Modeling spatial and temporal variation of suitable nursery habitats for Atlantic sturgeon in the Chesapeake Bay

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Abstract

For rare and endangered species, bioenergetics modeling can represent a valuable approach for understanding issues of habitat value and connectivity among potential habitats within nurseries in restoration programs. We used multivariable bioenergetics and survival models for Atlantic sturgeon to generate spatially explicit maps of potential production in the Chesapeake Bay. For the period 1993–2002, spatial and temporal patterns in water quality effects (temperature, dissolved oxygen [DO] and salinity) on potential production were evaluated. In addition, two forecasted scenarios were modeled: one implementing newly revised U.S. Environmental Protection Agency (EPA) DO-criteria for the Chesapeake Bay, and the other assuming a bay-wide increase of 1 °C due to an underlying trend in regional climate. Atlantic sturgeon's low (survival/growth) tolerance to temperatures >28 °C was a critical constraint during their first 1–2 summers of life. Hatched in freshwater (spring to mid-summer), young-of-the-year were predicted to occupy cooler (deeper) areas as temperature approached sub-lethal levels. While most thermal refuges were located down-estuary, a large fraction of potential refuges were unsuitable due to persistent hypoxia and/or salinity levels beyond the limited osmoregulatory capabilities of early juvenile Atlantic sturgeon. As a result, suitable summer habitats for juvenile Atlantic sturgeons in the Chesapeake Bay were predicted to be spatially restricted and variable between years, ranging from 0 to 35% of the modeled bay surface area. In critical (drought) years, almost no summer habitat was predicted to be available for juvenile Atlantic sturgeon. Value and size of nursery habitat was highly sensitive to climatic oscillations and anthropogenic interventions affecting freshwater inflow, water temperature and/or DO. Achieving EPA DO-criteria for the Chesapeake Bay was predicted to increase total suitable habitat by 13% for an average year, while increasing water temperature by just 1 °C bay-wide would reduce suitable habitat by 65%.
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1. Introduction

Habitat management in fisheries in the U.S. was accelerated by the new federal standard, Essential Fish Habitat (EFH), implemented in the 1994 Magnuson–Stevens Act. This act mandated management agencies to identify, conserve and enhance "the habitat necessary to fish for spawning, breeding, feeding, or growth to maturity". Most habitat evaluation procedures are based upon observed fish distribution and sets of

hypotheses aimed to explain the dependence of this distribution upon environmental parameters, mainly water quality and physical features, such as substrate, current speed and submerged aquatic vegetation (Wang et al., 1998). A widespread example of these methods is the habitat suitability index developed by the U.S. Fish and Wildlife Service as a planning and management tool for freshwater and terrestrial species (Terrel et al., 1996). Nonetheless, in many cases, the main or single criterion to designate EFH has been the presence or abundance of life stages of the target species or assemblages.

Basing EFH designation criteria only upon presence or abundance presents several problems. First, low

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abundance or absence of fish cannot be interpreted as unsuitable habitat. Current distribution represents the integral of anthropogenic and natural impacts, including overfishing, habitat degradation, regime shifts, recruitment cycles, and multi-species interactions (e.g., competition and predation). Further, for rare or endangered populations, little current or historical data exist, and they rarely fulfill the minimum spatial and temporal resolution needed, particularly for estuarine and marine species (Boisclair, 2001). Finally, field studies may need enormous sampling efforts to overcome high variability in time and space especially for motile species and species with complex life histories.

Beck et al. (2001) recently presented an approach to rank habitats based upon the relationship between juvenile habitats and adult recruitment (connectivity). Here, a higher ranked juvenile nursery area must show a greater contribution per unit of area to the production of recruits, than other nursery habitats. The contribution of juvenile habitats to adult recruitment can be inferred through methods such as conventional tagging or otolith microchemical assays (Beck et al., 2001; Kraus and Secor, 2004, in press), or can be assessed through prospective methods like spatially explicit demographic and energetic modeling (Rubec et al., 1998; Miller, 2003). The latter approaches are more feasible for endangered and rare species.

Here, we further develop spatially explicit energetic models as a method to evaluate likely recruitment rates from juvenile habitats for Atlantic sturgeon *Acipenser oxyrinchus* in the Chesapeake Bay. We follow Brandt and Kirsch' (1993) convention in developing a habitat suitability index using potential energy gain (growth). As a second step to more fully represent habitat-specific recruitment, we incorporate mortality as its reciprocal, resulting in an index of potential production, or net weight gain of a cohort (Werner and Gilliam, 1984; Houde, 1997; Secor, 1999).

Chesapeake Bay populations of Atlantic sturgeon collapsed during the late 19th and early 20th centuries, when Virginia mean annual landings dropped from ca. 300 metric tons during 1890–1899 to ca. 15 metric tons during 1920–1929 (Secor, 2002). The population crash was the result of over-exploitation (Secor and Waldman, 1999). Currently, Atlantic sturgeon populations along the East Coast of the United States are considered depleted, requiring immediate recovery measures (Anon., 1998). Essential fish habitat has not been defined for Atlantic sturgeon in estuarine waters, although a habitat suitability index for shortnose sturgeon in freshwater has been developed, mainly from observations of adult distribution and behavior (Crance, 1986).

We hypothesized that prominent anthropogenic changes in potential Atlantic sturgeon habitat in the Chesapeake Bay played a critical role in reducing populations or slowing the pace of population recovery.

Sedimentation of spawning grounds (Secor et al., 2000a) and increased frequency of hypoxia in nursery habitats (Officer et al., 1984; Cooper and Brush, 1991; Cronin and Vance, 2003) are two environmental changes that possibly had severe effects on these species in recent decades. In particular, we believed that systemic hypoxia in the Chesapeake Bay could limit or preclude juvenile production and resultant recruitment to the adult population due to high sensitivity of sturgeons to hypoxia (Klyashtorin, 1976; Secor and Gunderson, 1998; Secor and Niklitschek, 2002). Understanding the potential effects of low DO in concert with other key environmental inputs (temperature and salinity) could help hind-cast likely limits to sturgeon production, but also lead to predictions on scenarios of future environmental change (i.e., global warming) and habitat management measures (i.e., reduced eutrophication and increased DO levels). In this paper, we used bioenergetics and survival models developed by Niklitschek (2001) to index habitat value for juvenile Atlantic sturgeons in the Chesapeake Bay. Our main goal was to assess spatial, seasonal and inter-annual variability in suitable nursery habitats. Special emphasis was devoted to analyzing recent trends (1992–2001) in habitat suitability during the summer, when severe habitat reduction and fragmentation was expected for both species. To explore potential uses for this approach in environmental management we did a forecasting exercise to test the sensitivity of the Chesapeake Bay habitat value as a nursery for Atlantic sturgeon to two simplified scenarios of DO improvement and bay warming.

2. Material and methods

Potential production rate φ was defined as the instantaneous amount of biomass generated per unit of cohort biomass per day, considering both growth and the mortality rates. Instantaneous potential production (φ_{pp}) was calculated by subtracting the minimum mortality rate (Z_{min}) from the maximum growth rate (G_{max}), according to the following derivation:

$$P = \frac{W_0 e^{(Gt)} N_0 e^{-(Zt)}}{W_0 N_0}$$

$$P = e^{(G-Z)t} = e^{\varphi t}$$

$$\varphi = G - Z$$

$$\varphi_{pp} = G_{max} - Z_{min}$$

where P is the production per unit of cohort biomass; φ the daily instantaneous production rate, W_0 the average

individual weight at time 0; N_0 the cohort abundance at time 0; G the instantaneous growth rate; and Z the instantaneous mortality rate. Instantaneous potential production was calculated for each spatial cell in the mainstem and tributaries based upon the bioenergetics model described further below and presented in Appendix 1.

G and Z were estimated using bioenergetics and survival models (Appendix 1) developed by Niklitschek (2001) through extensive laboratory experiments and mesocosm validation. In these models, growth, survival, and therefore φ_{pp}, depend upon temperature, DO saturation, salinity and fish weight, with maximum φ_{pp} at 19 °C, 100% DO and 11.5 psu, for a 14.4 g fish (Fig. 1). In particular, survival, consumption, routine and active metabolism, and excretion rates were found and/or modeled to be dependent upon temperature, salinity and DO saturation. Post-prandial and egestion rates, on the other hand, were observed and therefore modeled to depend only upon temperature and DO saturation, while salinity had negligible effects upon these two components. Niklitschek (2001) measured
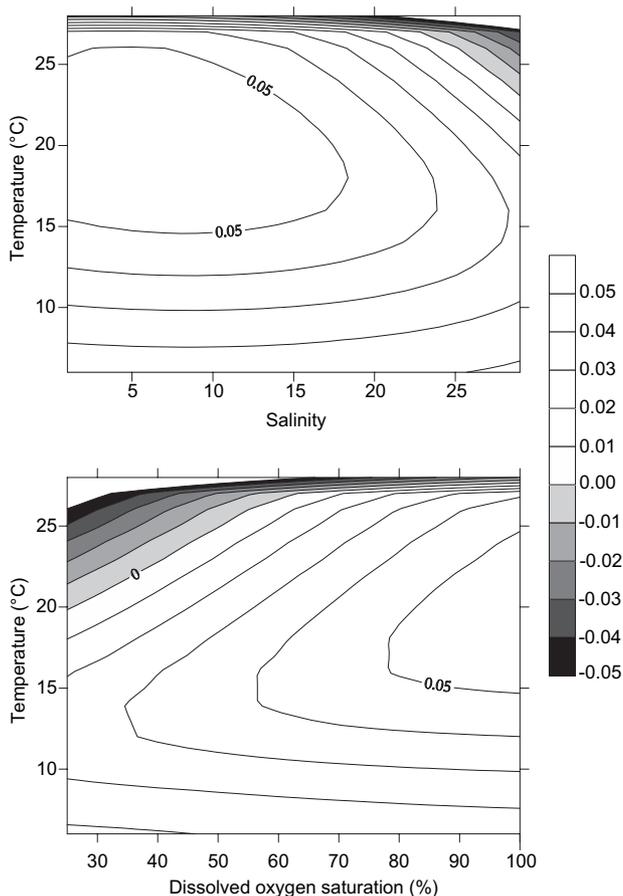

Fig. 1. Potential production as predicted by the bioenergetics/survival model derived by Niklitschek (2001). Upper panel shows temperature and salinity interactions, under a constant DO saturation of 100%. Lower panel shows temperature and DO interactions, under a constant salinity of 11. In both cases fish weight was set at 14.4 g.

individual survival and growth responses to abiotic factors, under unlimited food conditions. Although there was a significant correlation between growth and survival, the best survival model was obtained using salinity, temperature and DO, but not growth as explanatory variables (Appendix 1).

Instantaneous potential production rate was modeled for a cohort of 14.4 g juvenile Atlantic sturgeon (average size used by Niklitschek, 2001). Maximum growth and minimum survival rates were obtained by supplying the bioenergetics and survival models with bottom water quality data (<1 m from bottom) from the Environmental Protection Agency (Chesapeake Bay Program), corresponding to the 1993–2002 decade. Growth rate was maximum since it was estimated under maximum consumption rate ($kJ\,g^{-1}\,d^{-1}$) conditions. Survival was minimum since it only depended upon physiological stress from abiotic factors (Appendix 1), while no effects from predation or starvation were considered. Thus, growth and survival models did not entail secondary multi-species considerations (forage and predation). Our exercise here was to consider water quality inputs as key constraints in the distribution and production of a species hypothesized to be quite sensitive and susceptible to degradation of water quality in the Chesapeake Bay and elsewhere (Secor and Gunderson, 1998; Collins et al., 2000).

Data were available for 303 stations (Fig. 2), which had a sampling frequency between 1 and 3 times per month. No diel variation data were available. Water quality interpolation was conducted using the Chesapeake Bay Interpolator software (Bahner, 2001), which uses an inverse distance squared function as the main interpolation algorithm. We followed Bahner's (2001) division of the mainstem into 1 km^2 cells, and tributaries cells into 0.0025–0.25 km^2 cells. January, April, July and October were chosen as representative months for each season (Table 1). For inter-seasonal comparisons, we averaged and interpolated DO saturation, salinity and temperature data available from the 10-year period for each of the four representative months. For inter-annual comparisons, we computed monthly averages of the same environmental factors for each station and year.

Total suitable habitat (TSH) was calculated as the total area supporting positive potential production rates ($\varphi > 0$). Inter-annual variability in TSH for July, when habitats were most limited for Atlantic sturgeon, was then tested for correlation with inter-annual variability in individual factors: DO, salinity and temperature. We also evaluated the correlation between TSH and total freshwater inflow for July in the Susquehanna River. Freshwater inflow from this river was expected to explain a significant fraction of the variability observed in all three of the model inputs because the Susquehanna supplies >50% of total freshwater inflow into the Chesapeake Bay.
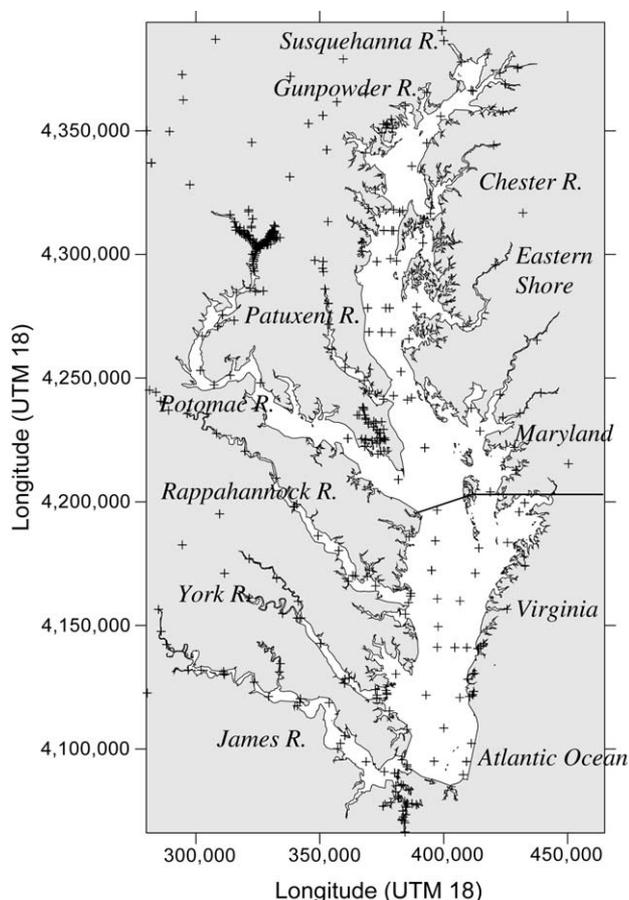
Fig. 2. Environmental Protection Agency (Chesapeake Bay Program) fixed stations used for water quality monitoring program. Those appearing outside the Chesapeake Bay are for upper nontidal rivers and streams. Rivers, states and other regional labels are provided for reference.

Distribution data for juvenile Atlantic sturgeon, caught in Chesapeake Bay between 1997 and 2001, were available from a reward program implemented by the U.S. Fish and Wildlife Service, USFWS (Secor et al., 2000b; Welsh et al., 2002). This data set was used to test habitat quality predictions generated by our potential production model. From a total of 1412 wild and hatchery-released Atlantic sturgeons we selected a subset

Table 1
Mean (1993–2002) water quality conditions (±1 standard deviation, SD) observed for Chesapeake Bay Program monitoring stations (see Fig. 1) for January, April, July and October

Month	Temperature (°C ± SD)	Salinity (± SD)	DO (% saturation ± SD)
January	4.3 ± 1.41	7.4 ± 9.28	93.7 ± 9.42
April	13.0 ± 2.28	6.5 ± 8.57	89.4 ± 13.8
July	25.8 ± 2.52	7.5 ± 9.38	72.0 ± 25.82
October	16.8 ± 2.74	8.2 ± 9.72	84.7 ± 14.51

Temperature, salinity, and DO data were drawn from measures taken <1 m from the bottom.

of 619 captures, recorded between 1997 and 1999 from 69 pound nets, all located in Maryland waters. The Maryland section of the Chesapeake Bay was selected because only the Maryland (as opposed to Virginia) reward program was continuous through the study period. The 1997–1999 interval was selected because this period comprised >50% of all captures, and provided a relatively high number of records per month. While many captures occurred in drift gillnets, we used only pound net captures because pound nets are passive and stationary gears, with less expected variability in catchability. Most captures in this sub-sample corresponded to hatchery fish, released into the Nanticoke River in 1996 (Secor et al., 2000b; Welsh et al., 2002).

We assessed the distribution of sturgeon captures in two ways. First, we used Poisson regression (Kleinbaum et al., 1998) to test the dependence of the total number of fish caught in each month and pound net, upon the average potential production index estimated for that period and sampling unit. Expected covariance between catches observed within a year, month and pound net, were modeled through a mixed model approach (Littel et al., 1996). Habitat quality data for each pound net (i.e., the cell that the net occupied) were averaged by month due to the lack of daily water quality records. Potential production was again estimated for a 14.4 g cohort of juvenile sturgeon since this was the average size used by Niklitschek (2001). Because recaptured fish were substantially larger than this, we conducted identical analyses for a cohort of 2080 g fish (average weight for captured fish). Those results, not shown here, were similar in pattern and amplitude.

As a second approach to calibrate model results with field data, we hypothesized that given no habitat effects, the distribution of fish captures would be proportional to the distribution of pound nets between modeled suitable and unsuitable habitats. We used a contingency table test (χ^2-test), considering either active selection of habitat by juveniles or increased mortality at unsuitable habitats as alternative hypotheses.

We used Niklitschek's (2001) model and monthly averaged water quality conditions to predict growth and weight for fish released into the Nanticoke River in July 1996 (Welsh et al., 2002). Growth and weight were predicted on a monthly basis from July 1996 to December 1999, for each Chesapeake Bay cell (Bahner, 2001). Using an initial weight of 38.6 g (Welsh et al., 2002), monthly averages were computed from weights predicted at all cells showing a growth rate ≥0 in Maryland waters. Predicted values were then contrasted with monthly weight averages computed from juvenile Atlantic sturgeon captured in Maryland waters, and identified as part of the Nanticoke hatchery cohort.

The sensitivity of TSH to habitat change was explored for July 1993–2002 under two scenarios. In the first scenario, a lower limit was set for the

environmental DO data set, in such a way that all bay segments fulfilled the new instantaneous minimum DO-criteria targeted by the EPA in the Chesapeake Bay (Table 2; Anon., 2003a). In some Bay segments, both deepwater and deep channel "designated use zones" (DO-criteria zones) were applicable. In these cases, bottom water cells above the lower pycnocline boundary were considered "deepwater", while those below were classified as "deep channel" cells (Table 2). Under the second scenario, the average temperature conditions observed in July were raised by 1 °C. Although simplistic, this was an attempt to illustrate the probable effects of climatic change on nursery habitat value in a temperate estuary (Table 2).

3. Results

3.1. Seasonal predictions

Potential production rates predicted for juvenile Atlantic sturgeon in the Chesapeake Bay showed strong seasonal cycles, with fall and spring months offering the best overall conditions (Fig. 3). April showed the highest easonal peak for daily potential production, $\varphi_{pp} = 0.017$, and 85% of the bay's surface area showed positive production. The worst seasonal conditions were predicted for July, which showed an average potential production rate $\varphi_{pp} = -0.133$, with less than 10% of the bay identified as suitable habitat (Fig. 3). As a result, summer represented the most critical season, where low or nil growth, and high mortality rates resulted from the combined effect of low DO with high temperatures and high salinities in most of the Chesapeake Bay.

During the summer, highest value habitats identified by the model occurred in the upper Bay, between the Gunpowder River and the Susquehanna Flats; in the upper tidal sections of the Potomac; areas around the Chester River mouth; and in regions of Maryland's Eastern shore. During spring and fall, tributaries and shallow areas were the most productive habitats for juvenile Atlantic sturgeon. Conversely, the mainstem and deeper tributaries were expected to serve important habitat roles in winter. During winter, a temperature-dependent period of growth stasis was predicted, with production rates slightly above zero expected for most of the bay. Presumably, sturgeons would seek zones of slightly warmer (deeper marine-source) water during this period.

Largest areas of negative summertime production corresponded to deepwater hypoxic zones occurring in summer along the central mainstem, and the lower Patuxent, Potomac and Rappahannock rivers (Fig. 3). Shallow areas and upper tributary waters had negative production, mostly driven by sub-lethal temperatures in those regions. Salinity-driven habitat quality reductions were predicted near the mouth of the mainstem and some sub-estuary tributaries (e.g., James River) among most seasons. During summer in these regions, optimal DO and temperature conditions were counter-balanced by the negative effects attributed to high salinity (Fig. 4).

3.2. Inter-annual variation

We predicted very large inter-annual variations in suitable habitat area for juvenile Atlantic sturgeon during the studied period. Modeled variations were especially large during the summer (Fig. 5), with two orders of magnitude difference between the TSH calculated for 1996 (2900 km^2) and 1999 (20 km^2) (Table 3). No consistent (increasing or decreasing) trend in habitat suitability was calculated for the evaluated 10-year period. Univariate correlation analysis between single water quality parameters and July TSH showed the latter to be more closely related to inter-annual fluctuations in bottom temperature ($r = -0.83$, $p < 0.01$) and salinity ($r = -0.67$, $p < 0.05$) than to changes in bottom DO ($r = 0.39$, $p > 0.1$). For instance, in 1996, a year exhibiting the highest suitable habitat area, average temperature and salinity were the second lowest in the studied period, while DO conditions were just above the average. Low correlation between TSH and DO during summer resulted from the persistence of sub-optimal and sub-lethal DO levels throughout most of the Chesapeake Bay for the studied period.

Total freshwater inflow from the Susquehanna River in July showed a positive correlation ($r = 0.61$, $p < 0.1$) with predicted TSH during the studied period. While

Table 2
Mean values (1993–2002) of DO, temperature and salinity by U.S. Environmental Protection Agency (EPA) designated use (Anon., 2003b) in July. Predicted DO values are presented for simulation Scenario 1 (fulfillment of EPA DO-criteria), and Scenario 2 (bay-wide increase of 1 °C)

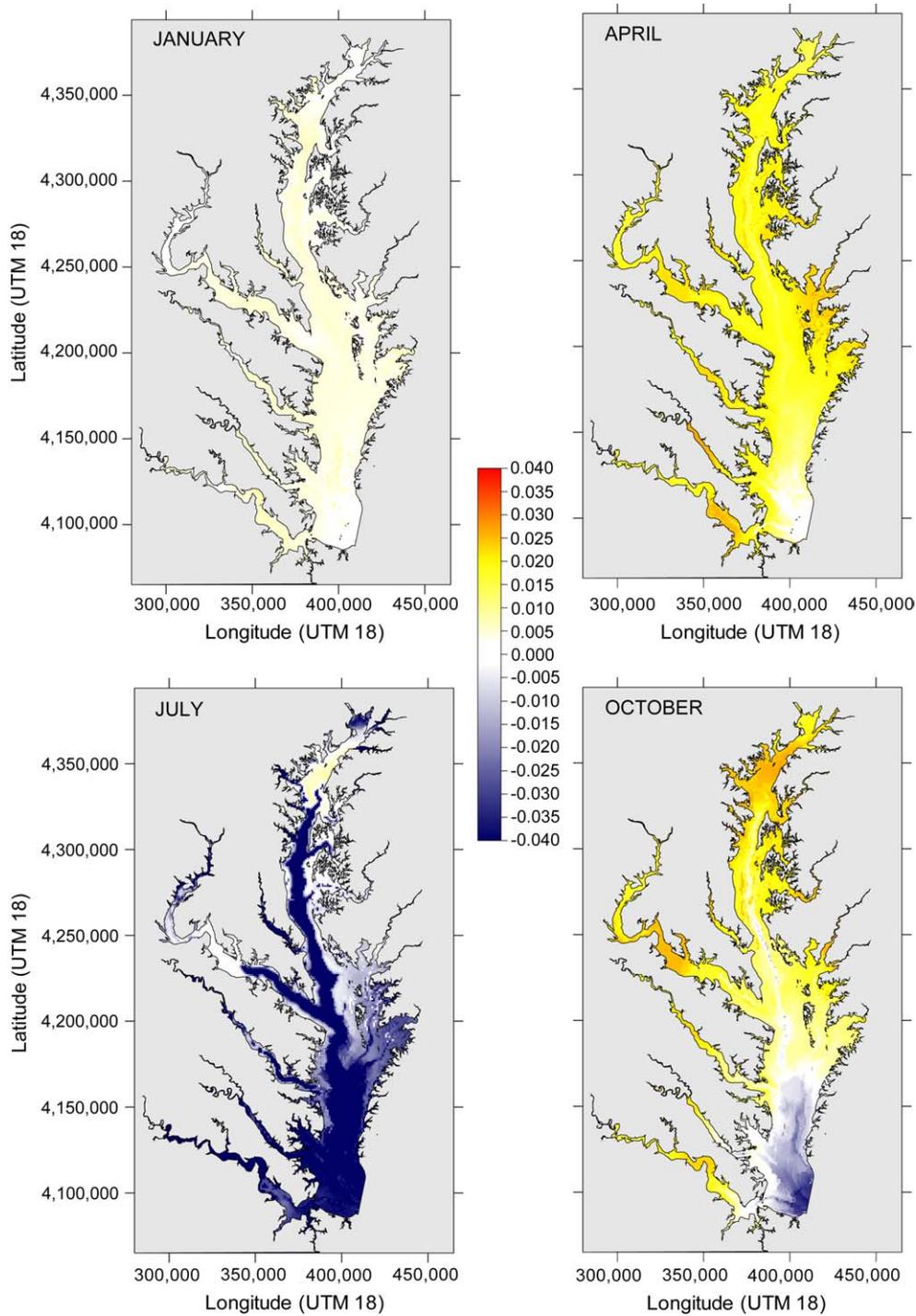| EPA-designated use	Mean values for July 1993–2002					Scenario 1	Scenario 2
	Surface area (km^2)	DO (mg l^{-1})	DO-criteria (mg l^{-1})	Temperature (°C)	Salinity	DO (mg l^{-1})	Temperature (°C)
Open/shallow water/ spawning tributary	5891	6.5	3.2	26.6	11.8	6.5	27.6
Deepwater	3792	4.3	2.3	25.1	18.8	4.5	26.1
Deep channel	1153	1.0	1.0	23.8	16.9	1.4	24.8
Overall total/mean	10836	5.1	2.7	25.8	14.8	5.3	26.8

Fig. 3. Instantaneous potential production rate (d^{-1}) for juvenile Atlantic sturgeon in Chesapeake Bay. Average conditions in January, April, July and October (1990–1999).

freshwater inflow was highly correlated with mean salinity ($r = -0.77$, $p < 0.01$), no evident association was found between July freshwater inflow and either mean temperature or mean DO for that month. The smallest summer suitable area was predicted for July 1999, when freshwater inflow was lowest and mean Bay salinity was highest over the time series.

3.3. Field observations

Poisson regression analysis showed that juvenile Atlantic sturgeon had a significantly higher ($p < 0.05$) probability of being caught in pound nets occurring in higher value habitats within each month than those associated with lower production rates. Most reported
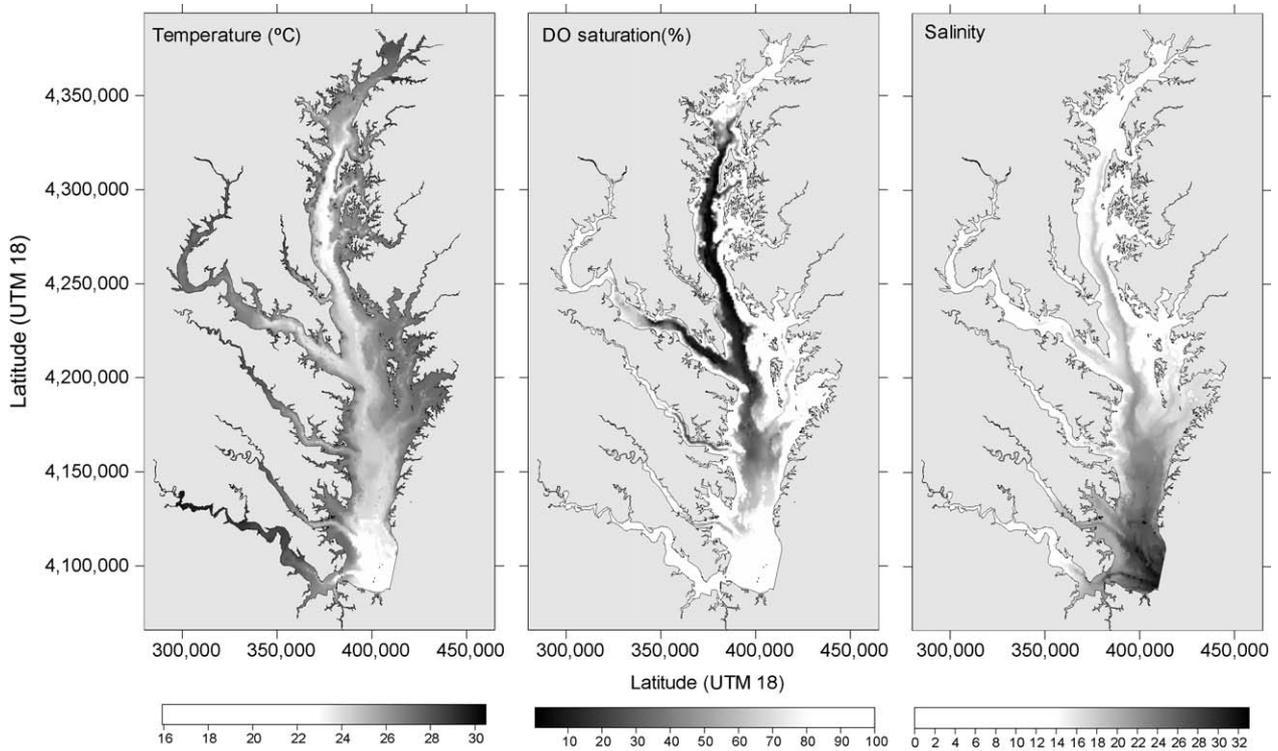
Fig. 4. Average water quality conditions in the Chesapeake Bay in July 1993–2002. (a) Temperature (°C); (b) DO; (c) salinity.

captures of juveniles occurred along the eastern portion of the Chesapeake Bay (Fig. 6) at an average recorded depth of 5.4 m. Thus, most captures occurred above the deeper layer of hypoxic waters and below the warmest superficial layer, with 76.6% of capture sites classified as suitable habitat by our model. Because an even larger proportion of captured fish (84.9%) were caught in those areas, there was a significant departure from
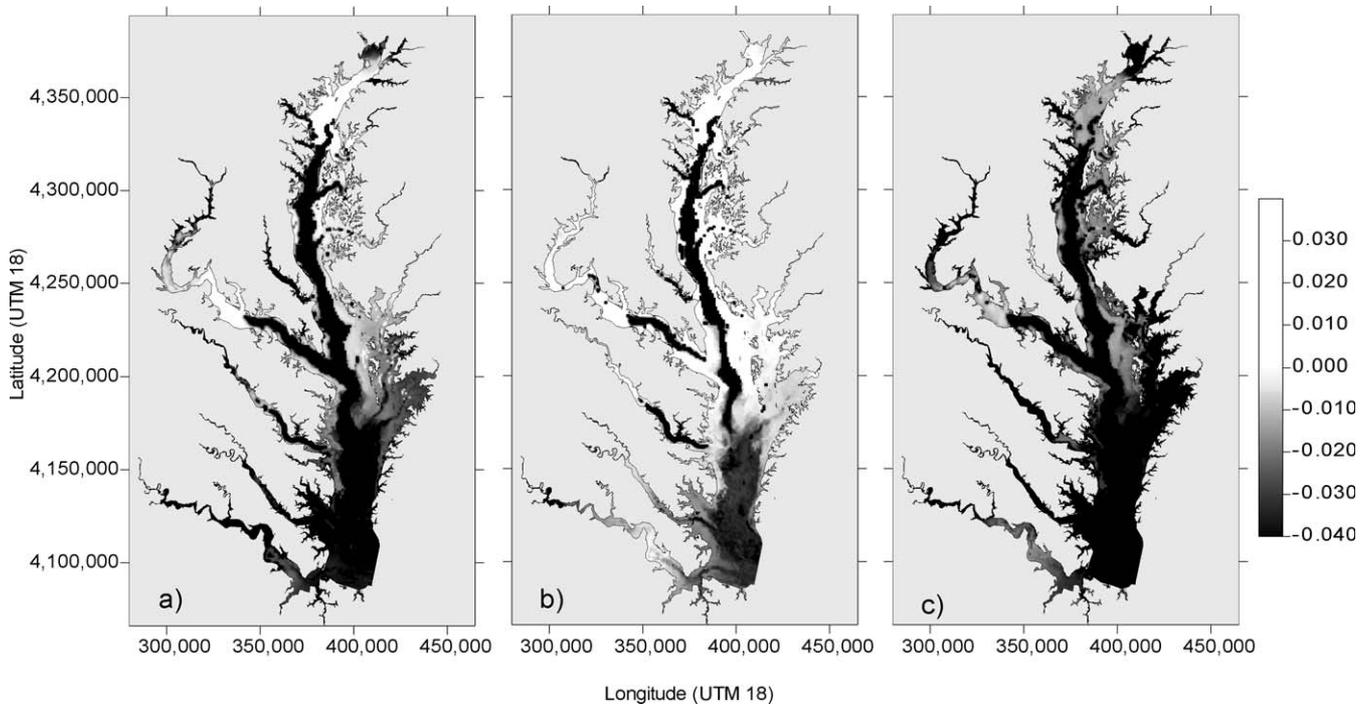

Fig. 5. Inter-annual variation in summer habitat quality (instantaneous potential production) for juvenile Atlantic sturgeon. (a) Average conditions July 1993–2002; (b) July 1996; (c) July 1999.

Table 3
Total suitable habitat (potential production >0) for juvenile Atlantic sturgeon in the Chesapeake Bay during July, under mean observed conditions and under two simulation scenarios. Scenario 1 implies fulfillment of the EPA DO-criteria and Scenario 2 represents a bay-wide temperature increase of 1 °C

Year	Mean July suitable habitat (km^2)	Scenario 1 July suitable habitat (km^2)	Scenario 2 July suitable habitat (km^2)
1993	377	493	37
1994	405	414	5
1995	351	365	32
1996	3822	4407	2394
1997	989	1145	197
1998	2922	3257	828
1999	10	11	0
2000	3244	3764	1331
2001	1125	1147	72
2002	863	895	14
Average (1993–2002)	1411	1590	491
Relative change	1.00	1.13	0.35

the null hypothesis of independence between capture location and habitat quality (χ^2, $p < 0.001$).

The alternative hypotheses of habitat selection by the fish and/or increased mortality in unsuitable habitats are qualitatively supported by contrasting observed and predicted weights at capture for sturgeons released in the 1996 experiment (Secor et al., 2000b; Welsh et al., 2002). Apparent growth rates were relatively consistent with seasonal and inter-annual predicted variations, but tended to exceed predicted weights in amplitude (Fig. 7), as might be expected if fish selected habitats favorable to growth.

3.4. Habitat sensitivity to environmental change

Model predictions for a DO improvement scenario (EPA DO-criteria for the Chesapeake Bay fully attained) showed an average increase of 13% in TSH for juvenile Atlantic sturgeon in the bay (Fig. 8b). This improvement ranged from 2% in 2001, to >30% in 1993 (Table 3). A much larger, and negative, change was predicted when Bay temperatures were increased by 1 °C for each of the modeled cells (Fig. 8c). Under this scenario we predicted an average reduction of 65% (37–100%) in summer TSH during July 1993–2002, with almost no suitable areas available in critical years (Table 3).

4. Discussion

4.1. Using potential production to index habitat suitability

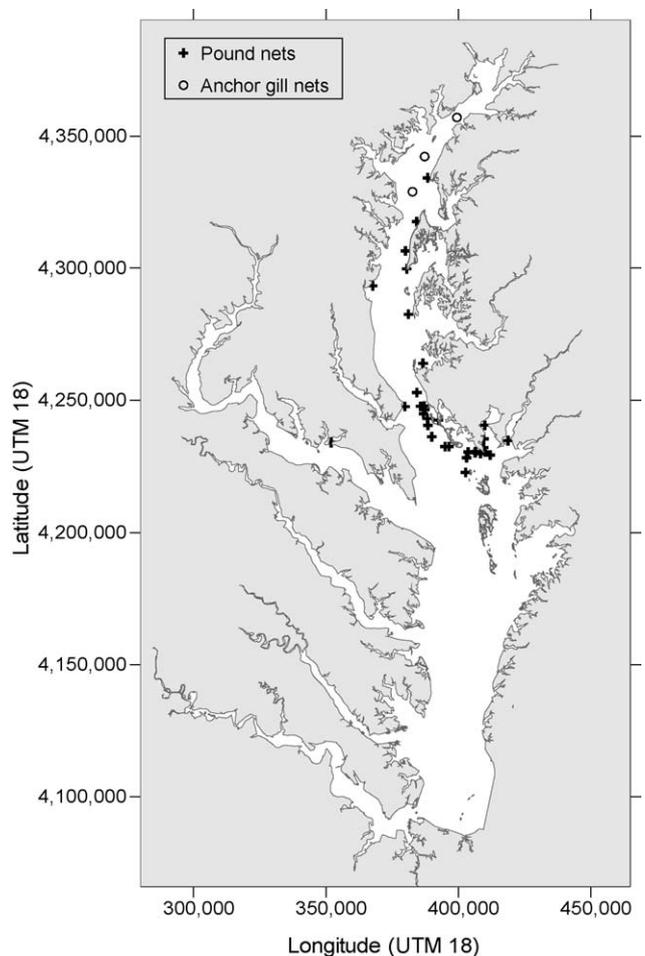Energetic modeling has not typically incorporated expected survival responses (Brandt and Kirsch, 1993;

Fig. 6. Capture location of recaptured hatchery and captured wild juvenile Atlantic sturgeon in Maryland waters of the Chesapeake Bay. June, 1997–1999.

Mason et al., 1995; Luo et al., 2001), yet under environmental extremes, lethal responses could make growth responses moot. For sturgeons, which are highly sensitive to current Chesapeake Bay conditions of high temperature, salinity and low DO, mortality is an important response, which we chose to integrate with growth as a potential production index. The present work shows the potential of lethal and sub-lethal effects, which we expect to be more acute had we data available at finer time scales. Although the Chesapeake Bay Program is one of the most intensively monitored systems in the world, we had to average data on a monthly basis to generate bay-wide synoptic information. This averaging approach masked relevant daily or hourly variations in habitat quality.

In contrast to Rubec et al. (1999) and related spatially explicit habitat suitability index measures, the approach taken here was to deduce a set of metabolic and survival responses from laboratory experiments, and apply these responses to a larger set of field conditions. Rubec et al. (1999) modeled densities of fish across habitat gradients from field data and then re-applied these general patterns
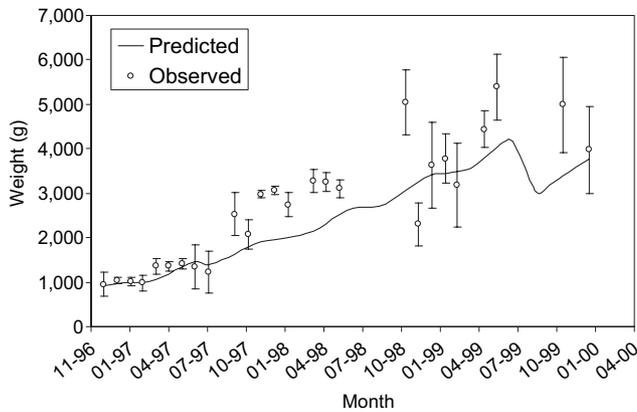
Fig. 7. Predicted and observed weight for hatchery-produced juvenile Atlantic sturgeon released in 1996 in the Nanticoke River (Welsh et al., 2002). Observed weight (g) correspond to average weight (±SE) of captured fish (reward program). Predicted weight corresponds to average model predictions for all the Chesapeake Bay cells (Bahner, 2001) where monthly survival was expected to be ≥0.

to that same set of field data. Validation of this approach is sought by developing the HSI model for one system and then applying it to another. An advantage of the more deductive approach we took is that the response is independent from the data used to derive the habitat suitability index. A limitation, however, is realism, which we sought to evaluate through observations (albeit limited) of distribution patterns of sturgeons captured by pound nets. Both approaches share limitations

derived from assuming a constant relationship between selected habitat variables and responses. Hence, compensatory physiological or behavioral responses are ignored beyond those implicit in field observations (HIS) or laboratory results (bioenergetics). Another shared assumption is independence between abundance, individual growth and survival, which is likely to hold at very low densities, such as those expected for Atlantic sturgeon in the study area.

Our modeling approach stressed abiotic parameters, excluding biotic inputs such as forage, predation and competition. While these relevant factors also need to be addressed, we focused on abiotic components as a first step, following available evidence that Atlantic sturgeon are quite sensitive to current abiotic conditions in the Chesapeake Bay (Secor and Gunderson, 1998; Collins et al., 2000) and the priority placed upon improving water quality conditions in the Chesapeake Bay and elsewhere as a means of improving habitats for living resources (Anon., 2003a, 2003b). Current models considering water quality criteria in estuaries are limited to single habitat variable considerations, and typically to predictions of short-term lethal responses (e.g., 50% lethality in 96 h). We believe the multivariable ecophysiological approach we have pursued here represents a substantial improvement in realism in estuarine habitat models than those merely based upon lethality.

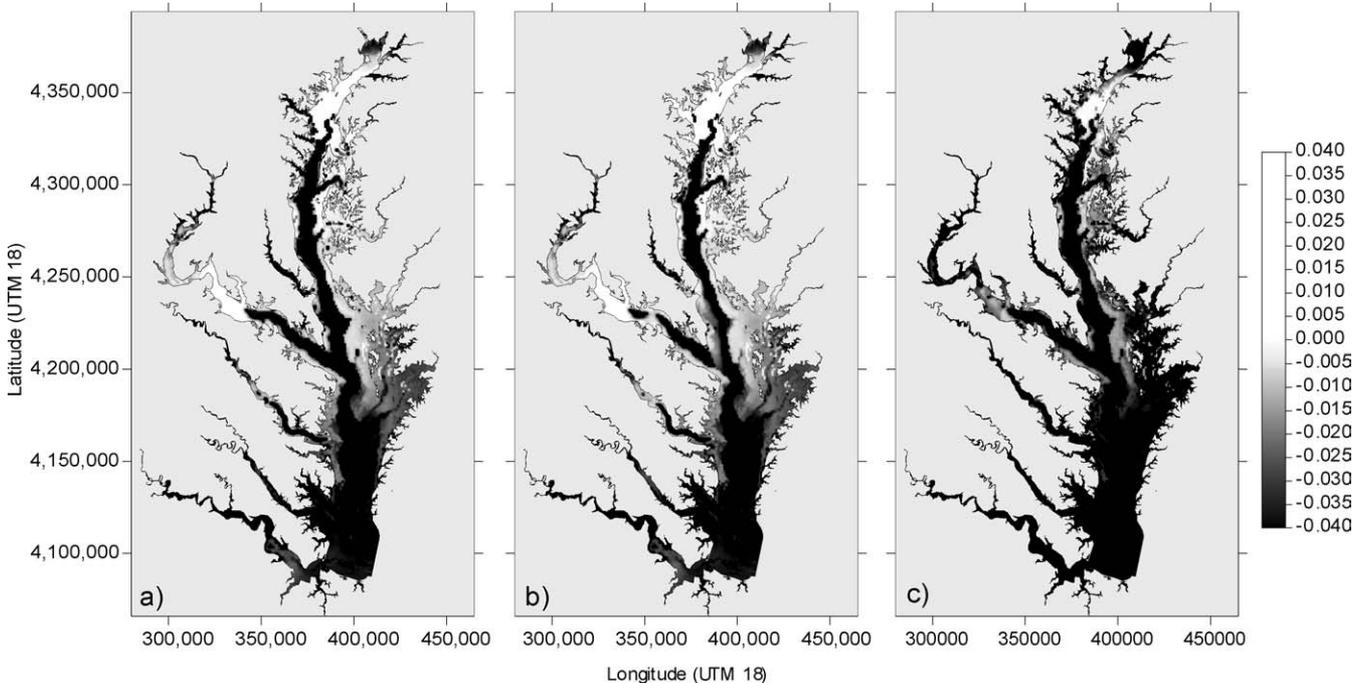Energetic modeling entails many limiting assumptions, but may be the only available approach in

Fig. 8. July instantaneous potential production for juvenile Atlantic sturgeon in the Chesapeake Bay under three scenarios: (a) average conditions 1993–2002; (b) average conditions 1993–2002, but all regions meeting newly revised U.S. Environmental Protection Agency DO-criteria; (c) average conditions 1993–2002, but temperature increased 1 °C bay-wide.

engaging issues of essential fish habitat and connectivity in threatened and endangered fishes. Energetic models are complex and require substantial knowledge of environmental and forage effects on metabolic processes. Even when all metabolic responses are known, experimental and natural sources of variance can result in substantial uncertainty in potential production responses. In some cases, such as active respiration, variations can be several-fold (Boisclair, 2001). Still, independent validation including field survey and mark-recapture studies and mesocosm studies can support energetic models (Rice and Cochran, 1984; Niklitschek, 2001). In the case of Chesapeake Bay sturgeons, individuals are too rare to evaluate specific energetic responses from field studies. Nonetheless, data from the 1996 release experiment showed consistency between predicted and observed growth rates for a period of three years (Fig. 7), and distribution patterns that corresponded to regions where positive productions were predicted.

Distributional data from the Hudson River, where a much larger Atlantic sturgeon population of juveniles uses mostly the brackish area of the river (Haley, 1999), also showed consistency with predictions from our model. Although spatial and temporal resolution of water quality data in this river is insufficient to replicate a modeling exercise like the one presented in this paper, it is possible to observe that the brackish section of the Hudson Rover tend to exhibit lower temperatures and higher DO concentrations than areas upstream.

4.2. Suitable habitat for juvenile Atlantic sturgeon in the Chesapeake Bay

Our results indicate that the Chesapeake Bay may continue to provide nursery habitat functions for juvenile Atlantic sturgeon, albeit on an inconsistent basis across years. Very high inter-annual variation in suitable habitat was predicted, largely due to severe reductions in suitable habitat under summer conditions. In extremely dry and warm summers, such as 1999, suitable habitat for juvenile Atlantic sturgeon was predicted to be nearly absent (<20 km^2). In a long lived species such as Atlantic sturgeon (Stevenson and Secor, 1999), it is important to note that high variability in growth and survival during early life stages of Atlantic sturgeon can be compensated by a periodic life-history strategy, which includes delayed maturity, repeated spawning, and a long life span (Winemiller and Rose, 1992; Gross et al., 2002).

The predicted pattern of improved habitat suitability during wet years resulted from a unique combination of spatial distributions of sub-optimal conditions of temperature, salinity and DO. Our model indicates that sturgeons undergo a three-way habitat squeeze during their first summer of life, where salinity and hypoxia,

respectively, set horizontal and vertical barriers to juvenile distribution, limiting suitable habitats to shallow areas of upper estuary and tributaries. These regions become increasing stressful (sub-lethal and lethal) as summertime temperatures rise. This situation is expected to be worse in dry years: since areas of high salinity advance up-estuary into tributaries. Thus, although overall hypoxia in the lower tributaries and mainstem usually decreases in dry years due to weaker density stratification, juveniles are shut-off from this region due to lethal salinity levels. In wet years, salinity in upper Bay estuaries becomes less of a barrier for dispersal into adjacent mainstem regions. In such years, mainstem bottom hypoxia rather than salinity limits summertime movements into favorable habitats. Still, because tributary habitat volumes are larger in wet years and buffered against high temperature to a greater extent, sturgeons might over-summer in their natal estuaries.

The continued presence of sturgeon nursery habitat in the Chesapeake Bay in some years was also confirmed by empirical evidence from the hatchery release experiment conducted in 1996 (Secor et al., 2000). These juveniles grew and dispersed at rates consistent with those of wild sturgeons in the Hudson and Delaware Estuaries (Secor et al., 2000) and those predicted from the bioenergetics model (Fig. 7). Further recapture rates, which exceeded 12% suggested high survival rates (Welsh et al., 2002). Interestingly, the first summer these fish experienced was 1996, corresponding to the year of largest predicted TSH in the series (Table 3).

The spatial distribution of fish captures recorded by the reward program was consistent with predicted distribution of suitable habitats, exhibiting further the patchy nature of summer refuges. According to the model results, at least four summer refuge areas were identified that may deserve special consideration in restoration efforts for this species: the upper Bay, above the mouth of the Chester River, areas of the Eastern shore, and the meso-oligohaline sections of the Potomac and James Rivers. In a future restoration program, we would look to these areas as those most likely to yield recruits to the adult population.

4.3. Sensitivity of Atlantic sturgeon habitat to environmental change

Large inter-annual fluctuations in value of summer-time habitat suggested that juvenile sturgeon could be especially sensitive to climatic oscillations, as well as to anthropogenic interventions affecting freshwater inflow, temperature, salinity and/or DO. In the Chesapeake Bay, these environmental factors have been displaced from historical levels by anthropogenic changes to freshwater flow, organic pollution and climate (Brush,

2001; Fisher and Schubel, 2001; Kennedy and Mount-ford, 2001). Temperature has probably served a histor-ical role as the most important habitat structuring force (Coutant, 1987) and summer habitat reduction to discrete thermal refuges has probably always occurred since formation of the modern Chesapeake Bay. These refuges may have included deeper areas in the mainstem, which are now unavailable due to hypoxia and/or increased salinity. Although the Bay mouth remains a well oxygenated, temperature-moderated refuge, it only becomes available to larger fish that are physio-logically able to live and grow under those high salinity conditions (>1-year-old fish; Niklitschek, 2001).

Responses to simulation scenarios highlighted phys-iological responses of juvenile Atlantic sturgeon, which showed temperature to have a larger influence on fish growth and production than salinity or DO for Chesapeake Bay conditions (Fig. 1). In this context, temperature was the key environmental factor structur-ing summertime habitat, where a simulated bay-wide increase of just 1 °C was predicted to lead to a major reduction of 65% in TSH. This scenario, while un-realistic in its application (e.g., temperature was changed, while other parameters remained fixed) pre-sented the view that any additional deterioration of habitat quality could shift the Chesapeake Bay from a marginal habitat to a completely dysfunctional nursery habitat. The result of temperature sensitivity is interesting in considering the estuarine/marine distribu-tion of Atlantic sturgeon in more southern estuaries, but may be consistent with the recent proposal that among sturgeons, Atlantic sturgeon may have had a more boreal ancestral distribution (Ludwig et al., 2002).

According to this simulation exercise, attaining the recently revised EPA DO-criteria had only a moderate impact, increasing by only 13% the TSH for juvenile Atlantic sturgeon. DO improvements occurring for large mainstem regions of the Chesapeake Bay, i.e., the effect of a 40% increase in average DO level in the deep channel, still resulted in hypoxic conditions for Atlantic sturgeon (here, an improvement from 1.0 to 1.4 mg l^{-1} in July; Table 3). Still, deep channel hypoxia is a natural feature (albeit exacerbated through anthropogenic organic inputs), and probably exhibited DO levels unsuitable for sturgeons prior to the 20th century (Anon., 2003b). Another issue, which might reduce expected benefits from DO improvement is the pre-dominant role of temperature and salinity within the three-way habitat squeeze, which led to the predicted low correlation between DO and TSH.

4.4. Extensions of the potential production model

The present work explored the use of potential production as a spatially explicit habitat assessment tool, which showed forecasting and simulation poten-tials, useful to understand some of the likely conse-quences of environmental change. In our view, the outputs from the current model approximate an upper limit of the likely extent of suitable habitat. As a first extension, we suggest to incorporate growth/survival effects from prey and predators abundance, as well as from physical factors, such as currents and substrate. By bringing in these elements the spatial extent of suitable habitats would be constrained to a subset of those predicted here. A further extension should incorporate relevant but hard to assess factors acting at and individual levels, including competition, density-depen-dence and physiological or behavioral compensatory mechanisms.

Proposed extensions of the model will require in-tensive and careful field experiments, perhaps using hatchery-released sturgeons and additional laboratory work. Salinity was a driving factor in potential pro-duction responses because juvenile Atlantic sturgeon are particularly vulnerable to salinities >20. By the end of their first year, however, sturgeons become fully tolerant to all salinity levels in the Chesapeake Bay. Indeed, a single tagged yearling released in the Nanticoke in the span of one year left the Chesapeake Bay and was recaptured in the Chowan River, North Carolina (Welsh et al., 2002). Anadromous fishes such as sturgeons, striped bass, shads, and salmons all have varying capacities to tolerate full salinity, which vary with ontogeny (Cataldi et al., 1999). Indeed, this is a critical component of connectivity within the live cycles of anadromous fishes. Thus to fully evaluate the premise that modeled habitat suitability for juvenile Atlantic sturgeon relates to recruitment to the adult, it will be necessary to model size-dependent responses to envi-ronmental factors beyond the first year of life.

One of the main difficulties for habitat evaluations based upon energetic models will be the intense laboratory work needed to model functional responses to environmental variables. Nonetheless, if stenotopic species are used to index habitat quality, this informa-tion might be used to define a bottom-line index of habitat quality for other less sensitive species. This is, in fact, the case for sturgeons, which have been shown to be especially sensitive to hypoxia (Klyashtorin, 1976). Thus, habitat quality predictions obtained from stur-geons should serve as a conservative reference to estimate habitat quality for other species in systems such as large estuaries, where seasonal hypoxia may prevail (Anon., 2003b).

Appendix 1. Survival and Bioenergetics model for juvenile Atlantic sturgeon (Niklitschek, 2001)

A.1. Notes

(a) Coefficient values from Niklitschek (2001) have been incorporated into the original equations, which have been simplified whenever possible.

(b) Value of coefficient d_{CF} was re-estimated and formulas for $f(DO)_{FC}$ re-arranged to allow extrapolation down to 0% DO saturation, observed in the Bay during the summer.

A.2. Symbols common to all equations

W = fish weight (g); T = temperature (°C); DO = water $DO_\%$; Sal = salinity.

A.3. Survival

$$S(t|Sal, T, DO) = 0.99^\xi \quad (day^{-1})$$

$$\xi = \exp(0.4(Sal - 10.3) + 0.8(T - 18.9) - 0.3(DO - 72.4))$$

A.4. Growth

$$G = FC - (RM + SDA + ACT) - (F + U) \quad (kJ \, day^{-1})$$

A.5. Food consumption (FC)

$$FC = 0.9 W^{0.20} f(T)_{FC} f(DO)_{FC} f(Sal)_{FC} \quad (kJ \, day^{-1})$$

$$f(T)_{FC} = KA_{FC} KB_{FC}$$

$$KA_{FC} = \frac{0.2 \exp(0.25(T - 26.8))}{1 + 0.2[\exp(0.25(T - 26.8)) - 1]}$$

$$KB_{FC} = \frac{0.6 \exp(2.91(26.8 - T))}{1 + 0.6[\exp(2.91(26.8 - T)) - 1]}$$

$$f(DO)_{FC} = \left| \begin{matrix} COK + \frac{[1-COK]KO_i}{KO_{max}}, & \text{for } DO < CDO_{crit} \\ 1, & \text{otherwise} \end{matrix} \right.$$

$$KO_i = (DO)e^{-c_{FC}(DO)}$$

$$c_{FC} = 0.04[2 - f(Sal, T)_{RM} - KA_{FC}]$$

$$KO_{max} = DO_{crit} e^{-c_{FC} DO_{crit}}$$

$$DO_{crit} = \frac{1}{c_{FC}}$$

$$COK = 1 - 0.39[f(Sal, T)_{RM} + f(T)_{FC}]$$

$$f(Sal, T)_{RM} = f(T)_{RM} f(Sal)_{RM}$$

$$f(Sal)_{FC} = -\frac{5.37 W^{-0.158}}{f(Sal, T)_{RM}} - 0.8$$

A.6. Routine metabolism

$$RM = 0.5 W^{-0.19} f(T)_{RM} f(DO)_{RM} f(Sal)_{RM} \quad (kJ \, day^{-1})$$

$$f(T)_{RM} = \left(\frac{0.15 e^{0.24(T-6)}}{1 + 0.15(e^{0.24(T-6)} - 1)} \right)$$

$$f(DO)_{RM} = \left| \begin{matrix} COK_{RM} + \frac{(1-COK_{RM})KO_i}{KO_{max}}, & \text{for } DO < RDO_{crit} \\ 1, & \text{otherwise} \end{matrix} \right.$$

$$KO_i = (DO_i)e^{-c_{RM} DO_1}$$

$$KO_{max} = KO_i \quad \text{at } RDO_{crit}$$

$$COK_{RM} = e^{-0.034T}$$

$$RDO_{crit} = \frac{1}{c_{RM}}$$

$$c_{RM} = \frac{0.018}{\log_e(T)}$$

$$f(\text{Sal})_{\text{RM}} = \frac{K_{\text{sa}} + K_{\text{sb}}}{5.37 W^{-0.158}}$$

$$K_{\text{sa}} = e^{0.05(29-\text{Sal})} W^{-0.158}$$

$$K_{\text{sb}} = e^{0.06(\text{Sal}-1)} W^{-0.158}$$

A.7. Post-prandial metabolism (SDA)

$$\text{SDA} = [0.12 + 0.01(\text{DO} - 79.6)]\frac{\text{FC}}{100} \quad (\text{kJ day}^{-1})$$

A.8. Active metabolism (A_m)

$$A_{\text{m}} = 1.5\text{FC} \quad (\text{kJ day}^{-1})$$

A.9. Egestion (F)

$$F = 0.074\text{FC}(T - 18)^{-0.5} e^{\text{CRO}} \quad (\text{kJ day}^{-1})$$

$$\text{CRO} = -0.3\frac{\text{FC}}{C_{\text{max}}} + 2.6\left[\frac{\text{FC}}{C_{\text{max}}}\right]^2 - 0.01(\text{DO} - 76.7)$$

C_{max} = maximum consumption rate at given size, temperature, salinity and DO conditions.

A.10. Excretion (U)

$$U = \text{RNE} + \text{XNE} \quad (\text{kJ day}^{-1})$$

$$\text{RNE} = 0.056 W^{0.71} \text{RM}_{T,\text{Sal},\text{DO}}$$

$$\text{XNE} = \frac{3.9\text{FC}}{100}$$

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