



# Population Connectivity in Marine Systems

## An Overview

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THERE IS GROWING consensus that life within the world's ocean is under considerable and increasing stress from human activities (Hutchings, 2000; Jackson et al., 2001). This unprecedented strain on both the structure and function of marine ecosystems has led to calls for new management approaches to counter anthropogenic impacts in the coastal ocean (Botsford et al., 1997; Browman and Stergiou, 2004; Pikitch et al., 2004). Spatial management, including Marine Protected Areas (MPAs), has been touted as a method for both conserving biodiversity and managing fisheries (Agardy, 1997). Continuing debates on the efficacy of MPAs have identified the need for models that capture the spatial dynamics of marine populations, especially with respect to larval dispersal (Willis et al., 2003; Sale et al., 2005). Theoretical studies suggest that *population connectivity*<sup>1</sup> plays a fundamental role in local and metapopulation dynamics, community dynamics and structure, genetic diversity, and the resiliency of populations to human exploitation (Hastings and Harrison, 1994; Botsford et al., 2001). Modeling efforts have been hindered, however, by the paucity of empirical estimates of, and knowledge of the processes controlling, population connectivity in ocean ecosystems. While progress has been made with older life stages, the larval-dispersal component of connectivity remains unresolved for most marine populations. This lack of knowledge represents a fundamental obstacle to obtaining a comprehensive understanding of the population dynamics of marine organisms. Furthermore, a lack of spatial context that such information would provide has limited the ability of ecologists to evaluate the design and potential benefits of novel conservation and resource-management strategies.

The spatial extent of larval dispersal in marine systems has traditionally been inferred from estimates of pelagic durations of larval dispersive stages, from the modeled movements of passive particles by ocean currents, or from analyses of variation in allele frequencies of mitochondrial or nuclear genes (Johnson, 1960; Scheltema, 1988; Planes, 2002). Observations of pelagic larval durations (PLDs) of many weeks to over one year in numerous marine species, coupled with predicted advection of passive particles by mean, low-frequency currents, imply that long-distance dispersal among subpopulations may be pervasive. A number of studies documenting genetic homogeneity over regional to basin-wide spatial scales provides further support for the existence of dispersal over long distances (e.g., Shulman and Birmingham, 1995). More recent research and careful reconsideration of the evidence, however, suggests this perception is likely inaccurate for many species, particularly over time scales of ecological relevance.

New hypervariable nuclear DNA assays show genetic differentiation among subpopulations of marine fish and invertebrates that were undetected by earlier, less-sensitive DNA analyses (Bentzen et al., 1996; Purcell et al., 2006; Gerlach et al., 2007). Novel tagging approaches demonstrate the potential for local retention of reef fish larvae (Jones et al., 1999, 2005; Almany et al., 2007), while constrained nearshore larval distributions of littoral invertebrate species (Barnett and Jahn, 1987) suggest localized retention in nearshore waters.

Finally, estimates of larval dispersal using advection/diffusion models with realistic mortality terms and vertical positioning behavior show more restricted movement than would be predicted from one-way oceanic currents acting on passive particles (e.g., Cowen et al., 2006). Taken together, these studies provide intriguing, albeit incomplete, evidence that subpopulations of marine organisms may be more isolated over smaller spatial scales than was previously thought. We are, nonetheless, a long way from a comprehensive understanding of population connectivity that would allow for quantitative predictions of specific natural or human impacts on marine populations.

Fundamental knowledge of larval dispersal and connectivity can be gained from (1) understanding the biological and hydrodynamic processes involved in the transport of larvae and (2) deriving larval origins and dispersal pathways using geochemical, genetic, or artificial

markers. Natal origins and destination points provide the basic data in connectivity studies (Box 1). However, a process-based understanding of dispersal is an essential component of population connectivity because it addresses how biological and hydrodynamic processes

interact on different spatial and temporal scales to disperse the larvae of marine organisms. Furthermore, a mechanistic understanding generates testable hypotheses of larval transport and dispersal in new environments or locations. The combination of marker and process-oriented approaches promises a truly predictive understanding of larval dispersal and connectivity.

The dominant scales of larval dispersal in coastal species are not known, and perceptions on this issue vary broadly within the academic community; opinions range from broad to restricted dispersal and from devout to agnostic. The few studies where natal origins have been empirically determined (Jones et al., 1999, 2005; Almany et al., 2007), and the case of endemic species on isolated islands where larvae must have originated from local sources (Robertson, 2001), demonstrate that limited dispersal occurs in marine environments.

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In contrast, observations that larvae of shallow-water species are found in ocean gyre systems, and examples of significant range extensions during narrow event windows, indicate dispersal on the scale of hundreds to thousands of kilometers is also possible (Johnston, 1960; Cowen,

<sup>1</sup> Population connectivity refers to the exchange of individuals among geographically separated subpopulations that comprise a metapopulation. Set in the context of benthic-oriented marine species, population connectivity encompasses the dispersal phase from reproduction to the completion of the settlement process (including habitat choice and metamorphosis).

1985; Sheltema, 1986; Victor, 1986; Newman and McConnaughey, 1987).

Identification of relevant temporal scales is also of critical importance to any discussion of population connectivity. For population maintenance, and associated conservation and resource-management objectives, the relevant time scale is ecological or demographic, rather than that relevant to evolutionary processes. Rates of exchange necessary to impact populations on ecological time scales are several orders of magnitude higher than those required to influence genetic structure. Consequently, both the time over which dispersal is measured and the amplitude of the relevant recruitment signal must be appropriate for ecological

contribution to population replenishment and maintenance.

Estimating population connectivity in marine ecosystems is inherently a coupled bio-physical problem. Important physical processes include boundary layer structure, particularly over the inner shelf, tides, internal tides and bores, fronts and associated jets, island wakes, and cross-shelf forcing via eddies, meanders, and lateral intrusions. However, physical processes alone do not determine the scales of connectivity. Time scales of larval development and behavioral capabilities, including vertical migration, also play an important role (Cowen, 2002).

Although the number of advective

and diffusive processes that relate to the dispersal and recruitment of marine organisms is potentially large, several general observations may help to define the connectivity problem. First, temporal and spatial correlation scales over continental shelves are often quite short—on the order of days and kilometers. Unfortunately, correlation scales near islands, reefs, and within estuaries are not well known. Careful selection of sampling strategies is therefore necessary to resolve the physical processes described above. Second, the relative contributions of these processes will likely change from site to site, depending on such factors as coastal geometry, proximity to estuaries, water-column

## BOX 1. QUANTITATIVE MEASURES OF POPULATION CONNECTIVITY

A mechanistic understanding of marine population connectivity requires resolution of the biological and physical processes involved in larval dispersal and transport. *Larval dispersal* refers to the intergenerational spread of larvae away from a source to the destination or settlement site at the end of the larval stage. This usage is widespread in the terrestrial lit-

erature where the basic description of dispersal is a *dispersal curve*, a one-dimensional representation of the number of settlers from a given source as a function of the distance from that source (see Figure A-1).

The dispersal curve becomes a *dispersal kernel* with an associated probability density function, in  $n$  dimensions. Formally, the dispersal kernel is the probability of ending up at position  $x$  given a starting position  $y$ . One quantitative measure of population connectivity is the source distribution matrix  $\rho_{ij}$  which gives the proportion of juveniles in population  $i$  that came from population  $j$ . In the absence of any data, let's assume that larval production in a population is a function of habitat area and that recruitment decays exponentially with distance from a natal population. In this case,

$$\rho_{ij} = \frac{\exp(-\alpha d_{ij}) A_j}{\sum_j \exp(-\alpha d_{ij}) A_j}$$

where  $d_{ij}$  is the distance between population  $i$  and  $j$ ,  $A_j$  is the area inhabited by population  $j$ , and  $\alpha$  scales the effect of distance on dispersal (Moilanen and Niemanen, 2002). Although simplistic, the model may provide an adequate representation of connectivity in metapopulations dominated by self-recruitment (Jones et al., 2005; Almany et al., 2007).

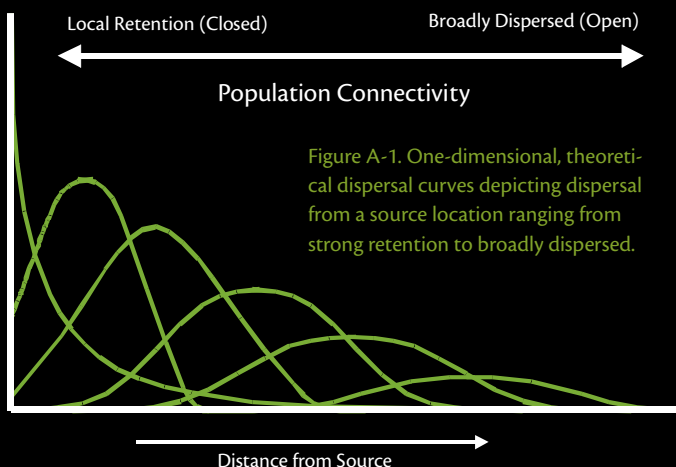
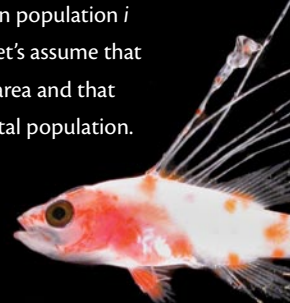


Figure A-1. One-dimensional, theoretical dispersal curves depicting dispersal from a source location ranging from strong retention to broadly dispersed.



stratification, and seasonal wind forcing (e.g., Werner et al., 1997; Epifanio and Garvine, 2001; Sponaugle et al., 2002; Pineda and Lopez, 2002). Third, the individual processes contain length and time scales that vary, and so physical transport and dispersal is inherently a multiscale process. This variability presents problems for modeling, as it is difficult at the present time to resolve mesoscale and small-to-intermediate scales simultaneously. Finally, there is a need for a higher degree of precision in knowledge of the flow fields in order to embed behavioral models on particles within physical models to test hypotheses involving bio-physical interactions.

This special issue of *Oceanography*

highlights recent advances, as well as challenges facing the oceanography community, as ocean ecologists seek a mechanistic understanding of marine population connectivity. The major challenges in this effort are to provide a quantitative understanding of the processes and scales controlling larval dispersal and

how connectivity influences the dynamics of affected populations. Resolving the mechanisms controlling larval dispersal will involve a coherent understanding of the relevant physical processes and how organisms mediate the physical outcome. Multiple scales will be important, and therefore understanding how

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Physical and coupled bio-physical hydrodynamic models can provide a more sophisticated parameterization of connectivity models. Here,

$$\rho_{ij} = \frac{p_{ij} A_j}{\sum_j p_{ij} A_j}$$

where  $p_{ij}$  represents the probability that a larva produced in population  $i$  settles in population  $j$  (Figure A-2). These probabilities are generated by coupling output of a hydrodynamic model with Lagrangian particle-tracking protocols that allow for virtual larvae to be assigned variable pelagic larval durations, vertical migration behaviors, and horizontal swimming abilities (e.g., Paris et al., in press). By using an individual-based approach, coupled bio-physical models have flexibility to incorporate characteristic life-history traits and behavioral capabilities of different taxa. However, to compare predictions from the various connectivity models, we need empirical estimates of larval dispersal to evaluate model performance. While new larval mark-recapture approaches are providing information on levels of self-recruitment to local populations, tracking larvae that disperse away from natal locations defines the critical challenge for field ecologists studying connectivity in marine systems.

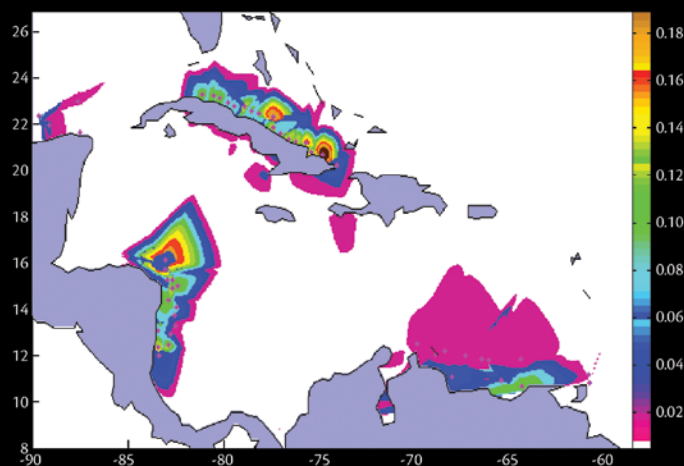


Figure A-2. Two-dimensional dispersal kernels calculated from a series of model runs using a coupled biological and physical model (Cowen et al., 2006; Paris et al., in press). Scale represents probability of successful dispersal from release sites indicated by red dots. Figure provided by C. Paris, University of Miami



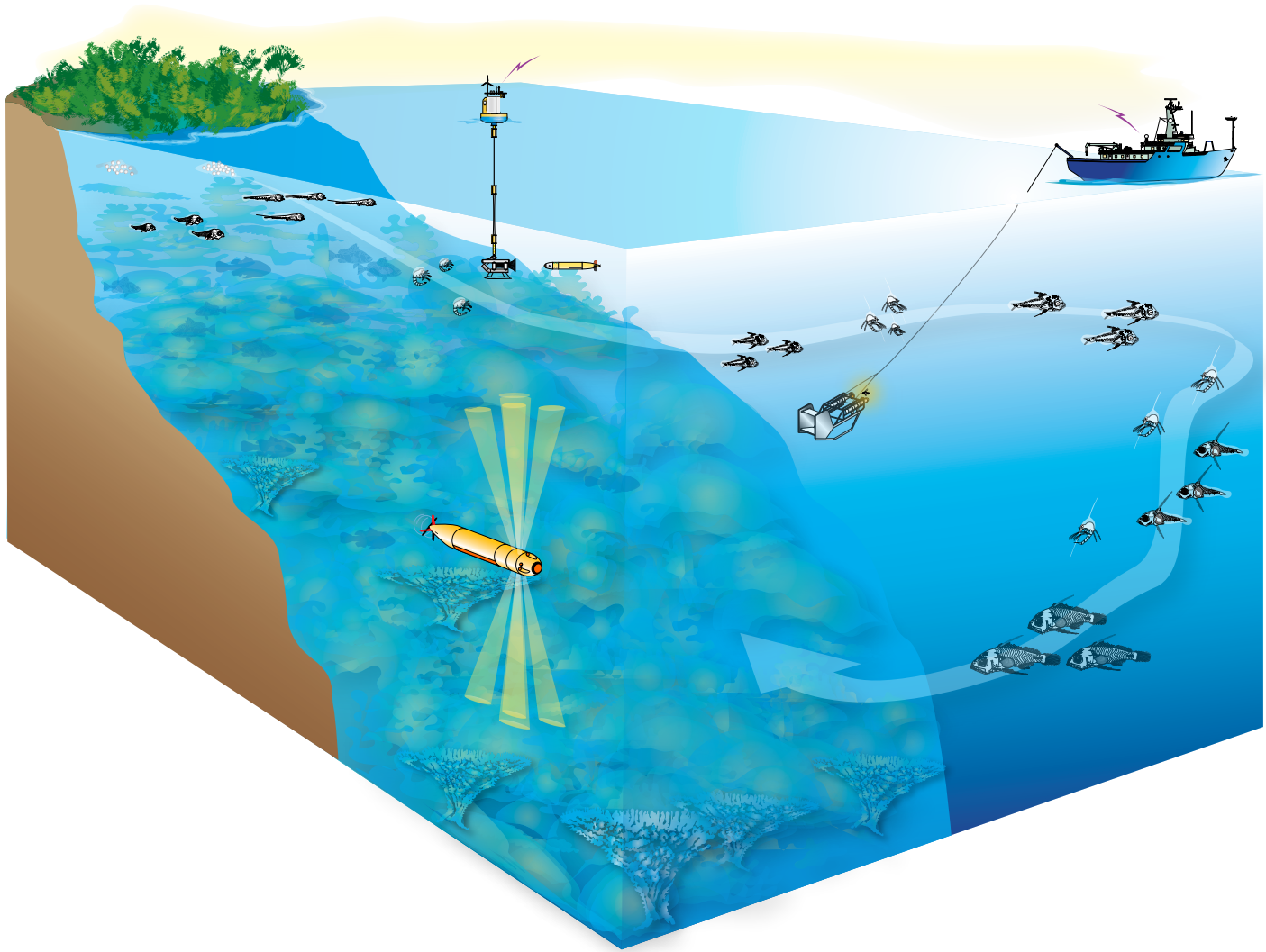


Figure 1. Population connectivity of benthic marine organisms occurs primarily during the pelagic larval phase when individuals either return to their natal location to settle, or disperse and settle some distance away from their natal population. While these larval movements are currently shrouded in mystery, new technologies promise to transform our understanding of population connectivity in ocean ecosystems. For instance, autonomous underwater vehicles (AUVs) could provide almost continuous real-time data on local hydrography that would then be streamed and assimilated into a coupled bio-physical model to predict the location of larvae spawned at a particular site. Model predictions could then be relayed to a research vessel conducting adaptive larval sampling using new in situ imaging systems that would, in turn, provide near-real-time distributions of target larvae. These distributions could then be used to optimize new mission targets for the AUVs during the following data-collection cycle.

the processes are coupled across scales is essential. Identifying patterns will need to involve efforts that focus on a variety of species with different life histories across diverse environments. In concert, the problem is multidisciplinary, but one requiring *interdisciplinary* research effort (Figure 1).

The core challenges or issues relevant to population connectivity can be parsed into four specific categories:

observation, explanation, consequences, and application. These issues can be captured, respectively, in the following general questions: (1) What is the spatial/temporal distribution of successful settlers originating from source populations? (2) What processes influence the shape of this dispersal kernel? (3) How do connectivity rates influence population and community dynamics? (4) How do we translate what we

learn into societal gains? Progress has been made in all four categories, but in most cases only at the periphery of the problem. This may be especially true of the second question, where answers are likely to be particularly challenging because a variety of physical and biological components contribute to the shape of the dispersal kernel. Although these components can be addressed separately, they will ultimately need to be examined

together due to the role of interactions. Ultimately, a process-oriented understanding is a prerequisite to achieving prognostic capability of marine-organism larval dispersal.

The series of papers in this volume demonstrates broad recognition of the relevance of and an active interest in the study of population connectivity across ocean science disciplines. These articles highlight the importance of spatio-temporal scales at a generally finer scale than previously considered in current hydrodynamic models and cross-shelf processes. The role of biological factors, such as larval behaviors that mediate the outcome of physical mixing and dispersal, is also evident. Similarly, the application of new methodologies (and the need for development of others) suggests exciting results and the potential for a transformative understanding of the importance of spatial processes in marine systems. As the processes and scale of connectivity are better understood, the applications of these findings are also being dissected to enhance management and conservation measures.

Each paper in this issue addresses the current state of knowledge, new and novel methods for studying connectivity-related processes, and a call for future work to bring the whole problem into focus. The first paper, by *Pineda, Hare, and Sponaugle*, discusses larval transport and larval dispersal and how they relate to population connectivity. The authors consider the concept of population connectivity, with an emphasis on understanding the role of planktonic processes on the success of the settlers. *Gawarkiewicz, Monismith, and Largier* explore the physical oceanogra-

phy of the coastal ocean, with an explicit perspective to physical processes potentially important to connectivity. *Werner, Cowen, and Paris* examine the state of biophysical modeling as it pertains to connectivity, emphasizing both the capabilities of the models and the assumptions (i.e., limitations) and pointing to areas of process-oriented research that are required to improve coupled models.

*Hedgecock, Barber, and Edmands* discuss the potential role and limitations of genetic methodologies in assessing population connectivity. These authors provide a dose of realism regarding the capabilities of genetic methods for inferring connectivity, but also a sense of optimism with the incorporation of newer integrative approaches. Similarly, *Thorrold, Zacherl, and Levin* examine new methods for direct measurements of connectivity in the field using natural and artificial tags. Their work focuses on geochemical signatures that exist within calcified structures of many marine organisms.

The last three papers explore the various implications and applications of

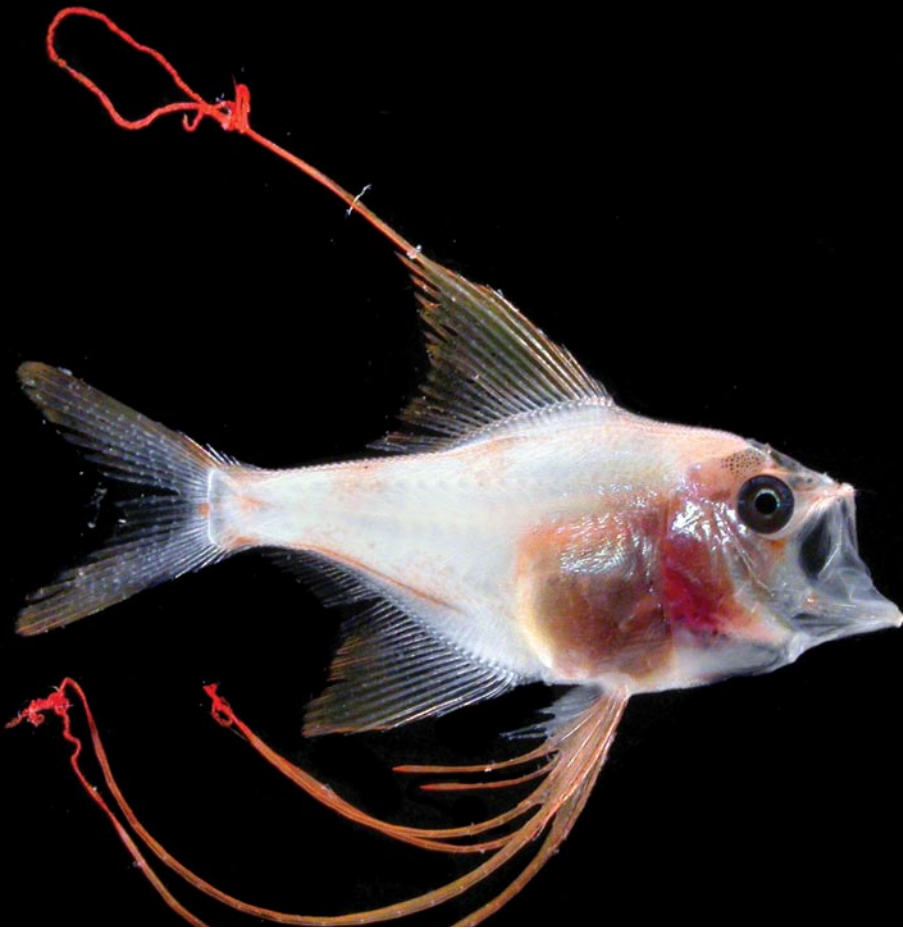
and offer broad theoretical contexts for addressing population ecology issues. *Jones, Srinivasan, and Almany* evaluate the significance of connectivity to the conservation of marine biodiversity. They provide recent evidence that the resiliency of marine populations to human exploitation may be linked to species richness, thereby highlighting the importance of maintaining biodiversity in marine communities. This theme is further discussed in the final paper by *Fogarty and Botsford*, who look into the central role of dispersal and connectivity in the dynamics of exploited marine systems. They discuss the critical importance of understanding dispersal processes controlling both larval export and movement of later life-history stages in the specification of effective spatial management strategies with an emphasis on marine reserves.

In summary, while these papers only touch on the scope of current work addressing various aspects of population connectivity in marine populations, they set the stage for a groundswell of

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connectivity in marine systems. *Gaines, Gaylord, Gerber, Hastings, and Kinlan* discuss the observational and theoretical advances and challenges in understanding the population consequences of larval dispersal and connectivity,

interdisciplinary scientific and community interest in marine population connectivity. Our hope is that through this combined effort, oceanographers may be able to establish a simplified yet useful set of guidelines (e.g., certain biologi-



cal processes, such as vertical behavior by larvae, may mediate or simplify the dispersive complexity of the physical environment). Until we do so, we may be relegated to resolving connectivity individually for every species and system of interest.

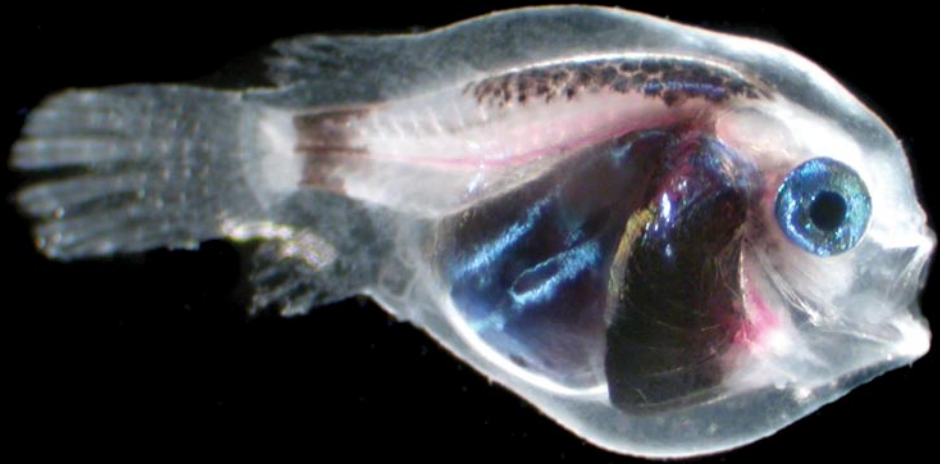
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## REFERENCES

- Agardy, T.S. 1997. *Marine Protected Areas and Ocean Conservation*, R.G. Landes Co., Austin, TX.
- Almany, G.R., M.L. Berumen, S.R. Thorrold, S. Planes, and G.P. Jones. 2007. Local replenishment of coral reef fish populations in a marine reserve. *Science* 316:742–744.
- Barnett, A.M., and A.E. Jahn. 1987. Pattern and persistence of a nearshore planktonic ecosystem off Southern California. *Continental Shelf Research* 7:1–25.
- Bentzen, P., C.T. Taggart, D.E. Ruzzante, and D. Cook. 1996. Microsatellite polymorphism and the population structure of Atlantic cod (*Gadus morhua*) in the northwest Atlantic. *Canadian Journal of Fisheries and Aquatic Sciences* 53:2,706–2,721.
- Botsford, L.W., J.C. Castilla, and C.H. Peterson. 1997. The management of fisheries and marine ecosystems. *Science* 277:509–515.
- Botsford, L.W., A. Hastings, and S.D. Gaines. 2001. Dependence of sustainability on the configuration of marine reserves and larval dispersal distance. *Ecology Letters* 4:144–150.
- Browman, H.I., and K.I. Stergiou. 2004. Perspectives on ecosystem-based management approaches to the management of marine Resources. *Marine Ecology Progress Series* 274:269–270.
- Cowen, R.K. 1985. Large scale pattern of recruitment by the labrid, *Semicossyphus pulcher*: Causes and implications. *Journal of Marine Research* 43:719–743.
- Cowen, R.K. 2002. Larval dispersal and retention and consequences for population connectivity. Pp. 149–170 in *Ecology of Coral Reef Fishes: Recent Advances*. P.F. Sale, ed., Academic Press, San Diego, CA.
- Cowen, R.K., C.B. Paris, and A. Srinivasan. 2006. Scaling of connectivity in marine populations. *Science* 311:522–527.
- Epifanio, C.E., and R.W. Garvine. 2001. Larval transport on the Atlantic continental shelf of North



- America: A review. *Estuarine and Coastal Shelf Science* 51:51–77.
- Gerlach, G., J. Atema, M.K. Kingsford, K.P. Black, and V. Miller-Sims. 2007. Smelling home can prevent dispersal of reef fish larvae. *Proceedings of the National Academy of Sciences of the United States of America* 104:858–863.
- Hastings, A., and S. Harrison. 1994. Metapopulation dynamics and genetics. *Annual Review of Ecology and Systematics* 25:167–188.
- Hutchings, J.A. 2000. Collapse and recovery of marine fishes. *Nature* 406:882–885.
- Jackson, J.B.C., M.X. Kirby, W.H. Berger, K.A. Bjorndal, L.W. Botsford, B.J. Bourque, R.H. Bradbury, R. Cooke, J. Erlandson, J.A. Estes, and others. 2001. Historical overfishing and the recent collapse of coastal ecosystems. *Science* 293:629–638.
- Johnson, M.W. 1960. The offshore drift of larvae of the California spiny lobster *Panulirus interruptus*. *California Cooperative Oceanic Fisheries Investigations Reports* 7:147–161.
- Jones, G.P., M.J. Millicich, M.J. Emslie, and C. Lunow. 1999. Self-recruitment in a coral reef fish population. *Nature* 402:802–804.
- Jones, G.P., S. Planes, and S.R. Thorrold. 2005. Coral reef fish larvae settle close to home. *Current Biology* 15:1,314–1,318.
- Moilanen, A., and M. Nieminen. 2002. Simple connectivity measures in spatial ecology. *Ecology* 83:1,131–1,145.
- Newman, W.A., and R.R. McConnaughey. 1987. A tropical Eastern Pacific barnacle, *Megabalanus coccopoma* (Darwin), in Southern California, following El Niño 1982–83. *Pacific Science* 41:31–36. *Resources* 29:31–68.
- Paris, C.B., L.M. Chérubin, A. Srinivasan, and R.K. Cowen. In press. Surfing, spinning, or diving from reef to reef: How does it change population connectivity? *Marine Ecology Progress Series*.
- Pikitch, E.K., C. Santora, E.A. Babcock, A. Bakun, R. Bonfil, D.O. Conover, P. Dayton, P. Doukakakis, D. Fluharty, B. Heneman, and others. 2004. Ecosystem-based fishery management. *Science* 305:346–347.
- Pineda, J., and M. López. 2002. Temperature, stratification and barnacle larval settlement in two Californian sites. *Continental Shelf Research* 22:1,183–1,198.
- Planes, S. 2002. Biogeography and larval dispersal inferred from population genetic analysis. Pp. 201–220 in *Ecology of Coral Reef Fishes: Recent Advances*. P.F. Sale, ed., Academic Press, San Diego, CA.
- Purcell, J.F.H., R.K. Cowen, C.R. Hughes, and D.A. Willams. 2006. Weak genetic structure indicates strong dispersal limits: A tale of two coral reef fish. *Proceedings of the Royal Society B* 273:1,483–1,490.
- Robertson, D.R. 2001. Population maintenance among tropical reef fishes: Inferences from small-island endemics. *Proceedings of the National Academy of Sciences of the United States of America* 98:5,667–5,670.
- Sale, P.F., R.K. Cowen, B.S. Danilowicz, G.P. Jones, J.P. Kritzer, K.C. Lindeman, S. Planes, N.V.C. Polunin, G.R. Russ, Y.J. Sadovy, and R.S. Steneck. 2005. Critical science gaps impede use of no-take fishery reserves. *Trends in Ecology and Evolution* 20(2):74–80.
- Scheltema, R.S. 1986. Long-distance dispersal by planktonic larvae of shoal-water benthic invertebrates among the Central Pacific islands. *Bulletin of Marine Science* 39:241–256.
- Shulman, M.J., and E. Birmingham. 1995. Early life histories, ocean currents, and the population genetics of Caribbean reef fishes. *Evolution* 49:897–910.
- Sponaugle, S., R.K. Cowen, A. Shanks, S.G. Morgan, J.M. Leis, J. Pineda, G.W. Boehlert, M.J. Kingsford, K.C. Lindeman, C. Grimes, J.L. Munro. 2002. Predicting self-recruitment in marine populations: Biophysical correlates and mechanisms. *Bulletin of Marine Science* 70(1):341–375.
- Victor, B.C. 1986. Larval settlement and juvenile mortality in a recruitment limited coral reef fish population. *Ecological Monographs* 56:145–160.
- Werner, F.E., J.A. Quinlan, B.O. Blanton, and R.A. Luettich Jr. 1997. The role of hydrodynamics in explaining variability in fish populations. *Journal of Sea Research* 37:195–212.
- Willis, T.J., R.B. Millar, R.C. Babcock, and N. Tolimieri. 2003. Burdens of evidence and the benefits of marine reserves: Putting Descartes before des horse? *Environmental Conservation* 30:97–103.