

A bio-oceanographic filter to larval dispersal in a reef-building coral

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Abstract

Gene flow was shown to be limited between western and eastern Caribbean populations of the reef-building coral, *Acropora palmata*. However, some mixing was detected among populations near Puerto Rico. Our genetic analyses categorize *A. palmata* samples from the east coast of the Dominican Republic with the western Caribbean population, suggesting a filter to gene flow east of the Dominican Republic. To test the hypothesis of a present day bio-oceanographic filter occurring between Puerto Rico and the Dominican Republic (i.e., in the Mona Passage), we used a Lagrangian stochastic model (LSM) of larval dispersal, coupling coral life history characteristics with physical forcing. The model operated at two spatial scales: Caribbean-wide and focusing on the Mona Passage area. Results from the Caribbean-wide study showed no significant virtual larval exchange between the two populations. The small-scale model indicated that virtual larvae do not readily traverse the Mona Passage during the corals' reproductive season. Larvae released from Mona Island, in the center of the passage, are retained in the lee within topographically steered eddies, which act, together with the larval competency period, as a de facto filter to dispersal. Combined, our findings reveal the location of a seasonal filter to gene flow and its mechanism.

Understanding the causes of population differentiation is an ongoing effort in evolutionary biology. The oceanic environment provides few obvious physical barriers that may prevent genetic exchange of pelagic larvae between populations, so it is difficult to understand how populations differentiate. The numeric (how many?) and geographic (over what distance?) scale of larval movements has been at the center of a long-standing debate. Pelagic larval stages may connect geographically distant populations by riding with fast ocean surface currents (Heck and McCoy

1978; Veron 1995). This view has been challenged by recent reports of localized recruitment and strongly structured populations (Thorrold et al. 2002). Biological factors such as reproductive strategy (Hohenlohe 2004), larval and/or recruit mortality (Schmidt and Rand 1999), and larval behavior (Carlson and Olson 1993; Altieri 2003; Fuchs et al. 2004) may interact with physical factors such as ocean currents (Alexander and Roughgarden 1996; Gaylord and Gaines 2000; Paris and Cowen 2004), eddies (often seasonal), and fragmented adult habitat (Johnson and Black 1995; Riginos and Nachman 2001) to restrict larval dispersal distance and influence its variance (Jackson 1986; Hohenlohe 2004). Understanding of the mechanism of such biophysical barriers to larval dispersal is the focus of this study.

Boundaries between biogeographic regions as described by multispecies distribution records are logical places to also look for present-day barriers to gene flow. A correspondence cannot be assumed a priori because historical discontinuities rather than restricted larval dispersal at the location of the faunal break may underlie the observed species distribution patterns (Hellberg 1998). Point Conception on the California coast has received much attention because a biogeographic boundary coincides there with an ocean current convergence zone that is predicted to restrict along-shore larval dispersal (Dawson 2001). However, evidence for restricted gene flow at Point Conception from genetic studies is equivocal (reviewed in Burton 1998). Hohenlohe (2004) simulated the distribution of genotypes after dispersal by incorporating life history and oceanographic data from the Point Conception area into a deterministic simulation model and found that seasonal variations in ocean currents result in a leaky (i.e.,

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seasonal) barrier to gene flow. Hence, reproductive timing plays an important role in determining the effectiveness of the Point Conception convergence zone, and maybe other bio-oceanographic barriers, in restricting larval dispersal.

In a previous study using microsatellite markers, Baums et al. (2005b) found that populations of the reef-building coral *Acropora palmata* experience little genetic exchange between the eastern and western Caribbean. Puerto Rico was identified as an area of mixing between the two subregions, suggesting that the Mona Passage may play a role in limiting genetic exchange between coral populations as well as fish populations, such as gobies (Taylor and Hellberg 2003) and blennies (Hastings and Springer 1994; Dennis et al. 2004). *Acropora palmata* historically has been a major reef builder in the Caribbean and, as such, has provided habitat for other reef organisms (Lirman 1999). It dominated the reef crest and shallow fore reef (0–5 m, Bruckner 2002), but populations drastically declined during the 1980s and are now considered for listing as “threatened” under the U.S. Endangered Species Act (Bruckner 2002). Knowledge of present-day dispersal patterns of *A. palmata* is potentially informative in regard to the generality of proposed phylogeographic breaks in the Caribbean, which are essential for estimating the likelihood of natural population recovery and thus are needed for conservation measures.

The goal of this study is to test the hypothesized filter to gene flow, find its exact location, and describe its mechanism. Guided by fine-scale genetic models, we investigate the Mona Passage as the location of a potential filter to *Acropora* larval dispersal. First, a Caribbean-wide larval dispersal model served to estimate the likelihood of larval dispersal between the two genetically identified subregions. Then, a smaller-scale numerical model reproduced the observed flow through the Mona Passage and was used to examine (1) the influence of the Mona Passage bottom topography on the flow pattern in the passage, (2) the resulting local circulation features such as small cyclones and their variability, (3) the seasonal influence of the large-scale circulation in the Caribbean Sea on the flow in the vicinity of the Mona Passage, and (4) the effect of the local flow patterns on the larval movements and the likelihood of dispersal across the passage. This study differs from previous modeling efforts (Roberts 1997; Kingsford et al. 2002; Hohenlohe 2004) in that it utilizes near-real-time climatological data and biological information in a stochastic model of larval dispersal operating at several temporal and spatial scales. It is further unique in its combination of fine-scale genetic and biophysical data to investigate barriers to gene flow in the Caribbean.

Materials and methods

Study organism—Distribution of the scleractinian coral, *A. palmata*, is restricted to the wider Caribbean. Once annually, *A. palmata* releases gametes into the water column, generally after the August full moon, in a synchronized spawning effort (Szmant 1986). Fertilization occurs near the surface. After 78 h, larvae have developed cilia, giving them the appearance of “fuzzy balls.” Motility is

observed at this stage (e.g., Baums et al. 2005b). It is generally assumed that larvae remain in surface waters during their early development due to their high lipid content (Szmant 1986). Similar to other invertebrate larvae, *Acropora* larvae show limited vertical migration in the laboratory (observed in a 1,000-mL measuring cylinder) (Fuchs et al. 2004, Szmant pers. comm.). Larvae begin settling out of the water column after 3–5 d; however, some delay settlement up to 20 d in aquaria (M. Vermeij unpubl. data, Margaret W. Miller and I.B. Baums pers. obs.). Pacific *Acropora* larvae show similar developmental patterns: first settlement is observed between 3 and 27 d (Harrison and Wallace 1990; Hayashibara et al. 1997; Nishikawa et al. 2003). This limited larval behavior is well suited for a modeling approach based on physical forcing, timing of settlement (based on larval precompetency and competency periods), and sensing suitable recruitment habitat.

Study region—In accordance with *A. palmata* habitat, the focus of this study is the wider Caribbean (59–90°W, 8–28°N; Fig. 1) and, in particular, the Mona Passage. The Mona Passage is one of the numerous passages between the Antilles islands in the eastern Caribbean. The Antilles form an arc extending from the Bahamas to the northern coast of South America and act as the western boundary of the North Atlantic subtropical gyre. Water enters the Caribbean through the passages in the island chain. Flow magnitude and variability have been studied in the southernmost passages through the Lesser Antilles (Stalcup and Metcalf 1972), and the northern Bahamian passages (Leaman et al. 1987; Atkinson et al. 1995). However, the only direct measurements of seasonal variation in flow through a passage are by Johns et al. (1999), who surveyed the Mona Passage with a shipboard acoustic Doppler current profiler (ADCP) in the upper 200 m of the water column. The Mona Passage was occupied five times between August 1989 and July 1996. The average flow from 0–200 m was predominantly southward (i.e., into the Caribbean) with a subsurface maximum greater than 20 cm s⁻¹ at mid-channel. In addition, there was a persistent countercurrent (i.e., out of the Caribbean) hugging the Puerto Rican shelf, with average speeds over 10 cm s⁻¹ (see fig. 6 in Johns et al. 1999). As such, the meridional transport in the Mona Passage, combined with currents flowing in opposite directions, may constitute a natural barrier against larval dispersion.

Genetic analysis—Samples of *A. palmata* were obtained from the Bahamas ($n = 16$ from Lee Stocking Island), the Dominican Republic ($n = 51$ from Punta Cana), Puerto Rico ($n = 50$ from Aurora Reef), and the U.S. Virgin Islands ($n = 50$ from Haulover Bay) (Fig. 1). Sample preservation, extraction, and genotyping followed Baums et al. (2005a,b). Briefly, two multiplex polymerase chain reactions (PCR) were performed per sample using fluorescent-labeled primers to assay five microsatellite loci containing the asparagine codon (AAT) repeats. The loci had previously been shown to satisfy assumptions of genetic models, i.e., they had mendelian inheritance and

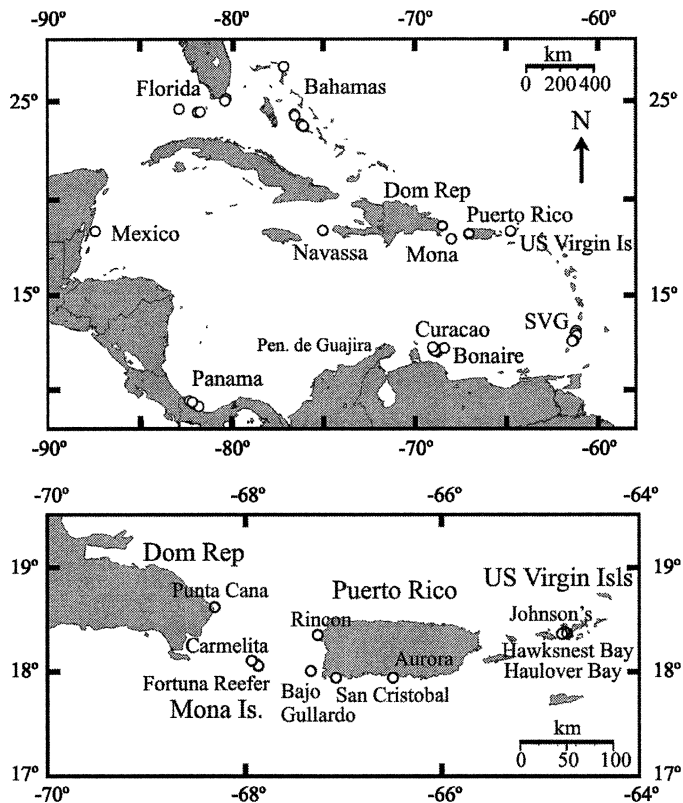


Fig. 1. Maps of sampling localities of *Acropora palmata* in the Caribbean used in the genetic model. Maps were created with Online Map Creation (OMC) (<http://www.aquarius.geomar.de/omc>).

were unlinked (Baums et al. 2005a). Unique genotypes ($n = 150$) were then added to the published Caribbean-wide data set of *A. palmata* genotypes obtained with the same methods in the same laboratory (Baums et al. 2005b). Genetic analysis was performed by STRUCTURE (Falush et al. 2003) and followed Baums et al. (2005b). STRUCTURE uses a Bayesian clustering algorithm to probabilistically assign genotypes to populations. Increasing the sample density around the area of interest (i.e., the Mona Passage) reduces potential bias introduced by unsampled “ghost” populations (Beerli 2004). The likely origin of samples from the Dominican Republic was investigated by designating them as “unknowns” under the assumption of no admixture in STRUCTURE. All other samples were assigned a priori to either the western or eastern Caribbean populations in concordance with earlier results (Baums et al. 2005b; Fig. 2).

Large-scale larval dispersal model—To evaluate the extent to which *Acropora* larvae disperse under a series of realistically varying spatial and temporal oceanographic conditions, we utilized a coupled particle-tracking dispersal (Lagrangian stochastic model, LSM) and recruitment (a geographical information system [GIS] of coral reefs in the Caribbean) model (C.B. Paris and A. Srinivasan, unpubl. data) running offline with the $1/12^\circ$ (~ 8 km horizontal resolution) Miami Isopycnal Coordinate Ocean Model

(MICOM; <http://oceanmodeling.rsmas.miami.edu/micom/>; Garraffo et al. 2001). The computational domain was the North and Equatorial Atlantic Ocean basin from 28°S to 70°N , including the Caribbean Sea, the Gulf of Mexico, and the Mediterranean Sea. Open ocean boundaries were treated as closed, but were outfitted with 3° buffer zones in which temperature (T) and salinity (S) were linearly relaxed toward their seasonally varying climatology values (Levitus 1982), with damping/relaxation time from 5 d at the wall to 30 d at the inner edge of the buffer zone. These buffer zones restore the T and S fields to climatology in order to approximately recover the vertical shear of the currents through geostrophic adjustment. After a 6-yr spin-up with monthly climatological forcing, the model was integrated using surface boundary conditions based on European Center for Medium-Range Weather Forecasting (ECMWF) daily atmospheric data from 1979 to 1986. The *Acropora* model was parameterized by biological factors such as maximum pelagic larval duration (PLD = 20–30 d), precompetent period (PC = 3–5 d), after which larvae can settle, and spawning strategies (2–3 d after the August full moon) of the coral.

Successful dispersal requires that larvae encounter suitable coral reef settlement habitat, which is fragmented and often covers only a small proportion of the total area of potential dispersal by currents. Thus, we restricted recruitment of virtual larvae to benthic habitat defined by the presence of coral reefs throughout the spatial domain of the model (i.e., the wider Caribbean: $59\text{--}90^\circ\text{W}$, $8\text{--}28^\circ\text{N}$; Fig. 1). We defined recruitment as the time when larvae sense suitable habitat (i.e., during the competent period), settle out of the plankton, and become part of the benthos. The coral reef habitat was parameterized by a series of polygons that were mapped as a 9-km buffer (similar to the model grid-cell resolution) around the coral reef area. Reef area was extracted from the World Resources Institute (WRI) Reefs at Risk in the Caribbean database (<http://marine.wri.org>), which is derived from remote-sensing observations and data produced by the World Conservation Monitoring Center (UNEP-WCMC). These polygons were partitioned in ~ 50 -km bins and were defined in the model as nodes (N_i), each of which represented a habitat patch i located by a spatial centroid (longitude, latitude).

A synchronous mass spawning event (1000 particles) was simulated at each of the nodes during August. To resolve interannual variability in transport within the entire region, this biophysical model was run for 5 consecutive real-wind years (i.e., 1979 to 1983) obtained from ECMWF. Successful larval recruitment was measured as the number of larvae reaching a suitable settlement habitat (i.e., node N_i) within the larval competent period. Virtual larvae were passive during the precompetent period (i.e., 3–5 d after their release), then they became active by sinking out from the water column and settling in the first reef habitat that their trajectory intercepted as a response to potential external stimuli from the suitable habitat. Individual particles continued their trajectory until intercepting a habitat patch (N_i) or until the end of the competent period (PLD, 20–30 d), after which they died. No quantitative information on population-level gamete pro-

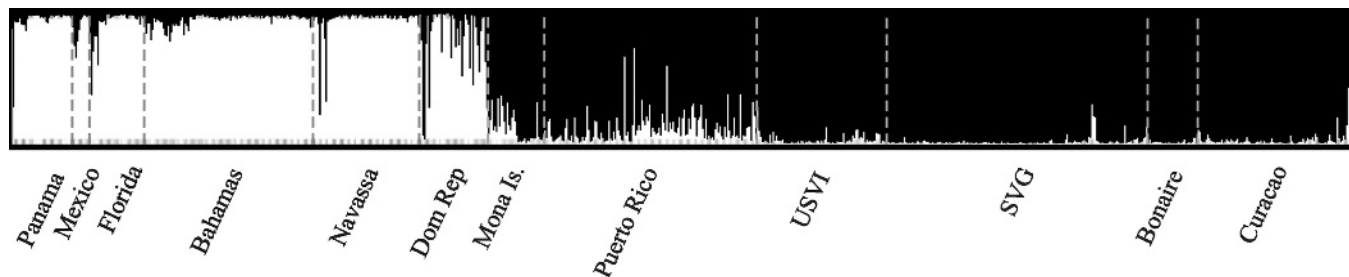


Fig. 2. Assignment of genotypes from the Dominican Republic (DR) to predefined eastern (white) and western (black) Caribbean clusters using STRUCTURE. Shown is the probability of ancestry in each cluster for all genets ($n = 859$). Genotypes from the DR clustered with the western population. The western population included genets from Panama, Mexico, Florida, the Bahamas, and Navassa. The eastern cluster included genets from Mona Island, Puerto Rico, the U.S. Virgin Islands (USVI), St. Vincent and the Grenadines (SVG), Bonaire, and Curacao. Sampling localities are delineated by gray vertical, dashed lines. Note that most genets from Mona Island and Puerto Rico showed varying degrees of western Caribbean ancestries.

duction and natural mortality rates of *Acropora* larvae were available. Thus, levels of recruitment were reported as the fraction of virtual larvae released that were settling onto available habitat without correcting for mortality in a source-recruitment matrix. These estimates should accurately reflect relative patterns of connectivity among localities. Dispersal and recruitment results are shown for the 23 nodes (Fig. 3) that corresponded to sampling localities of the genetic study (Fig. 1).

Small-scale numerical model—Local, small-scale dynamics of the Mona Passage were studied using the Regional Ocean Modeling System (ROMS), which is discretized in coastline- and terrain-following curvilinear coordinates (σ -coordinates model). The model has appropriate boundary conditions for an irregular solid bottom and coastline, free upper surface, and open-ocean sides away from the coastline (Marchesiello et al. 2003; Shchepetkin and McWilliams 2004). The boundary fluxes and initial conditions include temperature and salinity, the forcing influences of surface wind stress, heat and water fluxes, coastal river inflow, bottom drag, open-ocean outgoing wave radiation, and nudging toward the specified basin-scale circulation.

These boundary fluxes and initial states of the ocean were provided by the monthly Levitus climatology (Da Silva et al. 1994). The ocean boundaries were treated as open and were outfitted with buffer zone where T and S were relaxed toward their monthly varying climatology. Using monthly climatology surface fluxes and boundary conditions removed the high-frequency variability of the atmosphere and the ocean, but retained the seasonal variability and the annual signal. We chose a monthly time scale because we aimed to provide a general explanation for the long-term break in the *A. palmata* genetic differentiation between the western and the eastern subregions as it is related to the physical oceanography of the region. To reduce the computational burden, we released virtual larvae (see following) during two months only: the reproductive month of August and the month of January, which is representative of winter conditions.

The numerical experiment consisted of a child grid embedding the Mona Passage (Fig. 4A) with a $1/54^\circ$

(~ 2 km) horizontal resolution within a $1/18^\circ$ (~ 6 km) parent grid. This constituted 171 grid points in the x direction and 161 in the y direction (Fig. 4A). Twenty-five layers were used to discretize the water column in the vertical for both grids. The experiment started after a 6-month model spin-up when 4 to 100 virtual floats (depending on release depth) were released every 6 h, at two depths (5 and 10 m), over 2 months (August and January) at the beginning, the middle, and the end of each month. The model was run continuously until the end of the experiment, 45 d after the last release in January. The float release locations coincided with known locations of *A. palmata* colonies on both sides of the Mona Passage and on Mona Island (Figs. 1, 4B). Float trajectories were tracked for a maximum period of 62 d and were postprocessed with the GIS-based model (see above section—Large scale larval dispersal model) of the *Acropora* settlement habitat in the vicinity of the Mona Passage. The fraction of particles intercepting settlement habitat after 5 d (i.e., the conservative start of the competent period), and thereafter until a PLD maximum of 30 d, was computed to assess the magnitude of larval exchange across the passage.

Results

Origin of genets from the Dominican Republic—*A. palmata* genets from the Dominican Republic were clustered with the western Caribbean population (Fig. 2). Only 4 out of 40 genets from the Dominican Republic had a $<50\%$ probability of having originated in the west, and 2 of these had a $<10\%$ probability. Genets from Puerto Rico and Mona Island clustered mainly with the eastern Caribbean population (Fig. 2). However, most genets from Puerto Rico and Mona Island also showed some degree of western Caribbean ancestry (white portion of bars in genets from Mona Island and Puerto Rico in Fig. 2). Thus, the Mona Passage may act as a filter to coral larval dispersal, greatly reducing gene flow between the eastern and western Caribbean *A. palmata* populations.

Large-scale dispersal patterns—Dispersal of *Acropora* larvae among sampling localities around the Caribbean was assessed with the large-scale biophysical model. Self-

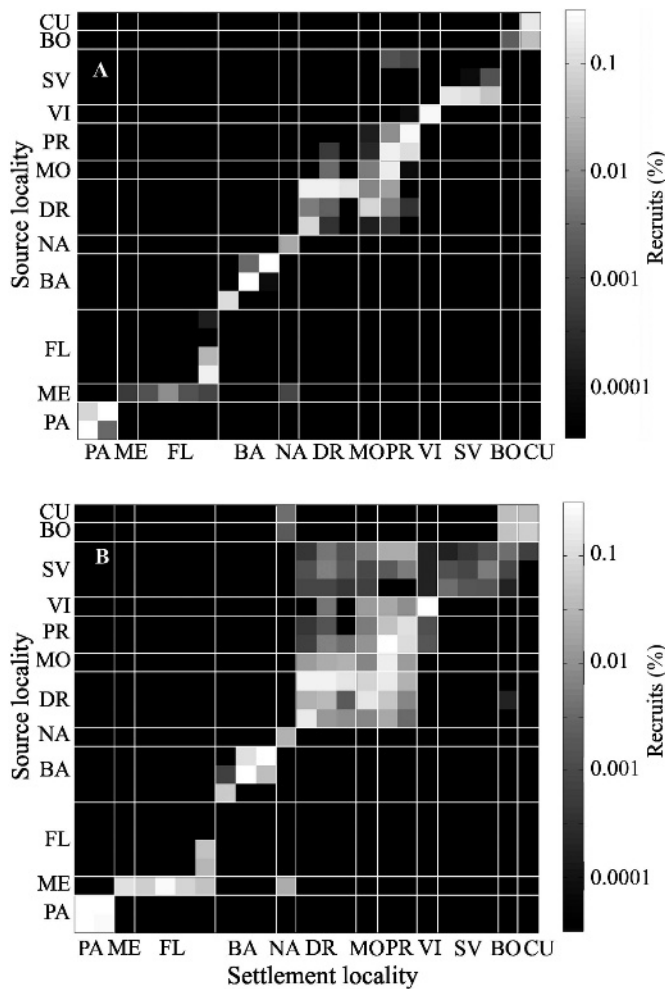


Fig. 3. Simulated exchanges of virtual *Acropora palmata* larvae among localities in the Caribbean: The large-scale model results are shown in a connectivity matrix of 23 nodes that correspond to sampling localities of the genetic model. Mass spawning during the August full moon was replicated in each node over a 5-yr period (1979–1983). Successful larval recruitment was measured as the number of larvae reaching suitable habitat within the larval competent period beginning 5 d after release (larvae were passive for 96 h after spawning) and ending after a maximum competency period of (A) 20 d or (B) 30 d. The relative amplitude of recruitment (Recruit %) contributing to each site is displayed in a \log_{10} scale and standardized by the total number of particles released at each site (no larval mortality was added). When the source and receiving locations are the same (along the diagonal), self-recruitment occurs. Thin white lines separate the sampling localities that encompass various numbers of nodes. Note that daily mortality rates for *Acropora* larvae are not known and therefore not reflected in the levels of recruitment in the dispersal matrix. Localities: Curacao (CU), Bonaire (BO), St. Vincent and the Grenadines (SV), U.S. Virgin Islands (VI), Puerto Rico (PR), Mona Island (MO), Dominican Republic (DR), Navassa (NA), Bahamas (BA), Florida (FL).

recruitment (i.e., recruitment along the diagonal) was predominant in most localities (Fig. 3). However, the large-scale model did not resolve the Mona Passage as a break. Although at levels order(s) of magnitude lower than self-recruitment, larvae were exchanged among Puerto

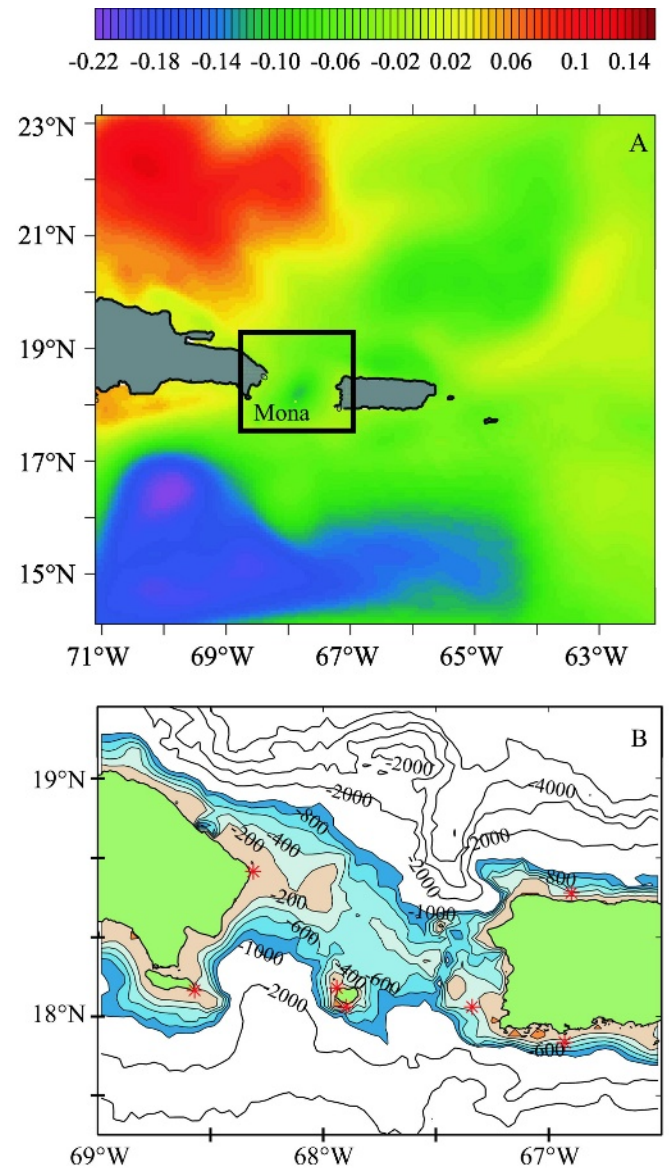


Fig. 4. (A) The Regional Ocean Modeling Systems (ROMS) model grid setup. The quadrant around Mona Island defines the child grid. Colors show the sea-surface height (SSH) in meters. (B) Bottom topography of the Mona Passage (in meters). Red stars show the location of particles released in the ROMS model in the vicinity of Mona Passage.

Rico (Puerto Rico), Mona Island (MO), and the Dominican Republic (DR) populations (Fig. 3). Outside of this area, no import or export occurred between the two subregions at 20 d PLD (e.g., empty nodes on the upper left corner and lower right corner of the matrix, Fig. 3A). The sole exception was St. Vincent and the Grenadines (SVG), which provided a small proportion ($\sim 0.1\%$) of larvae to Puerto Rico. Curacao and Bonaire were connected to each other but relatively isolated from other localities, yet placed in the eastern Caribbean, because they received recruits from the St. Vincent and the Grenadines when PLD was extended to 30 d (Fig. 3B).

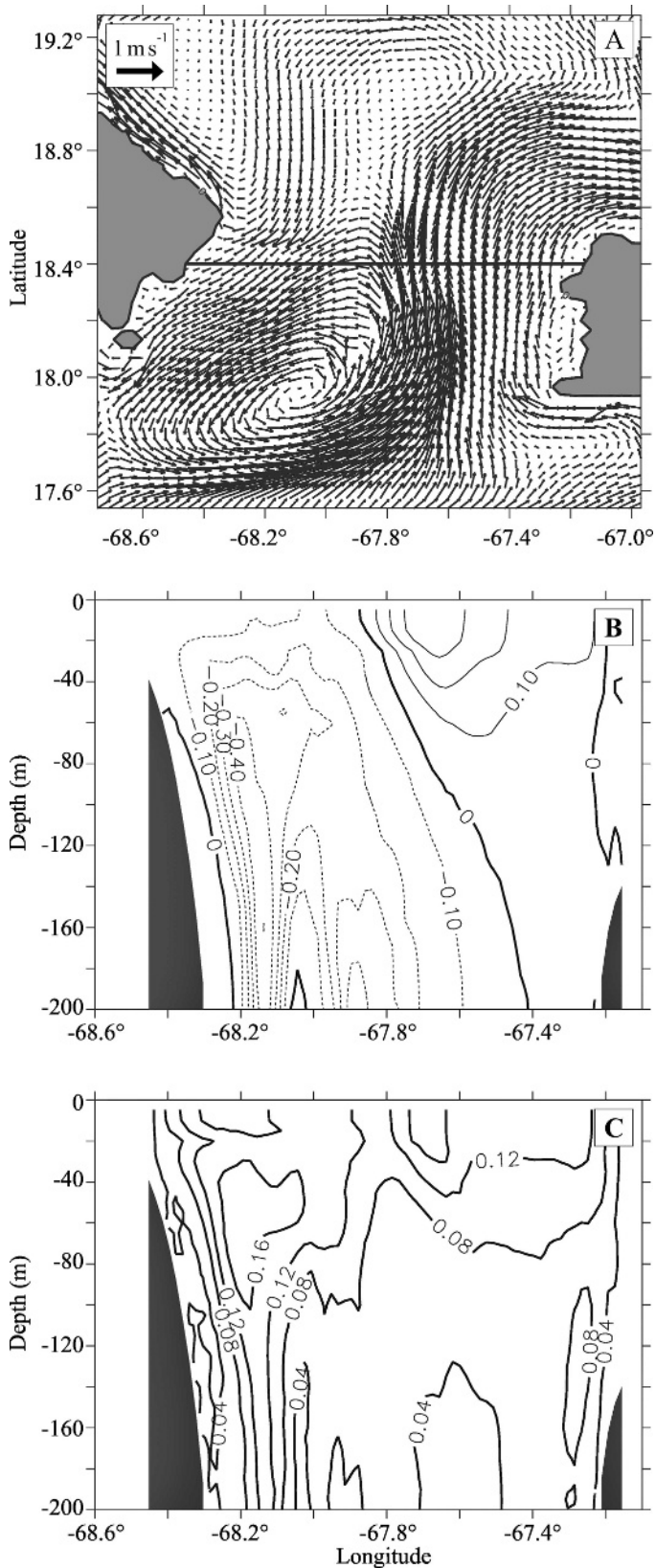


Fig. 5. (A) 20-d surface averaged flow in the Mona Passage. The transport is calculated through the section shown by the solid line. The crossed square indicates the location of Mona Island. (B) Mean meridional flow in model's month of August across

The total fraction of virtual larvae recruiting within the two subregions (standardized by the number of nodes in each subregion) was approximately 20% higher in the western Caribbean. However, when connectivity (C) was measured as the fraction of nodes with recruitment weighted by the mean distance (D) between nodes (i.e., $C = \sum N_{ij} / \langle D_{ij} \rangle \sum N_{ij}$), localities sampled in the east were approximately three times more connected to each other than those sampled in the west ($C_E/C_W = 0.34$). When larval duration was extended to 30 d, the levels of connectivity (i.e., number of virtual larvae recruiting in each node) increased in the western subregion, but the number of nodes connected (or connectedness) remained almost unchanged. The only new connection within the western Caribbean population was between Mexico and Navassa. In contrast, in the eastern subregion, recruitment levels decreased but connectedness increased when PLD was extended. The U.S. Virgin Islands (VI) became a new larval source for the Dominican Republic–Mona Island–Puerto Rico area. The Virgin Islands also received a small amount of larvae from Puerto Rico in return. The largest new larval source was the Grenadines, which provided propagules to all eastern locations and the Dominican Republic (Fig. 3B).

In summary, we found a division between the eastern and western Caribbean with distinct patterns of larval connectivity. Yet, larvae were exchanged between the two subpopulations in the Dominican Republic–Mona Island–Puerto Rico area.

Flow patterns in the Mona Passage—Figure 5A shows the surface velocity field over the child grid, averaged over 20 d in August (to encompass the estimated pelagic larval duration of *A. palmata*). The surface current is flowing southward on the western side and northward on the eastern side of the Mona Passage. The presence of both meridional currents is associated with a cyclonic eddy southwest of Mona Island, where its northern edge flows around the island. The average flow pattern exhibits two cores in the upper 200 m of the Mona Passage: to the west, a southward-flowing core, subsurface intensified ($>40 \text{ cm s}^{-1}$ at 60 m; Fig. 5B); to the east, a northward-flowing core surface intensified ($>30 \text{ cm s}^{-1}$). Both cores were highly variable, as shown by the standard deviation of the current speed in Figure 5C. In the first 200 m of the Mona Passage, the average transport in model month August across the section at 18.4°N (Fig. 5) is $-1.6 \times 10^6 \text{ m}^3 \text{ s}^{-1} \pm 0.66 \times 10^6 \text{ m}^3 \text{ s}^{-1}$. In contrast to the summer, the average flow in January is northward in the upper 50 m across the Mona Passage and southward below 50 m (not shown).

←

section at 18.4°N . Solid (dashed) lines are positive (negative or southward) velocities (m s^{-1}). Thick solid lines are the zero velocity contours. (C) Standard deviation of the model flow in panel B during August.

Topography and flow dynamics—The Antilles island arc constitutes a barrier to the flow in and out of the Caribbean Sea. Within the passages, flow is constrained by the bottom topography (e.g., sills, Figs. 4B). The depth in the Mona Passage decreases rapidly from 400 m at the top of the sill to below 2000 m. The sill connects the northeast coast of Hispaniola to the southwest coast of Puerto Rico across the passage. Mona Island forms a small mount with steep slopes just south of the sill at approximately mid-distance between the bigger islands of Puerto Rico and Hispaniola. The Regional Ocean Modeling Systems (ROMS) simulation from the child grid shows the evolution of eddies in the passage that are associated with the rapid changes in water depth north and south of the sill (Fig. 6). Namely, as the depth decreases above the sill, the flow moving toward the sill develops anticyclonic circulation. But as soon the flow reaches the deep waters on the other side of the sill, cyclonic circulation is created ad novo and strengthened as a result of the rapid depth increase. This effect is explained by the conservation of a quantity called the potential vorticity (Ertel 1942)

$$q = \frac{\zeta + f}{h},$$

where $\zeta = \partial_x v - \partial_y u$ is the rotation of the velocity field, also called relative vorticity, f is the Coriolis parameter, and h is the water depth. As this quantity (q) is conserved in an isopycnal layer, the depth change is compensated by the relative vorticity. Therefore, when the depth decreases (increases) as the water flows up (down) the sill, negative (positive) ζ anomaly is enhanced; this corresponds to anticyclonic (cyclonic) relative vorticity.

The effect is illustrated in Figure 6, which shows a snapshot of the formation of a cyclone by topographic constraint in the vicinity of Mona Island as it occurs in August in the ROMS simulation. The intensity of the cyclone decreases above the sill as depth decreases (Fig. 6B,C). As the cyclone reaches deep waters south of Mona Passage, its strength increases again (Fig. 6D,F). In the simulation, the cyclone became trapped around Mona Island for a period of 30–40 d until it moved back to the coast of Hispaniola and decayed (not shown).

In summary, with the cyclone trapped around Mona Island, the flow is to the north on the east side and to the south on the west side of the Mona Passage. This flow pattern can be strongly perturbed by large-scale eddies on either side of the Mona Passage, and they will then force southward or northward flow through the entire width of the passage (not shown).

Larval transport in the Mona Passage—Simulated larval exchanges among reef areas around the Mona Passage revealed that east-to-west (i.e., Puerto Rico to Hispaniola) and west-to-east (Hispaniola to Puerto Rico) crossing of a small fraction of particles (i.e., 1%) may occur in January (Fig. 7B) but not in August (Fig. 7A; Table 1). During *A. palmata* spawning, Mona Island is highly self-recruiting (i.e., 52% of particles are retained in the lee) with very little exchange toward the west (i.e., to Hispaniola, 2%). In contrast, during January, 3% of the total number of

particles released from Mona Island reach the coral reef habitat on the east of the passage (S-SW Puerto Rico). Self-recruitment to Mona Island is diminished by nearly half compared to the August release.

The presence of a zonal barrier to larval dispersal was verified with real float trajectories (Fig. 7C). Although the real surface floats were not released in the vicinity of the Mona Passage, nor were they all passing through the area specifically in August, none of the trajectories connected the eastern coast of Hispaniola with Puerto Rico. Some trajectories flushed through the passage after being subjected to small loops when passing on the sill, as predicted by the model.

Discussion

Evidence has been mounting that larval dispersal of marine organisms in general, and within the Caribbean basin in particular, is limited (Swearer et al. 2002; Taylor and Hellberg 2003; Cowen et al. 2006). Several coral reef associated organisms have strongly structured populations as suggested by genetic and other markers (Swearer et al. 2002). However, mechanisms explaining restricted larval dispersal in the Caribbean have rarely been investigated (Paris and Cowen 2004). Here, we identify the Mona Passage between the Dominican Republic and Puerto Rico as a filter to larval dispersal of an important reef-building coral. By integrating biological and physical parameters in a larval dispersal model, we reveal that a combination of reproductive timing, larval traits, and oceanographic features act together to greatly reduce dispersal between the western and eastern Caribbean populations of *A. palmata*. These findings validate not only the location of a filter to gene flow in a marine organism but also suggest its mechanism.

A filter to gene flow in the Caribbean—The Caribbean has traditionally been regarded as one marine biogeographic province (Veron 1995), partly due to the strong currents running through the basin. Indeed, several invertebrates appear to be panmictic (i.e., show no population structure) over their Caribbean-wide range (Mitton et al. 1989; Campton et al. 1992; Silberman et al. 1994). However, with the application of higher-resolution microsatellite markers, population structure has been detected in Bahamian populations of brooding gorgonians that can be divided into three subregions (Gutierrez-Rodriguez and Lasker 2004). Similar patterns of genetic breaks have been detected among lineages of a marine mussel (Lee and Foighil 2005).

The Mona Passage has been the focus of investigations into the presence of biogeographic barriers for marine fish in the Caribbean (Taylor and Hellberg 2003; Dennis et al. 2004). Some reef fish show only slight evidence of population structure throughout the Caribbean (Shulman and Bermingham 1995; Carlin et al. 2003). Several fish species, however, break at the Mona Passage as evidenced by species distribution records (Starck and Colin 1978) and genetic data (Taylor and Hellberg 2003). There is disagreement whether pre- or post-settlement processes underlie the

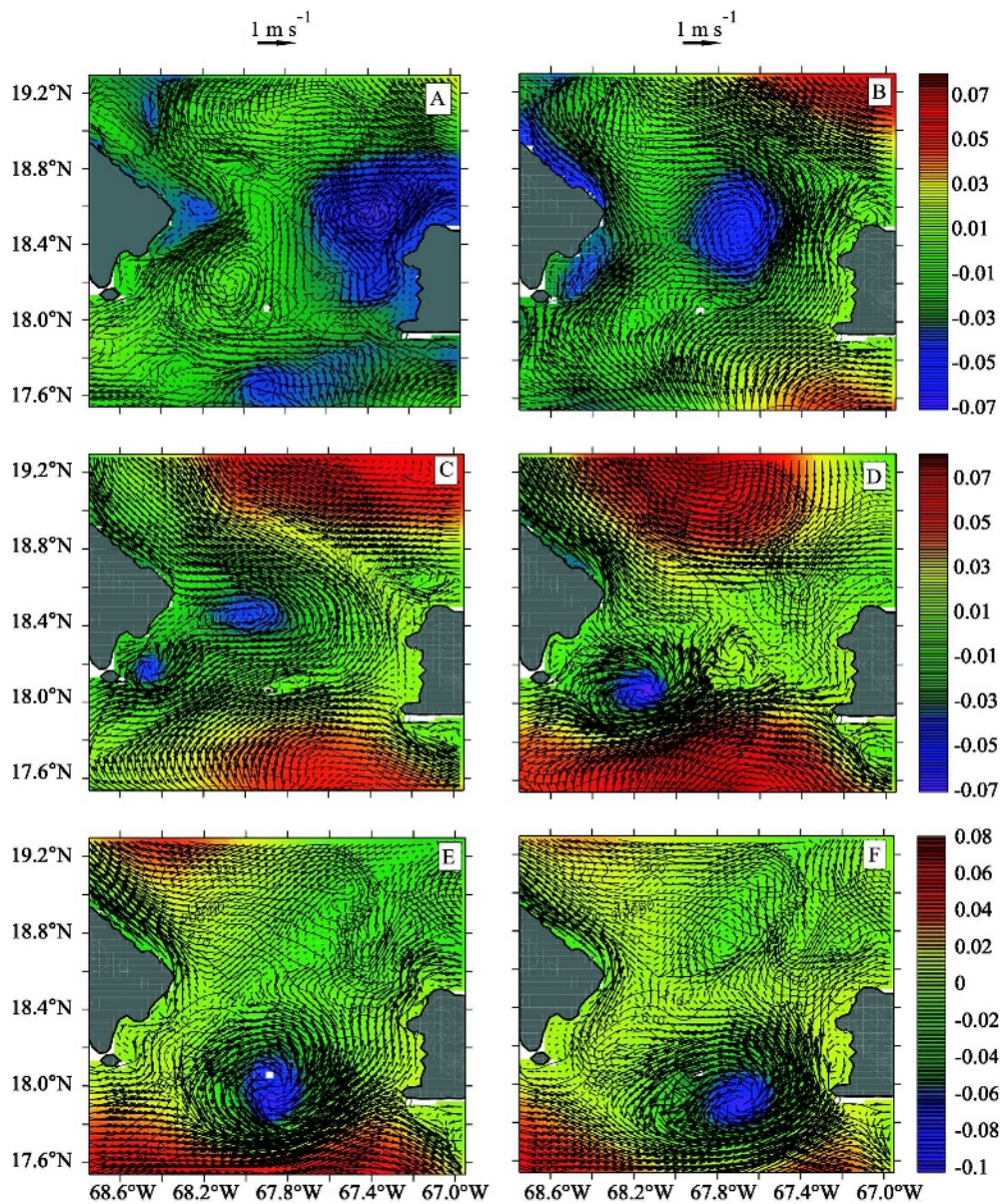


Fig. 6. (A–F) Time series of sea-surface height (SSH; in meters) from the child model showing the lifetime of a cyclone (blue contours) in the Mona Passage over three model months. Positive contours (red) correspond to anticyclonic flows; black arrows indicate the direction and intensity of currents (m s^{-1}).

observed pattern (Rocha et al. 2005; Taylor and Hellberg 2005). Here, we provide evidence that the Mona Passage has unique oceanographic features that may greatly limit larval dispersal across this narrow stretch of water during certain times of the year.

For the Elkhorn coral, *A. palmata*, Puerto Rico had been identified as an area of mixing between two Caribbean populations based on genetic evidence (Baums et al. 2005a,b). Samples from Navassa, northwest of Puerto Rico and from the U.S. Virgin Islands, southeast of Puerto Rico, clearly belonged to the western and eastern populations, respectively (Baums et al. 2005b). The accuracy of the genetic models used depends in part on the completeness of the sampling. Ghost populations (i.e.,

areas from which no samples were obtained) may bias the outcome of these models (Beerli 2004). We increased the sampling density around the area of interest (i.e., the Mona Passage) by including samples from the east coast of the Dominican Republic. These samples clearly grouped with the western Caribbean population, indicating that a potential break must be located to the east of the Dominican Republic (Fig. 2). Because some genets from the Dominican Republic, Mona Island, and Puerto Rico had mixed ancestries, occasional larval dispersal (i.e., over generations) likely occurs across the passage (Fig. 2). Thus, based on current genetic evidence, the Mona Passage maybe described as a filter to *A. palmata* larval dispersal.

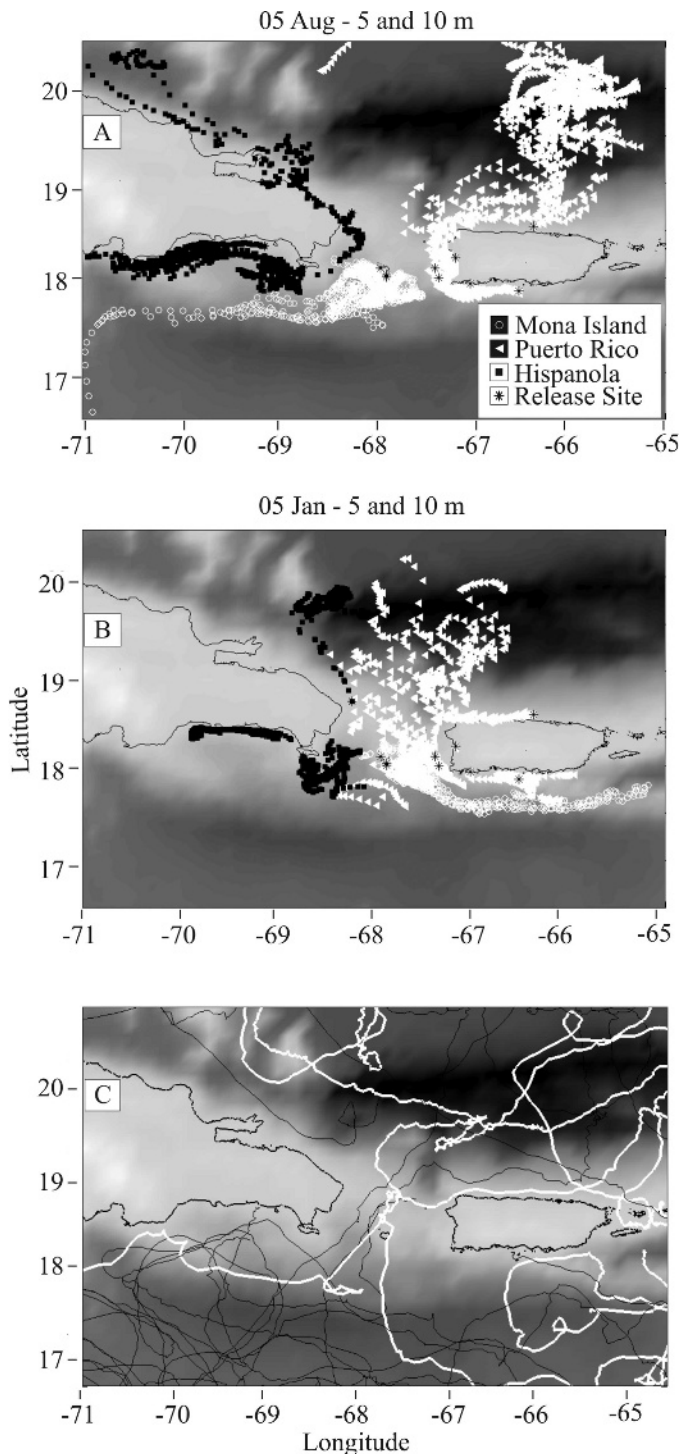


Fig. 7. Dispersal (daily position) of particles released in the ROMS at Mona Island, as well as east (Puerto Rico) and west (Dominican Republic) of the Mona Passage during the months of (A) August and (B) January. Particles are released every 6 h on the 05, 21, and 29 of August or January and tracked for 20 to 62 d. While there is no east-west exchange of particles during August, crossing from east to west and mixing at Mona Island occur during January. (C) Real float trajectories from the Global Lagrangian Drifter Database (GDL, <http://www.aoml.noaa.gov/phod/soto/gsc/data.php>). Floats passing through the model region between July and September are shown in white solid lines. Note

Potential mechanisms underlying a barrier to larval dispersal in *A. palmata* may act before or after larvae recruit (or during both periods). For example, some distinct lineages of a Caribbean mussel are maintained by postrecruitment processes rather than as a result of limited dispersal (Lee and Foighil 2005). This hypothesis is testable with reciprocal transplanting experiments of *A. palmata* larvae among habitats on either side of the Mona Passage. Note that such experiments would be difficult to conduct on this species because it produces larvae only once a year and matures over several years. Instead, the focus of this study was to investigate certain processes that may influence prerecruitment distributions of *A. palmata* larvae.

Large-scale larval dispersal patterns—The large-scale biophysical model supports the hypothesis that there are two, largely self-recruiting *A. palmata* populations, and mixing occurs around the Mona Passage (Fig. 3A). The break identified with the genetic model extended to the South American coast, between the sampling localities in Panama and the Netherlands Antilles (i.e., Bonaire and Curacao; Baums et al. 2005b). Data from the larger-scale biophysical model showed that virtual *Acropora* larvae released from Bonaire in August never reached the Colombian Basin, rather they crossed the Venezuelan Basin meridionally and eventually seeded Navassa when pelagic duration was extended (Fig. 3B). Westward larval exchange from the Venezuelan Basin to the Colombia-Panama gyre area was equally absent in a recent study of population connectivity (Cowen et al. 2006), and some goby species are separated from their cold-water tolerant cousins by Punta Guajira on the northern tip of Venezuela (Colin 1975). This area clearly warrants further study.

The effect of pelagic larval duration (PLD) on gene flow remains unpredictable (Doherty et al. 1995; Shulman and Bermingham 1995). It is commonly assumed that longer PLD results in higher connectivity; however, the degree of habitat fragmentation, larval behavior, and juvenile and adult habitat preferences may also be an important factor in determining recruitment distance (Riginos and Nachman 2001; Bierne et al. 2003). In the present study, an increase in competency period had little or no effect on the patterns of connectivity in the western Caribbean, while it resulted in an increase in connectivity in the eastern Caribbean (Table 1; Fig. 3). The most obvious difference between the subregions is the geomorphology of the reef habitat: while the eastern Caribbean is dominated by relatively isolated islands, the western Caribbean features continuous coastlines (the Mesoamerican and Florida reef tracts) and shallow bank reefs (the Bahamas). The continuous shelf areas in the western Caribbean result in a more uniform distribution of habitats (see <http://marine.wri.org> for Caribbean reef distribution maps). Thus, for a similar maximum competency period, modeled larvae remained

←

that the trajectories are looping as they pass over the sill north of Mona Island. Latitude and longitude are in degrees.

Table 1. Simulated exchanges of *Acropora palmata* larvae among reef areas around the Mona Passage (see Fig. 4 for release locations; data from the two sites of Mona Island are pooled) during August and January. Virtual larval transport between source (rows) and receiving (columns) locations was estimated using the velocity field from the small-scale coastal numerical model (ROMS). Larvae were competent (i.e., able to recruit) at day 5, and their (conservative) maximum pelagic duration was 30 d. Values (fraction of particles released per site) along the diagonal are recruitment within the same location (i.e., self-recruitment, italicized); underlined values indicate crossing of the Mona Passage. Note that crossing of the passage occurs only during January with the exception of larvae released from Mona Island in August. The latter originated from the south of Mona Island, traveled westward, and recruited to southeast coast of Hispaniola (H). In January, the predominant direction of larvae crossing the passage was eastward toward Puerto Rico (PR). Also, note that self-recruitment at Mona Island nearly doubles in August.

	H SE	H NE	Mona	PR SW	PR NW	PR W
Aug						
H SE	<i>0.32</i>	0.00	0.00	0.00	0.00	0.00
H NE	0.00	<i>0.13</i>	0.00	0.00	0.00	0.00
Mona	<u>0.02</u>	0.00	0.52	0.00	0.00	0.00
PR SW	<u>0.00</u>	0.00	0.00	<i>1.00</i>	0.00	0.00
PR NW	0.00	0.00	0.00	0.00	<i>0.98</i>	0.00
PR W	0.00	0.00	0.00	0.00	0.00	<i>0.03</i>
Jan						
H SE	<i>0.41</i>	0.00	0.01	0.00	0.00	<u>0.01</u>
H NE	0.00	<i>0.41</i>	0.00	0.00	0.00	<u>0.00</u>
Mona	0.00	0.00	<i>0.29</i>	<u>0.02</u>	0.00	<u>0.01</u>
PR SW	0.00	0.00	0.00	<i>1.00</i>	0.00	0.00
PR NW	<u>0.01</u>	0.00	0.02	0.00	<i>0.48</i>	0.02
PR W	<u>0.00</u>	0.00	0.03	0.00	0.00	<i>0.48</i>

pelagic for shorter periods in the western Caribbean where settlement habitat was abundant. Concordantly, Hohenlohe (2004) found that an increase in PLD beyond 30 d did not result in a further increase in modeled gene flow levels along a shoreline with continuous habitat.

In summary, the large-scale model based on larval behavior and physical forcing corroborated the findings of the genetic model; however, the exact location and mechanism by which the genetic break occurs was not apparent at this broader scale. Biological information for *Acropora* (i.e., larval mobility and natural mortality, maximum competency, patterns of settlement) is still needed to map dispersal kernels and their variance throughout the Caribbean.

Small-scale eddies as dispersal filters—Prevailing oceanographic conditions during the month of August result in a northward surface flow along the western coast of Puerto Rico, and a southwestern and western flow along the eastern and northern coasts of Hispaniola. Our results compare favorably with measurements reported by Johns et al. (1999), in terms of flow direction, strength, and variability (their figure 6). The current vectors on their figure 6 are characteristic of a turbulent flow, perturbed by small-scale eddies. Johns et al. (1999) measurements are the only such observations available for the Mona Passage. The ROMS-simulated double-core structure of the averaged flow in the Mona Passage is identical to the one observed by Johns et al. (1999) in August. Our estimated transport of 1.6 ± 0.66 Sv in the first 200 m in August is also in good agreement with

their measured transport for the same month. Therefore, this concordance between observations and the ROMS simulation allows us to obtain reliable particle trajectories aimed to simulate coral reef larvae advected by the flow from spawning areas in the Mona Passage.

The August flow pattern in the Mona Passage usually prevents larvae released from Mona Island from reaching Puerto Rico or Hispaniola and vice versa (Fig. 7A; Table 1). The geomorphology of the Mona Passage with Mona Island in its center (see Figs. 4B) contributes to the formation of small-scale cyclones in the vicinity of the island. The lifetime of small-scale eddies is generally less than 50 d (Stammer and Böning 1992), which compares favorably with the estimated 40-d life span of eddies in the vicinity of Mona Island in our simulation. However, this time scale exceeds the average larval competency period of *A. palmata* (M. Vermeij, unpubl. data, M.W. Miller and I.B. Baums, pers. obs.). Consequently, long-lived small-scale eddies may cause trapping of the simulated larvae in the vicinity of Mona Island, acting as a crossing barrier (Fig. 7A). Only when the small eddy collapses at the end of its life span on the eastern coast of Hispaniola can some of the *Acropora* larvae originating from Mona Island reach Hispaniola's reefs (~2%, Table 1). Although this amount of mixing may be insignificant over ecological time scales (sensu Cowen et al. 2000), these results substantiate the findings from the genetic model (addressing time scales of several to hundreds of generations) that there maybe some larval exchange between the eastern and western Caribbean *Acropora* populations (Fig. 2; Baums et al. 2005b).

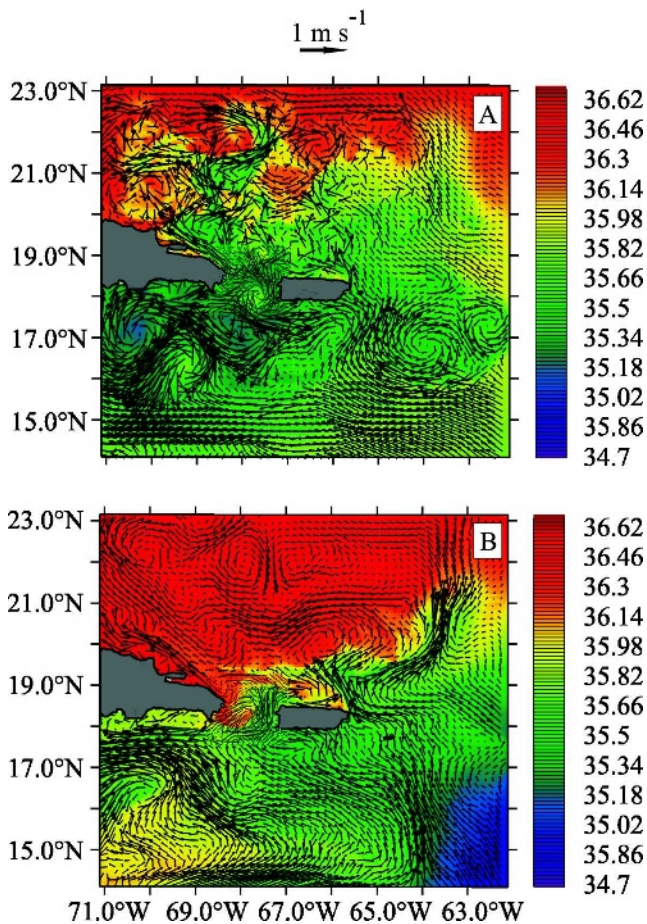


Fig. 8. Surface salinity in practical salinity units and current velocity vectors (m s^{-1}) for the beginning of (A) January and (B) August. Both grids of the Regional Ocean Model System (ROMS) simulation are shown. In January, the cyclone southwest of the Mona Passage is trapped between two anticyclones. August surface salinity patterns indicate the arrival of low-salinity water from the east.

Seasonality in small-scale eddy formation—Eddy formation and position in the Mona Passage appeared to be seasonal. During winter, the cyclone follows the westward propagation of large-scale anticyclones located south of the island chain (Fig. 8A), so that its lifetime in the vicinity of Mona Island is reduced to less than two weeks. The westward movement of the cyclone leads to weaker and more turbulent northward flow along the west coast of Puerto Rico, and stronger eastward flow sustained by the transiting anticyclones. Therefore, particles tend to be advected eastward by the neighboring anticyclone, favoring the crossing between Mona Island and Puerto Rico (Fig. 7B; Table 1). This is corroborated by lower self-recruitment of particles released from Mona Island in January (Table 1). In contrast, the cyclone is resident in the passage for longer periods during *Acropora* mass spawning events in August, so that eastward advection of particles is reduced. The position of the cyclone at the time of larval release and its propagation speed will strongly influence the connectivity between the reef habitats lining the Mona Passage. Thus, the Mona Passage can be described as

a dynamic filter to larval dispersal (rather than a barrier), and its effect upon coral reef connectivity will be largely determined by the reproductive timing of the species in question.

Recent methodological advances in empirical studies (Paris and Cowen 2004), theoretical modeling (Cowen et al. 2003), and genetic parentage analyses (Jones et al. 2005) emphasize the importance of the interaction between physical (i.e., currents, environmental cues) and behavioral mechanisms (James et al. 2002; Kingsford et al. 2002; Hohenlohe 2004) in facilitating larval retention (Sotka et al. 2004). The effect of regional and local environmental constraints on structuring populations via dispersal pathways has been stressed in zooplankton ecology, specifically for tidal and freshwater species. The present study provides evidence that a bio-oceanographic mechanism as revealed by a stochastic model of larval dispersal may be restricting larval movements over relatively short distances between islands.

Large-scale variability of flow in the Caribbean Sea—We argue here that Caribbean Current variability is a major factor in causing the flow patterns obtained in the ROMS simulation in the vicinity of Mona Island and that this large-scale variability is implicated in forming seasonal barriers to (virtual) larval dispersal across the Mona Passage.

The above-mentioned seasonal formation of the large-scale anticyclones south of the island chain is influenced by seasonal variation in surface salinity in the eastern Caribbean (Richardson and Chérubin unpubl. data). Low-salinity surface water originates from Amazon and Orinoco River discharges into the tropical Atlantic and is observed three to four months after the peak of seasonal rains occurring across northeastern South America. North Brazil Current (NBC) rings carry these low-salinity waters northward along the east coasts of the Lesser Antilles (Carton and Chao 1999; Murphy et al. 1999; Goñi and Johns 2001). As a result, low-salinity water extends across the Caribbean basin and increases from August–November to December–January (Corredor et al. 2004). Concurrently, Chérubin and Richardson (unpubl. data) observed that more anticyclones and cyclones are formed in the eastern Caribbean during the winter period. They propagate westward along the southern coast of the northern Antilles, as opposed to the stationary topographically steered eddies formed in the absence of the low-salinity waters in the Mona Passage.

The August to October period appears to be the transition period between the summer and the winter flow regimes. If a January-like circulation occurs earlier in August, then crossing of larvae from Mona to the west coast of Puerto Rico is enhanced. Therefore, variability in the onset of seasonal flow patterns could explain why some degree of western Caribbean ancestry is detected in *A. palmata* genotypes from Puerto Rico.

Stability of larval dispersal filter—The large- and small-scale biophysical models were forced by present-day climatology to elucidate potential mechanisms determining prerecruitment distributions of *A. palmata* larvae. On the

other hand, the observed distribution of *A. palmata* genotypes is the result of long-term processes that have occurred over the past hundreds to thousands or more generations (Falush et al. 2003). Because the genetic patterns correlate with the oceanographic mechanisms discussed here, despite the likely difference in temporal scale of the models, the argument that these mechanisms influence population connectivity over the long-term is strengthened. Integration of oceanographic, behavioral, and genetic processes into one model is needed to further study the stability of larval dispersal filters.

The present study shows for the first time a direct relationship between effective dispersal distances based on oceanography and life history traits, and gene flow in a marine organism. We found that geographic distance between living colonies of *A. palmata* was not the primary determinant of their population structure. Rather, the effective distance of larval dispersal is a major factor controlling local population connectivity and is driven by the oceanography of the region during mass spawning and throughout the pelagic larval phase of *Acropora*. The described biophysical filter is seasonal and thus leaky over generational time scales. Leakiness may be a common feature of biophysical filters to gene flow (Hohenlohe 2004). Realistic models of ocean currents that resolve adequate temporal and spatial scales from the source area of the target species to their entire range, as well as in-depth information on life history traits are necessary to estimate larval linkages. With this knowledge, conservation efforts will have a higher chance of securing continued larval supply for fragile marine ecosystems (Cowen et al. 2000; Sale et al. 2005).

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