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ARTICLE

## Detectability of Estuarine Fishes in a Beach Seine Survey of Tidal Tributaries of Lower Chesapeake Bay

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### Abstract

Detectability, the probability of encountering a species at a sampling site, is often overlooked in fisheries research despite its potential to obscure inferences on habitat use and lead to biased estimates of abundance. We used occupancy models to explore factors affecting detectability and occupancy ( $\Psi$ ), the probability that a species inhabits a site, for three fishes frequently captured in Chesapeake Bay seine surveys: young-of-the-year (age-0) striped bass *Morone saxatilis*, yearling Atlantic croaker *Micropogonias undulatus*, and spottail shiner *Notropis hudsonius*. Twelve repeat-sampling events occurred during the summers of 2008 and 2009 at 20 sites in the Mattaponi and Pamunkey rivers, Virginia. Although the environmental factors that influenced detection probabilities varied with species, the detectability of all species was positively related to effective net length (i.e., the maximum distance from shore that the seine was deployed). The mean detectability of age-0 striped bass, which occupied nearly every site ( $\Psi = 0.99$ , SE = 0.01), was 0.62 (SE = 0.06) and positively related to mean water temperature during sampling. The detectability of yearling Atlantic croakers was negatively related to water temperature at time of capture and was significantly greater in early summer than in late summer. In early summer, Atlantic croakers occupied all sampling sites; occupancy decreased in late summer ( $\Psi = 0.86$ , SE = 0.08) and was positively related to the mean salinity at the site. Unlike with Atlantic croakers, the mean detectability of spottail shiners was significantly greater in late summer than in early summer; detectability was positively related to turbidity at the time of sampling and reflected the increased availability of recently recruited individuals. Spottail shiners occupied fewer sites than did the two other species ( $\Psi = 0.59$ , SE = 0.21). Seasonal changes in detectability appeared to reflect changes in catchability associated with fish growth. Determining factors that influence detection probabilities is vital to improving our understanding of habitat use by fish and reducing the variation in fisheries sampling.

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Fisheries investigations that aim to understand the patterns and dynamics of habitat use rely on the ability of sampling gear to detect the species of interest in the sampled habitat. Detection occurs when the species occupies a site and is encountered during sampling. Some species may be undetected during sampling despite occurring at a site (MacKenzie et al. 2006). Estimates of habitat use, population size, and colonization rates are biased in the presence of imperfect detection (MacKenzie et al. 2006). Understanding factors that contribute to variation in detectability, defined as the probability that a species is detected during a sampling event (MacKenzie et al. 2006), could improve surveys

that seek to assess population characteristics (e.g., habitat use, relative abundance).

The failure to detect a species may be the result of true absences or 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 occurs at a site but is not captured (i.e., the species evaded capture). Unfortunately, true and false absences are confounded because the failure to detect a species can result from either process.

In addition to false absences, detectability is rarely constant and often highly variable because the factors that influence

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detectability vary. To detect a species, at least one individual must occur at the site, and, as expected, the odds of detection increase when a greater number of individuals are present. Thus, detectability is a function of the number of organisms vulnerable to capture and the probability of capture. For a given level of abundance, researchers can maximize detectability of a species by ensuring high catchability, which entails the deployment of efficient sampling gear during times and in locations where the species is available (Bayley and Peterson 2001). Catchability, or the proportion of a fish stock captured with a single unit of effort (Gulland 1983), is the product of availability and gear efficiency (Kimura and Somerton 2006). Availability refers to the proportion of the fish stock that occurs in locations where the gear is deployed, and gear efficiency is the proportion of fish 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 by fish behavior, as well as by the selectivity of the gear and the vulnerability of individual fish.

As with catchability and efficiency, few fisheries studies have estimated detectability,  $p$ . Detection probabilities vary among fish 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 when used in unobstructed waters than when used in nearshore areas containing snags and other obstructions. Similarly, the slope of the beach affects detection probabilities of young-of-the-year (age-0) striped bass *Morone saxatilis* (Hewitt et al. 2008). Environmental conditions, such as turbidity, that influence fish behavior also affect detectability. Because effective swimming speeds (and thus avoidance capabilities) are typically greater for larger fish, individual fish size may also affect detection probabilities. Given the variable nature of  $p$ , detection probabilities should be estimated to improve information from fisheries surveys. For instance, the Virginia juvenile striped bass seine survey (hereafter Virginia seine survey) provides estimates of recruitment from annual measures of the relative abundance of age-0 striped bass and other estuarine species. Here, as with most fishery surveys, relative abundance is estimated from the catch data assuming 100% detection. Fishery management plans for striped bass, Atlantic croaker *Micropogonias undulatus*, and other coastal and marine species are based on age-structured stock assessments, which rely on annual recruitment indices as input to the assessment. However, recruitment surveys typically do not address imperfect detection, and catch data are rarely evaluated for the effect of variable detection probabilities; yet such variation can lead to biased estimates of abundance.

The objective of our study was to determine factors that affect detection probabilities for the estuarine fishes encountered in beach seine surveys, which are commonly used to provide measures of recruitment. Hewitt et al. (2008) determined detection probabilities for age-0 striped bass in tributaries of the lower

Chesapeake Bay using long-term data from a seine survey, but limitations in sampling design resulted in imprecise estimates of the effects of factors that influenced detectability. In this study, we (1) explicitly estimated detection probabilities for fishes encountered by a beach seine in Chesapeake Bay tributaries, and (2) examined factors (such as temperature and turbidity) that affected these probabilities. Although other factors may have influenced detection probabilities, selected factors were those suspected to have the greatest effect on  $p$ . We used occupancy models (MacKenzie et al. 2002) to estimate detection probabilities for age-0 striped bass, yearling Atlantic croakers, and adult and juvenile spottail shiners *Notropis hudsonius*. Although not of primary interest, occupancy probabilities (the probability that a species inhabits a site within a region of interest) are also reported and discussed.

Age-0 striped bass, yearling Atlantic croakers, and adult and juvenile spottail shiners are frequently captured in Chesapeake Bay tributaries during the summer by the Virginia seine survey. The nearly ubiquitous distribution of age-0 striped bass and yearling Atlantic croakers in Virginia tidal rivers makes them ideal candidates for exploring factors that influence detection probabilities (because unoccupied sites provide no information on detectability). We elected to focus this study on striped bass and Atlantic croakers because the Chesapeake Bay supports important commercial and recreational fisheries for these species. In addition, both are managed by fishery management plans based on periodic stock assessments that use recruitment indices derived from beach seine surveys. Spottail shiners have a more limited distribution in the sampled rivers than either striped bass or Atlantic croakers, and thus provide a contrast to the two transient species.

## METHODS

*Field sampling.*—This study was conducted in the lower reaches of the Mattaponi and Pamunkey rivers, Virginia, two tidal tributaries that together with the York River form the York River system. The rivers are used as nurseries by many fishes of the region (Machut and Fabrizio 2009), including the three species of interest. 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 the summers of 2008 and 2009 (Figure 1); the same sites were sampled in both years. We assumed sites were independent between years because a different cohort of fish was sampled each year and environmental characteristics such as water temperature and salinity at each site varied annually. Sampled sites were representative of unobstructed nearshore locations in the Mattaponi and Pamunkey rivers and were similar to sites sampled by the Virginia seine survey. Sites were sampled during a 3-week period in early summer (July 2008 and 2009) and again in late summer (August 2008 and September 2009). Sampling occurred at the beginning and end of the summer

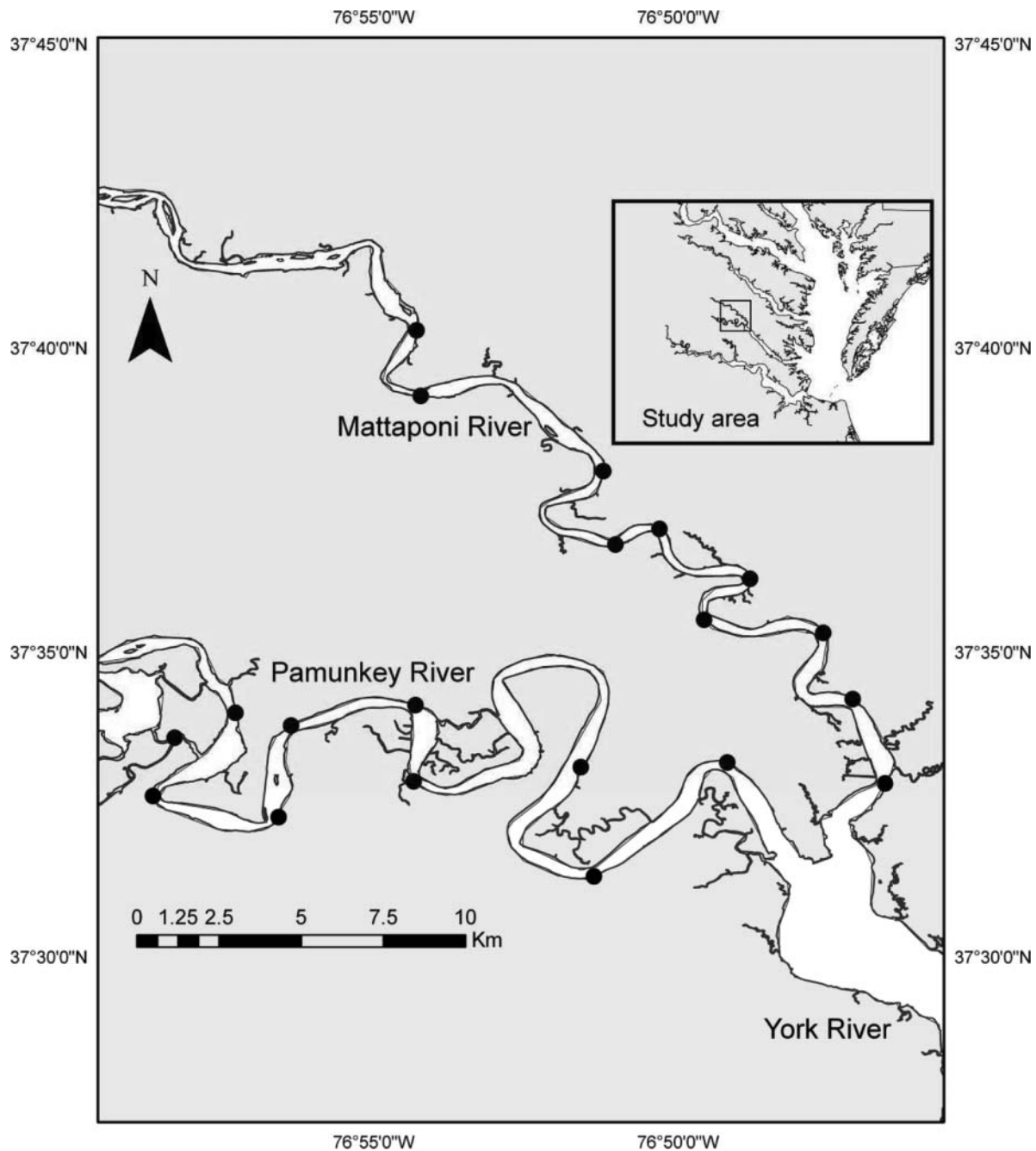


FIGURE 1. Locations of study area and sampling sites in the Mattaponi and Pamunkey rivers.

because observations from the Virginia seine survey suggested that catches declined as summer progressed, and because environmental factors that could potentially influence occupancy and detection probabilities also changed as summer progressed.

Because estimation of detection probabilities (and occupancy) requires collection of presence/absence data from multiple sites during repeated sampling occasions (MacKenzie et al. 2006), we sampled each site six times during each 3-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 conditions occasionally prohibited sampling (e.g., abnormally high or low tides, storms). The number of sites and sampling occasions per site were chosen based on occupancy-modeling guidelines (MacKenzie and Royle 2005; MacKenzie et al. 2006) and what was logistically feasible. We used preliminary estimates of occupancy and detection probabilities for age-0 striped bass (provided in Hewitt et al. 2008) to calculate the number of sampling

TABLE 1. Mean  $\pm$  SE salinity (Sal), water temperature (Temp), and turbidity (Turb) for early- and late-summer periods during 2008 and 2009 at 20 sites in the Mattaponi and Pamunkey rivers. Ranges are given in parentheses, and  $N$  is the number of observations (sampling events).

Variable	2008		2009	
	Early summer	Late summer	Early summer	Late summer
Sal (psu <sup>a</sup> )	2.16 $\pm$ 0.25 (0.03–9.78)	5.64 $\pm$ 0.41 (0.53–15.27)	2.47 $\pm$ 0.26 (0.05–9.07)	5.16 $\pm$ 0.41 (0.24–14.72)
Temp ( $^{\circ}$ C)	28.55 $\pm$ 0.11 (26.70–31.90)	26.22 $\pm$ 0.07 (24.04–28.86)	27.34 $\pm$ 0.08 (26.02–29.97)	23.39 $\pm$ 0.06 (21.34–24.89)
Turb (NTU)	56.40 $\pm$ 4.51 (3.14–322.00)	58.55 $\pm$ 6.02 (9.55–346.00)	52.38 $\pm$ 10.35 (6.62–889.35)	39.47 $\pm$ 7.83 (7.95–763.11)
$N$	115	108	109	105

<sup>a</sup>Practical salinity units.

occasions per site that would provide reasonable standard errors (i.e.,  $SE < 0.10$ ).

Fish were collected with a beach seine by using protocols consistent with juvenile fish surveys in Chesapeake Bay (Durell and Weedon 2009; Machut and Fabrizio 2009). The beach seine (30.5 m long  $\times$  1.2 m tall with 0.63-cm mesh) was deployed within 2 h 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 the residual flow and then back to shore. At some sites, excessive mud or deep water prohibited sampling with a fully extended net. Age-0 striped bass and yearling Atlantic croakers were counted, measured to the nearest millimeter (fork length for striped bass, total length for Atlantic croakers), and returned to the water.

At each sampling occasion, salinity, turbidity, and water temperature were recorded every 20 s with a multiparameter sonde (YSI 6920V2). Mean water temperature in early summer was greater than that during late summer (Table 1). Salinities ranged from 0.03 practical salinity units (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 nephelometric turbidity units (NTU) (Table 1). We also recorded weather conditions (clear, partly cloudy, or overcast–rain) at the time of sampling and the maximum distance (meters) the net was deployed from the shore (effective net length). 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 thought to contribute to variation in detectability of age-0 striped bass (Hewitt et al. 2008).

*Occupancy modeling.*—Like all models, occupancy models are fitted to data under certain assumptions. Those assumptions are as follows: (1) the occupancy of a site is constant within a study period (site closure), (2) sites are independent, and

(3) heterogeneity in occupancy and detection probabilities are explained by measured covariates (MacKenzie et al. 2006). Results from a tagging study with age-0 striped bass in the Mattaponi and Pamunkey rivers suggested that fish rarely move among sites within a 3-week sampling period in early or late summer and the site closure assumption is not violated (Williams 2010). Intersite movements of Atlantic croakers were deemed unlikely because yearling Atlantic croakers exhibit a high degree of site fidelity during summer (Miller et al. 2003). Because our study sites were separated by several kilometers, the site independence assumption seemed reasonable for all three species.

Factors hypothesized to affect occupancy and detection probabilities were treated as model covariates (Table 2). Site-specific covariates characterized the physical or relative condition of the sites (e.g., substrate or mean summer temperature), whereas sample-specific covariates characterized 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 each 3-week period.

Site-specific covariates included year, river (Pamunkey or Mattaponi), substrate (mud, hard bottom, or combination), beach slope, period (early versus late summer), mean water temperature, mean turbidity, and mean salinity. Site-specific means were calculated as the average value across the 12 sampling occasions per 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 modeled with period (early versus late summer) as a covariate. We 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 (six 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

TABLE 2. Factors postulated to affect occupancy ( $\Psi$ ) and detection ( $p$ ) probabilities for age-0 striped bass, yearling Atlantic croakers, and spottail shiners collected from the Mattaponi and Pamunkey rivers in 2008 and 2009. Substrate type was either sand, mud, or a combination, and period of sampling was early or late summer. "None" indicates factors that were not included as model covariates for a given parameter;  $i$  designates an individual sampling event. The abbreviations in parentheses are used in subsequent tables; DIST is also a measure of effective net length.

Factor	Effect on $\Psi$	Effect on $p$
Year (YR)	Year	Year
River (RV)	River	River
Substrate (SUB)	Substrate type	Substrate type
Slope (SL)	Slope of the beach	Slope of the beach
Period (PD)	Period of sampling	Period of sampling
Water temperature (TEMP)	Average water temperature at a site during a year	Water temperature at time of sampling
Turbidity (TURB)	Average turbidity at a site during a year	Turbidity at time of sampling
Salinity (SAL)	Average salinity at a site during a year	Salinity at time of sampling
Weather (WEA)	None	Weather at time of sampling
Distance from shore (DIST)	None	Maximum distance seine is deployed from shore
Fish length (LEN)	None	Average length of fish captured
Within-period sampling order (T1)	None	Order of sampling within a period ( $i = 1, 2, \dots, 6$ )
Within-year sampling order (T2)	None	Order of sampling within a year ( $i = 1, 2, \dots, 12$ )

assume a distinct detection probability (12 estimated  $p$ -values per year) and provided maximum flexibility in the estimation of detection probabilities.

Because different factors may influence occupancy and detection probabilities in the early- and late-summer periods, we used a multiseason occupancy model to estimate these probabilities in each period (early or late summer; MacKenzie et al. 2006). The multi-season occupancy model incorporates an estimate of colonization ( $\gamma$ ), the probability that an unoccupied site becomes occupied during the time between sampling periods. The model likelihood of the multiseason model takes the form

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

(MacKenzie et al. 2006). Models that incorporated covariates of colonization rarely converged, so we restricted our models to those that held colonization constant.

We fitted the models to the detection histories for each species by using the two-step approach described by MacKenzie et al. (2005) and used by Bailey et al. (2004). 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 presence/absence data are likely to be explained by this parameter (Bailey et al. 2004). We considered only additive effects of covariates because more complex relationships seemed unwarranted given the small number of sites we sampled and the likely loss of precision. The "best" model was selected by using  $AIC_c$ , a modification of Akaike's information criterion (AIC) corrected for small sample sizes (Burnham and Anderson 2002). The best model (the model with the lowest  $AIC_c$  value) from this step was used to identify the factors affecting  $p$ . Next, we constructed a suite of models by including the factors identified in step 1, as well as candidate factors for occupancy. All resulting models from step 2 were compared with the best overall model by calculating the difference in the  $AIC_c$  values,  $\Delta AIC_c$ . Models with  $\Delta AIC_c$  values from 0 to 2 are considered to have substantial support, those with  $\Delta AIC_c$  values from 4 to 7 have considerably less support, and those with  $\Delta AIC_c$  values greater than 10 are not supported by the data (in the tables that follow, we present only those models with  $\Delta AIC_c$  values less than 10; Burnham and Anderson 2002). Additionally,  $AIC_c$  weights can be used for model selection (MacKenzie et al. 2006). An  $AIC_c$  weight is interpreted 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). We estimated  $AIC_c$  weights to determine the level of support for a given covariate; when multiple models contained a single covariate, the level of support for that covariate was determined by summing the model weights of all models that included that covariate (Burnham and Anderson 2002). Model-averaged estimates of detectability and occupancy were calculated when several models were plausible, which allowed us to draw appropriate inferences (Burnham and Anderson 2002; MacKenzie et al. 2006). All modeling was performed with the program PRESENCE (Hines 2006).

## RESULTS

### Striped Bass

Detection probabilities for age-0 striped bass varied markedly, ranging from 0.096 to 1.0. Factors that best explained variation in  $p$  for age-0 striped bass were the distance from shore that the seine was deployed (effective net length), mean water temperature, and weather conditions at the time of sampling (Table 3). The model that included these three factors as covariates of  $p$  had an  $AIC_c$  weight of 0.895; however, the summed  $AIC_c$

TABLE 3. Models considered for identification of factors affecting the detectability of age-0 striped bass collected during summer 2008 and 2009 in the Mattaponi and Pamunkey rivers. Occupancy probabilities ( $\Psi$ ) and the probability of colonization ( $\gamma$ ) were held constant (represented by periods within parentheses). Models were ranked according to the Akaike information criterion corrected for small sample size ( $AIC_c$ );  $AIC_c$  weights and the number of estimated parameters ( $K$ ) are also reported. The factors considered in the models are from Table 2. For clarity, we omitted models with  $\Delta AIC_c$  values  $\geq 10$ .

Model	$AIC_c$	$\Delta AIC_c$	$AIC_c$ weight	$K$
$\Psi(\cdot)\gamma(\cdot)p(\text{DIST}+\text{TEMP}+\text{WEA})$	212.71	0.00	0.8954	6
$\Psi(\cdot)\gamma(\cdot)p(\text{DIST}+\text{TEMP}+\text{TURB})$	218.63	5.92	0.0464	6
$\Psi(\cdot)\gamma(\cdot)p(\text{DIST}+\text{TEMP})$	219.90	7.19	0.0246	5
$\Psi(\cdot)\gamma(\cdot)p(\text{DIST}+\text{TEMP}+\text{LEN})$	222.36	9.65	0.0072	6
$\Psi(\cdot)\gamma(\cdot)p(\text{DIST}+\text{TEMP}+\text{SL})$	222.58	9.87	0.0064	6
$\Psi(\cdot)\gamma(\cdot)p(\text{DIST}+\text{TEMP}+\text{YR})$	222.64	9.93	0.0062	6
$\Psi(\cdot)\gamma(\cdot)p(\text{DIST}+\text{TEMP}+\text{SUB})$	222.68	9.97	0.0061	6
$\Psi(\cdot)\gamma(\cdot)p(\text{DIST}+\text{TEMP}+\text{RV})$	222.68	9.97	0.0061	6

weights for effective net length and mean water temperature at the time of sampling was 0.999, which suggested these two factors alone are major determinants of detectability for age-0 striped bass.

The top-ranked occupancy model for striped bass, which included effective net length, mean water temperature at the time of sampling, and weather conditions to model the heterogeneity in  $p$  [ $\Psi(\cdot)\gamma(\cdot)p(\text{distance} + \text{temperature} + \text{weather})$ , where “ $\cdot$ ” denotes a constant; Table 4] indicated that occupancy did not vary during our study. However, our data also supported the notion that occupancy probabilities were influenced by beach slope, sampling period (early or late summer), and river (Table 4). We found less support for mean salinity and turbidity at a site affecting striped bass occupancy (Table 4).

Because all five candidate models were plausible (Table 4), model averaging was used to estimate detection and occupancy probabilities for age-0 striped bass. Detectability of

TABLE 4. Models considered for estimating occupancy probabilities for age-0 striped bass collected during summer 2008 and 2009 in the Mattaponi and Pamunkey rivers. The top-ranked models for estimated occupancy and detection probabilities were  $\text{logit}(\Psi_i) = 20.82$  and  $\text{logit}(p_{ij}) = -12.51 + 0.06\text{DIST} + 0.45\text{TEMP} + 0.18\text{WEA}$ . See Table 3 for additional details.

Model	$AIC_c$	$\Delta AIC_c$	$AIC_c$ weight	$K$
$\Psi(\cdot)\gamma(\cdot)p(\text{DIST}+\text{TEMP}+\text{WEA})$	212.71	0.00	0.4465	6
$\Psi(\text{SL})\gamma(\cdot)p(\text{DIST}+\text{TEMP}+\text{WEA})$	214.08	1.37	0.2251	7
$\Psi(\text{PD})\gamma(\cdot)p(\text{DIST}+\text{TEMP}+\text{WEA})$	215.05	2.34	0.1386	7
$\Psi(\text{RV})\gamma(\cdot)p(\text{DIST}+\text{TEMP}+\text{WEA})$	215.20	2.49	0.1286	7
$\Psi(\text{SAL}+\text{TURB})\gamma(\cdot)$	216.68	3.97	0.0613	8
$p(\text{DIST}+\text{TEMP}+\text{WEA})$				

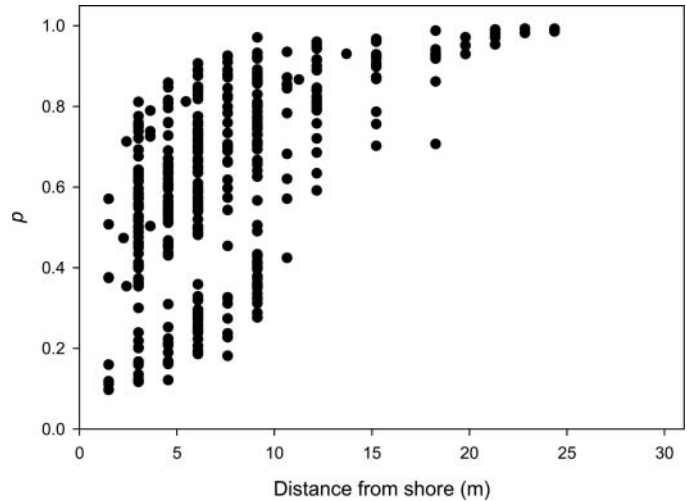


FIGURE 2. Relationship between estimated detection probability ( $p$ ) and effective net length (distance from shore that the seine was deployed) for age-0 striped bass captured by beach seine in summer 2008 and 2009 in the Mattaponi and Pamunkey rivers. Estimates of  $p$  were obtained from the model  $\Psi(\cdot)\gamma(\cdot)p(\text{Dist}+\text{Temp}+\text{Wea})$  (Table 3).

age-0 striped bass increased with increasing effective net length (Figure 2), and decreased as mean water temperatures declined in the river (Figure 3). 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 condition was small and estimated with poor precision (Table 5). Although, on average, detectability was moderate ( $p = 0.624$ ,  $SE = 0.058$ ), striped bass were

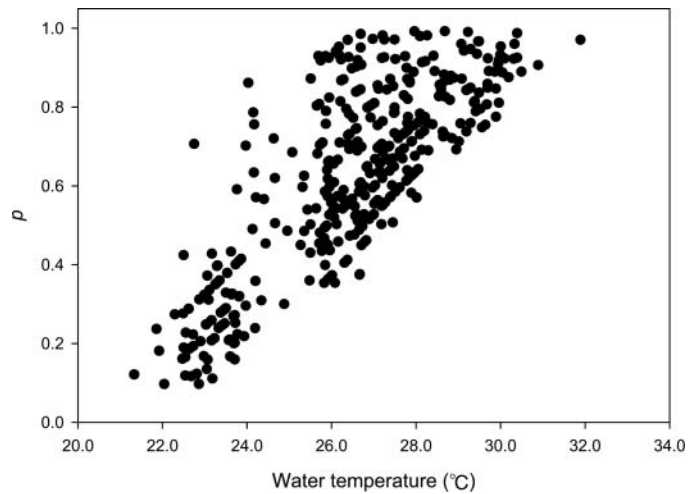


FIGURE 3. Relationship between estimated detection probability ( $p$ ) and water temperature at the time of sampling for age-0 striped bass captured by beach seine in summer 2008 and 2009 in the Mattaponi and Pamunkey rivers. Estimates of  $p$  were obtained from the model  $\Psi(\cdot)\gamma(\cdot)p(\text{Dist}+\text{Temp}+\text{Wea})$  (Table 3).

TABLE 5. Estimates and associated standard errors of covariate effects on occupancy ( $\Psi$ ) and detection ( $p$ ) probabilities from the top-ranked models for age-0 striped bass (Table 4), yearling Atlantic croakers (Table 6), and spottail shiners (Table 8). Asterisks indicate standard errors that are unusually large and associated with occupancy and detection probability estimates of 0.00 or 1.00.

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

likely to occupy nearly all sampled locations ( $\Psi = 0.993$ , SE = 0.012).

**Atlantic Croakers**

Three factors best explained the variation in detection probabilities for yearling Atlantic croakers: effective net length, whether sampling occurred in early or late summer (sampling period), and mean water temperature at the time of sampling. The model that included these factors had an  $AIC_c$  weight of 0.999; although we examined 19 other models, no other factors adequately modeled heterogeneity in  $p$ .

The top-ranked occupancy model indicated that Atlantic croaker occupancy varied with sampling period and mean site salinity [ $\Psi(\text{period} + \text{salinity}) \gamma(\cdot) p(\text{distance} + \text{period} + \text{temperature})$ ; Table 6]. Although the  $AIC_c$  weight for this model was 0.861, the six models we fitted to the data were within 10  $AIC_c$  units and thus plausible (Table 6). Model-averaged estimates of detection probabilities for Atlantic croakers were greater during early summer ( $p = 0.727$ , SE = 0.052) than during late summer ( $p = 0.375$ , SE = 0.067) by a factor of two. Within each period, detection probabilities were positively related to the effective net length and negatively related to mean water temperature at the time of sampling (Figures 4, 5). Yearling Atlantic croakers occupied more sites in early summer ( $\Psi = 1.0$ , SE = 0.001) than in late summer ( $\Psi = 0.863$ , SE = 0.083), when occupancy was restricted to sites with mean site salinities greater than 2.0 psu (Figure 6).

TABLE 6. Models considered for estimating occupancy probabilities for yearling Atlantic croakers collected during summer 2008 and 2009 in the Mattaponi and Pamunkey rivers. No other covariates or combination of covariates provided plausible models (i.e.,  $\Delta AIC_c \geq 10$ ) of the heterogeneity in  $p$ . The top-ranked models for estimated occupancy and detection probabilities were  $\text{logit}(\Psi_i) = 18.78PD1 - 2.71PD2 + 4.61SAL$  and  $\text{logit}(p_{ij}) = 0.03DIST + 5.98PD1 + 3.82PD2 - 0.20TEMP$ , where PD1 is early summer and PD2 is late summer. See Table 3 for additional details.

Model	$AIC_c$	$\Delta AIC_c$	$AIC_c$ weight	$K$
$\Psi(PD+Sal)\gamma(\cdot) p(DIST+PD+PD+TEMP)$	245.87	0.00	0.8612	8
$\Psi(\cdot)\gamma(\cdot) p(DIST+PD+TEMP)$	250.97	5.10	0.0672	6
$\Psi(PD+TURB)\gamma(\cdot) p(DIST+PD+TEMP)$	252.79	6.92	0.0271	8
$\Psi(TURB)\gamma(\cdot) p(DIST+PD+TEMP)$	253.46	7.59	0.0194	7
$\Psi(SL)\gamma(\cdot) p(DIST+PD+TEMP)$	253.93	8.06	0.0153	7
$\Psi(PD+SL)\gamma(\cdot) p(DIST+PD+TEMP)$	254.81	8.94	0.0099	8

**Spottail Shiners**

Estimated detection probabilities for spottail shiners ranged from 0.315 to 1.0 and varied with effective net length, sampling period (early versus late summer), and mean turbidity at the time of sampling [ $\Psi(\cdot) \gamma(\cdot) p(\text{distance} + \text{period} + \text{turbidity})$ ; Table 7]. Of the 19 models considered, only one other model was plausible; this model suggested that the effective net length,

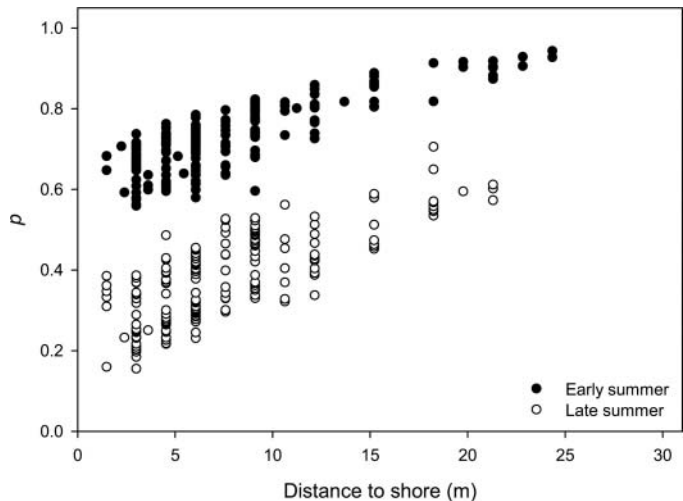


FIGURE 4. Relationship between estimated detection probability ( $p$ ) in early and late summer and effective net length (distance from shore that the seine was deployed) for yearling Atlantic croakers captured by beach seine in 2008 and 2009 in the Mattaponi and Pamunkey rivers. Estimates of  $p$  were obtained from the model  $\Psi(Pd+Sal.)\gamma(\cdot)p(Dist+Pd+Temp)$  (Table 6).



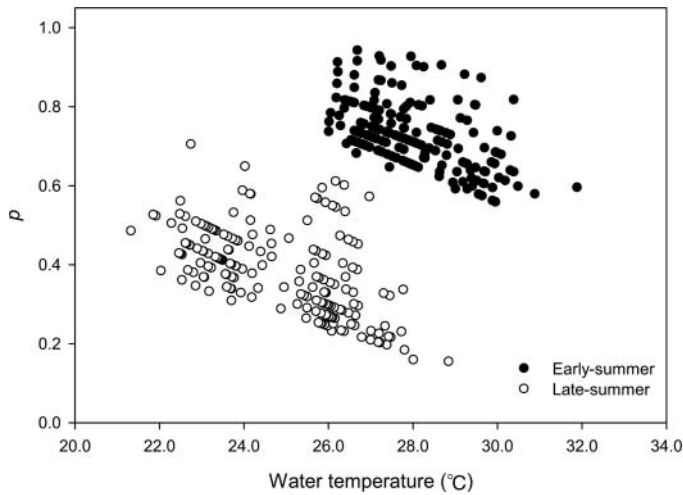


FIGURE 5. Relationship between estimated detection probability ( $p$ ) in early and late summer and mean water temperature at the time of sampling for yearling Atlantic croakers captured by beach seine in early and late summer 2008 and 2009 in the Mattaponi and Pamunkey rivers. Estimates of  $p$  were obtained from the model  $\Psi(\text{Pd}+\text{Sal})\gamma(\cdot)p(\text{Dist}+\text{Pd}+\text{Temp})$  (Table 6).

sampling period, and mean water temperature at the time of sampling best explained variation in detectability of spottail shiners (Table 7). Based on model weights, mean turbidity is more likely to influence the detectability of spottail shiners than mean water temperature (Table 7).

The top-ranked occupancy model for spottail shiners suggested that occupancy probabilities were most influenced by river [ $\Psi(\text{river})\gamma(\cdot)p(\text{distance} + \text{period} + \text{turbidity})$ ; Table 8]; this factor occurred in the top six models considered here (summed  $\text{AIC}_c$  weight = 0.923; Table 8). Occupancy was greater in the Pamunkey River ( $\Psi = 0.822$ ,  $\text{SE} = 0.095$ ) than in the Mattaponi River ( $\Psi = 0.362$ ,  $\text{SE} = 0.110$ ). Slope of the

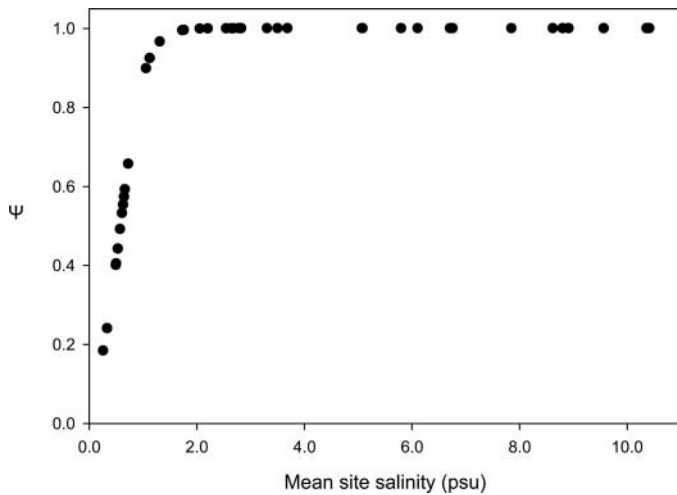


FIGURE 6. Relationship between estimated occupancy probability ( $\Psi$ ) in late summer and mean site salinity for yearling Atlantic croakers captured by beach seine in 2008 and 2009 in the Mattaponi and Pamunkey rivers. Estimates of  $\Psi$  were obtained from the model  $\Psi(\text{Pd}+\text{Sal})\gamma(\cdot)p(\text{Dist}+\text{Pd}+\text{Temp})$  (Table 6).

TABLE 7. Models considered for estimating detection probabilities for spottail shiners collected during summer 2008 and 2009 in the Mattaponi and Pamunkey rivers. See Table 3 for additional details.

Model	$\text{AIC}_c$	$\Delta\text{AIC}_c$	$\text{AIC}_c$ weight	$K$
$\Psi(\cdot)\gamma(\cdot)p(\text{DIST}+\text{PD}+\text{TURB})$	140.71	0.00	0.6964	6
$\Psi(\cdot)\gamma(\cdot)p(\text{DIST}+\text{PD}+\text{TEMP})$	142.37	1.66	0.3036	6

beach and substrate type were also identified as factors that influenced occupancy probabilities, although the summed  $\text{AIC}_c$  weight for each of these factors was less than 0.160 (Table 8).

Because several candidate models were plausible, model averaging was used to estimate detection probabilities for spottail shiners during early summer ( $p = 0.515$ ,  $\text{SE} = 0.130$ ) and late summer ( $p = 0.846$ ,  $\text{SE} = 0.070$ ). Estimated detection probabilities for spottail shiners were greater in late summer than in early summer, with a difference in  $p$  of about 0.35. The same relationship between detection probabilities and effective net length was found for spottail shiners as was found for striped bass and Atlantic croakers; detection probabilities increased with increasing effective net length (Figure 7). Regardless of sampling period, detection probabilities for spottail shiners improved as mean turbidity increased. When mean turbidity during a sampling event was greater than 150 NTU, detection probabilities were nearly always greater than 0.80 (Figure 8).

DISCUSSION

Detection probabilities varied among species and between early- and late-summer sampling periods, reflecting variation in

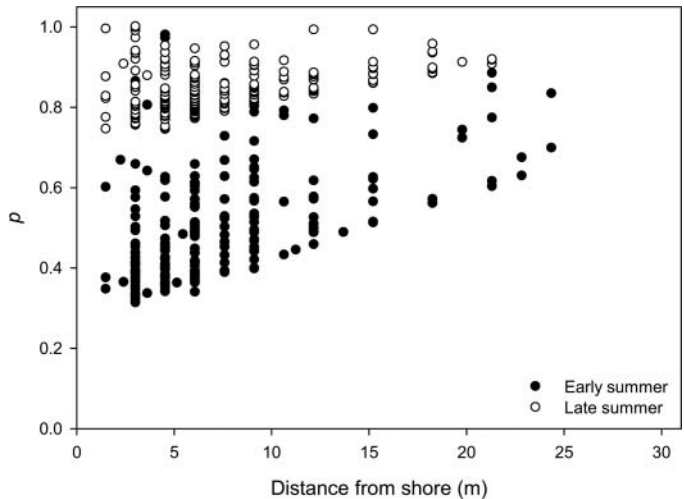


FIGURE 7. Relationship between estimated detection probability ( $p$ ) and effective net length (distance from shore that the seine was deployed) for spottail shiners captured by beach seine in early and late summer 2008 and 2009 in the Mattaponi and Pamunkey rivers. Estimates of  $p$  were obtained from the model  $\Psi(\text{Rv})\gamma(\cdot)p(\text{Dist}+\text{Pd}+\text{Turb})$  (Table 8).

TABLE 8. Models considered for estimating occupancy probabilities for spottail shiners collected during summer 2008 and 2009 in the Mattaponi and Pamunkey rivers. The top-ranked models for estimated occupancy and detection probabilities were  $\text{logit}(\Psi_i) = 1.53 - 2.10RV$  and  $\text{logit}(p_{ij}) = 0.02\text{DIST} - 1.11\text{PD1} + 0.68\text{PD2} + 0.02\text{TURB}$ . See Table 3 for additional details.

Model	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	AIC <sub>c</sub> weight	K
$\Psi(RV)\gamma(.) p(\text{DIST} + \text{PD} + \text{TURB})$	135.44	0.00	0.3224	7
$\Psi(RV + \text{SL})\gamma(.) p(\text{DIST} + \text{PD} + \text{TURB})$	136.89	1.45	0.1562	8
$\Psi(RV + \text{SUB})\gamma(.) p(\text{DIST} + \text{PD} + \text{TURB})$	137.22	1.78	0.1324	8
$\Psi(YR + RV)\gamma(.) p(\text{DIST} + \text{PD} + \text{TURB})$	137.35	1.91	0.1241	8
$\Psi(\text{PD} + RV)\gamma(.) p(\text{DIST} + \text{PD} + \text{TURB})$	137.69	2.25	0.1047	8
$\Psi(RV + \text{TEMP})\gamma(.) p(\text{DIST} + \text{PD} + \text{TURB})$	138.14	2.70	0.0836	8
$\Psi(.)\gamma(.) p(\text{DIST} + \text{PD} + \text{TURB})$	140.71	5.27	0.0231	6
$\Psi(\text{PD})\gamma(.) p(\text{DIST} + \text{PD} + \text{TURB})$	142.18	6.74	0.0111	7
$\Psi(YR)\gamma(.) p(\text{DIST} + \text{PD} + \text{TURB})$	142.65	7.21	0.0088	7
$\Psi(\text{SL})\gamma(.) p(\text{DIST} + \text{PD} + \text{TURB})$	143.25	7.81	0.0065	7
$\Psi(\text{TEMP})\gamma(.) p(\text{DIST} + \text{PD} + \text{TURB})$	143.39	7.95	0.0061	7
$\Psi(\text{SUB})\gamma(.) p(\text{DIST} + \text{PD} + \text{TURB})$	143.40	7.96	0.0060	7
$\Psi(YR + \text{PD})\gamma(.) p(\text{DIST} + \text{PD} + \text{TURB})$	144.56	9.12	0.0034	8
$\Psi(\text{PD} + \text{SUB})\gamma(.) p(\text{DIST} + \text{PD} + \text{TURB})$	145.05	9.61	0.0026	8
$\Psi(YR + \text{SL})\gamma(.) p(\text{DIST} + \text{PD} + \text{TURB})$	145.39	9.95	0.0022	8
$\Psi(YR + \text{SUB})\gamma(.) p(\text{DIST} + \text{PD} + \text{TURB})$	145.40	9.96	0.0022	8

the availability of fish, behavioral responses to the gear, and environmental factors. Detectability of age-0 striped bass, yearling Atlantic croakers, and spottail shiners was influenced by both gear-related factors (i.e., effective net length) and environmental conditions at the time of sampling (e.g., mean water temperature, mean turbidity). For the three species considered in this study, effective net length (the maximum distance from shore that the seine was deployed) was an important determinant of detection probabilities; this distance was a measure of the area

sampled. As 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 fish greater than 100 mm in length (Říha et al. 2008). In this study, the average length of yearling Atlantic croakers 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 age-0 striped bass and yearling Atlantic croakers 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, we 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 croakers and spottail shiners, but the direction of change varied with species. The decline in detection that occurred in late summer for yearling Atlantic croakers may reflect the fact that, in late summer, fish are larger and better able to avoid capture by the seine. The decline in detection could also be due to violations of the closure assumption, because juvenile Atlantic croakers may have moved out of the sampling area as the summer progressed. In New Jersey, juvenile Atlantic croakers emigrated from tidal marsh creeks in September and October (Miller and Able 2002). This out-migration may have occurred during, but not before, our late-summer sampling period in Virginia, thus violating the closure assumption. When this occurs, estimates of occupancy are high and estimates of

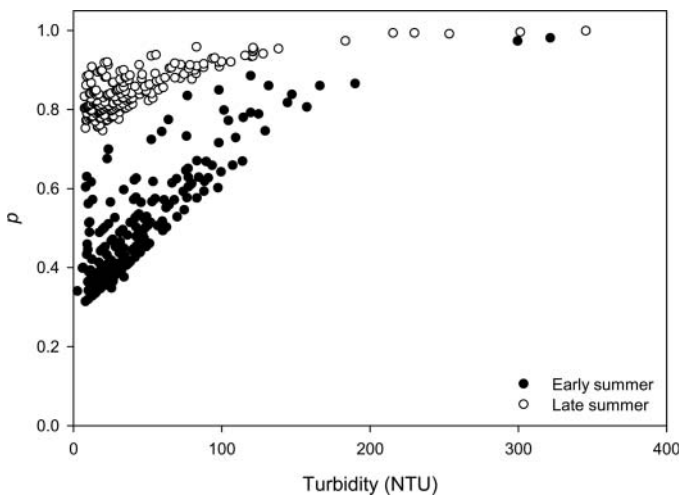


FIGURE 8. Relationship between estimated detection probability ( $p$ ) in early and late summer and turbidity at the time of sampling for spottail shiners captured by beach seine in 2008 and 2009 in the Mattaponi and Pamunkey rivers. Estimates of  $p$  were obtained from the model  $\Psi(RV)\gamma(.)p(\text{Pd} + \text{Dist} + \text{Turb})$  (Table 8).

detection probabilities are low, a pattern consistent with what we observed in late summer for this species.

Unlike with Atlantic croakers, spottail shiner detection probabilities increased in late summer. We 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 (Jenkins and Burkhead 1994) and may not have been fully recruited to the sampling gear by early summer (July). By late summer, juveniles are expected to be fully recruited and available to the gear. In addition, data from the Virginia seine survey indicate that relative abundance of spottail shiners generally increases later in the summer, which supports the notion that increases in local abundance could also result in greater detection probabilities. Our 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 croakers 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 fish (e.g., fyke nets, traps).

Mean water temperature at the time of sampling influenced the detectability of both age-0 striped bass and yearling Atlantic croakers during 2008 and 2009, but detectability varied among species. Optimal growth of age-0 striped bass occurs between 28.0°C 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 we sampled. Unlike age-0 striped bass, the detectability of yearling Atlantic croakers was negatively correlated with mean water temperature, but we believe that 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 croakers were high because fish were more vulnerable to capture owing 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 age-0 striped bass were higher on clear, sunny days than on days with cloud cover. We expected that a visual feeder such as age-0 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 in shallow, nearshore areas may have outweighed the risk of capture. Individuals that use 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 in situ light intensity 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 we observed in late summer for this species. 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). We postulate that escape behaviors of spottail shiners were less effective in turbid waters, which may explain the positive relationship between turbidity and detection probabilities we observed.

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 croakers and spottail shiners exhibited temporal and geographic variation. Although beach slope, mean site salinity, and mean site turbidity may affect age-0 striped bass occupancy, additional studies that include more unoccupied sites are needed to reveal these relationships. Yearling Atlantic croakers 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. This may indicate that fish exhibited decreased tolerance for low salinity (<2 psu) habitats as they completed their first summer of life, or that suitability of these low salinity habitats changed in late summer (e.g., alteration in prey quantity or quality). Based on observed occupancy, the Pamunkey River provided more suitable habitat for spottail shiners than did the Mattaponi River. Catch data from the Virginia seine survey indicate that spottail shiners are more abundant in the Mattaponi River than in the Pamunkey River (M. C. Fabrizio, personal observation). Together, these results imply that in the Pamunkey River, spottail shiners are less aggregated (lower site-specific abundances) and more evenly distributed among the habitats that we sampled.

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. Unfortunately, availability is difficult to quantify, particularly for juvenile fish. The effects of environmental factors and habitat characteristics on small-scale fish movements could be explored to better understand availability of juvenile fish to sampling gears. These individual fish movements may be examined with telemetry, hydroacoustics, or other emergent technologies.

The results from this study can be used to inform the design of fish surveys in Chesapeake Bay tidal tributaries, regardless of sampling gear. Although we recommend incorporation of repeat-sampling events to permit estimation of detection probabilities, particularly for habitat-use studies, we 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 with 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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