Seamount Genetics: Enabling the Understanding of Biodiversity, Connectivity, Evolution, and Endemism

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International Seabed Authority
Workshop on Deep Seabed Cobalt-rich crusts and the Diversity and Distribution Patterns of Seamount Fauna.
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Physical Oceanographic Processes

Important parameters affecting the flow around seamounts:

- Coriolis parameter (geographic location)
- Horizontal steady forces
- Stratification conditions
- Seamount geometry

Localized upwelling interacts with steady surface flows form anti-cyclonic eddies or Taylor columns and caps- these can aggregate mid-water fauna and larvae above a seamount; also inhibit the dispersal of larvae away from source population.

Ex. Great Meteor Seamount (Dower and Mackas 1996)

In contrast, populations can experience enhanced connectivity and gene flow via rectified flows along seamount chains, like the Northwest Hawaiian Seamount chain

Seamounts are a great place to look at the interaction of physical and biological processes- ideal laboratories to study isolation and speciation
Critical Questions Well-Suited to Genetic Approaches

- What are the key processes controlling seamount diversity, population connectivity, evolution, and endemism on seamounts?

- To what degree are seamount communities isolated, regulated by physical processes (extrinsic) vs. reproduction, life-history strategies (intrinsic)?

- What is the role of seamounts in creating and maintaining marine biodiversity? Are seamounts globally significant centers of speciation?

- Do seamount habitats provide stepping-stones for dispersal between distant populations?

- How does habitat loss (e.g., due to fisheries and mining activities) affect genetic diversity and the maintenance of species through gene flow?
Genetic Approaches to Assess Diversity, Connectivity and Evolution of Seamount Fauna

Molecular systematics
• address questions of taxonomic boundaries, identification and determination via comparison of morphological characters with genetic markers (DNA barcoding & identifying species-specific larvae)

Phylogenetics
• address questions of inter-specific/generic/familial relatedness; formation and radiation of diversity; speciation events; evolution of ecological adaptations of species and groups (interspecific approach)

Population genetics (includes phylogeography or historical population migrations)
• seeks to understand the history, formation, and persistence of the factors that inhibit, promote, and control dispersal; mechanisms of larval dispersal; identification of dispersal barriers, biogeographic boundaries, and stock structure for conservation and management (intraspecific approach)

“Community genetics”
• assessing host and associate relationships; co-evolution among species and populations; including congruence of dispersal patterns and mechanisms
Genetic Tools for Inferring Gene Flow and Isolation

• **Allozymes**
  – multiple, independent, codominant loci; relatively easy; low cost
  – not at the DNA level, subject to selection, state characters

• **Mitochondrial DNA**
  – relatively easy; maternally inherited; effectively haploid; non-recombining; modest cost; amenable to genealogical analysis
  – *Low variability in deep-water corals provides little utility*

• **Nuclear DNA sequences**
  – amenable to genealogical analysis;
  – diploid; recombination; start-up time may be considerable

• **AFLPs (Amplified Fragment Length Polymorphisms)**
  – nuclear markers; can get 100s of loci relatively easily
  – dominance; recombination; state characters; start-up time is considerable; mutation models not available

• **DNA microsatellites (and Expressed Sequence Tags)**
  – nuclear; can get dozens of loci relatively easily
  – recombination; state characters; start-up time and cost$ is great; problem with homoplasy in geographical studies; mutation must be taken into account in gene flow models
Sampled Seamounts

~250 sampled, out of >50,000 (>1000 m), “millions” (<1000 m)

(stolen from Malcolm Clark)
Published Seamount Genetic Studies of Microbes and Macrofauna

No. Publications

Year

Macrobiology
Microbiology
Genetics of Seamount-Related Fauna
Selected Phylogenetic and Systematic Examples:

• “What are the deeper evolutionary (and systematic) relationships among the Anthozoa?”
  Berntson et al., *Molecular Phylogenetics and Evolution* (1999) -18S rRNA nuclear gene sequences

• “What are the primary phylogenetic relationships within the Octocorallia?”
  Insertions-deletions (INDELS) and ribosomal RNA secondary structure

• “What are the evolutionary relationships among scleractinian corals? Are they aligned with taxonomic classifications?”
  16S rDNA gene sequences

• “Do combined molecular and morphological systematics resolve difficulties in anthozoan classification?”
  Won et al., *Coral Reefs* (2001) -18S rRNA nuclear gene sequences and 41 morphological characters
Hydrothermal vent and seep-endemic shrimp

Vent and seep siboglinid tubeworms

Compiled from:
Black et al. (1997) Marine Biology 130: 141-149
Halanych et al. (2001) Biological Bulletin 201: 65-75
McMullin et al. (2003) Symbiosis 34: 1-41
<table>
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<tr>
<th>Number of Species</th>
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<th>Number deeper than 50 m</th>
<th>Total</th>
<th>Deep Water</th>
<th>Molecular Approach</th>
<th>Comments</th>
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<td>Scleractinia</td>
<td>1482</td>
<td>615 (41.5%)</td>
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<td>3.5</td>
<td>1</td>
<td>2 students, 1 admin.</td>
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<td>Zoanthidea</td>
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<td>1</td>
<td>Gerardia, 1 student</td>
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<td>169 (75%)</td>
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<td>Octocoralllia</td>
<td>*2850</td>
<td>2140 (75%)</td>
<td>16</td>
<td>6.5</td>
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<td>220 (89%)</td>
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<td>0</td>
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<td>Milleporidae</td>
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<td>0</td>
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<tr>
<td><strong>TOTAL</strong></td>
<td><strong>4825</strong></td>
<td><strong>3145 (65.2%)</strong></td>
<td><strong>33</strong></td>
<td><strong>15</strong></td>
<td><strong>10</strong></td>
<td>8 students, 2 retired, 1 admin.</td>
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* estimate from S. Cairns
Morphology of the microscopic sclerites (the primary character used in octocorallian taxonomy) did not distinguish colonies that had divergent genetic haplotypes, including the most divergent (1.6%).

This suggests that there may be morphologically-cryptic species variation among seamount octocorals and reinforces the observation that octocoral taxonomy and systematics cannot rely solely on morphology of skeletal characters (Sánchez et al. 2003; Wirshing et al. 2005).

**Paramuricea** octocoral (New England Seamounts)

Molecular Systematics - determining diversity

Neighbor-joining phylogram (K2 distance) of *Paramuricea* (Octocorallia) based on 1367 bp of aligned msh1 sequences from 42 individuals (S. France, unpubl. data) showing four haplotypes from the NE Seamounts (S. France, unpublished data)
The Barcode of Life Initiative is an emerging collaborative effort to accelerate acquisition of and access to knowledge of biodiversity using mitochondrial DNA sequences (Cytochrome Oxidase I gene).

The Barcode of Life Data Systems (BOLD) is an online workbench that aids collection, management, analysis, and use of DNA barcodes.

Total Species Barcodes 96,356 (as of this morning)

NO barcode data from Seamounts exists in this database (>200 entries will be submitted by the end of 2006!)
Questions in Seamount-”Related” Coral Genetics
Selected Population Genetic Examples:

• “What is the effect of retention and dispersal of larvae on genetic population structure?”
  mitochondrial Cytochrome Oxidase I sequences

• “Are scleractinian populations in the Atlantic genetically isolated, and if so, to what extent?”
  Le Goff-Vitry and Rogers., In: *Cold Water Coral and Ecosystems* (2005)
  Internal Transcribed Spacer (ITS) 1 and 2 nuclear regional; 10 msatellite markers

• “What are the genetic units of precious coral populations, and are they genetically isolated?”
  Baco and Shank, In: *Cold Water Coral and Ecosystems* (2005)
  6 microsatellite markers
**Amphipods**

*Eurythenes gryllus* from the crest of 3 bathyal seamounts as well as from the summit and base of Horizon Guyot (Bucklin et al., 1987)

*Eurythenes gryllus* up to 15cm length

- high gene flow at similar depths
- no gene flow over a 3800m depth range on Horizon Guyot
Fish (Seamount associated)

Armorhead, *Pseudopentaceros wheeleri*, North Pacific Seamounts (Martin et al., 1992) Mitochondrial DNA, RFLP markers
• Different seamounts do not harbor genetically distinct populations

Blackspot seabream, *Pagellus bogaraveo* N. Atl. & Azores (Stockley et al., 2000), microsatellite markers
• showed little genetic differentiation

Blue-mouth red fish, *Helicolenus dactylopterus* N. Atl. & Azores (Aboim et. al., 2003; 2005) microsatellite and mitochondrial DNA
• showed population expansion after population bottleneck
Hawaiian Precious Corals

Red Coral

Corallium lauuense (regale)

(300 - 550 m)

Pink Coral

Corallium secundum

Population genetics - connectivity & isolation

Baco and Shank, 2005
Hawaiian Precious Corals

- Profitable fishery
- Only one “refuge” in entire Hawaiian chain
- Study of Mediterranean precious corals has shown limited dispersal ability and significant genetic structure between locations
Population genetics - connectivity & isolation

Main Islands

Far NWHI and Northern Populations

Near NWHI and Southern Populations

Corallium lauuense
6 Microsatellite loci
Population genetics - connectivity & isolation

Northwest Hawaiian Islands

Hancock Seamounts
Midway Island
Brooks Banks
Refuge

Far NWHI

Near NWHI

Main Islands

Hawaii

Main Hawaiian Islands

Oahu

Cross Seamount

20°N

25°N

160°W

155°W
Conclusions

• **Pink Coral:**
  Revealed genetic structure within “continuous populations”
  No significant structuring between populations on Oahu
  Some genetic structure between pops on Brooks Banks
  Evidence for isolation by distance
  Heterozygote deficiency (lack of diversity) at one locus

• **Red Coral:**
  Heterozygote deficiency at all sites - inbreeding?
  No evidence for isolation by distance
  Kauai population and Bank 8 population isolated from other populations

  2 sympatric species with different dispersal patterns
Sampled Seamounts

△ = published genetic studies
▲ = ongoing genetic studies
Host-associate systems on the New England and Corner Rise Seamounts

octocoral *Paramuricea*
brittle star *Asteroschema*

scleractinian coral *Lophelia pertusa* & polychaete worm *Eunice*

octocoral *Candidella* & brittle star *Ophioplinthaca* & scaleworm *Gorgoniapolynoe*

black coral *Parantipathes* & chirostylid crab

octocoral *Metallogorgia* & brittle star *Asteroschema*

brittle star *Ophioplinthaca* & *L. pertusa* & *Desmophyllum dianthus*
“Fisheries-related habitat damage” on the Corner Rise Seamounts (North Atlantic)

(A) broken *Paragorgia* branches (~40 cm long) (1450m depth);
(B) broken ground (mainly *Lophelia pertusa* rubble) resulting from heavy trawl gear on Lyman Seamount (1427m depth);
(C) parallel scour marks generated by chain-linked trawl nets on the edge of the summit plateau of Kukenthal Seamount (769m depth); and
(D) a single drag mark, perhaps from a metal weight suspended from the trawl footrope, that has cut through sponge communities (750m depth).

All pictures taken with ROV Hercules (DASS05_NOAA_IFE). (Waller et al., in prep)
Potential Impacts of Exploration and Mining

**Exploration** (mapping, imaging, precision/limited sampling, testing of recovery systems; evaluation of environmental, technical, economic, commercial factors):

Potential Positive Impacts:
- Discovery of new species, adaptations, evolutionary pathways
- Environmental and biological assessments of targeted seamount(s)
- Constraints on models of important integrated processes associated with seamounts

**Exploitation** (commercial recovery of cobalt crust):

Potential Negative Impacts:
- Loss of habitat, prohibiting connectivity and reducing genetic diversity
- Degradation of habitat quality
- Local, regional, or global extinction of endemic or rare taxa
- Decreased diversity (all levels: genetic, species, phylogenetic, habitat)
What Do We Need?

Want to know who is there?

- Tandem molecular and morphological systematic approaches hold the greatest promise for developing classification schemes that reflect evolutionary relationships that provide a framework for understanding the processes creating and maintaining biodiversity.

Want to know if and how seamount populations among Seamounts (chains or “distant” guyots) are connected?

- Measure physical oceanographic flows, habitat availability, rates of colonization, growth, and dispersal in concert with genetic data to understand mechanisms of connectivity and evolution.
What Do We Need?

Want to know what’s maintaining biogeographic boundaries and species’ migration patterns?

• combination of systematic and phylogenetic assessment among taxa is a prerequisite for understanding biogeographic patterns and the dispersion of species over evolutionary time (e.g., across ocean basins or between Smt chains)

Want to know the affects of mining on seamount populations?

• PRE-disturbance genetic characterization of connectivity to neighboring seamounts/habitats- develop conservation targets

• POST-disturbance genetic characterization of connectivity to neighboring seamounts/habitats
What Do We Need?

• to realize we cannot extrapolate dispersal/connectivity results of any taxa or seamount to another. For example, from the South Pacific to the Equatorial Pacific

• to realize that species characterized as having “limited larval dispersal” can travel large oceanic distances (e.g., deep-water clams)

• to realize what an “isolated seamounts” is- can define as “isolated” if the recent exchange of genetic information is not statistically significant (distance ≠ isolation)

• to realize that any plan to assess seamount diversity, endemism, and connectivity should include the integrated use of genetic approaches
USS San Francisco
crashed into 2-km tall uncharted Seamount

- Los Angeles class nuclear submarine ran aground in route from Guam to Brisbane, Australia - 8 January, 2005
- One sailor killed, 115 injured
- Crash depth ~160 m, speed 33 kn, Sonar measured a depth of 2000 m 4 minutes before crash
- 30-hour trip back to Guam, crew managed to keep the sub from sinking
Workshop Goal: to ascertain the potential impact of exploration and mining of deep-sea cobalt-rich ferromanganese crusts on seamount fauna

- assess patterns of diversity and endemism on seamounts and factors that drive these patterns

- identify gaps in current knowledge (encourage collaboration in these areas)

- provide suggestions and recommendations to assist the development of environmental guidelines for the protection of seamount fauna
Muir Seamount
New Zealand species of hydrothermal vent mussels


Molecular Phylogenetics - evolutionary relationships

Bathymodiolus

M. modiolus

0.05

0.05
Gene Flow Models

I. Stepping-Stone Model

II. Island Model

Gene Flow (log scale)

Distance (log scale)
Characteristics of seamount settings important to biology

• chemoautotrophic production present, but lower rates of primary productivity

• no flux of hydrothermal fluids, but sulfides may cap thermal systems and begin to flow once disturbed by mining activities (ODP experiences)

• with macrofaunal invertebrates, possibly some (or many) that are endemic, but much lower biomass; no known examples of symbioses

• habitat duration longer than that of active vents

• degree of isolation similar to that of active vents

• reproduction – relevant conditions different (e.g. habitat longevity, population density, food availability), so potential for different adaptations

• larval transport – plume-generated currents absent
“Bamboo corals”
Family Isididae

Bear Seamount, 1478 m

S.F. Keratoisidinae
Acanella  Gray, 1870
Australisis  Bayer & Stefani, 1987
Caribisis  Bayer & Stefani, 1987
Isidella  Gray, 1857
Keratoisis  Wright, 1869
Lepidisis  Verrill, 1883
Orstomisis  Bayer, 1990
Sclerisis  Studer, 1879

3 additional subfamilies

S. France, unpub. data
**Lepidisis:**

...simple *or branched*, the branches, when present, arising from the horny joints (Verrill 1883)

...*branched* from the nodes or the internodes... (Grant 1976)

“*Unbranched Keratoisidinae*” (Muzik 1978)

**Keratoisis:**

...branch from the internodes, *or are unbranched*... (Grant 1976)


Potential impacts of exploration and mining

“There is no imminent threat to the entire global vent fauna from mining or any other human activity.”

“Concentration of mining activities in areas such as the southwest Pacific back arc spreading centers will, however, produce local and even regional effects on vent organism abundance, to the point where the survival of some species could become an issue.”


“The anticipated consequences of sulphide mining will be the release of toxic elements and, more importantly, of fine particles.”

Scott, S. 2004. Abstract. Workshop for the establishment of environmental baselines at deep seafloor cobalt-rich crusts and deep seabed polymetallic sulphide mine sites in the Area for the purpose of evaluating the likely effects of exploration and exploitation on the marine environment. Kingston, Jamaica
Characteristics of active hydrothermal settings important to biology

Larval transport

Anticyclonic Circulation
Cyclonic Circulation

Sinking Larvae
Vortex Budding and Dispersal of Larvae

Entrained Larvae

from Mullineaux & France
Riftia free-swimming trocophore larvae - 40-day lifespan, plus current meter data suggest larval retention (~100km) within ridge segments on the East Pacific Rise.

(Marsh et al. 2002)
Population Genetic Structure of the Hawaiian Precious Coral, *Corallium secundum*, Based on Microsatellites

Amy Baco
Data required to establish environmental baselines in exploration areas

Standard criteria to be used in environmental assessment

- Characterization of the type of disturbance
- Estimation of the percent loss of [seafloor vent] habitats
- Identification of affected seafloor organisms
- Dose-response characteristics of plume fallout

Baseline information required

- Distribution of habitat within the potentially affected area
  - Species composition and community structure
  - Basic biology of species
Data required to establish environmental baselines in exploration areas

Key data, activities include:

- Detailed maps of the size and distribution of target sulfide deposits as well as of critical or special habitats such as non-target seamounts and the zone likely to be influenced by particle deposition.

- Measurement of the prevailing hydrographic regime and development of particulate fallout models to predict the suspended particulate and depositional gradients generated by mining activity, where critical habitats occur in the exploration area. This should include an assessment of the depositional shadow of specific minerals/metals potentially toxic to marine organisms (e.g., copper).

- Determination of the extent to which the biota of the region is endemic or cosmopolitan (using genetic data).

- Description of habitat through detailed imaging surveys
  - Determination of “intimacy” of host - associate (fauna can’t colonize seamounts if ho
  - Evolution of populations can provide evidence for sources and sink populations - dispersion of species over seamounts.
  - Modelling larve dispersal through physical oceanographic modeling
Data required to establish environmental baselines in exploration areas

Types of baseline data that will assist in assessment of impact of mining activities:

- Microbial diversity, biomass, primary productivity, biogeochemistry
- Taxonomic composition, species richness, diversity, evenness, biomass, abundance of
  - “strategic” sulfide-associated mega-, macro-, meiofaunal communities
  - background communities in areas within the depositional shadow
  - reference communities outside depositional shadow
- Genetic diversity of strategic species of background and sulfide habitats
- Trophic relationships among vertebrates, invertebrates, microbes, and mineral deposits
- Species ranges (can they be found outside the area likely to be impacted by mining) and degree of endemism of microbial, invertebrate taxa in association with sulfide deposits
- Identification of adaptations specialized for polymetallic mineral deposits
- Dose-response parameters especially for background fauna or fauna of critical habitats within the depositional shadow
Summary of Some Key Thoughts and Observations

• the connectivity of seamount fauna among seamounts is essentially unknown, but knowable

• fauna associated with seamounts are potentially of tremendous importance to biotechnology, remediation, and understanding the metabolic menus exploited by life on Earth and potentially elsewhere

• comparison of genetic information among seamount fauna can tell us the systematic (taxonomic) status and evolutionary relationships -important given the current problem dearth of taxonomists to undertake morphological descriptions of species

• baseline biological assessment of seamounts must consider whether neighboring non-mined habitats host same species and connected populations (the key to gene flow is the dispersal of larvae and available habitat)

• importance of reserves or sanctuaries as required in the ISA Draft Regulations cannot be underestimated, especially given our lack of knowledge of the biology of inactive seamounts— but these may not be easy to identify and require careful consideration and definition as to what is acceptable in a given region
seamounts??
Support unique biological