

Sensitivity of sand lance to shifting prey and hydrography indicates forthcoming change to the northeast US shelf forage fish complex

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Northern sand lance (*Ammodytes dubius*) and Atlantic herring (*Clupea harengus*) represent the dominant lipid-rich forage fish species throughout the Northeast US shelf and are critical prey for numerous top predators. However, unlike Atlantic herring, there is little research on sand lance or information about drivers of their abundance. We use intra-annual measurements of sand lance diet, growth, and condition to explain annual variability in sand lance abundance on the Northeast US Shelf. Our observations indicate that northern sand lance feed, grow, and accumulate lipids in the late winter through summer, predominantly consuming the copepod *Calanus finmarchicus*. Sand lance then cease feeding, utilize lipids, and begin gonad development in the fall. We show that the abundance of *C. finmarchicus* influences sand lance parental condition and recruitment. Atlantic herring can mute this effect through intra-guild predation. Hydrography further impacts sand lance abundance as increases in warm slope water decrease overwinter survival of reproductive adults. The predicted changes to these drivers indicate that sand lance will no longer be able to fill the role of lipid-rich forage during times of low Atlantic herring abundance—changing the Northeast US shelf forage fish complex by the end of the century.

Keywords: *Calanus*, changepoint, climate change, forage fish, recruitment, trophic ecology

Introduction

Small pelagic fishes, or forage fishes, are critical components of both neritic and oceanic food webs. They represent an important link between planktonic production and a diversity of larger predators, including numerous endangered species. However, forage fish abundance and recruitment are often sensitive to temperature and secondary production, leading to large fluctuations in abundance, making this trophic link highly variable in space and time (Chavez *et al.*, 2003; Clausen *et al.*, 2018; Thompson *et al.*, 2019; Sydeman *et al.*, 2020). Furthermore, numerous studies show that fluctuations in forage fish abundance can lead to marked effects on predator condition and breeding success (Barrett *et al.*, 2012; Kadin *et al.*, 2012; Engelhard *et al.*, 2013; Church *et al.*, 2019). Owing to the sensitivity of forage fish to climate regimes, and, in turn, the breeding and condition of their predators, there is great interest in understanding climate–forage fish relationships and using them to project forage fish abundances into the future (Fréon *et al.*, 2005; Alder *et al.*, 2008; Lindegren *et al.*, 2016; Checkley *et al.*, 2017).

Sand lances (family Ammodytidae) are one such group of quintessential forage fishes throughout temperate and sub-polar shelf ecosystems of the Northern Hemisphere. This is particularly true for northern sand lance (*Ammodytes dubius*) in the Northeast US Shelf ecosystem (Figure 1a). Of 72 regional predators consuming sand lance, populations of humpback whales (*Megaptera novaeangliae*) and numerous seabirds are particularly reliant on this resource (Staudinger *et al.*, 2020). However, the lack of a directed sand lance fishery and, therefore, regular assessments, has hampered our understanding of basic sand lance ecology that is needed to predict the species' characteristically large inter-annual fluctuations in abundance (Figure 1b and c; Nelson and Ross, 1991; Richardson *et al.*, 2014; Staudinger *et al.*, 2020).

Evidence indicates other sand lances of the genus *Ammodytes* are particularly sensitive to prey availability and temperature regimes at multiple life stages throughout their range (Winslade, 1974; Tomiyama and Yanagibashi, 2004; van Deurs *et al.*, 2011, 2014, 2015; Régnier *et al.*, 2017, 2018; Wright *et al.*, 2017; Clausen *et al.*, 2018; Murray *et al.*, 2019; Von Biela *et al.*, 2019). Larval prey availability and adult exposure to elevated overwintering temperatures are hypothesized to drive variability in catch of the species *A. marinus* (Régnier *et al.*, 2017; Wright *et al.*, 2017). Furthermore, significant reductions in size-at-age were observed for *Ammodytes personatus* off Alaska during the warm and zooplankton-poor “blob” event, and reductions in catch of *Ammodytes japonicus* were correlated with decreasing zooplankton abundance of Japan (Von Biela *et al.*, 2019; Nishikawa *et al.*, 2020). These relationships indicate that recruitment and condition of sand lances are linked to prey availability, although existing studies have not explicitly connected adult prey availability and condition to recruitment. Despite numerous studies on congeners, little to no information currently exists on the drivers of northern sand lance abundance throughout its range.

In addition to most forage fish species individually exhibiting population fluctuations, they often oscillate out-of-phase with one another, leading to one species replacing the role of the other when environmental conditions change (Bakun and Broad, 2003; Möllmann *et al.*, 2008; Alheit *et al.*, 2014). The Northeast US Shelf forage fish complex has historically exhibited an oscillation between dominance of northern sand lance and Atlantic herring (*Clupea harengus*; Sherman *et al.*, 1981; Richardson *et al.*, 2014).

The causes of this oscillation remain unknown, especially regarding sand lance. Intra-guild predation, zooplankton prey availability, and habitat suitability may be contributing factors (Sherman *et al.*, 1981; Fogarty *et al.*, 1991; Richardson *et al.*, 2014). Intra-guild predation, when a species not only competes with (e.g. for food) but also consumes another species, can lead to an overwhelming competitive advantage in food webs, driving oscillatory patterns of competitor abundance (Polis *et al.*, 1989). Zooplankton regimes in the region also fluctuate on seasonal to decadal scales, resulting in temporally inconsistent prey availability for small pelagic fishes (Kane, 2007; Morse *et al.*, 2017; Perretti *et al.*, 2017).

Beyond natural variability in zooplankton regimes, the Northeast US shelf has experienced dramatic warming of both surface and bottom waters throughout the late 20th and early 21st century. Warming has been linked to changes in heat flux from atmospheric forcing and changes in Gulf Stream dynamics that alter advective processes in the region (Greene and Pershing, 2007; Pershing *et al.*, 2015; Kavanaugh *et al.*, 2017; Gangopadhyay *et al.*, 2019; Chen *et al.*, 2020). This recent warming has negatively impacted temperate fish species occupying the shelf, driving both implied direct mortality and range shifts of numerous fishes (Pershing *et al.*, 2015; Henderson *et al.*, 2017; Kleisner *et al.*, 2017).

Here, we combine stomach content, lipid content, and growth analyses of sand lance to better understand their ecology and phenology, and then use these results to inform a mechanistic approach to understanding the drivers of sand lance population fluctuations across the Northeast US shelf. We hypothesize that northern sand lance abundance on the Northeast US shelf is controlled by a combination of adult prey availability, intra-guild predation on larvae, and winter hydrographic conditions. We then predict sand lance abundance throughout the 21st century on the Northeast US shelf using projections of the primary drivers of sand lance abundance that we identified: *Calanus finmarchicus* abundance, Atlantic herring abundance, and warm slope water proportions.

Material and methods

Seasonal feeding and reproductive ecology of sand lance

Sand lance collections

Adult sand lance (age 1+) were collected from Stellwagen Bank with a 1.0 × 0.5 m, small-mesh (0.63 cm) beam trawl (Figure 1a). Stellwagen Bank, a sandy bank in Massachusetts Bay within the Gulf of Maine, is a top predator hotspot and representative of typical sand lance habitat throughout the Northeast US shelf (Hazen *et al.*, 2009; Richardson *et al.*, 2014; Silva *et al.*, 2020). Thus, our insights from Stellwagen Bank collections were used to better understand the ecology and predict environmental drivers of this species across their range.

Collections occurred monthly in 2019 (except January, July, and December) and opportunistically on cruises from 2016 through 2018 (Supplementary Table S1). Trawl duration was 10 min and distances ranged from 0.5 to 1 km. Collected sand lance in 2019 were flash frozen in foil in liquid nitrogen upon retrieval. Sand lance collected prior to 2019 were placed in a –20°C freezer and then stored in ice for transportation. All specimens were collected in accordance with the guidelines and approval of Woods Hole Oceanographic Institution's Institutional Animal Care and Use Committee (approval #23453).

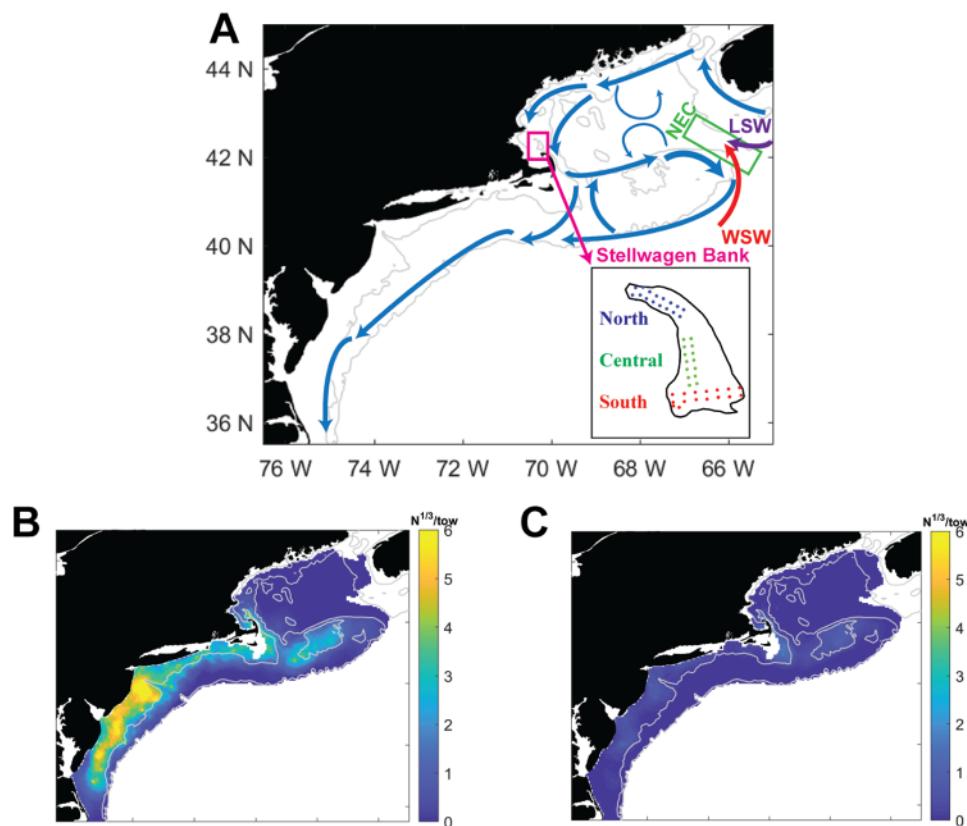


Figure 1. Hydrography of the Northeast US Shelf and sand lance abundance. (a) Overview of the Northeast US Shelf with blue arrows indicating prevailing surface currents of the region, red arrow indicating path of warm slope water entering the Northeast Channel (green box), and the purple arrow indicating flow of LSW entering the Northeast Channel. Inset displaying the 40 m isobath of Stellwagen Bank, and the three regions of the bank (north, central, and south) including trawl locations referenced throughout the text. (b) Mean interpolated cube-root catch of sand lance over the Northeast US shelf as part of the NEFSC spring bottom trawl survey from 1978 to 1982. (c) Same as (b), except for the period of 1991–1995.

Stellwagen Bank can be split into three “regions”, south, central, and north (Figure 1a). Collections aimed to cover both the northern and southern regions of Stellwagen Bank where sand lance density is historically high, except for February when collections solely occurred in the southern and central regions of the bank due to limited ship time.

Zooplankton collections

Simultaneous conductivity-temperature-depth (CTD) and zooplankton tows were performed at each station where sand lance were captured. A SeaBird 19plus was lowered to 1 m above the bottom, coupled with a 30-cm diameter, 150- μ m mesh zooplankton net that sampled vertically on the upcast. This resulted in a cast from 3 m above the bottom to the surface, allowing for the calculation of water volume sampled. Zooplankton samples were immediately preserved in 95% ethanol upon retrieval.

Prior to processing, zooplankton samples were reduced to ~500 organisms with a modified box splitter. Zooplankton were sorted, counted, and identified to the lowest possible taxa at the Polish Plankton Sorting and Identification Centre and in the lab at Woods Hole Oceanographic Institution following Kane (2007).

Sand lance dissections

Adult sand lance were thawed to near room temperature in the laboratory for dissections. Standard length, fork length, whole weight, eviscerated weight, liver weight, stomach content weight, and gonad weight were recorded for each fish. Stomach contents were preserved in 95% ethanol after weighing. Heads of each fish were removed for otolith extraction and ageing by making a vertical cut immediately posterior to the opercula. The remaining portion of each fish (both stomach contents and head removed) was weighed and freeze dried for subsequent lipid extraction (see lipid extractions). Gonadosomatic index was calculated as the ratio between gonad weight and somatic weight.

Stomach content identification

Stomach contents of each fish that contained prey were examined to identify the specific zooplankton prey of sand lance and how consumption varies seasonally. Details of stomach content identification methods can be found in the [Supplementary information](#). Feeding incidence was defined as the proportion of stomachs inspected on each sampling date that contained prey items. An overall proportion of prey taxa by number and biomass was also calculated for each month of collection.

For pre-2019 samples, feeding incidence was assessed as the presence or absence of prey in the stomach under a microscope after dissection. Samples collected before 2019 were not flash frozen, and thus prey items were often degraded and thus may have biased results towards items that were more robust to digestion. We therefore did not calculate diet by biomass or number for pre-2019 collected sand lance.

Age and growth

A subset of fish from March, April, June, August, and November of 2019 were haphazardly selected for otolith-based ageing. Full details of ageing analysis can be found in the [Supplementary information](#). For abundant age classes, a von-Bertalanffy growth curve was fit to standard length (SL) by month (m) for each age class with sufficient number of individuals ($n > 30$) following the equation:

$$SL_m = SL_{\infty}(1 - e^{-k(m-m_0)}),$$

where k is the growth coefficient. Von-Bertalanffy growth curves were fit primarily to estimate the parameter SL_{∞} in order to determine which month standard length of individuals in an age class approached their annual maximum when somatic growth ceases. The equation thus follows the standard von-Bertalanffy growth equation except for using month as the time scale. Von-Bertalanffy curve fitting was performed using the `vB` function in the `FSA` package in R ([Derek and Wheeler, 2020](#)).

Lipid extraction and content analysis

Lipid extractions were performed for opportunistically collected sand lance prior to 2019 following the exact modified Folch method presented in [Post and Parkinson, 2001](#)). For 2019 collected sand lance, up to 25 fish per month of collection were processed for lipid extraction following a further modified method to minimize lipid oxidation. Details of this method are described in the [Supplementary material](#).

Per cent lipid values were then fit with a cyclic penalized cubic regression spline with day of collection as the predictor and region of collection on Stellwagen Bank (north, central, and south) as a factor via the `mgcv` package in R to determine the effect of day of year (DOY) on sand lance lipid content while accounting for regional variability ([Wood, 2017](#)). Region of collection within Stellwagen Bank (north, central, and south) was included due to observed differences in zooplankton and hydrography by region (Supplementary Figures S1 and S2). The model was written as follows:

$$\text{Per cent Lipid} = \beta_0 + s(\text{DOY}) + \text{Region}.$$

Where per cent lipid represents per cent lipid of whole sand lance, $s(\text{DOY})$ represents the fitted smoothing function for DOY, and region is fit as a categorical predictor. We report change in deviance explained (ΔDE) from the full model for each variable as an estimate of their relative importance.

Eighteen individuals were selected for duplicates, encompassing two individuals from each month of collection, to determine intra-fish variability in lipid content estimates. Duplicates indicated $<3\%$ intra-fish difference.

Shelf-wide estimates and drivers of sand lance abundance

Northeast US shelf sand lance abundance

Estimations of Northeast US shelf sand lance abundance came from the spring Northeast Fisheries Science Center (NEFSC) bottom trawl survey, spanning from 1968 to present. During each survey, 300–400 stations are sampled in a random stratified design, ranging from the Western Scotian Shelf to Cape Hatteras ([Figure 1b and c](#)). At each station, all sand lance are weighed and individuals are measured, with sub-sampling occurring when catches were large. Further details of the survey and sampling gear are found within [Politis et al. \(2014\)](#). The log area weighted stratified mean abundance in catch of each survey was calculated to estimate inter-annual variability in sand lance abundance ([Richardson et al., 2014](#)). The spring survey typically occurs in March and April, well within the feeding window of sand lance (see Results section), and has largely been consistent in timing, gear, and vessel—allowing the survey to provide a consistent index of northern sand lance abundance ([Politis et al. 2014](#)). This is opposed to the fall survey, which occurs at a transitional window in sand lance life history from feeding to preparing for fall reproduction, leading to possible conflation of abundance trends with inter-annual variability in behaviour (see Results section; [Murray et al. 2019](#)). The survey is also not explicitly designed to sample sand lance habitat and thus there are rarely multiple trawls within a stratum that represent equivalent sand lance habitat quality. We therefore focused on the log area weighted stratified mean abundance for the entire survey region, assuming the broad spatial range and large sample size mitigated the likelihood of spurious or small-scale behavior-related biases in abundances estimates. Sand lance abundance exhibits major fluctuations, ranging orders of magnitude, allowing the survey to represent sand lance abundance trends despite being imprecise.

In 2009, the survey changed vessels and gear, notably switching the net liner from 1.27 to 2.54 cm, leading to a noticeable decrease in sand lance catchability during the calibration study ([Miller et al., 2010; Richardson et al. 2014](#)). The time series of sand lance abundance thus ends in 2008 to avoid conflation of gear selectivity with abundance trends. We do not have age estimates for each year of the survey, and thus all age classes of sand lance are included in the log area-weighted stratified mean abundance. The most comprehensive ageing of sand lance from the NEFSC spring trawl survey suggests >90% of individuals collected in the survey are age-2 or age-3 ([Nelson and Ross, 1991](#)). Due to this finding, we assumed that abundance of age-2 and age-3 individuals were responsible for the changes in overall sand lance abundance in the survey. While the survey provides a robust estimate of the abundance of age-2 and age-3 sand lance throughout the Northeast US Shelf, overall abundance of sand lance is likely underestimated due to low selectivity of age-1 individuals ([Nelson and Ross, 1991](#)).

Historical EcoMon zooplankton data

Calanus abundance anomalies were calculated following [Kane \(2007\)](#) and [Perretti et al., \(2017\)](#) from collections of the NEFSC EcoMon sampling programme spanning 1977 to present. Briefly, a mean abundance by date is computed by area for *C. finmarchicus*. This is accomplished by binning all samples for a given species to bi-monthly collection dates based on median cruise date, taking the mean abundance, then fitting a spline interpolation

between mean bi-monthly abundance to give expected abundance on any given day of the year. Data were spatially constrained to the Gulf of Maine ecological production unit (Lucey and Fogarty, 2013). All years (1977–2008) were used because annual sampling effort included at least 35% spatial coverage of the Gulf of Maine ecological production unit (Morse *et al.*, 2017). The Gulf of Maine was chosen as opposed to the full Northeast US shelf as this region serves as the source of *C. finmarchicus* for much of the Northeast US shelf. The Gulf of Maine has deep basins that provide habitat for diapausing *Calanus* and the general southward flow of the region advects *Calanus* to the other regions of the Northeast US shelf (Kane, 2005, 2007; Runge *et al.*, 2015; Ji *et al.*, 2017).

Zooplankton data were constrained to cruises centring around bi-monthly dates from January to July to correspond with our observed feeding patterns for sand lance. Winter-summer *Calanus* abundance anomalies were then lagged to approximate an average Gulf of Maine *Calanus* abundance at 3–4 years prior to the spring bottom trawl survey estimate of sand lance abundance. A 3- to 4-year lag was selected as this represents the years in which the parents of fish collected in the survey (age-2s and -3s) would be feeding on *Calanus* prior to spawning in the fall. The specific selection of this time lag was based upon our observations of sand lance feeding, growth, and lipid content being tightly coupled with their consumption of *Calanus*. The time lag used therefore represents a test of the parental condition hypothesis, whereby higher abundances of *Calanus* available to parents would result in either more or higher-quality eggs, and thus higher abundances of sand lance in the survey 3 and 4 years later when they become catchable in the survey as age-2 and age-3 individuals. We specifically focus on this time lag because of the results of our sampling of seasonal feeding and reproductive ecology of sand lance as opposed to testing multiple time lags to isolate the lag with the highest correlation coefficient.

Atlantic herring index

Atlantic herring are intra-guild predators of northern sand lance, meaning that adults of each species are competitors for prey but Atlantic herring also consume the larvae and juveniles of northern sand lance (Suca *et al.*, 2018). Hence, Atlantic herring may exert a strong top-down influence on northern sand lance abundance by consuming the early life stages of sand lance (Polis *et al.*, 1989).

Similar to sand lance, Atlantic herring catchability in the NEFSC bottom trawl survey changed during the time series. Catchability of Atlantic herring substantially increased in the survey in the mid-1980s, possibly due to a change in trawl doors (which has been consistently noted; Miller *et al.*, 2010; Northeast Fisheries Science Center, 2018). Richardson *et al.* (2014) thus developed a composite index of Atlantic herring abundance, from 1968 through 2010, combining numerous state and federal fisheries independent surveys of Atlantic herring using a non-linear least-square optimization procedure. This composite index represents an estimation of the overall Atlantic herring abundance on the Northeast US Shelf. It is worth noting that Atlantic mackerel likely also exert a top-down effect on sand lance via intra-guild predation but their transitory use of the region and tendency to avoid gear used in standardized surveys precluded effective use of Atlantic mackerel abundance as a predictor (Mbaye *et al.*, 2020).

The composite Atlantic herring index was lagged to represent Atlantic herring abundance 2–3 years prior to the bottom trawl survey estimate of sand lance. This lag indicates the abundance of

Atlantic herring on the Northeast US shelf when survey-collected sand lance were larvae and early juveniles and thus susceptible to predation by Atlantic herring. We specifically focus on this time lag because of the results of previous research (Polis *et al.*, 1989; Suca *et al.*, 2018) as opposed to testing multiple time lags to isolate the lag with the highest correlation coefficient.

Slope water proportions

We then further explored hydrographic drivers of variability in sand lance abundance on the Northeast US Shelf in conjunction with trophic (prey availability and predation) effects. We tested the hypothesis that increasing warm slope water proportion would have a direct detrimental effect on adult northern sand lance abundance on the Northeast US shelf. Slope waters enter the Gulf of Maine through the Northeast Channel (Figure 1) and are composed largely of two sources, colder and fresher Arctic-influenced Labrador slope water (LSW) and warmer, saltier Slope Sea and Gulf Stream-influenced “warm” slope waters (WSW) of which the relative proportions of each source vary inter-annually (Mountain, 2012). These slope waters then mix and circulate around the Gulf of Maine, becoming a substantial portion of the shelf water of the Northeast US shelf (Mountain, 2012), the primary habitat of northern sand lance on the Northeast US shelf. These warm slope waters have been shown to have deleterious effects to wintertime populations of *Calanus*, the primary prey of sand lance (Record *et al.*, 2019). This deleterious effect of warm slope water on *Calanus* does not appear to carry through the spring, with local production decoupling warm slope water proportions and integrated annual *Calanus* abundance (Record *et al.*, 2019). Thus the mechanism behind warm slope water’s effect on sand lance abundance could manifest in two ways: indirectly through decreasing prey availability to spawners—thus lowering parental condition and spawning output—or through a direct negative effect on over-winter survival of adult sand lance via elevated bottom temperatures and lower winter prey availability. Our observations suggest that the latter scenario is more likely as biological sampling showed that reproductive sand lance have their lowest energy reserves in winter, making mature individuals (age-2+) susceptible to mortality from increased metabolism and lack of prey availability from elevated warm slope water proportions. Thus, we hypothesized that increasing warm slope water proportions would have a deleterious effect at a 0-year lag, given the slope water conditions that either favour age-2+ survival or mortality would occur in the winter prior to the spring trawl survey (i.e. in the same year as the survey). We also note that warm slope water may influence the catchability of sand lance in the survey due to its effect on bottom temperature. However, schooling behaviour of congeners have been shown to be primarily linked to feeding and food availability (van Deurs *et al.* 2011), thus we believe this effect would be small relative the changes in true abundance given the survey overlaps with peak feeding for sand lance (see Results section). Additionally, hindcast bottom temperatures from a hydrographic model on the Northeast US shelf indicate that mean bottom temperatures during the survey do not correlate with sand lance abundance in the survey (Chen *et al.* 2011, see Supplementary information and Figures S13–S15).

Slope water proportions were extracted from the *ecodata* package in R (Fratantoni, 2019; Mountain, 2012). Slope water proportions were derived from bathythermograph data, CTD data, and water samples collected from Niskin bottles from Northeast

Fisheries Science Center surveys from the 1977 to present between 150 and 200 m in the Northeast Channel (42.2–42.6° N, 66–66.8°W, Figure 1). Data collected from 150 to 200 m are assumed to be waters sourced from three sources: Scotian Shelf water (2°C, 32 salinity), LSW (6°C, 34.7 salinity), and warm slope water from off the Northeast US Shelf (10°C, 35 salinity). The relative proportion of each source was calculated via a 3-point mixing algorithm following Mountain, (2012). These temperature and salinity end-member values of each water mass are assumed to be constant over time, though local heat fluxes and mixing likely alter these values. Despite these fluctuations, warm slope water proportion provides a reliable estimate of warmer waters entering the Gulf of Maine and provides an estimate of winter thermal conditions for sand lance over this period. While buoy data exist in the Northeast Channel from 2004 to 2018 (NERACOOS buoy N), annual estimates of slope water proportions were selected in order to extend the time series back to 1977, thus matching the length of available zooplankton data.

Sand lance abundance regression

Log sand lance abundance from NEFSC bottom trawl surveys were related to *Calanus* abundance, the composite Atlantic herring index, and warm slope water proportion using a multiple linear regression written as follows:

$$\log (SL_t) = \beta_0 + \beta_1 * \text{Calanus}_{t-3,4} + \beta_2 * \text{Atlantic herring}_{t-2,3} + \beta_3 * \text{WSW}_t,$$

where SL represents stratified mean spring trawl survey abundance of sand lance in year t , *Calanus* represents winter-summer *Calanus* abundance anomaly at a 3–4 year lag, *Atlantic herring* represents the Atlantic herring index at a 2- to 3-year lag, and WSW represents warm slope water proportion in year t . Predictor variables were not strongly correlated ($r < 0.5$). We inspected model residuals for temporal autocorrelation (see Supplementary Figure S11) and used generalized additive models to confirm linear relationships and use of linear regression. We also considered a model including a population dynamics term either in the form of a transformed response variable $\log(SL_t/SL_{t-3})$ and an autoregressive term (SL_{t-3}) to allow the model to represent the current abundance relative to the parent population.

We performed a leave-one-out cross-validation to test the predictive capability of our regression within our dataset. This method iteratively trains the model using $n-1$ observations and uses the model fitted to the training set to predict the left-out observation. The R^2 and root mean square error for the predicted vs. observed values were calculated to determine model predictive performance.

Change in slope water proportions with time

A changepoint beta regression was fit to the time series of warm slope water to determine if a changepoint occurred in warm slope water proportion after 2000, concurrent with other changes in regional hydrography near this time (Andres, 2016; McCarthy et al., 2018; Gangopadhyay et al., 2019; Friedland et al., 2020b). Beta distributions were used because warm slope water values are represented as proportions. The stepwise beta regression was written as follows:

$$\log \left(\frac{\text{WSW}}{(1 - \text{WSW})} \right) = \beta_0 + \beta_1 t + \beta_2 (t - \tau) I_{\tau}(t)$$

$$I_{\tau}(t) = 0 \text{ if } t \leq \tau$$

where WSW represents the proportion of warm slope water, t is time in years, and τ is the changepoint. The parameters β_0 , β_1 , β_2 , τ , and θ (the dispersion parameter) were fit via maximum log likelihood using the fmincon function in Matlab. Significance ($\alpha = 0.05$) was determined through parametric bootstrap (1000 simulations). The p -value was defined as the proportion of times the simulated difference in maximized log likelihood of the changepoint beta regression and the beta regression without a changepoint exceeded the difference between these regressions using our observed values, as described in the following equation:

$$p = \frac{\sum_{i=1}^{1000} X(i)}{1000}$$

$$X(i) = 1 \text{ if } (LL(i)_{CP_{sim}} - LL(i)_{\beta_{sim}}) > (LL_{CP_{obs}} - LL_{\beta_{obs}})$$

where LL represents the maximum log likelihood, CP represents the changepoint regression, and β represents the standard beta regression.

Projections of sand lance abundance

Log sand lance abundance was projected from 2020 to 2100 using multiple combinations of time-series predictor variables to represent several future scenarios. Eight scenarios were simulated, encompassed by four groupings (“current trajectory”, “optimistic”, “average herring”, “reduced warm slope water”; Table 1; Supplementary Figure S3). Owing to observed declines in Atlantic herring biomass and recruitment (NEFSC, 2018), predicted declines in *Calanus* abundance (Grieve et al., 2017), and our observation of increases in warm slope water proportion, we termed the predictors following this pattern as the “current trajectory” scenario. Long-term projections indicate suitable *Calanus* habitat throughout the Northeast US Shelf will decrease in the coming century, although there is regional variability in observations and projections of this trend (Reygondeau and Beaugrand, 2011; Grieve et al., 2017; Ji et al., 2017). Atlantic herring recruitment has been below average since 2013, with six of the eight worst recorded recruitment years occurring since 2013 (NEFSC, 2020). Herring spawning stock biomass is also below average and declining, despite stable to decreasing fishing mortality rates (NEFSC, 2020). Such declines, which are not easily attributable to fishing mortality, led to speculation that aspects of the rapidly changing Northeast US shelf ecosystem may be the cause of poor herring recruitment and result in continued declines in Atlantic herring (though egg predation by haddock may also be a cause; Richardson et al., 2011). While it is impossible to know if Atlantic herring populations will eventually recover, it will likely at least take multiple years for the stock to recover from the historically poor recruitment levels seen since 2013.

Table 1. Description of scenarios used in predictions of sand lance abundance through the end of the 21st century.

Scenario	Description	Calanus	Atlantic herring	Warm slope water
Current trajectory	<ul style="list-style-type: none"> • Declining <i>Calanus</i> • Low Atlantic herring • Increasing warm slope water 	Normal random variable with linearly decreasing mean (32% decrease in RCP 4.5, 50% decrease in 8.5). Constant variance with time corresponding to variance of used time series (1977–2008)	Normal random variable with mean and variance corresponding to previous decline (1973–1988)	Beta random variable with mean and dispersion parameter following fitted changepoint regression
Optimistic	<ul style="list-style-type: none"> • Declining <i>Calanus</i> • Average Atlantic herring • Pre-2009 warm slope water 	Normal random variable with linearly decreasing mean (32% decrease in RCP 4.5, 50% decrease in 8.5). Constant variance with time corresponding to variance of used time series (1977–2008)	Normal random variable where $\mu = 0, \sigma = 1$	Beta random variable with mean and dispersion parameter corresponding to pre-2009 time series (1977–2008)
Average Herring	<ul style="list-style-type: none"> • Declining <i>Calanus</i> • Average Atlantic herring • Increasing warm slope water 	Normal random variable with linearly decreasing mean (32% decrease in RCP 4.5, 50% decrease in 8.5). Constant variance with time corresponding to variance of used time series (1977–2008)	Normal random variable where $\mu = 0, \sigma = 1$	Beta random variable with mean and dispersion parameter following fitted changepoint regression
Reduced Warm Slope Water	<ul style="list-style-type: none"> • Declining <i>Calanus</i> • Low Atlantic herring • Pre-2009 warm slope water 	Normal random variable with linearly decreasing mean (32% decrease in RCP 4.5, 50% decrease in 8.5). Constant variance with time corresponding to variance of used time series (1977–2008)	Normal random variable with mean and variance corresponding to previous decline (1973–1988)	Beta random variable with mean and dispersion parameter corresponding to pre-2009 time series (1977–2008)

Importantly, in each of the four groupings of projection scenarios, *Calanus* abundance was represented by a normal random variable with a linearly decreasing abundance of *Calanus* from the mean of the existing time series to 68% of its mean to represent the projected decrease in *Calanus* under Representative Concentration Pathway (RCP) 4.5 or to 50% of its mean, representing the projected decrease in *Calanus* abundance under RCP 8.5 [variance was assumed to remain constant in time; rates of decline follow [Grieve et al. \(2017\)](#)]. Each predictor was simulated independently owing to the lack of strong correlation among predictor variables. Sand lance abundance was then estimated using our fitted multiple linear regression and these simulated regressors. This was then repeated 1000 times to get a mean simulated log sand lance abundance, along with interquartile range, for each year from 2020 to 2100.

Projection metrics

For each scenario, we calculated the per cent decline in sand lance abundance from the beginning of the simulation through the following equation:

$$\text{Percent Decline} = \left(\frac{\overline{SL}_x - \overline{SL}_{2020}}{\overline{SL}_{2020}} \right) * 100,$$

where \overline{SL}_x represents the average projected sand lance abundance in year x .

We also calculated the proportion of years in each simulation of each scenario that had below average sand lance abundance and proportion of years that had below-average abundances of both sand lance and Atlantic herring in the same year. This latter metric is perhaps most informative as this represents an ecosystem with below average abundance of both dominant lipid-rich forage fishes on the Northeast US shelf.

Results

Sand lance feeding, lipid accumulation, and growth

Feeding incidence (the percentage of stomachs with prey) varied monthly for sand lance collected in 2019, with highest values occurring in the winter and spring (52–84%; $n = 212$; [Figure 2a](#)). Feeding incidence decreased to zero in August and remained at zero through October, followed by a reappearance of prey in the guts in November—consistent with patterns of monthly feeding incidence from previous years ([Figure 2a; Supplementary Figure S4](#)). During months of feeding (other than November), the copepod *C. finmarchicus* (*Calanus* hereafter) dominated stomach contents, ranging from 30.4% of diet by biomass in February to 78% of the diet by biomass in April ([Figure 2b](#)).

Whole-body lipid content of sand lance varied significantly by DOY and by region within Stellwagen Bank, peaking throughout the bank in August ($n = 197$; deviance explained = 35.2%; [Figure 2c; Supplementary Figure S5](#)). Notably, lipid content decreased rapidly between October and November in connection with spawning during this time window as evidenced by the sharp increase and subsequent decrease in gonadosomatic index (DOY Δ DE = 32.5%, [Figure 2e](#)). Additionally, lipid content varied spatially within the bank, with highest lipid content values occurring on the northern portion of the bank in each month (region Δ DE = 3.0%).

Intra-annual size-at-age for both age-2 ($n = 54$) and age-3 ($n = 45$) fish approached their annual maximum in the summer, concurrent with the cessation of feeding and lipid accumulation ([Figure 2d](#)). Age-2 fish reached their annual maximum length in June (mean SL = 168.3 mm, median SL = 171.0 mm, $L_\infty = 170.8$ mm) and age-3 fish reached their annual maximum length by August (mean SL = 184.3 mm, median SL = 182.5 mm, $L_\infty = 184.0$ mm).

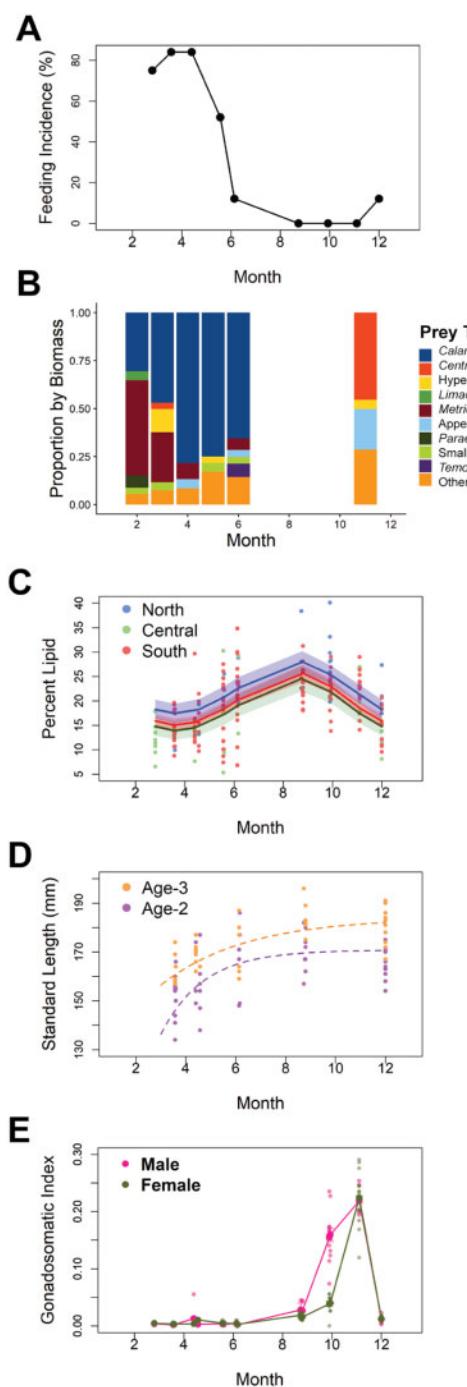


Figure 2. Ecology and phenology of adult sand lance collected on Stellwagen Bank in 2019. (a) Feeding incidence by DOY for fish collected in 2019 ($n = 202$). (b) Sand lance diet by proportion of biomass for each month ($n = 70$ fish containing prey, $n = 15$ prey). (c) Per cent lipid of whole fish for sand lance separated by region and DOY on Stellwagen Bank ($n = 197$). Solid lines represent fitted values from a generalized additive model including month and region with shading representing 95% confidence intervals (deviance explained = 38.5%). (d) Standard length by DOY for age-2 ($n = 54$) and age-3 ($n = 45$) and dashed lines represent fit von-Bertalanffy curves for each age class. (e) Gonadosomatic index (GSI) by DOYs for males ($n = 105$) and females ($n = 107$) along with mean \pm SEM GSI for each sex by monthly collection. Horizontal axis ticks in each plot represent first of the respective month.

Sand lance abundance regression

Sand lance abundance and lagged winter-summer *Calanus* abundance anomalies were significantly correlated throughout the time series ($R^2 = 0.21$, $p = 0.015$), and particularly well in the 1980s and 1990s ($R^2 = 0.46$, $p < 0.01$; Figure 3a). However, the relationship decouples later in the time series, concurrent with an increase in Atlantic herring in the region (Figure 3a). Lagged Atlantic herring index and sand lance abundance were negatively correlated ($R^2 = 0.28$, $p < 0.01$) throughout the time series, with Atlantic herring in low abundance during the 1980s “boom” of sand lance and in high abundance when the sand lance time series began to decouple from lagged *Calanus* abundances in the late 1990s and early 2000s (Figure 3a).

Warm slope water proportion was negatively correlated to log sand lance abundance ($R^2 = 0.52$, $p < 0.01$; Figure 3b). A cross-correlation analysis indicated that only a 0-year lag between warm slope water proportion and sand lance abundance was significant (adjusted for autocorrelation; Supplementary Figure S6). Incorporating 3–4 year lagged *Calanus* abundance, 2–3 year lagged Atlantic herring index, and unlagged warm slope water proportion in a multiple linear regression explains a majority of the inter-annual variance in the northern sand lance spring trawl survey, indicating these three mechanisms are likely the dominant drivers of northern sand lance throughout the Northeast US shelf ($R^2 = 0.76$; Figure 3; Table 2). Inclusion of population dynamics terms either as a transformed response variable or as an autoregressive term did not improve model fit and thus were not included.

Leave-one-out cross-validation indicated high predictive performance within the dataset ($R^2 = 0.68$, RMSE = 1.07) and showed no notable outliers between the predicted and observed values (Supplementary Figure S7).

Warm slope water changepoint

The fitted changepoint beta regression indicated a significant changepoint in 2009 ($p < 0.001$), with the rate of warm slope water proportions increasing with time rising by over tenfold after 2009 ($\beta_1 = 0.01$; $\beta_2 = 0.26$; Figure 3b; Table 3). Slope water proportions showed no significant mean change with time prior to this observed change point (i.e. from 1977 to 2008; Figure 3b; Table 3).

Projections of sand lance abundance

Rates of sand lance decline were similar for each RCP projection in the four scenarios (current trajectory, reduced warm slope water, average Atlantic herring, and optimistic). The average decline in sand lance abundance was 45.6 and 74.6% by 2100 for RCP 4.5 and 8.5, respectively (Figure 4). The minimum rate of decline for RCP 4.5 was in the “reduced warm slope water” scenario, with a per cent decline of 38.5%, and in the “optimistic” scenario for RCP 8.5 with a decline of 71.4%. The maximum per cent decline for RCP 4.5 was in the “average Atlantic herring” scenario at 52.0% and in the “current trajectory” scenario at 76.9% for RCP 8.5.

Scenarios varied drastically in both the proportion of years with below-average sand lance abundance and proportion of years with below-average sand lance and Atlantic herring abundance (Figure 4, Table 4). The “reduced warm slope water” scenario had the lowest average proportion of years with below-average sand lance abundance, with 34 and 47% of years having below-average sand lance abundance for RCP 4.5 and 8.5. The “average Atlantic herring” scenario resulted in the highest

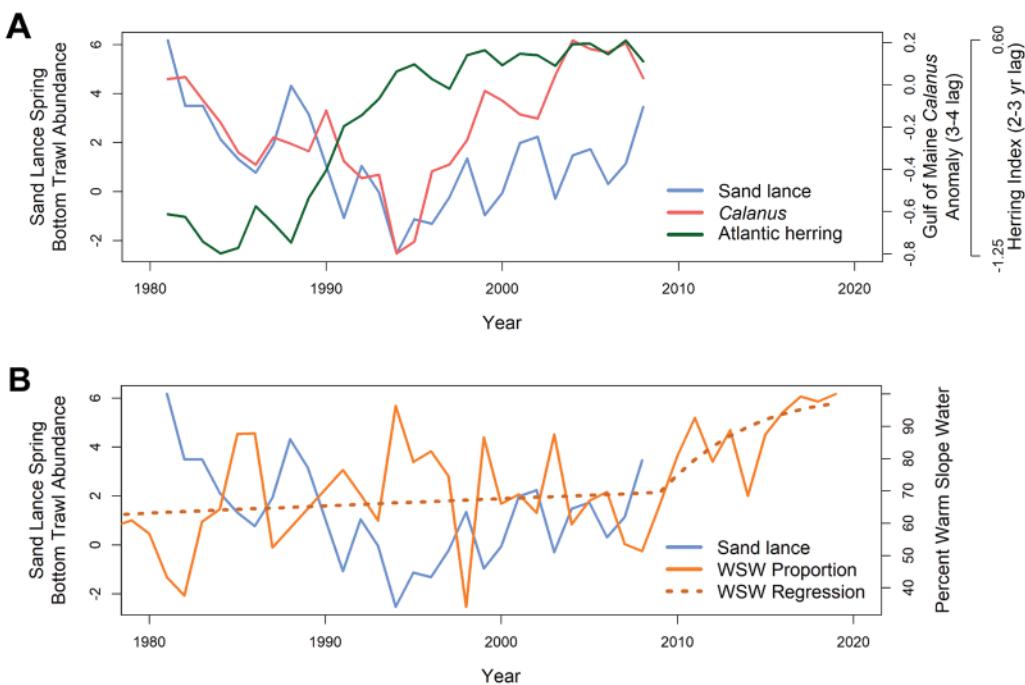


Figure 3. Time series of the environmental drivers of sand lance abundance. (a) NEFSC spring bottom trawl sand lance abundance (log scale; blue), 3- to 4-year lagged winter-summer *Calanus* abundance anomaly in the Gulf of Maine (red), and 2- to 3-year lagged Atlantic herring index (green). (b) NEFSC spring bottom trawl sand lance abundance (log scale; blue) and warm slope water proportion entering the Northeast Channel (gold). Dashed line indicates fitted changepoint beta regression (changepoint = 2009, $p < 0.001$).

Table 2. Fitted parameter estimates for the multiple linear regression of sand lance abundance anomaly ($n = 25$ years).

Regressor	Slope estimate	p-value
Gulf of Maine <i>Calanus</i> Anomaly	2.48	0.009
Atlantic herring index	-1.27	<0.001
Warm slope water proportion	-5.89	<0.001

Table 3. Fitted parameter estimates for the changepoint beta regression of warm slope water proportion with time ($n = 39$ years).

Parameter	Estimate
β_0	-18.8
β_1	0.01
β_2	0.2
τ	2009

Model p-value <0.001.

number of years with below-average sand lance abundance, averaging 97 and 98% of years for RCP 4.5 and 8.5, respectively.

When Atlantic herring are included in the calculation of below-average years of abundance, the “current trajectory” scenario represents the maximum amount of below-average years, while the “optimistic scenario” results in the lowest number of these years (Figure 5). An average of 20% of years in RCP 4.5 and 26% of years in RCP 8.5 of the “optimistic” scenario had both negative sand lance and negative Atlantic herring anomalies. However, an average of 95% of years in RCP 4.5 and 97% of years in RCP 8.5 of the “current trajectory” scenario had both negative sand lance and negative Atlantic herring anomalies indicating

nearly all years having below-average sand lance and Atlantic herring in the future.

Discussion

Our work indicates that the future of adult northern sand lance in the Northeast US shelf ecosystem is tenuous, owing to the observed and predicted changes in hydrography and prey availability across the region. The sensitivity of sand lance to these changing factors is linked to their capital breeding strategy, whereby the species has a defined feeding and growth period, and individual lipid reserves undergo a twofold change within one breeding season to allocate energy for reproduction. Furthermore, if ongoing declines in Atlantic herring recruitment and biomass persist for decades to come (NEFSC, 2018), our predictions suggest the Northeast US shelf will be in a state of low adult abundances of its two most dominant lipid-rich forage fishes for much of the 21st century.

Projections of long-term declines in sand lance abundance indicate marked change in the forage fish complex of one of the world’s most economically valuable shelf ecosystems (Hoagland *et al.*, 2005) as concurrent negative anomalies of northern sand lance and Atlantic herring have only occurred in 6 years from 1968 to 2008. Such a shift may open niche space for higher abundances of warm, temperate small pelagic species such as Atlantic butterfish (*Peprius triacanthus*) and Atlantic menhaden (*Brevoortia tyrannus*), diversifying the forage fish complex (Friedland *et al.*, 2020a). This, combined with and linked to changes to *Calanus*’ distribution, will likely alter the food web of the Northeast US shelf and represent a northward contraction of the region’s “lipidscape” (Record *et al.*, 2018). The timing and implications of a shift in forage fish community warrants

continued, targeted estimates of forage fish abundances and concurrent measurements of the condition of top predator taxa throughout the Northeast US shelf. Tropicalization and shifts in forage community are likely to be detrimental to lipid-rich piscivores, such as humpback whales and bluefin tuna (*Thunnus*

thynnus), while simultaneously ushering in piscivores commonly seen at lower latitudes such as black sea bass (*Centropristes striata*) and summer flounder (*Paralichthys dentatus*) (Henderson et al., 2017; Kleisner et al., 2017). This potential shift in community composition, from forage fish to top predators, would change much of the food web and fisheries of this region.

Declines in *Ammodytes* condition and catch have been documented in the Pacific, suggesting this key type of forage fish may be in global jeopardy due to shifting climate (Von Biela et al., 2019; Nishikawa et al., 2020). Suggestions of sensitivity of European congeners to temperature further this concern (Lindegren et al., 2018). Many protected species on the Northeast US shelf, such as humpback whales and seabirds, consistently target sand lance as their primary forage and may be in jeopardy from declining sand lance regardless of Atlantic herring's abundance (Staudinger et al., 2020). Populations of seabirds in the Northeast Atlantic suffer high chick mortality when local sand eel (*A. marinus*) abundances decline (Harris and Wanless, 1991; Rindorf et al., 2000). Recent reports indicate that declines in local sand lance populations even decrease adult survival of Arctic terns (*Sterna paradisaea*) in Iceland (Petersen et al., 2020). We may thus expect similar levels of repercussions to sand lance-reliant top predators on the Northeast US shelf within this century with recent data suggesting that declines in productivity of the endangered roseate tern (*Sterna dougallii*) in the Northeast US due to decreasing sand lance are already underway (J. Walsh, pers. comm.).

The lines of concurrent evidence of a capital breeding strategy for northern sand lance are consistent with observations of congeners around both the Pacific and Northeast Atlantic (Robards et al., 1999; Wright et al., 2017; Von Biela et al., 2019). However, one major difference is timing of the dormancy period. *Ammodytes* in the Northeast Atlantic are largely considered to be dormant in the winter, along with *A. dubius* populations in Greenland (van Deurs et al., 2011; Danielsen et al., 2016; Wright et al., 2017). Our observations of late summer dormancy indicate aestivation—a pattern observed in the warmer water *A. japonicus*—as opposed to hibernation observed in Northeast Atlantic congeners (Kuzuhara et al., 2019). Robards et al. (1999) also suggest that *A. personatus* in the Pacific undergo winter dormancy, though they did not analyse stomach contents and their observations of seasonal lipid accumulation match the pattern we observe. It is therefore possible *A. personatus* also undergoes aestivation and feeds in the winter, contrary to current theory.

Our work further supports the importance of prey availability, namely lipid-rich zooplankton, to the life history of *Ammodytes*.

Figure 4. Projections of sand lance abundance under various scenarios. Predicted sand lance abundance (log) under “reduced warm slope water” scenario (dotted lines), “optimistic” scenario (thin solid lines), “current trajectory” scenario (thick solid lines), and “average Atlantic herring” scenario (dashed lines). Colour represents the projected decline of *Calanus* under RCP 4.5 (blue) or the projected decline of *Calanus* under RCP 8.5 (red). Shaded regions represent bounds for the upper (75%) and lower (25%) quantiles. Black dashed line represents mean sand lance abundance from 1968 to 2008.

Table 4. Per cent sand lance decline under four scenarios and each RCP projection of *Calanus* decline and proportion of years from 2020 to 2100 with negative sand lance anomalies and both negative sand lance anomalies and negative Atlantic herring anomalies.

Scenario	RCP 4.5 Decline (%)	Proportion of Negative Sand Lance Anomalies	Proportion of Negative Sand lance and Herring Anomalies	RCP 8.5 Decline (%)	Proportion of Negative Sand Lance Anomalies	Proportion of Negative Sand lance and Herring Anomalies
Current trajectory	−51.6	0.96	0.95	−76.9	0.98	0.97
Reduced warm slope water	−38.5	0.34	0.33	−74.8	0.47	0.46
Average Atlantic herring	−52.0	0.97	0.47	−75.1	0.98	0.48
Optimistic	−40.4	0.64	0.20	−71.4	0.72	0.26

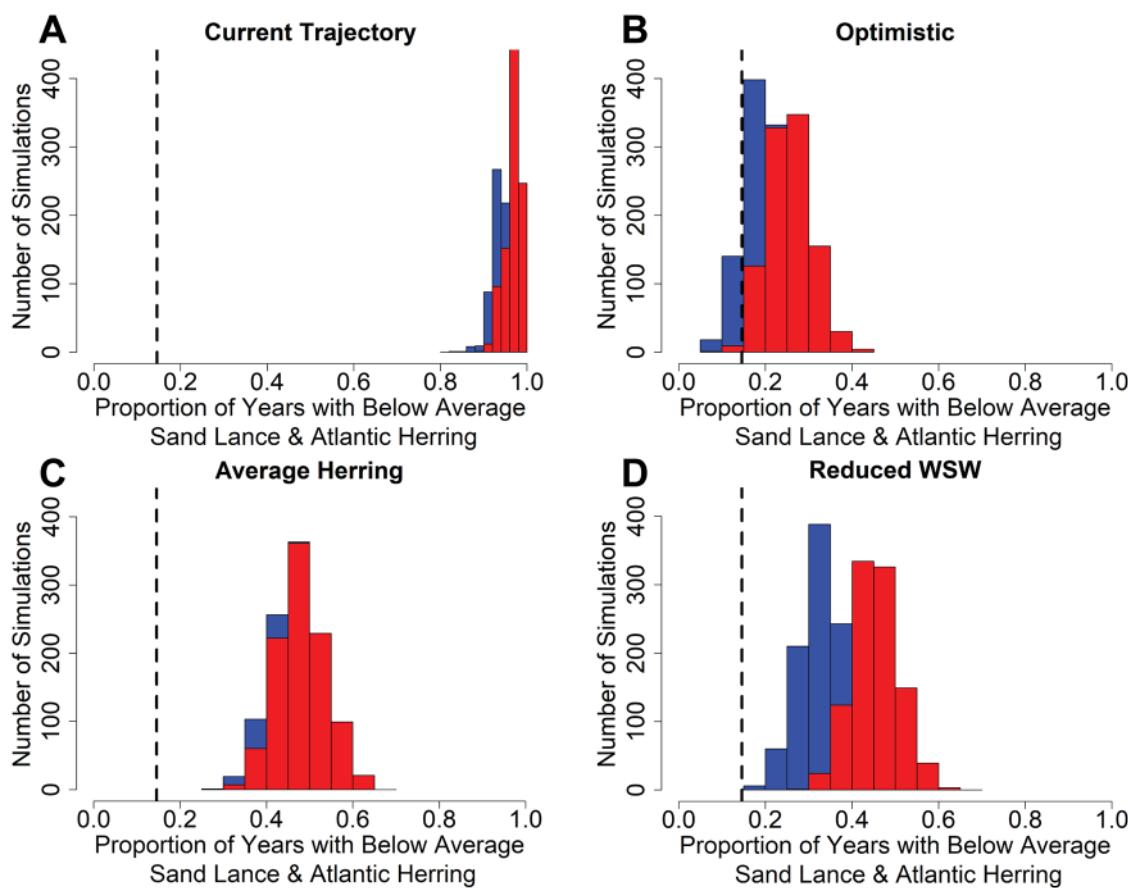


Figure 5. Histograms representing proportion of years between 2020 and 2100 that each simulation had negative sand lance abundance anomalies and negative Atlantic herring anomalies for (a) the “current trajectory” scenario, (b) “optimistic” scenario, (c) “average herring” scenario, and (d) “reduced warm slope water” scenario. Colour represents RCP 4.5 (blue) and 8.5 (red) rates of *Calanus* decline. Thick dashed line represents proportion of years from 1968 to 2008 with both negative sand lance and Atlantic herring anomalies.

Studies throughout the Pacific have indicated sand lance growth is linked to food availability (Kuzuhara *et al.*, 2019; Von Biela *et al.*, 2019) and, further, that recruitment follows changes in zooplankton abundance on decadal scales (Nishikawa *et al.*, 2020). We observed that the seasonal feeding pattern of *A. dubius* was consistent with times of historically high *Calanus* abundance in the Northeast US Shelf ecosystem where peaks in abundance typically occur from April through June, after which *Calanus* enter diapause in the late summer (Kane, 2007; Supplementary Figures S8 and S9). This suggests the timing of sand lance feeding and subsequent reproduction may be linked to the phenology of *Calanus*. Additionally, the overlap of lipid accumulation and somatic growth with feeding, and the subsequent cessation of feeding, growth, and lipid accumulation during gonad development, indicate that northern sand lance condition and reproduction may be sensitive to bottom-up forcing of prey availability. Indeed, even spatial differences in *Calanus* availability appear to drive differences in lipid accumulation in northern sand lance (Figure 2c). Elevated lipid content on the northern portion of Stellwagen bank corresponds with localized increases in seasonal *Calanus* abundance brought by the western Gulf of Maine Coastal Current that intercepts this region (Supplementary Figures S1 and S2). Such a link between sand lance condition and *Calanus* abundance indicates that projected decreases in *Calanus* on the Northeast US

shelf will likely lead to a decrease in availability of high-quality prey for sand lance, and thus may decrease parental condition and spawning output (Grieve *et al.*, 2017).

While consistent with other studies in indicating the importance of *Calanus* to *Ammodytes*, the mechanism suggested from our data differs from larval match-mismatch hypotheses proposed to drive *Ammodytes* recruitment in the Northeast Atlantic (Régnier *et al.*, 2017) in that our data suggest *Calanus* abundance is linked to adult condition. While the 3-year lag of sand lance behind *Calanus* abundance may represent both an effect of *Calanus* on parental condition of age-2 fish and larval feeding for age-3 fish, the strongest time-lag correlations between sand lance abundance and *Calanus* anomalies occur at a 3- to 4-year lag as opposed to a 2- to 3-year lag, indicating the effect of parental condition is, at the very least, more pronounced than an effect of *Calanus* abundance on larval feeding (Supplementary Figure S10). However, it is important to note that this does not exclude the possibility that *Calanus* abundance plays a role in the early life history of sand lance and further research is needed regarding this question. An effect of parental condition on offspring abundance and/or survival has been both theorized and observed in multiple systems (Green, 2008; Hare, 2014; Hixon *et al.*, 2014, Saenz-Agudelo *et al.*, 2015), including for haddock on Georges Bank (Friedland *et al.*, 2008), and has even been incorporated into population

models for herring in Iceland (Oskarsson and Taggart, 2010). It is noteworthy that this effect of *Calanus* on sand lance recruitment appears to be largely independent of the sand lance spawning stock as population dynamics terms did not improve model fit. This may be due to parental condition overwhelming an effect of abundance and/or the per capita benefit of increased *Calanus* on parental condition being reduced in years and areas with high densities of sand lance. Both scenarios could lead to present populations of sand lance being largely independent of the size of their parents' population, as observed here. We are also presently unsure if increased *Calanus* abundance only plays a role in lipid accumulation, or a role in both lipid accumulation and growth. Future studies are needed to assess changes in length at age and lipid accumulation for sand lance with changing zooplankton abundance and regimes.

In addition to the capital breeding strategy driving recruitment through parental condition, the large intra-annual change in lipid content for sand lance makes them susceptible to overwinter conditions. Individuals are at their lowest energy reserves after spawning and are thus sensitive to increased temperatures and shortages of prey. Such sensitivity to winter conditions has been shown in *Ammodytes marinus*, indicating this scenario is not unique to northern sand lance (van Deurs et al., 2011). This sensitivity becomes problematic for sand lance populations with recent shifts in hydrography, particularly the changepoint in warm slope water proportion entering the Northeast Channel (Figure 3). This changepoint in hydrography will likely lead to northern sand lance enduring winter regimes with consistently high temperatures and low prey (Record et al., 2019).

The changepoint in warm slope water proportion is noteworthy for the Northeast US shelf ecosystem. Other changepoints have been identified in advective processes in the Northeast US shelf region since 2000, notably a near doubling in the number of warm core rings shed from the Gulf Stream, a westward shift of the Gulf Stream destabilization point, and a rapid shift to an earlier spring transition date throughout the Northeast US shelf after 2008 (Friedland et al., 2015; Andres, 2016; Gangopadhyay et al., 2019). The cause of this changepoint is still undetermined, but hypotheses include a slowing of the Gulf Stream and warming of Slope Sea waters on the coastal side of the Gulf Stream (Andres, 2016; McCarthy et al., 2018; Gangopadhyay et al., 2019). While a change in survey gear precludes consistent estimates of northern sand lance abundance after 2008, this rapid increase in warm slope water proportion following 2009 is likely to be detrimental to sand lance populations throughout the Northeast US shelf via increasing overwinter mortality of this species.

Our work also indicates that sand lance populations may be heavily regulated by intra-guild predation from Atlantic herring. This mechanism has been proposed before (Fogarty et al., 1991; Polis et al., 1989), and subsequent diet studies indicate larval sand lance are important prey for Atlantic herring and Atlantic mackerel (though the overall abundance of the former is much greater; Suca et al., 2018). These dynamics largely allow either Atlantic herring or northern sand lance to be the dominant forage fish throughout the Northeast US shelf in any given year. However, when other drivers prevent a species from rebounding when their intra-guild predator is low, concurrent low abundances of both species can occur. While this has not happened often in the case of the Northeast US shelf, our projections indicate this situation of low northern sand lance and Atlantic herring abundances may

happen frequently in the coming decades, and thus the ecosystem level implications of this change require monitoring.

Perhaps the most alarming result of our projections is that the "current trajectory" scenario—based on current trends and knowledge regarding the future of *Calanus*, herring, and warm slope water—indicates the worst outcome for the future forage fish complex on the Northeast US shelf. These projections were also robust to the rate of decline of *Calanus*, with both RCP 4.5 and 8.5 rates of decline resulting in greater than 90% of years between 2020 and 2100 having below-average abundance of both sand lance and Atlantic herring. Given concurrent changepoints in warming rates and advection throughout the region (Andres, 2016; Gangopadhyay et al., 2019; Friedland et al., 2020b), and *Calanus'* sensitivity to changing temperature and salinity (Grieve et al., 2017), the least certain aspect of these projections is the future of Atlantic herring. However, even if Atlantic herring are to return to oscillating around their historic mean, it would take a drastic decline in warm slope water proportions to allow sand lance and Atlantic herring abundances on the Northeast US shelf to return to similar levels observed prior to 2008. Even this "optimistic" scenario results in a higher proportion of years with negative anomalies of sand lance and Atlantic herring than observed from 1968 to 2008, showing the projections of change to the forage fish complex on the Northeast US shelf—most notably a clear decline in sand lance—are consistent among projections. However, the true disappearance of northern sand lance may take longer than the NEFSC trawl survey indicates. The deleterious effect of warm slope water occurs for post-spawning adults (age-2+) and thus it is likely age-1 sand lance will be able to withstand this change in hydrography. These younger fish may not be sufficient for many predators though, as the ongoing decline in roseate tern productivity indicates (J. Walsh, pers. comm.). Furthermore, if warm slope water affects catchability of sand lance in the NEFSC spring survey, even if the effect is small relative to changes in abundance, this would lead to sand lance disappearing at a slower rate than many of our projections suggest. Such an effect would result in a future more closely following either the "reduced warm slope water" or "optimistic" scenario. Our analysis of seasonal bottom temperatures suggests a catchability effect is unlikely, but sand lance focused surveys could better resolve this question and refine projections of their abundance. While the future of the forage fish on the Northeast US shelf will certainly have a great degree of spatiotemporal complexity not incorporated or assessed in our projections, large-scale changes to sand lance abundance are likely to have ecosystem-wide effects and need to be considered in management and protection of top predator populations throughout the region.

Supplementary data

Supplementary material is available at the ICESJMS online version of the manuscript.

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Data availability

Data are available to those with inquiries upon request to the corresponding author. Code is also available to those with inquiries upon request to the corresponding author and at https://github.com/jsuca18/NES_Sand_Lance.

Author contributions

JJS, DNW, TLS, HB, LK, and JKL designed research; JJS, TLS, ARR, SG, EC, TG, MAT, and PH performed the research; JJS, DER, ARS, and JKL contributed to data analysis and interpretation; and JJS wrote the paper.

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