

Dispersal of an introduced larval cohort in a coastal lagoon

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Abstract

Patterns of larval dispersal influence the structure of marine biological communities, but many aspects of larval dispersal remain poorly understood. For example, much of our present understanding of larval dispersal is based on models that integrate aspects of physical oceanography and larval biology, but the predictions of those models are generally not tested because we lack the methodology for real-time larval tracking. In the present study, we used both modeled and measured data to track an introduced larval cohort essentially from fertilization to presumed settlement. Larvae of the hard clam *Mercenaria* were released into a labeled water parcel in the Banana River Lagoon, Florida, within 8.5 h of nursery production and then were tracked for the duration of their estimated 8-d pelagic life span. Comparisons of modeled versus measured larval distribution indicate that the fate of the larvae as predicted by a tracer model and by the concentration of coincidentally released sulfur hexafluoride (SF_6) did not agree with the fate of the larvae as predicted by the path of subsurface drifters and by a particle trajectory model. Thus, modeled predictions of larval dispersal must be interpreted with care. Additionally, one component of larval dispersal that was observed in the study but that was not accounted for in the model was the spread of larvae along the path of advection. That trail of larvae may have important consequences for patterns of recruitment and resultant community structure, but it is not considered in most treatments of larval dispersal.

The life history and dispersal of marine invertebrate larvae has long been a focal point for marine ecologists (Young 1990) because of the essential role that larvae play in the maintenance of many marine invertebrate populations (Grosberg and Levitan 1992). Larval dispersal influences the structure and connectivity of marine benthic communities

(Gaines and Roughgarden 1985; Warner and Cowen 2002), contributes to the success of marine fisheries (Bakun 1996), and influences the genetic mosaic underlying benthic marine species (Scheltema 1971). Thus, increased knowledge of larval life history and associated dispersal and recruitment processes is a necessary precursor to a fuller theoretical and practical understanding of marine biological processes.

Currently, ecologists are integrating the physical (Tremblay et al. 1994) and behavioral (Metaxas 2001) processes that influence larval dispersal in an effort to better understand and ultimately predict recruitment in marine invertebrate populations. Because of the inherent methodological difficulty associated with field studies of larval dispersal, much of our present understanding of dispersal has been developed from genetic (Palumbi 1995) or oceanographic (Largier 2003) models. Results from those studies indicate that the potential dispersal distance of most pelagic larvae is substantial (e.g., Scheltema 1971) but that local retention is a common outcome (Lundquist et al. 2004). Those conclusions are equivocal because, in the case of genetic studies, the input of very few propagules is sufficient to maintain

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genetic homogeneity, and in the case of modeling studies, it is difficult to account for larval behavior. Inclusion of a behavioral term in larval dispersal models is complicated by observational data that indicate that some (Baker and Mann 2003) but not all (Shanks et al. 2002) larvae exhibit an influential behavioral component, and in some cases, the larvae of a single species may exhibit a variety of behavioral patterns depending on the dynamic physical characteristics of the ambient environment (Rawlinson et al. 2004).

One impediment to successful characterization of larval dispersal has been the inability to follow larval cohorts from spawning through settlement (Levin 1990). Researchers have been able to track relatively large larvae (e.g., Olson 1985) or unusually distinctive patches of larvae (Willis and Oliver 1990), but such situations are not representative of most larval dispersal scenarios. For most broadcast spawning invertebrates, including many economically important species (Thorson 1950), the fate of a larval cohort is unknown. Field studies have sampled larval cohorts (Millar 1961) but generally have been unable to provide information concerning the origin or exact age of those cohorts (e.g., Wood and Hargis 1971; Shanks et al. 2002). Clearly, better knowledge of the in situ life history of marine invertebrate larvae would improve our understanding of the mechanisms that influence larval dispersal, would enhance our ability to model and predict recruitment, and would assist in clarifying interconnections among local or isolated populations.

Many ecologically and economically important invertebrate species reside in coastal estuaries and lagoons whose circulations are characterized by long residence times (Carriker 1961). The physical processes that control larval distribution in such settings include short spatial (10s of km) and temporal (days to weeks) scales. A good example is provided by species of hard clams of the genus *Mercenaria*, which inhabit coastal lagoons and estuaries along the eastern and Gulf of Mexico coasts of the United States. Hard clams are dioecious and release eggs that depend on external fertilization to initiate embryogenesis. Despite the ecological importance of *Mercenaria*, few studies of in vivo larval life history exist (Fegley 2001). Carriker (1961) estimated larval life span to be approximately 8 d during summer in Little Egg Harbor, New Jersey. A similar larval life span is reported for hatchery-reared clam larvae in the Indian River Lagoon (IRL; Leeming pers. comm.), where *Mercenaria* supports an important commercial fishery. Two species of hard clam (*Mercenaria mercenaria* and *Mercenaria campechiensis*) occur in the IRL system and they hybridize extensively (Bert and Arnold 1995). The two species and their hybrid forms are morphologically indistinguishable even in a hatchery setting, hence, our use of the generic *Mercenaria* to describe the animals that we worked with in this study. In the vertical dimension, early-stage *Mercenaria* larvae are often uniformly distributed at night and concentrated near the surface during the day, whereas late-stage larvae concentrate near the bottom (Carriker 1961). Competence to settle occurs as a visually distinctive foot develops at a shell length of approximately 200 μm (Carriker 2001). Spawning of hard clams in the IRL is almost continuous but has a springtime maximum (Hesselman et al. 1989).

The hard clam is an ideal organism for the study of larval

dynamics because of its ecological and economic importance, the wealth of available information concerning its basic biology, and the ease with which adult clams can be induced to spawn and the resultant larvae reared. Here, we use an integrated multidisciplinary approach to map the daily distribution of clam larvae in a coastal lagoon. To achieve this goal, we released a cohort of larvae into a labeled water mass and tracked both the larvae and the water parcel into which they were released. We then mapped our results to determine whether the larvae remained faithful to the labeled water parcel. Finally, we compared our empirical results with the output from a physical oceanographic model to assess how well the model predicted the dispersal pattern of the larvae and the labeled water parcel.

Materials and methods

Study location—The IRL (Fig. 1) is a system of bar-built lagoons along the east-central coast of Florida that experience little exchange with coastal waters. Such lagoon ecosystems are common but understudied coastal systems worldwide (Kjerfve 1994). The Banana River portion of the IRL, where our study was conducted, is microtidal (Smith 1987) and the flow is predominately wind driven (Smith 1983). The study site comprised an area of approximately 2.5 km². Average water depth was about 1.5 m and maximum water depth was <4 m. Although hard clams do occur in the Banana River, adults and juveniles have been absent from the study area in recent years (Arnold et al. 1997), and sampling during previous and subsequent studies (Arnold unpub. data) found no naturally occurring clam larvae or adults.

Clam spawning and release—On 16 May 2000, we spawned approximately 550 million hard clam eggs and a sufficient amount of sperm to ensure fertilization of all eggs. Spawning occurred in three batches beginning at 1200 h (Daylight Savings Time) and ending at 1600 h. After they were fertilized, the clam eggs were pooled in a seawater bath (salinity = 28) and distributed among nine 20-liter bags for transport to the study site. Each bag was then infused with O₂ to ensure an adequate supply of oxygen during transit. Transport from the hatchery (1800 h departure) to the Banana River release site (2030 h release) required approximately 2.5 h, so the embryos ranged in age from 4.5 to 8.5 h at the time of release. The water in which the larvae were transported from the hatchery to the release site was maintained at a temperature of 26°C and a salinity of 28, whereas water temperature at the release site (Fig. 1) was 28°C and salinity was 22.

Prior to larval release five noninstrumented CODE (Coastal Ocean Dynamics Experiment) subsurface drifters (Davis 1985) were deployed, with one at each corner of a square and one in the center, to track advective transport. The starting position for each drifter was recorded using a differential Geographic Positioning System (d-GPS). Within the box defined by the drifters, and also prior to larval release, approximately 1200 ml (at standard temperature and pressure) of the inert gas sulfur hexafluoride (SF₆) was bubbled into the water column approximately 0.5 m below the surface to

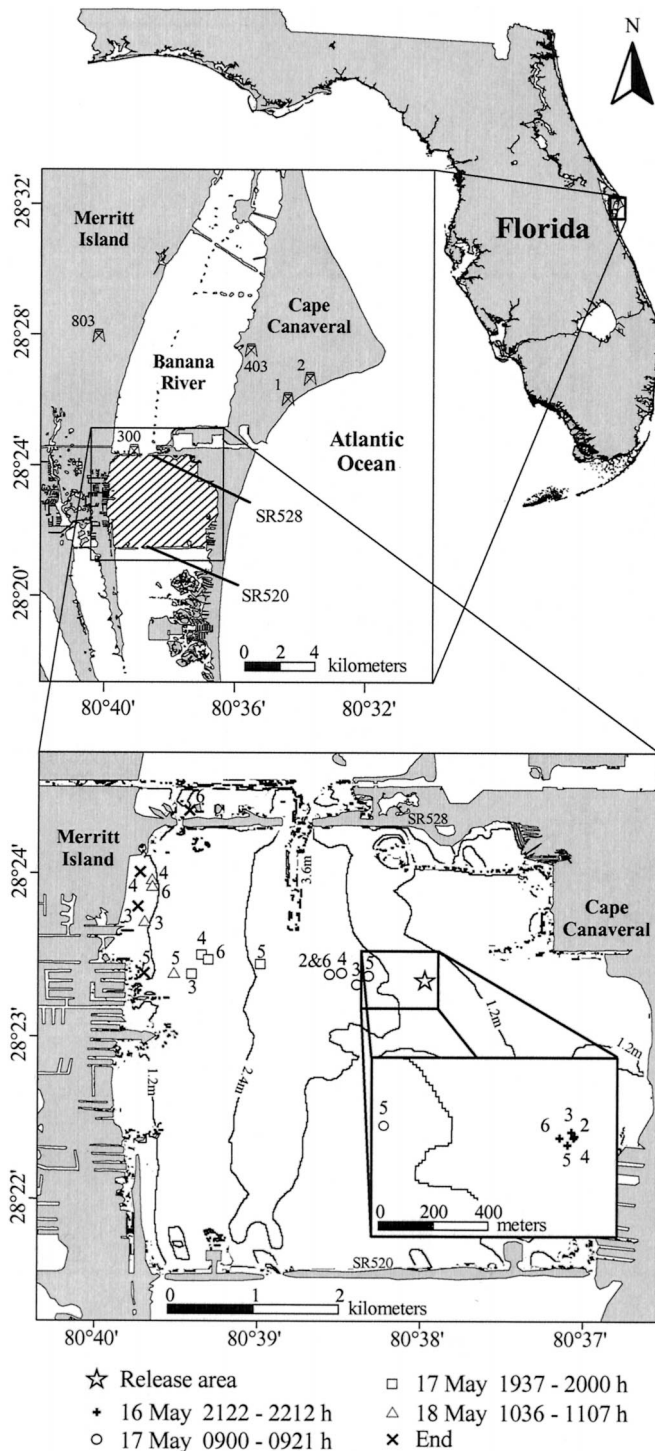


Fig. 1. Location of the study site (hatched area) in the Banana River Lagoon on the east-central coast of Florida, USA. The upper inset shows the State Road (SR) 520 (south), SR 528 (north), Merritt Island (west), and Atlantic Ocean coastal barrier island (east) boundaries of the study basin. Also included are the locations of meteorological towers 1, 2, 300, 403, and 803, from which wind data were obtained. The lower inset shows the path of the subsurface drifters. The expanded box provides better resolution of the release location for each individual drifter. Drifters were released at approximately 2030 h Daylight Savings Time on 16 May 2000, and their location recorded according to the schedule listed below the

track diffusive transport. The clam larvae were gradually acclimated within the holding containers and then released into the center of the drifter array approximately 0.5 m below the water surface.

Field sampling—During 17–24 May 2000, we used two small research vessels powered by outboard motors as platforms from which to track and sample the water parcel and associated larvae. To allow for efficient and contemporaneous sampling, one research vessel was devoted primarily to collecting samples for analysis of larval concentration and the other vessel was devoted primarily to collecting samples for SF_6 analysis. To track the water parcel during the early phase of the study, the subsurface drifters were visually relocated and the d-GPS position of each drifter recorded. Sample collection locations for hard clam larvae and for SF_6 were then determined based on the location and distribution of the drifters. Later in the study, in response to stranding of the drifters and the spread of the water parcel and associated larvae, a gridded sampling domain was initiated across the basin. Hard clam larval samples were obtained by collecting various volumes of water, which ranged in size from 150 to 282 liters (Table 1), depending on the projected density of larvae, using a Jabsco Model 34600-0000 diaphragm pump. To minimize disturbance by the research vessels to the sampled water parcel and associated larvae, each vessel was allowed to drift downwind at least 10 m from the anchor point prior to deploying the sample collection apparatus. Samples for larval analysis were then collected by drawing subsurface water (0.5-m depth) through a 300- μm -mesh sieve to remove large debris and then capturing the larvae in a 63- μm -mesh plankton net. Those mesh sizes encompass the size range of larval hard clams from spawned egg (Bricelj and Malouf 1980) through setting pediveliger (Loosanoff et al. 1951). The resultant samples were removed from the cod end of the plankton net and carefully concentrated to a volume of approximately 30 ml, transferred to a 50-ml screw-cap centrifuge tube, labeled, and frozen on ice for return to the laboratory and storage in an ultracold (-80°C) freezer.

Within 1 month of the completion of the study, frozen water samples were transported to the Skidaway Institute of Oceanography, where the presence of clam larvae in each sample was quantified. Clam larvae were quantified by direct deoxyribonucleic acid hybridization using a previously developed 18S ribosomal ribonucleic acid targeted oligonucleotide probe specific for *Mercenaria*. Larval quantification was accomplished essentially as previously described (Frischer et al. 2000), except that the oligonucleotide probe was labeled with ^{32}P [phosphorous]. The sequence of the *Mercenaria*-specific oligonucleotide probe used in this study (Mm-699) was 5' CAA GGG ACG GTA CGC CGG. This approach to identifying and quantifying bivalve larvae allows the discrimination of bivalve larvae even during their

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inset. Note that drifters 2 and 6 came in contact on the morning of 17 May, so drifter 2 was retrieved. Solid lines represent bathymetry in 1.2-m intervals.

Table 1. Date, location (decimal degrees), estimated number of larvae detected, volume of water collected, and number of larvae per sample liter for all stations at which larvae were collected during the course of the 16–24 May 2000 larval tracking study in the Banana River Lagoon, Florida.

Date	Station	Latitude	Longitude	No. of larvae	Volume sampled (liter)	Larvae L ⁻¹
16 May	release	28 23.318	80 37.964	550 million	N/A	N/A
17 May	14	28 23.374	80 39.014	368	282	1.3
19 May	5	28 23.368	80 39.288	280	150	1.9
19 May	9	28 22.909	80 39.288	1,238	150	8.3
20 May	11	28 22.905	80 38.182	838	150	5.6
20 May	15	28 22.430	80 38.733	907	150	6.0
20 May	23	28 21.964	80 37.071	729	150	4.9
21 May	1	28 23.849	80 39.289	1,015	150	6.8
21 May	6	28 23.380	80 38.740	952	150	6.3
21 May	10	28 22.893	80 38.723	1,178	150	7.9
21 May	15	28 22.428	80 38.744	603	150	4.0
21 May	16	28 22.432	80 38.188	973	150	6.5
21 May	18	28 22.433	80 37.080	570	150	3.8
21 May	19	28 21.988	80 39.290	597	150	4.0
21 May	24	28 24.367	80 39.519	820	150	5.5
21 May	27	28 24.381	80 38.773	1,459	150	9.7
21 May	29	28 24.204	80 39.297	301	150	2.0
21 May	30	28 24.191	80 38.729	428	150	2.9
21 May	32	28 23.845	80 39.695	417	150	2.8
22 May	1	28 23.844	80 39.289	513	150	3.4
22 May	5	28 23.375	80 39.268	693	150	4.6
22 May	6	28 23.353	80 38.753	937	150	6.2
22 May	9	28 22.917	80 39.294	489	150	3.3
22 May	17	28 22.440	80 37.603	479	150	3.2
22 May	19	28 21.973	80 39.267	416	150	2.8
22 May	20	28 21.997	80 38.742	387	150	2.6
23 May	3	28 23.839	80 38.167	675	150	4.5
23 May	4	28 23.857	80 38.019	705	150	4.7
23 May	5	28 23.364	80 39.272	1,094	150	7.3
23 May	6	28 23.362	80 38.729	259	150	1.7
23 May	7	28 23.367	80 38.177	346	150	2.3
23 May	8	28 23.372	80 37.702	280	150	1.9
23 May	9	28 22.892	80 39.286	660	150	4.4
23 May	10	28 22.895	80 38.736	413	150	2.8
23 May	15	28 22.436	80 38.730	248	150	1.7
23 May	19	28 21.952	80 39.277	266	150	1.8
23 May	24	28 24.355	80 39.502	922	150	6.1
23 May	29	28 24.204	80 39.280	1,109	150	7.4
23 May	30	28 24.184	80 38.709	603	150	4.0
24 May	17	28 22.436	80 37.627	531	150	3.5
24 May	22	28 21.970	80 37.596	633	150	4.2
24 May	23	28 21.957	80 37.063	1,154	150	7.7
24 May	24	28 24.357	80 39.509	307	150	2.0
24 May	29	28 24.224	80 39.309	518	150	3.5
24 May	30	28 24.193	80 38.736	592	150	3.9
24 May	31	28 24.188	80 38.204	242	150	1.6

earliest stages and is capable of detecting a single larva in a plankton sample (Frischer et al. 2000). Although it was possible to detect a single clam larva using the Mm-669 hybridization probe, actual detection sensitivity (i.e., larvae per liter) is a function of the initial volume of water collected and the amount of the resulting nucleic acid extract immobilized onto the hybridization membrane (Frischer et al.

2000). In this study, detection limits were estimated to be one larva in 30–40 liters of water (0.025–0.033 larvae L⁻¹) depending on the initial volume of water sampled (Table 1).

Samples for SF₆ analysis were collected by drawing subsurface water (0.5-m depth) into glass syringes at each station, ensuring that no air bubbles remained within the syringe. Syringes were stored under cooled lagoonal water to

prevent outgassing from the syringe or bubble formation within the syringe. Packaged syringes were transported to the Atlantic Oceanographic and Meteorological Laboratory in Miami, Florida, for analysis according to the procedures of Wanninkhof et al. (1991). All SF₆ samples were analyzed within 48 h of collection.

Modeled transport—To compare our empirically derived dispersal data with modeled dispersal, we employed a previously developed circulation and transport model (CH3D; Sheng 1989) and a Lagrangian particle-trajectory model (Sheng and Welter 1995). The numerical simulation was conducted with a $477 \times 43 \times 4$ curvilinear grid for the entire IRL, giving a horizontal grid with 50–500-m resolution and a time step of 60 s. Within the Banana River Lagoon, there was a total of 2,553 (111×23) horizontal grid cells, giving an average resolution of 400×400 m. For the simulated tracer dispersal calculation, a much finer horizontal numerical grid with 63,825 (555×115) grid cells (50 × 50-m resolution) was used for the Banana River to minimize numerical diffusion and better represent the bathymetry and geometry. Vertical turbulent mixing was calculated using a robust turbulence closure model (Sheng and Villaret 1989), while horizontal turbulence was calculated with an eddy coefficient that depends on local grid spacing and horizontal current speeds (Smagorinsky 1963). The particle trajectory model used the calculated flow field for advection but calculated the turbulent diffusion based on the random-walk method.

For the larval tracking simulation, CH3D was used to hindcast circulation in the Banana River portion of the IRL system. For that simulation, we used averaged wind data collected at five stations and provided by the National Weather Service (Fig. 1) and water levels determined at several tidal inlets (Ponce, Sebastian, Ft. Pierce, St. Lucie) by using a tidal prediction model (Foreman 1996). The three-dimensional advection–diffusion equation, which is part of the CH3D model, simultaneously calculated the simulated dispersal of the tracer and associated water parcel. The simulated flow fields were stored every hour and later used as input for the Lagrangian particle-tracking model. To calibrate the model, information on the ambient wind and tidal field during the prior 24–48 h was used to estimate the advection and diffusion of a hypothetical water parcel given the starting location of interest. In our case, the starting location was the point of deployment of the drifters, SF₆, and larval cohort, and the model was run daily from the time of release through 24 May 2000. Simulated tracer dispersal is presented as an average of the output acquired between 0800 h and 1700 h each day, concurrent with our daily field-sampling efforts.

Results

During the first day following larval release, the drifters were transported toward the west until they approached the western shore of the lagoon (Fig. 1). At approximately 0900 h on 17 May, we found that drifters 2 and 6 were in contact with one another, so we retrieved drifter 2 to minimize any confounding effects of this contact. We located the four re-

maining drifters between 1937 h and 2000 h on 17 May, at which time they were approaching the western shore and appeared to be turning to the north. Drifter 5 was trailing the other drifters by approximately 550 m, the most extreme example of a tendency for the drifters to become strung out along the main axis of movement. The following morning between 1036 h and 1107 h, drifters 3, 4, and 6 were moving to the north, but drifter 5 remained almost directly west of the release point. By the afternoon of 18 May, drifters 3, 4, and 5 had run aground and were stranded. Drifter 6 passed through a small bridge at the western end of the State Road (SR) 528 causeway and entered a separate basin, at which time the drifter was retrieved.

The modeled advection predicted a path similar to that observed for the drifters for the time period during which the drifters were in the water (Fig. 2A,B). However, the rate of advective drift predicted from the model was slower than the observed rate of movement of most of the drifters. The extent of the modeled advective path at 2100 h on 17 May (Fig. 2A) remained east of most of the drifter coordinates recorded at approximately 2000 h on that date, although drifter 5 was located within 600 m of the predicted position. The following morning, the location of drifter 5 remained relatively near the position predicted by the advective model (Fig. 2B), but the remaining drifters were located north-northwest of the predicted location at that time. By the evening of 18 May, all four drifters had become stranded so the temporal relationship between their location and the predicted location could not be determined, although the pathways were similar.

Although the drifters became stranded and were retrieved on the afternoon of 18 May, the predictive model was continued for the duration of the study. Modeled output for the entire study is depicted on a daily basis in the appropriate panels of Figs. 2 and 3. The modeled pathway became confined within the northwest corner of the basin on 19 May (Fig. 2C) and remained in that position on 20 May (Fig. 2D). The model indicated advective movement directly to the east along the southern shore of the SR 528 causeway on 21 May (Fig. 3A), then after a brief excursion through the main span of that causeway early on 22 May, movement directly south along the deep north–south axis of the basin on 22 May (Fig. 3B). During the evening of 22 May and throughout 23 May (Fig. 3C), the predicted advective pathway was confined to the center of the basin. The model predicted advective movement to the east on 24 May (Fig. 3D), with the final predicted position being almost directly south of the 16 May release point.

On the first day following release, the SF₆-labeled water parcel expanded in a diffusive manner around the original point of release but showed little advective movement (Fig. 2A). Modeled tracer dispersal also predicted that diffusive rather than advective processes were dominant on 17 May, although a small displacement to the northwest was observed. The distribution of SF₆ on 18 May suggests that the water parcel was advected to the northwest and stretched along a northwest–southeast axis, but diffusive processes still appear to have predominated (Fig. 2B). The model also predicted diffusion along a northwest–southeast axis, although the core of the modeled tracer remained near, or

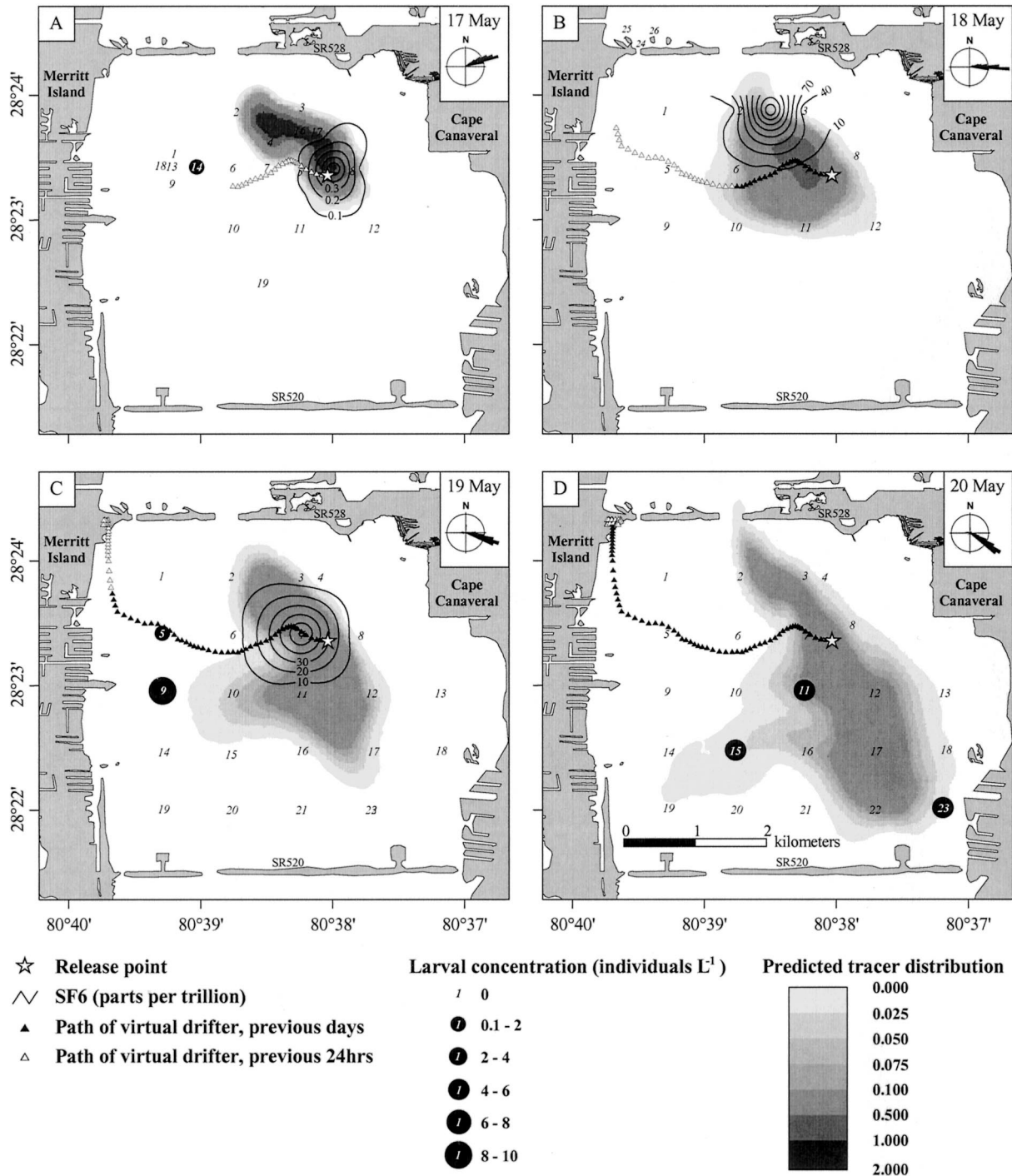


Fig. 2. (A) Location of larval sampling stations (italicized numbers) and estimated larval density (filled circle) of a hard clam (*Mer-
 cenaria* spp.) larval cohort in the Banana River Lagoon, Florida, on 17 May 2000. The size of the filled circle is positively proportional
 to larval density, and the station number is included within the circle. Open triangles represent the modeled hourly advective pathway
 beginning at 2100 h on 16 May and continuing for 24 h. Solid contour lines, derived using the inverse distance weighted method, represent
 17 May 2000 distribution of sulfur hexafluoride (SF₆), in parts per trillion, relative to the original release point. The contour cloud represents
 estimated tracer concentration calculated from the CH3D physical oceanographic model (see text for details). A 24-h wind rose is included
 as an inset in the upper right-hand corner. (B) Results from 18 May 2000. The legend follows from Fig. 2A with the exception that no
 larvae were recovered on 18 May so there are no filled circles. Open triangles represent the modeled hourly advective pathway beginning
 at 2100 h on 17 May and continuing for 24 h. Filled triangles represent the modeled hourly advective pathway for previous days. (C)
 Results from 19 May 2000. The legend follows from Fig. 2B. Filled circles represent the estimated larval density. The size of each filled
 circle is positively proportional to larval density, and the station number is included within the circle. Open triangles represent the modeled
 hourly advective pathway beginning at 2100 h on 18 May and continuing for 24 h. (D) Results from 20 May 2000. The legend follows
 from Fig. 2C with the exception that we did not sample for SF₆ on 20 May. Open triangles represent the modeled hourly advective pathway
 beginning at 2100 h on 19 May and continuing for 24 h.

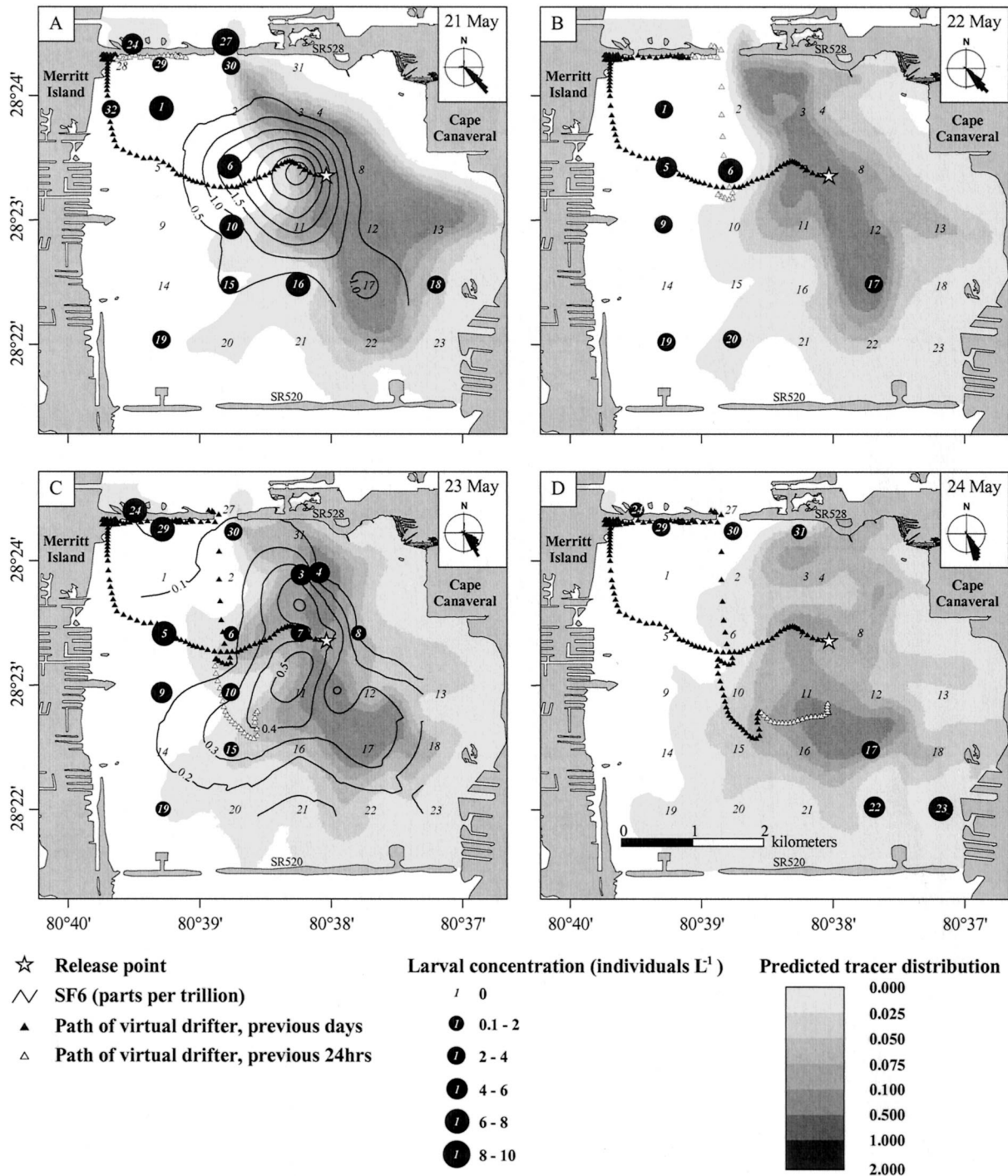


Fig. 3. (A) Results from 21 May 2000. The legend follows from Fig. 2C. Open triangles represent the modeled hourly advective pathway beginning at 2100 h on 20 May and continuing for 24 h. (B) Results from 22 May 2000. The legend follows from Fig. 2C with the exception that we did not sample for SF₆ on 22 May. Open triangles represent the modeled hourly advective pathway beginning at 2100 h on 21 May and continuing for 24 h. (C) Results from 23 May 2000. The legend follows from Fig. 2C. Open triangles represent the modeled hourly advective pathway beginning at 2100 h on 22 May and continuing for 24 h. (D) Results from 24 May 2000. The legend follows from Fig. 2C with the exception that we did not sample for SF₆ on 24 May. Open triangles represent the modeled hourly advective pathway beginning at 2100 h on 23 May and continuing for 24 h.

Table 2. Pertinent meteorological data for each full day of the 16–24 May 2000 larval tracking study in the Banana River Lagoon, Florida. Wind direction and speed data are averaged from data collected at five wind towers depicted in the inset of Fig. 1. Additional meteorological data were obtained from reports provided by Orlando International Airport, approximately 50 km west of the study site. PC, partly cloudy.

Date	17 May	18 May	19 May	20 May	21 May	22 May	23 May	24 May
Wind direction (°)								
Mean	67.5	89.8	104.8	121.3	132.4	137.8	134.5	153.4
Standard deviation (SD)	8.7	5.9	13.6	10.7	13.7	7.0	22.6	10.3
Min	0	58	0	0	0	108	0	0
Max	351	167	174	310	322	253	342	329
Wind speed (m s ⁻¹)								
Mean	3.8	4.1	3.3	3.6	4.6	4.9	3.5	3.8
Standard deviation (SD)	1.7	2.0	1.5	2.0	2.3	2.6	2.1	2.0
Min	0	0	0	0	0	0.5	0	0
Max	8.2	9.3	6.7	9.3	10.3	11.8	9.8	10.3
Air temp max (°C)	30.6	31.7	32.8	32.0	33.3	33.3	33.3	35.6
Air temp min (°C)	18.3	17.2	16.7	14.0	14.4	17.8	18.3	20.0
Cloud cover	PC	PC	PC	Clear	PC	PC	PC	PC
Precipitation (cm)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Sea-level pressure (hPa)	1,020	1,022	1,022	1,019	1,018	1,015	1,014	1,014

slightly west of, the 16 May release point. On 19 May, we found SF₆ only within the vicinity of the release point (Fig. 2C). The model similarly predicted little advective movement but continued diffusion along the northwest–southeast axis. The model also revealed the first evidence of a low-density tongue of particles moving into the southwest corner of the basin. We did not sample for SF₆ on 20 May, but the modeled distribution continued to expand along the northwest–southeast axis with a modal distribution to the southeast of the original release point (Fig. 2D). Modeled distribution on 20 May also predicted the most distinct extension of tracer into the southwest corner of the basin. On 21 May, SF₆ was considerably more spread out with a pronounced stretching along a northwest–southeast axis (Fig. 3A). The SF₆ distribution also provided evidence of the extension of the labeled water parcel into the southwest corner. The distribution of modeled tracer on 21 May was maintained along the northwest–southeast axis, but a substantial eastward spread was observed. The prediction of a relatively high tracer concentration east of the central trough and a relatively low tracer concentration west of the central trough (with the exception of the tongue of particles extending into the southwest corner) remained consistent for the last 3 d of the study (Fig. 3B–D). We sampled SF₆ a final time on 23 May (Fig. 3C), and those results provide additional evidence that the labeled water parcel was concentrated in the eastern portion of the basin. However, both the measured and modeled tracer distribution revealed that the labeled water mass was breaking up into discrete patches. Patch development is particularly evident in the modeled distribution on 24 May (Fig. 3D).

The distribution of SF₆ and the modeled tracer distribution appear to have been mediated principally by diffusive processes, whereas the distribution of larvae appears to have been governed by advective processes. We detected larvae at only one station on 17 May (Table 1; Fig. 2A), but that

station was in direct line with the drifters and with the predicted advective pathway (Figs. 1, 2A). Larvae were not detected at any of the stations on 18 May (Fig. 2B), but larvae were detected at two sampling stations on 19 May (Fig. 2C), and both of those stations were located along the western shore of the study basin. This observation is consistent with the predominately westerly winds at that time and with the westward shoaling of the actual drifters observed the previous day. Larvae were collected at three stations on 20 May (Fig. 2D), two of which were located in the center of the basin and the third of which was located in the southeast corner of the basin. Larvae were collected at 12 stations throughout the study basin on 21 May (Fig. 3A). Peak larval abundance on 21 May was in the northwest corner of the basin, including on the north side of the SR 528 causeway, and along the deep central trough of the basin. On both 21 and 22 May (Fig. 3B), the majority of larvae were captured at stations located either along or to the west of the central trough, including the southwest corner of the basin. However, a small patch of clam larvae, first detected on 20 May but also sampled on 21 and 22 May, was located in the southeast corner of the basin. Although we sampled in the southeast corner of the basin on 23 May, a larval patch was not detected (Fig. 3C). Instead, larvae were concentrated in the northwest corner and along the western shoreline of the basin. By 24 May (Fig. 3D), we detected larvae only along the shore of the SR 528 causeway and in the southeast corner of the basin.

At the beginning of the study, wind was predominately from the east-northeast (Fig. 2A) but gradually rotated in a clockwise direction during the course of the study, eventually blowing from the south-southeast on 24 May (Fig. 3D). Both mean and maximum wind speeds were relatively consistent from day to day, generally averaging 3.3–4.9 m s⁻¹, with maximum speeds between 6.7 and 11.8 m s⁻¹ (Table 2). We experienced no rainfall or major meteorological

events (e.g., cold fronts, storms) during the course of the 8-d study. With the exception of 20 May, when skies were clear, the skies were partly cloudy each day.

Discussion

We were able to successfully track a cohort of introduced hard clam larvae and to map the resultant distribution of those larvae during their projected 8-d larval life span. We also mapped the daily distribution of the labeled water parcel within which the larvae were initially introduced, and we applied advective and dispersive components of a physical oceanographic model to predict the trajectory of virtual particles released at the same time and location as the larval cohort. Our results suggest that the fate of the larvae as predicted by the tracer model and as estimated by SF_6 concentration and the fate of the larvae as predicted by the drifters and the particle trajectory model did not agree. Both the SF_6 distribution and the modeled tracer dispersal primarily reflect diffusive processes. In contrast, larval distribution and the path of the drifters appear to be primarily advective, with diffusion of the larvae predominating only in the shallow margins of the basin.

IRL waters are not homogeneous but instead can be subdivided into three compartments from east to west. In the shallow eastern and western margins of each basin, water motion tends to be circular or nondirectional (Evink and Morgan 1981). Within the eastern and western compartments, and especially in waters <1 m deep, diffusive properties are predominant and advection plays a minor role in the movement of particles (Carter and Okubo 1965). In contrast, water in the deeper central portion of the basin is characterized by relatively stronger uniform flow along the long axis of the lagoon, reflecting the funnel effect of the causeways and bridges (Evink and Morgan 1981). It is in the deeper central compartment that vertically stratified counter-current flow is strongest (Smith et al. 1987) and advective processes predominate (Carter and Okubo 1965). Despite the lack of vertical structure in the lagoon, evidence does support vertical shear (Evink and Morgan 1981). That vertical gradient in currents along the central axis of the basin may result in differential horizontal transport of particles, such as clam larvae, even though the distribution of conservative water properties (e.g., salinity) may not reflect vertical stratification because of rapid turbulent diffusion between vertical layers (Carter and Okubo 1965).

Bivalve larvae are not transported as a conservative property (Baker and Mann 2003). Hard clam larvae can swim up at a rate of at least 7–8 cm min⁻¹ (Turner and George 1955). Clam larvae congregate near the surface during the first 24 h after fertilization (Turner and George 1955; Carriker 2001) but have a relatively even vertical distribution during the straight-hinged and early umbral stages, especially at night (Carriker 1961, 2001). Late umbral larvae show a more positive geotactic response as they progress toward the pediveliger stage and settlement (Carriker 2001). In the horizontal dimension, at least partially as a result of their vertical swimming characteristics, larval distribution can be very patchy. A population of embryonic larvae may be tightly

constrained, but patches form as the veliger stage is achieved. It is probable that the larval cohort that we introduced was poorly sampled during the first 2 d of the study because the cohort was tightly constrained and only one (day 1) or none (day 2) of our sampling stations fell within the domain of the larval patch.

With some exceptions, most of the locations where larvae were detected coincided with the trajectory of the drifters and the predicted advective pathway. Both the drifters and the larvae moved west during the early stage of the study, but larvae were also found along the central axis and in the southeast corner of the basin as the study progressed. Later in the study, especially on 21, 22, and 23 May, some larvae were sampled in the southwest corner of the basin. That location differed from the predicted advective path but was consistent with spread of the SF_6 and with the modeled tracer dispersal. Most notably on 23 May, but beginning as early as 19 May, a patch of increased tracer density spread west from the main body of the labeled water parcel. That pattern appears to reflect the SR 520 causeway constraining flow (and some associated larvae) from north to south along the central basin and inducing spread toward the eastern and western margins of the basin. At least in the southern portion of the basin, spread of larvae into shallow nearshore waters appears from our model and sampling results to have switched from a primarily advective to a primarily diffusive process consistent with the findings of Carter and Okubo (1965).

The larvae did not move through the basin as a coherent patch but rather as a trail of larvae along the primary path of advection. The drifters spread out in a similar formation along the axis of their movement during transit. Many days after the leading edge of the larval cohort had passed a particular point, we continued to sample larvae at that point. For example, although the leading edge of the larvae reached the southern end of the basin on 20 May, larvae continued to be sampled in the northwest corner of the basin and along the SR 528 causeway as late as 24 May. As a result, larvae were dispersed throughout the basin in response to advection of a patch, diffusion from that patch, and as expatriate larvae left behind as the larval cohort progressed.

As noted by Janzen and Wong (1998), the shallow nature of coastal lagoons does not eliminate the importance of either physical or biological processes in the vertical dimension. Vertical distributional patterns of larval hard clams (Carriker 1961) and other marine invertebrate larvae (e.g., DiBacco et al. 2001) generally reveal a broad spread of larvae throughout the vertical water column. Even in shallow and apparently well-mixed coastal lagoons such as the IRL, larvae at different levels in the water column will be exposed to different transport processes (Smith et al. 1987). In our study, that differential transport may contribute to the trail of larvae that marked the path of advection. As noted by DiBacco et al. (2001), both retention and transport have advantages, depending on the life history of the organism. Our results suggest that the individual members of a hard clam larval cohort may be differentially influenced by dispersive versus retentive processes. Similarly, both the measured and modeled results of DiBacco et al. (2001) suggest that a single cohort of brachyuran larvae was also influenced by both

dispersive and retentive processes. In that study, DiBacco et al. (2001) showed that most *Pachygrapsus crassipes* larvae were exported from a San Diego estuary but that some portion of them were retained. The temporally varying success of dispersive and retentive processes will be an important determinant of long-term population maintenance.

In the microtidal IRL, advective processes exert a primary influence on the pattern of dispersal of a larval cohort, but diffusive processes also play a prominent role. Diffusive spread of a larval cohort may be advantageous because it serves to provide the larvae with access to a greater diversity of habitats, thereby increasing the likelihood that suitable settlement sites will be encountered. Particularly for long-lived marine organisms such as the hard clam, diffusive spread may be essential for the maintenance of the species within physically dynamic coastal estuaries and lagoons. This is because the distribution pattern of suitable habitats may change during the lifetime of the organism. Diffusive spread increases the likelihood that suitable habitats will be encountered if they exist (Strathmann et al. 2002) and, particularly in shallow nearshore and coastal habitats, may be a more important component of the larval dispersal process than has previously been recognized (Largier 2003).

Our research approach provides a novel method for determining the fate of a larval cohort. Previous studies have tracked larval cohorts (e.g., Jorgensen 1981), but those studies involved tracking of opportunistically discovered larval cohorts. The age and origin of the cohort were not known. Other studies have released large numbers of larval mimics (e.g., Levin 1983), although the faithfulness with which those mimics reflect the actual trajectory of larvae is not known. By releasing a larval cohort within hours of fertilization and tracking the cohort until it approaches the settlement phase, we have been able to follow the cohort throughout its projected larval life span (Carriker 1961; Leeming pers. comm.), thereby providing a comprehensive summary of the fate of that cohort.

Tracking an introduced larval cohort does have some disadvantages, but these may be less severe than intuition might suggest. For example, we are unsure how well our release of 550 million larvae mimics a natural spawning event. At high densities, hard clams can produce vast numbers of fertilized embryos, especially considering that the average clam might release a minimum of 1 million eggs during a single spawn (Bricelj and Malouf 1980). However, especially at low population densities representative of the hard clam population of the Banana River Lagoon during 2000 (Arnold et al. 1997), the percentage of released eggs that are actually fertilized may be 10% or less (Levitan 1995). Thus, 550 million fertilized embryos equate to a natural spawn from 500 to 5,000 mature female clams assuming 1–10% fertilization success and an average of 1 million eggs produced per female. Considering a 1:1 ratio of males to females in the Indian River clam population (Hesselman et al. 1989), the total contribution equates to 1,000–10,000 mature clams. Even at a population density of 1 clam m^{-2} , that constitutes an area of up to 10,000 m^2 supporting a contemporaneous spawn. Clam densities in the IRL were much less than 1 m^{-2} during the late 1990s, so our estimate of the equivalent concentration of spawners may be an overestimate. Specifically

for the IRL, it is also possible that our tracking efforts were confounded by the potential inclusion of two species of hard clam and hybrids of those two species in the cohort that we released. Behavioral differences between those groups may have contributed to the dispersion patterns recorded during our study.

In summary, our understanding of larval dispersal continues to be incomplete despite several decades of research (Young 1990). This report describes a methodology and initial results in the study of in situ life history characteristics of an intentionally released cohort of marine invertebrate larvae. Our results indicate that such in situ studies will be necessary to unravel the complex influence of physical (Largier 2003) and behavioral (Metaxas 2001) processes on the fate of larval cohorts. As we better define and quantify those processes, we will then be able to incorporate that information into models that more accurately predict the fate of pelagically dispersing larvae.

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