Bridging the spawner-recruit disconnect: trends in American lobster recruitment linked to the pelagic food web

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ABSTRACT.—In the Gulf of Maine, landings of American lobster, *Homarus americanus* H. Milne-Edwards, 1837, have doubled since the early 2000s, and are currently at record-breaking levels. Estimates of spawning stock biomass (SSB) are correspondingly high, but benthic recruitment of young-of-year (YoY) lobsters has been declining precipitously since 2012 and is currently at time-series lows. We analyzed a long-term time series of larval abundance collected off the coast of New Hampshire, USA, via neuston tows to explore linkages between trends in lobster SSB, larval abundance, and YoY recruitment. There was a significant increasing trend in stage I larvae in coastal New Hampshire, consistent with the increasing levels of SSB in the Gulf of Maine over the same period. However, the planktonic postlarvae from the same survey have been declining in recent years, which correlate well with diminishing benthic YoY recruitment at monitoring sites in the western Gulf of Maine, from mid-coast Maine to Cape Cod Bay, Massachusetts. Furthermore, we found that both postlarval and YoY lobster time series were significantly correlated with the abundance of the copepod, *Calanus finmarchicus* (Gunnerus, 1770), but not other potential zooplankton prey, gelatinous predators, or environmental indicators, such as temperature or wind advection. To our knowledge, these results are the first to (1) narrow the likely timing of the decoupling of spawner abundance and settlement to the few weeks of lobster planktonic larval development, and (2) suggest that variability in YoY recruitment, including recent widespread declines, may be linked to changes in the zooplankton assemblage at the base of the pelagic food web.

Recent studies in the Northwest Atlantic coastal and shelf waters of the US and Canada suggest shifts in the abundance of zooplankton may limit recruitment success and commercial yields of finfish at higher trophic levels (Morse et al. 2017, Perretti et al. 2017). To date, however, little attention has been given to whether changes in the zooplankton assemblage might also impact recruitment to commercially

important crustacean stocks that now dominate the region's fisheries. Currently, American lobster, *Homarus americanus* H. Milne-Edwards, 1837, is the most valuable single-species fishery in the United States and Canada (DFO 2017, NOAA 2017). The commercial harvest of American lobster ranges from Newfoundland to the offshore waters of the US mid-Atlantic states. The most recent population assessment for American lobster in the United States indicates that the Gulf of Maine/Georges Bank stock is at a time-series high and has doubled since the early 2000s (ASMFC 2015). Furthermore, estimates of spawning stock biomass (SSB) for American lobster are also at record high levels. Contrary to expectations, however, young-of-year (YoY) recruitment has been decreasing in recent years throughout the Gulf of Maine (ASMFC 2015, Oppenheim 2016, ALSI 2017), and current estimates of YoY recruitment are at or near time-series lows throughout the region. The enigma facing scientists, managers, and industry is the persistent disconnect between a stock that is currently at record high levels of abundance and low levels of YoY recruitment.

Quantifying the stock-recruitment relationship has been an elusive goal for many species of marine fish and invertebrates, where high levels of stochastic variation have been reported (Caddy 1986, Fogarty et al. 1991, Fogarty 1993, Myers 1998, Wahle 2003). This is also true for the American lobster (Bannister and Addison 1986, Fogarty and Idoine 1986, Wahle 2003). A highly variable relationship between SSB and subsequent recruitment is not unexpected, as a myriad of factors operating before and after larval settlement determine the eventual success of a year class. Larval advection, mortality by predation, and food limitation have traditionally been considered important sources of recruitment variability in marine populations, all being affected by changes in the physical environment (Roughgarden et al. 1984, Gaines and Roughgarden 1987, Olson and Olson 1989, Hudon and Fradette 1993, Wahle and Incze 1997, Purcell et al. 2007).

For more than a century, planktonic food supply has been recognized as a factor limiting fish recruitment at early life stages. Hjort (1914) suggested that food supply may determine recruitment success via starvation, or prolonged larval development heightening the risk of predation. In the northwest Atlantic Ocean, copepods dominate the zooplankton biomass as a significant consumer of phytoplankton. Their lipid stores form an energy-rich link fueling higher trophic levels, including the planktotrophic larvae of fishes and invertebrates. Over the past decade in this region, several researchers have linked decadal scale changes in recruitment success of marine fishes to regime shifts in the zooplankton assemblage consumed by fish larvae (Mountain and Kane 2010, Friedland et al. 2013, 2015, Perretti et al. 2017). These findings coincide with reports of unprecedented changes in northwest Atlantic shelf waters, particularly in the Gulf of Maine. In recent decades, coastal waters of the Gulf of Maine have been warming and acidifying at a pace faster than most of the world's oceans (Key et al. 2004, Salisbury et al. 2009, Gledhill et al. 2015, Pershing et al. 2015). Additionally, since 2005 there has been a stepwise downturn in chlorophyll-*a* concentration in nearshore waters, reflecting declines in primary production and species composition of the phytoplankton assemblage (Balch et al. 2012). Such regime shifts propagate up the pelagic food web bringing widespread changes in the abundance and composition of the zooplankton assemblage.

Food limitation has not been as widely studied for the planktonic larvae of benthic invertebrates as it has in marine finfishes, and for many species the relationship has not been well established (Olson and Olson 1989). The tanner crab, *Chionoecetes*

spp., is one of the few examples we are aware of for which starvation at the larval stage has been implicated to play an important role in subsequent recruitment success (Incze et al. 1987). American lobster larvae undergo three planktonic larval stages (I–III) followed by a metamorphosis to a postlarval stage (IV) that is initially neustonic and eventually settles to the seabed in shelter-providing habitat. The entire planktonic phase ranges in duration from approximately 4–6 wks, depending on temperature (Lawton and Lavalli 1995). Laboratory studies conducted with the American lobster indicate a strong dependence of larval survival and development on food quality and abundance (Templeman 1936, Eagles et al. 1986). However, to our knowledge, there has been no field research linking zooplankton food supply to lobster larval abundance in situ.

Over the past 40 yrs, American lobster production in the Gulf of Maine has soared as the center of production has shifted northward (Pinsky et al. 2013). While there is general agreement that warming temperatures and the depletion of large-bodied predatory groundfish have favored the increase of lobster and other benthic crustacean populations in this region (Jackson et al. 2001, Worm and Myers 2003, Boudreau and Worm 2010, Wahle et al. 2013a, ASMFC 2015), the recent decoupling between high levels of SSB and low numbers of YoY remains elusive. Here, we examine a unique long-term data set on lobster larval abundance along with other indicators of lobster spawner abundance, YoY recruitment, and zooplankton abundance to better understand the factors influencing fluctuations of YoY recruitment of this iconic species. We identify a previously undocumented correlation between recent declines in components of the copepod assemblage and declining trends in YoY lobster recruitment that suggests a linkage between North America's most valuable fishery and the pelagic food web.

Materials and Methods

Study Area

Zooplankton abundance trends, obtained from the Seabrook Station Environmental Monitoring (SSEM) program off the coast of New Hampshire were compared to SSB abundance via the Northeast Fisheries Science Center (NEFSC) trawl survey conducted outside of 3 nautical miles (4.8 km) from shore in federal waters and to YOY abundance via the American Lobster Settlement Index (ALSI) conducted along the entire coast of Gulf of Maine (Fig. 1). Moreover, we integrated several additional environmental datasets, all of which are described below.

Abundance Indices

Seabrook Station Environmental Monitoring (SSEM).—Normandeau Associates, Inc. (Normandeau) has conducted zooplankton monitoring off the New Hampshire coast since 1978 as part of the environmental impact studies of the Seabrook Power Station (Fig. 1; Normandeau 2016). Lobster larvae were sampled from three stations with a neuston net (1 m deep × 2 m wide × 4.5 m long, and 1 mm mesh) weekly between May and October. The net was deployed with depressor and flow meter to sample 0.5 m to the surface. Thirty-min tows were made during the day, sampling an average area of approximately 3730 m^2 (a volume of 1865 m^3). In our analysis, we used mean values for stage I and postlarval (stage IV) indices from 1988 through 2015; we did not analyze trends in stage II and stage III larvae as these stages are primarily
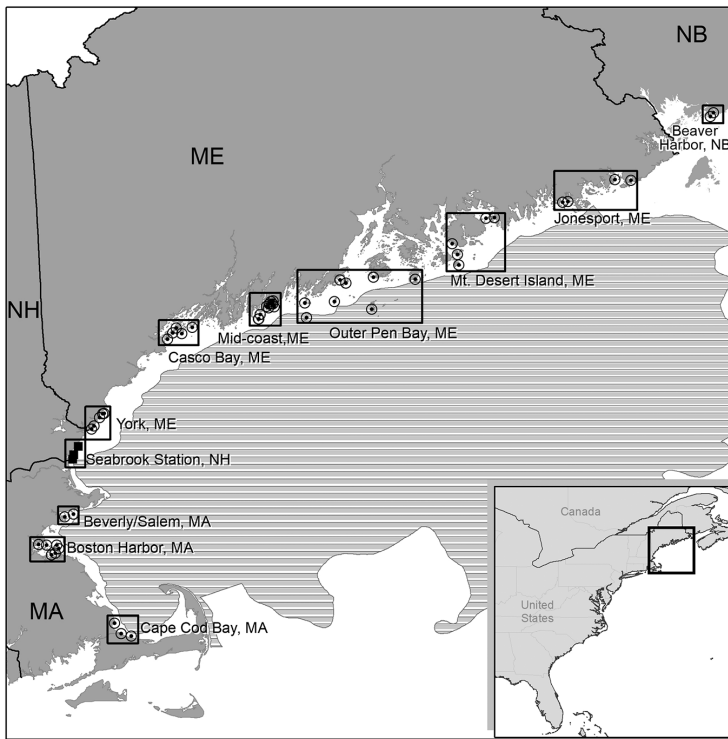
Figure 1. Spatial domain of this study, showing Seabrook Station Environmental Monitoring sampling sites (squares) in coastal New Hampshire in relation to American Lobster Settlement Index (ALSI; circles) and NEFSC Trawl Survey coverage (horizontal lines) throughout the Gulf of Maine. ALSI sample sites (circles) enclosed within labeled boxes representing study areas used in this analysis.

found at greater depths than can effectively be sampled by neuston net (Harding et al. 1987).

Macrozooplankton were sampled in a separate survey using a pair of 1-m diameter plankton hoop nets (0.505 mm mesh) in oblique tows at two stations along the New Hampshire coast between nautical sunset and sunrise twice a month, each month from 1989 to 2015. Nets with depressors and flow meters were towed for 10 min while varying boat speed, causing the net to sink to within 2 m of the bottom and then rise to the surface twice during the tow. The volume sampled averaged approximately 500 m^3. On retrieval, nets were rinsed with filtered seawater and contents preserved in 5%–10% buffered formalin. We used geometric mean values of annual macrozooplankton species abundance in a series of correlative analyses.

American Lobster Settlement Index (ALSI).—ALSI is a diver-based survey assessing the abundance of YoY lobsters repopulating coastal cobble nurseries annually at the end of the postlarval settlement period in late summer/fall (Wahle et al. 2009, 2013b). The survey effectively quantifies YoY and older juvenile lobster, as well as crabs and associated invertebrates (Wahle et al. 2013b, Hunt et al. 2017). At each sampling site, divers use an airlift suction device to sample between 12 and 20 0.5 m^2 quadrats. Samples were collected in separate mesh (1 mm) bags for each quadrat and sorted in the laboratory. We used data from surveys conducted at 10 study areas

from Cape Cod Bay, Massachusetts, in the western Gulf of Maine to Beaver Harbour, New Brunswick, in the eastern Gulf of Maine. Each study area contained from 2 to 10 fixed sampling sites (Fig. 1). The longest-standing sites, in the mid-coast Maine study area, have been sampled since 1989; the length of the time series used in this analysis for each study area is indicated in Table 1.

NEFSC Trawl Survey.—As a proxy for lobster spawning stock biomass in the Gulf of Maine, we used estimates of mature female lobster abundance from the National Marine Fisheries Service, NEFSC spring bottom trawl survey from 1988 through 2013. The survey utilizes a depth stratified random sampling design and spans the federal coastal and shelf waters from the Gulf of Maine to Cape Hatteras (ASMFC 2015).

Maine/New Hampshire (ME/NH) Trawl Survey.—To obtain an index of pelagic predator abundance, we used gelatinous zooplankton (scyphozoans, ctenophores, and tunicates) densities from the ME/NH trawl survey from 2003 through 2015. This survey utilizes a stratified random design modeled after the abovementioned NOAA trawl survey, but within state waters. A full description of procedures and gear can be found in Chen et al. (2005) and ASMFC (2015).

Climatic Indices

Wind Driven Transport.—We obtained time series of wind-driven Ekman transport in the surface layer for a single 1° × 1° grid cell centered at 42.5°N, 70.5°W derived at 6-hr intervals from modeled atmospheric pressure fields by the Fleet Numerical Meteorology and Oceanography Center (FMNOC) and served by NOAA's CoastWatch Program (http://coastwatch.pfeg.noaa.gov). Zonal and meridional components of transport were rotated to produce indices of cross-shelf and alongshore transport. From these time series, we calculated mean cross-shelf and alongshore transports (+1 SD) over the period from June to September for each year as an index of overall transport during the sampling season. We also calculated month-specific mean transports (+1 SD) and examined cumulative transport as it evolved over each year to evaluate whether short-term variability might differ among years in a manner correlated to patterns observed in the plankton time series.

North Atlantic Oscillation.—The North Atlantic Oscillation (NAO) index provides an indication of atmospheric effects across the North Atlantic and was used to assess linear relationships with indices of abundance for lobster postlarvae and *Calanus finmarchicus* (Gunnerus, 1770). We chose to use the seasonal index of July, August, and September as it closely matches the time period when larvae are in the water column; these data were obtained from https://climatedataguide.ucar.edu.

Sea Surface Temperature (SST).—Estimates of daily mean SST from 1991 to 2015 were extracted from NOAA's Optimally Interpolated Sea Surface Temperature (OISSTv2; AVHRR-only) data product (https://www.ncdc.noaa.gov/oisst; accessed via https://coastwatch.pfeg.noaa.gov/erddap/) for the grid cell centered at 42.875°N, 70.125°W directly off the New Hampshire coast. From this time series, we calculated mean SST June 1 to September 30 for each year to assess relationships with zooplankton abundance.

Statistical Analysis

We used Pearson's correlation coefficient (r) to assess linear relationships between variables. In cases where variables violated the normality assumption (as assessed via Shapiro Wilk test), Spearman's rank test was used to confirm the significance as calculated by Pearson's r. Significance in time series trends was assessed with the Mann Kendall test. Based upon Incze et al. (2006), we excluded 1990 neuston tows as an outlier from correlative analyses of SSEM postlarvae with both ALSI Midcoast Maine and SSEM *C. finmarchicus*. In addition to being an unusually high value (i.e., a statistical outlier), the observation was based on limited sampling, which limits our confidence that this data point adequately represents the zooplankton in that year. Additionally, 1990 was excluded from all correlative analyses with plankton-net-sampled macrozooplankton, as abundance estimates for some species were missing in that year. We conducted four sets of analyses to assess:

(1) correlations between Gulf of Maine SSB and SSEM stage I larvae, and between stage I larvae and postlarvae;
(2) spatial coherence of the SSEM postlarval time series and YoY recruitment at study areas along the Gulf of Maine coast;
(3) correlations of postlarvae with dominant zooplankton taxa from the SSEM, gelatinous zooplankton from trawl survey data, and selected environmental indicators; and finally,
(4) relationships between SSEM *C. finmarchicus* and YoY recruitment at eleven study areas along the Gulf of Maine coast.

To distinguish whether correlations were related to long-term trends, annual fluctuations, or both, we conducted correlative analyses for both raw and detrended data for all but the gelatinous zooplankton and environmental indicators. Detrended time series consisted of the residuals from the time trend regression (i.e., the difference of the raw value predicted from the regression model). All data were analyzed using the statistical software package JMP Pro 12.1.0.

Results

Spawning Stock Biomass, Larval, Postlarval Decoupling

Stage I lobster larvae increased significantly over the 27-yr neuston tow time series, and were near record high abundance during the most recent years (Mann Kendall: $P = 0.005$; Fig. 2). This correlates well with estimates of Gulf of Maine spawning stock biomass, which was also at historic highs based on the NEFSC Spring Trawl Survey ($r = 0.56$, $P = 0.002$). In contrast, planktonic postlarvae in the same collections have trended significantly downward over the same time period (Mann Kendall: $P = 0.022$; Fig. 3), particularly since the peak in 2007. The most recent four years (2012–2015) were below the time series median. Additionally, we found no significant correlation between stage I larval and postlarval abundance ($r = -0.16$, $P = 0.414$), representing the first evidence of a decoupling of early and late stage larval time series.

Spatial Coherence of Postlarvae and YoY Recruits

Planktonic postlarval abundance at SSEM correlated well with benthic YoY recruitment at the six western Gulf of Maine sites from Cape Cod Bay through midcoast Maine, for both the long term trend (raw time series) and annual variability
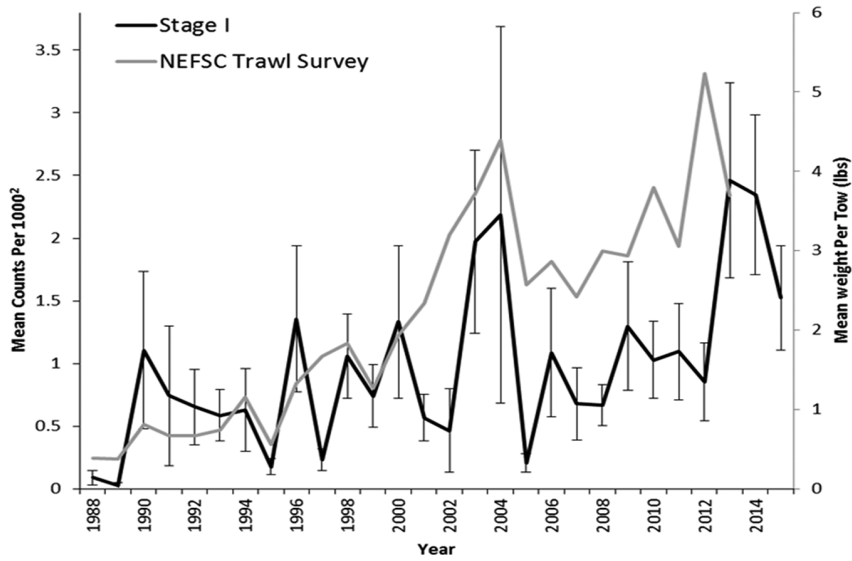
Figure 2. Seabrook Station Environmental Monitoring neuston-sampled stage I larvae (SE) and Northeast Fisheries Science Center spring trawl survey for mature female lobsters. The two indices are significantly correlated ($r = 0.56$, $P = 0.002$).
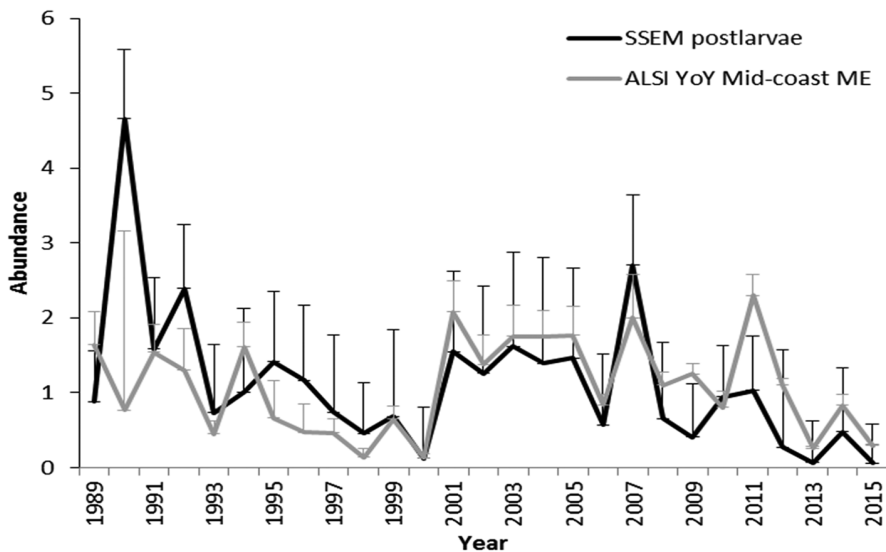

Figure 3. Parallel time series indicating the spatial coherence of Seabrook Station Environmental Monitoring neuston-sampled lobster postlarvae (SE) and American Lobster Settlement Index (ALSI) young-of-the year (YoY) (SE) from mid-coast Maine. Only positive error bars are displayed. These two indices were significantly correlated over the 27 yr time series ($r = 0.52$, $P = 0.006$). Refer to Table 1 for associated correlation statistics for additional ALSI study areas. Significant correlations between postlarvae and YoY lobsters were found throughout the western Gulf of Maine. Units of abundance for postlarvae, n 1000 m^{-2}; for YoY, n m^{-2}.

Table 1. Correlation statistics (raw and detrended) illustrating spatial coherence in the abundance of lobster postlarvae from neuston samples during Seabrook Station Environmental Monitoring and benthic young-of-the-year at 11 American Lobster Settlement Index study areas along the Gulf of Maine coast. Asterisks denote significant correlations ($P < 0.05$).

Location	Years	Pearson's r raw	P	Pearson's r detrended	P	Time series median
Beaver Harbor, NB	2000–2015	0.33	0.208	0.33	0.213	1.95
Jonesport, ME	2002–2015	0.36	0.198	0.27	0.335	0.35
Mt Desert Island, ME	2001–2015	0.40	0.157	0.43	0.120	0.33
Outer Penobscot Bay, ME	2001–2015	0.41	0.124	0.47	0.080	0.57
Mid-Coast, ME	1989–2015	0.64	<0.001*	0.69	<0.001*	1.10
Casco Bay, ME	2001–2015	0.80	<0.001*	0.61	0.015*	0.53
York, ME	2001–2015	0.68	0.008*	0.36	0.189	0.53
Beverly, MA	1995–2015	0.87	<0.001*	0.89	<0.001*	0.58
Boston Harbor, MA	1997–2015	0.71	<0.001*	0.70	<0.001*	0.11
Cape Cod Bay, MA	1995–2015	0.62	0.003*	0.62	0.003*	0.22

(detrended time series) (Table 1). Figure 3 is an example of this spatial coherence for mid-coast Maine, the longest of the ALSI time series, approximately 160 km from coastal New Hampshire, where postlarval collections were made. The only exception to this was the detrended ALSI time series for York, Maine. The postlarval-YoY relationship weakened substantially for the four ALSI study areas in the eastern Gulf of Maine, which were not significant correlated with the SSEM postlarval time series. Nonetheless, since 2012, both postlarval abundance at SSEM and YoY recruitment throughout the Gulf of Maine have been on a steady decline representing a recent period of strong spatial coherence. All YoY indices since 2012 have been below the time series median, except Mt. Desert, Maine, and Beaver Harbour, New Brunswick, in 2014.

Zooplankton–lobster Postlarval Correlations

Annually, from 1988 through 2015, >95% of the zooplankton (by abundance) in samples from SSEM was composed of the copepods *C. finmarchicus* (primarily co-pepodite) and *Centropages typicus* Krøyer, 1849 and larvae of the brachyuran crabs of the genus *Cancer*. Less than 5% of the total zooplankton samples consisted of *Neomysis americana* (S.I. Smith, 1873) and larvae of the caridean shrimp, *Crangon septemspinosa* Say, 1818. The time trend for *C. finmarchicus* correlated well with lobster postlarval abundance at SSEM, but we found no significant correlation for any of the other zooplankton species (Table 2). The time series abundance of lobster post-larvae and *C. finmarchicus* over the 27-yr period is depicted in Figure 4. Postlarval lobster abundance correlated significantly with *C. finmarchicus* for both raw and detrended time series at SSEM, indicating that postlarvae and copepods tracked closely, not only in the long-term trend, but also in annual variability. Similarly, YoY recruitment throughout much of the western Gulf of Maine correlated well with variability in *C. finmarchicus* abundance at SSEM, especially for the raw time series (Table 3). Raw YoY time series for five of the six ALSI study areas in the western Gulf of Maine were significantly correlated with *C. finmarchicus* abundance, whereas we found no such correlation for the four ALSI study areas in the eastern Gulf of Maine. Detrended time series for four of the six western Gulf of Maine ALSI study areas were also significantly correlated with detrended *C. finmarchicus* time series

Table 2. Correlation statistics (raw and detrended) for neuston-sampled lobster postlarvae vs the copepods, *Calanus finmarchicus* and *Centropages typicus,* crab larvae (*Cancer* spp.), *Neomysis americana* and *Crangon septemspinosa* from plankton samples, all collected at Seabrook Station Environmental Monitoring. Asterisks denote significant correlations ($P < 0.05$).

Zooplankton species	Pearson's r raw	P	Pearson's r detrended	P
Calanus finmarchicus	0.55	0.004*	0.63	<0.001*
Centropages typicus	−0.26	0.207	−0.34	0.089
Cancer spp.	0.05	0.792	−0.11	0.597
Neomysis americana	−0.07	0.726	−0.31	0.120
Crangon septemspinosa	0.33	0.057	0.20	0.318

at Seabrook, again suggesting close tracking in year-to-year variability between YoY lobster recruitment and copepods.

Environmental Correlations

Neither lobster postlarval or *C. finmarchicus* abundance correlated significantly with the following variables: temperature, wind driven transport (cross-shelf and alongshore), NAO index, or gelatinous zooplankton abundance (Table 4). Annual maximum and minimum (June–September) daily SST over the time series ranged from 17.84 to 21.88 and from 12.97 to 15.96, respectively, and did not exceed mortality thresholds for lobster postlarvae. Additionally, evaluation of wind-driven transport at shorter time scales (monthly means and cumulative transport paths) did not suggest that advection was a main driver of observed lobster postlarval or *C. finmarchicus* dynamics at Seabrook.

Discussion

The SSEM larval time series offers an important and previously unreported insight into the dynamics of stage-specific larval lobster abundance over a 27-yr period
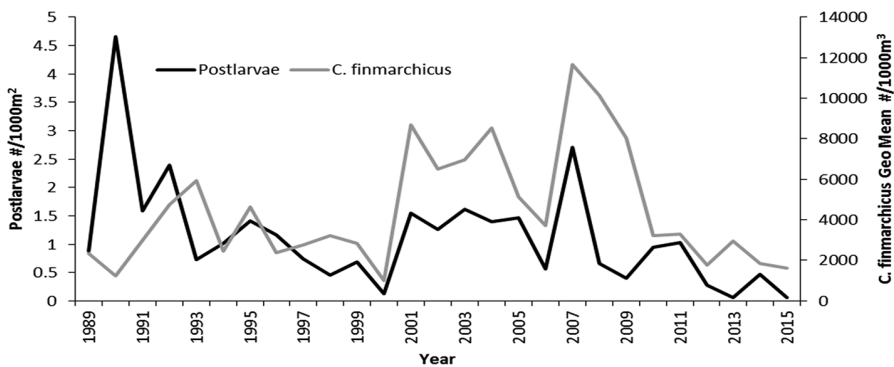

Figure 4. Parallel time series of neuston net-sampled lobster postlarvae and plankton net-sampled *Calanus finmarchicus* from Seabrook Station Environmental Monitoring (SSEM). The two indices were significantly correlated over the 27 yr time series ($r = 0.55$, $P = 0.0038$). Refer to Table 2 for associated correlation statistics evaluating the spatial coherence between *C. finmarchicus* at SSEM and young-of-the-year at American Lobster Settlement Index study areas throughout the Gulf of Maine.

Table 3. Correlation statistics (raw and detrended) illustrating the spatial coherence between Seabrook Station Environmental Monitoring plankton-sampled *Calanus finmarchicus* and young-of-the-year abundance by the American Lobster Settlement Index study area in the Gulf of Maine. Asterisks denote significant correlations ($P < 0.05$).

Location	Years	Pearson's r raw	P	Pearson's r detrended	P
Beaver Harbor, NB	2000–2015	0.39	0.132	0.43	0.098
Jonesport, ME	2002–2015	0.24	0.416	0.11	0.714
Mt Desert Island, ME	2001–2015	0.28	0.338	0.27	0.356
Outer Penobscot Bay, ME	2001–2015	0.13	0.649	0.08	0.783
Mid-Coast, ME	1989–2015	0.52	0.006*	0.52	0.005*
Casco Bay, ME	2001–2015	0.80	<0.001*	0.63	0.013*
York, ME	2001–2015	0.55	0.035*	0.10	0.719
Beverly, MA	1995–2015	0.70	<0.001*	0.70	<0.001*
Boston Harbor, MA	1997–2015	0.44	0.058	0.43	0.066
Cape Cod Bay, MA	1995–2015	0.52	0.015*	0.52	0.015*

and suggests the decoupling of SSB and YoY recruitment occurs during the developmental period between first larval and postlarval stages. Postlarval abundance is well documented to be a determinant of YoY recruitment success (Wahle and Incze 1997, Incze et al. 1997, Incze et al. 2006), and is further corroborated by correlations reported here between SSEM postlarvae and ALSI YoY abundance throughout the western Gulf of Maine. It is therefore plausible that stage-specific larval dynamics observed at SSEM represent more than a local anomaly and are general to a broader geographic area of the Gulf of Maine. These findings are also consistent with circulation patterns and larval transport modeling for the Gulf of Maine in which midcoast Maine represents the approximate boundary between the Eastern and Western Maine Coastal currents (Incze et al. 2010). Similar trends in the spatial coherence of YoY lobster recruitment have previously been reported in this region (Pershing et al. 2012).

To our knowledge, ours is the first analysis to identify a linkage between SSB and early stage lobster larval abundance, with subsequent decoupling of the linkage after the first larval stage. This decoupling suggests that factors apart from egg production begin to dominate larval dynamics during the later larval stages to become an important determinant of YoY recruitment. Declines in postlarval abundance at

Table 4. Correlation statistics for wind driven transport (cross-shelf and alongshore), North Atlantic Oscillation (NAO) index, and gelatinous zooplankton abundance for both lobster postlarvae and *Calanus finmarchicus*.

Variable 1	Variable 2	Pearson's r	P
Postlarvae	Sea surface temperature (1991–2015)	−0.35	0.078
Postlarvae	Wind transport cross shelf (1988–2015)	−0.09	0.652
Postlarvae	Wind transport alongshore (1988–2015)	−0.15	0.453
Postlarvae	NAO (1989–2015)	0.16	0.434
Postlarvae	Jellyfish (2003–2015)	−0.12	0.707
C. finmarchicus	Sea surface temperature (1991–2015)	−0.02	0.925
C. finmarchicus	Wind transport cross shelf (1988–2015)	0.13	0.509
C. finmarchicus	Wind transport cross shelf (1988–2015)	0.20	0.323
C. finmarchicus	NAO (1989–2015)	0.10	0.625
C. finmarchicus	Jellyfish (2003–2015)	0.23	0.443

SSEM and YoY recruitment throughout the Gulf of Maine since 2012 suggest levels of larval export or mortality have increased in recent years. Although we consider the role of several environmental factors and potential sampling artifacts below, our analysis and literature review suggest the abundance of postlarvae and subsequent YoY recruits in the western Gulf of Maine may be limited by the availability of *C. finmarchicus.*

Wind advection has been reported to affect spatial and temporal patterns of American lobster postlarval supply and YoY recruitment (Hudon and Fradette 1993, Incze et al. 1997, Wahle and Incze 1997, Pershing et al. 2012). Pershing et al. (2012) reported significant correlations of large scale atmospheric indicators with YoY recruitment at several of the ALSI monitoring sites through 2008. From our analysis using ALSI data through 2015, however, neither cross-shelf nor alongshore advection estimated for the coastal region near SSEM correlated well with postlarval abundance. Additionally, we did not detect evidence that monthly cumulative transport was a major driver of the observed lobster postlarval or *C. finmarchicus* dynamics. A more conclusive analysis of how advection might drive variability in abundance of late-stage larval lobster will likely require more detailed information on the spatial structure and variability of currents in the region.

Changes in predation could contribute to declines in postlarval abundance and YoY recruitment success. Gelatinous zooplankton (jellyfish and salps) represent a category of predator that could influence zooplankton and lobster larval dynamics. While there have been anecdotal accounts of increasing incidence of jellyfish and salps in the Gulf of Maine, few quantitative data are available on this important class of consumer in this region. Empirical data on the abundance of gelatinous zooplankton have only been consistently recorded since 2003 from the ME/NH trawl survey. The gelatinous zooplankton have been increasing in many parts of the world's oceans in response to anthropogenic effects, and can dramatically alter the pelagic food web dynamics through their feeding activity (Purcell 2005, Purcell et al. 2007). Although we found no correlation of gelatinous zooplankton with lobster postlarval abundance, we concede that these top-down impacts require additional study.

We have considered the possibility that the declining postlarval and YoY abundance trends may be a sampling artifact related to warming temperatures. For example, changes in thermal stratification could affect the availability of postlarvae to surface-sampling neuston nets giving inaccurate readings of postlarval abundance (Annis 2005). However, consistently robust correlations between postlarval abundance and YoY recruitment from ALSI regions throughout the western Gulf of Maine suggest that changes in sampling efficiency do not appear to have biased estimates of postlarval abundance. It is also possible that as water temperatures have warmed, larger areas of thermally suitable habitat have become available, allowing recruitment to spread over a much larger area of seabed (Steneck 2006), potentially reducing densities observed at shallow monitoring sites, and leading to underestimates of YoY recruitment trends. Although YoY lobster recruitment has been reported as deep as 80 m in the Gulf of Maine (Wahle et al. 2013b), and we recognize the potential for expanding deep-water settlement with warming temperatures, we currently have no direct evidence of its impact.

Warming temperatures have been widely invoked as a key driver behind the dramatic increases in lobster abundance in the Gulf of Maine over the past two decades through its direct effect on biological processes or indirect effect on species

interactions or disease prevalence. In the eastern Gulf of Maine, correlative evidence has linked warming temperatures to high levels of lobster recruitment through 2012, which likely played a role in the recent boom in US lobster landings (ASMFC 2015, Boudreau et al. 2015, LeBris et al. 2018). In the western Gulf of Maine, summer temperatures have largely stayed well within the optimal range of approximately 12–18 °C (MacKenzie 1988, Mills et al. 2013) for larval development, even as warming continues. This may explain the absence of a direct correlation in annual variability of temperature and postlarval abundance in the present study, but there are stronger thermal effects reported by other studies at the species' thermal range extremes (Boudreau et al. 2015, Jaini et al. 2018).

Our results point to a potential bottom-up effect on lobster YoY recruitment success in the western Gulf of Maine. We demonstrate a correlative link between lobster postlarvae and the copepod, *C. finmarchicus*, a known food source of larval lobster (Juinio and Cobb 1992, Lawton and Lavalli 1995). We hypothesize that the abundance of *C. finmarchicus* in nearshore waters is a significant factor influencing recruitment success in the American lobster. The following evidence is consistent with this hypothesis: (1) annual variability in postlarval lobster and YoY recruitment correlates well with *C. finmarchicus*, but not the other zooplankters that co-occur during the summer larval season; (2) if non-selective processes, such as wind advection or jellyfish predators, were influencing coastal zooplankton abundance, we would expect stronger coherence among co-occurring taxa, but we found no such correlation; (3) the seasonal peak of *C. finmarchicus* occurs just before the onset of the lobster larval season, and dominates the zooplankton assemblage at this time (Normandeau 2016); (4) lobster larvae of all stages readily consume *C. finmarchicus* in laboratory grazing experiments (D Fields, Bigelow Laboratory for Ocean Sciences, unpubl data), and have been found in guts of lobster larvae collected in the wild (Juinio and Cobb 1992); and (5) the reported time trends in *C. finmarchicus* from SSEM are consistent with those observed at a broader geographic scale (Meise and O'Reilly 1996, Pershing et al. 2010, EcoMon 2017).

To our knowledge, our results are the first in situ evidence linking trends in lobster postlarval abundance and YoY recruitment success to the availability of copepods. In the laboratory, lobster larval survival and rate of development to the postlarval stage has been reported to be strongly linked to food quality and quantity; high survival requires that first stage larvae encounter an abundance of food (Eagles et al. 1986). In early lobster larval rearing experiments conducted by Templeman (1936), reducing copepod prey densities by half reduced larval survival to the postlarval stage from 60% to 20%, and nearly doubled the development time to the postlarval stage from 25–30 to 50–55 d. Decreasing the food levels by half again resulted in no larvae reaching stage III. If the availability of *C. finmarchicus* is indeed a limiting factor in lobster recruitment success, it is imperative we gain a better understanding of this trophic interaction. Interestingly, there is also evidence that larger planktonic organisms promote growth and survival of lobsters throughout most of their first season of molting (Lavalli 1991).

Results from our study come at time when the Gulf of Maine ecosystem is undergoing unprecedented environmental changes and associated shifts in the composition of the pelagic food web (Balch et al. 2012, Morse et al. 2017). Recent comprehensive time series analyses have demonstrated strong linkages between zooplankton dynamics and finfish recruitment in the Gulf of Maine (Pershing et al. 2005, Castonguay

et al. 2008, Mountain and Kane 2010, Friedland et al. 2013, 2015, Morse et al. 2017, Perretti et al. 2017). Two comparisons between our study and Perretti et al. (2017) are noteworthy: (1) contrary to the finfish species cited by Perretti and colleagues, whereby population dynamics were linked to changes in the small-bodied fraction of the copepod assemblage, our analysis suggests lobster YoY recruitment success may be more tightly coupled to the large-bodied fraction of copepods dominated by *C. finmarchicus;* and (2) a dramatic shift occurred from 2000 to 2001, when lobster postlarval and YoY recruitment went up as finfish recruitment went down, corresponding to a shift from small to large copepod-dominated zooplankton assemblage. While these correlative studies suggest shifts in the zooplankton regime may be critical to fish yields, the mechanism of the trophic interaction remains poorly understood for most species. To our knowledge, no studies to date have examined such linkages for the commercially important crab and lobster taxa that now dominate fisheries in the Northeast US and Atlantic Canada, all of which have planktotrophic larvae. While recruitment bottlenecks could occur at any point before or after larval settlement to decouple the spawner-recruit relationship, here we provide suggestive evidence of a decoupling occurring between early and late planktonic larval stages that may be linked to the abundance of *C. finmarchicus*, a primary consumer at the base of the pelagic food web.

Recent projections under continued warming suggest that lobster recruitment potential within the western Gulf of Maine will diminish as the ratio of recruits-per-egg declines when temperatures exceed optimal limits in the future years (LeBris et al. 2018). The mechanism by which a temperature mediated decline in recruits-per-egg could occur is not explicit in the LeBris model, but evidence of changes in the pelagic food web associated with warming are accumulating and could have important implications for the planktonic larval stages of the American lobster that may already be manifesting themselves (Balch et al. 2012). Here we report evidence of a recent downturn in lobster postlarval abundance and YoY recruitment in the face of increasing SSB, suggesting that recruitment success per egg have been on the decline in recent years.

The present study is perhaps a prime example of why SSB has been a notoriously poor predictor of recruitment in many marine finfish and invertebrate fisheries (Myers 1998, Wahle 2003), and underscores the value of long-term, multi-life stage data sets to identify factors influencing year class strength. This work also reinforces the need to integrate single-species life history time series with other ecosystem indicators. As recent changes to the marine ecosystem outpace the ability of resource managers to react, our results provide another example of the need for an ecosystem-wide approach to fishery assessments and projections.

Literature Cited

Annis ER. 2005. Temperature effects on the vertical distribution of lobster postlarvae (*Homarus americanus*). Limnol Oceanogr. 50:1972–1982. https://doi.org/10.4319/lo.2005.50.6.1972

ALSI (American Lobster Settlement Index). 2017. American Lobster Settlement Index website. Accessed September 12, 2017. Available from: http://umaine.edu/wahlelab/american-lobster-settlement-index-alsi/american-lobster-settlement-index/

ASMFC (Atlantic States Marine Fisheries Commission). 2015. Stock Assessment Report No. 15-01 (Supplement) of the Atlantic States Marine Fisheries Commission. American Lobster Stock Assessment for Peer Review. ASMFC American Lobster Stock Assessment Subcommittee. 438 p.

Balch WM, Drapeau DT, Bowler BC, Huntington TG. 2012. Step-changes in the physical, chemical and biological characteristics of the Gulf of Maine, as documented by the GNATS time series. Mar Ecol Prog Ser. 450:11–35. https://doi.org/10.3354/meps09555

Bannister RCA, Addison JT. 1986. Effect of assumptions about the stock-recruitment relationship on a lobster (*Homarus gammarus*) stock assessment. Can J Fish Aquat Sci. 43:2353–2359. https://doi.org/10.1139/f86-287

Boudreau SA, Anderson SC, Worm B. 2015 Top-down and bottom-up forces interact at thermal range extremes on American lobster. J Anim Ecol. 84:840–850. https://doi.org/10.1111/1365-2656.12322

Boudreau SA, Worm B. 2010. Top-down control of lobster in the Gulf of Maine: insights from local ecological knowledge and research surveys. Mar Ecol Prog Ser. 403:181–191. https://doi.org/10.3354/meps08473

Caddy JF. 1986. Modelling stock-recruitment processes in Crustacea: some practical and theoretical perspectives. Can J Fish Aquat Sci. 43:2330–2344. https://doi.org/10.1139/f86-285

Castonguay M, Plourde S, Robert D, Runge JA, Fortier L. 2008. Copepod production drives recruitment in a marine fish. Can J Fish Aquat Sci. 65:1528–1531. https://doi.org/10.1139/F08-126

Chen YM, Kanaiwa M, Wilson C. 2005. Developing and evaluating a size structured stock assessment model for the American lobster, *Homarus americanus* fishery. N Z J Mar Freshw Res. 39:645–660. https://doi.org/10.1080/00288330.2005.9517342

DFO (Fisheries and Oceans Canada). 2017. Seafisheries landings. http://www.dfo-mpo.gc.ca/stats/commercial/sea-maritimes-eng.htm

Eagles MD, Aiken DE, Waddy SL. 1986. Influence of light and food on larval American lobsters, *Homarus americanus.* Can J Fish Aquat Sci. 43:2303–2310. https://doi.org/10.1139/f86-282

EcoMon. 2017. Gulf of Maine. Northeast Fisheries Science Center Marine Ecological Time Series database. Available from: https://www.st.nmfs.noaa.gov/copepod/time-series/us-50101/

Friedland KD, Kane J, Hare JA, Lough RG, Fratantoni PS, Fogarty MJ, Nye JA. 2013. Thermal habitat constraints on zooplankton species associated with Atlantic cod (*Gadus morhua*) on the US Northeast Continental Shelf. Prog Oceanogr. 116:1–13. https://doi.org/10.1016/j.pocean.2013.05.011

Friedland KD, Leaf RT, Kristiansen T, Large SI. 2015. Layered effects of parental condition and larval survival on the recruitment of neighboring haddock stocks. Can J Fish Aquat Sci. 72:1672–1681. https://doi.org/10.1139/cjfas-2015-0084

Fogarty MJ, Idoine JS. 1986. Recruitment dynamics in an American lobster (*Homarus americanus*) population. Can J Fish Aquat Sci. 43:2368–2376. https://doi.org/10.1139/f86-289

Fogarty JJ, Sissenwine MP, Cohen EB. 1991. Recruitment variability and the dynamics of exploited marine populations. Trends Ecol Evol. 6:241–246. https://doi.org/10.1016/0169-5347(91)90069-A

Fogarty MJ. 1993. Recruitment in randomly varying environments. ICES J Mar Sci. 50:247–260. https://doi.org/10.1006/jmsc.1993.1027

Gaines SD, Roughgarden J. 1987. Fish in offshore kelp forests affect recruitment to intertidal barnacle populations. Science. 235:479–481. https://doi.org/10.1126/science.235.4787.479

Gledhill DK, White MM, Salisbury J, Thomas H, Mlsna I, Liebman M, Mook B, Grear J, Candelmo AC, Chambers RC, et al. 2015. Ocean and coastal acidification off New England and Nova Scotia. Oceanography. 28:182–197. https://doi.org/10.5670/oceanog.2015.41

Harding GC, Pringle JD, Vass WP, Pearre S Jr, Smith SJ. 1987. Vertical distribution and daily movements of larval lobsters *Homarus americanus* over Browns Bank, Nova Scotia. Mar Ecol Prog Ser. 41:29–41. https://doi.org/10.3354/meps041029

Hjort J. 1914. Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. Rap PV Reun Cons Int Explor Mer 20. 228 p.

Hudon C, Fradette P. 1993. Wind-induced Advection of Larval Decapods into Baie de Plaisance (lles de la Madeleine, Quebec). Can J Fish Aquat Sci. 50:1422–1434. https://doi.org/10.1139/f93-163

Hunt H, Wahle RA, Tremblay J, Comeau M, Silva A, Rochette R. 2017. Spatial patterns of richness and abundance of benthic decapod crustaceans and fishes in the Northwest Atlantic as measured by passive cobble-filled collectors. Mar Biol Res. https://doi.org/10.1080/17451000.2017.1296161

Incze LS, Armstrong DA, Smith SL. 1987. Abundance of larval Tanner crabs (*Chionectes* spp.) in relation to adult females and regional oceanography of the southeastern Bering Sea. Can J Fish Aquat Sci. 44:1143–1156. https://doi.org/10.1139/f87-137

Incze LS, Wahle RA, Cobb JS. 1997. Quantitative relationships between postlarval production and benthic recruitment in lobsters, *Homarus americanus.* Mar Freshw Res. 48:729–743. https://doi.org/10.1071/MF97204

Incze LS, Wahle RA, Wolff N, Wilson C, Steneck R, Annis E, Lawton P, Xue H, Chen Y. 2006. Early life history and a modeling framework for lobster (*Homarus americanus)* populations in the Gulf of Maine. J Crustac Biol. 26:555–564. https://doi.org/10.1651/S-2764.1

Incze L, Xue H, Wolff N, Xu D, Wilson C, Steneck R, Wahle R, Lawton P, Pettigrew N, Chenc Y. 2010. Connectivity of lobster (*Homarus americanus*) populations in the coastal Gulf of Maine: part II. Coupled biophysical dynamics. Fish Oceanogr. 19:1–20. https://doi.org/10.1111/j.1365-2419.2009.00522.x

Jackson JBC, Kirby MX, Berger WH, Bjorndal KA, Botsford LW, Bourque BJ, Bradbury RH, Cooke R, Erlandson J, Estes JA, et al. 2001. Historical overfishing and the recent collapse of coastal ecosystems. Science. 293:629–637. https://doi.org/10.1126/science.1059199

Jaini M, Wahle RA, Thomas AC, Weatherbee R. 2018. Spatial surface temperature correlates of American lobster (*Homarus americanus*) settlement in the Gulf of Maine and southern New England shelf. Bull Mar Sci. 94(3):737–751. https://doi.org/10.5343/bms.2017.1141

Juinio MAR, Cobb JS. 1992. Natural diet and feeding habits of the postlarval lobster *Homarus americanus.* Mar Ecol Prog Ser. 85:83–91. https://doi.org/10.3354/meps085083

Key RM, Kozyr A, Sabine CL, Lee K, Wanninkhof R, Bullister J, Feely RA, Millero F, Mordy C, Peng T-H. 2004. A global ocean carbon climatology: results from GLODAP. Global Biogeochem Cycles. 18:GB4031. https://doi.org/10.1029/2004GB002247

Lavalli KL. 1991. Survival and growth of early-juvenile lobsters (*Homarus americanus*) through their first season while fed diets of mesoplankton, microplankton, and frozen brine shrimp. Fish Bull. 89:61–68.

Lawton P, Lavalli KL. 1995. Chapter 4. Postlarval, juvenile, adolescent, and adult Ecology. *In:* Factor JR, editor. Biology of the lobster *Homarus americanus.* Academic Press San Diego, CA. p. 47–83.

LeBris A, Mills KE, Wahle RA, Chen Y, Alexander MA, Allyn AJ, Schuetz JG, Scott JD, Pershing AD. 2018. Climate vulnerability and resilience in the most valuable North American fishery. Proc Natl Acad Sci USA. 115:1831–1836. https://doi.org/10.1073/pnas.1711122115

Meise CJ, O'Reilly JE. 1996. Spatial and seasonal patterns in abundance and age-composistion of *Calanus finmarchicus* in the Gulf of Maine and on Georges Bank: 1977–1987. Deep Sea Res Part II Top Stud Oceanogr. 43:1473–1501. https://doi.org/10.1016/S0967-0645(96)00048-3

MacKenzie BR. 1988. Assessment of temperature effects on interrelationships between stage durations, mortality, and growth in laboratory reared *Homarus americanus* Milne Edwards larvae. J Exp Mar Biol Ecol. 116:87–98. https://doi.org/10.1016/0022-0981(88)90248-1

Mills KE, Pershing AJ, Brown CJ, Chen Y, Chiang F-S, Holland DS, Lehuta S, Nye JA, Sun JC, Thomas AC, et al. 2013. Fisheries management in a changing climate: Lessons from the 2012 ocean heat wave in the Northwest Atlantic. Oceanography. 26:191–195. https://doi.org/10.5670/oceanog.2013.27

Morse RE, Friedland KD, Tommasi D, Stock C, Nye J. 2017. Distinct zooplankton regime shift patterns across ecoregions of the US Northeast continental shelf large larine ecosystem. J Mar Syst. 165:77–91. https://doi.org/10.1016/j.jmarsys.2016.09.011

Mountain DG, Kane J. 2010. Major changes in the Georges Bank ecosystem, 1980s to the 1990s. Mar Ecol Prog Ser. 398:81–91. https://doi.org/10.3354/meps08323

Myers R. 1998. When do environment-recruitment correlations work? Rev Fish Biol Fish. 8:285–305. https://doi.org/10.1023/A:1008828730759

NOAA. 2017. NOAA Office of Science and Technology. Commercial fisheries statistics. Accessed August 12, 2017. Available from: http://www.st.nmfs.noaa.gov/commercial-fisheries/commercial-landings/annual-landings/index

Normandeau (Normandeau Associates, Inc.). 2016. Seabrook Station 2015 environmental monitoring in the Hampton-Seabrook area: a characterization of environmental conditions. Prepared for FPL Energy Seabrook LLC.

Olson RR, Olson MH. 1989. Food limitation of planktotrophic marine invertebrate larvae: does it control recruitment success? Annu Rev Ecol Syst. 20:225–247. https://doi.org/10.1146/annurev.es.20.110189.001301

Oppenheim N. 2016. Recruitment forecasting and scientific knowledge production in the Gulf of Maine and southern New England American lobster fishery. MS Thesis. University of Maine.

Perretti CT, Fogarty MJ, Friedland KD, Hare JA. SM Lucey, RS McBride, TJ Miller, RE Morse, L O'Brien, JJ Pereira, et al. 2017. Regime shifts in fish recruitment on the Northeast US Continental Shelf. Mar Ecol Prog Ser. 574:1–11. https://doi.org/10.3354/meps12183

Pershing JW, Greene CH, Jossi JW, Obrien L, Brodziak JKT, Bailey BA. 2005. Interdecadal variability in the Gulf of Maine zooplankton community, with potential impacts on fish recruitment. ICES J Mar Sci. 62:1511–1523. https://doi.org/10.1016/j.icesjms.2005.04.025

Pershing JW, Head EHJ, Greene CH, Jossi JW. 2010. Pattern and scale of variability among Northwest Atlantic Shelf plankton communities. J Plankton Res. 32:1661–1674. https://doi.org/10.1093/plankt/fbq058

Pershing AJ, Wahle RA, Meyers PC, Lawton P. 2012. Large scale coherence in New England lobster (*Homarus americanus*), settlement and associations with regional atmospheric conditions. Fish Oceanogr. 21:348–362. https://doi.org/10.1111/j.1365-2419.2012.00629.x

Pershing AJ, Mills KE, Record NR, Stamieszkin K, Wurtzell KV, Byron CJ, Fitzpatrick D, Golet WJ, Koob E. 2015. Evaluating trophic cascades as drivers of regime shifts in different ocean ecosystems. Philos Trans R Soc Lond B Biol Sci. 370:20130265. https://doi.org/10.1098/rstb.2013.0265

Pinsky ML, Worm B, Fogarty MJ, Sarmiento JL, Levin SA. 2013. Marine taxa track local climate velocities. Science. 341:1239–1242. https://doi.org/10.1126/science.1239352

Purcell JE. 2005. Climate effects on formation of jellyfish and ctenophore blooms: a review. J Mar Biol Assoc. 85:461–476. https://doi.org/10.1017/S0025315405011409

Purcell JE, Uye S-i, Lo W-T. 2007. Anthropogenic causes of jellyfish blooms and their direct consequences for humans: a review. Mar Ecol Prog Ser. 350:153–174. https://doi.org/10.3354/meps07093

Roughgarden J, Gaines S, Iwasa Y. 1984. Dynamics and Evolution of Marine Populations with Pelagic Larval Dispersal. *In:* May RM, editor. Exploitation of marine communities. Dehlem Conferenzem. New York: Springer-Verlag. p. 111–128.

Salisbury J, Vandemark D, Hunt C, Campbell J, Jonsson B, Mahadevan A, McGillis W, Xue H. 2009. Episodic riverine influence on surface DIC in the coastal Gulf of Maine. Estuar Coast Shelf Sci. 82:108–118. https://doi.org/10.1016/j.ecss.2008.12.021

Steneck RS. 2006. Possible demographic consequences of intraspecific shelter competition among American lobsters. J Crustac Biol. 26:628–638. https://doi.org/10.1651/S-2753.1

Templeman W. 1936. The influence of temperature, salinity, light and food conditions on the survival and growth of the larvae of the lobster. J Biol Board Can. 2:485–497. https://doi.org/10.1139/f36-029

Wahle RA, Incze LS. 1997. Pre- and post-settlement processes in recruitment of the American lobster. J Exp Mar Biol Ecol. 217:179–207. https://doi.org/10.1016/S0022-0981(97)00055-5

Wahle RA. 2003. Revealing the stock-recruitment relationship in lobsters and crabs: Is experimental ecology the key? Fish Res. 65:3–32. https://doi.org/10.1016/j.fishres.2003.09.004

Wahle RA, Gibson M, Fogarty MJ. 2009. Distinguishing disease impacts from larval supply effects in a lobster fishery collapse. Mar Ecol Prog Ser. 376:185–192. https://doi.org/10.3354/meps07803

Wahle RA, Brown C, Hovel K. 2013a. The geography and body size dependence of top-down forcing in New England's lobster-groundfish interaction. Bull Mar Sci. 89:189–212. https://doi.org/10.5343/bms.2011.1131

Wahle RA, Bergeron C, Tremblay J, Wilson C, Burdett-Coutts V, Comeau M, Rochette R, Lawton P, Glenn R, Gibson M. 2013b. The geography and bathymetry of American lobster benthic recruitment as measured by diver-based suction sampling and passive collectors. Mar Biol Res. 9:42–58. https://doi.org/10.1080/17451000.2012.727428

Worm B, Myers RA. 2003. Meta-analysis of cod-shrimp interactions reveals top down control in oceanic food webs. Ecology. 84:162–173. https://doi.org/10.1890/0012-9658(2003)084[0162:MAOCSI]2.0.CO;2