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**“ORIGIN AND FATE OF SANDLANCE *AMMODYTES DUBIUS* OFFSPRING FROM STELLWAGEN
BANK, INFERRED FROM LAGRANGIAN DRIFT SIMULATIONS”**

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ORIGIN AND FATE OF SANDLANCE *AMMODYTES DUBIUS* OFFSPRING FROM STELLWAGEN BANK, INFERRED FROM LAGRANGIAN DRIFT SIMULATIONS

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Summary: Northern sandlance inhabit discontinuous sandbanks all along the northwest Atlantic shelf, but the connectivity and inter-reliance of these populations is currently not understood. We performed long-term (1990-2016) hydrodynamic drift simulations to investigate the spatial origin and fate of sandlance from Stellwagen Bank in the southern Gulf of Maine. Our findings suggest that the Stellwagen Bank sandlance population is highly connected to – and reliant on – spawning populations immediately to the north in the coastal and northern Gulf of Maine, while also indicating the potential for partial self-recruitment back to the bank. We further found that this productive spawning ground likely exports most of its offspring to suitable habitats in areas to the south and southeast of the bank, thereby potentially contributing to large, but interannually variable settlement pulses on Nantucket Shoals, Georges Bank, and mid-Atlantic Bight waters, including areas currently under development for offshore wind energy production. Available monitoring records of larval sandlance abundance on Stellwagen Bank (2008-2016) suggested that years of exceptional transport from far away areas in the northern Gulf of Maine produce exceptional larval settlement pulses, thus highlighting the potential role of variable transport patterns in generating the large spatio-temporal fluctuations typical for this important forage fish.

INTRODUCTION

Most marine metazoans have planktonic early life stages that disperse with ocean currents and are thus key to the connectivity of their populations (Cowen et al. 2000, Paris & Cowen 2004). Since circulation features vary seasonally and interannually they generate variability in offspring transport, which in turn affects offspring survival, growth, and the gene pool of populations. For marine fish, deducing the spatial origin and fate of annual larval cohorts can be predictive of recruitment success and thus aid management and conservation (Hinrichsen et al. 1997, Baumann et al. 2006). However, direct *in situ* measurements of ichthyoplankton transport are rarely feasible and if so, only over short time periods (Fortier & Leggett 1985, Davis et al. 1991). Alternatively, drift patterns can also be studied *in silico* via hydrodynamic simulations that allow scenario testing, backward and forward projections, and quantification of interannual drift variability. Over the past decades, these advantages have made hydrodynamic drift modeling a common, powerful approach in biological oceanography (Werner et al. 2007, Boucher et al. 2013, Liu et al. 2015).

Its basic premise is to couple a hydrodynamic model of appropriate resolution with a particle tracking routine that allows seeding and following virtual Lagrangian drifters anywhere within a model domain (Allain et al. 2003, Hinrichsen et al. 2005). Many approaches assume that ichthyoplankton drift can be sufficiently approximated by the displacement of ‘passive particles’ with their surrounding water parcels – at least until fish larvae develop into juveniles and start to settle, school, or exhibit directed swimming (Allain et al. 2003, Baumann et al. 2003). This dispersive period, or pelagic duration, varies greatly from a few days to many months among fishes.

Generally, hydrodynamic drift simulations find answers to two broad questions, i.e., ‘where did offspring come from?’ (Spatial origin) and ‘where has offspring gone to?’ (Spatial fate). These are addressed by backward and forward projections of particle drift,

respectively. Some models also include information on larval behavior (e.g., diel or ontogenetic vertical migration), while others further incorporate larval growth, mortality, and even modeled zooplankton fields into each simulated time step (Werner et al. 2007, Ji et al. 2012). In general, hydrodynamic simulations are most insightful when combined with observational data of larval fish abundance, distribution, or subsequent year class strength.

Here, we use hydrodynamic modeling to study interannual variability in origin and fate of larval Northern sandlance (*Ammodytes dubius*) from Stellwagen Bank, a national marine sanctuary in the southern Gulf of Maine and an abundance hot spot of this forage fish and its higher trophic predators (tuna, cod, seabirds, whales; Friedlaender et al. 2009, Silva et al. 2020). Sandlance are total spawners that deposit benthic eggs at the end of fall, a rare spawning time for fishes that results in the release of slowly developing larvae into cooling surface waters during winter (Staudinger et al. 2020). Previous analyses of sandlance otoliths (ear bones) suggested that larvae remain pelagic for up to three months (Suca et al. 2022) before settling onto shelf habitats with very specific sediment characteristics (coarse sand, low organic content).

We recently established that sandlance not just occur on Stellwagen Bank but indeed spawn there, mostly during a narrow window at the end of November (Baumann et al. unpublished data). Given the dynamic ocean conditions on the Bank generally, and specifically during fall and winter, the spatial fate of sandlance offspring produced here is an important but currently unanswered question. Because of their long pelagic duration, most if not all sandlance larvae could be advected off the Bank and subsequently contribute to settlement pulses in other regions. Such a scenario would also imply that the population on Stellwagen Bank relies heavily on influx of new recruits from other spawning grounds. Conversely, if offspring are hydrographically retained in the area, then Stellwagen Bank sandlance could be considered a self-recruiting population. These scenarios have important,

contrasting implications for the conservation of this species. For example, the ongoing development of the Northwest Atlantic shelf for wind energy production could overlap with areas to which new sandlance cohorts are transported. Testing such drift-related hypotheses falls squarely within the scope and strength of hydrodynamic simulations, which may ultimately elucidate, whether the high spatio-temporal variability of sandlance abundance on Stellwagen Bank is generated mostly by local or by external processes linked to variable ocean circulation patterns.

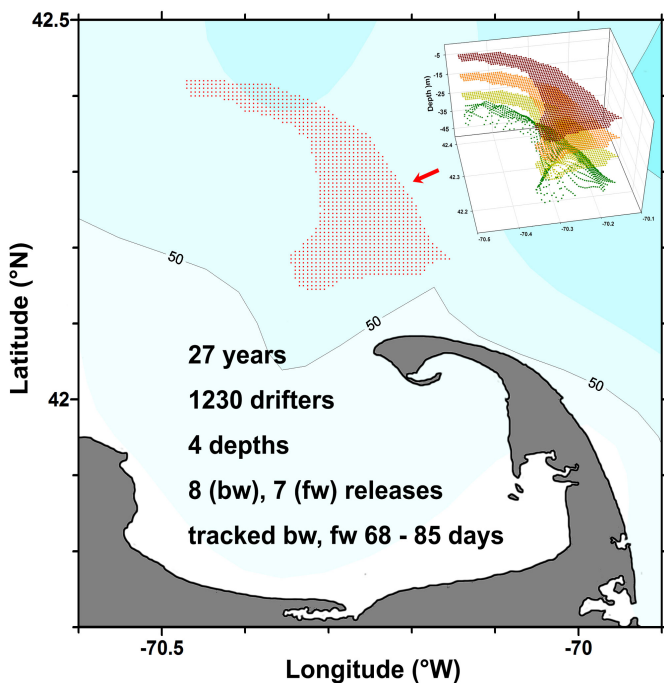


Fig.1: Set-up of the hydrodynamic drift simulations. We seeded 1230 Lagrangian drifters (red dots) on Stellwagen Bank in each of 4 depths (5, 15, 25, 35m, inset), 8 or 7 releases (backward, forward tracking, respectively), and each of 27 years and tracked them for 68 and 85 days backward (spatial origin) or forward (spatial fate).

METHODS

We used the third generation Gulf of Maine-Finite Volume Community Ocean Model (GoM-FVCOM; Chen et al. 2011) to generate hydrographic and hydrodynamic conditions with a horizontal resolution of 0.3 - 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, Xue et al. 2014, Ji et al. 2017). 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 2014). For our drift simulations, we added a particle tracking routine with a fourth order Runge-Kutta time stepping scheme to resolve advection (Ji et al. 2012, Boucher et al. 2013, Liu et al. 2015).

A suite of particle tracking experiments was conducted for each of 27 years (1990-2016). Particles were placed in a grid with 500m spacing in waters ≤ 40 m depth on Stellwagen Bank (bounded within the box 42.13-42.5°N, 70.5-70.12°W) resulting in 1230 drifters for each depth and day of release (Fig.1). Random walk routines were not incorporated due the high model resolution and the depth-keeping nature of the particle tracking runs. Previous work suggested that sandlance larvae below 28 mm length are almost evenly distributed within the water column, while larger 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 actually be the beginning of the settlement process. To represent the homogeneous vertical distribution of sandlance larvae, we used depth-keeping particle runs at 10m spacing in the upper 40m (5, 15, 25, and 35m; Fig.1). Given the absence of clear behavioral information we chose not to incorporate any diel vertical migration patterns into our simulations.

For backward projections, 1230 particles per year and depth stratum were released on each of eight days (17-31 March) and tracked backward in time for 68 days (to 9-23 January) and 85 days (to 23 December - 6 January). The two drift periods correspond to the range of pelagic durations estimated previously by

otolith microstructure analysis (Suca et al. unpublished data). This resulted in a total of 2,125,440 tracked particle positions (27 years × 4 depths × 8 days × 2 periods × 1230 drifters). Forward releases occurred on each of seven days during the first two weeks of January (1-13 January), consistent with estimated hatch dates of sandlance settlers caught on Stellwagen Bank (Suca et al. 2022). Again, 1230 particles per year and depth stratum were seeded and tracked forward in time for 68 days (to 8-20 March) and 85 days (to 25 March – 7 April), resulting in a total of 1,859,760 tracked particle positions (27 years × 4 depths × 7 days × 2 periods × 1230 drifters). Although drifter positions were internally carried through each simulation time step, our analyses focused only on their final distributions on days 68 and 85, i.e., the minimum and maximum estimate for the pelagic duration of sandlance larvae. For the purpose of this analysis, we considered all drifters released over a two week period (backward runs = 8 releases; forward runs = 7 releases) to comprise a years larval sandlance cohort and therefore calculated all metrics for pooled release days.

To visualize overall and annual particle distributions¹, particle coordinates were first binned into 0.25° longitude and 0.2° latitude bins, which were then used to calculate the percentage of particles in each bin for each year across all depth strata and drift periods. Contours of particle distributions were subsequently estimated via Kriging in Surfer (V8, Golden Software).

Metrics: We first calculated the median particle latitude (Lat_M) and longitude ($Long_M$) for each year, depth stratum, and drift duration. As a measure of dispersion, standard deviations of particle latitudes and longitudes (Lat_{SD} , $Long_{SD}$) were computed. In addition, we used the water depth at each particle position to calculate median depth ($Depth_M$) and SD ($Depth_{SD}$) for each year, depth stratum, and drift duration.

¹ Drifter distributions of individual years are accessible @ <https://befel.marinesciences.uconn.edu/sldrift/>

We calculated the distance ($Dist$, in km) of each particle i to the center of the release on Stellwagen Bank (42.34°N, 70.31°W) as

$$Dist = 1.852 \sqrt{\left((Lat_i - 42.34) * 60 \right)^2 + \left((Long_i - 70.31) * 60 * \cos\left(\frac{Lat_i + 42.34}{2} * \frac{\pi}{180}\right) \right)^2}$$

and then computed the median distance ($Dist_M$) and the standard deviation ($Dist_{SD}$) for each year, depth stratum, and drift duration.

To further quantify interannual variability in drift patterns, we classified particle positions in terms of six broad regions of the model domain (Fig.2) termed **Coastal Gulf of Maine** (R1: >70°W, >42.5°N), **Massachusetts Bay** (R2: >70°W, 41.65-42.5°N), **mid-Atlantic Bight waters** (R3: >70°W, <41.65°N), **Northern Gulf of Maine** (R4: <70°W, >43°N), **Outer Gulf of Maine** (R5: <70°W, 41.65-43°N), and **Outer shelf** (R6: <70°W, <41.65°N). We then computed the percentage of particles contained in each region per

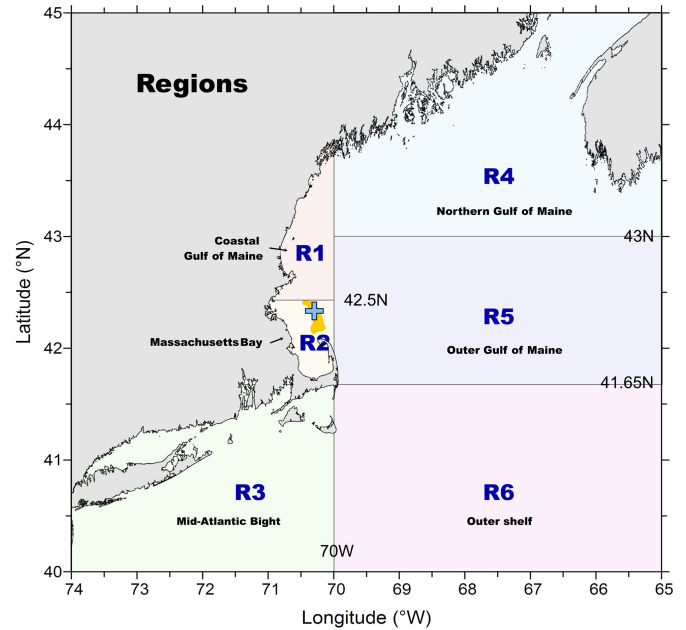


Fig.2: Dividing the model domain into six regions of interest to assess interannual variability in percent drifters originating from (backward tracking) or drifting to there (forward tracking).

year, depth stratum, and drift period.

To identify overarching drift scenarios, we created time-series of region-specific annual drifter percentages aggregated over all depths and drift periods. Excluding regions with zero or negligible percentage values (backward runs: R3 and R6; forward runs: R4 and R5), we used the remaining four time-series as input variables in principal component analyses (one for backward runs, one for forward runs) that extracted 2 principal components with eigenvalues > 1 and explained 82 - 84% of the interannual variability. Plots of annual PC1 vs. PC2 scores with overlaid component scores of the coefficient matrix were then used to identify similarities between years and the contributions of each region to these patterns. In addition, we used the same set of time-series (standardized to $m=0$, $\sigma=1$) to conduct non-hierarchical (K-means) cluster analyses for backward and forward runs to statistically distinguish 3 and 4, respectively, clusters of years with shared drift patterns. Cluster separation was then tested via ANOVAs with Bonferroni-adjusted post-hoc tests.

To investigate the potential overlap between the spatial fate of Stellwagen-produced sand lance and areas currently under development for offshore wind energy production, we extracted the outer coordinates of all current wind lease areas from the Bureau of Ocean Energy Management geodatabase (www.boem.gov/BOEM-Renewable-Energy-Geodatabase.zip). We then identified all $0.25^\circ \times 0.2^\circ$ bins (long/lat) in our model domain that matched the BOEM lease polygons, followed by calculating annual and overall percentages of forward-tracked particles that arrived there 68-85 days after their release on Stellwagen Bank.

Biological data: We accessed two data sources to relate simulated drift patterns to empirical observations of sand lance abundance. The first were monitoring data from the Northeast Gateway® Deepwater Port, an offshore liquid gas terminal located just north of Stellwagen Bank approximately

13 miles from shore in Massachusetts Bay. The facility has been maintaining a robust ichthyoplankton monitoring program since 2008 (Normandeau Associates, Inc.²) that has measured abundance for over 30 species of fish eggs and larvae, including sand lance yolk-sac and post-yolk sac stages. The sampling is conducted once or twice monthly at three replicate stations nearby the NEG facility. While the data report all sand lance as *Ammodytes americanus* (i.e., the nearshore congener of *A. dubius*), the distinction between the two species is difficult even for adults and close to impossible during the yolk-sac and post-yolk-sac stages. Given the offshore location of the monitoring, we assumed that all observed sand lance were in fact *A. dubius*. A sampling gap occurred in 2013 and 2014; hence, the temporal overlap with our drift simulations is limited to seven years. For the purpose of this analysis, we aggregated the abundance of both larval sand lance stages (ind m^{-3}) during the months of February – April to obtain an annual proxy for larval sand lance abundance on Stellwagen Bank.

Second, we accessed the sand lance abundance data of the annual spring bottom trawl survey of the Northeast Fisheries Science Center (NEFSC, NOAA) in Woods Hole, MA. While the full survey covers the entire Northwest Atlantic shelf (Cape Hatteras – Nova Scotia), we only selected survey stratum 26/1260 that includes Stellwagen Bank but has limited trawl coverage per year ($n \sim 5$). There are also known issues with sand lance catchability in NFMS bottom trawls, owing to the relatively large mesh size and the alternate burrowed/pelagic occurrence of the species, which likely results in stochastic and zero-inflated catches. Due to a gear change in 2009, we felt it prudent to exclude the most recent years and focused only on data from 1990 to 2008 in this analysis. Because bottom trawls do not catch sand lance larvae but adults age 2+; we used a two year lag of sand lance

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<https://www3.epa.gov/region1/npdes/offshoreIng/pdfs/draftma0040266permit.pdf>

abundance ($\log(SL(t))/SL(t-1)$) to account for the assumed delay between larval transport and appearance of age-2s in the survey.

Bivariate Pearson correlation analysis was used to relate all depth- and drift period-specific particle metrics from backward and forward runs to each sandlance time series, while adjusting the acceptable significance level to $p < 0.001$ to account for multiple comparisons. All metrics that showed significant correlations to either abundance proxy were subsequently used in a Principal Component Analysis to extract the first principal component that became the explanatory variable to test against sandlance abundance from NEG or the bottom trawl surveys.

All statistical analyses were performed in SPSS (V20, IBM).

RESULTS

Overall drift patterns across all 27 years suggested a clear answer to the question of sandlance spatial origin (Fig.3). Aggregate backward projections indicated that sandlance settling on Stellwagen Bank are predominantly produced to the north of the Bank, in the coastal areas of the northern Gulf of Maine, with smaller contributions from areas further to the north (Nova Scotia) and negligible contributions from offshore banks such as Georges Bank (Fig.3A). A considerable proportion of particles appears to originate from within Massachusetts Bay, thereby allowing for partial self-recruitment of Stellwagen Bank produced sandlance. Aggregate forward projections suggested that the majority of sandlance larvae from Stellwagen Bank are advected south, past Cape Cod, to shelf areas of Nantucket Shoals and coastal mid-Atlantic Bight habitats (Fig.3B). A considerable fraction of particles, however, appears to be retained within Massachusetts Bay, thus indicating potential self-recruitment back to Stellwagen Bank

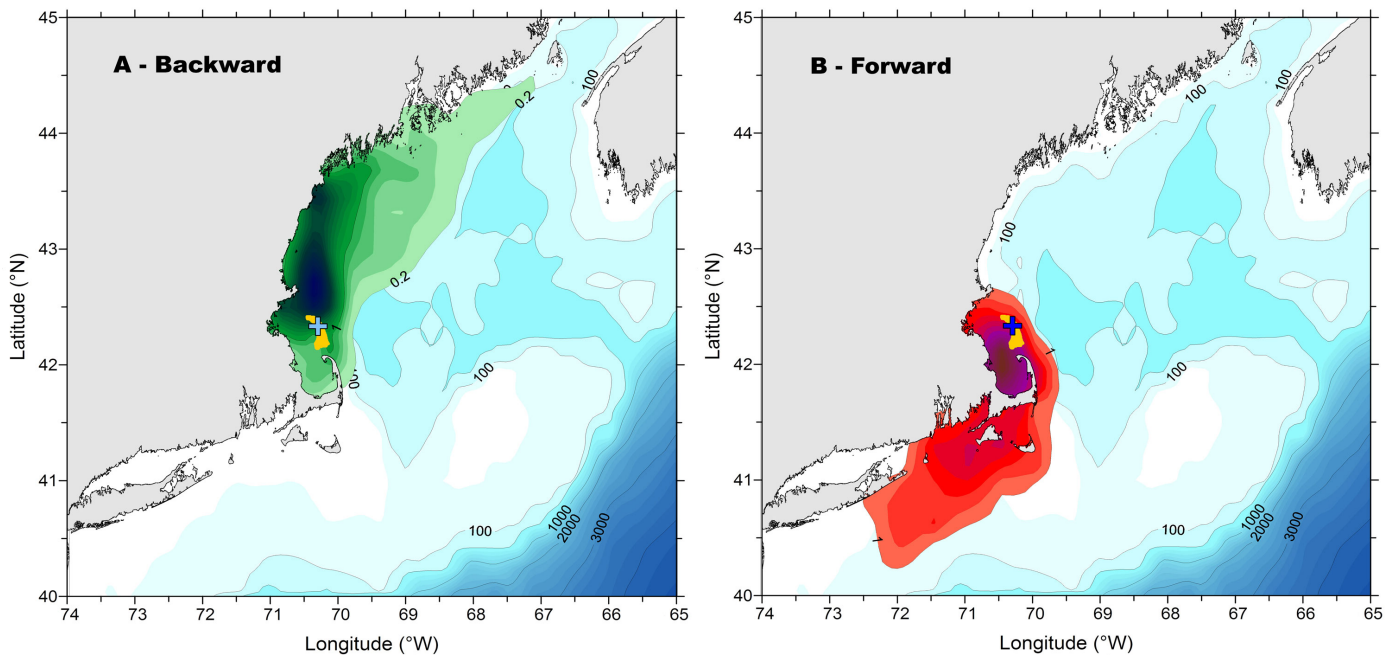


Fig.3: Aggregate backward (A) and forward (B) drift simulations to infer the spatial origin (A) and fate (B) of northern sandlance larvae settling (A) or produced (B) on Stellwagen Bank NMS. 1230 Lagrangian drifters were seeded (yellow area) in each of 27 years (1990-2016), each of 4 depths (5, 15, 25, 35m) and (A) each of 8 days (17-31 March) or (B) each of 7 days (1-13 Jan), and then tracked backward or forward for 68 and 85 days. Contours represent total aggregate percentages of particle distributions across all years and releases.

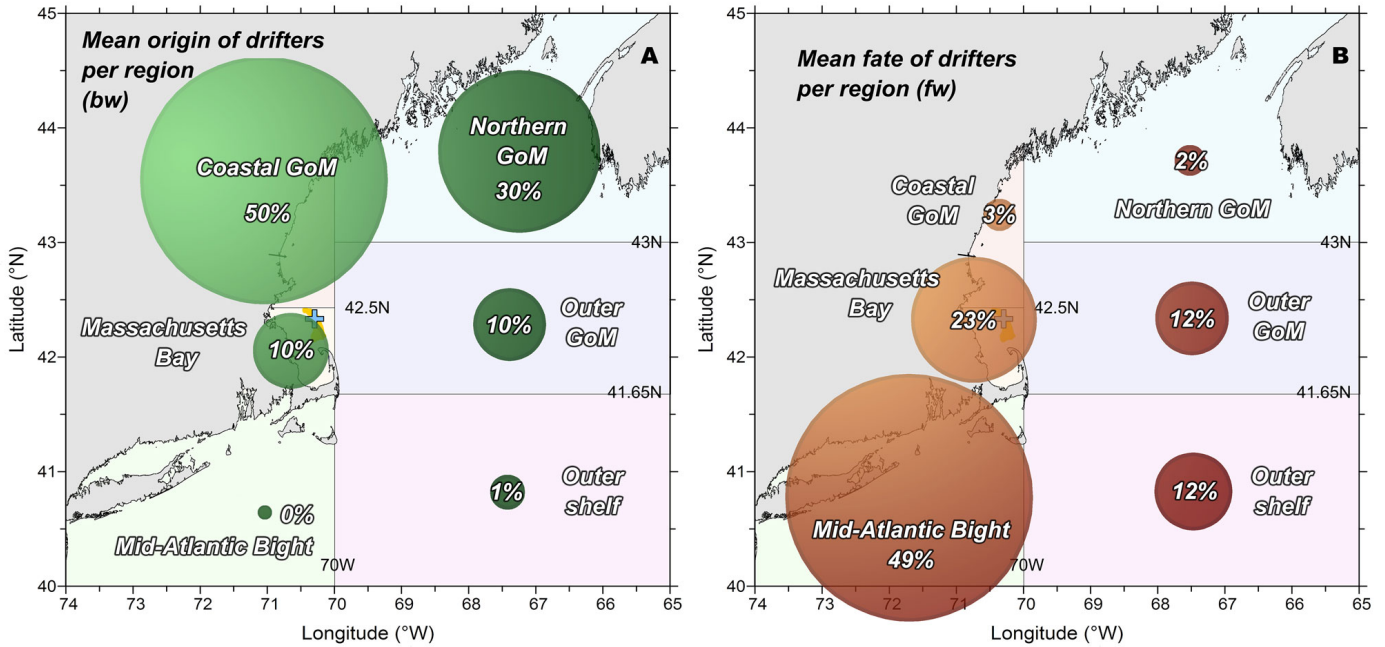


Fig.4: Bubble plot of the mean percentage of drifters (across all years, releases, periods, 15-35m depths) in (A) backward projections and (B) forward projections. Bubble sizes are scaled to percentages.

consistent with backward projections (Fig.3).

When dividing the model domain into six regions of interest, aggregate particle contributions could be quantified, revealing that, on average, 50% of all sandlance larvae settling on Stellwagen Bank are produced in the coastal Gulf of Maine areas adjacent to the north (R1, Fig.4A), while offspring from further away in the Northern Gulf of Maine (R2) contribute an average third to settlers on Stellwagen Bank. About 10% of sandlance settlers could be self-recruits from Massachusetts Bay, while the remaining 10% originate mostly from the outer Gulf of Maine (R5) and almost none from outer shelf or coastal mid-Atlantic Bight areas (< 1%, R3 & R6, Fig. 4A). Aggregate forward projections suggested that half (49%) of the Stellwagen produced sand lance larvae are advected into mid-Atlantic Bight waters by the time of settlement (R3, Fig.4B), while remaining on the coastal shelf. Almost a quarter (23%) are being retained on the spawning ground (Massachusetts Bay, R2), none end up north (<5% R1 & R4), while another quarter is being advected out onto the outer GoM and outer shelf regions (R5 & R6), thus potentially contributing

to sandlance settlers on Nantucket Shoals and Georges Bank (Fig.4B).

The percentage of particle contributions to each region showed substantial interannual variability (Fig.5). For example, backward projections revealed that the contribution of particles to Stellwagen Bank from R1 (coastal GoM) fluctuated between 16-90% interannually (mean \pm SD = 50 \pm 16%), whereas the largest interannual variability occurred in R4 (northern GoM), where contributions to Stellwagen Bank fluctuated between 0-69% (mean \pm SD = 30 \pm 19%). Potential self-recruitment from Massachusetts Bay varied between 1-33% interannually (mean \pm SD = 10 \pm 8%; Fig.5A). Similarly, forward projections mostly resulted in the majority of particles advected to coastal areas of the mid-Atlantic Bight (R3, Fig.5B), but interannual variability ranged from 1-96% (mean \pm SD = 49 \pm 26%). When not drifting into mid-Atlantic Bight waters, particles were either retained in Massachusetts Bay (R2, 0-65%; mean \pm SD = 23 \pm 17%) or advected into outer GoM (R5, 1-28%) or outer shelf areas (R6, 2-60%; Fig.5B).

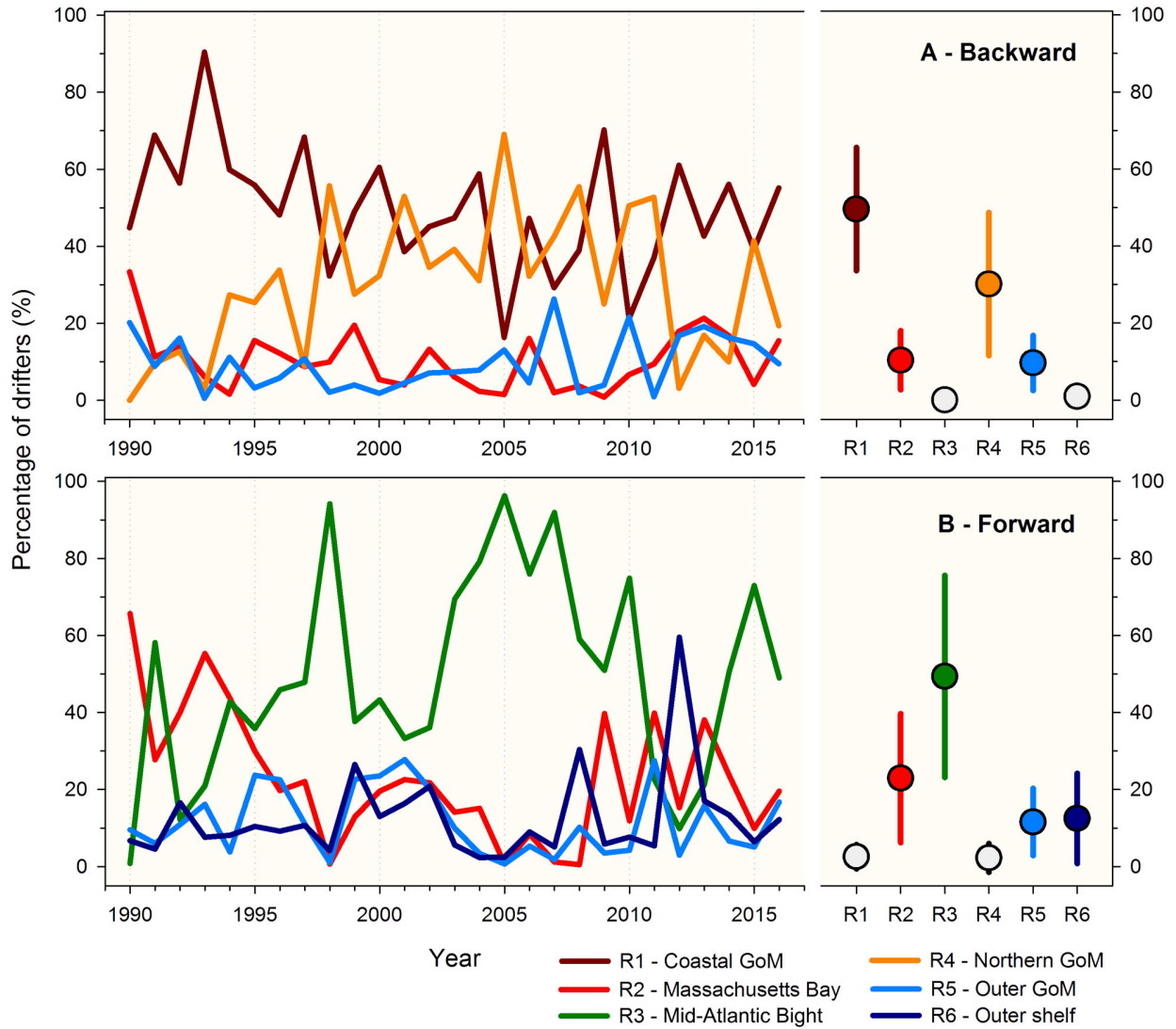


Fig.5: Time-series of annual drifter percentages for each of the six regions in (A) backward and (B) forward simulations (small value series omitted). Right panels show mean \pm SD of drifter percentages in each of 6 areas of the model domain. There are many interesting patterns here, e.g., (A) that the sand lance contribution from the coastal GoM fluctuates between 20-90% and often appears inverse to the Northern GoM timeseries (5-70%).

Principal component analysis on the four backward (R1, R2, R4, R5) and four forward time-series (R2, R3, R5, R6) of percent particle contributions revealed two principal components each, explaining 82 - 84% of the interannual variability (Fig.6). Northern GoM (R4) was highly correlated with PC1, whereas outer GoM was most highly associated with PC2. Hence, the PCA of backward run time-series suggested separation between years with high particle contributions from northern GoM (R4) vs. Massachusetts Bay (R2) and

coastal GoM (R1) on PC1, whereas separation along PC2 was between years with high spatial origin of drifters from outer vs. coastal GoM (R5 vs. R1, Fig.6A). Similarly, the PCA of forward run, particle percentage time series showed separation between years with strong drift into mid-Atlantic Bight vs. outer GoM and Massachusetts Bay (R2) along PC1, in addition to separation along PC2 distinguishing years of high particle drift to outer shelf (R6) vs. retention in Massachusetts Bay (R2, Fig.6B).

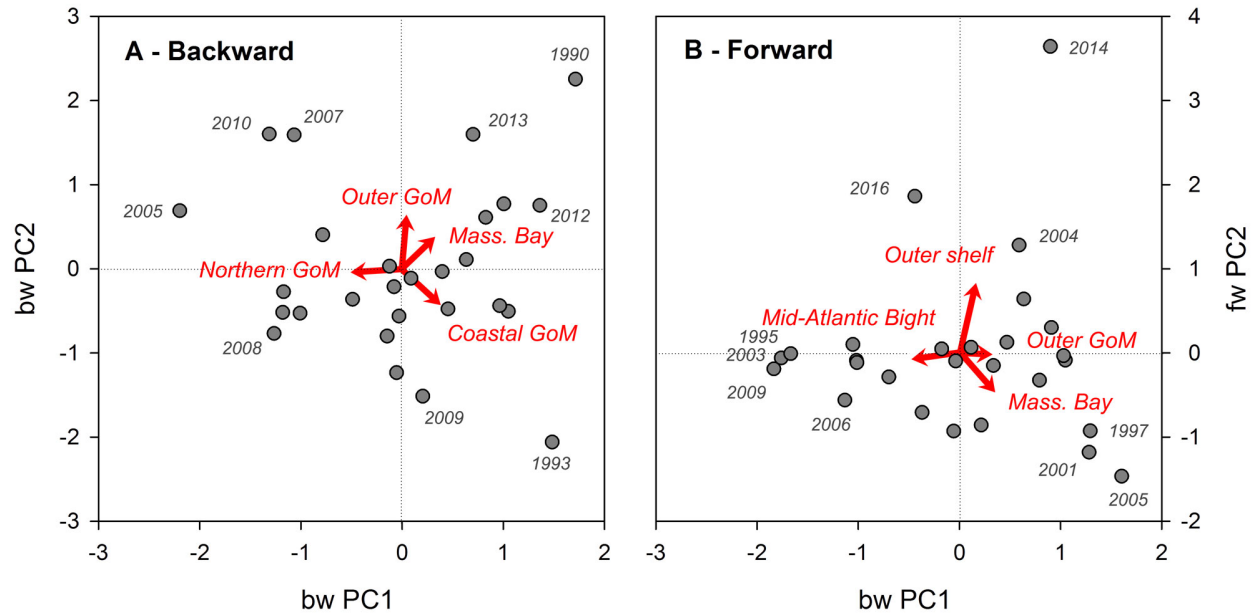


Fig.6: Principal component analyses of percent particle distribution time series in (A) backward and (B) forward simulations. The first and second principal component was extracted from 4 variables (2 low region variables excluded), and the annual PC1 and PC2 scores plotted. Red vectors denote the component scores of the coefficient matrix. Extreme years are labeled.

Cluster analysis of backward run time-series suggested 3 clusters as the most parsimonious separation of years with different spatial drifter origin (Fig.7A). Forward run time-series were best separated into 4 clusters, although the fourth cluster contained only a single year, 2014 (Fig.7B). As shown in Fig.8A (backward runs), the first cluster consisted of years with a high percentage of particles originating from northern GoM areas (R4), which is distinct from a second cluster of (most) years with limited drift from coastal GoM areas (R1) and a third cluster with strong self-recruitment from Massachusetts Bay (R2) or outer GoM (R5). Similarly, forward runs showed a distinct cluster of years characterized by large advection of particles to mid-Atlantic Bight waters (R3), as opposed to retention years in Massachusetts Bay (R2) or advection to outer GoM and outer shelf areas (R5 & R6). 2014 saw extreme levels of particle advection to outer shelf areas and thus comprised its own cluster (Fig.8B).

Our analysis of spatial drifter fate (forward runs) overlapping with current BOEM wind lease areas suggested only minimal transport onto areas 2-7 (mid-

Atlantic Bight, 0-2% annually), but indicated a much more considerable overlap with area 1 south of Nantucket Shoals. This wind lease area received on average 12% of sand lance settlers produced on Stellwagen Bank, with large interannual fluctuations ranging from 0.4% to 47% (Fig.9).

We correlated a total of 80 drifter-related proxies (40 backward run proxies, 40 forward run proxies) to the time-series of larval sand lance abundance (NEG data) and lagged adult sand lance abundance (NMFS bottom trawl, 26/1260 stratum). The latter was unrelated to any of our drift proxies ($P > 0.05$). However, several drift proxies (i.e., distance from destination and median longitude) showed strong correlations to the NEG larval sand lance data set (Pearson correlation, $P < 0.001$; Fig.10). The temporal overlap between drift and ichthyoplankton time-series was sadly limited to 7 years, and correlations were largely driven by the order-of-magnitude higher larval sand lance abundance in 2010 compared to all other years. However, this corresponded to a highly unusual drift pattern in that year, with particles coming from farther away (Fig. 10A) and from further to the east

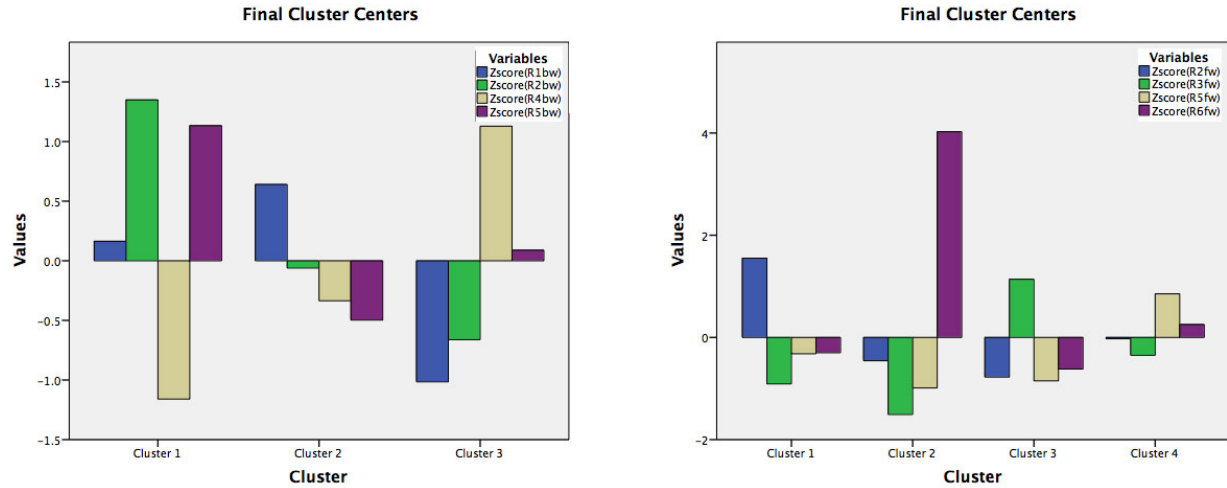


Fig.7: Non-hierarchical (K-Means) cluster analyses of backward and forward simulations based on annual percentages of drifters within the 6 domain regions. Time-series were standardized to zero mean and unit deviation, and 3 and 4 clusters were extracted, respectively. The plots show mean values of the final cluster centers based on 4 backward and forward variables.

(Fig. 10B) than in all other years. Similarly, the inverse relationship between larval abundance and median longitudes in forward runs suggested a much more western distribution of forward-tracked drifters in 2010, mostly along the mid-Atlantic Bight coast (R3), and a considerable retention within Massachusetts Bay (R2), likely enhancing self-recruitment back to Stellwagen Bank (Fig.10C). All other proxies that were

systematically tested for both forward and backward simulations (i.e., median latitude, median bottom depth at drifter location, drifter dispersion) were unrelated to larval sandlance abundance. Fig. 11 shows correlation coefficients (R) between individual drifter proxy time-series for specific drift depths and drift periods and larval sandlance abundance. This revealed that proxies from the shallowest drifter

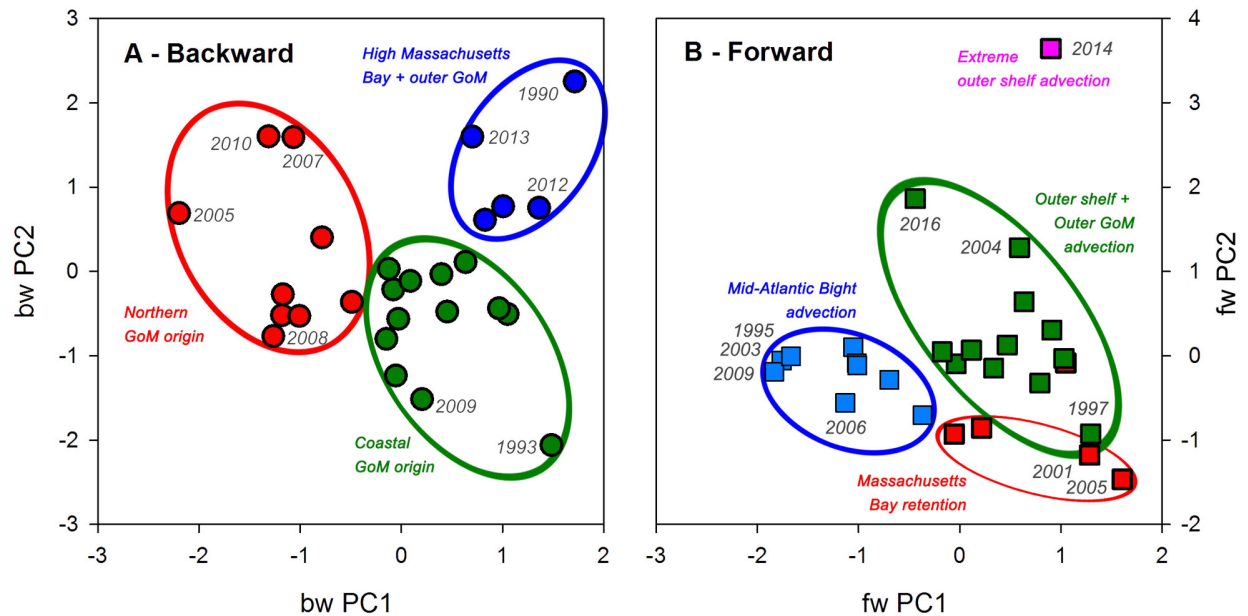


Fig.8: Combined Principal Component and Cluster analysis of particle percentages in 4 areas of the model domain in (A) backward and (B) forward simulations. 3 and 4 clusters could be statistically separated, respectively. Extreme years are labeled.

depth (5m) generally had the least explanatory power, while drifters at 15, 25, and 35m depth better correlated with larval sand lance abundance. Also, only the longer drift duration (85d) in the forward projection explained significant amounts of larval sand lance variability.

Conversely, in 2012 backward-tracked particles barely drifted at all, possibly indicating weak influx from northern sand lance spawning grounds. Between 1990-2016, these patterns occurred repeatedly, but for most years we lack corresponding larval abundance data.

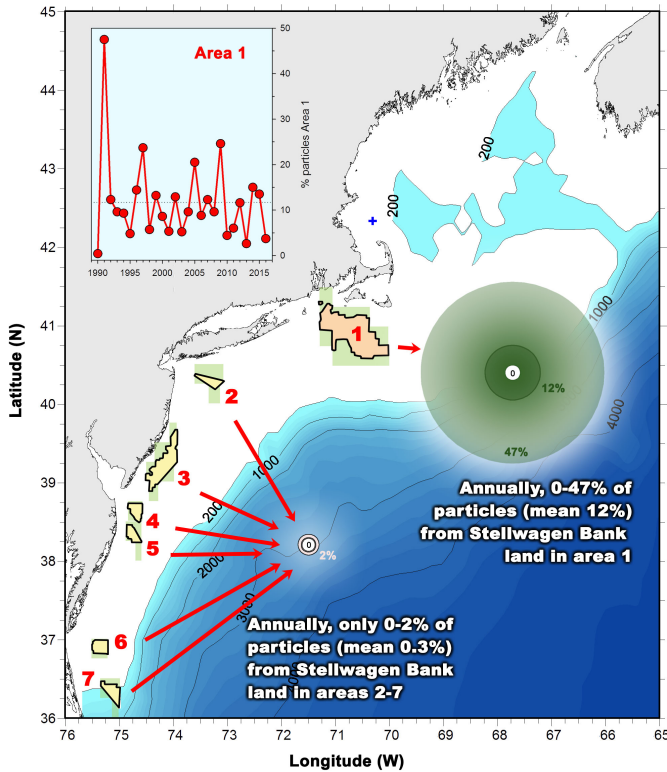


Fig. 9: Percentage of Stellwagen produced sand lance larvae drifting into BOEM Wind Lease areas at the time of settlement (68-85d), inferred from forward runs. Black outlines show wind areas 1-7 along the mid-Atlantic Bight (green squares = grid cells used to include drifters). Circles show minimum, mean, and maximum percentages of drifters. Inset shows time-series of area 1.

In Fig.12, we visualized backward and forward drift patterns (all releases, 2 drift periods, 15-35m depths) for two opposing years in terms of drift and larval sand lance abundance at the NEG facility (2010: $\sim 3 \text{ m}^{-3}$; 2012: $\sim 0.3 \text{ m}^{-3}$). This showed that in 2010, the majority of drifters arrived from furthest away in the northern Gulf of Maine, thereby perhaps transporting offspring from these productive spawning grounds to Stellwagen Bank and thus contributing to the extreme number of sand lance larvae recorded that year.

DISCUSSION

Despite the recognized ecosystem importance of northern sand lance as a critical forage resource for commercial fish stocks, seabirds, and marine mammals, surprisingly many aspects of the species ecology and population dynamics remain insufficiently understood to this day (Staudinger et al. 2020). Catchability issues in fishery-independent surveys and the absence fishery-dependent data impose large margins of uncertainty on even basic abundance metrics, while environmental drivers of contemporary and future sand lance productivity are only now becoming clearer (Suca et al. 2021). Like other forage fish species, especially their congeners on the northeast Atlantic shelf, northern sand lance populations, too, are comprised of very few year classes that exhibit large interannual fluctuations generated mostly during the early larval and juvenile stages (van Deurs et al. 2009). Recruitment pulses often appear localized to small regions or individual sand banks along their distributional range. These patterns may partially arise from variable offspring transport and are further amplified by the specific habitat requirements of the species, which relies on coarse grain sediment with minimal organic content to allow its partially buried, partially pelagic occurrence. Rather than one large population, northern sand lance might therefore be better understood as a collection of temporally variable abundance hotspots on disparate, insular offshore sand banks. The relationship between these localized populations, their inter-reliance, and genetic connectivity are currently unknown, and this represents a major obstacle to effective management and conservation strategies of the species.

Here we addressed this knowledge gap by investigating the spatial origin and fate of sandlance larvae settling and produced on Stellwagen Bank, which is a national marine sanctuary in the southern

Gulf of Maine and an exemplary local abundance hotspot of this species. We used a Lagrangian hydrodynamic modeling approach informed by recent findings on sandlance spawning, pelagic duration and

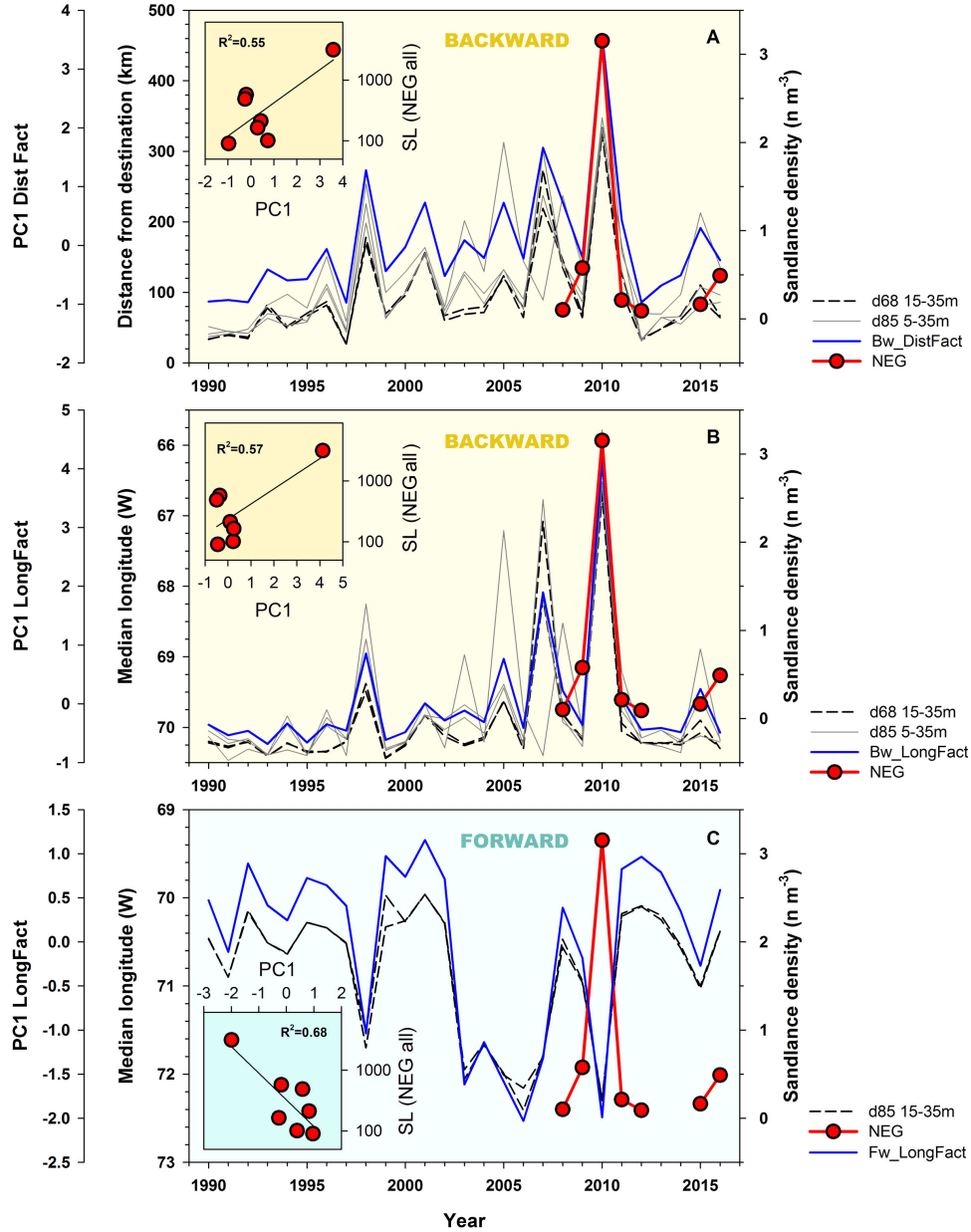


Fig.11: Time-series of drifter-derived proxies of interannual variability in backward and forward simulations (grey, black lines) and their relationship to independent measurements of larval sandlance occurrence (yolksac, post-yolksac) at the Northeast Gateway (NEG) facility near Stellwagen Bank (red circles, lines; 2008-2016). (A) Median distance of drifters from the mean arrival destination on Stellwagen Bank for different drift depths and tracking periods (but across all release days), (B) Median longitude of drifters from different depths and backward tracking periods (but across all release days), (C) mean longitude of drifters from different depths and forward tracking periods (but across all release days). The blue lines in each plot show the time-series of first principal component scores, calculated from all individual drifter time-series. Inserts show correlations between PC scores and the Feb-Apr sandlance larval abundance (ind m⁻³) recorded by NEG.

settlement times, which produced insights not only to the questions (i) where sandlance on Stellwagen Bank originate from and (ii) where sandlance produced on the bank are transported to, but also (iii) how interannual variability in transport patterns may affect abundance. We found that Lagrangian particles, and by inference sandlance larvae settling on Stellwagen Bank, are predominantly produced in coastal areas of the Gulf of Maine immediately to the north of Stellwagen Bank. This pattern is consistent with the direction of the prevailing Gulf of Maine Coastal Current, which is also critical for the supply of the key copepod, *Calanus finmarchicus*, to Stellwagen Bank and beyond (Runge et al. 2015). The strength of the coastal current is highly variable, and our analyses showed that in some years it has the potential to transport sandlance offspring from much further away

from other spawning grounds to the north, while a smaller fraction might comprise self-recruits from the bank itself. Perhaps unsurprisingly given the dominant north-to-south direction of the Gulf of Maine Coastal Current, sandlance on Stellwagen Bank do not appear to originate from any shelf areas to the southeast of Stellwagen Bank, for example Georges Bank.

Our forward drift simulations also offered clear insights about the spatial fate of Stellwagen produced sandlance offspring. Consistent with the direction of the Gulf of Maine Coastal Current, we found that most sandlance larvae (50%) are likely advected south into coastal waters of the mid-Atlantic Bight, thus contributing to sandlance settlement pulses in suitable habitats there. About another quarter of offspring are advected southeast and thus perhaps onto productive shelf habitats like Nantucket Shoals or

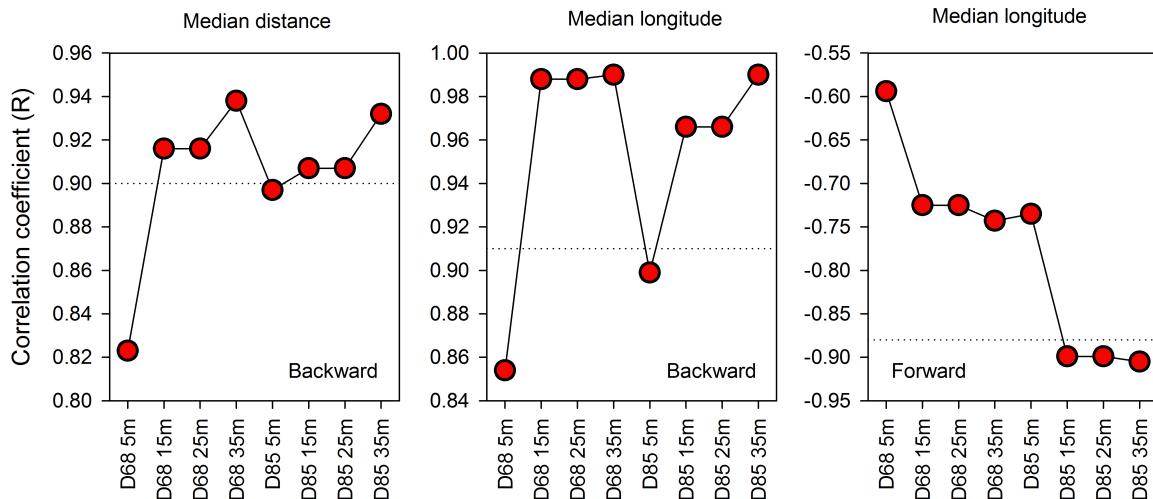


Fig.11: Correlation coefficients (R) between individual drifter proxy time-series for specific depths and drift periods and larval sandlance abundance (NEG data). Points above (bw) or below (fw) the dotted lines denote significant correlations ($P < 0.01$).

areas in the northern Gulf of Maine. At least in one year (2010), such extreme long-distance transport coincided with extremely high larval sandlance abundance on Stellwagen Bank. We also showed that a small but consistent percentage of drifters originated from within Massachusetts Bay, thereby indicating the potential for self-recruitment. Together, our findings suggest that sandlance on Stellwagen Bank likely depend on large pulses of offspring arriving

Georges Bank (Suca et al. 2022). Interestingly, a considerable fraction (23%) is actually retained in Massachusetts Bay, thereby implying a large, but interannually variable potential for self-recruitment back to Stellwagen Bank. We conclude that the Stellwagen Bank sandlance population could be partially self-replenishing, while exporting most produced offspring to other shelf habitats to the south and southeast of the Bank.

Both origin and fate patterns of sand lance larvae exhibited considerable interannual variability, suggesting that variable transport alone could account for the high spatio-temporal variability of sand lance settlers on Stellwagen Bank and in other areas. For example, the contribution of drifters from further away northern Gulf of Maine areas (R4) fluctuated

interannually between 0-69% and showed an inverse relationship with contributions from the nearer coastal Gulf of Maine area (R1, 16-90%, $R = -0.77$, $P < 0.001$). In short, for sand lance settlers on Stellwagen Bank we can discern years with predominantly short distance vs. long distance offspring origin, which at least for the years with corresponding observations of

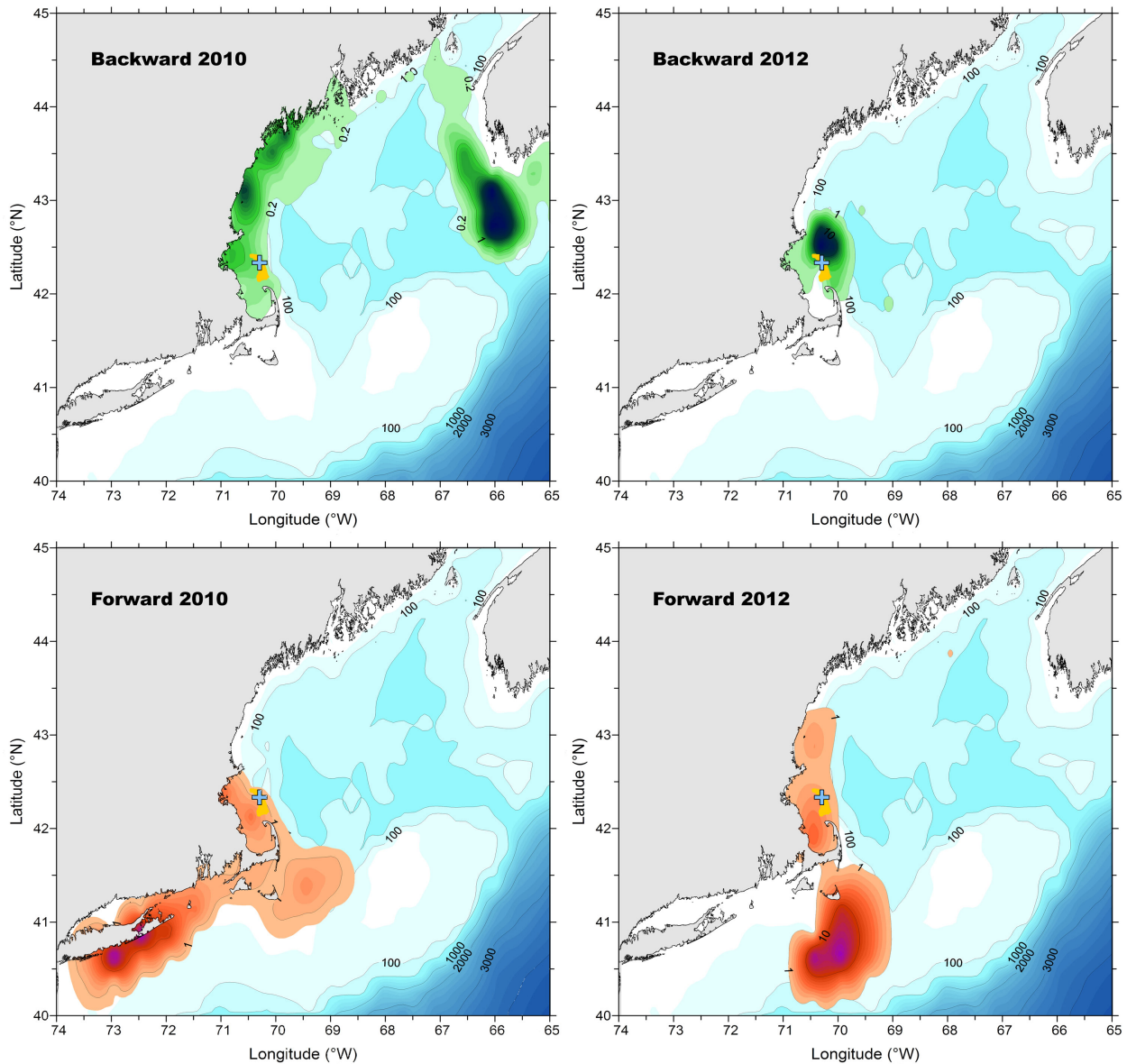


Fig.12: Distributions of backward and forward-tracked drifters in 2010 and 2012 (all releases, 2 drift periods, 15-35m depths), two extreme years in terms of drift and larval sand lance abundance at the NEG facility (2010: $\sim 3 \text{ m}^{-3}$; 2012: $\sim 0.3 \text{ m}^{-3}$). In 2010, the majority of drifters arrive from the further away in the northern Gulf of Maine, perhaps contributing to the record number of sand lance larvae recorded that year. Conversely, backward drifters barely moved in 2012, possibly indicating weak influx from northern sand lance spawning grounds. Contour labels denote percent of particles.

larval abundance appears to distinguish low from high settlement strength, respectively. It is therefore possible that the productive sand lance spawning grounds in the northern Gulf of Maine play an important role in the population dynamics of sand lance on Stellwagen Bank. Similarly, the drifter contributions from Stellwagen Bank to mid-Atlantic Bight waters (R3, forward runs) showed near total fluctuations between 1-96% interannually, with a similar negative correlation to drifters arriving in outer shelf areas (R6, 2-60%, $R = -0.46$, $P = 0.016$). This suggested a general distinction between years when sand lance offspring are predominantly advected either to mid-Atlantic Bight or outer shelf areas. Subsequent principal component and cluster analyses refined these patterns by suggesting 3 and 4 distinct drift scenarios for backward and forward projections, respectively, including years characterized by high self-recruitment or spawning ground retention of larval sand lance. However, at least for the seven years of available larval sand lance data, higher levels of self-recruitment to the bank did not result in larger than average sand lance abundance on the bank.

The rapid development of offshore wind energy production in the Mid-Atlantic Bight entails potential concerns for affected habitats and the biota that depend on them. Offshore sand banks are among the most suitable sites for wind turbine installations, however, those sandy habitats are also vital for sand lance. Our forward drift simulations showed that a considerable (12%), albeit interannually variable (0-47%) fraction of Stellwagen produced sand lance are regularly exported to one of the largest BOEM wind lease areas south of Nantucket Shoals at the time of settlement. At least during construction, this may negatively affect settlement success and therefore the productivity of the local sand lance population in this area. How operational offshore wind turbines may impact sand lance habitat suitability has yet to be explored.

While hydrodynamic drift simulations generally yield insightful patterns, their accuracy is linked to the assumption that planktonic fish larvae ‘behave’ like

passively drifting particles. Over the years, many studies have shown examples to the contrary by documenting how diel or ontogenetic vertical migrations or directed swimming of even small larval stages modulate their transport, mostly to reduce advection and increase retention of offspring on their spawning grounds (e.g., Taylor & Hellberg 2003, Paris & Cowen 2004). Our approach used depth-keeping drift simulations to reflect observed homogeneous vertical distributions of sand lance larvae in the water column, at least up to the size at settlement (Potter & Lough 1987). Whether sand lance larvae exhibit diel vertical migrations is unknown but could impact larval transport, since drift distance generally decreased with drift depth in our simulations. However, we strongly believe that the overall conclusions of our study are robust and unaffected by the inherent uncertainties of our modeling approach.

In summary, our modeling study suggested that the Stellwagen Bank sand lance population is highly connected to – and reliant on – populations to the north in the coastal and northern Gulf of Maine, while at the same time benefitting from retentive circulation features that allow for partial self-recruitment back to the bank. We further revealed that this productive spawning ground likely exports most of its offspring to suitable habitats in areas to the south and southeast of the bank, thereby potentially contributing to large, but interannually variable settlement pulses on Nantucket Shoals, Georges Bank, and mid-Atlantic Bight waters, including areas currently under development for offshore wind energy production. Moving forward, it is critical to maintain and expand ichthyoplankton monitoring efforts to better establish the relationship between sand lance abundance and drift patterns and better understand population connectivity using modern molecular approaches.

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Figure 1