

Connectivity of lobster (*Homarus americanus*) populations in the coastal Gulf of Maine: part II. Coupled biophysical dynamics

LEWIS INCZE,^{1,*}HUIJIE XUE,² NICHOLAS WOLFF,¹ DANYA XU,² CARL WILSON,³ ROBERT STENECK,² RICHARD WAHLE,⁴ PETER LAWTON,⁵ NEAL PETTIGREW² AND YONG CHEN²

¹Aquatic Systems Group, University of Southern Maine, Portland, ME 04101, USA

²School of Marine Sciences, University of Maine, Orono, ME 04469-5741, USA

³Maine Department of Marine Resources, West Boothbay Harbor, ME 04538, USA

⁴Bigelow Laboratory for Ocean Sciences, West Boothbay Harbor, ME 04538, USA

⁵St Andrews Biological Station, Department of Fisheries and Oceans, St Andrews, NB E5B 2L9, Canada

ABSTRACT

We used a coupled biophysical model to investigate larval transport and connectivity patterns in the Gulf of Maine lobster (*Homarus americanus*) population. Biological ‘particles’ were released at over 21 000 locations every 10 days over a 4-month hatching period, and were followed from hatching through late postlarval stage. In addition to circulation and dispersion, model calculations included spatial patterns of egg production, temporal patterns of hatching, temperature-dependent development, vertical distribution and mortality. We ran the model for three larval production seasons using the same hatching patterns and individual-based modeling parameters but different flow patterns in the coastal current system. Model results gave distribution and abundance patterns of competent postlarvae that closely resembled observed, alongshore patterns of lobster settlement density. We evaluated the relative contribution of all source regions to the total number of competent postlarvae in a series of medium-size zones along the coastal shelf, many of which are used in lobster

management. Connectivity depended on many factors, including patterns of egg production and transport, and the location and size of the receiving zones. Self recruitment ranged from a few percent to >90% of competent postlarvae. Although it was common for postlarvae to come from many, often distant, sources, most of the competent postlarvae in a zone originated within one to two zones in the prevailing ‘up-stream’ direction, forming shorter connections along the coast than the energetic currents might otherwise suggest. Inshore migrations during summer hatching may contribute to these shorter patterns of connectivity. Transport in the prevailing ‘upstream’ direction was also indicated.

Key words: advection, coastal current, connectivity, coupled biophysical model, egg production, hatching, *Homarus americanus*, individual-based model, larvae, lobster, mortality, postlarvae, transport

INTRODUCTION

Coupled biophysical models that embed ‘biological’ particles into simulated model flow fields provide important insights into potential patterns of transport and connectivity in populations of marine organisms with planktonic life stages (Cowen *et al.*, 2006; Miller, 2007; Briones-Fourzán *et al.*, 2008). As these models improve in resolution and realism (Fiksen *et al.*, 2007; Paris *et al.*, 2007) they can be used to address a growing number of questions concerning the conservation of marine biodiversity and development of sustainable fisheries practices. For example, larval development and mortality rates can be coupled with variability of ocean forcing to understand the spatial distribution of reproduction needed to sustain populations over their natural ranges (Botsford *et al.*, 2001; Shanks *et al.*, 2003). Although the study of the drivers of mortality in the sea and their variability form an inherently interesting and informative part of ecological and population studies (Gallego *et al.*, 2007), such specific, process-related estimates are usually not available over large areas and multiple years. In such cases, estimates of average

*Correspondence. e-mail: lincze@usm.maine.edu

Received 20 October 2008

Revised version accepted 21 July 2009

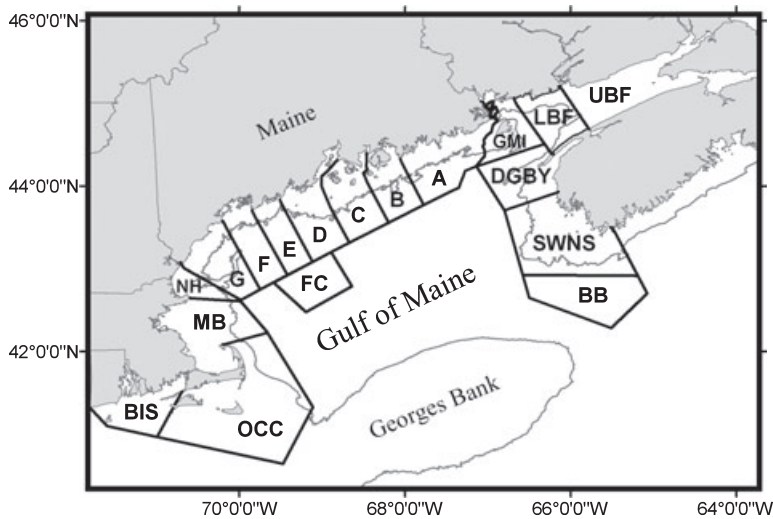


Figure 1. Gulf of Maine study area, showing 100 m isobath and zones used in the analyses. Abbreviations are: BB (Browns Bank); SWNS (Southwest Nova Scotia); DGBY (Digby); LBF and UBF (lower and upper Bay of Fundy); GMI (Grand Manan Island); A-G (Maine Lobster Management Zones A–G); NH (New Hampshire); MB (Massachusetts Bay and Cape Cod Bay); OCC (Outer Cape Cod); BIS (Block Island Sound); FC (Fippinnes and Cashes Ledges).

mortality serve to constrain estimates of connectivity over large scales (Cowen *et al.*, 2006).

In this study we used the circulation model of the Gulf of Maine Ocean Observing System (Xue *et al.*, 2005) to quantitatively examine connectivity of lobster (*Homarus americanus*) populations in the Gulf of Maine (Fig. 1). The operational nature of the model has led to extensive performance evaluation in all seasons and over several years, and has revealed distinct interannual differences in the summer residual circulation (Xue *et al.*, 2008). The objective of the present study was to understand the degree to which settlement (benthic recruitment) along different sections of the coast was driven by distant versus local egg production under these varying summer circulation patterns. Adjusting the model results of postlarval abundance to fit field observations of abundance provided estimates of average planktonic mortality that were higher than originally assumed.

The lobster fishery has become the most lucrative fishery in the coastal Gulf of Maine over the past two decades, due to an apparent increase in the abundance of lobsters as well as a decline in other historically important species (Incze *et al.*, 2006). Reproductive female lobsters carry their eggs attached to the ventral surface of the abdomen for 9–10 months, during which they may undertake seasonal movements into deeper water in fall and winter and shallower water during spring and summer (Lawton and Lavalli, 1995; Cowan *et al.*, 2007). Eggs hatch in late spring and summer (Ennis, 1995) to produce pelagic larvae (three stages) and postlarvae that remain in the water column for 2 or more weeks, depending on temperature (MacKenzie, 1988; Annis *et al.*, 2007). Approximately halfway through postlarval development, lobsters become competent to settle and can begin recruiting to the

bottom (Cobb *et al.*, 1989). Along the central coast of Maine, settlement begins in mid-July and lasts 6–8 or more weeks (Incze and Wahle, 1991; Incze *et al.*, 2000b). Settlement densities are positively correlated with postlarval abundance (Wahle and Incze, 1997; Incze *et al.*, 2000b) and can show large variations between years (Incze *et al.*, 2006). In addition, some sections of the coast have characteristically higher settlement densities than others (Incze *et al.*, 2006), although several factors may be involved, such as postlarval supply, predators, and environmental conditions (Wahle and Steneck, 1992; Steneck and Wilson, 2001). The total amount of settlement in an area is a function of habitat abundance and distribution, and is beyond the scope of this paper (but see Incze *et al.*, 2003 and Drew and Eggleston, 2006 for discussions).

Harding and Trites (1988) and Incze and Naimie (2000) demonstrated the potential for long-distance transport of lobster larvae in the cyclonic coastal current system that flows at speeds of 5–30 cm s⁻¹ around the Gulf of Maine during summer months (Pettigrew *et al.*, 2005). However, the quantitative aspects of transport and recruitment dynamics of lobsters are complex, and depend on numerous heterogeneous and variable aspects of the system and the behavior of the organisms themselves. These include spatial differences in egg production, spatial and temporal differences in the flow field and water temperature, the protracted period of hatching, stochastic processes, dispersion and mortality of the planktonic stages, and ontogenetic and environmentally stimulated changes in the vertical distribution of the planktonic life stages and their propensity to settle.

In an earlier paper (Xue *et al.*, 2008) we modeled the transport of particles released at 21 740 locations (approximately 4-km spacing) every 10 days

throughout the lobster hatching season, June through September, 2002–2004, in water depths ≤ 100 m. The particles occupied specific depths in the water column and ‘developed’ according to ambient temperatures at rates similar to lobster larvae, but there was no simulation of spatial or temporal differences in reproductive output and the particles experienced no mortality. The results provided an overview of potential transport patterns during summer months in 3 yrs in which the continuity of flow along the western margin of the Gulf of Maine varied significantly. The years were characterized as ‘blocked’ (low connectivity from east to west, 2002), ‘flow-through’ (2003), and intermediate (2004). In the present paper, we estimated the spatial and temporal patterns of egg hatching and weighted the particles according to these estimates at each place and time of release. We assigned a tentative, fixed mortality rate based on prior work (Ince *et al.*, 2003) and calculated connectivity based on patterns of larval production and transport coupled with dispersion and mortality. We compared the resulting postlarval abundances with field observations and adjusted the mortality rate to bring model and field data into agreement.

MATERIALS AND METHODS

Individual-based, coupled biophysical model

We used the operational circulation model of the Gulf of Maine Ocean Observing System [GoMOOS (<http://www.gomoos.org>); Xue *et al.*, 2005;] which is based on the Princeton Ocean Model (Mellor, 2003). The model uses an orthogonal curvilinear grid with 22

sigma-levels in the vertical and a horizontal resolution that varies from 3 to 5 km; it includes the Scotian Shelf, Gulf of Maine, Georges Bank, part of the Southern New England Shelf and the adjacent slope region (Fig. 2). The open boundaries are forced with daily ‘nowcasts’ from the Regional Ocean Forecast System (<http://polar.ncep.noaa.gov/cofs/>). Surface forcing within the model domain is obtained from the National Center for Environmental Prediction (NCEP) NAM 221 AWIPS Grid (<http://www.ncep.noaa.gov/pmb/products/nam/>), and daily fresh-water inputs from the Gulf’s six major rivers are obtained from the US Geological Survey. A particle-tracking subroutine (Bernsten *et al.*, 1994) is embedded in the circulation model to simulate transport and dispersion of particles in the water. A random walk term was used to approximate the effects of sub-grid scale processes on particle trajectories (Xue *et al.*, 2008). To simulate the development and transport of larvae and postlarvae, we used an individual-based model approach in which modeled ‘particles’ develop at temperature-dependent rates and follow simple ontogenetic changes in depth (see below).

In the first part of this study (Xue *et al.*, 2008) we established 15 analysis grids for summarizing particle distributions. Seven of these grids are formal Lobster Management Zones (LMZs) used in the state of Maine. The others – we added three more for a total of 18 in this study – are geographical units that we created for analysis (Fig. 1). For simplicity we refer to all of these as ‘zones’. These zones provide a practical scale for aggregating model results in geographic terms useful to the industry and management, and this step

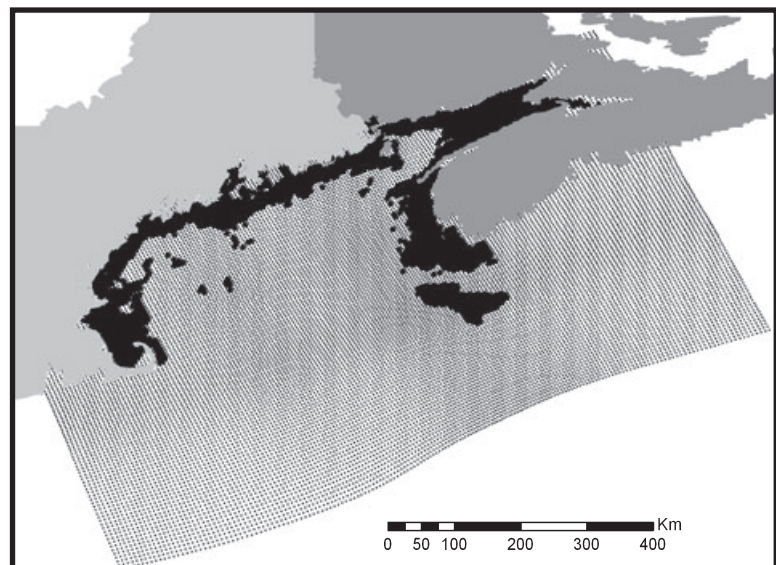


Figure 2. Model grid. Egg release points are shaded black and are inside the 100 m isobath.

avoids too much focus on small-scale patterns or results where prediction bears a high degree of uncertainty.

Larval production and timing

The spatial and temporal pattern of production ($n \text{ km}^{-2}$) of newly hatched Stage I larvae was derived from field data for each Maine LMZ and for the zone referred to as NH. No comparable data exist in the other zones. A series of calculations was required, beginning with the estimated abundance and size distribution of female lobsters. The base estimates came from 312 trawl samples collected at bottom depths of 8–97 m by the Maine Department of Marine Resources during September and October, 2000–2003. Abundance, sex, size, presence/absence of eggs, and egg development stage (Perkins, 1972) were recorded. The swept area of the trawl was used to estimate abundance ($n \text{ km}^{-2}$). This likely is an underestimate because trawling is conducted on relatively open bottom (thus missing rocky habitat) and because trawls probably fail to catch (because they over-ride) some individuals in the trawl path. We compared trawl-generated abundance estimates of large lobsters (carapace length, CL, ≥ 90 mm) with visual counts from ROV (remotely operated vehicle) and research submarine ('sub') surveys (a total of 102 dives for the two platforms). ROV and sub data were collected mostly over open bottom, sampling from 138 m^2 to 3516 m^2 per sample at depths from 8–122 m in July, August and September 1997, 1999 and 2001. We also compared trawl estimates of lobster abundance with SCUBA surveys ($N = 70$ dives) conducted at depths < 14 m in July and August, 1999. Comparisons were made only for lobsters with CL ≥ 90 mm. Comparisons were pooled across years and grouped by depth, proximity to each other, and zone. Although size (from all survey methods) and other biological data (from SCUBA) were available, sample sizes were too small to warrant further partitioning of the data.

To estimate the temporal and spatial patterns of hatching, we used data collected in collaboration with lobstermen during normal commercial fishing (trapping) operations. Data came from 45 309 trap hauls made during July and August, 1998–2002. Traps were located throughout the Maine coastal shelf to depths approaching 100 m, though most were in depths < 50 m. The timing of hatching was calculated from the proportion of lobsters carrying newly extruded versus late-stage eggs (Perkins, 1972). We binned the data over 10-day periods to compensate for generally low catch rates of ovigerous females. We first looked

for a difference in timing between eastern and western areas of Maine (Zones A–C and D–G, respectively; Fig. 1), and took the mean of the two polynomial fits when differences between the two areas were found to be small (≤ 6 days). The mean hatch curve was normalized to one (total hatch) to calculate the proportion of eggs hatched each day. To determine the spatial distribution of hatching, we examined the distribution of female lobsters with late-stage eggs or signs of recent hatching (remains of egg stalks on the ventral surface of the abdomen). Data were expressed as catch per trap haul (CPTH) and entered into a geographical information system (GIS) for analysis. CPTH was binned over 10-m-depth intervals after stratifying each zone for large-scale patterns such as the decreased abundance of ovigerous females in the middle and upper reaches of large bays and estuaries. The product of this analysis was a map of the spatial and temporal distribution of hatching within each zone. Potential sources of bias in the trap catches (Miller, 1990; Fogarty and Addison, 1997) could not be evaluated critically and are discussed later.

The numbers of Stage I (SI) larvae produced per year in NH and in each Maine LMZ were calculated by multiplying adult female lobster abundance per zone by the size distribution (CL) of lobsters, appropriate maturity ogives, a size–fecundity relationship, a spawning frequency, and an egg mortality rate. Size distribution was specific to each zone and maturity ogives varied from west to east. Maturity, defined as the proportion of females at size that are sexually mature, is given by the relationship $M = 1/[1 + e^{(\alpha + \beta * CL)}]$ where α and β have the following values: 14.898635 and 0.1738515 for zones NH, F and G; 23.28458085 and -0.264004712 for zones D and E, and 31.6769441 and -0.3444601 for zones A, B and C (Atlantic States Marine Fisheries Commission, 2000). Fecundity (N eggs per female) is given as $F = (6.06 * 10^{-4}) * CL^{3.7227}$ (Estrella and Cadrin, 1995). The spawning frequency is determined by the intermolt period. The minimum intermolt period for a sexually mature female lobster is 2 yrs, and this gradually increases to 7 yrs at 130 mm CL (we used real numbers instead of whole integers: Atlantic States Marine Fisheries Commission [ASMFC], 2000). We assumed an egg mortality rate of 0.40 from extrusion (when 'F' is calculated) to hatching (*cf.* Perkins, 1971; Campbell and Bratty, 1986).

SI production was distributed spatially and temporally according to our analysis of the commercial trap data (see above), and the spatial pattern was transferred to a 'grid' of polygons constructed about the nodes in the circulation model. Polygons were defined

by the midpoints along all possible lines connecting neighboring nodes, and thus were octagonal in shape and approximately 16 km² each. Trap and trawl data were not very abundant in the middle and upper portions of most bays, but these data and other observations showed that a reduction in larval production estimates was warranted for these areas. We reduced larval production to 50% of the nearest coastal values in the middle sections of large coastal embayments, and to 1% of coastal values in the upper reaches of these bays and in estuaries.

We did not have the full complement of data needed to calculate SI production for other areas of the Gulf of Maine. Consequently, for Canada, we used the Maine-wide average of the annual SI production for each depth interval (0–10, 10–20 m, etc.). For MB and OCC we used SI production data from zone F, which was better sampled than zone G. The effect of these estimations on model results is discussed later. Hatching, once initiated, was assumed to follow the same temporal curve as in Maine. The beginning date for hatching in NH was assumed to be the same as Maine (first appreciable SI on YD 152). Beginning dates were adjusted 10 days earlier in the south (for MB and OCC) and up to 40 days later in the north, as follows: YD 172 for Browns Bank; 182 for Southwest Nova Scotia and the Upper Bay of Fundy; and 192 for Grand Manan Island, Digby and Lower Bay of Fundy (Fig. 1). The northern (Canadian) adjustments were based on egg conditions from 101 792 trap hauls in Canadian lobster management districts (Lobster Fishing Areas) from May through November, 1977–1989.

Larval IBM and model runs

Larval development, vertical position in the water column and mortality were represented by a simple individual-based model (IBM, Table 1) coupled with the operational circulation model of the Gulf of Maine

Ocean Observing System, which has an average horizontal resolution of about 4 km (Xue *et al.*, 2005). Transport and dispersion were simulated using a particle-tracking subroutine with a random walk term (Xue *et al.*, 2008). Ten ‘super-particles’ (henceforth ‘particles’) were released at each model node where water depth was ≤100 m (Fig. 2), resulting in 21 740 particles per release. Particles were released on the 1st, 11th and 21st day of each month from 1 June through September, were independently subjected to the random walk term, and were followed for 60 days after release. Each particle represented a large number of individual larvae (see below), and developed through time according to the rate specified by the IBM and the ambient temperature. The model kept track of the proportion of accumulated development per stage, and the particle (representing a group of larvae) advanced to the next stage when the accumulated development equaled 1.0 (Xue *et al.*, 2008). In this study, particles representing stage I–III larvae were maintained at a fixed depth of 15 m. The depth immediately changed to 1 m when larvae advanced to stage IV (postlarvae, see Table 1).

The model was run with all particles being of equal rank and experiencing no mortality. Results (time, location and larval development within stage) were stored and post-processed to (1) weight the particles at the time of their release according to the spatial and temporal (seasonal) patterns of SI production ($n \text{ km}^{-2} \text{ day}^{-1}$), and (2) apply the mortality term. Each release included SI production for that date and the following 9 days (in some cases 10 days) to account for all hatching during a season. Model flow fields show strong consistency over this time interval during summer months. Converting from particles back to population estimates that were applicable to model polygons was technically easy (particle weights were originally defined by the number of larvae per

Table 1. Biological values used in the initial larval and postlarval individual-based model.

Property	Stages	Value	Source/explanation
V	SI–SIII	15 m	Incze, unpubl. field data
	PL	1 m	Annis (2005)
z	SI	0.3	This paper
	SII–PL	0.06	Incze <i>et al.</i> (2003), adjusted for faster development rates
D	SI	0.4[851(T–0.84)–1.91]	Annis <i>et al.</i> , 2007
	SII	0.4[200(T–4.88)–1.47]	Annis <i>et al.</i> , 2007
	SIII	0.4[252(T–5.3)–1.54]	Annis <i>et al.</i> , 2007
	PL	0.4[0.358833T ² – 14.316T + 156.895]	Annis <i>et al.</i> , 2007

V, vertical distribution (a single depth); z is the specific mortality rate, $z = -\ln(N_t/N_0)$, where N = number of larvae at the beginning (N_0) and end (N_t) of the stage, and t is measured in days; D = stage duration, in days; T is temperature (°C).

unit area), but could be unreliable if only a few particles were present. To avoid this, we binned the particles over 5-day periods, which gave large numbers of particles per polygon except for a few of the most offshore locations.

The model time-step was 216 s, but post-processing used daily time-steps beginning with the mid-night releases (hatching). The model was run for the egg hatching and larval transport seasons during 2002, 2003 and 2004, which offered the following contrasting flow conditions in the Coastal Current System along the Maine coast: a strong discontinuity between east and west; high flow-through from east to west; and intermediate conditions, respectively (Xue *et al.*, 2008). All runs used the same egg production patterns (the 2000–2003 average) and identical IBM properties.

Our analyses focused on the distribution and abundance of postlarvae – information carried by the location and biological ‘properties’ of individual particles. We calculated the average daily concentration of postlarvae ($n \text{ km}^{-2}$) in each model polygon (16 km^2) and summed the daily averages for each polygon over the season. Plots of the resulting data showed the spatial distribution of postlarvae (PL) in units $\text{PL-days km}^{-2} \text{ yr}^{-1}$, which we compared with field data (see Incze *et al.*, 2006 and later discussion). We examined within-year patterns of timing and peak abundance of postlarvae in Zone E, where we have extensive field data for comparison.

Postlarvae that were competent to settle were defined as stage 4.5 (halfway through postlarval development, Cobb *et al.*, 1989). The seasonal standing stock of competent postlarvae was tabulated for each zone after dividing into the following depth areas: $\leq 50 \text{ m}$, $51\text{--}100 \text{ m}$, and $>100 \text{ m}$. Using the histories of each particle, we constructed connectivity matrices for the above zone and depth areas to examine the relationships between source (egg hatching) and sink regions, where the sink was defined as the zone where the resulting postlarvae became competent to settle. Specifically, we were interested in the degree of self-recruitment versus allochthonous supply, or subsidy, in various zones. We also quantified exchanges between the inner (0–50 m) and outer (50–100 m) shelf regions, and ‘losses’ of reproductive effort to areas $>100 \text{ m}$ deep. We examined interannual differences in patterns of supply through an inverse analysis of release points contributing to zone E. Finally, we examined the effect of various mortality rates on the seasonal abundance patterns.

We used GIS tools to measure the area of each zone and the width (along-shelf direction) of each zone

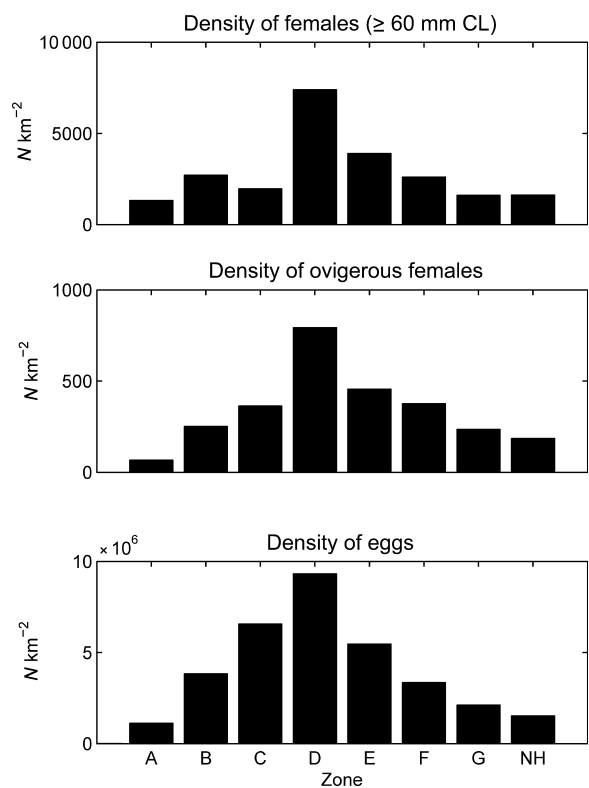
from A to NH, using a straight line or simple curve approximating the 50-m isobath.

RESULTS

Based on trawl data, the size frequency distribution of female lobsters $\geq 60 \text{ mm CL}$ (minimum size at sexual maturity) varied little along the coast of Maine and New Hampshire except that zone C had a greater proportion of lobsters $>85 \text{ mm CL}$. The density ($n \text{ km}^{-2}$) of all female lobsters $\geq 60 \text{ mm CL}$, as well as the density of ovigerous lobsters and annual egg production, was greatest in zone D and declined both to the north and south (Fig. 3). The proportion of female lobsters $\geq 60 \text{ mm CL}$ that were ovigerous, based on maturity ogives and molting frequency calculations, was minimum (0.05) in zone A and maximum (0.18) in zone C, with the other zones ranging from 0.09 to 0.15.

The mean density ($n \text{ km}^{-2}$) of large lobsters ($\geq 90 \text{ mm CL}$) from ROV and sub transects showed an increasing trend with increasing trawl densities, and averaged approximately 30% higher. However, the regression was not statistically significant and could

Figure 3. Characteristics of female lobster populations and egg production in Zones A–NH, 2000–2003.



not be used to adjust the trawl estimates. Likewise, SCUBA data were too variable to distinguish statistically between lobster abundance values over open areas (sampled by trawls, ROV and sub) compared with rocky bottom. Thus, we could not derive a habitat ‘correction’ for the trawl estimates of abundance. The autumn trawl data showed the same alongshore pattern of abundance as the traps (top panel in Fig. 3), and became the sole basis for estimating total egg production in each zone.

From the trap sampling, egg condition was recorded for 15 117 ovigerous lobsters, 4455 of which had developing eggs that would hatch that year. An additional 1597 lobsters had recently shed eggs. The average of the egg condition data indicates a hatching season extending from approximately YD 140 to YD 280 (mid May to early October) in Maine, with the majority of hatching taking place within a period of 80–90 days (Fig. 4). Data indicated a possibly later beginning to the hatching season in 1998, but the smaller sample size had negligible effect on the overall average. The polynomial fits to the hatching data (proportion of present-year eggs that had already hatched) were significant for both eastern (A–D) and western (E–G) zones: $r^2 = 0.88$ and 0.89 , $P = 0.005$ and 0.002 , respectively. Canadian data likewise showed that most hatching took place over a period of 90 days or less. The catch per trap haul of females with mature eggs in Maine indicates a strong tendency

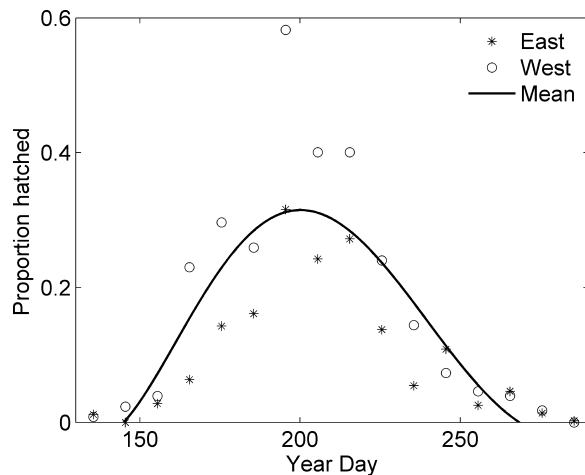
toward inner shelf locations at the time of hatching (Fig. 5).

Each model year generated more than 7 million records of date, larval stage with fractional proportion of within-stage development, and geographical location. Results for the yearly distribution and abundance of postlarvae on their first day of competence to settle (stage 4.5) are shown in Fig. 6, and for cumulative yearly postlarval days of all postlarvae (regardless of development) in Fig. 7. The abundances illustrated in Fig. 6 use a GIS classification scheme known as ‘natural breaks’ (Jenks), which divides classes at boundaries where there are relatively large jumps in data values. We added a zero to this scheme. Maps of seasonal abundance of postlarvae 10 days after attaining competence show patterns similar to Fig. 6 and are not shown here. Particularly high postlarval abundances, both competent and total, appear in the Upper Bay of Fundy, along the mid-coast of Maine, and in Cape Cod Bay. Chronically and conspicuously low abundance areas include zones A–C and NH. Other low values, for BB, SWNS, and OCC, should be considered only partial results because we did not model potential upstream sources of larvae for BB and SWNS, and did not model local egg production for OCC (Fig. 2). BIS did not receive any competent postlarvae from the modeled egg production zones and was dropped from further consideration.

Differences between the ‘blocked’ year (2002) and the ‘flow-through’ year (2003) occurred primarily in mid-coast Maine (zones D and E) and in Massachusetts/Cape Cod Bays (zone MB), with the ‘blocked’ year yielding higher total postlarval days (Fig. 7) and greater abundances of competent postlarvae (Fig. 8) in all three zones. Connectivity between all zones in the model domain is shown as a matrix of values in Table 2, emphasizing the perspective from the recipient zones (‘sinks’). Of the zones where we can reasonably account for all the plausible significant sources of SI production, the majority experienced substantial amounts of self-recruitment, wherein a large proportion of competent postlarvae originated from eggs within the zone. This was not true for zones LBF, A, E and G, which depended on upstream sources for most of their postlarvae.

We examined zone E more closely because it is the best-studied zone with respect to lobster early life histories (Incze *et al.*, 2006 and references therein). The majority of competent postlarvae in zone E came from its nearest upstream neighbor, zone D, in the blocked and intermediate years (Table 2), with a more inshore distribution of sources in the former (Fig. 9). In the flow-through year, the majority came from

Figure 4. Proportion of lobsters that have released eggs (post-hatch) compared to the total of pre- and post-hatch females in traps, binned over 10 days intervals, 1998–2002. East data are from zones A–C, and west from zones D–G. Solid line is the mean of the polynomial equations describing the two data sets.



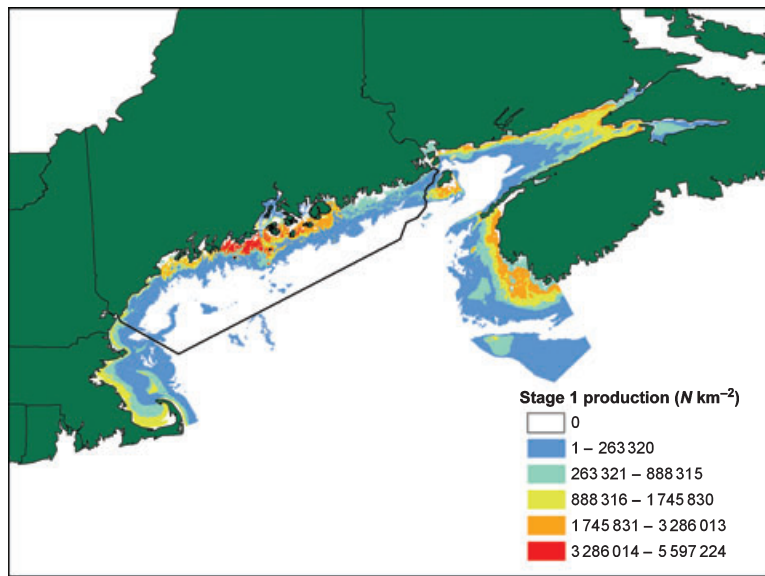


Figure 5. Stage I larval production predicted from the egg production estimates. Estimates in the upper bays were further reduced in model runs (see Materials and methods). Data for zones A–G (black outline, cf. Fig. 1) are based on trawl and trap data from the coastal shelf in each zone for the years 2000–2003. Values for areas to the north and the offshore banks and ledges were extrapolated from the mean depth-specific values for zones A–G; values to the south were extended from zone F.

Figure 6. Annual postlarval-days (PL-d) for competent postlarvae, summing daily average abundance in each 16 km² polygon. All runs used the SI larval production in Fig. 5.

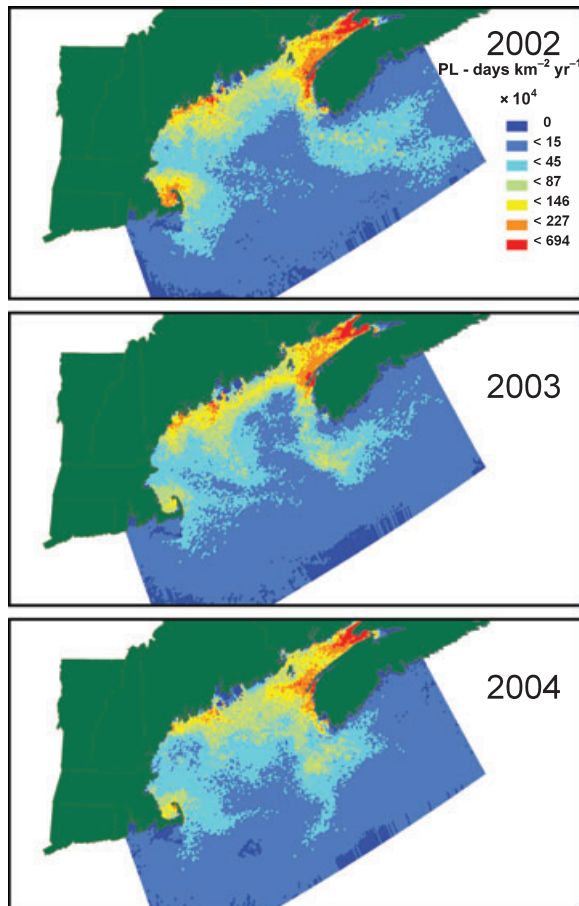
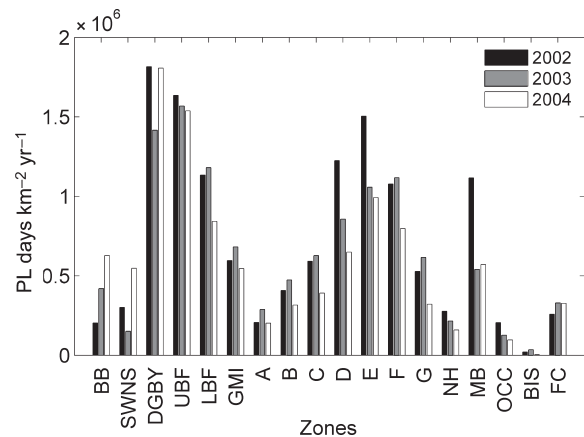


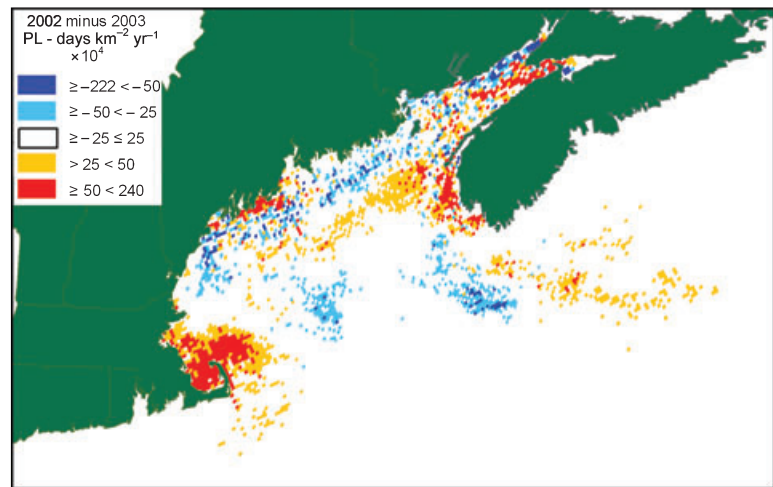
Figure 7. Integrated annual postlarval abundance (all molt-cycle stages) for areas ≤50 m: 2002 (black), 2003 (gray) and 2004 (white).



zone C, two zones away (Table 2). The maximum self-recruitment in zone E (10%) occurred in the blocked circulation of 2002. The pattern of contributions from zones other than C and D varied between years. Competent postlarvae in zone E came from as far away as Browns Bank to the north (Fig. 9B) and Cape Ann to the south (Fig. 9A,C). However, contributions from zones other than C and D were always small (Table 2).

The predicted temporal patterns of postlarvae in the inner coastal shelf (<50 m) of zone E show considerable within-year fluctuations and different inter-annual patterns (Fig. 10), with seasonal maxima mostly in the range of 20–35 PL 1000 m⁻² (note that the area units have been reduced here for convenience to match prior published results). Both in the model

Figure 8. The difference in annual abundance of competent postlarvae between the ‘blocked’ and ‘flow-through’ years, 2002 and 2003, respectively. Only differences $> \pm 250\,000\text{ km}^{-2}$ are shown. The best accounting of all stages is in the central coastal portion of the study area (Fig. 5).



and in field studies, the same postlarvae are counted on numerous succeeding days, except where mortality and/or advection intervene. This is knowable in the model, but not in the field; hence our use of PL-days for any summation over time. The seasonal postlarval abundance in zone E averaged approximately $1000\text{ PL-days } 1000\text{ m}^{-2}\text{ yr}^{-1}$. The maximum and total abundances are all high compared with field observations.

The across-shelf transport of larvae hatched in zones A–G (Maine) is summarized in Table 3. Of the SI larvae, 81% originated inside the 50-m isobath. Of those that survived to become competent postlarvae, 42–56% remained within the 50-m isobath somewhere in the Maine zones. A total of 22–37% had been transported to the outer coastal shelf (50–100 m) but remained in Maine, and 14–18% had been transported beyond the 100-m isobath. Losses to regions outside zones A–G totaled 6% or less. SI larvae produced in shelf depths 50–100 m deep in zones A–G accounted for 19% of SI hatched in Maine. Of the resulting postlarvae, 26–33% were still in that depth zone when they became competent to settle; 26–30% had been transported to areas inside the 50-m isobath; and 28–38% had been transported beyond the 100-m isobath. Losses to regions outside Maine ranged from 5 to 12% over the 3 yrs. A small number had ‘collided’ with the landward boundary of the model and were removed from the calculations (Xue *et al.*, 2008). Physical dimensions of the zones and areas are given in Table 4.

DISCUSSION

This paper is the first spatially explicit population model to cover the early life history from egg production through postlarval development for American

lobsters. We divide our discussion into three parts: an assessment of model inputs; a comparison of model predictions with field data; and a summary of transport patterns and connectivity in the Gulf of Maine population.

Model inputs

For the core of our calculations, we were fortunate to have inshore trawl surveys and collaborations with commercial lobstermen during the summer fishing season when eggs hatch. The extension of average southern Maine and average Maine and NH egg production values and depth patterns to areas south and north of these zones was of unknown accuracy, but by including these estimates we could follow the potential patterns of influence of sources throughout the region. Thus, while the magnitude of influence among these zones remains open to debate, the basic patterns of influence were captured and could be scaled up or down in the future. Based on the tentative Canadian egg production numbers, the influences of Canadian sources (mostly from UBF and GMI) appear to be significant as far south as zone D (generally $\geq 10\%$), but then diminish rapidly ($< 2\%$). Although we thought this would overestimate egg production because the Bay of Fundy lobster catch is approximately 10% that of Maine (Incze *et al.*, 2006), some Canadian expert opinions suggest it might be close.

Although we had an abundance of data from zones A–NH on which to base our estimates of egg and larval production, it is important to recognize that both trawl and trap data have biases in their representation of the lobster population. Trawl sampling was conducted over open bottom in the autumn, thus missing edge or rocky habitat, but sampling at a time when many lobsters were

Table 2. Connectivity between egg production (source zones, horizontal axes) and competent postlarvae (sink zones, vertical axes) based on model runs, 2002–2004. Values are proportions of competent postlarvae in each sink zone that originated from each source zone (values add up to one horizontally, but not vertically). Values <0.01 are denoted by '+', and zero values are left blank. Diagonal lines underscore self-recruitment values. Values ≥0.20 are shaded except where the modeling for egg production and likely larval inputs to sink regions is incomplete (zones BB, SWNS, and OCC). BIS received very few competent postlarvae from the modeled Gulf of Maine egg production and is not shown. Zones are shown in Fig. 1.

Year/sink	Source																
	BB	SWNS	DGBY	UBF	LBF	GMI	A	B	C	D	E	F	G	NH	MB	FC	OCC
2002																	
BB	1.00																
SWNS	+	1.00															
DGBY		0.86	0.13	+													
UBF		0.07	0.09	0.83	+												
LBF		0.84	0.12	0.03	0.01												
GMI		+	0.08	0.39	0.11	0.41	0.02										
A			+	0.61	0.19	0.10	0.07	0.03									
B				0.05	+	0.10	0.06	0.79	0.01								
C		+		0.02	0.01	0.01	0.03	0.04	0.85	0.04							
D			+	+	+	0.05	0.01	+	0.21	0.70	0.03	+					
E							0.02	0.04	0.33	0.49	0.10	0.01					
F					+		+	0.01	0.12	0.36	0.10	0.42	+				
G									0.10	0.31	0.20	0.31	0.07	0.01	+		
NH										0.01	0.04	0.18	0.17	0.60	+		
MB										0.01			+	0.02	0.98		
FC									0.79	0.02		+	+	+	0.66	+	0.19
OCC												+	+	+		+	0.33

Table 2. (Continued)

Year/sink	Source	BB	SWNS	DGBY	UBF	LBF	GMI	A	B	C	D	E	F	G	NH	MB	FC	OCC
2003	BB	1.00																
	SWNS		1.00															
	DGBY		0.84	0.16														
	UBF		0.04	0.05	0.90	+												
	LBF		0.64	0.16	0.14	0.07	+											
	GMI		0.11	0.03	0.38	0.06	0.41	0.01										
	A		0.17	0.01	0.56	0.13	0.10	0.02	+									
	B		+	+	0.05	0.05	0.03	0.08	0.79	+								
	C		+	+	+	0.01	0.14	0.05	0.11	0.50	0.19							
	D		+	+	+	+	0.11	0.02	0.03	0.15	0.69							
	E					+	0.02	0.01	+	0.80	0.13	0.03						
	F						0.02	+	0.01	0.15	0.40	0.12	0.33					
	G						+	+	+	0.18	0.24	0.17	0.34	0.07				
	NH							+	+	0.13	0.03	0.11	0.10	0.08	0.55	+		
	MB							+	+	+	+	+	+	+	0.02	0.96		
	FC								0.05	0.94	0.94	+	+	+	0.01	0.62		
	OCC		0.01						+	+	+	+	+	+	0.01	0.62		0.37
2004	BB	0.96																
	SWNS	+	1.00															
	DGBY	0.03	0.88	0.09		+												
	UBF		0.05	0.02	0.92	0.01												
	LBF		0.65	0.15	0.15	0.05	+											
	GMI		0.02	0.03	0.44	0.15	0.34	0.01										
	A		0.10	0.08	0.39	0.17	0.19	0.07	+									
	B		0.01	0.07	0.01	+	0.06	0.13	0.72	+								
	C		+	+	+	+	0.11	0.03	0.05	0.50	0.29							
	D		+	+	+	+	0.05	0.04	0.10	0.14	0.66	+						
	E			+			+	0.01	0.01	0.31	0.63	0.02	0.02	+				
	F							0.01	0.02	0.10	0.26	0.12	0.50	+				
	G		+	+	+		0.01	0.01	+	0.12	0.30	0.23	0.28	0.05	0.01			
	NH						+	+	+	0.08	0.62	0.01	0.03	0.02	0.23	0.01		
	MB							+	+	+	0.01	+	+	+	0.01	0.97		+
	FC																	
	OCC		1.00															0.43

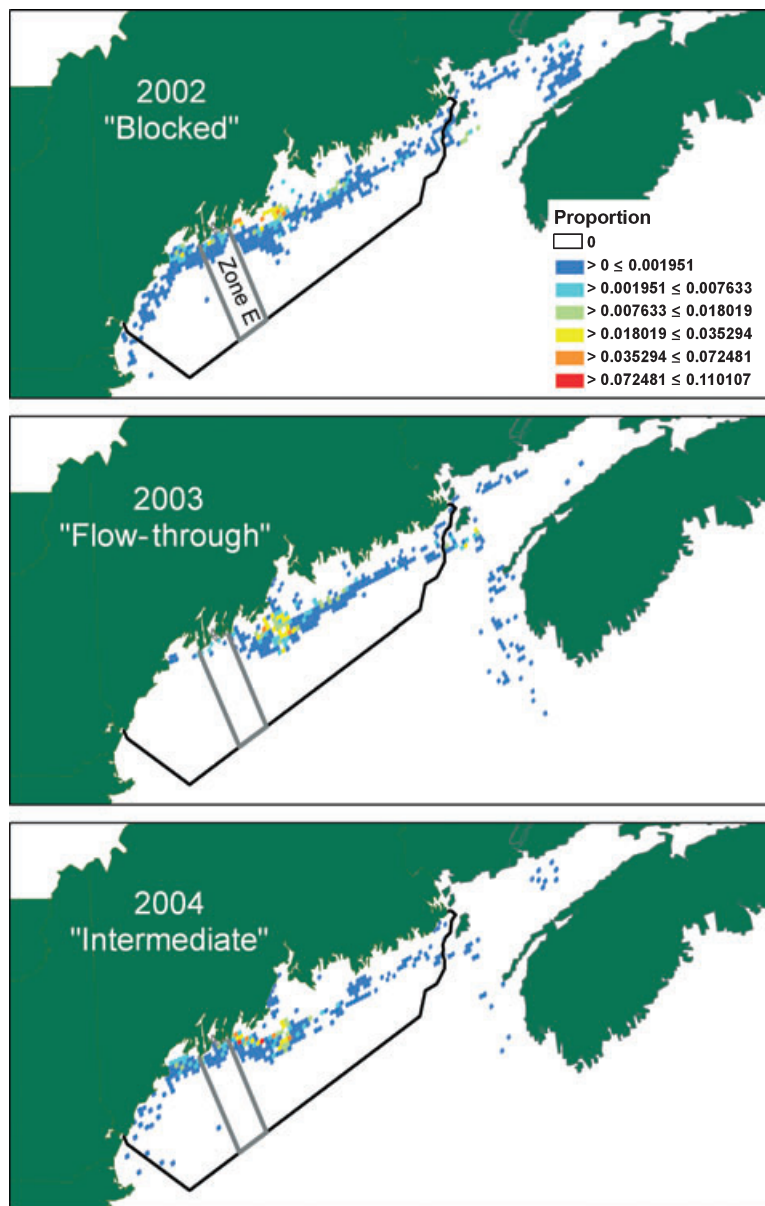


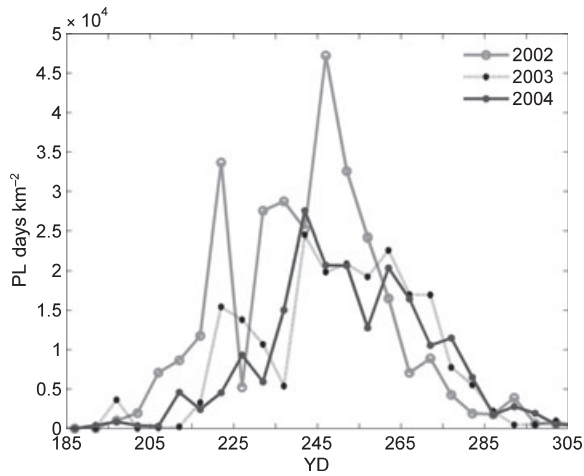
Figure 9. Source locations for larvae that became competent postlarvae inside the 50 m isobath in Zone E (gray polygon). The area with the best-resolved larval production (Zones A–G) is outlined in black.

migrating to deeper water. We assume that these two factors led to an underestimate of abundance overall, but we do not know by how much. Rocky habitat, especially boulders, has higher abundances of large lobsters (sampled by SCUBA during summer: Ste-neck and Wilson, 2001), but there is less of this habitat than there is open bottom. Over open bot-tom the trawls almost certainly under-sample lobsters, but we do not know the sampling efficiency for the large lobsters of interest at this time of year. We should note that another source of uncertainty is the estimate of area swept, which could be off in either direction. Importantly, patterns of abundance (dis-tribution) of large lobsters along the coast are similar

in the SCUBA (mostly summer) and trawl analyses, so the trawl data reflect regional population density patterns even if the absolute abundance estimates remain in question.

In Zones A–G, we distributed the calculated zonal egg production according to the trap catch rates (CPTH) of ovigerous females during the hatching season. We have no reason to doubt the dominance of inshore regions in terms of the overall pattern of hatching, but we caution that traps, trap density, lobster abundance, lobster behavior and commercial fishing practices present many sources of potential bias for this estimate (Miller 1995, Fogarty and Addison, 1997; Jury *et al.*, 2001), even though we focused on

Figure 10. Modeled seasonal pattern of postlarval abundance (all molt-cycle stages) for Zone E inside the 50 m isobath, years 2002–2004. Data shown are 5-days averages.



relative, rather than absolute, abundance. With so much fishing effort concentrated inshore during summer months (though not directed at ovigerous females, which cannot be kept), it is possible that we overestimated the proportion of hatching taking place in water ≤ 50 m (81%: Table 3), but other factors (see above) might have biased the estimate in the other direction. Of less concern, the binning of the ovigerous female density estimates by zones, sub-areas, and depth intervals led to artificially sharp boundaries in lobster distributions (Fig. 5). These artifacts probably had negligible impacts on the outcomes since planktonic stages drifted and dispersed for two or more weeks before they were reassessed as postlarvae, and abundances were averaged over large zones.

The single depth (15 m) assigned to larval stages I–III in the IBM is an oversimplification with some

Table 4. Zone areas and dimensions. The shelf areas inside 50 m and inside 100 m are given for each zone. Alongshore distances are given for Zones A–NH using a simple curve or a straight line at approximately 50 m depth.

Zone	Area ≤ 50 m ($\text{km}^2 \times 100$)	Area ≤ 100 m ($\text{km}^2 \times 100$)	Alongshore distance (km)
BB	0.4	29.2	
SWNS	27.5	61.7	
DGBY	7.2	19.2	
UBF	28.9	57.9	
LBF	3.8	17.6	
GMI	6.9	14.1	
A	9.4	26.2	108
B	5.3	13	44
C	8.3	17	49
D	7.3	17.6	49
E	2.8	6.3	32
F	5.5	9.6	32
G	7.8	19.3	69
NH	5.8	13.4	36
MB	30.9	52.6	
FIPCSH	0.1	1.8	
OCC	110.3	126.3	
BIS	35.8	36.2	

consequences. We have found all three stages at both deeper and shallower depths, but ontogenetic and environmental patterns of vertical distribution of the various stages are not well resolved and may be quite variable. Our data, for example, indicate that SI probably has a shallower mean depth in regions where the water column is stratified, but turbulence, light level and other factors may cause this to change. SI lasts a relatively short time, but SII and SIII have longer development times. Although the residual flow from 5 to 15 m does not have a strong vertical gradient in most locations, the net effect of varying vertical

Table 3. Transport fate of planktonic stages of larvae originating in zones A–G. The depth region and year of origin (hatching) are listed on the left. The other columns show where the resulting postlarvae were found at the time they became competent to settle.

Depth of origin	Proportion of resulting competent postlarvae found in Zones A–G or elsewhere, by depth					
	Zones A–G			Elsewhere		
	0–50 m	50–100 m	>100 m	0–50 m	50–100 m	>100 m
0–50 m						
2002	0.56	0.22	0.18	0.02	0.01	0
2003	0.5	0.3	0.17	0.01	0.01	0.01
2004	0.42	0.37	0.14	0.04	0.01	0.01
50–100 m						
2002	0.3	0.26	0.38	0.01	0.01	0.03
2003	0.29	0.31	0.29	0.03	0.03	0.06
2004	0.26	0.33	0.29	0.04	0.02	0.07

distribution on the end distributions of long-lived larvae cannot be ignored (Paris *et al.*, 2007), and the vertical distributions need to be better known. We selected one depth to maintain clarity through the analysis of outcomes, but larvae near the surface would probably experience more offshore transport, seen in extreme in the shallow postlarvae. An unintended consequence of the selected depth is that the cooler temperatures at 15 m probably led to slower development than larvae experience in stratified parts of the Gulf of Maine. We will return to this point later. The assignment of 1-m depth for postlarvae is reasonable (Annis 2005), and here the wind has a significant effect on transport, which can be seen in model results (Xue *et al.*, 2008).

Finally, neither the wind nor the circulation is properly resolved near shore. Our analysis of coastal wind data from buoys and offshore islands along the coast of Maine (unpublished data) shows an average diel rotation and acceleration of the dominant, southwesterly geostrophic wind during summer months (a diurnal sea breeze, Simpson, 1994). The shoreward rotation and intensification of the wind should favor transport to, and settlement in, shallow coastal waters at the end of the postlarval stage (Wahle and Incze, 1997; Incze and Naimie, 2000), but we do not deal here with this final step in the link between pelagic and early benthic life stages. Instead, 'background' coastal abundances of postlarvae generated by the present model can be used to estimate settlement potential in shallow subtidal habitat, with wind and other transport mechanisms (Wahle and Incze, 1997; Shanks *et al.*, 2000; Keafer *et al.*, 2005), biological processes (Incze and Wahle, 1991; Incze *et al.*, 2000b) and habitat distributions (Incze *et al.*, 2003, 2006) affecting realized settlement densities and finer-scale spatial patterns. Larger-scale wind-driven processes such as coastal divergence or convergence are captured by the model and may affect on- and offshore distributions and interactions with the along-shore flow field (Geyer *et al.*, 2004; Keafer *et al.*, 2005, and discussion below).

Comparisons with field data

In Fig. 6 and Table 2, we counted postlarvae that were in their first day of competence to settle, rather than mapping all competent postlarvae. We used a single developmental reference point for clarity, but adding older competent postlarvae (age 10 days post-competence) altered the results little because mortality reduced the numbers quickly relative to the influence of additional transport. In Fig. 7 we summed the daily counts of all postlarvae over the entire postlarval

season because this tabulation can be compared with field data, which generally do not have information on molt-cycle stage (for exceptions, see Incze *et al.*, 1997; Juinio and Cobb, 1994; James-Pirri and Cobb, 1997, Annis 2006).

Patterns of annual postlarval abundance shown in Fig. 7 qualitatively agree with patterns shown by field data collected from 1989–2003 in Zones A–NH: comparatively low abundances in zones A and B increased to a maximum in zone E and declined farther south (Incze *et al.*, 2006). Only a few zones were sampled after 2000, but some useful comparisons exist. In 2001, Annis *et al.* (2007) recorded 229 PL-days 1000 m^{-2} in the top 0.5 m in zones D and E, and Incze *et al.* (unpublished data) measured 222, 207, 269 and 215 PL-days 1000 m^{-2} in zone NH in 2001–2004, respectively. Field data show similar abundances in zones E and NH in most years (2001 and earlier: Incze *et al.*, 2000a), which does not agree with model predictions for the 3 yrs of this study. This outcome suggests that the model may underestimate transport into the coastal bight in zone NH, which warrants further scrutiny. The high values for MB are not unexpected based on earlier data for postlarvae (Fogarty and Lawton, 1983) and high settler densities (Incze *et al.*, 2006, and next paragraph), but the high values in the Bay of Fundy need to be corroborated with field data. We offer a reminder that the egg production and distribution estimates for Canadian waters were extrapolated from the Maine-wide average and warrant future examination.

We compared model results with contemporaneous settlement data using a time-series of settler densities, which are highly correlated with postlarval abundance (Wahle and Incze, 1997; Incze *et al.*, 2000b). Average settler densities in zones GMI, A, B, C, E, F, G and MB from 2002 to 2004 (Incze *et al.*, 2006) show a pattern similar to the average model-predicted annual postlarval abundances (Table 5). The agreement is surprisingly good, with a coefficient of determination (r^2) of 0.60 for the full dataset and 0.91 for data without GMI. In zone GMI, observed settlement is considerably higher than predicted by modeled postlarval abundance. Possible explanations are (1) sources of egg/larval production for this settlement region are greater than we used in the model, and/or (2) local conditions around the settlement sites are exceptionally favorable to postlarval delivery and do not represent the zonal average (see Incze and Wahle, 1991; Wahle and Incze, 1997).

The model predicted first appearance of postlarvae in zone E between YD 195 and YD 210, depending on the year (Fig. 10). We do not have field observations

Table 5. Comparison of 2002–2004 average observed settler density ($n\ m^{-2}\ yr^{-1}$) in subtidal cobble substrate, (Incze *et al.*, 2006) and model predictions of postlarval abundance for the same period (this study, Fig. 7, units converted to PL-days $m^{-2}\ yr^{-1}$). Data are means \pm 1 SE for settlers and \pm 1 SD for postlarvae. Settler data for zones GMI-G are the same as shown in Fig. 6 of Incze *et al.* (2006); MBB is an average of data from two sites in Massachusetts Bay and one in Cape Cod Bay. Linear regression for all zones: Settlers = $1.5032 * (\text{Postlarvae} - 0.109)$ ($r^2 = 0.60$); for zones A–MB, Settlers = $1.5594 * (\text{Postlarvae} - 0.2703)$ ($r^2 = 0.91$). The increase in concentration from postlarval to settler stages is due to time, advection and settling behavior (Incze *et al.*, 2000b).

Zone		GMI	A	B	C	E	F	G	MB
Observed settlers ($n\ m^{-2}\ yr^{-1}$)	Mean	1.68	0.18	0.18	0.37	1.63	1.26	0.78	0.85
	SE	0.72	0.05	0.12	0.09	0.21	0.56	0.4	0.53
Modeled postlarvae (PL-days $m^{-2}\ yr^{-1}$)	Mean	0.61	0.23	0.4	0.54	1.18	1	0.49	0.74
	SD	0.07	0.05	0.08	0.13	0.28	0.17	0.15	0.32

from Zone E in the modeled years, but data from earlier years are only slightly earlier, in the range YD 182–206 (Incze *et al.*, 1997; Annis *et al.*, 2007). In zone NH in the same years as the model runs, the first day of postlarvae was again slightly earlier in the field (YD 198, 190, and 194) than the model, but only by a few days (the two zones have similar first days). Because the model does not have sampling thresholds, whereas field sampling does, we might expect the opposite. However, the relatively small differences between model predictions and reality could be accounted for by small variations in the beginning of hatching, water temperature, vertical distributions of larvae, and the development rate equations. The temperature effect of the relatively deep modeled position of the larvae could by itself explain these differences (see earlier discussion).

Unlike the generally close agreement above, the modeled peak period of postlarval abundance in Zone E (Fig. 10) was longer and the end dates later than shown by earlier field data. For example, field data from 1989–1995 showed that postlarvae declined to very low levels by YD 240 and were rarely found after YD 260 (Incze *et al.*, 2006). There may have been a shift in the season length over time. In 2001, the field end date in Zones D and E was YD 275 (Annis *et al.*, 2007), and in Zone NH from 2001–2004 the end dates were YD 276, 275, 286 and 265, respectively (Incze *et al.*, unpublished data). These are still earlier than model results (*cf.* Fig. 10), but closer. We suspect that the model produced longer (later) seasons because larvae were developing at cooler temperatures in the model than in nature due to the single, 15-m, depth where we placed them (see earlier discussion of the larval IBM). Because the temperature difference between 15 m and shallower depths increases as the season progresses, the difference between model results and observations would be larger at the end of the season.

The temperature-dependent rates of larval development in our IBM were based on recent field data (Annis *et al.*, 2007) that shortened development relative to earlier laboratory results. These rates are always difficult to establish from field data and are inevitably imprecise, but they appear to work reasonably well. Possible explanations for faster development in the field include better nutrition, and biasing due to higher rates of survival of fast growers (Juinio and Cobb, 1994, Castro and Cobb 2005, James-Pirri and Cobb, 1997; Gonzalez-Gordillo and Rodriguez, 2000). Even after correcting for the probable temperature effect discussed above, the revised development rates do not appear to be too rapid.

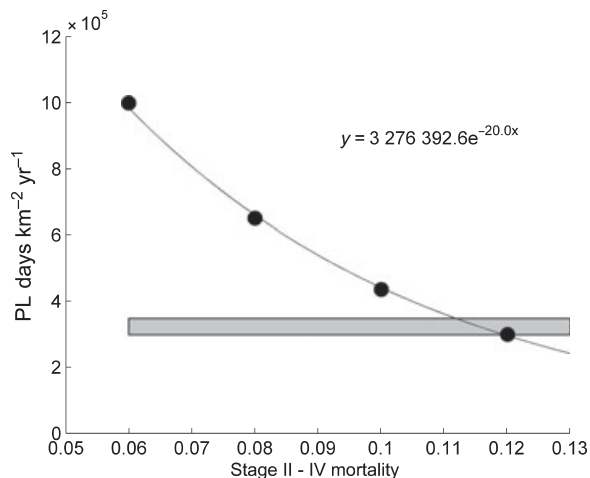
The final comparisons we make with field data are abundance estimates for postlarvae in zone E. Our original estimates of mortality (Table 1) gave model predictions of $\sim 20\text{--}35\ 1000\ m^{-2}$ over the inner shelf during the peak of the postlarval season (Fig. 10). Such densities are occasionally sampled in the field, but the daily averages over many samples are almost always lower. In 2001, we observed averages of $\sim 5\ 1000\ m^{-2}$ from YD 200–240 (Annis *et al.*, 2007), and about the same or only slightly higher in other years (Incze *et al.*, 1997, 2006). Field data came from the top 0.5 m of the ocean. Correcting for the fraction of postlarvae below this depth (Annis 2006) gives estimated field averages $\sim 8\ 1000\ m^{-2}$. The difference between model and field results thus appears to be on the order of $3\times$ or more.

It may be better to compare model and field data using the integrated seasonal abundances because they average over the high-frequency variations. The modeled seasonal postlarval abundance in Zone E (Fig. 7), at ≥ 1000 postlarval-days $1000\ m^{-2}\ yr^{-1}$, is a little more than three times greater than the field data when corrected for depth. From 1989 to 1995 there were ~ 200 PL-days $1000\ m^{-2}\ yr^{-1}$ in the upper 0.5 m in this zone (Incze *et al.*, 2000b); in 2001, there were

229 (Annis *et al.*, 2007). Using the depth correction, both sets of estimates give values from 307 to <350 PL-days $1000 \text{ m}^{-2} \text{ yr}^{-1}$. The 2002–2004 average depth-corrected field abundance in Zone NH (usually similar to Zone E) was 350 PL-days 1000 m^{-2} . As with the values from the middle of the postlarval season, the model estimates of seasonal abundance exceed field estimates by $\sim 3\times$ or more. We assume that this overestimation is typical, and the values used in Table 5 and shown in various figures should be adjusted accordingly.

The most likely source of error in our calculations is larval mortality. Egg mortality (already high), hatching distributions and advective losses are other possibilities, but it is difficult for these to account for the magnitude of difference in abundance between model and field data results. Our sensitivity analyses show that average speed (and the potential for advective losses) would be slightly greater if the larval stages had been located at 5 m rather than 15 m, but the potential for greater advective losses would have been opposed by faster development times at the warmer temperatures that exist near the surface. These findings suggest that the initial mortality rate estimates must be adjusted upward to bring model predictions and field data into alignment. All other things being equal, the daily mortality rate required to reduce model estimates to 300–350 PL-days $1000 \text{ m}^{-2} \text{ yr}^{-1}$ was in the range 0.11–0.12 for Stages II–IV (Fig. 11). The mortality rate for SI may be higher than the 0.03 we used, which would

Figure 11. Effects of daily mortality rate (z) for Stages II–IV on modeled seasonal abundance of postlarvae inside the 50 m isobath in zone E. The baseline of 1×10^6 postlarvae at $z = 0.06$ was chosen for simplicity from Fig. 7. Light gray box highlights the range of observed annual PL-d in zone E after depth corrections (see text).



reduce the estimate for subsequent stages. At the time we developed the initial larval IBM, we had field data suggesting that the mortality rate was as high as 0.5 for the first stage, but the data were limited and we chose to remain with a more conservative number. This rate needs to be more firmly established before any further adjustments of the SII–SIV rates can be justified. A higher SI mortality rate would reduce our estimates for remaining stages, which might also not be equal among stages or over time. Other factors also have to be considered. If larvae develop a little faster (see earlier discussion), it would imply higher mortality rates; likewise if egg production was underestimated. Thus, the range of 0.11–0.12 is a rough approximation and an overall average, useful for broad comparative purposes only. A more important focus would be the factors that might cause such rates to vary significantly over space and time.

Transport patterns and connectivity

The different circulation patterns of the 3 yrs resulted in generally small differences in patterns of source : sink relationships, except for the influence of zones C and D on downstream zones. These two zones currently have high egg production and are located in the transition area between eastern and western coastal currents. It is therefore not surprising that the degree of continuity of flow between the two segments of the coastal current system would have an impact on the distribution of resultant postlarvae. In general, the amount of self-recruitment throughout the study area was higher than we expected, and the amount of variation in lobster connectivity from year to year was less than might have been imagined from the striking differences in circulation among the 3 yrs. Both findings might be explained by the fact that most hatching, according to our analysis of the trap data, occurred inside the 50-m isobath, where patterns of flow are generally more complicated than in more offshore portions of the coastal current system. The inshore migration of lobsters in the spring is thus consequential in terms of increasing the chances for larval retention close to areas of reproduction, as well as producing larvae that remain relatively closer to shore, where settlement might be favored (Incze *et al.*, 2006). The blocked flow characteristic of summer 2002 produced a more variable temporal pattern of postlarval abundance in zone E than the other 2 yrs, possibly the result of greater variability in supply routes (Fig. 9). The suite of patterns, including the range of variations from week to week and the differences between years, are reminiscent of field observations (Incze *et al.*, 2000a).

Self-recruitment is the balance between retention of locally hatched larvae through to competent post-larvae, and inputs from other zones. Self-recruitment is affected by many factors: (1) development, mortality and dispersion rates; (2) relative egg production among the various zones; (3) the size of a zone (it is easier to have high self-recruitment in a large zone, other factors being equal); and (4) transport pathways affecting losses and gains. The small size of Zone E and its location downstream of high egg production zones C and D made outside sources of egg production particularly important: $\geq 90\%$ of competent postlarvae in Zone E originated as SI larvae in other zones. Zone A, though one of the largest, also had low self-recruitment because of relatively low egg production, low temperature (slow larval development), and a particularly strong coastal flow (Pettigrew *et al.*, 1998, 2005). Large zones such as UBF, B, C and D had high degrees of self recruitment, but still received outside subsidies of 17–50% (Table 2). The values in the connectivity matrix for the zones at the two ends of the model domain (BB, SWNS, OCC) are not true measures of connectivity because potential larval inputs to these zones were not complete, but they can be used to see which zones might interact through transport processes.

Variations in sources of larvae (egg hatching areas) contributing to the pool of competent postlarvae in Zone E were consistent with our initial characterization of the years (larval transport seasons) as ‘blocked’, ‘flow-through’ and ‘intermediate’ in terms of the general circulation (Fig. 9). In the ‘blocked’ year there apparently was considerable net drift in the ‘upstream’ direction, something that was nearly absent in the ‘flow-through’ year. In all years, postlarvae arriving in Zone E came from a large portion of the Gulf of Maine. However, quantitatively, distant sources contributed only a small proportion of the competent postlarvae to this zone in all 3 yrs. The largest contributors to zone E were the two large egg-producing areas one and two zones upstream, with changes in relative contribution consistent with the flow regimes (Table 2). Relatively more of the postlarvae originated from hatching locations closer to shore in the blocked season (Fig. 6), which is consistent with an energized offshore branch point of the current at such times (Pettigrew *et al.*, 1998, 2005). An unintuitive result was that more postlarvae in Zone E came from the Bay of Fundy in the blocked conditions, although these contributions were still small. This agrees with the apparent importance of the nearshore flow (‘inside track’) described for the transport of harmful algal blooms (Keafer *et al.*, 2005).

The blocked flow resulted in markedly higher PL-days per year in three zones: D (due to high self-recruitment), E (from zone D) and MB (self-recruitment; Fig. 7 and Table 2). The intermediate flow produced the highest PL-days in BB and SWNS compared with other conditions. Contributions to these two zones were not completely accounted for because they were at the upstream end of the study area, but it remains interesting that the differences were produced by circulation alone, since larval production and mortality were the same in all modeled scenarios. Zone FC received postlarvae mostly from zones C and D due to transport in the offshore branch of the Eastern Maine Coastal Current, demonstrating a potential recruitment pathway to offshore banks from the coastal population. Postlarval abundance at FC was similar to some of the less abundant coastal zones.

Average temperatures experienced by the larvae decreased from 2002 to 2003 and 2004 and accounted for an average 2 days’ longer larval development in 2003 and another 2 days in 2004. The mortality associated with these differences in development time does not account for the modeled differences in postlarval abundances in zones D, E and MB. Interannual differences in PL-days in the other zones were generally small, which agreed with small between-year differences in observed settlement densities over the same time period (Incze *et al.*, 2006).

Of the larvae hatched in Maine (zones A–G), a relatively high proportion of those that survived to become competent postlarvae remained within Maine and over the coastal shelf, defined as within the 100-m isobath. Nearly half (42–56%) of larvae hatched inside the 50-m isobath (inner shelf) that survived to become competent postlarvae were still in Maine and in this depth zone when they reached competency (Table 3). Model results showed postlarvae broadly distributed across the shelf, a condition confirmed by field observations for those zones where the data exist (Incze *et al.*, 2000a). In all, 22–37% of larvae hatched inside the 50-m isobath in Maine were transported to waters 51–100 m deep, and smaller but still significant portions (14–18%) were transported to waters >100 m deep (Table 3). The proportion of competent postlarvae that had been transported outside of Maine was small (3–6%, Table 2), most drifting to MB. These had originated as larvae in all Maine zones except in the blocked year, when only F and G contributed to postlarvae in MB. Larvae were transported against the prevailing direction of the coastal current system. While the

quantitative impact on the level of recruitment was small, the results agree with other studies suggesting that gene flow and biological invasions can take place in an upstream direction (Shanks and Eckert, 2005; Byers and Pringle, 2006). The scale and variability of dispersal in our study was thus much greater than corresponding patterns of major recruitment.

From the outer shelf, 51–100 m deep, less than a third (26–30%) of survivors to competent postlarvae had been transported to the inner shelf. About the same proportion (26–33%) remained in the outer shelf, and slightly more (29–38%) had been transported to deeper water. Up to 13% of postlarvae were transported to areas outside Maine. The greater losses from the deeper portion of the shelf can be ascribed to the fact that it has open boundaries on two sides, and that the along-shelf transport is more rigorous there compared to the inner shelf. According to these calculations, and considering only the inshore–offshore exchange within zones A–G, about 12% of competent postlarvae in the inner shelf originated offshore (from 51 to 100 m deep). This is relevant to the question of conserving offshore egg production as a management option (Fogarty, 1998). While modest at present, an offshore source of larvae could prove more important to the coastal fishery should the inshore component of egg production be reduced through factors such as disease, over-exploitation or a change in environmental conditions. To the extent that the trap data led to an overestimate of inshore egg production, the offshore contribution was correspondingly underestimated.

While we have focused on the life history of lobsters, our model results and calculations provide insight into the general patterns of along-shelf and across-shelf transport and connectivity in the Gulf of Maine under two significantly different and one intermediate transport regime. Consistent with earlier thinking, larvae can be transported over large distances in the Gulf of Maine. However, quantitatively, most competent postlarvae originated within two zones of the zone being considered, and self-recruitment was almost always important. This is similar to findings by Cowen *et al.* (2006), but at a smaller scale. The inshore concentration of hatching, coupled with faster development, contributed to the slower transport along the coast compared to prior estimates and assumptions, which were influenced by observations in the core of the coastal current. Anything that would change the distribution of ovigerous females at the time of hatching would have consequences for patterns of settlement and connectivity.

ACKNOWLEDGEMENTS

We thank F. Page, D. Greenberg, D. Townsend, D. Brooks, E. Annis, R. Strong and R. Losier for helpful discussions about modeling approaches and results; E. Annis for data; M. Strong, D. Robichaud and D. Pezzack for data mining; and S. Cousins for model runs and data archiving. M. Fogarty, J. Idoine and S. Cobb provided helpful insights during numerous conversations about this work, and the Maine Department of Marine Resources and the Canadian Department of Fisheries and Oceans provided data for our analysis. This work was sponsored by NOAA's Center for Sponsored Coastal Ocean Research, Grant #NA03NOS4780003, and received additional support from the Alfred P. Sloan Foundation (Gulf of Maine Area Program, Census of Marine Life) and the U.S. National Science Foundation (Grant 0709536). All are gratefully acknowledged.

REFERENCES

- Annis, E.R. (2005) Temperature effects on vertical distribution of lobster postlarvae (*Homarus americanus*). *Limnol. Oceanogr.* **50**:1972–1982.
- Annis, E.R., Incze, L.S., Wolff, N. and Steneck, R.S. (2007) Estimates of *in situ* larval development time for the lobster, *Homarus americanus*. *J. Crust. Biol.* **27**:454–462.
- Atlantic States Marine Fisheries Commission. (2000). *American lobster stock assessment report. Stock Assessment Report No. 00-01 (supplement)*. Washington D.C.: ASMFC American Lobster Stock Assessment Sub-Committee.
- Bernsten, J., Skagen, D.W. and Svendsen, E. (1994) Modeling the drift of particles in the North Sea with reference to sand eel larvae. *Fish. Oceanogr.* **3**:81–91.
- Botsford, L.W., Hastings, A. and Gaines, S. (2001) Dependence of sustainability on the configuration of marine reserves and larval dispersal distance. *Ecol. Lett.* **4**:144–150.
- Briónes-Fourzán, P., Candela, J. and Lozano-Álvarez, E. (2008) Postlarval settlement of the spiny lobster *Panulirus argus* along the Caribbean coast of Mexico: patterns, influence of physical factors, and possible sources of origin. *Limnol. Oceanogr.* **53**:970–985.
- Byers, J.E. and Pringle, J.M. (2006) Going against the flow: retention, range limits and invasions in advective environments. *Mar. Ecol. Prog. Ser.* **313**:27–41.
- Campbell, A. and Bratty, J. (1986) Egg loss from the American lobster, *Homarus americanus*, in relation to nemertean, *Pseudocarcinonemertes homari*, infestation. *Can. J. Fish. Aquat. Sci.* **43**:722–780.
- Castro, K.M. and Cobb, J.S. (2005) Behaviour of hatchery-reared and wild-caught 4th and 5th stage American lobsters, (*Homarus americanus*). *Marine Freshwater Res.* **39**(4):963–972.
- Cobb, J.S., Wang, D. and Campbell, D.B. (1989) Timing of settlement by postlarval lobsters (*Homarus americanus*): field and laboratory evidence. *J. Crust. Biol.* **9**:60–66.

- Cowan, D.F., Watson, W.H. III, Solow, A.R. and Mountcastle, A.M. (2007) Thermal histories of brooding lobsters, *Homarus americanus*, in the Gulf of Maine. *Mar. Biol.* **150**:463–470.
- Cowen, R.K., Paris, C.B. and Srinivasan, A. (2006) Scaling of connectivity in marine populations. *Science* **311**:522–527.
- Drew, C.A. and Eggleston, D.B. (2006) Currents, landscape structure, and recruitment success along a passive-active dispersal gradient. *Landscape Ecol.* **21**:917–931.
- Ennis, G.P. (1995) Larval and postlarval ecology. In: *Biology of the Lobster Homarus americanus*. J.R. Factor (ed.) San Diego, CA: Academic Press, pp. 23–46.
- Estrella, B.T. and Cadrin, S.X. (1995) Fecundity of the American lobster (*Homarus americanus*) in Massachusetts coastal waters. *ICES Mar. Sci. Symp.* **199**:61–72.
- Fiksen, Ø., Jørgensen, C., Kristiansen, T., Vikebø, F. and Huse, G. (2007) Linking behavioural ecology and oceanography: larval behavior determines growth, mortality and dispersal. *Mar. Ecol. Prog. Ser.* **347**:195–205.
- Fogarty, M.J. (1998) Implications of migration and larval interchange in American lobster (*Homarus americanus*) stocks: spatial structure and resilience. In: *Proc. North Pacific Symposium on Invertebrate Stock Assessment and Management*. G.S. Jamieson & A. Campbell (eds) *Can. Spec. Publ. Fish. Aquat. Sci.* **125**: 273–283.
- Fogarty, M.J. and Addison, J.T. (1997) Modelling capture processes in individual traps: entry, escapement and soak time. *ICES J. Mar. Sci.* **54**:193–205.
- Fogarty, M.J. and Lawton, R. (1983) An overview of larval American lobster (*Homarus americanus*) sampling programs in New England during 1974–1979. *NOAA Tech. Rep., NMFS SSRF* **775**:9–14.
- Gallego, A., North, E.W. and Pettigas, P. (2007) Introduction: status and future of modelling physical-biological interactions during the early life of fishes. *Mar. Ecol. Prog. Ser.* **347**:121–126.
- Geyer, W.R., Signell, R.P., Fong, D.A., Wang, J., Anderson, D.M. and Keafer, B.A. (2004) The freshwater transport and dynamics of the Western Maine Coastal Current. *Cont. Shelf Res.* **24**:1339–1357.
- Gonzalez-Gordillo, J.I. and Rodriguez, A. (2000) Larval development of *Philocheirus fasciatus* (Risso, 1816) (Decapoda, Caridea) reared in the laboratory, comparison with plankton larvae and occurrence of accelerated development. *J. Plankton Res.* **22**:1909–1924.
- Harding, G.C. and Trites, R.W. (1988) Dispersal of *Homarus americanus* larvae in the Gulf of Maine from Browns Ban1e. *Can. J. Aquat. Sci.* **45**(3):416–425.
- Incze, L.S. and Naimie, C.E. (2000) Modeling the transport of lobster (*Homarus americanus*) larvae and postlarvae in the Gulf of Maine. *Fish. Oceanogr.* **9**:99–113.
- Incze, L.S. and Wahle, R.A. (1991) Recruitment from pelagic to early benthic phase in lobsters, *Homarus americanus*. *Mar. Ecol. Prog. Ser.* **79**:77–97.
- Incze, L.S., Wahle, R.A. and Cobb, J.S. (1997) Quantitative relationships between postlarval production and benthic recruitment in lobsters, *Homarus americanus*. *Mar. Freshwater Res.* **48**:729–743.
- Incze, L.S., Aas, P., Ainaire, T. and Bowen, M. (2000a) Neustonic postlarval lobsters, *Homarus americanus*, in the western Gulf of Maine: spatial and interannual variations. *Can. J. Fish. Aquat. Sci.* **57**:755–765.
- Incze, L.S., Wahle, R.A. and Palma, A. (2000b) Advection and settlement rates in a benthic invertebrate: recruitment to first benthic stage in *Homarus americanus*. *ICES J. Mar. Sci.* **57**:430–437.
- Incze, L.S., Wolff, N. and Wahle, R.A. (2003) Can scientific observations of early life stages be scaled up to the level of a fished population? A case study using *Homarus americanus*. *Fish. Res.* **65**:33–46.
- Incze, L.S., Wahle, R.A., Wolff, N. et al. (2006) Early life history of lobster (*Homarus americanus*) populations in the Gulf of Maine. *J. Crust. Biol.* **26**:555–564.
- James-Pirri, M.J. and Cobb, J.S. (1997) Growth rates of planktonic and newly settled American lobsters *Homarus americanus*. *Mar. Ecol. Prog. Ser.* **160**:233–240.
- Juinio, M.A.R. and Cobb, J.S. (1994) Estimation of recent growth of field caught postlarval American lobsters, *Homarus americanus*, from RNA:DNA ratios. *Can. J. Fish. Aquat. Sci.* **51**:286–294.
- Jury, S.H., Howell, H., O'Grady, D.F. and Watson, W.H. III (2001) Lobster trap video: *in situ* video surveillance of the behavior of *Homarus americanus* in and around traps. *Mar. Freshwater Res.* **52**:1125–1132.
- Keafer, B.A., Churchill, J.H. and Anderson, D.M. (2005) Blooms of the toxic dinoflagellate, *Alexandrium fundyense*, in the Casco Bay region of the western Gulf of Maine: advection from offshore source populations and interactions in the Kennebec River plume. *Deep-Sea Res. II* **52**:2631–2655.
- Lawton, P.J. and Lavalli, K.L. (1995). Postlarval, juvenile, adolescent and adult ecology. In: *Biology of the Lobster Homarus americanus*. J.R. Factor (ed.) San Diego, CA: Academic Press, pp. 47–88.
- MacKenzie, B.R. (1988) Assessment of temperature effects on interrelationships between stage durations, mortality and growth in laboratory-reared *Homarus americanus* Milne-Edwards. *J. Exp. Mar. Biol. Ecol.* **116**:87–98.
- Mellor, G.L. (2003) *Users Guide for a Three-Dimensional, Primitive Equation, Numerical Ocean Model*. Princeton: Princeton University, p. 53.
- Miller, R.J. (1990) Effectiveness of crab and lobster traps. *Can. J. Fish. Aquat. Sci.* **47**:1228–1251.
- Miller, R.J. (1995) Catchability coefficients for American lobster (*Homarus americanus*). *ICES Marine Science Symposia.* **199**:349–356.
- Miller, T.J. (2007) Contribution of individual-based coupled physical-biological models to understanding recruitment in marine fish populations. *Mar. Ecol. Prog. Ser.* **347**:127–138.
- Paris, C.B., Cherubin, L.M. and Cowen, R.K. (2007) Surfing, spinning, or diving from reef to reef: effects on population connectivity. *Mar. Ecol. Prog. Ser.* **347**:285–300.
- Perkins, H. (1971) Egg loss during incubation from offshore northern lobsters (*Homarus americanus* Milne-Edwards). *Fish. Bull.* **69**:451–453.
- Perkins, H.C. (1972) Developmental rates at various temperatures of embryos of the northern lobster (*Homarus americanus* Milne-Edwards). *Fish. Bull.* **70**:95–99.
- Pettigrew, N.R., Townsend, D.W., Xue, H., Wallinga, J.P., Brickley, P.J. and Hetland, R.D. (1998) Observations of the Eastern Maine Coastal Current and its offshore extensions. *J. Geophys. Res.* **103**:30623–30640.
- Pettigrew, N.R., Churchill, J.H., Janzen, C.D. et al. (2005) The kinematic and hydrographic structure of the Gulf of Maine Coastal Current. *Deep-Sea Res. II* **52**:2369–2391.

- Shanks, A.L. and Eckert, G.L. (2005) Population persistence of California current fishes and benthic crustaceans: a marine drift paradox. *Ecol. Monogr.* **75**:505–524.
- Shanks, A.L., Largier, J., Brink, L., Brubaker, J. and Hoff, R. (2000) Evidence for shoreward transport of meroplankton by an upwelling relaxation front. *Limnol. Oceanogr.* **45**:230–236.
- Shanks, A.L., Grantham, B.A. and Carr, M.H. (2003) Propagule dispersal distance and the size and spacing of marine reserves. *Ecol. Appl.* (Suppl.) **13**: S159–S169.
- Simpson, J.E. (1994) *Sea Breeze and Local Wind*. Cambridge: University Press, p. 234.
- Steneck, R.S. and Wilson, C. (2001) Large-scale and long-term, spatial and temporal patterns in demography and landings of the American lobster, *Homarus americanus*, in Maine. *Mar. Freshw. Res.* **52**:1303–1319.
- Wahle, R.A. and Incze, L.S. (1997) Pre- and post-settlement processes in recruitment of the American lobster. *J. Exp. Mar. Biol. Ecol.* **217**:179–207.
- Wahle, R.A. and Steneck, R.S. (1992) Habitat restrictions in early benthic life: experiments on habitat selection and *in situ* predation with the American lobster. *J. Exp. Mar. Biol. Ecol.* **157**:91–114.
- Xue, H., Shi, L., Cousins, S. and Pettigrew, N.R. (2005) The GOMOOS nowcast/forecast system. *Cont. Shelf Res.* **25**:2122–2146.
- Xue, H., Incze, L.S., Xu, D., Wolff, N. and Pettigrew, N. (2008) Connectivity of lobster populations in the coastal Gulf of Maine. Part I. Circulation and larval transport potential. *Ecol. Modell.* **210**:193–211.