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Habitat Selection by Juvenile Striped Bass in Lower Chesapeake Bay Tributaries:
Inferences from Occupancy Models

Photo by Julia Ellis

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Contents

Executive Summary

1. Designations of nursery areas for juvenile fishes should rely on rigorous quantitative assessments of the *relative* value of available habitats, where value is determined by the *selection* of habitats by the species of interest.

2. Habitat analyses based on catches from standard fixed-station surveys provide weak inferences because they fail to account for nonrandom site selection and variation in species detectability. Detectability – the conditional probability that the target species will be captured given that it is present – has been largely ignored in habitat studies, but is critical to inference.

3. Data from surveys that sample fixed sites repeatedly within a relatively short time frame can be used in a new class of models – occupancy models – that account for detectability and permit solid inferences about habitat selection.

4. We used multi-state occupancy models and data from the Virginia Institute of Marine Science juvenile striped bass seine survey to assess habitat selection by juvenile striped bass in Virginia tributaries of the lower Chesapeake Bay.

5. We developed hypotheses about the relationships between site occupancy and various habitat variables based on the biology and ecology of juvenile striped bass, and evaluated the hypotheses in a model selection framework while specifically accounting for variation in detectability.

6. Detectability was high overall, but was substantially higher for sites where more than 10 individuals were collected ($\geq 95\%$) than for sites where 10 or fewer individuals were collected (70-79%). Detectability at sites where fewer than 10 individuals were collected declined through the sampling season, consistent with expectations that the ability of fish to escape increases as they grow. Detectability estimates were consistently less than 100%, reinforcing the importance of accounting for detectability in modeling habitat selection.

7. The effects of habitat variables on detectability were mostly small and unimportant. The only variable that was included in selected models was the bank slope. Detectability was higher at sites with greater slopes, in contrast to expectations that detectability would be lower at sites with shorter distances to deep water.

8. As expected, site occupancy probabilities were higher in years with above average spring precipitation (> 15 inches) than in years with below average precipitation (< 15 inches), and this effect was included in all selected models. Occupancy probabilities were higher for sites where 10 or fewer individuals were collected ($> 85\%$) than for sites where more than 10 individuals were collected (40-63%), indicating that most sites in our study tributaries host a small number of individuals and only select sites host large numbers of individuals.

9. In addition to the effect of spring precipitation, model selection results indicated that salinity was the only habitat variable important for modeling heterogeneity in site occupancy. Sites in areas of lower salinity were far more likely to host striped bass, and host them in higher abundance, than sites in higher salinity areas. This effect may be partly attributable to the fact that lower salinity areas are closer to striped bass spawning areas. Further work with occupancy models could include stratifying sites by salinity regime in order to refine assessments of the effects of other habitat variables on occupancy probabilities at a smaller scale.

Introduction

The importance of habitat

Much current ecological research focuses on the availability, quality, and importance of habitat to various life stages of animals. For example, the designation and protection of essential fish habitat (EFH) is now a mandated process in the management of marine and estuarine species in the U.S., with far-reaching and multifaceted implications (Benaka 1999). The concept of essential fish habitat links fish stock productivity with the maintenance of healthy habitats and has pushed single-species management toward an ecosystem-based, conservation-oriented approach (Rosenberg *et al.* 2000). The need to protect EFH is woven into recent concerns about the effects of various fishing activities on benthic habitats (Barnes & Thomas 2005). Research into essential fish habitat for juvenile life stages often focuses on delineating nursery areas – areas that are considered critical to juvenile survival and subsequent recruitment to the adult population.

Designation of EFH for adults and delineation of nursery areas for juveniles both depend on assumptions about what constitutes an *essential* habitat or provides characteristics of a *nursery*. Beck *et al.* (2001) review the history of the nursery concept for nearshore marine and estuarine species and note the ongoing struggle to clearly define the characteristics of nurseries. Early studies defined nurseries as areas that harbored higher densities of organisms than other nearby habitats; however, relative density has been shown to be an unreliable measure of relative habitat quality (Van Horne 1983; Rosenfeld 2003).

Focus of juvenile habitat research

Ideally, research on juvenile habitats focuses on the contribution of habitats to the primary components of fish production – growth, survival, and successful movement to adult habitats. Such research should ultimately identify habitats that contribute disproportionately to the adult population (Beck *et al.* 2001). However, the amount of resources required to study the various components of production simultaneously at reasonable spatial scales is often prohibitive, even for a single species. Survival rates in particular are notoriously difficult to estimate, although recent advances in technology have shown promise in small-scale studies (Adams *et al.* 2006). Production is difficult to measure at higher trophic levels, but stable isotopes may be useful for linking habitat to production as well as for monitoring the movement of juveniles into adult populations (Wainright *et al.* 1996; Hoffman *et al.* 2007). Comprehensive studies of the importance of various habitats for juvenile life stages are often

not feasible, and researchers often infer habitat importance by comparing the occurrence or abundance of target animals among available habitats.

We distinguish among habitat use, habitat selection, habitat preference, and habitat requirements following conventions in Rosenfeld (2003). Habitat *use* is an ambiguous term; it can simply imply the presence of an animal in some habitat at some point in time. Most studies of habitat use are distinguished from studies of distribution by their intention to demonstrate habitat *selection*, often resulting in a ranking of the habitats under study (i.e., some habitats being selected over others). Habitat selection is often inferred from snapshot observations of differential use (occupancy) of habitats in the field, or use that is disproportionate to availability. Such observations lack a mechanistic connection to habitat choice that differentiates selection from true *preference*. Habitat selection observed in the field can be considered *in situ* preference among the available habitats, but the suite of available habitats will always be limited by other factors. Furthermore, we concur with Rosenfeld (2003) that evidence for habitat selection falls short of demonstrating habitat *requirements*. Assessment of habitat requirements involves the fitness consequences of habitat use, a notion embedded in the concept of essential fish habitat. Nonetheless, field studies of habitat selection guided by *a priori* hypotheses that link the occurrence or abundance of animals to habitat features can provide inferences about the importance of various habitats.

Inferring the importance of habitats from survey data

In estuarine and coastal ecosystems, data from large-scale surveys are routinely used to identify environmental factors that influence the presence or abundance of fishes and invertebrates (Meng & Powell 1999; Wagner & Austin 1999; Bartol *et al.* 2002). However, the goals of fisheries surveys are typically more general, such as to describe the distribution of captured animals or to estimate indices of relative abundance (e.g., catch per unit effort, CPUE). The goals and fixed-station design of many standard fisheries surveys may conflict with the analytical goals of more specific investigations, making statistical inference difficult or impossible. Specifically, catch data (counts) from fisheries surveys are characterized by two problems related to survey design: [1] nonrandom and nonrepresentative site selection, and [2] imperfect detectability (Pollock *et al.* 2002; Tyre *et al.* 2003; MacKenzie 2005). Here, we focus on how site selection and detectability affect inferences about habitat selection based on catch data.

Site selection

Site selection in surveys is often restricted for logistical reasons, and limits the portion of the target population that is subject to capture. For example, seine surveys for juvenile striped bass are restricted to sites that are free of obstructions where the water is no deeper than about 120 cm. Similarly, trawl surveys are limited to areas that are deep enough for boat and trawl operation, which generally excludes water shallower than 120 cm. The inability to comprehensively sample both shallow and deep habitats restricts inferences about habitat to the portion of the population that is within the area that can be effectively sampled. Only supplemental comparative sampling can verify whether the sampled portion of the population is representative of the population as a whole. If a large enough portion of the population can be sampled, and there is no systematic difference between the portion of the population that is sampled and the portion that is not sampled, the bias introduced by partial sampling may be inconsequential to some analyses (e.g., indices of relative abundance).

A problem arises when the sampled portion of the population changes over time in a manner different from the unsampled portion or as a function of population density (Hubert & Fabrizio 2007). Catch data from the sampling effort would then partially reflect changes in distribution rather than changes in abundance, thus confounding inferences about habitat selection. Fish may be less abundant in a given habitat for reasons unrelated to the characteristics of the habitat itself.

Surveys of juvenile fish that sample across a relatively broad window of time target a population that is subject to constant change from growth and mortality (Rago *et al.* 1995). Cohorts of juveniles grow to a size at which they recruit to the habitats sampled by the gear and to the gear itself. During the same time, fish select habitats based on changing needs and a large portion of the cohort may succumb to natural mortality. All these factors are at work during the period of sampling and are added to the usual concerns about the effects of schooling behavior and gear selectivity on catches (Rago *et al.* 1995). As a result, catches from surveys that sample a restricted number of sites are difficult to use as a basis for inference about the population as a whole. Indeed, the population that is targeted by the sampling may be somewhat undefined and inconsistent through time.

When logistical restrictions on site selection are stringent, as in many beach seine surveys, the use of fixed sites is often necessary. The use of fixed sites introduces further concerns about the representativeness of the sampled population and concerns about the statistical basis of analyses. The characteristics of sites that can be sampled differ from sites that cannot be sampled. Discrepancies between sampled and unsampled sites may be particularly

problematic for studies of habitat selection if the sampled sites are not representative of the range of habitats available to the animal. Furthermore, without a random component to the selection of sampling sites, there is no basis for assessing the bias or accuracy of statistics calculated from the catch data (e.g., indices of relative abundance, Rago *et al.* 1995). Additional problems arise when sites are dropped or added to the "fixed" sampling frame.

Overall, inferences derived from survey data relate to the portion of the population that is subject to capture (i.e., not the entire population) and catches are difficult to interpret. Rago *et al.* (1995) concluded that it would be difficult to relate environmental variables (habitat) to site-specific catches from a fixed-station survey. We avoid some concerns about the interpretation of catch data by reducing the dimensionality of the data and focusing on site occupancy – whether the species selected the habitat or did not select the habitat. Nonetheless, our scope of inference is restricted to the portion of the juvenile striped bass population that is subject to capture at the fixed beach sites sampled by the seine survey.

Detectability

Detectability (p) is the conditional probability that an animal will be detected (here, captured) given that it is present at the site. Detectability can relate to the species as a whole (i.e., the probability of capturing at least one) or to individual animals (i.e., the probability of capturing any given animal). Where it relates to individual animals, detectability scales up synonymously with gear efficiency – the proportion of animals in an area that are captured. Many of the concerns about detectability are analogous to the concerns in fisheries about catchability, but catchability is a more complex issue (Ricker 1975; Arreguin-Sanchez 1996; Quinn & Deriso 1999). Wildlife scientists have struggled with detectability issues for some time (Thompson 2002; Williams *et al.* 2002), and designs for large-scale wildlife surveys routinely incorporate methods for estimating detectability (Pollock *et al.* 2002).

Based primarily on wildlife studies, Pollock *et al.* (2002) considered imperfect detectability ($p < 1.0$) to be a near-universal situation and suggested that detectability is rarely constant. Given similar convictions, Anderson (2001) argued that abundance indices uncorrected for detectability (e.g., CPUE) are simply poor foundations for inference and do not represent "data". MacKenzie (2005) described imperfect detection as a problem that must be addressed in most situations based on common sense.

The essential problem for survey data is that the probability of capturing an animal (or at least one animal) can vary among sites and over time, and the effects of changes in

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detectability are confounded with changes in observed catches. In almost all analyses based on survey data, catches (C; or CPUE) are interpreted as indices of local population size (N). The use of catch data in this manner requires the assumption that catch is proportional to the density, that animals occupy the same area, and that detectability is constant in both space and time; i.e., $C = pN$, where p is constant (Hubert & Fabrizio 2007). If detectability is not constant, catches at a given site can be larger because animals are easier to catch rather than because animals are more abundant. In fisheries surveys, we suspect that detectability will always be less than 1.0, as well as variable in space and time.

Pollock $et\ al.$ (2002) proposed three approaches for working with survey data in the face of imperfect and variable detectability:

1. Design the survey to ensure that detectability is constant over space and time;

2. Measure covariates that may influence detectability and attempt to remove changes in detectability by modeling the covariates;

3. Incorporate features in the survey design that allow detectability to be estimated (e.g., distance sampling or double sampling).

Despite the fact that detectability is often assumed to be constant, either explicitly or implicitly, we cannot envision any cases in fisheries surveys where approach [1] will be realistic. Approach [3] is the only approach that Pollock $et\ al.$ (2002) consider rigorous, and such an approach has been recommended by others (Tyre $et\ al.$ 2003; Gu & Swihart 2004; MacKenzie 2005). However, fisheries studies will need to adopt approach [2] until detectability becomes a focus in survey design. For example, considerable effort is expended in stock assessments to model the effects of covariates on catchability and remove trends in catchability from indices of abundance to derive so-called standardized CPUE (Collie & Sissenwine 1983; Maunder & Punt 2004).

The problem of individual detectability (capture efficiency) in fisheries surveys using seines has been recognized for over half a century, but has only recently gained general quantitative attention (Bayley & Herendeen 2000). Research using seines in streams, lakes, and tidal creeks has routinely shown that detectability can be low and highly variable among species and locations, and can be related to environmental conditions such as substrate type (Lyons 1986; Parsley $et\ al.$ 1989; Jennings 1991; Bayley & Herendeen 2000). Similarly, Peterson $et\ al.$ (2004) assessed detectability of stream-dwelling salmonids sampled with multipass electrofishing and called into question inferences based on removal estimates of abundance. They found that detectability varied with habitat characteristics and tended to decrease with

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subsequent passes, biasing estimates of abundance and inferences about habitat selection based on removal methods.

Overall, inferences about habitat selection from catch data will depend heavily on reliable estimation of, and correction for, detectability. Such estimation may not always be possible, but a solution that is appropriate in some circumstances is to reduce the data to presence/absence observations and estimate species-level detectability (MacKenzie *et al.* 2006). A key issue in presence/absence data has drawn considerable recent attention: the probability that observed absences (zero catches) do not represent true absences (Bayley & Peterson 2001; Tyre *et al.* 2003; Gu & Swihart 2004; MacKenzie 2005; MacKenzie *et al.* 2006). A species can be present at a site (probably in low numbers) but may not be captured, and the use of presence/absence data without accounting for this type of nondetection usually results in underestimates of site occupancy. Not surprisingly, Bayley & Peterson (2001) showed that species nondetection is a serious problem for seine sampling in streams. Accounting for nondetection is of particular importance to inferences that are made about habitat, as habitat features themselves can affect detectability (Gu & Swihart 2004; MacKenzie *et al.* 2006).

The estimation of the probability of nondetection is the focus of a relatively new class of models – occupancy models – that has developed rapidly in the last few years, primarily in the wildlife field (MacKenzie *et al.* 2006). Ball *et al.* (2005) provide an excellent example in a management context, and Donovan & Hines (2007) provide simple worked examples. The framework of occupancy modeling is a simple extension of capture-recapture models (Pollock *et al.* 1990) and provides a way to estimate detectability in a straightforward manner. The estimation procedure relies on repeated visits to the same sampling sites and a record of the presence or absence of the species at a site during each visit. In this study, we use occupancy models to make inferences about habitat selection by juvenile striped bass.

Striped bass recruitment in Chesapeake Bay

Recruitment of juvenile striped bass in tributary rivers of the Chesapeake Bay is evaluated as part of a coast-wide assessment program for striped bass coordinated by the Atlantic States Marine Fisheries Commission (ASMFC). Striped bass stocks along the East Coast crashed in the late 1970s and early 1980s, precipitating legislative and administrative actions that ultimately placed management oversight authority in the hands of ASMFC (Richards & Rago 1999). Annual surveys of juvenile striped bass abundance are conducted in states from North Carolina to Maine to generate juvenile relative abundance indices (JAIs) that inform management decisions. Surveys in the Chesapeake Bay are conducted with beach seines, as

are most of the surveys in other states (Rago *et al.* 1995). We use data from the Virginia Institute of Marine Science juvenile striped bass seine survey (hereafter, VIMS seine survey) in this analysis; the survey samples the major tributary rivers to the lower Chesapeake Bay in Virginia.

Since the late 1980s when the Chesapeake Bay spawning stock of striped bass began to recover, recruitment in Virginia rivers appears to have been positively correlated with the amount of spring precipitation [Figure 1; see also Wood (2000)]. Precipitation patterns have a strong influence on salinity, temperature, and turbidity conditions in the upper reaches of estuaries where larval striped bass are found. We developed hypotheses about the relationship between site occupancy and habitat variables based on the biology and ecology of juvenile striped bass. We assumed that striped bass select habitats to maximize their individual fitness and that individual habitat selection influences overall recruitment.
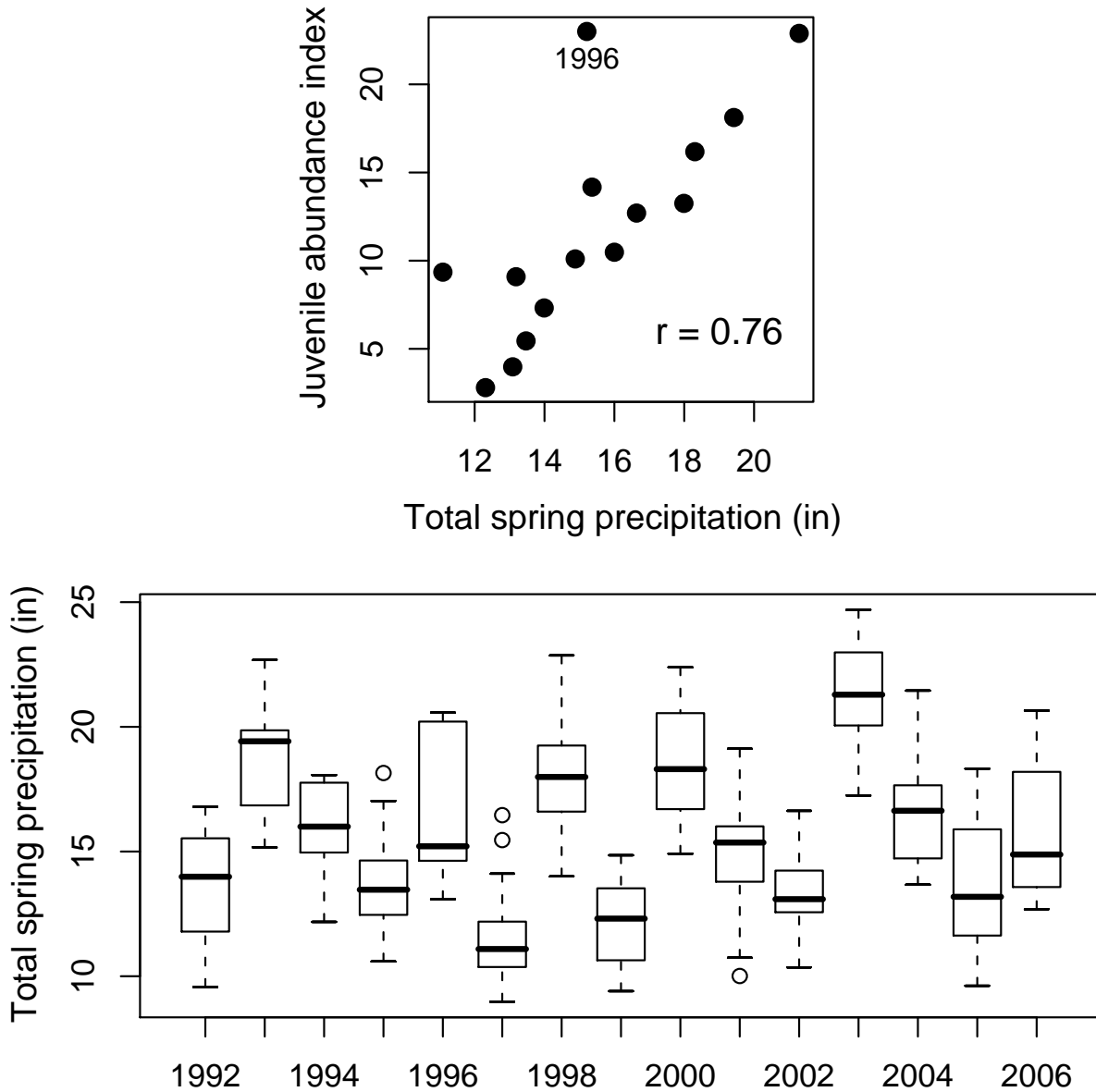
Figure 1: [TOP] The juvenile relative abundance index for striped bass calculated from the VIMS seine survey is positively correlated with total spring precipitation (March-June) in the Tidewater area of Virginia, 1992-2006. Annual juvenile abundance indices were taken from Hewitt *et al.* (2006) and precipitation data were obtained from the National Climatic Data Center (NCDC; `http://www.ncdc.noaa.gov/oa/climateresearch.html`). [BOTTOM] Boxplots of total spring precipitation were generated using all stations in the Tidewater division (01) of the NCDC database, but we only included records that were complete for all months (March-June). Boxplots in each year include data from 12-18 stations (mean = 16) and the annual medians are shown as dark horizontal bands in the boxplots. Annual medians are used as the precipitation values in the upper plot. If the outlier year (1996) is excluded, the correlation coefficient increases to 0.89.

Water quality (temperature and salinity)

The occurrence and extent of areas of low DO – hypoxia; DO < 2 mg/L – is a serious concern in the Chesapeake Bay (Kemp *et al.* 2005) and many other coastal ecosystems (e.g., the Gulf of Mexico). However, DO has exceeded 4 mg/L during most of our sampling (Figure 2) and striped bass are tolerant of DO as low as 3 mg/L (Coutant 1985). Therefore, we do not consider DO as a factor controlling habitat selection by juvenile striped bass.

Salinity plays a direct role in osmoregulation, and the development of euryhaline osmoregulatory capabilities appears to have evolved in concert with the evolution of an anadromous life history in striped bass. Salinity tolerance changes during ontogeny and is matched to the downstream transport of eggs, larvae, and juveniles into more saline portions of estuaries during growth and development. Based on a laboratory study, Secor *et al.* (2000) suggested that salinity and temperature should influence distribution (habitat selection) of striped bass juveniles in estuaries.

In Chesapeake Bay, adult striped bass spawn primarily in tidal freshwater reaches of rivers and eggs drift into upper estuarine areas by the time of hatching. The optimal range of salinity for egg survival appears to be between 0 and 9 ppt, and egg survival decreases rapidly with increasing salinity (Winger & Lasier 1994). After two days post-hatch, larvae require some amount of salinity (0 ppt is generally lethal), but can show substantially reduced survival at salinities above about 12 ppt. Older larvae are less sensitive to salinity and appear to survive best at moderate salinities (e.g., 6-18 ppt for larvae five days post-hatch).

Larvae and juveniles show increasing tolerance to salinity with age coincident with the maturity of euryhaline osmoregulatory capabilities (Winger & Lasier 1994). In the laboratory, Overton & Van Den Avyle (2005) found that survival, growth, and condition of 2 to 4.5 month old juveniles were relatively similar across salinities between 0 and 10 ppt, but Secor *et al.* (2000) noted increased mortality in salinities near freshwater conditions (0.5 ppt). Their results support the earlier findings of Bogenrieder (1997) that juvenile striped bass showed little preference for salinities between 5 and 15 ppt, but avoided freshwater (0 ppt). Similarly, Otwell & Merriner (1975) found that striped bass juveniles up to 2 months old were tolerant of salinities between 4 and 20 ppt, with some indication of a preference for higher salinities with increasing age. They concluded that fish less than one month old may prefer salinities below 20 ppt, but the evidence was not strong and temperature appeared to be more important (see also Krouse 1968). Secor *et al.* (2000) suggested that there was some evidence for increased growth performance of 1.5 to 3 month old juveniles at intermediate salinities (about 7 ppt), but the evidence was similarly weak. Hewitt *et al.* (2005) found

that growth of juvenile striped bass in Virginia appeared to be positively related to salinity (0-8 ppt; Figure 3).

Temperature optima for growth and survival also appear to be matched to the life history of striped bass. Egg hatching success and survival of two day post-hatch larvae are greatest between 16 and 20°C (Morgan *et al.* 1981), which generally coincides with water temperatures on the spawning grounds during spring in the Chesapeake Bay (Grant & Olney 1991). Metabolism and growth are generally greater at higher temperatures (Moyle & Cech 1996), but temperatures near upper or lower tolerance limits may reduce growth and survival. Juveniles in laboratory experiments showed high tolerance of temperatures between 18 and 24°C, but growth and survival were reduced at 12°C for fish less than one month old (Otwell & Merriner 1975). Overton & Van Den Avyle (2005) found faster growth rates at 28°C than at 25°C, and Secor *et al.* (2000) found that Chesapeake Bay striped bass juveniles grew faster at 28°C than at 20 or 24°C. In a laboratory experiment with much larger juveniles (> 60 g wet weight), Cox & Coutant (1981) found fastest growth rates between 24 and 26°C and noted that smaller juveniles were likely to have a higher optimal growth temperature. For larger juveniles, Cox & Coutant (1981) noted negative growth, increased mortality, and growth-related deformities at temperatures exceeding 33°C.

Overall, the influence of water quality variables such as salinity and temperature on juvenile striped bass presence or abundance is unclear when examined in the field, such as in the tributaries of lower Chesapeake Bay (Wagner & Austin 1999). The lack of relationships is partly due to the fact that conditions in lower Chesapeake Bay tributaries during the residence period for juvenile striped bass rarely exceed tolerance limits. Between 1992 and 2006, salinity ranged from 0 to 25 ppt but was almost always less than 20 ppt, and temperature generally ranged between 21 and 32°C at sites sampled by the VIMS seine survey. Nonetheless, growth and survival may be affected when suboptimal conditions persist for extended periods of time. In temperate latitudes, overwinter survival has been shown to be strongly size-dependent in a variety of freshwater and marine fishes, including striped bass (Hurst & Conover 1998); juveniles that obtain larger sizes by the onset of the first winter have greater fat reserves and are less vulnerable to starvation (Conover 1992). We evaluated the effects of salinity and temperature on the occurrence of juvenile striped bass by including the average value at a site (during July-August) in a given year as a covariate for occupancy probability.
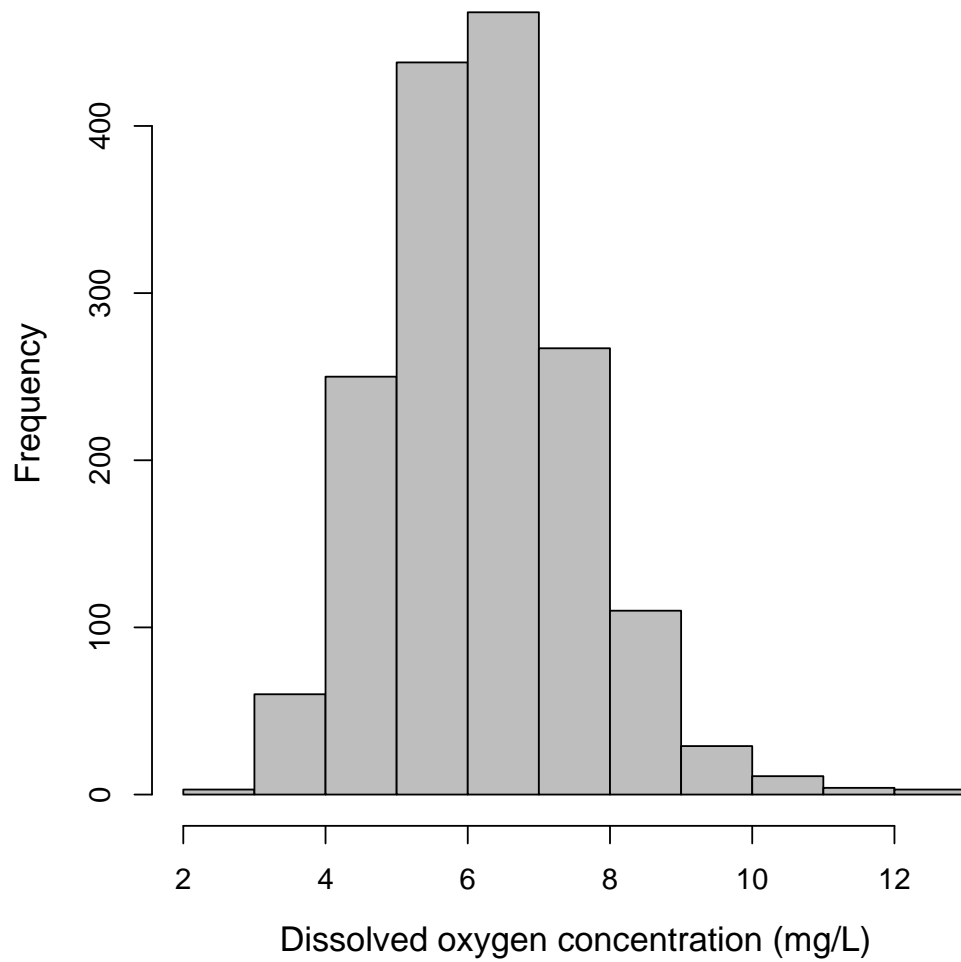
Figure 2: Histogram of dissolved oxygen concentrations measured during VIMS seine survey sampling, 1992-2006 ($N = 1,643$). Only data from the first three rounds of the survey are shown, as that is the data set used in our analysis (see Methods on page 17), but there is little difference in the distribution of dissolved oxygen measurements among the five rounds.

Figure 3: Based on VIMS seine survey data from 1992 to 2004, the growth rate of juvenile striped bass appears to be positively correlated with salinity. In each river system, the growth rate in a given year was calculated as the slope of a linear regression of median fork length (mm) against round. The corresponding annual salinity values were calculated as the means of all observations at seine survey sites in a given river system.

Physical habitat

In addition to water quality conditions, we considered characteristics of the physical habitat in rivers that may affect habitat selection by juvenile st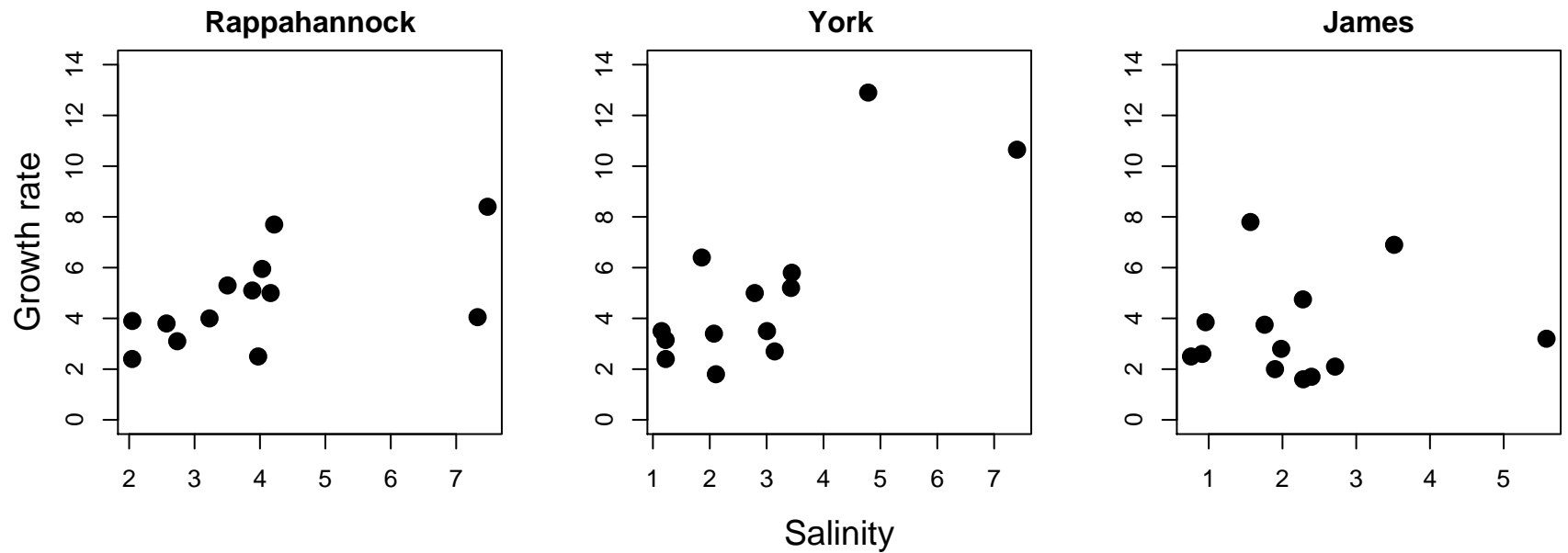riped bass. For example, Muffelman (2006) observed that the relative abundance of juvenile striped bass in the Rappahannock River, as measured by the VIMS seine survey, was consistently highest at a site located at river mile (rm) 55. She postulated that physical habitat features and water quality conditions interacted to create an environment supportive of high abundances of both juvenile striped bass and their prey, thus enhancing growth and potentially survival. Contributing features of the site at rm 55 included the presence of the main channel close to shore (about 11 m) and the existence of persistent eddies that presumably served to transport zooplankton prey from the channel to the shallows. We hypothesized that both physical habitat characteristics and water quality conditions contribute to habitat selection by juvenile striped bass, and we collected data on several physical habitat characteristics at each VIMS seine survey site in 2006.

Objective

We used data from the long-term VIMS seine survey to model habitat selection by juvenile striped bass in major Virginia tributaries to the lower Chesapeake Bay. We modeled the occupancy of seine survey sites by juvenile striped bass and examined selected water quality variables and physical habitat characteristics as covariates of occupancy and detectability.

Methods

Sampling procedure

We used catch data from the VIMS seine survey for the years 1992 to 2006. Although data were available for years prior to 1992, some of the water quality variables of interest were not consistently measured prior to that year. The survey includes sites in the drainages of the three major tributary rivers to the lower Chesapeake Bay in Virginia: the James, the York, and the Rappahannock (Figure 4). In a given year, the goal was to sample each site once during each of five two-week periods; each period is called a round. The first round typically began in mid to late July and the final round ended in September. We used data from only the first three rounds of the survey each year (July through early August) because

increasing fish size later in the season affected availability and catchability. Larger fish tend to disperse from the shallow habitats sampled by the survey, thus reducing their availability, and larger fish may also be better able to avoid capture by the seine, reducing catchability.

We used data from 40 sites that were consistently sampled between 1992 and 2006 (site JA0042 in the James River was sampled in only six years, but was included; Figure 5). Although 44 sites were sampled between 1992 and 2006, one site in the James River and one in the Rappahannock River (JA0077, RA0075) were sampled only in 2006, and so we excluded these two sites from consideration; two additional sites, one in the James and one in the Pamunkey (JA0040, PM0061), were excluded because of a lack of physical habitat measurements.

At each sampling event, fish were collected by standard seining methods and juvenile striped bass were enumerated from the catch (Hewitt *et al.* 2006). Collections were made at or near low tide with a 6.4 mm mesh bagless minnow seine that was 30.5 m long and 120 cm deep. One end of the net remained on shore and the rest of the seine was deployed perpendicular to the shoreline until either the net was fully extended or a depth of about 120 cm was encountered. The net was retrieved by pulling the offshore end down-current and back to shore. Only striped bass deemed to be young-of-year (YOY) fish were counted and measured. Young-of-year classification was based on size; individuals greater than 150 mm long were not considered to have been spawned in the current year.

The sampling frame for the survey includes some sites that are sampled twice on each visit to the site (i.e., two separate hauls of the seine). These sites are termed index stations because they are considered to be located in the core of the primary nursery areas and are used to calculate the relative abundance index (Hewitt *et al.* 2006; Figures 4 & 5). Following Wagner & Austin (1999) and recommendations in Rago *et al.* (1995), we used data from only the first seine haul at all sites sampled by the survey.
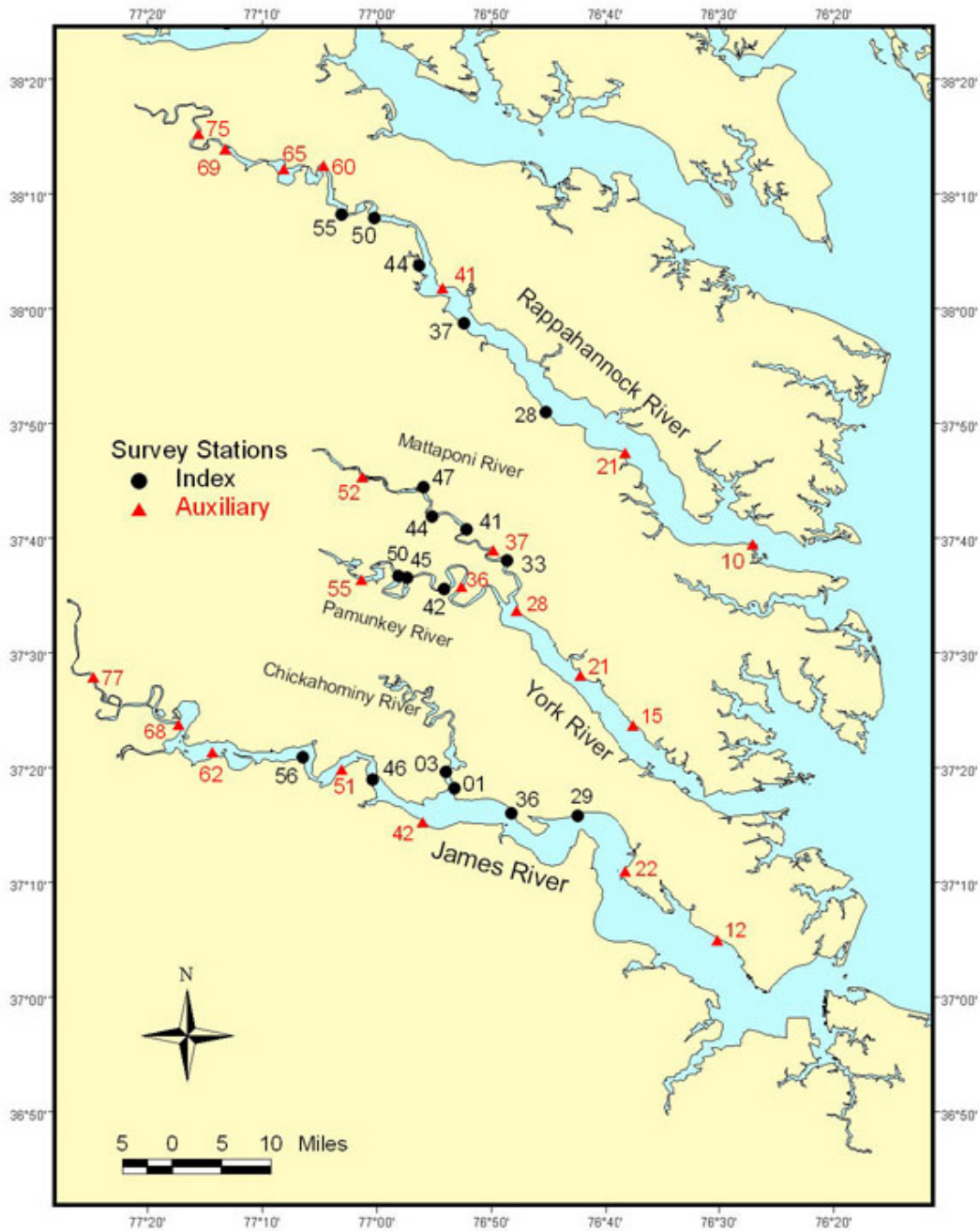
Figure 4: Locations of sites sampled by the VIMS seine survey in 2006. Number labels indicate the river distance in miles from the mouth of the river. Site 75 in the Rappahannock River was not used in our analysis, but we did use a site one mile farther upriver (site 76). In the James River, site 77 was not used in our analysis, but we did use nearby sites (sites 74 and 78). See Figure 5.

Figure 5: Timeline of the sampling frequency at the 40 sites sampled by the VIMS seine survey and used in our analysis. Site labels consist of a 2-letter designation of the river system and a number indicating distance from the river mouth in miles; JA=James, JC=Chickahominy [James drainage], MP=Mattaponi [York], PM=Pamunkey [York], RA=Rappahannock, YK=York. Shaded areas indicate sampled rounds and unshaded areas indicate missing observations. Rows for index stations are hatched.

We further restricted analyses to data for fish ≥ 40 mm long. Particularly in the first few rounds of the survey, some fish less than 40 mm are captured, but fish of this size may not be captured efficiently by the seine. We do not have specific information on the selectivity of our seine for juvenile striped bass. Bayley & Herendeen (2000) assessed the catch efficiency of a 25 m long seine with 5 mm mesh for a variety of species, seining methods, and habitat conditions in the Amazon floodplain in Brazil. In their analysis, species most similar to juvenile striped bass and sampling methods most similar to ours resulted in catch efficiencies that peaked at fish sizes near 40-50 mm and then declined with increasing size. For largemouth bass in a reservoir, Jackson & Noble (1995) compared the catch efficiency of a 9 m long seine with 6-9 mm mesh to that of handheld electrofishing and found that the seine captured 30-60 mm fish well, but did not adequately capture fish larger than about 60 mm. We selected the 40 mm cutoff based on these observations, our seine configuration, and our own experience that individuals ≥ 40 mm rarely pass through the net after retrieval.

Habitat variables

We considered two sets of habitat variables as covariates for site occupancy and detectability: [1] *in situ* water quality variables measured at the sampling sites, including salinity, temperature, and Secchi depth, and [2] variables measured to characterize physical properties of the sampling sites, including dominant substrate type, bank slope, and distance to the river channel. Salinity and temperature were measured with a YSI meter each time a site was sampled and Secchi depth was measured in the conventional way.

Physical habitat variables were measured at each site in 2006 (July to September). Substrate type was assessed visually using a modified Wentworth scale based on substrate particle size. We used five categories based on increasing particle size: silt, sand, pebble, cobble, and boulder. As expected, sand and silt were the most common substrate types and no sites were dominanted by cobble or boulder substrates (such substrates are avoided in site selection because they negatively affect seine sampling efficiency). Pebble substrate dominated at only two sites in the upper Rappahannock River (RA0065, RA0069), so we combined categories and redefined two substrate classes for use in modeling: fine substrate (silt) and coarse substrate (sand and pebble) (Table 1). Bank slope was defined as in Meng & Powell (1999) – the slope of the river bottom along a transect from, and perpendicular to, the shoreline. Water depth was measured 15 m from shore at three transects, one in the middle of the site and one at each edge. Bank slope was calculated as a dimensionless ratio of water depth (m) to distance from shore (15 m) and the average of the three measurements was used

in all analyses. The distance to the river channel was measured from, and perpendicular to, the shoreline and was used as an indicator of the extent of available shallow water habitat. Distance measurements were made at the sites when possible and other measurements were taken from nautical charts with geographic information system software. We assumed that physical habitat features had not changed substantially since 1992 and included our 2006 physical habitat data in models for all years. A general comparison of our substrate data with that reported by Wagner & Austin (1999) justified this assumption. Little had changed at the sites since 1990-1994, except perhaps an increase in the prevelance of silt at a few of the sites in the York River drainage. With regard to modeling and inference, we note that using the physical habitat variables as covariates introduces a form of pseudoreplication, in that single observations at a site from 2006 are repeated in the data set for that site in each year. The effect on results is that the precision of parameters related to these covariates is overestimated.

Modeling and inference

Occupancy models

The VIMS seine survey sampling scheme – repeat visits to the same sites within a year – provides an opportunity to use occupancy models to account for imperfect detection of juvenile striped bass at the sites. We follow the approach presented in MacKenzie (2005) and MacKenzie *et al.* (2006). Presence/absence observations are modeled as a function of two parameters: [1] occupancy (ψ), the probability that the site is occupied by striped bass, and [2] detectability (p), the conditional probability that striped bass are detected given that they are present. The objective was to estimate the probability that juvenile striped bass were present at the site but not captured by the survey sampling, and then correct estimates of occupancy to account for the probability of nondetection. Thus, detectability is mostly a "nuisance" parameter.

Observations from the first three rounds of the survey at each site in each year are used to estimate detectability. Histories of observed presence and absence at the sites (detection histories) in the three rounds provide the necessary information. For example, a detection history of 010 would indicate that striped bass were present at the site (the species was detected at least once) but were missed by sampling in the first and third rounds. Mathematically, the detection history is represented by a combination of the probabilities of occupancy and detectability; e.g.,

$$Pr(h = 010) = \psi(1 - p)p(1 - p).$$

Table 1: Physical habitat variables measured at VIMS seine survey sampling sites in the summer of 2006. Substrate classification was based on a modified Wentworth scale and condensed into two categories (see text on page 21): 1 = fine (silt), 2 = coarse (sand and pebble). Site labels are the same as in Figure 5.

Drainage	Site	Dominant substrate	Bank slope	Distance to river channel (km)
James	JA0012	2	0.078	2.69
	JA0022	2	0.063	1.08
	JA0029	2	0.054	0.55
	JA0036	2	0.044	0.82
	JA0042	2	0.028	0.31
	JA0046	2	0.056	0.13
	JA0051	2	0.054	0.06
	JA0056	2	0.055	0.67
	JA0062	2	0.042	0.67
	JA0068	2	0.091	0.05
	JA0074	1	0.067	0.07
	JA0078	1	0.035	0.08
	JC0001	1	0.037	0.10
	JC0003	1	0.162	0.05
York	MP0033	1	0.331	0.03
	MP0037	1	0.160	0.03
	MP0041	2	0.189	0.03
	MP0044	1	0.124	0.03
	MP0047	1	0.073	0.07
	MP0052	2	0.078	0.02
	PM0036	2	0.109	0.04
	PM0042	1	0.244	0.03
	PM0045	1	0.324	0.01
	PM0050	1	0.302	0.02
	PM0055	2	0.061	0.05
	YK0015	1	0.034	0.56
	YK0021	2	0.025	0.22
	YK0028	1	0.027	0.09
Rapp	RA0010	2	0.069	0.56
	RA0021	2	0.091	0.59
	RA0028	2	0.037	1.77
	RA0037	1	0.045	0.43
	RA0041	1	0.063	0.77
	RA0044	2	0.046	1.18
	RA0050	2	0.050	0.13
	RA0055	2	0.065	0.08
	RA0060	1	0.064	0.08
	RA0065	2	0.090	0.23
	RA0069	2	0.123	0.04
	RA0076	1	0.284	0.03

Of particular interest are the sites with 000 detection histories, which must be partitioned between sites where striped bass were absent $[1 - \psi]$ and those where striped bass were present but not detected $[\psi(1 - p)^3]$. The multinomial likelihood for 000 histories includes a summation of two terms that represent both possibilities. Detectability and occupancy probabilities are estimated by maximum likelihood using a likelihood function that combines the mathematical expressions for the detection histories at all sites. Missing observations at sites (see Figure 5), which occur when weather prohibits sampling, are simply handled by omitting probabilities associated with that observation from the likelihood (i.e., they do not contribute to estimation).

Occupancy models can be modified to include the effects of factors that might cause variation in occupancy and detectability among sites or rounds. In habitat studies, such factors (covariates) are of primary interest. Covariates are included by modeling occupancy or detectability as a function of the covariates (X) through a logit link function; e.g., to model the effect of a single covariate on occupancy, we use:

$$logit(\psi) = log(\psi/(1 - \psi)) = \beta_0 + \beta_1 X$$

or

$$\psi = e^{\beta_0 + \beta_1 X}/(1 + e^{\beta_0 + \beta_1 X}).$$

The parameters associated with the covariates (β_i) are estimated simultaneously with the detectability and occupancy probabilities.

Occupancy models are similar to logistic regression (Hosmer & Lemeshow 2000), which is commonly used to model habitat associations and has been used often in fisheries studies (e.g., Bartol *et al.* 2002; Tiffan *et al.* 2006). The key difference between occupancy models and logistic regression is that occupancy models account for uncertainty in observed absences. Habitat models based on logistic regression produce biased results when detectability is less than 100%, which is the typical situation (Tyre *et al.* 2003; Gu & Swihart 2004; MacKenzie 2005). In the face of imperfect detection, logistic regression models estimate and predict the characteristics of sites where the species is *found* rather than those that are actually occupied (MacKenzie *et al.* 2006).

Multi-state occupancy models

Preliminary modeling based on presence/absence data indicated that occupancy was high because at least one fish was captured at most sites in most rounds. Overall high occupancy limits our ability to model the effects of habitat variables because of limited contrast in occupancy. To incorporate some of the information present in the raw catch numbers, we used multi-state occupancy models, which are recent extensions of standard occupancy models (MacKenzie *et al.* 2006; Nichols *et al.* 2007). The approach we take also allows us to account for the effects of local population size on detectability (detectability is expected to increase with local population size), albeit in a somewhat ad-hoc way (see Royle & Nichols 2003). Multi-state occupancy models can be used to leverage the limited information in raw catch numbers (relative abundance) to better model habitat effects on occupancy (J. D. Nichols, Patuxent Wildlife Research Center, personal communication).

We adopted the multi-state approach by categorizing catches at survey sites into one of three abundance "states": 0 fish [state=0], 1-10 fish [state=1], > 10 fish [state=2] (Figure 6). Detection histories consist of 0, 1, or 2 for each visit to the site, and observations in the three states represent the following possibilities:

[0]   nondetection; possible true states are 0, 1, or 2

[1]   detected in low abundance; possible true states are 1 or 2

[2]   detected in high abundance; true state is 2.

Multi-state models are conditional on observations in one state being known with certainty, and we conditioned on the high abundance state [2]. In other words, when more than 10 juvenile striped bass were collected at a site in a given round, we assumed that they were indeed present in high abundance (i.e., greater than 10 fish at the site). In contrast, we allowed for uncertainty about state assignment for sampling events where 10 or fewer were collected. Juvenile striped bass could have been present in high abundance but we did not capture them in our seine or we only captured a small number of them. We assumed that juvenile striped bass were not misidentified and that errors in counting the catch, when present, did not influence state classification.
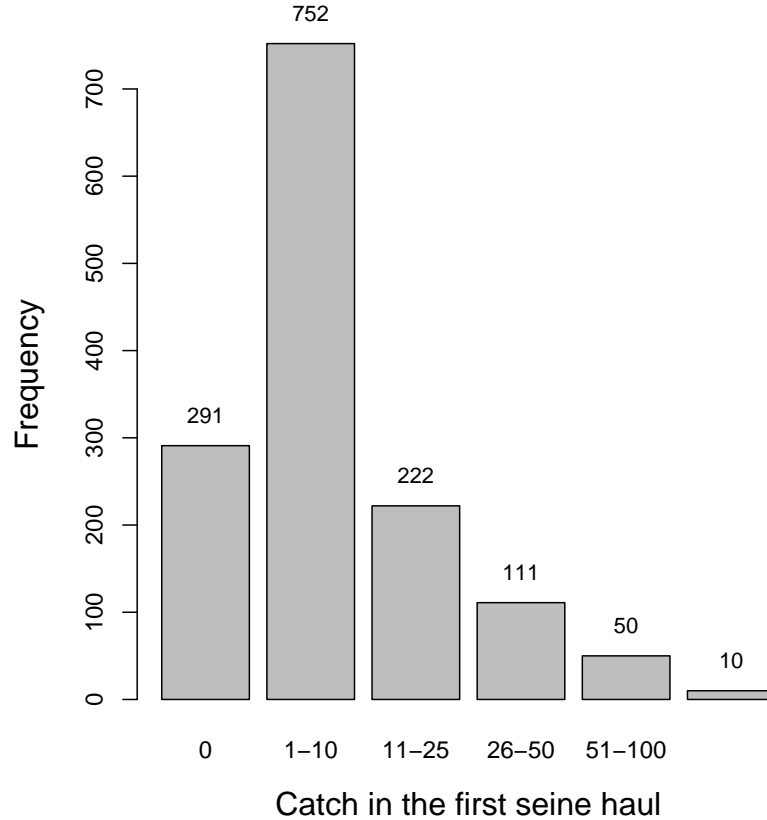
Figure 6: Histogram of catches from the first seine haul at each sampling site in the VIMS seine survey, 1992-2006 ($N = 1,458$). Data includes only the first three rounds of the survey in each year from the final data set used in analysis, and only striped bass ≥ 40 mm in length. Multi-state occupancy models were fitted to data summarized into three relative abundance categories ("states") shown by the first bar (zero catches), the second bar (catches of 1-10), and a sum of all remaining bars (catches > 10).

For computational convenience, occupancy in state 2 was modeled as being conditional on the site being occupied by at least one fish (state 1). Following Nichols *et al.* (2007), the parameters estimated for occupancy were defined as follows:

$$\psi^I = Pr(site\,is\,occupied)$$

$$\psi^{II} = Pr(site\,hosts\,high\,abundance,\,given\,that\,it\,is\,occupied).$$

The unconditional probability that the site is occupied and hosts a high abundance of stripers is calculated as $\psi^I \cdot \psi^{II}$, and the probability that the site is not occupied is simply $1 - \psi^I$. Similarly, probabilities of detection are estimated for each occupancy state as follows:

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$$p^I = Pr(occupancy\,is\,detected,\,given\,the\,true\,state\,is\,1)$$

$$p^{II} = Pr(occupancy\,is\,detected,\,given\,the\,true\,state\,is\,2).$$

An additional parameter δ is included to account for uncertainty in state classification for occupied sites. The δ parameter represents the probability that state 2 is observed given that juvenile striped bass were present in high abundance (> 10) and were detected. In other words, it is the probability of correctly classifying a site as hosting a high abundance of juvenile striped bass. In the detection histories, 1-δ represents an error where the sampling indicated state 1, but state 2 was the correct state (based on observing state 2 in either of the other rounds of the survey).

As an example, consider the detection history 120, which would be represented mathematically as

$$Pr(h = 120) = \psi^I \psi^{II} p^{II} (1 - \delta) p^{II} \delta (1 - p^{II}).$$

In this case, the site was known to support a high abundance of juvenile striped bass (observed in round 2), and the associated occupancy probability is $\psi^I \psi^{II}$. Because the site was known to be occupied in state 2, this history provides information about the detection probabilities only for state 2. Juvenile striped bass were detected in round 1 (p^{II}), but the round 1 observation incorrectly classified the site as being in state 1 ($1 - \delta$). Juvenile striped bass were again detected in round 2 (p^{II}) and the site was correctly classifed as being in state 2 (δ). No striped bass were detected in round 3 ($1 - p^{II}$).

Detection histories with no observations in state 2 involve more uncertainty about the correct state. In those cases, the mathematical expression for the history involves probabilities of occupancy in both states 1 and 2, detection probabilities for each state, and δ. Finally, detection histories of 000 involve the most uncertainty and include probabilities of occupancy in both states, detection probabilities for each state, δ, as well as the probability that the state was unoccupied ($1 - \psi^I$).

Coping with missing values

In occupancy models, missing values for round-specific covariates are not allowed. Missing values must either be imputed or the detection history must be dropped from the analysis. In our analysis, water quality variables are used as round-specific covariates for modeling detectability, and are also summarized across rounds to provide covariates for modeling occupancy. For a data set as large as ours, imputation is reasonable for a few missing values. However, detection histories in which more than one round has missing data are problematic

because there is only one other observation at a site in a given year to use for imputation. Many of the 587 detection histories in our data set were missing one or more water quality measurements in one or more rounds, either because water quality measurements were not taken when sampling occurred (e.g., the meter was not working) or because sites were not sampled (e.g., bad weather; see Figure 5). Secchi depth was by far the most troublesome variable, with 341 missing values. Salinity (21) and temperature (14) were less problematic, so we describe imputation for these variables first.

Salinity measurements were never missing (either because of instrument malfunction or missed sampling) for more than one round at a given location in a given year. Therefore, we simply imputed the average of the other two rounds for that location in that year for the missing values. When a site was not sampled in two of the three rounds in a given year, the detection history was dropped from the analysis. For water temperature, the detection histories for site JA0022 in 2000 and JA0078 in 1996 were missing measurements for two of the three rounds, so they were removed from the analysis. The other 12 missing values of temperature were imputed in the same way as for the missing values of salinity.

We treated missing values for secchi depth the same way we treated missing values for salinity and temperature. Detection histories were dropped if more than one round of secchi depth measurement was missing, and single missing values at a location in a given year were imputed from the other two rounds. The years 1994-1996 were particularly problematic, with many detection histories being deleted from the analysis due to missing secchi depth data (including all but a few of the histories that included missed sampling). A total of 99 detection histories was dropped from the analysis, and nearly 100 remaining missing values were imputed using averages of the other two rounds. However, secchi depth often did not vary much (or any) at a site across the three rounds in a given year, so the imputation approach seemed reasonable. After removing the 99 detection histories with two or more rounds of missing secchi depth and the two detection histories with two rounds of missing water temperature data, the final data set included 486 detection histories.

Inference about habitat selection

Occupancy models were developed based on considerations of how physical habitat characteristics and water quality variables would influence site occupancy and detectability for juvenile striped bass. Inferences about habitat selection followed an information-theoretic model selection framework as described by Burnham & Anderson (2002) and MacKenzie *et al.* (2006). Maximum likelihood parameter estimation and the calculation of model selec-

tion criteria were carried out with program MARK (maintained by Gary White, Colorado State University; see White & Burnham 1999; Cooch & White 2008). Models were developed and passed to MARK using the RMark package (Laake & Rexstad 2008) within the R software environment (R Development Core Team 2007). Model selection was based on the uncorrected Akaike Information Criterion (AIC) because the form of AIC corrected for small sample size (AICc) is not typically used with occupancy models (MacKenzie *et al.* 2006). Due to the repeated visits to the same sites, the definition of effective sample size in occupancy models remains unclear, particularly for multi-state models (J. D. Nichols, personal communication). Nonetheless, the difference between AIC and AICc for our models was trivial because of the size of the data set.

Given the number of parameters to be estimated, preliminary modeling using the multi-state approach indicated that the number of sites sampled by the survey in a given year (about 40) was sufficient to estimate the effects of only a few covariates on occupancy or detectability. To increase our effective sample size, we treated each of the 486 three-round detection histories as independent observations, regardless of the year in which the histories occurred. We considered this a reasonable approach because (1) the cohort of juvenile striped bass being sampled was newly spawned each year, (2) we included covariates to account for the dominant year-to-year environmental changes (e.g., salinity, temperature), and (3) we used multi-state models to explicitly capture some of the effects of fluctuations in abundance that occurred from year to year. In addition, because a dominant factor affecting recruitment of juvenile striped bass is the amount of spring precipitation (Figure 1), we added an additional categorical covariate for occupancy that identified detection histories as occurring in either dry or wet years. The 15 years included in the analysis were classified as dry or wet according to the total spring precipitation: years with more than 15 inches of spring precipitation (the median of the time series) were classified as wet years. We concluded that our modeling efforts should have accounted for major annual effects that might have caused detection histories to be more similar within a year than among years.

We first evaluated models that included covariates only for detectability in order to reduce the total number of parameters in models that also included covariates for occupancy. In these models, we constrained parameters for both occupancy states (ψ^I, ψ^{II}) and the state classification probability (δ) to be constant among detection histories. We estimated separate detectability parameters for the two occupancy states in all models because we expected detectability to be higher for the high abundance state [2]; i.e., p^I was never constrained to be equal to p^{II}. Preliminary results from simple models supported this expectation and also showed that p^{II} was high (≥ 0.95); when the true state was high abundance (catch of more

than 10), detection of striped bass at the site in at least one round was nearly certain. In the interest of parsimony, we held p^{II} constant in all models and modeled only p^{I} as a function of the covariates. We included the following factors as covariates for p^{I} in the initial models:

1. **Time**: Detectability was either held constant across rounds or allowed to vary by round under the hypothesis that growth of juvenile striped bass may lead to a decline in the capture efficiency of the seine through the summer.

2. **Secchi depth**: Detectability was modeled as a function of water clarity under the hypothesis that striped bass avoidance behavior may be reduced in more turbid water (detectability declines with increasing secchi depth [clearer water]).

3. **Substrate**: Detectability was modeled as a function of substrate particle size under the hypothesis that seine hauls are more effective over fine substrate (silt) than over coarse substrate (sand or pebble).

4. **Bank slope**: Detectability was modeled as a function of bank slope under the hypothesis that striped bass may be better able to avoid the seine in deeper water (detectability declines with increasing slope).

We fit a suite of models, including ones that included each of these covariates separately, ones that included combinations of the covariates, and a null model that did not include any covariates.

A full presentation of the results for these initial models for detectability are given under Results:Detectability on page 32. To facilitate explanation of the full model set that included covariates for both detectability and occupancy, we simply note that in the interest of parsimony we retained only bank slope and time effects on p^{I}. Detectability declined through the summer as expected, but bank slope had a positive effect on detectability, in contrast to our expectations.

Similar to the situation for p^{II}, preliminary model results indicated that the probability of occupancy in state 1 (ψ^{I}) was high (≥ 0.9), making it difficult to model ψ^{I} as a function of covariates. We followed the same approach that we used for detectability and estimated ψ^{I} as a constant in all models, including covariate effects only for ψ^{II} (except for the covariate for wet/dry years, see below). Thus, we estimated the effects of covariates on the probability that a site was occupied in high abundance given that it was occupied. In other words, we sought to determine what makes sites particularly attractive to juvenile striped bass. For

example, we estimated whether higher salinities increased the probability that sites would be occupied by high abundances of juvenile striped bass.

Our full models for estimating covariate effects on occupancy as well as detectability included the following factors as covariates for ψ^{II}:

1. **Temperature**: Occupancy was modeled as a linear (logistic) function of temperature under the hypothesis that striped bass would select sites with optimal temperatures for growth. Our literature review indicated optimal temperatures for juvenile striped bass of 28°C or perhaps higher. Because all but a few measurements of temperature in our data set were below expected thermal tolerance limits for juvenile striped bass (ca. 33°C), we modeled occupancy as a linear (logistic) function of temperature. In order to use temperature as a covariate for occupancy, we calculated the average temperature across the three rounds to characterize the overall temperature at a site.

2. **Salinity**: Occupancy was modeled as a linear function of salinity under the hypothesis that striped bass would select sites with optimal salinities for growth and survival. Based on our literature review, it appeared that salinity had weak effects on growth and survival in juvenile striped bass. The limited evidence suggests that juvenile striped bass may select areas with higher salinity, so we modeled occupancy as a linear (logistic) function of salinity. Salinity was treated similar to temperature for use as an occupancy covariate.

3. **Secchi depth**: Occupancy was modeled as a linear function of water clarity. Competing hypotheses could lead to both negative and positive effects of water clarity on occupancy. Because striped bass are sight feeders, one hypothesis posits that they would select sites with clearer water in order to optimize prey location and consumption. Another hypothesis posits that juvenile striped bass would select sites with more turbid water in order to avoid being detected by predators in shallow water. Secchi depth was treated similar to temperature and salinity for use as an occupancy covariate.

4. **Substrate**: Occupancy was modeled with a categorical covariate for substrate to assess whether juvenile striped bass differentially selected sites with fine (silt) or coarse (sand/pebble) substrate.

5. **Bank slope**: Occupancy was modeled as a linear function of bank slope, as a proxy for water depth. Competing hypotheses could lead to both negative and positive effects of bank slope on occupancy. Juvenile striped bass might be expected to prefer deeper

sites to avoid avian predators, but might be expected to prefer shallower sites to avoid larger fish predators.

6. **Distance to river channel**: Occupancy was modeled as a linear function of the distance to the river channel to evaluate the value of channel proximity. Juvenile striped bass might be expected to select sites with easier access to deep water refuges for predator avoidance (occupancy increases as distance to channel decreases). Sites closer to the channel might also be expected to have higher occupancy probabilities if the river channel serves as a conduit for juveniles dispersing downstream from the source spawning areas (same effect).

7. **Wet/dry year**: Occupancy was modeled with a categorical covariate for wet and dry years under the hypothesis that abundance and occupancy would be higher in wet years. The positive effect of spring precipitation on striped bass recruitment success appears to be well established, so we included this covariate in all models for both ψ^I and ψ^{II}. The hypothesis is that more sites are likely to be occupied in wet years, and that, given occupancy, sites are also more likely to be occupied in high abundance in wet years.

We fit a suite of models, including ones that included each of these covariates separately, ones that included combinations of the covariates, and a null model that did not include any covariates.

Results

Detectability

In the initial model set to investigate covariate effects on detectability (p^I), results indicated considerable model selection uncertainty and mostly small effects of the covariates. The top eight models all had essentially equal explanatory power ($\triangle$AIC within about two points of the top model) and were well separated from the null model and the model with only a time effect (Table 2). Within the subset of top models, bank slope and time were common covariates that appeared to represent important effects.

All of the top eight models included bank slope as a covariate, indicating that bank slope was a particularly important effect on p^I. However, the effect of bank slope was in the opposite direction of our hypothesis – detectability was higher at sites with larger slopes, or

Table 2: Model selection results for the initial set of models used to investigate the effects of habitat covariates on detectability. Only effects on p^I were investigated. Separate parameters were estimated for p^{II}, δ, ψ^I, and ψ^{II}, but they were held constant in all models. k is the number of parameters in the fitted model.

| Covariates on p^I	k	AIC	$\triangle$AIC	Model weight	$-2\log_e(\mathcal{L})$
bank slope, time	8	2581.91	0.00	0.19	2565.91
bank slope	6	2582.10	0.19	0.17	2570.10
bank slope, secchi, time	9	2582.31	0.40	0.16	2564.31
bank slope, secchi	7	2582.33	0.42	0.16	2568.33
bank slope, substrate, time	9	2583.84	1.94	0.07	2565.84
bank slope, substrate	7	2584.04	2.13	0.07	2570.04
bank slope, substrate, secchi	8	2584.12	2.21	0.06	2568.12
bank slope, substrate, secchi, time	10	2584.12	2.21	0.06	2564.12
time	7	2587.57	5.66	0.01	2573.57
NULL (p^I constant)	5	2587.86	5.95	0.01	2577.86
secchi, time	8	2587.88	5.97	0.01	2571.88
secchi	6	2588.00	6.09	0.01	2576.00
substrate, time	8	2588.95	7.04	0.00	2572.95
secchi, substrate, time	9	2589.50	7.59	0.00	2571.50
secchi, substrate	7	2589.63	7.72	0.00	2575.63
substrate	6	2653.81	71.90	0.00	2641.81
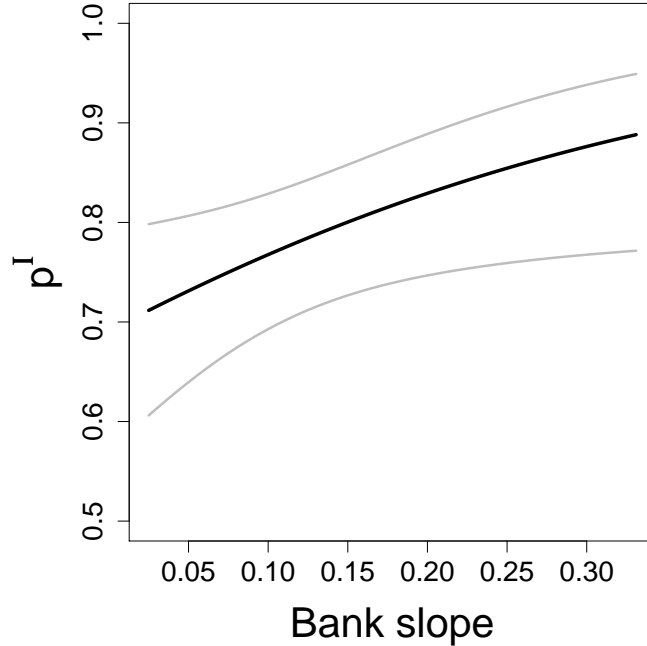
Figure 7: Illustration of the positive effect of bank slope on detectability at sites where striped bass were detected in low abundance (1-10 fish; p^I). Model-averaged point estimates and 95% confidence intervals are shown for round 1 only, but results were similar for the other two rounds.

deeper water (Figure 7). Parameter estimates for the time effect indicated that detectability declined through the sampling season, as expected, but the magnitude of the decline was rather small. Model-averaged estimates of p^I declined from 0.77 (se = 0.03) in round 1 to 0.76 (se = 0.03) in round 2 to 0.73 (se = 0.04) in round 3. Model-averaged estimates for the parameters that were held constant in each model were: $p^{II} = 0.96$ (se = 0.01), $\delta = 0.57$ (se = 0.02), $\psi^I = 0.92$ (se = 0.01), and $\psi^{II} = 0.54$ (se = 0.03).

We retained the bank slope and time effects in all of the models in the full analysis that included covariates on occupancy, but eliminated secchi depth and substrate. Although secchi depth and substrate were included in some of the top eight models, they appeared to partly be so-called "pretending variables" that were paired with important covariates but provided little additional explanatory power (Burnham & Anderson 2002). Three lines of reasoning led us to drop these other covariates for p^I in the full analysis:

1. Models that included these covariates in addition to bank slope were inferior to the models with only bank slope or bank slope and the time effect;

2. Models that included these covariates but did not include bank slope were inferior to
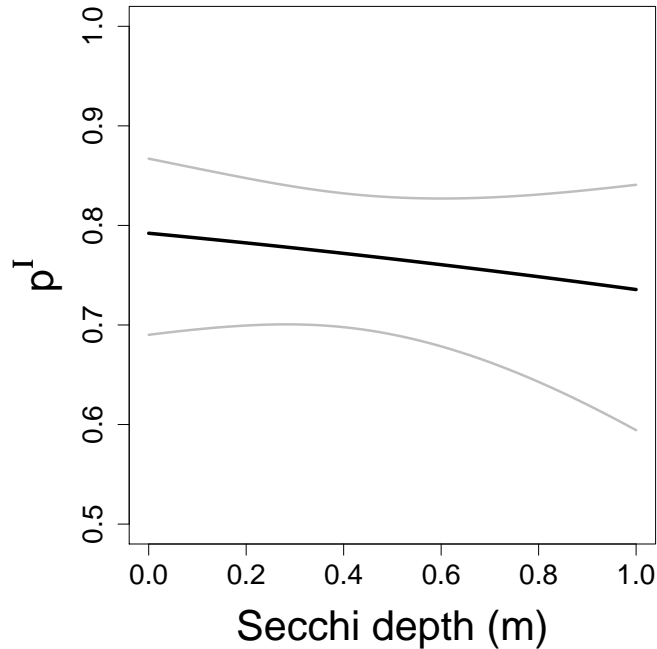
Figure 8: Illustration of the weak negative effect of secchi depth on detectability at sites where striped bass were detected in low abundance (1-10 fish; p^I). Model-averaged point estimates and 95% confidence intervals are shown for round 1 only, but results were similar for the other two rounds.

the null model;

3. The size of the effects for these covariates was small and estimated with relatively poor precision. Plots showed that the effect of secchi depth was much smaller than the effect of bank slope and the standard error for the effect was nearly as large as the estimate itself (Figure 8). For substrate, estimates of p^I varied by only 0.01-0.02 between substrate classes and the standard error for the effect was much greater than the estimate.

Although the large data set can apparently support some subtle effects of covariates on detectability, our primary interest was the effects of habitat covariates on the probability of site occupancy. In the interest of parsimoniously modeling the "nuisance" parameters for detectability, we retained only bank slope and the time effect as covariates for p^I in models that included covariates for occupancy. Recall that p^{II} was held constant and was estimated at ≥ 0.95.

Occupancy

Results from the model set used to investigate the effects of habitat covariates on occupancy showed that spring precipitation was clearly important (as expected), and provided strong evidence that salinity is the primary driver of habitat selection for juvenile striped bass when striped bass are present in high abundance (state 2). Although the probability of site occupancy for state 1 (low abundance) was high in all years, estimates of ψ^I were substantially different in wet and dry years and the parameters were estimated with high precision (wet years = 0.98 [se = 0.01], dry years = 0.88 [se = 0.02]). Differences in the estimates of ψ^{II} were greater between wet and dry years, with sites being far more likely to host high abundances of striped bass, given that they were occupied, in wet years (wet years = 0.63 [se = 0.04], dry years = 0.40 [se = 0.04]). Because estimates of ψ^I were large, the unconditional probabilities that a site hosted a high abundance of striped bass ($\psi^I * \psi^{II}$) in wet and dry years was similar to the results for ψ^{II} alone, but differences in occupancy were more pronounced (wet years = 0.62, dry years = 0.35).

The top model in the set included only salinity as a covariate for ψ^{II}, and all other covariates appeared in models only as "pretending variables" in conjunction with salinity (Table 3). In the top six models, the addition of single covariates with salinity increased the $\triangle$AIC by about two points, indicating no additional explanatory power in the additional covariate. Similarly, the seventh model included all of the covariates and had a $\triangle$AIC of 7.11, providing very little improvement in the model fit beyond the top model [as judged by -2log$_e$ ($\mathcal{L}$)] but paying a penalty for the addition of five more parameters. If the models with pretending variables are removed (models 2-7), there is no model selection uncertainty and all of the weight is placed on the top model with only the effect of salinity. In both wet and dry years, salinity had a strong negative effect on the conditional probability that a site would host a high abundance of juvenile striped bass, given that it was occupied (Figure 9). As expected, model-averaged estimates of the other parameters were similar to results from the model set for detectability: p^I declined from 0.77 (se = 0.03) in round 1 to 0.68 (se = 0.04) in round 3, p^{II} = 0.96 (se = 0.01), and δ = 0.55 (se = 0.03).

Table 3: Model selection results for the set of models used to investigate the effects of habitat covariates on occupancy, accounting for variation in detectability. Only effects on ψ^{II} were investigated, and all models included the wet/dry year covariate on ψ^{II} as well as the effects of bank slope and time on p^I (see Results:Detectability on page 32). Separate parameters were estimated for p^{II}, δ, and ψ^I, but they were held constant in all models (except for the wet/dry year covariate on ψ^I). k is the number of parameters in the fitted model.

| Covariates on ψ^{II}	k	AIC	$\triangle$AIC	Model weight	$-2\log_e\left(\mathcal{L}\right)$
salinity	11	2517.05	0.00	0.38	2495.05
salinity, bank slope	12	2518.87	1.83	0.15	2494.87
salinity, secchi	12	2518.95	1.91	0.15	2494.95
salinity, distance to channel	12	2519.04	2.00	0.14	2495.04
salinity, temp	12	2519.67	2.63	0.10	2495.67
salinity, substrate	12	2520.66	3.62	0.06	2496.66
salinity, bank slope, secchi, distance to channel, temp, substrate	16	2524.16	7.11	0.01	2492.16
distance to channel	11	2537.97	20.93	0.00	2515.97
NULL (wet/dry only)	10	2543.06	26.01	0.00	2523.06
bank slope	11	2544.62	27.57	0.00	2522.62
substrate	11	2544.64	27.60	0.00	2522.64
secchi	11	2544.74	27.69	0.00	2522.74
temp	11	2545.05	28.00	0.00	2523.05
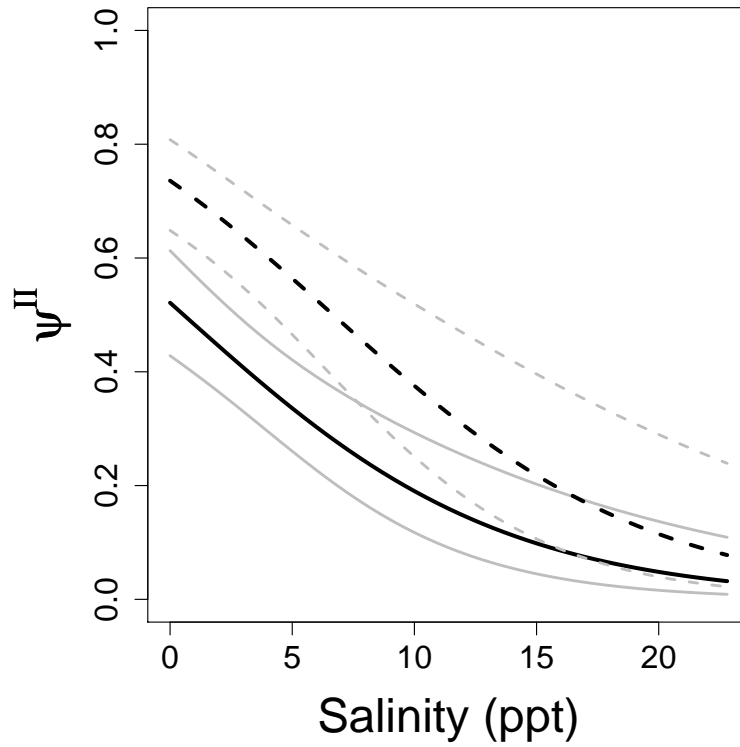
Figure 9: Average salinity showed a strong negative effect on the conditional probability that a site hosted a high abundance of striped bass, given that it was occupied (ψ^{II}). Model-averaged point estimates and 95% confidence intervals are shown separately for wet (dashed lines) and dry (solid lines) years.

Discussion

Summary of major findings

Results from multi-state occupancy models indicated that detectability of juvenile striped bass in the VIMS seine survey is less than 100%, and should be estimated when making inferences about habitat selection. We found that detectability declined through the summer sampling season and increased with the slope of the bank at sampling sites (deeper water). Although the magnitude of the effect was small, our hypothesis that striped bass would become less catchable as they grew through the summer appears to be supported. In contrast, our hypothesis that increasing bank slope (water depth) would reduce detectability was not supported. One possible explanation for the positive effect of bank slope is that fish are less likely to be startled and flee from the sampling area in deeper water. They might also be less likely to make directed movements towards the river channel and away from the sampling area in deeper water, but would almost certainly do so in shallower water. We acknowledge that this explanation is not particularly compelling, but given the strong support for the effect in our modeling results we suggest that future research with seine surveys consider evaluating the effect of water depth, and potentially other factors, on detectability or capture probability.

The probability of site occupancy by juvenile striped bass was high overall, indicating that most seine survey sampling sites in most years are occupied by at least one striped bass. More sites were occupied in wet years, consistent with evidence suggesting that higher amounts of spring precipitation are beneficial to striped bass recruitment in lower Chesapeake Bay tributaries (Wood 2000). Furthermore, and potentially more importantly, given that a site was occupied, the conditional probability that it would host a high abundance of juvenile striped bass increased by over 50% in wet years. Our modeling of this conditional probability as a function of physical habitat and water quality variables indicated that striped bass preferentially selected sites with lower salinity, and other habitat variables appeared to be unimportant. Sites in lower salinity areas were more likely to host high abundances of juvenile striped bass. Although previous evidence from laboratory studies is limited, our results appear to contradict expectations that juvenile striped bass would select higher salinity areas for growth and survival. Similarly, laboratory studies have suggested that the effect of temperature on growth of juvenile striped bass (Secor *et al.* 2000) would influence habitat selection, but our results indicate that the effects measured in the laboratory do not translate into selection differentials in the field, at least not across the range of temperatures

typically encountered in Virginia tributaries.

Limitations of our approach

Spatial scale

Our results concerning habitat selection are dependent on the spatial scale at which the analysis was performed. At a large scale, salinity appears to be the primary factor influencing habitat selection in juvenile striped bass. This result is predictable to some extent in that lower salinity areas are closer to the spawning areas. As juveniles grow and disperse from the spawning areas, sites that are closer would be expected to have higher probabilities of being occupied. An alternative explanation of our results would be that juvenile striped bass are simply more available to sites in lower salinity areas. Nonetheless, by modeling the effects of habitat variables specifically on ψ^{II}, the conditional probability that a site would host a high abundance of juvenile striped bass, we feel that our results provide strong evidence that salinity plays a role in the selection of habitats. The spatial scale of the analysis could be refined in further work to address this issue (see), but accounting for the movement of juveniles from the spawning areas would require more intensive sampling within a year.

Contrast in habitat variables

The contrast in some of the habitat variables that we included, especially substrate, may be inadequate to capture effects of those variables. For example, substrate is linked to benthic prey production and may indeed play a role in habitat selection, but the seine survey sampling sites only provided observations of substrate in two categories that may not differ much in their attraction to juvenile striped bass (silt vs. sand). Similar arguments could be made about water clarity (secchi depth) and temperature. In particular, water temperature at the seine survey sampling sites fluctuates within a fairly narrow window during the summer (averages ranged from about 26 to 31°C).

Model assumptions

Multi-state occupancy models provided a valuable new approach for investigating habitat selection while accounting for detectability and utilizing the limited information available in the raw catch data. The models are extensions of capture-recapture theory in which sites are treated as individuals (MacKenzie *et al.* 2006). Similar to capture-recapture models,

occupancy models are subject to a number of important assumptions. The models we used require three critical assumptions:

1. Detectability and the probability of occupancy is constant among sites except for heterogeneity accounted for by the inclusion of covariates. In other words, there is no remaining heterogeneity in detection or occupancy probabilities.

2. Detection of juvenile striped bass and the detection histories at each site are independent.

3. Survey sites are closed to changes in occupancy by juvenile striped bass throughout the first three rounds of the survey. In other words, detection histories represent a series of observations at sites that are either occupied or not occupied during the three rounds.

As with capture-recapture models, assumption 1 is not likely to ever be met in full (see Royle 2006), but we hope to have guarded against bias by a careful approach to modeling that included effects of local abundance on detectability (multi-state approach) and important covariates for both detectability and occupancy. We expect that assumption 2 was well met in our analysis because sampling sites are spaced far apart relative to the dispersal ability of juvenile striped bass. Overdispersion may be a remaining concern due to the tendency of juvenile fish to shoal together. As with capture-recapture models, goodness-of-fit (GOF) tests can be used with occupancy models to assess overdispersion and correct modeling results by way of a variance inflation factor ($\hat{c}$; MacKenzie *et al.* 2006). However, Nichols *et al.* (2007) found that the standard GOF tests do not perform well for multi-state occupancy models, and this is an area of continuing research. In our analysis, worries about overdispersion are tempered by the unequivocal support for a simple model with only salinity as a covariate for occupancy (i.e., no model selection uncertainty).

The last assumption is the most critical in obtaining unbiased estimated of detectability and is often of central concern in occupancy models. To estimate detectability, occupancy models require that repeated samples at a site be close together in time relative to the time scale over which changes in occupancy occur. For our sampling, the essential assumption is that sites are either occupied or not occupied throughout the first three rounds, a period of about six weeks. The ideal frequency of repeat samples will be dependent on the developmental stage of the organism being studied, and for juvenile striped bass the frequency should probably be shorter than once every two weeks (perhaps three consecutive days). In

general, this assumption is unlikely to be met in our analysis or most applications to fisheries survey data, but random changes in occupancy within a season still lead to unbiased estimates of occupancy (MacKenzie *et al.* 2006). When random changes in occupancy occur, as is expected for mobile species like juvenile striped bass, a more practical interpretation of occupancy is that of habitat "used" during the season rather than habitat "occupied" throughout the season (MacKenzie 2005). Such an interpretation is entirely reasonable for our purposes. When the closure assumption is violated, the parameters for detectability also absorb some of the probability that the species was present at the site, further reinforcing the importance of estimating detectability.

One additional concern related to assumption 3 is that sites may experience continuous loss of occupancy status, such as might occur if juvenile striped bass are leaving the sampling area continuously. Such directional changes in occupancy should result in inferences being strictly applicable only to conditions present near the start of the season, but with more than two sampling events (here, rounds) the true bias is not clear (MacKenzie *et al.* 2006). Some protection against bias is obtained if models are fitted with round-specific detectability, as in our case, because the detectability parameters absorb some of the effects of emigration. For example, a decline in detectability through the rounds might indicate that emigration is occurring, but the small size of this effect in our results indicates that it is not a serious concern. By focusing on the first three rounds of the survey, we aimed to estimate occupancy and detectability during a season in which juvenile striped bass are resident in a given river reach. Nonetheless, small directional changes in occupancy do not appear to have affected our inferences about habitat selection.

Suggestions for future research

1. The multi-state modeling framework could be extended to include stratification of the river systems into salinity zones. By accounting for the large-scale effects of salinity within appropriately defined strata, modeling could focus on the effects of habitat variables at smaller spatial scales and the relative importance of the effects that appeared unimportant at a large scale could be discerned.

2. The robustness of results to the chosen criteria for abundance state classification (two states split at a catch of 10 individuals) can be assessed by considering more or different classifications. For example, the high abundance state could be further divided into two states (medium, high).

3. Occupancy models could incorporate more complex relationships between habitat co-variates and occupancy and detectability. For example, occupancy could be modeled as a dome-shaped (polynomial) function of salinity to determine whether juvenile striped bass were selecting optimal, intermediate salinities.

4. Studies could be designed to estimate detectability and occupancy more generally for the juvenile striped bass population in order to more fully define important nursery areas. Our inferences pertain strictly to that portion of the population available in relatively shallow water at sites that can be sampled by beach seines. We do not know what proportion of the population is sampled by the survey and whether that proportion changes over the course of the summer. Studies aimed at the larger population would likely need to include more and different gears and a larger sampling frame.

5. Multi-state, multi-season occupancy models could be used to explore changes in occupancy among years (here season refers to the sampling season, the first three rounds of the seine survey). In our analysis, we used single-season models and accounted for expected annual changes in occupancy with covariates (e.g., wet/dry years). Multi-season models would specifically model the dynamics of occupancy at sites through time (MacKenzie *et al.* 2006). Although the cohort of juvenile striped bass is new each year, this approach could be used to investigate whether sites occupied by high abundances are more consistently occupied than sites that are occupied by low abundances. Sites with marginal habitat might be expected to experience more turnover in occupancy, perhaps associated with overall population abundance. Studies to investigate within-year changes in occupancy, as might be related to shifting distribution of fish, would need to be designed with more intensive sampling, as the seine survey data are not suited for that purpose.

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