Bull Mar Sci. 94(3):737–751. 2018
https://doi.org/10.5343/bms.2017.1141

research paper

Spatial surface temperature correlates of American lobster (*Homarus americanus*) settlement in the Gulf of Maine and southern New England shelf

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11th International Conference and Workshop on Lobster Biology & Management · Portland, Maine
4–9 June, 2017

Guest Editors:
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Section Editor:
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Date Submitted: 14 September, 2017.
Date Accepted: 10 January, 2018.
Available Online: 12 April, 2018.

ABSTRACT.—American lobster, *Homarus americanus* H. Milne-Edwards, 1837, populations along the east coast of North America are geographically distributed over some of the steepest latitudinal ocean temperature gradients in the world. A disconnect between spawner biomass and postlarval settlement, i.e., young-of-year (YoY) recruitment, to the sea bed at the end of the larval season highlights the role of external environmental factors. To understand the spatial dimension of sea surface temperature correlates of settlement, we compared over two decades of inter-annual variation in lobster settlement at three oceanographically contrasting areas: the Bay of Fundy, coastal Gulf of Maine, and southern New England, with satellite-derived sea surface temperature anomaly (SSTa) patterns over the coastal regions and shelf waters. Correlations were performed between the settlement time series and monthly SSTa maps at time lags relevant to larval hatching, development, transport, and settlement. Settlement was significantly and positively correlated with SSTa in southern New England, showing associations with upstream areas over Georges Bank and southern Nova Scotia during months when larvae are expected in the water column (July–August). The Gulf of Maine site was correlated with SSTa in the immediate vicinity of the settlement site, and only in the month of settlement sampling. Settlement at the Bay of Fundy site was not correlated to SSTa patterns. The observed associations are consistent with larval advection by residual oceanic flow structure in the region, and are further supported by studies on lobster larval supply and genetic connectivity reported in the literature.

Benthic recruitment in marine species with complex life histories is fundamentally a biophysical problem concerning egg production, fertilization, hatching, pelagic transport, and settlement. Improved understanding of the population dynamics of such organisms lies in the identification of the key physical and biological drivers of recruitment, and the scales at which they operate (Roughgarden et al. 1988, Eckman 1996, Pineda et al. 2009). Satellite data provide consistent and systematic spatial and temporal views of sea surface conditions. Widely used in many aspects of fisheries science, satellite data have been applied to questions concerning biological recruitment of commercially important benthic and pelagic species (Fielder et al. 1984, Roughgarden et al. 1988, Santos 2000, Platt et al. 2007, Koeller 2011), and thus can improve our understanding of oceanographic patterns and processes potentially linked to larval dispersal and survival (e.g., Caputi et al. 2001, Sponaugle et al. 2005, Fox et al. 2012, Lara et al. 2016).

With a collective value in excess of one billion US dollars (FAO 2016), the American lobster, *Homarus americanus* H. Milne-Edwards, 1837, fishing industry constitutes the most valuable fishery in the US and Canada, and the largest lobster fishery in the world (Wahle et al. 2012, DFO 2017, NOAA 2017). With relatively low postsettlement mortality compared to other decapod crustaceans (Wahle and Incze 1997, Palma et al. 1999), fishery recruitment is strongly dependent on the successful recruitment of young-of-year (YoY) lobsters when they first settle to the seabed (Fogarty and Idoine 1986, Steneck and Wilson 2001, Wahle et al. 2009a), and is therefore driven by pelagic larval supply (Incze and Wahle 1991, Incze et al. 2000, 2010). The American Lobster Settlement Index (ALSI), an international collaborative of marine resource agencies and academic institutions, monitors recently settled YoY lobsters at more than 100 sites along the coast of New England and Atlantic Canada. The ALSI has significantly improved our understanding of the dynamics of early benthic phase lobster populations (Incze and Wahle 1991, Wahle and Incze 1997, Xue et al. 2008, Incze et al. 2010, Burdett-Coutts et al. 2014) and their relationship to landings (Steneck and Wilson 2001, Wahle et al. 2009a). Despite local (0.1–10 km) patchiness in settlement (Wahle and Incze 1997, Sigurdsson et al. 2016), ALSI time series reveal large-scale (>100 km) spatial coherence, suggesting the considerable areas over which environmental drivers may operate in common (Pershing et al. 2012).

As is true for most ectothermic species, temperature is a key environmental variable to the development, growth, and survival of the American lobster. The species' geographic range in the northwest Atlantic Ocean spans one of the steepest latitudinal sea surface temperature gradients in the world, from shelf waters off Cape Hatteras in the south to Newfoundland in the north (Fogarty 1995). Shelf waters are influenced by the warm Gulf Stream from the south and the cold Labrador Current from the north (Townsend et al. 2006). Larvae hatch in early to mid-summer and spend 3–12 wks in the water column before metamorphosing into a postlarva and settling in shelter-providing habitats like cobble beds (Factor 1995, Ennis 1995). While variability in broodstock abundance fails to explain interannual variability in lobster settlement (DFO 2013, ASMFC 2015, Carloni et al. 2018), environmental effects of temperature and winds (Wahle and Incze 1997, Pershing et al. 2012, Wahle et al. 2013a), predators (Wahle et al. 2013b, Boudreau et al. 2015), and larval food supply (Carloni et al. 2018) have been implicated to play a role in spatial and temporal patterns of lobster larval supply and benthic recruitment. As seasonally-warming bottom temperatures stimulate egg development and trigger hatching (Aiken and Waddy 1986, Cobb and Wahle 1994, Ennis 1995), regions differ in the timing of the seasonal larval cycle. Larval development and growth is faster in warmer water (Templeman 1936, Hudon and Fradette 1988, Ennis 1995, Annis et al. 2013), although larvae from stocks at the northern extreme of the species range are reported to develop faster at cold temperatures than those from the south, suggesting evidence of cold adaption (Quinn et al. 2013). In turn, with the possible exception of the most northern populations, postlarval settlement tends to concentrate above the thermocline, typically above the 12 °C isotherm over most of the species range (Harding et al. 1987, Boudreau et al. 1992, Ennis 1995, Annis et al. 2013, Wahle et al. 2013a).

During the summer months of seasonal vertical stratification when lobster larvae are expected in the water column, oceanographic processes, such as coastal circulation, upwelling, and tidal mixing, are evident in satellite SST images. The southern New England shelf and southwestern Gulf of Maine become strongly thermally stratified, while the eastern Gulf of Maine and Bay of Fundy remain mixed by extreme tides (Fig. 1). A main feature of residual circulation of the Gulf of Maine is the Gulf of Maine Coastal Current, a cold near-surface, pressure-driven, cyclonic flow from east to west, with an eastern and western component that vary in strength on an interannual basis (Fig. 1; Fox et al. 2005, Pettigrew et al. 2005). The boundary between eastern and western components often acts as a barrier for alongshore biological connectivity (Leurssen et al. 2005, Xue et al. 2008). Flanking the southeast corner of the Gulf of Maine is Georges Bank, a highly productive and thermally distinct shallow (<100 m) submerged terminal glacial moraine. Georges Bank is characterized by clockwise residual circulation and strong tidal mixing (Fig. 1; Fox et al. 2005, Townsend et al. 2006). Water from the Gulf of Maine and Georges Bank moves into the southern New England shelf region either through, or over, the Great South Channel (Fig. 1).

In the present study, we compared interannual variability in lobster settlement at three oceanographically contrasting regions (Fig. 1) with concurrent monthly satellite-measured sea surface temperature anomalies (SSTa): the Bay of Fundy, New Brunswick, Canada (BOF); midcoast Maine, USA, in the central coast of the Gulf of Maine (GOM); and coastal Rhode Island, USA, in southern New England (SNE). Our goal was to identify and map areas of the sea surface that strongly correlate with inshore lobster settlement, and quantify the time lags at which relationships exist.

Methods

American Lobster Settlement Index.—We analyzed ALSI data from three study areas with relatively long time series: Beaver Harbor in the Bay of Fundy (BOF) 1991–2014, midcoast Maine in the Gulf of Maine (GOM) 1989–2014, and coastal Rhode Island in southern New England (SNE) 1990–2014 (Fig. 1). The ALSI survey employs diver-based suction sampling (Wahle and Steneck 1991, Incze and Wahle 1991) and vessel-deployed passive postlarval collectors (Wahle et al. 2009b, 2013a) to assess the annual settlement of American lobsters to inshore cobble nursery grounds.

Sampling is conducted at the end of the late summer–early autumn postlarval settlement season and lobsters measuring at or below the designated YoY size limit are used to calculate annual settlement density (Table 1, Wahle et al. 2010). Each of the three ALSI sampling regions comprise multiple fixed sites (<1 km^2 in size) of cobble-boulder nursery habitat where 12–20 quadrats are randomly sampled (Table 1). For each year, data from available sites were averaged to produce an annual regional metric of lobster settlement density.

Sea Surface Temperature.—Multiple daily sea surface temperature images of NOAA Advanced Very High Resolution Radiometer (AVHRR) data at full (1.1 km) spatial resolution were obtained for the entire study period. Data were cloud-masked

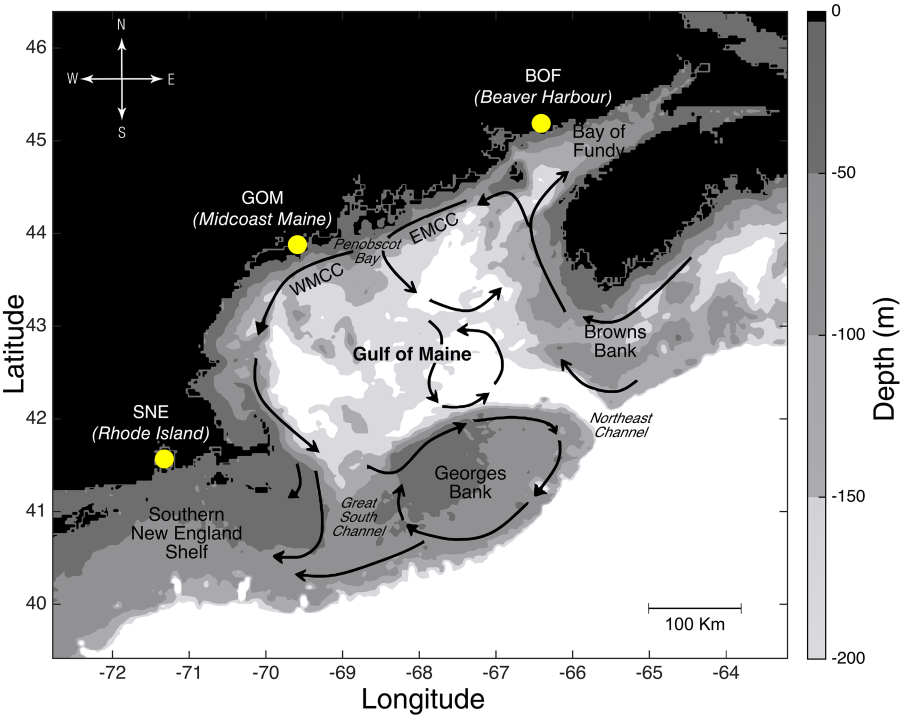

Figure 1. Gulf of Maine and surrounding shelf regions depicting regional bathymetry and major oceanographic features. Circles denote lobster settlement regions used in the present study (north to south): Bay of Fundy = BOF, Gulf of Maine = GOM, and southern New England = SNE along with the American Lobster Settlement Index (ALSI) region name. Black arrows demonstrate generalized summer surface (<75 m) circulation patterns including components of the Gulf of Maine Coastal Current (GMCC): the Eastern Maine Coastal Current (EMCC), and the Western Maine Coastal Current (WMCC), and the region of offshore bifurcation at Penobscot Bay (circulation arrows adapted from Pettigrew et al. 2005).

and subset to the study area (41.5°N –45°N, 66°W–71°W), and used to form monthly composites (average of all available images within a month) (e.g., Thomas et al. 2010). Composites for each calendar month were averaged over the available period (1985–2014) to produce monthly climatologies. Monthly SST anomaly (SSTa) fields were then calculated as deviations of each monthly composite from its respective monthly climatology.

Table 1. Details of American Lobster Settlement Index (ALSI) data used for the analysis of our study regions: Bay of Fundy (BOF, ALSI name = Beaver Harbour), Gulf of Maine (GOM, ALSI name = Midcoast Maint), and Southern New England (SNE, ALSI name = Rhode Island). Latitude and longitude indicate approximate central location of region. Annual averages were calculated using the maximum number of sites available. Most importantly, the regions differ in month of sampling (i.e., end of settlement season), year time series began, and the young-of-year (YoY) size limit (from American Lobster Settlement Index Collaborative: http://umaine.edu/wahlelab/american-lobster-settlement-index-alsi/american-lobster-settlement-index/).

Region	Latitude	Longitude	Sampling month	Years analyzed	YoY size (mm)	Quadrat size (m^2)	Number of sites	Approximate area (km^2)
BOF	44°58′12″N	66°48′36″W	October	1991–2014	≤13.0	0.25	2–5	250
GOM	43°45′36″N	69°31′12″W	September	1989–2014	≤10.5	0.50	8–10	500
SNE	41°25′12″N	71°18′00″W	August	1990–2014	≤13.0	0.50	2–6	500

Correlation Analysis.—We tested the relationship between the interannual variability of the three ALSI time series and monthly-averaged SSTa up to 4 mo prior to settlement sampling, as lobster larvae spend anywhere from 3 to 12 wks in the plankton (Ennis 1995). Time series were detrended with simple linear fits prior to calculation to avoid spurious correlations due to unresolved low frequency trends. We used the non-parametric Spearman's rank correlation to avoid violating assumptions about the unknown underlying distribution of the settlement data (Sokal and Rohlf 1981). Correlations with the SSTa fields were formed at each pixel location to produce maps of correlation values. To focus attention on shelf waters and avoid the high temperature variability of offshore Gulf Stream waters, that contribute little to inshore interannual lobster settlement, regions seaward of the shelf break 200 m bathymetric contour were excluded from the SSTa correlation analysis (Fig. 1).

Bootstrap Statistical Test.—Performing multiple correlations with a single data set (ALSI) greatly increases the risk of a Type 1 statistical error. Although a Bonferroni correction can help reduce this risk, it is known to be highly conservative and increases the risk of failing to observe an existing association (Perneger 1998, Narum 2006). To constrain our understanding of the significance of the correlations, we employed a bootstrap technique similar to that used by Barton et al. (2003) and Thomas et al. (2010). The detrended ALSI data were randomized and each correlation was carried out 100 times. For application to the SSTa fields, we calculated the fraction of times a larger number of ocean SSTa pixels correlated significantly (at 95% levels or better) with the randomized lobster time series compared to the results of the original analysis. Original results were deemed statistically significant when this fraction fell below 0.1 (90% significance) and 0.05 (95% significance).

Results

ALSI Time Series.—The ALSI time series show strong variability among regions, with BOF settlement two to three times as high as that in SNE or GOM (Fig. 2). Increasing and decreasing trends in lobster settler densities were evident for BOF and SNE, respectively, while GOM showed a declining trend through 2000, followed by a sharp upturn and sustained relative highs through 2012 (Fig. 2).

Correlations of Lobster Settlement with SSTa.—Interannual variability in lobster settlement time series correlated with SSTa over a variable area of the sea surface depending on lag and ALSI site, but was statistically significant only for SNE (Fig. 3, Table 2). All correlations of settlement with SSTa exceeding the 90% confidence level in the bootstrap analysis were positive, indicating increased settlement associated with increases in SST.

In SNE, interannual variation in ALSI did not correlate with SSTa from any area in May, but in June, July, and August, when larvae are in the water column, we found settlement at SNE to be significantly and positively correlated with temperature anomalies over a considerable area of the sea surface upstream of the site, including Georges Bank and parts of Browns Bank and southern Nova Scotia. Correlations were not present in immediately adjacent coastal waters ($P < 0.1$; Fig. 3A, Table 2).

The GOM settlement at Midcoast Maine was poorly correlated with SSTa over the shelf waters in June, July, and August (Fig. 3B). By September, the month of settlement sampling, however, the settlement index was positively correlated with SSTa in

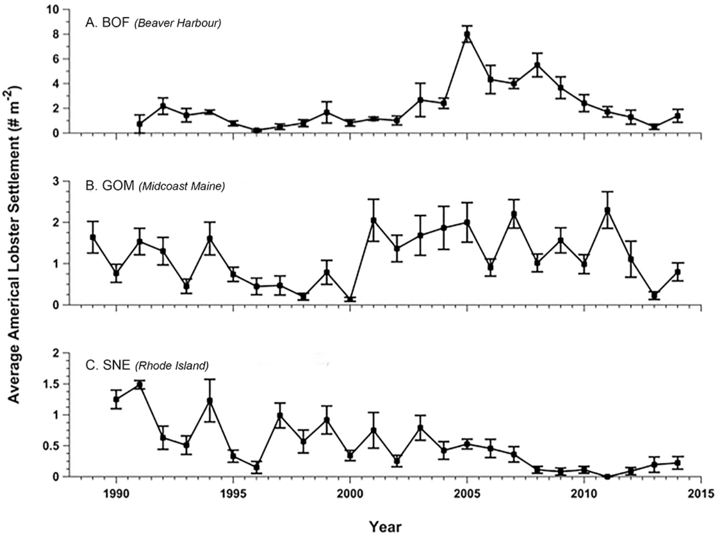

Figure 2. Interannual variability in American Lobster Settlement Index (ALSI) densities at (A) Bay of Fundy (BOF), (B) Gulf of Maine (GOM), and (C) southern New England (SNE) showing the original non-detrended trends until 2014. Error bars denote 1 SE (from American Lobster Settlement Index Collaborative: http://umaine.edu/wahlelab/american-lobster-settlement-index-alsi/american-lobster-settlement-index/).

a small area immediately adjacent to the settlement region over the 100 m isobath (Fig. 3B). Bootstrap analysis indicated that correlated areas of this size could occur by chance ($P > 0.1$, Table 2), so although a positive association with local SST is plausible, it should be interpreted with caution (Table 1, Fig. 3B).

The BOF settlement index correlated with SSTa only in small, disparate patches during August and September (Fig. 3C) and were not statistically significant in the bootstrap analysis ($P > 0.1$; Table 2).

Discussion

Our study demonstrates the spatial extent of SSTa correlations with lobster settlement at three monitoring locations extending from the Bay of Fundy to southern New England. The SNE settlement time series was positively associated with an extensive offshore area of SSTa over Georges and Browns banks. Settlement at the GOM study area was correlated with SSTa in a much more restricted area along the adjacent Maine coast. By contrast, we found no significant correlation between the BOF lobster settlement time series and SSTa over the evaluated sea surface area. Similar results were obtained when only part of the data sets (through 2008) were used (Jaini 2011).

Regional differences in the association between lobster settlement and SSTa are not unexpected given the steep temperature gradient across these study areas and the temperature dependence of larval biology. For example, in an evaluation of the spatial coherence and atmospheric correlates of lobster settlement time series along the New England coast, including the same three study regions as used in the present study, Pershing et al. (2012) found that the Rhode Island settlement time series stood apart from those within the Gulf of Maine. Furthermore, they reported that

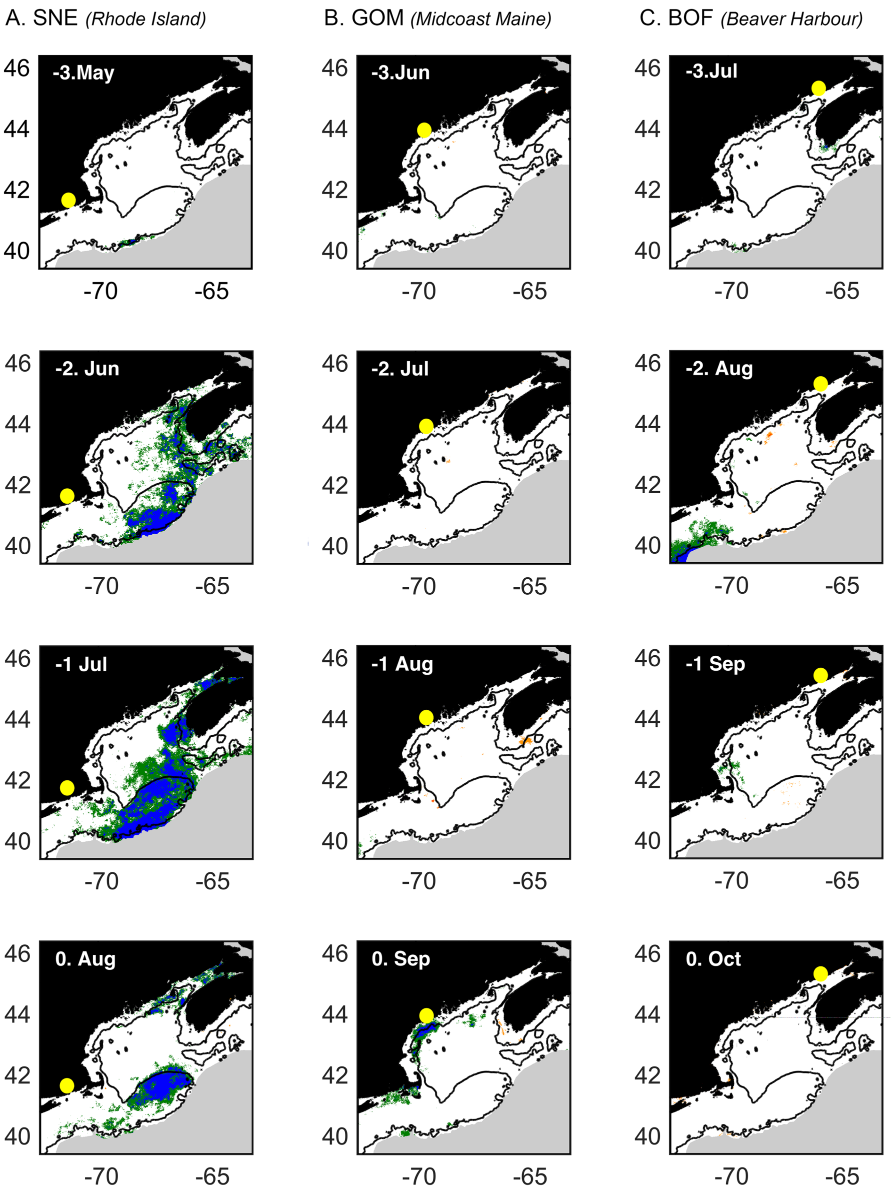

Figure 3. Correlation maps of detrended lobster settlement with detrended monthly sea surface temperature anomaly (SSTa) fields for (A) southern New England (SNE), (B) Gulf of Maine (GOM), and (C) Bay of Funday (BOF) (yellow dots) showing individual pixels of significant positive (blue and green) and negative (red and orange) correlation at 99% and 95% significance levels respectively, for a series of time lags (−3, −2, −1) leading up to the month (0) of settlement sampling. Black line indicates the 100 m isobath, gray area is the masked unanalyzed region. Bootstrap statistical test indicates that only the SNE correlation patterns observed in June and July are significant at a 95% confidence interval and in August at a 90% confidence interval (*see* Table 2).

Table 2. Bootstrap statistical test results for correlation analysis of American Lobster Settlement Index (ALSI) and sea surface temperature anomalies (SSTa) for Bay of Fundy, Gulf of Maine, and southern New England. Correlations are considered significant if the number of bootstrap tests exceeding the original area of significant correlation is <5 (95%, indicated by two asterisks) or <10 (90%, indicated by one asterisk) for 100 re-samplings.

		SSTa spatial correlation	
Region and time lag	Month	Original area of significant correlation (95% CI)	Number of bootstrap tests exceeding original area of significant correlation (95% CI)
Bay of Fundy			
−3	July	0.006	55
−2	August	0.058	29
−1	September	0.011	73
0	October	0.008	56
Gulf of Maine			
−3	June	0.003	86
−2	July	0.002	81
−1	August	0.007	82
0	September	0.054	31
Southern New England			
−3	May	0.007	66
−2	June**	0.297	3
−1	July**	0.372	4
0	August*	0.157	6

settlement in Rhode Island was more strongly influenced by atmospheric conditions in August, whereas the Gulf of Maine site was more strongly correlated with those in September. Thus, the two studies come to similar conclusions regarding regional differences in timing and strength of potential environmental drivers of settlement.

The most compelling and consistent result of our study is the correlation of the lobster settlement time series in SNE with SSTa over Georges and Browns banks, but the mechanism driving this association remains unclear. On one hand, SNE settlement and offshore SSTa could be correlated without direct larval connectivity. Because Georges and Brown banks are relatively shallow and the waters over them remain strongly mixed during the summer (Townsend et al. 2006, Brink et al. 2009), SSTa over these areas reasonably tracks interannual variability in integrated water column hydrographic conditions, and specifically bottom water temperatures, that could influence the timing and location of larval hatch in a way that would favor higher levels of settlement in coastal SNE. On the other hand, SNE settlement could benefit from an offshore larval subsidy. Coastal circulation around Georges Bank and along the SNE shelf could allow larval transport to coastal Rhode Island (Townsend et al. 2006, Xue et al. 2008, Manning et al. 2009, Incze et al. 2010) with a travel time of 2–9 wks (Manning et al. 2009), which is within the expected time of lobster larval development to the settlement stage. While the potential for transport from offshore hatching locations >100 km to inshore nurseries has long been recognized (Katz et al. 1994), the effective larval source for nurseries in coastal Rhode Island could very well extend as far as Georges Bank and southern New England's offshore canyons (ASMFC 2015). Interestingly, recent genetic studies that aim to understand meta-population dynamics of the American lobster found significant deviation between northern and southern populations, and genetic similarities over Georges Bank and the Southern New England Shelf (Kenchington et al. 2009, Benestan et al. 2015, 2016). Spatial patterns in genetic structure of the American lobster are attributed to past glaciation events and ocean current-mediated larval connectivity (Kenchington et al. 2009, Benestan et al. 2016).

To our knowledge, ours is the first study to employ satellite-derived data to provide spatial context to interannual differences in coastal settlement of clawed lobsters. Satellite data are commonly used in biophysical models of larval transport and settlement (Polovina et al. 1999, Chiswell and Booth 2008, Xue et al. 2008, Incze et al. 2010, Runge et al. 2010, Nolasco et al. 2013), have been instrumental in directly understanding recruitment processes in a number of marine species, and are commonly used in upwelling regions to understand the relationship between upwelling strength and pelagic species recruitment. This is true for: clupeoid, *Sardinops sagax* (Jenyns, 1842), recruitment in the northern Benguela upwelling system (Cole 1999, Hardman-Mountford et al. 2003); sardine, *Sardina pilchardus* (Walbaum, 1792), and horse mackerel, *Trachurus trachurus* (Linnaeus, 1758), recruitment off Portugal (Santos et al. 2001); intertidal invertebrate settlement in US west coast and Chilean upwelling zones (Roughgarden et al. 1988, Moreno et al. 1998, Broitman et al. 2008); and *Octopus vulgaris* Cuvier, 1797 recruitment off west Africa (Demarcq and Faure 2000). Similarly, satellite data were instrumental in detecting the role of eddies in the transport of reef fish larvae in Florida (Sponaugle et al. 2005) and Hawaii (Fox et al. 2012). Among crustaceans, satellite data helped demonstrate the direct relationship between western Australia rock lobster, *Panulirus cygnus* George, 1962, settlement and Leeuwin Current SST and strength (Caputi et al. 2001), and between barnacle recruitment and primary production in the Gulf of Maine and Gulf of St. Lawrence (Cole et al. 2011).

A variable not considered in our study is the role of brood stock abundance, as the abundance of breeders is not likely to change dramatically from one year to the next in such a long-lived species and our focus was on interannual variability. However, trends in local brood stock abundance may contribute to the considerable long-term increases in settlement in the BOF and declines in settlement in SNE (DFO 2013, ASMFC 2015). The mechanisms driving these diverging trajectories of the northern and southern lobster populations are not fully understood. Climate-related effects may be further compounded by the positive effects of depleted predatory fish depletion in the north, and the deleterious effects of shell disease in the south (Wahle et al. 2009a, 2013b, 2015, Steneck and Wahle 2013, Boudreau et al. 2015).

The most significant contribution of our study is in highlighting how regional differences in shelf SST are related to settlement variability, and in identifying specific areas of the sea surface, such as over Georges Bank, that may be particularly useful in predicting interannual variability in lobster settlement several months in advance. Such information is especially important from a management perspective in light of the strong climate-related SST trends observed in the northwest Atlantic Ocean and Gulf of Maine (e.g., Pershing et al. 2015, Thomas et al. 2017). The general association between SSTa and lobster settlement is not surprising as previous research has shown correlations between lobster landings and temperature with 6–8 yr time lags corresponding to the time between settlement and recruitment to the fishery (Dow 1969, 1978, Flowers and Saila 1972, Steneck 2005). While single variable relationships, such as the association between time-lagged temperature and lobster landings, fail to explain the increasing catch rates that began in the 1980s (Drinkwater et al. 1996), our analysis helps demonstrate the differing influence of a single variable in American lobster settlement dynamics in the Gulf of Maine and neighboring shelf areas. Along similar lines, a recent analysis of long-term settlement data of *Jasus edwardsii* (Hutton, 1875) in Australia and New Zealand has demonstrated complex ocean-atmospheric processes that help increase settlement in one region and decrease it in another (Hinojosa et al. 2017). The SSTa–lobster settlement associations detected in the present study may be related to the growing evidence of thermal adaptation in American lobster populations (Quinn et al. 2013, Benestan et al. 2016). This work illustrates the importance of the systematic and consistent collection, maintenance, and public availability of long-term ecological data sets. Using satellite data our spatial correlation analysis can be replicated in other species and systems to detect oceanographic features relevant to benthic recruitment.

Acknowledgments

This research work was originally conducted as a part of a master's thesis and constituted part of a grant from the US National Aeronautics and Space Administration-ROSES program (NASA grant NNX08AT92G) to the University of Maine. Partial support was also received from NSF Coastal SEES Program (OCE-1325484). We wish to thank R Steneck, A Pershing, P Lawton, L Incze, and H Xue for valuable discussion and perspectives on the study, J Churchill and J Gaudette for constructive feedback that helped improve this manuscript. ALSI data used in our study were collected by Department of Fisheries and Oceans, St. Andrews, Canada; Maine Department of Marine Resources and Rhode Island Department of Environmental Management, USA. SSTa data sets were acquired from the Satellite Oceanography Lab at the University of Maine.

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