SPATIAL DISTRIBUTIONS OF LAKE ERIE WALLEYE

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ABSTRACT

The spatial distributions of Lake Erie walleye stocks are examined from tagging data from 1990-2001. Releases and recoveries from four western basin tagging sites – Monroe, Chicken and Hen Islands, Sandusky Bay, and Sandusky River – and from one eastern basin site, Van Buren Bay, are analyzed. Walleye tagged at the Monroe, Chicken and Hen Islands, and Van Buren Bay are considered individual stocks and walleye tagged at the Sandusky Bay and Sandusky River sites are considered one stock. Spatial distributions are quantified by construction of a spatially-explicit population model that follows groups of releases from the first May after spring tagging through October of the second year after release and estimation of model parameters in a maximum-likelihood framework. Two different estimation frameworks are implemented that handle tag-loss rates and tag-reporting rates uniquely, so the effects of these ‘nuisance parameters’ can be analyzed. The results confirm previous tagging studies that show movement of western basin walleye

BIOGRAPHICAL SKETCH

James Thomas Murphy was born in Los Angeles, California, where he attended high school. James graduated from the University of California, Santa Cruz with a B.A. in Biology. Before attending Cornell, James worked in the environmental consulting industry in Northern California.

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Introduction

The spatial distributions and movement patterns of the walleye stocks of Lake Erie have important implications for the management of the associated recreational and commercial walleye fisheries. As the waters of Lake Erie are regulated by four American states, Michigan, Ohio, Pennsylvania, and New York and the Canadian province of Ontario , movement patterns can determine both the political entity that regulates the harvest of a particular fish and abundance levels for a given spatial-temporal strata. Strong spatial stratification of gear-types and fishing effort targeting walleye exists in Lake Erie; consequently, movement patterns of a stock, defined here as a spawning population or an aggregate of spawning populations, could result in different proportions of a stock being exposed to markedly different amounts and types of fishing effort, potentially determining the probability of harvest for a given proportion of a stock. Differential spatial distributions and movement patterns between stocks could have a similar consequence, with different stocks experiencing different harvest probabilities based on their movement patterns. Knowledge of stock-specific spatial distributions and movement patterns will allow consideration of the effects of management actions and fishery dynamics on specific stocks (e.g., the effect of spatial distribution of fishing effort) and may lead to more effective management actions through area-specific regulations.

The commercial gill net and recreational sport angling fisheries in Lake Erie proper are generally stratified by the U.S. - Canada border, which divides Lake Erie (Figure 1). Commercial gill net operations account for greater than 95 percent of walleye biomass harvested in Canadian waters and sport angling accounts for almost all walleye harvested in U.S. waters (Lake Erie Walleye Task Group 2005). From

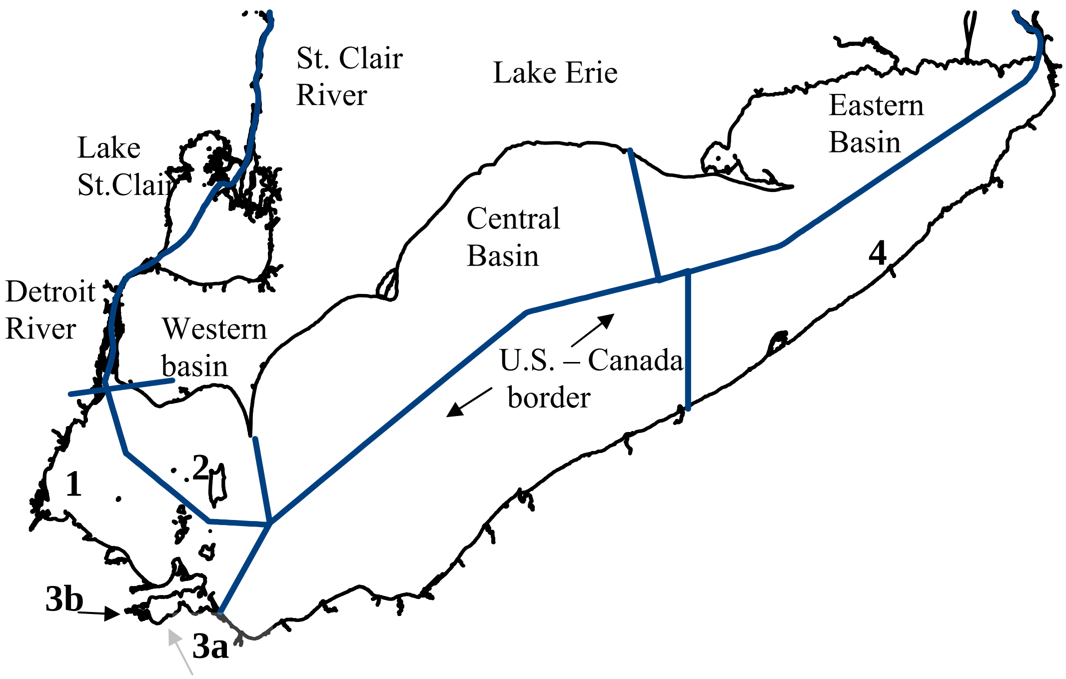


Figure 1. Lake Erie and Lake St. Clair area. Tagging sites: 1) Monroe; 2) Chicken and Hen Islands; 3a) Sandusky Bay; 3b) Sandusky River; 4) Van Buren Bay

2001 to 2004, the gill net fishery in Canadian waters accounted for 47 percent of the walleye harvest in Lake Erie and the recreational fishery in U.S. waters accounted for 43 percent. Due to seasonal movement, Lake Erie walleye stocks are also harvested in the connecting waters of the Lake St. Clair corridor by sport angling in both U.S. and Canadian waters and in southern Lake Huron by commercial gill net fisheries (Canadian waters only) and recreational fisheries (U.S. and Canadian waters).

Lake Erie is comprised of a western, central, and eastern basin with mean depths of 7.4 m, 18.5 m and 24.4 m respectively (Ryan et al. 2003). These basins have differing limnological characteristics and thermal regimes, resulting in ecological differences between the basins, exemplified by a shift from mesotrophic, coolwater habitat in the western basin to an oligotrophic, coldwater habitat in the eastern basin. The differences in thermal regimes and the dynamics of prey abundances among the basins are hypothesized to be important drivers of walleye movement in Lake Erie (Henderson and Wong 1994; Kershner et al. 1999). The principal inflow into Lake Erie is from the Detroit River. The Detroit River-Lake St. Clair (3.0 m mean depth) - St. Clair River corridor ('LSC', hereafter), lacking any structural barrier to fish movement, provides a physical and ecological connection between Lake Erie and upstream water bodies. Lake Erie flows into Lake Ontario to the east but the Niagara Falls complex precludes fish movement between the lakes.

The principal spawning grounds of walleye in Lake Erie are shallow, reef complexes in the western basin and in gravel beds of the Maumee and Sandusky Rivers, large tributaries to the western basin (Reiger et al. 1969). The walleye spawned in the western basin support commercial and sport fisheries in the western and central basins of Lake Erie as well as in the Lake St. Clair - southern Lake Huron region. These western basin walleye also contribute to the commercial and sport harvest in the eastern basin. Limited spawning grounds occur in the central basin and its tributaries. Spawning grounds in the eastern basin occur in shallow reef complexes and some tributaries along the Pennsylvania - New York shoreline (Reiger et al. 1969). Stock assessments estimate a 2004 population (age 2+) of forty-two million western basin walleye and a 2004 population (age 2+) of six hundred thousand for eastern basin walleye (Lake Erie Walleye Task Group 2005).

Broad-scale walleye movement patterns are known from previous tagging studies and can differ substantially between stocks (Ferguson and Derksen 1971; Einhouse and Haas 1994; Todd and Haas 1993; Wolfert et al. 1978). Eastern basin stocks remain almost entirely in the eastern basin of the lake. Post-spawning, a proportion of western basin stocks remain in the western basin and the remainder disperse throughout the lake and into the LSC system. Natal homing behavior is considered typical and individuals are presumed to generally return to their natal spawning grounds by the following spring (Reiger et al. 1969), though straying has been observed (Todd and Haas 1993). Mitochondrial DNA analyses show genetic divergence between spawning populations within Lake Erie with natal homing hypothesized to be the responsible mechanism (Stepien and Faber 1998). Western and central basin commercial gill net CPUE data from the late summer/early fall potentially indicate a westward return movement for western basin walleye that moved to the central and eastern basins after spring spawning (Henderson and Wong 1994).

In addition to stock affiliation, size is believed an important covariate of walleye movement. Creel surveys of walleye harvested in New York waters in the early 1990s indicated that large, older females, believed to be western basin walleyes that had moved into the eastern basin during the spring and summer months, comprised over

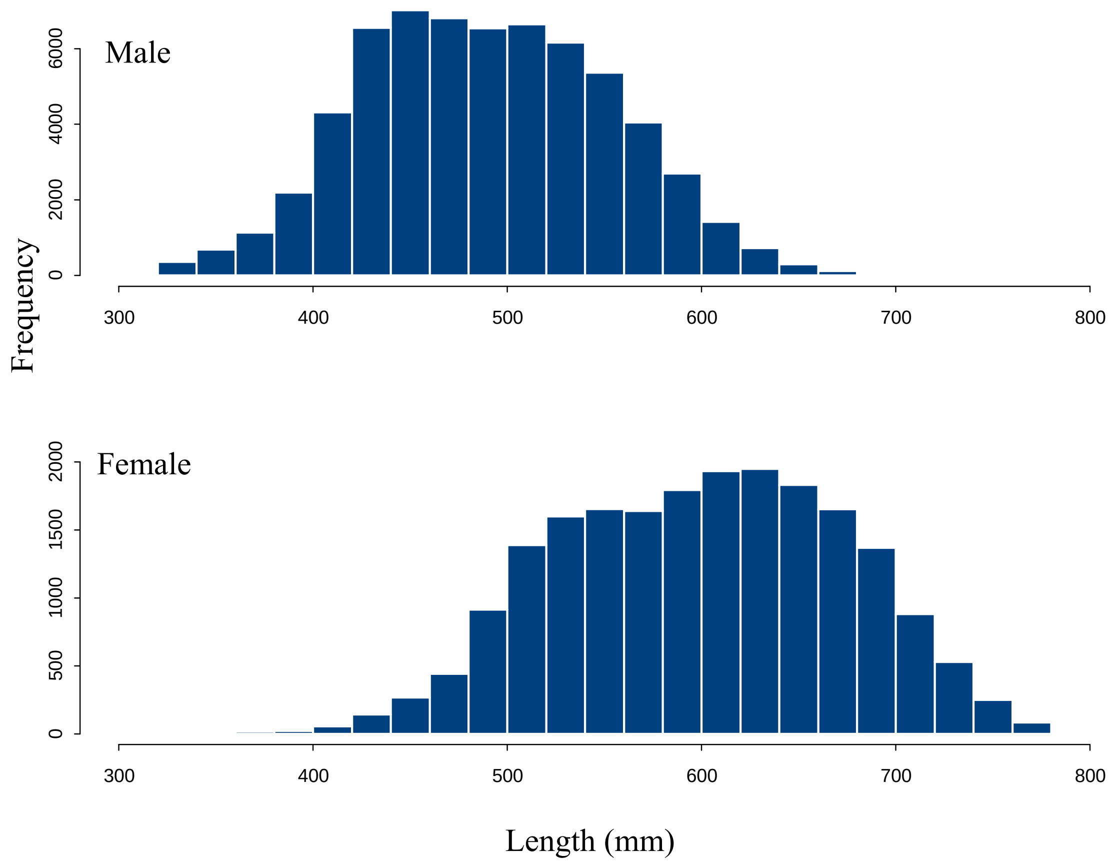


Figure 2. Length distributions (mm) of tagged walleye by sex in western basin of Lake Erie, 1990-2001.

80 percent of the harvest (Einhouse and Haas 1994). Due to the sexual dimorphic growth of walleye - with females growing larger than males - adult walleye length frequencies (used hereafter as a proxy for overall size) are partially stratified by sex, with proportionally more males in smaller length classes and proportionally more females in larger length classes (Figure 2).

The dynamics of walleye movement have been an increasing focus of interest for walleye managers. Various stocks are believed to make differential contributions to harvests in different areas of Lake Erie. Results of genetic analyses from 1995 and 1996 harvests from recreational sport derbies in the eastern basin and the commercial fishery in the eastern basin showed western basin stocks comprising at least 63 percent of the harvest from the sport derbies and 81 percent of the commercial fishery harvest (Gatt et al. 2002). Genetic analyses also showed Lake Erie western basin stocks comprising between 67 percent to 72 percent of the limited commercial fishery harvest in southern Lake Huron in 1994 and 1995 (McParland and Ferguson 1999). Tagging studies have shown the limited movement of eastern basin stocks to the central and western basins and thus a negligible contribution of eastern basin stocks to harvest outside the eastern basin can be inferred (Einhouse and Haas 1994). While a number of tagging studies of Lake Erie walleye exist, a formal statistical quantification of the spatial and temporal distribution of various walleye stocks has not been attempted with tagging data before this study.

Substantial tagging data (over 85,000 releases and 8,000 recoveries from 1990-2001), consisting of releases from agency personnel and voluntary recoveries from recreational and commercial fishers, exist for Lake Erie walleye; however, the tag releases are by necessity spatially and temporally constrained. Practically, tagging can occur only at or adjacent to a known spawning ground around the spring spawning time, when dense aggregations of adult walleye occur. Tagging operations outside of the spawning period are logistically more difficult and would require a substantial labor and time investment from the involved resource agencies due to the lower densities of walleye occurring away from the spawning grounds and potentially induce greater tagging-induced mortality associated with higher temperatures (for tagging operations during the summer months). In addition, the stock affiliation of releases tagged away from spawning grounds or outside the spawning period would be unknown due to the mixing of stocks outside the spawning period.

This constrained nature of the tag releases in turn impacts the types of estimates of movement that can be obtained from the available tagging data. Given a study area of n spatial strata, estimation of all possible n x n movements among all spatial strata for a given time period from tagging data requires that releases occur in all spatial strata during the time period (or just prior) and recovery effort occur in all spatial strata during the same time period (Schwarz et al. 1993). Lake Erie can be spatially stratified in various configurations, but with any configuration releases of a given stock cannot occur in all spatial strata. With any spatial configuration, the Lake Erie tagging data for a given stock consists of one release stratum (location of the spawning ground) and multiple recovery strata, preventing estimation of movements between all possible n x n spatial strata. Given these constraints of the tagging data, the specific movements for a given stock that can be quantified are movements between the release strata and the recovery strata, which does not account for the complete movement patterns of tagged fish as it does not account for potential movement through other spatial strata before being harvested in the recovery strata.

An alternative to estimating specific movement probabilities between release and recovery strata is to estimate the proportion of the tagged population that is in a given temporal-spatial strata given the observed recoveries. This approach allows for the estimation of proportions in spatial strata through time from which movement can then be inferred, though the actual movement patterns between spatial strata are not quantified. We implement this approach to estimate the proportions of tagged walleye populations from various Lake Erie stocks in seven spatial strata (the American and Canadian portions of the three Lake Erie basins and the Lake St. Clair – southern Lake Huron corridor, see Figure 1) at seasonal and annual time scales. Knowledge of movement and distribution patterns at finer spatial and temporal scales may elucidate ecological and behavioral mechanisms driving walleye movement; however, for developing management strategies at realistic spatial scales, such as the basin scale (which is the spatial scale used in this study, see Figure 1), quantifying stock-specific distribution patterns are an important first step toward integrating movement dynamics into a management framework for Lake Erie walleye.

Tag reporting rates and tag-loss rates (from tag shedding or tagging mortality) are known to bias parameter estimates from tagging data (Pollock et al. 2001). For the analysis of movements and spatial distributions of Lake Erie walleye, reporting rates by gear type are especially important due to the spatial stratification by gear type. Double tagging and reward tagging experiments have been periodically conducted with Lake Erie walleye to determine the rates of tag shedding and tag reporting. The results of these studies vary, with the agency conducting the tagging, the size of the fish (and the consequent size of the tag used), and the recovery gear all apparently influencing the results of the experiments (Einhouse and Haas 1994; Iserman and Knight 2005). To explore potential biases inherent in the walleye tagging data - and inherent in almost all fish tagging studies, especially those reliant on voluntary reporting of recoveries - two statistical modeling frameworks are implemented that each handle in unique manners the ‘nuisance’ parameters associated with tagging data.

The first framework follows Hilborn (1990) and requires explicit input values for tag loss rates and tag reporting rates. The second framework follows McGarvey and Feenstra (2002), and estimates movement probabilities independent of tag reporting and tag loss rates.

We develop simple walleye population models with movement that strive for biological realism given the constraints that the nature of the tagging data place on parameter estimation. This study differs from previous, more qualitative analyses by estimating actual spatial and temporal distributions of a stock. The objectives of our study are to analyze tagging data from 1990-2001 to 1) to estimate stock-specific distribution patterns of adult walleye 2) to analyze length as a covariate of this movement when appropriate and 3) to analyze the effect of 'nuisance' parameters associated with tagging data by implementing two different estimation frameworks.

Data organization

Tagging data

Between 1990 and 2001, the coordinated tagging programs among U.S. state resource agencies (Michigan, Ohio, Pennsylvania, and New York) and the Canadian province of Ontario have tagged approximately 85,000 adult walleye at various locations throughout Lake Erie, with over 80 percent of these releases in the western basin. Tagging operations occur at or adjacent to spawning sites during or shortly after spawning.

Tagging operations generally coincided with walleye spawning (or shortly thereafter), and occurred March to May in the western basin and during April and May in the eastern basin. Walleye were collected using either electro-shocking methods or trap and gill nets and seines. Collected walleye in good condition received an individually marked metal monel jaw-tag applied to the upper or lower mandible listing contact information for the involved agency. Biological data, including length and sex were recorded for each walleye. Sport and commercial fishers voluntarily reported recoveries. Latitude and longitude coordinates were assigned to each recovery location. Due to walleye spawning behavior, many more males are tagged than females. Males stay at spawning sites for up to several weeks while females are believed to spend at most several days.

We analyze 1990 – 2001 tagging data (non-reward tags only) from 5 tagging sites, four western basin sites representing three stocks and from one eastern basin site (representing one stock) (Figure 1 and Table 1).

Western basin stocks

- The Chicken and Hen Islands (CHI, hereafter; 11,497 releases analzyed) tagging site is a reef complex around the Chicken and Hen Islands in the Canadian waters of the central western basin and is the primary walleye tagging site for the Ontario Ministry of Natural Resources in the western basin.
- The Monroe tagging site (14,847 releases analyzed), is located off Monroe, Michigan (U.S.), and is the primary western basin walleye tagging site for the Michigan Department of Natural Resources. The Monroe tagging site is not a spawning ground but fish collected there are believed to be from the Maumee River (Ohio, U.S.) spawning population, located 24 km south.
- The Sandusky River tagging sites are at shallow gravel beds near Fremont, Ohio (U.S.); and the Sandusky Bay site is at the mouth of the Sandusky River (Ohio, U.S.) (15,440 combined releases analyzed). Preliminary analyses of recoveries from both sites showed similar spatial patterns and tagged fish from Sandusky Bay and Sandusky River sites are treated as one stock.

Table 1. Number of tag releases analyzed by year at five sites, 1990-2001.

Tagging site	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	Total releases*	Total recoveries**	Percent recovered
Van Buren Bay	587	1008	1086	825	786	924	711	993	452	1082	527	735	9716	419	4.3
Chicken and Hen Island	1872	1956	1039	1247	253	685	0	2587	295	0	884	679	11497	371	3.2
Sandusky Bay and River	1337	1482	2106	1881	1183	1927	1896	1211	0	0	1386	1031	15440	617	4.0
Monroe	1408	2359	1704	1330	1456	121	1746	1446	990	766	1521	0	14847	886	6.0

*Analyzed in this study
** Of releases analyzed in this study

Eastern Basin stock

- The Van Buren Bay site (9,716 releases analyzed), in the New York waters of the eastern basin is a shallow reef complex and the main tagging site for the New York Department of Environmental Conservation.

The western basin sites were chosen based on their geographic separation from each other and the large number of releases (Table 1 and Figure 1**)**. The Van Buren Bay site was the only eastern basin site chosen due to the large number of releases there, many times more than any other tagging site in the eastern basin. Tagging data from other western basin stocks/tagging sites exist but were not included as the number of releases occurring at the other sites were generally much less than the chosen western basin sites and maximizing sample size was the most important criterion. The western basin stocks chosen are sufficient to indicate trends and potential variability in spatial distribution patterns for western basin stocks.

Tag groups

Tag groups - subsets of tag releases sorted by stock affiliation, length, and year of release – are the population units followed. Only data from walleye 40 cm or greater were used for all release areas to ensure that tagged walleye met minimum length requirements of sport and commercial harvest regulations and because analysis by the authors of recovery data indicated size selective harvest occurring (or possibly size-selective reporting of recoveries) for fish less than 40 cm but not for larger sizes. To examine the effects of length at release, the Sandusky and Monroe stocks were organized into two length classes (< 60cm and ≥60cm). Relatively few larger walleyes (≥60cm) were tagged at Chicken and Hen Islands and this stock was not organized into separate length classes. Exploratory data analysis did not show a length effect on the spatial distribution of the Van Buren Bay stock and this stock was also not organized into separate length classes. Releases after April 30th for western basin stocks were not examined and releases. Recoveries before May 1st of the first year of release for western basin stocks or June 1st for the Van Buren Bay stock were not analyzed but were used to decrease the initial tag group size.

Spatial and Temporal Resolution

Choosing an appropriate spatial-temporal resolution is necessary to generate robust and realistic estimates of spatial distributions. The spatial-temporal resolution should incorporate biological realism but it will also be determined by the available data. Resource agencies estimate fishing effort data by month and consequently a monthly time-step is the minimum time step that can be used and was the time-step implemented; recoveries are thus organized by month of recovery. (Detailed sport angling effort data is not available for LSC and is set to be 15 percent of U.S. western basin monthly effort; this assumption is discussed further in Implications of Modeling Assumptions below.) As mentioned previously, the seven spatial strata outlined in Figure 1 are used to stratify recoveries; given the different limnological and biological characteristics of the Lake Erie basins (considering the Lake. St. Clair corridor a 'basin' for simplicity) that influence walleye movement (temperature, depth, prey abundance, etc.) they provide a logical basis to stratify recoveries. The small number of Lake Huron sport recoveries were grouped into the Lake St. Clair spatial strata while Lake Huron commercial recoveries were not analyzed.

Model Description: Movement , Survivorship, and Recovery

The basis of the statistical modeling approach used in the study is the construction of a population model of tag groups that includes survivorship of fishing and natural mortalities and movement. All tag groups are followed for two 'fishing seasons' after release, from May through October of the second year, though recoveries are only predicted for May through October. Output from the population model (predicted reported recoveries) is then compared with the actual reported recoveries as described below in Alternative Estimation Approaches. (Growth during this period is ignored.)

Model notation

The initial number of tagged walleye in tag group *i* (representing stock affiliation, length class, and year of release) is

$$N_{i,t=0} = T_i(1 - \alpha)$$

where α is the probability of tag loss through initial tag shedding or tagging mortality and T_i is the initial number of releases for tag group *i*. Based on results from Lake Erie walleye double tagging studies by Ohio Department of Natural Resources and New York Department of Environmental Conservation, α is set at 0.15 (Einhouse and Haas, 1995; Iserman and Knight, 2005).

The sequence of events in each time step in the population model is movement, survival relative to fishing mortality, and survival relative to natural mortality. The placement of natural mortality at the end of the time-step is arbitrary but the short monthly duration of each time-step minimizes the significance of its placement. Then, the population dynamics model in matrix notation is

$$N_{it} = S_M S_H P_{it} N_{it-1\bullet}$$

where $N_{it} = (N_{it1},...,N_{ita},...N_{itn_a})^t$ is a vector representing the number of walleye of tag group *i* in area *a* at time *t* and $N_{it-1\bullet} = \sum_a N_{it-1a}$ is a scalar quantity representing the sum of all survivors of tag group *i* in all areas from the previous time step. The vector of proportions of a tag group occurring in each area at time *t* is given by $P_{it} = (p_{it1,},\ldots, p_{ita,},\ldots p_{itn_a})^t$ with p_{ita} the proportion of tag group *i* occurring in area *a* at time *t*. Survivorship from harvest mortality is given by matrix

$$S_H = I - H_T$$

where I is the identity matrix and H_T is diagonal matrix composed of elements $\sum_g h_{atg}$, the total harvest probability for each area and time ($h_{atg} = q_g E_{atg}$, where q_g is the catchability of gear *g* and E_{atg} is the fishing effort by area, time, and gear). The survivorship of natural mortality is given by the diagonal matrix

$$S_M = [e^{-M/12}]$$

where *M* represents the annual instantaneous natural mortality rate (assumed to be 0.2). The expected number of recoveries per tag group, area, time, and gear type for a given tag group is given by the diagonal matrix

$$\hat{R}_{iatg} = \beta_g \left[H_G N_t \right]$$

where H_G is the diagonal matrix composed of elements h_{atg}, the harvest probability per area, time, and gear type *g*. β_g represents the reporting rate for gear *g*. Based on an analysis of high reward tag release and recovery data from 1990 and 2000 by the authors, we set the commercial and sport reporting rates to be 0.15 and 0.33, respectively, representing average values from the 1990 and 2000 high reward tagging results in the western basin.

The sum of the total estimated proportions are constrained to sum to one by the following formulation, as described in Heifetz and Fujioka (1991),

$$p_{ita} = \frac{\phi_{ita}}{\phi_{a\bullet}}\left(1 - \exp\{-\phi_{a\bullet}\}\right) \qquad \text{for } a \neq k$$

$$p_{ita} = \exp\{-\phi_{a\bullet}\} \qquad \text{for } a = k$$

$$\phi_{a\bullet} = \sum_{a \neq k}^{\text{all areas}} \phi_{ita}$$

where ϕ_{ita} is the actual parameter estimated, thus requiring six estimated spatial distribibution parameters for the seven spatial strata.

Model Variants

Three variants of the population model are implemented. All three variants estimate proportions for each of the seven spatial strata but differ by whether proportions are estimated seasonally (Model I) or annually (Model II and Model III) and whether proportions for different length classes are estimated (Model III). Implementation of these model variants for each stock allows analysis of both temporal and spatial distributions within a year and of the importance of length as a covariate of movement and spatial distribution. (See Table 2 for summary of models.)

Model I has three seasonal spatial distributions in a year for each stock: one for May-June (June only for the Van Buren Bay stock due to later release dates), July - August, and September – October. Model II has one annual spatial distribution for each stock in a year (i.e., no seasonal distributions) and this distribution can be considered the average spatial distribution over the spring – fall period. Model III, is similar to model II, but has one annual spatial distribution for two length classes (< 60cm and ≥60cm). These choices of length classes ensured that sufficient recoveries

Table 2. Summary of models

Model	Estimation framework	Length classes	Seasonal or annual distribution estimated	Catchability estimated? (sport and commercial)	Estimated parameters
Model I	Hilborn	1	Seasonal	yes	20
Model I	McGarvey	1	Seasonal	no	18
Model II	Hilborn	1	Annual	yes	8
Model II	McGarvey	1	Annual	no	6
Model III	Hilborn	2	Annual	yes	14
Model III	McGarvey	2	Annual	no	12

occurred in various spatial strata to allow for parameter estimation. Model III was not implemented for the CHI stock as very few fish >60cm were tagged for this stock, nor was Model III implemented for the Van Buren Bay stock as exploratory data analysis of the tagging data showed little influence of length on spatial distribution patterns for this stock.

We use Akaike's Information Criterion (AIC), which evaluates a model fit and parsimony relative to its likelihood score and number of estimated parameters (Burnham and Anderson, 1998), as a diagnostic tool to examine general model fit relative to the number of parameters. AIC is defined as

$$\mathrm{AIC} = -2\ln L(y \mid \hat{\theta}_k) + 2k$$

with $L(y \mid \hat{\theta}_k)$ representing the likelihood function (defined below) and k the number of estimated parameters.

Alternative Estimation Approaches

Statistical Models

Two statistical modeling approaches are implemented to estimate movement probabilities, Hilborn's simulation framework (Hilborn 1990) and McGarvey and Feenstra's 'conditioning on recapture' framework (McGarvey and Feenstra 2002; referred to as the 'McGarvey framework' hereafter). For our purposes, the important differences between the two modeling approaches are the requirement that tag-loss, tag-reporting rates, and natural mortality rates must be assumed known to estimate spatial distributions with the Hilborn framework but these rates are not actually used or required in the McGarvey framework. Hilborn's simulation framework assumes that recoveries follow a Poisson distribution, which nearly approximates a multinomial distribution when recoveries are infrequent or rare events. Each stock is modeled separately and a set of spatial distribution proportions and catchability coefficients are estimated for each stock. Model parameters are estimated by minimizing the negative log-likelihood of the predicted recoveries ($\hat{R}$) with observed recoveries (R) by tag group, time, area, and gear. The Poisson negative log-likelihood is

$$-\ln L(R_{itag} \mid \hat{R}_{itag}) = \sum_{itag} \hat{R}_{itag} - R_{itag} \ln(\hat{R}_{itag})$$

with the predicted number of recoveries a function of input parameters (fishing effort, tag loss rates, tag reporting rates, and natural mortality) and estimated parameters (population proportions per spatial strata and catchability by gear).

The second approach is based on McGarvey and Feenstra (2002). The same structure for the population and recovery models are used as under the Hilborn framework; however, the McGarvey framework does not predict actual number of reported recoveries. Rather, the relative proportions of recoveries occurring in each area per time step per tag group is predicted and these predicted proportions are fit to the data in the likelihood function. By assuming that tag shedding rates, tagging mortality rates, reporting rates by gear type, and natural mortality rates are uniform over all areas per time step, these nuisance parameters cancel from the predicted number of relative proportions of recoveries per time step, as well as the initial number of tag releases of the specified tag group. Importantly, these rates may vary between time steps but still cancel as they are assumed spatially uniform per time-step.

Denoting $f_1(a \mid igt)$ as the proportion of recoveries occurring in area a for tag group i, by gear g, at time t, the first time period of recoveries after release, then

$$f_1(a \mid itg) = \frac{\hat{R}_{itag}}{\sum_{a}^{\text{all areas}} \hat{R}_{itag}} = \frac{T_i (1-\alpha) p_{ita} h_{tag} \beta_g}{\sum_{a}^{\text{all areas}} T_i (1-\alpha) p_{ita} h_{tag} \beta_g}$$

where $\hat{R}_{itag}$ is the predicted number of recoveries for tag group *i* in area *a*, with gear type *g*, time *t* and $\sum_{a} \hat{R}_{itag}$ is the total number of recoveries of tag group by gear type *g*, over all areas, at time *t*. Then $f_1(a \mid itg)$ simplifies to

$$f_1(a \mid itg) = \frac{p_{ita} h_{agt}}{\sum_{a}^{\text{all areas}} p_{ita} h_{agt}}$$

as T_i, α, and β_g are assumed constant across all areas during each time-step and cancel out, and where h_{agt} is assumed known and p_{ita} are the estimated distribution proportions. This formulation is easily extended to recoveries occurring in subsequent time periods. Harvest rates by spatial-temporal strata are required data inputs and are calculated with effort data and catchability coefficients estimated by a Lake Erie walleye stock assessment model (-12.5 and –11.4 for commercial and sport catchabilities respectively, log-scale, with commercial effort in kilometers of gill net and sport effort in thousands of angler hours).

As outlined in McGarvey and Feenstra (2002) the likelihood of the predicted proportions of recoveries is based on the multinomial distribution and is the product of the probabilities for each observed outcome

$$L = \prod_{i=1}^{n_t} \prod_{r=1}^{n_r} f_i[r]$$

where n_t is the number of tag groups modeled and n_r is the number of reported recoveries for each tag group. The negative log likelihood,

$$-\ln L = -\sum_{i=1}^{n_i} \sum_{r=1}^{n_r} \log\left(f_i[r] \right)$$

is minimized to estimate the movement probabilities.

By using the two different estimation approaches, the influence of tagging-specific 'nuisance' parameters, tag shedding and tag reporting, can be potentially examined. Tag-shedding rates can vary due to differences between personnel applying the tags and due to changes or differences in methodologies used, such as different size tags for different size fish (Pollock et al, 2001). Also, tag reporting rates can be variable due to changes in sentiment of anglers or gill netters regarding reporting recovered tags and due to the influence of reward tag programs which can cause an increase in reporting of non-reward tags (Pollock et al, 2001). Our implementation of the Hilborn framework assumes that tag-shedding and reporting rates are known and remain constant throughout the study period (i.e., an average of the values over the study period) as insufficient data exists for multiple estimates of these parameters. These nuisance parameters cancel in the McGarvey framework and their influence on parameter estimation is presumed eliminated. If both frameworks produce similar movement estimates then we can assume that input values for the Hilborn framework were adequate or the estimates were not overly sensitive to the assumed values of the nuisance parameters.

Model Implementation

AD Model Builder non-linear optimization software (Otter Research Ltd., B.C., Canada) was used to construct and implement the above models and obtain parameter estimates. Estimates of the standard error for each parameter were determined using variance-covariance estimates derived from the inverse of the Fisher information matrix as calculated from the Hessian, a standard AD Model Builder output under a log-likelihood formulation.

Results

The estimated population distributions (Table 3 and Figure 3) show that western basin stocks move throughout the lake and appear to have moderate changes in seasonal distributions. The Sandusky stock moves almost entirely into the central and eastern basins; the Monroe stock moves mostly into LSC, the western basin, and the central Basin; the CHI stock is somewhat intermediate between the Sandusky and the Monroe stock with more movement into the western basin than the Sandusky stock and more movement to the Eastern Basin than the Monroe stock. The Van Buren Bay stock remains almost entirely in the Eastern Basin with some northward movement into Canadian waters. The two estimation frameworks are in general agreement.

The results for Model I (the seasonal distribution model) do not show major shifts in seasonal distributions between the May-June and July-August periods. The estimated proportions for the September-October period, however, show some surprising results, such as increased distributions in the Eastern Basin for the Monroe and CHI stocks, when it is expected that western basin stocks move westward during this time based on commercial CPUE data (Henderson and Wong 1994). The small number of recoveries for these stocks during this time period (32 for the CHI stock for 11 cohorts followed over two seasons and 63 recoveries for the Monroe stock for ten cohorts followed over two seasons) result in large confidence intervals for the estimated proportions and may not be sufficient for accurate estimates. The estimated proportions for the Van Buren Bay stock indicate movement from the U.S. Eastern Basin to the Canadian Eastern basin through the months of the study period.

Model II estimates a single set of estimated distribution proportions for each stock for the entire May – October period. For each stock, this set of estimated distributions

Table 3. Estimated spatial distributions of walleye stocks (with coefficient of variation).

				Spatial Strata						
Stock	**Model**	**Category**	**Framework**	**LSC**	**CA WB**	**US WB**	**CA CB**	**US CB**	**CA EB**	**US EB**
Monroe	Model I	May-June	McGarvey	0.288 (0.128)	0.153 (0.191)	0.134 (0.121)	0.138 (0.313)	0.167 (0.21)	0.0746 (0.66)	0.0465 (0.561)
		May-June	Hilborn	0.224 (0.119)	0.108 (0.171)	0.101 (0.094)	0.174 (0.245)	0.156 (0.194)	0.105 (0.462)	0.133 (0.27)
		July-August	McGarvey	0.322 (0.125)	0.0886 (0.302)	0.1 (0.126)	0.286 (0.18)	0.102 (0.199)	0.0593 (0.341)	0.0414 (0.285)
		July-August	Hilborn	0.34 (0.107)	0.0808 (0.3)	0.12 (0.107)	0.296 (0.144)	0.092 (0.207)	0.0509 (0.365)	0.0211 (0.409)
		Sept.-Oct.	McGarvey	0.499 (0.181)	0.000922 (>2)	0.0608 (0.41)	0.00697 (>2)	0.264 (0.301)	4.4e-05 (1.839)	0.169 (0.423)
		Sept.-Oct.	Hilborn	0.344 (0.233)	0.0442 (0.353)	0.0384 (0.383)	0.336 (0.267)	0.16 (0.324)	1.7e-06 (>2)	0.0771 (0.56)
	Model II	-	McGarvey	0.287 (0.088)	0.113 (0.146)	0.11 (0.085)	0.254 (0.138)	0.129 (0.136)	0.0561 (0.303)	0.0512 (0.221)
		-	Hilborn	0.271 (0.091)	0.0995 (0.14)	0.105 (0.087)	0.289 (0.125)	0.125 (0.137)	0.0588 (0.303)	0.0518 (0.22)
	Model III	<60cm	McGarvey	0.327 (0.088)	0.116 (0.157)	0.127 (0.087)	0.221 (0.159)	0.131 (0.144)	0.0497 (0.34)	0.0282 (0.318)
		<60cm	Hilborn	0.281 (0.094)	0.11 (0.138)	0.11 (0.088)	0.297 (0.128)	0.119 (0.148)	0.0554 (0.338)	0.0274 (0.319)
		>60cm	McGarvey	0.0543 (0.411)	0.0276 (0.732)	0.0149 (0.366)	0.534 (0.213)	0.0979 (0.403)	0.087 (0.686)	0.184 (0.347)
		>60cm	Hilborn	0.156 (0.303)	0.0262 (0.71)	0.0515 (0.249)	0.268 (0.28)	0.166 (0.328)	0.0781 (0.662)	0.254 (0.263)
Sandusky	Model I	May-June	McGarvey	0.0522 (0.209)	0.0255 (0.359)	0.0257 (0.149)	0.113 (0.379)	0.591 (0.095)	0.0727 (0.549)	0.12 (0.297)
		May-June	Hilborn	0.0547 (0.196)	0.0287 (0.276)	0.0269 (0.124)	0.141 (0.26)	0.566 (0.083)	0.076 (0.514)	0.107 (0.293)
		July-August	McGarvey	0.0624 (0.255)	0.0505 (0.394)	0.028 (0.163)	0.284 (0.151)	0.314 (0.103)	0.0835 (0.272)	0.177 (0.132)
		July-August	Hilborn	0.0624 (0.255)	0.0505 (0.394)	0.028 (0.163)	0.284 (0.151)	0.314 (0.103)	0.0835 (0.272)	0.177 (0.132)
		Sept.-Oct.	McGarvey	0.00912 (1.04)	0.0288 (0.542)	0.035 (0.423)	0.667 (0.151)	0.0593 (0.46)	0.0837 (0.594)	0.117 (0.428)
		Sept.-Oct.	Hilborn	0.0155 (1)	0.0154 (0.521)	0.0683 (0.259)	0.477 (0.174)	0.107 (0.333)	0.123 (0.511)	0.195 (0.291)
	Model II	-	McGarvey	0.05 (0.163)	0.0294 (0.232)	0.0264 (0.111)	0.244 (0.151)	0.384 (0.077)	0.0883 (0.221)	0.177 (0.115)
		-	Hilborn	0.0542 (0.158)	0.0278 (0.226)	0.0292 (0.105)	0.263 (0.144)	0.372 (0.077)	0.0872 (0.218)	0.167 (0.115)
	Model III	<60cm	McGarvey	0.0381 (0.223)	0.0464 (0.265)	0.0474 (0.134)	0.243 (0.192)	0.393 (0.104)	0.0907 (0.294)	0.141 (0.182)
		<60cm	Hilborn	0.038 (0.219)	0.0409 (0.231)	0.027 (0.12)	0.405 (0.123)	0.294 (0.111)	0.102 (0.284)	0.0925 (0.189)
		>60cm	McGarvey	0.0382 (0.238)	0.0198 (0.52)	0.0187 (0.193)	0.278 (0.219)	0.325 (0.125)	0.0857 (0.357)	0.235 (0.152)
		>60cm	Hilborn	0.0683 (0.217)	0.015 (0.502)	0.0236 (0.171)	0.192 (0.191)	0.398 (0.089)	0.063 (0.36)	0.24 (0.128)
Chicken and Hen Islands	Model I	May-June	McGarvey	0.0634 (0.322)	0.244 (0.168)	0.0626 (0.204)	0.297 (0.209)	0.247 (0.246)	0.0576 (0.95)	0.0286 (0.986)
		May-June	Hilborn	0.0674 (0.303)	0.27 (0.145)	0.0655 (0.157)	0.247 (0.21)	0.262 (0.228)	0.0596 (0.889)	0.0296 (0.976)
		July-August	McGarvey	0.0705 (0.391)	0.149 (0.299)	0.0242 (0.3)	0.294 (0.245)	0.292 (0.209)	0.0637 (0.48)	0.106 (0.301)
		July-August	Hilborn	0.0761 (0.369)	0.151 (0.277)	0.0287 (0.27)	0.295 (0.183)	0.286 (0.171)	0.0603 (0.479)	0.103 (0.278)
		Sept.-Oct.	McGarvey	8.58e-07 (>2)	0.0363 (0.926)	0.041 (0.71)	0.29 (0.817)	0.27 (0.57)	0.102 (0.924)	0.26 (0.619)
		Sept.-Oct.	Hilborn	1.11e-06 (>2)	0.023 (0.47)	0.047 (0.509)	0.265 (0.323)	0.27 (0.354)	0.148 (0.791)	0.247 (0.437)
	Model II	-	McGarvey	0.0529 (0.248)	0.174 (0.143)	0.0424 (0.153)	0.301 (0.147)	0.259 (0.149)	0.0682 (0.389)	0.103 (0.244)
		-	Hilborn	0.0588 (0.243)	0.192 (0.13)	0.0478 (0.149)	0.301 (0.137)	0.245 (0.149)	0.0646 (0.387)	0.0908 (0.242)
Van Buren Bay	Model I	May-June	McGarvey	7.35e-08 (>2)	1.23e-08 (>2)	1.11e-08 (>2)	0.00135 (1.2)	0.00689 (1.003)	0.0645 (0.67)	0.927 (0.048)
		May-June	Hilborn	8.16e-08 (>2)	4.5e-08 (>2)	1.29e-08 (>2)	0.00491 (1.02)	0.00753 (0.999)	0.134 (0.331)	0.853 (0.053)
		July-August	McGarvey	9.66e-08 (>2)	8.83e-08 (>2)	1.45e-08 (>2)	0.0217 (0.512)	0.00419 (1)	0.198 (0.174)	0.776 (0.049)
		July-August	Hilborn	9.96e-08 (>2)	1.18e-07 (>2)	1.47e-08 (>2)	0.0243 (0.453)	0.0042 (1)	0.205 (0.166)	0.766 (0.048)
		Sept.-Oct.	McGarvey	3.64e-07 >2)	0.00254 (1.114)	1.17e-07 (>2)	0.0479 (0.656)	0.0169 (1.018)	0.304 (0.321)	0.629 (0.18)
		Sept.-Oct.	Hilborn	4.1e-07 (>2)	0.00146 (1.03)	1.01e-07 (>2)	0.0385 (0.506)	0.0158 (0.994)	0.392 (0.225)	0.553 (0.166)
	Model II	-	McGarvey	3.63e-08 (>2)	0.000643 (1.033)	5.77e-09 (>2)	0.0165 (0.376)	0.00672 (0.577)	0.183 (0.154)	0.793 (0.039)
		-	Hilborn	4.12e-08 (>2)	0.000657 (1.024)	6.58e-09 (>2)	0.0176 (0.364)	0.00704 (0.577)	0.199 (0.15)	0.776 (0.042)

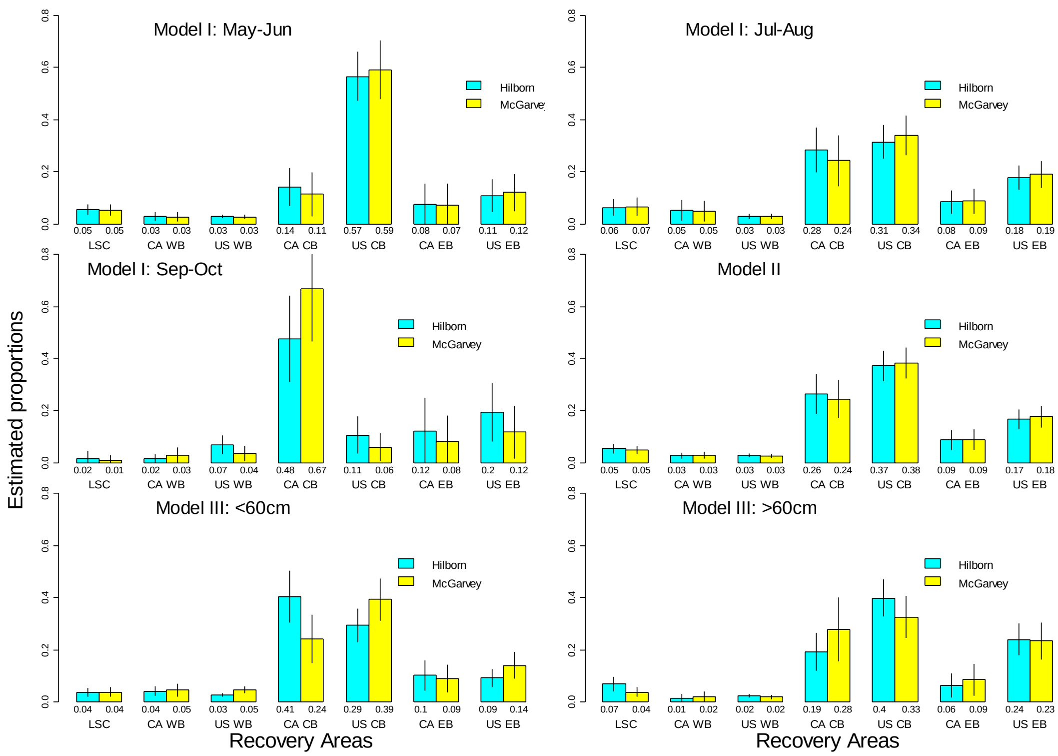


Figure 3a. Estimated spatial distributions of Sandusky stock with 95% CI by estimation framework and model variant. (LSC = Lake St. Clair corridor; WB = Lake Erie western basin; CB = Lake Erie central basin; EB = Lake Erie eastern basin; CA= Canada; US= United States; Model I = seasonal distribution with no length covariate; Model II = annual distribution with no length covariate; Model III = annual distribution with two length classes, fish length ≥ 60cm and length <60cm)

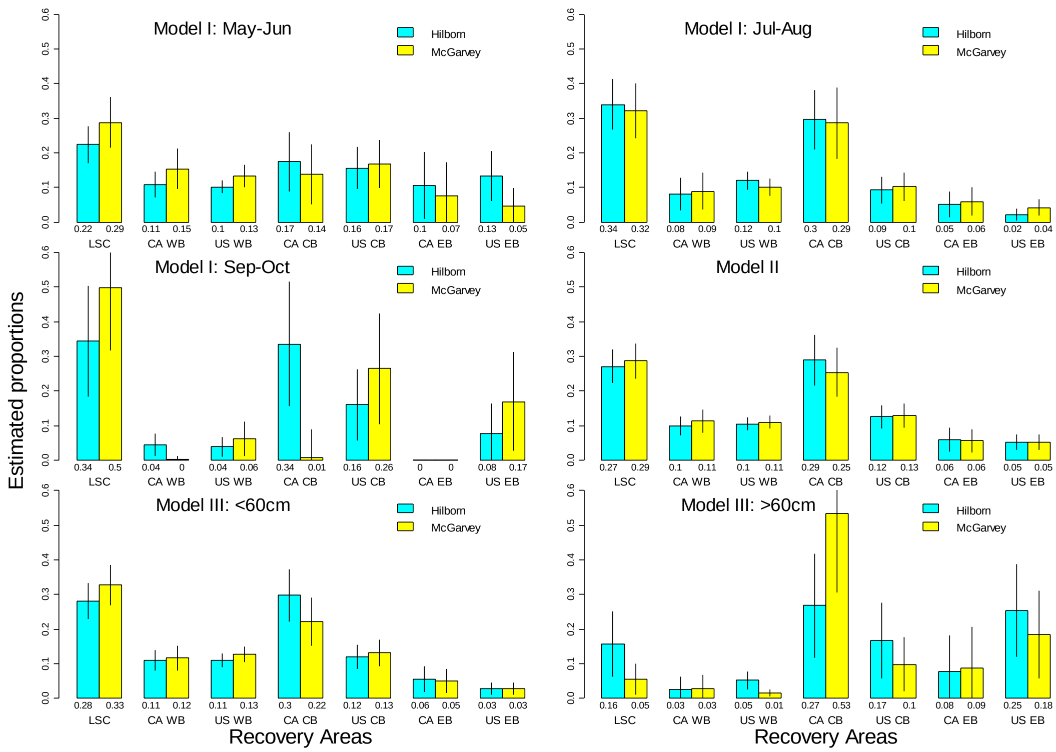


Figure 3b. Estimated spatial distributions of Monroe stock with 95% CI by estimation framework and model variant: Monroe. Abbreviations same as Figure 3a.

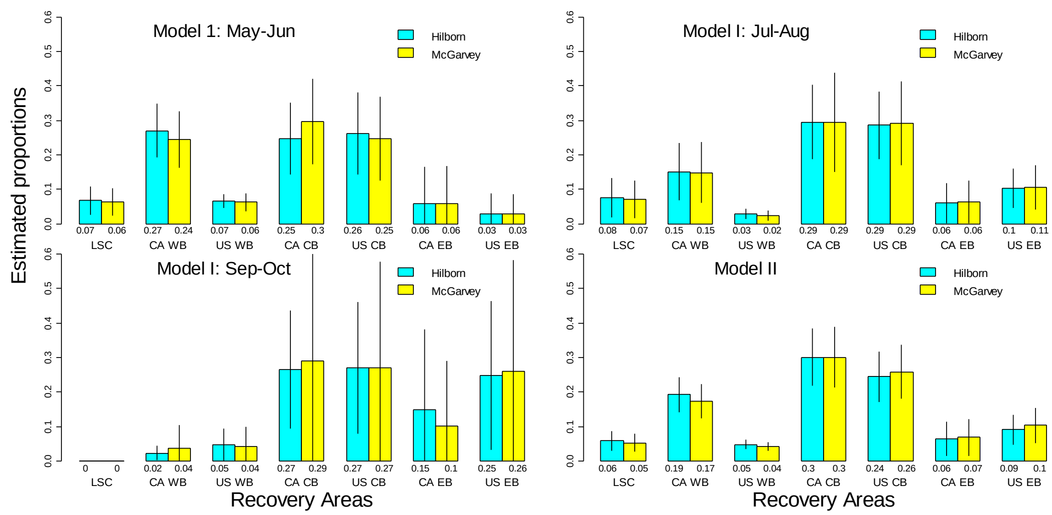


Figure 3c. Estimated spatial distributions of Chicken and Hen Island stock with 95% CI by estimation framework and model variant. Abbreviations same as Figure 3a.

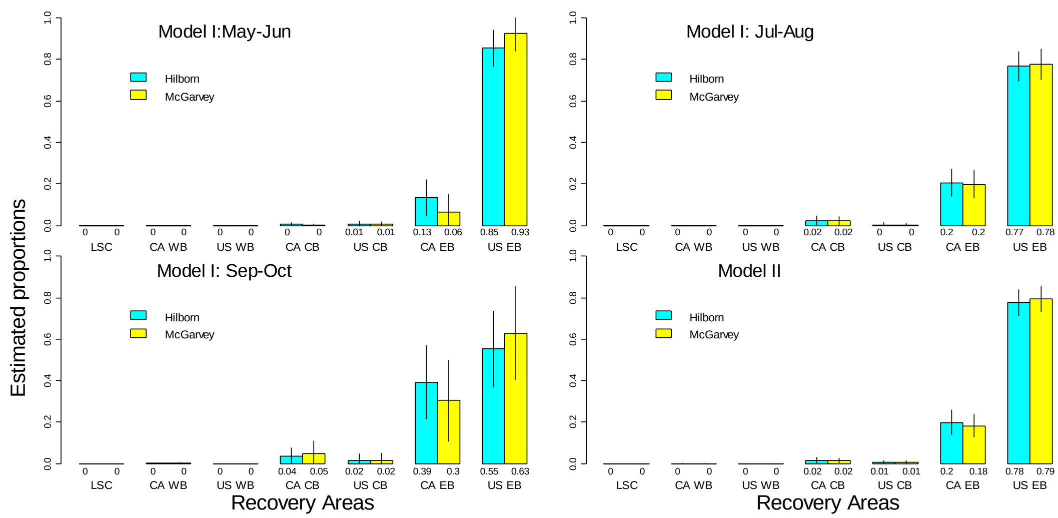


Figure 3d. Estimated spatial distributions of Van Buren Bay stock with 95% CI by estimation framework and model variant. Abbreviations same as Figure 3a.

is similar to the July-August estimates in Model I. As the majority of the recoveries come from July-August, this result is not surprising. Model II provides the most straightforward results to compare the average spatial distributions of a stock across the seasonal time-periods. Model II results indicate that the Monroe and the Sandusky stocks have the two most divergent distributions among western basin stocks and show that different western basin stocks can have distinct distributions and movement patterns. Over 25 percent of the Monroe stock is estimated to move to LSC while less than 5 percent is estimated for the Sandusky stock. Of the Monroe stock in the Central Basin about 40 percent is estimated to be in the Central Basin with twice the proportion estimated in Canadian waters than U.S. waters (25 to 29 percent versus 12 to 13 percent). Over 60 percent of the Sandusky stock is estimated to be in the Central Basin and the U.S. waters is estimated to have ~40 percent more of the stock than Canadian waters of the Central Basin (24 to 26 percent versus 37 to 38 percent). From 26 to 27 percent of the Sandusky stock is estimated to occur in the Eastern Basin while only 11 percent is estimated for the Monroe stock.

Model III estimates two sets of estimated distribution proportions for each stock for the entire May – October period, one set for fish <60 cm and one for fish >60 cm. The estimated proportions for the two length classes for the Sandusky stock do not differ greatly, though the larger length class has a greater proportion in the Eastern Basin than the smaller length class. Greater differences between the length classes exist for the Monroe stock with the smaller length class having a much higher proportion in LSC and the larger length class having a much higher proportion in the U.S. Eastern Basin. The confidence intervals for the <60cm group for the Monroe stock are much smaller than for the >60cm due to the smaller number of releases and recoveries of the larger length class. Model III results indicate larger western basin walleye move proportionately more to the eastern basin though differences exist between stocks on the extent of this length-based movement with a stronger length effect for the Monroe stock than for the Sandusky stock.

Both estimation frameworks produce fairly similar point estimates and standard errors overall, especially for Model II (Figure 3 and Table 2). The general concurrence of the two estimation frameworks indicates that the tagging-related input parameters (mainly the commercial and sport reporting rates) for the Hilborn framework were reasonably estimated. One significant difference in the results between the two estimation frameworks occurs with the Monroe stock in Model I. For the Monroe stock for the first two time periods, both estimation frameworks show strong movement in to LSC and the Central Basin; however for September-October, the Hilborn framework estimates 34 percent of the stock in the Canadian Central Basin while the McGarvey framework estimates only 1 percent of the stock. The reason for the large discrepancy between these two estimates is not clear.

Differences in estimated catchabilities between stocks may indicate different fishery dynamics for a given stock. For the western basin stocks, the estimated commercial catchabilities are similar (Figure 4). The estimated sport catchabilities for the Sandusky and Monroe stock are also similar but the CHI sport catchabilities are about 50 percent of the Sandusky and Monroe stocks. The CHI stock is the only stock in this study tagged by the Ontario Ministry of Natural Resources and thus the only stock with a Canadian agency on the tag as the contact agency. If this caused an increase in reporting rates by sport fishers, then the estimated catchability would decrease. If the stock had substantially lower tag loss rates then other stocks, decreases in both estimated sport and commercial catchabilities would be expected, but this did not occur. Besides differences in reporting rates for the CHI stock, other explanations are not apparent. The estimated catchabilities for the Van Buren Bay stock differ from the western basin estimates because they are based almost entirely on recoveries from the eastern basin, which is physically and biologically quite distinct from the other basins, resulting in possibly different catchability values. While the sport catchabilities are slightly to moderately higher than for the western basin stocks, the commercial catchabilities are generally much higher than those for the western basin stocks. Decreased reporting rates for tags labeled with the New York Department of Environmental Conservation as the contact agency relative to other resource agencies may explain this.

In AIC model selection, the lowest AIC value among models fit to the same data identifies the most parsimonious models with differences in AIC values of less than two indicating similar fits to the data, differences between two and ten indicating less support for the higher valued models, and differences greater than ten indicating little support for those models (Burnham and Anderson, 1998). Both estimation frameworks produced similar AIC results (Table 4), though the 'best fit' model differed among stocks (Model III for the Monroe stock, Model I for the Sandusky stock, Model I for the CHI stock and Model II for the Van Buren Bay). These results indicate that the pattern of tag returns indicate potentially different movement dynamics occur among the stocks and that different parameterizations may be more appropriate for particular stocks. An important point to emphasize is that these AIC values are based on the fit of the model variants to the tagging data. They do not imply that the biological/ecological processes that the model variants with higher AIC values represent (seasonal movement, length as a covariate of movement) are not valid, but only that the available data does not support the extra parameterizations they require.

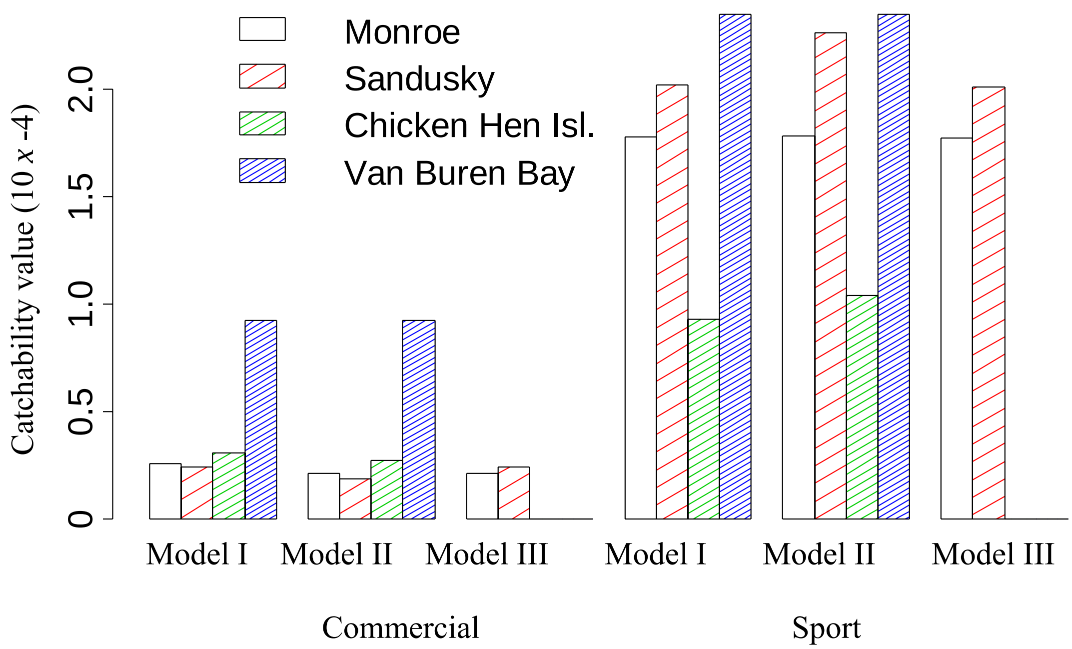


Figure 4. Estimated catchability values from Hilborn framework by stock, model variant, and gear type. (Sport values: per thousands of angler hours; commercial values: per kilometer of gill net)

Table 4. Likelihood and AIC values by stock and model

	Estimation framework					
Stock	**Hilborn**			**McGarvey**		
Monroe	Model I	Model II	Model III	Model I	Model II	Model III
No. of Parameters	20.00	8.00	14.00	18.00	6.00	12.00
-log likelihood	1603.01	1626.91	1604.45	907.26	927.87	891.70
AIC	3246.02	3269.82	3236.90	1850.53	1867.74	1807.40
Change in AIC	9.12	32.92	**0.00**	43.13	60.35	**0.00**
Sandusky	Model I	Model II	Model III	Model I	Model II	Model III
No. of Parameters	20.00	8.00	14.00	18.00	6.00	12.00
-log likelihood	1855.13	1893.84	1874.28	794.29	828.48	927.77
AIC	3750.26	3803.68	3776.56	1624.58	1668.97	1879.54
Change in AIC	**0.00**	53.42	26.30	**0.00**	44.39	254.96
Chicken and Hen Islands	Model I	Model II	Model III	Model I	Model II	Model III
No. of Parameters	20.00	8.00	-	18.00	6.00	-
-log likelihood	790.02	830.09	-	1294.12	1308.78	-
AIC	1620.05	1676.17	-	2624.24	2629.56	-
Change in AIC	**0.00**	56.13	-	**0.00**	5.32	-
Van Buren Bay	Model I	Model II	Model III	Model I	Model II	Model III
No. of Parameters	20.00	8.00	-	18.00	6.00	-
-log likelihood	5634.86	5642.99	-	8666.30	8672.54	-
AIC	11309.72	11301.98	-	17368.60	17357.08	-
Change in AIC	7.74	**0.00**	-	11.52	**0.00**	-

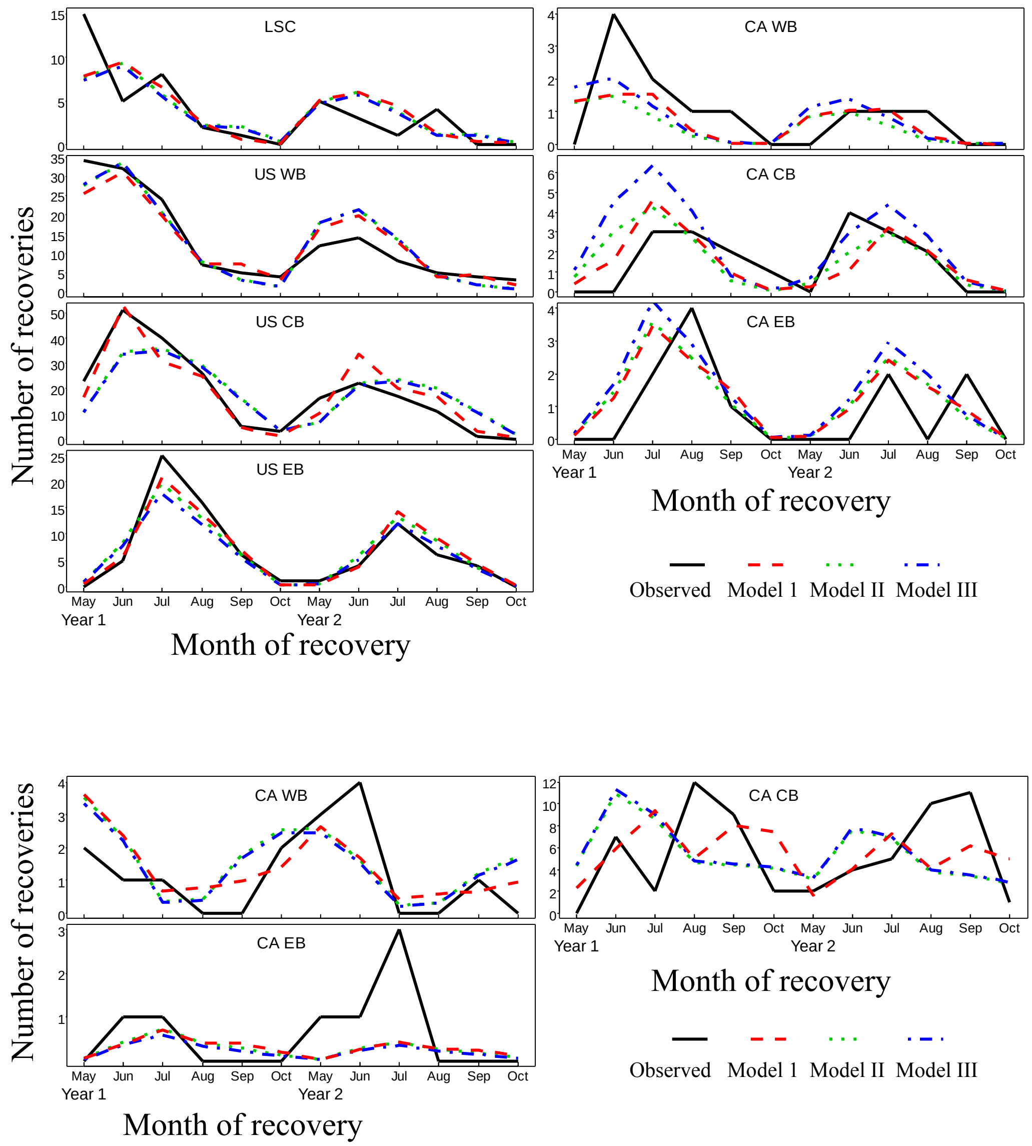


Figure 5a. Sandusky stock: observed and predicted recoveries aggregated from 1990-2001. (top, sport; bottom, commercial) Abbreviations same as Figure 3a.

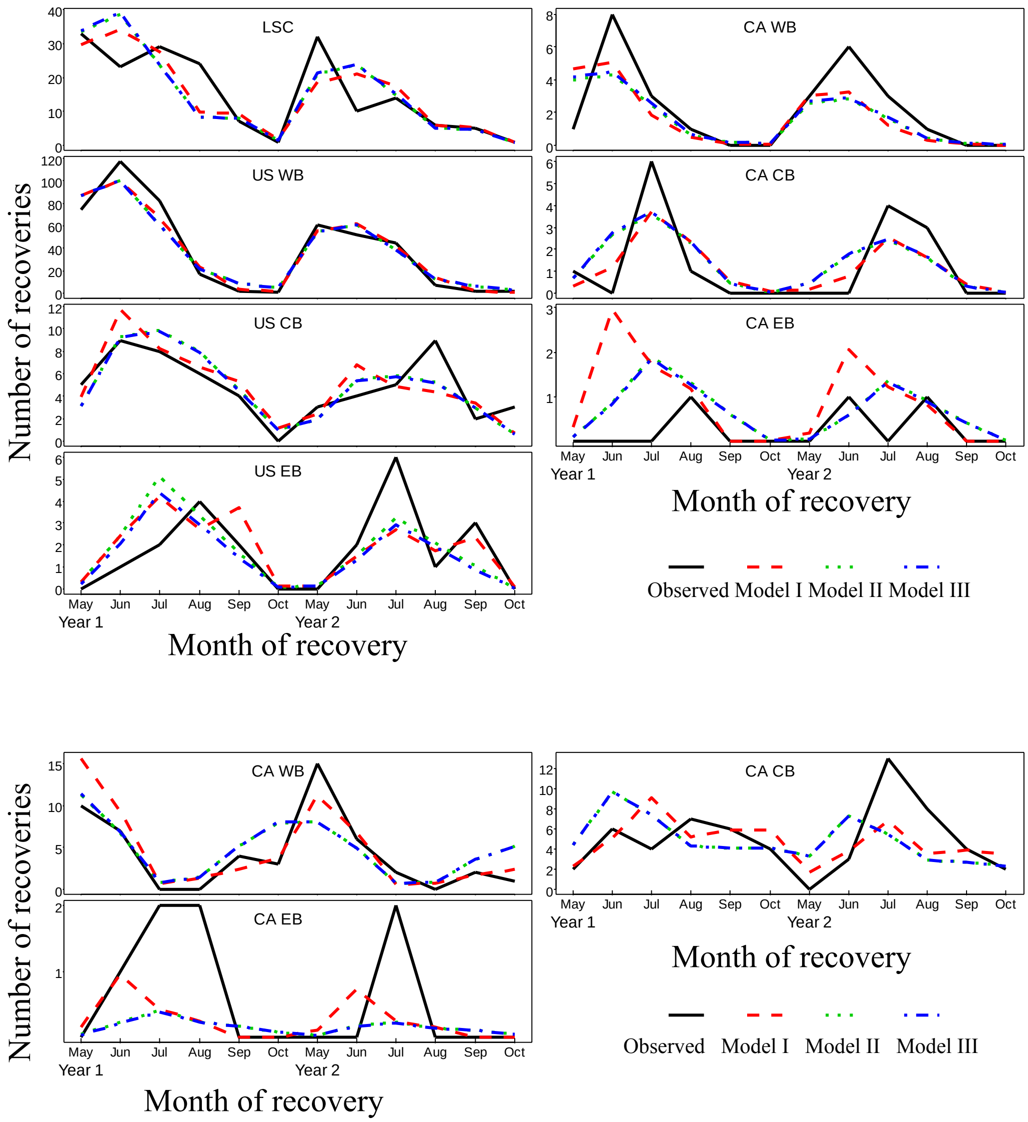
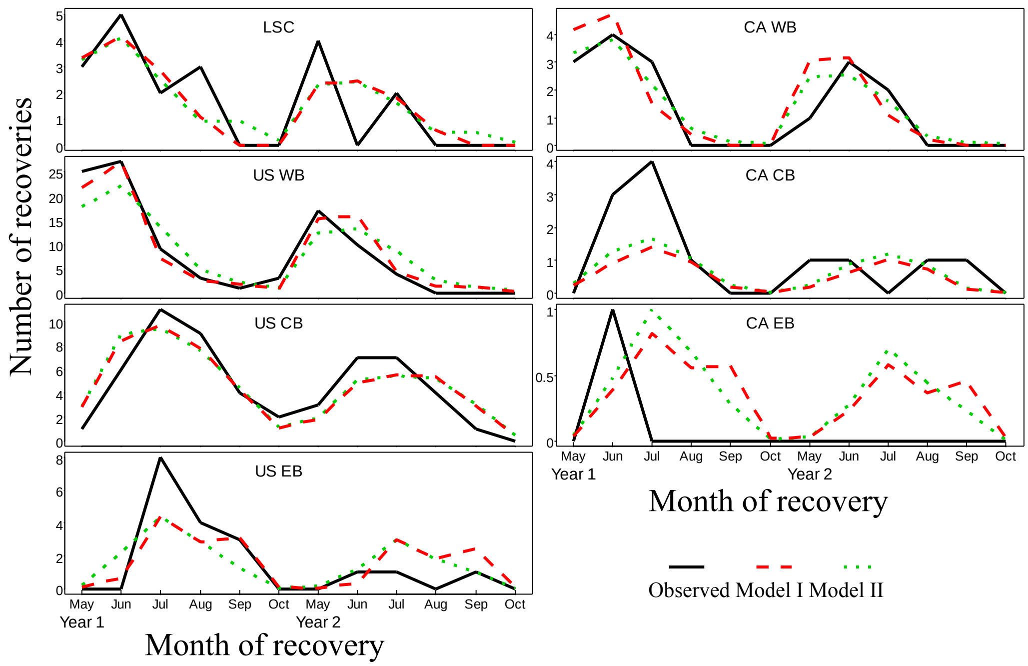


Figure 5b. Monroe stock observed and predicted recoveries aggregated from 1990-2001. (top, sport; bottom, commercial) Abbreviations same as Figure 3a.



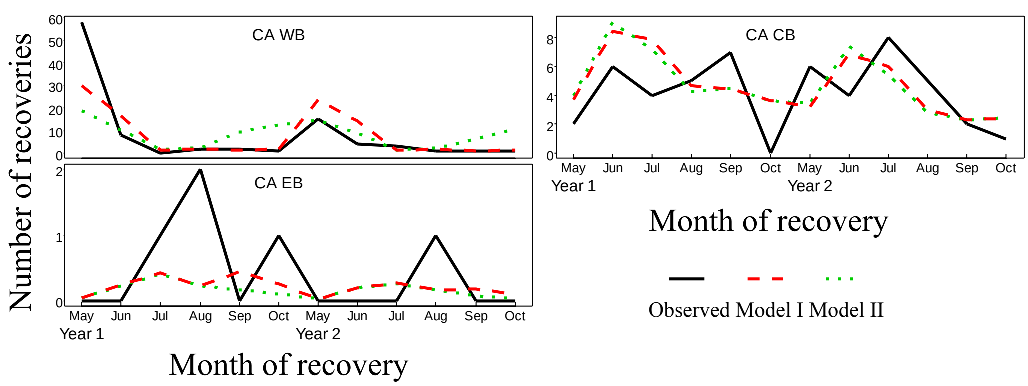


Figure 5c. Chicken and Hen Islands stock: observed and predicted recoveries aggregated from 1990-2001. (top, sport; bottom, commercial) Abbreviations same as Figure 3a.

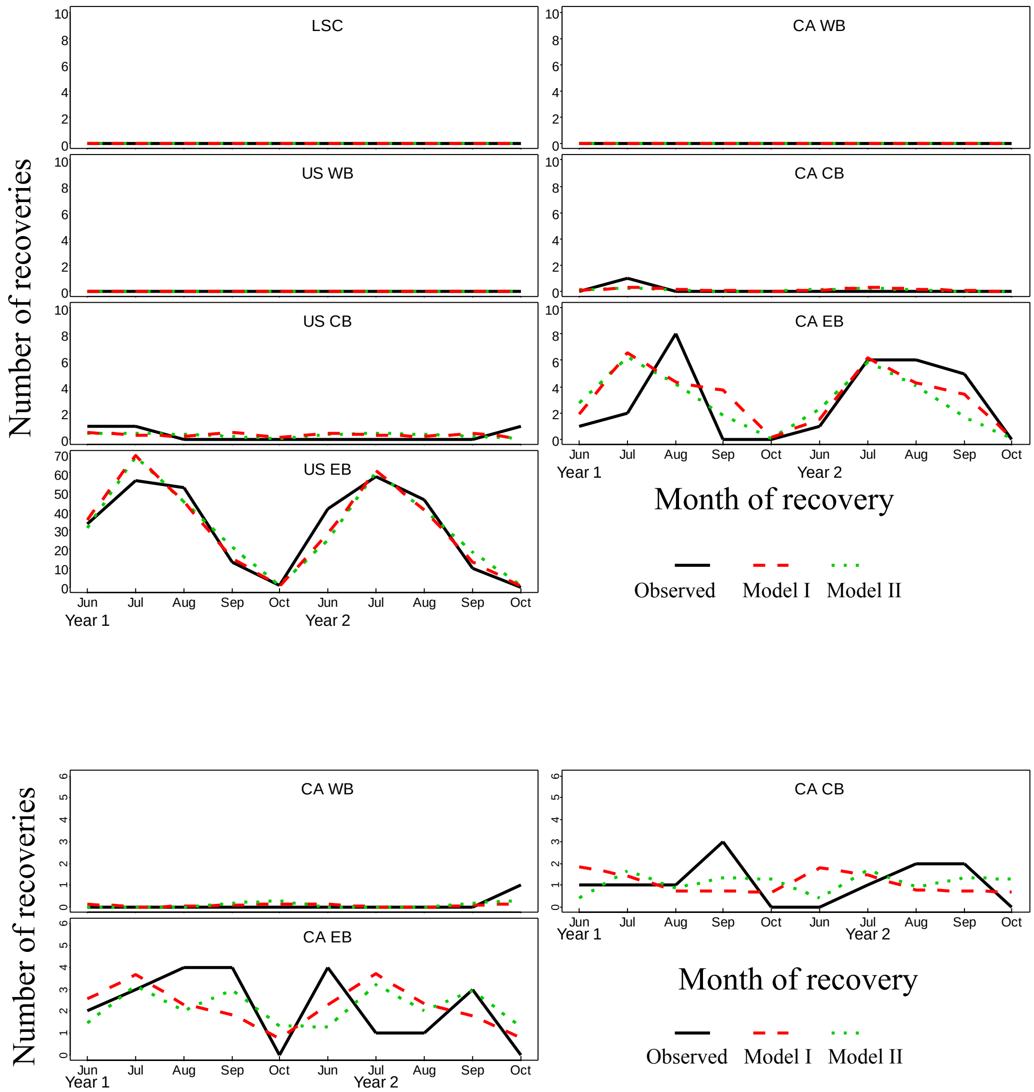


Figure 5d. Van Buren Bay stock: observed and predicted recoveries aggregated from 1990-2001. (top, sport; bottom, commercial) Abbreviations same as Figure 3a.

The Hilborn framework estimates a predicted number of recoveries per spatial-temporal strata and the pattern of observed versus predicted recoveries can be used as an informal model diagnostic. Figure 5 shows the aggregate observed versus predicted recoveries (the sum from all tag groups). The general patterns show generally good correspondence between observed and predicted recoveries. A significant deviation between observed and predicted recoveries occurs for the May commercial recoveries of the CHI stock, where the predicted recoveries range between 20 – 30 versus 60 for observed recoveries. This difference may arise from commercial gill net operations occurring in the close vicinity of the spawning grounds and harvesting the tagged walleye as they disperse from the spawning grounds. The different models produce nearly similar patterns of predicted recoveries, especially between Model II and Model III which are nearly identical in most cases. Thus, the different AIC results for a stock do not necessarily translate into large differences for the predicted recoveries.

Implications of Model Assumptions

Two important assumptions inherent in the analysis are the value of fishing effort in LSC and the lack of size selectivity in the estimation (Hilborn framework) or direct calculation (McGarvey framework) of the harvest rate. LSC monthly fishing effort was assumed to be 15 percent of the monthly U.S. western basin effort (Michigan and Ohio waters). As LSC effort data are sparse, it could be inaccurate. Assumed values for LSC effort affect estimates by decreasing movement to LSC as assumed effort increases in LSC and decreasing movement to other basins and strata. The sport and commercial fisheries were not assumed to be size-selective, based on a direct estimate of selectivity from the tagging data by the authors (Myers and Hoenig, 1997). While a particular gill net mesh size is highly size selective, enough different mesh sizes are evidently used by the gill net fishery such that size selectivity for fish >40 cm in length at time of tag application is not apparent from the tag return data.

Ignoring growth during the two years a tag group was followed is a simplifying assumption for examining the distribution of the two different length classes for the Monroe and Sandusky stocks. As walleye <60cm may grow seven to eight cm in a season, some walleye grouped in the smaller length class likely grew into the larger length class. However, the larger walleye also grew during this time, though more slowly, maintaining a relative size difference between the two length-classes. The inclusion of a growth function in the population dynamics model would add more realism but would not likely affect the estimates and would add complexity to the modeling with little additional insight gained. Experimental runs that fit data only to the first year of recoveries, thus minimizing the effect of growth on the composition of the two length classes, yielded almost identical results for Model III, but with larger standard errors.

The annual instantaneous rate of natural mortality of Lake Erie walleye is estimated to be 0.32 (LEWTG, 2000), but models for the Monroe stock failed to converge during the estimation process at this natural mortality rate. With natural mortality set at 0.20, convergence was achieved and the model parameters were successfully estimated. For consistency, 0.20 was used for all model runs for each stock. However, when natural mortality was set at 0.32 for the other stocks, nearly identical spatial distributions were estimated for the other stocks with a slight decrease in the estimated catchability coefficients for each gear type (typically about eight or nine percent).

Discussion

With the international boundary effectively bisecting sport and commercial fishing effort in Lake Erie, the proportion of a stock moving to either the U.S. or Canadian waters is of particular interest. Using Model II results to analyze average distribution patterns shows that some significant differences occur in distribution between U.S. and Canadian waters for particular basins for the western basin stocks. The Monroe stock is evenly distributed in the western and eastern basins but has a significantly higher proportion in Canadian waters in the central basin (25 to 29 percent versus 12 to 13 percent). The Chicken and Hen Island stock has a higher proportion in the Canadian waters of the western basin but not in the other basins. The western basin estimates likely result from the high number of commercial recoveries in the western basin shortly after spawning and before all walleye have undergone post-spawning dispersal. The Sandusky stock is fairly evenly distributed with moderately higher proportions occurring in the U.S. waters of the central and eastern basins, resulting in about 20 percent more of the stock occurring in U.S. waters than Canadian waters. The estimated proportions are based on fishing effort estimates that potentially have large uncertainties associated with them; slight to moderate differences in estimates between the U.S. and Canadian waters of a particular basin might be a result of the uncertainty in the estimated fishing effort rather than true differences between the proportions.

The catchability coefficients estimated in the Hilborn framework are correlated with tag-loss and tag-reporting rates. Tag-loss rates and estimated catchability are positively correlated, e.g., lower initial tag-loss rates result in lower estimated catchabilities; and reporting rates by gear-type are inversely correlated with catchabilities, e.g., lower reporting rates result in higher estimated catchabilities. Experimental runs show that if no tag-loss were assumed to occur and all tags were assumed reported, the Hilborn framework would estimate similar proportions, but the estimated catchabilities would be lower. Due to their strong correlations with tag loss and tag reporting rates, comparing the estimated catchabilities from this tagging study with estimated catchabilities from walleye stock assessments is problematic. Also, while it is believed that catchability varies by basin (as the differences between Van Buren stock's catchabilities and the western basin stock's catchabilities imply), estimating a separate catchability for each basin is not possible because those estimates are confounded with the proportion estimates. Experimental runs with the McGarvey framework indicate that the actual input values for the catchability coefficients are less important than the relative difference in magnitude between the sport and commercial values. If the relative magnitudes both change in parallel (e.g., both catchabilities increase by 10%) then the estimated proportions remain the same.

The McGarvey and Hilborn estimation frameworks have substantially different likelihood functions yet produce the same AIC values (in ranking the model variants for each stock) and generally similar point estimates. The agreement between the AIC values indicate that both estimation frameworks behave similarly in fitting the models to the data and this agreement is the most significant aspect of the AIC results. If the ranking of the AIC values differed among frameworks, this would potentially indicate that the estimation frameworks were different enough that comparison of the results might not be straightforward or appropriate. Besides showing similarity in model-fitting between the two estimation frameworks, the AIC results indicate that different model parameterizations may be more appropriate for different stocks. For example, for the Monroe stock with Model I having the lowest AIC value, one conclusion is that after dispersal from the spawning grounds, the general distribution of the stock does not change much during the period of the fishing season and therefore estimating seasonal distributions does not improve the model fit to the data;

but a strong length-based movement dynamic exists for the stock and having length-at-release as a covariate improves the fit to the data. Conversely, for the Sandusky stock, length-based movement does not seem to be as an influential covariate (i.e., the different length classes move similarly) as shown by the estimated proportions but distinct seasonal distributions appear and therefore Model I provides the best fit to the data. Estimating seasonal distributions improves the model fit for the CHI stock significantly but not for the Van Buren Bay stock.

The general agreement among the point estimates and standard errors of the two estimation frameworks indicate that the implementation of the McGarvey framework, where the tag loss and tag reporting rates cancel and do not influence the parameter estimation, did not generally result in significantly different parameter estimates from the Hilborn framework. However, results from the high-reward tagging efforts and the estimation of reporting-rates as input parameters for the Hilborn framework were likely necessary for the agreement between the two frameworks and the ability to estimate reasonable reporting rates minimizes the advantage of the McGarvey framework. A scenario well suited for the McGarvey framework are for tagging programs where tags are recovered from multiple fisheries with different gear-types with unknown and/or highly variable reporting rates that could be considered spatially uniform for a given time-step.

The McGarvey and Hilborn estimation frameworks have substantially different likelihood functions yet both frameworks identify the same model variants as the most parsimonious (i.e., having the lowest AIC value). The agreement between the AIC values indicate that both estimation frameworks behave similarly in fitting the models to the data and this agreement is the most significant aspect of the AIC results. If the ranking of the AIC values differed among frameworks, this would potentially indicate that the estimation frameworks were different enough that comparison of the results might not be straightforward or appropriate. Besides showing similarity in model-fitting between the two estimation frameworks, the AIC results indicate that different model parameterizations may be more appropriate for different stocks. For example, for the Monroe stock with Model I having the lowest AIC value, one conclusion is that after dispersal from the spawning grounds, the general distribution of the stock does not change much during the period of the fishing season and therefore estimating seasonal distributions does not improve the model fit to the data; but a strong length-based movement dynamic exists for the stock and having length-at-release as a covariate improves the fit to the data. Conversely, for the Sandusky stock, length-based movement does not seem to be as an influential covariate (i.e., the different length classes move similarly) as shown by the estimated proportions but distinct seasonal distributions appear and therefore Model I provides the best fit to the data. Estimating seasonal distributions improves the model fit for the CHI stock significantly but not for the Van Buren Bay stock.

The long-distance movement of western basin walleyes to the eastern basin is one of the most noteworthy aspects of walleye movement dynamics. Eastward movement of western basin walleye generally increases with size and as female walleye are significantly larger than males, females comprise a majority of western basin walleye that move to the eastern basin. While females comprised only five percent of releases from the Chicken and Hen Islands site and nine percent from the Monroe site, they were 22 percent of the Chicken and Hen Islands recoveries and 21 percent of the Monroe recoveries in the eastern basin. Results from a summer 1994 creel survey of walleye harvested in New York waters showed that over 80 percent of the harvest were large, older females, presumed to be western basin fish (Einhouse and Haas, 1995). However, the overall walleye harvest level in the eastern basin is relatively low; in 2004, an estimated 420,000 age 5+ walleye were harvested in the western basin alone versus 30,000 in the eastern basin (Lake Erie Walleye Task Group, 2005). Therefore, while large western basin females may constitute a substantial percentage of eastern basin harvest, their eastward movement may lower their probability of harvest due to the much lower fishing effort in the eastern basin.

Bioenergetic principles may explain much of the eastward movement of western basin walleye. Kershner et al. (1999) presented results from bioenergetic simulation models that indicated western basin walleye that migrate to the central basin (they did not consider movement to the eastern basin) achieved higher net energy gains than non-migratory walleye because the deeper and cooler central basin provides more optimal summer habitat than the shallower and warmer western basin. Optimal temperatures for walleye growth are less than 24°C which is often exceeded in the summer in the western basin but less often in the central basin and rarely in the eastern basin (Kershner et al., 1999). Walleyes may also be moving eastward towards their prey base. Adult walleyes prefer soft-rayed fish as prey and some trawling survey data indicate soft-rayed forage fish may occur more frequently in cooler waters such as found in the central and eastern basins (Wang, 2003). For the eastern basin walleye, which grow larger than western basin walleye, possibly no bioenergetic advantage is gained by leaving the deeper and cooler waters of the eastern basin. Additionally, as the population of age 2+ western basin walleye has fluctuated between 40 million and 20 million during the period of this study (1990-2001), walleye density may influence movement patterns and spatial distributions, though it was not considered in this study.

The Lake Erie ecosystem has experienced significant biological and physical changes in recent decades due in part to the reduction of phosphorous loading and the introduction of non-native species such as zebra mussel (*Dreissena polymorpha*) and quagga mussel (*Dreissena polymorpha bugensis*), resulting in the oligotrophication of the lake and increasing water clarity. This oligotrophication has led to an altered food web structure and to changes in abundances of prey fish and reduction of aquatic habitat for walleye based on water clarity (Lester et al., 2004). How these changes have affected walleye behavior is not clear, but as Lake Erie continues to undergo ecological and physical changes, walleye movement and spatial distributions may change as well in response. The results presented here may be one snapshot in time (1990-2001); to document potential changes in walleye behavior, the tagging data should be continually augmented by new releases and re-analyzed.

The estimated proportions give a 'big picture' overview of the spatial distributions of the walleye stocks. As any spatially-explicit management actions would likely occur on the basin-scale, the results here would be directly applicable to such actions. The modeling framework used here could also have finer spatial resolution if necessary. However, as the number of spatial strata increases the number of recoveries per strata will decrease and increase the error terms for parameter estimates. Our methodology and results are directly applicable to spatially-explicit stock assessments, whose development is under consideration by Lake Erie walleye managers. A spatially explicit catch-at-age or catch-at-length stock assessment requires additional estimation of a large number of parameters for each spatial stratum used in the model and such an assessment model would not likely be able to estimate the required parameters with the seven spatial strata used in this model, let alone with additional spatial strata.

Two recommendations to improve future analyses of the Lake Erie walleye tagging data are to regularly release high-reward tagging and to regularly estimate fishing effort in LSC. High-reward tags have been shown an effective way to increase the reporting rates of walleye tags though they have only occurred in 1990 and 2000.

However, it has been noted that high reward tags also influence the reporting rates of non-reward tags (i.e., standard tags are reported at a higher rate due to the expectation of a potential reward) (Pollock et al. 2001). Also, reporting rates may vary over time. By having a regular high-reward tagging program, the bias that a high-reward tagging program may have on the reporting of non-reward tags is minimized and changes in reporting rates can be effectively monitored. Additionally, a significant number of recoveries occur in LSC for some stocks (roughly 20 percent of Monroe recoveries though only 5 percent of Chicken and Hen Islands recoveries). By having regular estimates of fishing effort data for the LSC, a more accurate spatial distribution of walleye stocks can be estimated.

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