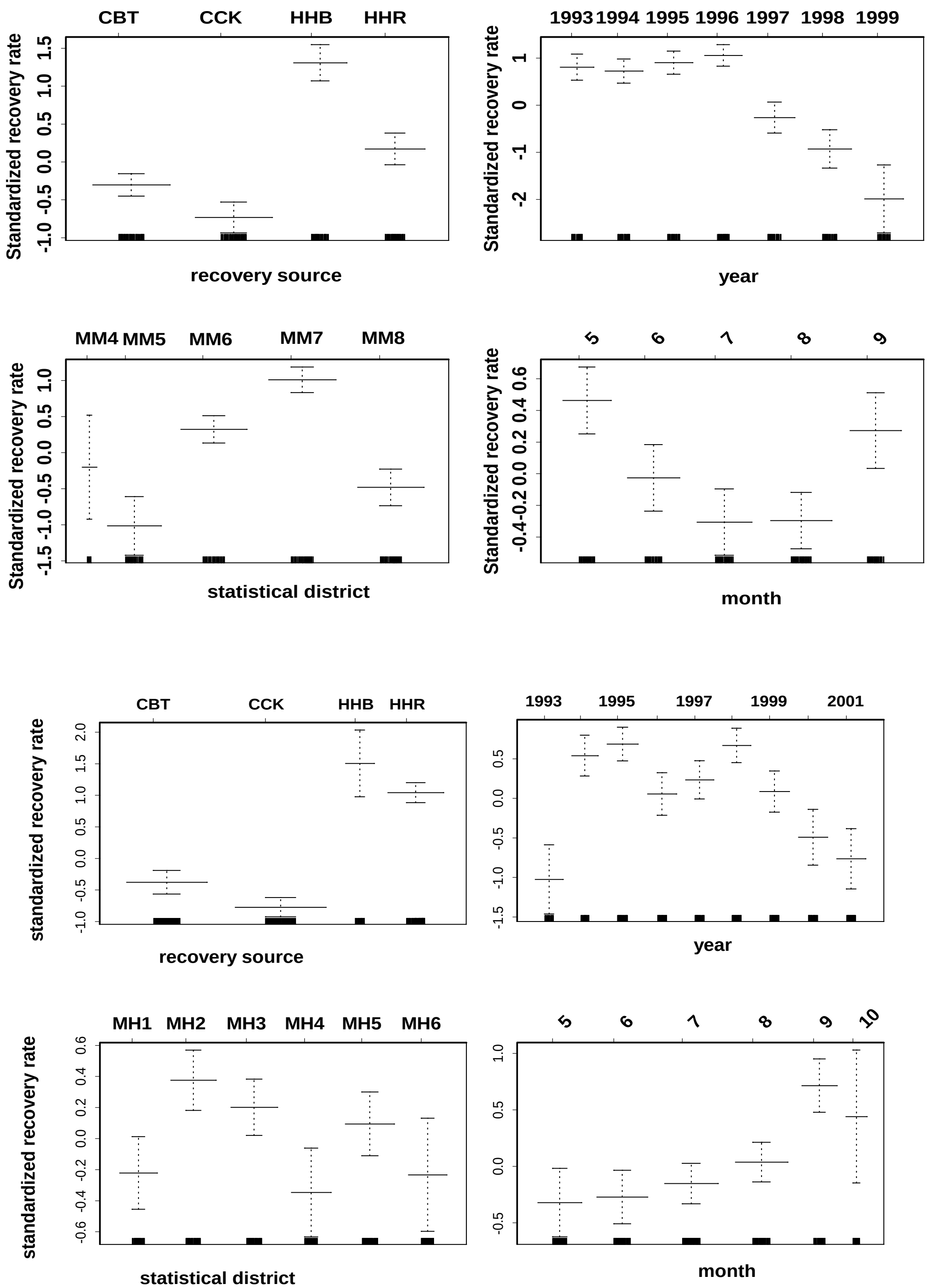

Figure 2. Main effects from generalized linear models of recovery rates of coded-wire-tagged Chinook salmon released in State of Michigan waters of Lake Michigan (MM4 – MM6) and U.S. waters of Lake Huron (MH1-MH6). Recovery sources: CCK=clerks from non-chartered trips, CBT=reported from chartered trips, HHR=headhunters (CWT collection specialists) from non-chartered trips, HHB=headhunters from chartered trips. Brackets represent 95% confidence intervals and y-axes are standardized so zero corresponds to mean recovery rates.

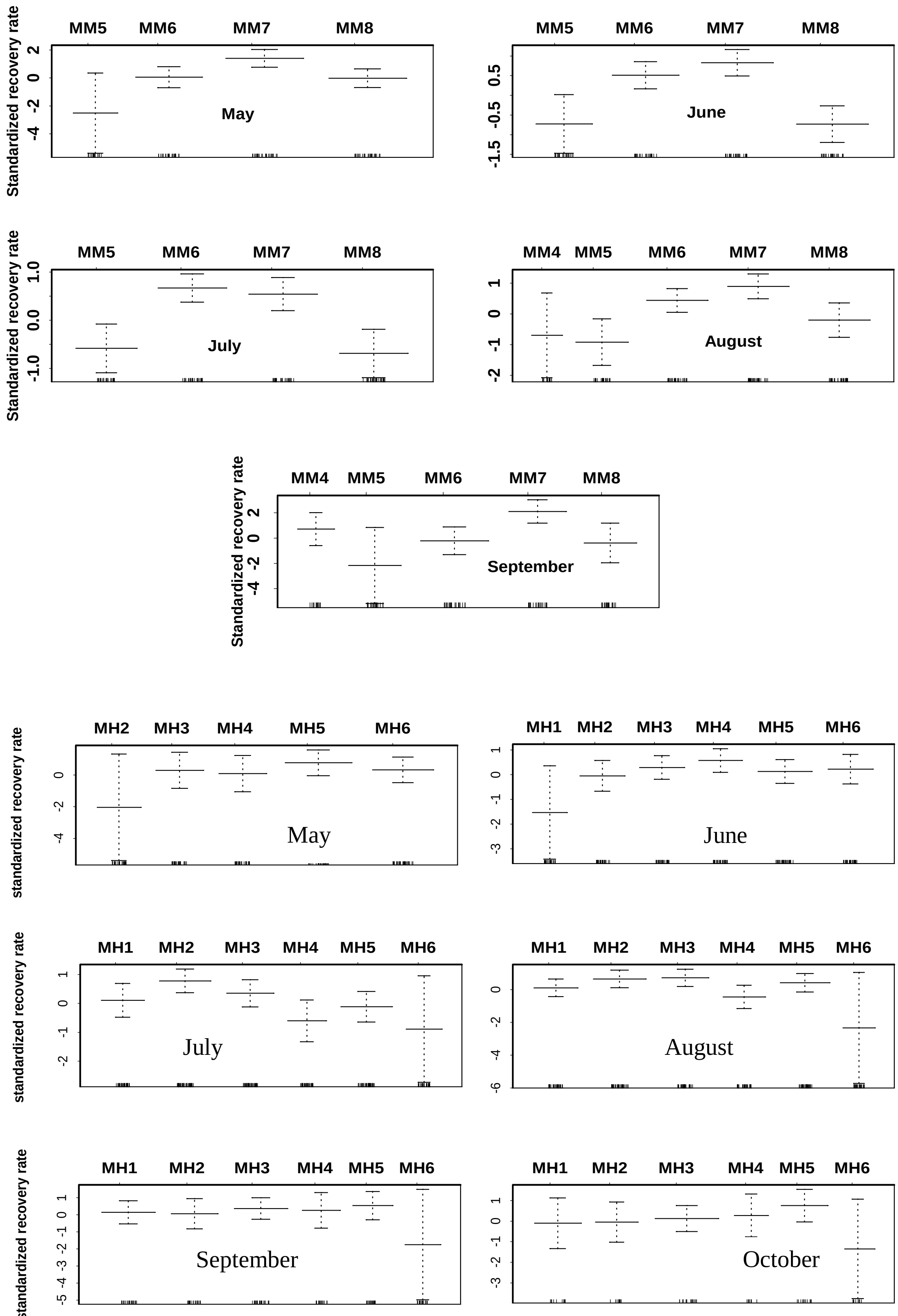

Figure 3. Fitted GLM effects for CWT recoveries of Chinook salmon by months as a function of statistical district. Other descriptions are as in Figure 2.

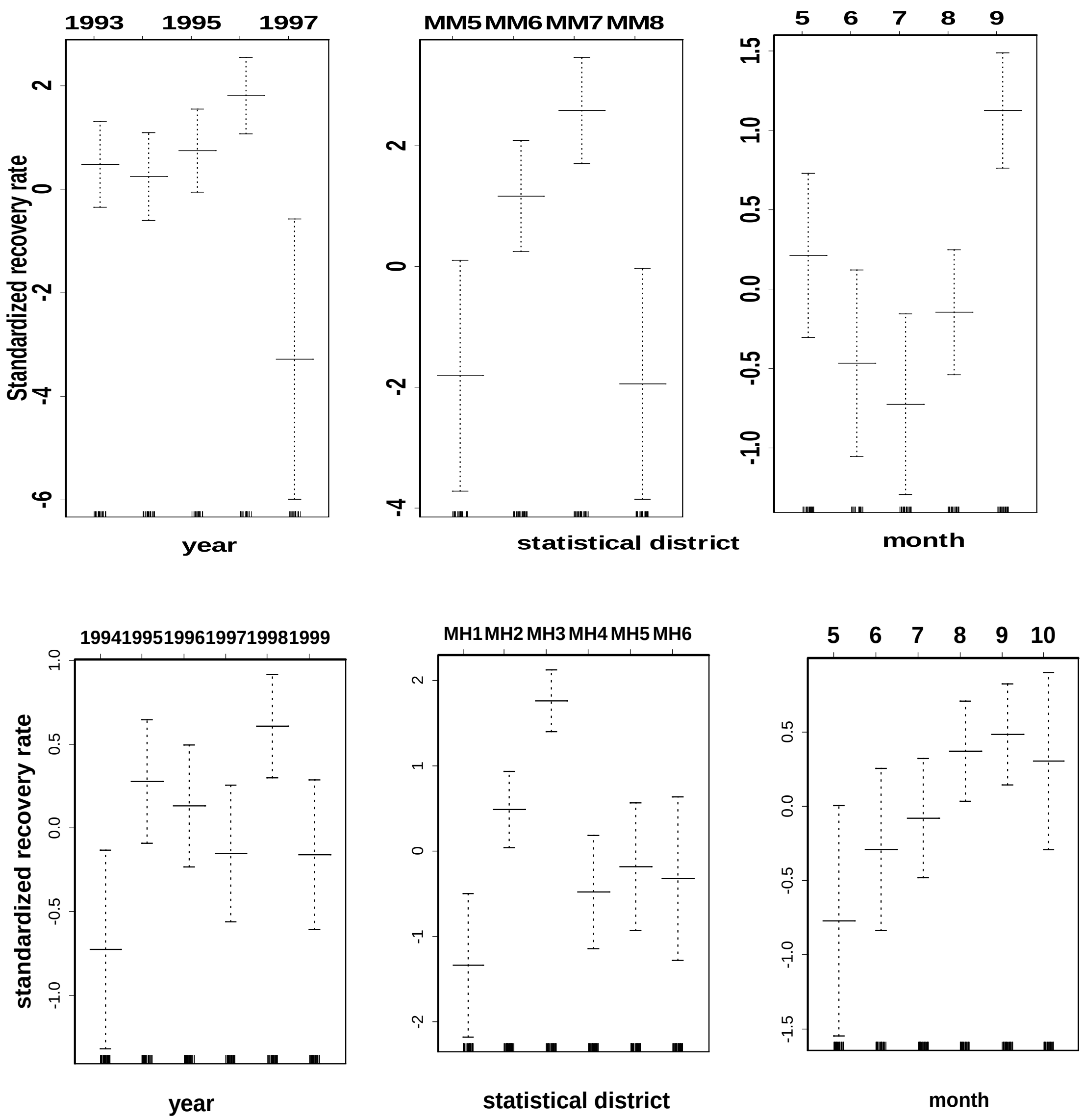

Figure 4. Effects of year, statistical district, and month of recovery from generalized linear models of tagged Chinook salmon recoveries by trip in recreational fisheries within the study period, from fish released in one statistical district among lakes Michigan and Huron. Additional information is similar to that in Figure 2.

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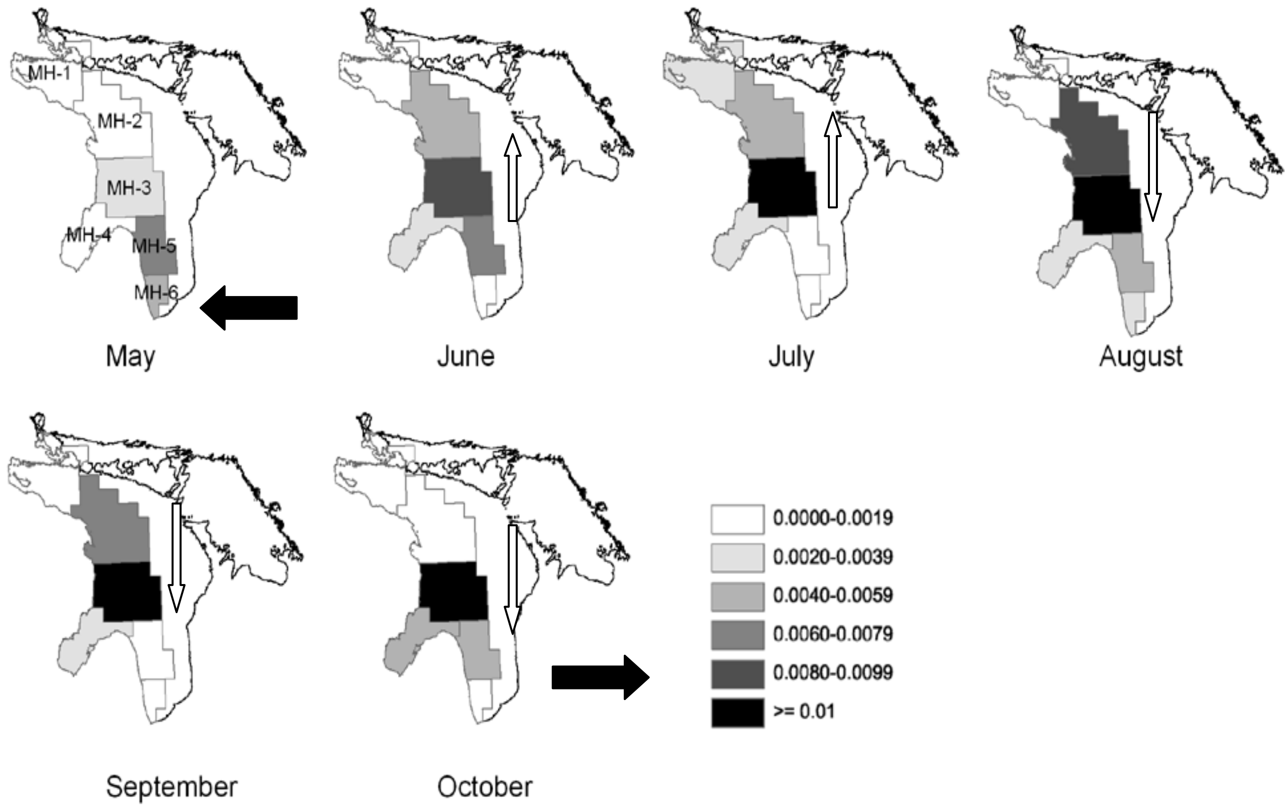

Figure 5. Generalized linear model predictions of the monthly distribution of coded-wire-tagged Chinook salmon based on standardized recoveries by trip of fish released in statistical district MH3 recovered from 1994 to 1999.

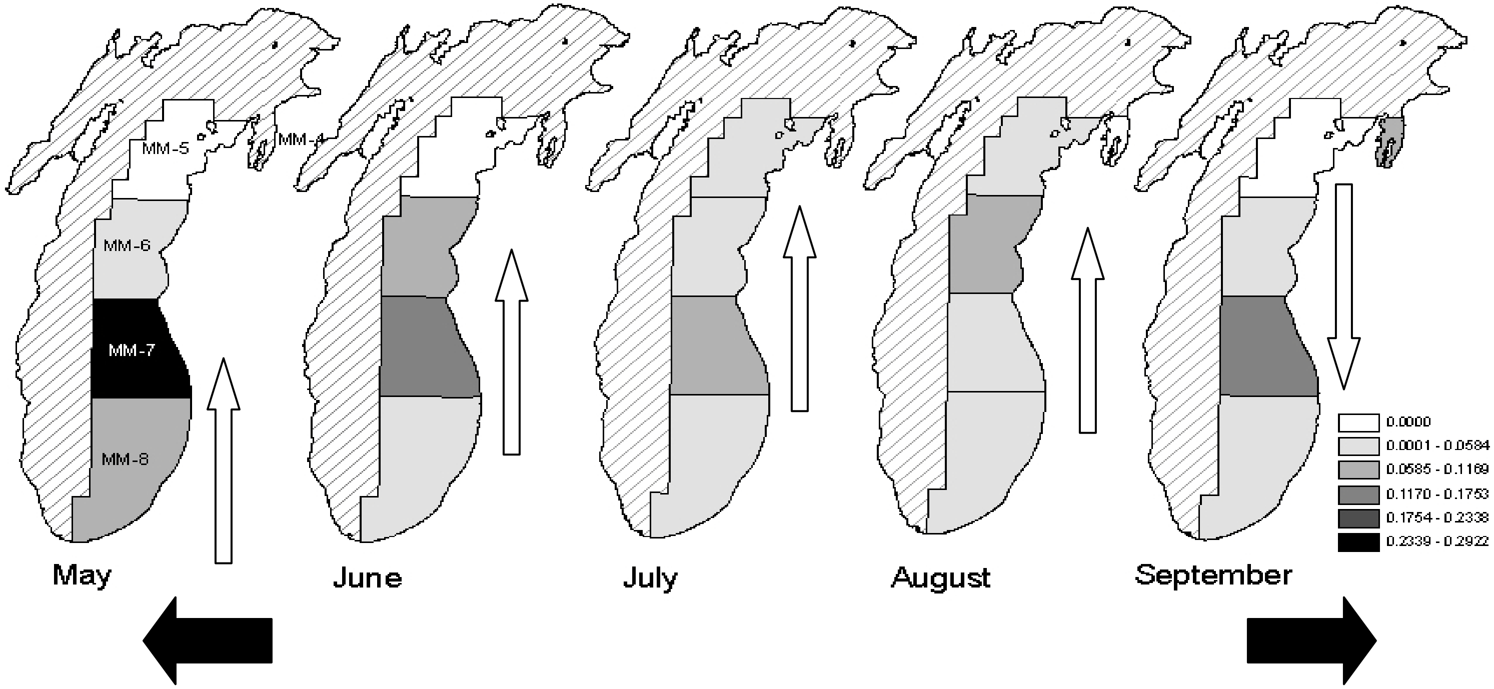

Figure 6. Generalized linear model predictions of the monthly distribution of coded-wire-tagged Chinook salmon based on standardized recoveries by trip. Patterns are the same as for predictions for fish released in statistical district MM7.