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# THE ROLE OF LONG DISTANCE DISPERSAL VERSUS LOCAL RETENTION IN REPLENISHING MARINE POPULATIONS

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*ABSTRACT* Early models and evidence from genetics suggested that long distance dispersal of larvae is likely a common event leading to considerable population connectivity among distant populations. However, recent evidence strongly suggests that local retention is more the rule, and that long distance transport is likely insufficient to sustain marine populations over demographic timescales. We build on earlier model results to examine the probability of larval dispersal to downstream islands within different regions of the Caribbean at varying distances from source populations. Through repeated runs of an ocean circulation model (MICOM), coupled with a random flight model estimating larval sub-grid turbulent motion, we estimate the likelihood of particular circulation events transporting large numbers of larvae to within 9km radii of downstream populations, as well as account for total accumulations of larvae over each year. Further, we incorporate realistic larval behavior and mortality estimates and production variability into our models. Our results are consistent with the hypothesis that marine populations must rely on mechanisms enhancing self-recruitment rather than depend on distant 'source' populations.

## INTRODUCTION

Marine reserve design and placement is predicated, in part, on the intended function of the protection goal (e.g., habitat preservation, source of spillover of targeted species, increased production of larvae for dispersal to distant, non-protected regions; Bohnsack 1993, Carr and Reed 1993, Rowley 1994, Allison et al. 1998, Murray et al. 1999). Yet, for successful achievement of any function of a marine reserve, certain assumptions must be met. In the case of marine reserves as a source of larvae for dispersal, one assumption is that dispersal is likely to be extensive owing to strong dispersive characteristics of the ocean's currents (Roberts 1997). Recent evidence (Jones et al. 1999, Swearer et al. 1999) and modeling efforts (Cowen et al. 2000), however, suggest that larval dispersal may be more limited than previously thought, leading to the need to re-evaluate the spatial scaling of marine reserves.

It is the goal of this study to assess the basic assumptions about larval dispersal within the confines of the greater Caribbean region. Specifically, we examine the potential distance over which demographically meaningful quantities of larvae might be expected to disperse. We use a combination of ocean circulation and Lagrangian modeling techniques, coupled with modeling scenarios intended to replicate the role of larval behavior, to evaluate: 1) spatial and temporal variability in dispersal outcomes; 2) differences between passive and active dispersal scenarios; and 3) dispersal distances as a measure of connectivity among several source locations with their respective downstream sites.

## MATERIAL AND METHODS

To simulate larval dispersal trajectories within a realistic ocean flow field, we utilized the Miami Isopycnic Coordinate Ocean Model (MICOM). MICOM is basin-scale numerical simulation of the ocean flow, configured with realistic topography and stratification, a Kraus-Turner mixed layer parameterization, and forced by monthly climatology from the Comprehensive Ocean-Atmosphere data Set (COADS) and by radiative and freshwater fluxes (Bleck et al. 1992). The very high horizontal grid resolution (1/12°, 6 km mean grid spacing) and Evaporation-Precipitation flux boundary conditions of the most recent MICOM simulations improves the model's behavior by reproducing eddy activity, especially in the Gulf Stream separation and North Brazil Current (NBC) retroflexion regions (Paiva and Chassignet, 2001). Consistent with observations (Fratantoni and Glickson, 2002), eddy activity in the model is present in the eastern Caribbean (Garraffo et al., in review) and modulates the westward advection of surface waters in the vicinity of the Lesser Antilles (Cowen et al., in review).

To track trajectories of larval fish launched in the upper most layer of the model (mixed layer) a Lagrangian integration is performed on the velocity field combined to a turbulent field to simulate diffusion (Okubo, 1994).

The turbulent field is produced through a random-flight scheme predicting diffusion (Thompson, 1986):

$$\delta x = ( U + u ) \, \delta t$$

where $\delta x$ is the horizontal displacement of a particle in the x-axis, U is the meridional component of the deterministic velocity, u is the meridional component of the turbulent velocity, and $\delta t$ is the integration time step. At constant time steps the turbulent component of the velocity moves the particle an extra ($\pm$) displacement from the deterministic displacement (MICOM velocities). The evolution of this turbulent velocity is assumed to be a Markov process such that each time the particle moves through the flow field, it looses a fraction of its momentum to the surrounding fluid and in turn receives a random impulse from a Gaussian random ($G_r$) number generator ($-1 < G_r < +1$; Dutkiewicz et al. 1993). The diffusion coefficient ($K = 2 \times 10^4 \, \text{cm}^2 \, s^{-1}$), resulting from the imposed stochastic movement, is modeled to match the horizontal eddy diffusivity characteristic of the spatial scales prescribed in the deterministic velocity field (Okubo, 1971). Qualitative validation of this transport model was performed by comparing *in situ* near-surface drifter data—from the Intra-Americas Sea YOTO drifter program (www.IASlinks.org)—with the trajectories of particles released at the same time-space scales (Paris et al., in press).

To evaluate the scope of temporal and spatial variability of potential larval dispersal within the Caribbean, we examined larval trajectories originating from six sites located around the Caribbean and released throughout the year (Figure 1). Specifically, larval patches of 5000 individuals were released from each site every other day for an entire year (total releases per site = 182). Tracking trajectories of 5000 successful larvae is equivalent to releasing ca. $2 \times 10^6$ larvae and applying an instantaneous mortality coefficient of 0.2 d$^{-1}$ for 30 days. This natural mortality rate was estimated from *in situ* tracking of larval cohorts in the vicinity of Barbados (Paris, Cowen and Sponaugle, unpubl. data) and also corresponded to the modal value of various larval mortality rate estimates of coastal, non-reef species (Morse et al., 1989).

Assimilating the above models (MICOM, Lagrangian/random-flight particle tracking, and mortality), larval fish transport in the Caribbean was then simulated in two modes, passive and retention. In the passive dispersion scenario, larvae are directly advected from their source into the background flow field. Virtual larvae from each release date that were within 9-

km of any coral reef habitat (as derived from satellite imagery - Reefs at Risk) at the end of their 30-d larval period were considered successfully recruited; those outside this buffer zone were not. Recruited larvae were then counted at the source-island (local retention) and downstream islands (dispersed). In the retention scenario, a fraction (25%) of larvae are retained around their reef of origin during the first four days of their planktonic duration, prior to the advection scheme; thereafter, any larvae that passes within 9 km of reef habitat (whether around the source island or downstream) is retained for the duration of their larval period (i.e., they are recruited). This biophysical retention model is based on *in situ* synoptic sampling of the flow field and larval densities throughout the larval duration of the bicolor damselfish (*Stegastes partitus*) in the vicinity of Barbados. Briefly, during the spring of two consecutive years, ontogenetic vertical behavior combined with local flow structure represented a retention mechanism for locally spawned larvae. On average, 25% of all larvae were still present (retained) around the island, after the first 4 days; thereafter, due to vertical movements of postflexion larvae in vertically stratified currents, nearly 100% of larvae within 9 km of shore were retained around the island for the duration of their larval period (day 5–30; Paris and Cowen, unpubl. data). As with the passive advection scenario, all recruited larvae are counted at the source and downstream islands at the end of the larval period for each separate release date (bi-daily basis releases throughout an entire year period).

Finally, for the comparison of dispersal distances among release locations, we standardized recruitment success relative to Barbados self-recruitment rates. Our reason for this is that we had extensive time series data (18 months) of daily production and recruitment rates for the bicolor damselfish (Dorsey and Cowen, unpubl. data) with which to compare the modeled results. Due to its upstream location, Barbados is predominantly a self-recruited site (Cowen and Castro 1994, Cowen et al. 2000), yet it supports a well-developed coral reef fish population comparable to many other locations throughout the Caribbean. Thus, observed recruitment rates at Barbados may serve as a proxy of 'typical' recruitment rates required to maintain similar population levels at other locations (whether due to self-recruitment, long-distance recruitment or a combination). This assumes that post-settlement survival rates do not vary significantly among locations; such variation could obviously alter this simplified scenario.
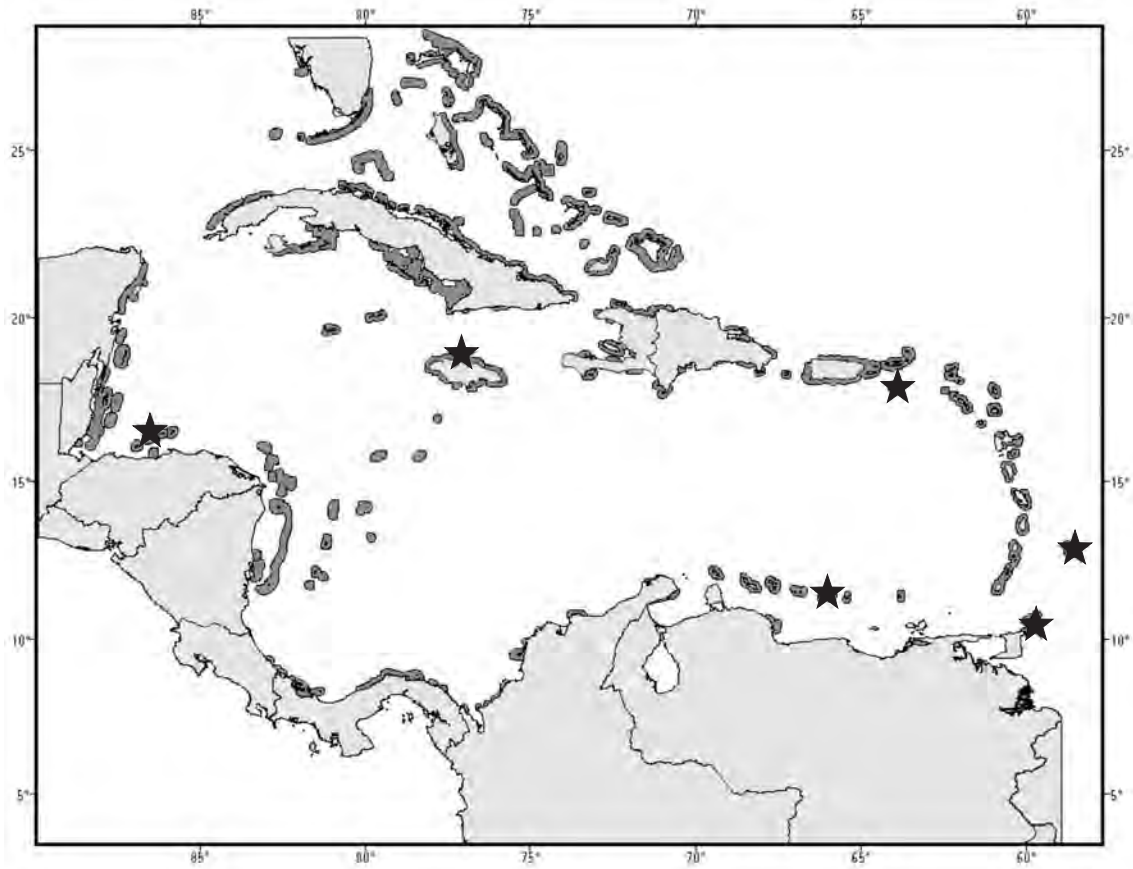
**Figure 1. Coral reef fish habitat with associated 9 km-retention zones in the Caribbean, derived from satellite imagery (Reef at Risk); stars indicate release locations for this study.**

## RESULTS

### Passive Mode

**Spatial variability of dispersal .** The spatial extent of larval dispersal varies depending on where the larvae originate. After 30 d, the spatial extent of larval dispersal released on the same date ranges from relatively small, coherent patches (*ca*. $2 \times 10^5$ km$^2$) in the vicinity of St. Croix to broadly dispersed larvae (*ca*. $10^6$ km$^2$) spread throughout much of the Caribbean (Figure 2). Further, at some locations, the larvae were spread somewhat linearly in a jetstream (e.g., western Caribbean boundary current), whereas in others, advection was limited and the spread was more evenly distributed around the source.

**Temporal variability in spatial context.** Similar scales of spatial variability are observed at individual sites when observed over time reflecting the spatial and temporal variability in ocean currents. For example, whereas larvae are dispersed from Barbados westward into the Caribbean following a July 1 release, the larvae spread north and east of the Lesser Antilles when released on October 1 (Figure 3). The direction and spatial extent of larval spread is also highly variable at other sites such as St. Croix where larvae at one time may be spread toward Puerto Rico to the west, while at other times they may spread out of the Caribbean to the northeast. When viewed over the whole year, it becomes apparent that certain times of year are potentially more favorable for retention of larvae near the source, and for dispersal to nearby locations at other times (Figure 4). However, there is no apparent trend in dispersal among islands; high retention does not necessarily predict low dispersal to a downstream location, nor does high dispersal to one location predict high dispersal to another, even if close by.

**Temporal variability coupled with production variability .** The above results concerning temporal variability involve a constant supply of larvae (i.e., constant egg production). However, for most, if not all, species, reproduction is temporally variable. When temporal variability in reproduction is incorporated into the model, the overall scenario, here viewed just in terms of retention around Barbados, changes substantially (Fig-
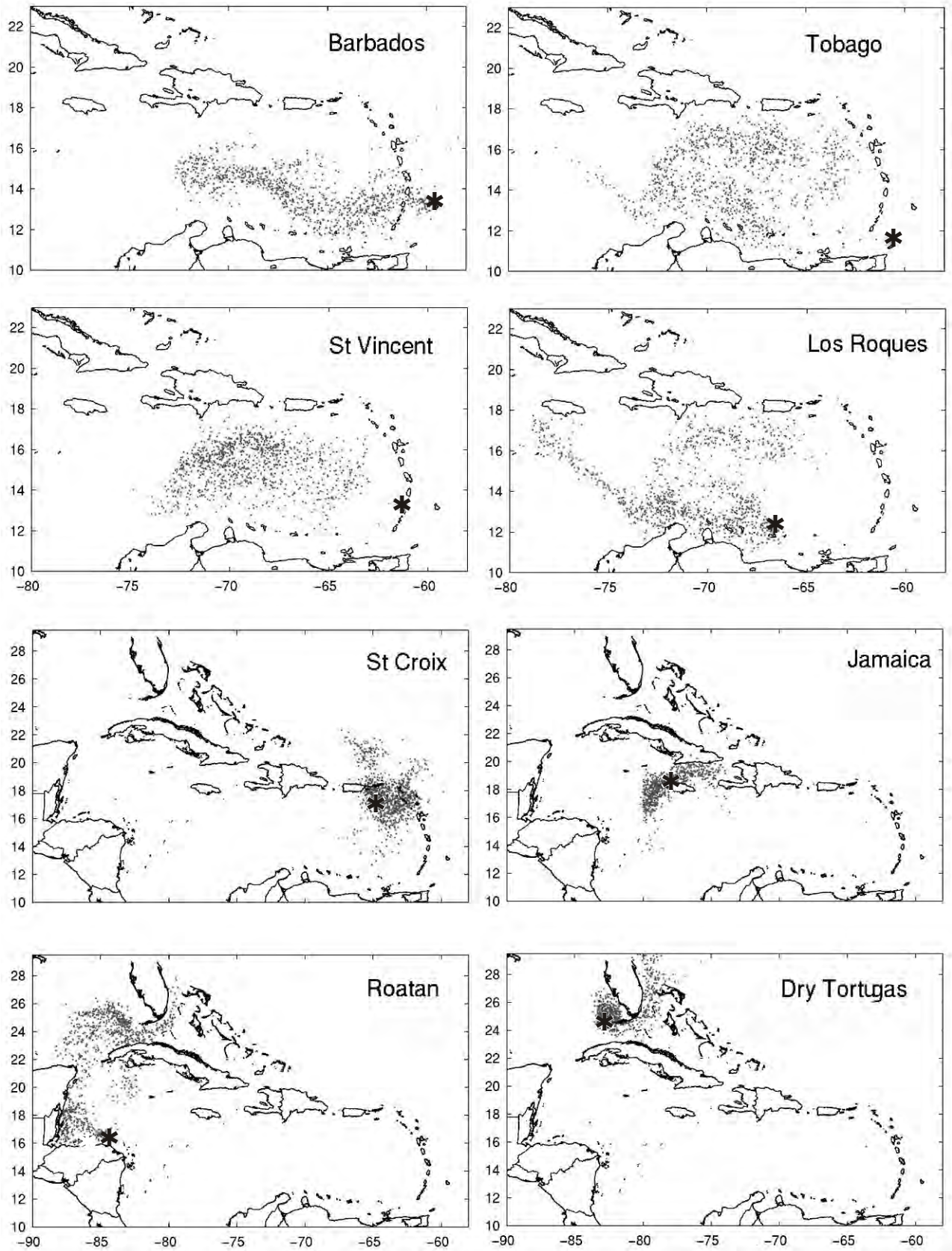
**Figure 2. Distribution at day 30 of 5000 larvae released on July 1 from various locations around the Caribbean as indicated by the asterisks.**
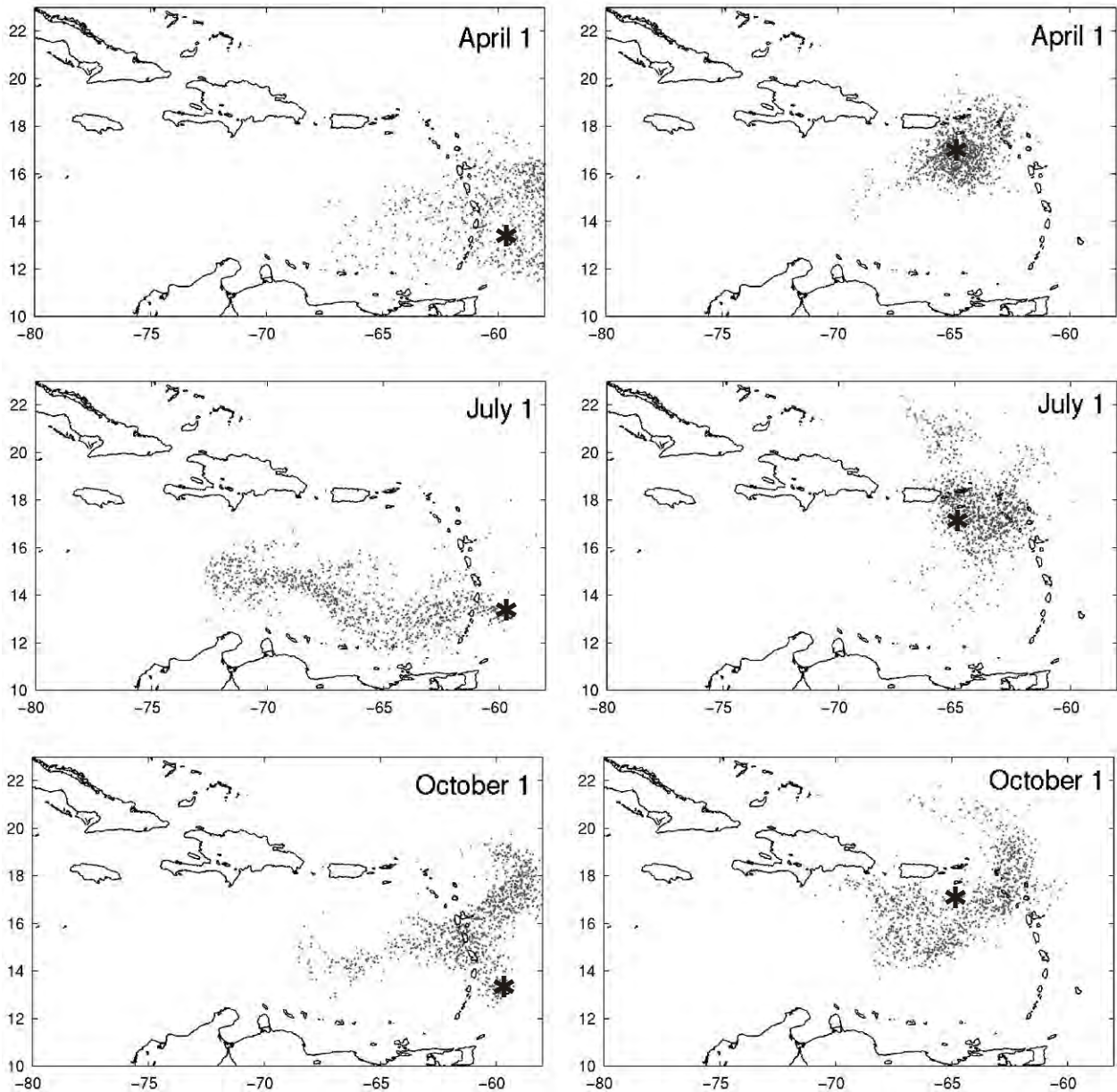
**Figure 3. Distribution at day 30 of 5000 larvae released during three different times of the year (April 1, July 1, and October 1) from Barbados (a) and St Croix (b); asterisks indicate release location.**

ure 5). Periods, which were highly favorable for retention of larvae, may be unimportant (e.g., December and January for the common reef fish *S. partitus*), if no reproduction is occurring.
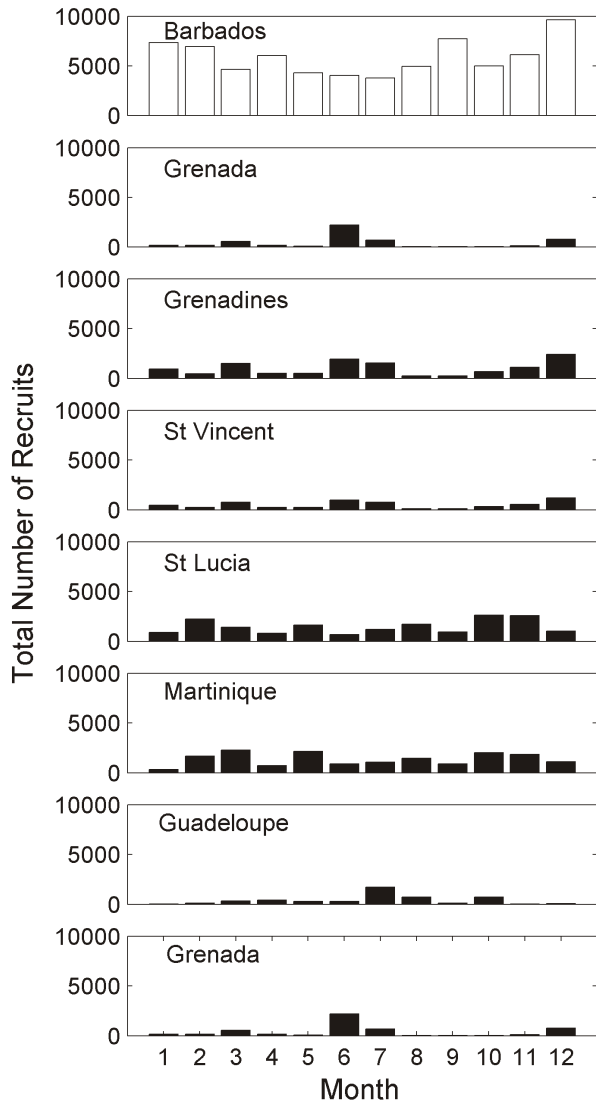
**Retention Mode**

**Comparison between passive/active scenarios.** The above spatial and temporal variability involved simple passive dispersal schemes. When compared with the model scenario that invokes the role of larval behavior, it becomes apparent that simple passive dispersal under-estimates retention, and may exaggerate the ex-

tent of downstream, long-distance dispersal (Figure 6). Under the active scenario, larvae are potentially retained near the source location by up to an order of magnitude more than with passive dispersal, with a mean trend of a *ca.* 4-fold increase. The passive scenario does not predict longer dispersal distance, but lower survival since fewer larvae are retained at any location. Consequently, the number of larvae successfully recruited to downstream sites rapidly diminishes with distance.

**Validation.** To place these model runs into context, we compared predicted recruitment rates (utilizing both

Figure 4. Monthly distribution of 30-d recruits to Barbados (local recruitment) and downstream locations (virtual larvae were released constantly on a bi-daily basis from Barbados); this shows temporal variability in retention and unpredictability of dispersal downstream based on recruitment at the source or at any other nearby location.

passive and active model scenarios) with observed recruitment rates around Barbados, after standardizing production rates and incorporating larval mortality rates (estimated at $z = 0.2d^{-1}$; Paris, Cowen and Sponaugle, unpubl. data). Based on mean observed production rates and settlement rates per m$^2$ around Barbados (Dorsey and Cowen, unpubl. data) we calculated self-recruitment as a ratio of the two (recruitment/production). Mean model outputs were similarly compared by calculating the same ratio, but utilizing total production (number released prior to mortality at the source) and total recruitment at the source. (Table 1). Circularity in

reasoning is avoided here because no duplicate use of variables occurs. Of the two model scenarios, that incorporating larval behavior closely approximates the observed recruitment rates, while the passive scenario underestimates local recruitment five-fold (i.e., it overestimates export away from the source). These results also validate the estimated larval mortality rate.

DISCUSSION

This model exercise serves to identify possible limits on the scope for extensive dispersal of larval fish within the Caribbean. By allowing for the potential role of active larval behavior, versus relying on simple passive drift models, we find that larval dispersal is greatly reduced, apparently in favor of retention. While such limits to dispersal have both evolutionary as well as management implications, we will focus our discussion on the management issue.

The primary finding of this study is that the abundance of potential larval recruits decreases very rapidly with distance from the source population, even after dispersal times of 30 d. Even though the model evaluated dispersal from a variety of sources positioned in very different ocean circulation environments, all dispersal outcomes converged on a similarly shaped curve (i.e. exponential decline). The critical values of the number of larvae (recruits) required to be demographically important have not been determined. However, if the assumption that observed recruitment rates and population size of fish populations at Barbados are typical of other Caribbean locations is valid, we can utilize the modeled results to examine realistic scenarios (Figure 7). For example, if some downstream location were receiving heavy fishing pressure (e.g., 40% of the population is being removed each year), then in order to sustain such fishing pressure, recruitment to the local population must be subsidized from upstream sources to the tune of about 40% of the total required, pre-fishery recruitment rates. Under this scenario, receipt of sufficient numbers of recruits would occur only if the source location were less than ca. 60 km away (see Figure 7); recruits coming from reefs located beyond this critical distance likely would not be sufficient to replenish the fishery.

Clearly, in many locations, more than one source location is possible, but the further away such source populations are located, their potential importance as recruit sources quickly declines. While specific local flow conditions will potentially modify these results, the general trend was consistent over a fairly diverse set
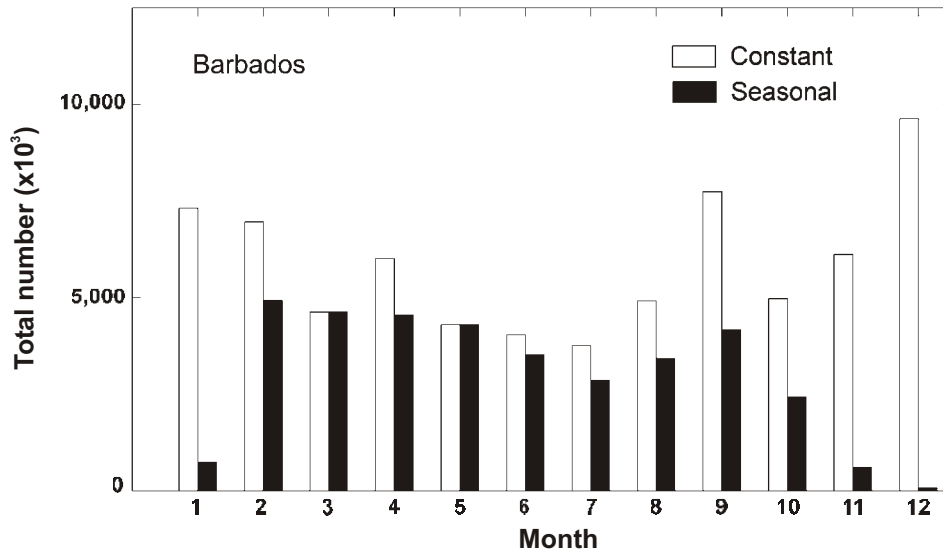
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**Figure 5. Monthly distribution of self-recruitment (retention) at Barbados resulting from constant reproduction and mean seasonal reproduction derived from observed daily egg production for the bicolor damselfish** *Stegastes partitus* **at Barbados (Dorsey and Cowen, unpubl. data).**

of flow environments. Thus, these results suggest that effective dispersal distances, over demographically meaningful time scales, and therefore, the critical management unit scale, is on the order of 10's of km rather than >100's km. Within such topographically diverse regions as the Caribbean, this can still lead to international management issues, but many island nations, particularly some of the larger ones (e.g., Cuba, Jamaica), may, in fact, be the primary source of their own reef resources. Thus, management strategies, especially

those utilizing no-take marine reserves, may need to rely more on within-island networks, rather than among-island networks.

The spatial and temporal variability observed in these model runs suggest care is warranted when utilizing model scenarios for design and placement of reserves. Notably, it is imperative that decisions not be made on the production of only a few model runs, since the full range of possible outcomes will be missed. Choice of the wrong time frame, for example, could lead
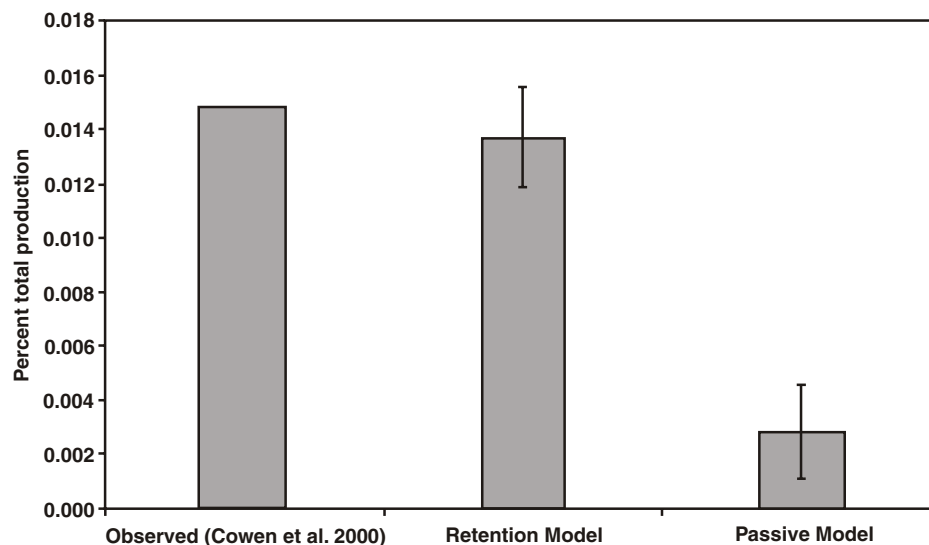


**Figure 6. Comparison of simple passive dispersal scheme (passive model) with the model scenario that invokes the role of larval behavior (retention model) and with observed recruitment at Barbados.**

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**TABLE 1**

**Self-Recruitment - Mean observed production rates and settlement rates per m² around Barbados (Cowen et al., 2000; Dorsey and Cowen, unpubl. data) serve to calculate self-recruitment as a ratio of the two (recruitment/production). This value is compared to self-recruitment estimated from model outputs of passive and retention modes. Mean self-recruitment for all release sites corresponds to the percent of annual production (total number of virtual larvae released bi-daily prior to mortality, identical for each site) retained at the source (mean annual recruitment).**

|  | Observed | Retention Model | Passive Model |
|---|---|---|---|
| Production (No. m⁻² day⁻¹) | 43.6 |  |  |
| Annual Production (No.) |  | 3.63E+08 | 3.63E+08 |
| Recruitment (No. m⁻² day⁻¹) | 0.00646 |  |  |
| Mean Annual Recruitment (No.) |  | 49792 | 10274 |
| Self Recruitment = R / P (%) | 0.0148% | 0.0137% | 0.0028% |
| Standard Error |  | 0.0019% | 0.0017% |
| Release Sites (n) |  | 6 | 6 |

to complete failure of a no-take marine reserve to achieve a goal of seeding towards a particular location, even if appropriate spatial scaling is utilized. Similar cautions can be made when utilizing drifter experiments to predict dispersal pathways. As seen in this analysis, drifter tracks from only one or a few deployments, will not likely provide the full range of possible dispersal outcomes, leading to the potential for mistaken placement of marine reserves, no matter how well inten-

tioned. Another related caution is that dispersal potential be evaluated (whether via models or field, i.e., drifter, efforts) at times and locations when spawning actually occur. Reliance on descriptions of flow fields from one season, regardless of how well resolved, may not be relevant when spawning is actually occurring.

***Limitations of the model.*** The retention scenario model proved to be a reasonable predictor of recruitment intensity, at least in the single case of Barbados.



$Y = 0.8646 * exp(-0.0112*x)$
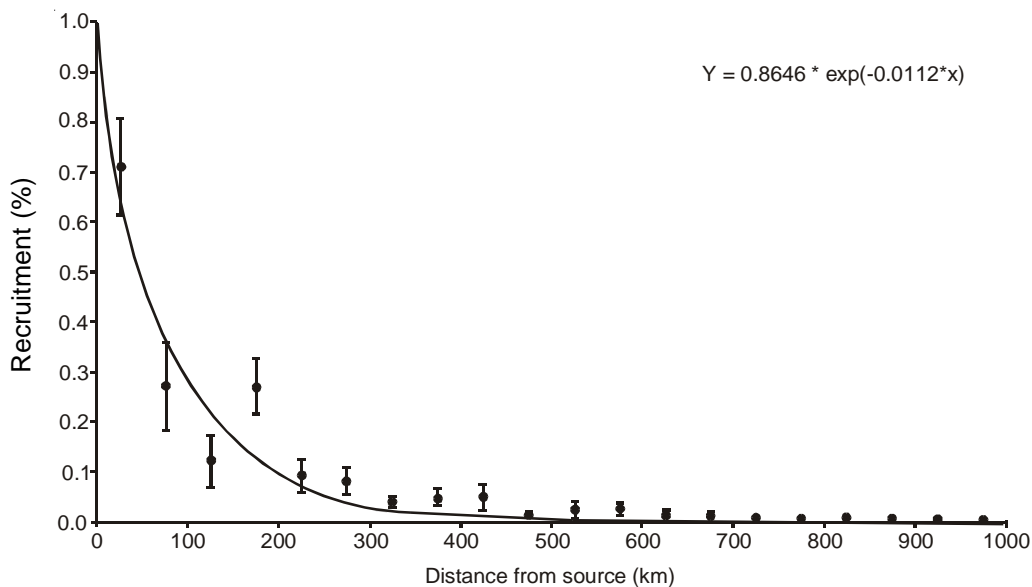
**Figure 7. Retention distances from the source: Recruitment to available reef habitat is estimated from constant bi-daily virtual larval (of 30-d pelagic duration) releases at 6 locations around the Caribbean. Number of larvae recruiting in each 50-km bin from the source is standardized by the recruitment value at Barbados (i.e., recruitment = 1 at Barbados), since its local population is assumed to be self-seeded; the larval transport model includes larval behavior (retention mode).**

The success of the model to estimate apparent retention of larvae around the island, of course, relies on a variety of model assumptions, many of which require direct measurements prior to accepting that these model premises are correct. Further, the observed rates and mechanisms of larval retention around Barbados are not verified for other regions of the Caribbean, though the biophysical processes involved are likely common in many coastal waters (Cowen 2002, Sponaugle et al. 2002). In general, the results of such models serve well to help estimate potential limits, particularly in the design of no-take marine reserve networks (sensu Botsford et al. in press). However, the results ultimately require validation prior to broad application to specific locales. The best use of such model results is to constrain (in a more conservative direction) what potential positive impacts might be derived from reserves, and to plan accordingly to maximize the likelihood of achieving the desired results.

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