Identifying Priority Areas for Protection and Restoration: Chesapeake Bay Striped Bass Spawning and Larval Nursery Areas as a Model

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Life History and Habitat

In simulations of fish population response to habitat perturbations, vastly different population sizes can result from a fixed change in mortality rate, depending on where and when it occurs, which life stages are impacted, and at which life stages the population is most sensitive to change (Schaaf et al. 1993). I extended this basic concept to select striped bass spawning areas and larval nurseries as priority habitat. These two areas are essentially one in the same spatially and are designated by regulation in Maryland and Virginia. Extended life cycle tests with several species of fish and a variety of toxicants found that early life stages were most sensitive and larvae were extremely sensitive to anthropogenic inputs to the environment (McKim 1997; Peterson et al. 1982; Bengston et al. 1993). I have evaluated risk to this critical striped bass habitat posed by general land-use (agriculture or development) rather than specific water quality factors (nutrients, chlorophyll, and DO). Best management practices (BMPs) for both agriculture and development are often targeted at reducing a specific impact (usually nutrients), but may ameliorate others that are harmful as well.

Human-related land use in the Bay watershed is dominated by agriculture (28.5% of watershed), but developed land (residential and commercial) is a major and growing use (3.6%; Chesapeake Bay Program or CBP; http://www.chesapeakebay.net/wspv31/(jczrasnky43gsp45dwsepr45)/WspAbout.aspx?basno=1&topic=5). Striped bass spawning areas are typically on the receiving end of large amounts of agricultural drainage because of their location at the junction of large fluvial systems and brackish estuaries. Some (Patuxent, Potomac, and James rivers) also receive drainage from large urban and suburban areas. Human population is projected to grow in all watersheds, displacing natural and agricultural landscapes in the process (CBP; http://www.chesapeakebay.net/wspv31/(jczrasnky43gsp45dwsepr45)/impacts1.aspx?basno=1) .

Striped bass are anadromous, long-lived, late maturing, highly fecund, and exhibit complex migrations (by age and sex; Boreman and Lewis 1987; Rago and Goodyear 1987; Rago 1991; Dorazio et al. 1994; Secor and Piccoli 2007). Population dynamics of striped bass are driven by dominant year-classes: longevity (in the absence of heavy fishing) ensures that these strong year-classes will reproduce over many years and dampen the effects of environmental variation (Rago and Goodyear 1987; Rago 1991).

Striped bass are sensitive to habitat perturbations because the population becomes concentrated in relatively small geographic areas at various life stages (Schaaf et al. 1993). This occurs to the extreme in spring when Chesapeake Bay Stock of spawning adults, their eggs, and their larvae (yolk-sac and postlarvae) are confined in limited reaches of 16 Bay tributaries (Hollis et al. 1967; Grant and Olney 1990; Schaaf et al. 1993; Table 1). Striped bass spawning and larval nursery areas are located in the fresh-low salinity tidal reaches within the coastal plain and the estuarine turbidity maximum is particularly important (North and Houde 2003). Year-class success of striped bass is largely determined by the first three weeks of life and is a product of egg abundance and survival through the postlarval stage (Uphoff 1989; 1993; Houde 1996).

Production from Chesapeake Bay spawning areas has been estimated to account for up to 90% of landings along the entire Atlantic Coast (Richards and Rago 1999). Generally, the dimensions of these spawning areas were determined by egg collections (Table 1); however, size was expressed as area in Maryland (Hollis et al. 1967) and volume in Virginia (Olney et al. 1991). Egg production has been estimated in some Maryland and Virginia rivers (see Table 1 for references), but comparisons are complicated by an absence of estimates for all systems and large differences in stock status when collections were made (Uphoff 1999).

Uphoff (1999) determined egg production was strongly related to area of spawning habitat for years of similar stock status (determined by egg-presence absence; Uphoff 1997) in six Maryland tributaries during 1989-1996 ($r^2 = 0.99$, $P < 0.0001$) and this relationship was used to fill in missing egg production estimates for Maryland spawning tributaries (Table 1). This relationship was described by the equation: $P = (49.2*H) + (8.67*10^8)$; where H is area of spawning habitat in m^2 and P is egg production. This strong relationship indicated the presence of a density-dependent mechanism that allocated egg production evenly among systems despite differences in year-class success among areas that should have distributed egg production differently if straying was minimal (Uphoff 1999).

Annual egg production in Virginia's spawning areas was estimated during 1980-1989 (Table 4 in Olney et al. 1991). Estimates for all four areas were only made during 1980-1983; this was a period of lower spawning stock status (indicated by egg presence-absence in Maryland). Estimates of average production in each of Virginia's four areas during 1980-1983 in Olney et al (1991) were rescaled to reflect the higher stock status when Maryland estimates were made. Average egg production for each Virginia river during 1980-1983 was multiplied by the ratio of Pamunkey River production during 1989 to Pamunkey River mean production during 1980 and 1983. Pamunkey River was the only Virginia spawning system with an estimate for 1989 (Olney et al. 1991), so I assumed that relative differences between the early and late 1980s were the same in remaining Virginia rivers. These rescaled estimates indicated that egg production in James and Rappahanock rivers was about 45-60% of Maryland's large Potomac River and Head-of-Bay spawning areas, while Pamunkey and Mattaponi rivers were comparable to the Nanticoke and Chester rivers, respectively (Table 1).

Throughout their range, striped bass have exhibited resistance or strong responses (both positive and negative) to spawning habitat changes. Location of the spawning area in the Head-of-Bay system, perhaps the Bay's largest spawning area, may have shifted during the early 20th century because of construction of dams on the Susquehanna River and conversion of the Chesapeake and Delaware Canal to a sealevel waterway (Dovel and Edmunds 1971). Hudson River has been severely contaminated with PCBs for decades (Schneider et al. 2007), yet indices of striped bass year-class success have not deteriorated noticeably (Atlantic States Marine Fisheries Commission or ASMFC 2005). Installation of secondary wastewater treatment in the Philadelphia area improved water quality and allowed striped bass spawning to become re-established in Delaware River after decades of poor water quality (Weisberg and Burton 1993). Alteration of natural river flow due to dam operation, water withdrawal, and harbor maintenance have been implicated in declines in Roanoke River (Rulifson and Maooch 1990), the Santee-Cooper System (Bulak et al. 1997), Savannah River (Reinert et al. 2005); and the Sacramento-San Joaquin Estuary (Stevens et al. 1985; Setzler-Hamilton et al. 1988). Restoration of “natural” salinity in Savannah River spawning habitat was followed by increased captures of wild larvae and juveniles (Reinert et al. 2005).

A severe and extended depression of Chesapeake striped bass year-class success lead to poor catches along the mid-Atlantic and New England during the mid-1970s and into the early 1990s (Richards and Rago 1999). Overfishing and poor water quality conditions for striped bass larvae were hypothesized as major contributors to the decline of Chesapeake Bay striped bass. Toxic water quality conditions (low conductivity, alkalinity, hardness, and pH and high levels of trace metals) and low water temperatures (< 12 °C) encountered by striped bass larvae were implicated in episodic mortalities in Chesapeake Bay tributaries in the 1980s (Uphoff 1989; 1992; Hall et al. 1993; Secor and Houde 1995; Richards and Rago 1999). Uphoff (1989; 1992) concluded that these factors operated independently; egg-prolarval survival was reflective of water temperature and postlarval mortality was associated with water quality conditions. Poor conditions at either or both stages would produce a poor year-class, while optimal conditions were needed at both stages for a good year-class.

Uphoff (1999; 2000) explored long-term early life stage survival of striped bass since 1955 (updated to present) for four major Maryland spawning tributaries (see Appendix 1 for methodology). Indices of juvenile and egg relative abundance that tracked recruitment (arithmetic mean catch of juveniles per standard seine haul in four Maryland spawning areas; Goodyear 1985) and spawning stock (egg-presence absence in plankton collections in Maryland spawning areas; Uphoff 1993; 1997) were combined in a tabular stock-recruitment analysis to derive 1955-2006 larval survival history. Larval survival was highly variable prior to the 1970s, but a sustained period of low survival occurred in the mid-1970s through the early 1980s (Figure 1). Reduced recruitment due to poor larval survival was rapidly followed by high fishing mortality and a decline in both resident and migratory biomass (biomass and fishing mortality described in Gibson 1993;

Uphoff 1993; Uphoff 1997; ASMFC 2005). Larval survival began to rise in the 1980s and recovered by the 1990s (Figure 1); rebuilding of stock biomass was concurrent with recovery of larval survival and conservative fishing rates. Timing and magnitude of recovery of larval survival was not the same in each system, which could have altered relative production of juveniles from these four spawning areas (Uphoff 1999).

Trends in year-class success of other anadromous fish in Maryland's portion of Chesapeake Bay offer support that early life stage habitat conditions greatly influenced population dynamics of striped bass. Yellow and white perch share the larval nursery of striped bass (Uphoff 1991; North and Houde 2001; 2003) and trends in juvenile indices (http://www.dnr.state.md.us/fisheries/juvindex/index.html) of these species are quite similar (Figure 2) despite different management strategies, maturation (Fishbase life history tool www.fishbase.org), migrations (white and yellow perch are semi-anadromous; Lippson 1973), spawning locations (upstream of striped bass; Lippson 1973), egg types (demersal and adhesive versus semi-buoyant; Lippson and Moran 1974), and adult trophic levels (Fishbase life history tool www.fishbase.org).

Agricultural Practices and Larval Survival

Agricultural pesticides and fertilizers were thought to be potential sources of toxic metals implicated in some episodic mortalities of striped bass larvae in Bay spawning tributaries (Uphoff 1992; Richards and Rago 1999). Agriculture has represented a declining portion of the Bay's watershed since the 1850s, but use of commercial fertilizers grew dramatically after the 1950s (Kemp et al. 2005). Other changes in the character of farming occurred between 1959 and 1974 (USDA 1978). On the Delmarva Peninsula, number of farms decreased, average farm size increased, while cash grain and poultry farming greatly increased and dairy and general farming declined (USDA 1978). Agricultural nutrient management led to downward trends in flow-adjusted nutrient concentrations in the watersheds of the major rivers of the Chesapeake Bay after 1985 (Sprague et al. 2000; Kemp et al. 2005), all of which were also striped bass spawning and larval nursery areas.

In 1994, the Caroline County Soil Conservation Service District Conservationist supplied records of implementation of nine major agricultural BMPs during 1980-1990. Caroline County borders a major portion of the Choptank River nursery and I assumed these records were indicative of measures implemented in the watershed (other counties did not have good records). An increasing trend in survival of postlarvae in Choptank River during 1980-1990 coincided with growth of agricultural land conservation programs that were designed to conserve soil and reduce nutrient runoff (Figure 3). A correlation analysis of these BMPs with estimates of postlarval survival (derived in Uphoff 2000; see Appendix 1 for methodology) indicated that as many as four BMPs were positively associated at a high level of significance (Table 2). Two measures that accounted for the greatest acreage, conservation tillage and cover crops, were most strongly associated with increased postlarval survival (r = 0.88 and 0.80, respectively; Table 2; Figure 3). A positive byproduct of agricultural BMPs in Choptank River watershed may have been reduced contaminant runoff, even though BMPs were aimed at reducing nutrients. Acidic deposition, pesticides, and phosphate ores in fertilizers could have been sources of toxic inorganic metals (Brady 1974; May and McKinney 1981; Peterson et al. 1982) implicated in episodic mortalities of postlarvae in Choptank River (Uphoff 1992).

These associations and coincidental trends may not indicate cause and effect, but they suggest that there is some chance that agricultural BMPs were beneficial for larval striped bass survival. Continuation, expansion, and enhancement of these practices reduce risk that detrimental conditions in the larval nurseries associated with runoff from agricultural areas could arise, regardless of the ultimate cause.

Urban Development and Striped Bass and Anadromous Fish Spawning and Larval Areas

Increasing urban sprawl associated with population growth has been identified as a threat to the Chesapeake Bay watershed (CBP 1999). Land is converted to impervious surface (IS; paved surfaces, buildings, and compacted soils) as human population grows (Beach 2002). A variety of studies have documented a deterioration of freshwater aquatic ecosystems as IS occupies more than 10% of a watershed (Cappiella and Brown 2001; Beach 2002) and similar impacts have been noted in Chesapeake Bay subestuaries (King et al. 2004; McGinty et al. 2006; Uphoff et al. 2007). Impervious surface increases runoff volume and intensity in streams, leading to physical instability, increased erosion, and sedimentation (Beach 2002). This runoff, warmer than water draining forests or other porous lands, becomes a source of thermal pollution. Impervious surface runoff transports a wide variety of excess nutrients that contribute to algae blooms, hypoxia, and anoxia. Toxic metals and detrimental organic compounds may also be found in this runoff (Beach 2002).

There are indications from other anadromous species that reproductive success of striped bass could be impaired by conditions associated with moderate to high levels of development. Anadromous fish egg densities (alewife and white perch) in the Hudson River exhibited a strong negative threshold effect to urbanization (Limburg and Schmidt 1990). White and yellow perch adults, eggs and larvae were far less likely to be found in Bush River streams during 2006 (≈13% IS) than 1973 (IS ≈9%; Uphoff et al. 2007). Anadromous fish spawning was detected more frequently in streams in less developed Aberdeen Proving Ground (≈3% IS in 1973 and 2006) than in streams in the adjacent Bush River watershed (Uphoff et al. 2007). Severn River (17% IS) yellow perch exhibited depressed egg and larval viability during 2001-2003 in comparison with other, less developed watersheds (Uphoff et al. 2005).

Siltation, impoundment, removal of substrate, physical alterations, toxic or organic pollution, and increased acidification were cited as possible mechanisms that would depress anadromous fish spawning as urbanization of the Hudson River watershed progressed (Limburg and Schmidt 1990). Salinity intrusion into the Severn River's upper tidal yellow perch spawning area and poor summer dissolved oxygen (DO) throughout juvenile and adult habitat were two significant issues potentially attributable to urbanization of the watershed (Uphoff et al. 2005). PCB concentrations in white perch and bottom DO levels in summer were closely related to impervious surface levels in Chesapeake Bay tributaries (King *et al*. 2004; McGinty et al. 2006; Uphoff et al. 2007).

Low DO and anthropogenic chemicals such as PCBs disrupt endocrine function associated with reproduction and are associated with depressed survival, malformation, and abnormal chromosome division of eggs and larvae (Longwell et al. 1992, 1996; Colborn and Thayer 2000, Rudolph *et al.* 2003).

Striped bass spawning areas were overlaid onto the CBP map of estimated development pressure (http://www.chesapeakebay.net/status.cfm?sid=197; Figure 4). Visually, all spawning area watersheds appeared to be under moderate to very high development pressure (Figure 4).

McGinty et al. (2006) proposed a general IS – fisheries management framework for Maryland's Chesapeake Bay tributaries. In systems with less than 5% IS, fish habitat would generally be considered unimpaired and harvest management actions should be effective; habitat preservation would also be desirable. Five percent might be considered a target level of IS representing a compromise between maintaining spawning area productivity while allowing for some development. As IS increases from 5 to 10%, habitat loss would increasingly have a negative influence on population dynamics. Fisheries managers would need to contemplate compensating for additional habitat-related losses by increasing adjustments to harvest or by lobbying successfully for land use changes, urban BMPs, or increased pollution control with responsible agencies. At or above this 10% IS threshold of habitat stress, successful preservation or restoration of resident stocks by traditional harvest adjustments becomes unlikely and habitat restoration would be the key to maintaining sustainable fisheries (McGinty et al. 2006).

Impervious surface reference points proposed by McGinty et al. (2006) were combined with projections of impervious surface in spawning area watersheds to quantitatively explore risk from development. Impervious surface thresholds in McGinty et al. (2006) were based on Towson University or Maryland Department of Planning (MDP) estimates. These methodologies were not identical, but estimates were generally close when both techniques were applied. However, these methodologies produced noticeably higher estimates than CBP RESAC-based analysis of satellite imagery. CBP watershed profiles (http://www.chesapeakebay.net/wspv31/(14e5iz450y3qys3sns0dycrz)/WspAbout.aspx?basno=1&topic=5) have RESAC estimates of IS, watershed area, and census estimates of human population for each of the striped bass spawning area watersheds. These estimates provided a basis for a series of regressions that translated CBP IS estimates into the same IS scale as those used to develop IS thresholds by McGinty et al. (2006). .

I used linear regression to estimate the relationship of people per square mile of watershed (2000 census) versus CBP IS for each of the spawning areas; whole watershed estimates were used. Watershed IS were represented by regional CBP estimates in some cases. Upper Eastern Shore region estimates described the Chester River watershed and the lower Eastern Shore region described Blackwater, Transquaking, Chicamicomico, Nanticoke, Wicomico, Manokin and Pocomoke River spawning area watersheds. This relationship was described by the equation: IS = (0 .000579*P) + 0.58; where IS = percent impervious surface and P = people per square mile ($r^2 = 0.88$, $P < 0.0002$, $N = 9$). This relationship was then used to estimate CBP IS in 2020 from projections of watershed population per square mile in 2020. I then developed a regression to convert CBP IS into the same IS currency as those of Towson University or MDP based on 13 watersheds (not striped bass spawning areas) studied by McGinty et al. (2006). This relationship was described by T = (2.09*R) + 1.5 ($r^2 = 0.86$, $P < 0.0001$); where T is percent impervious surface estimated by Towson University or MDP and R = CBP estimate of percent impervious surface. This convoluted path provided a means for applying McGinty et al. (2006) thresholds to 2000 and 2020 IS estimates.

Impervious surface estimates (Towson University or MDP units) for striped bass watersheds in 2000 ranged from 3.7% to 10.2% (Figure 5). In 2000, most watersheds fell below the 5% IS target, but Patuxent River met the 10% IS threshold and Potomac and James rivers fell between 5% and 10% IS. Projections of impervious surface in 2020 indicated that the three most urbanized spawning areas (Patuxent, Potomac, and James rivers) will experience the greatest proportional gains in IS, while remaining systems would stay just below the 5% IS target. These three urbanized spawning areas appeared most at risk from development. Potomac and James rivers are among the largest spawning areas in the Bay and their watersheds should be a priority area for urban BMPs.

Patuxent River may present a dilemma for prioritizing limited habitat restoration dollars. Patuxent River has a small striped bass spawning area, low egg production, and the watershed is projected to move beyond 10% IS by 2020 (Figure 5). Its upper region is located in a belt of high impervious surface expanding from the Washington – Baltimore corridor that could undergo more development than projected due to military base relocations to Fort Meade. Smaller tributaries within this western shore belt have experienced serious deterioration of fish habitat and declines in spawning success of white and yellow perch (Uphoff et al. 2005; McGinty et al. 2006). The cost of retrofitting stormwater measures in Anne Arundel County, where a substantial portion of Patuxent River and other impaired tributaries are located, has been estimated at $400 million and county residents and government have not endorsed the costs associated with this effort (Ferguson 2005).

Detecting changes in first year survival of striped bass in response to anthropogenic factors (such as impervious surface) is exceedingly difficult because of high natural variability in reproduction (Schaaf et al. 1987; Rago 1991). Retrospective analysis of egg-larval survival indicated that two to three year depressions in larval survival have not been uncommon throughout the time series, but sustained periods of four or more years may indicate deterioration of nursery habitat of striped bass (Figure 1; Uphoff 1999; 2000). Such a nadir (5-17 years of poor survival) occurred in the mid-1970s through the mid-1990s in the four major nurseries and was indicated by a low, flat spot in three-year moving averages of survival in three spawning areas and a steady decline in Head-of-Bay. During the 1990s, larval survival returned to patterns observed in the mid-1950s and 1960s. Rises and declines in larval survival occurred periodically prior to the 1970s, but a sustained period of low survival was only evident in these systems in the mid-1970s through the early 1980s (Uphoff 1999; 2000).

Certainly, urbanization is not the sole explanation if declines in larval survival are detected. Years of process oriented research and analysis might provide clues, maybe even definitive evidence of cause and effect, but this depends on forming correct hypotheses about what aspects of urbanization would be associated with a decline.

Threshold effects of urbanization have been observed for other anadromous fish (Limburg and Schmidt 1990; Uphoff et al. 2005) and this possibility exists for striped bass spawning. A threshold implies a sudden decline in resource status that cannot be easily reverted to an acceptable level; in some cases the changes are practically irreversible (www.thresholds-eu.org). Fortunately, the existence of an urbanization threshold for striped bass areas is undefined because it has not been crossed – yet. Experience with the decline of striped bass in the 1970s (Richards and Rago 1999) would indicate a lag in detection and action would be likely. As an alternative, we could attempt to manage growth, IS, and water quality now as broadly as possible to preserve natural infrastructure needed for successful striped bass spawning.

Assessment Needs

- Long-term data on agricultural practices and BMPs by watershed to compare with 1955-present larval survival estimates for the Choptank, Nanticoke, Patuxent, and Potomac rivers and Head-of Bay.
- Compare severity of agricultural "hot-spots" to tributary trends in larval survival.
- Better understanding of linkage of nutrients and conditions impacting larval survival.
- Determine relative importance of regions in spawning area watersheds. Are immediately adjacent areas more important than upstream?
- Develop a "standard" set of impervious surface estimates for use in analyses.
- Refine impervious surface projections by using individual watershed estimates and portions of watersheds adjacent to and upstream of spawning areas.
- Incorporate uncertainty of relationships used to translate units of IS (risk assessment).
- Initiate research to understand the effect of urban BMPs on success of anadromous fish spawning.
- Develop criteria for prioritizing areas for protection and restoration.

Management Needs

- Risk assessment / risk management strategies and tactics for land-use and BMPs for preserving spawning and larval habitats.
- Prioritization of spawning areas for management (decision tree?).
- Natural resource zoning that is capable of influencing local decisionmaking.

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Table 1. Comparison of Chesapeake Bay striped bass spawning area size and egg production in years of similar stock status. Years refers to the years where mean egg production was estimated; R 1989-1996 indicates that production was predicted from the linear regression of spawning area hectares to egg production estimates (Uphoff 1999); 1989 equivalent indicates mean estimates for 1980-1983 were rescaled to a 1989 equivalent. Reference refers to study that estimated egg production.

Spawning area	Hectares	Volume 10^6 m^3	Mean Egg Production 10^9	Years	Reference
Potomac	22162.2		11.3	1989	Rutherford and Houde 1997
Patuxent	1010.5		0.66	1991	Secor et al. 1994
Head-of-Bay	27225.4		14.6	1989	Rutherford and Houde 1999
Chester	785.5		1.6	1996	Burton et al. 1996
Choptank	1734.1		1.72	R 1989-1996	Uphoff 1999
Blackwater	238.4		0.98	R 1989-1996	Uphoff 1999
Transquaking & Chicamacomico	170.0		0.95	R 1989-1996	Uphoff 1999
Nanticoke	3033.6		2.6	1992 & 1994	Houde et al. 1996
Wicomico	648.7		1.19	R 1989-1996	Uphoff 1999
Manokin	22.7		0.88	R 1989-1996	Uphoff 1999
Pocomoke	417.2		1.07	R 1989-1996	Uphoff 1999
Rappahanock		183.36	6.4	1989 equivalent	Olney et al. 1991
Pamunkey		135.78	2.3	1989	Olney et al. 1991
Mattaponi		42.19	1.8	1989 equivalent	Olney et al. 1991
James		479.28	6.6	1989 equivalent	Olney et al. 1991

Table 2. Caroline County agricultural best management practices and their correlation (r) with estimates of Choptank River striped bass postlarval survival during 1980-1990. Minimum level for all practices was zero. Multiple comparisons indicated adjustment of P = 0.05 by dividing it by number of comparisons (9) would be prudent. This adjusted level of significance equaled 0.0045.

Practice	Units	Maximum	r	P
Waste management system	Number	49	0.24	0.468
Waste storage structure	Number	30	0.36	0.282
Conservation cropping system	Acres	10,658	0.36	0.28
Conservation tillage system	Acres	16,505	0.88	0.0004
Cover crops and green manure	Acres	16,621	0.80	0.0029
Critical area plantings	Acres	54	0.85	0.001
Crop residue use	Acres	10,425	0.33	0.32
Grade stabilizing structures	Number	61	0.58	0.06
Waste utilization	Acres	8,592	0.74	0.008

Figure 1. Baywide striped bass egg-larval survival (mean of 4 spawning area estimates). Horizontal lines indicate time period averages.

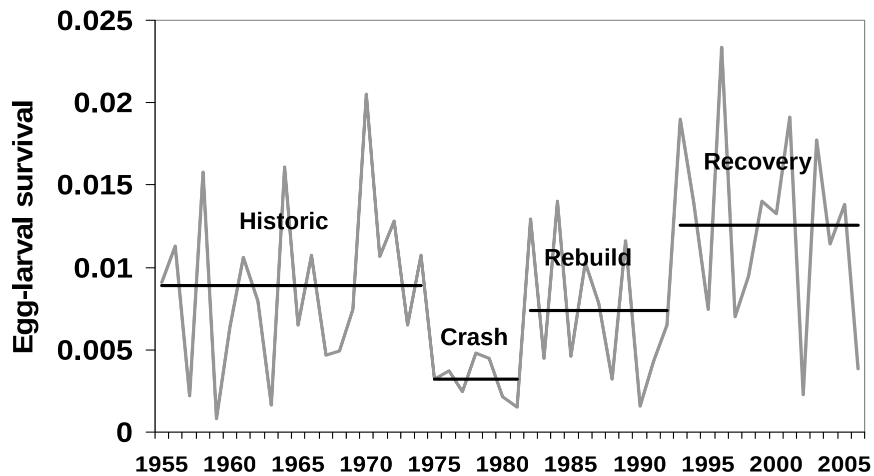


Figure 2. Standardized (z-transformed) Maryland juvenile indices of striped bass, white perch, and yellow perch. Indices are annual means of four spawning areas except for yellow perch.

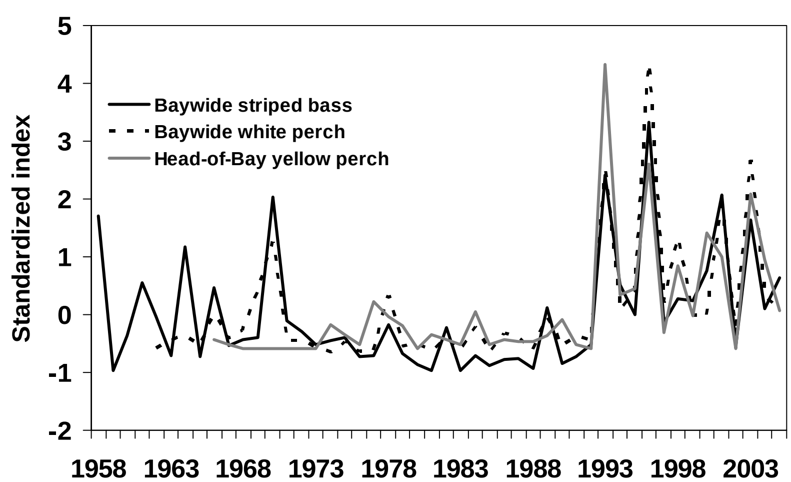


Figure 3. Choptank River striped bass postlarval survival and trends in two Caroline County, MD, agricultural BMPs. These BMPs were significantly correlated ($P < 0.05$) with postlarval survival (Table 2).

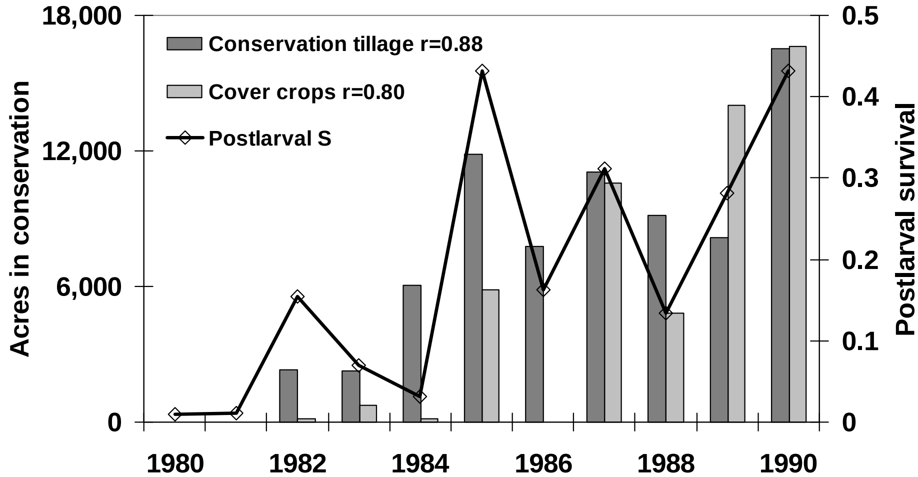


Figure 4. USGS projections of development pressure in the Bay watershed and approximate locations of striped bass spawning areas (black ovals). Some ovals contain multiple spawning areas. See Table 1 for a complete listing.

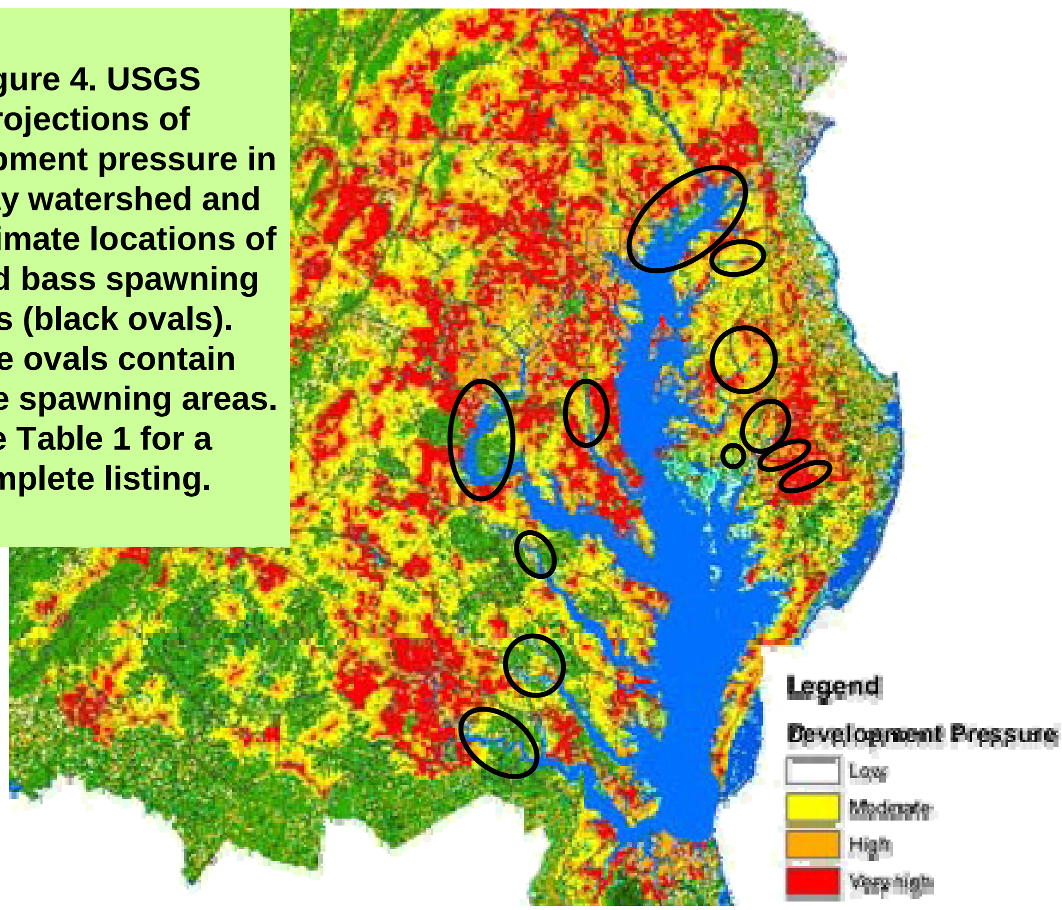
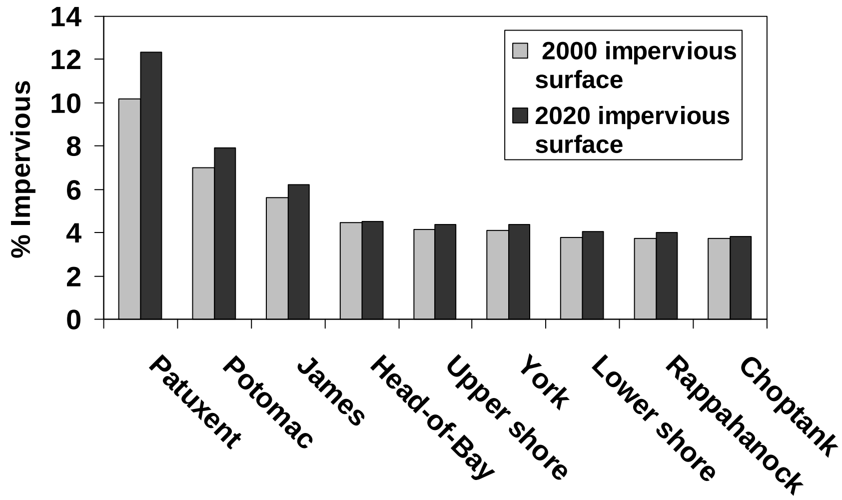


Figure 5. Estimated percent impervious surface in striped bass spawning area watersheds in 2000 and 2020.



Appendix 1 – Methods for estimating egg-larval survival

This description of methods is adapted from Uphoff (2000). The complete series of analyses related to this time-series can be provided.

An updated tabular stock-recruitment analysis provided a foundation for judging larval survival trends in each spawning system since 1955. Recruitment was measured by system-specific arithmetic mean juvenile indices of the Head-of-Bay and Potomac, Choptank, and Nanticoke rivers (Uphoff 1997). Spawning stock in each system was represented by baywide egg-presence absence (E_p; pooled estimate for systems sampled each year). Ranges of E_p and juvenile indices during 1955-1999 were broken into categories (E_p intervals of 0.1 and juvenile index intervals of 3.0). The lowest category of E_p consisted of values between 0.35 and 0.51; pooling these two intervals provided a larger sample size. Juvenile indices greater than 30 were pooled into a single interval.

I tested whether recruitment within E_p intervals was lognormally distributed with a Shapiro-Wilk test on $\log_e$-transformed juvenile indices (SAS Institute 1987). If lognormally distributed recruitment was indicated, I determined the mean, SD, and CV of the $\log_e$-transformed juvenile indices within each E_p interval to examine how average recruitment and its variation changed with spawning stock. Lognormal recruitment distributions have been found in many stock-recruitment data sets, were theoretically justified, and were a recommended starting assumption for stock-recruitment analyses (Hennemuth et al. 1980; Hilborn and Walters 1992).

The mean and standard deviation of the $\log_e$-transformed juvenile indices was used to generate a cumulative distribution of expected juvenile indices (N = 3,000) for each E_p category. These indices were transformed back to an arithmetic scale and used to depict the cumulative probability that system juvenile indices occurred at their value. This cumulative probability indexed relative larval survival (R_b) for each system. Low survival was indicated by a cumulative probability that approached 0 and high survival was indicated by a cumulative probability that approached 1.0. Cumulative percentages of a juvenile index occurring were fit to Weibull functions with SAS Proc NLIN to describe the R_b probability functions mathematically for each E_p category (SAS 1988). Juvenile indices ranged from 0-104 striped bass per standard seine haul in increments of 1 in the Weibull analyses. The asymmetric Weibull function is described by the equation $R_b = R_A\{1 - e^{[-(J\ /\ S)\wedge b]}\}$; where R_b is relative survival as cumulative percent; R_A = asymptotic percent where juvenile indices approach infinity; J = juvenile index; S = the value at which $R_b = 0.63 * R_A$; and b is a shape factor (Prager et al. 1989).

A predictive equation was developed from the regression of 1980-1990 Choptank River R_b and estimated proportions surviving from the egg to 12 mm total length (S_L; described below) during 1980-1990 to translate R_b for all years and systems into S_L; both estimates were $\log_e$-transformed because I expected total survival rates to be lognormally distributed because they were the product of independent survival of multiple life stages (Hilborn and Walters 1992). Relative abundances of larvae as small as 8 mm standard length or 10 mm total length have been correlated with juvenile indices and represented endpoints of processes that largely determine striped bass year-class success (Uphoff

1989, 1992; Houde 1996). Time trends in S_L for each system were estimated by using three year moving averages. Walters and Hilborn (2005) recommended using 3-year moving averages to recover historical changes in recruitment rates from relative abundance and catch data and I applied this smoothing to recover changes in larval survival rates. This smoothing overcomes variance caused by measurement error and improves reconstruction in cases with abrupt changes in recruitment (Walters and Hilborn 2005).

I estimated total survival from the egg through the postlarval stage (total larval surivival) in the Choptank River during 1980-1990 as the product of prolarval and postlarval survival. I used the methodologies described in Uphoff (1993) to estimate prolarval survival (number of 6-mm larvae / eggs) and postlarval survival, with one exception. Analysis of covariance (ANCOVA) was used to estimate daily instantaneous growth (*G*) and mortality (*Z*) rates of postlarvae instead of regression analysis. Year was treated as a covariate and 1980-1990 data were analyzed together rather than as separate regressions as in Uphoff (1993). ANCOVA provided more precise estimates of G or *Z* than regression analysis of each year (Dowdy and Weardon 1991). The ANCOVA (PROC GLM in SAS) tested for heterogeneity among the annual slopes of either length versus age or $\log_e$-transformed abundance versus age (Littel et al. 1991). If differences in slopes arose ($P \leq 0.05$) , annual estimates of *G* and *Z* were constructed. If slopes were not different, a common *G* or *Z* would be estimated. Postlarval survival was estimated as e^{-Zt}.