

Long distance dispersal versus local retention as a means of replenishing

Caribbean marine fish populations

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Early models and evidence from genetics suggested that long distance dispersal of marine larvae is likely a common event leading to considerable population connectivity among distant populations (Thorson 1950, Sheltema 1986, Shulman and Bermingham 1995, Roberts 1997). However, recent evidence strongly suggests that local retention is more the rule (Bentzen et al. 1996, Ruzzante et al. 1998, Shaw et al. 1999, Jones et al. 1999). and that long distance transport is likely insufficient to sustain ecologically marine populations (Cowen et al. 2000). Recent research has advanced the hypothesis that 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 adult habitat (Leis 1991, Lough & Potter 1993, Cowen and Castro 1994). This study examines the retention hypothesis (sensu Sinclair 1988) utilizing high resolution spatial and temporal measurements of the flow regime in the vicinity of an isolated oceanic island (Barbados) combined with three-dimensional surveys of larval reef fish distributions and long-term monitoring of recruitment to the reefs. Specific aims were to determine whether flow features and larval distributions are temporally and spatially consistent and whether larval distributions reflect behaviors capable of capitalizing on flows that promote return to the reef environment. The sampling was initiated at the time of peak spawning as determined from shore-based monitoring of the reproductive output. In principle, this allowed us to track, through intensive ichthyoplankton and oceanographic surveys, a cohort of fishes produced during one lunar cycle throughout its entire pelagic duration.

Based on our previous finding of the highest larval densities (Cowen and Castro 1994), the study region was located on the western shore of Barbados and limited to a 15x25-km array. Sampling involved repeated (sampling frequency ≈ 3 d), quasi-synoptic physical and biological measurements, each of 24 hr duration, to allow close integration of physical and biological processes. During day 1, CTD casts covered the domain in an grid pattern, and AOCF profiles were continuously recorded along the ship track. During day 2, 24 vertically-discrete ichthyoplankton sampling (MOCNESS 1 m²) were taken in a 12 day/12 night paired sampling protocol. Finally during day 3, satellite-tracked, GPS drifters were released and tracked within the study domain and additional 10 m² MOCNESS samples were taken. A total of 8 sampling rotations were conducted during May 1996 timed to correspond with high spawning and recruitment period of the target species. The entire experiment was repeated during the consecutive year (May 1997).

The experiment was designed to track specific cohorts of 2 species of damselfish (Pomacentridae), the bicolor damselfish, *Stegastes partitus* (Poey), and the longfin dam-selfish, *Sfegasfes diencaeus* (Jordan & Rutter). Typically the adult phase is associated with coral substrates. Females spawn demersal egg clutches in nests guarded by males. Peak spawning of the dominant pomacentrid, *S. partitus*, is between full and third quarter moon at Barbados (Sponaugle and Cowen 1996). The eggs hatch at night and larvae are released directly from the reef where they enter the pelagic realm. Larval duration of these pomacentrids is approximately 30 d. Early pre-flexion stages may be considered as passive, but behavioral capabilities (i.e. vertical and horizontal swimming) increase rapidly with development. However, processes such as advection and mortality operating during the larval duration affect the number of new recruits. The present study was designed to quantify these processes, and focal species were chosen to serve as a proxy for identifying general mechanisms in reef fish recruitment.

Fish larvae were sorted from the plankton samples and identified to the lowest taxonomic level in the laboratory. To isolate individual cohorts based on their birth-date, age information was obtained from the larval otolith. Once the larval identification and aging are performed, age-specific larval densities are computed to standardize catches. The resulting information is visualized through time series of 3-D

graphs representing specific larval distribution in the study box. Based on these field data, an age-dependent vertical migration (ontogenetic) scheme is used in modeling larval behavior. In addition, the observed distributions serve to validate the biophysical model of larval transport.

A multivariate objective analysis (Pedder 1989, Pinot et al. 1995) was used to obtain a coherent flow field by integrating all data (ADCP and CTD). The ADCP data were analyzed on 5 horizontal planes (every 20m) and returned in a regular mesh (12x12 grid). The mesh size of 1.1x2.2 km was determined by the density of observed data and is a compromise between increasing precision and minimizing error. A characteristic scale factor of 7 km was used in the objective analysis to determine the degree of smoothing of the output fields. This method smoothes noise due to small inertial and tidal currents via scale separation and predicts self-consistent maps of the residual flow field for the upper ocean. Multi-level maps of the horizontal flow field were generated for each rotation. In total, 16 maps of a 5-layer flow field, each being self-consistent were generated. Integration of 6 h time steps was used for dynamic interpolation of the flow field between maps, resulting in a continuous time series (dimensional realization $x, y, + \text{time}$). To track larval fish, we used a 'random flight' model scheme (Dutkiewicz et al. 1993), by which a turbulent velocity field is superimposed on the deterministic flow field.

Larval release was initialized in the surface layer (0-20 m) at the same location/day as the observed *S. partitus* larval patches of day 0-3 cohort. Four days later, the model accurately predicted the passive transport of the earliest larval stages as well as their density field (Fig. 1). These results validated the transport model and showed that flow features and reflexion larval distributions were temporally and spatially consistent. However, older larvae are not passive. While reflexion *S. partitus* larvae were located at surface (average depth of center of mass = 19 m) within the strong off shore Row region, postflexion stages migrate down, in the onshore flow region (average depth of center of mass = 40 m; Fig. 2). We tested explicitly whether vertical migration affected the outcome of the larval transport by releasing arbitrarily in the center of the domain a large patch of virtual larvae. Passive larvae released at the surface (0-20 m layer) were flushed out of the domain in less than 3 days. However, those that were released into the 40-60 m flow field layer were retained for over a week. By migrating vertically, fish larvae encounter the onshore, low flow found at depth, which enhances retention. We conclude that larval distributions reflected behaviors capable of capitalizing on flows that promote return to the reef environment.

During part of a larger temporal scale project which took place on the western shore of Barbados, daily record of egg production over 18 month and daily record of settlement over the same period was monitored. When the recruitment signal is lagged by 29 days, corresponding to the planktonic duration, the patterns do not translate. Recruitment is de-coupled from hatching (i.e. production), with among cohort variability greater in the recruitment signal than the egg production signal. To examine the role of pelagic transport processes contributing to the observed interannual variability, we utilized our simulation to compare the effect of flow conditions in May 96 (low recruitment) to May 97 (high recruitment). Hatching pulses were simulated by releasing virtual larval patches ($n = 1,000$) at 6 locations along shore in the flow conditions corresponding to May in each year. The results were consistent with the finding of higher recruitment in 1997. Basically, during 1996, the six group of larvae were rapidly mixed and carried out of the domain by strong currents within 3 d, whereas in 1997, the larvae converged and were carried to and retained nearshore for over 20 d (Fig.3).

The implications of these results are twofold. First they serve as further validation of our transport model since we are accounting for the inter-annual variability observed in cohort success, which may lead to a more thorough understanding of the processes underlying recruitment variability in reef fish populations. Moreover, these results indicate that the scale at which larval retention occurs is at the spatial scale of the island nearfield (the island radius was estimated as 15 km from the 100m isobath). With the potential of biophysical mechanisms of larval retention operating on such small scales, the scale of population connectivity may be smaller than often considered in the design of management strategies, particularly those involving Marine Protected Areas (MPAs).

Literature Cited:

- Bentzen, P., Taggart, et al. (1996). **Microsatellite** polymorphism and the population structure of Atlantic cod (*Gadus morhua*) in the northwest Atlantic. *Canadian Journal of Fisheries and Aquatic Sciences* 53: 2706-2721.
- Cowen, R. K. and L. R. Castro (1994). Relation of coral reef fish larval distributions to island scale circulation around Barbados, West Indies. *Bulletin of Marine Science* 54(1): 228-244.
- Cowen, R. K., K. M. M. Lwira, et al. (2000). Connectivity of marine populations: Open or closed? *Science* 287(5454): 857-859.
- Dutkiewicz, S., A. Griffa and D.B. Olson. 1993. Particle diffusion in a meandering jet. *J. Geophys. Res.*, 98(C9), 16,487 - 16,500.
- Jones, G. P., M. J. Milicich, et al. (1999). Self-recruitment in a coral reef fish population. *Nature* 402(6763): 802-804.
- Leis, J.M. 1991. The pelagic stage of reef fishes: The larval biology of coral reef fishes. In "The ecology of fishes on coral reefs" (P.F. Sale, Ed.), pp.183-230. Academic Press, San Diego.
- Lough, R.G. and D.C. Potter 1993, Vertical Distribution Patterns and Diel Migrations of Larval and Juvenile Haddock *Melanogrammus aeglefinus* and Atlantic Cod *Gadus morhua* on Georges Bank. *US Fish. Bull.* 91: 281-303.
- Pedder, M. A. 1989. Limited area kinematic analysis by a multivariate statistical interpolation method. *Mon. Wea. Rev.* 117: 175-1708.
- Pinot, J.M., J. Tintore, J. L. Lopez-Jurado, M. L. Fernandez De Puelles, and J. Jansa. 1995. Three-dimensional circulation of a mesoscale eddy/front system and its biological implications. *Oceanologica Acta* 18(4): 389-400.
- Roberts, C. M. (1997). Connectivity and management of Caribbean coral reefs. *Science* 278(5342):1454-1457.
- Ruzzante, D. E., C. T. Taggart, et al. (1998). A nuclear DNA basis for shelf- and bank-scale population structure in northwest Atlantic cod (*Gadus morhua*): Labrador to Georges Bank. *Molecular Ecology* 7(12): 1663-1680.
- Scheltema, R.S. 1986. On dispersal and planktonic larvae of benthic invertebrates: an eclectic overview and summary of problems. *Bull. Mar. Sci.* 39:290-322.
- Shaw, P. W., C. Turan, et al. (1999). Microsatellite DNA analysis of population structure in Atlantic herring (*Clupea harengus*), with direct comparison to allozyme and mtDNA RFLP analyses. *Heredity* 83: 490-499.
- Shulman, M. J. and E. Bermingham (1995). Early life histories, ocean currents and the population genetics of Caribbean reef fishes. *Evolution* 49: 897-910.
- Sinclair, M. 1988. Marine Populations: An Essay on Population Regulation and Speciation. Washington Sea Grant
- Sponaugle, S., and R.K. Cowen. 1996. Larval supply and patterns of recruitment for two Caribbean fishes, *Stegastes partitus* and *Acanthurus bahianus*. *Mar. Freshwater Res.* 47:433-447.
- Thorson, G. 1950. Reproduction and larval development of Danish marine bottom invertebrates, with special reference to the planktonic larvae in the Sound (Oresund), Meddr. Dommn. Danm. Fisk.-og Havunders. (Ser. Plankton) 4:1-529.

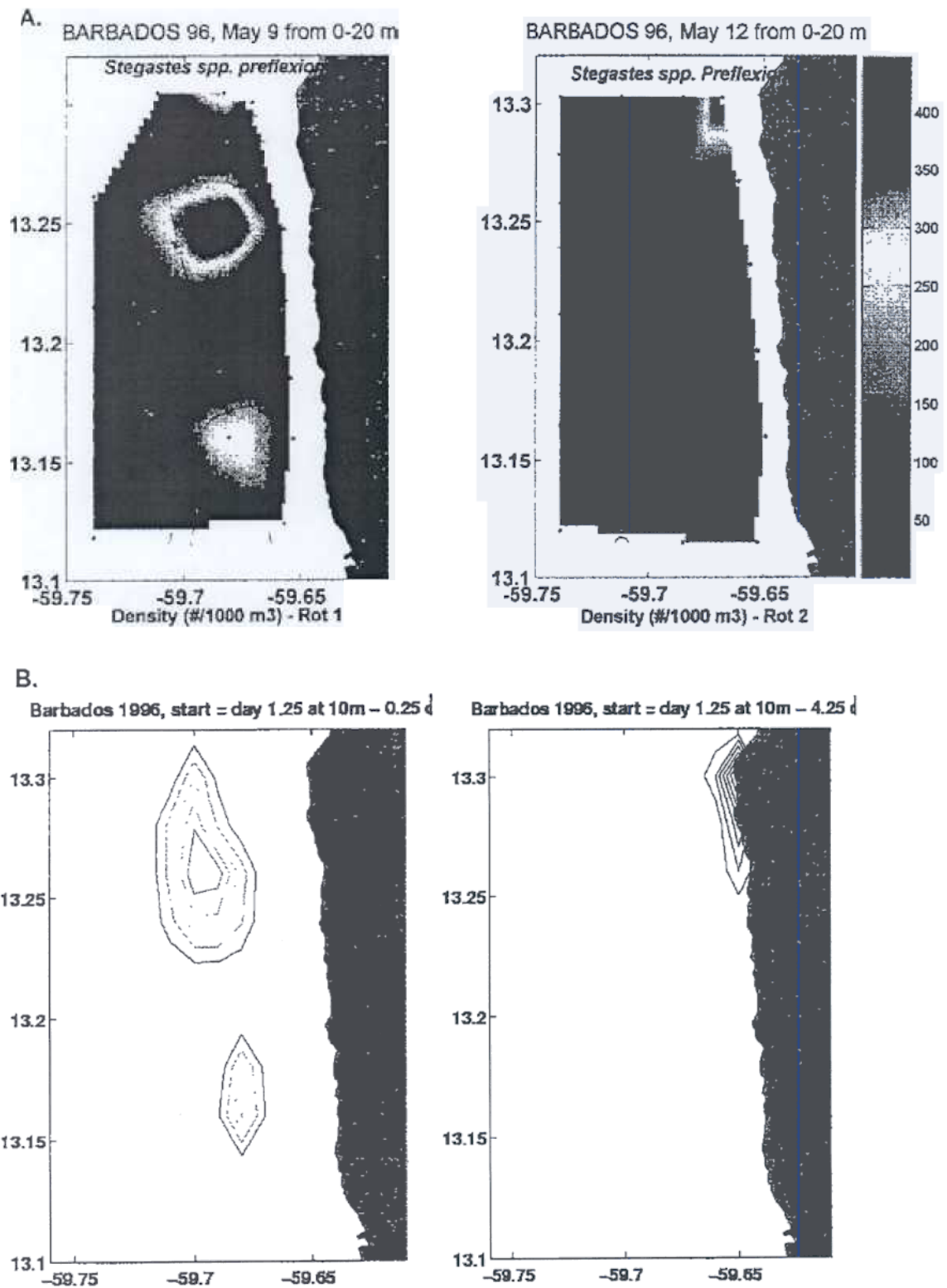


Fig.1. Comparison of results from the ichthyoplankton survey and model output. (A) Observed horizontal distributions of early stage *Stegastes* spp. larvae at 4 d interval surveys during May 1996; dots indicate sampling positions. (B) Modeled distributions for the same 4 d period.

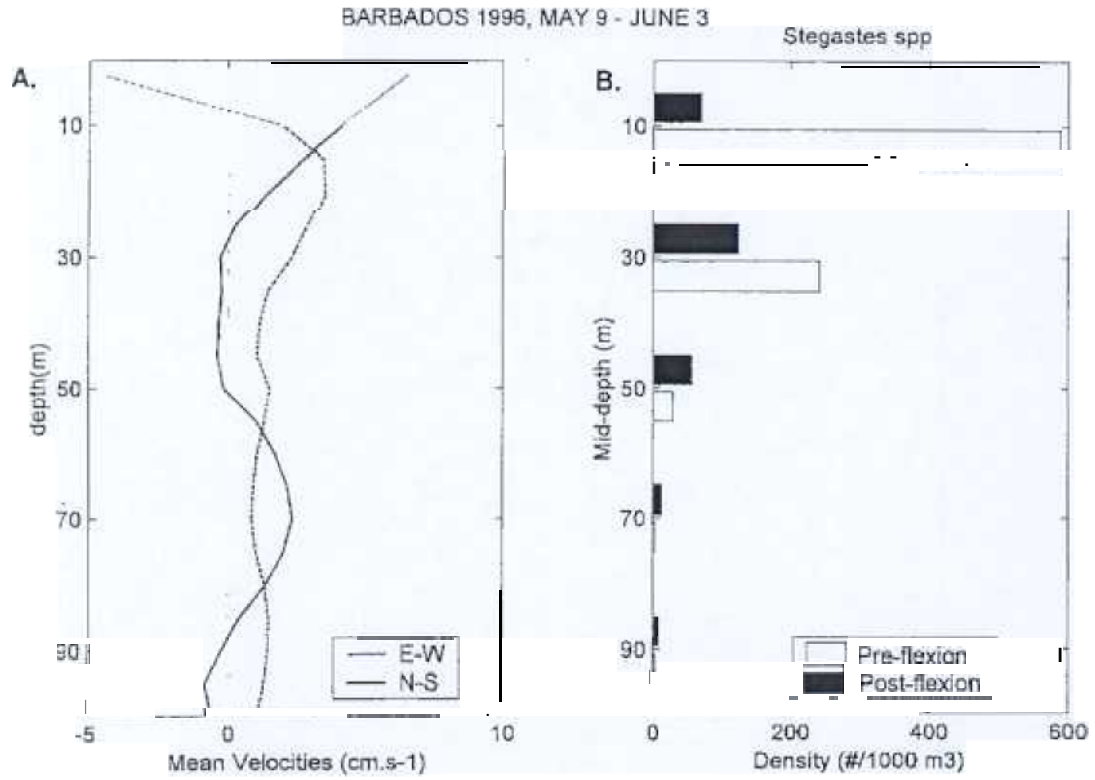


Figure 2. Vertical structure of flow and fish larvae during May 1996: (A) vertical profile of velocities on the western shore of Barbados; note the onshore (positive E/W) flow and low N/S flow at depth; (B) vertical distribution of preflexion and postflexion larvae of the genus *Stegastes* in 20 m depth bins.

A.

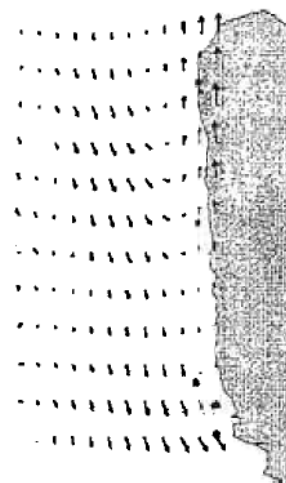
Barbados 96, start = day 5 at 10m - 0.25 d



Barbados 96, start = day 5 at 10m - 1 d



Barbados 96, start = day 5 at 10m - 2 d



B.

Barbados 97, start = day 5 at 10m - 0.25 d



Barbados 97, start = day 5 at 10m - 10 d



Barbados 97, start = day 5 at 10m - 20.25 d

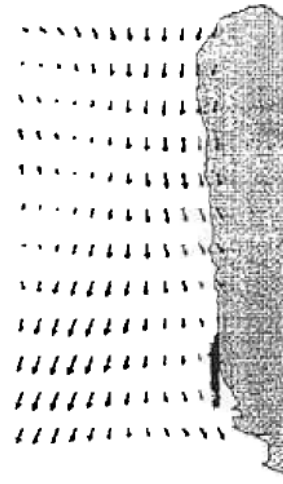


Fig.3. Comparison of simulated larval transport in the upper layer (0-20 m) on the western shore of Barbados for (A) May 1996 and (B) May 1997. Six hatching pulses were released along the reef track at day 5, corresponding to the observed spawning peaks in both years. Current velocity magnitude and direction, integrated over 20 m on a 6-hour time step basis (0.25 day) are also represented on a 1x2 km mesh grid. For May 1996, all larvae were carried out of the domain within 3 d, so only model results are shown for the initial, 1d and 2 d. For May 1997, larvae were still present at day 20, so initial, 10 d and 20 d modeled larval distributions are shown.