RESEARCH ARTICLE

Modeling population connectivity by ocean currents, a graph-theoretic approach for marine conservation

**Eric A. Treml · Patrick N. Halpin ·
Dean L. Urban · Lincoln F. Pratson**

Abstract The dispersal of individuals among marine populations is of great importance to meta-population dynamics, population persistence, and species expansion. Understanding this connectivity between distant populations is key to their effective conservation and management. For many marine species, population connectivity is determined largely by ocean currents transporting larvae and juveniles between distant patches of suitable habitat. Recent work has focused on the biophysics of marine larval dispersal and its importance to population dynamics, although few studies have evaluated the spatial and temporal patterns of this potential dispersal. Here, we show how an Eulerian advection–diffusion approach can be used to model the dispersal of coral larvae between reefs throughout the Tropical Pacific. We illustrate how this connectivity can be analyzed using graph theory—an effective approach for exploring patterns in spatial connections, as well as for determining the importance of each site and pathway to local and regional connectivity. Results indicate that the scale (average distance) of dispersal in the Pacific is on the order of 50–150 km, consistent with recent studies in the Caribbean (Cowen, et al. 2006). Patterns in the dispersal graphs highlight pathways for larval dispersal along major ocean currents and through island chains. A series of critical island 'stepping stones' are discovered providing potential pathways across the equatorial currents and connecting distant island groups. Patterns in these dispersal graphs highlight possible pathways for species expansions, reveal connected upstream/downstream populations, and suggest areas that might be prioritized for marine conservation efforts.

E. A. Treml (✉) · P. N. Halpin
Marine Geospatial Ecology Lab, Nicholas School of the Environment and Earth Sciences, LSRC, Duke University, Box 90328, Durham, NC 27708, USA
e-mail: eat4@duke.edu

D. L. Urban
Landscape Ecology Lab, Nicholas School of the Environment and Earth Sciences, LSRC, Duke University, Box 90328, Durham, NC 27708, USA

L. F. Pratson
Nicholas School of the Environment and Earth Sciences, Old Chem, Duke University, Box 90227, Durham NC 27708, USA

Introduction

For many marine species, life histories are characterized by a planktonic larval stage and a sessile, or sedentary, adult existence. Their spatially distributed adult populations are thought to be connected primarily through the dispersal of larvae by ocean

currents, often over great distances (Scheltema 1986; Shanks et al. 2003; Kinlan et al. 2005; Trakhtenbrot et al. 2005). Population connectivity, defined as the exchange of individuals among marine populations, is important for the persistence of isolated populations (Roughgarden et al. 1988; Gaylord and Gaines 2000; James et al. 2002), re-establishment of sites following disturbances, and the flow of genetic information (Palumbi 2003; Trakhtenbrot et al. 2005). In addition, for these populations, larval dispersal determines the rate and spatial patterns of population spread (Levins 1969; Gaines and Lafferty 1995; Gaylord and Gaines 2000)—a key factor in determining how a species might cope with global climate change (Trakhtenbrot et al. 2005). As a result, differences in population connectivity contribute greatly to the spatiotemporal patterns in the distribution of marine organisms (Levin 1992; Warner 1997), and need to be considered for their proper management (Gaines et al. 2003; Palumbi 2003). Here, we use a graph-theoretic framework for analyzing regional marine connectivity patterns and assigning conservation value to individual sites based on their role in contributing to this connectivity. In this case, a 'connection' exists between two reef sites or populations when there is potential for successful larval dispersal to occur between them. We evaluate the influence of pelagic larval duration (PLD) and the inter-annual variability in surface currents on regional connectivity and illustrate the utility of graph theory for marine population and conservation applications. Although this analysis is applied to a Pacific coral dispersal model, the graph analysis may be applied to connectivity estimates from Lagrangian biophysical models (James et al. 2002; Cowen et al. 2006), genetic estimates (Benzie and Williams 1997; Palumbi et al. 1997; Meyer et al. 2005), and community data (Connolly et al. 2005).

Understanding the physical and biological factors that contribute to marine connectivity is critical to the implementation of marine conservation and management strategies (Roberts 1997; Cowen et al. 2000; Kinlan et al. 2005; Sale et al. 2005; Trakhtenbrot et al. 2005). The design and management of marine reserves, in particular, should consider this connectivity (Gerber et al. 2003). Although there appears to be consensus that reserve networks should be a central management tool in conserving biodiversity (Sala et al. 2002; Gaines et al. 2003;

Lubchenco et al. 2003; Sale et al. 2005), two fundamental challenges remain with implementation: (1) quantifying dispersal/connectivity across the relevant spatial and temporal scales, and (2) integrating this connectivity explicitly in marine conservation planning. This is because direct measurements of connectivity are difficult and available for only a few marine species (Kinlan and Gaines 2003; Shanks et al. 2003). In addition, a methodological framework does not exist for directly incorporating dispersal connectivity in the design of an effective reserve network topology, such as the span of the network, spacing of individual sites, number of reserves, and their placement (Botsford et al. 2003; Lubchenco et al. 2003). For these reasons, marine conservation and management models rarely consider larval dispersal explicitly in their approach (Gaines et al. 2003). Yet the configuration of marine reserves, and conservation planning in general, should include the dispersal potential of the species of interest (Botsford et al. 2001; Warner and Cowen 2002; Palumbi 2004). The research presented here addresses some of these shortcomings by presenting a general method for quantifying potential dispersal and by illustrating how graph theory can inform the conservation process by providing a framework for exploring and analyzing connectivity estimates.

Quantifying marine connectivity

Quantifying the complex process of dispersal requires some degree of simplification due to the multiple spatial and temporal scales required and the many biological and physical factors involved. Connectivity between two populations is dependent on the larval characteristics of the species (e.g., competency period, dispersal duration, and swimming behavior), the health and abundance of the source population, the permeability of the intervening environment (speed and direction of ocean currents, temperature, salinity, etc.), and the availability and suitability of downstream habitat (Scheltema 1986; Veron 1995). As a result, when included in conservation planning, larval dispersal is often simplified using assumptions about larval supply (constant spatially uniform larval pool), larval exchange (larvae move between nearest neighbors only), or larval spread (a simple diffusion

process) (Gaines et al. 2003). The need to overcome these shortcomings has given rise to a number of research efforts that focus on building a theoretical foundation for dispersal modeling in idealized environments (Roughgarden et al. 1988; Possingham and Roughgarden 1990; Gaylord and Gaines 2000; Gaines et al. 2003; Largier 2003), and coupling larval dispersal parameters with realistic hydrodynamic data in biophysical models (Roberts 1997; Cowen et al. 2000; James et al. 2002; Gilg and Hilbish 2003; Paris et al. 2005). Following is a brief review of these studies highlighting the implications of modeling marine dispersal for ecological and conservation applications.

Theoretical foundations in larval dispersal modeling

The early modeling work of Roughgarden and others (Roughgarden et al. 1988, Possingham and Roughgarden 1990) formed a solid theoretical foundation for exploring the influence of ocean currents and larval supply on the distribution and abundance of benthic marine organisms. They concluded that there is a significant impact on downstream populations, and that larval transport needs to be an integral component of studying the population ecology of marine species (Possingham and Roughgarden 1990). These models were expanded to include a variety of flow fields representing common coastal oceanographic features (convergence, divergence, and eddy circulation), temporal variability in larval release, larval competency, and mortality (Gaylord and Gaines 2000). The expanded models supported earlier findings and found that simple oceanographic features could induce dispersal corridors and barriers (Gaylord and Gaines 2000). Gaines et al. (2003) continued this research and explored the impact of coastal oceanography on population persistence with respect to several different reserve configurations. Their work showed that advection by strong ocean currents can play a dominant role in determining the influence of reserve configuration on marine communities. These theoretical modeling exercises have clearly shown the potential impact of ocean currents on the connectivity of nearshore benthic populations, and emphasized the importance of including ocean dynamics in marine conservation planning.

Biophysical modeling of dispersal

Several studies have focused on coupling the biological parameters of larval dispersal with dynamic physical oceanographic data. Although these studies focus on different species, span a wide range in spatial scales, and vary in biological complexity, each offers unique insight into the patterns and consequences of larval dispersal and population connectivity. Collectively, they demonstrate the ability of hydrodynamic models to predict the spatial patterns in larval dispersal at various scales and for a variety of taxa: coral larvae (Gay and Andrews 1994; Sammarco 1994), estuarine dependent fishes (Hare et al. 1999; Ortner et al. 1999; Rice et al. 1999; Werner et al. 1999), mussels (Gilg and Hilbish 2003), and reef fish (Cowen et al. 2000, 2003, 2006; James et al. 2002; Paris et al. 2005). By simulating realistic flow regimes that incorporate daily to annual variability, it is possible to reveal patterns in the strength and persistence of dispersal connections between sites (Hare et al. 1999; Cowen et al. 2000, 2006; James et al. 2002). Empirical data on egg and larval distributions (Wolanski et al. 1989; Hare et al. 1999; Cowen et al. 2000), recruitment patterns (Sammarco and Andrews 1989; Sammarco 1994; Paris and Cowen 2004), and population genetics (Gilg and Hilbish 2003) offer indisputable evidence of the tight coupling between hydrodynamics and realized dispersal.

The role of larval behavior in biophysical dispersal modeling is believed to be crucial, although the degree to which it influences dispersal potential and local retention is debated, and probably species-specific (Cowen et al. 2000; Mora and Sale 2002; Warner and Cowen 2002; Sale 2004). This debate is most often focused on larval fish behavior, and may not pertain to those species with a more passive dispersal strategy or those confined to the upper water column for all or most of the pelagic dispersal stage. Marine organisms dispersed in the upper water column include those with buoyant larvae (or eggs), small ciliated larval forms (e.g., coral planula larvae), larvae with negative geotaxis and/or positive phototaxis behaviors (e.g., mussels), and those known to disperse on floating objects (Jackson 1986; Jokiel 1990; Jokiel and Cox 2003). Dispersal has been successfully modeled as an advection–diffusion process in sea surface flow fields for several species including corals (Richmond 1987; Andrews et al. 1988; Gay and Andrews 1994;

Sammarco 1994; Veron 1995; Glynn and Ault 2000; Gilg and Hilbish 2003), mussels (Gilg and Hillbish 2003), and many other invertebrates (Scheltema 1986; Kinlan and Gaines 2003).

In this study, we use a passive dispersal biophysical model to develop connectivity estimates between islands across the Tropical Pacific. Comparing model predictions with empirical data (e.g., genetics, community similarities) may highlight areas where biological or physical processes not included in the model play an important role in larval dispersal (Siegel et al. 2003). Once these models are validated and hypotheses tested, they can inform the marine conservation process and assist in marine reserve design.

Methods

To evaluate the patterns in connectivity throughout the Tropical Pacific, we use a spatially explicit biophysical model to simulate coral dispersal between coral reefs for three different years. Although our focus is on the dispersal potential of coral larvae, the methods and results may be applicable to any organism with equivalent larval dispersal traits. This two-dimensional (2D) Eulerian advection–diffusion model of coral dispersal incorporates realistic surface current velocity data and PLD estimates. PLD is defined as the period of a species larval development spent in the water column, susceptible to physical mixing and advection (Sponaugle et al. 2002). After dispersal simulations are

completed for all reef sites, the connectivity estimates (days) are used to populate a distance matrix representing the time it takes to disperse from every reef i to every other reef j. This distance matrix, along with the location of each reef site, is used to construct a graph model of the dispersal-based connectivity across the Pacific (Fig. 1). Graph analysis (West 2001; Newman 2003) is then used to explore the spatial and temporal patterns in connectivity, identify potential dispersal pathways, locate critical island stepping stones, and identify the connected upstream and downstream neighbors for each site. For graph definitions, see Table 1.

Hydrodynamic connectivity model

The spatial domain is defined using shorelines and reef locations derived from the Digital Chart of the World Server (Pennsylvania State University Libraries) and other sources (Spalding et al. 2001; Oliver et al. 2004) at a resolution of 1 km^2. The spatial data are aggregated up to 25×25 km^2 cells, creating a 279×490 grid cell modeling environment. A total of 457 independent reef patches among 35 countries are included between the latitudes of 30 North and 30 South and Longitudes 130 East and 120 West (Fig. 2). It has been shown that El Niño events can alter circulation patterns in the Pacific, and therefore dispersal pathways (Glynn and Ault 2000). To capture this variability, we model coral dispersal during a strong El Niño year (1997), a strong La Niña
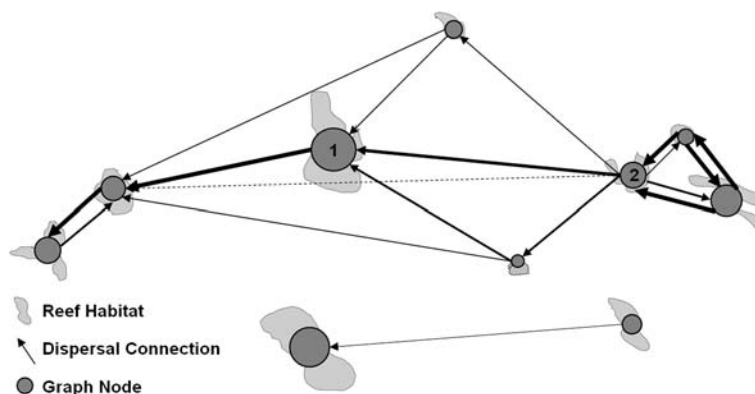

Fig. 1 A graph-theoretic illustration of marine connectivity. Coral reef habitat is represented by *nodes* within the graph framework. When larvae from a source reef reach a downstream reef site, a dispersal connection is made. This dispersal connection and direction is represented by an *arrow*, or '*edge*' within the graph. The thickness of the *arrow* reflects the strength of connection

Table 1 Primary graph definitions

Edge	An arrow, arc, or line representing a larval dispersal connection and direction
Node	A point or vertex showing the location of the centroid of reef habitat. Node attributes may include area, quality, protected status, etc.
Order	Total number of nodes within a graph. The graph in Fig. 1 has an order of 10
Size	Total number of edges within a graph. The graph in Fig. 1 has a size of 18
Component	A connected sub-graph. Figure 1 has two components
In-degree	Total number of edges coming into a node. Node number 1 in Fig. 1 has an in-degree of 3
Out-degree	Total number of edges leaving a node. Node number 1 in Fig. 1 has an out-degree of 1
Cut-node	With the removal of a cut-node, the graph is broken into additional components. In Fig. 1, node number 2 is a cut-node
Neighborhood	The connected upstream and downstream sites of a given node. In Fig. 1, node number 2 has an upstream neighborhood of two nodes and a downstream neighborhood of four nodes
Path	Any sequence of edges connecting two nodes through the graph framework. The length of the path is calculated either by counting the number of edges or summing the weights of all edges along the path
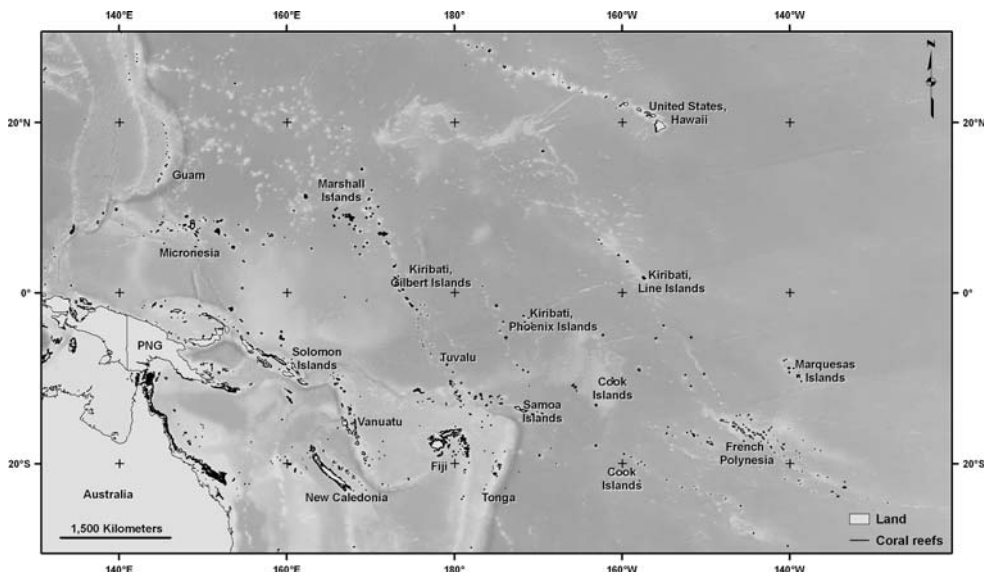
Fig. 2 Study area showing locations of reefs and land masses across the Tropical Pacific. Bathymetry is in *gray* with shallow areas in lighter shades

year (1999), and a neutral year (2001). Year selection was based on the Oceanic Niño Index published by the Climate Prediction Center of the National

Oceanic and Atmospheric Administration (NOAA) National Weather Service. Dispersal simulations were completed in every season for each year. These

scenarios were summarized by year, across years, and for the coral mass spawning season of October through November (Veron 1995). The average frequency of El Niño and La Niña events of ~2 decade^{-1} (Quinn et al. 1993; Dunbar et al. 1994) was used to calculate a weighted average connectivity distance matrix for all years from the annual simulations. These frequencies are also used to explore the relative persistence of dispersal pathways through time. The weekly averaged surface current velocities used in the larval dispersal model are from the NOAA Environmental Modeling Center's ocean analysis system (Ji et al. 1995). This Pacific Ocean general circulation model is driven by weekly mean surface winds and heat fluxes, and incorporates observed ocean temperatures and altimetry data from the TOPEX/Poseidon satellite.

Coral dispersal is implemented with a 2D Eulerian advection–diffusion-mortality model, similar to Cowen et al. (2000), to explore the passive dispersal of coral larvae from source reefs to all downstream sites:

$$\frac{\partial N}{\partial t} = -u\frac{\partial N}{\partial x} - v\frac{\partial N}{\partial y} + K\left(\frac{\partial^2 N}{\partial x^2} + \frac{\partial^2 N}{\partial y^2}\right) - \mu N \qquad (1)$$

where N is the concentration of larvae per cell, t the time, u the zonal velocity, v the meridional velocity, K the horizontal diffusion coefficient to represent sub-scale turbulence (Okubo 1994; Largier 2003), μ is the mortality coefficient, x and y are spatial coordinates. Diffusion is implemented using the finite difference approximation of Laplace's differential operator applied to the velocity fields, using MAT-LAB (2005). Biological parameters include larval

release time (t_0), initial larval density (N_0), species-specific PLD, and precompetency period (pc) (Table 2). In this implementation, a simulation consists of releasing 10,000 virtual larvae km^{-2} from an individual reef site and tracking the density of larvae through time (Cowen et al. 2000). This is repeated for each of the 457 individual reef sites in the model domain for every spawning season. Simulations are completed for PLDs up to a maximum of 80 days. This maximum is based on values for corals (Richmond 1987), and other marine taxa (Grantham et al. 2003; Kinlan and Gaines 2003). Model sensitivity analyses were completed and results show that the spatiotemporal patterns in connectivity are robust to moderate changes in all parameter values.

A distance matrix, **D**, is populated during a series of coral larval dispersal simulations for each season. During each simulation, virtual larvae are released and then transported downstream by ocean currents from an individual reef site (reef i). As the larvae are carried passively downstream, all other reef sites in the model are monitored. If the density of larvae at a downstream reef site exceeds 1 cell^{-1}, a connection is made between the two reef sites, and the time (days) it took for the larvae to drift between sites is recorded ($\mathbf{d}_{ij}$). After dispersal simulations are completed for all reef sites for a particular spawning season, a distance matrix is filled representing the dispersal-based connectivity of the Tropical Pacific for that season. The distance matrix is asymmetric due to the directionality of the currents; the time it takes to disperse from reef i to reef j is not the same as from reef j to reef i ($\mathbf{d}_{ij} \neq \mathbf{d}_{ji}$). A dispersal

Table 2 Parameters and values used in the coral dispersal biophysical modeling

		Units	Value
Δt	Time step	Day	0.1
Δx, Δy	Horizontal resolution	km	25
K	Horizontal eddy diffusivity	m^2 s^{-1}	50
N_0	Initial concentration of larvae	Larvae km^{-2}	10,000
t_0	Time of coral spawning	Day	Varies seasonally
μ	Larval mortality	% day^{-1}	0.0[a]
PLD	Pelagic larval duration	Days	15, 30, 60
pc	Larval precompetency duration	Days	1

Although a range of values were explored during the sensitivity analysis, the values above were used in the analyses presented here

[a] Mortality was implemented using a negative-exponential dispersal kernel after the biophysical modeling within the graph-theoretic framework

probability matrix, **P**, is then created by applying a negative-exponential dispersal kernel (Clark et al. 1999; Urban and Keitt 2001; Siegel et al. 2003; Kinlan et al. 2005) to the distance matrix to express the probability of successful dispersal between reef sites. We define the distance-decay coefficient, θ, based on the tail distance (maximum PLD) corresponding to the probability of successful dispersal, $P = 0.05$, as $\ln(0.05)\theta^{-1}$ (Urban and Keitt 2001). Setting the mortality coefficient to zero in the biophysical model and later calculating dispersal probabilities has the advantage of preserving potential, yet rare, dispersal events in **D**, while exploring the more likely dispersal connections and pathways in **P**.

The most often-used measurement for defining larval dispersal is geographic distance (Benzie and Williams 1997; Palumbi 2003; Kinlan and Gaines 2003; Gaines et al. 2003). Here, we use a larval dispersal 'distance' of days which should give a more realistic estimate of potential connectivity by integrating the influence of spatially and temporally variable ocean currents and the species-specific PLDs. For comparison, a geographic distance matrix, **G**, was created as a null connectivity model by measuring the geographic distance between all pairs of reef sites. The distance and probability matrices, along with the geographic position of all reef sites, were used to visualize and analyze the connectivity of the Pacific reefs with graph theory.

Graph analysis

Although graph theory has been applied in a number of fields (Newman 2003; Watts 2004), including ecology for the analysis of food webs (e.g., Dunne et al. 2002) and metapopulations (Fahrig and Merriam 1985), it has rarely been applied to spatial landscapes (Cantwell and Forman 1993; Keitt et al. 1997; Urban and Keitt 2001). This is the first study using graph theory to analyze the spatial and temporal patterns in marine connectivity. Modeling and exploring connectivity within a graph-theoretic framework offers many benefits to marine ecological and conservation applications, similar to those highlighted in the terrestrial literature (Cantwell and Forman 1993; Urban and Keitt 2001; Calabrese and Fagan 2004; Gastner and Newman 2006; Proulx et al.

2005). Graph theory provides a useful foundation for analyzing connectivity and exploring conservation scenarios because it efficiently handles very large and complex network topologies (Strogatz 2001; Newman 2003; Proulx et al. 2005) and satisfies three key ecological criteria: (1) a focus on the spatial configuration of patches within a network, (2) explicit use of the interactions between all elements, and (3) cross-scale comparisons of the first two criteria for any spatial habitat configuration and network size (Cantwell and Forman 1993). The two necessary characteristics of marine applications are the inherent directionality, or asymmetry in relationships, and the temporal variability in connectedness throughout the marine graphs. Taking this directionality and variability of marine larval dispersal into account is critical for revealing more realistic spatial predictions of population connectivity.

A graph data structure consists of a set of nodes (e.g., habitat patches, islands, populations, and reef sites), and a set of linkages (e.g., adjacency, dispersal probability, gene flow, and geographic distance) between all connected nodes (Fig. 1). When linkages are directional, they are referred to as arcs (West 2001); each arc consists of a *from* node, a *to* node, and a weight describing the strength of connectedness (e.g., geographic distance, PLD value, and dispersal probability). The information from the connectivity matrix is used to construct the arcs of the graph. We visualize the marine graph by plotting the nodes (reef sites) in geographic space and connecting appropriate nodes by arcs (arrows) reflecting the direction and strength of connectivity defined by the distance or probability matrix (Fig. 1). For the purpose of this paper, graph analyses will be summarized for the three selected years and for the PLD of 15, 30, and 60 days. These examples span most of the range reported for marine larvae (Richmond 1987; Grantham et al. 2003; Kinlan and Gaines 2003; Shanks et al. 2003) and will serve to highlight broad spatial and temporal patterns in connectivity across dispersal scales.

Several graph-level metrics correspond to key ecological processes and may be important to marine conservation efforts. For these coral dispersal simulations, the total number of nodes (the graph's *order*) remains constant, but the number, strength, and distribution of connections vary in space and time. The total number of connections within a graph for a

given simulation is referred to as the graph's *size* and reflects the overall network connectivity. A graph *component* is a connected sub-graph, a set of nodes that are inter-connected through arcs, but disconnected from some portion of the graph. These graph components, in an ecological context, may then represent isolated metapopulations, unique biogeographic regions, or distinct genotypes. A fundamental algorithm in graph theory is Dijkstra's (1959) solution to find the shortest route between any node and every other node within a network. These shortest paths can be used as a proxy for probable dispersal pathways, likely species/population expansion routes, or marine 'least-cost-paths.' The graph's *diameter* is the longest of all the shortest path distances for a network, and can also be used as a graph-level metric for overall connectedness. An alternative approach to quantifying and visualizing the network-wide patterns in connectivity is to calculate *betweenness* for every node and arc. The betweenness value is calculated as the proportion of shortest paths between all node pairs that pass through the particular node or arc of interest (Freeman 1997; Newman 2005). Mapping the betweenness scores on a dispersal graph highlights the 'most used' routes and may represent important dispersal pathways and highlight key stepping stones.

Node-level (reef site or island) metrics focus on local properties related to an individual reef's connectedness with its neighbors, its relative contribution of larvae to the local neighborhood, and its role in connecting distant sites. A node's *out-degree* refers to the number of connections linking to downstream neighbors and the *in-degree* is the number of connections from upstream sources. A node's *neighborhood* can be defined as the set of neighbors immediately upstream and downstream, or more generally, the set of nodes that are within a given number of connections from a primary node. Comparing the attributes of an individual node (area, health, protected status, etc.) to those of the entire neighborhood gives insight into the degree to which it acts as a local source or sink.

Following the methods of Urban and Keitt (2001) and Keitt et al. (1997), we also completed node removal scenarios to explore the implications of the loss of reef sites to the connectivity of the entire network. This node removal exercise resulted in a list of nodes (*cut-nodes*) which are critical to network-wide connectivity. With the removal of a cut-node, the original graph is severed into two or more components, isolating a portion of the graph. The impact of the cut-node's removal is evaluated using the new graph-level metrics. These nodes are considered critical stepping stones and should be considered for regional conservation efforts.

Results

At the scale of the Tropical Pacific, marine larval connectivity varied greatly depending on the dispersal model (PLD and time-series) and connectivity rules (probability or persistence) used (Table 3). As PLD increases, the Tropical Pacific becomes more connected. With increased PLD, the number of isolated components and islands decreases, and the order of the largest component and entire graph size increase. For example, the giant clam with a short PLD of 7–10 days (Benzie and Williams 1997) shows low-connectivity across the Pacific, whereas a coral with a PLD of more than 60 days (Richmond 1987) has a much greater connectivity. In general, connectivity during the coral mass spawning season of October through December (Table 3, g–i) is greater when compared to seasonal averages across years (Table 3, d–f). In addition, the average length of dispersal connections during this period is ~40% longer. After the negative-exponential dispersal kernel is applied to the distance matrices for the coral mass spawning season (Table 3, g–i), and the 0.5 probability of successful dispersal is selected, the Pacific-wide connectivity drops dramatically (Table 3, j–l). At this 0.5 probability, many more islands are isolated, previously connected components are disconnected, and the size of the marine graph drops to a fraction of the original connectivity estimates. When geographic distance between reef sites is used as a proxy for dispersal success, expected graph-level trends in connectivity appear. As the geographic distance threshold increases, Pacific-wide connectivity increases (Table 3, m–p).

Viewing the dispersal connectivity matrices as georeferenced graph models allows one to discern the spatial patterns in dispersal at a local-scale. Figure 3 highlights those dispersal connections that persist in more than 50% of the dispersal scenarios. Persistent pathways are drawn between reef sites for the PLD of

Table 3 A series of coral dispersal scenario were designed to explore the spatial and temporal patterns in coral population connectivity across the Pacific

	Connectivity rule	Time-series	Diameter (edges)	Components	Isolated islands	Size	Order of largest component	Mean edge length (km)	Median edge length (km)	Edge length STD (km)
	Marine graph summary									
(a)	30-day PLD	1997 (El Nino), all seasons	15	31	33	1,645	178	246	180	215
(b)	30-day PLD	1999 (La Nina), all seasons	25	31	20	1,492	147	214	152	203
(c)	30-day PLD	2001 (Neutral), all seasons	18	34	26	1,708	197	277	190	294
(d)	15-day PLD	Average: all years, all seasons	6	52	69	875	12	139	90	131
(e)	30-day PLD	Average: all years, all seasons	16	33	27	1,543	157	222	158	217
(f)	60-day PLD	Average: all years, all seasons	14	18	11	2,597	232	346	250	332
(g)	15-day PLD	Average: all years, October–December	20	32	45	1,343	57	212	152	188
(h)	30-day PLD	Average: all years, October–December	38	17	24	2,348	310	324	250	270
(i)	60-day PLD	Average: all years, October–December	18	9	10	4,290	349	538	425	430
(j)	P(15 days) > 0.5	Average: all years, October–December	14	64	140	410	27	77	56	43
(k)	P(30 days) > 0.5	Average: all years, October–December	15	47	111	643	41	116	79	97
(l)	P(60 days) > 0.5	Average: all years, October–December	9	38	74	975	120	194	125	186
(m)	Geographic, 100 km	–	8	76	127	333	19	66	71	20
(n)	Geographic, 250 km	–	29	27	31	1,109	122	146	150	65
(o)	Geographic, 500 km	–	55	6	6	2,777	418	287	301	134
(p)	Geographic, 1,000 km	–	43	2	1	7,679	437	594	626	270

The connectivity rule was based on a 15, 30, and 60-day pelagic larval duration (PLD) (a–i), and the 0.5 probability threshold after applying the negative-exponential dispersal kernel (j–l). For comparison, four geographic distance matrices were created and used to define connectivity at different distance thresholds (m–p). Annual and seasonal patterns in connectivity were investigated using 3 years; 1997, a strong El Niño year; 1999, a strong La Niña year; and 2001, a neutral year. October through December represents the coral mass spawning season (s–l). See text for graph definitions
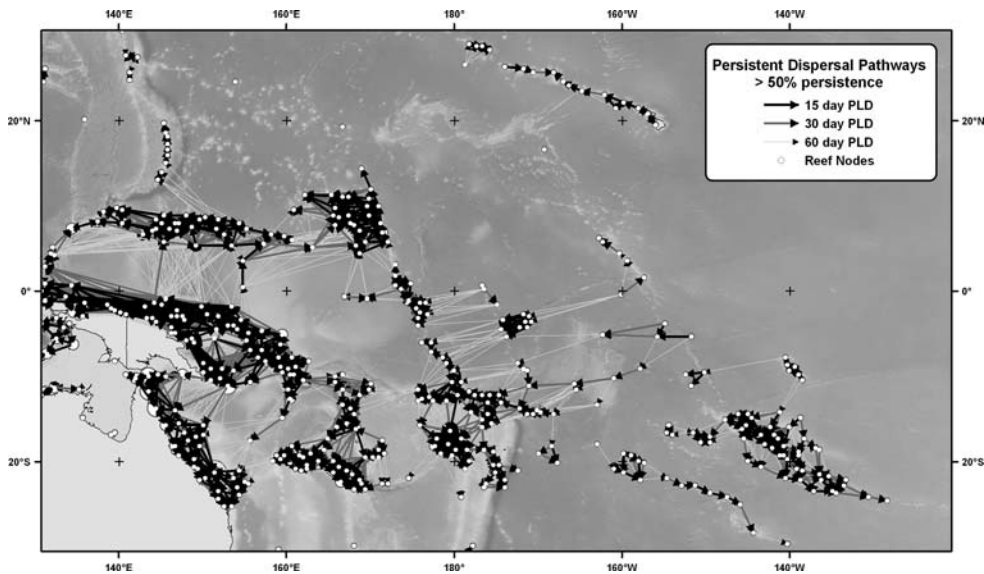
Fig. 3 Persistent dispersal pathways. This *graph model* represent dispersal connections that are estimated to be present more than 50% of the time based on the weighted average for all season. About 15, 30, and 60-day PLD dispersal simulations are included (Table 3, d–f)

15, 30, and 60 days. Many island groups form isolated graph clusters at a 15-day PLD. As PLD increases to 60 days, island clusters are joined together to form larger components, increasing the overall connectivity in the Pacific. Several cases exist where a PLD of more than 30 days is needed to connect island groups, such as between the Marshall Islands and the Gilbert Islands, between Tuvalu and the Gilbert Islands, between the Phoenix Islands and Tuvalu, and between Guam and the Caroline Islands. In addition, several dispersal barriers exist where a PLD of 60 days is not long enough to connect islands groups to the rest of the Pacific. These persistent dispersal barriers isolate several island groups including the Hawaiian Islands, the southern Cook Islands, French Polynesia, and several atolls.

The influence of the El Niño Southern Oscillation (ENSO) on sea surface currents and the impact on connectivity across the Pacific is shown in Fig. 4. Across most of the range in PLD, the El Niño event consistently increases overall connectivity. At dispersal distances >60 days, most of the Pacific becomes connected. As PLD decreases from ~60 days, the Pacific graph disconnects, resulting in an increased number of smaller components and isolated islands. At short PLDs (<20 days), most of the Tropical Pacific is disconnected and small,
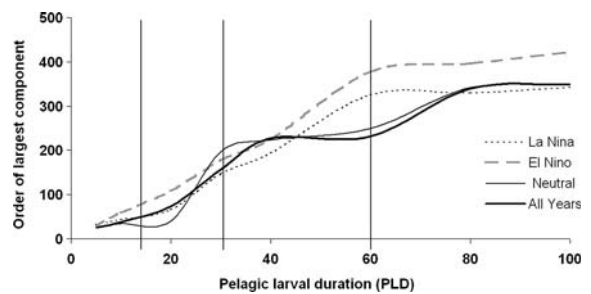

Fig. 4 Pacific-wide connectivity (number of inter-connected reef sites) plotted with respect to pelagic larval duration (*PLD*). The order of the largest component was calculated for each year and PLD. *Vertical bars* represent the PLD of 15, 30, and 60 days

isolated, island clusters are common. The spatial patterns associated with these trends in connectivity vary throughout the study area (Fig. 5). Consistent dispersal connections occurring in all years, through a 30-day PLD, are confined, in large part, to those between closely spaced islands within island groups. There are several unique dispersal connections occurring only during El Niño or La Niña events. In particular, El Niño events enhance the potential for connectivity from the Caroline Islands to the Gilbert Islands, from Papua New Guinea (PNG) to eastern Indonesia, as well as from Fiji to New Caledonia. La Niña events may provide rare dispersal opportunities
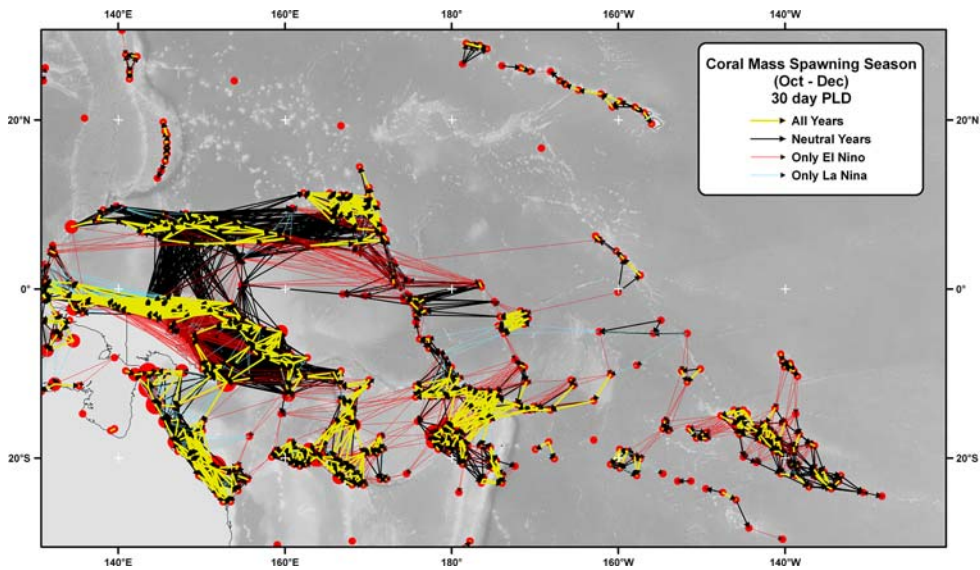
Fig. 5 Difference in connectivity between years for a 30-day PLD during the coral mass spawning season of October through December (Table 3, a–c). Dispersal connections common to all years are highlighted in *yellow*. Unique connections occurring in only 1 year are plotted for the El Niño (1997), La Niña (1999), and neutral year (2001)

north from the Gilbert Islands into the Marshall Islands, west from the Phoenix Islands into Tuvalu, and strengthen connectivity from PNG to the Great Barrier Reef (GBR). Dispersal connections confined to the neutral-year simulations are responsible for connecting the north coast of PNG to the Caroline Islands, and connectivity to the east into the Marshall Islands. The neutral-year scenarios also increase connectivity to the southeast through PNG and into the Solomon Islands.

When the negative-exponential dispersal kernel is applied to the distance matrices, and the probability of successful dispersal is 0.5 or greater, the number and extent of potential dispersal connections are drastically reduced (Table 3). Comparing the dispersal probability graphs to all other dispersal scenarios reveal the severity of fragmentation resulting from this more realistic dispersal probability estimate (Fig. 6). Despite regional fragmentation, many graph components remain as highly connected island clusters (e.g., Marshall Islands, Fiji, French Polynesia, the Solomon Islands, and the GBR). These localized regions of connectivity remain isolated from the rest of the Pacific despite PLD of up to 60 days.

Calculating betweenness reveals dispersal connections that are common to many dispersal routes in many seasons (Fig. 7). There are several commonalities in connectivity between scenarios, such as the dispersal pathways east across the Caroline Islands and into the Marshall Islands; the pathway from the Marquesas Island through French Polynesia and to the southeast; connectivity from Tuvalu and the Samoa Islands into Fiji; flow from Vanuatu south into New Caledonia; and dispersal southeast from PNG through the Solomon Islands. The common dispersal pathways revealed in this betweenness analysis represent a more realistic estimate of the dispersal connectivity in the Pacific. In general, dispersal connectivity is from west to east in the north Pacific, and from east to west in the south Pacific, following along the major ocean currents.

The neighborhood-level analysis focuses on the connected upstream and downstream sites from every reef node within the Pacific-wide dispersal graph. Upstream and downstream neighborhood characteristics vary greatly in the amount of reef habitat, the number of sites within a neighborhood, the degree of overlap in membership of the upstream and downstream neighborhoods, and the size and shape of the neighborhood (Fig. 8). The adjacent upstream and downstream neighborhoods of Chuuk Atoll, Santa Isabel Reef, and Makemo Atoll, for example, have a high degree of overlap and show little directionality. Each of these sites also has a relatively high degree
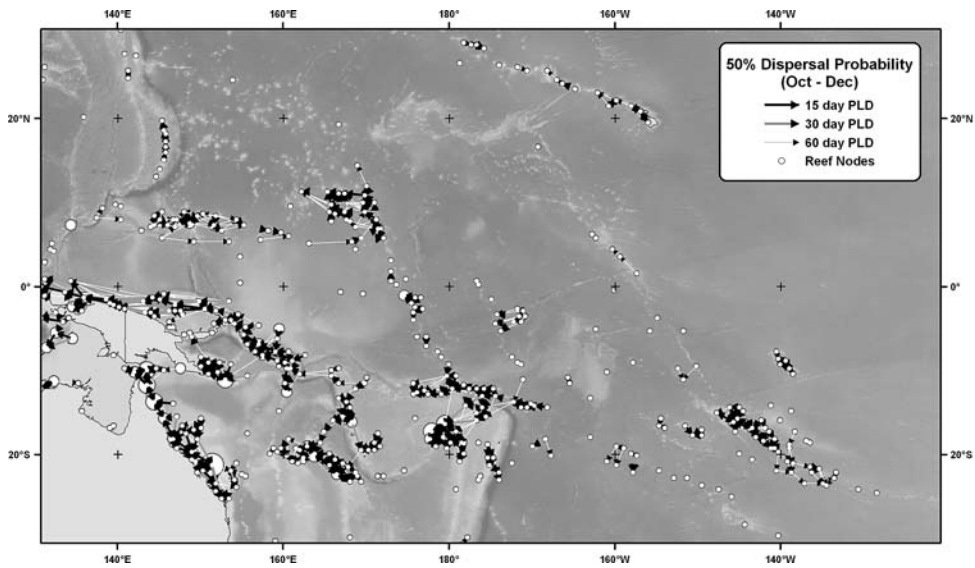
Fig. 6 A *graph* showing only those connections representing 50% or greater probability of successful dispersal between sites during the coral mass spawning season of October through December for all years (Table 3, j–l). The negative-exponential dispersal kernel was used
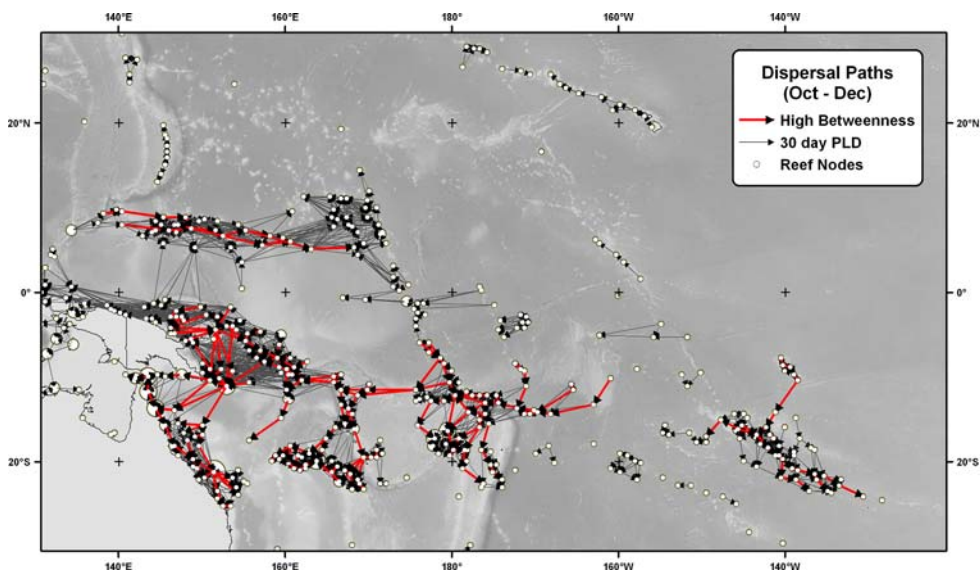

Fig. 7 Common dispersal pathways highlighted by the betweenness metric calculated for a 30-day PLD during all years and seasons (Table 3, e)

(upstream and downstream connections). The remaining sites highlighted in Fig. 8 show a high level of directionality, aligned along the dominant currents, and the upstream neighborhoods are distinct from the downstream neighborhoods. The size and direction of dispersal neighborhoods varies in time and space, and

is determined by the position of the reef site with respect to ocean currents, the PLD, and season.

Performing the node removal analysis on the dispersal graphs (Table 3, d–f), identifies those sites which are critical to local and/or regional connectivity. The cut-node reef sites identified in Fig. 9 are
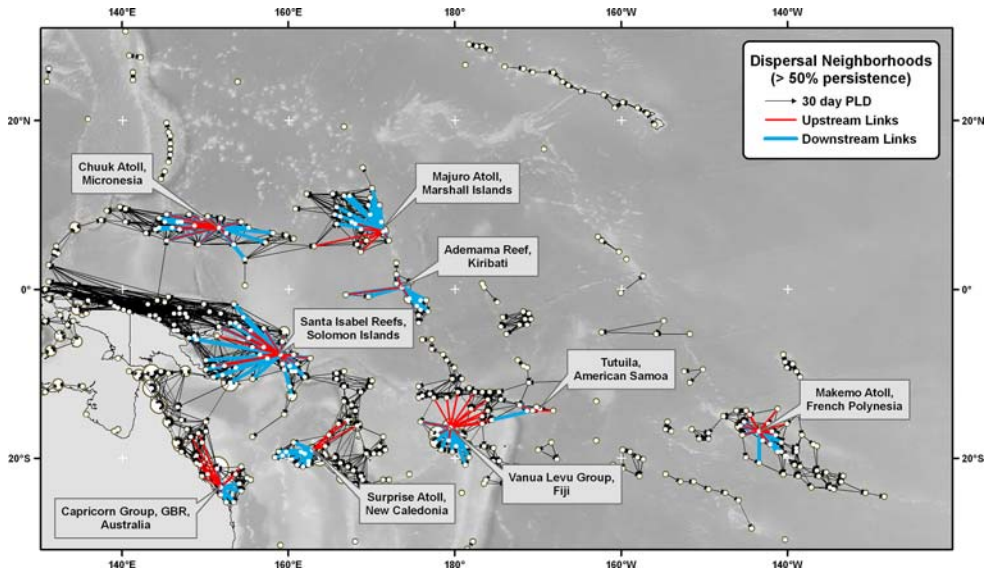
Fig. 8 Upstream and downstream dispersal neighborhoods. One dispersal connection upstream and downstream based on a 30-day PLD (Table 3, e)

important in preserving regional connectivity and may be considered critical stepping stone reefs. A series of these key stepping-stone reefs fall along the north–south island chain between the Marshall Islands and Tuvalu, and along the Hawaiian Islands. The cut-node reefs identified around the Cook Islands provide dispersal stepping-stones to/from French Polynesia and west to Samoa and Tuvalu. The number and location of cut-nodes is dependent on PLD and the time-series used to construct the dispersal graph.

The null connectivity model based on the geographic distance between all island pairs shares several characteristics with the dispersal-based
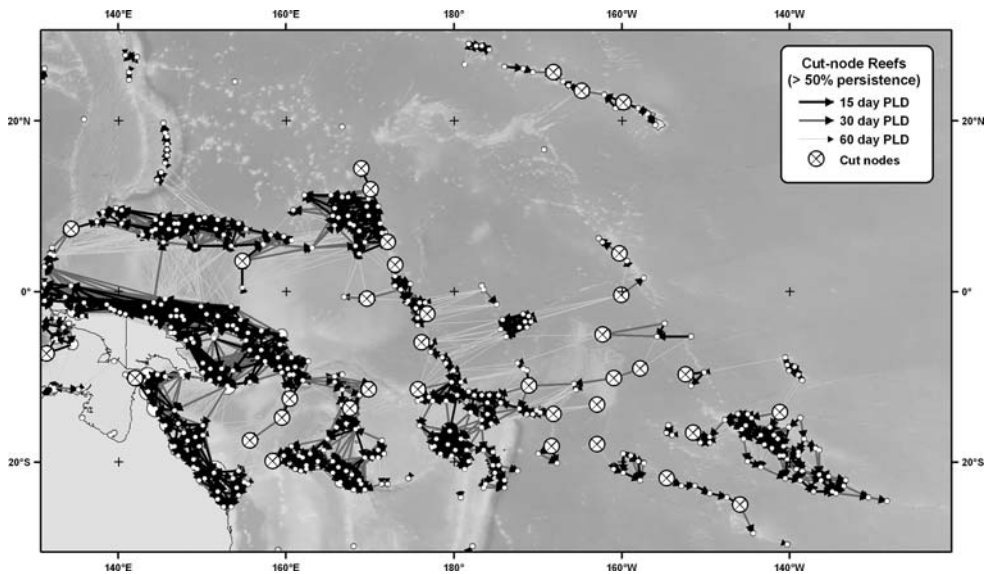

Fig. 9 Critical island stepping stones identified by the node-removal analysis based on a 15, 30, and 60-day PLD across all seasons and all years (Table 3, d–f)

graphs. Many of the same island clusters are grouped together in both the geographic and dispersal graphs (e.g., Marshall Islands, Fiji, French Polynesia, and GBR). In addition, some common pathways are identified in both models (Samoa to Tuvalu to Fiji, PNG to Solomon Islands and to Vanuatu and New Caledonia, and Caroline Islands to Marshall Island), although undirected in the geographic distance model. Critical difference exist in addition to the direction of connectivity. For example, the geographic distance model overestimates the connectivity through the Gilbert Islands between the Marshall Islands and Tuvalu and underestimates the connectivity from the Carline Islands to the Marshall Islands. In general, connectivity based on geographic distance is overestimated in regions of low-current flow or between islands aligned perpendicular to the dominant ocean currents, and underestimated in regions where islands fall upstream and downstream along swift surface currents.

Discussion

Marine ecologists and conservationist now realize the importance of integrating spatially explicit estimates of larval dispersal within their conceptualization and study of population dynamics and management strategies (Roberts 1997; Gaines et al. 2003; Gerber et al. 2003; Kinlan et al. 2005). The biophysical model and graph-theoretic approach presented here provides a robust and flexible analytical framework for the development and analysis of dispersal-based connectivity, and its integration into marine science and conservation. Our graph models of coral dispersal should be viewed as spatially explicit hypotheses regarding the strength and spatial structure of connectivity among reefs of the Tropical Pacific. Before they are included in the conservation process, these dispersal scenarios need to be parameterized based on the life history characteristics of the species of interest, and the connectivity analyses customized to fit management priorities. Although our graph analysis focused on the results of a coral dispersal model, this approach may be applied to a variety of marine connectivity data, including Lagragian biophysical connectivity matrices (Cowen et al. 2006), biogeographic data (Veron 1995; Connolly et al. 2003), and phylogeographic estimates (Benzie

and Williams 1997; Palumbi et al. 1997; Meyer et al. 2005).

This analysis of coral dispersal across the Tropical Pacific highlighted the value of applying graph theory to the study of marine connectivity. The results identify the spatial and temporal patterns in potential dispersal, an important factor in the population ecology and conservation of marine species (Gaylord and Gaines 2000; Gaines et al. 2003; Palumbi 2003). We found the scale of coral population connectivity across the Pacific to be on the order of 50–150 km (Table 3, j–l), consistent with estimates from the Caribbean (Cowen et al. 2006) and for other marine taxa (Kinlan and Gaines 2003). The estimates of connectivity vary with respect to PLD (Figs. 3, 6), the velocity and spatiotemporal variability in ocean currents (Figs. 3, 5), and the topology (spatial configuration) of reef habitat (Fig. 2). By exploring a variety of potential dispersal scenarios we were able to identify persistent patterns in coral dispersal (Fig. 3) and highlight common dispersal corridors, including their strength and direction (Fig. 7). The general patterns support current hypotheses regarding dispersal (Jokiel and Martinelli 1992; Veron 1995; Benzie and Williams 1997; Benzie 1999) and levels of endemism (Paulay and Meyer 2002; Meyer et al. 2005) throughout the Tropical Pacific, yet this analysis adds spatial resolution by identifying the specific island stepping stones, possible dispersal routes, and persistent dispersal barriers (Fig. 7). We were also successful in identifying areas of high connectivity (e.g., Marshall Islands, Fiji, French Polynesia, and New Caledonia), as well as regions of limited larval exchange (north and south of the Gilbert Islands across equatorial currents, west from French Polynesia, and west from Fiji) potentially isolating islands and island groups (Fig. 6). The neighborhood analysis adds greater resolution to these general patterns and identifies the potential flow of larvae to and from all individual sites (Fig. 8). A range of upstream/downstream neighborhood configurations exist, from those where the upstream and downstream neighborhoods are completely separate (Samoa, New Caledonia, Fiji, and the GBR), to those where there is a high degree of overlap (Caroline Islands, Marshall Islands, and the Solomon Islands). The configuration and persistence of the neighborhoods are dependent on the PLD, the strength of and variability in ocean currents, and the local topology

of the surrounding islands. This site-specific resolution is needed to evaluate the degree to which individual reef sites should be regarded as open or closed systems with respect to local population dynamics and marine management (Ogden 1997; Roberts 1997; Cowen et al. 2000; Mora and Sale 2002).

This connectivity research has implications for marine conservation planning at multiple scales. Perhaps most importantly, the spatial and temporal variability in dispersal across the Pacific requires the conservation approach be tailored toward the connectivity characteristics of the site and region of interest. These broad-scale patterns in connectivity should help in the design and implementation of regional management by linking the ecological dynamics with marine governance (Roberts 1997; Hughes et al. 2005). This graph approach may also help discover where dispersal limitations lead to isolated populations and geographically restricted species (Fig. 6). Such species may be at greater risk of recruitment failure and extinction than more widespread species (Roberts et al. 2002; Hughes et al. 2005). Therefore, regions containing isolated populations warrant additional scientific study and greater conservation efforts. At these board spatial scale, regional conservation efforts should also consider the importance of island stepping stones (Fig. 9) to the connectivity of critical species. Similarly, resource managers may need to include the connectivity of invasive species (e.g., crown of thorns starfish) in their conservation planning. Dependent on the degree of dispersal isolation, local management at these stepping stone sites may need to adjust their management approach to a more larval retention-based framework with a greater emphasis on preserving locally sustainable population levels.

At the local level, considering the direction and persistence of dispersal within the upstream/downstream neighborhood context would allow local managers to gain insight into potential larval sources and develop management solutions aligned with persistent dispersal routes and across the appropriate geopolitical boundaries (Roberts 1997; Palumbi 2004). Graph theory enhances our ability to integrate dispersal connectivity into the design and evaluation of marine protected area network topology (spatial arrangement, spacing, upstream, and downstream characteristics), complementing existing approaches to reserve design

(Gaines et al. 2003; Gerber et al. 2003; Halpern and Warner 2003; Guichard et al. 2004).

In addition to marine population and conservation applications, this framework may be used to test spatial predictions of biogeographic and phylogeographic patterns (Dyer and Nason 2004, E. Treml, in preparation). In this context, the persistent dispersal pathways (Fig. 3) and dispersal probabilities (Fig. 6) represent spatially explicit hypotheses regarding community similarity, the geographic structure of genetic variability, and patterns in endemism. Highly connected island clusters and persistent dispersal connections may explain population/genetic homogeneity (Benzie and Williams 1997; Palumbi et al. 1997; Palumbi 2003). Dispersal barriers (Fig. 6) may be responsible for population isolation, explaining genetic differentiation (Barber et al. 2002; Kirkendale and Meyer 2004), and the existence of endemic species (Paulay and Meyer 2002; Roberts et al. 2002; Meyer et al. 2005). These graph characteristics and distance measures offer more spatial explicit alternatives to geographic distance when exploring the spatial structure of population genetics at these spatial scales. This approach may also be used to explore the demographic and phylogenetic impacts of rare dispersal events. Rare, yet successful dispersal events may have lasting impacts on the marine population and community structure (Palumbi et al. 1997; Paulay and Meyer 2002; de Queiroz 2005). Alternative phylogeographic hypotheses may also be explored within this framework by adding reefs/islands that were present at lower sea level stands (Paulay 1990) and/or by altering the strength of currents throughout the Pacific to represent ocean circulation at different times throughout the Quaternary Period (Veron 1995) or under global climate change scenarios (Trakhtenbrot et al. 2005).

Although the graph-theoretic approach is applicable to a variety of distance/connectivity metrics, with few limitations regarding marine applications, the biophysical model presented here has several limitations. First, only 3 years of surface current data have been analyzed as a preliminary evaluation of the variability in connectivity across the Pacific (due to ENSO), and more years are needed to build confidence in the connectivity predictions. We are in the process of acquiring additional ocean current data at a higher resolution for the region to strengthen the analysis. These new data, at ∼12.5 km horizontal resolution,

resolves meso-scale eddies and better represents the complex flows occurring throughout the tropics. In addition, improving the estimates of nearshore hydrodynamics is of primary interest. The lack of realistic nearshore hydrodynamics is a limitation in our model's ability to quantify the degree of advection and retention within the coastal environment. Efforts are underway to nest a nearshore hydrodynamic model within the broad-scale model to investigate the impact of local advection and retention patterns on the Pacific connectivity. Finally, to broaden the applicability of this modeling approach to a wide variety of species, swimming behavior (e.g., diel vertical migration) may have to be integrated. The vertical layers of the new hydrodynamic model will provide the unique subsurface flow fields needed to add larval swimming behavior into the model.

We have shown that the advection–diffusion biophysical model effectively quantifies potential connectivity between coral reefs at the ocean-basin scale. We have also demonstrated the power and unique advantages of exploring patterns in connectivity within the graph-theoretic framework. Quantifying and exploring the spatial patterns in marine connectivity under a variety of dispersal scenarios and circulation patterns may help us understand the existing patterns in coral community structure, and help mitigate the current decline of coral reefs. The approach provides a powerful tool for directing a more robust marine conservation strategy.

References

Andrews JC, Gay S, Sammarco PW (1988) Influence of circulation on self-seeding patterns at Helix Reef-Great Barrier Reef. In: Proceedings of the 6th Int. Coral Reef Symposium, Townsville, Australia vol 2, pp 469–474

Barber PH, Palumbi SR, Erdmann MV et al (2002) Sharp genetic breaks among populations of *Haptosquilla pulchella* (Stomatopoda) indicate limits to larval transport: patterns, causes, and consequences. Mol Ecol 11:659–674

Benzie JAH (1999) Genetic structure of coral reef organisms: ghosts of dispersal past. Am Zool 39:131–145

Benzie JAH, Williams ST (1997) Genetic structure of giant clam (*Tridacna maxima*) populations in the west Pacific is not consistent with dispersal by present-day ocean currents. Evolution 51:768–783

Botsford LW, Hastings A, Gaines SD (2001) Dependence of sustainability on the configuration of marine reserves and larval dispersal distance. Ecol Lett 4:144–150

Botsford LW, Micheli F, Hastings A (2003) Principles for the design of marine reserves. Ecol Appl 13:S25–S31

Calabrese JM, Fagan WF (2004) A comparison-shopper's guide to connectivity metrics. Front Ecol Environ 2:529–536

Cantwell MD, Forman RTT (1993) Landscape graphs—ecological modeling with graph-theory to detect configurations common to diverse landscapes. Landsc Ecol 8:239–255

Clark JS, Silman M, Kern R et al (1999) Seed dispersal near and far: patterns across temperate and tropical forests. Ecology 80:1475–1494

Connolly SR, Bellwood DR, Hughes TP (2003) Indo-Pacific biodiversity of coral reefs: deviations from a mid-domain model. Ecology 84:2178–2190

Connolly SR, Hughes TP, Bellwood DR et al (2005) Community structure of corals and reef fishes at multiple scales. Science 309:1363–1365

Cowen RK, Lwiza KMM, Sponaugle S et al (2000) Connectivity of marine populations: open or closed? Science 287:857–859

Cowen RK, Paris CB, Olson D et al (2003) The role of long distance dispersal versus local retention in replenshing marine populations. Gulf Caribb Res 14:129–137

Cowen RK, Paris CB, Srinivasan A (2006) Scaling of connectivity in marine populations. Science 311:522–527

de Queiroz A (2005) The resurrection of oceanic dispersal in historical biogeography. Trends Ecol Evol 20:68–73

Dijkstra EW (1959) A note on two problems in connection with graphs. Numer Math 1:269–271

Dunbar RB, Wellington GM, Colgan MW et al (1994) Eastern Pacific sea-surface temperature since 1600-AD—the Delta-O−18 record of climate variability in Galapagos corals. Paleoceanography 9:291–315

Dunne JA, Williams RJ, Martinez ND (2002) Food-web structure and network theory: the role of connectance and size. Proc Natl Acad Sci USA 99:12917–12922

Dyer RJ, Nason JD (2004) Population graphs: the graph theoretic shape of genetic structure. Mol Ecol 13:1713–1727

Fahrig L, Merriam G (1985) Habitat patch connectivity and population survival. Ecology 66:1762–1768

Freeman LC (1979) Centrality in social networks conceptual clarification. Soc Netw 1:215–239

Gaines SD, Gaylord B, Largier JL (2003) Avoiding current oversights in marine reserve design. Ecol Appl 13:S32–S46

Gaines SD, Lafferty KD (1995) Modeling the dynamics of marine species: the importance of incorporating larval

dispersal. In: McEdward LR (ed) Ecology of marine invertebrate larvae. CRC Press, Boca Raton, pp 389–412

Gastner MT, Newman MEJ (2006) The spatial structure of networks. Eur Phys J B 49:247–252

Gay SL, Andrews JC (1994) The effects of recruitment strategies on coral larvae settlement distributions at Helix Reef. In: Sammarco PW, Heron ML (eds) The bio-physics of marine larval dispersal. American Geophysical Union, Washington, DC, pp 73–88

Gaylord B, Gaines SD (2000) Temperature or transport? Range limits in marine species mediated solely by flow. Am Nat 155:769–789

Gerber LR, Botsford LW, Hastings A et al (2003) Population models for marine reserve design: a retrospective and prospective synthesis. Ecol Appl 13:S47–S64

Gilg MR, Hilbish TJ (2003) The geography of marine larval dispersal: coupling genetics with fine-scale physical oceanography. Ecology 84:2989–2998

Glynn PW, Ault JS (2000) A biogeographic analysis and review of the far eastern Pacific coral reef region. Coral Reefs 19:1–23

Grantham BA, Eckert GL, Shanks AL (2003) Dispersal potential of marine invertebrates in diverse habitats. Ecol Appl 13:S108–S116

Guichard F, Levin SA, Hastings A et al (2004) Toward a dynamic metacommunity approach to marine reserve theory. Bioscience 54:1003–1011

Halpern BS, Warner RR (2002) Marine reserves have rapid and lasting effects. Ecol Lett 5:361–366

Hare JA, Quinlan JA, Werner FE et al (1999) Larval transport during winter in the SABRE study area: results of a coupled vertical larval behaviour-three-dimensional circulation model. Fish Oceanogr 8:57–76

Hughes TP, Bellwood DR, Folke C et al (2005) New paradigms for supporting the resilience of marine ecosystems. Trends Ecol Evol 20:380–386

Jackson JBC (1986) Modes of dispersal of clonal benthic invertebrates—consequences for species distributions and genetic-structure of local-populations. Bull Mar Sci 39:588–606

James MK, Armsworth PR, Mason LB (2002) The structure of reef fish metapopulations: modeling larval dispersal and retention patterns. Proc R Soc Lond B Biol 269:2079–2086

Ji M, Leetmaa A, Derber J (1995) An ocean analysis system for seasonal to interannual climate studies. Mon Weather Rev 123:460–481

Jokiel PL (1990) Long-distance dispersal by rafting—reemergence of an old hypothesis. Endeavour 14:66–73

Jokiel PL, Cox EF (2003) Drift pumice at Christmas Island and Hawaii: evidence of oceanic dispersal patterns. Mar Geol 202:121–133

Jokiel P, Martinelli FJ (1992) The vortex model of coral-reef biogeography. J Biogeogr 19:449–458

Keitt T, Urban D, Milne B (1997) Detecting critical scales in fragmented landscapes. Conserv Ecol 1:4. Available from http://www.ecologyandsociety.org/vol1/iss1/art4/ (accessed February 2007)

Kinlan BP, Gaines SD (2003) Propagule dispersal in marine and terrestrial environments: a community perspective. Ecology 84:2007–2020

Kinlan BP, Gaines SD, Lester SE (2005) Propagule dispersal and the scales of marine community process. Divers Distrib 11:139–148

Kirkendale LA, Meyer CP (2004) Phylogeography of the *Patelloida profunda* group (Gastropoda:Lottidae): diversification in a dispersal-driven marine system. Mol Ecol 13:2749–2762

Largier JL (2003) Considerations in estimating larval dispersal distances from oceanographic data. Ecol Appl 13:S71–S89

Levin SA (1992) The problem of pattern and scale in ecology. Ecology 73:1943–1967

Levins R (1969) Some demographic and genetic consequences of environmental heterogeneity for biological control. B Entomol Soc Am 15:237–240

Lubchenco J, Palumbi SR, Gaines SD et al (2003) Plugging a hole in the ocean: the emerging science of marine reserves. Ecol Appl 13:S3–S7

MATLAB (2005) The MathWorks, Inc. Natick, Massachusetts, US

Meyer CP, Geller JB, Paulay G (2005) Fine scale endemism on coral reefs: archipelagic differentiation in turbinid gastropods. Evolution 59:113–125

Mora C, Sale PF (2002) Are populations of coral reef fish open or closed? Trends Ecol Evol 17:422–428

Newman MEJ (2003) The structure and function of complex networks. SIAM Rev 45:167–256

Newman MEJ (2005) A measure of betweenness centrality based on random walks. Soc Netw 27:39–54

Ogden JC (1997) Marine managers look upstream for connections. Science 278:1414–1415

Okubo A (1994) The role of diffusion and related physical processes in dispersal and recruitment of marine populations. In: Sammarco PW, Heron ML (eds) The bio-physics of marine larval dispersal. American Geophysical Union, Washington, DC, pp 5–32

Oliver J, Noordeloos M, Yusuf Y et al (2004) ReefBase: a global information system on coral reefs. Available from http://www.reefbase.org/global_database/default.aspx (accessed February 2007)

Ortner B, Crowder LB, Hoss DE (1999) The South Atlantic Bight recruitment experiment: introduction and overview. Fish Oceanogr 8:1–6

Palumbi SR (2003) Population genetics, demographic connectivity, the design of marine reserves. Ecol Appl 13:S146–S158

Palumbi SR (2004) Marine reserves and ocean neighborhoods: the spatial scale of marine populations and their management. Annu Rev Environ Resour 29:31–68

Palumbi SR, Grabowsky G, Duda T et al (1997) Speciation and population genetic structure in tropical Pacific sea urchins. Evolution 51:1506–1517

Paris CB, Cowen RK (2004) Direct evidence of a biophysical retention mechanism for coral reef fish larvae. Limno Oceanogr 49:1964–1979

Paris CB, Cowen RK, Claro R, Lindeman KC (2005) Larval transport pathways from Cuban snapper (Lutjanidae) spawning aggregations based on biophysical modeling. Mar Ecol-Prog Ser 296:93–106

Paulay G (1990) Effects of late Cenozoic sea-level fluctuations on the bivalve faunas of tropical oceanic islands. Paleobiology 16:415–434

Paulay G, Meyer C (2002) Diversification in the tropical pacific: comparisons between marine and terrestrial systems and the importance of founder speciation. Integr Comp Biol 42:922–934

Possingham HP, Roughgarden J (1990) Spatial population-dynamics of a marine organism with a complex life-cycle. Ecology 71:973–985

Proulx SR, Promislow DEL, Phillips PC (2005) Network thinking in ecology and evolution. Trends Ecol Evol 20:345–353

Quinn TM, Taylor FW, Crowley TJ (1993) A 173 year stable-isotope record from a tropical South-Pacific coral. Quaternary Sci Rev 12:407–418

Rice JA, Quinlan JA, Nixon SW et al (1999) Spawning and transport dynamics of Atlantic menhaden: inferences from characteristics of immigrating larvae and predictions of a hydrodynamic model. Fish Oceanogr 8:93–110

Richmond RH (1987) Energetics, competence, long-distance dispersal of planula larvae of the coral *Pocillopora damicornis*. Mar Biol 93:527–533

Roberts CM (1997) Connectivity and management of Caribbean coral reefs. Science 278:1454–1457

Roberts CM, McClean CJ, Veron JEN et al (2002) Marine biodiversity hotspots and conservation priorities for tropical reefs. Science 295:1280–1284

Roughgarden J, Gaines S, Possingham H (1988) Recruitment dynamics in complex life-cycles. Science 241:1460–1466

Sala E, Aburto-Oropeza O, Paredes G et al (2002) A general model for designing networks of marine reserves. Science 298:1991–1993

Sale PF (2004) Connectivity, recruitment variation, the structure of reef fish communities. Integr Comp Biol 44:390–399

Sale PF, Cowen RK, Danilowicz BS et al (2005) Critical science gaps impede use of no-take fishery reserves. Trends Ecol Evol 20:74–80

Sammarco PW (1994) Larval dispersal and recruitment processes in Great Barrier Reef corals: analysis and synthesis. In: Sammarco PW, Heron ML (eds) The bio-physics of marine larval dispersal. American Geophysical Union, Washington, DC, pp 35–72

Sammarco PW, Andrews JC (1989) The helix experiment II. differential localized dispersal and recruitment pattern in Great Barrier Reef Corals. Limno Oceanogr 34:896–912

Scheltema RS (1986) Long-distance dispersal by planktonic larvae of shoal-water benthic invertebrates among central Pacific islands. Bull Mar Sci 39:241–256

Shanks AL, Grantham BA, Carr MH (2003) Propagule dispersal distance and the size and spacing of marine reserves. Ecol Appl 13:S159–S169

Siegel DA, Kinlan BP, Gaylord B et al (2003) Lagrangian descriptions of marine larval dispersion. Mar Ecol-Prog Ser 260:83–96

Spalding M, Ravilious C, Green EP (2001) World atlas of coral reefs. University of California Press, Berkely

Sponaugle S, Cowen RK, Shanks A et al (2002) Predicting self-recruitment in marine populations: biophysical correlates and mechanisms. Bull Mar Sci 70:341–375

Strogatz SH (2001) Exploring complex networks. Nature 410:268–276

Swearer SE, Shima JS, Hellberg ME et al (2002) Evidence of self-recruitment in demersal marine populations. Bull Mar Sci 70:251–271

Trakhtenbrot A, Nathan R, Perry G et al (2005) The importance of long-distance dispersal in biodiversity conservation. Divers Distrib 11:173–181

Urban D, Keitt T (2001) Landscape connectivity: a graph-theoretic perspective. Ecology 82:1205–1218

Veron JEN (1995) Corals in space and time: the biogeography and evolution of the Scleractinia. Comstock/Cornell, Ithaca

Warner RR (1997) Evolutionary ecology: how to reconcile pelagic dispersal with local adaptation. Coral Reefs 16:S115–S120

Warner RR, Cowen RK (2002) Local retention of production in marine populations: evidence, mechanisms, and consequences. Bull Mar Sci 70:245–249

Watts DJ (2004) The "new" science of networks. Annu Rev Sociol 30:243–270

Werner FE, Blanton BO, Quinlan JA et al (1999) Physical oceanography of the North Carolina continental shelf during the fall and winter seasons: implications for the transport of larval menhaden. Fish Oceanogr 8:7–21

West DB (2001) Introduction to graph theory, 2nd edn. Prentice-Hall, Uper Saddle River, NJ

Wolanski E, Burrage D, King B (1989) Trapping and dispersion of coral eggs around Bowden Reef, Great Barrier-Reef, following mass coral spawning. Cont Shelf Res 9:479–496