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The American lobster settlement index at 20 years: looking back - looking ahead

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Abstract

We review the accomplishments and future challenges of larval settlement monitoring for the American lobster (*Homarus americanus*), following a workshop convened in June 2009 observing the programme's twentieth anniversary. In the late 1980s the new emphasis on "supply-side ecology" energised researchers to look to larval transport and settlement processes to explain population dynamics of marine species with complex life cycles. At that time, larval settlement indices for spiny lobsters (*Panulirus cygnus*) in Australia were already demonstrating a capacity to forecast subsequent harvest trends and motivated the search for similar predictive power in the other lobster fisheries. The American Lobster Settlement Index (ALSI) was initiated in 1989 soon after diver-based suction sampling proved an effective way of sampling newly settled lobsters in shallow, cobble-boulder nursery habitats. The survey has expanded from a few sites in coastal Maine, USA, to encompass other lobster-producing regions of the Northeast United States and Atlantic Canada. Supported by state and provincial marine resource agencies, monitoring is conducted annually at the end of the late summer-early autumn postlarval settlement season. The settlement index has been the springboard for numerous research projects, contributing to some 24 peer reviewed publications and technical reports to date. Because of the interest in evaluating the predictive power of the time series for subsequent fishery trends, much research has focused on the pre- and post-settlement processes influencing lobster population dynamics. Owing in part to steep gradients in environmental conditions throughout the species' range, it is becoming evident ocean-atmospheric processes that influence annual fluctuations in larval supply vary on much larger spatial scales (100-1000 km) than do post-settlement processes, such as predation, disease and intra- and interspecific competition. Thus, unlike the Australian case, forecasting models for the American lobster will likely need to be regionally customised to account for differing regional dynamics. Since 2005, vessel-deployed passive postlarval collectors (plastic coated, wire mesh trays filled with cobbles) have been tested and deployed widely as an alternative to suction sampling to assess lobster settlement in waters where diving is unsafe or impractical. Indeed, collectors may become the tool of choice for settlement monitoring in some regions. As we enter the third decade of the region-wide collaboration, it will be important to continue to assess the value of the index as a tool for stock assessment, forecasting, and a mechanistic understanding of lobster recruitment processes.

Keywords: *Homarus americanus*, larva, recruitment, collector, suction sample

Introduction

The American Lobster Settlement Index (ALSI) is an annual diver-based survey of American lobster (*Homarus americanus*) nursery grounds in the coastal northeast US and Atlantic Canada. The survey is supported by participating states and provinces and gathers data not only on newly settled, young-of-year (YoY) lobsters, but older juveniles and associated crabs and fishes, as well. Data are compiled from all regions annually and disseminated to the participants, industry groups and interested parties. The time series is the largest-scale assessment of lobster nursery habitat available. It extends for more than 20 years at some locations and more than ten years at most. It has been the springboard for numerous research projects, contributing to more than two dozen peer-reviewed publications and technical reports (see Appendix 1, in reference section). It has been used to forecast local trends in the abundance of adult lobsters in nearshore trawl surveys (Wahle *et al*., 2009), and provided valuable insights into both pre- and post-settlement processes influencing lobster population dynamics (Incze *et al*., 1997; Wahle and Incze, 1997; Xue *et al*., 2008; Incze *et al*., 2010).

In June 2009 a workshop was held to celebrate the twentieth anniversary of the Index. Hosted by Bigelow Laboratory for Ocean Sciences and Maine Department of Marine Resources, the meeting convened some 40 scientists, fishery managers and industry members from New England and Atlantic Canada who have been involved in the monitoring and research over the years. We use the opportunity of these proceedings of the RALBAM conference to disseminate more widely the outcome of our regional workshop because we believe it serves to communicate the value of maintaining long-term multi-life-stage time series. In keeping with the workshop's two-part theme, the aim of this paper is to give a retrospective on the scientific contributions of ALSI to date, including a preview of work in progress, and to look ahead to the challenges and priorities still to be met in monitoring, research, data management, and outreach.

Early inspirations

The American Lobster Settlement Index was inspired by emerging developments in marine ecology and fisheries science the mid-1980s. At the time, marine ecologists were gaining a new appreciation of the role of "supply-side ecology" in the dynamics of intertidal populations and communities (Butman, 1987; Roughgarden *et al*., 1988; Ekman, 1990). While fisheries scientists had long appreciated that the vagaries of larval survival could dramatically influence cohort success (Hjort, 1914), few had been successful in harnessing the predictive power of gathering data on early life stages. By the mid-1980s, however, Australia's western rock lobster (*Panulirus cygnus*) biologists were already demonstrating an impressive capacity to forecast trends in the commercial harvest from time trends in the abundance of newly settled postlarvae on artificial collectors deployed at selected coastal locations, a time series that had begun in the late 1960s (Phillips, 1986; Caputi *et al*., 1995). Quite simply, we were inspired to see if we could emulate that success story with the American lobster.

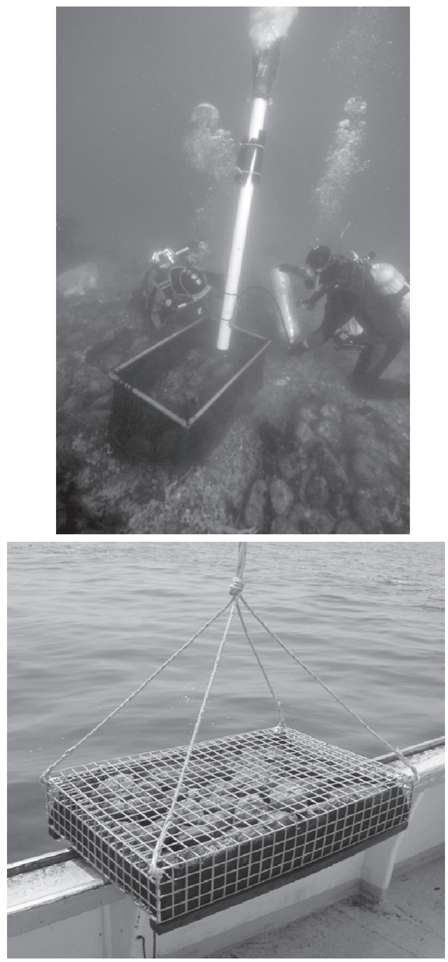

Fig. 1. Divers suction sampling (top), and a passive postlarval collector (below)

Paradoxically, for the large size of the American lobster fishery, and long history of scientific investigation, the means to quantify YoY lobster had still eluded science. Painstaking visual surveys by divers in the Magdalen Islands, southern Gulf of St. Lawrence, Canada, were giving the first numbers on recently settled lobsters, revealing the YoY as a well-defined mode in the size distribution of lobsters residing in rocky nurseries (Hudon, 1987). But the method depended on divers having good visibility and working slowly and methodically, an approach not practical for large scale surveys. Diver-based suction sampling was the key breakthrough (Fig. 1; Incze and Wahle, 1991; Wahle and Steneck, 1991). Since then, suction sampling has caught on as a lobster settlement monitoring tool among marine resource agencies and academics in the Northeast US and Atlantic Canada (Fig. 2). As the time series grew and expanded geographically, its value to our understanding of supply-side and post-settlement processes became increasingly apparent.

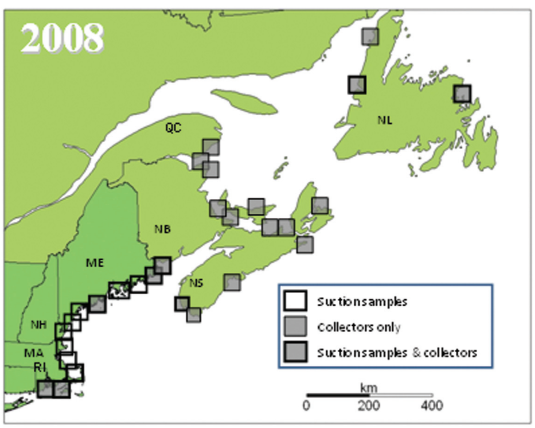

Fig. 2. Locations included in the American Lobster Settlement Index as of 2008 by diver-based suction sampling or passive postlarval collectors; each box represents a multi-site region

Understanding pre-settlement processes

Our understanding of the quantitative linkage between pelagic larval and subsequent benthic lobster life stages stems from a combination of field sampling and numerical modeling. By the mid-1990s parallel neuston and benthic sampling were revealing strong correlations in space and time between larval supply and benthic recruitment (Incze *et al*., 1997; Wahle and Incze, 1997). These results have helped confirm bio-physical model predictions of lobster larval transport trajectories (Lynch *et al*., 1996; Xue *et al*., 2008, Incze *et al*., 2010). Recent larval transport models suggest that in spite of the great potential for long distance larval dispersal, benthic recruitment is likely to be more locally derived than previously thought, and that larvae are more likely to be retained in local embayments if they are hatched nearshore (Incze *et al*., 2010).

New analyses by a University of Maine team, and supported by the US space agency, NASA, are currently evaluating correlations between the regional settlement time series and satellite-derived environmental data sets. These studies are enabling the refinement of hypotheses about the key drivers of spatial and temporal variability in larval settlement. Spatial coherence - the spatial scale at which annual settlement fluctuations are synchronous - can be an important indicator of the scale at which environmental drivers operate. New analysis by Andrew Pershing (University of Maine and Gulf of Maine Research Institute) are revealing coherence in the settlement indices collected among regions within, but not outside, the Gulf of Maine. Many of the regional settlement time series correlated significantly with regional indicators of atmospheric conditions. For example, the strength of atmospheric pressure gradients and resultant regional prevailing wind patterns during the larval production season show promise as predictors of regional fluctuations in lobster settlement.

In a separate analysis under the same project, University of Maine graduate student, Mahima Jaini, is using satellite-derived, high resolution maps of sea surface temperature to correlate annual fluctuations in lobster settlement at sampling sites and annual sea surface temperature anomalies far offshore. The settlement in coastal Rhode Island was higher than average, which was found to be correlated with warmer than average temperature anomalies over Georges Bank, about 150 km to the east. While the causal relationships in such correlations remain unclear, such analyses may help identify oceanographic features and processes important to lobster larval supply.

Genetic studies can also provide a greater understanding of whether these processes that influence larval supply and transport result in sufficient isolation to permit population differentiation and therefore stock definition. For example, the recent comprehensive analysis of the genetic structure of American lobster population throughout its geographic range by Kenchington *et al.* (2009), has generated new hypotheses about the history and process of population differentiation, albeit on a relatively coarse spatial scale. They suggest that the observed low levels of genetic diversity in the northern part of the species range may have arisen from only a few founder events reestablishing northern populations during and after the retreat of the Wisconsin ice sheet. Further analysis of genetic structure at finer spatial scales coupled with existing biophysical models of larval transport (Xue *et al*., 2008; Incze *et al*., 2010) would help further resolve lobster metapopulation structure.

Understanding post-settlement processes

Understanding demographic rates after larval settlement depends on the ability to follow cohorts through time and that requires the ability to distinguish age groups. While recently settled YoY lobsters are relatively easy to distinguish from older year classes by their small size, size-based age determination becomes less reliable as lobsters grow because of variable growth rates. Various methods have been used and are being explored to refine age estimates (Sheehy *et al*., 2001, reviewed in Wahle and Fogarty, 2006). In the absence of other reliable age indicators, body size remains the tool most commonly used. Tagging remains the most direct way to obtain measures of individual growth, but is a challenge with the smallest juveniles. While numerous tagging studies of lobsters in the harvestable range have been conducted over the years in different regions, growth studies of the smallest juveniles are rare. Detailed long-term tagging studies of juvenile lobsters in nurseries accessible in the intertidal zone of New England such as those undertaken by Diane Cowen (1999) will help complete our understanding of growth over the entire life cycle. Moreover, integrating tagging-based growth studies with modal analysis where age classes are well defined as size modes, work currently under way by the University of Maine graduate student, Charlene Bergeron, will provide the empirical data necessary to develop robust cradle-to-grave models of lobster growth.

Initial settlement densities are a prime determinant of the number of lobsters recruiting to subsequent ages (Incze *et al*., 1997; Wahle *et al*., 2004; Wahle *et al*., 2009). This seems intuitive, but it is not always the case in decapod crustaceans experiencing large early post-settlement mortality (e.g., Eggleston and Armstrong, 1995; Pile *et al*., 1996; Moksnes 1997; Palma *et al*., 1998). While the relationship between planktonic postlarval abundance and benthic young-of-year recruitment is essentially linear in the American lobster (Incze *et al*., 1997), the functional relationship between YoY and subsequent ages tends to be non-linear (Wahle *et al*., 2004, 2009a) as is true for the western rock lobster (Caputi *et al*., 1995) suggesting density-dependent mortality effects early in life. The mortality consequences of crowding remain poorly understood, however, there is evidence that the strength of habitat limitation bottlenecks may be mediated by the abundance of predators (Wahle, 2003). Future evaluation of trophic interactions is therefore an important part of understanding post-settlement effects on survival.

The first indication that the geography of the American lobster fishery may mirror the geography of settlement came with a coast-wide study in Maine during the late 1990s that included diver-based suction sampling, visual surveys, accompanied by at-sea sampling of the commercial catch (Steneck and Wilson, 2001). The multi-layered project demonstrated that settlement “hot spots” along the Maine coast correspond to harvesting hot spots, encouraging hopes that settlement could be a useful tool in fisheries forecasting.

Although forecasting trends in the American lobster fishery from a settlement index has not yet been realized at the geographic scale of the Australian model, we are seeing some important scientific advancements. The most promising results are coming by linking the settlement index to the subsequent abundance of older lobsters about to recruit to the fishery in nearshore trawl surveys conducted in adjacent waters by state marine resource agencies. In Rhode Island, USA, for example, nearshore trawl surveys had been under way for twelve years before the settlement survey began there in 1990. The parallel surveys have been linked in the first predictive model using the settlement index, but with a caveat (Wahle *et al*., 2009a). As the parallel time series grew, although a strong predictive relationship was emerging between settlers and sub-harvestable pre-recruits three years later in the trawl survey, from 1997 onwards that relationship began to lose predictive ability; the settlement survey on its own was no longer a good predictor of pre-recruits. In the previous year shell disease struck southern New England, and within a few years had affected 25-30% of the lobster population. Adding shell-disease prevalence to the predictive model in effect accounted for the elevated natural mortality after the onset of shell disease.

Success in developing a predictive model has been slower in Maine. This is in part because lobsters grow more slowly in the cooler waters of the Gulf of Maine. But also the state's trawl survey only began in 2000, so there has been less opportunity to link the parallel time series. Nonetheless, using a forecasting approach that accounts for variable growth (Wahle *et al*., 2004), preliminary results indicate that time trends of near-harvestable lobsters in the trawl survey are tracking fluctuations in the settlement index that occurred about seven to eight years earlier. Fortunately, shell disease is not a factor in Maine, but natural mortality rates may change over time, if for example, predatory fish abundance changes. Maintaining parallel environmental time series and fishery-independent surveys is therefore critical to forecasting. Being able to separate the influence of various environmental factors from the settlement signal on the abundance of lobsters in trawl surveys will be critical to fully understanding the sources of variability. University of Maine graduate student, Jui-Han Chang, described a habitat suitability model exploring the importance of factors such as substrate, depth, temperature, and salinity in predicting the spatial distribution of juvenile and adult lobsters found in Maine's nearshore trawl survey.

In the Gulf of St. Lawrence, forecasting trends in the Magdalen Island fishery may also be possible from the settlement index derived from diver visual surveys. Louise Gendron (Department of Fisheries and Oceans Canada) presented results of surveys of rocky lobster nurseries around the archipelago suggesting that inter-annual variability in settlement is correlated with both egg production and advection indices, and that it will be feasible to follow cohorts from rocky nurseries into trawl surveys, a transition suspected to occur at about three years of age. Growth rates vary, however, so not all lobsters from a year class recruit to the fishery at the same time. Wahle *et al*. (2004) developed a model that predicts time trends in fishery recruitment from the settlement index and accounts for variable growth. It will be important to parameterise this and other growth models with a better understanding of growth variability on a regional basis.

Emerging technology: passive postlarval collectors

Building on past success with diver-deployed passive postlarval collectors, a vessel-deployed version makes it possible to evaluate settlement at depths and locations that are otherwise unsafe or impractical for divers (Fig. 1; Wahle *et al*., 2009b). Collectors of various designs had been deployed by divers since the 1990s (Incze *et al*., 1997; Palma *et al*., 1999; Steneck and Wilson, 2001). A recent fisherman-scientist collaboration supported by NOAA's Northeast Consortium resulted in a redesign that allows collectors to be deployed with standard commercial trap hauling gear. Complementing deployments of collectors in New England waters to assess depthwise patterns of settlement, collector deployments undertaken in scientist-fishermen collaborations throughout Atlantic Canada since 2007 (presented by J. Tremblay and M. Comeau at the workshop) will considerably expand the potential geographic coverage of the settlement index if sustained for the long term (Fig. 2). Encouragingly, settlement densities compared favorably where side-by-side performance tests of collectors and suction sampling have been done (Wahle *et al*., 2009b). As the international collaboration evolves, it will be important to calibrate and consider the trade-offs of the two methods. For example, while suction sampling requires a single sampling trip at the end of the settlement season, collectors require two trips involving a considerable effort during deployment and retrieval, as well as maintenance. Collectors, on the other hand, provide the benefit of a standardised habitat unit and can be deployed where divers cannot go.

Prospects and challenges for the future

Workshop participants identified three areas on which to focus discussion about the future of the settlement index:

Survey methodology: Under survey methodology, the further refinement in size-frequency analysis was identified as a priority as applied to the development of growth models used to track cohorts through time. While the search for reliable age markers continues, refining these length-based methodologies will aid in estimating growth rates during the early benthic phase. Specifically, empirical data are desperately needed that characterise growth variability from the earliest juvenile stages through adulthood under environmentally contrasting conditions. Such studies will inform the development of generalised growth models that more realistically incorporate environmental effects such as temperature. Existing growth models such as those described by Wahle *et al*. (2004) and Chen *et al*. (in press) may be good starting points. In the absence of reliable age markers, integrating size-frequency-based approaches for early juveniles, and tagging-based approaches for older lobsters, may be a viable strategy to refine our understanding of the size-age relationships over a broad size spectrum of lobsters.

Seabed mapping was identified as a second survey-related priority vital to the future development of the settlement index. Mapping would not only aid site selection for diver-based and collector-based sampling, it would permit the quantification of suitable nursery habitat, and in turn, enable extrapolation from density estimates to total YoY recruitment in an area of interest, an important baseline for stock assessment. Historically, one of the impediments to large scale recruitment estimates has been the disparities in habitat classification schemes between the US and Canada and even among maps used by individual states. The group concluded that instead of relying on international or Federal habitat classification schemes, it would be more helpful to develop schemes that fit the habitat requirements for individual species or functional groups, including the American lobster. Groups such as the Gulf of Maine Mapping Initiative *(http://www.gulfofmaine.org/gommi/)* need to be made aware of these needs. A future workshop involving both biologists and geologists may be the best way of moving forward on this task.

Ecological processes: Knowing the ecological determinants of the post-settlement fate of a cohort is critical to forecasting time trends in the population. Recent correlative analyses underscore the importance of evaluating multiple time series of different segments of lobster life history, as well as other environmental factors that can influence rates of recruitment and natural mortality – such as predators, disease, and adverse environmental conditions. This will be especially important to consider in the context of long-term, large scale climate change, as well as short-term local scale environmental perturbations and disease. An important insight of our analyses is that because post-settlement mortality processes appear to vary over relatively short distances, it is likely that forecasting models will need to be regionally customised to incorporate environmental factors in addition to ALSI.

Inferences about metapopulation connectivity from recent population genetic analysis (Kenchington *et al*., 2009) have sparked much debate. Three advances would help us toward a better understanding of metapopulation structure: (i) finer spatial resolution of egg production for improved larval transport modeling, (ii) renewed tagging of benthic adults to improve our understanding of migratory exchange among populations during the benthic life phase, and (iii) finer spatial resolution of population genetic structure to compare to predictions of larval exchange models regarding gene flow among subpopulations.

Resource assessment: The ALSI has recently been included in the US stock assessment as a key indicator of the health of the lobster resource. In the months since the Settlement Index workshop fishery managers have defined a YoY recruitment reference point that will provide a useful threshold for management decisions. And it is playing a key role in the decision as to whether the lobster fishery in southern New England, which has been ravaged by more than a decade of shell disease, shall be subject to moratorium on fishing. The newly implemented reference point states that if stock abundance, as determined by trawl surveys, is running 25 to 50% below a long-term average, and the settlement index has fallen below 25% of its own long-term average for three of five consecutive years, a conservation measure will be triggered to rebuild the fishery. As part of the effort to make the settlement data more available to fishery managers, scientists and the fishing industry, a centralised data base is being constructed by the statistical branch of the Atlantic States Marine Fishery Commission. The more fishery scientists understand how YoY recruitment relates to the broodstock that produced them, or translates to subsequent fishery recruitment, the better they will be positioned to set guidelines for the use of settlement index reference points.

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Appendix 1

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