

ABSTRACT

KRAUSE, JACOB RICHARD. Sources, Magnitude, and Timing of Weakfish Mortality across the U.S. East Coast. (Under the direction of Dr. Jeffrey A. Buckel and Dr. Joseph E. Hightower).

Weakfish (*Cynoscion regalis*) is an important recreational, commercial, and ecological species along the U.S. Atlantic coast. The spawning stock biomass has declined since 1982 to historic lows in the late 2000s, despite increased regulatory measures. The cause of the decline is attributed to increased total mortality (Z), but uncertainty exists in the timing, magnitude, and sources of mortality. A coast-wide telemetry component using a Cormack-Jolly-Seber model provided insights into the magnitude and spatiotemporal component of mortality. Telemetered weakfish ($n=342$) were released across five estuaries ranging from North Carolina to New Jersey between 2006 and 2016. A joint model including all telemetered weakfish estimated an extremely low apparent survival of 0.002 (95% credible interval = 0.001-0.007). Despite a minimum of 61% of telemetered weakfish emigrating in the fall, only two out of 149 fish with long-lived transmitters were detected returning to estuaries the following year, an infinitesimal proportion for a species exhibiting spawning site fidelity. I infer that mortality occurring during the migration and overwinter periods account for the attrition of telemetered weakfish. A North Carolina conventional tag-return component analyzed using a Bayesian statistical framework provided estimates of the relative importance of seasonal and annual fishing mortality (F) and natural mortality (M) to Z . From November 2013 to May 2017, 3,672 weakfish were tagged, with 140 (3.8%) tags recovered and reported through October 2017. A constant annual instantaneous mortality rate was estimated to be 0.07 yr^{-1} for F (95% credible interval [CrI]: 0.06, 0.10) and 5.71 yr^{-1} for M (CrI: 4.40, 7.40) across the years 2014 to 2017. Annual estimates of Z from an independent catch-curve analysis were similarly high in magnitude and the seasonality in Z from catch-curve and conventional tags matched the telemetry tag results; a

large portion of mortality occurred from fall to spring, coinciding with weakfish migration and overwintering periods on the continental shelf. The weakfish tag-return study clarified the relative importance of F and M to Z , indicating that M consistently and significantly exceeded F . Insights into the timing and magnitude of M led to the hypothesis that predation was a source of increases in M . Five primary predators were identified based on published accounts of their diet, and their spatial and temporal overlap with that of weakfish. Predator consumption of weakfish was estimated and compared with the biomass attributable to M from the stock assessment. From 1982 to 2014, predators consumed on average 6,767 t of weakfish (80% CI 1,740 to 14,388 t), of which 55% was consumed by bottlenose dolphins (*Tursiops truncatus*), 21% by striped bass (*Morone saxatilis*), 17% by bluefish (*Pomatomus saltatrix*), 4% by summer flounder (*Paralichthys dentatus*), and 3% by spiny dogfish (*Squalus acanthias*). The sum of the stock assessment biomass attributable to M and total predator consumption were similar, indicating that high estimates of M are realistic and the cause is predation, as the average biomass from fishery landings in the last 10 years of the time-series was 29 times less than that from predator consumption. As the majority of biomass in the weakfish population has shifted toward age-0s, predators consuming late age-0s have resulted in a recruitment bottleneck, as evident by the mismatch in trends between decreasing age-1 recruits and consistent age-0 indices throughout the time-series. Multiple independent approaches indicate that weakfish mortality occurs during their migration and overwintering period, the annual Z is >90% on a discrete scale, and that the increasing Z was caused by M . The significant influence of predation on the United States east coast weakfish population highlights the importance of multi-species management for effective stock rebuilding.

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Sources, Magnitude, and Timing of Weakfish Mortality across the U.S. East Coast.

by
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BIOGRAPHY

I was born in Parkersburg, West Virginia, a small industrial city on the Ohio River. My fascination with water began with witnessing the river's annual flooding, and when our family moved to Pewaukee, Wisconsin, where I spent nearly all my summers on Pewaukee Lake. My first job at Smokey's Bait Shop kept me on the water and in the community, as I rented boats and sold tackle to local fishermen. I majored in Biology at Wisconsin Lutheran College under the guidance of Dr. Robert Anderson, who instilled in me the value of environmental monitoring in maintaining the long-term sustainability of natural resources. In my travels to Asia after graduating in 2009, I became aware of the importance of fisheries on sustaining a community, and the potential hazards of poor husbandry and management. I decided to pursue graduate studies in natural resources management, and in the summer of 2010, I was accepted in the M.S. program in Wildlife and Fisheries at South Dakota State University under Dr. Katie Bertrand. For my master's thesis, I developed a fish index of biotic integrity for small streams in the eastern region of the state, highlighting the importance of science-based management. My doctoral studies on the population dynamics of weakfish under Dr. Jeff Buckel and Dr. Joe Hightower, first undertaken in 2013 at North Carolina State University, has culminated in this dissertation.

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The administrative staff at North Carolina State University have been indispensable during my time in Raleigh and by the sea. Dawn Newkirk, Susan Marschalk, and Freha Legoas made my graduate school career a hundredfold easier for taking care of business on main campus. In Morehead City, Marlu Bolton made sure I did not get my head stuck too deeply in the sand, and Linda Dunn never judged when my dissertation data kept on gaining weight and needed more space. Although not administrative personnel, Greg Bolton was ever ready with an

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INTRODUCTION

Effective rebuilding of exploited fish stocks requires accurate fishing and natural mortality estimates. The fishing mortality rate (F) allows management to meet stock rebuilding goals through comparisons with target and threshold levels based on biological reference points (Hilborn and Walters 1992), whereas the natural mortality rate (M) affects estimates of stock size and productivity, which ultimately determines harvest rates (Clark 1999). Stock assessments typically estimate F indirectly by relating catch-at-age data to changes in stock abundance or size/age composition (Walters and Martell 2004), whereas M is difficult to measure since natural deaths are rarely observed in aquatic systems (Quinn and Deriso 1999). M is often estimated externally based on life history parameters and environmental variables (e.g., Pauly 1980; Hoenig 1983; Lorenzen 1996; Griffiths and Harrod 2007; reviewed by Kenchington 2014), and used as a fixed input parameter in fishery stock assessments (Vetter 1988). However, these estimates of M do not account for time- or location-specific differences and have an unknown certainty (Vetter 1988; Pascual and Iribarne 1993). Stock assessment models are particularly sensitive to input values of M (Clark 1999; Williams 2002), where overestimates of M may result in lost harvest, and underestimates may result in unsustainable exploitation rates and misguided management recommendations (Williams 2002; Legault and Palmer 2015).

Mortality estimates can be derived through acoustic telemetry and tag-return experiments (Pine et al. 2003). In acoustic telemetry studies, estimates of survival (converse of mortality) can be derived from a Cormack-Jolly-Seber (CJS) model, an open capture-recapture model that estimates detection probability and apparent survival. The latter is an estimate of a fish's probability of surviving and staying within the study area as compared to the subject's true survival (Hightower et al. 2015). Tag-return models partition instantaneous total mortality rate

(Z) into estimates of F and M (Hoenig et al. 1998), although precise estimates depend on key auxiliary parameters: tag-reporting rate (λ), tag loss (Ω), and survival from the tagging procedure (ϕ ; Pollock 1991; Pollock et al. 2001; Miranda et al. 2002; Brenden et al. 2010). Multi-year tagging studies of rigorous design can estimate the auxiliary parameters, generating reliable estimates of mortality (e.g., den Heyer et al. 2013; Kerns et al. 2015). Both approaches provide insight into the timing and causes of mortality, as the estimates can be applied to any time-scale and matched with seasonal stock locations (Hightower et al. 2001; Harris and Hightower 2017; Ellis et al. 2018), whereas most traditional stock assessments lack the enhanced spatiotemporal resolution.

Discerning the sources of mortality is essential for effective stock rebuilding. F is directly attributed to commercial and recreational fisheries based on harvest, whereas M consists of the removal of fish from the stock due to causes not associated with fishing such as predation. Quantification of predation, with uncertainty, can be done by estimating predator consumption using a Monte Carlo probability estimation approach (Overholtz 2006). The estimated biomass attributable to M from a stock assessment can then be compared with independent estimates of biomass consumed by predators to ascertain the relative proportion of predation to total natural mortality (Begoña Santos et al. 2014).

This dissertation investigates the sources, magnitude, and timing of weakfish (*Cynoscion regalis*) mortality across the U.S. east coast. Weakfish is an important recreational, commercial, and ecological species primarily inhabiting estuarine and coastal waters between North Carolina and Massachusetts. The spawning stock biomass has declined since 1982 to historic lows in the late 2000s, with the cause of the decline attributed to increased Z . Despite rigorous regulatory measures, stocks have failed to rebuild, and the most parsimonious explanation for the increase

in Z was an increase in M (ASMFC 2016). Efforts to improve stock assessment estimates of M resulted in a Bayesian statistical catch-at-age model which internally estimated a time-varying M (Jiao et al. 2012; ASMFC 2016). The prior distribution for the 1982 M estimate was based on external estimates, and subsequent M estimates were allowed to vary through the 1983-2014 time-series (ASMFC 2016). M was estimated to increase throughout the time-series to a high of 0.95 in 2008, however with considerable uncertainty and its cause unknown (ASMFC 2016). In addition, F and M are confounded in the stock assessment model (Johnson et al. 2015), therefore it is difficult to estimate both without additional information on M (Lee et al. 2011).

In Chapter 1, I estimated estuarine-specific and coast-wide apparent survival of weakfish using telemetry data from prior studies in New Jersey estuaries (Manderson et al. 2014; Turnure et al. 2015a; Turnure et al. 2015b), and conducting telemetry studies in North Carolina and Delaware Bay, providing insights into the magnitude and spatiotemporal component of mortality across the distribution of weakfish. In Chapter 2, the seasonality of mortality and relative importance of F and M to Z was established using a North Carolina tag-return study. Seasonal and annual Z estimates from the tag-return study were compared to those derived from a catch-curve based on a fishery-independent survey conducted by North Carolina Division of Marine Fisheries. The impact of predation on the weakfish stock was assessed in Chapter 3 by comparing estimates of predator consumption of weakfish to the biomass attributable to M from the stock assessment. In all, my dissertation provides new insights into the sources, magnitude, and timing of weakfish mortality, and enriches understanding of weakfish population dynamics towards effective stock rebuilding.

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CHAPTER 1. USING ACOUSTIC TELEMETRY TO ESTIMATE WEAKFISH SURVIVAL RATES ALONG THE U.S. EAST COAST

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ABSTRACT

Weakfish (*Cynoscion regalis*), an economically important species, has declined over the last 30 years, corresponding with an increase in total mortality according to the most recent stock assessment. We estimated estuarine-specific and coast-wide apparent survival of weakfish using a Cormack-Jolly-Seber model to provide insights into the spatiotemporal component of mortality. Telemetered weakfish (n=342) were released across five estuaries ranging from North Carolina to New Jersey between 2006 and 2016. In estuaries from Delaware Bay and northward, egress peaked around the third week of September, and in North Carolina, by the first week of November. For three estuaries with adequate sample size, apparent survival estimates were similar, and a joint model including all telemetered weakfish estimated an extremely low apparent survival, 0.002 (95% credible interval = 0.001-0.007). At the minimum, 61% of telemetered weakfish emigrated in the fall, but only 2 of 149 fish with long-lived transmitters were detected returning to estuaries the following year. This is a small proportion for a fish that exhibits spawning site fidelity. We conclude that the disappearance of telemetered fish is mortality that happens between emigration and the spring spawning period potentially during overwinter periods on the continental shelf. Our study provides insights on the magnitude, timing, and location of weakfish loss and facilitates improved understanding of weakfish population dynamics for use in stock rebuilding.

INTRODUCTION

The utilization of acoustic telemetry has proliferated, with most applications investigating fish behavior, physiology, movement, and habitat selection (Hussey et al. 2015). A lesser-utilized application of acoustic telemetry is estimating fish mortality (Hightower and Harris 2017). Traditional stock assessments rely on estimates of mortality to derive approximate stock size and biological reference points, resulting in uncertainty (Cadrin and Dickey-Collas 2015; Punt et al. 2015). Hence, comparing stock assessment model mortality input and outputs with that of acoustic telemetry allows for an independent parameter diagnostic. In addition, acoustic telemetry offers insights into the location and timing of mortality, since telemetry mortality estimates can be on any time-scale and matched with seasonal stock locations, whereas most traditional stock assessments lack the enhanced spatiotemporal resolution.

Telemetry mortality estimates have been estimated across multiple fish species using passive arrays in lakes, rivers, estuaries, and artificial reefs (e.g., Hightower et al. 2001; Heupel and Simpfendorfer 2002; Bacheler et al. 2009; Welch et al. 2009; Stich et al. 2015; Williams-Grove and Szedlmayer 2016). With advances in technology and the advent of cooperative telemetry networks such as OTN and ACT (Ocean Tracking Network and Atlantic Cooperative Telemetry Network, respectively), estimates of survival can now be expanded to include an entire fish stock over broad geographic ranges (Lindley et al. 2008; Rudd et al. 2014; Hightower et al. 2015). For instance, Hightower et al. (2015) estimated survival of Atlantic sturgeon (*Acipenser oxyrinchus oxyrinchus*), an anadromous fish, from four riverine substocks using detections from riverine and marine acoustic arrays along the southeast coast of the United States (SEUS). The authors used a Cormack-Jolly-Seber (CJS) model, an open capture-recapture model that estimates detection probability and apparent survival—the latter an estimate of a fish's

probability of surviving and being in the study area, in this instance, in the SEUS—as compared to the subject’s true survival. The multiple arrays in cooperative telemetry networks along the entire SEUS coast allowed for the study to encompass the entire range of the Atlantic sturgeon substocks, where emigrations into areas without receivers were temporary, and apparent survival estimates approximated true survival. We applied CJS modeling to the telemetry detections for weakfish (*Cynoscion regalis*), a migratory marine fish that spawns in estuaries along the U.S. east coast.

Historically, weakfish supported a vibrant commercial and recreational fishery at the height of its spawning stock biomass (SSB) in the 1980s (ASMFC 2016). The SSB has since declined to record lows in 2008 with no appreciable recovery thereafter, despite management efforts through continually reduced harvest, culminating in the 2010 regulation of recreational one-fish (greater than 305 mm) creel-limit and commercial 45-kg trip-limit. The lack of stock recovery was somewhat surprising since the stock has the capacity to rebuild quickly as weakfish sexually mature by age-1 (Merriner 1976; Shepherd and Grimes 1984; Nye et al. 2008). The reduced harvest combined with the lack of rebuilding prompted management to hypothesize that natural mortality (M) has increased in recent years (48th SAW 2009). In the latest stock assessment time-series from 1982-2014, the Bayesian statistical catch-at-age model estimated a time-varying M , in which 1982 M was estimated from an informed prior based on literature values of M and all subsequent years are allowed to vary using a random walk approach (ASMFC 2016). M was estimated to increase through the time-series to a high of 0.95 in 2008, with total mortality (Z) matching the increasing trends to a record high of 3.46 in 2007 (ASMFC 2016). However, these mortality estimates contain uncertainty, especially M , since none are based on directed field studies (ASMFC 2016). Therefore, reliable estimates of survival, along

with their spatial and temporal variability, are important for understanding the lack of rebuilding in the weakfish stock.

The bulk of the weakfish population ranges from New York to North Carolina (Mercer 1989). Weakfish of all ages (longevity is 17 years, Lowerre-Barbieri 1995) migrate southwards and/or offshore to overwinter on the continental-shelf and then return northward and/or to estuaries and the nearshore areas around inlets to spawn the following spring (Nesbit 1954; Bigelow et al. 2002; Mann and Grothues 2009). A large percentage of fish show natal homing (Thorrold et al. 2001). After spawning, weakfish may move out of estuaries, possibly to the inner continental shelf, or reside in estuaries until their fall emigration (Shepherd and Grimes 1984; Turnure et al. 2015a; Turnure et al. 2015b). Robust estimates of long-term survival from telemetry-tagged weakfish should be possible given their annual spawning migration into US east coast estuaries, many of which have receiver arrays.

Here, we estimate estuarine-specific and coast-wide apparent survival of weakfish using telemetry data from prior studies in two New Jersey estuaries (Manderson et al. 2014; Turnure et al. 2015a; Turnure et al. 2015b) and more-recently North Carolina State University (NCSU) collected telemetry-data from North Carolina and Delaware Bay. Combined, these studies cover the bulk of the distributional range of weakfish and the time-period (2004 to 2016) during weakfish population decline. We hypothesize that apparent survival will be low given the current age-structure (predominately age-0 to 4) from the most recent weakfish stock assessment (ASMFC 2016) and seasonally lowest in winter given the likely impact of predation (Chapter 3).

METHODS

Telemetered weakfish were released in five estuaries from New Jersey to North Carolina (Figure 1). For method details, refer to Manderson et al. (2014) for the Navesink and Turnure et

al. (2015a; 2015b) for Great Bay. Array placement and estuarine site descriptions for Delaware Bay can be found in Kilfoil et al. (2017), for the New River of North Carolina in Scheffel et al. (2018), and across multiple receiver arrays deployed from Florida to Maine by research groups participating in the Atlantic Coast Telemetry Network website based at Delaware State University (www.theactnetwork.com). This paper's methods are primarily focused on NCSU telemetered weakfish in Delaware Bay, New River, and Bogue Sound, and any major methodological differences between NCSU and that of our co-authors from the Navesink and Great Bay studies are highlighted.

Telemetry study site

Bogue Sound weakfish were passively tracked in the waters surrounding Beaufort inlet, North Carolina (Figure 2). Depths were generally less than 3 m in the lagoonal Bogue and Back Sounds and the partially mixed estuary of the Newport River. Depth increased to 4-7 m in navigable channels, and up to 12-16 m in the dredged shipping channel leading from Beaufort inlet to Morehead City port. The study area is dominated by tidal inflow with wind forcing causing polyhaline conditions (Logan et al. 2000). Commercial fishing is prohibited in the vicinity of the port, and therefore was primarily conducted on the ocean side of the barrier islands. The recreational fishery frequented the port and surrounding structure such as bridges.

The waters surrounding Beaufort inlet were selected for this study as they offered excellent accessibility to migrating weakfish, allowing for a series of collaborative acoustic arrays to provide extensive spatial coverage (Figure 2). In total, 22 core receivers were in place from the release of the first transmitters in September 2015 to the battery expiration of the last transmitters in late February 2018 (Figure 2). Additional receivers varied spatially and temporally with the initial receiver array consisting of 43 receivers in fall 2015 (Figure 2a), of

which 8 were maintained by Eastern Carolina University and retrieved in mid-November 2015 for a congruent study (pers. comm. Chuck Bangley 2018). In spring 2016, the array decreased to 36 receivers, of which a single receiver was briefly maintained by a citizen science project supervised by the Smithsonian Environmental Research Center, and provided weakfish detections during a 2-day period (Figure 2b). During fall 2016, a collaboration with University of North Carolina-Chapel Hill (IMS) researchers expanded the array to 76 receivers (Fig 2c). The number of receivers reached a maximum of 87 in mid-2017, then fell to and remained at 37 until the last transmitter expired on February 25th, 2018 after IMS retrieved their receivers in fall 2017 (Figure 2c). A total of 12 receivers were lost (2 fall 2015, 2 spring 2016, 1 fall 2016, 7 in 2017), and an additional one was broken. Receivers were retrieved for approximately one week each summer for maintenance. The variable detection range of receivers in highly dynamic locations (e.g., current, tide, boat traffic, wave prone areas) rendered receiver range testing impractical, and was not a requirement of our model assumptions. At the transmitter fish release site (Figure 2e), a control tag was placed within detection range of a receiver, to provide additional information on possible transmitter expulsions, surgery-related mortalities, and seasonal detection patterns.

Transmitter implantation

In Bogue Sound, weakfish were captured using hook-and-line within 1 mile of the Atlantic Beach Bridge in fall 2015, spring 2016, and fall 2016 (Figure 2a). Healthy individuals greater than 305 mm were transported in a 378 L container to the circular flow-through 1500 L holding tanks inside the Institute of Marine Sciences. In total, 211 uniquely coded ultrasonic transmitters (VEMCO, Bedford, Nova Scotia; model V13-1H, 13 x 36 mm, approximately 10.5 g in air, 69-kHz frequency) were deployed in Bogue Sound, 80 of which had 30-s to 90-s random

transmission rates and a typical battery life of ~184 days, and 131 had 50-s to 130-s random transmission rates with a battery life of ~513 days. The surgical methodology followed the guidelines outlined by Wagner et al. (2011), but were tailored specifically for weakfish with the assistance of the staff from North Carolina State University College of Veterinary Medicine (e.g., Harms and Lewbart 2011). Individual weakfish were anesthetized in a seawater solution of 40 mg/L Aqui-S (Aqui-S New Zealand LTD.; active ingredient proportion: 50% Isoeugenol) until unresponsive to the touch while still gilling (~2 minutes), measured (TL mm), weighed (wet weight in g), and implanted with a transmitter in the abdominal cavity. During the surgery, a continuous flow of 20 mg/L Aqui-S was pumped over the gills to maintain sedation. The incision was closed with 2-4 simple interrupted sutures (Ethicon Endo-Surgery, Inc.: PDS II synthetic absorbable suture in 3-0 thread size with FS-1 reverse cutting needle) and the fish was allowed to recover (i.e. re-establish equilibrium and exhibit normal swimming behavior) before release.

All New River weakfish had transmitters with 30-s to 90-s random transmission rate, whereas all Delaware Bay weakfish transmitters had a 50-s to 130-s random transmission rate. New River weakfish were captured using hook-and-line or strike net method, an approach outlined in Bacheler et al. (2009), with the singular difference being the use of a 183-m gillnet with 76-mm stretch mesh. Delaware Bay fish were captured using hook-and-line or beach seining (27 x 1.8-m seine with 25-mm mesh). New River weakfish were tracked with a 76-receiver array in 2014 (Scheffel et al. 2018), and in Delaware Bay, with an approximately 54-receiver array (Kilfoil et al. 2017). Of all NCSU released fish, only 12 New River weakfish were tagged with a single 63.5 mm long wire core internal anchor tag (FM-95W; Floy, Inc., Seattle, WA, which were red in color and stated “CUT TAG \$100 REWARD”, each with a unique tag number preceded by “NC” and a toll-free phone number. All NCSU fish followed the

aforementioned surgery protocol and had an average time for anesthetization of 1:59 min. (00:48 sd), surgery of 7:31 min. (2:17 sd), and recovery of 4:43 min. (2:12 sd). Lastly, all weakfish were released within 24 hours from the time of capture, and within 2 km of their original capture site.

Age-1+ Navesink weakfish (>224 TL mm) were captured using hook-and-line and transported to the James J. Howard Marine Sciences Laboratory in Highlands, New Jersey for surgery. Each weakfish was anesthetized with AquiS (AquiS New Zealand, Ltd., Lower Hutt, New Zealand) at a concentration of 54 mg/L, implanted with a uniquely coded ultrasonic transmitter (VEMCO, Bedford, Nova Scotia; model V9-6L, 9 x 20 mm, approximately 2 g in water, 69-kHz frequency, 40 to 120-s random transmission rate), and with a unique anchor tag inserted in the dorsal musculature. Fish were released at randomly selected Navesink locations within 8 days of their initial capture, and tracked with 27 receivers in 2006 and 33 receivers in 2007.

Reproductively mature Great Bay weakfish (>230 mm TL) were captured using hook-and-line, except one being caught in a stationary multi-mesh gill net (Turnure et al. 2015b). Weakfish were anesthetized with MS-222 in ambient seawater at 0.05 g/L and implanted with Lotek acoustic transmitters (Lotek Wireless, Inc., St. John's, Newfoundland, Canada; CAFT and MS series, 8.4-39.3 g, 5 s burst rate, maximum battery life 229-719 days), and tracked with a gated array of 6-9 wireless hydrophones (WHS-1100, Lotek Wireless, Inc.) as well as manually. Each fish was released within 100 m of its original capture location and 0-6 days of initial capture. A high-visibility external t-bar tag (Floy, Inc., Seattle, WA) was inserted between the first and second pterygiophores of the spiny dorsal fin to visually identify acoustically tagged fish.

Fates

Two independent readers analyzed weakfish movement patterns, then assigned death and temporary emigration fates via consensus, by analyzing average hourly movements within the estuary, speeds of transmitter movement, and detections patterns at receivers for each fish (Table 2). Although the CJS model is not a fates-based analysis, it does require information on known live fish, and consequently the fates of detected dead fish. The emigration fate provided insight into the temporal variation in survival estimates. In most cases, the fate of “death” was assigned if weakfish had continuous detections at the same receiver for multiple months, and were sub-categorized as a “cause unknown” death which includes natural mortality, catch-and-release mortality, transmitter expulsion, or surgery mortality. For some, a “predation” death was assigned as the fish exhibited erratic behavior, bypassed multiple receiver lines, and often registered maximum speeds of greater than 4 km/hr during these periods. Weakfish are an important prey item for bottlenose dolphin (Gannon and Waples 2004), whose speeds are greater than 4 km/hr (Bacheler et al. 2009), making probable the assumption of death by predation. Lastly, a “harvested” death was assigned to weakfish that were harvested and reported by anglers. A death date was assigned to a weakfish for the day previous to its activity cessation, the day of observed predation behavior, or the day of harvest. In the Navesink, weakfish detected alive at the dates of array retrieval on October 3, 2006 and October 31, 2007 were characterized as “alive in system”. A proportion of fish were released and “never detected”, and were censored from further analyses. For others, we felt confident in assigning them as a temporary “emigration” with an estuarine egress date, as their movements were detected within the estuary and were last detected at an estuarine inlet or ocean receiver. For fishes last detected alive in the

middle of the estuarine array, their classification under “disappear in array” includes unreported harvests, undetected emigrations, or undetected deaths.

Cormack-Jolly-Seber model

We analyzed data separately for each estuary to detect spatial variation in survival, and produced a pooled survival estimate for sexually mature weakfish (>224 mm TL; Nye et al. 2008). Each analysis was based on a capture history (CH) with rows for individual fish and columns for time in days. The matrix contained a “1” if one or more detections occurred for the selected date, and a “2” indicated a lack of detections. As weakfish had a staggered entry into the model, time periods when a fish was not yet released or unavailable to the model (e.g., harvested or battery expired) received a “0”. All weakfish were assigned an arbitrary year on the actual day of release, and all are assumed to be alive at the day of release. To minimize concerns about mortality due to capture, handling, and tag implantation, the analysis period for each individual started 1 week after tagging, and fishes were censored from the analysis if they were not detected alive after 7 days (Table 2), whereas those detected alive after the probationary period were assumed alive at day 8 regardless of an actual detection and received a 1. All capture histories were made using the library EasyMARK in R (R Core Team 2013; Waller 2014). The daily CH were then condensed to a weekly time frame for estuarine survival models, and into a monthly time frame for the pooled model. The period of analysis ranged from the first time a weakfish was released until the last battery expired or when an array was retrieved. The analysis time period was 16 weeks for Navesink (June to October Year 1), 119 weeks for Great Bay (April Year 1 to November Year 3), 97 weeks for Bogue (March Year 1 to February Year 3), with the pooled estimate of 27 months (April Year 1 to July Year 3).

Capture histories were analyzed using a multistate CJS model modified from Hightower et al. (2015), which estimates apparent survival and detection probability (Kéry and Schaub 2011). The multistate model distinguished between the true states of “alive” and “dead” based on observations of our capture histories. We implemented the model using Bayesian modeling framework through OpenBUGS software in R (Spiegelhalter et al. 2007; R Core Team 2013), in which individual weakfish were treated as the unit of observation (Otis and White 1999). Following Kéry and Schaub (2011), we used uninformative prior distributions to estimate apparent survival (ϕ ; uniform, 0-1) and detection probability (p), the latter the logit transformed sum of $\mu + \varepsilon_t$ (μ , uniform, 0-1; ε_t , normal, mean=0, sd=uniform, 0-10). Preliminary modeling indicated variability in ϕ and p among time-periods, therefore we modeled time-dependent ϕ as a fixed-effect factor and p as a random-effects factor on the logit scale (Kéry and Schaub 2011). Low sample size ($n < 10$) precluded us from running analyses by year for each estuary and for Delaware Bay and New River weakfish, as preliminary model estimates of uncertainty surrounding survival were biologically meaningless (ranged from ~0 to 1). For similar precision reasons, estimates were only shown when at least 10 fish were at-risk or considered alive by the model. We explored different time intervals in preliminary modeling, and found that weekly intervals among estuaries and monthly pooled across estuaries allowed for biologically relevant insights.

Model Assumptions

1. Survival rates are equal for all telemetered weakfish, as tagged fish across all study sites had a relatively narrow size range (Table 1).
2. The probability of transmitter failure or expulsion is negligible. Although Vemco transmitter failure has been reported or assumed (Dresser and Kneib 2007; Friedl et al. 2013), the

majority of studies report no transmitter failures (e.g., Hightower et al. 2001; Heupel and Simpfendorfer 2002; Bacheler et al. 2009; Ellis et al. 2017). All NCSU transmitters passed a functionality test prior to implantation, of which 3 working transmitters were returned by anglers and 5 from weakfish recaptured and subsequently released by researchers, and detections from our control tag until the end of its 513-day battery life suggest negligible transmitter failure. Manderson et al. (2014) implanted weakfish with replica V-9 transmitters for >120 days ($n>12$) and did not witness any expulsion. In one instance, NCSU researchers captured a weakfish bearing surgery scars without sutures approximately 7 days after release, however necropsy did not reveal a transmitter. Based on scar tissue healing, the veterinarian performing the necropsy believed that transmitter expulsion occurred within 4 days of initial release, with the most likely cause being suture discharge due to incising through thin anchor muscle and skin, incision dehiscence, and ultimately transmitter expulsion (Craig Harms DVM, personal communication). We assumed a negligible transmitter expulsion after the 7-day probationary period as many weakfish were detected alive for many weeks after release, the single known transmitter expulsion occurred shortly after surgery, and there was no evidence of transintestinal expulsion based in a tank holding study (Marty and Summerfelt 1986; Manderson et al. 2014).

3. Tagging mortality is negligible. The aforementioned tank holding experiment by Manderson et al. demonstrated 100% transmitter fish survival (2014). Field results from Turnure et al. recorded 7 out of 59 weakfish ceased to move within 7 days of release, whereas 6 out of 211 Bogue Sound weakfish from NCSU likewise ceased to move in the same time period, suggesting possible surgery mortality or transmitter expulsion (Table 2). To meet the assumption of negligible tagging mortality, we implemented the 7-day probationary period.

4. All detections are classified without error. As the weakfish were released by NCSU in Bogue Sound and New River during relatively short time periods and often congregated on structure (e.g., bridges), the probability of false detections increased. All false detections as deemed by the default settings of Vemco's VUE False Detection Analyzer (FDA) were removed from the analysis ($n=317$; Table 2). For weakfish released in the Navesink and Delaware Bay, we did not have the data to run the FDA analysis, but assumed negligible false detections based on the gradual release of fish across multiple locations. For Great Bay weakfish, which used Lotek equipment, the detections were cleaned post-hoc using a temporal filter (contacts-per-interval; Grothues et al. 2005). Since all detections need to come from living fish, transmitter returns from "harvested" fish received a 0 for all dates after harvest in the capture history, signifying to the model that these fish were no longer available to be detected. In addition, any fish that survived the probationary period but died from "predation" or "unknown cause", their detections after the death date were changed to non-detections (1 to 2 in capture history).
5. Bias in estimated survival due to the timing of tagging or detections was negligible, given short interval (weekly or monthly) for detection relative to the period of analysis (16, 97, or 119 weeks, or 27 months). Although most fish egressed within 3 months, the detection probabilities were high during those time-periods minimizing the timing bias in weekly and monthly estimates.
6. The fate of tagged fish is independent of the fate of other tagged fish. The assumption may be violated because weakfish aggregate on structure (i.e. bridges or deep holes) during the spring and fall for long periods of time (>1 month), but the extent of aggregation is not known. We often released weakfish during relatively short time periods (89 out of 92 Bogue

weakfish were released during a 24 hour period in fall 2015), and found that while many resided by structure with other transmitter fish, just as many moved to other estuary locations or emigrated within days of release. Violations of this assumption lowers precision but does not cause bias (Pollock et al. 2004).

7. There is no permanent emigration out of the study area. With the development of cooperative telemetry networks, the sampled area consists of the entire range of weakfish.

RESULTS

A total of 342 telemetered weakfish were released from 2006-2016, with sample sizes differing by estuary (Table 1), and median size of 361 mm TL across all studies (range 224-864; Table 1). A total of 178 long-lived transmitters contained batteries lasting greater than 300 days, of which 11 were released in 2007 and 18 in 2008 within Great Bay by Rutgers. For NCSU released weakfish in Delaware Bay, all 18 transmitters were long-lived, whereas in Bogue Sound, 12 long-lived transmitters were released in fall 2015, 60 in spring 2016, and 59 in fall 2015 (Table 1). Weakfish were detected 1,987,559 times across all studies, varying by estuary and temporal release (Table 1). Of the total detections, 158 were provided by the Smithsonian Environmental Research Center from within the Bogue Sound array (Figure 2b); no other detections were provided by cooperative telemetry networks. The majority of detections occurred between spring and fall, with a few fish apparently overwintering in Bogue Sound (Figure 3), though only two released with long-lived transmitters were detected after their overwintering period in the following spring and fall (Figure 3). The daily detections of the control transmitter indicated a seasonal difference, with the highest number of detections occurring during winter and the lowest in summer (Figure 4a), and the number of false detections increased with the increasing number of transmitters present in a given area (Figure 4b).

The fates of fish varied by estuary and season (Table 2). A total of 58 fish were censored from the analysis with 17 emigrating within 7 days of release, and the remaining 41 having died or not detected after the probationary period (Table 2). Overall, 284 weakfish were included in the modeling, of which 149 had transmitters with battery lives greater than 300 days. The fates of fish are as follows: 173 emigrations, 47 deaths, and 59 disappearances within the array (Table 2). Furthermore, the capture histories of 47 were updated to reflect deaths from “predation”, “cause unknown”, and “harvested” as noted in assumption 4 in the methods.

Emigration was evident across all estuaries (Table 2) and was steady across multiple weeks (Figure 5). For modeled fish, 61% were considered emigrations (Table 2). In estuaries from Delaware Bay and northward, egress peaked around the third week of September (week 39) and ended by the third week of November (week 47; Figure 5a). For North Carolina weakfish released in the spring, egress peaked around the second week of May (week 19) and ended for most fish by the third week of June (week 25; Figure 5b). For North Carolina weakfish released in the fall, egress peaked by the first week of November (week 45), continued throughout the winter, and into the early spring (weeks 53-67). The duration between the release of a weakfish in Bogue Sound and its emigration out of estuaries varied based on the season of release, as reflected by those released in the spring demonstrating the lowest median value of detection days at 22, as compared to the fall of 2015 with 47, and the fall of 2016 with 38 (Table 1).

Weekly estimates of apparent survival were similar among estuaries as evident by overlapping credible intervals (Figure 6b,d,f). The number of fish-at-risk, or those estimated to be alive by the model, decreased with seasonal emigration out of estuaries to areas on the shelf without receiver coverage (Figure 6b,d,f; Figure 5). Mean weekly median apparent survival estimates with 95% credible intervals (CrI) were 0.84 (CrI 0.80 to 0.89) for the Navesink, 0.87

(CrI 0.83 to 0.91) for Great Bay, and 0.78 (CrI 0.74 to 0.82) for Bogue Sound, when fish-at-risk is equal or greater than 10. Weekly median detection probabilities with 95% credible intervals were high among all estuaries; 0.91 (CrI 0.87 to 0.95) for Navesink, 0.82 (CrI 0.77 to 0.85) for Bogue Sound, and 0.50 (CrI 0.44 to 0.57) for Great Bay, when fish-at-risk is equal or greater than 10, with Great Bay having the most uncertainty (Figure 6a,c,e). Both the median and precision of apparent survival and detection probability estimates decreased as the number of fish-at-risk decreased.

For our model that pooled telemetry-tagged weakfish across all estuaries, monthly estimates of survival were made to better inform coast-wide management. Apparent monthly survival estimates varied across time (Figure 7b) and decreased with increased detected emigrations (Figure 7). Specifically, apparent survival of weakfish released in Bogue Sound in the spring decreased from 0.76 to 0.17 between April and May (months 4 and 5; Figure 7b); 40 out of 60 Bogue Sound weakfish were detected emigrating during that same period (Table 2; Figure 5b). The average median detection probability was high at 0.78 but declined as the number of fish-at-risk decreased through emigration in the spring and fall (Figure 7). The credible intervals widened for both apparent survival and detection probabilities when the number of fish-at-risk decreased (Figure 7). The highest value of fish-at-risk at 174 in September of year 1, dwindled to 1 by the following April, which corroborates the extremely low annual estimate of apparent survival at 0.002 (95% credible interval = 0.001-0.007).

DISCUSSION

We documented weakfish emigrating from estuaries in autumn. However we found almost no evidence of fish returning to spawn. The most likely explanation for the low number of weakfish detections after emigrating from estuaries is their movement to continental shelf

waters with limited receiver arrays. However, weakfish are estuarine spawners and have spawning site fidelity ranging from 60-81% (Thorrold et al. 2001); thus, we would expect telemetered weakfish to be detected the following spring in estuaries as all tagged fish were sexually mature and there is no evidence suggesting weakfish are skip spawners (Merriner 1976). Contrary to predictions based on spawning, only 2 out of 149 fishes with long-lived tags returned to estuarine release sites in subsequent years. Despite increased coverage across multiple estuaries from collaborative network receiver arrays, we observed no additional detections beyond the general vicinity of the tagging array in which the fish were released. We believe the lack of detections is due to the lack of weakfish, rather than detections of fish that were not shared within collaborative networks, as most fish were released by NCSU who were active participants in local collaborative receiver networks. Other potential reasons for the small number of telemetry-tagged weakfish returning to estuaries the following spring include surgery mortality, tag expulsion, and tag malfunction. In the assumptions section of the Methods, we provide evidence against each of these possibilities. Harvesting of telemetered fish may cause attrition of telemetered weakfish, but F has been low since 2006 given management regulations and primarily occurs in estuaries (estuarine defined as the environmental system consisting of the estuary and those transitional areas consistently influenced or affected by water from the estuary; ASMFC 2016; Chapter 2). Given the network of acoustic receivers on the US east coast, the most parsimonious explanation for the small number of weakfish detections is low survival.

Multiple studies support the hypothesis of low survival. The stock assessment's average Z from 2006-2014 was estimated as 2.42, an annual mortality of 91% (ASMFC 2016). Multiple weakfish conventional tagging studies have had low return rates, which can result from tag loss or low reporting rates, but can also occur due to high mortality. From 1996 to 1999, Virginia

Gamefish Tagging Program released 8,980 T-bar tagged, low-reward weakfish, of which 65 were returned (0.7% return rate), resulting in the eventual termination of the study (Lucy et al. 2000; Lucy and Bain 2001). In 2007, Delaware Division of Fisheries and Wildlife released 840 T-bar tagged weakfish with no returns (Clark 2008). NCSU released 3,622 high-reward (\$100), conventionally tagged coincident with the release of Bogue Sound telemetered weakfish, and had 140 returns (3.9% return rate). Although a higher return rate was measured in this study than in previous ones, 92% of the tag returns occurred within 100 days of release, which was reflected in an estimated annual 2016 Z of 7.25 (CrI 3.01 to 12.70; Chapter 2). In addition, a catch-curve from Pamlico Sound based on fisheries-independent data estimated a Z of 2.62 (CrI 1.83 to 3.70) for that same year, and annual median Z s from 2002-2017 ranged from 1.04 to 5.69 (Chapter 2). In summary, prior research supports our result of low apparent survival which likely represents true survival in the US east coast weakfish stock.

Weakfish mortality most likely occurred during the timespan between fall emigration from estuaries and spring return to estuaries. Our fate assignment determined that at least 61% of weakfish emigrated out of the estuary, and a further 20% of modeled fish disappeared in the array meaning we could not determine a fate. If the weakfish from the latter category were undetected emigrations, the percentage of estuarine emigrates could be as high as 81%. The model estimated lower apparent survival in periods when emigration away from estuarine receiver arrays occurred. Although spring-released telemetered weakfish emigrated rapidly away from estuarine receivers, NCSU conventionally tagged weakfish returns from spring-released weakfish indicated that many of these fish were migrating eastward and north and surviving till the fall (Chapter 2). Our work suggests weakfish mortality occurs between fall emigration out of their natal estuaries and their return in the following spring. The Virginia conventional tagging

study supports our finding, in which only 1 out of 65 total weakfish that had tag returns went through an overwintering period (Lucy and Bain 2001). Similarly, 4 out of 140 conventionally-tagged weakfish returns from the NCSU study overwintered (Chapter 2). In the fall, weakfish school and begin to move offshore. Predators of weakfish have similar migration and overwintering behaviors (e.g., striped bass, Overton et al. 2008; and bottlenose dolphin, Hayes et al. 2018); estimates of predator consumption rates of weakfish during winter periods suggest that predation mortality is the most likely mechanism for low survival (Chapter 3). The phenomenon of spatial/temporal specific mortality is not unique to weakfish, as the drastic decline of many salmon stocks are attributed to poor marine survival (McKinnell et al. 2001; Beamish et al. 2004; English et al. 2008), and evidence suggests predation could be the cause (Wright et al. 2007; Thomas et al. 2016; Chasco et al. 2017).

The fall emigration of weakfish is thought to commence with cooling water temperatures (Shepherd and Grimes 1984; Bigelow et al. 2002), and is supported by the initial telemetry work with Great Bay and Navesink weakfish, where egress began when water temperatures dropped below 24 °C (Manderson et al. 2014; Turnure et al. 2015b). Bogue Sound weakfish released in fall of 2015 resided longer in the estuary, corresponding with high water temperatures in December and January as compared to weakfish released in the fall of 2016 that left earlier. During the winter of 2015 into early 2016, some fish remained within Bogue Sound, suggesting estuary overwintering, a phenomenon also noted in Delaware Bay (Weinstein et al. 2009).

Our work indicates that weakfish emigration is gradual, especially in the fall, suggesting a process more complex than solely a change in water temperature. Manderson et al. (2014) found that egress was a product of salinity regimes and fish size as well as temperature. Out of 4 telemetered Great Bay weakfish released during spring 2007, the two largest (838 and 864 mm

TL) egressed within 4 days of tagging, whereas the smaller fish (381 and 648 mm TL) resided for 3-5 weeks post-tagging (Turnure et al. 2015b). Although limited by small sample size, the size-based emigration supports the hypothesis that older fish may spawn first in estuaries and egress immediately thereafter (Shepherd and Grimes 1984). Weakfish released from Bogue Sound in the spring had the shortest residence, which may be due to rapidly increasing water temperatures or that tagging occurred during the fish's north-bound migration.

Trends and magnitudes in weakfish apparent survival and detection probabilities were similar among estuaries. Time-varying apparent survival estimates were punctuated by downward spikes that matched the occurrences of weakfish emigrations, with the timing of spikes occurring earlier in northern latitudes. The detection probabilities were generally high at >0.4 with Great Bay being the lowest, as they had 6-9 stationary receivers as compared to the arrays of Navesink and Bogue Sound with >25 receivers. Hightower et al. (2015) investigated annual apparent survival estimates for Atlantic sturgeon and found them to be similar between four SEUS rivers. Their time-dependent detection probabilities had similarly low detection probabilities at ~ 0.2 while sturgeon were in coastal waters during the winter and increased to ~ 0.7 as fish returned to estuaries during spring and summer. Lindley et al. (2008) examined migrations of Green Sturgeon *Acipenser medirostris* in the northwest Pacific and found detections were highest as fish exited and entered rivers, but declined as fish moved to marine overwintering grounds without receivers.

Apparent survival can be lower than true survival, as the former is confounded by permanent emigration. We assumed permanent emigration was negligible due to extensive receiver coverage across the range of weakfish, at least for the majority of telemetered weakfish (NCSU released), as the number of receivers in collaborative telemetry networks have increased

substantially in recent years (www.theactnetwork.com). The use of Lotek equipment reduced the probability of Great Bay weakfish being detected on collaborative receiver arrays where Vemco acoustic technology is commonplace. As described above, fish moved to areas with minimal to no receiver coverage during their overwintering period. Normally, the fate of a tagged individual is made clear upon its return in spring or summer (Williams et al. 2002), which makes long-term apparent survival estimates unlikely to be biased by the low detection probabilities in winter. However, weakfish did not return for estuarine spawning as expected even with good receiver coverage in major east coast estuaries. More than half of weakfish had long-lived battery tags, and weakfish longevity is up to 17 years (Lowerre-Barbieri 1995). Therefore, the model accurately interpreted the low winter detection probabilities and subsequent lack of spring detections by estimating a low annual apparent survival that, in the case of weakfish, may approximate true survival.

Although this was not a fates (e.g., natural mortality, fishing mortality) driven model, we required some fate assignments to properly build the Cormack-Jolly-Seber observed states matrix. The subjectivity of assigning these fates was minimized by having individual capture histories read by a consistent pair of readers and maintaining an array until all transmitter batteries had expired. The ability to assign a fate increased with number of receivers in the array, as seen across seasonal releases in Bogue Sound. For our model, only capture histories of dead fish (e.g., predation, harvested, and cause unknown) were altered to reflect the assumption that detections only come from live fish. Although assigning predation may be the most subjective, we could discern non-weakfish behavior using metrics such as fish speed and location (e.g., Heupel and Simpfendorfer 2002; Bacheler et al. 2009; Friedl et al. 2013; Ellis et al. 2017). In addition, bias caused by erroneous assignment of predation fate or date-of-death was deemed

minimal, as the behavior leading to the assignment predominately occurred during the last detection day and the daily detections were condensed to weekly or monthly time steps. Additional information regarding catch-and-release and fishing mortalities could be acquired, if all fish had high reward external tags (Kerns et al. 2016; Hightower and Harris 2017), a condition only applicable to some of our telemetered weakfish. Many of our study estuaries were spatially large and had porous gates, which did not give us the ability to confidently assign a fate for 20% of all released fish that disappeared within the array, therefore we were unable to confidently subtract emigration from apparent survival to estimate true survival (Scheffel et al. 2019). In addition, emigration was consistent in spring and fall time-periods, therefore it was not possible to choose apparent survival estimates from time-periods with no emigration to estimate emigration by difference from apparent survival estimates with emigration. Instead, emigrations offered insight into the temporal variation in apparent survival estimates and allowed us to conclude that the bulk of fish emigrated out of estuaries.

Our modeling approach allowed for coast-wide survival estimates and provided insights into weakfish population dynamics. The multi-state CJS framework requires large amounts of data including sufficient recaptures, in order to determine whether an animal is present and not detected during a specific time period or has transitioned to another state (Joe and Pollock 2002; Coggins et al. 2006). For the model, an adequate total sample size is more important than the number of detections obtained for each individual (Otis and White 1999; Patterson and Pillans 2018), and this requirement was reflected in the lack of precision in estimates from time-periods with less than 10 fish-at-risk. The addition of Navesink and Great Bay weakfish increased the precision of our apparent survival estimates as well as the spatiotemporal scope of our findings. Lastly, telemetry allows for sufficient recaptures as reflected in higher detection probabilities as

compared to traditional mark-recapture methods (Pine III et al. 2001; Hewitt et al. 2010; McMichael et al. 2010; Dudgeon et al. 2015). The higher detection probabilities from telemetry studies increase parameter precision that allow for less restrictive models that can better detect trends in mortality estimates, diagnosing the causes of mortality, and directing effective management options (Johnson et al. 2010; Rudd et al. 2014).

Conclusion

Survival estimates are paramount to understanding population dynamics, especially for weakfish, whose stock has not rebuilt despite harvest reductions (ASMFC 2016). Incorporating previously published telemetry data allowed for coast-wide survival estimates which can be used to inform management (Crossin et al. 2017). Telemetry-tagged weakfish emigrated from estuaries and did not return in subsequent years, indicative of an extremely low apparent survival (<1%). Our estimate supports the low average annual survival probability from the 2016 weakfish stock assessment (ASMFC 2016). Telemetry also provided insight into the timing of mortality given the observed fall emigration from estuaries and then lack of spring detections. Conventional tagging studies and catch-curve mortality estimates support the timing and magnitude of mortality (see Chapter 2; Lucy et al. 2000; Lucy and Bain 2001; Clark 2008) and when combined with our telemetry findings, increases the power of our results, and can be used to formulate hypotheses for the cause of the weakfish stock decline such as predation mortality (Chapter 3).

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TABLES

Table 1. Summary of telemetry study results for weakfish including the estuary, year, sample size, first and last dates of release, minimum battery life of tags in days, median (Md) total length (TL) in mm with range, median raw detections per each telemetered fish with range, total raw detections, false detections, and median number of detection days with range. Blank cells indicate the data was not ascertainable.

Location	Year	Sample size	Release date	Battery life	Md TL (range)	Md det. (range)	Total det. ^a	False det. ^b	Md days (range) ^c
Navesink	2006	15	7/13-8/16	110	337 (224-535)	4040 (41-16568)	76056		33 (4-64)
	2007	26	6/29-10/9	110	389 (304-500)	1708 (31-11391)	143657		47 (6-88)
Great Bay	2007	26	4/30-8/31	229; 327; 627; 719	431 ^d (292-864)	242 (0-49892)	71986 ^e		9 (0-101)
	2008	33	6/11-9/11	229;438; 719	401 ^d (273-591)	142 (0-38283)	98681 ^f		27 (0-364)
New River	2014	13	6/2-10/28	184	342 (314-417)	2066 (50-126950)	182846	6	5 (1-39)
Delaware Bay	2015	18	8/24-9/17	513	318 (301-345)	36 (0-319)	1065		14 (2-37)
Bogue	2015	92	9/28-10/26	169;184; 513	361 (312-436)	1996 (2-51035)	589162	115	47 (1-192)
	2016	60	3/30-4/22	513	370 (315-485)	1337 (8-22072)	136929	82	22 (1-269)
	2016	59	9/22-9/28	513	350 (317-474)	5089 (122-140268)	857844	114	38 (0-136)
Total	2006-2016	342	3/30-10/26	110-719	361 (224-864)	1996 (0-140268)	1987559	317	33 (0-269)

Table 1 (continued).

^aIncludes false detections, detections of fish deemed as deaths, but not the control tag released in Fall 2016, ^bBased on the false detection analyzer (FDA) default setting in Vemco's proprietary VUE software, ^cNumber of days detected after altering capture histories for dead fish, ^dMean does not include censored fish in Table 2's Death within 7 day category (3 in 2007 and 4 in 2008), ^eTotal includes 25 active detections, ^fTotal includes 118 active detections

Table 2. Detected emigrations and fates for censored and model telemetered fish across multiple estuaries. Censored fish include temporarily emigrated or died within 7 days, or were never detected, or never detected alive after 7 days. Model fish include fish alive in system until receiver array pulled, temporary emigration after 7 days, death in the form of predation, harvest, or cause unknown, and finally disappear in array. For the Cormack-Jolly-Seber analysis, model fish within the death categories had their capture histories altered to meet the assumption that all detections were from live animals.

Location	Navesink		Great Bay		New River	Delaware Bay		Bogue		Total
Year	2006	2007	2007	2008	2014	2015	Fall 2015	Spring 2016	Fall 2016	2006-2016
Number released	15	26	26	33	13	18	92	60	59	342
Censored fish		1	10	12	8	10	8	7	2	58
Emigration within 7 d		1	2	1	5	1	5	2		17
Death within 7 d			3	4			2	4	2	15
Predation								1		1
Cause unknown			3	4			2	3	2 ^c	14
Not detected alive after 7 d			2	1	2 ^a	3	1	1		10
Never detected			3	6	1	6				16
Model fish	15	25	16	21	5	8	84	53	57	284
Alive in system	1	4								5
Emigration after 7 d	9	9	13	18	4	4	41	42	33	173
Death after 7 d	1		2		1		18	6	19	47
Predation							1	5	9	15
Harvested			2							5
Cause unknown	1				1		14	1	10	27
Disappear in array	4	12	1	3		4	25	5	5	59

Table 2 (continued).

^aA single fish was confirmed dead through active telemetry, ^bTwo fish harvested by recreational fisherman and 1 was recaptured and gut-hooked by researchers, ^cOne “Cause unknown” was a tag expulsion because the fish was recaptured with an incision wound but no transmitter.

FIGURES

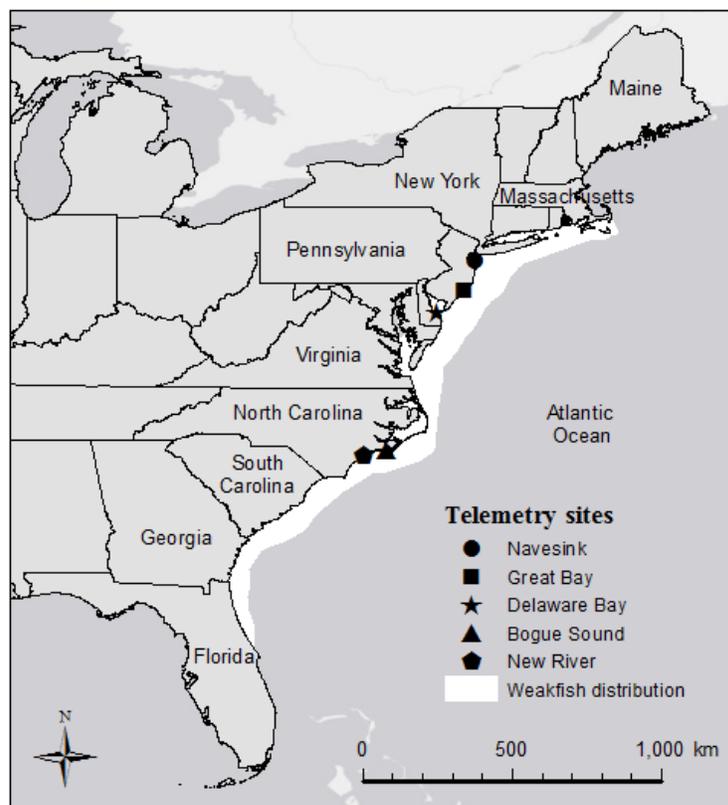
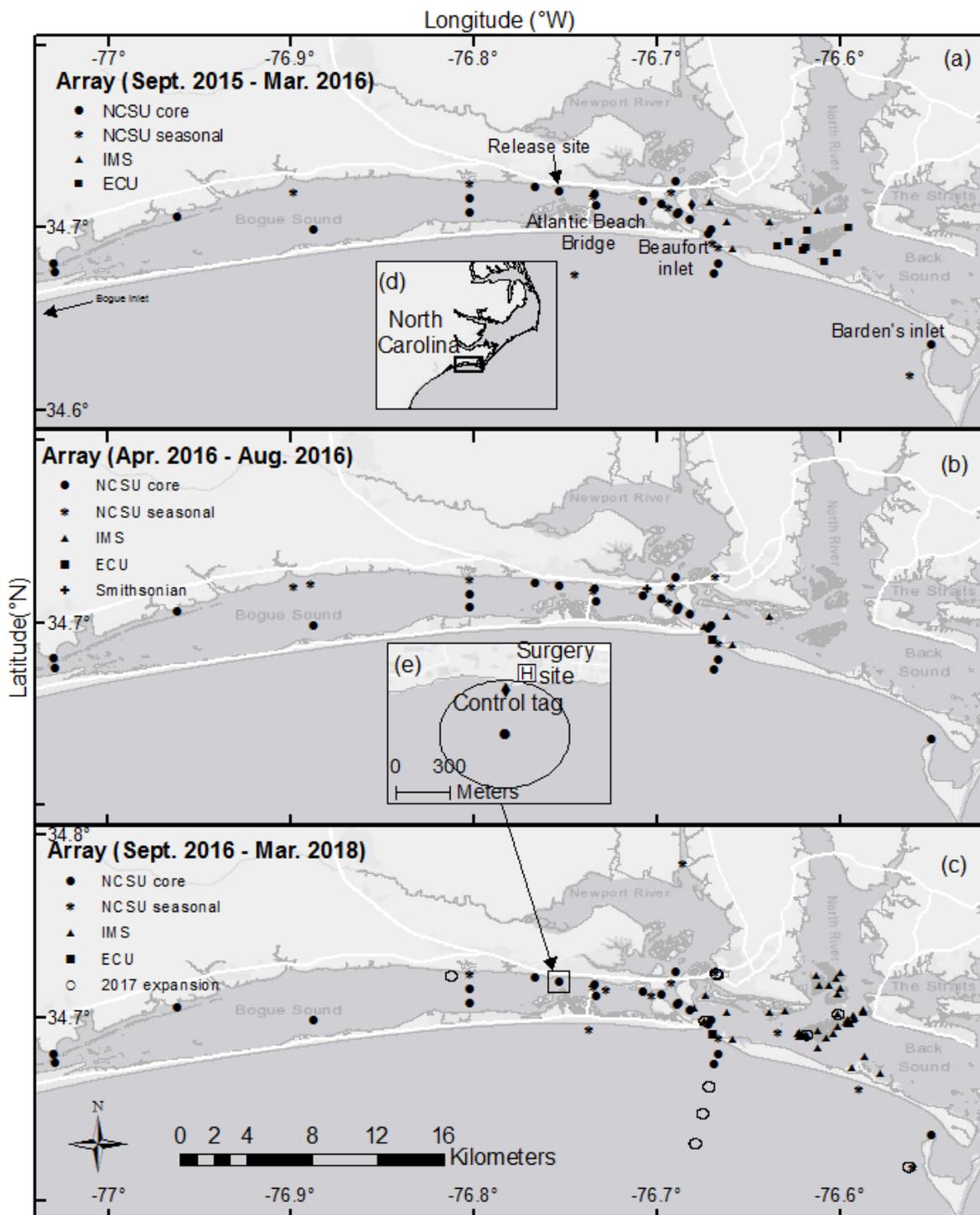


Figure 1. Telemetry release locations from 3 studies across the years 2006-2018 ($n=342$). Weakfish distribution ranges from Cape Canaveral, FL to Cape Cod, MA.

Figure 2. Bogue Sound array from September 2015 to March 2018 consisting of a variable receiver-array deployed by North Carolina State University (NCSU), North Carolina-Chapel Hill's Institute of Marine Sciences (IMS), Eastern Carolina University (ECU), and Smithsonian Environmental Research Center. The NCSU core locations were present from the first telemetered weakfish release till the last transmitter expired. Telemetered weakfish were detected in a) a 43 receiver-array from September 2015 to March 2016, b) a 35 receiver-array from April to August 2016, and c) a 76 receiver-array during fall 2016 that expanded to 87 receivers in 2017, of which 2017 additions are represented with hollow circles drawn to scale with a 300 m radius. d) Boxed inset location of Bogue Sound on the North Carolina coast. e) Surgery site inset with control tag location within the 300 m range of a receiver.



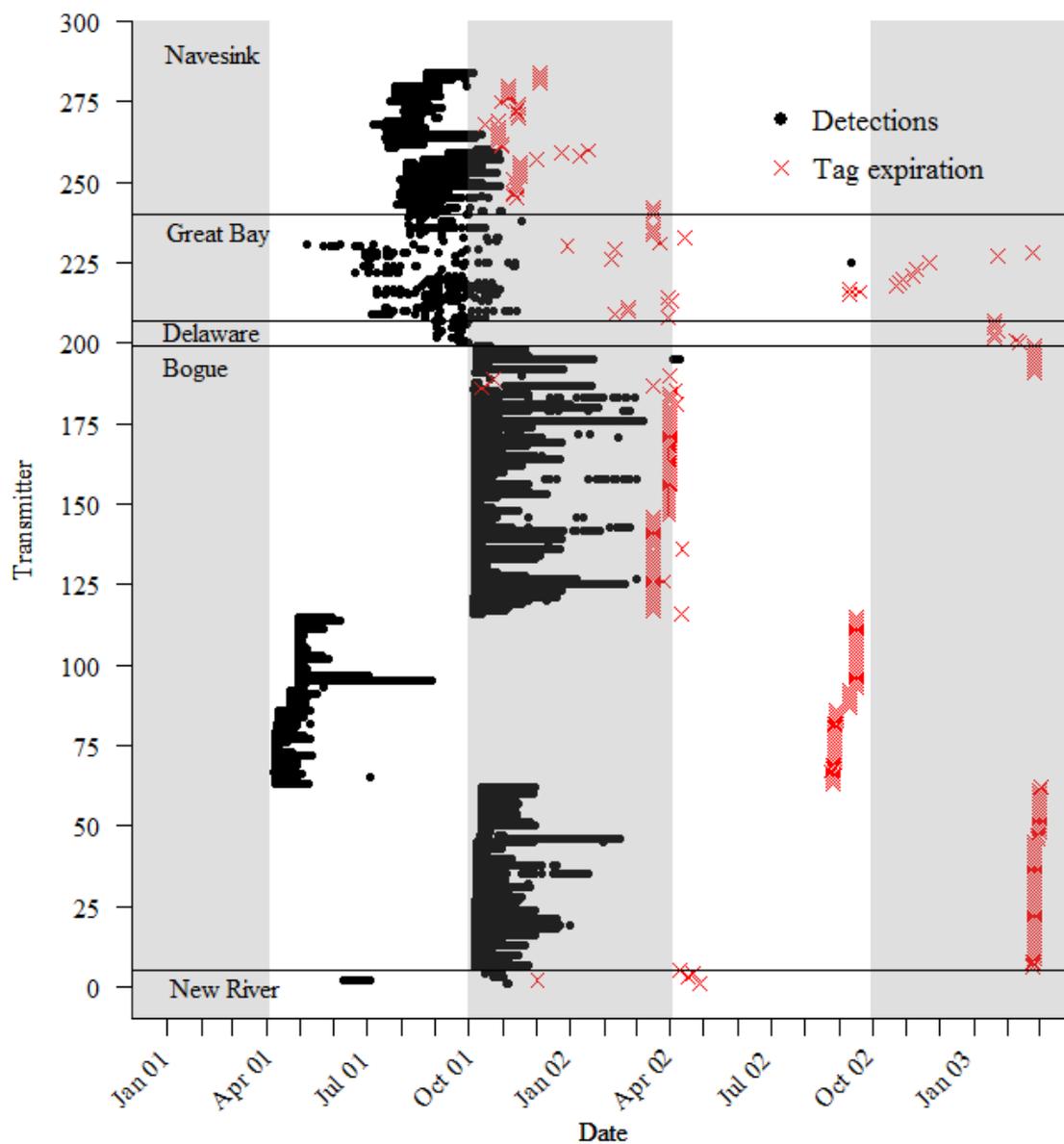


Figure 3. Abacus plot of daily weakfish detections across five estuaries arranged from north to south and by release date within each estuary. The red x indicate when the transmitter expired and grey shading indicates the weakfish overwintering time period from Oct 1 to the end of March. For the Navesink, the array was pulled before batteries expired on October 3 in 2006 and October 31 in 2007.

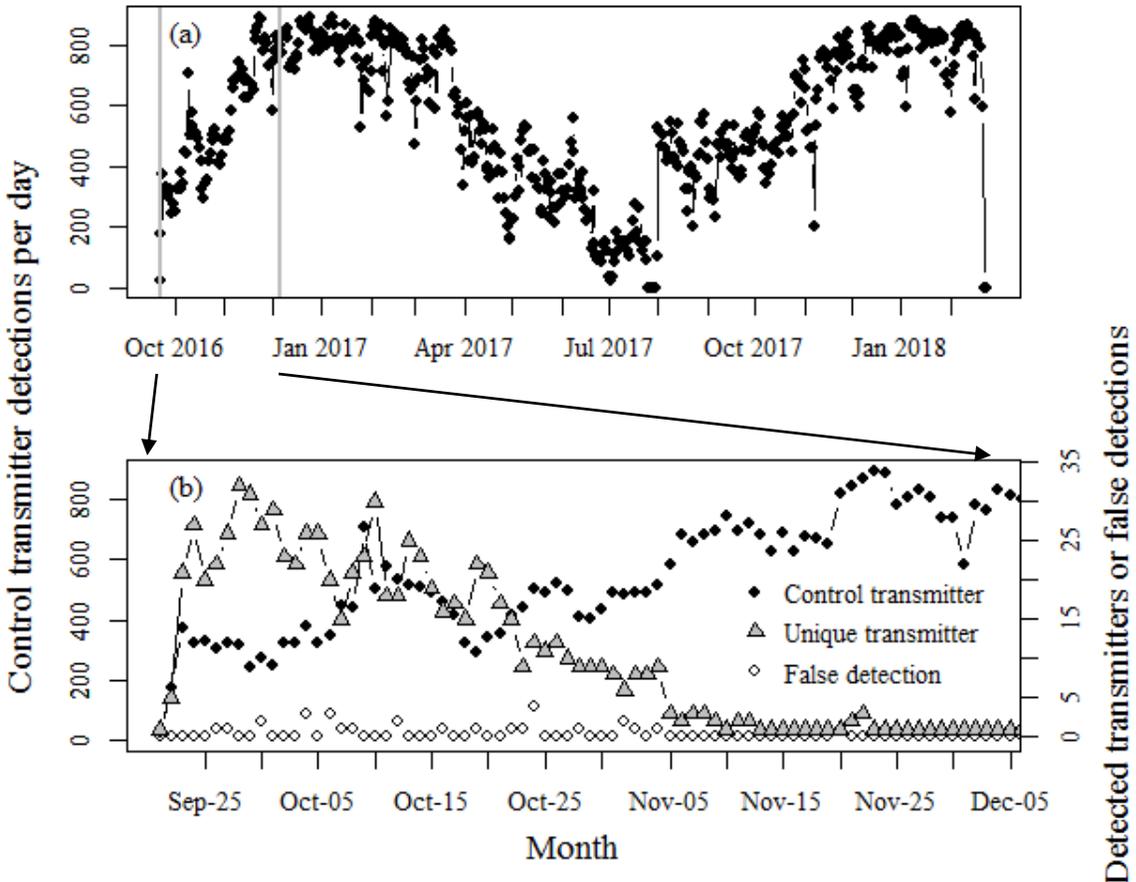


Figure 4. a) Daily detections of the control transmitter on a single receiver across the life of the transmitter. b) Inset of daily control transmitter detections from September 20th to December 6th 2017 compared to the number of unique transmitters detected and false detections.

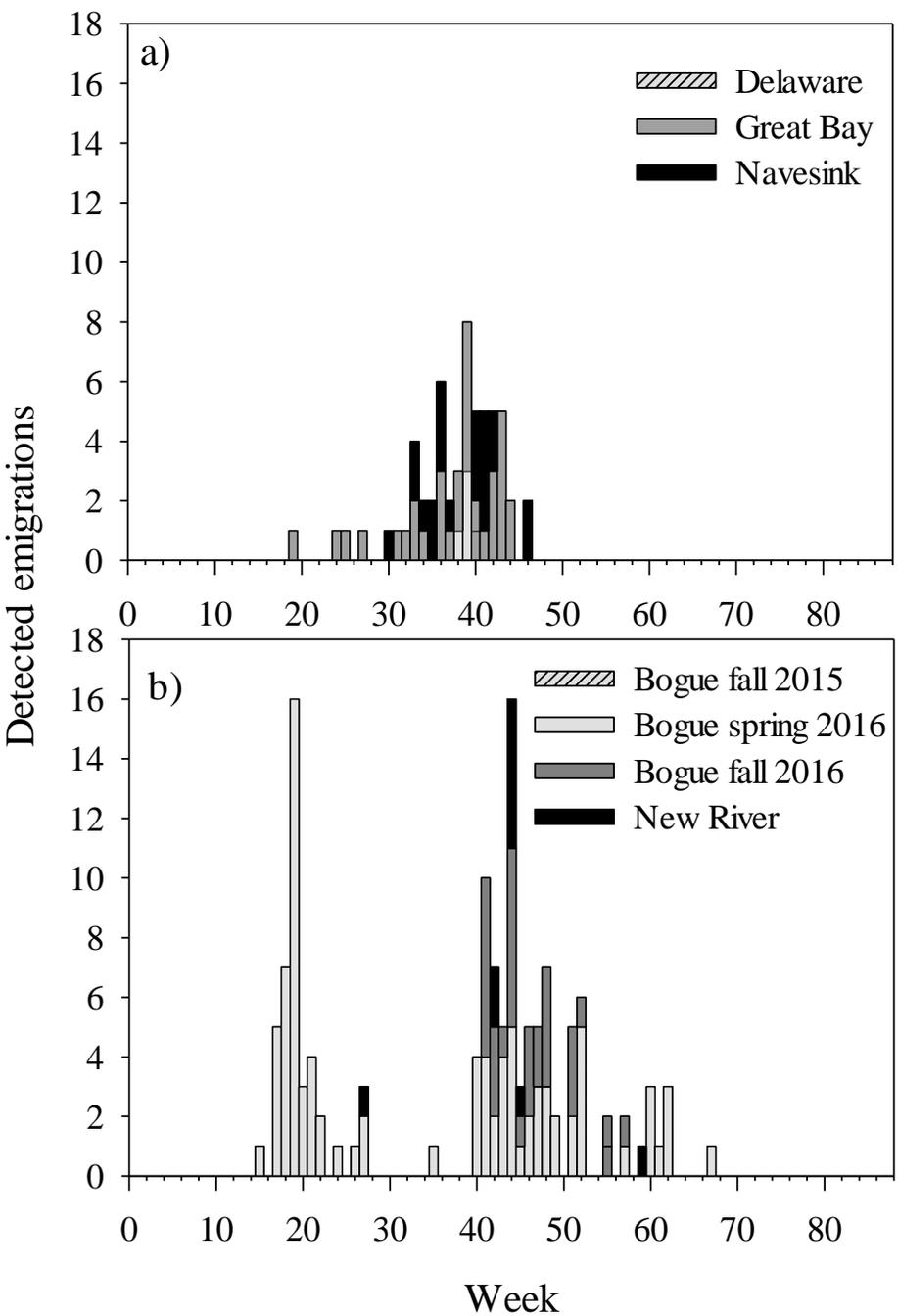


Figure 5. Detected weekly temporary emigrations of weakfish released a) north of Virginia and b) North Carolina.

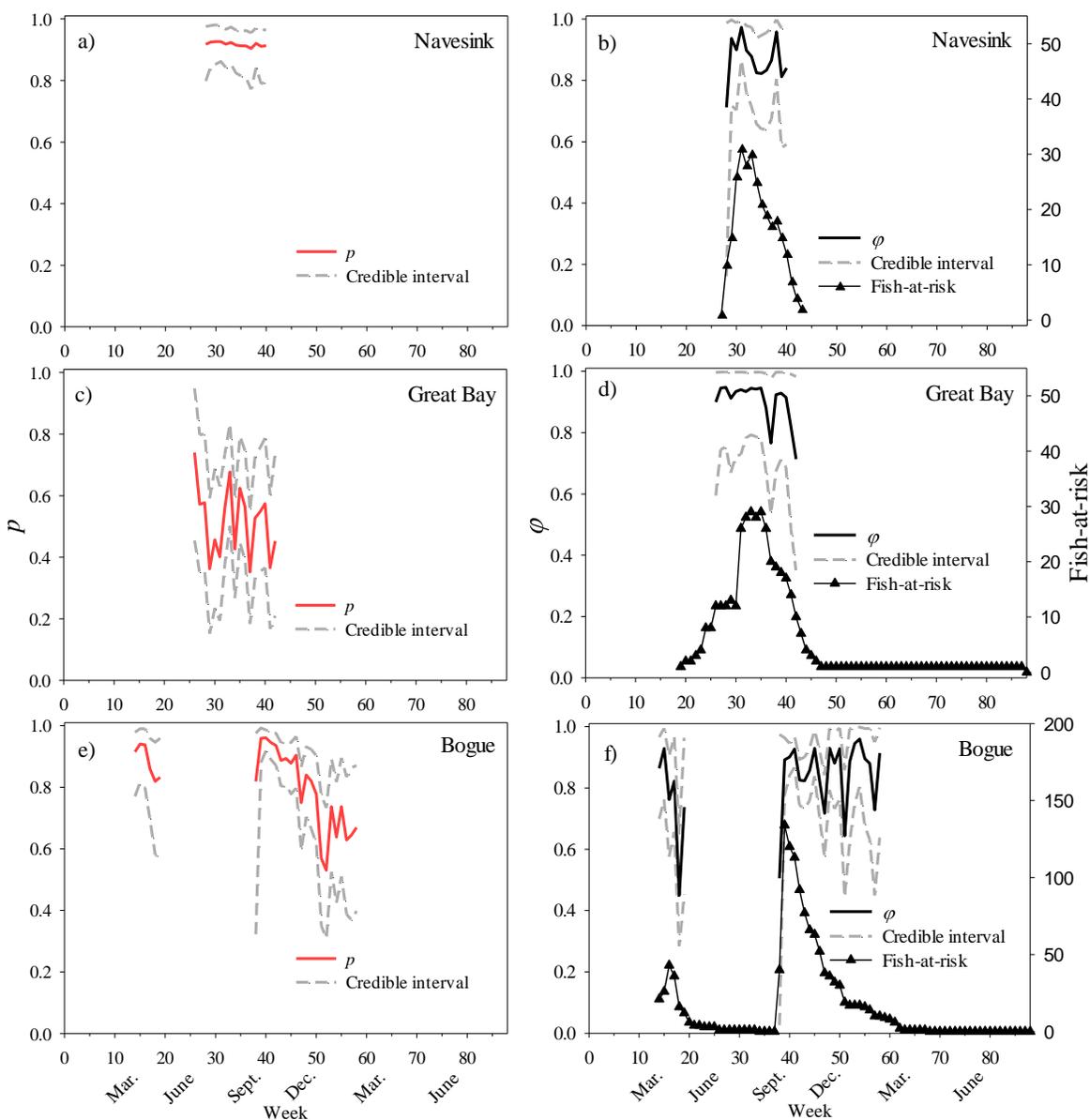


Figure 6. Weekly detection probabilities (p) and apparent survival estimates (ϕ) (with 95% credible intervals) for telemetry-tagged weakfish in the Navesink River, Great Bay, and Bogue Sound estuaries. Estimates are provided for those weeks where at least 10 fish were at-risk. Fish-at-risk data are presented for all time periods over which the model was run (b).

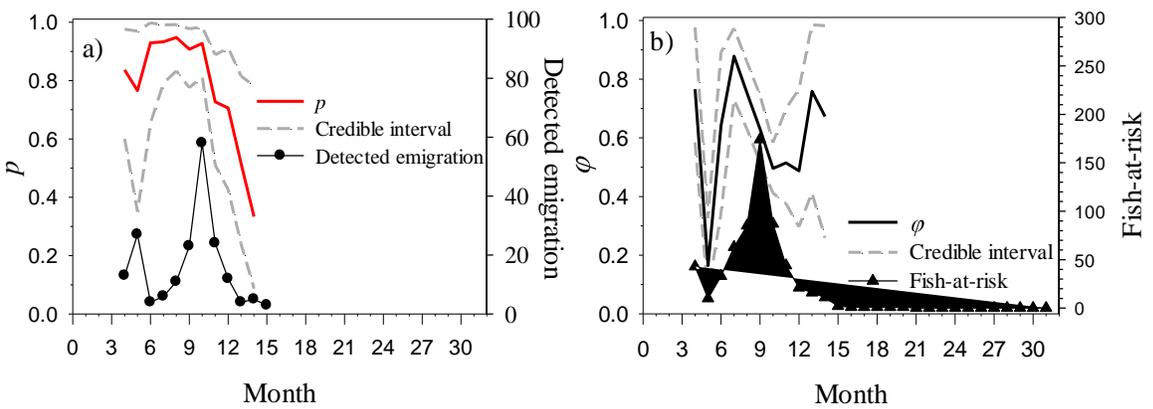


Figure 7. Monthly (a) detection probabilities (p) and (b) apparent survival estimates (ϕ) (with 95% credible intervals) for telemetry-tagged weakfish pooled across all estuaries. Detected emigrations ($n=190$) are all weakfish that showed clear signs of emigrating from estuaries (a). Estimates of ϕ and p are provided for those months where at least 10 fish were at-risk; fish-at-risk data are presented for all time periods over which the model was run (b).

CHAPTER 2. HIGH AND SEASONALLY-VARYING NATURAL MORTALITY FOR A FISH POPULATION AT LOW STOCK BIOMASS

Jacob R. Krause, Joseph E. Hightower, Stephen J. Poland, and Jeffrey A. Buckel

ABSTRACT

Rebuilding of exploited fish stocks at low biomass requires accurate mortality estimates. Weakfish (*Cynosion regalis*) abundance are at historical lows caused by an increasing total mortality (Z) in recent years, but uncertainty exists in the relative importance of F and M to Z . Data from a tag-return study of weakfish in North Carolina were analyzed using a Bayesian statistical framework to estimate seasonal and annual F and M . We accounted for key auxiliary parameters in a tag-return model (i.e., tag-reporting rate, tag loss, and tagging mortality) through field studies and experimental design including high-reward and double-tagging. From 2014 to 2017, we estimated a constant annual instantaneous mortality rate of 0.07 yr^{-1} (95% credible interval [CrI]: 0.06, 0.10) for F and 5.71 yr^{-1} (CrI: 4.40, 7.40) for M . Estimates of Z from an independent catch-curve analysis were similar in magnitude to our tag-return results. Both analyses indicate that a large portion of mortality occurred from fall to spring, coinciding with weakfish migration and overwintering periods on the continental shelf. Through independent datasets, our study provides insights into the magnitude, timing, and sources of weakfish mortality, and enhances understanding of weakfish population dynamics to facilitate effective stock rebuilding.

INTRODUCTION

Effective rebuilding of exploited fish stocks with a low biomass requires accurate fishing and natural mortality estimates. The fishing mortality rate (F) allows management to meet stock rebuilding goals through comparisons with target and threshold levels based on biological reference points (Hilborn and Walters 1992), whereas the natural mortality rate (M) affects

estimates of stock size and productivity, which ultimately determines harvest rates (Clark 1999). Stock assessments typically estimate F indirectly by relating catch-at-age data to changes in stock abundance or size/age composition (Walters and Martell, 2004), whereas M is difficult to measure since natural deaths are rarely observed in aquatic systems (Quinn and Deriso, 1999). M is often estimated externally based on life history parameters and environmental variables (e.g., Pauly 1980; Hoenig 1983; Lorenzen 1996; Griffiths and Harrod 2007; reviewed by Kenchington 2014), and used as a fixed input parameter in fishery stock assessments (Vetter, 1988). However, these estimates of M do not account for time- or location-specific differences and have an unknown certainty (Vetter 1988; Pascual and Iribarne 1993). Stock assessment models are particularly sensitive to input values of M (Clark 1999; Williams 2002). Overestimates of M may result in lost harvest, whereas underestimates can result in unsustainable exploitation rates and misguided management recommendations (Williams 2002; Legault and Palmer 2015).

Tag-return experiments can directly estimate F and M , thereby generating near real-time estimates of F to track fishery harvest trends, validating catch-at-age analysis, and determining if target harvest rates are being maintained (Walters and Martell 2004). These models partition the instantaneous total mortality rate (Z) into estimates of F and M (Hoenig et al. 1998a), however precise mortality estimates depend on key auxiliary parameters: tag-reporting rate (λ), tag loss (Ω), and survival from the tagging procedure (ϕ ; Pollock 1991; Pollock et al. 2001; Miranda et al. 2002; Brenden et al. 2010). Multi-year tagging studies of rigorous design can estimate the auxiliary parameters, generating reliable estimates of mortality (e.g., den Heyer et al. 2013; Kerns et al. 2015) and providing insight into the timing and causes of mortality because estimates are on varying time-scales (e.g., monthly or seasonally; Harris and Hightower 2017; Ellis et al. 2018).

Weakfish (*Cynoscion regalis*) are an important recreational, commercial, and ecological species that primarily inhabit estuarine and coastal waters between North Carolina and Massachusetts. The spawning stock biomass has declined since 1982 to historic lows in the late 2000s, with the cause of the decline attributed to increased Z . Despite rigorous regulatory measures, stocks have failed to rebuild, and the most parsimonious explanation for the increase in Z was an increase in M (ASMFC 2016). Efforts to improve stock assessment estimates of M resulted in a Bayesian statistical catch-at-age model that internally estimated a time-varying M (Jiao et al. 2012; ASMFC 2016). The prior distribution for the 1982 M estimate was based on external estimates (uniform prior 0.1 to 0.4), and subsequent M estimates were allowed to vary through the time-series (1983-2014) using a random-walk approach (ASMFC 2016). M was estimated to increase through the time-series to a high of 0.95 in 2008, however with considerable uncertainty, and the cause remains unknown (ASMFC 2016). Estimates of F from the stock assessment from 2000 onwards were considered a relatively minor portion of Z (ASMFC 2016), but have not been compared to direct estimates of F from a tag-return study.

We estimated monthly F and M for weakfish from a North Carolina tag-return study from 2013 to 2018. Our modeling approach follows the tag-return design of Ellis et al. (2018), which is based on the instantaneous rates formulation of the Brownie tag-return model (Brownie et al. 1985; Hoenig et al. 1998a; Hoenig et al. 1998b). We then compared seasonal and annual Z estimates from our tag-return study to those derived from a catch-curve (Ellis et al. 2018) based on a fishery-independent survey conducted by North Carolina Division of Marine Fisheries (NCDMF) from 2002 to 2017. Our study provides important information in timing and magnitude of weakfish mortality estimates, thereby enhancing precision of mortality estimates, and may promote effective management strategies to facilitate successful stock rebuilding.

METHODS

Data from two concurrent yet independent studies were used to model weakfish mortality: (1) a multi-year, high-reward external tagging initiative by North Carolina State University (NCSU) and (2) a fishery-independent gill net survey conducted by the NCDMF in Pamlico Sound. The methodologies used to collect and analyze these data are detailed below.

NCSU tag-return study

From November 2013 to May 2017, weakfish were continually tagged and released in North Carolina, with the highest concentration in the vicinity of Cape Lookout (Figure 1a,c). Researchers captured and released the majority of weakfish in this study (67%), while the remaining were captured and released by 11 compensated guides and recreational anglers using standard hook-and-line methods. All taggers were trained to ensure consistency in handling and tagging methodology. We also recruited the assistance of compensated guides in Delaware Bay during 2015 but tagging was discontinued in 2016 due to the low release ($n < 10$) and lack of returns.

We restricted tagging to mouth-hooked individuals greater than 305 mm total length (TL) that had no physical signs of trauma (e.g., bleeding or visible tissue damage). Three types of internal anchor tags were used in the project to test tag retention: polyetholin tubing over a stainless-steel wire core (steel), monofilament covered with vinyl tubing (mono), and vinyl tubing (vinyl; Model FM-95W, FM-89SL, and FM-84; respectively: Floy Tag, Inc., Seattle, WA). Each tag was red in color, with a tube length of 63.5 mm, and a laminated oval anchor disk measuring 4.8 x 15.9 mm. All tags were high-reward, with black text message “CUT TAG \$100 REWARD”, a unique tag number preceded by “NC”, and a toll-free phone number preceded by “NCSU” printed length-wise on the tube. Each anchor tag was inserted ventrally through a small

incision immediately posterior of the pelvic fin. Approximately one-third of weakfish were single-tagged with anchor placement on the left-lateral side, whereas the remaining two-thirds were double-tagged, bilaterally, to estimate tag loss. Initially, all taggers double-tagged every third fish, but after estimating a high tag-loss (~40%) on returns from 2014, we modified our protocol to increase the likelihood of returns by having researchers double-tag every fish. Treatments consisted of single steel, mono, and vinyl, and double-tagged steel x steel, steel x mono, and steel x vinyl in which steel tag was always placed on the left-lateral side. In a second approach to estimate tag loss, PIT tags (23 mm half duplex) were evenly implanted across all anchor tag treatments in 24% of total fish. The PIT tag was inserted into the coelomic cavity through the left-lateral incision prior to anchor tag insertion. For the year 2015, an additional treatment of PIT tag-only fish (n=109) was released to estimate survival from tagging procedure (ϕ ; i.e. compare return rates of conventionally tagged fish with PIT tag-only fish). Because this treatment had different detection probabilities when compared to conventionally tagged fish and only a single return, we excluded PIT tag-only releases and returns from all modeling and future results. Collaborators only performed single and double tagging using steel tags. The order of treatments was randomized (i.e. number of tags per fish and treatment type), and the tag number, date, fish TL (mm), and location associated with each individual release were recorded.

Information on recaptured weakfish in this study was provided by fishery participants and researchers. Reporting of tagged fish was promoted by advertising across several media outlets throughout the study. Recapture data ascertained during a follow-up phone interview included the tag number(s), date and location of recapture, fish TL, general condition and number of tags, fishery sector (commercial or recreational), picture of fish when available, and fate of the fish and tag (i.e., kept, released with tag intact, or released with tag cut off). Fishermen were required

to mail the tag(s) to researchers in order to collect reward. Weakfish captured by non-public personnel (NCDMF fisheries biologists, creel clerks, fish house samplers, collaborative taggers, and NCSU researchers) were scanned for PIT tags.

Tag-return assumptions

1. The tagged sample mix completely with the untagged population such that tagged fish are assumed to be representative of the entire population. Although we continually released weakfish over the study time-period, this assumption may have been violated over the spatial scale of North Carolina, as over 90% of fish were released in the vicinity of Cape Lookout.
2. All tagged individuals considered in the model have the same survival and recovery probabilities. Equal survival was ensured, as all fish were tagged within a narrow size range. Recovery probabilities were assumed equal, as 99.7% of tagged fish were >305 mm, the legal harvest size within the commercial and recreational sectors.
3. Tagged fish have independent fates. This assumption may be violated because weakfish aggregate around structures during spring and fall (i.e. bridges, rock jetties, deeper holes), allowing for individual anglers (n=14) to recapture multiple tagged fish, albeit never on the same day. Violations of this assumption make the precision lower than it appears, but violations do not cause bias (Pollock et al. 2004).
4. The month of tag recovery is correctly tabulated. We assumed anglers correctly reported the date of tag recovery.
5. Survival rates (ϕ) were not affected by tagging (i.e. 100% post-release survival), based on sound handling practices, and capture depth of <15 m to reduce barotrauma.

6. The tag reporting rate was 100% ($\lambda=1.0$), as all tags were high-reward at \$100 and double-tagged fish retaining both were worth \$200.
7. Tag loss can be estimated from the Barrowman and Myers (1996) exponential decay model. Monthly tag retention was estimated as a function of at-liberty days for double-tagged fish that were returned with either one or two tags. The model estimates tag retention from ρ , the probability of tag retention immediately after tagging and Ω , the chronic instantaneous rate of tag loss. For a recapture of individuals subsequently released with tags intact (i.e. a multi-recapture fish), only the first recapture was included in the model regardless of the method of capture (i.e. fishery or scientific sampling). The model assumes that double-tagged fish represent a random subset of all tagged weakfish, in which each of the two tags was lost or retained independently, regardless of placement laterality, and tag loss did not differ by laterality. The latter assumption may have been violated, as 12 out of 13 returns were lost on the right-lateral side, a percentage greater than expected as compared to random chance (i.e. 50%). In addition, we assumed that fish behavior, M , ϕ , and λ were unbiased by whether a fish was tagged with one versus two tags (Wetherall 1982; Hearn et al. 1991). Lastly, we assumed that retention by tag types was similar based on returns by tag type (see Results).

Tag-return model

We estimated F and M from the recoveries of single- and double-tagged weakfish following the tag-return model by Ellis et al. (2018). His model accounted for both harvest and catch-and-release (hereafter referred to as discard) mortality by following the approach of Jiang et al. (2007), where tags at-risk were modeled as opposed to tagged fish. This approach required that additional recaptures of individuals released with tags intact, beyond the first recapture, be

ignored (Bacheler et al. 2008). This effect on sample size was minimal, as only three tagged weakfish were caught and reported more than once. The model did not include fish caught by scientific sampling, as these mortalities were not associated with fishing. Our model differed from Ellis et al. (2018) by omitting internal estimation of the auxiliary parameters of Ω , λ by sector, and ϕ as they were externally estimated, with ϕ assumed to be 1.0 (see aforementioned assumptions). In accordance with Ellis et al. (2018), we assumed 100% reporting of \$100 high-reward tags, and externally estimated the initial tag-retention ρ which immediately reduced the effective population size of tagged fish. The tag-loss parameters Ω and ρ were externally estimated to allow for the use of extra information from a daily time-step as most fish were returned within 100 days and the incorporation of returns from scientific sampling. A monthly time-step was chosen for the tag-return model to examine seasonal variability in mortality.

Tag-returns were organized into nine tables (3x3): fishery type (recreational, commercial, discards) x tag type (single-tag released fish, double-tag released fish returned with 1 tag, and double-tag released fish returned with 2 tags). Recreational and commercial tables consisted of harvested fish from each sector. Discards (n=48) mostly consisted of fish captured recreationally, with only 3 commercial discard returns, therefore a single table represented catch-and-release from both fishing sectors. The recovery probabilities are described in Polacheck et al. (2006), and $\lambda=1$, as all our tags were high-reward. The recoveries were all assumed to follow a multinomial distribution (Polacheck et al. 2006; Ellis et al. 2018).

The model estimated instantaneous fishing mortality for commercial (F_c) and recreational fisheries (F_r), discards (F'), and M , all of which represent loss rates for tags. A 10% discard mortality was assumed in the latest stock assessment (ASMFC 2016), and F' was multiplied by 0.1 to provide an estimate of the mortality rate for discarded fish instead of the rate of discarding

(Jiang et al. 2007). The total fishing mortality (F_{fish}) was equal to $F_c + F_r + \text{adjusted } F'$, and total mortality (Z) equaled $F_{fish} + M$ for a specific time-period.

We implemented all models using the Bayesian statistical software package JAGS (Plummer 2003) called from R (R Core Team 2013). In the tag-loss model, uninformative prior distributions were used for ρ [uniform (0,1)] and Ω [uniform (0,2)]. The latter was uninformative as the estimated daily rate was very close to 0. For the mortality model, an uninformative prior distribution [uniform (-10,2)] was used for the natural logarithm of F_r , F_c , F' , and M . The model was run for 43 periods from June 2014 to December 2017, which corresponded to the first release and one month after the last return. We released 50 fish in November 2013, but had no returns and did not release any additional fish until June 2014; therefore with a paucity of releases and returns we did not include the months of November 2013 to May 2014 in the model. A preliminary model run with time-varying parameters (M43) indicated little variation in F parameters among periods, but strong seasonality in M . Therefore, we compared the M43 with models that had constant F parameters, and estimated a shared seasonal M (M4) or six-month M (M2). The seasons for M4 were winter, spring, summer, and fall which consisted of the months January to March, April to June, July to September, and October to December, respectively, and M2 were six-month intervals of October to March and April to September. The three candidate models were compared using deviance information criterion (DIC; Spiegelhalter et al. 2002) and its effective number of parameters (pD: Plummer 2002). Parameter posterior distributions from all models were estimated using three Markov chains of at least 50,000 samples, with the first 10,000 samples excluded to remove bias associated with initial parameter values. Chain convergence was determined by visually inspecting time-series plots of parameter values, and

through calculation of the Brooks-Gelman Robin statistic (Brooks and Gelman 1998). All parameter estimates are presented as posterior medians with a 95% credible interval (CrI).

NCDMF fishery-independent gill net survey

We used coast-wide fishery-independent gill net survey (IGNS) data collected by the NCDMF from February 2002 through December 2017 to estimate a seasonal Z for weakfish. The seasons were winter, spring, summer, and fall, consisting of the same month increments as the M4 tag-return model. Through a stratified random sampling design based on region and water depth (i.e., shallow <1.83 m and deep ≥ 1.83), 8 strata in Pamlico Sound were sampled from mid-February to mid-December each year. Strata were sampled only once in February and December months, and twice monthly in all other months. Specific detail on the sampling protocol and experiment gill net mesh sizes can be found in Ellis et al. (2018). Collected weakfish were enumerated and measured in TL, with a subsample retained for age analysis.

Analysis of survey data

We employed the catch-curve model described by Ellis et al. (2018) to estimate Z from catch-at-age data from the IGNS. Many weakfish captured in the IGNS were not aged; therefore, we used North Carolina weakfish aging data grouped by season within a year to convert IGNS-catch data in TL to an estimated age (Figure A1). These aging data were compiled by the NCDMF from multiple fishery-dependent and fishery-independent surveys across 15 years (February 2002 to December 2017; $n=7952$). Estimated survey catch by age was then summed across all length frequencies for each seasonal period and standardized across all seasonal periods. Standardization was achieved by calculating age-dependent catch-per-unit-effort (CPUE), the number of weakfish per age group captured per hour of gill net set in each seasonal period, and scaling CPUE upwards by 50,000 hours.

The model estimated an initial (relative) abundance of cohort i (N_i) and assumed the decline in numbers over time represented Z . By including all ages in our model (late age-0 to age-8), we assumed that weakfish within this age range share a common Z . The model accounted for age- and season-specific vulnerability of weakfish to the IGNS. The model estimated γ_a (the survey selectivity for age a) and α_p (the multiplier for seasonal p availability of weakfish to the survey). The γ_a was defined as asymptotic with a single increasing logistic function to estimate age-based selectivity of weakfish, where β_1 and β_2 are the intercept and slope parameters, respectively (Quinn and Deriso 1999; Ellis et al. 2018). Weakfish emigrate from estuaries during their overwintering migration to the continental shelf. As such, we accounted for the seasonal availability of weakfish to the IGNS. The α_p was assumed constant across ages and years.

We estimated Z seasonally, and calculated annual estimates of Z within the model. Uninformative prior distributions were used for the natural log of N_i [uniform (-15,15)], α [uniform (0,1)], β_1 [uniform -20,1], β_2 [uniform (1,12)], and Z [uniform (0,5)]. Preliminary modeling suggested the seasonal availability of weakfish to the IGNS was highest from April to June; therefore, the prior distribution of α_2 was fixed at 1.0 such that all other α_p were estimated relative to α_2 . A visual metric of model fit found agreement between the observed CPUE for each cohort within a season and that predicted by the model (Figure A2). In addition, a Pearson correlation test found a significant correlation ($r = 0.58$, $p = 0.03$) between N_i for 14 cohorts (2002 to 2015) with the Young-of-Year (YOY) index from NCDMF Pamlico Trawl Survey (Figure A3; Steve Poland, NCDMF, unpublished data). The index consists of standardized estimates of CPUE based on survey samples collected in June and September using a stratified-random sampling design. Parameter posterior distributions were estimated using three Markov chains of 50,000 samples with the first 10,000 samples excluded. The convergence of Markov

chains was assessed as previously described and all parameter estimates are presented as posterior medians with a 95% CrI.

RESULTS

A total of 3,672 weakfish were tagged in North Carolina from November 2013 through May 2017 (Figure 1a,c), consisting of 1,772 releases with a single high-reward tag (48%) and 1,900 releases with double high-reward tags (52%). Released weakfish ranged in TL from 262 to 612 mm, with an overall mean of 353 (± 0.6 SE) mm. A total of 140 fish were returned over four years, with the last on October 13, 2017. Of the returned fish, 3 were recaptured multiple times (i.e. fishermen only cut off one out of two tags upon initial capture, or the fish was released with all tags intact after being caught through scientific sampling).

Tagged weakfish were recovered throughout North Carolina estuarine and coastal waters (Figure 1b,d). Most recoveries were near the site of release (Figure 1a,c), with subtle differences based on the release month. For fish released in spring (February to July), recoveries occurred in areas north and east of release (i.e. Pamlico Sound; Figure 1d), whereas fish released in fall (August to January) were recovered in areas south and west of release (i.e. Onslow Bay; Figure 1b).

Of the 3,179 steel, 502 mono, and 505 vinyl tags used, 117 steel (3.7%), 26 mono (5.2%), and 24 vinyl (4.8%) were recovered. Fifty-five single-tagged and 82 double-tagged fish were recovered, with respective return rates of 1.5% and 2.2%. Out of the double-tagged returns, 13 fish shed a tag (1 mono and 12 steel), 12 from the right side and 1 from the left (Fig 2a).

Days-at-liberty averaged 49.6 (± 4.2 SE) with a range of 1 to 682, with the maximum value based on a second recapture. The percentage of all returns coming from fish at-liberty for at least 100 days was 8% and was higher for fish released in spring as compared to those in the

fall (Figure 2b). A total of 578 weakfish were released from March to June across study years, 28 were returned (4.8% return rate), of which 25% were recovered after 100 days-at-liberty. In contrast, a total of 3,014 weakfish were released from August to December, 112 were returned (3.7% return rate), of which only 3.6% were recovered after 100 days-at-liberty. Only 4 returns occurred after a weakfish was released in spring or fall and recovered post-winter in subsequent years.

The recreational fishing sector reported 89 external tags in total, comprised of 31 single-tagged and 58 double-tagged specimens, of which 45 (51%) were reported as discards. The commercial fishing sector reported 26 tags in total, comprised of 14 single-tagged and 12 double-tagged specimens, of which 4 (15%) were reported as discards. Almost all commercial returns were captured in a gill net ($n=23$), of which 17 occurred on the ocean side of coastal barrier islands (Figure 1b). Two were captured via hook-and-line, and the remaining one in an estuarine shrimp trawler. Most of the commercial returns ($n=18$) were in 2014, with minimal returns in subsequent years ($n=1, 3, \text{ and } 4$; respectively). During scientific sampling, a total of 25 fish were recaptured, of which 14 were released (1 subsequently recaptured by a recreational angler), and the remaining 11 sacrificed.

NCSU Tag-return study

The auxiliary parameters Ω and ρ were estimated from the returns of 82 fish that were originally double-tagged. These returns included 15 from scientific sampling and 67 from fisheries, accounting for only the first recapture of fish (out of multiple captures). The days-at-liberty were similar between fish that retained both tags (1 to 188 days) compared to the 13 fish that lost a tag (3 to 192; Figure 2a). The exponential decay model for tag retention converged on posterior median estimate of 0.95 (CrI: 0.88, 0.99) for ρ and 0.02 (CrI: <0.01, 0.07) for the

monthly Ω used in the tag-return model. On an annual scale, the probability of retaining a tag was 0.72 (CrI: 0.43, 0.91), and if the fish was double-tagged as a majority of fish were, the probability of retaining at least one tag increased to 0.92 (0.67, 0.99).

Model comparison found that M4 and M43 were similar in terms of overall fit according to DIC (within 2 DIC units; Spiegelhalter et al. 2002) and superior to M2. The M4 had a DIC of 569.0, within 2 DIC units of M43 at 569.8, whereas DIC for M2 was 584.7 (pD=6.6). For the superior models, the full M43 had a pD = 81 and the restrictive M4 had a pD = 6.2. The difference in pD and similar DIC indicates that M43 fit the likelihood component better than M4, but was offset by increased penalty in regard to estimated parameters. For transparency, we compared the estimated the output of monthly F and M using M43 with that of M4 (Figure 3). All annual and seasonal Z , F , and M rates were estimated using M4 due to its lower DIC, fewer parameters, greater precision (Figure 3), and ease in comparing with IGNS seasonal data.

For M43, F_{fish} was low and relatively constant, but imprecise for M43 (Figure 3a). For M4, F_{fish} was also low and constant by assumption (Figure 3b). In contrast, temporal variation was apparent in M for both models (Figure 3c,d). Winter M for every year in the time-frame was high (>2; Figure 3c,d). For M43, precision followed a bimodal pattern for F_{fish} and M , where credible intervals widened during winter and summer periods (Figure 3a,c). For both parameters estimated by M43, the upward spikes in medians and widening credible intervals during beginning and ending time-periods (pre-August 2014 and post-April 2017) are likely because of the small number of tags-at-risk. The reduced M4 had higher precision, with mortality peaking during winter as compared to the peaks in M occurring during November and December in M43. In addition, the winter monthly M of M4 was the highest at 1.56 (CrI: 1.16, 2.08), as compared to

spring at 0.08 (CrI: <0.01, 0.42), summer at 0.19 (CrI: <0.01, 0.52), and fall at <0.01 (CrI: <0.01, 0.16).

From June 2014 to December 2017, the annual F was low across fishing sectors and minimal compared to M (Figure 4). F' was 0.05 yr^{-1} (CrI: 0.04, 0.07), F_c was 0.02 yr^{-1} (CrI: 0.01, 0.03), and F_r was 0.04 yr^{-1} (CrI: <0.01, 0.06). When comparing F and M , F_{fish} was 0.07 yr^{-1} (CrI: 0.06, 0.10), whereas M was 5.71 yr^{-1} (CrI: 4.40, 7.40). Given the relatively low F values, the seasonal Z followed the same trend as M (Figure 5), with winter being the highest at 4.70 (CrI: 3.50, 6.26), as compared to spring at 0.27 (CrI: 0.02, 1.28), summer at 0.60 (CrI: 0.02, 1.56), and fall at 0.03 (CrI: 0.02, 0.51).

NCDMF fishery-independent gill net survey

A total of 3,805 weakfish were captured in the IGNS from February 2002 to December 2017, with TL ranging from 137 to 721 mm (mean \pm SE: 320.2 ± 1.0), and converted into fractional catches-at-age for ages that ranged from 0 to 8 (Figure A1). The majority (65%) of weakfish collected in the IGNS were age-2 (33%) and age-3 (32%). During the time-series, weakfish estimated to be ages 5 to 8 were present in catches from 2002 to 2007, but were nearly nonexistent from 2008 to 2017 (Figure A1).

Seasonal availability of weakfish to the IGNS was the highest during spring ($\alpha_3 = 1.0$), lowest during winter at 0.10 (CrI: 0.09, 0.13), and moderate during summer at 0.64 (CrI: 0.55, 0.76) and fall at 0.74 (CrI: 0.63, 0.85). Intercept (β_1) and slope (β_2) parameters of the age-selectivity logistic function (γ_a) were estimated to be -10.80 (CrI: -11.29, -10.34) and 3.5 (CrI: 3.42, 3.67), respectively, which corresponds to a precipitous increase from low selectivity at ages 0 and 1 to full selectivity at approximately age 3.

Seasonal estimates of Z were consistently highest during fall, winter, and spring during the IGNS time-series (Figure 6). The annual peak Z occurred in fall 7 times, 5 times in winter, and 5 times in spring, but never in summer (Figure 6). We averaged the seasonal Z to match the timing of the first and last fish released in the tag-return study (spring 2014 to spring 2017), and estimates were 1.06 for fall (CrI: 0.75, 1.40) and 0.95 for winter (CrI: 0.61, 1.28) compared to 0.27 for spring (CrI: 0.11, 0.49) and 0.45 for summer (CrI: 0.26, 0.65). The highest seasonal Z estimate occurred either in the fall or winter for both the survey and tag-return data (Figure 5). The annual estimates of Z from survey data (Figure 6) increased through the time-series ranging from 1.04 yr^{-1} (CrI: 0.58, 1.50) to 5.69 yr^{-1} (CrI: 3.20, 8.15), which is equivalent to the discrete rate of annual population loss of 65-99%. The 2017 Z is imprecise which is caused by the model having limited data informing the estimation. The IGNS survey data were incorporated as 1 of 14 fisheries-independent time-series into the 2016 weakfish stock assessment (ASMFC 2016), and the annual estimates of Z from our survey method were similar in trend and magnitude to the annual estimates of Z from the stock assessment (Figure 7). The annual tag-return Z (2014-2017) was 5.78 yr^{-1} (CrI: 4.46, 7.47), and was higher for all but the terminal year of the survey data, but similar to an apparent survival Z estimate from telemetry-tagged weakfish during the years 2006-2017 (Figure 7; Chapter 1). All methods indicate a high average annual population loss on a discrete scale: stock assessment at 90% (average 2006-2014), survey at 93% (average 2006-2017), telemetry at >99% (2006-2017; Chapter 1), and tag-return at >99% (2014-2017).

DISCUSSION

Weakfish stock biomass is low, and rebuilding is currently impeded by uncertainty in the sources of high mortality (ASMFC 2016). We used a tag-return study and fisheries-independent gill net survey to estimate mortality at a seasonal scale, allowing for insight into the timing and

possible causes of mortality. The relative importance of F and M has been a subject of considerable debate over the last 3 stock assessments (ASMFC 2006; 48th SAW 2009; ASMFC 2016). After accounting for key auxiliary parameters (i.e., tag-reporting rate, tag loss, and tagging mortality), our multi-year tag-return study conclusively shows that M is the driving force in weakfish population dynamics.

Annual estimates of overall F from our tag-return study were low at <0.1 from 2014 to 2017, and encompassed mortality from both the commercial and recreational fisheries in North Carolina. At a coast-wide scale, the estimated F was 0.28 in 2014 from the most recent stock assessment (ASMFC 2016). The recent stock assessment (ASMFC 2016) and our study both show that F is a relatively small component of Z ; thus, the current management plan appears to be effective in reducing harvest. Currently, commercial harvest is limited to a 45-kg daily trip-limit and recreational creel limit to one fish with TL over 305 mm (ASMFC 2016). With the implementation of stricter minimum size and bag limits, the number of discards tend to increase along with discard mortality (Harper et al. 2000). We accounted for discard mortality and found it similar between recreational and commercial fisheries. Despite the relatively high number of discards (49 out 115 tag returns), we assumed that only 10% of the released fish died (ASMFC 2016), and therefore, dead discards had minimal impact on the final estimates of overall F . The estimates of F and Z would be negatively biased should actual mortality of discarded fish be greater than 10%, either due to catch-and release-mortality or inaccurate reporting (i.e. reported as discard when fish was in fact harvested). However, even 100% mortality of discards would not affect the overall determination that M , relative to F , accounted for the majority of annual Z .

Annual tag-return estimates of M were consistently high and far exceeded F . Preliminary modeling indicated negligible variation in annual estimates of M , resulting in M4 estimating a

yearly M of 5.71 from 2015 to 2017. The most recent stock assessment aligns with the finding of a consistently high M , but lower, ranging from 0.84 to 0.95 from 2005 to 2014 (ASMFC 2016). Extensive periods of high M may be the cause for dramatic population fluctuations in the weakfish stock since the late eighteenth century (Cushing 1982; Jiao et al. 2012; ASMFC 2016). A periodic M is in direct contrast to the episodic M experienced by spotted seatrout (*Cynosion regalis*), a congener of weakfish. Spotted seatrout in North Carolina and Virginia experience elevated M based on winterkill events (Ellis et al. 2017; Ellis et al. 2018). However, both spotted seatrout and weakfish can endure high M , as they exhibit traits of relatively short-lived fish such as rapid growth, early maturation, a protracted spawning period and prolificacy (Merriner 1976; Shepherd and Grimes 1984; Lowerre-Barbieri 1995; Bortone 2003; Nye et al. 2008).

Weakfish estimates of M and Z indicated seasonal variability. The seasonal tag-return M and Z were estimated to be highest during winter, and based on the last 5 years of time-series, the IGNS estimated the highest Z occurring in the fall. In 17 years of IGNS data, the highest peaks in Z were always during fall, winter, and spring, aligning with the weakfish overwintering period where weakfish emigrate from natal estuaries to warmer continental shelf waters in the fall, and return to spawn the following spring (Chapter 1). The timing of weakfish estuarine emigration and immigration are year-dependent (Chapter 1), possibly causing the interannual seasonal variation in high Z across the time-series of IGNS data. As for the difference between the IGNS and tag-return Z during winter and fall, we are unsure of the reason why. Regardless of the exact timing of mortality, weakfish have low survival during the overwintering period. For the tag-return model, the high winter Z essentially eliminates all tags at-risk during this season. The timing of tag-returns match the model output, as only 4 out 140 weakfish returned after winter. Although mortality was not estimated (nor any key auxiliary parameters), the Virginia Gamefish

Tagging Program found similar results in the timing of returning fish (Lucy et al. 2000; Lucy and Bain 2001). A total of 8,980 T-bar tagged, low-reward weakfish were released from 1996 to 1999, of which only 1 out of 65 returns survived winter. In a coast-wide telemetry study, the paucity of post-overwintering fish aligned temporally and spatially with the release of conventionally tagged fish, where only 2 out of 149 fish with long-lived transmitters (>300 days) were detected alive in the subsequent year after overwintering (Chapter 1). The most likely explanation for the high estimates of M or Z during the overwintering period is predation (Chapter 3). Weakfish overwinter with their main predators on the continental shelf and total predator consumption was similar in magnitude to the sum of the stock assessment biomass attributable to M (Chapter 3).

Analyzing multiple independent datasets promotes robust estimates of mortality depending on the strengths of each approach. The spatial scales differed between each dataset (IGNS = Pamlico Sound, tag-return = North Carolina [heavily weighted toward the vicinity of Cape Lookout], telemetry = coast-wide [Chapter 1]), but multiple datasets augmented the spatial scope of our findings. The tag-return and IGNS models had high temporal resolution (i.e. month or seasons) in mortality estimates that both exhibited mortality peaks during the fall and winter. The tag-return study allowed for a partition of Z into F and M , whereas the catch-curve solely estimates Z . The tag-return estimate of Z and that of telemetry were significantly higher than all but the terminal year Z of the IGNS (Chapter 1).

Tag-return and telemetry models (Chapter 1) estimated an annual population loss >99% over multiple years, which intuitively appears to be biased high considering the ages of fish observed in the IGNS data set. The telemetry model estimated apparent Z , which can be higher than true Z as the parameter is confounded with permanent emigration (Chapter 1). Simulations

for telemetry models that estimate F and M , show M is biased high at low sample sizes ($n < 25$ telemetered fish; Hightower and Harris 2017). For our tag-return estimates, Z consists mostly of M , we hypothesize that the tag-return model M and Z may be similarly biased high by low numbers of fish-at-risk caused by extreme mortality. Future Z estimates (post-2014) from the next stock assessment may provide insight into the difference in Z between our tag-return and IGNS, specifically if the years of our tag-return study had exceptionally high Z (> 5). Regardless of the dataset, weakfish mortality is high, as evidenced by all studies estimating an annual discrete population loss of $> 90\%$ in recent years.

The weakfish stock is currently depleted and has been since 2001 (ASMFC 2016). The stock is considered depleted when the stock is below a spawning stock biomass (SSB) threshold of 30% (6.8 million kg), which is equivalent to 30% of the projected total weight of fish in a stock that are old enough to spawn under average M of 0.43 and no F . For reference, the SSB was 2.5 million kg in 2014. When M is high, a Z benchmark was recommended to prevent an increase in F . The target Z is 0.93 and the threshold is 1.36, with Z being below the threshold for more than one year before management measures are taken to reduce F (ASMFC 2016). Although the stock assessment Z was below the threshold in 2014 ($Z = 1.11$), both our tag-return and survey Z exceeded the threshold for the three ensuing years. Our tag-return estimates demonstrate that M is currently driving weakfish population dynamics, and further harvest restrictions would most likely be inefficacious for effectual stock rebuilding.

In addition to estimating mortality, tag-return studies can delineate the boundaries between fish stocks (e.g., Westrheim et al. 1992; Schwarz 2014). Our study neither confirms nor rejects the current management practice of a single weakfish stock (ASMFC 2016). Studies using mark recapture, scale circuli, and morphological data concluded multiple stocks of weakfish

inhabited the Middle Atlantic region (Nesbit 1954; Perlmutter et al. 1956; Seguin 1960), but genetic and otolith microchemistry concluded that weakfish populations were not sufficiently distinct to be considered separate stocks (Crawford et al. 1989; Graves 1992; Thorrold et al. 2001; Cordes and Graves 2003). Although all our fish were released and recaptured in North Carolina, the low number of returns combined with extremely high overwintering mortality could not adequately ascertain a separate North Carolina stock.

The accuracy of our tag-return mortality estimates relied on fulfilling model assumptions (see Methods), especially for the key auxiliary parameters ϕ , Ω , ρ , and λ . Given the strict landing, handling, and release requirements, and low catch-and-release mortality of 10% (Malchoff and Heins 1997; Swihart et al. 2000; ASMFC 2016), we assumed tagging mortality (ϕ) to be zero. Our field-based tag loss approach estimated a low immediate tag shedding (ρ) at 5%, but chronic loss (Ω) on a discrete scale was substantial at 24% annually. We based our tag type and procedure on Ellis et al. (2018), who estimated similar tag shedding rates on a congener species ($\rho = 3\%$; $\Omega = 27\%$ [discrete scale]), and through his comparison between field and laboratory study estimates of Ω suggested that field-based experiments should be the standard to estimate tag-loss. The apparent difference in tag loss laterality could not be adequately modeled based on the low number of returns, but any potential bias would not affect the findings that F is low relative to M . With minimal exploitation, weakfish were not an ideal candidate for testing tag types, and historically, tagging weakfish has yielded relatively low return rates with the use of t-bar tags at <1% (Lucy and Bain 2001; Clark 2008). Our study and that of Ellis et al. (2018), suggest return rates can be increased with the use of internal anchor tags. High-reward tags allowed us to simplify our model (i.e. fewer tag-return matrices) with the assumption of 100% reporting (Sackett and Catalano 2017), and along with double-tagging appeared to have

increased the percentage of tags returned compared to previous studies (Lucy and Bain 2001; Clark 2008). It is possible that the use of high-reward tags may have biased F high as fishermen may have been influenced to target weakfish. It is often argued that high-reward tagging programs are too expensive to conduct (Miranda et al. 2002; Meyer and Schill 2014); however for weakfish and others with low exploitation rates, tag-return studies would not be possible without the high-reward component (Pollock et al. 2001; Sackett and Catalano 2017). For long-term sustainability of valuable exploited stocks, management needs to weigh the importance of precise estimates of M against the monetary cost of a high-reward study.

Conclusion

Mortality estimates are paramount to understanding population dynamics, especially for weakfish, whose stock has not rebuilt despite harvest restrictions (ASMFC 2016). Our weakfish tag-return study clarified the relative importance of F and M to Z , elucidating that M consistently and significantly exceeded F . Peaks in mortality were highest fall to spring, providing additional evidence that the cause of the high M is predation during the weakfish migration and overwintering periods (Chapter 3). With natural mortality currently driving weakfish population dynamics, further harvest restrictions would most likely be ineffectual in stock rebuilding. As IGNS is conducted every year, new data can be incorporated into our model with relative ease, allowing for seasonal estimates of Z within 12 months of data collection. Hence, management can promptly respond to changes in Z using information from IGNS as compared to waiting multiple years until the next stock assessment. Estimating mortality through a comprehensive tag-return study and IGNS complements traditional stock assessment approaches by providing independent and reliable information on the sources and levels of mortality for a stock with low biomass.

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FIGURES

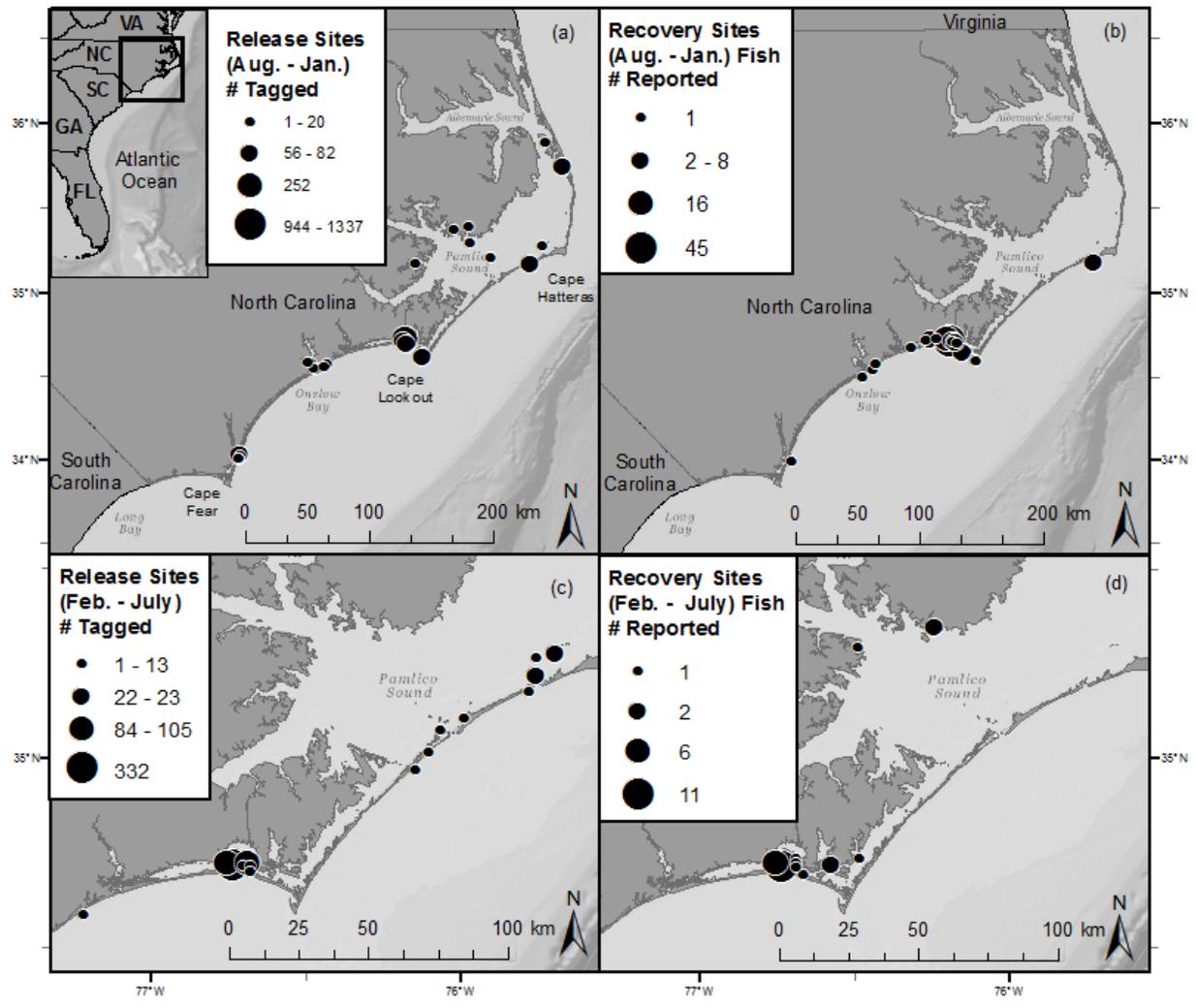


Figure 1. Maps showing the locations where weakfish were tagged and released in North Carolina during the months a) August to January (n=3063) and c) February to July (n=609) from November 2013 to May 2017. Reported recoveries from b) August to January tagged fish (n=28) and d) February to July tagged fish (n=112) from September 2014 to October 2017.

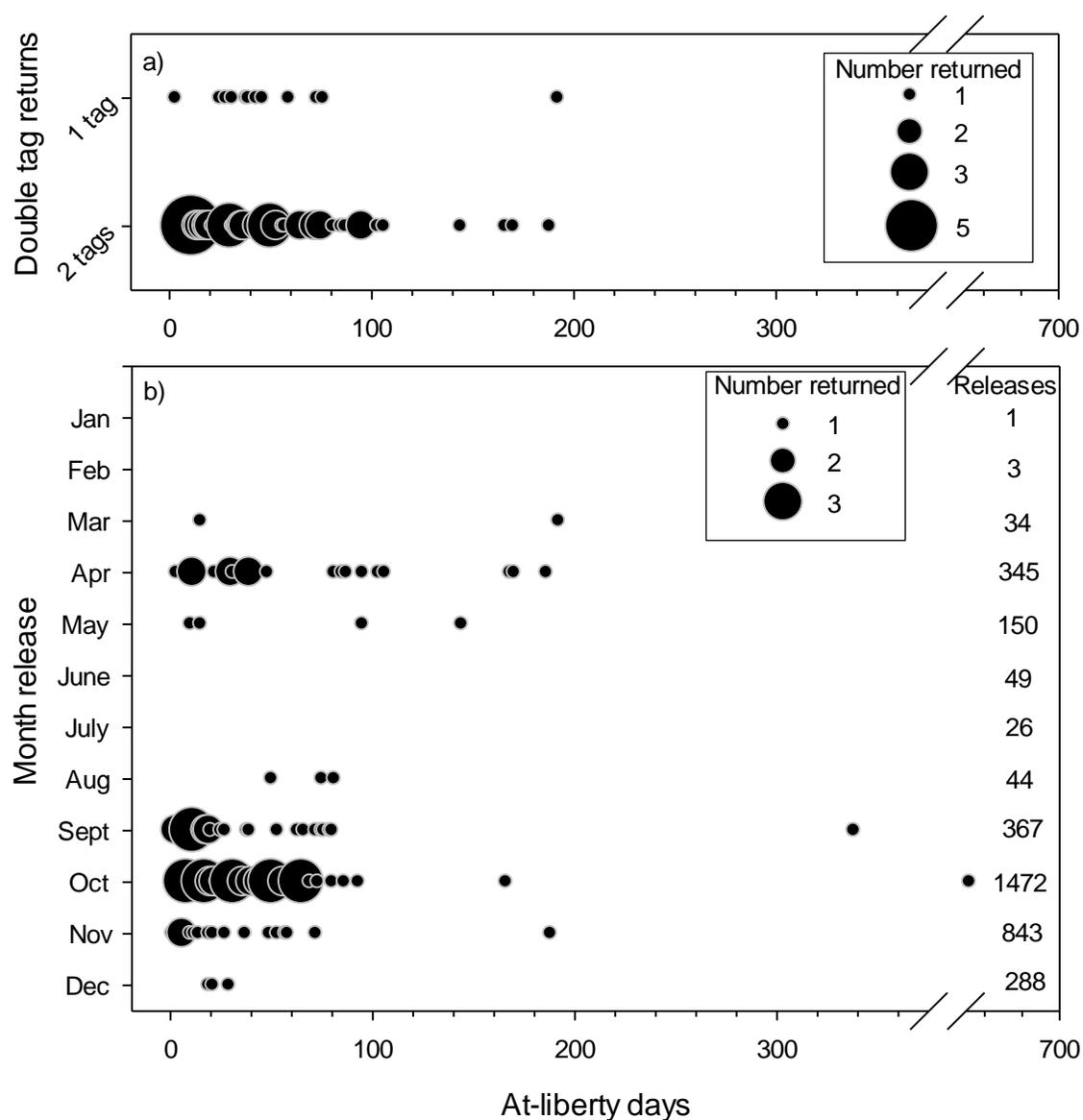


Figure 2. a) Double tag returns (n=82) by at-liberty days that lost a tag (1 tag, n=12) or were returned without tag loss (2 tags, n=70). b) Tags returns by at-liberty days according to the release month (n=140). The number of releases for a particular month are shown. All fish releases occurred from June 2014 to May 2017 in the state of North Carolina, and returns occurred from September 2014 to October 2017.

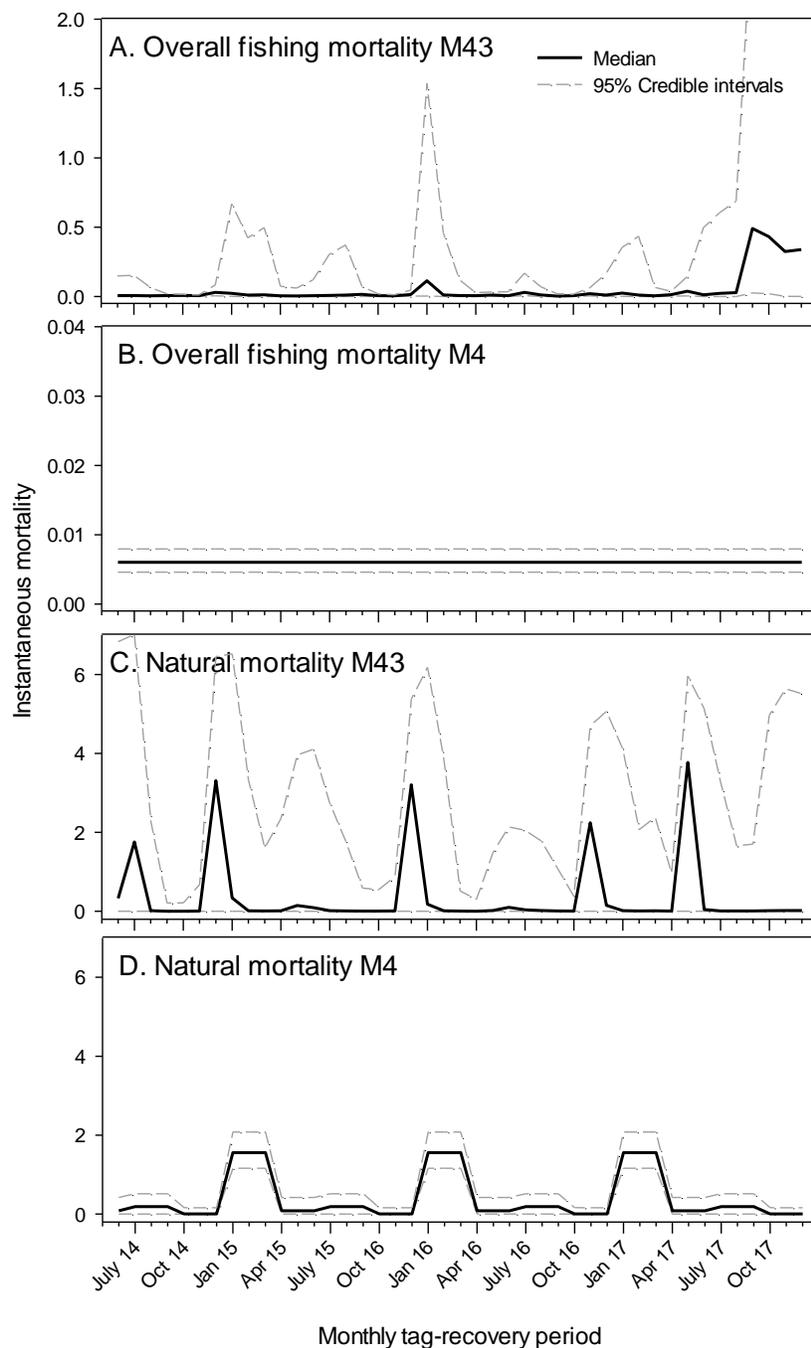


Figure 3. A comparison of F and M from between our best models: M43 (monthly F and M estimated monthly) and M4 (constant F and seasonal M estimated across years) across 43 monthly tag-recovery periods (June 2014–November 2017) from weakfish tagged in North Carolina waters. Instantaneous fishing mortality rate (i.e., commercial and recreational harvest and an assumed 10% discard mortality rate for both sectors) for a) M43 and b) M4. Instantaneous natural mortality rate estimated for c) M43 and d) M4. Note: y-axis scaling differs between plots.

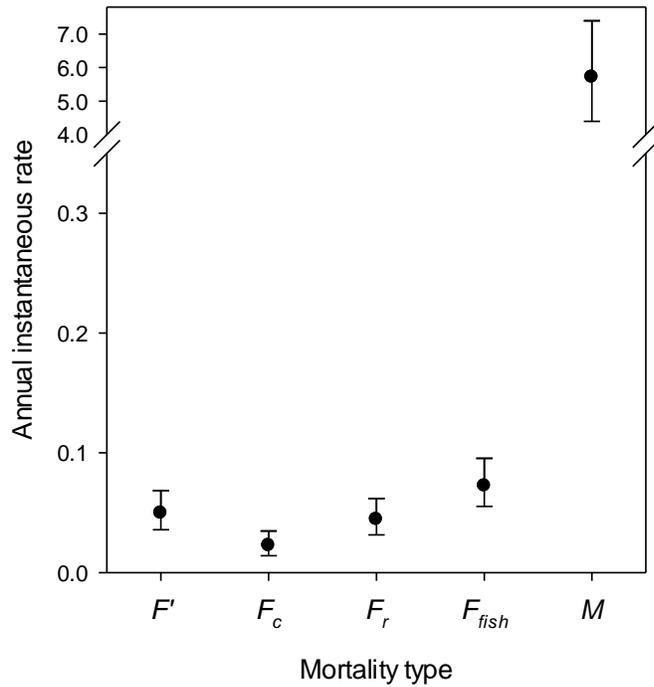


Figure 4. Annual instantaneous rates of discards (i.e. death of tags but fish released alive; F'), sector specific fishing mortality from recreational harvest (F_r), commercial harvest (F_c), and overall fishing mortality (total harvest plus an assumed 10% mortality for discards; F_{fish}), and natural mortality (M), estimated from the recoveries of weakfish tagged in North Carolina waters from 2013 to 2017. Median estimates of the posterior distribution with associated 95% credible intervals are shown and are estimated from the model run (M4), where M is shared seasonally and F is constant.

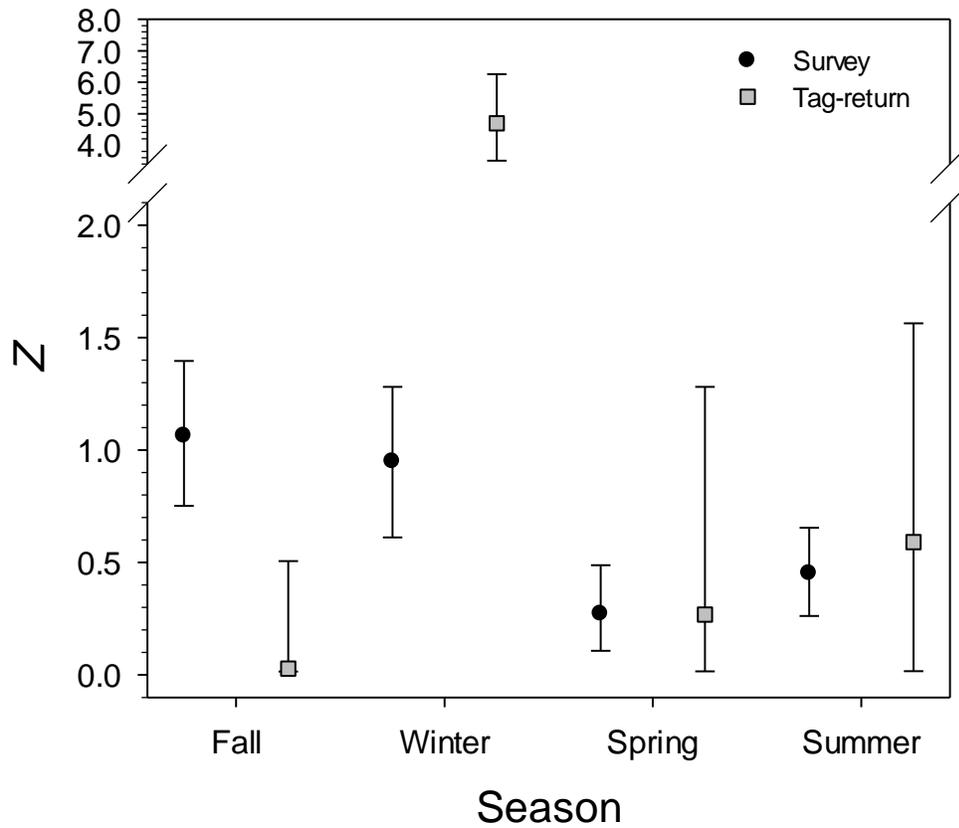


Figure 5. Seasonal estimates of instantaneous total mortality (Z) for fishery-independent gill net survey data and tag-return from 2014-2017. Seasonal periods are 3 months and consist of January to March, April to June, July to September, and October to December. Median estimates of the posterior distribution with associated 95% credible intervals are shown and are estimated from the model run (M4), where M is shared seasonally and F is constant.

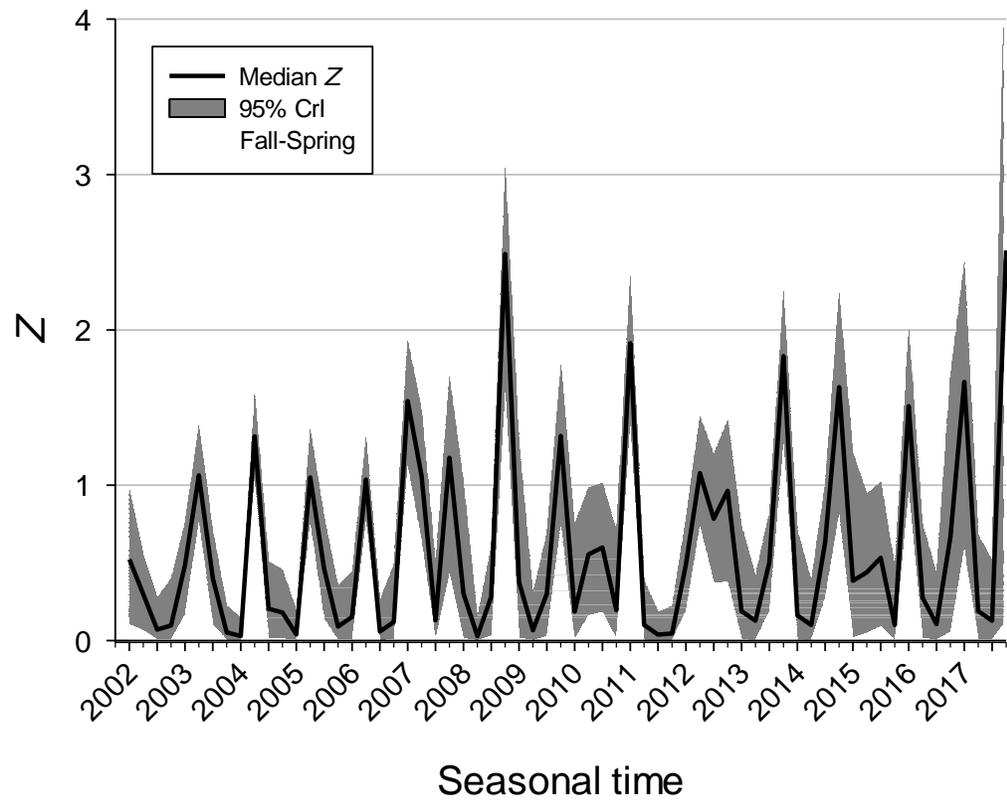


Figure 6. Seasonal estimates of instantaneous total mortality (Z) for fishery-independent gill net survey data from 2002-2017. Please refer to Figure 5 for breakdown of season by month. Median estimates of the posterior distribution with associated 95% credible intervals are shown and are estimated from the model run (M4), where M is shared seasonally and F is constant.

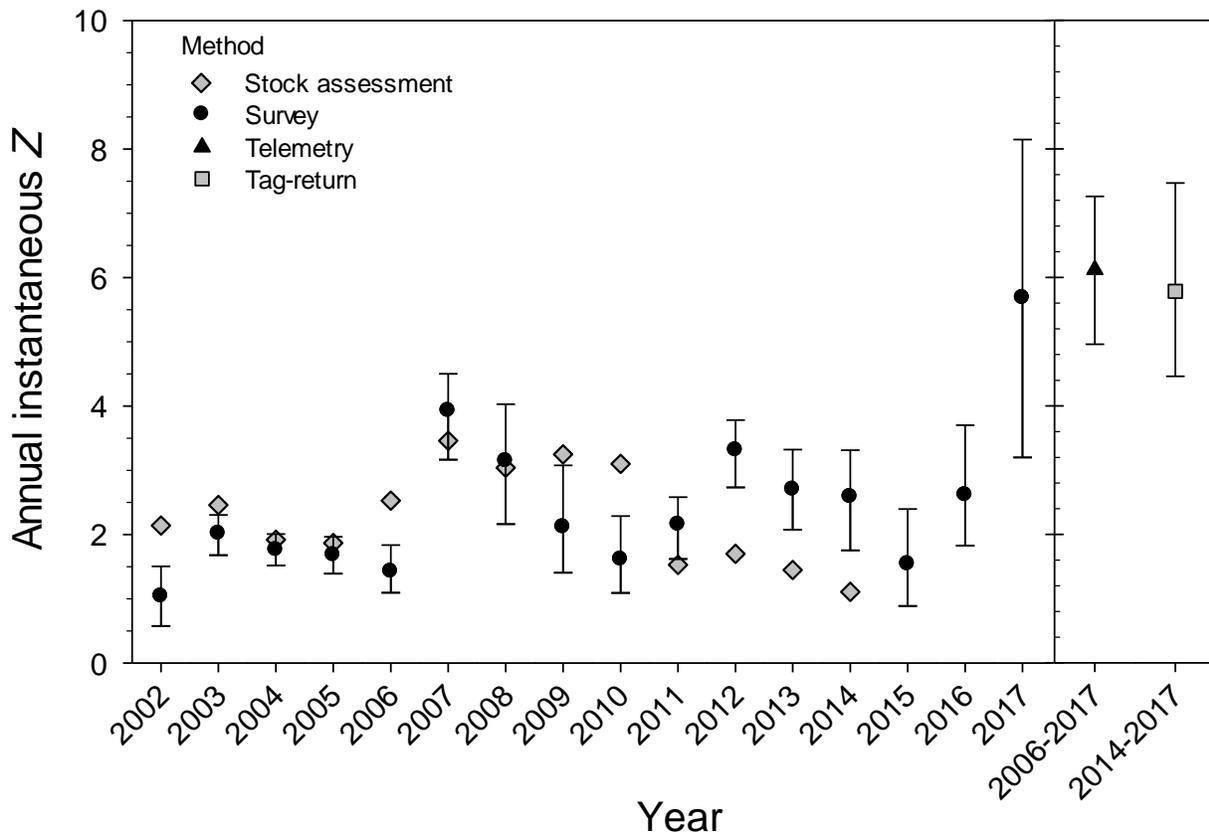


Figure 7. Annual instantaneous mortality rates (Z) from 2002-2017 from the 2016 weakfish stock assessment (ASMFC 2016), fishery-independent gill net survey data, tag-return from years 2014-2017, and apparent Z estimates from telemetry for the years 2006-2017 (Chapter 1). Median estimates of the posterior distribution with associated 95% credible intervals are shown and all tag-return estimates are from the model run (M4), where M is shared seasonally and F is constant.

CHAPTER 3. MARINE MAMMAL AND FINFISH PREDATION EXPLAIN HIGH NATURAL MORTALITY IN WEAKFISH

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ABSTRACT

Weakfish (*Cynoscion regalis*) along the US Atlantic coast has experienced a precipitous population decline from 1982 to 2014 despite fisheries regulations to reduce mortality. Concurrently, weakfish natural mortality increased (M), yet the cause for the increase is poorly understood. We identified five primary predators based on published accounts of diet and spatial and temporal distribution of weakfish and compared the predator consumption of weakfish with the biomass attributable to M . During 1982 to 2014, consumption biomass for these predators was estimated using compiled population size, diet, and energy requirements; uncertainty for consumption estimates was calculated using a Monte Carlo resampling method. Predators consumed on average 6,767 t of weakfish (80% CI 1,740 to 14,388 t) during the time-series, of which 55% was consumed by bottlenose dolphins (*Tursiops truncatus*), 21% by striped bass (*Morone saxatilis*), 17% by bluefish (*Pomatomus saltatrix*), 4% by summer flounder (*Paralichthys dentatus*), and 3% by spiny dogfish (*Squalus acanthias*). The sum of the stock assessment biomass attributable to M and total predator consumption were similar, indicating that high estimates of M are realistic and the cause is predation, as the average biomass from fishery landings in the last 10 years of the time-series was 29 times less than that by predator consumption. As the majority of biomass in the weakfish population has shifted toward age-0s, predators consuming late age-0s have resulted in a recruitment bottleneck, as evidenced by a mismatch in trends between decreasing age-1 recruits and consistent age-0 indices throughout the time-series. The significant influence of predation on the United States east coast weakfish population highlights the importance of multi-species management for effective stock rebuilding.

INTRODUCTION

Fisheries and marine mammal management are moving towards an integrated ecosystem-based approach, which examines ecosystem connections such as potential flows of energy and biomass among interacting populations (Arkema et al. 2006; Long et al. 2015). Quantifying trophic connections requires detailed predator/prey population size and structure, diet, and energetic requirements (Link 2010; Spitz et al. 2018). Predator consumption models assess trophic connections between a single prey and an array of possible predators, providing insight into the population dynamics of target prey species, which can be directly applied to current management practices within single-species stock assessments.

A predator/prey model that estimates consumption with uncertainty was developed by Overholtz (2006) using a Monte Carlo probability estimation approach. Overholtz (2006) estimated the consumption of Atlantic herring (*Clupea harengus*) by bluefin tuna (*Thunnus thynnus*) in the Gulf of Maine-Georges Bank, then expanded the model to include other herring predators such as demersal fishes, marine mammals, large pelagic fishes, and seabirds (Overholtz and Link 2007). The model has been adapted by many researchers across multiple geographic areas (e.g., Butler et al. 2010; Begoña Santos et al. 2014; Smith et al. 2015; Spitz et al. 2018), many of who have compared the predation estimates with fishery landings to give context for the magnitude of predation (e.g., Overholtz 2006; Butler et al. 2010; Begoña Santos et al. 2014; Smith et al. 2015).

Natural mortality (M) estimates used in stock assessments are often based on proxy estimates and are rarely compared to empirically derived estimates of predation, a major source of natural mortality. For most stock assessments, predation mortality is implicitly included as an unspecified proportion of natural mortality, often a fixed input (Vetter 1988) that is externally

estimated based on life history parameters and environmental variables (e.g., Pauly 1980; Hoenig 1983; Lorenzen 1996; Griffiths and Harrod 2007; reviewed by Kenchington 2014). However, these estimates of M do not account for time or location specific-differences and have an unknown certainty (Vetter 1988; Pascual and Iribarne 1993) and stock assessment models are particularly sensitive to input values of M (Clark 1999; Williams 2002). Although uncertainty is inherent to both predator consumption and M , estimated biomass attributable to M can be compared with independent data of biomass consumed by predators to verify if estimates are realistic. For example, Begoña Santos et al. (2014) compared the biomass consumption of four small cetaceans with the overall biomass attributable to M for two important prey fish stock assessments in Spanish waters. Although the authors acknowledged that additional consumption estimates of various predator fish species would be needed for a verification of M , their findings provide important information as to how fish stocks are impacted by marine mammal predation (Begoña Santos et al. 2014).

The target species for this study is weakfish (*Cynoscion regalis*), whose spawning stock biomass has declined since 1982 (ASMFC 2016). The cause of decline is attributed to increased total mortality (Z). With stricter fishing regulations not causing stock rebuilding, the most parsimonious explanation for the increase in Z was an increase in M (ASMFC 2016). As a result, efforts to improve estimates of M included estimating a time-varying M using a Bayesian statistical catch-at-age model in the latest stock assessment (Jiao et al. 2012; ASMFC 2016). The prior distribution for the 1982 M estimate was based on external estimates (uniform prior 0.1 to 0.4), and subsequent M estimates were allowed to vary through the time-series of 1983-2014 using a random-walk approach (ASMFC 2016). Consequently, M was estimated to increase through the time-series to a high of 0.95 in 2008, but there is uncertainty in the estimate, and the

cause for the increased M is unknown (ASMFC 2016). In addition, F and M are confounded in the stock assessment model (Johnson et al. 2015), therefore it is difficult to estimate both without additional information on M (Lee et al. 2011). Because M is modeled as the driver of the high Z during this time period, the weakfish stock is managed with a sustainable stock biomass (SSB) threshold (ASMFC 2016).

Various explanations have been proposed for the decline in weakfish stocks. The increase in M has been correlated with the Atlantic Multidecadal Oscillation (AMO), in which warm years of the oscillation have increased weakfish M (Jiao et al. 2012). However, this correlation does not provide a mechanism for the increased M . Hypothesized mechanisms include disease, toxins, and parasitism, but none can account for the magnitude of increase in M (48th SAW 2009). Similarly, unreported harvest and discards among the commercial and recreational fisheries would be included implicitly as components of M , but were deemed unlikely culprits for the magnitude of increase (48th SAW 2009). For unknown reasons, the age-structure of the population has shifted to younger individuals, whose females have lower batch fecundity and spawn less frequently than older weakfish (Nye et al. 2008). However, age-0 indices across the range of weakfish appear stable through time, indicating the lower reproductive potential does not appear to be the cause of the weakfish population decline (ASMFC 2016). Increased finfish predation, with striped bass (*Morone saxatilis*) being the leading predator, is purported as a likely explanation of increased M in the weakfish population (ASMFC 2006). However, this hypothesis did not encompass all possible predators of weakfish, including marine mammals such as the coastal morphotype of the common bottlenose dolphin (*Tursiops truncatus*, hereafter bottlenose dolphin or dolphin; Mead and Potter 1995; Hoelzel et al. 1998; Rosel et al. 2009).

Natural mortality may not be consistent throughout the year. Weakfish migrate during autumn from estuaries along Massachusetts to North Carolina to warmer waters on the continental shelf off Virginia and North Carolina (Nesbit 1954), then return to estuaries, often their natal estuaries to spawn the following spring (Thorrold et al. 2001). Conventional tagging and telemetry research indicate that the greatest mortality occurs during this overwintering period, as tagged fish are not returning to estuaries to spawn in subsequent years (Chapter 1 and 2). Of note, many top predators such as striped bass and bottlenose dolphin follow the same migration pattern (e.g., striped bass, Overton et al. 2008; and bottlenose dolphin, Hayes et al. 2018).

In this paper, 1) we compiled available information for 1982-2014 on population size, diet, and energy requirements for marine mammal and finfish predators whose overwintering migrations overlap with that of weakfish, 2) estimated the amount of weakfish removed by these predators, and 3) compared estimated biomass attributable to time-varying M from the stock assessment with the biomass consumed by predators. Our results show evidence for a mechanism causing the decline in weakfish stock size that will be useful for stock assessment scientists and managers, and a new understanding for the importance of weakfish as prey.

METHODS

Literature review

To identify a candidate pool of weakfish predators, a literature review was performed for accounts of diet for predators that overlap spatially and temporally across all seasons with the main distribution of weakfish (Cape Canaveral, FL to Cape Cod, MA). Diet studies, regardless of the confirmed presence of weakfish in the predator's diet, included all predators capable of consuming weakfish measuring greater than 100 mm, and was visually assessed from predator

size-prey size scattergrams or reconstructed prey-lengths (Scharf et al., 2000; Gannon and Waples, 2004). Our literature review examined 26 predator species, including 10 elasmobranchii, 9 teleostii, 3 birds, and 4 marine mammals (Tables B1-B12).

Diet studies excluded from model construction contained at least one of the following conditions: 1) predator diets using quantitative metrics other than volumetric or gravimetric for analyzing predator stomach contents, 2) water salinity being essentially fresh at <5% ppt, 3) studies occurring from June through August (Tables B1-B4), 4) combined data (e.g., across multiple seasons that include summer, or regions outside of weakfish range), and 5) minor diet items not being reported. For instance, the Northeast Fisheries Science Center (NEFSC) has long-term diet data (Bowman et al., 2000; Smith and Link, 2010), but did not include minor diet items nor classify data by region and season.

Inclusion criteria in the final consumption model constructions consisted of: 1) predators with reliable population data from stock assessments, and 2) average consumption of weakfish along the predator's overwintering period being greater than 1% percent mass ($\%M$) or the predator had a biomass greater than 100,000 metric tonnes. Predators that satisfied all inclusion criteria were summer flounder (*Paralichthys dentatus*), striped bass, and bottlenose dolphin with consumption greater than 1% M , and spiny dogfish (*Squalus acanthias*) and bluefish (*Pomatomus saltatrix*) with their biomass greater than 100,000 metric tonnes.

Non-modeled predators

Predators that did not meet inclusion criteria for consumption modeling are outlined in Tables B5-B8. Predators that consumed weakfish during fall and spring but did not have sufficient population or energetic data to inform Monte Carlo input parameters included Atlantic angel sharks (*Squatina dumeril*), Atlantic sharpnose shark (*Rhizoprionodon terraenovae*),

sandbar shark (*Carcharhinus plumbeus*), blacknose shark (*Carcharhinus acronotus*), dusky shark (*Carcharhinus obscurus*), smooth dogfish (*Mustelus canis*), smooth butterfly ray (*Gymnura micrura*), spiny butterfly ray (*Gymnura altavela*), and clearnose skate (*Raja eglanteria*) [Tables B5-B6]. Out of 7 bluefin tuna (*Thunnus thynnus*) studies and 17 goosefish (*Lophius piscatorius*) studies that coincided with the weakfish overwintering migration period, only one study for each predator species mentioned weakfish consumption (bluefin tuna 0.6% *M*, and goosefish 1.3% *M*; Table B7). Therefore, these two species were deemed minor weakfish predators and their consumption was not modeled. Atlantic cutlassfish (*Trichiurus lepturus*) and cobia (*Rachycentron canadum*) were not found to consume weakfish (Table B7). Striped searobin (*Prionotus evolans*), inshore lizardfish (*Synodus foetens*), and oyster toadfish (*Opsanus tau*) are common finfish predators overlapping with weakfish, but were not included because they did not consume weakfish >100 mm total length (TL; Bisker et al., 1989; Manderson et al., 1999; Cruz-Escalona et al., 2005). Although cannibalism is documented among weakfish, (Table B8) this is unlikely to account for overall population decline. Of potential avian predators, northern gannets (*Morus bassanus*), great cormorants (*Phalacrocorax carbo*), and double-crested cormorants (*Phalacrocorax auritus*) populations have increased during the time-series (Weseloh et al., 1995; Chardine et al., 2013); however, there are no diet studies during these birds' overwintering season in coastal North Carolina. Three marine mammal species, in addition to bottlenose dolphins, were identified as potential weakfish predators but did not make it into the final list. Humpback whales (*Megaptera novaeangliae*) were considered because weakfish were found in the stomachs of 3 stranded juvenile humpback whales recovered in Georgia, Virginia, and Massachusetts (Laerm et al., 1997). However, the small sample size and lack of regional studies precluded the inclusion of humpback whales in the modeling. Although gray seal

(*Halichoerus grypus*) abundance has increased in recent years, their overwintering range does not overlap with weakfish and they are uncommon in North Carolina (Hayes et al., 2017).

Harbor seals (*Phoca vitulina*) are more common than gray seals in North Carolina (Byrd et al., 2014) and Virginia (Rees et al., 2016), but their consumption of weakfish has not been reported (Toth et al., 2018).

Modeling

Overwintering population-level consumption of weakfish by predators was estimated as

$$C_{pop} = B * P * DR * W * T, \quad (1)$$

where B = biomass of predator (kg)

P = proportion of predator population overlapping with weakfish during the overwintering period

DR = predator daily ration (kg prey/ kg predator/day)

W = weakfish proportion by weight in predator stomachs

T = time in days that predators and weakfish overlap

Uncertainty in the C_{pop} was estimated using a Monte Carlo simulation (Overholtz, 2006).

All analyses were completed in R v.3.5.2 using RStudio interface with the libraries mc2d, colorspace, and truncnorm (Zeileis et al., 2009; Pouillot and Delignette-Muller, 2010; R Core Team, 2013; Mersmann et al., 2018). A distribution was created for each input variable in equation (1) for the years 1982-2014 (Table 1). For B and DR , a pert distribution was constructed based on the most likely (calculated as mean), minimum, and maximum input variables (Table 1). The pert distribution was chosen for its simplicity, symmetry, and insignificant tails (Overholtz 2006). Means were obtained from the literature; minimum and maximum values were calculated as one standard deviation (sd) below and above the calculated mean biomass based on

an assumed coefficient of variation (CV) of 0.3 (Overholtz 2006). For bottlenose dolphins, uncertainty in the population and mass estimates were modeled by splitting B into the input variables of B_p and B_w , where B_p was the population estimate in numbers and B_w was the average individual predator mass estimate. There were no quantitative estimates of P and T between weakfish and their predators, a uniform distribution was chosen to reflect uncertainty (Butler et al., 2010), with conservative bounds based on a synthesis of literature sources. A truncated normal distribution modeled W , in which the mean and sd were estimated from a weighted mean, based on literature values of sample size and $\%M$ converted to a proportion with the upper bound set at 1 to allow for model flexibility. The truncated normal distribution was used to incorporate the propensity of 0s in the data by having a lower bound set to negative infinity and changing all negative numbers to 0 (Figure B1). For literature values of $\%M$ informing W , independence was assumed if $\%M$ was categorized by season or time-frame. Therefore, if a study estimated a yearly $\%M$, each year would be a data point to estimate the weighted mean.

A random draw was made from each distribution to estimate C_{pop} , repeated 5,000 times for each predator during each year of the time-series. Uncertainty was based on 80% Confidence Intervals (CI), using the 10th and 90th percentiles of the C_{pop} distribution (Overholtz 2006, Smith et al. 2015). Sensitivity analyses were completed by regressing the 5000 estimates of the dependent variable C_{pop} against the independent variables consisting of the five Monte Carlo input parameters for each year in the time-series. Each variable in the regression was scaled by subtracting the mean and dividing by the sd. The coefficient values from 33 regressions were averaged across the time-series, and the magnitude of the resulting values indicated the relative rank of each dependent variable in changing C_{pop} . Detailed R code with Monte Carlo functions

for each predator, the raw data from the stock assessments, and figures depicting model outputs can be found in the supplementary appendix C.

Spiny dogfish

Annual biomass (B) estimates from 1982 to 2008 came from the most recent stock assessment and 2009 to 2013 from an update disseminated for peer-review (Figure 1; Rago and Sosebee, 2010; Rago and Sosebee, 2015). The stock assessment estimated B for a particular year as a 3-year average of the biomass of the year in question and the previous two years. As a point estimate for 2014 was missing, B for the year 2014 was calculated as the mean of the point estimates of 2012 and 2013. The most recent stock assessment categorized biomass for 370-790 mm and ≥ 800 mm sizes. Because the ontogenetic diet shift towards teleost fish occurs between 600 and 650 mm (Bangley, 2011); we used the ≥ 800 mm TL category which may negatively bias B for spiny dogfish. Spatial overlap (P) was assessed visually and the uniform distribution bounds were estimated as 0.05 to 0.3, using seasonal distribution and abundance maps from a NEFSC bottom trawl survey, in addition to movements of satellite-telemetered fish (Figure 2a; McMillan and Morse, 1999; Carlson et al., 2014). Daily ration (DR) was estimated from a linear model for female spiny dogfish at 0.006 with a sd of 0.001, which was applied to males of the same species (Table 1; Bangley and Rulifson, 2014). The proportion by weight (W) of weakfish in the diet of spiny dogfish was estimated as a weighted mean from 14 studies, at 0.004 with a sd of 0.020 (Table B9; Table 1). The time overlap (T) was estimated to be 60-150 days. Similar to weakfish, spiny dogfish undergo seasonal migrations southward in the fall and northward in the spring, and as a result, we conservatively assumed a minimum of 60 days to reflect a scenario where overlap only occurred during an arbitrarily picked 30-day migration period during spring

and fall. The upper value of 150 days was based on the maximum number of days spiny dogfish are found off the coast of North Carolina (Rulifson et al., 2012).

Summer flounder

Annual biomass estimates (1982-2012) of summer flounder were determined from annual abundance and mean weight-at-age data from a recent stock assessment (Figure 1; Northeast Stock Assessment Workshop, 2013). Biomass estimates for 2013 and 2014 were calculated as the mean value of B from 2011 and 2012. Since summer flounder greater than 300 mm (>age 3; Morson et al., 2015) can consume weakfish longer than 100 mm (Scharf et al., 2000), B included only summer flounder older than 3 years. A visual assessment from NEFSC winter trawl survey 1992-2007 data estimated spatial overlap to be 0.2 to 0.4 for the uniform distribution bounds (Figure 2b; Northeast Stock Assessment Workshop, 2013). The DR was estimated from consumption/biomass (Q/B), a standard approach used in Ecopath models (Pauly et al., 2000). A Q/B of 2.9 year⁻¹ was estimated for a Chesapeake Bay ecosystem model from an empirical equation available in FishBase (Froese and Pauly, 2004) that incorporated average environmental temperature ($Temp$), asymptotic weight (W_{inf}), fin aspect ratio, and food type (Christensen et al., 2009). The model assumed $Temp = 17$ °C, $W_{inf} = 12,000$ g, an aspect ratio of 1.32, and carnivorous diet (Christensen et al., 2009). These assumptions were valid for the physiology and trophic parameters as they take into account flounders throughout their entire distribution, and the mean monthly water temperature was ~17 °C from January to April on data buoy station 41025 in the middle of the weakfish overwintering grounds (National Data Buoy Center, 2018). The Q/B was converted to a DR of 0.008 by multiplying the total stock biomass for an individual year by Q/B , dividing the total by 365 followed by the same total stock biomass (Table 1). The W of weakfish in the diet of summer flounder was estimated as a weighted mean from 29 studies to be 0.030

with a sd of 0.076 (Table B10; Table 1). The T minimum was estimated to be 60 days based on the rationale for spiny dogfish, with a maximum T of 150 days as summer flounder leave estuaries in Virginia and North Carolina to overwinter and spawn on the continental shelf in October, and return inshore in March (Packer et al., 1999).

Bluefish

The annual estimates of B for age-2+ bluefish were obtained from a recent stock assessment (Figure 1; Celestino et al., 2015). Bluefish older than 2 years are greater than 200 mm (Salerno et al., 2001) and are capable of consuming weakfish longer than 100 mm (Scharf et al., 2000). A visual assessment from distributional maps estimated spatial overlap to be 0.3 to 0.7 for the uniform distribution bounds, as a large aggregation reported off Cape Hatteras, North Carolina (Figure 2c; Shepherd et al., 2006; Shepherd and Packer, 2006). A Q/B of 3.3 year⁻¹ was estimated for adult bluefish from the Chesapeake Bay ecosystem model using the same approach as summer flounder (Christensen et al., 2009). The model assumed $Temp = 17$ °C, $W_{inf} = 16,962$ g, aspect ratio of 2.55, and carnivorous diet, and input parameters were assumed valid for this study based on the rationale used for summer flounder (Christensen et al., 2009). The Q/B was converted to a DR of 0.009 (Table 1). The W of weakfish in the diet of bluefish was estimated as a weighted mean from 14 studies to be 0.010 with a sd of 0.040 (Table B11; Table 1). The T minimum was estimated to be 60 days based on the rationale for spiny dogfish, and a maximum T of 150 days was chosen as bluefish generally begin migrating southward in December towards continental shelf waters with temperatures >16 °C ranging from northeast Florida to North Carolina, and return northward beginning in May (Shepherd et al., 2006; Shepherd and Packer, 2006).

Striped bass

Annual estimates of abundance and mean weight-at-age data from a recent stock assessment (Figure 1; Atlantic Striped Bass Technical Committee, 2016) were multiplied to derive annual estimates of striped bass B . The B included only age-4+ striped bass, which on average measure >500 mm (Setzler et al., 1980), which are the migratory contingent of striped bass that overwinter off the coast of North Carolina and Virginia (Overton et al., 2008). A visual assessment from distributional maps estimated spatial overlap to be 0.6 to 0.9 for the uniform distribution bounds (Figure 2d; Holland Jr and Yelverton, 1973; Overton et al., 2008). A Q/B of 2.3 year^{-1} was estimated for migratory striped bass from the Chesapeake Bay ecosystem model (Christensen et al., 2009). The model assumed $Temp = 17 \text{ }^\circ\text{C}$, $W_{inf} = 115,760 \text{ g}$, aspect ratio of 2.31, and carnivorous diet, and input parameters were assumed valid for our study based on the rationale used for summer flounder (Christensen et al., 2009). The Q/B was converted to a DR of 0.006 (Table 1). The W in the diet of striped bass was estimated as a weighted mean from 22 studies to be 0.022 with a sd of 0.039 (Table B12; Table 1). The T was estimated to be 60 days based on the rationale for spiny dogfish, and a maximum T of 120 days was determined based on striped bass overwintering from December until the end of March (Holland Jr and Yelverton, 1973; Overton et al., 2008).

Bottlenose dolphin

Annual estimates of biomass were not available for bottlenose dolphins. Instead, bottlenose dolphin population abundance (B_p) and mean body weight (B_w) were estimated separately in the simulation to arrive at an estimate of B for three stocks that overlap with weakfish during their overwintering period: the Western North Atlantic Northern Migratory Coastal (NMCS), Northern North Carolina Estuarine System (NNCES), Southern North Carolina

Estuarine System (SNCES) stocks. Only point abundance estimates based on photo ID mark-recapture studies were incorporated into the model for the NNCES (2000=919, CV=0.13; 2006=950, CV=0.23; and 2013=823, CV=0.06; Read et al., 2003; Gorgone et al., 2014; Urian et al., 2014) and SNCES stocks (2000=141, CV=0.15; 2006=188, CV=0.19; Read et al., 2003; Urian et al., 2014). With abundance estimates being less than 1000 and appearing stable for the NNCES and SNCES throughout the time-series, the first point abundance estimate for a stock was assumed for each year prior to the second point abundance estimate, with all subsequent years assuming the abundance from the most recent point estimate. General abundance trends for the NMCS was assumed to be increasing based on the current no-take management and modeled based on abundance point estimates, unusual mortality events (UMEs), and the maximum productivity rate using the approach of Overholtz and Link (2007). The B_p through time was modeled by calculating a survival rate [$\ln(1+r)$, r being the yearly productivity rate], and decrementing the most recent abundance point estimate by the negative survival rate to estimate the previous year's population, and following the same procedure for each prior year until an abundance point estimate or the beginning of the time-series in 1982. The maximum net productivity rate for the NMCS was estimated to be 0.04 based on theoretical modeling (Barlow et al., 1995), and was modeled stochastically by drawing a yearly r from a uniform distribution bounded between 0 and 0.04. Three abundance point estimates for the NMCS stock were available (2010=14,314, CV=0.74; 2011=15,630, CV=0.29; 2016=6,639, CV=0.41), and estimates prior to 2010 were not used due to methodology differences (Hayes et al., 2018). The NMCS stock has experienced two UMEs as a result of morbillivirus epidemics in 1987-1988 and 2013-2015 (Lipscomb et al., 1994; Morris et al., 2015), in which overall mortality was estimated at 10-50% between 1987-1988 (Scott et al., 1988; Eguchi, 2002). For the year 1987, the UME

was modeled by drawing the r from a uniform distribution between 0.1 and 0.5 and multiplying by the 1988 abundance estimate. The 2013-2015 UME was not explicitly modeled because a population decrease was evident between the 2011 and 2016 point estimates. Instead, the 2012 abundance was modeled by adding the survival rate to the 2011 abundance point estimate. The modeled dolphin population estimates for each stock were the mean input value for a pert distribution. Minimum and maximum values were calculated as the CV from the abundance point estimate from which each year was estimated. For instance, the years 1982 to 2009 were decremented from the NMCS 2010 abundance point estimate, and its $CV=0.74$ would estimate the bounds for all 28 years. For the Monte Carlo output, the abundance from all stocks was combined.

A B_w of 126.5 kg was calculated from the mean body size of 178 male and female coastal morphotype bottlenose dolphins stranded along North Carolina between 1997 and 2008 (data provided by the National Marine Fisheries Service (NMFS) Marine Mammal Health and Stranding Response Database; see Byrd et al., 2014). The sample size did not include dolphins that were listed as emaciated or had incomplete TL measurements (e.g., flukes cut off by human interaction). For dolphins that were not weighed in the laboratory ($n=158$), weights were predicted based on a TL to weight regression found on the app WhaleScale (Barco et al., 2016; Harms et al., 2017), based solely on North Carolina stranded dolphins (Dr. Craig Harms, North Carolina State University, personal communication). The B_w included YOY even though many have not been fully weaned. We felt the bias was small as the reduced B_w offset the addition of YOY in abundance estimates, as a lack of age-structure knowledge precluded us from removing YOY from abundance estimates. Weights ranged from 7 to 283 kg, and the B_w was assumed the

same for all dolphin stocks. The minimum and maximum pert inputs for dolphin B_w were calculated from a $CV = 0.3$.

Tagging and photo-ID research indicate that all dolphin stocks have different distributional patterns affecting their overlap with weakfish. The NMCS stock occurs in coastal waters migrating from its summer distribution as far north as New Jersey to occur of North Carolina in winter (Hayes et al. 2018). During winter, central North Carolina (i.e., around Cape Lookout) is the southern limit of NMCS, with individuals rarely sighted north of the North Carolina/Virginia border (Urian et al., 1999; Garrison et al., 2016; Hayes et al., 2018). The NNCES stock occurs primarily within the Albemarle-Pamlico Sound estuaries during summer, but members of the stock move into nearby coastal waters during cold water months, and occupy coastal waters less than 3 km from shore between the New River and Oregon Inlet, North Carolina (Hall et al., 2013; Garrison et al., 2017). During summer, the SNCES stock inhabits coastal waters less than 3 km from shore and estuarine waters from Cape Lookout to the North Carolina and South Carolina borders, and in winter the northern range boundary shifts south of the New River (Read et al., 2003; Rosel et al., 2009; Hayes et al., 2018). Based on the combined winter ranges of all dolphin stocks, the spatial overlap was estimated as 0.7 to 0.9 for the uniform distribution bounds (Figure 2d).

We used the *DR* distribution for bottlenose dolphin from Smith et al. (2015), whose distribution incorporated uncertainty by including *DR* estimates from multiple sources including dolphin stocks spatially near to our modeled stocks. The mean *DR* of 0.046, with the min and max pert inputs consisting of the 80% confidence intervals of 0.029 to 0.061, (Table 1; Smith et al., 2015).

In order to calculate W , we examined stomach contents from 213 coastal morphotype dolphins stranded off the coast of North Carolina from 1998 to 2012. All stomach contents were primarily identified from otoliths and to a lesser extent squid beaks. All hard structures were graded according to Reccia and Read (1989) protocol. Only the least eroded grades (0-2) were used to reconstruct weight from hard structure sizes to weight regressions, and the average predicted weight from the least eroded grades within a stomach were applied to the most eroded grades (3-5). Weakfish weight was estimated from a sulcus length to weight regression (Byrd et al., 2019; in prep). Large and robust otoliths from a weakfish can bias W to be higher, as smaller and fragile otoliths degrade more quickly (Pierce and Boyle, 1991; Tollit et al., 1997). This bias was minimized by only analyzing the first of three bottlenose dolphin stomachs, which is assumed representative of the most recent feeding (Harrison et al., 1970). We assumed that stranded dolphin diet is comparable to free-ranging population (Dunsha et al., 2013; but see also Pierce and Boyle, 1991). We assumed that W for weakfish was representative for the entire bottlenose dolphin population, as stranded dolphins ranging from young-of-year (YOY, <184 cm TL; Read et al., 1993; Fernandez and Hohn, 1998) to mature adults feed on 100+ mm weakfish (Figure B2; Barros, 1993; Gannon and Waples, 2004). A W of 0.49 was calculated as the weighted mean with a sd of 0.138 from the number of stranded dolphins with stomach contents during the months of November to April (Figure B3; Table 1).

The minimum T for bottlenose dolphin was estimated at 90 days because for all dolphin stocks are found off coastal North Carolina from December to February (Hall et al., 2013); this distribution is supported by the absence of NMCS during aerial and ship surveys off the coast of New Jersey from November to February (Whitt et al., 2015). A maximum T of 180 days was

chosen since W is >0.2 from November to May (Figure B3), and both stocks undergo similar overwintering migrations spatially and temporally as weakfish (Hayes et al., 2018).

Comparison with stock assessment

The Atlantic States Marine Fisheries Commission (ASMFC) assessed the weakfish stock in 2016 using data from fishery landings and fishery-independent surveys from Florida to Massachusetts. For the assessment, the optimal model was a Bayesian statistical catch-at-age in which M was assumed constant over all weakfish age-classes and varied following a random walk process. The initial M was estimated to be 0.17 in 1982 and reached a high of 0.95 in the years 2008-2012. The stock assessment annual weights-at-age from 1982-2014 were multiplied by the total abundance of weakfish from age-1 to age-6+ (ASMFC, 2016). For the predator consumption simulation, weakfish greater than 100 mm were modeled as prey, which is the average length of an age-0 weakfish in September. Because the stock assessment only included age-1+ weakfish, the inclusion of biomass of age-0s from September to December was necessary for an equal comparison between the predator consumption simulation results and the stock assessment. A recruitment bottleneck at age-0 was hypothesized in the 2009 stock assessment (48th SAW 2009); the bottleneck was one explanation for the age-0 indices remaining stable while the age-1 abundance declined. The discrepancy is apparent in the most recent assessment. The recruited age-1 weakfish have declined through the time-series while a composite-YOY index indicates a stable trend through time (Figure 3a).

To estimate age-0 abundances, the year with the lowest composite-YOY index catch, 1984, had its age-1 abundance in 1985 from the stock assessment, divided by e^{-M} to predict the abundance of age-0s in 1984. M was estimated as 0.87 from Lorenzen's natural M equation (Lorenzen, 1996):

$$M_L = 3.0W^{0.288}, \quad (2)$$

where M_L is natural mortality and W is average weakfish weight. We used a $W = 73$ g that was calculated as the average of $n = 467$ age-0 weakfish caught in North Carolina between September to December (Steve Poland, North Carolina Division of Marine Fisheries, personal communication). The age-0 abundance for a particular year was estimated by scaling up the 1984 estimate using the ratio of the composite-YOY catch for that year divided by the composite-YOY catch for 1984. The average composite-YOY index for the years 1983-1985 was used for the missing 1982 value. An age-0 M was estimated by dividing the natural log of a year class's age-1 abundance by that year class's estimated age-0 abundance. Due to the lack of age-1 abundance in 2015, an average M was taken from 2011-2013 to estimate M for the 2014 year class. Lastly, the number of age-0s lost to M was divided by 3, to reflect only the 4-months, September to December, when weakfish were 100+ mm.

To calculate the numbers lost due to M , we applied the following equation where year (1982-2014) and age subscripts (age-0 through age-6+) were omitted for simplicity:

$$N_{mortality} = N * \frac{M}{M + (F_{com} * S_{com}) + (F_{rec} * S_{rec})} * (1 - e^{-(M + (F_{com} * S_{com}) + (F_{rec} * S_{rec}))}), \quad (3)$$

for each year and age, the N was the abundance from the assessment (ASMFC, 2016), whereas the M was the estimated natural mortality. Commercial fishing mortality (F_{com}) and recreational fishing mortality (F_{rec}) were the yearly F s for each fishing sector that were multiplied by age-selectivity to the fishery. All the gear selectivity values were approximated from figures in the 2016 weakfish stock assessment (ASMFC, 2016). The approximated commercial selectivity for ages-0 to age-6+ were 0, 0.2, 0.44, 0.72, 0.9, 1, and 0.95, respectively. The approximated recreational selectivity for the same ages were 0, 0.05, 0.22, 0.36, 0.77, 0.9, and 1 respectively for the years 1982 to 1995, and 0, 0.05, 0.26, 0.86, 1, 0.86, and 0.86 respectively for the years

1996-2014. We multiplied the numbers lost to natural mortality for each age after multiplying by the stock assessment's age-at-mass (ASMFC, 2016) and summed over all ages for a specific year to calculate $N_{mortality}$, the biomass lost to natural mortality.

The resulting biomass attributable to M for age-0s and age-1+ were combined and compared with the biomass lost to predation from the predator consumption simulation and to biomass lost due to each fishery sector. To estimate the numbers lost to fishing, we amended equation (3) by replacing the first appearance of M in the numerator with either $F_{com} * S_{com}$ or $F_{rec} * S_{rec}$. After converting numbers lost to biomass, the $N_{mortality}$ is then reflective of the biomass of weakfish lost to the specified F sector.

RESULTS

Predation and harvest

Finfish and marine mammal predators consumed on average 6,767 t of weakfish (80% CI 17,40 to 14,388 t) during the overwintering period off the coast of North Carolina across 1982-2014. During the time-series, harvest in the form of landings and discards decreased by ~98% as regulations increased (Figure 4), and harvest has not been greater than predation losses since 1993 (Figure 4). When harvest and predator consumption biomass are combined, the percentage attributable to predation averaged 54% from 1982-1998 and increased to an average of 84% in 1999-2014 (Figure 4).

Bottlenose dolphin were the top predator of weakfish averaging 3,706 t across the time-series, and accounted for 55% of the total weakfish biomass removed by all modeled predators (Figure 4). Trends in C_{pop} reflected changing dolphin biomass, as evidenced by two incidences of abrupt decline during 1988 and 2013 (Figure 5e). Even with the lowest predator biomass at less than 2.2 t, total C_{pop} mirrored bottlenose dolphin biomass (Figure 4, Figure 5e). The sensitivity

analysis indicated that during an individual year, changes in W most strongly affected C_{pop} , followed by changes in T . (Figure 6e). The normal truncated distribution from which W was derived ranged from 0.15 to 0.85 (Figure B1e).

Striped bass and bluefish on average accounted for 38% of the total weakfish biomass consumed by all modeled predators (21% and 17% respectively; Figure 4). Although trends in biomass differed pre-1995, the biomass of both predators since have generally increased, and is especially stark in striped bass (Figure 1). The C_{pop} reflected the changes in each predator's biomass (Figure 5c-d), even though the sensitivity analysis found that changes in W most strongly affected C_{pop} for both predators (Figure 6c-d). The normal truncated distribution from which W was derived was essentially the same for both predators ranging from 0 to 0.16, with slightly less than half of the distribution being 0 (Figure B1c-d).

Spiny dogfish and summer flounder were minor predators of weakfish, as each on average accounted for 3% and 4% of the total weakfish biomass consumed by all predators. Spiny dogfish had the greatest biomass of any predator (Figure 1), yet had the lowest weakfish consumption of all modeled predators (Figure 4, Figure 5a). Despite fluctuations in spiny dogfish biomass, their C_{pop} consumption did not change appreciably (Fig 5a). The sensitivity analysis indicated that during an individual year, changes in W most strongly affected C_{pop} (Figure 6a). The normal truncated distribution from which W was derived ranged from 0 to 0.08, with over half of the distribution being 0 (Figure B1a). Therefore, since the median W was <0.01 , a small change in W can increase spiny dogfish C_{pop} , due to this predator's large biomass. Although the average consumption was 4% across the time-series (Figure 4), summer flounder C_{pop} estimates increased substantially in post-2000 years as the stock rebuilt (Figure 1; Figure 5b). The sensitivity analysis found that changes in W most strongly affected C_{pop} (Figure 6b), and the

normal truncated distribution from which W was derived ranged from 0 to 0.24, with over half of the distribution being 0 (Figure B1b).

Comparison of total predator consumption with stock assessment

The inclusion of age-0s to the stock assessment's biomass attributable to M allowed for a realistic comparison to the predator consumption simulation. Biomass attributable to M from the stock assessment represents age-1+ weakfish and indicates, for biomass, an increase in the proportion of Z attributable to M during the time-series (Figure 3b). During this time period, the biomass of weakfish lost to age-1+ M has remained consistent with an average of 1,302 t (Figure 3b). The composite-YOY index indicates fairly consistent age-0 abundance; however, the estimates of age-1 abundance from the recent stock assessment show a declining trend since the 1990s (Figure 3a). Given the timing of age-0 surveys that make up the composite-YOY index, the loss of weakfish between age-0 and age-1 likely occurs between the fall of their spawned year and the following spring. The magnitude of this loss in biomass is apparent in that M for age-0s averaged 3.1 during the time-series (Figure 7), and with the exception of 2013, has remained greater than 3 since 2000 (Figure 7). When age-0 biomass is included in the biomass attributable to M from the stock assessment, the biomass lost to M is greater for age-0s when compared to age-1+ (Figure 3b). In comparing different mortality sources, natural mortality loss of age-0s in terms of biomass is greater than all other sources combined from 1992 onward (Figure 6b). That difference is especially large in the years 2004-2014 (Figure 6b). During these years, the population abundance of age-1+ were very small compared to previous years and the weakfish age-structure was truncated from age-6+ in the population to age-3 and age-4, thereby causing the bulk of weakfish biomass to come from age-0s (ASMFC, 2016).

The biomass attributable to M from the stock assessment is comparable to independent estimates for predator consumption simulation (Figure 8). The annual biomass attributable to M from the stock assessment, including age-0 weakfish, ranged from 2,431 to 15,445 t (years 1984 and 2006, respectively) and falls within the 80% CI of predator consumption estimates for every year except 1997 and 1998 (Figure 8). The pattern in yearly predator consumption estimates mirrored biomass trends in bottlenose dolphin (Figure 2; Figure 3e), and patterns in the estimates of biomass lost to stock assessment and age-0 M mirrored that of the composite-YOY (Figure 6a). Lastly, difference in time-scales between estimates should be noted, as the biomass attributable to M from the stock assessment was based on an annual scale with the exception of the inclusion of age-0 biomass for 4-months, whereas the predator biomass consumption only accounted for the 6-month overwintering period of weakfish.

DISCUSSION

Our findings indicate bottlenose dolphins are the top predator of weakfish, followed by striped bass, bluefish, summer flounder, and spiny dogfish. We integrated predator biomass, spatial overlap of predator and weakfish, diet, and consumption rates for these five weakfish predators to estimate their consumption of weakfish, and found the total consumption estimated during winter was similar in magnitude to the estimated biomass loss to M that was estimated in the most recent stock assessment (ASMFC, 2016). Our findings indicate that predation is largely responsible for the increase in total mortality observed in the weakfish population over the last 14 years.

Comparison with stock assessment

The similarity between the independent predator consumption estimates and biomass attributable to M from the stock assessment supports the latter's mortality estimates as realistic in

terms of a high M and increasing trend. During the 2000s, the decline in weakfish stock was attributable to a high Z caused by an increasing M (ASMFC, 2016). However, these yearly M estimates have uncertainty, in part because they are derived from priors based on calculations from life history and external parameters, and not mortality estimates from field studies (ASMFC, 2016). Estimating predator consumption and comparing the findings to a static M from stock assessment has been done in the past (Benoît et al., 2011; Begoña Santos et al., 2014), and we expanded on this approach by comparing time-varying predator consumption with annual biomass attributable to M in the stock assessment. The comparison allows for an independent check of M and the ability to test predation hypotheses for the effect on M . Begoña Santos et al. (2014) found that four small cetaceans consumed between 3% and 6% of the current Iberian sardine (*Sardina pilchardus*) stock biomass attributable to M , and between 92% and 214% of the M of the southern stock of hake (*Merluccius merluccius*). For the latter, bottlenose dolphin was responsible for 82% of M . Benoît et al. (2011) found that gray seal predation could explain up to 20 to 50% of M in adult white hake (*Urophycis tenuis*) and Atlantic cod (*Gadus morhua*). In addition, the similarity in magnitude of biomass estimates indicates that most weakfish mortality occurs during the overwintering period, as predator consumption was estimated during a 6-month period. Weakfish aggregate in predictable areas during their overwintering migrations to and from the continental shelf (Bigelow et al., 2002), which may increase predation as compared to summer months where fish are solitary (Neuenhoff et al., 2018). The minimal consumption of weakfish during summer, is further supported by our literature review (Table B1-B8, Figure B3). As spatio-temporal resolution increases with predator consumption model inputs, researchers can elucidate where and when predation occurs on specific prey types (Spitz et al., 2018).

The trend in estimated M from the stock assessment mirrors the increase in predator consumption for the recent time and indicates the cause of increased weakfish mortality. As weakfish biomass declined in the 2000s, all of the modeled predators were increasing as a result of management by maximum sustainable yields (MSY) or no-take policies (Figure 1). The difficulty in achieving populations at relatively high biomass levels simultaneously can be potentially detrimental to the population of mid-level predators such as weakfish (Hartman, 2003). As predation increased on weakfish in the late 2000s, age-3+ weakfish were greatly reduced and the majority of weakfish biomass was in younger age-classes (ASMFC, 2016), where increased predation may have caused a “pit” in which younger-age classes are consumed in such numbers that survival to older age classes becomes improbable (Swain and Benoît, 2015; Neuenhoff et al., 2018). The biomass consumption estimates of heavy mortality by predation is not limited to age-0s, as weakfish lengths-at-age variability caused by within-year spawned cohorts suggests predation pressure can continue up to age 2 or around 300 mm (Shepherd and Grimes, 1983; Szedlmayer et al., 1990; Hatch and Jiao, 2016). Data suggests weakfish may outgrow predation from bottlenose dolphin around 450 mm (Figure B2; Gannon and Waples, 2004), which corresponds with an age-3 fish (Lowerre-Barbieri, 1995). When considering the ability of modelled predators to consume 100+ mm weakfish and the weakfish population truncation at age-3 in recent years, almost the entire weakfish population is susceptible to predation.

Estimating age-0 biomass changed the current perspective on how weakfish biomass is distributed among age-classes. For an equal comparison between the stock assessment M and predator consumption, we included an estimated age-0 biomass lost to M to that of the stock assessment’s biomass of age-1+ weakfish. Through the inclusion, we found that the combined

age-1+ biomass has not been greater than age-0 biomass since 2000, an effect especially impressive since we only included biomass of age-0s from a mere 4-month period. In terms of age-0 biomass lost to M during our study, the stock assessment's total biomass lost to M increased on average over fivefold (1302 to 7148 t). The proportional biomass of age-0s lost to M has been large compared to age-1+ and consistent throughout the time-series, illustrating its role as both a mid-level predator (Hartman, 1993) and a forage fish (Binion-Rock, 2018). A biomass shift to age-0s and age-truncation are indicators of a heavily exploited stock (Berkeley et al., 2004; Ottersen, 2008; Hidalgo et al., 2011), weakfish share these indicators that increase the risk of recruitment failure and stock collapse (Brunel, 2010). In this instance, stock juvenation was caused by predation, as weakfish harvest has been minimal since 2000.

Recruitment appears to be determined during the late juvenile life stage of weakfish. Throughout the time-series, the composite-YOY index generally varied without a strong trend, regardless of extreme highs in SSB during the 1980s to record lows with age-truncation in the 2000s. It was concluded in the latest stock assessment that a reliable stock-recruit relationship could not be developed using age-0s (ASMFC, 2016). For our model, we assumed the composite-YOY index accurately mirrored weakfish age-0 abundance, and the mismatch in trends of age-0s and age-1s was reflective of a recruitment bottleneck. In order to estimate age-0 abundances, we assumed a weight-based estimate of Lorenzen's M for 1984 was valid to scale age-0 abundances to the composite-YOY index across the time series. Our work suggests that weakfish year-class regulation occurs during the late juvenile stage (>100 mm TL) as they undergo their first overwintering. It is generally accepted that recruitment strength is mainly determined at the pre-juvenile stage (e.g., Hjort, 1914; Crecco et al., 1983; Leggett and Deblois, 1994; Oeberst et al., 2009; Polte et al., 2013). Weakfish appear to be an exception that follow

Sissenwine's juvenile predation hypothesis (1984), where predation regulates recruitment during the later juvenile stage (i.e. post-larval to recruitment at age-1).

Predators

Bottlenose dolphin ranked as the top predator of weakfish. The trophic connection between weakfish and bottlenose dolphin in North Carolina was first reported in 1914, and in later Florida and South Carolina dolphin strandings (Townsend, 1914; Barros, 1993; Pate and McFee, 2012). A diet study from 186 stranded dolphins in North Carolina estimated an annual W of 0.36 and found that the percent numerical contribution of weakfish in the diet was 6% during the fall, peaked during winter at 47%, and tapered to 34% during spring (Gannon and Waples, 2004). Thus, weakfish is known to be an important seasonal prey for bottlenose dolphin for at least two decades: 1993-2001 (Gannon and Waples, 2004) and 1998-2012 (Barbie Byrd, unpublished data). The overall average biomass of bottlenose dolphin (1.6 t) was minimal relative to the other modeled predators. Even with relatively small biomass, bottlenose dolphins consumed large amounts of weakfish, as their DR is over four times that of any modeled fish predator because of endothermic energy requirements (Williams, 1999), and the W of ~ 0.5 was an order of magnitude higher than the other modeled predators. The ability of a marine mammal to consume more weakfish than all modeled finfish predators combined is not the norm in marine systems, where medium-sized predator fish are typically the leading consumers at the ecosystem level (Bax, 1991; Overholtz and Link, 2007). However, recent work suggests that individual marine mammal species can have disproportionately large effects on particular prey fish populations (Begoña Santos et al., 2014; Swain and Benoît, 2015; Chasco et al., 2017; Nelson et al., 2018; Neuenhoff et al., 2018).

Finfish consumed 45% of the average total weakfish biomass lost to all predators. Since 2000, all predator biomasses increased, with spiny dogfish, summer flounder, and striped bass all rebuilding after being “overfished”, thus leading to increased weakfish consumption. Variation in predator biomass was shown to affect demersal predator consumption of Atlantic herring, where consumption peaked in the early 1990’s, but declined after overfishing reduced the predator biomass (Overholtz and Link, 2007). The biomass of weakfish finfish predators was high (>100 t), and allowed for high consumption even when the contribution of weakfish to predator diets was low (<0.05). However, when W was heavily inflated towards 0, even a very high predator biomass does not equate to high weakfish consumption as evidenced by spiny dogfish. The increased consumption by the top weakfish predators (striped bass and bluefish) can have significant population effects as seen with forage fish. Striped bass were estimated to consume 40% of coast-wide Atlantic menhaden (*Brevoortia tyrannus*; Uphoff, 2003), and bluefish were estimated to consume 1 to 25% of bay anchovy (*Anchoa mitchilli*) biomass during the years 1994-1995 (Buckel et al., 1999a).

Modeling and uncertainty

Our selections of parameter values and distributions were conservative so that our estimates of weakfish consumption, if biased, would be biased low. Even with the uncertainty of bottlenose dolphin population size, its weakfish consumption may be underestimated because one additional stock, the Western North Atlantic Southern Migratory, was omitted but may prey on weakfish during the fall and spring of the weakfish migration (surveyed 2016 $n=3,751$ with $CV=0.6$; Hayes et al., 2018).

We were also conservative in our modeled distribution of W by accounting for sample size differences and diet studies of our modeled predators that did not find weakfish as a prey

item. Other modeling studies have incorporated temporal changes in W to reflect prey abundance changes (Overholtz and Link, 2007; Deroba, 2018), but the temporal distribution of predator diet studies did not allow for this approach with weakfish.

Arguably, the most subjective parameter is P , as weakfish and their predators cover vast regions of the continental shelf and beyond, and cannot be fully accounted spatially or temporally by a single sampling method (e.g., fisheries-independent trawl surveys). As additional data for our modeled species become available, P should reflect changing stock distribution shifts due to warming ocean waters in the Northeast United States continental shelf which may cause increase overlap between weakfish and their predators (Nye et al., 2009).

Estimates of finfish DR were calculated from lab studies and Q/B values, but bottlenose dolphin DR remain largely unexamined. We conservatively selected bottlenose dolphin DR estimates from Smith et al. (2015), derived from multiple captive animal studies. However, estimates from a Field Metabolic Rate (FMR) study for bottlenose dolphin in the US Atlantic and Gulf of Mexico suggests that our values may be biased low by up to a third, as it does not reflect the additional energy needed in the wild (Bejarano et al., 2017). As FMR estimations are dependent on prey caloric value, this particular method was unavailable to us in this study (Bejarano et al., 2017). Warming water temperatures in the Mid-Atlantic Bight may have caused the DR of ectotherm finfish predators to increase during the time-series. Basal metabolic rates increase exponentially with increases in temperature, thus requiring more food resources for predators in a warmer ocean (Daly and Brodeur, 2015).

The Monte Carlo modeling approach provides the most probable estimate of a predator's consumption, with an 80% CI incorporating the uncertainty in each input variable. The high uncertainty in predator consumption estimates is a product of the combined variance associated

with each parameter. The widening and narrowing of 80% CI reflects increase or decrease in a predator's abundance, first demonstrated by Overholtz (2006). An even greater effect on uncertainty for all five predators was W , the percentage of diet comprised by weakfish. Although the sensitivity analysis regression coefficients were an average across all modeling years, the importance of W was evident across the years, as there was minimal variation between yearly W regression coefficients for each predator. The finding indicates that even small increases in W can dramatically increase consumption. When modeling predator consumption of a specific prey such as weakfish, the effect of diet composition is generally the most influential (Shelton et al., 1997; Overholtz, 2006; Smith et al., 2015), whereas when modeling a predator's total consumption across all prey types, abundance and daily ration are generally the most significant parameters (Smith et al., 2015; Spitz et al., 2018). For weakfish and other specific prey items, overall model uncertainty can be reduced through targeted predator diet studies to better inform W (Overholtz and Link, 2007). Many of these studies need to be focused on predators during their overwintering period, as evidenced by some winter months having no diet data.

Our estimates of predator consumption are an underestimate because we could not include all possible predators and did not include predation during summer months. Insufficient biomass estimates, spatio-temporal information on overlap with weakfish, and daily ration estimates precluded us from modeling all possible predators. As additional studies are conducted, future consumption models should include juvenile humpback whales as they have to the capacity to eat large amounts of schooling prey (Laerm et al., 1997), cormorants and gannets based on their ubiquity off the North Carolina coast and recent population increases (Weseloh et al., 1995; Chardine et al., 2013), and lastly, the Atlantic sharpnose shark, which has increased by nearly a quarter in abundance (SEDAR 34, 2013). The timing of mortality and our literature

review suggested that predator consumption was minimal during the summer, therefore we did not include summer predator consumption, but could be included in future models.

The methods used in the current study can be applied to other studies to estimate predator consumption for comparison with estimated prey biomass attributable to M . All analyses were run in open-source R, with code easily modifiable for other species and systems. For example, Atlantic croaker along the US Atlantic and Gulf of Mexico share predators with weakfish and has estimates of M from a stock assessment. The code offers transparency, facilitates reproducibility by providing line-by-line record of the entire modeling process, and flexibility to experiment with different model inputs

Management implications

Linking trophic modeling to relevant management techniques such as stock assessments and reference points is an emerging field (Link, 2010). Similarly, the assumption of an estimated non-stationary M as a random walk over time is a recent development (Jiao et al., 2012; Swain and Mohn, 2012; Swain and Benoît, 2015), and is not recommended without strong empirical evidence due to the potential complications in the estimation of biological reference points (Legault and Palmer, 2015). For a species such as weakfish with an estimated increase in M , total predator consumption provided an independent means to support the use of a time-varying M , and a mechanistic understanding. With predation identified as the main cause of M , fisheries management can incorporate this information into the stock assessment to increase precision of M , such as partitioning M into M_1 and M_2 , where M_1 residual natural mortality and M_2 is predation natural mortality (Hollowed et al., 2000; Overholtz et al., 2008; Moustahfid et al., 2009a; Moustahfid et al., 2009b) or creating a predation pressure index (Richards and Jacobson, 2016). By explicitly incorporating predation mortality, biological reference points generally

become more conservative than those derived from traditional stock assessments (Link, 2010; Tyrrell et al., 2011), and allow for realistic recovery times (Harvey et al., 2008; Moustahfid et al., 2009b). Ultimately, weakfish could be managed with a multispecies approach, where M is allowed to vary with the abundances of predators and prey (Curti et al., 2013).

The difference between harvest and predator consumption biomass indicates that further reduction in F is unlikely to promote weakfish stock rebuilding, since the average predator consumption was over 29 times greater than the average combined commercial and recreational harvest from 2004 to 2014 (7,656 t to 259 t; respectively). Even with the inclusion of all unaccounted F biomass, it is improbable that harvest would rival predator consumption estimates. Furthermore, our work suggests that the cause for the recent weakfish population decline was a recruitment bottleneck between ages-0 to 1, whereas F across all sectors predominately selects for age-3+ weakfish. To further reduce F uncertainty, research should focus on fisheries that encounter age-0 weakfish. Therefore, increases in the weakfish population will require lower predator biomass or predators feeding on alternative prey for multiple and successive years; this could be tracked through age-0 M estimates as a yearly predation index, as weakfish from ages 0-2 are susceptible to predation.

Management requires a long-term perspective on the population dynamics of weakfish. In our dataset, fishing mortality was high during the 1980s and was probably the main driver of the initial weakfish population decline. As regulations increased in the 1990s, the stock was rebuilding until predation increased in the 2000s. Weakfish population fluctuations may be contingent on bottlenose dolphin numbers, which have had two mortality events caused by morbillivirus epidemics during our time-series (Lipscomb et al., 1994; Morris et al., 2015). These epidemics may reoccur over time as herd immunity is lost as the number of

immunologically naïve individuals increases (Duignan et al., 1996; Van Bresseem et al., 2014), and the effect of the 2013-2015 outbreak on weakfish is yet to be formally examined. Since the late eighteenth century, weakfish populations have undergone drastic population fluctuations with high abundance correlating with the warm years of the Atlantic Multidecadal Oscillation from 1930-2014 (Cushing, 1982; Jiao et al., 2012). Our work suggests the mechanism and cause for the correlation might be predation as shown in recent years. Roelofs (1951) classified periods of high weakfish abundance off New England from 1672 to 1917, and noted they matched periods when bluefish were scarce. Prior to a high period in the weakfish cycle from 1930-1948 (ASMFC, 2016), bottlenose dolphin populations were thought depleted, so much so that by 1930 the main dolphin harvester at Cape Hatteras, North Carolina stopped fishing (Cecelski, 2015). Further examination of marine mammal and finfish predator populations and the effects of fisheries management thereon is required to fully understand weakfish population dynamics.

Conclusion

Our work indicates that predation structures weakfish population dynamics, and only by understanding trophic connections and managing fisheries through a multi-species approach, can effective rebuilding occur. We explored weakfish trophic connections using a transparent and reproducible modeling framework which found predation to be the main cause of M . Comparing predator consumption to the estimated M in terms of biomass provided an independent check of M , one of the most influential and uncertain parameters in fisheries stock assessments (Vetter, 1988; Clark, 1999). Although weakfish are often categorized as a mid-level predator, our work highlights their additional importance as a forage species at younger ages for our modeled predators (Binion-Rock, 2018). With the recovery of many piscivorous marine mammal and finfish predator populations and the current practice of managing multiple species with MSY

principles or no-take (Costa et al., 2006; Stock status, 2017), predation may continue to prevent successful weakfish rebuilding (e.g., Hartman, 2003; Swain and Benoît, 2015; Chasco et al., 2017; Neuenhoff et al., 2018). Therefore, incorporating predation within an ecosystem-based approach is paramount for effective weakfish stock assessment and management.

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TABLE

Table 1. Distribution input parameters for predator consumption simulations, where B =biomass in kg, P =proportion of predator population overlapping with weakfish during the overwintering period, DR =daily ration (kg prey/kg predator/day), W =proportion by weight of weakfish in predator diet, T =time in days that predators and weakfish overlap, P =proportion of predator population overlapping with weakfish winter range. Distributions are pert, uniform (unif), truncated normal (trnorm), and unif (uniform). The Weighted (Wt.) mean was calculated using study sample size and proportion by weight of weakfish in predator stomachs. For bottlenose dolphin B , a separate pert distribution modeled each population stock abundance and a shared average dolphin population mass in kg that applied to all stocks.

	Spiny dogfish	Summer flounder	Bluefish	Striped bass	Bottlenose dolphin
<i>B</i>					
<i>Distribution</i>	pert	pert	pert	pert	pert
<i>P</i>					
<i>Bounds</i>	0.05-0.3	0.2-0.4	0.3-0.7	0.6-0.9	0.7-0.9
<i>Distribution</i>	unif	unif	unif	unif	unif
<i>DR</i>					
<i>Most likely</i>	0.006	0.008	0.009	0.006	0.046
<i>Minimum</i>	0.005	0.008	0.006	0.004	0.029
<i>Maximum</i>	0.006	0.010	0.012	0.008	0.061
<i>Distribution</i>	pert	pert	pert	pert	pert
<i>W</i>					
<i>Wt. mean</i>	0.004	0.030	0.010	0.022	0.489
<i>Sd</i>	0.020	0.076	0.040	0.039	0.139
<i>Bounds</i>	$-\infty$ to 1	$-\infty$ to 1	$-\infty$ to 1	$-\infty$ to 1	$-\infty$ to 1
<i>Distribution</i>	trnorm	trnorm	trnorm	trnorm	trnorm
<i>T</i>					
<i>Bounds</i>	60-150	60-150	60-150	60-120	90-180
<i>Distribution</i>	unif	unif	unif	unif	unif

FIGURES

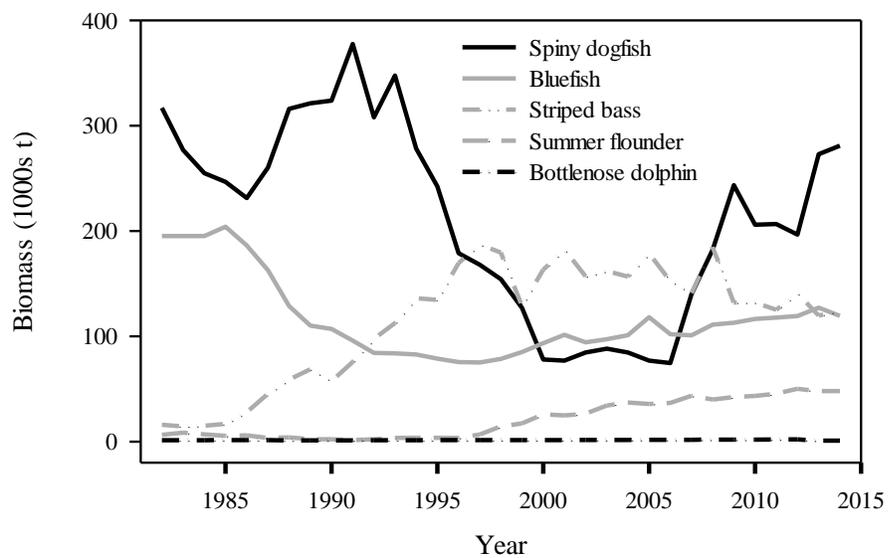


Figure 1. Predator biomass in 1000s of metric tonnes from 1982 to 2014.

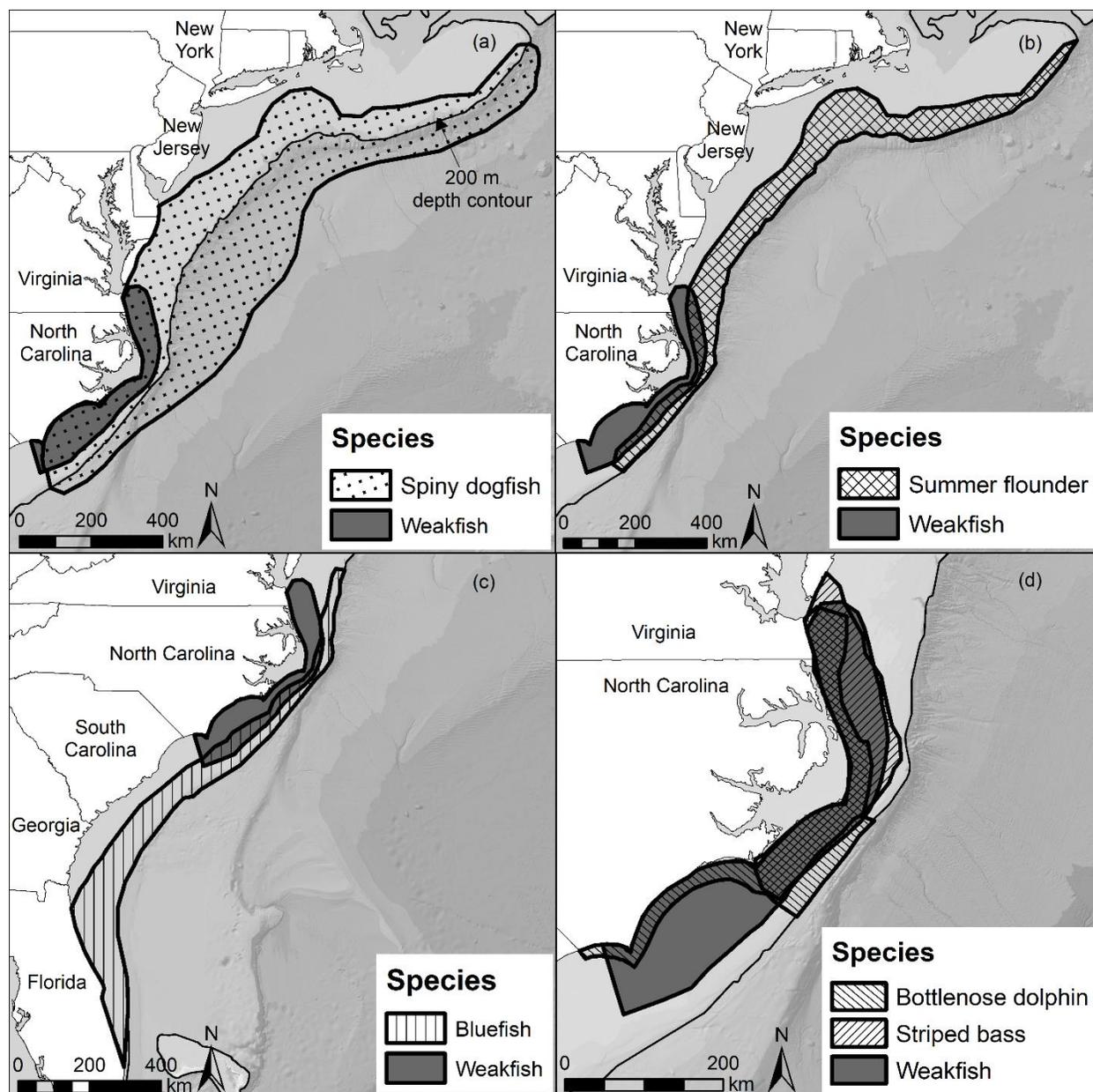


Figure 2. Spatial overlap during the height of winter (January) of weakfish with predators: spiny dogfish (a), summer flounder (b), bluefish (c), and bottlenose dolphin and striped bass (d).

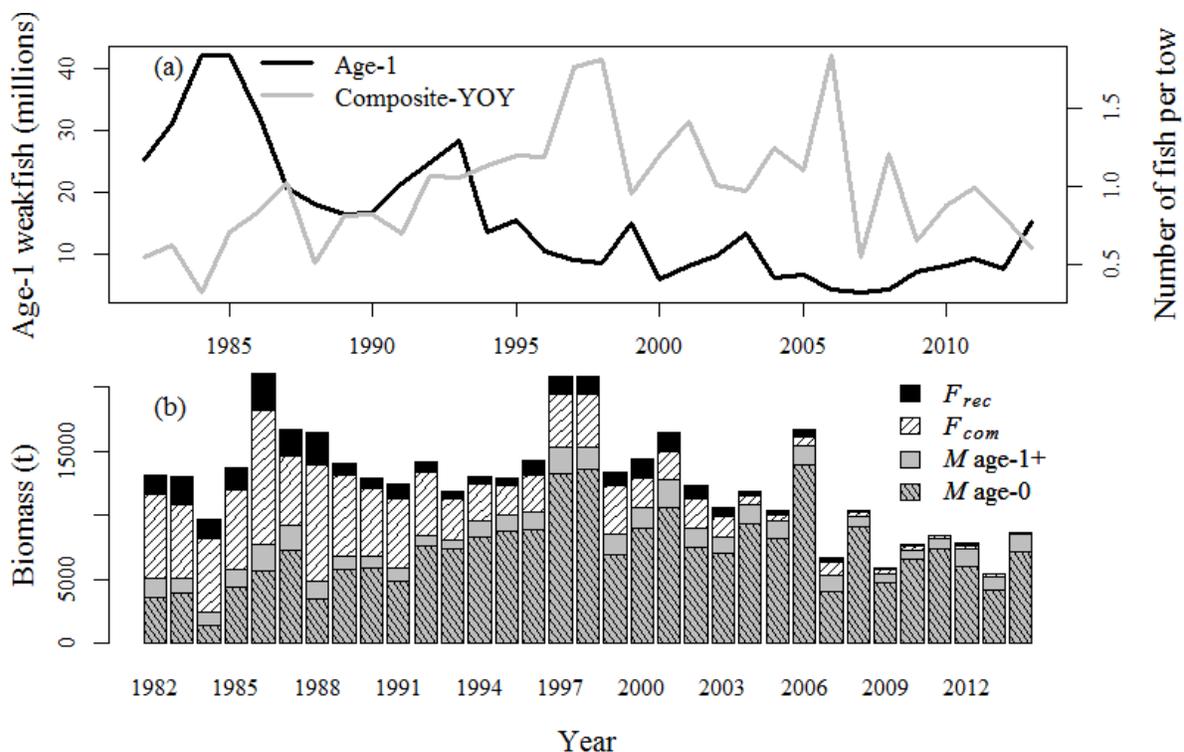


Figure 3. (a) The age-1 abundance of weakfish compared to a coast-wide composite-YOY (young-of-year) index. (b) Weakfish biomass in metric tonnes attributed to recreational harvest (F_{rec}), commercial harvest (F_{com}), and natural mortality of age-1+ (M_{age-1+}), and the addition of age-0 biomass attributable to natural mortality from September to December (M_{age-0} ; see Methods). All data were compiled from the 2016 weakfish stock assessment (ASMFC, 2016).

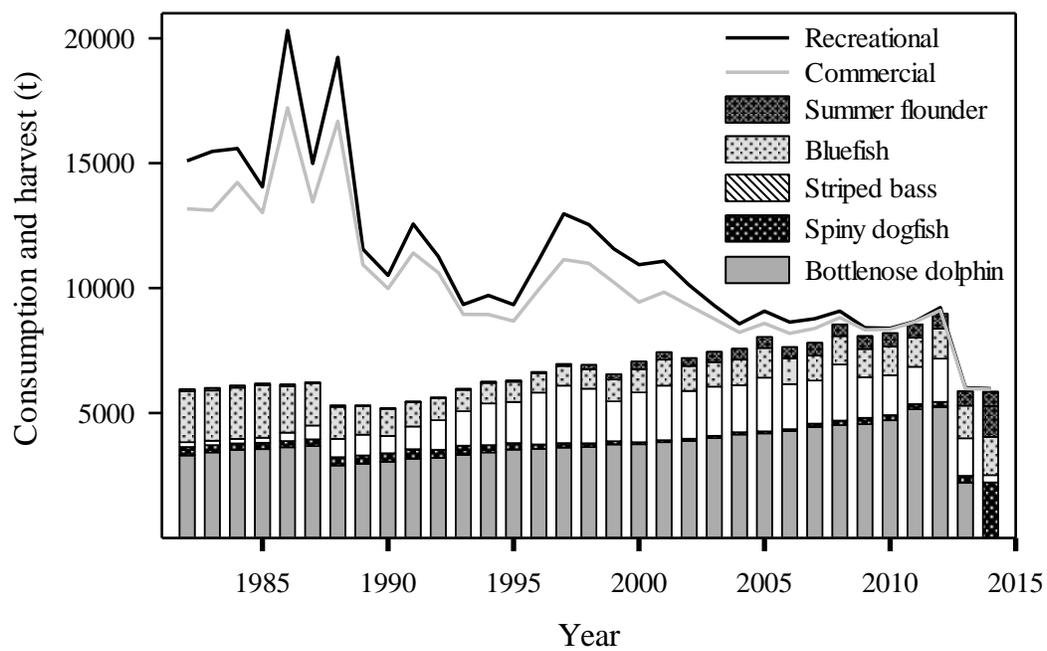


Figure 4. The aggregated weakfish biomass in metric tonnes lost to predator consumption and harvest (landings and discards) from each fishery sector.

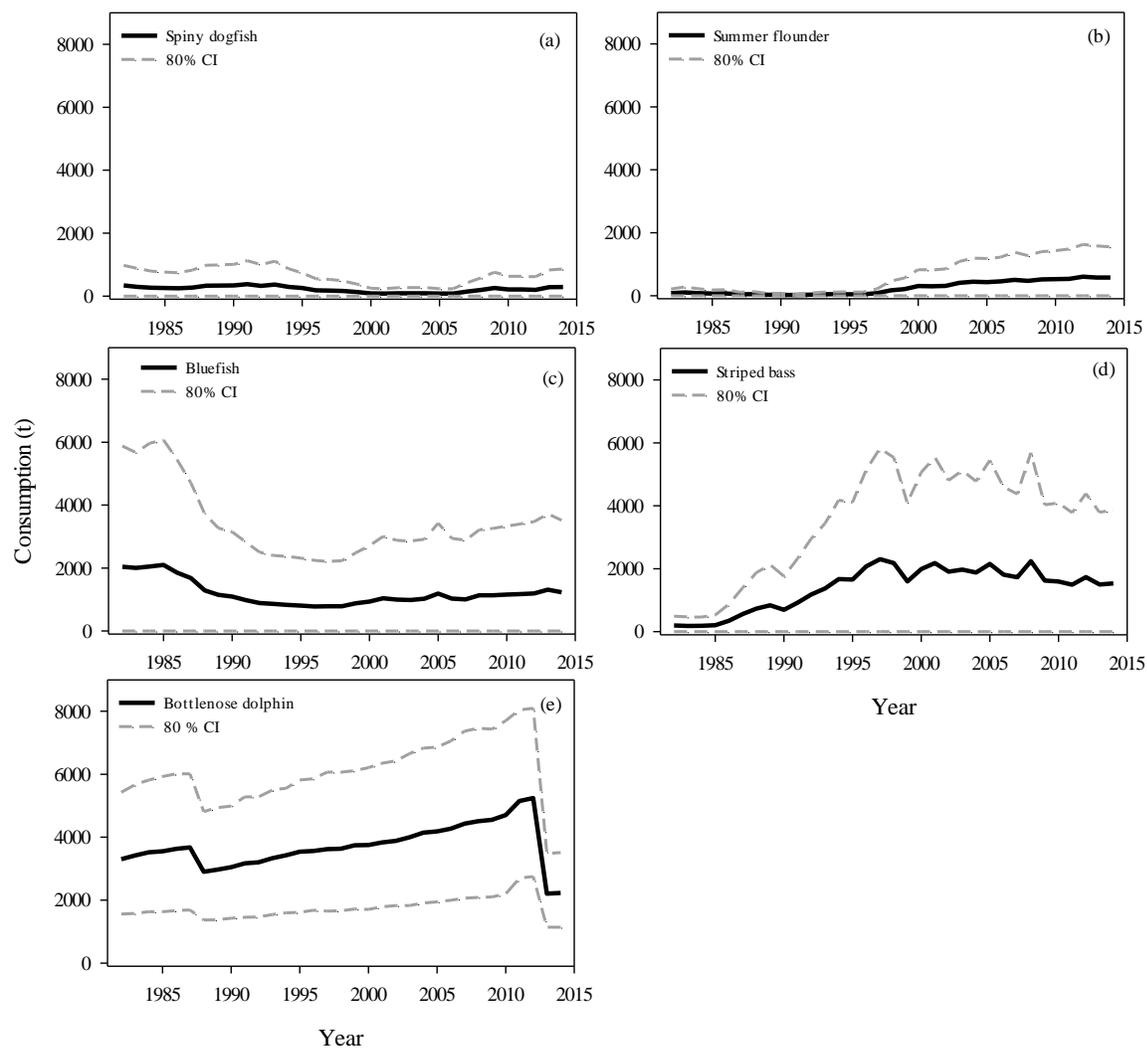


Figure 5. Predator consumption of weakfish in metric tonnes with 80% confidence intervals for spiny dogfish (a), summer flounder (b), bluefish (c), striped bass (d), and bottlenose dolphin (e).

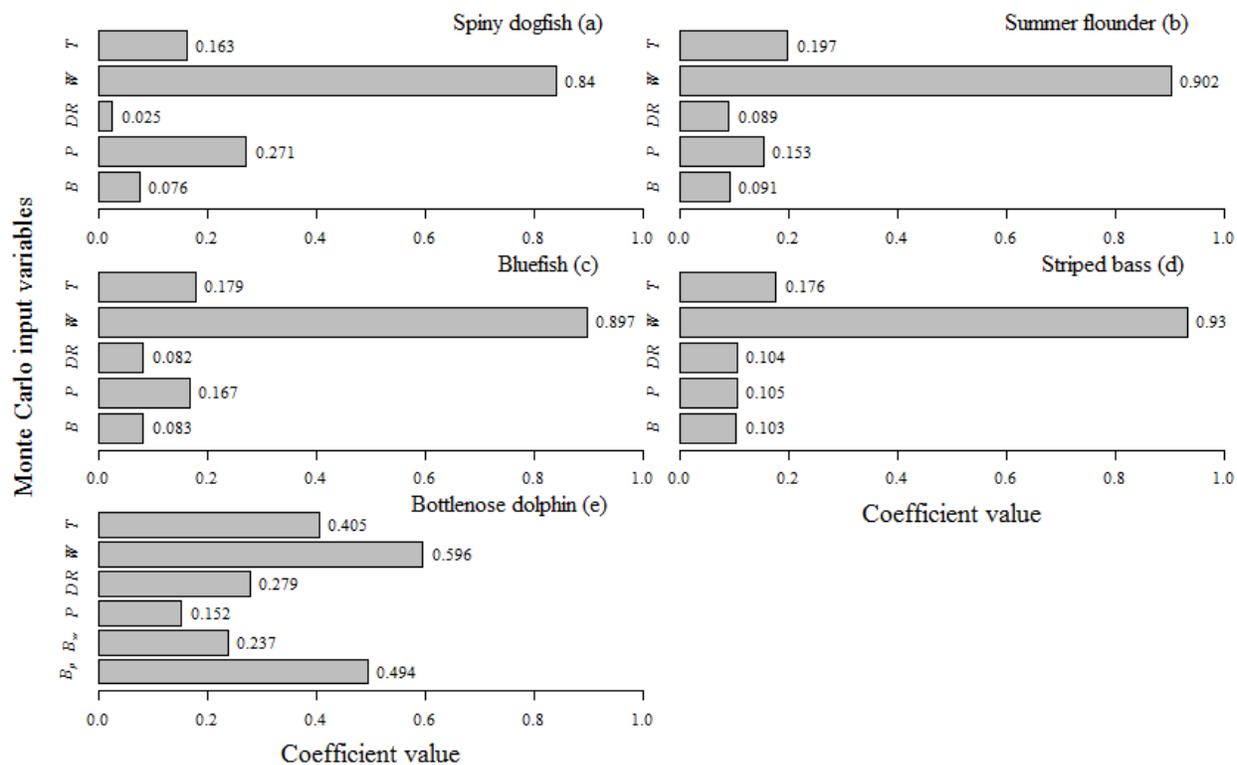


Figure 6. Regression sensitivity results of input variables (see Table 1 for definitions, the only exception being B_p =predator abundance and B_w =predator mass) versus weakfish consumption by predators: spiny dogfish (a), summer flounder (b), bluefish (c), striped bass (d), and bottlenose dolphin (e). Exact regression coefficients for each input variable are listed to the right of each bar.

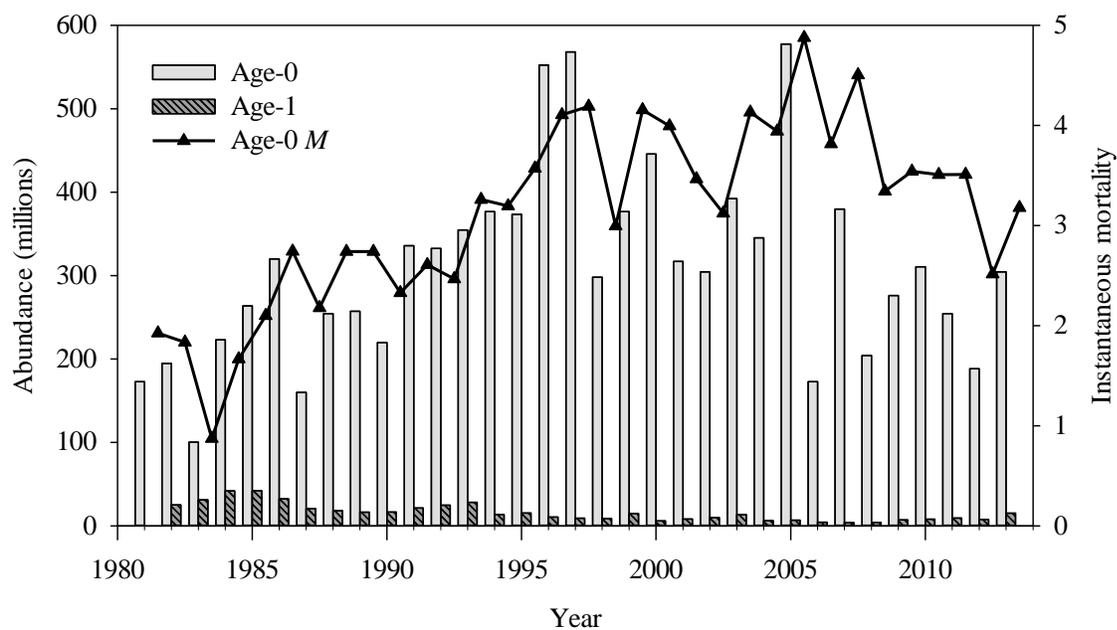


Figure 7. Age-0 and age-1 weakfish abundance from 1981 to 2014 with age-0 M as estimated by dividing the natural log of a year class's age-1 abundance from the stock assessment by that year class's estimated age-0 abundance. The large differences in age-0 and age-1 abundance levels highlight the magnitude of M for weakfish during their first year.

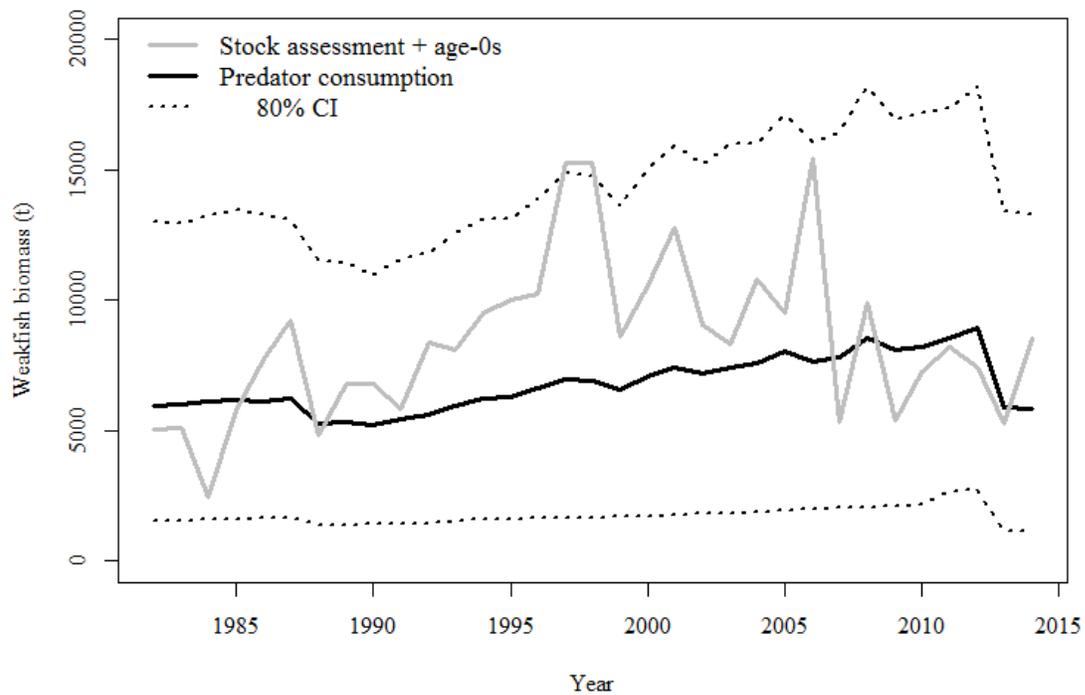


Figure 8. Weakfish biomass (t) attributable to predator consumption simulations with 80% confidence intervals as compared to the stock assessment biomass attributable to M that incorporates age-0s.

CONCLUSION

Weakfish population dynamics are driven by natural mortality, specifically winter predation. Multiple field and modeling approaches estimated a high average annual population loss on a discrete scale: catch-curve at 93% (2006-2017), telemetry at >99% (2006-2017), and tag-return at >99% (2014-2017), and were similar in magnitude to those of the stock assessment at 90% (2006-2014). The relative importance of F and M has been a subject of considerable debate over the last 3 stock assessments (ASMFC 2006; 48th SAW 2009; ASMFC 2016). After accounting for key auxiliary parameters (i.e., tag-reporting rate, tag loss, and tagging mortality), my multi-year tag-return study conclusively demonstrated that M consistently and significantly exceeded F . All field and modeling approaches indicated that weakfish mortality peaks during their migration and overwintering periods. Predator/prey modeling indicated that common bottlenose dolphins are the top predator of weakfish, followed by striped bass, bluefish, summer flounder, and spiny dogfish. The combined consumption by predators was similar in magnitude to the estimated biomass loss to M from the most recent stock assessment (ASMFC 2016), indicating that predation is largely responsible for the increase in natural mortality observed in the weakfish population in recent years.

Traditional management practices to decrease F may not be effective for weakfish stock rebuilding. From 2004 to 2014, the average biomass from fishery landings was 29 times less than that from predator consumption. Even with the inclusion of all unaccounted F biomass, it is improbable that harvest would rival predator consumption estimates. Furthermore, our work suggests that the cause for the recent weakfish population decline was a recruitment bottleneck from age 0 to 1, whereas F across all sectors predominately selects for age-3+ weakfish. Therefore, management will need to rely on low abundance years in predator population

dynamics to reduce weakfish predation. For example, weakfish population fluctuations may be contingent on bottlenose dolphin numbers, which have had two mortality events by morbillivirus epidemics during 1988 and 2013-2015 (Lipscomb et al., 1994; Morris et al., 2015). For a measurable rebuild in weakfish population, reduced predation will likely require multiple and successive years, as weakfishes of ages 0-2 are susceptible to predation.

The multiple estimates of F , M , and Z from this study may enhance the precision of stock size and mortality estimates in future stock assessments. The 2016 weakfish stock assessment estimated a non-stationary M (Jiao et al. 2012; ASMFC 2016), a new development best applied in tandem with strong empirical evidence, due to potential complications in the estimation of biological reference points (Legault and Palmer 2015). My total predator consumption estimates increased through the time-series and independently corroborated the adoption of a time-varying M . With predation identified as the main cause of M , fisheries management can apply our findings to enhance the precision of M in future stock assessments, for example, partitioning M into M_1 and M_2 , where M_1 signifies residual natural mortality and M_2 signifies predation natural mortality (Hollowed et al. 2000; Overholtz et al. 2008; Moustahfid et al. 2009a; Moustahfid et al. 2009b), or creating a predation pressure index (Richards and Jacobson 2016). By explicitly incorporating predation mortality, biological reference points generally become more conservative (e.g., recommend higher standing biomass) than those derived from traditional stock assessments (Link 2010; Tyrrell et al. 2011), and allow for realistic recovery times (Harvey et al. 2008; Moustahfid et al. 2009b). Ultimately, weakfish could be managed with a multi-species approach, where M is allowed to vary with the abundances of predators and prey (Curti et al. 2013).

My overall conclusion is that predation structures weakfish population dynamics. Although weakfish are often categorized as a mid-level predator, our work highlights their importance as a forage species at younger ages for our modeled predators (Binion-Rock 2018). With the recovery of many piscivorous marine mammal and finfish predator populations, the current practice of managing multiple species with MSY principles or no-take (Costa et al. 2006; Stock status 2017) may be ineffective towards successful weakfish rebuilding, due to high predation (e.g., Hartman 2003; Swain and Benoît 2015; Chasco et al. 2017; Neuenhoff et al. 2018). Therefore, the explicit incorporation of predation in weakfish stock assessment may allow for more effective management and stock rebuilding.

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APPENDICES

**APPENDIX A. CHAPTER 2 FIGURES ILLUSTRATING CATCH-CURVE MODEL
CATCH BY AGE AND FIT**

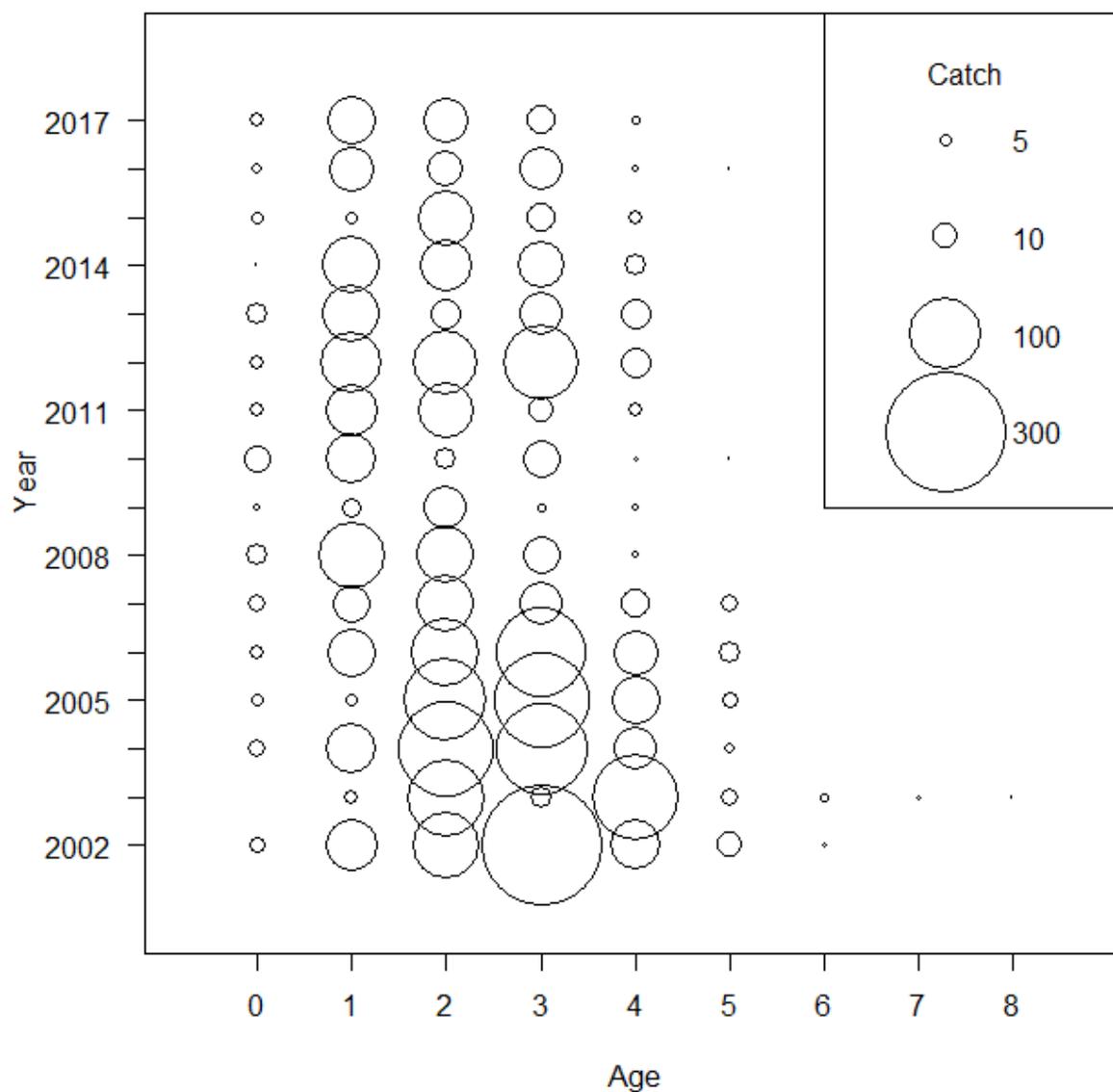
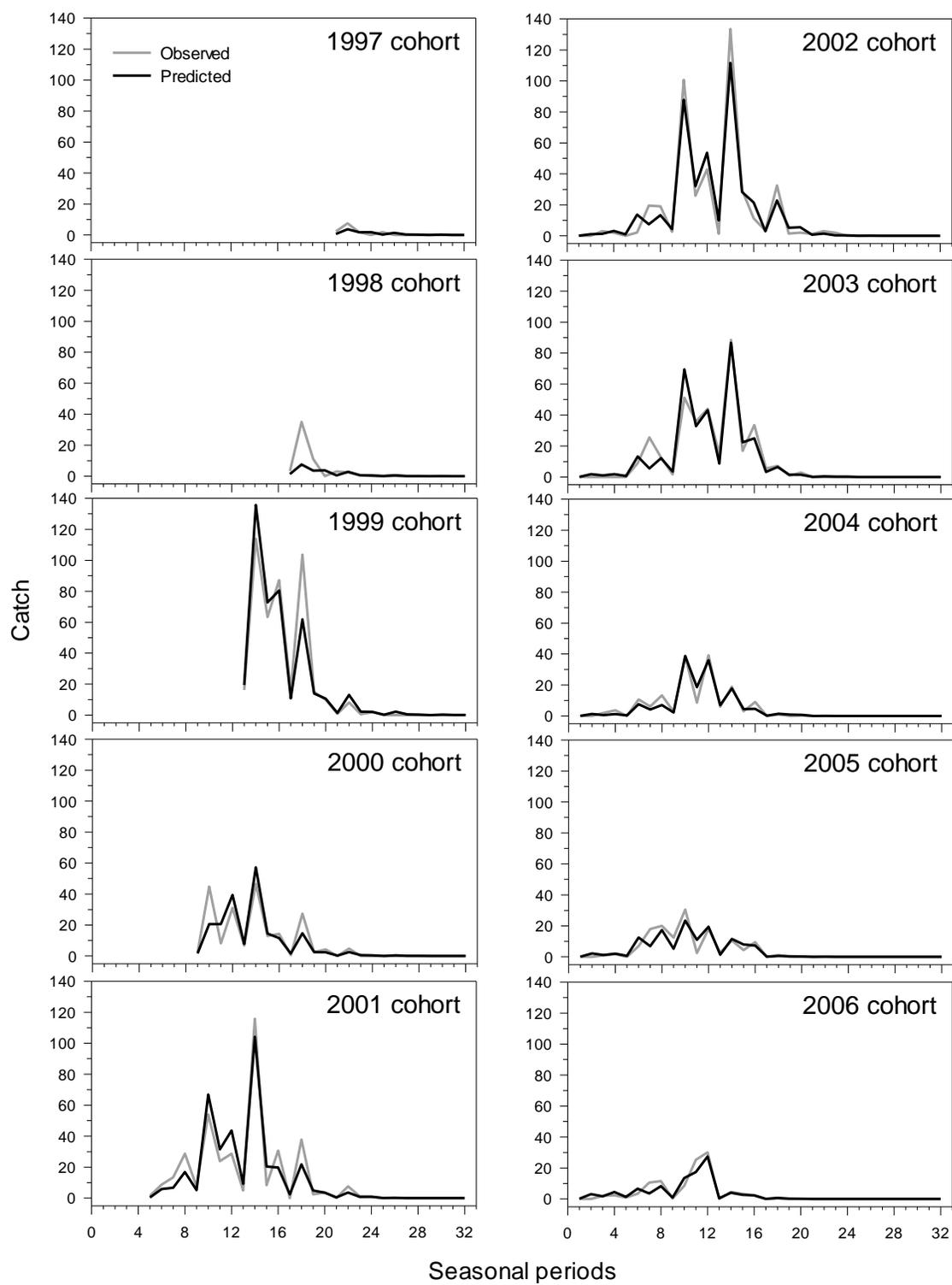
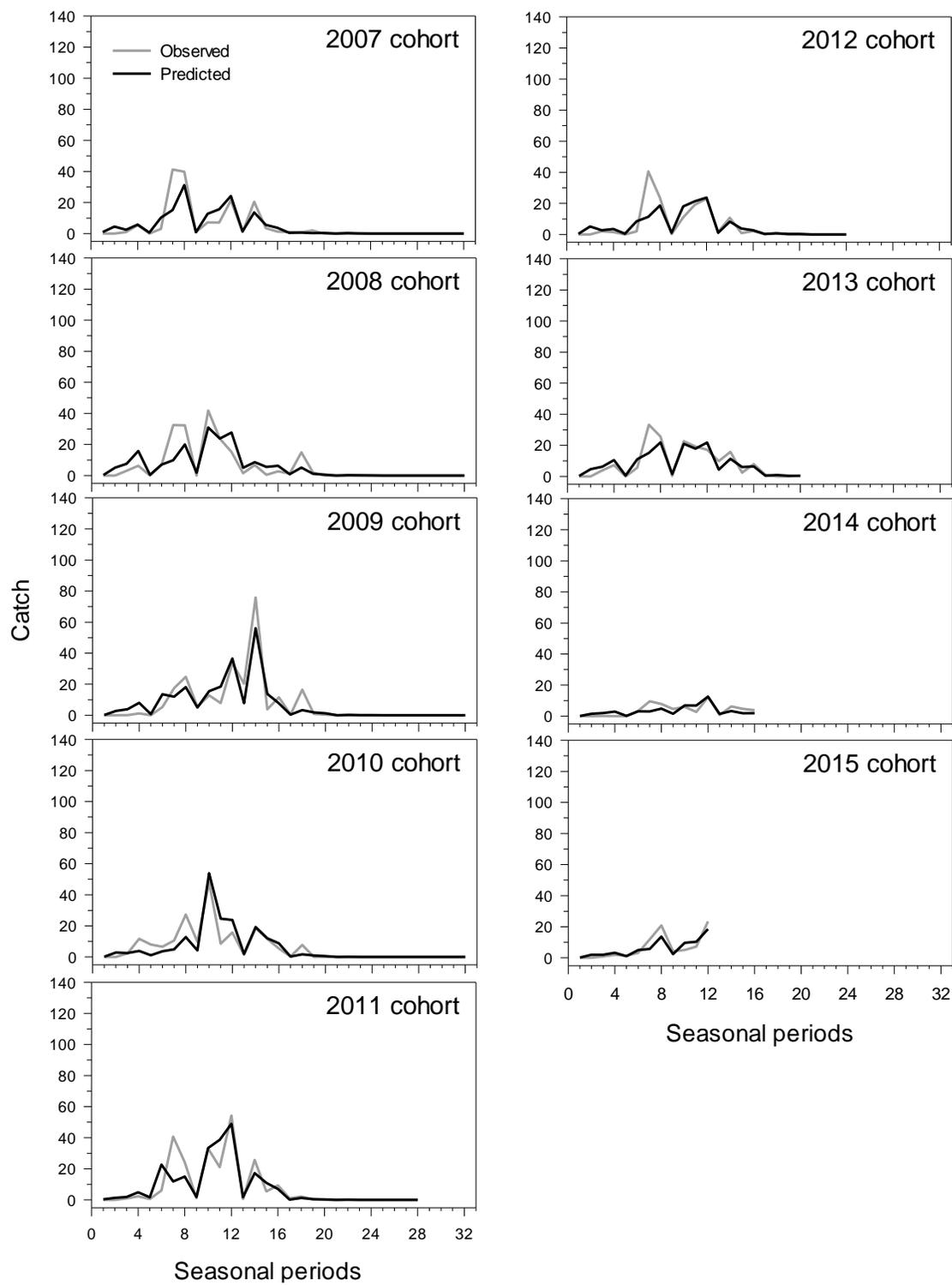


Figure A1. Estimates of catch by age from 2002 to 2017. Length data from North Carolina Division of Marine Fisheries (NCDMF) gill net survey in Pamlico Sound was converted to catch by age using an age-length key from concurrently collected age-length data from multiple state fisheries-independent surveys.

Figure A2. Survey predicted seasonal estimates of catch compared to the observed catches from fisheries-independent gill net survey data (IGNS) data for 19 cohorts tracked across 32 seasonal periods (8 years).





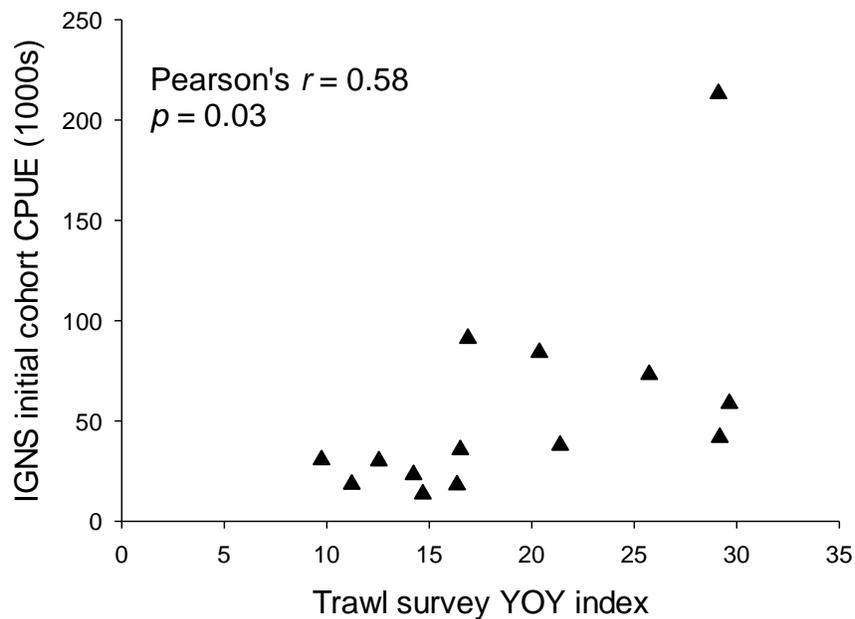


Figure A3. Initial cohort abundance CPUE estimated from IGNS compared to the NCDMF fisheries-independent Young-of-Year (YOY) trawl survey from Pamlico Sound during the years 2002 to 2015.

APPENDIX B. CHAPTER 3 PREDATOR DIET TABLES WITH REFERENCES AND FIGURES

Each predator diet table is organized by *Month* and *Year*. The *Regions* are SAB=South-Atlantic Bight (South of Cape Hatteras); MAB=Mid-Atlantic Bight (Cape Hatteras to New York/New Jersey state line); SNE=Southern New England (New York/New Jersey state line to Nantucket, Massachusetts). *Gears* include PN=pound net, SE=seine, HL=hook-and-line, EL=electrofishing, EX=explosives, FH=fish house, TR=trawl, GN=gill net, TM=trammel net, FY=fyke net, PS=purse seine, HA=handline, HP=harpoon, TL=trolling, CH=chumming, and RO=rotenone. The *Sample* is the number stomachs analyzed and the number of empty stomachs is in parentheses. *Mean* is the size in mm of predators with the standard error in parenthesis and *Range* is the minimum and maximum size of predators. The %*M* is the relative volume or percent mass that is the percent contribution of a food item to the total volume or mass of food found for the time period or group tabulated and parentheses are standard errors (Hyslop, 1980). *Reference* is the cited paper. Blank cells indicate the information was not ascertainable. Tables A1-A8 were not used in predator consumption models, and are followed by those used in simulations (Table A9-A12).

Table B1. Studies of spiny dogfish diets during summer months. These studies were not used in predator consumption simulations.

Month	Year	Region	Gear	Sample	Mean	Range	%M	Reference
June-Aug.	1973-1980	MAB	TR	22 (12)	312 (6) ^a	230-370 ^a	0 ^b	Rountree 2017
June-Aug.	1973-1980	SNE	TR	187 (78)	581 (2) ^a	230-1030 ^a	0 ^b	Rountree 2017
June-Aug.	1981-1990	MAB	TR	9 (8)	346 (8) ^a	310-400 ^a	0 ^c	Rountree 2017
June-Aug.	1981-1990	SNE	TR	10 (7)	934 (2) ^a	810-1010 ^a	0 ^c	Rountree 2017

^aTotal length; ^bCalculated by volume; ^cWet weight method

Table B2. Studies of summer flounder diets during summer months or where diet analyses were combined across multiple seasons including summer. These studies were not used in Monte Carlo simulations.

Month	Year	Region	Gear	Sample	Mean ⁱ	Range	%M	Reference
June-Oct.	1958-1959	SNE ^a	TR	1210 (404)		~240-700 ^{h,i}	0.2 ^k	Poole 1964
Mar.-Sept.	1971-1972	MAB ^b	TR; SN	42 (6)		201-476 ^j	0 ^l	Kimmel 1973
June-Aug.	1973-1980	SAB	TR	8 (8)	283 (18)	210-360 ⁱ	0 ^l	Rountree 2017
June-Aug.	1973-1980	SNE	TR	2 (2)	515 (135)	380-650 ⁱ	0 ^l	Rountree 2017
June-Aug.	1973-1980	MAB	TR	91 (50)	358 (9)	210-650 ⁱ	4.9 ^l	Rountree 2017
June-July	1986-1988	SAB ^c	TR; RO	51		50-313 ⁱ	0 ^l	Wenner et al. 1990
June-Aug.	1999	MAB ^d	TM	95 (40)		252-648 ⁱ	0 ^l	Manderson et al. 2000
June	2005	MAB ^e	TR	63 (21)		301-400 ⁱ	0 ^{m,n}	Wuenschel et al. 2013
June	2005	MAB ^e	TR	35 (9)		401-750 ⁱ	0 ^{m,n}	Wuenschel et al. 2013
July	2005	MAB ^e	TR	153 (79)		301-400 ⁱ	0 ^{m,n}	Wuenschel et al. 2013
July	2005	MAB ^e	TR	51 (39)		401-700 ⁱ	0 ^{m,n}	Wuenschel et al. 2013
Aug.	2005	MAB ^e	TR	245 (67)		301-400 ⁱ	0 ^{m,n}	Wuenschel et al. 2013
Aug.	2005	MAB ^e	TR	108 (46)		401-650 ⁱ	0 ^{m,n}	Wuenschel et al. 2013
July	2006	MAB ^f	TR	14		225-374 ⁱ	0 ^{h,k,n}	Buchheister and Latour 2011
July	2006	MAB ^f	TR	17		>375 ⁱ	0 ^{h,k,n}	Buchheister and Latour 2011
July	2007	MAB ^f	TR	29		225-374 ⁱ	0 ^{h,k,n}	Buchheister and Latour 2011
July	2007	MAB ^f	TR	14		>375 ⁱ	~18 ^{h,k,n}	Buchheister and Latour 2011
Apr.-Oct.	2007-2008	SNE ^g	TR; SN	141 (29)	382 (6.1)	260-649 ⁱ	3 ^{k,n}	Sagarese et al. 2011

^aGreat South Bay, New York; ^bMagothy Bay, Virginia; ^cSouth Carolina; ^dNavesink River, New Jersey; ^eCoastal New Jersey; ^fChesapeake Bay; ^gLong Island Bays, New York; ^hEstimated from figure; ⁱTotal length; ^jStandard length; ^kWet weight method; ^lCalculated by volume; ^mDry weight method; ⁿCluster sampling methodology for diet metric (Buckel et al. 1999b)

Table B3. Studies of bluefish diets during summer months or where diet analyses were combined across multiple seasons including summer. These studies were not used in predator consumption simulations.

Month	Year	Region	Gear	Sample	Mean	Range	%M	Reference
Aug.	1960	MAB; SAB ^a	SE; HL; FH	464 (215)		210-919 ^j	Trace ^{h,l}	Lassiter 1962
June	1961	MAB; SAB ^a	SE; HL; FH	68 (14)		210-919 ^j	0.2 ^l	Lassiter 1962
July	1961	MAB; SAB ^a	SE; HL; FH	72 (18)		210-919 ^j	0 ^{h,l}	Lassiter 1962
Aug.	1961	MAB; SAB ^a	SE; HL; FH	47 (26)		210-919 ^j	0 ^{h,l}	Lassiter 1962
June-Aug.	1973-1980	SAB	TR	50 (18)	259 (5) ^j	170-330 ^j	0 ^l	Rountree 2017
June-Aug.	1973-1980	SNE	TR	21 (6)	640 (19) ^j	480-800 ^j	0 ^l	Rountree 2017
June-Aug.	1977-1981	SAB ^b	HL	50		0-999	0 ^l	Naughton and Saloman 1985
June-Aug.	1981-1990	MAB	TR	6 (6)	480 (106) ^j	250-790 ^j	0 ^m	Rountree 2017
June-Aug.	1981-1990	SNE	TR	1 (0)	670 ^j	670 ^j	0 ^m	Rountree 2017
July-Aug.	1990-1991	MAB ^c	HL; TR; GN	24 (0)	Age-2+		0 ^{m,n}	Hartman 1993
Mar.-Dec.	1994	SNE ^d	GN	19 (4)		>350	0 ^m	Schulze 1996
May-Oct.	1998	MAB ^e	GN	~77 ⁱ	Age-1+	>300 ^j	0 ^m	Scharf et al. 2004
May-Oct.	1999	MAB ^e	GN	~117 ⁱ	Age-1+	>300 ^j	5.9 ^m	Scharf et al. 2004
June-Nov.	2001-2002	MAB ^f	GN;TR	2833 (1113)		78-395 ^k	1.2-4 ^{o,p,q}	Able et al. 2017
June	2005	MAB ^g	TR	6 (2)		301-732 ^k	0 ^{p,q}	Wuenschel et al. 2013
July	2005	MAB ^g	TR	3 (3)		301-732 ^k	0 ^{p,q}	Wuenschel et al. 2013
Aug.	2005	MAB ^g	TR	20 (3)		301-732 ^k	0 ^{p,q}	Wuenschel et al. 2013
Mar.-Nov.	2007-2014	MAB ^f	TR	10	Age-2+		0 ^{o,p}	VIMS ChesMMAP 2018

Table B3 (continued).

^aMorehead City to Hatteras, North Carolina; ^bSouth Carolina to North Carolina; ^cChesapeake Bay; ^dConnecticut River estuary; ^eNavesink River, New Jersey; ^fDelaware Bay creeks; ^gcoastal New Jersey; ^hOnly young-of-year and age-1 bluefish consumed weakfish; ⁱEstimated from figure; ^jTotal length; ^kFork length; ^lCalculated by volume; ^mWet weight method; ⁿReconstructed mass; ^oThe exact value for the five creek locations were 0.5, 4, 2.8, 1.3, and 1; ^pDry weight method; ^qCluster sampling methodology for diet metric (Buckel et al. 1999b)

Table B4. Studies of striped bass diets during summer months or where diet analyses were combined across multiple seasons including summer. These studies were not used in predator consumption simulations.

Month	Year	Region	Gear	Sample	Mean	Range	%M	Reference
Jan.-Dec.	1955-1959	MAB ^a	GN; PN; SN; EX	916 (319) ⁱ		170-1219 ⁱ	0 ^{k,l}	Griffin and Margraf 2003
Apr.-Nov.	1964	SNE ^b	SN	367 (78) ⁱ		275-940 ⁱ	0 ^m	Schaefer 1970
July-Aug.	1970-1971	MAB ^c	HL; GN; TR; SN	1094 ^j		125-714 ^j	3.13 ^m	Manooch 1973
May-June	1990-1991	MAB ^a	HL;GN	54	Age-3+		0 ^{k,l}	Hartman 1993
July-Aug.	1990-1991	MAB ^a	HL;GN	22	Age-3+		0 ^{k,l}	Hartman 1993
Mar.-Dec.	1994	SNE ^d	GN	646 (245)		>350	0 ^k	Schulze 1996
June-Oct.	1998	MAB ^e	GN	59 (7) ⁱ		212-670 ⁱ	0 ⁿ	Tupper and Able 2000
June-Aug.	1997-2000	SNE ^f	SN; TR	365 (192) ^j	675 ^j	305-1140 ^j	0 ^k	Nelson et al. 2003
May-Nov.	2001	MAB ^g	GN	235 ^j		140-740 ^j	0 ⁿ	Neuman et al. 2004
June-Nov.	2001-2002	MAB ^e	GN; TR	99 (23) ⁱ		>400 ⁱ	0 ^{n,o}	Able et al. 2017
Mar.-Nov.	2002-2015	MAB ^a	TR	838	Age-4+		0.01 ^{k,o,p}	VIMS ChesMMAAP 2018
Aug.	2005	MAB ^h	TR	27 (16) ⁱ		450-900 ⁱ	0 ^{n,o}	Wuenschel et al. 2013

^aChesapeake Bay; ^bLong Island, New York; ^cAlbemarle Sound, North Carolina; ^dConnecticut River estuary; ^eDelaware Bay;

^fMassachusetts; ^gHackensack River, New Jersey; ^hCoastal New Jersey; ⁱFork length; ^jTotal length; ^kWet weight method;

^lReconstructed mass; ^mCalculated by volume; ⁿDry weight method; ^oCluster sampling methodology for diet metric (Buckel et al. 1999b); ^pA weighted average of all 4+ fish %M

Table B5. Shark diet studies.

Season	Year	Region	Gear	Sample	Mean	Range	%M	Reference
<i>Atlantic angel shark (Squatina dumeril)</i>								
June-Aug.	1973-1980	MAB	TR	12 (4)	774 (97) ^h	320-1190 ^h	0 ^l	Rountree 2017
June-Aug.	1981-1990	MAB	TR	3 (1)	1163 (23) ^h	1120-1200 ^h	0 ^m	Rountree 2017
Sept.-Nov.	1973-1980	MAB	TR	8 (0)	631 (97) ^h	370-1200 ^h	0 ^l	Rountree 2017
Sept.-Nov.	1981-1990	MAB	TR	22 (4)	826 (63) ^h	370-1190 ^h	0 ^m	Rountree 2017
Mar.-May	1973-1980	MAB	TR	27 (1)	557 (22) ^h	349-890 ^h	0 ^l	Rountree 2017
Mar.-May	1973-1980	SAB	TR	5 (1)	732 (134) ^h	450-1100 ^h	0 ^l	Rountree 2017
Mar.-May	1981-1990	MAB	TR	32 (4)	562 (23) ^h	410-820 ^h	0 ^m	Rountree 2017
Mar.-May	1981-1990	SAB	TR	39 (17)	1042 (26) ^h	280-1180 ^h	2.05 ^m	Rountree 2017
<i>Atlantic sharpnose (Rhizoprionodon terraenovae)</i>								
June-Aug.	1973-1980	MAB	TR	11 (4)	779 (64) ^h	370-950 ^h	0 ^l	Rountree 2017
June-Aug.	1973-1980	SAB	TR	29 (11)	579 (50) ^h	340-1000 ^h	0 ^l	Rountree 2017
May-Oct.	1980-1992	MAB ^b	LL	208 (79)		810-1100 ^h	0 ^m	Gelsleichter et al. 1999
Sept.-Nov.	1973-1980	MAB	TR	5 (0)	948 (7) ^h	930-970 ^h	0 ^l	Rountree 2017
Sept.-Nov.	1973-1980	SAB	TR	24 (6)	669 (49) ^h	420-1000 ^h	0 ^l	Rountree 2017
Sept.-Nov.	1981-1990	MAB	TR	55 (12)	904 (13) ^h	500-990 ^h	0 ^m	Rountree 2017
Sept.-Nov.	1981-1990	SAB	TR	41 (12)	972 (21) ^h	430-1080 ^h	0 ^m	Rountree 2017
Mar.-May	1973-1980	SAB	TR	9 (1)	840 (29) ^h	700-940 ^h	0 ^l	Rountree 2017
Mar.-May	1981-1990	SAB	TR	9 (6)	1029 (90) ^h	760-1540 ^h	0 ^m	Rountree 2017
Spring & Fall ^a	2002-2015	MAB; SNE ^c	TR	6			52.7 ^{m,n}	VIMS NEAMAP 2018

Table B5 (continued).

Season	Year	Region	Gear	Sample	Mean	Range	%M	Reference
<i>sandbar (Carcharhinus plumbeus)</i>								
June-Aug.	1973-1980	SAB	TR	1 (1)	2040 ^h	2040 ^h	0 ^l	Rountree 2017
June-Aug.	2003-2006	MAB ^d	GN; LL	1169 (514)		~400-1250 ^{i,j}	6.2 ^m	McElroy 2009
Mar.-Sept.	1972-1984	MAB;SNE ^e	HL; LL	321	1380 ⁱ		0 ^l	Stillwell and Kohler 1993
May-Oct.	2001-2002	MAB ^f	GN; LL	89		<610 ^k	0 ^m	Ellis 2007
May-Oct.	2001-2002	MAB ^f	GN; LL	122		610-900 ^k	8.3 ^m	Ellis 2007
May-Oct.	2001-2002	MAB ^f	GN; LL	21		>900 ^k	0 ^m	Ellis 2007
Mar.-Nov.	2002-2010	MAB ^f	TR	26			3.3 ^{m,n}	VIMS ChesMMAP 2018
Sept.-Nov.	1973-1980	MAB	TR	2 (0)	895 (135) ^h	760-1470 ^h	0 ^l	Rountree 2017
Sept.-Nov.	1981-1990	MAB	TR	25 (9)	1242 (78) ^h	630-1750 ^h	0 ^m	Rountree 2017
Sept.-Nov.	1981-1990	SAB	TR	1 (0)	610 ^h	610 ^h	0 ^m	Rountree 2017
Mar.-May	1973-1980	SAB	TR	3 (0)	1317 (165) ^h	1040-1610 ^h	0 ^l	Rountree 2017
Mar.-May	1981-1990	MAB	TR	2 (2)	1165 (235) ^h	930-140 ^h	0 ^m	Rountree 2017
Mar.-May	1981-1990	SAB	TR	29 (9)	910 (50) ^h	630-1580 ^h	0 ^m	Rountree 2017
Spring & Fall ^a	2007	MAB; SNE ^c	TR	8			14.7 ^{m,n}	VIMS NEAMAP 2018
<i>blacknose shark (Carcharhinus acronotus)</i>								
Mar.-May	1981-1990	SAB	TR	1 (0)	1050 ^h	1050 ^h	0 ^m	Rountree 2017
Unknown	2003-2011	SAB ^g	GN; LL	90 (52)			3.8 ^{m,o}	Ford 2012

Table B5 (continued).

Season	Year	Region	Gear	Sample	Mean	Range	%M	Reference
<i>dusky shark (Carcharhinus obscurus)</i>								
June-Aug.	1973-1980	SAB	TR	2 (1)	665 (135) ^h	530-800 ^h	0 ^l	Rountree 2017
June-Aug.	1981-1990	MAB	TR	1 (0)	1070 ^h		0 ^m	Rountree 2017
Sept.-Nov.	1973-1980	MAB	TR	16 (4)	985 (34) ^h	830-1430 ^h	0 ^l	Rountree 2017
Sept.-Nov.	1973-1980	SAB	TR	1 (0)	2000 ^h		0 ^l	Rountree 2017
Sept.-Nov.	1981-1990	MAB	TR	12 (3)	1000 (81) ^h	490-1720 ^h	0 ^m	Rountree 2017
May-Oct.	1980-1992	MAB ^a	LL	153 (94)		850-3450 ^h	3.11 ^m	Gelsleichter et al. 1999
Mar.-May	1973-1980	SAB	TR	25 (5)	914 (56) ^h	630-2120 ^h	0 ^l	Rountree 2017
Mar.-May	1981-1990	MAB	TR	1 (0)	800 ^h		0 ^m	Rountree 2017
Mar.-May	1981-1990	SAB	TR	5 (0)	1194 (71) ^h	1000-1400 ^h	0 ^m	Rountree 2017
Mar.-May	1973-1980	MAB	TR	3 (0)	1040 (85) ^h	720-1360 ^h	6.8 ^l	Rountree 2017
<i>smooth dogfish (Mustelus canis)</i>								
June-Aug.	2003-2006	MAB ^c	LL	365 (7)		~300 to 1180 ^{i,j}	0.3 ^m	McElroy 2009
June-Aug.	1973-1980	MAB	TR	146 (7)	876 (14) ^h	400-1250 ^h	0 ^l	Rountree 2017
June-Aug.	1973-1980	SAB	TR	8 (1)	551 (63) ^h	290-930 ^h	0 ^l	Rountree 2017
June-Aug.	1973-1980	SNE	TR	46 (1)	962 (10) ^h	760-110 ^h	0 ^l	Rountree 2017
June-Aug.	1981-1990	MAB	TR	48 (1)	919 (19) ^h	630-1190 ^h	0 ^m	Rountree 2017
May-Oct.	1980-1992	MAB ^a	LL	64 (0)		460-1,260 ^{+h}	0 ^m	Gelsleichter et al. 1999
Mar.-Nov.	2002-2014	MAB ^f	TR	315			0 ^{m,n,p}	VIMS ChesMMAAP 2018
Sept.-Nov.	1973-1980	MAB	TR	226 (2)	891 (14) ^h	420-1020 ^h	0 ^l	Rountree 2017
Sept.-Nov.	1973-1980	SAB	TR	1 (0)	410 ^h		0 ^l	Rountree 2017
Sept.-Nov.	1973-1980	SNE	TR	59 (3)	893 (23) ^h	450-1180 ^h	0 ^l	Rountree 2017

Table B5 (continued).

Season	Year	Region	Gear	Sample	Mean	Range	%M	Reference
<i>smooth dogfish (Mustelus canis) continued</i>								
Sept.-Nov.	1981-1990	MAB	TR	1031 (38)	848 (7) ^h	430-130 ^h	0.06 ^m	Rountree 2017
Sept.-Nov.	1981-1990	SNE	TR	194 (38)	995 (6) ^h	720-1210 ^h	0 ^m	Rountree 2017
Mar.-May	1973-1980	MAB	TR	93 (4)	760 (17) ^h	480-1160 ^h	0 ^l	Rountree 2017
Mar.-May	1973-1980	SAB	TR	40 (2)	914 (25) ^h	540-1240 ^h	0 ^l	Rountree 2017
Mar.-May	1981-1990	MAB	TR	127 (23)	858 (16) ^h	470-1250 ^h	0 ^m	Rountree 2017
Mar.-May	1981-1990	SAB	TR	278 (41)	954 (9) ^h	510-1240 ^h	0.36 ^m	Rountree 2017
Spring & Fall ^a	2007-2014	MAB; SNE ^c	TR	2,790			0 ^{m,n,p}	VIMS NEAMAP 2018

^aSpring is March to May and Fall is September through November, ^bOffshore Chesapeake Bay, ^cCape Hatteras, North Carolina, to Cape Cod, Massachusetts, ^dDelaware Bay, ^eGeorges Bank to Cape Hatteras, North Carolina, ^fChesapeake Bay, ^gFlorida to North Carolina, ^hTotal length, ⁱFork length, ^jEstimated from figure, ^kPre-caudal length, ^lCalculated by volume, ^mWet weight method, ⁿCluster sampling method for diet metric (Buckel et al. 1999b), ^oResults questionable because weakfish were a diet prey across all stomachs, but were not a diet item in the male or female only %M analyses, ^pMay have had weakfish in "fish-other" category (always less than 3.9%), which we assumed to be 0.

Table B6. Ray diet studies.

Season	Year	Region	Gear	Sample	Mean ^d	Range ^d	%M	Reference
<i>smooth butterfly ray (Gymnura micrura)</i>								
Mar.-Nov.	2004-2014	MAB ^b	TR	44			7.3 ^{e,f}	VIMS ChesMMAP 2018
<i>spiny butterfly ray (Gymnura altavela)</i>								
June-Aug.	1973-1980	MAB	TR	7 (4)	561 (22)	510-680	0 ^g	Rountree 2017
Mar.-Nov.	2002-2014	MAB ^b	TR	72			4.2 ^{e,f}	VIMS ChesMMAP 2018
Sept.-Nov.	1981-1990	MAB	TR	15 (9)	981 (93)	580-1660	0 ^e	Rountree 2017
Mar.-May	1973-1980	SAB	TR	1 (0)	1120		0 ^g	Rountree 2017
Mar.-May	1981-1990	SAB	TR	27 (23)	964 (83)	570-1990	0 ^e	Rountree 2017
<i>clearnose skate (Raja eglanteria)</i>								
June-Aug.	1973-1980	MAB	TR	21 (2)	546 (12)	430-620	0 ^g	Rountree 2017
June-Aug.	1973-1980	SAB	TR	1 (0)	540		0 ^g	Rountree 2017
June-Aug.	1981-1990	MAB	TR	3 (0)	663 (35)	610-730	0 ^e	Rountree 2017
Mar.-Nov.	2002-2014	MAB ^b	TR	940			3.3 ^{e,f}	VIMS ChesMMAP 2018
Sept.-Nov.	1973-1980	MAB	TR	6 (0)	525 (32)	430-600	0 ^g	Rountree 2017
Sept.-Nov.	1973-1980	SAB	TR	1 (0)	444		0 ^g	Rountree 2017
Sept.-Nov.	1981-1990	MAB	TR	52 (14)	590 (12)	380-720	0 ^e	Rountree 2017
Sept.-Nov.	1981-1990	SAB	TR	7 (0)	584 (16)	520-630	0 ^e	Rountree 2017
Mar.-May	1973-1980	MAB	TR	13 (4)	544 (25)	380-640	0 ^g	Rountree 2017
Mar.-May	1973-1980	SAB	TR	2 (0)	575 (35)		43.6 ^g	Rountree 2017
Mar.-May	1981-1990	MAB	TR	53 (16)	584 (13)	270-720	0 ^e	Rountree 2017
Spring & Fall ^a	2007-2014	MAB; SNE ^c	TR	3,430			1 ^{e,f}	VIMS NEAMAP 2018

Table B6 (continued).

^aSpring is March to May and Fall is September through November, ^bChesapeake Bay, ^cCape Hatteras, North Carolina, to Cape Cod, Massachusetts, ^dTotal length, ^eWet weight method, ^fCluster sampling method for diet metric (Buckel et al. 1999b), ^gCalculated by volume

Table B7. Bony fish predator diet studies.

Season	Year	Region	Gear	Sample	Mean	Range	%M	Reference
<i>bluefin tuna (Thunnus thynnus)</i>								
June-Sept.	1970-1975	MAB; SNE ^c	HL; PS	220 (142)		<50 kg	0 ^s	Mason 1976
June-July	1986	MAB ^d	HL	97 (25)	900 (130) ^{o,p}	700-1320 ^p	0 ^s	Eggleston and Bochenek 1990
July-Oct.	1988-1992	SNE ^e	PS; HL; HA; HP	210 (27)	2210 (380) ^{o,p}		0 ^t	Chase 2002
July-Oct.	1988-1992	SNE ^f	PS; HL; HA; HP	57 (8)	1240 (300) ^{o,p}		0 ^t	Chase 2002
May-Sept.	1988-1989	MAB ^g	HL	220 (60)	840 ^p	544-1421 ^p	0 ^s	Barr 1991
Nov.-Jan.	2003-2006	SAB ^h	HL	124 (24)	1957 (5.2) ^p	1854-2057 ^p	0 ^t	Butler et al. 2010
Nov.-Jan.	2003-2006 ^b	SAB ^h	HL	324 (72)	2240 (7.1) ^p	>2057 ^p	0.31 ^t	Butler et al. 2010
Mar.-Apr.; July	1965-1966	SAB; MAB; SNE ⁱ	LL; PS	219 (148)		520-2670 ^p	0 ^s	Dragovich 1970
Unknown	1977	MAB; SNE ^j	PS; TL	296 (81)		<100 kg	0 ^{s,u}	Holliday 1978
Unknown	1977	SNE	CH	54 (2)		>270 kg	<1 ^s	Holliday 1978
<i>goosefish (Lophius piscatorius)</i>								
June-Aug.	1973-1980	MAB	TR	20 (7)	390 (56) ^q	70-1010 ^q	0 ^s	Rountree 2017
June-Aug.	1973-1980	SNE	TR	42 (21)	524 (38) ^q	140-1200 ^q	0 ^s	Rountree 2017
June-Aug.	1977	MAB ^k	TR	45 (4)			0 ^s	Sedberry 1983
June-Aug.	1981-1990	SNE	TR	6 (1)	465 (54) ^q	350-650 ^q	0 ^t	Rountree 2017
Aug.	1983	SNE	TR	40 (17)		201-400 ^q	0 ^{s,v}	Armstrong et al. 1996
Aug.	1983	SNE	TR	72 (33)		301-600 ^q	0 ^{s,v}	Armstrong et al. 1996
Aug.	1983	SNE	TR	38 (16)		>600 ^q	0 ^{s,v}	Armstrong et al. 1996
Sept.-Nov.	1973-1980	MAB	TR	29 (20)	469 (36) ^q	170-900 ^q	0 ^s	Rountree 2017

Table B7 (continued).

Season	Year	Region	Gear	Sample	Mean	Range	%M	Reference
<i>goosefish (Lophius piscatorius) continued</i>								
Sept.-Nov.	1973-1980	SNE	TR	121 (72)	540 (19) ^q	80-1019 ^q	0 ^s	Rountree 2017
Sept.-Nov.	1976	MAB ^k	TR	37 (15)			0 ^s	Sedberry 1983
Sept.-Nov.	1981-1990	MAB	TR	120 (65)	292 (11) ^q	130-730 ^q	0 ^t	Rountree 2017
Sept.-Nov.	1981-1990	SNE	TR	160 (90)	443 (16) ^q	130-960 ^q	0 ^t	Rountree 2017
Dec.-Feb.	1977	MAB ^k	TR	40 (9)			0 ^s	Sedberry 1983
Dec.-Feb.	1981-1990	MAB	TR	2 (0)	490 (160) ^q	330-650 ^q	0 ^t	Rountree 2017
Jan.-Apr.	2006-2008	SNE	GN	398 (265)	134 ^q	710-1180 ^q	0 ^t	Johnson et al. 2008
Jan.-Apr.	2006-2008	MAB	GN	291 (188)	103 ^q	710-1180 ^q	0 ^t	Johnson et al. 2008
Mar.-May	1977	MAB ^k	TR	18 (2)			0 ^s	Sedberry 1983
Mar.-May	1973-1980	MAB	TR	58 (36)	512 (31) ^q	160-1010 ^q	0 ^s	Rountree 2017
Mar.-May	1973-1980	SAB	TR	1 (1)	610 ^q	610 ^q	0 ^s	Rountree 2017
Mar.-May	1973-1980	SNE	TR	78 (38)	573 (27) ^q	210-1240 ^q	0 ^s	Rountree 2017
Mar.-May	1981-1990	MAB	TR	237 (162)	503 (15) ^q	130-1120 ^q	0 ^t	Rountree 2017
Mar.-May	1981-1990	SNE	TR	115 (83)	486 (16) ^q	110-930 ^q	0 ^t	Rountree 2017
Mar.-May	1981-1990	SAB	TR	33 (16)	770 (25) ^q	500-1000 ^q	0.6 ^t	Rountree 2017
Spring and Fall ^a	2007-2014	MAB; SNE ^l	TR	102	Age-0+		1.3 ^{t,w}	VIMS NEAMAP 2018
<i>Atlantic cutlassfish (Trichiurus lepturus)</i>								
June-Aug.	1973-1980	SAB	TR	11 (0)	485 (9) ^q	440-540 ^q	0 ^s	Rountree 2017
Mar.-Nov.	2006-2014	MAB ^m	TR	32			0 ^{t,w}	VIMS ChesMMAP 2018

Table B7 (continued).

Season	Year	Region	Gear	Sample	Mean	Range	%M	Reference
<i>cobia (Rachycentron canadum)</i>								
June-July	1997	MAB ^m	HL	114 (36)		370-1410 ^r	0 ^s	Arendt et al. 2001
Mar.-Aug.	1989-1990	SAB ⁿ	HL; TR; SN; TR	140 (30)		390-1420 ^r	0 ^t	Smith 1995
Sept.-Nov.	1981-1990	SAB	TR	4 (0)	770 (127) ^q	580-1130 ^q	0 ^t	Rountree 2017
Mar.-May	1973-1980	SAB	TR	3 (0)	947 (53) ^q	840-1000 ^q	0 ^s	Rountree 2017
Mar.-May	1981-1990	SAB	TR	2 (1)	995 (15) ^q	980-1010 ^q	0 ^t	Rountree 2017

^aSpring is March to May and Fall is September through November, ^bWeakfish only eaten from December 2005 to January 2006.

^cVirginia to Massachusetts, ^dVirginia, ^eGreat South Channel, Massachusetts, ^fSouth of Martha's Vineyard, Massachusetts, ^gRudee Inlet and Wachapreague, Virginia, ^hBeaufort and Morehead City, North Carolina, ⁱCarolinas to New York, ^jNorth Carolina to Massachusetts, ^kCoastal New Jersey and Delaware Bay, ^lCape Hatteras, North Carolina, to Cape Cod, Massachusetts, ^mChesapeake Bay, ⁿBeaufort to Hatteras, North Carolina, ^oStandard deviation in parenthesis, ^pCurved fork length, ^qTotal length, ^rFork length, ^sCalculated by volume, ^tWet weight method, ^uCombined purse seining and trolling together because both were 0 %M for weakfish, ^vNet feeding observed, therefore all "fresh" fish were removed from the analysis, ^wCluster sampling method for diet metric (Buckel et al. 1999b).

Table B8. Weakfish diet studies.

Month	Year	Region	Gear	Sample	Mean ⁱ	Range ⁱ	%M	Reference
<i>Summer</i>								
June-Aug.	1973-1980	MAB	TR	56 (21)	221 (18)	80-660	0 ^j	Rountree 2017
June-Aug.	1973-1980	SAB	TR	34 (6)	269 (5)	210-330	0 ^j	Rountree 2017
June-Jan.	1967-1970	SAB ^b	GN; SN; TR; PN	2159 (1342)	Age-0 to 4		2.6 ^j	Merriner 1975
July-Aug.	1990-1991	MAB ^c	TR; HL	96	Age-1		0 ^{k,l}	Hartman 1993
May-June	1990-1991	MAB ^c	TR; HL	27	Age-2		0 ^{k,l}	Hartman 1993
June-Nov.	2001-2002	MAB ^d	GN; TR	135 (18)		>300	0-25.7 ^{m,n,o}	Able et al. 2017
June	2005	MAB ^e	TR	1 (0)		365-565	0 ^{m,n}	Wuenschel et al. 2013
Aug.	2005	MAB ^e	TR	7 (2)		365-565	0 ^{m,n}	Wuenschel et al. 2013
Mar.-Nov.	2002-2014	MAB ^c	TR	3387	Age-1+		4.85 ^{l,n,p}	VIMS ChesMMAp 2018
<i>Fall</i>								
Sept.-Nov.	1973-1980	SAB	TR	56 (12)	246 (5)	160-340	0 ^j	Rountree 2017
Sept.-Nov.	1973-1980	SNE	TR	12 (1)	424 (62)	150-690	0 ^j	Rountree 2017
Sept.-Nov.	1973-1980	MAB	TR	171 (18)	258 (11)	70-750	0.5 ^j	Rountree 2017
Sept.-Nov.	1981-1990	MAB	TR	652 (201)	259 (4)	80-790	0.2 ^l	Rountree 2017
Sept.-Nov.	1981-1990	SAB	TR	18 (12)	247 (6)	190-311	0 ^l	Rountree 2017
Sept.-Nov.	1981-1990	SNE	TR	10 (1)	320 (75)	150-770	0 ^l	Rountree 2017
Sept.-Oct.	1990-1991	MAB ^c	TR; HL	452	Age-1		4.8 ^{k,l}	Hartman 1993
Sept.-Oct.	1990-1991	MAB ^c	TR; HL	27	Age-2		0 ^{k,l}	Hartman 1993
Nov.-Dec.	1990-1991	MAB ^c	TR; HL	16	Age-1		0.1 ^{k,l}	Hartman 1993
Sept.	2005	MAB ^e	TR	5 (0)		365-565	0 ^{m,n}	Wuenschel et al. 2013
Nov.	2005	MAB ^e	TR	86 (20)		365-565	0 ^{m,n}	Wuenschel et al. 2013

Table B8 (continued).

Month	Year	Region	Gear	Sample	Meanⁱ	Rangeⁱ	%M	Reference
<i>Spring</i>								
May	1919	MAB ^f	SN	30 (9)		240-390	0 ^j	Welsh and Breder 1923
Spring & Fall ^a	1969-1972	MAB; SNE ^g	TR	21 (2)			0 ^l	Maurer and Bowman 1975
Mar.-May	1973-1980	MAB	TR	18 (7)	284 (26)	140-550	0 ^j	Rountree 2017
Mar.-May	1973-1980	SAB	TR	20 (4)	305 (13)	190-420	0 ^j	Rountree 2017
Mar.-May	1981-1990	MAB	TR	39 (29)	369 (21)	160-590	0 ^l	Rountree 2017
Mar.-May	1981-1990	SAB	TR	40 (21)	238 (11)	140-510	0 ^l	Rountree 2017
Spring & Fall ^a	2007-2014	MAB; SNE ^h	TR	1,837	Age-1+		0.62 ^{l,n,p}	VIMS NEAMAP 2018

^aSpring is March to May and Fall is September through November; ^bPamlico Sound and Morehead City, North Carolina; ^cChesapeake Bay; ^dDelaware Bay; ^eCoastal New Jersey; ^fCape May, New Jersey; ^gCape Hatteras, North Carolina, to Nantucket, Massachusetts; ^hCape Hatteras, North Carolina, to Cape Cod, Massachusetts; ⁱTotal length; ^jCalculated by volume; ^kReconstructed mass; ^lWet weight method; ^mDry weight method; ⁿCluster sampling methodology for diet metric (Buckel et al. 1999b); ^oThe exact value for the five creek locations were 25.7, 16.3, 1.3, 0, and 6.4; ^pA weighted average of all 1+ fish %M

Table B9. Fall through spring spiny dogfish diet studies that were used in predator consumption simulations.

Month	Year	Region	Gear	Sample	Mean	Range	%M	Reference
<i>Fall</i>								
Sept.-Nov.	1973-1980	MAB	TR	59 (25)	538 (37) ^b	250-1050 ^b	0 ^c	Rountree 2017
Sept.-Nov.	1973-1980	SNE	TR	222 (97)	713 (14) ^b	260-1030 ^b	0 ^c	Rountree 2017
Sept.-Nov.	1981-1990	MAB	TR	143 (70)	366 (13) ^b	240-880 ^b	0 ^d	Rountree 2017
Sept.-Nov.	1981-1990	SNE	TR	1145 (594)	735 (5) ^b	240-1090 ^b	0 ^d	Rountree 2017
<i>Winter</i>								
Dec.-Feb.	1981-1990	MAB	TR	48 (32)	793 (11) ^b	680-1010 ^b	0 ^d	Rountree 2017
Feb.-Mar.	2006-2007	MAB ^a	TR	73 (24)			23.54 ^{d,e}	Bangley 2011
Feb.	2010	MAB ^a	TR	242 (53)			0 ^d	Bangley 2011
<i>Spring</i>								
Mar.-May	1973-1980	MAB	TR	389 (228)	679 (13) ^b	220-1070 ^b	0 ^c	Rountree 2017
Mar.-May	1973-1980	SAB	TR	17 (0)	934 (12) ^b	830-1000 ^b	0 ^c	Rountree 2017
Mar.-May	1973-1980	SNE	TR	146 (82)	584 (21) ^b	240-1030 ^b	0 ^c	Rountree 2017
Mar.-May	1981-1990	MAB	TR	6270 (3180)	761 (2) ^b	200-1130 ^b	0.26 ^d	Rountree 2017
Mar.-May	1981-1990	SAB	TR	382 (129)	858 (5) ^b	650-1090 ^b	3.98 ^d	Rountree 2017
Mar.-May	1981-1990	SNE	TR	2338 (1342)	663 (5) ^b	230-1140 ^b	0 ^d	Rountree 2017
Mar.	2010	MAB ^a	TR	132 (<25)		>650 ^b	0 ^d	Bangley 2011

^aHatteras inlet, North Carolina to Virginia; ^bTotal length; ^cCalculated by volume; ^dWet weight method; ^eSpiny dogfish were observed net feeding on weakfish at one station on the 2007 cruise

Table B10. Fall through spring summer flounder diet studies that were used in predator consumption simulations.

Month	Year	Region	Gear	Sample	Mean ^e	Range ^e	%M	Reference
<i>Fall</i>								
Sept.-Nov.	1973-1980	SAB	TR	51 (40)	275 (6)	180-400	0 ^f	Rountree 2017
Sept.-Nov.	1973-1980	SNE	TR	64 (26)	488 (11)	280-720	0 ^f	Rountree 2017
Sept.-Nov.	1981-1990	SAB	TR	3 (1)	260 (36)	210-330	0 ^g	Rountree 2017
Sept.-Nov.	1981-1990	SNE	TR	116 (57)	416 (9)	190-700	0 ^g	Rountree 2017
Sept.-Nov.	1981-1990	MAB	TR	694 (400)	339 (3)	150-620	0 ^g	Rountree 2017
Sept.	2005	MAB ^b	TR	117 (43)		301-400	0 ^{h,i}	Wuenschel et al. 2013
Sept.	2005	MAB ^b	TR	22 (914)		401-700	0 ^{h,i}	Wuenschel et al. 2013
Oct.	2005	MAB ^b	TR	134 (55)		301-400	9.5 ^{h,i}	Wuenschel et al. 2013
Oct.	2005	MAB ^b	TR	26 (13)		401-650	26.7 ^{h,i}	Wuenschel et al. 2013
Sept.	2006	MAB ^c	TR	49		225-374	~15 ^{g,i,j}	Buchheister and Latour 2011
Sept.	2006	MAB ^c	TR	16		>375	0 ^{g,i,j}	Buchheister and Latour 2011
Nov.	2006	MAB ^c	TR	97		225-374	~7 ^{g,i,j}	Buchheister and Latour 2011
Nov.	2006	MAB ^c	TR	16		>375	~62 ^{g,i,j}	Buchheister and Latour 2011
Nov.	2007	MAB ^c	TR	94		225-374	~5 ^{g,i,j}	Buchheister and Latour 2011
Nov.	2007	MAB ^c	TR	13		>375	~9 ^{g,i,j}	Buchheister and Latour 2011

Table B10 (continued).

Month	Year	Region	Gear	Sample	Mean ^e	Range ^e	%M	Reference
<i>Spring</i>								
Mar.-May	1973-1980	MAB	TR	153 (118)	337 (9)	150-770	0 ^f	Rountree 2017
Mar.-May	1973-1980	SAB	TR	13 (12)	278 (29)	210-520	0 ^f	Rountree 2017
Mar.-May	1973-1980	SNE	TR	19 (17)	279 (29)	410-820	0 ^f	Rountree 2017
Mar.-May	1981-1990	SAB	TR	45 (35)	280 (29)	180-510	0 ^g	Rountree 2017
Mar.-May	1981-1990	SNE	TR	97 (90)	281 (29)	180-670	0 ^g	Rountree 2017
Mar.-May	1981-1990	MAB	TR	350 (263)	282 (29)	170-720	0.7 ^g	Rountree 2017
Mar.	2006	MAB ^c	TR	16		225-374	0 ^{g,i,j}	Buchheister and Latour 2011
Mar.	2006	MAB ^c	TR	19		>375	0 ^{g,i,j}	Buchheister and Latour 2011
May	2006	MAB ^c	TR	23		225-374	0 ^{g,i,j}	Buchheister and Latour 2011
May	2006	MAB ^c	TR	31		>375	~45 ^{g,i,j}	Buchheister and Latour 2011
Mar.	2007	MAB ^c	TR	12		225-374	0 ^{g,i,j}	Buchheister and Latour 2011
May	2007	MAB ^c	TR	32		225-374	0 ^{g,i,j}	Buchheister and Latour 2011
May	2007	MAB ^c	TR	21		>375	~37 ^{g,i,j}	Buchheister and Latour 2011
Spring & Fall ^a	2007-2014	MAB; SNE ^d	TR	759	Age-3+		2.4 ^{g,i,k}	VIMS NEAMAP 2018

^aSpring is March to May and Fall is September through November; ^bCoastal New Jersey; ^cChesapeake Bay; ^dCape Hatteras, North Carolina, to Cape Cod, Massachusetts; ^eTotal length; ^fCalculated by volume; ^gWet weight method; ^hDry weight method;

ⁱCluster sampling methodology for diet metric (Buckel et al. 1999b); ^jEstimated from figure; ^kA weighted average of all 4+ fish %M

Table B11. Fall through spring bluefish diet studies that were used in predator consumption simulations.

Month	Year	Region	Gear	Sample	Mean	Range	%M	Reference
<i>Fall</i>								
Sept.	1960	MAB; SAB ^c	SE; HL; FH	53 (30)		210-919 ^k	0 ^m	Lassiter 1962
Oct.	1960	MAB; SAB ^c	SE; HL; FH	106 (55)		210-919 ^k	0 ^m	Lassiter 1962
Sept.-Nov.	1973-1980 ^b	MAB	TR	219 (41)	335 (10) ^k	90-780 ^k	0.2 ^m	Rountree 2017
Sept.-Nov.	1973-1980	SAB	TR	66 (23)	260 (5) ^k	180-350 ^k	0 ^m	Rountree 2017
Sept.-Nov.	1973-1980	SNE	TR	24 (4)	466 (39) ^k	190-760 ^k	0 ^m	Rountree 2017
Sept.-Nov.	1981-1990	MAB	TR	1184 (494)	386 (4) ^k	80-810 ^k	0.4 ⁿ	Rountree 2017
Sept.-Oct.	1994	MAB; SAB; SNE ^d	TR	65 (20)	451 (18) ^l	310-780 ^l	3.0 (12.9) ^{n,o}	Buckel et al. 1999a
Sept.-Oct.	1995	MAB; SAB; SNE ^d	TR	116 (32)	391 (11) ^l	310-730 ^l	0.1 (0.6) ^{n,o}	Buckel et al. 1999a
Sept.-Nov.	1977-1981	SAB ^e	HL	114		0-999	0 ^m	Naughton and Saloman 1984
Sept.-Nov.	1981-1990	SNE	TR	229 (75)	513 (13) ^k	120-880 ^k	0 ⁿ	Rountree 2017
Sept.-Oct.	1990-1991	MAB ^f	HL; TR; GN	47 (0)	Age-2+		0 ^{m,p}	Hartman 1993 Wuenschel et al.
Sept.	2005	MAB ^g	TR	5 (3)		301-732 ^l	0 ^{o,q}	2013 Wuenschel et al.
Oct.	2005	MAB ^g	TR	67 (15)		301-732 ^l	25.2 ^{o,q}	2013
<i>Winter</i>								
Dec.	1960	MAB; SAB ^c	SE; HL; FH	32 (15)		210-919 ^k	Trace ^{m,r}	Lassiter 1962

^aSpring is March to May and Fall is September through November; ^bBluefish consumption of weakfish only found in 1979;

^cMorehead City to Hatteras, North Carolina; ^dCape Hatteras, North Carolina, to Montauk, New York; ^eSouth Carolina to North Carolina; ^fChesapeake Bay; ^gCoastal New Jersey; ^hCape Hatteras, North Carolina, to Nantucket, Massachusetts; ⁱCape Hatteras, North Carolina, to Cape Cod, Massachusetts; ^jUsed max sample size in Monte Carlo model; ^kTotal length; ^lFork length; ^mCalculated by volume; ⁿWet weight method; ^oCluster sampling methodology for diet metric (Buckel et al. 1999b); ^pReconstructed mass; ^qDry weight method; ^rUsed 0.01 as trace in Monte Carlo model

Table B12. Fall through spring striped bass diet studies that were used in predator consumption simulations.

Month	Year	Region	Gear	Sample	Mean	Range	%M	Reference
<i>Fall</i>								
Sept.-Nov.	1981-1990	MAB	TR	2 (0)	645 (5) ⁱ	640-650 ⁱ	0 ^k	Rountree 2017
Sept.-Oct.	1990-1991	MAB ^b	HL;GN	27	Age-3+		0 ^{k,l}	Hartman 1993
Nov.-Dec.	1990-1991	MAB ^b	HL;GN	43	Age-3+		0 ^{k,l}	Hartman 1993
Sept.	1997-2000	SNE ^c	SN; TR	106 (39)	675 ⁱ	305-1140 ⁱ	0 ^k	Nelson et al. 2003
Oct.	2005	MAB ^d	TR	89 (52)		400-1050 ^j	6.9 ^{m,n}	Wuenschel et al. 2013
<i>Winter</i>								
Feb.-Mar.	1970	SAB; MAB ^e	TR; GN	50 (7)		424-1090 ^j	29.4 ^o	Holland and Yelverton 1973
Jan.-Feb.	1990-1991	MAB ^b	HL;GN	27	Age-3+		0 ^{k,l}	Hartman 1993
Jan.	1994	MAB ^f	TR	73 (1)	613.1 (72.3) ⁱ	425-765 ⁱ	0 ^k	Overton et al. 2008
Jan.	1995	MAB ^f	TR	19 (0)	639.7 (57.0) ⁱ	525-718 ⁱ	0 ^k	Overton et al. 2008
Jan.	1996	MAB ^f	TR	34 (9)	805.9 (75.6) ⁱ	666-955 ⁱ	0 ^k	Overton et al. 2008
Jan.	2000	MAB ^f	TR	50 (8)	561.3 (90.5) ⁱ	465-770 ⁱ	0 ^k	Overton et al. 2008
Jan.	2002	MAB ^f	TR	60 (14)	616.2 (180.0) ⁱ	373-941 ⁱ	1.4 ^k	Overton et al. 2008
Jan.	2003	MAB ^f	TR	19 (3)	836.6 (80.6) ⁱ	745-953 ⁱ	0 ^k	Overton et al. 2008
Dec.-Mar.	2004-2005	MAB ^f	FH	253 (195)	881.2 (94.5) ⁱ	509-1150 ⁱ	3.6 ^k	Overton et al. 2008
Dec.-Mar.	2005-2006	MAB ^f	FH	450 (324)	914.6 (87.9) ⁱ	720-1200 ⁱ	0.4 ^k	Overton et al. 2008
Dec.-Mar.	2006-2007	MAB ^f	FH	140 (27)	994.2 (99.0) ⁱ	760-1250 ⁱ	1.1 ^k	Overton et al. 2008
Jan.	2006-2007	MAB ^g	TR	64 (5)			0 ^k	Bangley 2010

Table B12 (continued).

Month	Year	Region	Gear	Sample	Mean	Range	%M	Reference
<i>Spring</i>								
Mar.-May	1973-1980	MAB	TR	1 (0)	1020 ⁱ		0 ^o	Rountree 2017
Mar.-May	1981-1990	MAB	TR	12 (7)	836 (53) ⁱ	600-1180 ⁱ	0 ^k	Rountree 2017
Mar.-Apr.	1990-1991	MAB ^b	HL;GN FH; GN;	38	Age-3+		0 ^{k,l}	Hartman 1993 Walter and Austin 2003
Mar.-May	1997-1998	MAB ^b	HL; EL; FY	1225 (537)	653.7 ⁱ	458-1151 ⁱ	2.51 ^k	2003
Spring & Fall ^a	2002-2015	MAB; SNE ^h	TR	227	Age-4+		0 ^{k,n,p}	VIMS NEAMAP 2018

^aSpring is March to May and Fall is September through November; ^bChesapeake Bay; ^cMassachusetts; ^dCoastal New Jersey; ^eCape Lookout, North Carolina, to Cape Charles, Virginia; ^fOregon inlet, North Carolina, to Chesapeake Bay, Virginia; ^gHatteras inlet, North Carolina to Virginia; ^hCape Hatteras, North Carolina, to Cape Cod, Massachusetts; ⁱTotal length; ^jFork length; ^kWet weight method; ^lReconstructed mass; ^mDry weight method; ⁿCluster sampling methodology for diet metric (Buckel et al. 1999b); ^oCalculated by volume; ^pA weighted average of all 4+ fish

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FIGURES

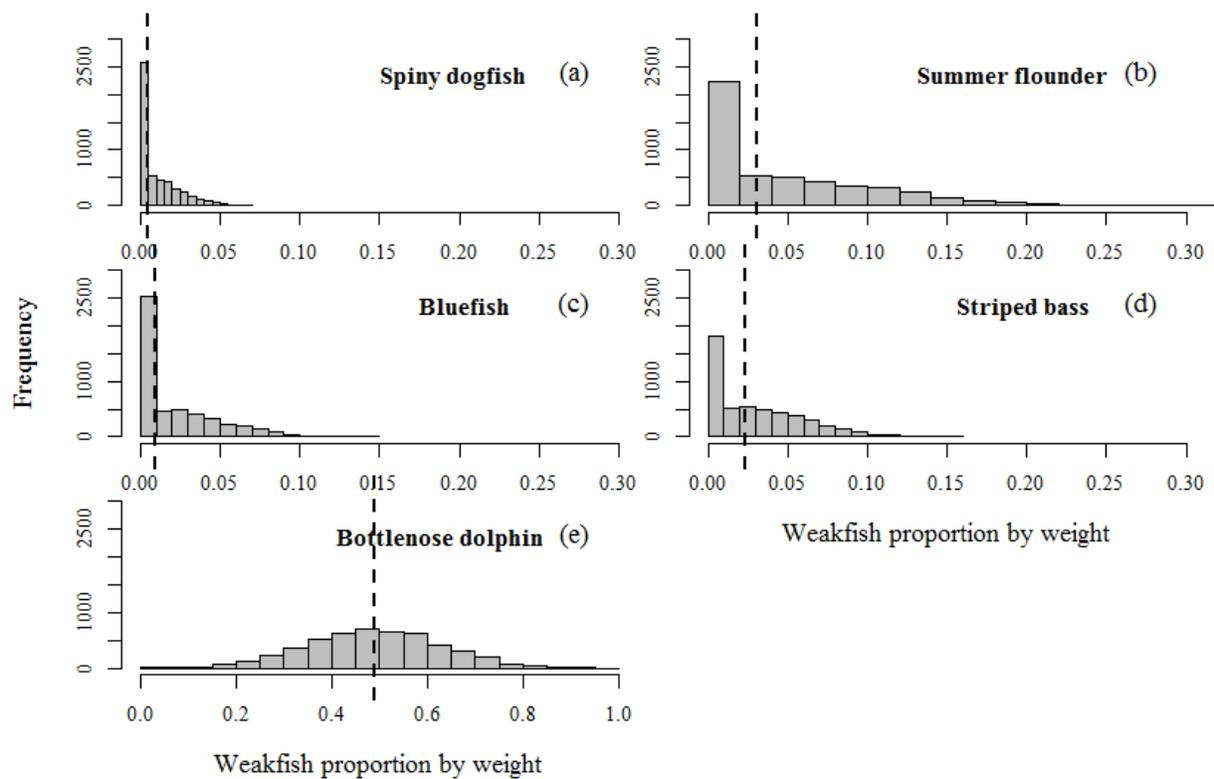


Figure B1. Comparison of truncated normal distributions for modelled weakfish predators. All negative values were changed to 0s. The dashed vertical line represents the median from 5000 Monte Carlo simulations and is the same as the weighted average mean from predator diet studies.

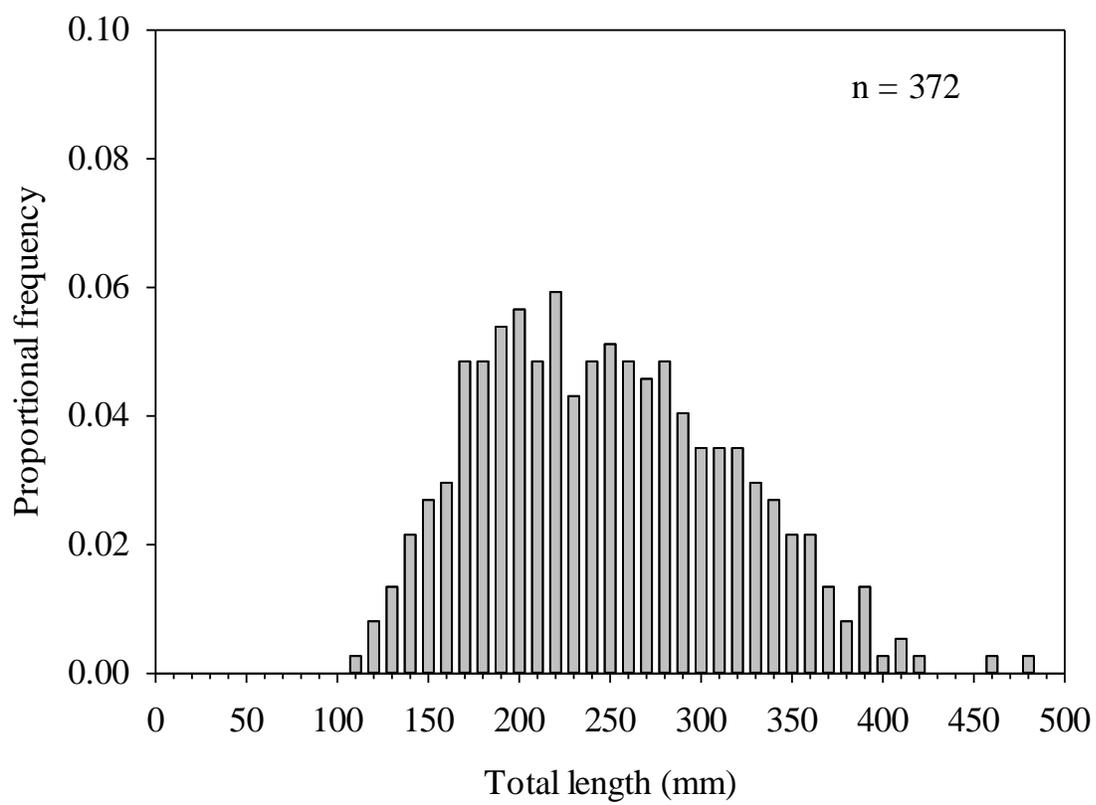


Figure B2. Length-frequency distributions of weakfish consumed by coastal bottlenose dolphin in North Carolina waters.

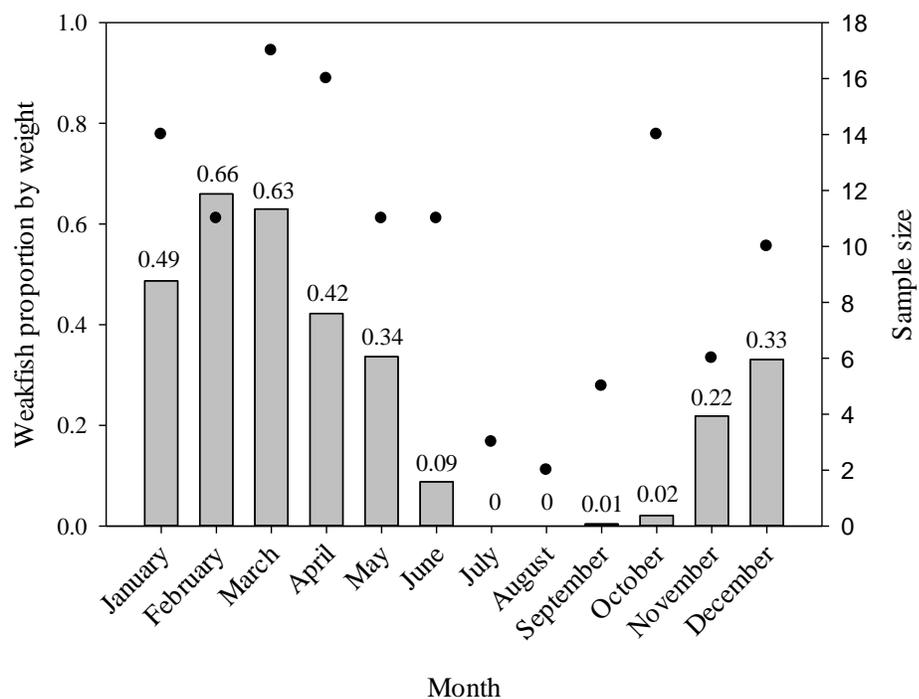


Figure B3. Comparison of bottlenose dolphin W of weakfish in diet by month. The exact W is listed above bars and the black dots are the sample size for each month. Only the W from November to April were used in the predator consumption simulations.

APPENDIX C. CHAPTER 3 MONTE CARLO SIMULATION CODE

```

#Estimate predator consumption of weakfish based on Monte Carlo simulations

#Code developed by Jacob Krause

#All code was run through the RStudio interface

#####
####Libraries####
#####

# install.packages("mc2d") #rpert distribution function
# install.packages("colorspace") #Color pallete
# install.packages("truncnorm") #truncnorm distribution function
library (mc2d)
library (colorspace)
library (truncnorm)

#####
####Set working directory to save files####
#####

#Change working directory for your computer
setwd("~/your working directory/")

#Reproduce exact results
set.seed(123) #Comment out line or change "123" to use different random numbers in
distributions

#####
####Bottlenose dolphin####
#####

#Estimate Northern North Carolina Estuarine System (NNCES) bottlenose dolphin stock from
1982-2014
#2000 population estimate was 919, 2006 population estimate was 950, and 2013 population
estimate was 823
#Taken from page 159 of the U.S. Atlantic and Gulf of Mexico Marine Mammal Stock
Assessments-2017

time<-seq(1982,2014,1) #Create vector representing time frame
NNCES_years_1982to2005<-rep(919,24) #Repeat 2000 population estimate for 1982 to 2005
NNCES_years_2006to2012<-rep(950,7) #Repeat 2006 population estimate for 2006 to 2012
NNCES_years_2013to2014<-rep(823,2) #Repeat 2013 population estimate for 2012 to 2014

```

```

estimate<-
c(NNCES_years_1982to2005,NNCES_years_2006to2012,NNCES_years_2013to2014)
#Combine yearly estimates into vector
NNCES_years<-as.data.frame(cbind(time,estimate)) #Combine columns into a dataframe

#Estimate Southern North Carolina Estuarine System (SNCES) bottlenose dolphin stock from
1982-2014
#2000 population estimate was 141 and 2006 population estimate was 188
#Taken from page 173 of the U.S. Atlantic and Gulf of Mexico Marine Mammal Stock
Assessments-2017

time<-seq(1982,2014,1) #Create vector representing time frame
SNCES_years_1982to2005<-rep(141,26) #Repeat 2000 population estimate for 1982 to 2000
SNCES_years_2006to2014<-rep(188,7) #Repeat 2006 population estimate for 2006 to 2012
estimate<-c(SNCES_years_1982to2005,SNCES_years_2006to2014) #Combine yearly estimates
into vector
SNCES_years<-as.data.frame(cbind(time,estimate)) #Combine columns into a dataframe

#Estimate Western North Atlantic Northern Migratory (NMCSES) bottlenose dolphin stock from
1982-2014
#Decriments or adds dolphin population size from 2010 to 2016 estimates (population = 6639 in
2016, 15630 in 2011, 14314 in 2010)
#by picking a net productivity rate from a uniform distribution between 0 and 0.4
#Taken from page 98 and 99 (Table 1) of the U.S. Atlantic and Gulf of Mexico Marine Mammal
Stock Assessments-2017

v <- Reduce(function(v, x) v- v*log(1+runif(1,0,0.04)), x=numeric(3), init=6639,
accumulate=TRUE) #Estimates NMCS population from 2016-2013
NMCS_years_2016to2013<-cbind(step = 0:3, v) #Binds yearly estimates
v <- Reduce(function(v, x) v + v*log(1+runif(1,0,0.04)), x=numeric(1), init=15630,
accumulate=TRUE) #Estimate NMCS population for 2012
NMCS_years_2012to2013<-cbind(step = 0:1, v)
v <- Reduce(function(v, x) v- v*log(1+runif(1,0,0.04)), x=numeric(22), init=14314,
accumulate=TRUE) #Estimates NMCS population from 2010-1988
NMCS_years_1988to2010<-cbind(step = 0:22, v)
#1987 population estimate based on a 10 to 50% increase from 1988. In 1988, a mass mortality
event decreased the stock size between 10 and 50%.
NMCS_years_1987<-
NMCS_years_1988to2010[22,2]+NMCS_years_1988to2010[22,2]*log(1+runif(1,0.1,0.5))
#Estimate 1987 NMCS population
v <- Reduce(function(v, x) v- v*log(1+runif(1,0,0.04)), x=numeric(5), init=NMCS_years_1987,
accumulate=TRUE) #Estimates NMCS population from 1987-1982
NMCS_years_1982to1987<-cbind(step = 0:5, v)
NMCS_years<-
as.data.frame(rbind(NMCS_years_2016to2013[3:4,],NMCS_years_2012to2013[2:1,],NMCS_je

```

```

ars_1988to2010,NMCS_years_1982to1987)) #Binds all population estimates into a vector
withina dataframe
NMCS_years$time<-rev(seq(1982,2014,1)) #Adds time columns to data frame
NMCS_years<- NMCS_years[dim(NMCS_years)[1]:1,] #Reorder from 1982-2014
NMCS_years$estimate<-NMCS_years$v #Rename column
NMCS_years<-NMCS_years[,-c(1:2)] #Remove unwanted step column

#Bottlenose dolphin Monte Carlo function
{
Ttconsumption<-function(n,year){

#Cpop=B*P*DR*Wp*T

#Cpop=consumption of predator population of weakfish (kg)
#B=biomass (kg) of predator*
#P=proportion of predator population overlapping with weakfish winter range
#DR=estimate of predator daily ration (kg prey/kg predator/day)
#W=proportion by weight of weakfish in predator stomach
#T=the time (days) that predator and weakfish are both present in the weakfish overwintering
grounds
#*Depending on stock assessment data format, the biomass (b) can be split into Bp * Bw, where
Bp is the predator abundance estimate and Bw is predator weight abundance depending on
predator data source

#Generate values:

###Bp###
#Northern North Carolina Estuarine System Stock
#CV decided by population estimate year
if(year>=1982 & year<=2005){
  NNCES_year_CV<-0.13 #2000 CV
} else {
if(year>=2006 & year<=2012){
  NNCES_year_CV<-0.23 #2006 CV
} else {
  NNCES_year_CV<-0.06 #2013 CV
}
}

NNCES_year_estimate<-NNCES_years$estimate[NNCES_years$time==year] #Matches year
with correct population estimate

#rpert distribution

```

```

Bp_NNCES<-rpert(n,min=NNCES_year_estimate-
(NNCES_year_CV*NNCES_year_estimate), mode = NNCES_year_estimate, max =
NNCES_year_estimate+(NNCES_year_CV*NNCES_year_estimate))
#Minimum estimate (min)=mean-CV*mode
#Most likely estimate (mode)=mean
#Most optimistic estimate (max)=mean+CV*mode

#Southern North Carolina Estuarine System Stock
#CV decided by population estimate year
if(year>=1982 & year<=2000){
  SNCES_year_CV<-0.15 #2000 CV
} else {
  SNCES_year_CV<-0.19 #2013 DV
}

SNCES_year_estimate<-SNCES_years$estimate[SNCES_years$time==year] #Matches year
with correct population estimate

#rpert distribution
Bp_SNCES<-rpert(n,min=SNCES_year_estimate-(SNCES_year_CV*SNCES_year_estimate),
mode = SNCES_year_estimate, max =
SNCES_year_estimate+(SNCES_year_CV*SNCES_year_estimate))

#Western North Atlantic Northern Migratory Stock
#CV decided by population estimate year using if else function
if(year>=1982 & year<=2010){
  NMCS_year_CV<-0.74 #2011 CV
} else {
if(year>=2011 & year<=2012){
  NMCS_year_CV<-0.29 #2012 CV
} else {
  NMCS_year_CV<-0.41 #2016 CV
}
}
}
NMCS_year_estimate<-NMCS_years$estimate[NMCS_years$time==year] #Matches year with
correct population estimate

Bp_NMCS<-rpert(n,min=NMCS_year_estimate-(NMCS_year_CV*NMCS_year_estimate),
mode = NMCS_year_estimate, max =
NMCS_year_estimate+(NMCS_year_CV*NMCS_year_estimate))

#Combine populations
Bp<-Bp_NNCES+Bp_SNCES+Bp_NMCS

###Bw###
#Predator weight (kg) same for both stocks

```

```

Bw_CV<-0.3 #Coefficient of variation
Bw_mean<-126.5 #Average mass
Bw<-rpert(n,min=Bw_mean-(0.3)*(Bw_mean), mode = Bw_mean, max =
Bw_mean+(0.3)*(Bw_mean))
#Minimum estimate (min)=mean-CV*mean;
#Most likely estimate (mode)=mean
#Most optimistic estimate (max)=mean+CV*mode

###P###
P<-runif(n,0.7,0.9)

###DR###
DR<-rpert(n,min=0.029, mode = 0.046, max = 0.061)
#Minimum estimate min=0.029
#Most likely estimate (mode)=0.046
#Most optimistic estimate max=0.061

###W###
#Only used months of November to April when NMCS is known to be in North Carolina waters
Tt_samplesize<-c(6,10,14,11,17,16) #Sample sizes by month
Tt_samplesize<-Tt_samplesize/sum(Tt_samplesize) # Divide by sum to equal 1
Tt_W<-c(21.9,33.1,48.7,66.0,63.0,42.2)
Tt_W_average<-sum(Tt_samplesize*Tt_W)/sum(Tt_samplesize) #Average %Mass
Tt_variaNNCES<-sum(Tt_samplesize*(Tt_W-Tt_W_average)^2) #VariaNNCES
Tt_sd<-sqrt(Tt_variaNNCES) #Standard deviation

#Truncated normal distribution
W<-rtruncnorm(n, a=-Inf, b=1, mean = Tt_W_average/100, sd = Tt_sd/100) #Divide by 100 to
get proportion
#a=lower bound
#b=upper bound that is truncated at 1
W[W<0]=0 #All negative values from the distribution are changed to 0s

###T###
T<-runif(n,90,180)
#Number of days of overlap

#Calculate consumption:
Cpop<-Bp*Bw*P*DR*W*T/1000 #Divide by 1000 to convert to metric tonnes

#Return result:
return(list("Cpop"=Cpop, "Bp"=Bp,"Bp_NNCES"=Bp_NNCES,"Bp_NMCS"=Bp_NMCS,
"Bw"=Bw, "P"=P, "DR"=DR, "W"=W, "T"=T))
}
}

```

```

#Summary of all years
Tt_output<-matrix(0,nrow(NNCES_years),19) #Create empty matrix
Tt_output[,1]<-seq(1982,2014,1) #First column is years
colnames(Tt_output)<-c("Year","Min.", "1st Qu.", "Median", "Mean", "3rd Qu.", "Max.", "10%
CI", "90% CI", "scale(Bp)", "scale(Bw)", "scale(P)", "scale(DR)", "scale(W)",
"scale(T)", "Dolphin Stock all", "Dolphin Stock NNCES", "Dolphin Stock NMCS", "Bw")
#Column names
name_list<-as.character(seq(1982,2014,1)) #Convert list to character for use in for loop

#Loop to extract data for every year
for(i in 1982:2014){
TtConsumption_Samples5000<-Ttconsumption(5000,i)
Tt_output[i-1981,2:7]<-summary(TtConsumption_Samples5000$Cpop) #Minimum, 1st
Quantile, Median, Mean, 3rd Quantile, Maximum
Tt_output[i-1981,8:9]<-quantile(TtConsumption_Samples5000$Cpop,c(0.1,0.9))
#ConfideNNCES interval quantiles at 10 and 90%
sensitivity <- lm(scale(Cpop) ~ scale(Bp) + scale(Bw) + scale(P) + scale(DR) + scale(W)+
scale(T), data=TtConsumption_Samples5000) #Sensitivity analysis regression
Tt_output[i-1981,10:15]<-summary(sensitivity)$coefficients[2:7,1] #Regression coefficients
from sensitivity analysis
Tt_output[i-1981,16]<-mean(TtConsumption_Samples5000$Bp) #Dolphin population all
Tt_output[i-1981,17]<-mean(TtConsumption_Samples5000$Bp_NNCES) #Dolphin population
NNCES
Tt_output[i-1981,18]<-mean(TtConsumption_Samples5000$Bp_NMCS) #Dolphin population
NMCS
Tt_output[i-1981,19]<-mean(TtConsumption_Samples5000$Bw) #Dolphin biomass
#Write files to directory
currentDate<-Sys.Date()#Saves files with current timestamp
TtConsumptioncsvFileName<-paste("_TtConsumption_",currentDate, ".csv", sep="") #File name
for Monte Carlo outputs
write.csv(TtConsumption_Samples5000, paste(i,TtConsumptioncsvFileName, sep = "")) #Write
csv for 5000 Cpop estimates for each year
Tt_outputcsvFileName<-paste("Tt_output_Summary_",currentDate, ".csv", sep="") #File name
for summary output
write.csv(Tt_output,Tt_outputcsvFileName) #Write csv of summary data across all years
}

```

```
#####
####Spiny dogfish####
#####

#Make vector of population estimates
time<-(seq(1982,2014,1)) #Create vector of years
#Ontogenetic diet shift happens at 650 mm, but stock assessment category only had dogfish from
360 to 790 mm.
#Biomass in 000s of metric tonnes of male, female, and unsexed spiny dogfish over 800 mm
from 1980-2013
#(Years 1981-2008 Table 1 page 30 in biological reference points for spiny dogfish)
#(Years 2009-2013 from page 22 Table 7 in Update on the Status of Spiny Dogfish in 2015 and
Projected Harvests at the Fmsy Proxy and Pstar of 40%)
Sa_800mm_Total<-
c(294,168,489,108,143,443,195,310,459,203,471,250,322,263,142,132,230,101,50,83,98,73,94,
87,50,87,283,177,271,170,179,241,399,203)
#Estimates were based on 3 year average of that year and the 2 previous
mav <- function(x,n){filter(x,rep(1/n,n), sides=1)} #Function to calculate 3 year moving average
av_estimate<-mav(Sa_800mm_Total,3)*1000*1000 #Convert averages to kg
estimate<-av_estimate[3:34] #Remove years 1980 and 1981
#No estimate from 2014 was available, instead estimated as the average biomass of 2012 and
2013
estimate<-append(estimate, mean(av_estimate[33:34]), after = length(32))
Sa_years<-as.data.frame(cbind(time,estimate))

#Spiny dogfish Monte Carlo simulation
{
Saconsumption<-function(n,year){

####B###
#30% CV used to calculate a standard deviation (sd) by multiplying 0.3 by the mean to get 1 sd
above or below the mean
Sa_year_CV<-0.3
Sa_year_estimate<-Sa_years$estimate[Sa_years$time==year] #Matches biomass estimates with
correct year

B<-rpert(n,min=Sa_year_estimate-(Sa_year_CV*Sa_year_estimate), mode = Sa_year_estimate,
max = Sa_year_estimate+(Sa_year_CV*Sa_year_estimate))

####P###
P<-runif(n,0.05,0.3)

####DR###
DR<-rpert(n,min=0.005, mode = 0.0056, max = 0.0062)

####W###
```

```

Sa_samplesize<-c(59,222,143,1145,48,73,242,389,17,146,6270,382,2338,132)
Sa_samplesize<-Sa_samplesize/sum(Sa_samplesize)
Sa_W<-c(0,0,0,0,23.54,0,0,0,0.26,3.98,0,0)
Sa_W_average<-sum(Sa_samplesize*Sa_W)/sum(Sa_samplesize)
Sa_variaNNCES<-sum(Sa_samplesize*(Sa_W-Sa_W_average)^2)
Sa_sd<-sqrt(Sa_variaNNCES)

#Truncated normal distribution
W<-rtruncnorm(n, a=-Inf, b=1, mean = Sa_W_average/100, sd = Sa_sd/100)
W[W<0]=0

###T###
T<-runif(n,60,150)

#Calculate consumption:
Cpop<-B*P*DR*W*T/1000

#Return result:
return(list("Cpop"=Cpop, "B"=B, "P"=P, "DR"=DR, "W"=W, "T"=T))
}
}

#Summary of all years
Sa_output<-matrix(0,nrow(Sa_years),15)
Sa_output[,1]<-seq(1982,2014,1)
colnames(Sa_output)<-c("Year", "Min.", "1st Qu.", "Median", "Mean", "3rd Qu.", "Max.", "10%
CI", "90% CI", "scale(B)", "scale(P)", "scale(DR)", "scale(W)", "scale(T)", "Spiny dogfish
biomass")
name_list<-as.character(seq(1982,2014,1))

#Loop to extract data for every year
for(i in 1982:2014){
  SaConsumption_Samples5000<-Saconsumption(5000,i)
  Sa_output[i-1981,2:7]<-summary(SaConsumption_Samples5000$Cpop)
  Sa_output[i-1981,8:9]<-quantile(SaConsumption_Samples5000$Cpop,c(0.1,0.9))
  sensitivity <- lm(scale(Cpop) ~ scale(B) + scale(P) + scale(DR) + scale(W)+ scale(T),
data=SaConsumption_Samples5000)
  Sa_output[i-1981,10:14]<-summary(sensitivity)$coefficients[2:6,1]
  Sa_output[i-1981,15]<-mean(SaConsumption_Samples5000$B) #Spiny dogfish biomass
  #Write files to directory
  currentDate<-Sys.Date()
  SaConsumptioncsvFileName<-paste("_SaConsumption_",currentDate, ".csv", sep="")
  write.csv(SaConsumption_Samples5000, paste(i,SaConsumptioncsvFileName, sep = ""))
  Sa_outputcsvFileName<-paste("Sa_output_Summary_",currentDate, ".csv", sep="")
  write.csv(Sa_output,Sa_outputcsvFileName)
}

```

```
#####
####Summer Flounder####
#####
```

```
#Make vector of population estimates
time<-(seq(1982,2014,1)) #Add column for years
```

```
#Biomass based on age 3+ summer flounder
```

```
#Mean weight (kg) at age of summer flounder catch (Table A36 in Summer Flounder Stock
Assessment for 2013)
```

```
Pd_wt_age3<-
```

```
c(1.447,1.075,1.046,1.109,1.16,1.14,1.13,1.04,1.162,1.186,1.226,1.478,1.349,1.058,1.076,0.862,
0.842,0.876,1.079,0.97,0.956,1.026,0.969,0.922,0.964,0.941,0.87,0.837,0.758,0.676,0.742)
```

```
Pd_wt_age4<-
```

```
c(1.906,1.257,1.5,1.726,1.739,1.941,1.738,1.474,1.538,1.812,1.392,1.671,2.092,1.643,1.629,1.2
44,1.324,1.423,1.783,1.454,1.382,1.526,1.361,1.187,1.271,1.279,1.162,1.084,1.047,0.998,1.022)
```

```
Pd_wt_age5<-
```

```
c(2.787,1.495,2.163,2.297,1.994,2.862,2.486,2.248,2.143,2.519,2.687,1.865,2.763,2.645,2.341,2
.257,2.444,1.944,2.702,2.171,2.107,2.072,1.788,1.512,1.661,1.734,1.559,1.497,1.398,1.501,1.47
3)
```

```
Pd_wt_age6<-
```

```
c(2.668,2.567,3.456,2.671,3.31,3.378,3.888,2.408,3.024,2.975,2.302,2.816,3.399,3.624,2.727,2.
609,2.745,2.736,2.645,2.611,2.734,2.794,2.409,1.897,2.24,2.22,1.92,1.943,1.899,1.864,1.845)
```

```
Pd_wt_age7plus<-
```

```
c(3.831,3.351,3.886,4.721,3.382,3.344,3.762,2.709,4.305,3.66,4.456,4.49,3.703,4.094,4.914,3.4
29,3.815,3.471,3.025,3.736,3.744,3.357,3.183,2.452,3.138,2.831,2.507,2.703,2.734,2.457,2.328)
```

```
Pd_wt_agematrix<-
```

```
as.matrix(cbind(Pd_wt_age3,Pd_wt_age4,Pd_wt_age5,Pd_wt_age6,Pd_wt_age7plus))
```

```
#Combine weights by age-class into a matrix
```

```
#Estimates of population abundance (000s) by age (Table A89 in Summer Flounder Stock
Assessment for 2013)
```

```
Pd_abundance3<-
```

```
c(2360,6350,4054,3140,3887,1656,2880,1788,1444,472,1585,1991,1866,2432,2627,7037,13028
,10380,10397,11094,10104,14481,15505,16143,11804,17947,11224,14922,15611,18984,21353)
```

```
Pd_abundance4<-
```

```
c(807,636,1220,652,557,533,286,283,267,351,91,311,431,436,322,511,2308,4647,4525,4474,52
80,5086,7473,7614,7868,6513,10535,7144,9559,9936,11819)
```

```
Pd_abundance5<-
```

```
c(252,285,175,293,169,119,135,48,64,87,96,25,93,136,59,64,170,838,2084,1994,2158,2689,265
9,3727,3777,4404,3898,6003,4120,5448,5405)
```

```
Pd_abundance6<-
```

```
c(172,96,87,47,84,41,34,26,12,22,26,29,8,32,24,14,24,69,403,989,1027,1164,1483,1407,1961,2
206,2718,2253,3513,2382,3001)
```

```

Pd_abundance7plus<-
c(124,103,52,33,20,23,16,8,8,6,8,10,12,6,7,8,9,14,40,214,633,921,1183,1455,1556,2100,2698,3
275,3401,4179,3855)
Pd_abundancematrix<-
as.matrix(cbind(Pd_abundance3,Pd_abundance4,Pd_abundance5,Pd_abundance6,Pd_abundance
7plus)) #Combine abundances by age-class into a matrix

#Calculate biomass
Pd_biomass<-Pd_wt_agematrix*Pd_abundancematrix #Estimate biomass by multiplying weight
and abundance matrices
colnames(Pd_biomass)<-
c("Pd_biomass3","Pd_biomass4","Pd_biomass5","Pd_biomass6","Pd_biomass7plus") #Create
column names
estimate<-rowSums(Pd_biomass)*1000 #Convert to kg
#No estimates for 2013-2014, calculated average of 2011 and 2012 for 2013-2014
post2012estimates<-rep(mean(estimate[30:31]),2) #Estimate 2013 and 2014 biomass from 2011
and 2012 average
estimate<-append(estimate,post2012estimates) #Add 2013-2014 estimates to biomass vector
Pd_years<-as.data.frame(cbind(time,estimate)) #Bind time and biomass columns

#Summer flounder Monte Carlo simulation

Pdconsumption<-function(n,year){

  ###B###
  #30% CV used to calculate a sd by multiplying 0.3 by the mean to get 1 sd above or below the
  mean
  Pd_year_CV<-0.3
  Pd_year_estimate<-Pd_years$estimate[Pd_years$time==year] #Matches estimate with year

  B<-rpert(n,min=Pd_year_estimate-(Pd_year_CV*Pd_year_estimate), mode =
Pd_year_estimate, max = Pd_year_estimate+(Pd_year_CV*Pd_year_estimate))

  ###P###
  P<-runif(n,0.2,0.4)

  ###DR###
  #Taken from Chesapeake Bay Stock ecopath model that had a Q/B of 2.9 for summer flounder
  Pd_QB<-2.9
  Pd_DR<-((Pd_years[1,2]*Pd_QB)/365)/Pd_years[1,2] #Convert Q/B to daily ration of 0.0079
  #30% CV used to calculate a sd by multiplying 0.3 by the mean to get 1 sd above or below the
  mean
  Pd_DR_sd<-Pd_DR*0.3 #Calculated sd is 0.0019

  DR<-rpert(n,min=Pd_DR-Pd_DR_sd, mode = Pd_DR, max = Pd_DR+Pd_DR_sd)

```

```

####W###
Pd_samplesize<-
c(51,64,3,116,694,117,22,134,26,49,16,97,16,94,13,153,13,19,45,97,350,16,19,23,31,12,32,21,7
59)
Pd_samplesize<-Pd_samplesize/sum(Pd_samplesize)
Pd_W<-c(0,0,0,0,0,0,9.5,26.7,15,0,7,62,5,9,0,0,0,0,0,0.7,0,0,0,45,0,0,37,2.4)
Pd_W_average<-sum(Pd_samplesize*Pd_W)/sum(Pd_samplesize)
Pd_variaNNCES<-sum(Pd_samplesize*(Pd_W-Pd_W_average)^2)
Pd_sd<-sqrt(Pd_variaNNCES)

#Truncated normal distribution
W<-rtruncnorm(n, a=-Inf, b=1, mean = Pd_W_average/100, sd = Pd_sd/100) #Divide by 100 to
get proportion
W[W<0]=0 #All negative values from the distribution are changed to 0s

####T###
T<-runif(n,60,150)

#Calculate consumption:
Cpop<-B*P*DR*W*T/1000

#Return result:
return(list("Cpop"=Cpop, "B"=B, "P"=P, "DR"=DR, "W"=W, "T"=T))
}

#Summary of all years
Pd_output<-matrix(0,nrow(Pd_years),15)
Pd_output[,1]<-seq(1982,2014,1)
colnames(Pd_output)<-c("Year","Min.", "1st Qu.", "Median", "Mean", "3rd Qu.", "Max.", "10%
CI", "90% CI", "scale(B)", "scale(P)", "scale(DR)", "scale(W)", "scale(T)", "Striped bass
biomass")
name_list<-as.character(seq(1982,2014,1))

#Loop to extract data for every year
for(i in 1982:2014){
  PdConsumption_samples5000<-Pdconsumption(5000,i)
  Pd_output[i-1981,2:7]<-summary(PdConsumption_samples5000$Cpop)
  Pd_output[i-1981,8:9]<-quantile(PdConsumption_samples5000$Cpop,c(0.1,0.9))
  sensitivity <- lm(scale(Cpop) ~ scale(B) + scale(P) + scale(DR) + scale(W)+ scale(T),
data=PdConsumption_samples5000)
  Pd_output[i-1981,10:14]<-summary(sensitivity)$coefficients[2:6,1]
  Pd_output[i-1981,15]<-mean(PdConsumption_samples5000$B) #Striped bass biomass
estimates
  #Write files to directory
  currentDate<-Sys.Date()
  PdConsumptioncsvFileName<-paste("_PdConsumption_",currentDate,".csv",sep="")

```

```
write.csv(PdConsumption_samples5000, paste(i,PdConsumptioncsvFileName, sep = ""))
Pd_outputcsvFileName<-paste("Pd_output_Summary_",currentDate,".csv",sep="")
write.csv(Pd_output,Pd_outputcsvFileName)
}
```

```
#####
####Bluefish####
#####

#Make vector of population estimates
time<-(seq(1982,2014,1)) #Add column for years

#Biomass estimates (t) are for age 2 to 6+ fish (~size when they can eat >100 mm weakfish)
#Taken from Table B7.6 in Bluefish Benchmark Stock Assessment for 2015
Ps_biomass2<-
c(19394,24664,13274,8760,6455,8672,15706,5154,8780,4342,5466,8921,6854,6886,8253,7381,
11268,6484,11229,10078,12566,7956,11720,12808,9362,8771,5985,6058,6528,6532)
Ps_biomass3<-
c(17701,21352,26463,13711,10386,7511,9140,17654,8825,11093,5913,6775,10991,8612,10026
,13634,11901,15941,9497,15650,13995,16360,8956,14972,15433,10048,9929,7292,9513,10345
)
Ps_biomass4<-
c(21571,16946,19571,21749,12689,11642,6646,8604,17371,9769,12493,6476,7372,13373,1110
1,14489,18702,14325,18521,10581,17917,14018,16923,10848,17070,15306,9661,11305,8827,1
2595)
Ps_biomass5<-
c(16102,18224,14256,15076,18388,11133,8864,5518,7713,15898,9168,12443,5797,7414,13459
,9924,13688,15505,12161,18209,11184,15936,12774,16332,11507,17286,19428,13513,15114,1
1981)
Ps_biomass6plus<-
c(129412,105194,89313,69457,62279,68090,55627,47325,41197,41647,45786,41051,44230,42
329,42198,48063,45906,42087,45885,46537,62611,47828,50569,56216,59551,65126,72867,811
11,87347,77925)
Ps_biomassmatrix<-
as.matrix(cbind(Ps_biomass2,Ps_biomass3,Ps_biomass4,Ps_biomass5,Ps_biomass6plus))
#Combine biomass by age-class into a matrix
estimate<-rowSums(Ps_biomassmatrix)*1000 #Convert to kg
#No estimates for 1982-1984, years estimated from average of 1985 and 1986
pre1985estimates<-rep(mean(estimate[1:2]),3) #Estimate 1982-1984 base on average of 1985
and 1986
estimate<-append(pre1985estimates,estimate) #Add 1982-1984 estimates to biomass vector
Ps_years<-as.data.frame(cbind(time,estimate)) #Combine year and biomass estimate columns

#Bluefish Monte Carlo simulation

Psconsumption<-function(n,year){

  ###B###
  #30% CV used to calculate a sd by multiplying 0.3 by the mean to get 1 sd above or below the
  mean
  Ps_year_CV<-0.3
```

```

Ps_year_estimate<-Ps_years$estimate[Ps_years$time==year] #Matches estimate with year

B<-rpert(n,min=Ps_year_estimate-(Ps_year_CV*Ps_year_estimate), mode = Ps_year_estimate,
max = Ps_year_estimate+(Ps_year_CV*Ps_year_estimate))

####P###
P<-runif(n,0.3,0.7)

####DR###
#Taken from Chesapeake Bay Stock ecopath model that had a Q/B of 3.3 for large bluefish
Ps_QB<-3.3
Ps_DR<-((Ps_years[1,2]*Ps_QB)/365)/Ps_years[1,2] #Convert Q/B to calculate daily ration of
0.0094
#30% CV used to calculate a sd by multiplying 0.3 by the mean to get 1 sd above or below the
mean
Ps_DR_sd<-Ps_DR*0.3 #Calculated sd is 0.0027

DR<-rpert(n,min=Ps_DR-Ps_DR_sd, mode = Ps_DR, max = Ps_DR+Ps_DR_sd)

####W###
Ps_samplesize<-
c(53,106,219,66,24,1184,65,116,114,229,47,5,67,32,39,86,11,31,53,46,29,46,210)
Ps_samplesize<-Ps_samplesize/sum(Ps_samplesize)
Ps_W<-c(0,0,0.2,0,0,0.4,3,0.1,0,0,0,0,25.2,0.01,0,0,0,13.9,0,0,0,0)
Ps_W_average<-sum(Ps_samplesize*Ps_W)/sum(Ps_samplesize)
Ps_variaNNCES<-sum(Ps_samplesize*(Ps_W-Ps_W_average)^2)
Ps_sd<-sqrt(Ps_variaNNCES)

#Truncated normal distribution
W<-rtruncnorm(n, a=-Inf, b=1, mean = Ps_W_average/100, sd = Ps_sd/100)
W[W<0]=0

####T###
T<-runif(n,60,150)
#Number of days of overlap

#Calculate consumption:
Cpop<-B*P*DR*W*T/1000

#Return result:
return(list("Cpop"=Cpop, "B"=B, "P"=P, "DR"=DR, "W"=W, "T"=T))
}

#Summary of all years
Ps_output<-matrix(0,nrow(Ps_years),15)
Ps_output[,1]<-seq(1982,2014,1)

```

```

colnames(Ps_output)<-c("Year", "Min.", "1st Qu.", "Median", "Mean", "3rd Qu.", "Max.", "10%
CI", "90% CI", "scale(B)", "scale(P)", "scale(DR)", "scale(W)", "scale(T)", "Bluefish biomass")
name_list<-as.character(seq(1982,2014,1))

#Loop to extract data for every year
for(i in 1982:2014){
  PsConsumption_samples5000<-Psconsumption(5000,i)
  Ps_output[i-1981,2:7]<-summary(PsConsumption_samples5000$Cpop)
  Ps_output[i-1981,8:9]<-quantile(PsConsumption_samples5000$Cpop,c(0.1,0.9))
  sensitivity <- lm(scale(Cpop) ~ scale(B) + scale(P) + scale(DR) + scale(W)+ scale(T),
data=PsConsumption_samples5000)
  Ps_output[i-1981,10:14]<-summary(sensitivity)$coefficients[2:6,1]
  Ps_output[i-1981,15]<-mean(PsConsumption_samples5000$B) #Bluefish biomass
  #Write files to directory
  currentDate<-Sys.Date()
  PsConsumptioncsvFileName<-paste("_PsConsumption_",currentDate,".csv",sep="")
  write.csv(PsConsumption_samples5000, paste(i,PsConsumptioncsvFileName, sep = ""))
  Ps_outputcsvFileName<-paste("Ps_output_Summary_",currentDate,".csv",sep="")
  write.csv(Ps_output,Ps_outputcsvFileName)
}

```

```
#####
####Striped Bass####
#####
```

```
#Make vector of population estimates
```

```
time<-(seq(1982,2014,1)) #Add column for years
```

```
#coastal migratory stock >500 mm or an age-4+ striped bass
```

```
#Catch weights-at age (kg) estimates are for age 4 to 13+ fish (Table 13 in Atlantic Striped Bass Stock Assessment Update 2016)
```

```
Ms_wt_age4<-
```

```
c(1.54,1.37,1.62,1.66,2.4,2.11,1.98,2.23,2.05,2.17,1.93,1.99,2.21,2.18,2.32,2.46,1.62,1.44,1.45,1.75,1.51,1.4,1.4,1.64,1.35,1.3,1.43,1.41,1.41,1.55,1.67,1.39,1.27)
```

```
Ms_wt_age5<-
```

```
c(2.42,2.37,2.67,2.19,2.44,2.5,3.12,3.06,2.35,2.62,2.81,2.77,2.85,2.77,3.23,2.81,2.25,1.91,1.96,2.21,2.18,2.2,2.43,2.22,1.96,2.1,2.14,1.92,1.99,2.2,2.3,2.27,2.15)
```

```
Ms_wt_age6<-
```

```
c(3.75,3.29,3.39,3.59,3.12,2.91,4.02,4.53,3.83,3.17,3.67,3.58,3.5,3.65,4.52,3.64,2.95,2.51,2.79,3.25,3.17,3.2,3.11,3.23,2.8,3.07,3.47,3.29,3.34,3.08,3.25,3.38,3.07)
```

```
Ms_wt_age7<-
```

```
c(4.83,3.77,5.07,4.91,3.95,3.61,4.38,5.37,4.91,4.81,4.9,4.8,4.94,5.38,6.39,4.51,4.69,3.36,3.89,4.12,4.19,4.1,4.14,4.18,3.84,4.31,5.05,4.49,4.27,4.1,4.44,4.14,4.28)
```

```
Ms_wt_age8<-
```

```
c(5.79,5.36,5.65,5.46,5.05,4.74,4.7,6.23,5.96,5.64,5.79,6.11,6.2,6.16,7.11,5.07,5.66,5.03,5.09,5.02,5.48,5.2,5.17,5.64,5.35,5.32,5.51,5.74,5.21,5.13,5.88,5.3,5.3)
```

```
Ms_wt_age9<-
```

```
c(6.2,6.01,6.76,6.77,5.44,5.52,5.24,6.04,5.7,6.46,6.96,7.03,6.8,7.27,7.81,6.73,6.82,6.56,7.11,6.36,6.03,6.1,6.07,6.38,6.7,6.89,6.69,6.87,6.27,6.41,6.57,6.69,6.99)
```

```
Ms_wt_age10<-
```

```
c(8.68,8.1,7.76,7.45,6.09,6.49,5.62,8.68,5.97,6.24,8.15,8.01,7.53,8.86,9.2,9.17,7.03,7.85,7.37,7.79,7.56,7.2,7.12,7.21,7.41,7.84,8.26,7.73,7.65,7.54,8.31,7.55,8.43)
```

```
Ms_wt_age11<-
```

```
c(10.8,9.57,8.41,9.7,7.75,7.77,8.58,8.94,7.44,9.46,9.77,9.53,9.73,7.57,9.31,9.94,7.76,8.69,9.7,8.65,9.09,8.5,8.18,8.51,8.58,9.39,9.19,8.81,8.97,8.2,9.05,9.26,9.17)
```

```
Ms_wt_age12<-
```

```
c(11.2,10.39,12.65,10.69,9.16,9.78,10.4,9.74,9.08,8.3,12.44,10.76,10.69,9.73,10.1,10.24,9.87,9.76,10.7,8.29,9.75,9.4,9.03,10.9,4,10.12,9.82,9.47,9.15,9.98,10.41,10.44,11.91)
```

```
Ms_wt_age13plus<-
```

```
c(14.05,11.11,12.38,13.91,12.78,13.15,13.27,13.36,12.6,14.22,13.97,14.55,12.73,16.66,13.7,14.78,11.87,11.98,13.55,10.87,11.52,11,10.71,12.19,12.05,12.77,12,12.24,11.59,13.08,13.84,13.14,14.29)
```

```
Ms_wt_agematrix<-
```

```
as.matrix(cbind(Ms_wt_age4,Ms_wt_age5,Ms_wt_age6,Ms_wt_age7,Ms_wt_age8,Ms_wt_age9,Ms_wt_age10,Ms_wt_age11,Ms_wt_age12,Ms_wt_age13plus)) #Combine weight by age-class into a matrix
```

#Estimates of population abundance by age (Table 25 in Atlantic Striped Bass Stock Assessment Update 2016)

Ms_abundance4<-

c(2456170,1128340,1317490,1634200,4463560,4143780,4087440,3280280,4372470,5687860,6312800,8454580,6906570,7005760,8959640,17855000,11449500,12502300,15536700,9835500,10108800,8035480,11851100,13780400,7600040,16567600,9460290,8806610,6533210,8511700,6053810,7428220,9450390)

Ms_abundance5<-

c(1445556,2115903,1856112,1784697,2759762,7743925,9131117,8734189,5372030,7809277,10905610,12019058,16330244,12791001,14737909,16574251,26621775,14560751,16517371,22653605,14343768,15041422,12905803,17306521,17567578,10349136,23051010,12006586,11515652,8681700,12807527,9033170,10406452)

Ms_abundance6<-

c(597337,892786,695173,814930,1131050,3097570,2926640,2854310,2285970,2980640,3881000,4339010,5729910,4617690,4562820,5898310,11831900,7623430,8427230,10250500,6579710,6837010,5311030,7795730,8963050,4928160,10771500,6253430,5786760,4340850,5568490,3979370,4840210)

Ms_abundance7<-

c(168737,110602,199343,443061,367829,467232,670182,1853710,1720960,1610180,1258490,1687210,2191470,2374210,2986010,2339070,2272470,2944480,6078680,3861930,4218970,5281990,3319280,3284190,2488440,3546700,4104050,2312380,5200510,3053400,2790930,2081370,2626430)

Ms_abundance8<-

c(114695,106820,83220,156637,352289,298010,390454,551196,1528690,1382950,1305430,1030900,1362750,1750310,1835020,2299490,1712860,1686420,2233310,4454540,2872520,3176320,3845110,2366610,2307700,1714320,2493230,2921890,1676690,3817930,2175430,2036390,1465940)

Ms_abundance9<-

c(87977,76692,80941,66046,123635,285098,248997,321362,456035,1245940,1132120,1075600,840198,1099160,1369470,1420100,1662780,1257100,1266710,1617000,3271280,2133160,2283730,2695530,1636270,1557160,1186320,1740310,2095470,1215850,2680750,1572490,1411080)

Ms_abundance10<-

c(99003,61016,58430,64682,51860,99995,238208,205088,266586,375598,1027450,937026,882709,682853,868242,1065060,1018220,1211360,938102,909809,1177110,2405920,1521060,1582310,1843290,1088310,1066190,816570,1239200,1506950,845316,1926260,1077580)

Ms_abundance11<-

c(77782,70385,46693,46923,50615,41939,83562,196356,170504,221230,311407,853296,772968,721532,543297,678367,759846,738609,900506,670643,658734,860349,1707300,1046180,1074850,1214920,740451,727233,579159,886774,1041530,605525,1311090)

Ms_abundance12<-

c(153578,56254,54065,37633,36639,40940,35056,68936,163543,142266,184148,259283,706605,634557,577187,426274,482801,550093,548070,642375,484177,479723,609161,1169550,708256,704869,824013,502340,515004,413450,611101,745352,410707)

```

Ms_abundance13plus<-
c(79516,171045,175532,185823,174171,170653,176964,175149,203782,308170,376570,46819
8,604962,1081410,1380900,1545890,1403300,1365540,1421280,1404890,1476430,1424570,13
48400,1338490,1696360,1572950,1544100,1601070,1491030,1431620,1270870,1348730,14188
70)
Ms_abundancematrix<-
as.matrix(cbind(Ms_abundance4,Ms_abundance5,Ms_abundance6,Ms_abundance7,Ms_abundan
ce8,Ms_abundance9,Ms_abundance10,Ms_abundance11,Ms_abundance12,Ms_abundance13plu
s)) #Combine abundance by age-class into a matrix

#Calculate biomass
Ms_biomass<-Ms_wt_agematrix*Ms_abundancematrix #Estimate biomass by multiplying
weight and abundance matrices
colnames(Ms_biomass)<-
c("Ms_biomass4","Ms_biomass5","Ms_biomass6","Ms_biomass7","Ms_biomass8","Ms_biomass
9","Ms_biomass10","Ms_biomass11","Ms_biomass12","Ms_biomass13")
estimate<-rowSums(Ms_biomass)
Ms_years<-as.data.frame(cbind(time,estimate))

#Striped bass Monte Carlo simulation

Msconsumption<-function(n,year){

###B###
#30% CV used to calculate a sd by multiplying 0.3 by the mean to get 1 sd above or below the
mean
Ms_year_CV<-0.3
Ms_year_estimate<-Ms_years$estimate[Ms_years$time==year]

B<-rpert(n,min=Ms_year_estimate-(Ms_year_CV*Ms_year_estimate), mode =
Ms_year_estimate, max = Ms_year_estimate+(Ms_year_CV*Ms_year_estimate))

###P###
P<-runif(n,0.6,0.9)

###DR###
#Taken from Chesapeake Bay Stock ecopath model that had a Q/B of 2.3 for coastal striped bass
Ms_QB<-2.3
Ms_DR<-((Ms_years[1,2]*Ms_QB)/365)/Ms_years[1,2] #Convert Q/B to calculate daily ration
of 0.0063
#30% CV used to calculate a sd by multiplying 0.3 by the mean to get 1 sd above or below the
mean
Ms_DR_sd<-Ms_DR*0.3 #Calculated sd is 0.0018

DR<-rpert(n,min=Ms_DR-Ms_DR_sd, mode = Ms_DR, max = Ms_DR+Ms_DR_sd)

```

```

####W###
Ms_samplesize<-c(2,27,43,106,89,50,27,73,19,34,50,60,19,253,450,140,64,1,12,38,1225,227)
Ms_samplesize<-Ms_samplesize/sum(Ms_samplesize)
Ms_W<-c(0,0,0,0,6.9,29.4,0,0,0,0,1.4,0,3.6,0.4,1.1,0,0,0,0,2.51,0)
Ms_W_average<-sum(Ms_samplesize*Ms_W)/sum(Ms_samplesize)
Ms_variaNNCES<-sum(Ms_samplesize*(Ms_W-Ms_W_average)^2)
Ms_sd<-sqrt(Ms_variaNNCES)

#Truncated normal distribution
W<-rtruncnorm(5000, a=-Inf, b=1, mean = Ms_W_average/100, sd = Ms_sd/100)
W[W<0]=0

####T###
T<-runif(n,60,120)

#Calculate consumption:
Cpop<-B*P*DR*W*T/1000

#Return result:
return(list("Cpop"=Cpop, "B"=B, "P"=P, "DR"=DR, "W"=W, "T"=T))
}

#Summary of all years
Ms_output<-matrix(0,nrow(Ms_years),15)
Ms_output[,1]<-seq(1982,2014,1)
colnames(Ms_output)<-c("Year", "Min.", "1st Qu.", "Median", "Mean", "3rd Qu.", "Max.", "10%
CI", "90% CI", "scale(B)", "scale(P)", "scale(DR)", "scale(W)", "scale(T)", "Striped bass
biomass")
name_list<-as.character(seq(1982,2014,1))

#Loop to extract data for every year
for(i in 1982:2014){
  MsConsumption_samples5000<-Msconsumption(5000,i)
  Ms_output[i-1981,2:7]<-summary(MsConsumption_samples5000$Cpop)
  Ms_output[i-1981,8:9]<-quantile(MsConsumption_samples5000$Cpop,c(0.1,0.9))
  sensitivity <- lm(scale(Cpop) ~ scale(B) + scale(P) + scale(DR) + scale(W)+ scale(T),
data=MsConsumption_samples5000)
  Ms_output[i-1981,10:14]<-summary(sensitivity)$coefficients[2:6,1]
  Ms_output[i-1981,15]<-mean(MsConsumption_samples5000$B) #Striped bass biomass
  #Write files to directory
  currentDate<-Sys.Date()
  MsConsumptioncsvFileName<-paste("_MsConsumption_",currentDate, ".csv", sep="")
  write.csv(MsConsumption_samples5000, paste(i, MsConsumptioncsvFileName, sep = ""))
  Ms_outputcsvFileName<-paste("Ms_output_Summary_",currentDate, ".csv", sep="")
  write.csv(Ms_output, Ms_outputcsvFileName)
}

```

```
#####
####Compare harvest and predation biomass removals ####
#####

#Sets dimensions to 1 plot a page
par(mfrow=c(1,1),family="serif")

#Harvest-landings and discards in kg
#Commercial harvest from 2016 stock assessment
com_landings<-
c(7214804,7107817,8129160,6840112,11075299,7224785,11375359,5632354,4778787,594854
3,4989202,2977992,2685453,2377591,3299692,4176464,4063253,3678530,2371374,2402930,2
094546,1319228,650318,547767,549138,577043,273678,252126,158388,101798,136512,10340
8,99065)
com_landings<-com_landings/1000 #Convert to metric tonnes
#Recreational harvest from 2016 stock assessment
rec_landings<-
c(1914835,2354049,1355816,1032561,3091958,1538154,2561072,619471,533925,1155785,644
501,389459,766680,660876,1173778,1830355,1549977,1334644,1500621,1240257,823842,534
366,340643,492815,446979,389810,257464,81217,42215,19949,109780,32116,24969)
rec_landings<-rec_landings/1000 #Convert to metric tonnes

#Assemble data
counts<-
as.matrix(t(cbind(com_landings,rec_landings,Tt_output[,5],Sa_output[,5],Ms_output[,5],Ps_outp
ut[,5],Pd_output[,5])))
rownames(counts)<-c("Commercial","Recreational","Bottlenose dolphin", "Spiny dogfish",
"Striped bass", "Bluefish", "Summer flounder")
colnames(counts)<-seq(1982,2014,1)

#Barchart
barplot(counts, main="Biomass removals of weakfish",
        xlab="Year", ylab="Biomass (t)",col=diverge_hcl(7,h=c(246,40),c=96),
        legend = rownames(counts))
```

```
#####
####Figure 6: Sensitivity analyses####
#####
```

```
#Standardized coefficients from each multiple regression
#Multipanel plot
par(mfrow=c(3,2),mar=c(1,1.4,2,0.6),oma=c(4,4,0.2,0.2),family="serif")
```

```
#Spiny dogfish
Sa_sensitivity<-as.matrix(t(colMeans(Sa_output[,10:14]))) #Calculate column means and format
data for barchart
colnames(Sa_sensitivity)<-c("B","P", "DR","W", "T")
Sa_barplot<-barplot(Sa_sensitivity, main=NULL,
                    xlab="Coefficient value", xlim=c(0,1), horiz=TRUE,
                    col="gray",names.arg=c(expression(italic(B),italic(P),italic(DR),italic(W),italic(T))))
text(Sa_sensitivity[1,],Sa_barplot,round(Sa_sensitivity[1,],3), cex = 1, pos=4) #Label bar chart
mtext("Spiny dogfish (a)", side = 3, line=-0.5,adj = 0.9)
```

```
#Summer flounder
Pd_sensitivity<-as.matrix(t(colMeans(Pd_output[,10:14]))) #Calculate column means and format
data for barchart
colnames(Pd_sensitivity)<-c("B","P", "DR","W", "T")
Pd_barplot<-barplot(Pd_sensitivity, main=NULL,
                    xlab="Coefficient value", xlim=c(0,1), horiz=TRUE,
                    col="gray",names.arg=c(expression(italic(B),italic(P),italic(DR),italic(W),italic(T))))
text(Pd_sensitivity[1,],Pd_barplot,round(Pd_sensitivity[1,],3), cex = 1, pos=4) #Label bar chart
mtext("Summer flounder (b)", side = 3, line=-0.5, adj = 0.9)
```

```
#Bluefish
Ps_sensitivity<-as.matrix(t(colMeans(Ps_output[,10:14]))) #Calculate column means and format
data for barchart
colnames(Ps_sensitivity)<-c("B","P", "DR","W", "T")
Ps_barplot<-barplot(Ps_sensitivity, main=NULL,
                    xlab="Coefficient value", xlim=c(0,1), horiz=TRUE,
                    col="gray",names.arg=c(expression(italic(B),italic(P),italic(DR),italic(W),italic(T))))
text(Ps_sensitivity[1,],Ps_barplot,round(Ps_sensitivity[1,],3), cex = 1, pos=4) #Label bar chart
mtext("Monte Carlo input variables",side=2,outer=TRUE, line=2,cex=1.1)
mtext("Bluefish (c)", side = 3, line=-0.5, adj = 0.9)
```

```
#Striped bass
Ms_sensitivity<-as.matrix(t(colMeans(Ms_output[,10:14]))) #Calculate column means and
format data for barchart
colnames(Ms_sensitivity)<-c("B","P", "DR","W", "T")
Ms_barplot<-barplot(Ms_sensitivity, main=NULL,
                    xlab=NULL, xlim=c(0,1), horiz=TRUE,
                    col="gray",names.arg=c(expression(italic(B),italic(P),italic(DR),italic(W),italic(T))))
```

```

text(Ms_sensitivity[1,],Ms_barplot,round(Ms_sensitivity[1,],3), cex = 1, pos=4) #Label bar chart
mtext("Coefficient value",side=1,outer=FALSE, line=3,cex=1.1)
mtext("Striped bass (d)", side = 3, line=-0.5, adj = 0.9)

```

```

#Bottlenose dolphin

```

```

Tt_sensitivity<-as.matrix(t(colMeans(Tt_output[,10:15]))) #Calculate column means and format
data for barchart

```

```

colnames(Tt_sensitivity)<-c("Bp","Bw","P", "DR", "W", "T")

```

```

Tt_barplot<-barplot(Tt_sensitivity, main=NULL,

```

```

      xlab=NULL, xlim=c(0,1), horiz=TRUE,

```

```

col="gray",names.arg=c(expression(italic(B[p]),italic(B[w]),italic(P),italic(DR),italic(W),italic(T)
)))

```

```

text(Tt_sensitivity[1,],Tt_barplot,round(Tt_sensitivity[1,],3), cex = 1, pos=4) #Label bar chart

```

```

mtext("Coefficient value",side=1,outer=FALSE, line=3,cex=1.1)

```

```

mtext("Bottlenose dolphin (e)", side = 3, line=-0.5, adj = 0.9)

```

```
#####
####Compare biomass estimates with stock assessment####
#####
```

```
#Stock assessment
```

```
#Natural mortality estimates from run best catch-at-age model run "S4" (Table 8.1.4.B in 2016 Weakfish Benchmark Stock Assessment and Peer Review Report)
```

```
M_yearly<-
```

```
c(0.17,0.16,0.16,0.16,0.16,0.16,0.16,0.16,0.16,0.16,0.15,0.14,0.14,0.14,0.14,0.15,0.17,0.2,0.25,0.3,0.38,0.48,0.55,0.63,0.74,0.87,0.93,0.95,0.95,0.95,0.95,0.95,0.92,0.84)
```

```
M_ages<-matrix(rep((M_yearly),6),nrow=33,ncol=6)
```

```
#Commercial mortality estimates from run S4 (Table 8.1.3.B in 2016 Weakfish Benchmark Stock Assessment and Peer Review Report)
```

```
F_Com<-
```

```
c(1.23,1.34,1.8,1.47,1.64,0.82,1.73,1.69,1.5,1.42,1.57,1.42,0.71,0.47,0.46,0.51,0.69,0.75,0.72,0.6,1.14,1.34,0.77,0.62,0.92,1.76,1.52,1.59,1.79,0.49,0.39,0.48,0.18)
```

```
F_Rec<-
```

```
c(0.38,0.76,0.8,0.73,0.87,0.57,0.76,0.38,0.36,0.55,0.44,0.44,0.28,0.24,0.18,0.19,0.23,0.22,0.52,0.45,0.61,0.66,0.6,0.58,0.84,0.89,0.67,0.82,0.42,0.1,0.41,0.06,0.11)
```

```
#F Selectivity estimated from figures (Figures 8.1.1.A and 8.1.1.B in 2016 Weakfish Benchmark Stock Assessment and Peer Review Report)
```

```
#Commercial
```

```
F_Com_Selectivity<-matrix(rep(c(0,0.2,0.44,0.72,0.9,1,0.95),33),nrow=33,ncol=7,byrow=TRUE)
```

```
#Recreational
```

```
F_Rec_Selectivity_1982to1995<-matrix(rep(c(0,0.05,0.22,0.36,0.77,0.9,1),14),nrow=14,ncol=7,byrow=TRUE)
```

```
F_Rec_Selectivity_1996to2014<-
```

```
matrix(rep(c(0,0.05,0.26,0.86,1,0.86,0.86),19),nrow=19,ncol=7, byrow=TRUE)
```

```
F_Rec_Selectivity<-rbind(F_Rec_Selectivity_1982to1995,F_Rec_Selectivity_1996to2014)
```

```
#Annual weight-at-age (kg) of weakfish (Table 2.3.1 in 2016 Weakfish Benchmark Stock Assessment and Peer Review Report)
```

```
Cr_wt_age0<-rep(0.073,33) #Based on the average weight of 422 age-0 North Carolina caught weakfish from (2000-2012)
```

```
Cr_wt_age1<-
```

```
c(0.095,0.07,0.086,0.069,0.137,0.078,0.081,0.098,0.1,0.11,0.09,0.08,0.12,0.11,0.1,0.19,0.12,0.11,0.11,0.097,0.15,0.117,0.113,0.104,0.185,0.194,0.202,0.178,0.123,0.105,0.139,0.117,0.107)
```

```
Cr_wt_age2<-
```

```
c(0.212,0.19,0.189,0.267,0.262,0.236,0.179,0.186,0.18,0.31,0.26,0.18,0.23,0.19,0.19,0.28,0.21,0.21,0.21,0.326,0.267,0.306,0.26,0.244,0.321,0.462,0.437,0.293,0.394,0.286,0.301,0.191,0.212)
```

```

Cr_wt_age3<-
c(0.307,0.368,0.379,0.579,0.758,0.524,0.398,0.383,0.54,0.68,0.6,0.36,0.41,0.31,0.32,0.41,0.35,0
.39,0.39,0.484,0.46,0.506,0.469,0.421,0.548,1.264,0.669,1.324,0.67,0.563,0.582,0.339,0.341)
Cr_wt_age4<-
c(0.483,0.885,0.758,1.235,1.759,1.234,0.796,0.769,1.04,1.12,1.02,0.59,0.63,0.46,0.49,0.57,0.52,
0.62,0.62,0.84,0.522,1.045,1.116,0.667,0.768,1.208,2.405,3.183,1.072,0.793,0.759,0.432,0.235)
Cr_wt_age5<-
c(1.076,1.395,1.583,1.748,2.819,2.127,1.494,1.417,1.58,1.6,1.48,0.86,0.89,0.63,0.68,0.74,0.71,0
.87,0.87,1.424,1.367,2.262,2.451,2.142,0.97,1.318,2.813,4.689,1.74,1.577,1.577,1.577,1.577)
Cr_wt_age6plus<-
c(3.033,2.862,2.536,3.055,3.173,2.536,3.026,3.348,2.39,2.33,2.19,1.33,1.32,0.94,1.02,1.03,1.04,
1.31,1.31,3.193,2.894,3.25,4.304,4.126,4.463,5.171,6.516,5.9,2.843,2.843,2.843,2.843,2.843)
Cr_wt_agematrix<-
as.matrix(cbind(Cr_wt_age0,Cr_wt_age1,Cr_wt_age2,Cr_wt_age3,Cr_wt_age4,Cr_wt_age5,Cr_
wt_age6plus))

#Total abundance estimated by the Bayesian age-structured model in millions of fish for run S4
(Table 8.1.5.1B. in 2016 Weakfish Benchmark Stock Assessment and Peer Review Report)
Cr_abundance1<-
c(21.8,25.2,31.1,42,42.1,32.3,20.6,18.1,16.4,16.6,21.4,24.7,28.2,13.6,15.4,10.5,9.1,8.6,14.9,5.9,
8.2,9.9,13.4,6.3,6.7,4.4,3.8,4.2,7.2,8,9.3,7.6,15.2)
Cr_abundance2<-
c(16.7,15,16.9,19.4,27.8,27,23.8,13,11.6,10.9,11.2,14.2,16.9,21.7,10.8,12.2,8.1,6.6,5.9,9.6,3.6,4.
1,4.5,6.2,2.7,2.4,1.3,1.1,1.2,2.1,2.9,3.3,2.8)
Cr_abundance3<-
c(8,8.1,6.7,6.2,8.3,10.8,15.3,9,5.3,5.1,4.9,4.8,6.5,10.6,14.6,7.3,7.9,4.7,3.6,2.9,4.6,1.2,1.2,1.5,2,0.
6,0.4,0.2,0.2,0.2,0.6,0.9,1.1)
Cr_abundance4<-
c(3.4,2.8,2.4,1.4,1.7,2.4,7,3.5,2.4,1.6,1.5,1.4,1.5,3.3,5.8,8.3,3.9,3.6,2,1.2,1,0.9,0.2,0.3,0.3,0.3,0,0
,0,0,0.1,0.1,0.2)
Cr_abundance5<-
c(1.3,0.8,0.5,0.3,0.2,0.2,0.6,0.6,0.6,0.5,0.3,0.3,0.3,0.6,1.6,2.9,4,1.5,1.3,0.5,0.3,0.1,0.1,0,0,0,0,0
,0,0,0,0)
Cr_abundance6plus<-
c(1.1,0.5,0.2,0.1,0,0,0.1,0.1,0.1,0.1,0.1,0.1,0.1,0.1,0.1,0.4,1,1.9,2.2,1.3,0.7,0.4,0.1,0,0,0,0,0,0,0,0
,0)

#Composite YOY
Composite_YOY<-
c(0.62,0.32,0.71,0.84,1.02,0.51,0.81,0.82,0.7,1.07,1.06,1.13,1.2,1.19,1.76,1.81,0.95,1.2,1.42,1.0
1,0.97,1.25,1.1,1.84,0.55,1.21,0.65,0.88,0.99,0.81,0.6,0.97)
Composite_YOY_1982<-mean(Composite_YOY[1:3]) # No value was available for 1982, so an
average of the years 1983-1985 was used
Composite_YOY<-append(Composite_YOY_1982,Composite_YOY) #Add 1982 value to age-0
vector

```

```

#Lorenzens M Correction factor
#Estimate M for age-0 and average age-1+ (using weight)
#Lorenzen's natural M equation  $M = \mu W^b$  where M is natural mortality,  $\mu$  is mortality at unit weight ( $\mu[\text{year}^{-1}]$ ), W is average weight for age class, and b is the weight exponent
 $\mu <- 3$ 
 $b <- (-0.288)$ 
#Average weight of age-0s is constant at 0.073 kg
Lorenzens_age0 <-  $\mu * (\text{Cr\_wt\_age0} * 1000)^b$  #Convert kg to g by multiplying by 1000

#Estimate age 0 abundance based on next years age 1 abundance and that years total mortality
and Lorenzens correction
 $\text{Cr\_abundance0\_1984} <- \text{Cr\_abundance1}[4] / \exp(-(\text{Lorenzens\_age0}[3]))$ 
 $\text{Cr\_abundance0} <- (\text{Cr\_abundance0\_1984} * (\text{Composite\_YOY} / \text{Composite\_YOY}[3]))$ 

#Calculate M by dividing age-1s from age-0s
 $M\_age0 <- -(\log(\text{Cr\_abundance1}[2:33] / \text{Cr\_abundance0}[1:32]))$ 
# No age 1 abundance for in 2015 to estimate age 0 abundance in 2014
#Averaged 2011-2013 M instead
 $M\_2014 <- \text{mean}(M\_age0[30:32])$ 
 $M\_age0 <- \text{append}(M\_age0, M\_2014)$ 
 $M <- \text{cbind}(M\_age0, M\_ages)$ 
Cr_abundancematrix <-
as.matrix(cbind(Cr_abundance0, Cr_abundance1, Cr_abundance2, Cr_abundance3, Cr_abundance4,
Cr_abundance5, Cr_abundance6plus))

#Calculate abundance lost to M
Cr_abundancematrix_MLost <- Cr_abundancematrix * M * (1 - exp(-
(M + (F_Com * F_Com_Selectivity) + (F_Rec * F_Rec_Selectivity)))) / (M + (F_Com * F_Com_Selectivity) + (F_Rec * F_Rec_Selectivity))
Cr_abundancematrix_MLost[,1] <- Cr_abundancematrix_MLost[,1] / 3 #Divide by 3 so number
lost to M is only for when the majority of age-0s are greater than 100 mm (assumed to be
September 1)
#This /3 does not need to be done for F sectors siNNCES these are not susceptible to fishing gear at
these lengths

#Calculate abundance lost to F_Com
Cr_abundancematrix_F_ComLost <- Cr_abundancematrix * (F_Com * F_Com_Selectivity) * (1 -
exp(-
(M + (F_Com * F_Com_Selectivity) + (F_Rec * F_Rec_Selectivity)))) / (M + (F_Com * F_Com_Selectivity) + (F_Rec * F_Rec_Selectivity))

#Calculate abundance lost to F_Rec
Cr_abundancematrix_F_RecLost <- Cr_abundancematrix * (F_Rec * F_Rec_Selectivity) * (1 - exp(-
(M + (F_Com * F_Com_Selectivity) + (F_Rec * F_Rec_Selectivity)))) / (M + (F_Com * F_Com_Selectivity) + (F_Rec * F_Rec_Selectivity))

```

```

#Calculate biomass for each mortality
#M
Cr_biomass_M<-as.data.frame(Cr_wt_agematrix*Cr_abundancematrix_MLost*1000000)
#Convert to actual numbers for biomass estimate for M
colnames(Cr_biomass_M)<-
c("Cr_biomass0","Cr_biomass1","Cr_biomass2","Cr_biomass3","Cr_biomass4","Cr_biomass5",
"Cr_biomass6plus")
Cr_biomass_M$Total<-rowSums(Cr_biomass_M)
time<-seq(1982,2014,1) #Add column for year
Cr_biomass_M<-cbind(time,Cr_biomass_M)
#F_Com
Cr_biomass_F_Com<-
as.data.frame(Cr_wt_agematrix*Cr_abundancematrix_F_ComLost*1000000) #Convert to actual
numbers for biomass estimate for F_Com
colnames(Cr_biomass_F_Com)<-
c("Cr_biomass0","Cr_biomass1","Cr_biomass2","Cr_biomass3","Cr_biomass4","Cr_biomass5",
"Cr_biomass6plus")
Cr_biomass_F_Com$Total<-rowSums(Cr_biomass_F_Com)
time<-seq(1982,2014,1) #Add column for year
Cr_biomass_F_Com<-cbind(time,Cr_biomass_F_Com)
#F_Rec
Cr_biomass_F_Rec<-
as.data.frame(Cr_wt_agematrix*Cr_abundancematrix_F_RecLost*1000000) #Convert to actual
numbers for biomass estimate for F_Rec
colnames(Cr_biomass_F_Rec)<-
c("Cr_biomass0","Cr_biomass1","Cr_biomass2","Cr_biomass3","Cr_biomass4","Cr_biomass5",
"Cr_biomass6plus")
Cr_biomass_F_Rec$Total<-rowSums(Cr_biomass_F_Rec)
time<-seq(1982,2014,1) #Add column for year
Cr_biomass_F_Rec<-cbind(time,Cr_biomass_F_Rec)

```

```
#####
##Figure 3: Biomass removals attributable to stock assessment F and M and the effect of YOY##
#####

#Sets format for multipanel plot
plot.new()
par(mfrow=c(2,1),pin=c(4,2),mar=c(2,1,1,1),oma=c(4,4,0.2,4),family="serif",cex=1)

#Panel a
#Plot
plot(Cr_abundance1[2:33]~time[1:32],type='l',lty=1,lwd=3,xlab="",ylab=NA)
par(new=T)
plot(Composite_YOY[1:32]~time[1:32],axes=F,type='l',lty=1,lwd=3,col="gray",xlab=NA,ylab=
NA)
axis (side=4)
legend(1985.3,2,legend=c("Age-1", "Composite-
YOY"),col=c("black", "gray"),lty=c(1,1),lwd=c(3,3),bty="n",cex=1.15)
mtext(side=4,line=3,'Number of fish per tow',cex=1.3)
mtext("Age-1 weakfish (millions)",side=2,outer=FALSE, line=2.5,cex=1.3)
mtext("(a)", side = 3, line=-1.2,adj = 0.05,cex=1.2)

#Panel b
#Compares F Rec, F Com, and M for age-0 M and age-1+

#Assemble data
Cr_biomass_M_age0<-Cr_biomass_M[,2]
Cr_biomass_M_age1plus<-rowSums(Cr_biomass_M[,3:8])
Cr_Mortality_Totals_Mdiff<-
as.matrix(t(cbind(Cr_biomass_M_age0,Cr_biomass_M_age1plus,Cr_biomass_F_Com$Total,Cr
_biomass_F_Rec$Total)))/1000 #Convert to metric tonnes
rownames(Cr_Mortality_Totals_Mdiff)<-c("F Rec", "F Com", "M age-1+", "M age-0")
colnames(Cr_Mortality_Totals_Mdiff)<-seq(1982,2014,1)

#Plot
barplot(Cr_Mortality_Totals_Mdiff,
        xlab=NULL,ylim=c(0,20000),ylab="Biomass (t)",density=c(100,100,20,100),
        angle=c(0,0,45,0),col=c("grey", "grey", "black", "black"))
barplot(Cr_biomass_M_age0/1000,ylim=c(0,20000),density=25, angle=125,col="black",add=T)
#Overlay on barplot to get shaded bars
mtext("Biomass (t)",side=2,outer=FALSE, line=2.5,cex=1.3)
mtext("Year",side=1,outer=TRUE, line=1,cex=1.3)
mtext("(b)", side = 3, line=-1.2,adj = 0.05,cex=1.2)
par(xpd=TRUE)
legend("topright", inset=c(0.01,-
0.1),legend=c(expression(italic(F)[italic(rec)]),italic(F)[italic(com)]),italic(M)~"age-
```

```
1+",italic(M)~"age-0")),density=c(NA,20,NA,NA) ,  
angle=c(0,45,0,0),fill=c("black","black","grey","grey"),box.lty=0,cex=1.15)  
legend("topright", inset=c(0.01,-  
0.1),legend=c(expression(italic(F)[italic(rec)],italic(F)[italic(com)],italic(M)~"age-  
1+",italic(M)~"age-0")),density=c(NA,20,NA,25) ,  
angle=c(0,45,0,125),fill=c("black","black","grey","black"),bg=NA,box.lty=0,cex=1.15)
```

```
#####
###Figure 8: Predator consumption compared to stock assessment biomass attributable to M###
#####
```

```
#Sets dimensions to 1 plot a page
plot.new()
par(mfrow=c(1,1),mar=c(5,5,3,5),oma=c(0.2,0.2,0.2,0.2),family="serif",cex=1)

#Assemble data
Monte_Carlo_mean<-Tt_output[,5]+Sa_output[,5]+Ms_output[,5]+Ps_output[,5]+Pd_output[,5]
Monte_Carlo_10<-Tt_output[,8]+Sa_output[,8]+Ms_output[,8]+Ps_output[,8]+Pd_output[,8]
Monte_Carlo_90<-Tt_output[,9]+Sa_output[,9]+Ms_output[,9]+Ps_output[,9]+Pd_output[,9]

plot(Monte_Carlo_mean~time,ylim=c(0,20000),type='l',lty=1,lwd=3,xlab="Year",ylab="Weakfish biomass (t)")
lines(Monte_Carlo_10~time,lty=3,lwd=2)
lines(Monte_Carlo_90~time,lty=3,lwd=2)
# Cr_biomass_M_NoYOY<-rowSums(Cr_biomass_M[,3:8])/1000
# lines(Cr_biomass_M_NoYOY~time,lty=1,lwd=3,col="gray")
lines(Cr_biomass_M$Total/1000~time,lty=1,lwd=3,col="gray")
legend(1981,21000,legend=c("Stock assessment + age-0s", "Predator consumption", "80% CI"),col=c("gray", "black", "black"),lty=c(1,1,3),lwd=c(3,3,2),bty="n",cex=1.1)
```

```
#####
####Fig B1: Compare W distributions across predators####
#####

set.seed(123)
plot.new()
par(mfrow=c(3,2),mar=c(1,1.4,1,0.6),oma=c(4,4,0.2,0.2),family="serif",cex=0.9)

#Spiny dogfish
Sa_samplesize<-c(59,222,143,1145,48,73,242,389,17,146,6270,382,2338,132) #Sample sizes of
diet studies
Sa_samplesize<-Sa_samplesize/sum(Sa_samplesize) #Divide by sum to equal 1
Sa_W<-c(0,0,0,0,0,23.54,0,0,0,0,0.26,3.98,0,0) #%Mass for each diet study
Sa_W_average<-sum(Sa_samplesize*Sa_W)/sum(Sa_samplesize) #Average %Mass
Sa_variance<-sum(Sa_samplesize*(Sa_W-Sa_W_average)^2) #Variance
Sa_sd<-sqrt(Sa_variance) #Standard deviation

#Truncated normal distribution
W<-rtruncnorm(5000, a=-Inf, b=1, mean = Sa_W_average/100, sd = Sa_sd/100) #Divide by 100
to get proportion
W[W<0]=0 #All negative values from the distribution are changed to 0s

hist(W,xlim=c(0,0.30),ylim=c(1,3000),main=NULL,ylab=NULL,xlab=NULL,col="grey")
abline(v=median(W),col="black",lty=2,lwd=2)
title("Spiny dogfish",line=-2,adj=0.7)
mtext("(a)", side = 3, line=-2.1,adj = 0.9,cex=1.2)

#Summer flounder
Pd_samplesize<-
c(51,64,3,116,694,117,22,134,26,49,16,97,16,94,13,153,13,19,45,97,350,16,19,23,31,12,32,21,7
59) #Sample sizes of diet studies
Pd_samplesize<-Pd_samplesize/sum(Pd_samplesize) #Divide by sum to equal 1
Pd_W<-c(0,0,0,0,0,0,0,9.5,26.7,15,0,7,62,5,9,0,0,0,0,0,0.7,0,0,0,45,0,0,37,2.4) #%Mass for each
diet study
Pd_W_average<-sum(Pd_samplesize*Pd_W)/sum(Pd_samplesize) #Average %Mass
Pd_variance<-sum(Pd_samplesize*(Pd_W-Pd_W_average)^2) #Variance
Pd_sd<-sqrt(Pd_variance) #Standard deviation

#Truncated normal distribution
W<-rtruncnorm(5000, a=-Inf, b=1, mean = Pd_W_average/100, sd = Pd_sd/100) #Divide by 100
to get proportion
W[W<0]=0 #All negative values from the distribution are changed to 0s

hist(W,xlim=c(0,0.30),ylim=c(1,3000),main=NULL,ylab=NULL,xlab=NULL,col="grey")
abline(v=median(W),col="black",lty=2,lwd=2)
title("Summer flounder",line=-2,adj=0.7)
```

```

mtext("(b)", side = 3, line=-2.1,adj = 0.9,cex=1.2)

#Bluefish
Ps_samplesize<-
c(53,106,219,66,24,1184,65,116,114,229,47,5,67,32,39,86,11,31,53,46,29,46,210) #Sample
sizes of diet studies
Ps_samplesize<-Ps_samplesize/sum(Ps_samplesize) #Divide by sum to equal 1
Ps_W<-c(0,0,0.2,0,0,0.4,3,0.1,0,0,0,0,25.2,0.01,0,0,0,13.9,0,0,0,0,0) #Mass for each diet study
Ps_W_average<-sum(Ps_samplesize*Ps_W)/sum(Ps_samplesize) #Average %Mass
Ps_variance<-sum(Ps_samplesize*(Ps_W-Ps_W_average)^2) #Variance
Ps_sd<-sqrt(Ps_variance) #Standard deviation

#Truncated normal distribution
W<-rtruncnorm(5000, a=-Inf, b=1, mean = Ps_W_average/100, sd = Ps_sd/100) #Divide by 100
to get proportion
W[W<0]=0 #All negative values from the distribution are changed to 0s

hist(W,xlim=c(0,0.30),ylim=c(1,3000),main=NULL,xlab=NULL,ylab=NULL,col="grey")
abline(v=median(W),col="black",lty=2,lwd=2)
title("Bluefish",line=-2,adj=0.7)
mtext("Frequency",side=2,outer=TRUE, line=2,cex=1.1)
mtext("(c)", side = 3, line=-2.1,adj = 0.9,cex=1.2)

#Striped bass
Ms_samplesize<-c(2,27,43,106,89,50,27,73,19,34,50,60,19,253,450,140,64,1,12,38,1225,227)
#Sample sizes of diet studies
Ms_samplesize<-Ms_samplesize/sum(Ms_samplesize) #Divide by sum to equal 1
Ms_W<-c(0,0,0,0,6.9,29.4,0,0,0,0,0,1.4,0,3.6,0.4,1.1,0,0,0,0,2.51,0) #Mass for each diet study
Ms_W_average<-sum(Ms_samplesize*Ms_W)/sum(Ms_samplesize) #Average %Mass
Ms_variance<-sum(Ms_samplesize*(Ms_W-Ms_W_average)^2) #Variance
Ms_sd<-sqrt(Ms_variance) #Standard deviation

#Truncated normal distribution
W<-rtruncnorm(5000, a=-Inf, b=1, mean = Ms_W_average/100, sd = Ms_sd/100) #Divide by
100 to get proportion
W[W<0]=0 #All negative values from the distribution are changed to 0s

hist(W,xlim=c(0,0.30),ylim=c(1,3000),main=NULL,ylab=NULL,xlab=NULL,col="grey")
abline(v=median(W),col="black",lty=2,lwd=2)
title("Striped bass",line=-2,adj=0.7)
mtext("(d)", side = 3, line=-2.1,adj = 0.9,cex=1.2)
mtext("Weakfish proportion by weight",side=1,outer=FALSE, line=3,cex=1.1)

#Bottlenose dolphin
#Only used months of November to April when Northern migratory stock is known to be in
North Carolina waters

```

```
Tt_samplesize<-c(6,10,14,11,17,16) #Sample sizes by month
Tt_samplesize<-Tt_samplesize/sum(Tt_samplesize) # divide by sum to equal 1
Tt_W<-c(21.9,33.1,48.7,66.0,63.0,42.2)
Tt_W_average<-sum(Tt_samplesize*Tt_W)/sum(Tt_samplesize) #Average %Mass
Tt_variance<-sum(Tt_samplesize*(Tt_W-Tt_W_average)^2) #Variance
Tt_sd<-sqrt(Tt_variance) #Standard deviation

#Truncated normal distribution
W<-rtruncnorm(5000, a=-Inf, b=1, mean = Tt_W_average/100, sd = Tt_sd/100) #Divide by 100
to get proportion
W[W<0]=0 #All negative values from the distribution are changed to 0s

hist(W,xlim=c(0,1),ylim=c(1,3000),main=NULL,ylab=NULL,xlab=NULL,col="grey")
abline(v=median(W),col="black",lty=2,lwd=2)
title("Bottlenose dolphin",line=-2,adj=0.7)
mtext("(e)", side = 3, line=-2.1,adj = 0.9,cex=1.2)
mtext("Weakfish proportion by weight",side=1,outer=FALSE, line=3,cex=1.1)
```