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Exploring interannual variability in potential spawning habitat for Atlantic bluefin tuna in the Slope Sea

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A B S T R A C T

The Slope Sea in the Northwest Atlantic Ocean, located between the Gulf Stream and the continental shelf of the Northeast United States, is a recently-documented possible major spawning ground for Atlantic bluefin tuna (*Thunnus thynnus*). Larval surveys and a habitat modeling study have shown that suitable spawning habitat occurs in the Slope Sea, but the degree to which this habitat varies interannually is an open question. Here, we perform a decade-long (2009–2018) numerical modeling analysis, with simulated larvae released uniformly throughout the Slope Sea, to investigate the interannual variability in the water temperature and circulation criteria deemed necessary for successful spawning. We also quantify the influence of Gulf Stream meanders and overshoot events on larval retention and their effect on habitat suitability rates throughout the Slope Sea, defined as the percentage of simulated larvae released at a given location that satisfy criteria related to water temperature and retention near nursery habitat. Average environmental oceanographic conditions over the decade are most favorable in the western part of the Slope Sea, specifically in the Slope Gyre and away from the immediate vicinity of the Gulf Stream. Variability in domain- and summertime-averaged yearly spawning habitat suitability rates is up to 25% of the mean decadal-averaged values. Yearly habitat suitability correlates strongly with the Gulf Stream overshoot but does not correlate well with other oceanographic variables or indices, so an overshoot index can be used as a sole oceanographic proxy for predicting yearly bluefin spawning habitat suitability in the Slope Sea. Selective spawning can weaken the correlation between habitat suitability and Gulf Stream overshoot. Effort should be put towards collecting observational data against which we could validate our findings.

1. Introduction

Atlantic bluefin tuna (*Thunnus thynnus*; bluefin hereafter) is a migratory fish of great economic and conservation value. Each year, bluefin migrate between coastal feeding areas in late summer and fall, deep water in winter and early spring, and spawning grounds in late spring and early summer. Catch data, electronic tagging, and larval surveys strongly suggest that bluefin tuna spawning largely occurs in waters between 23 °C and 28 °C, with the same temperature interval being required for successful egg hatching and larval development (Llopiz & Hobday, 2015; Muhling et al., 2010; Muhling et al., 2013; Reglero et al., 2018b; Rooker et al., 2007; Teo et al., 2007). In addition to water temperatures, advection by oceanic currents also plays a major role in spawning success rates by either enhancing or impeding retention of larvae in proximity to coastal nursery habitats (see Richards et al., 1989; Muhling et al., 2010; Lindo-Atichati et al., 2012; Domingues et al., 2016 for the studies in the Gulf of Mexico, Garcia et al., 2005 for the Mediterranean, and Rypina et al., 2019 for the Slope Sea). Thus, bluefin spawning success strongly depends both on water temperatures and circulation patterns.

Bluefin has been historically managed by the International Commission for the Conservation of Atlantic Tunas as two stocks—the western stock that spawns in the Gulf of Mexico and the eastern stock that spawns in the Mediterranean (Block et al., 2005; ICCAT, 2017; Rooker et al., 2008). However, recent collections of very young bluefin larvae in the Slope Sea—a geographical area located off the northeast United States between the shelf break and the Gulf Stream—have increased the focus on this region as a potential third major bluefin spawning ground (Richardson et al., 2016). Motivated by this recent discovery, Rypina et al. (2019) investigated the suitability of the Slope Sea for Atlantic bluefin tuna spawning using a realistic ocean circulation model. Their analyses suggest that in 2013—the year of larval collections by Richardson et al. (2016)—water temperatures and circulation patterns in the Slope Sea generally provided suitable conditions for bluefin spawning and larval development but with clear spatial variability.

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Here, we extend the analyses of Rypina et al. (2019) from one year (2013) to the decade 2009–2018 in order to investigate and quantify the inter-annual variability in bluefin spawning habitat suitability throughout the Slope Sea. As in Rypina et al. (2019), we compute a habitat suitability rate, defined as the percentage of simulated larvae released at each location that satisfy criteria related to water temperature and retention in proximity to nursery habitats (see Methods for details). While habitat suitability and spawning success initially seem related, spawning success depends not only on the availability of favorable habitat (habitat suitability), but also on the behavior of adults and the overall biomass of spawners. Since our simulated larvae are released evenly throughout the Slope Sea, which would not be occurring in reality, our spatially-explicit analysis is an examination of spawning habitat suitability rather than actual spawning success. We also explore the sensitivity of habitat suitability rates with respect to the retention criterion used to define successful larvae, i.e., strict retention inside the Slope Sea for the entire duration of bluefin larval development interval (taken to be 25 days here) versus the less strict requirement that larvae only end up in the Slope Sea at the end of the larval development interval. In addition, we compare the changes in habitat suitability rates obtained through the use of the time-evolving meandering Gulf Stream as the Slope Sea southern boundary versus the use of mean location of the Gulf Stream as the southern boundary. We also evaluate regions of the Northwestern Atlantic outside of the Slope Sea as possible spawning grounds and show that habitat suitability rates there are significantly smaller. We use statistical correlations to indicate which oceanographic variables, indices and processes have a major influence on the bluefin spawning habitat suitability in the Slope Sea, and we use a linear regression to construct a model for predicting habitat suitability based on an oceanographic index, specifically, the Gulf Stream overshoot index. We also explore the possible connection between habitat suitability and temperature fronts in the Slope Sea, and we investigate the effects of potential selective spawning strategies by bluefin, such as targeting waters with a more narrow temperature range (around 26 °C), and spawning in areas with the highest habitat suitability.

2. Methods

2.1. HYCOM model output and lagrangian simulations

Our numerical simulations are based on an ocean circulation model HYCOM (Hybrid Coordinate Ocean Model; Chassignet et al., 2006). We use the data-assimilative global numerical experiments GLBa008 experiments #90.8 through #91.2 with 1/12° spatial resolution that are publically available on the HYCOM website (http://tds.hycom.org/thredds/catalog.html). We use daily model velocities at 10 m below the surface. This depth was chosen because field surveys suggest that bluefin larvae do not exhibit vertical migrations, and that 10 m corresponds to the mean depth of larval distributions observed in the field (Habtes et al., 2014; Reglero et al., 2018a). Sensitivity tests (Appendix A; see also Rypina et al., 2019) suggest that results at 5 m are similar. Data assimilation and realistic atmospheric forcing ensure that the HYCOM model output that we use is representative of oceanographic conditions for the years 2009 to 2018, the time period of this study (Cummings, 2005; Cummings & Smedstad, 2013; Fox et al., 2002); see also https://www7320.nrlssc.navy.mil/GLBhycom1-12/ for verification statistics and model data comparisons).

For each year, we run bio-physical simulations of larval dispersal by releasing simulated larvae on a regular 0.25°-by-0.25° grid spanning the entire Slope Sea every day from 1 June to 20 September, which encompasses the spawning season with margins on both sides (Richardson et al., 2016). A total of approximately 75,000 simulated larvae were released within the Slope Sea each year (although the exact number changes from year to year due to the changes in the area of the Slope Sea). Sensitivity analysis with increased numbers of simulated larvae suggests that our results are statistically robust (see Appendix B). In one

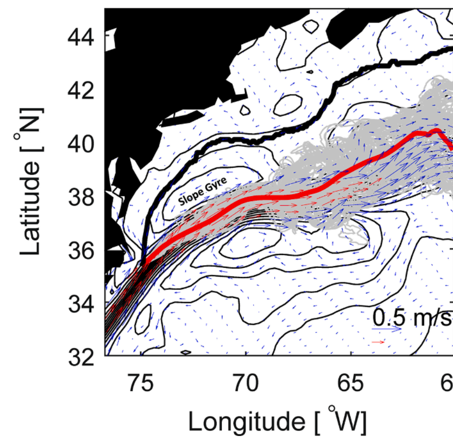

Fig. 1. Superposition of daily locations of the Gulf Stream northern wall (grey) and the mean location of the Gulf Stream northern wall (red) in Summer 2013. The thick black curve is the 200 m isobath. Thin black contours show the long-time mean (1993–2012) SSH contours, corresponding to the mean dynamic topography from https://cds.climate.copernicus.eu/cdsapp#!/dataset/satellite-sea-level-global?tab=overview. The Slope Gyre is marked. Red and blue arrows show mean geostrophic velocities derived from satellite altimeters (scale in the bottom right corner; data taken from the same website).

simulation we released simulated larvae in a wider region of the Northwestern Atlantic to investigate habitat suitability rates outside of the Slope Sea. In another targeted simulation, we assumed that larvae selectively spawn in geographical areas with the highest habitat suitability, and we released simulated larvae only within the habitat suitability "hot spots," defined by the upper 80th percentile contour of the highest habitat suitability rates for each year. (In this simulation, larvae are released uniformly throughout the hot spot areas, instead of throughout the entire Slope Sea.) Trajectories are integrated for 25 days, which corresponds to bluefin larval development time until reaching the juvenile stage and the onset of directed swimming (Fukuda et al., 2010), using the 4th order variable-step Runge-Kutta scheme (ode45 in Matlab) with a bi-linear interpolation between velocity grid points in time and space. Identical integration and interpolation schemes were used in Rypina et al. (2019), who also demonstrated that the 25-day integration is sufficiently short that the addition of horizontal diffusion does not significantly affect the results. Also, we did not impose active horizontal swimming because any directional swimming behavior of bluefin larvae is not known.

2.2. Working definitions of the Slope Sea, Gulf Stream northern wall, and overshoot events, and a brief description of ocean currents in the area

The Slope Sea was defined as the geographical region west of 60°W lying between the Gulf Stream northern wall and the 200 m isobath that delineates the shelf break. The northern wall of the Gulf Stream was defined following Fuglister (1955) as the 15 °C isotherm at 200 m depth. If the time-mean northern wall is used as the southern boundary of the Slope Sea, we refer to the resulting time-independent Slope Sea domain as the "time-mean Slope Sea." If the instantaneous position of the northern wall is used as the southern boundary, we refer to the resulting evolving in time Slope Sea domain as the "time-evolving Slope Sea."

The Gulf Stream typically separates from the N. American shelf near Cape Hatteras, but sometimes it "overshoots" further north along the coast; such events are called Gulf Stream overshoot events (Dengg et al., 1996; Dengo, 1993; Özgökmen et al., 1997; Pierini et al., 2011; Zhang & Vallis, 2007). Following Rypina et al. (2016), we define the Gulf Stream overshoot index as the mean latitude of the Gulf Stream between 75°W and 70°W. Overshoot events have been shown to affect slow-swimming

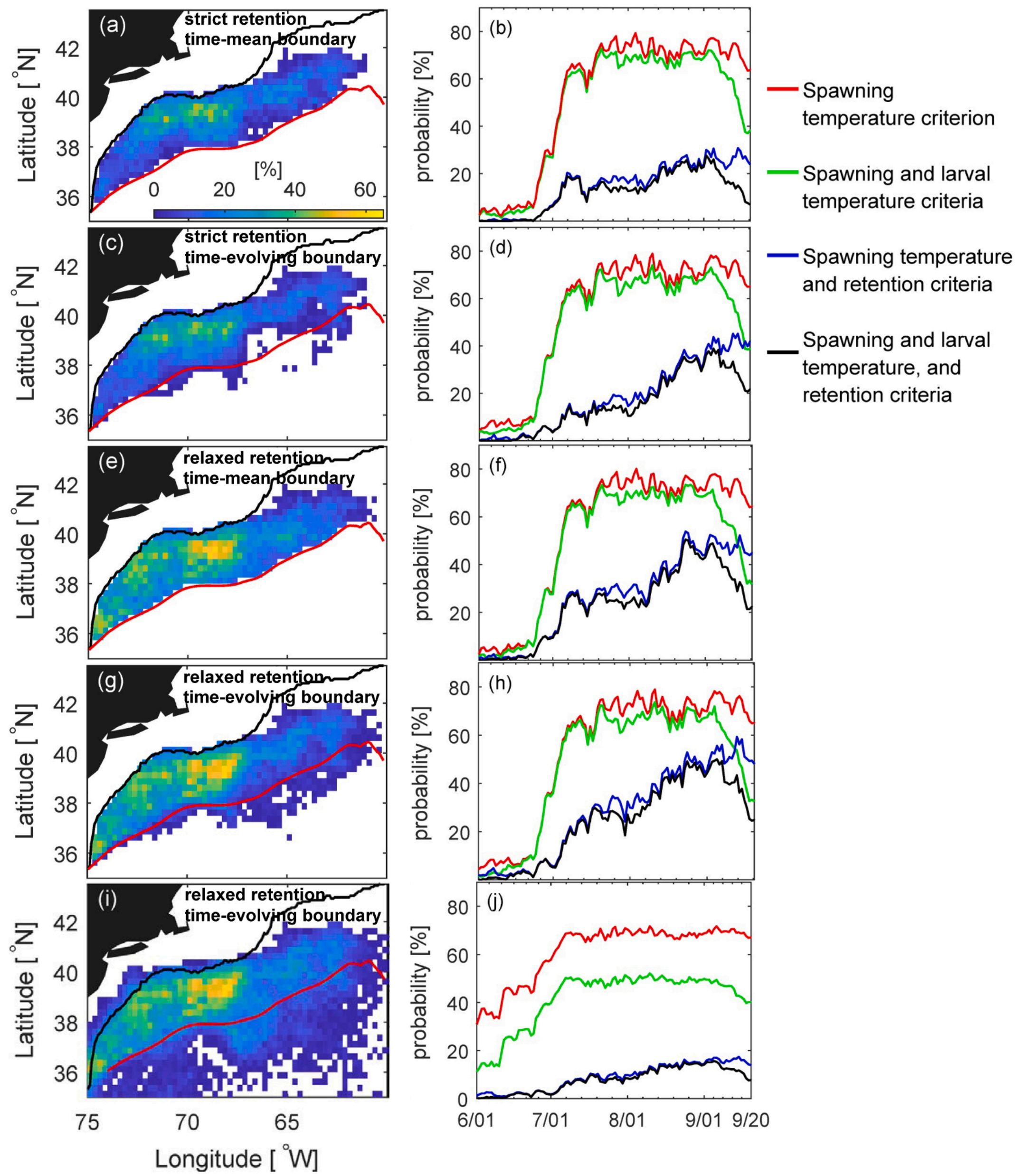

Fig. 2. Probability maps (left) and time series (right) of spawning habitat suitability rates in 2013 using strict (a-d) and relaxed (e-j) retention conditions for the time-independent Slope Sea domain (a,b,e,f), time-evolving (c,d,g,h) Slope Sea domain, and Northwestern Atlantic domain (i,j). In left panels, the red curve is the summer-mean Gulf Stream, and the black curve is the 200 m isobath. Red / green / blue / black in right panels correspond to rates for larvae satisfying spawning temperature / spawning and larval temperature / spawning temperature and retention / spawning and larval temperature and retention criteria.

biological organisms, specifically American eel larvae, in crossing the Gulf Stream and reaching coastal nursery areas (Rypina et al., 2016). Here, we show that Gulf Stream overshoot also significantly affects bluefin spawning habitat suitability in the Slope Sea.

Oceanic circulation in the western Slope Sea is dominated by two current systems: a generally southward flow over the continental shelf and slope, and the northeastward-flowing Gulf Stream Extension current (Fig. 1). These two systems produce, in the mean, a cyclonic recirculation called the Slope Gyre (Csanady & Hamilton, 1988); however, it can get shifted or disrupted by transient eddies and Gulf Stream rings that detach from the meandering Gulf Stream further east and propagate westward toward the coast. Several such Gulf Stream rings are produced each year (Brown et al., 1986) but not all reach the slope gyre because many get reabsorbed by the Gulf Stream.

2.3. Quantifying spawning habitat suitability

Habitat suitability criteria that we used in this study were based on knowledge of optimal temperatures for bluefin spawning and larval development (23–28 °C), as well as presumption of larval retention within the Slope Sea domain. Specifically, larvae were considered successful if they satisfied the following three criteria:

1) Spawning-temperature criterion: water temperature at time and location of larval release is between 23 °C and 28 °C;
2) Larval-temperature criterion: mean water temperature along the 25-day-long larval trajectory is between 23 °C and 28 °C; and
3) Retention criterion: larvae are located inside the Slope Sea 25 days after their release.

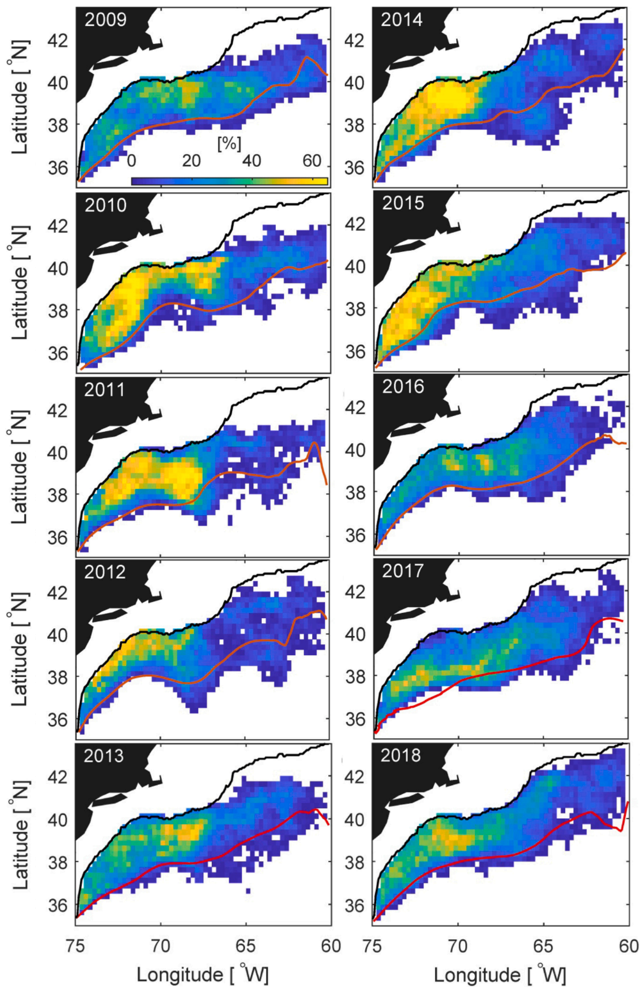

Fig. 3. Probability maps of spawning habitat suitability rates for individual years, evaluated for the time-evolving Slope Sea using the spawning and larval temperature, and relaxed retention criterion. The red curve is the summer-mean Gulf Stream for each year. The black curve is the 200 m isobath.

The formulation of the spawning temperature criterion is straightforward and simply uses information about the optimal spawning temperature interval. The larval temperature criterion, on the other hand, requires some assumptions about the ability of larvae to survive at suboptimal temperatures. Specifically, we assumed that larvae can survive temporarily outside of the optimal temperature interval, as long as the average temperature along the larval trajectory is within the stated range. Both temperature criteria were identical to those used in Rypina et al. (2019). In two additional simulations we used two narrower temperature intervals, 25–27 °C and 25.5–26.5 °C, for criteria 1 and 2. These targeted simulations are motivated by the fact that more larvae have been captured in waters with approximately 26 °C in the Gulf of Mexico and Mediterranean Sea (see Muhling et al., 2010). Our retention criterion is motivated by the assumption that bluefin nursery habitat is located inshore of the shelf break along the U.S. east coast (Galuardi & Lutcavage, 2012; Mather, 1995; Rooker et al., 2003). Those individuals that find themselves offshore of the Gulf Stream by the end of their larval development time (25 days in our case) would have to cross the Gulf Stream in order to reach coastal waters, which presents a major challenge for very young tuna. Thus, we impose that successful larvae are those that are located inside the Slope Sea after 25 days (regardless of where they traveled during those 25 days), allowing access to nursery habitats. We will refer to this retention criterion as the "relaxed retention criterion," which differs from the "strict retention criterion" used in Rypina et al. (2019) where successful larvae were retained within the Slope Sea for the entire 25 days. The reason for using the strict rather than relaxed retention criterion in Rypina et al. (2019) was that the model domain in that study was too small to allow tracking of larvae outside the Slope Sea, thus making it impossible to say whether larvae were coming back or staying outside once they left the Slope Sea. Note that the relaxed retention criterion also allows for successful larvae that start outside but end inside of the Slope Sea.

2.4. Statistical techniques: habitat suitability probability maps, correlation coefficients, linear regression, and maps of frontal occurrences

Following the methods employed by Rypina et al. (2011, 2014, 2016, 2019), we used statistical probabilities to identify times and regions of the Slope Sea (and in one simulation, of the wider geographical region of Northwestern Atlantic) that, on average, provide favorable environmental conditions for bluefin spawning and larval development. Specifically, habitat suitability probability maps were generated to show the time-averaged probability that a larva released at a certain geographical location satisfies success criteria 1, 2, and 3 (or, in some simulations, the narrower temperature interval in 1 and 2, or the strict version of 3). Associated with a time-averaged probability map there is a space-averaged time series, which quantifies the probability that larvae released on a given day anywhere in the Slope Sea satisfy the success criteria.

Our presentation will also utilize cross correlation analysis and linear

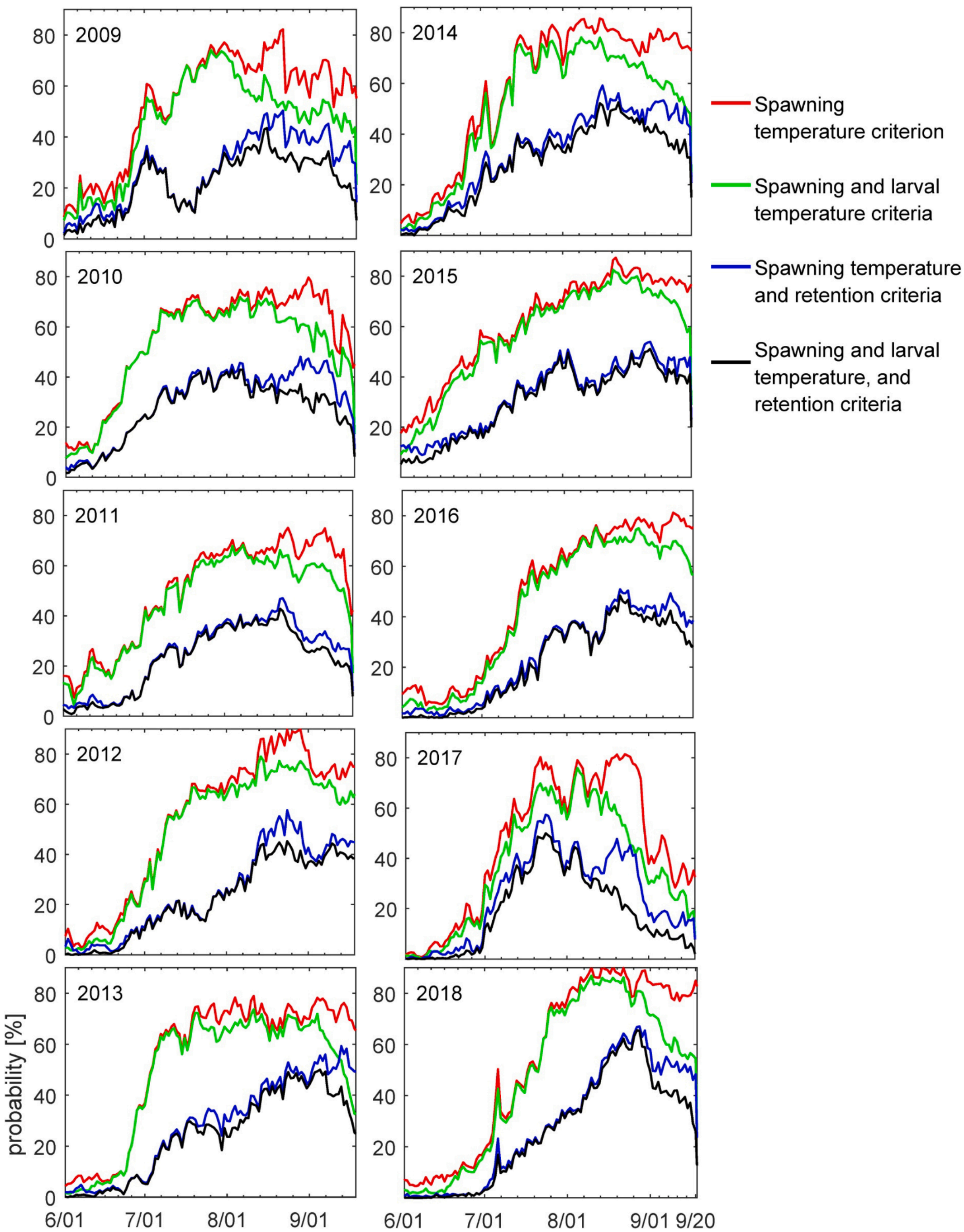

Fig. 4. Time series of habitat suitability rates for individual years. Red/green/blue/black show % of simulated larvae satisfying spawning temperature/spawning and larval temperature/spawning temperature and retention/spawning and larval temperature and retention criteria.

regression. The cross correlation coefficient between two discretely sampled time series, $(X_1, X_2, \cdots, X_N)$ and $(Y_1, Y_2, \cdots, Y_N)$ is defined as $R_{x,y} = \frac{\sum_{i=1}^{N}(X_i-\overline{X})(Y_i-\overline{Y})}{\sqrt{\sum_{i=1}^{N}(X_i-\overline{X})^2}\sqrt{\sum_{i=1}^{N}(Y_i-\overline{Y})^2}}$, where overbar denotes the mean value. For two identical time series the cross correlation coefficient is 1; if one of the two identical time series is flipped in sign, then the correlation coefficient becomes −1. Simple linear regression is used to determine how well the dependent variable—spawning habitat suitability rate (P)—might be predicted by the Gulf Stream overshoot index (O), i.e., P = b * O + a. The coefficients a and b that minimize the difference between true and predicted values of the dependent variable are given by b = $R_{P,O}STD(P)/STD(O)$ and a = $\overline{P} - b\overline{O}$, where STD denotes standard deviation.

Temperature fronts have been identified as locations where the local horizontal temperature gradient exceeds one STD above the domain- and summertime-averaged (from June 1 to September 20) mean value for a given year. For each year, frontal occurrence probability at each location was computed by dividing the number of days when a front was present by 111 (the number of days spanning 6/1 to 9/20). The decadally-averaged frontal occurrence map was computed by averaging together 10 maps for individual years.

3. Results

The instantaneous location and shape of the Gulf Stream can

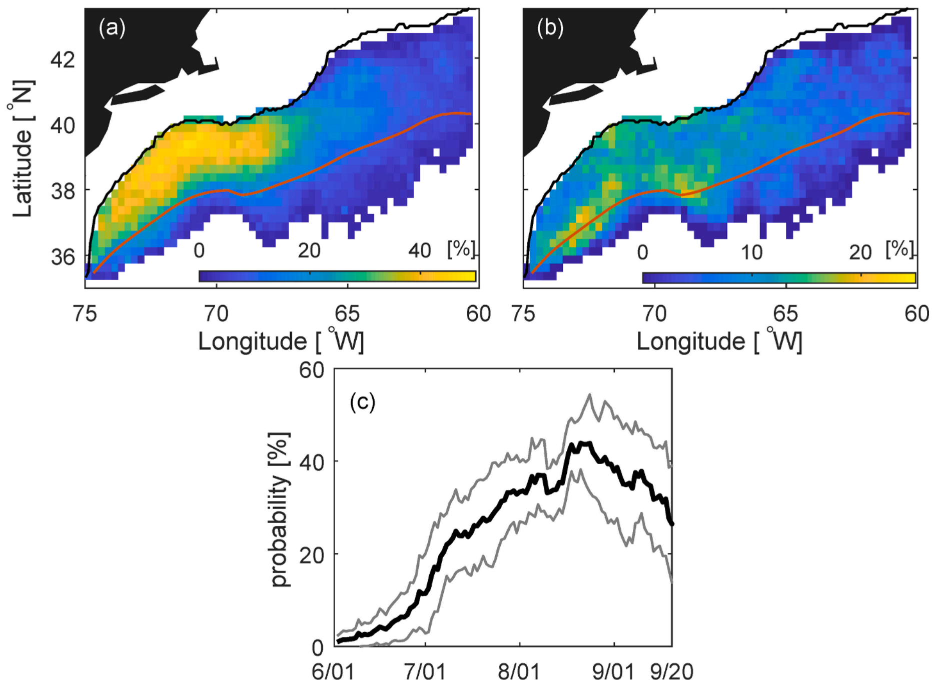

Fig. 5. (a) Mean and (b) STD of the 10 probability maps (i.e. years) in Fig. 3. The red curve shows the decadal average of the 10 summer-mean Gulf Stream curves in Fig. 3. The black curve is the 200 m isobath. (c) Mean and 1-std interval for the 10 time series in Fig. 4.

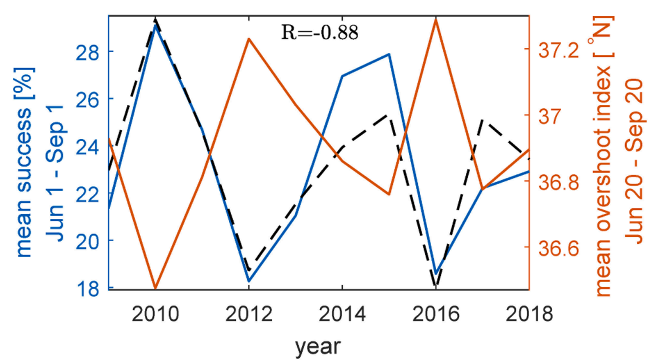

Fig. 6. Spatio-temporally averaged spawning habitat suitability rates, computed directly from simulated larval trajectories (blue) and reconstructed from overshoot index using linear regression method (black dashed), i.e., success = a*overshoot + b with a = -13.3187 and b = 514.4940. The Gulf Stream overshoot index is shown in red. R is the habitat-suitability-overshoot correlation coefficient.

significantly change in time over the summer season (Fig. 1). In order to quantify the influence of this variability on bluefin spawning habitat suitability throughout the region, we compare statistics of simulated habitat suitability rates in 2013 for the time-mean versus time-evolving Slope Sea domain (see Methods for definitions), and for the relaxed versus strict retention criteria (Fig. 2). The two temperature criteria—spawning temperature and larval temperature—are kept the same in all simulations. Our analysis suggests that the strict retention criterion inside the time-mean Slope Sea (Fig. 2a,b) is hardest to satisfy and produces the smallest habitat suitability rates (averaged over the entire Slope Sea domain and entire spawning season), whereas the relaxed retention criterion inside the time-evolving Gulf Stream (Fig. 2g,h) is overall easiest to satisfy and produces the largest habitat suitability rates. Simulations with the same (i.e., strict or relaxed) retention condition and different Slope Sea definition (i.e., time-independent versus time-evolving Slope Sea) are similar to each other, and simulations with the same Slope Sea definition and different retention conditions are dissimilar. All 4 simulations show zero success in the northeast, very small success in the east, rapidly diminishing success across the mean Gulf Stream, and elevated success in the western half of the Slope Sea, with a hot spot near 68°W and 39°N. In addition to the higher overall habitat suitability, simulations with the time-evolving Slope Sea show substantially higher values in the Slope Gyre. In order to investigate the possibility of successful spawning outside of the Slope Sea, we also performed one additional simulation (Fig. 2i,j), where we kept the 3 success criteria unchanged (as in Fig. 2g,h) but initialized larvae throughout the wider region of the Northwestern Atlantic, instead of only in the Slope Sea as in other simulations. The resulting probability map (Fig. 2i) is similar to Fig. 2g. All 5 time series in Fig. 2 show that in 2013 successful spawning started in late June, peaked in late August, and decreased through September. In all 5 simulations, probabilities to satisfy one or both temperature criteria (red and green curves in right panels) are close to each other (except at the end of the season when it becomes harder to satisfy the larval temperature criterion than the

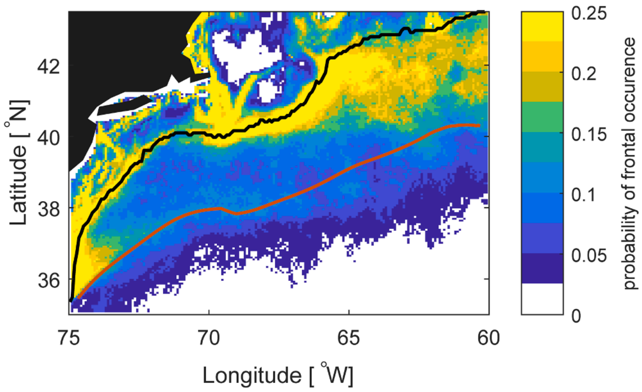

Fig. 7. Decadally-averaged frontal occurrence map showing the probability that a temperature front is present at a given location during a summer season. The red curve shows the mean location of the Gulf Stream, averaged over 10 summers from 2009 to 2018 (same as in Fig. 5a-b). The black curve is the 200 m isobath.

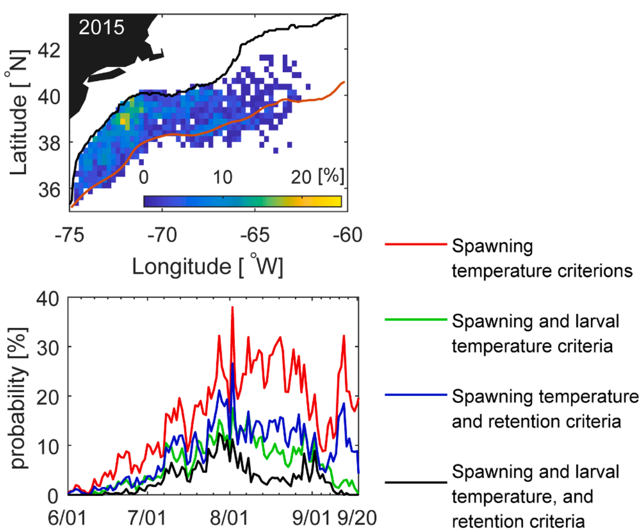

Fig. 8. For 2015, the probability map (top) and the corresponding time series (bottom) of habitat suitability rates in simulations with the most narrow suitable temperature interval (25.5–26.5 °C). In the top panel, the red curve is the summer-mean Gulf Stream for 2015. The black curve is the 200 m isobath.

spawning temperature criterion) and significantly different from those involving the retention condition (blue and black curved).

Next, we investigated the inter-annual variability in habitat suitability rates over the decade 2009 through 2018 (Figs. 3-5). Here and for the remainder of the analyses we use the relaxed retention criterion and the two temperature criteria (spawning temperature and larval temperature) to evaluate habitat suitability, as well as the time-evolving instantaneous Gulf Stream as the Slope Sea's southern boundary. Probability maps for all individual years (Fig. 3) show elevated habitat suitability in the western part of the Slope Sea, with diminishing values further to the northeast, down to near-zero and zero values in the northeastern corner of the domain. For any given year, the southern extent of the non-zero habitat suitability region coincides roughly with the mean path of the Gulf Stream for that year (i.e., there is almost no blue south of the red curves in Fig. 3). This is particularly true in the western part of the domain, where the Gulf Stream does not meander much (i.e., grey region in Fig. 1 is thin in the west and wide in the east). The spawning hot spots (regions with locally highest habitat suitability rates) vary from year to year in their values (from ~ 50% in low-habitat-suitability years such as 2016 to ~ 80% in 2014), locations (for example,

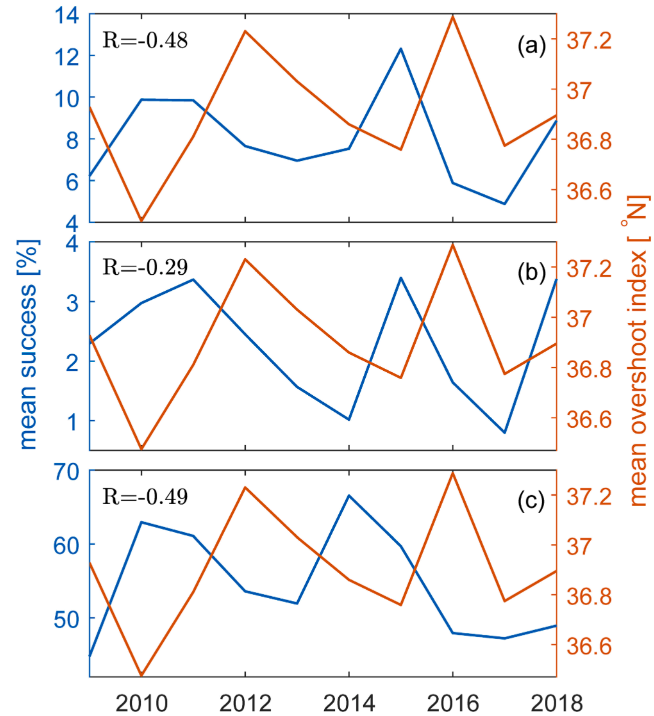

Fig. 9. Spatio-temporally averaged habitat suitability rates and the Gulf Stream overshoot index for simulations with the narrower suitable temperature ranges: (a) 25–27 °C, (b) 25.5–26.5 °C, and (c) simulations with selective spawning within the hot spots of habitat suitability. R is the correlation coefficient.

more western Slope Sea in 2015 versus more central location in 2014 or 2016), and geographical extent (more localized in 2014 versus more spread out in 2010). However, no hot spots are immediately adjacent to the Gulf Stream because larvae that originate too close to the Gulf Stream are swept away from the Slope Sea.

Time series of habitat suitability rates for individual years (Fig. 4) show that habitat suitability typically starts to increase in the second half of June or early July and diminishes in September, with largest values reaching 45–60% in August (black curve). In all years, the red and green curves (temperature-related criteria only) closely follow each other until late in the season, and the blue and black curves (temperature-related criteria with the retention criterion) closely follow each other, with the large differences between these two pairs illustrating the effect of the retention criterion. The details of the time series, however, vary between years, with 2010 and 2015 (2013 and 2017–2018) showing an early (late) onset of the increase in the habitat suitability rate at the beginning of summer, and 2017 showing the shortest, but not the overall least successful, summer season.

The mean of the 10 habitat suitability probability maps (Fig. 5a) reveal a pronounced hot spot with values up to 45% in the western Slope Sea, located over the Slope Gyre and extending to the east from it. Habitat suitability rates drop to below 20% east of 64°W and below 10% north of 41°N and south of the Gulf Stream. Variability in the habitat suitability rates (Fig. 5b) is small in low-suitability regions (where habitat suitability is consistently low in all 10 years) and in the Slope Gyre (where habitat suitability is consistently high in all 10 years). Variability is highest in the immediate vicinity of the Gulf Stream, where the Gulf Stream exhibits significant inter-annual variations in shape and location. The decadally-averaged time series (Fig. 5c) shows the onset and the end of the spawning season in June and September, respectively, with the maximum in mid to late August.

The 10-year time series of habitat suitability rates in the Slope Sea, spatially averaged over the Slope Sea and temporally averaged over the 3 summer months, is shown by a solid blue curve in Fig. 6. Average habitat suitability rate varies between 18 and 29%, with largest values in 2010 and 2014–2015, and lowest values in 2012 and 2016. The 10-year time series of the model-based overshoot index, averaged over Jun 20–Sep 20 period for each year from 2009 until 2018 is shown in red in Fig. 6. The spatially and temporally averaged habitat suitability rate for each year and the Gulf Stream overshoot are strongly anti-correlated, with the correlation coefficient R = -0.88. Because of the high anti-correlation between the Gulf Stream overshoot and habitat suitability, the former can be used to predict the latter using a simple linear regression (habitat suitability = a * overshoot + b, with a = -13.3187 and b = 514.4940). The resulting reconstructed habitat suitability rate is shown by the black dashed curve in Fig. 6. This method accurately captures the two minima in habitat suitability rates in 2012 and 2016 and the maximum in 2010, but underestimates the second maximum in 2015. Other oceanographic variables that we have tested, including Gulf Stream kinetic energy (i.e., sum of the squares of zonal and meridional velocity components), Gulf Stream meander amplitudes at 72/67/62°W (i.e., largest deviation in longitude at a fixed latitude), mean enstrophy in the Slope Sea (i.e., absolute value of vorticity), and NAO index (i.e., difference of atmospheric pressure at sea level between the Icelandic Low and the Azores High; see Hurrel (2003)), correlate poorly with habitat suitability, with correlation coefficients less than 0.2 in absolute value.

The map of decade-average probabilities of summer-time frontal occurrence at each geographical location throughout the Slope Sea (Fig. 7) shows that the probability of frontal occurrence is high along the entire length of the 200-m isobath, is relatively high in the eastern Slope Sea (east of 65°W), is slightly elevated near the northern wall of the Gulf Stream west of about 67°W, and is lowest in the interior of the western Slope Sea and in the general area of the Slope Gyre.

Figs. 8 and 9 show results of targeted numerical simulations, where we used narrower temperature intervals in our spawning- and larval-temperature success criteria 1 and 2. For 2015, the warmest year of the decade, Fig. 8 top, bottom shows the probability map and the corresponding time series of habitat suitability rates for the 25.5–26.5 °C temperature interval (probability maps for other years are in Appendix C). Compared to our baseline (23–28 °C temperature interval) simulations, the habitat suitability rates drop substantially throughout the entire Slope Sea, the suitable spawning season gets shorter, and the relative importance of the temperature-related criteria increases (as indicated by the shift of the green curve, which was close to the red curve in our baseline simulation, towards the black curve). The inter-annual variability of the habitat suitability rates for simulations with the narrower temperature intervals is presented in Fig. 9a,b. The anti-correlation with the Gulf Stream overshoot index decreases in magnitude with the decrease of the suitable temperature interval. The correlation coefficient drops to $R = -0.48$ for the 25–26 °C interval and to $R = -0.29$ for 25.5–26.5 °C.

Finally, Fig. 9c shows habitat suitability-overshoot correlation in our final targeted selective-spawning simulations, where we assumed that bluefin spawn exclusively within the hot spots, i.e., in geographical areas characterized by the highest habitat suitability. This leads to a strong increase in the habitat suitability rates (decadal mean of 55%) and a decrease in the anti-correlation with the Gulf Stream overshoot ($R = -0.49$).

4. Discussion

Our bio-physical numerical study of bluefin larval dispersal suggests that the Slope Sea consistently provided suitable environmental conditions for bluefin spawning and larval development during the summer season each year from 2009 to 2018. According to our model, and in agreement with Richardson et al. (2016), suitable conditions for successful spawning in this region starts in late June to early July, peaks in late August, and diminishes through September. Contemporaneous increases in habitat suitability rates (Fig. 4) in June for the different criteria scenarios illustrate the dominant influence of water temperature on habitat suitability in the beginning of summer, with June being the month when the Slope Sea waters become warmer than 23 °C. Similarly, during the ramp-down in September, the effect of water temperatures becoming too cold to meet the temperature-related (specifically, the larval-temperature) criterion is evident. In all years, the red and green curves closely follow each other until late in the season and the blue and black curves closely follow each other, with large difference between the pairs. This suggests that, at least until late in the season, larvae that spawn in warm waters will generally stay in warm waters during the subsequent 25 days. Many of these larvae, however, will get expelled from the Slope Sea and thus the retention criterion causes a substantial decrease in spawning habitat suitability (i.e., compare the red and green curves vs. black and blue curves in Fig. 4). This suggests that in all years retention (i.e., advection of larvae by the ocean circulation) is a significant factor in limiting the habitat suitability rates, at least until late in the season when the larval temperature criterion may become a limiting factor.

On average over a decade, as well as for the individual years, we find elevated habitat suitability rates in the western half of the Slope Sea, specifically in the Slope Gyre (i.e., within the semi-permanent cyclonic recirculation in the western Slope Sea) and towards the northwestern portion along the shelf break. Simulated larvae released there find themselves in warm enough waters (satisfying temperature criteria 1 and 2) with less chance of being entrained by the Gulf Stream and a greater chance of recirculating within the Slope Gyre (satisfying retention criterion 3). In the decadal average, habitat suitability rates reach 50% in that region. Values quickly diminish southward across the Gulf Stream and also eastward and northeastward due to a combination of eastward advection out of the domain and colder temperatures in the north. The exact locations of spawning hot spots within the western Slope Sea, as well as the exact on-set and duration of the spawning season vary between the years.

All of the main qualitative features of the spatial distribution of the bluefin spawning habitat suitability rates in the Slope Sea along with the associated time series of habitat suitability throughout the summer season are in full agreement with the 2013 results of Rypina et al. (2019). This similarity, despite the fact that this earlier paper used a higher-resolution (1 km/2km in the across-/along-shore direction) ocean circulation model compared to the 1/12° HYCOM used here, suggests that the retention characteristics of the Slope Sea are dominated by mesoscale rather than sub-mesoscale oceanic currents.

What oceanographic factors are responsible for the inter-annual variability of the spawning habitat suitability rates? Mean water temperature during the summer season is an obvious candidate. However, correlation between the model spawning habitat suitability rates and the summertime- and Slope-Sea-averaged model temperature at 10 m is poor (R = 0.11). The reason for this low correlation is that even in the coldest years, a large portion of the Slope Sea becomes warm enough (i.e., above 23 °C) to allow for successful spawning and larval development by bluefin. With larval retention in the Slope Sea being strongly influenced by the Gulf Stream, another oceanographic index—the Gulf Stream overshoot index—is a second obvious candidate for controlling the spawning habitat suitability. Indeed, yearly habitat suitability rate is strongly anti-correlated with the Gulf Stream overshoot index, defined here as the mean Gulf Stream latitude between 75°W and 70°W. The reason for the high correlation is that in years with the high overshoot index, the western Slope Sea (where the majority of the habitat suitability hot spots are located) is narrower than usual leading to fewer locations yielding successful larvae. Correlation between the summer-mean habitat suitability rate and overshoot is highest when overshoot is averaged from June 20 to September 20 (instead of June 1 – September 1) because retention, and thus overshoot, are secondary to temperature in controlling habitat suitability for larvae spawned in the beginning of June but are primary for larvae spawned in mid- to late-August. For comparison, without the shift, the correlation coefficient

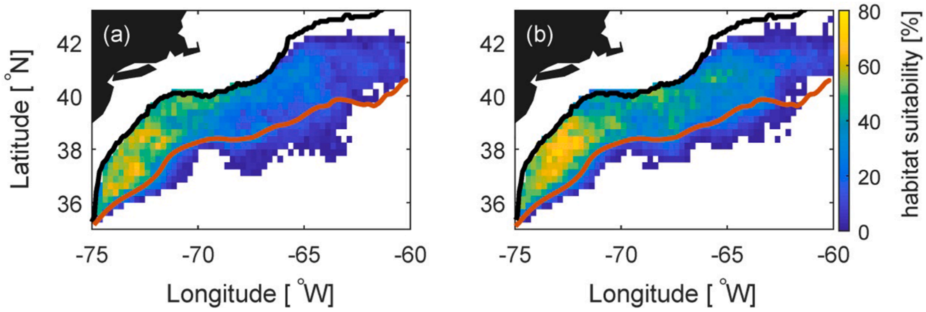

Fig. 10. Habitat suitability maps for 2015 computed using HYCOM velocities and temperatures at (a) 10 m and (b) 5 m below the surface. The spatio-temporally averaged habitat suitability rate (i.e., space average of the shown maps excluding white regions) is about 28% at 10 m and 29% at 5 m. The red curve is the summer-mean Gulf Stream for 2015. The black curve is the 200 m isobath.

between habitat suitability rates and overshoot averaged over the same summer time interval, June 1 – September 1, is −0.81 (compared to −0.88).

Because the western Slope Sea has significantly higher habitat suitability rates than the eastern Slope Sea, and because the Gulf Stream overshoot strongly affects the circulation and area of the western Slope Sea, the strong anti-correlation with the Gulf Stream overshoot index is not surprising. Note, however, that the habitat suitability map depends on both oceanographic properties and biological parameters used to define successful larvae, and thus can be different for different biological species. For example, if the habitat suitability hot spot was located in the eastern rather than western Slope Sea (which could be the case for a different species with shorter development interval, stronger swimming, and colder suitable temperatures), then the correlation with the Gulf Stream overshoot index would likely be weaker, since the eastern Slope Sea is affected less by the overshoot events, both in terms of area and circulation patterns. Note also that by taking a spatial average of the habitat suitability maps over the Slope Sea domain, which is different each year, we essentially eliminate, or at least minimize, the direct dependence of the yearly habitat suitability values in Fig. 6 on the area of the Slope Sea. For example, if the habitat suitability rates were uniform throughout the entire Slope Sea and the same for all years, then the domain-average habitat suitability values would also be the same for all years, even though the size (and shape) of the Slope Sea domain would change in concert with the Gulf Stream overshoot. Thus, it is the spatial distribution of the habitat suitability within the Slope Sea, and not the size of the Slope Sea, that matters most for the correlation with the Gulf Stream overshoot. In other words, it is the fact that the hot spots of bluefin habitat suitability happen to be located in the western Slope Sea that yields a strong anti-correlation with the Gulf Stream overshoot index.

Predicting spawning habitat suitability could be an important goal for fishery management. We propose a simple model based on a linear regression to reconstruct bluefin spawning habitat suitability from the overshoot index. The latter is much easier to monitor than the former because overshoot can be estimated from satellite data and/or mooring observations. Although multi-variable regressions could be superior to single-variable regressions in problems that are jointly controlled by several parameters, single-variable linear regression is a reasonable choice here because the variability in habitat suitability is dominated by a single parameter (i.e., Gulf Stream overshoot index). The reconstructed time series of habitat suitability rates correlates with the HYCOM-based "true" simulated habitat suitability with the correlation coefficient of 0.88. The model correctly captures the two minima in the time series and the maximum in 2010 but underestimates the second maximum in 2015 by about 11%. This underestimation is likely because in years with low overshoot index, when the western Slope Sea is wider than normal, habitat suitability might also depend on other physical parameters that govern retention. Gulf Stream overshoot events have been previously shown to exhibit influence over success rates of other organisms such as American eel larvae in its quest to reach coastal nursery areas of the Mid- and South Atlantic Bight (Rypina et al., 2016).

It is important to acknowledge the distinction between spawning habitat suitability as modeled here and the processes controlling stock productivity and recruitment. In the model simulations presented here, simulated larvae were released at regular intervals in time and space to assess when and where suitable spawning habitat occurs, but true spawning is likely to occur in a more patchy distribution through adult spawning aggregation behavior and adults being able to swim to where conditions might be more suitable (Richards et al., 1989; Reglero et al., 2014; Lindo-Atichati et al., 2012; Domingues et al., 2016, Garcia et al., 2005, Teo et al., 2007, Muhling et al., 2010). Our results, rather than predicting biological recruitment, demonstrate how widespread, persistent, and reliable the distribution of suitable spawning habitat is. If adult bluefin randomly spawn throughout the Slope Sea, then we expect our estimates of habitat suitability rates to correlate well with larval abundance and recruitment. Selective spawning, processes affecting adult abundance, and conditions influencing larval development such as food availability and mortality, which are not captured in our model, will influence larval abundance and recruitment. Valuable insights can be gained from comparing our modeling approach with surveys of larval bluefin in the Slope Sea, which we hope will increase in future years.

Habitat suitability rates outside of the Slope Sea are significantly lower than those inside this region. This is largely a consequence of the barrier effect of the Gulf Stream current (Bower et al., 1985; Burkholder & Lozier, 2011; Farazmand et al., 2014; Rypina et al., 2007; Rypina et al., 2014; Rypina et al., 2011), which prevents larvae originating on the southern side from entering the Slope Sea during the larval development stage. Because early-juvenile nursery habitat is thought to be in shelf and slope waters along the U.S. east coast (Galuardi & Lutcavage, 2012; Mather, 1995; Rooker et al., 2003) and because the Gulf Stream would be difficult to cross for post-metamorphic bluefin, larvae recruiting to Western Atlantic juvenile pools would need to end up on the inshore side of the Gulf Stream.

The Gulf Stream and its Extension form an energetic and strongly varying current system, whose instantaneous location and shape constantly change in time, producing time-evolving meanders that can entrain, expel and transport larvae both from and back into the Slope Sea, thus influencing larval retention and the resulting spawning habitat suitability. In order to quantify the influence of such time-evolving Gulf Stream meanders on habitat suitability rates in the Slope Sea, we performed additional simulations for one of the years (2013) using the mean Gulf Stream instead of the time-evolving Gulf Stream as the southern boundary of the Slope Sea. We also carried out simulations using a stricter retention condition that required that successful larvae continuously stay within the Slope Sea domain for 25 days since spawning. Similarity between simulations with the same retention condition (i.e., between panels a and c, as well as between e and g of Fig. 2) suggests that the retention condition has a greater impact on the resulting habitat suitability rates compared to the exact definition of the

Slope Sea southern boundary (i.e., time-independent versus time-evolving Gulf Stream).

The eastern boundary of the Slope Sea has been placed at 60°W in our study. However, additional sensitivity analyses that we have performed by moving the eastern boundary to 60.25°W suggest that the results are insensitive to small shifts in the longitude of the eastern boundary of the Slope Sea. This is because the temperature regime and circulation patterns in the eastern Slope Sea are generally unfavorable for bluefin tuna spawning.

Although spawning habitat suitability in the Slope Sea is still relatively high in September, it might be unfavorable for bluefin to spawn so late in the season, given limited time left for their larvae to develop and then for juvenile fish to reach a pre-winter size that would promote survival. Although little is known about juvenile growth and survival, previous work on the distribution of adults and larvae in the Gulf of Mexico and Mediterranean Sea suggests that bluefin tuna spawn preferentially at the beginning of the season, i.e. as soon as temperatures cross the critical threshold for egg hatching (Reglero et al., 2018b). Tagging data also indicates that tuna aged 2–5 begin moving inshore (onto the shelf and into the Gulf of Maine) in September (Galuardi & Lutcavage, 2012). Therefore, all probability maps in this paper were computed for the summer period, i.e., June 1-September 1; however, all maps for June 1-September 20 time interval (not shown) are qualitatively and quantitatively similar to our presented figures.

Selective spawning by bluefin has been inferred from larval presence and adult tagging in the Gulf of Mexico and Mediterranean Sea (Richards et al., 1989; Reglero et al., 2014; Lindo-Atichati et al., 2012; Domingues et al., 2016, Garcia et al., 2005, Teo et al., 2007). For instance, while bluefin larvae are found in waters between 23 and 28 °C in the Gulf of Mexico, the probability of larval presence peaks at sea surface temperatures of 26 °C (see Muhling et al., 2010). More larvae are also found near certain types of oceanic features, specifically near temperature and/or salinity fronts, in the Gulf of Mexico (e.g. Lindo-Atichati et al., 2012; Domingues et al., 2016) and in the Mediterranean Sea (e.g. Garcia et al., 2005). In a Gulf of Mexico tagging study, adults showed preferences for spawning in slope waters with temperatures of 24–27 °C, moderate eddy kinetic energy, low chlorophyll, and moderate wind speeds (Teo et al., 2007). Backtracking simulations of Atlantic bluefin tuna larvae collected in the Slope Sea in 2016 indicated that many of the collected larvae resulted from spawning activity in the Slope Gyre region and along the shelf break (Hernandez et al., 2020).

In order to explore the potential influence of preferential spawning near fronts, we compared our mean habitat suitability map (Fig. 5) with the map of frontal occurrences in the Slope Sea (Fig. 7). Frontal occurrence probability is highest along the shelfbreak, where colder shelf waters meet slope waters. Relatively high frontal occurrence probabilities can be observed in the eastern part of the Slope Sea, likely due to the abundance of recirculation features whose cores carry different water masses compared to the surrounding waters. Frontal occurrence probability is slightly elevated near the northern flank of the Gulf Stream where warmer Gulf Stream waters meet cooler Slope Sea waters. The frontal occurrence is lowest in the interior of the western part of the Slope Sea, with a minimum in the general area of the Slope Gyre. This spatial pattern differs dramatically from the habitat suitability map in Fig. 5. The habitat suitability hot spot in the Slope Gyre has very low frontal occurrence, whereas the low-suitability areas near the Gulf Stream, along most of the shelfbreak, and in the east are associated with high frontal occurrences. The only areas with relatively high frontal occurrence and relatively high habitat suitability rates are located along the shelfbreak in the western Slope Sea. Thus, our model suggests that, in contrast to the Gulf of Mexico and the Mediterranean Sea, spawning near most fronts in the Slope Sea (except for some fronts near the shelfbreak in the western Slope Sea) appears sub-optimal based on our habitat suitability criteria. This difference between the Slope Sea and the Gulf of Mexico and Mediterranean Sea is largely due to the different retention properties of the Slope Sea compared to the other two spawning areas. While spawning near fronts in the Gulf of Mexico and Mediterranean Sea leads to the high retention of larvae within these regions, or, for larvae spawned near fronts associated with the Loop Current, could bring larvae close to coastal nursery habitats along the South- and Mid-Atlantic bight after 25 days, spawning near the Gulf Stream front in the Slope Sea facilitates transport of larvae out of the Slope Sea.

Motivated by Muhling et al. (2010), who observed the highest probability of larval presence at 26 °C, we investigated the response of the habitat suitability rates to the changes in the suitable temperature interval. In two additional simulations, both spawning- and larval-temperature intervals in our suitability criteria 1 and 2 were narrowed to 25–27 °C and 25.5–26.5 °C (compared to 23–28 °C in our baseline simulations). The resulting habitat suitability rates strongly decrease with the decrease of the suitable temperature interval (Fig. 8&9 and Appendix C). This is because the suitable spawning season gets shorter, and a larger portion of the Slope Sea never reaches suitable temperatures above 25 °C or 25.5 °C (Fig. 8). Consequently, the relative importance of the temperature increases and the relative importance of retention decreases. As a result, the anti-correlation between the yearly habitat suitability rates and the Gulf Stream overshoot index (Fig. 9a,b) drops in magnitude from −0.88 in our baseline simulation to −0.48/-0.29 for 25–27 °C/25.5–26.5 °C, respectively. Note that in this case we have restricted both spawning temperature and the larval growth temperature for the most conservative analysis, while Reglero et al. (2018) showed that the preferred spawning temperature of Atlantic bluefin tuna was often colder than the optimal temperature for larval growth.

The persistent hot spot in the Slope Gyre, near the Mid-Atlantic Bight, is characterized by both geographic and oceanographic features that could enable repeated use by adult bluefin. This is explored in our final targeted numerical simulation, where we assumed that bluefin selectively spawn only in geographic areas with the highest habitat suitability, defined by the 80% contour of the largest yearly habitat suitability rates (i.e., we essentially only release simulated larvae within the corresponding 80th percentile contour each year). The effect of such selective behavior was quantified by re-computing the mean yearly habitat suitability rate, averaged within the hot spots only, instead of averaging over the entire Slope Sea, as in our baseline simulation (note that averaging the probability maps in Fig. 3 over the hot spots only is equivalent to only releasing larvae within the hot spots). In this case, the decadally-averaged habitat suitability increases to 55% (from 24% in the baseline simulation), and the anti-correlation with the Gulf Stream overshoot index drops to −0.5 (from −0.88). Overall, the results of our targeted numerical simulations suggest that selective spawning by bluefin can substantially influence habitat suitability rates in the Slope Sea, and can weaken the link between the habitat suitability and Gulf Stream overshoot index.

Our bio-physical model of bluefin larval dispersal has a number of limitations on both oceanographic and biological sides. The former includes fairly coarse spatio-temporal resolution of HYCOM, leading to unresolved oceanic currents in the submesoscale range. Note, however, that similarity between the HYCOM-based results and those from higher-resolution MABGOM-2 suggests that small scales have only minor influence on habitat suitability. On the biological side, shortcomings include the absence of active swimming, the uniform release of larvae in the domain and the absence of selective spawning behavior in our baseline simulations, the lack of spatially variable larval mortality, and fixed duration of the larval development interval. In light of the importance of these biology-related constraints, the limitations associated with the resolution of our oceanographic model likely play only a secondary role. As more information becomes available on the spawning by bluefin in the Slope Sea, all of these important biological effects could be implemented into our bio-physical model for an improved future study.

When trying to reconcile our model-based spatial habitat suitability maps with the limited data on observed larval catches in the Slope Sea (see Fig. 1 of Richardson et al., 2016), it is important to keep in mind the distinctions between our model-based habitat suitability hot spots, the actual bluefin spawning locations, and the resulting larval distributions, owing to several reasons. First, while habitat suitability hot spots highlight geographical areas with the most favorable temperature and circulation patterns, bluefin likely also consider food availability and other cues when spawning. Second, as shown in Rypina et al., 2019, habitat suitability maps are generally smoother and have more localized hot spots than the resulting simulated larval distributions, which are more filamented and more widespread due to the advection/dispersion of larvae by the oceanic currents during the larval development time. Thus, maps akin to Fig. 1 from Richardson et al., 2016 should to be compared to the model-based distribution of the successful simulated larvae in the Slope Sea (as was done in Rypina et al., 2019), rather than directly to the habitat suitability maps (as our Figs. 3 and 5). Carrying out a proper comparison for different years would require more comprehensive datasets of larval catch locations in the Slope Sea for multiple years, so this comparison is delegated to a future study.

Ultimately, this study attempts to advance our understanding of a relatively data-poor phenomenon: spawning by Atlantic bluefin tuna in the Slope Sea. Adequate larval surveys have so far been conducted in only 2013 and 2016, and the smaller individuals that are presumed to spawn in this region (Richardson et al., 2016) are under-sampled via tagging relative to giant bluefin. Our modeling approach incorporates field and laboratory data on larval biology with high-quality oceanographic models to determine that there is likely to be suitable spawning habitat in the Slope Sea region every year, supporting the idea that bluefin could spawn there regularly, instead of opportunistically. Our results also indicate the need for more larval surveys in the Slope Sea, which would greatly complement our approach and mutually increase the impact of both observations and modeling.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. . Sensitivity to depth

Habitat suitability rates were re-computed using velocities and temperatures at 5 m instead of 10 m for 2015 – the warmest year of the decade. The warmest year was used since the differences are expected to be amplified in warm years due to the increased stratification. The results at 5 and 10 m are qualitatively and quantitatively similar to each other (Fig. 10). Both maps show a hot spot of similar shape and size located in the Slope Gyre, and the differences between the 10- and 5-m simulations are significantly smaller than the year-to-year variations in the spatial structure of the habitat suitability maps (Fig. 3). The domain- and summer-averaged habitat suitability rates for the 10- and 5-m simulations are approximately 28% and 29%, respectively. While the 5-m simulation does lead to a slightly larger rate due to the overall warmer water temperatures, the difference of 1% is much smaller than the inter-annual variability in the habitat suitability rates (which reaches 11% between years with largest and smallest rates; see Fig. 6). This conclusion agrees with Rypina et al. (2019) who did similar sensitivity tests for 2013. Note that our analysis at 5 m is based on the output from a more recent HYCOM global simulation, GLBv008, because GLBa008 simulation that we used throughout the paper does not have output at depths between surface and 10 m.

Appendix B. . Sensitivity to the number of simulated larvae

(See Fig. 11)

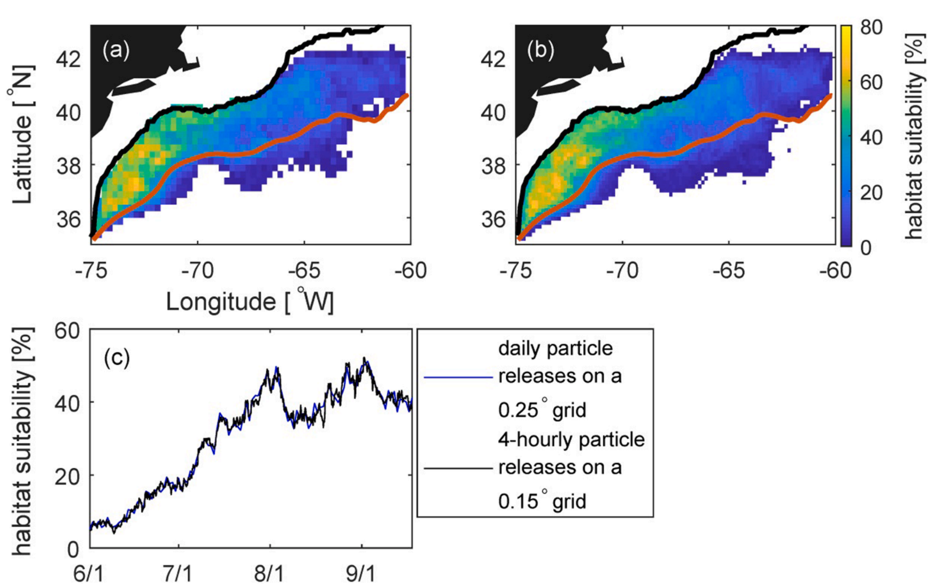

Fig. 11. For 2015, summer-mean habitat suitability rates computed using simulated larvae released (a) daily on a 0.25 × 0.25 deg grid, and (b) 4-hourly on a 0.15 × 0.15 deg grid. The red curve is the summer-mean Gulf Stream for 2015. The black curve is the 200 m isobath. (c) Time series of the habitat suitability rates for simulations with smaller and larger number of simulated larvae.

Appendix C. . Habitat suitability maps for targeted selective spawning simulations

(See Figs. 12-14)

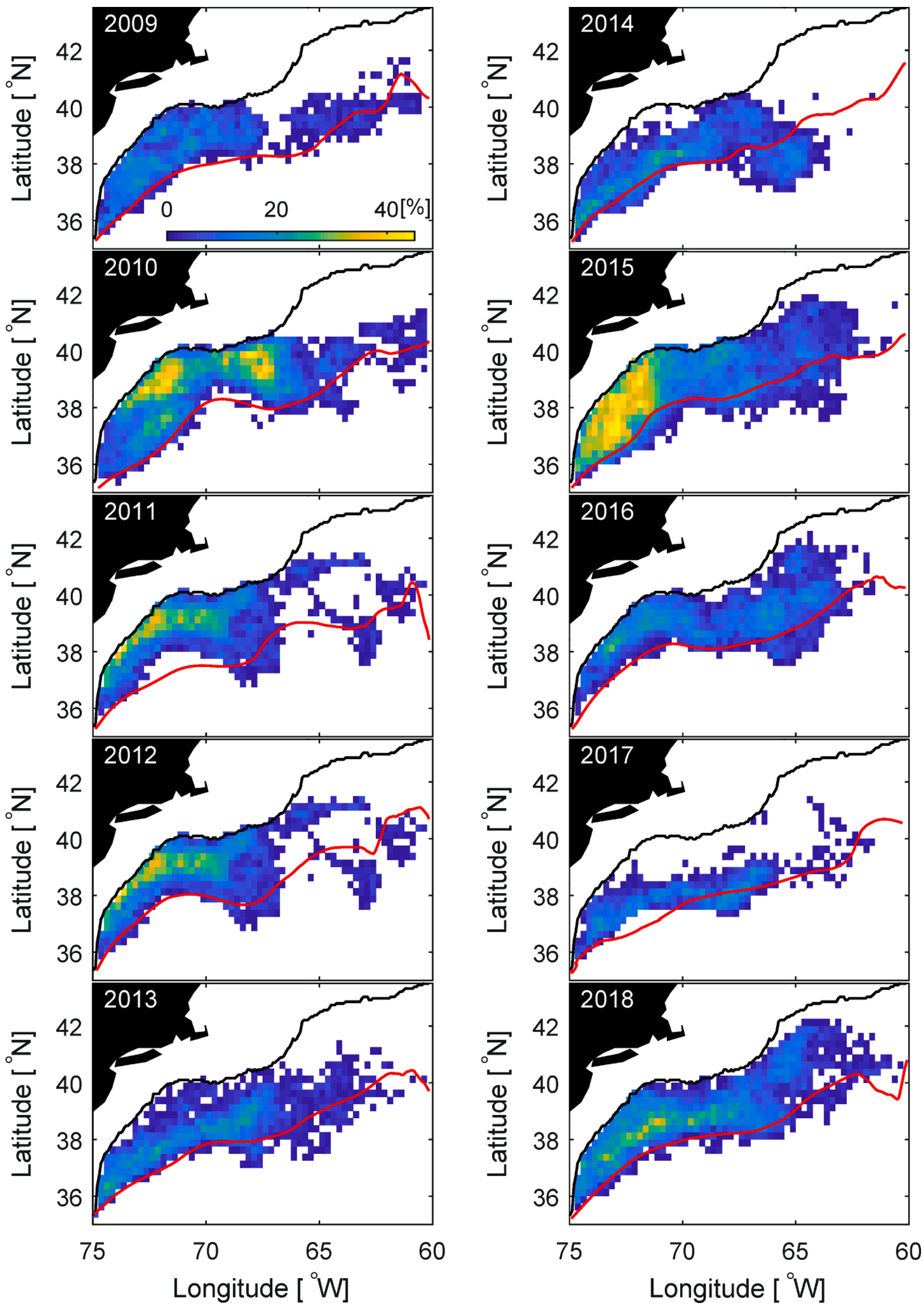

Fig. 12. Same as Fig. 3 but for the targeted simulation, in which both spawning- and larval-temperature intervals in our suitability criteria 1 and 2 were narrowed to 25–27 °C (compared to 23–28 °C in our baseline simulations in Fig. 3). Note the decreased color bar range in this figure compared to Fig. 3.

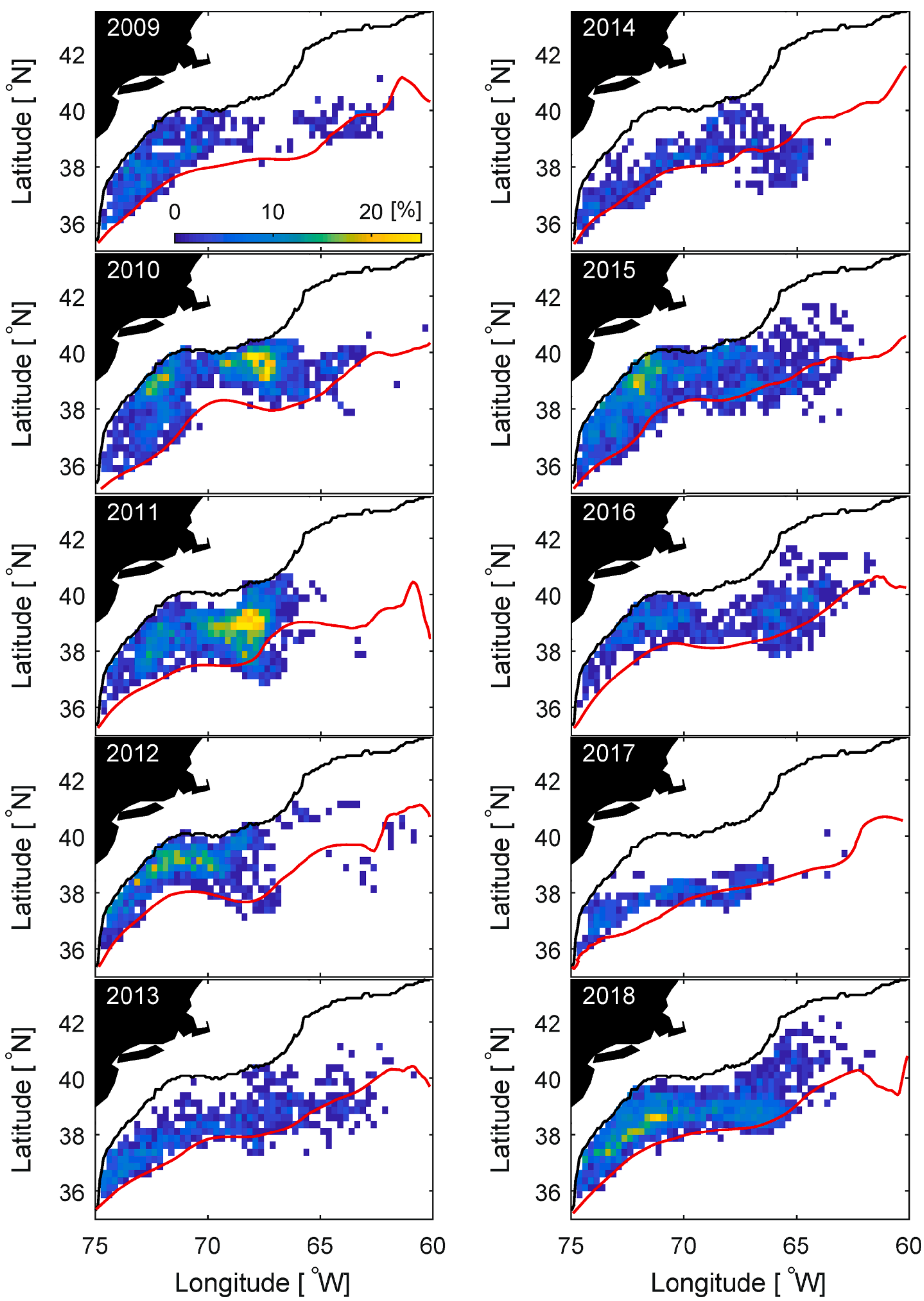

Fig. 13. Same as Fig. 3 but for the targeted selective spawning simulation, in which both spawning- and larval-temperature intervals in our suitability criteria 1 and 2 were narrowed to 25.5–26.5 °C (compared to 23–28 °C in our baseline simulations in Fig. 3). Note the decreased colorbar range in this figure compared to Fig. 3.

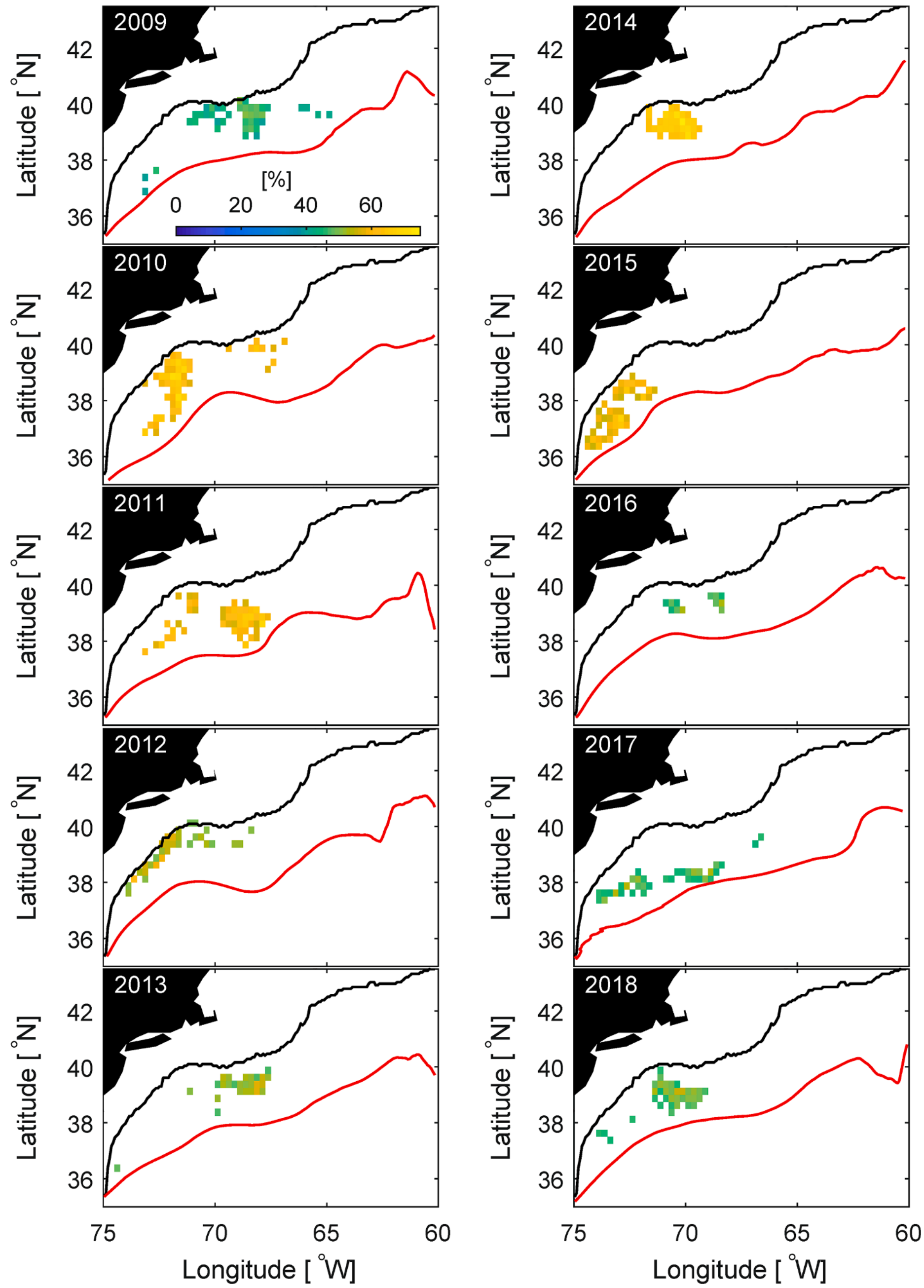

Fig. 14. Same as Fig. 3 but for the targeted selective spawning simulation, in which simulated larvae were released only within the habitat suitability "hot spots" (defined by the upper 80th percentile contour of the highest habitat suitability rates for each year), instead of everywhere in the Slope Sea.

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