





Larval transport pathways from three prominent sand lance habitats in the Gulf of Maine

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Abstract

Northern sand lance (*Ammodytes dubius*) are among the most critically important forage fish throughout the Northeast US shelf. Despite their ecological importance, little is known about the larval transport of this species. Here, we use otolith microstructure analysis to estimate hatch and settlement dates of sand lance and then use these measurements to parametrize particle tracking experiments to assess the source–sink dynamics of three prominent sand lance habitats in the Gulf of Maine: Stellwagen Bank, the Great South Channel, and Georges Bank. Our results indicate the pelagic larval duration of northern sand lance lasts about 2 months (range: 50–84 days) and exhibit a broad range of hatch and settlement dates. Forward and backward particle tracking experiments show substantial interannual variability, yet suggest transport generally follows the north to south circulation in the Gulf of Maine region. We find that Stellwagen Bank is a major source of larvae for the Great South Channel, while the Great South Channel primarily serves as a sink for larvae from Stellwagen Bank and Georges Bank. Retention is likely the primary source of larvae on Georges Bank. Retention within both Georges Bank and Stellwagen Bank varies interannually in response to changes in local wind events, while the Great South Channel only exhibited notable retention in a single year. Collectively, these results provide a framework to assess population connectivity among these sand lance habitats, which informs the species' recruitment dynamics and impacts its vulnerability to exploitation.

KEYWORDS

Gulf of Maine, larval retention, otolith microstructure, particle tracking, population connectivity, sand lance

1 | INTRODUCTION

Northern sand lance (*Ammodytes dubius*; hereafter sand lance) represent one of the most critically important forage fishes on the Northeast US shelf, serving as prey for at least 72 different predators including numerous commercially fished species, marine mammals, and seabirds (Staudinger et al., 2020). Sand lance exhibit extreme fluctuations in interannual abundance throughout the Northeast US shelf and are highly patchy in space (Fogarty et al., 1991; Richardson et al., 2014; Suca et al., 2021). Despite their abundance, no active fishery exists for sand lance in the Northwest Atlantic, a marked difference from congeners in the North Sea (Kvist et al., 2001; Pedersen et al., 1999). Due to the lack of a fishery, the dramatic interannual fluctuations in sand lance abundance and distribution are assumed to be linked to interannual variability in environmental conditions that cause large- and small-scale changes in recruitment and adult survival (Staudinger et al., 2020; Suca et al., 2021).

Little is known about the spawning time of sand lance throughout the Northeast US shelf, but studies suggest they are capital breeders with spawning occurring in the late fall or early winter (Murray et al., 2019; Nelson & Ross, 1991; Suca et al., 2021). After spawning, eggs are demersal, resulting in minimal transport between spawning and hatch (Smigielski et al., 1984; Wright & Bailey, 1996). Egg duration may last in excess of 50 days in laboratory conditions at 5–6°C (Murray et al., 2019), though more realistic temperature progressions indicate shorter egg durations (~27 days) are more likely (Baumann

et al., 2022). Larval duration for sand lance, however, is largely unknown, though estimates based on collections of larvae range from 1 to 3 months (Potter & Lough, 1987), similar to what has been observed for European (Wright & Bailey, 1996) and northeast Pacific congeners (Doyle et al., 2019).

Sand lance are unique among the forage fishes of the Northeast US shelf in their requirement of coarse-grained sandy substrate for burying when they are not actively feeding on zooplankton (Gilman, 1994). This requirement contributes to a defined settlement phase for sand lance larvae when they transition from a pelagic stage to a benthopelagic lifestyle of adults (Nanjo et al., 2017; van Deurs et al., 2009). While adult movement has not been studied for sand lance, congeners are assumed to have high site fidelity to their settlement area throughout the adult life, limited to ~30 km displacement for 1- to 3-year-old fish (*A. personatus*, Baker et al., 2019; *A. tobianus*, Laugier et al., 2015; *A. marinus*, van Deurs et al., 2013; Wright et al., 2019). This site fidelity and sediment requirement (coarse-grained sand, generally with <10% silt; Bizzarro et al., 2016; Endo et al., 2019; Wright et al., 2000) constrain sand lance habitats, defined here as areas where adult sand lance occur consistently in fisheries-independent surveys, similar to the northeast Pacific (Greene et al., 2020). In the Gulf of Maine/Georges Bank region (Gulf of Maine hereafter), there are three dominant habitats: Stellwagen Bank, the Great South Channel/Nantucket Shoals, and Georges Bank (Figure 1; Staudinger et al., 2020). These three habitats vary dramatically in size and hydrography, generating different patterns in sand lance

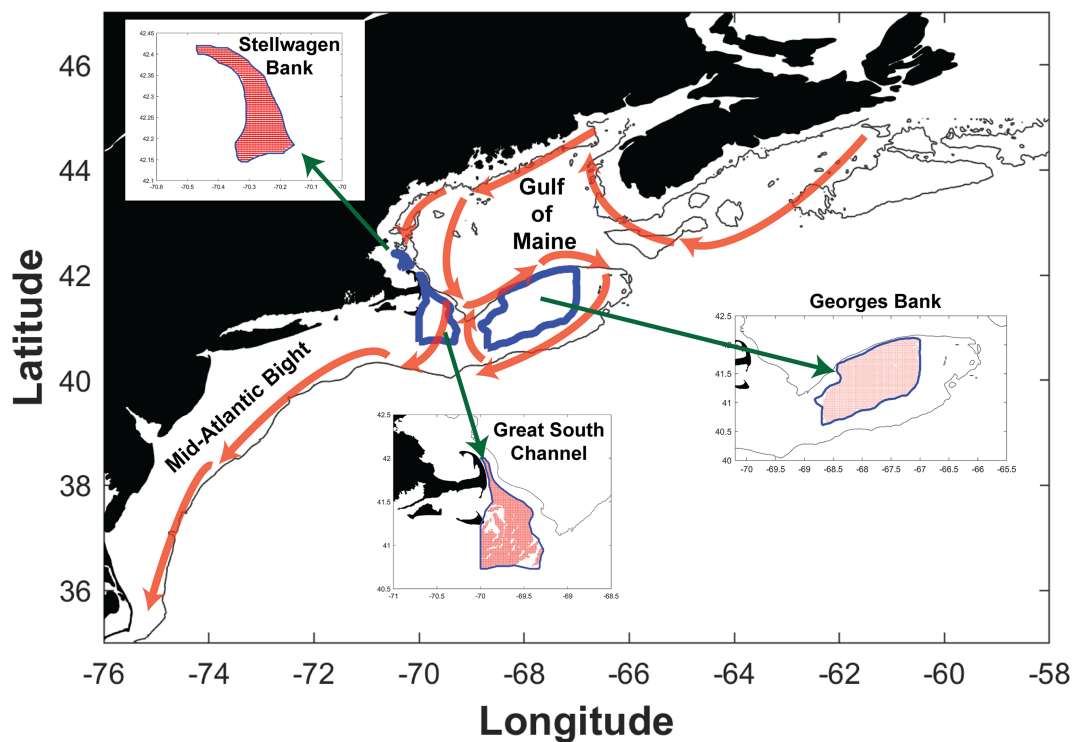


FIGURE 1 Map of regional sand lance habitats and particle seeding locations for Stellwagen Bank, the Great South Channel, and Georges Bank. Contours represent the coastline and 100 m isobath. White spaces in the Great South Channel are areas < 15 m. Transparent red arrows indicate prevailing surface currents of the region

abundance among the three habitats that likely oscillate independently of shelf wide abundance trends (Suca et al., 2021).

The most northern of the three habitats, Stellwagen Bank, is a relatively small, sandy bank located north of Provincetown on Cape Cod, MA, USA. Stellwagen Bank is well known as a top predator hotspot, particularly for marine mammals and seabirds (Powers et al., 2020; Silva et al., 2019; Silva, Wiley, & Fay, 2021) and is part of a national marine sanctuary. There is notable spatial heterogeneity of sand lance presence within Stellwagen Bank, with a shoal on the southwest corner representing the most persistent region of high sand lance abundance (Silva, Wiley, Thompson, et al., 2021; Wiley et al., 2003). The second habitat, the Great South Channel region (including Nantucket Shoals), is a large sandy region to the east and south of Cape Cod, MA, USA. The region has less clearly defined boundaries than Stellwagen Bank and Georges Bank but generally occupies the sandy shoals west of the deepest portions of the Great South Channel (Harris & Stokesbury, 2010). Similar to Stellwagen Bank, the Great South Channel region also represents a marine mammal and seabird feeding hotspot, particularly for sand lance-reliant predators such as roseate terns (*Sterna dougallii*) and great shearwaters (*Ardennagravis*; Goyert, 2014; Powers et al., 2020). The hydrography of the region varies seasonally based on stratification, but prevailing currents move along the isobaths of the region from the northeast to the southwest (Beardsley et al., 1985). The third habitat, Georges Bank, is one of the world's most productive fisheries regions and the largest sand lance habitat in this region (Cohen & Wright, 1979; Ji et al., 2008). The majority of substrate on Georges Bank represents suitable sand lance habitat (Harris & Stokesbury, 2010). Hydrography of the bank is also defined by a large, anti-cyclonic tidal rectification gyre that leads to high retention along the bank. However, this gyre is weakest in winter months and thus susceptible to off-bank transport from wind events (Lewis et al., 2001; Naimie et al., 1994).

While minimal research exists on the larval transport dynamics of sand lance to date, multiple particle tracking experiments have been performed for congeners, particularly those in the northeast Atlantic (known as sand eels). Collectively, these studies have suggested that variable larval transport modulates *Ammodytes* recruitment dynamics. This includes overlap between the observed distribution of recruiting sand eels and larval transport patterns (Proctor et al., 1998), identification of dominant transport pathways (Christensen et al., 2008), and local variability in the role of larval transport in recruitment success (Berntsen et al., 1994). Further, larval transport, particularly during the earliest stages of feeding, may be one of the leading indicators of regional recruitment success, allowing for short-term forecasts of recruitment (Henriksen et al., 2018). Therefore, these studies suggest that understanding larval transport patterns is essential for resolving regional and small-scale recruitment drivers of these fishes.

Here, we aim to better understand the larval transport pathways among the three prominent Gulf of Maine sand lance habitats (Stellwagen Bank, the Great South Channel, and Georges Bank), including their roles as larval sources or sinks of sand lance larvae. We first estimate hatch and settlement dates for sand lance through otolith microstructure analysis of settlers collected from two of these

habitats. We then use this information for tracking simulated sand lance larvae in forward and backward tracking experiments from each of the three habitats. Specifically, we hypothesize that sand lance larvae hatched on Stellwagen Bank, the most northerly habitat, will serve as a larval source of larvae to the Great South Channel, which in turn will serve as a local sink. Conversely, we predict that larvae hatched in the Great South Channel will be transported out of the study area, south to the Mid-Atlantic Bight. We also hypothesize that Georges Bank will represent a semi-closed population where most larvae hatched on Georges Bank are primarily retained on the bank with little contribution from the other two habitats. We expect general trends in larval transport to vary interannually, with local wind events enhancing or reducing retention.

2 | MATERIALS AND METHODS

2.1 | Sand lance collections

Settlement-stage sand lance were collected from the Great South Channel in May 2019 and from both the Great South Channel and Stellwagen Bank in June 2019 (Figure S1, Table S1). No settling sand lance were collected from Georges Bank due to ship time limitations and equipment constraints. Age-0 sand lance were collected with a 1.0 × .5-m, small-mesh (.63 cm) beam trawl as described in Suca et al. (2021). Trawl duration was 10 min and distances ranged from .5 to 1 km. Individual sand lance < 10 cm were immediately preserved in ethanol upon net retrieval to maintain otolith quality. These individuals represent a different set than those used in Suca et al. (2021) due to the differences in sizes and timing of collections.

2.2 | Otolith preparation and aging

We extracted sagittae from up to 60 individuals from each sampling region and month of collection, resulting in otoliths from 176 total individuals, though only 145 individuals were readable (82%). Right sagittae were mounted on a slide using cyanoacrylate. Sagittae were polished using 10- μ m lapping film until daily rings became apparent using a Leica DM2500 compound microscope with a 50 \times objective. Once daily rings were clearly visible, images of each sagitta were taken using a Leica MC120 HD camera and the Leica Application Suite software. Images were taken in horizontal sections across the otolith at 500 \times magnification, ranging from 3 to 6 sections. For each otolith section, multiple focal planes were captured and merged into multi-layer images to aid reading and interpreting the otolith microstructure (Pringle & Baumann, 2019). Otolith images were imported as stacks for reading and rings were counted using ImageJ software.

Settlement timing was estimated as the change in growth axis of each sagitta (Laugier et al., 2015; Wright & Bailey, 1996). We estimated the larval duration of each individual as the number of rings from the otolith core to the change in growth axis, which is assumed to correspond with the timing of metamorphosis (Figure S2). The

juvenile period until day of collection was estimated as the number of rings between the change in growth axis and the otolith edge. We assumed the final ring would correspond to the day of capture; thus, the day of settlement was estimated as the day of capture minus the number of days in the juvenile period. Hatch dates were estimated by subtracting the sum of days from the larval period and juvenile period from the date of capture. We assumed the first ring represents the first day post-hatch as has been shown for the congener *A. marinus* (Wright & Bailey, 1996).

Each sagitta was read by two independent readers. Estimates of larval and juvenile period from each reader were compared separately. We did this to ensure accurate estimates of larval duration and settlement dates and to avoid the potential for “false” agreement among reader estimates resulting from similar cumulative age estimates despite differing larval and juvenile period estimates. If a larval or juvenile period estimate differed by more than 5%, the period was re-read by the second reader. If the third read agreed with either of the previous two reads (± 1 day), the matching estimate was used for the length of the given period. If the third estimate did not agree, the otolith was deemed unreadable and was discarded from further analyses (18% of otoliths). Differences in hatch dates and larval period between individuals from Stellwagen Bank and the Great South Channel were compared using Student's *t*-tests.

2.3 | Bio-physical individual-based model

Hydrographic and hydrodynamic conditions were simulated using the third generation Gulf of Maine-Finite Volume Community Ocean Model (GOM-FVCOM; Chen et al., 2011) with horizontal resolution of .3–10 km, with finer resolution in coastal regions and tidal mixing fronts (e.g., Georges Bank) and coarser resolution at the boundaries near the shelf break (Chen et al., 2011; Ji et al., 2017; Xue et al., 2014). The GOM-FVCOM is itself nested within the FVCOM-global model to ensure water property conservation at its boundaries (Chen et al., 2011). Previous studies have confirmed that the GOM-FVCOM accurately recreates hourly to interannual variability in currents (Chen et al., 2011; Sun et al., 2016), including a comparison with actual drifter observations (Sun et al., 2016). For our drift simulations, a particle tracking routine with a fourth-order Runge–Kutta time stepping scheme was used to resolve advection, similar to the previous applications for the region, such as the tracking for haddock larvae (Boucher et al., 2013) and copepods (Ji et al., 2017).

A suite of particle tracking experiments, in both forward and backward tracking directions, was conducted at an annual scale for 27 years (1990–2016), totaling 5616 experiments (details below). Particles were released on a $.01^\circ \times .01^\circ$ grid in waters ≤ 40 m depth on Stellwagen Bank (bounding box $42.13\text{--}42.5^\circ\text{N}$, $70.5\text{--}70.12^\circ\text{W}$) and water depths of 15–40 m in the Great South Channel (bounding box $42.5\text{--}40.5^\circ\text{N}$, $70.0\text{--}69.0^\circ\text{W}$; Figure 1). Particles were placed on a coarser $.05^\circ \times .05^\circ$ grid in waters ≤ 60 m depth on Georges Bank (bounding box $42.33\text{--}40.0^\circ\text{N}$, $69.2\text{--}65.5^\circ\text{W}$; Table 1) to account for

TABLE 1 Experiment specifications based on release habitat

Region	Area of releases (km ²)	Depth range	Release depths	Spatial resolution	Otoliths used for hatch and settlement dates	Assumptions	Reference
Stellwagen Bank	272	0–40 m	5, 15, 25, 35 m	$.01^\circ \times .01^\circ$	Stellwagen Bank	Offshore bank representing <i>Ammodytes dubius</i> habitat.	Auster et al., 2001
Great South Channel	4780	15–40 m	5, 15, 25, 35 m	$.01^\circ \times .01^\circ$	Great South Channel	Waters < 15 m likely represent <i>A. americanus</i> habitat rather than <i>A. dubius</i> .	Nizinski et al., 1990
Georges Bank	14,500	0–60 m	5, 15, 25, 35 m	$.05^\circ \times .05^\circ$	Great South Channel	Great South Channel represents nearest collections. Sand lance are more frequently found at greater depth than other regions.	Staudinger et al., 2020; supporting information

computational constraints and deeper observed sand lance distribution (Potter & Lough, 1987; see supplementary methods; Figure S3). Although the presence of sand lance does not necessarily imply spawning at these depths, we use this proxy as it is our current state of knowledge. Changes in the maximum depth of release revealed minimal effects on dispersal trends (Figure S4). We also recognize that *Ammodytes* spp. have been observed at deeper depths (Baker et al., 2021), though rarely in the case of *A. dubius* (Staudinger et al., 2020), and thus, our habitat definitions may not encompass all possible spawning locations for *A. dubius* throughout the study area. In the Great South Channel, we avoided seeding particles in regions shallower than 15 m to minimize the inclusion of nearshore *A. americanus* habitat, which were not the focus of this study (Nizinski et al., 1990).

Particles were advected using 10-min time steps through interpolation of hourly mean velocity fields. Random walk routines were not incorporated due to the high model resolution and the depth-keeping nature of particle tracking runs (Ji et al., 2017). Previous work suggested that sand lance larvae below 28 mm length are almost evenly distributed within the upper water column, while older stages appear to move to greater depths later in spring (Potter & Lough, 1987). Observations of larger individuals at depth temporally overlap with our estimates of settlement; hence, this vertical movement might be the beginning of the settlement process. To represent the homogeneous vertical distribution of sand lance larvae, we used depth-keeping particle runs at 10 m spacing in the upper 40 m (5, 15, 25, and 35 m). We chose not to incorporate diel vertical migration patterns into our simulations due to sparse behavioral information on northern sand lance. For each forward and backward tracking simulation, this framework resulted in 1230 particles per depth per day per direction for Stellwagen Bank, 4152 particles per depth per day per direction for the Great South Channel, and 15,108 particles per depth per day per direction for Georges Bank.

Forward tracking particles were released based on the mean hatch date \pm standard deviation (SD) of hatch date. Particles were released from each location and depth each day at midnight. Preliminary analyses releasing particles hourly showed minimal differences in end location based on hour of releases; therefore, particles were released only once daily (see supplementary methods; Figure S5). For backward tracking, dates of release were based on the mean hatch date by region of collection \pm SD + mean larval duration for a given region. We did not use mean settlement date because hatch dates were more variable than settlement dates. Thus, our method encompassed the range of observed settlement dates while also ensuring a balanced number of releases between forward and backward tracking experiments. Since we did not collect any age-0 fish from Georges Bank, we used the hatch and settlement date values from our collections in the Great South Channel due to its similar hydrography and ecosystem dynamics (Lucey & Fogarty, 2013). This resulted in 972 backward and forward experiments for Georges Bank and the Great South Channel and 864 backward and forward experiments for Stellwagen Bank (due to narrower range of hatch dates).

2.4 | Temporal and spatial estimates of habitat connectivity

Particles were considered to have potentially “settled” (forward simulations) or “hatched” (backward simulations) in a given habitat if they occurred over the region either during the mean \pm SD of settlement or hatch dates. These values were set as the ranges from which the particles originated (i.e., Stellwagen Bank had a different set of hatch and settlement date ranges than the Great South Channel and Georges Bank based on otolith microstructure analysis).

Annual estimates of habitat “connectivity” were estimated as the proportion of release locations that had at least one particle at a given depth and day that potentially “settled” (forward connectivity) or “hatched” (backward connectivity) at a given habitat per day, by the following formula:

$$\text{Connectivity Metric from Hab}_a \text{ to Hab}_b = \left(\frac{\sum_{i=1}^N \frac{\text{Num. of Releases from Hab}_a \text{ reaching Hab}_b}{\text{Total num. of releases from Hab}_a}}{N} \right) * 100$$

where N is the number of days that particles were released in a given year and a “release” is considered the release of particles from a given seeding location at all used depths, resulting in a mean percentage. This framework focuses on location of release as the sampling unit as opposed to individual particles. This was done to have particles at each release location represent a group of hatching sand lance that distribute throughout the water column. We know very little about the actual larval behavior of sand lance so we assumed a particle released from any of the four release depths reaching a habitat may represent a connection between these habitats. Additionally, while there is some variability in transport by release depth, the mixed layer depth of the region during the larval duration of sand lance is greater than our release depths, leading to less variable flow in the vertical domain compared to stratified systems and seasons (Paris & Cowen, 2004; Townsend et al., 2015). A connectivity metric value of 100% represents a scenario where all release locations within a habitat had at least one particle that originated or settled in a given habitat per day of release. We thereby calculated the annual habitat connectivity for each release location and potential settlement location for both forward and backward tracking. We use the term habitat connectivity to refer to larvae potentially originating or settling from one habitat to another, while conceding that true population connectivity depends on settled individuals surviving to reproductive maturity, which we do not explore (Pineda et al., 2007). We further define retention as a metric for the connectivity of a habitat to itself (i.e., backward tracking of a particle back to the same habitat or forward tracking indicating potential “settlement” over that same habitat). The retention metric therefore indicates particles being retained over or near a given habitat through much of the larval transport simulations. We also provide a mean value of proportion of releases for each habitat that did not drift into any of the three habitats during the settlement or hatch window over the 27 years of experiments, indicating a mean loss or connectivity to other habitats not studied here.

Hence, particles not “connected” to any of the three habitats could still have “settled” or “hatched” in other habitats outside of the study area.

We also explored spatial trends in habitat connectivity. To do so, we estimated connectivity by release location through averaging annual habitat connectivity for each release location within a given habitat over the full 27 years of experiments. This was done to elucidate small spatial scale patterns in connectivity—particularly to see if certain release locations were favorable for retention in a given habitat. Note that figures depicting these analyses are scaled according to their maximum value to highlight spatial differences despite notable absolute differences in connectivity among habitats.

2.5 | Comparison with wind regimes

Based on the importance of wind as a driver of winter/spring retention of groundfish larvae and zooplankton in Massachusetts Bay (Jiang et al., 2007; Runge et al., 2010) and Georges Bank (Lewis et al., 2001; Mountain et al., 2008; Werner et al., 1996), we analyzed the relationship between local wind stress and retention for Stellwagen Bank and Georges Bank (no such analysis was needed for the Great South Channel due to the lack of observed retention; see Section 3). We tested the hypothesis that the frequency of strong northerly or southerly strong wind events influence retention on Stellwagen Bank and that strong northerly wind events on Georges Bank lead to lower retention. Daily mean wind stress estimates from GOM-FVCOM were spatially averaged into $.1^\circ \times .1^\circ$ grid cells within the bounding box defining each sand lance habitat from January to April of each year (see above for bounding box coordinates). For both northerly and southerly winds, we defined a strong wind day as a day where GOM-FVCOM wind stress estimates exceed $.146 \text{ Pa}$. This value corresponds to the wind stress generated from a mean daily wind velocity of 10 m s^{-1} (generating an approximate sea state of 6 on the Beaufort scale) based on the equations within Large and Pond (1981). There is no set value where we are certain that offshore transport or disruption may occur throughout our region; thus, we used 10 m s^{-1} which is generally known to generate transport and turbulence (Incze et al., 2001). The number of strong wind days was calculated for each $.1^\circ \times .1^\circ$ grid cell over a

given habitat and then averaged over the habitat area to get an annual mean number of strong wind days for a habitat. Annual retention metrics were then related to the mean number of strong wind days over a habitat through beta regression, as described in the following equation:

$$\log \left(\frac{\text{Ret.Metric}}{(1 - \text{Ret.Metric})} \right) = \beta_0 + \beta_1 (\text{Wind Metric})$$

where β_0 represents the intercept estimate and β_1 indicates the slope estimate for the relationship between days of strong wind conditions and a logit transform (the link function) of the retention metric. We estimate model fit through pseudo- R^2 values, the squared correlation of linear predictor and link-transformed response using the *betareg* package in R (Zeileis et al., 2016).

For Stellwagen, both northerly and southerly wind events were tested as both could lead to enhanced retention via different mechanisms. Near Stellwagen, northerly winds lead to onshore transport and thus retention in Massachusetts Bay directly west of Stellwagen Bank (Baumann et al., 2020; Jiang et al., 2007; Runge et al., 2010), while strong southerly winds move these retention zones eastward and generate a retentive feature over the southwest corner of Stellwagen Bank (Jiang et al., 2007). For Georges Bank, we focused only on northerly winds which push larvae to the southern flank of Georges Bank, into the slope current, transporting them away from Georges Bank (Mountain et al., 2008).

3 | RESULTS

3.1 | Hatch and settlement date estimates

Mean hatch dates and settlement dates varied by habitat and month of collection (Table 2; Figure 2). Settling individuals on Stellwagen Bank hatched significantly earlier than those collected in the Great South Channel ($p < .001$), with individuals hatching an average of 22.5 days earlier on Stellwagen Bank compared to the Great South Channel. Larval duration was also different between regions, with Stellwagen individuals having a longer mean larval duration (69.2 days) than individuals from the Great South Channel (65.5 days;

TABLE 2 Standard length, larval duration estimates, hatch dates, and settlement dates for age-0 sand lance from otolith aging analysis

Region	Month of collection	<i>n</i>	Standard length (mean ± SD; mm)	Larval duration (mean ± SD)	Hatch dates	Settlement dates
Great South Channel	May	50	45.36 ± 7.21	65.60 ± 7.87	Jan 21 to Feb 21	Mar 28 to Apr 25
Stellwagen	June	47	68.72 ± 8.41	69.23 ± 5.94	Dec 24 to Jan 24	Mar 5 to Apr 2
Great South Channel	June	48	54.52 ± 8.90	65.44 ± 6.98	Jan 10 to Feb 13	Mar 20 to Apr 17
Great South Channel	Total	98	50.54 ± 9.27	65.52 ± 7.41	Jan 15 to Feb 18	Mar 23 to Apr 21

Note: Great South Channel represents the Great South Channel. Hatch and settlement dates represent the range of dates corresponding to 1 standard deviation before and after the mean hatch or settlement date as these are the dates used for model parameterization. *n* represents the number of usable otoliths (see Section 2).

$p = .003$; Figure 2). Hatch dates varied by month of collection in the Great South Channel, but mean larval period was very similar (65.6 days in May and 65.4 in June; Table 2). Settlement dates ranged from March 5 to April 2 (mean \pm SD, mean \pm SD) on Stellwagen Bank

and from March 23 to April 21 (mean \pm SD, mean \pm SD) in the Great South Channel.

3.2 | Annual patterns in habitat connectivity

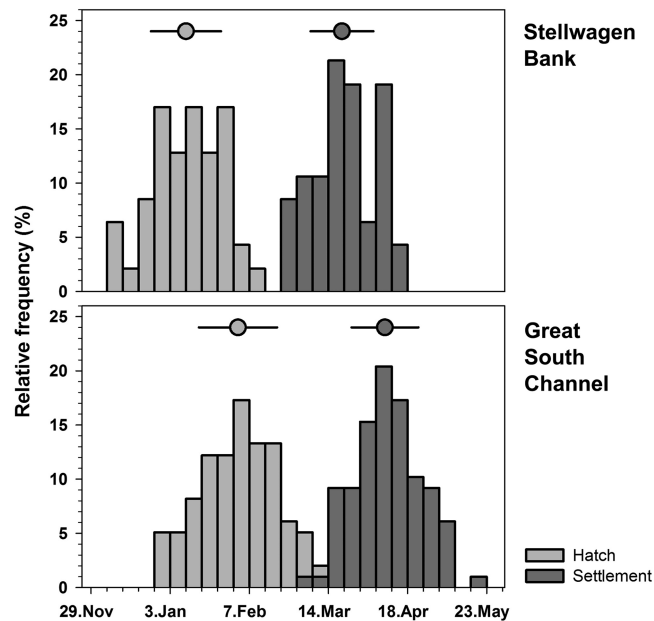


FIGURE 2 Relative frequency distributions of hatch dates (gray bars) and settlement dates (dark gray bars) of juvenile sand lance caught in June 2019 on Stellwagen Bank (upper panel) and May/June 2019 in the Great South Channel area (lower panel) using weekly bins. Symbols and error bars denote means \pm 1SD of hatch and settlement dates

Forward tracking experiments from Stellwagen Bank exhibited intermediate average retention (mean retention value = 8.5%), high connectivity with the Great South Channel (following dominant advection; mean connectivity value = 19.8%), and low connectivity with Georges Bank (mean connectivity value = 3.6%; Table 3; Figure 3a). Backward tracking experiments from Stellwagen Bank (Figure 3d) had intermediate retention (mean retention value = 7.5%), low connectivity with the Great South Channel (mean connectivity value = 1.5%), and Georges Bank (mean connectivity value < .1%). A mean of 71.5% of release sites from Stellwagen Bank did not indicate connectivity with the three studied habitats for forward runs, and 91.1% of release sites did not for backward releases.

Forward tracking experiments from the Great South Channel had minimal connectivity with all three habitats following the highly north to south advective environment (mean retention = 4.5%, mean connectivity to Stellwagen < .1%, mean connectivity to Georges Bank = 3.2%; Figure 3b). Backward tracking experiments from the Great South Channel had variable but generally low to intermediate connectivity with all three habitats (mean retention value = 6.6%, mean connectivity with Stellwagen = 9.0%, mean connectivity with Georges Bank = 6.7%; Figure 3e). A mean proportion of 93.5% release sites from the Great South Channel did not indicate connectivity with the three studied habitats for forward runs, and 79.4% of release sites did not for backward releases.

TABLE 3 Mean, standard deviation, and range of annual connectivity values from 1990 to 2016 experiments

Source habitat	Direction	End habitat	Mean (%)	SD (%)	Range (%)
Stellwagen	Forward	Stellwagen	8.5	8.7	.1-33.7
		Great South Channel	19.8	12.5	3.7-47.4
		Georges Bank	3.6	5.5	.0-19.2
	Backward	Stellwagen	7.5	6.6	.2-19.7
		Great South Channel	1.5	4.4	.0-20.9
		Georges Bank	.0	.1	.0-.4
Great South Channel	Forward	Stellwagen	.0	.1	.0-.3
		Great South Channel	4.6	11.6	.0-54.0
		Georges Bank	3.2	9.0	.0-45.0
	Backward	Stellwagen	6.1	3.8	.4-18.8
		Great South Channel	6.7	16.8	.1-88.1
		Georges Bank	9.0	10.7	.0-43.6
Georges Bank	Forward	Stellwagen	.0	.0	.0-.1
		Great South Channel	2.9	5.7	.0-29.9
		Georges Bank	48	16.7	10.0-80.9
	Backward	Stellwagen	.4	.8	.0-3.2
		Great South Channel	1.1	3.7	.0-19.0
		Georges Bank	63.2	19.4	24.0-93.0

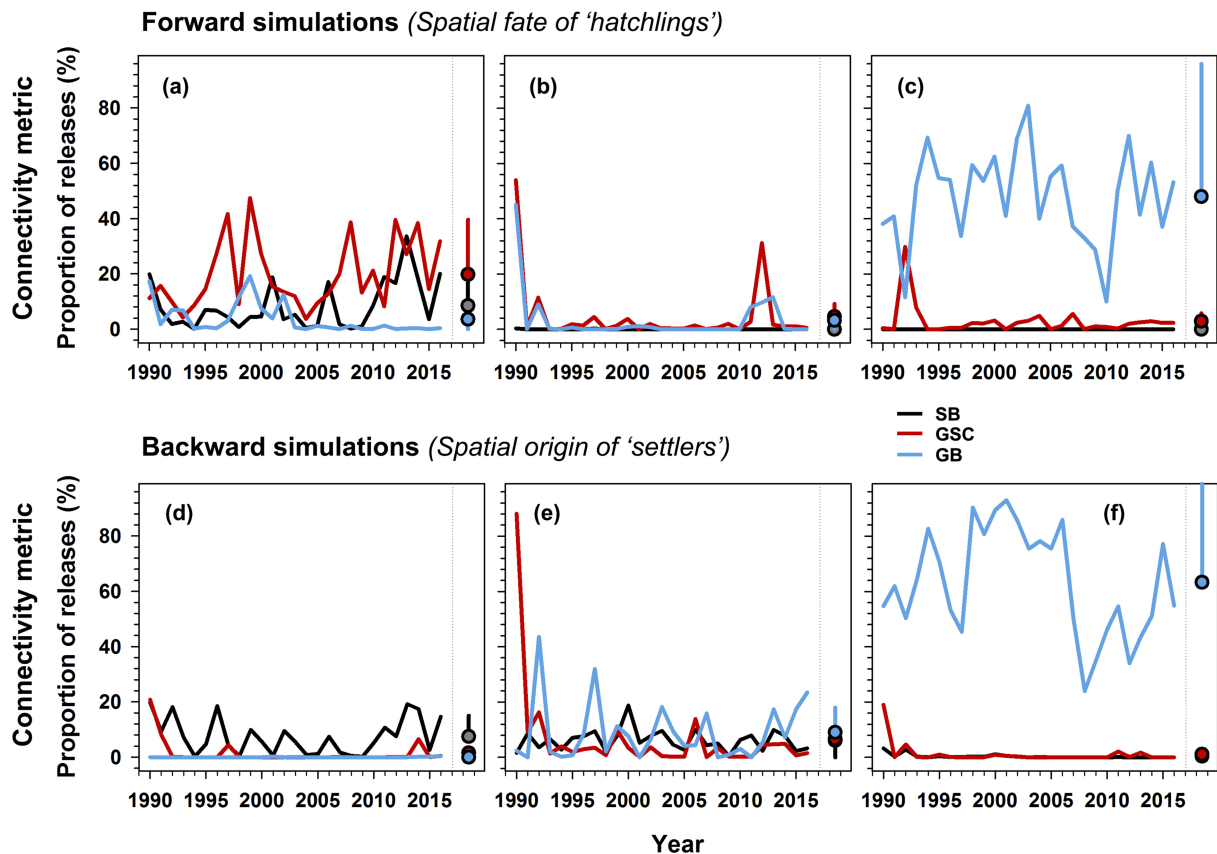


FIGURE 3 Interannual variability in connectivity between three important sand lance areas (SB, Stellwagen Bank; GSC, Great South Channel; GB, Georges Bank), based on forward (a–c) and backward (d–f) Lagrangian drift simulations. Lines depict proportions of particles releases that resulted in at least one particle “settling” (forward simulations) or “hatching” (backward simulations) in (a,d) SB (black), (b,e) GSC (red), or (c,f) GB (light blue). The seeding area is given next to each panel letter. Overall mean \pm 1SD proportions are given for each area to the right of each time series panel

Georges Bank particle tracking experiments indicated retention was high for both forward and backward runs, averaging retention of 48.0% for forward runs and 63.3% for backward runs (Figure 3c,f). Forward tracking experiments from Georges Bank showed minimal connection to Stellwagen Bank (mean connectivity value $<$.1%) and weak connection to the Great South Channel (mean connectivity value = 2.9%; Figure 3c). Backward tracking experiments from Georges Bank indicated minimal connection with Stellwagen Bank (mean connectivity value = .4%) and the Great South Channel (mean connectivity value = 1.1%). A mean proportion of 50.6% release sites from Georges Bank did not indicate connectivity with the three studied habitats for forward runs, and 36.0% of release sites did not for backward releases.

3.3 | Within-habitat patterns in connectivity

Stellwagen Bank had the strongest gradients of within-habitat spatial variability where both forward and backward particle tracking experiments had the highest values of retention on the southwest corner of

the bank, with average values reaching 15% (Figure 4a,b). This was most pronounced in the backward tracking experiments, while forward tracking experiments had high retention values along much of the western flank of the bank and on the northwest corner.

Forward connectivity from Stellwagen Bank to the Great South Channel was more evenly distributed throughout Stellwagen, though the northwest corner had the highest connectivity values with the Great South Channel with average connectivity values exceeding 25% (Figure 4c). Forward connectivity from Stellwagen to Georges Bank only occurred from the eastern flank of Stellwagen Bank, with no connectivity originating from the southwest corner (Figure 3e). Backward connectivity from Georges Bank and the Great South Channel to Stellwagen did not show noticeable patterns due to the very low overall connectivity in these cases (Figure 4d,f).

Spatial patterns in connectivity and retention in the Great South Channel followed the dominant upstream–downstream patterns of the region, with highest forward retention occurring from releases in the northern (upstream) portion of the Great South Channel and with lowest in the southwest portion (downstream; Figure 5c). Backward retention patterns showed the opposite pattern, with highest

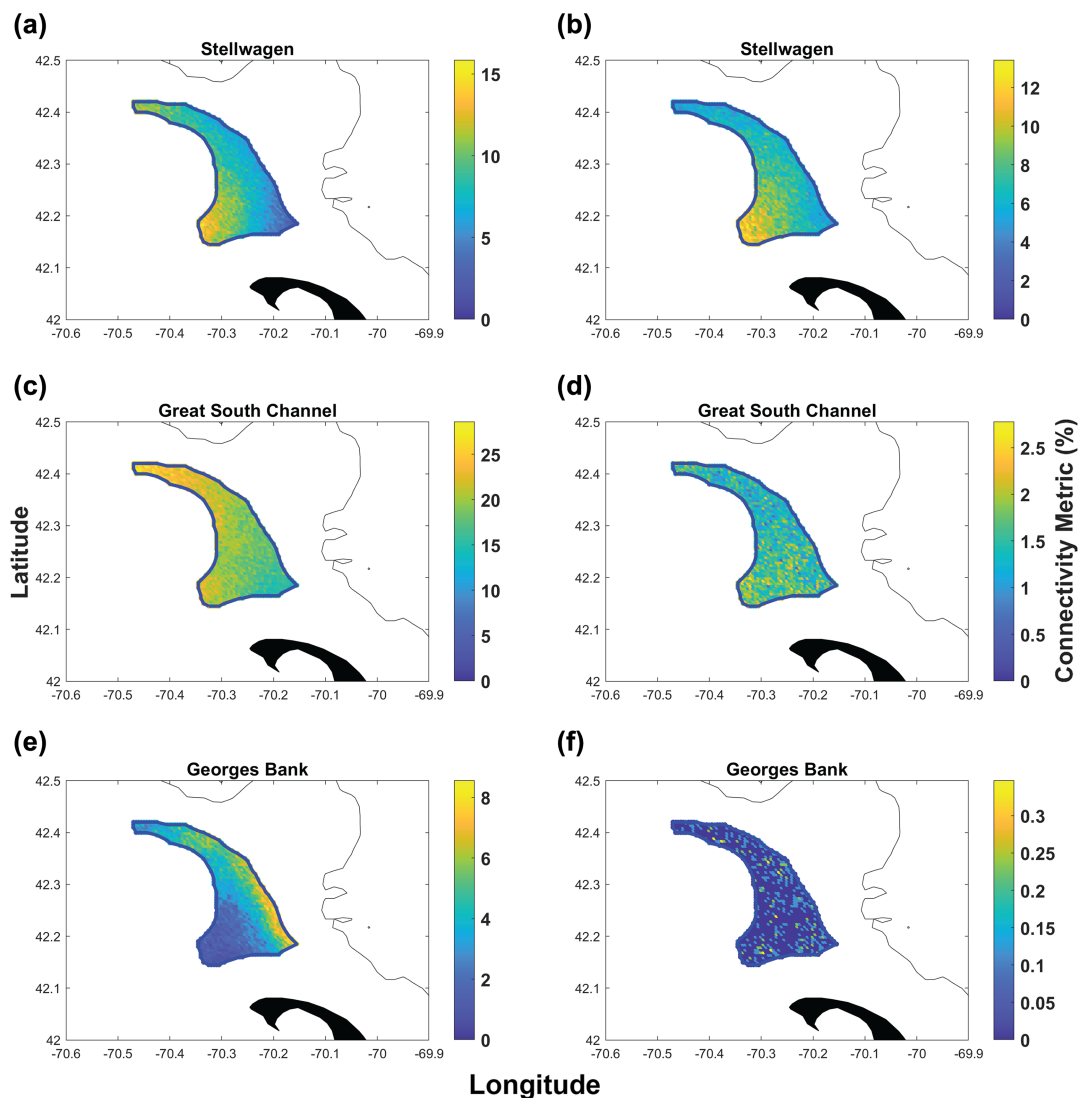


FIGURE 4 Spatial patterns in connectivity based on release locations from Stellwagen Bank for forward (a,c,e) and backward tracking (b,d,f) experiments. Titles represent the habitat pairs for the connectivity metric. Contours represent the coastline and 100 m isobath. Note that color bars for connectivity are scaled for each panel

backward retention occurring in the southwest (downstream) and minimal retention in the northern portion of the Great South Channel (upstream; Figure 5d). Backward connectivity from Stellwagen and Georges Bank to the Great South Channel was highest in the portions of the Great South Channel in closest proximity to these other habitats, with high connectivity to Stellwagen Bank in the northern portion of the Great South Channel (Figure 5b) and the highest connectivity to Georges Bank in the southeast portion of the Great South Channel (Figure 5f). Forward connectivity from the Great South Channel to Georges Bank was highest in the northern portion of the Great South Channel with intermediate values in the southern portion of the Great South Channel (Figure 5e). The Great South Channel had minimal forward connectivity with Stellwagen Bank (Figure 5a).

Spatial distribution of retention on Georges Bank varied between forward and backward tracking experiments (Figure 6e,f). Forward tracking experiments showed highest retention in the shallowest

region (western/central) of Georges Bank with average retention values reaching 80%, while backward retention was nearly homogeneous across Georges Bank, with the exception of lower retention near the most offshore portions of the bank (eastern and southern). Forward connectivity from Georges Bank to the Great South Channel was highest in the southwest portion of the bank, the region with the closest proximity to the Great South Channel (Figure 6c). All other connectivity metrics across Georges Bank were low (e.g., connectivity with Stellwagen Bank; Figure 6a,b).

3.4 | Relationship of interannual retention with wind metrics

The number of strong southerly wind days on Stellwagen Bank was significantly related to retention for both forward and

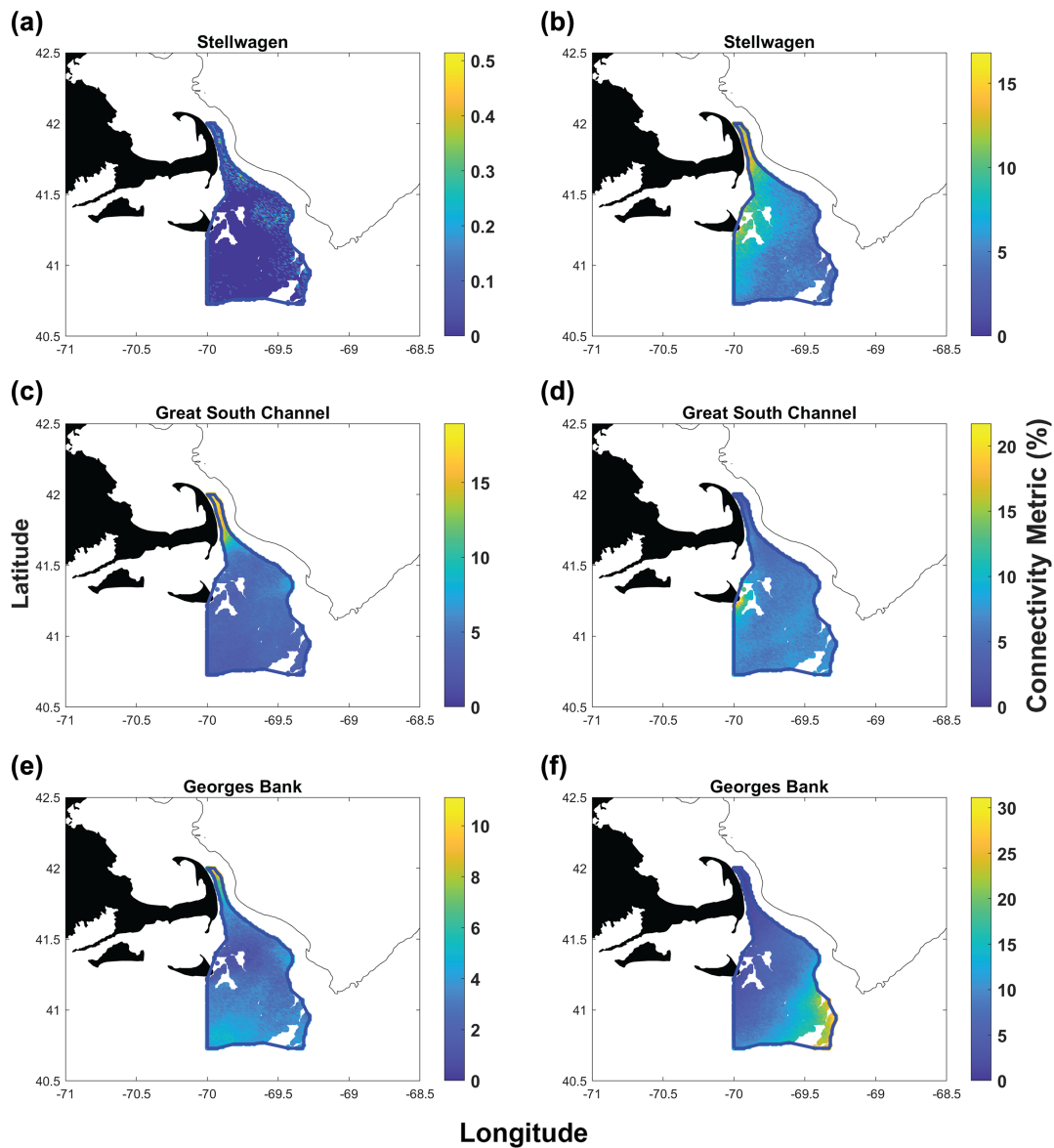


FIGURE 5 Spatial patterns in connectivity based on release locations from the Great South Channel for forward (a,c,e) and backward tracking (b,d,f) experiments. Titles represent the habitat pairs for the connectivity metric. Contours represent the coastline and 100 m isobath. Note that color bars for connectivity are scaled for each panel

backward tracking experiments (Table 4; Figure 7a,b). Years with few days of strong southerly winds resulted in many particles being swept to the south from Stellwagen Bank through the Great South Channel to the Mid-Atlantic Bight (Figure 7c). In backward tracking experiments, years with few strong southerly wind days resulted in particles largely originating from more northerly regions such as the Bay of Fundy and Scotian Shelf (Figure 7d). Years with >5 days of strong wind during the larval period resulted in particles remaining near Stellwagen Bank and in the western Gulf of Maine for both forward and backward tracking experiments (Figure 7e,f). The number of strong northerly wind days had no relationship with forward or backward retention on Stellwagen Bank (Table 4).

Retention on Georges Bank was significantly negatively related to the number of strong northerly wind days for both forward and backward particle tracking experiments (Table 4; Figure 8a,b). In years with few strong northerly wind days (<15 days during the larval period), particles remained largely over Georges Bank for both forward and backward tracking experiments (Figure 8c,d). In forward tracking experiments, years with large numbers of strong northerly wind days resulted in many particles being swept to the south from Georges Bank to the Mid-Atlantic Bight (Figure 8e). Patterns of particle distributions during years with many strong northerly wind days for backward tracking experiments led to more particles originating from locations such as the northeast peak of Georges Bank, than in years with few strong northerly wind days (Figure 8f).

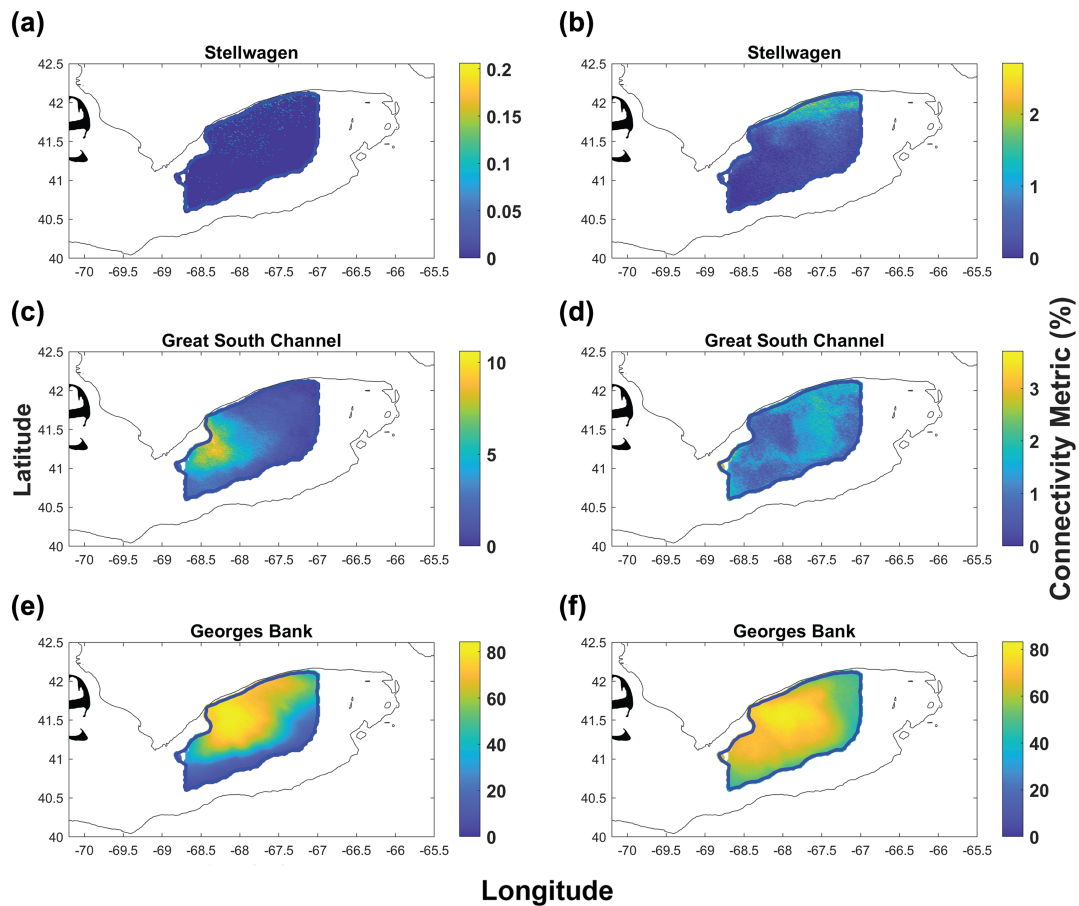


FIGURE 6 Spatial patterns in connectivity based on release locations from Georges Bank for forward (a,c,e) and backward tracking (b,d,f) experiments. Titles represent the habitat pairs for the connectivity metric. Contours represent the coastline and 100 m isobath. Note that color bars for connectivity are scaled for each panel

TABLE 4 Slope, pseudo- R^2 , and p -values for beta regressions between wind patterns for forward and backward retention metrics for Stellwagen and Georges Bank

Region	Direction	Regressor	Slope	Pseudo- R^2	p -value
Stellwagen	Forward	Strong northerly wind days	.025	.013	.560
Stellwagen	Backward	Strong northerly wind days	-.029	.018	.482
Stellwagen	Forward	Strong southerly wind days	.197	.089	.029
Stellwagen	Backward	Strong southerly wind days	.240	.152	.003
Georges Bank	Forward	Strong northerly wind days	-.038	.154	.030
Georges Bank	Backward	Strong northerly wind days	-.044	.148	.029

4 | DISCUSSION

Our results indicate that connectivity among the three most pronounced sand lance habitats in the Gulf of Maine varies notably on interannual and intraregional spatial scales. Drivers of these patterns are also linked to local wind forcing on Stellwagen Bank and Georges Bank, which are highly variable from year to year. While source-sink dynamics of these habitats vary interannually, some patterns are consistent. For example, retention is important for Georges Bank and Stellwagen Bank while the Great South Channel largely relies on other habitats for sources of larvae. Resolving these source-sink dynamics

among the three major Gulf of Maine sand lance habitats advances our understanding of how sand lance in each habitat are connected and scales that are important for sand lance recruitment.

4.1 | Interannual variability in connectivity

Habitat-specific differences in retention and connectivity indicate that each location plays a different role in the larger source-sink dynamics of the region. Notably, our results show that retention of simulated larvae can occur over Stellwagen Bank. This was evident in later years

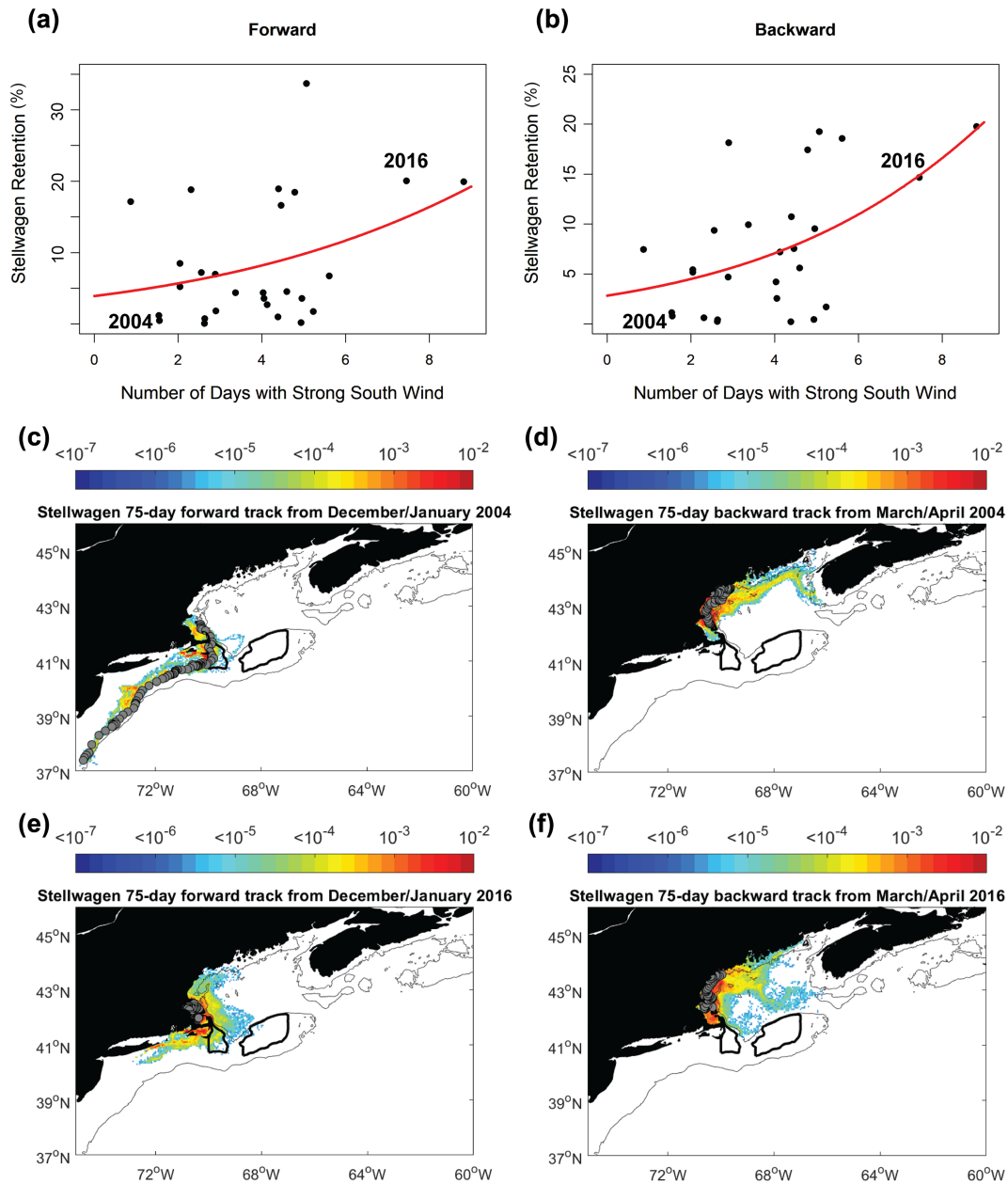


FIGURE 7 Relationship between number of days with strong southerly winds from January–April and (a) forward and (b) backward retention on Stellwagen Bank. Red lines represent fitted beta regression curves. Panels (c)–(f) show particle dispersal densities for 75-day forward (c,e) and backward (d,f) tracks during 2004 (c,d), a year with few days of strong southerly winds, and 2016 (e,f), a year with many days of strong southerly winds. In panels (c)–(f), tracks of a single particle are shown in gray

of the experiments, particularly after 2011. The hydrography of Stellwagen Bank is heavily tidally influenced with periodic influences of Ekman transport and the western Gulf of Maine Coastal Current, which at times may serve to collectively enhance retention (Churchill et al., 2011; Jiang et al., 2007). However, its small size has led to skepticism about retention and small-scale tidal gyre formation over the bank, including lack of observations of such retention from drifters from 1988 to 2007 (Manning et al., 2009). Interestingly, our results corroborate low retention over Stellwagen Bank during much of this window, with retention starting to increase later in the time series,

potentially due to shifts in wind patterns and behavior of the Gulf of Maine Coastal Current. Stellwagen was most strongly connected to the Great South Channel and, up until 2011, connectivity with the Great South Channel oscillated out of phase with retention on Stellwagen. This suggests oscillation in the western Gulf of Maine Coastal Current either enhanced transport southward to the Great South Channel or promoted retention. However, this pattern disappears later in the time series when both retention and connectivity to the Great South Channel were high, though the mechanism remains uncertain.

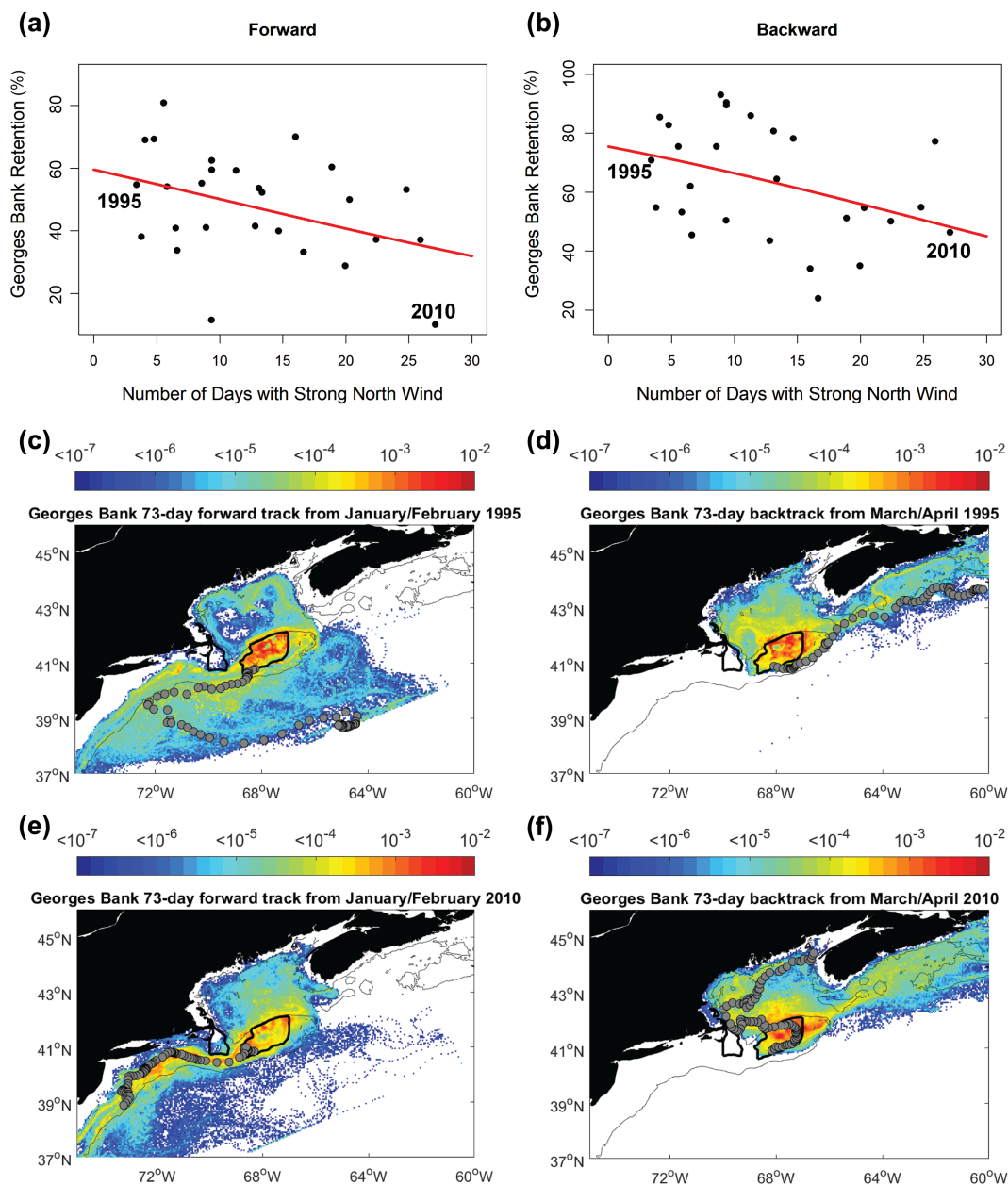


FIGURE 8 Relationship between number of days with strong northerly winds from January–April and (a) forward and (b) backward retention on Georges Bank. Red lines represent fitted beta regression curves. Panels (c)–(f) show particle dispersal densities for 73-day forward (c,e) and backward (d,f) tracks during 1995 (c,d), a year with few days of strong northerly winds, and 2010 (e,f), a year with many days of strong northerly winds. In panels (c)–(f), tracks of a single particle are shown in gray

Unlike the other habitats, the Great South Channel averaged little retention throughout our particle tracking experiments. Apart from 1990, a year with anomalously strong southerly winds leading to a reversal of flow from south to north (see supporting information), particles backtracked from the Great South Channel were mostly sourced from Stellwagen Bank and Georges Bank. This pattern indicates that the Great South Channel represents the most pronounced sink of sand lance larvae studied here and likely why it is one of the most consistent sand lance habitats on the Northeast US shelf. It is worth noting that particles released from the Great South Channel were transported to the Mid-Atlantic Bight, a region that historically

represented a sand lance habitat on the Northeast US shelf (Staudinger et al., 2020). Mid-Atlantic Bight sand lance habitat has largely disappeared in recent years (and was thus not included in this study; Suca et al., 2021), but it is likely that sand lance in the Great South Channel region served as a source population for this habitat prior to its decline. The exact cause of this decline is unknown, but given the upstream habitats (the Great South Channel and Georges Bank) have not had an increase in retention, we believe that a lack of larval supply via hydrographic shifts is not the root cause.

Georges Bank is almost exclusively connected with itself (retention) and likely represents a semi-closed population of sand lance that

episodically receives larvae from other habitats, though we presently lack genetic evidence to corroborate or challenge this finding. Future studies may illuminate this as analyses have shown a degree of reproductive isolation may occur for *A. marinus* in the North Sea (Jiménez-Mena et al., 2020). The important role of retention is consistent with other spawning fishes on Georges Bank, such as haddock (Mountain et al., 2008; Werner et al., 1993, 1996), Atlantic cod (Mountain et al., 2008; Werner et al., 1993, 1996), and Atlantic herring (Bakun et al., 2009; Jech & Stroman, 2012). The tidal rectification gyre over Georges Bank contributes to the high retention of particles on Georges Bank, though this gyre frequently breaks down on seasonal scales (Smith & Morse, 1985). One notable difference between the ecology of sand lance on Georges Bank compared to haddock and Atlantic cod is the much earlier spawning and hatching period for sand lance, resulting in larvae being present on the bank from January through April (Mountain et al., 2008; Potter & Lough, 1987; Werner et al., 1996). This results in the larval period of sand lance coinciding with the weakest tidal rectification currents and the greatest influence of wind patterns on circulation (Naimie et al., 1994), likely contributing to the “boom-bust” nature of this sand lance habitat (Staudinger et al., 2020).

4.2 | Within-habitat variability in retention

Despite its relatively small size, Stellwagen Bank showed notable spatial variability in larval retention patterns which may be a large contributor to the persistence of the southwest corner as a sand lance habitat. Retention was highest on the southwest corner of the bank, the region with highest occurrence of sand lance and dependent top predators like humpback whales and seabirds (Powers et al., 2020; Silva, Wiley, & Fay, 2021; Silva, Wiley, Thompson, et al., 2021). However, the drivers of the spatial heterogeneity in sand lance and sand lance predator distribution over Stellwagen Bank, namely, the cause of the localized habitat in the southwest corner (Hazen et al., 2009; Lutcavage et al., 2000; Wiley et al., 2003), have remained largely a mystery due to the broad availability of suitable substrate across the bank (Valentine & Cross, 2020). The spatial variability in larval retention patterns on Stellwagen Bank may be a large contributor to the persistence of the southwest corner as a sand lance habitat and serves as a viable hypothesis for the mechanism behind the spatial heterogeneity in sand lance observations in the southern and central portions of the bank. The observation of highest potential retention in this region suggests fish may be aggregating on the southwest corner either due to increased settlement of individuals in this area or formation of spawning aggregations that maximize retention on the bank. While we cannot distinguish between these two hypotheses in this work, this question warrants further exploration. However, our observations of spatial heterogeneity in retention metrics do not explain the episodic explosions of sand lance abundance on the northwest corner of Stellwagen Bank, which can intermittently exceed those on the southwest corner (Richardson et al., 2014). Given the lack of backward retention on the northwest corner, it appears sand lance

observed on the northwest corner must come from an external source, likely north of Stellwagen Bank due to the prevailing current structure (Bigelow, 1927; Brooks, 1985; Franks & Anderson, 1992; Townsend et al., 2015). The northwest and southwest corners of Stellwagen Bank also had the highest connectivity to the Great South Channel, supporting that this connectivity is likely “realized” given these areas correspond to high sand lance abundance. It also further provides context for why retention and connectivity to the Great South Channel tend to oscillate out-of-phase in time. Collectively, these patterns suggest that sand lance spawning on Stellwagen Bank are likely to reach settlement habitat in most environmental conditions.

Unlike Stellwagen Bank, spatial variability in retention within the Great South Channel generally followed an expected pattern, with north to south advections within the region leading to the observed patterns. Forward retention was highest in the most upstream locations (northern) and the most downstream and shallow locations (southwest). Additionally, backward connection from Stellwagen was highest in the northernmost region and connectivity was highest in the southeast region for Georges Bank, corresponding to the nearest regions to each habitat. Thus, the spatial patterns in connectivity and retention for the Great South Channel reflect the highly advective regime of the region as opposed to revealing localized small scale (e.g., Stellwagen) or larger scale (e.g., Georges Bank) retention.

Georges Bank had the least variable pattern in spatial differences in connectivity and retention. Retention was highest toward the center of the bank which corresponds to the shallowest regions of the bank with the weakest stratification (Boucher et al., 2013). Patterns in forward connectivity to the Great South Channel and retention indicate the larvae are transported clockwise around the tidal rectification gyre, emphasizing the importance of this feature for retention and connectivity on Georges Bank as it is for numerous other species (Mountain et al., 2008; Potter & Lough, 1987; Werner et al., 1996).

4.3 | Role of wind on retention

Our results show interannual variability in retention on Stellwagen Bank is coupled to local wind patterns, though it is noteworthy that patterns suggest a different mechanism than proposed for other species in the region. Unlike Atlantic cod, which see enhanced retention and recruitment in the western Gulf of Maine during years with strong northerly winds from onshore Ekman transport (Runge et al., 2010), the enhanced retention of sand lance on Stellwagen Bank appears to be driven by eastward movement of retentive features from Stellwagen Basin to the southwest corner of Stellwagen Bank during years with strong southerly winds (Jiang et al., 2007). This is further supported by our observation that backward retention metrics were highest for particles released from the southwest corner of Stellwagen Bank and that retention of particles on the southwest corner exceeded connectivity with other portions of the bank in many years in forward tracking experiments. The association of spatial and interannual patterns in retention with local wind forcing suggests

monitoring of wind strength over Stellwagen Bank is particularly important for understanding spatiotemporal patterns in local recruitment. However, we must note that, while statistically significant, the relationship between southerly winds and retention on Stellwagen Bank was weak. This is likely largely due to factors other than wind forcing modulating the western Gulf of Maine coastal current. Previous research has shown that flow patterns in the region are not solely controlled by wind forcing and more work is needed to elucidate the more complex drivers of these hydrodynamics, such as local eddies and meanders (Churchill et al., 2005).

Retention on Georges Bank was also linked to wind patterns during the larval period, with years with many days of strong northerly winds corresponding with poor retention. Northerly winds are able to both move forward tracked particles to the southwest and thus off Georges Bank in addition to increasing the proportion of larvae that would have originated from the northeast peak of Georges Bank (where sand lance are not abundant) for backward tracking experiments. The timing of sand lance spawning reinforces this dynamic, as winter is when the tidal rectification gyre is weakest and thus larvae would be most susceptible to off-bank transport from winds (Naimie et al., 1994). Lewis et al. (2001) observed similar patterns for simulated “plankton” across Georges Bank from 1968 to 1998, indicating both that this pattern is persistent through time and may have additional effects on sand lance larval survival through regulating prey availability on Georges Bank. The combination of strong northerly winds moving larval sand lance off Georges Bank and these winds potentially reducing prey availability may have notable effects on sand lance recruitment in this region.

4.4 | Limitations and future directions

Our study is primarily limited by the lack of understanding of larval sand lance biology. Potter and Lough (1987) represent the only study of larval sand lance vertical distribution, with their results showing a movement of larvae to deeper water as sand lance larvae grow to near settlement age. However, we lack understanding of sand lance movements, including diel vertical migration patterns or horizontal movements. If larvae do exhibit concerted vertical or horizontal movements prior to the settlement process, incorporating such behavior in our particle tracking experiments would likely alter our results. Numerous studies have shown that the inclusion of larval behaviors alter dispersal pathways (Faillettaz et al., 2018; Levin, 2006; Rypina et al., 2014). This is most notable for larvae that exhibit vertical movements in areas with high vertical velocity shear (Garwood et al., 2021; Tapia & Pineda, 2007). The Gulf of Maine in winter is well mixed and thus vertical velocity shears are low on banks for much of the larval duration of sand lance (Mountain & Manning, 1994), though waters begin to stratify in the spring and thus vertical gradients in velocity begin to increase as sand lance larvae approach settlement (Mountain & Manning, 1994; Naimie et al., 1994). It is possible that vertical movements do occur among larvae and that these movements could affect the results presented here. For example, studies suggest

that vertical migration may enhance survival of the congener *A. marinus* through increasing food availability and thus growth (Gurkan et al., 2012). While we did not incorporate mortality into our models, future work should focus on better understanding larval sand lance behavior and incorporating this behavior into dispersal models to see if emergent patterns in dispersal pathways and retention change among these three habitats.

An additional source of unexplored variability may lie within the settlement and hatch timing of sand lance. Our estimates of settlement timing and hatch dates may not be perfectly representative of the expected settlement and hatch dates of sand lance in a given region. Both metrics may be sensitive to origin of an individual, and since connectivity metrics vary interannually among these habitats, observed settlement and hatch dates in a region may be sensitive to the degree of connectivity of that region with other habitats. For example, if the settling individuals in the Great South Channel are primarily from the Great South Channel (e.g., 1990), the otoliths of settling individuals from the Great South Channel likely accurately reflect hatch dates. However, if the settling individuals are a distribution of individuals hatched in the Great South Channel, Georges Bank, and Stellwagen Bank, the observed hatch dates would reflect a mix of hatch dates from these regions and not truly represent the mean hatch date of larvae on the Great South Channel. Unfortunately, hydrographic and hydrodynamic forcing from GOM-FVCOM for 2019 was not available when the experiments were conducted for this study, but future work should explore the variability in hatch and settlement dates observed on these habitats based both on temperature regimes and the expected connectivity among the habitats.

A large remaining question for *A. dubius* is the degree to which larval transport modulates local recruitment and the extent to which it interacts with other aspects of sand lance life history. Our work focused exclusively on larval transport of simulated particles, but a full understanding of larval survival necessarily requires knowledge of the interaction of larvae with physical conditions (e.g., temperature), prey fields, and predators (Llopiz et al., 2014). Interactions with prey fields are likely highly important in understanding larval growth and survival, as has been suggested in numerous systems (Hermann et al., 2001; Régnier et al., 2017). While we do not attempt such a study here, similar work on the congener *A. marinus* can provide some potential insights into this interaction. *A. marinus* survival appears to rely closely on the spatiotemporal overlap of larval hatching and copepod egg production (Régnier et al., 2017), both of which are sensitive to temperature phenology (Régnier et al., 2019). For regions such as much of the North Sea, where large-scale larval transport is rare, understanding the drivers of this overlap is essential (Wright et al., 2019). The closest corollary to such a region in the Gulf of Maine is likely Georges Bank, whereby retention dominates larval transport patterns and thus local thermal and productivity regimes may be the key to understanding local recruitment fluctuations. For regions such as Stellwagen Bank, however, timing of productivity and hatch must also be coupled with the infrequent years of high retention for high sand lance recruitment to result. This pattern of trophic overlap with retention-favorable hydrodynamics has also been suggested to be important for

A. marinus larvae on Dogger Bank, indicating commonalities between these species (Henriksen et al., 2018). Future work in the Gulf of Maine should move toward coupling lagged abundances of adult sand lance (due to our lack of a recruitment index for the Gulf of Maine) with overlap in favorable transport and prey availability to generate a unified theory on drivers of habitat-specific sand lance recruitment. Such validation of dispersal modeling results is essential as, even with inclusion of detailed larval behavior, modeling results do not always corroborate observations of local recruitment and genetic analyses and indicate additional mechanisms are at play (Stockhausen et al., 2019). Similar efforts have been pursued in other regions, indicating potential for critical larval and juvenile data collection to validate dispersal modeling efforts (Siddon et al., 2019).

Our use of hydrographic and hydrodynamically coupled Lagrangian tracking models is another limitation when it comes to translating our results to realistic drivers of recruitment. Lagrangian particle tracking models are used frequently to estimate particle trajectories for movements of water parcels (Roach & Speer, 2019), plankton (e.g., Ji et al., 2017), and larval stages of organisms, including fishes (Baumann et al., 2006; Boucher et al., 2013; Churchill et al., 2011; Huret et al., 2007; Petrik et al., 2014) and shellfish species (e.g., Chen et al., 2021, and references therein) in our study area. However, fine-scale differences in velocity interpolation and chaotic trajectories near stagnation points can lead to vastly different trajectories for nearby placed particles within Lagrangian tracking models (see supplementary methods). These large discrepancies even appear when using small time steps if the particle tracking experiments last for long periods, as is the case in our work. Therefore, we must caution that our experiments represent a subset of the potential drift trajectories of water parcels (and thus larval sand lance) released from each of our habitats and not a full representation of the fate of larvae hatched or backtracked from each location. Discrepancies also arise when comparing forward and backward tracked particles. These discrepancies are not due to the random walk nature of the water parcels as illustrated by Christensen et al. (2007) because random walk is not considered in our calculation. Instead, they are largely due to the difference between the forward and backward velocities before and after a particle was tracked. However, this can result in a different location than the particle would be in a forward tracking experiment as multiple pathways can result in the same location. This leads to an impossibility of backtracking a particle to repeat the forward tracking path in a reversed direction which is particularly difficult at stagnation points or convergent flows where the Lagrangian coherence scale is small. While we believe that backtracking experiments (and backtracking experiments generally) can assess the dispersal probability and capture the general connectivity patterns, we must note caution against over-interpreting the results of such studies.

5 | CONCLUSIONS

Collectively, our results indicate that larval dispersal pathways among Stellwagen Bank, the Great South Channel, and Georges Bank vary

interannually and spatially within each habitat. Interannual variability and the spatial distributions of retention are also linked to local wind phenomena. This connection between retention and wind phenomena allows managers and stakeholders interested in local sand lance retention to focus on winter–spring wind patterns as indicators of likely strong or weak retention for Stellwagen Bank and Georges Bank. Given that settling sand lance are difficult to collect due to their small size and patchy distribution, these metrics may be helpful to ameliorate our lack of direct recruitment estimates from trawl surveys. However, wind events are not the sole driver of local retention and more research into other mechanisms is warranted, especially for retention over Stellwagen Bank. Our results indicate that local presence of sand lance may be linked to larval dispersal pathways and thus larval retention may play a role in local sand lance abundance if other conditions are stable. However, environmental conditions are rarely stable for multiple consecutive years, and thus, interannual changes in retention and dispersal must be paired with observations of drivers of adult sand lance abundance when ultimately predicting spawning stock biomass. Future research should work toward incorporating environmental drivers of adult abundance and larval dispersal pathways into a stock assessment and stock recruitment relationships for this critical, yet understudied forage fish.

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CONFLICT OF INTEREST

The authors have no conflicts of interest to declare.

AUTHOR CONTRIBUTIONS

JJS, RJ, HB, DNW, and JKL designed the study. JJS, TLS, KP, and JKL collected the data. JJS, RJ, ZF, and HB performed modeling and

statistical analyses. JJS, RJ, HB, and JKL contributed significantly to the drafting of the manuscript. All authors contributed to editing and approved the final manuscript.

DATA AVAILABILITY STATEMENT

All model run output is available to interested parties upon request.

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SUPPORTING INFORMATION

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