SYMPOSIUM

Dispersal of Marine Organisms and the Grand Challenges in Biology: An Introduction to the Symposium

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Synopsis Understanding dispersal and its complex variables is critical to understanding the ecology and evolution of life histories of species, but research on dispersal tends to reflect or emphasize particular disciplines, such as population genetics, functional morphology, evolutionary and developmental biology, physiology, and biophysics, or to emphasize a particular clade or functional group (e.g., fish, planktotrophs or lecithotrophs, pelagic or benthic organisms) in marine ecosystems. The symposium on "Dispersal of Marine Organisms" assembled an interdisciplinary group of outstanding young and established speakers to address dispersal in marine organisms in order to foster integration and cross-talk among different disciplines and to identify gaps in our knowledge and suggest areas for future research.

The oceans hold a rich diversity of organisms that help support life on the planet. In the first decadelong Census of Marine Life (2000-2010), teams of researchers sought to answer three questions: what lives in the ocean?, What has lived in the ocean? and What will live in the ocean? (Grassle 2010). Now in 2012, the Ocean Biogeographic Information System database developed as part of the census holds >30 million records of life in the ocean (www.iobis.org), and scientists are still identifying new species. In addition to knowing what lives in the ocean, understanding where, when, and how populations of organisms are distributed in the ocean is a central and significant topic in marine biological research. Moreover, gaining such understanding requires an integrative approach because, fundamentally, the dispersal and distribution of marine organisms reflect an integration of environmental characteristics and organisms' biology, physiology, and behavior.

As a topic of research, dispersal of marine organisms addresses many of the Grand Challenges in Organismal Biology proposed by Schwenk et al. (2009) (Table 1). For example, environmental conditions determine the fate of many propagules, and the plasticity of marine organisms' behavioral and

physiological responses to the environment can influence dispersal and subsequent patterns of distribution (Table 1, GC1). Similarly, some taxa use multiple dispersal mechanisms—does this flexibility enhance their resiliency or their ability to invade new habitats (CG1)? How is phenotypic plasticity in dispersing forms generated and maintained (GC4)? The oceans harbor tremendous biodiversity and provide food for a burgeoning human population. Yet, fishing activity by humans has reduced species diversity in some taxa. Conserving biodiversity of the oceans depends on understanding how connected marine populations are and the degree to which variation in dispersal determines connectivity (GC2). New research in dispersal and in marine connectivity requires the integration of physical oceanographic models with biological models. How do we link these two disparate systems with common currencies to allow integrated analysis of both living and physical systems (GC3)? This type of integration is critical to predicting how dispersal patterns, and therefore species' distributions, are likely to respond to the changing oceanic environment (GC5).

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Table 1 Dispersal of marine organisms exemplifies the integrative research proposed in the Grand Challenges in Organismal Biology (Schwenk et al. 2009)

Grand Challenge	Dispersal metaphor/questions
GC1: Understanding the organism's role in organism–environment linkages	How do the environment and organismal physiology and behavior interact to constrain or promote ability to disperse? Does flexibility in the mechanisms of dispersal enhance resiliency?
GC2: Utilizing the functional diversity of organisms	Do certain dispersal mechanisms promote hotspots in biodiversity or influence invasions by nonnative species? Can better understanding of dispersal mechanisms and constraints lead to sound management of marine resources?
GC3:Integrating living and physical systems analysis	Modeling population connectivity requires integrating physical environmental models and biological models. What are the common currencies and methods that will improve modeling?
GC4: Understanding how genomes produce organisms	How is phenotypic plasticity in dispersing forms generated and maintained?
GC5: Understanding how organisms walk the tightrope between stability and change	How does the changing oceanic environment affect dispersal capabilities of organisms? What are the evolutionary linkages between dispersal in stable deep-sea environments and those in shallower waters?

or emphasize a particular discipline (e.g., population genetics, functional morphology, evolutionary and developmental biology, and biophysics) or emphasize a particular taxon or functional groups (e.g., fish, planktotrophs or lecithotrophs, pelagic or benthic organisms). As the following synopsis describes, the symposium "Dispersal of Marine Organisms" brought together researchers from each of these perspectives to address the broad problem of dispersal in marine environments.

Although larval dispersal was a significant focus of the symposium, many marine organisms do not have a pelagic larval stage, and yet are able to expand their distributions and can even have "geographic distributions that are comparable to those with a pelagic dispersal stage" (Winston, 2012). Judith Winston considers the mechanisms by which marine plants and invertebrates disperse, even when they have no planktonic life stage, or have planktonic life stages of very limited duration. She also highlights several cases in which the observed distribution of species is not clearly related to the potential for larval dispersal. Dr. Winston's call for action, specifically cooperative and integrative research spanning oceanography, modeling, and genetic and ecological studies, was a theme echoed by most of the symposium speakers.

Research in marine larval ecology has a rich history and many of the questions asked by researchers today benefit from the basic research on larval development, form, function, and behavior conducted in the first half of the 20th century (reviewed by Young 1990). Karen Chan's contribution continues this theme, asking how larval swimming can impact dispersal potential, and highlighting research on sand dollar larvae that examines the intersection of

environmental change, larval morphology, biomechanics, and swimming performance. This topic is directly relevant to the first grand challenge in biology (Table 1).

Two symposium speakers considered dispersal in specific, "extreme" environments. Compared with other regions of the world's oceans, marine benthic invertebrates that live in the Southern Ocean produce fewer pelagic larvae or drifting stages. Yet, there is tremendous diversity of benthic organisms in Antarctic waters and the mechanisms leading to, and maintaining, this diversity have been the topic of debate for decades. Beginning with the context set by Thorson's Rule (that the dearth of species with pelagic larval forms at high latitudes is an adaptation to the mismatch between long developmental time and short periods of abundant food), and the bringing of new molecular biological evidence to the discussion, Sven Thatje argues that early life history characteristics and physiological adaptations of Antarctic benthic invertebrates affect their dispersal ability and lead to their diversity and resilience over evolutionary history. From the extreme environment of the Southern Ocean, Craig Young and colleagues take us to the extreme habitats of the deep sea, in a wonderful example of integrative biological research that partners insight gained from laboratory rearing experiments and from field sampling to determine the larval durations of seven bathyal invertebrates with hindcasts generated from a physical oceanographic model of oceanic circulation to explore questions concerning planktonic larval development, dispersal potential of deep-sea species, and how oceanic circulation modifies dispersal.

One of the champion-dispersing species highlighted by Young et al. (2012) was a sipunculan,

Phascolosoma turnerae, and its taxon has been the focus of considerable research in larval biology and in the role of dispersal in larval ecology. Sipunculan pelagosphera larvae are renowned for the duration of their larval stage (e.g., Rice 1967) and for their potential ability to disperse (Scheltema and Hall 1975). Anja Schulze and colleagues continue the focus on sipunculan larval dispersal and distribution, presenting a case study for integrating traditional morphological methods with molecular genetic analyses to evaluate the relationships among "cosmopolitan" species.

Once relatively separated, studies of population connectivity, species' distributions, life histories, phylogenetics, biophysics, and physical oceanography have become increasingly integrated (Levin 2006) and, aided by new and improving tools, including molecular biological approaches, this process continues (Cowen and Sponaugle 2009). Efforts in marine conservation and management increasingly rely on integrating the information gained from such studies. Paola Lopez-Duarte and colleagues explore the links between connectivity and metapopulation dynamics of eight species found on the southern Californian coast, synthesizing the results of 12 years of research using elemental-fingerprinting to determine larval origins and connectivity patterns, and highlighting how such studies can contribute to ecosystem management. Research by Eric Treml and colleagues uses a novel modeling approach to understand connectivity that explicitly considers the interaction between the physical environment and a given species' life history characteristics, especially those that influence larval dispersal. Their approach allows examination of multi-species population connectivity in the Indo-Pacific Ocean across multiple spatial and temporal scales. Finally, Erik Sotka explicitly considers the evolutionary timescale and explores geographic variation of phenotypes in the sea, focusing on local adaptation of marine populations. He suggests a framework for predicting when local adaptation versus phenotypic plasticity should be favored and outlines ways in which research in marine systems may contribute unique insights.

The symposium organizers hope that the presentations and discussions at the meeting, reinforced by the papers in this volume, will promote the exchange and integration across disciplines of ideas and knowledge of dispersal, and identify needed areas and approaches for future research. We challenge readers to consider the same questions that we posed to the symposium participants: How do physical environmental characteristics and organisms' physiology and behavior interact to affect the ability

of species to disperse? What are the ecological and evolutionary consequences of variation in dispersal? What common currencies should be measured and analytical approaches employed to better understand how dispersal of marine organisms will respond to the changing oceanic environment? Answering these questions will require an integrated approach, as many of the symposium participants noted. Indeed, Craig Young's (1990) call to action regarding the state of research on larval ecology at the beginning of the last decade of the 20th century resonates today: "Important advances will be made most quickly if ecologists interact with zoologists and physical oceanographers to use existing knowledge as a springboard for efficient progress toward new discoveries." We hope that the papers in this symposium volume provide that springboard.

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