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The American Lobster Settlement Index: History, lessons, and future of a long-term, transboundary monitoring collaborative

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Understanding the processes that influence recruitment variability in marine populations has been a long-standing challenge for resource management. Quantifying abundance at early life stages for marine fish and invertebrates with complex life histories can be difficult and require unconventional sampling approaches. However, the benefit of developing appropriate tools to sample early life stages is that, together with associated demographic and environmental information, the data can provide insights into the causes and consequences of recruitment variability, allowing prediction of older life stage abundance. Before the 1980s, the earliest benthic life stages of the American lobster (*Homarus americanus*) eluded quantitative field surveys. With the development of diver-based and vessel-deployed sampling methods over the past three decades, the American Lobster Settlement Index (ALSI) program has expanded into a regional, transboundary commitment to better understand lobster settlement processes and forecast future fishery trends for what has become the most valuable single-species fishery in North America. In this context, "settlement" is a shorthand for the annual recruitment of young-of-year lobster to coastal nurseries, as postlarvae settle to the seabed at the end of larval development. Here, we review the development and products of the ALSI program, first outlining the goals, methods, and data products of the program. We then highlight how the program has advanced the scientific knowledge on pre- and post-settlement processes that influence the fate of a cohort from egg hatch to harvest, which provides insight into the spawner-recruit relationship. Lastly, we provide guidance for future research recommendations building on the ALSI science to-date, some major elements of the program that have allowed for its success, and considerations for maintaining the ALSI program. By highlighting the uniqueness and contributions of the ALSI program, we hope it serves as a model for other scientists, managers, and industry collaborators aiming to understand recruitment processes for species over a broad geographic area.

KEYWORDS

American lobster, young-of-year, recruitment, abundance indices, settlement, forecasting

Introduction

Long-term fisheries monitoring programs are vital for inferring how marine populations change over time. Programs targeting early-life stages reveal species life cycle dynamics with several applications, including estimating spawning stock biomass (Richardson et al., 2010), describing habitat preferences (McManus et al., 2018), understanding planktonic food web ecology, and discerning environmental drivers of fish stocks (Caputi et al., 2014). Such data are particularly valuable in understanding recruitment processes and dynamics for marine populations. For more than a century, scientists have linked the variability in the abundance of adult fish to the variability in their numbers during the pre-recruit stages (Hjort, 1914). Identifying this relationship has often relied on survey data of life stages prior to fisheries recruitment, or the point at which new individuals become harvestable by the fishery. For example, passive collectors have been used to monitor Western Australian rock lobster (*Panulirus cygnus*) postlarval abundance and provide an early indicator of year class strength and predictor of subsequent recruitment to the fishery (Phillips, 1986; Caputi et al., 1995). In this case, the sum of periodic counts of postlarvae accumulated on collectors deployed in the water column provide an annual postlarval index. However, the time and effort to conduct frequent sampling over the year can be prohibitively costly, and such programs are not as pervasive as those that can be conducted with less frequency or with greater seasonal flexibility (e.g., trawl surveys). Further, contemporary larval surveys are typically designed to serve multipurpose ecosystem research objectives, limiting their usefulness for species with complex pelagic behavior, narrow spawning windows, and atypical spawning strategies.

These challenges have been true for crustaceans, including the American lobster (*Homarus americanus*). For many crustacean species, there often is a poor linkage between spawning stock biomass and recruit abundance, which historically has been attributed to the factors that decouple the spawner-recruit relationship, such as highly variable larval export or mortality up to the time of recruitment to the fishery (Wahle, 2003). These challenges have led researchers to investigate other methods for understanding the early-life history of lobster populations, and to construct better tools for informing future recruitment to the population and fishery.

The need to connect early life history stages to recruitment has led to the development of sampling strategies that target young-of-year American lobster. By directly sampling for lobsters recently settled from the pelagic environment to the benthos in their first year of life, young-of-year abundance information would inform research and management communities of variability in both pre- and post-settlement processes. After investigative studies during the 1980s on methods for quantifying recently settled lobsters (Wahle and Steneck, 1991), the American Lobster Settlement Index (ALSI) program began in 1989. The program's original, primary objective was to monitor newly settled lobsters in shallow, cobble-boulder nursery habitats (Wahle et al., 2010). The ALSI program originally sought to emulate Australia's western rock lobster (*P. cygnus*) postlarval index program, both to construct a proper monitoring program for newly settled lobsters and develop an early warning system for future commercial harvest (Caputi et al., 1995). However, the sampling method differed because American lobster larvae do not settle on fibrous substrates suspended in the water column as do spiny lobster postlarvae. Rather, diver-based suction sampling was the first method to reliably and efficiently quantify young-of-year lobsters in naturally occurring shallow cobble-boulder nurseries (Incze and Wahle, 1991). Subsequently, vessel-deployed cobble-filled collectors were added to the tool kit and expanded the survey into deeper waters and locations otherwise out of reach of divers (Wahle et al., 2009b; Wahle et al., 2013a). Since 1989, marine resource agencies, fishing industry partners and academics have conducted long-term diver-based suction sampling, and collector deployments, covering more than 11° in latitude, from Rhode Island, United States to Newfoundland, Canada (Figure 1).

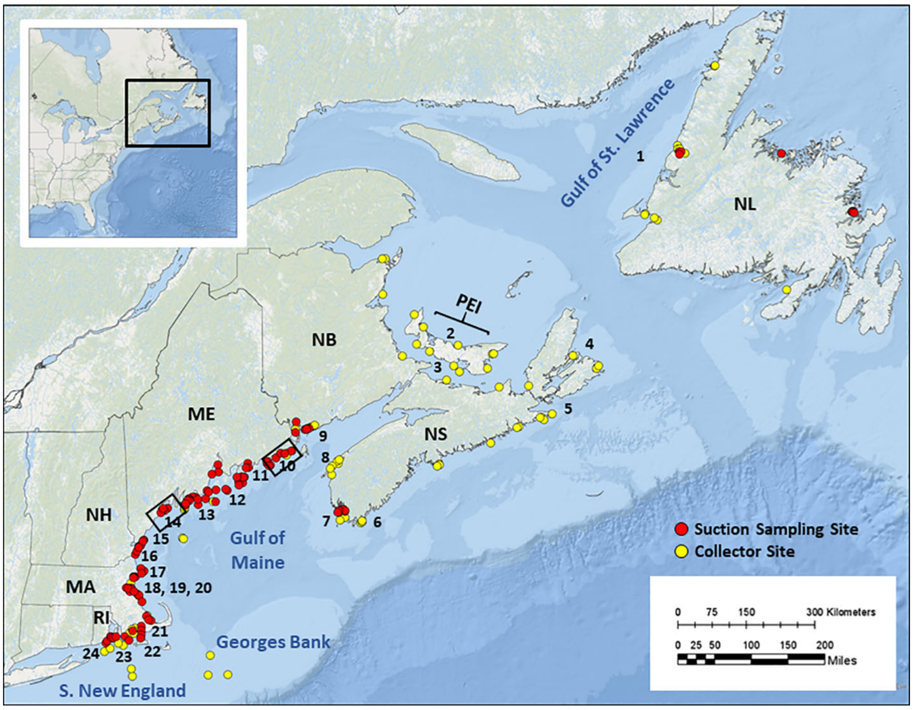

FIGURE 1
ALSI sampling sites in New England and Atlantic Canada using diver-based suction (red) and vessel-deployed collector (yellow) sampling locations. Inset map indicates coverage within eastern North America. Numbers correspond to study area descriptions and data presented in Supplement S2 and Figure 2. Abbreviations represent relevant geographic jurisdictions: Newfoundland (NL), Prince Edward Island (PEI), Nova Scotia (NS), New Brunswick (NB), Maine (ME), New Hampshire (NH), Massachusetts (MA), and Rhode Island (RI). Black rectangles denote collector deployment areas for deepwater settlement monitoring supported by Ready Seafood Co. in Maine.

Since its inception, the ALSI program has provided extensive insight into American lobster settlement dynamics in New England and Atlantic Canada, representing a unique transboundary scientific collaborative. The resulting time series have become a springboard for subsequent studies addressing a variety of research questions, especially regarding the processes operating before and after larval settlement to influence the fate of a cohort between the time of hatching and recruitment to the fishery. They include oceanographic drivers of lobster larval transport, pelagic-benthic coupling, the effect of substrate quality on postlarval settlement, spatial scale of settlement patchiness, cobble nursery community structure, settler-recruit dynamics, disease impacts, crustacean sampling designs, and forecasting commercial harvest (Incze et al., 1997; Butler et al., 2006; Steneck and Wahle, 2013; Sigurdsson et al., 2014; Ellis et al., 2015; Sigurdsson et al., 2016; Hunt et al., 2017; Goode et al., 2019; Oppenheim et al., 2019; White, 2022). The scientific questions addressed with this program have been critical to understanding the sustainability of the resource, which has become particularly important with the expansion of the lobster fishery over the past decade. Given the commercial and social significance of lobster for coastal communities in the northeast US and Atlantic Canada, the ALSI program is a tool to understand potential population vulnerabilities and for regional lobster management.

ALSI partners convene annually to share their results from yearly sampling and settlement-related research projects, and present new research initiatives. These annual meetings have served as symposia to share and learn from each other's research findings and logistical challenges running the program. With over three decades of ALSI sampling and program activities now complete, we present a roadmap that summarizes the advancement of the program, as well as how future research efforts should be prioritized. We begin by highlighting the uniqueness of the sampling strategies used to monitor recently settled lobsters as part of the ALSI program. We then summarize how the ALSI program has improved our understanding of lobster recruitment processes, and how American lobster science has been advanced due to the program. We present the outlook for the future of the program, specifically research recommendations and directions identified as high priority for American lobster recruitment dynamics in a changing ecosystem. Lastly, we outline the elements of ALSI that have allowed for its success and considerations for maintaining such long-term monitoring efforts. In doing so, we aim to showcase this program as a model for collating resources regionally to support long-term research and monitoring that can be applied to other marine resources.

Sampling methods and settlement indices

Since the late 1980s, the primary tool used to monitor lobster settlement has been suction sampling (Wahle and Steneck, 1991). Suction sampling is conducted after postlarvae have settled to the benthos, the timing of which varies with latitude, and practioners acknowledge that the settlement season may vary interannually as well, based on environmental conditions. The settlement season typically ends in late August-early September in southern New England, mid/late October in the northeast Gulf of Maine, and up to late-November in Newfoundland. For the suction sampling part of the ALSI program, between 10 and 20 haphazardly placed quadrats (0.5-m^2) are sampled per study site, within a nested sampling design of multiple fixed study sites nested within study areas. For the longest-running Atlantic Canada survey area (Beaver Harbour), smaller quadrats (0.25-m^2) are used to optimize survey logistics while diving within the large tidal ranges in the Bay of Fundy. The quadrat frame often includes an apron weighted with a chain to conform to irregularities of the seabed and prevent the escape of small lobsters. Passive postlarval collectors were more recently developed for monitoring lobster settlement in deeper locations that are either unsafe or inaccessible for divers (Wahle et al., 2013a). They have, however, become the preferred sampling method for some groups, due to various logistic considerations (e.g., lack of available dive teams) and monitoring goals (e.g., collectors are more effective at capturing small fish than suction sampling quadrats). Collector deployments have generally adopted the fixed site sampling protocol used in suction sampling. The sole exception is the long-term deep water settlement monitoring conducted by Ready Seafood Co. and the University of Maine that has partnered with a research trap survey conducted by Maine Department of Marine Resources that is sampled in a random stratified design across three depth strata (Figure 1). The collector design benefitted from close consultation with fishing industry collaborators, to make them amenable to deployment and retrieval from commercial fishing boats equipped with a lobster pot hauler, which is one factor that has contributed to the adoption of this method by different groups. Collectors are constructed with standard vinyl-coated trap wire mesh (38 mm); the floor and walls are lined inside with plastic mesh (1 mm) to retain organisms. The total rectangular footprint of the collectors is 0.56-m^2. The collectors are filled with rounded cobbles ranging in diameter from approximately 10 to 15 cm, which is also the size range targeted in suction sampling. The covers of collectors are made of the same wire mesh, to both contain the cobble and allow for larval settlement into the collectors. Collectors must be deployed before the settlement season has begun. Retrieval is on approximately the same schedule as suction sampling. The two sampling techniques have also provided insight into gear selectivity and lobster behavior *via* the size composition of lobster catch (Supplement S1). Additional details for suction and collector sampling can be found in Wahle et al. (2009a, 2010; 2013a).

In both sampling methods, lobster carapace length and sex are recorded, with additional information (e.g. claw or damage status) often noted. Although the ALSI survey was designed for lobsters, many from the collaborative have agreed to also enumerate and measure brachyuran crabs and fishes within the sample. Station or quadrat-level habitat information, including sea temperature, algal cover and cobble size composition, are also recorded by various partners. ALSI-derived settlement indices rely on a fixed-station sampling design, where sites are nested within larger study areas spread across the regions. Suction and collector sampling have occurred in waters throughout New England and Atlantic Canada (Wahle et al., 2013a), although only a subset of the sampling locations have been maintained over time to produce data for use in times series analyses. An evaluation of the fixed-station design in the Gulf of Maine has found that while this approach may underestimate the absolute number of settlers, the sampling design is effective in monitoring temporal changes in settler densities (Li et al., 2015). Both suction sampling and collector data are used to inform the annual settlement index, but the method used to calculate the index is consistent within a study area. Arithmetic mean settler abundance indices from ALSI have revealed important spatial and temporal patterns in young-of-year lobster population in the coastal Northwest Atlantic (Figure 2). The size threshold for defining young-of-year lobsters varies in space due to regional differences in growth (Wahle and Fogarty, 2006; Harrington et al., 2017; Morin and Wahle, 2019; Supplement S2). A fixed threshold has often been adopted for each study area and held constant over time; the Prince Edward Island study area is an exception to this, where the threshold varies annually based on interpretation of the length frequency distribution. Over time, supplemental suction and collector sampling have been conducted over larger geographic areas as part of dedicated research projects to understand various questions regarding lobster ecology, biodiversity, and sampling design (Supplement S2).

Annually, partners produce a two-page *ALSI Update* (reports can be found at https://umaine.edu/wahlelab/american-lobster-settlement-index-alsi/), which provide summaries of the most recent year's data, advancements in the indices for use in forecasting regional landings, and other ALSI related research. The timely production of these annual updates is aided by a shared online password protected ALSI database,

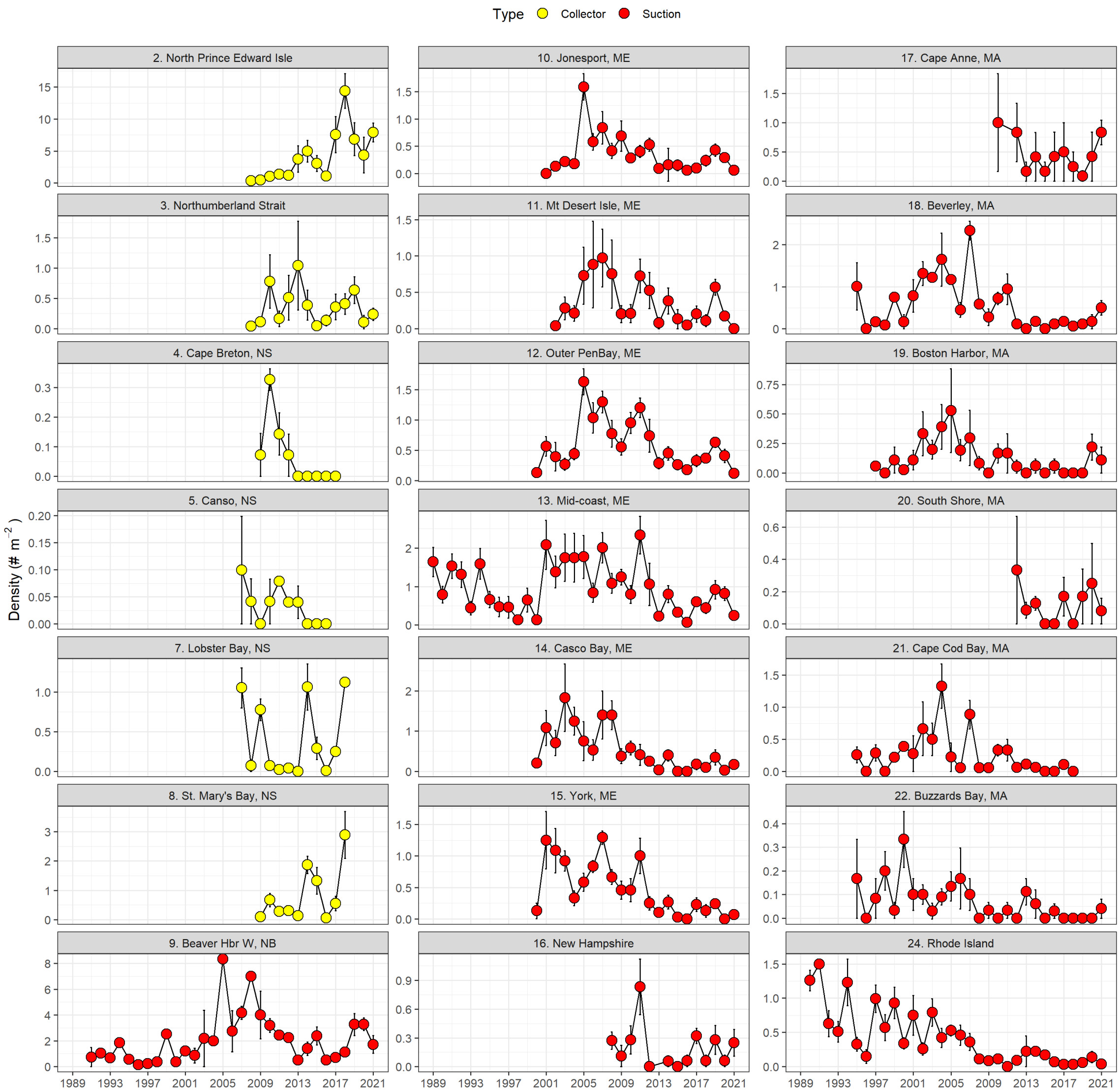

FIGURE 2
Mean (± 1 SE) annual indices for young-of-year (settler) American lobster (# m^{-2}) for select study areas enumerated in Figure 1, each consisting of 4-10 sampling sites. Indices are colored by collection method: suction sampling (red), passive collectors (yellow). For regions using both methods simultaneously, the prevailing method used to derive indices is presented.

where collaborators annually submit their data into systematic templates with quality assurance and control checks to ensure data are properly organized and comparable for regional analyses. The online database is accompanied by a data portal and query tool, which allow ALSI partners to access data across the sampling range and time series and provide partners with data products in user-specified formats.

The ALSI program indices have become increasingly incorporated into the science-informed management of lobster in the US and Canada, in large part due to evidence that the regional indices follow broader trends in lobster stocks. For example, local indices for sites within the Southern New England and Gulf of Maine lobster stock units indicate similar population signals as regionally corresponding trawl surveys: a decline in relative abundance in southern New England since the 1990s, and an increase in Gulf of Maine during the 2000s (ASMFC, 2020). As such, ALSI indices for US waters are presented in US American lobster stock assessments as model-free indicators to inform prospective changes in recruitment to the fishery in future years. The ALSI indices have been the focus of several

Atlantic States Marine Fisheries Commission (ASMFC) American Lobster Management Board discussions, particularly regarding how the trends should be used to inform lobster management. For example, recent declines in ALSI young-of-year indices for the Gulf of Maine region was the primary impetus for the ASMFC Lobster Board to initiate Addendum XXVII, which proposed additional biological conservation through additional spawning stock biomass protection *via* gauge and vent size changes. Beginning in 2022, ALSI indices are also one of three fisheries independent surveys annually presented to the ASMFC Lobster Board to provide direct scientific information on the population trajectories. Similarly, benthic recruitment data have been used in Canada as an indicator of lobster stock health to support stock assessment exercises for the Magdalen Islands (e.g., DFO, 2019) and southern Gulf of St. Lawrence (Rondeau et al., 2015), although not so far for the Bay of Fundy (DFO, 2021) despite the fact that ALSI time series trends measured in adjacent waters of the eastern Gulf of Maine have proven useful in forecasting harvest trends in those areas (Oppenheim et al., 2019). Overall, the conveyance of ALSI indices through these methods has provided fisheries managers additional information to evaluate the need for proactive management measures, and ultimately better integrate the program into stock assessment science for lobster.

Bridging the gaps: Settlement processes

Understanding the stock-recruit relationship for many crustaceans, including American lobster, has often been challenging due to a myriad of factors (Caddy, 1986; Fogarty et al., 1991; Fogarty, 1995; Wahle, 2003). The correlation between spawning stock biomass and subsequent recruitment to the fishery in American lobster is driven by both pre- and post-settlement processes, which cumulatively can span from 5 to 9 years (Wahle and Incze, 1997). These processes can be influenced by a suite of environmental or ecological factors, such as oceanography, predation, competition, food supply, disease, and habitat, which vary in time and space (Figure 3). Settlement monitoring for over thirty years has allowed us to better understand settlement processes and test stock-recruit and settlement-recruit hypotheses. Specifically, ALSI times-series data have been used to understand quantitative relationships between larval supply and recently settled young-of-year lobsters (Incze and Wahle, 1991; Incze et al., 1997; Wahle and Incze, 1997; Incze et al., 2006; Carloni et al., 2018), as well as between young-of-year lobsters and older juvenile or adult stages (Wahle et al., 2009b; Oppenheim et al., 2019; ASMFC, 2020; White, 2022).

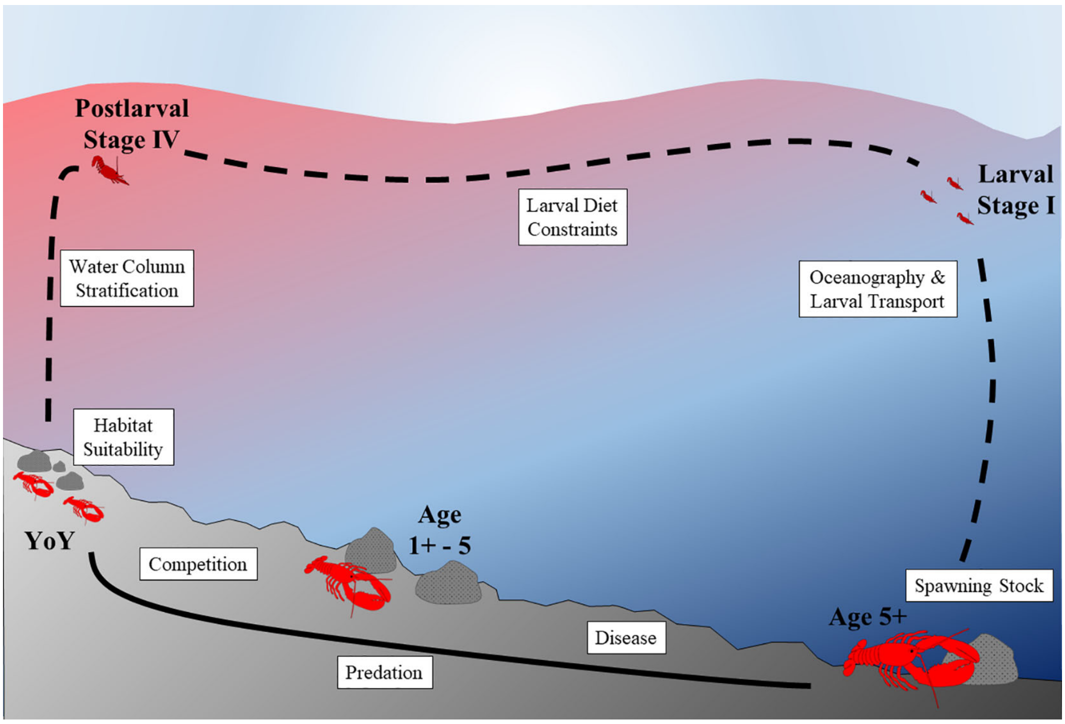

FIGURE 3
Conceptual model of American lobster life history and the settlement processes influencing recruitment to the fishery. Mechanisms influencing pre-settlement processes are indicated along the dashed line, and those influencing post-settlement processes are indicated using solid lines.

In combination with other survey data, the ALSI program has been used to analyze lobster populations using life cycle analyses. One such method is the Paulik diagram, which uses a set of plots to understand the linkage between individual life stages, and begin to determine the stage transitions that are more significant in dictating the strength of a stock-recruitment relationship (Paulik, 1973). This approach steps through the relationships between successive life stages in a clockwise fashion, with complete rotation returning back to the starting life stage, but in the next generation. In the example of American lobster, the Paulik Diagram can be used to visualize the linkage between life stages: adults-pelagic stages, pelagic stages-settlers, settlers-juveniles, and juveniles-adults (Figure 4; Supplement S3). For many regions within the American lobster native range, the abundance of fishery recruits and adult lobsters can be estimated from long-standing fishery-dependent or fishery-independent surveys, such as landings, at-sea surveys of the commercial catch, trawl surveys, and ventless trap surveys. Therefore, ALSI program data can fill a critical data gap in understanding American lobster population connectivity. These analyses are limited given long-term monitoring programs that quantify pelagic lobster larvae are exceedingly rare: only one multi-decade larval monitoring program that effectively captures lobster larvae is conducted throughout the species' geographic range (Carloni et al., 2018). This lack of information limits the locations where one could conduct a full life cycle analysis from spawners (e.g. adults; landings or trawl surveys) to larvae (neuston tows) to young-of-year (e.g. settlers; ALSI) to older juveniles (e.g. pre-recruits; ALSI, trawl, or ventless traps), and back to adult spawners (landings or trawl surveys). Estimated egg production may be a useful proxy for the pelagic larval stage in these analyses (Figure 4), but given its inherent reliance on the other surveys for estimation, it is likely an over-optimistic representation of the pelagic connectivity state to spawners and settlers. Nonetheless, the abundance indices for the remaining segments of the life history provide a rich database from which to make inferences about pre- and post-settlement processes influencing the fate of lobster cohorts.

Pre-settlement processes

Oceanographic effects on American lobster larval supply

While ALSI is primarily a metric to quantify spatiotemporal variation in post-settlement abundance, it can also contribute to our understanding of larval dispersal, as it is the conclusion of pre-settlement processes. In the early years of the ALSI monitoring, short-term and relatively small-scale field studies were conducted in mid-coast Maine and coastal Rhode Island in which pelagic larval sampling was paired with benthic suction sampling to quantify spatiotemporal links between larval/postlarval supply and resulting settlement densities, and to elucidate the factors affecting these links (Incze et al., 1997; Wahle and Incze, 1997). These studies underscored the importance of local oceanography, especially wind-driven currents, on local differences in postlarval supply and corresponding settlement densities. Experimental habitat

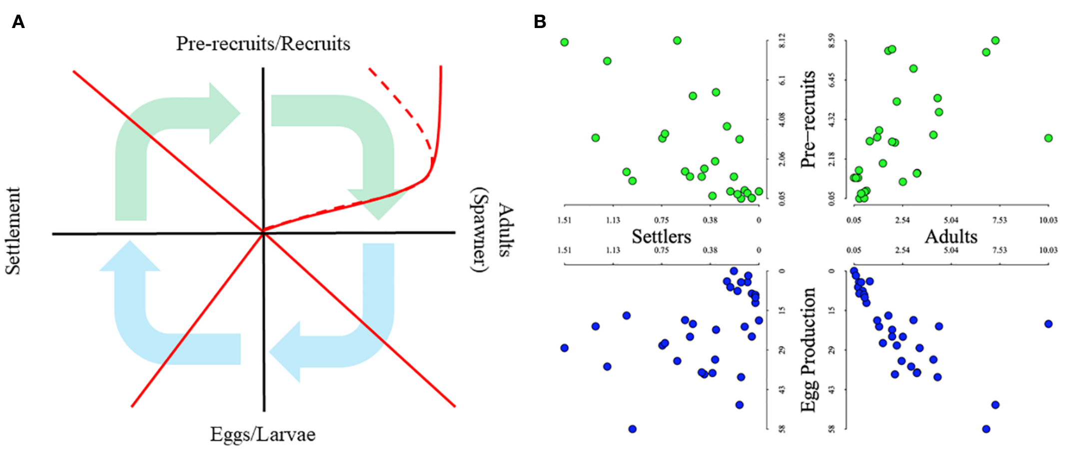

FIGURE 4
(A) Theoretical American lobster Paulik diagram adapted from Wahle (2004) between adult (spawners), pelagic stage (eggs/larvae), young-of-year (settlement) and pre-recruit or recruit lobsters. Arrows indicate the flow of life stages through the diagram for pre-settlement (blue) and post-settlement (green) stages. Red lines represent theoretical relationships between life stages. The solid and dashed lines for the upper right sub panel represent Beverton-Holt and Ricker stock-recruit functions. **(B)** Application of the Paulik diagram for American lobsters in southern New England (United States) with data from Rhode Island. Points represent relative abundance estimates by life stage and are colored by pre-settlement (blue) and post-settlement (green) stages. Details on data and methods can be found in Supplement S3.

manipulations also illustrated the importance of cobble cover as a determinant of post-settlement population densities. Subsequent deployments of passive collectors have been conducted to evaluate depth-wise patterns of lobsters, and have provided new insights on settlement in contrasting oceanographic settings over much of the species' range (Wahle et al., 2013a; Hunt et al., 2017).

Nearly a century ago, Huntsman (1923) speculated that the absence of small lobsters in the Bay of Fundy lobster fishery of that era was related to summer temperatures being too cold for lobster larvae to develop. By the end of the century, the ALSI program, in concert with the accumulated knowledge of larval biology over the decades, has advanced our understanding of thermal effects on larval settlement. Collector deployments in locations where waters become thermally stratified during the summer have shown settlement tends to be restricted to the warmer strata above the thermocline (Wahle et al., 2013a). This finding is consistent with earlier laboratory and field observations of postlarval diving behavior in a vertical temperature gradient (Boudreau et al., 1992; Annis, 2005). For example, Annis et al. (2013) observed in the field that postlarvae traversing a vertical thermocline will give up their dive as they encounter temperatures lower than about 12°C. By contrast, collector deployments where the water column is well mixed, such as the easternmost Gulf of Maine and Bay of Fundy, have shown that settlement is more uniform across depths, and can occur at depths greater than 80 m where water does not thermally stratify during the summer. Still, even in well mixed areas, collector-based data consistently reveal that settlement densities diminish with greater depth, perhaps reflecting a diminishing propensity to settle with greater depth that is independent of temperature and may reflect the availability of preferred substrate, predation, or energetic constraints during the act of post-larval settlement. These observations suggest the depth range of settlement may generally be controlled by the availability of thermally suitable nursery habitats, whereby colder years with a shallower thermocline may concentrate settlers nearshore, and warmer years with a deeper warm layer may spread them over a larger area offshore (Steneck, 2006; Steneck and Wahle, 2013; Goode et al., 2019). This "thermally-mediated settlement dilution" may have implications for the ALSI index if not accounted for in estimates of year class strength and derived fishery forecasts (Goode et al., 2019). Without the international collaboration of the ALSI program, these large-scale geographic patterns and associated abundance trajectories could not have been identified.

Recent research is providing new insight into the trophic interactions of larvae in the pelagic food web, and suggests the disconnect between recent high abundance of spawning stock biomass in the Gulf of Maine and sustained low levels of young-of-year abundance may be a function of larval food supply. Drawing upon the unique three-decade time series of larval lobster and zooplankton sampling off the New Hampshire coast, as well as the spawner biomass index from federal trawl surveys and young-of-year data from the ALSI program, Carloni et al. (2018) reported a series of correlations suggesting the spawner-recruit relationship for lobster decouples soon after larval hatch due to planktonic food limitation, principally the favored prey item *Calanus finmarchicus*. Although the abundance of newly hatched stage I larvae had been rising concomitant with unprecedented levels of spawning stock biomass since 2010, postlarval numbers were declining and decoupled from both stage I abundance and spawner biomass. This finding significantly aligned with the time series trend in young-of-year abundance measured at ALSI sites throughout the western Gulf of Maine. Further analysis of parallel zooplankton time series collected both locally on the New Hampshire coast, and regionally by federal plankton surveys, indicate especially strong correlations of the young-of-year lobster declines in the Gulf of Maine with time trends in the copepod, *Calanus finmarchicus*, and a few other cold-water copepods, but not with other members of the zooplankton community (Wahle et al., 2021).

These changes are concurrent with a dramatic shift in the influence of North Atlantic waters on the Gulf of Maine ecosystem. Satellite and *in situ* ocean observations after approximately 2010 indicate a weakening of the influence of the cold, nutrient-rich Labrador Shelf Waters on the Gulf of Maine, while the warm, salty and nutrient-poor Gulf Stream have increased, with adverse consequences for primary and secondary production (Grieve et al., 2017; Friedland et al., 2020; Gonçalves et al., 2021). Regional warming trends are also suspected to influence the phenology of the ecosystem, such as for early-stage lobster larvae and *C. finmarchicus*, which could widen mismatches in temporal overlap of predator and putative prey and contribute to the recent declines in lobster settlement. While evidence of larval lobster food limitation through changes in the zooplankton community remains correlative at this time, the topic is an area of active research that emerged through a comparison of ALSI data with parallel independent time series.

Bio-physical larval transport models developed to date provide a tool to incorporate the influence of egg production, larval development, postlarval swimming speed and oceanography on relative settlement strength along the coast (Katz et al., 1994; Xue et al., 2008; Chassé and Miller, 2010; Incze et al., 2010; Quinn et al., 2017; Quinn et al., 2022). Correlations between satellite-derived sea surface temperature and young-of-year densities from the ALSI program have been used to explain larval transport and connectivity between adjacent regions (Jaini et al., 2018); however, to date, there has not been a rigorous test of these models against empirical settlement densities as reported by ALSI partners.

Post-settlement processes

Interspecific interactions

Upon settlement to the benthos, young-of-year lobsters are subject to a different suite of factors than the pelagic larval and postlarval stages. Several factors influence the number of settled lobsters that survive and recruit to the fishery and spawning stock (Figure 3). However, distinguishing which factors are most prominent in dictating post-settlement survivorship can be challenging, not only because of the many potential factors involved, but also because testing different hypotheses requires extensive time-series data of the life stages and covariates of interest. Ascribing causation to post-settlement mortality is of particular interest whether populations are in decline, as in southern New England, or growing and expanding, as in the eastern Gulf of Maine and the Gulf of St. Lawrence.

Apart from the effects of water temperature and chemistry, which affect all life stages, several post-settlement factors can further influence recruitment to the fishery. These include density-dependent intra-specific effects, shelter limitation, food limitation, disease, interspecific competition and predation. Common demersal and benthic predators include cunner (*Tautogolabrus adspersus*), sculpins (*Myoxocephalus* spp.), black sea bass (*Centropristis striata*), scup (*Stenotomus chrysops*), among others, that have been documented through video monitored tethering experiments in the field (Wahle and Steneck, 1992; Wahle et al., 2013b). In a comparison of size-specific predation rates in southern and northern New England, Wahle et al. (2013b) documented a wider diversity of potential predators and a correspondingly higher risk of predation at the warmer, southern, end of the range. Moreover, the same study noted that in the Gulf of Maine, where ground fish populations have been widely depleted, the upward trend in lobster abundance between 1979 and 2007 was more strongly related to the collective declines in predator body size, than to predator biomass, as estimated from federal trawl surveys. Video surveys by remotely operated vehicles, also reported in Wahle et al. (2013b), further revealed that lobster in the relatively predator-free Gulf of Maine tended to be less strongly associated with shelter than those in the south. Similarly, a study involving passive collectors provided additional evidence that young lobsters successfully recruit to featureless mud seafloor in the relatively predator-poor Bay of Fundy (Dinning and Rochette, 2019). While predation pressure may have relaxed over the decades in the Gulf of Maine and Bay of Fundy because of intense groundfish harvesting, the introduction of new predators or competitors may be adding to the already more diverse assemblage of predators in southern New England. For example, the introduced Asian shore crab (*Hemigrapsus sanguineus*) has been implicated in the local decline of juvenile lobster populations in shallow nurseries of Narragansett Bay, which have receded in part from a warming climate (Wahle et al., 2015). Although *Hemigrapsus* is limited to a relatively shallow depth range, laboratory experiments indicate that it consistently excludes similar-sized juvenile lobsters from shelters (Baillie and Grabowski, 2018), suggesting that in shallow, relatively warm areas where their distributions do overlap, *Hemigrapsis* may have a competitive edge. Because many ALSI program partners quantify all fish, lobsters, and crabs in each half-square-meter quadrat or collector, it is possible to explore species associations and potential interactions at fine scales. To date, correlative analyses relating predator numbers to young lobster numbers in collectors have only revealed a significant inverse relationship for collectors deployed in southern New England, and only for older juvenile lobsters, not the young-of-year (Wahle et al., 2013b). The same study found no significant inverse relationship for collector deployments in mid-coast Maine, eastern Maine or Nova Scotia.

Forecasting the Trends in the Fishery

An ALSI-based forecasting tool is grounded in the idea that an accurate indicator of young-of-year abundance is likely to be a better predictor of subsequent recruitment to the fishery than indices of broodstock or larval abundance, because the cohort has already run the gauntlet and uncertainties of planktonic life (Wahle, 2003). Developing a forecasting tool faced several challenges. After quantifying the annual pulse of young-of-year abundance by way of suction sampling or vessel-deployed collectors, the next step was to deal with the inherent difficulties in projecting future trends of fishery recruitment for a long-lived species like the American lobster. The first challenge was to account for the fact that crustaceans are notoriously difficult to age, and while thermal regime can help predict lobster growth rates and therefore size at age, tremendous variability in growth are observed for the same thermal regime. This means that a given cohort of settlers will cross the legal-size threshold to recruit to the fishery over a range of ages, so that any year of fishery recruitment comprises a mix of ages (Oppenheim et al., 2019). The first predictive model (Wahle et al., 2004) began to account for that variability, but the forecasts were preliminary, spanned a relatively short time series, did not account for variable environmental conditions within an area, and were not validated against observed fishery recruitment or landings. In addition, as many studies have noted, the challenges of testing environmental effects on recruitment and survivor dynamics is that the correlations between them may not be stationary over time (Myers, 1998; Jacobson and McClatchie, 2013; Hare et al., 2015).

Rhode Island, for example, the location with one of the longest ALSI time series and fastest growth rates, began to show promising signs that settlement could reliably predict the abundance of pre-recruits measured in the state's fishery independent trawl survey some 4-5 years later. However, this predictive ability changed when epizootic shell disease became a significant source of natural mortality. When natural mortality remained relatively constant, the predictive relationship was robust. But in the late 1990s, when shell disease became prevalent, the ALSI forecasting model predictiveness weakened. The next generation ALSI-based predictive model, therefore, included a term for shell disease prevalence to accurately predict the downward trend in pre-recruits (Wahle et al., 2009b).

Subsequent predictive models have become more rigorous, by both including more environmental predictors and providing validation of the predictions against observed metrics of fishery recruitment across a broad range of study areas (Figure 5) (Oppenheim et al., 2019). The model was developed for 11 substock areas between Rhode Island and New Brunswick's Bay of Fundy shore and predicts landings trends as many as six years out. Landings time trends have been used as the indicator of fishery recruitment, as some 90% of the harvest consists of lobsters just entering the fishery (Acheson and Reidman, 1982; ASMFC, 2020). This new version of the ALSI forecast model accurately predicted landings time trends for 9 of the 11 substocks. The model continues to be updated annually, and since publication it has become apparent that while the model has consistently predicted landings accurately in most areas, it has underpredicted landings trends in the southwest Gulf of Maine. Possible explanations for why the model would underpredict landings in this region include the likelihood that the southwest is subsidized by recruits from the higher density populations in the northeastern Gulf of Maine, or that harvesters are increasingly exploiting federal waters outside their nearest fishing grounds. While the suction sampling-based ALSI index from shallow water in the Gulf of Maine and southern New England has provided considerable predictive power, early indications are that the building time series of collector-based sampling across a range of depths may provide a more complete picture of year-class strength (Goode et al., 2019).

A recent study developed individual-based models to forecast fisheries recruitment in three management areas in Canada, two in the Gulf of St. Lawrence and one in the Bay of Fundy, based on the three longest (16, 25 and 30 years as of 2021) lobster benthic recruitment time series obtained by DFO researchers using SCUBA (White, 2022). The modeling approach used in this study differed from that used in Oppenheim et al. (2019) in terms of how growth was modeled, although it too generated an annual fisheries recruitment index that was significantly correlated to annual biomass landed (in all three study regions). In particular, when constrained to the same time period, models developed in the two studies showed very similar skill at forecasting landings in LFA-36 based on the lobster settlement in Beaver Harbor, which speaks to the robustness of these benthic-fisheries recruitment linkages to different modeling approaches. Additional modeling work based on ALSI science is also being conducted in Canadian waters, including the prospective underprediction of Bay of Fundy landings in recent years (e.g., thermal expansion of settlement habitat, mismatch between recent values of landings and fisheries recruitment), and the expansion of forecasting abilities to other areas with shorter but expanding ALSI time series.

The future of ALSI: Opportunities and challenges

Next steps for lobster settlement science

Over the past three decades, the ALSI program has evolved and expanded during a period of rapid environmental and ecosystem changes brought about by a warming climate, human exploitation, and species introductions. Changes in oceanography influence regional suitability of lobster settlement habitat. Continuing to assess how these changes will translate into altered lobster settlement is crucial to our ability to determine the productivity and population bottlenecks for the stock (Goode et al., 2019). This is particularly true for deeper waters, where, historically, lobster settlement has been assumed to be minimal compared to coastal areas. The use of passive collectors to assess offshore lobster settlement in areas such as the Gulf of Maine will lead to better assessment of the stock's resilience and whether apparent declines in coastal areas of Gulf of Maine are compensated for by increases in deeper waters.

The broader use of collectors across deeper habitats would be beneficial across the species' range, such as Georges Bank (Figure 1). Large aggregations of egg-bearing lobsters and larvae and postlarvae (stages I-IV) have been documented on Georges Bank (Harding et al., 2005; Henninger and Carloni, 2016; Jury et al., 2019), yet recruitment dynamics are largely unknown. Temperatures and habitat are suitable for recruitment on Georges Bank, and preliminary biophysical modeling suggests retention within the gyre is possible (J. Churchill, personal communication). Due to the distance of this unique bathymetric offshore bank from shore, logistics associated with sampling have been difficult and initial attempts to deploy collectors there have been inconclusive (R. Wahle, personal communication). Deep water offshore areas and offshore banks with documented larval production also beg the question of how postlarval swimming ability influences spatial recruitment dynamics. In southern New England, Katz et al. (1994) found a higher abundance of earlier stage larvae in offshore areas (up to 150 km offshore), but more mature larvae closer to shore, suggesting that the larvae originating from eggs that hatched offshore recruit to inshore, shallow waters. An empirical trajectory model showed that passive drift of these larvae alone was not sufficient for these offshore populations to recruit

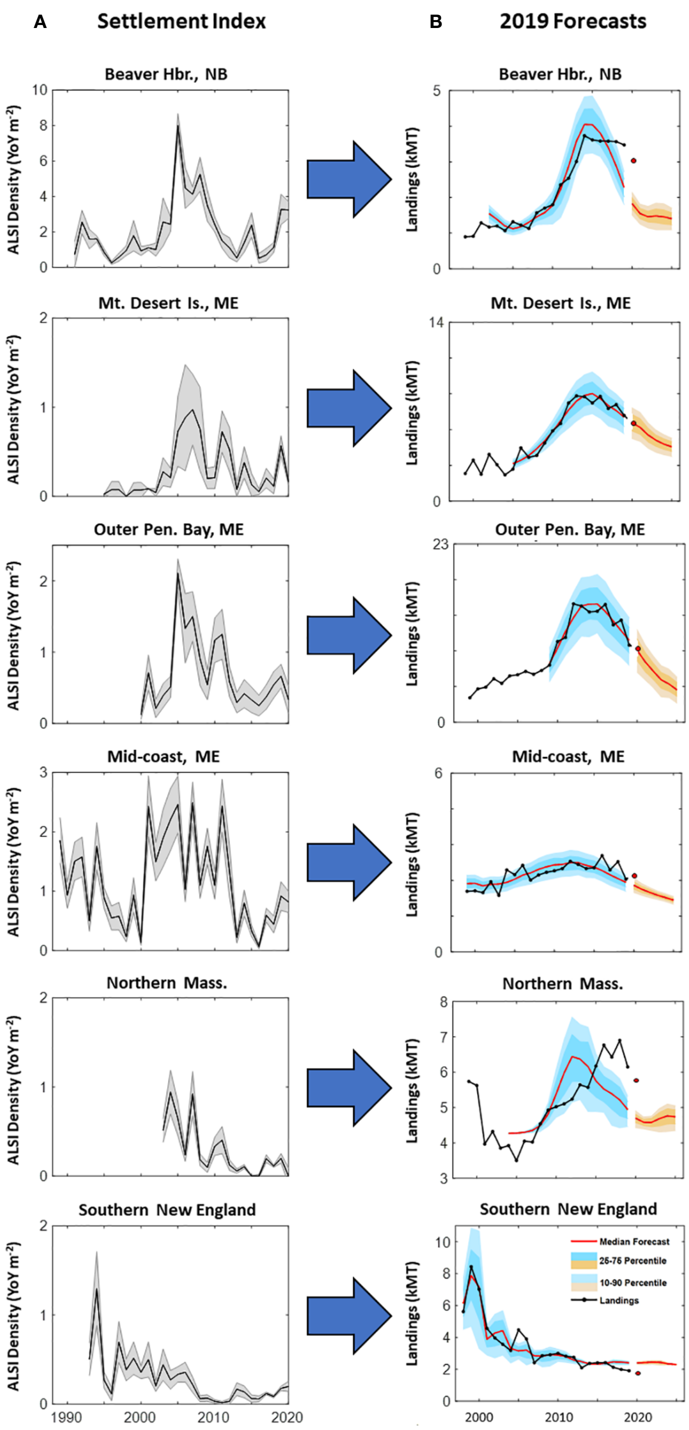

FIGURE 5
Settlement indices by region **(A)** and their corresponding forecast to landings **(B)**. Settlement indices include annual means and standard error. Forecasts include the settlement and landings relationship through 2019 (blue segment) and the skill of the forecast (orange) is assessed as landings accumulate. Methods for the forecast model can be found in Oppenheim et al., 2019. The 2020 landings are also presented (red dots).

inshore. However, when incorporating the swimming speed of postlarvae, transport and recruitment to inshore coastal waters was plausible. Thus, it is possible that in the Gulf of Maine and Georges Bank, eggs hatched farther offshore could recruit to inshore coastal nursery habitats. We expect that a future direction of the ALSI collaborative will be to investigate connectivity and recruitment dynamics around Georges Bank.

We present an application of the Paulik diagram here for the American lobster using a suite of survey data, including those from the ALSI program, but little has been done to quantify the relationship between the successive life-stages and the suite of variables that are known to influence survivorship between life stages. Several types of analyses have been used to test the relationship between successive life stages of marine organisms, such as key factor analysis (Langan et al., 2022). Exercises such as these allow for testing the drivers in survivorship variability between life stages, which is particularly valuable for discerning mechanisms in post-settlement processes. In southern New England, there is evidence of recruitment failure with productivity or recruits per spawner declining over the last two decades (ASMFC, 2020). Changes in oceanographic influence, stock-recruitment relationships, and management regulations pose a challenge to generating robust landing forecasts over long temporal scales, raising the need for frequent model re-evaluation and optimization to account for relationships that vary over time. The lack of direct age indicators has continued to challenge our ability to track the fate of cohorts over time in long-lived crustaceans like lobster. Recent exploration of potential direct indicators of age from band counts of histological sections of the gastric mill and eye stalk have sparked new interest but remain in doubt for lack of an understanding of the mechanism by which bands are formed and accumulate (Kilada et al., 2012; Huntsberger et al., 2020). In addition, addenda to legal harvest sizes and fishing effort will affect how landings volumes reflect annual fishery recruitment, potentially increasing the need to restructure forecasts based on catch per unit effort or fishery-independent estimates of recruitment (e.g., trawl surveys). As temperatures continue to rise, the probability of disease influence on northern stocks will increase alongside potential predation and intraspecific effects of novel species, which will also need to be considered in model development. The availability and use of deep nursery habitats as recruitment refuge will also need to be tested to evaluate their potential buffering of ocean warming effects on settlement and fishery recruitment. Future work should integrate these socio-environmental dynamics over oceanographically relevant scales to capture the extent to which changes translate to fishery productivity.

With over 30 years of ALSI data in certain regions, the young-of-year indices have provided managers a model-free indicator of year class strength that can be used to project recruitment to the fishery. However, to date, the ALSI data have not been included as input data to regional lobster stock assessment models (ASMFC, 2020). For US lobster stocks, one of the limiting factors thus far for including the ALSI data has been the need to extend the growth matrix to include smaller size classes. The University of Maine Model (UMM) used for the US lobster stocks currently models lobsters from 53 mm to 233 mm (carapace length), with 53-77 mm lobsters used to represent recruitment of the population in the models. Limiting the recruit abundances to lobsters greater than or equal to 53 mm results in not capturing population responses to processes driving recruitment between egg hatch and 53 mm. For ALSI abundance data to be used as relative abundance indicators of recruited lobsters, the growth matrix for the model would have to be expanded down to the corresponding size classes. Future work should integrate existing molt increment and probability information into the current growth matrix used in the UMM for inclusion of regional ALSI indices and size compositions into assessment models.

Much of our inference from ALSI indices is predicated on defining the size threshold of young-of-year lobsters. Lobster growth and molting frequency is known to vary geographically (ASMFC, 2020), including over small spatial scales for young-of-year and juvenile lobsters (McMahan et al., 2016), which is reflected in the size determination of study area-specific indices (Supplement S2). These geographic differences are often believed to be driven by regional differences in the environment that influence growth, such as temperature (Huntsberger et al., 2020). Such thermal influence on lobster molting and frequency over time has also been document for early-life lobsters (McMahan et al., 2016.) Given growth's dependency on temperature and documented interannual and long-term changes in the ecosystem, the size of young-of-year lobsters at given sites has likely not been static over time. Several studies have aimed to understand the sensitivity of changes in size threshold on resulting ALSI indices, and the relation between young-of-year size determination and sea temperature (Harrington et al., 2017; Morin and Wahle, 2019). However, we are still lacking the mechanistic relationship between lobster growth and the environment to employ a time varying threshold. Dedicated work toward defining this relationship would allow for a more realistic depiction of young-of-year lobsters annually, and ultimately improved ALSI indices.

The ALSI program was originally designed for the American lobster, but by enumerating associated crustaceans and fish, the monitoring program has also provided insight into the ecology of other species and potential species interactions (Wahle et al., 2013b; Wahle et al., 2015; Hunt et al., 2017). In US waters, for example, Jonah crab (*Cancer borealis*) has emerged as a viable fishery, but there is little demographic or ecological information on the early life stages to inform population assessments (Truesdale et al., 2019a; Truesdale et al., 2019b). The ALSI program has a long record of recently settled Jonah crabs, suggesting recent increases in abundance in the Gulf of Maine

(Figure 6). The program has subsequently been leveraged to better understand Jonah crab growth dynamics (Huntsberger, 2019). The ALSI program also provides insight into new emerging or invasive species. For example, these data have been valuable in tracking new taxa moving into lobster settlement habitats, such as Asian shore crabs in southern New England (Figure 6) and black sea bass in Gulf of Maine, and green crab in Newfoundland. To date there has been only one comprehensive analysis of the collector-based biodiversity throughout the range from Newfoundland to Rhode Island, which covered only a few years (Hunt et al., 2017), but the potential for a greater synthesis of regional and temporal changes in benthic biodiversity is increasing as the time series continues to expand.

Emerging new data streams can also extend to lobsters themselves. For example, epizootic shell disease became prevalent in southern New England lobsters in the mid-1990s (Castro and Somers, 2012), and shows diminishing prevalence along a northeastward gradient (Glenn and Pugh, 2006; Reardon et al., 2018). Shell disease has been linked to increased mortality from settler to pre-recruit stages (Wahle et al., 2009b). Shell disease is seldom seen in settlers and very young lobsters, though most lobster monitoring programs do not encounter lobsters in this size class. In southern New England, lobstermen have begun to observe disease on lobsters at increasingly smaller sizes, giving rise to concern that the more frequent molting of small lobsters may not be enough to mitigate future disease prevalence. The ALSI program is perhaps the best monitoring tool to be able to systematically capture epizootic shell disease prevalence in smaller size classes, further justifying monitoring into the future.

Program considerations

We identified the traits and values of the ALSI collaborative that have enabled its persistence over three decades:

(i) Interdisciplinary Mindset: While the program's original objective of monitoring newly settled lobsters (Wahle et al., 2010) has not changed through three decades of monitoring, the expansion of the program has given rise to a suite of new questions that have gained elevated research attention. Several scientific fields have been integrated into the work conducted under the ALSI program, including oceanography (physical, biological, and satellite), larval fish ecology, marine biology, and population dynamics, and most recently, molecular genetics, with DNA sequencing of larval gut contents

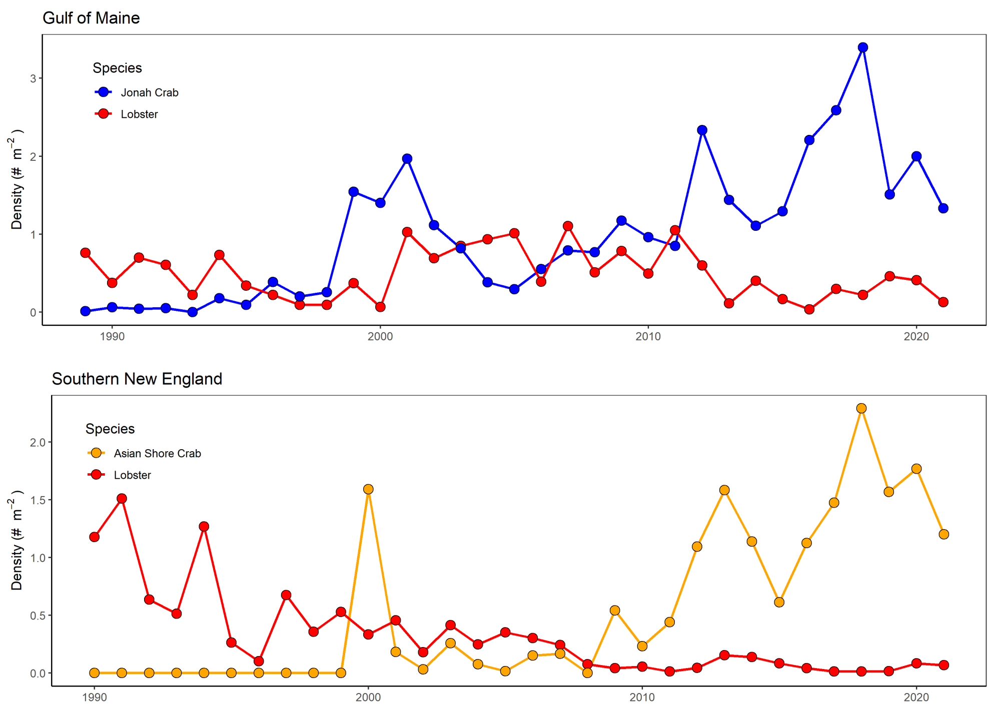

FIGURE 6
Depiction of emerging taxa in relation to young-of-year American lobster in US waters: Jonah crab in the Gulf of Maine (top) and Asian shore crab in southern New England (bottom). Gulf of Maine indices represent those from the Mid-coast Maine site and Southern New England indices are aggregated from Rhode Island and Buzzards Bay.

to improve our understanding of larval trophic interactions. A holistic interpretation of ALSI data leveraging these fields has allowed ALSI collaborators to maximize the knowledge that the program can provide. Doing so has allowed for continued funding success by showcasing the many applications of the program. We recommend that similar long term monitoring programs embrace an interdisciplinary perspective to maximize the utility of their data.

(ii) Continuous Questioning: The American lobster may be one of the most well-studied marine species of the Northwest Atlantic ecosystem. This legacy has surely informed the ALSI program. Still, many science gaps remain, and the boundaries of what we know continue to advance with new research. The ASLI partnerships have fostered honest conversations representing diverse perspectives, and a willingness to challenge the conventional wisdom. Open-mindedness and trust-building across partners and sectors have been a strength of the program, and we believe is vital for successful long-term monitoring programs.

(iii) Diverse Partnerships: The ALSI program has included an interdisciplinary team of scientists from a wide variety of disciplines and expertise, which have been leveraged to further the science. The regional recognition of the program's importance, and consideration of partner's varying needs as they vary geographically, has allowed for fruitful collaborations between the leading entities. Over the years, the cooperative research approach with the lobster industry has improved the science of the ALSI program. The shallow nature of the long-term monitoring sites has allowed for academic and agency scientists to survey them with SCUBA. However, the complement of collector deployments to monitor settlement at sites inaccessible to divers has necessitated assistance from the lobster fishery, and led to increased collaborations with fishermen by using commercial vessels as research platforms and designing sampling configurations. The relationship between lobster scientists and harvesters has grown, allowing for sharing of ecological knowledge, explaining scientific methods and analyses, and formulating new hypotheses related to lobster early life history. The collaborative nature of the program has led to co-development of hypotheses and methods between scientists, fisheries managers, and harvesters. With the growing use of collectors throughout the region to better understand deep water settlement patterns, we contend that reliance on industry collaborations will become increasingly important. Further, recording industry members' observations on the water in a continually changing environment will be imperative for ALSI partners to contextualize patterns from long-term monitoring sites. The partnership with the commercial fishery will continue to be important into the future.

(iv) Opportunistic Funding: Oceanographic and biological time series data are essential for our understanding of the mechanisms driving the dynamics of marine populations. However, funding long-term monitoring programs is not easy. It requires decades of data with sufficient spatial and temporal resolution, especially for the study of long-lived species such as the American lobster. Support for ALSI has proven sustainable for three key reasons: (1) the monitoring is not very costly relative to other monitoring programs, and (2) the cost has been shared by all partners by aggregating funds and effort from a broad spectrum of industry, academic and government sources, and (3) the results have been reported in a timely manner with outcomes meaningful to its stakeholders. The real strength of the ALSI effort is in the spatial aggregate and length of its time series, although in some cases changing priorities have left gaps, compromising its utility for fishery managers in certain regions. Sustaining long-term funding for the ALSI program remains both a challenge and priority for the region at-large.

Conclusion

ALSI has demonstrated that transboundary collaborative research among scientists, the fishing industry and government agencies can provide a valuable and cost-effective indicator of the health and near-term future of the iconic American lobster fishery. The sampling method taps into a pivotal and uniquely useful juncture of the lobster life history that provides insight into both the pre- and post-settlement processes that influence the fate of a cohort and recruitment to the fishery. Resulting forecasting tools under development show promise of becoming a useful tool giving stakeholders several years of lead time to consider business and sustainable management options, and to evaluate future scenarios. By highlighting both the successes and challenges of the program in this review, we illustrate how the ALSI program can serve as a model of collaborative long-term research and monitoring for other marine resources that may be challenged to find the resources to inform management decisions. Given the prospects of rapid environmental change in the coming century, continued long-term early life stage monitoring will be an essential tool to inform sustainable management of these lobster stocks and provide resiliency to the communities that depend on them.

Author contributions

MCM conceived this review, and led the writing and organization of the manuscript. RAW led the development of the sampling methodology and founded the ALSI collaborative. MCM, AGG, KK, and RAW executed figures and tables. All co-authors are members of the ALSI collaborative, have contributed to the sampling effort and analyzing data, and provided guidance, text, and revisions to the manuscript.

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Conflict of interest

Author CB was employed by Ready Seafood Company.

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2022.1055557/full#supplementary-material

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