

## Direct evidence of a biophysical retention mechanism for coral reef fish larvae

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### Abstract

We examine the hypothesis that reef fish larvae have some direct influence on their own dispersal and ability to recruit to their natal reef by tracking cohorts of bicolor damselfish (*Stegastes partitus*) from hatching to settlement onto the reef, about 30 d later. We conducted high-resolution sampling during two consecutive years in a small area (15 km × 20 km) off the west coast of Barbados, extending from depths of 0 to 100 m. Observations of discrete stage-specific larval patches of mean size of 29.4 and 13.2 km<sup>2</sup> for preflexion (1–5-d old) and flexion/postflexion (>5-d old) stages extending ca. 30 m in the vertical indicated that larvae initially dispersing as patches tend to stay in coherent patches throughout their pelagic duration. Highest concentrations of preflexion larvae within a patch were in the upper 20 m, while those of older larvae were always deeper. Downward migration of about 60 m throughout ontogeny within stratified currents represented a retention mechanism for locally spawned larvae. Most of the variability in estimated retention rates between daily cohorts occurred during the earliest stages as a result of the dynamic nature of surface currents experienced by larvae prior to the onset of vertical migration. Differences in residence time between experiments were consistent with observed intermonthly variability in recruitment strength, implying that pelagic processes can explain recruitment rates. These results provide empirical evidence for larval retention of coral reef fishes and stress the role of active behavior in larval transport.

The early life history of many marine benthic organisms includes pelagic larvae, which may act as agents of dispersal and gene flow. Previous larval and molecular studies suggest that long-distance dispersal of marine larvae is a common event over evolutionary time scales, leading to considerable genetic population connectivity among distant populations (Thorson 1950; Scheltema 1986). However, over ecological time scales, recruitment of fish larvae to adult populations often depends on local retention (Schultz and Cowen 1994; Doherty et al. 1995; Shaw et al. 1999), and models indicate that long-distance transport over hundreds of kilometers is likely insufficient to sustain marine populations (Cowen et al. 2000, 2003). Further, it has been suggested that some larvae may have evolved behaviors that allow them to exert control over their transport and reduce dispersal away from their natal reef and facilitate self-recruitment (Cowen and Castro 1994; Schultz and Cowen 1994; Bakun 1996). Larval behavioral capabilities could indeed create a wide variety of biophysical interactions.

Large-scale circulation patterns tend to disperse larval fishes, while small-scale processes and interactions of currents with the bathymetry may concentrate larvae locally and limit horizontal diffusion and advection (Black et al. 1990; Limouzy-Paris et al. 1997; Reiss et al. 2000). In the case of island circulation, processes limiting advection away from the island include trapped eddies and other island-mass ef-

fects such as topographically steered currents (Boden 1952; Sanders 1981; Boehlert et al. 1992). Because physical processes act throughout the larval life history of coral reef fishes, they have the potential to influence a range of behaviors, including the strategy and timing of adult spawning (Parrish et al. 1981; Hugget et al. 2003), the timing of settlement and metamorphosis to juvenile stages (Victor 1984; Sponaugle and Cowen 1994), as well as diel migrations and vertical preferences during larval ontogeny (Leis 1986). Vertical migrations can be used to move between vertically stratified water masses or currents. Including the effect of such active behavior in models of larval transport seems critical to fully explain observations (Werner et al. 2001; Hugget et al. 2003). However, active behavior is rarely incorporated in larval transport models because of lack of direct behavioral observations.

Consistent larval distribution patterns may reflect behaviors that are adapted to circulation features occurring in a wide variety of pelagic environments, thereby facilitating return to the natal habitat (Cowen and Castro 1994; Cowen 2002). Likewise, species living in a variable environment may have evolved abilities to quickly change their behavior or adopt one among several possibilities (Bakun 1996).

While adaptive behaviors during the pelagic phase are linked to transport processes, the environmental factors sampled rarely include direct (e.g., Boehlert and Mundy 1993) or even indirect current measurements (e.g., Moser and Pomeranz 1999), or are often not measured concurrently with and at the same scales as the biological processes (Rodríguez et al. 2001), limiting the interpretation of biophysical interactions. Studies that have demonstrated patterns of larval distribution have not adequately resolved the spatiotemporal scales to reveal a cause-effect relationship or to develop a process-oriented explanation of local retention. To date, there are no direct data demonstrating the importance of biological response, if any, in the effectiveness of physical processes in retaining or returning offspring. To observe such bio-

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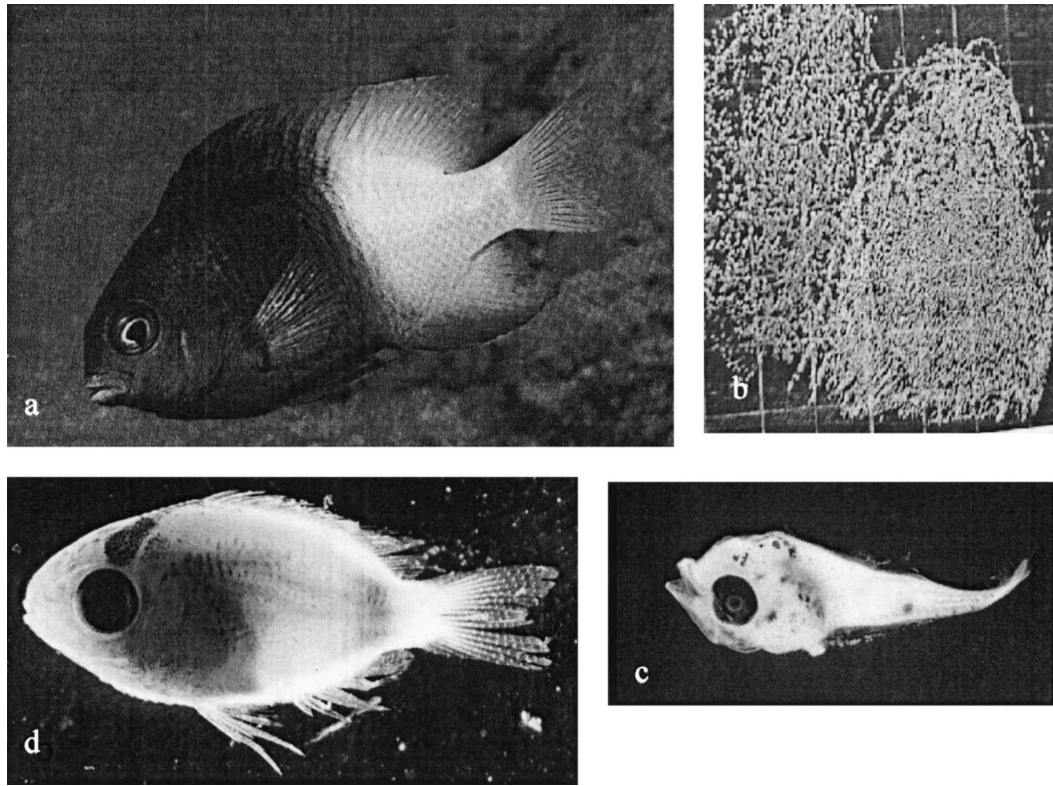


Fig. 1. Bipartite life cycle of the bicolor damselfish, *S. partitus*: The benthic phase includes the (a) adult stage (~60 mm SL), and (b) the egg clutches; while the pelagic phase is illustrated by (c) an early preflexion stage larva (2.3 mm SL) and (d) a late postflexion stage larva (11.5 mm SL).

physical interactions, it is necessary to investigate pelagic processes throughout the entire pelagic larval duration (PLD) of specific larvae. Frequent and simultaneous measurements of current fields and distributions of larvae until they are competent to settle should help explain in situ larval behavior.

In this paper we examine the hypothesis that retention of early life stages of coral reef fishes near their natal reef (sensu Sinclair 1988, i.e., the ability of species with a pelagic phase to maintain self-sustained populations within a particular geographic space) is a consequence of the influence that larvae exert over their dispersal through behavior-related mechanisms. This was achieved by direct observations of biophysical interactions using high-resolution spatiotemporal measurements of currents and larval patches in the vicinity of Barbados, West Indies. The rationale for selecting an isolated island, east of the Lesser Antilles, was to minimize the likelihood of larval input from upstream sources.

Our main objective was to investigate the mechanism by which coral reef fish larvae may maximize their return to the settlement habitat of the natal population. For this purpose, we needed to determine the role of larval behavior in controlling dispersal and horizontal advection and its relationship to the island-scale flow patterns. We proceeded stepwise by (1) identifying a potential retention mechanism by describing the three-dimensional in situ distribution of larval patches within their pelagic environment throughout the course of the larval life, (2) constructing a larval transport

model based on in situ current data collected during the same period, (3) validating the model by tracking virtual larvae and comparing changes in their spatial distribution to observed in situ changes in larval distributions, and (4) using the model to test the biophysical retention mechanism identified through observations. Findings are discussed in the terms of the degree to which pelagic processes shape recruitment strength.

## Methods

*Study species and general sampling scheme*—A focal species, the bicolor damselfish *Stegastes partitus* (Poey) (Pomacentridae), was chosen to serve as a proxy for identifying general mechanisms in reef fish recruitment (Fig. 1). This species is one of the most ubiquitous inhabitants of coral reefs in the western central Atlantic (Emery 1973), including Barbados (Butsh 1939). Typically the adult phase is associated with sparse cover coral substrates, rubble, and patch reefs in shallow waters. Female spawn demersal, single-layer egg clutches in nests guarded by males (Cole and Sadovy 1995). Peak spawning occurs during the third quarter and new moon at Barbados (Sponaugle and Cowen 1996a); the eggs hatch at night after a 4-d incubation period, and larvae are released directly from the reef where they enter the pelagic realm, at which point they quickly absorb their yolk sac (<12 h; Dorsey unpubl. data). The mean pelagic larval duration for *S. partitus* recruiting to Barbados is  $30.55 \pm$

0.58 d and ranges from 26 to 36 d (Sponaugle and Cowen 1996a). Our premise was to initiate sampling during the stage of the lunar cycle when peak hatching normally occurs based on simultaneous monitoring of the daily reproductive output (Dorsey and Cowen unpubl. data). In principle, this allowed us to track a monthly cohort of fishes throughout their pelagic larval stage.

*Study site and previous ichthyoplankton work*—Previous extensive plankton surveys around Barbados in 1990–1991 identified an area of high larval concentrations that was persistent in spite of the variable nature of the incident flow (Cowen and Castro 1994). Based on these previous findings, the experiments took place on the western shore of Barbados in the area of high larval concentration and were limited to an area of  $15 \times 20$  km (Fig. 2a). The island-scale flow at Barbados is dominated by a combination of large fluctuations in current direction (typically reversing twice every 20 d; Paris et al. 2002) and intrusions of low-salinity water entrained by North Brazil Current (NBC) rings originating from the Amazon (Kelly et al. 2000; Paris et al. 2002). External forcing by NBC rings is characterized by a strong signal on the local circulation (Paris et al. 2002), with a concomitant increased variability in local recruitment cycles (Sponaugle and Cowen 1996b).

*Biophysical sampling*—Integration of physical and biological processes was key to this study and was achieved by conducting a series of high-resolution, sequential hydrographic and planktonic surveys during two cruises on the R/V *Seward Johnson* carried in 1996 and 1997. Each cruise started in spring and lasted approximately 1 month (Table 1) and was timed to start near peak hatching (third quarter moon) of the bicolor damselfish.

The sampling protocol involved 3-d cycles of around-the-clock physical and biological measurements, continuously repeated for 27–29 d, except for two 1–2-d interruptions for port days. During day 1 of each sampling cycle (or 3-d survey), 26 conductivity–temperature–depth (CTD) casts typically covered the study area in 24 h, through an alongshore grid pattern (Fig. 2b). Along the ship track, a ship-mounted acoustic Doppler current profiler (ADCP; broad band 150 KHz) recorded velocity profiles (4-m vertical bin size, averaged every 4 min). During day 2, vertically discrete plankton samples were collected at 22 stations using a 1-m<sup>2</sup> multiple opening–closing net and environmental sensing system (MOCNESS) fitted with six nets of 333- $\mu$ m mesh. ADCP profiles continued to be recorded concurrently with MOCNESS tows. Sampling was carried out during 24 h (12-h day and 12-h night), covering the domain in a zigzag pattern (Fig. 2c). Each station was sampled with five nets at 20-m increments within the upper 100 m (net 1, 100–80; net 2, 80–60; net 3, 60–40; net 4, 40–20; net 5, 20–0 m), since few damselfish larvae were previously collected at depths greater than 100 m (Cowen and Castro 1994). Each net was towed at  $\sim 2$  knots in an oblique and upward fashion for 5 min in each stratum, resulting in a volume filtered of approximately 250 m<sup>3</sup> per net. During day 3, three to eight satellite-tracked, global positioning system drifters equipped with standard holey-sock drogues (1-m diameter, 10-m long)

were released offshore in clusters at various depths (2 m, 25 m, 50 m) and tracked within the study domain for up to 12 h to measure eddy diffusivity (*see* Paris et al. 2002 for drifter data). During day 3 of the 1997 cruise, a 10-m<sup>2</sup> MOCNESS fitted with five nets of 500- $\mu$ m mesh was used to capture late developmental stages (prior to settlement on the reef). For this purpose, the shoreward stations were sampled with four nets at 20-m increments within the upper 80 m during night hours. A total of eight sampling cycles (3-d survey) were conducted from 8 May to 3 June 1996, and the entire experiment was replicated from 29 April to 27 May 1997 (Table 1).

Ichthyoplankton were sorted from the samples and identified to the lowest taxonomic level in the laboratory. Substantial larval series of the Pomacentridae family allowed the identification of *S. partitus* (Paris-Limouzy 2001), which were separated in two groups according to their ontogenetic development. The first group of larvae was composed of preflexion stages (stage 1, ca. 1–5-d old) prior to the caudal fin development; the second group included flexion and postflexion stages (stage 2, ca. >5-d old), following Kendall et al. (1984). Larval densities in numbers per 1,000 m<sup>3</sup> of volume filtered were computed separately for these two groups to standardize catches and were designated as stage-specific densities.

Ontogenetic vertical migration was inferred from differences in the vertical distribution of larvae at the preflexion and postflexion stages and was used to model larval behavior. Larval patch coherence throughout ontogeny was explored by describing patch size including its vertical extent concurrently to the salinity and velocity fields. Larval patch shape is approximated to half an ellipsoid for the preflexion stages with highest densities at the surface and an ellipsoid for the postflexion stages where highest densities are deeper in the water column. The volume ( $V$ ) of an ellipsoid is measured by

$$V = 4\pi(a \times b \times c)/3$$

where  $a$  and  $b$  are the horizontal distances measured from the core of the patch to the mean density contour line in the north–south and east–west direction, respectively,  $c$  is the vertical extent of the patch estimated by the depth of penetration from the core.

*In situ larval fish transport (ISLAFIT)*—To reproduce the dynamic habitat of the larvae, in situ current velocities were reconstructed from multivariate objective analysis of the CTD and ADCP data (temperature, salinity, and total currents) and described in Paris et al. (2002). This optimal statistical technique was used to remove noise from scattered sampling and generated flow fields in a regular mesh ( $12 \times 12$  grid), integrated every 20 m on five horizontal planes (Fig. 2a). A total of eight, five-layer Eulerian maps of horizontal currents were produced for each sampling cycle. A 6-h time step was used to interpolate the currents between sampling cycles while the current from the last sampling cycle was maintained constant for 48 h, resulting in a continuous 30-d time series for each sampling experiment (1996 and 1997). Since oceanographic data were collected synoptically with ichthyoplankton, this 30-d coastal circulation

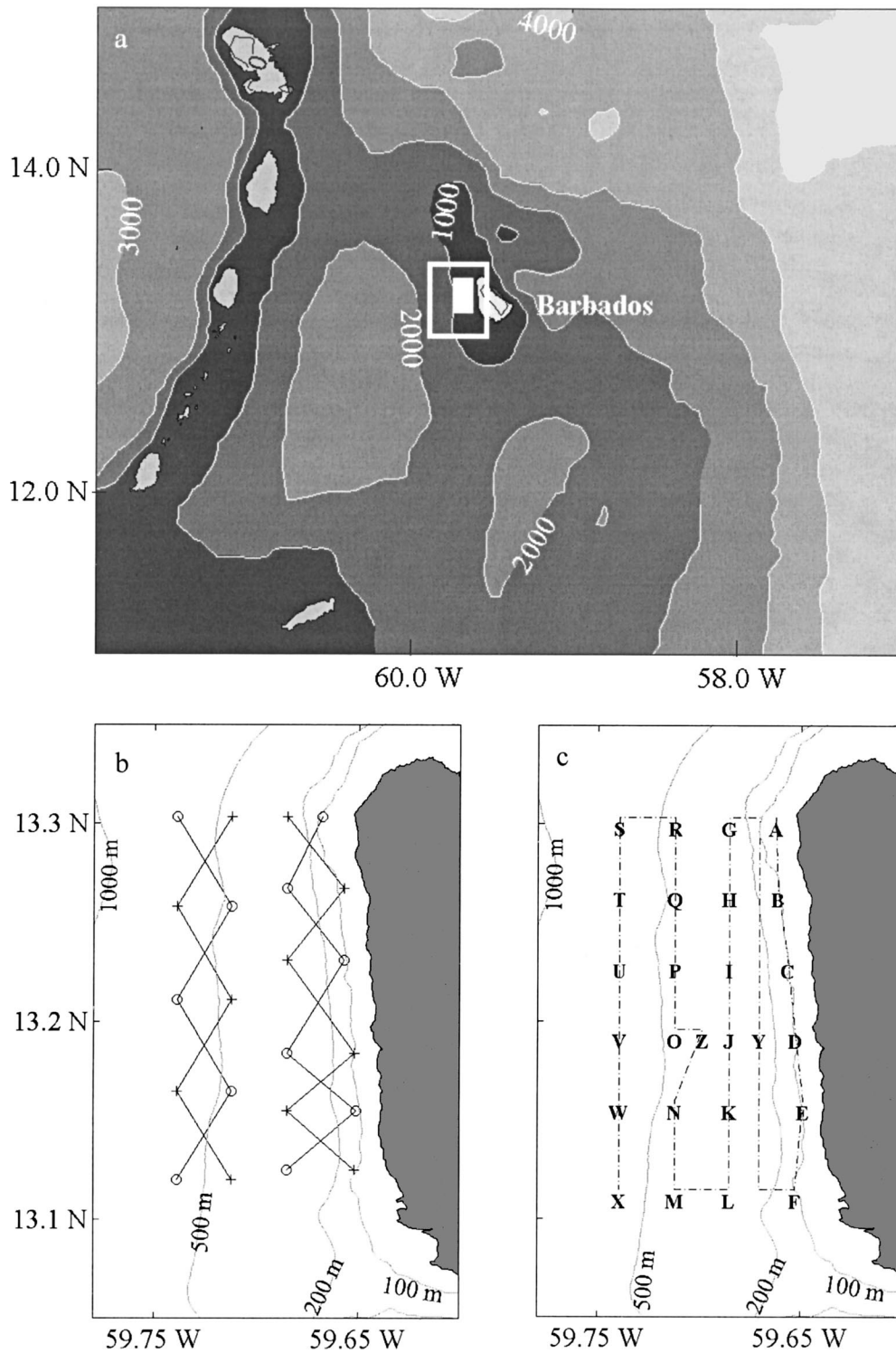


Fig. 2. Topography of the Lesser Antilles (depth in meters) in the vicinity of the island of Barbados, West Indies; (a) the study area (15 km × 20 km) is indicated by the white rectangle. Inserts indicated by the white frame in (a) illustrate (b) the biological sampling consisting of MOCNESS hauls during day (circle) and night (cross) stations and (c) the physical sampling consisting of CTD stations (letters) and ADCP track (dotted line).

Table 1. Schedule of biophysical sampling cycles for the 1996 and 1997 Barbados cruises. CT, conductivity-temperature recorder; ADCP, acoustic Doppler current profiler; MOC-1 and MOC-10, multiple opening-closing net and environmental sensing system (MOCNESS 1 m<sup>2</sup> and 10 m<sup>2</sup>).

Year	Sampling cycle (survey no.)	CT/ADCP	MOC-1	Drifters and MOC-10*
1996	1	8 May	9 May	13 May
	2	11 May	12 May	16 May
	3	14 May	15 May	18 May
	4	19 May	30 May	21 May
	5	22 May	23 May	24 May
	6	27 May	28 May	26 May
	7	30 May	31 May	29 May
	8	2 June	3 June	1 June
1997	1	30 April	1 May	29 April
	2	4 May	5 May	3 May
	3	7 May	8 May	9 May
	4	12 May	13 May	14 May
	5	15 May	16 May	18 May
	6	19 May	20 May	21 May
	7	22 May	23 May	24 May
	8	25 May	26 May	27 May

\* MOC-10 was only used during the 1997 cruise.

model operated at the same spatial and temporal scales as the biological processes and was used to track virtual larvae.

Larval advection in the horizontal plane was achieved via a Lagrangian stochastic technique following Dutkiewicz et al. (1993), by which horizontal diffusivity inherent to currents is modeled using a random-flight scheme. In summary, virtual larvae are moved by the deterministic velocity but are also allowed to diffuse against the mean velocity gradient through a random kick (or stochastic velocity), reproducing the small-scale eddy transport that is not well resolved by our deterministic flow field resolution or subgrid turbulent motion (Olson et al. 2001). This stochastic velocity is not totally random at each step. Rather, its evolution is assumed to be a first-order Markov process by which each time a particle moves through the flow field, it loses a fraction of its momentum to the surrounding fluid and in turn receives a random impulse from a Gaussian random number generator. The resulting stochastic (or turbulent) velocity is correlated to the previous value up to the Lagrangian time scale (or decorrelation time scale,  $T_L$ ). The stochastic displacement

of a particle in one dimension ( $x$ -axis) is then given by the following equations:

$$dx/dt = U + u' \quad (1)$$

The turbulent velocity is stationary so its mean  $\langle u' \rangle$  is constant with time and its evolution is given by

$$du' = -(u'/T_L) \times dt + R_G \times \langle u'^2 \rangle \quad (2)$$

The time parameters specified in Table 2 were at first estimated by computing the autocovariance function of the deterministic velocities and then adjusted by comparing trajectories of particles with floats (see Paris et al. 2002) and with observed displacements of larval patches (see Results section). In addition, the horizontal diffusivity coefficient ( $K_x$ ) resulting from this imposed stochastic movement was adjusted to match the horizontal eddy diffusivity characterized by the spatial scales prescribed by the Eulerian velocity grid size ( $L_x, L_y$ ; see Okubo 1971) and was estimated by

$$K_x \sim T_L \langle u'^2 \rangle \quad (3)$$

These parameters define the spatiotemporal scales at which the larval transport model is operating and are thus meaningful (Okubo 1994).

Boundary conditions prescribed a perfect reflection and no flux at the Barbados coastline (i.e., tracers cannot leave the box at the shoreline), while tracers may leave the domain at open boundaries. The biological component is introduced in the Lagrangian stochastic particle tracking code as vertical migration behavior, imposing sequential shifts in vertical distribution; this is achieved by displacing the distribution of particles or tracers from one 20-m horizontal flow field layer to the next. The onset of vertical migration behavior is initiated at flexion, which starts as early as 5 d after hatch for *S. partitus* (Paris-Limouzy 2001). At that stage, the gas bladder is already formed and active control by larva of this particular family is tangible (see Fisher et al. [2000] for development of critical swimming speed). Tracers are then moved into the next 20-m layer every 5-d until they reach the last layer (80–100 m).

Virtual larvae are introduced as tracers representing the horizontal density field of preflexion and postflexion larvae observed within the sampling area. They are also introduced as alongshore clusters of particles to simulate hatching events from the bank reef situated on the west coast of Barbados.

Qualitative validation was performed by comparing observed horizontal distribution of preflexion stages of *S. par-*

Table 2. Parameters used in the in situ larval fish transport (ISLAFIT) model.

	Random-flight turbulence		Lagrangian integration
$u'$	stochastic velocity	$U$	deterministic velocity
$\langle u'^2 \rangle$	variance of the stochastic velocity	$L_x, L_{xy}$	mesh size of the velocity grid in km = $1.1 \times 2.2$
$R_G$	Gaussian number generator with zero mean	$k$	number of layers = 5
$T_L$	decorrelation time scale of $u' = 2.5$ d	$dt$	deterministic time step = 6 s
$K_{x,y}$	horizontal diffusivity coefficient = $2 \times 10^4$ cm <sup>2</sup> s <sup>-1</sup>	$dt$	turbulent time step = 60 s

*titus* in the surface layer (0–20 m) with those of the model output. For this purpose, observed patches of early larvae (stage 1) were projected into the in situ larval transport model and tracked until the next sampling cycle (3–5-d interval), then compared to observed stage 1 *S. partitus* distributions.

**Retention rates**—Larval retention rates were calculated as a postprocess of the modeled larval tracking output from ISLAFIT with two main goals. First, retention rates were used to quantify the effect of active behavior (i.e., vertical migration) versus passive transport of reef fish larvae. Second, they were used to estimate the fate of hatching events observed on the western shore of Barbados by comparing the changes of modeled retention rates with the observed differences in settlement strength between experiments. Retention was defined as the daily percentage of tracers (or virtual larvae) remaining within the study area per 20-m strata or within the entire domain (0–100 m).

Water residence time in the sampling box was also calculated, and this was achieved by releasing a total of 15,000 tracers on a regular mesh of 30 locations across the 12 × 12 grid in each of the five horizontal layers. Model runs at those fixed depths are conducted for 20 consecutive days, and the distribution of residence times is represented as an average of all runs or as a maximum value among all runs. Residence times may be underestimated since tracers cannot be tracked for more than the length of each sampling experiment (e.g., if tracers are released on day 20, residence time cannot exceed 29 – 20 = 9 d). Water residence time indicates the passive role of the physical processes in limiting or enhancing dispersal.

To quantify the oceanographic component in transport variability between yearly cruises, daily hatching variability was homogenized by simulating alongshore hatching pulses every day for 20 consecutive days. This was accomplished by releasing simultaneously six patches of 1,000 tracers each along the coast. Releases were always initiated at the surface (0–20-m layer) and tracked until the end of the 29-d sampling period each year. Patch release was performed gradually throughout the first hatching day (1/4 of the tracers are released every 6-h for the 24-h period).

## Results

**Observed larval distribution**—Residual velocity profiles in the domain show vertical shear with surface (0–20 m) intensification to the northwest (offshore flow) and onshore flow at depth (20–100 m) in both years, with peak onshore flow at 25 m in 1996 and at 20 and 80 m in 1997 (Fig. 3a,c). In general, a vertical ontogenetic shift of larval densities from the upper layers to deeper layers was observed. While 50–60% stage 1 *S. partitus* larvae were located in the upper 20 m within the offshore flow region, most stage 2 are further down into the onshore flow region (Fig. 3b,d). The difference in larval vertical distributions between experiments, with deeper larvae in 1997, is due to gear selectivity rather than true difference. During the 1997 experiment, we also used a large net (10-m<sup>2</sup> opening) to capture older larval stages (>16-d old; unpubl. data) that were avoiding the small net (1-m<sup>2</sup> opening).

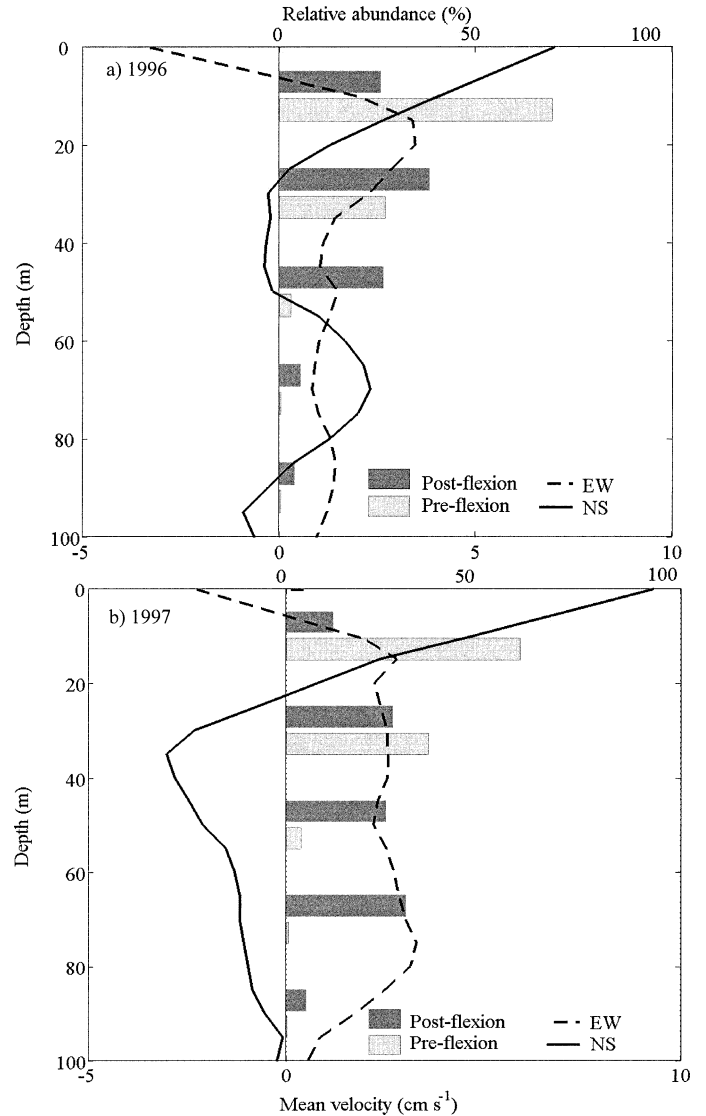


Fig. 3. Vertical structure of flow and fish larval abundance during (a) 8 May–3 June 1996 and (b) 30 April–27 May 1997. Vertical profile of residual ADCP velocities on the western shore of Barbados (surface values are estimated from drifters velocities); note the onshore (positive toward the east) flow at depth; vertical distribution of standardized catch of stage 1 and stage 2 larvae of *S. partitus* in 20-m depth bins derived from (a) 1-m<sup>2</sup> MOCNESS tows in 1996 and (b) from 1-m<sup>2</sup> and 10-m<sup>2</sup> MOCNESS tows in 1997.

Although stage 1 larvae were collected during all sampling cycles, there were fluctuations in the magnitude of post-hatching pulses, with peak densities in 1996. As expected by physical diffusion and natural mortality acting concurrently upon pelagic larvae, stage 2 larvae were less abundant and not confined to the coast (Fig. 4). For May 1996, in contrast to May 1997, high stage 1 densities were not matched in the following sampling cycle by high densities of stage 2, indicating high transport out of the study area during the 3–5-d interval.

**Larval patch dynamics**—The average shape of observed larval patches was slightly longer in the north–south along-

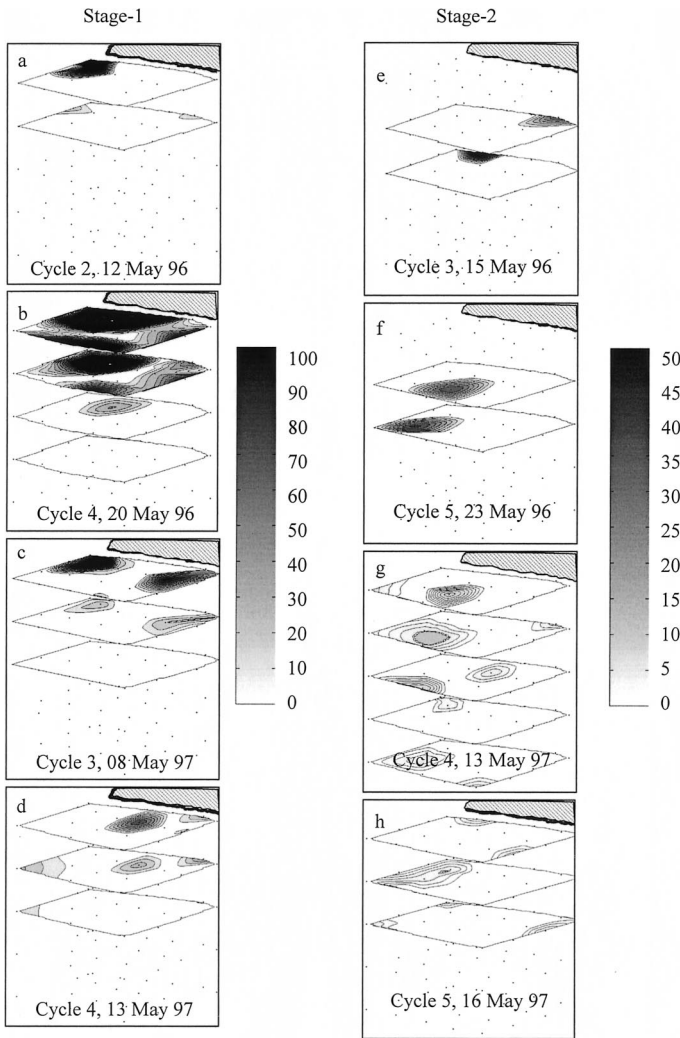


Fig. 4. Three-dimensional distribution of *S. partitus* larvae for the preflexion stages (stage 1 ~ 1–5 d after hatch [DAH]) during sampling cycles (a) 2, 12 May and (b) 4, 20 May of 1996, (c) 3, 8 May and (d) 4, 13 May of 1997, and 3–5 d later for the flexion and postflexion stages (stage 2 > 5 DAH) during sampling cycles (e) 3, 15 May and (f) 5, 23 May of 1996, (g) 4, 13 May and (h) 5, 16 May of 1997. Layers represent 20-m intervals from 0–100 m; contours of densities are in number of larvae per 1,000 m<sup>3</sup>; dots indicate sampling stations, and the bold line represents the western shore of Barbados.

shore direction of the prevailing currents (Table 3). Stage 2 larvae formed less distinct patches than stage 1 larvae, which is not surprising since this stage represents a greater mixing of cohorts. Mean patch density for stage 1 was 46 larvae per 1,000 m<sup>3</sup> and 10.2 larvae per 1,000 m<sup>3</sup> in the upper layer for 1996 and 1997, respectively, whereas for stage 2 it was 8.5 larvae per 1,000 m<sup>3</sup> and 3.7 larvae per 1,000 m<sup>3</sup> in the 20–40-m layer for 1996 and 1997, respectively. Patches of older larvae were consequently less dense and, on average, 44% smaller in size than those formed by early larvae, with an approximate surface area of 10.1 km<sup>2</sup> and 23.9 km<sup>2</sup>, respectively. In general, stage 1 larval patches were closer to shore with higher densities in the upper layer (0–20 m). At

Table 3. Spatial dimensions (mean length  $\pm$  SD) of larval patches of *Stegastes partitus* at the preflexion (stage 1), flexion, and postflexion (stage 2); distances are measured from density contour lines of 50 and 10 larvae per 1000 m<sup>3</sup> for stage 1 and stage 2, respectively, across the core of the patch. Note that the shape of stage 1 patch is half an ellipsoid that interfaces with the ocean surface, while that of stage 2 is an ellipsoid.

	North–South (km)	East–West (km)	Thickness (m)	Estimated volume (m <sup>3</sup> )
Stage 1 (n=10)	6.4 $\pm$ 1.1	4.6 $\pm$ 1.0	34.0 $\pm$ 13.5	518.4 $\times$ 10 <sup>6</sup>
Stage 2 (n=6)	5.5 $\pm$ 1.2	2.4 $\pm$ 0.4	30.0 $\pm$ 10.5	457.7 $\times$ 10 <sup>6</sup>

very high densities, their signature extended to the 40–60-m layer (Fig. 4b). Mean larval patch thicknesses were not significantly different between stages. Yet, stage 2 patches were found among all layers, with highest densities centered in deeper strata. Although some larval patches were found at flow convergences, additional analysis is necessary to clarify whether patch generation was due to passive accumulation of larvae rather than active aggregation.

In both experiments, NBC rings impinged on the island during survey 5 and persisted in the sampling domain throughout the rest of the surveys, disrupting the local circulation and bringing low-salinity water from the Amazon in the sampling domain (Paris et al. 2002). Despite the consistency in vertical position of stage-specific larval patches, during survey 6 of both years the core of stage 1 larval patches was no longer within the upper 20-m layer but in the 20–40-m stratum, confined within higher salinity (>35) than found at the surface (Fig 5). Coincidentally, stage 1 larval patches lost their ellipsoid structure and were spread unevenly throughout the domain during the following surveys. Stage 2 larval patches remained undisrupted after the low-salinity intrusion, yet they also were found deeper (Fig. 5).

*Comparison of predictions and observations: validation of ISLAFIT*—Large stage 1 larval patches observed during the first sampling cycle (survey 1) of 1996 were projected as tracers into ISLAFIT and tracked until the next sampling cycle (Fig. 6a,b). The two initial patches merged and moved onshore before translating alongshore, reaching the northern tip of the island by the end of the 4-d run; these tracers ended up in a similar configuration as the single larval patch of *S. partitus* observed during survey 2. This patch was further tracked into ISLAFIT and exited the domain before the next sampling cycle (survey 3); in fact, very low densities of stage 1 larvae were present during survey 3. Similarly in 1997, large stage 1 larval patches observed during the third sampling cycle (survey 3) were projected into ISLAFIT and tracked for 5 d until the next sampling cycle. By survey 4, a discrete and sparse larval patch was observed in the southern part of the domain (Fig. 6a, 1997), the location and spread of which were well predicted by the model output (Fig. 6b, 1997).

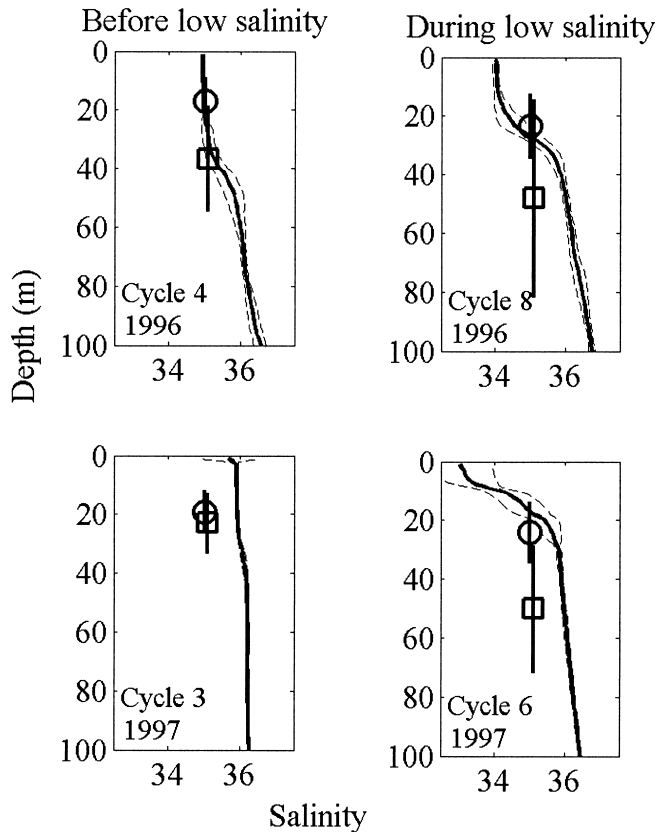


Fig. 5. Vertical profile of salinity (black line) and mean depth of center of mass for larval *S. partitus* stage 1 (circle) and stage 2 larvae (square) before and during the low-salinity event of 1996 and 1997. A total of 17–24 CTD casts and MOCNESS hauls was made during each survey; dotted lines and vertical bar represent 1 standard deviation around the mean salinity and mean depth of center of mass, respectively.

**Retention mechanism**—Residual currents in the sampling domain were vertically stratified (Fig. 3). Overall, they exhibited a strong shear in the upper 25 m with their meridional (east–west) component offshore at the surface and onshore at depth during both cruises. However, between-cruise variability was apparent in both direction and speed throughout the water column while vertical distributions of *S. partitus* were consistent among cruises. Preflexion larvae (stage 1) were predominantly located in the upper 40 m of the water column, with nearly 60% of their abundance near the surface (0–20 m) and within strong offshore currents. Older larvae (stage 2) were predominantly distributed within deeper layers, shifting their center of concentration downward into the onshore flow region. The consistency of larval distribution among stages and cruises typifies an ontogenetic vertical migration.

To examine the interaction of this ontogenetic shift with stratified currents, residence time of tracers released at the surface (0–20-m layer) was compared to that of tracers released in deeper layers (Fig. 7). In the 20–40-m layer, tracers were retained for about a week on average and had an onshore maximum residence time of more than 2 weeks. Deep-

er in the water column, retention increased and exceeded 20 d in the 60–80-m layer.

The effect of vertical migration on larval horizontal transport was further quantified by simulation of daily hatching near the coast and measuring cohort retention within the sampling domain. On average, for both years combined, 12%  $d^{-1}$  of the particles were flushed out during the first 5 d. Thereafter, the remaining tracers (ca. 25%) were retained at nearly 90%  $d^{-1}$  (Fig. 8). However, average retention rate did not represent the true picture. Among daily cohorts retention rates were highly variable ( $9.1\% < SD < 35\%$ ), indicating that some cohorts could quickly be flushed out while others could experience more favorable current conditions. At the onset of vertical migration, two groups of cohorts were prominent (Fig. 8, bottom panel). Essentially, one group of daily cohorts had a high retention rate as a consequence of current features that concentrate particles, even in the near surface layer. The second group of cohorts had a very low retention rate, but was still present in the domain at day 5. From then on, retention rates in both groups of cohorts increased substantially by downward migration.

**Recruitment variability**—Despite rather constant lunar cyclic egg production rates, the relative success of cohorts differed between years (Fig. 9). Lower recruitment from the May 1996 cohorts compared to that from May 1997 might have been due to less favorable current conditions. To examine the contribution of pelagic transport processes to the observed interannual variability, larval retention rates were compared using the flow conditions in May 1996 (low recruitment) with those of May 1997 (high recruitment). Before the onset of vertical migration, there was a significant difference in the retention rates between the two sampling experiments, with higher retention in 1997 (Fig. 10). Furthermore, the tracking of tracers simulating high hatching pulses observed in both sampling experiments (survey 1 of 1996, and survey 3 of 1997) revealed that while larval patches were denser in 1996 than in 1997, they were quickly dispersed (Fig. 11a). Conversely, the sparser hatching pulse of 8 May 1997 was retained in the domain until the end of the experiment (Fig. 11b). Essentially, during 1996, the six modeled larval patches were rapidly mixed and carried out of the domain by strong currents within 5 d, whereas in 1997 the patches converged and were retained nearshore for over 17 d. In both years, the modeled discrete hatching pulses merged in a single patch and translated alongshore, moving predominantly toward the northern tip of the island. These model outcomes were consistent with the horizontal distribution of larval patches when they concentrated in the northeast portion of the sampling box (Fig. 6) and with the finding of higher recruitment in 1997 by examination of time series of settlement of *S. partitus* on the western shore of Barbados (Fig. 9). During May of 1997, the residual onshore flow penetrated deeper while the zonal flow reversed from north to south at 25 m, leading to a more efficient retention mechanism (Fig. 3).

Variations in the flow field led to substantial differences in retention rates, manifested in the recruitment signal. The relative success of cohorts is further quantified by comparing residence times between years. During the 1996 experiment,

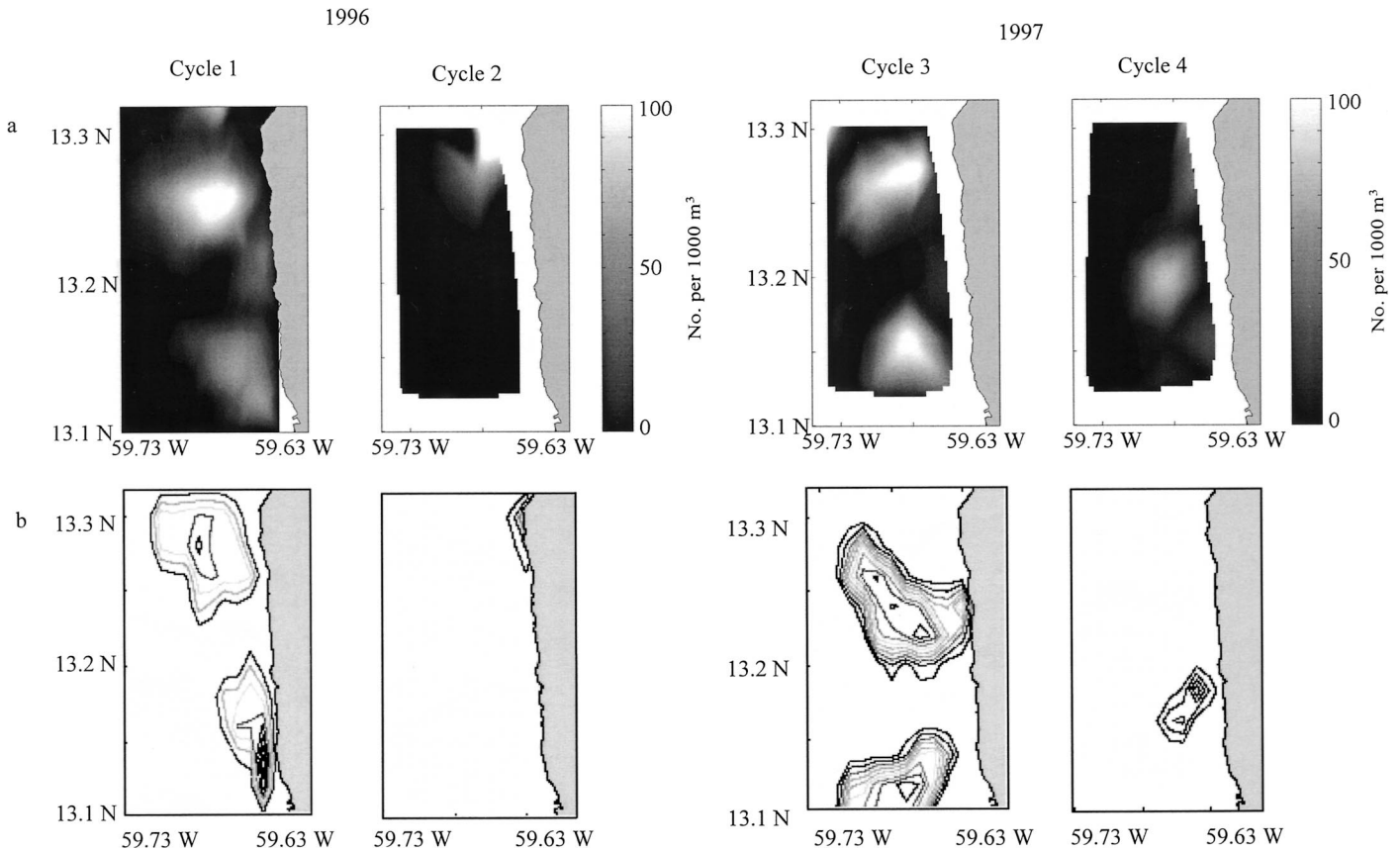


Fig. 6. Comparison of results from ichthyoplankton survey and ISLAFIT output. (a) Observed horizontal density distributions of early stage *S. partitus* larvae (no.  $10^{-3} \text{ m}^{-3}$ ) on 9 May (cycle 1) and 12 May (cycle 2) of 1996 and 8 May (cycle 3) and 13 May (cycle 4) of 1997; (b) simulated distributions for the same time periods of 1996 and 1997. Note that for cycle 1, 1996 and cycle 3, 1997 in (b), tracer densities are depicted 6 h after initial seeding into the flow field. Contour lines represent the horizontal density field of observed larval patches and have the same key.

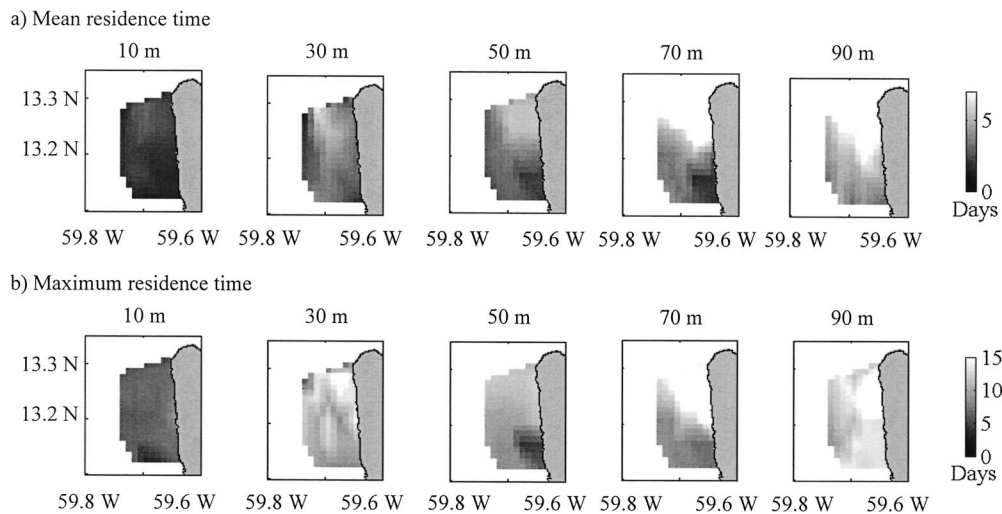


Fig. 7. Distributions of (a) mean residence time and (b) maximum residence time in days for each 20-m layer on the western shore of Barbados, from 8 May to 3 June 1996.

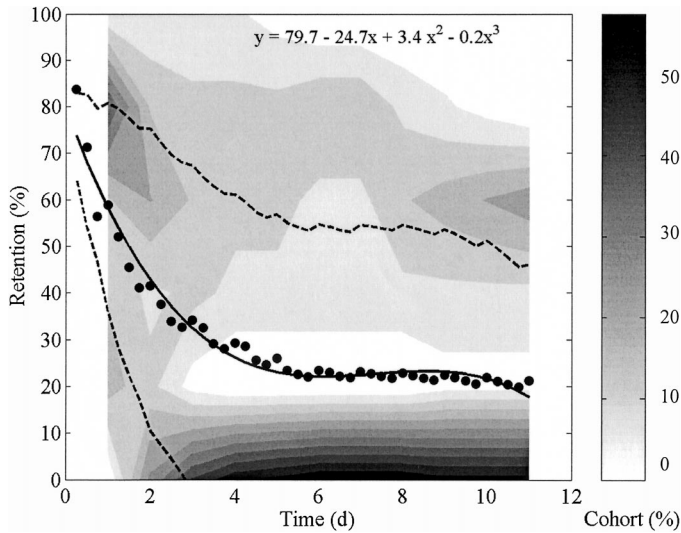


Fig. 8. Transport of daily cohorts of *S. partitus* on the western shore of Barbados during May of 1996 and 1997: Mean retention rate within the sampling domain is shown at every 6-h step (black dots) and fitted by a polynomial regression (solid line) with its standard deviation (dashed lines), indicating that transport is highly variable and levels off at the onset of vertical migration (day 5). The gray surface represents the percentage of daily cohorts at a specific retention rate (cohort %) and reveals that although among cohorts transport is variable, it is also strongly bimodal (i.e., low retention mode centered at ~5%, high-retention mode centered at ~70%).

retention was maximized for tracers released from the northern part of the western shore of Barbados, while during the 1997 experiment tracers released along the whole western shore of the island had a similar maximum residence time as the 1996 maximum values (ca. 15 d). Maximum residence time across the domain, integrated over 100 m and over a 20-d period, was ~30% higher in the 1997 experiment than in the 1996 (Fig. 12), which is consistent with observed differences in recruitment (36% higher in 1997; Fig. 9).

## Discussion

**Retention mechanism**—Previous analysis of the local circulation near the island of Barbados indicated that currents near the island are mostly vertically stratified (Paris et al. 2002), and so larvae could potentially avoid passive advection through vertical migration. Hare et al. (1999) modeled larval transport in the shelf region of the northwest Atlantic to investigate pathways from Atlantic menhaden and spot spawning grounds to nursery habitats. They concluded, in agreement with our findings, that general patterns in larval transport determined by circulation were altered by the vertical distribution of larvae. However, they did not find any apparent adaptive advantage for these biophysical interactions since no significant difference in the outcome of larval transport was found between passive and migrating larvae. In contrast, our results indicate that the ontogenetic behavior of *S. partitus*, which was found consistently between cruises, represents a response to common flow conditions (e.g., vertically stratified flow), allowing larvae to

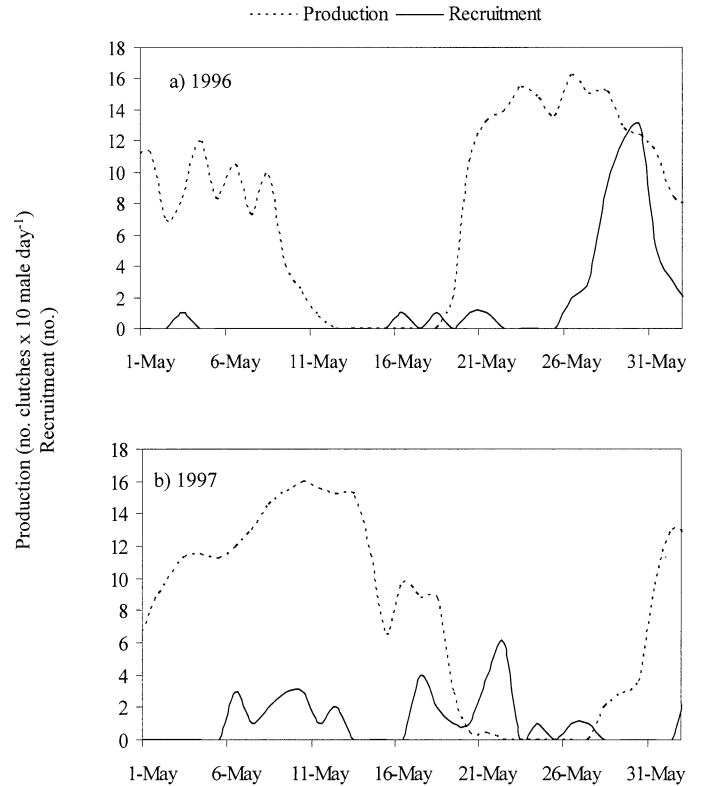


Fig. 9. *S. partitus* production and 34-d lagged recruitment during (a) May 1996 and (b) May 1997. Production peaked during the first half of the 1996 cruise and during the second half of the 1997 cruise (modified from fig. 4 in Cowen 2002). Production was measured as daily egg production in 75 nests. Recruitment was measured by collecting all the new recruits in 20 quadrates measuring  $1 \times 5 \text{ m}^2$  every 2 weeks, then back calculating settlement date from otolith analysis.

minimize strong advective loss in the surface layers, and is compatible with the retention hypothesis (sensu Sinclair 1988). Thus, reef fish larvae influenced their dispersal by using the vertical shear of the water column. The present findings are also consistent with earlier observations of typical (temporally and spatially persistent) flow features in the vicinity of Barbados (e.g., surface alongshore jet and on-shore flow at depth) associated with larval coral reef fish concentrations along the western shore of the island (Cowen and Castro 1994). Consequently, these results represent a validation to the modeling exercises of Armsworth (2000), which indicated that larvae would greatly influence their dispersal if they could position themselves in favorable currents through vertical movement.

Areas of low flow that could lead to retention of larvae without including any kind of behavior have been found around barrier reefs, in situations where the coral reefs rise from a shallow continental shelf platform (Black et al. 1990). In modeling for physical oceanographic use, Black et al. (1990) found that retention times tended to increase with reef size and decrease with shelf depth and currents and could be as high as 14 d, retaining as many as 20–40% of the particles. They found that in some cases, loss of tracers seemed to flatten off as a consequence of coral reef topo-

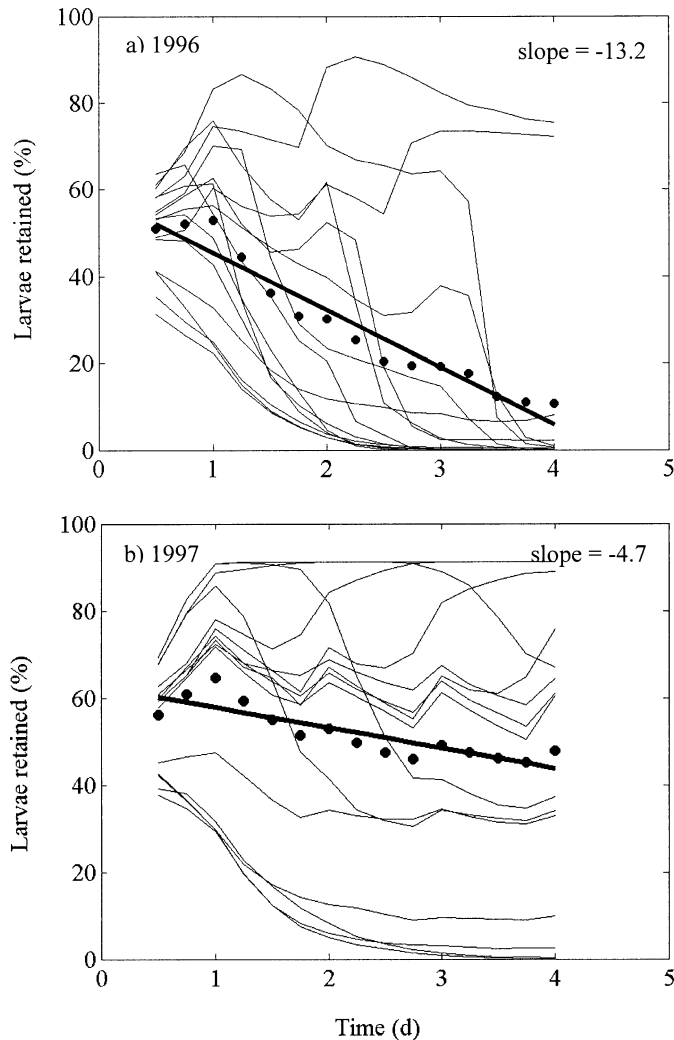


Fig. 10. Retention rates in the surface layer (0–20 m) during (a) May 1996 and (b) May 1997 for daily releases of six patches of 1,000 particles for 15 consecutive days along the bank reef off Barbados. The slopes of the regressions on the mean retention rates (dots) from daily consecutive releases (thin lines) indicate mean daily loss rates for the first 4 d after hatch (DAH) before the onset of vertical migration.

graphic features that concentrated them. Dight et al. (1990) also found that simulated larval clouds could remain reasonably coherent for as long as 28 d in the southern portion of the Great Barrier Reef because of passive concentration near lagoons. In the case of oceanic islands, the potential for dispersal is usually higher than near barrier reefs because the reef platform is narrow, bottom friction is reduced, and cur-

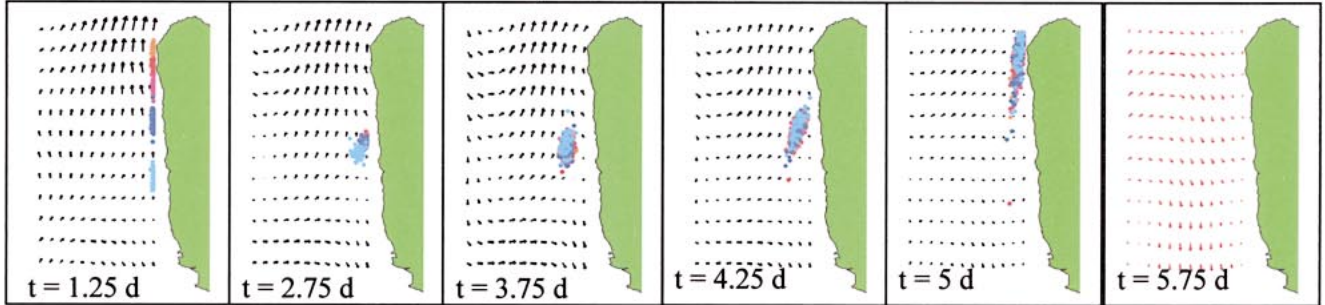
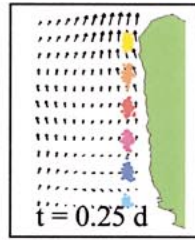
rents are more energetic. However in the vicinity of Barbados, biophysical interactions (i.e., ontogenetic vertical migration interacting with stratified currents) lead to retention rates comparable to those from the Great Barrier Reef area. In the case of Barbados, loss of tracers from the relatively small study domain stabilizes as a consequence of larval behavior and not of topographic effects.

*Larval patch dynamics*—Presumably, coral reef fish larvae and planktonic organisms in general occur in patches (Haury et al. 1978; Victor 1984), but direct evidence of the three-dimensional configuration of single-species, stage-specific coral reef fish larval patches has not been previously reported. Horizontal size estimates of *S. partitus* patches provided in this study (2–6 km) are in agreement with the findings of Williams and English (1992) of late-stage, multispecies larval patches of at least 6 km across, arriving onto the reef, but shy of estimates of patch size for presettlement wrasses of 20–46 km (Victor 1984). However, the estimates of Victor (1984) were from simultaneous settlement at multiple locations and not a true measure of larval patch size. It is possible to infer the approximate number of larvae in a patch, since the observed thickness of a larval patch in the present study is in the 30-m range (Table 3). At the preflexion stage,  $26 \times 10^6$  larvae may form a patch of 50 larvae per 1,000  $m^3$ , while an older larval patch (flexion and post-flexion stages) can be estimated to  $4.6 \times 10^6$  larvae (at an average density of 10 larvae per 1,000  $m^3$ ). This is conceivable, considering that the mean reproductive effort of *S. partitus* egg (demersal) in Barbados is  $43.6 \text{ eggs } m^{-2} d^{-1}$  (Cowen et al. 2000) on the west coast of the island (reef area of ca. 138  $km^2$  as derived from satellite imagery Reef at Risk) and generates ca.  $6 \times 10^9$  eggs  $d^{-1}$ .

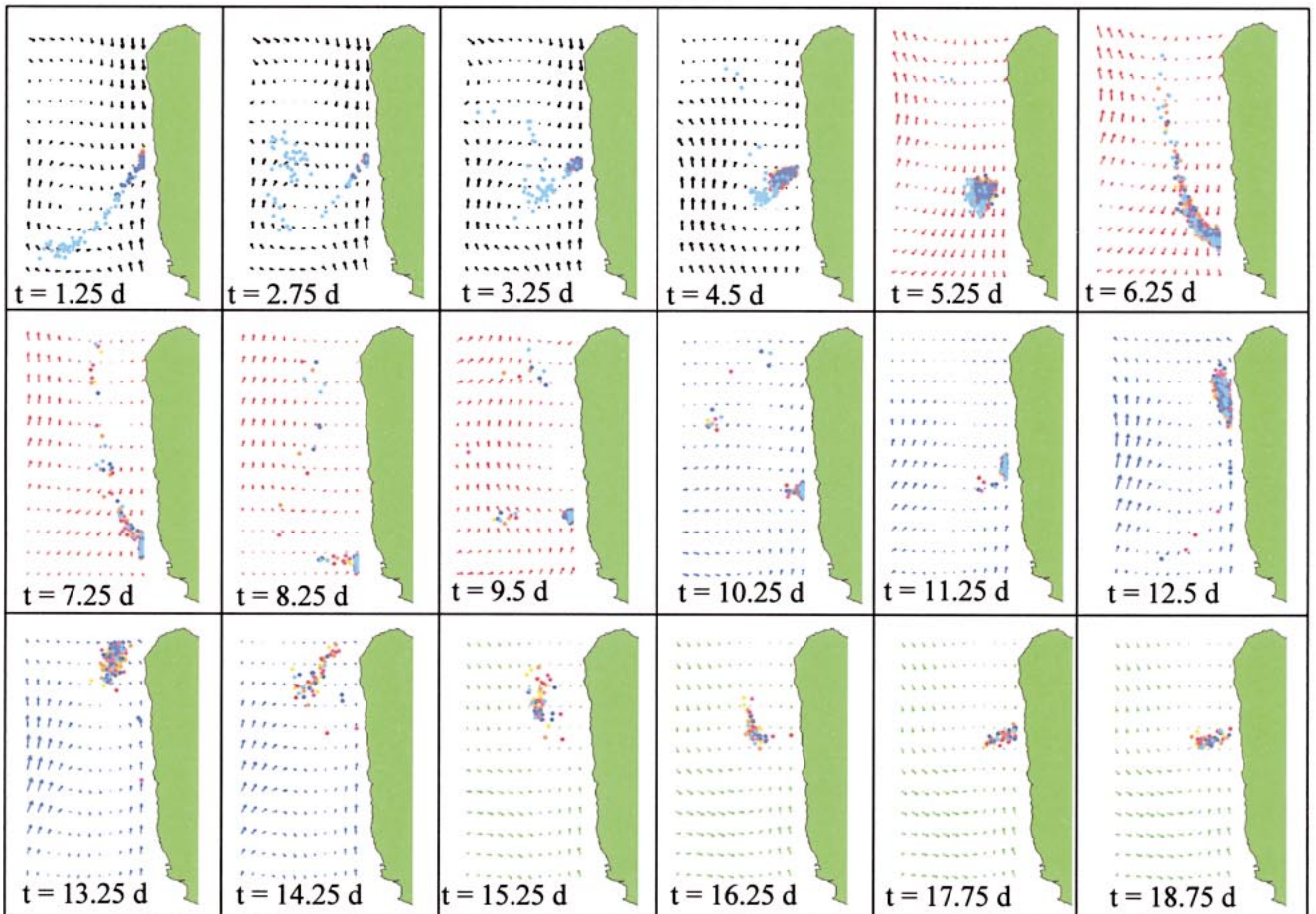
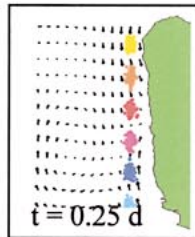
These results imply that larvae initially dispersing as patches tend to remain coherent, even perhaps until settlement. In fact, high variance in age observed within a settling cohort may not necessarily indicate that natal cohorts are dispersed, as suggested by Danilovicz and Sale (1999), but that discrete cohort patches may merge together passively or actively within specific local oceanographic features (e.g., convergences, accumulation area, strong gradients in habitat), which influence cohort characteristics (Victor 1984; Searcy and Sponaugle 2000). Patch generation and maintenance may be due to behavior-mediated aggregation in addition to passive accumulation (Boehlert and Mundy 1993). By migrating vertically, larvae may select flow conditions (direction and speed) that are favorable to retention and facilitate aggregation against dispersion; this particular subject requires further calculations of current convergences and divergences in relation to changes in *S. partitus* patch concentrations.

Fig. 11. Interannual variability of transport in the in situ flow field for particles released during the observed large hatching pulses of (a) 9 May 1996 and (b) 8 May 1997. Patches of tracers initially released along the bank reef (0–20 m,  $t = 0$ ) then moved vertically to the next 20-m strata every 5 d as indicated by a change in the velocity field color (black = 0–20 m; red = 20–40 m; blue = 40–60 m; green = 60–80 m). (a) All six patches released on 9 May 1996 are flushed out of the domain within 5 d (e.g., before the onset of vertical migration), while (b) tracers released on 8 May 1997 are still present after 15 d in the 60–80-m layer. Note that the six discrete initial patches, designated each by a different color, had merged into a single larger patch by day 3.

a) 1996



b) 1997



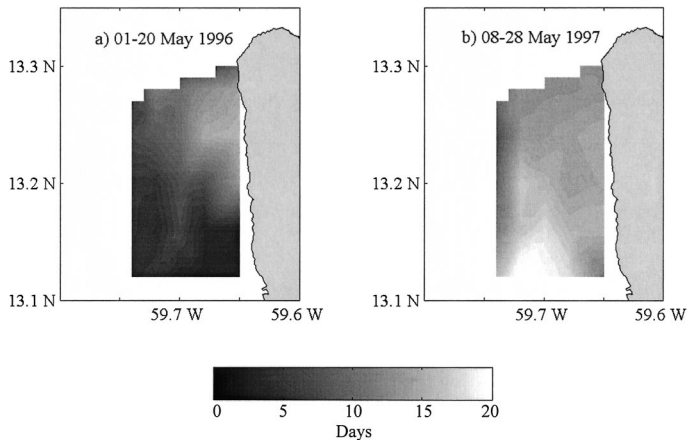


Fig. 12. Maximum residence time across the domain, integrated over 100 m and over a 20-d period for the (a) 1996 and (b) 1997 experiments.

Larval patch dynamics provided additional information on the daily variable nature of retention, indicating that usually (except for a narrow window of a few days) all simulated hatching would be lost if larvae were confined to the 0–20-m layer. Yet dense larval patches are also thick and can reach deeper layers (20–60 m) where advective loss is minimized. Even when surface currents are not all favorable, hatching peaks may generate low levels of recruitment (e.g., during the 1996 experiment), suggesting that vertical extent of dense preflexion larval patches maximizes the chances for retention.

**Recruitment variability**—Tracking virtual larvae revealed that flow conditions during the initial period after hatch (pre-flexion stage) are critical for the local survival of larval cohorts. High variability in the percent of larvae retained in the study domain during the early pelagic phase indicates that currents experienced by reef fish larvae before the onset of vertical migration play a large role in retention variability and consecutive recruitment.

Processes occurring at different scales can influence the supply of late-stage reef fish larvae in Barbados. Sponaugle and Cowen (1996a) found that sporadic physical larger scale events, which influenced the nearshore transport of larvae, were occasionally superposed on predictable cyclic peaks of settlement, synchronized to lunar periods and tidal amplitudes. Large current reversals of 20-d periodicity that constitute a major component of the local circulation at Barbados (Paris et al. 2002) may play an additional role in concentrating larvae by closing their Lagrangian trajectories into orbits.

In Barbados, large biological responses take place during freshwater intrusion events brought by North Brazil Current rings impinging on the island. Low salinity intruded halfway through the sampling experiments (sampling cycles 5–8 of both years), disrupting both the local circulation (Paris et al. 2002) and larval patch distributions. Damselfish larvae shifted downward, perhaps responding to a density signal. Such a change in patterns of ontogenetic vertical migration may decrease advection. Egg production of bicolor damselfish is

lunar cyclic and peaked during the first half of May 1996 and the second half of May 1997, or 6 d before the new moon. However, larger hatching pulses were observed during the first four sampling cycles of each experiment and were replaced by less discrete pulses in the following sampling cycles, suggesting that although spawning still occurred in lower salinity waters, posthatch mortality may have been higher. Because these low-salinity events are more frequent than previously thought (Kelly et al. 2000), local recruitment variability may often result from the influence of those events on larval retention and survival. Understanding and quantifying those processes will ultimately lead to coupling of time series of egg production and settlement and will be the focus of future research.

**Model strength and limitations**—Scales: The choice of spatiotemporal scales is critical to the accuracy of the results. The sampling frequency and station separation scales used in this study are resolving well the biophysical interactions, and the multivariate objective analysis minimizes sampling error. Faster time scales are not necessary unless tides are important in predicting the coastal circulation. We would, however, recommend extending the sampling domain offshore to better resolve possible exchange (observation of immigration of larvae). The size of the sampling box also affects computations of residence time: in all simulations, tracers reaching the open boundaries are permanently lost from the domain, while in reality larval patches may have reentered (e.g., during current reversal); this tends to underestimate retention and ultimately underestimate the magnitude of total recruitment.

**Role of behavior in larval transport model**: The present study revealed that biophysical interactions are largely expressed by vertical migration of *S. partitus* larvae, limiting horizontal dispersal. Our results concur with the theory of Bakun (1996) and the model of Armsworth (2000) of swimming behavior demonstrating that it is quite energetically efficient for fish larvae to exploit currents and control advection in a structured vertical shear. In fact, recent laboratory experiments on larval walleye pollock showed that larvae respond to gradients of flow by adjusting their vertical distribution (Davis 2001). Therefore, marked ontogenetic vertical zonation is important for larval transport as suggested by Boehlert and Mundy (1993) and Cowen and Castro (1994). Vertical zonation is likely modified by predator-prey interactions, which are found to relate to biophysical factors such as light intensity and predator risk/prey availability (Job and Bellwood 2000). Hence the role of larval behavior is critical to predicting and tracking larval trajectories when modeling larval transport.

The biological component of ISLAFIT was strictly introduced as ontogenetic vertical behavior; another important factor to consider in predicting larval transport is the range of behavioral capabilities (i.e., vertical and horizontal swimming) of the early life-history stages. Swimming behavior of late pelagic stages has been studied within the past decade in laboratory experiments (Stobutzki and Bellwood 1994) and by in situ observations (Leis et al. 1996). These studies revealed that presettlement reef fishes are competent swim-

mers, capable of actively modifying their dispersal, and mathematical modeling demonstrated that they can use these capabilities to orientate with respect to the reef in an efficient swimming fashion (Wolanski et al. 1997; Armsworth 2000). More recently, Fisher et al. (2000) examined the swimming abilities of larvae of a damselfish from northern Australia, *Pomacentrus amboinensis* (PLD ~ 20 d, size at settlement ~ 15 mm standard length [SL]; Fisher et al. 2000) throughout ontogeny, in both short-term and long-term locomotion. They found that critical swimming speed increased steadily with age, while the prolonged swimming abilities increased suddenly at ca. 10 d after hatch and was related to the development of propulsion area in the larvae. Assuming that its conspecific, *S. partitus* (PLD ~ 30 d, size at settlement ~ 12 mm SL; Sponaugle and Cowen 1996a) has similar capabilities, larvae may be able to enhance their retention near the island of Barbados halfway through their pelagic duration as well, at about 15 d after hatching. After this initial retention period, *S. partitus* may further use current-dependent and current-independent cues (Armsworth 2000) to remain in proximity of the island until settlement. The critical period during which larvae are more susceptible to advective losses is the preflexion stage, since they hatch in the upper layers where currents are stronger. Yet, posthatch larvae (12 h after hatching) of *P. amboinensis* were found to have critical swimming speeds of ca.  $3.5 \text{ cm s}^{-1}$ , as well as an average sustained swimming time of approximately 7 min (Fisher et al. 2000), enough to migrate vertically to ca. 15 m as indicated by the depth of penetration of stage 1 *S. partitus* patches. Small movement in the vertical, either by gas bladder adjustment or active swimming, can become significant in terms of differential advection within the strong vertical velocity shear encountered in a region such as Barbados.

**Larval trajectories as a hypothesis-testing tool:** This study demonstrates the limitations of inferring the role of larval movement from temporal snapshots of larval distributions, even considering the high temporal resolution of these sampling cycles. Building a continuous, four-dimensional representation of real currents was essential to the identification of biophysical retention mechanisms.

Predicting larval trajectories with real-time flow conditions is an important tool for answering ecological questions. Such an approach is relevant to study the effect of life-history traits (e.g., spawning strategies, larval duration) on retention and recruitment. For example, a wide range of larval durations among coral reef fish species has led to the hypothesis that they dictate dispersal strategies (Cowen and Castro 1994; Sponaugle and Cowen 1994; Victor and Wellington 2000). Tracking larval cohorts of various coral reef fish species/locations could serve in testing numerous hypotheses on the selection of traits through life-history strategies in coral reef fishes.

Tracking larval patches led to the quantification of the time dependence of retention within sampling cycles as well as between years and may further help in identifying circulation features and events responsible for recruitment success. Identifying circulation features and events responsible for recruitment variability is therefore possible and will rep-

resent an extension of this work. Larval trajectories also provided insight on patch dynamics, indicating that larvae initially dispersing as patches can in fact remain coherent throughout ontogeny and may merge with other larval patches formed by younger or older cohorts. Formation and maintenance of larval patches requires further calculations of current convergences and divergences in relation to changes in larval density. Larval patch dynamics are also key to understanding the effect of food condition on growth and survival of the pelagic stages and investigate functional linkages between pelagic and demersal stages (Searcy and Sponaugle 2000).

Our study reveals a proximate mechanism of biophysical retention with direct evidence from field observations. Retention of locally spawned larvae resulted from the exploitation of the vertical stratification of currents through ontogenetic vertical behavior, further suggesting that larvae may be adapted to persistent flow structures (baroclinic flow). We demonstrate that (1) larval vertical distributions reflect behaviors capable of capitalizing on flows that promote return to the reef environment, (2) flow conditions during the initial period after hatch (preflexion stages) are critical for the local survival of larval cohorts, and (3) retention of coral reef fish larvae is highly dependent on the interactions of the island near-field currents and larval behavior and is modulated by far-field currents. Although external forcing was similar between years, vertical shear was different between years, resulting in significant differences in retention further manifested in recruitment signals.

The present contribution also reveals that changes in larval fish distribution cannot be explained without invoking behavior. On average, larval movement in the vertical decreased advective loss by 20%, retaining approximately 20–25% of the larvae in the study area after 15 d. Retention is a function of ontogeny, and the vertical distribution maintained by *S. partitus* larvae serves as a biophysical mechanism to ensure maximum retention. These results stress the role of active behavior in larval transport in contrast to passive transport and have significant impact in studies of coral population connectivity. Further, this study confirms that, at ecological time scales, persistent local fish populations from Barbados are heavily self-seeded.

The implications of these results are twofold. First, in situ, high-resolution biophysical experiments are critical to accurately predict larval trajectories. Such experiments lead to a better understanding of physical processes occurring during the pelagic phase of a coral reef fish by defining the scales and patterns of processes underlying recruitment variability in reef fish populations. Second, the scales at which larval retention occurred were that of the island (i.e., in the order of tens of kilometers). The potential of biophysical mechanisms operating on such small scales also suggests that levels of larval exchange among distant populations may be considerably lower than previously assumed. These findings are important for management strategies, particularly those involving design of marine protected areas (MPA) network at local scales, facilitating site selection around the island where retention is optimized. They are also relevant to studies of population connectivity, whereby modeling long-distance larval transport should include behavioral fac-

tors (see Cowen et al. 2003). Further studies of species-specific behavior interacting with local circulation patterns from a variety of islands are needed for a better grasp of larval transport dynamics among coral reefs in the Caribbean.

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