Proposal for a SCOR Working Group to Investigate
Physical and Biological Determinants of Population Connectivity:
Are Perceived Temperate-Tropical Differences Real?

Abstract
The proposed working group, co-chaired by RR Warner and JM Leis, will address the perceived vs. real differences in connectivity of marine metapopulations through larval dispersal in temperate and tropical environments. Space-based management of coastal oceans, including no-take marine reserves, is being developed worldwide. Proper design of marine reserve networks depends on knowing the extent to which the changes inside a protected community are reflected in the connections to other communities (e.g., supplying larvae to fished areas, or connecting to other reserves in a network). There are few differences between temperate vs. tropical areas in the positive response within reserves to protection, but at this point we do not know if there are fundamental differences in connectivity associated with different coastal environments. Managers and designers are unsure if lessons learned about connectivity in one realm are applicable to another. The working group will establish the critical determinants of geographical variation in connectivity, with an aim of providing clear guidelines for spatial design and management.

There are a number of reasons to expect that the scale and processes of connectivity might differ geographically; some arise from contrasts in species composition and community structure, some from temperature influences on physiology and development, and others from differences in physical processes. We will explore these perceived differences to determine which are real, which may be due to the different perceptions, perspectives, and research agendas of those working in the different environments, and which require further research. The working group will bring together scientists with expertise in marine community ecology, conservation genetics, larval biology, physical oceanography, and fisheries to consider the critical factors affecting geographical variation in connectivity.

Many of the factors that may affect the scale and processes of connectivity on a geographical basis are also projected to be themselves affected by global environmental change. Therefore, we will use the findings of this working group to explore how connectivity might change over time in any particular geographical area due to climate change.

In addition to a major synthetic review, the working group will produce a practical guide to the factors that might affect connectivity in marine systems, with special attention paid to how these factors might vary on a geographic basis or over decades of environmental change. The second meeting of the group will integrate our findings into marine spatial planning criteria, with explicit acknowledgement that a single-minded approach is simply inappropriate for places as complex as the coastal ocean.

Background and Rationale
Marine spatial planning generates opposition from some stakeholders whose objections usually focus on the science behind marine reserve planning. Even when the science is sound, some claim that evidence gathered from one geographic area (say, temperate coastal waters) is not applicable to geographically distinct areas (such as coral reefs). The extent to which these are valid objections is unclear. For example, it has been suggested that the responses of organisms to protection in reserves may differ between temperate and tropical areas (Laurel and Bradbury, 2006). In contrast, Lester et al. (2009) demonstrated that temperate and tropical communities responded similarly to protection.

Most marine organisms have a pelagic propagule stage that poses a further challenge to spatial planning. Although the positive demographic responses of marine organisms to protection inside reserves are clear, we know much less about the fate of the increased
reproduction that occurs inside of reserves. This question is critical, because it addresses both the service function of reserves (e.g., export of larvae to fished areas) and the design of reserves (e.g., networks connected through larval exchange; Warner and Cowen, 2002; Sale et al., 2005). Evidence is accumulating about the extent of larval export from reserves (Pelc et al., 2010), and the degree to which larvae may be able to influence their settlement location (Leis, 2007, 2010). However, at this point we have little ability to respond to the suggestion that connectivity between marine populations might vary geographically (e.g., as a function of temperature or underlying demography; Laurel and Bradbury, 2006; O'Connor et al., 2006). As estimates of connectivity and dispersal are important criteria in marine spatial planning (Botsford et al., 2003; Roberts et al., 2003), this limits the confidence of designers and managers to apply general criteria to local problems. This working group will examine and evaluate the potential importance of geographically varying physical and biological factors in affecting dispersal and connectivity in coastal marine environments, and will produce clear guidelines for the practical application of our findings.

A recent symposium convened by Leis and Warner on this theme (Larval Fish Conference, 2009) confirmed this is a problem of general interest, particularly to managers. A SCOR working group is the ideal vehicle to complete this process. Connectivity demands a multi-disciplinary approach, and because we seek to examine regional differences, and must involve workers from different perspectives and with different goals, a SCOR working group is the best way to go. Workers and funding agencies have tended to focus on their own discipline or region, often both, but the question demands a broader, more integrated approach. We have identified scientists whose depth of knowledge and strong interactive ability make them ideal participants in an SCOR working group setting. Two advantages accrue from developing a working group out of a symposium: 1st, many of the data required to address the problem have already been organized, allowing us to work efficiently; 2nd, we are much more aware of critical information gaps.

On the biological side, information on connectivity comes from studies in genetics, tagging, otoliths, larval biology, oceanographic sampling, and physiology (Leis et al 2011). Data are rather sparse and the methods used vary from study to study. On the physical side, data from drifters, oceanographic models, and direct or remote measurements are more standardized, but the datasets can be enormous.

**Terms of Reference**

Working group activities will involve review of source-specific information assembled before the first meeting (Step 1 below), consideration the possible underlying causes for geographic variation (Step 2), publication of a synthetic review, including identification of research priorities (Step 3), and publication of specific guidelines for spatial planning (Step 4). Co-chairs Warner and Leis have track records of successful delivery of important 'group publications', including the much cited 'Open Populations' issue of Bull. Mar. Sci. (Warner & Cowen 2002), and Leis' larval-fish books (the most recent is Leis and Carson-Ewart 2004).

1. **Assemble geographically specific information on the scale of connectivity and dispersal arising from the following sources:**
   - Genetics
   - Recruitment patterns resulting from isolated sources
   - Marking of internal hard structures/recruit recapture
   - Naturally occurring elemental markers in internal hard structures/recruit recapture
   - Oceanographic sampling of larvae
   - Circulation modeling (tuned to species characteristics and latitudinal oceanographic variables, eg, thermocline depth, Coriolis force)
   - Direct or remote measurements of current patterns
2. Is there evidence of geographic variation in these estimates of connectivity? If so, ask two questions of the data:

**2A. Might the geographic differences arise from differing methodologies/research targets?** Listed below are some methodologies/research targets that may have a systematic tendency to influence the outcomes of a connectivity study, and may also have a geographic bias. In each case, the methodology/research target listed first tends to be associated with tropical studies, and the second with temperate, but fortunately there are many exceptions.

- Larval fish biology: Academic ecologists vs Agency fishery biologists
- Scale of study: Micro to mesoscale vs Meso to macroscale
- Study Species: Smaller, site-attached, non-exploited vs Larger pelagic/migratory, exploited species
- Research focus (Cowen & Sponaugle, 1997): variability in connectivity due to fluctuations in: Dispersal/retention vs Food availability
- Life-history styles – do they differ with latitude?
  - Anadromy – is it more important in temperate areas?
  - Spawning aggregations – are they more important in the tropics
- Definitions of “connectedness”: Demographic (input affects local population dynamics) vs Genetic (input detectable in local genetics)

**2B. If the differences are real, what are the underlying causes for geographic variation?** The real-world phenomena listed below could vary geographically and could have a direct or indirect effect on dispersal and connectivity. Characteristics that could have an inherent correlation with latitude are marked with an asterisk (*). In some cases, for example larval swimming speed, there is empirical support for geographic differences, but for most items, support is theoretical to equivocal, and requires further investigation.

- **Biological**
  - Species assemblages and characteristics (Leis, 2007, 2010)
    - Larval swimming ability
    - Pelagic larval duration
    - Larval size and survival
  - Habitat distributions
  - Temperature-related physiological processes*
    - Swimming speed
    - Developmental rate
- **Physical**
  - Current and wind velocities*
  - Mesoscale eddies* (Siegel et al., 2008)
  - Coriolis force*
  - Upwelling*
    - Effects on retention
    - Effects on productivity
  - Depth of mixed layer*
  - Viscosity of seawater*
  - Bathymetry (steered flows)
  - Geomorphology – Islands and capes (retention in wakes, discontinuous habitat)
3. What is the relative importance of those factors that appear to be affecting geographic variation in connectivity? The product will be a major synthetic review of the causes and consequences of geographic variation in dispersal and connectivity: an important section will be an identification of knowledge gaps and research priorities.

4. Given the important factors affecting geographic variation in connectivity, how can we incorporate this knowledge into criteria and guidelines for marine spatial planning? In our second meeting, we will convene with spatial planning experts and managers to produce a straightforward set of guidelines that incorporate considerations of connectivity into local planning efforts.

**Timetable of activities, products, and benefits**

We propose to meet only twice, but for five days each time. This will be more efficient, reduce the carbon footprint of the project, and will help the group finish its work more quickly. Because of the longer meeting times, the group will need the full amount normally budgeted for a SCOR working group. If this is not acceptable to SCOR, we can rearrange the timing of our tasks to make it possible to meet three times in three years.

1. **1st half of 2012:** Detailed instructions sent to workshop participants with expertise in particular data sources (see Step 1, above). Each participant assembles information on the scale of connectivity and dispersal, paying particular attention to geographical variation.

2. **Meeting one, TBA, possibly Sept 2012, 5 days:** Terms of reference 1-3.
   1. (Plenary) Receive reports of geographical variation (or lack thereof) in connectivity and dispersal based on different data sources.
   2. (Subgroups) In smaller, focused groups, resolve:
      (a) whether differences actually exist, or are more a function of methodology;
      (b) if differences exist, identify causes – is it inherent in latitude, or a function of underlying species composition, bathymetry/geomorphology, etc.?
      (c) given the differences, how great an effect will these factors actually have on connectivity?
   3. (Plenary) Entire working group reviews the subgroup reports and undertakes an initial ranking exercise to identify the most important factors that might affect connectivity on a geographic basis. This is not intended to give a simple answer as to whether connectivity might differ between tropical and temperate regions, but rather to assemble a list of the important factors to consider when estimating or modeling connectivity in a particular region.

3. **Date TBA: Publication of a synthetic review of the important factors affecting geographic variation in connectivity and dispersal.** This will include a formal comparison to explore the relative importance of these factors.

4. **Meeting two, date TBA late 2013/early 2014 (5 days):** Terms of reference 1-4.

   This meeting will consist of a subset of the participants from the first meeting. For the 1st 3 days, we will produce a working draft of the synthetic review. For the last 2 days, we will meet with a group of experts in marine spatial planning design and implementation. We will use our results to modify existing design criteria for marine spatial planning to take into account factors affecting connectivity that arise from community composition and physical setting of the areas under consideration. While these factors may often reflect a tropical vs. temperate setting, our detailed approach will identify important factors on a case-by-case basis, and will include those factors likely to be altered by global environmental change. These guidelines will be made available in downloadable booklet form, with an intended audience of managers, planners, stakeholders, non-governmental organizations, and the general public.

**Meeting Location**

Connectivity is a multidisciplinary problem, so, our working group members come from a variety of disciplines. As a result, there is no conference that a high proportion of the members would be likely to attend and to which we can append our meetings. We therefore propose to hold the meetings at the University of California at Santa Barbara (where co-chair Warner is based: therefore, he does not require SCOR funding to participate), which is
relatively centrally located to the working group members. The Marine Science Institute at USCB will host the meetings, and it is likely the working group will receive some support from the National Center for Ecological Analysis and Synthesis based at UCSB.

**Working Group Proposed Composition**

**Full Members**

<table>
<thead>
<tr>
<th>Name</th>
<th>Country</th>
<th>Expertise</th>
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<tbody>
<tr>
<td>Jeffrey Leis (co-Chair)</td>
<td>Australia</td>
<td>Larval-fish biology</td>
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<tr>
<td>Satoshi Mitarai</td>
<td>Japan</td>
<td>Marine biophysics</td>
</tr>
<tr>
<td>Ian Bradbury</td>
<td>Canada</td>
<td>Fishery &amp; conservation genetics</td>
</tr>
<tr>
<td>Emanuel Gonçalves</td>
<td>Portugal</td>
<td>Marine community ecology, behaviour</td>
</tr>
<tr>
<td>Jean-Olivier Irisson</td>
<td>France</td>
<td>Biological oceanography, dispersal modeling</td>
</tr>
<tr>
<td>Trond Kristiansen</td>
<td>Norway</td>
<td>Physical oceanography, biophysical processes</td>
</tr>
<tr>
<td>Elizabeth North</td>
<td>USA</td>
<td>Larval biology and dispersal</td>
</tr>
<tr>
<td>Mary O’Connor</td>
<td>Canada</td>
<td>Physiology of marine animals</td>
</tr>
<tr>
<td>George Branch</td>
<td>South Africa</td>
<td>Marine ecology and biogeography</td>
</tr>
<tr>
<td>Yvonne Sadovy</td>
<td>China</td>
<td>Reproductive physiology, spawning behaviour</td>
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**Full Member not requiring SCOR funding**

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<thead>
<tr>
<th>Name</th>
<th>Country</th>
<th>Expertise</th>
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<tbody>
<tr>
<td>Robert Warner (co-Chair)</td>
<td>USA</td>
<td>Marine ecology and demography</td>
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</tbody>
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**Associate Members**

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<tr>
<th>Name</th>
<th>Country</th>
<th>Expertise</th>
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<tbody>
<tr>
<td>Jennifer Caselle</td>
<td>USA</td>
<td>Marine ecology, population connectivity</td>
</tr>
<tr>
<td>Steven Swearer</td>
<td>Australia</td>
<td>Otolith microchemistry and dispersal</td>
</tr>
<tr>
<td>Robert Cowen</td>
<td>USA</td>
<td>Biological oceanography, larval dispersal</td>
</tr>
<tr>
<td>Paul Barber</td>
<td>USA</td>
<td>Marine phylogeography and genetics</td>
</tr>
<tr>
<td>Andrew Bakun</td>
<td>USA</td>
<td>Fisheries, biological oceanography</td>
</tr>
<tr>
<td>Ivan Nagelkerken</td>
<td>Netherlands</td>
<td>Marine ecology, population connectivity</td>
</tr>
<tr>
<td>Alan Shanks</td>
<td>USA</td>
<td>Larval invertebrate biology</td>
</tr>
<tr>
<td>Jon Hare</td>
<td>USA</td>
<td>Fisheries, larval biology</td>
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</tbody>
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**Literature cited**