Spatial and temporal scales of patches of crab larvae in coastal waters

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ABSTRACT: This study examined the spatial and temporal scales of patches of crab larvae in the coastal waters of the Middle Atlantic Bight near the mouth of Delaware Bay, USA (38.70° N, 75° W). The spatial scale of the patches was characterized by sampling along-shelf and across-shelf transects via series of continuous plankton tows. Autocorrelation of larval densities along each transect revealed that patch diameters ranged from about 0.5 to 2.5 km in both along-shelf and across-shelf dimensions. The ages of 12 different patches were estimated by comparing the proportions of Stage I and Stage II larvae composing each patch. One additional patch was tagged with a satellite-tracked drifter, and changes in the proportions of the 2 stages were observed over a 3 d period. Analysis indicated that the tagged patch had remained cohesive for at least 4 d and possibly as long as 6 d. Potential mechanisms for patch formation and maintenance include synchronous spawning events, associative larval behavior, and aggregative physical processes.

KEY WORDS: Patch · Transport · Larvae · *Callinectes sapidus* · Delaware Bay

INTRODUCTION

Marine zooplankton are rarely distributed uniformly, but rather are found in discrete patches (e.g., Greene et al. 1994). Both physical and biological processes contribute to this heterogeneity. Physical processes that produce plankton patches on small spatial scales (10 to 10^2 m) include internal waves and Langmuir circulation (Franks 1997). Other factors such as tidal fronts and internal tidal bores are important in creating patches on medium scales (10^2 to 10^4 m), while large-scale patches ($>10^4$ m) have been attributed to features such as gyres, eddies and meanders (Pineda 1991, Thiébaut 1996). Biological processes also aid in the formation of patches. For example, factors such as vertical migration, synchronous spawning events, or interaction with prey organisms may be important in the formation of small- to medium-scale patches (Fortier & Leggett 1984, Ouellet & Lefaivre 1993, Ashjian et al. 1994).

Regardless of the mode of formation, patches do not remain stable through time, but instead undergo dispersion in response to physical processes (Thiébaut 1996). Experiments in the coastal ocean have shown that small-scale turbulence associated with horizontal current shear may reduce concentration gradients and homogenize patches of inanimate tracers on time scales of days to weeks (Franks 1997). Patches of zooplankton occurring in shelf waters are subject to similar mixing processes. Therefore, zooplankton patches in the coastal ocean are likely to disperse over time scales pertinent to horizontal transport.

While the physical and biological factors that control formation and dispersion of patches are reasonably well understood, there have been few actual measurements of patch dimensions in nature (Gallager et al. 1996). Moreover, there has been little success in following changes in these dimensions through time (Lee et al. 1992). This is particularly true for larval forms of marine fish and invertebrates, where an appreciation of patch dynamics is an essential component of the overall understanding of larval transport (Garvine et

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al. 1997). Measurement of patch size for larval forms has been limited to relatively few studies (e.g., Gallager et al. 1996, Thiébaut 1996), and efforts to track patches through time have been restricted primarily to ichthyoplankton (Fortier & Leggett 1985, Stabeno et al. 1996).

The species of particular interest in our investigation was the blue crab *Callinectes sapidus*. In the Middle Atlantic region of North America, blue crab larvae are released in summer and are quickly exported from the mouths of estuaries to the coastal ocean. Over a period of 3 to 6 wk, the larvae develop through 7 zoeal stages in surface waters of the inner continental shelf. This is followed by a single postlarval stage of 1 to 2 wk duration that eventually settles and undergoes metamorphosis in nursery habitat within the estuary (Epifanio 1995 and references therein).

Details of blue crab larval transport in the Middle Atlantic region have been described in recent conceptual and mathematical models (Epifanio 1995, Garvine et al. 1997). These models stipulate initial transport of zoeae southward along the inner continental shelf within the buoyant estuarine plume. Transport back toward the estuary is provided by a wind-driven band of water flowing northward along the mid-shelf. Across-shelf transport to estuarine settlement sites is accomplished by coastal Ekman circulation associated with discrete southward wind events.

Although transport of blue crab larvae is described well by the models outlined above, the distribution (10^2 to 10^4 m) of larvae on the continental shelf remains unknown. Field observations and model experiments indicate that settlement of postlarvae in estuarine habitats occurs as discrete pulses in time that follow some, yet not all, southward wind events (Jones & Epifanio 1995, Garvine et al. 1997). This suggests that the distribution of post-larvae and larvae in coastal waters is patchy in nature. However, the existence of temporal pulses in settlement provides only circumstantial evidence for the assumption of patchiness in space, and patches of crab larvae have never been documented in the field.

In this paper we describe results of a field investigation that was designed to determine the length scales of patches of blue crab larvae along and across the continental shelf adjacent to Delaware Bay, USA. In addition, we estimated time scales (duration) of patches by determining the most prevalent larval stages found in the patches and calculating the maximum period of patch cohesiveness assuming a 3 to 6 d duration for each stage. We examined temporal changes in proportions of different larval stages by tagging one patch with a satellite-tracked Lagrangian drifter and following the patch for 3 d.

MATERIALS AND METHODS

Study area. Our study was conducted in the southern Middle Atlantic Bight at the mouth of Delaware Bay (Fig. 1). Subtidal flow in this area is influenced by a buoyant plume emanating from the bay. The plume flows southward along the coast and counter to the prevailing northward winds that are typical of summer in the region. These winds result in an upwelling circulation along the coast and also produce northward surface flow just offshore of the plume (Garvine et al. 1997). Early autumn is characterized by an increased frequency of southward wind events. These events drive downwelling circulation that causes an increase in sea level along the coast, followed by barotropic flow into the bay (Münchow & Garvine 1993).

Spatial scale. Sampling was conducted from July to September 1998, during the spawning season of *Callinectes sapidus*. The spatial scale of larval patches was determined via series of plankton tows (0.5 m diameter nets, 253 μm mesh) performed from an 8 m boat. The volume of water filtered through the nets was derived from flowmeters (General Oceanics Model 2030) secured in the center of the net. Distance towed was determined with differential GPS (global positioning system). Sampling was always conducted in a 2 h period around high slack water. Thus, towing speed
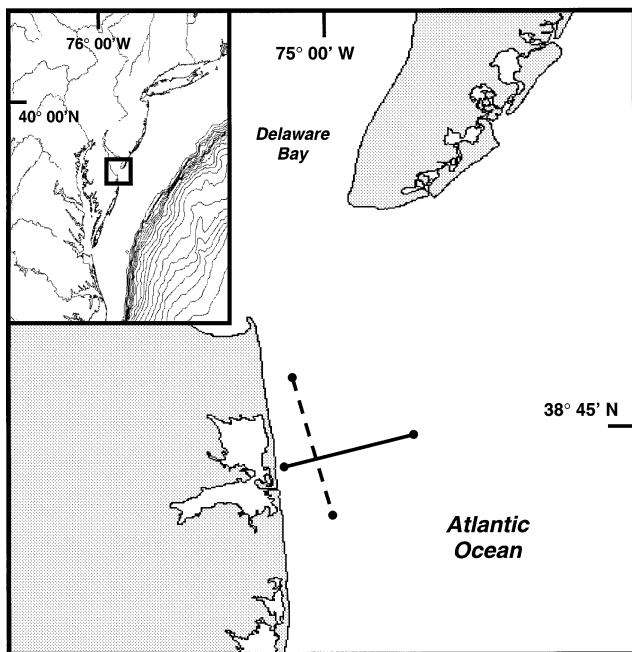

Fig. 1. Map of sampling area. Representative along-shelf (dashed line) and across-shelf (solid line) transects sampled in the summer of 1998. Inset: Middle Atlantic Bight, USA

was always much greater than the speed of tidal currents, and there was little displacement of water in relation to the sampling transects. Wind speed on sampling days was also generally low (<5 m s^{-1}), and therefore wind-driven surface currents were unlikely to affect the volume of water sampled with each tow.

Tows were taken along transects in both along-shelf and across-shelf directions (Fig. 1). Along-shelf transects were positioned parallel to the main channel of Delaware Bay. Across-shelf transects were perpendicular to the channel and always intersected the along-shelf transect. Because *Callinectes sapidus* larvae remain in the upper 2 m of the water column throughout development (Epifanio 1995 and references therein), surface tows were sufficient to determine spatial scales of the patches.

We conducted 2 types of sampling (*continuous* and *interval*) over the course of the study (Table 1). Individual tows were always 300 m in length and filtered about 35 m^3 of water. At the beginning of each tow, temperature and salinity were measured with a salinity-conductivity-temperature meter. Continuous sampling consisted of a series of tows wherein retrieval of one net always coincided with deployment of another. This method allowed a continuous record of larval density, but placed practical limitations on the length of each transect (maximum = 7.2 km). In contrast, interval sampling involved a series of 300 m tows taken at 800 m intervals. This allowed us to sample over a longer transect (maximum = 18.7 km), but required linear interpolation of larval densities across intervals. Overall, we sampled on 10 separate days. These consisted of 3 days during which we sampled in the along-shelf direction, 1 day on which we sampled in the across-shelf direction, 4 days during which we sampled in both along-shelf and across-shelf directions, and 2 days during which we sampled a tagged patch (see below).

Table 1. *Callinectes sapidus.* Dimensions of patches (m) of zoea larvae near the mouth of Delaware Bay, USA. Sampling method (continuous or interval) is described in the text. (–) Dimension was not sampled

Date (1998)	Method	Along-shelf dimension (m)	Across-shelf dimension (m)
13 Jul	Continuous	2000	–
15 Jul	Continuous	500	–
22 Jul	Continuous	–	1000
24 Jul	Continuous	1400	–
10 Aug	Continuous	2400	–
20 Aug	Continuous	1200	2200
21 Aug	Continuous	2200	1600
2 Sep	Interval	2000	2200
3 Sep	Interval	1600	1200

Samples were preserved and analyzed using standard techniques (Dittel & Epifanio 1982). Each sample was split 4 to 6 times using a Folsom plankton splitter, and 1 of the 16 to 64 resulting subsamples was selected randomly for analysis. Blue crab zoeae were separated from the rest of the plankton, staged, and counted (Sandifer 1972).

Temporal scale. Because transects were located near the blue crab spawning grounds in lower Delaware Bay, samples were always dominated by early-stage larvae. The age of a given patch was estimated by comparing the proportions of Stage I and Stage II zoeae in the samples. This approach was based on previous reports indicating that duration of each stage varies among individual larvae, but generally falls in the range of 3 to 6 d (Sulkin 1975, Epifanio 1995). Thus, a patch containing only Stage I larvae could have been as young as 1 d and as old as 6 d. Accordingly, patches containing high numbers of both Stage I and Stage II larvae were estimated to be 4 to 6 d old.

On one occasion (10 to 13 August) we were able to examine temporal changes in the proportion of larval stages in a patch, by deploying 4 satellite-tracked drifters (Horizon Marine, FHD/Holey Sock) while sampling an along-shelf transect. This was done by releasing a drifter during every 6th plankton tow, i.e., every 1800 m along the 7200 m transect. Samples from the drifter sites were analyzed immediately in the laboratory, where it was determined that 1 of the drifters had been deployed in a patch of Stage I larvae (density > 100 m^{-3}). This drifter was tracked by the Argos, a satellite system used for global data collection, and re-located with an automated radio-direction finder. Because of inclement weather, the area around the drifter was not sampled again until 13 August. By this time the patch had been transported approximately 25 km southward from its initial location. The second sampling was conducted along 2 orthogonal transects that crossed at the drifter. Each transect consisted of 6 contiguous 300 m tows centered on the drifter (Table 1). A 3rd sampling on 15 August determined that the drifter was no longer in the patch.

Statistical analysis of patch dimensions. We used autocorrelation analysis to determine patch dimensions in both the along-shelf and across-shelf directions (Chatfield 1984). In our analysis, observations of larval densities were correlated at successive lags (i.e., the distance between samples) of 300 m (continuous samples) or 800 m (interval samples). Autocorrelation coefficients were calculated for a total of 10 lags transect^{-1}.

We considered the point in space at which the larval densities first became decorrelated as the characteristic length scale of a patch (Rowe & Epifanio 1994). Decorrelation occurs when the value of the autocorrelation coefficient is not different from zero (Richerson

et al. 1977). In practice this is the point at which the value of the coefficient falls below the value of Bartlett's Standard Error (Box & Jenkins 1976). Bartlett's Standard Error is an estimate of the standard error of the autocorrelation function at each point in its

Table 2. *Callinectes sapidus*. Correlations of the respective abundances of Stage I and Stage II zoea larvae along transects spanning each patch. (–) No Stage II zoeae occurred within a patch. *p < 0.05, **p < 0.01

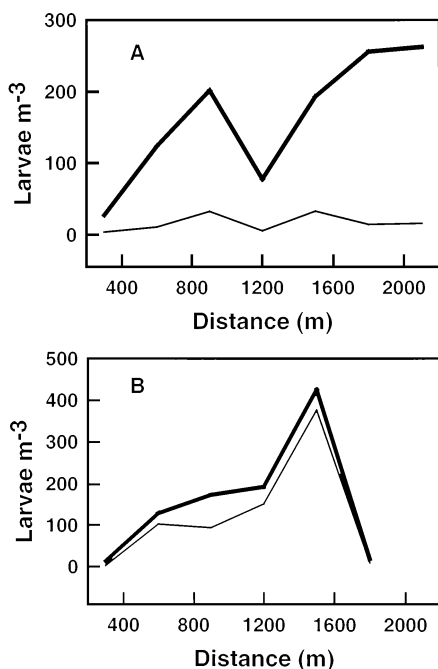| Date (1998)	Dimension	Correlation coefficient
13 Jul	Along-shelf	0.182
15 Jul	Along-shelf	0.737**
22 Jul	Across-shelf	–
24 Jul	Along-shelf	0.427*
10 Aug	Along-shelf	0.801**
13 Aug	Along-shelf	0.943**
13 Aug	Across-shelf	0.988**
20 Aug	Along-shelf	0.821**
20 Aug	Across-shelf	0.700**
21 Aug	Along-shelf	0.469*
21 Aug	Across-shelf	0.328
2 Sep	Along-shelf	0.422*
2 Sep	Across-shelf	0.926**
3 Sep	Along-shelf	0.847**
3 Sep	Across-shelf	0.809**

Fig. 2. *Callinectes sapidus*. Densities of Stage I (bold line) and Stage II (thin line) zoeae along a transect within a tagged patch. (A) 10 August 1998. Densities of the 2 stages are significantly correlated in space (R = 0.80, p < 0.01), but note the small percentage of Stage II. (B) 13 August 1998. Densities of the 2 stages are significantly correlated in space (R = 0.94, p < 0.01), but note the relatively high percentage of Stage II

domain. The characteristic length scale of a patch is half its linear dimension (Richerson et al. 1977). Hereafter, we characterize each patch by its entire along-shelf or across-shelf dimension, or twice the characteristic length scale.

We also ran simple correlations to determine the relationship between densities of Stage I and Stage II zoea larvae at the various sampling sites within a patch. Specifically, the spatial series of Stage I densities was correlated with the series of Stage II densities. We used the results of this analysis to support our estimates of patch age. For example, when there was a significant correlation between densities of Stage I and Stage II larvae within a patch (i.e., the relative proportions of the 2 stages remained constant within a patch), it was reasonable to conclude that all of the larvae were from the same spawning cohort, but that some individuals had already undergone a molt to the second stage. Because the duration of the 2 stages was known, it was then possible estimate the age of the patch (see above.)

RESULTS

Physical data suggested that patches of larvae were located mainly within the estuarine plume. The latter was indicated by warm surface temperatures and low salinities (~25°C, 30‰) that contrasted with the lower temperatures and higher salinities (~24°C, ~31‰) in adjacent shelf waters.

Results of autocorrelation analysis showed that dimensions of individual patches ranged from 500 to 2400 m in the along-shelf direction and 1000 to 2200 m in the across-shelf direction (Table 1).

There was a significant correlation between the densities of Stage I and Stage II zoeae in 12 of the 14 transects sampled, indicating that these patches had remained cohesive for 4 to 6 d (Table 2). The correlation between densities of sequential zoeal stages in the tagged patch provided additional evidence that patches remain cohesive through time (Fig. 2). On 10 August, the patch was dominated by Stage I larvae, with maximum density of ~300 m^{-3}. On 13 August the composition of the patch was split more evenly between Stage I and Stage II larvae. Moreover, there was a highly significant correlation (R = 0.988) between the densities of the 2 stages at the various sampling sites within the patch. This suggested that many of the Stage I zoeae in the initial sampling had since molted to Stage II and indicated that the age of the patch was between 4 and 6 d. Differences in overall abundance of larvae were probably due to the fact that we did not sample the exact same location in the patch on each of the sampling dates.

DISCUSSION

The results of our study show that early-stage blue crab larvae are distributed in discrete patches and that these patches are cohesive on a time scale of days to a week. The diameters of the patches ranged from 0.5 to 2.4 km. Because all samples in our investigation were dominated by Stage I zoeae, it is likely that patches were generated near the time of spawning. Patches of larval fish have been associated with large aggregations of spawning adults (Fortier & Leggett 1984), and this may be the mechanism that produced patches of crab larvae in our investigation (Provenzano et al. 1983). If the newly hatched larvae were released by aggregations of females within an area circumscribed by hundreds of meters to a few kilometers, they would have formed patches on the scales observed in this study. Patch diameters on the order of 10^3 to 10^4 m also correspond to the width of the main channel at the mouth of Delaware Bay, a feature that could concentrate newly released zoea larvae.

The length scales of the individual larval patches found in this study were nevertheless quite varied. Roman & Boicourt (1999) showed that upwelling-favorable (northward) winds spread the estuarine plume offshore, while downwelling-favorable winds condensed the plume. These processes may have affected the size of patches in our study; however, our data were insufficient to allow quantitative analysis of their effects.

The temporal scales determined in our study support existing models that postulate wind-driven transport of *Callinectes sapidus* larvae in the coastal ocean (Epifanio 1995, Garvine et al. 1997). Our results show that some patches remained cohesive for periods of at least 6 d, which constitutes nearly 30% of the entire period of zoeal development. This lends credence to the idea that the observed pattern of settlement in this species may result from across-shelf transport of discrete patches of postlarvae that have remained cohesive since spawning (Jones & Epifanio 1995).

There are a number of physical processes that promote the formation of patches in the coastal ocean. However, the spatial and temporal scales (km, days to weeks) of patches in this study more closely match the scales of dispersive processes (e.g., horizontal and vertical current shear and horizontal turbulence) This indicates that patches of larvae should disperse with time and implies that aggregative physical processes are insufficient to maintain patch integrity. Because blue crab larvae maintain a surface distribution throughout development, we can also discount diel vertical migration as a possible mechanism for maintenance of patches. However, horizontal swimming that results in swarming of the larvae is a possibility.

Associative behavior that assists in maintenance of patches is a common subject in the literature dealing with fish larvae (e.g., Davis & Olla 1995, Stabeno et al. 1996), but has received little attention among invertebrate species. Indeed, the literature dealing with transport of crustacean larvae is almost entirely devoted to swimming in the vertical plane (Sulkin et al. 1980, Tankersley & Forward 1994). Only the work of Harvey & Epifanio (1997) suggests horizontal swimming in response to pressure waves generated by co-occurring zooplankton, but that investigation did not include any direct measurements of larval behavior, and the implication of horizontal swimming is based solely on inference drawn from prey-selection experiments.

Regardless of uncertainties concerning the maintenance of patches, our study has provided clear evidence concerning their spatial scale in the coastal ocean. Our data indicate that patches form at the time of hatching and remain cohesive through the first 2 zoeal stages, in spite of a generally dispersive physical environment. Evidence from earlier studies suggests that the postlarval form of *Callinectes sapidus* is also distributed in discrete aggregations (Jones & Epifanio 1995, van Montfrans et al. 1995). It is unclear whether the intervening zoeal stages are distributed in patches or whether some physical process (e.g., Beardsley et al. 1996, Epstein & Beardsley 2001) results in aggregation of postlarvae as they return to the estuary.

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