Larval behavior, hydrodynamic transport, and potential offshore-to-inshore recruitment in the American lobster *Homarus americanus*

C. H. Katz[1], J. S. Cobb[1], M. Spaulding[2]

[1]Department of Zoology and [2]Department of Ocean Engineering, University of Rhode Island, Kingston, Rhode Island 02881, USA

ABSTRACT: Theoretical and field patterns of offshore larval dispersal were explored for the American lobster *Homarus americanus* on the southern New England (USA) continental shelf. Our field collections along an offshore–inshore transect revealed a gradient of larval stages with a greater proportion of earlier stage larvae in the vicinity of offshore canyons, and more mature stage III and IV larvae dominating larval distributions closer to coastal habitats. An empirical trajectory model integrating larval behavior and hydrodynamic properties was then constructed to evaluate potential dispersal mechanisms. Model simulations suggested that passive drift via surface currents and wind-induced transport were insufficient conditions for offshore recruitment subsidies to coastal populations. In contrast, directional swimming of the fourth stage larvae resulted in successful dispersal to the coast within the duration of the planktonic phase of *H. americanus*.

KEY WORDS: Recruitment · Larval dispersal · Transport model · American lobster · Swimming behavior · Surface currents · Wind-induced transport

INTRODUCTION

The demography of marine populations with complex life cycles requires an understanding not only of local adult life history traits, but of the dispersal and settlement of the planktonic larvae as well (Wallace 1876, Thorson 1950, Scheltema 1971, 1986, Underwood & Denley 1984, Strathmann 1985, Roughgarden et al. 1988, Black & Morgan 1991). In general, the population dynamics of these marine species are related to the integrated response of the adult and larval stages to biological and hydrodynamic factors (Phillips & McWilliam 1986). One source of population variation lies in the growth, survival and fecundity of the adult phase. The influences of predation, competition, space, food resources, disturbances, and harvesting upon adult traits are well documented for many marine species (Connell 1961, Paine 1966, Dayton 1971, Ambrose 1984, Katz 1985, Ortega 1986, Jones 1987, Holbrock & Schmitt 1989). The second major component of demographic variation occurs in the dispersal and colonization of the planktonic larvae (Loosanoff 1964, Scheltema 1966, Thorson 1966, Sale 1978, Keough 1983, 1984, Underwood & Denley 1984, Gaines &

Roughgarden 1985). In most instances, the supply of larvae is thought to originate from a number of populations within a specific region rather than result from local reproduction (Robertson 1964, Scheltema 1964, Caswell 1978, Hughes 1990). Further, larval abundances and regional as well as local ocean hydrodynamic characteristics can contribute to the dynamics of pelagic and benthic populations (Thorson 1961, Scheltema 1971, Jackson & Strathmann 1981, Caffey 1985, Possingham & Roughgarden 1990, Sutherland 1990). Although theoretical and empirical studies have focused on the important role of presettlement processes for over 70 yr, the specific mechanisms of larval recruitment and the variation in larval subsidies for many species remain central questions in marine population ecology and fisheries biology.

The complex process of recruitment in marine populations involves the developmental stages of the life cycle (e.g. spawning, growth, metamorphosis, survival, maturation), behavioral traits (e.g. directional swimming, vertical migration, habitat selection), and oceanographic properties (e.g. currents, wind-induced transport, tides, waves, turbulence). The role of oceanographic processes in larval dispersal (e.g.

Scheltema 1968, Lough 1976, Epifanio et al. 1984, Johnson et al. 1984, Roughgarden et al. 1985, Bartsch et al. 1989) has received increased attention in an attempt to discern the mechanisms of recruitment and the causes of fluctuations in population dynamics. Decopod and crustacean populations have been examined in an effort to integrate hydrodynamic transport with life history stages. For example, Phillips & McWilliam (1986) showed that recruitment of the Australian rock lobster *Panulirus cygnus* is affected by drift due to currents as well as behavioral mechanisms such as vertical migration and responses to lunar phases. Possingham & Roughgarden (1990) investigated theoretically the effects of coastal diffusion and advection on intertidal barnacles, and Davis (1984) modeled copepod dynamics in a simulated gyre designed to mimic the circulation on George's Bank (NW Atlantic). In each of these studies, the larvae are assumed to be passive particles or are limited to vertical migrations. Here, we investigate not only the role of oceanographic properties, but also the horizontal directional swimming behavioral traits of larvae of the American lobster *Homarus americanus*.

The purpose of this study was to explore the patterns and mechanisms of offshore larval dispersal in *Homarus americanus*, and ascertain the potential contributions from offshore recruitment to coastal populations. Specifically, our hypothesis submits that coastal lobster populations of Rhode Island and southeast Massachusetts, USA, are subsidized by larvae released in canyons near the continental slope. Our approach was to examine general larval dispersal patterns over the northeastern continental shelf, and to explore mathematically the oceanographic and behavioral mechanisms that may influence this larval dispersal. Initially, field collections were used to delineate the distribution of lobster larvae along a 150 km offshore-inshore transect. Next, we developed an empirical trajectory model to simulate larval movements. The model integrated surface currents, wind-induced surface transport, passive drift in the early stage lobster larvae, and directional swimming behavior of the final stage larvae. Stepwise increases in complexity of the model were used to generate offshore-onshore larval patterns. General insights from the model were used to qualitatively suggest the possible mechanisms necessary for the offshore recruitment given the constraints of the life history traits of *H. americanus*.

LIFE HISTORY AND EXPERIMENTAL METHODS

The complex life cycle of *Homarus americanus* consists of 4 larval stages, a juvenile benthic phase, and the mature adult. Similar to the dispersal of many other benthic invertebrate larvae, the first 3 developmental stages

of the lobster drift passively with geostrophic and wind-forced currents. Recent evidence suggests that the first 2 stages may exhibit diel vertical migration in deeper waters (Harding et al. 1987). More interestingly, observations reveal that the fourth stage larvae (classically referred to as the postlarvae) are active directional swimmers (Ennis 1986a). Short-term field observations (Cobb et al. 1989) of the fourth stage larvae at or very near the surface indicate that individuals in this life history stage are rapid swimmers with a mean velocity of 18 cm s^{-1} ± 0.049 (standard error), while swimming speeds noted in laboratory-reared larvae are slightly slower at 10.7 cm s^{-1} (Rooney & Cobb 1991). Furthermore, swimming is orientated in a northerly direction for a majority of larvae in the fourth stage. The average life span and, therefore, the dispersal time of the passive and swimming stages in 18 to 21 °C waters is 26 d (Herrick 1909, Templeman 1936, Wilder 1953). Specifically, the development times for stages I, II, III, and IV are 3, 3, 4, and 16 d respectively. Following the active dispersal phase, the stage IV larvae search for and settle in suitable sheltered habitats (Wahle & Steneck 1991).

In 1988, an offshore-inshore transect on the southern New England (USA) continental shelf was sampled to test the hypothesis that an offshore recruitment subsidy would result in a gradient of larval stages with a corresponding greater proportion of stage IV larvae nearer to the coastal habitats. The sampling procedure consisted of a series of surface neuston tows from approximately 40.1° N, 69.4° W to 41.05° N, 71.6° W. A 2 × 2 m neuston net with a 1000 µm mesh was used to determine abundances of lobster larvae during weekly tows between June 11 and August 16. The tows were made from a commercial lobster vessel and lasted 30 min at a speed of 2.8 to 3.0 knots. All larvae were washed into the cod-end with seawater, and the number of stage I to IV larvae was recorded for each date. A chi-square analysis was used to test the null hypothesis that the distribution of larval stages was independent of sample locations. The analysis was calculated on a Dell 386 33 MHz computer using SAS (1985, 1987) for personal computers.

DISPERSAL MODEL

A trajectory model was formulated to ascertain the relative importance of oceanographic processes and behavioral traits (e.g. swimming) on lobster larvae dispersal. The lobster larval transport model is based on an empirical hydrodynamic vector equation (see Spaulding 1988) and is denoted as:

$$\vec{U_L} = \vec{U}_{current} + \vec{U}_{wind-induced\ transport} + \vec{U}_{swimming} \quad (1)$$

where $\vec{U_L}$ is the resultant velocity of the larvae; $\vec{U}_{current}$

describes velocity of long-term mean shelf surface currents; and $\overrightarrow{U}_{swimming}$ incorporates swimming speed and direction of the fourth stage larvae, with $\overrightarrow{U}_{swimming} = 0.0$ for stages I, II, and III. $\overrightarrow{U}_{wind\text{-}induced\ transport}$ represents the transport of surface larvae due to winds and is described as:

$$\overrightarrow{U}_{wind\text{-}induced\ transport} = \overrightarrow{\lambda |U_{wind}|}. \tag{2}$$

Here, λ is a coefficient that describes the wind-induced transport as some percentage of the absolute wind speed ($|U_{wind}|$). For most objects in the upper meter of the water column, λ is equal to between 1 and 2% of the wind speed, while objects that float at the surface (e.g. oil) move at 3 to 4% of the wind speed (Stolzenbach et al. 1977). The wind-induced transport direction is to the right of the wind in the northern hemisphere due to the Coriolis force, with an angle θ varying between 0 and 25° (mean = 15°) depending on the velocity of the wind.

The continental shelf extending from 39° to 42.5° N and 68° to 75° W was divided into a horizontal grid with a cell size of 5 km². The mean shelf surface currents obtained from the U.S. Naval Oceanographic Office, ocean drifter data (Bumpus & Lauzier 1965), and current meter observations (Beardsley et al. 1976) were integrated into the model grid. Current speeds on the shelf ranged from 10 to 50 cm s^{-1} with a general flow to the west and southwest. The direction and speed of the wind were obtained hourly from the NOAA/National Weather Service Station at T. F. Green Airport in Warwick, Rhode Island. Observed wind direction was primarily out of the southwest in June and July 1988. Since offshore wind velocities are stronger than those measured at the land based stations, winds were compared with offshore buoys (Godshell et al. 1980, Gilhousen et al. 1983) and multiplied by a conversion factor of 2. Wind-induced transport (the coefficient λ) was set at either 0, 1, or 2% of the wind speed. In this model, stage I, II, and III larvae are assumed to be transported passively for 10 d. With metamorphosis to the stage IV larvae, the vector for directional swimming was set to either 10 cm s^{-1} or 18 cm s^{-1}. In addition, trajectories were generated either with continuous 24 h swimming or with diurnal swimming from 05:00 to 19:00 h. Swimming ori-

entation in each case was set towards magnetic north. The transport trajectories were determined by simulating the release of larvae at several locations along the canyons, and following their dispersal spatially and temporally over the continental shelf. Simulations were begun in mid-June of 1988 to coincide with the emergence of lobster larvae in the field. The model simulations were performed on a MicroVax II, and allowed to run for up to 40 d.

A 2-way analysis of variance (TANOVA) was calculated to determine the effects of larval swimming behavior and wind-induced transport on dispersal rates. In this case, the null hypothesis was that dispersal times from the offshore to inshore habitats were equal for each fixed treatment. The model used in this 2-way analysis was $Y_{ijk} = w + \alpha_i + \beta_j + \alpha\beta_{ij} + e_{ijk}$, where Y is the variation in dispersal, w is the overall mean, α is the effects of larval swimming behavior, β is the impact of wind-induced transport, $\alpha\beta$ is the interaction term, and e is the random deviation of the individual k samples from the ith and jth group. A priori comparisons of swimming speeds and duration were performed with orthogonal contrasts. These statistics were generated using the SAS (1985) GLM procedure.
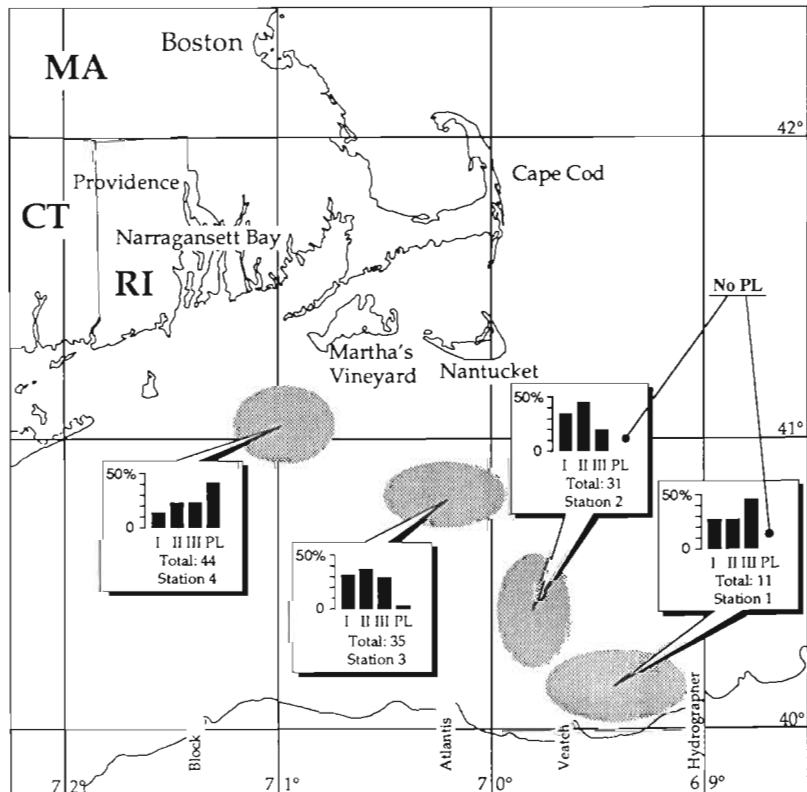

Fig. 1. *Homarus americanus*. Inshore-offshore transect showing the percent of lobsters in each larval stage at 4 locations off the New England (USA) coast. PL: postlarvae; Block, Atlantis, Veatch, Hydrographer: canyons in the continental slope
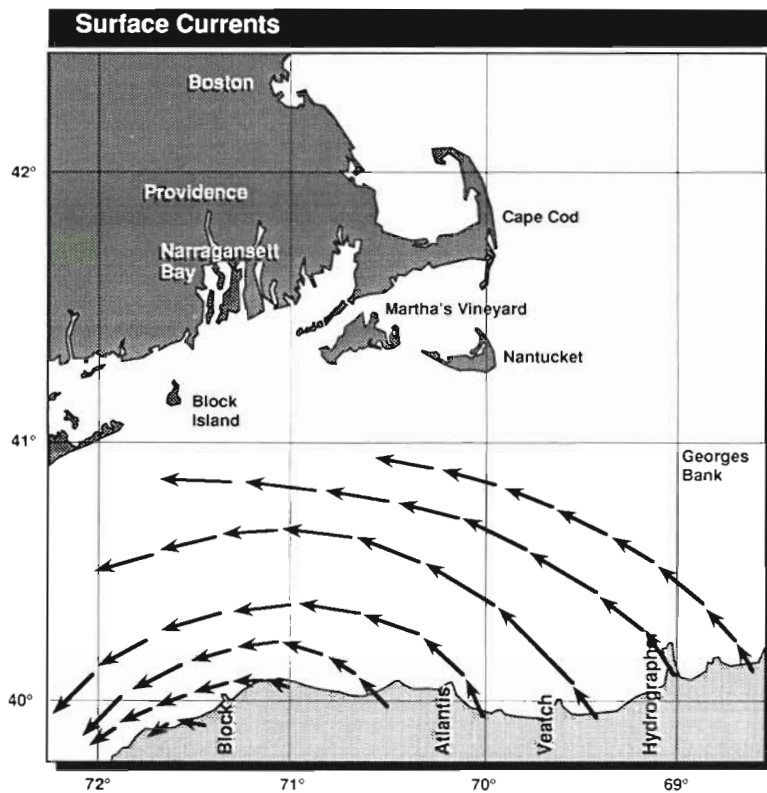
Fig. 2. Simulated passive dispersal of larvae of American lobster *Homarus americanus*, as influenced by surface currents. Dispersal trajectories are represented by arrows whose orientation indicates direction, and length denotes distance traveled over a 5 d interval
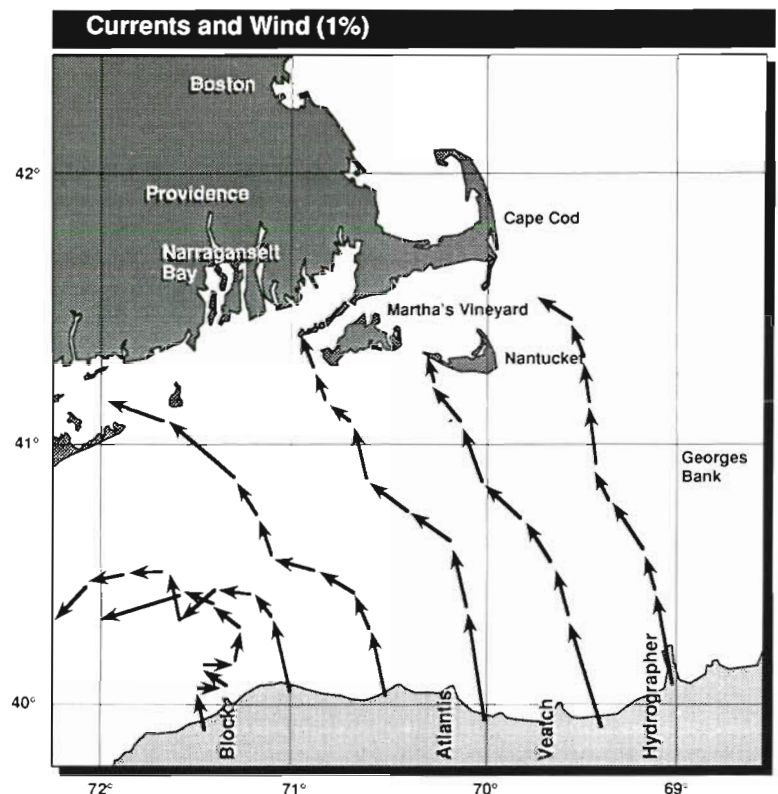
of the samples consisting of stage I larvae. Comparison of the number of individuals per stage revealed a significant difference in the larval distributions for the 4 areas (chi-square, $p < 0.05$).

In an effort to distinguish the relative potential effects of physical and biological mechanisms on dispersal rates, larval trajectories were first modeled with only the influence of surface currents, then as a vector sum of currents and wind-inducted transport, and finally as a vector sum of current, wind, and swimming. Initially, dispersal as a simple function of surface currents resulted in a southwest recruitment pattern over the continental shelf after a 40 d simulation (Fig. 2). Note that each arrow indicates the simulated dis-

RESULTS

The field distribution of the 4 larval stages showed a distinct pattern along the offshore–inshore transect (Fig. 1). In general, the transect showed a greater proportion of the earlier stage larvae in offshore waters, while the stage IV larvae predominated closer to the coast. At Stns 1 and 2 near the canyons, stage I, II, and III larvae comprised 100 % of the larval abundances. For example, stages I and II were observed to constitute 35 % and 45 % of the total samples respectively at Stn 2, and the remaining 19 % were stage III individuals. The intermediate sampling site (Stn 3) revealed a relatively even distribution of stage I, II and III, and the first evidence of stage IV larvae (3 %) in the water column. Conversely, Stn 4 was dominated by the fourth stage larvae at 41 % with only 14 %

Fig. 3. Simulated dispersal of *Homarus americanus* larvae as affected by currents and 1 % wind-induced transport. Arrows as in Fig. 2, except that arrows contacting the islands or mainland describe distances covered in ≤5 d
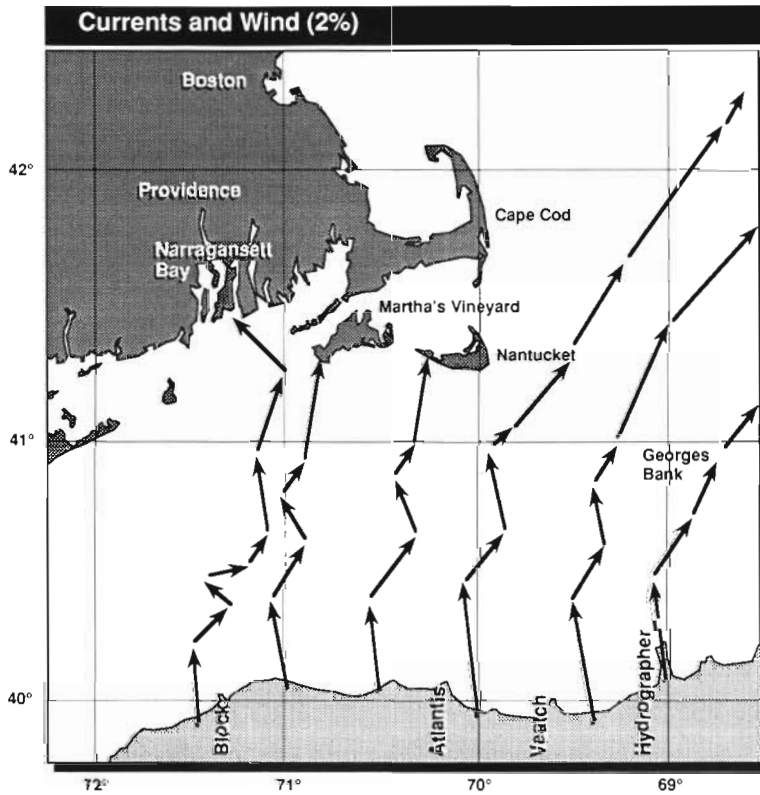
Currents and Wind (2%)

tance traveled by the larvae for 5 d intervals, and that the closest larvae remained approximately 45 km offshore. Given a mean planktonic duration of 26 d, passive drift appears to be an insufficient mechanism for coastal subsidies. Further, we would expect these larvae to begin settling and colonizing suitable habitats between the canyons and coasts. Next, incorporating 1 % wind-induced transport with mean currents, the larvae are shown to drift into the vicinity of Martha's Vineyard, Nantucket Island, and Block Island after 40 d (Fig. 3). In this instance, recruitment to the islands would occur if settlement were delayed for approximately 15 d. At 2 % wind-induced transport, trajectories shifted to the northeast (Fig. 4) as a consequence of southwesterly winds typical of the summer months in this region, and with higher wind-induction the larvae were blown away from the coast and towards George's Bank.

Integrating directional swimming of the stage IV larvae and the hydrodynamic properties (Table 1) had a significant effect on dispersal times (Table 2; TANOVA, $p < 0.01$) and general patterns of movement. Orthogonal contrasts revealed notable differences in dispersal times to the coast between diurnal and continuous swimming behavior at 18 cm s^{-1} ($p < 0.01$), and diurnal 10 cm s^{-1} and continuous 18 cm s^{-1} dispersal ($p < 0.01$). Conversely, dispersal was similar ($p = 0.33$) for stage IV larvae simulating continuous 10 cm s^{-1} behavior and diurnal 18 cm s^{-1} swimming for 0 %, 1 % and 2 % wind-induction. Specifically, the stage IV larvae reached mainland and island coastal populations within an average of 17 d (Fig. 5) in the model

Table 1. Mean simulated dispersal times of *Homarus americanus* larvae, in days, from the offshore canyons to coastal habitats as related to surface currents, wind-induced transport, and postlarval swimming. The means and standard errors were calculated from those trajectories that intersect islands or the mainland of the states of New York, Connecticut, Rhode Island, and Massachusetts, USA

| | | Wind-induced transport | | |
		0 %	1 %	2 %
Swimming	Continuous			
	10 cm s^{-1}	24.7 ± 1.2	21.3 ± 1.1	18.5 ± 1.6
	18 cm s^{-1}	17.4 ± 0.5	16.9 ± 0.7	15.3 ± 1.1
	Diurnal			
	10 cm s^{-1}	29.9 ± 1.2	25.8 ± 2.1	22.3 ± 1.1
	18 cm s^{-1}	23.2 ± 1.0	20.5 ± 1.0	17.8 ± 1.4

Table 2. Results of a 2-way analysis of variance examining the effects of swimming and wind-induced transport on dispersal rates of *Homarus americanus* larvae

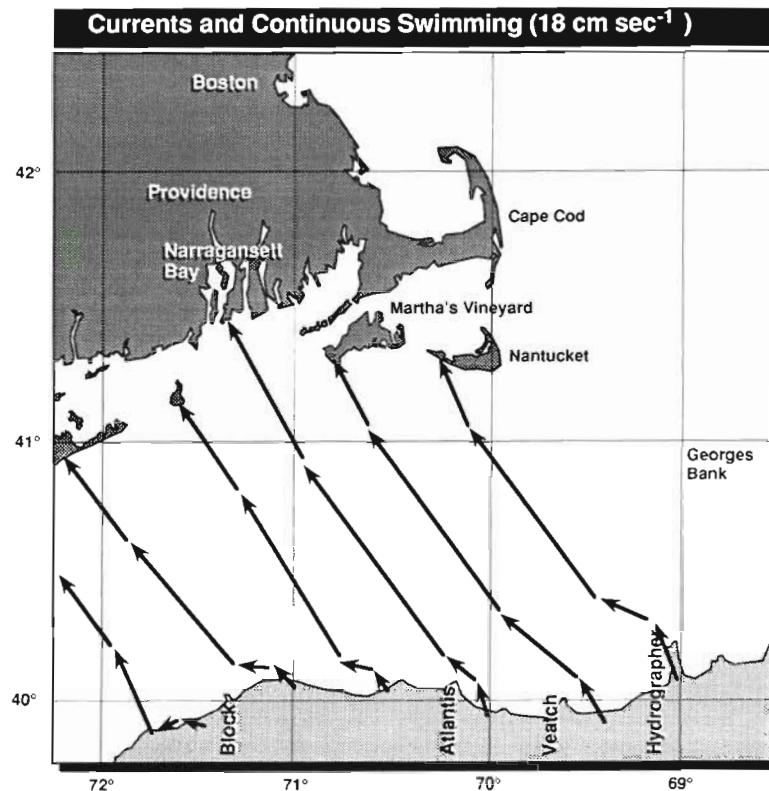| Source	df	SS	MS	F	p
Swimming	3	610.1895	203.3964	28.48	<0.01
Wind	2	250.9823	125.4907	17.57	<0.01
Swimming × Wind	6	38.8229	6.4705	0.91	0.4990
Error	46	328.5000	7.1413		
Total	57	1228.4938			

Currents and Continuous Swimming (18 cm sec⁻¹)

◀ Fig. 5. Simulated *Homarus americanus* larval dispersal as a result of surface currents and continuous stage IV larval swimming at 18 cm s⁻¹. Arrows as in Fig. 3

DISCUSSION

The current hypotheses of larval recruitment focus on advection and diffusion processes, Ekman transport, lunar phases, and vertical migrations (Wroblewski 1982, Johnson et al. 1984, Phillips & McWilliam 1986, Bartsch et al. 1989, Possingham & Roughgarden 1990). For *Homarus americanus*, offshore larvae are thought to be transported toward the coast by surface currents (Templeman 1937, 1939, Stasko 1978, Harding et al. 1983, Ennis 1986b) and possibly by modified vertical water column movements (Caddy 1979). In general, our lobster-larvae dispersal model suggests that surface currents and wind-induced transport in and of themselves are insufficient conditions for successful offshore recruitment subsidies to coastal populations in south-

simulating surface currents and continuous swimming at 18 cm s⁻¹. Notice that larval transport (stages I to III) during the first 10 d was passive and dictated by currents, while the directional swimming by the stage IV larvae traversed the majority of the distance (approximately 150 km) to the coast.

Assuming diurnal stage IV larval swimming at 18 cm s⁻¹ for 14 h d⁻¹, offshore larvae were noted along the coast in an average of 23 d. Transport mechanisms consisting of 1% and 2% wind-induced movement, surface currents, and diurnal swimming resulted in simulated arrival times of 20 d (Fig. 6) and 18 d, respectively. Given swimming speeds of 10 cm s⁻¹, offshore-inshore dispersal times were computed to range from 18 d with 2% wind-inducted transport and continuous swimming versus 30 d in the absence of wind and with diurnal swimming.

Fig. 6. Trajectories affected by currents, 1% ▶ wind-induced transport, and stage IV *Homarus americanus* larval swimming at 18 cm s⁻¹ between 05:00 and 19:00 h. Arrows as in Fig. 3

Currents, Wind (1%), and Diurnal Swimming (18 cm sec⁻¹)
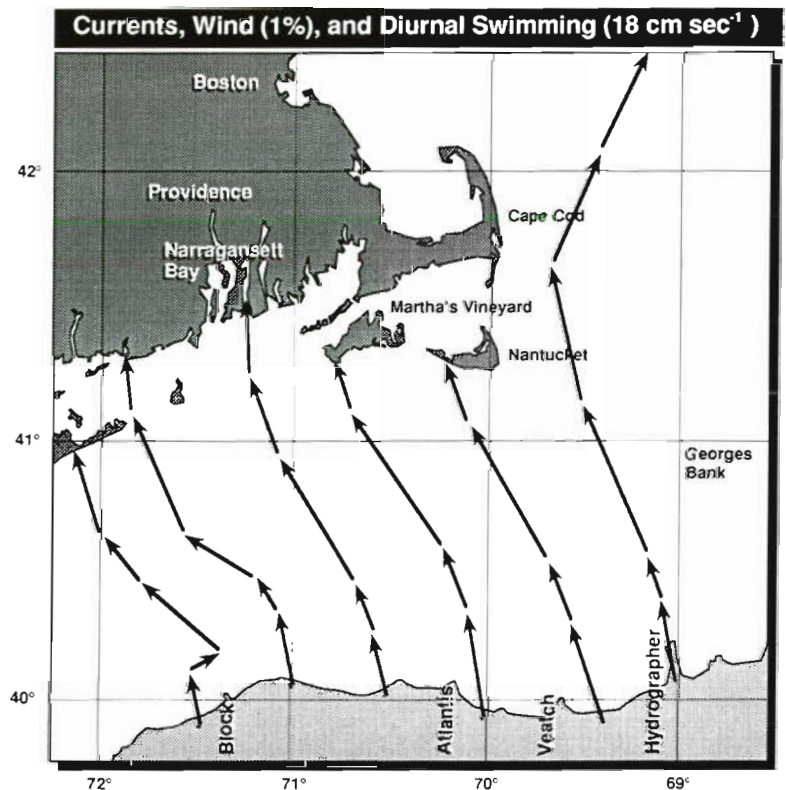
ern New England. Passive drift of the larvae reveals dispersal patterns that do not overlap with coastal habitats. Instead, drifting larvae would be transported to the southwest by the prevailing surface currents on the southern New England shelf. The integration of wind-induced movement with surface currents produces larval trajectories that intersect with the islands off the coast after 40 d. In order for these 2 physical oceanographic factors to actually serve as a mode of dispersal, the planktonic and pelagic stages of *H. americanus* would need to be delayed by approximately 2 wk assuming that the average developmental time is 26 d. In contrast, strong directional swimming of the stage IV larvae results in recruitment to coastal populations within the duration of the planktonic/pelagic phase. Continuous and diurnal swimming at 18 cm s^{-1} contributes to the traversing of the continental shelf within a range of 17 to 23 d. If the settlement to the benthos occurs halfway through the fourth larval stage as suggested by Scarratt (1973), then the number of days the larvae spend in the water column would be further constrained. For a larval phase of 18 d, potential dispersal mechanisms would be limited to continuous swimming at 18 cm s^{-1} or diurnal swimming (18 cm s^{-1}) with 2% wind-induced transport.

Several general insights concerning the mechanisms of larval recruitment can be generated from the simulations of the trajectory model. First, several authors have hypothesized that fourth stage larval swimming may be an important behavioral trait for selecting suitable benthic habitats during colonization (Ennis 1986b, Hudon et al. 1986, Cobb et al. 1989). Our field evidence and model imply that directional swimming could also be a key mechanism for long distance regional lobster larval dispersal. Second, increases in larval phase duration or reductions in larval swimming speed as a result of environmental factors (e.g. poor nutrition, cooler water temperatures) would increase the significance of wind-induced transport. The mosaic of transport mechanisms affecting successful larval dispersal to coastal habitats, therefore, could vary depending on the yearly fluctuations of biological and physical conditions. Lastly, the migrations of mature adults between coastal and offshore habitats provides another mechanism of population interdependency. Inshore migrations from the outer continental shelf during the spring (Cooper & Uzmann 1971) could lead to the direct transfer of eggs by benthic adult transport, or young could be released at some intermediate distance on the continental shelf to augment hydrodynamic and behavioral dispersal processes.

The overall conclusions from our field evidence and dispersal model pose important implications for the regional population dynamics and management of *Homarus americanus*. If lobsters in the canyons act as regional donors of larvae larval, then these recruitment subsidies would tend to buffer local coastal populations from over-exploitation. Conversely, if the offshore populations are heavily harvested and recruitment subsidies are diminished, then regional reductions in the lobster population would become more likely. Our future endeavors will be to experimentally evaluate the mechanisms of larval dispersal on the northeast continental shelf, and attempt to ascertain the percent contribution of larvae from offshore to coastal populations.

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