Current Biology 16, 1622–1626, August 22, 2006 ©2006 Elsevier Ltd All rights reserved DOI 10.1016/j.cub.2006.06.052

Report

Seascape Genetics: A Coupled Oceanographic-Genetic Model Predicts Population Structure of Caribbean Corals

Heather M. Galindo,[1,*] Donald B. Olson,[2] and Stephen R. Palumbi[1]

[1] Department of Biological Sciences
Stanford University
Pacific Grove, California 93950

[2] Rosenstiel School of Marine and Atmospheric Sciences
University of Miami
Miami, Florida 33149

Summary

Population genetics is a powerful tool for measuring important larval connections between marine populations [1–4]. Similarly, oceanographic models based on environmental data can simulate particle movements in ocean currents and make quantitative estimates of larval connections between populations possible [5–9]. However, these two powerful approaches have remained disconnected because no general models currently provide a means of directly comparing dispersal predictions with empirical genetic data (except, see [10]). In addition, previous genetic models have considered relatively simple dispersal scenarios that are often unrealistic for marine larvae [11–15], and recent landscape genetic models have yet to be applied in a marine context [16–20]. We have developed a genetic model that uses connectivity estimates from oceanographic models to predict genetic patterns resulting from larval dispersal in a Caribbean coral. We then compare the predictions to empirical data for threatened staghorn corals. Our coupled oceanographic-genetic model predicts many of the patterns observed in this and other empirical datasets; such patterns include the isolation of the Bahamas and an east-west divergence near Puerto Rico [3, 21–23]. This new approach provides both a valuable tool for predicting genetic structure in marine populations and a means of explicitly testing these predictions with empirical data (Figure 1).

Results

Oceanographic Model

Ocean simulations are based on the MICOM North Atlantic simulations [8] between 24°S and approximately 70°N (see [6, 24, 25]). The model uses wind data to estimate currents at 19 vertical layers and has been tested with ocean drifters [26]. To generate connectivity matrices for each model run, we released 1000 particles at 87 randomly chosen Caribbean locations for each of the years in the range from 1982–1986. Particles were released during the summer (Julian days 205–219) and had durations of 14 days, consistent with expected larval duration for staghorn corals [27]. Arrival calculations incorporated a buffer within 25 km of the model coastal boundary, which is set in MICOM at 25 m depth. For each model run, we used observations of particle arrival at each locality on day 14 to estimate a connectivity matrix (probability that a particle released at point *i* arrives at point *j*). (Access to the matrices is available from the authors upon request.)

Description of the Genetic Model

The genetic model uses a connectivity matrix to simulate the effects of dispersal and genetic drift on a one-locus, two-allele neutral marker without mutation. All populations begin with equal allele frequencies and diploid populations of approximately 100 individuals. In each nonoverlapping generation, 50% of individuals are randomly chosen for synchronous reproduction, and a larval pool is then created in Hardy-Weinberg equilibrium from the selected parents. The above assumptions are characteristic of basic population genetic models [4, 14]. (See Supplemental Data available with this article online for choice of parameters.)

Larval movement is simulated in two ways. The deterministic model uses a connectivity matrix to calculate the fraction of the larval pool that disperses between each pair of populations. In the individual-based stochastic model, entries in the same connectivity matrix are used as relative probabilities that a larva disperses to each of the other populations, is retained, or experiences mortality before settling. The two versions assess the relative impact of allowing genetic drift to occur only during reproduction (deterministic) or during both reproduction and dispersal (stochastic). After arrival, all larvae settle and enter the adult population. Allele frequencies vary across generations, but population sizes are reset to initial conditions every generation. Multiple runs of the single-locus model are interpreted as data from multiple loci because each run is independent. Five sets of ten runs each used the connectivity matrix for each of the years from 1982–1986. An additional set of simulations used the matrices for all five years in a repeated sequence (the "all-years" simulations). Each of these six sets was run for 100 generations with both the deterministic and stochastic model versions for a total of twelve oceanographic regimes. Last, we ran a set of ten runs with each of the two model versions by using a panmictic matrix to provide a null model for data analysis. (Additional runs with larger populations and longer durations are described in the Supplemental Data).

Genetic Results and Testing A Priori Hypotheses

We analyzed data from 120 model runs by using Arlequin 2.0 [28] to calculate genetic differences among populations (F_{ST}), among groups defined a priori (F_{CT}), and among populations within groups (F_{SC}). For all twelve oceanographic regimes, we found strong population genetic structure. Mean F_{ST} values for all 87

*Correspondence: hgalindo@stanford.edu

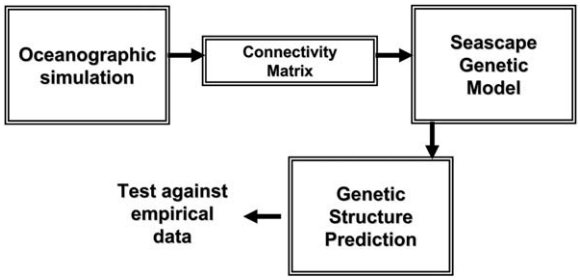

Figure 1. Conceptual Model of Coupled Oceanographic-Genetic Approach

populations fall between 0.115 and 0.568, with every value being significantly different from zero (data not shown). In contrast, the mean F_{ST} for the null panmictic model was −0.007; none of these runs were significant.

Next, data from the 87 populations were grouped in two ways. First, we created groups corresponding to collection sites across the Caribbean for a genetic analysis of staghorn corals (Vollmer and S.R.P., unpublished data). For the simulated populations, genetic differences were strong among regions, but not among populations within regions (data are displayed in Figure 2). Mean F_{CT} values ranged between 0.130 and 0.590 and were significant for 90%–100% of the runs in each oceanographic regime except for the 1984 deterministic regime (60% runs significant). In contrast, F_{SC} values were nonsignificant except for 10% of runs for the 1983 stochastic regime (F_{SC} = 0.095), 50% for the 1984 stochastic regime (F_{SC} = 0.015–0.206), and 100% for the 1984 deterministic regime (F_{SC} = 0.014–0.272). Mean F_{CT} values were 0.000 and 0.002 for the null deterministic and stochastic models respectively with only one stochastic run being significant. Null model F_{SC} values were all nonsignificant and had means of −0.010 to −0.005.

We then created an east-west comparison of all 87 Caribbean populations by separating them across a line running NE-SW between Puerto Rico and the Dominican Republic [29]. Compared to results for the coral groupings, evidence for an east-west divide in populations was less robust. Only 20%–70% of the runs under deterministic regimes showed significant F_{CT} values (mean values from 0.034–0.062). However, results from the stochastic model showed a higher east-west division; there were significant values in 60%–90% of the runs, with mean values ranging from 0.141–0.302. For all runs in both versions of the model, significant F_{SC} values indicated that variation within regions was substantial (mean values ranged from 0.077–0.285). Null model mean F_{CT}/F_{SC} values were 0.000/−0.010 and 0.000/−0.005 for the deterministic and stochastic models, respectively, with only two stochastic runs having significant F_{CT} values.

Overall, genetic structure from all-years simulations tended to be lower than those run for a single year at a time (Figure 2), reflecting differences in currents from year to year. The individual-based stochastic model often predicts higher genetic differentiation because of additional genetic drift during dispersal. However, the patterns are qualitatively the same as those of the deterministic model.

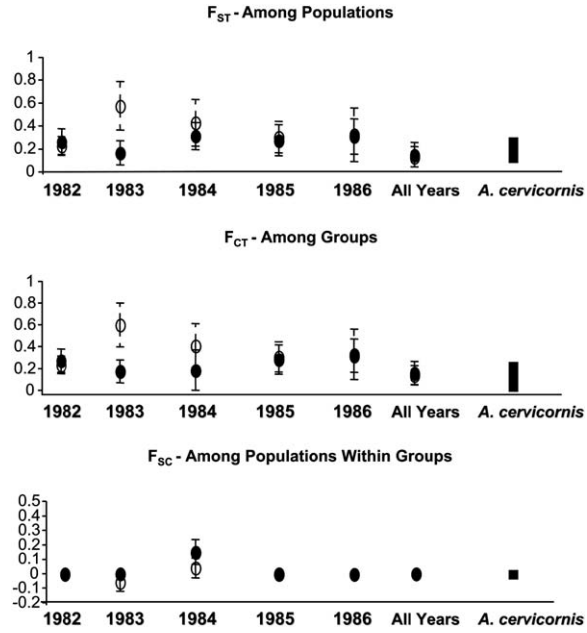

Figure 2. Fixation Indices across Oceanographic Models Run for 1982–1986 and All Years

Data show mean overall levels of genetic differentiation for model populations grouped according to *A. cervicornis* collection sites. Population groupings: Bahamas = 34, 35, 38; Turks and Caicos = 42; Puerto Rico = 16, 17; Curacao = 11, 12; Panama = 4, 5; Belize = 61, 70, 71; Yucatan = 63, Jamaica = 83, numbers from Figure 3.) Error bars represent one standard deviation. Results from the deterministic (closed circles) versus stochastic versions of the model (open circles) are shown. *A. cervicornis* data represent a range of values across mitochondrial and nuclear loci (Vollmer and S.R.P., unpublished data).

Geographic Inferences from Genetic Simulations

To explore geographic predictions of the model, we used two common clustering methods. First, we used PRIMER 5.0 [30] to calculate Bray-Curtis distances for all pairs of 87 populations across all ten loci and to produce dendrograms that clustered genetically similar populations. The reliability of population clusters was estimated by jackknifing across loci. Clusters that were robust across all twelve oceanographic regimes are shown in an insert in Figure 3. This approach is analogous to methods used to combine phylogenetic trees from genetic analyses to show population groups that have similar gene frequencies. Membership in some of these groups varies among runs or years. For example, population 42 (Turks and Caicos Isl.) sometimes joins the Hispaniola group. However, some regional groupings, especially those in the eastern Caribbean and those along the Meso-American Barrier Reef, were robust (Figure 3).

Next, we used the software STRUCTURE to define the most likely genetic clusters based on the relative probabilities of the data given a certain number of clusters (Pr(X|K)). Populations were then grouped according to the similarity of their patterns of relative membership (q values [31]) in each of the genetic clusters as determined by the model. (Details are available in the Supplemental Data).

When overlaid on a map of the Caribbean, results from both the PRIMER and STRUCTURE analyses indicate

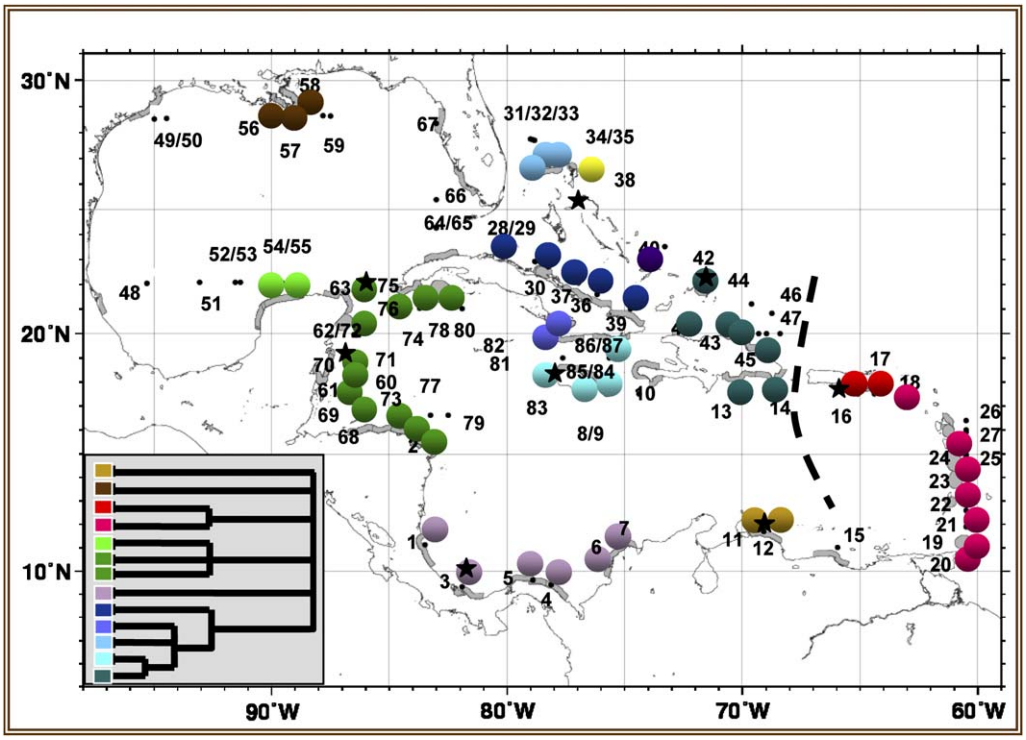

Figure 3. Results of Caribbean Model

The 87 randomly chosen larval-release locations are indicated here by black or colored circles. Each release location corresponds to a 25 km arrival zone (shaded gray) where larval arrivals were counted. Release locations were chosen along a rhumbline, which occasionally resulted in the locations being far from the coast (e.g., 48, 51, 79). Collection sites for *A. cervicornis* are indicated by black stars. Colored circles indicate arrival locations with genetically similar populations as determined by the consensus dendrogram (insert) from PRIMER. These groupings also represent the genetic cluster analysis from STRUCTURE. The curved dotted line demarks the east-west genetic boundary suggested by Baums et al. [47] and Taylor and Hellberg [3].

very similar geographic groupings of genetically clustered populations (Figure 3). These clusters include the northern Gulf of Mexico (Populations 56–58, brown circles in Figure 3), eastern Florida straits (31–33, light blue), the Bahamas (38, yellow), Panama (1, 3–7, lavender), and Turks and Caicos/Dominican Republic (13, 14, 41–47, dark green). Results from the two analyses differ slightly in a few cases. STRUCTURE indicates a single south Cuba/Jamaica cluster (8–10, 81–87), whereas PRIMER divides this cluster into two closely related groups (8–10, 83–87, turquoise; 81–82 purple). A similar situation occurs for the single north-Cuba cluster (28–30, 36, 37, 39, 40) from STRUCTURE and the two related clusters from PRIMER (28–30, 36–37, 39, dark blue; 40, dark purple). In contrast, STRUCTURE divides the Yucatan/Belize group (2, 60–65, 68–73, 77) from the group southwest of Cuba (74–76, 78, 80), whereas PRIMER put them in a single group (2, 60–80, green). Last, both analyses group the U.S. Virgin Islands (16, 17, red) separately from the Lesser Antilles (19–27, pink) but differ in their placement of population 18. Although results occasionally differ in their resolution, they are entirely consistent at the regional scale.

Comparison to Empirical Data

Staghorn corals, *Acropora cervicornis*, in the Caribbean have been recently shown to exhibit strong population structure, especially for populations more than 500 km apart (Vollmer and S.R.P, unpublished data). Across major regions of the Caribbean (Panama, Belize, the Bahamas, Turks and Caicos, Puerto Rico and Curacao), data from three nuclear introns and mtDNA indicate that genetic differentiation for staghorn corals is high, with an average F_{ST} of 0.021–0.235 (Vollmer and S.R.P., unpublished data). These values are similar to those from the AMOVA analysis on the coral groupings in the model data, particularly for the all-years simulations (Figure 2).

Comparing the model results to genetic data shows broad concordance at the regional scale. For collection sites across the east-west divide, analysis of *A. cervicornis* data gives a highly significant F_{CT} of 0.08 (p value, 0.001). Although differing quantitatively, results from analysis of the all-years stochastic dataset indicate a mean F_{CT} of 0.31 (significant for 60% of the runs). For comparison, the mean F_{CT} for the null panmictic simulations with the stochastic model was −0.001, with none of the runs being significant. Empirical results also indicate that the Bahamas are isolated from the rest of the Caribbean (F_{CT} = 0.06; p = 0.003). The all-years stochastic dataset has a high mean F_{CT} of 0.20 across runs, but none of the runs have a significant F_{CT} because of high variation among populations. Mean F_{CT} for the null model was 0.0009, with two of the runs being significant by chance. However, the STRUCTURE and PRIMER results clearly distinguish between the Bahamas (population 38) and the rest of the Caribbean (Figure 3).

Discussion

A New Tool for Investigation of Marine Larval Dispersal

We show that advanced oceanographic simulations can be used to predict genetic structure of marine populations and that these predictions can then be tested against empirical data. Larval dispersal connects many marine populations, and knowledge of these connections is fundamental to the design of marine managed areas, fisheries management, and conservation plans [1, 32, 33, 34]. However, tracking larval dispersal trajectories is very difficult [35], and a detailed understanding of marine connectivity requires integrating approaches from oceanography, marine ecology, tagging studies, and population genetics [1, 6]. The seascape model presented here is a step forward in explicitly using oceanography to predict population genetic structure and then directly comparing these predictions to empirical genetic results and known biogeographic patterns.

Among Caribbean corals, regional genetic differences for four species ([21–23] and Vollmer and S.R.P., unpublished data) are consistent with our modeling results. In addition, biogeographic and genetic studies of reef fish (e.g., [3, 29]) and reef faunal assemblages [36–38] highlighted an east-west biogeographic divide, as well as north-south distinctions, in the Caribbean. In general, our coupled model predicts genetic divisions for low-dispersal species from east to west and from north to south across the Caribbean Sea. However, these conclusions may not hold for species with wider dispersal, and empirical support for strong Caribbean genetic structure is rarer in these species [39–42].

Our simple oceanographic-genetic model successfully predicts broad-scale genetic structure and provides a seascape view of marine neighborhoods. However, larval behavior [43], local adaptation [44], or larval mortality may reduce connectivity to levels below those produced in our model [6]. Many marine species have longer planktonic durations than the simulations we perform here [1, 2], and genetic structure in these species may depend on factors other than oceanography. In these cases, deviations of empirical data from model predictions may signal important larval-dispersal features not explainable by simple oceanography.

Limitations

Although our coupled oceanographic-genetic model successfully predicts the qualitative pattern of genetic structure, it cannot accurately predict the magnitude of genetic differences (e.g., levels of F_{ST} in Figure 2). Better numerical predictions would require additional biological data (such as spawning, recruitment, mortality, and population sizes [26]) and further oceanographic information, particularly for species with complicated larval behavior. In addition, model areas that by chance have low density of particle releases may restrict stepping-stone dispersal. Because the rate of genetic drift and the build-up of F_{ST} depend strongly on difficult-to-measure parameters such as effective population size [13], accurate quantitative predictions of F_{ST} are unlikely. In addition, a more complex genetic model involving multiple alleles at several loci, mutation, and recombination would allow a drift-migration equilibrium to be attained and rare dispersal events to be incorporated. Finally, small-scale differences in genetic structure cannot be easily predicted by our current models because the oceanographic simulations do not perform well in shallow water [26]. Yet, some closely spaced marine populations have strong genetic differences ([3] and Vollmer and S.R.P., unpublished data). A higher-resolution oceanographic circulation model is needed to make comparisons with genetic datasets on a finer geographic scale.

Future Applications

Our genetic model provides a flexible framework applicable to any dispersal scenario for which a connectivity matrix can be provided. Sources of such matrices could include other oceanographic models or empirical data from natural or artificial tagging studies (e.g., [45, 46]). Model parameters such as population sizes, initial conditions, and reproductive patterns are easily modified to fit the life-history strategies for a wide variety of species. Comparisons between the deterministic and stochastic models indicate that both predict similar geographic patterns of genetic structure, but the added level of genetic drift during the dispersal phase in the stochastic model leads to more distinct structure. Data analysis with Arlequin, PRIMER, and STRUCTURE provide simple comparisons to empirical data sets and similar geographic clusters of related populations. The coupled seascape model can be a powerful source of insight into the role of oceanographic features in marine population biology.

Supplemental Data

Supplemental Data are available with this article online at http://www.current-biology.com/cgi/content/full/16/16/1622/DC1/.

Acknowledgments

We would like to thank Geoff Samuels for running the drift simulations and compiling the connectivity tables and Claire B. Paris for initial work on the oceanographic model. Paul R. Armsworth, Tom Oliver, Steven L.H. Teo, and Tomo Eguchi provided valuable help in the development of the genetic model. We thank Arjun Sivasundar, Mollie Manier, Liz Alter, Margaret McManus, Anna Pfeiffer-Hoyt, Paul Barber, Matt Hare, Richard Grosberg, and four anonymous reviewers for comments leading to the significant improvement of the manuscript and Steve Vollmer for use of coral data. The authors were supported through the Bahamian Biocomplexity Project sponsored by the National Science Foundation (NSF OCE-0119976), NOAA-FL Sea Grant NA16RG-2195, and grants from the David and Lucille Packard and Gordon and Betty Moore Foundations to PISCO. In addition, this material is based upon work supported under a National Science Foundation Graduate Research Fellowship awarded to H.M.G.

Received: April 7, 2006
Revised: June 9, 2006
Accepted: June 12, 2006
Published: August 21, 2006

References

1. Palumbi, S.R. (2004). Marine reserves and Ocean neighborhoods: The spatial scale of marine populations and their management. Annual Review of Environment and Resources *29*, 31–68.
2. Palumbi, S.R., and Hedgecock, D. (2005). The life of the sea: Implications of marine population biology to conservation policy. In Marine conservation biology: The science of maintaining the

sea's biodiversity, E.A. Norse and L.B. Crowder, eds. (Washington, D.C.: Island Press), pp. 33–46.
3. Taylor, M.S., and Hellberg, M.E. (2003). Genetic evidence for local retention of pelagic larvae in a Caribbean reef fish. Science *299*, 107–109.
4. Waples, R.S. (1987). A multispecies approach to the analysis of gene flow in marine shore fishes. Evolution Int. J. Org. Evolution *41*, 385–400.
5. Batteen, M.L., Cipriano, N.J., and Monroe, J.T. (2003). A large-scale seasonal modeling study of the California Current System. J. Oceanogr. *59*, 545–562.
6. Cowen, R.K., Paris, C.B., and Srinivasan, A. (2006). Scaling of connectivity in marine populations. Science *311*, 522–527.
7. James, M.K., Armsworth, P.R., Mason, L.B., and Bode, L. (2002). The structure of reef fish metapopulations: Modelling larval dispersal and retention patterns. Proc. R. Soc. Biol. Sci. B *269*, 2079–2086.
8. Paiva, A.M., Hargrove, J.T., Chassignet, E.P., and Bleck, R. (1999). Turbulent behavior of a fine mesh (1/12 degrees) numerical simulation of the North Atlantic. J. Mar. Syst. *21*, 307–320.
9. Young, E.F., Brown, J., Aldridge, J.N., Horsburgh, K.J., and Fernand, L. (2004). Development and application of a three-dimensional baroclinic model to the study of the seasonal circulation in the Celtic Sea. Continental Shelf Research *24*, 13–36.
10. Hohenlohe, P.A. (2004). Limits to gene flow in marine animals with planktonic larvae: models of *Littorina* species around Point Conception, California. Biol. J. Linn. S. Lond. *82*, 169–187.
11. Kimura, M., and Weiss, G.H. (1964). Stepping stone model of population structure and decrease of genetic correlation with distance. Genetics *49*, 561–576.
12. Nielsen, R., and Wakeley, J. (2001). Distinguishing migration from isolation: A Markov chain Monte Carlo approach. Genetics *158*, 885–896.
13. Rousset, F. (1997). Genetic differentiation and estimation of gene flow from F-statistics under isolation by distance. Genetics *145*, 1219–1228.
14. Slatkin, M. (1993). Isolation by distance in equilibrium and non-equilibrium populations. Evolution Int. J. Org. Evolution *47*, 264–279.
15. Wright, S. (1931). Evolution in Mendelian populations. Genetics *16*, 97–159.
16. Bohrer, G., Nathan, R., and Volis, S. (2005). Effects of long-distance dispersal for metapopulation survival and genetic structure at ecological time and spatial scales. J. Ecol. *93*, 1029–1040.
17. Guillot, G., Estoup, A., Mortier, F., and Cosso, J.F. (2005). A spatial statistical model for landscape genetics. Genetics *170*, 1261–1280.
18. Guillot, G., Mortier, F., and Estoup, A. (2005). GENELAND: A computer package for landscape genetics. Mol. Ecol. Notes *5*, 712–715.
19. Lurz, P.W.W., Shirley, M.D.F., Rushton, S.P., and Sanderson, R.A. (2002). Modelling the consequences of duck migration patterns on the genetic diversity of aquatic organisms: A first step towards a predictive tool for wetland management. Acta Oecologica *23*, 205–212.
20. Manel, S., Schwartz, M.K., Luikart, G., and Taberlet, P. (2003). Landscape genetics: Combining landscape ecology and population genetics. Trends Ecol. Evol. *18*, 189–197.
21. Baums, I.B., Miller, M.W., and Hellberg, M.E. (2005). Regionally isolated populations of an imperiled Caribbean coral, *Acropora palmata*. Mol. Ecol. *14*, 1377–1390.
22. Brazeau, D.A., Sammarco, P.W., and Gleason, D.F. (2005). A multi-locus genetic assignment technique to assess sources of *Agaricia agaricites* larvae on coral reefs. Mar. Biol. *147*, 1141–1148.
23. Fukami, H., Budd, A.F., Levitan, D.R., Jara, J., Kersanach, R., and Knowlton, N. (2004). Geographic differences in species boundaries among members of the *Montastraea annularis* complex based on molecular and morphological markers. Evolution Int. J. Org. Evolution *58*, 324–337.
24. Cowen, R.K., Paris, C.B., Olson, D.B., and Fortuna, J.L. (2003). The role of long distance dispersal versus local retention in replenishing marine populations. Gulf and Caribbean Research *14*, 129–137.
25. Olson, D.B., Paris, C.B., and Cowen, R.K. (2001). Lagrangian biological models. Encyclopedia of Ocean Sciences (New York: Academic Press), pp. 1438–1443.
26. Olson, D.B. (2006). Lagrangian biophysical dynamics. In Lagrangian Analysis and Prediction of Coastal and Ocean Dynamics, A. Griffa, A.D. Kirwan, A.J. Mariano, T. Ozgokmen, and T. Rossby, eds. (Cambridge, UK: Cambridge University Press), in press.
27. Vollmer, S.V., and Palumbi, S.R. (2002). Hybridization and the evolution of reef coral diversity. Science *296*, 2023–2025.
28. Schneider, S., Roessli, D., and Excoffier, L. (2000). A Software for Population Genetics Data Analysis (Geneva, Switzerland: Genetics and Biometry Laboratory, University of Geneva).
29. Colin, P.L. (2003). Larvae retention: Genes or oceanography? Science *300*, 1657–1659.
30. Clarke, K.R. (1993). Non-parametric multivariate analyses of changes in community structure. Aust. J. Ecol. *18*, 117–143.
31. Pritchard, J.K., Stephens, M., and Donnelly, P. (2000). Inference of population structure using multilocus genotype data. Genetics *155*, 945–959.
32. Botsford, L.W., Micheli, F., and Hastings, A. (2003). Principles for the design of marine reserves. Ecol. Appl. *13* (*Suppl 1*), S25–S31.
33. Roberts, C.M. (1997). Connectivity and management of Caribbean coral reefs. Science *278*, 1454–1457.
34. Sale, P.F., Cowen, R.K., Danilowicz, B.S., Jones, G.P., Kritzer, J.P., Lindeman, K.C., Planes, S., Polunin, N.V.C., Russ, G.R., Sadovy, Y.J., et al. (2005). Critical science gaps impede use of no-take fishery reserves. Trends Ecol. Evol. *20*, 74–80.
35. Sammarco, P.W., Andrews, J.C., and Risk, M.J. (1991). Coral reef geomorphology as a function of seasonal prevailing currents and larval dispersal. Palaeogeogr. Palaeoclimatol. Palaeoecol. *88*, 1–12.
36. Bouchon-Navaro, Y., Bouchon, C., Louis, M., and Legendre, P. (2005). Biogeographic patterns of coastal fish assemblages in the West Indies. J. Exp. Mar. Biol. Ecol. *315*, 31–47.
37. Briggs, J.C. (1974). Operation of zoogeographic barriers. Syst. Zool. *23*, 248–256.
38. Robins, C.R. (1971). Distributional patterns of fishes from coastal and shelf waters of the tropical western Atlantic. FAO Fisheries Research *71*, 249–255.
39. Mitton, J.B., Berg, C.J., and Orr, K.S. (1989). Population structure, larval dispersal and gene flow in the Queen Conch *Strombus gigas* of the Caribbean. Biol. Bull. *177*, 356–362.
40. Rocha, R.M., Faria, S.B., and Moreno, T.R. (2005). Ascidians from Bocas del Toro, Panama. I. Biodiversity. Caribb. J. Sci. *41*, 600–612.
41. Shulman, M.J., and Bermingham, E. (1995). Early life histories, ocean currents, and the population genetics of Caribbean reef fishes. Evolution Int. J. Org. Evolution *49*, 897–910.
42. Silberman, J.D., Sarver, S.K., and Walsh, P.J. (1994). Mitochondrial DNA variation and population structure in the spiny lobster *Panulirus argus*. Mar. Biol. *120*, 601–608.
43. Cowen, R.K., Lwiza, K.M.M., Sponaugle, S., Paris, C.B., and Olson, D.B. (2000). Connectivity of marine populations: Open or closed? Science *287*, 857–859.
44. Palumbi, S.R., and Warner, R.R. (2003). Why gobies are like hobbits. Science *299*, 51–52.
45. Jones, G.P., Planes, S., and Thorrold, S.R. (2005). Coral reef fish larvae settle close to home. Curr. Biol. *15*, 1314–1318.
46. Thorrold, S.R., Latkoczy, C., Swart, P.K., and Jones, C.M. (2001). Natal homing in a marine fish metapopulation. Science *291*, 297–299.
47. Baums, I.B., Paris, C.B., and Cherubin, L.M. (2006). A bio-oceanographic filter to larval dispersal in a reef-building coral. Limnol. Oceanogr., in press.