Fisheries Research 278 (2024) 107082

Contents lists available at ScienceDirect

Fisheries Research

journal homepage: www.elsevier.com/locate/fishres

Bridging the spawner-recruit disconnect II: Revealing basin-scale correlations between zooplankton and lobster settlement dynamics in the Gulf of Maine

Burton Shank[a,*], Joshua T. Carloni[b], Paul Geoghegan[c], David M. Fields[d], Andrew G. Goode[e], Harvey J. Walsh[f], Richard A. Wahle[e]

[a] *NOAA National Marine Fisheries Service, Northeast Fisheries Science Center, Woods Hole, MA, United States*
[b] *New Hampshire Fish and Game Department, United States*
[c] *Normandeau Associates, Inc, United States*
[d] *Bigelow Laboratory for Ocean Sciences, United States*
[e] *University of Maine, School of Marine Sciences, United States*
[f] *NOAA National Marine Fisheries Service, Northeast Fisheries Science Center, Narragansett, RI, United States*

A R T I C L E I N F O

Handled by: Nick Caputi

Keywords:
American lobster
Homarus americanus
Settlement
Larval trophic interactions
Recruitment
Zooplankton dynamics
Calanus finmarchicus
Ecosystem regime shift
Gulf of Maine

A B S T R A C T

In recent decades, recruitment of young-of-year lobsters to benthic nursery habitats in the Gulf of Maine was regionally synchronized and exhibited correlative links with changes in the abundance of the copepod *Calanus finmarchicus,* a foundational zooplankton species of the pelagic food web. The spatial scale at which recruitment dynamics were correlated indicated that recruitment processes were not as strongly coupled to trends in spawner abundance as might be expected, but, rather, were influenced by common, ecosystem-scale processes. Here we explored how local- and basin-scale zooplankton dynamics and oceanographic indicators in the Gulf of Maine correlated with lobster settlement indices and each other since the late 1980s. Our analysis indicates that lobster settlement trends in southwestern Gulf of Maine study areas, from Midcoast Maine to Cape Cod Bay, tend to be significantly correlated with basin-wide *C. finmarchicus* dynamics and the composition of waters entering the Gulf of Maine through the Northeast Channel. In contrast, lobster settlement in the northeastern Gulf, from Penobscot Bay to the Bay of Fundy, tended to correlate more strongly to *C. finmarchicus* variability in the Bay of Fundy region, which was distinct in earlier years but converged with the broader basin-scale processes in the latter years. Our results are consistent with the hypothesis that the combined effect of climate-related declines in abundance and phenological shifts of *C. finmarchicus* have contributed to declines in lobster settlement over the past decade, and justify further research into the mechanisms of this interaction. These changes also align with the weakening influence of cold Labrador Slope Water and strengthening effects of warm Gulf Stream waters that precipitated an ecosystem-wide regime shift in the Gulf of Maine over the past decade and may have greater implications for lobster recruitment than previously suspected.

1. Introduction

Climate change and ecosystem regime shifts have profoundly altered marine ecosystems globally with consequences and implications for the productivity and distribution of marine fisheries and other ecosystem services (Nye et al., 2009; Pinsky et al., 2013; Levin and Mollmann, 2015). The shelf and coastal waters of the Northwest Atlantic have historically supported some of the world's most productive fisheries (FAO, 2022). The American lobster fishery (*Homarus americanus*) of the Northeast United States and Atlantic Canada represents the most valuable single-species fishery of both nations, and together are more productive in volume than all other lobster fisheries globally (Wahle et al., 2020). More than 90 % of the United States' lobster production, and about one-third of Canadian, comes from the Gulf of Maine (henceforth referred to as the Gulf) and Bay of Fundy (ASMFC, 2020; DFO, 2024). Stakeholders are acutely interested in how environmental drivers will influence the population dynamics of this resource of immense ecological and economic importance (ASMFC, 2020).

* Corresponding author.
E-mail address: burton.shank@noaa.gov (B. Shank).

https://doi.org/10.1016/j.fishres.2024.107082
Received 3 April 2024; Received in revised form 7 June 2024; Accepted 10 June 2024
Available online 25 June 2024
0165-7836/Published by Elsevier B.V.

In a changing climate, the Gulf and adjacent shelf waters have been warming faster than more than 95 % of the global ocean (Pershing et al., 2015). The year 2010 marked a stepwise change in Northwest Atlantic oceanography that brought about an ecosystem-level regime shift in the Gulf that was strongly linked to rapid warming and ice melt in the Arctic (Bamber et al., 2012; Sévellec et al., 2017; Putrasahan et al., 2019; Dukhovskoy et al., 2019; Friedland et al., 2020a, b). The resulting warming and strengthening of the Western Atlantic Subpolar Gyre has weakened the influence of the cold Labrador Current that has historically fueled the Gulf's high productivity from the north (Gonçalves Neto et al., 2021; Tesdal, 2020; Townsend et al., 2023). As Labrador Slope water has receded, the northward flowing, warm Gulf Stream has encroached from the south. These changes have percolated up the food web, diminishing net primary productivity and altering the composition of the phytoplankton community (Balch et al., 2012, Friedland et al., 2020, Tesdal, 2020). Consequently, the zooplankton assemblage has also changed, with observed declines of the cold-water copepod, *Calanus finmarchicus*, a foundational member of the pelagic foodweb (Pershing and Stamieszkin, 2020). *C. finmarchicus* has been implicated in the decline of herring stocks, sea birds, and the endangered North Atlantic right whale, all of which depend on this copepod as an energy-rich forage food (Record et al., 2019; Friedland et al., 2020a, b; Pershing et al., 2021; Meyer-Gutbrod et al., 2021). Recent correlative evidence also suggests that the downturn in *Calanus* has led to declines in young-of-year (YoY) American lobster recruitment despite record high lobster broodstock levels and early-stage larval production (Carloni et al., 2018).

The Gulf's lobster population increased substantially in the 1990s following a period of stability from the 1950s through the 1980s. Scientific consensus generally supported the interpretation that the population boom was largely driven by the combination of a decline in predatory groundfish and the favorable effects of warming across critical thermal thresholds for larval development in historically cooler areas of the species' range (Steneck and Wahle, 2013; Goode et al., 2019). However, after three decades of record-breaking landings, the Gulf's lobster fishery began to decline after 2016, declines that were anticipated by earlier downward trends in the recruitment of YoY lobster to coastal nurseries some 5–8 years earlier (Oppenheim et al., 2019). Our understanding of the drivers of these declines in settlement, despite high broodstock levels, have motivated a heightened intensity of research, and have become a focus of interest to the scientific community (ASMFC, 2020).

Recently, insights have been gained from a unique 30-year time series of larval lobster and zooplankton collected along coastal New Hampshire, near the center of the Gulf of Maine. Carloni et al. (2018) reported a curious decoupling in what would otherwise be expected to be a straightforward relationship between lobster broodstock abundance and their progeny. While Carloni et al. (2018) found the expected correlation between the numbers of early-stage lobster larvae and rising abundance of spawners in adjacent shelf waters, surprisingly, the same relationship did not hold for the still-planktonic postlarval stage. After a systematic assessment of correlations with environmental factors, including temperature, advection, and associated zooplankton, they found postlarval lobster cohorts correlated most strongly with densities of the copepod *C. finmarchicus,* rather than their parental broodstock. Furthermore, postlarval abundance in the New Hampshire collections also correlated well with resulting YoY cohorts at multiple American Lobster Settlement Index (ALSI) study areas in the western Gulf of Maine. Since the YoY lobster have proven to be a useful predictor of subsequent recruitment to the fishery (Wahle et al., 2009; Oppenheim et al., 2019; McManus et al., 2023), the finding raised the question of whether lobster recruitment could be limited by, and predicted from, the supply of planktonic foods. These findings have motivated further study to evaluate linkages between lobster recruitment and the Gulf of Maine zooplankton assemblage. In recent years, several parallel studies have been conducted for further retrospective analyses of existing data time series, including the present study, as well as a new analysis by Carloni et al. (2024) documenting the diverging phenology of larval lobster and *C. finmarchicus*. Additional field and laboratory studies are providing a better understanding of the mechanism of the trophic interaction between larval lobsters and the zooplankton assemblage (Ascher, 2023; Ascher et al. in review; Layland, 2023; Layland et al. in review), as well as the consequences of warming temperature on lobster reproductive performance (Waller et al., 2021; Ascher, 2023; Ascher et al. in review) that may also influence recruitment success.

In this study, we build on the findings of Carloni et al. (2018), by capitalizing on more than three decades of zooplankton monitoring in the Gulf of Maine through NOAA's EcoMon database (NOAA, 2021) and Canada's counterpart zooplankton monitoring in the Bay of Fundy (Casault et al., 2020). This enabled us to investigate the links between lobster recruitment and zooplankton assemblages over a broader geographic and taxonomic scope than provided by the New Hampshire time series. Here we evaluated how local- and basin-scale zooplankton dynamics and oceanographic indicators in the Gulf of Maine and Bay of Fundy correlated with lobster settlement indices, and each other, over the three decades of seasonal sampling (1988–2018). We reasoned that if coherent relationships existed between basin-scale and coastal zooplankton dynamics, and lobster settlement patterns, we would have a more compelling evaluation of the environmental and ecological factors potentially influencing lobster recruitment success within a significant portion of its range.

2. Methods

2.1. Methods overview

To examine the relationships between lobster settlement, local- and basin-scale zooplankton dynamics, and broader oceanographic processes, we compared time trends across five data sets from the Gulf (Fig. 1): (1) the American Lobster Settlement Index (ALSI) from southern Nova Scotia to Cape Cod Bay, the abundance of *C. finmarchicus* in coastal seasonal surveys in (2) New Hampshire and (3) the mouth of the Bay of Fundy, (4) the abundance of *C. finmarchicus* and associated zooplankton from NOAA's Gulf-wide Ecosystem Monitoring (EcoMon) cruises, and (5) the composition of water entering the Gulf through the Northeast Channel, reported as the proportion of water originating from Labrador Slope Water (LSW). Data for each time series were aggregated into annual indices to represent the interannual variability in a given process plus some stochastic error due to sampling. To better estimate the actual process-level dynamics while filtering some of the sampling error, we applied state-space smoothers to each time series. Except for the ALSI index, we produced smoothed time series with a "Local Level" model (Petris, 2010) as:

$$X_y = \mu_{y\text{-}1} + \eta_y + \varepsilon_y$$

where X_y is the value of a time series in year *y*, observed with error, and ε_y is the observational error:

$$\varepsilon_y \sim \mathrm{NID}(0, \sigma_\varepsilon^2)$$

$\mu_{y\text{-}1}$ is the actual state of the time series in the previous year and η_y is the change in the state over year *y*, modeled as:

$$\eta_y \sim \mathrm{NID}(0, \sigma_\eta^2)$$

Thus, the resulting time series, μ, represents an optimal estimate of the trend with the sampling error removed. All analyses were conducted on the R statistical platform (R Core Team, 2023).

2.2. Lobster settlement time series

The time series for lobster settlement was based on suction sampling conducted by contributors to the American Lobster Settlement Index

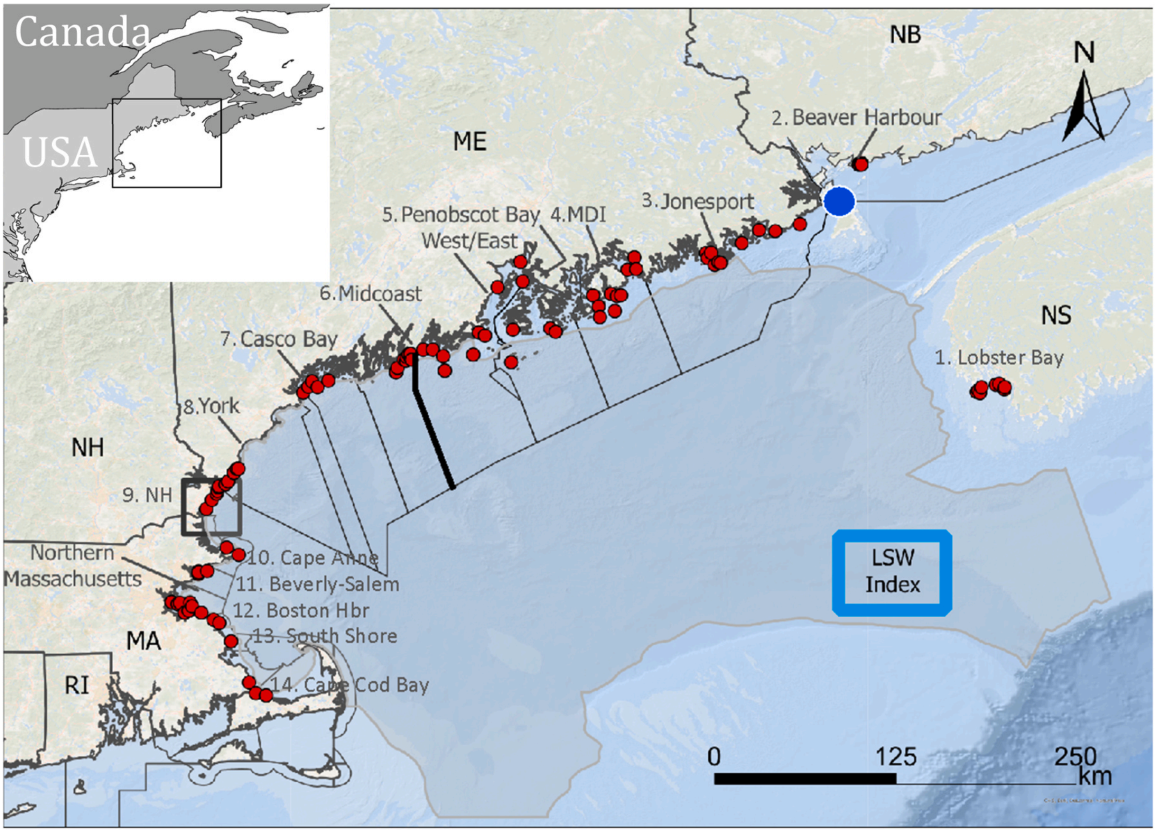

Fig. 1. Gulf of Maine region depicting ALSI study sites (red dots) within the 14 respective study areas (black boundaries; bold black line denotes boundary between northeast and southwest study areas); coastal New Hampshire larval lobster and zooplankton sampling sites (black box); DFO coastal Bay of Fundy zooplankton sampling station (blue dot); NEFSC basin-wide EcoMon sampling domain (darkened); and study area of the Northeast Channel used to calculate the Labrador Slope Water (LSW) index (blue box).

from 1989 to 2020 (ALSI, https://umaine.edu/wahlelab/american-lobster-settlement-index-alsi/, ACCSP, 2024). ALSI suction-sampling surveys at established fixed sites have a hierarchical sampling design with study areas containing multiple representative fixed study sites with multiple quadrats haphazardly sampled per study site annually, typically in August or September. We constrained the spatial domain to study areas within the Gulf, from southern Nova Scotia through Cape Cod, and study sites with a minimum of eight years of data, retaining 14 study areas, each composed of 4–10 study sites that collectively totaled 68 study sites. Observations of small lobsters were further constrained to individuals with a carapace length of 17 mm or less except for Massachusetts study areas where the constraint was set at 24 mm to account for a somewhat warmer regime with faster growth rates. These size bins are estimated to correspond to YoY and 1-Year-Olds, in effect representing two years of settlement. We chose to include two years of settlement because the delineation of just the YoY can be problematic and our intent is to characterize long-term trends and reduce observation errors rather than characterizing finer-scale inter-annual variability (Harrington et al., 2018).

We calculated time series for each study area within the Gulf and a combined region-scale index. To get time series for each of the study areas, we converted observations of young lobsters in quadrats to densities, based on quadrat size, then averaged across quadrats at a study site and sampling event. We then simply averaged together the mean observed density across study sites within a study area and year to get unsmoothed, yearly indices for each study area.

We calculated Gulf-wide indices using a hierarchical model-based method because ALSI survey sites were designed around local rather than regional monitoring, study areas are irregularly spaced along the coastline in the study region, and sampling did not begin in all study areas at the same time. We fitted the data to a state-space trajectory in log-space with study areas nested within the region study sites nested as random effects:

$$L_{asy} = \mu_{y\text{-}1} + \eta_y + \alpha_i + \beta_{ij} + \mathcal{E}_{asy}$$

where L_{asy} is the density of lobsters observed at study area a, and site s in year y, observed with error, and $\mathcal{E}_y$ is the sampling error:

$$\mathcal{E}_{asy} \sim \text{NID}(0, \sigma^2_{\mathcal{E}})$$

$\mu_{y\text{-}1}$ is the mean regional density of lobsters in the previous year and η_y is the change in the density over year y as above. α_i represents the offsets of study areas around the regional mean and β_{ij} are the offsets of all study sites within study area i. Both α_i and β_{ij} are assumed normally distributed with a mean of zero and their own variance. We fit the model using Template Model Builder (TMB, Kristensen et al., 2016).

With this structure, all study areas and study sites are assumed to have a common relative trajectory in time but to vary in scale across space, recognizing local variations in larval supply, habitat quality, predation rates, and other ecological processes. To obtain a predicted settlement time series from this model, we extracted the predicted dynamics for a single study site as a proxy for the estimated common trajectory among all study areas. The choice of study area is inconsequential for our purposes because our primary interest is in relative change over time and modeled predictions for all study sites have the same relative trend and exhibit the same relationships when correlated against another time series.

Because prior analysis suggested differences in trajectories among study areas in the northeastern and southwestern end of the Gulf (Pershing et al., 2012; Goode et al., 2019), we also split the region and fit two separate sub-regional models; one to northeastern study areas from

Penobscot Bay through Nova Scotia, and a second model including southwestern study areas from Midcoast Maine to Cape Cod (Fig. 1).

2.3. Coastal New Hampshire and Bay of Fundy copepod time series

We constructed coastal copepod abundance time series based on a zooplankton monitoring study conducted off New Hampshire, USA (Normandeau, 2016) and lower Bay of Fundy of coastal New Brunswick, Canada (Casault et al., 2020). In New Hampshire, macrozooplankton were sampled at two stations using oblique tows with a pair of 1-m diameter plankton hoop nets (505 µm mesh) (Fig. 1 and Fig. S-1). Nets were fitted with depressors and flow meters and towed for 10 minutes under variable speeds to allow nets to sample multiple depths within the water column with each tow sampling a volume of about 500 m^3. Samples were collected monthly from 1988–2018 and fixed in buffered formalin before enumeration. Annual geometric mean *C. finmarchicus* abundances were then calculated for each site. Because values for both sites were not available for all years, we merged the time series for coastal New Hampshire into a single time series by fitting a general linear model with fixed year effects and an offset for the two sites. We then extracted the calculated year effects and fit a local-level model to the merged New Hampshire time series.

Sampling for zooplankton at the mouth of the Bay of Fundy began in 1999 by Fisheries and Oceans Canada at fixed station “Prince 5” (Fig. 1) near Grand Manan Island (Casault et al., 2020). Monthly vertical tows were conducted year-round with 75-cm ring net (202 µm mesh net) for biomass (wet and dry weights) and numerical abundance. Samples were fixed in buffered formalin. Numerical abundance data were log transformed, expressed as standardized anomalies relative to the time series mean, and smoothed prior to conducting correlation analyses described below.

2.4. EcoMon Regional zooplankton time series

We used zooplankton data collected on NOAA, Northeast Fishery Science Center (NEFSC) Ecosystem Monitoring (EcoMon) cruises between 1988 and 2018 to examine regional dynamics of the zooplankton assemblage and specifically, *C. finmarchicus*, across the Gulf of Maine (Fig. 1). EcoMon sampling uses two 61 cm diameter Bongo nets with 333 µm mesh nets (Kane, 2007). While these surveys occurred year-round, we constrained the analysis to samples collected between August 7th and November 20th, (Day of Year 219 – 324, Fig. S-1). Even though the larval lobster season is likely to have begun earlier in the summer, EcoMon sampling rates for this period were low and inconsistent across years. Nonetheless, we found EcoMon’s *C. finmarchicus* index to be highly correlated with New Hampshire’s year-round index (Table S-1), suggesting EcoMon’s constrained data set sufficiently captured the annual variability. Additionally, Carloni et al. (2024) noted interannual variations in the onset and duration of lobster hatching seasons and trends for the season extending later into the fall and Ji et al. (2022) found the season-specific annual *C. finmarchicus* abundance anomalies of the deep basins (shown in their Fig. 2) were more correlated for summer and fall than other season combinations.

Thus, to allow for interannual variability in larval season and increase sample sizes to stabilize abundance indices, we also included plankton samples from October and November, which had more consistent sampling and exhibited similar temporal patterns to the summer months. All calculations were performed on zooplankton abundance (individuals per 10 m^2 sea surface area).

We explored cohesive dynamics among groups of zooplankton species represented in the EcoMon database for summer and fall using a principal components analysis (PCA) to understand if there were significant temporal shifts in community composition and with some expectation that dynamics across multiple correlated species may be more stable than for individual species, partially mitigating observation error. The PCA included the 21 most common species, occurring in

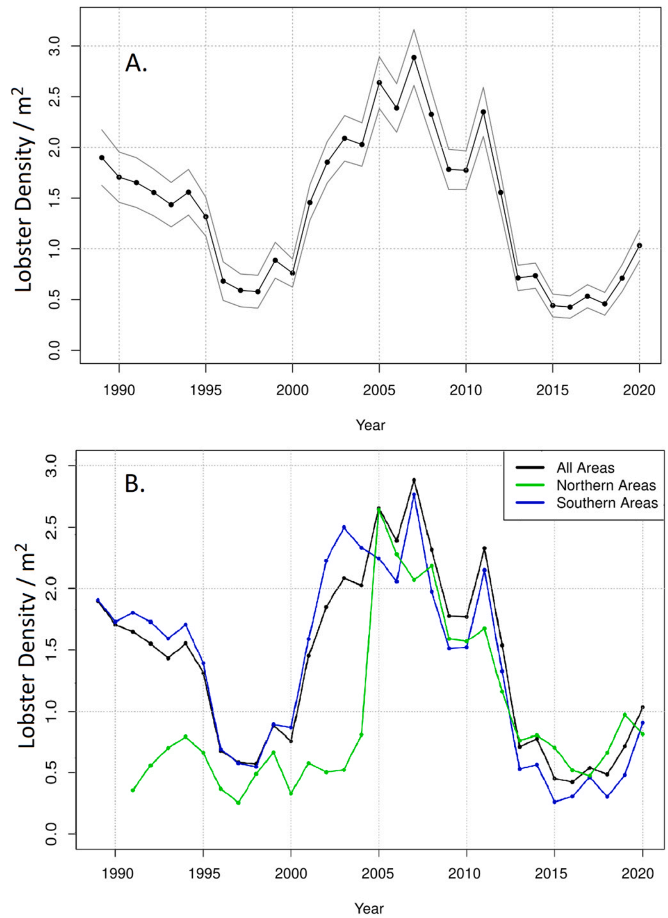

Fig. 2. A. Modeled ALSI settlement trends (+/- 2SE) for all combined study areas in the Gulf of Maine. B. Modeled ALSI settlement trends for all combined study areas, as in A, and separate trends for southwestern and northeastern study areas.

>20 % of plankton samples, as well as three less common species groups (*Calanus minor*, Ostracods and Protozoa) that exhibited strong temporal patterns. Abundances from individual tows for each species were log+1 transformed before averaging within survey stratum and year. We then performed a PCA on sample correlations by transforming the resulting mean abundances to z-scores within species and stratum across years, which gave each species and stratum equal influence in the analysis regardless of absolute abundances or frequency of observation. We retained a limited set of the resulting principal components based on the variance explained and identified the plankton species groups that were most highly correlated with each component. For these retained components, we averaged the PCA score for each year across strata and plotted this mean time series for the PCA.

To examine if there were spatially distinct trajectories for *C. finmarchicus* within the EcoMon sampling domain, we log-transformed and averaged copepod densities within strata and years, then calculated z-scores within each stratum across years, and conducted a cluster analysis on the standardized data. As this analysis did not support splitting the Gulf into sub-areas with distinct dynamics, we calculated a single stratified-mean survey index for the region as a whole. This survey index was then log-transformed and fitted to a local-level model.

2.5. Labrador Slope Water index

Water enters the Gulf of Maine primarily through the northeast channel and surface waters south of Nova Scotia (Fig. 1; Pettigrew et al., 2005; Runge et al., 2015). As part of the State of the Ecosystem Report (NEFSC, 2023), the NOAA's Northeast Fisheries Science Center maintains and updates a time series on the composition of water entering through the Northeast Channel, based on CTD data collected from a defined region encompassing the channel (Fig. 1) and a three-point mixing algorithm developed by Mountain (2012). Of the three potential water types observed here, most water is either Labrador Slope Water (LSW) or Warm Slope Water (WSW), with a third small fraction being Scotian Shelf Water. LSW primarily derives from the cold, low salinity Labrador Current system from the north, whereas the WSW is warm, high salinity water influenced by the Gulf Stream from the south. Thus, the LSW index provides an indicator for the temperature, salinity, and nutrient composition of water entering the Gulf, as well as the zooplankton community associated with these waters. We extracted the time series of the proportion of LSW entering the Gulf and fit a local-level model to represent shifting water compositions feeding the

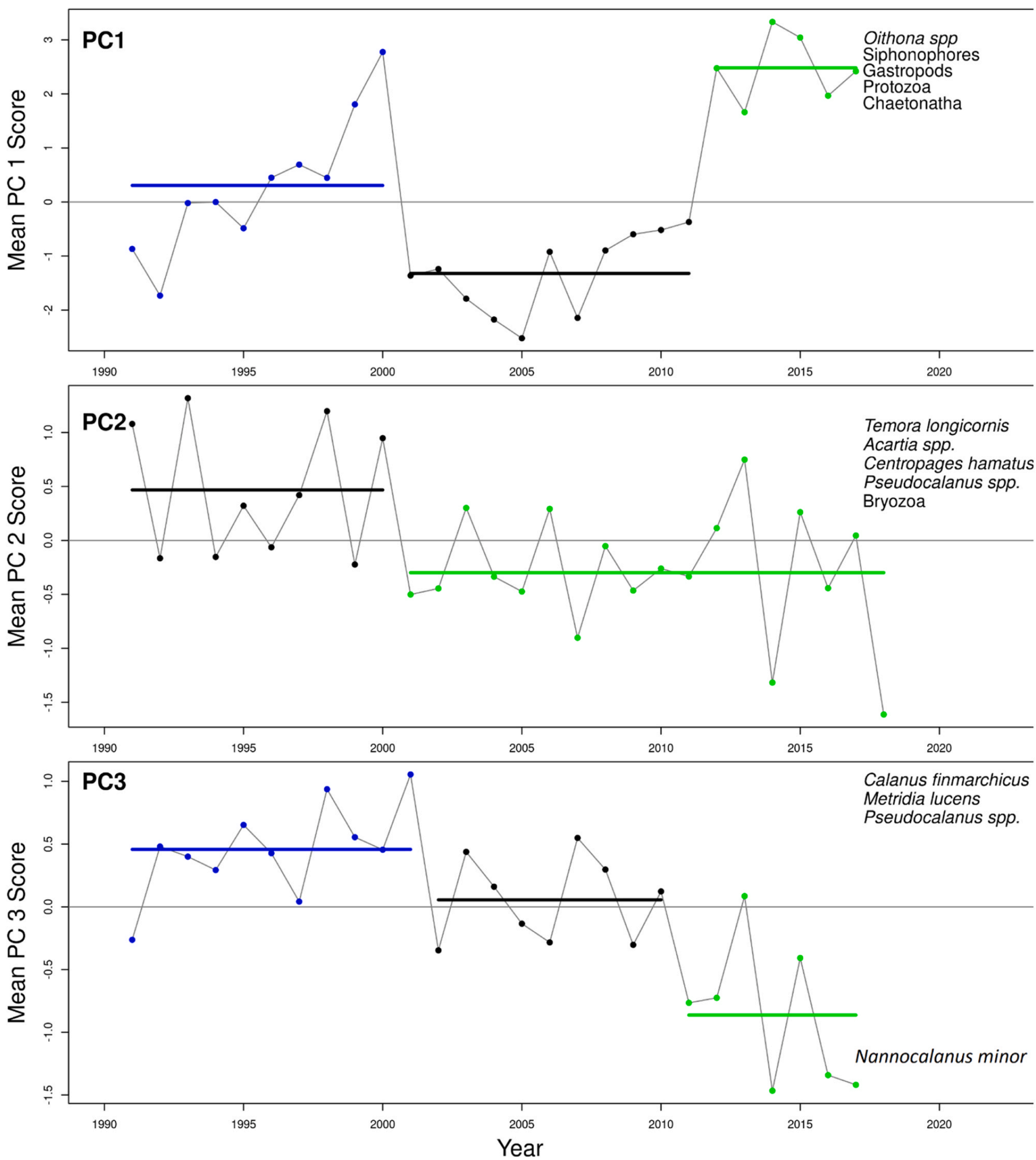

Fig. 3. Time series trajectories and associated species for the first three Principal Components (PC) analysis of EcoMon zooplankton assemblages. Horizontal bars indicate mean for the corresponding time series. Note precipitous increase in PC1 and decline in PC3 after 2010. Species listed comprise those correlating most strongly, either directly or inversely with the PC at a threshold value above 0.25 or below −0.25. In all cases species meeting these criteria correlated positively with their PC, with the exception of *Nannocalanus minor* in PC3.

Gulf ecosystem.

2.6. Correlation analysis

We first performed Pearson's correlations of *C. finmarchicus* from both the Gulf-wide EcoMon and Bay of Fundy to the unsmoothed lobster settlement time series for the 14 individual ALSI study areas, including lagging lobster settlement behind plankton dynamics by one year. We then correlated the smoothed Gulf-wide, northeast and southwest lobster settlement indices, against all combinations of the unsmoothed and smoothed *C. finmarchicus* indices from coastal New Hampshire, Bay of Fundy, and the Gulf-wide EcoMon domain, as well as the Labrador Slope Water index area.

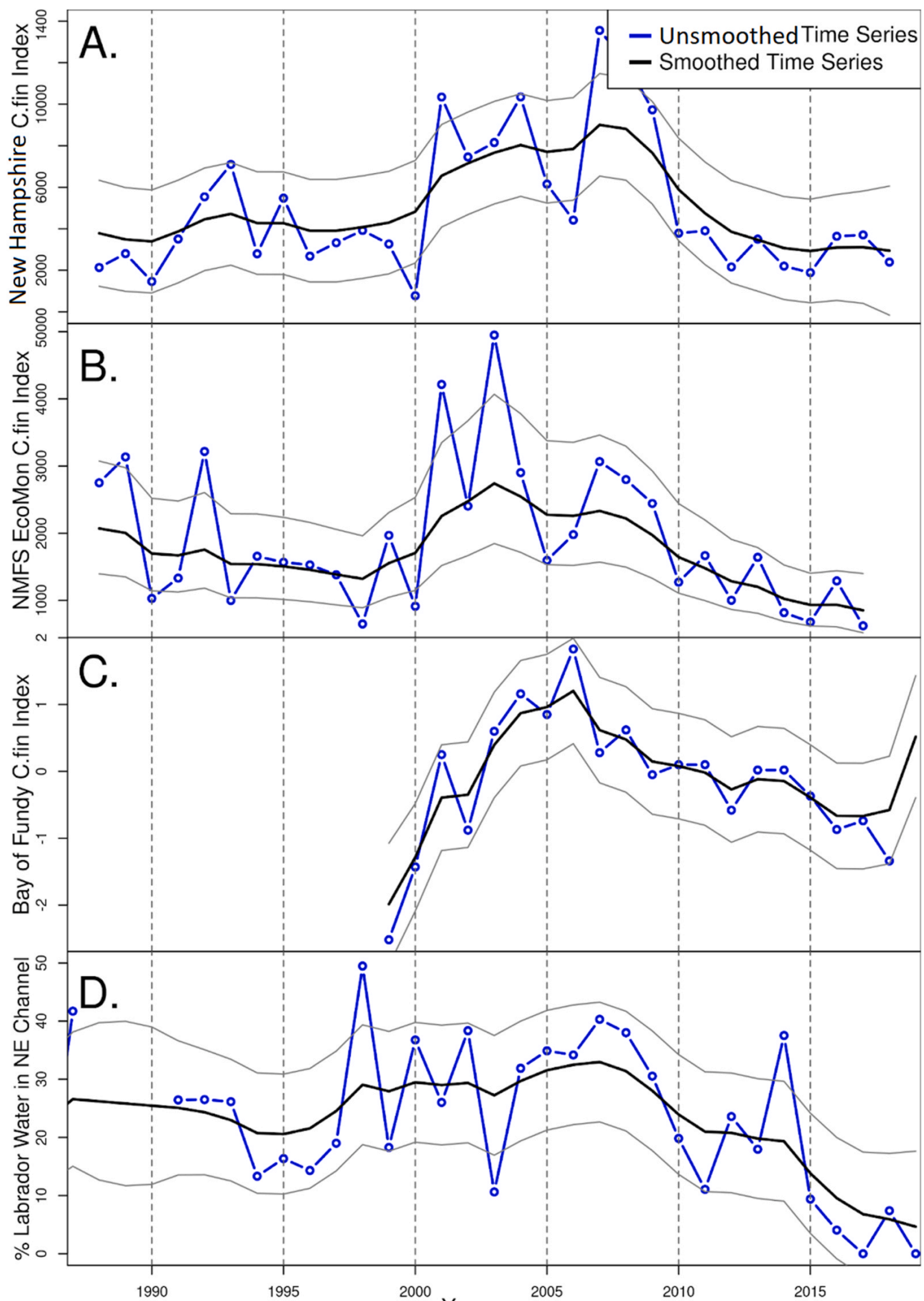

Fig. 4. *Calanus finmarchicus* indices for (A) coastal New Hampshire, (B) Gulf-wide EcoMon domain, and (C) Bay of Fundy. (D) Labrador Slope Water index measured at the Northeast Channel of the Gulf of Maine. Unsmoothed annual data (blue); smoothed (black) (+/- 2SE). See Fig. 1 for sampling locations.

3. Results

3.1. Lobster dynamics

The smoothed index for YoY and 1-year old lobsters indicated a period of moderate settlement density between 1990 and 1995, a drop to a period of low densities from 1996 to 2000, with a sharp rise to high settlement levels from 2003 to 2011, followed by another drop to low levels from 2013 to 2020 (Fig. 2a). Splitting the study areas into northeastern and southwestern sectors revealed distinct trajectories for the two areas (Fig. 2b). The trend for the Northeast area was consistently lower until 2004, followed by a sharp rise to match and exceed the southwestern study areas. The two sub-regions show remarkably cohesive dynamics for 2005–2020.

3.2. Zooplankton assemblage dynamics

Our broader taxonomic evaluation of temporal dynamics among the EcoMon zooplankton assemblage indicated complex trends in the first three Principal Components (Fig. 3). PC1 accounted for 21 % of the total variance and was primarily associated with five diverse taxonomic categories (*Oithona* spp., Siphonophora, Gastropoda, Protozoa, and Chaetognatha). PC1 showed three strong temporal regimes: an increasing trend prior to 2000, a consistently low regime through 2011, then a consistently high regime thereafter. PC2 accounted for 15 % of the variance and was primarily associated with four copepod groups (*Temora longicornis*, *Acartia* spp., *Centropages hamatus*, *Pseudocalanus* spp.), and bryozoan larvae. PC2 gradually declined throughout the time series with a potential regime shift around 2000. PC3 accounted for 8 % of the variance and comprised four copepod taxa: *C. finmarchicus, Pseudocalanus* spp., *Metridia lucens* and *Nannocalanus minor*. The first three were positively correlated with the component, while *N. minor* was

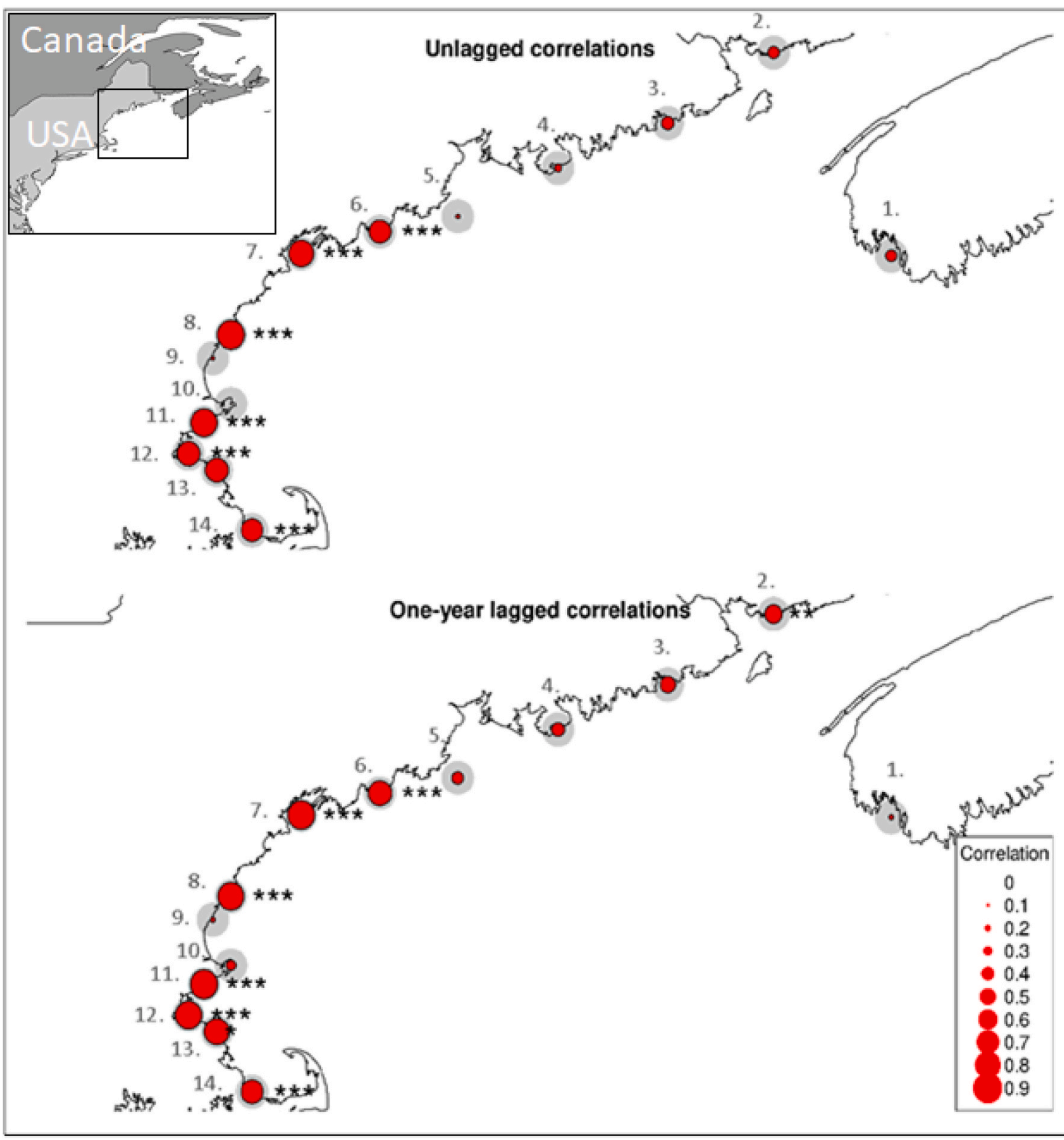

Fig. 5. Mapped correlations between unsmoothed settlement time series (YoY + 1Year Olds) for individual study areas and the smoothed EcoMon *C. finmarchicus* index for the period 1988–2018. Significant correlations are noted as * - p<0.05, ** - p<0.01, *** - p<0.001. Some higher correlations do not achieve the significance criteria due to shorter time series. Study area labels as in Fig. 1.

negatively correlated with the component. It is noteworthy that, of the four species, *N. minor* is associated with warmer water and has the most southern distribution (WORMS, 2021). PC3 had three stable regimes, starting above the time series mean prior to 2002, then remaining close to the mean through 2010, before dropping in 2011, ending at time-series lows in 2016 and 2017.

3.3. *Calanus finmarchicus* dynamics

There was a high-density regime in the *C. finmarchicus* index from coastal New Hampshire from 2001 to 2009 with low densities before and after this period (Fig. 4a). Similarly, the *C. finmarchicus* index from the EcoMon survey was low prior to 2001, increased through 2005, followed by a decline through the remainder of the time series, ending at or near record low values (Fig. 4b). The *C. finmarchicus* time series for the coastal Bay of Fundy region did not begin until 1999, but it was similarly low in its initial year and increased dramatically in the early 2000s to a time series peak in 2006 after which it declined monotonically through 2018 (Fig. 4c). The proportion of Labrador Slope Water advected into the Gulf of Maine has been declining in recent years: while there has been much interannual variability, the smoothed index was generally high, approaching 30 %, until the late 2000s followed by a decline to less than 10 % in the most recent years (Fig. 4d).

3.4. Correlations among time series

The Gulf-wide, smoothed EcoMon *C. finmarchicus* index from 1989 to 2018 tended to correlate more strongly with lobster settlement trends in the southwestern Gulf of Maine. EcoMon's copepod index significantly correlated with the unsmoothed lobster settlement trends in six of the 14 study areas when unlagged and eight of the 14 when lagged by one year. All of the significantly correlated study areas were located southwest of Penobscot Bay when unlagged, and all but one when lagged by one year (Fig. 5). By contrast, the Bay of Fundy smoothed *C. finmarchicus* index

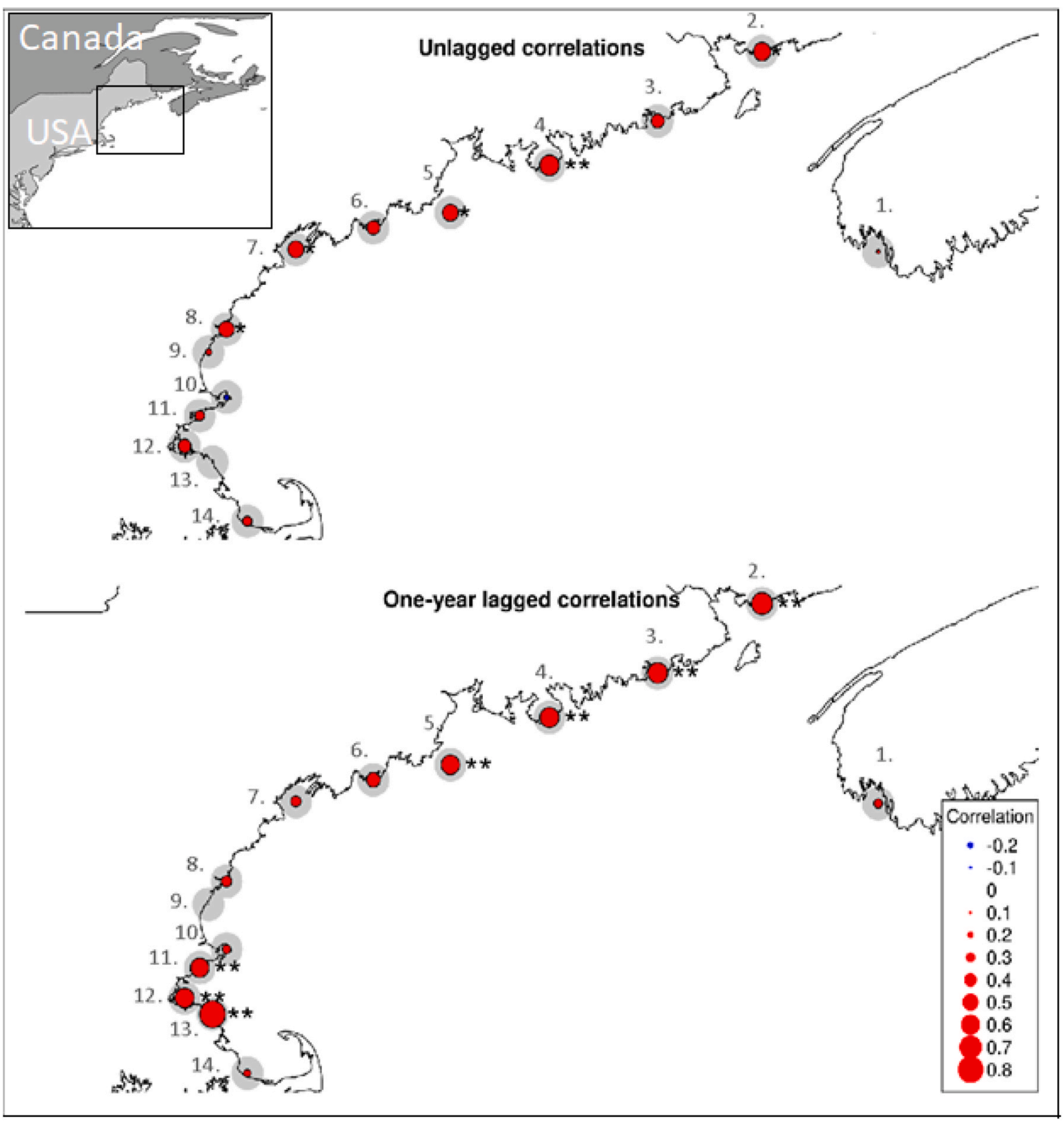

Fig. 6. Mapped correlations between unsmoothed settlement time series (YoY + 1Year Olds) for individual study areas and the smoothed Bay of Fundy *Calanus finmarchicus* index for the period 1999–2019 from Casault et al. (2020). Significant correlations are noted as * - p<0.05, ** - p<0.01, *** - p<0.001. Some higher correlations do not achieve the significance criteria due to shorter time series. Study area labels as in Fig. 1.

tended to correlate more strongly with lobster settlement dynamics in the northeastern Gulf. This copepod index correlated with the unsmoothed lobster settlement trends in five of the 14 study areas when unlagged, and seven when lagged by one year (Fig. 6). Three of the five significant unlagged correlations, and five of the seven lagged correlations, were with lobster study areas in the northeastern Gulf, from Penobscot Bay to Beaver Harbour. In short, this analysis suggests lobster settlement trends in the southwestern Gulf are more closely linked to basin-scale *C. finmarchicus* dynamics, while those in the northeastern sector may be more strongly tied to coastal dynamics in the Bay of Fundy and eastern Maine.

Fig. 7 and Table 1 provide a comparison of the correlation statistics for the aggregated and smoothed state-space lobster settlement time series (Fig. 3; north, south and combined study areas) with the smoothed New Hampshire, Bay of Fundy and EcoMon *C. finmarchicus* time series (Fig. 4a-c), as well as the smoothed Labrador Slope Water index (Fig. 4d). Correlations involving smoothed time series performed better than unsmoothed time series in virtually all cases. For brevity and clarity only correlations for the smoothed time series are given in Table 1. Sixteen of the 18 correlations presented in Table 1 were significant at $p<0.05$, and all correlations were positive. The coastal New Hampshire and Gulf-wide EcoMon *C. finmarchicus* time series, and the Labrador Slope water most strongly correlated with the ALSI lobster combined and southern time series, whereas *C. finmarchicus* trends in the Bay of Fundy correlated more strongly with lobster trends in the north. Moreover, we observed that *C. finmarchicus* dynamics in coastal New Hampshire are more highly synchronized with the Gulf-wide (EcoMon) *C. finmarchicus* dynamics than those in the Bay of Fundy. Similarly, variability in the Labrador Slope Water was strongly tied to *C. finmarchicus* trends in both New Hampshire and EcoMon, but not to the Bay of Fundy. In short, as with our finer spatial scale correlations depicted in Figs. 5 and 6, lobster settlement trends in the southwest Gulf of Maine appear to be generally correlated with basin-wide *C. finmarchicus* dynamics and the Labrador Slope Water index, whereas lobster settlement in the northeast tends to link more strongly to *C. finmarchicus* variability in the Bay of Fundy region, which also does not appear to be as strongly tied to changes in the Labrador Slope Water in the Northeast Channel.

4. Discussion

Our retrospective time series analysis reinforces our understanding of correlative linkages between American lobster recruitment and changes in the Gulf's pelagic food web. These linkages might have resulted from warming temperatures and changing oceanography over the past few decades, as characterized by relevant long-term

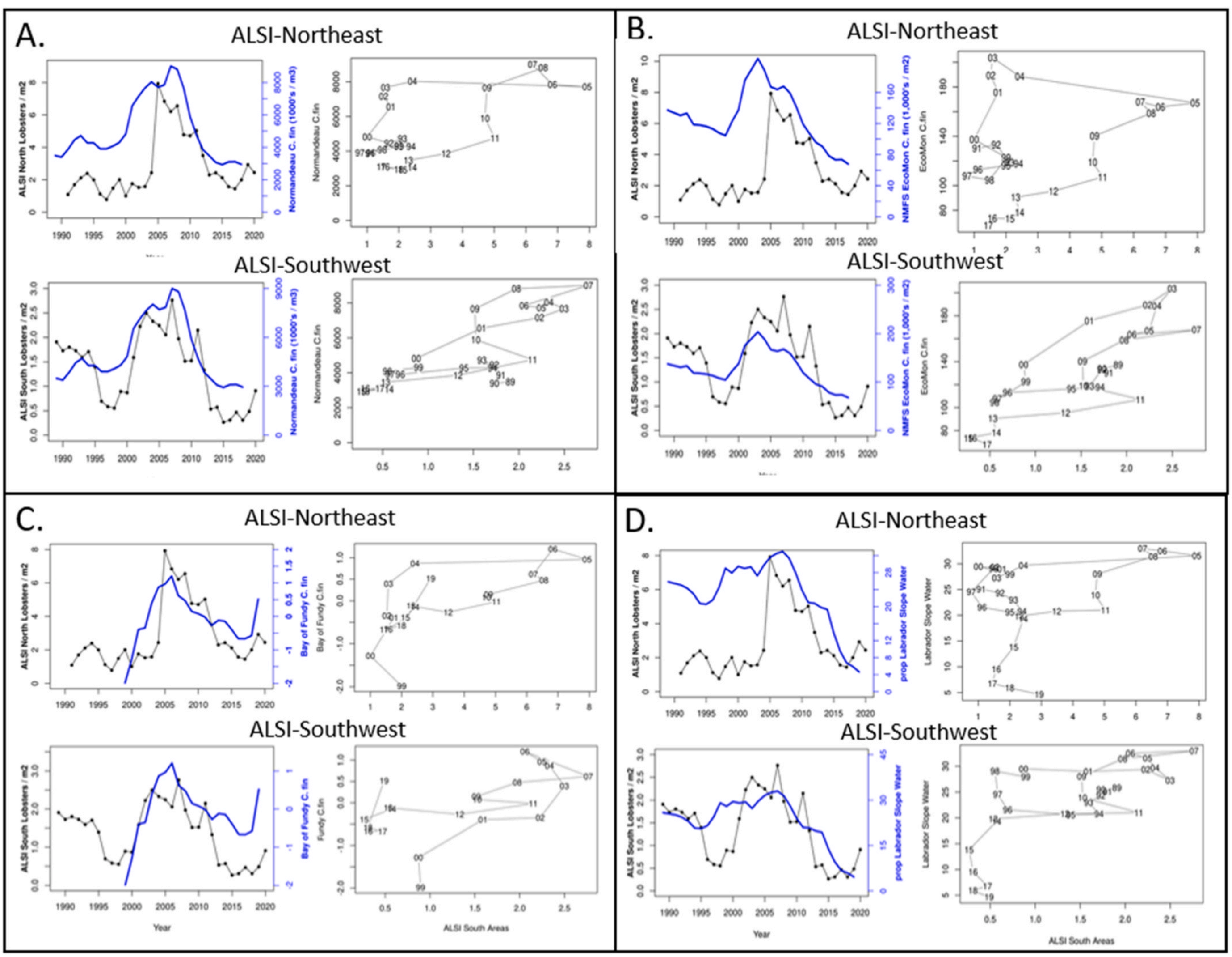

Fig. 7. Time series (left) and scatterplots (right) of northeast and southwest Gulf of Maine lobster settlement indices with (A) New Hampshire *C. finmarchicus* index, (B) NEFSC EcoMon *C. finmarchicus* index, (C) Bay of Fundy *C. finmarchicus* index and (D) Labrador Slope Water index. Numbers on scatterplots denote sampling year; lines connect consecutive years. See Table S-1 for correlation statistics.

Table 1
Pearson coefficients for correlations among constructed time series. Colors indicate statistical significance; legend in column at right. See Table S-1 for full comparison of correlations for unsmoothed and modeled indices.

	ALSI Lobster						
	Combined	Northeast Areas	Southwest Areas	NH Cfin	EcoMon Cfin	Fundy Cfin	
NH Cfin	0.78	0.65	0.76				NS
EcoMon Cfin	0.73	0.30	0.83	0.84			P < 0.05
Fundy Cfin	0.68	0.67	0.59	0.67	0.46		P < 0.01
LSW	0.66	0.37	0.70	0.73	0.82	0.28	P < 0.001

environmental time series (Figure S-2). Specifically, including NOAA's EcoMon, and DFO Canada's Bay of Fundy surveys have enabled us to expand databases used in the correlation analysis from the local scale of coastal New Hampshire (Carloni et al., 2018) to include a larger geographic scope of biological and oceanographic indicators.

The significant correlation between the local scale New Hampshire data set and the Gulf-wide scale EcoMon time series for *C. finmarchicus* indicated that time trends measured in coastal New Hampshire strongly reflect basin-scale dynamics for this species. This is important because, to date, evidence of larger scale coherence was only suggested by correlations between local *C. finmarchicus* variability measured in coastal New Hampshire and lobster settlement time series along the southwestern Gulf coast (Carloni et al., 2018). Similarly, in the present study we found that EcoMon's Gulf-wide *C. finmarchicus* index most strongly correlated with lobster settlement trends at study areas in the southwestern Gulf, but only weakly with those in the northeast. Accordingly, the addition of the *C. finmarchicus* trends measured from the northeastern area of the Gulf correlate more strongly with lobster settlement dynamics in that region (Casault et al., 2020). The Maine Coastal Current is an important transport pathway, connecting the northeast to the southwest Gulf. *C. finmarchicus* copepodites emerging from diapause enter the coastal current from eastern areas upstream (Bay of Fundy, Scotian Shelf, Wilkinson Basin) in the spring (Ji et al., 2017, 2022). The food rich environment of the coastal current can supply potential reproduction and growth of multiple generations of *C. finmarchicus* along the coast from spring to summer.

The biological implications of contrasting physical oceanographic conditions and dynamics in the northeast and southwest Gulf have long been recognized, especially as regards to the lobster fishery (Huntsman, 1923; Steneck and Wilson, 2001; Pershing et al., 2012;Goode et al., 2019). From the present analysis it is clear that the large surge in juvenile lobster observed in the northeast Gulf lagged a few years behind the smaller magnitude surge in the southwest, but over the last decade the two regions have been declining precipitously in tandem. One interpretation for the lag in the northeast lobster settlement surge, advanced by Goode et al. (2019), is that until the northeastern Gulf warmed sufficiently, larval settlement was suppressed by the relatively cool temperatures in that region. They argued that the relatively recent boom in lobster settlement in the northeastern Gulf in the mid-2000s was triggered by warming above a critical thermal threshold for larval development at approximately 12 °C (MacKenzie, 1988; Annis et al., 2005).

We caution that the spatial coverage of the ALSI settlement time series was relatively sparse prior to 2000 and the state-space model may not fully capture regional dynamics in the earlier years. Nonetheless, the state-space time series extrapolated back to the 1990s is grounded in an understanding of the scale of spatial coherence and justifies dividing the Gulf into northeastern and southwestern recruitment cells (e.g., Pershing et al., 2012; Goode et al., 2019), even if they may have become more convergent in recent years. In addition, the trends in early benthic phase lobster abundance are also robust to the selection of size definitions used for age 0+ and 1+ year lobsters. The size ranges we selected are based on previous analyses (e.g., Harrington et al., 2017, Morin and Wahle, 2019) and remain the subject of continuing refinement and interpretation.

Our analysis of the EcoMon database indicates the Northeast shelf ecosystem has experienced zooplankton regime shifts characterized by declines in overall abundance and the proportion of large-bodied copepods, accompanied by an increase in diversity (Morse et al., 2017; NEFSC 2023). *C. finmarchicus* had above average abundances from 2000 to 2010 in the Gulf of Maine, while smaller copepods, *Centropages typicus* and *Pseudocalanus* spp. had below average abundances (NEFSC, 2021). A reversal of abundance trends among the two size classes has occurred since 2012. In addition, potential copepod predators including gelatinous zooplankton (i.e., cnidaria) and krill have also increased in abundance post 2010 (NEFSC, 2021). Concurrent with these declines are dramatic oceanographic changes in the Gulf that have diminished primary and secondary productivity over the past decade, and may further be driven by environmental changes occurring in the Arctic that transferred to the Gulf along the Scotian Shelf (Friedland et al., 2020a,b; Gonçalez-Neto et al., 2021; Seidov et al., 2021). These reports, along with the declines in the Labrador Slope Water index trend reported here, suggest a weakening influence on the Gulf of the cold, nutrient rich waters of the Labrador Current and a concurrent strengthening effect of warm, nutrient poor waters from the Gulf Stream (Townsend et al., 2015, 2023; Pershing et al., 2021).

These results reinforce our previous work suggesting that the drivers of lobster recruitment may be linked to changes in the abundance and phenology of planktonic food for developing larvae (Carloni et al., 2018, 2024). Using a match/mismatch index (Cushing, 1990), Carloni et al., (2024) most recently provided evidence that the seasonal overlap of larval lobster and *C. finmarchicus* has declined in recent years. Since 2010, the *C. finmarchicus* season has been ending with increasing frequency before the peak abundance of stage I lobster larvae. We speculate that the reduced overlap between planktonic larval lobsters and their prey may have exacerbated the effects of diminished prey abundance on recent trends in lobster recruitment.

Similarly, in Western Australia, DeLestang et al. (2015), found consecutive low years of western rock lobster, *Panulirus cygnus*, recruitment were more strongly linked to timing of spawning relative to favorable environmental conditions for larval development than to the volume of egg production. Although the mechanisms may differ, our analysis also suggests the thermally controlled timing of the egg hatch is likely an important factor determining the co-occurrence of larvae with their planktonic foods. The seasonal overlap of American lobster larvae with *C. finmarchicus* remains poorly understood on a wider geographic scale because of the lack of larval lobster sampling. Recently initiated larval lobster and zooplankton sampling by several research groups in the Gulf of Maine will dramatically increase our understanding of larval lobster dynamics in the future.

New research is breaking ground on our understanding of the mechanism of the trophic interaction between larval American lobster larvae and their planktonic prey. Recent work by Ascher (2023) built on only two previous gut content analyses of larval American lobster stomachs from collections in the wild (Harding et al., 1987; Juinio and Cobb, 1992), by combining conventional microscopy with new DNA sequencing approaches. In the first gut content analysis of lobster larvae from the coastal Gulf of Maine, Ascher's metabarcoding analysis confirmed a range of taxa observed by microscopy, mainly dominated by crustaceans, prominently copepods and decapods, but also including taxa not readily identified visually, such as cnidarians and polychaetes and molluscs. In a more targeted analysis by qPCR, Ascher found both stage I larvae and postlarvae collected in coastal Maine to contain *C. finmarchicus* in disproportionately high numbers relative to the occurrence of this species in concurrent zooplankton samples. This was supported by laboratory studies showing that all lobster planktonic stages were able to capture and ingest *C. finmarchicus* (Layland et al., in review). Furthermore, swimming speeds, handling time and functional response of the four developmental stages to a range of prey densities showed an order of magnitude leap in predatory capacity in the transition to the postlarval stage. These results, together with experiments by Ascher et al. (in review) indicating postlarvae can survive starvation considerably longer than the larval stages, underscore the relative vulnerability of early larval stages to low planktonic food supplies.

While our focus in this study has been on the potential role of larval trophic interactions on lobster settlement trends, we recognize that other ecological and climate change-related factors come into play. Indeed, previous studies have demonstrated that dominant drivers of recruitment trends can change over time (Wahle et al., 2009; Li et al., 2018; Goode et al., 2019), and recent work has demonstrated considerable declines in maturation size of female lobsters (Waller et al., 2021) that may have important implications for larval production or performance (Ascher et al. in review). It is therefore important to be cognizant of the range of factors that can influence the recruit process. Because our previous correlation analysis (Carloni et al., 2018) found the spawner-recruit relationship to decouple between the first larval stage and the postlarva, we focused the present analysis on potential determinants of larval survival that could affect benthic recruitment. Lobster spawning stock biomass (SSB) or other proxies for egg production were therefore not included in the present analysis. Nonetheless, future research should involve efforts to understand the combined effects of SSB and environmental factors in determining reproductive success and the degree to which fishery management may be able to mitigate environmentally-induced declines in fishery productivity.

The Gulf of Maine is warming at an alarming rate, and although we are beginning to understand the effects of these changes on fisheries in this region (Pershing et al., 2015, 2021; Richards, 2016, Gonçalez-Neto et al., 2021), the evidence remains largely correlative. The disconnect first identified by Carloni et al. (2018) between lobster spawning stock biomass and postlarval abundance, despite the strong quantitative link between spawners and stage I larvae, narrowed the likely timing of decoupling of the spawner-recruit relationship to the early planktonic larval stages. With this report we provide supporting evidence that declines in *C. finmarchicus*, and perhaps other members of the zooplankton assemblage, may be linked to that decoupling. In the analysis of the coastal New Hampshire data, Carloni et al. (2018) found little evidence that variability in postlarval lobster was correlated with potential plankton predators, such as gelatinous zooplankton, chaetognaths or ichthyoplankton. The rising abundance of some of these planktonic carnivores evident in the EcoMon time series, suggests we cannot entirely rule out the potential role of top-down mechanisms as a driver of larval lobster survival (Jaspers et al., 2015). The gelatinous zooplankton particularly warrant more attention as they are especially difficult to sample, and few long-term time series exist. Increases in some planktonic species, on the other hand, may reflect northwardly shifting ranges of warmer water species, such as the copepod, *Nannocalanus minor,* for example.

The significant correlation between declines in both the Labrador Slope Water and *C. finmarchicus* begin to link changes in potential oceanographic drivers to subsequent changes in the zooplankton assemblage, and specifically the abundance and phenology of *C. finmarchicus* that may have important implications for lobster larval survival. While the evidence presented here remains correlative, it poses testable hypotheses for continued analysis regarding the mechanisms driving trends in lobster settlement, subsequent fishery recruitment and landings over the past decades.

Recent low levels of YoY lobster settlement in the Gulf have been a cause for concern to fishery managers, and although adult abundance is still near time series highs, there have been a clear signals of declines in both sublegal lobsters (ASMFC, 2023), and landings, as forecasted by Oppenheim (2019). Although the sustained low levels of settlement may be tempered to some degree by increased suitable thermal habitat in deep water (Goode et al., 2019), several surveys across a broad spatial domain corroborate a declining population and may be a harbinger of continued declines in the near-term. In response to these concerns, the Atlantic States Marine Fisheries Commission has approved an addendum that includes an increase in the minimum harvestable size to increase spawning stock biomass and provide additional resiliency to the Gulf of Maine-Georges Bank lobster stock. Le Bris et al. (2018) noted that conservation measures implemented in the Gulf in the 1990s to protect spawning stock biomass set the stage for the fishery to capitalize on favorable conditions for recruitment during the boom years, and these current proactive measures may prove to do the same. However, given the notorious decoupling of spawner abundance and subsequent recruitment in lobsters and other crustacean fisheries (Wahle, 2003; Carloni et al., 2018), there is no guarantee of a beneficial outcome. Indeed, the research presented here adds further support to the hypothesis that environmental factors, in this case those impacting the pelagic food web, may be critical to lobster recruitment.

CRediT authorship contribution statement

Burton Shank: Writing – review & editing, Writing – original draft, Visualization, Methodology, Formal analysis, Data curation, Conceptualization. **Paul Geoghegan:** Writing – review & editing, Writing – original draft, Data curation, Conceptualization. **Joshua Carloni:** Writing – review & editing, Writing – original draft, Methodology, Data curation, Conceptualization. **Richard Wahle:** Writing – review & editing, Writing – original draft, Supervision, Project administration, Investigation, Funding acquisition, Conceptualization. **Andrew Goode:** Writing – review & editing, Writing – original draft, Conceptualization. **David Fields:** Writing – review & editing, Writing – original draft, Funding acquisition, Conceptualization. **Harvey Walsh:** Writing – review & editing, Writing – original draft, Data curation.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper

Data Availability

Data will be made available on request.

Acknowledgements

This study was supported in part by a grant from the Maine Department of Marine Resources Lobster Research Collaborative to RW and DF. We are grateful to the following organizations for the use of data sets for our analyses: the American Lobster Settlement (ALSI) collaborative (Maine, New Hampshire, Massachusetts, Rhode Island, New Brunswick, Nova Scotia, and Prince Edward Island); Normandeau Associates, Inc. for use of the New Hampshire larval lobster and zooplankton tow data; NOAA for use of EcoMon zooplankton and Labrador Slope Water databases; and the Department of Fisheries and Oceans, Canada for their Prince 5 zooplankton data time series.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.fishres.2024.107082.

References

ACCSP 2024. American Lobster Settlement Index database portal. ⟨https://safis.accsp.org:8443/safis_prod/r/safis_prod/lsi/login⟩.
Annis, E.R., Incze, L.S., Wolff, N., Steneck, R.S., 2005. Estimates of *in situ* Larval Development Time for the Lobster, *Homarus americanus*. J. Crustace Biol. 27, 454–462. https://doi.org/10.1651/S-2758.1.
Ascher, A., 2023. Climate Change and an evolving fishery: do declining maternal size and planktonic foods affect lobster larval survival in the Gulf of Maine? UMaine PhD Diss. ⟨https://digitalcommons.library.umaine.edu/cgi/viewcontent.cgi?article=4838&context=etd⟩.
Ascher, A., Niemisto, M., Baughman, D., Andrews, G., Morris, C., Patrick, E., Wahle, R.A., Fields, D.M. *In review*. Climate induced declines in maternal size may come at a cost to embryonic investment and larval performance in the American lobster. *Fisheries Research* (submitted to Special Edition: Proceedings of the International Conference and Workshop on Lobsters).
ASMFC. 2020. Stock Assessment Report of the Atlantic States Marine Fisheries Commission. American Lobster Stock Assessment for Peer Review. ASMFC American Lobster Stock Assessment Subcommittee. ⟨http://www.asmfc.org/uploads/file/5fb2c4a82020AmLobsterBenchmarkStockAssmt_PeerReviewReport.pdf⟩.
ASMFC, 2023. Addendum XXVII to Amendment 3 to the Interstate Fishery Management Plan for American Lobster. Atlantic States Marine Fisheries Commission. ⟨https://www.asmfc.org/uploads/file/64651dabAmLobsterAddendumXXVII_May2023.pdf⟩.
Balch, W.M., Drapeau, D.T., Bowler, B.C., Huntington, T.G., 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.
Bamber, J., van den Broeke, M., Ettema, J., Lenaerts, J., Rignot, E., 2012. Recent large increases in freshwater fluxes from Greenland into the North Atlantic. Geophys. Res. Lett. 39 (19) https://doi.org/10.1029/2012GL052552.
Carloni, J., Wahle, R.A., Fields, D.M., Geoghegan, P., Shank, B., 2024. Phenological shifts in the relative timing of American lobster larvae and their zooplankton prey in a warming ocean. ICES J. Mar. Sci. https://doi.org/10.1093/icesjms/fsae051 (In press.).
Carloni, J.T., Wahle, R.A., Geoghegan, P., Bjorkstedt, E., 2018. Bridging the spawner-recruit disconnect: trends in American lobster recruitment linked to the pelagic food web. Bull. Mar. Sci. 94, 719–735.
Casault, B., Johnson, C., Devred, E., Head, E., Cogswell, A., Spry, J., 2020. Optical, chemical and biological oceanographic conditions on the Scotian Shelf and in the Eastern Gulf of Maine during 2019. *Fish. Oceans Can., Res. Doc.* 2020/071.
Cushing, D.H., 1990. Plankton production and year class strength in fish populations: an update of the match/mismatch hypothesis. *Adv. Mar. Biol.* 26 249–293.
DeLestang, S.D., Caputi, N., Feng, M., Denham, A., Penn, J., Slawinski, D., Pearce, D., How, J., 2015. What caused seven consecutive years of low puerulus settlement in the western rock lobster fishery in Western Australia? ICES J. Mar. Sci. 72 (Supplement 1), i49–i58. https://doi.org/10.1093/icesjms/fsu177.
DFO 2024 (Fisheries and Oceans Canada) ⟨https://www.dfo-mpo.gc.ca/stats/commercial/sea-maritimes-eng.htm⟩.
Dukhovskoy, D.S., Yashayaev, I., Proshutinsky, A., Bamber, J.L., Bashmachnikov, I.L., Chassignet, E.P., Lee, C.M., Tedstone, A.J., 2019. Role of greenland freshwater anomaly in the recent freshening of the subpolar north atlantic. J. Geophys. Res.: Oceans 124 (5), 3333–3360. https://doi.org/10.1029/2018JC014686.
FAO, 2022. The State of World Fisheries and Aquaculture 2022. Towards Blue Transformation. Food and Agriculture Organization, Rome. https://doi.org/10.4060/cc0461en.
Friedland, K.D., Langan, J.A., Large, S.I., Selden, R.L., Link, J.S., Watson, R.A., Collie, J. S., 2020b. Changes in higher trophic level productivity, diversity and niche space in a rapidly warming continental shelf ecosystem. Sci. Total Environ. 704, 135270 https://doi.org/10.1016/j.scitotenv.2019.135270.
Friedland, K.D., Morse, R.A., Shackell, N., Tam, J.C., Morano, J.L., Moisan, J.R., Brady, D.C., 2020a. Changing physical conditions and lower and upper trophic level responses on the US Northeast Shelf. Front. Mar. Sci. https://doi.org/10.3389/fmars.2020.567445.
Gonçalez-Neto, A., Langan, J.A., Palter, J.B., 2021. Changes in the Gulf Stream preceded rapid warming of the Northwest Atlantic Shelf. Commun. Earth Environ. 2, 74. https://doi.org/10.1038/s43247-021-00143-5.
Goode, A.G., Brady, D.C., Steneck, R.S., Wahle, R.A., 2019. The brighter side of climate change: How local oceanography amplified a lobster boom in the Gulf of Maine. Glob. Change Biol. 25, 3906–3917. https://doi.org/10.1111/gcb.14778.
Harding, G.C., Pringle, J.D., Vass, W.P., Pearre Jr., S., Smith, S.J., 1987. Vertical distribution and daily movements of larval lobsters *Homarus americanus* over Browns Bank, Nova Scotia. Mar. Ecol. Prog. Ser. 41, 29–41.
Harrington, A., Brady, D., Wahle, R., 2018. Technical report submitted to Maine Department of Marine Resources. Spatiotemporal Eff. Temp. size Young-.-. –year Am. Lobsters *(Homarus Am.)*.
Huntsman, A.G., 1923. Natural lobster breeding. Bulletin of the Biological Board of Canada. Biological Board of Canada.
Jaspers, C., Acuña, J.L., Brodeur, R.D., 2015. Interactions of gelatinous zooplankton within marine food webs. J. Plankton Res. 37, 985–988. https://doi.org/10.1093/plankt/fbv068.
Ji, R., Feng, Z., Jones, B.T., Thompson, C., Chen, C., Record, N.R., Runge, J.A., 2017. Coastal amplification of supply and transport (CAST): a new hypothesis about the persistence of *Calanus finmarchicus* in the Gulf of Maine. ICES J. Mar. Sci. 74 (7), 1865–1874. https://doi.org/10.1093/icesjms/fsw253.
Ji, R., Runge, J.A., Davis, C.S., Wiebe, P.H., 2022. Drivers of variability of *Calanus finmarchicus* in the Gulf ofMaine: roles of internal production and external exchange. ICES J. Mar. Sci. 79 (3) https://doi.org/10.1093/icesjms/fsab147.
Juinio, M.A.R., Cobb, J.S., 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.
Kane, J., 2007. Zooplankton abundance trends on Georges Bank, 1977–2004. ICES J. Mar. Sci. 64, 909–919.
Kristensen, K., Nielsen, A., Berg, C.W., Skaug, H., Bell, B.M., 2016. TMB: automatic differentiation and Laplace approximation. J. Stat. Softw. 70, 1–21.
Layland, 2023. Outgrowing the risks of planktonic life: Ontogeny of prey pursuit, handling, and ingestion by the larval stages of the American lobster. University of Maine Masters Thesis.
Layland, E., Patrick, E., Spencer, M., Lasley-Rasher, R., Fields, D.M., Wahle, R.A. *In review*. Outgrowing the risks of planktonic life: Ontogeny of prey pursuit, handling, and ingestion by the larval stages of the American lobster. *Fisheries Research* (submitted to Special Edition: Proceedings of the International Conference and Workshop on Lobsters).
Le Bris, A., Mills, K.E., Wahle, R.A., Chen, Y., Alexander, M.A., Allyn, A.J., Schuetz, J.G., Scott, J.D., Pershing, A.J., 2018. Climate vulnerability and resilience in the most valuable North American fishery. Proc. Natl. Acad. Sci. USA 115, 1831–1836.
Levin, P.S., Mollmann, C., 2015. Marine ecosystem regime shifts: challenges and opportunities for ecosystem-based management. Philos. Trans. R. Soc. B 370, 20130275. https://doi.org/10.1098/rstb.2013.0275.
Li, B., Cao, J., Guan, L., Mazur, M., Chen, Y., Wahle, R., 2018. Estimating spatial non-stationary environmental effects on the distribution of species: a case study from American lobster in the Gulf of Maine. ICES J. Mar. Sci. *75*, 1473–1482. https://doi.org/10.1093/icesjms/fsy024.
MacKenzie, B.R., 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.
McManus, M.C., Brady, D.C., Brown, C., Carloni, J.T., Giffin, M., Goode, A.G., Kleman, K., Lawton, P., Le Bris, A., Olszewski, S., Perry, D.N., Rochette, R., Shank B, B.V., Wilson, C.M., Wahle, R.A., 2023. The American Lobster Settlement Index: History, lessons, and future of a long-term, transboundary monitoring collaborative. Front. Mar. Sci. 9, 1055557 https://doi.org/10.3389/fmars.2022.1055557.
Meyer-Gutbrod, E., Greene, C., Davies, K., Johns, D., 2021. Ocean regime shift is driving collapse of the North Atlantic right whale population. Oceanography 34 (3), 22–31. https://doi.org/10.5670/oceanog.2021.308.
Morin, A., Wahle, R. 2019. Re-analysis of spatiotemporal effects of temperature on the size of young-of-year American lobsters (*Homarus americanus*). Technical Report submitted to Maine Department of Marine Resources.
Morse, R.E., Friedland, K.D., Tommasi, D., Stock, C., Nye, J., 2017. Distinct zooplankton regime shift patterns across ecoregions of the U.S. Northeast continental shelf Large Marine Ecosystem. J. Mar. Syst. 165, 77–91. https://doi.org/10.1016/j.jmarsys.2016.09.011.
Mountain, D.G., 2012. Labrador slope water entering the Gulf of Maine - response to the North Atlantic Oscillation. Cont. Shelf Res 47, 150–155.
NOAA 2021.NOAA's EcoMon Database. ⟨https://www.ncei.noaa.gov/access/metadata/landing-page/bin/iso?id=gov.noaa.nodc:0187513⟩.

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.

Northeast Fisheries Science Center (NEFSC). 2021. State of the Ecosystem – New England. https://doi.org/10.25923/6pww-mw45.

Northeast Fisheries Science Center (NEFSC). 2023. State of the Ecosystem – New England. ⟨https://www.fisheries.noaa.gov/new-england-mid-atlantic/ecosystems/state-ecosystem-reports-northeast-us-shelf⟩.

Nye, J.A., Link, J.S., Hare, J.A., Overholtz, W.J., 2009. Changing spatial distribution of fish stocks in relation to climate and population size on the Northeast United States continental shelf. Mar. Ecol. Prog. Ser. 393, 111–129. https://doi.org/10.3354/meps08220.

Oppenheim, N.G., Wahle, R.A., Brady, D.C., Goode, A.G., Pershing, A.J., 2019. The cresting wave: larval settlement and ocean temperatures predict change in the American lobster harvest. Ecol. Appl. 29 https://doi.org/10.1002/eap.2006.

Pershing, A.J., Alexander, M.A., Brady, D.C., Brickman, D., Curchitser, E.N., Diamond, A. W., McClenachan, L., Mills, K.E., Nichols, O.C., Pendleton, D.E., Record, N.R., Scott, J.D., Staudinger, M.D., Wang, Y., 2021. Climate impacts on the Gulf of Maine ecosystem: A review of observed and expected changes in 2050 from rising temperatures. Elem.: Sci. Anthr. 9 https://doi.org/10.1525/elementa.2020.00076.

Pershing, A.J., Alexander, M.A., Nernandez, C.M., Kerr, L.A., Le Bris, A., Mill, K.E., 2015. Slow adaptation in the face of rapid warming leads to collapse of the Gulf of Maine cod fishery. Science 350, 809–812.

Pershing, A.J., Stamieszkin, K., 2020. The North Atlantic ecosystem, from plankton to whales. Annu. Rev. Mar. Sci. 12, 1. https://doi.org/10.1146/annurev-marine-010419-010752.

Pershing, A.J., Wahle, R.A., Meyers, P.C., Lawton, P., 2012. Large-scale coherence in New England lobster (*Homarus americanus*), settlement and associations with regional atmospheric conditions. Fish. Oceanogr. https://doi.org/10.1111/j.1365-2419.2012.00629.x.

Petris, G., 2010. An R Package for Dynamic Linear Models. J. Stat. Softw. 36 (12), 1–16. https://doi.org/10.18637/jss.v036.i12.

Pettigrew, N.R., Churchill, J.H., Janzen, C.D., Mangum, L.J., Signell, R.P., Thomas, A.C., Townsend, D.W., Wallinga, J.P., Xue, H., 2005. The kinematic and hydrographic structure of the Gulf of Maine Coastal Current. Deep-Sea Res. II 52, 2369–2391.

Pinsky, M.L., Worm, B., Fogarty, M.J., Sarmiento, J.L., Levin, S.A., 2013. Marine taxa track local climate velocities. Science 341 (6151), 1239–1242. https://doi.org/10.1126/science.1239352.

Putrasahan, D.A., Lohmann, K., von Storch, J.-S., Jungclaus, J.H., Gutjahr, O., Haak, H., 2019. Surface flux drivers for the slowdown of the atlantic meridional overturning circulation in a high-resolution global coupled climate model. J. Adv. Model. Earth Syst. 11 (5), 1349–1363. https://doi.org/10.1029/2018MS001447.

R Core Team (2023). R: A Language and Environment for Statistical Computing_. RFoundation for Statistical Computing, Vienna, Austria. <⟨https://www.R-project.org/⟩>.

Record, N.R., Runge, J.A., Pendleton, D.E., Balch, W.M., Davies, K.T.A., Pershing, A.J., Johnson, C.L., Stamieszkin, K., Ji, R., Feng, Z., Kraus, S.D., Kenney, R.D., Hudak, C. A., Mayo, C.A., Chen, C., Salisbury, J.E., Thompson, C.R.S., 2019. Rapid Climate-Driven Circulation Changes Threaten Conservation of Endangered North Atlantic Right Whales. Oceanography 32 (2), 162–169. ⟨https://www.jstor.org/stable/26651192⟩.

Richards, R.A., O'Reilly, J.E., Hyde, K.J.W., 2016. Use of satellite data to identify critical periods for early life survival of northern shrimp in the Gulf of Maine. Fish. *Oceanogr.* 25, 3.

Runge, J.A., Ji, R., Thompson, C.R.S., Record, N.R., Chen, C., Vandemark, D.C., Salisbury, J.E., Maps, F., 2015. Persistence of *Calanus finmarchicus* in the western Gulf of Maine during recent extreme warming. *J. Plankton Res.* 37, 221–232.

Seidov, D., Mishonov, A., Parsons, R., 2021. Recent warming and decadal variability of Gulf of Maine and Slope Water. *Limnol. Oceanogr.* https://doi.org/10.1002/lno.11892.

Sévellec, F., Fedorov, A., Liu, W., 2017. Arctic sea-ice decline weakens the Atlantic Meridional Overturning Circulation. Nat. Clim. Change 7, 604–610. https://doi.org/10.1038/nclimate3353.

Steneck, R.S., Wahle, R.A., 2013. The American lobster dynamics in a brave new ocean. Can. J. Fish. Aquat. Sci. 70, 1612–1624. https://doi.org/10.1139/cjfas-2013-0094.

Steneck, R.S., Wilson, C., 2001. Long-term and large scale spatial and temporal patterns in demography and landings of the American lobster *Homarus americanus* in Maine. Mar. Freshw. Res 52, 1303–1319.

Tesdal, J.-E., 2020. Circulation changes associated with freshwater and heat content variability and implications for biological productivity in the subpolar North Atlantic Ocean (Doctoral theses). Dep. Earth Environ. Sci., (N. Y. Columbia Univ.). https://doi.org/10.7916/d8-36h5-xz52.

Townsend, D.W., Pettigrew, N.R., Thomas, M.A., Neary, M.G., McGillicuddy, D.J., O'Donnell, J., 2015. Water masses and nutrient sources to the Gulf of Maine. J. Mar. Res. 73, 93–122. https://doi.org/10.1357/002224015815848811.

Townsend, D.W., Pettigrew, N.R., Thomas, M.A., Moore, S., 2023. Warming waters of the Gulf of Maine: the role of shelf, slope and Gulf Stream water masses. Prog. Oceanogr. *215, 1–28*. https://doi.org/10.1016/j.pocean.2023.103030.

Wahle, R.A., 2003. Revealing the stock-recruitment relationship in lobsters and crabs: Is experimental ecology the key? Fish. Res. 65, 3–32.

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

Wahle, R., Linnane, A., Harrington, A., 2020. Wahle, R., Linnane, A., & Harrington, A. 2020. Chapter 3: Lobster Fisheries. In and G. Lovrich and M. Thiel (eds). The Natural History of the Crustacea. (Vol. 9). New York: Oxford Univ. Press. 554 pp. https://global.oup.com/academic/content/series/n/natural-history-of-crustacea-nhc/?lang=en&cc=us⟨https://global.oup.com/academic/content/series/n/natural-history-of-crustacea-nhc/?lang=en&cc=us⟩(In and).

Waller, J.D., Reardon, K.M., Caron, S.E., Jenner, B.P., Summers, E.L., Wilson, C.J., 2021. A comparison of the size at maturity of female American lobsters (*Homarus americanus*) over three decades and across coastal areas of the Gulf of Maine using ovarian staging. ICES J. Mar. Sci. https://doi.org/10.1093/icesjms/fsab034.

World Register of Marine Species (WORMS) 2021. Taxonomic and distributional information on *Nannocalanus minor* ⟨http://www.marinespecies.org/aphia.php?p=taxdetails&id=104469#distributions⟩ Accessed Sept 1, 2021.