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Estimating Detection Probabilities in Beach Seine Surveys for Estuarine Fishes

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Estimating Detection Probabilities in Beach Seine Surveys for Estuarine Fishes

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In Partial Fulfillment

of the Requirements for the Degree

Master of Science

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by

Branson D. Williams

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APPROVAL SHEET

This thesis is submitted in partial fulfillment of

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ABSTRACT

Detectability, the probability that a species is encountered if it inhabits a site, is often overlooked in fisheries research despite its potential to obscure habitat use inferences. Detectability can be estimated using models that also provide an estimate of occupancy (Ψ), the probability that a species inhabits a site. I used these models to estimate both probabilities, and to examine factors affecting detectability and occupancy for three fishes in Chesapeake Bay tributaries: young-of-the-year striped bass (*Morone saxatilis*), yearling Atlantic croaker (*Micropogonias undulatus*), and spottail shiner (*Notropis hudsonius*). Occupancy models were fitted to data from a seine survey conducted during summer, 2008 and 2009, in two Chesapeake Bay tributaries. Key assumptions of occupancy models relate to the extent and timing of fish movement: sites are independent, and no site-specific emigration or immigration occurs. A mark-recapture study of striped bass, and previously published studies of Atlantic croaker and spottail shiner, suggested that these assumptions were reasonable. Detectability differed among species and variation was explained by both gear-related and environmental factors. Effective net length (i.e., the distance from shore the seine was deployed) explained variation in detectability for all species; generally, when the effective seine length exceeded 12 m, detectability was higher and less variable. Detectability varied from early to late summer for Atlantic croaker and spottail shiner but not for striped bass. This variation may be attributed to increased net avoidance by Atlantic croaker during late summer and increased relative abundance of spottail shiner due to recruitment of individuals to the gear. Occupancy of striped bass and Atlantic croaker, both of which are transient species, was high (Ψ>0.80), whereas the resident spottail shiner occupied fewer sites (Ψ=0.59±0.21; mean±SE) and occupancy varied by river ($\Psi_{\text{Mattaponi}}$=0.36±0.11; Ψ_{Pamunkey}=0.82±0.10). Occupancy models are useful to identify factors affecting detectability of fishes captured by seines in Chesapeake Bay tributaries, but other fisheries studies would benefit from sampling design modifications that maximize detectability and improve habitat-use inferences.

Estimating detection probabilities in beach seine surveys for estuarine fishes

CHAPTER 1

Detectability of estuarine fishes in a beach seine survey of tidal tributaries of the lower Chesapeake Bay

ABSTRACT

Detectability, the probability that a species is encountered if it inhabits a site, is often overlooked in fisheries research despite its potential to obscure inferences on habitat use. Wildlife researchers use occupancy models to estimate detectability and occupancy (Ψ), the probability that a species inhabits a site within a region of interest. I used these models to estimate detectability and occupancy for three fishes frequently captured in Chesapeake Bay seine surveys and determined factors affecting those probabilities. Sites were repeatedly sampled during early- and late-summer periods during 2008 and 2009 in the Mattaponi and Pamunkey rivers of Virginia. Young-of-the-year (YOY) striped bass (*Morone saxatilis*) occupied nearly every site (Ψ=0.99, SE=0.01); mean detectability was 0.62 (SE=0.06) and positively related to the mean water temperature and weather conditions during the sampling event. Mean detectability of yearling Atlantic croaker (*Micropogonias undulatus*) was negatively related to the mean water temperature at sampling and greater during early-summer than during late-summer periods. The estimate of occupancy for this species was essentially one during early-summer but decreased during late-summer (Ψ=0.86, SE=0.08), when occupancy was positively related to the mean salinity at a site. Mean detectability of spottail shiner (*Notropis hudsonius*) was greater in late-summer than in early summer, and positively related to the mean turbidity during the sampling event. Spottail shiners occupied fewer sites than the other two species (Ψ= 0.59, SE= 0.21) and occupancy was greater in the Pamunkey River than the Mattaponi River. The detectability of all species was positively related to the maximum distance from shore that the seine was deployed. Both environmental and gear-related factors influenced detection probabilities for fishes, but the effects varied with species. Although determining factors that affect occupancy for these species was difficult, findings suggest a difference in occupancy between resident (i.e., spottail shiner) and transient species (i.e., striped bass, Atlantic croaker). Spottail shiners are resident to both river systems and occupied fewer sampled locations than both YOY striped bass and yearling Atlantic croaker, species that primarily use the rivers as summer nurseries. Variation in occupancy for spottail shiner was explained by the river in which sampling occurred but not by measured environmental factors, and suggests that one or more river-specific factors affect occupancy. Striped bass and Atlantic croaker occupancy was high, indicating that most habitats in the sampled area are suitable for these species during summer.

INTRODUCTION

Habitat loss from anthropogenic and other influences affects distribution and abundance of fish populations, yet patterns and dynamics of habitat use for many fishes are unknown. Many ecological investigations aim to determine the proportion of a habitat that a species occupies, and to identify factors that influence habitat use to better understand the ecology of a species. These studies rely on detection of the species of interest in the sampled habitat. Unfortunately, few species are always detected by research surveys, despite their occurrence at a site (MacKenzie et al. 2006). An imperfect ability to detect a species is a pervasive issue in many ecological investigations addressing habitat use and other population parameters of interest such as relative abundance, and colonization rates (Martin et al. 2005; MacKenzie et al. 2006; Arab et al. 2008). The detection of a species occurs when the species occupies the site and is encountered by researchers. The failure to detect a species may result from two processes: true absences and false absences. A true absence occurs when a species does not occupy a site, thus it cannot be detected. A false absence occurs when a species is not available for capture although it inhabits the site (i.e., the species is in another portion of its habitat), or when a species occurs at a site but is simply not captured (i.e., the species evaded capture). Unfortunately, true and false absences are confounded given that the failure to detect a species can result from either process. This poses problems for ecological studies aiming to identify habitats that are occupied (used) by a particular species.

Detectability is a function of the number of fishes vulnerable to capture and the probability of capture, and is affected by differences in catchability (Bayley and Peterson 2001). The probability of detection is rarely constant and often highly variable because the factors that influence it vary. In order to detect a species, at least one individual of the species must occur at a site and the odds of detection increase when a greater number of individuals occur at a site. Although the factors that influence detectability are dynamic (e.g., catchability, gear efficiency), true and false absences must be distinguished and detectability must be estimated when habitat use of a species is of concern.

Catchability, which is defined as the proportion of a fish stock captured with a single unit of effort (Gulland 1983; Jennings et al. 2001; Walters and Martell 2004), is the product of availability and gear efficiency (Kimura and Somerton 2006). Availability refers to the proportion of the stock that occurs in locations where the gear is deployed, and gear efficiency is the proportion of fishes captured from those that occurred within the sampled area (Kimura and Somerton 2006). Although often assumed constant, catchability is variable because availability and efficiency vary. For example, gear efficiency may be affected by environmental factors that alter gear performance and fish behavior, as well as the selectivity of the gear and the vulnerability of individual fish.

Detectability (*p*), is the probability that a species is detected during a sampling event (Bayley and Peterson 2001, MacKenzie et al. 2006). Like catchability and efficiency, few fisheries studies have estimated *p*. However, ignoring imperfect detection probabilities introduces biases into estimates of habitat use and population size (MacKenzie et al. 2006). Detection probabilities vary among species and with habitat characteristics (Bayley and Peterson 2001; Burdick et al. 2008; Hayer and Irwin 2008; Hewitt et al. 2008); for example, seines are more efficient and, thus have higher detection probabilities on open beaches than beaches with obstructions. Similarly, beach slope affects detection probabilities of young-of-the-year (YOY) striped bass (Hewitt et al. 2008). Turbidity and other environmental conditions that influence fish behavior may also affect detection. Because effective swimming speeds (and thus avoidance capabilities) are typically greater for larger fishes, fish size may also affect detection probabilities. Given the variable nature of p, detection probabilities should be estimated to improve habitat use information from fisheries studies. Estimates of relative abundance will also benefit from knowledge about detection probabilities.

The objective of this study was to determine factors that affect detection probabilities for fishes encountered in beach seine surveys conducted in estuarine environments. Hewitt et al. (2008) determined occupancy and detection probabilities for YOY striped bass in tributaries of the lower Chesapeake Bay using long-term data from a seine survey (VIMS juvenile striped bass survey), but limitations in sampling design resulted in imprecise estimates of the effects of factors that influenced detection probabilities. In this study, I modified the seine survey design to allow me to (1) explicitly estimate detection probabilities for fishes encountered in Chesapeake Bay tributaries, and (2) examine factors that affect these probabilities. I used occupancy models (MacKenzie et al. 2002) to simultaneously estimate detection probabilities for YOY striped bass (*Morone saxatilis*), yearling Atlantic croaker (*Micropogonias undulatus*), and adult and juvenile spottail shiner (*Notropis hudsonius*). Occupancy probabilities are also reported.

Species descriptions

YOY striped bass, yearling Atlantic croaker, and adult and juvenile spottail shiner are frequently captured by beach seines in Chesapeake Bay tributaries during summer, but habitat use may vary among species. The nearly ubiquitous distribution of YOY striped bass and yearling Atlantic croaker in Virginia tidal rivers makes them ideal candidates for exploring factors that influence detection probabilities. Spottail shiners have a more limited distribution in these rivers, and thus provide a contrast to the two transient species.

The striped bass is an anadromous, coastal fish that spawns in tidal freshwater tributaries during spring (North and Houde 2006). Although the species ranges from the Saint Lawrence River, Canada, to the Saint John's River, Florida, most spawning occurs during spring in the Hudson River, Delaware River, and tributaries of Chesapeake Bay (Klein-MacPhee 2002). Larvae hatch within several days of spawning, and are frequently retained in the estuarine turbidity maximum (North and Houde 2001). YOY fish occupy nearshore habitats of tributaries adjacent to and downstream of spawning areas (Able and Fahay 1998), where they grow and feed on a variety of prey items, including calanoid copepods and dipteran larvae (Muffelman 2006). By fall, YOY inhabit more saline waters downstream of natal habitats (Dey 1981; Robichaud-LeBlanc et al. 1998; Robinson et al. 2004).

Atlantic croaker is an abundant marine demersal fish that ranges from Massachusetts to Florida, and into the Gulf of Mexico, although the species is rare in waters north of New Jersey (Murdy et al. 1997). In the Mid-Atlantic Bight, Atlantic croaker spawn from September through April on the continental shelf (Hettler and

Chester 1990), and larvae are transported into estuaries by water currents during fall and winter (Norcross 1991). Young fish inhabit low-salinity areas of tributaries during summer, and yearlings leave these habitats in the fall (Miller et al. 2003; Ross 2003).

The spottail shiner is one of the widest ranging North American minnows and frequently occurs in large upland rivers and estuaries of Virginia (Jenkins and Burkhead 1994). Adults are small (60-90 mm standard length [SL]) and inhabit a variety of habitats ranging from clear, rocky streams to turbid, still waters (Rozas and Odum 1987a; Jenkins and Burkhead 1994). The species occupies tidal fresh and brackish waters, and tolerates salinities up to 12 psu. Spottail shiners are more abundant in open nearshore areas than among submerged vegetation (Rozas and Odum 1987b, Murdy et al. 1997), and feed on microcrustaceans, insects, mollusks, and plant matter. Most spottail shiners are mature at 55 mm total length (TL) (1-3 years of age) and females may produce up to 9,000 ova (Jenkins and Burkhead 1994). Eggs are deposited on sand or gravel from mid-April to mid-June in Virginia waters (Jenkins and Burkhead 1994), and juveniles recruit to shallow, nearshore habitats during summer.

METHODS

Occupancy models

Although originally designed to provide researchers with a means to estimate the probability that a species inhabits a site within a region of interest (occupancy), site occupancy models also allow the estimation of detection probabilities using a maximum likelihood framework (MacKenzie et al. 2002). These models use logistic regression to model the effect of environmental or other factors on detection and occupancy probabilities. A logit link function is used to restrict the possible parameter values (occupancy, detection) between 0 and 1.0 (MacKenzie et al. 2006). The probability that a single site (i) is occupied is:

$$1) \qquad logit(\Psi_i) = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \ldots + \beta_U x_{iU},$$

where the occupancy of a site (Ψ_i) is a function of U factors (MacKenzie et al. 2006). The effect (β_i) of each factor (x_i) is estimated, as well as an intercept parameter, β_0, using maximum likelihood estimation techniques.

Occupancy models have been used to estimate detection probabilities for a variety of terrestrial and aquatic species, as well as the prevalence of disease in salmonids (Thompson 2007). The models are similar to mark-recapture models and make use of the repeated sampling of sites to estimate parameters. In occupancy models, sites are the primary sampling unit and as such are analogous to individually tagged fish in mark-recapture modeling. In addition, multiple sampling occasions are similar to multiple attempts to recapture an individual in mark-recapture modeling (Vojta 2005). If a species is captured, it is assumed to inhabit the site. For occupied sites, the history of detections and nondetections of the species (whether or not the species was captured on a sampling occasion) is used to estimate detection probabilities. Unoccupied sites provide no information on detection probabilities.

Occupancy models use the history (h_i) of detections (1) and nondetections (0) for each site (i) to estimate occupancy and detection probabilities for a species. For example, a history of $h_i = 001$ represents a site that was sampled on three occasions. The species inhabits the site because it was detected on the third occasion. However, detection probabilities are less than one because the species was not detected during the first or second sampling occasions. The probability of observing this detection history is:

$$2) \qquad \Pr(h_i) = \Psi(1-p_1)(1-p_2)p_3,$$

where Ψ is the probability of occupancy, p_i is the probability of detection during a sampling occasion *i*, and $(1-p_i)$ represents the probability of not detecting a species during sampling occasion *i*. A detection history that indicates the species was never detected represents a unique case, and the probability of this detection history (h_i=000) must incorporate the probability that the species inhabits the site but was never detected, as well as the probability that the species does not inhabit the site. Thus, the probability of observing $h_i=000$ is:

$$3) \qquad \Pr(h_i = 000) = \Psi(1-p_1)(1-p_2)(1-p_3) + (1-\Psi),$$

where $\Psi(1-p_1)(1-p_2)(1-p_3)$ presents the probability that the species occurs at the site but was not detected and $(1-\Psi)$ represents the probability that the species does not occupy the site. The model likelihood is represented as:

$$4) \qquad L(\Psi, p|h_1, h_2, \ldots, h_s) = \prod_{i=1}^{s} \Pr(h_i),$$

where the likelihood (L) of observing a particular set of occupancy and detection probabilities given the observed detection histories (h_i) for sites i to s is calculated as the product of all detection histories.

Like all models, occupancy models are fitted to data under certain assumptions. Those assumptions are: (1) the occupancy of a site is constant within a study period, (2) sites are independent, and (3) heterogeneity in occupancy and detection probabilities are explained by measured covariates (MacKenzie et al. 2006). Covariates are factors that influence either occupancy or detection probabilities in a predictable manner. The first assumption is also known as the closure assumption: For the duration of the study period, occupied sites must remain occupied and unoccupied sites must not become occupied. Site independence occurs when the detection of a species at one site is not influenced by the detection of the species at another site. In this study, I conducted a beach seine survey to explore the effects of several covariates (e.g., water temperature, turbidity) on heterogeneity in detection probabilities for YOY striped bass, yearling Atlantic croaker, and spottail shiner from lower Chesapeake Bay tributaries.

Field sampling

This study was conducted in the lower reaches of the Mattaponi and Pamunkey rivers in Virginia, two tidal tributaries that together with the York River form the York River system. Both watersheds are dominated by marsh and forested land, with minimal development (Bilkovic et al. 2002). The rivers are used as nurseries by many fishes of the region, including striped bass, Atlantic croaker, and spottail shiner (Machut and

Fabrizio 2009). Sampling sites were typically free of obstructions and substrates were either mud, hard bottom (i.e., sand or shell), or a combination of the two.

Sampling occurred at 10 fixed sites in each river (20 total) during summer 2008 and 2009 (Figure 1). The same sites were sampled in both years. Each site was sampled during a three-week period in early-summer (July 2008 and 2009) and again in late-summer (August 2008, September 2009). Sampling occurred at the beginning and end of summer because observations from the VIMS juvenile striped bass survey suggested that catches declined as summer progressed (A.H. Hewitt, pers. comm.), and because environmental factors that could potentially influence occupancy and detection probabilities also change as summer progresses.

Each site was sampled six times during each three-week period (12 times per year). Sampling was completed on 235 occasions in 2008 and 221 occasions in 2009. The number of occasions is fewer than the planned 240 occasions because site conditions (e.g., abnormally high or low tides, storms) occasionally prohibited sampling. The number of sites and sampling occasions per site was chosen based on guidelines in MacKenzie et al. (2006) and what was logistically possible. I used preliminary estimates of occupancy and detection probabilities for YOY striped bass from 15 years of data from the VIMS juvenile striped bass survey to calculate the number of sampling occasions per site that would provide standard errors (SEs) less than 0.10 (Appendix) (estimates provided in Hewitt et al. 2008). I assumed sites were independent between years because a different year class of fish was sampled each year and environmental characteristics such as water temperature and salinity at each site varied annually.

Fishes were collected using a beach seine that was deployed using protocols consistent with the VIMS survey (Machut and Fabrizio 2009) and described by Hayes et al. (1996). The beach seine (30.5 m-long, 1.2 m-tall with 0.63 cm mesh) was deployed within two hours of low tide because beaches were typically not exposed or available for sampling outside of this timeframe. One end of the seine was held at the shoreline while the other end was taken offshore until the net was fully extended or a water depth of 1.2 m (the height of the net) was encountered. To complete the haul, the offshore end of the net was hauled in the direction of tidal flow and then back to shore. At some sites, excessive mud or deep water prohibited sampling with a fully extended net. The presence of YOY striped bass, yearling Atlantic croaker, and spottail shiners was noted. Additionally, YOY striped bass and yearling Atlantic croaker were counted, measured to the nearest mm (fork length [FL] for striped bass, TL for Atlantic croaker) and returned to the water.

At each sampling occasion, salinity, turbidity, and water temperature were measured and recorded every 20 seconds using a YSI 6920V2 multiparameter water quality sonde. I also recorded weather conditions (clear, partly cloudy, or overcast/rain), tidal direction (ebb or flood), and the maximum distance (m) the net was deployed from the shore. This distance is an indicator of the area sampled by the gear and can be used to estimate the slope of the beach (maximum water depth divided by the distance from shore), a factor that contributes to variation in detectability (Hewitt et al. 2008).

Sampled sites were representative of unobstructed nearshore locations in the Mattaponi and Pamunkey rivers and similar to those used by the VIMS juvenile striped bass survey. Water temperatures in early-summer were greater than those during late-summer (Table 1). Salinities ranged from 0.03 psu at the uppermost sites to 15.27 psu at the most downriver sites, and were greater in late-summer than in early-summer (Table 1). Turbidity was highly variable in both periods, ranging from 3.14 to 889.35 NTU (Table 1). Means and ranges were calculated using Proc Means in SAS (SAS Institute Inc., Cary, NC).

Modeling p and Ψ

Occupancy models were used to assess detection probabilities and occupancy for YOY striped bass, yearling Atlantic croaker, and spottail shiner under the assumptions of site closure and site independence. Findings from a tagging study with YOY striped bass suggest that fish rarely moved among sites within a period (Williams, Chapter 2). Because yearling Atlantic croaker exhibit a high degree of site fidelity during summer (Miller et al. 2003) and because my study sites were spaced several kilometers apart, I considered the movement of Atlantic croaker and spottail shiner among sites unlikely.

Factors hypothesized to affect occupancy and detection probabilities were treated as model covariates (Table 2). Site-specific covariates characterized the overall physical condition of the sites (e.g., substrate), whereas sample-specific covariates included factors that characterized the dynamic conditions at the time of sampling (e.g., salinity). Site-specific covariates are therefore constant across study periods, and may influence both occupancy and detection probabilities. Sample-specific covariates may influence detection probabilities, which can vary between sampling occasions, but not occupancy probabilities, which are assumed constant within a period.

Site-specific covariates included river (Pamunkey, Mattaponi), substrate (mud, hard bottom, or combination), beach slope, mean salinity, mean turbidity, and mean water temperature, where the site-specific mean was calculated as the average value across all 12 sampling occasions in each year. Beach slope was calculated for each site as the mean slope from measurements taken during all sampling occasions within a year. Temporal variation in detection probabilities was considered using period (early- vs. late-summer) as a covariate. I also considered two other types of temporal variation: sampling order within a period and sampling order within a year. Sampling order within a period allowed detection probabilities to vary by sampling occasion (6 total estimated p values per year); this type of temporal variability may be associated with fish behavioral responses to repeated seine deployments (e.g., trap shyness behavior observed in mark-recapture studies). Sampling order within a year allowed each sampling occasion to assume a distinct detection probability (12 total estimated p values) and allowed maximum flexibility in the estimation of detection probabilities.

Because different factors may influence occupancy and detection probabilities in the early- and late-summer periods, I used a multi-season occupancy model to estimate detection probabilities and occupancy for each period (early- or late-summer) (MacKenzie et al. 2006). This form of occupancy model allows researchers to understand changes in occupancy and detection probabilities through time, and is essentially a sequence of single-season models. The multi-season occupancy model also incorporates an estimate of colonization (γ), the probability that an unoccupied site becomes occupied in the time between periods. The model likelihood of the multi-season model takes the form:

5) $$L(\Psi,\gamma,p \mid h_1,h_2,\ldots,h_s)=\prod_{i=1}^{s}\Pr(h_i),$$

where the likelihood of observing a certain occupancy, colonization, and detection probability given the observed multi-seasonal detection histories (h_i) for each site (s) is equal to the product of the probability of observing those detection histories. Colonization was not a focus of my work so this parameter entered the model as a constant (no covariates).

I fit the models to the detection histories for each species using the two-step approach described by MacKenzie et al. (2005). First, occupancy and colonization probabilities were modeled as constants across sites (modeled without covariates) and candidate models that included covariates for detection probabilities were fitted to the data. Detection probabilities were modeled first because most of the variation in the presence-absence data is likely to be explained by this parameter. I considered only additive effects of covariates for detection because more complex relationships may be difficult to determine precisely given the small number of sites sampled (n= 40). The "best" model was selected using AICc, a modification of Akaike's Information Criterion (AIC) corrected for small sample sizes. AICc should be used when the ratio of the number of sampling units to the number of estimated parameters is less than 40 (Burnham and Anderson 2002). In this study, that ratio ranged from 2.9-13.3. All models were compared with the "best" model (the model with the lowest AICc value) using ΔAICc, the difference between AICc values for each model and the "best" model. The best model from this step was used to identify the covariates that affected p. Next, I constructed a suite of models by including the covariates affecting p (and identified in step 1), as well as candidate covariates for occupancy. Using ΔAICc, I selected the “best” overall model; models with ΔAICc values from 0 to 2 are considered to have substantial support (Burnham and Anderson 2002). Models with ΔAICc values from 4-7 have considerably less support, and those with ΔAICc values greater than 10 are not supported by the data (Burnham and Anderson 2002). Additionally, AICc weights can be used for model selection (MacKenzie et al. 2006). An AICc weight is the percentage of occasions that a given model is selected as the “best” model by AICc and serves as the weight of evidence in favor of a given model being the best model from a set of candidate models (Burnham and Anderson 2002; MacKenzie et al. 2006). I estimated AICc weights to determine the level of support for a given covariate; when multiple models contain a single covariate, the level of support for that covariate can be determined by summing the model weights of models that include the covariate (Burnham and Anderson 2002).

All modeling was performed using Program PRESENCE (Hines 2006). Differences between mean estimates of detection probabilities for a species were tested for significance using a two-tailed *t* test and the standard errors estimated by the multi-season occupancy model. This test was used because it is robust to deviations from normality and is appropriate when sample sizes (individual estimates of detection probabilities) are large (n>200) (Zar 1999). Model-averaging was used when several models were plausible, thus allowing me to draw appropriate inferences (Burnham and Anderson 2002; MacKenzie et al. 2006).

RESULTS

Seine surveys during 2008 and 2009 resulted in variable encounter rates of the three species such that the transient species (striped bass and Atlantic croaker) were present in at least 43% of samples in any given year, and resident spottail shiner were encountered in less than 31% of samples in any given year (Table 3). YOY striped bass were present in greater than 57% of all sampling events during early-summer, but less than 30% of sampling events during late-summer (Table 3). Yearling Atlantic croaker were present in greater than 57% of all sampling events, except for late-summer of 2009. Seasonal changes in the presence of spottail shiner were not observed (Table 3).

Striped bass

The top-ranked model for striped bass suggested occupancy is constant (denoted by '.'), but detection probabilities varied by distance from shore, mean water temperature at the time of sampling, and weather conditions (Ψ(.) γ(.) *p*(distance + temperature + weather); Table 4). This model best fit the data based on AICc model selection techniques; it also had an AICc weight nearly twice that of the second-ranked model (Ψ(slope) γ(.) *p*(distance + temperature + weather); Table 4). However, multiple models were plausible based on ΔAICc values. Other factors that may influence occupancy probabilities were beach slope, sampling period (early- or late-summer), river (Mattaponi or Pamunkey), the mean salinity at a site, and the mean turbidity at a site (Table 4).

Factors that best explained variation in *p* for YOY striped bass were the distance from shore that the seine was deployed and mean water temperature and weather conditions at the time of sampling. This model had an AICc weight of 0.895; however, an AICc weight of 0.046 was associated with a model that substituted mean turbidity at the time of sampling for weather conditions (Table 5). The third "best" set of covariates for p omitted weather conditions and turbidity and only included distance from shore and mean water temperature at the time of sampling. A review of the summed AICc weights of each of these covariates indicated that both the distance from shore that the seine is deployed and mean water temperature at the time of sampling occurred in 0.999 of all models.

Estimated detection probabilities were positively related to both the distance from shore that the seine was deployed and the mean water temperature at the time of sampling (Figure 2; Figure 3). Estimated detection probabilities were negatively related to weather conditions, such that fish were more likely to be detected on clear, sunny days (mean p= 0.658, SE=0.025) than on cloudy days (partly cloudy: mean p= 0.625, SE= 0.018; overcast/rainy days: mean p= 0.593, SE=0.020). However, the effect of weather conditions was small and estimated with poor precision (Table 6).

Because all candidate models were within 4 AICc units of each other, and thus plausible, model-averaging was used to estimate detection and occupancy probabilities for YOY striped bass. Although detectability was moderate (p= 0.624, SE=0.058), striped bass were likely to occupy nearly all sampled locations (Ψ= 0.993, SE=0.012; Table 7).

Atlantic croaker

The top-ranked model indicated that occupancy varied by sampling period and with mean site salinity; sampling period, distance from shore, and mean water temperature at the time of sampling were important in modeling variation in detection probabilities (Ψ(period + salinity) γ(.) *p*(period + distance + temperature); Table 8). Although this model had an AICc weight of 0.861, all fitted models were within 10 AICc units and thus plausible (Table 8). The second-ranked model (Ψ(.) γ(.) *p*(period+distance+temperature)) suggested that occupancy probabilities were constant.

Three factors best explained variation in detection probabilities for yearling Atlantic croaker: sampling period, the distance from shore that the seine was deployed, and mean water temperature at the time of sampling. The model that included these factors had an AICc weight of 0.999, and no other factors adequately modeled the variation in detection probabilities (Table 9).

Estimated detection probabilities for Atlantic croaker were significantly greater during early summer than late summer (t= 34.44, $P<0.05$), by a factor of two. Within each period, detection probabilities were positively related to the distance from shore the seine was deployed and negatively related to the mean water temperature at the time of sampling (Table 7; Figure 4; Figure 5).

The best model to describe occupancy and detection probabilities for Atlantic croaker had an AICc weight that was over 12 times as high as the second-ranked model; however other candidate models were plausible and I used model-averaging to estimate parameters. Model-averaged estimates of detection probabilities in early- and late-summer periods were p=0.727± 0.052 and p=0.375± 0.067. In addition, Atlantic croaker occupied more sites in early summer than in late summer. In late summer, occupancy was best explained by mean site salinity, such that Atlantic croaker occupied all sampled sites with mean site salinities greater than 2.0 psu (Table 4; Figure 6).

Spottail shiner

The top-ranked model for spottail shiner suggested occupancy probabilities varied between the Pamunkey (Ψ=0.822± 0.095) and Mattaponi rivers (Ψ=0.362± 0.110) (Table 10). This model indicated that detection probabilities varied by sampling period, distance from shore, and mean turbidity at the time of sampling (Ψ(river) γ(.) *p*(period + distance + turbidity); Table 10). The AICc weight of this model was twice that of the second-ranked model, which included river and beach slope as covariates for occupancy (Ψ(river+slope) γ(.) *p*(period + distance + turbidity); Table 10).

Sampling period (early- vs. late-summer), the distance from shore that the seine was deployed, and mean turbidity at the time of sampling best explained variation in detection probabilities for spottail shiner (AICc wgt=0.696; Table 11). Summed AICc weights indicated that sampling period and distance from shore that the seine was deployed occurred in all plausible models (summed AICc wgt=1.000). The mean turbidity at the time of sampling and the mean water temperature at the time of sampling occurred in 0.696 and 0.304 of candidate models, indicating that mean turbidity is more likely to influence detectability of spottail shiner than mean water temperature (Table 11).

Estimated detection probabilities for spottail shiners were significantly greater in late-summer than in early-summer (t = -30.24, P<0.05), with a difference in *p* of about 0.35. The same relationship between detection probabilities and the distance from shore that the seine was deployed was found for spottail shiners as was found for striped bass and Atlantic croakers; detection probabilities increased with increases in the maximum distance from shore that the seine was deployed (Table 7; Figure 7). Increases in mean turbidity resulted in increased detection probabilities for spottail shiner, regardless of sampling period. When mean turbidity during a sampling event was greater than 150 NTU, detection probabilities were nearly always greater than 0.80 (Figure 8).

Estimated occupancy probabilities for spottail shiners were most influenced by river, and this factor occurred in the top six models that I fit to the beach seine data (summed AICc weight= 0.923; Table 10). Slope and substrate were also identified as factors that influenced occupancy probabilities, although the summed AICc weight for each factor was less than 0.160 (Table 10).

Because most candidate models were plausible, model-averaging was used to estimate detection probabilities for spottail shiner during early-summer (p= 0.515, SE=0.130) and late-summer (p= 0.846, SE=0.070; Table 7) periods.

DISCUSSION

As expected, detection probabilities varied among species and between early- and late-summer sampling periods. The detection of YOY striped bass, yearling Atlantic croaker, and spottail shiner was influenced by both gear-related factors (i.e., the distance from shore that the seine is deployed) and environmental conditions at the time of sampling (e.g., mean water temperature, mean turbidity, weather conditions). Naïve estimates of fish detection (percentage of sampling occasions in which a species was encountered) confound true and false absences, and subsequent inferences of habitat use are negatively biased. As predicted, naïve estimates of detection for the three species studied here were less than estimates of detection probabilities from occupancy modeling.

For all species considered in this study, the distance from the shore that the seine was deployed was an important determinant of detection probabilities; this distance was a measure of the effective length of the net and area sampled. As the distance from shore increased (or effective net length increased), detection probabilities increased for all species. Beach seines sample a greater area and are more efficient when the entire length of the net is used, and this is particularly so when seines are used to capture fishes greater than 100 mm in length (Říha et al. 2008). In this study, the average length of yearling Atlantic croaker encountered by the seine was greater than 100 mm during late summer, a period when fish were more likely to escape capture, resulting in decreased detection probabilities. Thus, effective net length must be maximized when targeting fish greater than 100 mm. Furthermore, when effective net length exceeded 12-15 m, detection probabilities for YOY striped bass and yearling Atlantic croaker were less variable and often greater than when effective net lengths were less than 12 m. To limit variation and maximize detection probabilities in seine surveys within Chesapeake Bay, I recommend sampling at sites where the seine can be deployed at least 12-15 m from shore.

Temporal differences in detection probabilities were identified for yearling Atlantic croaker and spottail shiner, but the direction of change varied by species. The decline in detection that occurred in late summer for yearling Atlantic croaker may reflect the fact that, in late summer, fish are larger and better able to avoid the seine. The decline in detection could also be due to violations of the closure assumption, because juvenile Atlantic croaker may have moved out of the sampling area as the summer progressed. In New Jersey, juvenile Atlantic croaker emigrated from tidal marsh creeks in September and October (Miller and Able 2002). This out migration may have occurred during, but not prior to, my late-summer sampling period in Virginia, thus violating the closure assumption. When this occurs, estimates of occupancy are high and estimates of detection probabilities are low, a pattern consistent with what I observed during late summer.

Unlike Atlantic croaker, spottail shiner detection probabilities increased in late-summer. I attribute this increase to an increase in the number of juveniles that recruited to the gear after July. Spottail shiners spawn during spring in Virginia and by July (early summer), may not have been fully recruited to the sampling gear. By late summer, juveniles are expected to be fully recruited and available to the gear. In addition, data from the VIMS Seine Survey indicate that relative abundance of spottail shiner generally increases later in the summer, supporting the notion that increases in local abundance could also result in greater detection probabilities. My results suggest that selection of the appropriate sampling period can reduce variation in detection probabilities for estuarine species. For example, a seine survey targeting yearling Atlantic croaker is more effective if conducted early in the season when fish are readily captured and net avoidance is minimized. Similarly, investigations of habitat use of spottail shiners would benefit from late-summer sampling when juveniles are fully recruited to the gear. Alternatively, different sampling gears may be used to capture young fishes (e.g., fyke nets, traps).

Mean water temperature at the time of sampling influenced the detectability of both YOY striped bass and yearling Atlantic croaker during 2008 and 2009, but detectability varied among species. Optimal growth of YOY striped bass occurs between 28.0 and 30.0 °C (Kellogg and Gift 1983) and the positive relationship observed between detection probabilities and water temperatures may be due to an increase in availability of fish to the gear in the warm, nearshore waters that I sampled. Unlike YOY striped bass, the detectability of yearling Atlantic croaker was negatively correlated with mean water temperature, but this relationship may be confounded with fish length. Although mean water temperature was high (> 26.0 °C) during early summer, estimates of detectability for Atlantic croaker were high because fish were more vulnerable to capture due to their small size (<100 mm). Surprisingly, none of the top-ranked models identified mean fish length as an important covariate, probably because the range of mean fish lengths was too narrow to discern a relationship between fish size and detectability.

Although the effects of weather conditions were small and imprecisely estimated, detection probabilities of YOY striped bass were higher on clear, sunny days than on days with cloud cover. I expected that a visual feeder such as YOY striped bass would detect and avoid the seine more effectively in bright light conditions, thus yielding lower detection probabilities on clear days. However, striped bass are more successful foragers in bright light conditions (MacIntosh and Duston 2007), and on clear days, the benefits of foraging may have outweighed the risk of capture. Individuals using shallow habitats for foraging may thus be more vulnerable to the gear on clear days. Weather conditions were measured subjectively in this study and a direct measurement of light intensity in the water may provide more precise estimates of the effects of this factor on detectability.

Reduced escapement of spottail shiners in turbid conditions, coupled with an increase in relative abundance due to new recruits, may have contributed to the higher detection probabilities I observed in late summer. The effect of turbidity on the escape behavior of spottail shiners has not been studied, but in at least one member of the family Cyprinidae, increased turbidity resulted in the decreased ability of individuals to detect and avoid predators (fathead minnow (*Pimephales promelas*); Abraham and Kattenfeld 1997). I postulate that escape behaviors of spottail shiners were less effective in turbid waters, which may explain the positive relationship between turbidity and detection probabilities for this species.

Estimates of occupancy probability for striped bass exceeded 0.80 and precluded the identification of factors that influenced habitat use by this species. In contrast, occupancy probabilities for Atlantic croaker and spottail shiner exhibited temporal and geographic variation. Although beach slope, mean site salinity, and mean site turbidity may affect YOY striped bass occupancy, additional studies that include more unoccupied sites are needed to reveal these relationships. Yearling Atlantic croaker used all sampled habitats in early summer, but by late summer, overall occupancy declined and fish used sites where mean salinity exceeded 2.0 psu. Based on observed occupancy, the Pamunkey River provided more suitable habitat for spottail shiners than the Mattaponi River. Catch data from the VIMS seine survey indicated that spottail shiners were more abundant in the Mattaponi River than in the Pamunkey River. Together, these results imply that spottail shiner populations in the Pamunkey River are less aggregated and more evenly distributed among the habitats that I sampled.

The strength of inferences I made from this study depends on the validity of model assumptions, particularly those for site closure and site independence. The high degree of site fidelity exhibited by YOY striped bass and yearling Atlantic croaker suggests that the assumptions of site closure and site independence are reasonable (Miller et al. 2003; Williams, Chapter 2). Violations of the site closure assumption leads to negatively biased estimates of detection probabilities, and because my estimates of detection for spottail shiner were high, I believe that the site closure assumption was reasonable for this species. In addition, because detectability was generally estimated with precision for all species, the covariates I considered appeared to have sufficiently explained variation in detection probabilities.

The availability of fish to the beach seine clearly affected detectability. Although a fish may inhabit a site, the species may not be available for capture (i.e., fish may temporarily occupy portions of the site that are not sampled). Unfortunately, availability is difficult to quantify, particularly for juvenile fishes. The effects of environmental factors and habitat characteristics on small-scale fish movements could be explored to better understand availability of juvenile fishes to sampling gears. These individual fish movements may be examined using radio-telemetry, hydro-acoustics, or other emergent technologies.

Results from this study using beach seines in Chesapeake Bay tributaries can be used to inform the design of fish surveys, regardless of sampling gear. Although I recommend incorporation of repeat sampling events to permit estimation of detection probabilities, particularly for habitat use studies, I realize that logistical constraints and research goals may prohibit such modifications. Another option is to design a study that investigates the role of environmental and temporal factors on detectability. For instance, detectability may be maximized by selecting an appropriate time to sample when fish are fully recruited to the gear but net avoidance is low. Inferences about fish habitat use are best supported when detectability is directly estimated using occupancy models, or when detectability is maximized through the application of study designs that incorporate factors affecting the likelihood of detection.

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Table 1. Mean salinity (Sal, psu), water temperature (Temp, °C), and turbidity (Turb, NTU) for early- and late-summer periods during 2008, 2009 at 20 sites in the Mattaponi and Pamunkey rivers, Virginia. All measurements were collected using a YSI 6920V2 multiparameter water quality sonde. Means are reported ± standard errors; ranges are given in brackets; n is the number of observations (sampling events).

	2008		2009	
	Early-summer	Late-summer	Early-summer	Late-summer
Sal (psu)	2.16 ± 0.25	5.64 ± 0.41	2.47 ± 0.26	5.16 ± 0.41
	[0.03-9.78]	[0.53-15.27]	[0.05-9.07]	[0.24-14.72]
Temp (°C)	28.55 ± 0.11	26.22 ± 0.07	27.34 ± 0.08	23.39 ± 0.06
	[26.70-31.90]	[24.04-28.86]	[26.02-29.97]	[21.34-24.89]
Turb (NTU)	56.40 ± 4.51	58.55 ± 6.02	52.38 ± 10.35	39.47 ± 7.83
	[3.14-322.00]	[9.55-346.00]	[6.62-889.35]	[7.95-763.11]
n	115	108	109	105

Table 2. Covariates postulated to affect occupancy probabilities (Ψ) and detection probabilities (p) for YOY striped bass, yearling Atlantic croaker, and spottail shiner, and their hypothesized effects on each model parameter. 'None' indicates that the factor was not included as a covariate for a given parameter (Ψ or p).

Factor	Effect on Ψ	Effect on p
Year	varies by year	varies by year
River	varies by river (Mattaponi, Pamunkey)	varies by river
Substrate	varies with substrate type (sand, mud, combination)	varies by substrate type
Slope	varies by the slope of the beach sampled	varies by the slope of a sampled beach
Salinity	varies by average salinity at a site during a year	None
Water temperature	varies by average water temperature at a site during a year	varies by water temperature during the sampling occasion
Turbidity	varies by average turbidity at a site during a year	varies by turbidity during the sampling occasion
Tidal direction	None	varies by the direction of tidal flow (ebb or flood) during the sampling occasion
Weather	None	varies by the weather during the sampling occasion
Distance from shore	None	varies by the maximum distance the seine is deployed from shore
Fish length	None	varies by the average length of fish captured
Order of sampling within a period	None	varies by the order of sampling occasions within a period
Sample	None	varies by sampling occasion within a year

Table 3. The percentage of sampling occasions during which YOY striped bass, yearling Atlantic croaker, and adult and juvenile spottail shiner were captured during early- and late-summer 2008, 2009 at sites in the Mattaponi and Pamunkey rivers, Virginia. All fishes were captured using a 30.5-m long, 1.2-m tall beach seine.

Species	Year	Early-summer	Late-summer	Overall
Striped bass	2008	62.2%	23.3%	43.0%
	2009	57.6%	28.2%	43.9%
Atlantic croaker	2008	69.8%	57.8%	63.8%
	2009	61.9%	34.0%	48.9%
Spottail shiner	2008	27.7%	33.6%	30.6%
	2009	39.0%	33.9%	36.7%

Table 4. Rankings for occupancy models used to identify factors affecting occupancy probabilities for YOY striped bass collected during summer 2008, 2009 at sites in the Mattaponi and Pamunkey rivers, Virginia using covariates from the top-ranked model to explain detection probabilities for YOY striped bass (i.e., DIST= the maximum distance from shore the seine was deployed, TEMP= water temperature, WEA= weather; Table 5). For all models, colonization (γ) was held constant and represented by '.'. Models were ranked according to Akaike Information Criterion values corrected for small sample sizes (AICc) and the top-ranked model (lowest AICc) was used to compute the ΔAICc. AICc weights (AICc wgt) and K, the total number of estimated parameters, are also reported. Covariates for occupancy included: PD= period (early- or late-summer), RV= river (Mattaponi or Pamunkey), SAL= the mean salinity value at a site within a year, SL= the slope of the sampled beach, and TURB= the mean turbidity value at a site within a year.

Model	AICc	ΔAICc	AICc wgt	K
Ψ(.)γ(.) p(DIST+TEMP+WEA)	212.71	0.00	0.4465	6
Ψ(SL)γ(.) p(DIST+TEMP+WEA)	214.08	1.37	0.2251	7
Ψ(PD)γ(.) p(DIST+TEMP+WEA)	215.05	2.34	0.1386	7
Ψ(RV)γ(.) p(DIST+TEMP+WEA)	215.20	2.49	0.1286	7
Ψ(SAL+TURB)γ(.) p(DIST+TEMP+WEA)	216.68	3.97	0.0613	8

Table 5. Rankings for occupancy models used to identify factors affecting detectability of YOY striped bass collected during summer 2008, 2009 in the Mattaponi and Pamunkey rivers, Virginia. Occupancy probabilities (Ψ) and the probability of colonization (γ) were held constant and represented by '.'. Rankings were based on the Akaike Information Criterion values corrected for sample sizes (AICc) and the top-ranked model (lowest AICc) was used to compute the ΔAICc. AICc weights (AICc wgt) and K, the total number of estimated parameters, are also reported. Covariates considered in the model were: DIST= the maximum distance from shore that the seine was deployed, LEN= the mean length of fish captured on a sampling date, ORDER= sampling order within a period, PD= period (early- vs. late-summer), RV= river (Mattaponi or Pamunkey), SAMPLE= sampling order within a year, SL= beach slope, SUB= substrate type (sand, mud, combination), TEMP= mean water temperature during a sampling occasion, TIDE= direction of tidal flow (ebb or flood), TURB= median turbidity during a sampling occasion, WEA= weather (clear, partly cloudy, overcast or rain), and YEAR= 2008 or 2009.

Model	AICc	ΔAICc	AICc wgt	K
Ψ(.) γ(.) p(DIST+TEMP+WEA)	212.71	0.00	0.8954	6
Ψ(.) γ(.) p(DIST+TEMP+TURB)	218.63	5.92	0.0464	6
Ψ(.) γ(.) p(DIST+TEMP)	219.90	7.19	0.0246	5
Ψ(.) γ(.) p(DIST+TEMP+LEN)	222.36	9.65	0.0072	6
Ψ(.) γ(.) p(DIST+TEMP+SL)	222.58	9.87	0.0064	6
Ψ(.) γ(.) p(DIST+TEMP+YR)	222.64	9.93	0.0062	6
Ψ(.) γ(.) p(DIST+TEMP+SUB)	222.68	9.97	0.0061	6
Ψ(.) γ(.) p(DIST+TEMP+RV)	222.68	9.97	0.0061	6
Ψ(.) γ(.) p(PD+DIST+TEMP)	225.58	12.87	0.0014	7
Ψ(.) γ(.) p(DIST+TURB)	245.16	32.45	0.0000	5
Ψ(.) γ(.) p(DIST+WEA)	330.45	117.74	0.0000	5
Ψ(.) γ(.) p(DIST)	336.98	124.27	0.0000	4
Ψ(.) γ(.) p(DIST+LEN)	337.07	124.36	0.0000	5
Ψ(.) γ(.) p(TEMP+WEA)	372.59	159.88	0.0000	5
Ψ(.) γ(.) p(TEMP+TURB)	373.54	160.83	0.0000	5
Ψ(.) γ(.) p(TEMP)	378.19	165.48	0.0000	4
Ψ(.) γ(.) p(TURB)	419.11	206.40	0.0000	4
Ψ(.) γ(.) p(TIDE)	566.77	354.06	0.0000	4
Ψ(.) γ(.) p(WEA)	573.08	360.37	0.0000	4
Ψ(.) γ(.) p(PD)	577.79	365.08	0.0000	5
Ψ(.) γ(.) p(YR)	579.25	366.54	0.0000	4
Ψ(.) γ(.) p(SUB)	587.15	374.44	0.0000	4
Ψ(.) γ(.) p(SL)	589.07	376.36	0.0000	4
Ψ(.) γ(.) p(RV)	589.42	376.71	0.0000	4
Ψ(.) γ(.) p(.)	591.33	378.62	0.0000	3
Ψ(.) γ(.) p(LEN)	593.31	380.60	0.0000	4
Ψ(.) γ(.) p(SAMPLE)	600.70	387.99	0.0000	14
Ψ(.) γ(.) p(ORDER)	602.64	389.93	0.0000	8

Table 6. Estimates and associated standard errors (SE) of covariate effects on occupancy (Ψ) and detection probabilities (p) from the top-ranked occupancy models for YOY striped bass, yearling Atlantic croaker, and spottail shiner. An asterisk indicates a standard error that is unusually large, and associated with occupancy and detection probability estimates that were 0.00 or 1.00.

Species	Parameter	β estimate	SE(β)
Striped bass	$\Psi_{\text{intercept}}$	20.82	*
	$p_{\text{intercept}}$	-12.51	1.39
	p_{distance}	0.06	0.02
	$p_{\text{temperature}}$	0.45	0.05
	p_{weather}	-0.18	0.24
Atlantic croaker	$\Psi_{\text{early-summer}}$	18.78	*
	$\Psi_{\text{late-summer}}$	-2.71	3.60
	Ψ_{salinity}	4.61	6.19
	$p_{\text{early-summer}}$	5.98	1.69
	$p_{\text{late-summer}}$	3.82	1.51
	p_{distance}	0.03	0.01
	$p_{\text{temperature}}$	-0.20	0.06
Spottail shiner	$\Psi_{\text{intercept}}$	1.53	0.65
	Ψ_{river}	-2.10	0.80
	$p_{\text{early-summer}}$	-1.11	0.92
	$p_{\text{late-summer}}$	0.68	0.82
	p_{distance}	0.02	0.02
	$p_{\text{turbidity}}$	0.02	0.01

Table 7. Model-averaged estimates (mean and standard error in parentheses) of occupancy during early- and late-summer periods (Ψ_{Early}, Ψ_{Late}) and detection probabilities during early- and late-summer (p_{Early}, p_{Late}) for YOY striped bass, yearling Atlantic croaker, and spottail shiner. All fish were collected during summer 2008 and 2009 using a beach seine in the Mattaponi and Pamunkey rivers in Virginia. Values straddling the early and late columns indicate no difference in the parameter between early- and late-summer periods.

1. Probability	2. Striped bass	3. Atlantic croaker	4. Spottail shiner
5. Ψ_{Early}	6. 0.993(0.012)	7. 1.000(0.001)	8. 0.590(0.121)
9. Ψ_{Late}		10. 0.863(0.083)	
11. p_{Early}	12. 0.624(0.058)	13. 0.727(0.052)	14. 0.515(0.130)
15. p_{Late}		16. 0.375(0.067)	17. 0.846(0.070)

Table 8. Rankings for occupancy models used to identify factors affecting occupancy probabilities for yearling Atlantic croaker data collected during summer 2008, 2009 at sites in the Mattaponi and Pamunkey rivers, Virginia. For all models, colonization (γ) was held constant and represented by a '.'. Covariates included to explain variation in detection probabilities (*p*) were: PD=period, DIST= the maximum distance from shore the seine was deployed, and TEMP= the mean water temperature at the time of sampling (from Table 7). Rankings were based on the Akaike Information Criterion values corrected for small sample sizes (AICc) and the top-ranked model was used to compute ΔAICc. AICc weights (AIC wgt) and K, the total number of estimated parameters, are also reported. Covariates considered to affect occupancy probabilities are: PD= period (early- or late-summer), SAL= the mean salinity value at a site within a year, SL= the slope of the sampled beach, and TURB= the mean turbidity value at a site within a year.

Model	AICc	ΔAICc	AIC wgt	K
Ψ(PD+SAL)γ(.) p(PD+DIST+TEMP)	245.87	0.00	0.8612	8
Ψ(.)γ(.) p(PD+DIST+TEMP)	250.97	5.10	0.0672	6
Ψ(PD+TURB)γ(.) p(PD+DIST+TEMP)	252.79	6.92	0.0271	8
Ψ(TURB)γ(.) p(PD+DIST+TEMP)	253.46	7.59	0.0194	7
Ψ(SL)γ(.) p(PD+DIST+TEMP)	253.93	8.06	0.0153	7
Ψ(PD+SL)γ(.) p(PD+DIST+TEMP)	254.81	8.94	0.0099	8

Table 9. Rankings for occupancy models used to determine factors affecting detection probabilities for yearling Atlantic croaker data collected during summer 2008, 2009 in the Mattaponi and Pamunkey rivers, Virginia. Occupancy (Ψ) and colonization (γ) were held constant and represented by '.'. Rankings were based on the Akaike Information Criterion values corrected for small sample sizes (AICc) and the top-ranked model was used to compute ΔAICc. AICc weights (AIC wgt) and K, the total number of estimated parameters, are also reported. Covariates included for consideration were: DIST= the maximum distance from shore that the beach seine was deployed, LEN= the mean length (TL) of yearling croaker collected on a sampling day, ORDER= sampling order within a period, PD= period (early- or late-summer), RV= river (Mattaponi or Pamunkey), SAMPLE= sampling order within a year, SL= beach slope, SUB= substrate type (sand, mud, combination), TEMP= mean water temperature during a sampling occasion, TIDE= direction of tidal flow (ebb or flood), TURB= median turbidity during a sampling occasion, WEA= weather (clear, partly cloudy, overcast or rain), and YEAR= 2008 or 2009.

Model	AICc	ΔAICc	AICc wgt	K
Ψ(.) γ(.) p(PD+DIST+TEMP)	250.97	0.00	0.9999	6
Ψ(.) γ(.) p(DIST+TEMP)	270.11	19.14	0.0001	5
Ψ(.) γ(.) p(DIST+TURB)	277.21	26.24	0.0000	5
Ψ(.) γ(.) p(PD+DIST)	326.69	75.72	0.0000	5
Ψ(.) γ(.) p(PD+DIST+LEN)	328.99	78.02	0.0000	6
Ψ(.) γ(.) p(DIST)	364.40	113.43	0.0000	4
Ψ(.) γ(.) p(PD+DIST)	405.30	154.33	0.0000	5
Ψ(.) γ(.) p(TEMP)	418.13	167.16	0.0000	4
Ψ(.) γ(.) p(TURB)	420.66	169.69	0.0000	4
Ψ(.) γ(.) p(TIDE)	548.37	297.40	0.0000	4
Ψ(.) γ(.) p(PD)	551.10	300.13	0.0000	4
Ψ(.) γ(.) p(WEA)	557.30	306.33	0.0000	4
Ψ(.) γ(.) p(LEN)	566.54	315.57	0.0000	4
Ψ(.) γ(.) p(SL)	568.04	317.07	0.0000	4
Ψ(.) γ(.) p(SUB)	570.64	319.67	0.0000	4
Ψ(.) γ(.) p(.)	570.67	319.70	0.0000	3
Ψ(.) γ(.) p(YR)	571.50	320.53	0.0000	4
Ψ(.) γ(.) p(RV)	573.13	322.16	0.0000	4
Ψ(.) γ(.) p(ORDER)	574.26	323.29	0.0000	8
Ψ(.) γ(.) p(SAMPLE)	576.64	325.67	0.0000	14

Table 10. Rankings for occupancy models used to determine factors affecting occupancy probabilities for spottail shiner data collected during summer 2008, 2009 in the Mattaponi and Pamunkey rivers, Virginia. Colonization (γ) was held constant and represented by a '.'. Covariates included to explain variation in detection probabilities (p) were: PD= early- or late-summer, DIST= the maximum distance from shore that the seine was deployed, and TURB= the mean turbidity during a sampling occasion (from Table 11). Rankings were based on the Akaike Information Criterion values corrected for small sample sizes (AICc) and the top-ranked model was used to compute ΔAICc. AICc weights (AIC wgt) and K, the total number of estimated parameters, are also reported. Covariates considered to affect occupancy probabilities are: PD= period (early- or late-summer), RV= river (Mattaponi or Pamunkey), SL= the slope of the sampled beach, SUB= substrate type (sand, mud, combination of the two), TEMP= the mean water temperature (°C) at a site within a year, TURB= the mean turbidity value (NTU) at a site within a year, and YR= year (2008 or 2009).

Model	AICc	ΔAICc	AIC wgt	K
Ψ(RV)γ(.) p(PD+DIST+TURB)	135.44	0.00	0.3224	7
Ψ(RV+SL)γ(.) p(PD+DIST+TURB)	136.89	1.45	0.1562	8
Ψ(RV+SUB)γ(.) p(PD+DIST+TURB)	137.22	1.78	0.1324	8
Ψ(YR+RV)γ(.) p(PD+DIST+TURB)	137.35	1.91	0.1241	8
Ψ(PD+RV)γ(.) p(PD+DIST+TURB)	137.69	2.25	0.1047	8
Ψ(RV+TEMP)γ(.) p(PD+DIST+TURB)	138.14	2.70	0.0836	8
Ψ(.)γ(.) p(PD+DIST+TURB)	140.71	5.27	0.0231	6
Ψ(PD)γ(.) p(PD+DIST+TURB)	142.18	6.74	0.0111	7
Ψ(YR)γ(.) p(PD+DIST+TURB)	142.65	7.21	0.0088	7
Ψ(SL)γ(.) p(PD+DIST+TURB)	143.25	7.81	0.0065	7
Ψ(TEMP)γ(.) p(PD+DIST+TURB)	143.39	7.95	0.0061	7
Ψ(SUB)γ(.) p(PD+DIST+TURB)	143.40	7.96	0.0060	7
Ψ(YR+PD)γ(.) p(PD+DIST+TURB)	144.56	9.12	0.0034	8
Ψ(PD+SUB)γ(.) p(PD+DIST+TURB)	145.05	9.61	0.0026	8
Ψ(YR+SL)γ(.) p(PD+DIST+TURB)	145.39	9.95	0.0022	8
Ψ(YR+SUB)γ(.) p(PD+DIST+TURB)	145.40	9.96	0.0022	8
Ψ(SL+SUB)γ(.) p(PD+DIST+TURB)	146.04	10.60	0.0016	8
Ψ(SL+TEMP)γ(.) p(PD+DIST+TURB)	146.13	10.69	0.0015	8
Ψ(SUB+TEMP)γ(.) p(PD+DIST+TURB)	146.23	10.79	0.0015	8

Table 11. Rankings for occupancy models used to determine factors affecting detection probabilities for spottail shiner collected during summer 2008, 2009 in the Mattaponi and Pamunkey rivers, Virginia. Occupancy (Ψ) and colonization (γ) were held constant and represented by '.'. Rankings were based on the Akaike Information Criterion values corrected for small sample sizes (AICc) and the top-ranked model was used to compute ΔAICc. AICc weights (AIC wgt) and K, the total number of estimated parameters, are also reported. Covariates included for consideration were: DIST= the maximum distance from shore that the beach seine was deployed, ORDER= sampling order within a period, PD= period (early- or late-summer), RV= river (Mattaponi or Pamunkey), SAMPLE= sampling order within a year, SL= beach slope, SUB= substrate type (sand, mud, combination), TEMP= mean water temperature during a sampling occasion, TIDE= direction of tidal flow (ebb or flood), TURB= median turbidity during a sampling occasion, WEA= weather (clear, partly cloudy, overcast or rain), and YEAR= 2008 or 2009.

Model	AICc	ΔAICc	AIC wgt	K
Ψ(.) γ(.) p(PD+DIST+TURB)	140.71	0.00	0.6964	6
Ψ(.) γ(.) p(PD+DIST+TEMP)	142.37	1.66	0.3036	6
Ψ(.) γ(.) p(PD+DIST+WEA)	181.41	40.70	0.0000	6
Ψ(.) γ(.) p(PD+DIST+SUB)	190.06	49.35	0.0000	6
Ψ(.) γ(.) p(PD+DIST+TIDE)	192.42	51.71	0.0000	6
Ψ(.) γ(.) p(PD+DIST+SL)	194.11	53.40	0.0000	6
Ψ(.) γ(.) p(PD+DIST)	202.18	61.47	0.0000	5
Ψ(.) γ(.) p(PD+DIST+RV)	202.49	61.78	0.0000	6
Ψ(.) γ(.) p(PD+DIST+YR)	204.64	63.93	0.0000	6
Ψ(.) γ(.) p(DIST)	208.23	67.52	0.0000	4
Ψ(.) γ(.) p(TEMP)	224.05	83.34	0.0000	4
Ψ(.) γ(.) p(PD+TURB)	225.48	84.77	0.0000	5
Ψ(.) γ(.) p(PD+TEMP)	225.49	84.78	0.0000	5
Ψ(.) γ(.) p(TURB)	225.59	84.88	0.0000	4
Ψ(.) γ(.) p(WEA)	308.72	168.01	0.0000	4
Ψ(.) γ(.) p(TIDE)	321.01	180.30	0.0000	4
Ψ(.) γ(.) p(SUB)	327.46	186.75	0.0000	4
Ψ(.) γ(.) p(RV)	328.24	187.53	0.0000	4
Ψ(.) γ(.) p(PD)	328.45	187.74	0.0000	4
Ψ(.) γ(.) p(.)	333.09	192.38	0.0000	3
Ψ(.) γ(.) p(SL)	335.05	194.34	0.0000	4
Ψ(.) γ(.) p(YR)	335.50	194.79	0.0000	4
Ψ(.) γ(.) p(ORDER)	343.55	202.84	0.0000	8
Ψ(.) γ(.) p(SAMPLE)	351.62	210.91	0.0000	14

Figure 1. Map of the study area in the Mattaponi and Pamunkey rivers, tributaries of the York River, Virginia.

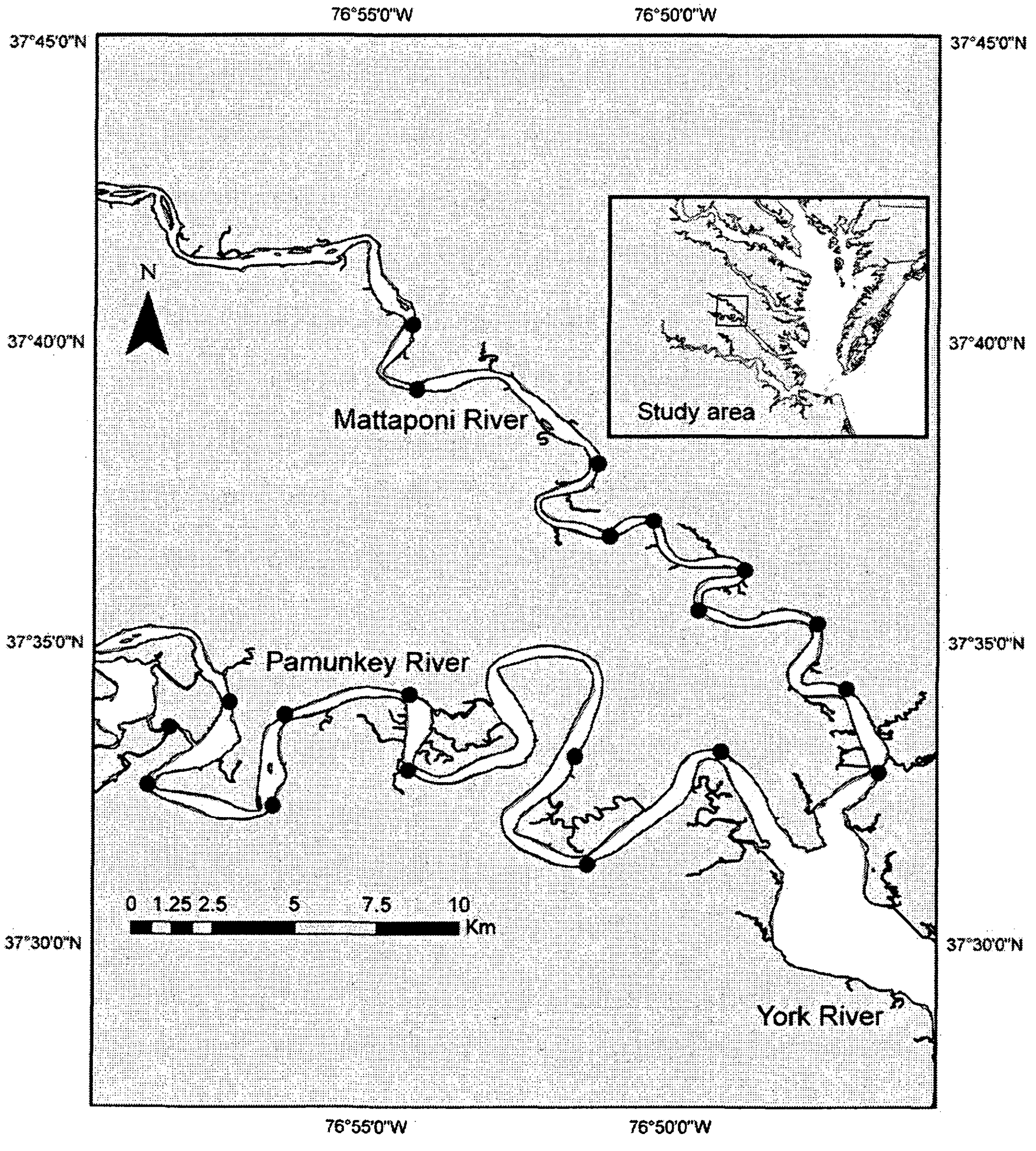


Figure 2. Relationship between estimated detection probabilities (*p*) and the effective net length for YOY striped bass collected during summer 2008, 2009 at sites in the Mattaponi and Pamunkey rivers, Virginia. Values were estimated from $\Psi(.)\gamma(.)p(\text{Dist+Temp+Wea})$ (Table 4).

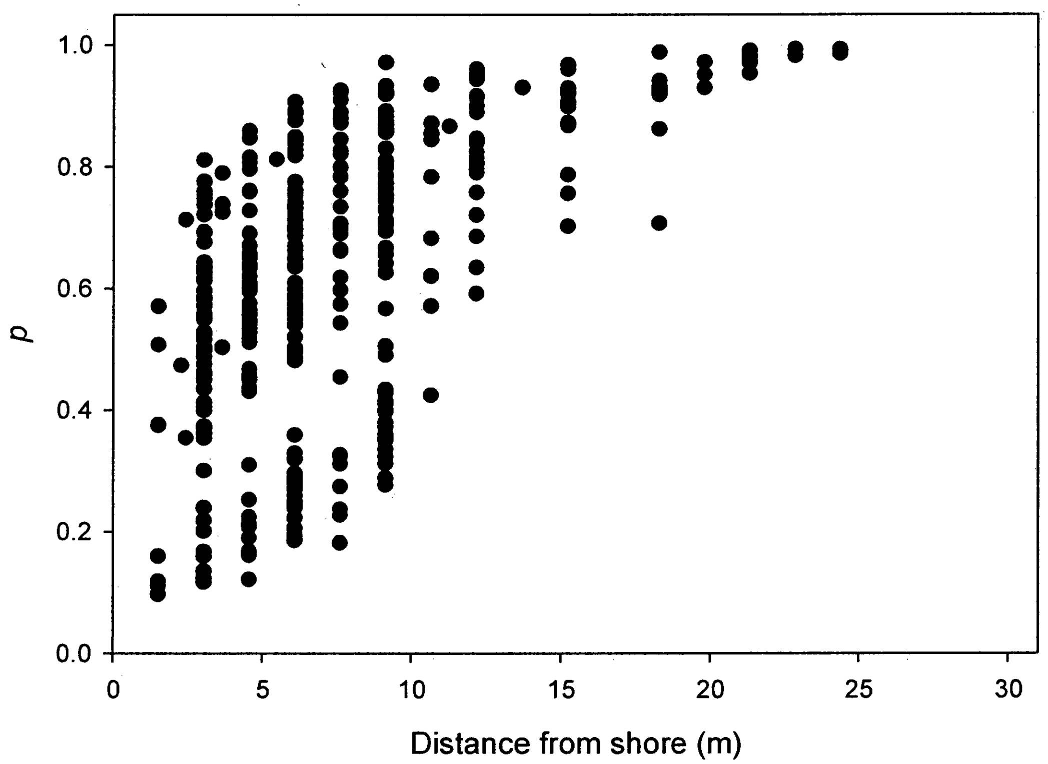


Figure 3. Relationship between estimated detection probabilities (*p*) and the water temperature at the time of sampling for YOY striped bass collected using a beach seine during summer 2008, 2009 at sites in the Mattaponi and Pamunkey rivers, Virginia. Values were estimated from $\Psi(.)\gamma(.)p$(Dist+Temp+Wea) (Table 4).

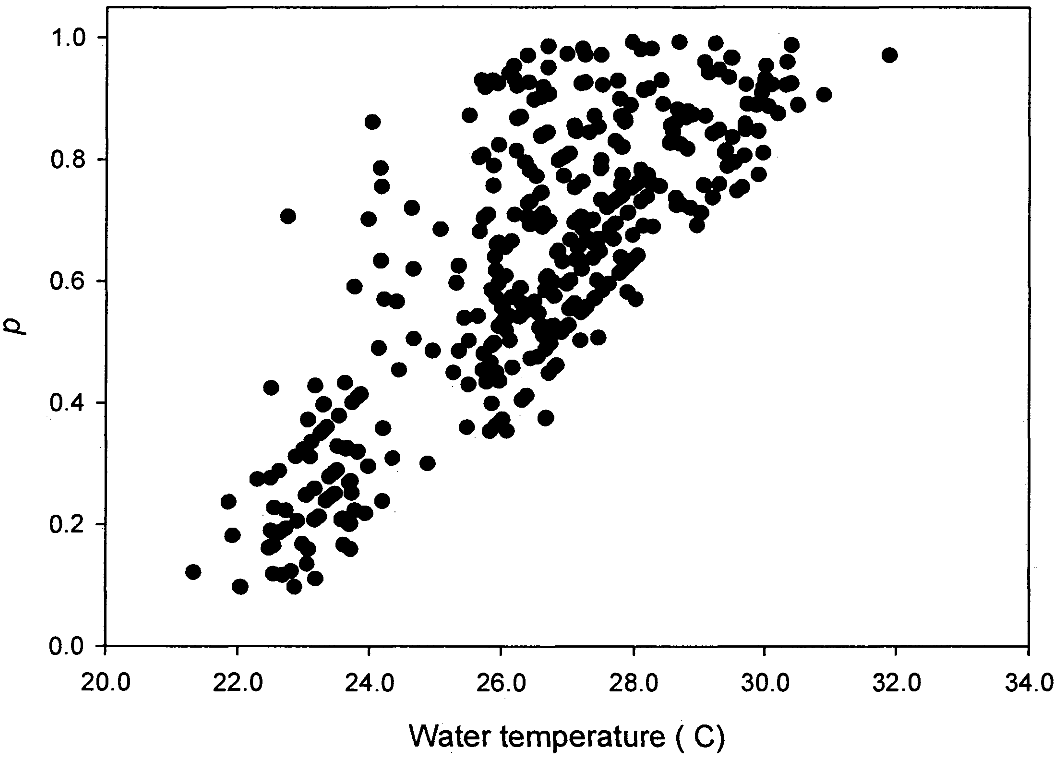


Figure 4. Relationship between estimated detection probabilities (*p*) and the effective net length for yearling Atlantic croaker collected during summer 2008, 2009 at sites in the Mattaponi and Pamunkey rivers, Virginia. Values were estimated from Ψ(Pd+Sal.)γ(.)*p*(Pd+Dist+Temp) (Table 8).

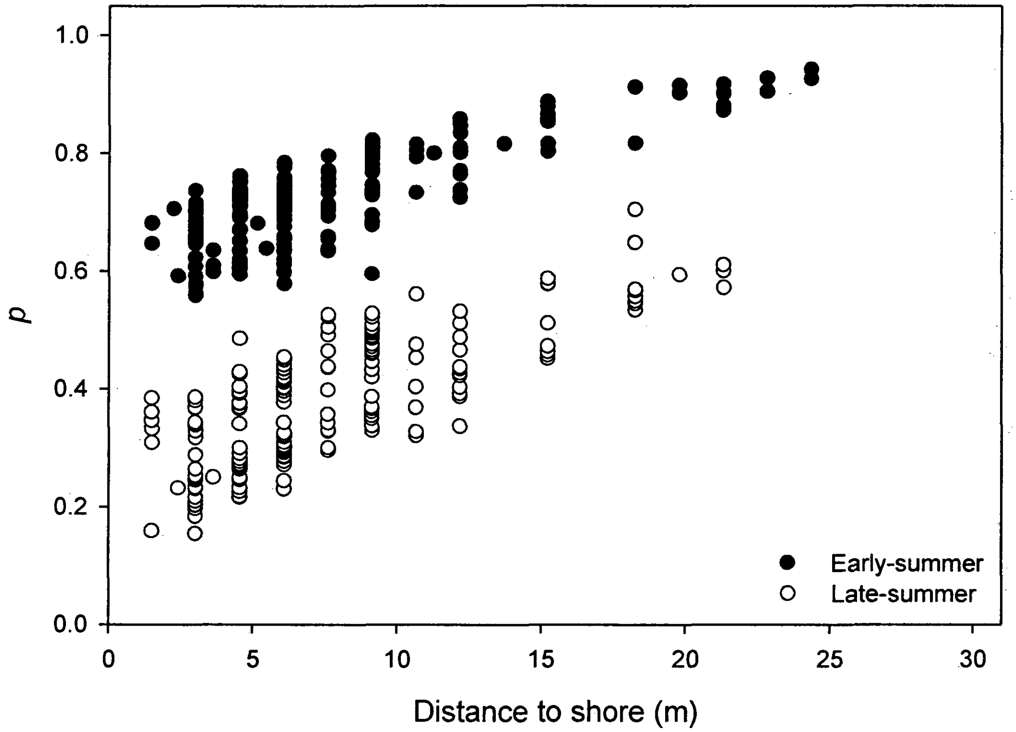


Figure 5. Relationship between estimated detection probabilities (*p*) and mean water temperature at the time of sampling for yearling Atlantic croaker captured using a beach seine during two periods (early-summer and late-summer) in 2008 and 2009 in the Mattaponi and Pamunkey rivers, Virginia. Values were estimated from Ψ(Pd+Sal.)γ(.)*p*(Pd+Dist+Temp) (Table 8).

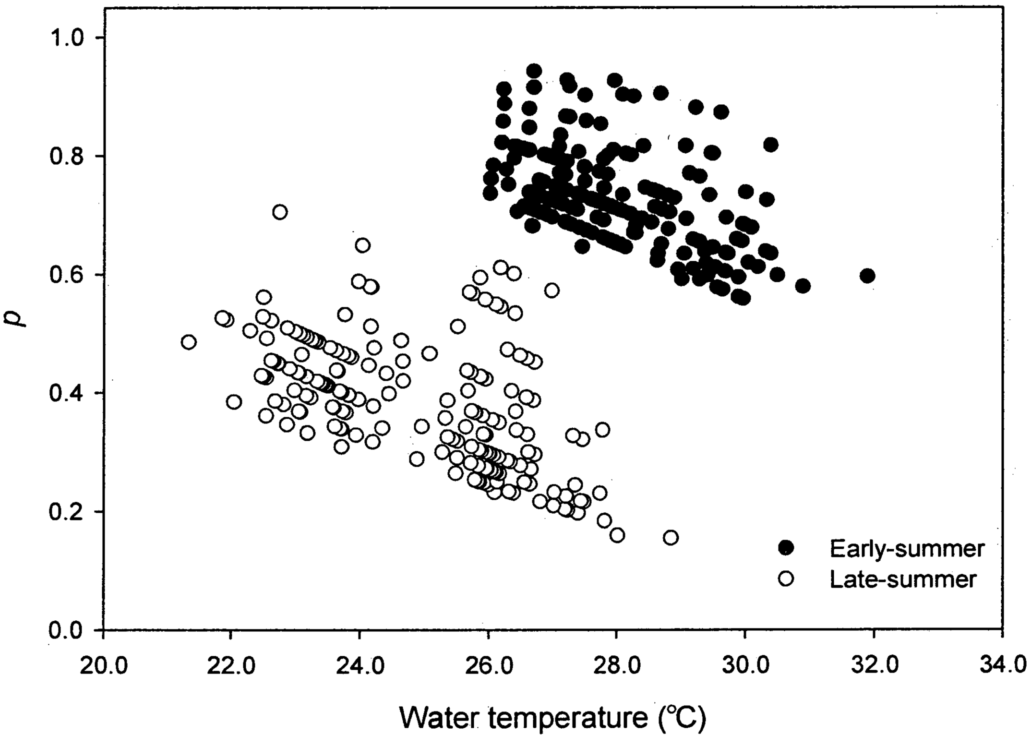


Figure 6. Relationship between estimated occupancy probabilities (Ψ) and the mean salinity of a site for yearling Atlantic croaker captured using a beach seine during two periods (early-summer and late-summer) in 2008 and 2009 in the Mattaponi and Pamunkey rivers, Virginia. Values were estimated from Ψ(Pd+Sal.)γ(.)p(Pd+Dist+Temp) (Table 8).

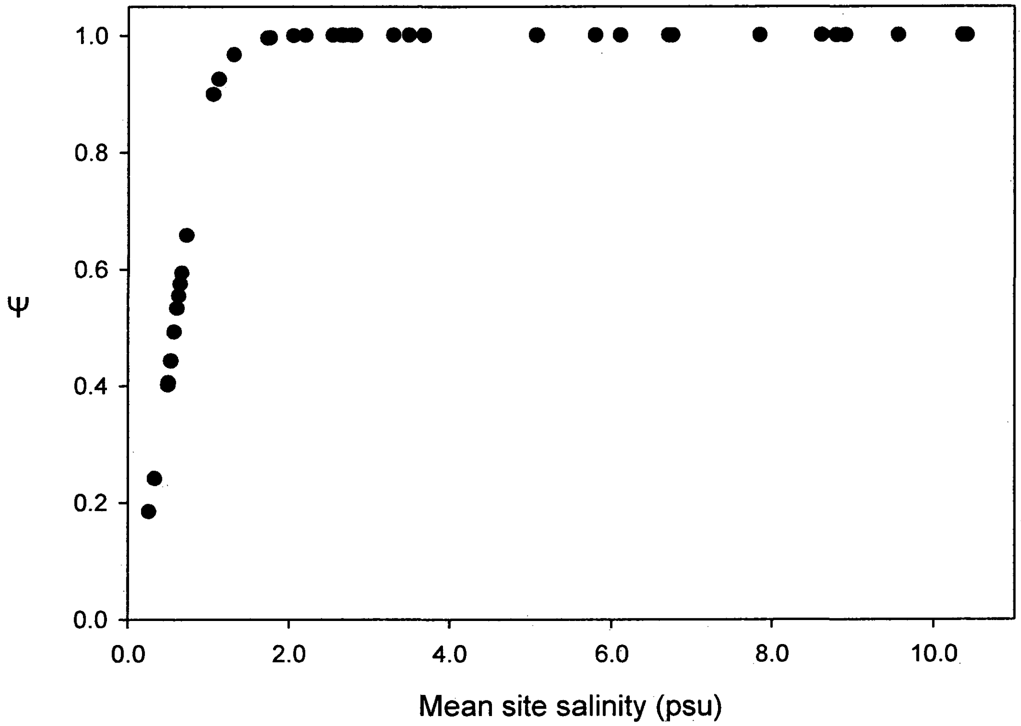


Figure 7. Relationship between estimated detection probabilities (*p*) and the effective net length for spottail shiner collected during early- and late-summer 2008, 2009 in the Mattaponi and Pamunkey rivers, Virginia. Values were estimated from $\Psi(Rv)\gamma(.)p(Pd+Dist+Turb)$ (Table 10).

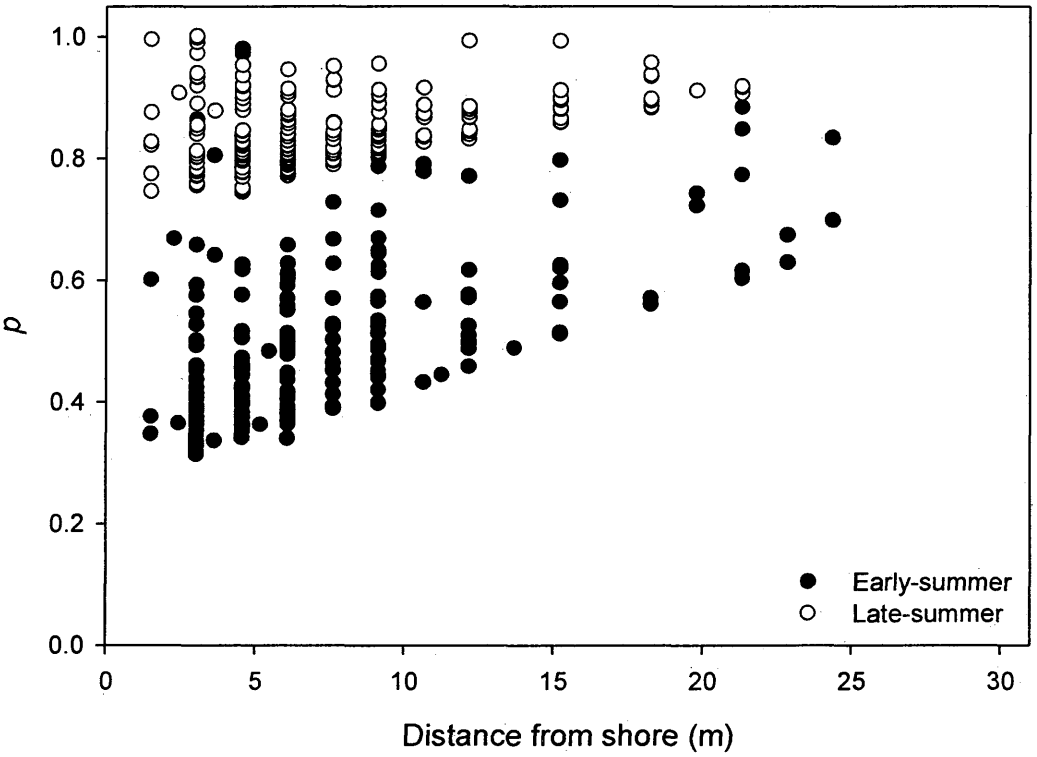
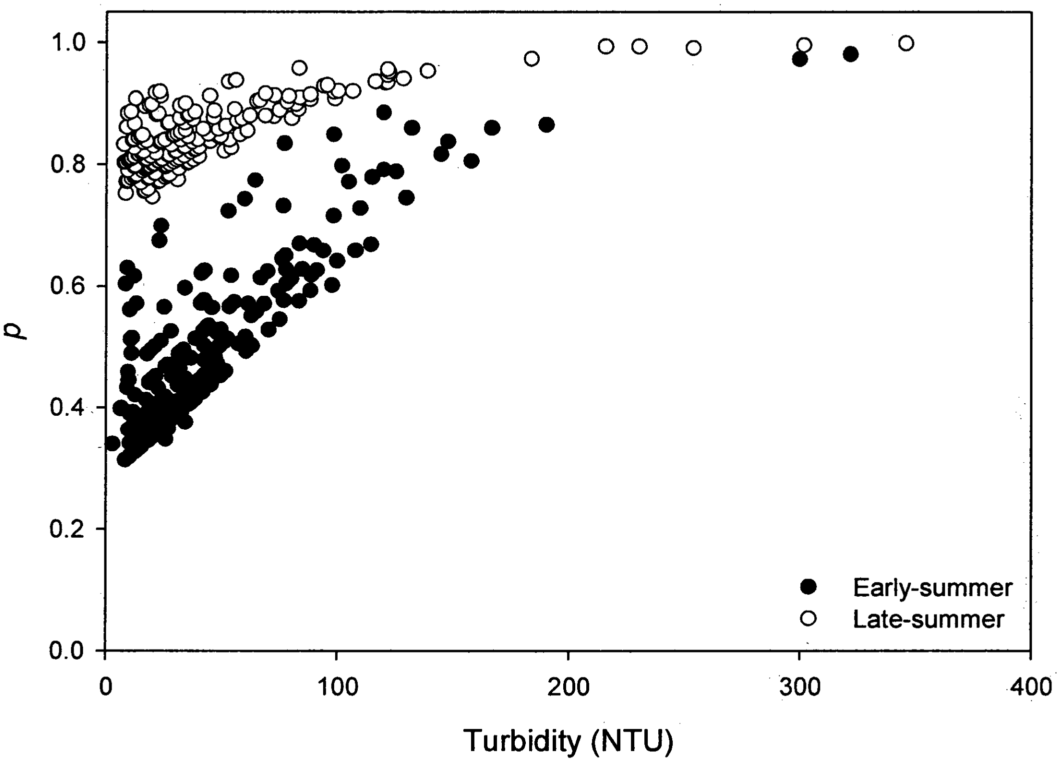


Figure 8. Relationship between estimated detection probabilities (*p*) and median turbidity at the time of sampling for spottail shiner collected during two periods (early-summer and late-summer) in 2008 and 2009 in the Mattaponi and Pamunkey rivers, Virginia. Values were estimated from $\Psi(\mathrm{Rv})\gamma(.)p(\mathrm{Pd+Dist+Turb})$ (Table 10).



CHAPTER 2

Movements of young-of-the-year striped bass in tidal tributaries of the lower Chesapeake Bay

ABSTRACT

Young-of-the-year (YOY) fishes use tidal tributaries of temperate estuaries as nurseries before moving into adult habitats farther downstream or in marine waters. Many anadromous species exhibit these habitat shifts during the first year of life. However, specific movements within natal tributaries are not well studied and may provide insight on the connectivity of nursery habitats as well as the role of dynamic habitat in mediating downstream movement. To elucidate the nature and direction of movements of young-of-the-year fishes in tidal tributaries, I conducted a tagging experiment with young-of-the-year striped bass. Small-scale movements (2-40 km) during early- and late-summer periods of 2008 and 2009 were studied using 1,094 coded-wire-tagged (CWT) fish that were captured and released in the Mattaponi and Pamunkey rivers in Virginia. A laboratory experiment indicated that retention of CWTs was high (>97%), but survival rates (S) differed between tagged and untagged (control) fish (χ^2= 7.09, $P<0.05$; S_{tagged}= 87.8± 13.8% (mean± standard error), $S_{control}$= 95.6± 3.9%). I was able to recapture 6.3% of tagged fish, and the mean time at liberty for these recaptured fish was 13 days (range: 2-70 days). Roughly 10% of recaptured individuals were recaptured at a site different from the tagging site. Movement occurred in both the upstream and downstream directions, although downstream movements were more common and were observed only in early- to mid-September. Site-specific catch data were examined for evidence of a change in the spatial distribution of YOY fish from early- to late-summer, but no such shift was observed. The mark-recapture study and spatially explicit catch records support the notion that YOY striped bass generally remain within a given nursery area during early- and late-summer periods in Chesapeake Bay tributaries. Although limited by low recapture rates, my findings suggest that, like other estuarine fishes, YOY striped bass exhibit a high degree of site fidelity in tidal tributaries of Chesapeake Bay during summer.

INTRODUCTION

Nearshore habitats in estuaries and tidal tributaries are used by the juvenile stages of many temperate species of fishes because these areas offer conditions suitable for growth and survival (e.g., abundant food resources and low predation risk; Beck et al. 2001; Dahlgren et al. 2006). However, increasing development of coastal watersheds has led to habitat alterations that negatively affect marine organisms (Beck et al. 2001). An understanding of nearshore habitat use by young fishes is vital for identification and development of protective measures. However, with a few exceptions (Miller and Able 2002; Ortega et al. 2009; Johnson et al. 2010), movement of juvenile fishes within estuarine habitats has not been well studied. Because many anadromous fishes move from upstream, freshwater habitats to downstream, brackish or marine habitats during their first year of life, these species are ideal candidates for exploring juvenile fish movement.

The striped bass (*Morone saxatilis*) is an anadromous fish that uses nearshore habitats of Chesapeake Bay tidal tributaries during the first year of life (Klein-MacPhee 2002). Spawning occurs in the freshwater portions of tidal tributaries in spring (Murdy et al. 1997), and larvae are hatched and retained within the zone of the estuarine turbidity maximum (ETM; North and Houde 2001). The ETM, which usually occurs at the 1.0 psu isohaline, provides larvae with high concentrations of prey items, and optimal salinity and temperature conditions for growth (Strathman 1982; North and Houde 2001). This zone also offers refuge from predation (Chesney 1989). Young-of-the-year (YOY) striped bass inhabit nearshore, shallow waters during summer (Dorazio et al. 1991), and as they grow, juveniles begin to use other portions of tributaries (Dey 1981). In regions north of Chesapeake Bay (i.e., Canadian waters, Hudson River), juveniles migrate to the lower reaches of tidal tributaries and out of their natal rivers by early fall (Dey 1981; Robichaud-LeBlanc et al. 1998; Robinson et al. 2004). Previous work in Chesapeake Bay focused on large-scale seasonal movement of YOY striped bass out of the tributaries (Dorazio et al. 1991), but small-scale movements of YOY striped bass during their first summer are unknown in Chesapeake Bay tributaries.

Fish movement can be inferred using mark-recapture studies or by monitoring temporal changes in the spatial distributions of fishes (Miller and Able 2002; Ross and Lancaster 2002; Miller et al. 2003; Robinson et al. 2004). In a mark-recapture study, observations on recaptured individuals can be used to determine movement away from the location of tagging. It should be noted that these studies rely on the following assumptions: (1) tags are not lost over the duration of the study, (2) the tagged portion of the population is representative of the total population of fish, and (3) all fish have an equal probability of capture (Pollock et al. 1990; Guy et al. 1996). Tag loss can be estimated using a double-tagging experiment in the field (Reinert et al. 1998; Henderson-Arzapalo et al. 1999), or by holding tagged individuals in the laboratory. Assumption 2 is reasonable if random samples of the population can be obtained. For example, individuals of all available size classes should be included in the tagged cohort. Equal capture probabilities (assumption 3) can be ensured by using appropriate capture methods and selecting a tagging process that does not influence fish behavior. For instance, tags should not impede swimming ability such that tagged fish are captured more readily than untagged fish. Furthermore, all tagged fish are assumed to mix uniformly into the population (Pollock et al. 1990).

Monitoring the temporal changes in the spatial distribution of a cohort can elucidate downstream or upstream movements of a cohort over large spatial scales (Robinson et al. 2004; Adlerstein et al. 2007). For example, with downstream movement, one would expect to observe a gradual decline in abundance of fish at upriver sites and a relative increase in abundance at downriver locations over a given time interval. Such movement could indicate a change in habitat use, for example, when fish move from freshwater sites to more saline sites.

Coded-wire-tags (CWTs) are frequently used to tag large numbers (>10,000) of small fishes, and have been used extensively to mark hatchery-reared salmonids since the 1960s (Jefferts et al. 1963; Klar and Parker 1986; Fletcher et al. 1987; Guy et al. 1996). CWTs are small (1.1 mm x 0.25 mm dia) sections of stainless steel wire, etched with unique numeric codes that allow identification of individuals. The tags are implanted into fishes, and tissue damage associated with the tagging process is minimal and heals quickly (Fletcher et al. 1987; Buckley and Blankenship 1990). Previous studies indicated high retention rates of CWTs implanted in the cheek of juvenile striped bass (92.4- 100% retention rates: Klar and Parker 1986; Wallin and Van Den Avyle 1994), and losses from mortality were low (31-40% mortality after >90 days: Klar and Parker 1986; Wallin and Van Den Avyle 1994). However, fish in those studies were hatchery-reared, and retention and survival rates may be different for wild-captured striped bass.

The objective of this study was to determine the movement of juvenile striped bass during their first summer in tributaries of the Chesapeake Bay. I conducted a mark-recapture experiment during 2008 and 2009 and examined the spatial distributions of YOY striped bass in early- and late-summer periods for evidence of movement. Because CWTs are associated with low tagging mortality rates and high retention rates, I elected to use CWTs for my study of YOY striped bass movement. Moreover, to verify the appropriateness of this approach for wild-captured fish, I conducted a laboratory experiment to determine tag retention rates and survival associated with the tagging process for juvenile striped bass.

METHODS

Tag retention and tag-related mortality rates

During early-summer 2009, YOY striped bass were collected using a 30.5-m long, 1.2-m tall beach seine with 0.63 cm mesh in the Rappahannock River, Virginia. Fish were transported to the lab and randomly assigned to one of six aerated, 340-L (91 gallon) circular aquaria. Water in each tank was independently filtered and maintained at 3.8±0.5 psu (mean±standard error [SE]) and 26.0±1.0 °C. Fish were exposed to a natural photoperiod for the duration of the experiment (49 days) and fed a commercial diet to satiation twice daily. Fish were allowed to acclimate to laboratory conditions for 72 hours prior to tagging; acclimation was evidenced by active feeding.

Three randomly selected aquaria held tagged fish (*n*= 73) and the remaining aquaria held control fish (*n*= 86). Fish from the control group were removed, measured to the nearest mm fork length (FL), and returned to their respective tank. Fish assigned to the tagged treatment were measured and implanted with individually numbered, sequentially coded wire tags (CWTs). Tags were implanted in the adductor mandibularis (cheek) muscle. Successful implantation was ensured prior to returning fish to aquaria using a handheld magnetic detector (Northwest Marine Technology, Inc.). At the beginning of the experiment, mean length of all fish (*n*=159) was 53.1 mm FL (range: 41-71 mm; Table 1). Mortalities of tagged and untagged fish were monitored daily; all dead fish were removed, and dead fish from the CWT treatment were scanned for the presence of CWTs. CWTs were then dissected from fish and read under a microscope to determine the individual identity of fish.

Because most tag loss occurs within several weeks of tagging (Heidinger and Cook 1988), tagged fish were removed after 15 days and checked for the presence of a CWT using the handheld wand detector. At the end of the experiment (49 days after tagging), both control and tagged fish were measured (FL) to evaluate tagging-induced changes in growth. Surviving fish were sacrificed, and scanned for CWTs (tagged group only) after 49 days. The experiment was terminated after 49 days because this timeframe was sufficiently long to span the time between field sampling in early and late summer (see Williams, Chapter 1). Overall, mean fish length after 49 days was 88.0 mm FL (range: 71-115 mm; Table 1). All fish were handled, maintained, and humanely euthanized in accordance with protocols approved by the Institutional Animal Care and Use Committee of the College of William & Mary.

Mean survival at 49 days (S) was calculated for control and tagged fish as:

$$S = \left(\sum_{1}^{n} \frac{N_{49}}{N_0} \right) \times \frac{1}{n} \times 100\%,$$

where n = number of replicates (aquaria) per treatment (3), N_{49}= number of fish remaining on day-49, and N_0 = number of fish at the beginning of the experiment. Estimated mean survival rates for each treatment were examined for equal variance and compared using a chi-squared test (Brown and Austen 1996).

The mean tag retention rate for YOY striped bass was determined at 15 and 49 days post-tagging. The percent of tags retained (R_t) was calculated as:

$$R_t = \left(\sum_{1}^{n} \frac{T_t}{N_t} \right) \times \frac{1}{n} \times 100\%,$$

where n = the number of replicates (3), N_t = the number of tagged fish alive on day t, and T_t= the number of fish alive on day t that retained CWTs.

Movement of tagged fish

YOY striped bass were captured during early- and late-summer periods of 2008 and 2009 (early period: July 8-28, 2008, July 13-30, 2009; late period: August 25-September 12, 2008; September 9-25, 2009). Sampling occurred twice weekly at 20 sites in the lower reaches of the Mattaponi and Pamunkey rivers in Virginia (Figure 1; Figure 2). Distances between sampling sites averaged 3.1±0.4 km in the Mattaponi River and 4.2±0.8 km in the Pamunkey River. A 30.5 m (100 ft) long, 1.2 m (4 ft) tall beach seine with 0.6 cm (0.25 in) mesh was used to capture fish using protocols consistent with the Virginia Juvenile Striped Bass Survey (Machut and Fabrizio 2009). All YOY striped bass were placed into aerated, water-filled buckets, and measured to the nearest mm fork length (FL). Captured striped bass ranged in length from 28 to 96 mm FL in 2008 and from 33 to 117 mm FL in 2009. During the first sampling event, live fish were tagged in the adductor mandibularis (cheek) muscle with a CWT using a modified 24-gauge syringe, and immediately returned to the river. During the second and all subsequent sampling events in the year, live fish were checked individually for the presence of CWTs with a handheld wand detector; if a tag was present the fish was sacrificed and returned to the laboratory for removal of the CWT. Live fish that did not have a tag were tagged and immediately returned to the river.

The locations and dates of initial tagging and recapture were compared to determine the direction of movement and the minimum distance traveled by individual fish, as well as the time at liberty. I also used the site-averaged catch per seine haul (mean CPUE) during early-summer and late-summer periods to describe the spatial distribution of YOY striped bass within each river.

RESULTS

Tag retention and tag-related mortality rates

The mean size of control and tagged fish did not differ at the beginning or at the end of the experiment (day-0: $t= -0.06$, $P>0.05$; day-49: $t= -0.27$, $P>0.05$). However, mean survival rates of control and tagged YOY striped bass were significantly different after 49 days ($S_{control}$=95.6±3.9%; S_{tagged}=87.9±13.8%; $\chi 2=7.09$, $P<0.05$; Table 2). The overall lower mean survival rate of tagged fish was due to the unusually low survival (S=72.0%) I observed among the group of fish that were tagged first in the experiment. Fish from this replicate fed less aggressively than fish from the other replicates, and may have experienced additional stress associated with the tagging process. Survival rates of tagged fish from the other two replicates were within the range of rates I observed for the control fish (S=93.3-100.0%). Overall, mean survival rates of my tagged fish exceeded values from similar studies with juvenile striped bass, although my experiment was conducted over a shorter time period (Klar and Parker 1986; Wallin and Van Den Avyle 1994).

The mean tag retention rate at 15 days post-tagging was 98±2.0% (n=64 fish) and 97±3.0% at 49 days (n=64 fish). These rates were similar to retention rates observed by others (Klar and Parker 1986; Wallin and Van Den Avyle 1994).

Movement of tagged fish

The mean CPUE ranged from 0 to 10.83 fish/haul during early summer and from 0 to 5.83 fish during late summer (Figure 3). As a result, more fish were tagged during early summer than during late summer. This finding is consistent with the decline in CPUE of YOY striped bass reported by the VIMS juvenile striped bass survey as summer progresses (Machut and Fabrizio 2009). No change in the spatial distribution of fish (upstream or downstream) was observed during either 2008 or 2009 (Figure 3), and suggested that movements during this time period were minimal.

Of 1,094 YOY striped bass tagged in this study, 6.3% (*n*=69) were recaptured during early- and late-summer sampling events (Table 3). Information from CWTs was obtained from 68 of the recaptured individuals because one recovered CWT was lost. Most fish were recaptured at the tagging site within two weeks of tagging (mean=13 days, range: 2-70 days; Figure 4) However, 10.3% of recaptured fish were recaptured at a site different from the tagging site; this group of fish represented 0.6% of tagged fish (Table 4).

Surprisingly, fish movement occurred in both the upstream and downstream directions (Table 5; Figure 5). In 2008, movement was observed for 2.9% (*n*=2) of recaptured striped bass. Those individuals were tagged at the same site on the same day, and were subsequently recaptured at the adjacent upstream site (4.9 km) three days later. In 2009, upstream movement was observed for only one (1.5%) recaptured fish, which traveled 12.6 km upstream. Four (5.9%) recaptured fish moved downstream in 2009 in the Mattaponi River and were recaptured during late summer. Three of these were recaptured at the adjacent downstream site 3.1 km away, including one fish that traveled that distance in six days. The fourth fish was recaptured 5.0 km downstream.

DISCUSSION

Both tagging and catch/haul data suggest that YOY striped bass exhibited limited movement during summer in tributaries of the lower Chesapeake Bay. Movements were observed in a small proportion (~ 10%) of recaptured fish, and most fish traveled less than 5.0 km from the site of tagging. Although movements occurred in both the upstream and downstream directions, downstream recaptures were observed only during late summer (mid-September) in 2009. No pattern in mean CPUE along the salinity gradient was discerned, nor did I detect a temporal shift in abundance as summer progressed.

The high degree of site fidelity I observed in YOY striped bass is not uncommon among juvenile fishes (e.g., Florida pompano, Gulf kingfish: Ross and Lancaster 2002; Atlantic croaker: Miller et al. 2003). However, my study focused on movements within short reaches of the sampled rivers (< 40 km) and over a short period of time (3 months), which may explain why I observed little movement in my study. The majority of fish was recaptured within several days of tagging, but fish were confirmed to remain at the tagging site for up to 70 days.

Recapture rates for this study were low (~ 6%) but within the range of reported recapture rates for similar studies of YOY fishes (Miller and Able 2002; Ross and Lancaster 2002). The high retention rates of CWTs observed in laboratory-held fish (>98.0 %) suggested that tag shedding was negligible in the field, and thus not likely to account for the low observed recapture rates. Instead, low recapture rates may be indicative of high population abundance or tagging-induced changes in fish behavior. Because growth and feeding in the laboratory were similar between control and tagged fish, neither the presence of tags nor the tagging process likely resulted in differential behavior between tagged and untagged fish in the field. Although mean survival rates were significantly different between tagged and untagged laboratory-held fish, differences were attributed to the low survival I observed in a single replicate of tagged fish. However, the spatial scale of my field study, as well as potentially different behaviors between tagged and untagged fish, may have affected the findings that upstream or downstream movements of YOY striped bass are uncommon during summer.

The spatial scale of my sampling design may have precluded observation of movement among YOY striped bass if the scale of fish movement was less than the distance between sites (~3-4 km). Each sampling area (site) was roughly 50 m in length, and separated from adjacent sites by several kilometers, thus, movements of fish to another portion of the river (e.g., a location as few as several meters out of the sampling area) would not be detected with my survey design.

In addition, if the behavior of tagged fish differed from that of their untagged conspecifics, inferences about the direction and likelihood of movement could be biased. Because only a small portion of the total population of striped bass within the rivers could be tagged each summer, it is possible that tagged fish did not fully represent the cohort of YOY striped bass. For instance, tagged fish may have moved away from the capture site to areas in the river that I did not sample, or they may have developed an aversion to disturbances at a site, such that during the next sampling event fish may have sought temporary refuge in areas not sampled (the "trap shy" response). Downstream movements were observed for only a small proportion of recaptured fish. All of these fish were recaptured during late summer 2009 when sampling extended into late-

September. These downstream movements may reflect changes in diets from small plankton prey at upriver sites to larger prey items (e.g., polychaete worms) at downriver locations (Cooper et al. 1998; Muffelman 2006). Alternatively, downstream movements may be related to changes in environmental conditions such as water temperature, and such relationships should be explored in future studies. Unfortunately, the effect of environmental variation on fish movement could not be discerned because sample sizes in my study were small (movement was observed for only seven fish).

Information on the spatial distribution of fish within the river supported the conclusions about movement derived from the tagging data and suggested that large-scale upriver or downriver movements of YOY striped bass do not occur during summer in lower Chesapeake Bay tributaries. Temporal changes in the spatial distribution of catches may be more appropriate for discerning fish movement when studies are conducted over large temporal and spatial scales instead of the small scale (several kilometers) which was the focus of this study. My study was designed to determine if large-scale movements of striped bass reported from summer to fall (Dey 1981; Dorazio et al. 1991; Robichaud-LeBlanc et al. 1998; Robinson et al. 2004) also occurred at a smaller scale during summer. The small scale of the study limited detection of gradual movements from the upriver areas in the Pamunkey and Mattaponi rivers used by striped bass to downriver sites in the York River; fish likely occupied locations both upstream and downstream of the study area.

Variations in gear efficiency may introduce uncertainty in relative abundance data and in the location of fish within the rivers. I used a beach seine to collect juvenile striped bass, but the efficiency of beach seines varies by species, and may be affected by physical and environmental conditions during sampling (Parsley et al. 1989; Steele et al. 2006; Williams, Chapter 1). The ability to detect YOY striped bass is affected by the maximum distance from the shoreline that a seine is deployed, and differs among sites due to beach slope and bottom-type conditions that may prohibit sampling farther from shore (Williams, Chapter 1). Site-specific differences in seine efficiency and detection of YOY striped bass may have contributed to variation in the relative abundance of fish for a given site, and may have impeded my ability to discern small-scale movements from temporal changes in mean CPUE data.

Future studies to examine small-scale movements of YOY striped bass would benefit from a greater number of tagged fish and additional effort to collect recaptures, as well as the expansion of the study area throughout the primary nursery grounds. A larger sample area, perhaps with more sites, would be useful to observe gradual changes in fish distribution.

Although some movement was observed for YOY striped bass during summer, little evidence from this study supported the notion that a large proportion of fish in Chesapeake Bay tidal tributaries undergoes such movement before early-September. Downstream movements of fish were observed only during mid-September, and suggest that directed downstream movements may be related to environmental factors such as water temperature. An understanding of the extent and timing of small-scale fish movements is essential to identify critical habitats for young-of-the-year fish.

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Table 1. Mean fork length (FL, mm) of control and coded wire tagged young-of-the-year striped bass on day-0 and day-49 of a tag retention experiment. The number of fish (N), mean FL, and standard deviation (SD) is also provided. Mean fork length was not significantly different between treatments on either day-0 (*t*= -0.06, P>0.05) or day-49 (*t*= 0.27, P>0.05).

Treatment		day-0			day-49	
	N	Mean FL	SD	N	Mean FL	SD
Control	86	53.05	6.43	82	87.80	7.38
Tagged	73	53.12	6.59	64	88.19	9.50
Overall	159	53.09	6.48	146	87.97	8.35

Table 2. Survival after 49 days of control (C) and tagged (T) young-of-the-year striped bass. Percent survival (*S*) was calculated as the proportion of fish at the onset of the experiment (N_0) that survived to the end of the experiment (N_{49}), and mean overall survival rates differed between treatments ($S_{control} = 95.6\%$; $S_{tagged}=87.9\%$: $\chi^2= 7.09$, $P<0.05$).

Treatment	N_0	N_{49}	S (%)
C	25	24	96.0
C	26	26	100.0
C	23	22	95.7
T	30	28	93.3
T	30	28	93.3
T	25	18	72.0
Overall	159	146	91.7

Table 3. Number of young-of-the-year striped bass that were tagged and recaptured at sites in the Mattaponi and Pamunkey rivers, Virginia during summer 2008 and 2009. Number of fish tagged, number of fish recaptured, and the number of recaptured fish that moved are provided. Percentages of recaptured fish and fish that moved are provided in parentheses.

Year	Number of fish tagged	Number of fish recaptured	Number of fish that moved
2008	503	44 (8.7)	2 (4.7)
2009	591	25 (4.2)	5 (20.0)
Overall	1,094	69 (6.3)	7 (10.3)

Table 4. Recaptured young-of-the-year striped bass (*n*=68) from a two-year tagging study conducted during summer 2008 and 2009 on the Mattaponi (M) and Pamunkey (P) rivers, Virginia. The year, fish identification number, river, tagging date, tagging site, recapture date, and recapture site are provided for each fish. The number of days at liberty is also provided. An asterisk next to the fish identification number indicates a fish that was recaptured at a site that differed from the tagging site.

River	Fish number	Tagging date	Tagging site	Recapture date	Recapture site	Days at liberty
			2008			
P	R016	8-Jul-2008	9	21-Jul-2008	9	13
M	R014	8-Jul-2008	11	25-Jul-2008	11	17
M	R011	9-Jul-2008	11	25-Jul-2008	11	16
P	R010	10-Jul-2008	3	15-Jul-2008	3	5
M	R005	16-Jul-2008	13	18-Jul-2008	13	2
P	R015	17-Jul-2008	1	21-Jul-2008	1	4
M	R006	18-Jul-2008	13	22-Jul-2008	13	4
M	R009	18-Jul-2008	12	22-Jul-2008	12	4
M	R002	18-Jul-2008	16	25-Jul-2008	16	7
M	R021	18-Jul-2008	19	3-Sep-2008	19	47
P	R001	21-Jul-2008	2	24-Jul-2008	2	3
P	R003*	21-Jul-2008	1	24-Jul-2008	2	3
P	R004*	21-Jul-2008	1	24-Jul-2008	2	3
P	R008	21-Jul-2008	3	28-Jul-2008	3	7
P	R029	21-Jul-2008	1	25-Aug-2008	1	35
P	R022	21-Jul-2008	3	28-Aug-2008	3	38
M	R012	22-Jul-2008	11	25-Jul-2008	11	3
M	R013	22-Jul-2008	11	25-Jul-2008	11	3
M	R042	22-Jul-2008	16	27-Aug-2008	16	36
P	R007	24-Jul-2008	1	28-Jul-2008	1	4
M	R019	25-Jul-2008	14	29-Aug-2008	14	35
P	R026	25-Aug-2008	9	28-Aug-2008	9	3
M	R025	27-Aug-2008	20	29-Aug-2008	20	2
M	R041	27-Aug-2008	11	29-Aug-2008	11	2
M	R037	27-Aug-2008	19	5-Sep-2008	19	9
M	R043	27-Aug-2008	19	8-Sep-2008	19	12
M	R024	28-Aug-2008	20	8-Sep-2008	20	11
P	R032	28-Aug-2008	9	12-Sep-2008	9	15
P	R033	28-Aug-2008	9	12-Sep-2008	9	15
M	R023	29-Aug-2008	11	3-Sep-2008	11	5
P	R018	2-Sep-2008	1	4-Sep-2008	1	2
P	R035	2-Sep-2008	5	4-Sep-2008	5	2
P	R036	2-Sep-2008	5	4-Sep-2008	5	2
P	R031	2-Sep-2008	4	12-Sep-2008	4	10

M	R034	3-Sep-2008	17	5-Sep-2008	17	2
M	R038	3-Sep-2008	19	5-Sep-2008	19	2
M	R039	3-Sep-2008	19	5-Sep-2008	19	2
M	R040	3-Sep-2008	19	5-Sep-2008	19	2
M	R027	3-Sep-2008	11	8-Sep-2008	11	5
M	R028	3-Sep-2008	17	8-Sep-2008	17	5
M	R030	3-Sep-2008	17	11-Sep-2008	17	8
M	R044	5-Sep-2008	19	8-Sep-2008	19	3
M	R017	5-Sep-2008	19	11-Sep-2008	19	6
			2009			
P	R054	13-Jul-2009	3	22-Jul-2009	3	9
P	R069*	13-Jul-2009	6	9-Sep-2009	10	58
P	R068	13-Jul-2009	6	10-Sep-2009	6	59
M	R052	14-Jul-2009	19	21-Jul-2009	19	7
M	R053	14-Jul-2009	16	21-Jul-2009	16	7
P	R058	15-Jul-2009	3	23-Sep-2009	3	70
M	R046	16-Jul-2009	16	29-Jul-2009	16	13
M	R048	16-Jul-2009	16	29-Jul-2009	16	13
P	R049	20-Jul-2009	6	22-Jul-2009	6	2
P	R055	20-Jul-2009	10	22-Jul-2009	10	2
P	R051	20-Jul-2009	5	28-Jul-2009	5	8
P	R050	22-Jul-2009	5	28-Jul-2009	5	6
P	R047	22-Jul-2009	10	30-Jul-2009	10	8
M	R065*	22-Jul-2009	16	15-Sep-2009	15	55
M	R064*	23-Jul-2009	16	15-Sep-2009	15	54
M	R056	27-Jul-2009	13	28-Jul-2009	13	1
M	R045	27-Jul-2009	16	29-Jul-2009	16	2
M	R061*	27-Jul-2009	16	17-Sep-2009	14	52
M	R063*	9-Sep-2009	16	15-Sep-2009	15	6
M	R062	9-Sep-2009	16	17-Sep-2009	16	8
M	R060	9-Sep-2009	11	22-Sep-2009	11	13
P	R057	10-Sep-2009	1	14-Sep-2009	1	4
M	R067	11-Sep-2009	18	15-Sep-2009	18	4
P	R066	14-Sep-2009	10	16-Sep-2009	10	2
P	R059	14-Sep-2009	1	23-Sep-2009	1	9

Table 5. Recaptured fish that had observed movement during a two-year tagging study of YOY striped bass conducted during summer 2008 and 2009 on the Mattaponi and Pamunkey rivers, Virginia. The year, fish identification number, tagging date, number of days at liberty, and minimum distance traveled are provided for each fish. Negative values for the minimum distance traveled indicate downstream movement while positive values indicate upstream movement.

Year	Fish number	Tagging date	Days at liberty	Minimum distance traveled (km)
2008	R003	21-Jul-2008	03	4.9
	R004	21-Jul-2008	03	4.9
2009	R069	13-Jul-2009	58	12.6
	R064	23-Jul-2009	55	-3.1
	R065	23-Jul-2009	55	-3.1
	R061	27-Jul-2009	52	-5.0
	R063	09-Sep-2009	06	-3.1

Figure 1. Map of the study area within the lower Chesapeake Bay. Sampled sites occurred within a 27.6 km stretch of the lower Mattaponi River, Virginia and a 39.1 km stretch of the lower Pamunkey River, Virginia.

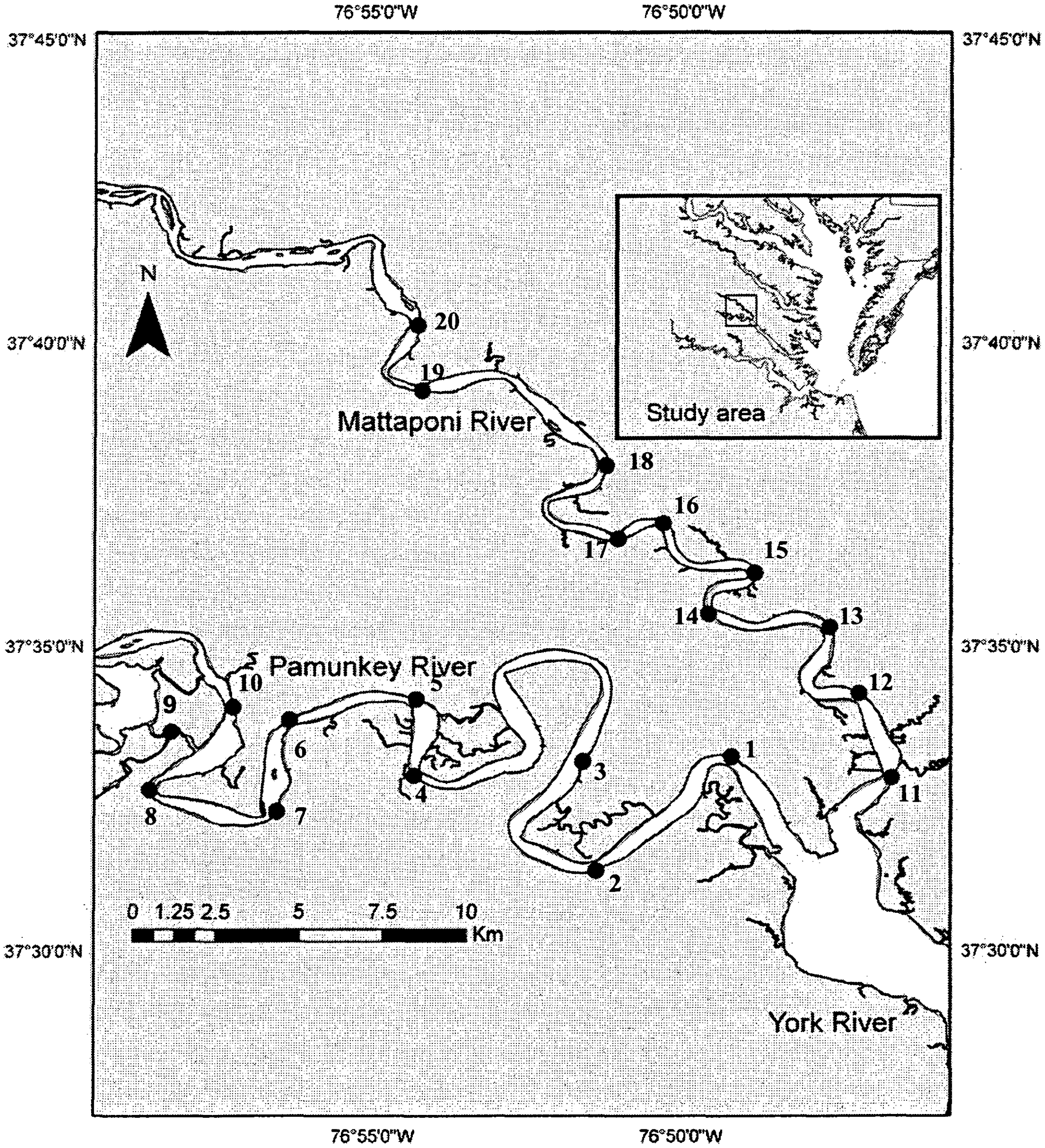


Figure 2. Number of young-of-the-year striped bass tagged at 20 sites in the Mattaponi and Pamunkey rivers, Virginia during summer 2008 and 2009. Fish were collected using a 30.5-m long beach seine on 12 sampling occasions.

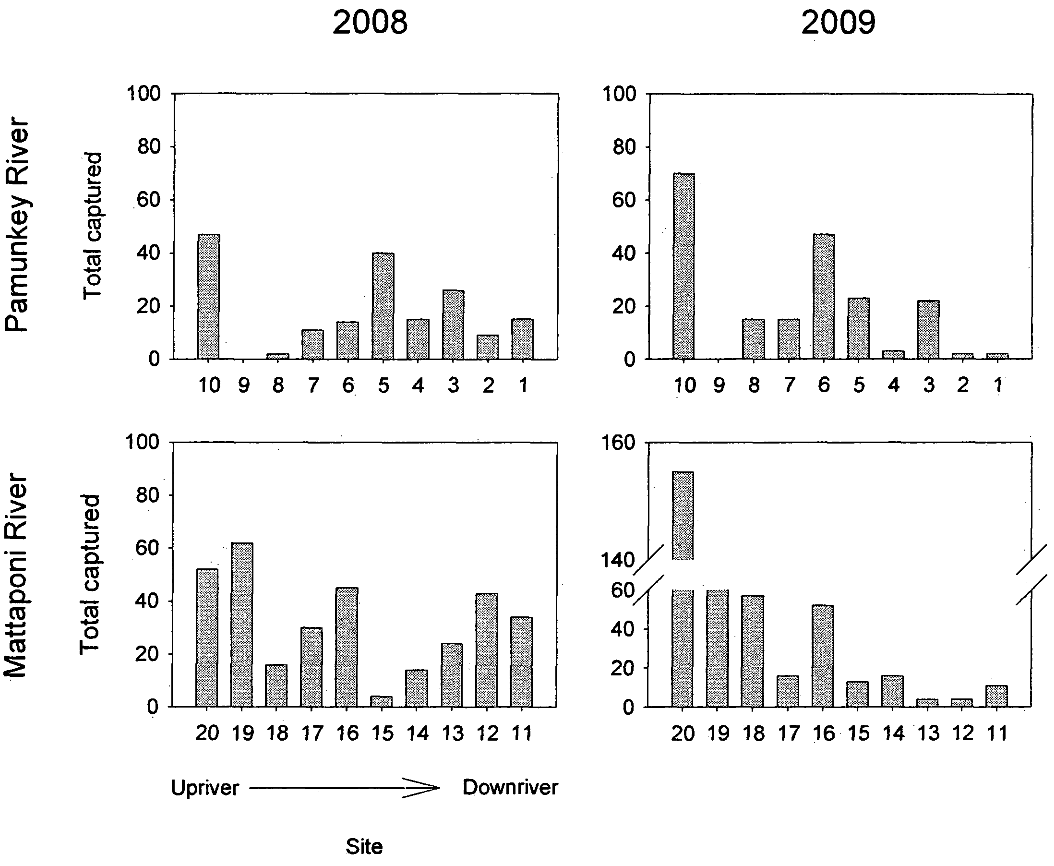


Figure 3. Mean CPUE for YOY striped bass from a tagging study conducted during early- and late-summer periods of 2008 and 2009 in the Mattaponi and Pamunkey rivers, Virginia. Fish were collected using a 30.5-m long beach seine at 10 sites in each river.

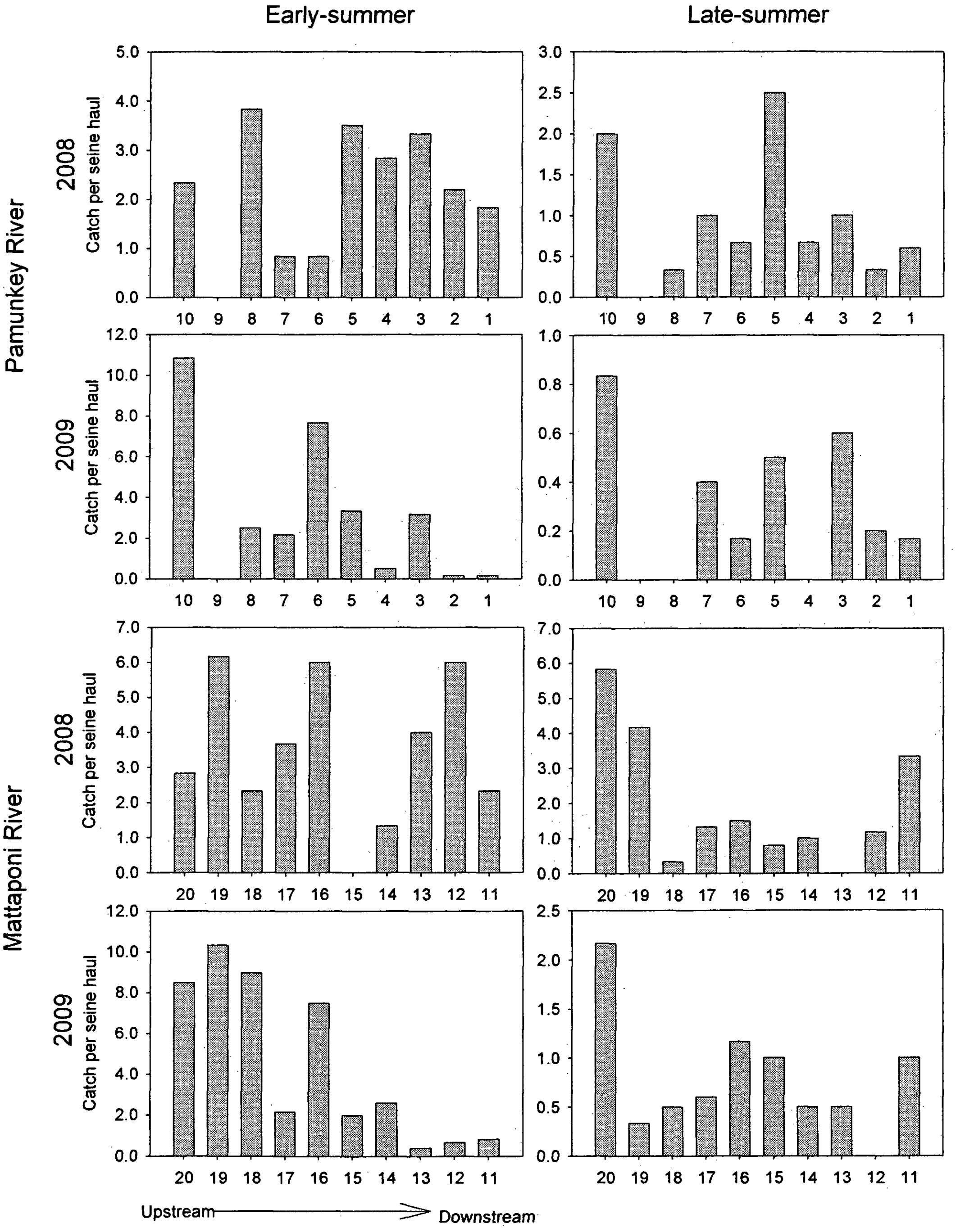


Figure 4. Days at liberty for 68 recaptured YOY striped bass during a tagging study conducted in summer 2008 and 2009 in the Mattaponi and Pamunkey rivers, Virginia.

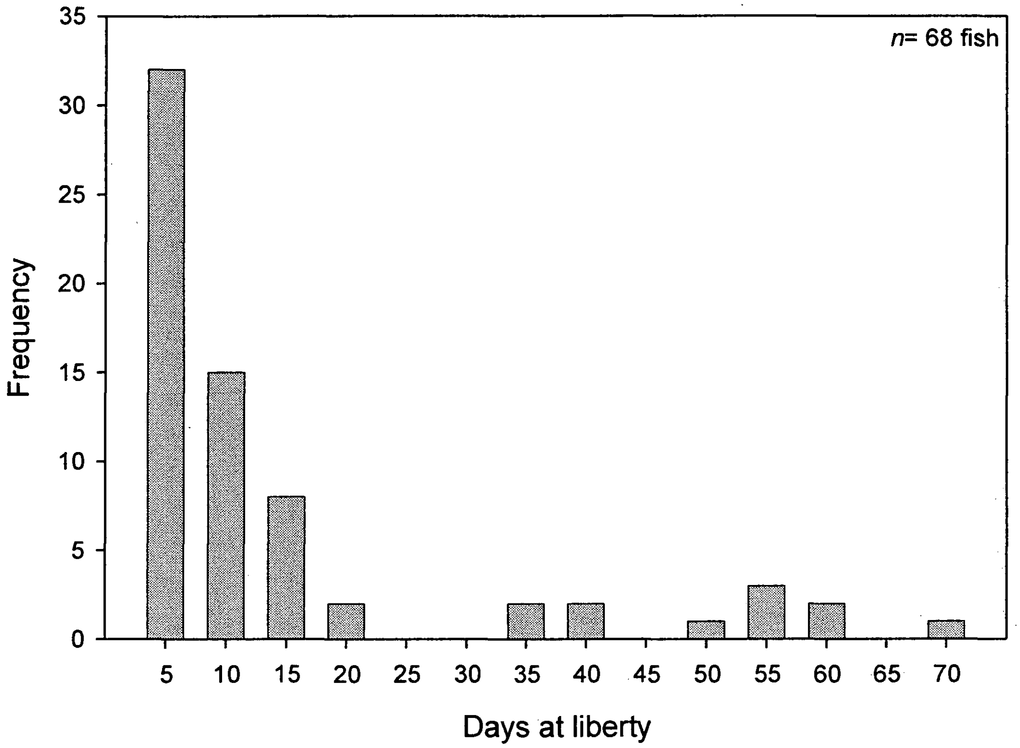
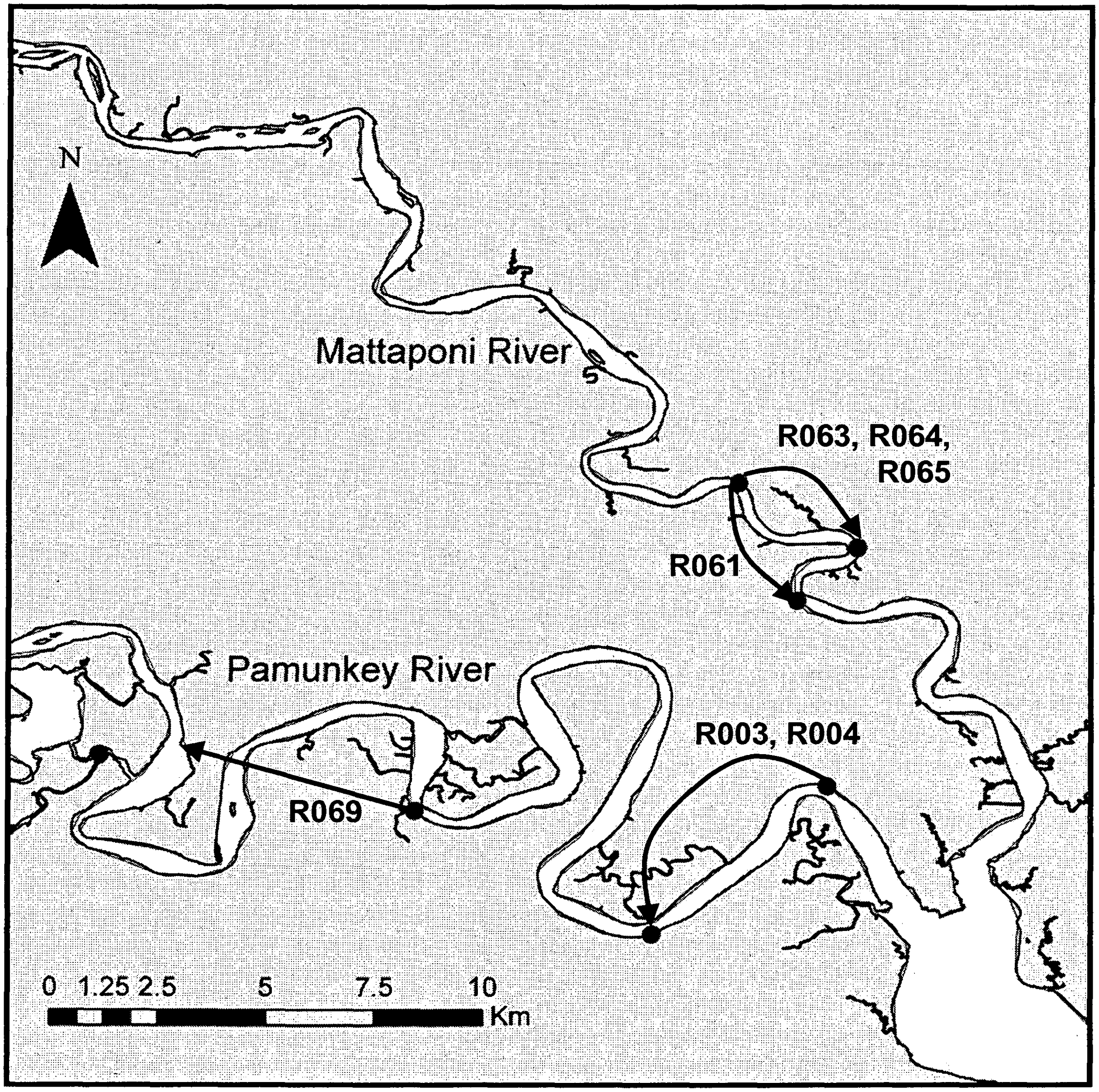


Figure 5. Movements of recaptured fish during a two-year tagging study conducted in the Mattaponi and Pamunkey rivers, Virginia. The direction of each arrow denotes the direction of travel (upriver or downriver) and fish identification numbers (e.g., R003) are provided.



APPENDIX

Survey design

Occupancy models rely on sampling a set of sites, s, on a given number of sampling occasions, K, to determine estimates of detection (*p*) and occupancy probabilities (Ψ). The number of sites and sampling occasions per site can be calculated assuming *a priori* values for detection and occupancy probabilities (Table A1; MacKenzie and Royle 2005). Generally, for rare species more sites should be sampled but on fewer occasions, whereas for common species such as striped bass and Atlantic croaker, a greater frequency of sampling is required but at fewer sites (MacKenzie et al. 2006). The expected precision of an estimate of occupancy (assuming occupancy is constant) is calculated as:

$$1) \qquad Var(\Psi) = \frac{\Psi}{s}\left[(1-\Psi) + \frac{(1-p^*)}{p^* - Kp(1-p)^{K-1}}\right],$$

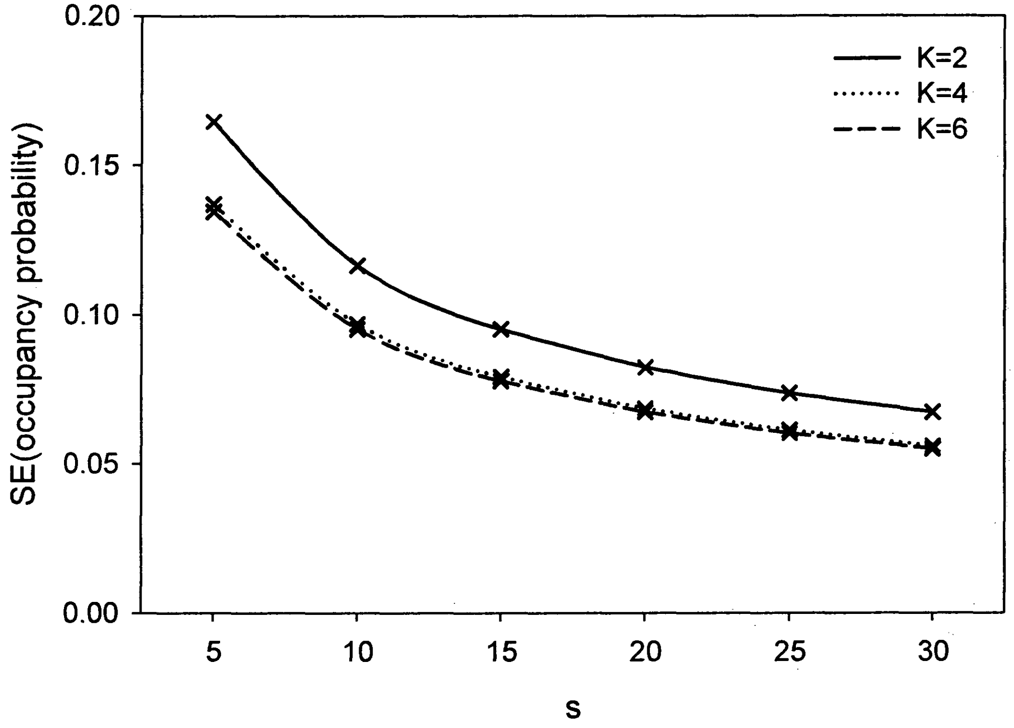
where var(Ψ) is the variance of the occupancy parameter, and $p^*=1-(1-p)^K$ is the probability that the species is detected during one or more of K occasions (MacKenzie et al. 2006).

Using estimates of Ψ (0.9) and *p* (0.7) from a previous study of YOY striped bass (see Hewitt et al. 2008), I determined that a minimum of three sampling occasions must be completed (Table A1). I examined the predicted precision of the estimate of occupancy probability for 5 to 30 sites and for 2, 4, and 6 sampling occasions per site (Figure A1). Because the predicted precision decreased rapidly as the number of sites increased, I selected 20 sites and 6 sampling occasions per site (K=6) as an appropriate sampling effort that would provide reasonable precision ($SE(\Psi)<0.10$) and yet still be logistically feasible (Figure A1). Additional gains in precision from sampling 25 or 30 sites were small (<0.013).

Table A1. Minimum number of sampling occasions per site for estimating occupancy (assuming it is constant) for various combinations of occupancy (Ψ) and detection (p) probabilities. Table reproduced from MacKenzie et al. (2006).

	Ψ								
p	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9
0.1	14	15	16	17	18	20	23	26	34
0.2	7	7	8	8	9	10	11	13	16
0.3	5	5	5	5	6	6	7	8	10
0.4	3	4	4	4	4	5	5	6	7
0.5	3	3	3	3	3	3	4	4	5
0.6	2	2	2	2	3	3	3	3	4
0.7	2	2	2	2	2	2	2	3	3
0.8	2	2	2	2	2	2	2	2	2
0.9	2	2	2	2	2	2	2	2	2

Figure A1. Standard error of the estimated occupancy probability for a given number of sampled sites (s), and a range of sampling occasions per site (K), when the probabilities of occupancy and detection are 0.9 and 0.7.



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Born in Princess Anne, Maryland on 21 July 1984. Graduated as the valedictorian from Washington High School in 2002. Graduated *summa cum laude* from the University of Maryland Eastern Shore with a Bachelor of Science in Environmental Science and a concentration in Marine Science in 2006. Entered the Master of Science program at the School of Marine Science, Virginia Institute of Marine Science, College of William & Mary in 2006.