



Sensitivity of a shark nursery habitat to a changing climate

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ABSTRACT: Nursery area habitats such as estuaries are vital for the success of many fish populations. Climate change is altering conditions in these areas, which can thus impact the availability of suitable nursery habitat. The sandbar shark *Carcharhinus plumbeus* uses Chesapeake Bay (USA) as a nursery habitat during the summer months from birth up to 10 yr of age. To assess the impacts of climate change on juvenile sandbar sharks, we developed a habitat model using long-line data collected from a fishery-independent survey within Chesapeake Bay. With this model, we projected contemporary and future distributions of suitable habitat for juvenile sandbar sharks in Chesapeake Bay under varying environmental regimes. Predicted suitable juvenile sandbar shark habitat was negatively impacted by future increases in temperature, but positively influenced by future decreases in dissolved oxygen. The latter trend was likely related to the habitat partitioning that occurs between different life stages. Changes in salinity had relatively small impacts. By end-of-century the projected amount of suitable bottom habitat decreased; however, when incorporating the entire water column, projected suitable habitat increased. This suggests that juvenile sandbar sharks may need to make a behavioral shift to avoid non-preferred conditions, which could alter their foraging ecology or refuge strategies. As nursery habitats change with climate change, it is crucial to understand how a species may be impacted during this vital life stage when trying to predict overall species success in the future.

KEY WORDS: Habitat modeling · Sandbar shark · *Carcharhinus plumbeus* · Chesapeake Bay · Climate change · Environmental variability · Habitat suitability

1. INTRODUCTION

Many shark species rely heavily on nursery habitats for juvenile survival. Young-of-year (YOY) and juvenile sharks can spend several years in a nursery habitat where they can avoid predation and find an abundance of prey (Morrissey & Gruber 1993, Heupel et al. 2007). Among others, environmental factors such as salinity, temperature, and dissolved oxygen influence the distribution of individuals within estuarine nursery habitats (Froeschke et al. 2010, Ward-Paige et al. 2015, Oh et al. 2017).

Due to their close proximity to human populations, coastal habitats such as bays and estuaries are often influenced by anthropogenic pressures, such as human-induced climate change (Muhling et al. 2018). The shallow nature of coastal habitats makes them particularly vulnerable to climate change and susceptible to sudden changes in temperature. Anthropogenic nutrient inputs coupled with warming have already led to increases in the extent and severity of hypoxic zones (Hagy et al. 2004, Rabalais et al. 2009, Najjar et al. 2010). As climate-change impacts intensify worldwide, larger environmental changes in

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coastal habitats are expected to follow suit (Rabalais et al. 2009, Hoegh-Guldberg & Bruno 2010, Najjar et al. 2010, Irby et al. 2018), which will likely affect juvenile fish species that utilize these areas as nurseries.

Future suitability of nursery areas may require species to adapt or modify behavior as available habitat varies. For example, a large-scale study on 288 coastal fish species in the Mediterranean Sea reported projected reductions in home ranges of 55 and 60% between 2040 and 2059 and between 2080 and 2099, respectively (Albouy et al. 2013). Some species may expand into new nursery habitats as a result of climate change. For example, juvenile bull sharks *Carcharhinus leucas* have expanded their nursery habitat range north into Pamlico Sound (North Carolina, USA) as a result of warming temperatures in the region (Bangley et al. 2018).

A powerful approach to estimate climate effects on marine species is through the combination of understanding the relationship between the environment and both a species' physiology and its habitat use or distribution. When changes occur in the environment, it is important to understand how physiology may be impacted and thus drive the response of a species to the change (Pörtner & Knust 2007, Somero 2010, Horodysky et al. 2015). For example, a species with a broad thermal tolerance range may be more successful under climate change compared to a species that has a limited thermal tolerance range (Somero 2010, Madeira et al. 2012). Furthermore, species with a greater hypoxia tolerance will have more success when exposed to lower oxygen levels in coastal habitats compared to a species with lower hypoxia tolerance. In recent years, numerous studies have generated species habitat modeling from habitat-use data to project distributions under various climate change scenarios (Pinsky et al. 2013, Kleisner et al. 2017, Muhling et al. 2017, Morley et al. 2018, McHenry et al. 2019). As a result of these changes, many fish species are expected to experience habitat reductions (Hare et al. 2012, Kleisner et al. 2017) or shifts poleward (Morley et al. 2018), although these changes are very species specific. Despite numerous habitat modeling studies, understanding habitat changes on a smaller spatial scale, particularly in nursery habitats, is lacking.

The sandbar shark *Carcharhinus plumbeus* is a large coastal shark species that uses bays and estuaries as a primary nursery habitat. The largest estuary in the USA and most important nursery habitat for the sandbar shark in the northwest Atlantic is Chesapeake Bay. Pupping occurs in this area in late spring/early summer where YOY remain through the

summer until they move offshore during the colder months. For the following 4–10 yr, juvenile sandbar sharks return to these nursery areas to forage and avoid larger predators (Grubbs & Musick 2007). As a species that is listed as overfished (SEDAR 2017), it is critical for younger sharks to successfully reach maturity within these nursery habitats to promote population growth. However, like other coastal estuaries, Chesapeake Bay is getting warmer and more hypoxic due to climate change and anthropogenic nutrient input (Hagy et al. 2004, Najjar et al. 2010, Irby et al. 2018). In a laboratory controlled experiment, juvenile sandbar sharks had a high incipient lethal temperature (~32°C), but a poor hypoxia tolerance (critical oxygen level: 3.5 mg l⁻¹, Crear et al. 2019). At these thresholds, sandbar shark metabolic rate and performance substantially decline, and some individuals stopped swimming, despite the sandbar shark being an obligate ram ventilator (Crear et al. 2019). Unlike the hypoxia threshold, juvenile sandbar sharks likely do not encounter their temperature threshold often. However, with Chesapeake Bay warming and becoming more hypoxic, the encounter rate of both thresholds will likely increase in the future, particularly later in the century. To complement the study of Crear et al. (2019), which provided mechanistic relationships between sandbar sharks and their changing environment, here we used fishery-independent survey data to develop a habitat model to predict contemporary and future distributions of juvenile sandbar sharks in Chesapeake Bay under changing environmental regimes.

2. MATERIALS AND METHODS

2.1. Field data collection

Sandbar shark habitat data were collected from the Virginia Institute of Marine Science (VIMS) Cooperative Atlantic States Shark Pupping and Nursery (COASTSPAN) longline survey that sampled in Chesapeake Bay during June, July, and August from 2013 to 2019. For each month, 20 longline sets were made and selected using a random stratified design defined by depth. Depth was divided into 3 strata: shallow (<7.6 m), mid (7.6–12.2 m), and deep (>12.2 m). Additional sets (n = 22) were made during the summer of 2019 in specific areas of Chesapeake Bay to sample catch in conditions that occurred less often in the survey. Sharks were sampled using a demersal longline, composed of a 305 m mainline with 3.0 mm diameter monofilament set with 50 gangions

and 12/0 circle hooks (Mustad) baited with Atlantic mackerel *Scomber scombrus*. The longline gear was soaked for 30 min, during which nearby hydrographic conditions were recorded, including depth, bottom temperature, bottom salinity, and bottom dissolved oxygen. Sharks were brought aboard, identified, measured, sexed, and released. The number of juvenile sandbar sharks (71+ cm total length; age 1+; Conrath & Musick 2007) caught were recorded for each set. To make the results of this study comparable to that of Crear et al. (2019), where sharks were strictly juvenile, young-of-year sharks were not included in this study (<71 cm total length). The survey was designed to catch immature sharks; therefore, adult sharks were never caught. Survey animal handling protocols were approved under the William and Mary Institutional Animal Care and Use Committee protocol number IACUC-2019-03-05-13473-jxgart.

2.2. Model development

Using the survey data, we characterized habitat preferences of juvenile sandbar sharks using a negative binomial generalized additive mixed effects model (GAMM; 'mgcv' package by Wood 2011 in R v.3.6.1, R Core Team 2019). A GAMM framework was selected because of its ability to handle nonlinear relationships with habitat data (Hastie & Tibshirani 1990, Wood 2017). The response variable was the number of juvenile sharks sampled per longline set, and effort was calculated as the number of hooks divided by soak time (h), then standardized for 50 hooks and 0.5 h sets. The log of effort was included as an offset variable in the model. Habitat covariates selected for modeling were temperature ($^{\circ}\text{C}$), salinity (ppt), and dissolved oxygen (mg l^{-1}). Year was included as a random effect because we were not concerned about its impact on sandbar shark distribution, but did want to allow the model to accommodate the variation in the data attributed to year. The smoothing functions for the covariates were thin plate regression splines, and the number of knots within each smoother was adjusted to remove unrealistic noise in the response output. Temporal and spatial autocorrelation were assessed in the residuals of preliminary model fits, but neither was present.

The performance of the model was quantified using 5-fold cross validation, where the observations were randomly divided into 5 equally sized groups. One group was selected as the test dataset and used for prediction, while the other 4 groups were used to train the model. This process was repeated such that

each of the 5 groups served as the test data. Root-mean-squared-error (RMSE) was calculated for the test and training data sets, and if the RMSE values were similar, the model was deemed appropriate for generating predictions. Mean absolute error (MAE) was calculated on the test dataset for the full model and for a null model, which did not include any covariates (only included the offset of effort). The ratio between MAE for the full model and null model is known as the mean absolute scaled error (MASE) and is used to assess forecast predictions, where a ratio value <1 means the full model does a better job at predicting shark relative abundance compared to the null model (Kleisner et al. 2017). The last metric we used to assess model performance was the Diebold-Mariano test statistic, which assesses the errors between the full and null models (Diebold & Mariano 1995). A significant result for this test indicates a rejection of the null hypothesis in favor of the alternative, indicating that the full model provides a better prediction than the null model (Kleisner et al. 2017, Hyndman et al. 2019). Predictions over each covariate were generated using marginal means (Searle et al. 1980). Estimates of uncertainty were generated from 1000 bootstrapped samples (Efron & Tibshirani 1993).

2.3. Projection scenarios

Projected environmental conditions for Chesapeake Bay were extracted from the ChesROMS-Estuarine-Carbon-Biogeochemistry (ECB) model for the summer months (June–August). This is a 3-dimensional coupled hydrodynamic–biogeochemical model that has roughly a 1 km \times 1 km horizontal resolution and 20 terrain-following vertical levels that are higher resolution near the surface and bottom of the water column (Feng et al. 2015, Irby et al. 2016, Da et al. 2018). Daily averaged model outputs of temperature, salinity, and dissolved oxygen were generated from the ChesROMS-ECB model over 2001–2010. These conditions were considered the baseline. These years were selected because conditions were starkly different among some years.

To understand the impact of individual variables on sandbar shark available habitat, we performed climate change sensitivity tests where we manipulated temperature, salinity, and dissolved oxygen output from the ChesROMS-ECB model separately. For temperature we added 1, 2, 3, 4, and 5 $^{\circ}\text{C}$ to the temperature output from the ChesROMS-ECB model, while keeping the other variables constant. For

salinity we added 0.5, 1.0, 1.5, and 2.0 ppt to the salinity of the output from the ChesROMS-ECB model, while keeping the other variables constant. We subtracted 0.25, 0.50, 0.75, 1.00, 1.25, and 1.50 mg l⁻¹ from the dissolved oxygen output from the ChesROMS-ECB model, while temperature and salinity remained constant. All scenarios were applied evenly through the entire water column, since observations suggest that climate change impacts the surface and subsurface water of Chesapeake Bay similarly (Preston 2004, Irby et al. 2018). Each sensitivity test scenario was conducted for the full 10 yr simulation (2001–2010).

To estimate available juvenile sandbar shark habitat in Chesapeake Bay for mid-century and end-of-century, we manipulated the 3 variables simultaneously such that environmental conditions would be similar to what may be expected for those time periods. For end-of-century we added 2 ppt salinity, added 5°C temperature, and subtracted 1.5 mg l⁻¹ dissolved oxygen, whereas for mid-century we added 1 ppt salinity, added 2°C temperature, and subtracted 0.5 mg l⁻¹ dissolved oxygen. We selected 2 ppt because it fell between salinity projections for 2100 by Najjar et al. (2010), which predicted an increase between 1.4 and 3.2 ppt. In addition, recent work suggests that a sea level rise of approximately 1 m by 2100 would cause a 2 ppt increase and a 0.5 m rise in sea level by 2050 would cause a 1 ppt increase (St-Laurent et al. 2019). A 5°C increase for end-of-century and a 2°C increase for mid-century are representative of atmospheric warming estimated by the Coupled Model Intercomparison Phase 5 projections for the Representative Concentration Pathway (RCP) 8.5 scenario and inferred from Muhling et al. (2018) and Saba et al. (2016). A 1.5 mg l⁻¹ reduction in dissolved oxygen for end-of-century and 0.5 mg l⁻¹ reduction for mid-century was based on estimated solubility changes, phytoplankton growth rates, and organic matter remineralization relative to a 5 and 2°C increase, respectively (Irby et al. 2018). As above, the mid-century and end-of-century scenarios were conducted on all 10 years.

The habitat model generated from the shark survey was applied to baseline, all sensitivity test scenarios, and both mid- and end-of-century scenarios (Table 1) for each of the 10 years where each output consisted of projected juvenile sandbar shark catch throughout the entire Chesapeake Bay at all 20 vertical levels. Because we are not trying to predict sandbar shark catch, the value should be interpreted as a suitable habitat value. Suitable habitat values were averaged for each grid cell over all 10 years for

Table 1. Scenarios for each year type (average, dry, wet) where salinity or temperature were added (+) to the baseline output (2001–2010) from the ChesROMS-ECB model or dissolved oxygen was subtracted (–) from the baseline output from the ChesROMS-ECB model. For the mid-century (~2050) scenarios, 1 ppt salinity was added, 2°C was added, and 0.5 mg l⁻¹ dissolved oxygen was subtracted. For the end-of-century (~2100) scenarios, 2 ppt salinity was added, 5°C was added, and 1.5 mg l⁻¹ dissolved oxygen was subtracted

Scenarios	
Salinity (+)	0.5, 1.0, 1.5, 2.0
Temperature (+)	1, 2, 3, 4, 5
Dissolved oxygen (–)	0.25, 0.50, 0.75, 1.00, 1.25, 1.50
Time period	Baseline, 2050, 2100

baseline, all sensitivity test scenarios, and both mid- and end-of-century scenarios. This resulted in an average baseline output, average output for each sensitivity test scenario, and average output for the mid- and end-of-century scenarios.

Because conditions in Chesapeake Bay substantially vary from year to year and depend on whether it is a wet or dry year, we also selected the driest year (2001) and wettest year (2003) during that 10 yr time span. The suitable habitat output for 2001 and 2003 without any manipulations was considered baseline for a dry and wet year, respectively. Each suitable habitat output from the sensitivity test scenarios and the mid- and end-of-century scenarios for 2001 and 2003 was representative of a dry and wet year, respectively, for those scenarios.

In total, there were 18 scenarios with suitable habitat outputs for an average year (over 2001–2010), dry year (2001), or wet year (2003) (Table 1). Those 18 scenarios included a baseline scenario, mid-century scenario, end-of-century scenario, 4 salinity scenarios, 5 temperature scenarios, and 6 dissolved oxygen scenarios. With 18 scenarios for each year type (average, dry, wet), a total of 54 scenarios were ultimately assessed (Table 1). Suitable habitat was assessed along the bottom and was determined as the mean suitable habitat at each grid cell within 1 m of the bottom. Although juvenile sandbar sharks are thought to primarily use and feed on the bottom, they have been found to spend 50 and 35% of their time 3 and 6 m off the bottom, respectively. They are thought to make short forays into the water column to feed at night, and pelagic fish have been found in their stomachs (e.g. menhaden *Brevoortia tyrannus* and bluefish *Pomatomus saltatrix*) (Medved & Marshall 1981, Grubbs 2001, Ellis & Musick 2007). Based on this information, we deemed it appropriate to also assess suitable habitat throughout the entire water column.

2.4. Metrics

To quantify juvenile sandbar shark habitat suitability in Chesapeake Bay over each scenario, we calculated 2 metrics for the bottom and the entire water column. The first metric was total habitat suitability (THS), where all suitable habitat values on the bottom and entire water column in each cell were summed. The second metric was the percent change of the THS for the bottom or entire water column for each scenario relative to baseline, where baselines were each average, dry, or wet year. To remove any influence of ocean data on the THS of Chesapeake Bay, suitable habitat values outside of Chesapeake Bay in either of the metrics were not included.

3. RESULTS

3.1. Habitat model

From June to August in 2013–2019, 412 longline sets were deployed in Chesapeake Bay and 248 juvenile sandbar sharks (>71 cm total length; age 1+) were sampled (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m652p123_supp.pdf). The se-

lected GAMM explained 21.4% of the deviance. Of the 5 iterations in the cross validation approach, training and testing RMSE values were considered similar (mean RMSE train: 1.190; test: 1.182). The full model outperformed the null model, with the mean MASE being <1 and the mean Diebold-Marino test statistic being <0.05. Based on these metrics, we determined that the model performed reasonably well and could predict juvenile sandbar shark relative abundance (catch, interpreted as a habitat suitability value), with a moderate level of accuracy. Therefore, final results should be interpreted with care. Marginal mean predictions of juvenile sandbar shark relative abundance (habitat suitability) over the observed domains of predictor covariates showed greater use of temperatures of 22–26°C, salinities of 19–24 ppt, and dissolved oxygen values of 3.5–5.4 mg l⁻¹, and catch (suitability) was maximized at 24.3°C, 22.2 ppt, and 4.5 mg l⁻¹ (Fig. 1).

3.2. Bottom suitable habitat

3.2.1. Baseline scenarios

When focusing just on baseline scenarios, the most suitable habitat for an average year occurred from

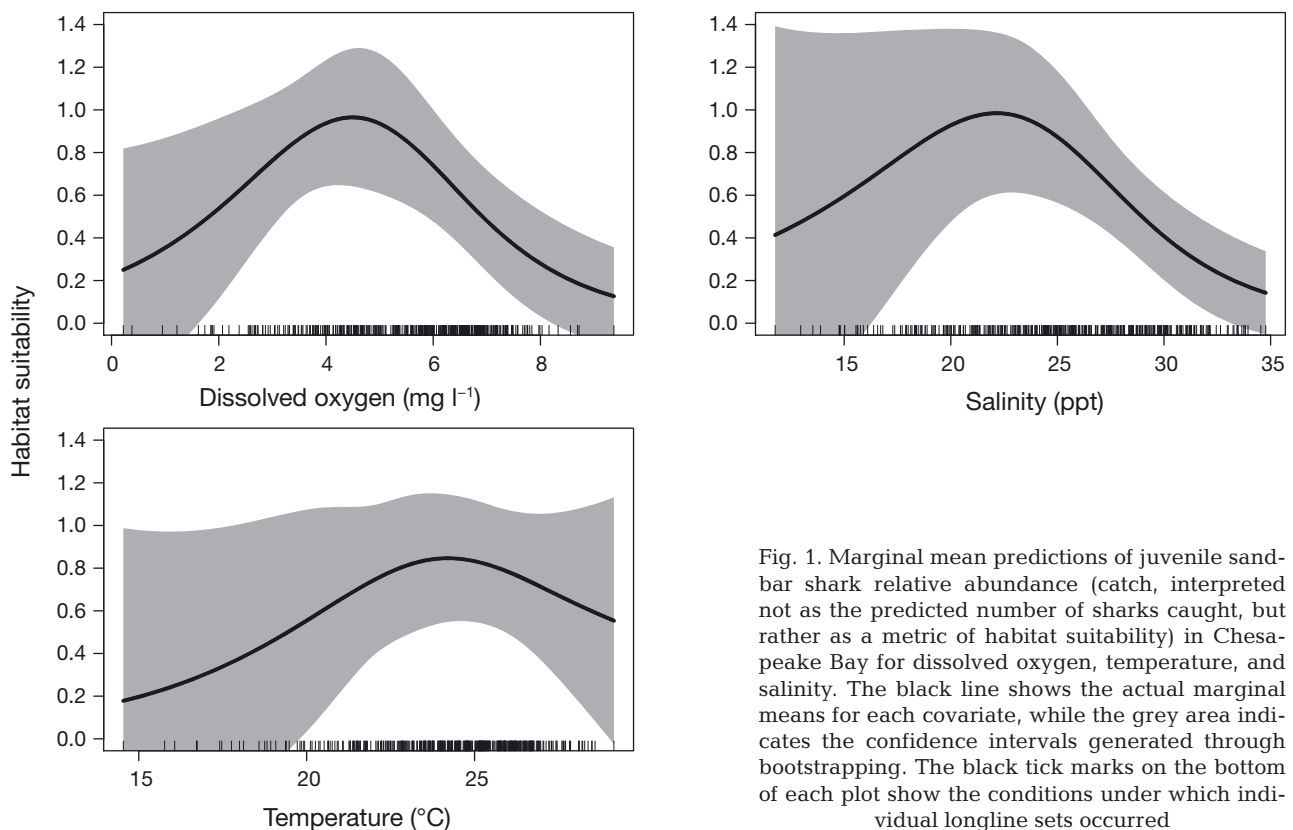


Fig. 1. Marginal mean predictions of juvenile sandbar shark relative abundance (catch, interpreted not as the predicted number of sharks caught, but rather as a metric of habitat suitability) in Chesapeake Bay for dissolved oxygen, temperature, and salinity. The black line shows the actual marginal means for each covariate, while the grey area indicates the confidence intervals generated through bootstrapping. The black tick marks on the bottom of each plot show the conditions under which individual longline sets occurred

the mouth of the Potomac River to south of Mobjack Bay (Fig. 2a). During a dry year, the most suitable habitat shifted further north compared to an average year and ranged from north of the Potomac River to areas south of the Rappahannock River (Fig. 2d). During a wet year, the most suitable habitat shifted farther south compared to an average year and ranged from Tangier Island to north of the mouth of the James River (Fig. 2g).

3.2.2. Sensitivity test scenarios

The THS for bottom habitat was always higher during a dry year, followed by an average year, and then a wet year regardless of the scenario (Fig. 3). As salinity increased, THS increased slightly (Fig. 3a), whereby an increase in 2 ppt only led to a <10% increase in THS for all year types (average, dry, wet) (Fig. 4a). THS increased with decreasing dissolved oxygen. For a dry year, THS increased at a faster rate as dissolved oxygen decreased (Fig. 3b). These trends were evident in the percent change metric, when dissolved oxygen was reduced by 1.5 mg l⁻¹, THS increased by 21, 13, and 1% for a dry, average, and wet year, respectively (Fig. 4b). As temperature increased, THS decreased; THS decreased fastest for a dry year, followed by an average year, and then a wet year (Fig. 3c). This was reflected by a decrease of 31, 29, and 12% for a dry, average, and wet year, respectively, when temperature increased by 5°C (Fig. 4c). During a wet year, THS did not change until temperatures increased by >2°C.

3.2.3. Time period scenarios

Between baseline and a mid-century year, THS decreased slightly during a dry and average year (1 and 2%, respectively), and slightly increased by 4% during a wet year (Figs. 3d & 4d). In addition, habitat loss occurred primarily between the mouths of the Potomac and Rappahannock Rivers for average, wet, and dry years, whereas small habitat gains occurred in areas towards the mouth of Chesapeake Bay and along areas closer to shore (Fig. 2b,e,h). Between baseline and an end-of-century year, THS decreased more substantially for an average (18%) and dry (15%) year, and decreased 7% for a wet year (Figs. 3d & 4d). Habitat loss occurred over a much wider area within Chesapeake Bay between baseline and end-of-century. For example, during an average year, habitat losses occurred along the entire main-

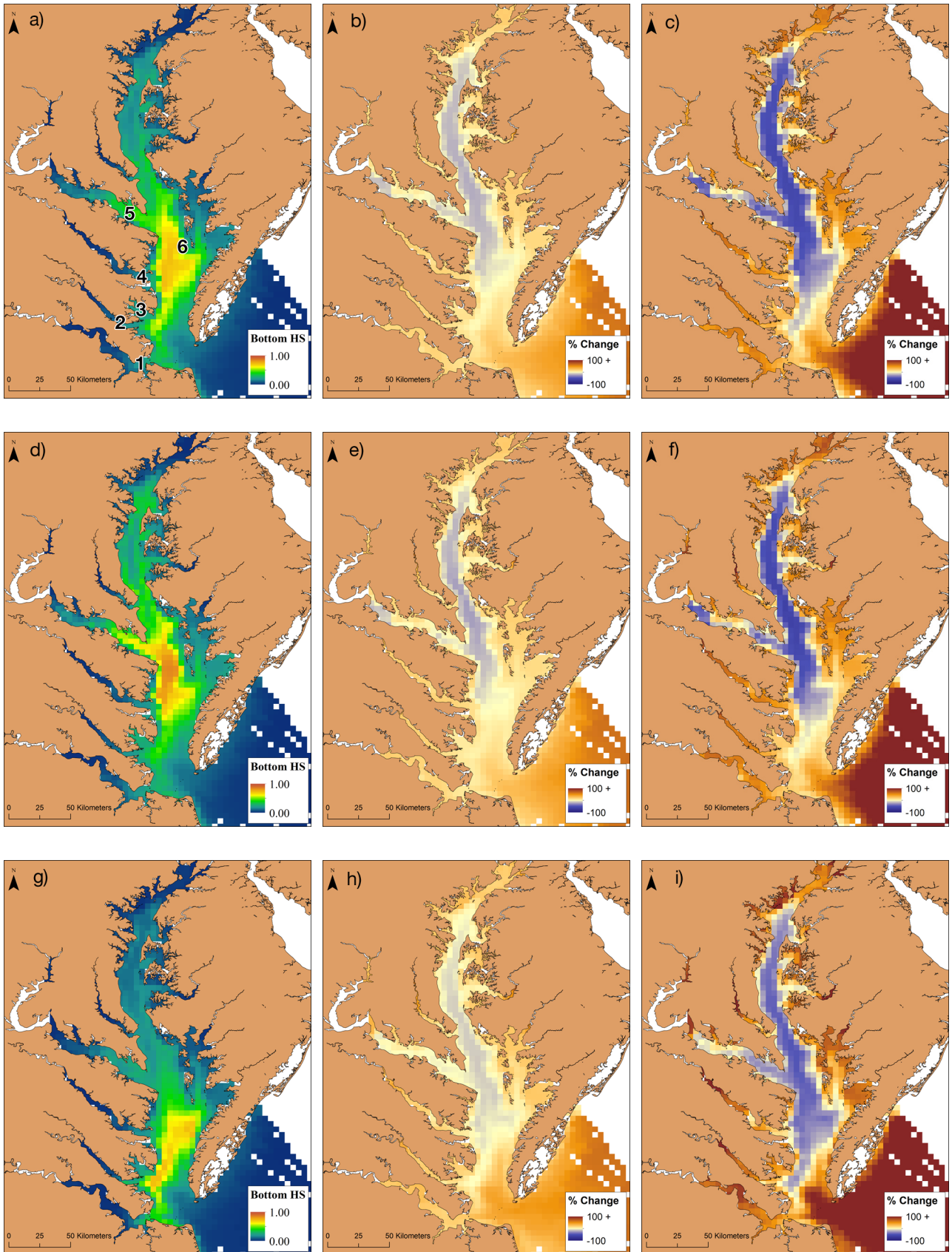
stem of Chesapeake Bay until the York River, with worse losses occurring in waters north of the Rappahannock River. Habitat gains occurred near the mouth of Chesapeake Bay and in shallower areas such as Mobjack Bay (Fig. 2c). During a dry year, habitat losses occurred primarily along the mainstem to south of the Rappahannock River. Like during an average year, habitat gains occurred in shallower areas and near the mouth of Chesapeake Bay (Fig. 2f). Lastly, during a wet year, habitat losses occurred along the entire mainstem to areas south of the York River, but habitat declines were not as great compared to an average or dry year. Habitat gains were more prevalent in shallow areas during a wet year compared to an average or dry year, and those gains occurred towards the mouth of the James River and Chesapeake Bay (Fig. 2i). Maps of projected suitable habitat values for mid-century and end-of-century for average, wet, and dry years are presented in Fig. S2.

3.3. Water column suitable habitat

3.3.1. Sensitivity test scenarios

The THS for the entire water column followed similar patterns for many of the scenarios as THS for the bottom habitat, but with greater magnitudes of change. The THS for the entire water column was always highest for the dry year, followed by the average and wet years (Fig. 5). THS increased slightly as salinity increased. More specifically, a 2 ppt increase resulted in a THS increase of only 10–15% for average, wet, or dry years (Fig. 6a). THS increased as dissolved oxygen decreased (Fig. 5b), but increased at the fastest rate in the dry year, followed by average and wet years. When dissolved oxygen was reduced by 1.5 mg l⁻¹, THS increased substantially by 53% in an average year, 62% in a dry year, and 39% in a wet

Fig. 2. Bottom habitat suitability (HS) maps for (a,b,c) an average year, (d,e,f) dry year, and (g,h,i) a wet year. Maps a, d, and g represent the baseline habitat distribution for juvenile sandbar sharks in Chesapeake Bay. HS values were divided by the maximized habitat suitability value (1.12) when salinity, temperature, and dissolved oxygen were optimal to put all baseline maps on a scale of 0–1. Maps b, e, and h are the percent change between the habitat suitability values from the baseline and 2050 from -100 to +100%. Maps c, f, and i are the percent change between the habitat suitability values from the baseline to 2100 from -100 to +100%. The numbers in (a) refer to key features referenced in the text and are as follows: 1, James River; 2, York River; 3, Mobjack Bay; 4, Rappahannock River; 5, Potomac River; 6, Tangier Island



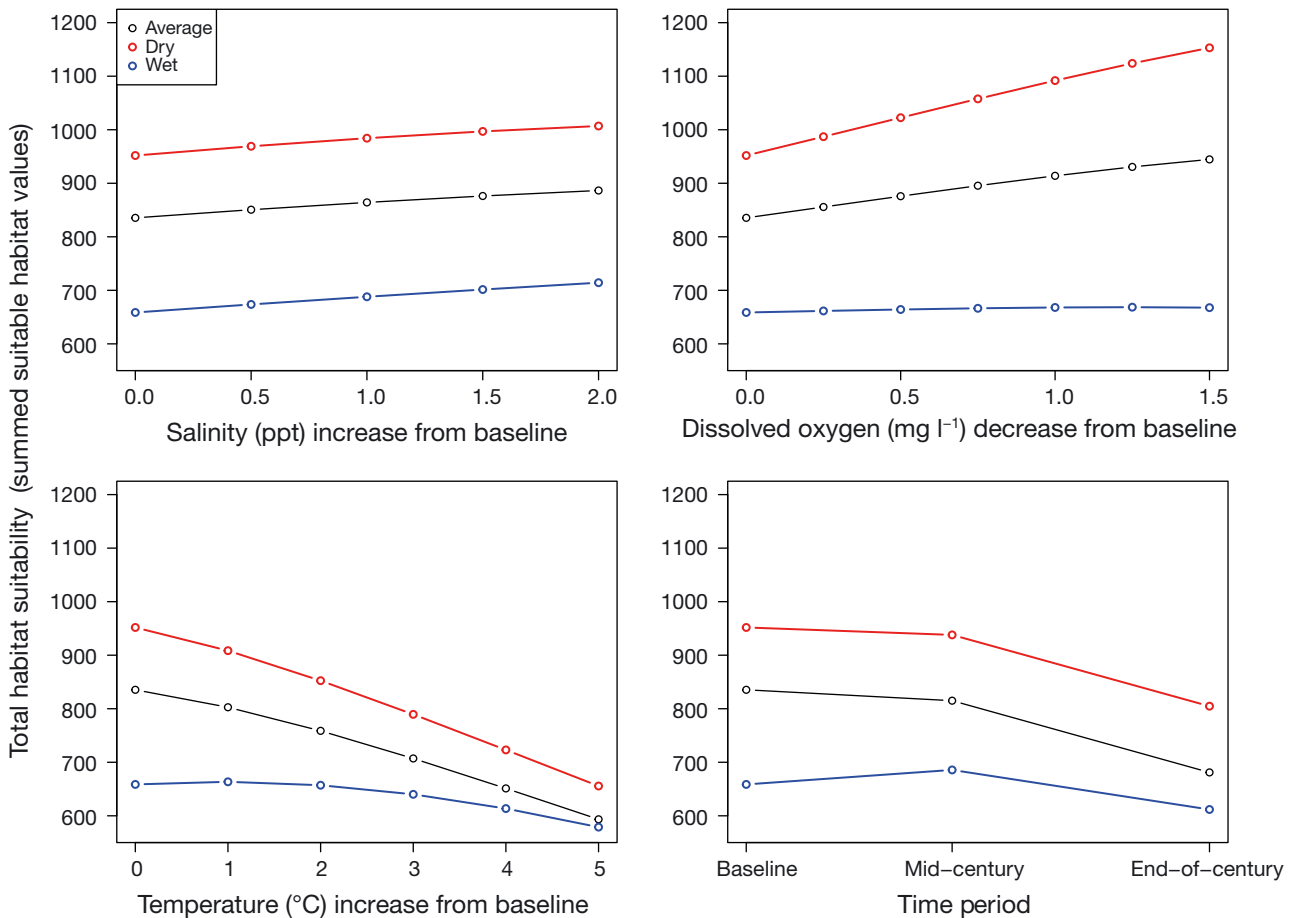


Fig. 3. Juvenile sandbar shark total habitat suitability values of bottom habitat (within 1 m of the bottom) within Chesapeake Bay for each environmental sensitivity (salinity, dissolved oxygen, and temperature) scenario and time period scenario for an average year, dry year, and wet year

year (Fig. 6b). THS decreased with increasing temperature (Fig. 5c), where at a 5°C increase, THS had decreased by 34, 35, and 22% for an average, dry, and wet year, respectively (Fig. 6c).

3.2.2. Time period scenarios

Compared to baseline, by mid-century for the entire water column, THS increased for average, dry, and wet years. Unlike for the bottom habitat, which showed a ~10–20% decrease in overall habitat by end-of-century (Fig. 4d), THS for the entire water column increased by the end of the century (Fig. 6d) by ~10–20%.

4. DISCUSSION

This study assessed the sensitivity of juvenile sandbar sharks to projected environmental changes in

Chesapeake Bay. It is clear that juvenile sandbar shark distribution shifts in latitude depending on whether environmental conditions are representative of an average, dry, or wet year. Assessing inter-annual variability in suitable habitat, although often ignored in most habitat modeling studies, is critical in understanding how a habitat may change (Crear et al. 2020), particularly in dynamic habitats (bays and estuaries). For juvenile sandbar sharks, a southward shift in suitable bottom habitat occurred during a wet year because the low-salinity water extended farther south, whereas during a dry year, the low-salinity water receded farther up Chesapeake Bay, resulting in a northward shift of suitable habitat. A reduced frequency of preferred bottom salinities (19.4–24.5 ppt) during a wet year (Fig. S5, cf. Fig. S3 for an average year) appeared to be the main driver of THS reduction compared to an average and dry year, whereas a higher frequency of preferred bottom salinities occurred during a dry year (Fig. S4). For

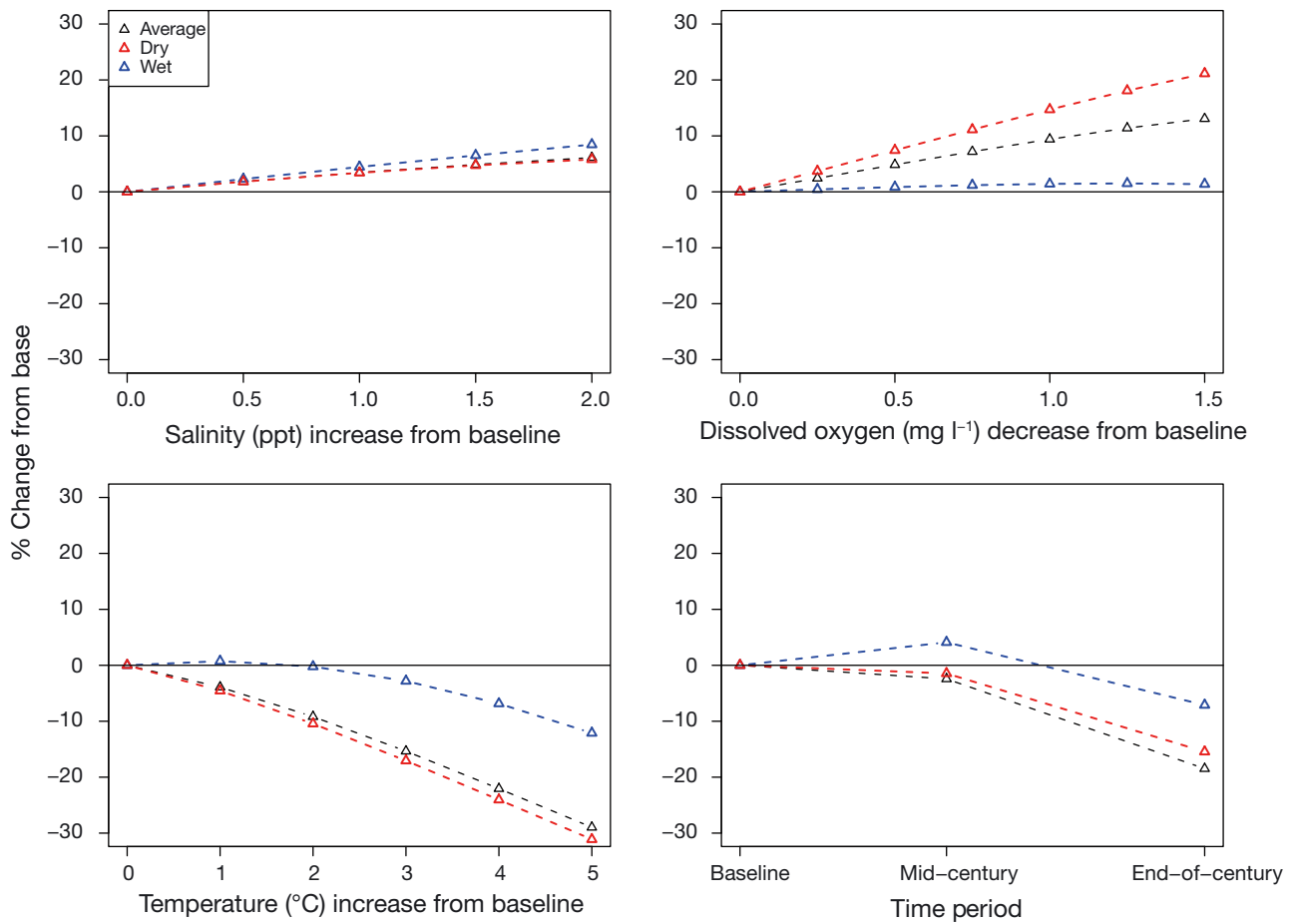


Fig. 4. Percent change of total habitat suitability of juvenile sandbar sharks along the bottom habitat (within 1 m of the bottom) within Chesapeake Bay for each environmental sensitivity (salinity, dissolved oxygen, and temperature) scenario and time period scenario relative to baseline for an average year, dry year, and wet year

baseline scenarios, salinity was the major driver of differences in suitable habitat distribution. Avoidance of low salinities is common among shark species that inhabit estuaries, and has been found to influence species distributions (Ubeda et al. 2009, Froeschke et al. 2010, Knip et al. 2011). This general finding was reported by Grubbs & Musick (2007), who examined sandbar shark distribution in Chesapeake Bay, although differences in the longlines used (i.e. mainline material, hook size, soak time) and sampling intensity when compared to our study make direct comparisons difficult.

Despite being sensitive to salinities in a wet versus dry year, juvenile sandbar sharks appeared to be impacted much less by increases in salinity compared to increases in temperature and decreases in dissolved oxygen. This is because differences in salinity between a dry and wet year (>3.5 ppt) and an average and wet year (>2 ppt) are larger than the

projected salinity changes. An increase of only 2 ppt from salinities that occur most frequently in Chesapeake Bay on average still does not overlap with the salinity preference of juvenile sandbar sharks (Figs. S3 & S6). Therefore, the 2 ppt increase expected by the end of this century is likely to benefit juvenile sandbar sharks, but should not elicit a massive change in distribution. An avoidance of higher salinities also suggests that juvenile sandbar sharks may be using salinity gradients in Chesapeake Bay as refugia from adult sandbar sharks that are inhabiting higher salinities. This avoidance behavior is a common theory behind nursery habitat use (Speed et al. 2010). To date, the occurrence of smaller sandbar sharks in the stomachs of large sandbar sharks is very rare, but other coastal carcharhinids like lemon sharks *Negaprion brevirostris* and bull sharks have been documented to cannibalize (Wetherbee et al. 1990, Ellis & Musick 2007). This potential threat may elicit a

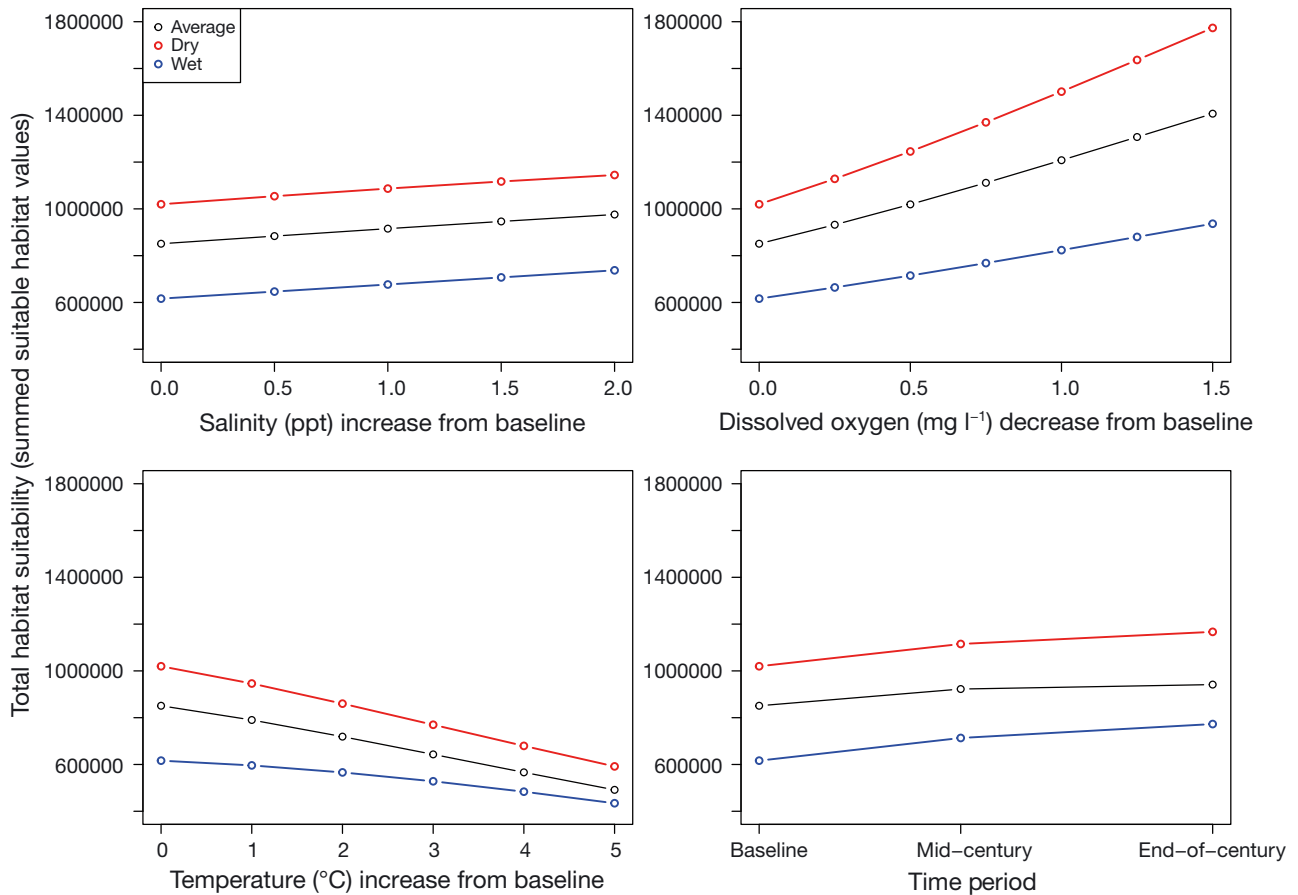


Fig. 5. Juvenile sandbar shark total habitat suitability values of the entire Chesapeake Bay water column for each environmental sensitivity (salinity, dissolved oxygen, and temperature) scenario and time period scenario for an average year, dry year, and wet year

tradeoff between predator avoidance and osmoregulatory costs associated with residence in lower salinities (Froeschke et al. 2010).

Despite the general trend that low dissolved oxygen is less favorable for many marine and estuarine species, our results indicated that juvenile sandbar sharks favor areas with lower dissolved oxygen levels. There are currently large areas with bottom dissolved oxygen levels above the preferred range for juvenile sandbar sharks; however, as dissolved oxygen levels drop, the amount of area within their preferred dissolved oxygen range is expected to increase (Figs. S3–S5). During a wet year, the decrease in dissolved oxygen had minimal impact because increases in freshwater stratifies the water column and leads to an increase in the flux of nutrients, primary production, and respiration, thus leading to larger hypoxic areas (Fig. S5) relative to an average or dry year. Therefore, when dissolved oxygen decreases further, the bulk of bottom water with low

dissolved oxygen levels is expected to have a smaller positive influence on THS during a wet year compared to an average year and especially compared to a dry year (Figs. S3–S5). The preference of juvenile sandbar sharks for areas with lower dissolved oxygen may be similar to habitat partitioning likely occurring across salinity gradients. The critical oxygen concentration (C_{crit}) or hypoxia threshold for juvenile sandbar sharks was 3.5 mg l⁻¹ at 24–32°C (Crear et al. 2019). Based on our results, it appears that juvenile sandbar sharks prefer dissolved oxygen concentrations between 3.5 and 5.4 mg l⁻¹, suggesting that higher relative abundances would be expected along the fringes of hypoxic areas. Juvenile sandbar sharks may be selecting these areas to avoid larger sharks, or because these are areas where their prey species are more abundant. Occupying areas just outside the hypoxic zone provides juvenile sandbar sharks the opportunity to make short forays inside hypoxic areas to forage on fish species that are

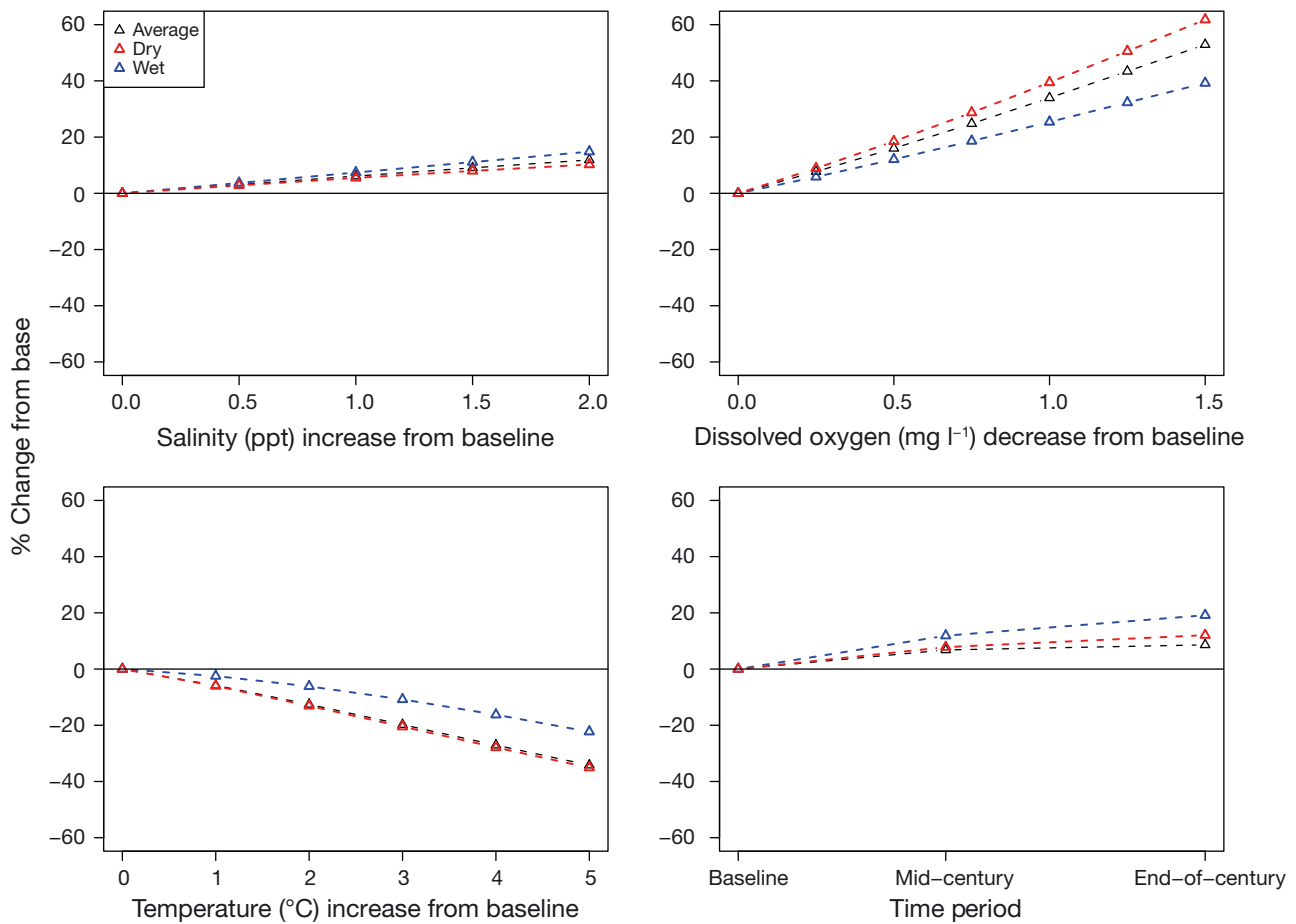


Fig. 6. Percent change of total habitat suitability of juvenile sandbar sharks for the entire Chesapeake Bay water column for each environmental sensitivity (salinity, dissolved oxygen, and temperature) scenario and time period scenario relative to baseline for an average year, dry year, and wet year

more hypoxia tolerant than they are, a predation behavior observed in other fish species (Breitbart et al. 2001, Ludsin et al. 2009). Although juvenile sandbar sharks appear to be sensitive to a decrease in dissolved oxygen, the overall influence appears positive.

Juvenile sandbar sharks also appear sensitive to increases in temperature. The gradual decline in THS was driven by a temperature preference (22–26°C) aligning with the most frequently occurring temperatures in Chesapeake Bay during baseline for average, dry, and wet years (Figs. S3–S5). As projected temperatures warm, the most frequently occurring temperatures quickly shift out of the temperature preference range of juvenile sandbar sharks, particularly for average and dry years, which contributes to at least a 30% decrease in THS at a 5°C increase. The performance of juvenile sandbar sharks quickly diminished during acute exposure (<72 h) at 32°C in a recent physiology study (Crear et

al. 2019). Interestingly, although juvenile sandbar sharks could handle 28°C during captivity and metabolic rate/behavioral trials (Crear et al. 2019), when given the option (in the wild) it appears they prefer lower temperatures. This suggests that juvenile sandbar sharks may actually have the capacity to withstand more of a temperature increase than our habitat model showed. Even if this was true, we are unaware of the physiological compromises (e.g. feeding efficiency, time to maturity) these sharks may have to make if required to inhabit warmer-than-preferred waters. Altogether, these results show the importance of conducting both laboratory and field experiments, where animals can be exposed to conditions that are not common in the wild (e.g. 32°C) and critical thresholds can be identified, while field data can assess relationships over a larger domain of a given variable.

Changes in suitable habitat likely occur on an interannual basis, whether there are wet, dry, cool, or

warm years, but under continued climate change these changes are expected to be more extreme. In the future, it appears that a wet year will have a smaller impact on the habitat availability of juvenile sandbar sharks in Chesapeake Bay, whereas a dry year will have a larger impact. Although bottom suitable habitat will generally decrease over the next century, habitat improvements in shallow areas will most likely result from dissolved oxygen levels dropping closer to more preferred levels. As climate change continues, extreme conditions (i.e. wetter and drier conditions) are expected to occur more frequently (Najjar et al. 2010, Singh et al. 2013); therefore, the magnitude of the fluctuations of the amount of suitable habitat interannually will increase. Furthermore, continued mitigation to reduce nutrient input into Chesapeake Bay will likely increase bottom oxygen, thus further complicating this situation.

By the end of this century, juvenile sandbar shark suitable habitat is likely to decline on the bottom, but to increase when the entire water column is considered. Specifically, the decline in bottom suitable habitat will occur because of the stronger negative effects of a 2 and 5°C increase compared to the positive effects of an increase in salinity and decrease in dissolved oxygen. However, the suitable habitat throughout the entire water column is expected to ultimately improve because the decline in dissolved oxygen in the more oxygenated water column (compared to just the bottom) would then result in a higher volume of water occurring within the juvenile sandbar shark preferred dissolved oxygen range (Figs. S6–S8).

Changes in suitable habitat along the bottom and throughout the water column will certainly impact juvenile sandbar shark behaviors. We expect that, as bottom habitat worsens, during a dry or average year, juvenile sandbar sharks may be forced to remain in a non-preferred habitat, move up in the water column, or shift to shallower habitats. Sandbar sharks are generalist feeders, which suggests that if they occupy waters off of the benthos, they could switch their current diet that is predominately crustaceans (e.g. mantis shrimp *Squilla empusa*) and benthic fishes (e.g. clearnose skate *Raja eglanteria*) to species that use more of the water column (e.g. menhaden and bluefish) (Ellis & Musick 2007). Predator avoidance is likely influencing juvenile sandbar shark habitat envelopes, which makes it appear that they prefer lower oxygen and salinity waters, but actually do not. This implies that juvenile sharks will continue to make tradeoffs to ultimately maximize fitness and ensure survival even as conditions change. Lastly, it appears that sandbar shark popula-

tions have been increasing in recent years despite being overfished (SEDAR 2017). This suggests that if reductions in bottom suitable nursery habitat occur, an increasing abundance of juvenile sandbar sharks could result in an increase in competition for resources. Such predications are tenuous, however, as the amplitude of fluctuations in the environmental conditions of Chesapeake Bay increase under the influence of climate change.

Projecting future habitat suitability in coastal habitats (e.g. bays and estuaries) is particularly difficult because environmental projections under climate change are often lacking compared to shelf or open-ocean ecosystems. Further, projecting the numerous processes shaping these coastal habitats in the future is difficult, especially as some bays and estuaries undergo restoration (e.g. Chesapeake Bay; Irby et al. 2018). The sensitivity approach we took is a simple method that is rarely used in habitat modeling, but can be valuable when trying to understand the drivers of habitat use change. The simplicity of this approach is also a limitation. For example, we applied each change throughout the entire water column, which likely will not occur in the future with climate change. In addition, like all end-of-century habitat projections, uncertainty is likely higher due to the uncertainty surrounding projected environmental conditions. Despite this, we believe this sensitivity approach portrays general trends and should be considered in future studies that assess habitat suitability of marine species when using coastal habitats, particularly as spawning, feeding, or nursery areas.

The suitability of nursery habitat areas is crucial to the population success of sandbar sharks. Expected environmental changes due to climate change are likely to create conditions that are less favorable along the bottom and more favorable throughout the water column. The capacity to adapt, such as making appropriate behavioral shifts, will be important for juvenile sandbar sharks to withstand the impacts of climate impacts. Whether the behavioral shifts will impact population success remains to be seen. As conditions in Chesapeake Bay and other estuaries shift under climate change, other species that use these habitats as nursery grounds may also need to behaviorally adapt. Without these abilities, species would be forced to leave habitats that have been used as nursery habitat for many generations and often frequented over consecutive years. As nursery habitats are modified with climate change, it is crucial to understand how a species may be impacted during this vital life stage when trying to predict overall species success in the future.

Acknowledgements. This research was supported by a grant from NOAA Fisheries (award NA16NMF4720218) and NOAA's National Centers for Coastal Ocean Science (award NA16NOS4780207). We thank the staff of the Multispecies Research Group at VIMS who collected the data for the COASTSPAN survey each summer in Chesapeake Bay and the marine technicians who operated the research vessels during the survey. We specifically thank Jim Gartland for his help in consolidating and processing the survey data. This work used the Extreme Science and Engineering Discovery Environment (XSEDE) supercomputer Comet at SDSC through allocation OCE-160013, which is supported by National Science Foundation grant number ACI-1548562. We also acknowledge William & Mary Research Computing (www.wm.edu/it/rc) for providing computational resources and/or technical support that contributed to the results reported within this manuscript. We appreciate the input and advice from Alistair Hobday and Rich Brill. Comments from the editor and 3 anonymous reviewers helped improve the manuscript. This is Virginia Institute of Marine Science contribution # 3954.

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Editorial responsibility: Robert M. Suryan,
Juneau, Alaska, USA

Submitted: April 29, 2020; Accepted: August 31, 2020
Proofs received from author(s): October 13, 2020