

UNDERSTANDING THE ECOLOGICAL PROCESSES THAT DRIVE PATTERNS IN FISHERY
SELECTIVITY AND SURVEY CATCHABILITY

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ABSTRACT OF THE DISSERTATION

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Being able to confidently count organisms is fundamental to estimating the dynamics of populations and to making inferences about what influences those dynamics. However, an accurate census is difficult to achieve because an entire population is almost never fully detectable. The population size of aquatic organisms can be particularly problematic to estimate because the environment is not conducive to human observation, and, particularly in the ocean, the entire habitat of the population in question can never be fully sampled. When we attempt to count the numbers of fish or shellfish in a population, for example to help manage a fishery or to increase our understanding of how a population is responding to shifts in climate, this impediment almost always results in at least some portion of the population being unobserved and unquantified. Having some information about the size and composition of this unobserved demographic is fundamental to population ecology and is particularly

essential when the relative contribution of the unobserved demographic to the true population changes in space and time.

Advancements in fisheries population dynamics and stock assessment science have resulted in the generally accepted application of two parameters that aid in estimating the unobserved portion of the population from the observed one. The first, selectivity, defines the proportion of a given demographic group, available to, and retained by, survey or fishing gear once it comes into contact with it. The second, catchability, is defined as the proportion of the population caught by a single unit of fishing or survey effort. Despite the influence these two parameters have on our perception of what controls fish and shellfish population dynamics, we still don't fully understand the underlying processes that influence them for many managed fisheries.

Using fishery and population survey data from two mid-Atlantic fisheries, summer flounder and Eastern oysters, I use the following four chapters to 1.) identify patterns in selectivity and catchability and understand the underlying ecological processes that drive them, and 2.) propose how we might better utilize this information to assess and manage these and other fisheries.

In Chapter 1 I use summer flounder data collected from commercial and recreational landings and a stock assessment trawl survey to evaluate the selectivity of the survey and fishing gear for different demographic groups. Some interesting patterns were identified, particularly that selectivity for female summer flounder is higher in the recreational fishery than in both the commercial fishery or the stock assessment trawl survey. This pattern suggested a highly female-biased recreational catch and that male and female summer flounder separate in space and time.

In Chapter 2 I explored, given the size- and sex-specific selectivity patterns and catch composition identified in Chapter 1, whether management actions could be taken to achieve a more sex-balanced harvest in the recreational fishery. I evaluated whether a series of slot limits, size regulations that require landed fish be between some minimum and maximum size, have the potential to simultaneously reduce mortality on large, fecund, females while maintaining or reducing total fishing mortality.

The patterns in summer flounder fishery catch composition and selectivity and the prescribed management actions identified and discussed in Chapters 1 and 2 should contribute significantly to our understanding of the life history, particularly relative to sex-specific habitat use, of summer flounder, and will likely be relevant to the stock assessment and management of this commercially and recreationally important fishery going forward.

In Chapter 3 I used a set of field experiments to derive empirical estimates of catchability for a survey dredge used in the stock assessment of eastern oysters in Delaware Bay. I identified an along-bay gradient in catchability that appeared to be driven by changes in oyster density. This density-dependent catchability lead to catch-per-unit-effort of the survey dredge being hyperstable at low oyster density, making catch-per-unit-effort (CPUE) an unreliable proxy for abundance at low oyster density.

In Chapter 4 I asked the question, given that evidence from Chapter 3 suggests a fixed catchability coefficient is not appropriate for estimating true density from survey CPUE, how do three alternative models perform in estimating the true density in the sampled area. In the first model, I corrected CPUE by applying spatially-explicit catchability coefficients, as opposed to a constant, that account for the along-bay gradient in density.

In the second, CPUE was corrected for by estimating catchability *in situ* for each tow using a logistic model fit to catch composition and tow covariates. For the third model, CPUE data were ignored entirely and a model that accounted for the proportion of the sample composition that was made up of oysters was applied to estimate oyster density *in situ* for each tow. The simplest model, which ignored both catchability of the survey gear and CPUE, and relied only on an estimate of the portion of the catch that was made up of oysters, performed best in estimating the true density in the sampled area.

The density-dependence in catchability identified for an oyster survey dredge in Chapter 3 is an important finding because it adds to a growing body of literature that density-dependent catchability, a phenomenon traditionally attributed to an interaction between fish and fishermen behavior, may be a common problem in standardized stock assessment survey data as well. In addition, Chapter 4 strongly suggests that when catchability varies at fine spatial and temporal scales, raw catch components may more accurately reflect the true density in the sampled area than an index derived from catch-per-unit-effort and catchability. Both findings should have application to how reef growing populations of organisms, and oysters in particular, are assessed and managed going forward.

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INTRODUCTION

While our ability to estimate the number of organisms in a population is central to applied ecology (Elphick 2008) and plays a major role in our understanding of biodiversity (Colwell and Coddington 1994) and species interactions (Faisal et al. 2010), identifying the most appropriate methodology used to count individuals, and the most appropriate data interpretations and transformations used to scale those counts to estimates of population size, continues to be a field of research rife with challenges (Jones 2011; Guthlin, et al. 2014; Maunder and Piner 2014). Some of the more common approaches to estimating abundance include stratified random sampling (Powel et al. 2008), mark-recapture methods (Grimm et al. 2014), depletion analyses (Young et al. 2004), and the application of complex models that account for the contribution of different demographic groups (Haddon 2011). Each method comes with a set of assumptions about how the true population relates to the sampled one, and attempts are made to account for these when drawing inferences about ecological phenomenon.

For population assessment scientists and natural resource managers and stakeholders, the necessity for reliable count data extends beyond the desire to advance theory and principles in ecology. When applied in a resource management context, unreliable, misused, or misinterpreted abundance data can result in ecological, social, and economic disasters. Marine fisheries management has a particularly storied, even if overstated, history of fisheries collapsing from what have been actual or perceived failures of population assessment scientists and/or the management system to

recognize important trends in the population dynamics of the species being managed (Hilborn and Hilborn 2012).

A major difficulty associated with counting and managing fisheries, as well as other mobile and inconspicuous organisms, was summarized famously by John Shepherd (1978) with, "Managing fisheries is hard; it's like managing a forest, in which trees are invisible and keep moving around." The fisheries literature is full of innovative attempts to overcome this reality (Hilborn and Walters 1992; Quinn and Deriso 1999). In addition, recent advancements in computing have made it possible to assess the fit of hundreds of non-linear model parameters simultaneously (Fournier et al. 2012) so that the evolution of population assessment might soon lead to models that mirror the complexity of a natural population. Yet, despite continued improvement to techniques for assessing population size and complex model fitting procedures, contemporary methods still cannot accurately depict key population parameters for the most recent years in a time series (Cadrin and Dickey-Collas 2014; Maunder and Piner 2014).

Selectivity and catchability are both stock assessment parameters that scale observations taken from a sample of a population to estimates of the true population size (Cadrin et al. 2016). Selectivity can be defined as the product of 1) the proportion of a given demographic group retained by survey or fishing gear once it comes into contact with it, also called contact selectivity, and 2) the proportion of the same demographic group available to the fishing or survey gear at the time and location it was fished, also called population selectivity (Maunder et al. 2014). Catchability is simply how much of the population is caught by a single unit of fishing or survey effort (Arreguin-Sanchez 1996). Although both are tightly linked with the life history and

behavior of the species being studied, experimental or field observation-based approaches to estimates are often neglected in favor of those derived inside the assessment model (Cadrin et al. 2016) where they are sometimes correlated with other model parameters (Arreguin-Sanchez 1996). Despite key stock assessment outputs, including total abundance and fishing mortality rate, being highly sensitive to misspecification of selectivity and catchability (Chen et al. 2003; Cardin et al. 2016), both remain poorly understood for most fisheries (Sampson and Scott 2011; Sampson 2013).

This work is aimed at understanding the driving forces influencing catchability and selectivity and intersects two fields, stock assessment science and natural history, that are now too often viewed as disparate. I present experimental and observational estimates of selectivity and catchability from two fisheries, summer flounder and eastern oysters. Two chapters are devoted to each fishery. In first chapter I endeavor to understand, through observation and experimentation, some of the underlying ecological processes that drive patterns in selectivity and catchability of fishing and survey gear. With a better understanding of these ecological processes, I then set out in the second chapter to evaluate how we might utilize this information to develop more appropriate tools and applications in fishery stock assessment and management.

I propose that one of the major complications with counting any organism is that our ability to do it well is directly dependent on how much we already know about the organism's life history (distribution, demography, growth rates, movement patterns). But such information can only be learned from properly designed population surveys, with unbiased interpretations of population data, so that a feedback loop forms

between the raw count data being used to model and assess the population and basic natural history information needed to collect the raw count data. The underlying processes (natural history) inform priors of the model parameters and generate more certain estimates of the size of the population, which in turn allow for stronger inference about the underlying processes, and so on. This is an admittedly trivial statement. To count, model, and manage a resource, of course one would need to understand the basic life history and ecology of that resource. However, financial and time constraints often lead to gross overgeneralizations of the underlying processes that make different species unique.

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CHAPTER 1

ESTIMATING THE SEX COMPOSITION OF THE SUMMER FLOUNDER CATCH USING FISHERY-INDEPENDENT DATA**

Abstract

Models that account for sex-specific behavior and population dynamics are becoming more common in the stock assessment of sexually dimorphic fishes. However, such models can be data-intensive and require some knowledge or assumptions about the sex ratio of fishery landings. A recent stock assessment review of Summer Flounder *Paralichthys dentatus* identified the need to account for sex-specific fishing mortality in the assessment model; however, no data on the sex composition of the catch were available. Fishery-independent sex-specific information is collected annually for this species by the National Marine Fisheries Service, Northeast Fisheries Science Center on their ocean trawl survey. Sex-at-age from the survey could be applied to the fishery landings if the probability of landing a given sex at a given age is equivalent for fish collected by the survey and in the landings. To generate the first regionally comprehensive database on the sex ratio of Summer Flounder landings and to determine the efficacy of using survey sex-at-age keys to sex the landings, I recorded the sex composition of the commercial and recreational Summer Flounder catch (n= 31,912) in 2010 and 2011. When (1) survey length data were left-truncated to simulate the minimum retention sizes in the fisheries and (2) age-length keys generated from

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fishery-dependent data were applied to length-frequency distributions from the survey to simulate the growth rates of fish landed in the catch, the sex-at-age pattern in the survey-derived data closely resembled the patterns in the catch. However, statistically significant differences in sex-at-age remained between the catch and the survey-derived data. I hypothesize that these differences are owed to differences in the spatiotemporal distribution of the sexes and the spatiotemporal distribution of the survey and fishing effort.

Introduction

Recent evidence suggests that including sex structure in stock assessment models is important for sexually-dimorphic fishes. For example, if growth rates or natural mortality differ between male and female fish (Wang et al. 2005; Su et al. 2013), if sex-specific migratory behavior and fishing effort are not evenly distributed in space and time (Okamura et al. 2014), or if fishery selectivity is sex-specific (Myers et al. 2014), not including sex-structure in the assessment model can bias biological reference points. In light of these recent findings, sex-structured assessment models are becoming more common in describing the population dynamics of fishes that have sexually-dimorphic characteristics and/or behavior (Clark 2006; Wang et al. 2007; Fenske et al. 2011; Su et al. 2011; McGilliard et al. 2013).

Female Summer Flounder *Paralichthys dentatus* grow faster (Poole 1961; King et al. 2001) and mature at a larger size (Able and Kaiser 1994; Packer et al. 1999) than males. In addition, the sex ratio of young fish is skewed in favor of males, probably due to a complex interaction between temperature and the biochemistry of sex determination

(Luckenbach et al., 2009). However, as the cohort ages the balance in sex ratio shifts toward females (Smith and Daiber 1977; Bonzek et al. 2009), a pattern that suggests a higher natural mortality rate for the males (Maunder and Wong 2011). Sexually-¹dimorphic life history characteristics of Summer Flounder suggest that a sex-structured assessment model would be appropriate for this species (Jones et al. 2013; NEFSC 2013), yet the most recent assessment applied a single-sex statistical catch-at-age model (NEFSC 2013).

Sex-structured assessment models can be difficult to implement because they are data-intensive, requiring either some prior knowledge about the sex composition of the catch or that assumptions be made about the sex-specific selectivity curve and its stability in space and time (Methot and Wetzel 2013; Myers et al. 2014). Sex-specific information is not collected from Summer Flounder landings as part of the annual assessment process because, like other flatfishes, there are no external characteristics that can be used to identify the sex and Summer Flounder cannot be dissected by port agents and still retain their market value. However, on the National Marine Fisheries Service, Northeast Fisheries Science Center (NMFS-NEFSC) bottom trawl survey, conducted twice annually in the spring and fall, sex-specific data are collected using fish dissection (NEFSC 2013).

When fishery-independent survey data are sex-specific and the probability of a given sex at a given length or age are similar between the survey and the catch, it may be possible to apply a sex-at-length or sex-at-age key developed from survey data directly to length or age data from the catch (Clark 2004). However, the sex composition of the

catch is influenced by a combination of the differences in the size-, age-, and sex-specific retention selectivity imposed by the minimum retention size in each fishery (Kendall and Quinn 2013), the size-, age-, and sex-specific vulnerability of fish resulting from their interaction with (Ryer 2008; Somerton et al. 2011), and/or their availability to (Okamura 2014; Sampson 2014), the fishing gears, and the spatial-, temporal-, and sex-specific growth rates of the fish being retained by the different sampling gears (Poole 1961; Planes et al. 1999; Wilderbuer and Turnock, 2009). For instance, different minimum retention size limits are implemented in the recreational and commercial Summer Flounder fisheries (NEFSC 2013) and some limited evidence suggests that the availability/vulnerability of the sexes at a given length to the fishing effort may vary seasonally and between the recreational fishery and the NMFS-NEFSC survey (Morson et al. 2012). These fishery-specific processes can result in differences in the sex-composition within the catch and between the catch and the survey, so an assumption of equal probabilities of sex-at-length or sex-at-age between catch and survey data may be incorrect.

In this chapter I examine trends in the sex composition of summer flounder landed in the recreational and commercial fisheries. Given these trends, I test the efficacy of applying NMFS-NEFSC survey-derived sex-at-age keys to catch data so that the stock assessment of Summer Flounder might implement a sex-specific model. Finally, I discuss some of the underlying ecological processes that may be driving the observed patterns in selectivity.

Methods

Data Collection

Summer Flounder *Paralichthys dentatus* were collected along the northeast and mid-Atlantic continental shelf of the USA in 2010 and 2011 from a fishery-independent survey (NFS) and from commercial (CFS) and recreational hook-and-line (RFS) fishery landings (Table 2.1). For all fish, total length, sex, and catch location were recorded. For a subset of the fish sampled, otoliths and/or scales were removed for aging (Table 2.1). Otoliths were removed from carcasses collected from the RFS. Scales were collected for specimens up to 60 cm and otoliths for fish greater than 60 cm from the CFS and the NFS. Otoliths were processed by selecting the right side otolith and center-aligned in a merchandise tag, embedded in black polyester resin, and then cross-sectioned through the core with a low-speed sectioning saw. After processing, otoliths were examined using a Leica MZ-6 dissecting microscope with transmitted light at between 8 and 60 times magnification. Annuli from otoliths were identified as narrow opaque bands and were counted along the ventral side of the sulcal groove. Scales were processed by selecting five or six samples from each fish and impressing them on acetate sheets. Impressions were examined using a microfiche reader with 20 and 29mm lenses. Annuli were identified in scales by using established protocols described in Pentilla and Dery (1988).

The National Marine Fisheries Service, Northeast Fisheries Science Center (NMFS-NEFSC) provided NFS data for Summer Flounder sampled from the spring and fall bottom trawl survey cruises at predetermined sampling strata at depths ranging from 27 m - 365 m from Cape Hatteras, North Carolina, USA to Nova Scotia, Canada. A

detailed description of the bottom trawl survey design can be found in Azarovitz (1981) and NEFSC (1988), but briefly between 350 and 400 stations are sampled each year with a bottom trawl that has a 1.5 cm stretch mesh liner and rollers for sampling hard substrate. Tows are conducted for 30 minutes at each station at a tow speed of 3.5 knots. CFS and RFS data were collected by sampling fish landed at marinas, packing houses, and fishing docks from North Carolina to Massachusetts (Table 2.2).

Sampling of the CFS occurred year-round wherever the fishery was operational. The minimum mesh size in the CFS was a 14 cm diamond mesh or 15 cm square mesh applied throughout the net body, extension, and codend. For each visit to a commercial dock, samples from up to 100 fish were collected haphazardly in each market category (medium, large, and jumbo) available from a given fishing trip. The market category is determined by each dock or packing house, but generally, small fish ranged from 35 cm - 45 cm, medium fish from 45 cm - 55 cm, and jumbo fish were greater than 55 cm. At these sizes, all fish sampled were sexually mature. Summer Flounder cannot be sexed using external characteristics; so, to avoid a reduction in market value, a developed a minimally-invasive technique for determining sex (Figure 2.1). A one-inch incision was made on the pigmented side of the fish in an area halfway between the anterior end of the anal fin and the center of the pectoral fin. Using forceps, the gonads were pulled out through this incision. Orange eggs or empty ovaries and the white testis tissue were used to differentiate female and male fish, respectively. Both male and female fish were easily identified even when sampling did not occur during the spawning season.

RFS ports were sampled once per week during the recreational fishing season (May-September) to collect racks (fileted carcasses) of all Summer Flounder caught that day

on all participating boats. Once Summer Flounder were fileted, the sex organs remained intact and visible on the rack. Boat captains and crew saved fish racks in a bin and those racks were collected upon arrival at a participating dock. In order to increase the number of fish available for collection, freezers were placed at each dock. Bags and waterproof tags were provided to the boat captains and crew and were available near the freezers so that samples could be accurately labeled with the date and location of the catch. Participating boat captains were asked to deposit all fish racks from the day's catch in these tagged bags and place the bags in the freezers. Freezers were emptied by scientists upon arrival at a dock to collect fresh racks. Morson et al. (2012) concluded that the change in Summer Flounder length from freezing was negligible. To ensure a representative sample of harvested Summer Flounder sex, length, and age, all fish caught on a fishing trip were sampled without regard to size. Sex was determined by macroscopic investigation of exposed gonad on filleted fish carcasses. Over ninety-nine percent of fish collected had reproductive organs intact and readily visible to the naked eye.

For all fish sampled from the RFS and CFS, a record was kept of the NMFS-NEFSC statistical area where the fish were caught (Figure 2.2 and Table 2.3). The CFS and RFS operate in different statistical areas so that there was not complete overlap between the two fisheries relative to fishing location. On the NFS, data were collected along stratified sampling strata. To make spatially-comparable comparisons between the NFS and the RFS/CFS, latitude and longitude from each NFS tow were used to assign NFS samples to NMFS-NEFSC statistical areas.

Data analysis

Age was determined for 23,020 of the 36,745 Summer Flounder sampled from the RFS, CFS, and NFS (Table 2.1). To utilize the full set of data to determine how well sex-at-age collected on the NFS described sex-at-age in the RFS and CFS, it was necessary to generate appropriately partitioned age-length keys (ALKs) and apply those keys to fish not aged empirically. Age-length data were partitioned by sex, region, and data source (SFS/CFS/RFS). Region was defined as north, which included all fish caught or collected north of 40° latitude; or south, which included all fish caught or collected south of 40° latitude. To compare ALKs, the age distribution at a given length was modeled using multinomial logistic regression (Gerritsen et al. 2006). The multinomial log-linear models were fit via neural networks using the function *multinom()* available in the R package *nnet* (Venables and Ripley 2002). This approach provided a simple and robust method for identifying significant differences between ALKs generated from data partitioned by sex, region, and data source. The best-fit model identified the most appropriate stratification of the data and ALKs were generated based on that stratification. ALKs were then applied to all fish not aged empirically based on a probability of each age given the length of each fish using the *ageKey* function in the R package *FSA* (Isermann and Knight 2005; Ogle 2014).

I used logistic regression to evaluate the efficacy of applying a sex-at-age key developed from NFS data to CFS and RFS age data. The probability of landing a female at given age was modeled as the dependent variable and the data source (NFS, CFS, and RFS) was modeled as the independent variable (Wilson and Hardy 2002; Morson et al. 2012). Significant differences between the NFS and both fishery data sources suggested

a sex-at-age key developed from raw NFS data would not be appropriate in describing the sex composition from either fishery. I hypothesized that the size-, age-, and sex-specific retention selectivity imposed by the minimum retention size (MRS) of 35 cm in the CFS and of between 46 cm and 53 cm in the RFS, as well as the differences in growth rates between fish collected from the three data sources, could explain the variability in sex-at-age among the datasets. Therefore, I simulated, independently for the CFS and RFS, the effects of these fishery-specific processes on the fishery-independent survey data and re-analyzed the resultant sex ratio-at-age.

First, to simulate the length-specific retention selectivity of the RFS and CFS, I left-truncated the NFS data at the MRS of each fishery. This approach provided a NFS-derived measure of sex-at-age comparable to the left-truncated sex composition in each fishery-dependent set of data. A 35-cm MRS was implemented coast-wide in the CFS during the sample-collection period, so NFS and CFS data were left-truncated at 35 cm for the CFS comparison. The recreational fishery MRS varied from 46cm -53 cm depending on the landing year and state. To avoid too many pair-wise comparisons using too little data, I left-truncated the NFS and RFS data at 46 cm and at 53 cm in two separate comparisons that together encompass the full range of potential comparisons.

To simulate the observed growth rates in the CFS and RFS, sex- and region-specific ALKs generated from CFS and RFS data were applied to the left-truncated sex- and region-specific NFS length data. This allowed us to assign age to the left-truncated distribution of lengths in the NFS data as if the NFS fish grew at the same rates as in each respective fishery.

Finally, as a proxy for evaluating the length-specific vulnerability of the sexes to the fisheries, I compared the left-truncated NFS-derived sex ratio-at-length to the measured sex-at-length from the CFS and RFS. Since the NFS utilizes a smaller mesh size than the regulation size in the CFS and the RFS-MRS is set higher than that in the CFS, all left-truncated NFS data in these comparisons come from fish that are fully recruited to the survey. A logistic regression model was fit to estimate the probability of landing a female at a given length for each pairwise comparison.

All statistical analyses were computed in R v3.0.3 (R Core Team 2014). Model selection followed Akaike Information Criterion (AIC). A model score that was two AIC units lower was accepted as evidence for better fit among competing models (Arnold 2010).

Results

Summer Flounder *Paralichthys dentatus* from 27 different NMFS-NEFSC statistical areas were sampled on the NMFS-NEFSC bottom trawl survey (NFS) and from the commercial (CFS) and recreational (RFS) fishery port sampling programs (Table 2.3). The samples collected from the CFS were distributed inshore and offshore across similar statistical areas as those collected on the NFS, but the RFS samples were limited to statistical areas located inshore (Figure 2.2 and Table 2.3).

The probability that a fish of a given length was a given age depended on its sex, region, and data source (NFS/CFS/RFS; Table 2.4). Sex was the most important effect in the model, followed by data source, and region.

The sex ratio-at-age in the NFS was significantly different than the CFS ($p < 0.0001$) and the RFS ($p < 0.0001$) when comparisons included all NFS data (Figure 2.3a and Figure 2.4a). A higher proportion of the catch-at-age is female in both fisheries (Figure 2.3a, 4a, and 5a). However, fish landed under a minimum retention size (MRS) had a higher mean length-at-age than fish collected by the NFS. The higher the MRS imposed on the landed fish, the higher the mean length-at-age (Figure 2.6). This effect was apparent for all ages containing the MRS within their length frequency. When NFS data were left-truncated to simulate the MRS in the CFS and RFS to account for this, the sex ratio-at-age pattern more closely approximated the pattern in the data collected directly from the fisheries (Figure 2.3b, 4b, and 5b). The proportions-at-age in the survey-derived data shifted dramatically toward female fish at younger ages (Figures 3b, 4b, and 5b). Applying, separately, sex- and region-specific age-length keys (ALK) generated from CFS and RFS data to left-truncated sex- and region-specific NFS length data resulted in a sex ratio-at-age pattern that further resembled the pattern of the data collected directly from the CFS and RFS (Figures 3c, 4c, and 5c). The shift in sex ratio-at-age suggests that the differences in growth between the fish landed in the fisheries and the fish collected on the survey is sex-specific. Females landed in both fisheries had grown faster than female fish collected from the NFS, and male fish landed in both fisheries had grown slower than male fish collected from the NFS. Thus, applying fishery-specific ALKs resulted in a shift in the sex ratio of younger fish further toward female and a shift in the sex ratio of older fish toward male (Figures 3b and 3c; Figure 2.4b, 4c, 5b, and 5c). For example, in the CFS comparison (Figure 2.3b and 3c), one-year-old survey-derived sex-at-age increased from approximately 40% female (Figure

2.3b) to approximately 65% female (Figure 2.3c) whereas six-year-old survey-derived sex-at-age decreased from approximately 75% female (Figure 2.3b) to approximately 50% female (Figure 2.3c). Even so, statistically significant differences remained between the CFS ($p < 0.0001$) and RFS ($p < 0.0001$) data and the NFS-derived data that were manipulated to simulate the fishery-specific MRS and growth processes within catches from the fisheries.

Given that accounting for the length-specific retention selectivity and the differences in growth rates between the fish landed in the fisheries and those collected on the survey did not remove all of the variability in sex-at-age between the survey and catch data, I attempted to estimate the difference in availability of the sexes to the survey and the fisheries. The length-specific vulnerability of the sexes to the gear, modeled as the probability of a fish being female at a given length, was similar, but statistically different ($p = 0.0037$) for the left-truncated NFS data and CFS data comparison (Figure 2.7a). The probability of landing a female at a given length is slightly higher in the CFS than in the left-truncated NFS (Figure 2.7a). In addition, the proportion female-at-length increased in both the CFS and the left-truncated NFS at similar rates until each reached the smallest MRS in the recreational fishery (~ 45 cm). At this point the female proportion-at-length remained unchanged or increased only slightly from one centimeter-increment to the next until reaching approximately the 50-cm length increment when the rate for both datasets returned to a logistic form (Figure 2.7). The probability of landing a female at a given length was much higher in the RFS than for the left-truncated NFS data ($p < 0.0001$; Figure 2.7b). In fact when a fish is landed in the recreational fishery at the smallest MRS (46 cm), there is an 80% chance that the fish

will be female and this probability rapidly approaches 100% with increasing size (Figure 2.7b).

Discussion

To determine whether the sex composition of Summer Flounder *Paralichthys dentatus* from a fishery-independent trawl survey could be used to estimate the sex composition of the Summer Flounder catch without collecting sex-specific data directly from the fisheries, I simulated fishery-specific processes on the survey data, including the minimum retention size (MRS) in each fishery and the growth rates of fish landed in both fisheries, and compared those survey-derived estimates to the actual sex composition in the catch.

Fish landed in the fisheries had grown at different rates than those collected from the survey, and at different rates from one another, suggesting that each gear is sampling a different part of the population. Furthermore, this effect was sex-specific; female fish landed in the fisheries had grown faster than those collected on the survey, while male fish collected on the survey had grown faster than male fish landed in the fisheries. This suggests that fisheries are selectively targeting faster-growing females and slower-growing males. Stari et al. (2010) offered that sampling location or gear selectivity could explain differences in age-length keys (ALK) for North Sea Haddock *Melanogrammus aeglefinus* collected from different gears. I propose the differences in ALKs found here could result from the spatial sex-specific segregation of Summer Flounder previously suggested (Morson et al. 2012), the influence of region on growth rates previously identified (Kraus and Musick 2001) and further confirmed with this

work, and the spatial and temporal distribution of fishing effort; though the influence of age-specific gear selectivity cannot be ruled out. I discuss spatiotemporal distribution of fish and fishing effort in more detail below.

The MRS in each fishery, operating on the sex-specific growth rates (Poole 1961; King et al. 2001), forces a higher fraction female-at-age in the catch than would be expected in a non-culled, fishery-independent sample. I was able to largely correct for this by left-truncating the survey data to mimic the MRS in each fishery and this transformation of the survey data recovered a sex-at-age pattern more closely resembling the one measured directly from the catch. Not surprisingly, when I applied ALKs developed from fishery-dependent data to left-truncated survey data, the result was a sex-at-age pattern in the survey-derived data that even more closely resembled the one measured directly from the catch.

This step-wise approach to simulating fishery-specific effects on fishery-independent data recovered the pattern of sex-at-age in the fisheries and it may therefore have application to other fisheries where biological data from the catch are limited and a desire exists to estimate sex-specific parameters in an assessment. However, these manipulations did not recover the exact proportions-at-age measured directly from the catch. I hypothesize that this is due to some difference in the spatiotemporal distributions in stock structure and fishing effort, such that the availability of the sexes to the survey and the fishing fleets was not equivalent. As evidence, I show that sex-at-length, used as a proxy for the availability of fish on the bottom to the fishing gears, varied slightly between the commercial fishery and the survey, and dramatically between the recreational fishery and the survey. The recreational fishery occurs

inshore from late spring to early fall, the commercial fishery occurs year-round inshore and offshore, and the NMFS-NEFSC survey occurs offshore once in March and once in September. As no overlap exists in space or time between the recreational fishery and the survey, the expectation is that if spatial and temporal structure to the sex composition exists in the population, then differences in the spatiotemporal availability of the sexes to the survey and recreational fishery will be reflected in the catch. This was observed, manifested in the large difference in sex ratio-at-length between the recreational catch and survey data.

As the commercial fishery overlaps both in time and space with the survey, the expectation is that sex-specific availability of fish to the commercial fishery and survey will be similar. Such a finding also was observed, manifested in the fairly close match in sex-at-length between the commercial catch and the survey data. This is the first evidence, to my knowledge, of sex-specific segregation of Summer Flounder in space and time.

Spatial and temporal segregation of fishes by sex is a common phenomenon and occurs in other sexually-dimorphic flatfishes (Morgan and Trippel 1996; Swain 1997; Swain and Morin 1997; Gorchinsky 1998; Richards et al. 2008; Gerritsen 2010; Sahin and Gunes 2010; Loher 2012; Loher and Hobden 2012). Explanations for sex-specific segregation include temperature (Swain 1997) and/or depth (Swain and Morin 1997) selection, sex-specific life history strategies that promote sexually-dimorphic characteristics (Gerritsen et al. 2010), and sex-specific foraging intensity and the spatial and temporal distribution of the forage base (Swain and Morin 1996). Any of these postulations could be advanced to explain the sex-specific distribution of Summer

Flounder in space and time. The importance, however, of estimating and understanding the sex-specific spatial and temporal distribution of Summer Flounder goes beyond these interesting ecological implications. Okamura et. al (2014) showed that biological reference points are highly sensitive to assumptions about effort allocation in space and time when seasonal migrations of Offshore Lingcod *Ophiodon elongatus* are sex-specific. A similar analysis for Summer Flounder is beyond the scope of this paper, but, minimally, the application of sex-aggregated ALKs to landings data should result in highly biased estimates of the catch-at-age given that female Summer Flounder grow much faster than males and that the recreational fishery lands female fish almost exclusively. Accounting for the complex spatiotemporal dynamics in the distribution of sex composition and fishing effort will undoubtedly complicate future stock assessments of Summer Flounder.

Given the importance of having an accurate estimate of the sex composition of the catch and the failure of my method to recover an exact match by applying sex-specific processes to survey data, because of what appear to be complex, time- and space-varying sex-specific fishery selectivities, it makes sense to explore other options for collecting sex-composition data directly from fishery landings. In the recreational fishery, this would be easy to incorporate into any port-sampling program that already collects length-frequency data from the catch. I show that even when Summer Flounder are fileted at sea, the gonad remains intact and readily visible to the naked eye. An observer measuring the length of a fish can determine the sex macroscopically with no additional time or cost. In the commercial fishery, collecting sex-specific information may prove more difficult because fish are not fileted at sea to expose the gonads and

fish are typically sold whole to market, which precludes full dissection of fish to determine the sex. I introduced a method for determining sex using a small incision in the gut cavity. Although this may still be too invasive for some fishing ports or fish sellers or buyers, I encountered no resistance on the part of the many commercial docks that I sampled. The Pacific Halibut Commission used microsatellite-based genetic techniques to measure the sex composition of the catch (Loher et al. 2012). This reduced the influence of spatial and temporal variability in survey and fishing effort when deriving sex composition of the catch using survey data because it provided a direct measure of the sex composition of the catch. A cost-benefit analysis of purchasing fish and dissecting them vs. the development of microsatellite techniques may shed some light on the most cost- and time-effective way forward for determining the sex composition of the commercial catch. No matter how the data are obtained though, if a program is instituted to collect sex composition data directly from the catch it would need to mirror the spatial and temporal distribution of the fishing effort since it appears male and female fish disaggregate in time and space.

The trends observed in the sex, length, and age of the catch may interact with fishing regulations and induce changes in population structure. The mean length-at-age of individuals in the Summer Flounder population is declining over time with no accompanying change in the length-weight relationship or condition index (NEFSC 2013) that one might expect from density-dependent influences on individual fish growth (Rose et al. 2001). Given the dynamic nature of climate change in the northwestern Atlantic Ocean (Scavia et al. 2002), and its influence on the fish stocks of this region (Rothschild and Jiao 2012; Sparrevohn et al. 2013), a simple

environmentally-determined change in growth rate in the Summer Flounder stock cannot be discounted. Nonetheless, I show a trend of increasing mean length-at-age with increasing MRS in the fishery landings. The MRS being implemented is selecting, at a given age, the fastest growing fish while leaving behind the slower growing fish to reproduce another year. A growing literature addresses the potential evolutionary effects of size-selective fishing (e.g., Conover and Munch 2002; Law 2007). Varying opinions exist concerning the time-scale and fishing pressure needed to induce evolutionary change as opposed to simple phenotypic change in a fish population (e.g., Anderson and Brander 2009; Enberg et al. 2009); however the possibility cannot be ruled out that the size-selective fishing pressure on the Summer Flounder population could be causing a shift in the genetic structure of the stock favoring slower growth and resulting in a decrease in the mean length-at-age over time.

Additionally, the proportion female-at-age in the Summer Flounder population is in decline (NEFSC 2013). If the MRS is selecting the faster growing fish in the population at a given age, those fish have to be disproportionately female because of the difference in growth rates between the sexes. My sampling found that the sex-at-age relationships from the recreational catch, and to a lesser extent from the commercial catch, are skewed toward female fish in comparison to the sex-at-age expected from survey data. Simulation of the effects of the MRS shows that this result accrues in part from the implementation of the MRS in each fishery. For example, the proportion of fish that are female increases with increasing length in the survey, as well as in the fisheries. But, interestingly, in both the commercial fishery data and survey data, at around the 5 cm increment that encompasses the range of MRS implemented in the recreational fishery

(45 cm - 50 cm), the sex ratio remains relatively unchanged, when the expectation is that it should increase as it does at each length increment before and after the 45 cm - 50 cm increment. This suggests the MRS implemented in the recreational fishery may have altered the population sex ratio within this range of sizes. One potential explanation, therefore, for the trend of decreasing proportion female-at-age in the population over the last decade (NEFSC 2013) could be the increases in MRS used to rebuild the stock over that same time period and the associated increases in female-specific fishing mortality. Sex-specific differences in fishery selectivity happen in other sexually-dimorphic flatfishes regulated by an MRS (Briggs 1965; Lohre and Hobden 2012). In fact, the sex composition estimates for commercial Pacific halibut *Hippoglossus stenolepis* landings indicate that males may never reach mean sizes associated with full fishery selectivity-at-age (Clark and Hare 2006).

If current management strategies are driving changes in the structure of the Summer Flounder stock, it is important for managers to consider the potential adverse effects of those changes. Size-selective fishing can alter the sex ratio of a population (Kendall and Quinn 2013) and influence the reproductive potential of the stock (Rowe and Hutchings 2003; Claereboudt et al. 2004; Rijnsdorp et al. 2010) and genetic traits selected against by implementing a MRS as a management strategy may be difficult to recover (Enberg et al. 2009).

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TABLES – CHAPTER 1

Table 1.1. Total number of fish sampled for sex and length and the subset of those fish that were also aged by examining annuli in otoliths and scales (see Methods).

Survey	Sex and length	Age
NMFS-NEFSC bottom trawl survey (NFS)	4,828	3,935
Commercial fishery survey (CFS)	18,685	11,809
Recreational fishery survey (RFS)	13,232	7,276
Total	36,745	23,020

Table 1.2. Locations where samples were collected from the recreational and commercial Summer Flounder fisheries.

Recreational Fishery		Commercial Fishery	
State	Port	State	Port
VA	Virginia Beach	NC	Wanchese
	Hampton	VA	Hampton
	Buckroe		Newport News
	James River	NJ	Cape May
	Capeville		Barnegat Light
	Wachapreague		
	Yorktown		
	Cape Charles		
	Mathews		Point Pleasant
MD	Ocean City	NY	Point Lookout
DE	Lewes		Hampton Bays
NJ	Cape May		Mattituck
	Fortescue		East Hampton
	Barnegat Light		Montauk
	Point Pleasant	CT	Stonington
	Atlantic Highlands	RI	Point Judith
NY	Freeport	MA	Westport
	Huntington		New Bedford
	Captree		Hyannis
	Port Jefferson		
	Moriches		
	Riverhead		
	Hampton Bays		
	Mattituck		
	Greenport		
	East Hampton		
	Montauk		
CT	Niantic		
RI	Point Judith		
MA	New Bedford		
	Hyannis		

Table 1.3. Total number of fish sampled, by NMFS-NEFSC statistical area (see Figure 1.2), from the NMFS-NEFSC bottom trawl survey, the commercial fishery, and the recreational fishery.

NMFS-NEFSC Statistical area	NMFS-NEFSC bottom trawl survey (NFS)	Commercial fishery (CFS)	Recreational fishery (RFS)
201			930
393			419
514	12		
521	3	40	
522	14	120	
525	71	401	
526	230	157	
537	741	1,596	
538	5	454	1,278
539	270	2,558	1,065
561		39	
562	27		
611		2,028	1,078
612	7	842	3,454
613	658	3,985	839
614	112	687	45
615	262	3,343	40
616	441	822	
621	421	434	4,080
622	289	508	
623	18		
625	178	176	22
626	493	488	
631	141		15
632	114		
635	293		
636	44	15	

Table 1.4. Akaike information criterion (AIC) for eight potential models describing the probability of a given age provided the length (null model) and the sex, region (north of 40° latitude or south of 40° latitude), and data source (data collected from the recreational fishery, the commercial fishery, or a fishery-independent trawl survey).

Model	DF	AIC	Delta AIC	Residual deviance
Sex, region, data source	65	59836	0	59668
Sex, region	56	60226	390	60114
Sex, data source	70	60268	432	60128
Sex	42	60605	769	60521
Region, data source	70	65590	5754	65450
Data source	56	65949	6113	65837
Region	42	66242	6406	66158
	28	66550	6714	66494

FIGURES – CHAPTER 1

Figure 1.1. Photographs showing a technique for determining the sex (A = Female; B = Male) of a Summer Flounder without dissecting the entire fish. A small incision is made along the gut cavity and the gonads are pulled through the incision with a pair of forceps.

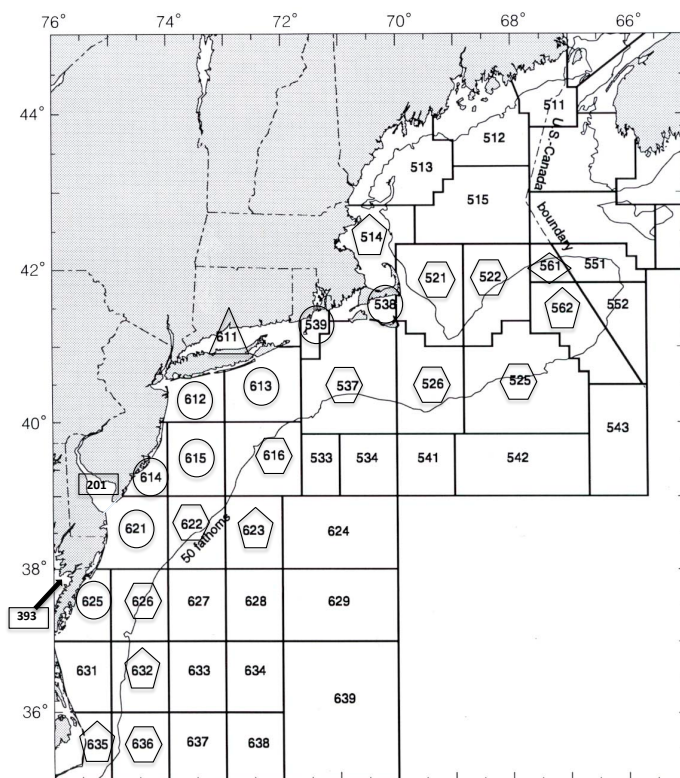


Figure 1.2. Map showing National Marine Fisheries Service, Northeast Fisheries Science Center statistical area units along the northeast USA and the western mid-Atlantic continental shelf (NEFSC 1997). The shapes around the statistical area number indicate the data source as NMFS-NEFSC bottom trawl survey (NFS), commercial fishery (CFS), or recreational fishery (RFS). Rectangles represent RFS only, diamonds represent CFS only, pentagons represent NFS only, triangles represent RFS and CFS, hexagons represent NFS and CFS, and circles represent RFS, CFS, and NFS.

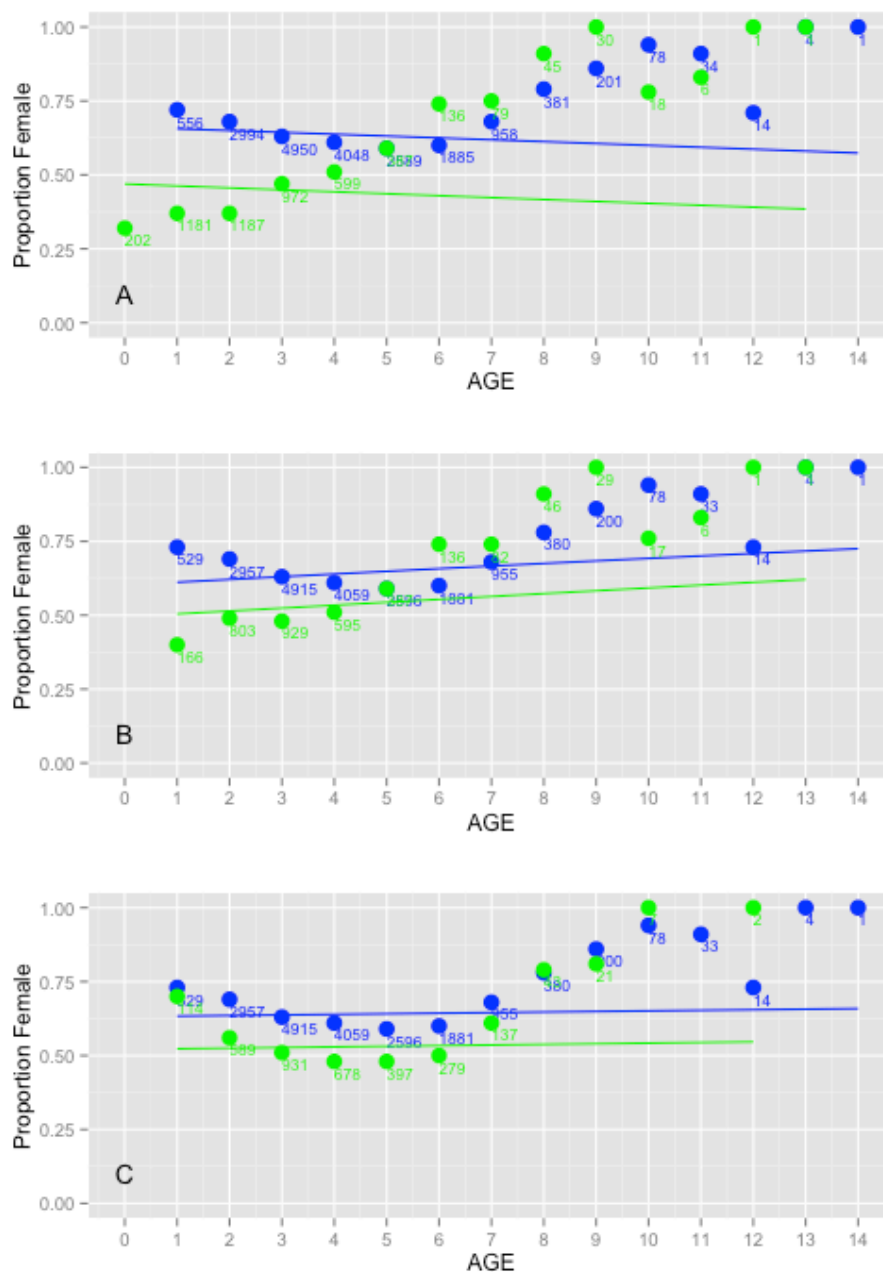


Figure 1.3. Proportion female Summer Flounder at-age in the commercial fishery (blue dots) and the National Marine Fisheries Service, Northeast Fisheries Science Center (NMFS-NEFSC) bottom trawl survey (green dots). Lines represent the probability of landing a female estimated by logistic regression (see text). Commercial fishery data are compared to (A) raw NMFS-NEFSC bottom trawl survey data, (B) NMFS-NEFSC bottom trawl survey data that were left-truncated at 35 cm to simulate the minimum retention size in the commercial fishery, and (C) NMFS-NEFSC bottom trawl survey data that were left-truncated at 35 cm and assigned age based on age-length keys generated from commercial fishery data.

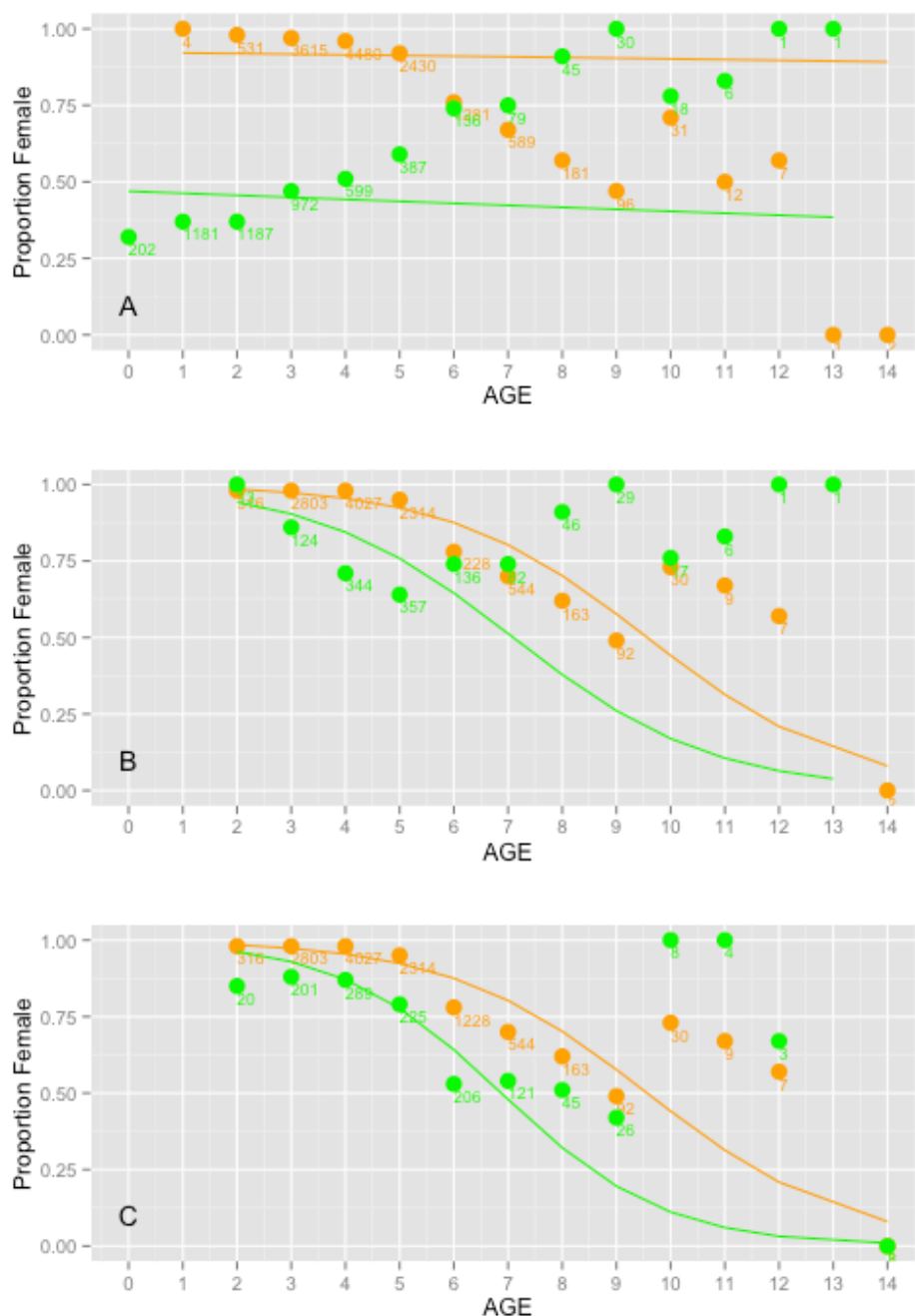


Figure 1.4. Proportion female Summer Flounder at-age in the recreational fishery (orange dots) and the National Marine Fisheries Service, Northeast Fisheries Science Center (NMFS-NEFSC) bottom trawl survey (green dots). Lines represent the probability of landing a female estimated by logistic regression (see text). Recreational fishery data are compared to (A) raw NMFS-NEFSC bottom trawl survey data, (B) NMFS-NEFSC bottom trawl survey data that were left-truncated at 46 cm to simulate the smallest minimum retention size in the recreational fishery, and (C) NMFS-NEFSC bottom trawl survey data that were left-truncated at 46 cm and assigned age based on age-length keys generated from recreational fishery data.

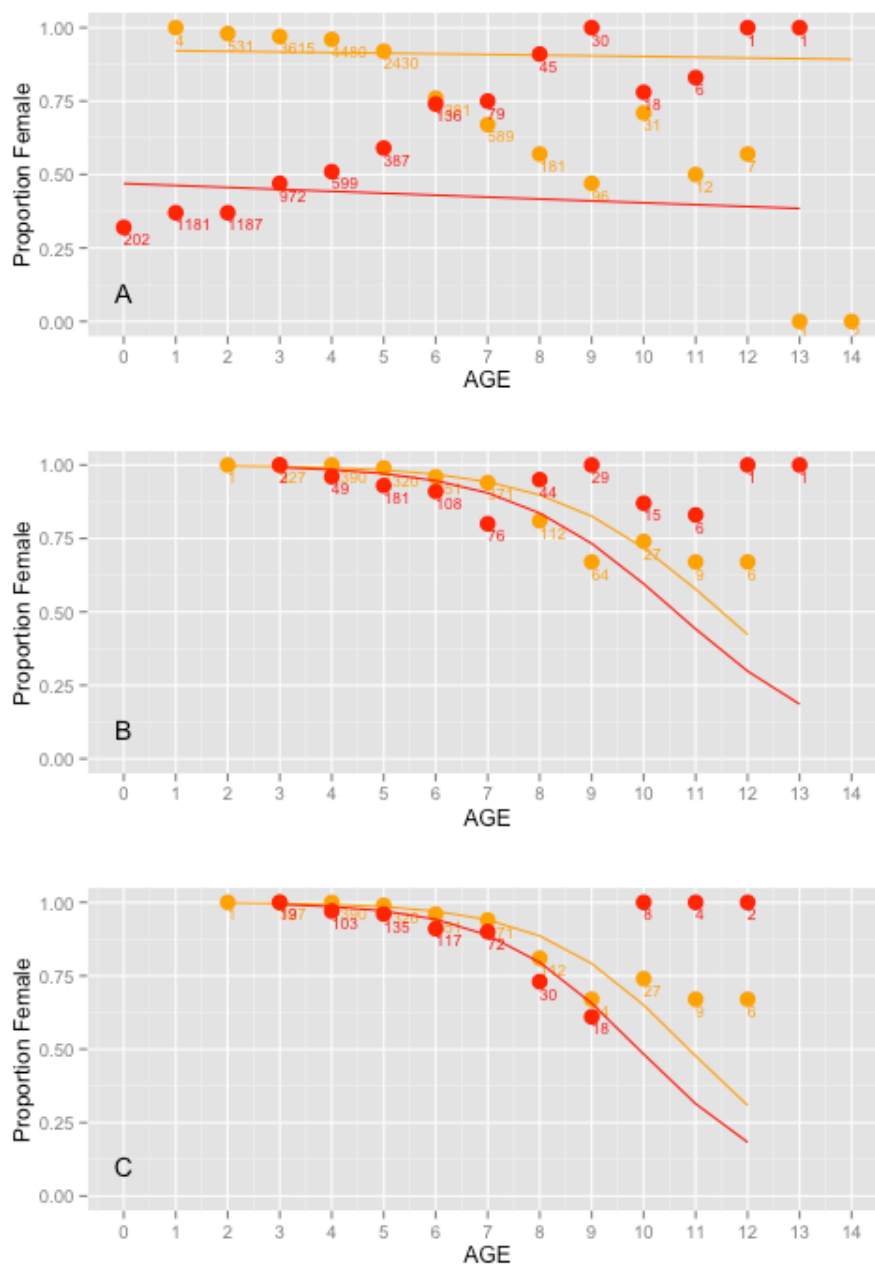


Figure 1.5. Proportion female Summer Flounder at-age in the recreational fishery (orange dots) and the National Marine Fisheries Service, Northeast Fisheries Science Center (NMFS-NEFSC) bottom trawl survey (red dots). Lines represent the probability of landing a female estimated by logistic regression (see text). Recreational fishery data are compared to (A) raw NMFS-NEFSC bottom trawl survey data, (B) NMFS-NEFSC bottom trawl survey data that were left-truncated at 53 cm to simulate the largest minimum retention size in the recreational fishery, and (C) NMFS-NEFSC bottom trawl survey data that were left-truncated at 53 cm and assigned age based on age-length keys generated from recreational fishery data.

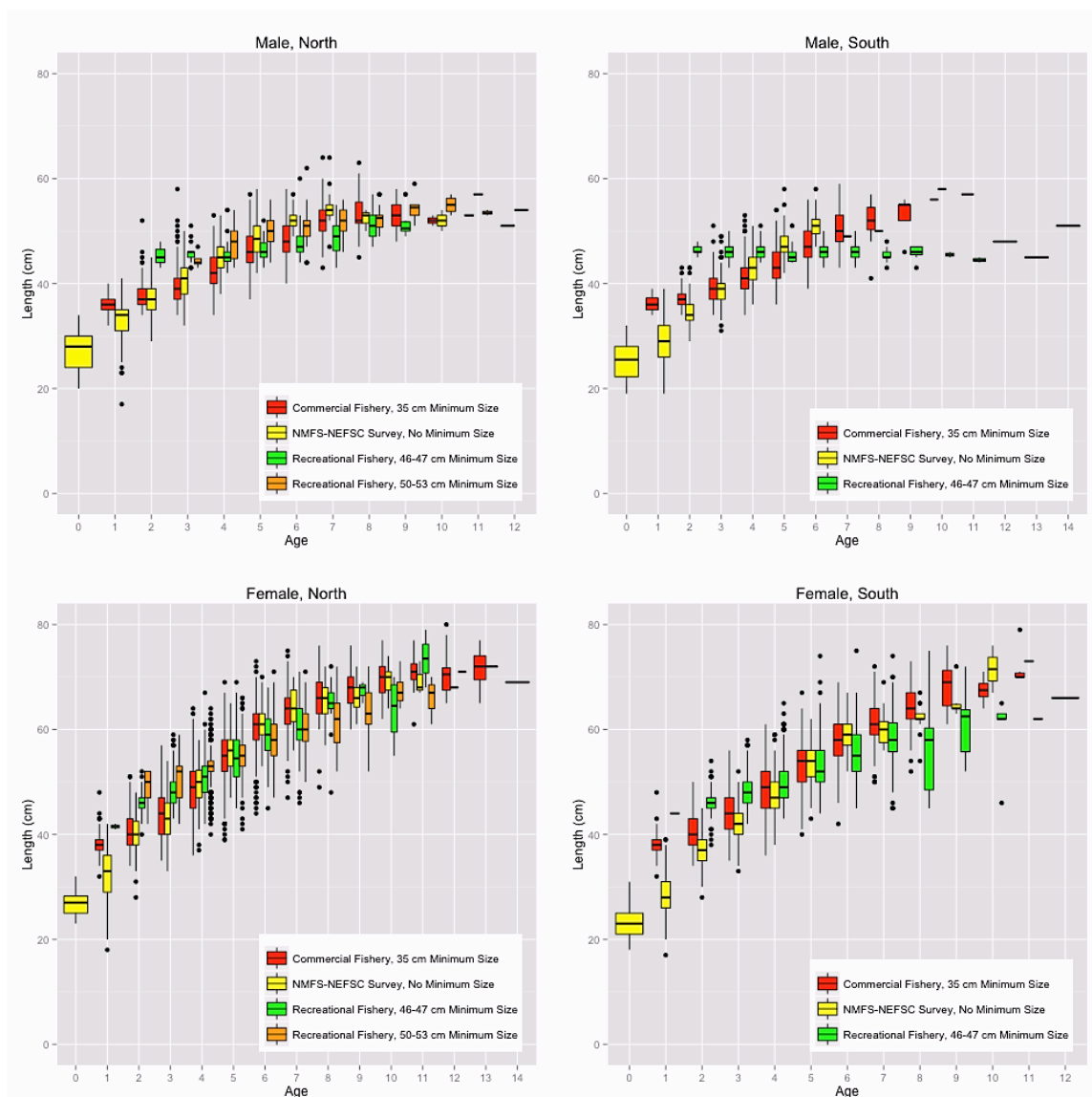


Figure 1.6. Box and whisker plots of the mean length-at-age of Summer Flounder under different minimum retention size regulations. Plots are organized by region (north and south) and sex (male and female). Black horizontal lines are the mean, boxes are the interquartile ranges, black vertical lines are the 5th and 95th percentiles, and dots are outliers.

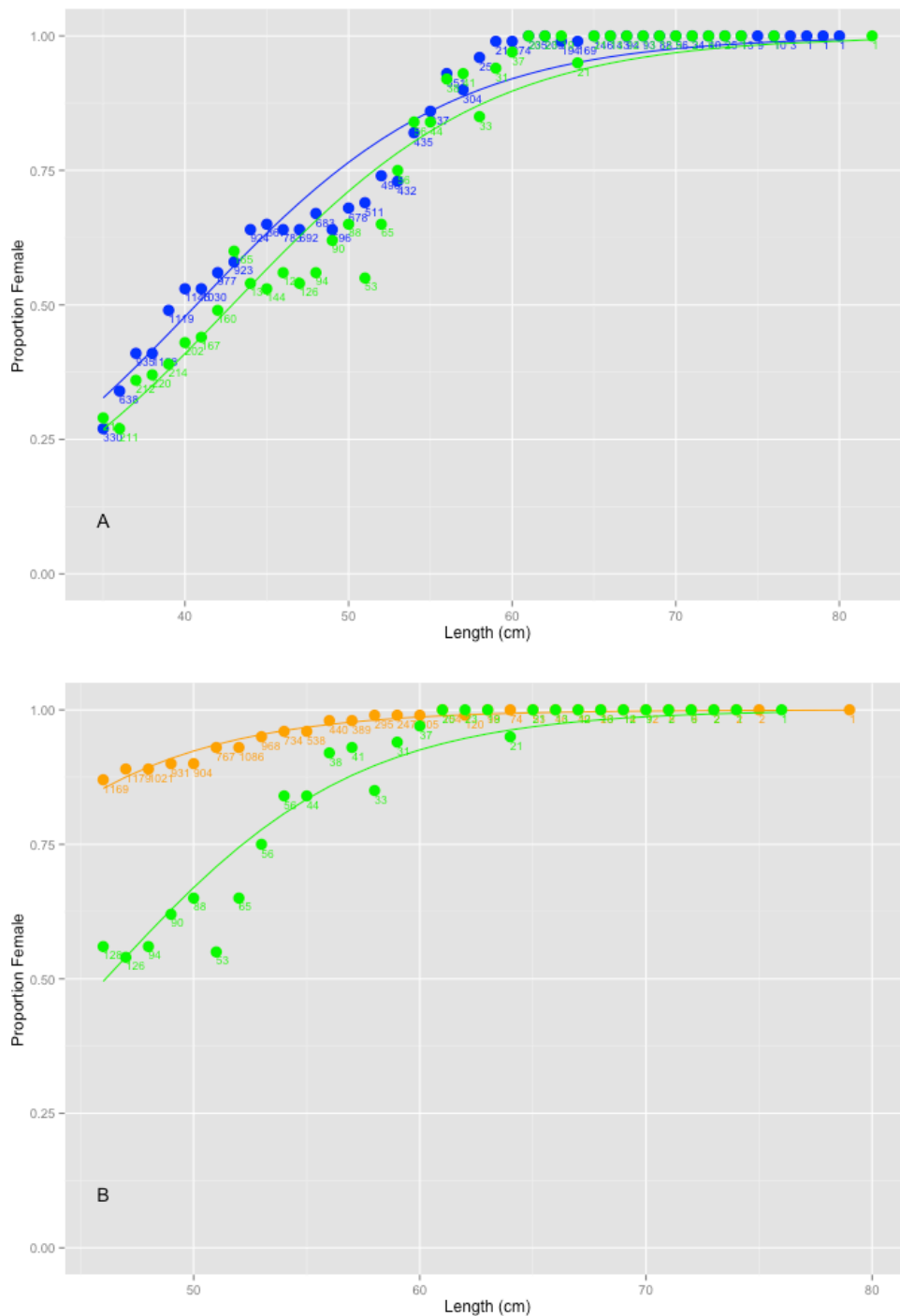


Figure 1.7. Proportion female Summer Flounder at-length in the commercial fishery (blue dots), the recreational fishery (orange dots), and the National Marine Fisheries Service, Northeast Fisheries Science Center (NMFS-NEFSC) bottom trawl survey (green dots). Lines represent the probability of landing a female estimated by logistic regression (see text). NMFS-NEFSC bottom trawl survey data are truncated according to the minimum retention size in the (A) commercial fishery (35 cm) and (B) recreational fishery (46 cm).

CHAPTER 2

**EVALUATING THE POTENTIAL FOR A SEX-BALANCED HARVEST
APPROACH IN THE RECREATIONAL SUMMER FLOUNDER *PARALICHTHYS*
DENTATUS FISHERY****

Abstract

Summer Flounder (*Paralichthys dentatus*) support important recreational and commercial fisheries along the northeast and mid-Atlantic coasts of the USA. In the recreational sector, management efforts to constrain harvest below the maximum allowable catch have typically involved increasing the minimum landing size; however, females grow faster than males. Thus, reliance on increased minimum size limits as a management strategy has resulted in approximately 90% of the recent recreational landings being large, female fish. I evaluated the potential for slot limits to produce a sex-balanced harvest in the recreational Summer Flounder fishery. To estimate the size- and sex-specific vulnerability I sampled the landed and discarded fish (n=3,290) caught by recreational anglers on select party boats from New Jersey to Rhode Island during the 2016 recreational fishing season. I then examined the performance of a wide array of slot limits to estimate which would have promoted a more sex-balanced harvest while maintaining a fixed fishing mortality given the observed catch composition. I demonstrate that slot limits applied to the recreational Summer Flounder fishery have the potential to simultaneously meet multiple management objectives, including conservation of female biomass while maintaining a fixed fishing

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mortality; however, no single slot limit performed best at all sampling locations.

Results should therefore be viewed as optimal given the observed catch composition for the year, fishing mode, and locations that were observed and further evaluation of interannual, spatial, and fishing mode variability is warranted.

Introduction

Targeted fishing of certain species within an ecosystem or a particular demographic within a population is known as selective fishing, an activity that may lead to detrimental imbalances (Law 2000; Bundy et al. 2005; Daan et al. 2005; Jorgensen et al. 2007; Anderson et al. 2008). Distributing a moderate fishing mortality across the widest possible range of species, stocks, and demographics in an ecosystem in proportion to their natural productivity could reduce the negative effects of selective fishing on biodiversity and population productivity (Zhou et al. 2010; Garcia et al. 2012). This ‘balanced harvest’ approach has gained traction as ecosystem-based strategies to fisheries management become more popular, but the purported necessity and benefits of a blanket balanced harvest approach continue to be debated (Jacobsen et al. 2013; Froese et al. 2015; Breen et al. 2016; Anderson et al. 2016; Froese et al. 2016; Kolding et al. 2016). There is, however, strong evidence that at least sex-selective harvesting can have a negative impact on reproductive rates and stock productivity, as well as alter sex ratio and life history (Clark and Tait 1982; Orensanz et al. 1998; Alonzo and Mangel 2004; Hamilton et al. 2007; Hutchings and Rowe 2008). When feasible, fishing regulations that promote exploitation of male and female fish in equal

proportions are therefore often preferred over those that result in a female-biased harvest.

Summer Flounder, *Paralichthys dentatus*, support important recreational and commercial fisheries along the northeast and mid-Atlantic coasts of the USA. In 2015, an estimated 12.5 million summer flounder were caught in the recreational fishery alone (Terceiro 2016). In this sector, management efforts to constrain harvest below the maximum allowable catch have typically involved increasing the minimum landing size; however, Summer Flounder are sexually dimorphic. Females grow faster and mature at a larger size than males (Poole 1961; Morse 1981; Packer et al. 1999). Thus, reliance on increased minimum size limits as a management strategy has resulted in approximately 90% of the recent recreational landings being female fish (Morson et al. 2012, 2015). Furthermore, the female fish that are targeted are also the largest, and therefore potentially the most fecund fish in the population (Morse 1981; Berkeley et al. 2004; Birkeland and Dayton 2005; Hixon et al. 2013; Shelton et al. 2015; Stige et al. 2017).

Slots limits offer an alternative management approach to traditional minimum size limits in that they restrict landings to some intermediate range of sizes while large and small fish are released (Gwinn et al. 2013). In the Summer Flounder recreational fishery, it was previously demonstrated that slot limits have the potential to increase landings in numbers under a fixed fishing exploitation rate by weight (Bochenek et al. 2010; Powell et al. 2010). If smaller males are vulnerable to recreational fishing effort, a similar approach that redirects some fraction of the fishing mortality toward smaller-sized fish may also balance the fishing mortality with respect to sex. However, the only

information available on the sex composition of the Summer Flounder recreational catch comes from fish that were landed and are therefore larger than the minimum size limit (Morson et al. 2012, 2015). Without an estimate of the sex composition for fish below the minimum landing size, it is not possible to evaluate the sex-specific outcomes of such alternative management options.

Given the highly sex-biased catch composition identified in Chapter 1 for the recreational Summer Flounder fishery, in this chapter I evaluate the potential for slot limits to produce a more sex-balanced harvest. To estimate the full size- and sex-specific vulnerability I sampled additional landings, as well as all discarded fish, caught by recreational anglers on select party boats from New Jersey to Rhode Island during the 2016 recreational fishing season. I then examined the performance of a wide array of slot limits to estimate which would have promoted a more sex-balanced harvest while maintaining a fixed fishing mortality given the observed catch composition.

Materials and Methods

Field program

Data collection focused on three states: New Jersey, New York, and Rhode Island; and one fishing mode: for-hire mode. In 2016, these states accounted for 82% of the total catch by state; however, the for-hire fishing mode accounted for only 5% of the total catch by mode. While the for-hire mode accounted for only a small fraction of the total catch, the private mode, which accounted for 89%, operated across a similar spatial scale. In 2016, 34% and 31% of the total catch in the for-hire and private modes, respectively, came from open ocean waters less than or equal to three miles from the

coast. In the same year, 42% and 54% of the total catch in the for-hire and private modes, respectively, came from inland waters (personal communication from the National Marine Fisheries Service, Fisheries Statistics Division, 5/25/17). Given the two fishing modes access the same areas, data collection focused on the for-hire mode. The larger, for-hire vessels had space for up to 75 anglers which significantly increased the sample size potential on any one sampling trip.

Data collection spanned one entire recreational fishing season from May 23, 2016 through September 16, 2016. Fish were collected bi-weekly aboard participating fishing vessels from Cape May (8 trips) and Atlantic Highlands (8 trips), NJ, Captree (9 trips) and Montauk (10 trips), NY, and Point Judith, RI (6 trips) (Figure 2.1). The total length of every Summer Flounder caught, whether landed or discarded, on each trip was measured. In addition, the sex for all landed Summer Flounder was recorded. Since Summer Flounder must be dissected to determine sex, ten discarded fish were also sacrificed within predetermined fish length and water depth bins on each sampling trip (Table 2.1). A sex ratio, by depth bin, length bin, and trip, was applied to any unsexed discarded fish to assign sex to the entire discarded portion of the catch (Table 2.1).

Analysis

To estimate the effect of different slot limits on three performance metrics, the total number of dead fish (landings + dead discards), the biomass of dead females, and the ratio of dead discards to total number dead, I simulated outcomes from twenty-one potential slot limits. The smallest lower size limit evaluated was 14 inches, the minimum size limit in the commercial fishery, and the largest upper size limit evaluated

was 21 inches, the largest minimum size ever implemented in the recreational Summer Flounder fishery. The width of the slots limits varied from a minimum width of two inches to a maximum width of seven inches.

A slot limit can be defined several ways, but here I am referring to a regulation where only fish within a minimum and maximum size limit *could* be kept while all fish that are greater than the maximum size or less than the minimum size *must* be discarded. Since I did not record catch-rate-per-angler, and could therefore not evaluate alternative bag limits within a given slot limit, all fish between the minimum retention size and maximum retention size of a slot limit were assumed to be kept (no bag limit). Each slot-limit was imposed on the observed catch and catch composition data overall, as well as by location and depth category, assuming effort was fixed at what was observed. Finally, 10% mortality was applied to all discarded fish in conformity with the recreational discard mortality rate currently applied in the Summer Flounder stock assessment (Terceiro 2016).

To convert observed individual fish lengths (in inches) to estimated individual fish weights (in pounds) I applied sex-specific parameters from Morse (1981) for the equation,

$$w(l) = \alpha l^{\beta}$$

The total number dead, N_d , for each simulated slot limit s , was calculated as:

$$N_{d_s} = N_{L_s} + (0.10 * N_{D_s})$$

where N_L is the total number of fish that were landed and N_D is the total number of fish that were discarded. The biomass of dead females, F_d , was calculated as:

$$F_{d_s} = \left[\sum_{i=1}^n W_{i_{L_{f_s}}} + \left(0.10 \times \sum_{i=1}^n w_{i_{D_{f_s}}} \right) \right]$$

where w is the weight in pounds of fish i and f denotes female fish. Finally, the ratio of dead discards to total dead was calculated as:

$$R_{d_s} = \frac{(0.10 * N_{D_s})}{N_{d_s}}$$

The influence of each slot limit on these metrics was evaluated separately using the observed catch composition at each sampling location. For each slot limit, I calculated the proportional change from the observed metric at an 18-inch minimum retention size to the calculated metric given the slot limit. Slot limits that produced a 10% or less change, whether negative or positive, in the total number of dead fish, were deemed suitable alternatives in that they would not have resulted in a significant change in fishing mortality given total catch and total effort was fixed at what was observed. In other words, only slot limits that kept fishing exploitation rate near constant were viewed as potential alternatives to the 18-inch minimum retention size.

Results

Observed catch composition

Under an 18-inch minimum size restriction, I observed a total catch of 3,290 Summer Flounder by recreational anglers on forty-one directed party boat trips (Table 2; Figure 2). Of the total catch, 2,645 (80%) were discarded, however the proportion of the catch that was discarded varied by region and by depth category (Table 2). The discard proportion was lower in deeper water and in more northern ports (Table 2) where smaller fish occurred less frequently (Figures 3, 4). The proportion female increased with size resulting in 87% (n=558) of the landings and 38% (n=1,011) of the discards being female overall (Figure 2). However, the sex ratio at length varied by location and by depth category. At a given length, the sex ratio was more heavily skewed toward female fish in shallower water and in more southern ports (Table 2; Figures 3, 4).

Simulated catch composition

Slot limits that kept the total number dead at or near that observed under the 18-inch minimum size limit, herein referred to as “suitable”, were all narrow, ranging from two to four inches wide. Of the suitable slot limits, most contained 18 inches within the slot limit and only once did the bottom of the slot limit fall below 16 inches, when a 15- to 17-inch slot limit was suitable in Atlantic Highlands, NJ. All suitable slot limits reduced the total biomass of dead females, one of which, referred to herein as “optimal”, produced the greatest reduction in total biomass of dead females. Few suitable slot limits had a significant impact on the proportion of the total dead made up of dead discards (Table 3).

No single optimal slot limit minimized dead female biomass at every location. Variation in length frequency and sex ratio at length observed across the different

sampling locations produced varying suitable and optimal slot limits at each sampling location (Figure 3; Table 3). In Cape May, New Jersey a 17- to 19-inch slot would have been optimal, reducing dead female biomass by 31% (from 262.37 lb to 181.59 lb), while in the same state, in Atlantic Highlands, a 15- to 17-inch slot would have been optimal, producing a 58% reduction in dead female biomass (from 537.85 lb to 226.89 lb). Similarly, in New York, the catch composition from Captree would have generated a 21% reduction in dead female biomass (from 181.1 lb to 143.93 lb) at an 18- to 20-inch optimal slot limit, while in Montauk, the optimal slot limit was 16 to 18 inches, which would have produced a 55% reduction (from 533.27 lb to 238.04 lb). Finally, in Pt. Judith, Rhode Island, among slot limits deemed suitable, a three-inch slot from 17 to 20 inches would have been optimal, generating a 55% reduction in dead female biomass (from 222.94 lb to 100.48 lb). At some sampling locations, the potential to reduce dead female biomass came primarily from males being more accessible at lower sizes, for example in Atlantic Highlands, NJ (Figure 3b) and in Montauk, NY (Figure 3d), while in other sampling locations it came primarily from the protection of larger females, for example in Cape May, NJ (Figure 3a) and in Captree, NY (Figure 3c) and less from accessing smaller males at lower sizes.

Discussion

The overall sex composition and the spatial and depth-dependent trends in sex ratio of large fish matched what has been previously reported for the recreational Summer Flounder fishery (Morson et al. 2012, 2015). Furthermore, the overall discard rate, 80%, is similar to the 79% discard rate estimated for the entire for-hire fishing mode in

2016 (personal communication from the National Marine Fisheries Service, Fisheries Statistics Division, 5/25/17). The proportion female in the larger size classes is higher than that observed in the commercial catch or on the NMFS-NEFSC trawl survey (Morson et al. 2015). However, while the observed sex ratio pattern for the larger fish suggests large males do not come inshore and are therefore not available to the recreational fishery when and where it takes place, I show here that smaller-sized males are both available inshore and show up in the recreational catch at smaller sizes. This is an important finding for two reasons. First, it suggests that any sex-specific movement or habitat use that produces such a highly skewed sex ratio in the landings must also be size-specific. That is, while large male fish may remain offshore where they are less likely to be accessible to the recreational fishery, smaller males do move inshore in the spring/summer where they are available to the recreational fishing effort. Sex- and size-dependent separation in space and time has been well documented in other sexually dimorphic flatfishes (Swain 1997; Swain and Morin 1997; Sahin and Gunes 2010; Loher and Hobden 2012), so the occurrence of this behavior in Summer Flounder is not surprising and ecological theory for intraspecific partitioning of resources along a life history is well established (Schoener 1968). Second, the availability of male fish at lower sizes enables changes in size regulations to influence the sex composition of the catch. This second point is especially important given how much of the fishing mortality is being directed at the female portion of the stock in this fishery under the current minimum size restrictions and the desire to evaluate alternative management options that could promote a more sex-balanced harvest (Morson et al. 2012, 2015).

Slot limits have been demonstrated to produce higher harvest numbers, maintain natural age structure in the population, reduce discard mortality, positively influence recruitment potential, and conserve biomass across a variety of fish life histories (Birkeland and Dayton 2005; Powell et al. 2010; Koehn and Todd 2012; Law et al. 2012; Gwinn et al. 2013; Sanchez-Hernandez et al. 2016). Here I add additional support to a growing body of literature that suggests slot limits can simultaneously achieve a number of desired management goals and demonstrate that, for fish with sexually-dimorphic growth, slot limits have the potential to distribute sex-biased fishing exploitation more evenly across both sexes. In the Summer Flounder recreational fishery, there is an obvious trade-off available to managers where the catch of large, heavy, female fish could be replaced by a similar number of smaller, lighter, male and female fish.

One important consideration in the evaluation of any slot limit relative to a minimum size limit is whether the lifetime spawner reproductive potential is negatively affected. Since nearly all of the lower ends of the slot limits prescribed here as optimal are only an inch or two smaller than the current 18-inch size limit, both the current 18-inch size limit and the prescribed optimal slot limits would allow fish the opportunity to spawn multiple times before recruiting to the fishery. Nevertheless, to fully evaluate the long-term impacts of varying slot limits on stock productivity, a spawning stock biomass per recruit analysis would be necessary (Haddon 2011). A more appropriate method for evaluating viable slot limit options and potential outcomes therefore is a management strategy evaluation that links annual management decisions on slot limits with a stock assessment model and includes annual, seasonal, and spatial dynamics in the

population, the catch composition given the prescribed slot, and the fishing effort (Punt et al. 2014). Such an evaluation is beyond the scope of this work, however the sex composition data now exist for the full range of sizes available to the recreational fishery so the development of such a model is an obvious next step.

Several important limitations are inherent in the data and analysis I present herein. First, my approach assumes effort would have remained constant under alternative management scenarios. If, for example, a given slot limit would encourage more anglers to participate in the fishery than participated in it under an 18-inch minimum size limit, the total catch under any alternative scenario may have increased, resulting in a higher total catch, and mortality, relative to the observed. Second, this work focused on the catch of the for-hire mode and did not sample the private or shore-based modes. It is possible the catch size and catch length and sex composition vary across these other fishing modes, which would alter the observed catch as well as the simulated outcomes of different slot limits. Finally, the observed catch is only representative of the catch in the year in which it was collected. Having observed a catch composition that appears to support a specific slot limit this year does not guarantee the same measure would be appropriate in any other year. For this reason, slot limits as a general strategy have the potential to be highly successful in achieving multiple management goals, particularly relative to a sex-balanced harvest in the recreational Summer Flounder fishery, but should be viewed as optimal given the observed catch composition for the year, locations, and mode I sampled and further evaluation of interannual, spatial, and mode-specific dynamics is warranted.

In conclusion, the availability of male fish to the recreational fishing effort at smaller sizes, identified here for the first time, suggests the conservation of large, female fish is achievable in this fishery with prescribed management actions. I demonstrate a few viable options that would have achieved either a more sex-balanced harvest or a reduction in dead female biomass under the catch conditions in the mode, location, and time I observed. However, a more robust, spatially- and temporally-dynamic management strategy evaluation could be used to estimate how alternative applications, including slot limits and trophy limits, would perform for this fishery in any given year so that multiple management goals, including limiting mortality of large females, increasing angler satisfaction, and balancing harvest sex ratio under a fixed harvest rate might be achieved simultaneously.

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TABLES – CHAPTER 2

Table 2.1. Length and depth categories for sub-sampling the sex of discarded fish.

Length bins (inches)	Depth bins (feet)
8.0 - 9.9	0-25.4
10.0 - 11.9	25.5-50.4
12.0 - 13.9	50.5-75.4
14.0 - 15.9	75.5+
16.0 - 17.9	

Table 2.2. Total number of summer flounder sampled by port, depth range, outcome (landed/discarded), and sex. A dash indicates a given cell was not sampled while a zero indicates there were zero fish for that cell.

State	Port	Depth Range (ft)	Outcome	Female	Male
New Jersey	Cape May	0-25	Landed	-	-
			Discarded	-	-
		25-50	Landed	-	-
			Discarded	-	-
		50-75	Landed	60	4
			Discarded	144	229
		75+	Landed	28	0
			Discarded	37	138
	Atlantic Highlands	0-25	Landed	0	0
			Discarded	9	24
		25-50	Landed	166	16
			Discarded	150	209
		50-75	Landed	8	2
			Discarded	75	118
		75+	Landed	-	-
			Discarded	-	-
New York	Captree	0-25	Landed	42	2
			Discarded	163	169
		25-50	Landed	13	0
			Discarded	53	74
		50-75	Landed	8	5
			Discarded	70	85

Rhode Island	Montauk	75+	Landed	0	0
			Discarded	0	1
		0-25	Landed	9	0
			Discarded	9	6
		25-50	Landed	120	12
			Discarded	214	390
	Point Judith	50-75	Landed	38	9
			Discarded	48	62
		75+	Landed	-	-
			Discarded	-	-
		0-25	Landed	4	8
			Discarded	0	2
		25-50	Landed	0	0
			Discarded	1	1
		50-75	Landed	31	13
			Discarded	26	50
		75+	Landed	31	16
			Discarded	12	70

Table 2.3. Observed (18-inch minimum size limit, top row) and simulated incremental slot limit performance metrics, including total number dead (N_d), dead female biomass (F_d), and ratio of dead discards to total dead (R_d). In parentheses are the percent changes in a given performance metric relative to the observed (18-inch minimum size limit). Slot limits in bold are within +/-10% of the observed total number dead.

State	Port	Bottom of Slot Limit	Top of Slot Limit	Total Number Dead	Dead Female Biomass	Ratio of Dead Discards to Total Dead
New Jersey	Cape May	18.00	-	147	262.37	0.37
		14.00	15.99	321 (118%)	117.35 (-55%)	0.11 (-70%)
		14.00	16.99	411 (180%)	187.01 (-29%)	0.06 (-84%)
		14.00	17.99	447 (204%)	244.6 (-7%)	0.05 (-86%)
		14.00	18.99	487 (231%)	321.34 (22%)	0.03 (-92%)
		14.00	19.99	506 (244%)	369.87 (41%)	0.03 (-92%)
		14.00	20.99	519 (253%)	409.91 (56%)	0.03 (-92%)
		15.00	16.99	273 (86%)	153.98 (-41%)	0.15 (-59%)
		15.00	17.99	310 (111%)	211.57 (-19%)	0.12 (-68%)
		15.00	18.99	349 (137%)	288.31 (10%)	0.09 (-76%)
		15.00	19.99	368 (150%)	336.84 (28%)	0.08 (-78%)
		15.00	20.99	382 (160%)	376.88 (44%)	0.08 (-78%)
		16.00	17.99	190 (29%)	174.52 (-33%)	0.26 (-30%)
		16.00	18.99	230 (56%)	251.26 (-4%)	0.2 (-46%)
		16.00	19.99	249 (69%)	299.79 (14%)	0.18 (-51%)
		16.00	20.99	262 (78%)	339.83 (30%)	0.16 (-57%)
		17.00	18.99	141 (-4%)	181.59 (-31%)	0.4 (8%)
		17.00	19.99	159 (8%)	230.13 (-12%)	0.34 (-8%)
		17.00	20.99	173 (18%)	270.17 (3%)	0.3 (-19%)
		18.00	19.99	123 (-16%)	172.54 (-34%)	0.47 (27%)
		18.00	20.99	136 (-7%)	212.58 (-19%)	0.41 (11%)
		19.00	20.99	96 (-35%)	135.84 (-48%)	0.63 (70%)
	Atlantic Highlands	18.00	-	251	537.85	0.23
		14.00	15.99	301 (20%)	154.23 (-71%)	0.18 (-22%)
		14.00	16.99	411 (64%)	259.93 (-52%)	0.1 (-57%)
		14.00	17.99	466 (86%)	327.79 (-39%)	0.07 (-70%)
		14.00	18.99	545 (117%)	461.88 (-14%)	0.05 (-78%)
		14.00	19.99	575 (129%)	539.13 (0%)	0.04 (-83%)
		14.00	20.99	602 (140%)	616.99 (15%)	0.03 (-87%)
		15.00	16.99	277 (10%)	226.89 (-58%)	0.2 (-13%)
		15.00	17.99	332 (32%)	294.75 (-45%)	0.15 (-35%)
		15.00	18.99	411 (64%)	428.84 (-20%)	0.1 (-57%)

New York	Captree	15.00	19.99	441 (76%)	506.09 (-6%)	0.08 (-65%)
		15.00	20.99	467 (86%)	583.95 (9%)	0.07 (-70%)
		16.00	17.99	242 (-4%)	254.37 (-53%)	0.25 (9%)
		16.00	18.99	322 (28%)	388.46 (-28%)	0.16 (-30%)
		16.00	19.99	352 (40%)	465.71 (-13%)	0.13 (-43%)
		16.00	20.99	378 (51%)	543.57 (1%)	0.12 (-48%)
		17.00	18.99	212 (-16%)	282.76 (-47%)	0.3 (30%)
		17.00	19.99	242 (-4%)	360 (-33%)	0.25 (9%)
		17.00	20.99	269 (7%)	437.86 (-19%)	0.21 (-9%)
		18.00	19.99	188 (-25%)	292.14 (-46%)	0.35 (52%)
		18.00	20.99	214 (-15%)	370 (-31%)	0.29 (26%)
		19.00	20.99	134 (-47%)	235.91 (-56%)	0.53 (130%)
	Montauk	18.00	-	132	181.1	0.47
		14.00	15.99	285 (116%)	162.17 (-10%)	0.16 (-66%)
		14.00	16.99	366 (177%)	243.48 (34%)	0.1 (-79%)
		14.00	17.99	393 (198%)	283.12 (56%)	0.08 (-83%)
		14.00	18.99	436 (230%)	357.99 (98%)	0.06 (-87%)
		14.00	19.99	445 (237%)	380.35 (110%)	0.06 (-87%)
		14.00	20.99	454 (244%)	406.74 (125%)	0.06 (-87%)
		15.00	16.99	213 (61%)	175.18 (-3%)	0.25 (-47%)
		15.00	17.99	240 (82%)	214.82 (19%)	0.21 (-55%)
		15.00	18.99	283 (114%)	289.7 (60%)	0.16 (-66%)
		15.00	19.99	292 (121%)	312.05 (72%)	0.15 (-68%)
		15.00	20.99	301 (128%)	338.45 (87%)	0.14 (-70%)
		16.00	17.99	177 (34%)	167.65 (-7%)	0.32 (-32%)
		16.00	18.99	219 (66%)	242.53 (34%)	0.24 (-49%)
		16.00	19.99	228 (73%)	264.88 (46%)	0.22 (-53%)
		16.00	20.99	237 (80%)	291.28 (61%)	0.21 (-55%)
		17.00	18.99	138 (5%)	161.22 (-11%)	0.44 (-6%)
		17.00	19.99	147 (11%)	183.57 (1%)	0.41 (-13%)
		17.00	20.99	156 (18%)	209.97 (16%)	0.38 (-19%)
		18.00	19.99	120 (-9%)	143.93 (-21%)	0.52 (11%)
		18.00	20.99	129 (-2%)	170.33 (-6%)	0.48 (2%)
		19.00	20.99	87 (-34%)	95.45 (-47%)	0.77 (64%)
		18.00	-	261	533.27	0.28
		14.00	15.99	404 (55%)	207.19 (-61%)	0.14 (-50%)
		14.00	16.99	529 (103%)	312.22 (-41%)	0.08 (-71%)
		14.00	17.99	573 (120%)	361.73 (-32%)	0.07 (-75%)
		14.00	18.99	627 (140%)	448.41 (-16%)	0.05 (-82%)
		14.00	19.99	656 (151%)	511.83 (-4%)	0.04 (-86%)
		14.00	20.99	699 (168%)	635.37 (19%)	0.03 (-89%)
		15.00	16.99	326 (25%)	249.51 (-53%)	0.2 (-29%)

		15.00	17.99	370 (42%)	299.03 (-44%)	0.16 (-43%)
		15.00	18.99	424 (62%)	385.71 (-28%)	0.13 (-54%)
		15.00	19.99	453 (74%)	449.13 (-16%)	0.11 (-61%)
		15.00	20.99	496 (90%)	572.66 (7%)	0.09 (-68%)
		16.00	17.99	261 (0%)	238.04 (-55%)	0.28 (0%)
		16.00	18.99	315 (21%)	324.71 (-39%)	0.21 (-25%)
		16.00	19.99	344 (32%)	388.13 (-27%)	0.19 (-32%)
		16.00	20.99	387 (48%)	511.67 (-4%)	0.15 (-46%)
		17.00	18.99	190 (-27%)	219.69 (-59%)	0.43 (54%)
		17.00	19.99	219 (-16%)	283.11 (-47%)	0.35 (25%)
		17.00	20.99	262 (0%)	406.64 (-24%)	0.28 (0%)
		18.00	19.99	175 (-33%)	233.59 (-56%)	0.47 (68%)
		18.00	20.99	218 (-16%)	357.13 (-33%)	0.36 (29%)
		19.00	20.99	164 (-37%)	270.45 (-49%)	0.51 (82%)
Rhode Island						
	Point Judith	18.00	-	119	222.94	0.14
		14.00	15.99	86 (-28%)	35.75 (-84%)	0.23 (64%)
		14.00	16.99	135 (13%)	57.61 (-74%)	0.11 (-21%)
		14.00	17.99	162 (36%)	76.54 (-66%)	0.07 (-50%)
		14.00	18.99	201 (69%)	110.67 (-50%)	0.04 (-71%)
		14.00	19.99	215 (81%)	130.69 (-41%)	0.03 (-79%)
		14.00	20.99	232 (95%)	168.04 (-25%)	0.02 (-86%)
		15.00	16.99	104 (-13%)	54.87 (-75%)	0.17 (21%)
		15.00	17.99	132 (11%)	73.8 (-67%)	0.11 (-21%)
		15.00	18.99	171 (44%)	107.93 (-52%)	0.06 (-57%)
		15.00	19.99	184 (55%)	127.95 (-43%)	0.05 (-64%)
		15.00	20.99	201 (69%)	165.3 (-26%)	0.04 (-71%)
		16.00	17.99	103 (-13%)	68.2 (-69%)	0.17 (21%)
		16.00	18.99	142 (19%)	102.33 (-54%)	0.1 (-29%)
		16.00	19.99	155 (30%)	122.34 (-45%)	0.08 (-43%)
		16.00	20.99	172 (45%)	159.7 (-28%)	0.06 (-57%)
		17.00	18.99	93 (-22%)	80.46 (-64%)	0.21 (50%)
		17.00	19.99	107 (-10%)	100.48 (-55%)	0.17 (21%)
		17.00	20.99	124 (4%)	137.83 (-38%)	0.13 (-7%)
		18.00	19.99	79 (-34%)	81.55 (-63%)	0.26 (86%)
		18.00	20.99	96 (-19%)	118.9 (-47%)	0.2 (43%)
		19.00	20.99	57 (-52%)	84.78 (-62%)	0.4 (186%)

FIGURES – CHAPTER 2

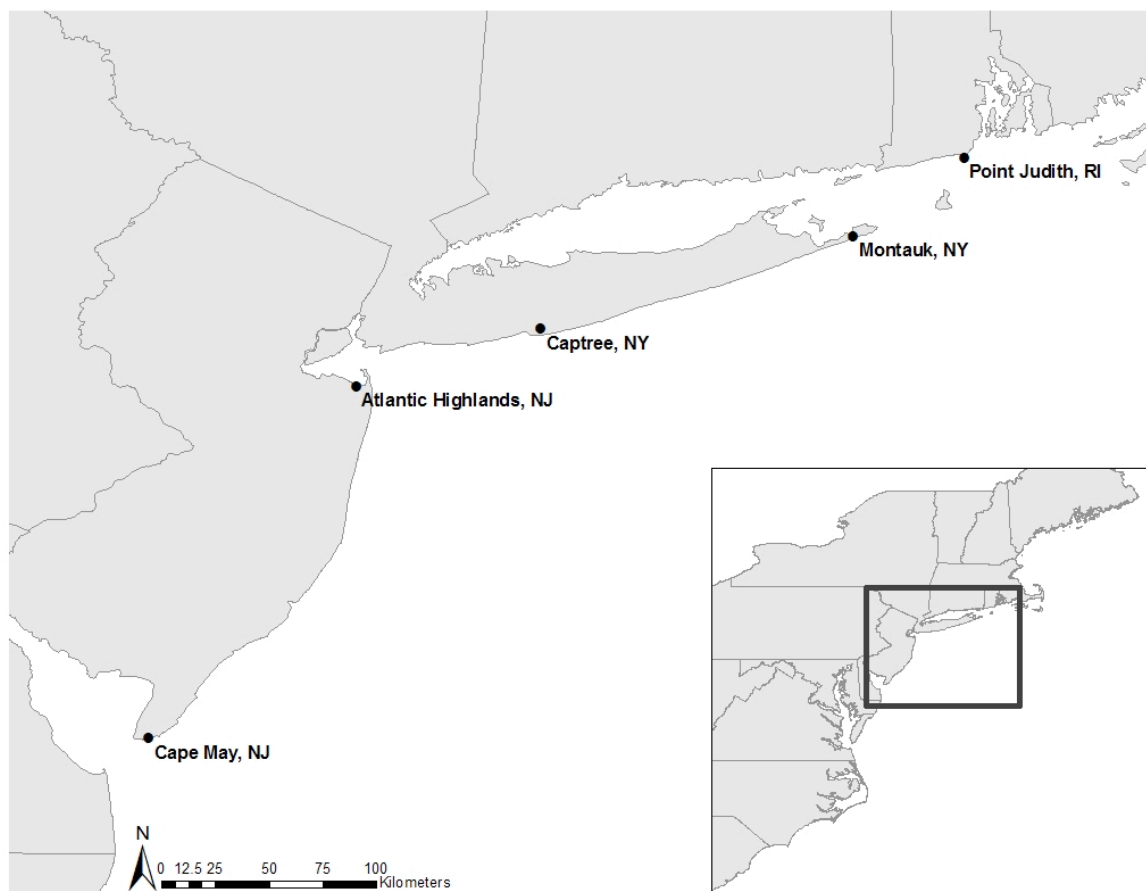


Figure 2.1. Map of sampling locations.

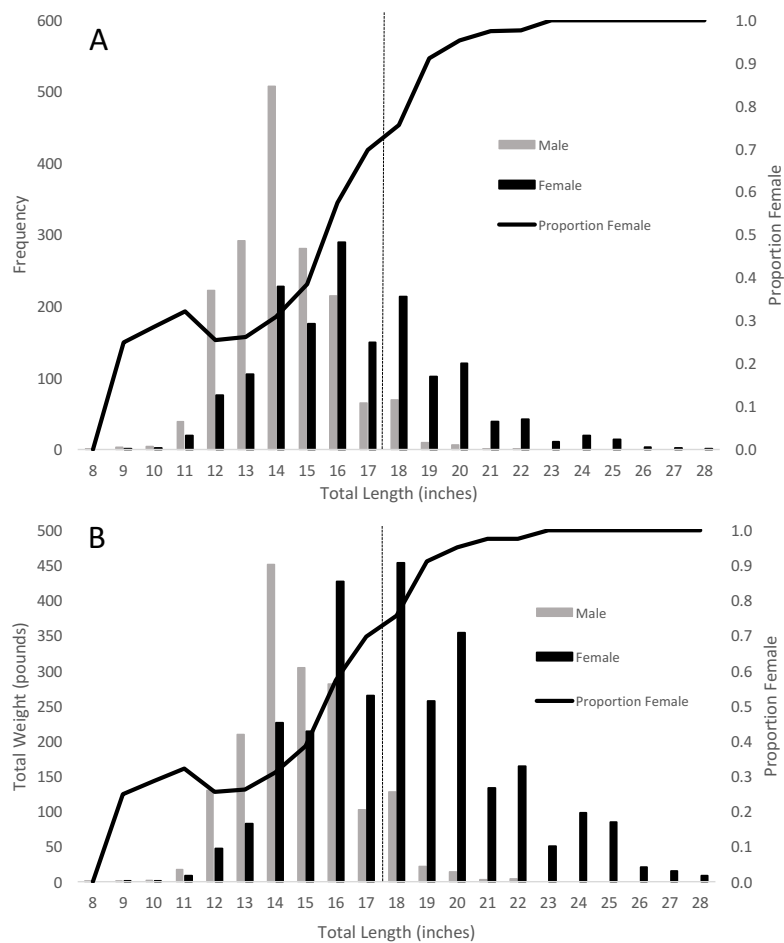


Figure 2.2. Total number (A) and weight (B) of male and female Summer Flounder collected at each 1-inch length bin. Solid black line represents proportion female-at-length. Vertical dashed line represents the 18-inch minimum landing size in 2016.

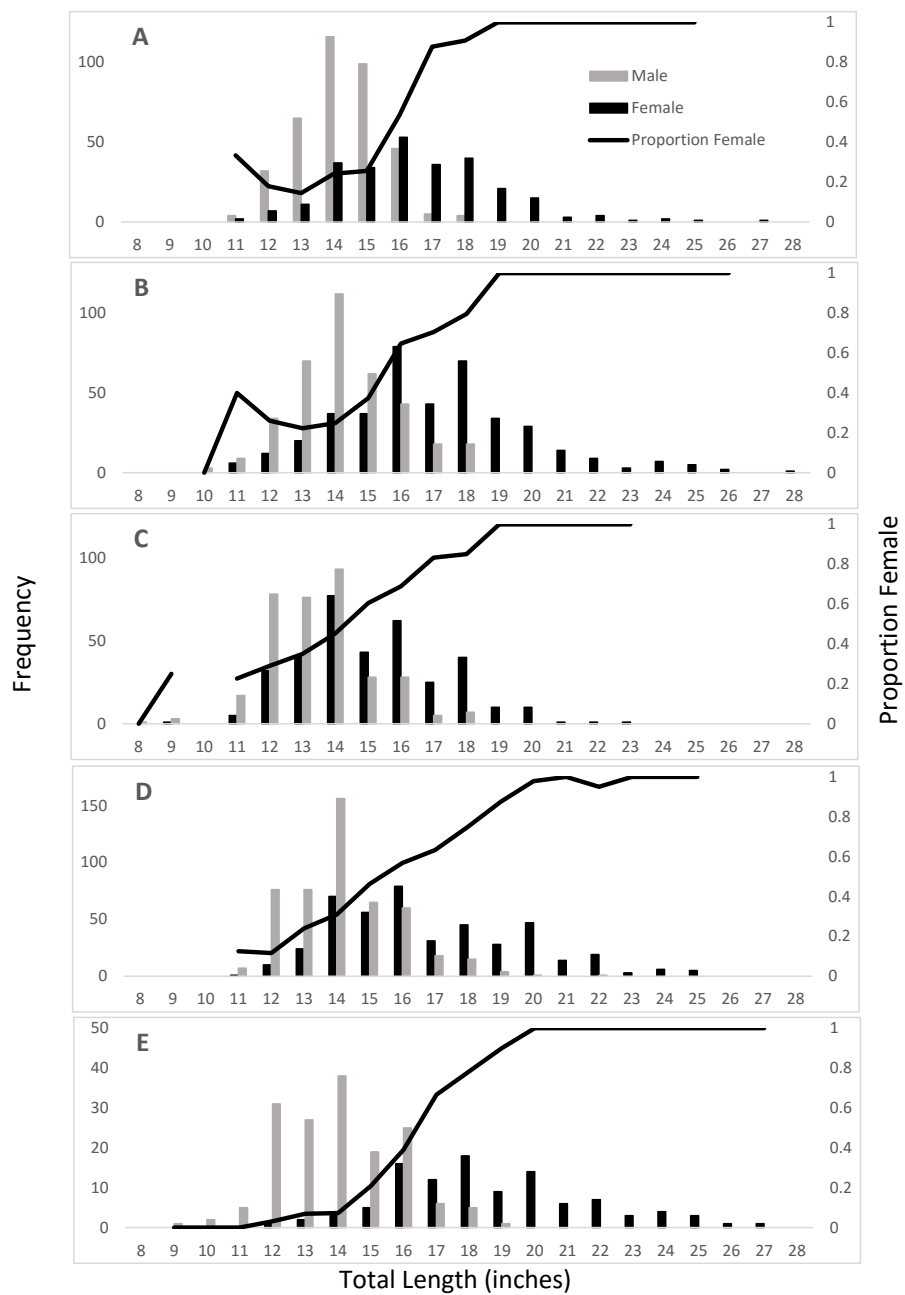


Figure 2.3. Total number of male and female Summer Flounder collected at (A) Cape May, NJ, (B) Atlantic Highlands, NJ, (C) Captree, NY, (D) Montauk, NY, and (E) Pt. Judith, RI in each 1-inch length bin. Solid black line represents proportion female-at-length. Note differences in primary y-axis for each panel.

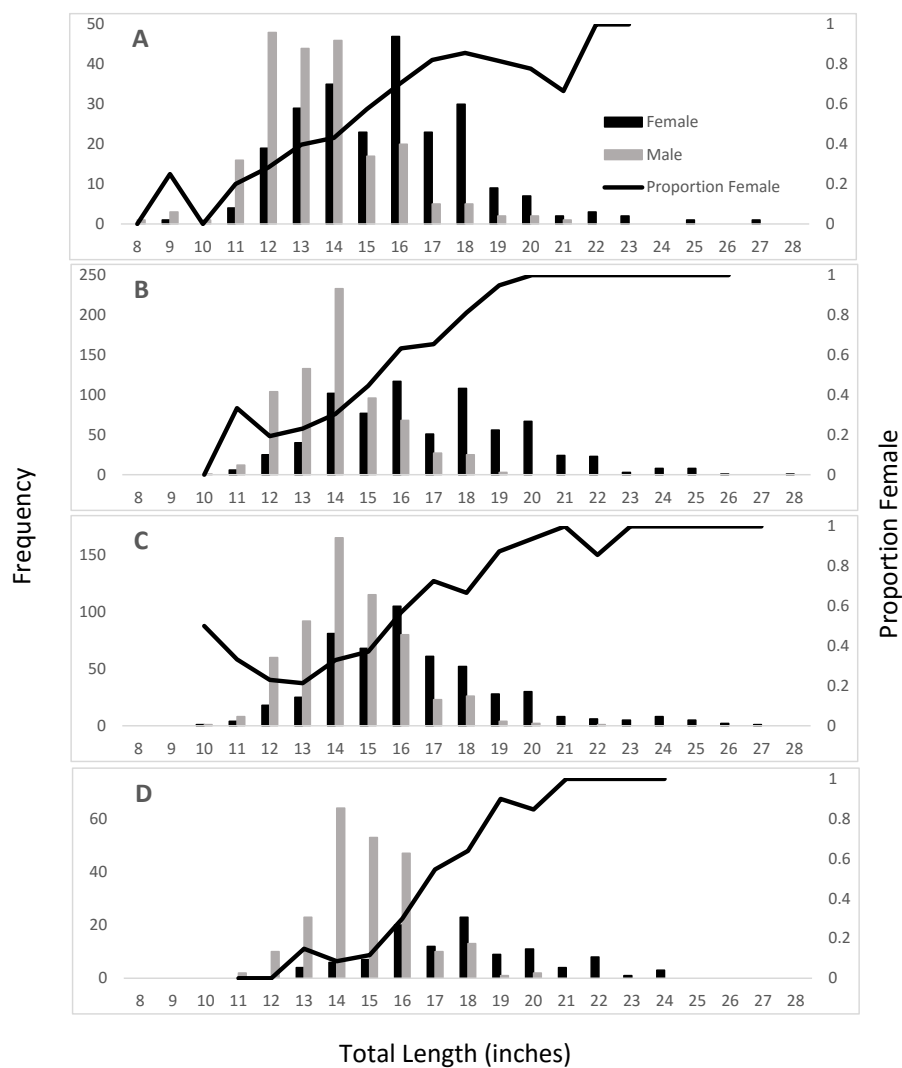


Figure 2.4. Total number of male and female Summer Flounder collected in (A) 0-25 feet (B) 25-50 feet (C) 50-75 feet, and (D) 75+ feet of water at each 1-inch length bin. Solid black line represents proportion female-at-length. Note differences in primary y-axis for each panel.

CHAPTER 3

**DENSITY-DEPENDENT CAPTURE EFFICIENCY OF A SURVEY DREDGE AND
ITS INFLUENCE ON THE STOCK ASSESSMENT OF EASTERN OYSTERS
CRASSOSTREA VIRGINICA IN DELAWARE BAY**

Abstract

A reliable measure of gear capture efficiency is required to calculate unbiased estimates of population size and fishing mortality from survey data in a stock assessment. However, capture efficiency can vary spatially and temporally due to changes in abundance, stock area, the environment, and the sampling gear itself. Therefore, periodic reassessment of this parameter is necessary to ensure that the catchability coefficients being applied accurately reflect the capture efficiency of the survey sampling gear, especially when catchability is being estimated outside of the stock assessment model. Using data from field experiments conducted in 1999, 2000, 2003, and 2013, I evaluated spatial and temporal variability in capture efficiency for a commercial dredge used to conduct a fishery-independent survey of the eastern oyster (*Crassostrea virginica*) population in Delaware Bay, USA. A spatial gradient in capture efficiency was detected, but no temporal trend. Capture efficiency was a function of the density of oysters in the sampled area. To my knowledge this is the first time density-dependent capture efficiency has been identified for a sessile invertebrate stock survey. Since density dependence in capture efficiency leads to hyperstable catch-per-unit-effort, caution is advised when deriving oyster abundance from dredge survey catch-

per-effort data, especially at low oyster density and when high spatial resolution estimates of survey dredge capture efficiency are not available.

Introduction

Stock assessment of oyster populations is typically done using data collected from surveys that employ one of three types of sampling gear. Diver quadrat sampling and patent tongs are nearly 100% efficient for collecting oysters within the area sampled (Chai et al. 1993; Mann et al. 2004). However, patent tongs can be destructive to the reef and can only sample a small area per unit of effort; therefore, some have advocated against their long-term use for surveying natural resources (Rothschild et. al 1994). Diver sampling suffers from the same limitation in sample size and typically also suffers from limited sample numbers due to the time required per sample. Alternatively, a commercial dredge can be used to sample a large area, providing a high sample density at relatively low cost, but is also inefficient (Powell et al. 2002; Mann et al. 2004; Powell et al. 2007; Marenghi et al. 2017). When the sampling gear captures less than 100% of the individuals in the sampled area, it is important to estimate the efficiency of the gear and to account for this when converting survey catch-per-unit-effort (CPUE) data to an index of population size (Hilborn and Walters 1992; Arreguin-Sanchez 1996).

The capture efficiency of survey gear, and the catchability coefficient derived from capture efficiency, can be estimated within the stock assessment model (Fournier et al. 1998) or can be explicitly defined, either as a fixed value (Powell et al. 2007), or by some functional relationship (Wilberg et al. 2010). Field and experimental observations from depletion experiments (Lasta and Iribarne 1997; Gedamke et al.

2004; Rago et al. 2006; Hennen et al. 2012; Wilberg et al. 2013) and simultaneous sampling of survey gear and gear that is 100% efficient (Powell et al. 2002; Mann et al. 2004; Powell et al. 2007; Singh et al. 2014) have been used to estimate catchability of shellfish survey dredges directly. Often the capture efficiency will vary spatially (Powell et al. 2002, 2007; Doray et al. 2010; Marengi 2017) and temporally (Walters and Martell 2004; Powell et al. 2007), likely due to changes in abundance, stock area, the environment, and the sampling gear (Wilberg et al. 2010). For this reason, periodic reassessment of survey dredge capture efficiency has been advised (Powell et al. 2007; Marengi et al. 2017).

The dredge survey used in the annual stock assessment for the eastern oyster *Crassostrea virginica* in Delaware Bay dates back to 1953 and provides one of the longest continuous abundance records of any shellfish population (Powell et al. 2008). Field experiments conducted in 1999, 2000 and 2003 identified spatial and temporal trends in the capture efficiency of the dredge used for this survey (Powell et al. 2002, 2007). To account for these, time- and location-specific catchability coefficients have been applied in the stock assessment to estimate an index of abundance from survey CPUE (Ashton-Alcox et al. 2015). However, Powell et al. (2007) suggest that capture efficiency of this survey gear may change rapidly, over only a few years at any one location. If the catchability coefficients currently being applied in the Delaware Bay oyster stock assessment no longer accurately reflect the capture efficiency of the sampling gear, this will lead to biased estimates of population size and exploitation rate (Pope and Shepherd 1985; Wilberg and Bence 2006) with the magnitude of the bias linked directly to the magnitude of the error in the estimate of capture efficiency used.

In this chapter I use data from a set of field experiments to update estimates of capture efficiency for the survey dredge used to estimate abundance in the stock assessment of the Delaware Bay eastern oyster population. I evaluate whether the time- and location-specific coefficients calculated from earlier experiments (1999, 2000, and 2003), which have been applied in the stock assessment, are still appropriate given new data collected during an experiment in 2013.

Methods

Field sampling

Capture efficiency was estimated at twelve oyster reef locations in Delaware Bay in 1999, 2000, 2003, and 2013 (Figure 3.1). At each location, three measurements of capture efficiency were collected within a 0.2' latitude by 0.2' longitude grid (approximately 25 acres). For the 1999-2003 experiments, measurements consisted of paired dredge tows and diver transect samples. Paten tongs and divers are equally efficient at sampling oysters (Chai et al. 1992). Since patent tongs were more readily available at the time, measurements from the 2013 experiment consisted of paired dredge tows and patent tong transect samples. For each replicate, a one-minute tow was conducted by the *F/V Howard W. Sockwell* using a standard 1.27-m commercial dredge and twelve haphazardly placed 0.25 m² diver quadrats or six haphazardly placed 0.89 m² patent tong samples were taken by a second boat in a transect parallel to but not in the dredge path. The time and GPS coordinates were recorded when the dredge tow began and ended. The total volume caught in each tow was measured as 37-L bushels in a pre-calibrated hopper. If the dredge was full after the 1-minute tow,

the tow time was reduced to 45s so that the total number of bushels of material collected in the swept area could be determined. A single bushel was collected from each tow as a representative sub-sample of the catch and the remaining catch was discarded overboard. The entire tong or diver quadrat sample, minus the sediment, were retained for analysis. Both dredge and tong or diver samples were sorted into oysters, cultch (oyster shell), and boxes (dead oysters with the hinge still intact). Volumes and weights of each component of the catch were recorded and all oysters and boxes in each sample were counted and measured.

Data analyses

Deriving capture efficiency

The swept area, sa , for each dredge tow, in square meters, was calculated as

$$(1) \quad sa = d * w$$

where d is the distance towed in meters determined by tallying the distances between GPS coordinates every 10 seconds during the tow, and w is the dredge width in meters. The apparent density, ad , of oysters on the bottom for a given tow was calculated as

$$(2) \quad ad = (o * b) / sa$$

where o is the total number of oysters present in the bushel sample from a given tow and b is the total number of bushels caught in that tow. The correct density, cd , of oysters on the bottom for a given tow was calculated as

$$(3) \quad cd = (\sum_{n=6}^{n=6} od) / (n * ta)$$

where od is the total number of oysters collected by patent tong or diver sample taken along a given tow path, n is the total number of patent tong or diver samples taken along that same tow path, and ta is the area sampled by the patent tong or diver quadrat. Oyster dredge capture efficiency, e , was calculated as

$$(4) \quad e = ad / cd .$$

Preliminary evaluation of e suggested that at values of cd below 25 oysters/m², e was commonly estimated to be greater than 1 and sometimes greater than 2. Since the tong/diver samples cover a much smaller spatial area than the dredge, the low abundance at these locations likely lead to tong/diver undersampling bias (Powell et al. 2017) and therefore an overestimate of capture efficiency. Therefore, I did not include any capture efficiency estimates in subsequent analyses that were derived from cd observations below 25 oysters/m².

Finally, catchability, q , was calculated as

$$(5) \quad q = 1/e .$$

Evaluating size-specific retention probability

I evaluated the size-dependent retention probability of the survey dredge using a logistic model that was fit to selectivity at a given length $s(l)$ calculated as

$$(6) \quad s(l) = D_{l,d} / (D_{l,t} + D_{l,d}),$$

where $D_{l,d}$ was the experiment-wide density of oysters at a given length collected in the dredge and $D_{l,t}$ was the experiment-wide density of oysters at that same length

collected in the tong/diver samples. Given the results of this analysis (no size selectivity), I used the full range of sizes for oysters in all further analyses.

Evaluating spatial and temporal variation in capture efficiency

Logistic regression was applied to assess spatial and temporal effects on the capture efficiency of the survey dredge. To evaluate temporal variability, the dataset was truncated to include only locations that were sampled in all years. Given the results of this analysis (no temporal variability), the decision was made to include data from all years in subsequent spatial analyses.

Spatial analyses identified three statistically significant groups of oyster reef locations relative to capture efficiency. Additionally, these groups were different from those identified in the 2003 experiment (Powell et al. 2007) which have been applied in the stock assessment since 2005 (Ashton-Alcox et al. 2016). To evaluate the impact of changing the capture efficiency of the survey gear, and the catchability coefficients derived from capture efficiency, on the stock assessment, mean catchability coefficients were derived separately from capture efficiency based on analyses conducted by Powell et al. (2007) and on analyses conducted with this work. Powell et al. (2007) analyzed capture efficiency separately for different-sized oysters and while they found no change over time in capture efficiency for all oysters, a significant effect was detected for market-sized oysters. Therefore, time-specific catchability coefficients have been applied in the stock assessment and the most recent part of time series uses regional mean catchability coefficients derived from data collected during the 2003 experiment only to convert CPUE to abundance. However, since I detected no size selectivity of the dredge, and no temporal trend in capture efficiency, I derived regional mean

catchability coefficients from the full set of experimental data (1999, 2000, 2003, and 2013) and calculated regional means based on the statistically significant reef groupings from this work. The proportional change in abundance or exploitation rate P from the previously applied catchability coefficients for the stock assessment (Powell et al. 2007; Ashton-Alcox 2015) to the application identified as most appropriate with this work was calculated as

$$(7) \quad P = [(\delta_{new} - \delta_{old}) / \delta_{old}] * 100$$

where δ represents abundance or exploitation rate, *new* represents the application of catchability coefficients identified with this work as most appropriate and *old* represents the application of catchability coefficients that have been used in the stock assessment (Ashton-Alcox 2015), based on previous analyses by Powell et al. (2007).

Estimating uncertainty in capture efficiency and modeling density-dependence

Uncertainty in the estimate of e can be defined by the variation in intra-tong/diver quadrat density used to estimate cd for a given sample. For each estimate of e , six tong density measurements or twelve quadrat density measurements were drawn at random with replacement from the set of observed densities and cd and e were recalculated using these random draws. This was repeated 1,000 times in a bootstrap simulation and the variance, σ^2 , of the simulated distribution of e was used subsequently as a measure of uncertainty.

A power function is commonly used to describe density-dependence in catchability for many fisheries (Wilberg et al. 2010) and has been used to describe density-dependence in survey capture efficiency for trawl surveys in at least one instance

(Kotwicki et al. 2014). Therefore, to determine whether e of the survey dredge was density-dependent here, I modeled e as a power function of cd

$$(8) \quad e \sim \alpha * cd^{-\phi},$$

where α and ϕ are model parameters, using weighted non-linear least squares regression. The weights wt for each observation of e were the reciprocal the σ^2

$$(9) \quad wt = 1/\sigma^2$$

where σ^2 was estimated by bootstrap simulation as described above.

Results

The patent tongs and diver samples, assumed to have collected 100% of the oysters in the sampled area, had the same size frequency distribution as the commercial oyster dredge (Figure 2). Hence, oyster length was not a significant ($p = 0.82$) predictor of retention probability and all subsequent analyses were conducted without separating oysters by size class or correcting for size-specific retention probability.

When data were truncated to include only experiments done at reefs sampled in all three years, year was not a significant predictor of capture efficiency ($p = 0.29$), and neither was the interaction between year and reef ($p = 0.44$), but reef was significant ($p = 0.003$). Capture efficiency was nearly constant across all three years sampled (Figure 3).

For the full set of data, reef ($p = 0.004$) remained a significant predictor of capture efficiency. Efficiency is more variable, and higher in the lower bay, decreases and becomes less variable in the middle section of the bay, and increases in the upper bay (Figure 4). Reefs formed statistically significant groups relative to capture efficiency

and these groups were different from those estimated by Powell et al. (2007), who used data collected during the set of experiments conducted in 2003 only.

When updated location-specific catchability coefficients that included data from all experiments (1999, 2000, 2003, and 2013) were applied to calculate 2015 abundance and exploitation rate, the proportional change varied with region (Table 1). For instance, on the Very Low Mortality region and on the Round Island reef in the Low Mortality region, the estimated abundance of oysters decreased by 67%; however, on the Shell Rock region, the estimated abundance of oysters increased by 166% and the estimated exploitation rate decreased by 62%. Overall, the 2015 estimated abundance decreased by 9% and the exploitation rate increased by 11%.

Uncertainty in estimates of capture efficiency increased with decreasing oyster density (Figure 5). Oyster density significantly influenced the capture efficiency of the survey dredge. A two-parameter power function described the relationship between capture efficiency and oyster density (Table 2). Capture efficiency declined with increasing oyster density but at a slower rate at oyster densities greater than approximately 100 oysters/m² (Figure 5).

Discussion

Density-dependent capture efficiency

Density-dependent capture efficiency or catchability, and the hyperstability/hyperdepletion of CPUE that results from density-dependence, are typically thought to be processes that make fishery catch data disproportionate to abundance because of the interaction between organism and fisher behavior (Hilborn

and Walters 1992). CPUE data collected from fishery-independent surveys, however, were traditionally thought to provide reliable indices of abundance because survey design is standardized (Godo 1994). More recently, though, evidence for density-dependent catchability in fishery-independent bottom-trawl surveys has been described as well (Godo et al. 1999; Kotwicki et al. 2013, 2014). To my knowledge this is the first time density-dependent capture efficiency has been identified and modeled for a sessile invertebrate stock survey. For bottom-trawl fishery-independent surveys, density-dependence likely results from fish reacting, such as schooling or gear avoidance behaviors at high density, to the survey gear (Godo et al. 1999; Hoffman et al. 2009). Oysters are sessile and immobile, so density-dependent capture efficiency is not manifested in behavioral responses to survey gear. For oysters, density dependence may be explained by their gregarious setting behavior and the three-dimensional structure of reefs that become consolidated and cemented at high density. When oyster density is low, the dredge is likely to capture most oysters in the dredge path, but as density increases, the vertical relief of the reef, cementation, and consolidation likely increase as well making it more difficult for the dredge to capture 100% of the oysters in the dredge path.

Since the efficiency of the survey gear evaluated here is density-dependent, one must caution against biased interpretation of survey data due to the likelihood of hyperstability in survey CPUE. Hyperstability describes a situation where CPUE remains stable while true density or abundance declines (Hilborn and Walters 1992). Density-dependence in capture efficiency and catchability have been shown to cause hyperstability in CPUE for fisheries and for fishery-independent surveys (Hilborn and

Walters 1992; Rose and Kulka 1999; Godo et al. 1999; Wilberg et al. 2010; Ward et al. 2013; Kotwicki et al. 2013, 2014). As true density or abundance declines, if the efficiency of a fishing fleet or of a survey gear increases, CPUE will remain stable. For the oyster population in Delaware Bay this means increases or declines in oyster density are likely to be difficult to detect, especially at low densities, because capture efficiency increases rapidly with declining density. Interpreting temporal trends from survey CPUE may be particularly problematic for reefs in the lower bay where heavy disease pressure keeps oyster density low.

Interestingly, above 100 oysters/m² the capture efficiency declines at a much lower rate. Since density-dependent capture efficiency of survey gear has not been modeled for other sessile invertebrates it is difficult to speculate on the broader ecological significance of this inflection point. However, it is possible that much of the change in density above 100 oysters/m² comes from recruitment of small oysters that, due to limitations on space and resources within a square meter of habitat, do not survive to larger sizes. If this is the case, then these oysters would not contribute substantially to increasing vertical relief of the reef, cementation, and consolidation, which I suggest might be influencing the capture efficiency of the survey gear. As similar information becomes available for oyster reefs in different regions with different resource availability, it will be informative to compare how parameters of the power model I used to model capture efficiency vary.

Size-selectivity and spatiotemporal variability in capture efficiency

In many cases, the size of the organism being surveyed provides an accurate estimate of capture probability because survey and fishing gears are designed to retain

individuals above a certain size threshold (Millar 1992). The lack of any size selectivity here, however, is in agreement with previous work that evaluated capture efficiency separately for different sized oysters (Powell et al. 2007; Marenghi et al. 2017). Size-dependent retention should be rare because oysters grow in aggregations with the larvae cementing onto existing oyster substrate.

The probability that a given clump of oysters will be retained by the dredge is therefore a function of the size of the entire clump and not of the size of any one oyster in that clump.

No temporal change in capture efficiency was detected, but reefs formed statistically significant regional groups within Delaware Bay along the salinity gradient in the lower, middle, and upper bay. The same was true when an earlier subset of these data were evaluated (Powell et al. 2007), though the specific reefs in each group changed slightly. Since I have identified a strong density-dependence in capture efficiency, this suggests that density at each of the sampled locations has changed relatively little from 1999, when the first experiment was conducted, to 2013, when the last experiment was conducted. In fact, relative to the long-term time series, the oyster population in Delaware Bay, NJ has been stable over this time period (Ashton-Alcox 2016). While spatial and temporal variability in survey gear capture efficiency can create biased estimates of abundance and exploitation rate (Pope and Shepherd 1985; Wilberg and Bence 2006), progress continues to be made on innovative ways to deal with both (Wilberg et al. 2010; Cadrin et al. 2016), and the region-specific mean catchability coefficients being applied in the stock assessment of Delaware Bay oysters appear to adequately account for the spatial variation in oyster density and catchability.

However, as has been recommended by others (Powell et al. 2007; Marenghi et al. 2017), periodic re-evaluation of spatial patterns in density is advised to detect and correct for any temporal changes in survey gear catchability. Alternatively, coupled acoustic methods have the potential to accurately map different forms of oyster habitat (Allen et al. 2005; Legare and Mace 2017). Advancement in these and other acoustic methods may allow oyster density estimation without the need to correct for capture efficiency or catchability of dredge survey gears.

Stock assessment implications for updating catchability coefficients

The catchability coefficients derived from the 2003 experimental data using statistically significant regional group means (Powell et al. 2007), herein referred to as *old-q*, differed from those derived from the present analysis, herein referred to as *new-q*. Given that the exploitation rate is fixed at the number of oysters harvested divided by the estimated population size at that time, the only variables that can change from updating catchability coefficients from *old-q* to *new-q* are the estimate of what the population size is and/or the estimate of how heavily the population is being exploited. For instance, on the Shell Rock region if the total number of oysters harvested was 5 million, it remains 5 million whether the exploitation rate (Table 1) was calculated to be 0.069 at a population size of 78 million oysters or 0.026 at a population size of 208 million oysters. Therefore, the management implications for updating to *new-q* values may appear inconsequential because the harvest remains fixed. However, there is inherent value in knowing, with as much certainty as possible, both the actual abundance of the population on which the fishery is prosecuted, and how heavily that population is being exploited. This is because sustainable rates of exploitation for *C.*

virginica populations in one system, e.g. Delaware Bay, can influence how a fishery is managed in another system. In the case of Shell Rock in particular, a 7% exploitation rate would appear suitable to sustain the population there based on *old-q* values, however, the exploitation rate there is much closer to 2.5%, based on *new-q* values. Given that recent simulation modeling suggests oyster populations can sustain exploitation rates of approximately 2%, and that this is robust across different systems and fisheries (Powell et al. in press), the 7% exploitation rate was likely artificially high and an artifact of a misspecified catchability coefficient. Hence, as has been identified in other fisheries (Pope and Shepherd 1985; Wilberg and Bence 2006), inaccurate catchability coefficients can lead to biased estimates of abundance and exploitation rate in oyster fisheries.

Applying *new-q* values to 2015 stock assessment survey data resulted in a 9% reduction in total abundance and an 11% increase in exploitation rate. However, it is important to recognize that the change in catchability is not unidirectional for all regions evaluated; whether the effect of the *new-q* values results in an increase or a decrease in total stock size depends on the relative contribution of any one region to the total stock size in any given year. For years and regions where catchability is now estimated to be higher and the region makes up a larger relative portion of the total stock, the result will be an overall increase in stockwide abundance, and associated decrease in exploitation rate, not an increase.

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TABLES – CHAPTER 3

Table 3.1. Oyster abundance and exploitation rate calculated using different catchability coefficients for each of the managed regions in 2015 (See Figure 3.1). The proportional change in abundance from the catchability coefficients using 2003 data only, to the application identified with this work as being most appropriate (1999, 2000, 2003, and 2013 data), is given in parentheses next to each abundance estimate in the lower half of the table. * The Low Mortality region was split out into separate sections (Arnolds / Upper Arnolds and Round Island) based on the results of analysis for spatial trends in capture efficiency (see Results section and Figure 3.4).

	Experimental Data Used To		Exploitation Rate	Catchability Coefficients
	Calculate Catchability Coefficient	Oyster Abundance		
All	2003	1,701,095,858	0.018	-
Very Low Mortality	2003	485,588,439	0	7.3
Low Mortality* - <i>Round Island</i>	2003	57,480,614	0	7.3
Low Mortality* - <i>Arnolds/Upper Arnolds</i>	2003	182,871,268	0.025	7.3
Medium Mortality Transplant	2003	412,269,327	0.024	7.3
Medium Mortality Market	2003	234,268,474	0.017	7.3
Shell Rock	2003	78,433,103	0.069	3.11
High Mortality	2003	250,184,633	0.03	3.11
All	1999, 2000, 2003, 2013	1,552,939,034 (-9%)	0.02 (11%)	-
Very Low Mortality	1999, 2000, 2003, 2013	160,310,704 (-67%)	0 (0%)	2.41
Low Mortality* - <i>Round Island</i>	1999, 2000, 2003, 2013	18,976,477 (-67%)	0 (0%)	2.41
Low Mortality* - <i>Arnolds/Upper Arnolds</i>	1999, 2000, 2003, 2013	206,920,093 (13%)	0.022 (-12%)	8.26
Medium Mortality Market	1999, 2000, 2003, 2013	466,485,568 (13%)	0.021 (-13%)	8.26
Medium Mortality Transplant	1999, 2000, 2003, 2013	265,076,384 (13%)	0.015 (-12%)	8.26
Shell Rock	1999, 2000, 2003, 2013	208,314,288 (166%)	0.026 (-62%)	8.26
High Mortality	1999, 2000, 2003, 2013	226,855,520 (-9%)	0.033 (10%)	2.82

Table 3.2. Power function model parameters describing density-dependent capture efficiency.

Model	Parameter	Coefficient	Standard error	T statistic	P value
Power function; density-dependence					
	α	1.9104	0.3252	4.12	0.0013
	ϕ	0.5190	0.0781	5.012	<0.0001

FIGURES – CHAPTER 3

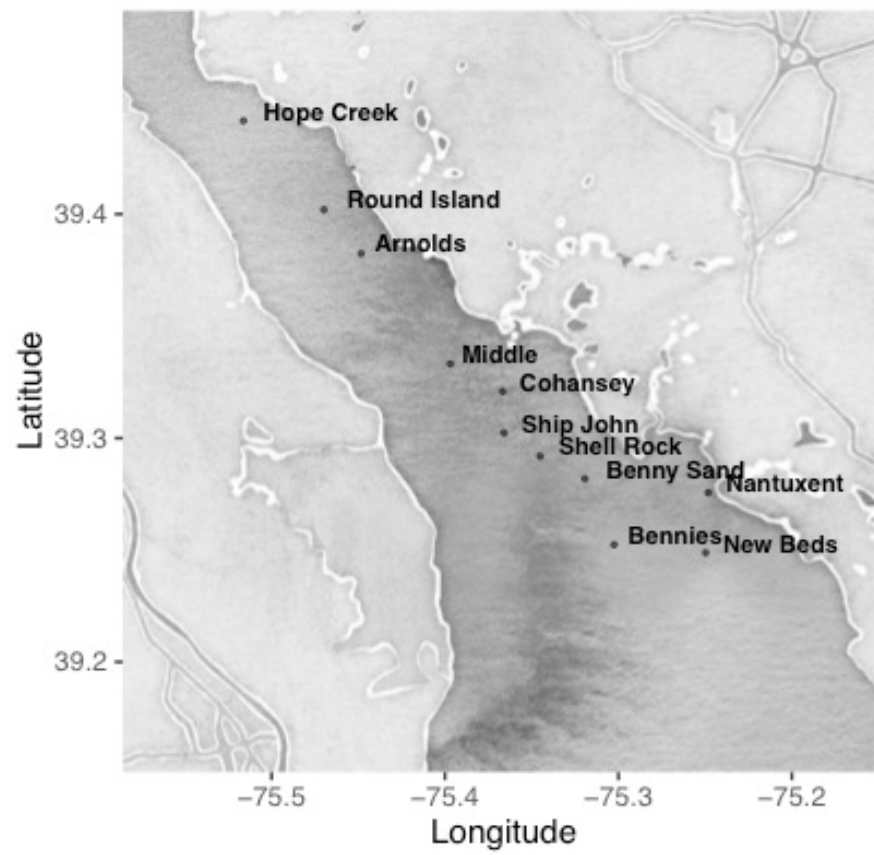


Figure 3.1. Map of sampling locations.

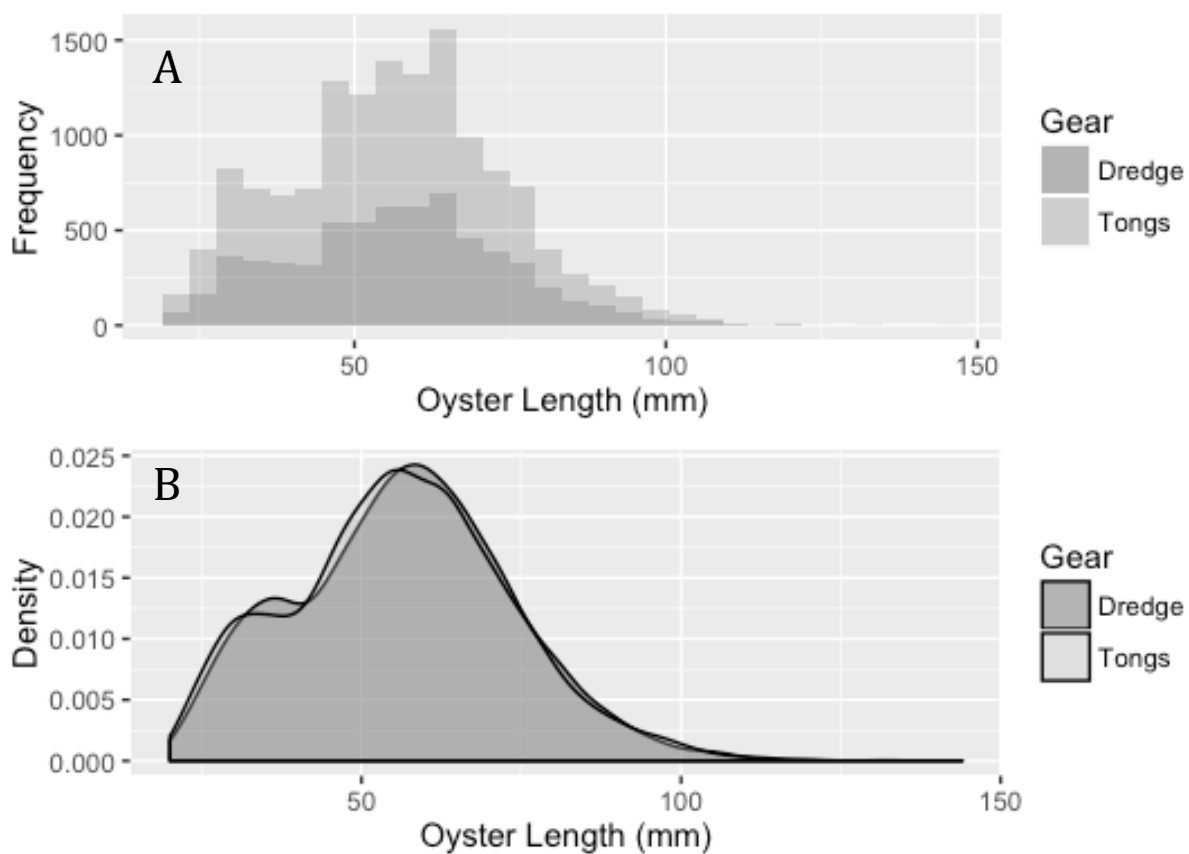


Figure 3.2. Length frequency (A) and probability density length distribution (B) for oysters collected at the same locations with a commercial oyster dredge and patent tongs.

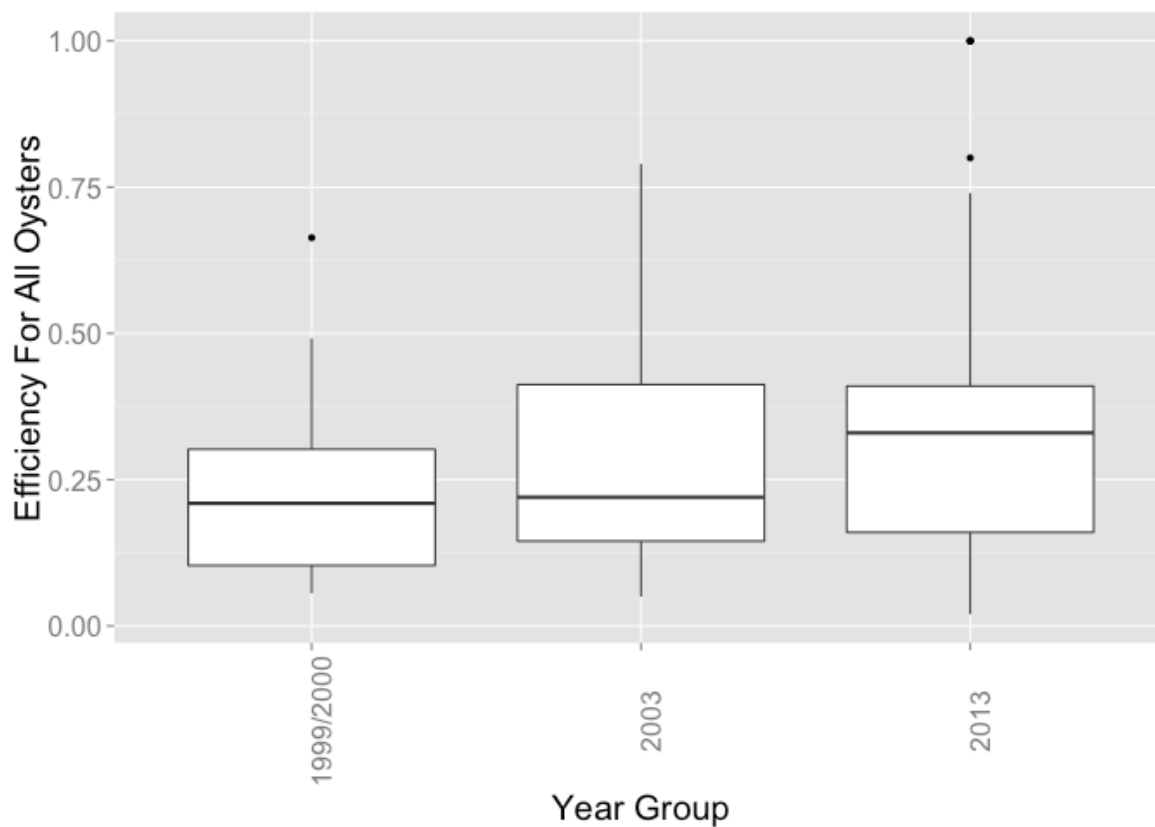


Figure 3.3. Box and whiskers plot of mean capture efficiency of a commercial oyster dredge estimated in 2000, 2003, and 2013 at the same sampling locations. Bold horizontal lines represent the mean, boxes encompass the interquartile range, black whiskers extend to the 5th and 95th percentiles, and dots are outliers.

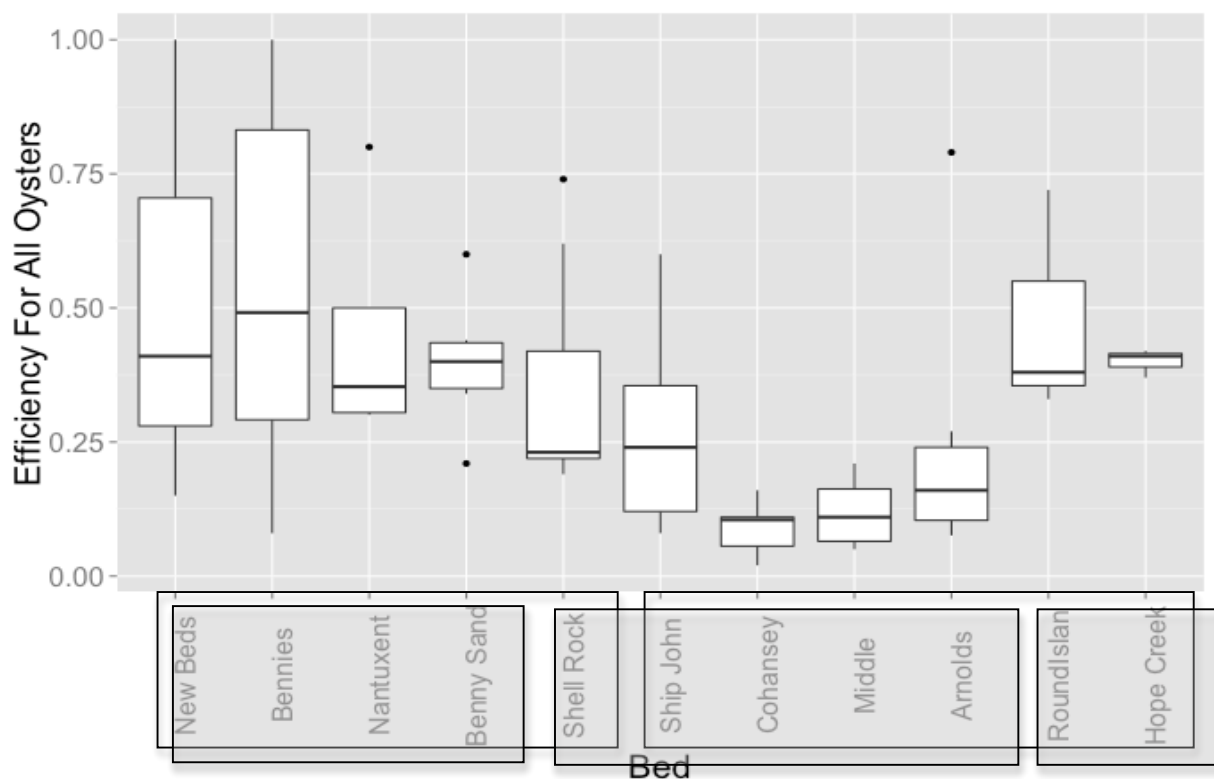


Figure 3.4. Box and whiskers plot of mean capture efficiency of a commercial oyster dredge at different oyster reef locations along the Delaware Bay, USA. Reef locations are organized on the x-axis from the lower bay (left side) to the upper bay (right side). Empty black boxes around the reef names represent the regional grouping of bed-specific catchability coefficients applied in the 2015 Delaware Bay oyster stock assessment based on data collected from the 2003 experiments (Powell et al. 2007). Shaded, offset boxes, represent the regional groupings of bed-specific catchability coefficients identified as statistically appropriate with this work. Bold horizontal lines represent the mean, boxes encompass the interquartile range, black whiskers extend to the 5th and 95th percentiles, and dots are outliers.

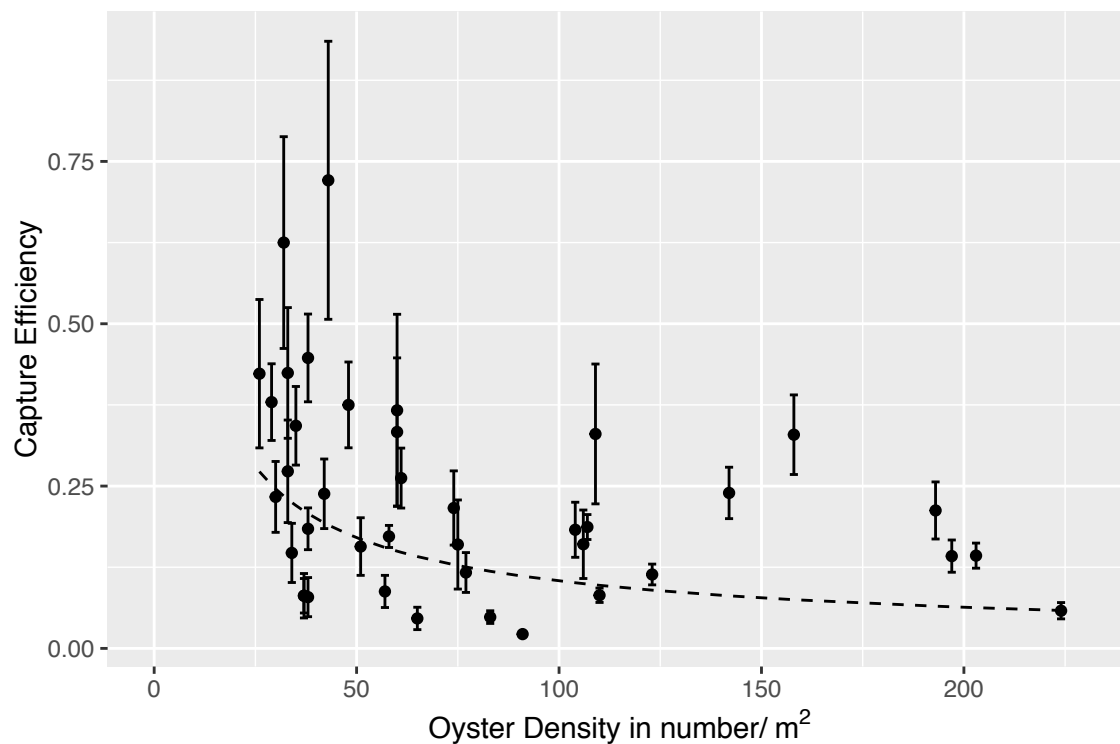


Figure 3.5. Survey gear capture efficiency as a function of true oyster density. Error bars represent the standard deviation from 1,000 bootstrap simulations. Line indicates the best fit power model estimated by weighted nonlinear least squares. See methods section for details.

CHAPTER 4

ALTERNATIVE MODELS TO ESTIMATE DENSITY OF EASTERN OYSTERS *CRASSOSTREA VIRGINICA* USING A HYDRAULIC DREDGE

Abstract

Catchability (q) is a parameter used in stock assessments to describe how much of the population is caught by a single unit of fishing or survey effort. In some cases, q can be density-dependent, causing survey CPUE to be hyperstable across a range of animal densities. In these instances, CPUE can be an unreliable proxy for true density in the sampled area. In Delaware Bay, USA, there is a natural, along-bay gradient in the density of eastern oysters *Crassostrea virginica*. In addition, the q of the survey dredge used in the assessment of the oyster population there is density-dependent. Using data collected during two separate field experiments, one in 2003 and one in 2013, I evaluated three potential methods for estimating true oyster density in an area sampled with an oyster dredge. For the first model, CPUE was corrected for by applying spatially-explicit q coefficients that account for the along-bay gradient in density. In the second, CPUE was corrected for by estimating q *in situ* for each tow using a logistic model fit to catch composition and tow covariates. For the third model, CPUE data were ignored entirely and a model that accounted for the proportion of the sample composition that was made up of oysters was applied to estimate oyster density *in situ* for each tow. Models were trained on one set of experimental data and tested on an independent set. The mean square error (MSE) was calculated for each train-test pairing and the modeling approach with the lowest average MSE score was chosen as

the best approach. The model that utilized the proportion of the total catch that was made up of oysters to estimate the oyster density performed best. Where time and financial constraints prevent a more quantitative approach that measures CPUE and estimates q for the sampling gear, or where q varies at fine spatial and temporal scales, a simpler evaluation of the relative components that comprise a tow may adequately describe the density of oysters in the sampled area.

Introduction

Catchability (q) is a parameter used in stock assessments to describe how much of the population is caught by a single unit of fishing or survey effort (Arreguin-Sanchez 1996). Fishery and survey q can vary in space and time, sometimes due to changes in the density of the sampled organism (e.g., Rose and Kulka 1999; Godo et al. 1999; Kotwicki et al. 2014). In such instances, interpreting survey or fishery catch-per-unit effort (CPUE) is difficult because they are rarely proportional to the actual abundance (Hilborn and Walters 1992; Maunder et al. 2006).

The conditions that produce density-dependent q in observations collected from fishing data are well established (Hilborn and Walters 1992; Rose and Kulka 1999). For example, as abundance declines, fish may aggregate in a behavioral response to declining abundance, and fishermen will likely aggregate around the fish, causing CPUE to remain constant while abundance declines. This makes abundance especially difficult to estimate from fishery-dependent data because it can result in fishery CPUE being hyperstable at different levels of abundance (Erisman et al. 2011).

Evidence for density-dependent q is now becoming more prominent in fishery-independent survey data as well (Godo et al. 1999; Kotwicki et al. 2013, 2014). While the behavior of the survey gear may be standardized, reducing or eliminating the influence of human behavior, the surveyed animal may still respond to that gear differently at varying densities (Kotwicki et al. 2014). This can make relative abundance or CPUE indices generated from a fishery-independent survey unreliable as well.

The q for commercial dredges used to survey oyster reefs in Delaware Bay varies spatially and temporally (Powell et al. 2002, 2007) likely due to changes in oyster density (Chapter 3). Furthermore, density-dependent q leads to survey CPUE being hyperstable at low oyster density (Chapter 3). This raises the question then, how does one confidently estimate the density of oysters in an area sampled with a dredge?

Highly variable dredge q has been identified for other oyster populations (Fu et al. 2016; Marenghi et al. 2017). One recommended course of action to account for this is to treat oyster resource surveys as relative indices with prior probabilities that incorporate uncertainty in dredge efficiency (Fu et al. 2016). However, this approach generates highly uncertain abundance estimates, making it difficult to interpret how an oyster resource is responding to prescribed management actions or environmental drivers (Ashton-Alcox 2016).

In this chapter, given the density-dependence in q of the survey gear used to assess the oyster population in Delaware Bay, described in Chapter 3, I evaluate the accuracy of three different approaches to estimating true oyster density (td) in the sampled area from a survey dredge tow. In the first approach, herein referred to as the average

model (AM), the estimated density (ed) was calculated by multiplying the sample CPUE by a region-specific, mean q . The AM approach is what is used to calculate ed in the sampled area for the stock assessment of oysters in Delaware Bay (Ashton-Alcox 2016) and is supported by statistical analyses of the spatial trend in oyster density along the bay gradient (Powell et al. 2002, 2007; Chapter 3). However, the AM approach depends on having an independent, experimentally-derived estimate of q , and since q is density-dependent (Chapter 3), this approach requires q estimates be periodically updated to account for any temporal changes in density in a given region.

In the second approach, herein referred to as the logistic model (LM), a tow-specific q was modeled by logistic regression using a list of tow and catch composition variables, and applied to CPUE to calculate ed . When catch composition and variables that describe the conditions of the tow explain some of the variability in q , this information can potentially be used to estimate q *in situ* for each individual tow (Powell et al. 2007). Since the LM approach estimates catchability directly for each tow *in situ*, this method does not require periodic reassessment of q .

The third approach evaluated, herein referred to as the power model (PM), does not utilize survey CPUE data, but rather models ed in the sampled area directly as a power function of the proportion of the survey dredge tow that was made up of oysters. Since the PM approach relies only on an estimate of the contents in a given tow, it does not require an estimate of CPUE for the tow or independent estimates of q . This approach is akin to an historic management rule called the “40% rule” used in the management of the Delaware Bay oyster fishery from 1953 to 1996, before q had been estimated. Under

this rule, if the average survey dredge catch in a given area was comprised of less than 40% oysters, the fishery in that area would close (Ford 1997).

Material and Methods

Field sampling

Survey dredge CPUE and true oyster density, td , were estimated at twenty-four locations in Delaware Bay in 2003 and 2013 (Figure 4.1). Detailed protocol for estimating CPUE and td can be found in Chapter 3, but briefly, the *F/V Howard W. Sockwell* was used to tow the survey dredge for 1-minute at each sampling location. If the dredge was full after the 1-minute tow, the tow time was reduced to 45s so that the total number of bushels of material collected in the swept area could be determined. Swept area and an estimate of the total number of oysters caught in the dredge were used to calculate CPUE as oysters/m² for each tow. To estimate td , six, 0.89 m² patent tong grabs, assumed to be 100% efficient, were collected parallel to, but not inside, the tow track and td was estimated as total oysters/m² from these six grabs.

For each dredge tow, a one bushel subsample was collected, brought back to the lab, and sorted into catch component classes of oysters, cultch (oyster shell), boxes (dead oysters with the hinge still intact), and debris. Volumes and weights of each catch component were recorded and all oysters and boxes in each sample were counted and individual lengths measured. In addition, wire scope, swept area, total catch in bushels, and change in bottom depth were recorded for each tow.

For each tow, this approach resulted in an observation of survey dredge CPUE (or apparent density (ad)), an estimate of td adjacent to the survey tow, and a record of tow

and catch composition data that could be evaluated for their effect on survey dredge performance.

Data Analysis – Model Descriptions

Average Model (AM)

The model estimated density ed_{tr_i} for each test data set t , region r , and tow i was

$$ed_{tr_i} = q_{tr_r} * ad_{tr_i}, \quad (1)$$

where for each tow i , the apparent density, or CPUE, ad_i of oysters in the tow track was

$$ad_i = \frac{opb_i * b_i}{sa_i} \quad (2)$$

where opb represents the number of oysters collected in a 37-L bushel subsample, b represents the total number of bushels in the tow, and sa represents the swept area (m^2) covered by the tow. The mean catchability parameter q_{tr_r} for each training data set tr and region r was

$$q_{tr_r} = \frac{1}{n} \sum_{i=1}^n \left(\frac{1}{e_{i_{tr_r}}} \right) \quad (3)$$

where for each tow i

$$e_i = \frac{ad_i}{td_i} \quad (4)$$

Finally, the density of oysters td_i collected parallel to tow track i was

$$td_i = \frac{\sum_{j=1}^6 o_j}{5.34} \quad (5)$$

where j represents a 0.89 m^2 tong sample collected parallel to tow i and o represents the number of oysters collected in each tong sample j .

Logistic Model (LM)

Powell et al. (2007) used data from the 2003 experiment to evaluate whether information collected during the tow, information from the catch composition, and information about the fishing intensity in the sampled area could be used to model tow-specific q of the dredge *in situ*. This approach is attractive because it does not rely on having independent observations of q or require periodic reevaluation of q . In addition, it takes advantage of the available information that describes the tow and catch conditions. Finally, it allows for q to be estimated at the individual tow level, instead of being a fixed, region-specific coefficient. With the LM approach, I build on this previous work by reevaluating the influence of the same set variables used in the Powell et al. (2007) analysis, but by including data from the 2013 experiment as well, by including additional independent catch and tow composition variables, and by altering the modeling approach from estimating q with linear multiple regression to estimating the probability of capture e with multiple logistic regression.

In many cases, the size of the organism being surveyed provides an accurate estimate of capture probability because survey and fishing gears are designed to retain individuals above a certain size threshold (Millar 1992). However, this is not true for oysters (Powell et al. 2007; Marenghi et al. 2017; Chapter 3), likely because oysters grow in interconnected reefs and the probability that a given clump of oysters will be retained by the dredge is a function of the size of the entire clump and not of the size of any one oyster in that clump. For this reason, the mean length of oysters caught in the dredge tow was not included as a potential variable in the LM analyses. Catch composition variables that were evaluated included the proportion of the 37-L bushel sub-sample that was made up of cultch, the area (length*width in mm) of the ten largest

clumps in each sub-sample, where clump refers to a particle of material in the subsample, and the total haul volume (in bushels). Variables evaluated that were related to the tow included the change in depth from the beginning to the end of the tow, the wire scope, calculated as the amount of chain let out by the boat divided by the average depth for the tow, the total swept area covered, and a variable that measures the relationship between the direction of the tow and the direction and intensity of the tide, herein referred to as the tow-tide variable. The tow-tide variable tt_i for each tow i was calculated as

$$tt_i = dir_i * tide_i, \quad (6)$$

where the adjusted tow direction dir_i for tow i was

$$dir_i = 45 - tdir_i, \quad (7)$$

for actual tow direction $tdir_i < 136$, and

$$dir_i = tdir_i - 225, \quad (8)$$

for $136 \leq tdir_i \leq 315$, and

$$dir_i = 405 - tdir_i, \quad (9)$$

for $tdir_i > 315$. The magnitude of the tide $tide_i$ for equation (6) was calculated as

$$tide_i = T_i - 6, \quad (10)$$

for ebbing tides, and

$$tide_i = T_i, \quad (11)$$

for flooding tides, where T_i represents the time in hours since slack tide at the time and location of tow i . The final variable evaluated was weighted industry coverage in the

sampled area. This was estimated as a weighted average of the fishing effort on the reef from the three years prior to when a given tow was conducted.

For each test data set t , the estimated density ed_{t_i} was calculated separately for each tow i . This transforms equation (1) to

$$ed_{t_i} = q_{t_i} * ad_{t_i}, \quad (12)$$

where apparent density ad_{t_i} , or CPUE, is still estimated by equation (2), but where q_{t_i} is now estimated separately for each individual tow i and test data set t *in situ* by

$$q_{t_i} = \frac{1}{e_{t_i}}, \quad (13)$$

and

$$e_{t_i} = \left[\frac{\exp(\beta_{0_{tr}} + \beta_{1_{tr}}x_{1_{t_i}} + \beta_{2_{tr}}x_{2_{t_i}} \dots \beta_{j_{tr}}x_{j_{t_i}})}{1 + \exp(\beta_{0_{tr}} + \beta_{1_{tr}}x_{1_{t_i}} + \beta_{2_{tr}}x_{2_{t_i}} \dots \beta_{j_{tr}}x_{j_{t_i}})} \right], \quad (14)$$

where β_{0_t} is the estimated y-intercept parameter for test data set t , x_{j_t} is a vector of catch composition, tow, and industry effort variables, as described above, j for test data set t , and $\beta_{j_{tr}}$ is a vector of j estimated parameters for each x_{tr} in training data set tr .

For each training data set tr the best set of variables for vector x_{j_t} was estimated using backward, stepwise Akaike Information Criteria

Power Model (PM)

A preliminary analysis of oyster density across different variables measured during the field experiments revealed that oyster density increased in a non-linear, predictable fashion, with the proportion of the 37-L bushel sub-sample from each tow that was

made up of oysters. Therefore, the oyster volume relative to the total volume ov_i in the bushel sub-sample was used to calculate the estimated oyster density ed_{t_i} for each test data set t in the sampled area for tow i directly with

$$ed_{t_i} = \alpha_{tr} * ov_{t_i}^{\theta_{tr}} \quad (15)$$

where α_{tr} and θ_{tr} are estimated parameters for training data set tr .

Data Analysis – Evaluating Model Performance

To evaluate the accuracy of each approach in estimating td in the sampled area, I split the experimental data up six ways, creating three pairs of training and test data sets. In the first pairing, the 2003 experimental data served as training data and the 2013 experimental data served as test data. In this case, the 2003 experimental data were used to estimate the parameters of the models. The models parameterized with the 2003 data were then used calculate ed in the sampled area for the 2013 data and this model-estimated density was evaluated against td for the 2013 data. For a second pairing, this process was repeated using the 2013 data as training data and the 2003 experimental data as test data. For the final pairing, 24 of the 48 observations (including data from both the 2003 and 2013 experiments), were drawn at random and labeled as the training data set, while the remaining 24 observations were labeled as the test data set. For each training-test combination, the mean squared error MSE_m for each model m was calculated as,

$$MSE_m = \frac{1}{n} \sum_{i=1}^n (\widehat{td}_i - ed_{m_i})^2 \quad , \quad (16)$$

where \widehat{td}_i represents what was estimated to be the true density in the sampled area from the tongs for tow i and ed_{m_i} represents the density estimated by model m for tow

i. The approach with lowest average MSE score across all three training-test data combinations was selected as the best modeling approach.

Results

The parameters for each modeling approach varied across the three training data sets (Table 4.1). For the AM approach, mean q coefficients calculated from experiments conducted in the lower bay were always lower than those from experiments conducted in the upper bay and q varied in the upper bay across the different training data sets.

For the LM approach, the variables that contributed significantly to the capture efficiency (e) varied with the training data set (Table 4.1). Only two variables, total haul volume and the proportion of the subsample made up of cultch, were significant predictors of e for all three training data sets. A higher proportion cultch in the subsample and a higher total catch volume resulted in a higher capture efficiency, and this was consistent across all three training data sets (Figure 4.2).

The PM approach achieved the lowest mean MSE score and outperformed all other models in all but one pairing, the AM 2003 training/2013 test data combination (Table 4.2). The mean MSE score for the AM approach was inflated by a high 2013 training/2003 test pairing MSE score (Table 4.2). The LM approach achieved a consistently poorer fit than either the AM or PM approach. The LM 2003 training/2013 test pairing, in particular, resulted in an order of magnitude poorer fit (131,440) than any training-test pairing of any of the three modeling approaches. The LM approach typically produced large overestimations of ed relative to td , while the AM approach produced a disproportionate number of underestimates (Figure 4.3).

The td in the sampled area increased with an increase in the proportion of the bushel subsample that was made up of oysters (Figure 4.4). PM parameters estimated from a random draw of observations from the 2003 and 2013 experiments performed best in estimating the td in the sampled area (Table 4.2, Figure 4.4).

Discussion

Fishery-independent surveys of natural resources are historically believed to provide indices that are proportional to abundance (Godo 1994; Kotwicky et al. 2014) and these indices are utilized regularly in stock assessments and models of population and community dynamics. However, we know now that even when collected using a standardized, fishery-independent survey design, CPUE may still not be proportional to abundance because q of the survey gear can be highly variable in space and time (Hoffman et al. 2009; Wilberg et al. 2010; Kotwicky et al. 2014; Chapter 3).

Density-dependence in survey q offers an interesting challenge because to convert CPUE or ad in the sampled area to td , one would need to know td *a priori* since q is density-dependent. However, with an estimate of the td in the sampled area, there would be no need for q or ad . Since oyster td cannot be estimated directly in an area sampled with an oyster dredge because the dredge is not 100% efficient (Powell et al. 2003, 2007; Marengi et al. 2017), and since the capture efficiency of the dredge varies with density (Chapter 3), with this work I evaluated three alternative approaches to applying a singular q coefficient to estimate td of oysters in an area sampled with a dredge. In the first, I attempted to control for density-dependence in q in a direct way with spatially-explicit q coefficients (the AM model). In the second I use an indirect

application to estimate q for each tow *in situ* using available information about the tow and catch composition (the LM model). In the final application, I ignored CPUE data all together and adapted a version of a historically-applied method to estimate td *in situ* from the proportion of the bushel sub-sample that was made up of oysters (the PM model).

I expected the LM model to perform best because it utilized a suite of variables that described the tow conditions and catch composition, as well as the exploitation history in the sampled area, to estimate q . This fine scale information, however detailed, turned out to be uninformative relative to the information contained in the competing models. Not only did the LM approach not perform best, but it performed significantly worse than either of the alternative approaches. Tow and environmental conditions, as well as catch composition, are known to influence survey catchability for marine and freshwater species with a variety of life histories (Hoffman et al. 2009; Somerton et al. 2013; Sagarese et al. 2016; Korman and Yard 2017), and this is true for surveys of oyster reefs as well (Powell et al. 2007). However, since q is density-dependent, and since neither density nor some proxy for density are included as independent variables in the LM approach, perhaps the poor performance of this method relative to the other two should not have been surprising.

The AM model, which outperformed the LM model by a large margin, also did not include density as a model parameter, however, by utilizing regional mean q coefficients for a population where density varies in a predictable way along the bay gradient, this model did contain a proxy for density. The regional q coefficients could be viewed as pseudo-density-dependent since density varies by region. While the

application of spatially-explicit q coefficients appear to be rare in the assessment of oyster populations (but see Ashton-Alcox 2016), this approach likely has widespread application to other dredge surveys where oyster density occurs non-randomly in space.

Since CPUE is not proportional to true abundance when q is density-dependent, it should probably not be surprising that the one application that ignores CPUE data entirely, the PM model, performed best. While one could devise a situation where this model would generate highly biased estimates of td , such situations occurred at low enough frequency that the mean MSE for the PM model was lower than either of the other two applications evaluated. For instance, if a given tow covered a 100 m² area and the only thing the dredge picked up over that tow was 1 oyster, the apparent density would be 0.01 oysters/m² and the proportion of the sample made up of oysters would be 100%. Depending on the training data set used in the estimation, this would have resulted in an ed of between 142 and 362 oysters/m². This estimate would almost certainly be biased extremely high given that a single oyster was collected over a 100 m² area.

To my knowledge, there are no other instances where a PM approach, or even something similar, has been used to estimate oyster density for a survey. The Delaware Bay oyster fishery used to be managed on a single reference point. If 40% or more of the average catch was made up of oysters, then the fishery in that area would remain open, but if the catch composition fell below 40% oysters, it would close (Ford 1997). For all four PM models this suggests 40% and lower would have equated to 50 oysters/m² and lower. While the “40% rule” was a relative index of the catch

composition, perhaps it worked well because it provided an accurate and quantitative proxy for when td fell below the 50 oysters/m² threshold.

Where q varies at fine spatial and temporal scales, the PM model may offer advantages over more traditional applications for estimating oyster density in an area sampled with a dredge. First, a significant amount of additional time and effort is needed to quantify both the swath area and the number of oysters for a given tow to calculate CPUE. Since both the AM and LM models require a measure of CPUE, and since both performed more poorly relative to the PM method, the dedicated time and resources spent to estimate CPUE may not be necessary. In addition, while the AM model performed nearly as well as the PM model, it requires some independent and up-to-date estimate of td over a coarse region. With increasing spatial shifts in density along the bay gradient over time, the application of the AM model will become progressively poorer. Since the PM model does not require independent knowledge of td , similar shifts in density along the bay gradient should not affect the accuracy of the AM approach.

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TABLES – CHAPTER 4

Table 4.1. Coefficients for model parameters for average (AM), logistic (LM), and power (PM) models. In parentheses next to each coefficient is the p-value associated with that parameter. NS = not selected by backward stepwise AIC (see Methods).

	Parameters	2003 Training Data	2013 Training Data	Random Training Data
Average Model				
Lower Bay	q	3.04	3.30	3.15
Upper Bay	q	6.48	10.55	6.97
Logistic Model				
Intercept	β_0	-2.021	-1.981	1.425
Total Haul Volume (bushels)	β_1	0.5307 (<0.001)	0.6257 (<0.001)	0.0817 (0.007)
Prop. of Subsample Made of Cultch	β_2	0.0441 (<0.001)	0.0270 (<0.001)	0.0253 (<0.001)
Average Clump Area in Subsample	β_3	NS	-0.0001 (0.003)	0.0001 (0.002)
Change in Depth	β_4	NS	0.2965 (<0.001)	0.0923 (0.01)
Scope	β_5	-1.8471 (<0.001)	0.3109 (<0.001)	NS
Swept Area	β_6	NS	-0.0264 (<0.001)	-0.0392 (<0.001)
Tow-Tide	β_7	-0.0008 (<0.001)	NS	-0.0012 (<0.001)
Weighted Industry Coverage	β_8	0.2105 (<0.001)	-0.2764 (<0.001)	NS
Power Model				
	α	362.43 (0.03)	142.95 (0.003)	264.15 (0.05)
	θ	2.22 (0.01)	1.39 (0.009)	2.16 (0.03)

Table 4.2. Model performance estimated using the mean squared error (MSE) for each modeling approach (average, logistic, and power) and each training-test data combination. The overall reported mean for each method is the mean of the MSE scores for each training-test combination.

	Average	Logistic	Power
2003 Training / 2013 Test	1,389	18,599	2,074
2013 Training / 2003 Test	18,119	131,440	4,218
Random Training / Random Test	2,312	12,421	1,935
Mean	7,273	54,153	2,742

FIGURES – CHAPTER 4

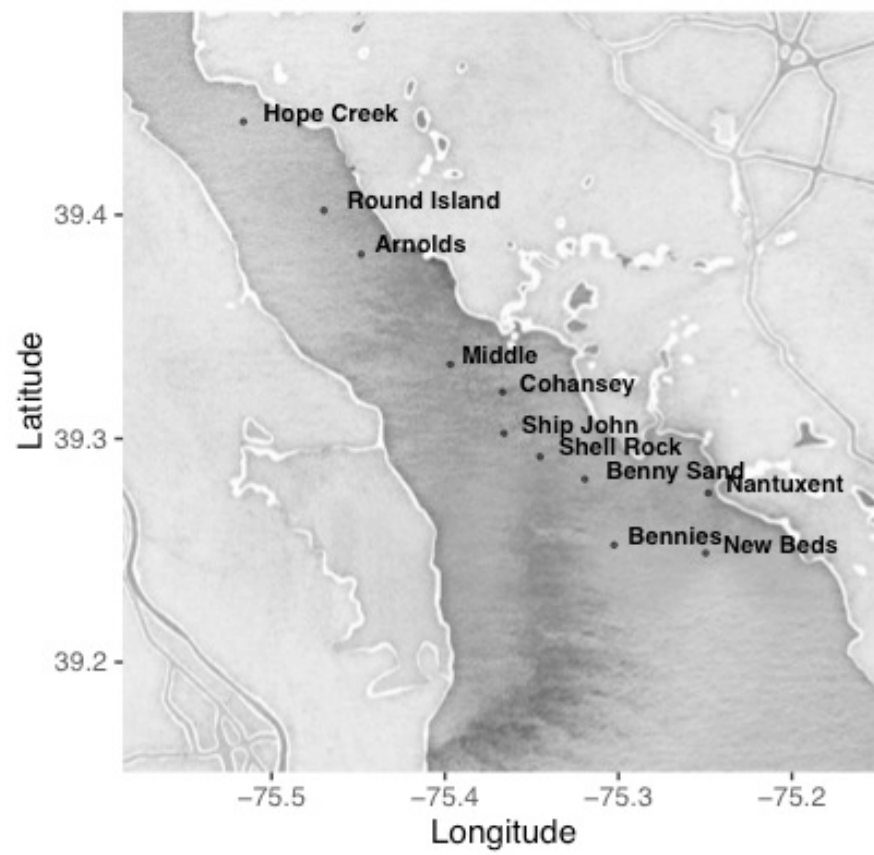


Figure 4.1. Map of sampling locations.

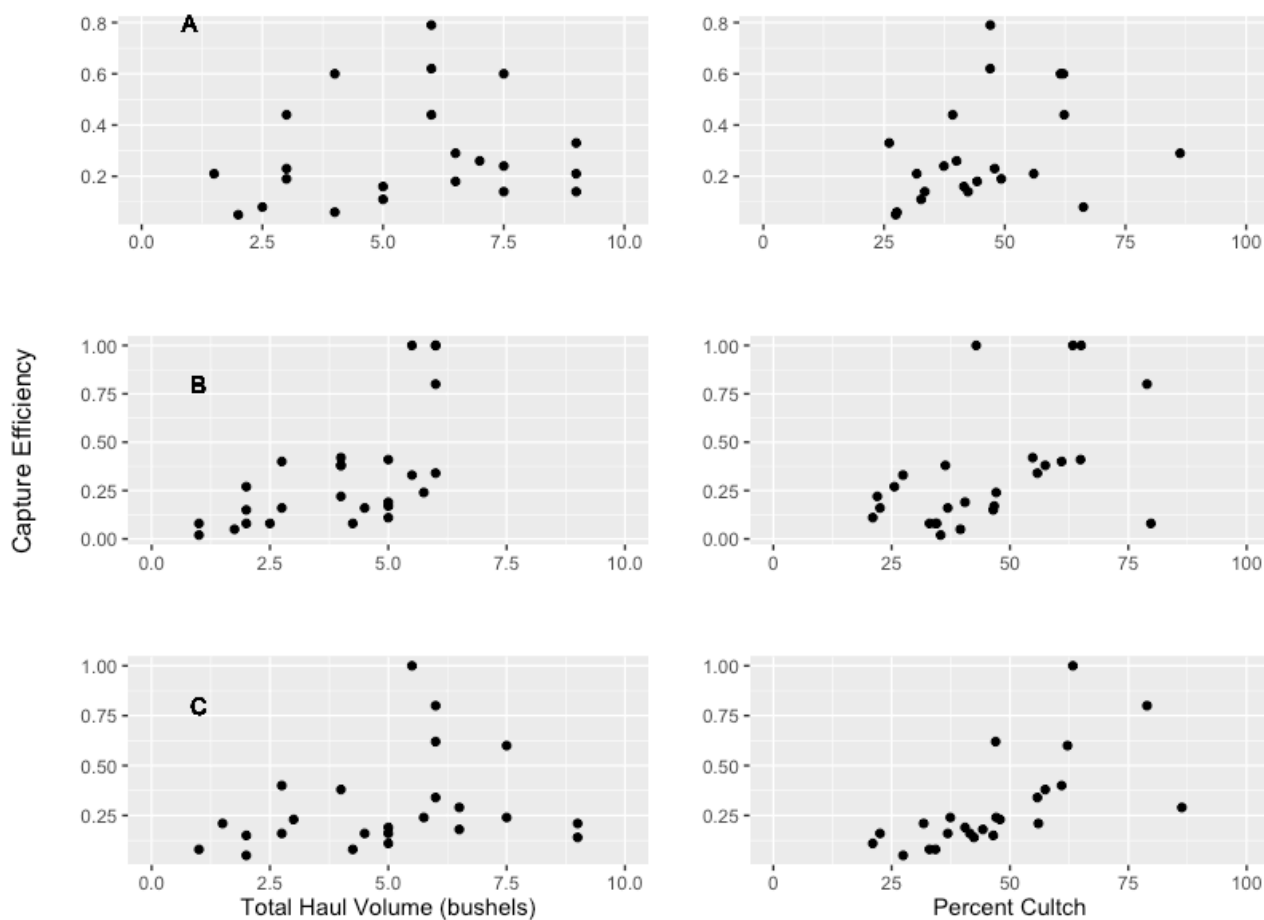


Figure 4.2. Capture efficiency as a function of two variables, total haul volume (left panels) and proportion of the sub-sample that was made up of cultch (right panels) for all three training-test pairs of data (A = 2003 training data, B = 2013 training data, C = random training data).

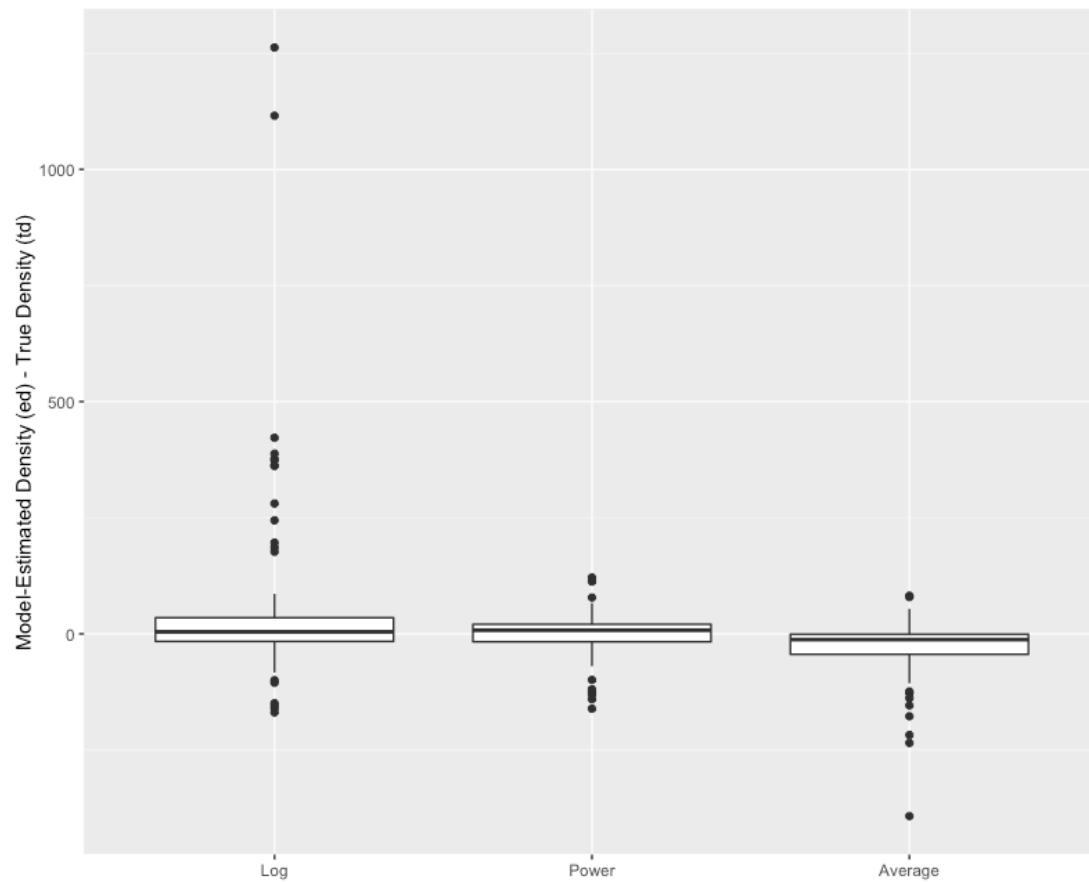


Figure 4.3. Residuals (model-estimated density ed – true density td) calculated from three approaches, a logistic model (LM), a power model (PM), and an average model (AM), to estimating true density in the sampled area. See Methods for model descriptions.

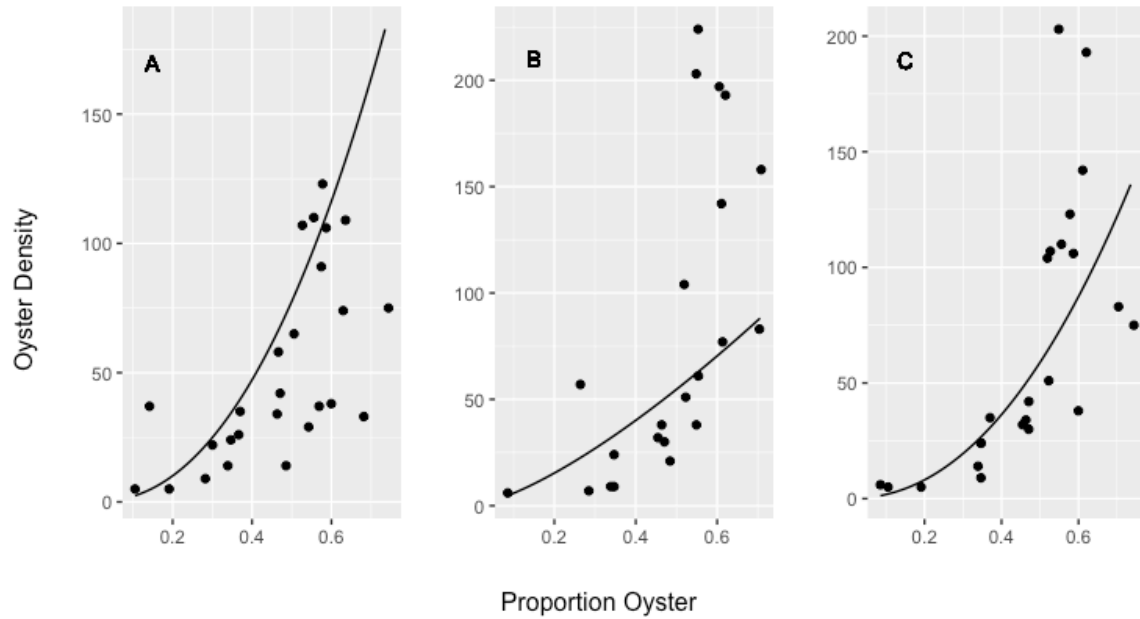


Figure 4.4. The true density (td) of oysters in the sampled area as a function of the proportion of the sample that was made up oysters. (A) 2003 data were used to train and estimate power model (PM) parameters for the predicted line while the points plotted are the 2013 observations, (B) 2013 data were used to train and estimate power model parameters for the predicted line while the points represent the 2003 data, and (C) a random draw of 24 of the 48 experimental observations (2003 and 2013 experimental data) were used to train and estimate parameters for the predicted line while the points represent the remaining 24 data points.

CONCLUSIONS

Our ability to evaluate the response of a fished population to changes in the ecosystem or changes in fishing exploitation rate is dependent on how confident we are in stock assessment results. Output from stock assessments, including abundance and biological reference points, are highly sensitive to misspecification of fishery and survey catchability and selectivity (Harley et al. 2001; Chen et al. 2003; Francis 2011; Jonsson et al. 2013; Butterworth et al. 2014; Cadrin et al. 2016). Despite this, the processes that drive patterns in selectivity and catchability remain poorly understood for many fisheries (Sampson 2013; Maunder and Piner 2014; Wang and Maunder 2017).

Traditionally, selectivity and catchability are parameters that are estimated inside the stock assessment model where they conform with the model input data and assumptions. However, since catchability and selectivity can be highly correlated with other model parameters (Arreguin-Sanchez 1996) and can be highly variable in space and time (Wilberg et al. 2010), more recently a call for experimental and field observation-based approaches to estimates of selectivity and catchability are becoming common. For example, Somerton et al. (1999) state, “Cooperative studies by experimentalists and modelers are needed to derive a better understanding of the situations in which experimentally derived estimates of catchability can improve knowledge of stock size or fishing mortality rates”, and Cadrin et al. (2016) suggest, “Considering the sensitivity of stock assessments to the assumed form of selectivity and estimates of catchability, as well as their importance for fishery management advice, we

suggest that the selection pattern and catchability (or relative efficiency) should be evaluated from a field experiment whenever possible to reduce uncertainties in stock assessments.”

One could view this dissertation, in part, as an answer to these calls. However, I suggest that we not only endeavor to derive estimates of catchability and selectivity through experimentation and observation, but that we should attempt to understand the underlying ecology that drives variability in these parameters so that we can better understand and predict how shifts in life history, distribution, and behavior will influence perceived dynamics of a population. Wang and Maunder (2017), state in reference to assessment model misspecification, “Therefore, we recommend that more work be done to ensure that models are correctly specified. Unfortunately, there is a lack of understanding and uncertainty in the fundamental biological and fishing processes of most, if not all, fish stocks, making the removal of model misspecification difficult.” The unique characteristics of a species require similarly unique applications and an understanding of the underlying ecological processes that make them unique. While it is likely not feasible, nor necessary, to develop a unique stock assessment modeling approach for every species, research on the underlying ecology of each individual species could lead to species-level applications of parameters like selectivity and catchability that account for unique life history within more general modeling frameworks.

My work is not the only research attempting to intersect underlying ecological processes with parameters used in stock assessments, of course. For instance, the most recent butterfish (*Peprilus triacanthus*) stock assessment used a thermal niche model to

develop temperature-dependent estimates of catchability that account for the availability of butterfish to the survey gear in the water temperature where it was deployed (Adams et al. 2014). In this application, the organisms's unique thermal niche is being used to develop realistic estimates of survey catchability when and where the survey occurred. Additional examples exist for temperature- and density-dependent catchability, predator-dependent catchability, and selectivity patterns that account for unique migration patterns (Wilberg et al. 2010; Chakraborty et al. 2012; O'Boyle et al. 2016). Each method is similar in that the knowledge of the underlying ecology of the organisms is used to define direct estimates, or estimate bounds, for catchability and selectivity.

In Chapter 1 I identified a selectivity pattern in the recreational summer flounder fishery that was significantly skewed toward female fish relative to the selectivity patterns in the commercial fishery or the survey. As discussed, this pattern likely results from sex- and age-specific movement and habitat use. In Chapter 2, given the identified selectivity pattern in the recreational fishery and its influence on the catch composition, I evaluated alternative management actions that could reduce fishing pressure on large, fecund female fish. The unique characteristics of summer flounder, that they likely separate out by sex and age in space and time, require a separate selectivity pattern be modeled for this fishery than for the commercial catch or the survey. Furthermore, given this behavior results in a highly biased female catch in the recreational fishery, management action may need to be taken to evaluate alternatives measures that could reduce fishing pressure on female fish.

In Chapter 3 I discovered that we cannot treat oysters as we would surf clams or scallops relative to survey gear catchability. Oysters have a unique catchability characteristic such that changes in density lead to changes in gear performance, and this is likely related directly to their need to grow in a three-dimensional reef structure. One of the unique ecological characteristics of oysters, that they grow in three-dimensional reefs, requires a unique application to how we sample, assess, and manage them. In Chapter 4, I worked on developing these applications and evaluating the performance of each so that a method that accounts for density-dependence in catchability could be incorporated into the stock assessment of oysters in Delaware Bay.

Without an understanding of summer flounder availability relative to fishing effort, one would never reevaluate the sex- and age-specific selectivity patterns in the recreational fishery. Similarly, without knowing how oysters interact with an oyster dredge at high density, one would never seek to develop density-dependent models of catchability for that survey. Hare (2014) calls for “a multi-hypothesis, integrative and multidisciplinary approach to fishery assessment and management” and Able (2016) states, “The development of our understanding of fish and other marine fauna, including my own over several decades, has proceeded from basic natural history to ecology and evolution, but we often need to return to natural history to address deficiencies in our attempts to manage fisheries, conserve habitats, and model ecosystems”. I agree with both sentiments and I hope this work contributes evidence in support of the notion that accurate assessment and sustainable management of marine resources depends on our ability to collaborate as fishermen, stock assessment

scientists, ecologists, ocean modelers, resource managers, biologists, and natural historians.

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