

Scaling of Connectivity in Marine Populations

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Defining the scale of connectivity, or exchange, among marine populations and 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 typical larval dispersal distances of ecologically relevant magnitudes on the scale of only 10 to 100 km for a variety of reef fish species and show the importance of the early onset of larval behavior mediating the dispersal potential. Larval subsidies, in addition to self-recruitment, are required to sustain most populations, although larval 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.

Identification of the scaling of marine larval dispersal remains one of the fundamental challenges to marine ecology and oceanography. Most coastal marine species have limited adult movement, so the relatively short, pelagic larval phase represents the primary opportunity for dispersal. While 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 modes (i.e., long-distance) of dispersal for marine populations (12, 13). The rates, scale, and spatial structure of successful exchange, or connectivity, among local populations of marine organisms drive population replenishment, and, have profound implications for population dynamics and genetics of marine organisms, as well as spatially oriented resource management (e.g., MPAs), and the 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 exist 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 snap shot 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 utilizing 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 (e.g., spacing of marine reserves) (15, 20–22), yet such studies do not provide realistic renditions of ocean circulation nor 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 (i.e., effective geographical distances among reef fish populations) under realistically varying spatial and temporal oceanographic conditions, the circulation model was run for five 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 (i.e., vertical and horizontal swimming capabilities), and adult spawning strategies (i.e., season and frequency). Successful dispersal also requires larvae (real or virtual) to encounter suitable settlement habitat, which is fragmented and often

covers a very 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 (i.e., the wider Caribbean including the Bahamas and Florida). Contiguous coral reef habitat was further divided into 50-km segments, setting the spatial scale for self-recruitment in this study. Virtual larvae had to be near (i.e., within 9 km) available settlement habitat at the end of their larval period in order to be considered successful (i.e., settle).

Though dispersal of a few organisms may be widespread, ecologically significant levels of dispersal (i.e., those necessary to replenish annual mortality) may be significantly more restricted in spatial extent (12, 20). To make reasonable predictions of ecologically meaningful dispersal curves or kernels, the required relative level or amplitude 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 (i.e., maintain it at a constant population level) by balancing the natural juvenile and adult mortality, and accommodating any additional mortality (i.e., fishing). Settlement rates (i.e., number of settlers/year), therefore, were matched to estimated adult mortality rates utilizing simple population growth models (i.e., $N_t = N_0 e^{rt}$) set to a constant age 1+ population size. Based on these estimates (27) (table S1), we found that the required level of potential settlers (i.e., larvae that survived their entire pelagic duration) range between 10 and 100% for long-lived (i.e., longevity > 15 years) to short-lived species (i.e., longevity *ca.* 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 a large region with complex, highly diverse flow regimes and spatially heterogeneous habitat (i.e., the wider Caribbean: 8° N-28° N, 57° W-90° W, *ca.* 2,100 km × 3,300 km, Fig.1), that typical larval dispersal distances providing ecologically-significant numbers of settlers were only on the scale of 50-100 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 (i.e., subsidized) larvae varied, largely as a result of variation in the abundance of imported larvae. Consequently, some populations experience generally lower recruitment levels than others. The fine scale of dispersal, on top of specific suitable settlement habitat and oceanographic boundaries, creates several sub-regions 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 behavior. These results suggest that passive dispersal is insufficient for population replenishment. The foremost difference between a purely passive model and one incorporating larval behavior is the prevalence of local or self-recruitment enhanced with early onset of behavior and modified by the fragmentation pattern of available settlement habitat (i.e., clustered vs. isolated), while the converse of greater long distance dispersal under the passive scenario was not realized (Fig. 2). Overall, the passive scenario resulted in recruitment levels which were 1-2 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 larval durations, which also increase connectivity. These results underscore the role of larval traits and behavior when modeling both dispersal and recruitment and demonstrate that biological (i.e., PLD, larval capabilities) and physical constraints (i.e., oceanographic boundaries) are similarly important in resolving dispersal kernels and connectivity among fish populations.

In most areas, when larval behavior was invoked, total recruitment (i.e., recruitment accruing from subsidy from all sites and from 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 (high-turnover) species (Fig 3A). Two regions (i.e., WIND and MEXI) stood out as being strongly recruitment-limited (i.e., total recruitment falls well below that necessary for sustaining populations), while most regions appear to receive sufficient recruitment levels such that post-settlement (i.e., density-dependent) processes may be important at moderating population fluctuation. When parsed between recruitment from local sources (i.e., self-recruitment) versus imported (or subsidized) 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 at supplying adequate numbers of young only with larval behavior, but a variety of sites appear to be poor at self-seeding. In contrast, subsidy is generally less variable, particularly under passive scenarios, though certain sites (e.g., Windward Islands, Yucatan Peninsula in northern Mexico) are apparently devoid of sources within a critical upstream distance, resulting in low recruitment levels. Life histories and larval behavior emerge as factors that strongly influence self-recruitment, while oceanographic regimes appear to control subsidies.

Caribbean-wide, self-recruitment accounted for *ca.* 21% of the recruits to an average site, with subsidy from within 50 km (or less since 50 km is the resolution of the 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 a large regional domain (i.e., 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 of the semi-permanent Panama-Colombia Gyre). In the latter case, the high proportion of self-recruitment was partially due to low levels of subsidy from upstream locations, resulting in a generally low overall level of recruitment. Generally, significant additional contributions of recruits do not accumulate from farther than 200-300 km. The exception is in regions upstream of very strong western boundary currents (e.g., Florida). However, even though additional larvae accumulated from well upstream in such areas (e.g., Mexico), the overall recruitment levels were relatively low (Fig. 2). The typical shape of the cumulative dispersal curve, therefore, is strongly skewed near the origin, with a near-zero level tail starting as close as a few hundred km (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 approximately 67-70°W, or from the western end of Puerto Rico down 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 with the Leeward Islands being mostly self-recruiting and constituting 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 northern-most 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 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 Jamaica, 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, 10), as well as, 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 five years of monthly spawning appears sufficiently robust to allow region-scale genetic isolation as shown in other oceanographically/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 where 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 (34) (i.e., storage effect). 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 five years, long term rare events (e.g., 25, 50, and 100-yr. 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 approximately 5% of the time at distances up to 200 km, but less than 1% (i.e., 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 (e.g., rare events) if the frequency of spawning decreases as compared to that of short-lived species.

The modeling approach taken in this study utilized 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 predictions 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 bio-physical 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.

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Supporting Online Material

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Materials and Methods

Fig. S1

Table S1

References and notes

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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 represents a small fraction of the entire oceanic and coastal areas. Subregions within the wider Caribbean region are color coded and segmented in a total of 260 polygons (9×50 km) or nodes (N_i).

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 site N_j after completion a 30-d pelagic larval duration (PLD) (i.e., 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 (i.e., $i = j = 260$) 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, while 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 (i.e., $N_i = N_j$, along the diagonal), self-recruitment occurs. Lunar cyclic spawning (i.e., monthly) of the modeled coral reef fish (e.g., Damselfish) is replicated in each node for a 5-year period of ocean circulation model (i.e., MICOM) daily currents, while larval dispersal trajectories are simulated at various degree of larval behavior: (A) onset of larval behavior (i.e., retention within 9km of available settlement habitat) half-way through the pelagic phase (i.e., day 15); (B) early onset of active behavior (i.e., day 5); (C) delayed onset of active behavior for passive larvae at the end of PLD (i.e., 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 & Mona Islands; HISW, Hispaniola West (Haiti); HISE, Hispaniola East (Dominican Republic); JAMA, Jamaica Island & Pedro Bank; CAYM, Cayman Islands, Rosario & Misteriosa Banks; CUSE, Southeast Cuba; CUSW, Southwest Cuba; CUNW, Northwest Cuba; CUNC, North central Cuba; TCIS, Turks & Caicos Islands; BAHA, Bahamas Bank & Southeast Bahamian Islands; GRBA, Grand Bahamas; FLOR, Florida Keys & West coast reefs; MEXI, Mexican Caribbean & 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 A Dios); PANA, Panama & Coasta Rica; COLO, Gulf of Colombia.

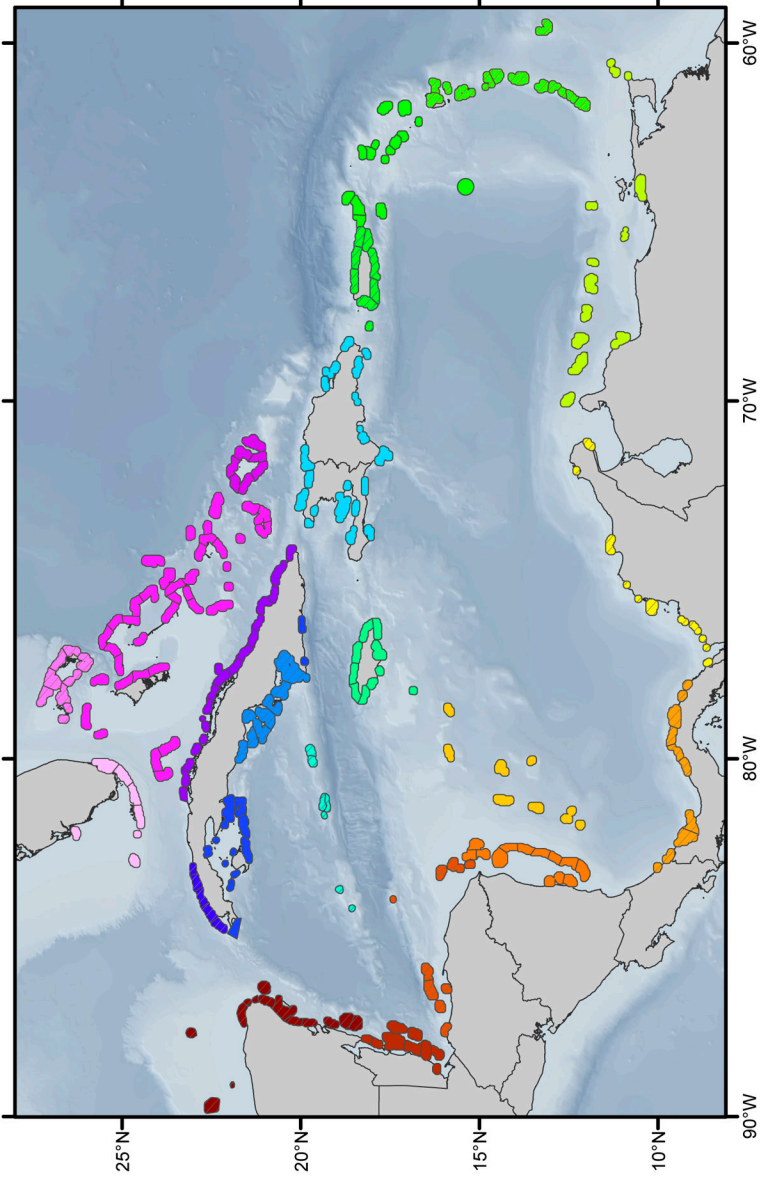
Fig. 3. Simulated (A) total, (B) self, and (C) subsidy recruitment as a proportion of surviving virtual larvae reaching each coral reef settlement site (i.e., node N_j) within subregions of the wider Caribbean. Larval dispersal trajectories were simulated at various degrees of larval behavior, whereby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

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 Turks & Caicos Islands, and the Nicaraguan Archipelago, which are both strongly intra-connected. The Panama-Colombian Gyre sub-region 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 significantly to ecological connectivity but are shown here because they may become significant 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 (i.e., necessary to replace the adult populations of each representative species) in the wider Caribbean region and for sub-regions (e.g., individual islands, group of islands, 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 recruit. (prop. surv.)	Self-recruit. (% total recruit.)	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

- Florida Keys & West Coast Reefs
- Grand Bahama
- Bahamas Bank & SE Bahamas Island
- Turks & Caicos Islands
- Northcentral Cuba
- Northwest Cuba
- Southwest Cuba
- Southeast Cuba
- Hispaniola
- Cayman Islands, Rosario & Misteriosa
- Jamaica & Pedro Bank
- Puerto Rico & Mona Islands
- Leeward Islands
- Windward Islands
- Venezuelian Corridor (Tobago-Aruba)
- Gulf of Colombia
- Colombian Archipelagos
- Panama & Costa Rica
- Nicaraguan Rise Islands
- Gulf of Honduras
- Belize
- Mexican Caribbean & Campeche Bank



Settlement Node (Nj)

