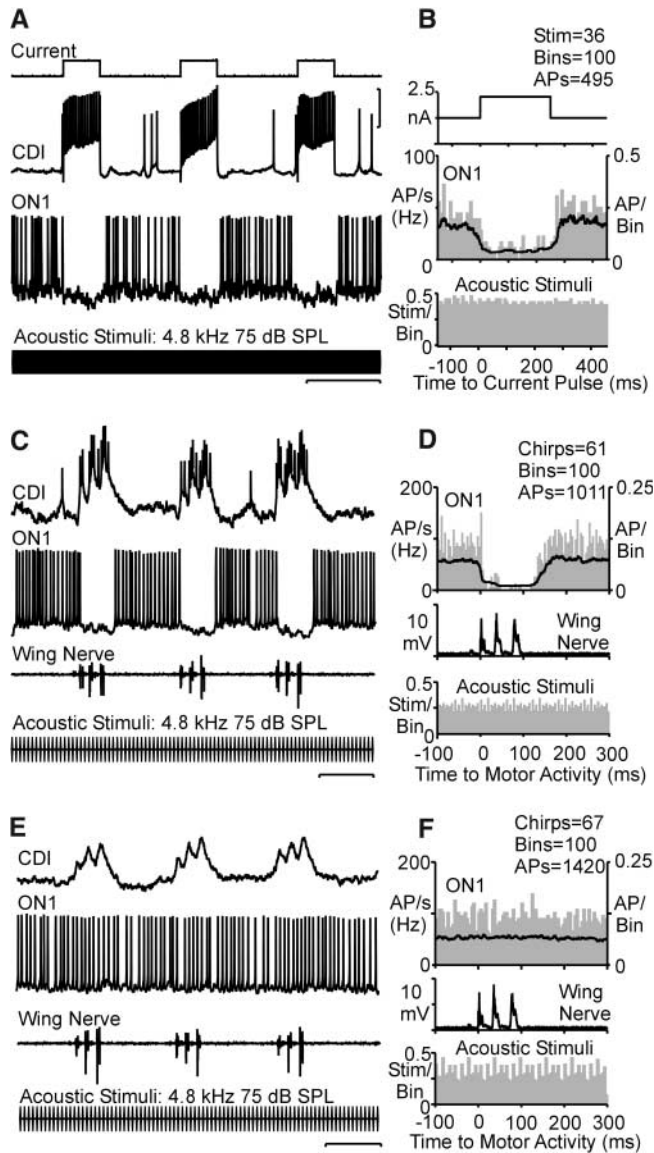


**Fig. 4.** The effect of CDI on sound processing. **(A)** ON1's response to a continuous sequence of 4.8 kHz, 75 dB SPL sound pulses, 8 ms in duration with intervals of 7 ms, is completely inhibited during periodic current injection in CDI. **(B)** PSTH and superimposed instantaneous spike frequency of ON1 averaged over 36 trials demonstrate that ON1 activity is reduced during CDI stimulation. **(C)** In an animal with the contralateral prothoracic-to-mesothoracic connective cut, ON1 responds with a train of spikes during the chirp intervals, but it fails to respond during the chirp if CDI is spiking. **(D)** The PSTH and instantaneous spike frequency of ON1 highlights the reduction in ON1 response during the chirp. **(E)** When CDI is prevented from spiking by hyperpolarizing current injection, ON1 responds to sound during the chirp and the chirp interval. **(F)** When CDI spikes were suppressed by inhibitory current injection, the PSTH and instantaneous spike frequency show no reduction in the activity of ON1 during chirps. Vertical scale bar, current: 2.5 nA (A); CDI: 20 mV [(A) and (E)], 10 mV (C); ON1: 20 mV [(A), (C), and (E)]; horizontal scale bars, 500 ms (A), 200 ms [(C) and (E)].



**References and Notes**

1. K. G. Pearson, *Annu. Rev. Neurosci.* **16**, 265 (1993).
2. R. W. Sperry, *J. Comp. Physiol. Psychol.* **43**, 482 (1950).
3. E. von Holst, H. Mittelstaedt, *Naturwissenschaften* **37**, 464 (1950).
4. M. Zaretsky, C. H. F. Rowell, *Nature* **280**, 583 (1979).
5. M. A. Sommer, R. H. Wurtz, *Science* **296**, 1480 (2002).
6. J. F. A. Poulet, B. Hedwig, *Nature* **418**, 872 (2002).
7. K. T. Sillar, P. Skorupski, *J. Neurophysiol.* **55**, 678 (1986).
8. K. T. Sillar, A. Roberts, *Nature* **331**, 262 (1988).
9. S. J. Blakemore, D. Wolpert, C. D. Frith, *Nat. Neurosci.* **1**, 635 (1998).
10. C. C. Bell, *Science* **214**, 450 (1981).
11. J. E. Roy, K. E. Cullen, *J. Neurosci.* **24**, 2102 (2004).
12. J. F. A. Poulet, B. Hedwig, *J. Neurosci.* **23**, 4717 (2003).
13. J. F. A. Poulet, B. Hedwig, *J. Exp. Biol.* **204**, 1281 (2001).
14. J. F. A. Poulet, B. Hedwig, *J. Neurophysiol.* **89**, 1528 (2003).
15. See supporting material on Science Online.
16. R. M. Hennig, *J. Comp. Physiol. A* **167**, 629 (1990).
17. K. Michel, *Z. Morph. Tiere* **77**, 285 (1974).
18. K. Schildberger, D. W. Wohlert, F. Huber, in *Crick Behavior and Neurobiology*, F. Huber, T. E. Moore, T. E. Loher, Eds. (Cornell Univ. Press, Ithaca, NY, 1989), pp. 423–458.
19. M. D. Kirk, J. J. Wine, *Science* **225**, 854 (1984).
20. F. Clarac, D. Cattaert, *Exp. Brain Res.* **112**, 163 (1996).
21. P. Rudomin, R. F. Schmidt, *Exp. Brain Res.* **129**, 1 (1999).
22. J. F. A. Poulet, B. Hedwig, data not shown.
23. M. G. Weeg, B. R. Land, A. H. Bass, *J. Neurosci.* **25**, 5967 (2005).
24. C. C. Bell, K. Dunn, C. Hall, A. Caputi, *J. Comp. Physiol. A* **177**, 449 (1995).
25. W. C. Li, S. R. Soffe, A. Roberts, *J. Neurosci.* **22**, 10924 (2002).
26. S. C. Rosen, M. W. Miller, E. C. Cropper, I. Kupfermann, *J. Neurophysiol.* **83**, 1621 (2000).
27. K. E. Cullen, *E. Curr. Op. Neurobiol.* **14**, 698 (2004).
28. C. C. Bell, K. Grant, *J. Neurosci.* **9**, 1029 (1989).
29. T. G. Nolen, R. R. Hoy, *Science* **226**, 992 (1983).
30. M. Dambach, H.-G. Rausche, G. Wendler, *Naturwissenschaften* **70**, 417 (1983).
31. We thank S. Atkinson, M. Burrows, C. Petersen, and S. Rogers for comments on the manuscript. Supported by the UK Biotechnology and Biological Sciences Research Council, the Royal Society, and the Human Frontier Science Program.

**Supporting Online Material**

www.sciencemag.org/cgi/content/full/311/5760/518/DC1  
 Materials and Methods  
 References

3 October 2005; accepted 20 December 2005  
 10.1126/science.1120847

# Scaling of Connectivity in Marine Populations

R. K. Cowen,<sup>1\*</sup> C. B. Paris,<sup>1</sup> A. Srinivasan<sup>2</sup>

Defining the scale of connectivity, or exchange, among marine populations and determining the factors driving this exchange are pivotal to our understanding of the population dynamics, genetic structure, and biogeography of many coastal species. Using a high-resolution biophysical model for the Caribbean region, we report that typical larval dispersal distances of ecologically relevant magnitudes are on the scale of only 10 to 100 kilometers for a variety of reef fish species. We also show the importance of the early onset of active larval movement mediating the dispersal potential. In addition to self-recruitment, larval import from outside the local area is required to sustain most populations, although these population subsidies are very limited in particular systems. The results reveal distinct regions of population isolation based on larval dispersal that also correspond to genetic and morphological clines observed across a range of marine organisms.

Identifying the scale of marine larval dispersal remains one of the fundamental challenges to marine ecology and ocean-

ography. Most coastal marine species have limited adult movement, so the relatively short, pelagic larval phase represents the pri-

mary opportunity for dispersal. Although larvae have the potential for long-distance dispersal (1, 2), evidence is mounting that larval dispersal may be limited (3–11). These studies challenge assumptions about the dominant distance mode of dispersal for marine populations (whether larvae typically travel a long or short distance) (12, 13). The rates, scale, and spatial structure of successful exchange, or connectivity, among local populations of marine organisms drive population replenishment and, therefore, have profound implications for population dynamics and genetics of marine organisms; spatially oriented resource management (e.g., marine protected areas); and the

<sup>1</sup>Marine Biology and Fisheries, <sup>2</sup>Meteorology and Physical Oceanography, Rosenstiel School of Marine and Atmospheric Science, University of Miami, 4600 Rickenbacker Causeway, Miami, FL 33149, USA.

\*To whom correspondence should be addressed. E-mail: rcowen@rsmas.miami.edu

spread of invasive species (9, 14, 15). However, realistic scaling estimates of connectivity are lacking. With major declines in fishery stocks, rapid degradation of natural coastal habitat, and calls for ecosystem-based management, identification of the spatial scale of population connectivity over demographically relevant time scales is critical.

Data on dispersal distances have been collected for only a handful of species, mostly those with short larval durations (hours to days) and very short distance dispersal (16, 17). These studies generally provide a snapshot of dispersal, representing only one possible dispersal scenario. It is impossible to capture empirically the full range of spatial and temporal variability that is expressed as a result of oceanographic conditions and larval behavior. Thus, the task of estimating dispersal kernels (the spatial probability of dispersal) for multiple species from a variety of potential spawning sites is only feasible with the use of high-resolution, hydrodynamic models.

For marine systems, early estimates of dispersal have relied on either simplified advection-diffusion models or passive particle models that use mean currents to define the potential for spread (18, 19). Advection-diffusion modeling studies and those based on statistics of oceanographic flow fields provide good theoretical frameworks for viewing potential scaling issues related to larval dispersal, such as spacing of marine reserves (15, 20–22); yet, such studies do not provide realistic renditions of ocean circulation or reveal how biological factors may mediate the dispersal outcome driven by ocean

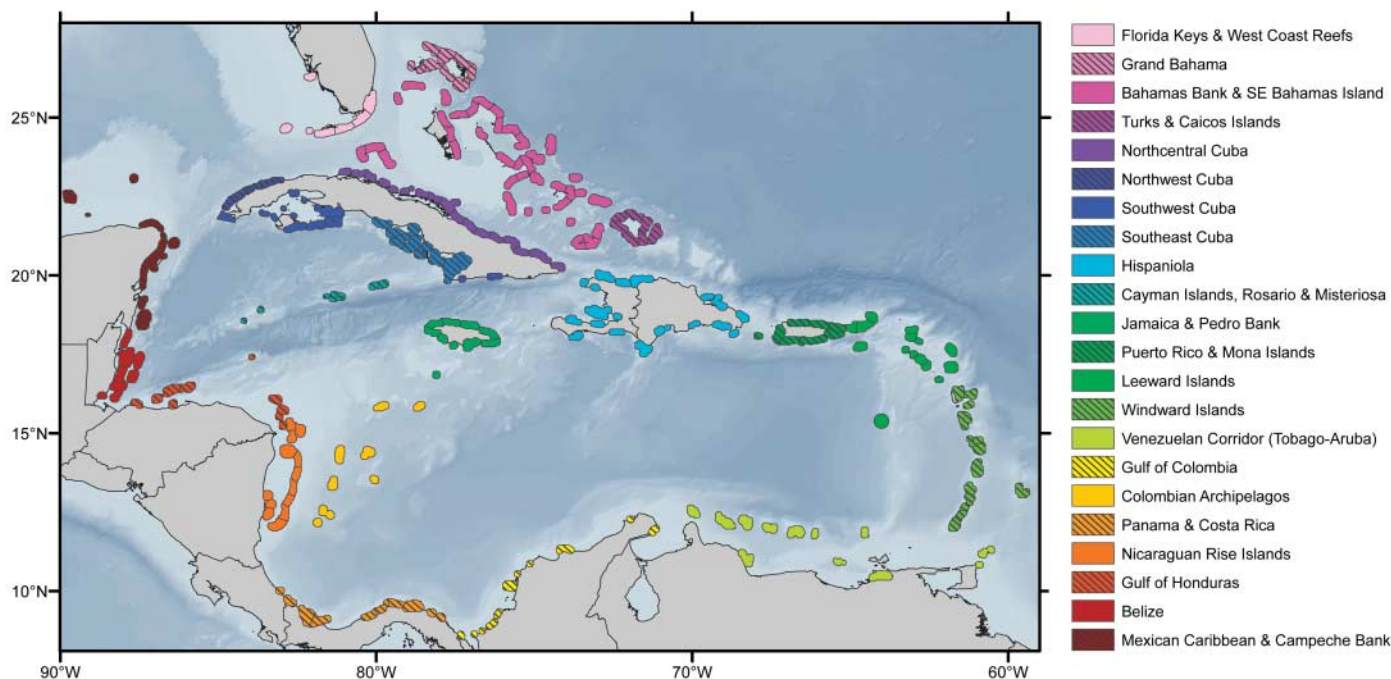
conditions. Critical evaluation of the role of behavior in modifying flow-mediated trajectories, as well as assessing variability in seasonal and spatial aspects of flow over and among heterogeneous coral reef systems along complex coastlines, requires more realistic, coupled biological-physical models (23–26).

We used flow trajectories from a high-resolution ocean circulation model in a Lagrangian stochastic scheme, generating an individual-based model (IBM) for larval dispersal (27). To evaluate the spatial scales over which larvae may be dispersed, that is, the effective geographic distances among reef fish populations, under realistically varying spatial and temporal oceanographic conditions, we ran the circulation model for 5 years of real wind data, resolving interannual variability in transport within the entire region. The IBM model includes a number of biological parameters such as pelagic larval duration (PLD), larval behavior (vertical and horizontal swimming capabilities), and adult spawning strategies (season and frequency). Successful dispersal also requires larvae (real or virtual) to encounter suitable settlement habitat, which is fragmented and often covers a small proportion of the area of potential dispersal by currents. Therefore, we included benthic habitat defined by the presence of coral reefs throughout the spatial domain of the model—the wider Caribbean including the Bahamas and Florida. Contiguous coral reef habitat was further divided into 9-km by 50-km segments, setting the spatial scale for self-recruitment in this study. Virtual larvae had to be near (within 9 km of) available settlement

habitat at the end of their larval period in order to be considered successful, that is, able to settle.

Although dispersal of a few organisms may be widespread, ecologically significant levels of dispersal—those necessary to replenish annual mortality—may be substantially more restricted in spatial extent (12, 20). In order to make reasonable predictions of ecologically meaningful dispersal curves or kernels, the required number or relative level of successful settlers arriving at any destination population must be estimated. This level was set to reflect the settlement rates required to replenish the local population, so as to maintain it at a constant population level by balancing the natural juvenile and adult mortality and by accommodating any additional mortality, such as from fishing. Settlement rates (the number of settlers per year), therefore, were matched to estimated adult mortality rates by using simple population growth models ( $N_t = N_0 e^{rt}$ ) set to a constant age 1+ population size. On the basis of these estimates (27) (table S1), we found that the required level of potential settlers, those that survived their entire pelagic stage, ranges between 10 and 100% for long-lived and short-lived species (longevity >15 years to ~1 year), respectively. Increasing mortality due to fishing pressure would similarly increase the required level of potential settlers, but would generally fall within this range. Estimating relevant recruitment levels is essential to scaling the extent of dispersal, which otherwise would be meaningless at ecological time scales.

We show for the wider Caribbean—a large region with complex, highly diverse flow re-



**Fig. 1.** Coral reef fish settlement habitat in the Caribbean region buffered by a 9-km larval sensory zone. The coral reef mosaic is largely fragmented and restricted to shallow water near continental coastlines or around islands and

isolated seamounts, and it represents a small fraction of the entire oceanic and coastal areas. Subregions within the wider Caribbean region are color coded and segmented into a total of 260 polygons (9 km by 50 km) or nodes ( $N_i$ ).

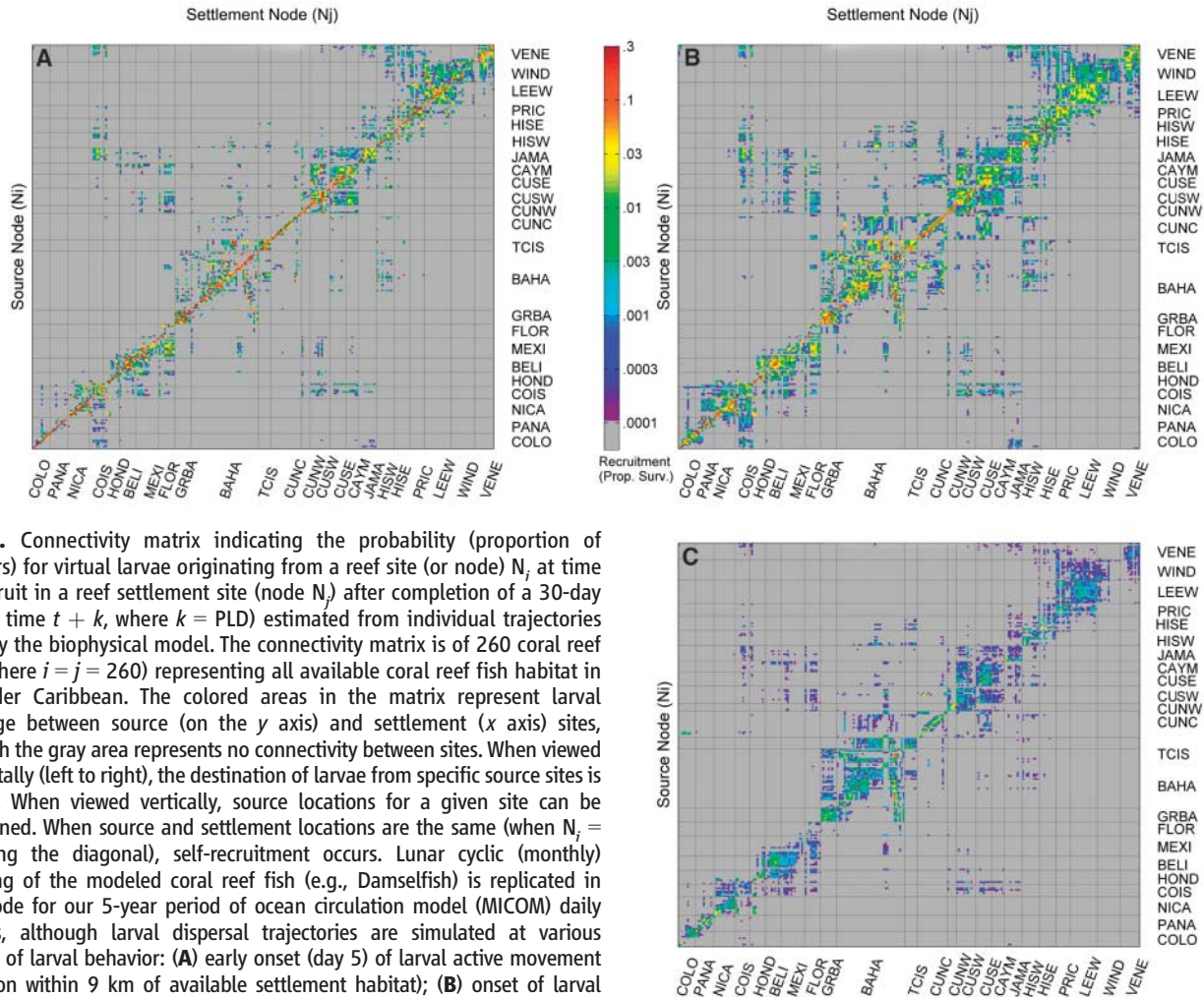
gimes and spatially heterogeneous habitat (8°N to 28°N, 57°W to 90°W, about 2100 km × 3300 km) (Fig. 1)—that typical larval dispersal distances providing ecologically significant numbers of settlers were only on the scale of 50 to 100 km for most species, with a relatively high rate of local retention or recruitment from adjacent locations. The role of population subsidy from distant locations was greatest for species with high natural (or fishing-related) mortality rates. Across the region, the relative importance of locally retained versus imported larvae varied, as a result of variation in the abundance of imported larvae. Consequently, some populations experience generally less recruitment than others. The fine scale of dispersal, on top of specific suitable settlement habitat and oceanographic boundaries, creates several subregions that are ecologically isolated

from each other, which may translate into biogeographic regions of genetic heterogeneity.

At the broadest scale of comparison, there was considerable spatial variation in the exchange of larvae among sites, which interacted strongly with the degree of larval active movement. These results suggest that passive dispersal is insufficient for population replenishment. The foremost difference between a purely passive model and one incorporating larval active movement is the prevalence of local or self-recruitment enhanced with early onset of swimming behavior and modified by the fragmentation pattern of available settlement habitat, whether clustered or isolated, whereas the converse of greater long-distance dispersal under the passive scenario was not realized (Fig. 2). Overall, the passive scenario resulted in recruitment levels that were one to two orders of magnitude

below that necessary for successful population replenishment and considerably reduced population connectivity (Fig. 2C). Greater dispersal distances can be achieved with longer duration of the larval stage, which also increases connectivity. These results underscore the role of larval traits and behavior when both dispersal and recruitment are modeled and demonstrate that biological and physical constraints (such as oceanographic boundaries) are equally important in resolving dispersal kernels and connectivity among fish populations.

In most areas, when active larval movement was invoked in the model, total recruitment [subsidy recruitment and self-recruitment] met or exceeded the demographic minimum required to sustain stable populations of long-lived species, but only a few locations were able to regularly sustain short-lived or severely fished



**Fig. 2.** Connectivity matrix indicating the probability (proportion of survivors) for virtual larvae originating from a reef site (or node  $N_i$ ) at time  $t$  to recruit in a reef settlement site (node  $N_j$ ) after completion of a 30-day PLD (at time  $t + k$ , where  $k = \text{PLD}$ ) estimated from individual trajectories given by the biophysical model. The connectivity matrix is of 260 coral reef sites (where  $i = j = 260$ ) representing all available coral reef fish habitat in the wider Caribbean. The colored areas in the matrix represent larval exchange between source (on the  $y$  axis) and settlement ( $x$  axis) sites, although the gray area represents no connectivity between sites. When viewed horizontally (left to right), the destination of larvae from specific source sites is evident. When viewed vertically, source locations for a given site can be determined. When source and settlement locations are the same (when  $N_i = N_j$  along the diagonal), self-recruitment occurs. Lunar cyclic (monthly) spawning of the modeled coral reef fish (e.g., Damselfish) is replicated in each node for our 5-year period of ocean circulation model (MICOM) daily currents, although larval dispersal trajectories are simulated at various degrees of larval behavior: (A) early onset (day 5) of larval active movement (retention within 9 km of available settlement habitat); (B) onset of larval active movement halfway through the pelagic phase (day 15); and (C) delayed onset of active swimming for passive larvae at the end of PLD (day 30). The model domain is grouped (thin gray lines) into 23 subregions: VENE, Venezuelan Corridor (from Tobago to Aruba); WIND, Windward Islands; LEEW, Leeward Islands; PRIC, Puerto Rico and Mona Island; HISW, Hispaniola West (Haiti); HISE, Hispaniola East (Dominican Republic); JAMA, Jamaica Island and Pedro Bank; CAYM, Cayman Islands and Rosario and Misteriosa Banks; CUSE, southeast Cuba; CUSW, southwest Cuba; CUNW, northwest

Cuba; CUNC, north central Cuba; TCIS, Turks and Caicos Islands; BAHA, Bahamas Bank and southeast Bahamian Islands; GRBA, Grand Bahamas; FLOR, Florida Keys and west coast reefs; MEXI, Mexican Caribbean and Campeche Bank; BELI, Belize; HOND, Gulf of Honduras; COIS, Colombian Archipelagos (from San Andres to Serrena Bank); NICA, Nicaraguan Rise Islands (from Mosquito Coast to Cabo Gracias á Dios); PANA, Panama and Costa Rica; COLO, Gulf of Colombia. Prop. surv., proportion surviving.

(high-turnover) species (Fig. 3A). Two regions, the Windward Islands and the Mexican Caribbean and Campeche Bank, stood out as being strongly recruitment-limited (total recruitment falls well below that necessary for sustaining populations), while most regions appear to receive sufficient recruitment levels such that post-settlement, density-dependent processes may be important at moderating population fluctuation. When parsed between recruitment from local sources (i.e., self-recruitment) versus importation from adjacent or distant sources, the pattern is highly variable across space, as well as in recruitment intensity (Fig. 3, B and C). Self-recruitment was close to sufficient for supplying adequate numbers of young only with active larval movement, but a variety of sites appear to be poor at self-seeding. In

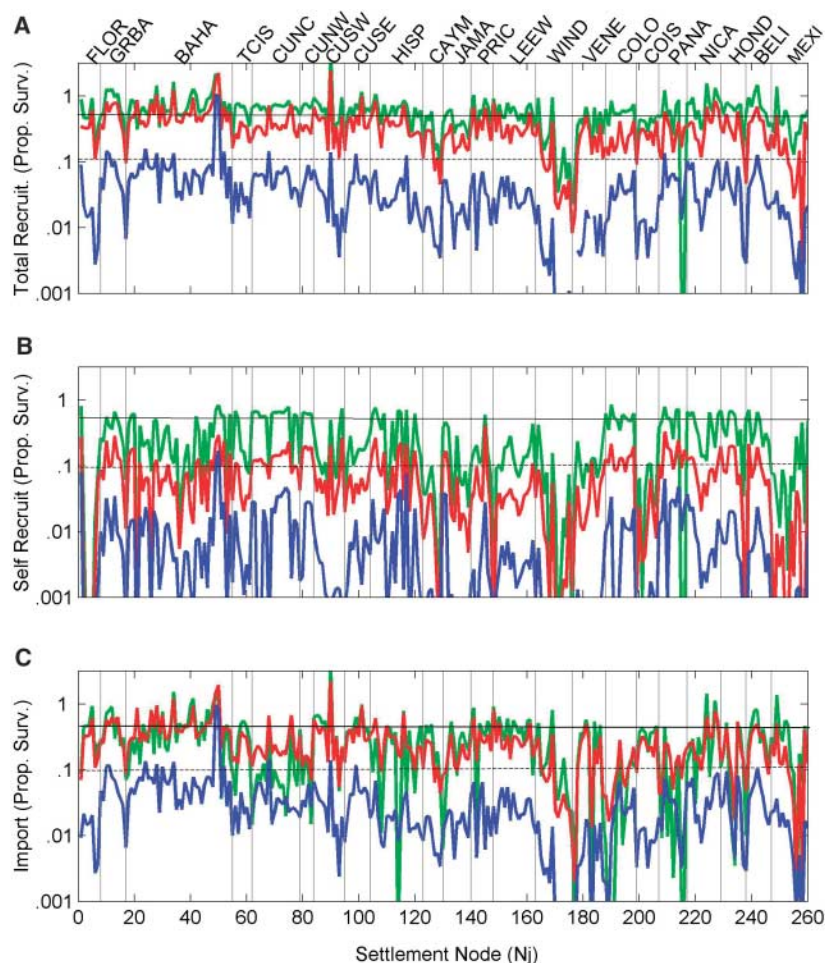
contrast, population subsidy is generally less variable, particularly under passive scenarios, though certain sites (e.g., the Windward Islands and the Yucatan Peninsula in northern Mexico) are apparently devoid of sources within a critical upstream distance, which results in low recruitment levels. Life histories and larval capabilities emerge as factors that strongly influence self-recruitment, whereas oceanographic regimes appear to control population subsidies.

Caribbean-wide self-recruitment accounted for ~21% of the recruits to an average site, with subsidy from within 50 km or less—since 50 km is the resolution of the Geographic Information Systems (GIS)-based habitat model—necessary to achieve recruitment levels required to sustain long-lived species and within 200 km

at the most to sustain typical reef-fish life histories (Table 1). These values robustly simulate dispersal distances over the wider Caribbean, strongly suggesting that the relevant scaling of dispersal is much smaller than believed. Regionally, self-recruitment varied from 9% (off Mexico in proximity to a strong western boundary current) to almost 57% (off Colombia in proximity to the semipermanent Panama-Colombia Gyre). In the latter case, the high proportion of self-recruitment was partially due to low importation from upstream locations, which resulted in generally low overall recruitment. Generally, important additional contributions of recruits do not accumulate from farther than 200 to 300 km. The exception is in regions upstream of strong western boundary currents (such as those along Florida). However, even though additional larvae accumulated from well upstream in such areas (e.g., Mexico), the overall recruitment was relatively low (Fig. 2). The typical shape of the cumulative dispersal curve, therefore, is strongly skewed near the origin, with a near-zero tail starting as close as a few hundred kilometers (fig. S1).

Population connectivity via larval dispersal can produce biogeographic patterns within the broader Caribbean region (Fig. 4). The western and eastern Caribbean are moderately isolated from each other along a meridional break centered at about 67° to 70°W, or from the western end of Puerto Rico south to Aruba off the coast of Venezuela, which may constitute a clear ecological barrier from the Colombian gyre area to the west. The northeast Caribbean (Puerto Rico, Leeward Islands) is relatively isolated from the remainder of the eastern Caribbean; the Leeward Islands are mostly self-recruiting and constitute a sink for north-south larval exchange with the Windward Islands. However, there is also westerly exchange among the more southern Windward Islands and those along the north coast of South America. The Bahamas and the Turks and Caicos Islands form an enclave of high connectivity in the northern Caribbean, which is largely isolated from the remaining Caribbean domain, except for minor exchange from the north coast of Cuba and Haiti. The southern Mesoamerican (or Gulf of Honduras) reef area, including Belize and Honduras, is weakly isolated from the northernmost Mesoamerican Barrier Reef and strongly isolated from islands along the coast of Nicaragua to the east and south. Reefs along the Panama-Colombia Gyre are also isolated from the remainder of the Caribbean.

The Caribbean region emerges as four broadly defined regions of connectivity, the eastern Caribbean, the western Caribbean, the Bahamas and the Turks and Caicos Islands, and the region at the periphery of the Colombia-Panama Gyre, with lesser areas of isolation within each region. The more central portion of the Caribbean, including Hispaniola and Ja-



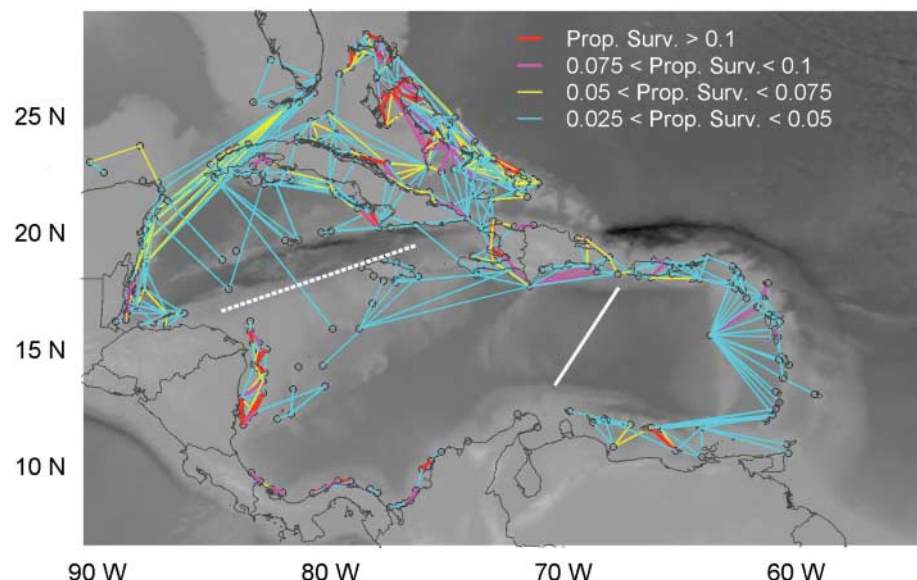
**Fig. 3.** Simulated larval (A) total recruitment, (B) self-recruitment, and (C) subsidy recruitment (importation) as a proportion of surviving virtual larvae reaching each coral reef settlement site (node  $N_j$ ) within subregions of the wider Caribbean. Larval dispersal trajectories were simulated at various degrees of larval activity, whereby the onset of active movement is on day 5 (green line), day 15 (red line), and day 30 (blue line; same as passive). Threshold levels required to sustain damselfish (30% of surviving larvae) and snapper (10% of surviving larvae) populations are indicated by the solid and dotted black lines, respectively. Although recruitment levels from passive larvae rarely met the threshold, the early onset of active larval movement typically enhanced both self-recruitment and subsidy. Abbreviations for the subregions are the same as for Fig. 2; prop. surv., proportion surviving.

maica, represents a zone of mixing among several of these other regions. The prominence of the boundaries of these regions is highlighted in genetic-based and morphological studies. These regions roughly define the same regions of genetically (and morphologically) distinct populations of the goby, *Elacatinus evelynae* (7, 11), and the coral, *Acropora palmata* (28). Thus, short-distance, stepping-stone population connectivity (29) may occur within regions, but the finding of limited exchange among regions over 5 years of monthly spawning appears sufficiently robust to allow regional scale genetic isolation as shown in other oceanographically and geographically complex regions (8). Faunal breaks, which are typically attributed to temperature or salinity differences inferring physiological constraints, may, in fact, be influenced (or alternatively, driven) by circulation constraints on dispersal (17, 30–32).

Ecological connections may be extended in some situations by rare, extreme dispersal events in which unusually large numbers of larvae are exported to distant locations (30, 33). When such events occur frequently enough (in terms of the demographic longevity of a species), populations may be sustained by the storage effect (34). Extending longevity in a species has been suggested as a means of capturing dispersal-related variability in flow events (20, 21, 33). In these simulations, which only covered 5 years, long-term rare events (25-, 50-, and 100-year events) were not evident. However, when viewed as cohort-specific events for short-lived species that spawn on a monthly (or more frequent) basis, rare events (defined as recruitment intensity of demographic relevance) occurred ~5% of the time at distances up to 200 km, but less than 1% (less than 1 out of 100 cohorts) at distances greater than 200 km. Thus, the storage effect may occur more as a range extension [e.g., extension of the short-lived blue-

phase goby into Turks and Caicos waters (7)], with local scale processes maintaining the population thereafter, than as occasional events maintaining a population. Moreover, lengthening adult life does not necessarily increase opportunity to capture variability (as from rare events) if the frequency of spawning decreases as compared with that of short-lived species.

The modeling approach taken in this study used an advanced combination of theoretical tools (26) that allowed an unprecedented overview of the spatial and temporal context over which population connectivity in marine species occurs. The passive (water circulation) component of this model has been well validated (27). Moreover, results of this model suggest testable hypotheses, with specific pre-



**Fig. 4.** Connectivity network for reef fish populations in the wider Caribbean plotted for various levels of larval exchange (proportion surviving) between each reef site (or node  $N_i$ , where center location is represented by a small gray circle; note that there is no directionality represented in the exchange). Two major meridional biogeographic breaks are identified: one in the eastern Caribbean Sea (white line) and the other one at the northern edge of the Nicaraguan Rise (dotted white line), which separate the eastern and western Caribbean. Two enclaves stand out: the Bahamas Bank, including the Turks and Caicos Islands, and the Nicaraguan Archipelago, which are both strongly intraconnected. The Panama-Colombian Gyre subregion is also largely isolated from the rest of the Caribbean, with little connection between Panama and Colombia. Note that connections at levels below 0.05% (proportion surviving) are not likely contributing appreciably to ecological connectivity but are shown here because they may become important when accumulated from different sources at one particular location.

**Table 1.** Estimates of total recruitment, proportion of self-recruitment, and dispersal distances at which various thresholds of recruitment are met, those necessary to replace the adult populations of each representative species, in the wider Caribbean region and for subregions

(e.g., individual islands, groups of islands, and complex continental shelf and lagoon areas). N/A means not attainable: Not enough larvae could accumulate at a site to accommodate such high levels of recruitment.

Region	Total recruitment (proportion surviving)	Self-recruitment (% total recruitment)	Source distance (km) for recruitment levels			
			0.01	0.1	0.3	1
Caribbean	0.39	20.7	<50	<50	200	N/A
Bahamas	0.63	21.5	<50	<50	100	N/A
Haiti	0.45	26.9	<50	<50	100	N/A
Cuba	0.43	25.0	<50	<50	150	N/A
Belize	0.37	26.4	50	<100	<100	N/A
Dominican Republic	0.36	27.0	<50	<50	300	N/A
Honduras	0.33	36.2	<50	<100	100	N/A
Florida	0.32	14.9	<50	300	950	N/A
Panama-Colombia	0.24	55.2	<50	<50	<100	N/A
Greater Antilles	0.23	12.9	<50	50	<250	N/A
Venezuela Corridor	0.22	16.4	50	<150	N/A	N/A
Jamaica	0.22	24.4	50	100	N/A	N/A
Cayman	0.18	9.8	50	200	N/A	N/A
Mexico	0.17	9.0	50	250	N/A	N/A

dictions about dispersal distances, the role of larval traits, and biogeographic and genetic patterns, which are consistent with emerging empirical data (6, 28, 35). Further experimental tests of model predictions, as well as incorporation of higher resolution biophysical models, will serve to improve the predictability of dispersal kernels, our understanding of the processes driving the dispersal outcome for explicit locations, and, ultimately, application of appropriate scaling to spatial management of marine populations.

#### References and Notes

- G. Thorson, *Meddr. Kommn. Danm. Fisk.-og Havunders. (Ser. Plankton)* **4**, 1 (1950).
- R. S. Scheltema, *Bull. Mar. Sci.* **39**, 290 (1986).
- G. P. Jones, M. J. Milicich, M. J. Emslie, C. Lunow, *Nature* **402**, 802 (1999).
- S. E. Swearer, J. E. Caselle, D. W. Lea, R. R. Warner, *Nature* **402**, 799 (1999).
- S. R. Thorrold, C. Latkoczy, P. K. Swart, C. M. Jones, *Science* **291**, 297 (2001).
- C. B. Paris, R. K. Cowen, *Limnol. Oceanogr.* **49**, 1964 (2004).
- M. S. Taylor, M. E. Helberg, *Science* **299**, 107 (2003).
- P. H. Barber, S. R. Palumbi, M. V. Erdmann, M. K. Moosa, *Nature* **406**, 692 (2000).
- S. Palumbi, *Ecol. Appl.* **13**, S146 (2003).
- G. P. Jones, S. Planes, S. R. Thorrold, *Curr. Biol.* **15**, 1314 (2005).
- P. L. Colin, *Neon Gobies* (TFH Publications, Neptune, NJ, 1975).
- R. K. Cowen, K. M. M. Lwiza, S. Sponaugle, C. B. Paris, D. B. Olson, *Science* **287**, 857 (2000).
- R. R. Warner, R. K. Cowen, *Bull. Mar. Sci.* **70**, 245 (2002).
- J. Roughgarden, S. D. Gaines, H. P. Possingham, *Science* **241**, 1460 (1988).
- L. Botsford, W. A. Hastings, S. D. Gaines, *Ecol. Lett.* **4**, 144 (2001).
- P. W. Sammarco, J. C. Andrews, *Limnol. Oceanogr.* **34**, 896 (1989).
- A. L. Shanks, B. A. Grantham, M. H. Carr, *Ecol. Appl.* **13**, S159 (2003).
- A. E. Hill, *Mar. Ecol. Prog. Ser.* **64**, 217 (1990).
- C. M. Roberts, *Science* **278**, 1454 (1997).
- J. L. Largier, *Ecol. Appl.* **13**, S71 (2003).
- S. D. Gaines, B. Gaylord, J. L. Largier, *Ecol. Appl.* **13**, S32 (2003).
- D. A. Seigel, B. P. Kinlan, B. Gaylord, S. D. Gaines, *Mar. Ecol. Prog. Ser.* **260**, 83 (2003).
- F. E. Werner, J. A. Quinlan, R. G. Lough, D. R. Lynch, *Sarsia* **86**, 411 (2001).
- E. Wolanski, P. Doherty, J. Carleton, *Naturwissenschaften* **84**, 262 (1997).
- M. K. James, P. R. Armsworth, L. B. Mason, L. Bode, *Proc. Biol. Sci.* **269**, 2079 (2002).
- B. deYoung *et al.*, *Science* **304**, 1463 (2004).
- Materials and Methods are available on *Science Online*.
- I. B. Baums, M. W. Miller, M. E. Hellberg, *Mol. Ecol.* **14**, 1377 (2005).
- M. H. Carr, D. C. Reed, *Can. J. Fish. Aquat. Sci.* **50**, 2019 (1993).
- R. K. Cowen, *J. Mar. Res.* **43**, 719 (1985).
- W. R. Coe, *Ecology* **34**, 225 (1953).
- I. E. Efford, *Crustaceana* **18**, 293 (1970).
- B. Gaylord, S. D. Gaines, *Am. Nat.* **155**, 769 (2000).
- R. R. Warner, P. L. Chesson, *Am. Nat.* **125**, 769 (1985).
- S. Planes, in *The Ecology of Fishes on Coral Reefs*, P. F. Sale, Ed. (Academic Press, San Diego, 2002), pp. 201–220.
- The authors thank S. Sponaugle, J. Llopiz, J. Kool, and D. Richardson for discussion and review of an earlier draft of this paper. We also thank K. Lindeman of Environmental Defense and the National Science Foundation (OCE-0119976 and OCE-0095955) for supporting this work. Z. Garraffo and E. Chassignet provided help and support with using the output of the Miami Isopycnal Coordinate Ocean Model (MICOM).

#### Supporting Online Material

www.sciencemag.org/cgi/content/full/1122039/DC1

Materials and Methods

Fig. S1

Table S1

References and Notes

31 October 2005; accepted 18 November 2005

Published online 15 December 2005;

10.1126/science.1122039

Include this information when citing this paper.

## Nonrandom Processes Maintain Diversity in Tropical Forests

Christopher Wills,<sup>1\*</sup> Kyle E. Harms,<sup>2,3</sup> Richard Condit,<sup>3</sup> David King,<sup>4</sup> Jill Thompson,<sup>5</sup> Fangliang He,<sup>6</sup> Helene C. Muller-Landau,<sup>7</sup> Peter Ashton,<sup>4</sup> Elizabeth Losos,<sup>8</sup> Liza Comita,<sup>9</sup> Stephen Hubbell,<sup>9</sup> James LaFrankie,<sup>10</sup> Sarayudh Bunyavejchewin,<sup>11</sup> H. S. Dattaraja,<sup>12</sup> Stuart Davies,<sup>4</sup> Shameema Esufali,<sup>13</sup> Robin Foster,<sup>14</sup> Nimal Gunatilleke,<sup>13</sup> Savitri Gunatilleke,<sup>13</sup> Pamela Hall,<sup>15</sup> Akira Itoh,<sup>16</sup> Robert John,<sup>17</sup> Somboon Kiratiprayoon,<sup>18</sup> Suzanne Loo de Lao,<sup>3</sup> Marie Massa,<sup>8</sup> Cheryl Nath,<sup>12</sup> Md. Nur Supardi Noor,<sup>19</sup> Abdul Rahman Kassim,<sup>19</sup> Raman Sukumar,<sup>12</sup> Hebbalalu Satyanarayana Suresh,<sup>12</sup> I-Fang Sun,<sup>20</sup> Sylvester Tan,<sup>21</sup> Takuo Yamakura,<sup>16</sup> Jess Zimmerman<sup>5</sup>

An ecological community's species diversity tends to erode through time as a result of stochastic extinction, competitive exclusion, and unstable host-enemy dynamics. This erosion of diversity can be prevented over the short term if recruits are highly diverse as a result of preferential recruitment of rare species or, alternatively, if rare species survive preferentially, which increases diversity as the ages of the individuals increase. Here, we present census data from seven New and Old World tropical forest dynamics plots that all show the latter pattern. Within local areas, the trees that survived were as a group more diverse than those that were recruited or those that died. The larger (and therefore on average older) survivors were more diverse within local areas than the smaller survivors. When species were rare in a local area, they had a higher survival rate than when they were common, resulting in enrichment for rare species and increasing diversity with age and size class in these complex ecosystems.

Most of the mechanisms that have been proposed for the maintenance of species diversity in ecosystems do not assume that locally rare species will survive preferentially. These mechanisms include the intermediate disturbance hypothesis and classic niche differentiation (1); lottery competition for space, coupled with storage effects, which can take place in a variable environment or when recruitment is limited (2); the source-sink hypothesis (3); and the neutral theory of bio-

diversity (4). The last of these assumes that within a trophic level of an ecosystem—such as the trees of a tropical forest—ecological drift governs local community dynamics.

Three important models invoke frequency-dependent mechanisms that lead to higher survival of locally rare species. The first of these is the Janzen-Connell hypothesis (5, 6), in which diversity is maintained by frequency- or density-dependent interactions between hosts and specialized pathogens, herbivores, or

predators. The Janzen-Connell model predicts that diversity should increase as a group of individuals ages, because more common species are selectively removed by pathogens and predators. The mix of surviving species will also depend on the past history of local host-pathogen or plant-resource interactions, so that it is likely to vary over both time and space. There is experimental evidence for the Janzen-Connell model (7–11).

The second of these models, the niche complementarity hypothesis (12, 13), posits that species differ in the sub-environments or resources they exploit, and as a result, individuals compete more intensively with conspecifics than with individuals of other species. Because locally rare species are subject to relatively less conspecific competition than more common species, they are at a relative advantage (14). In this model, an increase in diversity can be traced to variations in the physical characteristics of the environment rather than the effects of pathogens and predators. In the third model, facilitation (15), diversity may increase if an individual facilitates (benefits) nearby nonspecifics. Similar to the niche complementarity hypothesis, facilitation has the effect of making interspecific interactions more positive than intraspecific interactions and thus provides an advantage to locally rare species.

Possible frequency-dependent effects have recently been proposed for six forest sites (16), but these postulated effects are based on extrapolations from theory rather than actual birth and death rates. Frequency-dependent recruitment and mortality have been observed