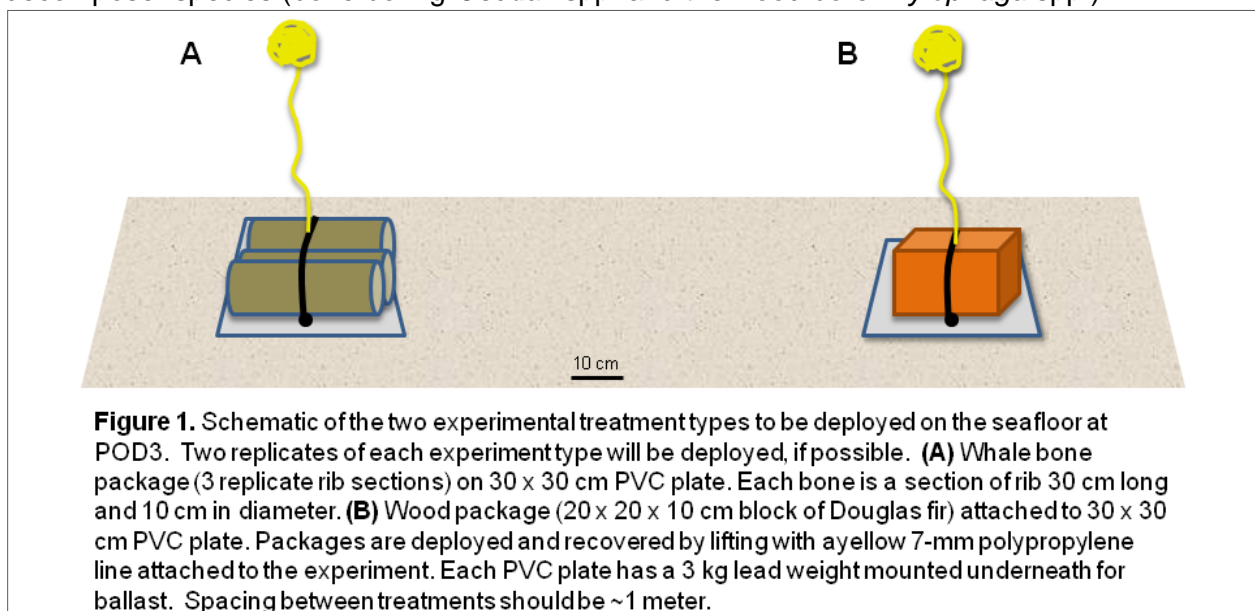


Biodiversity, connectivity and ecosystem function in organic-rich whale-bone and wood-fall habitats in Barkley Canyon

PIs Craig R. Smith¹ and Fabio De Leo²
¹University of Hawaii at Manoa, ²ONC

Background: Organic-rich habitat islands support specialized communities throughout natural ecosystems and often play fundamental roles in maintaining alpha and beta diversity, thus facilitating adaptive radiation and evolutionary novelty. In the deep sea, whale-bone and wood falls occur widely and may contribute fundamentally to biodiversity and evolutionary novelty; nonetheless, large-scale patterns of biodiversity, connectivity and ecosystem function in these organic-rich metacommunities remain essentially unexplored. **We propose to deploy whale bones and wood in Barkley Canyon at ONC POD3 as part of a novel comparative experimental approach, in which bone and wood substrates are being used to evaluate bathymetric, regional and inter-basin variations in biodiversity and connectivity, as well as interactions between biodiversity and ecosystem function, in whale-bone and wood-fall habitats at the deep-sea floor.** The experiments in Barkley Canyon will test fundamental hypotheses concerning biodiversity and biogeography of resource-rich habitats in energy- and oxygen-limited deep-sea environments, and explore the utility of whale-bone and wood falls as model experimental systems to address patterns of connectivity and decomposer function in the deep sea.

General Study Design: Two packages of humpback (*Megaptera novaeangliae*) ribs, and two blocks of Douglas Fir (*Pseudotsuga menziesii*), will be deployed by ROV on the seafloor at 890-m depth in Barkley Canyon, within view of the POD3 Video Camera (Fig. 1). After deployment, video monitoring of the bone/wood packages will occur every three hours for 5 minutes, with a different experimental package monitored during each 3-h interval; thus, each package will be monitored for two 5-minute periods per day. This will allow (1) observation of the nature and rates of faunal colonization by microbial mats, macrofauna and megafauna on each bone/wood package, (2) observations of feeding activities and biotic interactions, including grazing on microbial mats and predation of bone/wood fauna (e.g., crabs preying on *Osedax*), and (3) observations of rates of boring and breakdown of the bone and wood substrates by specialized decomposer species (bone boring *Osedax* spp. and the wood borer *Xylophaga* spp.).



After approximately one year, the experimental packages will be recovered by ROV by placing each package in a separate sealing “biobox” to allow quantitative transfer of wood/bone packages and associated biota (microbial mats, macrofauna and megafauna) to the surface ship for detailed study. Molecular genetic, taxonomic, and functional studies of macrofaunal and microbial assemblages of recovered bone/wood substrates will then be conducted within the framework of our US NSF funded project (*Collaborative Research: Biodiversity, connectivity and ecosystem function in organic-rich whale-bone and wood-fall habitats in the deep sea*, C. R. Smith and K. Halanych, PIs, Project Summary attached), in which similar bone/wood substrates have been deployed at 1500 and 3000 m depths along the Washington-Oregon margin. The Barkley Canyon experiments will allow us to address the following hypotheses:

- 1) *The identity and diversity of dominant bone/wood species differs in the relatively oxygen-poor Barkley Canyon at 890 m from bone/wood fauna at deeper, better oxygenated depths on the Washington-Oregon margin.*
- 2) *The Barkley Canyon site at 890 m has much greater genetic (and species) connectivity with 1500 m deep sites, than with 3000 m deep sites, on the Washington-Oregon margin.*
- 3) *Rates of bone/wood volume loss and faunal biomass growth and production on bone/wood substrates are reduced in the low oxygen (~ 0.3 ml/L) Barkley-Canyon site due to reduced colonization by specialized macrofaunal decomposers (Osedax/Xylophaga).*
- 4) *Total macrofaunal species richness and trophic complexity on bone/wood substrates are reduced in the low-oxygen Barkley Canyon waters compared to deeper, better oxygenated depths on the Washington-Oregon margin.*

Expected Outcomes: We expect our Barkley Canyon bone/wood studies to (1) reveal how bone/wood substrates are colonized and consumed over a broad range of time scales (days to one year) at ~900 m depths on the Canadian margin, (2) elucidate how reduced bottom-water oxygen may influence bone/wood colonization and degradation, (3) provide new insights into the locomotion and feeding activities of specialized bone/wood fauna and generalized deep-sea predators and detritivores, and (4) help to elucidate how population and community connectivity can vary with isolation by depth, distance, and oxygen concentration for specialized and generalized components of the bone/wood biota. These results will yield fundamental insights into processes of colonization, community development and connectivity within organic-rich habitat island systems in the deep sea. We also expect Barkley Canyon experiments to (5) help show how the diversity of ecosystem engineers (bone-eating *Osedax* and wood-eating *Xylophaga*) interacts with the structure and function of whale-bone/wood-fall assemblages, to potentially control such key ecosystem attributes as species richness and rates of bone/wood decomposition. The Barkley-Canyon work will be an important component of the first experimental study of interactions between the diversity of key engineering species and ecosystem function in the deep sea, allowing us to test the generality of models developed in detritus-based terrestrial and freshwater ecosystems in the largest detritus-based ecosystems in the biosphere.

Broader Impacts – Integration of Barkley Canyon Studies into the Friday Harbor Laboratories Summer Program: Real-time video observations and data collection from our bone/wood experiments at POD3 in Barkley Canyon will be integrated into our summer field course at Friday Harbor Laboratories titled *Deep-Sea Biodiversity, Connectivity and Ecosystem Function* (<http://depts.washington.edu/fhl/studentSummer2014.html>). This course, offered to 15

graduate students and advanced undergraduate students from July 21 - Aug 22, 2014, will use our bone/wood experiments (including the Barkley Canyon experiments) as model systems to address fundamental questions concerning biodiversity, connectivity and ecosystem function in the deep sea. The ONC link will provide an extraordinary, novel experience for very talented students to learn to use ONC tools to observe *in situ* processes on bone/wood substrates in the deep sea while working with more traditional preserved material from our deep-sea bone/wood experiments recovered from the WA-OR margin. We anticipate that Dr. De Leo will present lectures and tutorials on ONC Canada, and then lead a field trip from FHL to the ONC facilities in Victoria, BC, to provide extraordinary educational opportunities for the class. We anticipate that new users and enthusiasts for ONC will be developed from this course experience.

CERTIFICATION PAGE

Certification for Authorized Organizational Representative or Individual Applicant:

By signing and submitting this proposal, the Authorized Organizational Representative or Individual Applicant is: (1) certifying that statements made herein are true and complete to the best of his/her knowledge; and (2) agreeing to accept the obligation to comply with NSF award terms and conditions if an award is made as a result of this application. Further, the applicant is hereby providing certifications regarding debarment and suspension, drug-free workplace, lobbying activities (see below), responsible conduct of research, nondiscrimination, and flood hazard insurance (when applicable) as set forth in the NSF Proposal & Award Policies & Procedures Guide, Part I: the Grant Proposal Guide (GPG) (NSF 11-1). Willful provision of false information in this application and its supporting documents or in reports required under an ensuing award is a criminal offense (U. S. Code, Title 18, Section 1001).

Conflict of Interest Certification

In addition, if the applicant institution employs more than fifty persons, by electronically signing the NSF Proposal Cover Sheet, the Authorized Organizational Representative of the applicant institution is certifying that the institution has implemented a written and enforced conflict of interest policy that is consistent with the provisions of the NSF Proposal & Award Policies & Procedures Guide, Part II, Award & Administration Guide (AAG) Chapter IV.A; that to the best of his/her knowledge, all financial disclosures required by that conflict of interest policy have been made; and that all identified conflicts of interest will have been satisfactorily managed, reduced or eliminated prior to the institution's expenditure of any funds under the award, in accordance with the institution's conflict of interest policy. Conflicts which cannot be satisfactorily managed, reduced or eliminated must be disclosed to NSF.

Drug Free Work Place Certification

By electronically signing the NSF Proposal Cover Sheet, the Authorized Organizational Representative or Individual Applicant is providing the Drug Free Work Place Certification contained in Exhibit II-3 of the Grant Proposal Guide.

Debarment and Suspension Certification (If answer "yes", please provide explanation.)

Is the organization or its principals presently debarred, suspended, proposed for debarment, declared ineligible, or voluntarily excluded from covered transactions by any Federal department or agency? Yes No

By electronically signing the NSF Proposal Cover Sheet, the Authorized Organizational Representative or Individual Applicant is providing the Debarment and Suspension Certification contained in Exhibit II-4 of the Grant Proposal Guide.

Certification Regarding Lobbying

The following certification is required for an award of a Federal contract, grant, or cooperative agreement exceeding \$100,000 and for an award of a Federal loan or a commitment providing for the United States to insure or guarantee a loan exceeding \$150,000.

Certification for Contracts, Grants, Loans and Cooperative Agreements

The undersigned certifies, to the best of his or her knowledge and belief, that:

- (1) No federal appropriated funds have been paid or will be paid, by or on behalf of the undersigned, to any person for influencing or attempting to influence an officer or employee of any agency, a Member of Congress, an officer or employee of Congress, or an employee of a Member of Congress in connection with the awarding of any federal contract, the making of any Federal grant, the making of any Federal loan, the entering into of any cooperative agreement, and the extension, continuation, renewal, amendment, or modification of any Federal contract, grant, loan, or cooperative agreement.
- (2) If any funds other than Federal appropriated funds have been paid or will be paid to any person for influencing or attempting to influence an officer or employee of any agency, a Member of Congress, an officer or employee of Congress, or an employee of a Member of Congress in connection with this Federal contract, grant, loan, or cooperative agreement, the undersigned shall complete and submit Standard Form-LLL, "Disclosure of Lobbying Activities," in accordance with its instructions.
- (3) The undersigned shall require that the language of this certification be included in the award documents for all subawards at all tiers including subcontracts, subgrants, and contracts under grants, loans, and cooperative agreements and that all subrecipients shall certify and disclose accordingly.

This certification is a material representation of fact upon which reliance was placed when this transaction was made or entered into. Submission of this certification is a prerequisite for making or entering into this transaction imposed by section 1352, Title 31, U.S. Code. Any person who fails to file the required certification shall be subject to a civil penalty of not less than \$10,000 and not more than \$100,000 for each such failure.

Certification Regarding Nondiscrimination

By electronically signing the NSF Proposal Cover Sheet, the Authorized Organizational Representative is providing the Certification Regarding Nondiscrimination contained in Exhibit II-6 of the Grant Proposal Guide.

Certification Regarding Flood Hazard Insurance

Two sections of the National Flood Insurance Act of 1968 (42 USC §4012a and §4106) bar Federal agencies from giving financial assistance for acquisition or construction purposes in any area identified by the Federal Emergency Management Agency (FEMA) as having special flood hazards unless the:

- (1) community in which that area is located participates in the national flood insurance program; and
- (2) building (and any related equipment) is covered by adequate flood insurance.

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- (2) for other NSF Grants when more than \$25,000 has been budgeted in the proposal for repair, alteration or improvement (construction) of a building or facility.

**Certification Regarding Responsible Conduct of Research (RCR)
(This certification is not applicable to proposals for conferences, symposia, and workshops.)**

By electronically signing the NSF Proposal Cover Sheet, the Authorized Organizational Representative of the applicant institution is certifying that, in accordance with the NSF Proposal & Award Policies & Procedures Guide, Part II, Award & Administration Guide (AAG) Chapter IV.B., the institution has a plan in place to provide appropriate training and oversight in the responsible and ethical conduct of research to undergraduates, graduate students and postdoctoral researchers who will be supported by NSF to conduct research. The undersigned shall require that the language of this certification be included in any award documents for all subawards at all tiers.

AUTHORIZED ORGANIZATIONAL REPRESENTATIVE		SIGNATURE	DATE
NAME			
TELEPHONE NUMBER	ELECTRONIC MAIL ADDRESS	FAX NUMBER	

* EAGER - EARly-concept Grants for Exploratory Research
** RAPID - Grants for Rapid Response Research

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AUTHORIZED ORGANIZATIONAL REPRESENTATIVE		SIGNATURE		DATE
NAME		Electronic Signature		Aug 15 2011 10:14AM
John M Mason				
TELEPHONE NUMBER	ELECTRONIC MAIL ADDRESS	FAX NUMBER		
334-844-4438	ospadmn@auburn.edu	334-844-5953		

* EAGER - EARly-concept Grants for Exploratory Research

** RAPID - Grants for Rapid Response Research

Collaborative Research: Biodiversity, connectivity and ecosystem function in organic-rich whale-bone and wood-fall habitats in the deep sea

Project Summary

Intellectual Merit: Organic-rich habitat islands support specialized communities throughout natural ecosystems and often play fundamental roles in maintaining alpha and beta diversity, thus facilitating adaptive radiation and evolutionary novelty. Whale-bone and wood falls occur widely in the deep-sea and contribute fundamentally to biodiversity and evolutionary novelty; nonetheless, large-scale patterns of biodiversity, connectivity and ecosystem function in these organic-rich metacommunity systems remain essentially unexplored. **We propose a novel comparative experimental approach, using bottom landers carrying bone and wood, to evaluate bathymetric, regional and inter-basin variations in biodiversity and connectivity, as well as interactions between biodiversity and ecosystem function, in whale-bone and wood-fall habitats at the deep-sea floor.** Our experiments will test fundamental hypotheses concerning biodiversity and biogeography of resource-rich habitats in energy-limited deep-sea environments, and explore the utility of whale-bone and wood falls as model experimental systems to address patterns of connectivity and decomposer function in the deep sea. Six replicate bone/wood landers will be deployed at two depths (1500 and 3000 m), 250 – 500 km apart, in the NE Pacific and SW Atlantic basins, with quantitative recovery of bone/wood macrofaunal assemblages 15 month later. Through molecular genetic, taxonomic, and functional studies of macrofaunal and microbial assemblages on bone/wood substrates, we will address the following hypotheses:

- 1) *The identity and diversity of dominant bone/wood species varies between depths and ocean basins.*
- 2) *Genetic (and species) exchange is much greater within a depth zone than between depth zones (i.e. genetic connectivity is greater along versus across isobaths).*
- 3) *Bone/wood specialists exhibit genetic/evolutionary isolation by basin (i.e., different species complexes occur in different basins suggestive of distinct adaptive radiations).*
- 4) *Rates of bone/wood mass loss, faunal biomass production, and the nature and rates of aerobic and anaerobic microbial processes on bone/wood substrates are directly related to the abundance and species richness of specialized macrofaunal decomposers (*Osedax*/*Xylophaga*).*
- 5) *Total macrofaunal and microbial species richness and trophic complexity on bone/wood substrates are directly related to the diversity and abundance of specialized bone/wood decomposers.*

We expect our quantitative bone/wood lander studies to reveal how population and community connectivity can vary with isolation by depth, distance, and ocean basin for specialized and generalized components of the bone/wood biota, yielding fundamental insights into processes of dispersal and evolution in the deep sea. We also expect to show how the diversity of ecosystem engineers (bone-eating *Osedax* and wood-eating *Xylophaga*) interacts with the structure and function of whale-bone/wood-fall assemblages, to potentially control such key ecosystem attributes as species richness, the nature of microbial metabolism, and rates of bone/wood decomposition. *To our knowledge, this will be the first experimental study of interactions between the diversity of key engineering species and ecosystem function in the deep-sea, allowing us to test the generality of models developed in detritus-based terrestrial and freshwater ecosystems in the largest detritus-based ecosystems in the biosphere.*

Broader Impacts: Our project will have broader impacts in four areas: (1) At least two graduate students will conduct PhD research, and three undergraduate students will participate in research cruises and develop their senior theses, within the project. In addition, project results will be incorporated into undergraduate and graduate courses at two universities. (2) We will develop a new a graduate-level summer course at Friday Harbor Laboratories, titled *Deep-Sea Biodiversity, Connectivity and Ecosystem Function*, around our bone/wood lander studies. A similar course will be offered at the University of Sao Paulo in Brazil at no cost to NSF. (3) Public outreach will include project web sites and cruise blogs at both UH and Auburn, and presentations at UH and Auburn open houses. (4) We will present results at international scientific meetings and conservation forums (e.g., the annual meeting of Pew Fellows in Marine Conservation), and will publish our results in top-tier, peer reviewed scientific journals.

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Table of Contents	1	_____
Project Description (Including Results from Prior NSF Support) (not to exceed 15 pages) (Exceed only if allowed by a specific program announcement/solicitation or if approved in advance by the appropriate NSF Assistant Director or designee)	15	_____
References Cited	9	_____
Biographical Sketches (Not to exceed 2 pages each)	2	_____
Budget (Plus up to 3 pages of budget justification)	6	_____
Current and Pending Support	1	_____
Facilities, Equipment and Other Resources	1	_____
Special Information/Supplementary Documents (Data Management Plan, Mentoring Plan and Other Supplementary Documents)	19	_____
Appendix (List below.) (Include only if allowed by a specific program announcement/ solicitation or if approved in advance by the appropriate NSF Assistant Director or designee)	_____	_____
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Collaborative Research: Biodiversity, connectivity and ecosystem function in organic-rich whale-bone and wood-fall habitats in the deep sea

A) Results From Prior NSF Support

Craig Smith: *Collaborative Research: Benthic-Pelagic Coupling on the West Antarctic Peninsula Shelf: The Impact and Fate of Bloom Material at the Seafloor.* OPP-9816049, 6/1/1999 – 5/31/2003; \$315,493;

C. Smith, *Collaborative Research: Benthic Faunal Feeding Dynamics on the Antarctic Shelf and the Effects of Climate Change on Benthic-Pelagic Coupling.* OPP-0636806, 9/15/2007-5/31/2012, \$447,135. In the first project (FOODBANCS), we examined benthic ecological impacts of intense summer plankton blooms on the West Antarctic Peninsula (WAP) shelf. Over 15 months, we found strongly seasonal POC flux and accumulation of phytodetritus at the seafloor (Mincks et al. 2005, Smith et al. 2006, 2008).

Nonetheless, macrobenthic response to seasonal flux was surprisingly muted, with deposit feeding, spawning, and recruitment occurring year round (Galley et al. 2003, 2005, 2008, Mincks and Smith 2007, McClintic et al. 2008, Wigham et al. 2008). We concluded that summer blooms create a benthic “food bank” of labile material that nourishes benthic detritivores throughout ice-covered winter months (Mincks et al. 2005, Smith et al. 2006, 2008).

During the 2nd project (FOODBANCS2), we have explored changes in WAP shelf ecosystem structure and function along a strong latitudinal sea-ice gradient (1.4 to 7.6 mo y⁻¹) from 63°- 68° S. Most benthic parameters are surprisingly resistant to differences in sea-ice duration, suggesting ecosystem robustness to climate change. However, we do find a major N-S shift in megafaunal trophic structure from suspension feeders to deposit feeders, suggesting a latitudinal increase in the importance of benthic “food banks.” These projects have supported: (a) 5 MS and 2 senior theses, 4 PhD dissertations, 5 postdoctoral scholars; (b) Antarctic experience for 32 graduate/undergraduate students, 2 teachers, and 5 international colleagues; (c) project web sites & cruise blogs receiving >3,000 visits from a total of 81 countries, (d) >30 presentations and 2 special sessions at scientific meetings; (e) 23 refereed publications (indicated by * in the References), including *Deep-Sea Research II Vol. 55/22-23* (2008), and (f) material for undergraduate/graduate courses at UHM, NCSU, U. of Barcelona, and U. of Sao Paulo.

Ken Halanych: *Collaborative Research: Relevance of Planktonic Larval Dispersal to Endemism and Biogeography of Antarctic Benthic Invertebrates.* OPP 0338218, 2/04 – 1/07 (no cost extension until 1/08), \$373,412; The overarching goal of this grant was to develop an evolutionary understanding of how benthic organisms have been influenced by the formation of, and geological history of, the Drake Passage and surrounding waters. More specifically, we were interested in how organisms can maintain genetic continuity (ie non-endemicity) across the Drake Passage despite the presence of strong oceanographic currents that form the sub-Antarctic and Antarctic Polar Fronts. We explored phylogeographic patterns in several species groups that span the Antarctic Polar Front using a combination of phylogenetic and coalescent approaches. Whether these fronts have acted as barriers to gene flow is species specific (e.g., Wilson et al 2009, Thornhill et al 2008, Hunter & Halanych 2008). However, genetic divergence values suggest that all examined trans-Drake species were separated <5 mya, even if one assumes a slow mtDNA substitution rate. This work has included 7 undergraduate researchers (4 female, 3 male), and women and minority participants on research cruises. Three postdocs (1 female, 2 male) and 2 graduate students (both female) have been trained. Web-based journals were an effective outreach mechanism, producing visits from thousands of unique I.P. addresses (www.auburn.edu/antarctica). Fourteen papers have been published (indicated by ** in the Reference section). The molecular approaches used in the current proposal build directly on methods and experience of this prior support.

B) Introduction

Patterns of biodiversity and adaptive radiation are often driven by unusual ecological opportunity, especially in extreme environments. For example, high local energy availability against an oligotrophic background has led to extraordinary biodiversity, evolutionary novelty, and animal-microbe interactions adapted to exploit chemical energy at hydrothermal vents and cold seeps, in spite of often harsh physico-chemical conditions (van Dover, 2000; Boetius, 2005; Martin et al., 2008; Dubilier, 2008). Similarly, falls of organic-rich materials, such as whale bones and wood, can provide ecological and evolutionary opportunity at the deep-sea floor by increasing local organic-carbon flux by orders of magnitude (e.g., Turner, 1973, 1977; Grassle and Morse-Porteus, 1987; Butman et al., 1996; Smith et al., 1989;

Snelgrove and Smith, 2002; Smith and Baco, 2003; Rouse et al., 2004; Goffredi et al., 2004, 2005, 2008; 2010; Glover et al., 2005; Smith, 2006). However, as at hydrothermal vents, energy exploitation at organic-rich bone/wood habitat islands may require special adaptations, especially to release organic material from recalcitrant bone or wood matrices (Distel and Roberts, 1997; Rouse et al., 2004; Smith, 2006; Goffredi, 2005; Dubilier et al., 2008). **Our overarching goals are (1) to explore interactions between biodiversity, ecosystem function and connectivity in resource-rich habitat islands embedded in a resource-poor landscape, the vast ecosystems of the deep sea, and (2) to test the utility of controlled experimental whale-bone and wood fall implantations for elucidating patterns of connectivity in deep-sea ecosystems.**

Organic-rich habitat islands support specialized microcommunities throughout natural ecosystems and often play fundamental roles in maintaining alpha and beta diversity, thus facilitating adaptive radiation and evolutionary novelty. Non-marine examples include tree falls in forest ecosystems, ungulate dung piles in fields and savannahs, mammalian carcasses in tropical to polar habitats, and leaf-litter accumulations in forests and streams (e.g., Schoenfly and Reid, 1987; Schaetzel et al., 1989; Hanski and Cambefort, 1991; Ulanova, 2000; Hanski and Gilpin, 1997). Each of these island habitat types harbors a characteristic biota distributed in metacommunities, in which connectivity, adaptation and co-evolution shape decomposer, trophic, and successional interactions, in turn influencing patterns of taxonomic, genetic, and functional diversity over a broad range of scales. Such organic-rich habitat islands have provided model systems for exploring processes of biodiversity maintenance, ecosystem function, metapopulation dynamics, and evolution in terrestrial and freshwater ecosystems (e.g., Hanski and Gilpin, 1997; Gessner et al., 2010).

Organic-rich habitat islands, such as whale bones and wood falls, are now known to occur widely in the deep sea. These bone/wood islands may support diverse, trophically complex macrofaunal assemblages and in some cases appear to have sustained radiations of decomposer taxa (*Osedax* and xylophagain bivalves, respectively) adapted to exploit concentrated organic matter trapped within a recalcitrant bone/wood matrix (Turner, 1973; 1977, 2002; Pailleret et al., 2007; Smith and Baco, 2003; Voight, 2007, 2009; Richer de Forges et al., 2009; Lundsten et al., 2010b). For example, whale falls in the deep North Pacific may support diverse macrofaunal assemblages (>200 species per fall), with >50 new species described since 1987 (Baco and Smith, 2002; Smith and Baco, 2003; Rouse et al., 1995; Smith, 2006; Fujiwara et al. 2007; Braby et al., 2007; Lundsten et al., 2010b). Faunal diversity on whale bones includes ~26 putative species in the bone-eating *Osedax* clade (Vrijenhoek et al., 2009; Glover et al., in prep.; Honig et al., in prep.) whose engineering activities may facilitate rapid decomposition of the bone matrix, fostering colonization by heterotrophic species (e.g., Lundsten et al., 2010b). Whale bones also harbor speciose polychaete groups (e.g., Chrysopetalidae, Dorvilleidae) thought to specialize on microbes decomposing complex organic compounds in the bones (Smith and Baco, 2003; Dahgren et al., 2004; Glover et al., 2005; Wiklund et al. 2009a, Wiklund et al. 2009b). Deep-sea whale falls thus may support a core, bone-inhabiting fauna with specialized life histories and adaptive strategies (e.g., the bone-eating worm *Osedax*, snails in the genus *Rubyspira*, the sipunculan *Phascolosoma saprophagicum*), chemosynthetically dependent fauna (e.g., vesicomyids, bathymodiolins), and a large suite of heterotrophic species (e.g., deposit feeders and suspension feeders) from the background community (Gibbs, 1987; Smith et al., 1989; Bennett et al., 1994; Baco and Smith, 1999; Distel et al., 1999; Smith and Baco, 2003; Kiel and Goedert, 2006; Samadi et al., 2007; Lorion et al., 2009; Lundsten et al., 2010a & b; Johnson et al., 2010). Similarly, deep-sea wood falls support diverse macrofaunal assemblages, including wood-boring decomposers (≥ 41 species of bivalves in the subfamily Xylophaginae), and a substantial number of specialists (some with chemoautotrophic endosymbionts) utilizing wood falls for nutrition and habitat (Turner 1973, 1977, Wolff 1979, Distel and Roberts, 1997; Distel et al., 1999; Stoeckle, 2006; Pailleret et al. 2007, Voight 2007, 2009; Gros et al., 2007; Bernardino et al., 2010; Rodriguez and Daly, 2010). As on whale bones, the diverse communities on wood falls may be heavily influenced by ecosystem-engineering activities of substrate decomposers, i.e., xylophagain bivalves, which modulate food and habitat availability (Turner, 1973; 1977; Wolff, 1979; Stoeckle, 2006; Voight, 2007, 2008).

In addition, recent molecular studies suggest that some whale-bone/wood-fall taxa share evolutionary histories with the fauna of hydrothermal vents and cold seeps, raising the possibility that bone/wood falls have played a role in the evolution and connectivity of deep-sea faunas exploiting other energy-rich habitat islands in the oligotrophic deep sea (Baco et al., 1999; Distel et al., 2000; Halanyc et

al., 2001; Schulze and Halanych, 2003; Rouse et al., 2004; Glover et al., 2005; Jones et al., 2005; Kiel and Little, 2006; Samadi et al., 2007; Lorion et al., 2009).

While it is clear that whale-bone and wood-fall habitats may contribute fundamentally to biodiversity and evolutionary novelty at the deep-sea floor, large-scale patterns of biodiversity, connectivity and ecosystem function in these organic-rich metacommunity systems remain essentially unexplored. For example, deep-sea whale-bone macrofaunal communities have only been quantitatively sampled in the North Pacific, and new species continue to be discovered at a high rate in this region (Baco and Smith, 2003; Dahlgren et al., 2004; Rouse et al., 2005; Smith, 2006; Fujiwara et al., 2007; Pleijel et al., 2008; Vrijenhoek et al., 2009; Wiklund, 2009). *Osedax* and *Xylophaga* are thought to be widely distributed in the deep-sea, but these genera have been reported from fewer than 10 sites south of the Equator in a hemisphere containing 60% of the world ocean (Stoeckle, 2006; Voight et al., 2009; information available on OBIS). This extreme knowledge gap results from the inaccessibility of deep-sea habitats, which makes quantitative sampling and manipulation of deep-sea whale bones and wood falls very difficult. In general, current knowledge of inter-basin and bathymetric connectivity in the deep-sea is very poor outside of hydrothermal vent and cold seep habitats (reviewed in Vrijenhoek, 2010) primarily because sampling efforts needed to obtain the number of organisms outside such environments is difficult, if not prohibitive. Nonetheless, efforts to assess connectivity in other deep-sea environments such as seamounts (e.g., White et al., 2009; Miller et al., 2010, 2010; Cho and Shank, 2010) and the deep Antarctic shelf and slope (e.g., Strugnell et al., 2008) are taking place. Most of these studies are still regional in spatial scale and with only a few (outside of vents and seeps) addressing connectivity between deep-sea basins. In particular, Zardus et al. (2006) showed that the bivalve *Deminucula atacellana* had more divergence within a basin at different depths than across thousands of kilometers at the same depth. The impact of depth-related divergence has since been observed in other organisms and systems (e.g., brittle stars on seamounts – Cho and Shank 2010; polychaetes in the Antarctic – Schüller 2011; corals in the Pacific - Miller et al., 2011). Zardus et al. (2006) went on to hypothesize that isolation by distance explains much of the inter-basin variation. Based on these studies, mechanisms that maintain or promote genetic divergence along a depth gradient appear to be fundamentally different from mechanisms controlling genetic divergence within depth zones in the deep sea.

We propose a novel comparative experimental approach (cf. Menge et al., 2002, 2003) to begin to evaluate bathymetric, regional, and inter-basin variations in the biodiversity and connectivity, as well as interactions between biodiversity and ecosystem function, in organic-rich whale-bone and wood-fall habitats at the deep-sea floor. Our experiments will test fundamental hypotheses concerning biodiversity and biogeography of resource-rich habitats (e.g., whale bone and wood falls) in an energy-limited environment, and explore the utility of whale-bone and wood falls as model experimental systems to address patterns of connectivity and decomposer function in deep-sea ecosystems. We expect deep-sea whale-bone and wood falls to be highly useful for exploring population connectivity and barriers to dispersal over a variety of scales because bone/wood islands can be implanted anywhere, are easily standardized, and foster large resident populations with a range of ecological and life-history characteristics (from bone/wood specialists to heterotrophic species from the background community, e.g., Lundsten et al., 2010b). They thus can provide ample genetic material for broad-based studies of population connectivity, a major challenge in deep-sea ecosystems where population densities are typically extremely low. In addition, we expect whale-bone/wood-fall communities to be useful for exploring interactions between diversity and ecosystem function in marine decomposer communities. A number of studies (e.g., Stoeckle, 2006; Voight, 2007, 2009; Lundsten et al., 2010b) indicate that there are regional and bathymetric variations in the diversity of *Osedax* and *Xylophaga*, i.e., in key engineering taxa that facilitate the decomposition of bone and wood in the deep sea. With a controlled experimental system, such regional and bathymetric variations can be used to explore how decomposer diversity is related to rates of bone/wood degradation, allowing testing of diversity-decomposition models developed in freshwater and terrestrial ecosystems (e.g., contrasting systems with high versus low background productivity and recalcitrant detrital input, Gessner et al., 2010).

C) Proposed Research

i. Hypotheses to be tested

We propose to use a “comparative experimental approach” (Menge et al., 2002, 2003) to assess bathymetric and regional variations in biodiversity, connectivity and ecosystem function in whale-bone

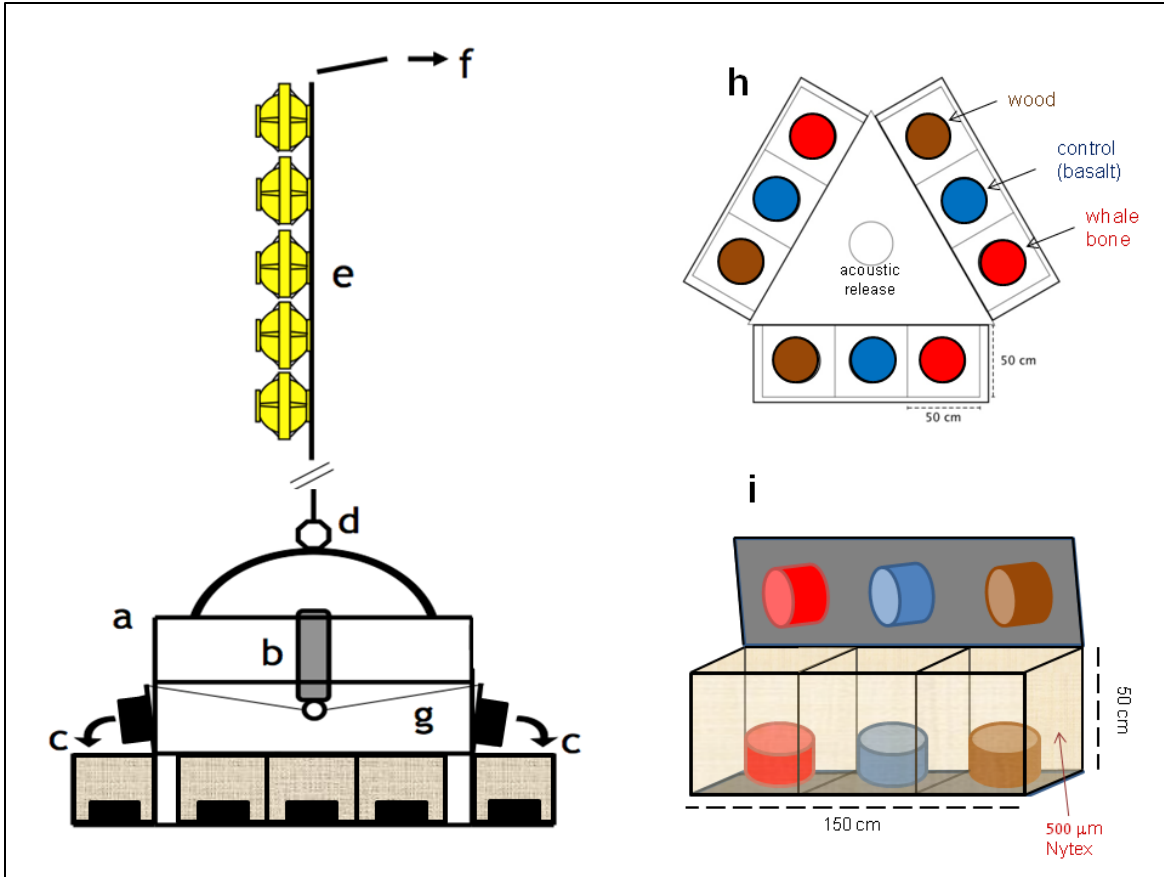


Figure 1. Conceptual design of free-vehicle bone/wood landers (BOWLs). BOWLs will consist of triangular frames (with one set of *bone - control (basalt) – wood treatments*) in open bins on each side of the lander; positions of bone and wood bins on each side will be randomized. Each treatment will be deployed in an open 500- μ m mesh bin, with substrates exposed to flow within bin and on bin lids throughout the 15-month seafloor deployment. At recovery, an acoustic release (b) will drop ballast and allow hinged bin lids to fall and close, quantitatively retaining macrofaunal assemblages for recovery at the sea surface. (a) Side view of a BOWL at the seafloor with bins open and substrates exposed. (b) Acoustic release, which will release bin doors (c,g) and drop the free-vehicle ballast weight (not shown) on an acoustic signal. (d) Flotation line and (e) glass flotation. (f) Attachment point for radio beacon and strobe light to allow rapid location of vehicles at sea surface for recovery. (h) Plan view of three Nitex mesh bins showing position of substrates. (i) Lateral view of one set of mesh bins, with lid open. Similar free-vehicles with acoustic releases are widely used in oceanography to deploy and close experimental apparatus at the deep-sea floor (e.g., Gage and Tyler, 1991).

and wood-fall habitat islands in the deep sea. Specifically, we will use free-vehicle landers to deploy standardized whale-bone, wood and control (basalt) substrates at the deep-sea floor. Six replicate experimental landers (each with three replicated sets of substrates, Fig. 1) will be deployed in a stratified design at each of two seafloor depths (~ 1500 m and ~ 3000 m) on the NW Pacific Margin (Fig. 2); experimental substrates and associated macrofaunal communities will then be *quantitatively* recovered 15 months later. A parallel set of experiments, with a similar experimental design, will be conducted with Brazilian collaborators, with funding in hand from FAPESP Brazil, on the SW Atlantic Margin (Fig. 2) (see letters of collaboration from Drs. Sumida and Bernardino). This comparative experimental approach will allow us to test the following hypotheses:

- 1) *The identity and diversity of dominant bone/wood species varies between depths and ocean basins.*
- 2) *Genetic (and species) exchange is much greater within a depth zone than between depth zones (i.e. genetic connectivity is greater along versus across isobaths).*
- 3) *Bone/wood specialists exhibit genetic/evolutionary isolation by basin (i.e., different species complexes occur in different basins suggestive of distinct adaptive radiations).*

- 4) *Rates of bone/wood mass loss, faunal biomass production, and the nature and rates of aerobic and anaerobic microbial processes on bone/wood substrates, are directly related to the abundance and species richness of specialized macrofaunal decomposers (Osedax/Xylophaga).*
- 5) *Total macrofaunal and microbial species richness and trophic complexity on bone/wood substrates are directly related to the diversity and abundance of specialized bone/wood decomposers.*

In addition, our inferences on connectivity and biodiversity from bone/wood lander experiments will be placed in a global context using bone/wood fall samples from other ocean basins available in the PI's collections and from collaborators (Fig. 3).

Below we explain the rationales for our hypotheses and describe our approach for testing them.

ii. Rationales and Approaches for Testing of Hypotheses

Hypotheses 1, 2, and 3

Rationale: The macro- and megafauna of detritus-based deep-sea habitats, as well as the fauna of vents and seeps, exhibit both bathymetric and regional turnover of species (see Van Dover, 2000; Van Dover et al., 2002; Levin et al., 2003; Carney, 2005; Rex et al., 2005; Cordes et al., 2007; Rex and Etter, 2010; Menot et al., 2010; Krylova and Sahling, 2010; Rodriguez and Daly, 2010). The soft-sediment macrofauna, in particular, shows substantial species turnover between depths of 1500 and 3000 m, often with an alpha diversity maximum at mid-slope depths (1000-2500 m), and a diversity decline into the abyss (Levin et al., 2001; Carney, 2005; UNESCO et al., 2010; Rex and Etter, 2010). A variety of mechanisms have been proposed to explain the decline in macrofaunal diversity from bathyal to abyssal depths; the exponential decline in organic-carbon flux (i.e., food availability) with depth is thought to be a major factor (e.g., Levin et al., 2001; Rex et al., 2005; Carney, 2005; Rex and Etter, 2010). Deep-sea vent and cold-seep communities also show species turnover with depth, but these changes do not appear to be associated with a bathymetric diversity gradient, and are postulated to be driven by adaptations to hydrostatic pressure and variations in habitat stability and/or fluid geochemistry rather than by depth related clines in sinking organic-carbon flux (e.g., Van Dover, 2000; Desbruyeres et al., 2000; Cordes et al., 2007). Whale-bone and wood-fall communities also show species turnover with depth (e.g., Rouse et al., 2005; Braby et al., 2007; Fujiwara et al., 2007; Voight, 2007, 2009; Lundsten et al., 2010b) but changes in macrofaunal community structure and diversity are very poorly characterized because of the paucity of controlled, quantitative, community-level studies. Thus, it is extremely difficult to predict levels of turnover or changes in macrofaunal species diversity between depths (e.g., 1500 versus 3000 m) and ocean

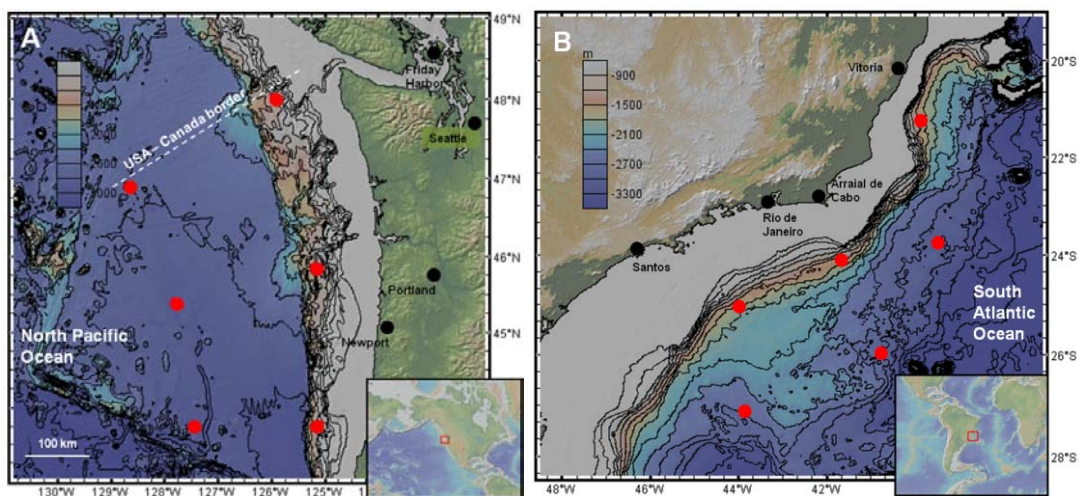


Figure 2. Design of field deployments in the Northeast Pacific on the Washington-Oregon margin (**A**) to be funded by this project, and in the Southwest Atlantic on the Brazilian margin (**B**) funded by collaborations with Brazilian scientists (see letters from Sumida and Bernardino). On each margin, six replicate landers (red circles) will be deployed with approximately ~250-km spacing; three BOWL landers at ~1500 m (± 200) and three landers at ~3000 (± 300) m depths. Landers will be deployed in the boreal spring (a season of whale migration and driftwood input along these margins), and recovered 15 mo later (see Fig. 4 for time table).

basins (NE Pacific versus SW Atlantic) in these organic-rich habitats. Nonetheless, we do expect substantial differences between depths (and regions) in bone/wood macrofaunal diversity, as well as in the abundance and diversity of the key decomposer taxa *Osedax* and *Xylophaga*, as observed along the California margin (Braby et al., 2007; Voight 2007, 2009; Lundsten et al., 2010b), allowing us to examine interactions between diversity and ecosystem functions in our controlled experimental substrates.

In soft-sediment, detritus-based deep-sea ecosystems, species ranges and gene flow generally appear to be much greater along than across depth zones; i.e., connectivity is higher along 1500 m and 3000 m isobaths than between them (Etter and Rex, 1990, Etter et al., 1995; Carney, 2005; Zardus et al., 2006; Rex and Etter 2010). If this pattern holds for whale-bone/wood-fall substrates (i.e., if *Hypothesis 2* is correct), this will suggest that the drivers of connectivity in whale-bone/wood-fall assemblages are similar to those for detritus-based, soft-sediment deep-sea communities. This is an important condition for broader use of whale-bone/wood-fall landers as model, comparative experimental systems to explore population connectivity and barriers to dispersal over a variety of scales in the deep sea.

Approach: Hypotheses 1 will be addressed by quantitatively comparing, between depths and basins, species structure, diversity, and apparent population sizes of dominant whale-bone/wood-fall taxa including the genus *Osedax*, bivalves in the subfamily xylophaginae, the gastropod *Rubyspira*, pyropeltid limpets, bathymodiolin mussels, and dorvilleid, chrysopetallid, and polynoid polychaetes (e.g., Smith and Baco, 2003; Rouse et al., 2004; 2009; Dahlgren et al., 2004; Glover et al., 2005; 2008; Fujiwara et al., 2007; Wiklund et al., 2009, 2010; Johnson et al., 2010) using a broad range of morphological, molecular genetic and statistical approaches. *Hypotheses 2* and *3* will be tested by examining species overlap and genetic structure for our experimental bone/wood/control substrates within landers, within depth zones, between depth zones (~1500 m versus ~3000 m), and between ocean basins (the NE Pacific versus the SW Atlantic) using morphological and genetic approaches (see **Description of Experimental Approach** and **Data Collection and Analyses** for details). In addition, the quantitative studies from our bone/wood landers will be augmented by comparisons for selected components of bone/wood fauna from other regions and ocean basins, based on material available in the collections of the PIs (southern California, the Weddell Sea, and the Bellingshausen Sea), from our collaborators (Glover et al. for the North Atlantic and Indian Ocean, Chilean collaborators for the eastern South Pacific, New Zealand collaborators for the New Zealand margin (Baco et al., 2009)), and from GenBank (a variety of locations in the North Pacific)(Fig. 3). In total, this will provide a very large, inter-basin scale context for our quantitative connectivity studies with bone/wood landers.

Hypotheses 4 and 5

Rationale: Bone-eating worms in the genus *Osedax*, and wood-boring bivalves in the subfamily Xylophaginae, appear to act as ecosystem engineers (cf., Jones et al., 1994; Bruno et al., 2003) in deep-sea whale-bone and wood-fall habitats by directly decomposing the bone/wood material, by creating and destroying habitat structure, by modulating the availability of food resources to other species, and by facilitating colonization by other species and functional groups (e.g., Turner, 1973, 1977, 2002, Wolff, 1979; Voight, 2007, 2008, 2009; Rouse et al., 2005; Braby 2007; Lundsten, 2010a & b; Treude et al., 2009; Higgs, 2010). For example, *Osedax*/xylophagains burrow into the recalcitrant bone/wood matrix, enhancing the penetration of electron acceptors and heterotrophic microbes into subsurface layers of the bone/wood. The burrow structures of *Osedax*/xylophagains likely increase the attachment area and niche complexity for microbes, and provide refugia and basic habitat for animals living as endofauna within the bone/wood (e.g., Turner, 1977; Wolff, 1979; Stoeckle, 2006; Voight, 2007). *Osedax*/xylophagains also are likely to increase food availability for detritivores, microbial grazers and predators by freeing organic material (e.g., bone lipids) from the solid bone/wood matrix, stimulating microbial growth, degrading refractory wood compounds (cellulose and lignin) into more labile material (e.g., xylophagain feces), and providing faunal biomass for predators (e.g., Turner, 1973, 1977; Wolff, 1979; Goffredi et al., 2005; Braby et al., 2007; Fujiwara et al., 2007; Voight, 2007, 2009). Ultimately, *Osedax*/xylophagains may lead to the destruction of habitat by hastening the decomposition the bone/wood habitat island (Turner, 1977; Braby et al., 2007; Lundsten et al., 2010b). In many respects, *Osedax*/xylophagains may be deep-sea functional analogs of dermestid beetles and boring insects in terrestrial forests, whose engineering activities substantially influence biodiversity and ecosystem function (e.g., rates of wood decomposition, alpha diversity) in saproxylic communities inhabiting large bones and woody debris (e.g., Grove, 2002). Thus, key ecosystem structure and function in whale-bone/wood-fall

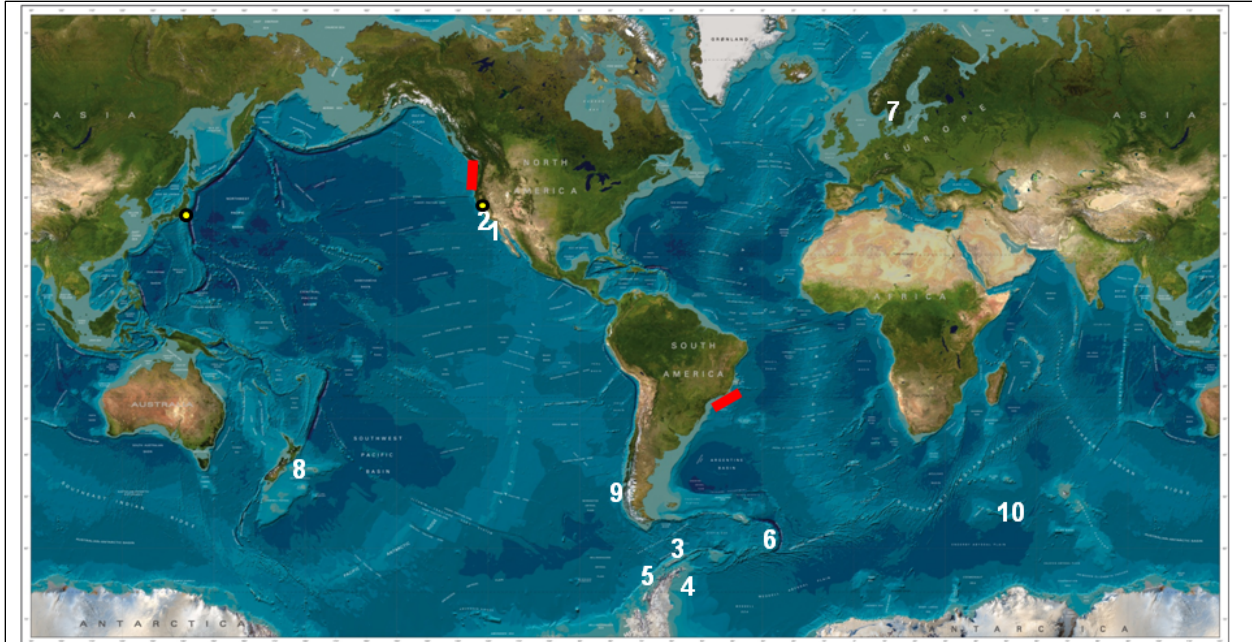


Figure 3. Sites from which selected whale-bone/wood-fall fauna genetic material is available from the PIs and collaborators for global studies of phylogenetic connectivity. **Red bars:** Field areas proposed here for quantitative bone/wood lander studies in the NE Pacific and SW Atlantic. **(1)** Santa Catalina Basin (1200 m) and **(2)** Santa Cruz Basin (1670 m) from which diverse whale-bone and wood-fall material (including *Osedax* and xylophagains) is available in PI collections. **(3-5)** Sites (600 m) in the Bellinghousen and Weddell Seas from which *Osedax* and other whale-bone species are in hand (C. Smith, collaborators). **(6)** Scotia Arc, Southern Ocean (1500 m) and **(7)** Skagerrak, Sweden (125 m), from which *Osedax* and other whale-bone species are available from collaborators (Glover, Dahlgren). **(8-10)** New Zealand (700-1100 m) and Chile margins, and Indian Ocean, where ongoing collaborations will yield whale-bone and wood collections in the next 3 yr (Rowden, Sellanes, Glover). **Yellow dots:** Sites along Japan (Fujikura et al., 2006; Fujiwara et al., 2007) and in Monterey Canyon (Rouse et al., 2005; Braby et al., 2007; Vrijenhoek et al., 2009; Johnson et al., 2010; Lundsten et al., 2010b) from which DNA sequences are available in GenBank for *Osedax* and other whale-bone fauna.

habitats, including substrate decomposition, production of faunal biomass, biodiversity, and food-web complexity, are likely to be strongly modulated by the engineering activities of *Osedax*/xylophagains.

Because deep-sea bone/wood falls are patchy, relatively ephemeral and food rich, these detrital habitat islands appear to have selected for opportunistic life histories in some species, including high dispersal ability, and rapid population growth and resource utilization (e.g., Turner 1973; 1977; Rouse et al., 2005, 2009; Voight et al., 2007; 2009; Braby et al., 2007; Lundsten et al., 2010b). Nonetheless, both *Osedax* and xylophagains appear to have substantial global species richness in the deep sea (≥ 26 and ≥ 41 species respectively, despite limited sampling); these bone/wood decomposers can also sustain high local species richness, with at least four *Osedax*/xylophagain species capable of occurring simultaneously on single pieces of bone/wood (Voight, 2007, 2009; Vrijenhoek et al., 2009; Honig et al., unpub. data for the Antarctic). For suites of *Osedax*/xylophagain species occurring simultaneously in single bone/wood habitat islands, there is evidence of between species differences in functional traits, including differences in adult size and morphology, and burrow depth and shape (e.g., Voight, 2007, 2009; Vrijenhoek et al., 2009; Higgs et al., unpublished data; Honig et al., unpublished data). **We predict that these functional differences will in combination facilitate bone/wood decomposition, such that higher local *Osedax*/xylophagain species richness yields more rapid loss of bone/wood mass in these habitat islands.** Specifically, we predict “transgressive overyielding” wherein greater detritivore species richness is associated with more rapid detrital decomposition rates, a situation documented in some stream systems where detrital accumulations are food-rich but unstable compared to the background ecosystem (Gessner et al., 2010). The presence of transgressive overyielding in bone/wood habitats islands in the deep sea would suggest that ecosystem function in these habitats may be highly sensitive to regional differences in *Osedax*/xylophagain diversity resulting from natural or anthropogenic processes. For example, in regions with low detrital wood input such as the Southern Ocean or central oceanic gyres, low habitat availability is likely to yield low xylophagain diversity, causing low wood decomposition rates

(and high archeological preservation potential). Similarly, loss of sunken bone/wood habitats resulting from deforestation or whaling may have led, or be leading, to bone/wood fauna extinction in the deep sea, altering ecosystem function in these habitats (Butman et al., 1995, 1996; Smith, 2006).

Approach: Hypotheses 4 will be addressed by comparing essential ecosystem functions in our experimental bone/wood substrates to variations in the abundance and diversity of macrofaunal bone/wood decomposers (*Osedax/xylophagains*). Ecosystem functions addressed will include rates of bone/wood mass and volume loss, macrofaunal biomass production, and the activity of anaerobic bone/wood decomposers (sulfate-reducing bacteria and methanogenic archaea) evaluated using a broad range of techniques (presented in detail in the **Data Collection and Analyses** section below). Comparisons between ecosystem functions versus *Osedax/xylophagain* diversity and abundance will be made within landers, within depth zones, between depth zones (~1500 versus ~3000 m), and between ocean basins (the NE Pacific versus the SW Atlantic)(see letters of collaboration from Drs. Sumida and Bernardino). To test Hypothesis 5, we will evaluate species richness and trophic complexity in both macrofaunal and microbial communities for comparison to the abundance and diversity of macrofaunal bone/wood decomposers (*Osedax/xylophagains*) within and between landers, depth zones, and ocean basins. We will use morphological, molecular and functional-group analyses to assess macrofaunal species richness and trophic structure, focusing for this hypothesis on macrofauna attached to bone/wood surfaces (sessile epifauna) or collected from bone/wood pore spaces (endofauna). Microbial diversity and trophic structure will be assessed using metagenomic approaches by Drs. Marie-Anne Van Sluys and Vivian Pellizari, University of Sao Paulo (see letter of collaboration from Van Sluys). The abundance of dominant groups of anaerobic microbial decomposers in bone/wood will be determined by Catalyzed Reporter Deposition Fluorescence In Situ Hybridization (CARD-FISH) in collaboration with Dr. Tina Treude of IFM-Geomar (see letter of collaboration). More complete details are provided in **Description of Experimental Approach** and **Data Collection and Analyses** below.

iii. Description of Experimental Approach

We will employ a “comparative experimental approach” (Menge et al., 2002, 2003) to evaluate variations in bone/wood community diversity, connectivity, and ecosystem function over a variety of spatial scales. This approach, which uses identically designed, replicated experiments placed at different sites along and across environmental gradients, has proven to be a powerful tool to investigate factors influencing community structure and dynamics on local to regional scales (Menge et al., 2002, 2003). In our experiments, we will deploy replicated whale-bone, wood and control (basalt) substrates on free-vehicle landers (Fig. 1) in the NE Pacific at intervals of ~250 km along the Washington-Oregon margin at two depths (~1500 and ~3000 m) in a nested design (Fig. 2). Parallel experiments, using a similar experimental design, are being conducted collaboratively with Brazilian colleagues along the SW Atlantic margin off Brazil (Fig. 2)(see letters from Drs. Sumida and Bernardino).

Study Regions

NE Pacific: Our primary study region, the Washington-Oregon margin between 43° and 48° N (Fig. 2), lies in the Cascadia Basin, where annual humpback and gray-whale migrations occur (Gaskin, 1982; Johnson and Wolman, 1984; Jones et al., 1984; Moore et al., 2003), providing whale-fall habitats (e.g., Smith and Baco, 2003). Other large cetacean species also feed in and migrate through this region (e.g., Calambokidis and Barlow, 2004). While substantial commercial whaling occurred in the region in the 19th and 20th centuries (e.g., Estes et al., 2006), the abundance of coastal migratory great-whale species is still high in this region relative to global standards. The coastal zone is also heavily forested, providing a major source of detrital wood, including coarse woody debris, to the marine environment (Ritter et al., 2002; Voight, 2007). Deep-sea whale-bone communities (including an undetermined species of *Osedax*) and wood-fall communities are known from the deep Cascadia Basin (Stoeckle, 2006; Voight, 2007, 2008; Lundsten et al., 2010a; Glover, personal communication) and the NE Pacific in general appears to be a biodiversity hotspot for both *Osedax* and *Xylophaga*, i.e., for key deep-sea bone/wood ecosystem engineers (Stoeckle, 2006; Voight, 2007, 2008; Vrijenhoek et al., 2008). The species composition, abundance, and diversity of *Osedax* and *Xylophaga* in the region vary locally (e.g., within single carcasses and wood piles), along isobaths, and across depths (e.g., Vrijenhoek et al., 2009; Voight et al., 2009; Bernardino et al., 2010; Smith et al., in prep.), so we expect the diversity of *Osedax/Xylophaga*

within our experiments to vary on local, along-isobath and especially across-isobath scales. The deep-water circulation and water-mass properties of our target region in the Cascadia Basin have recently been studied and modeled (Hautala et al., 2009) providing an excellent physical oceanographic context for our examination of biodiversity and connectivity along and across the WA-OR slope. Pacific Deep Water occurs at depths of 900-1900 m in the Cascadia Basin, with slow mean southward flow (of order 1 cm s^{-1} on monthly time scales) along the slope driven by the North-Pacific-Basin-scale anticyclonic gyre (Hautala et al., 2009). At $\sim 1500 \text{ m}$ (our shallow deployment depth), bottom waters are well oxygenated ($>1 \text{ ml l}^{-1}$) (Hartnett and Devol, 2003). Below depths of 2400 m in the Cascadia Basin (including at our deep sites), the slope is bathed by well oxygenated Cascadia Basin Bottom Water ($[\text{O}_2] >2 \text{ ml l}^{-1}$) with weak mean northerly flow ($\sim 1 \text{ cm s}^{-1}$) (Hautala et al., 2009) fed by water from the broader Pacific passing through deep gaps in the Blanco Fracture Zone to the southwest (Hautala et al., 2009). Studies of faunal zonation for a number of benthic taxa suggest a middle-slope faunal zone centered at $\sim 1600 \text{ m}$ (roughly our shallow study depth) and a lower slope-abyssal faunal zone centered at $\sim 2800 \text{ m}$ (roughly our deep study depth) within the Cascadia Basin (Carney, 2005).

SW Atlantic: Our second study region (addressed in collaboration with Brazilian scientists) is between 21° and 25° S in the Brazil Basin on the Brazil margin (Fig. 2). This region harbors migrating and breeding humpback whales, and provides feeding grounds for other large baleenopterid species (e.g., Zerbini et al., 1997, 2008). However, the populations of great whales were heavily depleted during whaling in the 20th century, and populations sizes of many species, including humpbacks, still are low relative to pre-exploitation levels (Zerbini et al., 1997, 2008). Thus, current whale-fall habitat abundance is likely reduced relative to evolutionary time scales. The coastal zone in this region also contains the formerly vast Atlantic rainforest of southeast Brazil as a source of wood detritus. However, over historical times, heavy deforestation has occurred in this region, leaving only $\sim 12\%$ of the original forest (Brooks et al., 1999). Thus, while detrital wood input is likely to have been substantial over evolutionary time scales, wood input to this margin has declined dramatically within the last century. Three major water masses are found along the Brazilian margin: Antarctic Intermediate Water (AAIW), North Atlantic Deep Water (NADW), and Antarctic Bottom Water (AABW) (De Madron & Weatherly 1994; Silveira *et al.* 2000). In our study region in the Brazil Basin, NADW generally flows southward at depths of 1200-3000 m to $\sim 32^\circ \text{ S}$ (McCartney 1993). Below $\sim 3000 \text{ m}$, AABW generally flows northward (De Madron & Weatherly 1994; Hogg and Owen, 1999), so that our deep study sites ($\sim 3300 \text{ m}$ on this margin) will be bathed by a different water mass (AABW) with potentially different larval sources than our shallower depth ($\sim 1500 \text{ m}$). Dissolved oxygen is high ($>2 \text{ ml l}^{-1}$) throughout the water column between 21° and 25° S (Tomczak and Godfrey, 1994). Faunal depth zonation along the Brazil margin is very poorly studied, but the generalized zonation scheme of Carney (2005) suggests that our shallow ($\sim 1500 \text{ m}$) and deep ($\sim 3300 \text{ m}$) study depths will be dominated by different faunas (an Upper Boundary Biota and a Lower Boundary Biota, respectively). The biotas of whale-bone and wood falls along the deep Brazil margin remain wholly unsampled, to our knowledge (see OBIS).

BOne/Wood Landers (BOWLs)

Our bone/wood landers are designed to expose replicate bone, wood, and basalt substrates at the deep-sea floor for colonization, and then to **quantitatively** recover experimental substrates and their macrofaunal assemblages, from the seafloor in sealed 500- μm Nitex bins. Test versions of the BOWLs, with whale-bone substrates, have been successfully deployed for 13 months at bathyal depths off Antarctica, and resulted in quantitative recovery of dense and diverse whale-bone communities (Smith and Honig, in prep.). BOWLs will be three sided, with replicates of each treatment type located along each side to stratify the effects of directional bottom currents across treatment types (Fig. 1). The positions of whale-bone and wood substrates on each side will be randomized on either side of the control basalt treatment. Recovery of bone/wood/basalt substrates from the seafloor in protected, sealed 500- μm Nitex bins is essential to study macrofaunal biodiversity and ecosystem function at the community level; previous, submersible and ROV-based quantitative studies of deep-sea bone and wood assemblages indicate that a substantial number of macrofaunal individuals and species may be washed from unprotected substrates during recovery from the seafloor (e.g., Turner, 1978; Baco and Smith, 2003; Smith and Baco, 2003; Voight, 2007; Bernardino et al., 2010).

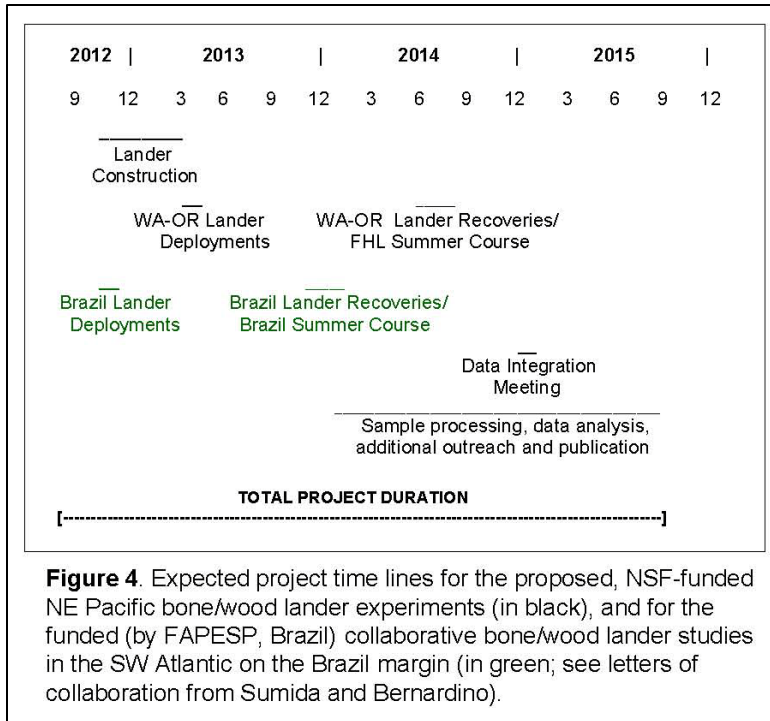


Figure 4. Expected project time lines for the proposed, NSF-funded NE Pacific bone/wood lander experiments (in black), and for the funded (by FAPESP, Brazil) collaborative bone/wood lander studies in the SW Atlantic on the Brazil margin (in green; see letters of collaboration from Sumida and Bernardino).

subsample of bone ~1 cm thick will be cut from the middle of each vertebra and frozen for later geochemical and microbial analyses to document t=0 conditions. One whale-bone cylinder will be fastened to the bottom and one to the lid of each whale-bone bin, with sectioned surfaces against the PVC bottom/lid (Fig. 1). Wood substrates will be similarly sized and sub-sampled pieces of raw (untreated) Douglas fir (*Pseudotsuga menziesii*), a member of a genus distributed from boreal to tropical latitudes, and now widely farmed in the Southern Hemisphere. Douglas fir is a low density wood in the pine family that undergoes rapid, exponential decomposition in terrestrial environments (e.g., Stone et al., 1998); fir and other species of the pine family have been heavily colonized and bored within one year in deep-sea experiments on the Pacific and Atlantic margins (e.g., Turner, 1977; Voight, 2007; Tyler et al., 2007; Bernardino et al., 2010). Control substrates will consist of porous basalt similar in size to bone/wood substrates, but free of organic material. Prior to deployment, all substrates will be waterlogged in the dark in clean seawater, wet weighed, and internal pore-space volume determined by water loss after removal from immersion. Similar measurements will be made immediately after substrate recovery following 15 mo deployments, and mass loss and changes in pore volume per unit mass determined by difference to evaluate decomposition (cf. Robertson and Paul, 2000).

Precise immersed volume measurements also needed.

We are confident that the bone/wood substrates within our BOWL bins deployed along the WA-OR margin will be heavily colonized by *Osedax/Xylophaga* and other components of the bone/wood assemblage, especially at ~1500 m (Voight, 2007; Lundsten et al., 2010a & b). *Osedax/Xylophaga* and diverse macrofaunal assemblages have established high densities on deep-sea bone/wood substrates elevated ≥ 50 -cm above the seafloor on natural skeletons and sunken logs, experimental wood and bone parcels, and free-vehicle landers (e.g., Turner, 1977; Glover et al., 2005; Braby et al., 2007; Tyler et al., 2007; Jones et al., 2008; Lundsten et al., 2010a & b; Bernardino et al., 2010; C. Smith, T. Dahlgren, and D. Honig, in prep.). Especially rapid colonization and bone/wood decomposition by *Osedax/Xylophaga* has been documented for depths of 1000-2000 m along the NE Pacific margin (Braby et al., 2007; Tyler et al., 2007; Jones et al., 2008; Hannides, 2008; Lundsten et al., 2010a & b; Bernardino et al., 2010).

Control basalt substrates will be included in the middle bin on each side of BOWLS to (1) minimize interactions between organic-rich whale-bone and wood substrates, and (2) provide a control for the provision of open hard substrate (versus organic enrichment) on whale-bone/wood substrates. Species found in similar or greater abundance, body size and biomass on basalt, relative to bone and wood substrates, will be considered to be hard-substrate respondents.

Bone/wood/basalt substrates will be standardized where possible across treatments in terms of size and quality. Whale-bone substrates will consist of lumbar vertebrae from adult humpback whales (*Megaptera novaeangliae*), a species widely distributed in all oceans with migration routes and/or breeding grounds along the coasts of WA-OR and Brazil (Calambokidis et al., 2004; Zerbini et al., 2004; 2006). A suitable supply of humpback vertebrae (stored in freezers) and permits for conducting these experiments are available for both the NE Pacific and the Brazil margins (see letters from Sumida and Bernardino for Brazil). Vertebral processes will be removed from humpback vertebrae and each centrum transversely sectioned to produce two standard-sized cylinders of whale bone ~30 cm diameter and ~15 cm long. A transverse

Fieldwork Design

Six BOWLs will be deployed on the Washington-Oregon margin: three at ~1500 m depth (below the maximum depth of commercial trawling), and 3 at ~ 3000 m (Fig. 2). Distances between landers will be ~200-250 km, with total distances along and across isobaths of ~ 500 km (Fig. 2); recent work on the OR-CA margin on dorvillied polychaetes from methane seeps suggests that 500 km is an adequate scale to exhibit genetic structure within a depth zone (Halanych, in prep.). The use of similar distance scales within and between depth zones will facilitate distinguishing the effects of bathymetric change versus geographic distance on faunal connectivity (e.g., correlations to genetic structure). Landers will be deployed in spring (when whale migrations and natural wood inputs occur) and left on the seafloor for 15 months (Fig. 4). Previous studies of deep-sea bone/wood implantations on forested continental margins indicate that substantial colonization and substrate decomposition by bone/wood decomposers, including *Osedax/Xylophaga*, commonly occurs within 15 mo (Tuner, 1973, 1977; Smith and Baco, 2003; Braby et al. 2007; Voight et al., 2007; Stoeckle et al., 2007; Palacios et al., 2009; Lundsten et al., 2010a & b; Bernardino et al., 2010).

Deployments and recoveries of BOWLs on the WA-OR margin will be conducted during two 12-day cruises using a UNOLS vessel (e.g., the *RV Wecoma*) out of Newport, OR or Seattle, WA. BOWLs will be designed and built at UH, shipped to the University of Washington's Friday Harbor Laboratories for experimental substrate attachment and field testing (using 3 days of *RV Centennial* time), and then transported to Newport, Oregon or Seattle for deployment. Following BOWL recoveries, experimental substrates will undergo initial processing on shipboard; all experimental substrates will then be off-loaded from the research vessel at Friday Harbor Laboratories for more complete analyses. Processing and initial analyses of faunal samples from bone, wood, and basalt substrates will be conducted within the framework a summer field course at Friday Harbor Laboratories, titled *Biodiversity, Connectivity and Ecosystem Function in the Deep Sea* to be taught by C. Smith and K. Halanych (see **Broader Impacts** section, and letter of support from Ken Sebens, Director of Friday Harbor Laboratories).

During the BOWL recovery cruise, multiple coring will also be conducted from the ship to collect background sediment-microbial assemblages for comparison with bone/wood/basalt microbial communities (see **Activity and abundance of anaerobic bone/wood decomposers and chemoautotrophs**). Parallel BOWL deployments will be conducted on the Brazil margin under the direction of Drs. Sumida and Bernardino (see Fig. 2 and letters of collaboration).

Data Collection and Analysis

Shipboard sample processing. Immediately after shipboard recovery, experimental substrates will be subsampled for microbiology and then immersed in sterile chilled seawater in a cold room and quantitatively photographed to allow displacement volume estimation and mapping of epifauna. Water volume loss after removal from immersion (pore-space volume) and wet weight of each experimental substrate will then be rapidly measured to allow assessment of mass and volume loss during deployment. Each substrate will be x-rayed using a portable x-ray machine to facilitate for counting of *Osedax/Xylophaga* and analysis of the distribution and volume of their burrows (c.f. Tyler et al., 2007). Whale bones will then be further subsampled for microbial and lipid-content analyses (see Microbial Studies below; for lipid analyses, see Schuller et al. (2004)) and the macrofauna quantitatively removed from bone/wood/basalt substrates using the methods of Baco and Smith (2002). Box wash from BOWL bins will be carefully washed on 500- μ m sieves and fauna retained for analyses. Specimens will be catalogued, and selected subsamples fixed as appropriate for taxonomic (10% formalin), molecular genetic (95% ethanol, -80 C frozen), microscopic (glutaraldehyde), and stable isotopic (-80 C frozen) studies. Macrofaunal subsamples to be frozen or immediately distributed to other investigators (e.g., systematists), will be photographed under dissecting microscope to allow biovolume estimates for calculation of biomass. Following removal of macrofauna, experimental substrates will be quantitatively retained and frozen to allow later biogeochemical analyses (e.g., erosion of bone mass).

Macrofaunal Sorting and Taxonomic Identifications. During the Friday Harbor Laboratories course and subsequently in the laboratory at UH, macrofauna from experimental substrates will quantitatively sorted to family/genus, and biomass determined nondestructively by wet weight, or by photomicrography and biovolume models (e.g., Briones-Escobar and Soto, 1997). Macrofauna will then be identified to

species with existing UH expertise and the aid of taxonomic experts (as in Baco and Smith, 2002). The following experts will collaborate in taxonomic/phylogenetic analyses (see letters of collaboration): Adrian Glover, Thomas Dahlgren, Helena Wiklund, polychaetes; Janet Voight, xylophaginae). Other taxonomists have expressed interest in our material as follows: A. Waren (gastropods), M. Sheador (amphipods), E. Vetter (leptostracans), John Taylor and Emily Glover (lucinids), and Gordon Paterson (cirratulids and nereids).

Macrofaunal Species Diversity. Experimental substrates on our landers will be standardized in size, and associated macrofaunal assemblages quantitatively recovered, facilitating biodiversity comparisons. We will follow the general recommendations of Magurran (2004), using species richness per standardized sampling unit (bin), rarefaction diversity, Simpson's index, and Pielou's Evenness to explore diversity variations across treatment types, lander positions, depths, and ocean basins (cf. Bernardino et al., 2010).

Faunal genetic, phylogenetic and phylogeographic studies. To investigate phylogenetics of the fauna of bone/wood/basalt experimental substrates, we will focus on key taxa (e.g., *Osedax*, *Xylophaga*, dorvilleids, chrysopetallids, polynoids), using a variety of analytical techniques, including light and electron microscopy, DNA sequencing and microsatellite analyses. Because this project is examining diversity and variation at multiple spatial scales, we will use a multi-tiered approach to cover a range of evolutionary time scales. First, specimens will be identified using external morphological characters and placed within the existing systematic framework. Secondly, for taxa or individuals of interest, phylogenetic analyses will be undertaken using both nuclear and mitochondrial gene loci (including 18S rRNA, cytochrome oxidase 1 and cytochrome b, which provide a range of temporal scales and will allow comparison to existing data). This effort will be augmented by existing collections in the laboratories of Smith, Halanych, Glover, and Dahlgren to provide a broader spatial scale. Halanych has considerable experience with invertebrate phylogenetics and thus we will follow the data collection and analyses protocols used daily in his lab (eg Passamaneck and Halanych 2004, Thornhill et al., 2008). Lastly, species obtained in appropriate numbers (within and across basins and bathymetric ranges) will be subjected to population-genetic analyses using microsatellite markers. We have opted for microsatellites because of (1) the advantages of this multilocus approach, and (2) cost efficiency once primers have been developed. We are aware that some taxa are reportedly notorious for their lack of microsatellite regions (lepidopterans - Meglec et al 2004, birds - Primmer et al 1997), but the use of a next generation sequencing approach will provide numerous potential primer pairs. We will follow standard enrichment protocols (Zane et al 2002, Glenn & Schable 2005, Selkoe & Toonen 2006) to isolate fragments with di-, tri- and tetranucleotide repeats. Libraries will be subjected to next-gen sequencing, which is a fast, low-cost and effective means for generating such markers (Abdelkrim et al 2009, Rasmussen & Noor 2009). Previously, we have used 454 sequencing but we will use the most cost effective and appropriate approach when the work is undertaken. Following data assembly, primers will be designed for fragments containing 6-10 repeats and appropriate flanking regions. Once optimized, products will be run on a Beckman CEQ8000 with a size standard, and suitability of each locus assessed. We propose to identify ~15 appropriately polymorphic loci for at least 4 species (e.g., an *Osedax* sp., a *Xylophaga* sp., and 2 others). Numbers of individuals to be analyzed will depend on sampling, but we expect approximately 250-400 individuals per species. Following allele scoring, analytical methods will be used to identify potentially problematic loci (eg excess homozygotes with MICROCHECKER - Van Oosterhout et al 2004; linkage disequilibrium using MICROSATELLITE ANALYZER - Dieringer & Schlötterer 2003; neutrality DETSEL -Vitalis et al 2003). In order to infer genetic structure, and ultimately degrees of connectivity between populations, we will use STRUCTURE 2.2 (Pritchard et al 2000) and BAPS 3.1 (Corander et al 2003), as well as ARLEQUIN v3.1.

These studies will be conducted in collaboration with experts on polychaetes, including *Osedax* (Drs. Adrian Glover, Thomas Dahlgren and Helena Wiklund) and on xylophaginae (Dr. Janet Voight, see letters of collaboration). As appropriate, species descriptions for new taxa will be created.

Ecosystem Function Measurements: Ecosystem functioning involves a variety of processes, including organic matter decomposition, biomass production, transfer of organic matter to higher trophic levels, organic matter consumption, and nutrient regeneration (e.g., Danovaro et al., 2008). We will measure key functions of organic matter decomposition and production of biomass by decomposers, total macrofauna, and predators on our bone/wood/control substrates. We will also evaluate aspects of community structure

highly relevant to ecosystem function, in particular the development of food-web complexity in bone/wood fall substrates. Functional parameters measured will include: bone/wood mass loss, bone/wood volume loss, lipid depletion in whale bones, total macrofaunal biomass production, higher trophic level (predator) biomass production, and development of food-web complexity including chemoautotrophic and methanotrophic pathways (based on trophic-group, species-richness analyses, and selected δC^{13} , δN^{15} , and $\delta^{34}S$ analyses) over the 15-month deployment period. Methods employed will be similar to those used or reviewed in Smith and Baco (2003), McCutchan et al. (2003), Schuler et al. (2004), Demopoulos et al. (2007), McLoed et al. (2007, 2010), Thurber et al. (2009), and Bernardino et al. (2010).

Activity and abundance of anaerobic bone/wood decomposers and chemoautotrophs (to be conducted by Dr. Tina Treude, IFM-GEOMAR, Kiel, Germany, see letter of collaboration): Anaerobic microbial pathways of organic carbon degradation, such as sulfate reduction and methanogenesis, depend on the delivery of short-chained intermediates produced by the more powerful aerobic degradation pathway as well as by fermentation (Jørgensen, 2000). In whale bones and wood, the microbial symbionts of *Osedax* and *Xylophaga*, respectively, contribute to the initial decompositional step of long-chained organic compounds, which can then fuel affiliated anaerobic degradation processes (Palacios et al., 2006; Treude et al., 2009). After the recovery of whale bones and wood parcels, we will study the activity of sulfate-reducing bacteria and methanogenic archaea, as part of the anaerobic degradation pathways, applying radiotracer techniques with ^{35}S -labeled (Kallmeyer et al., 2004) and ^{14}C -labeled substrates (Finke et al., 2007; Treude et al., 2007). After radiotracer incubations, hot spots of sulfate-reducing and methanogenic activity will be identified by 2D beta-microimaging of ^{35}S and ^{14}C that precipitated or is assimilated, respectively, into the bone and wood matrix (Treude et al. 2007, Treude et al. 2009). The potential activity of aerobic methanotrophic bacteria, which could establish at the bone/wood periphery due to methane production inside the bone/wood matrix, will be studied in incubations with ^{14}C -labeled methane (Treude and Ziebis, 2010). Two-dimensional distributions of dominant bacterial and archaeal groups that could be involved in anaerobic degradation pathways or chemosynthesis (methane and sulfide oxidation) will be determined by CARD-FISH (Pernthaler et al., 2002) in bone/wood thin sections produced under cryostat (Treude et al. 2007). Oligonucleotide-probes for CARD-FISH analyses will be selected according to metagenomic data bases produced from the same materials (see Microbial Metagenomic Analyses below). Finally, 2D activity (radiotracer technique) and abundance of dominant bacterial and archaeal groups (CARD-FISH) will be compared. In order to study the background sedimentary microbial community from which the bone/wood substrate could be colonized, background sediments (0-25 cm depths from multiple cores) near each lander position will be analyzed for microbial activity (sulfate reduction, methanogenesis, methane oxidation; Jørgensen, 1978) as well as the abundance of important microbial groups that were identified in bones/wood.

Microbial Metagenomic Analyses (To be conducted by Drs. Marie-Anne Van Sluys and Vivian Pellizari, University of Sao Paulo, see letter of collaboration): Microbial metagenomic analyses of the whale-bone and wood microbial assemblages be addressed by the use of standard procedures for DNA sample extraction with no need for organism isolation. Total DNA will be prepared according to high through-put sequencing technology basically for longer reads (500 bp in 454-Roche platform, or other appropriate technology). The resulting high quality reads will be analyzed using online databases such as MG-RAST (<http://metagenomics.anl.gov/>) and MEGAN 4 (<http://ab.inf.uni-tuebingen.de/software/megan/>) to provide up-to-date environmental information. Initially, a panel of the general diversity of the Bacteria and Archaea, as well as potential Eukarya and Viruses, will be defined based on phylogenetic properties of the sequenced DNA. Then, a specific metabolic map for each bone/wood sample location plus a comparative map will be achieved by laying the genetic potential revealed by the sequenced reads onto KEEG metabolic maps.

Statistical Analyses: Data will be tested for adherence to assumptions of normality, independence of error terms, and equality of variance and transformed where possible to meet assumptions. Nested analysis of variance will be used to address lander, position (i.e., along isobath), bathymetric, and basin effects. Correlation and regression analyses (including Generalized Linear Models for non-normal data sets) will be used to explore the degree of association among different factors (cf. Quinn and Keogh, 2002; Menge et al., 2003). ANCOVA will be used to explore relationships between decomposer (i.e., *Osedax* /*Xylophaga*) diversity and abundance, and the diversity of other macrofauna and microbial assemblages.

Additional community comparisons across treatment types, depths, and ocean basins will be addressed using multivariate analyses (e.g., non-Metric Multidimensional Scaling, PCA) in Primer 6 software.

Scientific Team – Responsibilities and Coordination

We have built an integrated team to evaluate biodiversity, connectivity and ecosystem function in deep-sea whale-bone and wood falls. Craig Smith, who will serve as overall project leader, has worked extensively on the biodiversity and ecology of organic-rich falls, and has substantial experience engineering and building free-vehicle systems for studies of deep-sea ecosystems. Smith will build and test the bone/wood landers, organize and run the WA-OR field program, oversee sample collection and distribution, and conduct the macrofaunal biodiversity and ecosystem function studies in his laboratory. Kan Halanych has extensive experience in molecular studies of invertebrate evolution, phylogenetics and connectivity; he will lead the macrofaunal molecular studies, overseeing faunal sampling and conducting molecular analyses. Both PIs will participate in the FHL field course and outreach activities. Key collaborators will also contribute substantially to this project (see letters of collaboration). Janet Voight, an expert in xylophagian taxonomy and biology (Voight, 2007, 2008, 2009), will participate in the BOWL recovery cruises, will identify all xylophagian species collected, and will describe those new to science. Benthic ecologists Paulo Sumida and Angelo Bernardino will run the Brazil Margin field program with funding already in hand from FAPESP, Brazil. They will build and deploy a parallel set of BOWLS, and process Brazilian samples. Microbial ecosystem function studies will be conducted by Tina Treude, who has extensive experience studying the activity and abundance of anaerobic bone/wood decomposers and chemoautotrophs. To compliment Treude's efforts, metagenomic analyses of microbial biodiversity will be conducted by the Brazilian collaborators Marie-Ann Van Sluys and Vivian Pellizari, who have extensive experience and resources for such studies at the University of Sao Paulo. Taxonomic identification of collected polychaetes, including *Osedax*, will be conducted in collaboration with the polychaete experts Adrian Glover and Thomas Dahlgren.

Cruise logistics and sampling requirement for PIs and collaborators will be coordinated at the beginning of the project through conference calls, and through formulation of a detailed plan for sampling and sample distribution, developed with input and concurrence of all PIs and collaborators. All PIs and collaborators (or their representatives) will participate in the bone/wood lander recovery cruise on the WA-OR margin, and most will participate in bone/wood lander recoveries on the Brazil margin. In the third year of the project, all PIs and key collaborators will participate in a two-day data integration workshop to present initial project results, integrate data sets, and to plan collaborative, integrated publications and outreach efforts (e.g., press releases associated with publications).

iv. Outreach and Broader Impacts

This project is designed to have broader impacts in four areas: (1) graduate and undergraduate education within our institutions, (2) development of a new summer course on *Deep-Sea Biodiversity, Connectivity and Ecosystem Function* at Friday Harbor Laboratories (FHL) and at the University of Sao Paulo, Brazil, (3) outreach to the general public through websites, blogs and open houses, and (4) scientific contributions. (1) At least two graduate students will conduct their PhD research within this project, training future researcher in biological oceanography. In addition, we will take several undergraduate students from UH's Global Environmental Sciences degree program, undergraduates from Auburn University, and graduate/undergraduate students participating in the FHL course on our BOWLS recovery cruise on the WA-OR margin. We will advise UH and Auburn undergraduate students in the development of senior theses on topics within the BOWLS project. Finally, material from this project will be incorporated into undergraduate and graduate courses we currently teach in the Global Environmental Sciences and Marine Biology programs at UH and Auburn. (2) We will develop a new a summer field course at in the second year of this project, using, in part, BOWLS samples collected during the recovery cruise. Availability of these novel deep-sea samples will substantially broaden the materials and organisms available for the course. The 14 student course will be titled *Deep-Sea Biodiversity, Connectivity and Ecosystem Function*, and will include guest lectures from many of our international collaborators, who will be disembarking from the BOWL recovery cruise. We will use the resources and expertise of FHL to ensure the participation of under-represented minorities (see letter of support from Ken Sebens of FHL). We have requested \$24,000 in stipends to help support participation of top-level graduate and advanced undergraduate students in the course; additional resources for student

scholarships will be made available on a competitive basis by FHL. A similar course, at no cost to NSF, will be offered by Smith and Halanych through the University of Sao Paulo in Brazil (see letters of collaboration from Bernardino and Sumida), leading to significant international capacity building from this project. (3) Public outreach will include: maintenance of project web sites and cruise blogs at both UH and Auburn (previous cruise blogs have received hits from >80 countries); and presentations on our project at SOEST and Auburn open houses, which are attended by >1000 people annually (see Outreach Office letter from Ewald at Auburn). (4) We will present our project results at international scientific meetings and at international conservation forums (e.g., the annual meeting of Pew Fellows in Marine Conservation), and will publish our results in top-tier, peer reviewed scientific journals.

v. Significance of Proposed Research

Patterns of biodiversity, connectivity and ecosystem function in whale-bone/wood-fall faunas remain very poorly studied on large (i.e., regional to inter-basin) scales even though these metacommunity systems are widely distributed in the deep sea and may offer important insights into dispersal, adaptive radiation, and ecosystem function in the ocean. We expect our quantitative bone/wood lander studies to (1) reveal how population and community connectivity can vary with isolation by depth, distance, and ocean basin for specialized and generalized components of the bone/wood biota, yielding fundamental insights into processes of dispersal and evolution in the deep sea. We also expect to show (2) how the diversity of ecosystem engineers (*Osedax* and *Xylophaga*) interacts with the structure and function of whale-bone/wood-fall assemblages, potentially controlling such key ecosystem attributes as species richness (for both microbes and macrofauna), the nature of microbial metabolism, and rates of bone/wood decomposition. **To our knowledge, this will be the first experimental study of interactions between the diversity of key engineering species and ecosystem structure and function in the deep-sea, allowing us to test the generality of models developed in detritus-based terrestrial and freshwater ecosystems in the largest detritus-based ecosystems in the biosphere.** Ultimately, whale-bone and wood falls may provide useful models of adaptive radiation in ephemeral, ecologically favorable (i.e., food-rich) habitats imbedded in extreme ecosystems (in particular, the oligotrophic deep sea).

Our studies of whale-bone/wood falls also may provide insights into the response of deep-sea ecosystems to anthropogenic forcing. The inputs of whale bones and wood to the deep sea have been substantially altered by human activities such as whaling and deforestation (e.g., Butman et al., 1995; 1996; Smith, 2006; Voight, 2009) and our two primary study regions, the NE Pacific and SW Atlantic, have different histories of whaling, whale population recovery, and deforestation. For example, great whales in the SW Atlantic were heavily depleted early in the 20th century, and the main coastal migratory species along the SE Brazilian coast, the humpback (*Megaptera novaeangliae*), remains at a small fraction of its original population (Andriolo et al., 2006). In contrast, in NE Pacific the coastally migrating gray whale has rebounded to substantial population levels (Alter et al., 2007), and other great whale stocks in the North Pacific were depleted in the mid 20th century, leaving little time lag for extinction of whale-bone fauna (Smith 2006). In addition, historical deforestation has been relatively minor in NE Pacific and very heavy in Atlantic rainforests of Brazil (Brooks et al., 1999). It seems very likely that regional patterns of biodiversity, population size, connectivity, and ecological function in whale-bone/wood-fall assemblages have been impacted by these varying regional patterns of whale/wood resource use and ecosystem alteration by humans; we expect that our standardized whale-bone and wood fall implantation experiments (i.e., the “comparative experimental approach” (Menge et al., 2002, 2003) should help substantially to elucidate these anthropogenic impacts.

Finally our bone/wood landers (or BOWLs) have the potential to provide standardized experimental systems, which yield adequate samples sizes of a range of species and life-history types, to elucidate general patterns of connectivity and barriers to dispersal in the deep ocean. Our experimental results on the WA-OR and Brazil margins should indicate whether BOWLs may be useful to explore general patterns of connectivity in the detritus-based deep sea.

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- **Wilson, N.G., Hunter R.L., Lockhart S.J., Halanych K.M. 2007 Absence of panmixia in the Antarctic 'circumpolar' crinoid *Promachocrinus kerguelensis* Carpenter, 1888. *Marine Biology* 152, 895-904.
- **Wilson, N.G., Schrodli M., Halanych, K.M. 2009 Ocean barriers and glaciation: evidence for explosive radiation of mitochondrial lineages in the Antarctic sea slug *Doris kerguelensis* (Mollusca, Nudibranchia). *Molecular Ecology* 18, 965-984.
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Curriculum Vitae
CRAIG RANDALL SMITH

Address:

Department of Oceanography
University of Hawaii at Manoa
1000 Pope Road

Honolulu, HI 96822 Telephone: 808-956-7776 email: craigsmi@hawaii.edu

Birthplace: Bay Shore, NY

Date: 28 Aug 1954

Education:

B.S., 1977, with high honors, Biological Science, Michigan State University

Ph.D., Dec 1983, Biological Oceanography, University of California at San Diego, Scripps
Institution of Oceanography

Professional Experience:

1995-present: Professor, Department of Oceanography, University of Hawaii at Manoa

1995-1998, 2004-2007: Chair, Biological Oceanography Division, University of Hawaii at
Manoa

1988-1995: Associate Professor, Department of Oceanography, University of Hawaii at Manoa

1986-1988: Research Assistant Professor, School of Oceanography, University of Washington

1985-1986: Postdoctoral Res. Associate, School of Oceanography, University of Washington

1983-1984: Postdoctoral Scholar, Woods Hole Oceanographic Institution

Major Research Interests:

Seafloor ecology and oceanography including processes of disturbance, colonization and
community succession, deep-sea reducing habitats, pelagic-benthic coupling and anthropogenic
impacts on the ocean, climate change in Antarctica

**Five Publications Most Relevant to this Proposal (out of 122 published or in press, H Index
= 34):**

Smith, C.R. and A. R. Baco. 2003. The ecology of whale falls at the deep-sea floor. *Oceanogr.
Mar. Biol. Ann. Rev.*, 41: 311-354.

Schuller, D., D. Kadko, and C. R. Smith. 2004. Use of $^{210}\text{Pb}/^{226}\text{Ra}$ disequilibria in the dating of
deep-sea whale falls. *Earth Planet. Sci. Lett.* 218:277-289.

Smith, C. R. 2006. Bigger is better: The role of whales as detritus in marine ecosystems. *In
Whales, Whales, Whaling and Ocean Ecosystems*, J.A. Estes, D.P. DeMaster, R.L.
Brownell Jr., D.F. Doak, and T.M. Williams (eds)., Editors. University of California
Press, Berkeley, CA, USA, pp. 286 – 301.

Treude, T., C. R. Smith, F. Wenzhöfer, E. Carney, A. F. Bernardino, A. K. Hannides, M. Krüger,
A. Boetius. 2009. Biogeochemistry of a deep-sea chemosynthetic whale fall: rates and
patterns of microbial sulfur and carbon metabolism. *Mar. Ecol. Progr. Ser.* 382: 1–21.

Bernardino, A.F., C.R. Smith, I. Altamira, A.R. Baco-Taylor, and P. Sumida. 2010. Macrofaunal succession in sediments around kelp and wood falls in the deep NE Pacific and community overlap with other reducing habitats. *Deep-Sea Research I*, 57: 708–723.

Five Additional Publications:

Distel, D.L., A.R. Baco, E. Chuang, C. Cavanaugh, W. Morrill and C.R. Smith. 2000. Do mussels take wooden steps to deep-sea vents? *Nature*, 403: 725-726.

Baco, A. R. and Smith, C. R. 2003. High biodiversity levels on deep-sea whale skeletons. *Mar. Ecol. Progr. Ser.* 260: 109-114.

Demopoulos, A.W.J., B. Fry, B. and C.R. Smith. 2007. Food-web structure in exotic and native mangroves: a Hawaii-Puerto Rico comparison. *Oecologia*, 153:675–686.

Smith, C.R. , F. DeLeo, A. Bernardino, A. Sweetman, and P. Martinez. 2008. Abyssal Food Limitation, Ecosystem Structure and Climate Change. *Trend. Ecol. Evol.* 23: 518-528.

Smith, C.R., L. Grange, D. L. Honig, L. Naudts, B. Huber , L. Guidi, and E. Domack. 2011. A large, population of king crabs in Palmer Deep on the West Antarctic Peninsula and potential invasive impacts. *Proceedings of the Royal Society B*, in press.

Synergistic Activities (selected): 2003: Keynote speaker and discussion leader, 5th International Conference on the Environmental Future, *Future of Aquatic Ecosystems*, Zurich, Switzerland. 2004: Co-Organizer, *Ecology of the Antarctic Sea Ice Zone – Final Symposium*, Korcula, Croatia. 2004-2007: Pew Fellow in Marine Conservation, Design of Marine Protected Areas for Deep-Sea Seamounts, Nodule Fields, and Chemosynthetic Habitats; 2003-2010: Co-PI *CoML Census of Diversity of Abyssal Marine Life*; 2004-2010: Steering Committee, CoML ChEss program; 2007-2009: Organizer, Pew Foundation workshops to *Design Marine Protected Areas for Seamounts and the Abyssal Nodule Province in Pacific High Seas*; 2006 onward: Associate Editor *Marine Ecology*; 2008: NSF review panel for Antarctic Organisms and Ecosystems Program; 2009 onward: Associate Editor *Marine Biodiversity*; 2011: Invited speaker, Gordon Research Conferences on Polar Marine Science, *Exploring Complex Systems in Polar Marine Science*, Ventura, CA; 2011: UNOLS Polar Research Vessel Committee.

Graduate Students and Postdoctoral Advisees: Steven Brumsickle (M.S. 1989), Bruce Bennett (M.S. 1990), Helmut Kukert (M.S. 1990), Shawn Doan (M.S. 1994), Paul Parnell (M.S. 1992, Ph.D. 2000), Daniel Hoover (M.S. 1995), Amy Baco (PhD 2002) , Robert Miller (M.S. 1997), Amanda Demopoulos (M.S. 2000, PhD 2004), Sarah Mincks (PhD 2005), Bryan Nakahara (M.S. 2007), Angelo Bernardino (PhD 2009), Pavica Srsen, Fabio Cabrera de Leo, Dr. Paulo Sumida, Dr. Adrian Glover, Dr. Leniack Menot, Dr. Elizabeth Galley, Dr. Sarah Mincks, Dr. Andrew Sweetman, Dr. Victor Evrard, Dr. Laura Grange.

Additional Collaborators and Co-authors in Last Five Years: Amy Baco, Lisa Levin, Paul Tyler, Eva Ramirez, Eugene Domack, Scott Ishman, Amy Leventer, Bruce Huber, Rhian Waller

Graduate Advisor: Robert R. Hessler

Postdoctoral Advisors: Howard L. Sanders, Peter A. Jumars

Biographical Sketch

Name: Kenneth M. Halanych
Address: Biology Dept., 101 Rouse Bld.
Auburn University
Auburn, AI 36849
Phone: (334) 844-3222 **FAX:** (334) 844-2333 **Email:** ken@auburn.edu

Professional Preparation

postdocs

Rutgers University	Marine Invert. Systematics	1996 – 1998
Southern Methodist University	Aging	1995 - 1996
University of Pretoria	Mammal Systematics	1994 – 1995 + 1996

education

University of Texas	Zoology	Ph.D. 1994
Wake Forest University	Biology	B.S. 1988

Appointments

Auburn University –	Professor	2009 – present
	Associate Professor	2003 – 2009
Woods Hole Oceanographic Institution	Associate Scientist	2002
	Assistant Scientist	1998 – 2002
Marine Biological Laboratory -	Adjunct Scientist	1999 – 2002

Publications

(i). Five publications most closely related to proposal (out of ~80 total):

- Mahon, A.R., D.J. Thornhill, J.L. Norenburg, **K.M. Halanych**. DNA discovers missing Antarctic nemerteans and exposes a decades-old cold case of asymmetric inventory. *Polar Biology*. **33**:193-202. (2010)
- Wilson, N.G., M Schrödl, and **K.M. Halanych**. Ocean barriers and glaciation: explosive radiation of Pleistocene lineages in the Antarctic sea slug *Doris kerguelenensis* (Mollusca, Nudibranchia). *Molecular Ecology* **18**: 965–984. (2009)
- Thornhill, D. J., A. R. Mahon, J. L. Norenburg, and **K. M. Halanych**. Open-ocean barriers to dispersal: a test case with the Antarctic Polar Front and the ribbon worm *Parborlasia corrugatus* (Lineidae: Nemertea). *Molecular Ecology*. **17**: 5104-5177. (2008)
- Thornhill, D. J., A. A. Wiley, A. L. Campbell, F. F. Bartol, A. Teske, and **K. M. Halanych**. Endosymbionts of *Siboglinum fiordicum* and the phylogeny of Siboglinidae (Annelida) endosymbionts. *Biological Bulletin*. **214**:135-144. (2008)
- Shank T.M. and **K.M. Halanych**. Toward a mechanistic understanding of larval dispersal: insights from genomic fingerprinting of the deep-sea hydrothermal vent tube-worm *Riftia pachyptila*. *Marine Ecology* **28**:25-35. (2007)

ii). Five other significant publications:

- Kocot, K.M., J.T. Cannon, C. Todt, M.R. Citarella, A.B. Kohn, A. Meyer, S.R. Santos, C. Schander, L.L. Moroz, B. Lieb & K.M. Halanych. **Phylogenomics reveals deep molluscan relationships**. *Nature* (in press).
- Struck, T.H., N. Schult, T. Kusen, E. Hickman, C. Bleidorn, D. McHugh, and **K.M. Halanych**. 2007. Annelid phylogeny and origins of Sipuncula and Echiura. *BioMed Central: Evol. Biol.* **7**: 57 (11 pages). (2007)

- Halanych, K. M.** 2005. Molecular phylogeny of siboglinid annelids (a.k.a. pogonophorans): A review. *Hydrobiologia* **535**:297-307. (2005)
- Halanych, K. M.** The new view of animal phylogeny. *Annual Reviews of Ecology, Evolution and Systematics*. **35**: 229-256. (2004)
- Halanych, K.M.,** R. A. Feldman, and R.C. Vrijenhoek. Molecular evidence that *Sclerolinum brattstromi* is closely related to vestimentiferans, not frenulate pogonophorans (Siboglinidae, Annelida). *Biological Bulletin* **201**: 65-75. (2001)

Synergistic Activities

- Tree of Life - Metazoan page author
 Marine Lab course -
 Evolution and Development (w/ BJ Swalla) Friday Harbor Labs 5X 2001-2011
 Participation in WHOI summer student fellow program for undergraduates
 SICB symposium co-organizer – “Evolutionary Relationships of Metazoan Phyla” – 1998
 Organizer – “WormNet: Recent advances in annelid systematics, development, and evolution” 2005
 Co-Secretary - Division of Evolutionary Developmental Biology, Society of Integrative and Comparative Biology 2001
 Chair – Division of Systematic and Evolutionary Biology, Society of Integrative and Comparative Biology 2004-2006
 Associate Editor – *Biological Bulletin*. Jan. 2005- present, Editorial Board since Jan 2002.
 Editorial Board – *Marine Biology Research*. Jan 2005-present.
 Zoologica Scripta. Advisory Council. Jan 2006 – present.
 Marine Ecology – An Evolutionary Perspective. May 2008 – 2010.
 Participation in NSF Teacher Enhancement Award, College of Science and Math AU Explore outreach day, outreach sessions to help recruit scholarship students to AU College of Science and Math.
 Presentations to a total of 300 children in K thru 2nd at 3 different schools (groups of ~30)

Collaborators & Other Affiliations

Collaborators - Boore, J., Joint Genome Institute (on going); **Dahlgren, T. G.**, Goteborg University (on going, coauthor); **Raymond Lee**, Washington State University (co-PI) **Lisa Levin**, Scripps Institution of Oceanography (co-PI) **Martindale, M.**, University of Hawaii (ongoing); **McHugh, D.**, Colgate University, (on going); Levin, L. Scripps Institute of Oceanography (ongoing); **Rouse, G.W.** Scripps Institution of Oceanography (joint advisor) **Swalla, B. J.**, University of Washington (co-instructor); **Schander, C.**, Univ. of Bergen, (ongoing); **Scheltema, A.**, WHOI, (ongoing); **Scheltema, R.**, WHOI (ongoing); **Seaver, E.** Univ. of Hawaii (on going), **Wiebke Ziebis**, Univ. of Southern California (co-PI);

(ii) Graduate and Post Doctoral Advisors

David M. Hillis,	University of Texas	Dissertation
Robert C. Vrijenhoek	MBARI	Postdoctoral
Terence J. Robinson	Stellenbosh University, South Africa	Postdoctoral
William C. Orr	Southern Methodist University	Postdoctoral

(iii) Thesis Advisor and Postgraduate-Scholar Sponsor

N Wilson, T Struck, TM Shank, TG Dahlgren, D Thornhill, A Mahon, E Borda – postdocs.
 Y Passamaneck, RM Jennings, R Belcher, A Janosik, J. Cannon, K. Kocot – Ph.D students