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EARLY LIFE HISTORY AND A MODELING FRAMEWORK FOR LOBSTER (*HOMARUS AMERICANUS*) POPULATIONS IN THE GULF OF MAINE

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ABSTRACT

Beginning in the late 1980s, lobster (*Homarus americanus*) landings for the state of Maine and the Bay of Fundy increased to levels more than three times their previous 20-year means. Reduced predation may have permitted the expansion of lobsters into previously inhospitable territory, but we argue that in this region the spatial patterns of recruitment and the abundance of lobsters are substantially driven by events governing the earliest life history stages, including the abundance and distribution of planktonic stages and their initial settlement as Young-of-Year (YOY) lobsters. Settlement densities appear to be strongly driven by abundance of the pelagic postlarvae. Postlarvae and YOY show large-scale spatial patterns commensurate with coastal circulation, but also multi-year trends in abundance and abrupt shifts in abundance and spatial patterns that signal strong environmental forcing. The extent of the coastal shelf that defines the initial settlement grounds for lobsters is important to future population modeling. We address one part of this definition by examining patterns of settlement with depth, and discuss a modeling framework for the full life history of lobsters in the Gulf of Maine.

INTRODUCTION

The population of American lobster (*Homarus americanus* Milne Edwards, 1837) in the Gulf of Maine has surged over the past two decades, fueling a lucrative fishery that now accounts for $> 80\%$ of the value of all commercially landed fish and shellfish in the State of Maine. Marked increases in landings also occurred elsewhere in New England, and in Canada (Fig. 1). Since the fishery operates at a very high rate of removal of legally harvested lobsters, the increased landings that began in the late 1980s are thought to largely reflect an increase in abundance (Fogarty, 1995). This is not to say that changes in effort and reporting have not also contributed to the upsurge, but no one doubts that there has been a substantial increase in the population itself. This increase can be seen in fishery-independent bottom-trawl surveys conducted by the U.S. National Marine Fisheries Service (Northeast Fisheries Science Center, Woods Hole, Massachusetts), but those surveys are conducted mostly in deep water and outside the main resource area for lobsters. Those data are now augmented by an inshore survey along the New Hampshire and Maine coasts (since 2000) that can be paired with the longer history of inshore surveys conducted by the state of Massachusetts to the south (since 1978). These surveys begin to detect demographic shifts 2-3 years before lobsters become legally harvestable, but several years of early life remain unaccounted for by trawl sampling (Lawton and Lavalli, 1995), and it is therefore difficult to ascertain the major factors that may be driving abundance and fishery production.

Fishing effort has been expanding farther offshore as increased income from landings enabled investment in larger and faster vessels, and advances in electronic navigation improved the speed and efficiency of relocating fixed gear. Some contend that the fishery is now exploiting a portion of the population that hitherto had been spared such pressure, and that this may account for a significant amount of the increase in landings. This is of concern because the offshore region may have served as a refugium for lobsters, and the offshore portion of the population might subsidize inshore recruitment, perhaps through larval supply (Fogarty, 1998). An alternative interpretation of these trends is that expansion of the fishery offshore followed an expansion of the population into territory that was previously less densely occupied by this species. Fishermen report that they catch lobsters in places that have never before been worth fishing (Fogarty and Gendron, 2004). Possible reasons for such an expansion include density-related pressures from the growing population inshore and more hospitable conditions offshore created by reduced predation from the now diminished groundfish populations (Steneck, 1997). While changes in predator populations probably shifted controls on the upper limits of population size, evidence presented by Incze et al. (1997, 2000b), Wahle et al. (2004) and later in this paper suggests that postlarval supply and settlement also are major drivers of adult population changes. Other frequently cited hypotheses to explain the multi-year increase in lobster landings include: (H_1) effective conservation of reproductive females has increased egg production (Steneck and Acheson 1997); and (H_2) the diet of lobsters has been augmented by the growing number of baited traps (Saila et al., 2002). The role of each of these factors is difficult to evaluate without comprehensive models of the full life history.

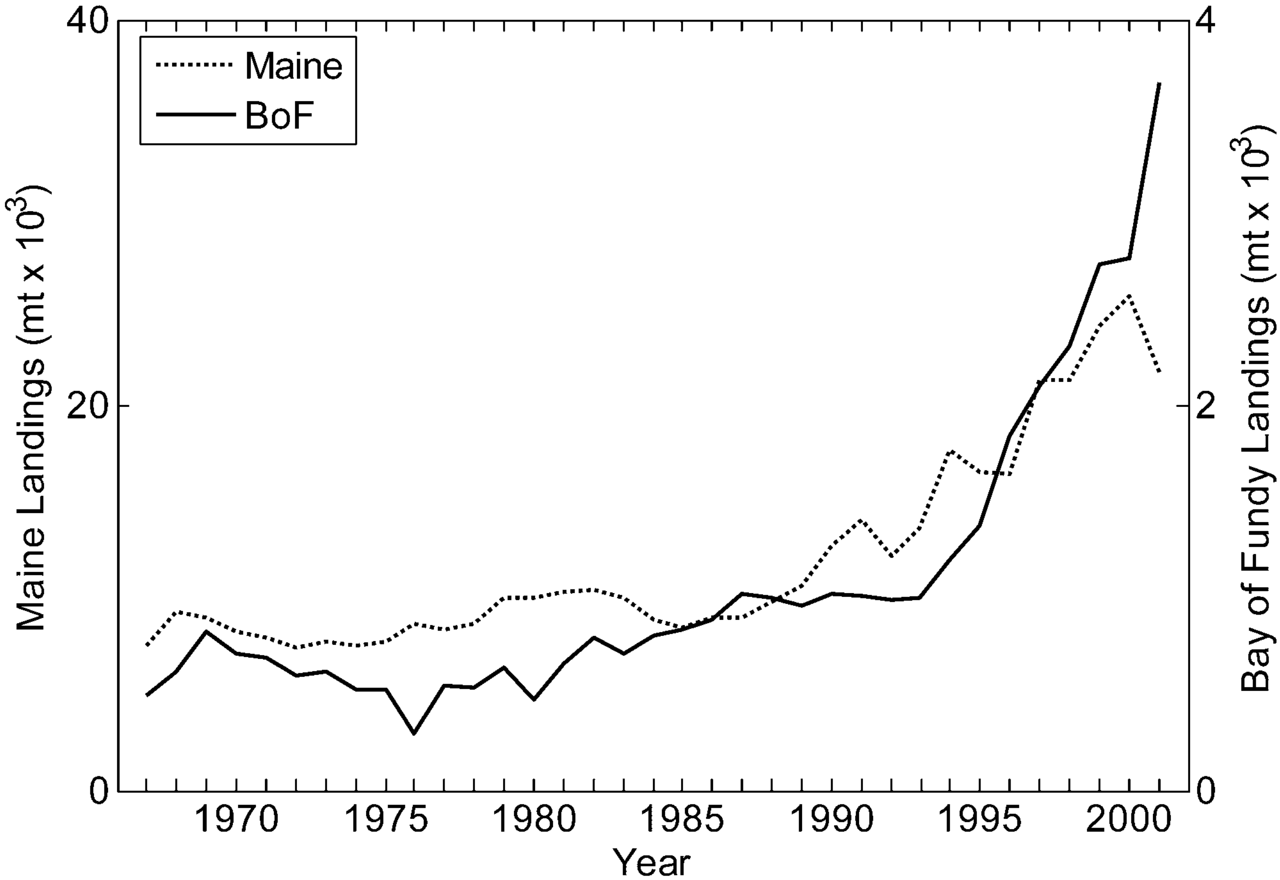

Fig. 1. Lobster landings in Maine, USA and Bay of Fundy (BoF), Canada, 1967-2001.

Quantitative, mechanistic models for evaluating or testing the various hypotheses do not exist. The rapid growth of data on various life history stages of American lobsters over the past two decades, and the need to improve our understanding of population trends and governing factors, make the effort at model-building realistic and timely. In the short term, models probably cannot meet urgent management needs, but strategies that combine management and curiosity-driven research can benefit both areas of endeavor. One strategy is to make modeling results available at spatial scales and life stages of interest to managers. Another is to develop interest in shared measurements, such as the abundance of Young-of-Year (YOY) lobsters that can serve as an "early warning" of possible future trends in recruitment to legal size (ASMFC, 2000; Wahle et al., 2004). Indices based on settlement can provide a greater lead time for management and the industry, and at the same time the data provide insight into the factors that drive recruitment. Dual-purpose indicators such as this can help sustain observational and modeling efforts that are essential for developing the forecasting skill that will be useful in the future.

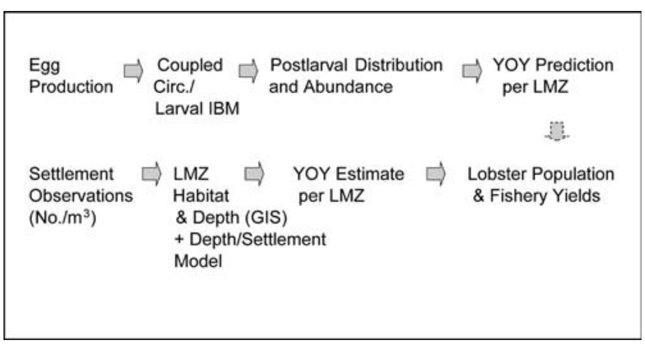

Fig. 2. Schematic of modeling effort in which postlarval and settlement data will be used. Upper model is the pelagic phase, using a coupled circulation/larval IBM (a 4 km resolution operational model used by the Gulf of Maine Ocean Observing System). The model incorporates egg hatching distributions and timing and proceeds through postlarval development. An empirical estimate of Young-of-Year (YOY) settlement is possible. The lower model is driven by empirical observations of settlement density, followed by submodels that calculate YOY populations per Lobster Management Zone (LMZ) and subsequent population growth. Model predictions can be compared with each other at the YOY stage. GIS = Geographic Information System; LMZ = Lobster Management Zone.

We are presently involved in a synthesis of field data and the development of spatially-explicit models to follow the life stages of lobsters in the western Gulf of Maine. We have divided our modeling into two parallel efforts dealing with planktonic and benthic life stages (Fig. 2). The planktonic model begins with the spatial pattern of egg hatching throughout the model domain shown in Fig. 3, and ends with postlarval abundance, from which a qualitative prediction of settlement (high, medium or low) might be possible based on empirical relationships. The model incorporates hatching throughout the season so that temporal and spatial variations in larval inputs, temperature and transport processes are included. The benthic population model begins with an estimate of YOY populations derived from field data and settlement models, and ends with the adult population and the fishery. The models operate at different grid scales. The planktonic phase is based on the regional circulation model used by the Gulf of Maine Ocean Observing System (Xue et al., 2000, 2005), which has a spatial resolution of approximately 4 km. The benthic model uses Maine's Lobster Management Zones (LMZs, Fig. 3) as its unit for population estimation. Output from the higher resolution planktonic model can be aggregated at the larger grid scale of LMZs so that postlarval supply can be related to geographic units that are meaningful to management and the industry. Studies published previously (Incze et al., 1997, 2000b) and additional analyses presented here show that lobster settlement is highly correlated with postlarval abundance.

In this paper, we present data from three components of our synthesis: a summary of spatial and temporal patterns of abundance of lobster postlarvae and young-of-year lobsters, and data describing variations in settlement with depth. This paper is part of a presentation made at a conference recognizing the lifetime contributions of Professor Stanley J. Cobb to lobster biology, ecology, behavior and fisheries science (Philips, this volume). Professor Cobb's work includes numerous papers on postlarval biology, behavior and settlement (Cobb et al., 1989a, b; Juinio and Cobb, 1994; James-Pirri et al., 1996, 1997; James-Pirri and Cobb, 2000) and early recognition that coupled biological, behavioral and physical models might answer long-standing questions about source and sink relationships in lobster recruitment (Katz et al., 1994). Professor Cobb has also championed the positive relationship between basic science and fisheries management. While the Gulf of Maine was not the geographic focus of Cobb's own field work, we note that he worked with L. Incze to make the first intensive measurements of lobster postlarvae in Maine's midcoast region in 1988, and was instrumentally involved in some of the early work that built a foundation for our ongoing synthesis (Incze et al., 1997).

METHODS

Postlarval Distributions

Lobster postlarvae were sampled from 1988 to present using neuston samplers equipped with 500 or 1000 μm mesh nets. Most collections from Zone C south (except Seabrook, New Hampshire; Fig. 3) used samplers that were 1 m wide × 0.5 m deep (portion below the surface) that were towed 10-15 minutes at approximately 2.8 km h^{-1}. Samplers were equipped with flow meters so that the sampled area could be determined. Most tows from Zone D south (except Seabrook) sampled 600-650 m^2, and thus had a nominal threshold for detecting postlarvae of about 1.5/1000 m^2. At Seabrook, investigators used a 2 m wide net towed at approximately 3.7 km h^{-1} for an average sampled area of 1860 m^2 (and a corresponding detection threshold of approximately 0.5 postlarvae/1000 m^2). Most of these tows remained very standardized over the time series, although the data sets include some exploratory sampling (different locations) and longer tows. Sample variances are discussed by Incze et al. (2000a). In Zones A through C (Fig. 3), postlarvae were less abundant and sampling effort was increased. Initially this was done by increasing the towing time for the 1.0 m wide samplers, averaging 850-1200 m^2. We ultimately went to larger samplers (2.0 m wide × 0.5 m deep) for work in Zones A and B, averaging 1400 m^2 per tow. Postlarvae were counted in the field or were transported live to

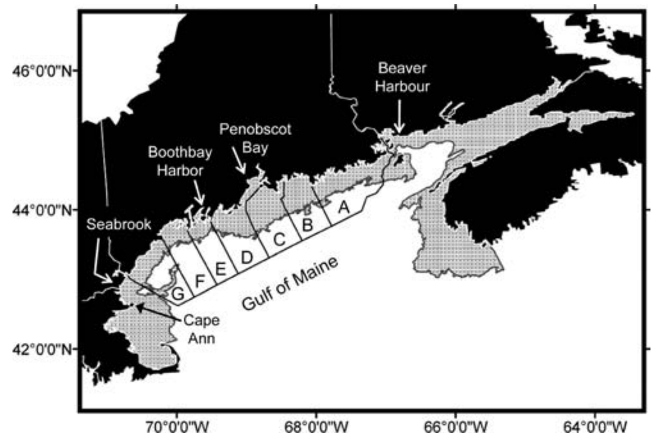

Fig. 3. Gulf of Maine, showing the coastal shelf <100 m deep (grey) where larvae are hatched in the model. Zones A-G are Lobster Management Zones used for population models. Geographic names are referred to in the text.

the lab and returned to the sea after counting them and making other measurements or observations. All postlarval densities are reported directly from the sample catches and were not corrected for the proportion missed by the neuston samplers (Annis, 2005).

Collections were made mostly along the outer coast and islands, but we also sampled offshore to the 100 m isobath and beyond. Some of the data have been published in earlier studies that can be consulted for details (Incze and Wahle, 1992; Incze et al., 1997, 2000a, b, c; Wahle and Incze, 1997; Wahle et al., 2004; Annis, 2005). Samples from Zones C and D, not previously published, include outer and some middle portions of Penobscot Bay (Fig. 3). Collections from Zones A and B include coastal bays, none of which are very large, and waters out to 100 m deep. In all cases where offshore samples were collected, they were part of a sampling grid or transect that included inshore stations for comparison. Data from all years were grouped by zone, except that F and G, for which there were only a small number of samples, were grouped with Seabrook.

Interannual time-series were examined for the mid-coast, Maine region in Zone E (1989-1995; 12 sampling stations) and for Seabrook (1989-2005; 3 sampling stations). In both areas the sampling locations and effort were fixed and sampling extended through most of the postlarval season. We used linear interpolation of postlarval (PL) abundance between sampling dates (nominally one week apart) and added the resulting estimates of daily standing stocks (PL/1000 m^2) to arrive at the total number of PL-days/1000 m^2/year at each site. The standard error of the estimate was calculated as the sum of the daily standard errors divided by the square root of the sampling intervals.

YOY Settlement Patterns

Young-of-Year lobsters were defined as those $\leq$ 10.5 mm carapace length (CL) and were collected by suction sampling in cobble areas approximately 5-10 m below MLW (Wahle and Incze, 1997). In the U.S., SCUBA divers tossed a 0.5 m^2 quadrat onto a cobble area, and the circumscribed area was sampled by removing the cobbles by hand while operating the suction sampler around the cobble and through the underlying sediment to a depth of about 7 cm. A mesh apron attached to the sides of the quadrat created a barrier to prevent lobsters from escaping laterally from the area being sampled. Sampling was conducted by two divers so that while one operated the sampler, the other removed rocks and watched for escapees (larger lobsters) and captures by the curtain. Samples were retained in a mesh bag attached to the end of the sampler and returned to the laboratory where lobsters were counted and measured. Twelve quadrats were taken at each sampling site. In Canada (Beaver Harbour, New Brunswick; Fig. 3), a 0.25 m^2 quadrat was used with the same procedures. Sampling was conducted once late in the year after postlarval numbers became low, late-September to mid-October in the U.S. and early to mid-October in Canada. Exceptions were studies where within-season settlement was investigated (Incze et al., 2000c).

Systematic sampling began in 1989 in the mid-coast region of Maine (near Boothbay Harbor in Zone E, Fig. 3) and the data have been used in

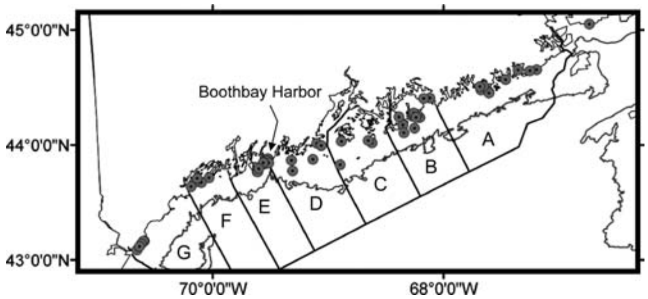

Fig. 4. Distribution of sampling areas for monitoring benthic settlement (YOY), with Lobster Management Zones A-G and 100 m isobath. Beaver Harbour is shown in the upper right. The eight long-term monitoring sites for mid-coast Maine (off Boothbay Harbor; 1989-2005; Table 2) are identified.

a series of studies (Incze and Wahle, 1991; Incze et al., 1997; Wahle and Incze, 1997; Wahle et al., 2004). Sampling expanded to other study sites beginning in the mid 1990s. In 1995, we established the Boothbay sites (n = 12) as a time-series which continues to the present. In 2000, funding was obtained to include other sites as part of a monitoring network to examine spatial and interannual patterns of settlement (Fig. 4). Data from Massachusetts and Rhode Island are not included in this analysis.

The pattern of settlement with depth was examined by two studies at 13 locations in the western Gulf of Maine where at least one depth was sampled in each of the following three categories (depths are below MLW): 0 or 5 m, 7 or 10 m, and 20 or 25 m. In addition, there were three locations where samples were taken at 60 m but at no other depths. Locations and depths are given in Table 1A and B. Suction samples were taken as above by SCUBA divers except at 60 m, where they were taken from a suction sampler operated by a robotic arm from the submersible *Clelia* (Harbor Branch Foundation). The submersible collected 6 samples per dive from 2 dives per site, each sample having an area of 0.5 m^2. All data were collected in 1997 and 1998. The data were plotted from all sites combined to examine the general trends of abundance with depth. Since this mixed sites with high and low abundance, we also analyzed the trends at each site by calculating the density at each depth as a proportion of the maximum density at that site. Thus, the maximum density at a site had a value of "1.0", and all other concentrations were scaled proportionately. At the 60 m sites, where we sampled at no other depths, we gave the densities only.

Table 1A. Sampling locations for depth-settlement patterns, 1997-1998. Geographic positions are for the general area, not for specific sampling sites. Zone locations for Maine (ME) are shown in Fig. 4. The two Massachusetts (MA) sites are south of Cape Ann, which is labeled in Fig. 3.

Name	Location (°N)	Location (°W)	Zone	Depths sampled (m)
Bass Harbor, ME	44.2345	68.3519	B	0, 7, 25
Long Island, ME	44.1063	68.3438	B	0, 7, 25
Isle au Haut 1, ME	44.0389	68.6526	C	5, 10, 20
Isle au Haut 2, ME	44.0175	68.6198	C	5, 10, 20
Mount Desert Rock, ME (2 sites)	44.0316	68.1469	B	60
Ragged Island, ME (2 sites)	43.8280	68.8959	C	5, 10, 20
Muscongus Bay, ME (2 sites)	43.8261	69.3167	D	60
Monhegan Island	43.7752	69.3088	D	5, 10, 20
Pemaquid Point, ME	43.8353	69.5132	E	0, 7, 25
Kresge Point, ME	43.8367	69.5179	E	5, 10, 20
Fisherman's Island, ME	43.7938	69.6021	E	5, 10, 20
Damariscove Island, ME (2 years)	43.7666	69.6132	E	5, 10, 20 and 0, 7, 25
Canoe Beach, Nahant, MA	42.4211	70.9069	-	0, 7, 25
Stellwagen Bank, MA (2 sites)	42.3563	70.2253	-	60

Table 1B. Depth distribution of YOY as a proportion (P) of the maximum concentration at each site. Data are: n (number of locations/years that a depth was sampled), and the range, mean and median proportions at each depth. The last column gives the number of times that a depth contained (or tied) the maximum concentration of YOY for a given location/year. Raw data are shown in Fig. 8. Maximum YOY densities ranged from 0.67 to 9.67/m^2 with mean = 3.63, SD = 2.94. Samples from 60 m contained no YOY but are not included here because they came from sites without sampling at other depths. Samples at a site came either from 0, 7 and 20 m or from 5, 10 and 25 m (see Table 1A.).

Depth (m)	n	Range of P	Mean	Median	Times = Max.
0	5	0.00-1.00	0.28	0.20	1
5	7	0.43-1.00	0.81	0.88	4
7	5	1.00	1.00	1.00	5
10	7	0.50-1.00	0.77	0.79	2
20	7	0.32-1.00	0.59	0.51	2
25	5	0.00-0.52	0.11	0.00	0

Results

A total of 3687 neuston samples were analyzed and recorded from 1989-2003 along the Maine and New Hampshire coasts. Most zones did not contain enough data for us to examine interannual patterns of abundance, so data were combined across all years to evaluate average seasonal and spatial patterns (Fig. 5). Zone E had higher average concentrations of postlarvae than the other zones, a difference that was not due simply to temporal biasing. That is, the lower abundances in zones A through C did not result from sampling in low abundance years alone. Most of the samples in those zones were collected in 2001-2003, when postlarvae were abundant in Zone E. The timing of the postlarval season from Zones C south through Seabrook appears to be similar, with possibly a later start in C and an earlier end at Seabrook. Data were not plotted beyond 2003 because the only collections were at Seabrook.

The time series data on postlarvae in the mid-coast Maine region (1989-1995) and at Seabrook (1989-2005) are given in Table 2, along with YOY data from the mid-coast Maine sites. Despite a geographic separation of about 140 km, the Seabrook annual postlarval abundance and the mid-coast Maine settlement densities are positively correlated ($P < 0.001$; Fig. 6). Both data sets (Table 2) show variable abundances from 1989-1995, generally lower abundances from 1995 through 2000, and high numbers from 2001-2005. The 1990 value for Seabrook was extraordinarily high due to a single sampling day and was not included in the regression.

The regional settlement patterns (Fig. 7) show several features of interest. First, settlement in 2000 was low everywhere it was measured in Maine (Zones B through G), but not at Beaver Harbour, Canada, where it was comparable to the four years that followed. Second, from 2001-2004, Zones A through D showed considerably lower settlement than at E. Settlement decreased from E to G. Both trends are consistent with the postlarval abundance patterns shown in Fig. 5. Third, there was a dramatic shift in settlement patterns in 2005. While settlement in Zone E in

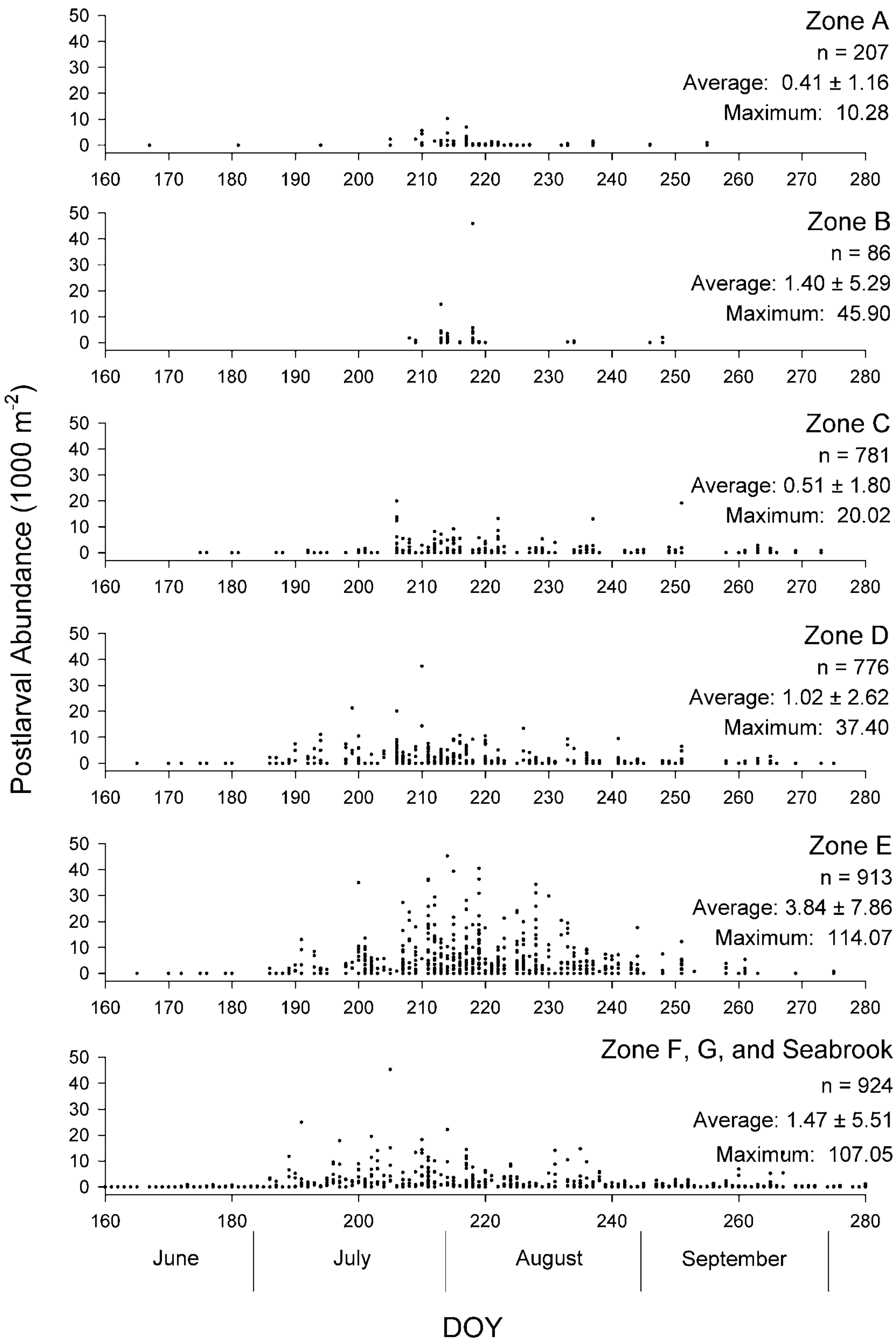

Fig. 5. Postlarval abundance in each LMZ (Fig. 2) from 1989 to 2003. Data are individual tows (n = 3,687). Three data points from Seabrook (DOY 225) and four from Zone E (DOY 211, 217, 219, 232) were > 50/1000 m 2 and do not appear in the figure. Only Zone E and Seabrook had regularly sampled stations, and the time series are given in Table 2.

Table 2. Young-of-year (YOY) densities and the seasonal abundance of postlarvae (PL-days) from two time series stations: mid-coast Maine (in Zone E) and Seabrook, New Hampshire (zone NH).

	YOY (No./m^2)		Postlarvae (PL − days/1000 m^2/year)			
	Mid-coast ME		Seabrook		Mid-coast ME	
Year	Mean	SE	Mean	SE	Mean	SE
1989	1.64	0.38	214.5	70.2	192.8	102.4
1990	0.77	0.22	668.0	91.4	246.7	131.9
1991	1.54	0.32	248.9	44.4	278.4	139.8
1992	1.30	0.33	338.8	71.5	193.0	96.9
1993	0.45	0.17	100.6	21.5	96.0	56.2
1994	1.61	0.40	198.7	60.2	318.3	104.5
1995	0.66	0.21	190.0	59.7	149.8	71.9
1996	0.47	0.25	164.1	44.1		
1997	0.46	0.28	87.6	24.5		
1998	0.14	0.08	63.7	18.7		
1999	0.65	0.31	115.6	35.6		
2000	0.13	0.06	17.8	5.7		
2001	2.08	0.64	223.8	56.0		
2002	1.38	0.41	207.3	57.5		
2003	1.75	0.61	269.0	103.7		
2004	1.75	0.63	214.9	52.2		
2005	1.77	0.56	184.0	51.7		

2005 was typical for that zone, and settlement decreased slightly to the south as it had in the earlier years, settlement in all zones north of E was well above average. In particular, settlement densities in Zones A and C were unprecedented and virtually equal to E, and there was record settlement in Beaver Harbour, three to four fold higher than previous measurements.

Vertical patterns of settlement in cobble substrate indicate maximum settlement at the 5-10 m level, and declining densities shallower and deeper (Fig. 8). Analysis of the data at individual sites shows that maximum settlement densities most often occurred at the 5 and 7 m (below Mean Low Water, MLW) sampling depths. Samples from 10 and 20 m below MLW rarely contained the maximum concentration at a site, but still had appreciable concentrations (> 30%) relative to the maximum (Table 1). No YOY were found in samples from 60 m depth.

Discussion

The Gulf of Maine has a tidal amplitude ranging from a few meters in the south to more than 15 m at the head of the Bay of Fundy, resulting in strong tidal currents and mixing (Loder and Greenberg, 1986). The Gulf is also characterized by a generally cyclonic (counter-clockwise) residual circulation and a buoyancy-driven coastal current system (Brooks, 1985) with residual velocities of 5-15 cm s-1 in the southwestern portion of the Gulf (Western Maine Coastal Current) and 15-30 cm s-1 along the northern and northwestern coasts (Eastern Maine Coastal Current; Pettigrew et al., 1998). Thus, there is an expected northeast to southwest drift of larvae with potentially large distances covered (Harding and Trites, 1988; Incze and Naimie, 2000).

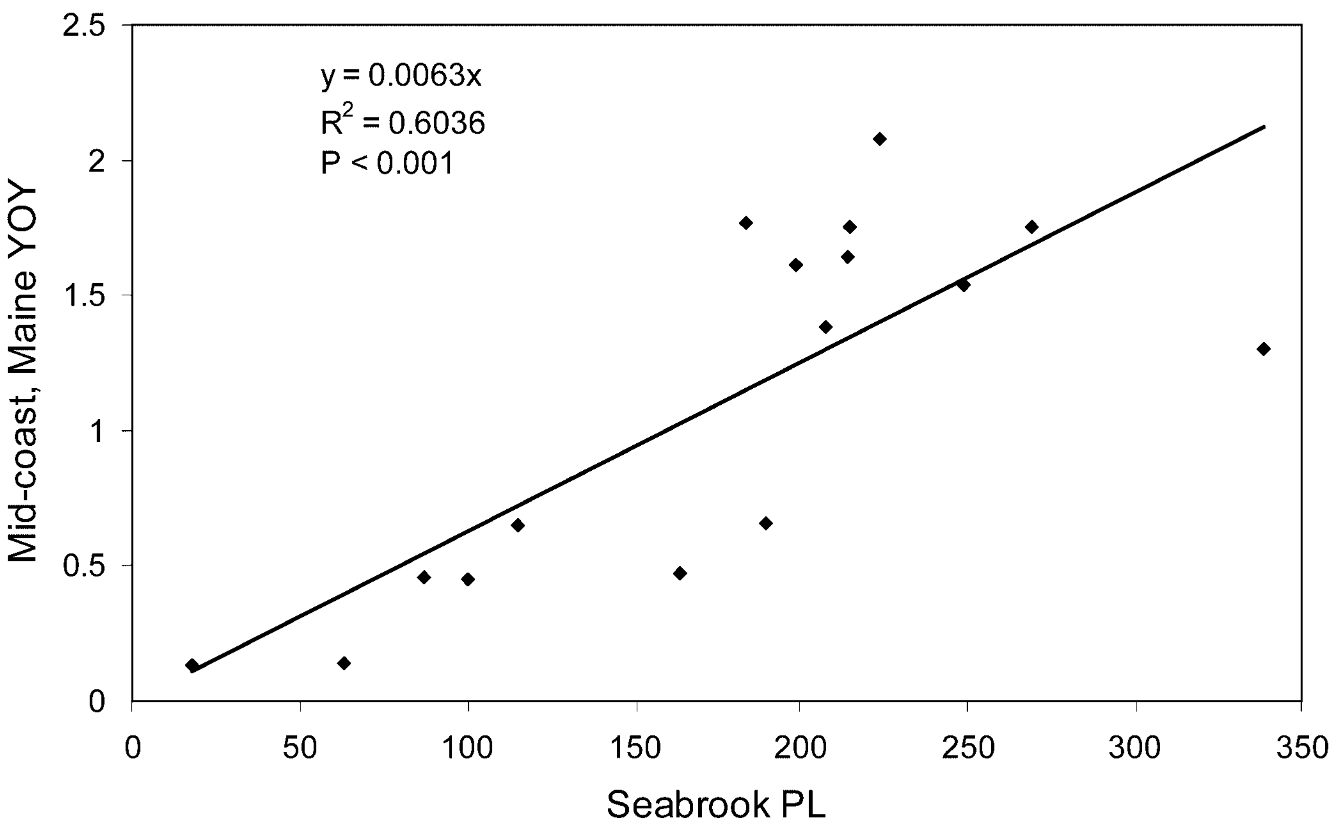

Fig. 6. Linear regression of mid-coast Maine YOY densities (No./m^2) vs. Seabrook postlarval abundance (No./1000 m^2), 1989-2003, with the1990 datum (x = 668.0, y = 0.77) removed. The low slope results from a low instantaneous settlement rate (Incze et al., 2000).

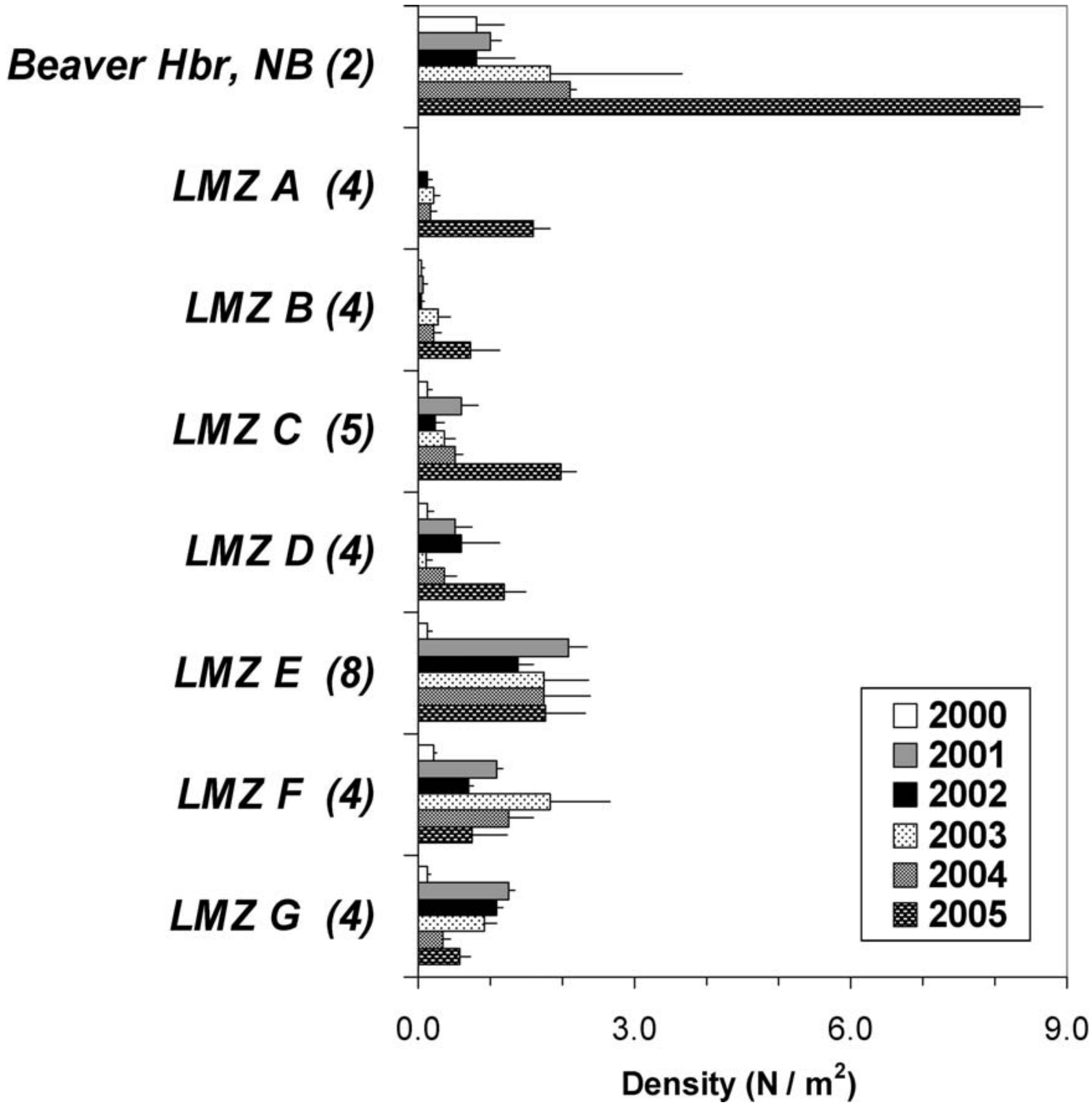

Fig. 7. Spatial and temporal patterns of YOY recruitment, 2000-2005. LMZ A was not sampled in 2000 or 2001. Numbers in parentheses are the number of sites sampled within each area. Sampling locations are shown in Figure 4.

The modeling framework presented here adds to more than two decades of interest in the transport of larvae and the relationship between source and sink regions in the population dynamics of lobsters in the northwestern Atlantic (Hudon, 1987; Harding and Trites, 1988; Katz et al., 1994; Incze and Naimie, 2000; Harding et al., 2004). The potential for long distance transport has never been questioned. Rather, the challenge has been to quantitatively understand the principal patterns of connectivity. Stated from the perspective of settlement within a particular region: what is the contribution of local egg and larval production relative to other sources? How are these patterns and over-all recruitment affected by variations in environmental forcing? Understanding these connections for lobsters would be of value to the industry and management, especially at times when patterns of recruitment and fishery production change. Developing the modeling tools and supporting observational data sets to monitor and understand changing population levels or distributions for an important commercial fishery provides insight into the dynamics of other coastal marine populations as well. The approach we are using may be the first to be based on an operational model from an ocean observing system. While considerable effort is still needed to perform calculations with the coupled biology included, the underlying circulation model benefits from the types of validation and improvement that its operational status requires.

Coupled biophysical models require well-grounded biological inputs as well as data sets with which to evaluate model performance. The depth-settlement patterns we present here for cobble habitats are essential for linking the pelagic portion of the population model to the benthic portion. The data reinforce previous suggestions that settlement is primarily a coastal, "shallow-water" phenomenon (Wahle and Steneck, 1991; Wilson, 1999), but we have better defined that as being primarily less than 25 m. It would be useful for

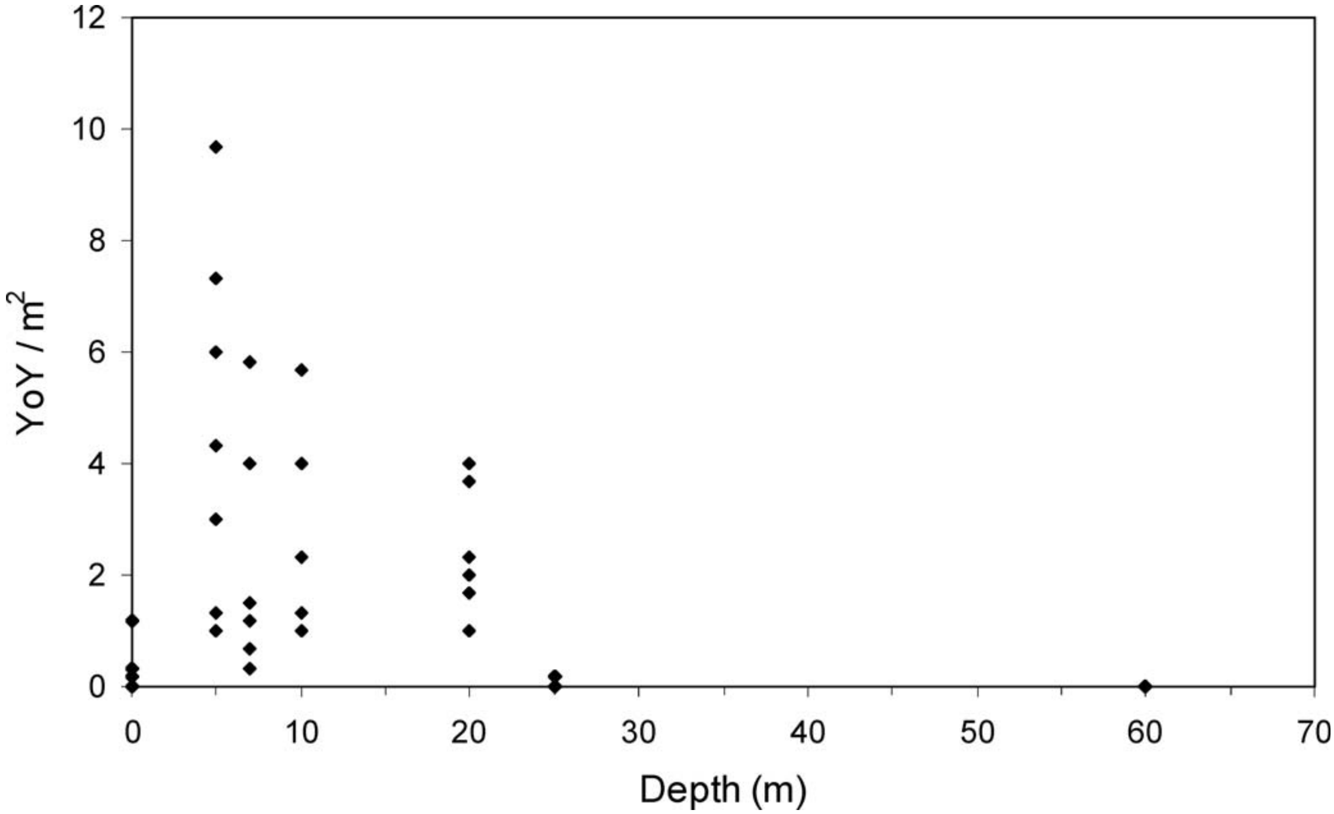

Fig. 8. Depth distribution of YOY in 15 samplings (12 locations ≤ 25 m, one of them sampled in two years; 3 locations at 60 m), 1997-1998, in the western Gulf of Maine. Locations and details are given in Table 1.

future work to determine if this lower depth is influenced by water column stratification, bottom water temperature or other conditions.

The depth-settlement data provide a basis for estimating populations of settlers. This can be done by combining settlement densities from field measurements in cobble with knowledge of differential settlement rates on various substrates and accurate area estimates of substrates by depth throughout the region. Such information is becoming more commonly available for coastal areas through sea bed mapping and Geographic Information Systems (Barnhardt et al., 1998). These data must be coupled with information on broad-scale patterns of larval supply and settlement (such as decreased settlement up estuaries and bays: Wahle, 1993; Palma et al., 1999). Area-depth-substrate data can then be combined with settlement data (densities at "index" monitoring sites) to estimate YOY populations in the various management zones. There are sizeable uncertainties involved in such extrapolations, but Incze et al. (2003) showed that the estimates of YOY populations in Zone E fit quite well with what was needed to support the fishery in that area. At a minimum, it should be possible to distinguish high, medium and low recruitment levels given the range of settlement densities we have observed (Fig. 7 and Table 2). Wahle et al. (2004) made projections for future harvests based on settlement indices and growth models, and the predictions will be evaluated with fishery-independent survey and landings data over the next few years.

Patterns of settlement between years and along the coast show some remarkable features that provide insights into possible mechanisms influencing recruitment. The very low settlement in 2000 was recorded at many sites (Fig. 7) and indicates geographically broad forcing, although the underlying mechanism(s) have not been identified. In Zone E where the time series extends back to 1989, it is evident that this (2000) was an extreme event (Table 2). Previous studies in Zone E (Wahle and Incze, 1997; Incze et al., 2000b) showed that settlement was highly correlated with postlarval supply. The only full-season sampling for postlarvae in 2000 was at Seabrook, and postlarvae there were unprecedentedly low (Table 2). The correlation between Seabrook postlarvae and the midcoast Maine settlement is quite good, and the co-occurrence of record lows in both regions suggests that low planktonic supply was responsible for the low recruitment along the coast. Interestingly, this followed a multi-year downward trend in settlement (Zone E) and postlarvae (Seabrook) that began in 1995 (Table 2). Possible explanations include changes in transport, especially those affecting across-shelf distributions; changes in planktonic mortality; and shifts in the distribution of ovigerous lobsters when eggs were hatching. We hypothesize that hatching farther inshore favors retention along the coast, and that the springtime inshore movement of lobsters may vary sufficiently to cause differences in where eggs hatch. This, in turn, interacts with the along-shore current system to affect larval transport. Settlement is a protracted process (Incze et al., 2000b), so short-term events are not likely to affect an entire season's settlement unless the events have long-lasting impacts. The strong spatial and temporal signals in the data provide an opportunity to search for important forcing mechanisms. For example, the abrupt shift from record low recruitment in 2000 to high recruitment in 2001 may provide such an opportunity. In this paper we report the postlarval numbers as sampled in the neuston. Recent studies (Annis, 2005) indicate that a substantial portion (average of 35%) of the water column population may be missed, at least along the mid-coast of Maine.

The pattern of generally low settlement in Zones A and B, with gradual increases south to E, and then a gradual decrease south to Seabrook, was consistent for several years and closely resembled the patterns of postlarval supply sampled through 2003 (Fig. 5). Other factors, such as water temperature, predation and the propensity of postlarvae to settle, may also influence settlement (Incze and Wahle, 1991). The patterns are nonetheless consistent with our predictions that the coastal current system may limit recruitment in Zones A and B due to rapid removal of locally hatched larvae and low supply of postlarvae from upstream locations (Incze and Naimie, 2000). Apparently, conditions departed from this pattern in 2005.

The unprecedented northward shift of high settlement in 2005 suggests a significant change in forcing. Because postlarvae were rare along the eastern Maine coast (Zones A and B) in 2001-2003, when they were abundant to the south, we conclude that the unusually high settlement of 2005 was the result of postlarvae being present in high numbers along shore in Zones A-C. The change in D was not nearly as dramatic, and Zone E was normal, so the forcing may have been restricted to the eastern portion of the coastal current system. Mechanisms to explore include convergence of offshore waters with the coast, relaxation of the coastal current along this portion of the coast, and an abundant supply of postlarvae transported along the coast from the western side of the Bay of Fundy. The last explanation would be consistent with the record high settlement at Beaver Harbour. It seems less likely that the high settlement of 2005 was due to a change in the settlement process alone, because postlarvae typically have been so much less abundant in these zones, and it is not clear how such low postlarval numbers could have produced settlement densities similar to those in Zone E.

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