

ESTIMATION OF REGIONAL MORTALITY RATES FOR LAKE ERIE WALLEYE
SANDER VITREUS USING SPATIAL TAG-RECOVERY MODELING

By

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ABSTRACT

ESTIMATION OF REGIONAL MORTALITY RATES FOR LAKE ERIE WALLEYE *SANDER VITREUS* USING SPATIAL TAG-RECOVERY MODELING

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Since 1990, Lake Erie Walleyes *Sander vitreus* have been tagged annually with jaw tags to better understand population dynamics and ecological characteristics of individual spawning populations. Although data collected from this tagging have been used for a variety of purposes, there has been only cursory examination of mortality and movement rates from the recoveries of this long-term tagging program. I used double-tagging and high-reward tagging experiments to estimate tag shedding and reporting rates for jaw-tagged Walleyes. Agency-specific model-averaged estimates of immediate tag retention ranged from 95 to 99%; for chronic shedding, model-averaged instantaneous rates (annual) ranged from 0.07 to 0.28. In general, tag reporting rates were higher for recreational fisheries (range 33-55%) than commercial fisheries (range 10-17%). Reporting rates for both fisheries and tagging basins declined between 1990 and 2000. I then fit a spatial tag-recovery model to jaw-tag recovery data that incorporated tag shedding and reporting rate estimates. As part of this spatial tag-recovery model, I estimated region- and age-specific mortalities and regional movement probabilities. The best performing model based on overdispersion-adjusted Akaike information criteria comparison had age-group-specific movement probabilities, age- and region-specific natural mortalities, and age-group- and region-specific annual fishing mortalities. Commercial fishing mortalities varied considerably during the study, while recreational fishing mortalities were more static. Natural mortalities of age-5 and older Walleyes were lower than those of younger fish in all regions, with natural mortalities ranging from 0.30 to 0.40 for age-4 and younger fish and 0.13 to 0.27 for age-5 and older fish.

In Lake Erie's western basin, age-4 natural mortality was lower than that of age-3 fish. To provide guidance with regards to designs of future tagging studies for Lake Erie Walleye, I used stochastic simulations to evaluate bias and precision of fishery and demographic parameter estimates from spatial tag-recovery models under different combinations of high- and low-reward tagging levels, allocations of tags to different age groups, and patterns in age-specific natural mortalities. Parameter precision increased as number of tags released increased and proportion of high-reward tags released increased. Additionally, aside from one exception (i.e., the oldest age group), precision in the estimated mortality rates also increased when I compared a skewed versus balanced tag allocation design. These trends in parameter precision were consistent among different population dynamic scenarios (i.e., assumed natural mortality rates in the data-generating model). The findings presented in this dissertation provide managers with information needed to update the current stock assessment model used to establish safe harvest levels for Lake Erie Walleye as well as insight into how future tagging studies should be conducted to ensure that meaningful fishery and population dynamic parameters can be estimated.

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CHAPTER 1

DISSERTATION INTRODUCTION

Walleye Life History

Walleye *Sander vitreus* is an ecologically and economically important fish species across much of North America (Barton 2011). With a native range extending from northern Canada to the Mississippi River delta region in the southern United States, Walleye are habitat generalists able to survive in both lotic and lentic systems. Spawning activity generally commences when water temperatures approach 5-6° C and peaks once water temperature approaches 10° C. Timing, intensity, and duration of spawning are mediated by photoperiod (Scott and Crossman 1973). Prior to spawning, mature Walleyes stage on or near spawning grounds, which typically consist of open-water reef complexes or riffle areas within rivers. Once spawning is completed, fish make directed movements toward summer feeding grounds to replenish energy resources exhausted during spawning (Wang et al. 2007). Depending on locale and stock, post-spawn movements may be limited to areas near spawning grounds or over a vast geographic area. As water temperatures decline, Walleyes begin moving toward wintering grounds, often near the spawning grounds, where they continue to replenish energy reserves for the upcoming spawning period.

Lake Erie Walleye fishery

The Lake Erie Walleye population supports one of the most important commercial and recreational freshwater fisheries in North America. Given the value and importance of the fishery, sustainable management of the Walleye population is imperative for the four U.S. states (Michigan, Ohio, Pennsylvania, and New York) and one Canadian province (Ontario) that border the lake. Walleye harvest is regulated through quotas determined by the Lake Erie Committee (LEC), which consists of a representative from each fisheries management agency bordering the

lake (Knight 1997). Harvest quotas (i.e., total allowable catches) are intended to promote a sustainable fishery in the western and central basins and are calculated annually based on projected population abundance for the upcoming year and a harvest policy that adjusts target fishing rate depending on estimated abundance.

Commercial exploitation of Lake Erie Walleye began in the 1920s shortly after collapse of the Lake Herring *Coregonus artedii* population (Hatch et al. 1987; Nepszy et al. 1991). With expansion of commercial and recreational fishing, Walleye population levels declined precipitously during the late 1950s (Colby et al. 1991). Multiple factors are believed to have contributed to this decline in abundance, including nutrient enrichment, invasive species, over-exploitation, spawning habitat degradation, dam construction, and introgression with Blue Pike *Sander vitreus glaucus* and Sauger *Sander canadensis* (Regier et al. 1969). Following this decline, Walleye harvest remained low until the fisheries in Michigan, Ohio and Ontario waters were closed in 1970 due to mercury contamination that caused a consumption moratorium. The recreational Walleye fishery reopened in Ontario waters in 1973, but only nominal incidental commercial harvest occurred until the commercial fishery was fully reopened in 1976 (Cowan and Paine 1997). Recreational harvest was also reopened in Ohio and Michigan waters in 1976, but the commercial fisheries in these states never reopened due to the states choosing to emphasize recreational fishing opportunities over commercial fishing interests. The Walleye fisheries in the eastern basin remained open during the western basin moratorium; however, New York's commercial harvest ceased after 1985 and Pennsylvania's commercial gill-net fishery closed in 1996 (Baldwin et al. 1979) although a small commercial trap-net fishery persisted. As a result of reduced exploitation and improvements in water quality in Lake Erie, the Walleye population increased rapidly and harvest quickly rebounded once the fisheries were re-opened

with recreational harvest composing the majority of harvest (Hatch et al. 1987; Colby et al. 1991). Despite the rebound, Walleye abundance and harvest have fluctuated considerably since the fisheries reopened as a consequence of highly variable recruitment (Locke et al. 2005)

Since 1990, statistical catch-at-age (SCAA) modeling has been used to annually estimate abundances and mortality rates of Walleye in the western and central basin (Statistical Districts 1-3) for the purpose of setting harvest quotas (WTG 2013). The current SCAA model framework uses Walleye harvest, catch, and effort data from the western and central basin fisheries. Additionally, fishery-independent trends in abundance (i.e., population assessment gill net catch rates) are incorporated into the SCAA model as auxiliary data sources to help characterize changes in abundance. Although the SCAA model incorporates considerable complexity in the model structure (e.g., age structure, multiple fisheries, fishery independent data sources), there are several assumptions implicit in the SCAA model that likely do not match Lake Erie Walleye biology or ecology. For one, natural mortality in the SCAA model is assumed to be constant across ages and years (WTG 2013), with the assumed value based on limited analysis of a long-term tagging study conducted on the lake (see below). In actuality, natural mortality likely varies spatially, temporally, and among age-classes due to factors such as disease incidence, predator abundance, environmental conditions, and fishing pressure (Ricker 1975; Vetter 1988; Hansen et al. 2011). An additional assumption that is made in the SCAA model is that the Lake Erie Walleye population is homogenous and well mixed (Zhao et al. 2011; Berger et al. 2012). However, previous research has found that the Lake Erie Walleye population exhibits complex spatial structuring, which has been attributed to metapopulation dynamics, complex fish movements, and regional differences in water quality, trophic structure, and incidence of invasive species (Wang et al. 2007; Berger et al. 2012). Ignoring spatial

structuring when it comes to the assessment of fish populations is not uncommon, despite the fact that doing so can result in biased abundance and mortality estimates for spatially-structured populations (Fournier et al. 1998; Kell et al. 2009; Kerr et al. 2010).

Background on the Lake Erie Walleye Tagging Program

As part of their management of the Walleye fishery, LEC agencies have cooperated in an interagency tagging study commonly referred to as the Lake Erie Walleye tagging program (LEWTP). The LEWTP was initiated in 1990 and has involved annual tagging of Walleyes through the maxillary or mandible (Scott and Crossman 1973) using size-10 or size-12 Monel® butt-end bands (jaw tags) (Einhouse and Haas 1995). The recovery and reporting of jaw tags by commercial and recreational fishers, as well as by scientific personnel, has formed the basis for drawing conclusions regarding, among other things, Walleye movements and stock dynamics in Lake Erie (Isermann and Knight 2005; Wang et al. 2007; Zhao et al. 2011).

Multiyear tagging studies such as the LEWTP are commonly used by fisheries biologists to estimate migration patterns, stock intermixing, and mortality rates of fish stocks (Nielsen 1992). Brownie et al. (1985) established much of the theory underpinning tag-recovery models for the purpose of estimating survival and exploitation rates; as a consequence, tag-recovery models are quite often referred to simply as Brownie models. The underpinning theory of Brownie models was greatly expanded upon by work conducted by Hoenig et al. (1998a), Hoenig et al. (1998b), Pollock et al. (1991), Pollock et al. (2001), Hearn et al. (2003), Jiang et al. (2007), and Bacheler et al. (2008). Arguably, one of the most important developments in Brownie models from a fisheries management standpoint concerned parameterization of the models in terms of natural and fishing mortality components and guidance for estimating these

different mortality components by either assuming reporting rates as known or employing methods that allowed reporting rates to be estimated (Hoenig et al. 1998a; Pollock et al. 2001, 2002; Hearn et al. 2003). Estimation of mortality components through Brownie models is facilitated through the availability of data analysis programs such as SURVIV (White 1983) and MARK (White and Burnham 1999); however, there are numerous assumptions associated with Brownie models (Pollock et al. 2001) and violations of these assumptions can lead to biased estimates (Miranda et al. 2002; Brenden et al. 2010). According to Pollock et al. (2001), assumptions of Brownie tag-recovery models are the following: 1) the tagged sample is representative of the target population, 2) there is no tag loss, 3) survival rates are not affected by tagging, 4) the year of tag recovery is correctly reported, 5) the fate of each tagged fish is independent of another, 6) all tagged fish within a cohort have the same annual survival and recovery rates and 7) fishing and natural mortality processes are additive.

Although estimating mortality rates was the primary impetus for initiating the LEWTP, efforts to consolidate and analyze jaw-tag recoveries for the purpose of estimating mortality components have been limited. Thomas and Hass (1994, 2000, 2005) analyzed recoveries of Walleyes tagged in Michigan waters of Lake Erie using Brownie models as implemented in the program ESTIMATE (Thomas and Hass 1994, 2000, 2005). Zhao et al. (2011) analyzed recoveries from tagging conducted by the NYSDEC in Lake Erie's eastern basin at the Van Buren Bay spawning site. Wright et al. (2005) conducted the most comprehensive analysis to date based on recoveries from multiple tagging sites in the western basin. In each of these previous attempts at analyzing jaw tag recoveries of fish from the LEWTP, the possibility of spatial, temporal, or age-related differences in natural mortality rates were not accounted for and there were questionable assumptions made with regards to tag shedding and tag reporting.

Previous analyses of recoveries from the LEWTP have generally assumed that shedding of tags has not occurred, which, if shedding does occur, can result in biases in both fishing and natural mortality rates. Tag shedding can occur shortly after tags have been applied (immediate shedding) and chronically through time (Fabrizio et al. 1996; Pollock et al. 2001). Regardless of tag type, some level of tag loss has been observed during tag shedding evaluations (Muoneke 1992; Pegg et al. 1996; Newman and Hoff 1998; Miranda et al. 2002); however, few published estimates of jaw tag loss rates for multi-year tagging studies exist. Newman and Hoff (1998) reported annual jaw tag loss rates for Walleyes between 17.5 to 27.8% for fish recovered by angling and trap nets, respectively. The authors suggested that the disparity between the tag loss rates may have been associated with jaw tags becoming entangled in the netting material during the recapture period, which may have inflated tag loss rate for Walleye captured in the trap nets. On Lake Erie, several jaw tagging studies with Walleyes have been conducted; however, these studies have produced conflicting results. During a short-term (i.e., 5 month) tagging experiment conducted in hatchery ponds by the Michigan Department of Natural Resources (MDNR) during 1991, jaw-tag (sizes 10 and 12) loss was 0% (B. Haas, MDNR, unpublished data). Similarly, Einhouse and Haas (1995) reported no annual tag loss (0%) for size-12 jaw tags, but a 41% tag loss of size-10 tags for Walleyes tagged and released in New York waters of Lake Erie. More recently, Isermann and Knight (2005) conducted a shedding study in the Ohio waters of Lake Erie and documented a 60% loss rate for size-10 jaw tags and a 30% loss rate for size-12 jaw tags. Based on the finding of Einhouse and Haas (1995) and Isermann and Knight (2005), an assumption of perfect tag retention for the LEWTP likely cannot be justified.

Although there are many factors that can lead to biased mortality estimates in Brownie models, imperfect tag reporting is considered to be one of the largest potential sources of bias

(Miranda et al. 2002; Brenden et al. 2010). There are several ways for estimating tag-reporting rates, such as releasing high-reward tags (Pollock et al. 2001), use of fishery observers (Pollock et al. (2002), or plantings of tags (Hearn et al. 2003). As part of the LEWTP, high-reward tags were released in 1990 and 2000 for the purpose of estimating tag reporting rates. A \$100 USD reward was offered for the recovery and reporting of a high-reward tag. This same reward level has been used for high-reward tags in other tagging studies (Nichols et al. 1991; Bacheler et al. 2009; Wood and Cadrin 2013), although as noted by Pollock et al. (2002) the level of reward needed to elicit 100% reporting will vary by species, location, and time. Although high-reward tagging was incorporated in the LEWTP, the results from this tagging have not been studied in depth. In particular, there has been no attempt to compare reporting rates between commercial and recreational fishers or to assess spatial and/or temporal differences in reporting rates. There are a number of factors that can influence fishers' motivations to return tags, which is why both spatially and temporally varying rates are frequently reported in studies characterizing tag reporting (Jenkins et al. 2000; Pollock et al. 2002; Polacheck et al. 2006; Taylor et al. 2006), and it is conceivable, if not likely, that such motivations could differ between commercial and recreational fishers and/or areas and management jurisdictions in Lake Erie.

Review of Spatial Tagging Models

As previously indicated, the Lake Erie Walleye population is recognized as exhibiting complex spatial structuring as a result of metapopulation dynamics, complex fish movements, and regional differences in water quality, trophic structure, and incidence of invasive species (Wang et al. 2007; Berger et al. 2012). Although marine fishes have received much of the attention concerning population spatial structuring, it is increasingly being recognized as

important in management of freshwater fish populations as well (Zimmerman and Krueger 2009). Because of the potential for assessment models to produce biased estimates of abundance and mortality for spatially-structured populations (Fournier et al. 1998; Kell et al. 2009; Kerr et al. 2010), Berger et al. (2012) fit an SCAA model with spatially-referenced vulnerabilities and catchabilities [i.e., “fleets as areas” approach to dealing with spatial structuring (Hurtado-Ferro et al. in press)] to Lake Erie Walleye harvest at age and survey data. This spatial SCAA model was found to perform better than the non-spatial model. Consequently, Berger et al. (2012) recommended the development of a spatially-explicit SCAA model to be used for management purposes.

To facilitate development of a spatially-explicit SCAA model for the Lake Erie Walleye fishery, it would be beneficial to have regional estimates of natural mortality rates to aid in the model’s parameterization. While estimation of natural mortality rates within SCAA models is theoretically possible, accuracy and precision of the estimates are data dependent (Hilborn and Walters 1992; Wang and Liu 2006; Lee et al. 2011). Thus, it is fairly common for natural mortality estimates from tagging models (e.g., Brownie model) to be incorporated in SCAA models. For a spatially-explicit SCAA model, region- and perhaps age-specific estimates of natural mortality would likely be of greatest use. A variety of spatial tag-recovery models have been proposed for region-specific estimates of mortality components (Hilborn 1990; Brownie et al. 1993; Schwarz et al. 1993; Joe and Pollock 2002; Cowen et al. 2009; Eveson et al. 2009). Each of the models can be considered a type of multi-state model, with the spatial regions of the modeled system corresponding to the different model states (Brownie et al. 1993; Joe and Pollock 2002; Eveson et al. 2009). The approaches differ primarily with respect to how movement among regions is treated (Markovian versus non-Markovian; constant versus time

varying), assumed distributions for the recovery data (Poisson versus multinomial), and how survival rates are estimated (overall survival versus separate fishing and natural mortality components). With a Markovian approach, movement to time step (t+1) depends only on location at time step (t) (i.e., the process is memoryless), whereas, with non-Markovian models location in time step (t+1) is dependent upon current (t) and previous (t-1) time steps. In terms of assumed distributions for the recovery data, past evaluations have found that the different approaches produce nearly identical estimates (Hilborn 1990). Although early descriptions of spatial tag-recovery models appeared more than 20 years ago, thus far applications have mostly been limited to marine fishes (e.g., Skipjack Tuna *Euthynnus pelamis*, Hilborn 1990; Sablefish *Anoplopoma fimbria*, Heifetz and Fujioka 1991; Pacific Herring *Clupea harengus pallas*, Schwarz et al. 1993; Yellowtail Flounder *Limanda ferruginea*, Cowen et al. 2009). It is not clear why spatial-tagging models either have not or rarely been applied to freshwater fish populations. Regardless, given the potential importance of spatially varying demographic rates to the management of both spatially structured and non-spatially structured fish populations, wider adoption of spatial tag-recovery models would likely prove beneficial to freshwater fisheries management.

Dissertation Goal and Objectives

The goal of this dissertation was to provide fisheries managers with estimates of important fishery and demographic parameters (e.g., natural mortality, fishing mortality, inter-regional movements) based on recoveries from a large-scale multi-year tagging program after accounting for potential biases associated with the tagging process, fisher behavior, and population spatial structuring. Furthermore, I wanted to provide managers with recommendations regarding the

design of future tagging studies. The purpose of chapter 2 was to conduct an in-depth examination of jaw-tag shedding and tag reporting rates associated with a large-scale multi-year tagging program. In chapter 3, I estimated regional- and age-specific movement and mortality components for a highly migratory fish using tag recovery data. My aim was to provide movement and mortality information that could be used in the development of a more spatially explicit assessment model as part of a quota-management system. A secondary objective was to demonstrate the application of spatial tag-recovery models to a freshwater fish population in the hopes that it might encourage additional use of these models in freshwater systems. In chapter 4, I evaluated how bias and precision of parameter estimates from a spatial tag-recovery model varied among different tagging design features for a population exhibiting complex fishing and demographic spatial structuring. In conducting these evaluations, I assumed inter-regional movements of tagged individuals could be treated as fixed (i.e., known) values under an assumption that external estimates would be available from an electronic tracking study. It is my desire that the results of this dissertation will prove useful to Lake Erie fishery resource managers and will be of interest and utility to the broader fisheries science community.

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CHAPTER 2

ESTIMATION OF TAG SHEDDING AND REPORTING RATES FOR LAKE ERIE JAW TAGGED WALLEYE

Abstract

Since 1990, Lake Erie Walleyes *Sander vitreus* have been tagged annually with jaw tags to better understand population dynamics and ecological characteristics of individual spawning populations. Although the data collected from this tagging have been used for a variety of purposes (e.g., estimating migration patterns, stock intermixing, and mortality rates), there has been only cursory examination of shedding and reporting rates associated with the long-term tagging program. I used double-tagging and high-reward tagging experiments to estimate tag shedding and reporting rates for jaw tagged Walleyes in Lake Erie. Double tagging of Walleyes with jaw and passive integrated transponder (PIT) tags suggested that tagging method and tagging agency contributed to observed variability in both immediate (within 21 days of tagging) retention and chronic jaw tag shedding rates. Agency-specific model-averaged estimates of immediate tag retention ranged from 95 to 99%; for chronic shedding, model-averaged instantaneous rates (annual) ranged from 0.07 to 0.28. Jaw tag reporting rates, estimated via releases of high reward tags in 1990 and 2000, varied among tagging year, tagging basin, and commercial and recreational fishery. In general, tag reporting rates were higher for the recreational fishery (range 33-55%) than for the commercial fishery (range 10-17%); reporting rates for both fisheries and tagging basins were found to have declined between 1990 and 2000. Uncertainty in the tag reporting rates was greater for the recreational fishery than for the commercial fishery. The results of this study will be beneficial for the management of the economically important Lake Erie Walleye fishery by providing managers with robust tag shedding and reporting rate estimates. These estimates will allow for more reliable estimates of important dynamic rates such as fishing and natural mortality because recoveries from the long-term jaw tagging dataset can be corrected for these previously unaccounted for biases.

Introduction

The Walleye *Sander vitreus* fishery in Lake Erie consists of a large commercial fishery in Canadian waters and an equally large recreational component in U.S. waters (Walleye Task Group 2011). Between 1990 and 2008, annual Walleye harvest by commercial and recreational fishers averaged approximately 2.7 and 1.9 million fish, respectively (Walleye Task Group 2011). The fishery is managed cooperatively by a bi-national committee (Lake Erie Committee) comprised of resource managers from the Ontario Ministry of Natural Resources (OMNR), Michigan Department of Natural Resources (MDNR), Ohio Department of Natural Resources (ODNR), Pennsylvania Fish and Boat Commission (PFBC), and the New York State Department of Environmental Conservation (NYSDEC). As part of their management of the Walleye fishery, Lake Erie Committee (LEC) agencies have cooperated in an interagency tagging study commonly referred to as the Lake Erie Walleye tagging program (LEWTP). The LEWTP was initiated in 1990 and has involved annual tagging of Walleyes through the maxillary or mandible (Scott and Crossman 1998) using size-10 or size-12 Monel® butt-end bands (jaw tags) (Einhouse and Haas 1995). The recovery and reporting of jaw tags by commercial and recreational fishers, as well as by scientific personnel, has formed the basis for drawing conclusions regarding, among other things, Walleye movements and stock dynamics in Lake Erie (Isermann and Knight 2005; Wang et al. 2007; Zhao et al. 2011).

Multiyear tagging studies such as the LEWTP are commonly used by fisheries biologists to estimate migration patterns, stock intermixing, and mortality rates of fish stocks (Nielsen 1992). Brownie models (Brownie et al. 1985) have become the standard analytic approach for estimating mortality rates from tagging studies due in part to their flexibility (Pollock et al. 1991; Hearn et al. 1998; Hoenig et al. 1998; Pollock et al. 2001; Jiang et al. 2007). Although

estimation of mortality rates through Brownie models is facilitated through the availability of data analysis programs such as SURVIV (White 1983) and MARK (White and Burnham 1999), it is important to recognize that there are a variety of assumptions associated with these models (Pollock et al. 2001) and that violations of these assumptions can lead to biased estimates if not properly accounted for in the estimation process (Miranda et al. 2002; Brenden et al. 2010).

One of the most widely recognized assumptions of mark-recapture studies is that of no tag loss. I characterize this assumption as widely recognized because of the large number of studies that have evaluated tag shedding (Pierce and Tomcko 1993; Fabrizio et al. 1999; Latour et al. 2001; Miranda et al. 2002; Isermann and Knight 2005; Livings et al. 2007). Tag shedding can occur soon after tags are first applied (i.e., type-I tag loss) or chronically through time (i.e., type-II tag loss) (Beverton and Holt 1957; Pollock et al. 2001). Several studies have evaluated jaw tag shedding in Lake Erie Walleyes, but the results of these studies have been inconsistent. As part of a short-term experiment conducted in the early 1990s, 0% shedding over a 5-month period was observed for adult Walleyes tagged with size-10 and size-12 jaw tags and held in hatchery ponds (R. Haas, MDNR, unpublished data). Einhouse and Haas (1995) reported 0% tag shedding over a 1-year period for Walleyes tagged with size-12 jaw tags and released in New York jurisdictional waters of Lake Erie; however, they also reported a 41% tag shedding over a 1-year period for Walleyes tagged with size-10 tags. More recently, Isermann and Knight (2005) reported 60% and 30% shedding rates over a 1-year period for size-10 and size-12 jaw tags, respectively, for Walleyes tagged and released in Ohio waters of Lake Erie. The disparities in the results of these studies are likely due to a variety of factors, such as study environment, duration of study, size of fish tagged, and variations in tagging methodology. Regardless, the inconsistency in the results suggests that there remains substantial uncertainty as to what actual

tag shedding rates have been for the LEWTP and what factors may contribute to shedding.

Incomplete reporting of tags recovered by fishers is another source of bias that can affect conclusions drawn from multiple-year tagging studies (Pollock et al. 1991). Although tag reporting rates can be estimated as part of the process of fitting Brownie models (Pollock et al. 2001, 2002; Hearn et al. 1998), it is not uncommon for tag reporting rates to be estimated separately and later incorporated into Brownie model recovery probabilities (Latour et al. 2001; Taylor et al. 2006; Cadigan and Brattey 2008; Ebener et al. 2010). Reporting rates can be estimated by covertly planting tags in harvested fish (Matlock 1981; Green et al. 1983), distributing surrogate postcards to simulate fisher encounters with tagged fish (Zale and Bain 1994), using creel or port observers to monitor the harvest of tagged fish (Pollock et al. 1991; Polacheck and Hearn 2003), and releasing high-reward tags along with standard reward tags (Pollock et al. 2001). For the LEWTP, periodic (once in 1990 and then again in 2000) releases of high-reward jaw tags have been used to estimate reporting rates. The amount offered for the return of a high-reward tag has been US\$100, which was based in part on the findings of Nichols et al. (1991) that this amount was sufficient to elicit near 100% return of tags for recaptures of Mallards *Anas platyrhynchos*. Similar reward amounts have been used in high reward tagging of fishes as well (Denson et al. 2002; Taylor et al. 2006; Cadigan and Brattey 2006). Although this high reward tagging has been conducted on Lake Erie Walleyes, the results have only been cursorily examined. When using jaw tag return data to estimate mortality rates for Lake Erie Walleyes, a constant reporting rate that is assumed to apply to both commercial and recreational fisheries and all agencies and years has been incorporated in the Brownie model structure (Walleye Task Group 1991). However, there are a number of factors that can influence fishers' motivations to return tags, which is why both spatially and temporally varying rates are

frequently reported in studies characterizing tag reporting (Jenkins et al. 2000; Pollock et al. 2002; Polacheck et al. 2006; Taylor et al. 2006). It is conceivable, if not likely, that such motivations could differ between commercial and recreational fishers and/or areas and management jurisdictions, which could lead to biased mortality estimates if unaccounted for in Brownie model recovery probabilities.

The purpose of this study was to conduct an in-depth examination of Lake Erie Walleye tag shedding and reporting in the hopes that this would answer some lingering questions regarding the accuracy of values currently used for estimation of mortality rates as part of the LEWTP. Improved estimates of tag shedding and reporting will provide managers with the necessary information to “correct” the tag return data collected from the LEWTP and should result in more reliable estimates of important dynamic rates (e.g., fishing and natural mortality), which is imperative for ensuring sustainable management of Lake Erie Walleye stocks (Locke et al. 2005).

Methods

Tag Shedding

To assess jaw tag shedding, Walleyes from eight Lake Erie spawning populations were double tagged with jaw and passive integrated transponder (PIT) tags by agency personnel from the MDNR, ODNR and NYSDEC during 2005, 2006, and 2007 and the OMNR in 2005. Passive integrated transponder tags were selected as the second tagging method because these tags generally have high (>95%) retention (Prentice et al. 1990; Gries and Letcher 2002; Rude et al. 2011), although, variable (56-100%) retention rates have also been observed in some instances (Dieterman and Hoxmeier 2009). Each management agency collected and tagged fish using

similar collection and tagging protocols as previous tagging efforts. Tagging occurred from late-March to early-May in each year when Walleyes were congregated in tributaries or on open-water reefs to spawn.

As previously indicated, two sizes of jaw tags constructed of the stainless-metal alloy Monel® were used for tagging Walleye in the LEWTP, size-10 (inside diameter 7.95 mm) and size-12 (inside diameter 9.53 mm) tags. I used both tag sizes in my shedding evaluation to determine if shedding rates differed between tag sizes as the results of Einhouse and Haas (1995) and Isermann and Knight (2005) suggested. For the ODNR, Walleyes <500 mm were tagged with size-10 jaw tags, while Walleyes >500 mm were tagged with a size-12 jaw tag, all fish were tagged on the mandible. For the NYSDEC, Walleyes <450 mm received a size-10 jaw tag on the mandible, while Walleyes 450-650 mm received a size-10 tag on the maxillary and Walleye >650mm received a size-12 tag on the maxillary. The MDNR used size-12 jaw tags exclusively; however, jaw tags were affixed to the mandible or maxillary without an *a priori*, size-based criterion. Size-10 and -12 jaw tags were randomly allocated by the OMNR among Walleye of all sizes. Each jaw tag was affixed to the maxillary or mandible (Figure 2.1, Panel A) of tagged fish using one of two methods. For method 1, which is used by MDNR and NYSDEC personnel, the end of a jaw tag was inserted through the flesh around the maxillary or mandible and the ends of the tag were overlapped firmly with a pair of pliers. For method 2, which is used by ODNR and OMNR personnel, the jaw tag was crimped onto the mandible with a specialized pair of pliers with the overlapping ends of the tag facing the interior of the mouth cavity. Each jaw tag was inscribed with agency-specific fish identification numbers and tag reporting information.

Passive integrated transponder tags (length 12 mm, 134.2-kHz ISO, Destron-Fearing, St. Paul, Minnesota) were inserted into the subcutaneous musculature of the isthmus using a

modified, 12-gauge syringe-style hypodermic needle (Figure 2.1, Panel B). After PIT tags were implanted, fish were scanned with a radio-frequency identification (RFID) tag reader (Pocket Reader, Pocket Reader EX, or FS2001F-ISO, Destron-Fearing, St. Paul, Minnesota) to ensure the tag was functioning properly. Prior to release, corresponding jaw and PIT tag identification numbers were recorded, as was fish total length (to the nearest mm) and sex. All Walleyes captured during tagging operations and routine population assessment surveys from 2005 to 2009 were visibly examined for jaw tags and scanned with an RFID reader to determine whether tags of either type had been shed during the time at liberty.

Tag shedding rates were estimated using methodology described in Barrowman and Myers (1996). The probability that a jaw tag was shed at year t after release was modeled as

$$Q_A(t) = \rho_A \exp(-\phi_A t),$$

where $Q_A(t)$ was the retention rate at year t , ρ_A was the probability that a jaw tag was retained immediately (within 21-d) after release and ϕ_A was the instantaneous (annual) rate of chronic shedding. Retention rate of PIT tags ($Q_B(t)$) was similarly modeled with ρ_B and ϕ_B used to distinguish immediate retention and instantaneous shedding rate parameters for PIT tags. From these retention rates, the probability of observing a PIT and jaw tagged fish ($p_{AB}(t)$), a jaw tagged only fish ($p_A(t)$), or a PIT tagged only fish ($p_B(t)$) at time t after release for fishes that were initially double tagged could be calculated as

$$p_{AB}(t) = Q_A(t)Q_B(t),$$

$$p_A(t) = Q_A(t)\{1 - Q_B(t)\},$$

and

$$p_B(t) = Q_B(t)\{1 - Q_A(t)\}.$$

Reporting rates did not factor into the above equations because only recaptures examined by

tagging agency personnel were used to estimate shedding rates; thus, reporting rates were assumed to be 1.0. The parameters of the shedding rate equations were estimated by maximum likelihood estimation as described in Barrowman and Myers (1996). Because all tagging was conducted within a 21-day window, annual releases of double tagged individuals were considered to be simultaneous. For each tagged cohort, the log likelihood (ℓ) of observed recaptures of double tagged and single tagged fish conditional on observed recapture times was

$$\ell = \sum_{j=1}^{n_{AB}} \log_e \frac{p_{AB}(t_j)}{p_{AB}(t_j) + p_A(t_j) + p_B(t_j)} + \sum_{j=1}^{n_A} \log_e \frac{p_A(t_j)}{p_{AB}(t_j) + p_A(t_j) + p_B(t_j)} + \sum_{j=1}^{n_B} \log_e \frac{p_B(t_j)}{p_{AB}(t_j) + p_A(t_j) + p_B(t_j)},$$

where n_{AB} , n_A , and n_B were the number of recaptures with both jaw and PIT tags, a jaw tag only, or a PIT tag only, respectively, and t_j was the time after release (0= within 21 d, 1= 1 year at liberty, 2= 2 years at liberty and 3= 3 years at liberty) that a recapture of a particular tag combination occurred. Model estimation was conducted in SAS using PROC NLP (SAS Institute Inc. 2010a).

I fit a series of models to the tag shedding data using a set of explanatory variables that were hypothesized *a priori* to influence tag loss. The explanatory variables used to evaluate tag shedding included tagging agency, tagging method (for jaw tags), tag size (for jaw tags), and different combinations of these variables. The simplest (null) model estimated model parameters as constant across the explanatory variables, while the most complex model estimated model parameters separately for each tagging agency and tag size. Because there were only a few recaptures of jaw tag only fish, I was unable to include explanatory variables for the PIT tag shedding models; thus, PIT tag shedding was assumed to be the same for all tagging agencies

and years. Akaike information criterion (AIC) was used to evaluate the performance of the different candidate models (Burnham and Andersen 2002). Empirical support (i.e., plausibility) for a particular candidate model was evaluated via AIC differences. Models with AIC differences < 3.0 were considered to have strong plausibility as being the “best” model. If more than one model had an AIC difference of less than 3.0, model averaging of tag shedding parameters using the Akaike weights for the models was used to incorporate the results of all strongly plausible models (Burnham and Andersen 2002).

Tag Reporting Rates

Jaw tag reporting rates were estimated from tag return data collected via the high-reward tagging conducted in 1990 and 2000 through the LEWTP. Walleye were tagged by the OMNR, MDNR, ODNR and NYSDEC from western (1990 and 2000) and eastern (2000) basin spawning stocks (Figure 2.2). The high-reward tags were identical to the jaw tags used to estimate tag loss, with the exception that the high reward tags included the inscription “REWARD \$100”. Tag returns were solicited via posters, news releases and informational meetings from the recreational and commercial fisheries throughout Lake Erie and fishers were encouraged to report tags, regardless of tag type, from harvested fish.

With high reward tagging studies, reporting rates are estimated by comparing the number of standard (R_S) to reward (R_R) tags reported by fishers relative to the number of standard (N_S) and reward (N_R) tags released under the assumption that 100% of high reward tags are returned by fishers (Pollock et al. 1991). For simplicity, the number of recaptures observed between 1990 and 1999 from the 1990 release of high reward tags and between 2000 and 2009 from the 2000 release of high reward tags were used for the analysis. There were only a few

($n=4$) high reward tags returned after more than 10 years at liberty so this data censoring had little effect on estimated rates.

As described in Cadigan and Brattey (2008), the statistical distribution of the return of standard jaw tags conditional on the sum of standard and high reward jaw tag returns is binomial with probability

$$p(t) = \frac{\lambda(t)N_S}{\lambda(t)N_S + N_R},$$

where $p(t)$ is the conditional probability of the return of standard jaw tag in year t and $\lambda(t)$ is the reporting rate for year t . Cadigan and Brattey (2006, 2008) noted that with a logit link function, this conditional probability can be expressed as

$$\log_e \left\{ \frac{p(t)}{1 - p(t)} \right\} = \log_e \{ \lambda(t) \} + \log_e \left(\frac{N_S}{N_R} \right),$$

where $\log_e \left(\frac{N_S}{N_R} \right)$ is an offset constant that adjusts for the number of standard and high reward tags released for the experiment. As noted by Cadigan and Brattey (2008), reporting rates using the above formulation can be estimated through either fixed-effects or mixed-effects logistic regression (MELR). I used MELR because of the benefits identified in Cadigan and Brattey (2008), including the ability to estimate yearly reporting rates even with sparse data. As was done with tag shedding, I evaluated several factors that were identified as possibly influencing reporting rates. These factors were tagging year (1990 and 2000), basin (eastern and western basin), agency (OMNR, MDNR, ODNR and NYSDEC), and recapture fishery (commercial and recreational). I did not include tag size in the evaluations as I had little reason to suspect that reporting rates differed by tag size and because my tag shedding evaluations provided little support for tag loss differing by tag size (see Results section). The factors mentioned above, and various combinations of these factors, were incorporated in the MELR as fixed effects. The

random effect included in each of the MELR models was the interaction between year of recapture and all the fixed effects included in a particular model (Cadigan and Brattey 2008). The MELR models were fit by the Laplace approximation of the marginal likelihood function in SAS using the GLIMMIX procedure (SAS Institute Inc. 2010b). Performances of the fitted models were compared with AIC. As was done with tag shedding, plausibility of models were evaluated based on AIC differences, with model averaging conducted if more than one model had AIC differences less than 3.0.

Results

Tag Shedding

Between 2005 and 2007, 15,695 Walleyes ranging in total length from 317 to 817 mm (\bar{x} = 509 mm; SE = 0.6) were double tagged with jaw and PIT tags. Approximately equal numbers of fish were tagged with size 10 ($n=8,281$) and 12 ($n=7,414$) jaw tags (Table 2.1). Between 2005 and 2009, a total of 930 Walleyes that had retained at least one of the tag types were recaptured. The proportion of fish recaptured with at least one tag type from the initial tagging efforts ranged from 1.0 to 9.0% among the tagging agencies with an overall weighted mean proportion of 6.0%. The majority (89%) of recaptures occurred within 1-year of tagging. There were very few ($n=17$) recaptures of double-tagged fish by OMNR because tagging only occurred in 2005 due to sampling constraints during the study. The low number of recaptures caused convergence problems in some of the evaluated models; as a result, I excluded the OMNR data when fitting the tag shedding models.

Of the double-tagged fish recaptured, only around 2% ($n=16$) had shed PIT tags. Of the fish that had shed a PIT tag, 94% (15 of 16) were originally tagged and subsequently recaptured

by the NYSDEC. Although the higher PIT tag shedding rates observed by the NYSDEC may be attributed solely to tag loss, malfunctioning RFID tag readers may also explain the increased incidence of PIT tag loss by the NYSDEC; however, this phenomenon was not quantified. Regardless, because PIT tag shedding was so low I assumed that PIT tag shedding was constant across tagging agencies, which seemed more appropriate than assuming absolutely no PIT tag loss for some agencies.

Of the evaluated tag shedding models, two models had AIC differences less than 3.0 (Table 2.2). The best-performing model (i.e., the model with the lowest AIC value) had tagging-method specific parameters for jaw tag shedding probabilities. The next best performing model had tagging-agency specific parameters. The AIC difference for the tagging-method model versus the tagging-agency model was approximately 2.1, indicating fairly similar levels of support for these two models. The next best performing model had tagging-method and tag-size specific parameters for jaw tag shedding models; however, the AIC difference for this model was 5.7 relative to the tagging-method model indicating relatively little support for this model (Table 2.2). All other models had AIC differences greater than 30.0, indicating virtually no empirical support for these models. I did attempt to fit a tagging-agency×tag-size specific model, but this model had convergence issues that could not be resolved and as a result parameter estimates for this model were not available.

Based on the estimated parameters for the jaw-tagging method model, tagging method 1 (tag end inserted through the flesh around the maxillary or mandible and the ends overlapped and crimped with a pair of pliers) had higher immediate retention and lower chronic shedding rates than method 2 (Table 2.3). Likewise, the tagging agencies that used method 1, MDNR and NYSDEC, had higher immediate retention and lower chronic shedding rates than the ODNR,

which used method 2. The model-averaged parameter estimates for immediate jaw tag retention were similar (range 95-99%) among the tagging agencies; however, there was considerable variation among the tagging agencies with respect to chronic tag loss. Instantaneous jaw tag shedding rates were highest for ODNR (0.28), followed by MDNR (0.08) and NYSDEC (0.07) (Table 2.3). Using these model-averaged parameter estimates of immediate tag retention and chronic tag shedding, the probability that a jaw tag was retained 1, 2, and 3 years after tagging for MDNR applied tags was 92, 85 and 79%, respectively (Figure 2.3). The probability that a jaw tag was retained 1, 2, and 3 years after tagging for the NYSDEC was 93, 87 and 81%, respectively and the probability that a jaw tag was retained 1, 2, and 3 years after tagging for the ODNR was 72, 55, and 42%, respectively (Figure 2.3). For the most part, the model-averaged tag shedding models fit the observed tag loss rates well (Figure 2.3). The only obvious disparity between the observed and predicted probabilities of retention was observed for fish at liberty for 3 years for the NYSDEC model. However, this disparity may have been caused by a low number of recaptures ($n=10$) observed 3 years after release. As for PIT tag shedding, immediate PIT tag retention was estimated to be 99% (95% CI: 99-100%), with an instantaneous shedding rate of 0.03 (95% CI: 0.02-0.05).

Tag Reporting Rates

During the 1990 and 2000 high-reward tagging releases, 1,551 high-reward and 11,748 standard jaw tags were released at various spawning sites in the western and eastern basins of Lake Erie (Table 2.4). The ratio of standard: reward tags released in the western basin of Lake Erie in 1990 and 2000 was 7:1 and 9:1, respectively; in the eastern basin the ratio was 8:1 in 2000. The majority of tags released (92%) and harvested (92%) during the reporting rate studies

originated from western basin tagging sites. Overall, the reporting rate ratio for tags released in the western basin in 1990 and subsequently reported by the recreational fishery (1.7:1) was 29% higher than the commercial fishery (1.2:1). In 2000, the recreational fishery reporting rate ratio was 81% higher (3.3:1) than the commercial fishery (0.6:1). For tags released in the eastern basin in 2000 the reporting rate ratio was 3.2:1 for the recreational fishery. There were only three high-reward and two standard jaw tags returned by the commercial fishery for fish tagged in the eastern basin of Lake Erie; thus I did not attempt to estimate reporting for this fishery component from fish tagged in this basin.

Of the evaluated tag reporting models, two models had AIC differences less than 3.0 (Table 2.5). The model with the lowest AIC value had a tagging-year×fishery fixed effect and a tagging-year×fishery×recapture year random effect. The next best performing model had a tagging-year×tagging-basin×fishery fixed effect and a tagging-year×tagging-basin×fishery×recapture year random effect (Table 2.5). The AIC difference for the best performing model compared to the next performing model was approximately 0.5, suggesting both models had nearly equal probability of being the best model. The next best performing models had fishery, tagging-basin×fishery, or tagging-year×tagging-agency×fishery fixed effects; the AIC differences for these models ranged from 3.7 to 5.8 (Table 2.5). The worst performing models had tagging-agency×fishery, tagging-basin, or tagging-agency as fixed effects, which had AIC differences in excess of 30 (Table 2.5). Models with tagging-year or tagging-year×tagging-basin fixed effects did not converge during the fitting process.

Because there was more than one model with AIC differences less than 3.0, model averaging was used to estimate reporting rates based on the results of the tagging-year×fishery and tagging-year×tagging-basin×fishery models. Based on these model-averaged estimates, the

reporting rate of jaw tags was on average (without added random effects) lower in the 2000s than in the 1990s for both basins and fishery components (Figure 2.3). For the western basin, reporting rate for the commercial fishery was on average (without added random effects) lower than for the recreational fishery in the 1990s (17% vs. 55%) and 2000s (10% vs. 33%; Figure 2.3). Recreational fishery reporting rates in the 2000s on average (without annual random effects) was slightly higher (39% vs. 33%) in the eastern basin than in the western basin (Figure 2.3). Uncertainty in the tag reporting rates was greater for the recreational fishery than for the commercial fishery based on the widths of confidence intervals around the annual reporting rate estimates (Figure 2.3). Uncertainty in the tag reporting rates for the recreational fishery in the western basin was similar to the uncertainty for the recreational fishery in the eastern basin (Figure 2.3).

Discussion

Isermann and Knight (2005) noted that there are a variety of factors that can influence tag shedding, including attachment technique, tag construction, fish behavior, recapture method, and tag size. In the present study, I was able to evaluate the influence of some, but not all, of the factors Isermann and Knight (2005) identified. Based on my results, tag size did not appear to have a large effect on tag shedding, however, tag attachment method did. Both NYSDEC and MDNR use the method 1 approach (tag end inserted through the flesh around the maxillary or mandible and the ends overlapped firmly with a pair of pliers) for attaching tags, while ODNR and OMNR use the method 2 approach (tags crimped onto the mandible with a specialized pair of pliers). Based on predicted retention probabilities, retention of NYSDEC and MDNR applied tags after only three years at liberty were approximately twice that of tags applied by ODNR

personnel. Newman and Hoff (1998) theorized that jaw tag shedding could be minimized if the ends of the tags were slightly overlapped prior to crimping. The results of my research lends strong support to this suggestion and I recommend that future jaw tag studies use the method 1 approach for applying tags in order to reduce tag loss.

While the influence of attachment method on tag shedding was clearly evident, the fact that the tagging-agency model had moderate support based on AIC values suggests that perhaps subtle variations in how tags are applied can also influence tag shedding. Even though NYSDEC and MDNR used the same general method for attaching tags, the results of the tagging-agency model suggested that NYSDEC applied tags had lower (0.05 vs. 0.10) chronic shedding rates than MDNR applied tags. At this point, it is unclear what might lead NYSDEC applied tags to have lower chronic shedding rates. One major difference in how NYSDEC and MDNR applied tags was that NYSDEC personnel applied jaw tags exclusively to the mandible of fishes except those > 650 mm, while MDNR personnel applied tags to both the maxillary and mandible of fishes. This suggests that tag shedding could perhaps be minimized by applying tags exclusively to the mandible. However, there could be other subtle variations in how NYSDEC and MDNR applied tags that could also explain the differences in chronic shedding observed between the agencies, such as how firmly the ends are overlapped or where the tags are inserted through the jaw. The present study was not designed to evaluate such subtle differences in tagging methods or differences in shedding between maxillary and mandible applications. To further improve understanding of jaw tag shedding, it may be worthwhile for future studies to attempt to address how subtle variations in tagging and maxillary versus mandible tagging can affect jaw tag loss.

My finding that tag shedding was not greatly affected by tag size differed from the results from other jaw tag studies that have been conducted on Walleyes. Einhouse and Haas (1995)

and Isermann and Knight (2005) each found retention to be higher in size-12 than in size-10 jaw tags. However, Newman and Hoff (1998) found size-8 (inside diameter: 6.75 mm) jaw tags to have better retention than size-10 (inside diameter 8.33 mm) tags for Walleyes tagged in Lake Escanaba, Wisconsin. Newman and Hoff (1998) noted that perhaps the size-10 tags they used in their research were not large enough for some of the larger fish that were tagged as a part of their study. Although I did not find tag size to have a large influence on tag shedding, I do not necessarily discount the findings of these other studies as there are likely strong interactions between tag size, fish size, growth rates, and application methods that could have influenced tag loss.

As previously indicated, there has been wide discrepancy in the results of studies that have attempted to quantify jaw tag shedding in Lake Erie Walleyes. The results of the present research may provide some explanation as to why these discrepancies have been occurred. Based on the results of the current study, one would expect that tag shedding would have been greater in the Isermann and Knight (2005) study (tagged by ODNR personnel) than in the Einhouse and Hass (1995) study (tagged by NYSDEC personnel), which indeed was the case. Overall, Einhouse and Hass (1995) observed an approximately 28% shedding rate one-year after tagging, while Isermann and Knight (2005) observed an approximately 43% shedding rate. The shedding rates observed by both studies after one year at liberty were higher than what the current study predicted, although this could be a result of their using fin clipping and punching to secondarily mark their fish, whereas PIT tags were used to double tag fish for this study. Fin clipping for assessing chronic shedding can be problematic as complete fin regeneration can occur relatively quickly after clipping (Eipper and Forney 1965; Deroba et al. 2007). Additionally, natural abrasions on fins can be easily confused for partial fin clips (Guy et al.

1996), which could lead to an overestimation of tag shedding as it might be concluded more fish had lost tags than what actually had occurred. The injection of PIT tags subcutaneously in the isthmus served as an excellent secondary tagging method for evaluating jaw tag loss and I highly recommend this tag type and approach for evaluating tag shedding. As has been found in other studies (Prentice et al. 1990; Gries and Letcher 2002; Rude et al. 2011), retention of PIT tags was excellent and after 3 years at liberty, retention was still predicted to be in excess of 90%. As previously noted, most of the PIT tag loss observed in this study was from fish tagged by the NYSDEC. I do not know why PIT tag loss was higher for this agency compared to the other agencies as the same tagging method was used by all agencies; however, Buzby and Deegan (1999) noted that PIT tag retention rates can vary among tagging crews. Additionally, differences in PIT tag reader efficiencies have been observed in previous studies (Fuller et al. 2008). During the course of the current study, NYSDEC personnel occasionally experienced difficulties with the PIT tag reader (D. Einhouse, personal observation). Whether there was a difference in the efficiency of the NYSDEC PIT tag reader than those used by other agencies is not presently known, but if so could explain the higher PIT tag shedding rates observed in this study.

Previous jaw tag shedding studies that have been conducted on Lake Erie Walleyes have assessed tag loss to one year after tagging; in the current study I estimated tag loss to three years after tagging. A common belief with tagging programs is that at some point shedding rates stabilize. For example, if a tag is retained after the first year, that tag will be retained indefinitely. Perhaps this is one reason why jaw tag shedding studies have generally only lasted one year. From my research, however, I saw little indication of tag shedding stabilizing even after three years of tagging. This may have important bearing on the LEWTP, particularly for

ODNR tagged fish, as based on my estimates in as little as five years more than 75% of jaw tagged fish will have lost their tags, which if unaccounted for could have large impacts on estimated mortality rates. Considering that it is not uncommon for Lake Erie Walleyes to live upwards of 15 to 20 years (C. S. Vandergoot, unpublished data), conducting even longer tag shedding studies than what was conducted here may be worthwhile to determine if shedding rates stabilize or even accelerate as time-at-liberty following tagging increases.

My finding that tag reporting rates of Lake Erie jaw tagged Walleyes varied both spatially and temporally matches findings from studies conducted on species such as Red Drum *Sciaenops ocellatus* (Denson et al. 2002) and Atlantic Cod *Gadus morhua* (Cadigan and Bratney 2006). In general, variable tag reporting rates are common in exploited fish populations (Pollock et al. 2001; Polacheck et al. 2006; Taylor et al. 2006; Cadigan and Bratney 2006), even though they are frequently assumed to be constant over both space and time in tagging models. The high-reward tagging studies conducted with Lake Erie Walleye provided a unique opportunity to compare recreational and commercial fishery reporting rates, which to my knowledge is not routinely done [see Bratney et al. (2010) for an exception]. For both tagging periods, tag reporting rates for the recreational fishery were higher than the commercial fishery. This observation is opposite to the observations of Bratney et al. (2010) who found that reporting rates for commercial fishers were higher than recreational fishers for the inshore Atlantic Cod fishery in Newfoundland. Several studies have theorized as to why fishers may be more apt to report tags than others (Densen et al. 2002; Polacheck and Hearn 2003; Schmalz et al. 2004; Cadigan and Bratney 2006; Taylor et al. 2006). In general, recreational fishers are supportive of tagging studies because they derive personal satisfaction from the experience of catching a tagged fish and have a concern for the management of the fishery which serves as sufficient incentives for

reporting tags (Schmalz et al. 2004; Taylor et al. 2006). However, angler ambivalence leading to reduced cooperation may cause recreational fishers to neglect reporting tagged fish when caught (Denson et al. 2002). For commercial fishers, the perception that reporting tags may adversely impact their financial interests (Polacheck and Hearn 2003) or the lack of a financial incentive (Taylor et al. 2006) may deter them from reporting harvested tagged fish. Regardless of the motives, the disparity in reporting rates between commercial and recreational fishers underscores the need for fishery specific reporting rates when estimating mortality parameters via tag returns for the Lake Erie Walleye as well as other exploited fish populations.

Similar to the variable reporting rates observed between fisheries, the degree of precision in the estimates also varied between fisheries in the current study. Denson et al. (2002) suggested that due to a lack of novelty, individuals who caught fewer fish were more likely to report tags compared to those who caught them frequently. While this phenomenon may explain why the reporting rates were higher for the recreational fishery compared to commercial fishery, it also may provide some insight into the precision of these estimates. Unlike the recreational fishery where access is open, the harvest of Walleye in the commercial fishery is restricted to license holders who retain a portion of the commercial quota (Cowan and Paine 1997; Vandergoot et al. 2010). Because there are fewer commercial than recreational fishers, individual commercial fishers had a higher probability of harvesting a tagged fish during the course of the current study than a recreational fisher. Thus, for the commercial fishery, the probability that an individual tag is reported may be contingent upon previous recaptures (i.e., lower variability in reporting rates), whereas in the recreational fishery tag returns may be independent of each other due to individual reporting tendencies (i.e., higher variability in reporting rates). Therefore, it appears as if individuals from the commercial fishery report tags

in a consistent manner; however, similar to the recommendations of Denson et al. (2002) and Brenden et al. (2010), additional research is needed to further understand individual reporting tendencies for Lake Erie fishers.

The decline in reporting rates for both fisheries from the 1990 and 2000 high-reward tagging experiments is possibly related to fisher apathy of the LEWTP (Hoenig et al. 1998; Denson et al. 2002). The tagging program has been in effect for more than 20 years and it is possible that anglers may be unaware of the valuable information that has been gathered from this program or how management of the Lake Erie Walleye fishery has benefitted from the program. As noted by Pollock et al. (2001) there are steps that can be taken to combat angler apathy to a tagging program and stimulate anglers' desire to return tags. Given the length of time this tagging has been conducted on Lake Erie (i.e., since 1990), it may be worthwhile to implement some of the recommendations proposed by Pollock et al. (2001) if this program continues into the future. This may include adjustments to the amount of reward offered for tags, alternative methods of advertising the tagging program, and better dissemination of how the results from the program are aiding management of the fishery.

The Lake Erie Walleye population is generally considered to be comprised of eastern and western basin spawning stocks (Einhouse and MacDougall 2010; Vandergoot et al. 2010). Although Stepien et al. (2010) showed that there can be substantial genetic variation among Walleye spawning aggregations within the western basin, fish originating from the western basin exhibit similar inter- and intra-basin movement patterns (Wang et al. 2007). Consequently, for population modeling purposes, mortality parameters for the western basin spawning aggregations are estimated separately from eastern basin spawning aggregations as fish from the eastern basin exhibit little inter-basin movement (Einhouse and MacDougall 2010). Currently for the western

basin stock, mortality parameter estimates are based on pooled tag recoveries across basins (Walleye Task Group 2011). However, based on the findings of my research, it may prove useful to separate out western and eastern basin fishery components to account for differences in tag reporting rates between the basins.

One issue concerning reporting that this study did not address was tag detection (i.e., the probability of detecting a tagged fish) in either fishery component. Jaw tag detection rates for both commercial and recreational fisheries in Lake Erie are unknown; however, tags are sometimes reported to agency personnel by fish processors, implying that the fisher who caught the fish either failed to recognize the tag or recognized the tag but did not remove it and thus the tag would otherwise have gone unreported. A similar phenomenon has been observed in the coastal Cod commercial fishery in Iceland, where 20% of the tag returns were from fish processors (Björnsson et al. 2011). Björnsson et al. (2011) reported improved detection and reporting rates for double-tagged coastal cod compared to single-tagged fish and recommended that future tagging studies adopt a strategy of double-tagging all fish to increase tag detection. While initially double tagging may seem a logical strategy to incorporate into the LEWTP, several studies have demonstrated reduced growth and survival rates in fish tagged with single jaw tags (DeRoche and Bond 1955; MacCrimmon and Robbins 1979; Zerrenner et al. 1997), so while double jaw tagging may improve detection rates, tagging mortality could also increase as a result.

In conclusion, the most recent natural mortality rate for Lake Erie Walleyes was estimated assuming 100% retention of jaw tags and a constant non-reporting rate between the fisheries and among years. Because inaccurate estimates of tag shedding and reporting can lead to significant errors in mortality and exploitation estimates (Pollock et al. 2001; Miranda et al.

2002; Isermann and Knight 2005; Brenden et al. 2010), the accuracy of the current natural mortality rate estimates should be considered suspect and I highly recommend that tag recovery data from the LEWTP be reanalyzed taking advantage of the tag shedding and reporting rate estimates that have resulted from this research. This also draws into the question the accuracy of current estimates of fishing mortality rates for the Lake Erie Walleye stocks. Inaccurate estimates could lead to more harvest on the stocks than what they can sustain and ultimately lead to stock collapse (Myers et al. 1996, 1997). The importance of reanalyzing the data from the LEWTP cannot be overemphasized given the ecological and economic importance of the Lake Erie Walleye fishery.

APPENDIX

Table 2.1.—Number of Walleye double-tagged (*N*) by jaw tag size (size-10 and size-12) between 2005 and 2007 by the Michigan Department of Natural Resources (MDNR), New York State Department of Environmental Conservation (NYSDEC), Ohio Department of Natural Resources (ODNR) and Ontario Ministry of Natural Resources (OMNR) to assess jaw tag retention. Also shown are the number of Walleyes recaptured with both jaw and passive integrated (PIT) tags present, a jaw tag only, or a PIT tag only during each recovery period (0= within 21 d, 1= 1 year at liberty, 2= 2 years at liberty and 3= 3 years at liberty).

Agency	Jaw size	Tags retained	<i>N</i>	Recaptures by recovery period			
				0	1	2	3
MDNR	10	Jaw, PIT	833	46	5	0	0
		Jaw only		0	0	0	0
		PIT only		0	0	0	0
	12	Jaw, PIT	3,657	220	89	12	0
		Jaw only		0	0	0	0
		PIT only		2	11	1	0
NYSDEC	10	Jaw, PIT	3,767	116	128	41	9
		Jaw only		1	10	3	1
		PIT only		2	9	8	0
	12	Jaw, PIT	212	6	1	0	0
		Jaw only		0	0	0	0
		PIT only		0	1	0	0
ODNR	10	Jaw, PIT	2,949	42	46	12	0
		Jaw only		0	1	0	0
		PIT only		2	21	7	1
	12	Jaw, PIT	2,760	37	18	2	0
		Jaw only		0	0	0	0

Table 2.1.(cont'd)

		PIT only		2	2	4	0
OMNR	10	Jaw, PIT	732	0	3	0	0
		Jaw only		0	0	0	0
		PIT only		0	1	0	0
	12	Jaw, PIT	785	4	8	1	0
		Jaw only		0	0	0	0
		PIT only		0	0	0	0

Table 2.2.—Ranking of models fit to the Lake Erie Walleye tag shedding data. Shown are the number of estimated parameters (K), AIC values (AIC), AIC differences (Δ AIC), and AIC weights (w_i) for each fitted model.

Model	K	AIC	Δ AIC	w_i
Tagging method	6	567.6	0.0	0.71
Tagging agency	8	569.7	2.1	0.25
Tagging method×jaw tag size	10	573.3	5.7	0.04
Null model	4	597.9	30.3	0.00
Jaw tag size	6	601.6	34.0	0.00

Table 2.3.—Immediate retention (i.e., < 21 d post release; ρ_A) and chronic instantaneous (annual) shedding rate (θ_A) estimates for the double-tagging experiments conducted between 2005 and 2009 by the Michigan Department of Natural Resources (MDNR), New York State Department of Environmental Conservation (NYSDEC) and Ohio Department of Natural Resources (ODNR) in Lake Erie. The parameter estimates were calculated by model averaging the parameter estimates from the tagging method and tagging agency shedding models. The model-averaged 95% confidence interval for each parameter estimate is shown in parentheses.

Model	Parameter	Agency		
		MDNR	NYSDEC	ODNR
Tagging method	ρ_A	0.99 (0.98-1.00)	0.99 (0.98-1.00)	0.95 (0.89-0.99)
	ϕ_A	0.07 (0.04-0.10)	0.07 (0.04-0.10)	0.28 (0.17-0.40)
Tagging agency	ρ_A	0.98 (0.95-1.00)	0.99 (0.98-1.00)	0.95 (0.89-0.99)
	ϕ_A	0.10 (0.05-0.21)	0.05 (0.02-0.09)	0.28 (0.17-0.40)
Model average	ρ_A	0.99 (0.97-1.00)	0.99 (0.97-1.00)	0.95 (0.89-0.99)
	ϕ_A	0.08 (0.04-0.12)	0.07 (0.04-0.10)	0.28 (0.17-0.40)

Table 2.4.—Number of Walleye tagged and released by tagging with high-reward and standard jaw tags in the western and eastern basins of Lake Erie during 1990 and 2000. The number of tags returned between 1990 and 2009 for each cohort by commercial and recreational fisheries, respectively, is shown in parentheses.

Release year	Tagging site	Tag type	
		Reward	Standard
Western basin			
1990	Hen/ Chick Islands	400 (57, 44)	1,971 (71, 86)
	Sandusky Bay	149 (2, 14)	1,344 (7, 81)
	Sugar Rock	178 (13, 39)	1,333 (17, 133)
	Raisin River	218 (23, 58)	1,675 (23, 58)
2000	Hen/ Chick Islands	115 (31, 5)	1,091 (23, 33)
	Sandusky Bay	162 (5, 15)	1,460 (6, 37)
	Raisin River	208 (33, 45)	1,874 (14, 143)
Eastern basin			
2000	Lackawanna Shoreline	29 (1, 7)	239 (0, 23)
	Van Buren Bay	92 (2, 18)	761 (2, 57)

Table 2.5.—Ranking of models fit to the Lake Erie Walleye tag reporting data. Shown are the number of estimated parameters (K), AIC values (AIC), AIC differences (Δ AIC), and AIC weights (w_i) for each fitted model.

Model	K	AIC	Δ AIC	w_i
Tagging year×fishery	4	369.0	0.0	0.47
Tagging year×tagging basin×fishery	5	369.5	0.5	0.37
Fishery	3	372.7	3.7	0.07
Tagging basin×fishery	4	373.1	4.1	0.06
Tagging year×tagging agency×fishery	7	374.8	5.8	0.03
Tagging agency×fishery	6	380.2	11.2	0.00
Tagging year×tagging basin	3	427.8	60.9	0.00
Tagging year	2	434.1	65.2	0.00
Tagging basin	3	435.7	66.7	0.00
Null model	2	439.8	70.8	0.00
Tagging agency	5	440.8	71.8	0.00

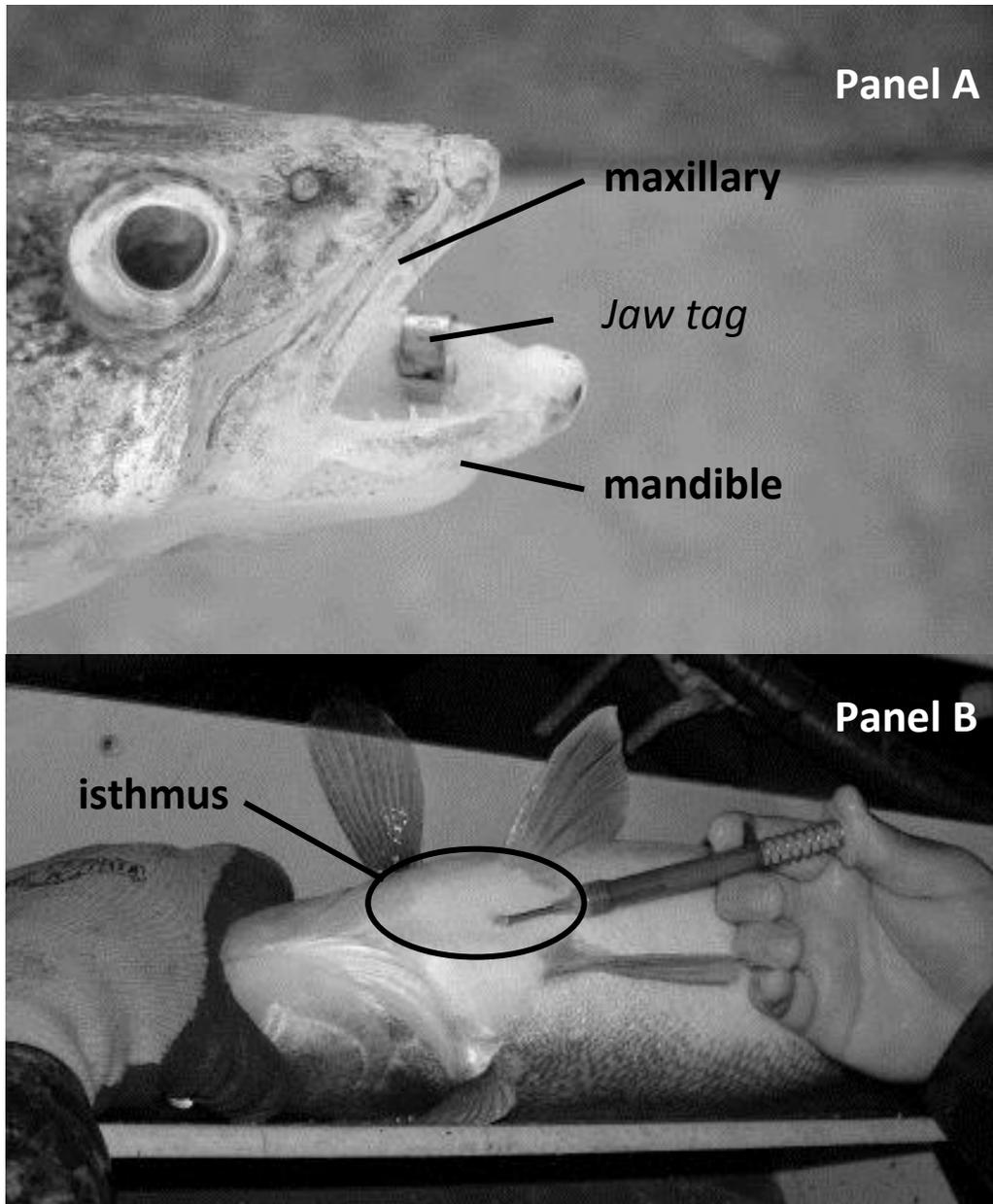


Figure 2.1.—Photographs of jaw and passive integrated transponder (PIT) tag placement. Panel A shows where the jaw tags were placed on the mandible or maxillary and panel B shows a tagging needle injecting a PIT tag subcutaneously.

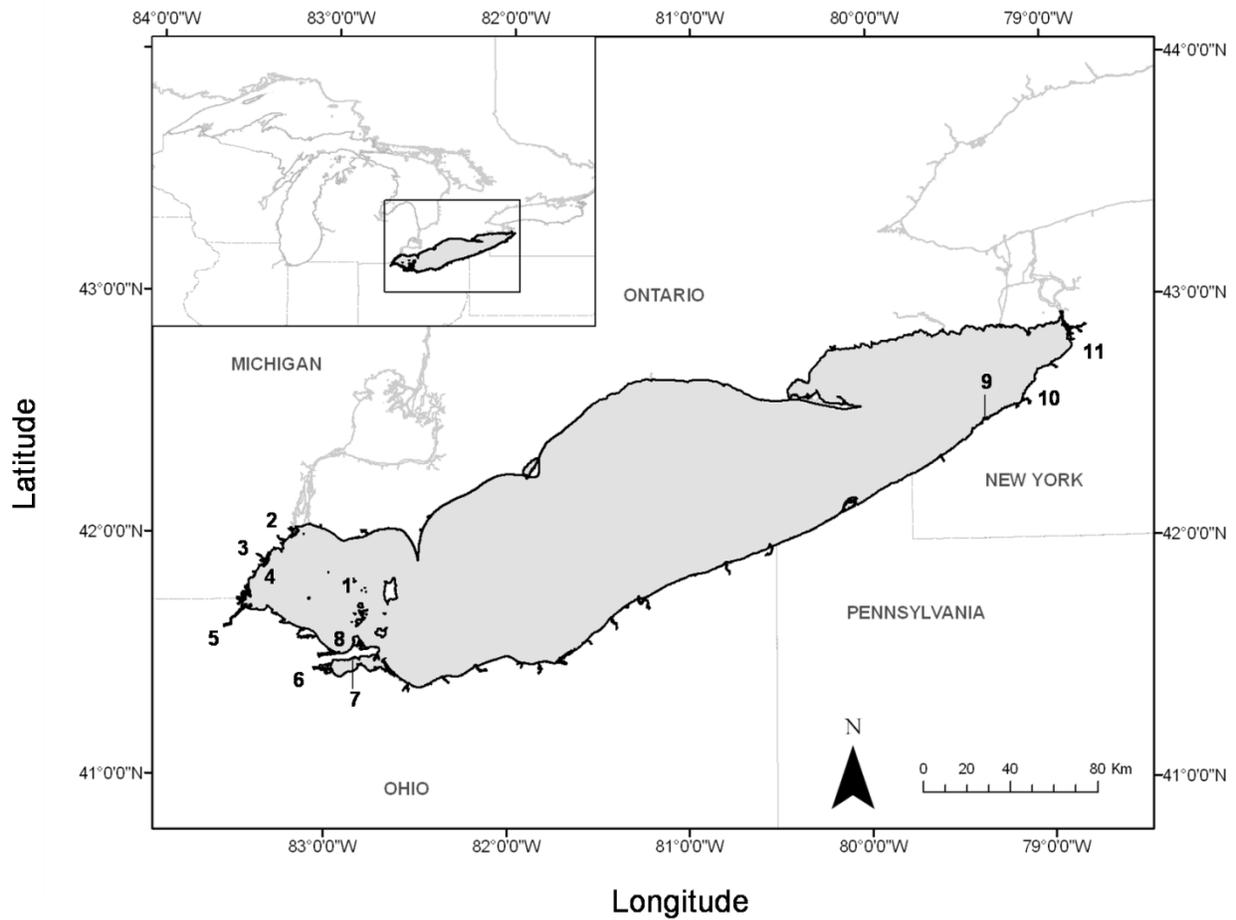


Figure 2.2.—Spawning populations of Walleye in Lake Erie used in the double tagging and high reward tagging experiments used to estimate jaw tag shedding (†) and reporting rates (*). Walleye were tagged in the western basin of Lake Erie by the Ontario Ministry of Natural Resources (1= Hen/ Chick Islands^{†*}), Michigan Department of Natural Resources (2= Huron River[†], 3= Rasin River^{*}, and 4= Monroe[†]), Ohio Department of Natural Resources (5= Maumee River[†], 6= Sandusky River[†], 7= Sandusky Bay^{†*} and 8= Sugar Rock^{*}) and in the eastern basin by the New York State Department of Environmental Conservation (9= Van Buren Bay^{†*}, 10= Cattaraugus Creek^{*} and 11= Lackawanna Shoreline^{*}).

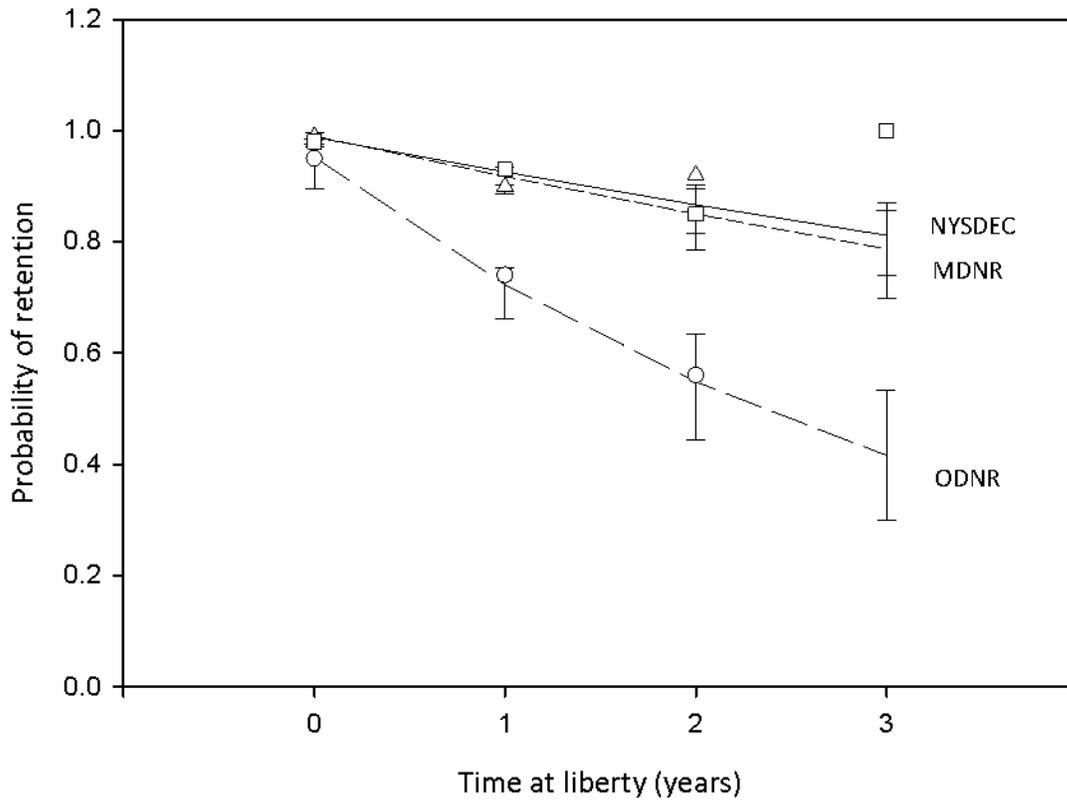


Figure 2.3.—Probability of retention for 0, 1, 2, and 3 years at liberty for jaw tags applied by the Michigan Department of Natural Resources (MDNR; short dashed line), New York State Department of Environmental Conservation (NYSDEC; solid line), and Ohio Department of Natural Resources (ODNR; long dashed line). Error bars are 95% confidence intervals for the predicted tag shedding rates at year 0, 1, 2, and 3 for each agency. Observed tag retention rates, based on recaptures observed for each time period, are shown for the MDNR (open triangles), NYSDEC (open squares), and ODNR (open circles) agencies.

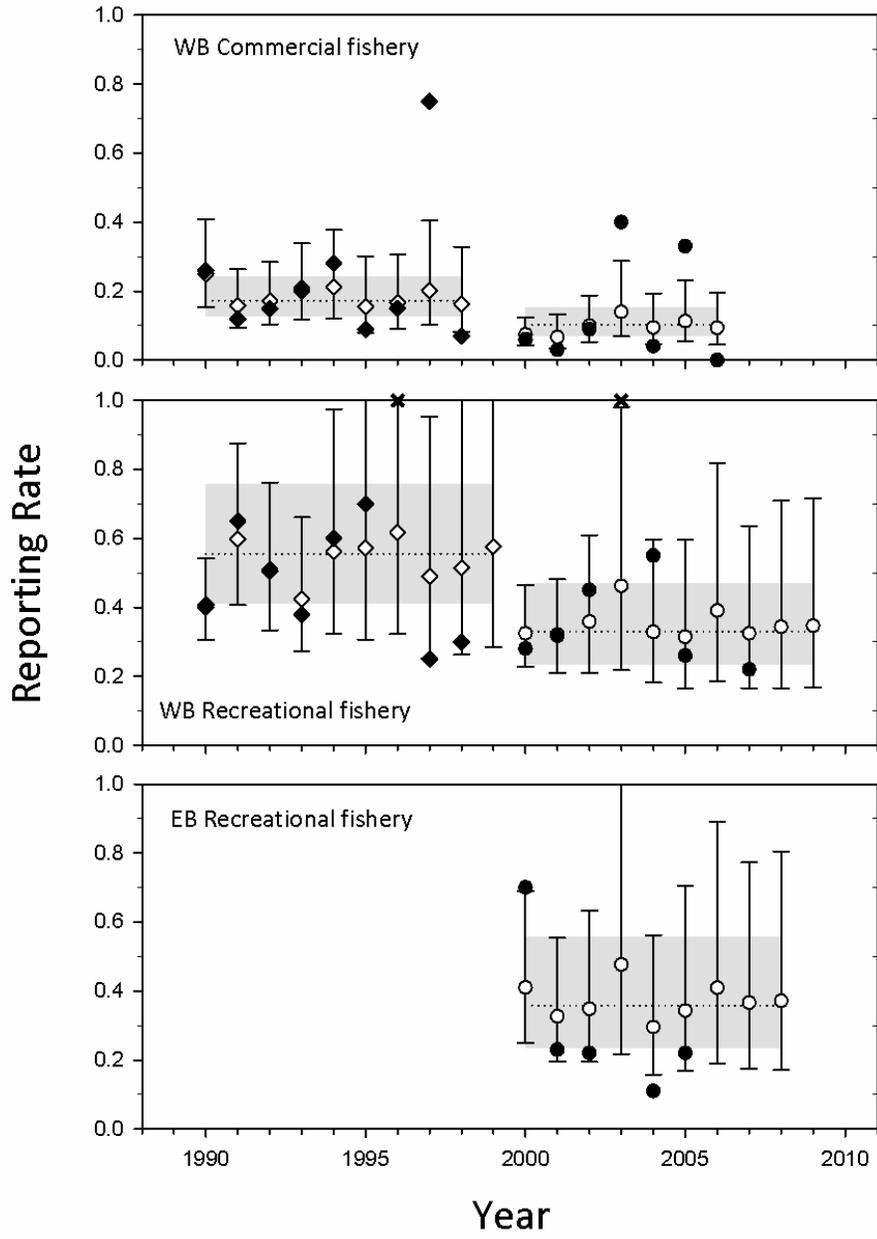


Figure 2.4.—Model averaged annual reporting rates, with associated 95% confidence intervals, for the commercial and recreational fisheries for the 1990 (diamonds) and 2000 (circles) high reward tagging studies in the western (WB) and eastern (EB) basins of Lake Erie. Darkened symbols for each basin and fishery represent the actual reporting rates as described by Pollock et al. (1991). Reporting rates for the recreational fishery which exceeded 1.0 are represented by an “X” symbol. Dashed lines and shaded areas in each panel indicate the mean reporting rate, and associated 95% confidence intervals, respectively, for each tagging year absent the model random effects.

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CHAPTER 3

SPATIALLY-VARYING POPULATION DEMOGRAPHICS AND FISHERY CHARACTERISTICS OF LAKE ERIE WALLEYE (*SANDER VITREUS*) INFERRED FROM A LONG-TERM TAG-RECOVERY STUDY

Abstract

Although the Lake Erie Walleye (*Sander vitreus*) population exhibits complex spatial structuring, the extent to which population demographics also vary spatially is unknown. Using a spatial tag-recovery model, I estimated region- and age-specific mortalities and regional movement probabilities using recoveries from a jaw-tagging study initiated in 1990. The best performing model based on QAIC comparison had age-group-specific movement probabilities, age- and region-specific natural mortalities, and age-group- and region-specific annual fishing mortalities. Commercial fishing mortalities varied considerably during the study, while recreational fishing mortalities were more static. Natural mortalities of age-5 and older Walleyes were lower than those of younger fish in all regions, with natural mortalities ranging from 0.30 to 0.40 for age-4 and younger fish and 0.13 to 0.27 for age-5 and older fish. In Lake Erie's western basin, age-4 natural mortality was lower than that of age-3 fish. Sensitivity analyses indicated that some natural mortality estimates were sensitive to prior probability distributions assigned to mortality components and assumed movement probabilities in regions where no tagging was conducted. The decline in natural mortalities with age in Lake Erie's western basin matches what has been found for other populations, suggesting that such patterns are perhaps common in exploited Walleye populations. Movement probabilities in the western basin were greater than those in the central/eastern basin. The mortalities and movement probabilities estimated in this study should assist in the parameterization and scaling of a spatially-explicit Lake Erie Walleye assessment model, the development of which has been recommended for lake's quota-management system. My study is believed to be one of the first to apply a spatial-tag recovery model to a freshwater fish population for the estimation of mortality components. I encourage wider use of this method for improving the understanding of how mortality components and movements vary regionally within freshwater systems.

Introduction

Complex spatial structuring is increasingly being recognized as a common attribute of fish populations (Smedbol and Wroblewski 2002; Smedbol et al. 2002; Kritzer and Sale 2004; Small et al. 2005; Dunn and Forman 2011). Spatial structuring can arise genetically from populations comprising multiple local breeding sub-populations that are inter-connected via immigration and emigration (i.e., meta-populations; Levins 1969; Hanski and Gilpin 1991; Kritzer and Sale 2004). The existence of population contingents that differ in life history tactics and ultimately select for differing habitat types, but which does not result in genetic differences, also can give rise to spatial structuring (i.e., contingent structuring; Secor 1999; Kerr et al. 2010; Dunn and Forman 2011).

Regardless of the underlying cause, spatial structuring can be beneficial for long-term population stability and sustainability because it increases resilience to environmental perturbations (Berkeley et al. 2004; Hsieh et al. 2010; Kerr et al. 2010); however, it also poses challenges to fisheries managers. For one, it raises concern about possible extirpation of population components and consequences that this could have on overall population health (Stephenson 1999). Further, detecting whether particular population components require management intervention can be difficult when structuring occurs (Cooper and Mangel 1998; Kell et al. 2009). Some of the highest profile stock collapses that have occurred, such as northern Atlantic Cod (*Gadus morhua*) and Pacific Northwest salmon (*Oncorhynchus* spp.) collapses (Morishima and Henry 1999; Smedbol and Wroblewski 2002), have been attributed partly to population spatial structuring and failure to account for this in management. Failure to account for complex spatial structuring is also believed to have contributed to declines in

Atlantic Herring (*Clupea harengus*) and several North American groundfish stocks (Stephenson 1999; Berkeley et al. 2004).

To date, marine fishes have received much of the attention concerning population spatial structuring, although it also has bearing on management of freshwater fish populations (Zimmerman and Krueger 2009). The Lake Erie Walleye (*Sander vitreus*) population, which supports large and economically important recreational and commercial fisheries in the Laurentian Great Lakes region of North America (Roseman et al. 2013), is one example of a freshwater fish population exhibiting complex spatial structuring. The structuring has been attributed to several factors, including metapopulation dynamics and regional differences in water quality, trophic structure, and incidence of invasive species (Wang et al. 2007; Berger et al. 2012). As is often the case when stock assessment models are developed for spatially structured fish populations (Botsford et al. 2009; Goethel et al. 2011), the statistical catch-at-age (SCAA) model used to set harvest levels as part of the Lake Erie Walleye quota management system has assumed the population is homogenous and well-mixed (Zhao et al. 2011; Berger et al. 2012). Because of the potential for assessment models to produce biased estimates of abundance and mortality for spatially-structured populations (Fournier et al. 1998; Kell et al. 2009; Kerr et al. 2010), Berger et al. (2012) fit an SCAA model with spatially-referenced vulnerabilities and catchabilities to Lake Erie Walleye harvest at age and survey data. This spatial SCAA model was found to perform better than the non-spatial model. Consequently, Berger et al. (2012) recommended the development of a spatially-explicit SCAA model to be used for management purposes.

An important issue that remains unresolved with regard to the Lake Erie Walleye fishery is the extent to which demographics of the population also vary spatially, as this can further

complicate the management of spatially structured populations (Ralston and O'Farrell 2008; Shepard et al. 2011). Two Lake Erie Walleye demographic features that in particular could inform development of a spatially explicit SCAA model are inter-regional movement patterns and regional estimates of natural mortality. When developing spatially explicit assessment models, understanding degree of movement among different regions of a system is considered vital for appropriate scaling of the model (Smedbol and Wroblewski 2002; Goethel et al. 2011). Movement of Walleyes among different regions of Lake Erie was assessed by Wang et al. (2007) based on harvest of fish from a jaw-tagging study; however, their analyses excluded commercial fishery tag returns and did not account for tag shedding, which subsequently was found by Vandergoot et al. (2012) to be quite high for some tagging agencies. Thus, questions remain as to how much movement actually occurs within the lake.

Although natural mortalities generally have been treated as constant in the Lake Erie Walleye SCAA models (Berger et al. 2012), in actuality these rates likely vary regionally, as well as temporally and/or by fish age, due to factors such as disease incidence, predator abundance, environmental conditions, and fishing pressure (Vetter 1988; Hansen et al. 2011). Natural mortalities for Lake Erie Walleyes have previously been estimated (Thomas and Haas 1994, 2000, 2005; Zhao et al. 2011); however, past studies have generally not attempted to estimate regional or age-specific natural mortalities, have not accounted for tag shedding or imperfect tag reporting, and have been based on tagging from only a limited number of sites. Recently, Hansen et al. (2011) found that Walleye natural mortalities declined with fish age in Escanaba Lake, Wisconsin and noted specifically that similarly varying natural mortalities could prove problematic for Lake Erie's Walleye quota-management system. One of the

recommendations from their study was wider consideration of the degree to which Walleye mortalities varies within populations to help inform management decisions (Hansen et al. 2011).

Here, I estimate regional- and age-specific movement and mortality components for Lake Erie Walleyes using data from a lakewide long-term jaw-tagging study. My aim was to provide movement and mortality information that could be used in the development of a more spatially explicit assessment model as part of the Lake Erie Walleye quota-management system. A secondary objective was to demonstrate the application of spatial tag-recovery models to a freshwater fish population in the hopes that it might encourage additional use of these models in freshwater systems. Wider adoption of spatial tag-recovery models would prove beneficial for gauging the extent to which freshwater fish populations are spatially structured and assist in formulating management policies that protected this structuring.

Methods

Tagging Experiment Study Design

Lake Erie is the shallowest and most productive of the Laurentian Great Lakes. The lake consists of three distinct basins (Figure 3.1; Ryan et al. 2003). The western basin is the shallowest with a mean depth of 7.4 m, followed by the central (mean depth = 18.5 m) and eastern (mean depth = 24.5 m) basins. Most of the lake is classified seasonally as coolwater (20-28° C) with coldwater (<20° C) habitat limited to the eastern basin and portions of the central basin (Hokansen 1977). For the purpose of this study, Lake Erie was partitioned into four regions (Figure 3.1). The western basin was partitioned into two regions (regions 1 and 2) corresponding to waters under Canadian (i.e., Ontario; region 1) and U.S. (i.e., Michigan and Ohio; region 2) management authority. Similarly, the combination of central and eastern basins

(hereafter referred to as central/eastern basin) were partitioned into two regions (regions 3 and 4) corresponding to waters under Canadian (i.e., Ontario; region 3) and U.S. (i.e., Ohio, Pennsylvania, and New York; region 4) management authority. Total mortality rates between Ontario and U.S. waters were believed *a priori* to differ because in Ontario waters Walleyes are exploited by commercial and recreational fisheries, while in U.S. waters only recreational fishing occurs. Finer-scale partitioning (e.g., by quota management units) was not possible because tagging was generally limited to the lake's western and eastern basins. The central basin was combined with the eastern basin for partitioning because habitat and fishery characteristics are more similar to the eastern basin than the western basin. Because of the possibility of tagged fish moving to the Huron-Erie corridor (i.e., Detroit River, Lake St. Clair, St. Clair River) or Lake Huron, these areas were combined into an additional region (region 5; Figure 3.1).

Between 1990 and 2007, mature Walleyes were collected from tributary and open-water reef spawning locations during the spring, affixed with a jaw tag (butt-end style, constructed of the alloy Monel®) to the mandible or maxillary, and released. Tagging in region 1 was conducted by the Ontario Ministry of Natural Resources (OMNR). Tagging in region 2 was conducted by both the Michigan Department of Natural Resources (MDNR) and Ohio Department of Natural Resources (ODNR). Tagging in region 4 was conducted by the New York State Department of Environmental Conservation (NYSDEC). Tagging in regions 3 and 5 did occur during the course of this study; however, releases were generally few in number and tagging was sporadic, so recoveries and releases of these tagging efforts were not included in my analyses. Although there were some differences among agencies with respect to tag size and how tags were affixed, tagging was administered consistently within agencies during the course of the study (Zhao et al. 2011; Vandergoot et al. 2012).

Structures for aging Walleyes were not collected at time of tagging, but sex and total lengths were recorded. Ages of tagged fish were thus estimated using year-, sex-, and tagging-basin-specific age-length keys (Ricker 1975). Age-length keys were developed from age estimates determined from scale samples collected during population assessment surveys conducted the fall prior to tagging under the assumption that growth during the winter was limited (C. Vandergoot, unpublished data). Tagged fish were assigned to one of four ages (2, 3, 4, or 5+). Age-5 and older fish were combined into a single age-group to minimize errors associated with ageing Walleyes with scales (Erickson 1983; Isermann et al. 2003).

Estimation Model

Demographic and fishery characteristics for Lake Erie Walleyes were estimated with an age-specific, spatial Brownie model similar to that described in Eveson et al. (2009). The spatial Brownie model described by Eveson et al. (2009) allows for movement of fish among different areas of the system and is parameterized to obtain separate estimates of fishing and natural mortality rates. The full model described in Eveson et al. (2009) included a component for estimating abundances within tagging regions under a closed-population assumption. I did not include this abundance-estimation component in my tagging model as releases did not occur in all regions, thus abundances could only have been estimated for a subset of regions.

Individual tagged cohorts were considered to be agency-, year-, and age-group specific. Recovery probabilities were defined in terms of survival, movement, exploitation, tag reporting, and tag retention, with tag shedding and reporting rates treated as known using the results of Vandergoot et al. (2012). The probabilities of fish from a tagged cohort being harvested in a given year, region, and by a particular fishery were represented as

$$p_{t,a,ty,fy,f} = \begin{cases} \pi_a^k D(u_{a,fy,f}) D(\lambda_{fy,f}) \phi_{t,fy-ty} & fy = ty \\ \pi_a^k D(S_{a,ty}) \dots \pi_{a+(fy-ty)-1} D(S_{a+(fy-ty)-1,fy-1}) \pi_{a+(fy-ty)} D(u_{a+(fy-ty),fy,f}) D(\lambda_{fy,f}) \phi_{t,fy-ty} & fy > ty \end{cases} \quad (1)$$

(see Table 3.1 for a listing and description of all equation symbols used herein). This formulation of recovery probabilities assumed that movement occurs immediately after tagging, which was deemed appropriate given tagged Walleyes are frequently recovered from other regions of the lake shortly after tagging. Exploitations for a given age, year, fishery, and region were modeled as

$$u_{a,fy,f}^k = \frac{s_{a,f} F_{fy,f}^k}{\sum_f s_{a,f} F_{fy,f}^k + M_{a,fy}^k} (1 - S_{a,fy}^k), \quad (2)$$

with survival equal to

$$S_{a,fy}^k = \exp\left(-\left(\sum_f s_{a,f} F_{fy,f}^k + M_{a,fy}^k\right)\right). \quad (3)$$

In regions 1, 3, and 5, Walleyes were exploited by both commercial and recreational fisheries, while in regions 2 and 4 fish were only exploited by recreational fisheries. Fishing mortalities were the product of age-specific relative vulnerabilities (i.e., selectivities) and a fully-selected instantaneous fishing mortality rate that was year, fishery, and region specific. Age-3 and older Walleyes are generally considered fully selected to both commercial and recreational fisheries in Lake Erie (WTG 2011), thus selectivities for these age groups were set equal to 1.0. For age-2 Walleyes, fishery-specific selectivities were estimated as

$$s_{2,f} = \frac{\exp(\theta_f)}{1.0 + \exp(\theta_f)}, \quad (4)$$

which constrained selectivities to be between 0.0 and 1.0. Selectivities for a particular fishery were assumed to be the same for all regions of the lake as fishers generally use similar angling methods throughout the lake.

Movement probabilities of tagged fish were allowed to vary among age-groups but were assumed to be constant across years. Time-varying movements were not considered because this would have greatly increased the number of estimated parameters. Because no tagging was conducted in regions 3 and 5, informative data for estimating movement probabilities for these regions were lacking. As a consequence, movement probabilities for regions 3 and 5 were assumed known. For simplicity, I assumed that if fish moved into regions 3 or 5 then they would remain in those regions until being harvested or dying of natural causes. For regions where movements were estimated, age-group and region-specific movement probabilities were estimated as

$$\pi_a^{k,k'} = \frac{\exp(\gamma_a^{k,k'})}{1 + \sum_{k'=1}^4 \exp(\gamma_a^{k,k'})} \quad k' = 1, \dots, 4$$

$$\pi_a^{k,5} = \frac{1}{1 + \sum_{k'=1}^4 \exp(\gamma_a^{k,k'})}$$
(5)

Tag retention rates for the different tagging agencies were calculated as

$$\phi_{t, fy-ty} = \alpha_t \exp(-\beta_t (fy - ty + 0.5))$$
(6)

When calculating tag retentions, 0.5 was added to the time at large ($fy - ty$) so that rates represented retention at the mid-point of the year. For MDNR, ODNR, and NYSDEC, α_t was assumed to be 0.99, 0.95, and 0.99, respectively, and 0.08, 0.28, and 0.08, respectively, for β_t (Vandergoot et al. 2012). Retention of tags applied by OMNR, which was not quantified by

Vandergoot et al. (2012), was assumed to be the same as that of ODNR due to similar tagging methods.

Reporting rates incorporated in recovery probability calculations were fishery- and region-specific estimates from high-reward tagging studies conducted in 1990 and 2000 (Vandergoot et al. 2012). Specific rates assumed for this research were the model-averaged marginal linear predictors estimated for each region, fishery, and time block (1990 to 1999, 2000 to 2007) in Vandergoot et al. (2012). For recreational fisheries in regions 1 and 5, reporting rates of 0.55 and 0.33 were assumed for the periods of 1990 to 1999 and 2000 to 2007, respectively. In regions 3 and 4, a reporting rate of 0.39 was assumed for the period of 1990 to 2007. For commercial fisheries in regions 1, 3, and 5, reporting rates of 0.17 and 0.10 were assumed for the periods of 1990 to 1999 and 2000 to 2007, respectively. I chose to not use annual reporting rate estimates because high-reward tags were only released twice during the course of the study, thus reporting rates in most years were based on recoveries of only a few tags, which resulted in considerable uncertainty in the reporting rate estimates (Vandergoot et al. 2012). As part of sensitivity analyses, I assessed how mortality and movement estimates changed when annual, as opposed to time-block, reporting rates were incorporated in the recovery probability calculations (see below).

The spatial Brownie model was estimated in AD Model Builder (Fournier et al. 2012). Model parameters ($F_{fy,f}^k$, $M_{a,fy}^k$, θ_f , and $\gamma_a^{k,k'}$) were estimated by highest posterior density estimation. Models were considered to have converged on a solution when the maximum gradient of the parameters with respect to the objective function was less than 1.0×10^{-3} . The objective function consisted of the sum of the negative log-prior components and the negative log-likelihood components corresponding to the recoveries of each tagged cohort of fish.

Multinomial distributions were assumed for the negative log-likelihood components for the recoveries of the tagged cohorts of fish. The negative log-likelihoods for the recoveries of a tagged cohort of fish were calculated (with ignorable constants removed) as

$$L_{t,a,ty} = \left(N_{t,a,ty} - \sum_k \sum_{fy} \sum_f R_{t,a,ty,fy,f}^k \right) \log_e \left(1.0 - \sum_k \sum_{fy} \sum_f P_{t,a,ty,fy,f}^k \right) + \sum_k \sum_{fy} \sum_f R_{t,a,ty,fy,f}^k \log_e P_{t,a,ty,fy,f}^k \quad (7)$$

Log-normal prior probability distributions were assigned to the $F_{fy,f}^k$ and $M_{a,fy}^k$ parameters based on values estimated or assumed in the Lake Erie Walleye SCAA model (WTG 2011). For the $F_{fy,f}^k$ parameters, log-normal priors with medians of 0.165 and log_e-scale dispersions of 0.2 were assumed. For the $M_{a,fy}^k$ parameters, log-normal priors with medians of 0.3 and log_e-scale dispersions of 0.2 were assumed. For the other parameters, diffuse, uniform (on a logit scale) priors were specified to help keep the optimization algorithm from flat parts of the likelihood surface.

Candidate Models and Model Evaluation

Sixteen tag-recovery models were evaluated that differed as to whether natural mortality rates were constant (M) or varied among ages (M_{age}), regions (M_{region}), time blocks ($M_{time\ block}$), or different combinations of these factors ($M_{age,region}$, $M_{age,time\ block}$, $M_{region,time\ block}$, $M_{age,region,time\ block}$), and whether movement probabilities were constant (π) or varied among age groups (π_{age}). For natural mortality, age-specific models assumed that rates differed among each age class, time-block specific models assumed that rates differed among the 1990-1994, 1995-1999, and 2000-2007 time periods, and region-specific models assumed that rates differed among the regions, with the exception that natural mortalities in region 2 were assumed to be the same as that of

region 1 due to the environmental similarity between these regions. For movement probabilities, age-group-specific models assumed that movement probabilities for age-4 and younger Walleyes were different from those of age-5 and older fish.

Overdispersion in the tag-recovery data was evaluated by calculating the variance inflation factor for the global (i.e., most heavily parameterized) model. The variance inflation factor was calculated by dividing the chi-square value of the Pearson goodness-of-fit test for the global model by its degrees of freedom (Burnham and Anderson 2002). The variance inflation factor for the global model was 4.98, suggesting that the tag-recovery data were indeed overdispersed. Consequently, candidate models were evaluated using a quasi-likelihood Akaike information criterion (QAIC) approach (Burnham and Anderson 2002). Standard errors associated with the parameter estimates for all fitted models were increased by the square root of the estimated variance inflation factor to account for overdispersion. Although inflating the standard errors by the square root of the variance inflation factor is an approximation, this has been shown to be a reasonable, although somewhat variable, approach for non-spatial Brownie models (Polacheck et al. 2006; Eveson et al. 2007).

Sensitivity Analysis

Sensitivity analyses were conducted to determine how parameter estimates were affected by assumed movement probabilities for regions 3 and 5 (i.e., regions where no tagging occurred), the prior probability distributions assumed for the natural mortality parameters, and the reporting rates assumed for the different regions and fisheries. The sensitivity analyses involved refitting the best performing model as determined by QAIC comparison with different assumed movement probabilities, prior probability distributions, or reporting rates and evaluating how

model parameter estimates changed. As previously indicated, my assumption when evaluating candidate models was that if fish moved to regions 3 or 5 then they would stay in these regions. As part of the sensitivity analyses, the probabilities of fish remaining in regions 3 or 5 were reduced from 100% to between 0 and 75% (Table 3.2). The probabilities of fish moving from region 3 to regions 1, 2, or 4 were assumed to be equal (keeping in mind that movement probabilities needed to sum to 100%), with the probability of moving to region 5 set at 0%. For region 5, the probabilities of fish moving to regions 1 or 2 for the sensitivity analyses were assumed to be equal, with the probabilities of moving to regions 3 or 4 set at 0%. In terms of sensitivity of parameter estimates to the assumed priors for the natural mortality parameters, I refit the best performing model assuming the medians of the log-normal prior probability distributions equal 0.2 or 0.4. In terms of sensitivity to reporting rates, I refit the best performing model with the model-averaged annual reporting rate estimates for each region and fishery presented in Vandergoot et al. (2012).

Comparison of Fishing Mortality Rates

For comparative purposes, the fishery and region-specific fishing mortality rates estimated in this study were compared with those from the SCAA model currently used as part of the Lake Erie Walleye quota-management system (WTG 2011), as well as with those from the SCAA model with spatially-referenced vulnerabilities and catchabilities described in Berger et al. (2012). Each of the SCAA models were analyzed under two different natural mortality scenarios. The first scenario assumed that the natural mortality rate for all ages was 0.32 (i.e., age-invariant), which is the rate currently assumed in both SCAA models (WTG 2011; Berger et al. 2012). For the second scenario, the natural mortality rates were assumed to be 0.34 for age-2,

0.40 for age-3, 0.35 for age-4 Walleyes and 0.13 for the age-5+ age group (i.e., age-specific). These assumed rates were similar to the values estimated for regions 1 and 2 from the best performing model (see results below). Because the WTG (2011) SCAA model is not parameterized to estimate region-specific fishing mortalities, I assumed that fishing mortalities were directly proportional to fishing effort. Thus, the fishing mortalities estimated from the WTG (2011) SCAA model were multiplied by the proportion of effort expended by each fishery in each region [regions 1 and 2 in my model equate to management unit 1 and regions 3 and 4 equate to management units 2 and 3 in the WTG (2011) model].

Results

Between 1990 and 2007, a total of 109,939 Walleyes were tagged and released with jaw tags, with approximately 80% of releases occurring in the western basin (regions 1 and 2) (Table 3.3). In both the central/eastern and western basins, age-5 and older Walleyes were the most commonly tagged age group (Figure 3.2). Age-2, age-3, and age-4 Walleyes represented 4, 18, and 21% of the fish tagged in the western basin and 3, 6, and 10%, in the central/eastern basin, respectively. A total of 8,658 tags were harvested and reported by commercial and recreational fishers between 1990 and 2007 (Table 3.3). Overall, recreational fishers returned approximately 5.7 times more tags than commercial fishers (7,368 versus 1,290), although this is not reflective of the relative levels of harvest of the fishery components, given that recreational fishery reporting rates have been estimated to be three times greater than commercial fishery reporting rates (Vandergoot et al. 2012).

After accounting for overdispersion, the model with age-group specific movements and age- and region-specific natural mortalities ($\tau_{age}M_{age,region}$) was found to be the best performing

model (Table 3.4). The second best performing model had age-group specific movements and age-specific natural mortalities ($\pi_{age}M_{age}$); however, the QAIC difference for this model was 5.2, suggesting that there was much less empirical support for it being the best model (Burnham and Anderson 2002). All other evaluated models had QAIC differences greater than 13, indicating essentially no empirical support for these models being the best model (Burnham and Anderson 2002).

Recreational and Commercial Fishing Mortalities

Commercial and recreational fishing mortalities for fully-selected age-groups from the QAIC selected model exhibited both spatial and temporal variation. In regions 1 and 3, commercial fishing mortalities generally increased during the early 1990s and plateaued during the mid-1990s (Figure 3.3). For region 1, commercial fishing mortalities peaked at an instantaneous rate of around 0.43, while for region 3 commercial fishing mortalities peaked at around 0.55. In both regions, commercial fishing mortalities subsequently declined during the late 1990s and 2000s, with year-to-year variability in fishing mortalities increasing in the mid- to late-2000s (Figure 3.3). In region 5, commercial fishing mortalities were low throughout the course of this study, with estimates ranging between 0.0 and 0.02 between 1990 and 2007 (Figure 3.4). The commercial fishery selectivity for age 2 Walleyes in all regions was estimated at 0.94 (SE=0.47).

Compared to commercial fishing mortalities, recreational fishing mortality rates were more stable at least for Lake Erie regions. For regions 1 through 4, recreational fishing mortality rates ranged from 0.05 to 0.16 (Figure 3.3). In regions 1 and 2, recreational fishing mortalities were slightly higher during the last 5 years of the study than they were in the 1990s and early

2000s (Figure 3.3). Such increases were not observed for regions 3 and 4. For region 5 (i.e., Lake Huron and the Huron-Erie Corridor), there was considerably more variability in the recreational fishing mortality estimates compared to Lake Erie regions. Instantaneous recreational fishing mortalities in region 5 ranged from 0.10 to 0.37 with an overall mean of 0.18 during the time period of study. The recreational fishery selectivity for age-2 Walleyes in all regions was estimated at 0.50 (SE=0.07).

Natural Mortalities

Natural mortalities from the QAIC selected model were fairly similar across regions particularly for younger ages (Table 3.5). In regions 3, 4, and 5, natural mortalities for age-4 and younger Walleyes ranged between 0.30 and 0.34. In regions 1 and 2, naturally mortality generally declined with Walleye age, the only exception was that age-2 natural mortality was less than that of age-3 Walleyes. The biggest decrease in natural mortalities was between age 4 and age-5 and older Walleyes, Region 5 was the only region where natural mortality was greater for age-5 and older Walleyes than for younger fish. At the basin scale, natural mortalities of age-5 and older Walleyes was lower in the western basin than in the central/eastern basins.

Inter-Regional Movements

In terms of movements, Walleyes in the western basin (regions 1 and 2) were more likely to move to other regions than fish in in region 4 (Table 3.6). For region 1, the probability that age-4 and younger fish remained in the region was 42%, while for age-5 and older fish the probability of remaining in region 1 was 56%. Fish in region 1 were far more likely to move to region 2 than other regions regardless of fish age (Table 3.6). For region 2, the probability of

Walleyes remaining in the region were 79 and 69% for age-4 and younger and age-5 and older fish, respectively. For age-4 and younger Walleyes, the probabilities of moving from region 2 to other regions ranged from 1% (movement to region 3) to 11% (movement to region 5) (Table 3.6). For age-5 and older Walleyes, the probabilities of moving from region 2 to other regions ranged from 4% (movement to region 3) to 14% (movement to region 4) (Table 3.6). The vast majority of Walleyes in region 4 remained in that region regardless of fish age, although when movement occurred Walleyes were most likely to move to region 3 than the other regions (Table 3.6). In terms of basin-level fidelity, (i.e., probability of fish either staying within a region or moving to the other region within a basin), fidelities ranged from 74 to 100% (Table 3.6).

Sensitivity Analyses

Fishing mortalities (Figure 3.4) and movement probabilities (Figure 3.5) were generally insensitive to assumed movement probabilities for regions 3 and 5, assumed prior probability distributions for natural mortality parameters, and assumed reporting rates. The most sensitive parameters were commercial fishing mortalities in region 3 (Figure 3.4), recreational fishing mortalities in region 3 (Figure 3.4), and the age-5 and older movement probabilities in region 1 (Figure 3.5). For example, in region 3 during 1996, instantaneous commercial fishing mortality estimates ranged from approximately 0.40 to 0.52 depending on the assumed movement probabilities (Figure 3.4). Recreational fishing mortalities in region 3 in the 1990s were lower when annual reporting rates were incorporated in the recovery probabilities, although this discrepancy was not evident later in the time series (Figure 3.4). In terms of movement probabilities, the probability of Walleyes staying in region 1 decreased from 56% to around 40% depending on the assumed movement probabilities for regions 3 and 5, while movement to other

regions correspondingly increased. Despite the variation in parameter estimates, results remained qualitatively similar depending on the assumed movement probabilities or prior probability distributions.

Compared to fishing mortalities and movement probabilities, natural mortalities were more sensitive to assumed movement probabilities for regions 3 and 5, assumed prior probability distributions for natural mortality parameters, and assumed reporting rates, at least for some ages and regions. Age-3, age-4, and age-5 and older natural mortalities for regions 1 and 2 were relatively insensitive to movement probabilities, prior probability distributions for natural mortality parameters, and fishery reporting rates (Figure 3.6). The natural mortality estimate for age-5 and older Walleyes in region 4 was also insensitive (Figure 3.6). Conversely, the age-2 natural mortalities for all regions and the age-3 and age-4 estimates for regions 3, 4, and 5 were very sensitive to the assumed medians for the log-normal prior probability distributions on the natural mortality parameters. In essence, the sensitivity analyses indicated that the tag-recovery data were not informative about natural mortalities for these ages and regions and as a consequence the estimates remained centered on the location of the assumed prior probability distributions. The natural mortality estimate for age-5 and older Walleyes in region 5 was insensitive to the assumed prior probability distributions for the natural mortality parameters, but was sensitive to the assumed movement probabilities for regions 3 and 5 (Figure 3.6). As the probability of fish moving out of region 5 increased, the natural mortality estimate for age-5 and older fish decreased (Figure 3.6). The natural mortality estimate for age-5 and older fish in region 3 was sensitive to both the assumed prior probability distributions for the natural mortality parameters and the assumed movement probabilities for regions 3 and 5. Depending on the

assumption, the natural mortality estimate for this age group and region ranged from 0.18 to 0.35 (Figure 3.6).

Comparisons with SCAA Model Estimates

The trends in fishing mortalities estimated from the spatial-tag recovery model were similar to those from the WTG (2011) and Berger et al. (2012) SCAA models; however, there were some notable discrepancies in estimates on an annual basis. For example, although all three models estimated that commercial fishing mortalities increased throughout the 1990s in regions 1 and 3, the fishing mortalities from the spatial tag-recovery model were higher than those from the SCAA models regardless of the assumed natural mortalities (Figure 3.3). Additionally, for both regions the SCAA models estimated a larger decline in commercial fishing mortalities during the late 1990s and 2000s and the year-to-year variability in the estimates were lower than the spatial-tag-recovery estimates (Figure 3.3).

For the recreational fishery in region 2, the magnitude of fishing mortality rates were similar among the models; however, the annual patterns varied between my estimates and the SCAA models (Figure 3.3). The SCAA models, regardless of the assumed mortality rates, suggested that recreational fishing mortalities peaked during the late 1990s and early 2000s and declined during the mid and late 2000s while my model suggested that recreational fishing mortalities in region 2 peaked during the mid and late 2000s (Figure 3.3). In region 4, the annual pattern in recreational fishing mortality rates were similar among the models; however, the estimates derived from my model were consistently, albeit slightly, greater than the estimates from the SCAA models (Figure 3.3).

Discussion

Through spatial tag-recovery analysis of a long-term jaw-tagging study, I found that Lake Erie Walleyes exhibited age and spatial variability in movements and mortality components. Perhaps most notable was that Walleyes in the eastern/central basin were less likely to move to other regions than fish in the western basin. Additionally, natural mortality of Walleyes in Lake Erie's western basin declined with age and, at least for age-5 and older fish, was lower than the natural mortalities in the eastern/central basins. My ability to draw definitive conclusions regarding other aspects of Walleye natural mortalities in Lake Erie or the Huron-Erie corridor and Lake Huron was affected by the sensitivity of mortality estimates to assumptions made during the model fitting process. Some of these assumptions were necessary because of how the original jaw-tagging study was conducted and this information can aid in designing future tagging studies for which spatial movement and mortality components hope to be estimated.

Although recoveries from the jaw tagging that has been conducted on Lake Erie have previously been used to estimate natural mortalities, my study is the most comprehensive to date in terms of estimating age- and region-specific estimates and analyzing lakewide recoveries and releases. Thomas and Hass (1994, 2000, 2005) analyzed western basin recoveries of Walleyes tagged in Michigan waters of Lake Erie since the jaw-tagging program was first initiated. Their estimates of instantaneous natural mortalities pooled across all ages and regions ranged from 0.17 to 0.36 (Thomas and Hass 1994, 2000, 2005), which is similar to the range of natural mortalities estimated in this study. Zhao et al. (2012) analyzed returns from tagging conducted by the NYSDEC in Lake Erie's eastern basin at the Van Buren Bay spawning site and estimated an instantaneous natural mortality rate of 0.22. The natural mortality estimate from Zhao et al. (2012) is comparable to my estimate for age-5 and older Walleyes in the central/eastern basin,

but somewhat lower than my estimates for age-4 and younger fish, although admittedly my estimates for younger fish were highly sensitive to the prior probability distributions for the natural mortality parameters. Zhao et al. (2012) limited their analyses to only fish tagged with the largest jaw tags, which based on the age-length keys developed for my study suggests that they effectively limited their analyses to age-5 and older Walleyes. Thus both the Zhao et al. (2012) natural mortality estimate and my reliable estimate were for older Walleyes, which helps explain why the estimates were so closely aligned.

As previously noted, Hansen et al. (2011) found that natural mortalities decreased with fish age in Escanaba Lake, Wisconsin, which is similar to what I found in the western basin of Lake Erie. Hansen et al. (2011) attributed the decrease in natural mortality with fish age to the possible inverse relationship between natural and fishing mortalities as a result of mortalities being compensatory and to older fish simply being less vulnerable to natural mortality than younger fish. In addition to the explanations offered by Hansen et al. (2011), another possible explanation is that older fish may have behavioral characteristics that result in lower natural mortalities. Lake Erie Walleyes have been identified as highly migratory, with older fish actively seeking areas where thermal regimes are more conducive to growth (Kershner et al. 1999; Wang et al. 2007) despite the increased energetic costs associated with migrating (Northcote 1978; Hinch et al. 2006).

Although variability in age-specific natural mortality rates is commonplace, the precise relationship between mortality rate and ages varies. Beverton and Holt (1957) theorized that natural mortalities should increase with age, at least once fish got past pre-recruit stages, as a result of the physiological costs associated with sexual maturation (Cushing 1975; Moyle and Cech 1996). Positive relationships between mortalities and ages have been observed for species

including Pacific Herring (*Clupea pallasii*; Tanasichuk 2000), Muskellunge (*Esox masquinongy*; Muir 1964), and Lake Trout (*Salvelinus namaycush*; Kennedy 1954). Conversely, inverse relationships between natural mortalities and ages have been observed for several tuna species in the Pacific Ocean (Hampton 2000) and for Striped Bass (*Morone saxatilis*) in Chesapeake Bay (Jiang et al. 2007b). My findings of declining natural mortalities with fish age in the western basin of Lake Erie, in combination with the findings of Hansen et al. (2011) for Escanaba Lake, Wisconsin, suggests that this relationship between natural mortality and age may be a common feature of exploited Walleye populations. Although I found that natural mortalities in region 5 did not decrease with fish age, the sensitivity of natural mortality estimates in this region to assumptions about movement probabilities and prior probability distributions means that the precise relationship between Walleye age and natural mortality in this region remains unclear. Mosindy et al. (1987) reported that natural mortalities of Walleyes in a small Ontario boreal lake increased with fish age, however, this lake was closed to fishing, which, if fishing and natural mortalities are compensatory (Hansen et al. 2011), could explain why the expected relationship was not observed in this lake. Additional studies that estimate age-specific mortalities of Walleyes in populations with varying exploitation levels will be needed to determine how strong of a relationship there might be between natural mortalities and fish age.

There were some notable differences between the fishing mortality rates estimated in this study and those from SCAA models that have been developed for Lake Erie Walleyes. In particular, the commercial fishing mortalities that I estimated were greater than those from the SCAA models regardless of assumed natural mortality rates. In other studies that have compared fishing mortality estimates between assessment and tag-recovery model, deviations between estimates have also been observed (Myers et al. 1996; Ebener et al. 2010; D. G. Fielder personal

communication) and examination of the assumptions associated with the models is necessary to explain the disparity between the estimates (although this will not necessarily help determine which estimates are more accurate). For example, although I accounted for tag shedding in my analyses, I used information presented in Vandergoot et al. (2012), which only looked at shedding for up to 3 years post-tagging. The tagging database analyzed for this study included recoveries up to 14 years post tagging; it is possible that the retention model parameters that I assumed did not adequately characterize the long-term tag retention rates (Fabrizio et al. 1996). As well, the reporting rates assumed in my analyses may not have adequately characterized actual reporting by the different fishery components. Although most parameter estimates were not sensitive to whether time-block or annual reporting rates were incorporated in the recovery probability calculations, as previously indicated, the reporting rates estimated in Vandergoot et al. (2012) were based on few releases of high-reward tags and thus there was a considerable amount of uncertainty in some of the reporting rate estimates. Additional assumptions that, if violated, may have resulted in my estimates deviating from those of the SCAA models or from actual Lake Erie mortalities include incomplete mixing of tagged fish with the at-large Walleye population and failure to fully account for the complex migratory behavior (e.g., age specific, inter-annual variability) of Lake Erie Walleye.

For the SCAA model estimates of fishing mortalities, among the assumptions that if violated could result in the model producing biased estimates is that the Lake Erie Walleye population is well mixed and homogeneously distributed. This has been shown to be unfounded in several prior research projects (Wang et al. 2007; Berger et al. 2012), as well as based on the movement probabilities estimated in this study. Rather than being well mixed, the Lake Erie Walleye population in actuality is likely patchily distributed, consisting of localized clumps of

fishes that vary in abundance levels depending on availability of resources and environmental conditions. As a result, the actual fishing mortality rates associated with the various fishery components and lake regions could differ considerably from the mortalities predicted in the SCAA models depending on the localized abundance levels.

Understanding movement patterns of Lake Erie Walleye is important because of the interjurisdictional management of the fishery (Knight 1997; Roseman et al. 2013). The movement probabilities estimated in this study were similar to those estimated in previous studies. That is, there was a general tendency for fish to remain within their respective basins, with western basin fish exhibiting more movement than central/eastern basin fish (Wang et al. 2007). I also found that in at least some parts of Lake Erie's western basin older Walleyes were more likely to move to the central/eastern basin than younger fish, which matches the findings of Wang et al. (2007) and Berger et al. (2012). Movement from Lake Erie to the Huron-Erie Corridor and Lake Huron did occur, with estimated movement probabilities for some regions very similar to the 10% level that Todd and Haas (1993) estimated. However, despite my efforts, as well as those of others to characterize inter-regional movement patterns of Lake Erie Walleye, there remains much that has yet to be determined, including annual variability and age-specific movements particularly for older Walleyes. In terms of future studies examining Lake Erie Walleye movement patterns, I do not suggest continuing to rely on tagging studies where recoveries are derived primarily from commercial and recreational fisheries as such studies are at best weakly informative of fish movements. Rather, studies that allow for multiple recaptures of tagged fish would help elucidate movement patterns of individual fish and determine, for example, how long fish remain in the Huron-Erie Corridor and Lake Huron before possibly returning to Lake Erie. Advances in telemetry techniques in recent years (Adams et al. 2012;

Leber and Blankenship 2012) provide an opportunity for estimating movement and mortality parameters with fishery-independent data rather than relying solely on traditional fishery-dependent tag-recovery data (Pine et al. 2003). Detailed insight into the migratory behavior of Lake Erie Walleye also could be accomplished using autonomous logging of data transmitted from tagged fish (e.g., Adams et al. 2012; Heupel and Weber 2012).

The natural mortality and inter-regional movement probabilities estimated in this study should ultimately prove beneficial for developing a spatially explicit SCAA model for the Lake Erie Walleye population. Although assuming constant natural mortalities is a common for population modeling purposes (Beverton and Holt 1957; Hewitt and Hoenig 2005; Jiang et al. 2007a; Hewitt et al. 2010), from a biological standpoint such an assumption is difficult to justify considering what is known about the variability in natural mortality estimates (Vetter 1998). When the assumption of constant natural mortalities is violated, bias in assessment model parameter estimates can result and ultimately influence management decisions (Cadrin and Secor 2009; Hansen et al. 2011). Both Roseman et al. (2013) and Hansen et al. (2011) have recommended that assessment models used as part of the Lake Erie Walleye quota management system be updated with more biologically appropriate natural mortalities given their potential influence on recommended harvest levels. The natural mortalities that I estimated in this study could either be the new rates assumed for the SCAA models or they could be used to specify prior distributions for models that attempt to estimate natural mortalities as part of the assessment model fitting process. Finally, although I question the appropriateness of incorporating the movement probabilities estimated in this study directly into a spatially explicit SCAA model, the inter-regional movement patterns that I estimated can be used in part to determine the appropriate spatial scaling (i.e., regional groupings) for a new assessment model.

One of my objectives for conducting this research was to demonstrate the application of a spatial tag-recovery model to a freshwater fish population and the information that is generated from this type of analysis to encourage wider use of this method in freshwater systems. A variety of spatial tag-recovery models have been proposed for estimating movement probabilities and spatial variability in mortality components (Hilborn 1990; Brownie et al. 1993; Schwarz et al. 1993; Joe and Pollock 2002; Cowen et al. 2009; Eveson et al. 2009). However, applications of these models, as far as I am aware, have to date been limited to marine fishes (e.g., Skipjack Tuna *Euthynnus pelamis*, Hilborn 1990; Sablefish *Anoplopoma fimbria*, Heifetz and Fujioka 1991; Pacific Herring *Clupea harengus pallas*, Schwarz et al. 1993; Yellowtail Flounder *Limanda ferruginea*, Cowen et al. 2009). I am unsure why spatial tag-recovery models have not been applied to freshwater systems as, in my opinion, the estimates from these models are just as relevant and would be just as beneficial for formulating management decisions as they are for marine systems. Spatial structuring of freshwater fish populations has been demonstrated in both large lentic and lotic systems (Gresswell et al. 1994; Zimmerman et al. 2009; Murphy et al. 2012; Peterson and Farrae 2011), and there is little doubt that spatial tag-recovery models would be beneficial for clarifying how mortality components and movements differed between spatial regions for such systems. However, even in smaller water bodies, fish populations can have complex spatial structure from a myriad of factors, such as differing migration patterns, predation vulnerabilities, and agonistic interactions with conspecifics (Werner and Hall 1988; Ruzycski and Wurtsbaugh 1999; Kerr et al. 2010; Collins et al. 2013). Thus, even in small systems there could be considerable benefits in using spatial tag-recovery models and studies for obtaining regional mortality and movement estimates and in using this information to formulate management decisions.

As I have demonstrated in this study, difficulties can be encountered when attempting to fit spatial tag-recovery models to studies that were not necessarily designed for such purposes. In particular, fitting spatial tag-recovery models can be problematic if tagging has not been conducted in all regions. Although Eveson et al. (2009) found that it was not necessary for tagging to be conducted in every region in all years, estimation problems can arise if there are regions in the study area where no tagging is conducted, and resulting estimates can be sensitive to assumptions made to deal with lack of tagging in all regions. As well, estimation problems can arise when particular population components (i.e., ages) are not well represented in the tagging or recovery aspects of the study, as was demonstrated in my results. Although the design of any tagging study necessitates close consideration of factors that may influence parameter estimability (Pollock et al. 2001), spatial models such as the one implemented in this research arguably necessitate closer consideration because of the greater model complexity and the interdependence of movement and mortality components (Schwarz et al. 1993). Additional research would be beneficial for understanding how parameter estimability and uncertainty is affected by tagging levels, tagging composition, amount of movement, and complexity of the modeled system (i.e., number of regions).

APPENDIX

Table 3.1.—List of equation symbols used in modeling spatially varying population demographics and fishery characteristics of Lake Erie Walleye.

Symbol	Description
Indicator variables	
t	Tagging agency (MDNR, ODNR, OMNR, NYSDEC)
a	Age class (2, 3, 4, 5+)
k	Lake region (1, 2, 3, 4, 5)
f	Fishery (recreational, commercial)
ty	Tagging year (1990 – 2007)
fy	Fishing year (1990 – 2007)
Estimated parameters	
$F_{fy,f}^k$	Instantaneous fishing mortality rate in year fy for fishery f in region k
$M_{a,fy}^k$	Instantaneous natural mortality rate at age a in year fy in region k
θ_f	Fishery f specific parameter for estimating age-2 selectivities for each fishery
$\gamma_a^{k,k'}$	Parameters for estimating age-group specific probabilities of moving from region k to the other 4 regions of the system or alternatively staying in region k (k can be equal to k')
Calculated and assumed quantities	
$S_{a,f}$	Selectivity at age a for fishery f
$P_{t,a,ty,fy,f}^k$	Probability that a fish tagged by agency t at age a and released in year ty is harvested in year fy by fishery f in region k

Table 3.1 (cont'd)

$\mathbf{p}_{t,a,ty,fy,f}$	A 1×5 vector with $p_{t,a,ty,fy,f}^k$ as its elements
$u_{a,fy,f}^k$	Exploitation rate at age a in year fy for fishery f in region k
$\mathbf{u}_{a,fy,f}$	A 1×5 vector with $u_{a,fy,f}^k$ as its elements
$S_{a,fy}^k$	Survival rate at age a in year fy in region k
$\mathbf{S}_{a,fy}$	A 1×5 vector with $S_{a,fy}^k$ as its elements
$\pi_a^{k,k'}$	The probability of moving from region k to region k' (k can be equal to k') at the beginning of the year for a particular age group
$\boldsymbol{\pi}_a^{k'}$	A 1×5 vector consisting of the probability of moving to region k' from one of the other regions (dependent on tagging agency) for a particular age group
$\boldsymbol{\pi}_a$	A 5×5 matrix with $\pi_a^{k,k'}$ as its elements
$\lambda_{fy,f}^k$	Tag reporting rate in year fy by fishery f in region k
$\boldsymbol{\lambda}_{fy,f}$	A 1×5 vector with $\lambda_{fy,f}^k$ as its elements
$\phi_{t,fy-ty+0.5}$	Tag retention rate for a fish tagged by agency t captured $fy-ty$ years after tagging (time at-large)

Observed Data

$N_{t,a,ty}$	Total number of fish tagged by agency t at age a and released in year ty
$R_{t,a,ty,fy,f}^k$	Total number of recapture of fish tagged by agency t at age a and released in year ty in year fy by fishery f in region k

Matrix Operators

Table 3.1 (cont'd)

$D(\)$ A matrix operator that converts a 1×5 vector into a 5×5 diagonal matrix with the elements of the vector along the diagonal

Likelihood Components

$L_{t,a,ty}$ Negative log likelihood corresponding to the cohort tagged and released by agency t at age a in year ty

Table 3.2.—List of the movement probabilities from regions 3 and 5 to other regions for assessing parameter sensitivity to assumed movement probabilities.

Model	Region of origin	Region moved to				
		1	2	3	4	5
Movement 1	3	0.08	0.08	0.75	0.09	0.00
	5	0.12	0.13	0.00	0.00	0.75
Movement 2	3	0.16	0.17	0.50	0.17	0.00
	5	0.25	0.25	0.00	0.00	0.50
Movement 3	3	0.25	0.25	0.25	0.25	0.00
	5	0.37	0.38	0.00	0.00	0.25
Movement 4	3	0.33	0.33	0.00	0.34	0.00
	5	0.50	0.50	0.00	0.00	0.00

Table 3.3.—Number of jaw-tagged Walleye released in the western (regions 1 and 2) and eastern (region 4) basin of Lake Erie and the number of tags returned (by age-group) by the commercial and recreational fisheries in each region (i.e., regions 1-5) between 1990 and 2007.

Region	Number released	Age-group	Recoveries by region (commercial/recreational)				
			1	2	3	4	5
1	144	2	0/0	0/2	0/0	0/2	0/0
	2715	3	35/4	0/36	13/6	0/12	0/3
	4368	4	94/7	0/68	41/7	0/49	0/18
	7544	5+	148/16	0/111	94/23	0/89	0/19
2	2975	2	17/4	0/98	6/2	0/9	0/35
	13354	3	53/20	0/572	21/4	0/47	0/233
	14338	4	47/22	0/590	61/12	0/100	0/214
	43213	5+	185/77	0/1609	323/138	0/950	2/583
4	536	2	0/0	0/0	1/5	0/18	0/0
	1341	3	0/0	0/2	4/7	0/58	0/1
	2235	4	0/0	0/1	11/23	0/106	0/2
	17176	5+	1/0	0/1	133/135	0/1204	0/14

Table 3.4.—Model rankings for the models (see text for a description of models) used to estimate mortality parameters from the tag-return study conducted with Lake Erie Walleye between 1990 and 2007. Shown are the number of estimated parameters (K), overdispersion-adjusted AIC (QAIC) values, and QAIC differences (Δ_i) for the fitted models. The number of parameters listed for each model includes the estimation of the variance inflation factor for the assessment of overdispersion for the global model.

Model	K	QAIC	Δ_i
$\pi_{age}M_{age, region}$	187	22817.1	0.0
$\pi_{age}M_{age}$	175	22822.3	5.2
$\pi_{age}M_{age, time block}$	183	22830.5	13.4
$\pi_{age}M_{region, time block}$	183	22841.0	23.9
$\pi_{age}M_{region}$	175	22843.2	26.1
$\pi M_{age, region}$	175	22852.3	35.2
$\pi_{age}M_{age, region, time block}$	219	22854.8	37.6
$\pi_{age}M$	172	22856.3	39.2
$\pi_{age}M_{time block}$	174	22858.2	41.1
πM_{age}	163	22869.5	52.4
$\pi M_{age, time block}$	171	22877.2	60.0
$\pi M_{region, time block}$	171	22885.3	68.2
πM_{region}	163	22888.2	71.1
$\pi M_{age, region, time block}$	207	22890.5	73.4
πM	160	22900.3	83.2
$\pi M_{time block}$	162	22902.5	85.3

Table 3.5.—Instantaneous natural mortality rate estimates for age-2, age-3, age-4, and age-5+ Lake Erie Walleye by region. Estimates are from the model with the lowest QAIC value ($\pi_{age}M_{age, region}$). Values in parentheses are 95% confidence limits.

Region	Age-group			
	2	3	4	5+
1&2	0.34 (0.17– 0.50)	0.40 (0.25 – 0.55)	0.35 (0.22 – 0.47)	0.13 (0.09 – 0.16)
3	0.30 (0.15 – 0.46)	0.31 (0.15 – 0.46)	0.30 (0.15 – 0.46)	0.27 (0.16 – 0.39)
4	0.31 (0.15 – 0.46)	0.33 (0.17 – 0.50)	0.33 (0.17 – 0.48)	0.21 (0.17 – 0.25)
5	0.31 (0.15 – 0.47)	0.33 (0.16 – 0.49)	0.34 (0.16 – 0.52)	0.45 (0.30 – 0.59)

Table 3.6.—Age-group specific movement probabilities Walleye moving from tagging regions 1, 2, or 4 to regions 1, 2, 3, 4, or 5. Estimates are from the model with the lowest QAIC value ($\pi_{age}M_{age, region}$). Values in parentheses are 95% confidence limits. Because no tagging was conducted in regions 3 and 5, fish moving into these regions were assumed to remain there until harvested or died from natural causes.

Region	Region moved to				
	1	2	3	4	5
Age 2 to Age 4					
1	0.42 (0.27 – 0.58)	0.37 (0.21 – 0.53)	0.07 (0.02 – 0.13)	0.12 (0.02 – 0.21)	0.02 (0.00 – 0.05)
2	0.05 (0.03 – 0.07)	0.79 (0.74 – 0.83)	0.01 (0.00 – 0.02)	0.04 (0.02 – 0.06)	0.11 (0.08 – 0.14)
4	0.00 (0.00 – 0.00)	0.01 (0.00 – 0.04)	0.07 (0.01 – 0.14)	0.91 (0.93 – 0.98)	0.01 (0.00 – 0.02)
Age 5+					
1	0.56 (0.46 – 0.66)	0.23 (0.14 – 0.32)	0.09 (0.05 – 0.14)	0.11 (0.05 – 0.16)	0.01 (0.00 – 0.03)
2	0.05 (0.03 – 0.06)	0.69 (0.66 – 0.73)	0.04 (0.03 – 0.06)	0.14 (0.12 – 0.16)	0.07 (0.05 – 0.09)
4	0.00 (0.00 – 0.00)	0.00 (0.00 – 0.00)	0.06 (0.04 – 0.08)	0.94 (0.92 – 0.96)	0.00 (0.00 – 0.00)

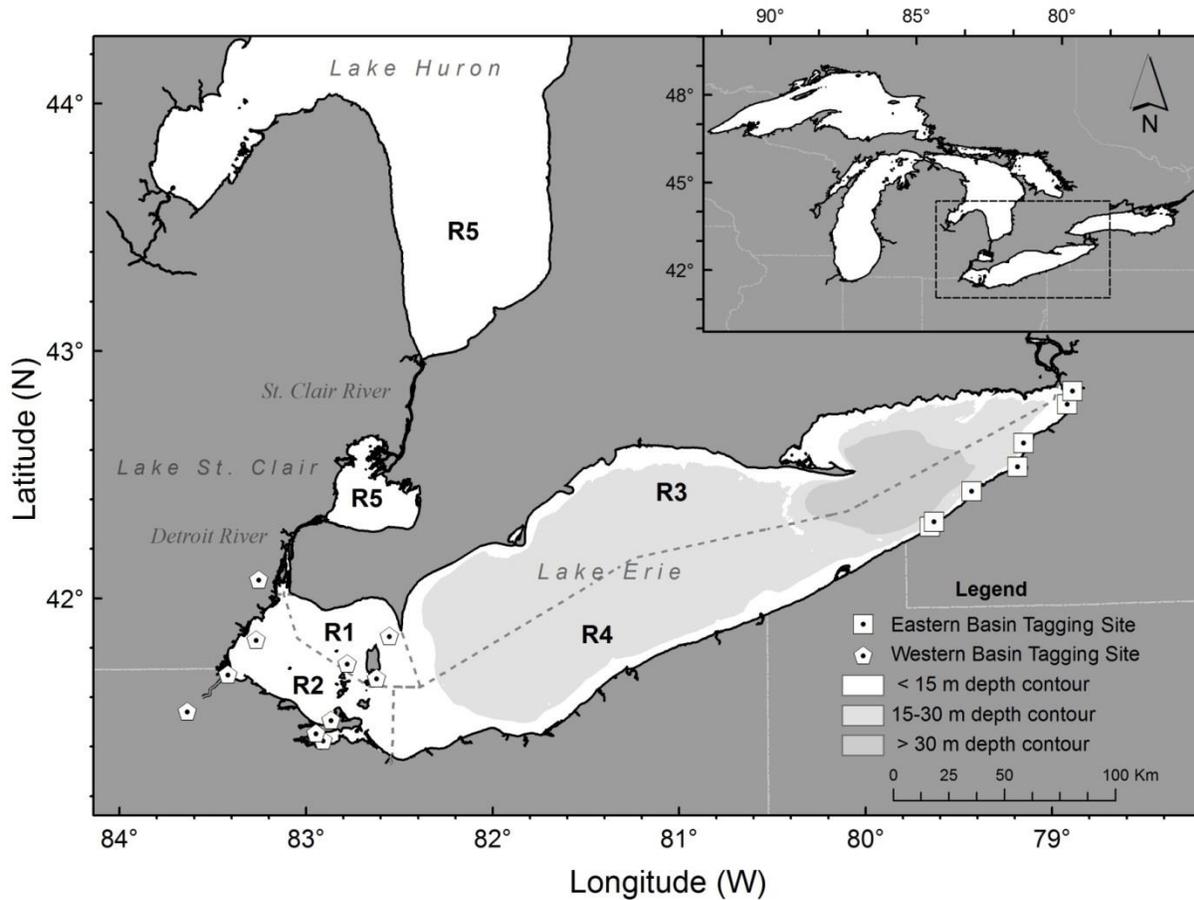


Figure 3.1.—Map of Lake Erie showing the sites where jaw-tagged Walleyes were released as part of the jaw-tagging study. Also shown are the different regions (separated by dashed lines) where demographic and fishery parameters were estimated in Lake Erie (regions 1 through 4) and the Huron-Erie corridor (i.e., Detroit River, Lake St. Clair, St. Clair River) and Lake Huron (region 5). Depth contours only apply applicable to Lake Erie.

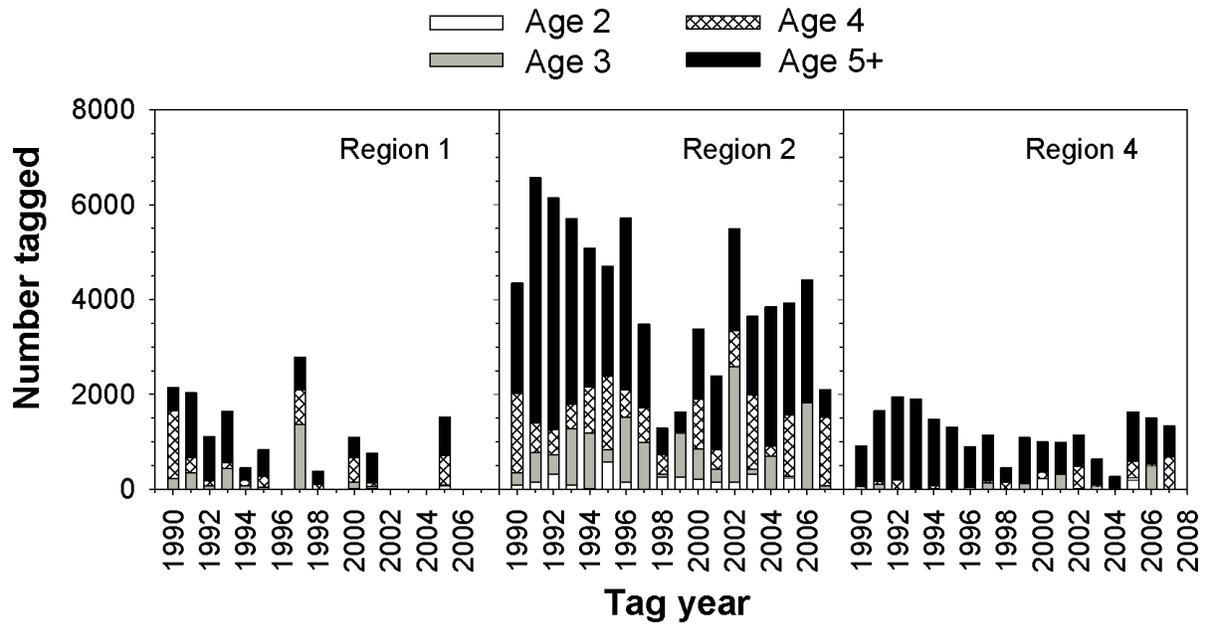


Figure 3.2.—Number of jaw-tagged Walleyes released (by age-group) in the western (regions 1 and 2) and eastern (region 4) basins of Lake Erie between 1990 and 2007.

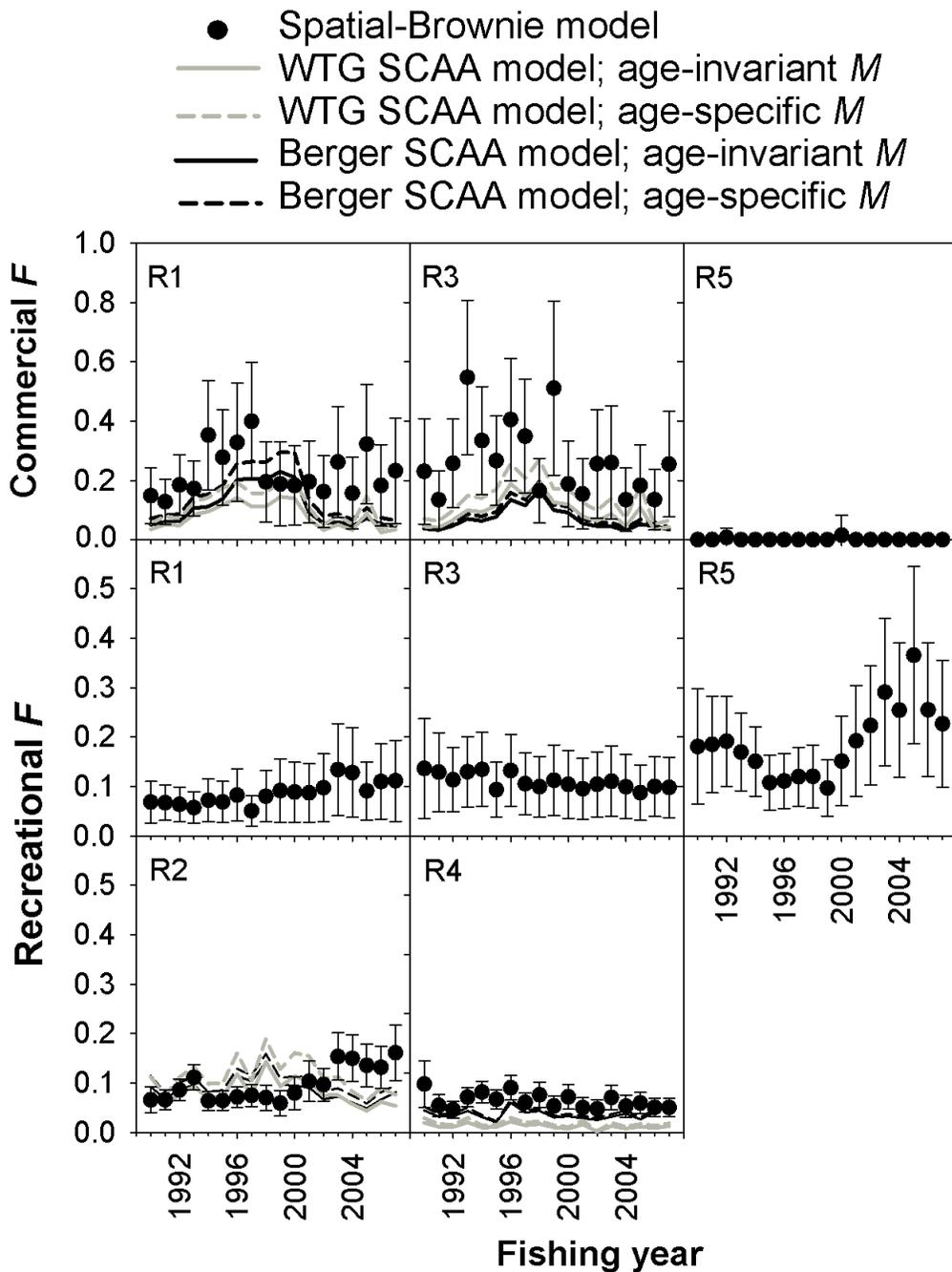


Figure 3.3.—Region-specific, instantaneous fishing mortality (F) rates (black circles with associated 95% confidence intervals) for fully recruited ages (i.e., age-3+) estimated using a spatial-Brownie model for the commercial and recreational Walleye fisheries in Lake Erie, 1990-2007. Also shown are region-specific estimates of F from the statistical catch at age (SCAA) models reported by the Lake Erie Walleye Task Group (WTG 2011) and Berger et al. (2012) assuming age-invariant (thick solid lines) and age-specific (thick dashed lines) natural mortality (M) rates. Note the difference in the y-axis scales (i.e., estimates of F) for the commercial and recreational fisheries.

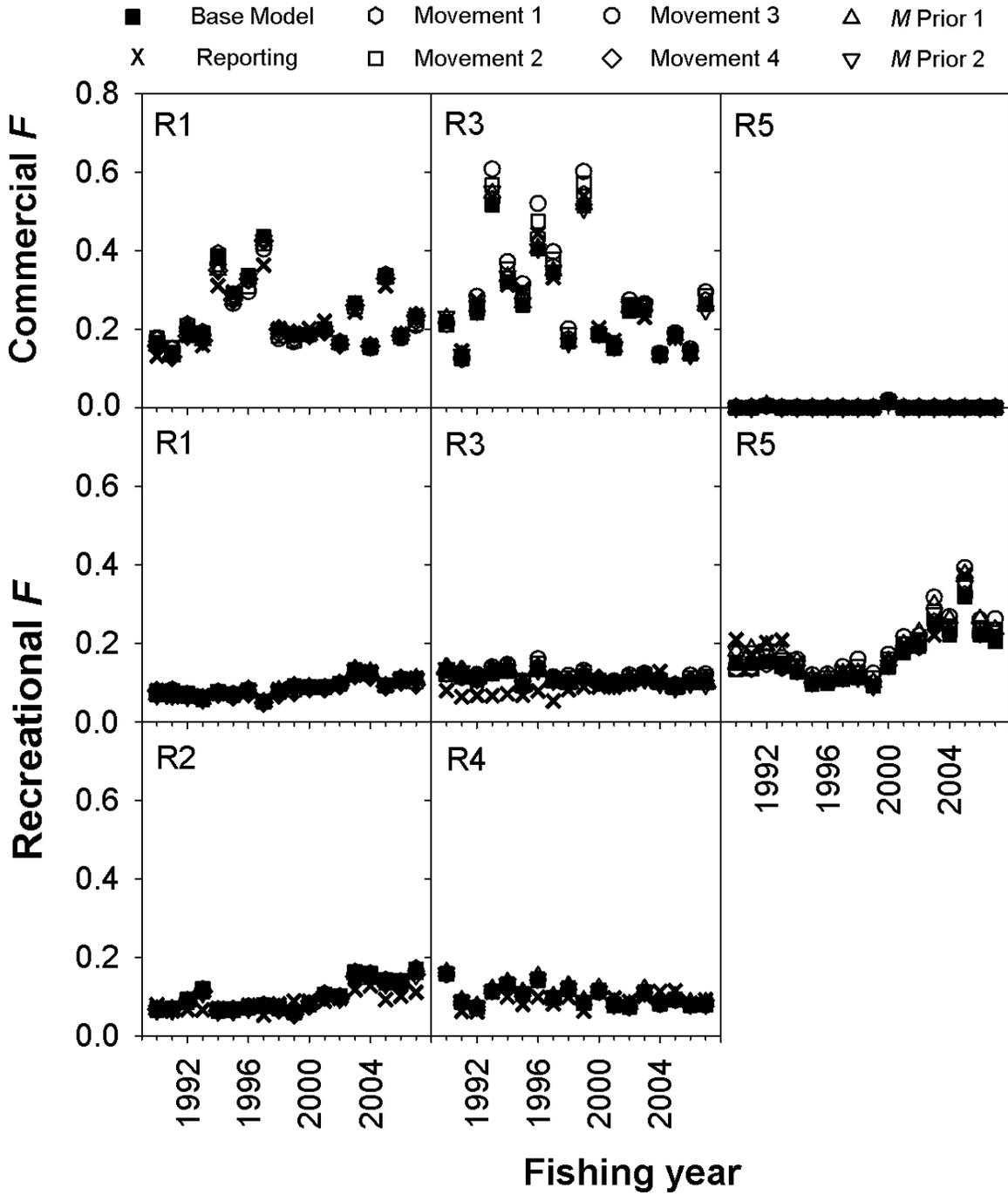


Figure 3.4.—Sensitivity plots of the instantaneous fishing mortality (F) rates for Lake Erie Walleye (regions 1-5) in the commercial and recreational fisheries assuming five different movement scenarios (Table 3.2) for Walleye in regions 3 and 5, two different prior probability distributions for natural mortality (prior 1: log-normal median = 0.40; prior 2: log-normal median = 0.20) and the year-, fishery-, and region-specific reporting rates presented by Vandergoot et al. (2012).

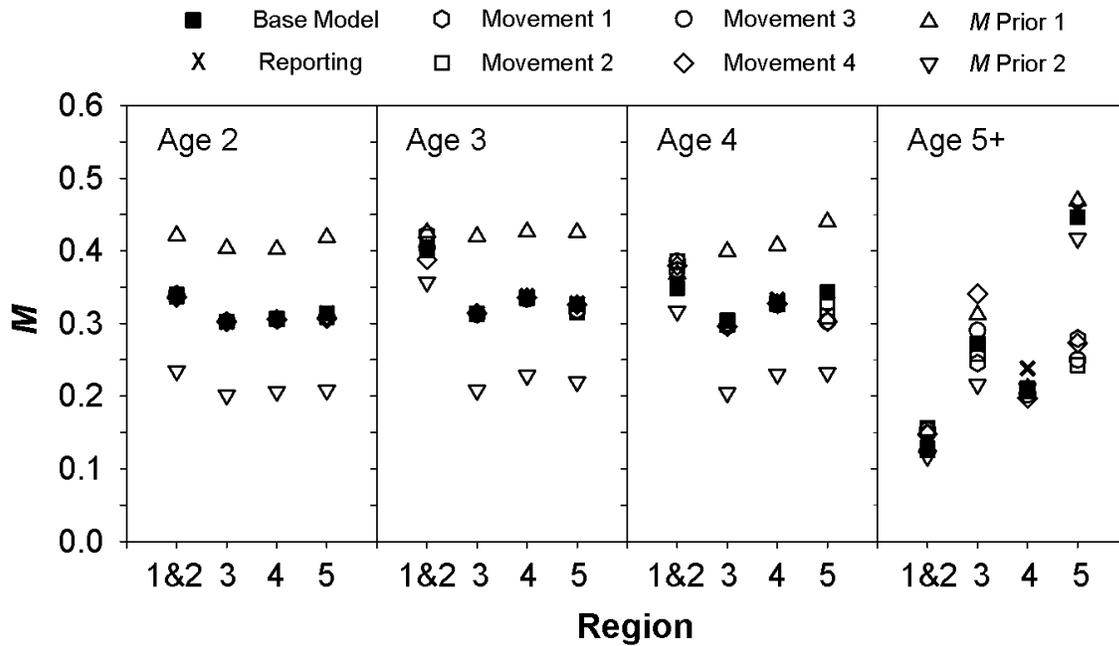


Figure 3.5.—Sensitivity plots of the estimated movement probabilities Lake Erie Walleye from tagging regions 1, 2, and 4 to the adjacent regions assuming five different movement scenarios (Table 3.2) for Walleye in regions 3 and 5, two different prior probability distributions for natural mortality (prior 1: log-normal median = 0.40; prior 2: log-normal median = 0.20) and the year-, fishery-, and region-specific reporting rates presented by Vandergoot et al. (2012).

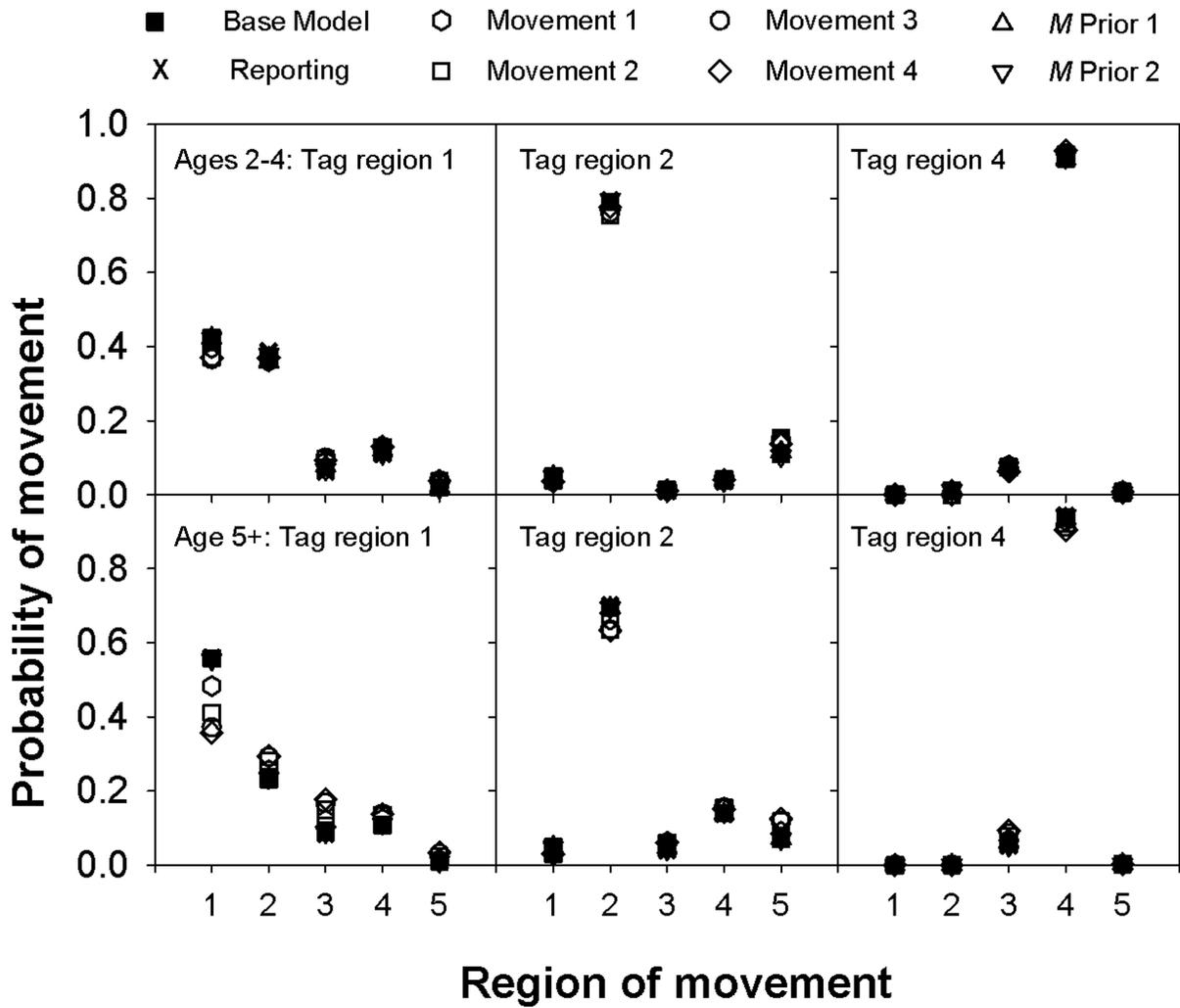


Figure 3.6.—Sensitivity plots of the instantaneous natural mortality (*M*) rates for Lake Erie Walleye (regions 1-5) assuming five different movement scenarios (Table 3.2) for Walleye in regions 3 and 5, two different prior probability distributions for natural mortality (prior 1: log-normal median = 0.40; prior 2: log-normal median = 0.20) and the year-, fishery-, and region-specific reporting rates presented by Vandergoot et al. (2012).

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CHAPTER 4

BIAS AND PRECISION OF FISHERY AND DEMOGRAPHIC ESTIMATES FROM A SPATIAL TAG-RECOVERY MODEL WHEN INTER-REGIONAL MOVEMENTS ARE TREATED AS FIXED

Abstract

I used stochastic simulations to evaluate bias and precision of fishery and demographic parameter estimates from spatial tag-recovery models under different combinations of high- and low-reward tagging levels, allocations of tags to different age groups, and patterns in age-specific natural mortalities. My evaluations were based on information available for the Walleye *Sander vitreus* population in Lake Erie, which has been found to exhibit complex spatial structuring and which also supports economically important recreational and commercial fisheries. My simulation framework included a data-generating model that was a mathematical representation of the “true” dynamics of tagged cohorts, and a tag-recovery estimation model that used recoveries from the data-generating model to estimate reporting rates, fully-selected fishing mortality rates, age-specific selectivities, and age-specific natural mortalities. The modeled system consisted of three regions that were intended to correspond to west/central (region 1) and eastern (region 2) basins of Lake Erie and the adjacent St. Clair/Detroit River/Lake Huron area (region 3). In conducting my evaluations, I assumed inter-regional movements of tagged individuals could be treated as fixed (i.e., known) values under an assumption that external estimates would be available from an appropriately designed movement study. Parameter precision increased as the number of tags released increased and the proportion of high-reward tags released increased. Additionally, aside from one exception (i.e., the oldest age-group), precision in the estimated mortality rates also increased when I compared a skewed versus balanced tag allocation design. These trends in parameter precision were consistent among different population dynamic scenarios (i.e., assumed natural mortality rates in the data-generating model). My simulations were useful for understanding how parameter precision varied for a fish population exhibiting spatial stock structuring assuming various tagging

scenarios and provides researches with insight for designing future tagging studies so that fishery and demographic parameters of interest are estimable.

Introduction

Spatial structuring is a common characteristic of marine and freshwater fish populations. This phenomenon can be caused by numerous factors, including metapopulation dynamics (Levins 1969; Hanski and Gilpin 1991; Kritzer and Sale 2004), population contingents selecting different habitats based on varying life history tactics (Secor 1999; Botsford et al. 2009; Kerr et al. 2010; Dunn and Forman 2011), and environmental variability (Lande et al. 1999). Spatial structuring also can arise from regional variations in fishery fleet dynamics, such as variable fishing effort or gear use (Booth et al. 2000; Guan et al. 2013). Regardless of its origin, previous research has established that individual populations components can be overexploited if management decisions do not account for spatial structuring (Stephenson 1999; Ying et al. 2011; Guan et al. 2013), which is of concern because loss of individual components can affect long-term sustainability because of limited resilience to perturbations (Stephenson and Kenchington 2000).

Despite spatial structuring being a common attribute of fish populations, it is frequently overlooked in actual assessment of freshwater and marine stocks (Hutchings 2000; Cadrin and Secor 2009; Ying et al. 2011; Wilson et al. 2013; Al-Humaidhi et al. 2013). Statistical catch-at-age (SCAA) and tag-recovery models are two approaches routinely used in the assessment of exploited fish stocks. With SCAA assessment models, as well as similar modeling methods such as virtual population analysis, the primary assessment purpose is often stock reconstruction for documenting historical changes in abundances, mortality rates, or recruitment levels (Walters and Martell 2004). Conversely, the focus of tag-recovery models is often quantifying current population dynamics of fish stocks (Walters and Martell 2004). In practice, estimates from tag-

recovery models, in particular natural mortality rates, frequently are incorporated in stock reconstruction assessment models either as assumed (i.e., fixed) values or as coefficients for prior probability distributions (Lee et al. 2011; Jiao et al. 2012). While estimation of natural mortality rates within SCAA models is theoretically possible, accuracy and precision of estimates are data dependent (Hilborn and Walter 1992; Wang and Liu 2006; Lee et al. 2011). Spatial versions of SCAA and tag-recovery models do exist; however, application of these models is infrequent and there is much that needs to be learned about their performance. Explicit parameterization of the spatial dynamics of spatially-structured populations within SCAA assessment models necessitates that tagging data be incorporated in the assessment modeling framework, although there are simpler approaches for accounting for spatial structure in SCAA assessment models, such as the “fleets-as-areas” approach used by Berger et al. (2012) and Hurtado-Ferro et al. (*in press*). Even with these simpler approaches, it is likely that estimation of natural mortality rates via SCAA assessment models will continue to be a challenge, particularly if regional estimates of natural mortality rates are desired. Consequently, I anticipate that spatial tag-recovery models will frequently be used in conjunction with spatial SCAA assessment models to aid in their parameterization, much in the same way that non-spatial tag-recovery models are used to inform non-spatial assessment models.

There are many factors that can affect accuracy and precision of estimates from tag-recovery models, including tagging levels (i.e., number of tagged individuals), number of recaptures, tag shedding, tag non-reporting, and delayed mixing of tagged individuals with at-large populations (Pierce and Tomcko 1993; Fabrizio et al. 1996; Hoenig et al. 1998; Latour et al. 2001; Pollock et al. 2001; Eveson et al. 2009; Brenden et al. 2010; Vandergoot et al. 2012). For non-spatial tag-recovery models, various studies have been conducted evaluating features of

different tagging study designs (e.g., Hoenig et al. 1998; Pollock et al. 2001; Brenden et al. 2010). Far less attention has been paid to study designs for spatial tag-recovery models. Xiao (1996) evaluated how tagging level affected precision and bias of inter-regional movement probabilities when other parameters, such as catchability coefficients, natural mortality rates, and tag shedding rates, were treated as fixed quantities using the spatial tag-recovery model of Hilborn (1990). Using an alternative spatial tag-recovery model formulation (one that included as a component the estimation of population abundances at the start of the tagging study), Eveson et al. (2009) investigated how different model parameterizations affected precision of multiple parameters, including inter-regional movement probabilities, fishing mortalities, and natural mortalities; however, these evaluations were based mostly on a single tagging design.

The purpose of this study was to evaluate how bias and precision of parameter estimates from a spatial tag-recovery model varied among different tagging design features for a population exhibiting complex fishing and demographic spatial structuring. In conducting this research, I assumed inter-regional movements of tagged individuals could be treated as fixed (i.e., known) values under an assumption that external estimates would be available from an electronic tracking study. Although tag-recovery models often rely solely on anglers or commercial fishers for the return of tagged individuals, information pertaining to movement can be limited with these studies as it is only known where individuals were tagged and where they were recovered (Pollock et al. 2001; Bolle et al. 2005; Vandergoot and Brenden 2014). Conversely, advances in electronic fish tracking technologies, such as acoustic telemetry, allow detailed information on fish movement to be collected without having to rely on angler or commercial fisher catch (Heupel and Simpfendorfer 2002; Adams et al. 2012; McKenzie et al. 2012). While methods do exist for estimating population dynamics of fish stocks based on

electronic fish tracking “recoveries” (see Pine et al. 2003), increased tag costs limit how many individuals can be tagged. As a result, there can be concerns about how representative demographic rate estimates are because of low sample sizes (Le Bris et al. 2013), although as noted by Kurota et al. (2009) electronic tags can have high reporting rates by virtue of reward levels and better publicity so that the number of recovered electronic tags can be proportionately greater than that of conventional tags. As a consequence of their lower cost, conventional tagging studies can tag larger segments of populations and thus have been identified as being better suited for making broad-scale (i.e., population-level) inferences (Le Bris et al. 2013). Because of their respective characteristics, there may be considerable benefits to using a combination of conventional and electronic fish tracking technologies in tagging studies (Kurtado et al. 2009; Eveson et al. 2012; Hightower and Pollock 2013). For example, an integrated tag-recovery model could be fit to the recoveries of conventional and electronic tags (Kurtado et al. 2009; Eveson et al. 2012). Alternatively, information from electronic tagging studies could be used to help inform movement parameterization of spatial tag-recovery models that are fit to recoveries from conventional tagging studies, similar to how natural mortality estimates from tagging studies are often used to inform SCAA assessment models.

Lake Erie Walleye as a Simulation Basis

As a basis for my research, I used information available for Lake Erie Walleye *Sander vitreus*. Spatial structuring in the Lake Erie Walleye population has been attributed to several factors, including metapopulation dynamics and regional differences in water quality, trophic structure, and incidence of invasive species (Wang et al. 2007; Berger et al. 2012). In addition to functioning as an apex predator (Ryan et al. 2003), the Walleye population supports important

commercial and recreational fisheries throughout Lake Erie with most fishing activity localized in the western and central basins (Roseman et al. 2011; Zhao et al. 2011). Harvest quotas are set annually to promote sustainability of this economically and ecologically important fishery (Roseman et al. 2011). Under the current harvest policy, quotas fluctuate with population abundance, which is estimated using an age-structured SCAA model (Vandergoot et al. 2010; Zhao et al. 2011).

Despite evidence to the contrary, existing SCAA assessment models for west-central and eastern basin Walleye stocks assume that the population is well mixed (i.e., homogeneously distributed) and that natural mortality does not vary with age or through time (Locke et al. 2005; Zhao et al. 2011; Berger et al. 2012). Using a spatial tag-recovery model and recoveries from a long-term jaw-tagging study, Vandergoot and Brenden (2014) found that Lake Erie Walleyes exhibited age and spatial variability with respect to movement and mortality components. For example, Vandergoot and Brenden (2014) found that Walleyes in the Lake Erie's western basin were more likely to move to other regions of the lake than eastern basin fish, which was consistent with previous movement studies that have been conducted (Wang et al. 2007; Zhao et al. 2011). Natural mortalities of age-5 and older Walleyes were lower than those of younger fish in both the lake's western and eastern basins (Vandergoot and Brenden 2014).

Given the complex spatial structuring of Lake Erie Walleye, there has been interest in using a spatial SCAA assessment model in conjunction with the lake's quota management system (Berger et al. 2012). Additionally, in recent years, there has been significant investment in the deployment of acoustic telemetry receivers in Lake Erie and its connecting waterways for the purpose of obtaining detailed intra- and inter-lake movements of fish (see <http://data.glos.us/glatos>). In 2010, acoustic telemetry arrays were deployed throughout the St.

Clair/Detroit River system for the purpose of monitoring fish movement between lakes Huron and Erie. In 2013, acoustic-telemetry “curtains” were deployed that bisected Lake Erie for the purpose of studying movement of fishes between the lake’s basins.

Methods

My stochastic simulation framework included a data-generating model that was a mathematical representation of the “true” dynamics of tagged cohorts, and a tag-recovery estimation model that used recoveries from the data-generating model to estimate reporting rates, fully-selected fishing mortality rates, age-specific selectivities, and age-specific natural mortalities. The modeled system consisted of three regions that were intended to correspond to west/central (region 1) and eastern (region 2) basins of Lake Erie and the adjacent St. Clair/Detroit River/Lake Huron area (region 3). For the simulations, tagging was assumed to be conducted annually over a 20-year period in both regions 1 and 2, with tags being recovered over the same time period. No tagging was assumed to be conducted in region 3. The purpose of including region 3 was to have a sink to which tagged fish could emigrate although they still would be vulnerable to exploitation and thus tags could be recovered in this region. I was concerned about dynamics in region 3 only insofar as their possible influence on parameter estimates in regions 1 and 2. Commercial and recreational fisheries were assumed to operate in each region, with the level of exploitation and probability of reporting recovered tags differing between the fisheries, which is similar to what has been observed in Lake Erie (Vandergoot and Brenden 2014). Both high- and low-reward tags were assumed to be released annually. The age range in both the data-generating and tag-recovery estimation models was age 2 to age 5, with the last age class an aggregate group including age-5 and older fish. This is the same age range

that Vandergoot and Brenden (2014) used in their spatial tag-recovery analysis of Lake Erie Walleyes and reflects the uncertainty associated with aging older Walleyes with some methodologies. Both the data-generating and tag-recovery estimation models were programmed in AD Model Builder (Fournier et al. 2012). Simulations were conducted in parallel on general purpose compute clusters of the Michigan State University High Performance Computing Center. The examined scenarios consisted of different low- and high-reward tagging levels, allocation of tags to different age groups, and patterns in natural mortalities (total number of scenarios = 80). A total of 500 iterations were conducted for each investigated scenario. A listing and description of all variables and equation symbols used herein are presented in Table 4.1.

Data-Generating Model

Tag-recovery data were simulated using a model structured after the spatial tag-recovery model described by Vandergoot and Brenden (2014) for Lake Erie Walleye, which was based on a model described by Eveson et al. (2009). For my simulations, individual tagged cohorts were region-, year-, age-group, and reward-level specific. Recovery probabilities were defined in terms of survival, movement, exploitation, tag reporting, and tag retention. The probabilities of low- or high-reward tagged fish being harvested in a given year, region, and by a particular fishery were represented as

$$\mathbf{p}_{a,ty,fy,f}^{low} = \begin{cases} \boldsymbol{\pi}^{k'} \mathbf{D}(\mathbf{u}_{a,fy,f}) \mathbf{D}(\boldsymbol{\lambda}_f) \phi_{fy-ty} & fy = ty \\ \boldsymbol{\pi}^{k'} \mathbf{D}(\mathbf{S}_{a,ty}) \dots \boldsymbol{\pi} \mathbf{D}(\mathbf{S}_{a+(fy-ty)-1,fy-1}) \boldsymbol{\pi} \mathbf{D}(\mathbf{u}_{a+(fy-ty),fy,f}) \mathbf{D}(\boldsymbol{\lambda}_f) \phi_{fy-ty} & fy > ty \end{cases}$$

$$\mathbf{p}_{a,ty,fy,f}^{high} = \begin{cases} \boldsymbol{\pi}^{k'} \mathbf{D}(\mathbf{u}_{a,fy,f}) \phi_{fy-ty} & fy = ty \\ \boldsymbol{\pi}^{k'} \mathbf{D}(\mathbf{S}_{a,ty}) \dots \boldsymbol{\pi} \mathbf{D}(\mathbf{S}_{a+(fy-ty)-1,fy-1}) \boldsymbol{\pi} \mathbf{D}(\mathbf{u}_{a+(fy-ty),fy,f}) \phi_{fy-ty} & fy > ty \end{cases} \quad (1)$$

The only difference between recovery probabilities for the different tag reward levels was that with high-reward tags it was assumed there was perfect (100%) reporting of harvested tags. The formulations in Equation 1 assumed that movement occurred immediately after tagging. Alternative formulations (e.g., movement occurring at the end of the year) could have been used as well, but in the case of Lake Erie Walleye, tagged fish are frequently recovered in other regions of the lake shortly after tagging (Wang et al. 2007).

For the purpose of my simulations, inter-regional movement probabilities were treated as constant among ages. This assumption was not anticipated to have a large influence on simulation results since inter-regional movement probabilities were treated as known in the estimation model. For fish tagged in region 1, the probability of a fish remaining in region 1 was 80%, while the probabilities of moving to regions 2 or 3 were both set at 10%. For fish tagged in region 2, the probability of fish remaining in region 2 was 95%, while the probabilities of moving to regions 1 or 3 were 5% and 0%, respectively. Because I assumed region 3 served as a sink for western basin walleye, tagged fish that moved into region 3 remained there until being harvested (i.e., movement occurred prior to the fishing season) or died of natural causes.

Retention of tags was represented through an exponential function

$$\phi_{fy-ty} = \exp(-0.08(fy - ty + 0.5)). \quad (2)$$

This function assumed that immediate tag retention was 100%, with an annual instantaneous chronic shedding rate of 0.08. This function was based on the results obtained from a lakewide double-tagging study conducted with jaw- and passive-integrated-transponder tagged Walleye on Lake Erie (Vandergoot et al. 2012). When modeling tag retentions, 0.5 was added to the time at large so that rates represented retention at the mid-point of the year.

The reporting rates incorporated in the recovery probability calculations were based on fishery- and region-specific estimates from high-reward tagging studies conducted on Lake Erie Walleye (Vandergoot et al. 2012). Reporting rates assumed for low-reward tags were 40% for recreational fisheries and 15% for commercial fisheries in each region. As previously indicated, reporting rates for high-reward tags were assumed to be 100% for all fisheries and regions. I made no assumption as to what reward level was necessary to elicit perfect reporting of high-reward tags, but I address this important aspect of tagging study designs in the Discussion.

Exploitation for a given age, year, fishery, and region were modeled as

$$u_{a,fy,f}^k = \frac{s_{a,f} F_{fy,f}^k}{\sum_f s_{a,f} F_{fy,f}^k + M_{a,fy}^k} (1 - S_{a,fy}^k), \quad (3)$$

with survival equal to

$$S_{a,fy}^k = \exp\left(-\left(\sum_f s_{a,f} F_{fy,f}^k + M_{a,fy}^k\right)\right). \quad (4)$$

In each region, both commercial and recreational fisheries were assumed to operate. Fishing mortalities were calculated as the product of age-specific relative vulnerabilities (i.e., selectivities) and a fully-selected instantaneous fishing mortality rate that was year, fishery, and region specific. Age-3 and older fish were considered fully selected for both commercial and recreational fisheries, thus selectivities for these age groups were set equal to 1.0. Age-2 selectivities were set equal to 0.30 for both commercial and recreational fisheries. Selectivities were assumed to be the same for all modeled regions. For the data-generating model, fully-selected recreational fishing mortalities were set equal to 0.20. Fully-selected commercial fishing mortalities varied from 0.15 in years 1 to 5, 0.35 in years 6 to 15, and 0.20 in years 16 to 20 in both regions 1 and 2. The respective fully-selected recreational and commercial fishing patterns

for regions 1 and 2 were similar to the mortality rates estimated for Lake Erie Walleyes by Vandergoot and Brenden (2014). In region 3, commercial and recreational fishing mortalities were held constant at 0.10 over the modeled time period. Assumed natural mortality rates depended on the investigated scenario (*see below*). Natural mortalities were age-group specific with age-2 and age-3 fish having the same natural mortalities and age-4 and age-5 fish having different natural mortalities (Vandergoot and Brenden 2014).

Cohort-specific tag recoveries were generated from multinomial distributions where the number of trials equaled the assumed tagging level for an evaluated scenario and the cell probabilities equaled the recovery probabilities specified in equation 1. Because actual tag-recovery data frequently are overdispersed (i.e., exhibit greater variability than what is expected under the assumed model), when generating the tag-recovery data process error was incorporated in the fishing and natural mortality parameters in equation 3. Process errors were distributed lognormal with log-scale means and standard deviations equal to 0 and 0.2, respectively.

Tag-Recovery Estimation Model

Structurally, the tag-recovery estimation model was similar to the data-generating model (Vandergoot and Brenden 2014). The major difference with the estimation model was that region- and fishery-specific reporting rates, fishery-specific age-2 selectivities, year-, region-, and fishery-specific fully-selected fishing mortalities, and year-, region-, and age-group-specific natural mortalities were parameters to be estimated during the model fitting process. As part of the estimation model, tag-shedding and inter-regional movement rates were treated as fixed and set equal to the values assumed in the data-generating model. To aid in estimation, age-2 fishery-specific selectivities were estimated through an inverse-logit function

$$\hat{s}_{2,f} = \frac{\exp(\theta_f)}{1.0 + \exp(\theta_f)}, \quad (5)$$

which constrained selectivities to be between 0.0 and 1.0, while allowing the estimated parameter to be any real number. Fishery- and region-specific reporting rates were similarly estimated

$$\hat{\lambda}_f^k = \frac{\exp(\gamma_f^k)}{1.0 + \exp(\gamma_f^k)} \quad (6)$$

As with the data-generating model, selectivities for a particular fishery were assumed to be the same for all regions (Vandergoot and Brenden 2014). As part of the tag-recovery estimation model, annual fully-selected fishing mortality rates were estimated; however, age-group specific natural mortality rates were estimated in 5-year time blocks. Five-year time blocks were used for natural mortality rates based on my belief that for stock assessment purposes, it may be undesirable to make frequent adjustments to natural mortality values as it results in discontinuity in the assessment procedure. As in the data-generating model, natural mortality rates for age-3 fish were assumed to be the same as that of age-2 fish.

Model parameters were estimated by maximum likelihood estimation and were considered to have converged on a solution when the maximum gradient of the parameters with respect to the objective function was less than 1.0×10^{-3} . For some simulations, meeting the convergence criterion was problematic (i.e., maximum gradients were greater than 1.0×10^{-3}), but upon further inspection the distributions of parameter estimates from models that converged and those that did not converged overlapped thus all parameter estimates were retained. The objective function consisted of the sum of the negative log-likelihood components corresponding to the recoveries of each tagged cohort of fish. Multinomial distributions were assumed for the negative log-likelihood components for the recoveries of the tagged cohorts of fish. The negative

log-likelihoods for the recoveries of a tagged (both high- and low-reward tags) cohort of fish were calculated (with ignorable constants removed) as

$$L_{a,ty}^k = \left\{ \left(N_{a,ty}^{low,k} - \sum_k \sum_{fy} \sum_f R_{a,ty,fy,f}^{low,k} \right) \log_e \left(1.0 - \sum_k \sum_{fy} \sum_f p_{a,ty,fy,f}^{low,k} \right) + \sum_k \sum_{fy} \sum_f R_{a,ty,fy,f}^{low,k} \log_e p_{a,ty,fy,f}^{low,k} \right\} + \left\{ \left(N_{a,ty}^{high,k} - \sum_k \sum_{fy} \sum_f R_{a,ty,fy,f}^{high,k} \right) \log_e \left(1.0 - \sum_k \sum_{fy} \sum_f p_{a,ty,fy,f}^{high,k} \right) + \sum_k \sum_{fy} \sum_f R_{a,ty,fy,f}^{high,k} \log_e p_{a,ty,fy,f}^{high,k} \right\} . \quad (7)$$

Simulation Scenarios

The evaluated tagging scenarios consisted of different combinations of the number of low- and high-reward tags released annually, how tags were allocated among population age-groups, and the assumed patterns in natural mortality rates. Simulations were conducted at five different low-reward tagging levels (region 1: 1,250, 2,500, 5,000, 7,500 and 10,000 tags/ year; region 2: 250, 500, 1,000, 1,500 and 2,000 tags/ year). The mid-range tagging level (5,000 tags in region 1 and 1,000 tags in region 2) roughly corresponded to the average number of Walleyes tagged in Lake Erie between 1990 and 2007 (Vandergoot and Brenden 2014). The other low-reward tagging levels were chosen to evaluate how precision of parameter estimates changed under greater or lower tagging intensities, while still being in the range of feasible tagging levels for Lake Erie Walleye.

In addition to releasing low-reward tags, it was assumed that a smaller number of high-reward tags were also released for the purpose of estimating tag reporting rates. Imperfect tag-reporting rates can seriously affect parameter estimates from tag-recovery models and there are a number of ways for estimating tag-reporting rates, such as release of high-reward tags (Pollock et al. 2001, 2002; Hearn et al. 2003). The release of high-reward tags is frequently used to

measure tag-reporting rates (Latour et al. 2001; Taylor et al. 2006; Ebener et al. 2010a; Vandergoot and Brenden 2014), although depending on what reward level is needed to elicit 100% reporting and the level of exploitation that a stock experiences it also has the potential to considerably increase tagging study costs. For my simulations, I evaluated two levels of high reward releases. In the first, the number of high reward released was 10% of the low reward releases. In the second, the number of high reward released was 20% of the low reward releases. As a consequence, the total number of tags released each year depended on what reward-level scenario was being evaluated.

Historically, the age composition of Walleye tagged in Lake Erie has been skewed toward older individuals (Vandergoot and Brenden 2014). This skewness stems from older Walleyes arriving on Lake Erie spawning grounds before younger fish (Pritt et al. 2013), which is when Walleye tagging is generally conducted on Lake Erie. Typically, tagging continues until the annual tagging quota is achieved, which often occurs before younger individuals return to the spawning grounds. Such skewness can result in different levels of precision in estimates for parameters that are age specific. Thus as part of investigated scenarios, I evaluated how precision of parameter estimates changed under a skewed tag allocation design versus a balanced tag allocation design. Tagging age composition under the skewed tag allocation design was 10% (age 2), 10% (age 3), 10% (age 4), and 70% (age 5 and older). Tagging age composition for the balanced design was 25% for each of the age groups.

Four different natural mortality patterns for the regions were evaluated (Table 4.2). Natural mortality patterns that were examined were the following: constant through time (NMS1), linear increase throughout the course of study (NMS2), linear increase during the first

10 years of the study followed by a linear decrease during the last 10 years of the study (NMS3), cyclical with a peak in years 5 and 6 and a peak in years 15 and 16 (NMS4).

Data Analysis

For each parameter, relative error between the tag-recovery model estimates and the values assumed for the data generating model were calculated. My primary interest was on the relative error in the natural mortalities given that estimates of these parameters from tag-recovery models frequently are used to parameterize SCAA models and thus can be important for determining safe harvest levels for a fishery. Despite this being my primary focus, relative errors were calculated for all estimated parameters. As previously mentioned, I limited my analyses to the parameter estimates for regions 1 and 2 as region 3 was just a sink to which Walleyes could emigrate. The median relative error calculated across all simulations for a particular scenario was used to evaluate parameter estimate bias, while the interquartile range of the relative error calculated across all simulations was used to evaluate precision.

Results

When natural mortality rates were assumed to be constant over time, parameter estimates were mostly unbiased (when referring to bias it is in the context of median bias) regardless of how tags were allocated to age the age groups. With a balanced tag-allocation design, there were some positive biases evident in natural mortality rate estimates at lower tagging levels, particularly for region 2 and under a 10% proportional release of high-reward tags (Figure 4.1). These biases became more pronounced under a skewed tag-allocation design (Figure 4.2). Biases were also evident in estimated fishery selectivities and fishery reporting rates at the lower

tagging levels under both tag allocation designs, with biases again becoming more pronounced for the skewed design relative to the balanced design (Figure 4.3). In particular, at the lowest tagging level, commercial and recreational fishery reporting rates in region 2 were positively biased in region 2, whereas fishery selectivities were negatively biased under a skewed tag allocation design and a 10% proportional release of high-reward tags.

For the other examined natural mortality patterns, biases in parameter estimates became more evident than compared to natural mortality patterns NMS1; however, this was to be expected given the mismatch between what was assumed in the data-generating model regarding natural mortality rates and how they were estimated in the tag-recovery estimation model for these other patterns. For natural mortality pattern NMS2, age-2 and 3 natural mortality estimates were negatively biased early in the time series, but became unbiased later in the time series. This pattern was evident for both the balanced (Figure 4.4) and skewed (Figure 4.5) tag-allocation designs across all tagging levels. As was observed for natural mortality pattern NMS1, there was some bias evident in natural mortality estimates in region 2 at the lowest tagging level for both tag allocation designs (Figures 4.4-4.5), but at higher tagging levels the estimates became unbiased. At lower tagging levels, there were some positive biases in fishery reporting rates for the regions, with larger biases in region 2 and under the skewed tag allocation design and the 10% proportional release of high-reward tags (Figure 4.6). Also, there was a small negative bias in fishery selectivities at the lowest tagging level under a skewed tag allocation and 10% proportional release of high-reward tags (Figure 4.6).

For natural mortality pattern NMS3, natural mortality estimates for all ages were relatively unbiased early in the time series, but were positively biased later in the time series regardless of region and proportional releases of high-reward tags. This was observed for both

balanced (Figure 4.7) and skewed (Figure 4.8) tag-allocation designs. Compared to natural mortality patterns NMS1 and NMS2, more bias was observed in fully-selected fishing mortality rates across regions and proportional releases of high-reward tags for natural mortality pattern NMS3 (Figures 4.7-4.8). Patterns in bias for fishery selectivity and fishery reporting rates for natural pattern NMS3 were similar to the other examined scenarios. There were positive biases in fishery reporting rates at lower tagging levels particularly for region 2 and under the skewed tag allocation design and the 10% proportional release of high-reward tags (Figure 4.9). As well, there was small negative biases in fishery selectivities at the lowest tagging level under a skewed tag allocation and 10% proportional release of high-reward tags (Figure 4.9).

The greatest bias in parameter estimates was observed for natural mortality pattern NMS4, although again this was to be expected given the assumed natural mortality patterns in the data-generating model and how they were estimated in the tag-recovery estimation model. Across the time series, both fishing and natural mortalities estimates alternated between being positively and negatively biased for both regions with tagging level and proportional release of high-reward tags generally not having much of an effect (Figures 4.10-4.11). Bias in age-5 and older natural mortality estimates was smaller for the skewed tag-allocation design (Figure 4.11) compared to the balanced tag-allocation design (Figure 4.10) by virtue of there being more fish of this age-class being released under the skewed design. Patterns in bias for fishery selectivity and fishery reporting rates for natural pattern NMS4 were similar to the other examined scenarios (Figure 4.12).

In terms of evaluating precision of parameter estimates, I chose to focus my attention on natural mortality rate estimates as this is most often the parameter associated with tag-recovery models that is incorporated in assessment models when for setting safe harvest levels for

exploited fish stocks. For the other parameters, I simply note that precision of parameter estimated increased along with increases in tagging levels, which was to be expected, although gains in precision were somewhat lower at the higher tagging levels than at the lower tagging levels. Looking at overall precision of natural mortality estimates in relation to tagging level, where overall precision was defined as the arithmetic average of the mean inter-quartile ranges of the natural mortality relative errors (averaged over the four time blocks), there was a clear leveling off of precision around the mid-range tagging level (i.e., 5,000 tags in region 1 and 1,000 tags in region 2) across the examined scenarios (Figure 4.13). Comparing overall precision in natural mortality estimates across balanced and skewed tag-allocation design, precision improved by approximately 28% for age-4 and younger fish with a balanced design compared to a skewed design for both regions (Figure 4.12). Conversely, precision decreased by around 20% for age-5 and older fish for both regions with a balanced design compared to a skewed design. Increasing the proportion of high-reward tags released annually from 10 to 20% increased precision in natural mortality rates for all age groups regardless of the assessed scenario (Figure 4.12). On average, precision was roughly 20% greater when the proportion of high-reward tags released annually was 20% rather than 10%.

Discussion

When it comes to the assessment of spatially-structured fish populations, the availability of tag-recovery data from an appropriately designed tagging study can be beneficial for multiple purposes. Tag-recovery data can be directly incorporated into an assessment model framework for the purpose of estimating spatial dynamics of fish populations. Alternatively, parameter estimates from tag-recovery models can be used to aid in parameterization of assessment models

or serve as the primary basis for making management decisions. Regardless of how tag-recovery data will be used, study design is important so that actual recoveries are appropriate for their intended purpose. Whether for spatial or non-spatial purposes, costs of tagging studies can be substantial (Guy et al. 1996), and inadequate recovery and reporting of tags can lead to imprecise and/or biased parameter estimates. Thus, biologists and managers can prevent a significant waste of resources by conducting preliminary evaluations on possible tagging study designs. Recovery of tags is affected by a variety of factors, including tagging levels, issues with the tagging process (e.g., tag shedding, handling mortality), fishery characteristics (e.g., tag non-reporting, level of harvest), and fish population dynamics (e.g., movement patterns, natural mortality) (Pierce and Tomcko 1993; Fabrizio et al. 1996; Hoenig et al. 1998; Latour et al. 2001; Miranda et al. 2002; Brenden et al. 2010; Vandergoot et al. 2012). Because of this, it is important to examine precision and bias of parameter estimates across a range of design features, and stochastic simulations, such as that employed herein, have been identified as useful in this regard (Pollock et al. 2001).

Although I found that precision in parameter estimates increased along with increases in tagging levels, gains in precision were not consistent. Greater gains in precision occurred between the first three tagging levels (region 1: 1,250, 2,500, and 5,000 low-reward tags; region 2: 250, 500, and 1,000 low-reward tags), with smaller gains at the higher tagging levels. These results suggest that for the type of conditions considered herein, the mid-range tagging level (i.e., 5,000 tags in region 1 and 1,000 tags in region 2) likely would suffice for estimating spatially varying population demographic rates. Slightly better precision could be obtained at higher tagging levels; however, this gain in precision would come at greater expense due to a larger payout for recovered and reported tag and greater initial tagging costs. Whether the gains in

precision would be worth the added expense is unclear but would likely be context specific. In some cases, it may be important for parameter estimates to be as precise as possible and thus tagging at a higher level may be warranted. In other cases, a lower level of precision may be tolerable and tagging levels could be reduced to a lower tagging level. I would not advise reducing the number of fish tagged to the lowest possible tagging level considered herein given that biases in some parameter estimates were observed even under consistent natural mortality rate patterns, but again such a decision might be warranted in certain circumstances.

I observed a modest increase in parameter precision when the proportion of high-reward tags released annually was increased from 10 to 20%. The purpose of releasing high-reward tags is to allow estimation of tag-reporting rates associated with a tagging study, which in turn allows for separate estimation of fishing and natural mortality rates (Pollock et al. 2001). Thus, while the focus of releasing high-reward tags is for estimating reporting rates, it also influences the estimation of other model parameters. An overarching assumption when high-reward tags are used for estimating reporting rates is that the offered reward is sufficient to elicit 100% reporting of high-reward tags (Pollock et al. 2001). If there is not 100% reporting, then fishing mortality estimates will be negatively biased while natural mortality estimates will be positively biased (Pollock et al. 2001). In my simulations, I used reporting rates estimated from a tagging study conducted on Lake Erie Walleyes in which \$100 USD was offered for the return of high-reward tags (Vandergoot et al. 2012); however, it is not known with certainty whether this reward elicited 100% reporting. This same reward level has been used for high-reward tags in other tagging studies (Nichols 1991; Bacheler et al. 2009; Wood and Cadrin 2013), although as noted by Pollock et al. (2002) the level of reward needed to elicit 100% reporting will vary by species, location, and time. This variation in what reward level will result in perfect reporting of high-

reward tags is why studies such as the one conducted by Taylor et al. (2006) are so beneficial as they can be used to determine what reward level will result in perfect reporting.

The added expense of increasing the proportion of high-reward tags released annually from 10 to 20% depends in part on the difference in payout between high- and low-reward tags. From a design standpoint, Pollock et al. (2001) recommended that rewards be offered for all tags as otherwise tag reporting rates are likely to be low and possibly will vary over different segments of the fishing population. Based on the average number of tags returned for the different scenarios, if the difference in payout between high- and low-reward tags was 10:1 (e.g., \$50 versus \$5), the cost of a tagging study would increase by approximately 79 to 80% if the proportion of high-reward tags released annually was 20% rather than 10%. Likewise, if the difference in payout between high- and low-reward tag ratios was 20:1 (e.g., \$100 versus \$5), the cost of a tagging study would increase by approximately 88%. At 30:1 (e.g., \$150 versus \$5), the cost of a tagging study would increase by approximately 92%. Similar to what was discussed regarding tagging levels, whether the increase in precision of parameter estimates that would result from increasing the proportion of high-reward tags released annually would be worth the added expense would likely be context specific. As is evident by the cost differences presented above, releasing high-reward tags can greatly increase tagging study cost. Even at a 10:1 difference in payout between low- and high-reward tags, it is perhaps doubtful that a 20% improvement in precision of parameter estimates would justify an 80% increase in tagging study cost. Admittedly, in my research, I considered a very simple scenario (i.e., time invariant) in terms of reporting rates. With a more complex reporting rate scenario, the benefits of releasing more high-reward tags perhaps would become more evident.

With a balanced tag-allocation design, the precision of all parameter estimates, except for age-5 and older natural mortality rates and fishery reporting rates, was greater than with a skewed tag-allocation design. The largest gains in precisions were for commercial and recreational age-2 selectivities and for age-4 and younger natural mortalities. The impetus for my evaluation of the different tag allocation designs was the results presented in Vandergoot and Brenden (2014) in which difficulties were encountered when estimating natural mortality rates for certain ages of Lake Erie Walleyes. This difficulty in estimating natural mortality rates was attributed to inadequate tagging of younger Walleyes due to tagging being conducted early in the spawning period before younger fish have migrated to spawning grounds. Age-related differences in temporal patterns of spawning is not uncommon (Berkeley et al. 2004), and, from an operational standpoint, it is likely attractive to coincide tagging with spawning events due to individuals congregating in small areas. The results from my simulations, as well as the difficulties that Vandergoot and Brenden (2014) encountered, suggests that if age structure is going to be incorporated in the tagging model than some forethought may need to go into how tags will be allocated to different age groups. As with other aspects of this research, it is difficult to generalize whether a balanced tag-allocation design would always be preferable to a skewed design as this is again context specific. For example, there may be instances where achieving more precise parameter estimates for older age-groups at the expense of the younger age-groups is perhaps warranted because older fish compose most of the harvested stock. In other circumstances, such as the case of Lake Erie Walleye, younger cohorts may be an important component of the fishery and thus it may be just as important to have accurate population dynamics for younger ages as it is for older ages. In which case, adopting a balanced tag-allocation design would likely be advantageous.

How tags are allocated to different age-groups can influence the cost of a tagging study; however, it is difficult to generalize results as it depends on how demographic rates vary among ages. Based on the conditions considered herein, a skewed tag-allocation design could be expected to be between 11 and 14% more expensive than a balanced tag-allocation design by virtue of younger fish have higher natural mortality rates and age-2 experiencing lower fishing mortality rates. Alternative assumptions about natural and fishing mortality rates for the different age groups could have led to the exact opposite being true (i.e., a lower cost for a skewed tag allocation design). To achieve a balanced allocation of tags, there also could be additional sampling costs as a result of varying age-specific vulnerabilities to the sampling gear and/or as a result of age-related temporal variation in spawning. As previously indicated, generalizing tagging costs is difficult because of the factors that influence them, but I nevertheless draw attention to the aforementioned factor as costs are an important feature to consider for any tagging study.

In my evaluations, I assumed that inter-regional movement rates of tagged cohorts were known quantities based on an assumption that detailed and accurate information on individual fish movement would be available from electronic tracking studies conducted for the population of interest. In recent years, there have been remarkable advances in electronic fish tracking technology, including development of autonomous passive receivers, reductions in size of telemetry transmitters, and development of biologging devices (Adams et al. 2012; Heupel and Webber 2012). Application of these technologies for studying fish movement has also increased. For example, in the Great Lakes region of North America, there are between 10 and 15 ongoing or recently completed projects that have entailed acoustic telemetry tagging and tracking of tagged fish (<http://data.glos.us/glatos/about>). Additionally, electronic fish tracking technologies

have been recently used to monitor survival and activity centers of American Shad (*Alosa sapidissima*) in a North Carolina river (Raabe et al. 2014), movement of Unicorn fish (*Naso unicornis* and *Naso lituratus*) in a Guam marine reserve (Marshall et al. 2011), and for spatial planning of preserves and aquatic protection areas (Chapman et al. 2005; Cooke et al. 2005; Le Bris et al. 2013). Continued increasing use of electronic tracking technologies in fishery populations will undoubtedly assist in both the assessment and management of spatially structured fish populations, and ultimately may aid in the protecting of individual spawning components. In my application, I assumed that the inter-regional movement estimates from electronic tracking studies were incorporated in tag-recovery models as fixed (i.e., known estimates). Rather than treating the estimates as fixed, these estimates could have been incorporated as coefficients for prior probability distributions to help inform the estimation of movement rates from conventional tagging studies. Alternatively, the information from electronic tracking studies could be incorporated along with conventional tagging data in an integrated tag-recovery model for simultaneous estimation of mortality rates and inter-regional movement rates (Kurtado et al. 2009; Eveson et al. 2012).

Although typically used to understand movement patterns, electronic fish tracking data have also been used to estimate mortality rates for freshwater and marine fish stocks. Unlike conventional tagging studies, electronic fish tracking studies can provide direct information about the fate (i.e., alive or dead) of study fish as long as individuals remain within the study area after release and tagged individuals are encountered periodically during the study (Pincock and Johnston 2013). Recent attention has been given to estimating mortality parameters by combining information from electronic and conventional tag-return studies. Pollock et al. (2004) presented the initial model parameterizations for a combined approach. Bacheler et al. (2009)

demonstrated how this approach can be effective for estimating mortality components using a field test with estuarine Red Drum *Sciaenops ocellatus*. The model used by Pollock et al. (2004) and Bacheler et al. (2009) did not assume spatial structuring in the tag-recovery model; however, Kurota et al. (2009) and Eveson et al. (2012) each presented a framework for combining conventional and electronic tags for the estimation of fishing mortalities, natural mortalities, and movement rates. I predict that combined tagging approaches will become more common as electronic fish tracking technologies become more affordable and scientists become more familiar with the methods and the information that can be garnered from application of these methods. In the Laurentian Great Lakes of North America alone, there are numerous fish species that exhibit complex spatial structuring and for which a spatial tag-recovery study would provide beneficial information for management, including Chinook Salmon *Oncorhynchus tshawytscha*, Lake Trout *Salvelinus namaycush*, Lake Whitefish *Coregonus clupeaformis*, Lake Sturgeon *Acipenser fulvescens*, and Yellow Perch *Perca flavescens*. For some of these species, how the populations are structured spatially is believed to have changed in recent years as a result of environmental changes in the Great Lakes region (Ebener et al. 2010b); however, management policies have been slow to adjust to these changes, which could put some population components at risk of overharvest (Molton et al. 2012, 2013).

I used stochastic simulations to evaluate how precision of parameter estimates varied under different spatial tag-recovery experimental designs. Although the fishery and population characteristics I evaluated in my simulations were complex (i.e., multiple fisheries, multiple age-groups, and stock-specific movement rates) and specific to Lake Erie Walleye, the framework reflected actual conditions and processes for a spatially-structured fish population and the investigated features were reflective of possible tagging studies. The results presented herein

provide insight into how future tagging studies can be designed for spatially structured fish populations improved and proved beneficial for determining if parameters of interest were estimable given finite tagging resources and complex fishery and population spatial structuring. I recommend that additional simulation studies be conducted exploring spatial tag-recovery study designs as there is still much that needs to be learned regarding the performance of spatial tag-recovery models under different assumptions pertaining to tagging processes, fishery characteristics, and fish population dynamics. In particular, I believe it would be beneficial to conduct simulations exploring precision when parameters such as reporting rates and age-specific vulnerabilities exhibit temporal and/or spatial variation. Additionally, I recommend that simulations be conducted exploring accuracy of estimating movement rates in addition to other parameters in spatial tag-recovery models applied to conventional tagging data alone and the combination of conventional tagging and electronic fish tracking data. Regarding the latter, Eveson et al. (2012) has conducted useful evaluations based on archival tagging data; however, there are numerous other forms of electronic fish tracking methods that could be combined with conventional tagging data for which simulations would be useful.

APPENDIX

Table 4.1.—List of equation symbols used in modeling spatially varying population demographics and fishery characteristics of Lake Erie Walleye.

Symbol	Description
	Indicator variables
a	Age class (2, 3, 4, 5+)
k	Region (1, 2, 3)
f	Fishery (recreational, commercial)
ty	Tagging year (1 – 20)
fy	Fishing year (1 – 20)
	Model inputs
$N_{a,ty}^{low,k}$	Number of fish tagged with low reward tags in region k at age a in year ty
$N_{a,ty}^{high,k}$	Number of fish tagged with high reward tags in region k at age a in year ty
$\pi^{k,k'}$	The probability of moving from region k to region k' (k can equal k') at the beginning of the year
$\boldsymbol{\pi}^{k'}$	A 1×3 vector consisting of the probability of moving to region k' from one of the other regions (dependent on tagging region)
$\boldsymbol{\pi}$	A 3×3 matrix with $\pi^{k,k'}$ as its elements
	Model parameters (assumed for data-generating model and estimated in the tag-recovery estimation model)
$F_{fy,f}^k$	Fully-selected instantaneous fishing mortality rate in year fy for fishery f in region k
$M_{a,fy}^k$	Instantaneous natural mortality rate at age a in year fy in region k
θ_f	Fishery f specific inverse logit parameter for age-2 selectivities
γ_f^k	Region k and fishery f specific inverse logit parameter for tag reporting of low reward tags
	Derived variables
$s_{a,f}$	Selectivity at age a for fishery f
$p_{a,ty,fy,f}^{low,k}$	Probability that a fish tagged (low reward tags) in a region at age a and released in year ty is harvested in year fy by fishery f in region k
$p_{a,ty,fy,f}^{high,k}$	Probability that a fish tagged (high-reward tags) in a region at age a and released in year ty is harvested in year fy by fishery f in region k
$\mathbf{p}_{a,ty,fy,f}^{low}$	A 1×3 vector with $p_{low,t,a,ty,fy,f}^k$ as its elements
$\mathbf{p}_{a,ty,fy,f}^{high}$	A 1×3 vector with $p_{high,t,a,ty,fy,f}^k$ as its elements
$u_{a,fy,f}^k$	Exploitation rate at age a in year fy for fishery f in region k
$\mathbf{u}_{a,fy,f}$	A 1×3 vector with $u_{a,fy,f}^k$ as its elements
$S_{a,fy}^k$	Survival rate at age a in year fy in region k
$\mathbf{S}_{a,fy}$	A 1×3 vector with $S_{a,fy}^k$ as its elements
λ_f^k	Tag reporting rate for low-reward tags by fishery f in region k

Table 4.1 (cont'd)

$\lambda_{fy,f}$	A 1×3 vector for low-reward tags with λ_f^k as its elements
$R_{a,ty,fy,f}^{low,k}$	Total number of recoveries in year fy by fishery f in region k of fish tagged with low reward tags in region k at age a and year ty
$R_{a,ty,fy,f}^{high,k}$	Total number of recoveries in year fy by fishery f in region k of fish tagged with high reward tags in region k at age a and year ty
Matrix Operators	
$D(\)$	A matrix operator that converts a 1×3 vector into a 3×3 diagonal matrix with the elements of the vector along the diagonal
Likelihood Components	
$L_{a,ty}^k$	Negative log likelihood corresponding to low and high reward cohorts tagged and released in region k at age a in year ty

Table 4.2.— Age-specific natural mortality scenarios (NMS) assumed for fish in regions 1 (R1) and 2 (R2) in the data-generating model.

Year	NMS1				NMS2				NMS3				NMS4			
	R 1&2		R1	R2												
	Age 2	Age 4	Age 5+	Age 5+	Age 2	Age 4	Age 5+	Age 5+	Age 2	Age 4	Age 5+	Age 5+	Age 2	Age 4	Age 5+	Age 5+
1	0.32	0.32	0.15	0.20	0.30	0.15	0.05	0.10	0.20	0.15	0.05	0.10	0.20	0.15	0.05	0.10
2	0.32	0.32	0.15	0.20	0.32	0.17	0.06	0.11	0.24	0.19	0.07	0.12	0.30	0.25	0.10	0.15
3	0.32	0.32	0.15	0.20	0.33	0.19	0.07	0.12	0.29	0.24	0.09	0.14	0.40	0.35	0.15	0.20
4	0.32	0.32	0.15	0.20	0.35	0.21	0.08	0.13	0.33	0.28	0.12	0.17	0.50	0.45	0.20	0.25
5	0.32	0.32	0.15	0.20	0.36	0.23	0.09	0.14	0.38	0.33	0.14	0.19	0.60	0.55	0.25	0.30
6	0.32	0.32	0.15	0.20	0.38	0.26	0.10	0.15	0.42	0.37	0.16	0.21	0.60	0.55	0.25	0.30
7	0.32	0.32	0.15	0.20	0.39	0.28	0.11	0.16	0.47	0.42	0.18	0.23	0.50	0.45	0.20	0.25
8	0.32	0.32	0.15	0.20	0.41	0.30	0.12	0.17	0.51	0.46	0.21	0.26	0.40	0.35	0.15	0.20
9	0.32	0.32	0.15	0.20	0.43	0.32	0.13	0.18	0.56	0.51	0.23	0.28	0.30	0.25	0.10	0.15
10	0.32	0.32	0.15	0.20	0.44	0.34	0.14	0.19	0.60	0.55	0.25	0.30	0.20	0.15	0.05	0.10
11	0.32	0.32	0.15	0.20	0.46	0.36	0.16	0.21	0.60	0.55	0.25	0.30	0.20	0.15	0.05	0.10
12	0.32	0.32	0.15	0.20	0.47	0.38	0.17	0.22	0.56	0.51	0.23	0.28	0.30	0.25	0.10	0.15
13	0.32	0.32	0.15	0.20	0.49	0.40	0.18	0.23	0.51	0.46	0.21	0.26	0.40	0.35	0.15	0.20
14	0.32	0.32	0.15	0.20	0.51	0.42	0.19	0.24	0.47	0.42	0.18	0.23	0.50	0.45	0.20	0.25
15	0.32	0.32	0.15	0.20	0.52	0.44	0.20	0.25	0.42	0.37	0.16	0.21	0.60	0.55	0.25	0.30
16	0.32	0.32	0.15	0.20	0.54	0.47	0.21	0.26	0.38	0.33	0.14	0.19	0.60	0.55	0.25	0.30
17	0.32	0.32	0.15	0.20	0.55	0.49	0.22	0.27	0.33	0.28	0.12	0.17	0.50	0.45	0.20	0.25
18	0.32	0.32	0.15	0.20	0.57	0.51	0.23	0.28	0.29	0.24	0.09	0.14	0.40	0.35	0.15	0.20
19	0.32	0.32	0.15	0.20	0.58	0.53	0.24	0.29	0.24	0.19	0.07	0.12	0.30	0.25	0.10	0.15
20	0.32	0.32	0.15	0.20	0.60	0.55	0.25	0.30	0.20	0.15	0.05	0.10	0.20	0.15	0.05	0.10

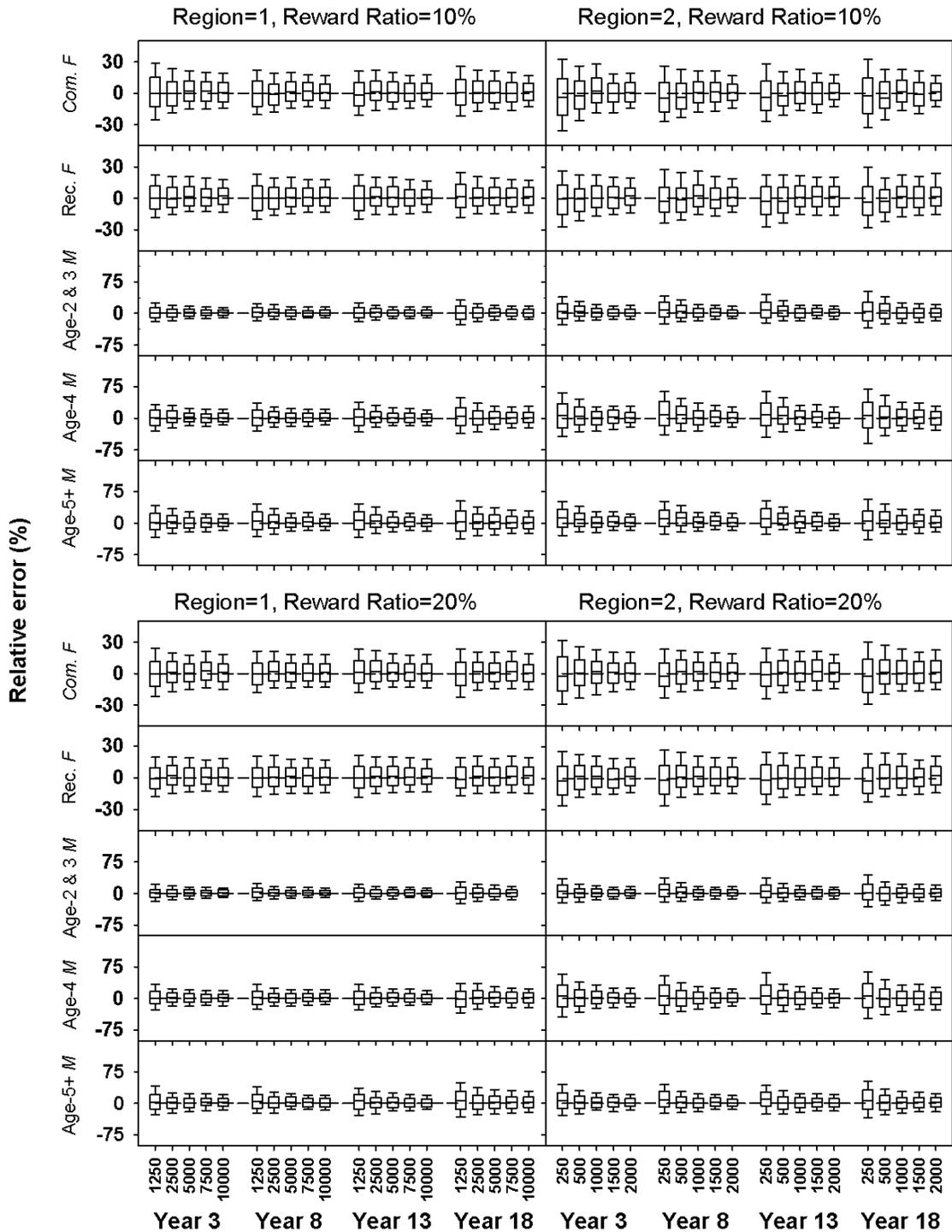


Figure 4.1.—Sensitivity plots of the instantaneous natural mortality (M) rates for Lake Erie Walleye (regions 1-5) assuming five different movement scenarios (Table 3.2) for Walleye in regions 3 and 5, two different prior probability distributions for natural mortality (prior 1: log-normal median = 0.40; prior 2: log-normal median = 0.20) and the year-, fishery-, and region-specific reporting rates presented by Vandergoot et al. (2012).

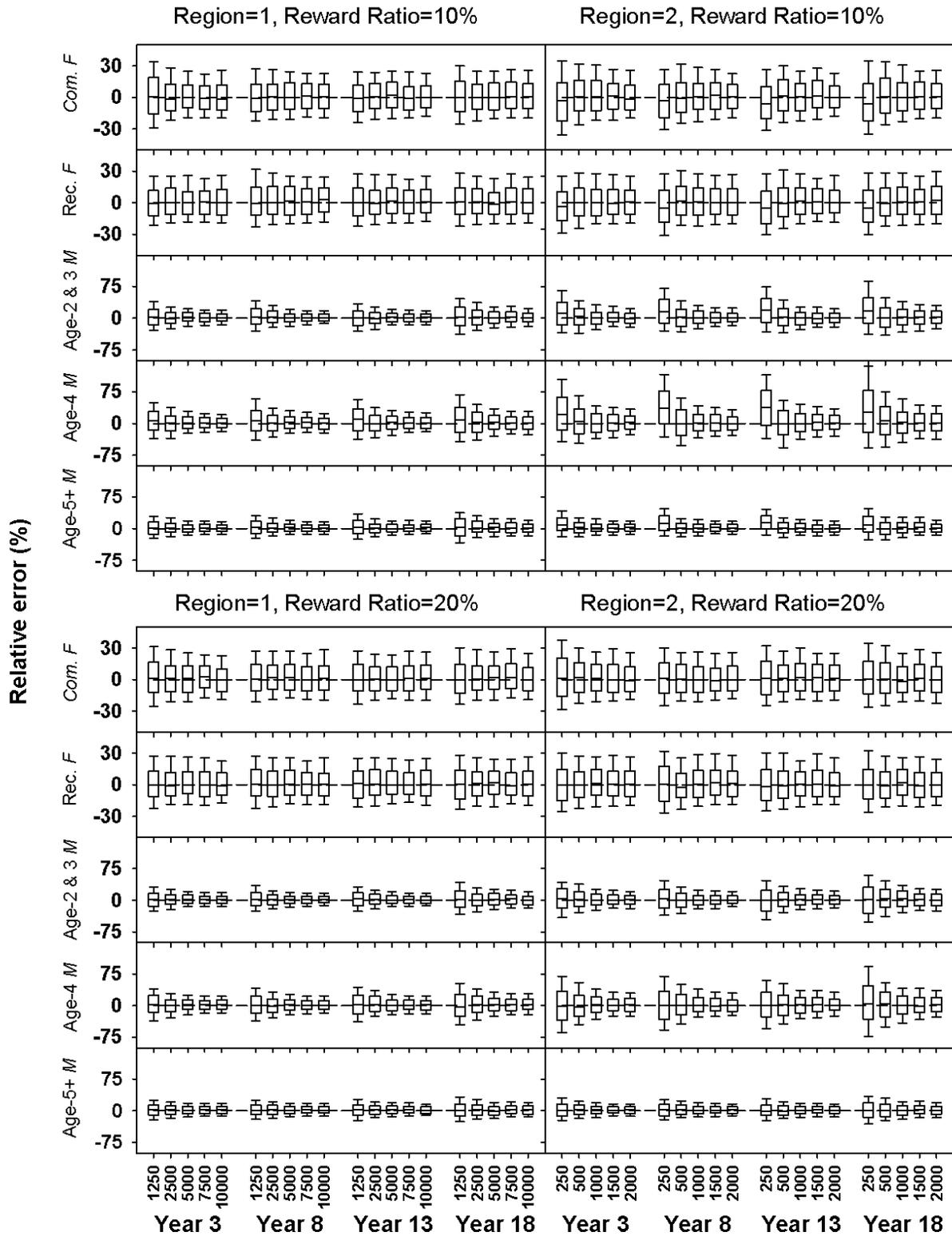


Figure 4.2.—As in Figure 4.1 except for a skewed tag-allocation design.

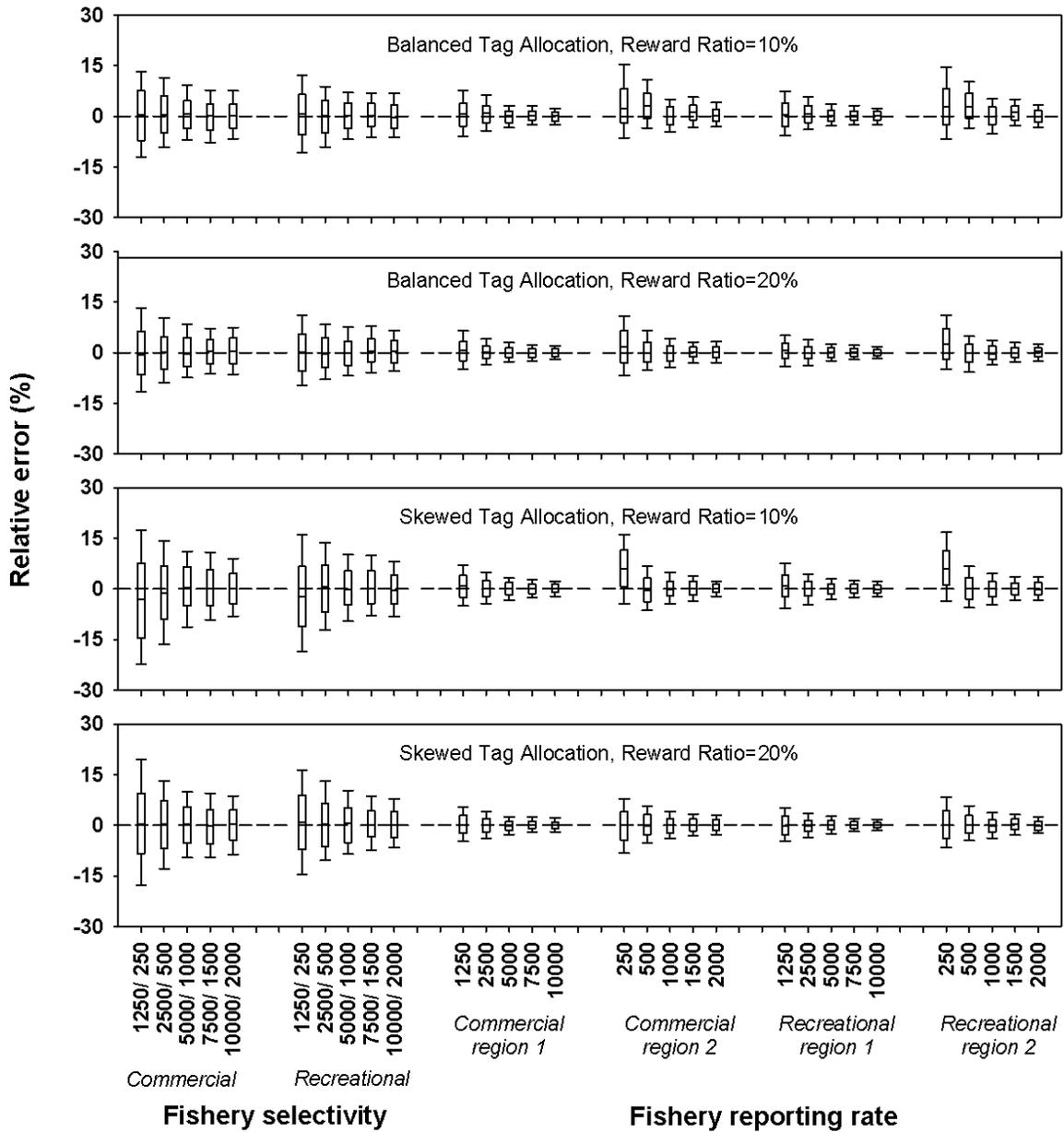


Figure 4.3.—Distributions of relative errors in fishery-specific selectivities and fishery- and region-specific reporting rates for skewed and balanced tag-allocation designs under high-reward tagging proportions of 10 and 20% (reward ratios). The relative error values shown are for natural mortality pattern NMS1. Results are only shown for simulation years 3, 8, 13, and 18 for conciseness

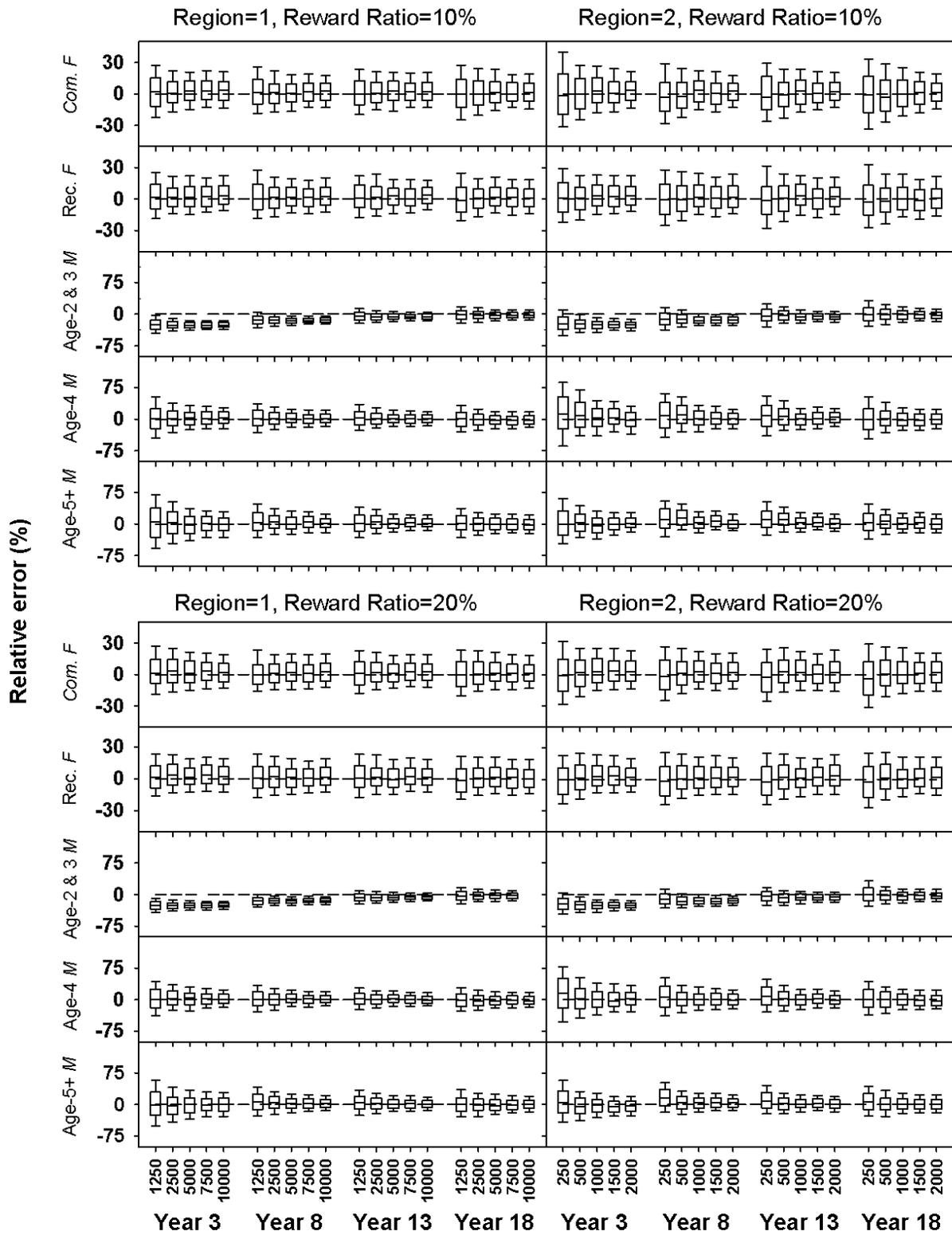


Figure 4.4.—As in Figure 4.1 except for natural mortality pattern NMS2.

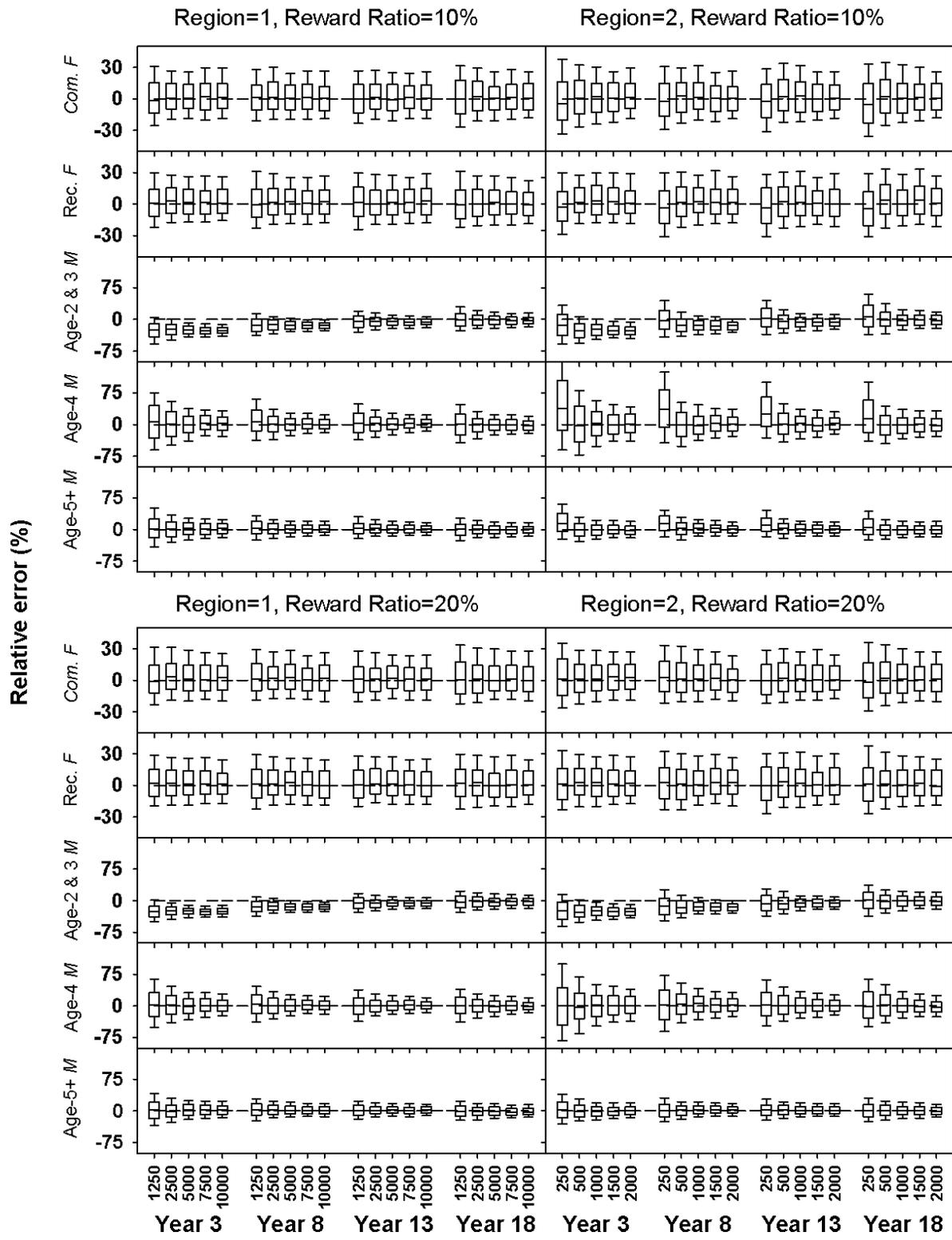


Figure 4.5.—As in Figure 4.2 except for natural mortality pattern NMS2.

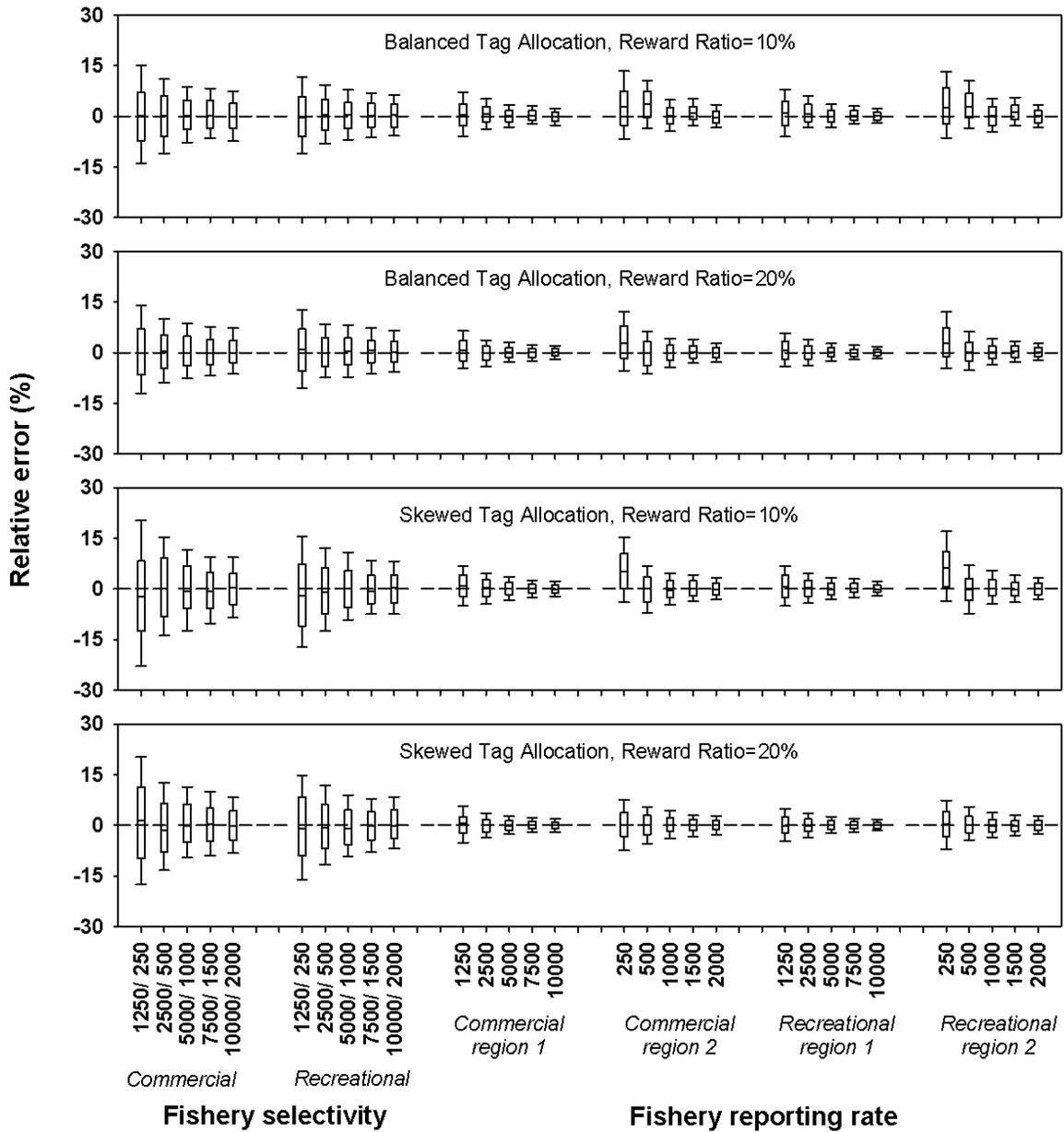


Figure 4.6.—As in Figure 4.3 except for natural mortality pattern NMS2.

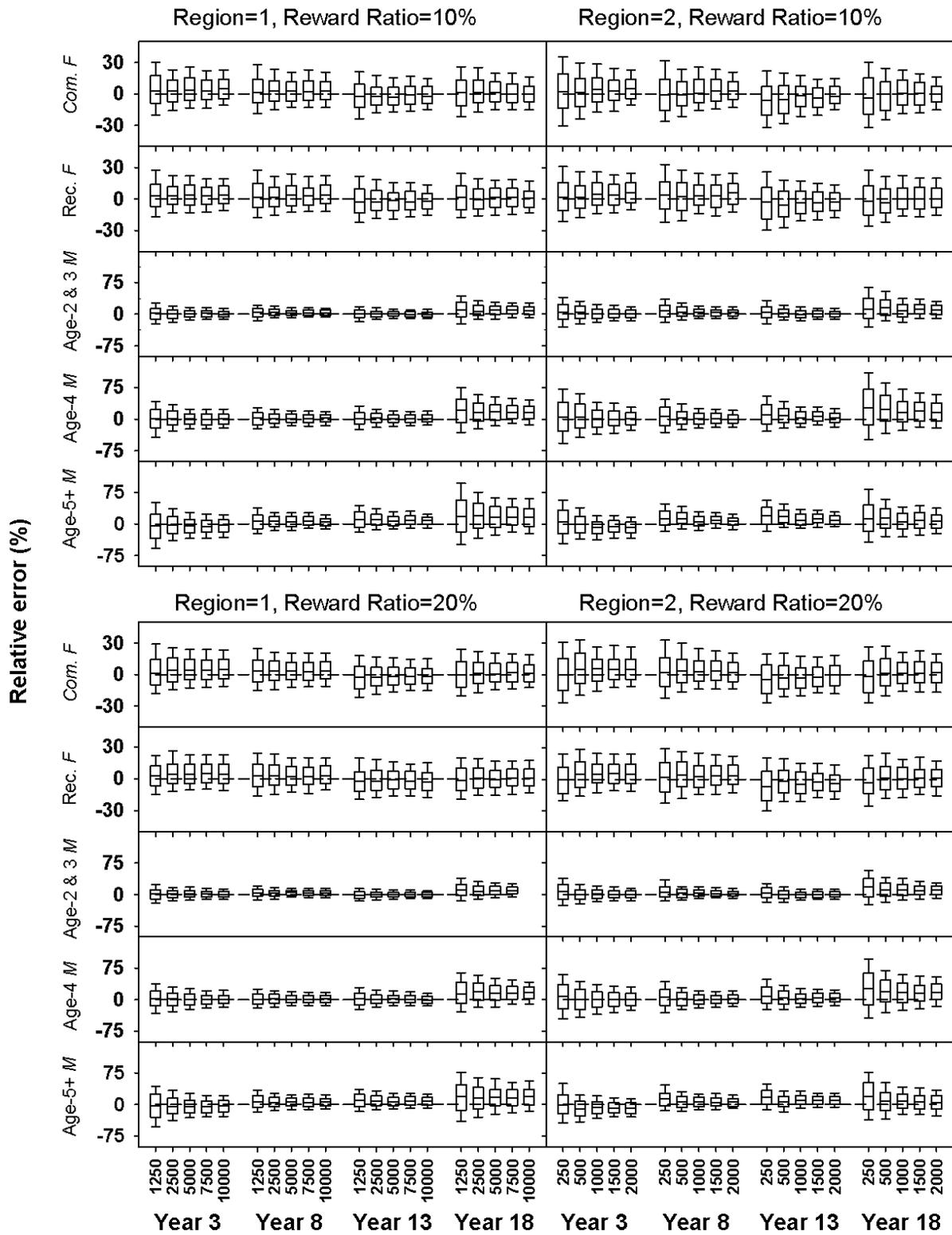


Figure 4.7.—As in Figure 4.1 except for natural mortality pattern NMS3.

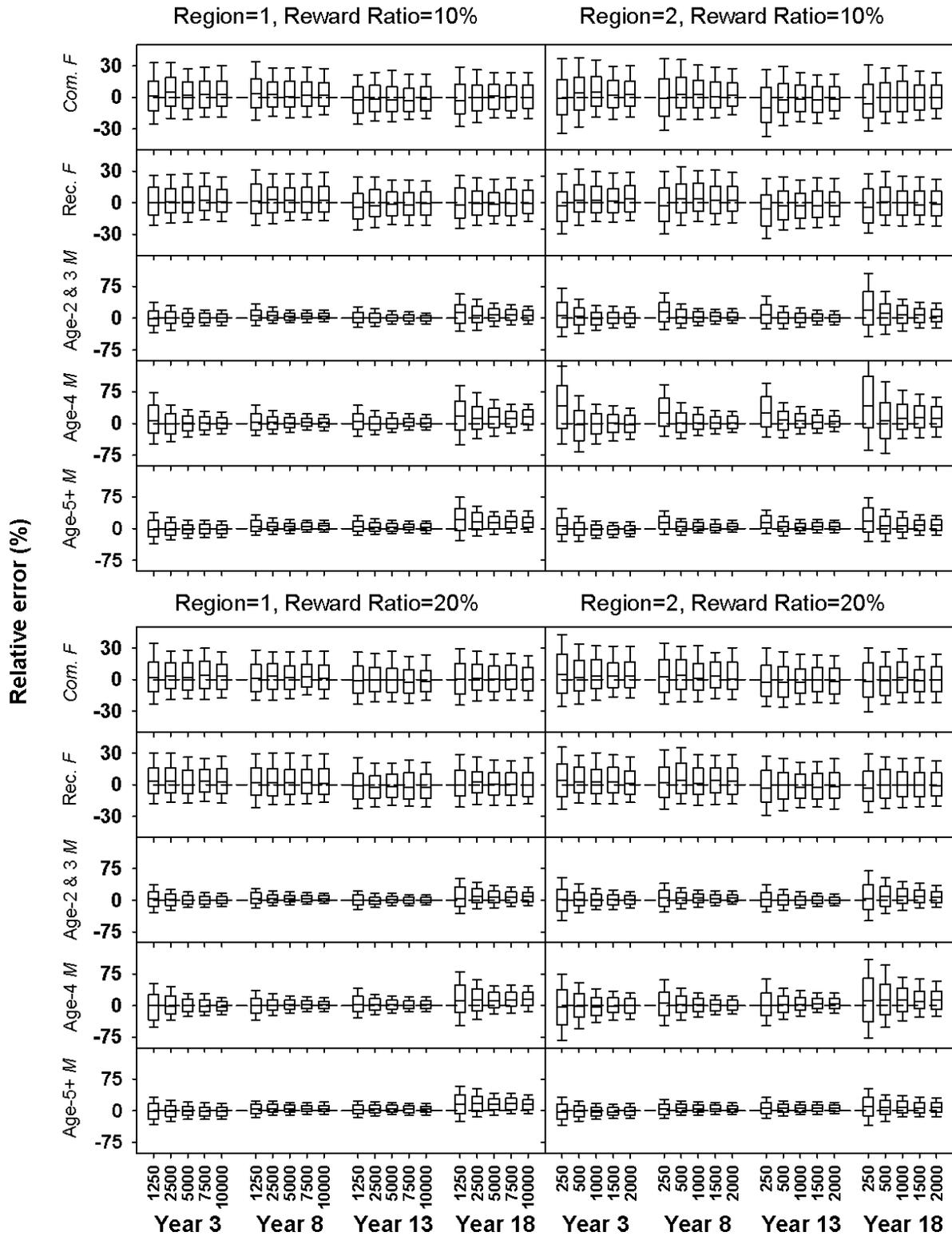


Figure 4.8.—As in Figure 4.2 except for natural mortality pattern NMS3.

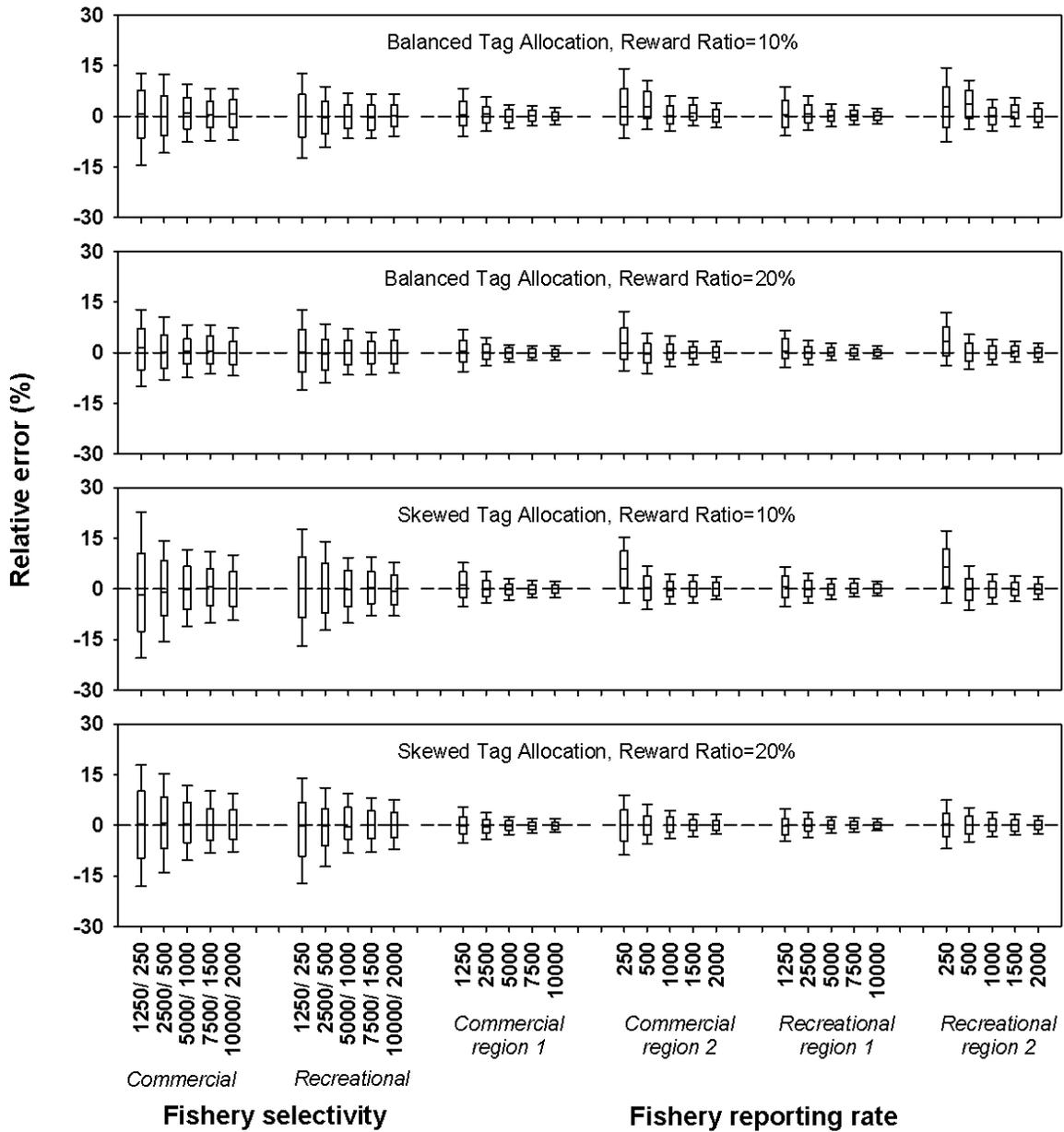


Figure 4.9.—As in Figure 4.3 except for natural mortality pattern NMS3.

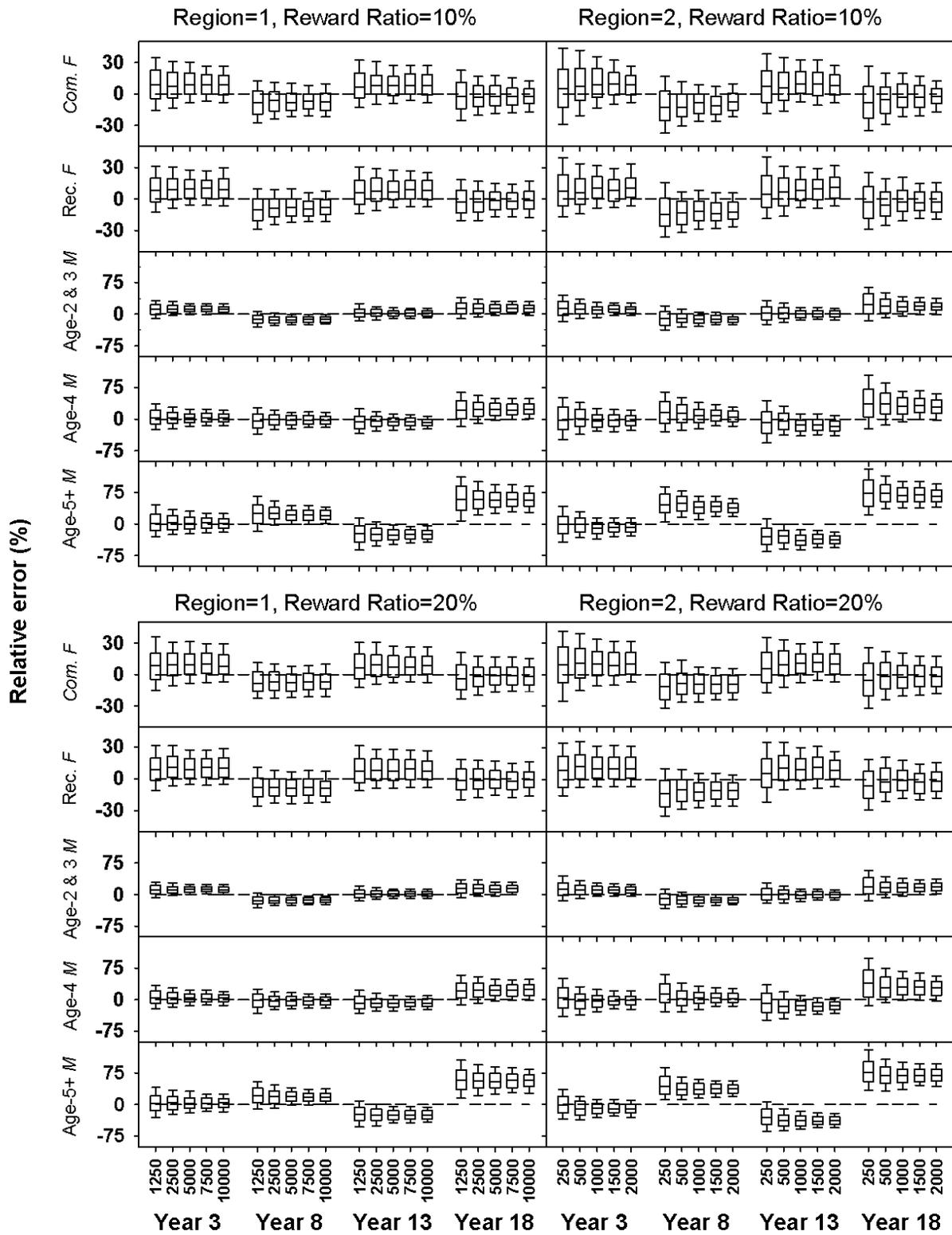


Figure 4.10.—As in Figure 4.1 except for natural mortality pattern NMS4.

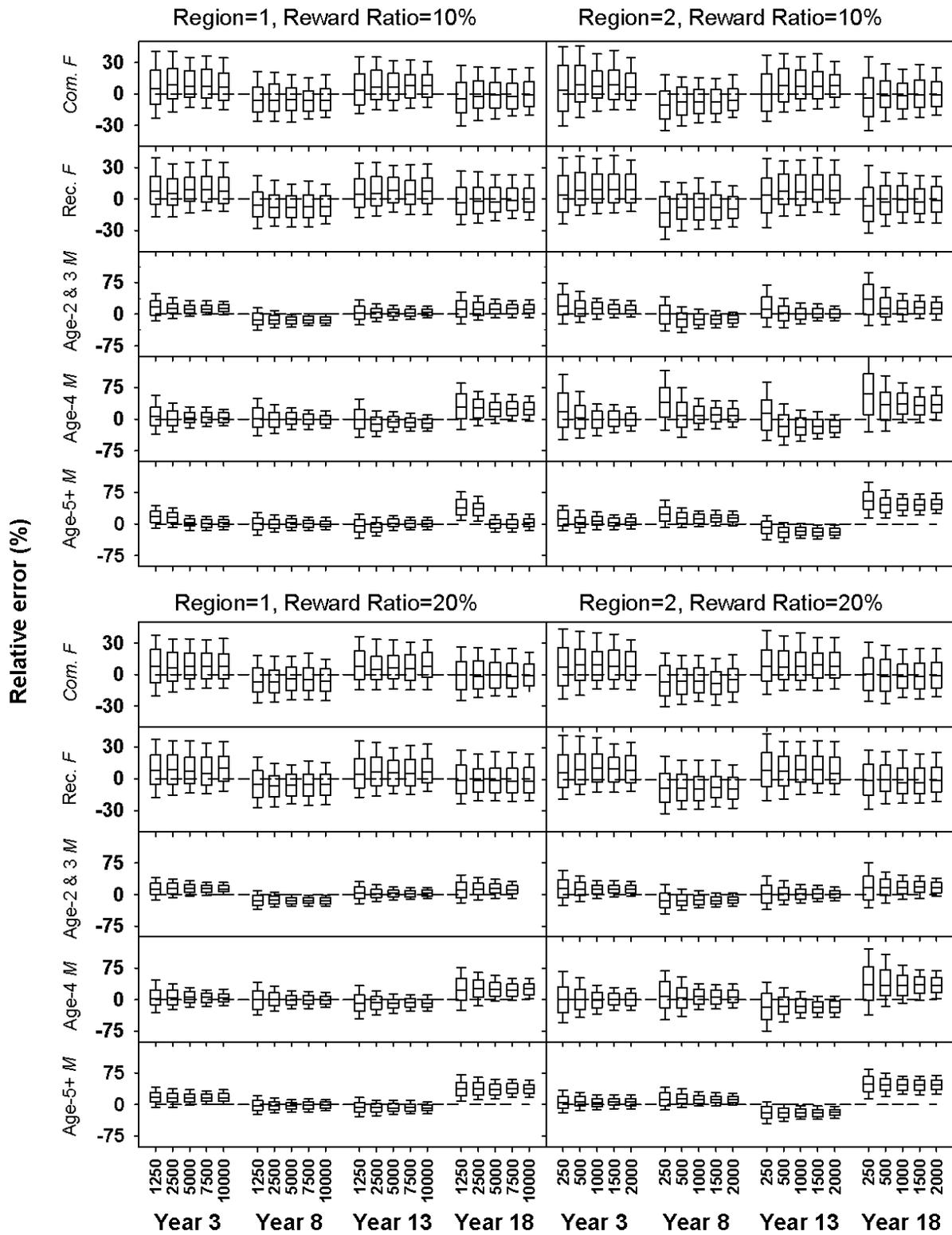


Figure 4.11.—As in Figure 4.2 except for natural mortality pattern NMS4.

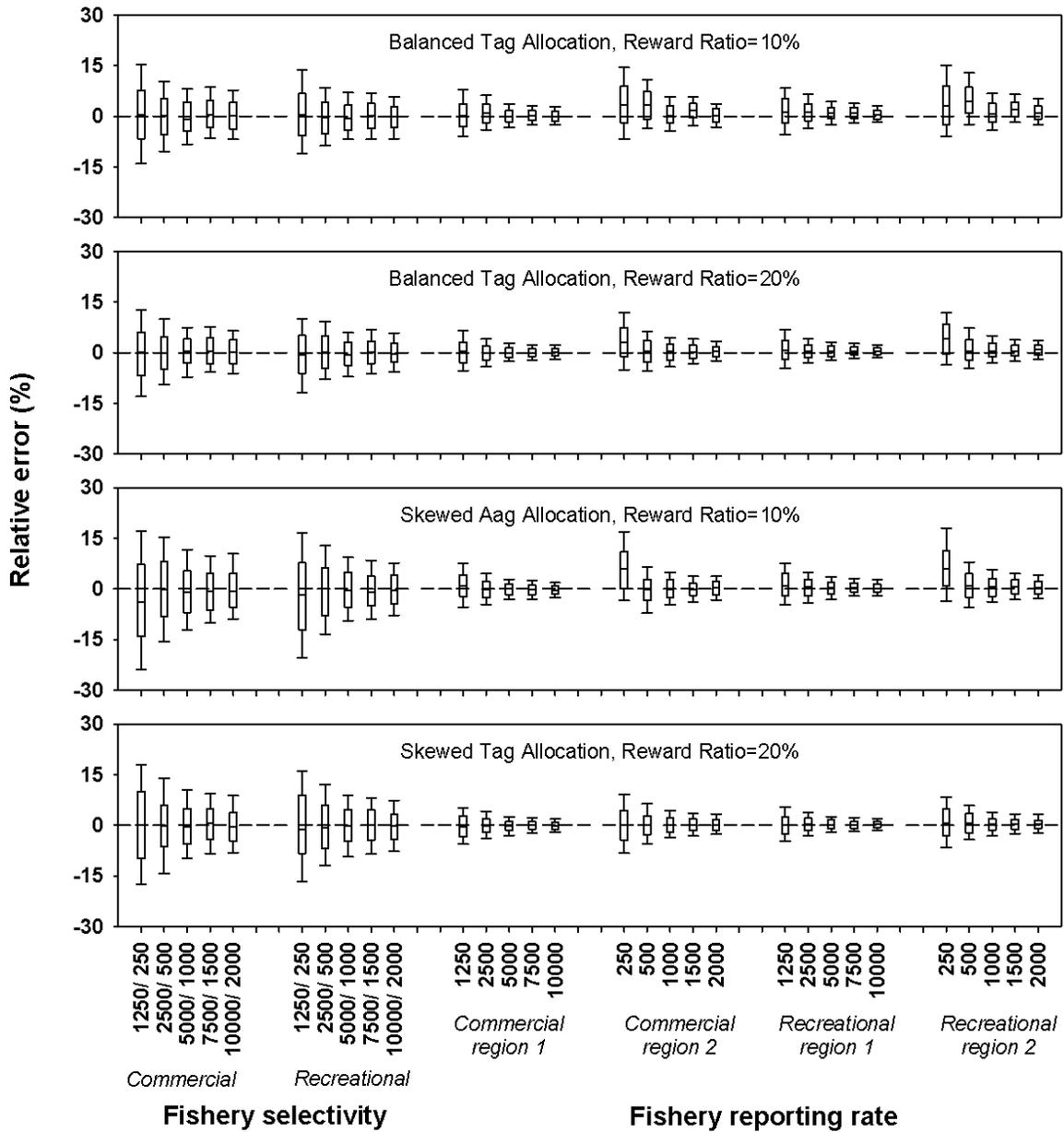


Figure 4.12.—As in Figure 4.3 except for natural mortality pattern NMS4.

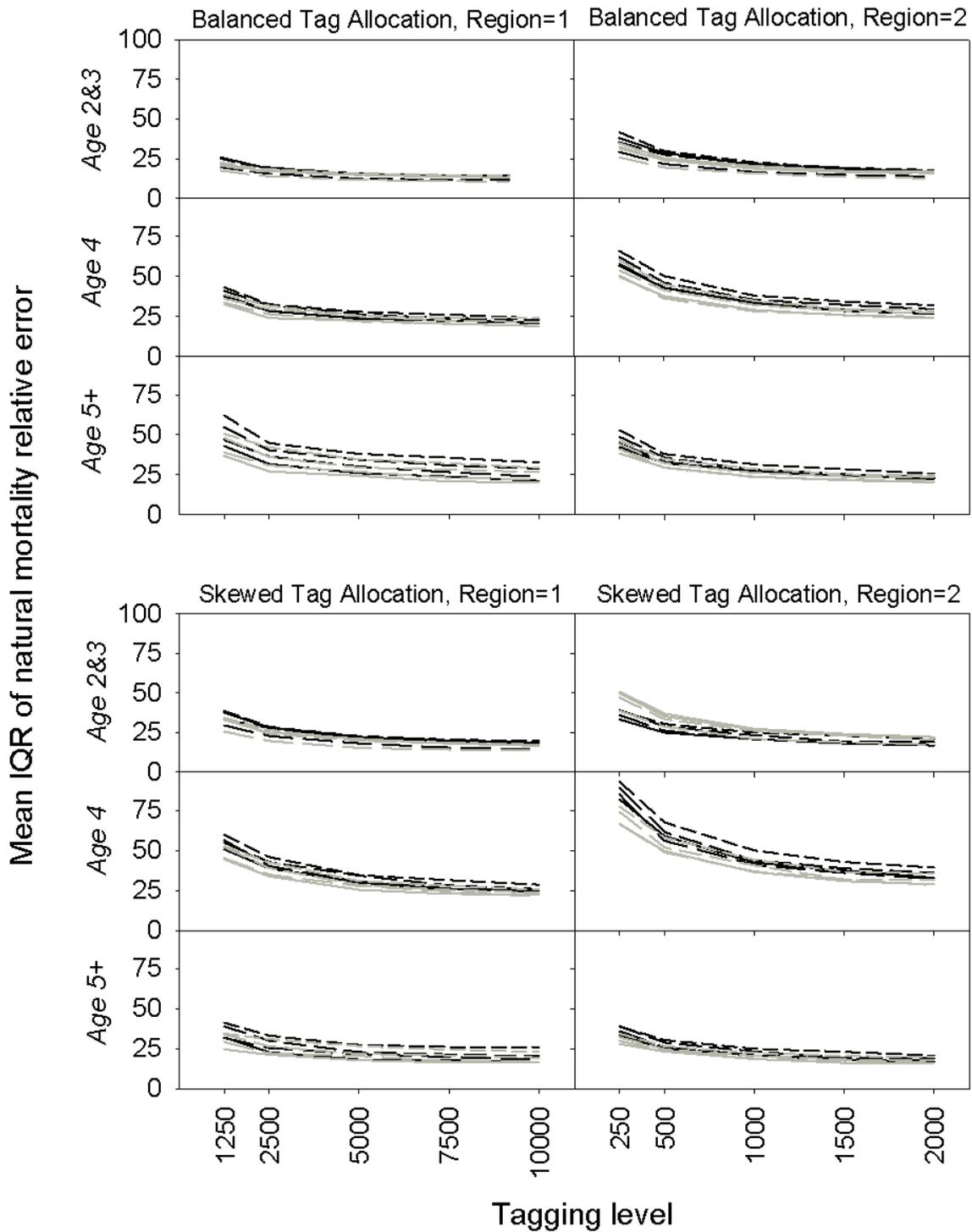


Figure 4.13.—Mean interquartile ranges of the relative errors in the age-group-specific natural mortalities (averaged across the four time blocks) by tagging level for regions 1 and 2 and for balanced and skewed tag allocation designs (solid line = NMS1; long-dash line = NMS2; medium-dash line = NMS3; short-dash line = NMS4; black lines = 10% high-reward tagging proportions; gray lines = 20% high-reward tagging proportions [reward ratios]).

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CHAPTER 5

MANAGEMENT RECOMMENDATIONS

Although the LEWTP concluded in 2009, the findings presented in this dissertation will aid in the management of Lake Erie Walleye stocks and efforts to design future tagging studies. The results presented in Chapter 2 *Estimation of Tag Shedding and Reporting Rates for Lake Erie Jaw Tagged Walleye* demonstrate the necessity of quantifying tag retention and reporting rates, as well as other factors that have the potential to influence tag recoveries, such as tagging-related mortality and delayed mixing of tagged individuals with at-large populations. Because 1) tag-retention rates varied between tagging methods and among agencies and 2) reporting rates varied between fisheries, basins, and time periods, the accuracy of parameter estimates based on analyses of recoveries from the LEWTP that did not account for shedding or imperfect tag reporting are highly suspect. The results also demonstrate the importance of rigorous evaluation of assumptions regarding factors such as tag shedding and tag reporting at the onset of a tagging study rather than as an afterthought a few years prior to the tagging study being concluded. The results presented in Chapter 3 *Spatially-Varying Population Demographics and Fishery Characteristics of Lake Erie Walleye (Sander vitreus) Inferred from a Long-Term Tag-Recovery Study* provide region- and age-specific mortalities and regional movement probabilities for Lake Erie Walleye, which should assist in the parameterization and scaling of a spatially-explicit assessment model for use as part of the lake's quota-management system. Finally, the results in Chapter 4 *Precision of Parameter Estimates from a Spatial Tag-recovery Model When Inter-regional Movements are Known* should provide beneficial information regarding the design of future tagging studies for Lake Erie Walleye for the purpose of estimating region- and age-

specific mortality components through a spatial tag-recovery model while taking advantage of the investment in acoustic telemetry equipment in the Great Lakes region. The results suggest that under conditions similar to the LEWTP programming, a tagging level of approximately 5,000 fish in the west/central basin and 1,000 fish in the eastern basin would be sufficient for obtaining precise estimates of mortality rates. Additionally, the results suggest that a balanced tag-allocation design would increase precision in age-4 and younger natural mortality rates by approximately 28% and decrease precision in age-5 and older natural mortality by approximately 20% for age-5 and older fish.

Listed below are some specific recommendations for future Walleye tagging studies and refinements to the current stock assessment model based on the findings of my dissertation research:

Tag retention should be evaluated routinely under conditions that tagged fish will encounter while at liberty. The double-tagging experiment conducted as part of Chapter 2 indicated that depending on the application method shedding of jaw tags may be problematic. In previous analyses of LEWTP tag recovery data, tag shedding was assumed to not occur based on relatively brief studies conducted in experimental ponds. This discrepancy in results highlights the importance of evaluating tag shedding under conditions that tagged fish are likely to encounter while at liberty. Furthermore, the variability in tag shedding associated with slight variation in methods of application rates underscores the need to design shedding studies that consider such application differences. Regardless of the tag type used in future tag-recovery studies (i.e., jaw tag, anchor tags, etc.), turnover in agency personnel necessitates that routine tag retention studies be conducted to account for this potential source bias. If the LEWTP is re-

instituted using jaw tags, I recommend that participating agencies adopt the tag attachment method (i.e., wrapping tag around jaw rather than crimping it on) utilized by the Michigan Department of Natural Resources and the New York State Department of Environmental Conservation.

High-reward tagging studies should be conducted to determine the monetary value required to elicit complete (i.e., 100%) reporting of tags. In the current study, although high-reward tags were used to estimate tag-reporting rates it is unclear if complete reporting (i.e., 100% of harvested high-reward tags) of these tags is achieved by offering a reward of \$100USD. If reporting of high-reward tags is incomplete, the tag reporting rates presented in this study would be over-estimated; consequently, fishing mortality rates would be under-estimated and natural mortality rates over-estimated. The Lake Erie Walleye fishery is unique in that large commercial and recreational fisheries exploit this resource, and Walleye are highly migratory. As a result, it is necessary to consider what reward level would elicit 100% reporting accounting for different areas and types of fishers.

Future tagging studies should estimate fishery-specific reporting rates on an annual basis using a study design where high and low reward tags are released simultaneously. As part of the LEWTP, high-reward tags were only released in 1990 and 2000. Because of this limited release of high-reward tags, reporting rate estimates in some years were based on recoveries of very few tags. As a consequence, the accuracy of annual reporting rate estimates is questionable. Not concurrently releasing low- and

high-reward tags in each year can also lead to a problem of unaccounted for temporal changes in reporting rates.

During the tagging process, tags should be allocated among population components of interest so these parameters can be estimated reliably. When the interagency tagging study was initiated, meeting site-specific tagging quotas was the primary concern; consequently, allocating tags to specific population components of interest (i.e., by age-group) was a low priority. Because of this, low numbers of young fish were tagged annually and when it came to estimating natural mortality rates for these younger age classes, problems were encountered. Careful consideration to how tags are allocated to different population components should be given when future tagging studies are designed to ensure parameters of interest can be estimated. Given the consumptive nature of the Lake Erie Walleye fishery, precise and accurate mortality estimates for younger fish are likely just as important as estimates for older fish.

Adequate numbers of tags should be applied to male and female Walleye in future tagging studies so that sex-specific mortality rates can be estimated. Due to the way tags were allocated in the current study, i.e., the majority (>90%) of fish tagged were males; the rates presented here are most applicable to this demographic component even though the parameter estimates presented are for combined sexes. Consequently, future tagging studies should focus on tagging adequate numbers of fish of both sexes so sex-specific rates can be estimated. This recommendation stems from that fact that previous studies have suggested that the timing and extent of movement is influenced by fish sex.

For example, female movements are thought to encompass a greater spatial extent than males, thus mortality rates may vary due to this behavior.

Additional research should be conducted to determine optimum tagging levels which take into account trade-offs between parameter precision and financial constraints.

In the current study, parameter precision varied considerably depending on the tagging scenario evaluated. For example, as the number of fish tagged increased and more high-reward tags were released, there was a concomitant increase in precision of the fishery and demographic parameters estimated. Consequently, an increase in the cost of the tagging study would be associated with each of these scenarios. Although increased project costs might be justified, particularly for intensively managed fisheries like Lake Erie Walleye, at some point obtaining higher precision may not be worth the additional expenditure. While the goal of this study was not to evaluate what level of precision is required for stock assessment purposes or how to achieve this level given limited financial resources, future tagging study evaluations should include a cost/ benefit analysis to identify the least expensive way to implement a tagging study while achieving a desired precision level.

Future tag recovery models used to estimate mortality rates for Lake Erie Walleye should be parameterized to estimate spatial fishery characteristics and demographic population parameters.

Based on the tag-return data analyzed in this study, there is no evidence to support the assumption that mortality rates for Lake Erie Walleye are spatially homogeneous. Previous attempts to estimate tag-based mortality rates have neglected to account for spatial structuring, thus the mortality rates estimated in these

studies overlooked an important consideration for understanding the population dynamics of this important fishery resource. Consequently, future tagging studies (e.g., tag-recovery or telemetry) should be designed to validate the movement rates presented in this study and estimate mortality rates at spatial scales appropriate to management. Ideally, the tag-recovery model would have been parameterized to estimate mortality rates for each basin (i.e., western, central and eastern). However, since tagging did not occur in the central basin, it was impossible to treat this area of the lake as separate regions (i.e., similar to the western basin with Ontario and US waters separate). Instead tagging data (i.e., releases and recaptures) from the central basin was combined with the eastern basin due to the similarity in bathymetry, limnology (i.e., thermal stratification) and fish community (e.g., forage base). Thus, future studies should focus on estimating mortality parameters independently for the western, central and eastern basins to provide a better representation of the spatial extent of Lake Erie Walleye.

Natural mortality and movement rates should be estimated on time scales that are realistic from a biological standpoint. Even though the best tag-recovery model used to estimate natural mortality and movement rates in Chapter 3 treated these parameters as being time-invariant (i.e., over the 17 year study), from a biological standpoint this may be unrealistic given what is known about the population dynamics of wild fish stocks. For all but the most complex natural mortality pattern scenarios evaluated, the results presented in Chapter 4 suggest that natural mortality rates can be estimated reliably on shorter time intervals (e.g., 5 year) provided sufficient numbers of fish are released. This is important because it is unrealistic to assume that the mortality and movement rates

remain static over extended time periods. Additionally, future studies should be designed to estimate natural mortality and movement rates based on fishery-independent surveys.

Recently, Lake Erie fishery managers adopted a new harvest policy for establishing safe harvest levels for Walleye utilizing a process involving stakeholders. The harvest policy selected during this process used the current stock assessment model (i.e., non-spatial) to evaluate how the population would respond to different harvest strategies. Although the population model used ignores inter and intra-lake movements and variable natural mortality rates, the results of the current study suggests these rates do vary regionally and by age. While re-structuring the Lake Erie Walleye stock assessment model to more accurately reflect the demographic processes described in this study would be justifiable from a scientific standpoint, managers should be aware that doing so would likely require re-evaluating the current harvest policy since accounting for spatial variability represents a considerable change to the model structure. The following are suggestions for incorporating spatial structure into the stock assessment model for Lake Erie Walleye.

The demographic parameters presented in this study could be used to develop a “lakewide” Walleye stock assessment model. Currently, quota management for Lake Erie Walleye is based on the abundance of western basin spawning stocks (i.e., Lake Erie Walleye Management Units 1-3); but, this approach only partially captures the dynamics of this complex population. In fact, it is well established that Walleye originating from the western basin migrate to the eastern basin (i.e., Lake Erie Walleye Management Units 4 and 5) during the summer months where they mix with eastern basin fish. Since the

current Western Basin stock assessment model fails to account for fish harvested in the eastern basin, the population estimates are inherently biased. The stock-specific movement and natural mortality rates presented in this study provide the information necessary to initiate preliminary lakewide stock assessment modeling attempts.

However, a reliable mechanism (e.g., genetic, microchemistry, or tagging studies) for determining stock contribution (i.e., fish originating from the eastern and western basin spawning stocks) is essential for obtaining plausible population estimates.

The movement rates presented in this study could be used to account for spatial structuring. In the current study, tag-recovery information was used to quantify movement patterns of Lake Erie Walleye. Consequently, the movement rates presented in Chapter 3 could be incorporated into a spatial stock assessment model to more accurately reflect the spatial structuring of the Walleye population. For example, even though it is widely accepted that western basin Walleye migrate to the eastern basin, the current stock assessment model fails to account for this phenomenon because the degree to which this occurred thus far remains unquantified. Similarly, emigration of western basin Walleye from Lake Erie via the Detroit River also remains unaccounted for in the current stock assessment model. Furthermore, the age-specific movement rates presented here provides a level of detail that also has been lacking; thus, the age- and region specific movement rates presented here provide a mechanism for accounting for these dynamics in a spatially explicit stock assessment model to more accurately mimic reality.

The age and region specific natural mortality rates could be used to inform a spatial stock assessment model for Lake Erie Walleye. In the current study, the tag recovery data indicated natural mortality rates varied by age and region which is in stark contrast to the previous assumption that natural mortality for Lake Erie Walleyes were constant among ages and across regions. Thus, similar to the movement rates, the natural mortality rates presented here represent an in-depth understanding about the demographics of Lake Erie Walleye and provide a means for informing a spatial stock assessment model to account for demographic heterogeneity which is currently ignored. Furthermore, because the natural mortality rates estimated in Chapter 3 are corrected for tag loss and non-reporting (Chapter 2), these estimates are more robust to the assumptions associated with tag-recovery models than previous estimates. However, additional studies designed to estimate natural mortality rates for Walleye < age-5+ are needed because some of the estimates presented in the current study were uninformative.