

# Population Connectivity in Marine Systems

**Report of a Workshop to  
Develop Science Recommendations  
for the National Science Foundation**

**November 4-6, 2002  
Durango, Colorado**

**Workshop Convenors:**

**Robert K. Cowen  
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# MARINE POPULATION CONNECTIVITY

## 1. Executive summary

A central goal of marine ecology is to achieve a mechanistic understanding of the factors regulating the abundance and distribution of marine populations. With such an understanding, it should be possible to generate theory capable of predicting the effects of changes in physical and biological parameters on the dynamics of these populations. A critical component of the above goal is to quantify rates of exchange, or **connectivity**, among subpopulations of marine organisms. We have, however, little more than a rudimentary understanding of the spatial scales over which marine populations are connected by larval dispersal. This lack of knowledge represents a fundamental obstacle to any 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 fisheries scientists to evaluate the design and potential benefits of novel, spatially-explicit management strategies including marine protected areas (MPAs).

One of the key ecological questions identified by the OEUVRE Workshop (1998) was focused on the resolution of the mechanisms contributing to and the spatial scales over which marine populations are connected via dispersal of early life stages of marine organisms. Resolution of this problem has direct impact on our knowledge of marine population and community ecology, mechanisms of genetic divergence and evolution, and marine biogeography as well as direct societal applications such as stewardship of marine resources and dynamics of infectious diseases. The report noted that the inability to accurately predict dispersal makes it impossible to determine the effect of climate change and/or human exploitation on marine ecosystems. Thus, there is a clear need for an interdisciplinary effort to address this issue and the consequential need for programmatic funding in support of this effort.

This report summarizes the outcome of a workshop that was convened to specifically address the scientific issues and needs relevant to resolving marine population connectivity. Participants at the workshop were charged with developing a Science Action Plan targeting a process-oriented understanding of population connectivity in marine systems and, in so doing, to make recommendations to facilitate the successful implementation of the plan. Recognizing the highly interdisciplinary nature of the problem, the specific recommendations to NSF may be summarized as:

**Programmatic development focused on Marine Population Connectivity to ensure adequate resources and overview aimed at:**

### **i) Development and application of key technologies**

– The nature of the connectivity problem will require a diverse toolbox of techniques (e.g., molecular, genetic, microchemistry, modeling, tracers and “smart” drifters) applied in an interdisciplinary framework. Many techniques are at the cusp of being developed, others are available but have yet to be applied in ways relevant to assessing the mechanisms and outcome of larval dispersal and population connectivity. Such specific technologies and applications require programmatic support to expedite their development and, thereby, availability for simultaneous application in multi-pronged research efforts.

### **ii) Integration with Ocean Observing Systems and Observatories**

– The focused study of population connectivity should be carefully integrated with the planning of future coastal ocean observatories and observing systems. Observatories will provide intensive process-oriented data on key factors determining connectivity, while observing systems will provide sustained measurements over larger spatial scales. These observing approaches are complementary and are both necessary. Because of the potentially small spatial scales of processes affecting connectivity, and the short temporal scales of processes affecting dispersion, we advocate the use of integrated and re-locatable observatory components which would allow redeployment in varying environments (e.g., broad shelves, islands, and estuaries). In parallel to the deployment of observatories, the implementation of permanent observing systems spanning large (eventually basin-wide) geographic domains is critically important to provide the backdrop to the more focused strategy of the observatories and provide critical data to population connectivity issues given the inter-annual to decadal temporal variability associated with larval dispersal processes.

### **iii) Need for application of multiple techniques/disciplines simultaneously**

– resolving the scope and mechanisms involved in larval dispersal and population connectivity will require joint application of biological and physical oceanographic studies, with the inclusion of a variety of techniques. Such a multi-disciplinary, multi-investigator research effort will involve large teams and require sufficient resources. Current limits to our resolution of the population connectivity problem have been, in part, due to limited resources restricting the size and scope of research teams. Programmatic support is therefore required to ensure substantial commitment and participation across multiple disciplines in well-coordinated, interdisciplinary studies.

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**iv) Transfer of information: fostering cross-training and collaboration** – Identifying the scales of population connectivity and incorporating these data into resource management practices requires bringing together expertise that includes ecology, genetics, physical oceanography, fluid dynamics, applied mathematics, computer science, policy and management. To achieve the integration of disciplines, support is recommended at two levels:

- In the short term, cross-training is recommended in the form of graduate and post-doctoral traineeships, intensive workshops, summer courses and symposia. Programs including UCAR, NCAR, and NCEAS should be considered in the structuring of intensive courses and workshops to allow for formal approaches to be developed in this technology transfer.
- In the longer term, we recommend the creation of a **Center for Integrative Marine Ecology (CIMEC)**. In the next five years, integration of observations and modeling in marine environments will be elevated to levels that will revolutionize the way we view the coastal ocean.

Observations will be available in near-real time for many coastal regions and models. These will provide information in space and time we have never seen. To systematically take advantage of this information and use it to answer longstanding questions in ecology, conservation biology and resource management, the Center would provide a site where access to this information is provided. It would bring together academic, government and private sectors with the goal of developing quantitative approaches to the conservation and sustainable management of marine ecosystems based on these observational and modeling products. In addition to a core staff, the Center would support leading experts (e.g., on short leaves from their institutions) of the various disciplines to come together periodically to conduct basic research on marine ecology and resource management, as well as to run workshops and dedicated courses.

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## 2. Introduction

There is a growing consensus that the living organisms within the world's oceans are under considerable and increasing stress from human activities. Most marine-capture fisheries continue to be exploited at levels above those required for sustainable use of the resource. The combined effects of fishing mortality, habitat degradation and pollution have led to alarming reductions in the numbers of many marine fishes, shellfishes, mammals, turtles, and birds. Finally, ecosystem services provided by marine environments are under increasing threat from the effects of human habitation of the coastal zone. A large proportion of the world's population lives within 100km of the coast, likely leading to further exacerbation of marine ecosystem stress.

**The absence of empirical data on population connectivity represents a fundamental obstacle to any comprehensive understanding of the population dynamics of marine organisms**

particular, have been touted as methods for both maintaining biodiversity and managing fisheries. Continuing debates on the efficacy of MPAs have identified the need for spatial models that accurately capture marine population dynamics. Theoretical studies suggest that population connectivity (the exchange of individuals among geographically-separated sub-populations that comprise a metapopulation) plays a fundamental role in local and metapopulation dynamics, community structure, genetic diversity, and the resiliency of populations to human exploitation. Modeling efforts have been hindered, however, by the paucity of empirical data on population connectivity. While progress has been made with older life stages, connectivity as a function of larval dispersal remains unresolved for most marine populations. This lack of knowledge represents a fundamental obstacle to any 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 fisheries scientists to evaluate the design and potential benefits of novel management strategies.

The magnitude and spatial extent of larval dispersal in marine systems has traditionally been inferred from

The unprecedented strain on both the structure and function of marine ecosystems has led to calls for new management approaches to counter anthropogenic impacts in coastal oceans. Spatial management options, in general, and marine protected areas (MPAs) in

the pelagic duration of the larval dispersive stage, from the modeled movements of passive particles by low-frequency currents, or from analyses of population variation in mitochondrial or nuclear genomes. Observations of pelagic larval durations in many marine species of weeks to years, coupled with predicted advection of passive particles by 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 provide further support for the existence of long-distance dispersal (e.g. 100's to 1000's km). However, more recent research and careful reconsideration of the evidence suggests this perception is likely inaccurate for many species, particularly over time scales of ecological relevance.

New hyper-variable nuclear DNA assays have found genetic differentiation among sub-populations of marine fish and invertebrates that went undetected by earlier, less sensitive, DNA analyses. Novel tagging approaches have demonstrated the potential for local retention of reef fish larvae. 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. Taken together, these studies provide intriguing, albeit incomplete, evidence that subpopulations of marine organisms may be semi-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 numerical predictions of specific natural or human impacts on marine populations.

Justification of Question: A recent NSF report (OEUVRE, 1998) identified marine population connectivity as a key question in biological oceanography – “Over what spatial scales are marine populations connected via dispersal of early life stages?” The report noted that the inability to accurately predict larval dispersal makes it impossible to determine the effects of natural or anthropogenically induced variability on marine ecosystems. More specifically, the report identified five objectives that could be addressed with adequate information on population connectivity:

- Population and community ecology:** Determine kinds and strengths of interspecific interactions in which open versus closed populations engage.
- Evolution:** Compare degrees of isolation with rates of genetic divergence.
- Biogeography:** Evaluate the extent to which range limits are set by barriers to dispersal rather than physical tolerances of adults

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## **Management, conservation and biodiversity:**

Evaluate the efficacy of extant reserves as determined by regional dispersal patterns

**Dynamics of infectious diseases:** Evaluate the role of linkages in the epidemiology of diseases.

Ultimately, patterns of connectivity among subpopulations of marine organisms are determined by interactions between biological phenomena including life history characteristics and larval behavior, and physical processes of advection and diffusion. Population connectivity is relevant to a fundamental understanding of marine ecological processes and is directly applicable to critical human and environmental issues. Thus, there is a clear need for an interdisciplinary initiative in Marine Population Connectivity and concomitant programmatic funding in support of the effort. In response to this need, a workshop was held in Durango, CO, on November 4-6, 2002 with the goal of developing a Science Action Plan for an initiative in Marine Population Connectivity. The workshop was also charged with identifying means of effective engagement between scientists and those agencies responsible for the conservation and sustainable management of marine ecosystems.

## **3. Background**

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 inter-generational spread of larvae away from a source to the destination or settlement site. This usage is widespread in the terrestrial literature where the basic description of dispersal is a *dispersal curve*, a 1-dimensional representation of the number of settlers from a given source as a function of the distance from that source. The dispersal curve becomes a *dispersal kernel* with an associated probability density function, in  $n$  dimensions.

On the other hand, larval *transport* is used to describe the horizontal translocation of larvae between two points, often in cross- ( $u$ ) and along-shore ( $v$ ) directions for coastal environments. Note, however, that although high dispersal implies significant larval transport, restricted dispersal is not necessarily correlated with reduced larval transport. As defined

**The dominant scales of larval dispersal in coastal species are not known**

above, restricted dispersal with high larval transport may occur when larvae return to their original birth sites after traveling long distances. In addition, retention in shadow zones near islands or reefs, and

in estuaries, further serves to complicate the problem. 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. A process-based understanding of dispersal is an essential component of population connectivity because it addresses how biological and hydrodynamic processes at different spatial and temporal scales interact in the dispersal of marine organisms. Furthermore, a mechanistic understanding generates testable predictions of larval transport and dispersal in unstudied situations. The combination of marker and process-oriented approaches promises a full mechanistic 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, or in the case of endemic species on isolated islands where larvae must be from local sources, suggest that limited dispersal is possible in marine environments. In contrast, observations that larvae of shallow water species are found in gyre systems, and examples of significant range extensions during narrow event windows indicate dispersal on the scale of hundreds to thousands of kilometers is possible.

Of critical bearing on this issue is clarification of the relevant time scale. For population maintenance, and associated conservation and resource management objectives, the fundamentally relevant time scale is ecological or demographic, rather than that relevant to evolutionary processes. 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.

The problem of population connectivity is inherently a coupled bio-physical problem. Physical processes which are important to this problem include boundary layer structure, particularly over the inner shelf, tides, internal tides and bores, fronts and associated jets, and onshore/offshore forcing via eddies, meanders, island wakes, and lateral intrusions. However, physical processes alone do not determine the scales of connectivity. Time scales of larval development and behavioral issues including vertical migration play an important role.

From this potentially large number of advective and diffusive processes which relate to the dispersal and recruitment of marine organisms, general points can be extracted which help define the connectivity

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problem. First, the temporal and spatial correlation scales over continental shelves may be relatively short; on the order of days and kilometers. Correlation scales near islands, reefs and within estuaries are not well known. This necessitates careful selection of sampling strategies to resolve the various processes described above. Second, the relative contributions of these various processes will likely change from site to site, depending on such factors as coastal geometry, proximity to estuaries, and seasonal stratification and wind forcing. Third, the individual processes contain length and time scales which vary, and so the physical transport and dispersion is inherently a multi-scale process. This presents problems for modeling, as it is difficult at the present time to resolve mesoscale and small- to intermediate-scales simultaneously. Finally, we need a high degree of precision in our knowledge of the flow fields in order to embed behavioral models on particles within physical models to test hypotheses involving bio-physical interactions.

## 4. Challenges

### Mechanistic understanding of larval dispersal and larval transport must be hypothesis driven

The major challenges in this effort are to provide an adequate, quantitative understanding of the processes and scales controlling larval dispersal and how it influences the dynamics of the affected populations. Resolving the mechanisms controlling larval dispersal will involve a coherent understanding of the relevant physical processes and how organisms mediate the

**Resolving the mechanisms controlling larval dispersal will involve a coherent understanding of the relevant physical processes and how organisms mediate the physical outcome**

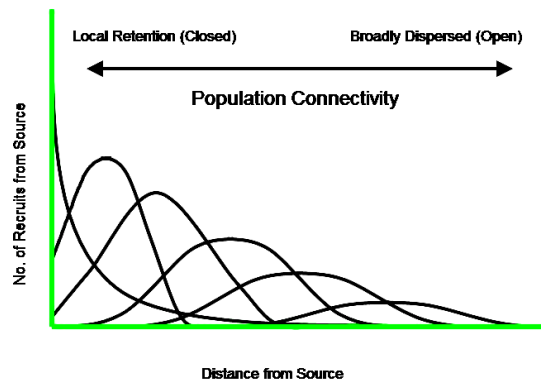
physical outcome. Multiple scales will be important, and therefore understanding how the processes are coupled across scales is essential. Identifying patterns will involve efforts that focus on a variety of species with different life histories across various

environments. In concert, the problem is multidisciplinary, but one requiring *interdisciplinary* research effort.

The following questions were identified as core to the broad issue of connectivity of marine populations. They are separated into four specific categories relating to, respectively, observation, explanation, consequences and application.

### 4.1. What is the spatial/temporal distribution of successful settlers originating from source populations?

A formal approach to address this question is via the definition of a dispersal kernel. Simply, the dispersal kernel provides the probability of ending up at position  $x$  given a starting position  $y$ . In terrestrial systems, for example, a dispersal kernel can be constructed by catching seeds from trees and plotting their abundance as a function of distance from source. Knowing the dispersal kernel and the spatial distribution of adult lifetime egg production ( $R_0$ ) over space we can estimate the persistence or sustainability of the population, for specific populations, but there is limited understanding of what leads to persistence in general. In marine systems, dispersal kernels can be constructed by either tagging larvae and collecting successful recruits or following organisms in the field. Dispersal kernels may also be estimated via particle releases (passive or behaviorally active, if possible) in model flow fields. However, given spatial and temporal variation in circulation, as well as



Theoretical dispersal curves depicting dispersal ranging from strong retention to broadly dispersed

reproduction, empirical determination of larval dispersal represents a basic challenge in resolving the scale of population connectivity.

### 4.2. What influences the shape of the dispersal kernel?

Beyond empirical descriptions of dispersal kernels, we also need to answer the question: "What **drives** the observed dispersal kernels?" Answering this question is perhaps one of the greatest challenges due to the inherent sources of variability, and a process-oriented understanding is a pre-requisite to achieving prognostic capability. 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.

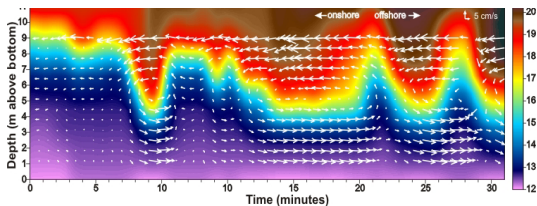


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## The shape of the dispersal kernel is determined by:

*Advection and diffusion:* Passive transport is the simplest case and can be defined as transport of neutrally buoyant larvae in a turbulent flow field without behavior. However, dispersed marine larvae do not typically encounter a homogeneous substrate in which to settle; neither are most marine larvae behavior-free. Therefore, complexity is introduced even in this simplistic case.

*Larval behavior:* Ocean, coastal and nearshore circulation often exhibits strong vertical structure. Vertically-stratified flows coupled with larval behaviors such as vertical migration can significantly affect larval dispersal and, potentially, the shape of the dispersal kernel. For example, dispersal kernels of surface-seeking larvae are likely to be very different from larvae that are found deeper in the water column. Thus, a challenge before us is to identify critical behavioral capabilities characteristic of each portion of the larval phase.



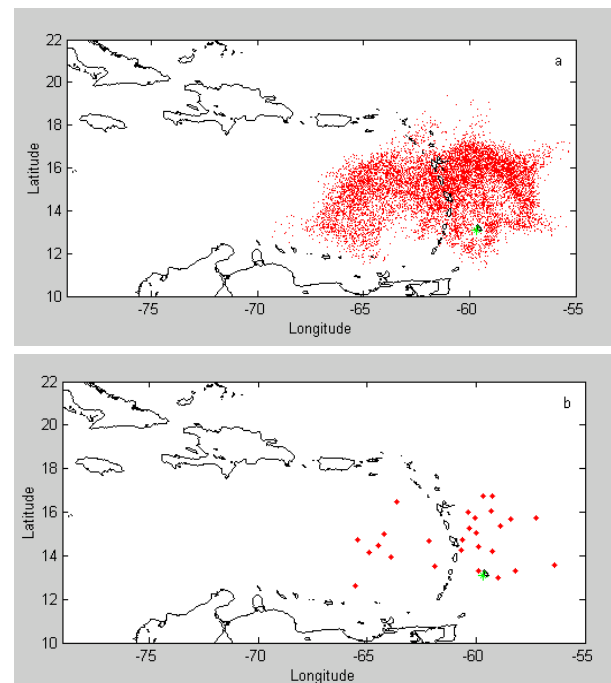
**Temperature and circulation in an internal bore warm front off Southern California, at about 11 m water depth. Horizontal currents rotated in the direction of front propagation. (Modified from Pineda, J. 1999, L&O 44:1400).**

*Along-trajectory mortality:* Induced either by starvation or predation, mortality of larvae along their transit will contribute to the shape of the dispersal kernel. An example is shown (right) where the distribution of larvae (particles) without starvation mortality (upper panel) is compared to that with starvation (lower panel). The result of the mortality is a significant reduction in effective dispersal. Differential survivorship will not confound the estimation of dispersal kernels if survivorship is determined empirically using a mark-recapture approach. However, spatially-structured mortality presents a significant problem for attempts to construct dispersal kernels using coupled bio-physical models. Similarly, the environment that larvae experience will determine their growth and survival.

*Process interactions across scales:* Environmental factors, in general, will be highly variable from year to year and from one location to another. On short time and space scales, extreme temperatures can stress larvae (and can be fatal), as can low oxygen conditions. Longer period variability of oceanic conditions (such as El Niño-Southern Oscillation - ENSO and the North Atlantic Oscillation - NAO) can also provide an inter-annual and longer modulation to

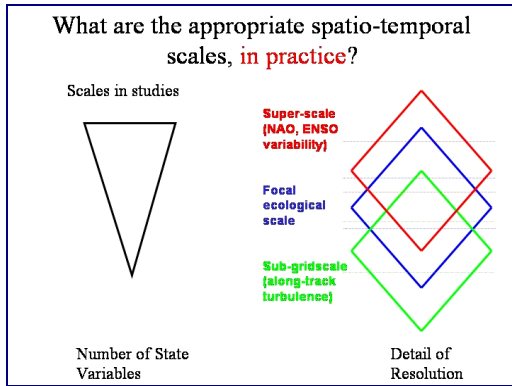
the dispersal kernel. We suggest that models focus on specific space-time scales and that they be linked in defining the modulation of the higher frequencies and smaller scales as illustrated (see figure on next page). The focal ecological scales are restricted by larval duration and mean dispersal distance. Advances are needed to couple across scales, e.g., how does the information of a detailed large eddy simulation scale up to ecological scales? Conversely, how does basin-scale variability downscale to ecological scales?

Modeling of population connectivity poses several unique challenges. First, many source regions are located in the nearshore environment, where there remain fundamental issues in resolving nearshore physics and their coupling to inner shelf processes and models. Physical transport models are also in need of improvement at the edge of the continental shelf, where shallow shelf waters abut deeper waters often influenced by strong boundary currents. However, an absolutely critical aspect of the modeling necessary for understanding population connectivity is the incorporation of behavior into models. There is not general agreement at the present time on the best way to do this, though the use of agent-based (or individual-based) modeling is crucial to successful modeling. A general issue is the disparate range of time and length scales for physical processes, e.g. internal waves, fronts, eddies, gravity currents, as compared to the time and length scales set by the larvae, such as vertical position in the water column, larval duration, and length and timing of spawning.



**Dispersal of 10,000 virtual larvae after 30 d following release from Barbados (•) (upper panel); and same after effect of larval mortality (lower panel). (Modified from Cowen et al. 2000, Science 287:857).**

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**Graphic depicting the need for linking models focused on scale-specific processes**

### 4.3. How do connectivity rates influence population and community dynamics?

An empirical determination of larval dispersal will provide an estimate of the sources of larvae that eventually recruit to adult populations. The challenge, however, is to integrate these data into spatially explicit models of marine populations. From dispersal kernels, we can calculate an  $n \times n$  population connectivity matrix  $P_{ij}$ , which gives the proportion of recruits in population  $i$  that came from population  $j$ , and where  $n$  is the number of populations. Accurate parameterization of metapopulation models will, in turn, allow ecologists to examine the stability and persistence of marine populations. We need a general understanding of the combinations of habitat spatial patterns and dispersal kernels that lead to persistence.

Ultimately, we need to understand the role that connectivity plays in the dynamics of marine ecosystems. For instance, inter-specific interactions that drive community structure may depend upon the degree to which populations recruit from local or distant sources. The resilience of marine communities to pathogens and biological invasions will similarly be determined by dispersal patterns of local populations and invasive or infective agents. Estimates of population connectivity will be required to explain patterns of genetic divergence as a function of geographic isolation, and to determine the extent to which larval dispersal influences the geographic range of coastal species.

### 4.4. How do we translate what we learn to societal gains?

The management of living marine resources is inherently spatially-dependent. Understanding how marine populations are connected in space and time will provide an essential component to management of marine resources that is presently not available. For instance, the design of marine protected areas (MPAs), requires a quantitative description of population connectivity. An understanding of spatial linkages

over populations will also contribute to the explanation of variability in fisheries.

One of the challenges is to generate a joint approach to the study of connectivity that considers both the scientific and the management components. The workshop participants recognized that while enhancements in modeling capabilities will continue, present-day models and the methods used to generate dispersal kernels need to be made available to ecologists and managers in a format that non-specialists can use. Not having these tools available has been an impediment to the testing of ecological theories, field experimental design and management practices. A desirable byproduct of the release of the models (or model products) to the community is that relevant directions in model development may be more quickly identified. Therefore, models need to be of appropriate complexity, and sufficiently modular to allow for incremental hypothesis testing (e.g., Ocean System Simulation Experiments [OSSE]). It was also recognized that transfer of the models from the computational fluid dynamics community to the resource managers, will require the transformation of “research codes” into community-accessible models. This activity necessitates joint collaboration with the computer science community.

## 5. Opportunities

Addressing the above challenges will require a highly integrated effort across multiple disciplines and technologies. Success will be significantly enhanced by capitalizing on opportunities that exist within the ocean science community and related fields. Specifically, community recognition of the importance and scope of the connectivity issue, the state of technological advancements applicable to the science, and existing, complementary programs will all contribute to facilitating a thorough understanding of marine population connectivity. Each of these opportunities was identified by workshop participants and their specific relevance was identified.

**5.1. Timeliness** – In defining future research priorities, the ocean science community has recognized the need for resolving the scaling and processes driving the spatial dynamics of marine populations. Community interest in such problems is more than an academic exercise; it also reflects clear recognition of the societal relevance of the problem. Moreover, calls by marine resource managers for more specific information applicable to spatial management objectives are directly relevant to the connectivity issue. This broad interest among the science and management communities is also reflected in legislative mandates for development of ecosystem-based, sustainable management strategies (see Reykjavik Declaration <ftp://ftp.fao.org/docrep/fao/005/y2198t/y2198t00.pdf>; pp. 105-108; see also, World Summit on Sustainable Development: Plan of

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Implementation [http://www.johannesburgsummit.org/html/documents/summit\\_docs/2309\\_planfinal.htm](http://www.johannesburgsummit.org/html/documents/summit_docs/2309_planfinal.htm).

Given the state of many of our marine resources, there is a clear sense of urgency for effective action. Thus, timing is optimal for building strong community support and action.

In a related perspective, there currently exists broad community recognition of the need for more integrated research efforts when focusing on complex systems. This call for greater interdisciplinary action has been both grass roots and top down in origin. Indeed, NSF has instituted a variety of mandates and opportunities for greater interdisciplinary research efforts.

**5.2. Emerging Technologies** – A broad range of tools is needed to address the challenges of determining population connectivity in the marine environment. Many technologies are currently available or emerging, enabling a rapid start. Other technologies

will require additional development but promise important capabilities for scientists. Tools for high resolution and rapid measurements of physical properties are quite advanced, however, the present day capability of observing systems for determining larval distributions lag behind the capability to observe physical fields. Real-time, *in situ* observing systems will be immediately useful in the short term in defining the oceanographic environment, including variability of the hydrographic and velocity fields, and in determining the Lagrangian pathways of identifiable larvae from source areas. Similarly, remote observing systems are needed to identify episodic events (and trigger intensive sampling), and temporal variability over long time scales.

We can loosely divide the tools into four major areas of application: (1) empirical estimates of dispersal pathways, (2) *in situ*, near real-time larval sampling, (3) remote biophysical Eulerian sampling, and (4) modeling (Table 1).

**Table 1. Emerging Technologies/uses of technologies – Status for use in connectivity studies, ranging from 1 (Completely developed) to 5 (Conceptual only, needs complete development).**

<u>Emergent Technologies</u>	<u>Status</u>
<b>Defining dispersal patterns</b>	
Geochemical signatures in calcified structures	2
Hyper-variable population genetic techniques	2
Natural/Artificial tags	3
Dyes	2
Smart drifters (larval mimics)	4
Passive drifters	2
<b>High resolution and near real-time larval sampling</b>	
Acoustics	4
<i>In situ</i> visual imaging (moored and shipboard)	3
Microarrays	4
Immuno-fluorescence	3
<b>Biological and physical remote sampling</b>	
Satellites	2
AUVs	2
Radar – OSCAR, CODAR, WERA	2
Remote sampler arrays	5
Larval pumps/tubes	3
Settlement samplers	2
Doppler current meters	1
<b>Models</b>	
Nearshore hydrodynamic models	4
Shelf hydrodynamic models	2
Model nesting	3
Bio/physical coupled models	2
Behavior	4
Neural networks	3
Agent-based (IBM's)	3
Real-time data assimilation	4
Marine metapopulation models	3

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At present, the most common methods for assessing dispersal pathways are geochemical signatures in calcified structures, artificial tags, isotopes, and population genetic techniques. Natural geochemical signatures have seen limited use in assessing larval dispersal, although analytical techniques are maturing and we expect to see the technique applied to connectivity issues in the near future. Population genetic approaches suffer from limitations because demographic isolation among sub-populations over evolutionary time scales is required to generate significant heterogeneity in gene frequencies. However new hyper-variable genetic techniques show promise because they evolve more rapidly than mitochondrial markers. Passive drifters and dyes will be helpful in separating the relative contribution of behavior and physical transport in larval transport. Drifters that incorporate simple behaviors such as changing buoyancy to achieve vertical migration (larval mimics) may offer a more realistic Lagrangian understanding of potential connectivity.

High resolution larval sampling is limited at the present time, though modification of existing systems (e.g. optical methods) used for small zooplankters may be a good starting point. Currently, the field of view in most optical systems is generally very small, and therefore these systems are hampered by the large volumes of water necessary to resolve low larval concentrations. Since such systems may enable the rapid assessment of finescale larval concentrations, and could also be useful in determining larval behaviors, concerted efforts should be aimed at increasing resolution capabilities over larger fields of view with improved digital technologies. Other possible technologies exist that may enhance rapid, high resolution sampling. For example, fluorescent probes and microarray immuno-assays offer the prospect of near real-time species identification in plankton samples using either ship-board or moored observing systems.

Remote Eulerian methods are more mature, with acoustic Doppler current profilers (ADCP), remote sensing of sea surface temperature, color, and height, among others, offering the means to resolve a variety of space and time scales, with data being increasingly available in near real time. An important tool which is currently gaining in usage is autonomous underwater vehicles (AUV). They provide the opportunity for relatively low cost sampling of hydrographic and velocity fields at a relatively modest cost. Coastal radars, such as OSCAR and CODAR, are important in obtaining well-resolved maps of surface currents continuously.

Modeling of physical and biological systems is rapidly increasing in terms of the spatial and temporal resolution achieved and the complexity of processes involved. Computing capabilities have enabled highly sophisticated ocean circulation models, and the ability

to couple biological and geochemical processes to the circulation models. Methods developed for nesting models, increased computing power and an expanding development of models into various shallow water environments provide opportunities for resolving more realistic transport pathways of larvae. Use of Individual Based Modeling (IBM) approaches also allows better opportunity for accurate parameterization of biological variables required for modeling larval dispersal.

**5.3. Linkage with other programs** – The Population Connectivity initiative is unique but shares some common concerns with other existing programs. For example, cross-shelf transport processes are studied in the Coastal Ocean Processes (CoOP), and the larger problem of ecosystem dynamics is considered in GLOBEC. Genetic techniques will be a shared concern with the NSF Genomic Program, and existing programs within the Office of Naval Research (ONR) on autonomous vehicles and adaptive sampling will be relevant for our programmatic goals. The development of conceptual approaches to population connectivity is relevant to fisheries management, development of Marine Protected Areas and Networks, habitat restoration in a range of environments from kelps and reefs to wetlands, and coral reef conservation. There are many programs in NOAA, EPA, and Non-Governmental Organizations (NGOs), including the World Bank, that would benefit from the anticipated results of this initiative.

Among the most relevant programs is the Coastal Ocean Observing Module of GOOS (the Global Ocean Observing System – see also OCEAN.US). We anticipate that both GOOS and relevant observatories being considered in the Ocean Observatories Initiative (OOI) near selected field sites will be critical for providing larger scale information on the ocean environment, providing far-field boundary conditions for coastal problems and mesoscale eddy fields for island problems. Moreover, such ocean observatories would provide ideal opportunities for interjecting various remote biological samplers, in addition to the physical samplers, into a common framework. **Thus, Population Connectivity represents a very timely opportunity to apply a specific science question to a newly established observing system.**

## 6. Recommendations

Workshop participants recognized the broadly interdisciplinary nature of the research required to address population connectivity. Discussion topics included the limitations that exist in the current model of single or small multi-PI research efforts addressing such complex problems. Small research groups often may be limited in the scope and/or scale of a given

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process under study as well as in the tools being applied. More rapid advancement may well be served by bridging multiple scales and processes with a coordinated research effort. Consequently, an **overall recommendation** was made calling for –

### **Programmatic development focused on Marine Population Connectivity to ensure adequate resources and oversight aimed at:**

**i) Development and Application of Key Technologies** - The nature of marine population connectivity will require a diverse toolbox of techniques applied in an interdisciplinary framework. Many techniques are at the cusp of being developed, others are available but have yet to be applied in manners relevant to assessing the mechanisms and outcome of larval dispersal and population connectivity. Such specific technologies and applications require programmatic support to expedite their development and, thereby, availability for simultaneous application in multi-pronged research efforts.

**ii) Integration of Population Connectivity Science Issues into Planning and Implementation of Ocean Observing Systems and Observatories** – The development of ocean and coastal observing capabilities is an important component in enabling long-term studies of population connectivity across a variety of marine environments. Observing systems will provide a large scale framework to examine the inter-annual variability of connectivity as it relates to known climate signals such as El Niño and the North Atlantic Oscillation. Because of the sensitivity of advection and dispersion to both large scale signals such as wind stress anomalies as well as small scale signals such as modulation of internal tides, we advocate the inclusion of oceanographic instrumentation which is capable of resolving transport processes as well as relevant biological sensors such as optical plankton recorders.

Observatories will also play a fundamental role in defining and quantifying the processes determining population connectivity. As such, we recommend the incorporation of connectivity issues into the planning and development of ocean observatories. We advocate the development of re-locatable observatories suggested by the Coastal Ocean Processes (CoOP) program. Because the testing of specific hypothesis about connectivity may involve a variety of possible environments such as estuaries, broad shelves, and islands, we encourage the development of systems which can be deployed in a range of environments for ecologically relevant time scales (e.g. 1-3 months).

**iii) Application of multiple techniques from several disciplines simultaneously** - Resolving the scope and mechanisms involved in population connectivity will

require the simultaneous application of a number of biological and physical oceanographic techniques over a range of spatio-temporal scales. For instance, determining natal origins of recently-settled larvae using artificial tags in otoliths could be used to estimate a connectivity ( $P_{ij}$ ) matrix for a marine fish metapopulation at one place in time. These data could also be used, however, to test a coupled bio-physical model that would have more general application, providing sufficient physical information to adequately parameterize the coupled model was collected during the tagging experiment. Similarly, high resolution ichthyoplankton sampling immediately after egg release, perhaps directed by real-time assimilation of hydrodynamic data, would assist with the recovery of marked individuals after settlement and allow for a direct assessment of the behavioral component of the bio-physical model. It is unlikely, based on the cumulative experiences of researchers to date, that any of these approaches in isolation will lead to significant advancement in our understanding of larval dispersal. However, an integrated research program combining multiple biological and physical techniques across relevant scales has the potential to revolutionize our ability to describe and model population connectivity in marine systems.

Traditionally, the use of research vessels requires months to years of anticipated planning. On the other hand, resolving larval transport by event-driven phenomena will require the availability of sampling platforms with very short notice. Use of research vessels for adaptive sampling will require new models of usage of the oceanographic fleet.

A truly interdisciplinary, multi-investigator research effort will necessarily involve large teams and considerable resources. Limits to our resolution of population connectivity have been, in part, due to limited resources restricting the size and scope of research teams. Programmatic support is therefore required to ensure substantial commitment and participation across multiple disciplines in well-coordinated, interdisciplinary studies.

**iv) Transfer of information – fostering cross-training and collaboration** – The determination of population connectivity and its incorporation into resource management practices requires bringing together expertise that includes ecology, genetics, physical oceanography, fluid dynamics, applied mathematics, computer science, policy and management. To achieve the integration of disciplines, support is recommended at two levels:

- In the short term, cross-training is recommended in the form of graduate and post-doctoral traineeships, intensive workshops, summer courses and symposia. Programs including UCAR, NCAR, and NCEAS should be considered in the structuring of intensive courses

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and workshops to allow for formal approaches to be developed in this technology transfer.

- In the longer term, we recommend the creation of a **Center for Integrative Marine Ecology (CIMEC)**. In the next five years, integration of observations and modeling in marine environments will be elevated to levels that will revolutionize the way we view the coastal ocean. Observations will be available in near-real time for many coastal regions and models. These will provide information in space and time we have never seen. To take advantage of this information systematically and use it to answer longstanding questions in ecology, conservation biology and

resource management, the Center would provide a site where access to this information is provided. It would bring together academic, government and private sectors with the goal of developing quantitative approaches to the conservation and sustainable management of marine ecosystems based on these observational and modeling products. In addition to a core staff, the Center would support leading experts (e.g., on short leaves from their institutions) of the various disciplines to come together periodically to conduct basic research on marine ecology and resource management, as well as to run workshops and dedicated courses.

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## Appendix I – Workshop Agenda

### WORKSHOP ON POPULATION CONNECTIVITY IN MARINE SYSTEMS

**Science goal:** To provide a mechanistic understanding of larval dispersal trajectories of marine organisms, and to develop a predictive theory of population connectivity in marine systems.

**Background:** A central goal of marine ecology is to achieve a mechanistic understanding of the factors regulating the abundance and distribution of marine populations. With such an understanding, it should be possible to generate theory capable of predicting the effects of changes in physical and biological parameters on the dynamics of these populations. A critical component of the above goal is to quantify rates of exchange, or connectivity, among subpopulations of marine organisms (OEUVRE, 1998). Theoretical studies suggest that these linkages play a fundamental role in local and metapopulation dynamics, community structure, genetic diversity, and the resiliency of populations to human exploitation (Fogarty, 1998). We have, however, little more than a rudimentary understanding of the spatial scales over which marine populations are connected by larval dispersal. This lack of knowledge represents a fundamental obstacle to any 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 fisheries scientists to evaluate the design and potential benefits of novel management strategies such as marine protected areas (MPAs).

The magnitude and spatial extent of larval dispersal in marine systems has traditionally been inferred from the pelagic duration of the larval dispersive stage, from the calculated trajectories of passive particles by low-frequency currents, or from analyses of variation in mitochondrial or nuclear genomes. Observations of pelagic larval durations in many marine species of weeks to years, coupled with predicted advection of passive particles by one-way low-frequency currents, imply that long distance dispersal among subpopulations may be pervasive (Roberts, 1997). A number of studies documenting genetic homogeneity over regional to basin-wide spatial scales provide further support for the existence of long-distance dispersal (Ward et al., 1994). However, more recent research and careful reconsideration of the evidence suggests this perception is likely inaccurate, particularly over time scales of ecological relevance.

New hyper-variable nuclear DNA assays have found genetic differentiation among subpopulations of marine fish and invertebrates that were not detected by earlier, less sensitive, DNA analyses (e.g. Pogson et al., 2001; Wirth and Bernatchez, 2001). Novel

marking approaches have similarly demonstrated the potential for local retention and recruitment of reef fish larvae with pelagic larval durations of several weeks (Jones et al., 1999) to months (Swearer et al., 1999). Estimates of larval dispersal using advection/diffusion models with realistic mortality terms and vertical positioning behavior show more restricted larval dispersal than would be predicted from one-way oceanic currents acting on passive particles (Cowen et al, 2000), and flows unique to the nearshore may diminish large-scale larval dispersal. Taken together, these studies provide intriguing, albeit incomplete, evidence that subpopulations of marine organisms may be semi-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 numerical predictions of specific natural or human impacts on marine populations.

Ultimately, patterns of connectivity among subpopulations of marine organisms are determined by interactions between biological (life history characteristics and larval behavior) and physical processes (advection and diffusion). Thus, there is a clear need for an interdisciplinary effort to address this issue and the consequential need for programmatic funding in support of this effort.

**Justification of Question:** A recent study (OEUVRE, 1998) identified marine population connectivity as a key question in biological oceanography – “Over what spatial scales are marine populations connected via dispersal of early life stages?” The report noted that the inability to accurately predict dispersal makes it impossible to determine the effect of climate change and/or human exploitation on marine ecosystems. More specifically, the report identifies 5 objectives that could be addressed with adequate information on population connectivity.

- *Population and community ecology: Determine kinds and strengths of interspecific interactions in which open versus closed populations engage.*
- *Evolution: Compare degrees of isolation with rates of genetic divergence.*
- *Biogeography: Evaluate the extent to which range limits are set by barriers to dispersal rather than physical tolerances of adults*
- *Management, conservation and biodiversity: Evaluate the efficacy of extant reserves as determined by regional dispersal patterns*
- *Dynamics of infectious diseases: Evaluate the role of linkages in the epidemiology of diseases.*

The scope of the question and its associated implications is clearly far reaching. It bears on both a fundamental understanding of marine ecological processes and direct application of critical human and environmental issues.

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**Justification of Approach:** At issue is the basic question as to what extent population connectivity in marine organisms is constrained by various biological and physical processes, acting primarily on larval dispersal. Multiple factors and processes are operating at different temporal and spatial scales resulting in a complex problem. Resolution of this issue has been limited by the spatial and temporal scales of the problem, rendering the single investigator approach ineffectual. Clearly, the problem is interdisciplinary, requiring all relevant disciplines be involved in the planning to ensure compatibility of spatial and temporal scales in sampling strategies and model development.

A predictive model of connectivity will require both empirical estimates of larval exchange among subpopulations and, more generally, a mechanistic understanding of larval dispersal. The prospect of connectivity models also raises significant questions for physical oceanographers, given that hydrodynamic processes undoubtedly play a dominant role in larval dispersal. Alongshore flows are generally more energetic and spatially coherent than cross-shelf flows, and have been the subject of considerable study by the physical oceanographic community. Cross-shelf flows are less well understood, but are likely more important because cross-shore gradients in ecological variables are stronger than the corresponding alongshore gradients (e.g. Mullin, 1993), and because coherence length scales of cross-shelf flows are more closely coupled with that of realized larval dispersal. For instance, particle exchange in the cross-shelf dimension may be generated by alongshore flow instabilities, steered by topographic features, and dominated by transient events (Pineda, 1991; Gawarkiewicz *et al.*, 1996). These observations are in accord with data from researchers studying larval supply to benthic marine habitats, where consistent spatial patterns of recruitment are superimposed on large, episodic recruitment events. Larvae of many marine species also cross the boundary between open ocean and coastal waters regularly, interjecting multiple scales of physical processes that ultimately contribute to larval transport.

A final complication for both physicists and biologists studying dispersal is that larvae are ultimately delivered to benthic habitats by nearshore flows in very shallow water. Little is known of the dynamics of such flows, and how meso- and large-scale flows modulate them. For example, when episodic larval transport is correlated with the occurrence of meso- or large-scale hydrodynamic events, it is not clear if the larval transport is driven by the large-scale forcing, or by the modulation of nearshore flows by these larger events.

Overall, development of a program to address this highly complex problem, operating over multiple spatio-temporal scales, must:

- Resolve the fundamental physical and biological questions to be addressed, and identify the appropriate spatio-temporal scales of interest.
- Incorporate bio-physical measurements and integrate coupled bio-physical models over the same spatial and temporal scales.
- Take advantage of recent methodological developments, including geochemical tracers and genetic markers.
- Highlight processes capable of explaining and ultimately predicting observed patterns of connectivity among subpopulations.
- Evaluate the ecological, evolutionary, and applied implications of generalized models of population connectivity in the marine environment.

**Workshop Goals:** Considering the significance of this problem and the obvious need for an integrated, interdisciplinary approach, a workshop is proposed to:

- 1) Develop an appropriate Science Action Plan, and
- 2) Estimate resource needs to successfully execute this plan.

The proposed workshop will draw scientists from across the broad biological and physical oceanographic community, with additional representation, as needed, from other disciplines, especially those capable of providing unique methodologies applicable to the resolution of this problem.

**By developing an appropriate Science Action Plan through consultation of scientists across multiple disciplines, the requisite interdisciplinary approach can be achieved.**

**Plan of Action:** There are two phases to this effort, the workshop itself and the production of a written product based on the workshop discussions.

The workshop will be structured as follows: a combination of plenary and break-out groups will be utilized. Break-out groups (total of 4) will be composed of a mixture of personnel across disciplines, with each group discussing the same group of questions (1-6, see below). Opportunity for cross-fertilization of ideas will be available during Plenary sessions wherein each group will present a brief overview of their discussions. After all six questions are addressed by the groups, each group will spend an afternoon preparing a final report outlining their conclusions and ideas for each of the questions in preparation for presenting at the final plenary (and providing a summary document by the end of the workshop).

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## Primary Discussion Questions:

1. What are the fundamental physical and biological questions to be addressed? What are the appropriate spatio-temporal scales of interest?
2. What research approaches are required to definitively address these primary research questions?
3. What are the necessary model requirements for synthesis of component biological and physical processes critical to determination of population connectivity?
4. Is there need for development of new research methods and/or approaches to adequately address these research questions?
5. What are the attributes of ideal model systems for addressing these issues? What are the minimum number of model systems required to adequately test these questions across a diversity of habitats, life histories, etc.?
6. What resources are required to address the science goals?

## Proposed Schedule:

Day 1 – Plenary session

AM Introductions  
Several Keynote presentations  
Charge to group –  
Develop of a Science Action Plan  
Research Priorities – Questions  
Research Methodologies  
Study Systems  
Open Discussion of Charge, basic issues

PM Break-out groups – Question 1  
Break-out groups – Question 2

Day 2 –

AM Plenary – review of group findings on Questions 1-2  
Break-out groups – Question 3

PM Break-out groups – Question 4  
Plenary – review of group findings on Questions 3-4

Day 3 –

AM Break-out groups – Question 5  
Break-out groups – Question 6

PM Plenary – review of Questions 5-6  
Plenary - Discussion of final writing tasks/format/timelines  
Break-out groups – Preparation of report

**Post Workshop** – Writing will involve synthesizing of the 4 break-out group reports, coupled with incorporation of plenary discussion points. This task will be headed by the workshop organizers, with the draft document being circulated to the entire workshop group for final comments. Final product will be disseminated to NSF for review/comment then, once those comments are incorporated, it will be available for dissemination to the broader community via NSF.

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## MARINE POPULATION CONNECTIVITY

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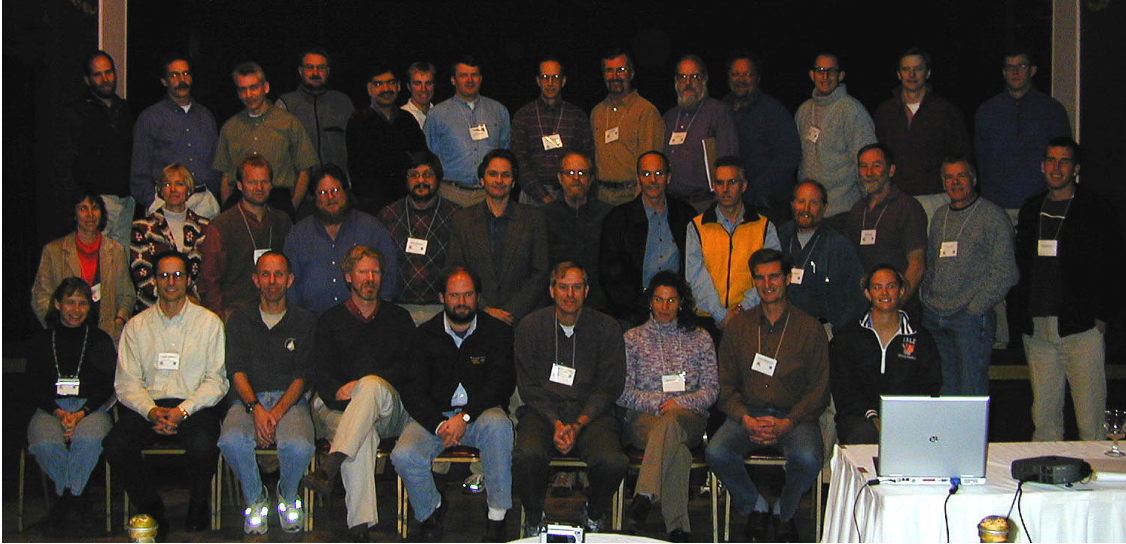
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## MARINE POPULATION CONNECTIVITY

### Group Photos



Conference Venue – The Historic Strater Hotel, Durango Colorado



Group Visit to Mesa Verde National Park