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Movements, Growth, and Mortality of Chesapeake Bay Summer Flounder Based on Multiple Tagging Technologies

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Movements, Growth, and Mortality of Chesapeake Bay Summer Flounder Based on Multiple Tagging Technologies

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Presented to

The Faculty of the School of Marine Science

The College of William and Mary in Virginia

In Partial Fulfillment

of the Requirements for the Degree of

Doctor of Philosophy

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by

Mark J. Henderson

2012

APPROVAL SHEET

This Dissertation is submitted in partial fulfillment of

the requirements for the degree of

Doctor of Philosophy

Mark J. Henderson

Approved, by the Committee, August 2012

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DEDICATION

For my wife, Nikki, and our dog, Keta. They continually reminded me that the most important things in life rarely have to do with work.

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ABSTRACT

The research projects presented in this dissertation used multiple tagging technologies to examine the movements, growth, and mortality rates of summer flounder tagged and released in Chesapeake Bay. In the first two chapters, I used acoustic, archival, and conventional tags to examine the behavior of summer flounder on different spatial scales. Investigating the movement behavior of individuals on different scales is an important step towards understanding how large-scale distributions of a population are established. Based on the observed behaviors of summer flounder, I hypothesize that the movements of these fish are primarily related to foraging behavior while they are resident in Chesapeake Bay. In the third chapter, I use growth models to investigate hypotheses regarding recreational angler noncompliance with minimum size regulations in Virginia. Angler noncompliance with management regulations can severely degrade the ability of fishery managers to prevent overexploitation of fish populations. Using a growth model fit to recreational angler mark-recapture data, I demonstrate that recreational anglers in Virginia responded to changes in summer flounder management regulations, but considerable levels of noncompliance were detected in years when management agencies drastically increased the minimum size regulations. In the final chapter, I attempt to estimate natural and fishing mortality rates of summer flounder using conventional mark-recapture data collected by an angler tagging program. These mortality rates were estimated using a Barker model, which is a generalization of the Cormack-Jolly-Seber tagging model. Results from this study indicated that sublegal summer flounder experience different emigration or mortality processes than do larger fish. Furthermore, handling and tagging mortality rates of summer flounder were much larger than the recreational discard mortality rate currently used in the stock assessment, implying that the recreational discard mortality rate should be reexamined. The research presented in this dissertation provides information that could be used by management agencies to further understand the behavior of summer flounder, and how to most effectively manage this population.

AUTHORS NOTE

The chapters of this dissertation were written in manuscript format for publication. Thus, each chapter was written in the third person to represent my co-authors. The citations for the chapters are as follows:

Chapter 1
Henderson MJ, Fabrizio MC, Lucy JA (In review) Movement patterns of summer flounder near an artificial reef: Effects of fish size and environmental cues. Marine Ecology Progress Series.

Chapter 2
Henderson MJ, Fabrizio MC, Lucy JA (In prep) Using archival and conventional tags to observe summer flounder movements at different spatial scales.

Chapter 3
Henderson MJ and Fabrizio MC (In prep) Using mark-recapture growth models to discern recreational angler noncompliance with minimum length regulations.

Chapter 4
Henderson MJ and Fabrizio MC (In prep) Estimation of summer flounder mortality rates using mark-recapture data from a recreational angler tagging program.

Movements, Growth, and Mortality of Chesapeake Bay Summer Flounder Based on Multiple Tagging Technologies

INTRODUCTION

Summer flounder *Paralichthys dentatus* are one of the most targeted and valuable fish species of the US Atlantic coast, making effective management essential to ensure the sustainability of the population (Terceiro, 2002). Regulations of the summer flounder fishery in the mid-Atlantic region have been especially critical in recent years, during which the Atlantic States Marine Fisheries Commission and the Mid-Atlantic Fishery Management Council instituted a rebuilding plan for the summer flounder population in response to large declines in abundance observed during the early 1990s. Summer flounder range from Nova Scotia to Florida but are primarily targeted by the commercial and recreational fisheries from Massachusetts to North Carolina, where the population abundance is high (Terceiro, 2002). The commercial fishery primarily occurs offshore during the winter months when summer flounder spawn along the edge of the continental shelf (Morse 1981, Kraus and Musick 2001). In contrast, the recreational fishery primarily occurs in the spring and summer when fish return to coastal bays and estuaries to feed (Kraus and Musick 2001). The success of the rebuilding plan depends on instituting effective management regulations, which rely on understanding the ecology, growth, and mortality rates of the summer flounder population (Hilborn and Walters 1992, NRC 2000).

One important aspect of summer flounder ecology that is not well understood is their behavior while fish are resident in inshore habitats.

Understanding habitat use and movement patterns of individual fish is becoming increasingly important as researchers recognize the connection between individual behavior and a population's vital rates (e.g., recruitment, mortality, and emigration; Sutherland 1996). Linkages between habitat, movement behaviors, and population dynamics have been investigated using individual-based models (Lomnicki 1999, Humston et al 2004, Hayes et al 2009), which provide a mechanism to understand how large-scale species distributions are established from small-scale behavioral decisions (Roshier et al 2008, Humston et al 2004). However, such models often suffer from a lack of information on the movement behaviors of individual fish relative to environmental conditions (Humston et al 2004, Hayes et al 2009). In the case of summer flounder, large-scale seasonal migrations have been well studied with conventional mark-recapture techniques, but few studies have examined the fine- (<1 meter) and small- (100s of meters) scale movements of these fish. The small-scale studies that have been conducted indicate that summer flounder behavior is related to tidal state (Szedlmayer and Able 1993), dissolved oxygen levels (Miller 2010), and time of day (Capossela 2010, Miller 2010). Although suggestive, these studies primarily observed dispersal patterns or individual behaviors over brief time periods (24-48 hours). Further investigation into the long-term (i.e. months) movement patterns of these fish on different spatial scales could provide a better understand of how the population will respond to variations in environmental conditions, such as those associated with climate change.

Although understanding fish behavior is necessary to properly manage an exploited population, it is also crucial that management agencies implement regulations that ensure the sustainability of the species while also considering the interests of the different fishing sectors. To regulate the harvest of the summer flounder recreational fishery, managers throughout the Atlantic states have primarily implemented bag and size limits that change annually. However, accurately estimating the catch of the recreational fishery sector is challenging, which may partially explain why the recreational fishery has exceeding its allotted quota in multiple years (Terceiro 2002). Angler noncompliance with management regulations can severely degrade the ability of fishery managers to prevent overexploitation of fish populations (Gigliotti and Taylor 1990, Sullivan 2002, Hicks 2002). A simulation study indicated that even moderate levels of noncompliance could result in severe declines in the number of legal sized fish harvested (Gigliotti and Taylor 1990). Quantifying the extent of angler noncompliance is a challenging task, because noncompliance is difficult to measure accurately (Schill and Kline 1995, Sullivan 2002). For example, Pierce and Tomcko (1998) found that angler noncompliance estimates based on creel surveys and citation records were biased low and concluded that anglers concealed their sublegal catches from creel clerks and enforcement officers. Developing a method to accurately quantify noncompliance with regulations would allow managers to assess the effectiveness of different policies and to determine if any modifications might be necessary to increase the compliance rate. One method that could provide some indication of the level of angler noncompliance would be to use a mark-recapture growth model to investigate if the length measurements of tagged fish that were recaptured by recreational anglers suffered from any biases, especially if the recaptured fish was harvested by the angler.

Another important component of fisheries management is developing accurate stock assessments that can be used to estimate the optimal exploitation rate and target spawning stock biomass. The instantaneous natural mortality rate (M), which is the rate that individuals are lost from the population due to reasons other than exploitation (e.g., death, predation, permanent emigration, etc.), is integral to the stock assessment and influences the estimates of stock productivity, optimal exploitation rate, and the target spawning stock biomass. Estimation of M is notoriously difficult because *in situ* natural mortality processes cannot be observed directly, and currently M is one of the greatest uncertainties in the summer flounder stock assessment (Maunder and Wong 2011). For summer flounder stock assessments, M was historically assigned a value of 0.2, which is a value commonly used in many fisheries stock assessments and appeared to be a suitable estimate for summer flounder (NEFSC 1997; NRC 2000). For the 2009 summer flounder stock assessment, M was revised to account for potential age-based differences in natural mortality rates (Terceiro 2009). Using the revised estimates of age-specific M (mean = 0.25), the 2009 stock assessment concluded that overfishing was not occurring and the summer flounder stock was classified as not overfished. However, stock assessments are highly sensitive to estimates of M. For example, if a constant value of 0.2 was used for M, the summer flounder stock would have been considered overfished and overfishing would have been occurring (NEFSC 2008). For these assessments, estimates of M were obtained using life-history-based models that relate natural mortality to longevity, growth, reproductive effort, or maximum size. None of these life-history-based models were specifically designed to estimate M for summer flounder (Maunder and Wong 2011), but were instead, developed to provide estimates of M for multiple species. Due to the importance of M in the summer flounder stock assessment, it is critical that studies on summer flounder are conducted to develop a more accurate estimate of this parameter. One recent study suggested that a tagging program may be the best option for accurately estimating M for summer flounder (Maunder and Wong 2011).

Dissertation Objectives

In this dissertation, I use three types of tags (i.e., acoustic, archival, and conventional) to: 1) observe and describe summer flounder movements in Virginia waters on different spatial scales (Chapters 1 and 2), 2) assess angler noncompliance with minimum size limits based on predictions of growth from mark-recapture data collected by an angler tagging program in Virginia (Chapter 3), and 3) estimate mortality rates of summer flounder using 12 years of mark-recapture data (Chapter 4). This research should be useful to ecologists and managers who seek a better understanding of this species to ensure its sustainability for future generations.

References

Capossela KM (2010) Migration dynamics, within-estuary behaviors and cardiorespiratory responses of summer flounder to selected estuarine conditions. MS thesis, College of William and Mary, Williamsburg, VA

Gigliotti LM and Taylor WW (1990) The effect of illegal harvest on recreational fisheries. North American Journal of Fisheries Management, 10: 106-110.

Hayes D, Jones M, Lester N, Chu C, Doka S, Netto J, Stockwell J, Thompson B, Minns CK, Shuter B, and Collins N (2009) Linking fish population dynamics to habitat conditions: insights from the application of a process-oriented approach to several Great Lakes species. Reviews in Fish Biology and Fisheries 19: 295-312.

Hicks RL (2002). *Stated preference methods for environmental management: recreational summer flounder angling in the Northeastern United States.* Washington D.C.: National Marine Fisheries Services, NFFKS-18.

Hilborn R and Walters CJ (1992) Quantitative fisheries stock assessment: choice, dynamics and uncertainty. Chapman and Hall, New York.

Humston R, Olson DB, and Ault JS (2004) Behavioral assumptions in models of fish movement and their influence on population dynamics. Transactions of the American Fisheries Society 133: 1304-1328.

Kraus RT and Musick JA (2001) A brief interpretation of summer flounder, *Paralichthys dentatus*, movements and stock structure with new tagging data on juveniles. Marine Fisheries Review 63: 1-6.

Lomnicki A (1999) Individual-based models and the individual-based approach to population ecology. Ecological Modelling 115:191-198.

Maunder MN and Wong RA (2011) Approaches for estimating natural mortality: application to summer flounder (Paralichthys dentatus) in the U.S. mid-Atlantic. Fisheries Research 111: 92-99.

Morse WW (1981) Reproduction of the summer flounder, *Paralichthys dentatus* (L.). Journal of Fish Biology 19: 189-203.

Northeast Fisheries Science Center (NEFSC) (1997) *Report of the 25th Northeast Regional Stock Assessment Workshop (25th SAW): Stock Assessment Review Committee (SARC) Consensus Summary of Assessments.* Northeast Fisheries Science Center Reference Document 97-14. National Marine Fisheries Service, Woods Hole, Massachusetts.

Northeast Fisheries Science Center (NEFSC) (2008) 47th Northeast regional stock assessment workshop (47th SAW) Assessment report. Northeast Fisheries Science Center Reference Document 08-11. National Marine Fisheries Service, Woods Hole, Massachusetts.

National Research Council (NRC). 2000. Improving the collection, management and use of marine fisheries data. Washington, DC. National Academy Press. 222 p.

Pierce RB and Tomcko CM (1998) Angler noncompliance with slot length limits for northern pike in five small Minnesota lakes. North American Journal of Fisheries Management, 18: 720-724.

Roshier DA, Doerr VAJ, Doerr ED (2008) Animal movement in dynamic landscapes: interaction between behavioural strategies and resource distributions. Oecologia, 156: 465-477.

Schill DI and Kline PA (1995) Use of random response to estimate angler noncompliance with fishing regulations. North American Journal of Fisheries Management, 15: 721-731.

Sullivan MG (2002) Illegal angling harvest of walleyes protected by length limits in Alberta. North American Journal of Fisheries Managemen,t 22: 1053-1063.

Sutherland WJ (1996) From individual behavior to population ecology. Oxford University Press, Oxford, 213 p.

Szedlmayer, S. T. and K. W. Able. 1993. Ultrasonic telemetry of age-0 summer flounder *Paralichthys dentatus*, movements in a southern New Jersey estuary. Copeia 3: 728-736.

Terceiro M (2002) The summer flounder chronicles: science, politics, and litigation, 1975-2000. Reviews in Fish Biology and Fisheries, 11: 125-168.

Terceiro M (2009) Stock assessment of summer flounder for 2009. US Dept. Commer, Northeast Fish Sci Cent Ref Doc. 09-17; 134 p. [http://www.nefsc.noaa.gov/publications/]

CHAPTER 1

Movement Patterns of Summer Flounder Near an Artificial Reef: Effects of Fish Size and Environmental Cues

Abstract

Acoustic telemetry was used to understand the influence of fish size and environmental cues on the behavior of summer flounder near an artificial reef in the lower Chesapeake Bay. Recent studies have used acoustic telemetry to monitor summer flounder dispersal patterns and movements throughout large regions, but less is known about factors that influence the small-scale movements of this species during their inshore residency period. We used passive acoustic telemetry to monitor the small-scale (100s of meters) 2-dimensional movements of 42 summer flounder while fish were resident at the artificial reef site. The mean residency time for summer flounder at the artificial reef was 54 ± 10.7 days, which was a sufficient duration to observe movements relative to a spectrum of tidal stages, times of day, lunar phases, and temperatures. To understand the importance of biological and environmental factors on summer flounder behavior, we fit repeated measures generalized linear mixed models to these data. Results suggest that summer flounder are generally sedentary while residing in inshore habitats, but that activity levels are influenced by fish size, tidal stage, and the interaction between time of day and lunar phase. In general, the highest activity levels were observed among small fish and all fish were more likely to move during the rising tide and on nights nearest the quarter moons. Based on these movement patterns, we hypothesize that summer flounder activity levels were predominantly influenced by the behavior of their preferred prey.

Introduction

Understanding habitat use and movement patterns of individual fish is becoming increasingly important as researchers recognize the connection between individual behavior and a population's vital rates (e.g., recruitment, mortality, and emigration; Sutherland 1996). Linkages between habitat, fish movements, and population dynamics have been investigated using individual-based models, but such models often suffer from a lack of information on the behavior of individual fish relative to environmental conditions (Lomnicki 1999, Humston et al 2004, Hayes et al 2009). Fish move over a range of spatial and temporal scales in response to ontogenetic changes (Dahlgren and Eggleston 2000) and various environmental cues, including tidal currents (Szedlmayer and Able 1993, Hartill et al 2003, Childs et al 2008), light level (Cote et al 2002, Payne et al 2010), lunar phase (Vinagre et al 2006, Hanson et al 2008), and season (Kraus and Musick 2001, Hunter et al. 2003). In this study, we investigate the short-term movement patterns of summer flounder relative to these biological and environmental factors.

Artificial reefs are ideal locations to study small-scale fish movements because many species are attracted to these complex habitats and can remain resident for long durations (Lowe and Bray 2006, Topping and Szedlmayer 2011). The attraction of fish to structured habitats, such as artificial reefs, is primarily due to the increased availability of shelter and prey resources (Allen 1985, Eklund 1997). Previous studies have used passive acoustic telemetry to show that some species remain closely associated with a single artificial reef for extended durations, in some cases for nearly two years (Reynolds et al. 2010, Topping and Szedlmayer 2011). Although passive acoustic telemetry is primarily used to observe whether individuals are present or absent within a habitat, it is also possible to use this technology to observe small-scale movements of marine species (Simpendorfer et al. 2002, Humston et al. 2005). We chose to focus our study on the movement patterns of summer flounder (*Paralichthys dentatus*), one of the most targeted and commercially valuable fish species on the US Atlantic coast.

Summer flounder exhibit a seasonal migration pattern and are known to use different offshore and coastal habitats throughout their life history (Morse 1981, Kraus and Musick 2001). The recreational fishery targets adult summer flounder in the spring and summer when they migrate into coastal and estuarine waters to feed, grow, and prepare for spawning. In Chesapeake Bay, adult and juvenile summer flounder inhabit the estuary from March through November (Desfosse 1995, Fabrizio et al. 2007, Latour et al. 2008). Adult fish migrate towards the continental shelf break from October through December to spawn off the coast of New Jersey, Virginia, North Carolina, or south of Cape Hatteras (Desfosse 1995, Kraus and Musick 2001). Although large-scale movement patterns of summer flounder are well known, only recently have researchers begun to study their small-scale movements during their residency in inshore waters.

Summer flounder are generally associated with structured habitats during their residency periods in coastal waters. Conventional mark-recapture program have shown that some individuals remain associated with structured sites (e.g., piers, bridges, and artificial reefs) in Chesapeake Bay for as long as 150 days during the period of inshore residency (Lucy and Bain 2007). Recreational anglers often target these sites, an observation which implies that summer flounder aggregate near structured habitats. However, data from conventional tagging programs do not provide information on summer flounder behavior between the times of release and recapture.

In recent years, summer flounder acoustic telemetry studies, conducted while fish occupied inshore habitats, have provided information on their residency, habitat preferences, and behavior. Using acoustic telemetry, researchers have shown that summer flounder remain resident in coastal bays and lagoons from 40-86 days (Sackett et al. 2007, Capossela 2010), prefer habitats with increased temperatures and dissolved oxygen levels (Sackett et al. 2008), and move in response to changes in tidal currents (Szedlmayer and Able 1993). Although suggestive, previous studies were designed primarily to observe dispersal patterns, occupancy within large (10s of km^2) regions, and individual behaviors over brief time periods (24-48 hours). As a result, these studies do not provide insight into the small-scale movements of summer flounder during their inshore residency. Only one previous study used acoustic telemetry to continuously monitor summer flounder movement over a small-scale (100s of meters) for an extended period of time (Fabrizio et al. 2005). Preliminary results from that study, which took place on the continental shelf, suggest that activity decreases with increasing size of fish.

However, it is unknown if summer flounder on the continental shelf exhibit similar movement patterns to those within an enclosed estuary, such as Chesapeake Bay.

The goal of this study was to understand the distribution and movement patterns of summer flounder near an artificial reef in the lower Chesapeake Bay. The specific objectives were: 1) to estimate duration of summer flounder residency at an artificial reef in Chesapeake Bay, 2) to observe habitat preferences and behaviors of both small and large summer flounder, and 3) to examine how exogenous cues influenced summer flounder movement patterns.

Methods

Study site

The Back River artificial reef in lower Chesapeake Bay was selected as the study site due to the known presence of summer flounder at the site throughout the summer (J. Lucy, personal observation). The artificial reef is located 3 nautical miles east of Virginia's western shore of the Chesapeake Bay and consists of over 2250 metric tons of concrete igloos, rubble, pipe, piles, and bridge sections spread over an area of approximately 49 hectares (Figure 1). The bathymetry of the artificial reef is relatively flat, but there is a deep navigation channel near the northeast corner of the reef and the bottom along the western edge of the reef slopes from 7 m to 4.5 m. The mean tidal range observed at the site throughout this study was 67 cm, which is typical of mid-Atlantic estuaries.

Prior to deployment of acoustic receivers at the study site, we conducted a range test to determine the maximum distance at which an *in situ* acoustic transmitter could be detected. Range tests are essential for telemetry studies because the detection range of acoustic transmitters varies depending on site-specific environmental parameters (depth, salinity, vegetation, etc.). We conducted range tests from a small vessel using a single moored VR2 (VEMCO) receiver equipped with an omnidirectional hydrophone. In order to determine the distance at which the receiver no longer detects the acoustic signal emitted by a transmitter, we placed an acoustic transmitter (V9-2L-R256, transmitting at 69 kHz; VEMCO) near the bottom of the water column at progressively greater distances from the receiver. Based on results from this test, we estimated the optimal detection distance at Back River Reef was 400 m (Fabrizio et al. 2007). On 13 June 2006 we deployed 12 acoustic receivers around the artificial reef ensuring that the detection range of adjacent receivers overlapped slightly (Figure 1). Each receiver was placed approximately 3 meters from the seafloor and tethered to a 91 kg mushroom anchor. In addition to the receivers, we also deployed temperature loggers directly above the receivers on the moorings at the corners of the array to record water temperatures throughout the study. The location of each receiver was marked with a surface buoy. Data from the acoustic receivers were downloaded on two occasions: 22 August 2006 and 27 March 2007. Receivers were redeployed only after the August retrieval, as the study was completed in March. We were unable to recover five receivers during the March retrieval due to missing surface buoys. Scuba divers subsequently retrieved three of the five missing receivers in June 2007.

Acoustic Tagging

Summer flounder (258 to 612 mm TL), captured by hook and line and small trawls, were implanted with acoustic transmitters between 15 June 2006 and 10 July 2006 and released in lower Chesapeake Bay. Forty fish were captured and released near Back River reef and an additional 80 fish were released at two nearby sites as part of a related study (Fabrizio et al. 2007). Each fish was surgically implanted with an acoustic transmitter designed to emit a unique acoustic code to allow identification of individual fish. Transmitters were configured to emit signals every 60 to 180 seconds to ensure battery power through the one-year duration of the study. To implant the transmitters we used surgical procedures previously established for summer flounder (Fabrizio and Pessutti 2007). Briefly, fish were anesthetized with 60 mg L^{-1} AQUI-S (a clove oil derivative approved for use as an anesthetic in Australia and New Zealand), a small incision was made on the non-pigmented side of the fish, a beeswax- coated transmitter (9mm x 30 mm; V9-2L-R256, VEMCO) was inserted into the peritoneal cavity, and the incision was stitched using non-absorbable sutures in an interrupted pattern. While the fish remained under anesthesia, size and weight measurements were collected, and an individually numbered T-bar anchor tag (Hallprint tags) was inserted into the dorsal musculature near the tail. Anchor tags were labeled with a phone number so that recreational anglers could report their recaptures. Fish were then resuscitated using ram ventilation and released near the center of the acoustic array at Back River reef.

Quality assurance

Information downloaded from acoustic receivers was carefully examined to remove erroneous data resulting from multiple detections of the same signal at adjacent receivers, spurious detections due to acoustic noise, or detections after mortality or tag loss. Occasionally, the same acoustic signal, or ping, was detected and recorded at multiple receivers because the detection ranges of adjacent receivers overlapped slightly. To simplify the data, and remove redundancies, detections of the same transmitter signal that occurred within 60 seconds were removed from the database. Sixty seconds was chosen because this was the minimum duration between pings for individual transmitters. We also deleted a small number of data records (n=83) that were known to be spurious. Examples of spurious detections include those that were recorded from: 1) transmitters prior to implantation and release, 2) transmitters known to be at another site based on detection history, and 3) transmitters removed from the study following angler capture. These erroneous detections are most likely the result of acoustic noise or simultaneous detections of multiple pings. Finally, the detections from one transmitter were removed because that transmitter was recorded at a single receiver throughout the study. This anomaly indicated that the fish either succumbed to tagging-related mortality or shed the transmitter shortly after release.

Residency and distribution

We used simple descriptive statistics to estimate residency durations and the size distributions of all summer flounder detected at Back River artificial reef, including fish that were released at other sites. Summer flounder residency was defined as the number of days an individual was detected at Back River reef, without an absence of more than one week. To examine the distribution patterns of summer flounder near the artificial reef, we calculated the number of detections per individual recorded by each acoustic receiver. Size-related distribution patterns around Back River reef were examined using a weighted mean length for fish detected by each receiver. The weighted mean length at each receiver ($\bar{L}_r$) was calculated using:

$$\bar{L}_r = \frac{\sum_{i=1}^{n}(L_i \cdot d_{i,r})}{\sum_{i=1}^{n} d_{i,r}} \qquad (1)$$

where L_i is the length at time of tagging for an individual fish (i), $d_{i,r}$ is the total number of detections of fish (i) at receiver (r), and n is the total number of fish detected at receiver (r).

Minimum distance traveled

Movements of summer flounder around the artificial reef were examined by calculating the minimum distance traveled (MDT) by a fish that would yield the observed detection history within the acoustic array. Although it is impossible to know the exact location of an individual fish within a receiver's detection range, an approximate location could be estimated for fish that moved between adjacent receivers. If the detection ranges of the two receivers overlapped, the approximate location was the mid-point between the two receivers. If the detection ranges of the receivers did not overlap, the approximate locations were estimated assuming: 1) the detection range of each receiver was 400 m, and 2) the fish moved in a straight line between the receivers. All locations were estimated using Universal Transverse Mercator (UTM) coordinates. The MDT was then calculated as the total distance traveled between all the approximate locations within a given time period. Using these calculations, a fish may have an MDT of zero during a given time period if that fish was detected at a single receiver, or if that fish was detected consecutively at two adjacent receivers (because the detection ranges of adjacent receivers overlap it was possible for a fish to be detected at two different receivers without moving). Thus, it is important to note that we could not observe fine-scale movements and, therefore, we limit our discussion to summer flounder movement patterns on the scale of 100s of meters.

Statistical analysis

We restricted our analysis to dates when we were confident that observed movement patterns represented the behavior of summer flounder resident at Back River reef. To ensure that the movement patterns we observed were not influenced by the tagging procedure, we excluded detections within the first 48 hours after release. Likewise, to ensure that the observed behaviors were representative of resident fish, we excluded detections within one week of dispersal from the site. Based on these criteria, we observed movements of 42 fish from 22 June through 4 October 2006.

To examine summer flounder movements relative to various environmental cues, we examined subsets of the data based on tidal stage and determined the time of day, lunar phase, and mean temperature for each tidal stage over all days considered. Finite time periods were selected to compare changes in movement patterns with respect to: tidal stage, time-of-day, lunar phase, and temperature. Because tides were reported to influence movements of summer flounder (Szedlmayer and Able 1993, Miller 2010), we used 1.5 hour time periods centered around four tidal stages: low, rising (the mid-point between low and high tide), high, and falling (the mid-point between high and low tide). Although the 1.5-hour time period meant that we excluded approximately half the detections in our data set, this strategy increased the independence between successive observations. Tidal predictions for Messick Point, estimated with the Tides and Currents ® 2.0 software program, were used to determine tidal stages at Back River reef. Messick Point is approximately 5 nautical miles west of Back River reef and was expected to have similar tidal patterns. We also used Tides and Currents® to estimate times of sunrise and sunset, which were then used to assign a time of day to each tidal stage. If the mid-point of the tidal time period occurred prior to sunrise or after sunset the time of day was considered 'night,' otherwise the time of day was considered 'day'. Lunar phase was assigned based on the moon phase output from Tides and Currents®. Based on the proportion of the moon that was illuminated, the lunar cycle was categorized in eight phases: new moon, wax crescent, 1st quarter, wax gibbous, full, wan gibbous, 3rd quarter, wan crescent. Temperatures at receiver locations that did not have associated temperature loggers were estimated using inverse distance weighting. All temperatures were rounded to the near degree Celsius, except for those at the extreme high and low ends. To avoid problems with small sample sizes, we assigned 22 observations between 21.0 and 21.5°C to the 22°C temperature bin. We also assigned five observations at 29.1°C to the 28°C temperature bin.

Two linear mixed models were used to investigate the movement patterns of summer flounder relative to biological and environmental factors. Fish length and hours-at-large were centered (i.e., the mean was subtracted from individual observations) to reduce collinearity between continuous variables (Quinn and Keough 2002). Our data were characterized by a large number of time periods for which the observed MDT for an individual fish was zero, and thus the data were non-normal. This violates one of the assumptions of general linear models, so we used two separate models to analyze these detection data. The first model was a generalized linear mixed model (GzLMM) fit to a binomial response (moved vs. not-moved) to examine the influence of various factors on the probability of movement. The second model was a general linear mixed model (GLMM) fit to the positive values of MDT to determine the effect of biological and environmental factors on the distance traveled by an individual fish during periods of activity.

Prior to fitting the GLMM, we transformed the positive values of MDT using a Box-Cox transformation (Box and Cox 1964) to meet the normality assumption of this model. The Box-Cox transformation is calculated by:

$$y_i^{(\lambda)} = \begin{cases} \dfrac{y_i^{\lambda} - 1}{\lambda}, & \text{if } \lambda \neq 0 \\ \log(y_i), & \text{if } \lambda = 0 \end{cases} \tag{2}$$

Where $y_i^{(\lambda)}$ is the transformed response, y_i is the untransformed response, and λ is a power parameter. The value of λ was estimated with maximum likelihood using the solver function in Microsoft ® Excel (2010).

A repeated measures approach was used to fit the general and generalized linear mixed models due to the temporal autocorrelation between repeated observations of individuals through time. Repeated measures models incorporate specialized variance-covariance structures to account for these serial correlations (Littell et al. 2006, Rogers and White 2007). Mixed models were used because a combination of fixed effects (i.e., fish length, hours at large, tidal state, time of day, lunar phase, and temperature) and a random effect due to individual fish was included in the models (Littell et al. 2006, Bolker et al. 2008). The GLIMMIX procedure in SAS/STAT (version 9.2) was used to fit the repeated measures GzLMM, with a logit link function, to the binomial response (moved vs. not moved). We used the MIXED procedure in SAS/STAT (version 9.2) to fit the repeated measures GLMM to the transformed MDT data. We selected the most appropriate model (i.e., most parsimonious with the best fit to the data) using a three-step process (Figure 2).

The first step was to select a preliminary variance-covariance structure and then determine if the between-subject variability contributed to the total random variation. We refer to the combination of the variance-covariance structure and the individual fish random effect as the 'random effects structure.' The preliminary random effects structure was selected using a model that contained the six fixed effects with no interactions. Restricted maximum likelihood (REML) was used to fit

GLMM models with different random effects and variance-covariance structures (Pinheiro and Bates 2000, Zuur et al 2007). Because GzLMMs do not have an exact likelihood solution, we used Laplace's method to integrate over the random-effects distribution and to approximate the likelihood function. This method is believed to be a more appropriate approximation technique than pseudo-likelihood, which is the default computation method in SAS software (Bolker et al. 2008). Models were fit using the following variance-covariance structures to describe the correlations between the repeated measures: variance components, compound symmetry, first-order autoregressive, and first-order autoregressive-moving average (Verbeke and Molenberghs 2000, Littell et al. 2006). For each variance-covariance structure, we fit models that included and excluded individual fish as a random effect. For the GLMM, we used the Kenward-Roger approximation to calculate the denominator degrees of freedom and adjust the estimated standard errors (Littell et al. 2006, Bolker et al. 2008). We used the containment method to estimate the denominator degrees of freedom for the GzLMM because the Kenward-Roger approximation is not possible when using Laplace's method to approximate the likelihood (SAS 2009). For both models, we selected the preliminary random effects structure that best described the data as the model with the lowest value of Akaike's Information Criterion corrected for small sample size (AICc; Akaike 1973, Burnham and Anderson 2002).

The second step was to develop a global model to use in selecting the final random effects structure. A global model includes all the potential main effects as well as any potential interactions between those main effects (Zuur et al. 2007). To avoid testing every possible combination of interactions, we individually added each potential two-way or three-way interaction to the model that included the main effects only. All possible two-way interactions, and all three-way interactions that included fish length, were included in this analysis. For the models that included three-way interactions, we also included all the component two-way interactions, as inclusion of lower order interactions is necessary to correctly interpret linear models (Hox 2010). The GzLMM models were fit using the procedure previously described to select the preliminary random effects structure. For the GLMM, each model was fit using maximum likelihood (ML) and the preliminary random effects structure previously discussed. We then compared the main effects-only model with the more complex model. All interactions that reduced the AICc value by more than 1 unit were graphically examined to determine if the interactions were of ecological interest or were the result of random variation (potentially due to small sample sizes). Interactions were included in the global model if they reduced the AICc value and were not the result of random variation. Using the global model, we then repeated the procedure used to select the preliminary random effects structure. This was necessary because changing the mean structure (i.e., the fixed effects included in the model) will influence the random effects model selection criteria calculated with REML (Littell et al. 2006). Thus, we needed to validate that the correct random effects structure was used to develop the global model. If a different random effects structure was selected using the global model, we repeated the process until there was no difference between the random effects structure selected and the global model selected.

Our final step was to select the fixed effects and interactions that best described the variation in movement behavior and to verify that the data satisfied the assumption of homogeneity of variance. For the GLMM and the GzLMM, we fit models with all possible combinations of main effects and the interactions selected when building the global model. To fit the GzLMM, we continued using Laplace's method to approximate the likelihood and the containment method to estimate the denominator degrees of freedom. Because we were comparing models with different fixed effects, all of the GLMM models were fit using maximum likelihood. Once again, the degrees of freedom for the GLMM were estimated using the Kenward-Roger approximation and we used AICc to select the most parsimonious model with the best fit to the data. Once we selected the most appropriate model for the GLMM, we used REML to estimate the effect of each variable because the standard deviations calculated with REML are generally less biased than those estimated by maximum likelihood (Zuur et al. 2007, Bolker et al. 2008). After fitting both models, residual plots were used to verify that the assumption of homogeneity of variance was satisfied.

Results

Residency and site fidelity

Residency of fish detected at Back River reef differed depending on whether the fish was released at the reef or at one of the other two sites in lower Chesapeake

Bay. Mean residency time for fish released at Back River reef was 54.2 ± 10.7 days. Of the 39 fish released alive at the reef, over half (54%) were resident through mid-August (figure 3). Only four fish did not remain resident at the reef for longer than two weeks following release. In addition, 21 fish that were not released at Back River reef were detected at the reef before mid-December 2006 (figure 3). Ten of these fish were first detected during summer (24 June – 30 July 2006) and had a mean residency time of 11.1 ± 7.5 days. The other 11 fish were first detected during fall (28 September – 7 December 2006) and had shorter residency periods (1.1 ± 0.5 days).

Dispersal from Back River reef was nearly constant during the summer, but a few fish established residency at the site during fall and winter. Fish that were resident at Back River reef for longer than two weeks dispersed in nearly equal numbers in July (nine fish), August (14 fish), September (10 fish), and October (five fish). Dispersal date was not related to fish length (Figure 4). Within one week in late August, 13 of the 18 (72%) fish remaining at the reef dispersed (Figure 5). Measurements from a nearby meteorological station revealed that this period of rapid dispersal occurred prior to, and during, a precipitous drop in barometric pressure and exceptionally high wind speeds associated with Tropical Storm Ernesto (Figure 6). Of the 13 fish that dispersed prior to the landfall of Ernesto, nine subsequently returned to the reef within one month. Three of the fish released at Back River reef were resident at the reef from October through late November/early December. Interestingly, each of these fish had left the detection range of the acoustic array for extended durations (26-64 days) prior to their fall residency at the reef. From December 2006 through March 2007, only three tagged fish were detected at Back River reef. Two of these fish were tagged elsewhere in Chesapeake Bay and the third fish had not been detected for nearly 2 months prior to assuming winter residency at the reef.

Several summer flounder released at Back River Reef returned to the site the following spring, suggesting fidelity to this site. Ten of the 39 fish (26%) released alive at Back River reef were subsequently detected within the acoustic array between March and June 2007. An additional six fish released at other sites in Chesapeake Bay were also detected at Back River reef during this time period. These numbers represent a minimum estimate of site fidelity for multiple reasons: 1) the acoustic transmitters were near the end of their battery life so some fish that returned may not have been detected, 2) most of the receivers were retrieved in March 2007, leaving only three receivers to detect acoustic transmitters from March through June, 3) some fish may have returned to the site after the last receivers were retrieved in June, and 4) some fish may have been captured in the commercial fishery during the winter.

Within-site distribution

Summer flounder did not use all areas within the study site equally as evidenced by the number of detections at each receiver (Figure 7). Fish at Back River reef were more often detected at the receivers closest to the artificial reef structure, although the receivers on the slope to the southwest of the artificial reef also had a large number of detections. We also observed variations in the mean length of fish at individual receivers (range: 347.23 - 487.05 mm; Figure 7); interestingly, the largest individuals were observed at the receiver with the most detections per individual, whereas the smallest fish were observed at the receiver with the fewest detections per individual. In general, larger fish were detected in close proximity to the artificial reef structure and smaller fish were detected near the slope between the artificial reef and shallow nearshore areas.

Movement patterns

Many summer flounder established residency at Back River reef for long durations, but these fish were generally sedentary during their residency. Thirty-six of the fish released at Back River reef, and six fish released at other sites, were resident at the reef for longer than two weeks, which provided sufficient data to model their movement patterns. The mean number of tidal periods during which resident fish were present within the acoustic array was 234 (range: 8 to 646), and the combined total number of tidal periods for all fish was 9821. Only 35 resident fish exhibited non-zero MDT during 370 (3.8 %) of these tidal periods. The mean number of tidal periods that these fish were active was 10.6 (range: 1 to 57). Only 16 fish had non-zero MDT for more than five tidal periods and only 11 fish had non-zero MDT for more than 10 tidal periods.

Developing the global model for the GzLMM revealed that individual fish had different activity levels and that interactions existed between several of the main effects. The most appropriate variance-covariance structure was a simple variance components model (Appendix I). There was strong support for including individual fish as a random effect, as those models had much lower AICc values (66-70 units). In developing the global model, evidence existed for including the interaction between time of day and lunar phase (the AICc value for this model was 7.38 units less than the model with only main effects) as well as the interaction between length and hours at large (the AICc value for this model was 5.3 units less than the model with only main effects). Upon further graphical examination, we concluded that the interaction between length and hours at large was random through time and did not have an ecological interpretation (Appendix I). Thus, we chose to omit the interaction between length and hours-at-large in the global model. The same random effects structure (i.e., variance components with individual fish as a random effect) was selected using this global model.

The most appropriate fixed effects structure, based on AICc model selection criteria, included length, tide, and the interaction between time of day and lunar phase (Table 1; Appendix I), although there was some support (ΔAIC = 3.04) for the second best model, which excluded length as a main effect (Table 2). The statistical form for the model with the lowest AICc was:

$$\text{logit}(y_{ijkl}) = \mu + \lambda_i + \varphi_j + \tau_k + \phi_l + (\tau\phi)_{kl} + \gamma_i + \varepsilon_{ijkl}$$

where logit is the link function, y_{ijkl} is the binomial response for fish (i) during tidal period (j), time of day (k), and lunar phase (l), μ is the overall mean, λ is the length of fish (i), φ is the tidal state (j=low, rising, high, falling), τ is the time of day (k=day, night), ϕ is the lunar phase (l = new, wax crescent, 1st quarter, wax gibbous, full, wan gibbous, 3rd quarter, wan crescent), $\tau\phi$ is the interaction between time of day and lunar phase, γ is the random effect for fish (i), and ε is the random unexplained error. Based on this model, fish movement probability was inversely proportional to fish size. Although the largest summer flounder were generally sedentary, fish smaller than 550 mm exhibited both mobile and sedentary behavior patterns throughout the summer (Figure 8). Fish exhibited a higher tendency to move during rising tides, but movement probabilities were similar during other tidal phases (Figure 9). The interaction between time-of-day and lunar phase indicated that fish were slightly more active during the day near the quarter moons (Figure 10a). This pattern was more pronounced during the nighttime periods, when fish were much less active during nights closest to the new and full moons (Figure 10b).

The small sample size of nonzero MDT values limited our ability to fit GLMMs and to make inferences regarding factors that influenced distances traveled by individual fish. The most appropriate preliminary variance-covariance structure was first-order autoregressive and there was no evidence that sufficient between-subject variability existed to include individual fish as a random effect (Appendix I). The global model selection procedure indicated there was no support for including any of the candidate interactions in the model (Appendix I). Considering the fixed-effects structure of the model, eight different models were plausible (Table 3). Each of these models included fish length and time of day as a fixed effect. Only half the top models included hours at large, tide, and temperature. None of the top models included lunar phase. Based on these results, we selected the model that included only length and time-of-day as fixed effects (Table 4, Appendix I). Parameter estimates from this model indicate that the MDT by individual fish decreases with increasing fish size and that fish tend to move longer distances at night (Table 4).

Discussion

Prior to our study, summer flounder in Chesapeake Bay were thought to exhibit some degree of site fidelity to structured sites, but the degree of fidelity and the small-scale movement patterns of individuals were unknown. Here, we showed that summer flounder remain associated with a single artificial reef for long periods of time (54 days) during their residency within Chesapeake Bay. Furthermore, at least 26% of the fish released at the site were detected near the artificial reef the following spring. The observed residency period in this study was shorter than that observed within Mid-Atlantic coastal harbors (86 days; Sackett et al. 2008) and lagoons (130 days; Capossela 2010). Likewise, the degree of site fidelity in our study (26%) was slightly less than the 35-39% previously observed (Sackett et al. 2007, Capossela 2010). However, we note that the scale of observation in our study was considerably smaller, making direct comparisons with previous work difficult. The smaller spatial extent of our study provided an opportunity to observe summer flounder movements on the scale of 100s of meters and over long durations, which revealed patterns that were not apparent in previous studies. These observed small-scale movements indicated that summer flounder were primarily sedentary during their residency at the reef, but that activity levels were influenced by fish size, tidal stage, time of day, and lunar phase. Although previous studies have also indicated that summer flounder movements are influenced by tidal stage (Szedlymayer and Able 1993, Miller 2010) and time of day (Capossela 2010, Miller 2010), this is the first published study to discern behavioral differences due to fish size and lunar phase.

We hypothesize that the size-related differences in distribution and activity levels we observed are the result of competitive exclusion and ontogenetic changes in foraging behaviors. In general, larger summer flounder were found in close proximity to the artificial reef structure, whereas smaller fish were more often detected closer to the slope habitats at the margins of our site. This may be the result of larger fish exhibiting territoriality and excluding smaller fish from optimal foraging habitat closest to the artificial reef structure. Such competitive exclusion has often been suggested as an explanation for distributions of small and large fish (Lowe and Bray 2006). This habitat segregation, as well as differences in movement patterns with fish size, is most likely related to ontogenetic changes in the diet of summer flounder. A recent trophic dynamics study of summer flounder in Chesapeake Bay found that the diet of fish smaller than 375 mm was primarily dominated by mysids, and fish became more piscivorous with increasing length (Latour et al. 2008). Summer flounder primarily use ambush and active pursuit tactics to capture prey items (Staudinger and Juanes 2010), and different foraging strategies may have been employed to capture preferred prey items. Mysids generally exhibit a patchy distribution (Jumars 2007) and have a low caloric content, so smaller fish may need to use more active foraging behaviors to find sufficient prey to meet their metabolic requirements. In contrast, the more piscivorous diet of larger fish would allow them to reach their metabolic requirements with fewer meals. Furthermore, as the prey fish of larger flounder will generally be more evasive than invertebrates consumed by smaller flounder, larger fish are more likely to employ the more sedentary tactic of ambush predation.

We also hypothesize that observed behavioral differences in response to environmental cues were related to foraging behavior, although predator avoidance may also have been a factor. Movement patterns of fish are primarily related to foraging behaviors, predator avoidance, and spawning behavior (Lowe and Bray 2006). Spawning behavior can be excluded as an explanation for the observed localized movements, because summer flounder spawn on the continental shelf during fall and winter (Kraus and Musick 2001). Similarly, adult summer flounder comprise only a minor component of the diets of large predators, including different species of shark (Bowman 2000, Link et al. 2002, Ellis 2003); therefore, predator avoidance is most likely not a primary consideration affecting the behavior of summer flounder at Back River reef. Tidal state has previously been shown to influence the movements of summer flounder (Szedlmayer and Able 1993, Miller 2010) as well as other flatfish (Hunter et al. 2003). These studies suggest that flatfishes use tidal currents to reduce the energetic requirement associated with moving to a new location. Although this may be true for long-distance movements, we postulate that the increased localized movement probabilities associated with the rising tide is due to summer flounder feeding on prey that may be moving in association with the incoming tide. Zooplankton communities are associated with tidal fronts (Gomez-Gutierrez 2007), and increased density of zooplankton associated with the incoming tide may elicit summer flounder foraging behavior at this location. In addition, studies on the behavior and distribution of mysid shrimp have shown that these crustaceans are generally more abundant in the water column at night and that they respond to lunar periodicity (Hampel et al. 2003, Marques et al. 2009). Mysids may be more active near the quarter moons in response to changes in tidal currents. During the quarter moons the tidal range is at its minimum, decreasing the potential that mysids will be swept away from their preferred habitats by tidal currents (Kaartvedt 1989). Previous studies have also found that summer flounder activity increases at night (Capossela 2010, Miller 2010), but these studies did not investigate the influence of the lunar cycle. Unfortunately, we did not sample for potential summer flounder prey near Back River reef during the course of this study, so our conclusions regarding the relationship between summer flounder foraging behavior and the observed movement patterns remain conjectural.

Even though summer flounder activity responded to changes in environmental conditions, most individuals had low movement probabilities throughout their residency at the artificial reef. Due to the design of our study, individuals had to move at least 400 m within 1.5-hour time periods to have a non-zero movement probability. As a result, movement probabilities were low even when conditions were optimal (i.e., rising tide or on nights near the quarter moon).

Even the most active individuals in our study rarely moved large distances and had movement probabilities between 10 and 15% while they were resident at the artificial reef. This corroborates results from a previous acoustic telemetry study that found that actively tracked summer flounder rarely moved more than 180 m^2 within 3 to 6 hours (Sackett et al. 2008). Although the individuals in that study did not move large distances, they did remain in motion 74 ± 19% of the time they were tracked, implying that summer flounder are quite active but tend to inhabit small areas once they establish residency. We investigate the fine-scale movement patterns of Chesapeake Bay summer flounder in another study (ms. in prep.).

In addition to improving our understanding of summer flounder localized movement patterns, this study also revealed that summer flounder move to different habitats in anticipation of an oncoming storm front. Near the end of August a large percentage (72%) of the fish that were resident at Back River reef dispersed to habitats outside the detection range of the acoustic receivers. This dispersal event was immediately followed by a storm with strong winds that approached 90 km h^{-1}. In the weeks following the storm, the majority (70%) of individuals that had dispersed in anticipation of the storm subsequently returned to the artificial reef; implying that this dispersal event occurred in response to changing environmental conditions related to the storm event. A similar dispersal behavior was observed with juvenile blacktip sharks (*Carcharhinus limbatus*) that were resident in a coastal nursery area in Florida (Heupel et al. 2003). The authors of that study concluded that fish dispersed in response to declining barometric pressure associated with the storm. Similarly, summer flounder are believed to disperse from coastal estuaries in response to changes in barometric pressure (Sackett et al. 2007). It is unclear from our results if the storm related dispersal was in response to changes in barometric pressure, or to other unobserved environmental cues. Summer flounder began to disperse as the barometric pressure declined, but continued dispersing when the barometric pressure returned to normal levels prior to the landfall of the storm. Based on these results, we suspect that summer flounder may not rely solely on barometric pressure to initiate dispersal prior to a storm.

The detection histories of summer flounder released at Back River reef, and at other sites in the lower Chesapeake Bay, also provide some insight into the timing of seasonal dispersal from these sites. Back River reef is approximately 28 km from the mouth of Chesapeake Bay, and is closer to the mouth than either of the other two sites where fish were released (Fabrizio et al. 2007). Most of the fish that were resident at Back River reef throughout the summer had dispersed from the site by the end of October. Eleven fish that were not released at Back River were detected at the site for brief periods between October and December. The brief duration that individual fish remained at the reef during the fall months may indicate that these fish were exhibiting directed movement towards the mouth of the Chesapeake Bay as part of their annual spawning migration; this is consistent with the results from previous tagging studies in which summer flounder were observed dispersing from Chesapeake Bay from October through December (Desfosse 1995, Kraus and Musick

2001). The protracted time period over which these 'migrating' fish were detected suggests that fish travel independently and do not respond to a common exogenous cue (e.g., temperature, photoperiod) to initiate dispersal out of the bay. Only three fish were detected at Back River reef after December 2006, indicating that most of the tagged fish had dispersed from the site (possibly moving to offshore spawning locations). It is unclear if the fish that were detected during the winter had remained resident in Chesapeake Bay throughout the year or if they had participated in the spawning migration prior to, or following, their winter residency at Back River Reef. We suggest further work is necessary to elucidate the proximate factors that initiate summer flounder dispersal from Chesapeake Bay.

To our knowledge, we used the most appropriate telemetry techniques available at the time of our study, but results from a recent study suggest acoustic transmitter detection rates may be biased by fluctuating environmental conditions. Diel variations in receiver detection rates may influence the interpretation of acoustic telemetry data (Payne et al. 2010). One possible explanation for diel variation in detection rates is the interference with receiver detection efficiency by nocturnally active crustaceans (e.g. shrimp). The authors of that study recommend correcting the observed study animal detection probabilities using observed changes in the detection rate of stationary 'control' transmitters. In our study, which lacked control transmitters, we must assume that the detection rates were consistent through time and, therefore, that our observations were representative of summer flounder behavior.

We also must offer some caveats with regards to fitting generalized linear mixed models. To our knowledge, we used the best available model fitting and model selection techniques; however, the application of this modeling tool is an area of active study in statistics and there is uncertainty regarding the most appropriate method to fit these models. Using the wrong likelihood approximation technique could produce biased parameter estimates and inaccurate model inferences (Zhang et al 2011). We recommend that ecologists consult with statisticians on the best available practice regarding GzLMMs before using them in their own analyses.

Based on our experiences, we suggest that future acoustic telemetry studies consider sampling prey availability, measuring tidal currents, using tags that record water temperature, and designing acoustic arrays to observe dispersal. Our study did not sample the prey field available to summer flounder near Back River reef. We hypothesize that prey availability was the primary factor influencing summer flounder activity levels and believe that future acoustic telemetry studies would benefit from concurrently sampling prey field abundance. We also used tidal prediction models from a nearby site to estimate the tidal state at Back River reef. We believe that tidal current would be a better predictor of fish movement, but we chose not to use output from a tidal current prediction model because predictions were not available for Back River reef and because substantial variation in currents occur between different locations. Thus, we suggest deployment of water current meters in future studies where tidal currents are believed to influence movement patterns. Similarly, our measurements of water temperature were recorded by temperature loggers fixed to the receiver moorings on the periphery of the array and may not be representative of temperatures experienced by the fish occupying the inner portion of the site. As temperature is often associated with fish physiological processes (Claireaux and Lagardere 1999), distribution patterns (Harrison and Whitfield 2006), and activity levels (Staaks et al. 1999), future studies may consider acoustic transmitters that also provide measurements of water temperature. Finally, we believe that it would be beneficial to deploy an acoustic array across the mouth of Chesapeake Bay to determine the timing of fish dispersal from the bay. Multiple species are known to use the bay during only part of the year, and observing the timing of individual dispersal from the bay would be useful to identify proximate factors that initiate seasonal migrations for different species. Each of these suggestions could improve the interpretability of data collected using acoustic telemetry, but researchers should also understand that the potential benefits might not outweigh the increased costs associated with gathering additional data.

References

Akaike H (1973) Information theory and an extension of the maximum likelihood principle. *In* Petran BN and Csàaki F (eds.) *International Symposium on Information Theory*, 2nd ed. pp. 267-281. Akadèemiai Kiadi, Budapest, Hungary.

Allen LG (1985) A habitat analysis of the nearshore marine fishes from southern California. Bulletin of the Southern California Academy of Sciences, 84: 133-155.

Bolker BM, Brooks ME, Clark CJ, Geange SW, Poulsen JR, Henry M, Stevens H, and White J-SS (2008) Generalized linear mixed models: a practical guide for ecology and evolution. Trends in Ecology and Evolution, 24: 127-135.

Bowman RE, Stillwell CE, Michaels WL, and Grosslein MD (2000) Food of Northwest Atlantic Fishes and Two Common Species of Squid. Tech. Rep. NMFS-NE-155. National Marine Fisheries Service, Mashpee, MA.

Box GEP and Cox DR (1964) An Analysis of Transformations. Journal of the Royal Statistical Society, Series B, 26: 211-252.

Burnham KP and Anderson DR (2002) Model selection and inference: a practical information-theoretic approach. Springer-Verlag, New York.

Capossela KM (2010) Migration dynamics, within-estuary behaviors and cardiorespiratory responses of summer flounder to selected estuarine conditions. MS thesis, College of William and Mary, Williamsburg, VA

Childs A-R, Cowley PD, Næsje TF, Booth AJ, Potts WM, Thorstad EB, and Økland F (2008) Do environmental factors influence the movement of estuarine fish? A case study using acoustic telemetry. Estuarine, Coastal, and Shelf Science, 78: 227-236.

Claireaux G and Lagardére J-P (1999) Influence of temperature, oxygen, and salinity on the metabolism of European sea bass. Journal of Sea Research, 42: 157-168.

Cote D, Ollerhead LMN, Gregory RS, Scruton DA, and McKinley RS (2002) Activity patterns of juvenile Atlantic cod (*Gadus morhua*) in Buckley Cove, Newfoundland. Hydrobiologia, 483: 121-127.

Dahlgren CP and Eggleston DB (2000) Ecological processes underlying ontogenetic habitat shifts in a coral reef fish. Ecology, 81: 2227-2240.

Desfosse JC (1995) Movements and ecology of summer flounder, *Paralichthys dentatus*, tagged in the southern Mid-Atlantic Bight. PhD dissertation, College of William and Mary, Williamsburg, VA

Eklund AM (1997) The importance of post-settlement predation and reef resources limitation on structure of reef fish assemblages. Proceedings of the 8th international coral reef symposium, 2: 1139-1142.

Ellis JK (2003) Diet of the sandbar shark, *Carcharhinus plumbeus*, in Chesapeake Bay and adjacent waters. MS thesis, College of William and Mary, Williamsburg, VA

Fabrizio MC, Pessutti JP, Manderson JP, Drohan AF, and Phelan BA (2005) Use of the historic area remediation site by black sea bass and summer flounder. Final report to US Army Corps of Engineers.

Fabrizio MC and Pessutti JP (2007) Long-term effects and recovery from surgical implantation of dummy transmitters in two marine fishes. Journal of Experimental Marine Biology and Ecology, 351:243-254.

Fabrizio MC, Henderson MJ, and Lucy JA (2007) Understanding localized movements and habitat associations of summer flounder in Chesapeake Bay using passive acoustic arrays. Final report to VMRC, December 2007. [http://www.mrc.state.va.us/vsrfdf/pdf/RF06-11_Dec07.pdf]

Gómez-Gutiérrez J, Martínez-Gómez S, and Robinson CJ (2007) Influence of thermo-haline fronts forced by tides on near-surface zooplankton aggregation and community structure in Bahía Magdalena, Mexico. Marine Ecology Progress Series, 346: 109-125.

Hampel H, Cattrijsse A, and Vincx M (2003) Tidal, diel, and semi-lunar changes in the faunal assemblage of an intertidal salt marsh creek. Estuarine, Coastal and Shelf Science, 56: 795-805.

Hanson KC, Arrosa S, Hasler CT, Suski CD, Philipp DP, Niezgoda G and Cooke SJ (2008) Effects of lunar cycles on the activity patterns and depth use of a temperate sport fish, the largemouth bass, *Micropterus salmoides*. Fisheries Management and Ecology, 15: 357-364.

Harrison TD and Whitfield AK (2006) Temperature and salinity as primary determinants influencing the biogeography of fishes in South Aftrican estuaries. Estuarine, Coastal and Shelf Science, 66: 335-345.

Hartill BW, Morrison MA, Smith MD, Boubée J, and Parsons DM (2003) Diurnal and tidal movements of snapper (*Pagurs auratus*, Sparidae) in an estuarine environment. Marine and Freshwater Research, 54: 931-940.

Hayes D, Jones M, Lester N, Chu C, Doka S, Netto J, Stockwell J, Thompson B, Minns CK, Shuter B, and Collins N (2009) Linking fish population dynamics to habitat conditions: insights from the application of a process-oriented approach to several Great Lakes species. Reviews in Fish Biology and Fisheries, 19: 295-312.

Hox JJ (2010) Multilevel Analysis: Techniques and Applications – 2nd ed. Routledge. New York, USA.

Humston R, Olson DB, and Ault JS (2004) Behavioral assumptions in models of fish movement and their influence on population dynamics. Transactions of the American Fisheries Society, 133: 1304-1328.

Humston R, Ault JS, Larkin MF, and Luo J (2005) Movements and site fidelity of the bonefish *Albula vulpes* in the northern Florida Keys determined by acoustic telemetry. Marine Ecology Progress Series, 291: 237-248.

Hunter E, Aldridge JN, Metcalfe JD, and Arnold GP (2003) Geolocation of free-ranging fish on the European continental shelf as determined from environmental variables. Marine Biology, 142: 601-609.

Jumars PA (2007) Habitat coupling by mid-latitude, subtidal, marine mysids: Import-subsidised omnivores. Oceanography and Marine Biology: An Annual Review, 45: 89-138.

Kaartvedt S (1989) Retention of vertically migrating suprabenthic mysids in fjords. Marine Ecology Progress Series, 57: 119-128.

Kraus RT and Musick JA (2001) A brief interpretation of summer flounder, *Paralichthys dentatus*, movements and stock structure with new tagging data on juveniles. Marine Fisheries Review, 63: 1-6.

Latour RJ, Gartland J, Bonzek CF, and Johnson RA (2008) The trophic dynamics of summer flounder (*Paralichthys dentatus*) in Chesapeake Bay. Fisheries Bulletin, 106: 47-57.

Link JS, Garrison LP and Almeida FP (2002) Interactions between elasmobranchs and groundfish species (*Gadidae* and *Pleuronectidae*) on the Northeast U.S. Shelf. I: Evaluating Predation. North American Journal of Fisheries Management, 22: 550-562.

Littell RC, Milliken G, Stroup WW, Wolfinger R, and Schabenberger O (2006) SAS for mixed models, 2nd edition. SAS Institute, Cary, North Carolina.

Lomnicki A (1999) Individual-based models and the individual-based approach to population ecology. Ecological Modelling, 115:191-198.

Lowe CG and Bray RN (2006) Movement and Activity Patterns. *In* Allen LG, Pondella DJ, and Horn MH (eds.). *The Ecology of Marine Fishes: California and adjacent waters.* University of California Press, Los Angeles, CA.

Lucy JA and Bain III CM (2007) Virginia game fish tagging program annual report. Virginia Marine Resource Report Number 2007-1. VA Sea Grant, Gloucester Point, VA. [http://www.vims.edu/adv/recreation/2006%20Annual%20Report/MRR2007_1.pdf]

Marques SC, Azeiteiro UM, Martinho F, Viegas I, and Pardal MA (2009) Evaluation of estuarine mesozooplankton dynamics at a fine temporal scale: the role of seasonal, lunar and diel cycles. Journal of Plankton Research, 31: 1249-1263.

Miller MH (2010) Movement of summer flounder (*Paralichthys dentatus*) in relation to hypoxia in an estuarine tributary. MS thesis, University of Delaware, Lewes, DE

Morse WW (1981) Reproduction of the summer flounder, *Paralichthys dentatus* (L.). Journal of Fish Biology, 19: 189-203.

Otis DL and White GC (1999) Autocorrelation of location estimates and the analysis of radiotracking data. The Journal of Wildlife Management, 63: 1039-1044.

Payne NL, Gillanders BM, Webber DM, and Semmens JM (2010) Interpreting diel activity patterns from acoustic telemetry: the need for controls. Marine Ecology Progress Serie,s 419: 295-301.

Pinheiro JC and Bates DM (2000) Mixed-effects models in S and S-Plus. Statistics and Computing Series, Springer-Verlag, New York, NY.

Quinn G and Keogh M (2002) Experimental design and data analysis for biologists. Cambridge University Press. Cambridge, UK.

Reynolds BF, Powers SP, and Bishop MA (2010) Application of acoustic telemetry to assess residency and movements of rockfish and lingcod at created and natural habitats in Prince William Sound. PLoS ONE, 5: e12130. doi:10.1371/journal.pone.0012130.

Rogers KB and White GC (2007) Analysis of movement and habitat use from telemetry data. *In* Guy CS and Brown ML (eds.) *Analysis and Interpretation of Freshwater Fisheries Data*, pps 625-676. American Fisheries Society, Bethesda, Maryland.

Sackett DK, Able KW, and Grothues TM (2007) Dynamics of summer flounder, *Paralichthys dentatus*, seasonal migrations based on ultrasonic telemetry. Estuarine, Coastal and Shelf Science, 74: 119-130.

Sackett DK, Able KW, and Grothues TM (2008) Habitat dynamics of summer flounder *Paralichthys dentatus* within a shallow USA estuary, based on multiple approaches using acoustic telemetry. Marine Ecology Progress Series, 364: 199-212.

SAS Institute Inc. (2009) SAS OnlineDoc® 9.2. Cary, NC: SAS Institute Inc.

Simpendorfer CA, Heupel MR, and Hueter RE (2002) Estimation of short-term centers of activity from an array of omnidirectional hydrophones and its use in studying animal movements. Canadian Journal of Fisheries and Aquatic Sciences, 59: 29-32.

Staaks G, Kirschbaum F, and Williot P (1999) Experimental studies on thermal behavior and diurnal activity rhythms of juvenile European sturgeon (*Acipenser sturio*). Journal of Applied Ichthyology, 15: 243-247.

Staudinger MD and Juanes F (2010) Feeding tactics of a behaviorally plastic predator, summer flounder (*Paralichthys dentatus*). Journal of Sea Research, 64: 68-75.

Sutherland WJ (1996) From individual behavior to population ecology. Oxford University Press, Oxford, 213 p.

Szedlmayer, S. T. and K. W. Able. 1993. Ultrasonic telemetry of age-0 summer flounder *Paralichthys dentatus*, movements in a southern New Jersey estuary. Copeia, 3: 728-736.

Topping DT and Szedlmayer ST (2011) Home range and movement patterns of red snapper (*Lutjanus campechanus*) on artificial reefs. Fisheries Research, 112: 77-84.

Verbeke G and Molenberghs G (2000) Linear mixed models for longitudinal data. Springer, New York.

Vinagre C, Franca S, and Cabral HN (2006) Diel and semi-lunar patterns in the use of an intertidal mudflat by juveniles of Senegal sole, *Solea senegalensis*. Estuarine, Coastal, and Shelf Science, 69: 246-254.

Zhang H, Lu N, Feng C, Thurston SW, Xia Y, Zhu L, and Tu XM (2011) On fitting generalized linear mixed-effects models for binary responses using different statistical packages. Statistics in Medicine, 30: 2562-2572.

Zuur A, Leno EN, and Smith GM (2007) Analysing Ecological Data. Springer, New York.

Table 1. Model selection table for the repeated measures generalized linear mixed model designed to identify factors that influence the movement probability of summer flounder resident at Back River reef from June through September 2006. The model is based on a binomial response (moved vs not moved) for 42 individuals observed during 9821 time periods. The table shows the factors and interactions included in the top five models selected based on AICc model selection criteria. Possible factors include: fish length, hours at large, tidal stage (low, rising, high, or falling), time of day (day or night), lunar phase (new, wax crescent, 1st quarter, wax gibbous, full, wan gibbous, 3rd quarter, and wan crescent), and water temperature (Temp). The ΔAICc value is the difference in AICc values between a given model and the model with the lowest AICc.

Length	Hours-at- large	Tide	Time of day	Lunar	Temp	Time of day * lunar	AICc	ΔAICc
X		X	X	X		X	2838.6	0
		X	X	X		X	2841.6	3.0
X	X	X	X	X		X	2843.7	5.1
X		X		X			2846.0	7.4
X		X	X		X	X	2847.2	8.6

Table 2. Parameter estimates from the generalized linear mixed model with the lowest AICc value (see Table 3). Estimates for different tidal states are relative to the rising tide and estimates for the interaction of time-of-day and lunar phase are relative to nights during the same lunar phase. See text for description of factors.

Variable	Tide	Time-of-day	Lunar Phase	Degrees of Freedom	Estimate	Standard Error
Intercept				41	-3.83	0.35
Length				9718	0.00	0.00
Tide	High			9718	-0.64	0.15
Tide	Falling			9718	-0.69	0.15
Tide	Low			9718	-0.83	0.16
Tide	Rising			.	0.00	.
Time-of-day * Lunar phase		Day	New	9718	0.21	0.55
Time-of-day * Lunar phase		Day	Wax Cresent	9718	-0.23	0.47
Time-of-day * Lunar phase		Day	1st Quarter	9718	-0.86	0.43
Time-of-day * Lunar phase		Day	Wax Gibbous	9718	-1.26	0.53
Time-of-day * Lunar phase		Day	Full	9718	0.44	0.61
Time-of-day * Lunar phase		Day	Wan Gibbous	9718	-1.12	0.49
Time-of-day * Lunar phase		Day	3rd Quarter	9718	-0.75	0.47
Time-of-day * Lunar phase		Day	Wan Cresent	.	0.00	.

Table 3. Model selection table for the general linear mixed model developed to identify factors that influenced the minimum distance traveled by 35 individual summer flounder resident at Back River reef from June through early-October 2006. This model is based on non-zero movements during 370 different time periods. The table shows the factors included in the top eight models selected based on AICc model selection criteria. Possible factors included: fish length, hours at large, tidal stage (low, rising, high, or falling), time of day (day or night), lunar phase (new, wax crescent, 1st quarter, wax gibbous, full, wan gibbous, 3rd quarter, and wan crescent), and water temperature. The ΔAICc value is the difference in AICc values between a given model and the model with the lowest AICc value.

Length	Hours-at-large	Tide	Time of day	Lunar	Temperature	AICc	ΔAICc
x			x		x	646	0
x		x	x			646.2	0.2
x			x			646.3	0.3
x	x		x		x	646.4	0.4
x	x		x			646.5	0.5
x	x	x	x			646.7	0.7
x		x	x		x	647.2	1.2
x	x	x	x		x	647.8	1.8

Table 4. Parameter estimates for the general linear mixed model that included length and time of day as predictors of minimum distance traveled (See Table 1). The estimate reported for 'day' is relative to the estimate for 'night'.

Variable	Degrees of Freedom	Estimate	Standard Error
Intercept	313	2.294	0.047
Length	231	-0.001	0.0004
Day	348	-0.121	0.060

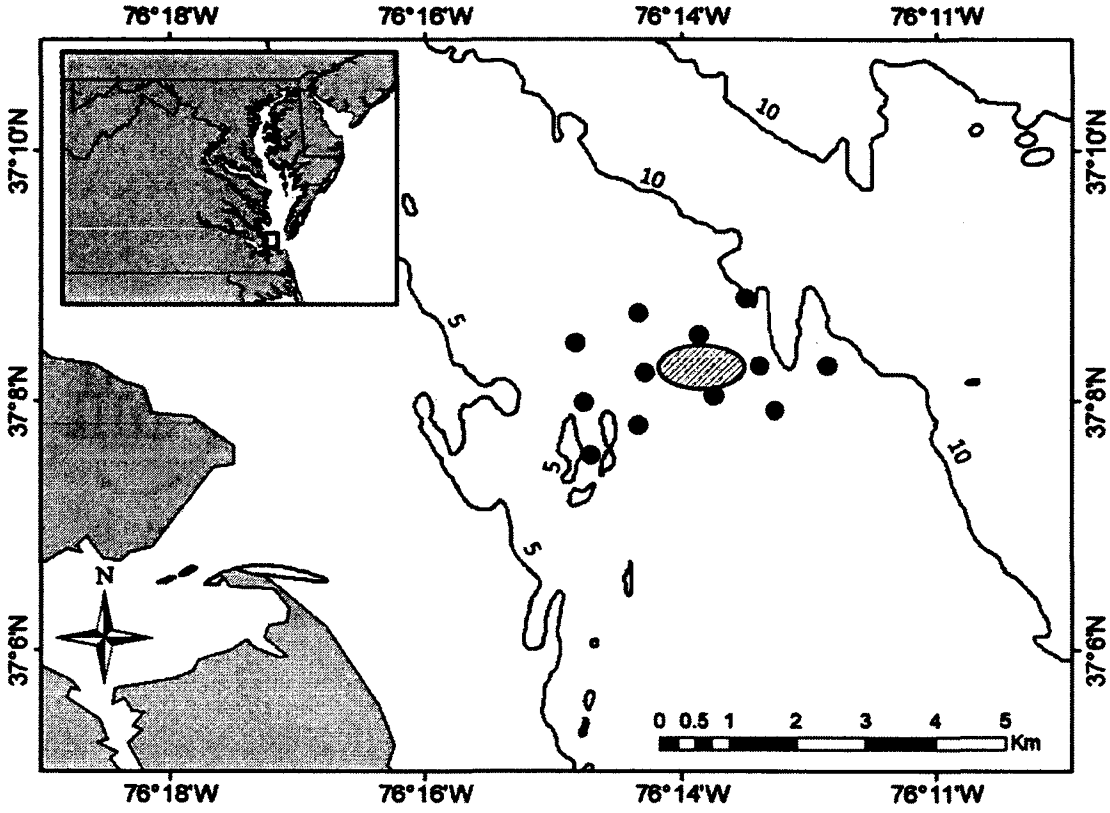


Figure 1. Location of Back River artificial reef (hashed ellipse) and acoustic receivers (black circles) in lower Chesapeake Bay (inset). Contour lines depict water depths (m).

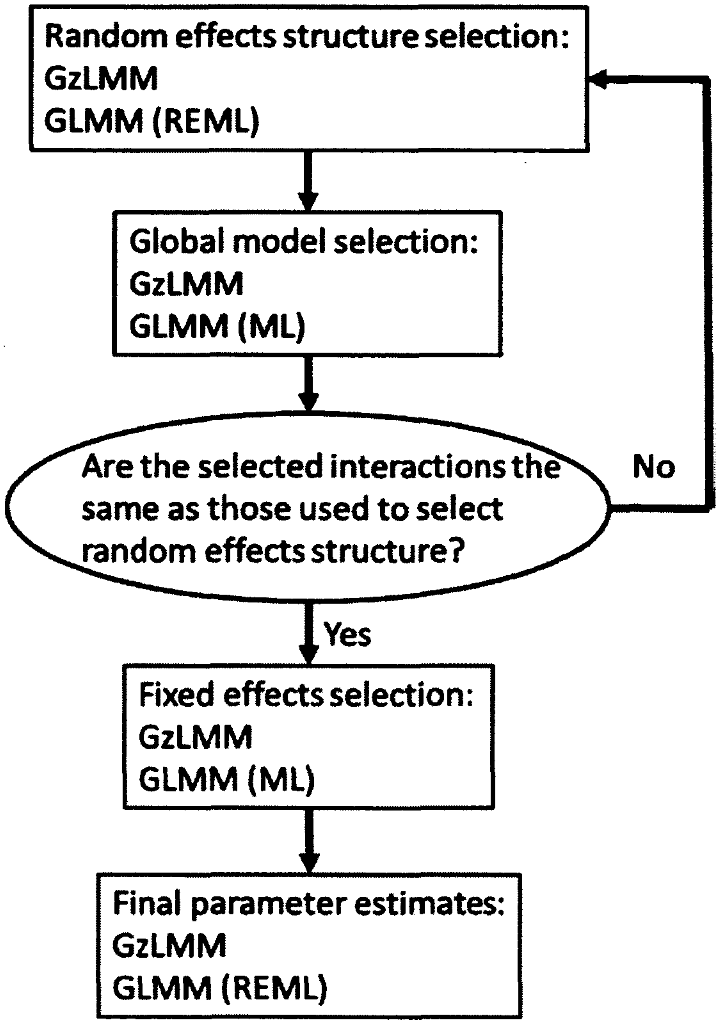


Figure 2. Conceptual diagram of the process used to select the most appropriate generalized (GzLMM) and general (GLMM) linear mixed model. For the GLMM we also show at each step whether the model was fit using restricted maximum likelihood (REML) or maximum likelihood (ML). The Laplace method was used to the fit the GzLMM at each step. The 'random effects structure' is comprised of the variance-covariance structure and whether or not individual fish is included in the model as a random effect. The 'global model' is the model that includes all the potential main effects as well as any interactions that may be of interest. In the 'fixed effect selection' step we determine which of the main effects and interactions best describe the observed data. The 'final parameter estimates' are the estimates from the most appropriate model and are presented in the results section.

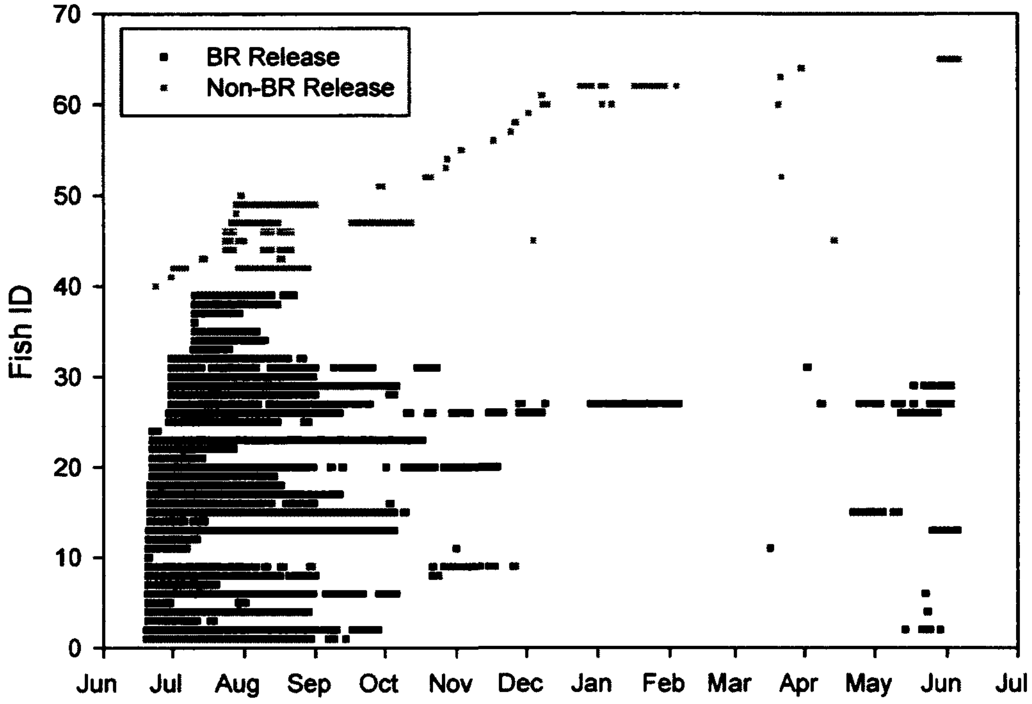


Figure 3. Individual detection histories at Back River (BR) reef for 39 fish released at Back River (black) and 26 fish released at other sites (Non-BR) in Chesapeake Bay (gray).

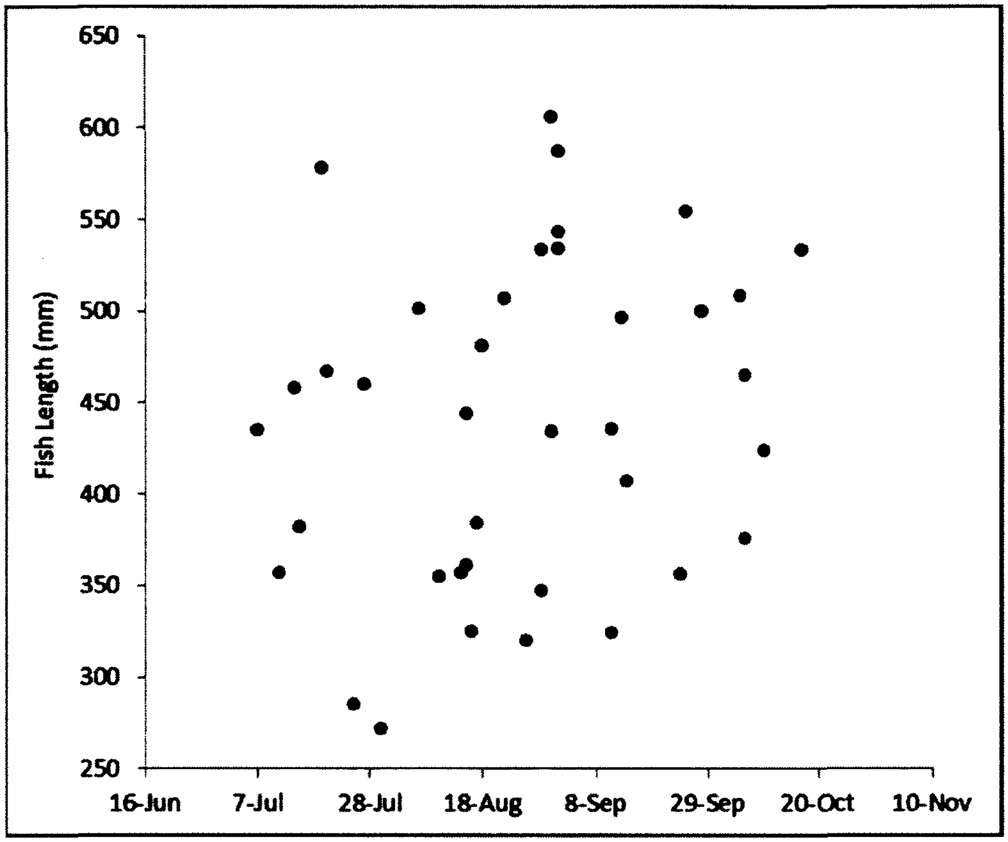


Figure 4. Size (total length) and date of dispersal for 39 summer flounder released with acoustic transmitters at Back River reef during summer 2006.

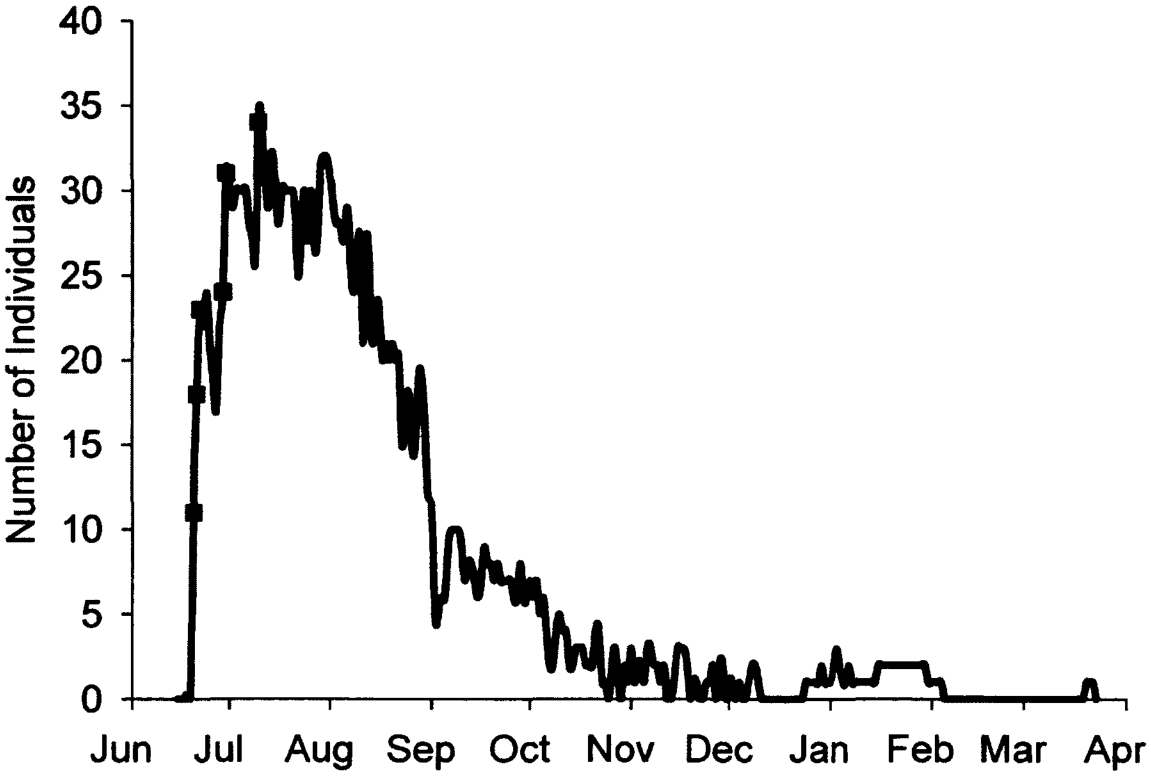
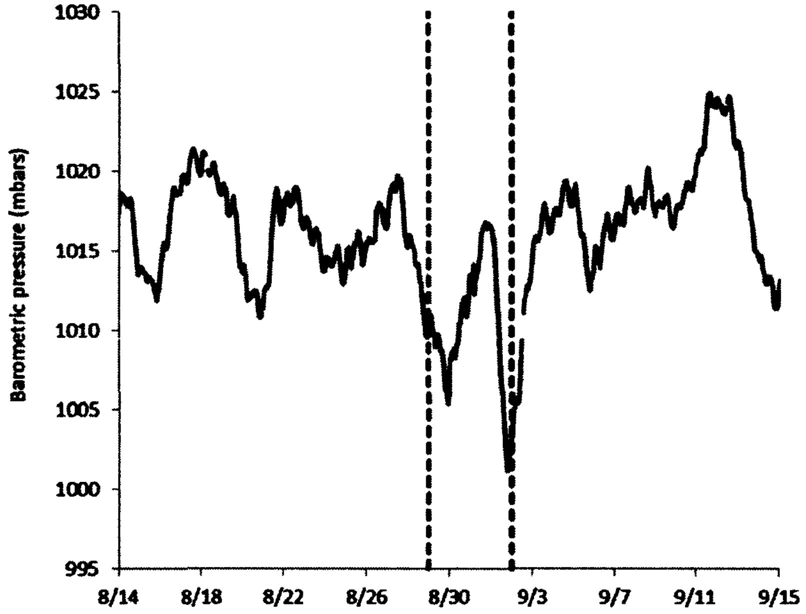


Figure 5. Number of individual summer flounder detected daily at Back River Reef from June 2006 through March 2007. The six black squares identify release dates for fish implanted with acoustic transmitters.

a)



b)

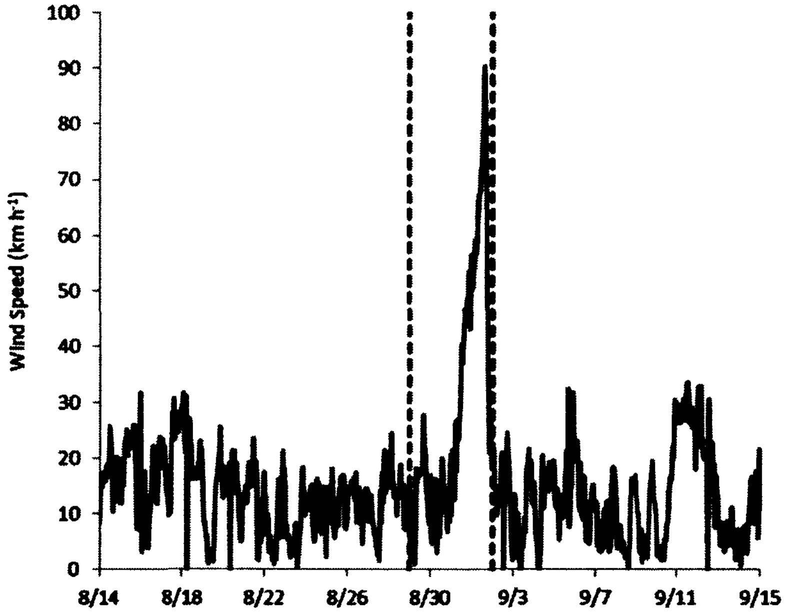


Figure 6. Measurements of barometric pressure (a) and wind speed (b) recorded at a meteorological station in the lower Chesapeake Bay from mid-August through mid-September 2006 (gray lines). The time period when summer flounder rapidly dispersed away from Back River reef is indicated by the dashed black lines.

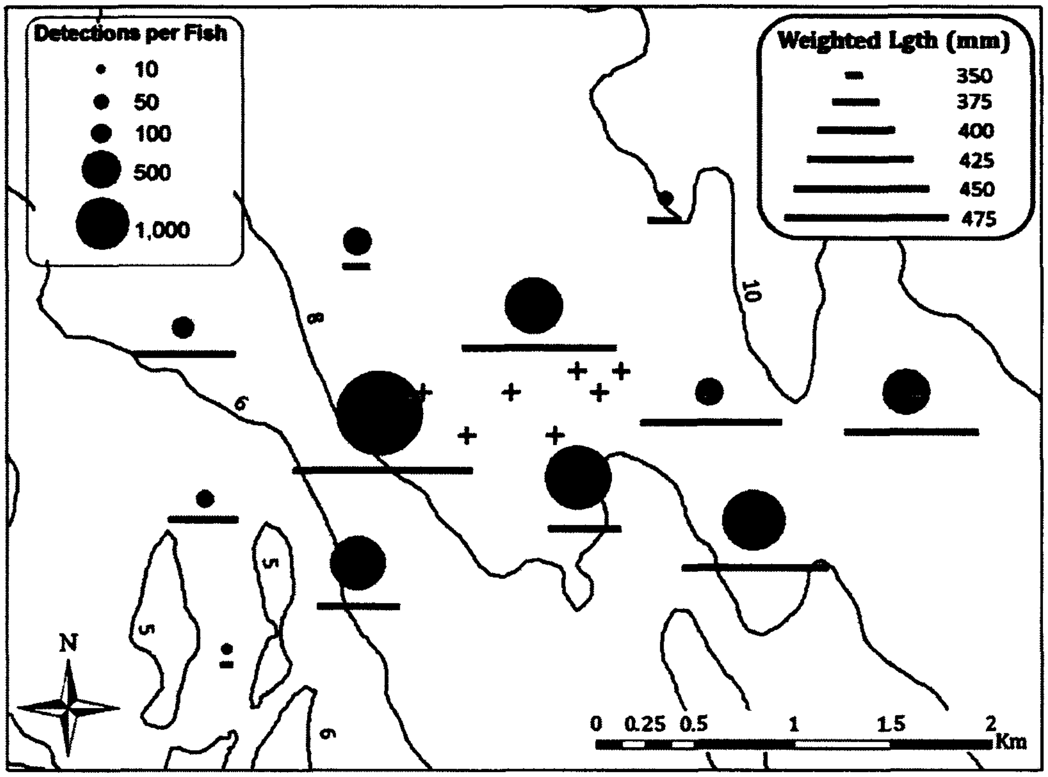


Figure 7. Number of detections per fish (gray circles) and weighted mean length of summer flounder (black bars) at each acoustic receiver from June through early-October 2006. Also depicted is the artificial reef structure (+) and the water depth in meters (contour lines).

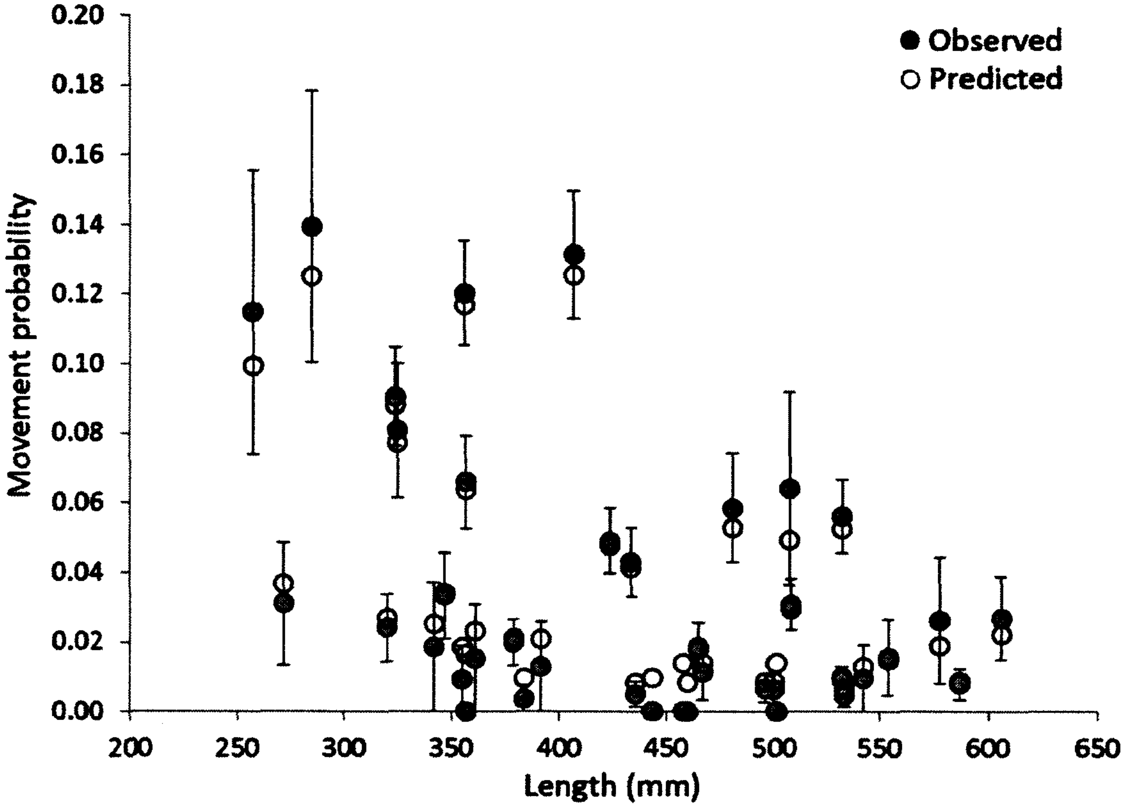


Figure 8. Mean movement probability and total length of 42 summer flounder resident at Back River reef from June through September 2006. Plot depicts the observed movement probabilities (filled circles) and movement probabilities predicted from the generalized linear mixed model (open circles). Error bars (± 1 SE) are shown for the observed probabilities.

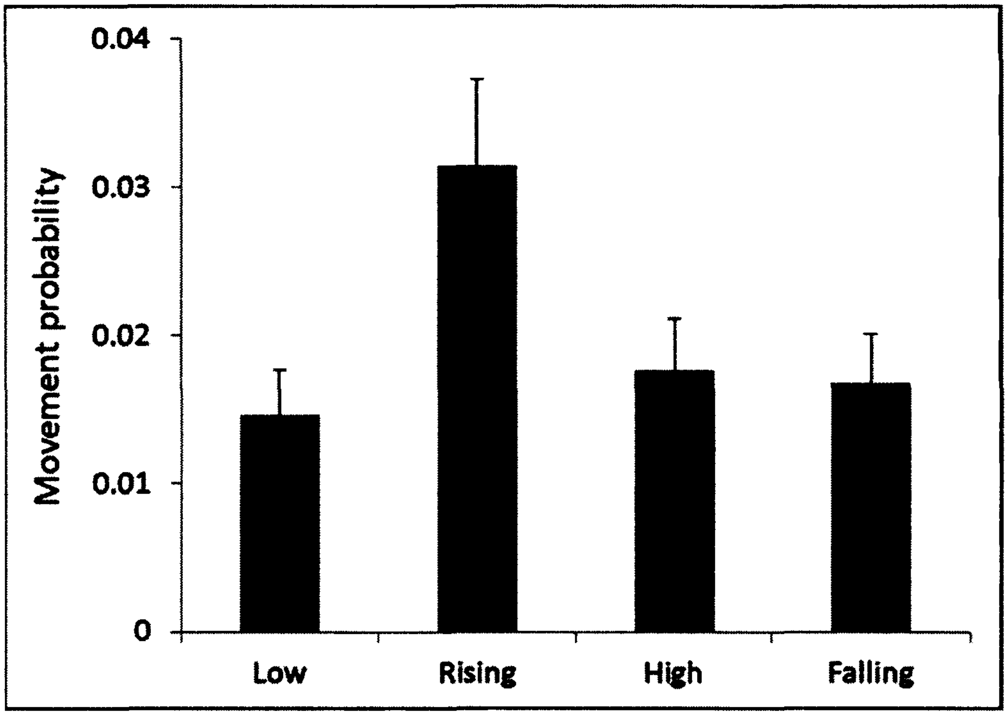


Figure 9. Mean movement probability for 42 summer flounder at low, rising, high, and falling tides during June through September 2006. Error bars are ± 1 standard error.

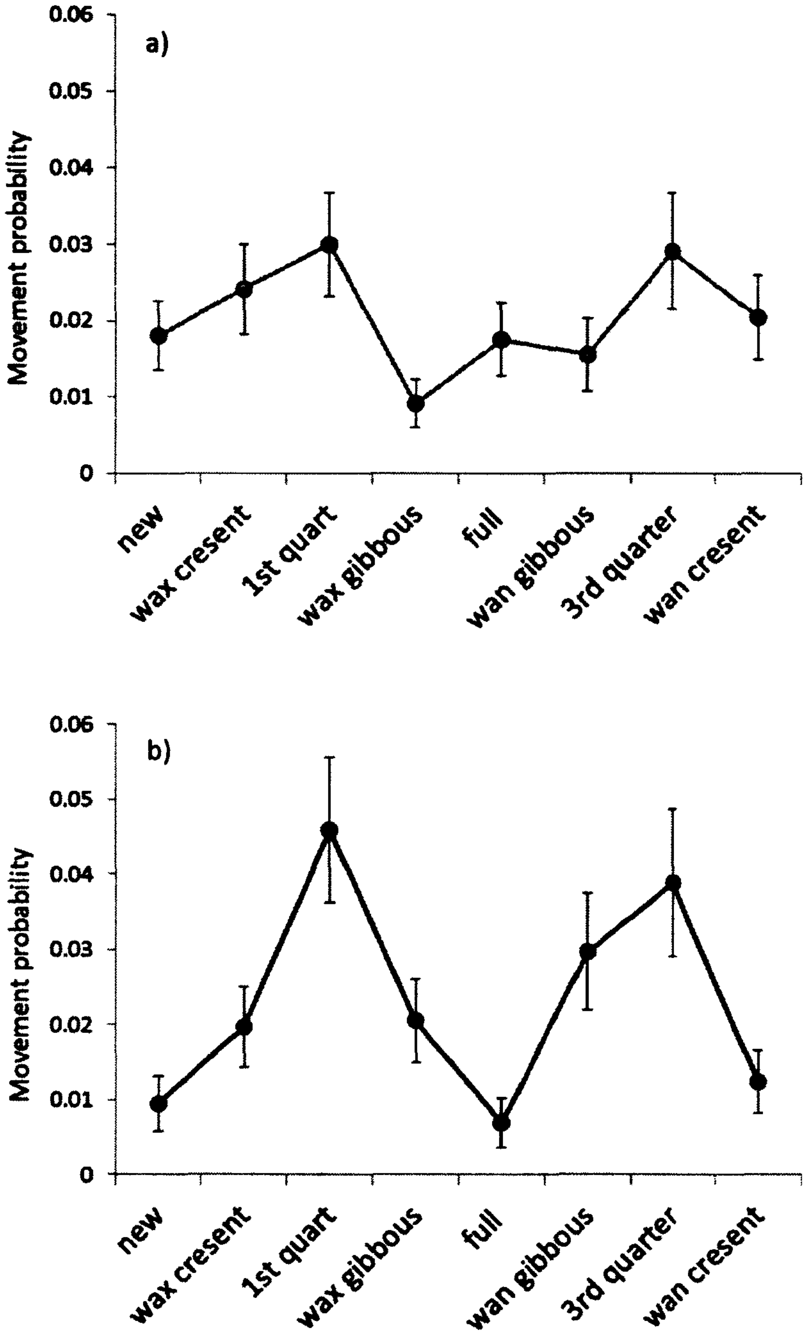


Figure 10. Influence of lunar phase on the daytime (a) and nighttime (b) movement probabilities of 42 summer flounder resident at Back River reef from June – September 2006. Error bars are ± 1 standard error.

CHAPTER 2

Using Archival and Conventional Tags to Observe Summer Flounder Movements at Different Spatial Scales

Abstract

Although large-scale movement patterns of summer flounder are well studied, factors that influence the small-scale movements of this species are not as well understood. We therefore used conventional and archival tags to examine the movement patterns of summer flounder across various spatial scales. Conventional tagging data were used to observe monthly movements, inter-annual site fidelity, and emigration of over 60,000 summer flounder tagged in Chesapeake Bay. We also used temperature and depth data collected with archival tags attached to 15 summer flounder to investigate how fish of different size responded to changes in tidal state, time-of-day, lunar phase, and temperature. Results suggest that summer flounder remain in relatively small regions while resident in Chesapeake Bay and that a high percentage (63.1 ± 2.2%) return to the same regions in subsequent years. Fish that migrated from Chesapeake Bay were more likely to move north during the spring and summer and to move south during the winter. Fish activity levels were higher as water temperature increased, but this primarily occurred during the rising and the falling tides. Furthermore, flounder smaller than 400 mm were more active at night, whereas activity of larger fish was not influenced by the time-of-day. Results from this study fill a void in understanding the factors that influence small-scale movements of summer flounder, and could be incorporated into individual based models to understand how large-scale distributions arise from small-scale behavioral decisions.

Introduction

Observing animal movements on different spatial scales provides a mechanism to understand how large-scale species distributions are established from small-scale behavioral decisions (Roshier et al. 2008, Humston et al. 2004). Individuals within a population alter their behavior in response to environmental heterogeneity to minimize physiological stress, minimize predation risk, and maximize foraging success (Wannamaker and Rice 2000, Lowe and Bray 2006). These individual behaviors subsequently influence the distribution and structure of populations (Humston et al. 2004). The scale of an individual's movement is expected to be proportional to the scale of variation in environmental conditions and resource availability (Roshier et al. 2008). As a result, examining animal movements on a range of spatial scales often provides greater insights into the factors that drive individual behavioral decisions. Although the large-scale distributions of populations are often well studied, movements of individuals on smaller spatial scales are not well known. In this study, we use conventional and archival tags to examine the movement patterns of summer flounder on three spatial scales: 1) within the Mid-Atlantic Bight (large scale; 100s of km), 2) within Chesapeake Bay and coastal Virginia waters (regional scale; 10s of km), and 3) within habitats while resident in Chesapeake Bay (fine scale; <1 m).

Summer flounder are an economically, and ecologically, important fish species that range throughout the east coast of North America. This species is one of the most highly targeted and valuable commercial and recreational fish species of the US Atlantic coast (Terceiro 2002). In addition to their economic value, summer flounder are a valuable member of the ecosystem as an upper-trophic-level predator (Latour et al. 2008). Based on their consumption, summer flounder have the potential to influence community dynamics in coastal habitats through trophic interactions (Overholtz et al. 2000, Link et al. 2002). Thus, as fisheries management moves towards ecosystem-based approaches, it is important to understand the processes that influence summer flounder movement and distribution.

Large-scale, seasonal migration patterns of summer flounder are well known from conventional mark-recapture studies conducted throughout most of their range (Poole 1962, Murawski 1970, Lux and Nichy 1981, Monaghan 1992, Desfosse 1995, Burke et al. 2000, Kraus and Musick 2001). During fall and early winter, summer flounder migrate to the continental shelf to spawn. The initiation of the spawning migration is earlier in the north and progressively later at more southern latitudes. After spawning is complete, individuals return to coastal habitats, where they reside during the spring and summer. These fish tend to return to the same inshore location in subsequent years, but fish that emigrate tend to be recaptured in coastal habitats to the north of their release location.

In contrast to these well documented seasonal migration patterns, movements between different coastal habitats (e.g., rivers, bays, seaside lagoons) during the period of inshore residency have not been examined, with the exception of one unpublished dissertation (Desfosse 1995). In his dissertation, Desfosse examined 3 years (1987-1989) of mark-recapture data and found that summer flounder were generally recaptured near their tagging location within a few months after release. With only 3 years of data on a relatively sedentary species, Desfosse did not have sufficient tag-returns to discern intra-annual regional movement patterns. However, with sufficient tag-return data it should be possible to determine if fish are more likely to move into certain regions, and less likely to move into other regions. According to the ideal free distribution theory (reviewed in Kennedy and Gray 1993) we would expect more individuals to move into regions with the highest density of resources. Thus, observing these regional movements could provide some indication of relative habitat quality. Furthermore, observing the temporal variation in regional movements provides insight into the timing of the seasonal migration.

Another way to gain insight into summer flounder behavior is to examine the small- and fine-scale movement patterns of individual fish relative to environmental conditions. For example, studies using acoustic telemetry have found that summer flounder move in response to changes in tidal state (Szedlmayer and Able 1993, Chapter 1), low dissolved oxygen concentrations (Miller 2010), oncoming storms (Sackett et al. 2007, Chapter 1), and decreased light levels at night (Capossela 2010, Miller 2010, Chapter 1). These studies examined movements over relatively large scales (100s to 1000s of meters) but could not discern fine-scale (<10 m) movements in response to environmental variations. Archival tags continuously record environmental information (i.e., depth and temperature) over long durations, making them an ideal technology for observing the fine-scale movements of fish (Block et al. 2001, Wilson et al. 2005). Furthermore, sequential measurements of fish depth and temperature can be used to examine large-scale migration patterns and identify spawning grounds (Hunter et al. 2003). Understanding these fine-scale behaviors is a critical component in developing individual-based models to examine how species distributions develop in response to various environmental conditions (Roshier et al. 2008, Humston et al. 2004).

In this paper, we use conventional and archival tags to examine large-, regional-, and fine-scale movement patterns of summer flounder tagged in Chesapeake Bay and coastal waters of Virginia. The Chesapeake Bay is the largest estuary in the range of summer flounder and is believed to be an important seasonal habitat for both juveniles and adults (Packer et al. 1999). We used conventional tagging data from a recreational angler tagging program to examine the seasonal migration pattern of summer flounder (large-scale). These mark-recapture data are also used to investigate the movements of summer flounder within Chesapeake Bay and coastal waters of Virginia (regional-scale). Finally, we use temperature and depth data recorded with archival tags to observe fine-scale movements of summer flounder during their residency within, and dispersal from, Chesapeake Bay.

Methods

Large- and regional-scale movements

Anglers participating in the Virginia Game Fish Tagging Program (VGFTP) have tagged and released summer flounder in Virginia waters since March 2000. Recreational anglers are trained to properly tag and release their catch and to record all salient information about their tagged releases, such as fish length, tag number, release location, and release condition (Musick and Gillingham 2010). Small rewards (i.e., t-shirts, tackle boxes, and pewter pins) are offered to encourage commercial and recreational fishers to report their recaptures. Between 2000 and 2009, participants in the VGFTP released 60,930 tagged summer flounder in Virginia waters. Tagging locations were primarily within Chesapeake Bay and its tributaries, but fish were also released in the nearshore coastal waters off Virginia Beach and the Eastern Shore (Figure 1, Table 1). Fish were tagged in the dorsal musculature near the tail with T-bar anchor tags (Hallprint). Each tag was labeled with a unique identifying number, a phone number to report recaptures, and a reward notice.

Summer flounder tag and recapture data from all years were used to investigate monthly movement patterns and inter-annual site fidelity. Data from all years were combined under the assumption that movement patterns did not differ considerably among years. To examine the monthly movements of summer flounder, we calculated the monthly proportion of recaptured fish that were tagged and encountered in different regions (see Figure 1 for region boundaries). Inter-annual site fidelity was quantified as the proportion of fish released and recaptured in the same region, after being at liberty through a spawning season (November-March). We restricted the site fidelity analysis to fish recaptured between May and October to decrease the probability that the observed movements were related to the seasonal spawning migration.

We also used the conventional tagging data from the VGFTP to understand regional-scale movements of summer flounder within Virginia and large-scale migrations to locations outside of Virginia. Within-year movements between regions in Virginia were calculated as the proportion of fish released in a given region and subsequently recaptured elsewhere. Regions with less than 250 releases during the 10-year study period were excluded from the analysis to avoid potential biases due to small sample sizes. Finally, we used the VGFTP recapture data to examine the seasonal migration patterns of summer flounder to locations outside of Virginia. Due to lingering questions regarding the existence of two summer flounder stocks along the Atlantic coast (Kraus and Musick 2001, NRC 2000), we were primarily interested in determining if fish tagged in Virginia waters subsequently moved north or south. These data were summarized as the proportion of fish recaptured outside of Virginia that moved in a given direction (i.e., north or south) during a given season (i.e., spring, summer, fall, and winter). We used a chi-square test to determine if the proportion of fish that moved north or south varied among seasons. A multiple comparison test for proportions was used to determine the season in which proportions differed. These test statistics were calculated using the methods described by Zar (1999), and were assessed using a significance level of 0.05. We also used an analysis of variance (ANOVA), implemented in R, to determine if the mean length at tagging differed between summer flounder that moved north or south in a given season. Tukey's honestly significant difference method was used to test for equality of mean fish length for fish moving in a given direction each season.

Fine-scale movements

During 16 days in August and September 2009 we released 262 summer flounder in the lower Chesapeake Bay with archival tags. Fish were primarily captured with hook-and-line gear near the mouth of the Chesapeake Bay. A small percentage of fish (1.5%) were captured in September 2009 using a 13.7-m bottom trawl towed for 30-minutes at a single site in the eastern portion of the lower Chesapeake Bay (Chesapeake Bay Multispecies Monitoring and Assessment Program; Bonzek et al. 2010). The total length for each fish was measured prior to the external attachment of a Star-Oddi DST milli-L archival tag measuring 12.5 mm in diameter by 38.4 mm in length and weighing 5 g in water. To maintain consistency in the tagging procedure, only one scientist (MJH) attached all 262 archival tags. These tags recorded water temperature (range: -1 to +40 °C, resolution: ± 0.03 °C) and depth (range: 1 to 250 m, resolution: ± 0.08 m) of the habitat occupied by each fish. Tags were configured to record temperature every 60 minutes and depth every 20 minutes. To maximize survival of fish after tag attachment, and avoid abnormal behaviors associated with application of a tag that was too heavy, only fish that exceeded 290 mm total length were tagged (range: 295 - 714 mm; mean: 413 mm).

Archival tags were attached externally to allow for identification by recreational anglers and commercial fishers upon recapture (Figure 2a). The external attachment method was modified from a procedure used to attach similar archival tags to yellowtail flounder (Cadrin and Moser 2006). Tags were attached to the pigmented side of the fish with 2 nickel pins that pierced the dorsal musculature. On the non-pigmented side of the fish, small plastic discs were used to protect the fish's epidermis from the nickel pins (Figure 2b). We allowed about 4 mm of space between the plastics discs and the epidermis of the fish to permit growth. A rubber earring backing was used to secure the plastic discs, and nickel pins were clipped and crimped around the earring backing to secure the archival tag to the fish. A T-bar anchor tag (Hallprint) was also inserted into the dorsal musculature as a secondary identification tool and to ascertain shedding rates of archival tags.

It was necessary to recover the archival tags to retrieve the recorded temperature and depth data, which were subsequently examined to remove erroneous or spurious recordings. To increase the probability that recovered archival tags were returned, we offered a $200 reward and instituted an extensive advertising campaign at ports and fish processing houses throughout the Mid-Atlantic coast. Data from recovered tags were downloaded and processed to remove all temperature and depth measurements recorded prior to the tag's deployment date and after the tag's retrieval date. Negative depth measurements (i.e., above the sea surface) were reassigned to a depth of 1 meter. These small number of negative depth measurements were most likely the result of inaccurate recordings when the fish occupied very shallow or near-surface waters.

We used depth data recorded by the archival tags to examine the fine-scale movement patterns of summer flounder during their residency in Chesapeake Bay. To ensure that the observed movement patterns were not influenced by the tagging procedure, we excluded recordings within 24 hours of release. We also restricted our analysis to dates prior to 15 October 2009 to ensure that we had at least 5 fish available to observe movements. This prevented potential biases related to small sample size. Fine-scale summer flounder movements were inferred from changes in depth between subsequent measurements from the same fish. While fish were resident in Chesapeake Bay, we corrected for tide-related changes in depth by subtracting the predicted change in tidal amplitude from the observed depth change; tidal amplitudes were estimated using the Tides and Currents® software program. Because we did not know an exact location for each fish, we calculated a mean tidal amplitude for the lower Chesapeake Bay. Based on tidal corrections used to predict tides at various locations in the lower Chesapeake Bay, we estimate that the mean tidal amplitudes were within 20 minutes of the actual tides experienced by our tagged fish.

We followed procedures described in Chapter 1 to estimate the tidal stage, time-of-day, and lunar phase during finite time periods while fish were resident within Chesapeake Bay. Due to importance of tidal state in the movements of summer flounder (Szedlmayer and Able 1993, Chapter 1), we elected to examine movements during 1.5-hour time periods centered around four tidal stages: low, rising (the mid-point between low and high tide), high, and falling (the mid-point between high and low tide). The time-of-day for each tidal period was assigned based on the times of sunrise and sunset, which were obtained from Tides and Currents®. If the mid-point of the tidal time period occurred prior to sunrise, or after sunset, the time-of-day for that time period was specified as 'night', otherwise the time-of-day was specified as 'day'. Lunar phase was assigned using the moon phase output from Tides and Currents software program. Based on the percent of the moon illuminated, the lunar cycle was divided into eight phases: new moon, wax crescent, 1st quarter, wax gibbous, full, wan gibbous, 3rd quarter, wan crescent.

We developed a general linear mixed model (GLMM) to investigate the effect of fish length, tidal state, time-of-day, lunar phase, and temperature on the movements of summer flounder resident in Chesapeake Bay. Length and temperature data were centered (i.e., the mean was subtracted from each observation) to reduce collinearity (Quinn and Keogh 2002). The response variable, which was the cumulative absolute depth change observed in each tidal period, was transformed using a Box-Cox transformation (Box and Cox 1964). The data were transformed because the untransformed data did not satisfy the linear model assumption of normality. The Box-Cox transformation is calculated by:

$$y_i^{(\lambda)} = \begin{cases} \dfrac{y_i^{\lambda} - 1}{\lambda}, & \text{if } \lambda \neq 0 \\ \log(y_i), & \text{if } \lambda = 0 \end{cases} \tag{1}$$

Where $y_i^{(\lambda)}$ is the transformed response, y_i is the untransformed response, and λ is a power parameter. The most appropriate value for λ was estimated with maximum likelihood using the solver function in Microsoft® Excel (2010). We then used the MIXED procedure in SAS to fit a repeated measures GLMM to the transformed depth-change data. A mixed model was used because our data included both fixed effects (i.e., fish size, tidal state, time-of-day, lunar phase, and temperature) as well as an individual fish random effect (Littell et al. 2006, Bolker et al. 2008). A repeated measures model was used because observations of the same fish recorded closely in time were serially correlated. The repeated factor in the model was the number of hours an individual was at liberty. To account for this serial correlation and to estimate unbiased model parameters, a repeated measures model incorporates a specialized variance-covariance structure (Rogers and White 2002, Littell et al. 2006). We selected the most parsimonious model using a three-step process.

The first step was to identify a preliminary variance-covariance structure and determine if the between-subject variability contributed to the total random variation. We refer to the combination of the variance-covariance structure and the individual fish random effect as the 'random effects structure'. We selected a preliminary random effects structure using models that contained the five main effects and no interactions. Restricted maximum likelihood (REML) was used to compare models with different random effects structures (Pinheiro and Bates 2000, Zuur et al. 2007). The variance-covariance structures tested were: variance components, compound symmetry, first order autoregressive, and first order autoregressive-moving average. These variance-covariance structures allowed us to model the correlation between the repeated measures response, which for these data was depth change recorded by the archival tags. As recommended for repeated measures models, the Kenward-Roger approximation was used to calculate the degrees of freedom and adjust the estimated standard errors (Littell et al. 2006, Bolker et al. 2008). We selected the preliminary random effects structure that best described the data as the model with the lowest value of Akaike's Information Criterion corrected for small sample size (AICc; Akaike 1973, Burnham and Anderson 2002). Although we believed our sample sizes were sufficient, Burnham and Anderson (2002) recommend using AICc because it is a more appropriate criterion at small sample sizes and converges with AIC as sample sizes increase.

After identifying the random effects structure we developed a global model that included all the main effects as well as any potential interactions (Zuur et al. 2007). To avoid testing thousands of models with every combination of main effects and interactions, we individually added each two-way or three-way interaction to the model with only the main effects. All possible two-way interactions and all three-way interactions that included fish length were evaluated in this analysis. For models with three-way interactions we also included the component two-way interactions to ensure correct interpretation of the model (Morrell et al. 1997). In this step, all models were fit using maximum likelihood (ML) and the preliminary random-effects structure previously discussed. 'Important' interactions were identified as those interactions that reduced the AICc value by more than 1 unit. We graphically examined the 'important' interactions to determine if such interactions were due to small sample sizes and simply reflected noise. Only informative interactions were added to the global model. The procedure used to evaluate the random-effects structure was repeated using the global model. This step was necessary because a change in the mean structure (i.e., the fixed effects included in the model) affects the random-effects model selection criterion calculated with REML (Littell et al. 2006). Thus, we validated that the correct random-effects structure was used to develop the global model. We repeated this entire process until there was no difference between the random-effects structure selected in step 1 and the global model selected in this step.

Our final step was to identify the fixed effects and interactions that best described the variation in summer flounder movement behaviors. Here, we used ML to fit models using all possible combinations of main effects and the interactions identified in step 2 (Littell et al. 2006, Zuur et al. 2007). Once again, the degrees of freedom were estimated using the Kenward-Roger approximation, and AICc was used to select the most parsimonious model with the best fit to the data. The final model parameters reported for the 'best' model were estimated using REML (Zuur et al. 2007).

We used the tidal location method developed by Hunter et al. (2003) to determine if fish that emigrated from Chesapeake Bay moved north or south on the continental shelf. The tidal location method uses the differences in tidal patterns between locations to approximate the geographic position of individual fish. The tidal frequency and amplitude at a fish's location is determined using archival-tag depth measurements recorded while the fish is sedentary on the seafloor. If differences in tidal cycles between locations are sufficiently large, the tidal information from the archival tag can be compared with tidal model predictions over a range of locations to approximate the fish's location. We used the Oregon State University East Coast tidal inversion model (Egbert et al. 1994) to predict tides at various locations. Because we were primarily interested in determining if fish moved north or south, we examined tidal predictions only off the coast of Delaware and North Carolina. Least squares were used to compare the times of high and low tide at the fish's location to the times of high and low tide predicted by the model at locations off Delaware and North Carolina.

Results

Large- and regional-scale movements

Summer flounder were recaptured primarily within the region in which they were tagged, and these recaptures generally occurred shortly (less than 90 days) after release. A total of 5669 (9.3%) conventionally tagged summer flounder was recaptured during 2000-2009. Some of these individuals were recaptured multiple times, resulting in a total of 6395 recapture reports. Most fish were recaptured in the lower bay (26.6%), the York River (26.2%), or near the mouth of the bay (21.1%). These three locations also comprised 73.1% of the releases of tagged summer flounder (Table 1). The mean time at liberty was 59.0 days (range: 0 – 1775 days). The majority (87.5%) of recaptures occurred within 90 days of release. Throughout the 10 years of this study, only 235 (4.2%) fish were at liberty for more than 1 year prior to recapture. Due to the short periods at liberty observed and the relatively sedentary nature of summer flounder, only a small percentage of fish (9.1%) were recaptured outside of the region in which they were tagged. Summer flounder were more likely to move to a different region, primarily outside of Virginia waters, between November and April (Figure 3). Most fish (63.11%) at liberty throughout the winter (November-April) were recaptured in their release region the following summer (May-October; Figure 4).

No obvious seasonal pattern existed in fish movements during residency in Virginia waters, but the VGFTP data suggest that fish were more likely to move between adjacent regions in the lower bay than they were to move between any other regions. Based on the timing of the spawning migration, we originally postulated that fish movements within Virginia water would exhibit seasonality, such that fish would move towards the head of the bay during spring (April-June) and towards the mouth of the bay during late summer/early fall (August-October). The data from recaptured fish did not support this hypothesis, and instead suggested that no discernible seasonal pattern existed for fish within Chesapeake Bay. For simplicity, we pooled data from the spring (April-June), summer (July-September), and fall (October-December) to examine regional movement patterns (Table 2). Of the fish that moved, the largest proportion moved from their release location into the lower bay and mouth of the bay. With the exception of fish tagged in the James River, less than 1% of tagged fish were released and recaptured in a different region. A slightly larger proportion (1.2%) of fish tagged in the James

River were recaptured in another region, primarily in the adjacent lower bay. The lowest proportions of fish that were released and recaptured in a different region were tagged in the York River, Virginia Beach, and the Eastern Shore regions. In spite of the large number of releases in the York River, we observed only a few recaptures of these fish in other regions. Relatively little exchange was evident between the Eastern Shore, Virginia Beach, and the Bay. Although a small proportion of fish tagged on the Eastern Shore (0.2%) and in Virginia Beach (0.3%) were recaptured within the Bay, exchanges between the Eastern Shore and Virginia Beach were not observed. In addition, a small proportion (0.1%) of fish tagged within Chesapeake Bay were recaptured in these two regions. This implies there was limited exchange across the mouth of the Bay or between the Bay and the coastal waters of Virginia.

The conventional tagging data indicated a seasonal trend existed in summer flounder movements to locations outside of Virginia. Recaptures were reported as far north as Rhode Island and as far south as South Carolina (Musick and Gillingham 2010). The proportion of fish that migrated north and south varied with season (χ^2=47.62, df = 3, p<0.001; Figure 5a). Fish tagged and released within Chesapeake Bay were more likely to be recaptured in northern locations during spring and summer. In contrast, fish tagged and released within Chesapeake Bay were more likely to be recaptured south of Chesapeake Bay during winter.

We used an ANOVA to test if the mean length at tagging differed between fish that moved north or south in a given season. This ANOVA revealed there was a significant interaction between direction and season (F=3.26, df = 3, p=0.024). Tukeys honestly significant difference test indicated that this interaction primarily resulted from 5 large fish recaptured north of Virginia during the winter (Figure 5b), and may be the result of small sample bias.

Fine-scale movements

Similarly to the conventionally tagged fish, summer flounder with archival tags were recaptured primarily within Chesapeake Bay shortly after release. To date, 15 archival tags have been recovered (6% recapture rate) from summer flounder that were at large from 1 to 810 days (Table 3). With the exception of two fish, all recaptures occurred within 90 days of release. One of the tags recovered after 90 days at liberty was found on a beach in North Carolina unattached to a fish. This tag may have been shed as a result of failure in the attachment method, tagging related mortality, or predation. Due to the uncertain fate of this fish, we chose to exclude it from analyses. Of the remaining recaptured fish, 7 (50%) were from a single release date (25 August 2009). We could not discern an obvious reason (e.g., mean fish length, water temperature, release location, or recapture location) for this anomaly; therefore, we assumed these fish were independent samples in our analyses.

Most summer flounder remained sedentary for long periods (>2 consecutive weeks) while residing in Chesapeake Bay. During this time, observed depth changes were associated with tidal fluxes. Sedentary intervals were occasionally interspersed with rapid changes in depth when fish moved either within the water column or to deeper or shallower habitats. These types of movements can be differentiated by: 1) the magnitude and duration of depth changes, and 2) the depths occupied before and after movement (Figure 6). Movements within the water column were generally of a higher magnitude (2-10 m) and lasted about 20-40 minutes. Movements to new locations were characterized by a 2-5 m shift in the fish's mean depth.

Summer flounder movements modeled with a GLMM provided insights about factors that influenced the behavior of these fish. The first-order autoregressive moving average was identified as the preliminary variance-covariance structure, and the model also included the random effect associated with individual fish. Using this random-effects structure, we identified a global model that included several interactions to account for the observed variation in depth-change behavior of summer flounder. The interactions that reduced the AICc value by at least 1 unit from the base model (i.e., model with only main effects) were: length*time of day, tidal state*temperature, time of day*temperature, lunar phase*temperature, length*time of day*temperature, and length*time of day*lunar phase. After graphical examination of these interactions (Appendix II) we excluded from consideration the interaction between lunar phase and temperature and the interaction between fish length, time of day, and temperature. We excluded the lunar phase*temperature interaction because different temperature ranges were often observed in different lunar phases. As a result, the interactions appeared to be the result of small sample sizes and we felt that the model may be overfit by including this interaction. Similarly, we excluded the size*time of day*temperature interaction because we had sufficient sample sizes in each size class (at least 3 individuals) only within the 20-25 C temperature range. Within this temperature range, interactions between size classes were not discernible. Our preliminary global model therefore had the following form:

$$\begin{aligned} Y_{ijklm} = {} & \mu + \beta_1 \bullet \mathrm{lgth}_i + \beta_2 \bullet \mathrm{tide}_j + \beta_3 \bullet \mathrm{tod}_k + \beta_4 \bullet \mathrm{lun}_l + \beta_5 \bullet \mathrm{temp}_m + \beta_6 \bullet \mathrm{tide}_j * \mathrm{temp}_m \\ & + \beta_7 \bullet \mathrm{lgth}_i * \mathrm{tod}_k + \beta_8 \bullet \mathrm{tod}_k * \mathrm{temp}_m + \beta_9 \bullet \mathrm{lgth}_i * \mathrm{lun}_l + \beta_{10} \bullet \mathrm{tod}_k * \mathrm{lun}_l + \\ & \beta_{11} \bullet \mathrm{lgth}_i * \mathrm{tod}_k * \mathrm{lun}_l + \gamma_\iota + \varepsilon_{ijklm} \end{aligned}$$

where Y_{ijklm} is the Box-Cox transformed response for fish (i) during tidal stage (j), time of day (k), lunar phase (l) and temperature (m), μ is the overall mean, the βs are the parameter estimates for the fixed effects and the interactions between the fixed effects, lgth is the length of fish (i), tide is the tidal stage (j=low, rising, high, falling), tod is the time of day (k= day, night), lun is the lunar phase (l = new, wax crescent, 1st quarter, wax gibbous, full, wan gibbous, 3rd quarter, wan crescent), temp is the mean water temperature during time period (m), γ is the random effect for fish (i), and ε is the random error. Note that the length*lunar phase and time of day*lunar phase interactions were included because they are components of the three-way interaction between length, time of day, and lunar phase. Using this global model, we repeated the random-effects selection procedure and validated that the preliminary random effects structure was appropriate for selecting fixed effects (Table 4).

The most parsimonious model with the best fit to these data indicated that movements were related to fish length, tidal stage, time of day, and temperature:

$$Y_{ijkm} = \mu + \beta_1 \bullet lgth_i + \beta_2 \bullet tide_j + \beta_3 \bullet tod_k + \beta_5 \bullet temp_m + \beta_6 \bullet tide_j * temp_m + \beta_7 \bullet lgth_i * tod_k + \gamma_\iota + \varepsilon_{ijkm}$$

For this model, the individual fish random effect (γ=0.19) was small compared with the residual error (σ_ε^2=2.58). The autoregressive and moving average terms of the arma(1,1) variance-covariance structure were 0.96 and 0.18, respectively. The large autoregressive term implies that fish depth changes during adjacent tidal periods were highly correlated. The top five models included tidal stage, time of day, and temperature as important factors, as well as the tidal stage* temperature interaction. Support was more moderate for including length and the length*time-of-day and time-of-day*temperature interactions in the model (Table 5, Appendix II). None of the top models included lunar phase as a factor, despite the fact that the model that included the main effects and the length*time-of-day*lunar phase interaction had an AIC value 1.7 units lower than the model with just the main effects (Appendix II). Based on parameter estimates of the top model (Table 6), summer flounder depth changes increased with increasing temperature, but these movements occurred mainly during rising and falling tides (Figure 7). Fish smaller than 400 mm TL had larger depth changes at night, whereas time of day had less of an influence on activity of larger fish (Figure 8).

In addition to the information on small-scale depth changes, two archival tags provided data on the timing of summer flounder dispersal from Chesapeake

Bay and the movement of fish prior to dispersal. Examination of the depth histories of these fish indicate periods when the mean daily depth of the fish increased rapidly, which we assume to indicate the date of dispersal from Chesapeake Bay. One fish was recovered approximately 5 miles east of Virginia Beach after the fish had been at large for 86 days. Based on the depth history of this fish we believe the fish dispersed from Chesapeake Bay in mid-October 2009 when water temperatures fell below 20°C (figure 9a). The second fish was recovered in November 2011 after being at liberty for 810 days. Unfortunately, tag memory was exceeded after 452 days so no data were recorded after November 2010. This fish experienced temperatures as high as 27 °C in summer and as low as 6 °C during winter. Based on the fish's depth history we believe that it dispersed from the bay in late November 2009, and returned to the bay the following June, where it resided until early November 2010 (figure 9b). In both years, this fish dispersed from the bay when temperatures decreased to approximately 14 °C. The mean daily depth changes of both fish increased dramatically immediately prior to their dispersal from Chesapeake Bay and remained at an elevated level throughout the winter. The mean daily depth change either doubled (Tag 199) or quadrupled (Tag 241) following dispersal from Chesapeake Bay (Figure 9 c,d).

Although the fish that was at liberty throughout the winter (Tag 241) provided sufficient data to implement the tidal location method, we could not successfully approximate the fish's location because tidal patterns were similar throughout the Mid-Atlantic Bight. Between December 2009 and May 2010, the daily depth changes experienced by this fish were larger than those experienced while the fish was resident in Chesapeake Bay (Figure 9d); however, this individual frequently remained sedentary on the sea floor (presumably on the continental shelf) throughout multiple tidal cycles during winter. Tidal predictions off the coast of Delaware and North Carolina showed a similar pattern to the depth data recorded by the archival tag, but we found little differences in the time of high and low tides in North Carolina and Delaware (Figure 10). In fact, the mean difference between either tidal extremes (high and low tides) at these two locations was 10 minutes or less (range: 5.1 – 10.3 minutes) for the time periods during which the fish was sedentary. Due to this small difference between tidal patterns at these two locations within the Mid-Atlantic Bight, we were unable to discern the direction of migration after the fish departed from Chesapeake Bay.

Discussion

This study demonstrated that observing individual fish movements on different spatial scales reveals intricacies in their behaviors that may not be apparent from observations on a single scale. Conventional mark-recapture data provide an important overview of fish distribution and movements between large geographic regions (e.g., Mid-Atlantic Bight), but do not provide insight into factors that drive behavioral decisions of individual fish. Previous research on small-scale (i.e., within a coastal lagoon) summer flounder movements indicated that individuals move in response to tidal stage (Szedlymayer and Able 1993) and time of day (Capossela 2010, Miller 2010). A recent telemetry study indicated that fish length, tidal stage, and the time of day*lunar phase interaction influenced summer flounder movements on the order of a few hundred meters (Chapter 1). Movement patterns (i.e., depth changes) observed with archival tags revealed more intricate patterns than could be observed with the coarser spatial scales of acoustic telemetry studies. Using data from archival tags, we have shown that not only does tidal stage affect summer flounder movement, but also that water temperature influences levels of activity observed during rising and falling tides. Furthermore, behavioral differences between large and small fish are most pronounced at night. Such results could be incorporated into individual-based models to determine how fine-scale behavioral decisions produce the observed distribution of summer flounder within Chesapeake Bay. Individual-based models could also be used to understand responses of summer flounder behavior and distribution to environmental variability and climate change (Humston et al. 2004).

Based on behaviors observed with archival tags, as well as those previously observed with acoustic telemetry, we believe that summer flounder movements within Chesapeake Bay are primarily related to foraging. Hunger has previously been shown to influence fish activity levels because fish that are not satiated will increase their foraging activity to improve their chances of encountering prey (reviewed in Gibson 2005). Summer flounder are believed to migrate inshore in the spring and summer to feed and increase their energetic reserves for spawning during the winter months (Packer et al. 1999). Thus, movements of individual fish in Chesapeake Bay are likely to be related to foraging activity. Increased movements of small summer flounder (<400 mm) at night may be in response to the increased abundance of their preferred prey during this time. Mysids, which are the primary component of the diet of summer flounder smaller than 375 mm (Latour et al. 2008, Buchheister and Latour 2011), are generally more active at night (Hurlburt 1957) and may elicit increased movements of smaller summer flounder during this time of day. In contrast, larger summer flounder that are primarily piscivorous (Latour et al. 2008) may use ambush tactics to feed (Staudinger and Juanes 2010). This predation technique requires that the fish remain sedentary, which would explain why larger fish are less active than smaller fish during night. However, individual differences in behavior were observed. For example, some fish larger than 450 mm were more active at night than would be expected based on predictions from the GLMM. This implies that these fish employed different foraging strategies than other fish of similar size. Summer flounder were previously observed using multiple foraging strategies in the lab (Staudinger and Juanes 2010), but this is the first study that links *in situ* behavior with presumed feeding activity.

Although the observed changes in depth that occurred in response to tidal stage and temperature may be related to foraging behavior, summer flounder may also be using tidal currents to move into different habitats. Archival tag data indicate that summer flounder maintain a relatively constant level of activity during high and low tides, but activity levels during rising and falling tides increase proportionally with increasing water temperatures. In a laboratory experiment, feeding rates of summer flounder were observed to increase with increasing water temperatures (Malloy and Target 1991). The relationship between feeding rates and temperature is most likely an adaptation to meet increased metabolic requirements at higher temperatures (Malloy and Target 1991, Fonds et al. 1992, Claireaux and Lagardere 1999). Thus, summer flounder may increase their activity levels during rising and falling tides to feed on prey items that are moving in association with tidal fronts, such as mysids and zooplanktivorous fish (Taggart et al. 1989, Gomez-Gutierrez 2007). An alternative hypothesis is that summer flounder use tidal currents associated with rising and falling tides to move between habitats. Tidal stream transport has previously been suggested as an energy-saving mechanism used by summer flounder to move between locations (Szedlmayer and Able 1993, Sackett et al. 2007, Miller 2010). To our knowledge, studies examining diets of summer flounder relative to tidal stage are lacking. Such studies would assist in determining if summer flounder use tidal currents: 1) to feed, 2) as a means of dispersal to new habitats, or 3) a combination of both.

Based on previous research, and the results presented here, we were moderately surprised that none of the top linear models included the interaction between length, time-of-day, and lunar phase. Preliminary results from developing the global model indicated that this interaction was significant in a classical sense ($p = 0.001$), using an F-test with type III sums of squares. Graphical examination of this interaction indicated that smaller fish were more active during nights closest to the quarter moons (Appendix II). A nearly identical relationship was observed in a previous acoustic telemetry study (Chapter I). Observation of the same pattern using two independent tagging technologies provides evidence that this was not an artifact of either data set or the model-building procedure. However, the AICc model selection criterion did not support the inclusion of this 3-way interaction in the final model developed here; we believe this may have been the result of insufficient sample size of fish observed through multiple lunar cycles. Together, results from the acoustic and archival tagging studies suggest that smaller summer flounder in Chesapeake Bay may be more active on nights near the quarter moon, probably in response to changes in the behavior of their prey. Mysids have been shown to alter their diel vertical migration behavior in response to changes in ambient light levels (Boscarino et al. 2009), which are influenced by lunar illumination levels. Alternatively, mysids may also be more active near the quarter moons in response to changes in tidal currents. Tidal range is at its minimum (i.e., neap tides) during the quarter moons, thus decreasing the potential that mysids will be swept away from their preferred habitats by tidal currents (Kaartvedt 1989). Due to the small sample size of our study, future research is warranted to elucidate the relationship between the lunar cycle and summer flounder foraging behavior.

Fine-scale summer flounder movement patterns changed in response to environmental cues, but these fish were generally sedentary while resident within Chesapeake Bay. Conventional mark-recapture data collected by the VGFTP also suggested that summer flounder recaptured within one year of tagging did not move much between regions (e.g., lower Bay, mid-Bay, rivers) between May and October, which was consistent with previous tagging studies (Desfosse 1995). Furthermore, acoustic telemetry studies estimated that summer flounder remain within 1-km^2 areas for periods of hours to weeks during their residency in coastal estuaries and bays (Sackett et al. 2008, Chapter 1). Data from archival tagged fish support this conclusion, indicating that while fish were resident in Chesapeake Bay they often remained in the same location for days or weeks. During these periods, the only observed depth changes were those related to tidal cycles. This may be indicative of the feeding periodicity of these fish.

Fish that dispersed from Virginia waters were recaptured primarily in southern waters during winter and in northern waters during spring and summer. These results from the VGFTP corroborate the findings of a previous tagging study with summer flounder conducted in Virginia (Desfosse 1995). Because most (63%) of the recaptured summer flounder returned to the same region following the spawning migration, we believe that fish recaptured in coastal habitats to the north during spring and summer had permanently emigrated out of Virginia waters. This inference is not novel, as numerous tagging studies conducted since the 1960s have reached similar conclusions based on observations from conventional tags (Lux and Nichy 1981, Desfosse 1995). In contrast, conventionally tagged fish recaptured in southern waters during winter were most likely participating in the seasonal spawning migration, and would therefore be expected to return to Virginia waters. Although these results are suggestive, our analysis may be confounded by differences in fishing effort and reporting rates among commercial and recreational fishers along the east coast (Hilborn 1990). Based on the success of previous studies that used archival tag data to approximate the locations of plaice and yellowtail flounder (Hunter et al. 2003, Cadrin and Westwood 2006), we had hoped to use data from our archival tags to more accurately determine the direction traveled by summer flounder after dispersing from Chesapeake Bay. Unfortunately, we recaptured only a single fish that had been at large throughout the winter spawning season, and we were unable to determine the direction traveled by that fish using the currently available tidal prediction models. Based on our analysis, the tidal location method is not suitable for fish resident within the Mid-Atlantic Bight.

Although our sample size was small, results from fish observed migrating from Chesapeake Bay indicated that dispersal timing varied between individuals and that individuals may respond to temperature as a cue to initiate dispersal. In 2009, the two fish we observed dispersing from the Bay left nearly 1.5 months apart (mid-October and late November). The fish observed dispersing from Chesapeake Bay in two consecutive years, left the Bay when water temperatures declined to approximately 14°C in both years, even though this occurred nearly a month earlier in 2010 than in 2009. This suggests that this fish responded to changes in water temperature rather than other seasonal cues (e.g., photoperiod). The possibility that fish were responding to temperature to initiate dispersal was also postulated by Capossela (2010), who observed that emigration rates from a coastal lagoon were associated with decreasing water temperatures. If summer flounder are responding to temperature to initiate dispersal, it appears that individuals within the Chesapeake Bay population have different temperature thresholds; however, a larger sample size is necessary to fully explore this hypothesis.

Archival tags are an excellent technology to further investigate the importance of environmental cues on fish movement patterns, but we recommend that future studies conducted in nearshore habitats consider surgically implanting these tags in fish. A large percentage (26.7%) of recovered archival tags were entangled in gillnets or fishing line. We hypothesize that the low recovery rate of archival-tagged summer flounder was related to the external attachment procedure, which increased the likelihood of gear entanglement and fish mortality. Previous studies that have externally attached archival tags to flatfish released the fish in offshore locations that, presumably, were characterized by homogeneous bottom types without potential snags (Hunter et al. 2003, Cadrin and Moser 2006). In contrast, we released summer flounder in structured habitats subject to high recreational and commercial fishing pressure and these habitats contained a number of potential snags. Surgical implantation of acoustic tags reduces the risk of entanglement and has a minimal tag-related mortality rate for summer flounder (Fabrizio and Pessutti 2007). We believe that surgically implanting the archival tags in our fish would have eliminated the entanglement risks, and could have increased our tag recovery rate.

References

Akaike H (1973) Information theory and an extension of the maximum likelihood principle. pp. 267-281. *In* Petran BN and Csàaki B (eds.) *International Symposium on Information Theory*, 2nd ed. Akadèemiai Kiadi, Budapest, Hungary.

Block BA, Dewar H, Blackwell SB, Williams TD, Prince ED, Farwell CJ, Boustany A, Teo SLH, Seitz A, Walli A, and Fudge D (2001) Migratory movements, depth preferences, and thermal biology of Atlantic bluefin tuna. Science, 293: 1310-1314.

Bolker BM, Brooks ME, Clark CJ, Geange SW, Poulsen JR, Henry M, Stevens H, and White J-SS (2008) Generalized linear mixed models: a practical guide for ecology and evolution. Trends in Ecology and Evolution, 24: 127-135.

Bonzek CF, Gartland J, and Latour RJ (2010) Annual Report: The Chesapeake Bay Multispecies Monitoring and Assessment Program. Project Number F-130-R-5. Virginia Institute of Marine Science. Gloucester Point, VA.

Boscarino BT, Rudstam LG, Mata S, Gal G, Johannsson OE, and Mills EL (2009) Predicting the vertical distribution of the opossum shrimp, *Mysis relicta*, in Lake Ontario: a test of laboratory-based light preferences. Canadian Journal of Fisheries and Aquatic Science, 66: 101-113.

Box GEP and Cox DR (1964) An Analysis of Transformations. Journal of the Royal Statistical Society, Series B, 26: 211-252.

Buchheister A and Latour RJ (2011) Trophic ecology of summer flounder in lower Chesapeake Bay inferred from stomach content and stable isotope analyses. Transactions of the American Fisheries Society, 140: 1240-1254.

Burnham KP and Anderson DR (2002) Model selection and inference: a practical information-theoretic approach. Springer-Verlag, New York.

Cadrin SX and Moser J (2006) Partitioning on-bottom and off-bottom behavior: a case study with yellowtail flounder off New England. ICES CM 2006/Q:14.

Cadrin SX and Westwood A (2004) The use of electronic tags to study fish movement: a case study with yellowtail flounder off New England. ICES CM 2004/K:81.

Capossela KM (2010) Migration dynamics, within-estuary behaviors and cardiorespiratory responses of summer flounder to selected estuarine conditions. M.Sc. thesis. College of William and Mary, Williamsburg, VA. 106 pp.

Claireaux G and Lagardére J-P (1999) Influence of temperature, oxygen, and salinity on the metabolism of European sea bass. Journal of Sea Research, 42: 157-168.

Desfosse JC (1995) Movements and ecology of summer flounder, *Paralichthys dentatus*, tagged in the southern Mid-Atlantic Bight. Ph.D. dissertation, College of William and Mary, Williamsburg, VA. 187 pp.

Egbert GD, Bennett AF, and Forman MGG (1994) TOPEX/POSEIDON tides estimated using a global inverse model. Journal of Geophysical Research, 99(C12): 24821-24852.

Fabrizio MC and Pessutti JP (2007) Long-term effects and recovery from surgical implantation of dummy transmitters in two marine fishes. Journal of Experimental Marine Biology and Ecology, 351:243-254.

Fonds M, Cronie R, Bethaak AD, van der Puyl P (1992) Metabolism, food consumption and growth of plaice (*Pleuronectes platessa*) and flounder (*Platichthys flesus*) in relation to fish size and temperature. Netherlands Journal of Sea Research, 29: 127-143.

Gibson RN (2005) The behavior of flatfishes. *In* Gibson R (ed.) *Flatfishes: Biology and Exploitation,* pp. 213-239. Blackwell Science, Oxford, UK.

Gómez-Gutiérrez J, Martínez-Gómez S, and Robinson CJ (2007) Influence of thermohaline fronts forced by tides on near-surface zooplankton aggregation and community structure in Bahía Magdalena, Mexico. Marine Ecology Progress Series, 346: 109-125.

Hilborn R (1990) Determination of fish movement patterns from tag recoveries using maximum likelihood estimators. Canadian Journal of Fisheries and Aquatic Sciences, 47: 635-643.

Humston R, Olson DB, and Ault JS (2004) Behavioral assumptions in models of fish movement and their influence on population dynamics. Transactions of the American Fisheries Society, 133: 1304-1328.

Hunter E, Aldridge JN, Metcalfe JD, and Arnold GP (2003) Geolocation of free-ranging fish on the European continental shelf as determined from environmental variables. Marine Biology, 142: 601-609.

Hurlburt E (1957) The distribution of *Neomysis Americana* in the estuary of the Delaware River. Limnology and Oceanography, 2: 1-11.

Kaartvedt S (1989) Retention of vertically migrating suprabenthic mysids in fjords. Marine Ecology Progress Series, 57: 119-128.

Kennedy M and Gray RD (1993) Can ecological theory predict the distribution of foraging animals? A critical analysis of experiments on the Ideal Free Distribution. Oikos, 68: 158-166.

Kraus RT and Musick JA (2001) A brief interpretation of summer flounder, *Paralichthys dentatus,* movements and stock structure with new tagging data on juveniles. Marine Fisheries Review, 63: 1-6.

Latour RJ, Gartland J, Bonzek CF, and Johnson RA (2008) The trophic dynamics of summer flounder (*Paralichthys dentatus*) in Chesapeake Bay. Fisheries Bulletin, 106: 47-57.

Link JS, Bolles K, and Milliken CG (2002) The feeding ecology of flatfish in the Northwest Atlantic. Journal of Northwest Atlantic Fishery Science, 30: 1-17.

Littell RC, Milliken G, Stroup WW, Wolfinger R, and Schabenberger O (2006) SAS for mixed models, 2nd edition. SAS Institute, Cary, North Carolina.

Lowe CG and Bray RN (2006) Movement and Activity Patterns. *In* Allen LG, Pondella DJ, and Horn MH (eds.). *The Ecology of Marine Fishes: California and adjacent waters.* University of California Press. Los Angeles, CA.

Lux FE and Nichy FE (1981) Movements of tagged summer flounder, *Paralichthys dentatus*, off southern New England. NOAA Tech. Rep. NMFS SSRF-752. 16 p.

Malloy KD and Targett TE (1991) Feeding, growth and survival of juvenile summer flounder *Paralichthys dentatus*: experimental analysis of the effects of temperature and salinity. Marine Ecology Progress Series, 72: 213-223.

Miller MH (2010) Movement of summer flounder (*Paralichthys dentatus*) in relation to hypoxia in an estuarine tributary. M.Sc. thesis. University of Delaware, Lewes, DE. 103 pp.

Monaghan JP Jr. (1992) Migration and population dynamics of summer flounder (*Paralichthys dentatus*) in North Carolina. Study 3A. Completion Rep. Proj. F-29. North Carolina Dep. Environ., Health, and Nat. Res., Div. Mar. Fish. Morehead City, NC. 36 p.

Morrell CH, Pearson JD, and Brant LJ (1997) Linear transformations of linear mixed-effects models. The American Statistician, 51: 338-343.

Murawski WS (1970) Results of tagging experiments of summer flounder, *Paralichthys dentatus*, conducted in New Jersey waters from 1960-1967. New Jersey Div. Fish, Game and Shellfish. Misc. Rep. No. 5M. Lebanon, NJ. 72 p.

Musick S and Gillingham L (2010) Annual report: Virginia Game Fish Tagging Program. VIMS Marine Resource Report No. 2011-5. 61 p.

National Research Council (NRC). 2000. Improving the collection, management and use of marine fisheries data. Washington, DC. National Academy Press. 222 p.

Overholtz WJ, Link JS, and Suslowicz LE (2000) Consumption of important pelagic fish and squid by predatory fish in the northeaster USA shelf ecosystem with some fishery comparisons. ICES Journal of Marine Science, 57: 1147-1159.

Packer DB, Griesbach SJ, Berrien PL, Zetlin CA, Johnson DL, and Morse WW (1999) Summer flounder, *Paralichthys dentatus*, life history and habitat characteristics. NOAA Tech. Memo. NMFS-NE-151. Woods Hole, MA. 88 p.

Pinheiro JC and Bates DM (2000) Mixed-effects models in S and S-Plus. Statistics and Computing Series, Springer-Verlag, New York, NY.

Poole JC (1962) The fluke population of Great South Bay in relation to the sport fishery. N.Y. Fish Game Journal, 9: 93-117.

Quinn G and Keogh M (2002) Experimental design and data analysis for biologists. Cambridge University Press. Cambridge, UK.

Rogers KB and White GC (2007) Analysis of movement and habitat use from telemetry data. pps 625-676 *In* Guy CS and Brown ML (eds.) *Analysis and Interpretation of Freshwater Fisheries Data*, American Fisheries Society, Bethesda, Maryland.

Roshier DA, Doerr VAJ, Doerr ED (2008) Animal movement in dynamic landscapes: interaction between behavioural strategies and resource distributions. Oecologia, 156: 465-477.

Sackett DK, Able KW, and Grothues TM (2007) Dynamics of summer flounder, *Paralichthys dentatus*, seasonal migrations based on ultrasonic telemetry. Estuarine, Coastal and Shelf Science, 74: 119-130.

Sackett DK, Able KW, and Grothues TM (2008) Habitat dynamics of summer flounder *Paralichthys dentatus* within a shallow USA estuary, based on multiple approaches using acoustic telemetry. Marine Ecology Progress Series, 364: 199-212.

Staudinger MD and Juanes F (2010) Feeding tactics of a behaviorally plastic predator, summer flounder (*Paralichthys dentatus*). Journal of Sea Research, 64: 68-75.

Szedlmayer ST and Able KW (1993) Ultrasonic telemetry of age-0 summer flounder *Paralichthys dentatus*, movements in a southern New Jersey estuary. Copeia, 3: 728-736.

Taggart CT, Drinkwater KF, Frank KT, McRuer J, and LaRouche P (1989) Larval fish, zooplankton community structure, and physical dynamics at a tidal front. Rapp. P.-v. Réun. Cons. Int. Explor. Mer., 191: 184-194.

Terceiro M (2002) The summer flounder chronicles: science, politics, and litigation, 1975-2000. Reviews in Fish Biology and Fisheries, 11: 125-168.

Wannamaker CM and Rice JA (2000) Effects of hypoxia on movements and behavior of selected estuarine organisms from the southeastern United States. Journal of Experimental Marine Biology and Ecology, 249: 145-163.

Wilson SG, Lutcavage ME, Brill RW, Genovese MP, Cooper AB, and Everly AW (2005) Movements of Bluefin tuna (*Thunnus thynnus*) in the northwestern Atlantic Ocean recorded by pop-up satellite archival tags. Marine Biology, 146: 409-423.

Zar JH (1999) Biostatistical analysis. 2nd ed. Prentice-Hall, Englewood Cliffs, N.J.

Zuur A, Leno EN, and Smith GM (2007) Analysing Ecological Data. Springer, New York.

Table 1. Number of conventionally tagged summer flounder released in Virginia and number of tagged fish subsequently recaptured at any location.

Tag Region	Tagged	Subsequently recaptured	Percent recaptured
Bay Mouth	18365	1319	7.18
Lower Bay	13708	1485	10.83
Mid-Bay	1489	53	3.56
Upper-Bay	73	1	1.37
James River	3054	180	5.89
York River	12447	1486	11.94
Rappanhannock River	230	9	3.91
Virginia Beach - ocean side	5583	921	16.50
Eastern Shore - ocean side	5981	215	3.59
Total	60930	5669	9.30

Table 2. Number of summer flounder released during the period of coastal residency (May-October) and recaptured in Virginia. Numbers in parentheses are the percentage of fish released from a given region that moved into the recapture region. Recaptures of fish within the release region are omitted to highlight fish movements, but were included in the estimation of percent recaptured by region. Note that in most cases, less than 1% of tagged fish were released and recaptured in different regions.

Release Region	Releases	Recapture Region							
		Bay Mouth	Lower Bay	Mid-Bay	James River	York River	Virginia Beach	Eastern Shore	Total
Bay Mouth	17353		106 (0.61)	5 (0.03)	8 (0.05)	4 (0.02)	4 (0.02)	1 (0.01)	128 (0.74)
Lower Bay	13541	76 (0.56)		2 (0.01)	36 (0.27)	7 (0.05)	2 (0.01)	1 (0.01)	124 (0.92)
Mid- Bay	1476	5 (0.34)	1 (0.07)			3 (0.20)			10 (0.61)
James River	3020	10 (0.33)	25 (0.83)			1 (0.03)			36 (1.19)
York River	12539	7 (0.06)	3 (0.02)				1 (0.01)		13 (0.09)
Virginia Beach	5643	7 (0.12)	5 (0.09)		4 (0.07)				16 (0.28)
Eastern Shore	5050	7 (0.14)		1 (0.02)					8 (0.16)
Total	58622	113 (1.55)	140 (1.62)	10 (0.06)	48 (0.38)	15 (0.31)	7 (0.05)	2 (0.01)	338 (3.98)

Table 3. Release and recapture information for 15 summer flounder tagged in Chesapeake Bay with archival tags.

Tag #	Tagging length (mm)	Release Date	Tagging Region	Recapture Date	Recapture Region	Days at large
11a	321	12Aug2009	Bay Mouth	23Aug2009	Bay Mouth	11
11b	440	15Sept2009	Bay Mouth	08Oct2009	Bay Mouth	23
37	398	14Aug2009	Bay Mouth	19Oct2009	Bay Mouth	66
98*	322	20Aug2009	Bay Mouth	23Oct2009*	Unknown	64
123	324	20Aug2009	Bay Mouth	13Sept2009	Mid-Bay	24
154	331	25Aug2009	Bay Mouth	20Sept2009	Bay Mouth	26
155	473	25Aug2009	Bay Mouth	30Sept2009	Bay Mouth	36
157	397	25Aug2009	Bay Mouth	06Oct2009	Bay Mouth	42
162	398	25Aug2009	Bay Mouth	09Sept2009	Bay Mouth	15
191	443	21Aug2009	Bay Mouth	23Oct2009	Bay Mouth	63
199	541	25Aug2009	Bay Mouth	19Nov2009	Off Virginia Beach	86
207	437	25Aug2009	Bay Mouth	16Oct2009	Bay Mouth	52
209	414	25Aug2009	Bay Mouth	26Aug2009	Bay Mouth	1
241	454	27Aug2009	James River	15Nov2011	Bay Mouth	810
299	501	15Sept2009	Bay Mouth	01Oct2009	Bay Mouth	16

*This tag was recovered on a beach in North Carolina; it is unknown if the fish shed the tag or was consumed by a predator or scavenger. Recapture date was the last date during which the tag recorded non-tidal changes in depth.

Table 4. Random-effects model selection for the general linear mixed model fit to depth change data recorded for 14 summer flounder carrying archival tags in the lower Chesapeake Bay from August through early-October 2009. Each of these random-effects structures was fit to the global model. The model with the lowest Akaike's Information Criterion (AICc) was selected. The delta AICc (ΔAICc) is the difference in value between each model and the model with the lowest AICc. Covariance structures were: variance components (vc), compound symmetry (cs), autoregressive with a lag of 1 (ar(1)), and autoregressive moving average with a lag of 1 (arma(1,1)).

Model	Random tag effect	Covariance structure	AICc	ΔAIC
1	x	arma(1,1)	12736.7	0
2		arma(1,1)	12748.8	12.1
3	x	ar(1)	12851.2	114.5
4		cs	12907.3	170.6
5	x	vc	12907.3	170.6
6	x	cs	12909.3*	172.6*
7		ar(1)	12977.8	241.1
8		vc	13101.9	365.2

*Note: final hessian not positive definite because the between-subject variance and the compound symmetry covariance are not identifiable (Littell et al. 2006)

Table 5. Fixed-effects model selection table showing the fixed factors -- length (lgth), tide, time of day (tod), and temperature (temp) -- and interactions included in the top five models.

Model	AICc	ΔAIC	lgth	tide	TOD	temp	lgth* TOD	tide* temp	TOD* temp
1	12573.2	0	x	x	x	x	x	x	
2	12576.2	3		x	x	x		x	x
3	12576.4	3.2	x	x	x	x	x	x	x
4	12578	4.8	x	x	x	x		x	x
5	12579.9	6.7		x	x	x		x	

Table 6. Parameter estimates, standard errors, and degrees of freedom (df) for the general linear mixed model selected to describe depth changes of individual fish (see table 5). Tidal stage estimates are relative to the rising tide. Time-of-day estimates are relative to night. This model included an individual fish random effect and was fit with a arma(1,1) covariance structure with an autoregressive term of 0.96 and a moving average term of 0.18 (see table 4). The residual error (σ_{ε}^2) was 2.58 and random variation due to individual fish (σ_{fish}^2) was 0.19.

Effect	Tide	Time of Day	Estimate	Standard Error	df
Intercept			3.14	0.147	12.8
Length			-0.002	0.002	12.6
Tide	Falling		-0.046	0.072	2690
Tide	High		-0.474	0.071	2504
Tide	Low		-0.61	0.072	2501
Tide	Rising		0	.	.
Time of day		Day	-0.164	0.052	3129
Time of day		Night	0	.	.
Temperature			0.116	0.038	649
Length*Time of day		Day	0.002	0.001	3126
Length*Time of day		Night	0	.	.
Tide*Temperature	Falling		0.021	0.042	2684
Tide*Temperature	High		-0.105	0.042	2513
Tide*Temperature	Low		-0.008	0.04	2555
Tide*Temperature	Rising		0	.	.

Note: Estimates are based on Box-Cox transformed data and the effects of length and temperature are for centered data.

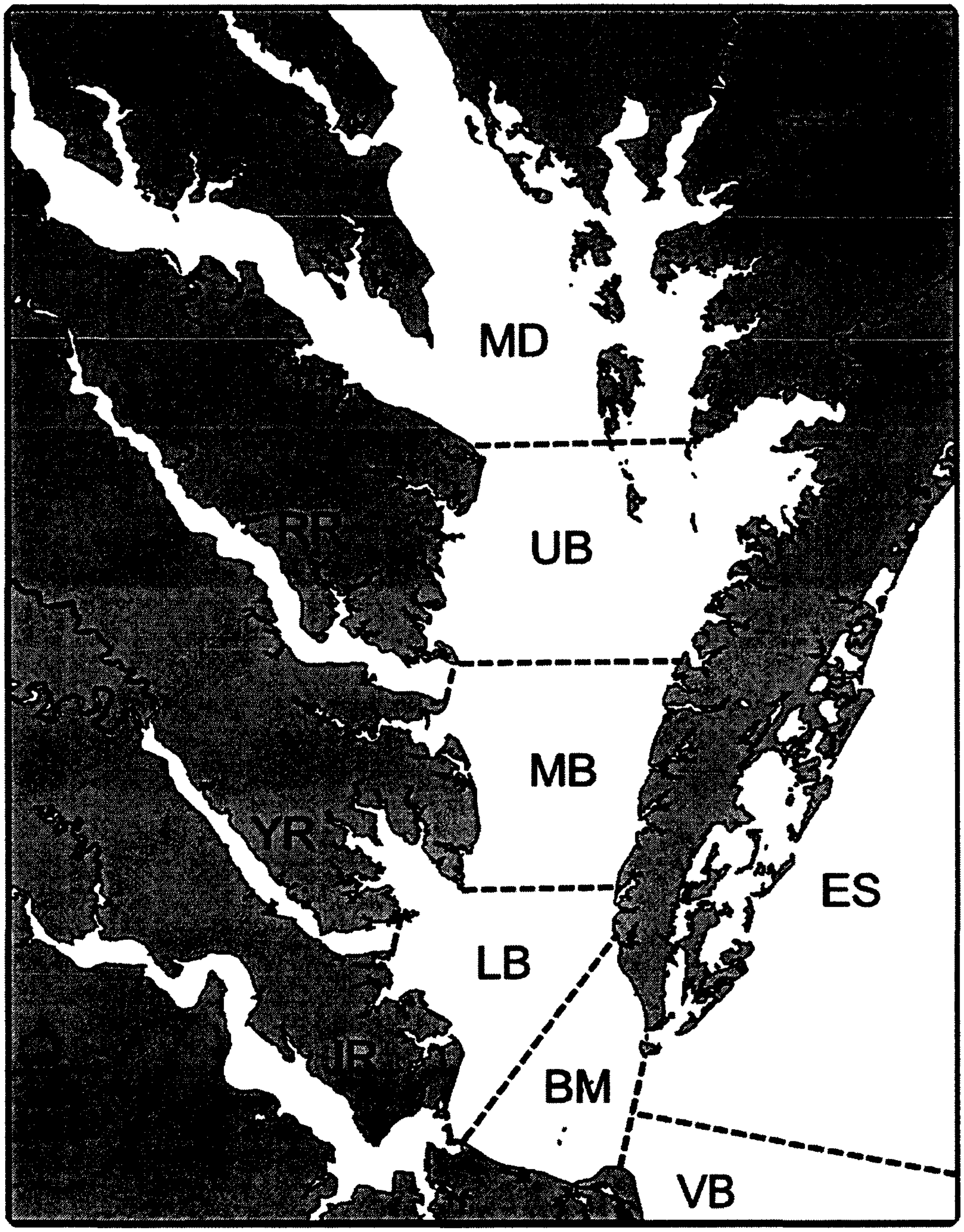


Figure 1. Region boundaries (dashed lines) used to examine large-scale movements of summer flounder from conventional mark-recapture data. Region abbreviations are: MD – Maryland, UB – Upper Bay, RR – Rappahannock River, MB – Mid-Bay, YR – York River, LB – Lower Bay, JR – James River, BM – Bay Mouth, ES – Eastern Shore, VB – Virginia Beach. Fish were tagged and released in all regions except Maryland.

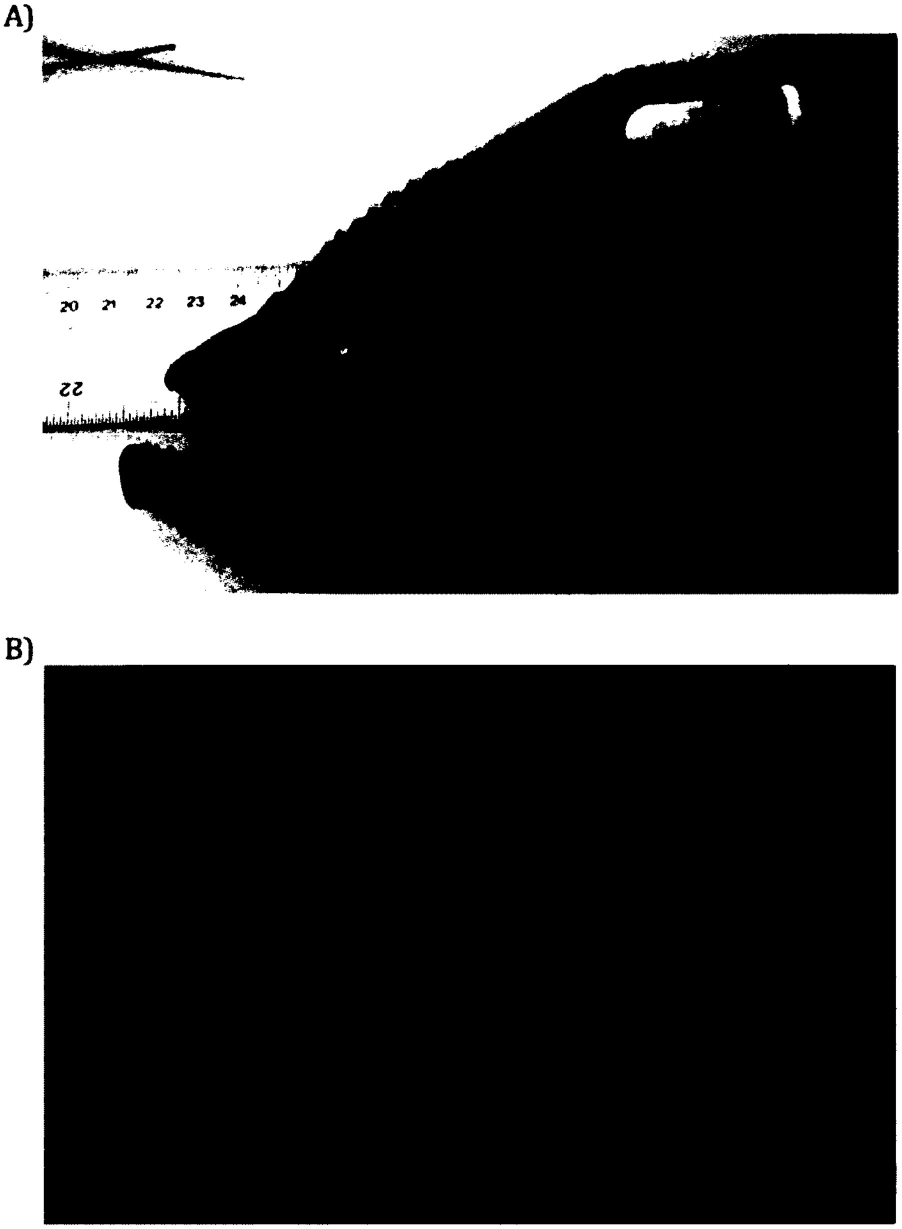


Figure 2. (A) Placement and orientation of the externally attached Star-Oddi DST milli-L archival tag on a 436 mm TL summer flounder. (B) plastic discs and earring backings used on the non-pigmented side of the fish to secure the archival tag.

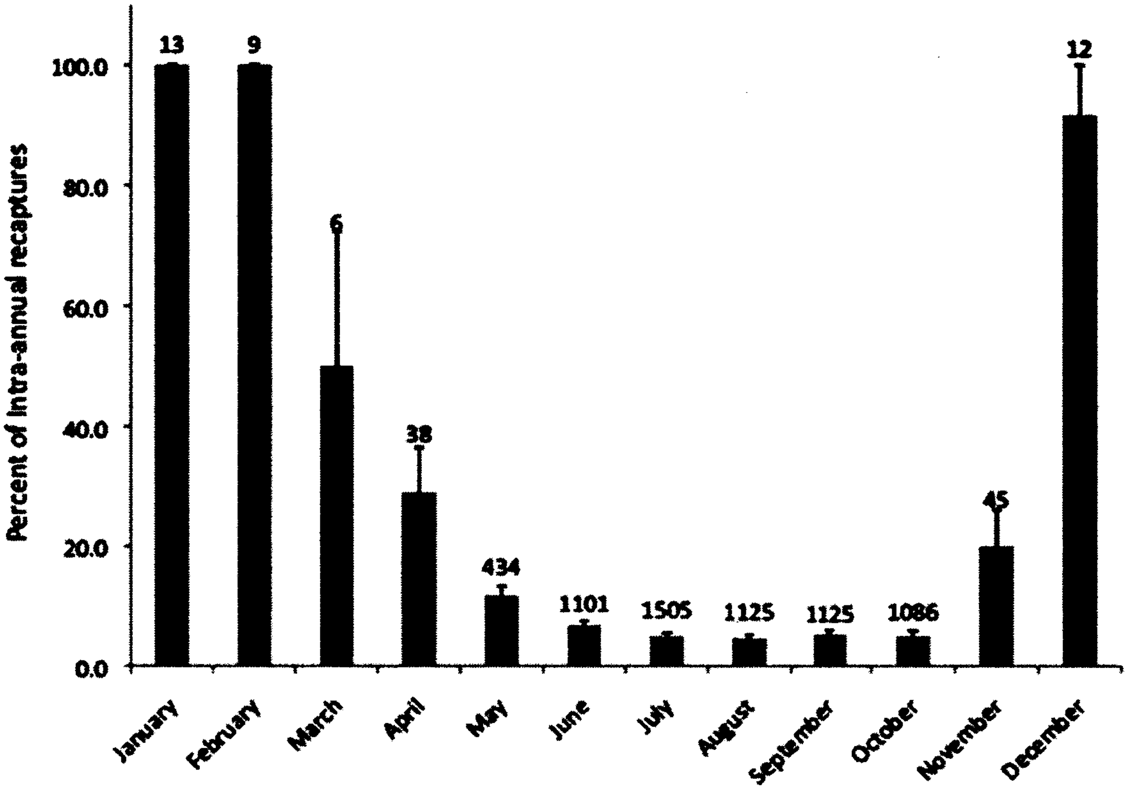


Figure 3. Proportion of summer flounder captured within one year of release that were released and recaptured in different regions. All fish were released within Chesapeake Bay from 2000-2009. Error bars are ± 1 standard error. Monthly sample sizes (number of recaptures) are shown above each error bar.

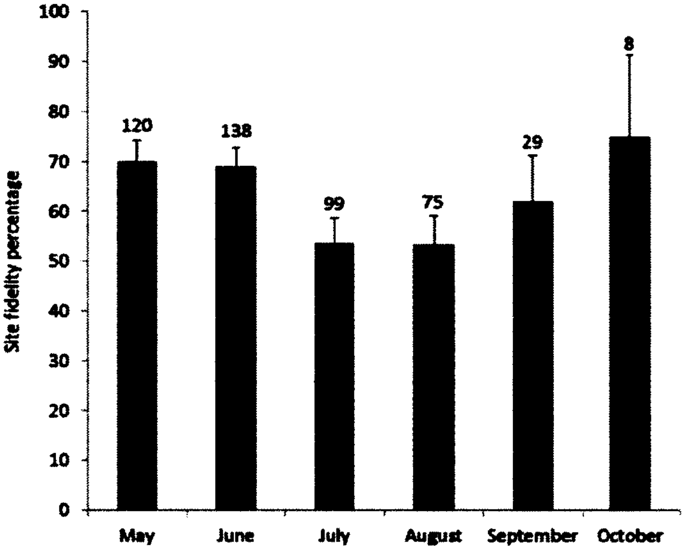


Figure 4. Proportion of summer flounder recaptured after one year at liberty that exhibited site fidelity by returning to the region from which they were released. All fish were released within Chesapeake Bay from 2000-2009. Error bars are ± 1 standard error. Monthly sample sizes (number of recaptures) are shown above each error bar. On average, 63% of recaptures after one year at liberty occurred in the same region in which the fish was released.

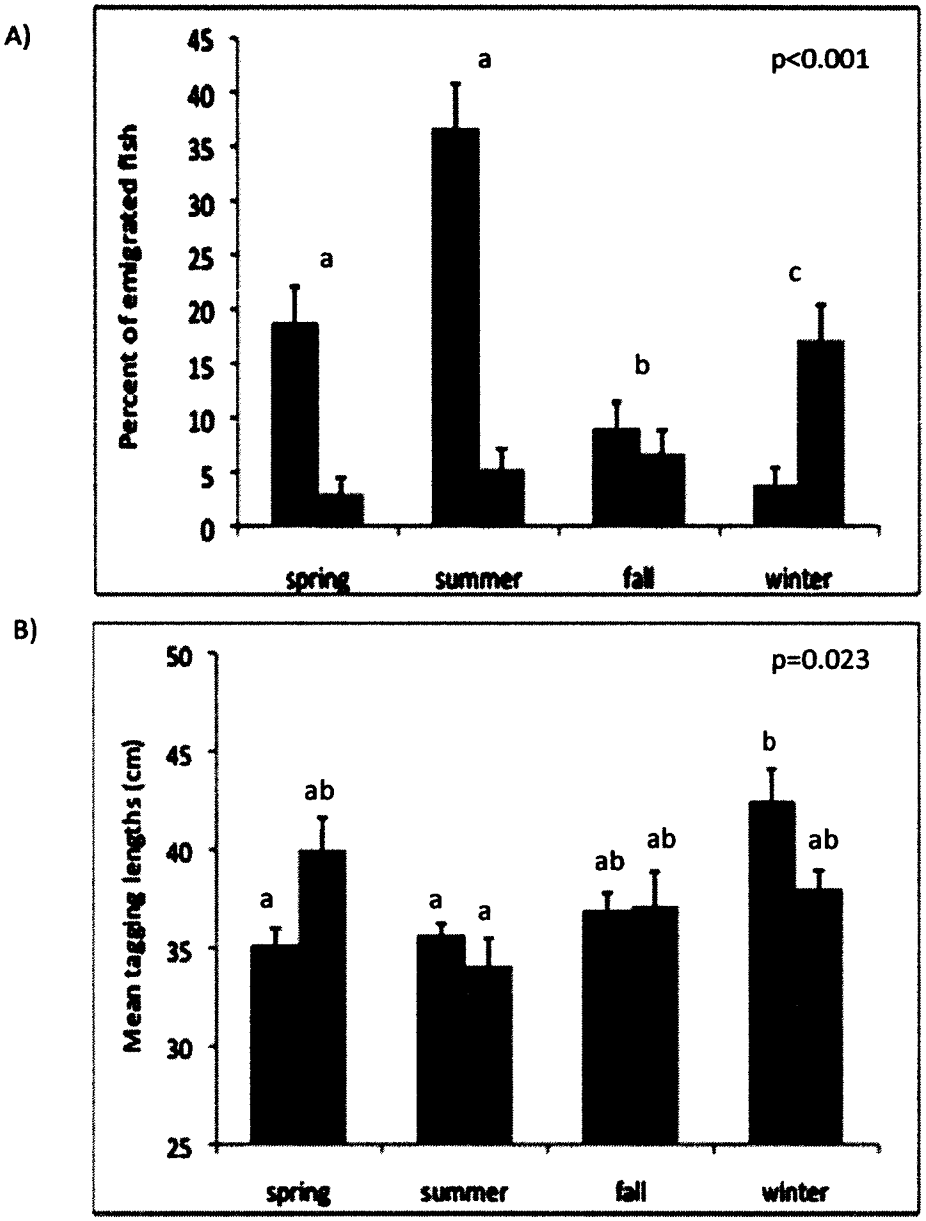


Figure 5. (A) Proportion of summer flounder and (B) mean length at tagging for summer flounder that migrated to locations north (black) and south (gray) of Virginia by season. All fish were released within Chesapeake Bay from 2000-2009. Error bars are ± 1 standard error. The p-value in (A) was calculated with a chi-square test with the null hypothesis of no difference in the proportion of fish moving north and south in each season. The letters above each proportion depict which seasons were significantly different from the others based on a multiple comparison for proportions test. The p-value in (B) is for the interaction between season and direction (North or South) calculated with an ANOVA. The letters above each bar represents groups that are significantly different based on Tukey's honestly significant difference method for multiple comparisons.

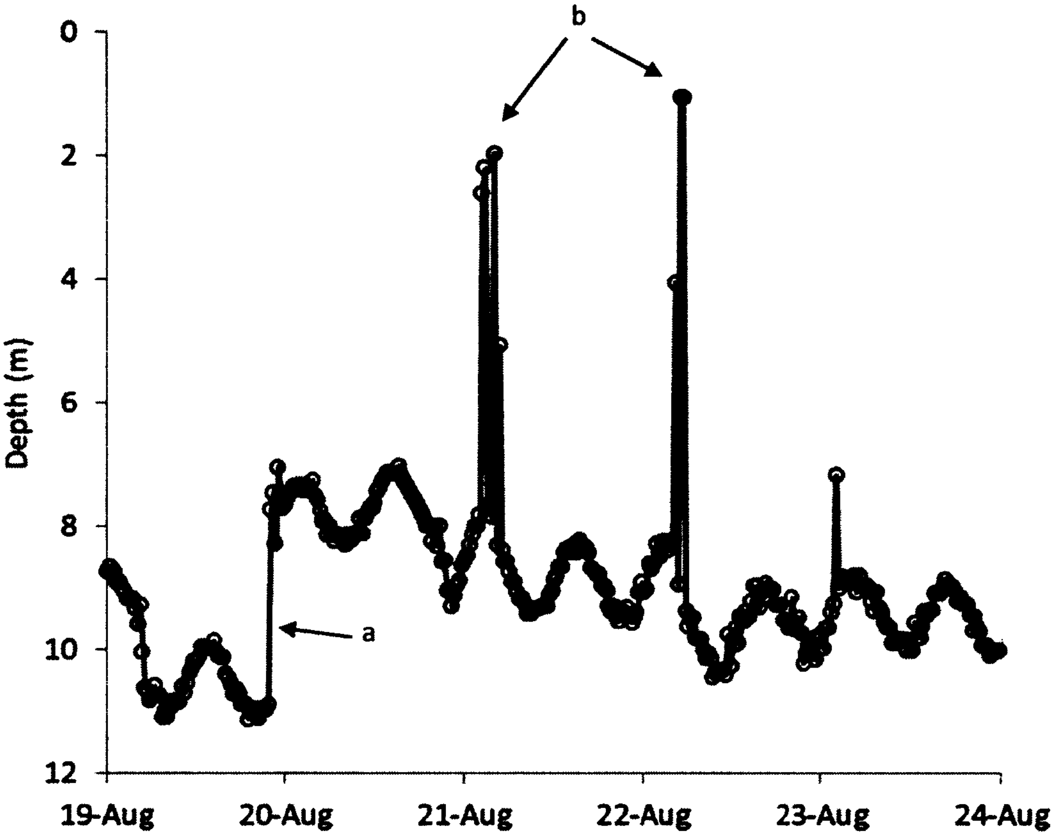


Figure 6. Example of a 5-day depth history for an individual summer flounder released with an archival tag (Tag 37) within Chesapeake Bay in 2009. The regular pattern in depth change is a result of tidal cycles when the fish was sedentary on the seafloor. Also shown are movements to a shallower habitat (a) and movements within the water column (b).

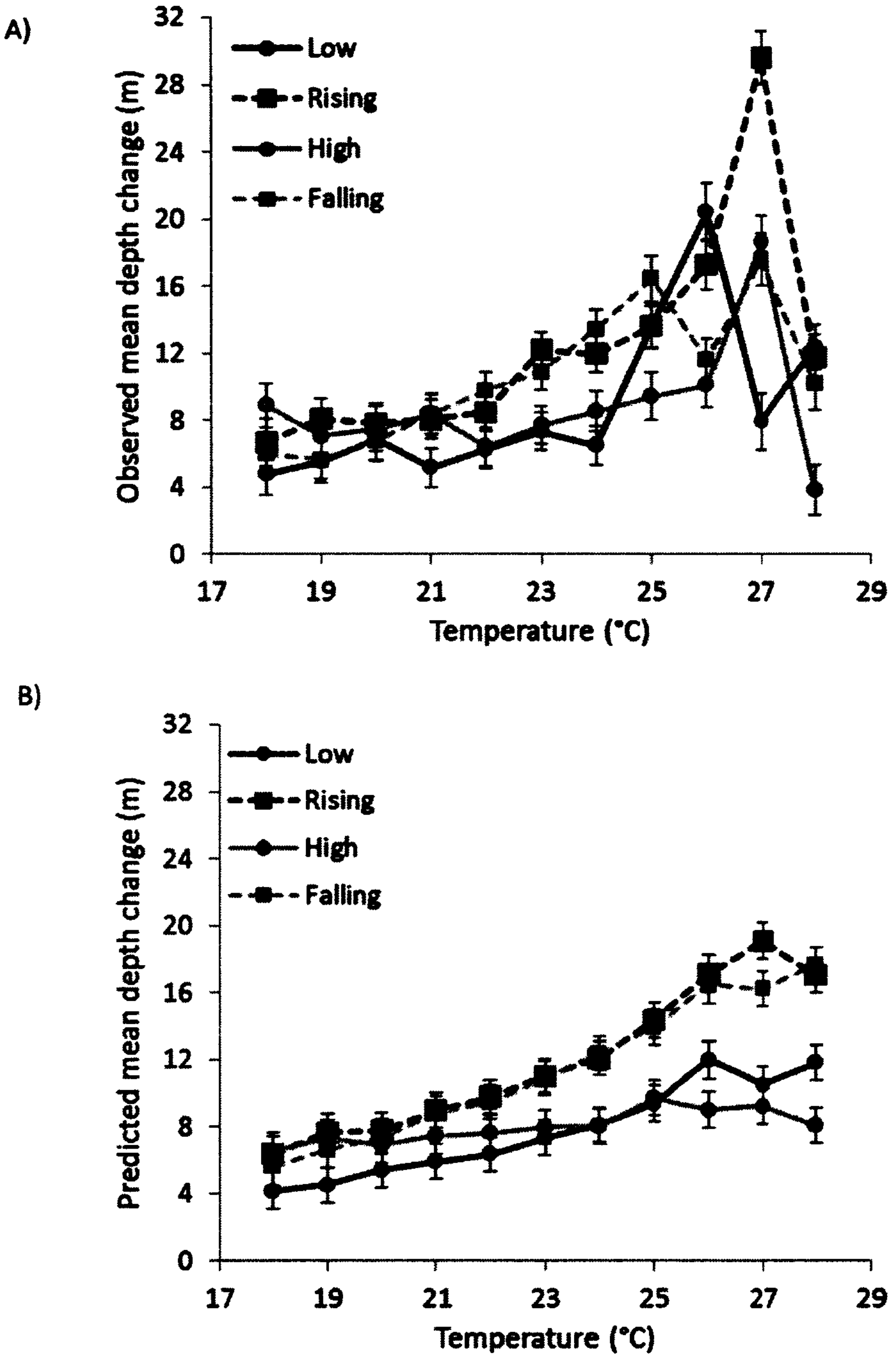


Figure 7. (A) Observed and (B) predicted interaction between temperature and tidal stage on the cumulative mean depth change (back transformed after Box-Cox transformation) for summer flounder tagged with archival tags within Chesapeake Bay in the summer of 2009. For this analysis, depth changes were observed during 1.5-hour time periods around low (black circles), rising (black squares), high (gray circles), and falling (gray squares) tides. Error bars are ± 1 standard error.

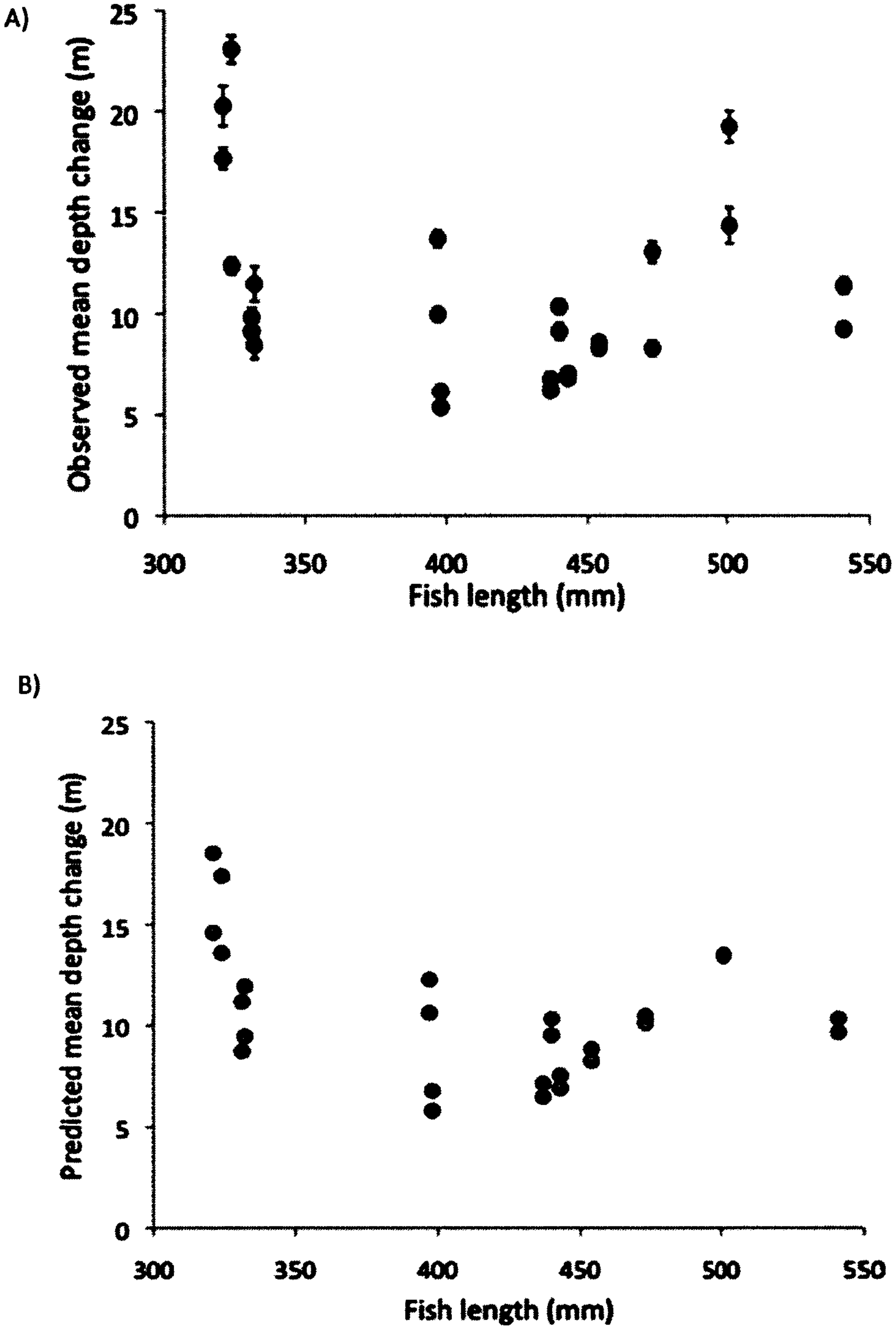


Figure 8. (A) Observed and (B) predicted cumulative mean depth change (back transformed after Box-Cox transformation) for summer flounder of various lengths during day (gray circles) and night (black circles). All fish were tagged and released within Chesapeake Bay during the summer of 2009. Error bars are ± 1 standard error.

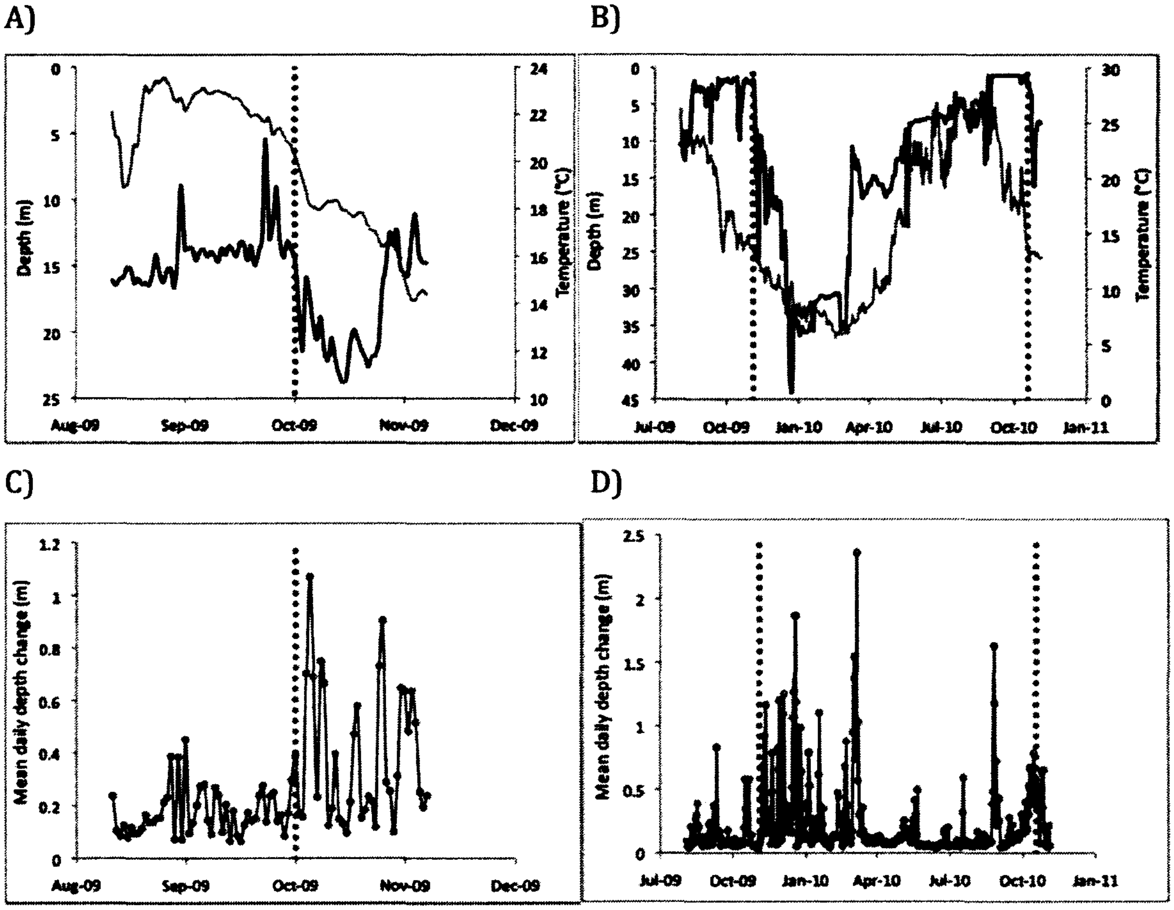


Figure 9. (A,B) Temperature (grey lines) and depth profiles (solid black lines), and (C,D) mean daily depth changes of two summer flounder with archival tags that dispersed from Chesapeake Bay. In each graph, the dotted black line represents the presumed dates of dispersal from Chesapeake Bay. Profiles depicted in A, C were from a fish that was recaptured in a gillnet off Virginia Beach (tag 199). Profiles depicted in B, D were from a fish that was recaptured in Chesapeake Bay in 2011 (Tag 241). Note that different time, depth, and temperature scales were used for each fish.

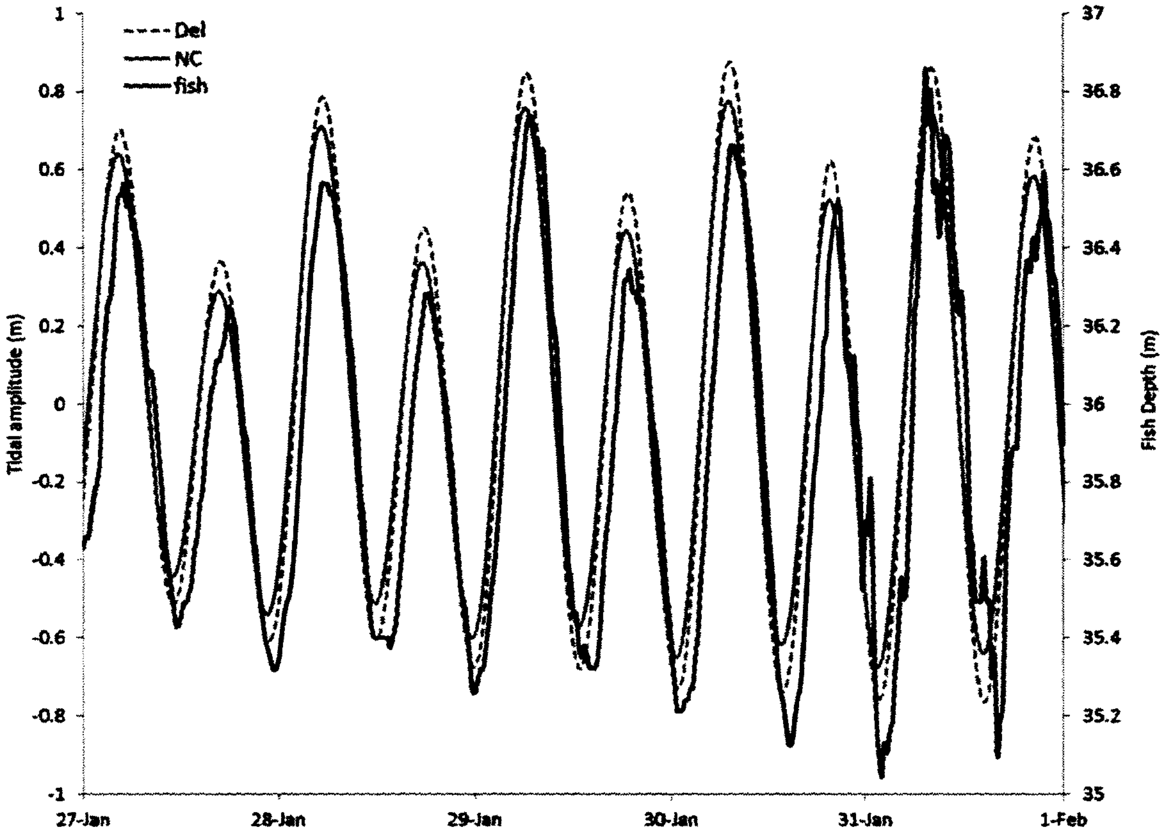


Figure 10. Comparison of archival tag depth recordings (black line) and tidal predictions off the coast of Delaware (gray, dashed line) and North Carolina (gray, solid line) during a period when the fish was mostly sedentary on the continental shelf in late January 2010.

CHAPTER 3

Using Mark-Recapture Growth Models to Discern Recreational Angler Noncompliance with Minimum Length Regulations

Abstract

We used mark-recapture growth models to investigate recreational angler compliance with minimum size regulations in a popular Chesapeake Bay fishery. Angler noncompliance can severely degrade the ability of fishery managers to avoid overexploitation and achieve objectives of rebuilding plans. To discern noncompliance in the summer flounder recreational fishery, we fit a series of growth models to 3474 recapture records from a tagging study involving volunteer anglers in Virginia from 2000-2011. The growth model included individual variability in fish growth, two growth phases, separate measurement error terms for fish recaptured by trained anglers and those recaptured by untrained anglers, and a process error term that was linearly related to the fish's time at liberty. Summer flounder growth patterns changed at 34.7 cm, which may represent the length when the majority of fish reach maturity. Length measurement errors reported by trained anglers were about 1.5 cm less than measurement errors reported by untrained anglers. Reported length measurements of harvested fish that were predicted to be sublegal had a positive bias of 2.2 ± 0.5 cm. The predicted mean size of harvested fish increased through time in response to increases in minimum size regulations, though sublegal fish continued to be harvested. Throughout the 12 years of this study, 33-79% of the reported harvest was predicted to be sublegal based on the growth model. The percentage of sublegal fish that were harvested increased dramatically when large ($\geq$5 cm) increases in minimum size limits were implemented. We conclude that Virginia recreational anglers responded to management regulations by adjusting the minimum size of harvested fish, but also continued to harvest sublegal fish.

Introduction

Noncompliance with management regulations can severely degrade the ability of fishery managers to prevent overexploitation of fish populations (Gigliotti and Taylor 1990, Sullivan 2002, Hicks 2002) and achieve objectives of rebuilding plans. In recent decades, recreational fishing effort has increased considerably and been implicated in the decline of some fish stocks (Post et al. 2002, Coleman et al. 2004, Cooke and Cowx 2004). The most common method for managing recreational fisheries is to implement regulations that limit the impacts of individual anglers on the population (e.g., season, bag, and size limits). Unfortunately, angler noncompliance with management regulations is common, and can be as high as 90% (Glass and Maughan 1984, Paragamian 1984, Schill and Kline 1995, Pierce and Tomcko 1998, Sullivan 2002). A simulation study indicated that even moderate levels of noncompliance could result in severe declines in the number of legal-sized fish harvested (Gigliotti and Taylor 1990). Quantifying the extent of angler noncompliance is a challenging task because noncompliance is difficult to measure accurately (Schill and Kline 1995, Sullivan 2002). Previous studies of angler noncompliance have used primarily creel surveys, citation records, or angler interviews. Each of these methods has inherent weaknesses and biases that stem from anglers concealing their sublegal catch. For example, Pierce and Tomcko (1998) found that estimated levels of angler noncompliance (i.e., percent of harvest that was sublegal) based on creel surveys and citation records were biased low and concluded that anglers concealed their sublegal catches from creel clerks and enforcement officers. Their results indicated that estimates of noncompliance based on voluntary tag returns were more accurate than those based on other methods. In this study, we use data collected from a recreational angler-tagging program in the Chesapeake Bay region to quantify angler noncompliance with minimum size regulations.

The Virginia Game Fish Tagging Program (VGFTP) is a cooperative project between the Virginia Marine Resources Commission and the Virginia Institute of Marine Science that trains recreational anglers to tag and release popular game fishes throughout the waters of Virginia. Since the program was initiated in 1995, up to 200 recreational anglers per year volunteer to tag fish during their normal fishing activities. The large numbers of participants in the program release thousands of tagged fish annually throughout the marine and estuarine waters of Virginia. Benefits of this program include a relatively low cost and a collaborative relationship between scientists and the angling community (Lucy and Davy 2000). One disadvantage is that the data quality may not meet scientific standards. For example, fish tagged and released as black sea bass have been recaptured and reported as summer flounder. Despite data quality issues, the large number of releases and recaptures remaining after quality assurance checking provides sufficient data to model fish growth and to examine compliance with established management regulations. We chose to analyze the mark-recapture data collected for summer flounder, which are one of the most targeted commercial and recreational fish species of the U.S. Atlantic coast (Terceiro 2002).

Due to the extensive fishing pressure on summer flounder, the effective management of this population is critical to ensure the sustainability of the population, which has been under a rebuilding plan since 2000. The Mid-Atlantic Fisheries Management Council and the Atlantic States Marine Fisheries Commission jointly managed this species through regulations on both the commercial and recreational fisheries (Terceiro 2002). Currently, 40% of the quota is allocated to the recreational fishery and the remaining 60% is allocated to the commercial fishery. The recreational fisheries sector has exceeded its allotted quota in multiple years, most likely due to the difficulties inherent in monitoring recreational angler activities (Terceiro 2002). To reduce the harvest of the recreational fishery, managers throughout the Atlantic states have primarily implemented bag and size limits that change annually. To gain insight into the rate of recreational angler noncompliance, we fit growth models to the mark-recapture data collected by the VGFTP and compared reported sizes of recaptured fish with predicted sizes.

Individual growth models are a valuable tool in fisheries science because understanding how fish grow is critical to many aspects of fish stock dynamics. Growth models are most commonly applied to size-at-age data, but these models can also be fit to mark-recapture data consisting of sizes and dates when fish were released and recaptured (Haddon 2011). Growth models are typically used to estimate parameters for stock assessments, but they have also been used to observe ontogenetic changes (Ross et al. 1995, Hearn and Polacheck 2002). For example, Hearn and Polacheck (2002) found that a two-phase growth model better represented the growth of southern bluefin tuna than the standard single-phase von Bertalanffy growth model. They concluded that the two growth phases might be the result of changes in fish behavior related to ontogeny. We suspect that similar changes in growth may occur with ontogeny in summer flounder, because these fish undertake large spawning migrations from coastal bays and estuaries to spawning grounds on the continental shelf (Kraus and Musick 2001).

In this study, we use mark-recapture growth models to observe trends in recreational angler noncompliance with summer flounder minimum size limits in Virginia. Although previous studies used recapture data to assess angler noncompliance (Pierce and Tomcko 1998), the incorporation of a growth model into this analysis allowed us to better quantify the extent of noncompliance relative to changes in the minimum size regulations. In addition, the growth model provided a means to investigate changes in growth related to ontogeny (i.e., length at maturity) and differences in measurement error between trained taggers and untrained anglers.

Methods

Tagging Program

The VGFTP trains volunteer anglers to tag and release game fishes as part of their routine fishing activities. All volunteer taggers were provided with tagging equipment and trained to properly measure, handle, and tag multiple fish species (Lucy et al. 2002). Based on this training, we assume throughout this paper that the length measurements reported by VGFTP taggers were accurate within rounding error. Taggers were also provided with data sheets to record information pertinent to their releases, such as tag number, species, date, total length, release location, and release condition (i.e., excellent, good, fair, and poor). These data sheets were submitted to the VGFTP and compiled into a database that was queried when recreational and commercial fishers reported recaptures.

During the period 2000-2011, VGFTP participants released 47513 tagged summer flounder throughout the Chesapeake Bay (see Chapter 2 for a more detailed description of release regions). Nearly all tagged fish were captured by hook-and-line because VGFTP taggers were almost entirely recreational anglers. All summer flounder were tagged with a Hallprint t-bar anchor tag inserted in the dorsal musculature near the tail. Each tag was labeled with a unique identifying number, a phone number to report recaptures, and a reward notice. Tagged fish had a truncated length range (21-60 cm; Figure 1) compared to that observed in fishery-independent surveys (Bonzek et al. 2010) because most fish larger than the recreational size limit were harvested by the taggers. During this study the minimum size limit varied between 39 and 48 cm total length.

A total of 7061 summer flounder recaptures was reported to the VGFTP, but some of these data were excluded from the growth analysis because they were outliers, tagged as exceptionally small fish (< 25 cm), or not at liberty for a sufficient duration to observe or measure growth. We used only those recapture records that included a recapture date and a measurement of fish length. Through personal discussion with anglers we learned that some of the reported length "measurements" were actually approximations that were visually estimated by the angler. Unfortunately, the type of length measurement (measured or estimated) was not recorded, so we were unable to quantify the accuracy and bias associated with length method estimation. We removed nine obvious outliers from the dataset based on the following criteria: 1) if the fish was recaptured within six months of release and the difference between release and recapture lengths was more than 25 cm, or 2) if the fish was recaptured after more than 1 year at liberty and the length at tagging exceeded the length at recapture by more than 5 cm. We also excluded data from fish that were smaller than 25 cm, fish at liberty for less than 10 days, and fish at large for more than 4 years. Fish smaller than 25 cm were excluded because we suspected that the tagging process influenced their growth and survival. Fish at liberty for less than 10 days were excluded from the growth analysis because these fish were not likely to exhibit observable growth; however, because these fish should have nearly identical lengths upon release and recapture, we used these data to determine the bias of the reported lengths of recaptured fish. To do this, we calculated the mean difference between the lengths at release and recapture and used a t-test to determine if this mean was significantly different from zero. Finally, we excluded 4 observations from fish at liberty for more than 4 years to avoid biases in parameter estimates resulting from small sample size. We thus retained information from 3474 recaptures and used those data to model summer flounder growth (Figure 2).

Growth Models

We used four growth models to investigate growth rates, growth phases and individual variability in growth patterns in summer flounder. The first -- the Fabens (1965) model -- is a modification of the von Bertalanffy growth equation for mark-recapture data. For all recaptured individuals (i), this model has the form:

$$E[\Delta l_i] = (L_\infty - l_{1_i})(1 - e^{-k(t_{2_i} - t_{1_i})}) + \varepsilon_i \tag{1}$$

where Δl_i is the growth increment, L_∞ is the asymptotic maximum length of the population, l_{1i} is the length at tagging, k is the growth coefficient, t_{1i} is the release date, t_{2i} is the recapture date, and ε_i is the unexplained error which includes model error and measurement error. The second model, developed by Hearn and Polacheck (2002), expands on the Fabens model by estimating a length at which growth patterns change, possibly due to fish reaching maturity. In this model, the Fabens equation is solved to estimate growth during two or more phases of life depending on when the fish was released and recaptured relative to the length at which the growth rates change (L*):

$$E[\Delta l_i] = \begin{cases} (L_\infty - l_{1_i})(1 - e^{-k_1(t_{2_i} - t_{1_i})}) + \varepsilon_i & \text{if } t_{2_i} \le t^*_i \\ (L^* - l_{1_i}) + (L_\infty - L^*)(1 - e^{-k_2(t_{2_i} - t^*_i)}) + \varepsilon_i & \text{if } t_{1_i} < t^*_i \text{ and } t_{2_i} > t^*_i \\ (L_\infty - l_{1_i})(1 - e^{-k_2(t_{2_i} - t_1)}) + \varepsilon_i & \text{if } t_{1_i} \ge t^*_i \end{cases} \tag{2}$$

where k_1 is the growth coefficient during the first growth phase, k_2 is the growth coefficient during the second growth phase, and t^*_i is the date when an individual reaches L*. Note that t^*_i is not an estimated parameter but is calculated by:

$$t^*_i = t_{1_i} - \left(\frac{\log\left(1 - \frac{L^* - l_{1_i}}{L_\infty - l_{1_i}}\right)}{k_1} \right) \tag{3}$$

Hearn and Polacheck (2002) estimated L_∞ values for each of two growth phases; however, their results showed limited support for that complex a model and biologically it seems more plausible to expect that a population would have a single asymptotic maximum length. Thus, we chose to reduce the number of parameters by estimating a single L_∞. The third model, developed by Wang (1998), modified the Fabens model by incorporating an additional factor to allow for individual variability in growth associated with the observed length at tagging. This model takes the form:

$$E[\Delta l_i] = \left(L_\infty + \beta(l_{1_i} - \overline{l_{1_i}}) - l_{1_i}\right)\left(1 - e^{-k(t_{2_i} - t_{1_i})}\right) + \varepsilon_i \tag{4}$$

where β is an estimated parameter whose magnitude indicates the amount of individual variability in growth. Note that this model is a generalization of the Fabens model, as it reduces to the Fabens model when β equals zero. The final model combined the two-stage model of Hearn and Polacheck (2002) and the individual growth variability model developed by Wang (1998):

$$E[\Delta l_i] = \begin{cases} (L_\infty + \beta(l_{1_i} - \overline{l_{1_i}}) - l_{1_i})(1 - e^{-k_1(t_{2_i} - t_{1_i})} + \varepsilon_i & \text{if } t_{2_i} \le t_i^* \\ (L^* - l_{1_i}) + (L_\infty + \beta(l_{1_i} - \overline{l_{1_i}}) - L^*)(1 - e^{-k_2(t_{2_i} - t_i^*)} + \varepsilon_i & \text{if } t_{1_i} \le t_i^* \text{ and } t_{2_i} < t_i^* \\ (L_\infty + \beta(l_{1_i} - \overline{l_{1_i}}) - l_{1_i})(1 - e^{-k_2(t_{2_i} - t_{1_i})} + \varepsilon_i & \text{if } t_{1_i} \ge t_i^* \end{cases} \tag{5}$$

Once again, t^*_i is not an estimated parameter, but is calculated by:

$$t^*_i = t_{1_i} - \left(\frac{\log\left(1 - \dfrac{L^* - l_{1_i}}{L_\infty + \beta(l_{1_i} - \overline{l_{1_i}}) - l_{1_i}}\right)}{k_1} \right) \tag{6}$$

This model will be referred as the Wang-L* model. To fit these models we pooled growth data for all years, under the assumption that growth patterns were consistent throughout this study (2000 - 2011).

Model parameters were estimated using maximum likelihood, with various error structures designed to account for known biases associated with estimating growth parameters from mark-recapture data. It is well documented that growth models based on mark-recapture data can suffer from biases when individual variability exists in growth parameters, particularly if the L_∞ parameter varies with individual fish (Francis 1988, Hampton 1991, James 1991, Wang 1998, Laslett 2002). As a result of this individual variability, the variance in the expected growth increment increases with increasing time at liberty (James 1991, Hampton 1991, Hearn and Polacheck 2002). To partially compensate for this bias we expressed the variance of the expected growth increment ($V[\Delta l_i]$) using five error structures. These error structures were:

1) a single constant error (σ):

$$V[\Delta l_i] = \sigma^2 \tag{7}$$

2) a single error (σ) that is linearly related to time at liberty:

$$V[\Delta l_i] = \sigma^2 (t_{2_i} - t_{1_i}) \tag{8}$$

3) the sum of two error terms: measurement error (σ_m) and process error (σ_p), which is linearly dependent on time at liberty:

$$V[\Delta l_i] = \sigma_m^2 + \sigma_p^2 (t_{2_i} - t_{1_i}) \tag{9}$$

4) conditional error terms: one for fish measured by a tagger trained by the game fish tagging program (σ_m), and an additional error term for fish measured by an untrained angler (σ_a):

$$V[\Delta l_i] = \begin{cases} \sigma_m^2 & \text{if recaptured by VGFTP tagger} \\ \sigma_m^2 + \sigma_a^2 & \text{if recaptured by untrained angler} \end{cases} \tag{10}$$

and,

5) conditional error terms with process errors: tagger measurement error (σ_m), angler measurement error (σ_a), and process error (σ_p) that is linearly dependent on the time at large:

$$V[\Delta l_i] = \begin{cases} \sigma_m^2 + \sigma_p^2(t_{2_i} - t_{1_i}) & \text{if recaptured by VGFTP tagger} \\ \sigma_m^2 + \sigma_a^2 + \sigma_p^2(t_{2_i} - t_{1_i}) & \text{if recaptured by untrained angler} \end{cases} \tag{11}$$

Although we refer to "measurement" and "process" errors, these two error terms are confounded and are not separately estimable because we do not have independent estimates of measurement error. Therefore, for error structures 3 and 5, the error term (σ_m^2) should be considered a composite of measurement error and components of the process error that are not related to time at liberty (Hearn and Polacheck 2002). Under the assumption that the growth increment was normally distributed (which was empirically supported by the data based on a comparison between the fit of the normal and the lognormal distributions to the growth increment response using the fitdistr function in R) the parameters for the various models and error terms were estimated by minimizing the following negative log-likelihood:

$$-\log(L)=\frac{1}{2}\sum_{i=1}^{n}\left[\log(2\pi(V[\Delta l_i])+\frac{(\Delta l_i-E[\Delta l_i])^2}{V[\Delta l_i]}\right] \qquad (12)$$

This was accomplished using the bounded BFGS minimization method (Byrd et al. 1995) implemented with the 'optim' function in R. To improve the efficiency of the minimization procedure we constrained the L_∞, k, k_1, k_2, and L* parameters to be greater than zero. The model that best described the data was selected using Akaike's information criterion (AIC; Akaike 1973).

None of the models implemented in this study were designed to account for individual variability in the growth coefficient (k). It would be reasonable to assume that if individuals have variability in the L_∞ parameter, then there may also be variability in the k parameter, because these parameters are highly correlated. Both maximum likelihood (Sainsbury 1980, Evenson et al. 2007) and Bayesian (Fabrizio et al. 2001, Zhang et al. 2009) methods have been developed to analyze growth data from mark-recapture experiments with assumed variability in L_∞ and k parameters. However, these methods are more computationally intensive than those employed in this study and simulation studies indicate it is unnecessary to model individual variability in the growth coefficient to accurately estimate the von Bertalanffy growth parameters (Hampton 1991, Wang et al. 1995, Wang 1998).

Angler Noncompliance

We used the residuals from the selected growth model to examine the bias in the length measurements reported by recreational anglers. The residual growth was calculated as the difference between the observed and predicted growth. We first plotted the residuals against the release length and time at liberty to determine if residuals were centered at zero throughout the range of observations. We next partitioned the data into two sets: fish that were released after recapture and fish that were harvested. Finally, we partitioned the data for harvested fish into two groups: 1) fish whose predicted size indicated they were sublegal upon recapture, and 2) fish whose predicted size indicated they were legal upon recapture. Note that we are using recaptures from recreational anglers only. Commercial fishers did not report enough recaptures for us to reliably estimate rates of noncompliance by that sector. In analyzing the residuals from recreational angler recaptures, our null hypothesis was that there was no length measurement bias and, thus, the mean residual was equal to zero. We tested this hypothesis for each group of residuals (i.e., released fish, harvested fish, harvested fish expected to be sublegal, harvested fish expected to be legal) using t-tests at a significance level of 0.05.

We used the predicted estimates of fish length to investigate changes in lengths of harvested fish through time and compared these changes with changes in minimum size limits for summer flounder in Virginia. We calculated the annual mean predicted length of all harvested fish (MPL - H), the annual mean predicted length of harvested fish that were predicted to be sublegal (MPL – S), and the annual percentage of harvested fish that were predicted to be sublegal. The 95% confidence intervals for all means and percentages were calculated using methods described in Zar (1999).

Results

Recaptures were more likely to occur shortly after release and the growth increment data were highly variable (Figure 2). Throughout the 12 years of this study, the majority (91.23 %) of summer flounder were recaptured within 6 months of release. The length measurements of summer flounder recaptured within six months of release ranged from 25 cm larger or 25 cm smaller than their length at time of release. This implies large inaccuracies in the measurements reported by either the taggers or the anglers that recaptured and reported the fish. Some of these inaccuracies may have been the result of rounding error. Nearly half of the reported recapture lengths were reported to the nearest inch, and an additional 30% were reported to the nearest half-inch (Table 1). A similar pattern was also apparent in the lengths reported by the trained taggers. Despite the lack of precision, the reported length measurements were not biased. The mean observed growth for the fish at large less than 10 days was 0.11 ± 0.14 cm and was not significantly different from zero ($t=1.63$, $df=1137$, $p = 0.10$).

The Wang – L* model with three error terms (error structure 5) best described the summer flounder growth data from the VGFTP (Table 2, Figure 3). Although this model had 8 parameters (more than any other in the study), AIC weights indicated a 99.7% probability that this was the best model among the candidate models. The estimated L_∞ from the Wang-L* model was considerably smaller than estimates reported in previous studies (Table 3). We suspect this is due to the nature of the tagging program. Because the taggers were recreational anglers who tend to harvest the legal-sized fish they catch, very few large fish are tagged. The estimated length at which growth patterns changed (L*) was 34.69 cm. The likelihood profile plot for this parameter shows that likelihood values do not differ greatly when the L* value ranges between 32 and 35 cm (Figure 4), suggesting variability in the length at which an individual's growth pattern changes. The model estimated value for the beta parameter, which represents the degree of individual variability in the L_∞ parameter, was quite large compared to beta estimates reported by Wang (1998). This implies that summer flounder exhibit large amounts of individual variation in growth (specifically L_∞), but this may also reflect the considerable measurement error observed with these data.

Regardless of the growth model, the most appropriate error structure included terms for tagger measurement error, non-tagger measurement error, and process error (error structure 5). The different error structures used to fit the models affected the AIC values more so than the differences in model parameterization. In particular, inclusion of separate error terms for tagger and non-tagger measurement error reduced AIC by more than 250 units regardless of growth model considered (Table 2). In these models, the non-tagger error term was nearly 1.5 cm larger than that for the trained tagger. Considerable support for inclusion of an additional process error term that was linearly related to time-at-liberty was also evident. Inclusion of the process and measurement error terms reduced AIC by approximately 40 units when compared with models containing a single error term.

No pattern was evident in the residuals from the Wang-L* model relative to fish size or time-at-large, but a pattern did emerge when residuals were examined relative to the status of recaptured fish – either harvested or released. Regardless of the size of the fish at tagging, model residuals were centered at zero (Figure 5a). As the size at tagging increased, the variance appeared to decrease, but this was most likely due to reduced sample sizes for fish tagged at 40 cm or larger. A similar pattern was observed for growth relative to time at liberty (Figure 5b). A positive bias in residuals was evident for fish that were harvested upon recapture (Figure 6). Of the 398 fish harvested by recreational anglers in this study, over half (54.02%) were expected to be sublegal according to the Wang-L* growth model. The residuals from the growth model were centered at zero for harvested fish that were predicted to be of legal size (Figure 7a) and the mean residual for these fish was 0.62 ± 0.45 cm. This was significantly different from zero (t=2.71, df=183, p=0.007) indicating a slight positive bias, which could be the result of rounding error. A majority (86.51%) of the harvested fish that were predicted to be sublegal had positive residuals (Figure 7b) and the mean residual for these fish was 2.87 ± 0.53 cm, which was significantly different from zero (t=10.72, df=214, p<0.001). Based on the large percentage of residuals that were positively biased and the magnitude of the mean residual, it is unlikely that the observed measurement bias for fish that were predicted to be sublegal was due to rounding error.

Recreational anglers responded to changes in minimum size regulations in Virginia, but still continued to harvest sublegal summer flounder. From 2000 to 2006, the mean predicted length of harvested fish (MPL-H) was nearly equal to, or greater than, the minimum size limit (Figure 8a). Between 2007 and 2011, the minimum size limit increased (over 47 cm), and the MPL-H was consistently less than the minimum size limit. The mean predicted length of harvested fish expected to be sublegal (MPL–S) also varied with the minimum size limit regulations (Figure 8b). The difference between the MPL-S and the minimum size limit ranged from

1.14 to 4.46 cm and tended to increase as the minimum size limit increased (Figure 9). The proportion of the harvested fish that were expected to be sublegal was also related to the minimum size limit. Throughout this study, 33-79 % of harvested fish reported to the VGFTP were expected to be sublegal but the confidence intervals for expected size at recapture were quite large due to small sample sizes (Figure 8c). The percent of sublegal harvest increased in 2002 and 2007, years when the minimum size limit regulation increased considerably (5 cm) from the previous year. The percent of sublegal harvest was also relatively high in 2009 and 2010. Although minimum size limits were relatively consistent during those years, statements made at angler club meetings and on online discussion boards (e.g., www.tidalfish.com) implied that anglers perceived those size limits as excessively large (M. Henderson, personal observation).

Discussion

Growth models fit to recreational angler mark-recapture data can provide insight into recreational angler noncompliance with minimum-size-limit regulations. These models allowed us to observe biases in the length measurements reported for sublegal summer flounder harvested by recreational anglers in Virginia. Based on model predictions, recreational anglers appeared to respond to changes in size regulations by adjusting the minimum length of fish they harvested; however, these anglers continued to harvest summer flounder that were approximately 1 - 4 cm smaller than the minimum size limit. The largest differences between the minimum size limit regulation and the mean size of harvested sublegal fish were observed during years when the minimum size limits were largest. Furthermore, the highest proportions of sublegal fish were harvested during years when minimum size limits changed substantially (e.g., in 2002 and 2007) or were maintained at large lengths for consecutive years (2006 – 2010). These increases in noncompliance were most likely because the larger size limits reduced the catch rate of legal sized fish (Sullivan 2002).

Although we believe our results concerning noncompliance are representative of the recreational summer flounder fishery in Virginia, there are limitations to using data collected by an angler-tagging program. First, the VGFTP relies on anglers to voluntarily report recaptures. Small rewards (e.g., t-shirts, pins, and tackle boxes) were offered as incentives to report recaptures, but the overall reporting rate in this program remains unknown. Anglers that harvest sublegal fish may be less likely to report recaptures under the assumption that they could be fined. If reporting rates were lower for harvested sublegal fish, then our estimate for the percentage of the recreational harvest that was illegal is conservative. A second limitation of using angler-tagging data is that summer flounder tagged and released by the VGFTP were disproportionally sublegal. As a result, the observed proportions of harvested fish that were sublegal most likely cannot be used to make inferences regarding the recreational fishery as a whole. Because very few larger fish were tagged and released as part of the VGFTP, we suspect that the proportion of harvested fish that were sublegal was lower in the recreational fishery than that indicated in Figure 8c. However, even low levels of noncompliance can degrade the benefits derived from instituting minimum size regulations (Gigliotti and Taylor 1990). Despite the limitations of the data, we believe our results provide useful observations on the habits of recreational anglers in response to changes in harvest regulations, and confirm the belief among managers that increasing minimum size regulations may increase angler noncompliance.

Results from this study also provided indication of the bias and precision of length measurements by recreational anglers. Length measurements from summer flounder that were recaptured by recreational anglers within 10 days of release were reported to have lengths that differed up to 25 cm from the length reported at time of tagging, but these recapture measurements were not positively or negatively biased. This lack of precision in angler measurements is large compared with that observed in other studies (Ferguson et al. 1984, Page et al. 2004), which may be the result of some recreational anglers in Virginia estimating, instead of measuring, the lengths of recaptured fish that were obviously sublegal. Another explanation may be recall bias. Some anglers reported recaptures days or weeks after the actual recapture event, and provided a length from memory. The lack of precision was also due to rounding error. Nearly 50% of the reported length measurements were rounded to the nearest inch, and an additional 30% were rounded to the nearest half-inch. This pattern was not surprising for the recapture lengths, as recreational angler rounding error has previously been noted in studies of inland fisheries (Ferguson et al. 1984, Page et al. 2004), but we had expected that trained taggers would provide more precise length measurements because they were trained to measure and report fish length to the nearest quarter inch. Based on these results it appears that many trained anglers reverted to the common habit of rounding to the nearest whole inch. Although measurements made by trained anglers may also suffer from rounding error, results from the growth model imply that their measurements are more accurate than those reported by an untrained angler. Measurement error associated with untrained anglers was an additional 1.5 cm greater than those reported by trained taggers.

Despite the biases and lack of precision in the length measurements reported by recreational anglers, we were able to fit a relatively complex growth model to these data. Summer flounder growth appears to be related to ontogeny, with the growth coefficient decreasing at approximately 35 cm, which may be the approximate length at which summer flounder reach maturity. We hypothesize that growth rates decline after maturity because fish begin to expend more energy on gonad production and seasonal spawning migrations (Lester et al. 2004, Rijnsdorp and Witthames 2007). The likelihood profile plot for the change point in the growth model indicated that individuals might reach this change point (maturity) between 32 and 35 cm total length. This relatively large range indicates that changes in individual fish growth rates do not occur immediately upon maturation, but may be manifested over a long period of time as fish progressively dedicate more energy towards reproduction. Previous studies based on macroscopic examination of whole gonads have indicated that the length at which 50% of summer flounder are mature is approximately 30 cm (summarized in Packer 1999). It is possible that as the summer flounder population has increased, and the age structure has become less truncated (Terceiro 2011), the length at which summer flounder become mature has increased. This conclusion is supported by data presented in Terceiro (2002) that indicate female summer flounder reached maturity at a larger length in the 1990s (high stock abundance) than they had in the 1980s (low stock abundance).

In designing this study, we selected only a small subset of growth models but other models may be more appropriate to describe summer flounder growth patterns. We chose to fit models based on the von Bertalanffy growth function primarily because it has been used previously to model summer flounder growth (Table 3). The specific models we selected allowed us to test hypotheses regarding length-at-maturity and individual variability in the asymptotic maximum length but we did not test for differences in seasonal growth (Cloern and Nichols 1978, Pauly et al. 1992) or individual variability in the growth coefficient (Sainsbury 1980, Fabrizio et al. 2001, Evenson et al. 2007, Zhang et al. 2009). It is possible that these additional complexities may improve our understanding of summer flounder growth, but such complexities may demand more precision from the angler-tagging data than is currently available. The models we selected were sufficient to investigate our questions regarding angler noncompliance with summer flounder minimum size regulations.

We caution that the growth parameters reported here are not representative of the mid-Atlantic summer flounder population. Summer flounder are known to exhibit sexually dimorphic growth (Poole 1961, Fogarty 1981), but we were unable to model male and female growth separately because sex cannot be determined without sacrificing the animal to examine gonads. Surveys of the summer flounder population in Chesapeake Bay indicate that females comprise nearly 80% of the adult summer flounder population within the Bay (Bonzek et al. 2008). Therefore, we believe our results are primarily representative of female growth patterns. Another reason that the growth parameters estimated in this study may not be representative of the mid-Atlantic population is that less than 1% of the tagged fish and only 3% of the recaptured fish were larger than 50 cm. Summer flounder can reach and exceed 65 cm total length within Chesapeake Bay (Bonzek et al. 2010), and exclusion of the larger fish from the angler-tagging program most likely biased our estimates of L_∞ and k. Due to the well-known correlations between the L_∞ and k parameters, reliable estimates of growth beyond the length range of the data cannot be obtained (Hearn and Polacheck 2002). This may partially explain our low estimates of L_∞, and high estimates of k, compared to previously published growth models based on length at age data (Table 3).

The results from this study have management implications for the summer flounder fishery in Virginia and for recreational fisheries in general. The upper range of the estimated summer flounder length-at-maturity (35 cm) is nearly identical to the current minimum size limit for summer flounder commercial fisheries along the coast (35.6 cm). This suggests that more research is warranted to determine if the minimum size limit for the commercial fishery should be increased to improve that probability that summer flounder will have the opportunity to spawn prior to becoming vulnerable to the commercial fishery. Our results also suggest that angler behavior should be incorporated into management decisions in order to improve the efficacy of regulations, as has been previously suggested (Hilborn and Walters 1992, Ludwig et al. 1993, Radomski et al. 2001, Beard et al. 2003). In a large body of water, such as Chesapeake Bay, it is infeasible to have a significant enforcement presence to prevent sublegal harvest of regulated species. Angler compliance may be maximized by implementing: 1) gradual changes in minimum size limits, or 2) minimum size limits that result in sufficiently high catch rates of legal sized fish to satisfy anglers. If population levels are depleted such that drastic management actions are required to rebuild the biomass of the stock, we suggest conducting a survey to determine angler preferences for fishing constraints (Dawson and Wilkins 1981, Renyard and Hilborn 1986).

References

Akaike H (1973) Information theory and an extension of the maximum likelihood principle. pp. 267-281 *In* Petran BN and Csàaki F (eds.) *International Symposium on Information Theory*, 2nd ed. Akadèemiai Kiadi, Budapest, Hungary.

Beard Jr TD, Cox SP, and Carpenter SR (2003) Impacts of daily bag limit reductions on angler effort in Wisconsin walleye lakes. North American Journal of Fisheries Management, 23: 1283-1293.

Bonzek CF, Latour RJ and Gartland J (2008) Final Report: Data collection and analysis in support of single and multispecies stock assessments in Chesapeake Bay: The Chesapeake Bay Multispecies Monitoring and Assessment Program. Virginia Institute of Marine Science. Gloucester Point, VA.

Bonzek CF, Gartland J, and Latour RJ (2010) Annual Report: The Chesapeake Bay Multispecies Monitoring and Assessment Program. Project Number F-130-R-5. Virginia Institute of Marine Science. Gloucester Point, VA.

Byrd RH, Lu P, Nocedal J, and Zhu C (1995) A limited memory algorithm for bound constrained optimization. SIAM Journal on Scientific Computing, 16: 1190-1208.

Cloern JE and Nichols FH (1978) A von Bertlanffy growth model with a seasonally varying coefficient. Journal of the Fisheries Research Board of Canada, 35: 1479-1482.

Dawson CD and Wilkins BT (1981) Motivations of New York and Virginia marine boat anglers and their preferences for potential fishing constraints. North American Journal of Fisheries Management, 1: 151-158.

Evenson JP, Polacheck T, and Laslett GM (2007) Consequences of assuming an incorrect error structure in von Bertalanffy growth models: a simulation study. Canadian Journal of Fisheries and Aquatic Sciences, 64: 602-617.

Fabens A (1965) Properties and fitting of the von Bertalanffy growth curve. Growth, 29: 265-289.

Fabrizio MC, Dorazio RM, and Schram RM (2001) Dynamics of individual growth in a recovering population of lake trout (*Salvelinus namaycush*). Canadian Journal of Fisheries and Aquatic Sciences, 58: 262-272.

Ferguson MO, Green AW, and Matlock GC (1984) Evaluation of the accuracy and precision of volunteered size data from tagged red drum returns. North American Journal of Fisheries Management, 4: 181-185.

Fogarty MJ (1981) Review and assessment of the summer flounder (*Paralichthys dentatus*) fishery in the northwest Atlantic. U.S. National Marine Fisheries Service Northeast Fisheries Center Woods Hole Laboratory Reference Document No. 81-25, 54 p.

Francis RICC (1988) Maximum likelihood estimation of growth and growth variability from tagging data. New Zealand Journal of Marine and Freshwater Research, 22: 42-51.

Gigliotti LM and Taylor WW (1990) The effect of illegal harvest on recreational fisheries. North American Journal of Fisheries Management, 10: 106-110.

Glass RD and Maughan E (1984) Angler compliance with length limits on largemouth bass in an Oklahoma reservoir. North American Journal of Fisheries Management, 4: 457-459.

Haddon M (2011) *Modelling and Quantitative Methods in Fisheries, 2nd ed.* Chapman and Hall/CRC, New York.

Hampton J (1991) Estimation of southern Bluefin tuna *Thunnus maccoyii* growth parameters from tagging data, using von Bertalanffy models incorporating individual variation. Fishery Bulletin, 89:577-590.

Hearn WS and Polacheck T (2002) Estimating long-term growth-rate changes of southern Bluefin tuna (*Thunnus maccoyii*) from two periods of tag-return data. Fishery Bulletin, 101: 58-74.

Hilborn R and Walters CJ (1992) Quantitative fisheries stock assessment: choice, dynamics and uncertainty. Chapman and Hall, New York.

James IR (1991) Estimation of von Bertalanffy growth curve parameters from recapture data. Biometrics, 47: 1519-1530.

Laslett GM, Eveson JP, and Polacheck T (2002) A flexible maximum likelihood approach for fitting growth curves to tag-recapture data. Canadian Journal of Fisheries and Aquatic Sciences, 59: 976-986.

Lester NP, Shuter BJ, and Abrams PA (2004) Interpreting the von Bertalanffy model of somatic growth in fishes: the cost of reproduction. Proceeding of the Royal Society of London, Series B, 271: 1625-1631.

Lucy J and Davy K (2000) Benefits of angler-assisted tag and release programs. Fisheries, 25: 18-23.

Lucy JA, Bain CM, and Arendt MD (2002) Virginia Game Fish Tagging Program: trained anglers making a contribution to fisheries research, management, and conservation. Pgs 195-200 *In* Lucy JA and Studholme AL (eds.) *Catch and Release in Marine Recreational Fisheries.* American Fisheries Society, Symposium 3, Bethesda, Maryland.

Ludwig D, Hilborn R, and Walters C (1993) Uncertainty, resource exploitation, and conservation: lessons from history. Science, 206: 17.

Page KS, Grant GC, Radomski P, Jones TS, and Bruesewitz RE (2004) Fish total length measurement error from recreational anglers: causes and contribution to noncompliance for the Mille Lacs walleye fishery. North American Journal of Fisheries Management, 24: 939-951.

Paragamian VL (1984) Angler compliance with a 12.0-inch minimum length limit for smallmouth bass in Iowa streams. North American Journal of Fisheries Management, 4: 228-229.

Pauly D, Soriano-Bartz M, Moreau J, and Jarre A (1992) A new model accounting for seasonal cessation of growth in fishes. Australian Journal of Marine and Freshwater Research, 43: 1151-1156.

Pierce RB and Tomcko CM (1998) Angler noncompliance with slot length limits for northern pike in five small Minnesota lakes. North American Journal of Fisheries Management, 18: 720-724.

Poole JC (1961) Age and growth of the fluke in Great South Bay and their significance to the sport fishery. N.Y. Fish and Game Journal, 8: 1-18.

Radomski PJ, Grant GC, Jacobson PC, and Cook MF (2001) Visons for recreational fishing regulations. Fisheries, 26: 7-18.

Renyard TS and Hilborn R (1986) Sports angler preferences for alternative regulatory methods. Canadian Journal of Fisheries and Aquatic Sciences, 43: 240-242.

Rijnsdorp AD and Witthames PR (2007) Ecology of Reproduction. pp. 68-93 *In* Gibson R (ed.) *Flatfishes: Biology and Exploitation.* Blackwell Science, Oxford, UK.

Ross JL, Stevens TM, and Vaughan DS (1995) Age, growth, mortality, and reproductive biology of red drums in North Carolina waters. Transactions of the American Fisheries Society, 124: 37-54.

Sainsbury KJ (1980) Effect of individual variability on the von Bertalanffy growth equation. Canadian Journal of Fisheries and Aquatic Sciences, 37: 241-247.

Schill DI and Kline PA (1995) Use of random response to estimate angler noncompliance with fishing regulations. North American Journal of Fisheries Management, 15: 721-731.

Sullivan MG (2002) Illegal angling harvest of walleyes protected by length limits in Alberta. North American Journal of Fisheries Management, 22: 1053-1063.

Terceiro M (2002) The summer flounder chronicles: science, politics, and litigation, 1975-2000. Reviews in Fish Biology and Fisheries, 11: 125-168.

Terceiro M (2011) Stock assessment of summer flounder for 2011. US Dept. Commer, Northeast Fish Sci Cent Ref Doc. 11-20; 141 p. [http://www.nefsc.noaa.gov/publications/]

Wang Y-G, Thomas MR, and Somers IF (1995) A maximum likelihood approach for estimating growth from tag-recapture data. Canadian Journal of Fisheries and Aquatic Sciences, 52: 252-259.

Wang Y-G (1998) An improved Fabens method for estimation of growth parameters in the von Bertalanffy model with individual asymptotes. Canadian Journal of Fisheries and Aquatic Sciences, 55: 397-400.

Zar JH (1999) Biostatistical analysis. 2nd ed. Prentice-Hall, Englewood Cliffs, N.J.

Zhang Z, Lessard J, and Campbell A (2009) Use of Bayesian hierarchical models to estimate northern abalone, *Haliotis kamtschatkana*, growth parameters from tag-recapture data. Fisheries Research, 95: 289-295.

Table 1. Precision of length measurements for summer flounder released by Virginia Game Fish Tagging Program participants and recaptured fish that were subsequently reported. Precision is categorized by the whole inch, half inch, and other (i.e., more precise units such as quarter or eighth inches). All fish were released within Chesapeake Bay from 2000 to 2011.

Measurement Precision	Number (%)	
	Releases	Recaptures
inch	23645 (49.8)	1728 (49.7)
half inch	14422 (30.4)	1047 (30.1)
other	9446 (19.9)	699 (20.1)

Table 2. Parameter estimates, number of parameters (npar), and AIC model selection criteria (AIC, ΔAIC, and AICw) for growth models fit to 3474 summer flounder released within Chesapeake Bay from 2000 to 2011 and subsequently recaptured and reported to the VGFTP. Structure of growth models and error terms are described in text. Estimated parameters are asymptotic maximum length (L_∞), length at which growth coefficient changes (L^*), growth coefficient for models with one growth phase or for fish smaller than L^* (k_1), growth coefficient for fish larger than L^* (k_2), individual growth variability parameter (β), constant error or trained tagger measurement error (σ_m), untrained angler measurement error (σ_a), and process error linearly related to time at liberty (σ_p). The standard error for each estimated parameter is shown in parentheses.

Model	Error	L_∞	L^*	k_1	k_2	β	σ_m	σ_a	σ_p	npar	AIC	ΔAIC	AIC_w
Fabens	1	56.82 (1.58)	-----	0.38 (0.04)	-----	-----	3.31 (0.04)	-----	-----	4	18177	347	0
Fabens	2	52.41 (2.24)	-----	0.59 (0.09)	-----	-----	-----	-----	11.01 (0.13)	3	18970	1140	0
Fabens	3	55.45 (1.69)	-----	0.43 (0.05)	-----	-----	3.07 (0.06)	-----	2.62 (0.27)	4	18136	306	0
Fabens	4	56.57 (1.57)	-----	0.38 (0.04)	-----	-----	2.15 (0.05)	1.44 (0.07)	-----	4	17910	80	0
Fabens	5	55.52 (1.65)	-----	0.42 (0.04)	-----	-----	1.92 (0.06)	1.49 (0.08)	2.31 (0.23)	5	17865	35	0
Hearn and Polacheck	1	69.99 (7.31)	33.99 (0.22)	0.33 (0.06)	0.19 (0.05)	-----	3.29 (0.04)	-----	-----	5	18151	321	0
Hearn and Polacheck	2	59.27 (5.74)	34.52 (0.76)	0.49 (0.1)	0.35 (0.11)	-----	11.00 (0.13)	-----	-----	5	18971	1141	0
Hearn and Polacheck	3	65.01 (4.44)	33.98 (0.58)	0.39 (0.05)	0.24 (0.05)	-----	3.08 (0.05)	-----	2.46 (0.27)	6	18116	286	0
Hearn and Polacheck	4	69.11 (5.61)	33.5 (0.44)	0.34 (0.05)	0.2 (0.04)	-----	2.14 (0.05)	1.44 (0.07)	-----	6	17880	50	0

Table 2 cont.

Model	Error	L_∞	L^*	k_1	k_2	β	σ_m	σ_a	σ_p	npar	AIC	ΔAIC	AIC$_w$
Hearn and Polacheck	5	70.00 (7.11)	34.55 (0.44)	0.32 (0.06)	0.19 (0.05)	-----	1.94 (0.06)	1.48 (0.07)	2.15 (0.23)	7	17843	12	0.002
Wang	1	47.68 (1.15)	-----	0.78 (0.1)	-----	0.52 (0.06)	3.3 (0.04)	-----	-----	4	18153	323	0
Wang	2	44.2 (1.73)	-----	1.27 (0.29)	-----	0.59 (0.11)	-----	-----	10.99 (0.13)	4	18963	1133	0
Wang	3	45.45 (1.02)	-----	1.04 (0.15)	-----	0.6 (0.06)	3.05 (0.05)	-----	2.63 (0.26)	5	18108	277	0
Wang	4	47.83 (1.18)	-----	0.75 (0.1)	-----	0.51 (0.07)	2.15 (0.05)	1.43 (0.07)	-----	5	17888	58	0
Wang	5	46.4 (1.15)	-----	0.9 (0.13)	-----	0.55 (0.07)	1.93 (0.06)	1.47 (0.08)	2.29 (0.23)	6	17843	13	0.002
Wang – L*	1	51.59 (2.31)	34.57 (0.52)	0.77 (0.12)	0.47 (0.09)	0.63 (0.09)	3.28 (0.04)	-----	-----	6	18133	303	0
Wang – L*	2	45.22 (2.47)	34.34 (1.21)	1.24 (0.32)	1.01 (0.34)	0.64 (0.13)	-----	-----	10.99 (0.13)	6	18965	1135	0
Wang – L*	3	48.87 (1.66)	34.13 (0.13)	0.94 (0.12)	0.61 (0.11)	0.66 (0.08)	3.07 (0.05)	-----	2.44 (0.26)	7	18098	268	0
Wang – L*	4	52.78 (2.77)	34.69 (0.49)	0.69 (0.12)	0.41 (0.09)	0.62 (0.1)	2.14 (0.05)	1.43 (0.07)	-----	7	17866	36	0
Wang – L*	5	50.17 (2.42)	34.69 (0.56)	0.81 (0.14)	0.52 (0.12)	0.65 (0.1)	1.94 (0.06)	1.47 (0.07)	2.13 (0.23)	8	17830	0	0.997

Table 3. Estimates of von Bertalanffy growth model parameters for summer flounder from individual length-at-age data.

Source	Date	Calcified Structure	Sex	L_∞ (cm)	k (yr)	t_0
Shepherd 1980	1977-1978	otoliths	both	96.88	0.16	-0.01
Shepherd 1980	1977-1978	scales	both	116.32	0.13	-0.16
Fogarty 1981	1976-1979	scales	male	72.72	0.18	-0.26
Fogarty 1981	1976-1979	scales	female	90.61	0.16	0.05
Anonymous 1986	1976-1983	scales	male	67.49	0.18	-1.66
Anonymous 1986	1976-1983	scales	female	82.67	0.17	-1.04
Desfosse 1995	1987-1990	scales	male	55.87	0.33	-0.79
Desfosse 1995	1987-1990	scales	female	75.78	0.29	-0.53
Desfosse 1995	1987-1990	scales	both	85.90	0.22	-0.69
Brust 2008*	1999-2006	unknown	male	65.25	0.23	-1.50
Brust 2008*	1999-2006	unknown	female	78.49	0.22	-1.12

*parameters were estimated using mean length at age data

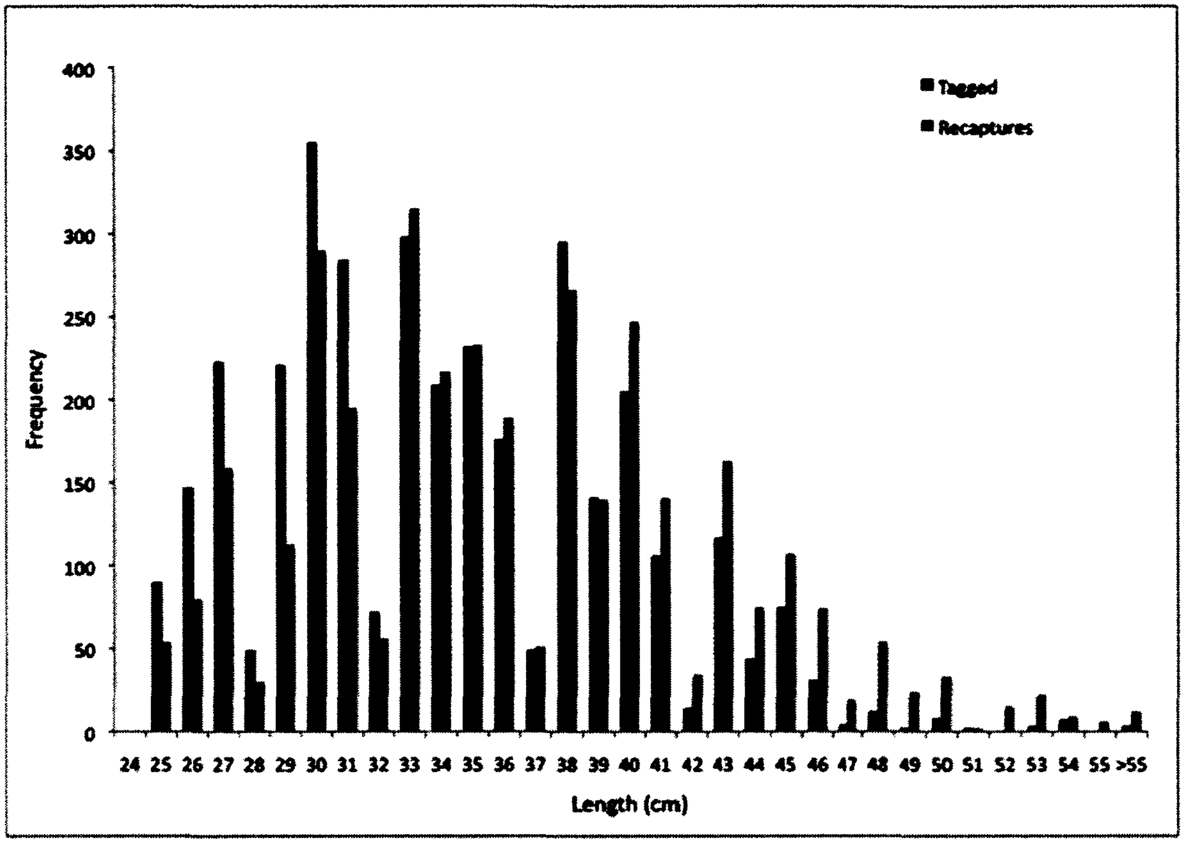


Figure 1. Length frequency of recaptured summer flounder at the time of tagging (black bars) and recapture (gray bars). All fish were tagged in the Chesapeake Bay between 2000 and 2011 by participants in the Virginia Game Fish Tagging Program.

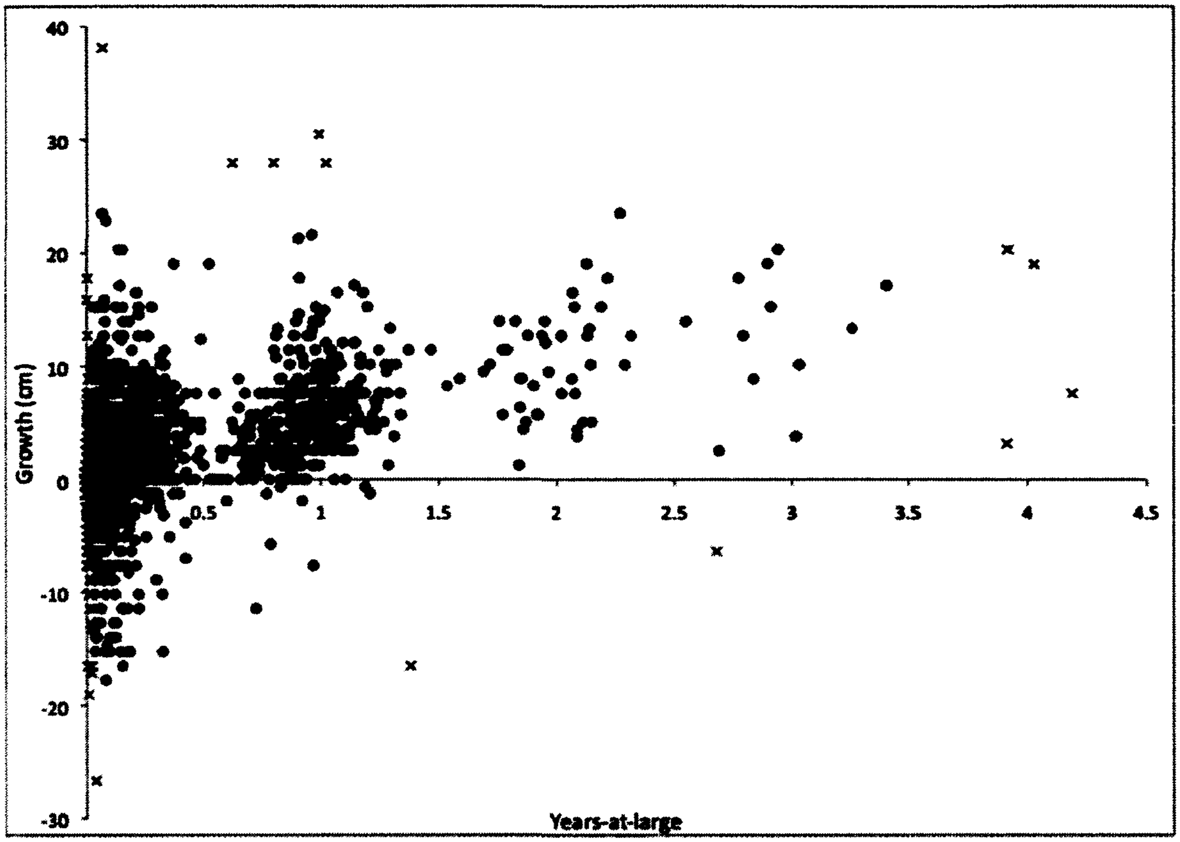


Figure 2. Observed growth (cm·yr^{-1}) of summer flounder based on reported length at tagging and recapture. Fish were tagged and released in Chesapeake Bay between 2000 and 2011. Data excluded from the growth model are plotted as (x); these data were excluded because fish were at liberty: 1) less than 10 days, 2) less than 6 months and the release and recapture lengths differed by more than 25 cm, 3) more than 1 year and the release length exceeded the recapture length by more than 5 cm, or 4) more than 4 winters.

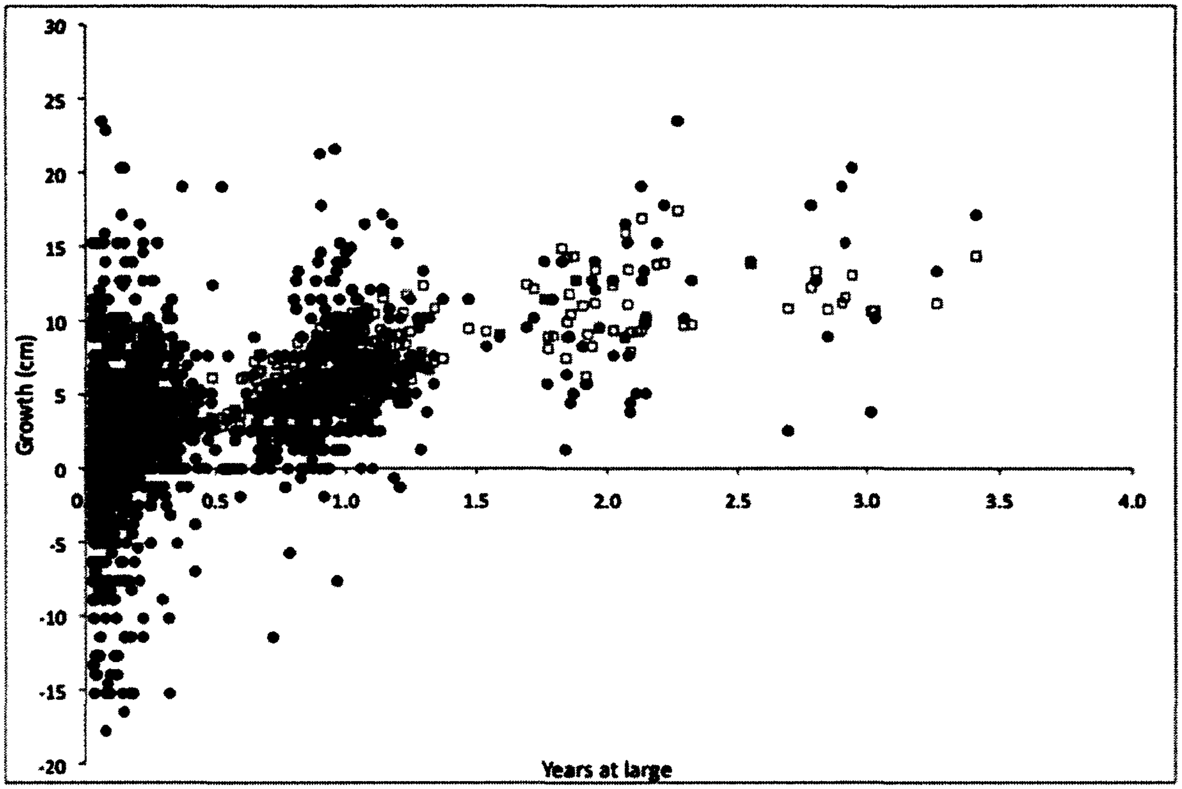


Figure 3. Observed summer flounder growth (cm·yr^{-1}) based on reported lengths at time of tagging and recapture (black circles) and the Wang-L* growth model predictions (gray open squares). All fish were tagged and released in Chesapeake Bay from 2000 to 2011.

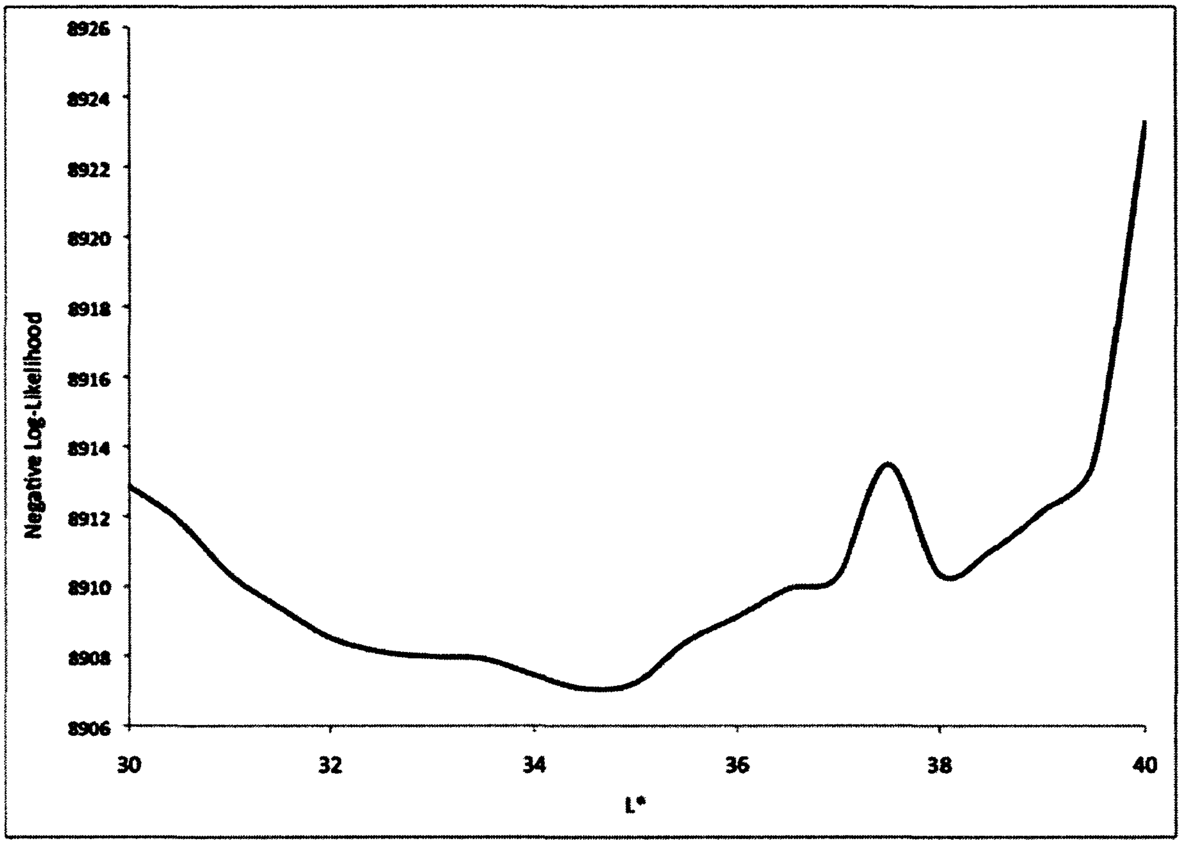
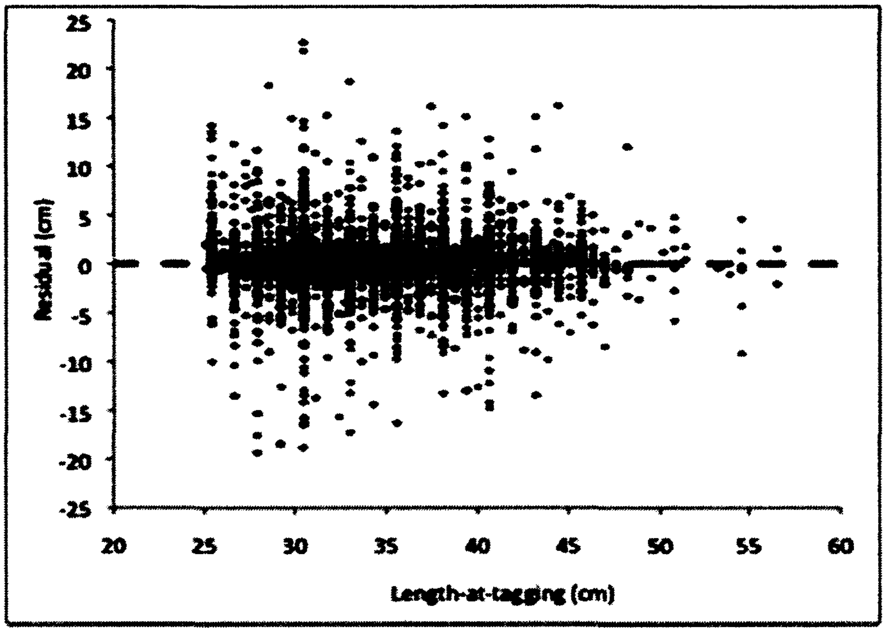


Figure 4. Likelihood profile plot for the length at which von Bertalanffy growth coefficients changed (L*) based on the Wang – L* model for summer flounder tagged by participants in the Virginia Game Fish Tagging Program (2000-2011). The negative log-likelihood values are those calculated when the L* parameter is held constant and all other parameters are estimated.

a)



b)

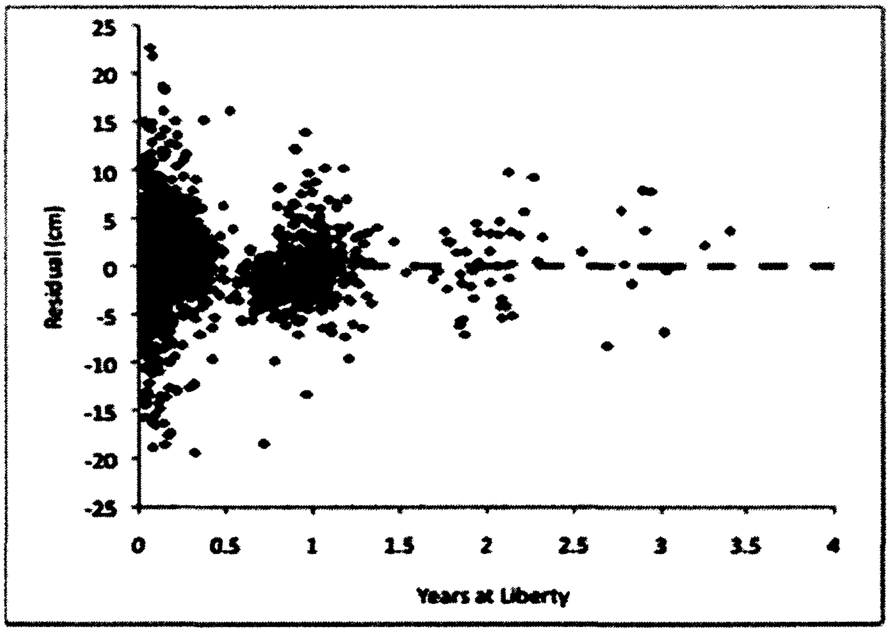


Figure 5. Residuals from the Wang – L* model for summer flounder growth increments estimated from lengths at release and recapture. Residuals are plotted against (a) length at time of tagging (cm), and (b) years at liberty. The zero line, around which all residuals should be centered, is shown as a dashed gray line in both plots. All fish were released in Chesapeake Bay from 2000 to 2011 by participants in the Virginia Game Fish Tagging Program.

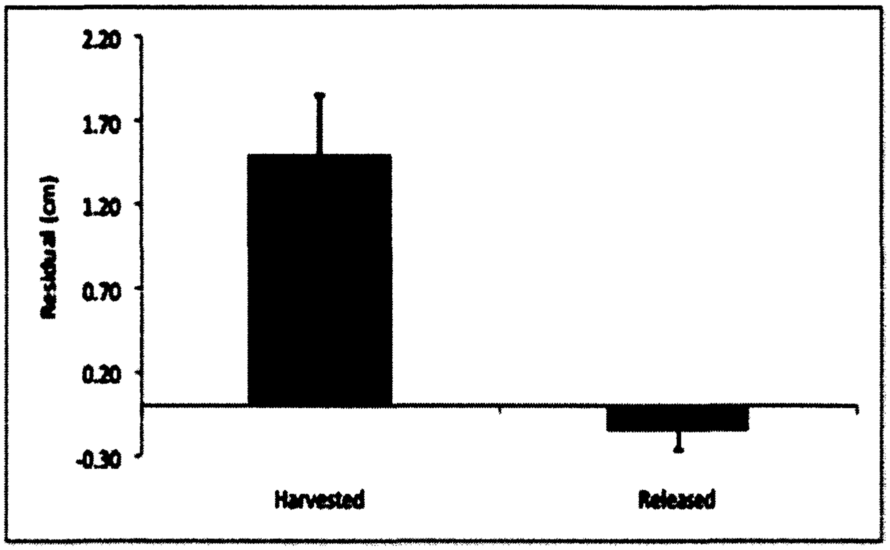
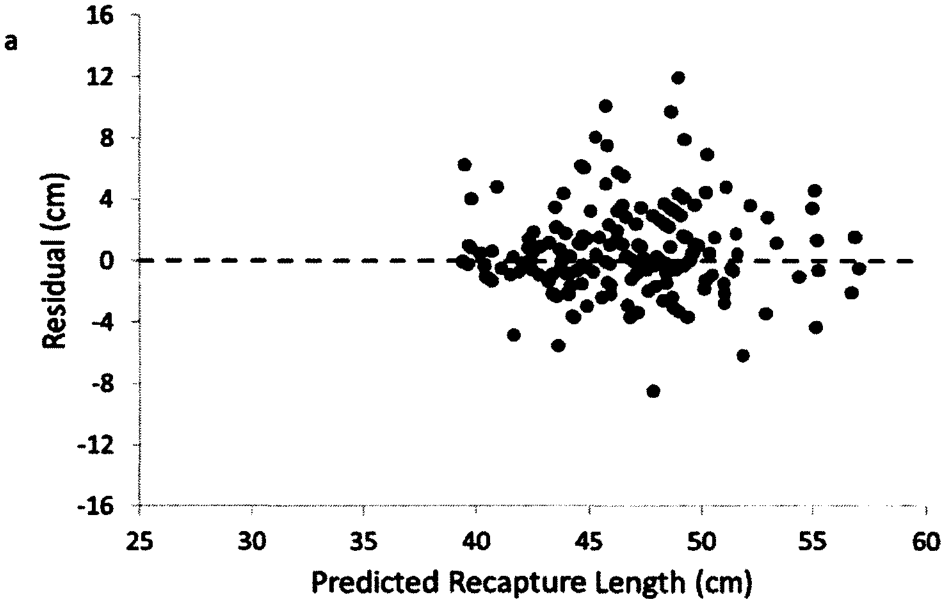


Figure 6. Mean residuals from the Wang-L* growth model for summer flounder tagged in Chesapeake Bay by participants in the Virginia Game Fish Tagging Program (2000-2011). Residuals are shown for individuals that were harvested (n = 449) and released (n= 3025). Error bars are 95% confidence intervals on the mean.



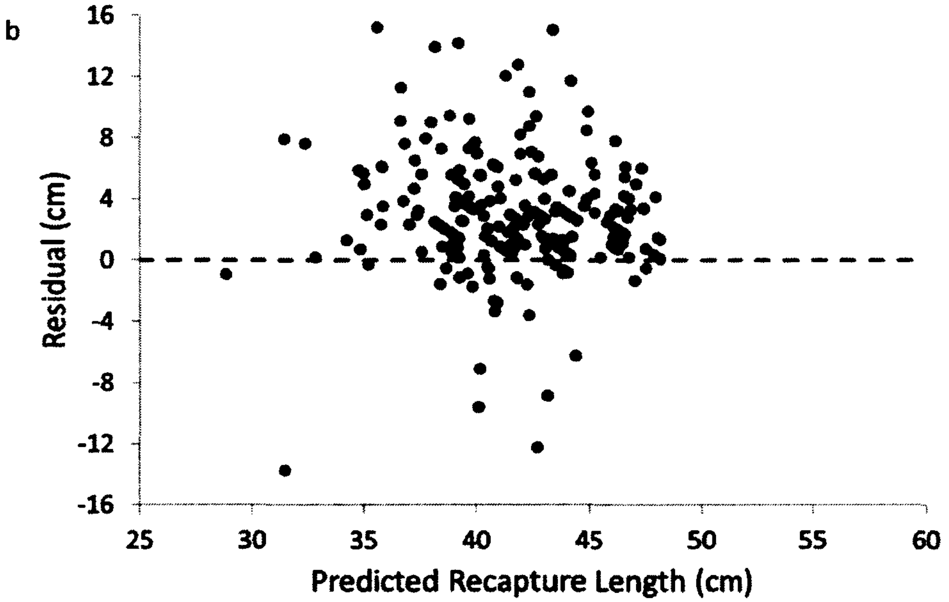


Figure 7. Residuals from the Wang – L* growth model for summer flounder harvested between 2000 and 2011 that were: (a) predicted to be of legal size at time of recapture (n = 183), and (b) predicted to be of sublegal size at time of recapture (n = 215). The zero line, around which all residuals should be centered, is displayed as a dashed gray line in both plots.

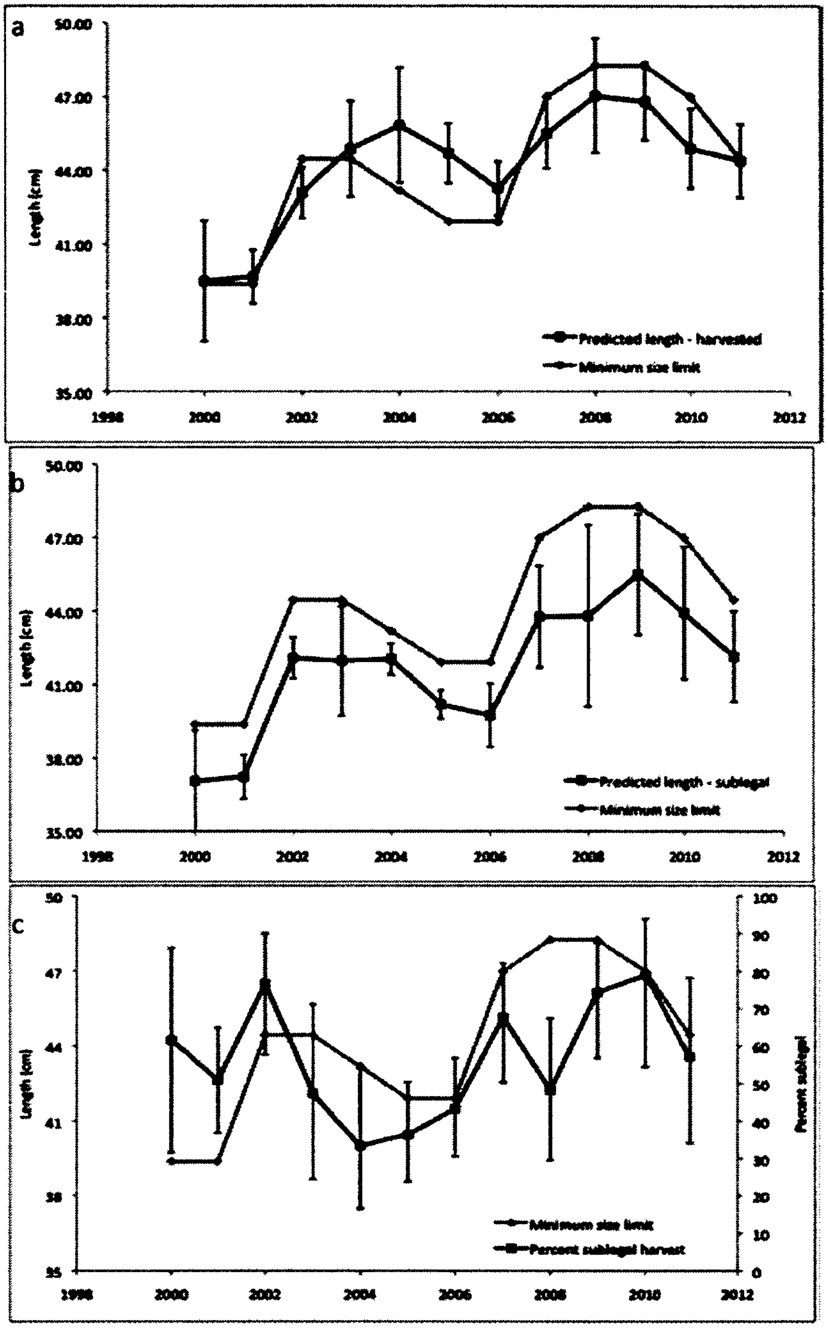


Figure 8. The minimum size limit for summer flounder in the Virginia recreational fishery between 2000 and 2011(gray line) and (a) mean predicted length of harvested fish reported to the Virginia Game Fish Tagging Program (VGFTP; black line), (b) mean predicted length of harvested fish reported to the VGFTP that were predicted to be of sublegal size at time of recapture (black line), and (c) percent of harvested fish reported to the VGFTP that were expected to be of sublegal size at time of recapture (black line). Error bars are 95% confidence intervals on the mean.

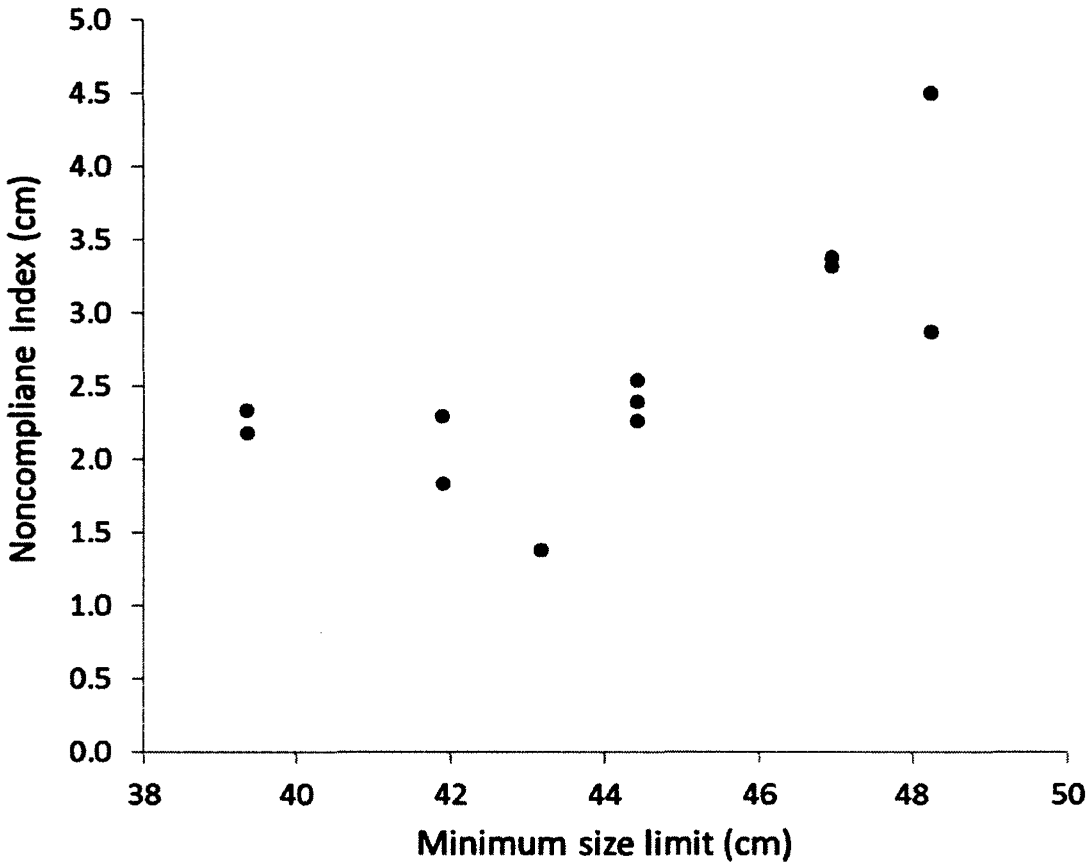


Figure 9. Effect of changes in the minimum size limit for summer flounder in Virginia waters on the noncompliance index (calculated as the difference between the minimum size limit in Virginia and the mean predicted length of sublegal fish harvested by recreational anglers in a given year; see figure 8b). Data are from summer flounder released and recaptured between 2000 and 2011. The noncompliance index represents the mean increment below the minimum size limit that anglers were willing to harvest summer flounder.

CHAPTER 4

Estimation of Summer Rlounder (*Paralichthys dentatus*) Mortality Rates Using Mark-Recapture Data from a Recreational Angler Tagging Program

Abstract

Tagging programs that rely on volunteer anglers to tag fish have the potential to become a valuable tool for researchers interested in estimating mortality rates. Standard tagging models (e.g., Cormack-Jolly-Seber) cannot be used to estimate mortality rates from mark-recapture data collected by angler tagging programs because the design of these programs violates the assumption that fish are released and recaptured instantaneously. It is possible to address this assumption violation by: 1) using tagging models that allow encounters of individuals to occur continuously after release, and 2) adjusting parameter estimates (e.g., survival rates) for variations in an individual's release date. We apply this approach to summer flounder mark-recapture data collected by an angler tagging program in Virginia. Since summer 2000, recreational anglers tagged and released 47513 summer flounder in Virginia waters of Chesapeake Bay, and 3240 of these fish were subsequently encountered. To account for heterogeneity in survival rates arising from size-based variation in fishing pressure, we categorized individuals into size states and used a growth model to predict recruitment of fish into each size state. Due to concerns regarding tag loss, a double-tagging study was conducted from 2009-2011 and revealed that summer flounder tag retention rates were low (0.5 ± 0.08 per year). After correcting for tag loss, the estimated mortality rates for the 30-day period following release were approximately 60% for sublegal fish (< 36 cm) and 65% for larger fish. After compensating for short-term (30-day post-release) mortality, we found that sublegal summer flounder experience greater annual mortality rates than larger fish. This may reflect actual differences in mortality or may reflect an increased likelihood of permanent emigration of smaller fish to locations with reduced encounter probabilities. We conclude that angler-tagging projects are a cost- effective way to gain insight on fish mortality rates, but that assumption violations of standard mark-recapture models must be addressed and an adequate number of recaptures must be available to permit reasonable precision of the mortality estimate obtained from such data.

Introduction

Summer flounder are one of the most targeted recreational and commercial fish species on the U.S. east coast, making effective management essential for the sustainability of this species (Terceiro 2002). For an exploited population, estimates of the fishing mortality rate as well as estimates of the natural mortality rate are necessary for determining the status of the stock and are critical to development of effective fisheries management plans. The instantaneous natural mortality rate (M) is the rate at which individuals are removed from the stock due to reasons other than exploitation (e.g., death, predation, permanent emigration, etc.). The estimate of M is directly related to several key outputs of the stock assessment including: stock productivity, optimal exploitation rate, and the target spawning stock biomass. Estimation of M is notoriously difficult because *in situ* natural mortality processes cannot be observed directly, and currently M is one of the greatest uncertainties in the summer flounder stock assessment (Maunder and Wong 2011). To date, stock assessment scientists have used a value for M estimated from longevity data or life history characteristics (i.e., growth parameters, reproductive effort, maximum size); however, none of these life-history-based methods were specifically designed to estimate M for summer flounder (Maunder and Wong 2011). In this study, we attempt to estimate natural and fishing mortality rates for summer flounder using mark-recapture data collected by a recreational angler tagging program.

If designed and analyzed properly, tagging studies are one of the most reliable methods of estimating M (Maunder and Wong 2011). The natural mortality rate of a population open to births, deaths, and migration is estimated with the Cormack-Jolly-Seber (CJS) mark-recapture model (Pollock et al. 1990, Lebreton et al. 1992). The CJS model uses recapture histories of marked cohorts of fish to estimate capture and survival probabilities. Over the past few decades the basic form of the CJS model has been generalized to allow encounters of fish from sources other than scientific research surveys (Burnham 1993, Barker 1997, Barker et al. 2004). For example, Burnham (1993) developed a model that allowed live recaptures of individuals during tagging operations and dead recoveries of animals that were killed (i.e., harvested) in between tagging occasions. The Burnham (1993) model was further extended to allow live resightings (e.g., catch and release) of animals between tagging occasions (Barker 1997, Barker et al. 2004). Although the Barker model (Barker 1997, Barker et al. 2004) is extremely versatile, it has been implemented only rarely (Hall et al. 2001, Slattery and Alisauskas 2001, Casale et al. 2007). One benefit of permitting the use of data from multiple sources (live/dead encounters) is that the estimates of the model parameters (such as survival rates) will generally be more precise (Lebreton et al. 1995, Barker 1997, Barker et al. 2004). An additional benefit is that it is no longer a requirement for the researcher to conduct the tagging operations and to recapture tagged individuals, thereby providing an opportunity to utilize data collected by non-researchers, including commercial and recreational (e.g., angler tagging programs) fishers.

Recreational angler tagging programs have multiple advantages, as well as some disadvantages, relative to mark-recapture studies that rely on scientists to tag, release, and recapture individuals. Compared with the costs of scientific personnel and vessel time, angler tagging programs are relatively inexpensive. The major costs in operating these studies consists of maintaining the tagging database, conducting training workshops, and purchasing tags, tagging equipment, and rewards (Lucy and Davy 2000, Gillanders et al. 2001). In addition, the large number of volunteers that participate in these programs may be able to release a greater number of fish than would be logistically possible with scientific personnel alone (Lucy and Davy 2000). Furthermore, angler participants generally capture and release individuals in multiple locations, providing the opportunity to investigate movement and survival of fish released in different areas (Lucy and Davy 2000, Gillanders et al. 2001). Finally, involving anglers in research projects enhances the relationship between the angling community and the research or management organization (Lucy and Davy 2000). In our experience, this familiarity with the program increases the likelihood that anglers will report encounters of tagged fish, providing increased numbers of recapture reports that are useful for movement and survival analyses. One of the disadvantages of angler tagging programs is that the quality of the data reported by recreational fishers may not meet scientific standards. For example, volunteer anglers that participate in these programs may not measure the size of the tagged fish with the precision preferred by researchers (Gillanders et al. 2001; Chapter 3). Despite these potential data quality issues, we believe that most data collected by angler tagging programs are useful for survival analyses as long as the assumptions of the selected statistical model are not violated.

In this paper, we used a Barker model (Barker 1997, Barker et al. 2004) to estimate mortality rates for summer flounder using tagging data from a recreational angler tagging program. The data were collected between 2000 and 2011 by the Virginia Game Fish Tagging Program (VGFTP), which utilizes trained volunteer anglers (approximately 200 per year) to tag and release game fishes within Virginia waters (Lucy et al. 2002). One of our goals was to provide guidance on ways to address tagging-model assumption violations when using mark-recapture data from angler tagging programs. With that goal in mind, we estimated mortality rates for different size classes of summer flounder tagged within Chesapeake Bay and explored potential management implications of these estimates.

Methods

Angler Tagging Program

The Virginia Game Fish Tagging Program (VGFTP) trains volunteer anglers to measure, handle, and tag 10 species of popular game fishes during their normal fishing activities (Lucy et al. 2002). All volunteer taggers are provided with tagging equipment and data sheets to record information pertinent to their releases, such as tag number, species, date, total length, release location, and release condition. These data are submitted to the VGFTP and compiled in a searchable database. Because taggers are primarily recreational anglers, all the tagged fish were captured by hook-and-line. All summer flounder were tagged with a t-bar anchor tag (Hallprint) inserted in the dorsal musculature near the tail. Each tag was labeled with a unique identifying number, a phone number to report recaptures, and a reward notice. Rewards consisted of t-shirts, tackle boxes, and pewter pins and served to encourage commercial and recreational fishers to report their recaptures.

Data collected by the VGFTP from 2000-2011 were examined for reliability prior to analysis. For example, release data were deleted if the reported tag number had not been distributed or if the tagger was uncertain about critical information related to the release (e.g., species, tag number, release date). If the tagger neglected to record the length of the fish upon release – which occurred only in 0.1% of the records used in this analysis - an individual's release length was estimated as the average length of at least five other summer flounder released within one week from the same region. We also omitted erroneous recapture data, such as encounters with fish that had been previously harvested by another angler. We restricted our analysis to fish larger than 25 cm that were tagged within Chesapeake Bay between May and October, which is the time that summer flounder are primarily resident in inshore habitats (Chapter 2). Fish smaller than 25 cm were excluded because they were recaptured in lower proportions than larger fish and we suspected that the smaller fish might be more susceptible to tagging- or handling-related mortality.

In the period 2000-2011 volunteer taggers working with the VGFTP released 47513 summer flounder within Chesapeake Bay, of which 3240 were subsequently encountered. At the time of tagging, the majority of fish were smaller than the recreational size limit (Figure 1; Table 1). Nearly half (47.7%) of the encounters occurred within 30-days of release and another 39.2% of encounters occurred within the remaining months of the release year (up to 12 months post-release). Only 1.9% of encounters occurred after the fish was at liberty through two or more winters (Table 1).

Tagging Model

Data from the VGFTP were analyzed using a Barker model (Barker 1997, Barker et al. 2004) because tagged fish were captured and released (hereafter referred to as a resighting) or harvested throughout the tagging year. A Barker model was used because the CJS model allows encounters of tagged individuals that occur only "instantaneously" during tagging operations (Seber 1982; Pollock et al. 1990; Lebreton et al. 1992). The Barker model includes parameters to estimate the probability of survival, harvest, resighting, and resighting before death (Figure 2). The resighting- before- death parameter is necessary to account for fish that die after being resighted but prior to the start of the next tagging season. Although the full Barker model includes additional parameters related to whether or not an individual is vulnerable to capture during tagging operations, those parameters are not pertinent to this study and are therefore not described here. The data input for this model are the encounter histories of marked individuals, which record the fate of each fish during each interval in the study. For this study, we used twelve intervals (i.e., years) ranging from May 1st of a given year through April 30th of the following year.

Parameter estimation using this implementation of the Barker model assumes: 1) all marked animals have the same probability of being resighted or harvested, 2) survival is equal for every marked animal, 3) survival rates are not influenced by tagging, 4) marks are not lost or overlooked, 5) the fate of each tagged fish is independent of the fate of other tagged fish, 6) resightings are independent events that have no influence on subsequent survival (Seber 1982, Pollock et al.

1990, Lebreton et al. 1992, Barker et al. 2004). We consider how data collected by angler tagging programs may violate each of these assumptions throughout this paper.

Within the first year after tagging, we hypothesized that all model parameters were influenced by a fish's release date. For example, a fish released in October 2001 would be less likely to be resighted prior to the start of the next interval (May 2002) compared with a fish released in June 2001. To incorporate such a relationship, we included the release date of each fish as a covariate in the model and estimated the parameter of interest (e.g., survival rate) using a generalized linear model with a logit link:

$$S_i = \frac{1}{1 + e^{-(\beta_0 + \beta_1 (t_i))}} \tag{1}$$

where S_i is the survival of the i^th^ individual, β_0 and β_1 are the intercept and slope of the regression, and t_i is the release date of the i^th^ individual. A similar approach was used to estimate survival and encounter rates for sea turtles tagged and released throughout multiple months (Casale et al. 2007). A logit link is a common function used to model the effect of individual covariates on parameters estimated with mark-recapture models. Such parameters represent probabilities and the logit link conveniently constrains estimates of the apparent survival rate to values between 0 and 1 (Lebreton et al. 1992). Survival probabilities estimated from the generalized linear model were forced to increase during a given interval by restricting the regression slope (β_1) to positive values. This was done because fish released in the later portion of the tagging interval are more likely to survive to the start of the subsequent interval than fish released in the early portion of the tagging interval. We did not restrict the regression slope of the encounter parameters. Variances of the parameters estimated with the generalized linear model were calculated using the delta method. This method is based on a first-order Taylor series expansion and approximates the variance of a parameter that is the function of other random variables, each with their own estimate of variance (Seber 1982, Powell 2007). The delta method is an appropriate method to approximate variances assuming that the transformation is linear over the expected range of the parameter (Powell 2007), which we assume is true for our data. The parameter and variance estimates reported in this study are those corresponding to the first day of the tagging interval (i.e., May 1st). By arbitrarily setting this date equal to zero, the slope parameter of the logit link function could be eliminated from the delta method variance calculation.

Data collected by the VGFTP violated the Barker model assumption that all individuals have the same probability of survival and harvest, because the smallest fish in the study were not subject to (legal) harvesting and hence, were not susceptible to fishing mortality. In addition, minimum- size- limit regulations differed for commercial and recreational fishers in Virginia. Throughout this study (2000-2011) the minimum size for the commercial fishery remained at 36 cm whereas the minimum size for the recreational fishery ranged from 39 to 48 cm (Table 2). Due to differences in minimum size limits among these sectors, fish of different lengths had different probabilities of harvest and were also expected to have different survival probabilities. To accommodate these differences in survival and harvest rates, we partitioned the data into three groups based on size: 1) smaller than the commercial size limit, 2) larger than the commercial size limit but smaller than the recreational size limit, and 3) larger than the recreational size limit. We used the Wang – L* growth model (Chapter 3) to determine the interval in which each fish became vulnerable to the commercial and recreational fisheries. In a few instances, the reported recapture length indicated the fish was in a size class different than that predicted by the growth model. When this occurred, we used the size class reported for the recapture, rather than the model-based designation. Multi-state models have previously been used to investigate the influence of animal size on survival probabilities (Nichols et al. 1992, Kendall and Nichols 2002), but a multi-state Barker model has not yet been described. Furthermore, due to the increased number of parameters required for a multi-state model, and the low number of encounters of fish at liberty for more than 2 years, data collected by the VGFTP may not be sufficient to fit a multi-state model. The deterministic growth model that we employed may artificially reduce the variance of our estimated parameters over those estimated with a multi-state model. We do not suspect this was a large concern because we used the growth model only to predict the interval (i.e., year) in which a fish became vulnerable to each fishing sector, thus, our predictions of growth did not need to be highly precise.

One important benefit of partitioning the tagging data into size classes was that it provided a means to estimate summer flounder natural and fishing mortality rates because each size class experienced different levels of fishing pressure. The smallest size class was not subject to fishing mortality, so the estimated total apparent survival probability for this size class could be used to estimate an instantaneous natural mortality rate (M) for summer flounder. Finite survival probabilities (S) estimated with the Barker model for all size classes were converted to instantaneous total mortality rates (Z) by the well-known relationship:

$$Z = -\ln(S) \tag{2}$$

We hypothesized that the instantaneous fishing mortality rate could be estimated as the difference between the estimate of M and the estimates of Z obtained from the larger size classes. This approach assumes that the instantaneous natural and fishing mortality rates are additive and that natural mortality rates were constant for all size classes, which are common assumptions in the fisheries literature. We assumed that sublegal fish (< 36 cm) that were reported as dead upon recapture were not intentionally killed and harvested. We believe this was a reasonable assumption because recreational anglers generally exaggerated the length of sublegal fish that were harvested and reported to the VGFTP (Chapter 3); thus, fish that were killed and reported as sublegal were most likely incidental mortalities. This assumption also allowed us to reduce the number of parameters in the model because the harvest probability for sublegal fish could be constrained to be zero. Fish were also considered incidental mortalities based on remarks provided by anglers in their recapture report (e.g., gut-hooked fish). Incidental mortalities, as well as fish whose tags were removed prior to release, were treated as though they were resighted but the probability of future encounters for these fish was set equal to zero (Barker et al. 2004).

In addition to the known violations of the Barker tagging model described above, we also investigated the combined effect of handling and tagging on summer flounder survival rates. One common method of estimating tagging-related mortality is to estimate an additional parameter for the survival rate within the release year and compare that estimate with estimates of survival for fish released in previous years (i.e., comparing survival rates during a given year for two or more cohorts of tagged fish; Burnham et al. 1987). We could not use this approach with the VGFTP data because a negligible number of encounters occurred after fish were at large for more than 2 years (Table 1). Thus, we did not have confidence in our mortality estimates during years following the release year. Due to this limitation, we divided the release year into two intervals, each with its own estimate of survival and encounter probabilities. This approach allowed us to estimate mortality associated with the handling and tagging process during a short period following the initial release. The first interval, referred to as the tagging interval, was designated as the 30-day period following release; we assumed that all tagging-related mortality would occur within this interval. The second interval comprised the remainder of the year (days 31 to 365) and will hereafter be referred to as the release year. We formulated the model to allow us to test the hypothesis that survival during the tagging interval was different from the average monthly survival observed in the release year. If this hypothesis is not rejected, then handling mortality is insignificant or could not be detected with the data in hand. If handling mortality was insignificant, then the overall model could be simplified by removing this parameter. If survival in the tagging interval differed significantly from monthly survival during the remainder of the release year, then we used the survival estimate for the remainder of the release year to calculate the annual survival probability. We adjusted the release year survival probability to an annual survival probability using:

$$S_i' = S_i^{\frac{12}{11}} \tag{3}$$

where S_i' is the annual survival for interval (*i*), and S_i is the survival for release year interval (*i*) estimated by the Barker model. The fraction in the exponent was necessary because we are using a survival probability estimate from the release year interval, which is 11 months in duration, to calculate a survival probability for a full year (12 months).

Due to the potential biases associated with tag loss (Arnason and Mills 1981), a double- tagging experiment was conducted from 2009-2011 to estimate tag loss rates for the t-bar anchor tags applied by VGFTP taggers. This experiment was implemented by seven VGFTP taggers who volunteered to tag summer flounder with a Petersen disc tag in addition to the standard t-bar anchor tag used by the VGFTP. Due to the small number of encounters of tagged fish from the double-tagging experiment, data were pooled among the seven taggers. Retention rates for the t-bar tags were calculated as the proportion of double-tagged flounder encounters that retained a t-bar tag. These proportions were estimated separately for sublegal fish (<36 cm) and legal-sized fish (>36 cm); we had insufficient data to estimate tag retention rates for all three size classes. To determine when tag loss occurred, we calculated the proportion of fish that retained tags within the first 10 days at liberty, within the remainder of the first 30 days at liberty, and then in each subsequent 30-day period. To ensure that the estimates of tag retention were not biased by small sample size, if at least 10 fish in a given size class were not recaptured in a given 30-day period, we pooled results with the subsequent month. Using this approach we identified five periods during which we could estimate tag retention: 1) less than 10 days, 2) 10-29 days, 3) 30-59 days, 4) 60-149 days), and 5) 150 or more days. For each period, we compared the proportion of fish that lost tags in the two size classes using a z-test. Survival rates estimated with the Barker model were corrected for tag loss with:

$$S'' = \frac{S}{\theta} \tag{4}$$

where S" is the tag-loss-adjusted survival rate, S is the survival rate estimate, and θ is the tag retention rate or 1 minus the tag loss rate (Pollock et al. 1990). As before, the delta method was used to calculate the variance of the adjusted survival estimates, S". This assumes that survival and tag loss rates are independent, which is a reasonable assumption because we used different data to estimate the two parameters (Pollock et al. 2007).

Parameter estimation and model selection

All parameters were estimated using maximum likelihood implemented with Automatic Differentiation Model Builder (ADMB; Fournier et al. 2011). The Barker model available in Program MARK assumes that fish remain in the same state (i.e., size class) throughout the experiment (Barker et al. 2004). Thus, we used ADMB to integrate the growth model, which allowed fish to grow into the next size class, into our analysis (Appendix IV). The growth model was used to determine the size class for each fish during each tagging interval (year), and the associated survival and encounter probabilities for that size class were used to build the likelihood. For tagging models, maximum likelihood estimation consists of constructing the multinomial likelihood that expresses the probability of observing a given encounter history as a function of the unknown parameters (Table 3, Table 4). Parameter estimates that maximize this likelihood function are determined iteratively. Because maximum likelihood is an asymptotic method, standard deviations of the parameters are estimated as the square root of the variances, which are estimated as the inverse of the Hessian matrix (i.e., the matrix of second derivatives; Lebreton et al. 1992). Simulated data were used to compare the results of the model coded in ADMB (excluding the growth model component) with results from Program MARK. In all cases, parameter estimates and standard deviations obtained from the ADMB code were identical to those produced by Program MARK. We also used simulated data that included growth to validate that the model coded in ADMB returned the correct parameter estimates.

Multiple models were fit to the summer flounder tagging data and Akaike's information criterion (AIC; Akaike 1973) was used to select the most appropriate model. The model permits each parameter (e.g., survival rate in the tagging interval) to vary by size class and time (year). In terms of size classes, we allowed each model parameter to either: 1) remain constant among size classes, 2) differ between sublegal fish (<36 cm) and legal fish (>36 cm), or 3) differ among the three size classes. Furthermore, each parameter included in the model was allowed to remain constant throughout the study (2000-2011) or to vary by year. With four rate parameters (i.e., survival, harvest, resighting, and resighting before death), each of which could vary by year and by size class during the tagging, release year, and post-release year intervals, we calculated that $1.96*10^{12}$ different parameter combinations was possible. The most complex of these models contained 649 parameters. Due to the large number of candidate models, we developed an approach to select the most appropriate model based on a set of reasonable hypotheses regarding summer flounder survival and encounter probabilities. We first fit a starting model that assumed all parameters were invariant with size class and time, with the exception of harvest probability, which was assumed to vary among the three size classes. We varied harvest probabilities by size class because sublegal fish were constrained to have a harvest probability of zero, whereas fish that were vulnerable to both commercial and recreational fishers had an increased harvest probability relative to fish that were subject to harvest in the commercial fishery only. In the starting model, we also estimated the probabilities of harvest and resighting in the release year as a function of release date using a logit link. This was done because fish released later in the year were at liberty for a shorter duration and therefore had a lower probability of harvest or resighting prior to the beginning of the following year. For the starting model, we did not assume that survival in the release year depended on release date because it is likely that mortalities primarily occurred during the winter and, thus, would not be influenced by the release date (recall that fish were released between May and October).

After fitting the starting model, we developed a series of potential models to address six questions: 1) does survival in the *release year* vary with release date, 2) how many size classes are needed to model survival and encounter probabilities in the *release year*, 3) how many size classes are needed to model survival and encounter probabilities in the *tagging interval*, 4) how many size classes are needed to model survival and encounter probabilities *after the release year*, 5) do survival and encounter probabilities in the *release year* vary inter-annually, and 6) do survival and encounter probabilities in the *tagging interval* vary inter-annually? Due to the paucity of releases (n=1169) and encounters (n=118) of fish in the largest size class, we could only fit models that allowed differences in the probabilities of survival and resighting between fish in the sublegal (<36 cm) and legal (>36 cm) size classes. Likewise, due to the lack of encounters of fish at liberty for more than two years, we did not construct models with time-varying survival and encounter probabilities in the post-release year intervals. For each of the above questions, the model with the lowest AIC value was selected and used as the base model for the subsequent question. Although this may not be the ideal procedure for identifying the most parsimonious model, the large number of possible models effectively precluded other approaches.

Results

Participants in the double- tagging study released a total of 2682 fish, of which 314 were subsequently encountered. A higher proportion of sublegal fish (<36 cm) retained their tags between 10 and 59 days compared with fish in the larger size classes (Figure 3). Between 10- and 29-days after release, 93% and 78%

of the sublegal and legal sized fish, respectively, had retained their t-bar tags (z=2.04, p=0.04). However, after fish were at liberty for more than 60 days, tag retention rates were comparable among size classes (Table 5). Based on this observation, we pooled the data for the different size classes after 60 days at liberty and, using the proportion of encountered fish (n=40) recaptured with a t-bar tag (n=20), calculated a tag retention rate of 0.5 ± 0.08. Tag retention rates were comparable for fish at liberty between 60-149 days and those at liberty for longer than 150 days, indicating that no chronic tag loss occurred after fish were at liberty for 60 days. However, it is difficult to make definitive conclusions regarding long-term chronic tag loss because of small sample sizes (e.g., only three double-tagged fish were recaptured after 365 days at liberty).

The most appropriate survival model contained multiple survival and encounter rates that varied among size classes but variations through time could not be detected for most model parameters (Table 6; Appendix IV). Within the tagging interval, the single parameter that was not influenced by fish size was the probability of being resighted before death. In addition, the probabilities of survival and resighting in the tagging interval varied throughout the 12 years of this study. Within the remainder of the release year, the probability of being resighted was the only parameter that was not different between the size classes. During the release year interval, the probability of a fish being resighted before death was the only parameter that varied by year. Perhaps not coincidentally, within the release year, the probability of being resighted before death was also the only parameter that did not depend on the release date of the fish. In many cases, models that used the generalized linear model to adjust survival rate estimates by date of release often produced non-positive definite Hessian matrices when the adjusted parameters were allowed to vary through time (Appendix IV), indicating a lack of sufficient data to estimate the parameters of the logit link model for each year of the study. Not surprisingly, the few recaptures after fish were at liberty for more than two years did not provide sufficient information to detect size-based differences in survival or encounter probabilities after the release year.

Apparent survival rates of summer flounder during the tagging interval were low and may have resulted from stress in response to the e handling and tagging process. Our results indicate that approximately 60% of sublegal fish, and 65% of larger fish, do not survive beyond the first 30 days after release. After correcting for tag loss in the first 30 days after release, the probability of a sublegal fish (< 36 cm) surviving the tagging interval ranged from 0.21 ± 0.08 to 0.66 ± 0.23 depending on year (mean = 0.40; Figure 4). Similarly, the tag-loss corrected estimate of the apparent survival probability for legal-sized fish (> 36 cm) ranged from 0.18 ± 0.09 to 0.50 ± 0.24 (mean = 0.35; Figure 4). In many years the estimates of survival in the tagging interval were comparable between the two size classes, but in some years the probability of survival was greater for the sublegal fish. This was a counterintuitive result because we expected that the smaller fish would be more susceptible to the stresses associated with the capture, handling, and tagging processes and thus would exhibit lower survival rates during the 30 days post-release.

Of the fish that survived the beyond the tagging interval, annual total mortality rates were greater for sublegal fish than for fish subject to fishing mortality. Using the estimate of survival probability in the release year, the tag-loss corrected instantaneous mortality rate for sublegal summer flounder was 1.37 yr^{-1}, whereas the tag-loss corrected instantaneous mortality rate for legal-sized summer flounder was 0.49 yr^{-1} (Figure 5). This is another counterintuitive result, but appears to be an accurate representation of the data. Throughout this study, a greater proportion of legal fish were encountered after the release year than sublegal fish (Figure 6). One explanation for this apparent difference in survival rates is that a larger proportion of sublegal fish permanently emigrated from Chesapeake Bay to locations with lower encounter rates. To investigate this *post-hoc* hypothesis, we calculated the proportion of sublegal and legal individuals that were recaptured outside of Virginia during the months that summer flounder generally occupy inshore habitats (May through October). Nearly 15% of the sublegal summer flounder, but only 8% of the legal-sized fish, were encountered outside of Virginia after the release year (Figure 7); these two proportions were significantly different ($z=1.98$, $p=0.047$). Although we received recapture reports from fishers throughout the east coast, it is probable that the reporting rate, and thus, encounter probabilities, were lower for locations outside of Virginia. Unfortunately, our model could not account for these heterogeneous encounter probabilities, which could result in reduced estimates of apparent survival rates because most of the fish that permanently emigrated would be considered losses and therefore, these individuals contributed to the estimate of apparent mortality.

Discussion

Our study demonstrated that data from volunteer angler tagging programs have great potential to aid in estimating fishing mortality rates, but that the weaknesses of the data must be considered and addressed in these analyses. Due to the design of the VGFTP, a number of the common assumptions of mark-recapture models were violated, making it difficult to accurately estimate the parameters of interest (i.e., survival). One of the assumptions violated was that marked individuals were released continuously throughout the tagging interval. A potential way of addressing this violation would have been to restrict the analysis to fish released during a brief time period (e.g., two weeks) at the beginning of each tagging year in the study. This would consequently result in ignoring the majority of the tagging data, and thus, reduce the precision of the estimates of survival and encounter probabilities. Our method of using a generalized linear model to adjust survival and encounter probabilities based on the release date makes use of all the data; however, we suspect that a consequence of using the release-date adjustment was that we were unable to estimate inter-annual variability of adjusted parameters. We also caution that the quality of the data from volunteer taggers does not always meet scientific standards. Though rare, on some occasions, volunteer anglers did not report all of the requested information (i.e., release location, release date, tagging length). Also, a small number of the reported encounters exhibited peculiarities. For example, a few fish were allegedly encountered nearly a month prior to the release date reported by the tagger. This may have been the result of a misread tag, poor record keeping by the tagger, or anglers misrepresenting the encounter to receive a reward. Although we are certain that some data have been compromised, we believe that most of the tagging and encounter data used in our analysis were accurate.

Summer flounder released by participants in the VGFTP exhibited low survival rates within 30 days of release. Average estimates of survival within the first 30 days of release were approximately 40% for sublegal fish and 35% for legal-sized fish. These rates are comparable to the rate reported in an unpublished report by the New York Department of Environmental Conservation. In that tagging study, the total survival probability for sublegal fish was reported to be 47% (Weber 1984, cited in Terceiro 2011). We suspect that the low survival rates observed in our study is primarily due to the stress associated with the capture and handling process rather than the tagging process, which is generally completed within one minute of the fish being landed. All fish included in this analysis were released between May and October, which are the months when the warmest water temperatures are recorded in the Chesapeake Bay. Increased water temperatures have often been associated with decreased catch-and-release survival rates of multiple species, with some studies reporting summer mortality rates greater than 80% (Muoneke and Childress 1994, Nelson 1998, Wilde et al. 2000, Bettinger et al. 2005, Gale et al. 2011). The recreational discard mortality rate for summer flounder used in the current stock assessment is 10% (Terceiro 2011), a rate that is based on experiments that estimated mortality within 72 hours of release (Malchoff et al. 2002). The 10% estimate of post-release mortality was supported by a study that observed the frequency of hooking-related injuries for summer flounder (Powell et al. 2011). Our results indicate that the recreational discard mortality may be higher than that used by stock assessment scientists, possibly because post-release mortality may not be manifested within 72 hours of release (e.g., Fabrizio et al 2008). In addition, post-release mortality may result from physiological stresses other than those associated with hooking injuries. We believe that further study is warranted to provide a more accurate estimate of post-release mortality from the recreational fishery. Given the potential for high post-release mortality rates, we also suggest that management policies to reduce discard mortality in summer flounder be considered. Results from a simulation study indicated that alternative management strategies such as slot limits or cumulative size limits could considerably reduce recreational discard mortality rates (Powell et al. 2010), but such approaches have not been implemented.

During the remainder of the release year, sublegal fish had considerably greater mortality rates than legal-sized fish. We had originally hypothesized that the total mortality rate estimated for the sublegal fish could serve as an estimate of the natural mortality rate for adult summer flounder, but our estimate of the instantaneous total mortality rate for sublegal fish ($Z_{sublegal}$=1.37) is unrealistically high and is considerably larger than the instantaneous total mortality rate of fish subject to fishing mortality (Z_{legal}=0.49). This suggests that sublegal and legal-sized fish experience different mortality rates, movement processes, or both. A *post-hoc* analysis of emigration indicated that sublegal fish exhibit a lower degree of site fidelity to Chesapeake Bay than larger fish. Thus, we postulate that the apparent mortality rates of sublegal fish may be higher because fish that have emigrated are encountered at lower rates than fish that return to Chesapeake Bay. We believe that reporting rates, and therefore encounter rates, are lower outside of Chesapeake Bay because the VGFTP is not advertised widely outside of Virginia.

Other potential explanation for the apparent high mortality rate of sublegal summer flounder is that these fish do not survive the stresses associated with the spawning migration in the fall/winter or experience high discard mortality rates after capture by the commercial trawl fishery. Summer flounder mature at about 1.5 years, when they reach a size of approximately 28-35 cm, and immature fish (juveniles) generally remain inshore during the winter months (Smith and Daiber 1977, Morse 1981, O'Brien et al. 1993, Chapter 3). This implies that many of the sublegal fish that were tagged and released by the VGFTP had yet to participate in an offshore spawning migration. If these fish attempted the spawning migration without sufficient energy reserves, they may experience greater mortality than larger conspecifics in better condition. Another potential explanation for the greater mortality rate observed for sublegal fish is the high discard mortality rate of these individuals from the commercial fishery that primary operates offshore during the winter. In the current stock assessment, the discard mortality rate of sublegal summer flounder captured by the commercial offshore trawl fishery is assumed to be 80% (Terceiro 2011), an estimate that is supported by a recent acoustic telemetry study (Yergey et al. 2012). Because of their lower swimming endurance capabilities, smaller flatfish may be more susceptible to capture in bottom trawl nets (Winger et al. 1999). Lower endurances and high discard mortality rates may contribute to the higher mortality rates of smaller summer flounder observed in this study. However, we suspect that these high observed mortality rates for sublegal summer flounder are not due to a single cause, but are more likely due to a combination of the hypotheses discussed above – permanent emigration, insufficient energy reserves, and high discard mortality rates.

Smaller summer flounder tagged in Chesapeake Bay are less likely than larger fish to return in subsequent years, implying that some juveniles use Chesapeake Bay only as a nursery area. Other researchers have suggested this based on the observation that small summer flounder tend to be recaptured in areas north of the area in which they were tagged (Poole 1962, Lux and Nichy 1981, Desfosse 1995, Kraus and Musick 2001, Chapter 2). Furthermore, Fogarty (1981) found that smaller fish (<30.5 cm) were generally absent from northern portions of their range, which is consistent with the hypothesis that eggs and larvae are passively carried primarily into bays and estuaries in the southern portion of the mid-Atlantic Bight (Rogers and van den Avyle 1983, cited in Kraus and Musick 2001). This suggests that southern bays and estuaries, such as Chesapeake Bay, act as sources of young fish (recruits) and that northern areas are sinks whose populations are partially maintained by nursery habitats to the south (Dias 1996). As such, southern bays and estuaries are essential fish habitat for juvenile summer flounder.

The emigration of both small and large summer flounder from the Chesapeake Bay suggests that a multi-state model may be required to estimate summer flounder mortality rates from tagging data. One assumption of the modified Barker model we applied is that survival and encounter rates are equal among individuals. As previously described, fish that permanently emigrate from the Chesapeake Bay may have lower encounter rates. These fish could have lower survival rates due to different minimum size limits in other coastal states; thus, individuals that are considered sublegal in Virginia may be legally harvested in other states, and vice-versa. These different minimum size limits result in heterogeneous harvest probabilities as well as heterogeneous survival rates for fish emigrating from Virginia. Our model does not address this heterogeneity, but a multi-state Barker model could be developed to estimate these probabilities for fish that remain within Virginia and for fish that emigrate from Virginia waters. Not only would a multi-state model provide more accurate estimates of survival and encounter probabilities, but such a model would also provide an estimate of the probability of emigration for different size classes of fish (Arnason 1973, Schwarz et al. 1993, Nichols and Kendall 1995, Lebreton and Pradel 2002, Conn et al. 2004). Of course, such a complex model would require an exceptional amount of data (most notably significantly more recapture records from Atlantic coastal states); it is not likely possible to fit such a model with the current data from the VGFTP.

Using estimates of the total mortality rate for legal-sized fish, it appears that the fishing mortality rate on summer flounder has been maintained at a reasonable level since 2000. Assuming that the instantaneous natural and fishing mortality rates are additive, and that the instantaneous natural mortality rate for legal sized fish is 0.25 (the mean rate currently used in the stock assessment; Terceiro 2011), we estimate that the instantaneous fishing mortality rate for legal-size fish (>36 cm) was approximately 0.24. This estimate is within the range of annual instantaneous fishing mortality rates estimated by the stock assessment from 2001 through 2010 (0.22 - 0.5; Terceiro 2011). Our estimated fishing mortality rate is slightly below the target fishing mortality of 0.254 recommended by the stock assessment review committee (NEFSC 2008), suggesting that management practices have been effective in maintaining exploitation at levels necessary to rebuild the stock.

One of the major sources of uncertainty in our analysis is the low tag retention rate (0.5 ± 0.08), which vastly reduces the precision of the estimates of summer flounder survival. High rates of tag shedding pose a difficult problem for researchers because the number of encounters after increasing periods at large is inversely proportional to the tag shedding rate – the higher the tag shedding rate, the lower the number of encounters with tagged fish. The precision of our estimated tag retention rate was somewhat low due to the small sample sizes in the double-tagging experiment from which these estimates were derived. This uncertainty is propagated into the survival estimates that are corrected for tag loss. Unfortunately, the high tag loss and imprecision of this estimate from this study resulted in survival estimates with large confidence intervals. One method that has been used to reduce the uncertainty due to the "propagation of error" is to incorporate tag-loss parameters into the likelihood model (Fabrizio et al. 1999, Conn et al. 2004, Cowen and Schwarz 2006). Unfortunately, as with the multi-state model, survival models that incorporate tag loss would require considerably more encounter data, from both single and double-tagged individuals, than are available from the VGFTP. Based on the estimates of tag loss that were observed in this study and the potential for angler-based tagging programs to exhibit high and variable tag loss rates, we recommend that researchers conduct independent tag-loss experiments, with multiple tag types (one of which should be a permanent tag or mark with 100% retention), prior to initiating an angler-tagging project. Such an approach will provide necessary guidance in the selection of the most appropriate tag type and tag placement, thereby providing better quality data for future analyses (Arnason and Mills 1981).

Another aspect of this research that requires further attention is the question of overdispersion of the data. Mark-recapture data may exhibit overdispersion due to a number of reasons, but researchers generally focus on the lack of independence between individuals as the source of overdispersion (Anderson et al. 1994). For example, fish from the same school are not independent and data collected from fish in the same school would be overdispersed. Although overdispersion will not bias the estimates of the parameters, the precision of the estimates will be overestimated (McCullagh and Nelder 1989); furthermore, model selection via AIC will tend to favor overfitted models (Anderson et al. 1994). One approach to correcting for overdispersion is to estimate the variance inflation factor (c-hat); however, estimation of c-hat is not straightforward in cases with multiple recapture events. One method that appears to offer the most promise in estimating the overdispersion in capture-recapture models is the median c-hat method (Cooch and White 1993). This method simulates data at increasing levels of overdispersion and compares a deviance metric from the simulated data to that estimated from the observed data. The value for c-hat is obtained from a logistic regression, where the binomial response is whether the simulated deviance metric is larger or smaller than the observed deviance metric and the predictor is the value of c-hat. Unfortunately, the median c-hat method cannot be applied to models that consider individual covariates, such as release date in our model. We suspect our data exhibit considerable overdisperion because: 1) the high rates of tag shedding reduced the number of fish encountered after two years at liberty and hence, the number of possible encounter histories considered by the model, and 2) individual tagger effects may be present, such as tagging-related mortality or differential tag loss, which could result in heterogeneous survival rates. We plan to use Program MARK to estimate the variance inflation factor for the VGFTP data and will subsequently use this estimate to adjust the estimated survival rate variances and to verify that we did not select an overfitted model.

We believe that additional research is required to estimate a natural mortality rate for summer flounder. We agree with the statement of Maunder and Wong (2011) that "a well designed and implemented tagging program may be the best approach to produce reliable estimates of M for summer flounder". Because CJS models cannot separately estimate natural and fishing mortality rates, we suggest using a Brownie-type model based on fish harvests throughout the US Atlantic coast (Brownie et al. 1985). For example, Jiang et al. (2007) developed a generalized Brownie model that, similar to the Barker model, allows fish to be encountered through harvesting or resighting. The natural and fishing mortality rate estimates derived from these models are highly dependent on the reporting probabilities, which can be estimated using a high reward tagging study (Pollock et al. 2001, 2002) or by planting a known number of tagged fish in the catch and observing the number of returns (Hearn et al. 2003). Due to the importance of the natural mortality rate in providing an accurate assessment of the summer flounder stock abundance, we believe it is imperative that such a tagging study is initiated in the near future.

References

Akaike H (1973) Information theory and an extension of the maximum likelihood principle. Pgs. 267-281. *In* Petran BN and Csàaki F (eds.) *International Symposium on Information Theory*, 2nd ed. Akadèemiai Kiadi, Budapest, Hungary.

Anderson DR, Burnham KP, and White GC (1994) AIC model selection in overdispersed capture-recapture data. Ecology, 75: 1780-1793.

Arnason AN (1973) The estimation of population size, migration rates, and survival in a stratified population. Researches in Population Ecology, 15: 1-8.

Arnason AN and Mills KH (1981) Bias and loss of Precision due to tag loss in Jolly-Seber estimates for mark-recapture experiments. Canadian Journal of Fisheries and Aquatic Sciences, 38: 1077-1095.

Barker RJ (1997) Joint modeling of live-recapture, tag-resight, and tag-recovery data. Biometrics, 53: 666-677.

Barker RJ, Burnham KP, and White GC (2004) Encounter history modeling of joint mark-recapture, tag-resighting and tag recovery data under temporary emigration. Statistica Sinica, 14: 1037-1055.

Bettinger JM, Tomasso JR, and Isely JJ (2005) Hooking mortality and physiological responses of striped bass angled in freshwater and held in live-release tubes. North American Journal of Fisheries Management, 25: 1273-1280.

Brownie C, Anderson DR, Burnham KP, and Robson DS (1985) Statistical inference from band recovery data: a handbook, 2nd ed. United States Fish and Wildlife, Resource Publication 131, Washington, DC.

Burnham KP, Anderson DR, White GC, Brownie C, and Pollock KH (1987) Design and Analysis Methods for Fish Survival Experiments Based on Release-Recapture. American Fisheries Society Monograph 5, 1-437.

Burnham KP (1993) A theory for combined analysis of ring recovery and recapture data. *In* Lebreton JD and North P (eds.) *Marked Individuals in Bird Population Studies* pgs 193-214. Birkhauser Verlag, Basel, Switzerland.

Casale P, Mazaris AD, Freggi D, Basso R, and Argano R (2007) Survival probabilities of loggerhead sea turtles (Caretta caretta) estimated from capture-mark-recapture data in the Mediterranean Sea. Scientia Marina, 71: 365-372.

Conn PB, Kendall WL, and Samuel MD (2004) A general model for the analysis of mark-resight, mark-recapture, and band-recovery data under tag loss. Biometrics, 60: 900-909.

Cooch E and White G (2009) *Program MARK: A gentle introduction. 8th ed.* [http://www.phidot.org/software/mark/docs/book/]

Cowen L and Schwarz CJ (2006) The Jolly-Seber model with tag loss. Biometrics, 62: 699-705.

Dias P (1996) Sources and sinks in population biology. Trends in Ecology and Evolution, 11: 326-330.

Desfosse JC (1995) Movements and ecology of summer flounder, *Paralichthys dentatus*, tagged in the southern Mid-Atlantic Bight. Ph.D. dissertation, College of William and Mary, Williamsburg, VA. 187 pp.

Fabrizio MC, Nichols JD, Hines JE, Swanson BL, and Schram ST (1999) Modeling data from double-tagging experiments to estimate heterogeneous rates of tag shedding in lake trout (*Salvelinus namaycush*). Canadian Journal of Fisheries and Aquatic Sciences, 56: 1409-1419.

Fabrizio MC, Scharf FS, Shepherd GR, and Rosendale JE (2008) Factors affecting catch-and-release mortality of bluefish. North American Journal of Fisheries Management, 28: 533-546.

Fournier DA, Skaug HJ, Ancheta J, Ianelli J, Magnusson A, Maunder MN, Nielsen A, and Sibert J. (2011) AD model builder: using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. Optimization Methods and Software, 27: 233-249.

Gale MK, Hinch SG, and Donalson MR (2011) The role of temperature in the capture and release of fish. Fish and Fisheries, doi: 10.1111/j.1467-2979.2011.00441.x

Gillanders BM, Ferrell DJ, and Andrew NL (2001) Estimates of movement and life-history parameters of yellowtail kingfish (*Seriola lalandi*): how useful are data from a cooperative tagging programme? Marine and Freshwater Research, 52: 179-192.

Hall AJ, McConnel BJ, and Barker RJ (2001) Factors affecting first-year survival in grey seals and their implications for life history strategy. Journal of Animal Ecology, 70: 138-149.

Hearn WS, Hoenig JM, Pollock KH, and Hepworth DA (2003) Tag reporting rate estimation: 3. Use of planted tags in one component of a multiple-component fishery. North American Journal of Fisheries Management, 23: 66-77.

Jiang H, Pollock KH, Brownie C, Hoenig JM, Latour RJ, Wells BK, and Hightower JE (2007) Tag return models allowing for harvest and catch and release: evidence of environmental and management impacts on striped bass fishing and natural mortality rates. North American Journal of Fisheries Management, 27: 387-396.

Kendall WL and Nichols JD (2002) Estimating state-transition probabilities for unobservable states using capture-recapture/resighting data. Ecology, 83: 3276-3284.

Kraus RT and Musick JA (2001) A brief interpretation of summer flounder, *Paralichthys dentatus*, movements and stock structure with new tagging data on juveniles. Marine Fisheries Review, 63: 1-6.

Lebreton JD, Burnham KP, Clobert J, and Anderson DR (1992) Modeling survival and testing biological hypotheses using marked animals: A unified approach with case studies. Ecological Monographs, 62: 67-118.

Lebreton JD, Morgan BJT, Pradel R, and Freeman SN (1995) A simultaneous survival rate analysis of dead recovery and live recapture data. Biometrics, 51: 1418-1428.

Lebreton JD and Pradel R (2002) Multistate recapture models: modeling incomplete individual histories. Journal of Applied Statistics, 29: 353-369.

Lucy J and Davy K (2000) Benefits of angler-assisted tag and release programs. Fisheries, 25: 18-23.

Lucy JA, Bain CM, and Arendt MD (2002) Virginia Game Fish Tagging Program: trained anglers making a contribution to fisheries research, management, and conservation. Pgs 195-200 *In* Lucy JA and Studholme AL (eds.) *Catch and Release in Marine Recreational Fisheries.* American Fisheries Society, Symposium 3, Bethesda, Maryland.

Lux FE and Nichy FE (1981) Movements of tagged summer flounder, *Paralichthys dentatus*, off southern New England. NOAA Tech. Rep. NMFS SSRF-752. 16 p.

Malchoff MH, Gearhart J, Lucy J, and Sullivan PJ (2002) The influence of hook type, hook wound location, and other variables associated with post catch-and-release mortality in the U.S. summer flounder recreational fishery. Pgs 101-105 *In* Lucy JA and Studholme AL, (eds.) *Catch and Release in Marine Recreational Fisheries.* American Fisheries Society, Symposium 3, Bethesda, Maryland.

Maunder MN and Wong RA (2011) Approaches for estimating natural mortality: application to summer flounder (*Paralichthys dentatus*) in the U.S. mid-Atlantic. Fisheries Research, 111: 92-99.

McCullagh P and Nelder JA (1989) Generalized linear models, 2nd ed. Chapman and Hall, New York, United States.

Morse WW (1981) Reproduction of the summer flounder, *Paralichthys dentatus* (L.). Journal of Fish Biology, 19: 189-203.

Muoneke MI and Childress WM (1994) Hooking mortality: a review for recreational fisheries. Reviews in Fisheries Science, 2: 123-156.

Nelson KL (1998) Catch-and-release mortality of striped bass in the Roanoke River, North Carolina. North American Journal of Fisheries Management, 18: 25-30.

Nichols JD, Sauer JF, Pollock KH, and Hestbeck JB (1992) Estimating transition probabilities for stage-based population projection matrices using capture-recapture data. Ecology, 73: 306-312.

Nichols JD and Kendall WL (1995) The use of multistate capture-recapture models to address questions in evolutionary ecology. Journal of applied statistics, 22: 835-846.

O'Brien L, Burnett J, and Mayo RK (1993) Maturation of nineteen species of finfish off the northeast coast of the United States, 1985-1990. NOAA Tech. Rep. NMFS 113. 66 pp.

Pollock KH (2002) The use of auxillary variables in capture-recapture modeling: an overview. Journal of Applied Statistics, 29: 85-102.

Pollock KH, Nichols JD, Brownie C, and Hines JE (1990) Statistical inference for capture-recapture experiments. Wildlife monographs, 107, pp. 1-97

Pollock KH, Hoenig JM, Hearn WS, and Calingaert B (2001) Tag Reporting rate estimation: 1. An evaluation of the high-reward tagging method. North American Journal of Fisheries Management, 21: 521-532.

Pollock KH, Hoenig JM, Hearn WS, and Calingaert B (2002) Tag Reporting rate estimation: 2. Use of high reward tagging and observers in multicomponent fisheries. North American Journal of Fisheries Management, 22: 727-736.

Pollock KH, Yoshizaki J, Fabrizio MC, and Schram ST (2007) Factors affecting survival rates of a recovering lake trout population estimated by mark-recapture in Lake Superior 1969-1996. Transactions of the American Fisheries Society, 136: 185-194.

Poole JC (1962) The fluke population of Great South Bay in relation to the sport fishery. N.Y. Fish Game Journal, 9: 93-117.

Powell, EN, Bochenek, EA, and DePersenaire J (2010) Evaluation of bag- and size-limit options in the management of summer flounder *Paralichthys dentatus*. Fisheries Research, 105: 215-227.

Powell EN, Bochenek EA, DePersenaire J, and King SE (2011) Injury frequency for discarded summer flounder in the recreational fishery of the Mid-Atlantic Bight: influence of landing size regulations. Pgs 171-187 *In* Beard TD, Arlinghaus R, and Sutton SG (eds.) *The Angler in the Environment: Social, Economic, Biological and Ethical Dimensions.* American Fisheries Society, Symposium 75.

Powell LA (2007) Approximating variance of demographic parameters using the delta method: a reference for avian biologists. The Condor, 109: 949-954.

Rogers SG and Van Den Avyle MJ (1983) Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (South Atlantic) - summer flounder. U.S. Department of the Interior, Fish and Wildlife Service. FWS/OBS-82/11.15 14 pp.

Northeast Fisheries Science Center (NEFSC) (2008) 47th Northeast Regional Stock Assessment Workshop (47th SAW) Assessment Report. US Dept Commerce, NEFSC Ref Doc. 08-12a, 335 p.

Schwarz CJ, Schweigert JF, and Arnason AN (1993) Estimating migration rates using tag-recovery data. Biometrics, 49: 177-193.

Seber GAF (1982) The estimation of animal abundance and related parameters. Griffin, London.

Slattery SM and Alisauskas RT (2001) Use of the Barker model in an experiment examining covariate effects on first-year survival in Ross's Geese (*Chen rossii*): a case study. Journal of Applied Statistics, 29: 497-508.

Smith RW and Daiber FC (1977) Biology of the summer flounder, *Paralichthys dentatus*, in Delaware Bay. Fishery Bulletin, 75: 823-830.

Terceiro M (2011) Stock assessment of summer flounder for 2011. US Dept. Commer, Northeast Fish Sci Cent Ref Doc. 11-20; 141 p. [http://www.nefsc.noaa.gov/nefsc/publications/]

Weber AM (1984) Summer flounder in Great South Bay: survival of sub-legals caught by hook-and-line and released. New York State Department of Environmental Conservation, Division of Marine Resources. Stony Brook, NY. 27 pp.

Wilde GR, Muoneke MI, Bettoli PW, Nelson KL, and Hysmith BT (2000) Bait and temperature effects on striped bass hooking mortality in freshwater. North American Journal of Fisheries Management, 20: 810-815.

Winger PD, He P, and Walsh SJ (1999) Swimming endurance of American plaice (*Hippoglossoides platessoides*) and its role in fish capture. ICES Journal of Marine Science, 56: 252-265.

Yergey ME, Grothues TM, Able KW, Crawford C, and DeCristofer K (2012) Evaluating discard mortality of summer flounder (*Paralichthys dentatus*) in the commercial trawl fishery: developing acoustic telemetry techniques. Fisheries Research, 115-116: 72-81

Table 1. Number of summer flounder released, resighted, and harvested for fish tagged as A) sublegal fish (< 36 cm), B) fish vulnerable to the commercial fishery (>36 cm) but smaller than the recreational size limit (see Table 2), and C) fish vulnerable to both the recreational and commercial fishery. The numbers in the encounter year columns are the number of resighted fish / harvested fish.

A			Encounter Year												
		Releases	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	total
	2000	1283	57/2	9/5	0/2	0/3	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0	78
	2001	3198		231/9	9/2	2/0	0/0	1/0	0/0	0/0	0/0	0/0	0/0	0/0	254
	2002	945			64/0	6/0	0/1	0/0	0/0	0/0	0/0	0/0	0/0	0/0	71
	2003	1819				144/0	3/0	1/0	0/0	0/0	0/0	0/0	0/0	0/0	148
	2004	2291					101/0	4/6	1/2	0/0	1/1	0/0	0/0	0/0	116
Release Year	2005	2371						126/1	14/5	3/2	0/1	1/0	0/0	0/0	153
	2006	2035							123/3	13/2	2/1	1/0	0/0	0/0	145
	2007	3678								212/2	17/1	3/1	0/0	0/0	236
	2008	2027									73/1	11/0	1/1	0/0	87
	2009	4130										313/1	18/1	1/0	334
	2010	1778											87/0	3/4	94
	2011	711												21/0	21
	total	26266	59	254	77	155	105	139	148	234	98	331	108	29	1737

Table 1 cont.

B			Encounter Year												
		Releases	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	total
Release Year	2000	510	10/6	1/3	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0	20
	2001	1407		61/26	12/6	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0	105
	2002	1553			58/12	8/7	0/0	0/1	0/0	0/0	0/0	0/0	0/0	0/0	86
	2003	804				27/7	5/4	0/0	0/0	1/0	0/0	0/0	0/0	0/0	44
	2004	1750					71/15	8/16	0/1	2/1	0/0	0/0	0/0	0/0	114
	2005	1494						75/15	13/15	2/3	0/1	0/0	0/0	0/0	124
	2006	1640							91/17	21/6	1/2	0/1	0/0	0/0	139
	2007	2249								99/16	16/14	1/2	1/0	0/0	149
	2008	3206									145/12	14/22	0/1	0/0	194
	2009	2268										121/15	7/5	0/2	150
	2010	2291											89/13	2/6	110
	2011	906												33/6	39
	total	20078	16	91	88	49	95	115	137	151	191	176	116	49	1274

Table 1 cont.

C			Encounter Year												
		Releases	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	total
	2000	107	3/6	0/0	1/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0	10
	2001	163		5/9	2/1	1/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0	18
	2002	53			3/3	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0	6
	2003	46				1/2	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0	3
	2004	145					5/9	1/3	0/1	0/0	0/0	0/0	0/0	0/0	19
Release Year	2005	210						5/14	0/3	0/1	0/0	0/0	0/0	0/0	23
	2006	239							9/13	0/5	0/0	0/0	0/0	0/0	27
	2007	53								0/4	0/2	0/0	0/0	0/0	6
	2008	35									0/2	0/0	0/0	0/0	2
	2009	28										0/0	0/0	0/0	0
	2010	29											0/0	0/0	0
	2011	61												1/3	4
	total	1169	9	14	10	4	14	23	26	10	4	0	0	4	118

Table 2. Minimum size limits (total length) for the summer flounder recreational fishery in Virginia from 2000 through 2011.

Year	Minimum recreational size limit (cm)
2000	39.4
2001	39.4
2002	44.5
2003	44.5
2004	43.2
2005	41.9
2006	41.9
2007	47.0
2008	48.3
2009	48.3
2010	47.0
2011	44.5

Table 3. Parameters of the Barker model used to analyze summer flounder mark-recapture data collected by an angler tagging program in Virginia from 2000-2011. The full Barker model (Barker 1997, Barker et al. 2004) includes three additional parameters to estimate the vulnerability of animals to recapture during scientific research surveys. Note that the R' parameter is necessary because encounters can occur continuously throughout an interval, and thus, resighted animals do not necessarily survive to the start of the subsequent interval.

Parameter	Description
S_i	The probability that an animal alive at time *i* is alive at time *i*+1
R_i	The probability that an animal is resighted alive during the interval (*i*, *i*+1)
h_i	The probability that an animal is harvested during the interval (*i*, *i*+1)
R'_i	The probability that an animal is resighted alive prior to death during the interval (*i*, *i*+1)

Table 4. Possible encounter histories and corresponding encounter probabilities for animals released in the first sampling interval of a 3-interval study. Encounter history codes are: resightings = 1, harvests = -1, and no encounter = 0. The associated probabilities are based on a Barker model (Figure 1). χ represents the probability that an animal is never encountered again. See Table 1 for description of the remaining parameters.

Encounter history			Probability
1	1	1	$S_1R_1S_2R_2((1\text{-}S_3)(1\text{-}h_3)R'_3 + S_3R_3\chi_4)$
1	1	-1	$S_1R_1S_2R_2(1\text{-}S_3)r_3$
1	0	1	$S_1R_1S_2(1\text{-}R_2)\ ((1\text{-}S_3)(1\text{-}h_3)R'_3 + S_3R_3\chi_4)$
1	0	-1	$S_1R_1S_2(1\text{-}R_2)(1-S_3)h_3$
0	1	1	$S_1(1\text{-}R_1)S_2R_2((1\text{-}S_3)(1\text{-}h_3)R'_3 + S_3R_3\chi_4)$
0	1	-1	$S_1(1\text{-}R_1)S_2R_2(1-S_3)h_3$
0	0	1	$S_1(1\text{-}R_1)S_2(1\text{-}R_2)((1\text{-}S_3)(1\text{-}h_3)R'_3 + S_3R_3\chi_4)$
0	0	-1	$S_1(1\text{-}R_1)S_2(1\text{-}R_2)(1-S_3)h_3$
1	1	0	$S_1R_1((1\text{-}S_2)(1\text{-}h_2)R'_2 + S_2R_2\chi_3)$
1	-1	0	$S_1R_1(1\text{-}S_2)h_2$
0	1	0	$S_1(1\text{-}R_1)((1\text{-}S_2)(1\text{-}h_2)R'_2 + S_2R_2\chi_3)$
0	-1	0	$S_1(1\text{-}R_1)(1\text{-}S_2)h_2$
1	0	0	$(1\text{-}S_1)(1\text{-}h_1)R'_1 + S_1R_1\chi_2$
-1	0	0	$(1\text{-}S_1)h_1$
0	0	0	χ_1

Where:

$$\chi_i = \begin{cases} (1-S_i)(1-r_i)(1-R'_i)+S_i(1-R_i)\chi_{i+1} & \text{if } i \le j \\ 1 & \text{if } i = j+1 \end{cases}$$

i = sampling interval

j = final interval

Table 5. Numbers (n) and proportion (prop) of sublegal and legal-sized double-tagged summer flounder that retained the t-bar anchor tag for various time intervals after tagging; z is the test statistic used to test equality of proportions between sublegal and legal fish and P is the probability of observing a larger z value, given the null hypothesis of no difference.

Days at liberty	sublegal			legal			z	p
	n	retained	prop	n	retained	prop		
<10	113	107	0.05	17	16	0.06	0.10	0.92
10-29	84	78	0.07	23	18	0.22	2.04	0.04
30-59	23	22	0.04	14	11	0.21	1.62	0.10
60-149	11	6	0.45	12	5	0.58	0.62	0.54
>150	8	4	0.50	9	5	0.44	0.23	0.82

Table 6. Model structure of the top three models used to estimate survival (S), harvest (h), resighting (R), and resighting before death (R') probabilities for summer flounder during for the first 30-days at liberty (tagging interval), remainder of release year (release year), and subsequent intervals (post release year). All fish were released within Chesapeake Bay between 2000 and 2011 by participants in the Virginia Game Fish Tagging Program. The most parsimonious model was selected using Akaike's information criterion (AIC). Also shown are the number of parameters (npar), the negative log-likelihood (NegLL), and the difference between a given model's AIC value and the minimum AIC value for all models considered (ΔAIC). Notations within parentheses indicate if the parameter: 1) was constant for all size classes and throughout the study (.), 2) varied between sublegal and legal sized fish (2sz), 3) varied among fish that were sublegal, vulnerable only to the commercial fishery, or vulnerable to both the commercial and recreational fishery (3sz), 4) varied throughout the 12 years of the study (t), or 5) varied between sublegal and legal fish as well as through time (2sz*t). Parameters that are estimated with a generalized linear model, using release date as a covariate, are subscripted with Logit. Parameter estimates for the best model are provided in Appendix 5.

Model	Tagging Interval	Release Year	Post Release Year	npar	NegLL	AIC	Δ AIC
1	S(2sz*t)h(3sz)R(2sz*t)R'(.)	$S_{Logit}(2sz)h_{Logit}(3sz)R_{Logit}(.)R'(2sz*t)$	S(.)h(3sz)R(.)R'(.)	90	15546.1	31272.1	0
2	S(2sz*t)h(3sz)R(2sz*t)R'(t)	$S_{Logit}(2sz)h_{Logit}(3sz)R_{Logit}(.)R'(2sz*t)$	S(.)h(3sz)R(.)R'(.)	101	15539.6	31281.2	9.1
3	S(2sz*t)h(3sz)R(2sz)R'(t)	$S_{Logit}(2sz)h_{Logit}(3sz)R_{Logit}(.)R'(2sz*t)$	S(.)h(3sz)R(.)R'(.)	79	15568.5	31294.9	22.8

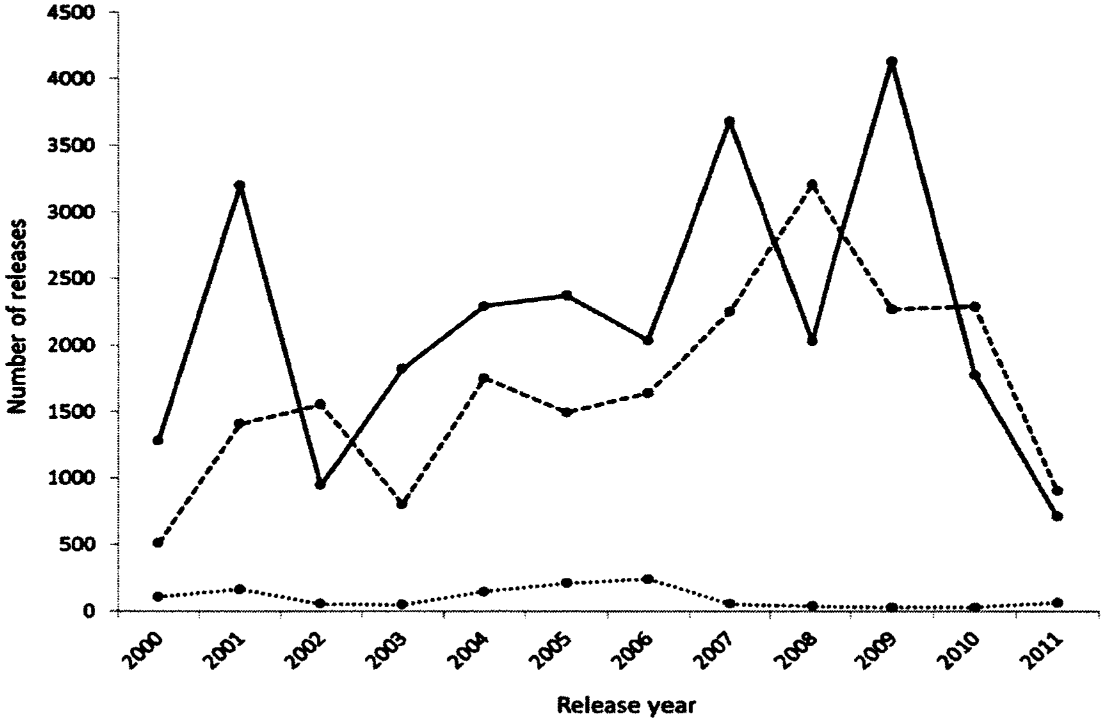


Figure 1. Number of tagged summer flounder released between 2000 and 2011 in Virginia waters. Three size classes of fish are represented: sublegal (solid line), vulnerable only to the commercial fishery (dashed line), and vulnerable to both the commercial and recreational fishery (dotted line).

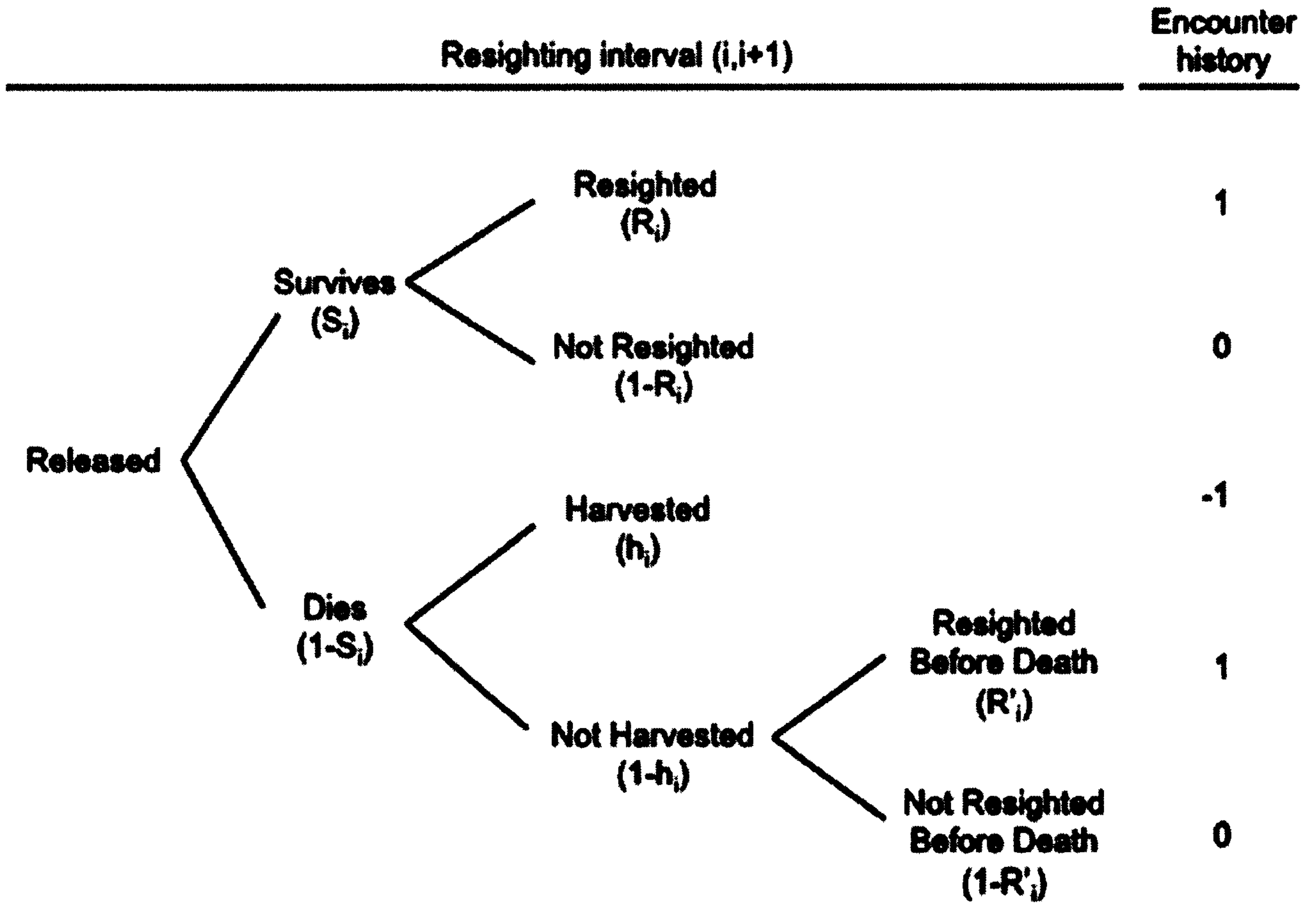


Figure 2. Tree diagram of possible fates of tagged animals during a single sampling interval (i, i+1), and the resulting encounter history codes, for the Barker model used to estimate survival probabilities of summer flounder tagged and released within Chesapeake Bay by an angler tagging program (modified from Barker et al. 2004).

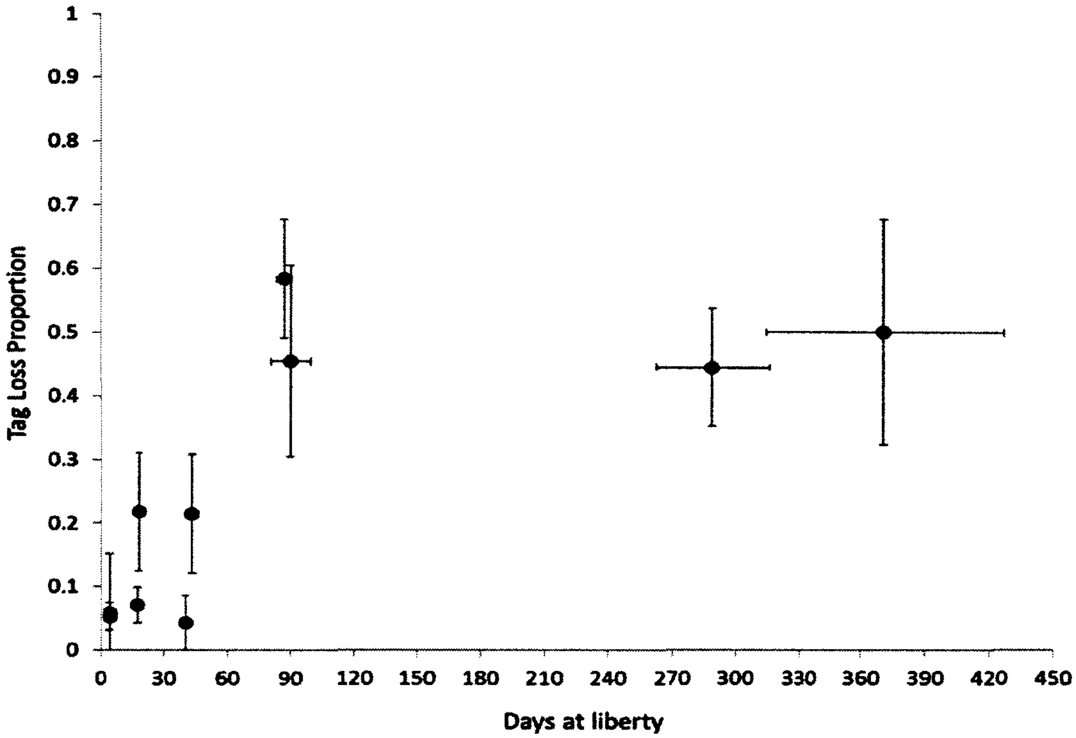


Figure 3. Proportion of sublegal (<36 cm; gray circles) and legal (>36 cm; black circles) sized double- tagged summer flounder that shed t-bar anchor tags. Fish were double tagged with a t-bar anchor tag and a Peterson disc tag between 2009 and 2011 and released in Virginia waters. Error bars are 1 standard error.

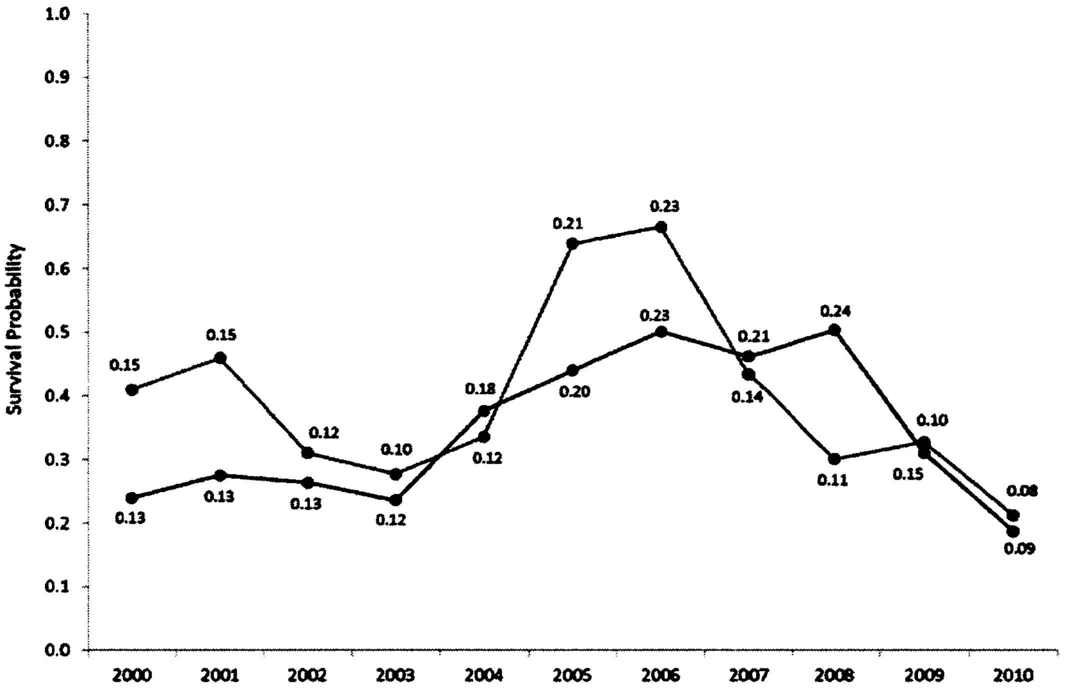


Figure 4. Tag loss corrected probability of survival of sublegal (<36 cm; gray line) and legal (>36cm; black line) sized summer flounder during the first 30-days at liberty. Standard errors, corrected for the uncertainty in tag loss using the delta method, are shown near each point.

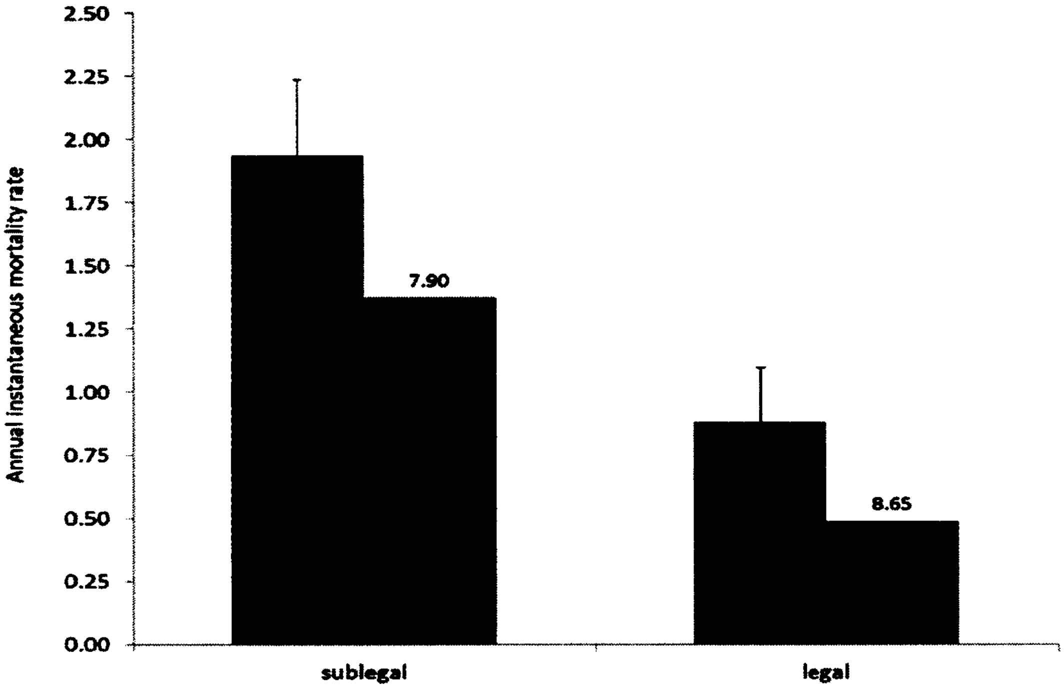


Figure 5. Barker model (black bars) and tag- loss corrected (gray bars) estimates of total annual instantaneous mortality rates for sublegal and legal-sized summer flounder. Error bars for the Barker model estimates represent one standard error. Standard errors for tag-loss-corrected estimates are shown above the gray bars and were estimated using the delta method. These large errors are the result of the large variance in the estimate tag loss rate.

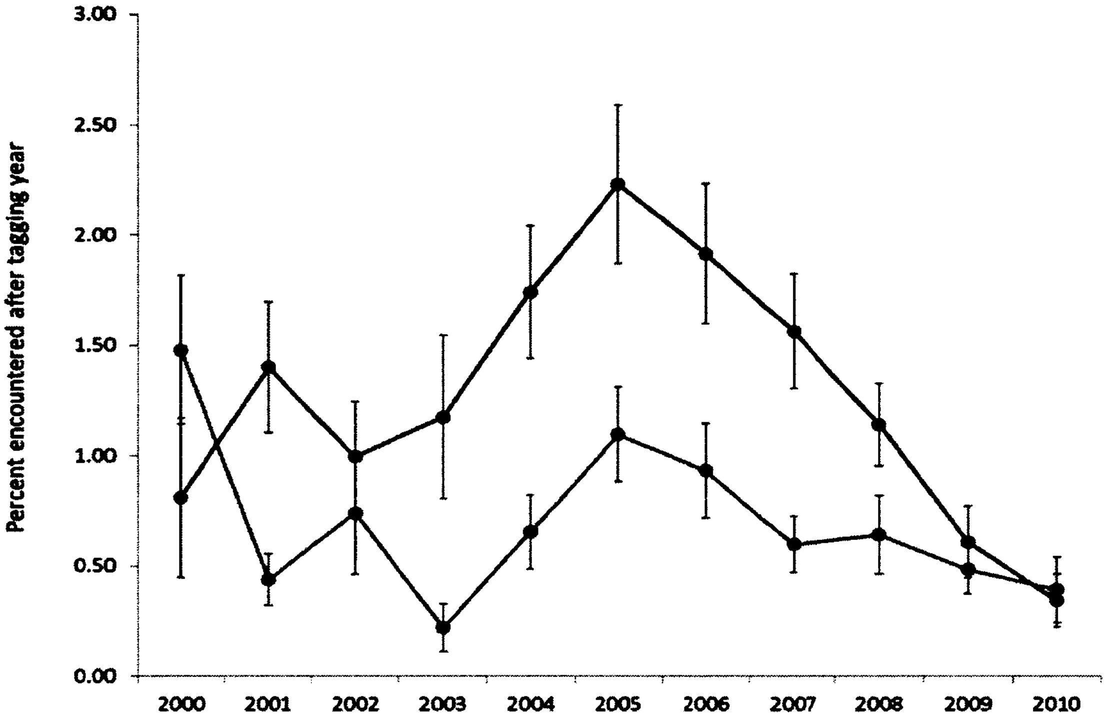


Figure 6. The proportion of summer flounder encountered after the release year that were sublegal (gray) or legal (black) at the time of tagging. Error bars are one standard error.

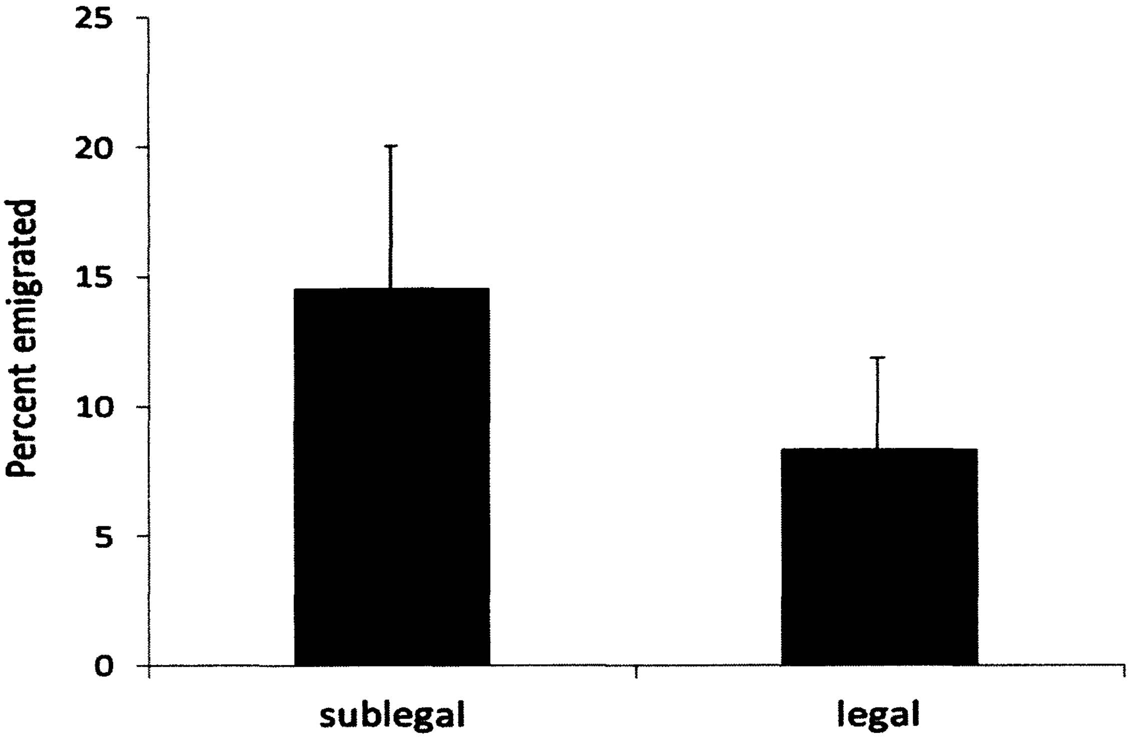


Figure 7. Proportion of summer flounder that emigrated from Chesapeake Bay between 2000 and 2011. A fish was considered to have emigrated if it was encountered after the release year and was resighted or harvested outside of Virginia between May and October. Sublegal (<36 cm) and legal (36 cm) size class categories are based on the size of the fish at tagging. Error bars are 95% confidence intervals.

CONCLUSIONS

In this dissertation I used multiple tagging technologies to examine the movements, growth, and mortality rates of summer flounder tagged and released in Chesapeake Bay. Each tag type used in this research -- acoustic, archival, and conventional -- provided different information on summer flounder behavior that yielded a more complete understanding when observations from these individual studies were combined. The results presented in this dissertation provide information that could be used by management agencies to further understand the behavior of these fish, and how to most effectively manage this population.

In the first two chapters, archival and acoustic telemetry were used to investigate factors that influenced summer flounder movements on relatively small spatial scales. The smallest scale (<1 meter) movements were observed with archival tags that continuously recorded depth and water temperature. These data indicated that summer flounder exhibited complex movements within Chesapeake Bay from August through early October. These movements were primarily influenced by: 1) tidal stage and temperature, and 2) fish length and time of day. Increases in water temperature corresponded with increases in fish activity, but this generally occurred during rising and the falling tides. Smaller summer flounder tended to be more active than larger individuals, and this difference in activity level was most apparent during night. These fine-scale movements were similar to behaviors observed on a slightly larger scale (100s of meters) using acoustic telemetry. From June through early October 2006, summer flounder movements within an array of passive acoustic receivers in the lower Chesapeake Bay were influenced mainly by fish size, tidal stage, and time of day. Similar to what I observed from archival-tagged fish, smaller summer flounder tended to be more active than larger individuals. In addition, the probability of movement was higher during the rising tide compared with other tidal phases. Finally, summer flounder tended to be more active at night, and this increased activity was more pronounced near the quarter moons. Observations from the archival telemetry study also suggested that summer flounder movements were influenced by fish size, time of day, and lunar phase; unfortunately, very few archival- tagged fish were observed through multiple lunar phases, which precluded any definitive conclusions regarding the effect of lunar phase on fish movements based on these data. The results from the archival and acoustic telemetry projects revealed similar patterns in summer flounder behavior, although the finer-scale observations of the archival tag indicated a temperature effect that was not detected with acoustic telemetry. The periods of increased movements observed with both archival and acoustic telemetry correspond to the times when mysids are most active. Mysids are one of the main prey items of smaller summer flounder (Latour et al 2008), suggesting that summer flounder behavior is related to foraging activity while resident in inshore habitats (e.g., Chesapeake Bay).

Results from the archival, acoustic, and conventional tagging data also revealed patterns in the timing of summer flounder dispersal from Chesapeake Bay, extent of site fidelity, and trends in the direction that fish moved after emigration. Two archival-tagged fish emigrated from Chesapeake Bay and provided information on timing of dispersal. One fish dispersed from the Bay in mid-October 2009 and was subsequently captured and harvested east of Virginia Beach prior to returning to Chesapeake Bay. The second fish dispersed from the Bay in early November 2009, returned to Chesapeake Bay in June 2010, and dispersed again in late November 2010. Interestingly, in both years this fish left the Bay when water temperatures reached 14 C, even though this occurred nearly a month earlier in 2009. Based on the acoustic telemetry study conducted in 2006, summer flounder moved towards the mouth of the bay between October and December. Approximately 90% of the fish that were resident at an artificial reef in the lower Bay had dispersed from the reef site by the end of October. Eleven fish that were released elsewhere in Chesapeake Bay with acoustic transmitters were detected at the artificial reef for brief periods between October and December. The brief duration that these individual fish remained at the reef during the fall months may indicate that these fish were exhibiting directed movement towards the mouth of the Chesapeake Bay as part of their annual offshore migration. The protracted time period over which these 'migrating' fish were detected suggests that individuals move independently and do not respond to a single common exogenous cue (e.g., temperature or photoperiod) to initiate dispersal from the bay. Conventionally tagged summer flounder that dispersed from Chesapeake Bay were primarily recaptured south of the Bay during winter and north of the Bay during spring and summer. This implies that Chesapeake Bay summer flounder primarily spawn on the southern shelf, off the coast of North Carolina, but fish that permanently emigrate from Chesapeake Bay tend to move north. Recaptures of conventionally tagged summer flounder also indicate that fish smaller than 36 cm were more likely than larger fish to be recaptured outside of Virginia during the spring and summer, indicating that these smaller fish had permanently emigrated from Chesapeake Bay. The period of dispersal, as well as emigration patterns, observed in this dissertation are consistent with results from previous tagging studies (Desfosse 1995, Kraus and Musick 2001), indicating that these behaviors have been consistent through time.

A growth model fit to summer flounder conventional tagging data revealed that recreational anglers harvested fish that were 2-4 cm below the minimum size limit in Virginia, and that the extent of noncompliance tended to increase as minimum size limits increased. This growth model was fit to mark-recapture data collected by an angler tagging program operating in Virginia from 2000 to 2011. Comparing the growth model predictions with the reported lengths of summer flounder recaptured by recreational anglers indicated that a measurement bias existed only for fish predicted to be below the minimum size. Of the harvested fish that were predicted to be sublegal, 85% were reported to be 2.78 ± 0.54 cm larger than expected upon recapture. Furthermore, the extent of noncompliance appeared to be related to changes in management regulations. The proportion of harvested sublegal fish increased dramatically in years following large (5 cm) increases in the minimum size limit or during years when the minimum size limit was perceived by recreational anglers to be excessively large. These increases in noncompliance with minimum size regulations were most likely the result of the reduced catch rate of legal sized fish due to the more strict regulations (Sullivan 2002).

Due to low encounter rates of sublegal summer flounder (<36 cm), it was not possible to estimate the natural instantaneous mortality rate of these fish based on conventional mark-recapture data, but results from this study did reveal high rates of handling mortality for all fish and high mortality rates of sublegal fish compared with legal sized fish (> 36 cm). For summer flounder released in Chesapeake Bay from 2000 to 2011 by participants in a recreational angler tagging program, the average estimates of mortality within the first 30 days of release were approximately 60% for sublegal fish and 65% for legal-sized fish. These estimates of short-term mortality following tagging are similar to the 53% total mortality rate observed in a tagging study conducted of sublegal summer flounder captured by hook-and-line (Weber 1984, cited in Terceiro 2011). Due to the relatively low impact of the tagging process, it is likely that the mortality observed in my study (30-days post-release) is primarily the result of stress induced by handling of fish. Surprisingly, of the summer flounder that survived the first 30 days after tagging, sublegal fish had higher rates of total apparent mortality than fish susceptible to exploitation by the fishery. This high mortality rate for sublegal fish may be the result of: 1) sublegal fish emigrating outside of Virginia waters, where they might be encountered at a lower rate than larger fish that tend to return to Virginia waters, 2) sublegal fish suffering high rates of mortality during their first spawning migration, or 3) sublegal fish suffering high rates of discard mortality from the commercial trawl fishery that primarily operates on the continental shelf during winter. Based on these results, more research is necessary to investigate the recreational fishery discard mortality and to estimate the summer flounder natural mortality rate.

Results from this dissertation can be used to guide the development of management regulations for summer flounder in Virginia and the mid-Atlantic region. Based on the observed noncompliance of Virginia's recreational anglers with the summer flounder minimum size regulations, it would be prudent for management agencies to consider angler behavior when developing regulations. When the minimum size limit was below 45 cm, anglers harvested fish approximately 2 cm below the size limit; however, in years when the minimum size limit exceeded 45 cm, anglers harvested fish 3-4.5 cm below the size limit. Thus, Virginia anglers harvested fish of approximately the same size even though minimum size limits increased. This noncompliance behavior could negate the expected benefit of increasing minimum size limit for the fishery. Based on the results of this dissertation, angler compliance with harvest size regulations may be maximized by: 1) small incremental changes in minimum size limits, or 2) minimum size limits that result in sufficiently high catch rates of legal sized fish to satisfy anglers. Managers could also consider modifying recreational fishery regulations to reduce discard mortality from the recreational fishery. Based on the high handling mortality observed in this dissertation, alternative management strategies, such as slot limits or cumulative size limits (Powell et al. 2010), should be considered to reduce recreational discard mortality.

References

Desfosse JC (1995) Movements and ecology of summer flounder, *Paralichthys dentatus*, tagged in the southern Mid-Atlantic Bight. Ph.D. dissertation, College of William and Mary, Williamsburg, VA. 187 pp.

Kraus RT and Musick JA (2001) A brief interpretation of summer flounder, *Paralichthys dentatus*, movements and stock structure with new tagging data on juveniles. Marine Fisheries Review, 63: 1-6.

Latour RJ, Gartland J, Bonzek CF, and Johnson RA (2008) The trophic dynamics of summer flounder (*Paralichthys dentatus*) in Chesapeake Bay. Fisheries Bulletin, 106: 47-57.

Powell, EN, Bochenek, EA, and DePersenaire J (2010) Evaluation of bag- and size-limit options in the management of summer flounder *Paralichthys dentatus*. Fisheries Research 105: 215-227.

Sullivan MG (2002) Illegal angling harvest of walleyes protected by length limits in Alberta. North American Journal of Fisheries Management, 22: 1053-1063.

Terceiro M (2011) Stock assessment of summer flounder for 2011. US Dept. Commer, Northeast Fish Sci Cent Ref Doc. 11-20; 141 p. [http://www.nefsc.noaa.gov/nefsc/publications/]

Weber AM (1984) Summer flounder in Great South Bay: survival of sub-legals caught by hook-and-line and released. New York State Department of Environmental Conservation, Division of Marine Resources. Stony Brook, NY. 27 pp.

APPENDIX I -

Acoustic Telemetry Model Selection Tables and Figures

Table 1. Global model selection table for the generalized linear mixed model fit to the binomial response (moved vs. not moved) for 42 summer flounder implanted with acoustic transmitters in the lower Chesapeake Bay during summer 2006. The global model included all the main effects -- fish length (Length), tidal stage (Tide), time of day (TOD), lunar phase (Lunar), temperature (Temp), and hours at liberty (HAL) – as well as the interactions listed. All three-way interactions also included the component two way interactions. Any interaction that decreased Akaike's information criterion corrected for small sample size (AICc) by more than 1 unit from the main effects only model (Model 1) was examined graphically (see Chapter 1 and this Appendix).

Model	Interactions	AICc	ΔAIC
1		2860.14	0
2	Length*Tide	2859.96	-0.18
3	Length*TOD	2861.79	1.65
4	Length*Lunar	2869.27	9.13
5	Length*Temp	2865.67	5.53
6	Tide*TOD	2860.65	0.51
7	Tide*Lunar	2877.07	16.93
8	Tide*Temp	2872.31	12.17
9	TOD*Lunar	2852.76	-7.38
10	TOD*Temp	2862.18	2.04
11	Lunar*Temp	2894.89	34.75
12	Length*Tide*TOD	2862.12	1.98
13	Length*Tide*Lunar	2897.35	37.21
14	Length*Tide*Temp	2884.49	24.35
15	Length*TOD*Lunar	2866.83	6.69
16	Length*TOD*Temp	2877.06	16.92
17	Length*Lunar*Temp	2928.7	68.56
18	Length*HAL	2854.84	-5.3
19	Tide*HAL	2863.25	3.11
20	TOD*HAL	2859.46	-0.68
21	Lunar*HAL	2867.85	7.71
22	Temp*HAL	2860.92	0.78
23	Length*HAL*Tide	2855.65	-4.49*
24	Length*HAL*TOD	2857.71	-2.43*
25	Length*HAL*Lunar	2858.66	-1.48*
26	Length*HAL*Temp	2863.01	2.87

*NOTE – these interactions were not considered in the final model because the AIC values indicate the model with just the Length*HAL interaction is more parsimonious.

Table 2. Random-effects model selection for the generalized linear mixed model fit to the binomial response (moved vs. not moved) for 42 summer flounder implanted with acoustic transmitters in the lower Chesapeake Bay during summer 2006. The model with the lowest Akaike's Information Criterion (AICc) was selected. The delta AICc (ΔAICc) is the difference in value between each model and the model with the lowest AICc. Covariance structures were: variance components (vc), compound symmetry (cs), autoregressive with a lag of 1 (ar(1)), and autoregressive moving average with a lag of 1 (arma(1,1)).

Model	Random tag effect	Covariance structure	AICc	ΔAIC
1	x	VC	2852.76	0
2		VC	2919.1	66.34
3		AR(1)	2921.11	68.35
4		CS	2921.11	68.35
5		ARMA(1,1)	2923.12	70.36
6	x	AR(1)	NA*	NA*
7	x	ARMA(1,1)	NA*	NA*
8	x	CS	NA*	NA*

*Note: fitting these models resulted in g-matrices that were not positive definite, implying that the random tag effect should not be included for those covariance structures.

Table 3. Fixed-effects model selection table showing the factors -- Fish Length (Length), hours at liberty (HAL), Tidal stage (Tide), time of day (TOD), Lunar phase (Lunar), and water temperature (Temp) -- and interactions for the generalized linear mixed models fit to the binomial response (moved vs. not moved) for 42 summer flounder implanted with acoustic transmitters in the lower Chesapeake Bay during summer 2006. Also shown are the values of Akaike's Information Criterion corrected for small sample size (AICc) and the difference in AICc values between a given model and the model with the lowest AICc.

Model	Length	HAL	Tide	TOD	Lunar	Temp	Interactions	AICc	ΔAIC
1	x		x	x	x		TOD*Lunar	2838.6	0
2			x	x	x		TOD*Lunar	2841.64	3.04
3	x	x	x	x	x		TOD*Lunar	2843.72	5.12
4	x		x		x			2846.02	7.42
5	x		x	x	x	x	TOD*Lunar	2847.22	8.62
6			x		x			2848.82	10.22
7		x	x	x	x		TOD*Lunar	2849.66	11.06
8			x	x	x	x	TOD*Lunar	2850.31	11.71
9	x	x	x		x			2850.73	12.13
10	x		x		x	x		2853.92	15.32
11		x	x		x			2856.51	17.91
12			x		x	x		2856.72	18.12
13		x	x	x	x	x	TOD*Lunar	2858.72	20.12
14	x	x	x		x	x		2859.02	20.42
15		x	x		x	x		2864.87	26.27
16	x			x	x		TOD*Lunar	2866.22	27.62
17				x	x		TOD*Lunar	2869.26	30.66
18	x	x		x	x		TOD*Lunar	2871.13	32.53
19	x			x	x	x	TOD*Lunar	2875.15	36.55
20		x		x	x		TOD*Lunar	2876.92	38.32
21				x	x	x	TOD*Lunar	2878.18	39.58
22	x				x			2878.18	39.58
23	x	x		x	x	x	TOD*Lunar	2880.32	41.72
24					x			2880.55	41.95
25	x		x					2882.83	44.23
26	x	x			x			2882.86	44.26
27	x		x	x				2883.07	44.47
28	x	x	x					2883.89	45.29
29	x	x	x	x				2884.02	45.42
30			x					2885.52	46.92
31			x	x				2885.76	47.16
32		x		x	x	x	TOD*Lunar	2886.15	47.55
33		x	x					2886.44	47.84

Table 3 cont.

Model	Length	HAL	Tide	TOD	Lunar	Temp	Interactions	AICc	ΔAIC
34	x				x	x		2886.51	47.91
35		x	x	x				2886.57	47.97
36		x			x			2888.53	49.93
37					x	x		2889.27	50.67
38	x		x			x		2890.81	52.21
39	x	x			x	x		2891.41	52.81
40	x		x	x		x		2892.43	53.83
41			x			x		2893.79	55.19
42			x	x		x		2893.97	55.37
43	x	x	x			x		2895.51	56.91
44	x	x	x	x		x		2895.89	57.29
45		x			x	x		2897.16	58.56
46		x	x			x		2901.11	62.51
47		x	x	x		x		2901.47	62.87
48	x							2910.68	72.08
49	x			x				2911.35	72.75
50	x	x						2911.69	73.09
51	x	x		x				2912.25	73.65
52								2913.31	74.71
53				x				2913.97	75.37
54		x						2914.17	75.57
55		x		x				2914.74	76.14
56	x					x		2918.24	79.64
57	x			x		x		2919	80.4
58	x	x				x		2919.45	80.85
59						x		2920.89	82.29
60				x		x		2921.65	83.05
61		x				x		2921.98	83.38
62		x		x		x		2922.62	84.02
63	x	x		x		x		2923.82	85.22

Table 4. Global model selection table for the general linear mixed model fit to the positive values of minimum distance traveled for 35 summer flounder implanted with acoustic transmitters in the lower Chesapeake Bay during summer 2006. The global model included all the main effects -- fish length (Length), tidal stage (Tide), time of day (TOD), lunar phase (Lunar), temperature (Temp), and hours at liberty (HAL) – as well as the interactions listed. All three-way interactions also included the component two way interactions. None of the interactions decreased Akaike's information criterion corrected for small sample size (AICc) by more than 1 unit, and thus, none were considered in the final model.

Model	Interactions	AICc	ΔAIC
1		652.4	0
2	Length*Tide	655.3	2.9
3	Length*TOD	654	1.6
4	Length*Lunar	665.5	13.1
5	Length*HAL	654.4	2
6	Length*Temp	654.1	1.7
7	HAL*Tide	656.5	4.1
8	HAL*TOD	654.1	1.7
9	HAL*Lunar	658.8	6.4
10	HAL*Temp	654.4	2
11	Tide*TOD	655.1	2.7
12	Tide*Lunar	667.3	14.9
13	Tide*Temp	658.2	5.8
14	TOD*Lunar	661.1	8.7
15	TOD*Temp	654.6	2.2
16	Lunar*Temp	657	4.6
17	Length*HAL*Tide	667.4	15
18	Length*HAL*TOD	659.1	6.7
19	Length*HAL*Lunar	683.2	30.8
20	Lengh*HAL*Temp	659.6	7.2
21	Legnth*Tide*TOD	664.4	12
22	Length*Tide*Lunar	727.1	74.7
23	Length*Tide*Temp	668.8	16.4
24	Length*TOD*Lunar	675.7	23.3
25	Length*TOD*Temp	660.1	7.7
26	Length*Lunar*Temp	679.2	26.8

Table 5. Random-effects model selection for the generalized linear mixed model fit to the positive values of minimum distance traveled for 35 summer flounder implanted with acoustic transmitters in the lower Chesapeake Bay during summer 2006. The model with the lowest Akaike's Information Criterion (AICc) was selected. The delta AICc (ΔAICc) is the difference in value between each model and the model with the lowest AICc. Covariance structures were: variance components (vc), compound symmetry (cs), autoregressive with a lag of 1 (ar(1)), and autoregressive moving average with a lag of 1 (arma(1,1)).

Model	Random tag effect	Covariance structure	AICc	ΔAIC
1		AR(1)	694.4	0
2	x	AR(1)	695.4	1
3		ARMA(1,1)	696.2	1.8
4	x	ARMA(1,1)	697.3	2.9
5		CS	706.2	11.8
6	x	VC	706.2	11.8
7		VC	706.7	12.3
8	x	CS	708.2	13.8

Table 6. Fixed-effects model selection table showing the fixed factors -- Fish Length (Length), hours at liberty (HAL), Tidal stage (Tide), time of day (TOD), Lunar phase (Lunar), and water temperature (Temp) -- and interactions for the generalized linear mixed models fit to the positive values of minimum distance traveled for 35 summer flounder implanted with acoustic transmitters in the lower Chesapeake Bay during summer 2006. Also shown are the values of Akaike's Information Criterion corrected for small sample size (AICc) and the difference in AICc values between a given model and the model with the lowest AICc.

Model	Length	HAL	Tide	TOD	Lunar	Temp	Interactions	AICc	ΔAIC
1	x			x		x		646	0
2	x	x		x		x		646.4	0.4
3	x		x	x				646.2	0.2
4	x			x				646.3	0.3
5	x	x		x				646.5	0.5
6	x	x	x	x				646.7	0.7
7	x		x	x		x		647.2	1.2
8	x	x	x	x		x		647.8	1.8
9	x	x						648.4	2.4
10			x	x				648.4	2.4
11	x							648.4	2.4
12	x					x		648.5	2.5
13	x	x				x		648.7	2.7
14	x		x					648.9	2.9
15				x		x		649.1	3.1
16		x	x	x				649.2	3.2
17	x	x	x					649.2	3.2
18			x	x		x		649.6	3.6
19				x				649.6	3.6
20		x		x		x		649.8	3.8
21		x		x				650.2	4.2
22	x		x			x		650.3	4.3
23	x		x	x	x			650.3	4.3
24	x	x	x	x	x			650.4	4.4
25		x	x	x		x		650.5	4.5
26	x	x	x			x		650.7	4.7
27			x					651.3	5.3
28	x	x		x	x			651.7	5.7
29								651.8	5.8
30						x		651.9	5.9
31		x	x					651.9	5.9
32	x			x	x			652	6
33	x		x	x	x	x		652.2	6.2

Table 6 cont.

Model	Length	HAL	Tide	TOD	Lunar	Temp	Interactions	AICc	ΔAIC
34		x						652.3	6.3
35			x	x	x			652.4	6.4
36		x				x		652.5	6.5
37	x	x		x	x	x		652.6	6.6
38	x			x	x	x		652.7	6.7
39			x			x		652.7	6.7
40		x	x	x	x			652.9	6.9
41	x		x		x			653.3	7.3
42	x	x	x		x			653.4	7.4
43		x	x			x		653.5	7.5
44	x	x			x			654	8
45			x	x	x	x		654.3	8.3
46	x				x			654.3	8.3
47		x	x	x	x	x		654.9	8.9
48				x	x			655.3	9.3
49	x	x			x	x		655.4	9.4
50	x		x		x	x		655.4	9.4
51	x	x	x		x	x		655.5	9.5
52	x				x	x		655.6	9.6
53		x		x	x			655.6	9.6
54			x		x			655.6	9.6
55				x	x	x		655.9	9.9
56		x	x		x			656.1	10.1
57		x		x	x	x		656.4	10.4
58			x		x	x		657.6	11.6
59					x			657.8	11.8
60		x			x			658	12
61		x	x		x	x		658.2	12.2
62					x	x		658.9	12.9
63		x			x	x		659.3	13.3

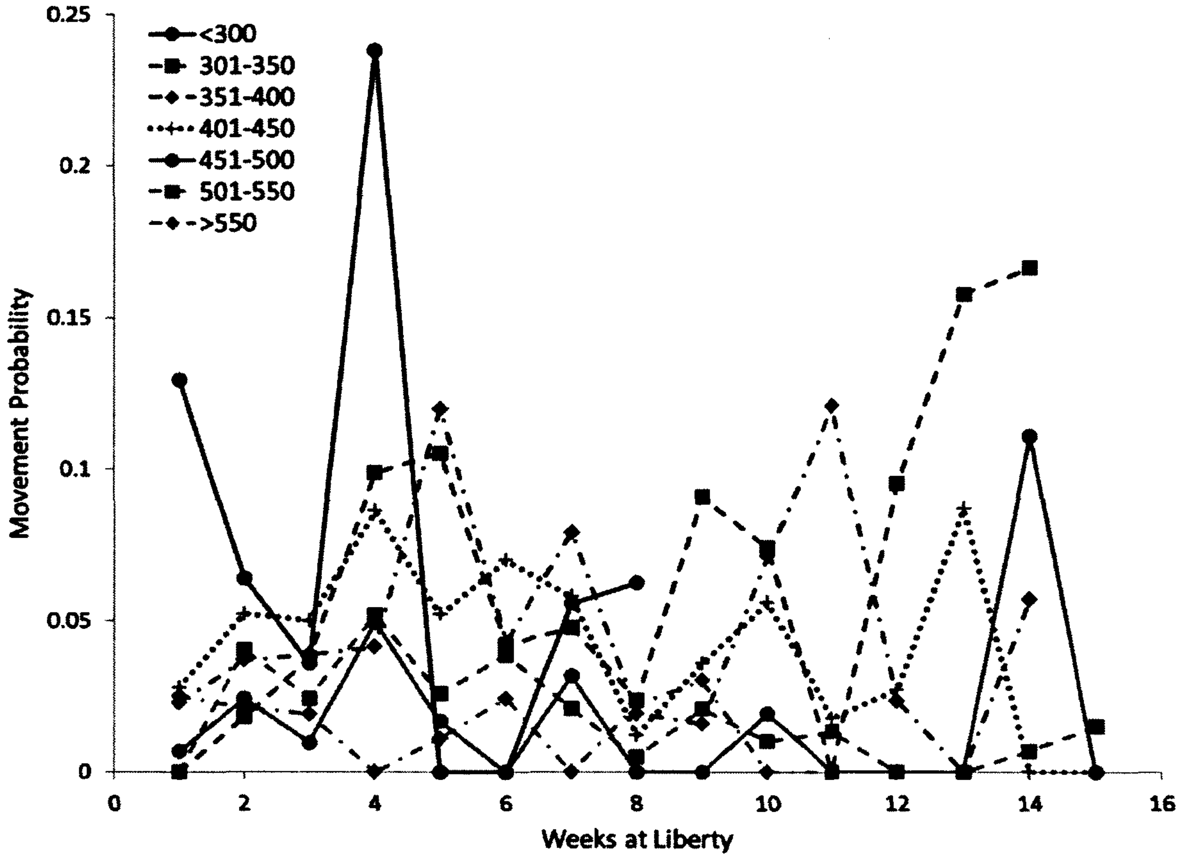


Figure 1. Observed interaction between fish length and time at liberty on the movement probability of summer flounder within an acoustic array. Movements were observed for 42 summer flounder implanted with acoustic transmitters and released near an artificial reef in the lower Chesapeake Bay during the summer of 2006. Due to the complexity of the interaction, time at liberty is displayed as weeks at liberty and fish were grouped into 50 mm length bins. Although including this interaction decreased the AICc values (see Table 1), it was excluded from the generalized linear mixed model fit to the binomial response (moved vs. not moved) because the interaction appeared to be random through time and did not have an ecological interpretation.

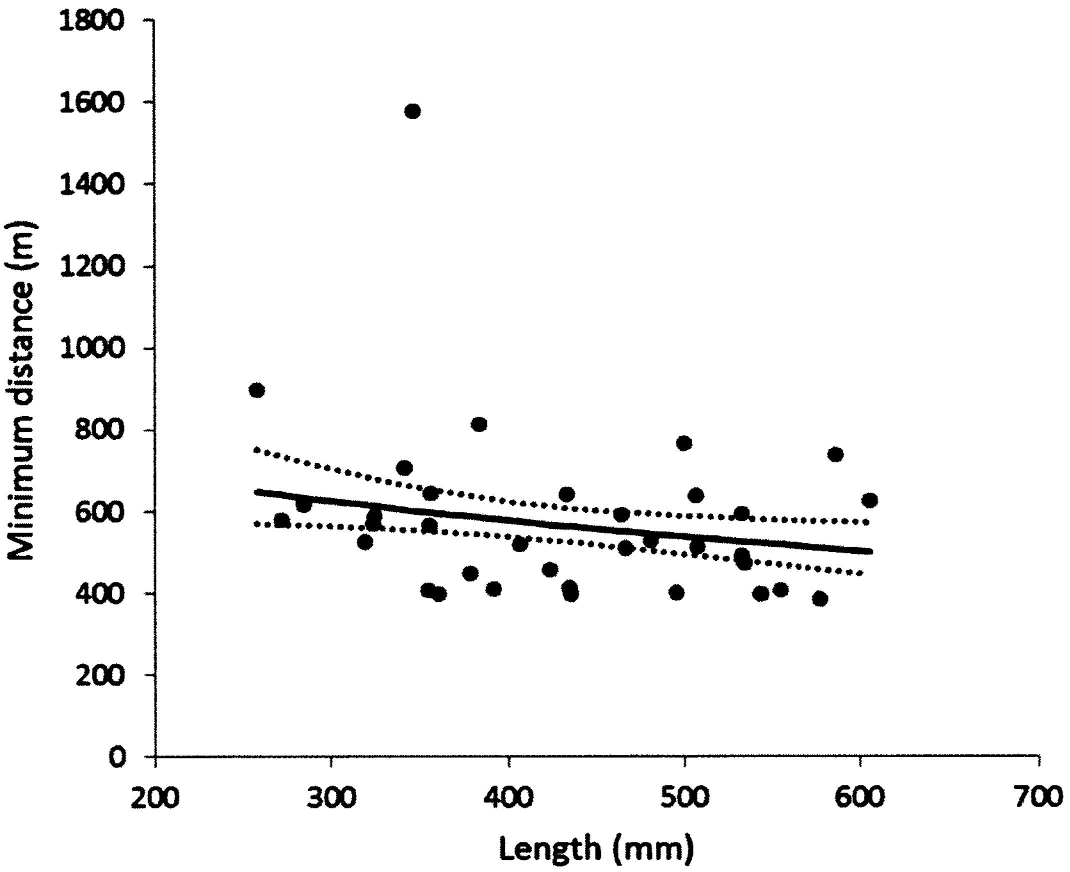


Figure 2. Minimum distance traveled and total length of 35 summer flounder observed moving between acoustic receivers while resident at Back River reef from June through September 2006. Also shown are the model predicted relationship (black line) and 95% confidence interval (dotted line) between fish length and minimum distance traveled.

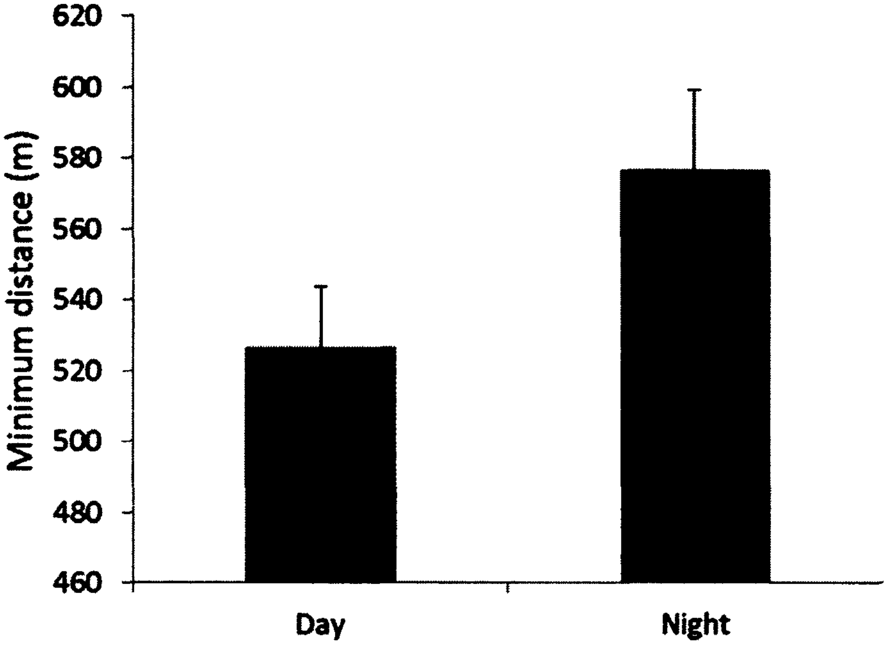


Figure 3. Mean minimum distance traveled during the day and night for 35 summer flounder observed moving between acoustic receivers while resident at Back River reef from June through September 2006. Error bars are ± 1 standard error.

APPENDIX II -

Archival Telemetry Model Selection Tables and Figures

Table 1. Global model selection table for the general linear mixed model fit to the depth change data from 14 summer flounder carrying archival tags in the lower Chesapeake Bay during summer 2009. The global model included all the main effects – fish length (Length), tidal stage (Tide), time of day (TOD), lunar phase (Lunar), and temperature (Temp) – as well as the interactions listed. All three-way interactions also included the component two way interactions. Any interaction that decreased Akaike's information criterion corrected for small sample size (AICc) by more than 1 unit from the main effects only model (Model 1) was examined graphically. A figure for the interactions included in the final model (Length*TOD and Tide*Temp) were provided in Chapter 2 – figures 7 & 8. Figures for the other interactions considered (TOD*Temp, Lunar*Temp, Length*TOD*Lunar, and Length*TOD*Temp) are provided in this appendix.

Model	Interactions	AICc	AIC
1		12593	0
2	Length*Tide	12597.1	4.1
3	Length*TOD	12588.6	-4.4
4	Length*Lunar	12600.1	7.1
5	Length*Temp	12593	0
6	Tide*TOD	12598.3	5.3
7	Tide*Lunar	12618.1	25.1
8	Tide*Temp	12588.9	-4.1
9	TOD*Lunar	12598.1	5.1
10	TOD*Temp	12589.4	-3.6
11	Lunar*Temp	12583.5	-9.5
12	Length*Tide*TOD	12599.6	6.6
13	Length*Tide*Lunar	12646.7	53.7
14	Length*Tide*Temp	12594.8	1.8
15	Length*TOD*Lunar	12591.3	-1.7
16	Length*TOD*Temp	12589.3	-3.7
17	Length*Lunar*Temp	12600.8	7.8

Table 2. Fixed-effects model selection table showing the fixed factors -- Fish Length (Length), Tidal stage (Tide), time of day (TOD), Lunar phase (Lunar), and water temperature (Temp) -- and interactions for the general linear mixed models fit to depth change data for 14 summer flounder carrying archival tags in the lower Chesapeake Bay during summer 2009. Also shown are the values of Akaike's Information Criterion corrected for small sample size (AICc) and the difference in AICc values between a given model and the model with the lowest AICc.

Model	Length	Tide	TOD	Lunar	Temp	Interactions	AICc	ΔAIC
1	x	x	x		x	Length*TOD, Tide*Temp	12573.2	0
2		x	x		x	Tide*Temp, TOD*Temp	12576.2	3
3	x	x	x		x	Length*TOD, Tide*Temp, TOD*Temp	12576.4	3.2
4	x	x	x		x	Tide*Temp, TOD*Temp	12578	4.8
5		x	x		x	Tide*Temp	12579.9	6.7
6		x	x		x	TOD*Temp	12580.4	7.2
7	x	x	x		x	Length*TOD, TOD*Temp	12580.7	7.5
8	x	x	x		x	Length*TOD	12581.4	8.2
9	x	x	x		x	Tide*Temp	12581.7	8.5
10	x	x	x		x	TOD*Temp	12582.3	9.1
11		x	x	x	x	Length*Lunar, Tide*Temp, TOD*Temp	12583.4	10.2
12	x	x	x	x	x	Length*TOD, Length*Lunar, Tide*Temp, TOD*Temp	12583.7	10.5
13		x	x		x		12584.1	10.9
14	x	x	x	x	x	Length*TOD, Length*Lunar, Tide*Temp	12584.5	11.3

Table 2 cont.

Model	Length	Tide	TOD	Lunar	Temp	Interactions	AICc	ΔAIC
15	x	x	x	x	x	Length*Lunar, Tide*Temp, TOD*Lunar, TOD*Temp	12585.2	12
16	x	x	x		x		12585.9	12.7
17	x	x	x	x	x	Length*TOD, Length*Lunar, Tide*Temp, TOD*Lunar, TOD*Temp, Length*TOD*Lunar	12586	12.8
18		x	x	x	x	Length*Lunar, Tide*Temp	12587.1	13.9
19		x	x	x	x	Length*Lunar, TOD*Temp	12587.5	14.3
20	x	x	x	x	x	Length*TOD, Length*Lunar, TOD*Temp	12587.8	14.6
21		x			x	Tide*Temp	12587.9	14.7
22	x	x	x	x	x	Length*TOD, Length*Lunar, Tide*Temp, TOD*Lunar, Length*TOD*Lunar	12588	14.8
23	x	x	x	x	x	Length*TOD, Length*Lunar	12588.6	15.4
24	x	x	x	x	x	Length*Lunar, Tide*Temp, TOD*Lunar	12588.9	15.7
25	x	x	x	x	x	Length*TOD, Length*Lunar, TOD*Lunar, TOD*Temp, Length*TOD*Lunar	12589.3	16.1
26	x	x	x	x	x	Length*Lunar, TOD*Lunar, TOD*Temp	12589.4	16.2
27	x	x			x	Tide*Temp	12589.7	16.5
28	x	x	x			Length*TOD	12590.6	17.4
29		x	x	x	x	Length*Lunar	12591.1	17.9

Table 2 cont.

Model	Length	Tide	TOD	Lunar	Temp	Interactions	AICc	ΔAIC
30	x	x	x	x	x	Length*TOD, Length*Lunar, TOD*Lunar, Length*TOD*Lunar	12591.3	18.1
31		x			x		12592	18.8
32	x	x	x	x	x	Length*Lunar	12593	19.8
33	x	x			x		12593.9	20.7
34		x	x				12594.1	20.9
35		x		x	x	Length*Lunar, Tide*Temp	12595	21.8
36	x	x	x				12595.2	22
37	x	x		x	x	Length*Lunar, Tide*Temp	12596.9	23.7
38	x	x	x	x		Length*TOD, Length*Lunar, TOD*Lunar	12597.2	24
39		x		x	x	Length*Lunar	12599.1	25.9
40	x	x	x	x		Length*TOD, Length*Lunar, TOD*Lunar, Length*TOD*Lunar	12599.1	25.9
41		x	x	x		Length*Lunar, TOD*Lunar, TOD*Temp	12600.7	27.5
42	x	x		x	x	Length*Lunar	12600.9	27.7
43		x					12601.8	28.6
44	x	x	x	x		Length*Lunar	12601.9	28.7
45	x	x					12602.9	29.7

Table 2 cont.

Model	Length	Tide	TOD	Lunar	Temp	Interactions	AICc	ΔAIC
46		x		x		Length*Lunar, TOD*lunar	12608.4	35.2
47	x	x		x		Length*Lunar, TOD*lunar	12609.6	36.4
48			x		x	TOD*Temp	12682	108.8
49	x		x		x	Length*TOD, TOD*Temp	12682.3	109.1
50	x		x		x	Length*TOD	12682.7	109.5
51	x		x		x	TOD*Temp	12683.8	110.6
52			x		x		12685	111.8
53	x		x		x		12686.8	113.6
54	x		x			Length*TOD	12689.9	116.7
55			x	x	x	Length*Lunar, TOD*Lunar, TOD*Temp	12690.5	117.3
56	x		x	x	x	Length*TOD, Length*Lunar, TOD*Lunar, TOD*Temp	12690.9	117.7
57					x		12691.1	117.9
58	x		x	x	x	Length*TOD, Length*Lunar	12691.3	118.1
59	x		x	x	x	Length*Lunar, TOD*Lunar, TOD*Temp	12692.3	119.1
60	x				x		12692.9	119.7
61			x				12693.1	119.9

Table 2 cont.

Model	Length	Tide	TOD	Lunar	Temp	Interactions	AICc	ΔAIC
63			x	x	x	Length*Lunar, TOD*Lunar	12693.5	120.3
64	x		x				12694.2	121
65	x		x	x	x	Length*TOD, Length*Lunar, TOD*Lunar, Length*TOD*Lunar	12694.6	121.4
66	x		x	x	x	Length*Lunar	12695.3	122.1
67	x		x	x		Length*TOD, Length*Lunar, TOD*Lunar	12698.2	125
68							12699	125.8
69				x	x	Length*Lunar, TOD*Lunar	12699.6	126.4
70	x						12700.1	126.9
71	x		x	x		Length*TOD, Length*Lunar, TOD*Lunar, Length*TOD*Lunar	12700.8	127.6
72			x	x		Length*Lunar, TOD*Lunar	12701.2	128
73	x			x	x	Length*Lunar, TOD*Lunar	12701.4	128.2
74	x		x	x		Length*Lunar	12702.4	129.2
75				x		Length*Lunar, TOD*Lunar	12707.1	133.9
76	x			x		Length*Lunar, TOD*Lunar	12708.3	135.1

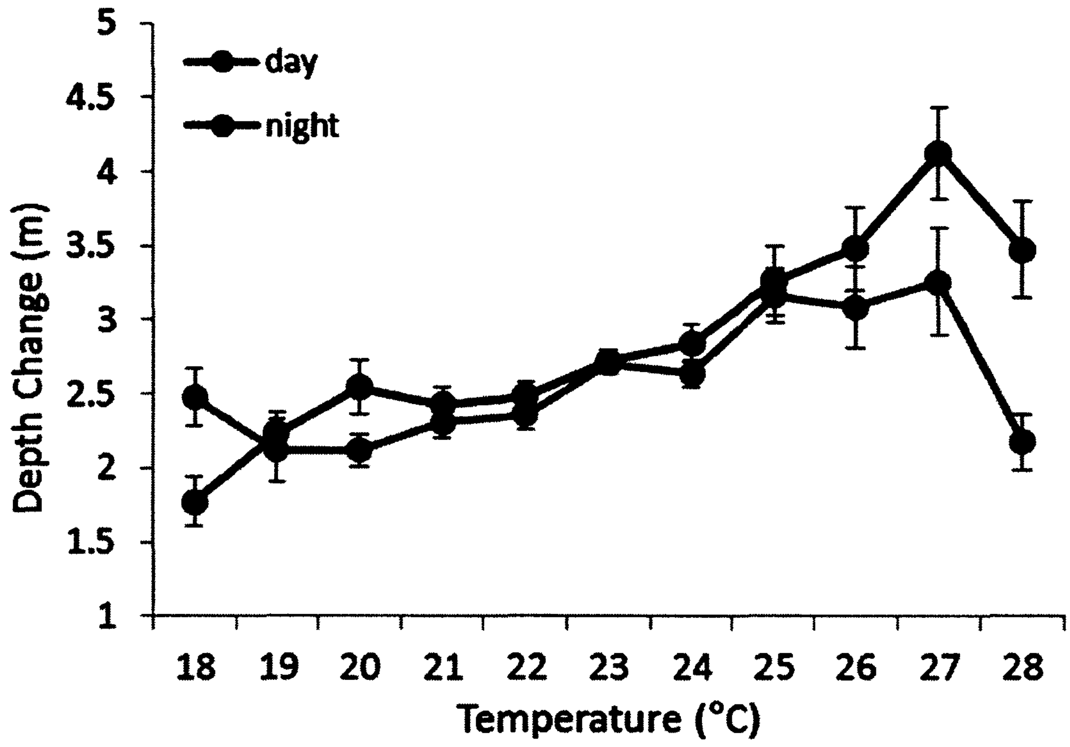


Figure 1. Interaction between water temperature and time of day on the movements of summer flounder based on depth changes observed with archival tags. Movements were observed for 14 summer flounder in the lower Chesapeake Bay during the summer of 2009. This interaction decreased the AICc values from the model with no interactions (see Table 1) and was selected in the second best model based on the fixed effects model selection (see Table 2).

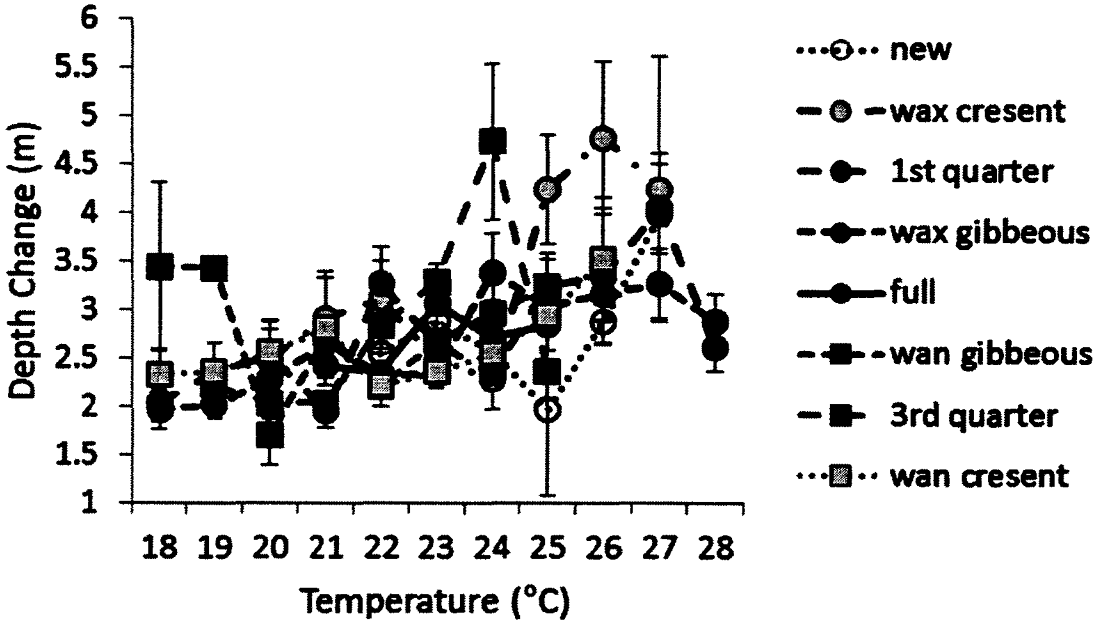


Figure 2. Interaction between water temperature and lunar phase on the movements of summer flounder based on depth changes observed with archival tags. Movements were observed for 14 summer flounder in the lower Chesapeake Bay during the summer of 2009. Although including this interaction decreased the AICc value (see Table 1), it was excluded from the mixed because the interaction appeared to be random and did not have an ecological interpretation.

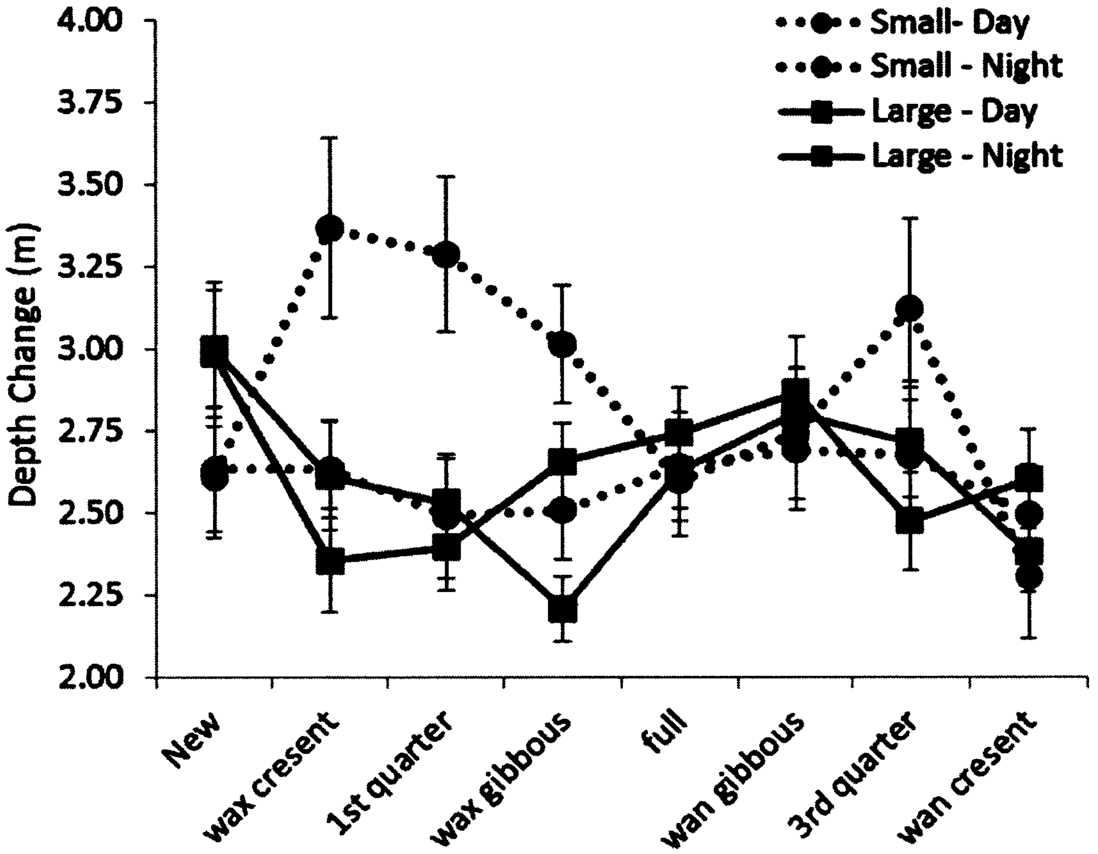


Figure 3. Interaction between lunar phase and fish size -- categorized as small (<400 mm) and large (>= 400 mm) -- on the movements of summer flounder based on depth changes observed with archival tags. Movements were observed for 14 summer flounder in the lower Chesapeake Bay during the summer of 2009. Although including this interaction decreased the AICc value (see Table 1), it was not selected as an interaction in the final model, potentially due to small sample size.

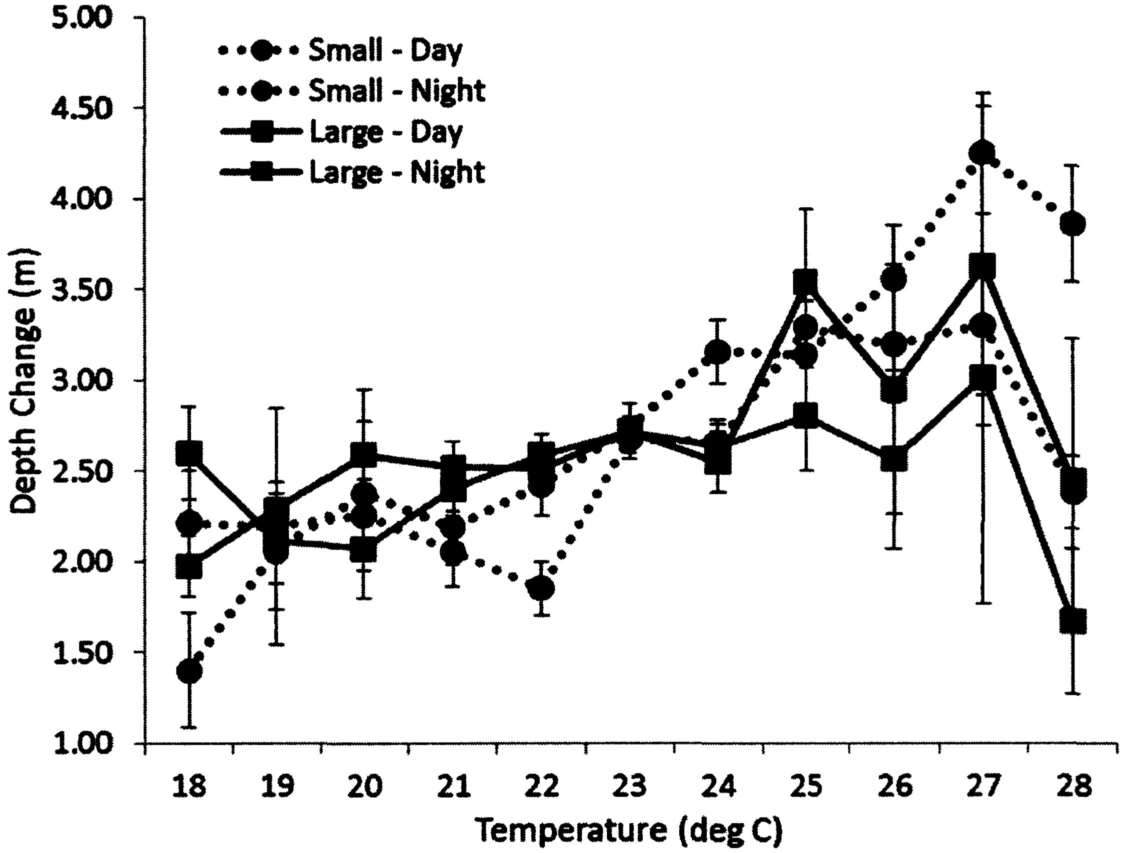


Figure 4. Interaction between water temperature, time of day, and fish size-- categorized as small (<400 mm) and large (>= 400 mm) -- on the movements of summer flounder based on depth changes observed with archival tags. Movements were observed for 14 summer flounder in the lower Chesapeake Bay during the summer of 2009. This interaction was excluded from the fixed-effects model selection because the interaction was primarily apparent only at temperatures less than 19 C and greater than 25 C. At these temperatures the sample sizes were less than 5 fish.

APPENDIX III –

ADMB Tagging Model Code

Automatic differentiation model builder (ADMB) code used to fit a Barker model to summer flounder mark-recapture data collected by the Virginia Game Fish Tagging Program from 2000 to 2011. This program uses individual encounter histories to estimate the following parameters: 1) survival probability, 2) probability of resighting (i.e. catch-and-release), 3) probability of recovery (i.e. harvest), and 4) probability of being resighted-before-death within a year. Parameters can vary annually or be considered constant throughout the study. Parameters can also vary based on fish size and can either be: 1) constant regardless of fish size, 2) differ between sublegal (< 14") and legal sized fish, or 3) differ between sublegal fish, fish subject to harvest by the commercial fishery only, or fish subject to both the commercial and recreational fishery.

```
DATA_SECTION
 //read in data from file
 init_int nEH; //number of encounter histories in dataset
 init_int intervals; // number of encounter intervals
 init_number tagdur; //duration of tagging related mortality interval in months
 init_int Stag_link; //use a logit link to model tagging related survival as a function of the release
    date (0 = no, 1 = yes)
 init_int rtag_link; //use a logit link to model recovery in the tagging interval as a function of the
    release date (0 = no, 1 = yes)
 init_int Rtag_link; //use a logit link to model resighting in the tagging interval as a function of
    the release date (0 = no, 1 = yes)
 init_int Rdtag_link; //use a logit link to model resighting- before- death in the tagging interval
    as a function of the release date (0 = no, 1 = yes)
 init_int Sstar_link; //use a logit link to model survival in the first season as a function of the
    release date (0 = no, 1 = yes)
 init_int rstar_link; //use a logit link to model recoveries in the first season as a function of the
    release date (0 = no, 1 = yes)
 init_int Rstar_link; //use a logit link to model resightings in the first season as a function of the
    release date (0 = no, 1 = yes)
 init_int Rdstar_link; //use a logit link to resightings-before-death in the first season as a
    function of the release date (0 = no, 1 = yes)
 init_int Stag_size; // does tagging related survival vary with size - 3 groups (<comm,
    >comm/<rec, >rec), 2 groups (<comm, >comm), 1 group, or there is no additional tagging
    related mortality (0)
 init_int Stag_time; // does tagging related survival vary with time (Yes = #intervals, No = 1) or
    there is no additional tagging related mortality (0)
```

init_int rtag_size; // does recovery in the tagging interval vary with size - 3 groups (<comm, >comm/<rec, >rec), 2 groups (<comm, >comm), or 1 group, or is equal to monthly recovery in the release year (0)

init_int rtag_time; // does recovery in the tagging interval vary with time (Yes = #intervals, No = 1) or there is no additional tagging related mortality (0)

init_int Rtag_size; // does resighting in the tagging interval vary with size - 3 groups (<comm, >comm/<rec, >rec), 2 groups (<comm, >comm), or 1 group, or is equal to monthly recovery in the release year (0)

init_int Rtag_time; // does resighting in the tagging interval vary with time (Yes = #intervals, No = 1) or there is no additional tagging related mortality (0)

init_int Rdtag_size; // does resighting- before- death in the tagging interval vary with size - 3 groups (<comm, >comm/<rec, >rec), 2 groups (<comm, >comm), or 1 group, or is equal to monthly recovery in the release year (0)

init_int Rdtag_time; // does resighting- before- death in the tagging interval vary with time (Yes = #intervals, No = 1) or there is no additional tagging related mortality (0)

init_int Sstar_size; // does survival in the first season vary with size - 3 groups (<comm, >comm/<rec, >rec), 2 groups (<comm, >comm), or 1 group

init_int Sstar_time; // does survival in the first season vary with time (Yes = #intervals, No = 1, survivial is not different in the first season = 0)

init_int rstar_size; // does recovery probability in the first season vary with size - 3 groups (<comm, >comm/<rec, >rec), 2 groups (<comm, >comm), or 1 group

init_int rstar_time; // does recovery probability in the first season vary with time (Yes = #intervals, No = 1, recovery is not different in the first season = 0)

init_int Rstar_size; // does resighting probability in the first season vary with size - 3 groups (<comm, >comm/<rec, >rec), 2 groups (<comm, >comm), or 1 group

init_int Rstar_time; // does resighting probability in the first season vary with time (Yes = #intervals, No = 1, Resighting is not different in the first season = 0)

init_int Rdstar_size; // does probability of resighting-before-death in the first season vary with size - 3 groups (<comm, >comm/<rec, >rec), 2 groups (<comm, >comm), or 1 group

init_int Rdstar_time; // does probability of resighting-before-death in the first season vary with time (Yes = #intervals, No = 1, Resighting-before-death is not different in the first season = 0)

init_int S_size; // does survival in VA vary with size - 3 groups (<comm, >comm/<rec, >rec), 2 groups (<comm, >comm), 1 group, or equal to a fraction of Sstar (0)

init_int S_time; // does survival in VA vary with time (Yes = #intervals, No = 1) or is equal to a fraction of Sstar (0)

init_int r_size; // does recovery probability in VA vary with size - 3 groups (<comm, >comm/<rec, >rec), 2 groups (<comm, >comm), 1 group, or is a fraction of rstar (0)

init_int r_time; // does recovery probability in VA vary with time (Yes = #intervals, No = 1) or is a fraction of rstar (0)

init_int R_size; // does resighting probability in VA vary with size - 3 groups (<comm, >comm/<rec, >rec), 2 groups (<comm, >comm), or 1 group

```
init_int R_time; // does resighting probability in VA vary with time (Yes = #intervals, No = 1) or
   is a fraction of rstar (0)
init_int Rd_size; // does probability of resighting-before-death in VA vary with size - 3 groups
   (<comm, >comm/<rec, >rec), 2 groups (<comm, >comm), or 1 group
init_int Rd_time; // does probability of resighting-before-death in VA vary with time (Yes =
   #intervals, No = 1) or is a fraction of rstar (0)

//correct the size and and time for each parameter that is set to zero. This is book-keeping so
   that the matrices in the parameter section are established correctly
!!if(Sstar_time==0 || Sstar_size==0) {Sstar_size=S_size; Sstar_time=0;}
!!if(rstar_time==0 || rstar_size==0) {rstar_size=r_size; rstar_time=0;}
!!if(Rstar_time==0 || Rstar_size==0) {Rstar_size=R_size; Rstar_time=0;}
!!if(Rdstar_time==0 || Rdstar_size==0) {Rdstar_size=Rd_size; Rdstar_time=0;}

!!if(Stag_time==0 || Stag_size==0) {Stag_size=Sstar_size; Stag_time=0;}
!!if(rtag_time==0 || rtag_size==0) {rtag_size=1; rtag_time=0;}
!!if(Rtag_time==0 || Rtag_size==0) {Rtag_size=1; Rtag_time=0;}
!!if(Rdtag_time==0 || Rdtag_size==0) {Rdtag_size=1; Rdtag_time=0;}

!!if(S_size==0 || S_time==0) {S_size=Sstar_size; S_time=0;}
!!if(r_size==0 || r_time==0) {r_size=rstar_size; r_time=0;}
!!if(R_size==0 || R_time==0) {R_size=Rstar_size; R_time=0;}
!!if(Rd_size==0 || Rd_time==0) {Rd_size=Sstar_size; Rd_time=0;}

init_matrix data(1,nEH,1,intervals+7); //read in matrix of encounter histories and tagging
   related information
vector tagID(1,nEH); //tag ID for each fish
vector tagint(1,nEH); //tagging interval for each fish
vector tagsize(1,nEH); //size state when tagged
vector comint(1,nEH); //interval when fish recruits to the commercial fishery
vector recint(1,nEH); //interval when fish recruits to the recreational fishery
matrix EH(1,nEH,1,intervals); //the capture history matrix
vector nind(1,nEH);  //number of fish with a capture history - includes negatives for fish
   harvested, released with/tags, or killed incidentally
vector tagday(1,nEH); //day within the tagging interval that each fish was tagged

//extract data on tag number, tagging interval, tagging size state, number of individuals, and
   tag day from the data matrix
!!tagID=column(data,1);
!!tagint=column(data,2);
!!tagsize=column(data,3);
!!comint=column(data,4);
```

```
 !!recint=column(data,5);
 !!nind=column(data,intervals+6);
 !!tagday=column(data,intervals+7);

PARAMETER_SECTION
 //in this section we have to initialize different sets of matrices. Let xx represent the name of a
    parameter (e.g. Stag, Sstar, Rstar, etc.)
 //The "xx_solve" matrices hold the values of the estimated parameters.  The "xx" matrices fill
    in values from the "xx_solve" matrices for every interval in the study.  The values in the "xx"
    matrices are the ones that are actually used in the likelihood.

 //initialize different matrices of estimated parameters depending on if the model uses a logit
    link to estimate tagging related survival parameters
 !!if (Stag_link==1)
 !!  {
    init_bounded_matrix Stag_alpha_solve(1,Stag_time,1,Stag_size,-100,100);
    init_bounded_matrix Stag_beta_solve(1,Stag_time,1,Stag_size,0,100);

    matrix Stag_alpha(1,intervals,1,Stag_size);
    matrix Stag_beta(1,intervals,1,Stag_size);
 !!  }
 !!else
    init_bounded_matrix Stag_solve(1,Stag_time,1,Stag_size,0,1);

 !!int s;
 !!if (rtag_size==1) s=1; else s=2;

 !!if (rtag_link==1)
 !!  {
    init_matrix rtag_alpha_solve(1,rtag_time,s,rtag_size);
    init_matrix rtag_beta_solve(1,rtag_time,s,rtag_size);

    matrix rtag_alpha(1,intervals,1,rtag_size);
    matrix rtag_beta(1,intervals,1,rtag_size);
 !!  }
 !!else
    init_bounded_matrix rtag_solve(1,rtag_time,s,rtag_size,0,1);

 !!if (Rtag_link==1)
 !!  {
    init_matrix Rtag_alpha_solve(1,Rtag_time,1,Rtag_size);
    init_matrix Rtag_beta_solve(1,Rtag_time,1,Rtag_size);
```

```
   matrix Rtag_alpha(1,intervals,1,Rtag_size);
   matrix Rtag_beta(1,intervals,1,Rtag_size);
!!  }
!!else
   init_bounded_matrix Rtag_solve(1,Rtag_time,1,Rtag_size,0,1);

!!if (Rdtag_link==1)
!!  {
   init_matrix Rdtag_alpha_solve(1,Rdtag_time,1,Rdtag_size,2);
   init_matrix Rdtag_beta_solve(1,Rdtag_time,1,Rdtag_size,2);

   matrix Rdtag_alpha(1,intervals,1,Rdtag_size);
   matrix Rdtag_beta(1,intervals,1,Rdtag_size);
!!  }
!!else
   init_bounded_matrix Rdtag_solve(1,Rdtag_time,1,Rdtag_size,0,1,2);

//initialize different matrices of estimated parameters depending on if the model uses a logit
   link to estimate survival in the first season
!!if (Sstar_link==1)
!!  {
   init_bounded_matrix Sstar_alpha_solve(1,Sstar_time,1,Sstar_size,-100,100);
   init_bounded_matrix Sstar_beta_solve(1,Sstar_time,1,Sstar_size,0,100);

   matrix Sstar_alpha(1,intervals,1,Sstar_size);
   matrix Sstar_beta(1,intervals,1,Sstar_size);
!!  }
!!else
   init_bounded_matrix Sstar_solve(1,Sstar_time,1,Sstar_size,0,1);

//initialize different matricies of estimated parameters depending on if the model uses a logit
   link to estimate encounter probabilities in the
first season
!!if (rstar_size==1) s=1; else s=2;

!!if (rstar_link==1)
!! {
   init_matrix rstar_alpha_solve(1,rstar_time,s,rstar_size);
   init_matrix rstar_beta_solve(1,rstar_time,s,rstar_size);

   matrix rstar_alpha(1,intervals,1,rstar_size);
```

```
    matrix rstar_beta(1,intervals,1,rstar_size);
!! }
!!else
   init_bounded_matrix rstar_solve(1,rstar_time,s,rstar_size,0,1);

!!if (Rstar_link==1)
!! {
    init_matrix Rstar_alpha_solve(1,Rstar_time,1,Rstar_size);
    init_matrix Rstar_beta_solve(1,Rstar_time,1,Rstar_size);

    matrix Rstar_alpha(1,intervals,1,Rstar_size);
    matrix Rstar_beta(1,intervals,1,Rstar_size);
!! }
!!else
   init_bounded_matrix Rstar_solve(1,Rstar_time,1,Rstar_size,0,1);

!!if (Rdstar_link==1)
!! {
    init_matrix Rdstar_alpha_solve(1,Rdstar_time,1,Rdstar_size,2);
    init_matrix Rdstar_beta_solve(1,Rdstar_time,1,Rdstar_size,2);

    matrix Rdstar_alpha(1,intervals,1,Rdstar_size);
    matrix Rdstar_beta(1,intervals,1,Rdstar_size);
!! }
!!else
   init_bounded_matrix Rdstar_solve(1,Rdstar_time,1,Rdstar_size,0,1,2);

//initialize matrices for the parameters that will be used in the likelihood. When logit link
    functions are used, the values within these matrices are set equal to the logit link of the
    estimated alpha and beta parameters
matrix Stag(1,intervals,1,Stag_size);
matrix rtag(1,intervals,1,rtag_size);
matrix Rtag(1,intervals,1,Rtag_size);
matrix Rdtag(1,intervals,1,Rdtag_size);
matrix Sstar(1,intervals,1,Sstar_size);
matrix rstar(1,intervals,1,rstar_size);
matrix Rstar(1,intervals,1,Rstar_size);
matrix Rdstar(1,intervals,1,Rdstar_size);

//initialize matrices for the estimated and likelihood parameters representing survival and
    encounters probabilites for fish in Virginia
```

```
 !!int t;
 !!if (S_time==intervals && Sstar_time!=0) t=2; else t=1;
 init_bounded_matrix S_solve(t,S_time,1,S_size,0,1);
 !!if (r_time==intervals && rstar_time!=0) t=2; else t=1;
 !!if (r_size==1) s=1; else s=2;
 init_bounded_matrix r_solve(t,r_time,s,r_size,0,1);
 !!if (R_time==intervals && Rstar_time!=0) t=2; else t=1;
 init_bounded_matrix R_solve(t,R_time,1,R_size,0,1);
 !!if (Rd_time==intervals && Rdstar_time!=0) t=2; else t=1;
 init_bounded_matrix Rd_solve(t,Rd_time,1,Rd_size,0,1,2);

 matrix S(2,intervals,1,S_size);
 matrix r(2,intervals,1,r_size);
 matrix R(2,intervals,1,R_size);
 matrix Rd(2,intervals,1,Rd_size);

 number chitag; //probability of never seeing a fish after tagging
 number chistar; //probability of never seeing a fish after the first year
 vector chi(1,intervals+1); //probability of never seeing a fish again
 vector probs(1,nEH); //probability of observing a particular likelihood

 number npar; //number of parameters estimated in the model
 number AIC; //Akaikes information criterion

 objective_function_value negLL; //the likelihood to minimize

PRELIMINARY_CALCS_SECTION
 int i,j;

 //initialize capture history matrix
 EH = 0;

 //build capture history matrix
 for (i=1;i<=nEH;i++) for (j=1;j<=intervals;j++) EH(i,j) = data(i,j+5);

 //calculate the number of parameters estimated for the model depending on size and time
    dependence of each parameter
 npar = Stag_size*Stag_time + rtag_size*rtag_time + Rtag_size*Rtag_time +
    Rdtag_size*Rdtag_time;
 if(rtag_size!=1) npar -= rtag_time;
 npar += Sstar_size*Sstar_time + rstar_size*rstar_time + Rstar_size*Rstar_time +
    Rdstar_size*Rdstar_time;
```

```
if(rstar_size!=1) npar -= rstar_time;
npar += S_size*S_time + r_size*r_time + R_size*R_time + Rd_size*Rd_time;
if(S_time==intervals) npar -= S_size; //correct for the last tagging interval, which only has an
   Stag and Sstar
if(r_time==intervals)
 {
  if(r_size==1)
   npar -= 1;
  else
   npar -= r_size-1; //correct for the last tagging interval, which only has an rtag and rstar
 }
if(R_time==intervals) npar -= R_size; //correct for the last tagging interval, which only has an
   Rtag and Rstar
if(Rd_time==intervals) npar -= Rd_size; //correct for the last tagging interval, which only has an
   Rdtag and Rdstar
if(r_size!=1) npar -= r_time;

if(Stag_link==1)
 npar += Stag_size*Stag_time;

if(rtag_link==1)
 {
  npar +=  rtag_size*rtag_time;
  if(rtag_size!=1) npar -= rtag_time;
 }

if(Rtag_link==1)
 npar += Rtag_size*Rtag_time;

if(Rdtag_link==1)
 npar += Rdtag_size*Rdtag_time;

if(Sstar_link==1)
 npar += Sstar_size*Sstar_time;

if(rstar_link==1)
 {
  npar +=  rstar_size*rstar_time;
  if(rstar_size!=1) npar -= rstar_time;
 }

if(Rstar_link==1)
```

```
  npar +=  Rstar_size*Rstar_time;

 if(Rdstar_link==1)
  npar +=  Rdstar_size*Rdstar_time;

PROCEDURE_SECTION
 int i,j,t,day;

 //determine what parameter estimates to use for the likelihood depending on if a link is used,
        the number of size classes and time periods for each parameter in the first season
 for(i=1;i<=intervals;i++)
  for(j=1;j<=Sstar_size;j++)
   if (Sstar_link==1)
    {
     if(Sstar_time==intervals)
      {
           Sstar_alpha(i,j)=Sstar_alpha_solve(i,j);
       Sstar_beta(i,j)=Sstar_beta_solve(i,j);
      }
     else
      {
       Sstar_alpha(i,j)=Sstar_alpha_solve(1,j);
       Sstar_beta(i,j)=Sstar_beta_solve(1,j);
      }
    }
   else
    {
     if(Sstar_time==intervals)
      Sstar(i,j)=Sstar_solve(i,j);
     else if (Sstar_time != 0)
      Sstar(i,j)=Sstar_solve(1,j);
     else
      {
       if(S_time==intervals)
        Sstar(i,j)=S_solve(i,j);
       else
        Sstar(i,j)=S_solve(1,j);
      }
    }

 for(i=1;i<=intervals;i++)
  for(j=1;j<=rstar_size;j++)
```

```
  {
   if(rstar_size>1 && j==1) j=2;

   if (rstar_link==1)
    {
     if(rstar_time==intervals)
      {
       rstar_alpha(i,j)=rstar_alpha_solve(i,j);
       rstar_beta(i,j)=rstar_beta_solve(i,j);
      }
     else
      {
       rstar_alpha(i,j)=rstar_alpha_solve(1,j);
       rstar_beta(i,j)=rstar_beta_solve(1,j);
      }
    }
   else
    {
     if(rstar_time==intervals)
      rstar(i,j)=rstar_solve(i,j);
     else if (rstar_time != 0)
      rstar(i,j)=rstar_solve(1,j);
     else
      {
       if (r_time==intervals)
        rstar(i,j)=r_solve(i,j);
       else
        rstar(i,j)=r_solve(1,j);
      }
    }
  }

for(i=1;i<=intervals;i++)
 for(j=1;j<=Rstar_size;j++)
  if (Rstar_link==1)
   {
    if(Rstar_time==intervals)
     {
      Rstar_alpha(i,j)=Rstar_alpha_solve(i,j);
      Rstar_beta(i,j)=Rstar_beta_solve(i,j);
     }
    else
```

```
       {
        Rstar_alpha(i,j)=Rstar_alpha_solve(1,j);
        Rstar_beta(i,j)=Rstar_beta_solve(1,j);
       }
     }
    else
     {
      if(Rstar_time==intervals)
       Rstar(i,j)=Rstar_solve(i,j);
      else if (Rstar_time != 0)
       Rstar(i,j)=Rstar_solve(1,j);
      else
       {
        if (R_time==intervals)
         Rstar(i,j)=R_solve(i,j);
        else
         Rstar(i,j)=R_solve(1,j);
       }
     }

for(i=1;i<=intervals;i++)
  for(j=1;j<=Rdstar_size;j++)
    if (Rdstar_link==1)
     {
      if(Rdstar_time==intervals)
       {
            Rdstar_alpha(i,j)=Rdstar_alpha_solve(i,j);
        Rdstar_beta(i,j)=Rdstar_beta_solve(i,j);
       }
      else
       {
        Rdstar_alpha(i,j)=Rdstar_alpha_solve(1,j);
        Rdstar_beta(i,j)=Rdstar_beta_solve(1,j);
       }
     }
    else
     {
      if(Rdstar_time==intervals)
       Rdstar(i,j)=Rdstar_solve(i,j);
      else if (Rdstar_time != 0)
       Rdstar(i,j)=Rdstar_solve(1,j);
      else
```

```
      {
       if (Rd_time==intervals)
        Rdstar(i,j)=Rd_solve(i,j);
       else
        Rdstar(i,j)=Rd_solve(1,j);
      }
    }


//establish matrices when tagging related mortality is estimated
for(i=1;i<=intervals;i++)
 for(j=1;j<=Stag_size;j++)
  if (Stag_link==1)
   {
    if(Stag_time==intervals)
     {
      Stag_alpha(i,j)=Stag_alpha_solve(i,j);
      Stag_beta(i,j)=Stag_beta_solve(i,j);
     }
    else
     {
      Stag_alpha(i,j)=Stag_alpha_solve(1,j);
      Stag_beta(i,j)=Stag_beta_solve(1,j);
     }
   }
  else
   {
    if(Stag_time==intervals)
     Stag(i,j)=Stag_solve(i,j);
    else if (Stag_time != 0)
     Stag(i,j)=Stag_solve(1,j);
    else
     {
      //use the Sstar parameters to estimate survival probabilites as a function of the tagging
         season duration (VGFTP is either 30 or 90 days)
      if(Sstar_link==0)
       Stag(i,j)=pow(Sstar(i,j),tagdur/(365-tagdur));
      else
       Stag(i,j)=pow(mfexp(Sstar_alpha(i,j) + Sstar_beta(i,j))/(1+mfexp(Sstar_alpha(i,j) +
         Sstar_beta(i,j))),tagdur/(365-tagdur));
     }
   }
```

```
for(i=1;i<=intervals;i++)
 for(j=1;j<=rtag_size;j++)
  {
   if(rtag_size>1 && j==1) j=2;

   if (rtag_link==1)
    {
     if(rtag_time==intervals)
      {
          rtag_alpha(i,j)=rtag_alpha_solve(i,j);
        rtag_beta(i,j)=rtag_beta_solve(i,j);
      }
     else
      {
       rtag_alpha(i,j)=rtag_alpha_solve(1,j);
       rtag_beta(i,j)=rtag_beta_solve(1,j);
      }
    }
   else
    {
     if(rtag_time==intervals)
      rtag(i,j)=rtag_solve(i,j);
     else if (rtag_time != 0)
      rtag(i,j)=rtag_solve(1,j);
     else
      rtag(i,1)=0;
    }
  }

for(i=1;i<=intervals;i++)
 for(j=1;j<=Rtag_size;j++)
  if (Rtag_link==1)
   {
    if(Rtag_time==intervals)
     {
      Rtag_alpha(i,j)=Rtag_alpha_solve(i,j);
      Rtag_beta(i,j)=Rtag_beta_solve(i,j);
     }
    else
     {
      Rtag_alpha(i,j)=Rtag_alpha_solve(1,j);
```

```
        Rtag_beta(i,j)=Rtag_beta_solve(1,j);
       }
     }
    else
     {
      if(Rtag_time==intervals)
        Rtag(i,j)=Rtag_solve(i,j);
      else if (Rtag_time != 0)
        Rtag(i,j)=Rtag_solve(1,j);
      else
        Rtag(i,1)=0;
     }

 for(i=1;i<=intervals;i++)
  for(j=1;j<=Rdtag_size;j++)
    if (Rdtag_link==1)
     {
      if(Rdtag_time==intervals)
       {
        Rdtag_alpha(i,j)=Rdtag_alpha_solve(i,j);
        Rdtag_beta(i,j)=Rdtag_beta_solve(i,j);
       }
      else
       {
        Rdtag_alpha(i,j)=Rdtag_alpha_solve(1,j);
        Rdtag_beta(i,j)=Rdtag_beta_solve(1,j);
       }
     }
    else
     {
      if(Rdtag_time==intervals)
        Rdtag(i,j)=Rdtag_solve(i,j);
      else if (Rdtag_time != 0)
        Rdtag(i,j)=Rdtag_solve(1,j);
      else
        Rdtag(i,1)=0;
     }

 //determine what parameter estimates to use for the likelihood depending on the number of
          size classes and time periods for each parameter
in Virginia after the first season
 for(i=2;i<=intervals;i++)
```

```
 for(j=1;j<=S_size;j++)
  if(S_time==intervals)
    S(i,j)=S_solve(i,j);
  else if (S_time!=0)
    S(i,j)=S_solve(1,j);
  else
   {
    //use the Sstar parameters to estimate survival probabilites as a function of the tagging
         season duration (30 or 90 days for VGFTP)
    if(Sstar_link==0)
     S(i,j)=pow(Sstar(i,j),365/(365-tagdur));
    else
     S(i,j)=pow(mfexp(Sstar_alpha(i,j) + Sstar_beta(i,j))/(1+mfexp(Sstar_alpha(i,j) +
         Sstar_beta(i,j))),365/(365-tagdur));
   }

for(i=2;i<=intervals;i++)
 for(j=1;j<=r_size;j++)
  {
   if(r_size>1 && j==1) j=2;

   if(r_time==intervals)
    r(i,j)=r_solve(i,j);
   else if (r_time!=0)
    r(i,j)=r_solve(1,j);
   else
    {
     if(rstar_link==0)
      r(i,j)=pow(rstar(i,j),365/(365-tagdur));
     else
      r(i,j)=pow(mfexp(rstar_alpha(i,j) + rstar_beta(i,j))/(1+mfexp(rstar_alpha(i,j) +
         rstar_beta(i,j))),365/(365-tagdur));
    }
  }

for(i=2;i<=intervals;i++)
 for(j=1;j<=R_size;j++)
  if(R_time==intervals)
   R(i,j)=R_solve(i,j);
  else if (R_time!=0)
   R(i,j)=R_solve(1,j);
  else
```

```
    {
     if(Rstar_link==0)
      R(i,j)=pow(Rstar(i,j),365/(365-tagdur));
     else
      R(i,j)=pow(mfexp(Rstar_alpha(i,j) + Rstar_beta(i,j))/(1+mfexp(Rstar_alpha(i,j) +
         Rstar_beta(i,j))),365/(365-tagdur));
    }

 for(i=2;i<=intervals;i++)
  for(j=1;j<=Rd_size;j++)
   if(Rd_time==intervals)
    Rd(i,j)=Rd_solve(i,j);
   else if (Rd_time!=0)
    Rd(i,j)=Rd_solve(1,j);
   else
    {
     if(Rdstar_link==0)
      Rd(i,j)=pow(Rdstar(i,j),365/(365-tagdur));
     else
      Rd(i,j)=pow(mfexp(Rdstar_alpha(i,j) + Rdstar_beta(i,j))/(1+mfexp(Rdstar_alpha(i,j) +
         Rdstar_beta(i,j))),365/(365-tagdur));
    }

 CalculateLikelihood();

 //initialize and calculate the AIC value
 AIC=0;
 AIC=(2*negLL)+(2*npar);

//-------------- Functions --------------------------------------------//

//calculate the likelihood based probability of capture for each capture history

FUNCTION CalculateLikelihood

 //declare and initialize the parameters that are only needed in this function
 int i, j, k, e, first, com, rec, last, ind, tagsz, sz, Stagsz, rtagsz, Rtagsz, Rdtagsz, Sstarsz, rstarsz,
    Rstarsz, Rdstarsz;
 first = com = rec = last = ind = tagsz = sz = Stagsz = rtagsz = Rtagsz = Rdtagsz = Sstarsz = rstarsz =
    Rstarsz = Rdstarsz = 0;
 double day;
 ivector Ssz(1,intervals);
```

```
ivector rsz(1,intervals);
ivector Rsz(1,intervals);
ivector Rdsz(1,intervals);

//initialize the negative log-likelihood, which is the value to be minimized in this function
negLL=0;

//this is the start of the main loop and is repeated for every fish in the encounter history. From
   here on out individual fish are identified by (i)
for (i = 1; i <= nEH; i++)
 {
  //get values for each fish that are either input in the data file or are calculated with the
   LastObs function
  ind = nind(i);
  first = tagint(i);
  tagsz = tagsize(i);
  com = comint(i);
  rec = recint(i);
  last = LastObs(i);
  if (last==0) last=first;

  //determine the size of each fish throughout every interval in the study.  Then determine
   which size class to use for each variable depending on the number of size classes modeled
   for that variable
  //Note: I determined the intervals when a fish recruited to the commercial fishery (com) and
   the recreational fishery (rec) using a growth model that I fit to the tagging data.  This was
   done in another program.

  if (Stag_size==1) Stagsz = 1;
  else if (Stag_size==2)
   {
    if (tagsz==2 || tagsz==3) Stagsz = 2;
    else Stagsz = 1;
   }
  else Stagsz = tagsz;

  if (rtag_size==1) rtagsz = 1;
  else if (rtag_size==2)
   {
    if (tagsz==2 || tagsz==3) rtagsz = 2;
    else rtagsz = 1;
   }
```

```
else rtagsz = tagsz;

if (Rtag_size==1) Rtagsz = 1;
else if (Rtag_size==2)
 {
  if (tagsz==2 || tagsz==3) Rtagsz = 2;
  else Rtagsz = 1;
 }
else Rtagsz = tagsz;

if (Rdtag_size==1) Rdtagsz = 1;
else if (Rdtag_size==2)
 {
  if (tagsz==2 || tagsz==3) Rdtagsz = 2;
  else Rdtagsz = 1;
 }
else Rdtagsz = tagsz;

if (first<com) sz=1;
else if (first>=com && first<rec) sz=2;
else sz=3;

if (Sstar_size==1) Sstarsz = 1;
else if (Sstar_size==2)
 {
  if (sz==2 || sz==3) Sstarsz=2;
  else Sstarsz=1;
 }
else Sstarsz=sz;

if (rstar_size==1) rstarsz = 1;
else if (rstar_size==2)
 {
  if (sz==2 || sz==3) rstarsz=2;
  else rstarsz=1;
 }
else rstarsz=sz;

if (Rstar_size==1) Rstarsz = 1;
else if (Rstar_size==2)
 {
  if (sz==2 || sz==3) Rstarsz=2;
```

```
  else Rstarsz=1;
 }
else Rstarsz=sz;

if (Rdstar_size==1) Rdstarsz = 1;
else if (Rdstar_size==2)
 {
  if (sz==2 || sz==3) Rdstarsz=2;
  else Rdstarsz=1;
 }
else Rdstarsz=sz;

for (j=1; j<=intervals; j++)
 {
  if (j < first) sz=tagsz;
  else if (j>=first && j<com) sz=1;
  else if (j>=com && j<rec) sz=2;
  else sz=3;

  if (S_size==1) Ssz(j) = 1;
  else if (S_size==2)
   {
    if (sz==2 || sz==3) Ssz(j)=2;
    else Ssz(j)=1;
   }
  else Ssz(j)=sz;

  if (r_size==1) rsz(j) = 1;
  else if (r_size==2)
   {
    if (sz==2 || sz==3) rsz(j)=2;
    else rsz(j)=1;
   }
  else rsz(j)=sz;

  if (R_size==1) Rsz(j) = 1;
  else if (R_size==2)
   {
    if (sz==2 || sz==3) Rsz(j)=2;
    else Rsz(j)=1;
   }
  else Rsz(j)=sz;
```

```
    if (Rd_size==1) Rdsz(j) = 1;
    else if (Rd_size==2)
     {
      if (sz==2 || sz==3) Rdsz(j)=2;
      else Rdsz(j)=1;
     }
    else Rdsz(j)=sz;
   }

///////////////////////////////////    Link functions ////////////////////////////////////////////

  //link function to estimate tagging related survival as a function of when a fish was tagged
    during the tagging interval
  if (Stag_link==1)
   {
    day=tagday(i);
    Stag(first,Stagsz)=mfexp(Stag_alpha(first,Stagsz) +
        Stag_beta(first,Stagsz)*day)/(1+mfexp(Stag_alpha(first,Stagsz) +
        Stag_beta(first,Stagsz)*day));
   }

  //link function to estimate recovery in the tagging related mortality interval as a function of
    when a fish was tagged within an interval
  if (rtag_link==1)
   {
    day=tagday(i);
    //set recovery probability equal to zero if the fish is smaller than the commercial size limit
    if(rtag_size!=0 && rtagsz==1) rtag(first,rtagsz)=0;
    rtag(first,rtagsz)=mfexp(rtag_alpha(first,rtagsz) +
        rtag_beta(first,rtagsz)*day)/(1+mfexp(rtag_alpha(first,rtagsz) +
        rtag_beta(first,rtagsz)*day));
   }

  //link function to estimate resighting in the tagging related mortality interval as a function of
    when a fish was tagged within an interval
  if (Rtag_link==1)
   {
    day=tagday(i);
    Rtag(first,Rtagsz)=mfexp(Rtag_alpha(first,Rtagsz) +
        Rtag_beta(first,Rtagsz)*day)/(1+mfexp(Rtag_alpha(first,Rtagsz) +
        Rtag_beta(first,Rtagsz)*day));
```

```
   }

   //link function to estimate resighting before death in the tagging related mortality interval as
    a function of when a fish was tagged within an
interval
    if (Rdtag_link==1)
    {
     day=tagday(i);
     Rdtag(first,Rdtagsz)=mfexp(Rdtag_alpha(first,Rdtagsz) +
          Rdtag_beta(first,Rdtagsz)*day)/(1+mfexp(Rdtag_alpha(first,Rdtagsz) +
          Rdtag_beta(first,Rdtagsz)*day));
    }

   //link function to estimate survival in the first year as a function of when a fish was tagged
    during the tagging interval
   if (Sstar_link==1)
    {
     day=tagday(i);
     Sstar(first,Sstarsz)=mfexp(Sstar_alpha(first,Sstarsz) +
          Sstar_beta(first,Sstarsz)*day)/(1+mfexp(Sstar_alpha(first,Sstarsz) +
          Sstar_beta(first,Sstarsz)*day));
    }

   //link function to estimate recovery in the first year as a function of when a fish was tagged
    within an interval
   if (rstar_link==1)
    {
     day=tagday(i);
     //set recovery probability equal to zero if the fish is smaller than the commercial size limit
     if(rstar_size!=0 && rstarsz==1) rstar(first,rstarsz)=0;
     rstar(first,rstarsz)=mfexp(rstar_alpha(first,rstarsz) +
          rstar_beta(first,rstarsz)*day)/(1+mfexp(rstar_alpha(first,rstarsz) +
          rstar_beta(first,rstarsz)*day));
    }

   //link function to estimate resighting in the first year as a function of when a fish was tagged
    within an interval
   if (Rstar_link==1)
    {
     day=tagday(i);
```

```
  Rstar(first,Rstarsz)=mfexp(Rstar_alpha(first,Rstarsz) +
       Rstar_beta(first,Rstarsz)*day)/(1+mfexp(Rstar_alpha(first,Rstarsz) +
       Rstar_beta(first,Rstarsz)*day));
 }

//link function to estimate resighting before death in the first year as a function of when a
  fish was tagged within an interval
if (Rdstar_link==1)
 {
  day=tagday(i);
  Rdstar(first,Rdstarsz)=mfexp(Rdstar_alpha(first,Rdstarsz) +
       Rdstar_beta(first,Rdstarsz)*day)/(1+mfexp(Rdstar_alpha(first,Rdstarsz) +
       Rdstar_beta(first,Rdstarsz)*day));
 }

//////////////////////          Calculate chis       ////////////////////////////////////////

//calculate probabilities that a fish is never seen again when the fish was last known to be
  within Virginia
for (j=intervals+1;j>=2;j--)
 {
  if (j == intervals+1)
    chi(j) = 1; //after the final sampling season the probability of encounter is zero (or the log
  of 1)
  else
   {
    if (r_size>1) r(j,1)=0;
    chi(j) = (1-S(j,Ssz(j)))*(1-r(j,rsz(j)))*(1-Rd(j,Rdsz(j))) + S(j,Ssz(j))*(1-R(j,Rsz(j)))*chi(j+1);
   }
 }

//calculate probabilities that a fish is never seen again after the first year
if (rstar_size>1) rstar(first,1)=0;
chistar = (1-Sstar(first,Sstarsz))*(1-rstar(first,rstarsz))*(1-Rdstar(first,Rdstarsz)) +
    Sstar(first,Sstarsz)*(1-Rstar(first,Rstarsz))*chi(first+1);

//calculate probabilities that a fish is never seen again after being tagged
if (rtag_size>1) rtag(first,1)=0;
chitag = (1-Stag(first,Stagsz))*(1-rtag(first,rtagsz))*(1-Rdtag(first,Rdtagsz)) +
    Stag(first,Stagsz)*(1-Rtag(first,Rtagsz))*chistar;

///////////////////////         Calculate probabilities        /////////////////////////////
```

```
probs(i) = 0;

//This is the loop to estimate probabilities for each fish's encounter history.  Encounter
  histories can have values of:
// 0.1 - fish that are encountered within the first year
// 1 - fish that are encountered in Virginia after the first year
// 2 - fish that are encountered outside Virginia - we assume that fish do not emigrate in the
      tagging interval so this can only happen after the first year
// 999 - the recapture location of this fish is unknown. These recaptures are ignored if the
      occur between the last resighting in VA and the first resighting outside of VA, but they
      are included in the likelihood if they are the last known encounter of this fish and the
      fish was not previously encountered outside of VA
// Negative values within the encounter history indicate that this fish was killed incidentally
      by the recapture fisher, or that the tag was removed by the recapture angler.

for (j = first; j <= last; j++)
 {
  //if there is no emigration set every encounter to have occurred within Virginia
  if (EH(i,j) == 2 || EH(i,j) == 999)
   EH(i,j) = 1;
  else if (EH(i,j) == -2 || EH(i,j) == -999)
   EH(i,j) = -1;

 // probabilities between tagging and last known encounter
 if (j < last)
  {
   //estimate tagging related survival, first season survival, and first season resighting based
      on encounter history
   if (j == first)
    {
     if (EH(i,j) == 1.1)
      probs(i) += log(Stag(j,Stagsz)*Rtag(j,Rtagsz)*Sstar(j,Sstarsz)*Rstar(j,Rstarsz));
     else if (EH(i,j) == 1)
      probs(i) += log(Stag(j,Stagsz)*(1-Rtag(j,Rtagsz))*Sstar(j,Sstarsz)*Rstar(j,Rstarsz));
     else if (EH(i,j) == 0.1)
      probs(i) += log(Stag(j,Stagsz)*Rtag(j,Rtagsz)*Sstar(j,Sstarsz)*(1-Rstar(j,Rstarsz)));
     else
      probs(i) += log(Stag(j,Stagsz)*(1-Rtag(j,Rtagsz))*Sstar(j,Sstarsz)*(1-Rstar(j,Rstarsz)));
    }
   //estimate probabilities while a fish is known to still be within Virginia waters
   else
```

```
    {
     if (EH(i,j) != 0)
       probs(i) += log(S(j,Ssz(j))*R(j,Rsz(j)));
     else
       probs(i) += log(S(j,Ssz(j))*(1-R(j,Rsz(j))));
    }
 }
 //probabilities a fish is recovered, indicated by a negative number of individuals
else if (EH(i,j)>0 && ind == -1)
  {
   if (EH(i,j) == 0.1)
     probs(i) += log((1-Stag(j,Stagsz))*rtag(j,rtagsz));
   else if (EH(i,j) == 1.1)
     probs(i) += log(Stag(j,Stagsz)*Rtag(j,Rtagsz)*(1-Sstar(j,Sstarsz))*rstar(j,rstarsz));
   else if (EH(i,j) == 1 && j == first)
     probs(i) += log(Stag(j,Stagsz)*(1-Rtag(j,Rtagsz))*(1-Sstar(j,Sstarsz))*rstar(j,rstarsz));
   else if (EH(i,j) == 1)
     probs(i) += log((1-S(j,Ssz(j)))*r(j,rsz(j)));
  }
//probabilities a fish is killed incidentally or released without tag
else if (EH(i,j)<0)
  {
   if (EH(i,j) == -0.1)
     probs(i) += log((1-Stag(j,Stagsz))*(1-rtag(j,rtagsz))*Rdtag(j,Rdtagsz) +
                     Stag(j,Stagsz)*Rtag(j,Rtagsz));
   else if (EH(i,j) == -1.1)
     probs(i) += log(Stag(j,Stagsz)*Rtag(j,Rtagsz)*((1-Sstar(j,Sstarsz))*(1-
                     rstar(j,rstarsz))*Rdstar(j,Rdstarsz) + Sstar(j,Sstarsz)*Rstar(j,Rstarsz)));
   else if (EH(i,j) == -1 && j == first)
     probs(i) += log(Stag(j,Stagsz)*(1-Rtag(j,Rtagsz))*((1-Sstar(j,Sstarsz))*(1-
                     rstar(j,rstarsz))*Rdstar(j,Rdstarsz) + Star(j,Sstarsz)*Rstar(j,Rstarsz)));
   else if (EH(i,j) == -1)
     probs(i) += log((1-S(j,Ssz(j)))*(1-r(j,rsz(j)))*Rd(j,Rdsz(j)) + S(j,Ssz(j))*R(j,Rsz(j)));
  }
//probabilities a fish is last resighted and released alive with tag
else if (EH(i,j)>0)
  {
   if (EH(i,j) == 0.1)
     probs(i) += log((1-Stag(j,Stagsz))*(1-rtag(j,rtagsz))*Rdtag(j,Rdtagsz) +
                      Stag(j,Stagsz)*Rtag(j,Rtagsz)*chistar);
   else if (EH(i,j) == 1.1)
```

```
      probs(i) += log(Stag(j,Stagsz)*Rtag(j,Rtagsz)*((1-Sstar(j,Sstarsz))*(1-
                 rstar(j,rstarsz))*Rdstar(j,Rdstarsz) + Sstar(j,Sstarsz)*Rstar(j,Rstarsz)*chi(j+1)));
     else if (EH(i,j) == 1 && j == first)
      probs(i) += log(Stag(j,Stagsz)*(1-Rtag(j,Rtagsz))*((1-Sstar(j,Sstarsz))*(1-
                 rstar(j,rstarsz))*Rdstar(j,Rdstarsz) + Sstar(j,Sstarsz)*Rstar(j,Rstarsz)*chi(j+1)));
     else if (EH(i,j) == 1)
      probs(i) += log((1-S(j,Ssz(j)))*(1-r(j,rsz(j)))*Rd(j,Rdsz(j)) + S(j,Ssz(j))*R(j,Rsz(j))*chi(j+1));
     }
    //probabilities if a fish is never encountered after release
    else if (EH(i,j) == 0)
     probs(i) += log(chitag);
   }
  //sum up the probabilities for all fish in the encounter history.  This is the value that is
   minimized.
  negLL += -(fabs(ind)*probs(i));
  }

//determine the last time a fish was encountered
FUNCTION int LastObs(int x)
 int i, Last=0;
 for (i=1; i<=intervals; i++)
       if (EH(x,i)!=0)
         Last = i;
 return Last;
```

APPENDIX IV

Tagging Model Selection Table and Final Tagging Model Parameter Estimates

Table 1. Model selection table for the various Barker models fit to summer flounder mark-recapture data collected by the Virginia Game Fish Tagging Program from 2000-2011. These models were used to estimate survival (S), harvest (h), resighting (R), and resighting before death (R') probabilities for summer flounder during the first 30-days at liberty (tagging interval), remainder of release year (release year), and subsequent intervals (post release year). To select the most parsimonious model we first fit a simple starting model and then developed a series of potential models to address six questions: 1) does survival in the *release year* vary with release date, 2) how many size classes are needed to model survival and encounter probabilities in the *release year*, 3) how many size classes are needed to model survival and encounter probabilities in the *tagging interval*, 4) how many size classes are needed to model survival and encounter probabilities *after the release year*, 5) do survival and encounter probabilities in the *release year* vary inter-annually, and 6) do survival and encounter probabilities in the *tagging interval* vary inter-annually? For each of the above questions, the model with the lowest Akaike's information criterion (AIC) value was selected (shown in bold) and used as the base model for the subsequent question. Also shown are the number of parameters (npar) and the difference between a given model's AIC value and the minimum AIC value for all models considered (ΔAIC). Notations within parentheses indicate if the parameter: 1) was constant for all size classes and throughout the study (.), 2) varied between sublegal and legal sized fish (2sz), 3) varied among fish that were sublegal, vulnerable only to the commercial fishery, or vulnerable to both the commercial and recreational fishery (3sz), 4) varied throughout the 12 years of the study (t), or 5) varied between sublegal and legal fish as well as through time (2sz*t). Parameters that are estimated with a generalized linear model, using release date as a covariate, are subscripted with Logit.

Model	Tagging Interval	Release Year	Post Release Year	npar	AIC	Δ AIC
Start	S(.)h(3sz)R(.)R'(.)	$S(.)h_{\text{Logit}}(3sz)R_{\text{Logit}}(.)R'(.)$	S(.)h(3sz)R(.)R'(.)	18	31505.6	233.5
1.1	**S(.)h(3sz)R(.)R'(.)**	$\mathbf{S_{\text{Logit}}(.)h_{\text{Logit}}(3sz)R_{\text{Logit}}(.)R'(.)}$	**S(.)h(3sz)R(.)R'(.)**	**19**	**31480.5**	**208.4**

*Note – Hessian not positive definite

Table 1 cont.

Model	Tagging Interval	Release Year	Post Release Year	npar	AIC	Δ AIC
2.1	S(.)h(3sz)R(.)R'(.)	$S_{Logit}(.)h_{Logit}(3sz)R_{Logit}(2sz)R'(2sz)$	S(.)h(3sz)R(.)R'(.)	22	33241.2	1969.1*
2.2	S(.)h(3sz)R(.)R'(.)	$S_{Logit}(2sz)h_{Logit}(3sz)R_{Logit}(2sz)R'(2sz)$	S(.)h(3sz)R(.)R'(.)	24	31477.9	205.8
2.3	S(.)h(3sz)R(.)R'(.)	$S_{Logit}(.)h_{Logit}(3sz)R_{Logit}(2sz)R'(.)$	S(.)h(3sz)R(.)R'(.)	21	31482.6	210.5
2.4	S(.)h(3sz)R(.)R'(.)	$S_{Logit}(2sz)h_{Logit}(3sz)R_{Logit}(2sz)R'(.)$	S(.)h(3sz)R(.)R'(.)	23	31478.8	206.7
2.5	S(.)h(3sz)R(.)R'(.)	$S_{Logit}(.)h_{Logit}(3sz)R_{Logit}(.)R'(2sz)$	S(.)h(3sz)R(.)R'(.)	20	33054.6	1782.5*
2.6	**S(.)h(3sz)R(.)R'(.)**	**$S_{Logit}(2sz)h_{Logit}(3sz)R_{Logit}(.)R'(2sz)$**	**S(.)h(3sz)R(.)R'(.)**	**22**	**31475.9**	**203.8**
2.7	S(.)h(3sz)R(.)R'(.)	$S_{Logit}(2sz)h_{Logit}(3sz)R_{Logit}(.)R'(.)$	S(.)h(3sz)R(.)R'(.)	21	33003.1	1731
3.1	S(0)h(3sz)R(2sz)R'(2sz)	$S_{Logit}(2sz)h_{Logit}(3sz)R_{Logit}(.)R'(2sz)$	S(.)h(3sz)R(.)R'(.)	23	38046.9	6774.8*
3.2	S(.)h(3sz)R(2sz)R'(2sz)	$S_{Logit}(2sz)h_{Logit}(3sz)R_{Logit}(.)R'(2sz)$	S(.)h(3sz)R(.)R'(.)	24	31443.3	171.2
3.3	S(2sz)h(3sz)R(2sz)R'(2sz)	$S_{Logit}(2sz)h_{Logit}(3sz)R_{Logit}(.)R'(2sz)$	S(.)h(3sz)R(.)R'(.)	25	31399.8	127.7
3.4	S(0)h(3sz)R(2sz)R'(.)	$S_{Logit}(2sz)h_{Logit}(3sz)R_{Logit}(.)R'(2sz)$	S(.)h(3sz)R(.)R'(.)	22	54262.8	22990.7*
3.5	S(.)h(3sz)R(2sz)R'(.)	$S_{Logit}(2sz)h_{Logit}(3sz)R_{Logit}(.)R'(2sz)$	S(.)h(3sz)R(.)R'(.)	23	31422.6	150.5
3.6	**S(2sz)h(3sz)R(2sz)R'(.)**	**$S_{Logit}(2sz)h_{Logit}(3sz)R_{Logit}(.)R'(2sz)$**	**S(.)h(3sz)R(.)R'(.)**	**24**	**31401.6**	**129.5**
3.7	S(0)h(3sz)R(.)R'(2sz)	$S_{Logit}(2sz)h_{Logit}(3sz)R_{Logit}(.)R'(2sz)$	S(.)h(3sz)R(.)R'(.)	22	40392.7	9120.6*
3.8	S(.)h(3sz)R(.)R'(2sz)	$S_{Logit}(2sz)h_{Logit}(3sz)R_{Logit}(.)R'(2sz)$	S(.)h(3sz)R(.)R'(.)	23	31427	154.9
3.9	S(2sz)h(3sz)R(.)R'(2sz)	$S_{Logit}(2sz)h_{Logit}(3sz)R_{Logit}(.)R'(2sz)$	S(.)h(3sz)R(.)R'(.)	24	31413.7	141.6
3.10	S(0)h(3sz)R(.)R'(.)	$S_{Logit}(2sz)h_{Logit}(3sz)R_{Logit}(.)R'(2sz)$	S(.)h(3sz)R(.)R'(.)	21	31558	285.9
3.11	S(2sz)h(3sz)R(.)R'(.)	$S_{Logit}(2sz)h_{Logit}(3sz)R_{Logit}(.)R'(2sz)$	S(.)h(3sz)R(.)R'(.)	23	31413.9	141.8

*Note – Hessian not positive definite

Table 1 cont.

Model	Tagging Interval	Release Year	Post Release Year	npar	AIC	Δ AIC
4.1	S(2sz)h(3sz)R(2sz)R'(.)	$S_{\mathrm{Logit}}(2sz)h_{\mathrm{Logit}}(3sz)R_{\mathrm{Logit}}(.)R'(2sz)$	S(.)h(3sz)R(2sz)R'(2sz)	26	31405.4	133.3
4.2	S(2sz)h(3sz)R(2sz)R'(.)	$S_{\mathrm{Logit}}(2sz)h_{\mathrm{Logit}}(3sz)R_{\mathrm{Logit}}(.)R'(2sz)$	S(2sz)h(3sz)R(2sz)R'(2sz)	27	31407.4	135.3
4.3	S(2sz)h(3sz)R(2sz)R'(.)	$S_{\mathrm{Logit}}(2sz)h_{\mathrm{Logit}}(3sz)R_{\mathrm{Logit}}(.)R'(2sz)$	S(.)h(3sz)R(2sz)R'(.)	25	31403.6	131.5
4.4	S(2sz)h(3sz)R(2sz)R'(.)	$S_{\mathrm{Logit}}(2sz)h_{\mathrm{Logit}}(3sz)R_{\mathrm{Logit}}(.)R'(2sz)$	S(2sz)h(3sz)R(2sz)R'(.)	26	31405.6	133.5
4.5	S(2sz)h(3sz)R(2sz)R'(.)	$S_{\mathrm{Logit}}(2sz)h_{\mathrm{Logit}}(3sz)R_{\mathrm{Logit}}(.)R'(2sz)$	S(.)h(3sz)R(.)R'(2sz)	25	31414.7	142.6
4.6	S(2sz)h(3sz)R(2sz)R'(.)	$S_{\mathrm{Logit}}(2sz)h_{\mathrm{Logit}}(3sz)R_{\mathrm{Logit}}(.)R'(2sz)$	S(2sz)h(3sz)R(.)R'(2sz)	26	31405.4	133.3
4.7	S(2sz)h(3sz)R(2sz)R'(.)	$S_{\mathrm{Logit}}(2sz)h_{\mathrm{Logit}}(3sz)R_{\mathrm{Logit}}(.)R'(2sz)$	S(2sz)h(3sz)R(.)R'(.)	25	31403.6	131.5
5.1	S(2sz)h(3sz)R(2sz)R'(.)	$S_{\mathrm{Logit}}(2sz*t)h_{\mathrm{Logit}}(3sz*t)R_{\mathrm{Logit}}(t)R'(2sz*t)$	S(.)h(3sz)R(.)R'(.)	156	31420.2	148.1*
5.2	S(2sz)h(3sz)R(2sz)R'(.)	$S_{\mathrm{Logit}}(2sz*t)h_{\mathrm{Logit}}(3sz*t)R_{\mathrm{Logit}}(t)R'(2sz)$	S(.)h(3sz)R(.)R'(.)	134	31801.2	529.1*
5.3	S(2sz)h(3sz)R(2sz)R'(.)	$S_{\mathrm{Logit}}(2sz*t)h_{\mathrm{Logit}}(3sz*t)R_{\mathrm{Logit}}(.)R'(2sz*t)$	S(.)h(3sz)R(.)R'(.)	134	32511.4	1239.3*
5.4	S(2sz)h(3sz)R(2sz)R'(.)	$S_{\mathrm{Logit}}(2sz*t)h_{\mathrm{Logit}}(3sz*t)R_{\mathrm{Logit}}(.)R'(.)$	S(.)h(3sz)R(.)R'(.)	112	31391.7	119.6
5.5	S(2sz)h(3sz)R(2sz)R'(.)	$S_{\mathrm{Logit}}(2sz*t)h_{\mathrm{Logit}}(3sz)R_{\mathrm{Logit}}(t)R'(2sz*t)$	S(.)h(3sz)R(.)R'(.)	112	33190.6	1918.5
5.6	S(2sz)h(3sz)R(2sz)R'(.)	$S_{\mathrm{Logit}}(2sz*t)h_{\mathrm{Logit}}(3sz)R_{\mathrm{Logit}}(t)R'(2sz)$	S(.)h(3sz)R(.)R'(.)	90	32336.5	1064.4*
5.7	S(2sz)h(3sz)R(2sz)R'(.)	$S_{\mathrm{Logit}}(2sz*t)h_{\mathrm{Logit}}(3sz)R_{\mathrm{Logit}}(.)R'(2sz*t)$	S(.)h(3sz)R(.)R'(.)	90	31418.7	146.6*
5.8	S(2sz)h(3sz)R(2sz)R'(.)	$S_{\mathrm{Logit}}(2sz*t)h_{\mathrm{Logit}}(3sz)R_{\mathrm{Logit}}(.)R'(2sz)$	S(.)h(3sz)R(.)R'(.)	68	31793.2	521.1*
5.9	S(2sz)h(3sz)R(2sz)R'(.)	$S_{\mathrm{Logit}}(2sz)h_{\mathrm{Logit}}(3sz*t)R_{\mathrm{Logit}}(t)R'(2sz*t)$	S(.)h(3sz)R(.)R'(.)	112	31411.8	139.7
5.10	S(2sz)h(3sz)R(2sz)R'(.)	$S_{\mathrm{Logit}}(2sz)h_{\mathrm{Logit}}(3sz*t)R_{\mathrm{Logit}}(t)R'(2sz)$	S(.)h(3sz)R(.)R'(.)	90	31390.4	118.3
5.11	S(2sz)h(3sz)R(2sz)R'(.)	$S_{\mathrm{Logit}}(2sz)h_{\mathrm{Logit}}(3sz*t)R_{\mathrm{Logit}}(.)R'(2sz*t)$	S(.)h(3sz)R(.)R'(.)	90	31399.3	127.2*

***Note – Hessian not positive definite**

Table 1 cont.

Model	Tagging Interval	Release Year	Post Release Year	npar	AIC	Δ AIC
5.12	S(2sz)h(3sz)R(2sz)R'(.)	S_{Logit}(2sz)h_{Logit}(3sz*t)R_{Logit}(.)R'(2sz)	S(.)h(3sz)R(.)R'(.)	68	32218.9	946.8*
5.13	S(2sz)h(3sz)R(2sz)R'(.)	S_{Logit}(2sz)h_{Logit}(3sz)R_{Logit}(t)R'(2sz*t)	S(.)h(3sz)R(.)R'(.)	68	31365.8	93.7
5.14	S(2sz)h(3sz)R(2sz)R'(.)	S_{Logit}(2sz)h_{Logit}(3sz)R_{Logit}(t)R'(2sz)	S(.)h(3sz)R(.)R'(.)	46	31360.7	88.6
5.15	**S(2sz)h(3sz)R(2sz)R'(.)**	**S_{Logit}(2sz)h_{Logit}(3sz)R_{Logit}(.)R'(2sz*t)**	**S(.)h(3sz)R(.)R'(.)**	**46**	**31352.6**	**80.5**
6.1	S(2sz*t)h(3sz*t)R(2sz*t)R'(t)	S_{Logit}(2sz)h_{Logit}(3sz)R_{Logit}(.)R'(2sz*t)	S(.)h(3sz)R(.)R'(.)	123	31296.5	24.4
6.2	S(2sz*t)h(3sz*t)R(2sz*t)R'(.)	S_{Logit}(2sz)h_{Logit}(3sz)R_{Logit}(.)R'(2sz*t)	S(.)h(3sz)R(.)R'(.)	112	31304.2	32.1
6.3	S(2sz*t)h(3sz*t)R(2sz)R'(t)	S_{Logit}(2sz)h_{Logit}(3sz)R_{Logit}(.)R'(2sz*t)	S(.)h(3sz)R(.)R'(.)	101	31310.1	38
6.4	S(2sz*t)h(3sz*t)R(2sz)R'(.)	S_{Logit}(2sz)h_{Logit}(3sz)R_{Logit}(.)R'(2sz*t)	S(.)h(3sz)R(.)R'(.)	90	31325.1	53
6.5	S(2sz*t)h(3sz)R(2sz*t)R'(t)	S_{Logit}(2sz)h_{Logit}(3sz)R_{Logit}(.)R'(2sz*t)	S(.)h(3sz)R(.)R'(.)	101	31281.2	9.1
6.6	**S(2sz*t)h(3sz)R(2sz*t)R'(.)**	**S_{Logit}(2sz)h_{Logit}(3sz)R_{Logit}(.)R'(2sz*t)**	**S(.)h(3sz)R(.)R'(.)**	**90**	**31272.1**	**0**
6.7	S(2sz*t)h(3sz)R(2sz)R'(t)	S_{Logit}(2sz)h_{Logit}(3sz)R_{Logit}(.)R'(2sz*t)	S(.)h(3sz)R(.)R'(.)	79	31294.9	22.8
6.8	S(2sz*t)h(3sz)R(2sz)R'(.)	S_{Logit}(2sz)h_{Logit}(3sz)R_{Logit}(.)R'(2sz*t)	S(.)h(3sz)R(.)R'(.)	68	31310.8	38.7
6.9	S(2sz)h(3sz*t)R(2sz*t)R'(t)	S_{Logit}(2sz)h_{Logit}(3sz)R_{Logit}(.)R'(2sz*t)	S(.)h(3sz)R(.)R'(.)	101	31332.2	60.1
6.10	S(2sz)h(3sz*t)R(2sz*t)R'(.)	S_{Logit}(2sz)h_{Logit}(3sz)R_{Logit}(.)R'(2sz*t)	S(.)h(3sz)R(.)R'(.)	90	31332.5	60.4
6.11	S(2sz)h(3sz*t)R(2sz)R'(t)	S_{Logit}(2sz)h_{Logit}(3sz)R_{Logit}(.)R'(2sz*t)	S(.)h(3sz)R(.)R'(.)	79	31343.2	71.1
6.12	S(2sz)h(3sz*t)R(2sz)R'(.)	S_{Logit}(2sz)h_{Logit}(3sz)R_{Logit}(.)R'(2sz*t)	S(.)h(3sz)R(.)R'(.)	68	31366.5	94.4
6.13	S(2sz)h(3sz)R(2sz*t)R'(t)	S_{Logit}(2sz)h_{Logit}(3sz)R_{Logit}(.)R'(2sz*t)	S(.)h(3sz)R(.)R'(.)	79	31318.3	46.2
6.14	S(2sz)h(3sz)R(2sz*t)R'(.)	S_{Logit}(2sz)h_{Logit}(3sz)R_{Logit}(.)R'(2sz*t)	S(.)h(3sz)R(.)R'(.)	68	31318.6	46.5
6.15	S(2sz)h(3sz)R(2sz)R'(t)	S_{Logit}(2sz)h_{Logit}(3sz)R_{Logit}(.)R'(2sz*t)	S(.)h(3sz)R(.)R'(.)	57	31329.2	57.1

*Note – Hessian not positive definite

Table 2. Estimates of encounter probabilities during the first 30-days after release for summer flounder released in Chesapeake Bay by participants in the Virginia Game Fish Tagging Program from 2000-2011. Parameter estimates and standard deviations (SD) are based on the most parsimonious Barker model (model 6.6 in table 1). The various size classes were: 1) commercial only - fish that were greater than 14" but less than the recreational size limit, 2) commercial and recreational - fish that were larger than the recreational size limit, 3) sublegal – fish that were less than 14", 4) legal - fish that were greater than 14", and 5) all – parameter is constant regardless of fish size. Parameters that varied inter-annually are distinguished by year, otherwise the model assumed the parameter was contant throughout the study.

Parameter	Size class	Year	Estimate	SD
Harvest probability	Commercial only	All	0.0036	0.0006
Harvest probability	Commercial and Recreational	All	0.0334	0.0068
Resighting probability	Sublegal	2000	0.0701	0.0183
Resighting probability	Sublegal	2001	0.0823	0.0144
Resighting probability	Sublegal	2002	0.0951	0.0278
Resighting probability	Sublegal	2003	0.1796	0.0373
Resighting probability	Sublegal	2004	0.0713	0.0167
Resighting probability	Sublegal	2005	0.0404	0.0081
Resighting probability	Sublegal	2006	0.0481	0.0096
Resighting probability	Sublegal	2007	0.0827	0.0148
Resighting probability	Sublegal	2008	0.0596	0.0172
Resighting probability	Sublegal	2009	0.1414	0.0224
Resighting probability	Sublegal	2010	0.1235	0.0321
Resighting probability	Sublegal	2011	0.2969	0.1758
Resighting probability	Legal	2000	0.0274	0.0304
Resighting probability	Legal	2001	0.0958	0.0223
Resighting probability	Legal	2002	0.0429	0.0177
Resighting probability	Legal	2003	0.0648	0.0292
Resighting probability	Legal	2004	0.0724	0.0154
Resighting probability	Legal	2005	0.0620	0.0131
Resighting probability	Legal	2006	0.0517	0.0106
Resighting probability	Legal	2007	0.0463	0.0101
Resighting probability	Legal	2008	0.0334	0.0077
Resighting probability	Legal	2009	0.0780	0.0173
Resighting probability	Legal	2010	0.1047	0.0281
Resighting probability	Legal	2011	0.1235	0.0564
Resighting-before-death probability	All	All	0.0084	0.0053

Table 3. Estimates of encounter probabilities during the release year for summer flounder released in Chesapeake Bay by participants in the Virginia Game Fish Tagging Program from 2000-2011. Parameter estimates and standard deviations (SD) are based on the most parsimonious Barker model (model 6.6 in table 1). Parameters that were estimated using a logit-link have an intercept (β_0) and a slope (β_1). The various size classes were: 1) commercial only - fish that were greater than 14" but less than the recreational size limit, 2) commercial and recreational - fish that were larger than the recreational size limit, 3) sublegal – fish that were less than 14", 4) legal - fish that were greater than 14", and 5) all – parameter is constant regardless of fish size. Parameters that varied inter-annually are distinguished by year, otherwise the model assumed the parameter was contant throughout the study.

Parameter	Size class	Year	Estimate	SD
Harvest probability - β_0	Commercial only	All	-4.8340	0.4003
Harvest probability - β_1	Commercial only	All	2.0478	0.8214
Harvest probability - β_0	Commercial and Recreational	All	-0.8834	0.3980
Harvest probability - β_1	Commercial and Recreational	All	0.5656	0.7883
Resighting probability - β_0	All	All	-1.8201	0.2802
Resighting probability - β_1	All	All	-3.4505	0.4759
Resighting -before-death probability	Sublegal	2000	0.0457	0.0388
Resighting -before-death probability	Sublegal	2001	0.0975	0.0354
Resighting -before-death probability	Sublegal	2002	0.3370	0.1378
Resighting -before-death probability	Sublegal	2003	0.2289	0.0826
Resighting -before-death probability	Sublegal	2004	0.0557	0.0300
Resighting -before-death probability	Sublegal	2005	0.0421	0.0234
Resighting -before-death probability	Sublegal	2006	0.0274	0.0206
Resighting -before-death probability	Sublegal	2007	0.0526	0.0247
Resighting -before-death probability	Sublegal	2008	0.0687	0.0396
Resighting -before-death probability	Sublegal	2009	0.1563	0.0428
Resighting -before-death probability	Sublegal	2010	0.1325	0.0690
Resighting -before-death probability	Sublegal	2011	0.0000	0.0001
Resighting -before-death probability	Legal	2000	0.1575	0.0965
Resighting -before-death probability	Legal	2001	0.2853	0.0950
Resighting -before-death probability	Legal	2002	0.3293	0.1257
Resighting -before-death probability	Legal	2003	0.2718	0.1126
Resighting -before-death probability	Legal	2004	0.0794	0.0483
Resighting -before-death probability	Legal	2005	0.0673	0.0439
Resighting -before-death probability	Legal	2006	0.0760	0.0452

Table 3 cont.

Parameter	Size class	Year	Estimate	SD
Resighting -before-death probability	Legal	2007	0.0948	0.0464
Resighting -before-death probability	Legal	2008	0.0999	0.0539
Resighting -before-death probability	Legal	2009	0.2102	0.0754
Resighting -before-death probability	Legal	2010	0.2540	0.1058
Resighting -before-death probability	Legal	2011	0.2799	0.1912

Table 4. Estimates of survival and encounter probabilities after the release year for summer flounder released in Chesapeake Bay by participants in the Virginia Game Fish Tagging Program from 2000-2011. Parameter estimates and standard deviations (SD) are based on the most parsimonious Barker model (model 6.6 in table 1). The various size classes were: 1) commercial only - fish that were greater than 14" but less than the recreational size limit, 2) commercial and recreational - fish that were larger than the recreational size limit, and 3) all – parameter is constant regardless of fish size. Each of these parameters were assumed to be contant throughout the study.

Parameter	Size class	Year	Estimate	SD
Survival probability	All	All	0.1458	0.0154
Harvest probability	Commercial only	All	0.0039	0.0011
Harvest probability	Commercial and Recreational	All	0.0491	0.0102
Resighting probability	All	All	0.0200	0.0197
Resighting -before-death probability	All	All	0.0223	0.0062

VITA

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