BIODIVERSITY, ECOSYSTEM ENGINEERING, AND TROPHIC ECOLOGY OF WHALE-BONE AND WOOD-FALL HABITATS IN THE DEEP NE PACIFIC: A CONTROLLED EXPERIMENTAL APPROACH

A DISSERTATION SUBMITTED TO THE GRADUATE DIVISION OF THE UNIVERSITY OF HAWAIʻI AT MĀNOA IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF

DOCTOR OF PHILOSOPHY
IN
OCEANOGRAPHY

MAY 2023

By
Emily L. Young

Dissertation Committee:

Craig R. Smith, Chairperson
Jeffrey C. Drazen
Kyle F. Edwards
Kenneth M. Halanych
Les E. Watling

Keywords: organic falls, deep sea, wood, whale bone, biodiversity, ecology

I dedicate this work to my family, Martin, Marivic, and Rachel Young, for their endless support, love, and encouragement.

ACKNOWLEDGEMENTS

First, I would like to express my deepest gratitude to my advisor, Dr. Craig Smith, for all the guidance, support, and opportunities he provided me throughout my PhD. I also extend my deep appreciation to my dissertation committee members, Drs Jeff Drazen, Kyle Edwards, Ken Halanych, and Les Watling, for their advice and contributions throughout my dissertation work. From each of you I have learned to become a better scientist, and for that I am truly grateful.

The research was primarily funded by National Science Foundation grants awarded to Drs Craig Smith and Kenneth Halanych. I am also grateful for funding support from the Denise B. Evans Fellowship in Oceanographic Research, the Field Museum of Natural History Visiting Scholarship, the University of Hawaiʻi at Mānoa Graduate Student Organization Travel Grant, the Graduate Women in Science Hawaiʻi Chapter Research and Travel Grant, the STAR Achievement Scholarship and the J. Watumull Merit Scholarship.

I sincerely thank all collaborators for their contributions to this work, including Drs Janet Voight, Diva Amon, Nicholas Higgs, Angelo Bernardino, Paulo Sumida, Mauricio Shimabukuro, Tina Treude, and Stefan Krause. My special thanks goes to Iris Altamira, who contributed indispensable expertise and many hours sorting and identifying macrofaunal samples. Thanks to all of those involved in the fabrication, fieldwork, and processing of the BoWLs experiments.

I am deeply grateful to support provided by the Department of Oceanography over the years. My thanks especially go to Anne Lawyer, Kristin Momohara, Catalpa Kong, Mireya Inga, and Dr Margaret McManus for their support. I also extend my thanks to all professors from whom I have learned to become an oceanographer and an academic.

Finally, my warmest thanks go to my friends and family, near and far, especially Drs Sabrina Diemert, Tobias Friedrich, Jesse van der Grient, Jessica Perelman, and Sarah Tucker, as well as Katherine Ackerman, Camille Adkison, Anamica Bedi de Silva, Amber Estes, Richard La, Kristen Miyano, Hannah Shadrach, and Gabrielle Stedman. This PhD would not have been possible without your friendship, love, and support.

ABSTRACT

Organic-fall habitat islands are established when large organic-rich parcels, such as whale bones or wood, sink to the generally food-poor deep-sea floor. Organic-fall communities may pass through a succession of ecological stages, modulated by key ecosystem engineers that influence the availability of habitat and food resources in these ecosystems. Because biodiversity and ecosystem functions at organic falls are likely to vary with substrate type, size, and deployment times, comparisons between ocean regions and depths are problematic. In this study, a replicated experimental approach has been used to control the effects of substrate type, size, and deployment times. Three major aspects of organic-fall ecology were explored: patterns and drivers of biodiversity, the importance of a wood-boring ecosystem engineer to ecosystem structure and function, and variations in trophic structure between whale-bone and wood-fall assemblages. Four benthic landers containing replicate whale-bone, wood, and inorganic control substrates were concurrently deployed for 15 months on the Washington-Oregon margin; two each at depths of ~1600 and ~2800 m, separated by distances of > 200 km. Whale-bone, wood, and inorganic substrates supported assemblages with different community structures, even within landers. Community composition was significantly different between depths and between landers within a depth, indicating variability on bathymetric and regional scales. Wood blocks at ~1600 m were heavily degraded by wood-boring xylophagaid bivalves, which consumed up to ~90% of wood-block mass. Xylophagaid boring and defecation increased habitat availability and complexity as well as the range of nutritional niches; this led to a high abundance of macrofauna inhabiting the borings inside the wood. Xylophagaid colonization was absent to mild in deeper wood blocks at sites further offshore, which we hypothesize results partly from lower propagule supply at increased distances from terrestrial forests. Bulk stable isotope analyses revealed that co-located whale-bone and wood assemblages had different trophic structures. Whale-bone and wood were dominant basal food sources; however, the relative importance of background particulate organic matter (POM) to faunal diets varied among taxa, functional groups, and between whale-bone and wood substrates, with background POM less important on wood. We hypothesize that labile particulate organic material in xylophagaid feces provides an especially important food resource at wood falls. This dissertation provides deeper insight into drivers of variability and quantifies some important aspects of organic-fall ecology.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1

Introduction

1.1 DEEP-SEA BIOLOGY

This dissertation addresses fundamental processes at the bathyal seafloor, a zone from 1000-4000 m depths that covers about 30% of the ocean floor. Bathyal habitats generally occur on continental margins and are sediment covered, providing habitat for a huge range of organisms, from microbes to megafauna (Wei et al., 2010). Continental margins are regions of high macrofaunal species diversity, in part due to high habitat heterogeneity and the presence of prominent environmental gradients (Grassle & Mackiolek, 1992; Levin & Dayton, 2009; Levin & Sibuet, 2012). The down-slope depth gradient is accompanied by environmental variations in pressure, temperature, oxygen and food availability, which are important drivers of species turnover and faunal standing stocks (Carney, 2005; Rex et al., 2006; Wei et al., 2010). Deep-sea ecosystems are generally considered food-poor; most nutrition sinks from the euphotic zone to the seafloor as particulate organic material (POM), with the supply attenuating with water depth and increasing distances from regions of high photosynthetic productivity (Lutz et al., 2007). However, hydrothermal vents, cold seeps, and organic-fall habitats provide important local exceptions to the food-poor deep-sea paradigm.

1.2 ORGANIC FALLS

Organic falls are habitat islands formed by organic-rich substrates sunken to the seafloor. These pulses of organic matter lead to enrichment of the otherwise food-poor deep-sea floor, providing nutrition and habitat for a range of organisms. As discussed below, organic falls influence the biodiversity, ecosystem function, and geochemistry of seafloor ecosystems, and are an important contribution to beta diversity on the deep-sea floor.

1.2.1 Organic-fall types

Organic-fall habitats can form on a range of large organic-rich substrates, including sunken carcasses of whales, large fish, cephalopods, reptiles, and jellyfish, as well as sunken plant material, such as wood and kelp (Turner, 1977; Smith, 1985; Smith & Baco, 2003; Bernardino et al., 2010; Sweetman & Chapman, 2011; Hoving et al., 2017; Bryant et al., 2022). This dissertation focusses on the organic-fall habitats created by sunken whale bones and wood. Sunken whale carcasses create “whale-fall” habitats (Smith & Baco, 2003). A 40-ton carcass, comprised of lipid-rich soft tissues and bones, contains around 1.6×10^6 grams of labile carbon

(Smith, 2007). Whale falls have been found in most ocean basins, with occurrences concentrated along migration routes and in calving and feeding grounds, typically around ocean margins (Smith et al., 2015). Terrestrial woody debris is an important component in many aquatic ecosystems (Maser & Sedell, 1994), and is regionally abundant in the deep sea (Wolff, 1979). Most wood is expected to enter the ocean from coastlines and river mouths, and storm-triggered landslides can move millions of metric tons of wood into the ocean in single events (West et al., 2011). Wood falls are also concentrated along continental margins, especially offshore of heavily forested coastlines. Although whale bones and wood are compositionally different, they are both hard substrates with high organic carbon content. Whale-fall and wood-fall can share some species (Smith & Baco, 2003; Amon et al., 2017a), and because of similarities in geochemical conditions to other reducing habitats such as vents and seeps, whale and wood falls may have played an important role in the radiation of deep-sea lineages (Distel et al., 2000; Baco-Taylor, 2002; Lorion et al., 2009; Lorion et al., 2013; Thubaut et al., 2013).

1.2.2 Successional stages

The decomposition of organic-rich substrates progresses through a series of overlapping successional stages, which are accompanied by changes in community structure, food sources and geochemical (reducing) conditions. Four overlapping stages are documented for whale falls (Smith & Baco, 2003). The "mobile scavenger" stage first occurs upon arrival of a whale carcasses to the sea floor, wherein soft tissues are consumed primarily by megafaunal scavengers, such as hagfish, sharks, and crustaceans. The fragmentation of the soft tissues by scavengers leads to localized enrichment surrounding the carcass and the establishment of the "enrichment opportunist" stage, wherein low-diversity, high-density assemblages of opportunistic polychaetes and crustaceans dominate. Anaerobic, sulfidic conditions are established by sulfate-reducing microbes in the "sulfophilic stage", both in the sediments surrounding the carcass, as well as within the lipid-rich bones. Sulfidic conditions fuel the chemoautotrophy of free-living and symbiotic sulfide-oxidizing microbes and support a range of chemosynthetically-dependent species. Finally, after organic matter has been exhausted from the skeleton, the inorganic remains provide a complex reef structure during the "reef stage". Similarly, Pop Ristova et al. (2017) described four successional stages at wood falls at the deep-sea floor. First, they describe a "specialist stage" beginning when specialist wood-boring fauna, most commonly xylophagaid bivalves, begin to degrade the wood. Next, they describe an "opportunist stage," wherein wood-borer biomass attracts and supports opportunistic detritus feeders, predators, and bacterivores. This is followed by the third, "sulfophilic stage," during which enhanced cellulose degradation leads to the development of sulfidic conditions, which support chemosynthetic organisms. Finally, a "senescence stage" is described, during which the wood-fall assemblage abundance declines as the wood is disintegrated and dispersed over surrounding sediments. The Pop Ristova et al. (2017) successional model does not consider either an initial microbial stage on wood falls (Kalenitchenko et al., 2018a; Kalenitchenko et al., 2018b) or the possibility of a reef stage. While these successional models are applicable to many observed organic-falls, temporal-spatial variability of the onset, duration, and biodiversity of organic-fall stages are expected due variations in environmental parameters, transport processes, and proximity of source populations, yet drivers of such variability remain poorly understood. It is often speculated that key ecosystem engineering taxa are important influencers of the establishment, duration, and progression of organic-fall successional stage (Turner, 1973; Grassle & Morse-Porteous, 1987).

1.2.3 Key ecosystem engineers

Key ecosystem engineers are organisms that significantly control the availability of biotic and abiotic resources to other organisms by modifying, maintaining, and/or creating habitats (Jones et al., 1994, 1997). At deep-sea organic falls, bone-eating *Osedax* siboglinid polychaetes and wood-boring xylophagaid bivalves have been widely regarded as key ecosystem engineers due to their specialization on, and modification of, bone and wood substrates, respectively (Wolff, 1979; Turner, 1973; Rouse et al., 2004).

Female *Osedax* polychaetes inhabit sunken whale bones by secreting acid to dissolve the inorganic carbonate matrix, and digest bone nutrients via endosymbiotic heterotrophic bacteria (Goffredi et al., 2005; Goffredi et al., 2007; Tresguerres et al., 2013; Moggioli et al., 2022). Bioerosion by *Osedax* alters bone habitats by (1) increasing structural complexity, (2) modifying oxygen and reduced-compound fluxes, and (3) destroying juvenile bones, which, in turn, influence microbial and macrofaunal assemblages, as well as the duration and progression of successional stages (Braby et al., 2007; Lundsten et al., 2010b; Higgs et al., 2011a; Amon et al., 2013; Smith et al., 2015; Alfaro-Lucas et al., 2017).

Xylophagaid bivalves are typically the primary drivers of wood degradation in the deep sea (Turner, 1973; Tyler et al., 2007; Voight, 2007; Bienhold et al., 2013). Xylophagaids create boreholes by rasping wood and digest cellulose from wood fragments via endosymbiotic cellulolytic bacteria (Distel & Roberts, 1997). The boreholes then provide habitat for xylophagaids and other organisms. The nitrogen content of wood is low, thus xylophagaids obtain their nitrogenous nutrition either via nitrogen-fixing endosymbionts, or by filtering particulate organic material from the water column (Voight et al., 2020). Wood boring activity by xylophagaids modifies the structural complexity of wood falls (initially increasing habitat space, and later destroying the overall wood-fall habitat), and xylophagaid fecal material may include wood-degrading microbes that serve as a labile food resource for other wood-fall fauna (Harbour et al., 2021a). Xylophagaids may also control reducing conditions throughout wood and surrounding sediments by (1) modifying oxygen and reduced compound fluxes between borehole interiors and wood surfaces, and (2) producing labile fecal material which provides organic enrichment, leading to the development of sulfidic niches (Bienhold et al., 2013; Kalenitchenko et al., 2018a). However, the implications of xylophagaid ecosystem engineering activity on wood-fall assemblage diversity, biomass, and abundance has yet to have been quantified.

1.2.4 Food sources and trophic ecology

Whale bones are rich in lipids and proteins, and wood in cellulose and lignin, but the organic components are only directly accessible to substrate specialists (Gessner, 2005; Higgs et al., 2011b). Specialist heterotrophic microbes can also decompose whale bone (Borchert et al., 2021) and wood (Bienhold et al., 2013; Fagervold et al., 2014) directly. Reduced compounds produced by microbial organic-matter decomposers can further fuel the growth of free-living and symbiotic chemoautotrophic bacteria (Deming et al., 1997; Smith & Baco, 2003; Treude et al., 2009; Kalenitchenko et al., 2015; Kalenitchenko et al., 2018b). Dense biofilms composed of heterotrophic and chemoautotrophic microbes on wood and bone surfaces, as well as on surrounding sediments can serve as an important food source for grazers and bacterivores (Bennett et al., 1994; Deming et al., 1997; Kalenitchenko et al., 2018b; Wiklund et al., 2009). Waste products of substrate specialists may be an important food source for organisms unable to utilize wood and bone directly. Xylophagaid fecal material contains partially digested wood fragments and microbial biomass that can be colonized by wood-decomposing microbes (Fagervold et al., 2014; Harbour et al., 2021a), which in turn may serve as labile and physically accessible food components for bacterivorous and deposit-feeding macrofauna. While fluxes of background, photosynthetically-derived POM at organic-falls may be many orders of magnitude lower than the organic carbon provided by organic-rich substrates (Smith, 2007), background POM may still may be an important food resource for at least some organic-fall fauna (Limén et al., 2007; Portail et al., 2016; Pereira et al., 2022) living on bone/wood substrates. The availability and relative importance of various food resources are likely to be highly dependent on organic-fall successional stage.

1.2.5 Variability in organic-fall ecology

Multiple drivers may lead to variability in various facets of organic-fall ecology, including organic-fall community composition and structure, progression of successional stages, ecosystem engineering activity, and trophic structure. For example, organic-fall community composition is influenced by the size (including volume and surface-area-to-volume ratio) and quality (which varies within and between tree and whale species) of organic-rich substrates (Lamlom & Savidge, 2003; Smith & Baco, 2003; McClain & Barry, 2014; Smith et al., 2015; Judge & Barry, 2016; Alfaro-Lucas et al., 2017). In addition, drivers/correlates of biodiversity and ecosystem function considered to be important for background deep-sea ecosystems, including depth, biogeographic region, and physicochemical conditions, may also influence organic-fall habitats (Braby et al., 2007; Voight, 2007; Fagervold et al., 2012; Romano et al., 2013; Smith et al., 2015; Amon et al., 2017a; Pop Ristova et al., 2017; Saeedi et al., 2019).

1.2.6 Organic-fall research

The serendipitous discovery of whale and wood-fall habitats and fauna has occurred throughout the world's oceans during seafloor imaging, during dives with remotely-operated and human-occupied vehicles (Smith et al., 1989; Amon et al., 2013; Sumida et al., 2016; Amon et al., 2017b), as well as through trawled wood and bone substrates (e.g., Dell, 1987; Gibbs, 1987; Marshall, 1987; McLean, 1992; Pailleret et al., 2007; Schwabe et al., 2015; Nishimoto et al., 2009). Such discoveries provide valuable insights into the natural ecology of organic-falls; however, important contextual information can be difficult to determine, such as the original volume/quality and species of the substrates, as well as the time of arrival of the substrate at the seafloor. High-resolution taxonomic identifications can be difficult to gain through imagery alone, and quantitative determinations of biodiversity may be unreliable following the recovery of single substrates and organisms by ROVs, HOVs and trawling.

The experimental implantation of organic-rich substrates in the deep-sea has contributed valuable insights into organic-fall ecology (Smith & Baco, 2003; Fujiwara et al., 2007; Gaudron et al., 2010; Bienhold et al., 2013; Cunha et al., 2013; McClain & Barry, 2014; Judge & Barry, 2016; Saeedi et al., 2019; Harbour et al., 2021b). Controlled experimental approaches (Menge et al. 2002; 2003) involving variations in selected independent variables (such as depth, location, and substrate types), while controlling for other variables (e.g., substrate volume and seafloor duration), can help elucidate important drivers of biodiversity, community structure, and ecosystem function through rigorous hypothesis testing.

1.3 THIS DISSERTATION

This dissertation investigates the ecology of deep-sea organic-fall habitats in the NE Pacific. Specifically, the (1) drivers of community structure and biodiversity, (2) ecosystem engineering activity, and (3) the trophic ecology at organic fall habitats, are explored via a comparative-experimental approach (Menge et al., 2002; Menge et al., 2003). Four benthic Bone and Wood Landers (BoWLs) carrying replicate whale-bone, wood, and control (inorganic) substrates were deployed to two depths (~1600 and ~2800 m) and spaced 200 – 400 km apart on the Washington-Oregon margin seafloor, for a total of 15 months (Figure 1.1). Analyses of the recovered substrates and associated biota provided the opportunity to quantify various aspects of organic-fall ecology under various environmental conditions.

Chapter 2 introduces the experimental approach, and documents how depth and substrate type influence community structure and diversity of wood and whale-bone habitats on the northeast Pacific margin. This chapter also addresses the natural history of dominant fauna.

Chapter 3 explores the ecosystem engineering role of xylophagaid bivalves by quantifying relationships between xylophagaid bivalve biomass and wood mass loss, as well as relationships between xylophagaid bivalve biomass and non-xylophagaid macrofaunal biomass, species richness, and evenness.

Chapter 4 elucidates the trophic structure of whale bone and wood assemblages and asks (1) whether trophic structure varies by substrate type, (2) whether organic-rich substrates are the primary food source for organic-fall macrofauna, and (3) how important background POM is as a food resource for various functional guilds.

Finally, **Chapter 5** summarizes the major conclusions of each data chapter, integrates discussion of the findings across chapters and other studies, outlines the significance of this research, and identifies future research directions to build on the results of this dissertation.

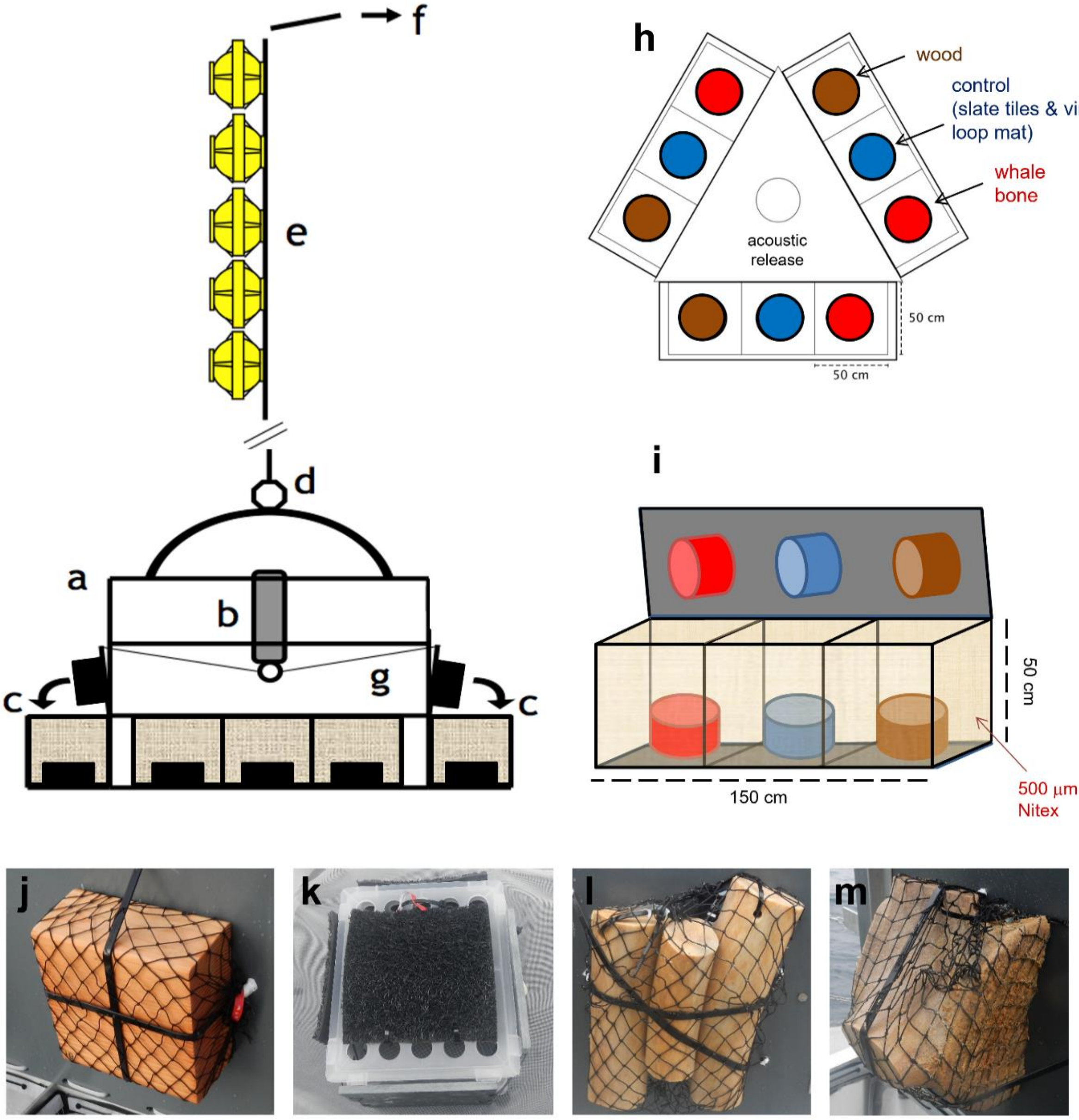

Figure 1.1 Schematic diagram and photos of Bone and Wood Landers. (a) Side view of a BoWL at the seafloor with bins open and substrates exposed. (b) Acoustic release releases bin doors (c,g) and drop the free-vehicle ballast weight (not shown) on an acoustic signal. (d) Flotation line and (e) glass flotation. (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. (j) Douglas fir wood substrate. (k) Control substrate, consisting of an upturned plastic crate with three 15 × 15 cm squares of vinyl loop mat and two 15 × 15 cm slate tiles attached. (l) Humpback whale rib bone packages. (m) Humpback whale vertebral half.

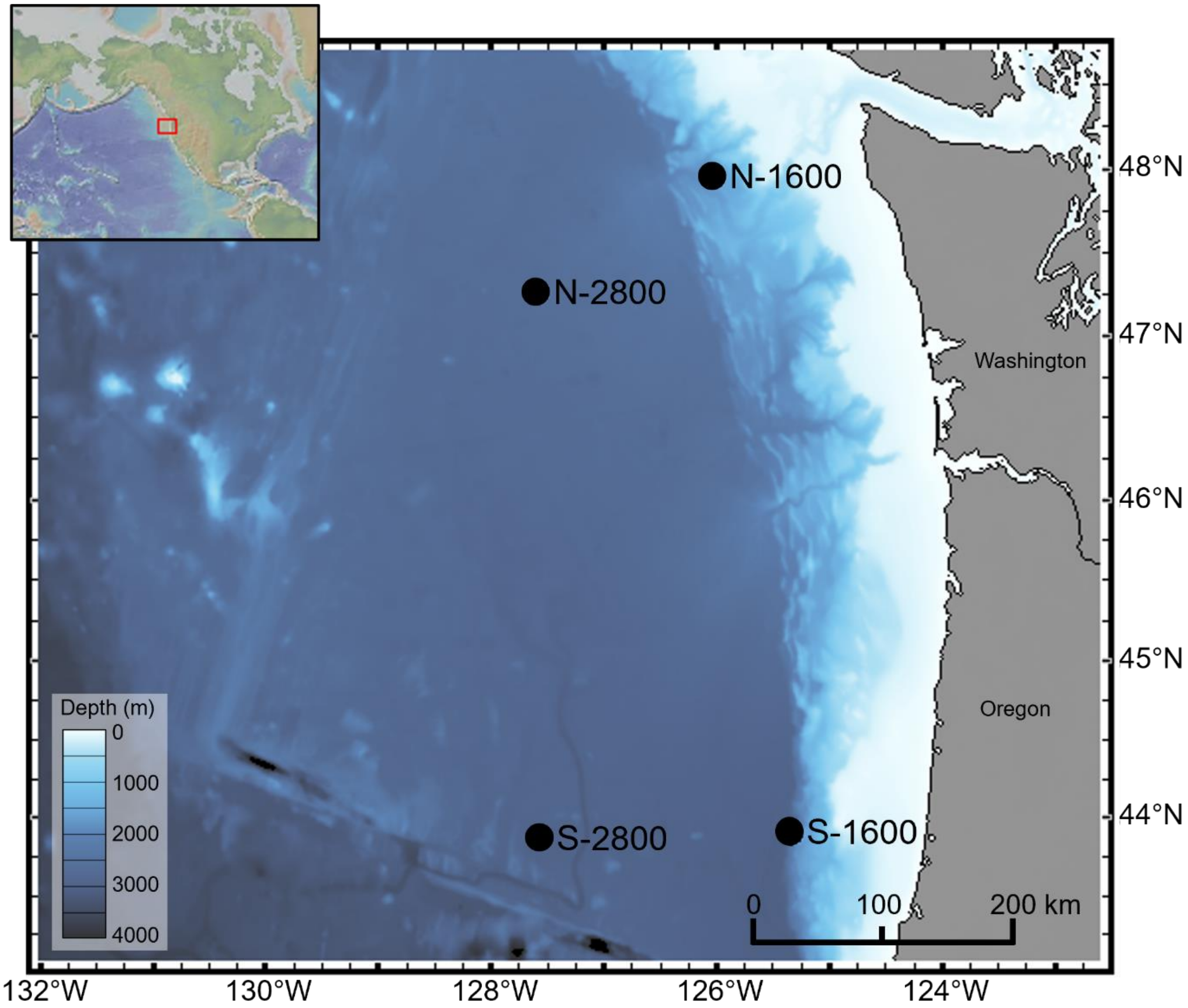

Figure 1.2 Positions of bone and wood landers on the Washington-Oregon (USA) margin, NE Pacific. Station names reflect geographic position (N: north; S: south) and approximate depth (1600 or 2800 m). Made with GeoMapApp (www.geomapapp.org)

CHAPTER 2

Depth and substrate type influence community structure and diversity of wood and whale-bone habitats on the deep NE Pacific margin

Published as: Young EL, Halanych KM, Amon DJ, Altamira I, Voight JR, Higgs ND, Smith CR (2022) Depth and substrate type influence community structure and diversity of wood and whale-bone habitats on the deep NE Pacific margin. *Mar Ecol Prog Ser* 687:23-42.
https://doi.org/10.3354/meps14005

2.1 ABSTRACT

Whale bones and wood on the deep-sea floor provide resource pulses that support characteristic faunal assemblages in an otherwise food-poor environment. To isolate the role of bathymetric and geographical drivers of organic-fall diversity and community structure, the study of organic-rich substrates of similar sizes, qualities, and seafloor durations is necessary. We used a comparative experimental approach to examine the roles of depth, location, and substrate type in structuring organic-fall faunal assemblages. Four free-vehicle landers containing replicate wood, whale-bone, and inorganic hard (control) substrates were deployed for 15 mo at depths of ~1600 and ~2800 m, spaced at ~400 km along the Washington-Oregon (USA) margin. The landers collected a total of ~84890 macrofaunal individuals of 144 species. Wood, bone, and control substrates supported assemblages with different community structures on all landers. Community composition was significantly different between depths and between locations at similar depths, indicating variability on regional and bathymetric scales. Wood blocks at ~1600 m were heavily degraded by wood-boring xylophagaid bivalves. Xylophagaid colonisation was lower in deeper wood blocks, which we hypothesize results partly from lower propagule supply as wood falls decrease in abundance with distance from terrestrial sources of wood. Bone-eating *Osedax* colonized whale bones, but bone degradation was low compared to some NE Pacific whale falls of similar duration; nonetheless, bones exhibited reducing conditions and supported sulfophilic species. Our study demonstrates quantitatively that co-located wood falls and whale bones support highly distinct, species-rich assemblages and thus promote biodiversity on the deep-sea floor.

Keywords: Deep sea; Organic falls; Wood; Whale bone; Community structure; Biodiversity; Continental margin

2.2 INTRODUCTION

Resource pulses are events of elevated, episodic, and ephemeral resource availability that influence ecological processes in a wide range of terrestrial and aquatic ecosystems (Yang et al., 2008). A pulsed provision of food to a system, such as carrion (Barton et al., 2013) and dead wood (Stokland et al., 2012) in terrestrial ecosystems, can have direct effects on consumer populations as well as indirect effects on community structure (Yang et al., 2010). The input of large, nutrient-rich parcels of organic matter into food-poor, deep-sea environments creates food-rich oases known as ‘organic falls’. Sunken animal carcasses, including those of whales ('whale falls'; Smith & Baco, 2003; Fujiwara et al., 2007; Lundsten et al., 2010a), large fish (Smith, 1985; Higgs et al., 2014), cephalopods (Hoving et al., 2017), and jellyfish (Sweetman & Chapman, 2011) , as well as sunken plant material such as wood (Turner, 1977; Romano et al., 2013; McClain et al., 2016) and kelp (Bernardino et al., 2010), can increase local organic-carbon flux to the seafloor by orders of magnitude (Smith, 2007; Smith et al., 2014). Organic-rich substrates, such as wood and whale bones, provide nutrition and habitat to a wide range of organisms on the deep-sea floor, and influence local geochemistry and ecology (Treude et al., 2009; Bernardino et al., 2010; Bienhold et al., 2013; Smith et al., 2014; Smith et al., 2015). Organic falls provide ecological and evolutionary opportunity and habitat heterogeneity, and ultimately promote biodiversity on the deep-sea floor.

Wood and whale falls can contribute fundamentally different forms of nutrition and habitat to deep-sea benthos but also share some ecological similarities. Both wood and whale bones are hard, organic-rich substrates with energy-rich components in largely inaccessible forms. Wood is mainly composed of recalcitrant, nitrogen-poor cellulose and lignin (Enríquez et al., 1993; Schowalter & Morrell, 2002; Gessner, 2005) and bone lipids and collagen are locked within a hard, inorganic apatite matrix (Smith et al., 2015). Wood-boring xylophagaid bivalves (with their nitrogen-fixing bacteria) and bone-eating *Osedax* polychaetes are notable examples of specialist ecosystem engineers that make the recalcitrant or inaccessible resources more available to non-specialist organisms through production of biomass and fecal material (Turner, 1977; Alfaro-Lucas et al., 2017). Boring of wood and bone by xylophagaids/*Osedax* also modifies the physical structure of these organic-rich substrates, both creating and destroying habitat niches for fauna living within the substrate (Amon et al., 2017a). Localized organic enrichment of the surrounding seafloor can sustain generalized opportunistic fauna, and anaerobic decomposition of organic matter can also provide reducing conditions that fuel chemoautotrophy and support chemosynthetically dependent species (Smith & Baco, 2003; Bienhold et al., 2013; Smith et al., 2015). Wood falls are expected to occur more frequently along continental margins than in the open ocean as a consequence of nearby terrestrial sources of wood. Whale falls may have an ocean-wide distribution, but many great whale migration routes and whale mortality are concentrated along coastlines and ocean margins (Green et al., 1995; Calambokidis et al., 2000; Smith et al., 2015). Because of these similarities, a portion of whale- and wood-fall assemblages on continental margins could be shared across the 2 habitat types.

The biodiversity and community structure of deep-sea communities often are driven by physical environmental conditions (Levin et al., 2001; Carney, 2005). Physicochemical properties, including bottom-water temperature and oxygen concentration, hydrodynamic and disturbance regimes, as well as topographic and sediment characteristics, can particularly influence diversity and spatial distributions/ranges of macrofauna on continental margins. The detrital flux of particulate organic carbon (POC) sinking from overlying photic zones provides the primary food to deep-seafloor animals, and thus strongly influences the abundance, biomass, and community structure of deep-sea communities (Smith et al., 2008; Rex & Etter, 2010; Smith et al., 2018). Because these drivers frequently co-vary regionally and with depth, deep-sea detritus-based communities often exhibit bathymetric and regional variations in community structure (Smith et al., 2008; Rex & Etter, 2010; Wei et al., 2010). Community structure on organic falls may be additionally influenced by the size (McClain & Barry, 2014) and type (e.g., species of wood; Judge & Barry, 2016); adult vs. poorly calcified juvenile whale bones, (Smith & Baco, 2003; Smith et al., 2015) of organic-rich substrates. Organic-fall assemblages also change with time on the seafloor, passing through successional stages related to the changing availability of habitat and nutritional sources as the organic-rich substrates are degraded (Smith & Baco, 2003; Smith et al., 2015; Bienhold et al., 2013; Pop Ristova et al., 2017). Overall, multiple drivers may influence the biodiversity and community structure of organic-fall communities.

Because drivers of wood-fall and whale-bone communities vary in space and time, simultaneous deep-sea deployments of replicate wood and whale bones are necessary to compare and contrast community structure on these substrate types. Results from simultaneous deployments of wood and whale bones in the deep sea have been reported from several locations: off Vanuatu (along with other types of organic substrata, Lorion et al., 2009), on the deep Antarctic shelf where there are no natural sources of wood (Glover et al., 2013), and on 2 seamounts in the Indian Ocean (Amon et al., 2017a). However, entire wood and whale-bone communities have not yet been quantitatively compared in soft-sediment areas typical of most of the deep sea. In addition, robust comparisons of the drivers of wood-fall and whalebone communities require deployments of inorganic substrata to serve as controls for the provision of hard substrate alone. Bathymetric zonation in substrate-specialized taxa has been reported (Braby et al., 2007; Voight, 2009; Shimabukuro & Sumida, 2019), but only a few published studies have looked at bathymetric patterns in entire organic-fall communities (Cunha et al., 2013; Saeedi et al., 2019), and these have not compared wood and whale-bone substrates. Because the study of natural organic falls is often serendipitous and costly, and because the species, original size, and/or time of arrival at the seafloor are often poorly constrained or unknown, controlled deployments are an invaluable approach for the study of organic falls. A comparative experimental approach (Menge et al., 2002), using standardized substrates, deployment times, and depths is essential to parse the roles of substrate type and depth as drivers of biodiversity and community structure in organic-fall habitats.

We employed a comparative experimental approach similar to that of Menge et al. (2002; 2003) to investigate patterns and drivers of organic-rich habitat biodiversity and community structure in the deep sea on the Washington−Oregon, USA, margin. Replicate wood blocks, whale bones, and inorganic control substrates were deployed to 4 seafloor locations at 2 depths (~1600 and ~2800 m) for a duration of 15 mo. In addition to describing the colonization of the experimental substrates, we addressed the following 4 hypotheses:

(1) Community structure differs between wood, bone, and control substrates deployed for similar times at similar locations.
(2) Macrofaunal abundance, as well as species richness and dominance, are greater on organic-rich substrates than on food-poor control substrates.
(3) Community structure of wood, whale-bone, and control assemblages differ with depth.
(4) Control assemblages have greater abundances at shallower depths, where detrital fluxes of POC are greater.

2.3 MATERIALS AND METHODS

2.3.1 Experimental design

Free-vehicle landers holding replicate whale-bone, wood, and control substrates (named Bone and Wood Landers, BoWLs) were designed by C. R Smith for the BoWLS project (Figure S2.1), and first deployed on the Washington-Oregon margin (this study). Similar landers using the BoWLs design were subsequently deployed in collaborative projects in the SW Atlantic (Saeedi et al., 2019; Shimabukuro & Sumida, 2019) and in a Norwegian fjord (Harbour et al., 2021b). For this study, 4 BoWLs were deployed in April 2013 from the RV 'Oceanus' to flat, sediment-covered areas of seafloor at 2 depths, ~1600 and ~2800 m, spaced ~400 km along the continental margin, and recovered after approximately 15 mo (Table 2.1, Figure 2.1). A further 2 landers located at 45° 51.2' N, 125° 09.3' W and 45° 32.3' N, 127° 49.1' W were deployed at the same time but were not recovered due to apparent failure of acoustic releases. Landers were 3-sided, with each side composed of 50 × 50 × 50 cm, open-sided bins (n = 3) lined with 500 μm Nitex mesh and a single closing lid (Figure 2.2; Figure S2.1). Replicate colonization substrates were affixed to the bottom of each bin and to the overlying lid. Colonization substrates consisted of: (1) ~3060 cm^3 (18.3 × 19.0 × 8.8 cm) blocks of untreated Douglas fir *Pseudotsuga menziesii*, (2) sections of adult humpback whale *Megaptera novaeangliae* vertebrae and ribs, and (3) inorganic hard substrates (controls) with a total surface area of 1125 cm^2, consisting of 2 slate tiles (15 × 15 cm) and 3 squares (15 × 15 cm) of vinyl loop mat affixed to the outsides of a plastic crate. Humpback whale-bone substrates consisted of either halves of lumbar vertebrae (average volume of 3790 cm^3) with vertebral processes removed, or of packages of 2 or 3 sections of rib bones (~30 cm, average volume of 2240 cm^3). Rib bones have comparable lipid and protein content to lumbar vertebrae (Higgs et al. 2011) and were used due to a limited availability of replicate lumbar vertebrae. Each bin contained 1 type of substrate, with control substrates located in the middle bin of each lander side, and 1 set of wood and bone substrates on either side in randomized locations. The lids of the landers remained open during vehicle descent and for 15 mo on the seafloor; lids closed, sealing contents in bins, as the ballast was dropped by a central acoustic release, causing the landers to become positively buoyant and ascend to the sea surface for recovery (Figure S2.1).

Table 2.1 Bone and wood lander location, deployment, and bottom water information. Deployments occurred on RV ‘Oceanus’ cruise OC1304A, and recoveries on RV ‘Oceanus’ cruise OC1406. Dissolved oxygen, temperature, and salinity from CTD casts: n = 3 at locations N-1600 and N-2800, n = 2 at S-2800 and S-1600. Particulate organic carbon (POC) flux estimates for the time period 1998-2010 calculated by Sweetman et al. (2017) using a model developed by Lutz et al. (2007). Dates are given as yr.mo.d

Location name	Lat. (N)	Lon. (W)	Depth	Deployment date	Recovery date	$[O_2]$ (ml L^{-1} ± SD)	Temp. (°C ± SD)	Sal. (ppt ± SD)	POC flux (g C m^2 yr^{-1})
N-1600	47° 57.46'	126° 2.12'	1596	2013.04.05	2014.06.22	0.7 ± 0.1	2.5 ± 0.1	34.5 ± 0.04	27.34
S-1600	43° 54.52'	125° 10.42'	1605	2013.04.09	2014.06.27	0.9 ± 0.1	2.3 ± 0.1	34.6 ± 0.00	26.78
N-2800	47° 16.20'	127° 35.57'	2666	2013.04.06	2014.06.23	1.8 ± 0.3	1.8 ± 0.03	34.6 ± 0.02	4.63
S-2800	43° 52.70'	127° 33.93'	2917	2013.04.08	2014.06.26	2.1	1.7	34.7	4.07

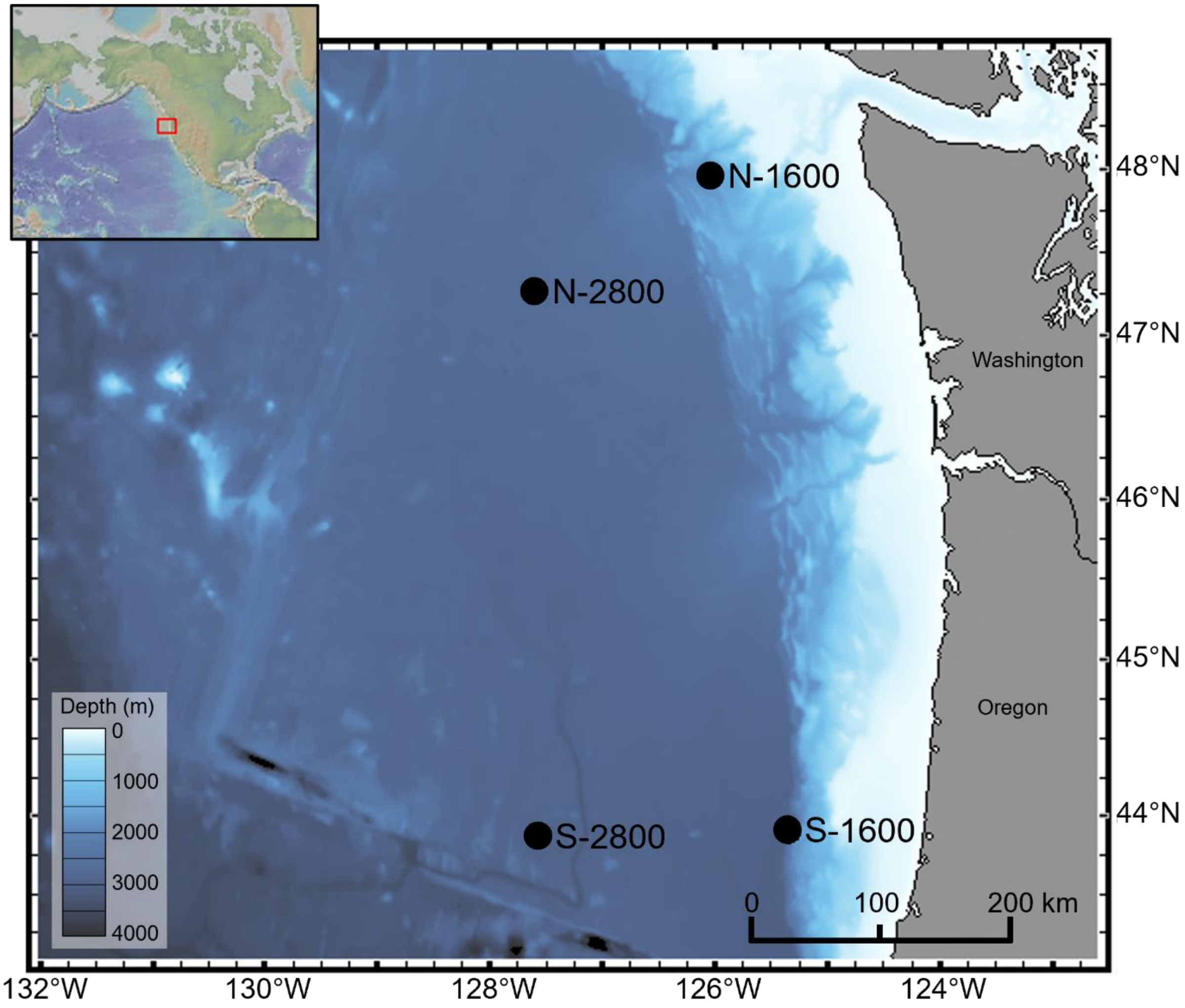

Figure 2.1 Positions of bone and wood landers on the Washington- Oregon (USA) margin, NE Pacific. Station names reflect geographic position (N: north; S: south) and approximate depth (1600 or 2800 m). Made with GeoMapApp (www. geomapapp.org)

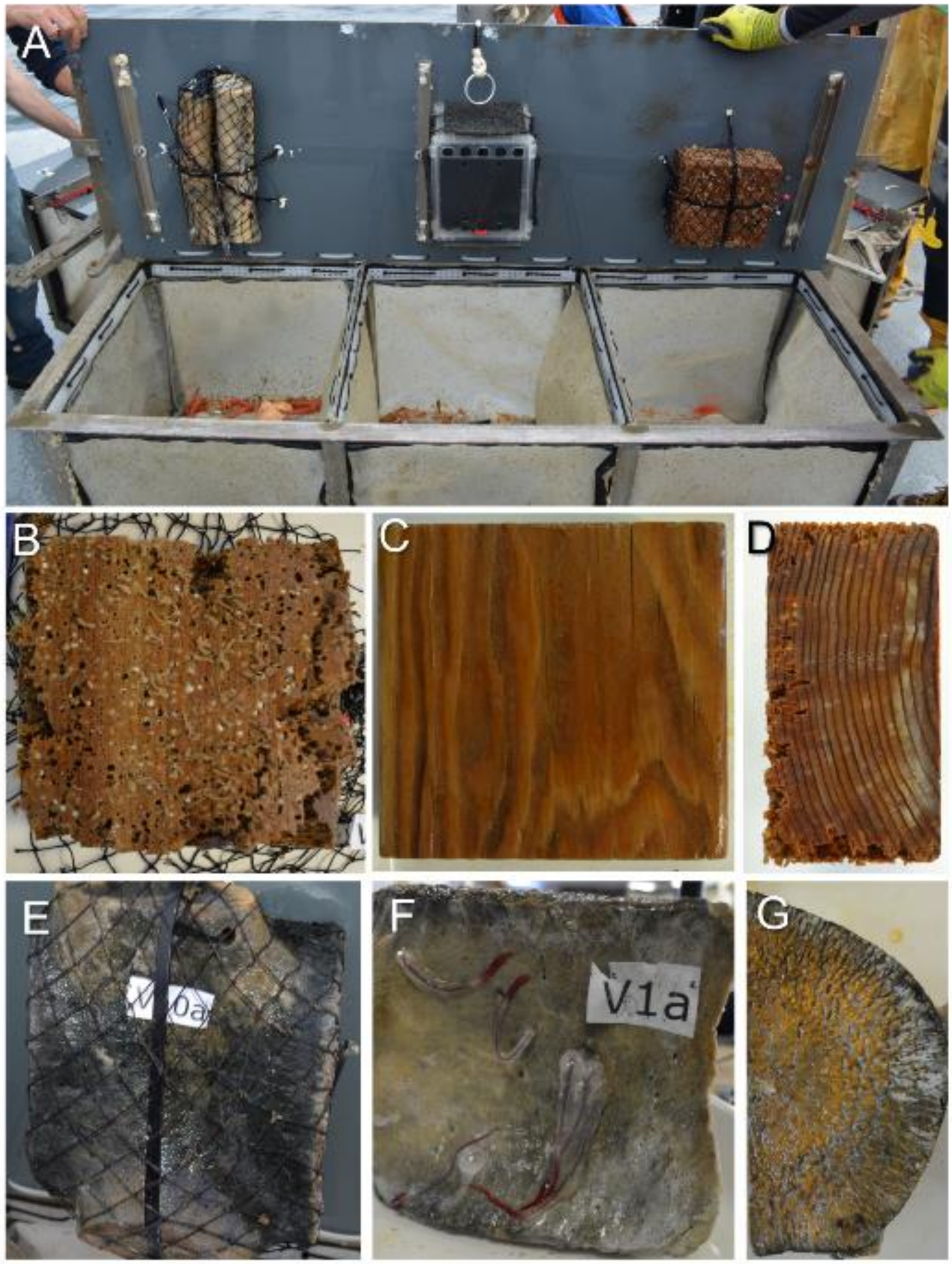

Figure 2.2 Photographs of substrates following recovery. (A) One side of the N-1600 lander, showing bone (rib package), control, and wood substrates attached to lid. (B) N-1600 wood block, (C) S-2800 wood block, (D) N-2800 wood block, (E) S-1600 whale vertebra, (F) N-1600 whale vertebra with *Osedax rubiplumus*, and (G) N-1600 whale vertebra

2.3.2 Sample processing

Upon lander recovery, all substrates were photographed on the lander, carefully removed, and transferred to chilled 20-μm filtered seawater. Organic substrates (wood blocks and whale bones) were cut into quarters. One quarter was frozen at −20°C, one was preserved in 95% ethanol, one in 10% formalin-seawater solution, and the fourth was allocated to either ethanol or formalin. If no fauna were present, the substrate was air dried. The contents of the mesh bins were washed on a 300 μm sieve and preserved in either 95% ethanol or 10% formalin−seawater solution. In the laboratory, contents of all mesh bins were sorted and identified to morphospecies using a dissecting microscope. Taxonomic experts who identified species, and distinguished undescribed species, included I. Altamira (annelids), J. Voight (mollusks), Les Watling (crustaceans), and Ronald Sluys (platyhelminths). Herein, sampling units consist of the contents of each mesh bin. Sampling units thus include all fauna collected from inside the mesh bin and picked from the surface of the substrate at the bottom of the bin, as well the estimated abundance of infauna residing inside the experimental substrata in bins. One quarter of each wood block preserved in formalin was dissected, fully sorted, and multiplied by 4 to estimate total infaunal abundance in the block. To account for the various whale-bone microenvironments (Alfaro-Lucas et al., 2017), subsampling of each whale vertebra consisted of sorting all macrofauna from within (1) 3 × 1 cm^3 randomized blocks from the surface of the vertebral body, (2) the outer edge of the vertebral body (1 cm^2 around the perimeter), (3) 3 × 1 cm^3 randomized blocks of the cut surface in contact with the bottom of the mesh bin, and (4) a 1 cm thick slice of the surface exposed by pre-deployment removal of the vertebral process (Figure S2.2). Subsampling of whale ribs involved sorting (1) 3 × 1 cm wide and 1 cm deep bands around the ribs, and (2) a 1 cm deep slice of the proximal and distal cut edges (Figure S2.2). In all bones, no macrofauna were found deeper than 1 cm from bone surfaces. Faunal abundances were extrapolated to the total surface area of the bone, based on the total area of each surface type. Surface areas (cm^2) of bones were estimated as in Bennett et al. (1994) by (1) covering vertebral quarters and rib sections with a single smooth layer of aluminum foil, (2) weighing the foil, and (3) multiplying by the surface area per unit mass of foil. Surface areas of wood blocks and controls were determined from the measured dimensions of the substrates. Volumes (cm^3) of wood and bone substrates were determined by water displacement prior to deployment. All epifauna were removed and sorted from the control substrates (slate tiles and vinyl loop mats). Meiofaunal (e.g., nematodes, hydrozoans, entoprocts, ectoprocts, copepods, and ostracods) and pelagic (e.g., salps and chaetognaths) taxa were excluded from analyses. Where reasonable, a preferred habitat type was identified for each morphospecies. Habitat preference was determined in 2 ways: based on (1) the relative abundance on each substrate type, and (2) information on habitat occurrence of similar morphospecies/genera/families in the peer-reviewed literature and archived data from collections of C. R. Smith (Table S2.1). A species was assumed to prefer an individual substrate type if ≥ 75% of its abundance across our entire study occurred on that substrate type. If ≥ 75% of a species' abundance occurred on both wood and bone combined, a preference for organic enrichment was assumed (generalized-enrichment respondents). Because species responding to organic enrichment generally attain high abundances (Pearson & Rosenberg, 1978; Smith et al., 2014), rare species (with ≤ 5 individuals across all landers) were assumed to be background species from surrounding soft sediments, unless taxonomic information suggested otherwise. The remaining undescribed morphospecies occurring on control and other substrates were assumed to be generalists attracted to hard substrata/structure. The habitat preference for known species was based on collection locations for these species reported in the literature and archived data from the Smith collections. A substantial number (24) of collected species could be differentiated as morphospecies within genera or families but could not be assigned to a described species. In such cases, congeneric or confamilial information was used to inform habitat preference (Table S2.1). Habitats of congeners were listed and considered for morphospecies identified to genus and 'cf. species' level. Preferred habitats of morphospecies identified to family level or higher were only assigned if there was strong evidence of substrate preference at the family level or higher. Final designation of habitat type considered both means of determination. Species authorities are included in Table S2.1.

2.3.3 Statistical analyses

2.3.3.1 Community structure

Multivariate analyses were used to evaluate community structure of assemblages using PRIMER 7 software (Version 7; Clarke & Gorley, 2015b). For community structure analyses, species abundance data were log(x + 1) transformed to allow rare and common species to contribute to patterns. A resemblance matrix was constructed using Bray-Curtis similarity and ordinated with non-metric multidimensional scaling (nMDS). Resemblance matrices performed on presence/absence data and on a dataset with xylophagaid bivalves and *Osedax* polychaetes removed were also compared to the transformed data using the Spearman's rank correlation method by the 2STAGE analysis in PRIMER 7. Significant differences in community structure were tested using permutational multivariate analysis of variance (PERMANOVA; Anderson, 2001; Anderson et al., 2008) in a 3-factor design including the factors Depth (fixed with 2 levels: 1600 or 2800 m), Substrate (fixed with 3 levels: Bone, Control, or Wood), and Location (random with 4 levels, nested within Depth). Main and pairwise PERMANOVAs were performed with 9999 permutations under a reduced model. Approximate p-values obtained using Monte Carlo random draws were calculated due to the limited number of possible permutations.

2.3.3.2 Abundance and diversity

To test abundance and diversity hypotheses, we employed a linear mixed-effect model approach (Zuur et al., 2009) using the packages 'lmerTest' (Kuznetsova et al., 2017), 'RLRsim' (Scheipl et al., 2008), and 'effects' (Fox, 2003; Fox & Weisberg, 2019) in R version 4.0.3 (R Core Team, 2020).

Diversity metrics (response variables) were calculated for each sampling unit, including assemblage abundance (N), species richness (S), Pielou's evenness (J), Shannon-Wiener diversity index (H'), expected species richness rarefied to 30 individuals (ES(30)), and total species richness estimated using the Chao1 index ('Chao1'; Chao, 1984). Species richness was rarefied to only 30 individuals to allow comparisons across samples with low abundances and to other studies (Cunha et al., 2013). Because some assemblages had fewer than 20 individuals, it was not possible to calculate ES(30) for 2 control assemblages (at site S-1600; see Figure 2.1). Response variables were first checked for normality and homogeneity of variances by inspecting diagnostic plots (Zuur et al., 2010). A log-transformation was applied to abundance and Chao1 data to meet the assumptions of the tests. Response variables were modelled as a function of fixed covariates Depth (categorical with 2 levels: ~1600 and ~2800 m), Substrate (categorical with 3 levels: Wood, Bone, and Control) and an interaction term of Depth × Substrate. Location was included as either a random intercept, (1|Location), or as a random intercept and a random slope of Substrate within Location, (1+Substrate|Location), to account for any location-based differences and the hierarchical structure of the experimental design. Final models were determined by iteratively assessing the significance of effects, starting with the full model:

Response variable = Depth + Substrate + Depth × Substrate + (1+Substrate|Location). Optimal models were assessed using Akaike's information criterion (AIC), likelihood ratio, and chi-squared tests to determine the optimal random effect structure and using F-tests to determine significant fixed-effect structure. Model assumptions were checked during model selection procedures. We used a significance level of $\alpha = 0.05$.

2.4 RESULTS

2.4.1 Overall colonization and condition of substrates

We estimated that the lander bins combined collected a total of ~84 890 macrofaunal individuals after accounting for the subsampling of wood and bone substrates. Abundances overall, and on organic-rich substrates at all landers, were dominated by annelids (53.6%) and amphipods (23.1%, Figure 2.3A). Annelids were the most species-rich taxon (67 of 144 morphospecies), with Dorvilleidae the most abundant (n = 16 635 of 36 008 individuals) and species-rich ($S = 13$) family overall, and within 9 of the 12 substrate-lander combinations (Figure 2.3B−D).

Half (n = 72) of all morphospecies were considered background taxa and 68 of these were represented by ≤ 5 individuals across all landers (Table S2.1). Generalized-enrichment respondents, along with wood and whale-bone specialists, dominated abundances and species richness of organic-rich assemblages (Figure 2.3E,F). Control assemblages were often dominated by hard substrate (generalist) taxa; however, control assemblages at site N-2800 were dominated by generalized-enrichment respondents. Wood/bone specialists and generalized-enrichment respondents constituted between 30.6 and 81.6% of control assemblage abundance across the 4 landers (Figure 2.3E). Across the 4 landers, approximately half (48.1−52.7%) of morphospecies occurred only on a single substrate type, and 17.7−31.6% of morphospecies were found on all 3 substrate types (Figure 2.4).

Figure 2.3 Taxonomic composition of assemblages. (A,C,E) Relative abundances and (B,D,F) number of species of all fauna by major taxonomic grouping (A,B), by polychaete families (C,D), and by habitat type (E,F). Error bars are SE from n = 3 replicates. Ar: Arthropoda, M: Mollusca

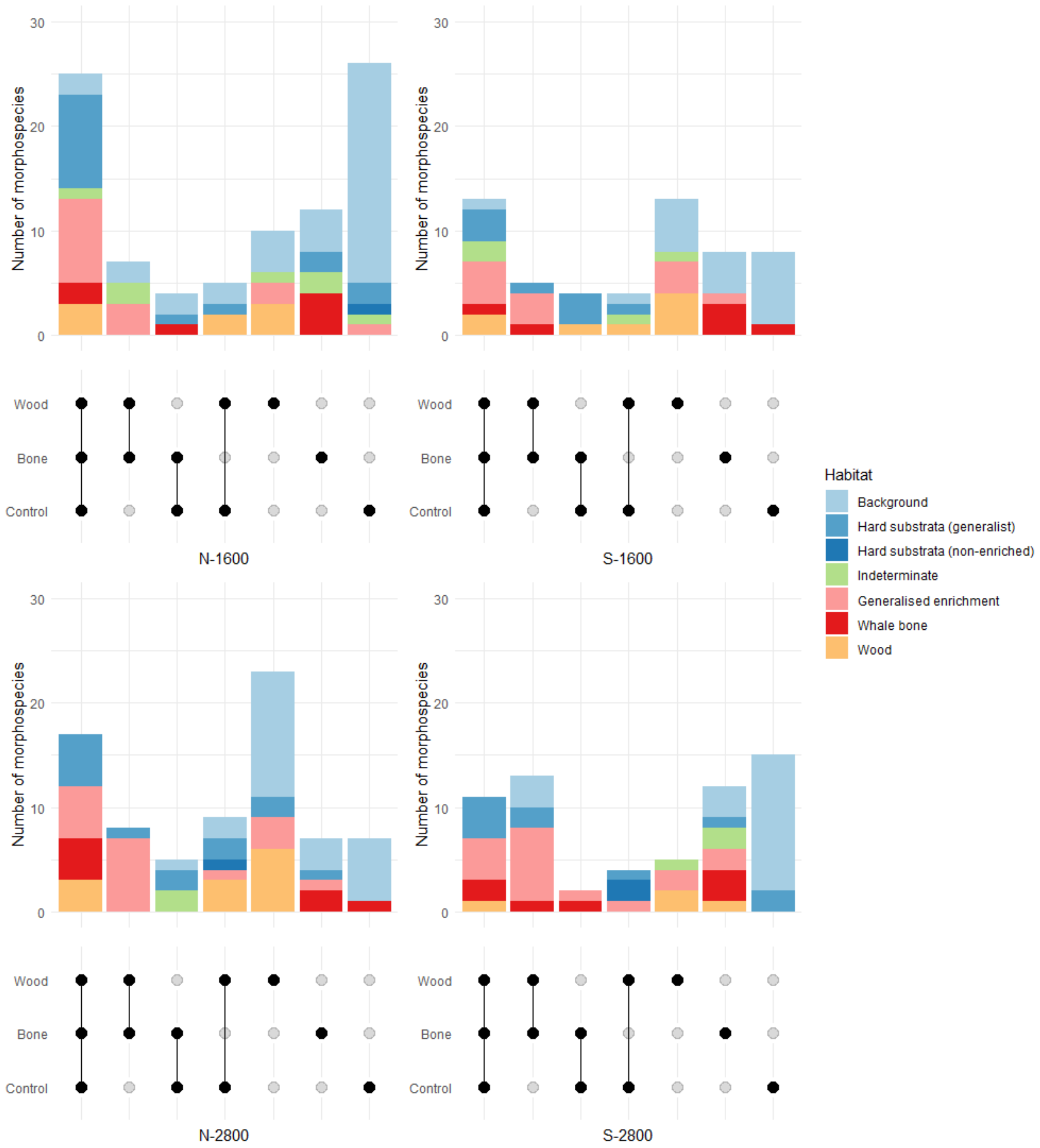

Figure 2.4 UpSet plot (Lex et al., 2014; Krassowski, 2020) indicating substrate types at which morphospecies were present. Black dots indicate substrate types, or combinations of substrate types when connected. UpSet plots for each depth and for all landers combined are displayed in Supplementary Figure 2.6.

2.4.1.1 Wood

Wood blocks at N-1600 were crumbling upon recovery (Figure 2.2B) due to heavy boring by 2 species of xylophagaid bivalve: mostly *Xylophaga oregona* (mean density ± SE = 0.90 ± 0.18

ind. cm^{-3}) with several individuals of *X. microchira* (0.0033 ± 0.0033 ind. cm^{-3}). Wood borings contained considerable amounts of fecal material produced by xylophagaid bivalves. The remainder of the wood infaunal community was dominated by the dorvilleid annelid *Ophryotrocha langstrumpae* (4.54 ± 1.18 ind. cm^{-3}), 2 ampharetid morphospecies (*Decemunciger* sp., 0.30 ± 0.09 ind. cm^{-3} and ampharetid sp. 22, 0.09 ± 0.01 ind. cm^{-3}), and a triclad platyhelminth (0.27 ± 0.09 ind. cm^{-3}). Strikingly, wood blocks in the bins at S-1600 were recovered fully intact with no xylophagaid colonization, despite heavy colonization of wood blocks on the lid directly above. Because the lid wood blocks at S-1600 were heavily colonized and crumbling, S-1600 wood bins included xylophagaid bivalves and other wood-infauna that had fallen from the lid into the mesh bins.

Wood blocks on N-2800 were recovered largely intact and lightly bored by xylophagaid bivalves of 4 species, with an overall mean density of 0.73 ± 0.38 ind. cm^{-3} (Figure 2.2D). *Xylonora zierenbergi* dominated 2 of the wood replicates, and the third was co-dominated by *X. muraokai* and *X. zierenbergi*. Seven dorvilleid morphospecies were recovered from wood substrates at N-2800, dominated by *O. batillus* (0.14 ± 0.05 ind. cm^{-3}). Wood blocks from S-2800 were fully intact (Figure 2.2C), with occasional empty boreholes ~2 mm in diameter.

Patches of black discoloration on non-bored wood surfaces were observed at each lander, and the thiotrophic bivalve *Idas washingtonius* was found at N-1600 (0.004 ± 0.001 ind. cm^{-3}), S-1600 (0.002 ± 0.001 ind. cm^{-3}), and N-2800 (0.001 ± 0.001 ind. cm^{-3}).

2.4.1.2 Bone

Whale bones from all landers displayed black discoloration indicating reducing conditions (Figure 2.2E–G). Eight large female *Osedax rubiplumus* individuals protruded from burrows in bin-affixed rib bones at N-1600 (0.004 ind. cm^{-2} bone surface area). A further 25 female *O. rubiplumus* were recovered from lid-affixed bones across N-1600 (n = 22) and S-1600 (n = 3), but were not included in the present analyses which concern only bin fauna. Colonization by a small (trunk length ~2 mm) *Osedax* sp. B varied across landers, with an average of 0.81 ± 0.63 ind. cm^{-2} in bones at N-2800, and 0.005 ± 0.005, 0.004 ± 0.004, and 0.010 ± 0.010 ind. cm^{-2}, respectively, in bones at landers N- 1600, S-1600, and S-2800. Dorvilleids were also found living within the bones at all landers. Bone substrates supported the highest abundances of any substrate type at N-2800, dominated by annelids (including *Osedax* sp. B and *Parophryotrocha* sp. A) and the amphipod *Accedomoera* sp. A. Bone assemblages included taxa characteristically reported from whalefalls and reducing habitats, including at least 5 species of dorvilleid polychaete, the thiotrophic bivalve *Idas washingtonius* , the polychaetes *Peinaleopolynoe santacatalina*, *Vrijenhoekia balaenophila*, and species in the gastropod genera *Hyalogyrina* and *Dillwynella* (Table S2.1).

2.4.1.3 Control

Control substrates supported visibly less fauna on substrate surfaces and in bins than did organic-rich substrates (Figure 2.2A). Slate surfaces were largely free of attached epifauna. Vinyl loop mats at N-1600, N- 2800, and S-1600 often had visible detritus trapped within 'spaghetti' loops, and detritus was more common on upward-facing surfaces. Across all landers, control bins collected between 18 and 560 individuals. Organic-rich substrate specialists and generalized-enrichment respondents constituted between 30.6 and 81.6% of control assemblage abundances across the 4 landers (Figure 2.3E). Control assemblages included species and genera likely from background soft-sediment faunas, including the annelids *Anobothrus apaleatus*, *Harmothoe* cf. *fragilis*, *Hesiospina* cf. *aurantiaca*, *Sosane wahrbergi*, and *Prionospio* cf. *ehlersi* (Table S2.1). Background megafauna included the octopus *Graneledone pacifica* directly underneath a clutch of eggs attached to a lid-affixed control substrate at S-1600, and a zoarcid fish in a control bin at N-2800.

2.4.2 Community structure

The nMDS analysis of morphospecies assemblages shows clustering according to depth, lander location, and substrate type (Figure 2.5). PERMANOVA indicated that communities at ~1600 and ~2800 m deployments were significantly different (Monte Carlo random draws; $p < 0.05$), and depth explained the greatest proportion of variation in community structure (29.1%, Table 2.2). Within a depth, assemblages differed significantly between lander locations (Monte Carlo random draws; $p < 0.05$), with lander location accounting for 17.8% of the total variation in community structure (Table 2.2). Morphospecies assemblages were also significantly different between substrate types (Monte Carlo random draws; $p < 0.05$). Significant interactions between substrate and both depth and lander location (Monte Carlo random draws; both $p < 0.05$) are evident in Figure 2.5, where clustering of substrate types varies within and across individual lander locations and depths.

Within landers, assemblages were often (8 out of 12 comparisons) significantly different by substrate type (Table S2.2). Bone assemblages were significantly different between depths (pairwise PERMANOVA; Monte Carlo random draws; $p < 0.05$, Table S2.2), while depth-related differences in wood (Monte Carlo random draws; $p = 0.07$) and control (Monte Carlo random draws; $p = 0.10$) assemblages could be considered marginally significant given the limited number of depths ($n = 2$) in the experimental design. Resemblance matrices of presence-absence data, as well as those with the abundant, substrate-obligate xylophagaids and *Osedax* removed, were highly correlated with the main data (2STAGE Spearman rank correlation = 0.92 and 0.99, respectively), indicating that less abundant species contributed to these patterns.

The community structure of wood assemblages on average was more similar at ~1600 m (61.9%) than at ~2800 m (41.5%). N-1600 and S-1600 wood assemblages shared dominant species and had similar community structure (> 40%, Figure 2.5) despite the lack of colonization of the bin-affixed wood blocks on S-1600. In contrast, average similarity of bone assemblage community structure was greater within lander locations at ~2800 m depth (54.9%) than at ~1600 m (39.4%).

2.4.3 Abundance and diversity

2.4.3.1 Patterns across different locations

The density (ind. cm^{-2} of substrate surface) and diversity (*S*, *J*, and Chao1) of assemblages varied greatly according to lander location, as indicated by the significance of location, or an interaction between location with substrate type, as a random effect in all mixed models (Table 2.3). Within each depth, density and species richness at each substrate type were greater at the northern deployments than at southern deployments, except for *S* of bone assemblages at ~2800 m, which were equal (Figure 2.6; however, see Section 2.5.1 for a discussion about low densities at S-1600). Assemblage densities of each substrate type at S-1600 were 1-2 orders of magnitude lower than for assemblages of the same substrate types at other locations.

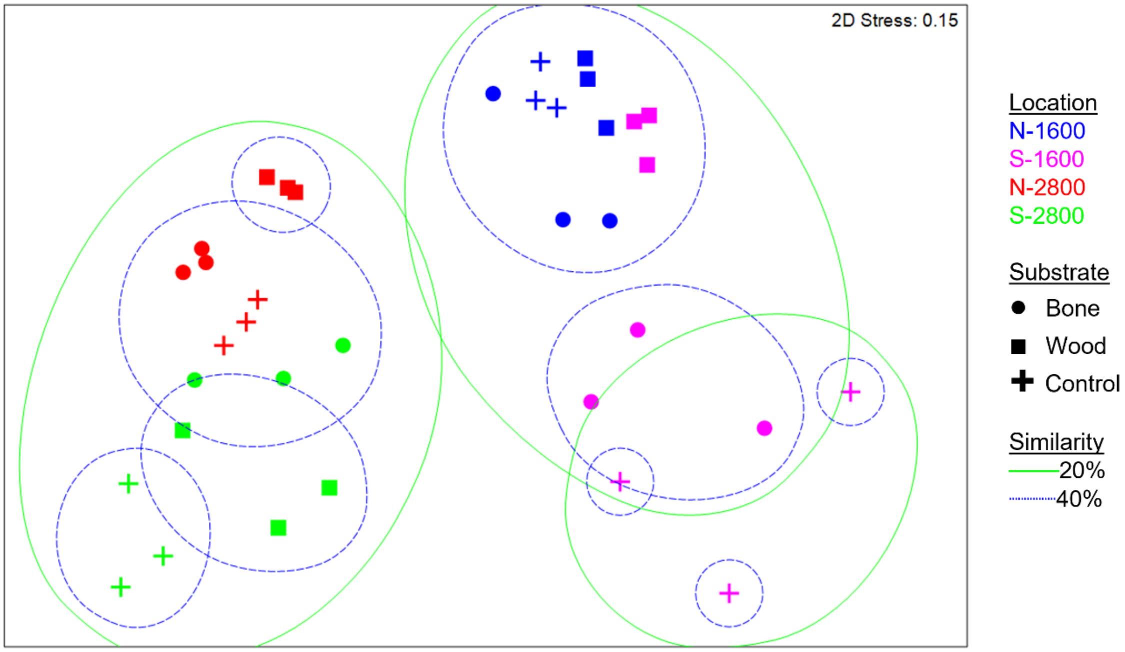

Figure 2.5 Nonmetric multidimensional scaling (nMDS) ordinations of wood, control, and bone assemblages from 4 experimental colonization landers deployed on the Washington-Oregon margin, based on Bray-Curtis dissimilarities of log(x + 1) transformed abundances.

Table 2.2 PERMANOVA partitioning and analysis of bone, wood, and control assemblages based on Bray-Curtis dissimilarities of log(x + 1) transformed abundances. P-values were obtained using 9999 permutations under a reduced model. P-values determined by Monte Carlo random draws (p(MC)) are shown due to limited number of permutations. Location is a random factor, nested within Depth. All other factors are fixed

Source	df	MS	Pseudo-F	p (perm)	Unique permutations	p (MC)	Variation explained (%)
Depth	1	30508.0	3.86	0.332	3	0.035	29.1
Substrate	2	7873.4	3.37	0.009	9942	0.001	10.7
Location(Depth)	2	7898.8	8.14	0.000	9921	0.000	17.8
Depth:Substrate	2	4756.6	2.04	0.044	9909	0.019	9.4
Location(Depth):Substrate	4	2334.2	2.40	0.000	9851	0.000	10.5
Residual	24	970.6					22.5

Table 2.3 Generalized linear mixed model summary information. Full mixed model information is included in Table S2.4. LRT: likelihood ratio test; Chisq: chi-squared test. **Bold** indicates significant ($p < 0.050$) terms. *S*: species richness; J: evenness; Chao1: estimated total species richness; R^{2}m: marginal R^2 value; R^{2}c: conditional R^2 value

Response	Final Model	Fixed terms	F-value	p-value	R^{2}m	Random terms	Test statistic	p-value	R^{2}c
log(ind/cm^2)	Depth + Substrate + (1+Substrate|Location)	Depth	72.96	< 0.001	0.38	(1+Substrate|Location)	Chisq = 22.00	0.001	0.98
		Substrate	14.88	0.025					
S	Depth + Substrate + (1+Substrate|Location)	Depth	5.27	0.072	0.18	(1+Substrate|Location)	Chisq = 20.27	0.001	0.93
		Substrate	0.36	0.724					
J	Depth*Substrate + (1|Location)	Depth	0.58	0.527	0.32	(1|Location)	LRT = 31.36	<0.001	0.87
		Substrate	7.22	0.003					
		Depth:Substrate	23.85	< 0.001					
log(Chao1)	Depth + Substrate + (1|Location)	Depth	0.52	0.545	0.04	(1|Location)	LRT = 1.06	0.040	0.27
		Substrate	0.07	0.929					

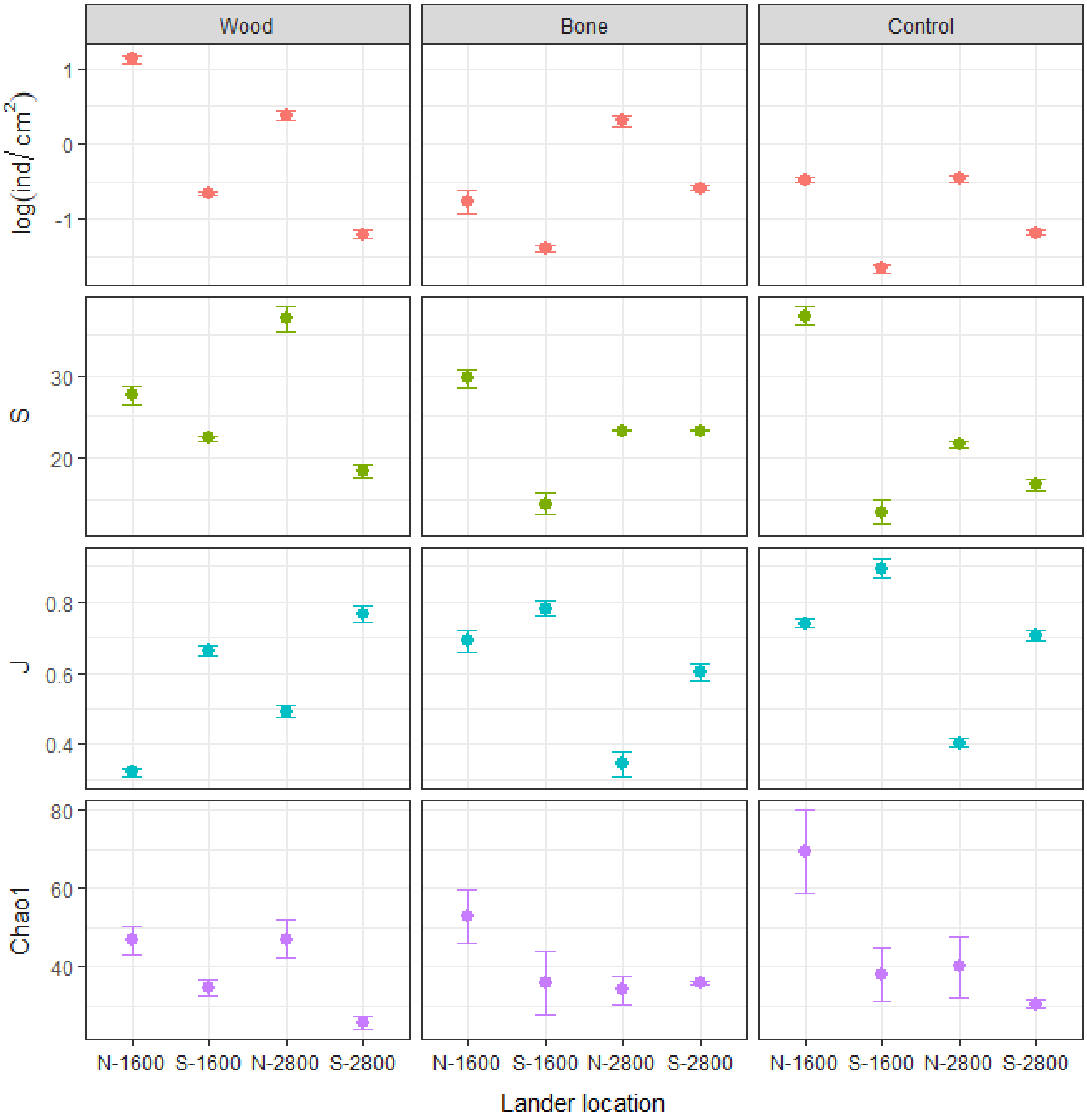

Figure 2.6 Faunal density (log(ind. cm^{-2} substrate surface area)) and diversity metrics (*S*: species richness; *J*: evenness; Chao1: estimated total species richness) by substrate type and lander location. Plotted as mean ± SE (n = 3). Abundances are estimates based on subsampling of wood and bone substrate infauna.

2.4.3.2 Patterns across different depths

Because lander location is nested within depth, the strong location effects made depth effects on diversity difficult to detect given the limited replication (2 depths, and 2 landers within each depth). Nonetheless, there were strong significant effects of depth ($p < 0.05$) on the density of assemblages, and of the interaction between depth and substrate type ($p < 0.05$) on the evenness

(*J*) of assemblages (Table 2.3). Within northern and southern locations, patterns of log(ind. cm^{-2}), *S*, and *J* with depth were inconsistent across the different substrate types (Figure 2.6). Densities of control assemblages had no clear pattern with depth (Figure 2.6).

2.4.3.3. Patterns across different substrate types

Substrate type overall had significant effects on densities ($p < 0.05$) and on evenness (Depth:Substrate, $p < 0.05$; Substrate, $p < 0.05$; Table 2.3). There were no consistent patterns of densities or diversity (*S*, *J*, or Chao1) across substrate types within individual landers (Figure 2.6).

2.4.3.4 Additional measures of diversity

Estimated species richness (Chao1) showed no pattern with depth or substrate, but differences between locations were significant ($p < 0.05$, Table 2.3, Figure 2.6). Patterns of *H’* and ES(30) closely resembled patterns of evenness, *J* (Figure S2.4, Table S2.3). Rarefaction and extrapolated species richness curves, estimated with Chao1, showed no consistent patterns with location or substrate type (Figure S2.5).

2.5 DISCUSSION

This study revealed that the abundance, diversity, and community structure of replicate whale-bone, wood-block, and control assemblages after 15 mo on the Washington-Oregon margin varied with lander location, substrate type, and depth. Our results support our first 3 hypotheses, i.e., that (1) community structure differs by substrate type; (2) abundance, species richness, and dominance are greater on organic-rich than control substrates; and (3) within a substrate type, community structure differs with depth. Our fourth hypothesis, i.e., that control substrates have greater abundance at shallower depths, was partially supported. However, because the large variability between individual lander locations influenced our ability to test the hypotheses, we first consider locational variability before discussing our hypotheses in detail.

2.5.1 Variability by location

We found significant location differences in community structure and diversity within substrate types at similar depths separated by distances of ~400 km. Because locations within each depth experienced similar environmental conditions (water masses, temperature, dissolved oxygen concentrations, and POC fluxes) and because organic-rich substrates were replicates, our results suggest that north-south differences in other factors, such as local larval supply, influenced our results. For example, the northern region of our study area, offshore of British Columbia (Canada) and northern Washington, is (1) more heavily forested, (2) features more fjords and other estuaries that could export wood (Emmett et al., 2000; Allen & Pavelsky, 2018), and (3) has more submarine canyons that could transport water-logged wood downslope than Oregon and California farther south (Harris & Whiteway, 2011). Therefore, the transport of wood to the deep seafloor is more likely in the northern regions, which would imply a greater abundance of wood falls and hence a higher supply of larvae from wood-fall specialists.

The variable occurrence and size of organic-rich substrates on the deep-sea floor likely results in high spatio-temporal variability of organic-rich habitats, and hence in larval sources for particular sites on the Washington-Oregon margin. Such variability is likely to yield locational differences in faunal recruitment and community composition on organic falls. For example, Voight (2007) observed variability in the composition of xylophagaid species at replicate wood blocks deployed < 10 km apart, and Tyler et al. (2007) observed substantial temporal variability in xylophagaid recruitment on replicate wood blocks. Thus, the spatial heterogeneity we observed within depths is consistent with other organic-fall colonization studies in the deep sea (Saeedi et al., 2019). Continental margins are characterized by high habitat heterogeneity (Levin & Sibuet, 2012), and the heterogeneity provided by different types of organic-fall habitats clearly contributes further to beta diversity along continental margins.

An additional source of variability in this study is the lack of xylophagaid bivalves and other colonization of wood blocks in bins at S-1600; this is surprising given the heavy colonization in blocks attached to the lid above. It is unclear whether recruitment was limited for other substrate types in bins at S-1600. Relatively low abundances across all substrate types at S-1600 suggest this might be the case, yet we exercise caution in this interpretation given the high variability of abundances across all landers. Bottom-water oxygen concentrations (~0.9 ml l^{-1}) did not appear to be stressful to deep-sea benthos at either of the shallow locations (Levin, 2003), and localized oxygen depletion within the bins is unlikely over such small scales. Sediment burial of the substrates during the deployment period also appears unlikely given the scarcity of annelid families in the S-1600 bins that are characteristic of soft sediments on the NE Pacific margin (e.g., Paraonidae, Lumbrineridae, and Cirratulidae; Fauchald & Hancock, 1981; Blake, 2006). Despite these apparent issues, the community compositions of S-1600 wood assemblages are most similar to wood assemblages of the other shallow lander (N-1600), apparently because fauna from the heavily bored wood blocks attached to the lid on S-1600 fell into the bins below. Additionally on S-1600, bone assemblages included specialist bone taxa, and control assemblages were comprised of typical background taxa, suggesting that the assemblages of S-1600 resembled the expected community composition of organic-rich and inorganic hard substrates. Because of the seemingly anomalous abundance and diversity of S-1600, we refrained from making statistical inferences on bathymetric abundance and diversity patterns, and instead only broadly interpret patterns across the remaining 3 locations (see Section 2.5.3.2).

2.5.2 Variability with substrate type — Hypotheses 1 and 2

Wood, bone, and control substrates were colonized by statistically different communities (Table 2.2) in spite of locational variability, a result consistent with Hypothesis 1: Community structure differs between wood, bone, and control substrates deployed for similar times at similar locations. Organic-rich substrates generally supported assemblages with higher abundances, species richness, and dominance than control substrates, which is consistent with Hypothesis 2: Macrofaunal abundance as well as species richness and dominance are greater on organic-rich substrates than on food-poor control substrates. Below, we discuss in more detail the community structure of individual substrate types, and then consider overlap between substrate types.

2.5.2.1 Wood

Wood blocks in this study were colonized by 5 of the 6 xylophagaid species previously described from wood deployments in the NE Pacific (Voight, 2007). Xylophagaid assemblages at N-1600 and on lid wood blocks at S-1600 closely resembled those recovered in wood blocks at comparable depths on Axial Volcano on the Juan de Fuca Ridge, where high densities of *Xylophaga oregona* had seemingly outcompeted an early colonizer, *X. microchira* (Voight, 2007). Although Voight (2007) did not report *X. oregona* densities, comparisons of photographs and descriptions of recovered wood (i.e., ‘crushable by hand’) suggest that similar xylophagaid densities and extent of wood degradation were found in both studies. However, xylophagaid assemblage identity at N-2800 did not resemble those of wood blocks deployed at comparable depths only ~50 km away (Voight, 2007), further highlighting the spatiotemporal variability of wood-fall assemblages. The coexistence of 4 xylophagaid species in the lightly bored wood blocks at N-2800 may represent an early stage of wood colonization, wherein wood surface area and internal space are not yet limited. Intraspecific competition among xylophagaid bivalves is also likely influenced by seasonality in recruitment, reproductive mode, and biotic interactions (Tyler et al., 2007; Voight, 2007; MacIntosh et al., 2012). Xylophagaid densities measured in this study are greater than those measured at many other wood falls (Gaudron et al., 2010; Bienhold et al., 2013; Romano et al., 2013). Reports of higher xylophagaid densities (Tyler et al., 2007; Amon et al., 2015; Gaudron et al., 2016) are associated with average xylophagaid shell lengths smaller than those of this study (~5-12 mm in our study, ~1-10 mm elsewhere). Further studies involving measurements of body size/biomass and the volume of remaining wood are necessary to infer the extent of resource competition among xylophagaids.

Degradation of our wood blocks by xylophagaid bivalves allowed an abundant fauna of a few species to inhabit the wood interior. Thousands of *Ophryotrocha langstrumpae* dominated the heavily degraded wood blocks at N-1600, and hundreds of *O. batillus* occurred inside the lightly-bored wood at N-2800. Dorvilleid polychaetes, especially those in the genus *Ophryotrocha*, are often found in organically enriched and chemically reducing habitats, such as at wood falls and whale falls (Smith & Baco, 2003; Wiklund et al., 2009; Wiklund et al., 2012; Amon et al., 2013; Smith et al., 2014; Ravara et al., 2021), in sediments below fish farms (Paxton & Davey, 2010), near sewage outfalls (Paavo et al., 2000), and at cold seeps and hydrothermal vents (Levin et al., 2009; Levin et al., 2013). *O. langstrumpae* was described from both wood and whale falls (Wiklund et al., 2012), but our data indicate an overwhelming preference for wood.

Stable-isotope analyses revealed that *Ophryotrocha* spp. occurring at high densities in sediments surrounding wood and kelp falls off southern California consumed plant material and sulfur-oxidizing bacteria (Bernardino et al., 2010). *Ophryotrocha* spp. inside xylophagaid-bored wood blocks are likely omnivorous, deriving nutrition from the labile fecal material produced by the xylophagaid bivalves, which also may include sulfur-oxidizing bacteria (Harbour et al., 2021b). Xylophagaid fecal material could also be a food source for surface deposit-feeding ampharetids living in the wood borings made by xylophagaids. Specialist ampharetids occur commonly in reducing habitats, where they are thought to feed on chemosynthetic bacteria (Thurber et al., 2010; Eilertsen et al., 2017). The high densities of triclad flatworms found inside our wood blocks have not been reported elsewhere, and the ecology of these wood-dwelling triclads remains poorly known. Polyclad flatworms in wood at N-2800 were morphologically similar to *Anicellidus profundus* described from wood blocks in the Cascadia Basin and are possibly xylophagaid predators or scavengers (Quiroga et al., 2006; Voight, 2007). *Dillwynella* gastropods were the second most abundant taxon (after the amphipod *Accedomoera* sp. A) on the unbored wood blocks on lander S-2800, and this entire gastropod genus is associated with wood or plant material in the deep sea, likely adapted to feeding on microbial mats on wood surfaces (Marshall, 1988).

2.5.2.2 Bone

Bone assemblages were often dominated by a few species of mobile crustaceans, contributing to the high abundance and low evenness of bone assemblages. Dense populations of the pontogeneid amphipod *Accedomoera* sp. at N-2800 may have been attracted to odor produced by soft tissues on the bones; however, amphipods in this family have rarely been reported as scavengers (Bowman, 1974). Bone assemblages at N-1600 attracted amphipods in the family Lysianassidae, which contains many scavengers attracted to whale and other carcass falls (Smith, 1985; Smith & Baco, 2003; Lundsten et al., 2010a; Smith et al., 2014). High abundances of *Osedax* sp. B and dorvilleid polychaetes were also found in interiors of bones. The dorvilleid *Parophryotrocha* sp. A was abundant just under the bone surface on deep landers and appears to be a bone-interior specialist. Habitat space for *Parophryotrocha* sp. A inside the bones may have been facilitated by *Osedax* sp. B. Capitellid polychaetes were very abundant inside whale bones at an abyssal seafloor in the South Atlantic (Silva et al., 2016; Sumida et al., 2016), yet only a few adult individuals were recovered from bone interiors in this study. However, we did find tens of unidentified juvenile capitellids inside bones, suggesting that capitellids are also utilizing whale bones opportunistically as an infaunal habitat at NE Pacific whale falls. Bones also supported mollusk genera known from reducing environments (e.g., *Laeviphitus*, *Hyalogyrina*, and *Idas*), albeit in low densities, which indicates an early reducing, sulfophilic successional stage for our bones (Smith & Baco, 2003).

The majority of taxa (by abundance and richness) in our bone assemblages were substrate specialists plus generalized-enrichment respondents. Species identified as preferring background soft-sediment or hard substrates contributed to the richness of bone assemblages, but the majority of these were represented by only a few individuals. Previous studies suggesting that the majority of species found at whale skeletons are from the background fauna were conducted using only video surveys, so these observations are biased towards megafaunal organisms and do not provide species-level identifications, complicating the resolution of specialist taxa (Lundsten et al., 2010a; Lundsten et al., 2010b). The collection of macrofauna, especially those residing in substrata interiors, is required to fully quantify the relative contribution of background taxa to whale-bone communities (Bennett et al., 1994; Baco & Smith, 2003; Hilario et al., 2015; Smith et al., 2017; Alfaro-Lucas et al., 2017).

2.5.2.3 Control

Within depths, control substrates generally supported low faunal densities, which is expected since the substrates themselves provided no exogenous organic input. High abundances of organic-rich species (wood and bone specialists, as well as generalized organic enrichment opportunists) occurring on control substrates were likely due to mass effects (Leibold et al., 2004), whereby high dispersal or spill-over from nearby abundant wood/bone populations enabled species to establish on normally unfavorable (organic-poor) substrata. This mass effect very likely inflated community densities, species richness, and dominance in control assemblages. Mass effects can generally increase the abundance and diversity of assemblages in areas near organic falls which should be considered in interpretations of similar organic-fall experiments involving different habitat types in close proximity (Jones et al., 2008; Rouse et al., 2011; Saeedi et al., 2019; Harbour et al., 2021b). Other than organic-rich species present due to mass effects, control assemblages were dominated by taxa such as mobile crustaceans (*Eurycopinae* sp. A, *Schisturella* sp. A), anemones, and limpets apparently exploiting the hard substrates.

2.5.2.4 Species overlap between substrates

The majority of the morphospecies (82 of 144) were found at multiple substrate types. This can be partly attributed to mass effects, as well as generalized-enrichment respondents (Pearson & Rosenberg, 1978; Baco & Smith, 2003). One example is *O. batillus*, a dominant dorvilleid at wood blocks at N-2800 and on bones at N-1600. As expected from mass effects, species overlap between substrate types occurred commonly in highly mobile species. Reducing conditions at both wood and bone substrates likely allowed chemoautotrophic symbiont-bearing *Idas washingtonius* (Deming et al., 1997) to inhabit both our wood blocks and whale bones. *Idas* bivalves have often been reported among the most abundant taxa at reducing habitats on wood and whale falls (Smith & Baco, 2003; Amon et al., 2017a). The relatively low *I. washingtonius* densities on our bone and wood deployments suggest that sulfidic conditions were low, either because of the small substrate sizes, or because the substrates were in early stages of development after 15 mo.

2.5.3 Variability with depth — Hypotheses 3 and 4

2.5.3.1 Community structure

The community structure of wood, bone and control assemblages differed between depths of ~1600 and ~2800 m, which is consistent with Hypothesis 3: Community structure of wood, whale-bone, and control assemblages differ with depth. Differences in taxonomic composition between the 2 depths are consistent with faunal zonation observed in the background deep sea in the Cascadia Basin, which has a middle slope fauna centered at 1600 m and a lower slope abyssal fauna centered at 2800 m (Carney, 2005). The 2 depths in this study were bathed by different water masses flowing in opposite directions (southward-flowing North Pacific Deep Water at 1600 m and northward-flowing Cascadia Basin Bottom Water at 2800 m; Hautala et al., 2009) and thus each was likely carrying different larval pools. Temperature, dissolved oxygen concentration, and hydrostatic pressure vary between the 2 depths (Table 2.1) and may also influence taxonomic composition through physiological adaptations. Gradients in POC flux are likely less important in controlling these differences because most of the fauna appear to be responding directly to the organic-rich substrates, but levels of POC flux may still influence the background species that colonized the landers. Bathymetric differences in taxonomic composition are a widespread feature in deep-sea communities (Carney, 2005) and our findings, along with others (Braby et al., 2007; Cunha et al., 2013; Saeedi et al., 2019), suggest that depth-related processes also influence organic-fall communities.

2.5.3.2 Abundances

Because POC flux is implicated as an important driver of bathymetric patterns of faunal densities (Smith et al., 2008; Rex & Etter, 2010; Wei et al., 2010), we predicted Hypothesis 4: Control assemblages have greater abundances at shallower depths, where detrital fluxes of POC are greater. Because control assemblage densities were influenced by mass effects, and because of the abnormalities at S-1600, we were unable to robustly test Hypothesis 4. However, following the exclusion of organic-rich substrate specialists and generalized-enrichment respondents from control assemblages (assuming their presence at control substrates is due to mass effects), faunal densities were indeed greatest at N-1600 and lower at N-2800 and S-2800 (Figure S2.7). In contrast, faunal densities of wood and bone assemblages were much more variable between locations and were not always greater at shallower depths. These results suggest that organic-rich assemblage abundances are not primarily driven by the bathymetric gradients of POC flux that drive abundances of control assemblages. Drivers influencing the larval availability of organic-fall specialists, such as the geographic distribution of wood and whale falls and water-mass effects, are likely more important than gradients in POC flux in controlling abundances in organic-fall assemblages on the NE Pacific margin.

Wood falls are expected to occur more frequently closer to terrestrial sources of wood, i.e., at shallower depths nearer to continental margins. Thus, we expect that propagule densities and connectivity are greater for wood falls at shallower depths and decline with increasing depth and distance from shore on the NE Pacific margin (also postulated for the North Atlantic by Cunha et al. (2013) and by Voight (2015)). This should allow shallower wood blocks to be colonized more rapidly by the wood-fall fauna than blocks at deeper locations. As indicated earlier, the presence and extent of xylophagaid bivalve colonization can greatly influence the abundances, species richness, and dominance of wood-fall communities. Our findings of greater xylophagaid colonization, overall abundances, dominance, and community structure similarity at ~1600 m wood blocks (~100 km from shore) compared to wood blocks at ~2800 m depth (~250 km from shore) are consistent with this proposed mechanism. Bathymetric variability of xylophagaid propagule density is likely a more important driver of wood-fall community abundance, structure, and diversity than gradients in POC flux.

The southward-flowing North Pacific Deep Water at a depth of 1600 m might be expected to transport more xylophagaid larvae from the heavily wooded margins off British Columbia than does the northward-flowing Cascadia Basin Bottom Water at 2800 m coming from the California margin. However, for ~2800 m deployments, xylophagaid densities were much higher on the northern landers (Table S2.6). We hypothesize that a greater local abundance of wood falls at the seafloor in the northern region is more important to xylophagaid recruitment than water masses transporting larvae from more distant sources.

Similarly, we can hypothesize that whale-fall community structure is, at least in part, influenced by the distribution and abundance of living whale populations. Whether there are bathymetric patterns in whale-fall distributions is unclear (Smith et al., 2019; Carretta et al., 2020). However, the regional distribution of whale populations, and whale migration routes, may provide some insight into differences in the abundance of whale-fall assemblages along the NE Pacific margin (Smith et al., 2015; Smith et al., 2019). Great whales are relatively abundant and have migration routes apparently closer to shore in Central California (including Monterey Bay), whereas abundances are lower and migration routes are further offshore along the Washington and Oregon margin (Barlow & Forney, 2007; Forney, 2007). This is likely to yield greater whale-fall abundance in Monterey Bay and thus greater propagule supply and connectivity between whale falls for whale-fall specialists (based on the model of Smith et al., 2019) in Monterey Bay. This may help explain the rapid and dense colonization of whale skeletons by multiple *Osedax* species in Monterey Bay (Lundsten et al., 2010b), compared to elsewhere in the NE Pacific (Smith & Baco, 2003; Smith et al., 2015). Because *Osedax* can influence the biodiversity (Alfaro-Lucas et al., 2017) and perhaps longevity of juvenile whale-fall habitats (Lundsten et al., 2010b; Smith et al., 2015; Smith et al., 2019), 'hot spots' of whale abundance could be important in determining global patterns of whale-fall community structure (Smith et al., 2019). Clearly, further studies on whale-fall communities and distributions along the NE Pacific margin, along which humpback, gray, and blue whales migrate (Carretta et al., 2020), and elsewhere are required to address this hypothesis.

Globally, inputs of whale bones and wood to the deep seafloor have been substantially altered by historical and ongoing human activities, such as whaling, deforestation, and the modulation of river geomorphology and watersheds (Butman et al., 1995; Smith; Wohl, 2014; Voight, 2015; Brazier et al., 2021). Modelling studies have suggested that whaling-induced declines in the abundance and mean size of whales have exerted extinction pressure on deep-sea whale-fall specialists and will continue to do so even at proposed sustainable yield scenarios (Smith et al., 2019). These ‘downstream’ impacts of anthropogenic forcing on organic-fall biodiversity remain to be fully evaluated.

2.6 CONCLUSIONS

The composition and diversity of faunal assemblages colonizing wood, whale-bone, and inorganic hard (control) substrata varied between depths and locations on the NE Pacific margin. Each substrate type supported a distinct assemblage, although enrichment opportunists and mass effects yielded some faunal overlaps. Most wood/bone colonists were substrate specialists or organic-enrichment opportunists, and organic-rich substrates supported higher macrofaunal abundances, and greater species richness and dominance than control assemblages nutritionally dependent on sinking POC flux. Differences in community composition of organic-fall assemblages with depth were consistent with the faunal zonation in background communities in the Cascadia Basin, but these differences seem unlikely to be driven simply by the decrease in small POC flux with depth. In particular, downslope differences in biodiversity of wood-fall assemblages are also likely influenced by a decline in the occurrence of wood-fall habitats with increasing distance from terrestrial sources of wood. We hypothesize that regions with greater supply of wood and/or whale falls experience greater propagule supply and connectivity of the organic-fall fauna, enhancing regional organic-fall biodiversity. The experimental approach and results of this and similar studies are critical to monitor and understand the implications of human activities, such as whaling and modulation of forests and waterways, on deep-sea biodiversity.

2.7 ACKNOWLEDGEMENTS

We thank Pavica Srsen and Bob Butler for help in obtaining the whale bones used in this study. We also thank Mario Williamson and P. Srsen for their assistance with lander design and construction, and Ian Butler, B. Butler, Damien Waits, and Matt Galaska for assistance with lander assembly. We thank the captain and crew of the RV ‘Oceanus’ for support at sea. Special thanks go to cruise participants Cassandra Turner, Amanda Ziegler, D. Waits, M. Galaska, Nathan Whelan, Stefan Krause, Paulo Sumida, Angelo Bernardino, and Mauricio Shimabukuro for help at sea. We thank C. Turner and the participants of the 2014 Friday Harbor Laboratories Deep-Sea Biology course for their contribution towards macrofaunal sorting. We also thank

Amber Cobley and Kevin Christensen for assistance sorting multicore samples, Les Watling for assisting with the identification of crustaceans, and Ronald Sluys for identifying platyhelminths. We thank Travis Washburn for providing POC flux values. Jesse van der Grient and Kyle Edwards provided excellent advice on statistical analyses. We thank Rachel Young for producing Figure S2.2. We are grateful to Friday Harbor Laboratories for providing facilities for assembly and testing landers, and processing samples. This is contribution no. 11494 from the School of Ocean and Earth Science and Technology, University of Hawai‘i at Mānoa.

CHAPTER 3

The ecosystem engineering role of xylophagaid bivalves at deep-sea wood falls

In prep as: Young EL, Treude T, Voight JR, Altamira I, Krause S, Halanych KM, Smith CR. The ecosystem engineering role of xylophagaid bivalves at deep-sea wood falls

3.1 ABSTRACT

Wood-boring xylophagaid bivalves are postulated to be key ecosystem engineers at deep-sea wood falls. Xylophagaid bivalves are thought to modulate food, habitat, and redox conditions and thus influence the biomass and diversity of entire wood-fall assemblages; however, these xylophagaid influences have been poorly quantified. Here, we evaluate the ecosystem engineering roles of xylophagaid bivalves collected from controlled wood-fall experiments in the NE Pacific. Replicate wood blocks were deployed to the seafloor at ~1600 and ~2800 m depth in the Cascadia Basin for 15 months. Xylophagaid bivalves were the primary drivers of wood loss with their biomass strongly positively correlated with wood mass loss. Xylophagaid biomass was positively correlated with non-xylophagaid macrofaunal biomass and species richness, and negatively correlated with non-xylophagaid macrofaunal evenness. Sulfate reduction rates in the wood blocks varied substantially but were generally low in comparison to those reported from other organic fall and reducing deep-sea environments. We did find evidence of enhanced sulfate reduction rates deeper in wood blocks with xylophagaid borings. Based on results and other studies, we outline five wood-fall successional stages: (1) microbial stage; (2) wood-borer stage; (3) opportunist stage; (4) wood disintegration stage; and (5) reef stage; and suggest that sulfidic conditions may occur during each of these stages.

3.2. INTRODUCTION

Coarse woody detritus provides an important source of nutrition and habitat in many aquatic ecosystems (Maser & Sedell, 1994). In the deep sea, sunken wood forms distinct, organic-rich habitats known as wood falls which deliver large pulses of organic matter to an otherwise food-poor deep-sea floor (Turner, 1973; Bienhold et al., 2013) However, wood is a recalcitrant resource and requires specialized decomposers to convert it into more labile forms for use by non-specialized organisms. The decomposition of wood on the seafloor follows an ecological succession in community structure and ecosystem function, likely mediated by key ecosystem engineers (Bienhold et al., 2013; Hendy et al., 2014).

Wood-boring xylophagaids bivalves are postulated to be the key ecosystem engineers at deep-sea wood falls, transforming available habitat, food resources and redox conditions of sunken wood. The creation of xylophagaid boreholes initially increases and diversifies the available habitat, allowing non-boring organisms to colonize the interior of wood parcels (Turner, 1973; Wolff, 1979). Extensive boring by xylophagaids can ultimately lead to the complete disintegration of the wood-fall habitat (Tyler et al., 2007; Romano et al., 2013). Xylophagaids ingest rasped wood particles, and digestion of wood material is expected to be aided by cellulolytic and nitrogen-fixing endosymbiotic bacteria (Distel & Roberts, 1997), although some species may also obtain nitrogen from particulate organic material filtered from the water column (Voight et al., 2020). Some xylophagaid species are known to line their boreholes with their fecal material, comprised of undigested lignin (Pesante, 2018; Dore & Miller, 1923), bacteria (Fagervold et al., 2014; Harbour et al., 2021a), and mucus (Purchon, 1941).The non-lignin component of the fecal material is relatively labile compared to wood, and is likely a significant food source for other animals that can't directly digest wood. Microbial decomposition of the fecal material, as well as the wood substrate, can lead to reducing conditions supporting chemoautotrophic metabolic pathways (Kalenitchenko et al., 2018a). Overall, the ecosystem engineering activities of xylophagaids may control the biomass, abundance, and biodiversity of wood-fall assemblages, as well as the distribution of sulfidic conditions throughout the wood, but their engineering activities are poorly quantified.

The progressive decay of wood in terrestrial and marine environments yields a succession of faunal and microbial communities (Stokland et al., 2012; Nishimoto et al., 2015; Fukasawa & Matsukura, 2021), as well as changes in the physicochemical properties of the wood and surrounding area (Fojutowski et al., 2014; Johnson et al., 2014). Pop Ristova et al. (2017, p.21) have proposed four overlapping (faunal and microbial) successional stages, quoted below:

"1) A specialist stage (McClain & Barry, 2014) occurring within the first couple of months of the wood arrival at the sea floor and characterized by invasion of woodborers that initialize the degradation of wood;

2) An opportunist stage (McClain & Barry, 2014; Bernardino et al., 2010), initiated already before the sulphophilic stage and lasting for 1-2 years, with a peak during the main growth of woodborer populations, when detritus-feeders and predatory organisms, e.g., sipunculids, pycnogonids, sea urchins, as well as bacterivores get attracted by the accumulation of biomass;

3) A sulfophilic stage (duration > 1–2 years; Bienhold et al., 2013; Kalenitchenko et al., 2015; Kalenitchenko et al., 2016; Yücel et al., 2013), during which enhanced cellulose degradation

leads to sulfidic conditions and a colonization by chemosynthetic organisms, i.e., *Idas* sp., siboglinids, takes place;

4) A senescence stage, initiated after the third year of degradation, characterized by the disintegration of wood logs, the dispersal and burial of the wood-chips, as well as a decline of numbers of large faunal organisms including reduction of woodborer biomass."

While there is some empirical support for these successional stages, the biomass and community structure of wood-fall assemblages, including xylophagaids, as well as rates of wood mass loss, across these stages remain poorly quantified in the deep sea. Quantitative studies of wood falls are required to better elucidate the nature of successional processes and role of ecosystem engineers in detritus-based ecosystems.

Here, we evaluate the ecosystem engineering role of xylophagaid bivalves collected from controlled experimental deployments of wood blocks in oxygenated bottom-water conditions in the NE Pacific (Young et al., 2022). Although the experiments were deployed for the same amount of time, bathymetric and local variability in wood-fall colonization yielded blocks spanning a broad range of decomposition stages. Because xylophagaids are thought to be major ecosystem engineers at deep-sea wood falls, their boring activities during the early-to-mid stages of wood decomposition might be expected to yield a number of successional patterns. First, xylophagaid biomass is expected to be correlated with wood-mass loss. If xylophagaids drive habitat availability and the diversity of food sources inside the wood, xylophagaid biomass should be correlated with species richness and biomass of the non-xylophagaid wood-fall assemblage. If xylophagaid fecal material substantially increases the availability of labile organic material at the wood fall, then xylophagaid biomass should be correlated with declining species evenness as enrichment opportunists increasing dominate the assemblage. Finally, xylophagaid boring may increase the availability of labile organic material and sulfate inside the wood, stimulating sulfate reduction deeper in the wood. Thus, for our wood blocks in early-to-mid successional stages of decomposition, we test the following hypotheses:

(1) Xylophagaid biomass is positively correlated with wood mass loss.
(2) Xylophagaid biomass is positively correlated with non-xylophagaid macrofaunal biomass and species richness.

(3) Xylophagaid biomass is negatively correlated with non-xylophagaid macrofaunal species evenness.

(4) The presence of xylophagaid bivalves enhances sulfate-reduction activity inside wood blocks.

Based on our results and a review of the literature, we also discuss modifications to the successional framework outlined by Pop Ristova et al. (2017).

3.3. MATERIALS AND METHODS

3.3.1 Experimental design

Detailed descriptions of the experimental and lander design are given in (Young et al., 2022). Briefly, four benthic landers holding whale-bone, wood, and inorganic control substrates were deployed at ~1600 and ~2800 m depth on the Washington-Oregon margin (Table 3.1, Figure S3.1). Landers were deployed in April 2013, and recovered after 15 months, by the *R/V Oceanus*. Each lander comprised nine 500-µm mesh bins (50 × 50 × 50 cm) arranged in an equilateral triangle, with one wood, one whale bone, and one control bin on each side of the triangle. Lids were attached to cover each bin upon recovery. Each bin held two replicate whale bone/wood/control substrates: one affixed to the bottom of the bin and one to the overlying lid. The lids of the landers remained open during lander descent and while on the seafloor. An acoustically-controlled release dropped the ballast and triggered lid closure, sealing contents inside the bins; the positively buoyant landers then ascended to the sea surface for recovery.

Table 3.1 Position, location, deployment durations, volumes, and successional stages (as per Pop Ristova et al. 2017) of wood blocks experimentally deployed in the Cascadia Basin. Dates of deployment and recovery are presented in Young et al. 2022. Initial volumes presented to 3 significant figures.

Wood block	Station	Position	Lat. (W)	Lon. (N)	Depth (m)	Deployment time (days)	Initial volume	Successional stage as per Pop Ristova et al. 2017
W27	N-2800	Lid	47° 16.20'	127° 35.57'	2666	443	3080	specialist
W18	N-2800	Lid	47° 16.20'	127° 35.57'	2666	443	3080	specialist
W35	N-2800	Lid	47° 16.20'	127° 35.57'	2666	443	3080	specialist
W1	N-2800	Bin	47° 16.20'	127° 35.57'	2666	443	3080	specialist
W26	N-2800	Bin	47° 16.20'	127° 35.57'	2666	443	3080	specialist
W28	N-2800	Bin	47° 16.20'	127° 35.57'	2666	443	3080	specialist
W36	N-1600	Lid	47° 57.46'	126° 2.12'	1596	443	3080	senescence
W15	N-1600	Lid	47° 57.46'	126° 2.12'	1596	443	3080	opportunist
W32	N-1600	Lid	47° 57.46'	126° 2.12'	1596	443	3080	opportunist
W30	S-1600	Lid	43° 54.52'	125° 10.42'	1605	444	3080	opportunist
W23	S-1600	Lid	43° 54.52'	125° 10.42'	1605	444	3080	opportunist
W22	S-1600	Lid	43° 54.52'	125° 10.42'	1605	444	3080	opportunist
W13	S-2800	Lid	43° 52.70'	127° 33.93'	2917	444	3080	specialist
W4	S-2800	Lid	43° 52.70'	127° 33.93'	2917	444	3080	specialist
W17	S-2800	Lid	43° 52.70'	127° 33.93'	2917	444	3080	N/A

Wood substrates were replicate blocks of untreated Douglas fir (*Pseudotsuga menziesii*) wrapped in 2-mm mesh nylon netting. Wood blocks had an average dimension of 18.4 × 19.0 × 8.8 cm, a volume of 3080 cm^3, and a surface area to volume ratio of ~ 0.44:1 (Table 3.1). Upon lander recovery, wood blocks were photographed whole, cut into quarters using a reciprocating saw, and preserved in 10% formalin-seawater solution, 95% ethanol, or air dried if no macrofauna were present. Samples for bacterial sulfate reduction were treated as described in 3.3.4.

3.3.2 Macrofaunal processing

To obtain data from wood blocks spanning a range decomposition states, quantitative macrofaunal data were collected from 12 formalin-fixed wood-block quarters: nine from lid-affixed wood blocks from three locations (N-2800, N-1600, and S-1600), and three from bin-affixed wood blocks at N-2800. Wood blocks were broken open to remove all macrofauna retained on a 300-µm sieve, macrofauna were then counted, sorted to morphospecies, and identified to the lowest possible taxonomic level. Taxonomic experts who identified species and distinguished undescribed species included co-authors I. Altamira (annelids) and J. Voight (mollusks), as well as Les Watling (crustaceans), and Ronald Sluys (platyhelminths). Epifauna were also picked from three unbored, lid-affixed wood blocks at S-2800. Because these epifauna were collected from whole blocks (not quarters), we consider these epifauna separately from the main data.

All wood from each sorted quarter was rinsed with deionized water over a 1.4-mm sieve to separate remaining wood from xylophagaid fecal material. Wood remaining on the sieve was dried at 60°C to a constant weight to determine post-deployment dry weight of each quarter. The pre-deployment dry weight of each quarter was estimated from pre-deployment weights of whole blocks, after accounting for (1) initial moisture content, and (2) wood mass loss during cutting. Initial moisture content (11.97 % ± 0.72 SD) was determined by drying four non-deployed blocks at 60°C to a constant weight. Mass change due to cutting (1.94 % ± 4.03 SD) was estimated by quartering the four non-deployed dried whole wood blocks with a similar reciprocal saw and blades. Wood mass loss (%) was calculated from the ratio of post-deployment dry weight to pre-deployment dry weight for each quarter. For comparisons with other studies, volumetric wood consumption rates (cm^3 wood lost per year) were estimated by converting wood mass into wood volume, based on measurements of dry wood density (0.45g/cm^3).

Macrofaunal biomass was measured as ash-free dry weight (AFDW; Mason et al., 1983). Specimens were dried at 60°C to a constant weight, and then combusted (ashed) at 550°C for 4 hours. The AFDW of organism fragments unidentifiable to species were also measured to estimate biomass more completely. AFDW was not determined for 76 animals that were too small to measure with estimated dry masses of < 0.0001 g per wood quarter, i.e., < 0.05 % of measured biomass on these quarters (Table S3.1). The AFDWs of 19 xylophagaid bivalve individuals stored in reference collections prior to biomass measurements were estimated from the mean body masses of conspecifics measured in this study.

3.3.3 Statistical analyses

Linear models were used to test hypotheses regarding relationships between xylophagaid biomass and 1) wood mass loss, 2) non-xylophagaid macrofaunal biomass, 3) non-xylophagaid macrofaunal species richness (S), and 4) non-xylophagaid macrofaunal evenness (J). Linear model analyses were performed using the “lme4” package (Bates et al., 2015) in the software R version 4.1.1 (R Core Team, 2021).

Macrofaunal assemblage similarity was visualized in a cluster dendrogram based on Bray-Curtis similarity performed on fourth-root transformed species-abundance data and using the group average linking method. Results of a SIMPROF test (Clarke et al., 2008) performed with 999 permutations were overlaid on the cluster dendrogram to indicate statistical significance of clusters. Differences between macrofaunal assemblage structure at different location/positions were tested using a one-way ANOSIM analysis. Cluster, SIMPROF, and ANOSIM analyses were performed using Primer-e software (Clarke & Gorley, 2015a).

3.3.4 Sulfate-reduction activity

Sulfate-reduction activity was measured in four wood blocks; W3 from N-1600-Bin, W13 from S-2800-Lid, W18 from N-2800-Lid, and W25 from S-1600-Bin. Block W3 was colonized by 0.57 inds per cm^3 wood (Young et al. 2022), while the other three blocks had no xylophagaid colonization. After wood pieces were split into halves or quarters, subsamples with dimensions of ~ 1 × 1 × 2 cm (each with a weight of ~1-3 g) were cut out with a sterile knife in 2-cm increments along the wood cross section. Individual wood pieces (two replicates per depth) were then each stored cold and dark in 12-ml glass serum crimp vials with sterile-filtered anoxic seawater until further treatment at GEOMAR, Germany a few days later. In the laboratory, the vials were injected with 6 µL of carrier-free $^{35}SO_4^{2-}$ radiotracer (dissolved in water, 370 kBq/sample, specific activity 37 TBq mmol^{-1}) and incubated in the dark at 0.5°C for 4 days. Sterile-filtered anoxic seawater incubated in 12 ml glass serum crimp vials without wood served as controls. After incubation, the sample liquid was poured into 50-ml plastic centrifugation vials filled with 15-ml 20% zinc-acetate solution to stop microbial activity and to precipitate sulfide. Samples were frozen and later analyzed to determine sulfate reduction rates according to the cold-chromium distillation method (Kallmeyer et al., 2004). The remaining wood pieces were then weighed wet to determine bacterial sulfate reduction rates per wood wet weight. Estimations of sulfate-reduction rates per surface area of wood (m^2) per day (integrated over the top 6 cm of wood) were calculated using wet wood density measurements taken upon wood recovery and were based on the assumption that that the surface area subsampled was 1 cm^2.

3.4 RESULTS

3.4.1 General state of decomposition

The wood blocks were recovered in varying states of decomposition. The three blocks from the S-2800-Lid were completely intact, except for several 1 - 3 mm diameter limnoriid boreholes on the outward facing surface of W13 (Figure 3.1A) and a 3 mm wide, 9 mm long, and ~2 mm deep bored trough on the lid-facing surface of W4 (not shown). Traces of microbial mat were patchily distributed across the surfaces of these wood blocks. Because W13 and W4 were colonized by woodborers, they represented the “specialist” successional stage as defined by Pop Ristova et al. (2017). W17 was not bored by woodborers and was not represented in the successional stage framework defined by Pop Ristova et al. (2017). Wood blocks from N-2800 (Figure 3.1B) were lightly bored by xylophagaid bivalves and were interpreted to be in the “specialist” successional stage defined by Pop Ristova et al. (2017), except for W36 which was in the “senescence” stage (see section 3.4.4). Surfaces of N-2800 wood blocks also had blackened patches and traces of microbial mats upon recovery. Lid-attached wood blocks at N-2800 were recovered intact with numerous small (< 1 mm wide) borehole openings, sometimes blackened, on wood surfaces, yet many boreholes were shallow and vacant (Figure 3.1B). Bin-attached wood blocks at N-2800 were also largely intact, covered with small boreholes and with some degradation of wood-block corners and edges (Figure 3.1C). Wood blocks from N-1600-Lid and S-1600-Lid were so heavily bored that the blocks were crumbling and easily crushable by hand (Figure 3.1D), interpreted as representing the "opportunist" successional stage as defined by Pop Ristova et al. (2017). Boreholes from N-1600-Lid (Figure 3.1D) and S-1600-Lid (not shown) contained significant amounts of fecal material and wood chips, and in some areas were blackened and smelled of sulfide.

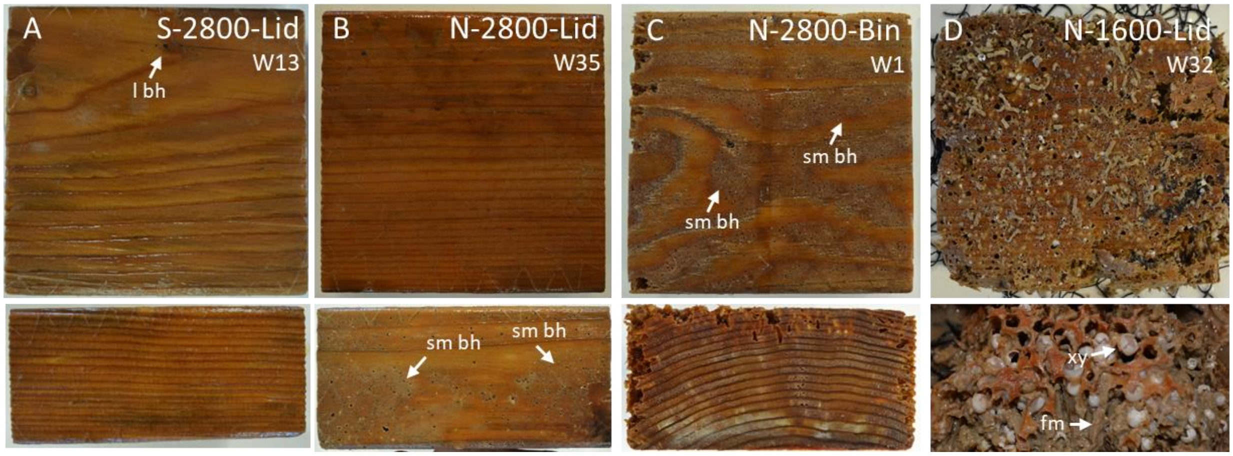

Figure 3.1 Representative wood blocks recovered from four different landers after 15 months analyzed in this study. Two exposed surfaces (front and side) of each block are shown. Arrows indicate examples of limnoriid bore holes on W13 (l bh), small bore holes (sm bh), and xylophagaids (xy) and fecal material (fm). Here, W13, W35, and W1 are interpreted to represent the "specialist" stage, and W32 represents the "opportunist" stage, as defined by Pop Ristova et al. (2017).

3.4.2 Macrofaunal community structure

A total of 25,423 macrofaunal individuals belonging to 33 morphospecies were collected from the 12 wood block quarters (Table 3.2). Phylum Annelida was the most abundant (69% of total individuals) and species rich, with 17 morphospecies belonging to 10 families. Mollusca was the second most abundant phylum (27% of total individuals across 9 morphospecies), the majority of which were 7 different morphospecies of xylophagaid wood-boring bivalve. The third most abundant phylum was Platyhelminthes, with 4.7% of the total abundance represented by a single triclad morphospecies, found only at N-1600-Lid and S-1600-Lid. Assemblages at each location/position were significantly different from one another (ANOSIM, $R = 0.759$, $p < 0.05$), yet N-1600-Lid and S-1600-Lid assemblages clustered with > 73.5% similarity (Figure 3.2).

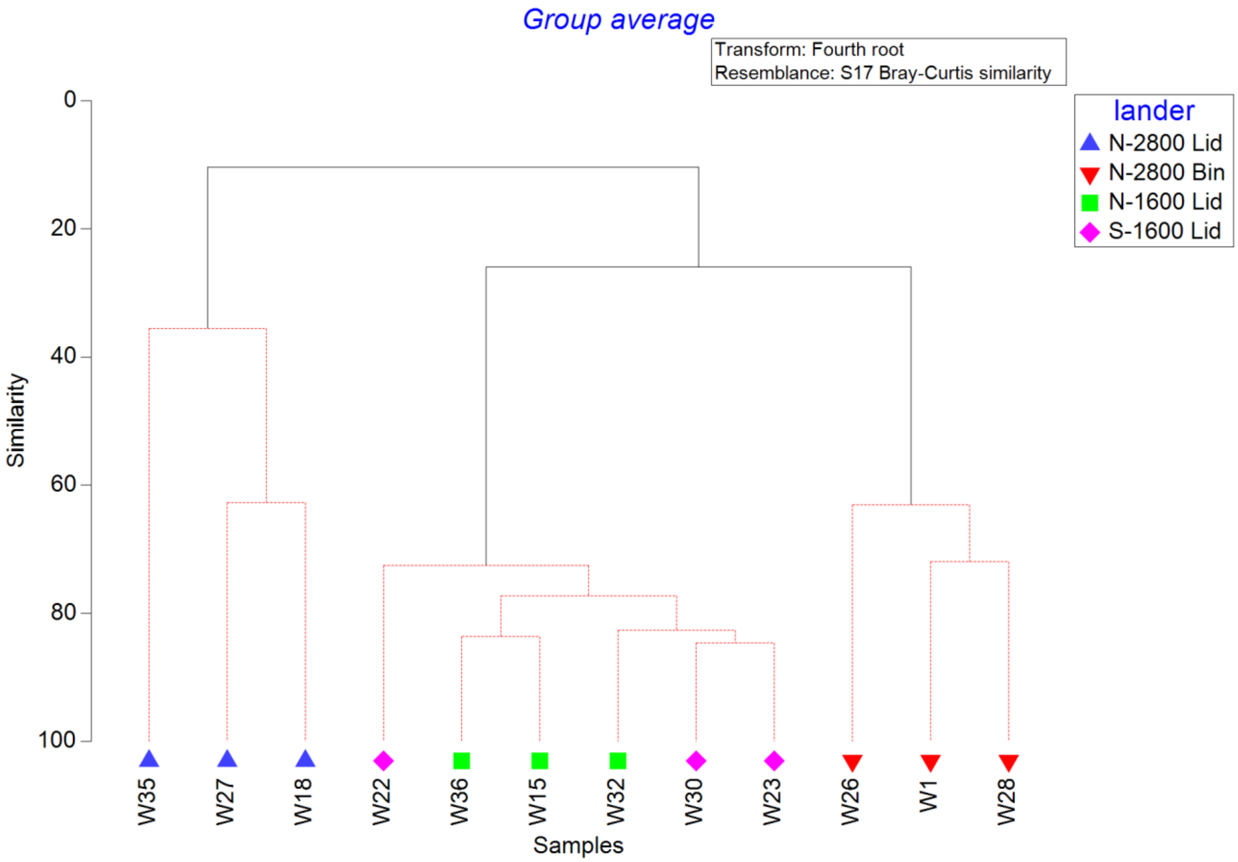

Figure 3.2 Cluster dendrogram of wood-block macrofaunal assemblages. Red lines indicate structure with no statistical support and black lines indicate structure with statistical support, according to SIMPROF analyses (significance level 5%).

At S-2800-Lid, a single amphipod belonging to the genus *Bathyceradocus* and two wood-boring limnoriid isopods were picked from one whole wood block, two anemones were picked from another block, and the third block had no associated macro-epifauna.

N-2800-Lid wood blocks were colonized by a few macrofaunal individuals (Table 3.2; Table S3.2). Despite numerous small boreholes the wood surfaces (Fig 3.1B), only two xylophagaid species at low densities (0-50 individuals, < 0.0636 individuals per cm^3) were recovered from any of these blocks and other macrofaunal species were rare (Table 3.1).

N-2800-Bin blocks were colonized by an average density of 0.870 macrofaunal individuals per cm^3 of wood (± 0.416 SE, Table 3.2). Xylophagaid assemblages were co-dominated by *X. zierenbergi* (58.8%) and *X. muraokai* (35.1%) and also included two less-abundant xylophagaid species, *Xylophaga corona* and *Xylopholas crooki*. Non-xylophagaid assemblages at N-2800-Bin blocks were dominated by dorvilleids (*Ophryotrocha batillus*, 61.1%; dorvilleid sp. 55, 15.67%;

and *O. langstrumpae*, 11.5%), and also included 11 other annelid, arthropod, and mollusk morphospecies.

N-1600-Lid blocks were colonized by an average of 3.28 macrofaunal individuals per cm^3 of wood (± 0.805 SE, Table 3.2). Xylophagaid assemblages were heavily dominated by *Xylophaga oregona* (96.9%). Non-xylophagaid assemblages were composed of 13 morphospecies dominated by *O. langstrumpae* (78.9%), followed by the platyhelminth Triclad sp. A (15.6%), and the ampharetid *Decemunciger* sp. A (3.9%). Notably, W36 had ~2-3 times fewer xylophagaid individuals than the other two N-1600-Lid blocks.

S-1600-Lid assemblages were colonized by an average of 6.84 individuals per cm^3 of wood (± 2.75 SE, Table 3.2) and had a similar composition to N-1600-Lid assemblages (Figure 3.2). Xylophagaid assemblages were heavily dominated by *X. oregona* (99.7%) and also included *X. microchira* (0.3%). Non-xylophagaid assemblages were composed of 16 morphospecies dominated by *O. langstrumpae* (94.8%), followed by the Triclad sp. A (2.8%), the ampharetid *Decemunciger* sp. A (1.1%), and the capitellid *Capitella* cf. *capitata* (0.6%).

Species richness of xylophagaids and non-xylophagaids, as well as the other diversity parameters of non-xylophagaid species, varied non-uniformly by lander and wood-block position (Table 3.2).

Table 3.2 Density (mean ± SE) of wood infauna (individuals per cm^3 deployed wood) per lander/position. Counts and densities (inds.cm^{-3} wood) for each wood block are presented in Tables S3.2 and S3.3. S: species richness; H' Shannon-Wiener diversity index; J: evenness.

Phylum, Family	Species/Morphospecies	N-2800-Lid	N-2800-Bin	N-1600-Lid	S-1600-Lid
Annelida					
Ampharetidae	Ampharetid sp. 22	-	0.000433 ± 0.000433	0.0178 ± 0.0111	0.0251 ± 0.00697
	Decemunciger sp. A	-	0.00693 ± 0.00385	0.0919 ± 0.00964	0.0605 ±0.00510
Capitellidae	*Capitella* cf. *capitata*	-	0.00390 ± 0.00150	0.000433 ± 0.000433	0.0342 ± 0.00607
Cirratulidae	*Chaetozone* sp. B	-	0.000867 ± 0.000867	-	-
Ctenodrilidae	Ctenodrillid sp. 2	-	-	0.00173 ± 0.00173	-
Dorvilleidae	Dorvilleid sp. 15	-	0.00606 ± 0.00338	-	-
	Dorvilleid sp. 32	-	-	0.000433 ± 0.000433	-
	Dorvilleid sp. 54	-	-	-	0.00173 ± 0.00173
	Dorvilleid sp. 55	-	0.0295 ± 0.00830	-	-
	Ophryotrocha langstrumpae	-	0.0217 ± 0.0112	1.85 ± 0.517	5.26 ± 2.63
	Ophryotrocha batillus	-	0.115 ± 0.0409	0.00650 ± 0.00270	0.00650 ± 0.00225
Flabelligeridae	Flabelligerid sp. A	-	-	-	0.000433 ± 0.000433
Hesionidae	*Sirsoe* cf. *hessleri*	-	-	-	0.0013 ± 0.0013
Nereididae	Nereidid sp. 6	-	-	0.000433 ± 0.000433	0.0013 ± 0.000751
Protodrilidae	Protodrilid sp. 1	-	-	-	0.000867 ± 0.000867
Spionidae	*Laonice* sp. A	-	-	-	0.0013 ± 0.000751
Syllidae	*Sphaerosyllis* sp. A	-	0.000867 ± 0.000433	-	0.000433 ± 0.000433
Arthropoda					
Amphipoda	*Accedomoera* sp. A	0.000867 ± 0.000867	-	-	-
	Lysianassid sp. A	0.000433 ± 0.000433	0.000867 ± 0.000867	0.00477 ± 0.00413	-
	Sebidae sp. A	-	0.000433 ± 0.000433	0.00216 ± 0.00156	0.000867 ± 0.000867
Isopoda	Limnoriid sp. A	-	-	-	0.000433 ± 0.000433

Table 3.2 (Continued) Density (mean ± SE) of wood infauna (individuals per cm^3 deployed wood) per lander/position. Counts and densities (inds.cm^{-3} wood) for each wood block are presented in Table S3.2 and S3.3. S: species richness; H' Shannon-Wiener diversity index; J: evenness.

Phylum, Family	Species/Morphospecies	N-2800-Lid	N-2800-Bin	N-1600-Lid	S-1600-Lid
Tanaidacea	Tanaid sp. A	-	0.000433 ± 0.000433	-	-
Cnidaria					
Actinaria	Actinarian sp. A	-	-	0.000867 ± 0.000433	-
Mollusca					
Bivalvia	*Idas washingtonius*	-	0.000867 ± 0.000867	-	0.000867 ± 0.000433
	Abditoconus heterosiphon	-	-	0.000433 ± 0.000433	-
	Xylonora muraokai	0.00260 ± 0.00150	0.239 ± 0.232	-	-
	Xylonora zierenbergi	0.0195 ± 0.0195	0.401 ± 0.140	-	-
	Xylophaga corona	-	0.00381 ± 0.0213	-	-
	Xylophaga microchira	-	-	0.0286 ± 0.00846	0.00346 ± 0.00114
	Xylophaga oregona	-	-	0.907 ± 0.282	1.28 ± 0.318
	Xylopholas crooki	-	0.00303 ± 0.00156	-	-
Gastropoda	*Dillwynella* sp. A	-	0.000433 ± 0.000433	-	-
Platyhelminthes					
	Triclad sp. A	-	-	0.366 ± 0.0267	0.155 ± 0.0864
	Total density	0.0013 ± 0.00106	0.870 ± 0.416	3.28 ± 0.805	6.84 ± 2.75
	Xylophagaid density	0.0221 ± 0.0208	0.682 ± 0.370	0.936 ± 0.281	1.29 ± 0.0329
	Xylophagaid *S*	1 ± 0.578	3.33 ± 0.333	2.33 ± 0.333	2 ± 0
	Non- xylophagaid *S*	0.667 ± 0.667	8.33 ± 0.667	8.33 ± 1.20	10.3 ± 2.96
	Non-xylophagaid *H'*		1.25 ± 0.173	0.704 ± 0.0972	0.302 ± 0.0303
	Non-xylophagaid *J*		0.588 ± 0.0614	0.336 ± 0.0363	0.141 ± 0.0298

3.4.3 Macrofaunal biomass

Macrofaunal biomass ranged from 0 - 0.0056 g AFDW per cm^3 of deployed wood across the 12 blocks (Figure 3.3). Biomass was lowest at N-2800-Lid blocks, intermediate at N-2800-Bin blocks, and highest at N-1600-Lid and S-1600-Lid blocks. Biomass was particularly variable at N-1600-Lid, with W36 having relatively low biomass. Xylophagaids dominated biomass (> 95%) at all wood blocks, with *Xylonora zierenbergi* dominating at 2800-m deployments, and *Xylophaga oregona* dominating at 1600 m. Non-xylophagaid biomass contributed 1.2 to 4.6% of total biomass across landers and positions (Figure 3.3). Although macrofauna were present at N-2800-Lid blocks, the non-xylophagaid biomass was too small to be measured (Table S3.1). Non-xylophagaid biomass was dominated by annelid fragments and *Capitella* cf. *capitata* at N-2800-Bin blocks, by *Decemunciger* sp. A, *Ophryotrocha langstrumpae,* and Triclad sp. A at N-1600-Lid blocks, and by *Ophryotrocha langstrumpae* and *Capitella* cf. *capitata* at S-1600-Lid blocks.

Estimated net xylophagaid production (mean ± SE) ranged from 0.2 ± 0.4 and 4.2 ± 0.1 g AFDW per liter of wood per year, and between 6.7 and 128.6 g AFDW per square meter of exposed wood per year (Table S3.4)

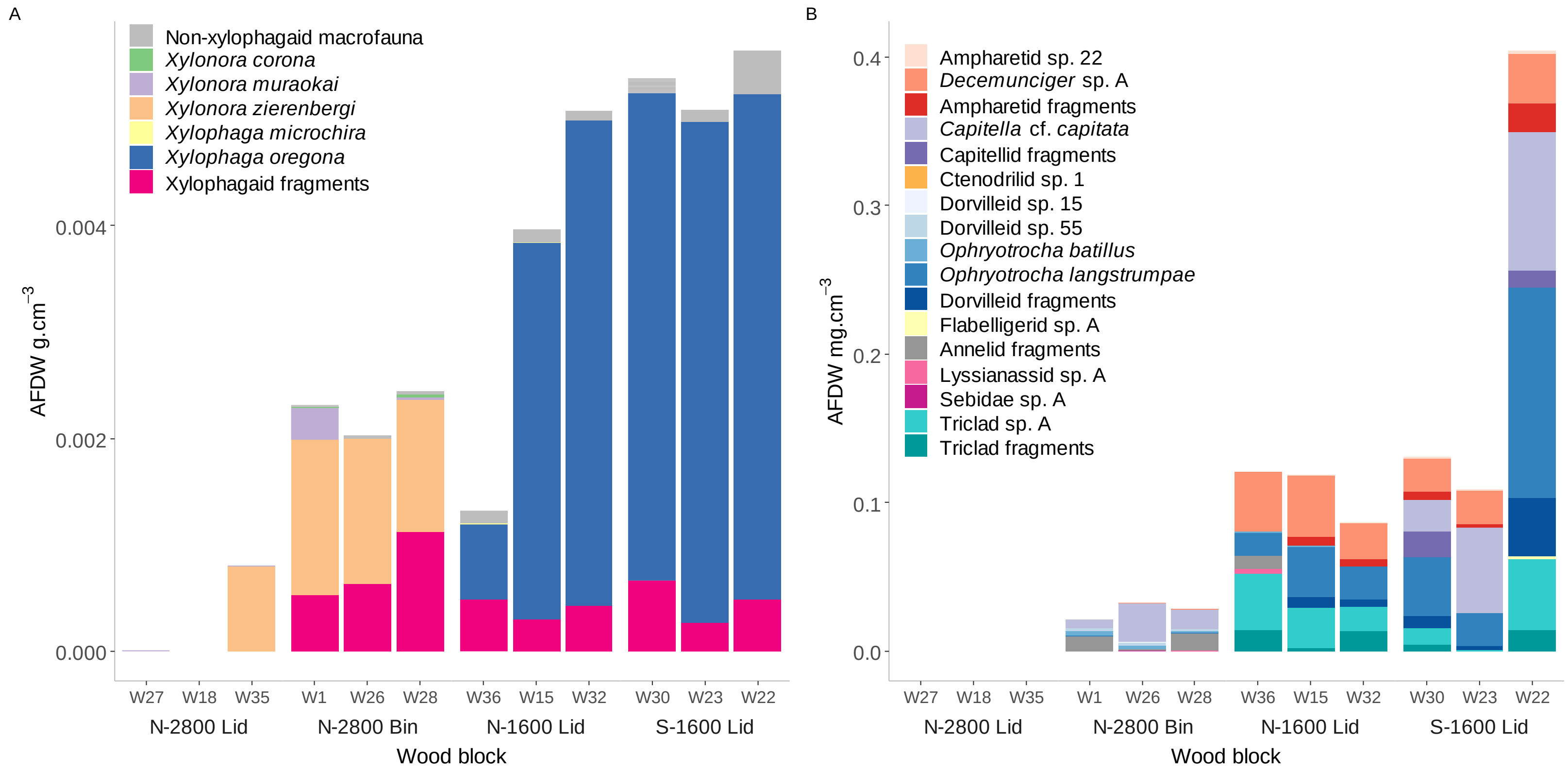

Figure 3.3 Biomass of A) total assemblages (AFDW, grams per cm^3 wood), and B) non-xylophagaid infauna Biomass (AFDW, mg per cm^3 wood). Individuals with unmeasurable biomass (dry weight > 0.0001 g) are indicated in Table S3.1.

3.4.4 Wood mass loss rates

Wood mass loss (% loss after 15 mo) varied substantially across location/positions. Mass loss was lowest at N-2800-Lid blocks, intermediate at N-2800-Bin blocks and highest at N-1600-Lid and S-1600-Lid blocks (Table 3.3). As expected, wood loss rates (cm^3 wood bored per year) increased with the qualitatively assessed successional decomposition stage of each location-position group (N-2800-Lid and Bin in the "specialist" stages, N1600-Lid and S-1600-Lid in the "opportunist" stages). However, at W36 (N-1600-Lid), the combination of low xylophagaid abundance and high % wood mass loss suggests that this block resembled the more advanced stage of decomposition, during which xylophagaid populations are in decline, resembling the "senescence" stage defined by Pop Ristova et al. (2017).

Table 3.3 Wood mass loss rates and xylophagaid densities.

Location, Position	Wood block	% wood mass loss over 15 months	Number of xylophagaid individuals per 770 cm^3 wood	Maximum wood consumption rate by all xylophagaids (cm^3 wood bored per year)	Maximum wood consumption rate per individual xylophagaid (cm^3 wood bored per year)
N-2800-Lid	W27	1.7	2	10.7	5.35
	W18	8.9	0	54.6	N/A
	W35	10.2	49	56.9	1.16
	mean ± SD	6.9 ± 4.6	17.0 ± 27.7	40.7 ± 26.0	3.26 ± 2.97
N-2800-Bin	W1	23.0	1087	139.1	0.13
	W26	25.8	166	178.0	1.07
	W28	29.5	321	180.5	0.56
	mean ± SD	26.1 ± 3.2	524.7 ± 493.1	165.9 ± 23.2	0.59 ± 0.47
N-1600-Lid	W36	91.2	342	511.6	1.50
	W15	86.7	1091	517.1	0.47
	W32	80.5	729	530.9	0.73
	mean ± SD	86.1 ± 5.4	720.7 ± 374.6	519.9 ± 9.9	0.90 ± 0.53
S-1600-Lid	W30	84.3	1039	521.5	0.50
	W23	91.2	945	574.8	0.61
	W22	91.3	985	582.9	0.59
	mean ± SD	88.9 ± 4.0	989.7 ± 47.2	559.8 ± 33.3	0.56 ± 0.06

3.4.5 Relationships between xylophagaid biomass, wood mass loss and macrofaunal community structure

Because we are testing hypotheses concerning wood blocks in the “specialist” and “opportunist” stages of decomposition, four blocks were omitted from the following analyses to test our hypotheses: W36, which is interpreted to be in the “senescence” stage, and the S-2800-Lid blocks lacking xylophagaids. Xylophagaid biomass was significantly positively correlated with percentage wood mass loss (Figure 3.4A), non-xylophagaid macrofaunal biomass (Figure 3.4B), and non-xylophagaid macrofaunal species richness (Figure 3.4C). Xylophagaid biomass was significantly negatively correlated both with non-xylophagaid macrofaunal evenness (Figure 3.4D).

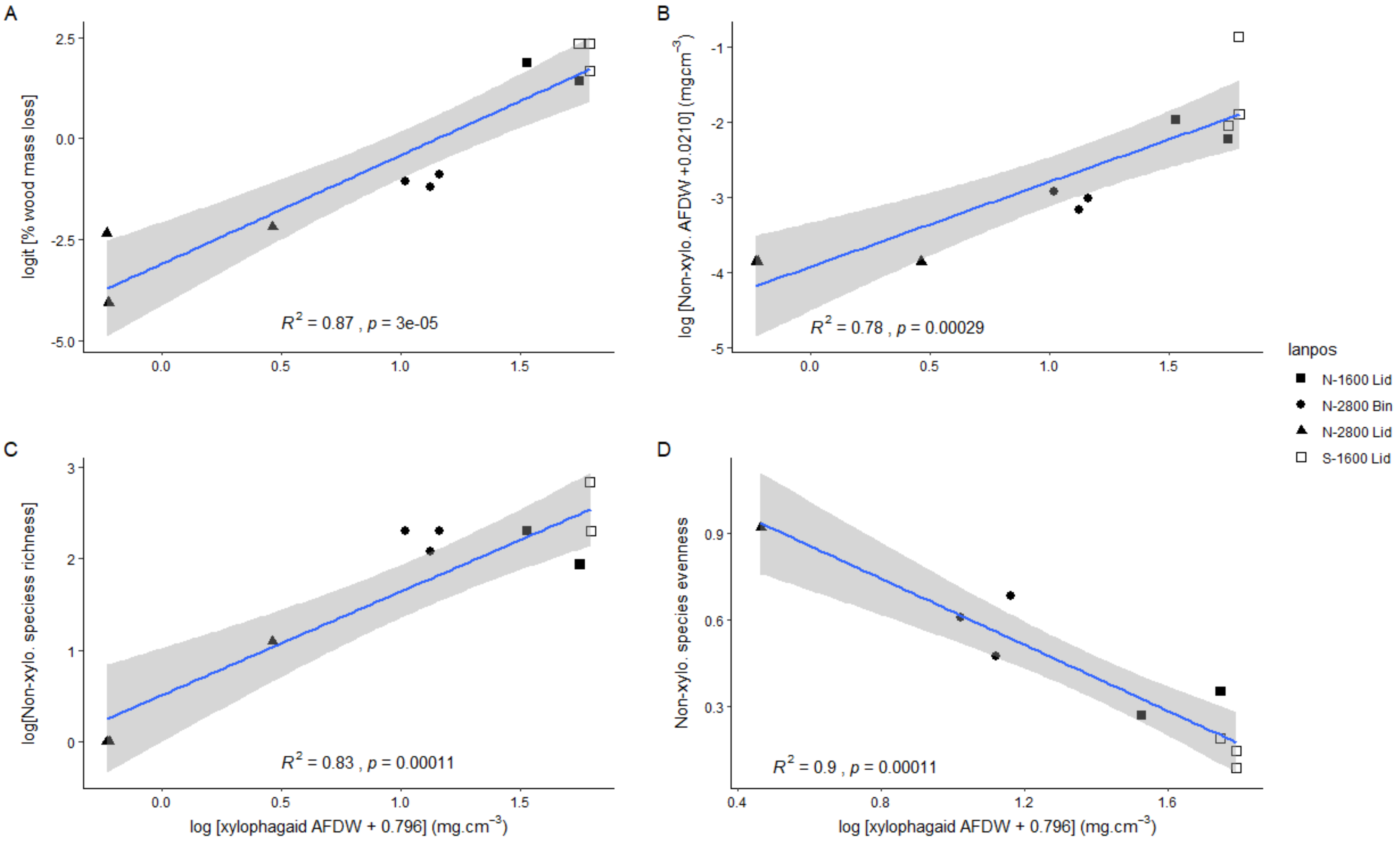

Figure 3.4 Relationships between xylophagaid biomass and A) percentage wood mass loss, B) non-xylophagaid macrofaunal AFDW, C) non-xylophagaid macrofaunal species richness, and D) non-xylophagaid macrofaunal evenness in wood blocks classified as falling into the “specialist and “opportunist” stages.

3.4.6 Sulfate-reduction activity

All wood blocks but W13 showed activity of bacterial sulfate reduction. Maximum activity ranged between 0.3 nmol SO_4^{2-} g^{-1} WW d^{-1} (W18) and 3.7 nmol SO_4^{2-} g^{-1} WW d^{-1} (W25, 0-2 cm). In W18 and W25, the highest activity was found in the surface layer (0-2 cm), while in W3, the highest activity was detected at 4-6 cm layer. Average sulfate reduction rates integrated over 6 cm of wood depth were greatest for W25, lowest for W18, and intermediate for W3 heavily bored by xylophagaids (Figure 3.5, Table 3.4).

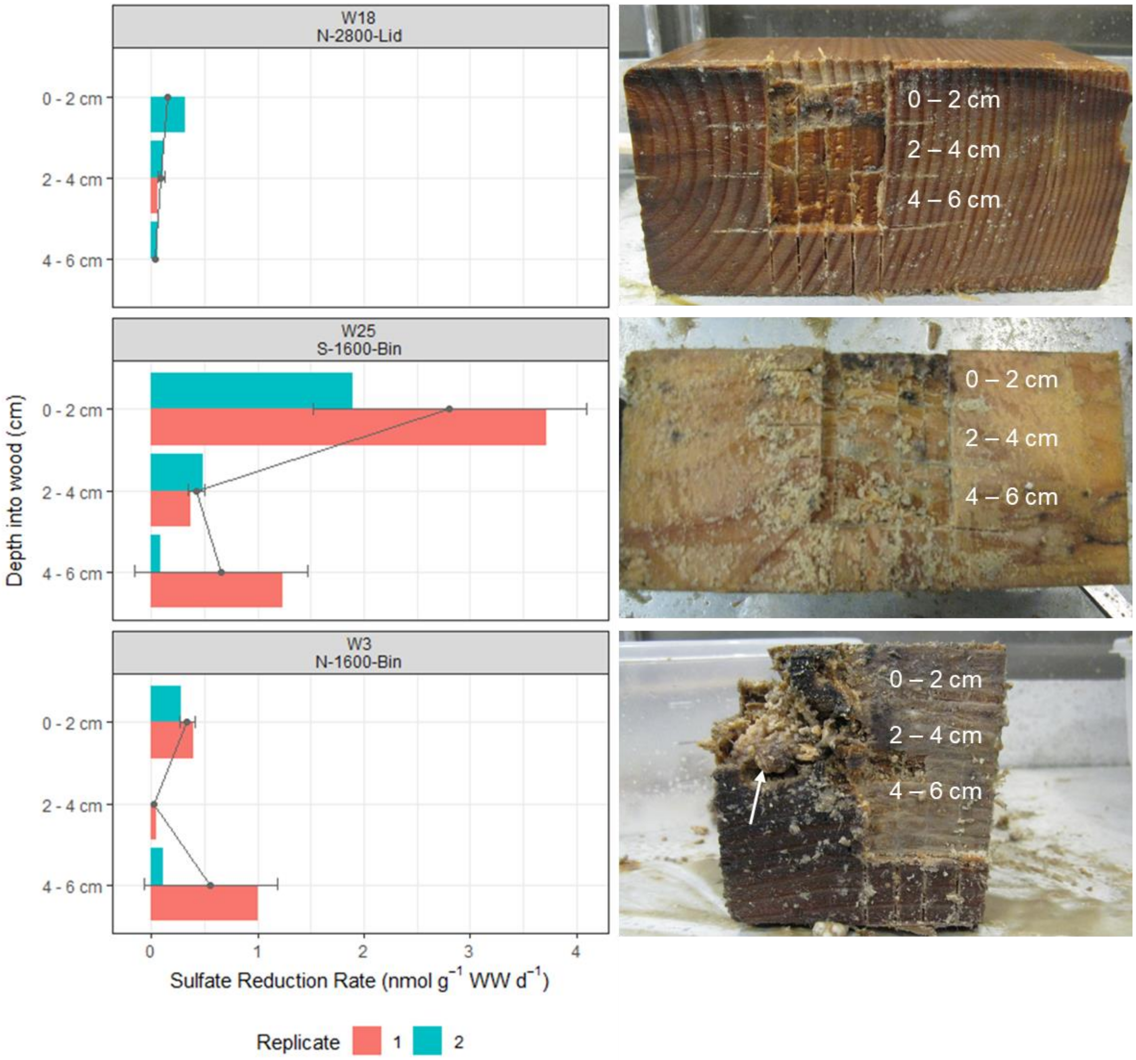

Figure 3.5 Sulfate reduction activity determined in wood. Points and error bars indicate mean and standard deviation values of replicate profiles. Left side: Sulfate reduction rates plotted against depth into wood (two replicates per depth). Right side: Wood showing subsampled depths for sulfate reduction determination. Wood blocks W18 and W25 were not colonized by xylophagaid bivalves. Wood block W3 was bored by xylophagaids (indicated by arrow). Note that no sulfate reduction activity was detected in wood block W13 (not shown).

Table 3.4 Summary of sulfate reduction rates (SRR) at wood blocks and at/surrounding other wood and whale bone deployments. Results from this study are reported as averages of two replicate measurements ± SD.

	SRR	Integrated depth	Reference
	(nmol cm^{-2} d^{-1})	(cm)	
W25, S-1600-Bin	3.9 ± 2.0	6	This study
W18, N-2800-Lid	0.3 ± 0.3	6	This study
W3, N-1600-Bin	0.9 ± 0.7	6	This study
W13	0	6	This study
Sediments, 0.5 m from wood	130 - 200	10	Bienhold et al. 2013
Cold seep sediments, 10 m from wood	250	10	Bienhold et al. 2013
Pelagic sediments, 10 m from wood	10	10	Bienhold et al. 2013
Sulfide-producing areas of whale bones	89	5	Treude et al. 2009

3.5 DISCUSSION

Our controlled experimental study of wood blocks deployed at the deep-sea floor for 15 months in the NE Pacific floor indicate, in agreement with previous studies, that xylophagaid bivalves dominate macrofaunal biomass at deep-sea wood falls. In addition, our results provide strong, quantitative evidence that xylophagaids influence important ecosystem functions/properties on wood falls, including wood-mass loss, biodiversity of wood-inhabiting assemblages, and reducing conditions within the wood.

3.5.1 Xylophagaids and wood mass loss

The strong positive correlation between xylophagaid biomass and percent wood mass loss (Figure 3.4) supports our Hypothesis 1, and provides strong quantitative evidence that xylophagaids can control the degradation of wood in the deep sea (Turner, 1973; Bienhold et al., 2013). We observed minimal mass loss in wood blocks with no xylophagaid colonization, and a uniform, highly significant pattern of increasing mass loss with increasing xylophagaid biomass.

Wood degradation was extensive at our 1600-m deployments, where ~90% of wood mass was lost after 15 months on the seafloor. In another study, Douglas fir deployed at comparable depths (1520 m) was similarly consumed after 10 months following colonization by the same xylophagaid species (Voight, 2007). The rapid and near-total degradation of wood blocks suggests that wood may be a substantial and important food source for specialized benthic communities at depths of 1500-1600 m in the Cascadia Basin, offshore of heavily wooded coastlines. Rapid (< 1 year) and total destruction of wood blocks has been reported elsewhere in the deep sea (Tyler et al., 2007; Romano et al., 2013), suggesting that very rapid, near total fragmentation resulting from xylophagaid boring can be one fate of wood material on the deep-sea floor on continental margins.

In contrast, xylophagaid biomass was low or absent, and between 1.7 and 29.5% of wood mass was lost after 15 months at our deeper, 2800 m deployments. There was no visible evidence of unsuccessful xylophagaid settlement (e.g., small, empty boreholes) on our southerly S-2800 blocks suggesting limited larval supply, despite previous reports of xylophagaid recruitment within ~140 km on wood at comparable depths after longer, 24-month deployments (Voight, 2007). This suggests that larval supply in this area is patchy in space and/or time. The presence of numerous shallow and or vacant boreholes at our northerly, N-2800 location suggests that xylophagaid larvae had settled but may have disappeared due to post-settlement predation; tanaids, galatheids and acotylean polyclad flatworms were collected from the bins surrounding N-2800 wood blocks (Young et al., 2022). Each of these taxa are considered to be potential xylophagaid predators at other wood falls (Turner, 1977; Voight, 2007; McClain & Barry, 2014). Thus, processes influencing recruitment and post-settlement survival of xylophagaids may limit xylophagaid population growth and biomass production, in turn influencing decomposition and community succession of wood-fall habitats in the deep sea.

While it is clear that xylophagaid boring is directly responsible for the vast bulk of wood-mass loss in ours and in other deep-sea experiments, it is worth noting that wood-mass loss in the deep sea may result from other processes as well. For example, wood at our 1600-m deployments was highly fragmented and crumbling, and wood fragments are likely to have fallen, or have been eroded, from our mesh bags prior to complete xylophagaid consumption. Other wood consumers, e.g., limnoriid isopods, can also play a role in wood-mass loss, although their contribution in our experiments was minimal. A single wood-boring limnoriid isopod with extremely small biomass was collected from our wood block at S-1600-Lid, and two further limnoriids were found at a S-2800-Lid block. Limnoriids often cause significant wood decay in shallow marine environments (Borges et al., 2014), but their presence at deep sea wood-falls has been reported infrequently (Kussakin & Malyutina, 1989; Schotte, 1989; Judge & Barry, 2016) with little indication of a substantial contribution to wood-mass loss.

Some mass loss may also have occurred from microbial decay. Fungi are major wood decomposers in terrestrial environments (Lustenhouwer et al., 2020) and their contribution to mass loss in marine environments is still being documented (Björdal, 2012). Under *in vitro* experimental conditions inaccessible to xylophagaid larvae, fungi from tropical and sub-tropical shallow marine habitats caused up to 10% of mass loss of submerged wood over 6 mo at 25°C (Bucher et al., 2004), although the wood had a surface area to volume ratios 10-fold greater than the blocks in our study. A few species of fungi have been described from sunken wood in the deep sea (Dupont et al., 2009; Kohlmeyer, 1977; Nagano et al., 2019) but their contribution to mass loss remains undocumented. However, the extent of fungal decomposition in our experiments is likely small compared to degradation by wood-boring bivalves, since the unbored wood in our experiments sustained very little wood-mass loss.

3.5.2 Xylophagaids influence on the non-xylophagaid macrofauna

As predicted in our Hypotheses 2 and 3, xylophagaid biomass was significantly correlated with non-xylophagaid macrofaunal species richness, evenness, and biomass. Our results quantify some of the ecosystem engineering roles of xylophagaid bivalves during succession and decomposition at wood-fall habitats.

Prior to colonization of wood by xylophagaids, food resources and habitat complexity appear to be relatively low at sunken wood, which thus support wood-fall assemblages with low abundances and species richness. Wood surfaces did serve as an attachment substrate for anemones, but these are likely to be suspension feeders or planktivorous predators, and not reliant on the wood as a food source. Microbial mats and films on our wood surfaces may have also provided a labile food source for bacterial grazers such as *Dillwynella* gastropods (Young et al., 2022) or wood-associated *Bathyceradocus* amphipods (Larsen & Krapp-Schickel, 2007; Judge & Barry, 2016).

Colonization by wood-boring xylophagaid bivalves mediates a change in the wood-fall habitat and biotic assemblage. The creation of boreholes increases habitat area and complexity, and the production of fecal material provides a more labile food source (compared to wood) for other organisms. As xylophagaid biomass further increased in our experiments, the apparent large production of fecal material appears to have supported assemblages dominated by opportunists, such as thousands of dorvilleid polychaetes, large capitellid polychaetes, and surface-deposit-feeding ampharetids. We hypothesize that the food source for these opportunists is xylophagaid fecal material, which may be rich in labile bacterial biomass (Fagervold et al., 2014; Harbour et al., 2021a) but also include xylophagaid mucus (Purchon, 1941) and undigested wood material rich in lignin (Dore & Miller, 1923; Pesante, 2018). Xylophagaid fecal material and tissue contains a higher proportion of nitrogen than wood (Voight et al., 2020), and thus the provision of nitrogen to the wood-fall assemblage is an additional important ecosystem engineering role of those xylophagaid species with nitrogen-fixing endosymbionts. Detailed trophic analyses of wood-fall food sources, e.g., through stable-isotope analyses, are merited to better elucidate food webs on deep-sea wood falls. The increase in food and space facilitated by the xylophagaids also appears to allow other less abundant trophic types, such as scavengers and other deposit feeders, to inhabit wood-falls enhancing species richness the overall assemblage.

One wood block in our experiments appeared to be in the “senescence” stage (Pop Ristova et al., 2017), in which xylophagaid populations have declined, leading to low xylophagaid biomass combined with high wood mass loss. While the non-xylophagaid assemblage at this block appeared no different from other blocks in the “opportunist” stage, we hypothesize that a reduction in xylophagaid biomass will eventually lead to a reduction in fecal material and a decrease in opportunists dependent on this rich, labile food resource.

3.5.3 Xylophagaids and sulfate-reduction activity

Xylophagaids may be predicted to modulate sulfidic conditions on wood falls in two ways; (1) through the production of labile fecal material, inside burrows, on wood surfaces, and dispersed to nearby sediments, providing a substrate for sulfate-reducing bacteria (Bernardino et al., 2010; Kalenitchenko et al., 2018b), and (2) by pumping seawater sulfate and electron acceptors (e.g., oxygen and nitrate) via siphons through bore holes inside the wood (Kalenitchenko et al., 2018a). Sulfide production can also occur, independently of xylophagaid colonization, from sulfate-reducing bacteria consuming small, labile organic components of the wood (Kalenitchenko et al., 2018b; Kalenitchenko et al., 2018a).

Our findings support some of these predictions. We observed sulfate-reduction activity, albeit at low levels, in three of four wood blocks, including two blocks that were not colonized by xylophagaid bivalves. Sulfate reduction activity was generally greater at the surfaces of unbored wood block than in the interior. In a wood block bored by xylophagaids (W3), one profile indicated sulfate-reduction activity 2-3 times greater at a depth of 6 cm than on the wood surface, consistent with our Hypothesis 4 that xylophagaids facilitate sulfate reduction deeper into the wood (Kalenitchenko et al., 2018a). A replicate measurement in the same wood layer, however, indicated very low levels of sulfate reduction activity (Figure 3.5), suggesting this phenomenon is heterogeneous. More replicate observations, carefully oriented to xylophagaid boreholes and fecal material, are required to further elucidate the relationship between xylophagaids and sulfate reduction within wood falls.

Overall, sulfate-reduction rates in wood blocks were very low, and even absent on one wood block (Table 3.4). Sulfate-reduction rates on our wood surfaces were 2-3 orders of magnitude lower than those measured in sediments surrounding wood blocks deployed around methane seepage in the Eastern Mediterranean, which were colonized by chemosynthetic *Idas* mussels (Bienhold et al., 2013; Table 3.4). Sulfate-reduction rates were also up to 2 orders of magnitude lower than at sulfophilic-stage whale bones, which were also colonized by chemosynthetic bacterial mats, vesicomyid clams, and *Idas* mussels (Treude et al., 2009). Low sulfide production rates may explain why only a few *Idas* mussel individuals, which gain nutrition via chemosynthetic sulfide-oxidizing symbionts (Deming et al., 1997; Duperron et al., 2008) , occurred our wood blocks.

3.5.4 Wood-fall successional stages

Biotic communities and geochemical properties on deep-sea wood falls change over time, and wood-boring xylophagaid bivalves are clearly important facilitators of these successional changes. While we did observe wood blocks consistent with the “specialist”, “opportunist”, and “senescence” successional stages, some wood blocks in our study were not adequately described by the successional stages outlined by Pop Ristova et al. (2017). Based on our results and those of other studies (McClain et al., 2018; Bernardino et al., 2010; Bienhold et al., 2013; Pop Ristova et al., 2017; Kalenitchenko et al., 2018a), we propose an updated characterization of successional stages during the colonization and decomposition of deep-sea wood falls. These stages are continuous (i.e., overlapping) and are named after the dominant functional groups and the overall characteristics of the wood-fall habitat, similarly to the identified successional stages on whale falls (Smith & Baco, 2003; Smith et al., 2015). These wood-fall successional stages are as follows: (1) a *microbial stage*; (2) a *wood-borer stage*; (3) an *opportunist stage*; (4) a *wood disintegration stage*; and (5) a *reef stage*. Based on our measurements and other studies, propose that sulfidic conditions, albeit often at low levels, can occur during each of these stages. A conceptual diagram of wood mass remaining, macrofaunal biomass, and sulfidic conditions through these hypothesized wood-fall successional stages is presented in Figure 3.6.

3.5.4.1 Microbial stage

Several studies indicate that microbes can dominate the early phases of wood-fall decomposition, before colonization by xylophagaid bivalves (Bienhold et al., 2013; Kalenitchenko et al., 2018a). The Pop Ristova et al. (2017) model did not describe any stages prior to woodborer colonization. Marine bacterial genera that may produce cellulases have been found on wood surfaces after as little as 1 day of immersion (Bienhold et al., 2013). Microbial communities themselves exhibit temporal succession in community structure on wood falls, including a transition in dominant metabolic strategies from heterotrophy to chemoautotrophy associated with a shift from localized aerobic to anaerobic conditions (Palacios et al., 2006; Palacios et al., 2009; Fagervold et al., 2012; Kalenitchenko et al., 2016). Microbial biofilms and/or mats likely serve as a labile food source for bacterial grazers during early phases, such as nematodes (Schwabe et al., 2015) and gastropods of *Dillwynella* (Nishimoto et al., 2009).

3.5.4.2 Wood-borer stage

This stage is characterized by the colonization and transformation of deep-sea wood parcels by wood-boring bivalves. Initial settlement of xylophagaids to wood in the deep sea can occur within 2-3 months (Turner, 1973, 2002; Tyler et al., 2007; Romano et al., 2013). Xylophagaid boreholes increase habitat complexity and can provide shelter for many organisms, even when inhabited by xylophagaids (Wolff, 1979; Schander et al., 2010). Labile food resources are also increased and diversified throughout this stage for a range of functional groups including opportunists, scavengers, and predators, through the provision of xylophagaid biomass and fecal material. Because wood contains little nitrogen, some xylophagaid species with nitrogen-fixing endosymbionts provide wood-fall assemblages with significant sources of organic nitrogen (Distel & Roberts, 1997; Voight et al., 2020). This stage most closely aligns with the “specialist” stage defined by Pop Ristova et al. (2017), but specifically highlights the importance of wood-boring specialists.

3.5.4.3 Opportunist stage

This stage is characterized by wood-fall assemblages numerically dominated by opportunist taxa, such as dorvilleid and capitellid polychaetes, likely responding to organic enrichment from increased production of labile xylophagaid fecal material and/or xylophagaid biomass. This opportunist stage was defined by Pop Ristova et al. (2017), has also been observed in sediments surrounding wood falls (Bernardino et al., 2010), and is analogous to the enrichment-opportunist stage described at whale-fall habitats (Smith & Baco, 2003; Smith et al., 2015).

The establishment and extent of the opportunist stage at wood-falls may be highly dependent on the dominant species of xylophagaids at a wood fall. Not all xylophagaids line their boreholes heavily with fecal material; This trait may be largely restricted to one subclade of xylophagaids, which includes *X. dorsalis, X. washingtona, X. oregona,* and *X. crooki* (Voight et al., 2019). For example, *Xylonora zierenbergi*, which belongs to a xylophagaid subclade that does not heavily line burrows with fecal material, was the dominant xylophagaid collected from wood at ~3200 m in the NE Pacific, and non-xylophagaid assemblages did not appear to support dense assemblages of enrichment opportunists as described in our study (McClain & Barry, 2014). In our study, *X. zierenbergi* and *X. muraokai* (also belonging to the same subclade) dominated xylophagaids at intermediately bored wood at N-2800, and opportunists, while present, were reduced in abundance compared to the 1600 m wood parcels where *X. oregona* was dominant. Further investigation is required to determine whether wood intensely bored (versus intermediately bored) by *X. zierenbergi* and/or *X. muraokai* can support abundant opportunist populations.

3.5.4.4 Wood disintegration stage

Eventually, xylophagaid populations may reach carrying capacity as wood parcels can no longer support additional boreholes. During this stage, a decrease in xylophagaid biomass and fecal material will be followed by a decrease in the biomass/abundance of opportunists and predators, and other species relying on xylophagaids. The disintegration of the wood block, potentially aided by mechanical fragmentation from bottom currents, can disperse wood chips into the surrounding sediment, enriching the benthos for years after the initial fragmentation of the wood (Bernardino et al., 2010; Bienhold et al., 2013). Pop Ristova et al. (2017) described a similar stage as a “senescence stage”, however it is unclear whether this refers to the senescence of the wood-borer populations, or the senescence of the entire wood-fall ecosystem. While this stage may represent the terminal stage of wood-fall succession, particularly for small and/or heavily infested wood parcels, it is also possible that the wood-fall persist into a reef stage (see next section). We propose the name “wood disintegration stage” to unambiguously describe the physical characteristics of this successional stage.

3.5.4.5 Reef stage

While some studies have indicated rapid total disintegration (within 9-13 months) of deep-sea wood falls (Tyler et al., 2007; Romano et al., 2013), others document persistence of wood with vacant xylophagaid boreholes after 5.5 to 7 years (Bernardino et al., 2010; McClain & Barry, 2014; Pereira et al., 2022). Vacant xylophagaid boreholes can provide habitat for other infauna, and the intact wood parcel may serve as hard substrate for species feeding on organic carbon independent of the wood parcel (e.g., background particular organic-carbon flux), analogously to the reef stage observed for whale falls (Smith & Baco, 2003; Smith et al., 2015). The establishment and duration of a reef stage at wood falls may depend heavily on factors influencing the colonization and survivorship of wood-boring bivalves, such as predation pressure and/or low oxygen conditions (Pereira et al., 2022). The size and surface-area-to-volume ratios of wood parcels likely also influence the establishment and persistence of a reef stage. Because the depth of boring by xylophagaids is limited by siphon lengths, it is likely that xylophagaids bore to a maximum and then die out before fragmenting very large wood parcels. This stage was not captured by the previous successional stage model proposed by Pop Ristova et al. (2017).

3.5.4.6 Sulfidic conditions

Sulfidic conditions likely occur within most of the wood-fall successional stages, although the origin of the sulfidic conditions appears to vary over time. During the microbial stage, anaerobic bacterial decomposition of labile wood components by sulfate-reducing bacteria may provide sulfide for chemoautotrophic bacterial mats on the wood surface (Kalenitchenko et al., 2018b; Kalenitchenko et al., 2016; Kalenitchenko et al., 2018a; Yücel et al., 2013). During the wood-borer and opportunist stages, xylophagaid fecal material provides rich labile organic substrates for sulfate-reducing bacteria (Fagervold et al., 2014; Kalenitchenko et al., 2018a). Under heavy xylophagaid colonization, fragmentation of the wood, and or fecal ejection by some xylophagaid species, may disperse xylophagaid fecal material onto the surrounding sediments, which also may become sulfidic (Bernardino et al., 2010; Bienhold et al., 2013).

At whale falls, the sulfophilic stage is characterized by a dominant, high density, species-rich, and trophically complex assemblage dependent on chemoautotrophic production (Smith & Baco, 2003; Smith et al., 2015). While typical, chemosynthesis-associated fauna, such as *Idas* mussels (Bienhold et al., 2013; Pop Ristova et al., 2017; Romano et al., 2013) and siboglinid polychaetes, have been reported at wood falls, assemblages numerically dominated by chemosymbiotic fauna have not been documented at sunken wood at locations far from geologically-mediated reducing conditions. The limited wood-fall food-web studies have not identified chemoautotrophic production as an major food source for wood-fall assemblages (Nishimoto et al., 2009; Harbour et al., 2021a) however, chemosynthetic nutrition does appear to be important for multiple species inhabiting sediments surrounding late-stage wood falls (Bernardino et al., 2010).

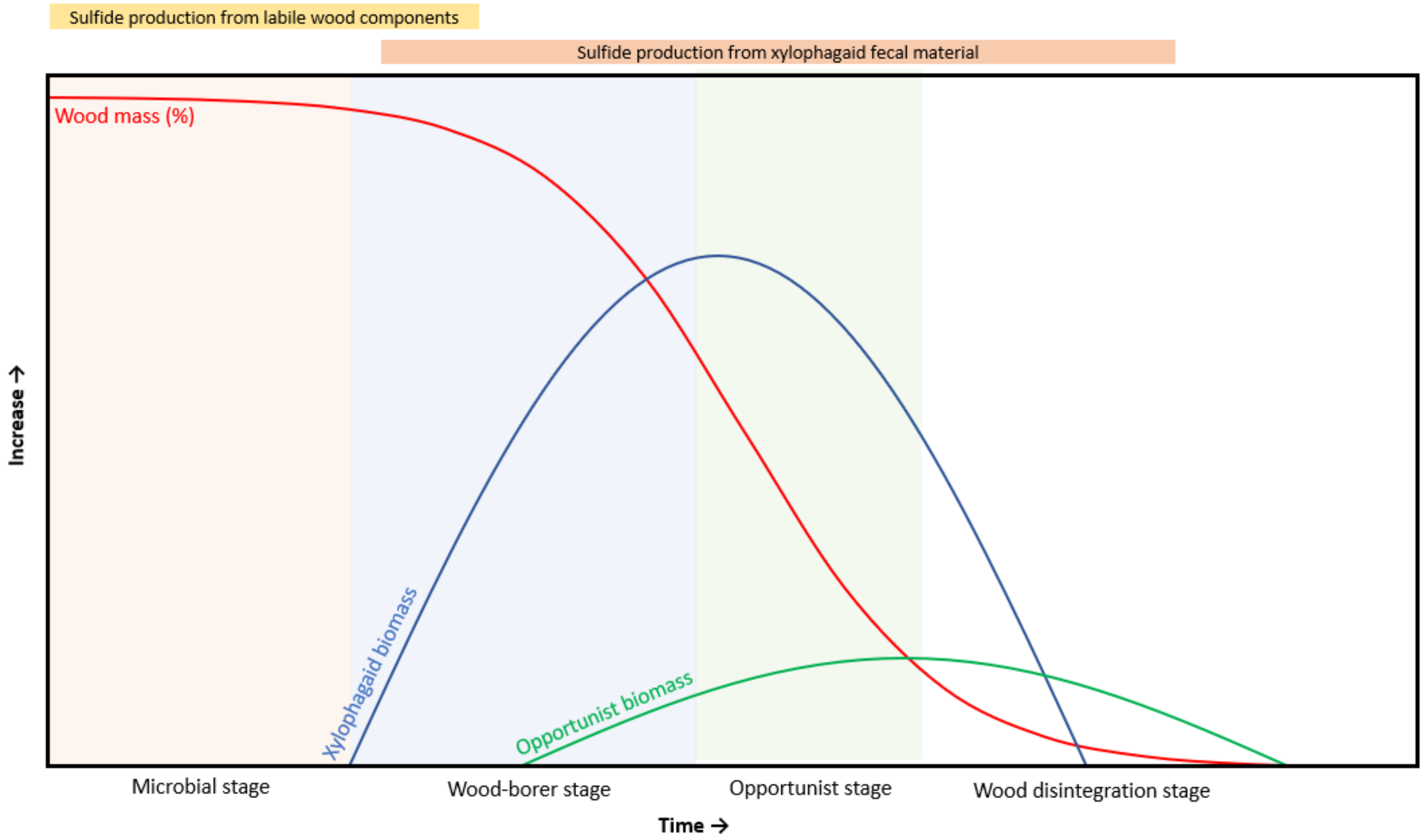

Figure 3.6 Hypothesized changes in biomass, wood mass remaining, and sulfidic conditions throughout the proposed successional stages of deep-sea wood-falls, assuming ultimate total disintegration of the wood substrate. Initial colonization of sunken wood by microbial assemblages during the "microbial stage" may lead to a low rate of wood-mass loss. Once wood is successfully colonized by wood-boring xylophagaids, a subsequent increase in xylophagaid biomass coincides with rapid rates of wood-mass loss throughout the "wood-borer stage". An increase in xylophagaid biomass and xylophagaid fecal material supports an increase in opportunist biomass during the "opportunist stage". During the "wood disintegration stage". continued xylophagaid boring leads to fragmentation and disintegration of the wood substrate, yielding a reduction in xylophagaid biomass as wood resources available for boring become depleted and habitat loss for wood-fall macrofauna. Sulfidic conditions may occur during all successional stages, first primarily sustained by microbial utilization of labile components of the wood, and later sustained by microbes decomposing xylophagaid fecal material and other biomass.

Many factors likely influence the general applicability of our proposed wood-fall successional stages (Figure 3.6). For example, available species pools and larval supply rates will vary between biogeographic regions and depths (Young et al., 2022), and wood-parcel size and wood characteristics may influence wood-fall community structure, diversity, and ecosystem functions (Judge & Barry, 2016; McClain et al., 2018). In addition, proximity to other reducing habitats may influence the colonization and development of sulfidic assemblages (Gaudron et al., 2010; Cunha et al., 2013; Pereira et al., 2022). Additionally, temporal progression and degree of overlap between stages likely depends heavily on the identity, colonization rate, and boring characteristics of xylophagaid bivalves. More standardized, controlled wood-fall experiments, such as conducted here, are highly desirable to further result the nature and variability of wood-fall succession.

3.6 ACKNOWLEDGEMENTS

We thank all of those involved in the fabrication, deployment, recovery, and procesing of the Bone and Wood Landers. Special thanks go to Kathleen Ruttenberg who provided access to a muffle furnace, to Philip Rapoza for providing help with sectioning wood blocks, and to Kevin Christensen and Hailee Neal for their help sorting wood samples. This research was supported by the National Science Foundation (grants OCE-1155703 awarded to C.R.S and OCE-1155188 awarded to K.M.H).

CHAPTER 4

Trophic ecology of whale-bone and wood-fall habitats in the deep NE Pacific

In prep as: Young EL, Halanych KM, Bernardino AF, Drazen JC, Smith CR. Trophic ecology of whale-bone and wood-fall habitats in the deep NE Pacific

4.1 ABSTRACT

Organic-fall habitat islands are important components of deep-sea benthic ecosystems, providing concentrations of organic carbon at the otherwise food-poor seafloor. We used stable isotope analyses to investigate and compare the trophic structure and nutritional sources of macrofaunal assemblages collected on whale-bone and wood substrates experimentally deployed in the NE Pacific, at a depth of 1605 m for 15 mo. The overall trophic structure of whale-bone and wood-fall assemblages differed. Bayesian-mixing models indicated that organic-rich substrates were the dominant basal food sources for the majority of the 14 wood taxa and 9 whale-bone taxa sampled. The relative importance of background particulate organic matter (POM) to faunal diets varied among taxa and functional groups. Three deposit-feeding and omnivorous species were sampled from both substrate types, and background POM was of greater importance to those three species collected on whale bones compared to wood. We suggest that this is due to the greater availability of labile particulate material produced by key ecosystem engineering, wood-boring xylophagaid bivalves at wood falls. In contrast, bone-eating *Osedax* annelid ecosystem engineers did not contribute to the production of particulate food resources on this 15-month time scale, but microbial biomass on whale bone substrates may have been an important particulate nutritional source for fauna. We conclude that bone and wood falls provide an important nutritional source to specialized consumers and also to trophic generalist macrofaunal types in the deep sea.

4.2 INTRODUCTION

Most deep-sea benthic habitats are nutritionally dependent on the flux of particulate organic matter (POM) from overlying surface waters. Large organic-rich substrates, such as sunken whale carcasses and wood, create seafloor habitat islands known as organic falls (whale-falls and wood-falls, respectively), and can provide the benthos with a pulse of organic carbon many orders of magnitude greater than provided by background POM flux (Smith & Baco, 2003). Organic falls are becoming increasingly recognized as common features on the deep-sea benthos and play an important role in maintaining biodiversity and ecosystem functioning in the deep sea (Smith et al., 2015; McClain & Barry, 2014; Harbour et al., 2021b).

Organic-fall habitats support faunal assemblages that include a range of functional groups (Smith et al., 2015; Harbour et al., 2021b). Specialist taxa, with specific adaptations that allow for the utilization and alteration of the otherwise inaccessible and recalcitrant components of whale bone and wood, are particularly important components of organic-fall assemblages. At whale-falls, specialists include bone-eating *Osedax* siboglinid annelids. *Osedax* produce acid to bore into bone (Tresguerres et al., 2013), and, aided by endosymbiotic bacteria, consume the collagen, and possibly lipids, locked within bone material (Goffredi et al., 2005; Goffredi et al., 2007; Moggioli et al., 2022). Wood-eating xylophagaid bivalves are the most notable specialists at deep-sea wood falls. Xylophagaids rasp wood to create boreholes, simultaneously ingesting the rasped wood particles and digesting the cellulose via cellulolytic endosymbiotic bacteria (Distel & Roberts, 1997). Because wood is nitrogen poor, xylophagaids obtain nitrogenous nutrition either via nitrogen-fixing endosymbionts, or by filtering POM from the water column (Voight et al., 2020). Both *Osedax* annelids and xylophagaid bivalves are considered key ecosystem engineers (Jones et al., 1994) at organic-falls because they modulate the physical environment, including habitat and food availability, which in turn can regulate the structure and biodiversity of the entire organic-fall assemblage (Alfaro-Lucas et al., 2017; Alfaro-Lucas et al., 2018; Chapter 3). Organic-fall assemblages often include “enrichment opportunist” taxa (Smith & Baco, 2003), such as deposit-feeding capitellid polychaetes (Alfaro-Lucas et al., 2017), omnivorous/bacterivorous (Chapter 3) dorvilleid polychaetes (Cunha et al., 2013; Wiklund et al., 2009; Young et al., 2022), and grazing gastropods (Smith & Baco, 2003; Cunha et al., 2013). Predatory and/or scavenging carnivores can constitute the higher trophic levels of organic-fall food webs (Turner, 1973; Smith & Baco, 2003; Bernardino et al., 2010).

A variety of food sources are available to fauna at organic falls. While organic-fall substrates (e.g., whale bone and wood) themselves are energy rich, the carbon is not necessarily directly available to the entire assemblage. In addition to the substrate specialists mentioned previously, consortia of free-living, heterotrophic microbial decomposers can also utilize whale-bone and wood materials (Bienhold et al., 2013; Fagervold et al., 2014; Borchert et al., 2021). The reduced compounds produced by heterotrophic bacteria decomposing the organic matter can also fuel the growth of free-living chemoautotrophic bacteria, sometimes forming dense mats on wood or bone surfaces and surrounding sediments (Bennett et al., 1994; Kalenitchenko et al., 2018b).

Both heterotrophic and chemoautotrophic biofilms may serve as an important food source for bacterivores (Deming et al., 1997; Wiklund et al., 2009). Another potentially important food source for fauna unable to directly utilize organic-fall substrates are the waste products of specialist decomposers. Xylophagaids produce fecal material composed of partially digested wood fragments which include lignin (Pesante, 2018; Dore & Miller, 1923), wood-decomposing bacteria and fungi (Fagervold et al., 2014), and mucus (Purchon, 1941). One particular xylophagaid clade, which includes *Xylophaga dorsalis* and *X. oregona*, characteristically accumulates fecal material inside boreholes and around siphons (Voight et al., 2019); this fecal material may serve as an important food source for particulate-feeding deposit feeders and bacterivores (Chapter 3). Photosynthetically-derived POM is also a food source available to fauna at organic falls and may be especially important for deposit feeders on organic-fall surfaces. While the diets of organic-fall fauna may be hypothesized by the natural history of functional groups, stable isotope analyses can provide more direct evidence of the relative importance of each food source (Nishimoto et al., 2009; Alfaro-Lucas et al., 2018; Harbour et al., 2021a).

Here we use stable isotope analyses (Deniro & Epstein, 1981; Peterson & Fry, 1987) to elucidate the (1) trophic structure, and (2) relative contributions of dietary sources to fauna collected from whale bones and wood in the deep sea. We conducted an experimental study of organic-fall habitats, whereby replicate parcels of whale-bone and wood were concurrently deployed for ~15 months at a single site, S-1600, on the Washington-Oregon margin seafloor at a depth of ~1605 m (Young et al., 2022). Upon collection, the whale bones were essentially intact but very lightly bored by multiple species of bone-eating *Osedax* polychaetes, and colonized by enrichment-opportunists (Smith & Baco, 2003). Dark patches and thin bacterial mats on bones suggested early signs of a sulfophilic successional stage (Young et al., 2022). The wood blocks were in an advanced “wood disintegration stage” (Chapter 3) as evidenced by heavy colonization and boring by xylophagaid bivalves, as well as by the presence of opportunistic and predatory taxa. Assemblages on whale-bone and wood substrates were distinct, yet some species occurred on both substrate types (Young et al. 2022). Using the isotopic signatures of fauna and dietary sources collected in this experiment, we address the following hypotheses for replicate, co-located whale-bone and wood substrates deployed at the deep-sea floor for 15 months:

(1) Whale bone and wood falls display different food-web structure.
(2) On average, a greater proportion of the diet of organic-fall fauna comes from the organic-fall source, rather than from background POM.
(3) Deposit feeders and omnivores on wood obtain a lower proportion of their diet from background POM sources than the same species on bone substrates, because of the increased availability of particulate xylophagaid fecal material at wood compared to particulate food sources at whale bones.

4.3 MATERIALS AND METHODS

4.3.1 Study area

The study site is on the continental slope ~100 km offshore of Washington and Oregon, USA, and is heavily sedimented and features numerous canyons and channels. The Washington and Oregon coastlines are heavily wooded, and multiple rivers provide natural sources of sunken wood to the continental margin (Young et al., 2022). Resident and migrating populations of large cetacean species (Green et al., 1995; Calambokidis & Steiger, 1997; Barlow & Forney, 2007), and natural whale falls (Lundsten et al., 2010a) are present in this region. Areas of methane seepage and gas-hydrate deposits are also present along the Washington-Oregon margin (Suess, 1985; Kastner et al., 1998). Site S-1600 (43° 54.52’ N, 125° 10.42’ W) has a water depth of ~1605 m, and the seafloor is bathed by slowly southward-flowing North Pacific Deep water (mean flow of ~1 cm s^{-1}; Hautala et al., 2009). Mean (± SD, n = 2) seafloor water temperatures (2.3°C ± 0.1), salinity (34.6 ± 0.0) and oxygen concentrations (0.9 ml l^{-1} ± 0.1) were measured during lander deployment in April 2013 (Young et al., 2022).

4.3.2 Experimental design

Benthic landers holding replicate whale-bone, wood, and inorganic control substrates were deployed on the Washington-Oregon margin seafloor in April 2013 and were recovered after ~15 months. This present study addresses stable-isotope data collected from wood and bone substrates from site S-1600 (Young et al., 2022). The lander was comprised of nine 500-µm mesh bins (50 × 50 × 50 cm) arranged in an equilateral triangle. Plastic lids spanning the three bins on each lander side were held open while the lander was on the seafloor and closed to seal bin contents during the ascent and recovery of the lander. Each lander side contained one bin each with whale bone, a control slate substrate (always positioned in the middle), and a wood block, with replicate colonization substrates attached to both the bottom and the lid of each bin. Whale bone substrates were sections of adult humpback whale (*Megaptera novaeangliae*) lumbar vertebral halves (~3790 cm^3) or ribs (~2240 cm^3), and wood substrates were 18.4 × 19.0 × 8.8 cm (~3080 cm^3) blocks of untreated Douglas fir (*Pseudotsuga menziesii*). The whale bones in this study were blackened upon recovery which indicated reducing conditions (Young et al. 2022), and some bone and surfaces appeared white, which we interpret as the presence of bacterial mats that were largely washed off during lander ascent to the surface (Figure S4.1). Whale-bone surfaces were colonized by four large *Osedax rubiplumus* individuals, as well as an average 7.3 individuals of a small *Osedax* species per bone (*Osedax* sp. B, averaged across 3 bones; Young et al. 2022). Wood blocks attached to the lid were crumbling due to heavy colonization by xylophagaid bivalves, while wood blocks attached to the bottom of mesh bins were not colonized by xylophagaid bivalves and were blackened, with no evidence of microbial mats (Figure S4.1). Woody debris from lid wood blocks had fallen into the mesh bins below. To obtain an estimated isotopic signature of background POM, surface plankton was sampled at site S-1600 and between sites N-1600 and N-2800 (Young et al., 2022) by towing a 63µm-mesh plankton net from the RV ‘Oceanus’ on June 22nd , 23rd, and 27th, 2014. Contents of the nets were washed with 20-µm filtered seawater into sterile vials and large zooplankton were removed under a dissecting microscope before samples were frozen.

4.3.3 Stable isotope analysis

Upon lander recovery, the mesh bins and substrates were immediately transferred to chilled 20-µm filtered seawater. Bone and wood substates were cut into quarters using a reciprocating saw and preserved in either a 10% formalin-seawater solution, or 95% ethanol. Mesh bags were rinsed with chilled 20-µm filtered seawater and contents were split in half; one half preserved in a 10% formalin-seawater solution, and the other in 95% ethanol. Stable isotope measurements were conducted on three occasions (Batch 1, Batch 2, and Batch 3). “Batch 1” macrofauna were identified and picked from substrates and mesh bins immediately following lander recovery, placed in sterile plastic vials (using sterile forceps) which were immediately frozen, later transported to the University of Hawai'i at Mānoa, and stored at -20°C until tissue preparation in November 2016. “Batch 2” macrofauna were prepared in July 2017, either directly from formalin-preserved wood blocks, or from mesh bin contents preserved in 10% formalin and later transferred to 80% ethanol. “Batch 3” macrofauna were prepared in July 2022 from whale bone and wood mesh bin contents preserved in either 95% ethanol or preserved in 10% formalin and later transferred to 80% ethanol. Different preservatives and storage durations have been reported to have taxon-variable effects (no effect, enrichment, or depletion) on stable isotopic signatures (Fanelli et al., 2010). Because no universal corrections are appropriate, and because effects on stable isotope signatures are expected to be minor in comparison to the observed differences in isotopic signature between nutritional sources, we report the data with no corrections applied.

Macrofauna were sorted and identified to lowest possible taxonomic level. We attempted to sample as much of the community as possible, especially taxa that contributed most to the overall biomass, where sufficient material was available for analyses (Young et al.2022; Chapter 3). For small organisms, multiple individuals were pooled to obtain a sufficient sample mass (Table S4.1). Tissue subsamples of the bivalve *Xylophaga oregona* were taken only from the siphon. Macrofauna/tissues were rinsed in deionized water, placed in individual glass vials in a 60°C oven and dried to a constant weight. Tissues were ground to a fine powder using a sterile ceramic mortar and pestle, and 0.5 mg of material was transferred to tin capsules, sealed, and sent to stable isotope facilities.

Surface plankton and whale bone subsamples were dried at 60°C, ground to a fine powder, and 0.5 mg of material was placed in each tin capsule and included in Batch 1 analyses. Small pieces of wood were subsampled from areas of bulk-frozen wood-block quarters with no visual evidence of biological colonization and were similarly dried and ground to a powder. Because wood has an extremely low nitrogen content, ~2 mg of powder was prepared for each wood sample and were analyzed in Batch 2. Xylophagaid fecal material was identified as another potential food source for wood organisms. Xylophagaid fecal material was subsampled from xylophagaid burrows in wood block quarters that were preserved (1) in 10% formalin-seawater solution, (2) in 10% formalin-seawater solution and later transferred to 80% ethanol, and (3) frozen. Dried and powdered xylophagaid fecal material samples weighing 0.5-1.0 mg were analyzed in Batch 2. Because we were unable to sample enough bacterial mat from whale bones deployed in this study, we instead use carbon and nitrogen isotopic signatures of bacterial mats (including *Beggiatoa* spp.) collected from a natural (not implanted) blue or fin whale skeleton sampled at 1240 m depth in the Santa Catalina Basin in 1991 and 1999 (Baco-Taylor, 2002; Smith & Baco, 2003).

Batch 1 and Batch 2 samples were analyzed for carbon and nitrogen weight and isotopic composition ($^{13}C/^{12}C$ and $^{15}N/^{14}N$) at Washington State University using a Costech elemental analyzer interfaced with a Micromass Isoprime isotopic ratio mass spectrometer. Batch 3 samples were analyzed for carbon and nitrogen weight and isotopic composition ($^{13}C/^{12}C$ and $^{15}N/^{14}N$) at the Biogeochemical Stable Isotope Facility at the University of Hawaii at Manoa using a Costech ECS 4010 elemental combustion system coupled to a Thermo Scientific Delta V Advantage isotope ratio mass spectrometer. Measurements are reported in δ notation relative to international standards (atmospheric nitrogen for $\delta^{15}N$ and Peedee belemnite for $\delta^{13}C$) in per mil (‰) units.

4.3.4 Statistical analyses

Each species/taxon was assigned to a functional group (bone/wood specialist, deposit feeder, microbial grazer, omnivore, mobile generalist, or carnivore) based on a literature review (Table 4.1). Taxa known to specialize on organic-rich substrates were categorized as bone/wood specialists. Feeding guilds of polychaetes (deposit feeders and omnivores) have been well defined by Jumars et al (2015). All gastropods in this study were determined to be microbial grazers. Taxa were categorized as mobile generalists if they had the capacity of mobility between experimental bins, and also occurred on multiple substrate types. Carnivores included predatory or scavenging taxa with limited mobility, relative to the experimental bins. A lipid correction was mathematically applied to the $\delta^{13}C$ of macrofaunal samples with C/N values > 3.5, ($\delta^{13}C_{\text{corrected}} = \delta^{13}C_{\text{uncorrected}} - 3.32 + 0.99 \times \text{C:N}$) according to (Post et al., 2007). Mann-Whitney U tests were used to compare $\delta^{13}C$ and $\delta^{15}N$ signatures of bone and wood taxa, and xylophagaid fecal material and wood sources, because isotopic data were not normally distributed.

Community-wide Layman metrics (Layman et al., 2007) were estimated in a Bayesian framework (Jackson et al., 2011) to quantify and compare the trophic structure of bone and wood food webs and functional groups in bivariate ($\delta^{13}C$ and $\delta^{15}N$) isotopic space. The following metrics were calculated: $\delta^{13}C$ range (CR), $\delta^{15}N$ range (NR), total area of the convex hull containing the means of functional groups (TA), mean distance of functional group means to the centroid (CD), mean nearest neighbor distance of functional group means (MNND), and standard deviation of nearest neighbor distance (SDNND). Interpretations of these metrics are addressed in the discussion. Isotopic niche-width metrics were determined in order to describe and compare the isotopic niche size of bone and wood functional groups. Standard ellipse areas corrected for sample size (SEA_C) and Bayesian estimates (and 95% credible intervals) of standard ellipse areas (Jackson et al., 2011) were calculated. The SEA_B of *Capitella* cf. *capitata* populations collected on bone and wood substrates were also estimated and compared.

Layman and isotopic niche width metrics were estimated using the Stable Isotope Bayesian Ellipse (SIBER) package (Jackson et al., 2011) in R version 4.1.1 (R Core Team, 2021) based on model runs with two Markov chains of 20,000 iterations, with a burn-in of 1,000 and a thinning of 10. Pair-wise comparisons of metric estimates were conducted by calculating the proportion of overlapping posterior distributions, and were considered significant when probability of overlap exceeded 95% (Jackson et al., 2011). Bone omnivore (n = 1) and wood microbial grazer (n = 1) data points were omitted from the calculation of Layman and isotopic niche width metrics due to insufficient sample sizes.

Bayesian mixing models (MixSIAR) were used to estimate the proportional contributions of different food sources to the diets of bone and wood fauna (Moore & Semmens, 2008). Potential food sources for each functional group were determined by conducting a literature review (Table 4.1). Because we were unable to measure the isotopic signature of wood bacterial mats, we instead used a combined wood signature (average of wood and xylophagaid fecal material signatures) to infer wood as the basal source of nutrition for wood microbial grazers and wood omnivores. If *X. oregona* is truly xylophagous, it is expected to obtain carbon from wood and nitrogen via endosymbiotic bacteria (Distel & Roberts, 1997; Voight et al., 2020). Therefore, to determine the dietary contributions to *X. oregona*, we used the $\delta^{13}C$ signature of “Wood” sources measured in this study along with the $\delta^{15}N$ signature of organic-matter produced by N-fixing bacteria (Hoering & Ford, 1960; Delwiche & Steyn, 1970; Macko et al., 1987; Minagawa & Wada, 1986; Carpenter et al., 1997). Trophic enrichment factors ($\delta^{13}C$: 0.1‰ ± 2.2 SD n = 157; $\delta^{15}N$: 2.6‰ ± 2.0 SD n = 155) from the literature determined from controlled feeding experiments of aquatic invertebrates (Brauns et al., 2018), and were adjusted for each functional group according to inferred trophic level (TEF × 1.5 for omnivores and mobile generalists, TEF

× 2 for carnivores; Table 4.1). MixSIAR models with uniform priors and a process × residual error structure were run using the MixSIAR package (Stock & Semmens, 2016; Stock et al., 2018) in R (R Core Team, 2021). Model runs were comprised of 3 Markov chain runs, each with 1,000,000 iterations, a burn in of 500,000 and a thinning rate of 500. Model convergence was assessed by examining Gelmin-Rubin and Heidelberger-Welch and Geweke diagnostic tests. Three data points were identified as potential outliers following the estimation of 95% confidence mixing (Smith et al., 2013) and are indicated as such throughout. Estimates for model runs with all functional groups supplied with all potential sources (Wood combined, Whale bone, Bone bacteria and Surface plankton) are presented in Tables S4.3 and S4.4 and Figure S4.3.

Table 4.1 Whale-bone and wood taxa sampled in this study, along with potential food sources and assumed trophic enrichment factors (TEF). Bo, bone; SP, surface plankton; Ba, whale bone bacteria; Wo, wood; XF, xylophagaid fecal material, Wo(c), wood (combined; wood and xylophagaid fecal material). **Xylophaga oregona* potential sources are wood (Wo) for carbon and nitrogen-fixing bacteria (NF) for nitrogen.

Substrate	Functional group	Taxa	Class, Family	Potential Sources	TEF	References
Bone	Bone specialist	*Osedax rubiplumus*	Polychaeta, Siboglinidae	Bo, SP	+1	(Rouse et al., 2004)
	Deposit feeder	*Laonice* sp. A	Polychaeta, Spionidae	Bo, Ba, SP		(Jumars et al., 2015)
		Capitella cf. *capitata*	Polychaeta, Capitellidae		+1	(Jumars et al., 2015)
		Capitella cf. *ovincola*	Polychaeta, Capitellidae			(Jumars et al., 2015)
	Microbial grazer	*Hyalogyrina* sp. A	Gastropoda, Hyalogyrinidae	Ba, SP		(Marshall, 1988; Warén et al., 1996; Åström et al., 2019)
		Dillwynella sp. A	Gastropoda, Skeneidae		+1	(Marshall, 1988; Nishimoto et al., 2009)
	Omnivore	*Ophryotrocha* batillus	Polychaeta, Dorvilleidae	Bo, Ba, SP	+1.5	(Wiklund et al., 2009; Bernardino et al., 2010; Jumars et al., 2015; Alfaro-Lucas et al., 2018)
	Mobile generalist	Ophiuroid	Ophiuroidea	Bo, Ba, Wo(c),SP		(Pearson & Gage, 1984; Smith, 1985)
		Amphipoda sp. K	Malacostraca		+1.5	(Bowman, 1974; Bousfield & Hendrycks, 1997; Cadien, 2015)
		Eurycopinae sp. A	Malacostraca, Munnopsidae			(Wolff, 1962, 1976)

Table 4.1 (Continued) Whale-bone and wood taxa sampled in this study, along with potential food sources and assumed trophic enrichment factors (TEF).

Substrate	Functional group	Taxa	Class, Family	Potential Sources	TEF	References
Wood	Wood specialist	*Xylophaga oregona*	Bivalvia, Xylophagaidae	Wo,NF*	+1	(Voight et al., 2020)
	Deposit feeder	*Laonice* sp. A	Polychaeta, Spionidae	XF, SP		(Jumars et al., 2015)
		Capitella cf. *capitata*	Polychaeta, Capitellidae			(Jumars et al., 2015)
		Decemunciger sp. A	Polychaeta, Ampharetidae			(Zottoli, 1982; Jumars et al., 2015)
		Ampharetid sp. 22	Polychaeta, Ampharetidae		+1	(Jumars et al., 2015)
		Flabelligerid sp. A	Polychaeta, Flabelligeridae			(Jumars et al., 2015)
	Microbial grazer	Limpet sp. A	Gastropoda	Wo(c), SP	+1	(Lesicki, 2009; Haszprunar et al., 2022)
		Ophryotrocha batillus	Polychaeta, Dorvilleidae			(Wiklund et al., 2009; Bernardino et al., 2010; Jumars et al., 2015; Alfaro-Lucas et al., 2018)
		Ophryotrocha langstrumpae	Polychaeta, Dorvilleidae			(Wiklund et al., 2009; Bernardino et al., 2010; Jumars et al., 2015; Alfaro-Lucas et al., 2018)
	Omnivore	Dorvilleid sp. 54	Polychaeta, Dorvilleidae	Wo(c), SP	+1.5	(Jumars et al., 2015)

Table 4.1 (Continued) Whale-bone and wood taxa sampled in this study, along with potential food sources and assumed trophic enrichment factors (TEF).

Substrate	Functional group	Taxa	Class, Family	Potential Sources	TEF	References
	Carnivore	Triclad sp. A	Phylum Platyhelminthes, Tricladida	Wo(c), SP		(Sluys, 1989)
		Polynoid sp. A	Polychaeta, Polynoidae			(Jumars et al., 2015)
		Sirsoe cf. *hessleri*	Polychaeta, Hesionidae			(Jumars et al., 2015)
		Nemertean sp. A	Phylum Nemertea		+2	(Thiel & Kruse, 2001)

4.4 RESULTS

4.4.1 Stable isotope signatures

A total of 91 faunal samples (25 collected from whale bones, 66 collected from wood), and 32 source samples were analyzed (Figure 4.1; Table 4.2). Stable isotopic signatures were obtained for 14 (out of 36) wood taxa, which included 9 of the 10 most numerous taxa (Young et al. 2022), and 7 of the 8 most dominant by biomass (Chapter 3). Nine (out of 30) whale bone taxa were analyzed, which included 6 of the 10 most numerous taxa (Young et al. 2022).

Potential food sources had distinct $\delta^{13}C$ and $\delta^{15}N$ signatures, although signatures of wood and xylophagaid fecal material were similar (Figure 4.1; Table 4.2). Xylophagaid fecal material $\delta^{13}C$ was lower than wood by an average of 1.1 ‰ ($U = 9$, $p = 0.01$). The $\delta^{15}N$ of xylophagaid fecal material was not significantly different from that of wood ($U = 41.5$, $p = 0.401$). Whale bone was had the highest $\delta^{13}C$ and $\delta^{15}N$ values. Both surface plankton and bone bacteria sources had $\delta^{13}C$ signatures intermediate to whale bone and wood, and surface plankton $\delta^{15}N$ was higher (by 8.4 ‰) than the $\delta^{15}N$ of whale-bone bacteria. Wood fauna had lower $\delta^{13}C$ values than bone fauna (median for wood fauna = -21.6 ‰, median for bone fauna = -20.2 ‰; $U = 340.5$, $p < 0.01$) and $\delta^{15}N$ (median for wood = 2.15, median for bone = 9.7; $U = 48.5$, $p < 0.01$). Estimates of all Layman metrics were significantly greater for bone macrofauna compared to wood macrofauna, indicating a different trophic structure between the two substrate types (Table 4.3).

The standard ellipse areas of functional groups on bone and wood substrates varied (Table 4.4). Bone specialist SEA_B was significantly greater than wood specialist SEA_B. The SEA_B of wood deposit feeders was not significantly greater than bone deposit feeders ($p = 0.851$) and they did not overlap. The SEA_B of *Capitella* cf. *capitata* on wood was not significantly greater than on bone ($p = 0.805$) and they did not overlap.

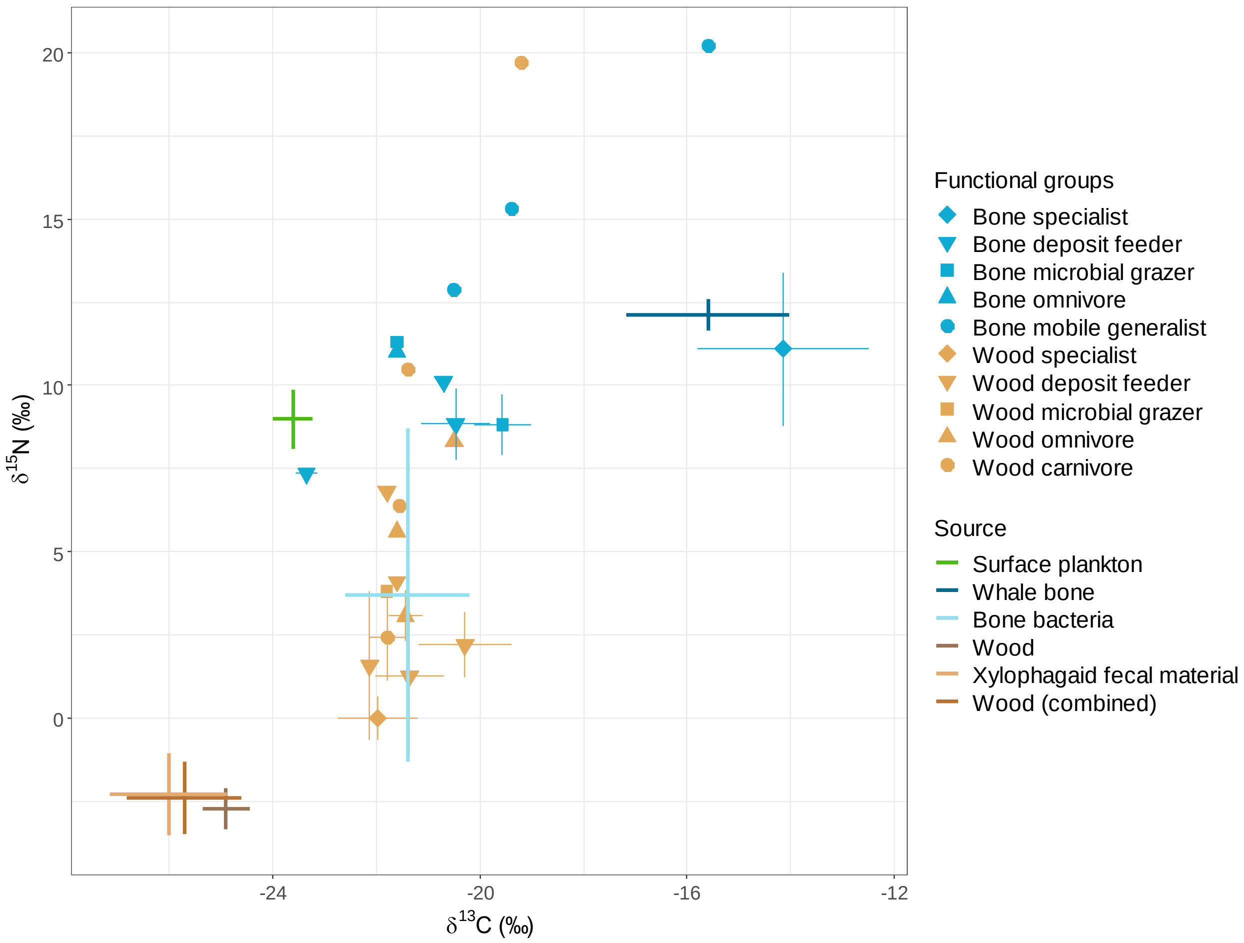

Figure 4.1 Stable isotope biplot of species collected from whale-bone and wood substrates, and potential food sources. Points/intersections indicate mean values and error bars indicate standard deviations.

Table 4.2 Means and standard deviations (SD) of $\delta^{13}C$, $\delta^{15}N$, and carbon/nitrogen ratio (C/N) of whale-bone and wood-fall taxa. *Mean and SD calculated from n = 2 values. †Whale-bone bacteria from Baco-Taylor 2002.

				$\delta^{13}C$ (‰)		$\delta^{15}N$ (‰)		C/N	
Substrate	Functional group	Taxa	n	Mean	SD	Mean	SD	Mean	SD
Sources		Surface plankton	3	-23.6	0.4	9.0	0.9	8.5*	1.4*
		Whale bone	6	-15.6	1.6	12.1	0.5	3.9	0.9
		Whale-bone bacteria†	3	-20.4	0.9	0.6	3.6	NA	NA
		Wood	5	-24.9	0.5	-2.7	0.6	297.6	18.7
		Xylophagaid fecal material	13	-26.0	1.1	-2.3	1.2	65.7	41.7
Bone	Bone specialist	*Osedax rubiplumus*	4	-14.2	1.7	11.1	2.3	5.8	1.0
	Deposit feeder	*Laonice* sp. A	2	-23.4	0.2	7.4	0.1	3.7	0.1
		Capitella cf. *capitata*	7	-20.5	0.7	8.8	1.1	4.0	0.3
		Capitella cf. *ovincola*	1	-20.7	-	10.1	-	4.2	-
	Microbial Grazer	*Hyalogyrina* sp. A	6	-19.6	0.5	8.8	0.9	3.8	0.1
		Dillwynella sp. A	1	-21.6	-	11.3	-	3.7	-
	Omnivore	*Ophryotrocha batillus*	1	-21.6	-	11.0	-	4.4	-
	Mobile generalist	Ophiuroid sp. A	1	-19.4	-	15.3	-	5.7	-
		Amphipod sp. K	1	-15.6	-	20.2	-	4.6	-
		Eurycopinae sp. A	1	-20.5	-	12.9	-	3.9	-

Table 4.2 (Continued) Means and standard deviations (SD) of δ^{13}C, δ^{15}N, and carbon/nitrogen ratio (C/N) of whale-bone and wood-fall taxa.

				δ^{13}C (‰)		δ^{15}N (‰)		C/N	
Substrate	Functional group	Taxa	n	Mean	SD	Mean	SD	Mean	SD
Wood	Wood specialist	*Xylophaga oregona*	15	-22.0	0.8	0.0	0.7	5.0	0.7
	Deposit feeder	*Laonice* sp. A	5	-21.4	0.7	1.3	2.4	4.3	0.7
		Capitella cf. *capitata*	15	-20.3	0.9	2.2	1.0	6.0	2.0
		Decemunciger sp. A	3	-22.1	0.1	1.6	2.2	4.3	0.3
		Ampharetid sp. 22	1	-21.8	-	6.8	-	4.3	-
		Flabelligerid sp. A	1	-21.6	-	4.1	-	3.6	-
	Microbial grazer	Limpet sp. A	1	-21.8	-	3.8	-	4.4	-
	Omnivore	*Ophryotrocha batillus*	1	-21.6	-	5.6	-	3.9	-
		Ophryotrocha langstrumpae	10	-21.4	0.3	3.1	0.8	4.8	0.8
		Dorvilleid sp. 54	1	-20.5	-	8.3	-	3.8	-
	Carnivore	Triclad sp. A	9	-21.8	0.4	2.4	1.3	4.4	0.7
		Polynoid sp. A	1	-21.4	-	10.5	-	3.7	-
		Sirsoe cf. *hessleri*	2	-21.6	0.1	6.4	0.0	3.7	0.0
		Nemertean sp. A	1	-19.2	-	19.7	-	4.2	-

Table 4.3 Bayesian estimates (posterior mode and 95% credible intervals) of community-wide Layman metrics for bone and wood assemblage trophic structure.CR = δ13C range. NR = δ15N range, TA = total area of the convex hull containing the means of functional groups, CD = mean distance of functional group means to the centroid, MNND = mean nearest neighbor distance of functional group means, and SDNND = standard deviation of nearest neighbor distance.

	Bone		Wood	
Metric	Mode	95% CI	Mode	95% CI
NR	7.5	5.6, 9.4	5	4.2, 5.8
CR	6.9	5.3, 8.5	1.1	0.6, 1.8
TA	23.2	15.7, 31.1	2.5	1.1, 4
CD	3.9	3.2, 4.6	1.7	1.5, 2
MNND	3.8	3.1, 4.6	1.7	1.4, 2
SDNND	2.9	1.9, 3.7	0.6	0.2, 1.1

Table 4.4 Standard ellipse areas (SEA) of functional groups. SEA_B (Bayesian-inferred) estimates are posterior modes and credible interval (CI). SEA_C (small-sample corrected) ellipses are plotted in Figure S4.2.

Substrate	Functional Group	n	SEA_C	SEA_B	SEA_B 95% CI
Bone	Bone specialist	4	13.7	8.9	2.2, 30.9
	Deposit feeder	10	3.8	3.3	1.8, 7
	Microbial grazer	7	3.5	2.8	1.2, 6.7
	Mobile generalist	3	6.8	17.5	3, 81.6
Wood	Wood specialist	15	1.5	1.4	0.8, 2.4
	Deposit feeder	25	6	5.7	3.8, 8.4
	Omnivore	12	2	1.8	0.9, 3.3
	Carnivore	13	6.2	6.6	3.8, 12.2
Bone	*Capitella* cf. *capitata*	7	1.9	1.6	0.7, 3.8
Wood	*Capitella* cf. *capitata*	15	3	2.6	1.5, 4.6

4.4.2 Dietary sources

Overall, organic-fall sources were the dominant basal food source of macrofauna analyzed (Figure 4.2; Tables 4.5-4.8). Averaged across all taxa, organic-fall sources (the total of wood, xylophagaid fecal material, whale bone and whale-bone bacteria sources) accounted for 68.8% of diet source (range 33.7 – 95.8%), and surface plankton had an average contribution of 31.2% (range 4.2 – 66.3%; Figure 4.2).

Whale bone and wood comprised most of the diet of bone and wood specialists, respectively, although the diet of *O. rubiplumus* contained a higher proportion of surface plankton than that of *X. oregona*.

Wood deposit feeders derived most of their diets from xylophagaid fecal material, with varied contribution of surface plankton (median proportion 0.11 – 0.42). The contribution of surface plankton to the diet of *Laonice* sp. A collected from whale bones was ~3 times greater (median proportion = 0.3) than the contribution of surface plankton to *Laonice* sp. A collected from wood (median proportion = 0.11). The probability that the dietary proportion of surface plankton of *Laonice* sp. A collected from whale bones was greater than the dietary proportion of surface plankton of *Laonice* sp. A collected from wood was 0.787. Similarly, the contribution of surface plankton to the diet of *Capitella* cf. *capitata* collected from whale bones (median proportion = 0.26) was greater than the contribution of surface plankton to *Capitella* cf. *capitata* diets collected from wood (median proportion = 0.19; probability = 0.711).

Most of the diet of bone and wood microbial grazers was derived from bone and wood sources, respectively. Dietary proportions of omnivores varied between species, but organic-fall sources were most important. The median proportion of diet derived from surface plankton sources ranged between 0.15 and 0.58 across the three dorvilleid polychaetes taxa collected from wood. The contribution of surface plankton to the diet of *O. batillus* collected from bone (median = 0.44) was greater than at wood (0.37; probability = 0.607).

Whale bone was the dominant food source of the three mobile generalist taxa collected from whale bones. Wood was the dominant food source of Triclad sp. A. However, two carnivores from the wood substrate assemblages had surface plankton dominated the diets (Polynoid sp. A, and Nemertean sp. A), and wood and surface plankton co-dominated the diet of *Sirsoe* cf. *hessleri*.

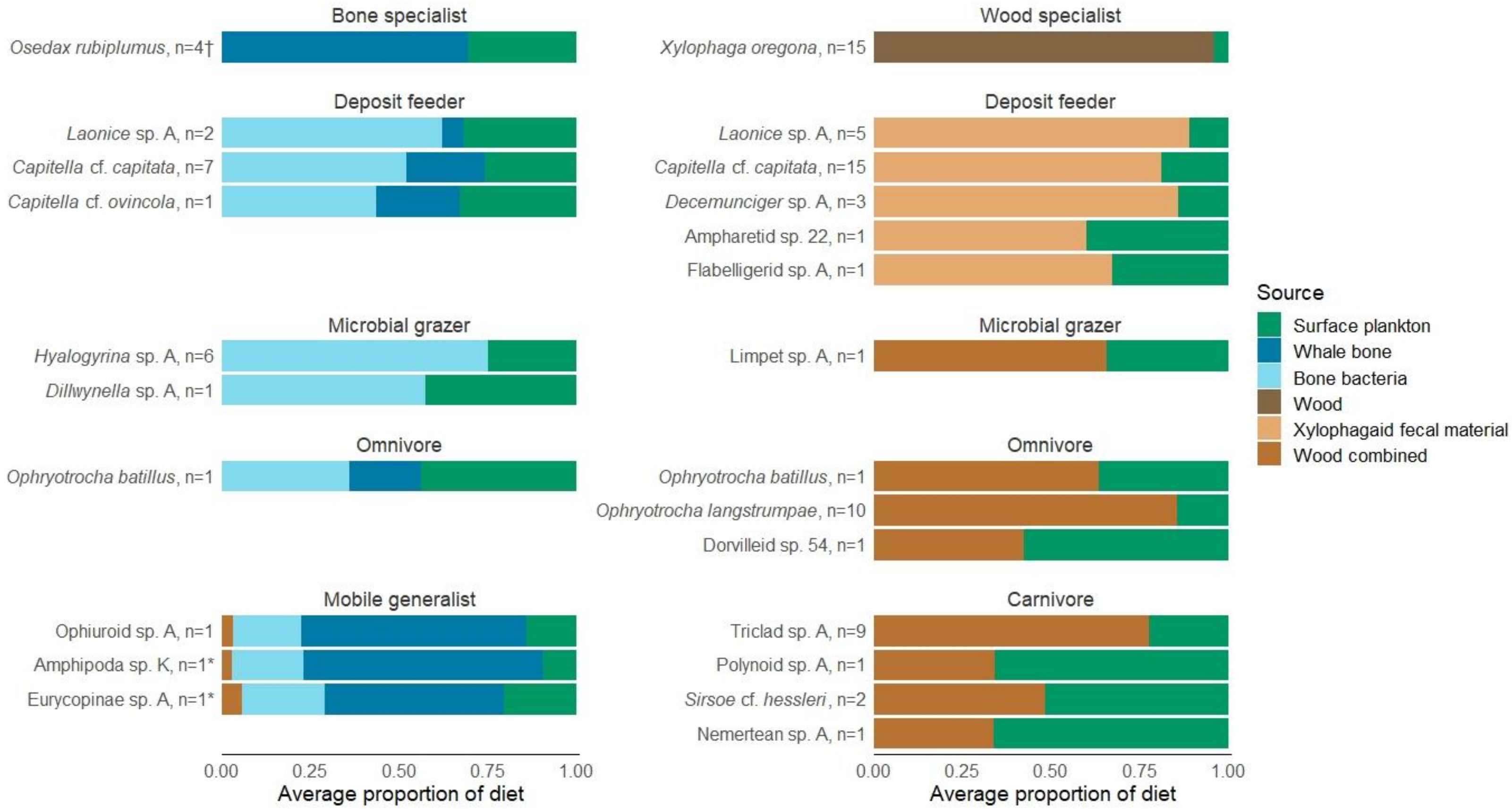

Figure 4.2 Average dietary proportions for whale-bone and wood fall taxa, determined by MixSIAR modelling. *Isotopic signature outside of mixing polygon. † n = 1 isotopic signature outside of mixing polygon.

Table 4.5 Dietary proportions (mean ± SD) of whale-bone taxa, determined by MixSIAR modelling. Calculated from Bayesian posterior distributions.

Substrate	**Functional group**	**Taxa**	Wood (combined)	Whale bone	Bone bacteria	Surface plankton
Bone	Bone specialist	*Osedax rubiplumus*	-	0.69 ± 0.22	-	0.31 ± 0.22
	Deposit feeder	*Laonice* sp. A	-	0.06 ± 0.05	0.62 ± 0.22	0.32 ± 0.22
		Capitella cf. *capitata*	-	0.22 ± 0.07	0.52 ± 0.13	0.26 ± 0.12
		Capitella cf. *ovincola*	-	0.23 ± 0.12	0.44 ± 0.19	0.33 ± 0.2
	Microbial grazer	*Hyalogyrina* sp. A	-	-	0.75 ± 0.16	0.25 ± 0.16
		Dillwynella sp. A	-	-	0.58 ± 0.23	0.42 ± 0.23
	Omnivore	*Ophryotrocha batillus*	-	0.2 ± 0.14	0.36 ± 0.21	0.44 ± 0.23
	Mobile generalists	Ophiuroid sp. A	0.03 ± 0.04	0.63 ± 0.23	0.19 ± 0.22	0.14 ± 0.16
		Amphipoda sp. K	0.03 ± 0.03	0.67 ± 0.21	0.2 ± 0.21	0.1 ± 0.08
		Eurycopinae sp. A	0.06 ± 0.07	0.5 ± 0.23	0.23 ± 0.23	0.21 ± 0.2

Table 4.6 Dietary proportions (mean ± SD) of wood-fall taxa, determined by MixSIAR modelling. Calculated from Bayesian posterior distributions.

Substrate	**Functional group**	**Taxa**	Wood (combined)	Wood	Xylophagaid fecal material	Surface plankton
Wood	Wood Specialist	*Xylophaga oregona*	-	0.96 ± 0.03	-	0.04 ± 0.03
	Deposit feeder	*Laonice* sp. A	-	-	0.89 ± 0.06	0.11 ± 0.06
		Capitella cf. *capitata*	-	-	0.81 ± 0.05	0.19 ± 0.05
		Decemunciger sp. A	-	-	0.86 ± 0.07	0.14 ± 0.07
		Ampharetid sp. 22	-	-	0.6 ± 0.13	0.4 ± 0.13
		Flabelligerid sp. A	-	-	0.67 ± 0.14	0.33 ± 0.14
	Microbial grazer	Limpet sp. A	0.66 ± 0.17	-	-	0.34 ± 0.17
	Omnivore	*Ophryotrocha batillus*	0.63 ± 0.07	-	-	0.37 ± 0.07
		Ophryotrocha langstrumpae	0.85 ± 0.03	-	-	0.15 ± 0.03
		Dorvilleid sp. 54	0.42 ± 0.07	-	-	0.58 ± 0.07
	Carnivore	Triclad sp. A	0.78 ± 0.13	-	-	0.22 ± 0.13
		Polynoid sp. A	0.34 ± 0.24	-	-	0.66 ± 0.24
		Sirsoe cf. *hessleri*	0.48 ± 0.22	-	-	0.52 ± 0.22
		Nemertean sp. A	0.34 ± 0.20	-	-	0.66 ± 0.20

Table 4.7 Dietary proportions (median, and 2.5% and 97.% confidence intervals) of whale-bone taxa, determined by MixSIAR modelling. Calculated from Bayesian posterior distributions.

Substrate	**Functional group**	**Taxa**	Wood (combined)	Whale bone	Bone bacteria	Surface plankton
Bone	Bone specialist	*Osedax rubiplumus*	-	0.73 (0.17, 0.99)	-	0.27 (0.01, 0.83)
	Deposit feeder	*Laonice* sp. A	-	0.05 (0.01, 0.18)	0.63 (0.15, 0.96)	0.3 (0.01, 0.79)
		Capitella cf. *capitata*	-	0.22 (0.07, 0.35)	0.51 (0.28, 0.78)	0.26 (0.03, 0.49)
		Capitella cf. *ovincola*	-	0.23 (0.02, 0.49)	0.41 (0.1, 0.85)	0.32 (0.01, 0.74)
	Microbial grazer	*Hyalogyrina* sp. A	-	-	0.77 (0.39, 0.98)	0.23 (0.02, 0.61)
		Dillwynella sp. A	-	-	0.58 (0.15, 0.96)	0.42 (0.04, 0.85)
	Omnivore	*Ophryotrocha batillus*	-	0.18 (0.01, 0.51)	0.34 (0.03, 0.83)	0.44 (0.03, 0.85)
	Mobile generalists	Ophiuroid sp. A	0.02 (0, 0.15)	0.67 (0.12, 0.97)	0.09 (0, 0.8)	0.08 (0, 0.56)
		Amphipoda sp. K	0.02 (0, 0.1)	0.73 (0.16, 0.93)	0.11 (0, 0.73)	0.08 (0, 0.29)
		Eurycopinae sp. A	0.03 (0, 0.25)	0.5 (0.08, 0.94)	0.16 (0, 0.81)	0.14 (0, 0.68)

Table 4.8 Dietary proportions (median, and 2.5% and 97.% confidence intervals) of wood-fall taxa, determined by MixSIAR modelling. Calculated from Bayesian posterior distributions.

Substrate	**Functional group**	**Taxa**	Wood (combined)	Wood	Xylophagaid fecal material	Surface plankton
Wood	Wood Specialist	*Xylophaga oregona*	-	0.96 (0.89, 1)	-	0.04 (0, 0.11)
	Deposit feeder	*Laonice* sp. A	-	-	0.89 (0.76, 0.98)	0.11 (0.02, 0.24)
		Capitella cf. *capitata*	-	-	0.81 (0.72, 0.9)	0.19 (0.1, 0.28)
		Decemunciger sp. A	-	-	0.86 (0.71, 0.98)	0.14 (0.02, 0.29)
		Ampharetid sp. 22	-	-	0.58 (0.36, 0.88)	0.42 (0.12, 0.64)
		Flabelligerid sp. A	-	-	0.67 (0.4, 0.94)	0.33 (0.06, 0.6)
	Microbial grazer	Limpet sp. A	0.66 (0.27, 0.96)	-	-	0.34 (0.04, 0.73)
	Omnivore	*Ophryotrocha batillus*	0.63 (0.49, 0.79)	-	-	0.37 (0.21, 0.51)
		Ophryotrocha langstrumpae	0.85 (0.79, 0.91)	-	-	0.15 (0.09, 0.21)
		Dorvilleid sp. 54	0.42 (0.29, 0.57)	-	-	0.58 (0.43, 0.71)
	Carnivore	Triclad sp. A	0.79 (0.47, 0.96)	-	-	0.21 (0.04, 0.53)
		Polynoid sp. A	0.29 (0.02, 0.9)	-	-	0.71 (0.1, 0.98)
		Sirsoe cf. *hessleri*	0.49 (0.05, 0.91)	-	-	0.51 (0.09, 0.95)
		Nemertean sp. A	0.29 (0.09, 0.87)	-	-	0.71 (0.13, 0.91)

4.5 DISCUSSION

Stable isotope analyses revealed that food web structure at experimental (co-located and concurrent) organic-fall deployments differed between whale-bone and wood substrates. Organic-fall substrates were the dominant basal food source for the faunal assemblages, and the importance of photosynthetically-derived, background POM varied among taxonomic groups and between whale-bone and wood substrates. Results of this study were consistent with each of our three hypotheses, which we discuss below following a discussion of the potential dietary sources used in this study.

4.5.1 Dietary sources at organic-falls

The overall divergent isotopic signatures of whale bone, wood, and surface plankton provides a strong basis for determining the relative importance of basal food resources in organic-fall assemblages. Both whale bone and wood are complex materials comprising organic components with differing labilities and isotopic signatures.

Whale bones (considered as organs, versus tissues) consist of a mineralized proteinaceous matrix surrounding marrow and interstitial organic material within bone spaces. Collagen, the dominant protein found within the bone tissue matrix, and lipids, stored inside bone spaces, are the two major food sources available to whale bone fauna, and make up ~10–20% and ~10–50% of bone composition, respectively (Higgs et al., 2011b). Previous isotopic studies of whale bones suggest that the $\delta^{13}C$ of collagen is greater (by ~5–8 ‰) compared to lipids (Stott et al., 1997; Baco-Taylor, 2002; Onishi et al., 2018), and the $\delta^{13}C$ signature of whale bones measured in this study are more resemblant of bone collagen. Whale bone sources in this study were sampled from the exterior of bone substrates, which may have contained less lipids, possible due to prior bacterial degradation and/or seepage from bone spaces (Allison et al., 1991; Deming et al., 1997; Schuller et al., 2004) and due to the less porous outer layers of the bone (Higgs et al., 2011b). The microbiome of bone surfaces in marine environments comprises a consortium of heterotrophic and chemoautotrophic microbes, with a range of metabolisms specialized for various reactions associated with bone decomposition (Borchert et al., 2021). Many studies have reported the presence of conspicuous sulfide-oxidizing microbial mats on and surrounding whale bones on the deep-sea floor (Smith et al., 1989; Smith & Baco, 2003; Sumida et al., 2016). The isotopic signatures of our whale bones were similar to those of lipid-depleted bones reported by Baco-Taylor (2002), and therefore use of their values for whale bone bacteria is likely appropriate. The large range in bacterial δ^{15}N values (-0.7 – +7.8 ‰) reported by Baco-Taylor (2002) warrants further investigation into the basal food sources and metabolic strategies (e.g., heterotrophy, autotrophy) of microbial communities on whale bones. Whale-bone bacteria δ^{13}C values reported by Alfaro-Lucas et al. (2018; ~ -30 ‰) were considerably lower than those of Baco-Taylor (2002; ~ -21 ‰) and Deming et al. (1997; ~ -21 ‰). Lower δ^{13}C signatures (~35 ‰) are frequently interpreted as a signal of chemosynthetically produced organic matter (Ruby et al., 1987). However, the whale bones from which the bacterial mats were collected (Alfaro-Lucas et al. 2018) had particularly lower δ^{13}C values (~ -27 ‰, A. Bernardino, pers comm). Therefore, we cannot be certain that the whale-bone bacteria signatures reflect a chemosynthetic origin versus the signature of the whale-bone material itself. It is possible that the greater δ^{13}C values of bacteria reported by Baco-Taylor (2002) and Deming et al. (1997) may incorporate a greater signal from the heterotrophic versus chemoautotrophic components in the microbial mat.

Holocellulose (α-cellulose and hemicellulose) and lignin are the dominant constituents of wood, and each have distinct isotopic signatures. The δ^{13}C signature of holocellulose is ~ 1 ‰ greater, and the δ^{13}C signature of lignin is ~ 2 ‰ lower relative to the isotopic signature of bulk wood (Loader et al., 2003). The differential isotopic signatures within wood explains why xylophagaids, which utilize (via symbionts) the cellulose component of wood, have much greater δ^{13}C values compared to the bulk wood signature (Nishimoto et al., 2009; Harbour et al., 2021a; Voight et al., 2020). The lower δ^{13}C values of xylophagaid fecal material compared to bulk wood has been observed in other studies (Voight et al., 2020; Harbour et al., 2021a) and likely reflects the greater proportion of lignin in fecal material after xylophagaid symbionts have digested the cellulose components (Dore & Miller, 1923; Pesante, 2018). Lignin is highly refractory and an unlikely direct food source for most macrofauna, but it may be decomposed by bacteria and fungi (Kohlmeyer, 1977; Dupont et al., 2009; Ohta et al., 2012; Fagervold et al., 2014; Nagano et al., 2019), which may, in turn, serve as a labile food component for bacterivorous macrofauna. We found no evidence of filamentous bacterial mats on wood blocks upon recovery, although mats could have been washed off during recovery, and other microbial films may have been present (Fagervold et al., 2014). White filamentous sulfur-oxidizing bacterial mats collected from sunken wood blocks and kelp bundles in a Norwegian fjord had isotopic signatures lower in $\delta^{13}C$ by ~1 ‰ and greater in $\delta^{15}N$ by ~4 ‰ compared to bulk wood signatures (Harbour et al., 2021a). Microbial mat signatures were also similar to those of xylophagaid fecal material, which may indicate a predominance of sulfur-oxidizing bacteria on fecal material but could alternatively reflect the greater proportion of $\delta^{13}C$-depleted lignin. Future studies should investigate in more detail the macromolecular composition of xylophagaid fecal material, as well as the isotopic signatures and fractionation of heterotrophic and chemoautotrophic microbes living on and metabolizing whale bone and wood substrates.

We used isotopic signatures of surface plankton as a proxy for the isotopic signature of background POM at the seafloor. The actual isotopic signatures of detrital plankton material available to benthic organisms may differ from this surface signal. An enrichment in POM $\delta^{15}N$ with depth due to progressively increased microbial degradation as particles sink throughout the water column is well documented (Saino & Hattori, 1980; Altabet et al., 1999; Hannides et al., 2013) and has been reflected in greater $\delta^{15}N$ of benthic organisms with depth (Mintenbeck et al., 2007; Bergmann et al., 2009). The $\delta^{15}N$ of surface plankton reported here are greater (~ 4 ‰) than POM signatures collected from surface, 0.7 µm-filtered seawater samples in a nearby region (Miller et al., 2010) which is likely due to the presence of zooplankton material in our samples.

4.5.2 Whale bone and wood falls display different trophic structure

Bulk stable isotope analyses revealed that fauna collected from co-located whale bones and wood blocks after 15 months had different isotopic signatures according to substrate type. Broadly, isotopic signatures of fauna collected from wood blocks more resembled the isotopic signatures of wood sources (wood substrate and xylophagaid fecal material) and were different to isotopic signatures of fauna collected from whale bones, which more resembled isotopic signatures of whale bone and background POM sources. Moreover, the isotopic signatures of three faunal species collected from both whale bone and wood substrates differed by substrate type, further highlighting the differing provision and assimilation of food resources at co-located organic-rich habitats.

Comparable studies of co-located (cow) bone and wood deployments found the opposite result: isotopic signatures of co-located bone and wood fauna were similar to one another, and trophic niches of bone and wood fauna overlapped (Pereria et al., 2022). The cow bone and wood deployments of Pereira et al., (2022) were conducted at and near regions of active methane seepage, and chemosynthetic carbon sources derived from seepage were hypothesized to contribute a greater source of carbon to organic-fall fauna than the organic substrates themselves. Notably, xylophagaid colonization was light to absent at the wood blocks examined by Pereira et al. (2022). We hypothesize that these wood blocks experienced a weaker ecosystem engineering role of xylophagaids on nutritional resources, compared to wood blocks examined in our study, and this plays an important role in driving differences in wood assimilation and trophic structure by organic-fall fauna.

In this present study, estimations of Layman metrics (Layman et al., 2007; Jackson et al., 2011) were used to quantify various components of community trophic structure; however the traditional interpretations of each metric may not be directly applicable to these organic-fall systems (Hoeinghaus & Zeug, 2008). For example, greater $\delta^{15}N$ range (NR) values are often interpreted to suggest more trophic levels within a system, yet here the greater NR at whale bone more likely reflects the greater $\delta^{15}N$ values of whale bone as basal food source compared to wood. Whale bone bacteria also had a large range in $\delta^{15}N$ signatures. Similarly, greater $\delta^{13}C$ range (CR) values are suggested to indicate a greater diversity of basal food sources, yet the greater CR of whale bone fauna compared to wood fauna in this study more likely reflects the greater difference between the $\delta^{13}C$ of whale bone and surface plankton, compared to wood and surface plankton. Mean distance to centroid (CD) is a measure of the overall trophic diversity, mean nearest neighbor distance (MNND) is a measure of trophic redundancy, the standard deviation of the nearest neighbor distance (SDNND) informs the evenness of trophic niche distributions in isotopic space, and total area TA is a measure of overall trophic diversity. In our study, each of these metrics may have been influenced by incomplete sampling of whale bone and wood assemblages, which may have excluded key functional groups. Nonetheless, quantification and statistical comparison of the isotopic data available do indicate differences in the assimilation of food sources between co-located whale bone and wood faunal assemblages.

4.5.3 Greater contribution of organic-fall sources versus background POM sources to diets

Results of MixSIAR modelling indicated that that most of the organic matter entering the food web came from the respective organic fall sources, and a relatively minor component appeared to be derived from background POM sources. This finding aligns with our expectations, because the supply of background POM to S-1600 (Young et al., 2022; Lutz et al., 2007) represents a small fraction of the organic carbon supplied by the organic-rich substrates, provided the organic-rich substrate material is made accessible by bacterial degraders and/or substrate specialists. For comparison, we estimate that each wood block in our study contained ~7500 g C, assuming that wood is 50% carbon (Lamlom & Savidge, 2003), and each vertebral half contained ~1300 g organic matter, assuming that cetacean bones are 28.6% organic matter (Kim et al., 2014).

The relative importance of background POM to diets varied across functional groups and species. Background POM was of minor importance to substrate specialists, *X. oregona* and *O. rubiplumus,* which confirms their specialization on organic-rich substrates. The contribution of background POM to the diet of *O. rubiplumus* (~ 30%) is likely an unreliable estimate, because *Osedax* does not appear to have the capacity to consume particulate material (Rouse et al., 2004), and indeed other stable isotopic studies have indicated that *Osedax* is assimilating whale-bone collagen (Goffredi et al., 2007; Alfaro-Lucas et al., 2018; Onishi et al., 2020). Our result may drive from a single outlying data point (Figure 4.2), or because TEF factors are less reliable when endosymbionts are involved. Microbial grazers on whale bones examined in this study were predominantly consuming whale-bone bacteria, with some contribution of background POM sources indicated by the model. This result aligns with other studies, where congenerics of *Hyalogyrina* and *Dillwynella* at organic-fall habitats (Nishimoto et al., 2009; Smith et al., 2014), as well as at other reducing habitats (Åström et al., 2019), are thought to be predominantly microbial grazers. Whether wood-fall limpets consume microbes associated with rasped wood fragments (Wolff, 1979; Marshall, 1985) or are consuming wood material itself (Zbinden et al., 2010), has been widely considered for various limpet-like groups (Lesicki, 2009; Haszprunar et al., 2022). Wood was a primary basal food source for the unidentified limpet examined in our study; however, without a specific isotopic signature of the wood microbial community, we are unable to determine a specific feeding strategy. The mobile generalists collected on whale bones were mostly dependent on whale-bone sources (including whale bone bacteria), suggesting that they do not travel between different substrate types, although more replicate samples including of individuals collected from wood substrates are desirable to make stronger inferences on their trophic strategy. Carnivores collected from wood, except for Triclad sp. A, derived a greater proportion of their diet from background POM, as indicated by MixSIAR modelling. The greater δ^{15}N values could alternatively suggest these carnivores are feeding at a higher trophic level than considered in the MixSIAR model (TL = 3) or that they were more mobile than expected and foraged outside of the experimental bins. The utilization of background POM in deposit and omnivores are discussed in more detail below (Section 4.4).

4.5.4 Availability of particulate food sources at whale bones and wood

The provision of available, labile food resources at organic-fall habitats is especially important to deposit feeding and omnivorous/bacterivorous taxa and varies between whale bone and wood substrates. These taxa consistently fed more on wood sources of organic matter than on bone at their respective organic fall enrichment sites (Figure 4.2). Three species in our study were found on both whale bone and wood substrates. Because substrates in our study were co-located, we can assume that both substrate types received equal amounts of background POM food resources, yet taxa on whale bones appeared to derive a greater proportion of their diet from background POM than did wood-fall taxa. We hypothesize that this is because of the lesser availability/volume of particulate food sources at our whale bones compared to our wood block substrates. Free-living microbes on bone surfaces are likely the major whale-bone-derived food source accessible to deposit-feeding and omnivorous/bacterivorous taxa at early-stage, whale-bone substrates (Wiklund et al., 2009; Alfaro-Lucas et al., 2018). While we were unable to quantify the microbial resource, the biomass was undoubtedly smaller than that of the particulate xylophagaid fecal material present at the highly degraded wood blocks, because boreholes were filled with fecal material.

These findings highlight the differences between organic-fall ecosystem engineers and the food webs they facilitate. *Osedax* annelids do not create particulate material, and their presence appears to be negatively correlated with and/or inhibit the production of microbial biomass on bone surfaces (Higgs et al., 2011b; Alfaro-Lucas et al., 2017). Xylophagaid bivalves that produce abundant fecal material provide a particulate food source to deposit and bacterivorous species in, on and surrounding the wood substrates and may also influence within-matrix and surface sulfur cycling and microbial biomass production (Kalenitchenko et al., 2018b). For those xylophagaid species that do not produce abundant fecal chimneys, or at earlier stages of wood degradation, background POM is likely to be a relatively more important food source (Harbour et al., 2021a).

4.5.5 Generalizability to other organic-fall food webs

This study investigated the trophic structure of whale-bones in an early-reducing stage, and wood blocks in a late “wood-disintegration” stage at a single location in the NE Pacific Ocean. The trophic structure and dominant nutritional sources of whale-bone and wood assemblages is strongly influenced by the degradational stage of the organic-rich substrates. Stable-isotopic studies have demonstrated a transition in dominant nutritional sources throughout whale-fall successional stages, from a primary reliance on whale soft tissues during mobile scavenger stages, to including bone lipids during enrichment opportunist stages, and then an increasing reliance on chemosynthetic organic matter from early to late sulphophilic stages (Baco-Taylor, 2002; Smith & Baco, 2003; Alfaro-Lucas et al., 2018; Onishi et al., 2020). We expect that the transition to “reef stage” of succession would be accompanied by a transition to nutritional dominance of background POM.

Similarly, dominant nutritional sources are expected to vary throughout the successional stages of wood-fall decomposition (Chapter 3). Following the arrival of wood at the seafloor and the onset of the microbial stage (Chapter 3), microbial (heterotrophic and chemoautotrophic) biomass may become an important food source, especially for grazers. At this stage, background POM is likely also important to suspension feeders such as anemones utilizing the wood as an attachment substrate. During the wood-boring stage, wood-derived carbon is the dominant food source for wood-borers and other functional groups. Nitrogen-fixing bacteria or background POM can contribute organic nitrogen to xylophagaids and the base of the food web (Voight et al., 2020). In cases of light degradation by wood borers, background POM and microbial biomass likely remain important for non-specialist wood-fall taxa (Harbour et al., 2021a; Pereira et al., 2022). During the opportunist stage, increased biomass of opportunistic taxa is sustained by the production of xylophagaid fecal material and/or xylophagaid biomass. The increased opportunist biomass may also support a greater biomass of carnivores, increasing the length of the overall food web. During the wood disintegration stage, wood-derived material (wood particles and xylophagaid fecal material) becomes an increasingly dominant food resource for surrounding sediment infauna, and the accompanying organic enrichment supports the production of chemosynthetic organic matter throughout surrounding sediments (Bernardino et al., 2010). Wood blocks that instead transition to a reef stage (instead of a terminal disintegration stage) would host assemblages increasingly dependent on background POM nutritional sources.

Overall, the establishment and duration of organic-fall successional stages, and hence organic-fall trophic structure, is influenced by many factors. The extent of colonization by substrate-specialist ecosystem engineers is an important driver of organic-fall successional stages (Chapter 3; Alfaro-Lucas et al., 2017), and is influenced by larval supply, which may vary regionally and with depth (Young et al., 2022). The size (McClain & Barry, 2014), quality (e.g., juvenile versus adult whale skeletons; Smith & Baco, 2003; bone lipid content; Higgs et al., 2011b; Smith et al., 2015; and wood species; Judge & Barry, 2016) of organic-rich substrates also influence organic-fall assemblages and successional stage progression. Proximity of organic-rich substrates to reducing habitats can also influence the contribution of chemosynthetically-derived nutritional sources, and hence trophic structure (Pereira et al., 2022). Standardized experimental studies of organic-fall habitats, such as used here, positioned at different depths, biogeographic regions, and spanning multiple successional stages are important to further our understanding of trophic structure and nutritional sources at organic-fall habitats.

4.6 ACKNOWLEDGEMENTS

We thank all of those involved in the fabrication, deployment, recovery, and processing of the Bone and Wood Landers. Special thanks go to R. Lee and N. Wallsgrove for their help with stable isotope analyses. This research was supported by the National Science Foundation (grants OCE-1155703 awarded to C.R.S and OCE-1155188 awarded to K.M.H).

CHAPTER 5

Conclusions

5.1 DISSERTATION OVERVIEW

Organic-falls are important components of deep-sea seafloor ecosystems. In particular, sunken whale bones and wood foster widespread, specialized, organic-rich ecosystems at the generally food-poor deep-sea floor. Through a comparative-experimental approach, this dissertation explored three general aspects of whale-bone and wood-fall ecology at the deep-sea floor: patterns and drivers of biodiversity (**Chapter 2**), the role of a key ecosystem engineer in modulating community structure and ecosystem function (**Chapter 3**), and trophic structure (**Chapter 4**).

5.2 CHAPTER 2

Chapter 2 reports the overarching findings of the controlled, experimental emplacement of replicate bone, wood, and inorganic hard substrates at four locations and two depths (~1600 and ~2800 m) on the Washington-Oregon margin. These experiments tested four fundamental hypotheses regarding patterns of community structure and biodiversity, i.e., (1) Community structure differs between wood, bone, and control substrates deployed for similar times at similar locations, (2) Macrofaunal abundance, as well as species richness and dominance, are greater on organic-rich substrates than on food-poor control substrates, (3) Community structure of wood, whale-bone, and control assemblages differ with depth, and (4) Control assemblages have greater abundances at shallower depths, where detrital fluxes of POC are greater. After 15 months on the seafloor, a total of ~84,890 macrofaunal individuals of 144 species had colonized the 36 bins and bin-affixed substrates (4 landers × 3 substrate types × 3 replicates). Whale bones at all locations were in an early sulfophilic stage, whereas wood substrates stages varied by depth and location, ranging from a microbial stage (intact and uncolonized by xylophagaid bivalves) to a wood disintegration stage (wood crumbling from heavy colonization and boring by xylophagaid bivalves). Overall, the community structure of assemblages varied with substrate type, depth, and at different locations within a depth, which highlights how organic-rich substrates (even of standardized sizes and qualities) can contribute greatly to beta-diversity of continental margins.

This study asked whether generalized bathymetric patterns of biodiversity observed in other detritus-based deep-sea ecosystems also apply to organic-falls. The bathymetric distribution of organic-fall community composition was indeed consistent with faunal zonation of background benthic communities in the Cascadia Basin (Carney, 2005). Control assemblages, after accounting for mass effects from nearby dissimilar substrates, exhibited patterns of faunal abundance similar to studies of deep-sea detritus-based ecosystems, with greater abundances at shallower depths where POC fluxes are greater (Wei et al., 2010). Conversely, organic-fall assemblage abundance and diversity was highly variable across the four locations and did not conform with bathymetric patterns expected of background detritus-based ecosystems. Because *Osedax* polychaetes and xylophagaid bivalves appear to regulate the biodiversity of whale-bone and wood organic-fall assemblages, respectively (e.g., Alfaro-Lucas et al., 2017), drivers that influence the larval availability of key ecosystem engineers and hence successional stages are hypothesized to be more important for organic-fall faunal density and diversity than bathymetric gradients of POC flux.

Because of equipment failures, only two (rather than three) landers were recovered from each depth zone during this study. Additional experiments, with greater replication within each depth horizon could help to determine whether the generally greater abundance and species richness at northern locations was a localized phenomenon, or a feature of a latitudinal, along-margin gradient.

5.3 CHAPTER 3

The importance of xylophagaid bivalves and their roles as ecosystem engineers at deep-sea wood falls has long been the subject of speculation (Turner, 1973), but not directly studied. In **Chapter 3**, the ecosystem engineering effects of xylophagaid bivalves on wood falls was quantified by exploring relationships between xylophagaid abundance/biomass and (1) wood mass loss, (2) macrofaunal assemblage abundance and diversity, and (3) microbial sulfate reduction. Xylophagaids were the primary drivers of wood mass loss. Wood mass loss rates have only been reported on a few other occasions (Fagervold et al., 2014; Amon et al., 2015), and this information is valuable for understanding the longevity of wood-falls and inferring remineralization rates of terrestrial organic matter in the deep-sea. The presence and biomass of xylophagaid bivalves had significant implications for the wider wood-fall assemblage. Xylophagaid bivalve biomass increased through early-to-mid successional stages wood of decomposition; during these stages, non-xylophagaid macrofaunal biomass, species richness and dominance were directly related to xylophagaid biomass. Wood boring by xylophagaids increased habitat availability and complexity, which allowed a greater biomass and species richness of other non-boring macrofauna to also inhabit wood parcels. High dominance within wood-fall assemblages during early-mid stages was due to large populations of opportunistic dorvilleid, capitellid and ampharetid polychaetes. We hypothesize here that the abundant and relatively labile (compared to wood) xylophagaid fecal material was a key food source for these opportunists (addressed further in **Chapter 4**). Sulfate-reduction rates in wood blocks were low but were enhanced deeper in one wood block where xylophagaid borings were present. Future studies involving more replicate measurements, carefully oriented to xylophagaid boreholes and fecal material, are required to better elucidate the hypothesized role of xylophagaids in modulating the development of sulfidic niches in wood blocks (Kalenitchenko et al., 2018a).

Based on findings in this chapter and the scientific literature, I presented a revised model of four to five successional stages on wood falls after arrival at the deep-sea floor. (1) The first is a "microbial stage", during which biofilms of heterotrophic and/or chemoautotrophic microbes develop, supporting bacterivores. (2) This is followed by the "wood-borer stage" which diversifies habitat and food resources. Xylophagaid bivalves, through boring and fecal production, appear to be the key drivers of this successional stage in the deep sea. (3) The "opportunist stage" follows, during which enrichment opportunists dominate wood assemblages; this is analogous to the enrichment-opportunist stage at whale-fall habitats (Smith & Baco, 2003; Smith et al., 2015). Eventually, xylophagaid growth slows, and the reduction in biomass and fecal production provides less nutritional support to the wider wood-fall assemblage. (4) The terminal phases of wood-fall decomposition may exhibit a "wood disintegration stage", wherein the wood substrate is fragmented and dispersed throughout surrounding sediments , and/or (5) a "reef stage" wherein xylophagaids have died out and remaining wood structure provides attachment sites primarily for hard-substrate species feeding on background POM. A number of deep-sea wood fall studies (Bienhold et al., 2013; Pop Ristova et al., 2017) have suggested the presence of an additional "sulfophilic stage" of wood-fall decomposition, analogous to that described at whale falls (Smith & Baco, 2003), characterized by high density, species-rich, and trophically complex assemblages dominated by a few species trophically dependent on chemoautotrophic production. In this study, we found little evidence to support such a sulfophilic stage at wood-falls. There was no dominance of taxonomic groups suspected to host chemosynthetic endosymbionts (**Chapter 2**), sulfate reduction rates at wood were low (**Chapter 3**), and we failed to find stable-isotope signatures characteristic of chemoautotrophic production within the wood-fall food web (**Chapter 4**).

The data used in this chapter was collected from wood blocks deployed for similar times (15 months) at multiple locations/depths that exhibited different levels of xylophagaid colonization and wood degradation. Future studies, in which replicate wood blocks are sampled at multiple time points from single locations could test this successional model, and further elucidate how wood-fall decomposition and succession vary by location and depth.

5.4 CHAPTER 4

In **Chapter 4,** bulk stable-isotopic analyses were employed to investigate the trophic structure of whale bone and wood assemblages at a single location. Organic-rich substrates were the dominant basal food sources for the majority of taxa sampled on whale-bone and wood, as indicated by Bayesian-mixing model analyses. These finding indicate that whale-bone and wood organic materials are important in providing nutrition (as well as habitat) for numerous species in found in these habitats. Background particulate organic matter (POM) had variable but minor importance in the diets of the organic-fall faunas. The availability of particulate material derived from organic-rich substrates varied between wood and whale bones; xylophagaid bivalves produced abundant labile particulate fecal material allowing wood derived carbon to support many deposit-feeding and omnivorous taxa on wood parcels. The availability of background POM was expected to be similar at the co-located whale-bone and wood substrates, yet background POM was more important to the whale-bone than the wood-fall fauna. This finding highlights the importance of key ecosystem engineers in the trophic ecology of wood-falls, and especially the importance of xylophagaid bivalves that produce abundant particulate fecal material (**Chapter 3**).

A variety of studies could build on the results of this research. Firstly, more complete sampling of whale-bone and wood assemblages will provide an improved understanding of the overall trophic structure. Better characterization of potential food sources is especially important for mixing model analyses. The importance of microbial activity, especially at various stages of wood-fall succession, is becoming increasingly recognized (Kalenitchenko et al., 2018b), and future studies quantifying the importance of heterotrophic and chemoautotrophic microbial biofilms as food sources in whale-bone and wood-fall communities could be very informative. Similarly, xylophagaid fecal material clearly contains a range of organic compounds (including microbial biomass) so detailed compositional and isotopic characterization of these components would be a valuable contribution to the field. Compound-specific stable isotope analyses would be a powerful tool to help elucidate the incorporation of microbial food sources (Potapov et al., 2019).

This stable isotope study focused on (a) whale bones lightly bored by *Osedax* in the early sulfophilic stage, and (b) on wood blocks in the wood-borer to opportunistic stages of succession. The relative importance of various food resources is hypothesized here to change across whale-bone and wood-fall successional stages, and the nature and duration these successional stages are hypothesized to vary with depth and the regional larval supply of key ecosystem engineers (**Chapter 2**). Time series studies of succession on whale bones and wood falls at multiple depths and different regions are needed to test these hypotheses. It is also hypothesized here that the relative importance of background POM decreases with depth (**Chapter 2**), which also could be addressed via standardized time-series studies across bathymetric gradients.

5.5 FUTURE STUDIES

The BoWLs experimental approach has been successfully deployed in the northeast Pacific (this dissertation), the southwest Atlantic (Saeedi et al., 2019; Shimabukuro et al., 2022), in a Norwegian fjord (Harbour et al., 2021b; Harbour et al., 2021a), and in the Southern Ocean (Craig Smith, pers. comm). In aggregate, these studies suggest that organic-fall communities vary by region and depth, and, even while being largely independent from background POM flux, exhibit bathymetric differences in community structure (Saeedi et al., 2019; Shimabukuro et al., 2022). Further standardized BoWLs experiments will help to elucidate particular bathymetric and regional patterns, for example indicating whether the diversity of whale-bone and wood-fall assemblages varies across ocean basins with different abundances and exploitation histories of whales and forests. Target locations for future BoWLs deployments may be informed by distributional models of cetacean migration pathways and mortality hot spots (Johnson et al., 2022), as well as distributional models of oceanic woody debris. If deployed far from terrestrial sources of wood, the deployment of standardized BoWLs experiments could reveal particularly interesting biodiversity and ecological findings underlying oligotrophic surface waters and beneath ocean gyres that may accumulate natural and anthropogenic woody debris (Amon et al., 2017b; Lebreton et al., 2018).

Future BoWLs experiments might next focus on the temporal succession of organic-fall assemblages, by deploying multiple landers in one location and recovering individual landers sequentially. These experiments could allow study of successional stages of wood decomposition, as well as providing information on the rates of initial colonization and succession of ecosystem engineers, and the amount of time taken for substrates to disintegrate and/or form a reef stage. To capture all successional stages, lander recovery schedules would likely need to vary with water depth and substrate types. For instance, for wood at ~1600 m depth on the Washington-Oregon margin, I recommend recoveries at 3, 6, 12, and 18 months to capture all stages of wood-fall succession. At ~2800 m depth, recoveries at 12, 18, 21, and 24 months may be more appropriate. Longer deployment durations are advised for studies prioritizing whale-bone degradation, because depletion of large lipid reserves may be slow (Smith et al., 2015; Smith et al., 2019).

A major feature of the BoWL lander design is the use of 500-μm mesh bins that retain substrates and fauna. The benefit of this approach is that the entire organic-rich substrates and communities can be collected, which has provided us important quantification of whale-bone and wood communities, as well as accurate estimates of substrate decomposition rates. However, this approach limits direct contact with underlying sediments, which may be an important feature of natural organic falls. This may have prevented some fauna with limited mobility, such as burrowing organisms, to colonize the substrates and mesh bins. This also may have had implications for the geochemistry and decomposition of the substrates themselves; In this experiment, some whale bone sections attached to lander legs that had direct contact with the sediments showed strong evidence of reducing conditions (blackened) and had outer-bone layers that were heavily disintegrated (Figure S5.1). Alternative experimental organic-fall approaches have involved placing and recovering organic-rich substrates, wrapped in coarse (~2-5 mm) mesh netting, directly on/from the seafloor using an ROV (e.g., McClain & Barry, 2014; Amon et al., 2017a). This approach has the advantage of collecting faunal assemblages not biased by mobility and allows for visual observations and push-core collections of surrounding sediments and sediment fauna (Bernardino et al., 2010, McClain & Barry, 2014).

However, fauna are inevitably lost during the collection of these parcels, and estimations of faunal richness and abundances are therefore considered as lower limits (Amon et al., 2017a). A future modification of the BoWLs lander could have organic-rich substrates affixed to solid surfaces that are designed to be partially buried into sediments and involve a mechanism to enclose the entire solid surface, surrounding sediments, and organic-rich substrates in a fine (500 or 300 µm) mesh netting upon collection of the lander. Future studies might investigate and quantify the compositional and functional differences between organic-rich assemblages that were deployed with and without direct contact to surrounding sediments to better understand the implications of varying experimental collection designs.

The research presented within this dissertation has provided important advancements to the growing field of deep-sea organic-fall ecology, which has relevant implications for science and society. Further organic-fall research is especially required in lesser-studied regions already threatened by anthropogenic seafloor activities (including deep-sea mining and trawling) to investigate their importance and value to local and regional biodiversity, as well as to inform appropriate management practices (Amon et al., 2017b). Although seemingly far removed from Earth's atmosphere, there are multiple ways in which deep-sea habitats are vulnerable to the effects of climate change (Sweetman et al., 2017). Regarding organic-fall habitats specifically, climate change is hypothesized to particularly impact the distribution and supply of organic-rich materials to the deep-sea by influencing whale mortality and migration pathways, and by enhancing the transportation of wood to the seafloor via rivers and coastlines due to an increased frequency and intensity of extreme climatic events. Advancements in the field of organic-fall ecology are critically required to identify, predict, and track impacts of climate change on organic-falls and to inform management and conservation of deep-sea habitats. Proposals to deposit on the deep-sea floor large amounts of organic carbon in the form of macroalgae and woody debris are increasingly gaining attention as a carbon dioxide removal (CDR) strategy to contribute towards climate mitigation (Zeng, 2008; Strand & Benford, 2009; Keil et al., 2010; Kokubu et al., 2019; Ricart et al., 2022), despite a current lack of scientific evidence and regulation. Organic-fall research revealing decomposition rates and geochemical impacts, such as presented within this dissertation, are a crucial precursor to elucidating the feasibility, management approaches, and potential consequences of such endeavors.

APPENDICES

SUPPLEMENTARY MATERIAL FOR CHAPTER 2

Table S2.1 Habitat designation of each morphospecies. Based on relative abundances across substrate types (Table S5), morphospecies were assigned to: Bo: bone; Wo: wood; Co: control; GE: generalized enrichment (bone and wood); HS-Ge: hard substrates, generalists across all substrate types; and Bac(Ra): rare morphospecies (with < 5 individuals across all locations) considered background taxa. Based on information presented in the literature, morphospecies were assigned to the following habitat types: Wha: whale fall, Wo: wood fall, Ke, kelp fall, Ma: non-cetacean mammal bone, GE: organic enrichment, Ve: hydrothermal vent, Se: cold seep, MH: methane hydrate, Ba: background, ss: soft sediment, and n/a (itr): habitat information not available, insufficient taxonomic resolution. Habitats of morphospecies based on literature searches are not always exhaustive but highlight occurrences at organic falls and other reducing habitat types. (CRS) indicates habitat information provided by collections of Craig R. Smith. Final habitat designation was determined from both relative abundances and literature/archived information, and justifications are provided under comments. Final habitat designations are as follows: Bac: Background, HS-Ge: Hard substrate (generalist), HS-NE: Hard substrate (non-enrichment), Ind: Indeterminate, GE: Organic enrichment, Wha: Whale bone, Wo: Wood.

Morphospecies	**Habitat**			**Comments**
	Relative abundance	Lit./Archived data.	Final	
ANNELIDA				
POLYCHAETA				
ACROCIRRIDAE				
Acrocirrid sp. 3	Bac(Ra)	n/a (itr)	Bac	Benthic forms associated with sediments (Jumars et al. 2015).
Flabelligella cf. *macrochaeta*	Bac(Ra)	Ba, Wo	Bac	Genus widely occurring in deep-sea sediments (Blake & Narayanaswamy 2004). Previously found on wood falls (CRS).
AMPHARETIDAE				
Anobothrus apaleatus Reuscher, Fiege & Wehe, 2009	HS-Ge	Cs, Ve, Wha	HS-Ge	Described from Cascadia Margin cold seeps and from an inactive hydrothermal vent on the Pacific-Atlantic ridge (Reuscher 2009). Reported from southern California whale falls (CRS).
Ampharetid sp. 21	Co	n/a (itr)	Bac	Speciose family, mostly associated to sediments (Jumars et al. 2015). Some species associated with reducing habitats (Eilersten et al. 2017, Quieros et al. 2017). Most abundant on control substrates.
Ampharetid sp. 22	Wo	n/a (itr)	Wo	Abundant in wood interior.
Ampharetid sp. 23	Bac(Ra)	n/a (itr)	Bac	Speciose family, mostly associated to sediments (Jumars et al. 2015). Some species associated with reducing habitats (Eilersten et al. 2017, Quieros et al. 2017).

Table S2.1 (Continued) Habitat designation of each morphospecies.

Morphospecies	**Habitat**			**Comments**
	Relative abundance	Lit./Archived data.	Final	
Decemunciger sp.	Wo	Wo	Wo	Abundant in wood interior. Only described species is found in sediments surrounding decaying wood (Eilersten et al. 2017). Found at wood falls (CRS).
Sosane wahrbergi (Eliason, 1955)	Bac(Ra)	Ba(ss)	Bac	Described from soft sediments (Eliason, 1955)
Sosane sp. A	Bac(Ra)	Ba, Wha	Bac	Speciose genus from soft sediment habitats (Read & Fauchald 2021a). Found on whale bones (CRS).
CAPITELLIDAE				
Capitella cf. *capitata*	GE	GE	GE	Genus frequently associated with organic enrichment in the deep sea (e.g., Grassle & Morse-Porteous 1987). Previously found at wood falls (CRS).
Capitella cf. *ovincola*	Bo	GE	GE	Genus frequently associated with organic enrichment in the deep sea (e.g., Grassle & Morse-Porteous 1987)
Capitellid sp. 10	HS-Ge	n/a (itr)	HS-Ge	Family associated to organic enrichment but also present in background multicores (Table S6). Occurs at all substrate types.
Capitellid sp. 13	Bac(Ra)	n/a (itr)	Bac	Family associated to organic enrichment but also present in background multicores (Table S6). Rare (doubleton) suggests background.
CIRRATULIDAE				
Chaetozone sp. A	Bac(Ra)	Ba, Wha	Bac	Genus includes species that are most dominant at bathyal depths off northern California (Blake 2006). Previously found in association to whale bones (CRS).
Chaetozone sp. B	Bac(Ra)	Ba, Ke	Bac	Genus includes species that are most dominant at bathyal depths off northern California (Blake 2006). Previously found in association to kelp falls (CRS)
Cirratulid sp. 14	Bac(Ra)	Ba(ss)	Bac	A dominant family in continental-slope soft-sediments off northern California (Blake 2006) and in background multicores (Table S6).
CTENODRILLIDAE				
Ctenodrillid sp. 2	Bac(Ra)	n/a (itr)	Bac	taxon inquirendum (Read & Fauchald 2021b) but may be associated to organically enriched substrata (Jumars et al. 2015). Rare (doubleton) suggests background.

Table S2.1 (Continued) Habitat designation of each morphospecies.

Morphospecies	**Habitat**			**Comments**
	Relative abundance	Lit./Archived data.	Final	
DORVILLEIDAE				
Dorvilleid sp. 15	GE	n/a (itr), Wha	GE	Most abundant on organic substrates. Previously found inside whale bone (CRS).
Dorvilleid sp. 32	Bac(Ra)	n/a (itr)	Ind	Speciose family often associated to enrichment but also present in background multicores (Table S6). Here found on wood and previously found at wood falls (CRS). Indeterminate because there is only one individual here.
Dorvilleid sp. 39	Bac(Ra)	n/a (itr), Wo, Bo	GE	Speciose family often associated to enrichment but also present in background multicores (Table S6). Previously found in association with wood and bone (CRS).
Dorvilleid sp. 54	HS-Ge	n/a (itr)	HS-Ge	Speciose family often associated to enrichment but also present in background multicores (Table S6). Occurs at all substrate types.
Dorvilleid sp. 55	Wo	n/a (itr)	Wo	High abundance on wood substrates.
Dorvilleid sp. 56	Bac(Ra)	n/a (itr)	Ind	Speciose family often associated to enrichment but also present in background multicores (Table S5). Rarity suggests background is likely.
Dorvilleid sp. 58	Bac(Ra)	n/a (itr)	Ind	Speciose family often associated to enrichment but also present in background multicores (Table S5). Rarity suggests background is likely.
Ophryotrocha batillus	GE	Wha, Wo	GE	Described from whale bones and wood (Wiklund et al. 2012).
Wiklund et al., 2012	GE	Wha, Wo	GE	Described from whale bones and wood (Wiklund et al. 2012).
Ophryotrocha craigsmithi	Bac(Ra)	Wha	Wha	Described from whale bone (Wiklund et al. 2009).
Wiklund, Glover & Dahlgren, 2009	Bac(Ra)	Wha	Wha	Described from whale bone (Wiklund et al. 2009).
Ophryotrocha langstrumpae	Wo	Wha, Wo	Wo	Described from whale bones and wood (Wiklund et al. 2012).
Wiklund et al., 2012	Wo	Wha, Wo	Wo	Described from whale bones and wood (Wiklund et al. 2012).
Ophryotrocha longicollaris	Bac(Ra)	Wha	GE	Described from whale bones (Wiklund et al. 2012). Here also found on wood.
Wiklund et al., 2012	Bac(Ra)	Wha	GE	Described from whale bones (Wiklund et al. 2012). Here also found on wood.
Ophryotrocha magnadentata	GE	Wha, Wo	GE	Described from whale bones and wood (Wiklund et al. 2012).

Table S2.1 (Continued) Habitat designation of each morphospecies.

Morphospecies	**Habitat**			**Comments**
	Relative abundance	Lit./Archived data.	Final	
Wiklund et al., 2012				
Parophryotrocha sp. A	Bo	n/a (itr)	Wha	Habitat information of genus is scarce/inaccessible, but one species is described from background deep-sea sediments (Hilbig & Blake 1991). Highly abundant in bone interior in this study.
FLABELLIGERIDAE				
Flabelligerid sp. 7	Bac(Ra)	n/a (itr)	Bac	Speciose family, infaunal in sediments or hard substrates, sometimes commensal on echinoderms (Jumars et al. 2015). Rarity suggests background is likely.
HESIONIDAE				
Gyptis sp. A	HS-Ge	Ba, Wha	HS-Ge	Speciose genus, although some species described from whale carcass (Summers et al. 2015). Found on whale bones and kelp falls (CRS).
Hesiocaeca sp. A	GE	Wha, Ve, Se, MH	GE	Taxon inquirendum, closely related to *Sirsoe* with conspecifics from reducing habitats (see *Sirsoe* cf. *hessleri*). Previously found in association with whale bones (CRS).
Hesiopina cf. *aurantiaca*	Bac(Ra)	Ba, Ve	Bac	*Hesiopina aurantiaca* is widely distributed and *H. vestimentidera* is associated with east Pacific hydrothermal vents (Pleigel 2004).
Sirsoe cf. *hessleri*	Wo	Wha, Ve, Se, MH	GE	Congenerics described from whale falls (Summers et al. 2015), hydrothermal vents (Blake 1991) methane hydrates (Desbruyères & Toulmond 1998), and cold seeps (Rouse et al. 2018).
Vrijenhoekia balaenophila Pleijel, Rouse, Ruta, Wiklund & Nygren, 2008	Bo	Wha, Wo,	Wha	Described from whale bones (Pleigel et al. 2008) but also associated with wood (Saeedi et al. 2019, this study). Previously found in association with bones (CRS).
LUMBRINERIDAE				
Lumbrinerid sp. 1	Bac(Ra)	n/a (itr)	Bac	Highly speciose family, most of which are infaunal (Jumars et al. 2015). Family has been reported at whale falls (Fujiwara et al. 2007) and associated with sunken wood (Samadi et al. 2010). Rarity suggests background is likely.

Table S2.1 (Continued) Habitat designation of each morphospecies.

Morphospecies	Habitat			Comments
	Relative abundance	Lit./Archived data.	Final	
MALDANIDAE				
Maldane sp. A	Bac(Ra)	Ba(ss)	Bac	Specoise genus, congenerics reported dominating soft sediments (e.g., Kendall 1996, Holte & Gulliksen 1998, Åström et al. 2016).
NEREIDIDAE				
Nereidid sp. 6	Bo	n/a (itr)	Ind	Highly speciose family from a variety of habitats (Jumars et al. 2015). More abundant on bone, but not very abundant overall.
OPHELIIDAE				
Opheliid sp. 4	Bac(Ra)	n/a (itr)	Bac	Speciose family mostly found in sandy sediments (Parapar et al. 2021) but also found associated with wood (e.g., Harbour et al. 2021, McClain et al. 2016) and whale falls (Fujiwara et al. 2007). Rarity suggests background is likely.
Opheliid sp. 5	Bac(Ra)	n/a (itr)	Bac	Speciose family mostly found in sandy sediments (Parapar et al. 2021) but also found associated with wood (e.g., Harbour et al. 2021, McClain et al. 2016) and whale falls (Fujiwara et al. 2007). Rarity suggests background is likely.
Opheliid sp. 6	Bac(Ra)	n/a (itr)	Bac	Speciose family mostly found in sandy sediments (Parapar et al. 2021) but also found associated with wood (e.g., Harbour et al. 2021, McClain et al. 2016) and whale falls (Fujiwara et al. 2007). Rarity suggests background is likely.
PARAONIDAE				
Aricidea cf. *rubra*	Bac(Ra)	Ba, Wha, Wo	Bac	Highly speciose genus. Previously found associated with bones and in sediments 2 m from wood fall (CRS).
Paraonides sp. A	Bac(Ra)	Ba(ss)	Bac	Congenerics described from background deep-sea sediments (e.g., Hartman & Fauchald 1971). Family commonly dominates deep-sea sediment communities (Jumars et al. 2015, Table S6).
PECTINARIIDAE				
Pectinariid sp. 1	Bac(Ra)	n/a (itr)	Bac	Family inhabits sediments (Jumars et al. 2015). Rarity suggests background is likely.

Table S2.1 (Continued) Habitat designation of each morphospecies.

Morphospecies	**Habitat**			**Comments**
	Relative abundance	Lit./Archived data.	Final	
PHOLOIDAE				
Pholoid sp. 1	Bac(Ra)	n/a (itr)	Bac	Family inhabits sediments (Jumars et al. 2015).
PHYLLODOCIDAE				
Sige brunnea (Fauchald, 1972)	Bac(Ra)	Ba(ss)	Bac	Described from fine, silty sediments (Blake 1992, Fauchald 1972). Found in association with whale bone and in sediments surrounding 5 yr. wood fall (CRS).
POLYNOIDAE				
Harmothoe cf. *fragilis*	HS-Ge	Ba, Wo, Wha, Ke	HS-Ge	Most abundant on control substrates. Speciose genus, three species described from organic falls (Pettibone 1985, 1993). Previously found in association with kelp and whale bones (CRS).
Peinaleopolynoe santacatalina Pettibone, 1993	GE	Wha, Ke	GE	Described from whale bone (Pettibone 1993), but more abundant on wood in this study. Previously found in association with kelp and whale bones (CRS).
SCALIBREGMATIDAE				
Scalibregmatid sp. 2	Bac(Ra)	n/a (itr)	Bac	Family found in soft sediments, with at least one occurring at hydrothermal vents (Jumars et al. 2015, Parapar et al. 2011). Rarity suggests background is likely.
SERPULIDAE				
Serpulid sp. 1	Bac(Ra)	n/a (itr)	Bac	Highly speciose family, generally attached to hard substrata (Jumars et al. 2015). Rarity suggests background is likely.
SIBOGLINIDAE				
Osedax rubiplumus Rouse, Goffredi & Vrijenhoek, 2004	Bo	Wha	Wha	Species is bone substrate specialist (Rouse et al. 2004).
Osedax sp. B	Bo	Wha	Wha	Species is bone substrate specialist (Rouse et al. 2004).
SPHAERODORIDAE				
Sphaerodorid sp. 1	Bac(Ra)	n/a (itr)	Bac	Most species found in sediments, some species reported in sediments surrounding whale falls (Shimabukuro et al. 2017), seeps (Levin & Mendoza 2007) and hydrothermal vents (Aguado & Rouse 2006). Rarity suggests background is likely.

Table S2.1 (Continued) Habitat designation of each morphospecies.

Morphospecies	**Habitat**			**Comments**
	Relative abundance	Lit./Archived data.	Final	
SPIONIDAE				
Aurospio cf. *dibranchiata*	Bac(Ra)	Ba(ss)	Bac	Common background deep-sea polychaete genus (Guggolz et al. 2020).
Spionid sp. 13	Bac(Ra)	Ba(ss)	Bac	Highly speciose family from a variety of habitats (Jumars et al. 2015) including whale falls (e.g. Lundsten et al. 2010a, Fujiwara et al. 2007), hydrothermal vents (e.g. Blake & Mackiolek 1992) and seeps (e.g. Blake & Ramey-Balci 2020). Dominant family in background multicores (Table S6).
Laonice sp. A	HS-Ge	Ba, Wha, Ke, Wo	Bac	Common background deep-sea polychaete genus. Previously found at whale, kelp, and wood falls (CRS).
Prionospio cf. *ehlersi*	Bac(Ra)	Ba(ss)	Bac	Common background deep-sea polychaete genus (Guggolz et al. 2020). Previously found in sediments surrounding organic falls (CRS).
Prionospio sp. A	Bac(Ra)	Ba(ss)	Bac	Common background deep-sea polychaete genus. Previously found in association with whale bones (CRS).
SYLLIDAE				
Syllid sp. 13	Bac(Ra)	n/a (itr)	Bac	Highly speciose family found in all benthic habitats (Jumars et al. 2015), mostly found on hard substrata. Rarity suggests background is likely.
Proceraea sp. A	Bac(Ra)	n/a (itr)	Bac	Speciose genus from a variety of habitat types (Nygren 2004). Subfamily and genus often specialised carnivores of sedentary invertebrates (Martin et al. 2017). Rarity suggests background is likely.
Sphaerosyllis sp. A	HS-Ge	Wha, Se, Ve, Ba	HS-Ge	Highly speciose genus from a range of habitat types, including NE Pacific hydrothermal vents (Blake & Hilgib 1990) and surrounding seeps (Bernardino et al. 2010b). Here found across all substrate types and previously found in association with whale bones (CRS).
TEREBELLIDAE				
Terrebellid sp. 8	Bac(Ra)	n/a (itr)	Bac	Highly speciose family found in a variety of habitats (Jumars et al. 2015). Rarity suggests background is likely.
Neoamphitrite sp. A	Bac(Ra)	Ba(ss), Ve	Bac	Genus includes 13 species of tube-dwelling polychaetes from soft-sediment habitats, one species described from sediments surrounding hydrothermal vent (Reuscher et al. 2012). Previously found in association with whale bones (CRS).
CLITELLATA				
HIRUDINEA				
Hirudinid sp. A	GE	n/a (itr)	HS-Ge	Was also present on lander floats, with egg cases.

Table S2.1 (Continued) Habitat designation of each morphospecies.

Morphospecies	**Habitat**			**Comments**
	Relative abundance	Lit./Archived data.	Final	
ARTHROPODA				
AMPHIPODA				
Amphipod sp. G	Bo	n/a (itr)	Ind	More abundant on bone, but not very abundant overall. Insufficient taxonomic information.
Amphipod sp. H	HS-Ge	n/a (itr)	HS-Ge	Insufficient taxonomic resolution, occurs across all substrate types.
Amphipod sp. J	GE	n/a (itr)	GE	Occurs in high abundances on bone and wood substrates.
Amphipod sp. K	HS-Ge	n/a (itr)	HS-Ge	Insufficient taxonomic resolution, occurs across all substrate types.
Bathyceradocus sp. A	Wo	Wo	Wo	Genus exclusively associated to wood (Jażdżewska & Ziemkiewicz 2019).
Euonyx sp. A	Bac(Ra)	Ba	Bac	Genus is ectoparasitic on echinoids (Lowry & Kilgallen 2014).
Isaeid sp. A	HS-Ge	n/a (itr)	HS-Ge	Speciose family from a variety of habitats (Horton et al. 2021a). Occurs at all substrate types.
Lysianassid sp. A	GE	GE	GE	Common deep-sea scavenging family (e.g., Smith 1985).
Oedicerotid sp. A	Bac(Ra)	n/a (itr)	Bac	Speciose family from a variety of habitats (Horton et al. 2021b). Rarity suggests background is likely.
Schisturella sp. A	HS-Ge	Wo, Ve, Ba	HS-Ge	Currently seven species recognised from general or undefined deep-sea habitats (Kilgallen & Lowry 2014) but including one species associated with wood near hydrothermal vents on the Juan de Fuca ridge (Larsen 2007). Occurs at all substrate types.
Sebid sp. A	GE	Wo, Ma, Ve	GE	Species have been associated with wood falls (e.g., Larsen 2007, Amon et al. 2017), cow carcasses (Hilário et al. 2015) and hydrothermal vents (e.g. Wang et al. 2019).
CARIDEA				
Caridean sp. A	Bac(Ra)	Ba	Bac	Common, highly mobile deep-sea taxa.
CUMACEA				
Cumacean sp. A	Bac(Ra)	n/a (itr)	Bac	Insufficient taxonomic information. Rarity suggests background is likely.
DECAPODA				
Chionocetes sp. A	Bac(Ra)	Ba, Wha	Bac	Genus known as scavengers and predators in the deep sea, also previously associated with whale falls (e.g., Lundsten et al. 2010a)
Paralomis sp. A	Bac(Ra)	Ba, Wha	Bac	Genus known as scavengers in the deep sea, also previously associated with whale falls (e.g., Williams et al. 2000).

Table S2.1 (Continued) Habitat designation of each morphospecies.

Morphospecies	**Habitat**			**Comments**
	Relative abundance	Lit./Archived data.	Final	
GALATHEOIDEA				
Galatheid sp. E	Bac(Ra)	n/a (itr)	Bac	Occurs in all marine habitat types. Abundant and diverse, especially in the Pacific Ocean (Macphearson et al. 2010). Rarity suggests background is likely.
Munidopsis albatrossae W.E. Pequegnat & L.H. Pequegnat, 1973	Bo	Ba(ss), Wha, Ma	Wha	Widely distributed soft-bottom species (Pequegnat & Pequegnat 1973, García Raso et al. 2008), also found on cow bones (Dong et al. 2019) and whale bones (Lundsten et al. 2010a).
Munidopsis cascadia Ambler, 1980	Bo	Ba, Wha	Wha	Described from regional background fauna (Ambler 1980) but also reported in high densities at California whale skeletons (Williams et al. 2000).
Munidopsis cf. *antonii*	GE	Ba, Wo, Wha	GE	Genus known from background, but frequently associated with wood and whale falls (e.g., Williams et al. 2000, Smith & Baco 2003, Kemp et al. 2006, Jones & Macphearson 2007, Hoyoux et al. 2012, Macphearson et al. 2014, Sumida et al. 2016, Dong et al. 2019).
Munidopsis cf. *lignaria*	GE	Ba, Wo, Wha	GE	Genus known from background, but frequently associated with wood and whale falls (e.g., Williams et al. 2000, Smith & Baco 2003, Kemp et al. 2006, Jones & Macphearson 2007, Hoyoux et al. 2012, Macphearson et al. 2014, Sumida et al. 2016, Dong et al. 2019).
ISOPODA				
Eurycopinae sp. A	HS-Ge	n/a (itr)	HS-Ge	Speciose subfamily from a variety of habitats (Bokyo et al. 2008b).
Eurycopinae sp. B	Bac(Ra)	n/a (itr)	Bac	Speciose subfamily from a variety of habitats (Bokyo et al. 2008b). Rarity suggests background is likely.
Ilyarachna profunda Shultz, 1966	GE	Ba(ss), Wha, Wo	GE	Species described from deep-sea soft sediment habitat (Shultz 1966) but has been reported in high densities at whale falls (Smith & Baco 2003), surrounding wood falls (Bernardino et al. 2010a), and in association with tube worms (C. R. Smith, unpubl. data).
Ischnomesid sp. A	Bac(Ra)	n/a (itr)	Bac	Speciose family from a variety of habitats (Bober et al. 2019). Rarity suggests background is likely.
Isopod sp. H	Bac(Ra)	n/a (itr)	Bac	Insufficient taxonomic resolution. Rarity suggests background is likely.
Isopod sp. J	Bac(Ra)	n/a (itr)	Bac	Insufficient taxonomic resolution. Rarity suggests background is likely.
Isopod sp. K	Bac(Ra)	Wha, Wo	Bac	Insufficient taxonomic resolution. Rarity suggests background is likely.
Janirid sp.	GE	n/a (itr) Wha, Wo	GE	Speciose family from a variety of habitats (Bokyo et al. 2008a). Species of the family Janiridae have been reported in high abundances at shallow-water whale falls (Linse et al. 2014) and associated to decaying plant material in marine environments (e.g., Wolff 1979).

Table S2.1 (Continued) Habitat designation of each morphospecies.

Morphospecies	**Habitat**			**Comments**
	Relative abundance	Lit./Archived data.	Final	
MYSIDA				
Mysid sp. A	Bac(Ra)	n/a (itr)	Bac	Insufficient taxonomic resolution. Rarity suggests background is likely.
NEBALIIDAE				
Nebalia sp. A	HS-Ge	Ba, Ve	HS-Ge	Only two deep-sea species known, one from hydrothermal vent (Hirata et al. 2019) and the other from general deep-sea habitat (Haney et al. 2001).
Nebalia sp. B	Bac(Ra)	Ba, Ve	Bac	Only two deep-sea species known, one from hydrothermal vent (Hirata et al. 2019) and the other from general deep-sea habitat (Haney et al. 2001).
TANAIDACEA				
Tanaid sp. A	Co	n/a (itr)	HS-NE	Insufficient taxonomic resolution. Most abundant on control substrates.
Tanaid sp. B	Bac(Ra)	n/a (itr)	Bac	Insufficient taxonomic resolution. Rarity suggests background is likely.
Tanaid sp. C	Bac(Ra)	n/a (itr)	Bac	Insufficient taxonomic resolution. Rarity suggests background is likely.
Tanaid sp. D	Bac(Ra)	n/a (itr)	Bac	Insufficient taxonomic resolution. Rarity suggests background is likely.
Tanaid sp. E	Bac(Ra)	n/a (itr)	Bac	Insufficient taxonomic resolution. Rarity suggests background is likely.
Tanaid sp. F	Bac(Ra)	n/a (itr)	Bac	Insufficient taxonomic resolution. Rarity suggests background is likely.
PYCNOGONIDA				
Pycnogonid sp. A	Co	n/a (itr)	HS-NE	Insufficient taxonomic resolution. Occurs mostly on control substrates.
CHORDATA				
ACTINOPTERYGII				
Zoarcid sp. A	Bac(Ra)	Ba	Bac	Common in deep-sea and scavenging fish communities (Pearcy et al. 1982).
CNIDARIA				
ACTINARIA				
Actinarian sp.	HS-Ge	n/a (itr)	HS-Ge	Insufficient taxonomic resolution, occurs across all substrate types.
ECHINODERMATA				
GORGONOCEPHALA				
Gorgonocephalan sp. A	Bac(Ra)	n/a (itr)	Bac	Insufficient taxonomic resolution. Rarity suggests background is likely.

Table S2.1 (Continued) Habitat designation of each morphospecies.

Morphospecies	**Habitat**			**Comments**
	Relative abundance	Lit./Archived data.	Final	
OPHIUROIDEA				
Ophiophthalmus normani (Lyman 1879)	HS-Ge	Ba, GE	Bac	Common background species (e.g. Summers & Nybakken 2000), also associated with organic enrichment (e.g. macroalgal falls: Smith & Hamilton 1983, jellyfish: Shepard & Marshall 1975, dead fish: Smith 1985).
Ophiuroid sp. B	Bac(Ra)	n/a (itr)	Bac	Insufficient taxonomic resolution. Rarity suggests background is likely.
Ophiuroid sp. C	Bac(Ra)	n/a (itr)	Bac	Insufficient taxonomic resolution. Rarity suggests background is likely.
MOLLUSCA				
APLACOPHORA				
Aplacophoran sp. A	GE	n/a (itr)	GE	Insufficient taxonomic information. Occurs only on organic-rich substrates.
BIVALVIA				
Bathypecten sp. A	HS-Ge	Ba, GE	Ind	Genus has two species, including one from hydrothermal vent (Schein-Fatton 1985). Low overall abundances.
Bivalve sp. B	HS-Ge	n/a (itr)	HS-Ge	Insufficient taxonomic resolution, occurs across all substrate types.
Bivalve sp. E	HS-Ge	n/a (itr)	HS-Ge	Insufficient taxonomic resolution, occurs across all substrate types.
Bivalve sp. F	GE	n/a (itr)	Ind	More common on organic-rich substrates, although low abundances overall. Insufficient taxonomic information.
Bivalve sp. G	Bo	n/a (itr)	Wha	Most abundant on whale bones.
Bivalve sp. H	Bac(Ra)	n/a (itr)	Bac	Insufficient taxonomic resolution. Rarity suggests background is likely.
Bivalve sp. I	Bac(Ra)	n/a (itr)	Bac	Insufficient taxonomic resolution. Rarity suggests background is likely.
Idas washingtonius (Bernard, 1978)	GE	Wha, Wo, Se, Ve	GE	Thousands of individuals found at Pacific whale skeletons (Smith et al. 1989, Bennet et al. 1994). Also found in association with wood (Dell 1987, Smith & Baco 2003) and hydrothermal vents and seeps (Bennet et al. 1994).
Xylonora corona (Voight, 2007)	Wo	Wo	Wo	Wood substrate specialist (Voight 2007).
Xylophaga microchira (Voight 2007)	Bac(Ra)	Wo	Wo	Wood substrate specialist (Voight 2007).
Xylonora muraokai (Turner 2002)	Wo	Wo	Wo	Wood substrate specialist (Turner 2002).
Xylophaga oregona Voight,2007	Wo	Wo	Wo	Wood substrate specialist (Voight 2007).
Xylonora zierenbergi (Voight, 2007)	Wo	Wo	Wo	Wood substrate specialist (Voight 2007).
Xylopholas crooki Voight, 2007	Wo	Wo	Wo	Wood substrate specialist (Voight 2007).

Table S2.1 (Continued) Habitat designation of each morphospecies.

Morphospecies	**Habitat**			**Comments**
	Relative abundance	Lit./Archived data.	Final	
GASTROPODA				
cf *Laeviphitus* sp.	Bo	Ve, Se	Wha	Putative genus associated with vents (e.g. Mullineaux et al. 2005) a brine pool (Vestheim & Kaartvedt 2016) and cold seeps (Ritt et al. 2010).
Dillwynella sp. A	Wo	Wo, Wha	Wo	Majority of species within this genus are described from wood-falls (e.g., Kunze et al. 2011) but also reported at whale falls (Fujiwara et al. 2007). Highly abundant on wood at S-2800.
Eulimid sp. A	Bac(Ra)	Parasitic	Bac	Family exclusively parasitic to echinoderms (Warén 1983).
Gastropod sp. H	Bac(Ra)	n/a (itr)	Bac	Insufficient taxonomic resolution. Rarity suggests background is likely.
Gastropod sp. I	Bac(Ra)	n/a (itr)	Bac	Insufficient taxonomic resolution. Rarity suggests background is likely.
Gastropod sp. J	Bac(Ra)	n/a (itr)	Bac	Insufficient taxonomic resolution. Rarity suggests background is likely.
Gastropod sp. K	Bac(Ra)	n/a (itr)	Bac	Insufficient taxonomic resolution. Rarity suggests background is likely.
Gastropod sp. L	HS-Ge	n/a (itr)	Ind	Insufficient taxonomic resolution and low overall abundances.
Gastropod sp. M	Bac(Ra)	n/a (itr)	Bac	Insufficient taxonomic resolution. Rarity suggests background is likely.
Gastropod sp. N	Bac(Ra)	n/a (itr)	Bac	Insufficient taxonomic resolution. Rarity suggests background is likely.
Hyalogyrina sp. A	Bo	Wo, Se, Wha, Ke	Wha	Congenerics described from wood (Marshall 1988, Warén et al. 1996, Hasegawa 1997), vents, and seeps (Warén & Bouchet 1993, 2001, 2009). Also reported from whale falls (Smith & Baco 2003) and kelp falls (Bernardino et al. 2010a).
Provanna cf. *macleani*	GE	Wha, Ve, Se, Wo	GE	Genus found commonly at hydrothermal vents (e.g., Warén & Bouchet 1986, Linse et al. 2019) and reported from whale falls (Smith & Baco 2003). Also found at fossil seeps, whale falls and wood falls (e.g., Amano & Little 2014, Kiel & Goedert 2006).
LIMPET				
Limpet sp. A	Wo	n/a (itr)	Wo	High abundance on wood substrates.
Limpet sp. B	Bac(Ra)	n/a (itr)	Bac	Insufficient taxonomic resolution. Rarity suggests background is likely.
NUDIBRANCH				
Ziminella abyssa Korshunova, Martynov, Bakken, Evertsen, Fletcher, Mudianta, Saito, Lundin, Schrodl & Picton, 2017	Co	Ba(ss)	Bac	Described from soft-sediment habitats (Korshunova et al. 2017).

Table S2.1 (Continued) Habitat designation of each morphospecies.

Morphospecies	**Habitat**			**Comments**
	Relative abundance	Lit./Archived data.	Final	
OCTOPODIDAE				
Graneledone pacifica Voss & Pearcy, 1990	Bac(Ra)	Ba	Bac	General deep-sea species that broods eggs attached to hard surfaces (Robinson et al. 2014).
NEMERTEA				
Nemertean sp.	GE	n/a (itr)	GE	Insufficient taxonomic resolution. Most abundant on organic-rich substrates.
PLATYHELMINTHES				
Triclad sp. A	Wo	n/a (itr)	Wo	Abundant in wood interior.
Polyclad sp. A	Wo	Wo	Wo	Similar to polyclad flatworms found in association with sunken wood in the Cascadia Basin (Voight 2007, Quiroga et al. 2006).

References cited in Table S2.1

Adams DK, Mullineaux LS (2008) Supply of gastropod larvae to hydrothermal vents reflects transport from local larval sources. Limnol. Oceanogr. 53:1945–1955

Aguado MT, Rouse GW (2006) First record of Sphaerodoridae (Phyllodocida: Annelida) from hydrothermal vents. Zootaxa 1383:1–21

Amano K, Little CT (2014) Miocene abyssochrysoid gastropod *Provanna* from Japanese seep and whale-fall sites. Acta Palaeontol Pol 59:163–172

Ambler JW (1980) Species of *Munidopsis* (Crustacea, Galatheidae) ocurring off Oregon and in adjacent waters. Fish Bull (Wash D C) 78:13–34

Amon DJ, Copley JT, Dahlgren TG, Horton T, Kemp KM, Rogers AD, Glover AG (2017) Observations of fauna attending wood and bone deployments from two seamounts on the Southwest Indian Ridge. Deep Sea Res II 136:122–132

Åström EK, Carroll ML, Ambrose WG, Carroll J (2016) Arctic cold seeps in marine methane hydrate environments: impacts on shelf macrobenthic community structure offshore Svalbard. Mar Ecol Prog Ser 552:1–18

Bennett BA, Smith CR, Glaser B, Maybaum HL (1994) Faunal community structure of a chemoautotrophic assemblage on whale bones in the deep northeast Pacific Ocean. Mar Ecol Prog Ser 108:205–223

Bernard FR (1978) New bivalve Mollusca, subclass Pteriomorpha, from the Northeastern Pacific. Venus 37:61-75

Bernardino AF, Li Y, Smith CR, Halanych KM (2017) Multiple introns in a deep-sea Annelid (*Decemunciger*: Ampharetidae) mitochondrial genome. Sci Rep 7:4295

Bernardino AF, Smith CR (2010) Community structure of infaunal macrobenthos around vestimentiferan thickets at the San Clemente cold seep, NE Pacific. Mar Ecol 31:608–621

Bernardino AF, Stiller J, Baco AR, Altamira I, Sumida PY (2010) Macrofaunal succession in sediments around kelp and wood falls in the deep NE Pacific and community overlap with other reducing habitats. Deep Sea Res I 57:708–723

Blake JA (1991) A new species of *Hesiocaeca* (Polychaeta: Hesionidae) from hydrothermal vents at the Mariana back-arc basin with notes on other polychaetes. Proc Biol Soc Wash 104:175–180

Blake JA (1992) New species and records of Phyllodocidae (Polychaeta) from the continental shelf and slope off California. Proc Biol Soc Wash 105:693–708

Blake JA (2006) New species and records of deep-water Cirratulidae (Polychaeta) from off Northern California. Sci Mar 70:45–57

Blake JA, Hilbig B (1990) Polychaeta from the Vicinity of Deep-sea Hydrothermal Vents in the Eastern Pacific. ll. New Species and Records from the Juan de Fuca and Explorer Ridge Systems. Pac Sci 44:219–253

Blake JA, Maciolek N (1992) Polychaeta from deep-sea hydrothermal vents in the eastern Pacific. III. A new genus and two new species of Spionidae (Polychaeta) from hydrothermal vents at the Guaymas Basin and Juan de Fuca ridge with comments on a related species from the Western North Atlantic. Proc Biol Soc Wash 105:723–732

Blake JA, Narayanaswamy BE (2004) Benthic infaunal communities across the Weddell Sea Basin and South Sandwich Slope, Antarctica. Deep Sea Res II 51:1797–1815

Blake JA, Ramey-Balci PA (2020) A new genus and species of spionid polychaete (Annelida, Spionidae) from a deep-water cold seep site in the Eastern Mediterranean Sea off Turkey. Zoosymposia 19:121–134

Bober J, Brandt A, Frutos I, Schwentner M (2019) Diversity and distribution of Ischnomesidae (Crustacea: Isopoda: Asellota) along the Kuril-Kamchatka Trench – A genetic perspective. Prog Oceanogr 178:102174

Boyko CB, Bruce NL, Hadfield KA, Merrin KL, Ota Y, Poore GCB, Taiti S, Schotte M, Wilson GDS (2008a). World Marine, Freshwater and Terrestrial Isopod Crustaceans database. Janiridae G. O. Sars, 1897. Accessed through: World Register of Marine Species at: http://www.marinespecies.org/aphia.php?p=taxdetails&id=118258

Boyko CB, Bruce NL, Hadfield KA, Merrin KL, Ota Y, Poore GCB, Taiti S, Schotte M, Wilson GDS (2008b). World Marine, Freshwater and Terrestrial Isopod Crustaceans database. Eurycopinae Hansen, 1916. Accessed through: World Register of Marine Species at: http://www.marinespecies.org/aphia.php?p=taxdetails&id=325351

Dell R (1987) Mollusca of the Family Mytilidae (Bivalvia) associated with organic remains from deep water off New Zealand, with revisions of the genera *Adipicola* Dautzenborg, 1927 and Idasola Iredale, 1915. National Museum of New Zealand Records 3:17–36

Desbruyères D, Toulmond A (1998) A new species of hesionid worm, *Hesiocaeca methanicola* sp. nov. (Polychaeta: Hesionidae), living in ice-like methane hydrates in the deep Gulf of Mexico. Cah Biol Mar 39:93–98

Dong D, Xu P, Li X-Z, Wang C (2019) *Munidopsis* species (Crustacea: Decapoda: Munidopsidae) from carcass falls in Weijia Guyot, West Pacific, with recognition of a new species based on integrative taxonomy. PeerJ 7:e8089

Eilertsen MH, Kongsrud JA, Alvestad T, Stiller J, Rouse GW, Rapp HT (2017) Do ampharetids take sedimented steps between vents and seeps? Phylogeny and habitat-use of Ampharetidae (Annelida, Terebelliformia) in chemosynthesis-based ecosystems. BMC Evol Biol 17:222

Eliason A (1955) Neue oder wenig bekannte Schwedische Ampharetiden (Polychaeta). Göteborgs Kungliga vetenskaps- och vitterhets-samhälles handlingar. Sjätte Följden 6:1–17

Fauchald K (1972) Benthic polychaetous annelids from deep water off western Mexico and adjacent areas in the Eastern Pacific Ocean. Allan Hancock Monographs in Marine Biology 7:1–575

Fujiwara Y, Kawato M, Yamamoto T, Yamanaka T, Sato-Okoshi W, Noda C, Tsuchida S, Komai T, Cubelio SS, Sasaki T, Jacobsen K, Kubokawa K, Fujikura K, Maruyama T, Furushima Y, Okoshi K, Miyake H, Miyazaki M, Nogi Y, Yatabe A, Okutani T (2007) Three-year investigations into sperm whale-fall ecosystems in Japan. Mar Ecol 28:219–232

Galkin SV, Goroslavskaya EI (2010) Bottom fauna associated with *Bathymodiolus azoricus* (Mytilidae) mussel beds in the hydrothermal fields of the Mid-Atlantic Ridge. Oceanology (Mosc) 50:51–60

García Raso JE, García Muñoz JE, Manjón-Cabeza ME (2008) First record of *Munidopsis albatrossae* (Crustacea: Decapoda: Galatheidae) from Antarctic waters. Polar Biol 31:1281-1285

Grassle J, Morse-Porteous LS (1987) Macrofaunal colonization of disturbed deep-sea environments and the structure of deep-sea benthic communities. Deep Sea Res I 34:1911–1950

Guggolz T, Meißner K, Schwentner M, Dahlgren TG, Wiklund H, Bonifácio P, Brandt A (2020) High diversity and pan-oceanic distribution of deep-sea polychaetes: *Prionospio* and *Aurospio* (Annelida: Spionidae) in the Atlantic and Pacific Ocean. Org Divers Evol 20:171–187

Haney TA, Hessler RR, Martin JW (2001) *Nebalia schizophthalma*, a new species of leptostracan (malacostraca) from deepwaters off the east coast of the United States. J Crustac Biol 21:192–201

Harbour RP, Smith CR, Simon-Nutbrown C, Cecchetto M, Young E, Coral C, Sweetman AK (2021) Biodiversity, community structure and ecosystem function on kelp and wood falls in the Norwegian deep sea. Mar Ecol Prog Ser 657:73–91

Hartman O, Fauchald K. (1971) Deep-water benthic polychaetous annelids off New England to Bermuda and other North Atlantic Areas. Part II. Allan Hancock Monographs in Marine Biology 6:1-327

Hasegawa K (1997) Sunken wood-associated gastropods collected from Suruga Bay, Pacific side of the Central Honshu, Japan, with descriptions of 12 new species. Nat Sci Mus Monogr 12:59–124

Hilário A, Cunha MR, Génio L, Marçal AR, Ravara A, Rodrigues CF, Wiklund H (2015) First clues on the ecology of whale falls in the deep Atlantic Ocean: results from an experiment using cow carcasses. Mar Ecol 36:82–90

Hilbig B, Blake JA (1991) Dorvilleidae (Annelida: Polychaeta) from the U.S. Atlantic slope and rise. Description of two new genera and 14 new species, with a generic revision of Ophryotrocha. Zool Scripta 20:147–183

Hirata T, Fujiwara Y, Kikuchi T (2019) A new species of *Nebalia* (Crustacea, Leptostraca) from a hydrothermal field in Kagoshima Bay, Japan. ZooKeys 897:1–18

Holte B, Gulliksen B (1998) Common macrofaunal dominant species in the sediments of some north Norwegian and Svalbard glacial fjords. Polar Biol 19:375–382

Horton T, Lowry J, De Broyer, C, Bellan-Santini, D, Coleman CO, Corbari L, Costello MJ, Daneliya M, Dauvin, J-C, Fišer C, Gasca R, Grabowski M, Guerra-García JM, Hendrycks E, Hughes L, Jaume D, Jazdzewski K, Kim Y-H, King R, Krapp-Schickel T, LeCroy S, Lörz A-N, Mamos T, Senna AR, Serejo C, Sket B, Souza-Filho JF, Tandberg AH, Thomas JD, Thurston M, Vader W, Väinölä R, Vonk R, White K, Zeidler W (2021a). World Amphipoda Database. Isaeidae Dana, 1852. Accessed through: World Register of Marine Species at: http://www.marinespecies.org/aphia.php?p=taxdetails&id=101388

Horton T, Lowry J, De Broyer, C, Bellan-Santini, D, Coleman CO, Corbari L, Costello MJ, Daneliya M, Dauvin, J-C, Fišer C, Gasca R, Grabowski M, Guerra-García JM, Hendrycks E, Hughes L, Jaume D, Jazdzewski K, Kim Y-H, King R, Krapp-Schickel T, LeCroy S, Lörz A-N, Mamos T, Senna AR, Serejo C, Sket B, Souza-Filho JF, Tandberg AH, Thomas JD, Thurston M, Vader W, Väinölä R, Vonk R, White K, Zeidler W (2021b). World Amphipoda Database. Oedicerotidae Lilljeborg, 1865. Accessed through: World Register of Marine Species at: http://www.marinespecies.org/aphia.php?p=taxdetails&id=101400

Hoyoux C, Zbinden M, Samadi S, Gaill F, Compère P (2009) Wood-based diet and gut microflora of a galatheid crab associated with Pacific deep-sea wood falls. Mar Biol 156:2421–2439

Jażdżewska AM, Ziemkiewicz A (2019) A new abyssal amphipod species (Crustacea) from sunken wood described using integrative taxonomy. Progr Oceanogr 172:1–13

Jones WJ, Macpherson E (2007) Molecular phylogeny of the east Pacific squat lobsters of the genus *Munidopsis* (Decapoda: Galatheidae) with the descriptions of seven new species. J Crustac Biol 27:477–501

Jumars PA, Dorgan KM, Lindsay SM (2015) Diet of worms emended: an update of polychaete feeding guilds. Ann Rev Mar Sci 7:497–520

Kaartvedt, S (2016) A Deep Sea Community at the Kebrit Brine Pool in the Red Sea. Mar Biodivers 46:59–65

Kemp KM, Jamieson AJ, Bagley PM, McGrath H, Bailey DM, Collins MA, Priede IG (2006) Consumption of large bathyal food fall, a six month study in the NE Atlantic. Mar Ecol Prog Ser 310:65–76

Kendall MA (1996) Are Arctic soft-sediment macrobenthic communities impoverished? Polar Biol 16:393–399

Kiel S, Goedert JL (2006) A wood-fall association from Late Eocene deep-water sediments of Washington State, USA. Palaios 21:548–556

Kiel S, Sami M, Taviani M (2018) A serpulid-Anodontia-dominated methane-seep deposit from the upper Miocene of northern Italy. Acta Palaeontol Pol 63:569–577

Kilgallen NM, Lowry JK (2014) The Tryphosa group (Crustacea: Amphipoda: Lysianassoidea: Lysianassidae: Tryphosinae). Zootaxa 3768:501–545

Korshunova TA, Martynov AV, Bakken T, Evertsen J, Fletcher K, Mudianta IW, Saito H, Lundin K, Schrödl M, Picton B (2017) Polyphyly of the traditional family Flabellinidae affects a major group of Nudibranchia: Aeolidacean taxonomic reassessment with descriptions of several new families, genera, and species (Mollusca, Gastropoda). ZooKeys 717:1–139

Kunze T (2011) *Dillwynella voightae* new species, a new skeneimorph gastropod (Turbinidae) from the western Atlantic and a new record of *Dillwynella modesta* (Dall, 1889). Nautilus 125:36–40

Larsen KI (2007) Amphipoda (Crustacea; Peracarida) from the Hydrothermal vent system of the Juan De Fuca Ridge, Escabana trough and Gorda ridge, Northeast Pacific. Part I. Lysianassidae and Sebidae. Zootaxa 1445:1–26

Levin LA, Mendoza GF (2007) Community structure and nutrition of deep methane-seep macrobenthos from the North Pacific (Aleutian) margin and the Gulf of Mexico (Florida escarpment). Mar Ecol 28:131–151

Linse K, Jackson JA, Malyutina MV, Brandt A (2014) Shallow-water northern hemisphere *Jaera* (Crustacea, Isopoda, Janiridae) found on whale bones in the Southern Ocean deep sea: ecology and description of *Jaera tyleri* sp. nov. PloS one 9:e93018

Linse K, Nye V, Copley JT, Chen C (2019) On the systematics and ecology of two new species of *Provanna* (Gastropoda: Provannidae) from deep-sea hydrothermal vents in the Caribbean Sea and Southern Ocean. J Mollus Stud 85:425–438

Lowry JK, Kilgallen NM (2014) A generic review of the lysianassoid family Uristidae and descriptions of new taxa from Australian waters (Crustacea, Amphipoda, Uristidae). Zootaxa 3867:1–92

Lundsten L, Schlining KL, Frasier K, Johnson SB, Kuhnz LA, Harvey JB, Clague G, Vrijenhoek RC (2010a) Time-series analysis of six whale-fall communities in Monterey Canyon, California, USA. Deep Sea Res I 57:1573–1584

Lyman T (1879) Ophiuridae and Astrophytidae of the “Challenger” expedition. Part II. Bulletin of the Museum of Comparative Zoology at Harvard College, Cambridge, Mass. 6:17-83

Macpherson E, Amon D, Clark PF (2014) A new species of *Munidopsis* from a seamount of the Southwest Indian Ocean Ridge (Decapoda: Munidopsidae). Zootaxa 3753:291–296

Marshall BA (1988) Skeneidae, Vitrinellidae and Orbitestellidae (Mollusca: Gastropoda) associated with biogenic substrata from bathyal depths off New Zealand and New South Wales. J Nat Hist 22:949–1004

Martin D, Nygren A, Cruz-Rivera E (2017) *Proceraea exoryxae* sp. nov. (Annelida, Syllidae, Autolytinae), the first known polychaete miner tunneling into the tunic of an ascidian. PeerJ 5:e3374

McClain CR, Barry JP, Eernisse. D, Horton T, Judge J, Kakui K, Mah C, Warén A (2016) Multiple processes generate productivity—diversity relationships in experimental wood-fall communities. Ecology 97:886–898

McClain CR, Barry JP, Webb TJ (2018) Increased energy differentially increases richness and abundance of optimal body sizes in deep-sea wood falls. Ecology 99:184–195

Mullineaux LS, Mills SW, Sweetman AK, Beaudreau AH, Metaxas A, Hunt HL (2005) Vertical, lateral and temporal structure in larval distributions at hydrothermal vents. Mar Ecol Prog Ser 293:1–16

Nishimoto A, Mito S, Shirayama Y (2009) Organic carbon and nitrogen source of sunken wood communities on continental shelves around Japan inferred from stable isotope ratios. Deep Sea Res II 56:1683–1688

Nygren A (2004) Revision of Autolytinae (Syllidae: Polychaeta). Zootaxa 680:1–314

Ockelmann KW, Dinesen GE (2011) Life on wood – the carnivorous deep-sea mussel *Idas argenteus* (Bathymodiolinae, Mytilidae, Bivalvia). Mar Biol Res 7:71–84

Okutani T (2000) Marine mollusks in Japan. Toaki University Press

Parapar J, Gambi MC, Rouse GW. 2011. A revision of the deep-sea genus *Axiokebuita* Pocklington and Fournier, 1987 (Annelida: Scalibregmatidae). Ital J Zool 78:148–162

Pearcy WG, Stein DL, Carney RS (1982) The deep-sea benthic fish fauna of the Northeastern Pacific Ocean on Cascadia and Tufts abyssal plains and adjoining continental slopes. Biological Oceanography 1:375–428

Pequegnat WE, Pequegnat LH (1973) *Munidopsis albatrossae,* a new species of deep-sea Galatheidae (Decapoda, Anomura) from the eastern Pacific Ocean. Crustaceana 24:163–168

Pettibone MA (1985) New genera and species of deep-sea Macellicephalinae and Harmothoinae (Polychaeta: Polynoidae) from the hydrothermal rift areas off the Galapagos and western Mexico at 21°N and from Santa Catalina Channel. Proc Biol Soc Wash 98:740–757

Pettibone MA (1993) Polynoid polychaetes associated with a whale skeleton in the bathyal Santa Catalina basin. Proc Biol Soc Wash 106:678–688

Pleijel F (2004) A revision of *Hesiospina* (Psamathini, Hesionidae, Polychaeta). J Nat Hist 38:2547–66

Pleijel F, Rouse GW, Ruta C, Wiklund H, Nygren A (2008) *Vrijenhoekia balaenophila*, a new hesionid polychaete from a whale fall off California. Zool J Linn Soc 152:625–634

Queirós JP, Ravara A, Eilertsen MH, Kongsrud JA, Hilário A (2017) *Paramytha ossicola* sp. nov. (Polychaeta, Ampharetidae) from mammal bones: Reproductive biology and population structure. Deep Sea Res II 137:349–358

Quiroga SY, Bolaños MD, Litvatis MK (2006) First description of deep-sea polyclad flatworms from the North Pacific: *Anocellidus* n. gen. *profundus* n. sp. (Anocellidae, n. fam.) and *Oligocladus voightae* n. sp. (Euryleptidae). Zootaxa 1317:1–19

Read G, Fauchald K (2021a). World Polychaeta Database. *Sosane* Malmgren, 1866. Accessed through: World Register of Marine Species at: http://www.marinespecies.org/aphia.php?p=taxdetails&id=129179 on 2021-06-2

Read G, Fauchald K (2021b) World Polychaeta Database. Ctenodrilidae Kennel, 1882. Accessed through: World Register of Marine Species at: http://www.marinespecies.org/aphia.php?p=taxdetails&id=905 on 2021-06-28

Reuscher M, Fiege D, Wehe T (2009) Four new species of Ampharetidae (Annelida: Polychaeta) from Pacific hot vents and cold seeps, with a key and synoptic table of characters for all genera. Zootaxa 219:1–40

Reuscher M, Fiege D, Wehe T (2012) Terebellomorph polychaetes from hydrothermal vents and cold seeps with the description of two new species of Terebellidae (Annelida: Polychaeta) representing the first records of the family from deep-sea vents. J Mar Biol Assoc UK 92:997–1012

Ritt B, Sarrazin J, Caprais J-C, Noël P, Gauthier O, Pierre C, Henry P, Desbruyères D (2010) First insights into the structure and environmental setting of cold-seep communities in the Marmara Sea. Deep Sea Res I 57:1120–1136

Robison B, Seibel B, Drazen J (2014) Deep-sea octopus (*Graneledone boreopacifica*) conducts the longest-known egg-brooding period of any animal. PloS one 9:e103437

Rouse GW, Carvajal JI, Pleijel F (2018) Phylogeny of Hesionidae Aciculata, Annelida), with four new species from deep-sea eastern Pacific methane seeps, and resolution of the affinity of Hesiolyra. Invertebr Syst 32:1050–1068

Rouse GW, Goffredi SK, Vrijenhoek RC (2004) *Osedax*: bone-eating marine worms with dwarf males. Science 305:668–71

Saeedi H, Bernardino AF, Shimabukuro M, Falchetto G, Sumida PY (2019) Macrofaunal community structure and biodiversity patterns based on a wood-fall experiment in the deep South-west Atlantic. Deep Sea Res I 145:73–82

Samadi S, Corbari L, Lorion J, /Hourdez S, Haga T, Dupont J, Boisellier M-C, Richer de Forges B (2010) Biodiversity of deep-sea organisms associated with sunken-wood or other organic remains sampled in the tropical Indo-Pacific. Cah Biol Mar 51:459–466

Sasaki T, Okutani T, Fujikura K (2005) Molluscs from Hydrothermal Vents and Cold Seeps in Japan: A Review of Taxa Recorded in Twenty Recent Years (1984-2004). Venus 64:87–133

Schein-Fatton E (1985) Découverte sur la ride du Pacifique oriental à 13° N d'un Pectinidae (Bivalvia, Pteriomorphia) d'affinités paléozoïques. CR Acad Sci Paris Ser III 301:491–496

Schultz GA (1966) Submarine canyons of southern California. Part 4. Systematics: Isopoda. Allan Hancock Pacific Expeditions 27:1–56

Shepard FP, Marshall NF (1975) Dives into outer Coronado Canyon system. Mar Geol 18:313–323

Shimabukuro M, Rizzo AE, Alfaro-Lucas JM, Fujiwara Y, Sumida PY (2017) *Sphaerodoropsis kitazatoi* a new species and the first record of Sphaerodoridae (Annelida: Phyllodocida) in SW Atlantic abyssal sediments around a whale carcass. Deep Sea Res II 146:18–26

Smith CR (1985) Food for the deep sea: utilization, dispersal, and flux of nekton falls at the Santa Catalina basin floor. Deep Sea Res I 32:417–442

Smith CR, Baco AR (2003) Ecology of whale falls at the deep-sea floor. Oceanogr Mar Biol Annu Rev 41:311–394

Smith CR, Hamilton SC (1983) Epibenthic megafauna of a bathyal basin off southern California: patterns of abundance, biomass, and dispersion. Deep Sea Res I 30:907–928

Smith CR, Kukert H, Wheatcroft RA, Jumars PA, Deming JW (1989) Vent fauna on whale remains. Nature 341:27–28

Smith KL, Baldwin RJ (1982) Scavenging deep-sea amphipods: Effects of food odor on oxygen consumption and a proposed metabolic strategy. Mar. Biol. 68:287–298

Sumida PYG, Alfaro-Lucas JM, Shimabukuro M, Kitazato H, Perez JAA, Soares-Gomes A, Toyofuku T, Lima AOS, Ara K, Fujiwara Y (2016) Deep-sea whale fall fauna from the Atlantic resembles that of the Pacific Ocean. Sci Rep 6:22139

Sumida PYG, Yoshinaga MY, Madureira LASP, Hovland M (2004) Seabed pockmarks associated with deepwater corals off SE Brazilian continental slope, Santos Basin. Mar Geol 207:159–167

Summers AC, Nybakken J (2000) Brittle star distribution patterns and population densities on the continental slope off central California. (Echinodermata: Ophiuroidea). Deep Sea Res II 47:1107–1137

Summers M, Pleijel F, Rouse GW (2015) Whale falls, multiple colonisations of the deep, and the phylogeny of Hesionidae. (Annelida). Invertebr Syst 29:105–123

Tunnicliffe V, McArthur AG, McHugh D (1998) A Biogeographical Perspective of the Deep-Sea Hydrothermal Vent Fauna. In: Blaxter, J, H, S, Southward, A, J, Tyler PA (eds) Advances in Marine Biology: Elsevier, p 353–442

Turner RD (2002) On the subfamily Xylophagainae. Bull Mus Comp Zool 157:223–307

Vestheim H, Kaartvedt S (2016) A deep sea community at the Kebrit brine pool in the Red Sea. Mar Biodiv 46:59–65

Voight JR (2007) Experimental deep-sea deployments reveal diverse Northeast Pacific wood-boring bivalves of Xylophagainae (Myoida: Pholadidae). J Molluscan Stud 73:377–391

Voss GL, Pearcy WG (1990) Deep-water octopods (Mollusca: Cephalopoda) of the northeastern Pacific. Proc Cali Acad Sci 47: 47–94

Wang Y, Zhu C, Sha Z, Ren X (2019) Description of *Seba longimera* sp. nov. from hydrothermal vents in the Okinawa Trough, Northwest Pacific (Amphipoda, Amphilochoidea, Sebidae). ZooKeys 899:141–149

Warén A (1983) A Generic Revision of the Family Eulimidae (Gastropoda, Prosobranchia). J Molluscan Stud 49:1–96

Warén A, Bouchet P (1986) Revision of the northeast Atlantic bathyal and Abyssal Aclididae, Eulimidae, Epitoniidae (Mollusca, Gastropoda): Four new species of *Provanna* Dall (Prosobranchia, Cerithiacea?) from East Pacific hydrothermal sites. Zool Scripta 15:157–164

Warén A, Bouchet P (1993) New records, species, genera, and a new family of gastropods from hydrothermal vents and hydrocarbon seeps. Zool zool j 22:1–90

Warén A, Bouchet P (2001) Gastropoda and Monoplacophora from Hydrothermal Vents and Seeps; New Taxa and Records. Veliger 44:116–231

Warén A, Bouchet P (2009) New gastropods from deep-sea hydrocarbon seeps off West Africa. Deep Sea Res II 56:2326–49

Warén A, Carozza F, Rocchini R (1996) Description of two new species of Hyalogyrinidae (Gastropoda, Heterobranchia) from the Mediterranean. Boll Malacol 32:57–66

Wiklund H, Altamira I, Glover AG, Stiller J, Baco AR, Dahlgren TG (2012) Systematics and biodiversity of *Ophryotrocha* (Annelida, Dorvilleidae) with descriptions of six new species from deep-sea whale-fall and wood-fall habitats in the north-east Pacific. Syst Biodivers 10:243–259

Wiklund H, Glover AG, Dahlgren TG (2009) Three new species of *Ophryotrocha* (Annelida: Dorvilleidae) from a whale-fall in the North-East Atlantic. Zootaxa:43–56

Williams, Austin, B, Smith CR, Baco AR (2000) New species of *Paralomis* (Decapoda, Anomura, Lithodidae) from a sunken whale carcass in the San Clemente basin off Southern California. J Crustac Biol 20:281–285

Wolff T (1979) Macrofaunal utilization of plant remains in the deep. Sarsia 64:117–136

Table S2.2 Pairwise PERMANOVA comparisons of bone, wood, and control assemblages, based on Bray-Curtis dissimilarities of log(*x*+1) transformed abundances. P-values were obtained using 9999 permutations under a reduced model. p-values determined by Monte Carlo random draws (P(MC)) are shown due to limited number of permutations. Significant differences in community composition (p(MC) < 0.050) after Bonferroni correction for multiple comparisons are indicated in bold. Location is a random factor, nested within Depth. All other factors (Substrate, Depth) are fixed.

Location	**Groups**	**t**	**P(perm)**	**Unique perm.**	**P(MC)**	**Average similarity %**
For pairs of substrate types, within each lander location.						
N-1600	Wood, Bone	2.324	0.098	10	**0.021**	42.2
	Wood, Control	2.729	0.104	10	**0.011**	49.2
	Bone, Control	1.730	0.102	10	0.064	49.7
S-1600	Wood, Bone	2.388	0.103	10	**0.020**	25.2
	Wood, Control	2.162	0.101	10	**0.026**	19.7
	Control, Bone	1.627	0.101	10	0.077	21.0
N-2800	Wood, Bone	3.570	0.101	10	**0.004**	41.5
	Wood, Control	2.708	0.099	10	**0.011**	41.9
	Control, Bone	2.338	0.101	10	**0.017**	48.9
S-2800	Wood, Bone	1.713	0.098	10	0.063	35.8
	Wood, Control	1.766	0.096	10	0.060	33.6
	Control, Bone	2.094	0.094	10	**0.030**	29.6
For pairs of depths, within each substrate type.						
Wood	2800 m, 1600 m	1.881	0.327	3	0.07	17.7
Bone	2800 m, 1600 m	1.946	0.329	3	**0.044**	19.4
Control	2800 m, 1600 m	1.602	0.334	3	0.103	10.7

Table S2.3 Generalized linear mixed model summary for *H'* and ES(30) response variables.

Response	**Final Model**	**Fixed terms**	**F-value**	**Pc(> F)**	**R^2m**	**Random terms**	**Test statistic**	**p-value**	**R^2c**
H'	Depth*Substrate + (1|Location)	Depth	1.27	0.377	0.36	(1|Location)	LRT = 4.99	**< 0.001**	0.62
		Substrate	1.58	0.224					
		Depth:Substrate	**10.48**	**< 0.001**					
ES(30)	Depth*Substrate + (1|Location)	Depth	1.10	0.404	0.42	(1|Location)	LRT = 15.53	**< 0.001**	0.80
		Substrate	**7.91**	**0.00**					
		Depth:Substrate	**21.92**	**< 0.001**					

Table S2.4 Generalized linear mixed model supplemental information.

Model	Fixed Effects				Random effects	
	Name	**Estimate**	**Std. Error**	**t value**	**Name**	**Variance**
log(N) ~ Depth + Substrate + (1+Substrate|Location)	(Intercept)	1.69	0.38	4.43	Location (Intercept)	0.52
	Depth2800	1.80	0.22	8.02	SubstrateControl	0.15
	SubstrateControl	-0.49	0.21	-2.32	SubstrateWood	1.01
	SubstrateWood	0.45	0.51	0.87	Residual	0.05
S ~ Depth + Substrate + (1+Substrate|Location)	(Intercept)	18.03	4.57	3.95	Location (Intercept)	63.58
	Depth2800	9.27	4.04	2.30	SubstrateControl	32.61
	SubstrateControl	-0.42	3.16	-0.13	SubstrateWood	69.23
	SubstrateWood	3.67	4.37	0.84	Residual	10.84
J' ~ Depth*Substrate + (1|Location)	(Intercept)	0.74	0.12	5.97	Location (Intercept)	0.03
	Depth2800	-0.26	0.17	-1.50	Residual	0.01
	SubstrateControl	0.08	0.05	1.72		
	SubstrateWood	-0.24	0.05	-5.15		
	Depth2800:SubstrateControl	0.00	0.07	0.01		
	Depth2800:SubstrateWood	0.40	0.07	5.99		
H' ~ Depth*Substrate + (1|Location)	(Intercept)	2.19	0.27	8.15	Location (Intercept)	0.10
	Depth2800	-0.70	0.38	-1.85	Residual	0.14
	SubstrateControl	0.28	0.22	1.28		
	SubstrateWood	-0.63	0.22	-2.90		
	Depth2800:SubstrateControl	-0.16	0.31	-0.52		
	Depth2800:SubstrateWood	1.13	0.31	3.68		

Table S2.4 (Continued) Generalized linear mixed model supplemental information.

Model	**Fixed Effects**				**Random effects**	
	Name	**Estimate**	**Std. Error**	**t value**	**Name**	**Variance**
ES(30) ~ Depth*Substrate + (1|Location)	(Intercept)	10.88	1.61	6.76	Location (Intercept)	4.40
	Depth2800	-3.87	2.28	-1.70	Residual	2.33
	SubstrateControl	2.62	1.00	2.61		
	SubstrateWood	-4.07	0.88	-4.61		
	Depth2800:SubstrateControl	-1.66	1.34	-1.24		
	Depth2800:SubstrateWood	6.45	1.25	5.17		
log(Chao1) ~ Depth + Substrate + (1|Location)	(Intercept)	3.68	0.22	16.87	Location (Intercept)	0.05
	Depth2800	-0.20	0.27	-0.72	Residual	0.18
	SubstrateControl	0.06	0.17	0.37		
	SubstrateWood	0.02	0.17	0.09		

Table S2.5 Abundance (individuals per mesh bin) of fauna collected from BoWLs landers. Values are averages ± SE (n = 3).

PHYLUM, CLASS/ORDER, FAMILY, Morphospecies	N-1600			S-1600			N-2800			S-2800		
	W	B	C	W	B	C	W	B	C	W	B	C
ANNELIDA												
POLYCHAETA												
ACROCIRRIDAE												
Acrocirrid sp. 3	-	-	-	-	-	-	-	-	-	-	-	0.33 ± 0.33
Flabelligella cf. *macrochaeta*	2.67 ± 2.67	-	-	0.33 ± 0.33	-	-	-	-	-	-	-	-
AMPHARETIDAE												
Anobothrus apaleatus	-	0.33 ± 0.33	2 ± 1	-	-	-	2 ± 1.53	-	2.67 ± 0.33	-	-	1.67 ± 0.88
Ampharetid sp. 21	-	-	4.33 ± 2.33	-	-	-	0.33 ± 0.33	-	-	-	-	-
Ampharetid sp. 22	288 ± 37.55	-	10.67 ± 3.76	16.67 ± 5.46	0.33 ± 0.33	0.33 ± 0.33	1.33 ± 1.33	0.33 ± 0.33	0.33 ± 0.33	-	-	-
Ampharetid sp. 23	-	-	0.33 ± 0.33	-	-	-	-	-	-	-	-	-
Decemunciger sp.	918.33 ± 265.54	0.67 ± 0.33	1.67 ± 0.67	40 ± 22.48	-	-	11.33 ± 5.04	-	0.67 ± 0.67	0.33 ± 0.33	-	-
Sosane wahrbergi	-	-	0.33 ± 0.33	-	-	-	-	-	-	-	-	-
Sosane sp. A	-	-	1 ± 0.58	-	-	-	0.33 ± 0.33	-	-	-	-	-
CAPITELLIDAE												
Capitella cf. *capitata*	9.33 ± 3.53	1 ± 0	0.67 ± 0.33	3 ± 1.73	6 ± 3.46	0.67 ± 0.33	12.67 ± 6.57	-	1.33 ± 1.33	1 ± 1	8 ± 1.53	-
Capitella cf. *ovincola*	0.33 ± 0.33	2 ± 1.15	0.33 ± 0.33	1 ± 1	9 ± 2.65	0.33 ± 0.33	4 ± 4	-	-	-	5 ± 4	0.67 ± 0.33
Capitellid sp. 10	-	-	-	-	-	-	1.33 ± 0.67	1 ± 0.58	3 ± 3	1.67 ± 0.33	2.33 ± 2.33	10.33 ± 9.84

Table S2.5 (Continued) Abundance (individuals per mesh bin) of fauna collected from BoWLs landers. Values are averages ± SE (n = 3).

PHYLUM, CLASS/ORDER, FAMILY, Morphospecies	N-1600			S-1600			N-2800			S-2800		
	W	B	C	W	B	C	W	B	C	W	B	C
Capitellid sp. 13	-	-	-	-	-	-	-	-	0.67 ± 0.33	-	-	-
CIRRATULIDAE												
Chaetozone sp. A	-	-	0.33 ± 0.33	-	-	0.33 ± 0.33	-	-	-	-	-	-
Chaetozone sp. B	-	-	-	-	-	-	2.67 ± 2.67	-	-	-	-	-
Cirratulid sp. 14	0.33 ± 0.33	-	-	-	-	-	-	-	-	-	-	-
CTENODRILLIDAE												
Ctenodrillid sp. 2	-	-	-	-	-	-	-	-	0.67 ± 0.67	-	-	-
DORVILLEIDAE												
Dorvilleid sp. 15	2.67 ± 1.33	11.33 ± 6.98	0.33 ± 0.33	1.67 ± 0.67	1.33 ± 1.33	-	25.67 ± 11.05	19.33 ± 15.38	0.33 ± 0.33	-	1.33 ± 0.88	-
Dorvilleid sp. 32	1.33 ± 1.33	-	-	-	-	-	-	-	-	-	-	-
Dorvilleid sp. 39	-	-	-	-	-	-	-	1 ± 1	-	-	-	-
Dorvilleid sp. 54	3 ± 2	4 ± 3.51	7.33 ± 3.53	3 ± 2	0.67 ± 0.33	-	0.67 ± 0.67	0.67 ± 0.67	-	0.67 ± 0.67	0.33 ± 0.33	-
Dorvilleid sp. 55	-	-	-	-	-	-	105 ± 27.79	-	-	-	-	-
Dorvilleid sp. 56	0.33 ± 0.33	0.67 ± 0.67	0.33 ± 0.33	-	-	-	-	-	-	-	-	-
Dorvilleid sp. 58	-	0.33 ± 0.33	-	-	-	-	-	-	-	-	-	-
Ophryotrocha batillus	81 ± 11.53	277.67 ± 246.8	71 ± 4.51	14.33 ± 3.18	9.67 ± 8.21	0.67 ± 0.67	430 ± 158.88	13 ± 5.57	21.33 ± 9.61	2.33 ± 1.33	18 ± 17.01	-

Table S2.5 (Continued) Abundance (individuals per mesh bin) of fauna collected from BoWLs landers. Values are averages ± SE (n = 3).

PHYLUM, CLASS/ORDER, FAMILY, Morphospecies	N-1600			S-1600			N-2800			S-2800		
	W	B	C	W	B	C	W	B	C	W	B	C
Ophryotrocha craigsmithi	-	0.33 ± 0.33	-	-	-	-	-	-	-	-	-	-
Ophryotrocha langstrumpae	13897 ± 3611.89	6 ± 2	28.67 ± 12.57	84.67 ± 14.52	-	0.67 ± 0.33	83.67 ± 40.58	0.33 ± 0.33	2.33 ± 1.2	-	0.33 ± 0.33	-
Ophryotrocha longicollaris	-	-	-	-	-	-	0.33 ± 0.33	0.33 ± 0.33	-	1 ± 1	-	-
Ophryotrocha magnadentata	2 ± 1.15	7.33 ± 5.33	0.67 ± 0.67	2.67 ± 0.67	0.33 ± 0.33	-	-	-	-	-	-	-
Parophryotrocha sp. A	-	28.33 ± 28.33	-	0.33 ± 0.33	0.33 ± 0.33	-	0.33 ± 0.33	601.67 ± 164.29	1.67 ± 0.88	-	193.67 ± 118.55	0.67 ± 0.67
FLABELLIGERIDAE												
Flabelligerid sp. 7	-	-	-	0.33 ± 0.33	-	0.33 ± 0.33	-	-	-	-	-	-
HESIONIDAE												
Gyptis sp. A	0.33 ± 0.33	2.67 ± 2.19	6.33 ± 3.18	-	-	-	-	1 ± 0.58	0.33 ± 0.33	-	-	-
Hesiocaeca sp. A	1.33 ± 1.33	0.33 ± 0.33	-	-	-	-	0.67 ± 0.33	-	-	0.67 ± 0.33	0.33 ± 0.33	-
Hesiopina cf. *aurantiaca*	-	0.33 ± 0.33	0.33 ± 0.33	-	-	-	0.33 ± 0.33	-	-	-	-	-
Sirsoe cf. *hessleri*	0.33 ± 0.33	-	-	4 ± 1.53	0.33 ± 0.33	-	1 ± 1	1.33 ± 0.67	-	0.67 ± 0.67	-	-
Vrijenhoekia balaenophila	1.33 ± 1.33	0.33 ± 0.33	0.33 ± 0.33	-	0.33 ± 0.33	-	4.33 ± 0.33	12.67 ± 1.45	0.33 ± 0.33	-	4.33 ± 1.67	-

Table S2.5 (Continued) Abundance (individuals per mesh bin) of fauna collected from BoWLs landers. Values are averages ± SE (n = 3).

PHYLUM, CLASS/ORDER, FAMILY, Morphospecies	N-1600			S-1600			N-2800			S-2800		
	W	B	C	W	B	C	W	B	C	W	B	C
LUMBRINERIDAE												
Lumbrinerid sp. 1	-	-	0.33 ± 0.33	-	-	-	-	-	-	-	-	-
MALDANIDAE												
Maldane sp. A	-	0.33 ± 0.33	0.33 ± 0.33	-	-	-	-	-	-	-	-	-
NEREIDIDAE												
Nereidid sp. 6	1.33 ± 1.33	0.33 ± 0.33	-	0.33 ± 0.33	-	-	-	-	-	-	1.67 ± 1.2	-
OPHELIIDAE												
Opheliid sp. 4	-	-	-	-	-	-	0.33 ± 0.33	-	-	-	-	-
Opheliid sp. 5	-	-	-	-	-	-	0.33 ± 0.33	-	0.33 ± 0.33	-	-	0.67 ± 0.67
Opheliid sp. 6	-	-	-	-	-	-	-	-	-	-	-	0.33 ± 0.33
PARAONIDAE												
Aricidea cf. *rubra*	-	-	-	-	0.33 ± 0.33	-	-	-	-	-	-	-
Paraonides sp. A	-	-	-	-	-	-	-	-	-	-	-	0.33 ± 0.33
PECTINARIIDAE												
Pectinariid sp. 1	-	-	0.33 ± 0.33	-	-	-	-	-	-	-	-	-
PHOLOIDAE												
Pholoid sp. 1	-	-	0.33 ± 0.33	-	-	-	-	-	-	-	-	-

Table S2.5 (Continued) Abundance (individuals per mesh bin) of fauna collected from BoWLs landers. Values are averages ± SE (n = 3).

PHYLUM, CLASS/ORDER, FAMILY, Morphospecies	N-1600			S-1600			N-2800			S-2800		
	W	B	C	W	B	C	W	B	C	W	B	C
PHYLLODOCIDAE												
Sige brunnea	0.33 ± 0.33	-	-	-	-	-	-	-	-	-	-	-
POLYNOIDAE												
Harmothoe cf. *fragilis*	2.67 ± 1.2	1.67 ± 0.88	13.67 ± 4.33	0.67 ± 0.33	0.67 ± 0.67	1 ± 0.58	-	-	-	-	-	-
Peinaleopolynoe santacatalina	0.33 ± 0.33	-	-	0.33 ± 0.33	-	-	0.33 ± 0.33	-	-	0.67 ± 0.67	0.67 ± 0.67	-
SCALIBREGMATIDAE												
Scalibregmatid sp. 2	-	-	0.33 ± 0.33	-	-	-	-	-	-	-	-	-
SERPULIDAE												
Serpulid sp. 1	-	-	0.67 ± 0.67	0.67 ± 0.67	-	-	-	-	-	-	-	-
SIBOGLINIDAE												
Osedax rubiplumus	-	2.67 ± 2.67	-	-	-	-	-	-	-	-	-	-
Osedax sp. B	-	9.33 ± 9.33	-	-	7.33 ± 7.33	-	-	1194.67 ± 918.27	-	-	12 ± 12	-
SIGALIONIDAE												
Sigalionid sp. 3	-	-	-	-	-	-	-	-	-	-	-	0.33 ± 0.33

Table S2.5 (Continued) Abundance (individuals per mesh bin) of fauna collected from BoWLs landers. Values are averages ± SE (n = 3).

PHYLUM, CLASS/ORDER, FAMILY, Morphospecies	N-1600			S-1600			N-2800			S-2800		
	W	B	C	W	B	C	W	B	C	W	B	C
SPHAERODORIDAE												
Sphaerodorid sp. 1	1.33 ± 1.33	-	-	-	-	-	-	-	-	-	-	-
SPIONIDAE												
Aurospio cf. *dibranchiata*	-	-	-	-	-	-	-	0.33 ± 0.33	-	-	-	-
Spionid sp. 13	-	-	-	-	-	-	-	-	-	-	0.33 ± 0.33	-
Laonice sp. A	2.33 ± 0.33	6.33 ± 2.19	7.67 ± 2.73	1.67 ± 0.88	2.67 ± 1.2	1 ± 1	2 ± 0.58	-	1.67 ± 1.2	0.33 ± 0.33	0.67 ± 0.67	-
Prionospio cf. *ehlersi*	-	-	0.33 ± 0.33	-	-	-	-	-	-	-	-	-
Prionospio sp. A	-	-	-	-	-	-	-	-	-	0.33 ± 0.33	0.67 ± 0.33	-
SYLLIDAE												
Syllid sp. 13	-	-	-	-	-	-	-	-	0.67 ± 0.33	-	-	0.33 ± 0.33
Proceraea sp. A	-	-	-	-	-	-	0.33 ± 0.33	-	-	-	-	-
Sphaerosyllis sp. A	2 ± 1	1 ± 0.58	13 ± 10.15	0.67 ± 0.33	0.33 ± 0.33	0.33 ± 0.33	22.33 ± 6.69	0.33 ± 0.33	2 ± 1.53	4.67 ± 3.71	2 ± 1.53	-
TEREBELLIDAE												
Terrebellid sp. 8	0.33 ± 0.33	-	0.67 ± 0.67	-	-	-	0.33 ± 0.33	-	-	-	-	-

Table S2.5 (Continued) Abundance (individuals per mesh bin) of fauna collected from BoWLs landers. Values are averages ± SE (n = 3).

PHYLUM, CLASS/ORDER, FAMILY, Morphospecies	N-1600			S-1600			N-2800			S-2800		
	W	B	C	W	B	C	W	B	C	W	B	C
Neoamphitrite sp. A	0.67 ± 0.33	0.33 ± 0.33	-	-	-	-	-	-	-	-	-	-
CLITELLATA												
HIRUDINEA												
Hirudinid sp. A	-	0.67 ± 0.33	-	1.33 ± 1.33	2.67 ± 2.19	0.33 ± 0.33	-	0.33 ± 0.33	-	-	-	1 ± 0.58
ARTHROPODA												
AMPHIPODA												
Accedomoera sp. A	-	-	-	-	-	-	703.33 ± 117.94	1447 ± 531	280 ± 67.12	30 ± 19.43	72 ± 46.49	15 ± 4.51
Amphipod sp. G	-	0.67 ± 0.33	-	-	-	-	-	1 ± 0.58	0.67 ± 0.33	-	0.33 ± 0.33	-
Amphipod sp. H	-	1.67 ± 0.88	-	-	-	-	0.67 ± 0.67	0.33 ± 0.33	1 ± 0.58	0.33 ± 0.33	-	0.33 ± 0.33
Amphipod sp. K	1.67 ± 1.67	17.67 ± 11.61	26.33 ± 10.35	-	0.33 ± 0.33	0.33 ± 0.33	1.33 ± 1.33	-	1.33 ± 1.33	-	-	-
Bathyceradocus sp. A	-	-	-	-	-	-	6 ± 1.53	-	0.67 ± 0.67	3.67 ± 1.86	-	-
Euonyx sp. A	-	-	0.67 ± 0.67	-	-	-	-	0.67 ± 0.33	-	-	0.33 ± 0.33	-
Isaeid sp. A	-	-	3.67 ± 2.67	-	-	-	1 ± 1	-	-	-	0.67 ± 0.67	-
Lysianassid sp. A	9.67 ± 7.31	20.67 ± 18.22	12.33 ± 3.76	-	-	-	8 ± 2.65	0.67 ± 0.33	-	2.67 ± 0.67	-	0.33 ± 0.33
Oedicerotid sp. A	-	-	-	-	-	-	-	-	0.67 ± 0.67	-	-	-

Table S2.5 (Continued) Abundance (individuals per mesh bin) of fauna collected from BoWLs landers. Values are averages ± SE (n = 3).

PHYLUM, CLASS/ORDER, FAMILY, Morphospecies	N-1600			S-1600			N-2800			S-2800		
	W	B	C	W	B	C	W	B	C	W	B	C
Schisturella sp. A	2.67 ± 1.76	26.67 ± 25.17	48.33 ± 26.96	-	-	-	-	1.33 ± 0.67	1 ± 0.58	0.67 ± 0.33	1 ± 0	0.33 ± 0.33
Sebidae sp. A	8.33 ± 2.19	2 ± 1	4.33 ± 1.45	1 ± 0.58	-	-	3.67 ± 1.76	1.33 ± 0.67	-	0.67 ± 0.67	0.33 ± 0.33	-
CARIDEA												
Caridean sp. A	0.67 ± 0.67	-	0.67 ± 0.33	-	-	0.33 ± 0.33	-	-	-	-	-	-
CUMACEAN												
Cumacean sp. A	-	-	-	-	-	-	-	-	-	-	0.33 ± 0.33	-
DECAPODA												
Chionocetes sp. A	-	-	0.33 ± 0.33	-	-	-	-	-	-	-	-	-
Paralomis sp. A	-	0.33 ± 0.33	-	-	-	-	-	-	-	-	-	-
GALATHEOIDEA												
Galatheid sp. E	-	0.33 ± 0.33	-	-	-	-	-	-	-	-	-	-
Munidopsis albatrossae	-	-	-	-	-	-	-	-	-	0.33 ± 0.33	3 ± 2.52	0.67 ± 0.67
Munidopsis cascadia	-	-	-	-	-	-	2.67 ± 0.67	16.33 ± 2.19	1.33 ± 0.33	1 ± 0.58	4.67 ± 2.73	0.67 ± 0.67
Munidopsis cf. *antonii*	-	-	-	-	-	-	16.33 ± 2.85	17.33 ± 5.36	7 ± 1	1 ± 0.58	6 ± 2.52	1 ± 0.58

Table S2.5 (Continued) Abundance (individuals per mesh bin) of fauna collected from BoWLs landers. Values are averages ± SE (n = 3).

PHYLUM, CLASS/ORDER, FAMILY, Morphospecies	N-1600			S-1600			N-2800			S-2800		
	W	B	C	W	B	C	W	B	C	W	B	C
Munidopsis cf. *lignaria*	-	-	-	-	-	-	1.33 ± 0.88	1.33 ± 1.33	-	4.67 ± 2.6	2 ± 1	0.67 ± 0.33
ISOPODA												
Eurycopinae sp. A	-	-	0.33 ± 0.33	-	1.33 ± 1.33	2 ± 2	11.67 ± 3.84	120.67 ± 78.68	48.67 ± 16.22	2.67 ± 2.19	28.67 ± 20.42	24 ± 8.02
Eurycopinae sp. B	-	-	-	-	-	-	-	0.33 ± 0.33	0.33 ± 0.33	-	-	-
Ilyarachna profunda	0.33 ± 0.33	2 ± 1.53	-	-	0.33 ± 0.33	-	-	-	-	3.67 ± 1.45	8.33 ± 1.2	1.33 ± 0.88
Ischnomesid sp. A	-	-	-	-	-	-	-	-	-	-	-	0.67 ± 0.33
Isopod sp. H	-	-	-	-	-	-	-	-	-	-	-	0.33 ± 0.33
Isopod sp. J	-	-	-	-	0.33 ± 0.33	-	-	-	-	-	-	-
Isopod sp. K	-	-	0.67 ± 0.67	-	-	-	-	-	-	-	-	-
Janirid sp.	-	-	-	-	-	-	-	-	-	2 ± 1.53	1 ± 0.58	-
MYSIDA												
Mysid sp. A	-	-	0.33 ± 0.33	-	-	-	-	-	-	-	-	-
NEBALIIDAE												
Nebalia sp. A	1 ± 1	1.33 ± 0.88	5.33 ± 2.85	-	-	-	-	-	-	-	-	-
Nebalia sp. B	-	-	-	-	-	-	1.67 ± 0.88	-	-	-	-	-
TANAIDACEA												
Tanaid sp. A	-	-	0.33 ± 0.33	-	-	-	2 ± 1.15	-	3.33 ± 1.86	0.33 ± 0.33	-	3 ± 1

Table S2.5 (Continued) Abundance (individuals per mesh bin) of fauna collected from BoWLs landers. Values are averages ± SE (n = 3).

PHYLUM, CLASS/ORDER, FAMILY, Morphospecies	N-1600			S-1600			N-2800			S-2800		
	W	B	C	W	B	C	W	B	C	W	B	C
Tanaid sp. B	-	0.33 ± 0.33	-	-	-	0.33 ± 0.33	-	-	-	-	-	0.33 ± 0.33
Tanaid sp. C	-	-	0.33 ± 0.33	-	0.33 ± 0.33	-	-	-	-	-	-	-
Tanaid sp. D	-	-	-	-	-	-	-	-	-	-	-	0.33 ± 0.33
Tanaid sp. E	-	-	-	-	-	-	-	-	0.33 ± 0.33	-	-	-
Tanaid sp. F	-	-	-	-	-	-	0.33 ± 0.33	-	-	0.33 ± 0.33	0.33 ± 0.33	-
PYCNOGONIDA												
Pycnogonid sp. A	-	-	-	-	-	-	-	-	-	2.33 ± 2.33	-	7 ± 3.06
CHORDATA												
ACTINOPTERYGII												
Zoarcid sp. A	-	-	-	-	-	-	-	-	0.33 ± 0.33	-	-	-
CNIDARIA												
ACTINARIA												
Actinarian sp.	0.67 ± 0.33	-	0.33 ± 0.33	-	-	-	3.33 ± 0.88	1.33 ± 0.33	3.33 ± 0.67	1.67 ± 0.88	1 ± 0.58	0.33 ± 0.33
ECHINODERMATA												
GORGONOCEPHALA												
Gorgonocephalan sp. A	-	0.33 ± 0.33	-	-	-	-	-	-	-	-	-	-

Table S2.5 (Continued) Abundance (individuals per mesh bin) of fauna collected from BoWLs landers. Values are averages ± SE (n = 3).

PHYLUM, CLASS/ORDER, FAMILY, Morphospecies	N-1600			S-1600			N-2800			S-2800		
	W	B	C	W	B	C	W	B	C	W	B	C
OPHIUROIDEA												
Ophiophthalmus normani	1.33 ± 0.88	3 ± 1.53	5 ± 2.31	-	-	0.33 ± 0.33	-	-	-	-	-	-
Ophiuroid sp. B	-	-	-	-	0.33 ± 0.33	-	-	-	-	-	-	-
Ophiuroid sp. C	-	-	-	-	-	-	-	-	-	-	-	0.33 ± 0.33
MOLLUSCA												
APLACOPHORA												
Aplacophoran sp. A	3.33 ± 3.33	2 ± 1.53	-	-	-	-	-	-	-	-	-	-
BIVALVIA												
Bathypecten sp. A	-	-	0.67 ± 0.67	1 ± 0.58	0.33 ± 0.33	0.33 ± 0.33	-	0.33 ± 0.33	0.33 ± 0.33	0.33 ± 0.33	-	-
Bivalve sp. B	19 ± 4.51	17 ± 2.08	23.67 ± 3.53	0.33 ± 0.33	-	5 ± 2.08	-	-	-	-	-	-
Bivalve sp. E	0.33 ± 0.33	2.67 ± 2.19	6.67 ± 1.2	-	0.67 ± 0.67	1 ± 1	0.33 ± 0.33	-	-	-	-	-
Bivalve sp. F	1.33 ± 1.33	0.67 ± 0.67	-	1 ± 1	0.67 ± 0.67	0.33 ± 0.33	-	-	-	-	-	-
Bivalve sp. G	-	1.67 ± 1.2	0.33 ± 0.33	-	0.67 ± 0.33	-	-	0.33 ± 0.33	-	-	-	-
Bivalve sp. H	-	-	0.33 ± 0.33	-	-	-	0.33 ± 0.33	-	-	-	-	-
Bivalve sp. I	-	-	-	-	-	-	-	-	-	-	-	0.33 ± 0.33

Table S2.5 (Continued) Abundance (individuals per mesh bin) of fauna collected from BoWLs landers. Values are averages ± SE (n = 3).

PHYLUM, CLASS/ORDER, FAMILY, Morphospecies	N-1600			S-1600			N-2800			S-2800		
	W	B	C	W	B	C	W	B	C	W	B	C
Idas washingtonius	13 ± 3	9.67 ± 1.86	3 ± 1.73	7.33 ± 3.28	9.67 ± 5.24	0.33 ± 0.33	2.67 ± 2.67	2.33 ± 0.33	-	-	0.67 ± 0.67	-
Xylonora corona	-	-	-	-	-	-	119 ± 65.29	-	-	-	-	-
Xylophaga microchira	1 ± 1	-	-	0.33 ± 0.33	-	-	-	-	-	-	-	-
Xylonora muraokai	-	-	-	-	-	-	736.67 ± 718.69	-	-	-	-	-
Xylophaga oregona	2751.33 ± 555.59	-	-	25.33 ± 3.28	-	-	-	-	-	-	-	-
Xylonora zierenbergi	-	-	-	-	-	-	1280.67 ± 412.66	-	-	-	-	-
Xylopholas crooki	-	-	-	-	-	-	11.33 ± 3.48	-	-	-	-	-
GASTROPODA												
cf *Laeviphitus* sp.	-	-	-	-	-	0.67 ± 0.67	6.67 ± 4.41	47 ± 2.65	5 ± 1.53	0.33 ± 0.33	1.67 ± 0.88	-
Dillwynella sp. A	0.33 ± 0.33	-	-	-	0.33 ± 0.33	0.33 ± 0.33	2 ± 1.53	0.33 ± 0.33	0.33 ± 0.33	17 ± 1	0.67 ± 0.67	2.33 ± 1.33
Eulimid sp. A	0.33 ± 0.33	0.67 ± 0.67	-	-	-	-	-	-	-	-	-	-
Gastropod sp. H	-	-	0.33 ± 0.33	0.33 ± 0.33	-	-	0.33 ± 0.33	-	-	-	-	-
Gastropod sp. I	-	-	0.33 ± 0.33	-	-	-	-	-	-	-	-	-
Gastropod sp. J	-	-	-	1 ± 1	-	-	-	-	-	-	-	0.33 ± 0.33

Table S2.5 (Continued) Abundance (individuals per mesh bin) of fauna collected from BoWLs landers. Values are averages ± SE (n = 3).

PHYLUM, CLASS/ORDER, FAMILY, Morphospecies	N-1600			S-1600			N-2800			S-2800		
	W	B	C	W	B	C	W	B	C	W	B	C
Gastropod sp. K	-	-	-	-	-	-	0.33 ± 0.33	-	-	-	-	-
Gastropod sp. L	-	-	-	1.33 ± 0.33	-	1 ± 0	-	-	-	-	-	-
Gastropod sp. M	-	-	0.67 ± 0.33	-	-	-	-	-	-	-	-	-
Gastropod sp. N	-	-	-	-	-	0.33 ± 0.33	-	-	-	-	-	-
Hyalogyrina sp. A	4 ± 2.52	45.33 ± 13.86	3 ± 0.58	0.33 ± 0.33	12.33 ± 8.35	1 ± 0.58	-	-	1.67 ± 1.67	-	1.33 ± 0.88	-
Provanna cf. *macleani*	-	-	-	-	-	-	4 ± 2	1.67 ± 0.67	-	-	-	-
LIMPET												
Limpet sp. A	0.67 ± 0.67	-	1 ± 0.58	24.33 ± 18.56	0.67 ± 0.67	5 ± 2.08	0.67 ± 0.67	-	-	-	-	-
Limpet sp. B	-	-	-	0.33 ± 0.33	-	-	-	0.33 ± 0.33	-	-	-	-
NUDIBRANCH												
Ziminella abyssa	-	-	1.67 ± 0.33	1 ± 1	-	1.67 ± 0.88	-	-	-	-	-	-
OCTOPODIDAE												
Graneledone pacifica	-	-	-	-	-	0.33 ± 0.33	-	-	-	-	-	-
NEMERTEA												
Nemertean sp.	-	-	0.67 ± 0.33	0.67 ± 0.67	-	-	1.67 ± 0.88	0.67 ± 0.67	0.67 ± 0.67	1.67 ± 1.67	0.67 ± 0.33	-

Table S2.5 (Continued) Abundance (individuals per mesh bin) of fauna collected from BoWLs landers. Values are averages ± SE (n = 3).

PHYLUM, CLASS/ORDER, FAMILY, Morphospecies	N-1600			S-1600			N-2800			S-2800		
	W	B	C	W	B	C	W	B	C	W	B	C
PLATYHELMINTHES												
Triclad sp. A	819 ± 274.53	2.67 ± 1.76	60 ± 18.03	58 ± 33.05	-	-	-	-	-	-	-	-
Polyclad sp. A	-	-	-	-	-	-	17.33 ± 2.91	-	0.33 ± 0.33	-	-	-

Table S2.6 Density (individuals per cm^2 substrate surface area) of fauna collected from BoWLs landers. Values are averages ± SE (n = 3).

PHYLUM, CLASS/ORDER, FAMILY, Morphospecies	N-1600			S-1600			N-2800			S-2800		
	W	B	C	W	B	C	W	B	C	W	B	C
ANNELIDA												
POLYCHAETA												
ACROCIRRIDAE												
Acrocirrid sp. 3	-	-	-	-	-	-	-	-	-	-	-	3.0e-04 ± 3.0e-04
Flabelligella cf. *macrochaeta*	2.0e-03 ± 2.0e-03	-	-	2.5e-04 ± 2.5e-04	-	-	-	-	-	-	-	-
AMPHARETIDAE												
Anobothrus apaleatus	-	1.6e-04 ± 1.6e-04	1.8e-03 ± 8.9e-04	-	-	-	1.5e-03 ± 1.1e-03	-	2.4e-03 ± 3.0e-04	-	-	1.5e-03 ± 7.8e-04
Ampharetid sp. 21	-	-	3.9e-03 ± 2.1e-03	-	-	-	2.5e-04 ± 2.5e-04	-	-	-	-	-
Ampharetid sp. 22	2.1e-01 ± 2.8e-02	-	9.5e-03 ± 3.3e-03	1.2e-02 ± 4.0e-03	1.8e-04 ± 1.8e-04	3.0e-04 ± 3.0e-04	9.9e-04 ± 9.9e-04	2.2e-04 ± 2.2e-04	3.0e-04 ± 3.0e-04	-	-	-
Ampharetid sp. 23	-	-	3.0e-04±3.0e-04	-	-	-	-	-	-	-	-	-
Decemunciger sp.	6.8e-01 ± 2.0e-01	3.8e-04 ± 2.0e-04	1.5e-03 ± 5.9e-04	3.0e-02 ± 1.7e-02	-	-	8.4e-03 ± 3.7e-03	-	5.9e-04 ± 5.9e-04	2.5e-04 ± 2.5e-04	-	-
Sosane wahrbergi	-	-	3.0e-04 ± 3.0e-04	-	-	-	-	-	-	-	-	-
Sosane sp. A	-	-	8.9e-04 ± 5.1e-04	-	-	-	2.5e-04 ± 2.5e-04	-	-	-	-	-

Table S2.6 (Continued) Density (individuals per cm^2 substrate surface area) of fauna collected from BoWLs landers. Values are averages ± SE (n = 3).

PHYLUM, CLASS/ORDER, FAMILY, Morphospecies	N-1600			S-1600			N-2800			S-2800		
	W	B	C	W	B	C	W	B	C	W	B	C
Capitella cf. *capitata*	6.9e-03 ± 2.6e-03	5.4e-04 ± 5.5e-05	5.9e-04 ± 3.0e-04	2.2e-03 ± 1.3e-03	3.7e-03 ± 1.9e-03	5.9e-04 ± 3.0e-04	9.4e-03 ± 4.9e-03	-	1.2e-03 ± 1.2e-03	7.4e-04 ± 7.4e-04	5.9e-03 ± 1.5e-03	-
Capitella cf. *ovincola*	2.5e-04 ± 2.5e-04	1.2e-03 ± 7.6e-04	3.0e-04 ± 3.0e-04	7.4e-04 ± 7.4e-04	5.3e-03 ± 1.3e-03	3.0e-04 ± 3.0e-04	3.0e-03 ± 3.0e-03	-	-	-	3.2e-03 ± 2.5e-03	5.9e-04 ± 3.0e-04
Capitellid sp. 10	-	-	-	-	-	-	9.9e-04 ± 4.9e-04	6.2e-04 ± 3.5e-04	2.7e-03 ± 2.7e-03	1.2e-03 ± 2.5e-04	2.0e-03 ± 2.0e-03	9.2e-03 ± 8.7e-03
Capitellid sp. 13	-	-	-	-	-	-	-	-	5.9e-04 ± 3.0e-04	-	-	-
CIRRATULIDAE												
Chaetozone sp. A	-	-	3.0e-04 ± 3.0e-04	-	-	3.0e-04 ± 3.0e-04	-	-	-	-	-	-
Chaetozone sp. B	-	-	-	-	-	-	2.0e-03 ± 2.0e-03	-	-	-	-	-
Cirratulid sp. 14	2.5e-04 ± 2.5e-04	-	-	-	-	-	-	-	-	-	-	-
CTENODRILLIDAE												
Ctenodrillid sp. 2	-	-	-	-	-	-	-	-	5.9e-04 ± 5.9e-04	-	-	-

Table S2.6 (Continued) Density (individuals per cm^2 substrate surface area) of fauna collected from BoWLs landers. Values are averages ± SE (n = 3).

PHYLUM, CLASS/ORDER, FAMILY, Morphospecies	N-1600			S-1600			N-2800			S-2800		
	W	B	C	W	B	C	W	B	C	W	B	C
DORVILLEIDAE												
Dorvilleid sp. 15	2.0e-03 ± 9.9e-04	5.6e-03 ± 3.3e-03	3.0e-04 ± 3.0e-04	1.2e-03 ± 4.9e-04	7.3e-04 ± 7.3e-04	-	1.9e-02 ± 8.2e-03	1.2e-02 ± 9.9e-03	3.0e-04 ± 3.0e-04	-	9.1e-04 ± 5.4e-04	-
Dorvilleid sp. 32	9.9e-04 ± 9.9e-04	-	-	-	-	-	-	-	-	-	-	-
Dorvilleid sp. 39	-	-	-	-	-	-	-	6.5e-04 ± 6.5e-04	-	-	-	-
Dorvilleid sp. 54	2.2e-03 ± 1.5e-03	2.0e-03 ± 1.7e-03	6.5e-03 ± 3.1e-03	2.2e-03 ± 1.5e-03	3.7e-04 ± 1.8e-04	-	4.9e-04 ± 4.9e-04	4.6e-04 ± 4.6e-04	-	4.9e-04 ± 4.9e-04	2.3e-04 ± 2.3e-04	-
Dorvilleid sp. 55	-	-	-	-	-	-	7.8e-02 ± 2.1e-02	-	-	-	-	-
Dorvilleid sp. 56	2.5e-04 ± 2.5e-04	4.4e-04 ± 4.4e-04	3.0e-04 ± 3.0e-04	-	-	-	-	-	-	-	-	-
Dorvilleid sp. 58	-	1.6e-04 ± 1.6e-04	-	-	-	-	-	-	-	-	-	-
Ophryotrocha batillus	6.0e-02 ± 8.5e-03	1.4e-01 ± 1.2e-01	6.3e-02 ± 4.0e-03	1.1e-02 ± 2.4e-03	5.4e-03 ± 4.6e-03	5.9e-04 ± 5.9e-04	3.2e-01 ± 1.2e-01	8.7e-03 ± 4.0e-03	1.9e-02 ± 8.5e-03	1.7e-03 ± 9.9e-04	1.1e-02 ± 1.1e-02	-
Ophryotrocha craigsmithi	-	1.6e-04 ± 1.6e-04	-	-	-	-	-	-	-	-	-	-

Table S2.6 (Continued) Density (individuals per cm^2 substrate surface area) of fauna collected from BoWLs landers. Values are averages ± SE (n = 3).

PHYLUM, CLASS/ORDER, FAMILY, Morphospecies	N-1600			S-1600			N-2800			S-2800		
	W	B	C	W	B	C	W	B	C	W	B	C
Ophryotrocha langstrumpae	1.0e+01 ± 2.7e+00	3.5e-03 ± 1.5e-03	2.5e-02 ± 1.1e-02	6.3e-02 ± 1.1e-02	-	5.9e-04 ± 3.0e-04	6.2e-02 ± 3.0e-02	2.2e-04 ± 2.2e-04	2.1e-03 ± 1.1e-03	-	2.9e-04 ± 2.9e-04	-
Ophryotrocha longicollaris	-	-	-	-	-	-	2.5e-04 ± 2.5e-04	2.3e-04 ± 2.3e-04	-	7.4e-04 ± 7.4e-04	-	-
Ophryotrocha magnadentata	1.5e-03 ± 8.5e-04	3.7e-03 ± 2.6e-03	5.9e-04 ± 5.9e-04	2.0e-03 ± 4.9e-04	1.8e-04 ± 1.8e-04	-	-	-	-	-	-	-
Parophryotrocha sp. A	-	1.4e-02 ± 1.4e-02	-	2.5e-04 ± 2.5e-04	1.8e-04 ± 1.8e-04	-	2.5e-04 ± 2.5e-04	3.9e-01 ± 1.1e-01	1.5e-03 ± 7.8e-04	-	1.3e-01 ± 7.1e-02	5.9e-04 ± 5.9e-04
FLABELLIGERIDAE												
Flabelligerid sp. 7	-	-	-	2.5e-04 ± 2.5e-04	-	3.0e-04 ± 3.0e-04	-	-	-	-	-	-
HESIONIDAE												
Gyptis sp. A	2.5e-04 ± 2.5e-04	1.4e-03 ± 1.1e-03	5.6e-03 ± 2.8e-03	-	-	-	-	6.2e-04 ± 3.5e-04	3.0e-04 ± 3.0e-04	-	-	-
Hesiocaeca sp. A	9.9e-04 ± 9.9e-04	1.6e-04 ± 1.6e-04	-	-	-	-	4.9e-04 ± 2.5e-04	-	-	4.9e-04 ± 2.5e-04	2.3e-04 ± 2.3e-04	-
Hesiopina cf. *aurantiaca*	-	1.6e-04 ± 1.6e-04	3.0e-04 ± 3.0e-04	-	-	-	2.5e-04 ± 2.5e-04	-	-	-	-	-

Table S2.6 (Continued) Density (individuals per cm^2 substrate surface area) of fauna collected from BoWLs landers. Values are averages ± SE (n = 3).

PHYLUM, CLASS/ORDER, FAMILY, Morphospecies	N-1600			S-1600			N-2800			S-2800		
	W	B	C	W	B	C	W	B	C	W	B	C
Sirsoe cf. *hessleri*	2.5e-04 ± 2.5e-04	-	-	3.0e-03 ± 1.1e-03	1.8e-04 ± 1.8e-04	-	7.4e-04 ± 7.4e-04	8.7e-04 ± 4.4e-04	-	4.9e-04 ± 4.9e-04	-	-
Vrijenhoekia balaenophila	9.9e-04 ± 9.9e-04	1.6e-04 ± 1.6e-04	3.0e-04 ± 3.0e-04	-	1.9e-04 ± 1.9e-04	-	3.2e-03 ± 2.5e-04	8.3e-03 ± 1.1e-03	3.0e-04 ± 3.0e-04	-	3.2e-03 ± 1.3e-03	-
LUMBRINERIDAE												
Lumbrinerid sp. 1	-	-	3.0e-04 ± 3.0e-04	-	-	-	-	-	-	-	-	-
MALDANIDAE												
Maldane sp. A	-	2.2e-04 ± 2.2e-04	3.0e-04 ± 3.0e-04	-	-	-	-	-	-	-	-	-
NEREIDIDAE												
Nereidid sp. 6	9.9e-04 ± 9.9e-04	2.2e-04 ± 2.2e-04	-	2.5e-04 ± 2.5e-04	-	-	-	-	-	-	1.1e-03 ± 7.4e-04	-
OPHELIIDAE												
Opheliid sp. 4	-	-	-	-	-	-	2.5e-04 ± 2.5e-04	-	-	-	-	-

Table S2.6 (Continued) Density (individuals per cm^2 substrate surface area) of fauna collected from BoWLs landers. Values are averages ± SE (n = 3).

PHYLUM, CLASS/ORDER, FAMILY, Morphospecies	N-1600			S-1600			N-2800			S-2800		
	W	B	C	W	B	C	W	B	C	W	B	C
Opheliid sp. 5	-	-	-	-	-	-	2.5e-04 ± 2.5e-04	-	3.0e-04 ± 3.0e-04	-	-	5.9e-04 ± 5.9e-04
Opheliid sp. 6	-	-	-	-	-	-	-	-	-	-	-	3.0e-04 ± 3.0e-04
PARAONIDAE												
Aricidea cf. *rubra*	-	-	-	-	1.8e-04 ± 1.8e-04	-	-	-	-	-	-	-
Paraonides sp. A	-	-	-	-	-	-	-	-	-	-	-	3.0e-04 ± 3.0e-04
PECTINARIIDAE												
Pectinariid sp. 1	-	-	3.0e-04 ± 3.0e-04	-	-	-	-	-	-	-	-	-
PHOLOIDAE												
Pholoid sp. 1	-	-	3.0e-04 ± 3.0e-04	-	-	-	-	-	-	-	-	-

Table S2.6 (Continued) Density (individuals per cm^2 substrate surface area) of fauna collected from BoWLs landers. Values are averages ± SE (n = 3).

PHYLUM, CLASS/ORDER, FAMILY, Morphospecies	N-1600			S-1600			N-2800			S-2800		
	W	B	C	W	B	C	W	B	C	W	B	C
PHYLLODOCIDAE												
Sige brunnea	2.5e-04 ± 2.5e-04	-	-	-	-	-	-	-	-	-	-	-
POLYNOIDAE												
Harmothoe cf. *fragilis*	2.0e-03 ± 8.9e-04	8.2e-04 ± 4.3e-04	1.2e-02 ± 3.9e-03	4.9e-04 ± 2.5e-04	3.7e-04 ± 3.7e-04	8.9e-04 ± 5.1e-04	-	-	-	-	-	-
Peinaleopolynoe santacatalina	2.5e-04 ± 2.5e-04	-	-	2.5e-04 ± 2.5e-04	-	-	2.5e-04 ± 2.5e-04	-	-	4.9e-04 ± 4.9e-04	4.5e-04 ± 4.5e-04	-
SCALIBREGMATIDAE												
Scalibregmatid sp. 2	-	-	3.0e-04 ± 3.0e-04	-	-	-	-	-	-	-	-	-
SERPULIDAE												
Serpulid sp. 1	-	-	5.9e-04 ± 5.9e-04	4.9e-04 ± 4.9e-04	-	-	-	-	-	-	-	-

Table S2.6 (Continued) Density (individuals per cm^2 substrate surface area) of fauna collected from BoWLs landers. Values are averages ± SE (n = 3).

PHYLUM, CLASS/ORDER, FAMILY, Morphospecies	N-1600			S-1600			N-2800			S-2800		
	W	B	C	W	B	C	W	B	C	W	B	C
SIBOGLINIDAE												
Osedax rubiplumus	-	1.3e-03 ± 1.3e-03	-	-	-	-	-	-	-	-	-	-
Osedax sp. B	-	4.6e-03 ± 4.6e-03	-	-	4.1e-03 ± 4.1e-03	-	-	8.1e-01 ± 6.3e-01	-	-	1.0e-02 ± 1.0e-02	-
SIGALIONIDAE												
Sigalionid sp. 3	-	-	-	-	-	-	-	-	-	-	-	3.0e-04 ± 3.0e-04
SPHAERODORIDAE												
Sphaerodorid sp. 1	9.9e-04 ± 9.9e-04	-	-	-	-	-	-	-	-	-	-	-
SPIONIDAE												
Aurospio cf. *dibranchiata*	-	-	-	-	-	-	-	2.3e-04 ± 2.3e-04	-	-	-	-
Spionid sp. 13	-	-	-	-	-	-	-	-	-	-	2.9e-04 ± 2.9e-04	-
Laonice sp. A	1.7e-03 ± 2.5e-04	3.5e-03 ± 1.3e-03	6.8e-03 ± 2.4e-03	1.2e-03 ± 6.5e-04	1.5e-03 ± 6.1e-04	8.9e-04 ± 8.9e-04	1.5e-03 ± 4.3e-04	-	1.5e-03 ± 1.1e-03	2.5e-04 ± 2.5e-04	5.8e-04 ± 5.8e-04	-

Table S2.6 (Continued) Density (individuals per cm^2 substrate surface area) of fauna collected from BoWLs landers. Values are averages ± SE (n = 3).

PHYLUM, CLASS/ORDER, FAMILY, Morphospecies	N-1600			S-1600			N-2800			S-2800		
	W	B	C	W	B	C	W	B	C	W	B	C
Prionospio cf. *ehlersi*	-	-	3.0e-04 ± 3.0e-04	-	-	-	-	-	-	-	-	-
Prionospio sp. A	-	-	-	-	-	-	-	-	-	2.5e-04 ± 2.5e-04	4.3e-04 ± 2.2e-04	-
SYLLIDAE												
Syllid sp. 13	-	-	-	-	-	-	-	-	5.9e-04 ± 3.0e-04	-	-	3.0e-04 ± 3.0e-04
Proceraea sp. A	-	-	-	-	-	-	2.5e-04 ± 2.5e-04	-	-	-	-	-
Sphaerosyllis sp. A	1.5e-03 ± 7.4e-04	5.4e-04 ± 2.9e-04	1.2e-02 ± 9.0e-03	4.9e-04 ± 2.5e-04	1.8e-04 ± 1.8e-04	3.0e-04 ± 3.0e-04	1.7e-02 ± 4.9e-03	2.2e-04 ± 2.2e-04	1.8e-03 ± 1.4e-03	3.5e-03 ± 2.7e-03	1.3e-03 ± 9.3e-04	-
TEREBELLIDAE												
Terrebellid sp. 8	2.5e-04 ± 2.5e-04	-	5.9e-04 ± 5.9e-04	-	-	-	2.5e-04 ± 2.5e-04	-	-	-	-	-
Neoamphitrite sp. A	4.9e-04 ± 2.5e-04	1.6e-04 ± 1.6e-04	-	-	-	-	-	-	-	-	-	-

Table S2.6 (Continued) Density (individuals per cm^2 substrate surface area) of fauna collected from BoWLs landers. Values are averages ± SE (n = 3).

PHYLUM, CLASS/ORDER, FAMILY, Morphospecies	N-1600			S-1600			N-2800			S-2800		
	W	B	C	W	B	C	W	B	C	W	B	C
CLITELLATA												
HIRUDINEA												
Hirudinid sp. A	-	3.3e-04 ± 1.6e-04	-	9.9e-04 ± 9.9e-04	2.0e-03 ± 1.7e-03	3.0e-04 ± 3.0e-04	-	2.3e-04 ± 2.3e-04	-	-	-	8.9e-04 ± 5.1e-04
ARTHROPODA												
AMPHIPODA												
Accedomoera sp. A	-	-	-	-	-	-	5.2e-01 ± 8.7e-02	9.5e-01 ± 3.7e-01	2.5e-01 ± 6.0e-02	2.2e-02 ± 1.4e-02	5.2e-02 ± 3.1e-02	1.3e-02 ± 4.0e-03
Amphipod sp. G	-	3.3e-04 ± 1.6e-04	-	-	-	-	-	6.2e-04 ± 3.5e-04	5.9e-04 ± 3.0e-04	-	2.1e-04 ± 2.1e-04	-
Amphipod sp. H	-	8.2e-04 ± 4.3e-04	-	-	-	-	4.9e-04 ± 4.9e-04	2.0e-04 ± 2.0e-04	8.9e-04 ± 5.1e-04	2.5e-04 ± 2.5e-04	-	3.0e-04 ± 3.0e-04
Amphipod sp. K	1.2e-03 ± 1.2e-03	9.4e-03 ± 5.6e-03	2.3e-02 ± 9.2e-03	-	2.5e-04 ± 2.5e-04	3.0e-04 ± 3.0e-04	9.9e-04 ± 9.9e-04	-	1.2e-03 ± 1.2e-03	-	-	-
Bathyceradocus sp. A	-	-	-	-	-	-	4.4e-03 ± 1.1e-03	-	5.9e-04 ± 5.9e-04	2.7e-03 ± 1.4e-03	-	-
Euonyx sp. A	-	-	5.9e-04 ± 5.9e-04	-	-	-	-	4.3e-04 ± 2.2e-04	-	-	2.3e-04 ± 2.3e-04	-

Table S2.6 (Continued) Density (individuals per cm^2 substrate surface area) of fauna collected from BoWLs landers. Values are averages ± SE (n = 3).

PHYLUM, CLASS/ORDER, FAMILY, Morphospecies	N-1600			S-1600			N-2800			S-2800		
	W	B	C	W	B	C	W	B	C	W	B	C
Isaeid sp. A	-	-	3.3e-03 ± 2.4e-03	-	-	-	7.4e-04 ± 7.4e-04	-	-	-	4.5e-04 ± 4.5e-04	-
Lysianassid sp. A	7.2e-03 ± 5.4e-03	1.0e-02 ± 9.0e-03	1.1e-02 ± 3.3e-03	-	-	-	5.9e-03 ± 2.0e-03	4.2e-04 ± 2.1e-04	-	2.0e-03 ± 4.9e-04	-	3.0e-04 ± 3.0e-04
Oedicerotid sp. A	-	-	-	-	-	-	-	-	5.9e-04 ± 5.9e-04	-	-	-
Schisturella sp. A	2.0e-03 ± 1.3e-03	1.3e-02 ± 1.2e-02	4.3e-02 ± 2.4e-02	-	-	-	-	8.7e-04 ± 4.4e-04	8.9e-04 ± 5.1e-04	4.9e-04 ± 2.5e-04	7.2e-04 ± 7.3e-05	3.0e-04 ± 3.0e-04
Sebidae sp. A	6.2e-03 ± 1.6e-03	1.0e-03 ± 4.7e-04	3.9e-03 ± 1.3e-03	7.4e-04 ± 4.3e-04	-	-	2.7e-03 ± 1.3e-03	8.9e-04 ± 4.4e-04	-	4.9e-04 ± 4.9e-04	2.1e-04 ± 2.1e-04	-
CARIDEA												
Caridean sp. A	4.9e-04 ± 4.9e-04	-	5.9e-04 ± 3.0e-04	-	-	3.0e-04 ± 3.0e-04	-	-	-	-	-	-
CUMACEAN												
Cumacean sp. A	-	-	-	-	-	-	-	-	-	-	2.3e-04 ± 2.3e-04	-

Table S2.6 (Continued) Density (individuals per cm^2 substrate surface area) of fauna collected from BoWLs landers. Values are averages ± SE (n = 3).

PHYLUM, CLASS/ORDER, FAMILY, Morphospecies	N-1600			S-1600			N-2800			S-2800		
	W	B	C	W	B	C	W	B	C	W	B	C
DECAPODA												
Chionocetes sp. A	-	-	3.0e-04 ± 3.0e-04	-	-	-	-	-	-	-	-	-
Paralomis sp. A	-	1.6e-04 ± 1.6e-04	-	-	-	-	-	-	-	-	-	-
GALATHEOIDEA												
Galatheid sp. E	-	2.2e-04 ± 2.2e-04	-	-	-	-	-	-	-	-	-	-
Munidopsis albatrossae	-	-	-	-	-	-	-	-	-	2.5e-04 ± 2.5e-04	2.1e-03 ± 1.7e-03	5.9e-04 ± 5.9e-04
Munidopsis cascadia	-	-	-	-	-	-	2.0e-03 ± 4.9e-04	1.1e-02 ± 1.6e-03	1.2e-03 ± 3.0e-04	7.4e-04 ± 4.3e-04	3.2e-03 ± 1.6e-03	5.9e-04 ± 5.9e-04
Munidopsis cf. *antonii*	-	-	-	-	-	-	1.2e-02 ± 2.1e-03	1.1e-02 ± 3.1e-03	6.2e-03 ± 8.9e-04	7.4e-04 ± 4.3e-04	4.2e-03 ± 1.6e-03	8.9e-04 ± 5.1e-04
Munidopsis cf. *lignaria*	-	-	-	-	-	-	9.9e-04 ± 6.5e-04	8.2e-04 ± 8.2e-04	-	3.5e-03 ± 1.9e-03	1.5e-03 ± 7.7e-04	5.9e-04 ± 3.0e-04

Table S2.6 (Continued) Density (individuals per cm^2 substrate surface area) of fauna collected from BoWLs landers. Values are averages ± SE (n = 3).

PHYLUM, CLASS/ORDER, FAMILY, Morphospecies	N-1600			S-1600			N-2800			S-2800		
	W	B	C	W	B	C	W	B	C	W	B	C
ISOPODA												
Eurycopinae sp. A	-	-	3.0e-04 ± 3.0e-04	-	7.5e-04 ± 7.5e-04	1.8e-03 ± 1.8e-03	8.6e-03 ± 2.8e-03	7.6e-02 ± 4.8e-02	4.3e-02 ± 1.4e-02	2.0e-03 ± 1.6e-03	2.0e-02 ± 1.4e-02	2.1e-02 ± 7.1e-03
Eurycopinae sp. B	-	-	-	-	-	-	-	2.3e-04 ± 2.3e-04	3.0e-04 ± 3.0e-04	-	-	-
Ilyarachna profunda	2.5e-04 ± 2.5e-04	1.0e-03 ± 7.4e-04	-	-	1.9e-04 ± 1.9e-04	-	-	-	-	2.7e-03 ± 1.1e-03	5.9e-03 ± 4.7e-04	1.2e-03 ± 7.8e-04
Ischnomesid sp. A	-	-	-	-	-	-	-	-	-	-	-	5.9e-04 ± 3.0e-04
Isopod sp. H	-	-	-	-	-	-	-	-	-	-	-	3.0e-04 ± 3.0e-04
Isopod sp. J	-	-	-	-	1.8e-04 ± 1.8e-04	-	-	-	-	-	-	-
Isopod sp. K	-	-	5.9e-04 ± 5.9e-04	-	-	-	-	-	-	-	-	-
Janirid sp.	-	-	-	-	-	-	-	-	-	1.5e-03 ± 1.1e-03	6.4e-04 ± 3.6e-04	-
MYSIDA												
Mysid sp. A	-	-	3.0e-04 ± 3.0e-04	-	-	-	-	-	-	-	-	-

Table S2.6 (Continued) Density (individuals per cm^2 substrate surface area) of fauna collected from BoWLs landers. Values are averages ± SE (n = 3).

PHYLUM, CLASS/ORDER, FAMILY, Morphospecies	N-1600			S-1600			N-2800			S-2800		
	W	B	C	W	B	C	W	B	C	W	B	C
NEBALIIDAE												
Nebalia sp. A	7.4e-04 ± 7.4e-04	6.5e-04 ± 4.4e-04	4.7e-03 ± 2.5e-03	-	-	-	-	-	-	-	-	-
Nebalia sp. B	-	-	-	-	-	-	1.2e-03 ± 6.5e-04	-	-	-	-	-
TANAIDACEA												
Tanaid sp. A	-	-	3.0e-04 ± 3.0e-04	-	-	-	1.5e-03 ± 8.5e-04	-	3.0e-03 ± 1.6e-03	2.5e-04 ± 2.5e-04	-	2.7e-03 ± 8.9e-04
Tanaid sp. B	-	2.2e-04 ± 2.2e-04	-	-	-	3.0e-04 ± 3.0e-04	-	-	-	-	-	3.0e-04 ± 3.0e-04
Tanaid sp. C	-	-	3.0e-04 ± 3.0e-04	-	1.9e-04 ± 1.9e-04	-	-	-	-	-	-	-
Tanaid sp. D	-	-	-	-	-	-	-	-	-	-	-	3.0e-04 ± 3.0e-04
Tanaid sp. E	-	-	-	-	-	-	-	-	3.0e-04 ± 3.0e-04	-	-	-
Tanaid sp. F	-	-	-	-	-	-	2.5e-04 ± 2.5e-04	-	-	2.5e-04 ± 2.5e-04	2.1e-04 ± 2.1e-04	-

Table S2.6 (Continued) Density (individuals per cm^2 substrate surface area) of fauna collected from BoWLs landers. Values are averages ± SE (n = 3).

PHYLUM, CLASS/ORDER, FAMILY, Morphospecies	N-1600			S-1600			N-2800			S-2800		
	W	B	C	W	B	C	W	B	C	W	B	C
PYCNOGONIDA												
Pycnogonid sp. A	-	-	-	-	-	-	-	-	-	1.7e-03 ± 1.7e-03	-	6.2e-03 ± 2.7e-03
CHORDATA												
ACTINOPTERYGII												
Zoarcid sp. A	-	-	-	-	-	-	-	-	3.0e-04 ± 3.0e-04	-	-	-
CNIDARIA												
ACTINARIA												
Actinarian sp.	4.9e-04 ± 2.5e-04	-	3.0e-04 ± 3.0e-04	-	-	-	2.5e-03 ± 6.5e-04	8.8e-04 ± 2.5e-04	3.0e-03 ± 5.9e-04	1.2e-03 ± 6.5e-04	7.9e-04 ± 5.1e-04	3.0e-04 ± 3.0e-04
ECHINODERMATA												
GORGONOCEPHALA												
Gorgonocephalan sp. A	-	2.2e-04 ± 2.2e-04	-	-	-	-	-	-	-	-	-	-

Table S2.6 (Continued) Density (individuals per cm^2 substrate surface area) of fauna collected from BoWLs landers. Values are averages ± SE (n = 3).

PHYLUM, CLASS/ORDER, FAMILY, Morphospecies	N-1600			S-1600			N-2800			S-2800		
	W	B	C	W	B	C	W	B	C	W	B	C
OPHIUROIDEA												
Ophiophthalmus normani	9.9e-04 ± 6.5e-04	1.7e-03 ± 9.5e-04	4.4e-03 ± 2.1e-03	-	-	3.0e-04 ± 3.0e-04	-	-	-	-	-	-
Ophiuroid sp. B	-	-	-	-	1.9e-04 ± 1.9e-04	-	-	-	-	-	-	-
Ophiuroid sp. C	-	-	-	-	-	-	-	-	-	-	-	3.0e-04 ± 3.0e-04
MOLLUSCA												
APLACOPHORA												
Aplacophoran sp. A	2.5e-03 ± 2.5e-03	9.8e-04 ± 7.5e-04	-	-	-	-	-	-	-	-	-	-
BIVALVIA												
Bathypecten sp. A	-	-	5.9e-04 ± 5.9e-04	7.4e-04 ± 4.3e-04	1.9e-04 ± 1.9e-04	3.0e-04 ± 3.0e-04	-	2.0e-04 ± 2.0e-04	3.0e-04 ± 3.0e-04	2.5e-04 ± 2.5e-04	-	-
Bivalve sp. B	1.4e-02 ± 3.3e-03	9.4e-03 ± 2.0e-03	2.1e-02 ± 3.1e-03	2.5e-04 ± 2.5e-04	-	4.4e-03 ± 1.9e-03	-	-	-	-	-	-
Bivalve sp. E	2.5e-04 ± 2.5e-04	1.4e-03 ± 1.1e-03	5.9e-03 ± 1.1e-03	-	5.0e-04 ± 5.0e-04	8.9e-04 ± 8.9e-04	2.5e-04 ± 2.5e-04	-	-	-	-	-

Table S2.6 (Continued) Density (individuals per cm^2 substrate surface area) of fauna collected from BoWLs landers. Values are averages ± SE (n = 3).

PHYLUM, CLASS/ORDER, FAMILY, Morphospecies	N-1600			S-1600			N-2800			S-2800		
	W	B	C	W	B	C	W	B	C	W	B	C
Bivalve sp. F	9.9e-04 ± 9.9e-04	4.4e-04 ± 4.4e-04	-	7.4e-04 ± 7.4e-04	3.6e-04 ± 3.6e-04	3.0e-04 ± 3.0e-04	-	-	-	-	-	-
Bivalve sp. G	-	1.0e-03 ± 8.0e-04	3.0e-04 ± 3.0e-04	-	4.3e-04 ± 2.3e-04	-	-	2.3e-04 ± 2.3e-04	-	-	-	-
Bivalve sp. H	-	-	3.0e-04 ± 3.0e-04	-	-	-	2.5e-04 ± 2.5e-04	-	-	-	-	-
Bivalve sp. I	-	-	-	-	-	-	-	-	-	-	-	3.0e-04 ± 3.0e-04
Idas washingtonius	9.6e-03 ± 2.2e-03	5.4e-03 ± 1.4e-03	2.7e-03 ± 1.5e-03	5.4e-03 ± 2.4e-03	5.6e-03 ± 2.8e-03	3.0e-04 ± 3.0e-04	2.0e-03 ± 2.0e-03	1.5e-03 ± 2.7e-04	-	-	4.5e-04 ± 4.5e-04	-
Xylonora corona	-	-	-	-	-	-	8.8e-02 ± 4.8e-02	-	-	-	-	-
Xylophaga microchira	7.4e-04 ± 7.4e-04	-	-	2.5e-04 ± 2.5e-04	-	-	-	-	-	-	-	-
Xylonora muraokai	-	-	-	-	-	-	5.4e-01 ± 5.3e-01	-	-	-	-	-
Xylophaga oregona	2.0e+00 ± 4.1e-01	-	-	1.9e-02 ± 2.4e-03	-	-	-	-	-	-	-	-
Xylonora zierenbergi	-	-	-	-	-	-	9.5e-01 ± 3.1e-01	-	-	-	-	-

Table S2.6 (Continued) Density (individuals per cm^2 substrate surface area) of fauna collected from BoWLs landers. Values are averages ± SE (n = 3).

PHYLUM, CLASS/ORDER, FAMILY, Morphospecies	N-1600			S-1600			N-2800			S-2800		
	W	B	C	W	B	C	W	B	C	W	B	C
Xylopholas crooki	-	-	-	-	-	-	8.4e-03 ± 2.6e-03	-	-	-	-	-
GASTROPODA												
cf *Laeviphitus* sp.	-	-	-	-	-	5.9e-04 ± 5.9e-04	4.9e-03 ± 3.3e-03	3.1e-02 ± 2.4e-03	4.4e-03 ± 1.4e-03	2.5e-04 ± 2.5e-04	1.3e-03 ± 6.3e-04	-
Dillwynella sp. A	2.5e-04 ± 2.5e-04	-	-	-	1.8e-04 ± 1.8e-04	3.0e-04 ± 3.0e-04	1.5e-03 ± 1.1e-03	2.3e-04 ± 2.3e-04	3.0e-04 ± 3.0e-04	1.3e-02 ± 7.4e-04	4.5e-04 ± 4.5e-04	2.1e-03 ± 1.2e-03
Eulimid sp. A	2.5e-04 ± 2.5e-04	4.4e-04 ± 4.4e-04	-	-	-	-	-	-	-	-	-	-
Gastropod sp. H	-	-	3.0e-04 ± 3.0e-04	2.5e-04 ± 2.5e-04	-	-	2.5e-04 ± 2.5e-04	-	-	-	-	-
Gastropod sp. I	-	-	3.0e-04 ± 3.0e-04	-	-	-	-	-	-	-	-	-
Gastropod sp. J	-	-	-	7.4e-04 ± 7.4e-04	-	-	-	-	-	-	-	3.0e-04 ± 3.0e-04
Gastropod sp. K	-	-	-	-	-	-	2.5e-04 ± 2.5e-04	-	-	-	-	-
Gastropod sp. L	-	-	-	9.9e-04 ± 2.5e-04	-	8.9e-04 ± 7.7e-20	-	-	-	-	-	-

Table S2.6 (Continued) Density (individuals per cm^2 substrate surface area) of fauna collected from BoWLs landers. Values are averages ± SE (n = 3).

PHYLUM, CLASS/ORDER, FAMILY, Morphospecies	N-1600			S-1600			N-2800			S-2800		
	W	B	C	W	B	C	W	B	C	W	B	C
Gastropod sp. M	-	-	5.9e-04 ± 3.0e-04	-	-	-	-	-	-	-	-	-
Gastropod sp. N	-	-	-	-	-	3.0e-04 ± 3.0e-04	-	-	-	-	-	-
Hyalogyrina sp. A	3.0e-03 ± 1.9e-03	2.6e-02 ± 1.0e-02	2.7e-03 ± 5.1e-04	2.5e-04 ± 2.5e-04	8.8e-03 ± 6.6e-03	8.9e-04 ± 5.1e-04	-	-	1.5e-03 ± 1.5e-03	-	9.1e-04 ± 5.4e-04	-
Provanna cf. *macleani*	-	-	-	-	-	-	3.0e-03 ± 1.5e-03	1.1e-03 ± 4.8e-04	-	-	-	-
LIMPET												
Limpet sp. A	4.9e-04 ± 4.9e-04	-	8.9e-04 ± 5.1e-04	1.8e-02 ± 1.4e-02	3.7e-04 ± 3.7e-04	4.4e-03 ± 1.9e-03	4.9e-04 ± 4.9e-04	-	-	-	-	-
Limpet sp. B	-	-	-	2.5e-04 ± 2.5e-04	-	-	-	2.2e-04 ± 2.2e-04	-	-	-	-
NUDIBRANCH												
Ziminella abyssa	-	-	1.5e-03 ± 3.0e-04	7.4e-04 ± 7.4e-04	-	1.5e-03 ± 7.8e-04	-	-	-	-	-	-

Table S2.6 (Continued) Density (individuals per cm^2 substrate surface area) of fauna collected from BoWLs landers. Values are averages ± SE (n = 3).

PHYLUM, CLASS/ORDER, FAMILY, Morphospecies	N-1600			S-1600			N-2800			S-2800		
	W	B	C	W	B	C	W	B	C	W	B	C
OCTOPODIDAE												
Graneledone pacifica	-	-	-	-	-	3.0e-04 ± 3.0e-04	-	-	-	-	-	-
NEMERTEA												
Nemertean sp.	-	-	5.9e-04 ± 3.0e-04	4.9e-04 ± 4.9e-04	-	-	1.2e-03 ± 6.5e-04	4.1e-04 ± 4.1e-04	5.9e-04 ± 5.9e-04	1.2e-03 ± 1.2e-03	4.3e-04 ± 2.2e-04	-
PLATYHELMINTHES												
Triclad sp. A	6.1e-01 ± 2.0e-01	1.3e-03 ± 8.7e-04	5.3e-02 ± 1.6e-02	4.3e-02 ± 2.4e-02	-	-	-	-	-	-	-	-
Polyclad sp. A	-	-	-	-	-	-	1.3e-02 ± 2.1e-03	-	3.0e-04 ± 3.0e-04	-	-	-

Table S2.7 Density (individuals per cm^3 substrate) of fauna collected from BoWLs landers. Values are averages ± SE (n = 3).

PHYLUM, CLASS/ORDER, FAMILY, Morphospecies	N-1600		S-1600		N-2800		S-2800	
	W	B	W	B	W	B	W	B
ANNELIDA								
POLYCHAETA								
ACROCIRRIDAE								
Acrocirrid sp. 3	-	-	-	-	-	-	-	-
Flabelligella cf. *macrochaeta*	8.7e-04 ± 8.7e-04	-	1.1e-04 ± 1.1e-04	-	-	-	-	-
AMPHARETIDAE								
Anobothrus apaleatus	-	8.1e-05 ± 8.1e-05	-	-	6.5e-04 ± 5.0e-04	-	-	-
Ampharetid sp. 21	-	-	-	-	1.1e-04 ± 1.1e-04	-	-	-
Ampharetid sp. 22	9.4e-02 ± 1.2e-02	-	5.4e-03 ± 1.8e-03	8.0e-05 ± 8.0e-05	4.4e-04 ± 4.4e-04	8.6e-05 ± 0.0e+00	-	-
Ampharetid sp. 23	-	-	-	-	-	-	-	-
Decemunciger sp.	3.0e-01 ± 8.7e-02	1.6e-04 ± 8.2e-05	1.3e-02 ± 7.3e-03	-	3.7e-03 ± 1.6e-03	0.0e+00 ± 1.1e-04	1.1e-04 ± 1.1e-04	-
Sosane wahrbergi	-	-	-	-	-	-	-	-
Sosane sp. A	-	-	-	-	1.1e-04 ± 1.1e-04	-	-	-
CAPITELLIDAE								
Capitella cf. *capitata*	3.1e-03 ± 1.2e-03	3.1e-04 ± 6.2e-05	9.8e-04 ± 5.7e-04	1.6e-03 ± 8.5e-04	4.1e-03 ± 2.1e-03	0.0e+00 ± 3.3e-04	3.3e-04 ± 3.3e-04	2.6e-03 ± 3.3e-04

Table S2.7 (Continued) Density (individuals per cm^3 substrate) of fauna collected from BoWLs landers. Values are averages ± SE (n = 3).

PHYLUM, CLASS/ORDER, FAMILY, Morphospecies	N-1600		S-1600		N-2800		S-2800	
	W	B	W	B	W	B	W	B
Capitella cf. *ovincola*	1.1e-04 ± 1.1e-04	4.9e-04 ± 2.9e-04	3.3e-04 ± 3.3e-04	3.3e-03 ± 1.5e-03	1.3e-03 ± 1.3e-03	-	-	1.2e-03 ± 8.0e-04
Capitellid sp. 10	-	-	-	-	4.4e-04 ± 2.2e-04	2.7e-04 ± 2.0e-04	5.4e-04 ± 1.1e-04	7.1e-04 ± 7.1e-04
Capitellid sp. 13	-	-	-	-	-	-	-	-
CIRRATULIDAE								
Chaetozone sp. A	-	-	-	-	-	-	-	-
Chaetozone sp. B	-	-	-	-	8.7e-04 ± 8.7e-04	-	-	-
Cirratulid sp. 14	1.1e-04 ± 1.1e-04	-	-	-	-	-	-	-
CTENODRILLIDAE								
Ctenodrillid sp. 2	-	-	-	-	-	-	-	-
DORVILLEIDAE								
Dorvilleid sp. 15	8.7e-04 ± 4.4e-04	3.2e-03 ± 1.6e-03	5.4e-04 ± 2.2e-04	3.2e-04 ± 3.2e-04	8.4e-03 ± 3.6e-03	5.2e-03 ± 4.8e-04	-	3.2e-04 ± 1.9e-04
Dorvilleid sp. 32	4.4e-04 ± 4.4e-04	-	-	-	-	-	-	-

Table S2.7 (Continued) Density (individuals per cm^3 substrate) of fauna collected from BoWLs landers. Values are averages ± SE (n = 3).

PHYLUM, CLASS/ORDER, FAMILY, Morphospecies	N-1600		S-1600		N-2800		S-2800	
	W	B	W	B	W	B	W	B
Dorvilleid sp. 39	-	-	-	-	-	2.6e-04 ± 0.0e+00	-	-
Dorvilleid sp. 54	9.8e-04 ± 6.5e-04	1.7e-03 ± 1.5e-03	9.8e-04 ± 6.5e-04	2.3e-04 ± 1.3e-04	2.2e-04 ± 2.2e-04	3.5e-04 ± 3.5e-04	2.2e-04 ± 2.2e-04	1.9e-04 ± 1.9e-04
Dorvilleid sp. 55	-	-	-	-	3.4e-02 ± 9.1e-03	-	-	-
Dorvilleid sp. 56	1.1e-04 ± 1.1e-04	1.7e-04 ± 1.7e-04	-	-	-	-	-	-
Dorvilleid sp. 58	-	1.4e-04 ± 1.4e-04	-	-	-	-	-	-
Ophryotrocha batillus	2.6e-02 ± 3.8e-03	1.2e-01 ± 1.1e-01	4.7e-03 ± 1.0e-03	4.1e-03 ± 3.8e-03	1.4e-01 ± 5.2e-02	5.5e-03 ± 3.7e-03	7.6e-04 ± 4.4e-04	4.0e-03 ± 3.7e-03
Ophryotrocha craigsmithi	-	1.4e-04 ± 1.4e-04	-	-	-	-	-	-
Ophryotrocha langstrumpae	4.5e+00 ± 1.2e+00	1.7e-03 ± 4.3e-04	2.8e-02 ± 4.7e-03	-	2.7e-02 ± 1.3e-02	8.6e-05 ± 0.0e+00	-	1.0e-04 ± 1.0e-04
Ophryotrocha longicollaris	-	-	-	-	1.1e-04 ± 1.1e-04	1.8e-04 ± 1.8e-04	3.3e-04 ± 3.3e-04	-
Ophryotrocha magnadentata	6.5e-04 ± 3.8e-04	2.9e-03 ± 2.4e-03	8.7e-04 ± 2.2e-04	8.0e-05 ± 8.0e-05	-	-	-	-

Table S2.7 (Continued) Density (individuals per cm^3 substrate) of fauna collected from BoWLs landers. Values are averages ± SE (n = 3).

PHYLUM, CLASS/ORDER, FAMILY, Morphospecies	N-1600		S-1600		N-2800		S-2800	
	W	B	W	B	W	B	W	B
Parophryotrocha sp. A	-	1.2e-02 ± 1.2e-02	1.1e-04 ± 1.1e-04	8.0e-05 ± 8.0e-05	1.1e-04 ± 1.1e-04	2.1e-01 ± 9.1e-02	-	5.1e-02 ± 2.1e-02
FLABELLIGERIDAE								
Flabelligerid sp. 7	-	-	1.1e-04 ± 1.1e-04	-	-	-	-	-
HESIONIDAE								
Gyptis sp. A	1.1e-04 ± 1.1e-04	1.1e-03 ± 9.7e-04	-	-	-	2.7e-04 ± 1.8e-04	-	-
Hesiocaeca sp. A	4.4e-04 ± 4.4e-04	1.4e-04 ± 1.4e-04	-	-	2.2e-04 ± 1.1e-04	0.0e+00 ± 1.1e-04	2.2e-04 ± 1.1e-04	1.9e-04 ± 1.9e-04
Hesiopina cf. *aurantiaca*	-	1.4e-04 ± 1.4e-04	-	-	1.1e-04 ± 1.1e-04	-	-	-
Sirsoe cf. *hessleri*	1.1e-04 ± 1.1e-04	-	1.3e-03 ± 5.0e-04	8.0e-05 ± 8.0e-05	3.3e-04 ± 3.3e-04	5.3e-04 ± 3.0e-04	2.2e-04 ± 2.2e-04	-
Vrijenhoekia balaenophila	4.4e-04 ± 4.4e-04	1.4e-04 ± 1.4e-04	-	1.5e-04 ± 1.5e-04	1.4e-03 ± 1.1e-04	4.5e-03 ± 2.0e-03	-	1.2e-03 ± 3.7e-04

Table S2.7 (Continued) Density (individuals per cm^3 substrate) of fauna collected from BoWLs landers. Values are averages ± SE (n = 3).

PHYLUM, CLASS/ORDER, FAMILY, Morphospecies	N-1600		S-1600		N-2800		S-2800	
	W	B	W	B	W	B	W	B
LUMBRINERIDAE								
Lumbrinerid sp. 1	-	-	-	-	-	-	-	-
MALDANIDAE								
Maldane sp. A	-	8.3e-05 ± 8.3e-05	-	-	-	-	-	-
NEREIDIDAE								
Nereidid sp. 6	4.4e-04 ± 4.4e-04	8.3e-05 ± 8.3e-05	1.1e-04 ± 1.1e-04	-	-	-	-	3.9e-04 ± 2.5e-04
OPHELIIDAE								
Opheliid sp. 4	-	-	-	-	1.1e-04 ± 1.1e-04	-	-	-
Opheliid sp. 5	-	-	-	-	1.1e-04 ± 1.1e-04	-	-	-
Opheliid sp. 6	-	-	-	-	-	-	-	-
PARAONIDAE								
Aricidea cf. *rubra*	-	-	-	8.0e-05 ± 8.0e-05	-	-	-	-
Paraonides sp. A	-	-	-	-	-	-	-	-

Table S2.7 (Continued) Density (individuals per cm^3 substrate) of fauna collected from BoWLs landers. Values are averages ± SE (n = 3).

PHYLUM, CLASS/ORDER, FAMILY, Morphospecies	N-1600		S-1600		N-2800		S-2800	
	W	B	W	B	W	B	W	B
PECTINARIIDAE								
Pectinariid sp. 1	-	-	-	-	-	-	-	-
PHOLOIDAE								
Pholoid sp. 1	-	-	-	-	-	-	-	-
PHYLLODOCIDAE								
Sige brunnea	1.1e-04 ± 1.1e-04	-	-	-	-	-	-	-
POLYNOIDAE								
Harmothoe cf. *fragilis*	8.7e-04 ± 3.9e-04	5.9e-04 ± 3.8e-04	2.2e-04 ± 1.1e-04	3.0e-04 ± 3.0e-04	-	-	-	-
Peinaleopolynoe santacatalina	1.1e-04 ± 1.1e-04	-	1.1e-04 ± 1.1e-04	-	1.1e-04 ± 1.1e-04	-	2.2e-04 ± 2.2e-04	3.7e-04 ± 3.7e-04
SCALIBREGMATIDAE								
Scalibregmatid sp. 2	-	-	-	-	-	-	-	-

Table S2.7 (Continued) Density (individuals per cm^3 substrate) of fauna collected from BoWLs landers. Values are averages ± SE (n = 3).

PHYLUM, CLASS/ORDER, FAMILY, Morphospecies	N-1600		S-1600		N-2800		S-2800	
	W	B	W	B	W	B	W	B
SERPULIDAE								
Serpulid sp. 1	-	-	2.2e-04 ± 2.2e-04	-	-	-	-	-
SIBOGLINIDAE								
Osedax rubiplumus	-	1.1e-03 ± 1.1e-03	-	-	-	-	-	-
Osedax sp. B	-	4.0e-03 ± 4.0e-03	-	3.3e-03 ± 3.3e-03	-	5.8e-01 ± 5.3e-01	-	3.6e-03 ± 3.6e-03
SIGALIONIDAE								
Sigalionid sp. 3	-	-	-	-	-	-	-	-
SPHAERODORIDAE								
Sphaerodorid sp. 1	4.4e-04 ± 4.4e-04	-	-	-	-	-	-	-
SPIONIDAE								
Aurospio cf. *dibranchiata*	-	-	-	-	-	1.8e-04 ± 1.8e-04	-	-
Spionid sp. 13	-	-	-	-	-	-	-	1.0e-04 ± 1.0e-04

Table S2.7 (Continued) Density (individuals per cm^3 substrate) of fauna collected from BoWLs landers. Values are averages ± SE (n = 3).

PHYLUM, CLASS/ORDER, FAMILY, Morphospecies	N-1600		S-1600		N-2800		S-2800	
	W	B	W	B	W	B	W	B
Laonice sp. A	7.6e-04 ± 1.1e-04	2.1e-03 ± 9.8e-04	5.4e-04 ± 2.9e-04	8.1e-04 ± 2.6e-04	6.5e-04 ± 1.9e-04	0.0e+00 ± 1.1e-04	1.1e-04 ± 1.1e-04	2.0e-04 ± 2.0e-04
Prionospio cf. *ehlersi*	-	-	-	-	-	-	-	-
Prionospio sp. A	-	-	-	-	-	-	1.1e-04 ± 1.1e-04	2.6e-04 ± 1.6e-04
SYLLIDAE								
Syllid sp. 13	-	-	-	-	-	-	-	-
Proceraea sp. A	-	-	-	-	1.1e-04 ± 1.1e-04	-	-	-
Sphaerosyllis sp. A	6.5e-04 ± 3.3e-04	2.5e-04 ± 1.4e-04	2.2e-04 ± 1.1e-04	8.0e-05 ± 8.0e-05	7.3e-03 ± 2.2e-03	8.6e-05 ± 0.0e+00	1.5e-03 ± 1.2e-03	4.6e-04 ± 3.2e-04
TEREBELLIDAE								
Terrebellid sp. 8	1.1e-04 ± 1.1e-04	-	-	-	1.1e-04 ± 1.1e-04	-	-	-
Neoamphitrite sp. A	2.2e-04 ± 1.1e-04	8.1e-05 ± 8.1e-05	-	-	-	-	-	-

Table S2.7 (Continued) Density (individuals per cm^3 substrate) of fauna collected from BoWLs landers. Values are averages ± SE (n = 3).

PHYLUM, CLASS/ORDER, FAMILY, Morphospecies	N-1600		S-1600		N-2800		S-2800	
	W	B	W	B	W	B	W	B
CLITELLATA								
HIRUDINEA								
Hirudinid sp. A	-	2.3e-04 ± 1.2e-04	4.4e-04 ± 4.4e-04	8.9e-04 ± 6.7e-04	-	1.8e-04 ± 1.8e-04	-	-
ARTHROPODA								
AMPHIPODA								
Accedomoera sp. A	-	-	-	-	2.3e-01 ± 3.9e-02	5.9e-01 ± 3.7e-01	9.8e-03 ± 6.3e-03	3.5e-02 ± 2.7e-02
Amphipod sp. G	-	2.3e-04 ± 1.2e-04	-	-	-	2.7e-04 ± 1.8e-04	-	7.2e-05 ± 7.2e-05
Amphipod sp. H	-	5.9e-04 ± 3.8e-04	-	-	2.2e-04 ± 2.2e-04	9.0e-05 ± 1.0e-04	1.1e-04 ± 1.1e-04	-
Amphipod sp. K	5.4e-04 ± 5.4e-04	6.8e-03 ± 5.3e-03	-	1.1e-04 ± 1.1e-04	4.4e-04 ± 4.4e-04	-	-	-
Bathyceradocus sp. A	-	-	-	-	2.0e-03 ± 5.0e-04	0.0e+00 ± 5.4e-04	1.2e-03 ± 6.1e-04	-
Euonyx sp. A	-	-	-	-	-	2.7e-04 ± 1.5e-04	-	1.9e-04 ± 1.9e-04
Isaeid sp. A	-	-	-	-	3.3e-04 ± 3.3e-04	-	-	3.7e-04 ± 3.7e-04

Table S2.7 (Continued) Density (individuals per cm^3 substrate) of fauna collected from BoWLs landers. Values are averages ± SE (n = 3).

PHYLUM, CLASS/ORDER, FAMILY, Morphospecies	N-1600		S-1600		N-2800		S-2800	
	W	B	W	B	W	B	W	B
Lysianassid sp. A	3.2e-03 ± 2.4e-03	8.6e-03 ± 8.0e-03	-	-	2.6e-03 ± 8.6e-04	1.8e-04 ± 1.9e-04	8.7e-04 ± 2.2e-04	-
Oedicerotid sp. A	-	-	-	-	-	-	-	-
Schisturella sp. A	8.7e-04 ± 5.8e-04	1.1e-02 ± 1.1e-02	-	-	-	5.3e-04 ± 3.0e-04	2.2e-04 ± 1.1e-04	3.6e-04 ± 1.0e-04
Sebidae sp. A	2.7e-03 ± 7.1e-04	7.4e-04 ± 4.9e-04	3.3e-04 ± 1.9e-04	-	1.2e-03 ± 5.8e-04	5.2e-04 ± 3.1e-04	2.2e-04 ± 2.2e-04	7.2e-05 ± 7.2e-05
CARIDEA								
Caridean sp. A	2.2e-04 ± 2.2e-04	-	-	-	-	-	-	-
CUMACEAN								
Cumacean sp. A	-	-	-	-	-	-	-	1.9e-04 ± 1.9e-04
DECAPODA								
Chionocetes sp. A	-	-	-	-	-	-	-	-
Paralomis sp. A	-	1.4e-04 ± 1.4e-04	-	-	-	-	-	-

Table S2.7 (Continued) Density (individuals per cm^3 substrate) of fauna collected from BoWLs landers. Values are averages ± SE (n = 3).

PHYLUM, CLASS/ORDER, FAMILY, Morphospecies	N-1600		S-1600		N-2800		S-2800	
	W	B	W	B	W	B	W	B
GALATHEOIDEA								
Galatheid sp. E	-	8.3e-05 ± 8.3e-05	-	-	-	-	-	-
Munidopsis albatrossae	-	-	-	-	-	-	1.1e-04 ± 1.1e-04	1.6e-03 ± 1.4e-03
Munidopsis cascadia	-	-	-	-	8.7e-04 ± 2.2e-04	5.9e-03 ± 2.8e-03	3.3e-04 ± 1.9e-04	1.2e-03 ± 4.9e-04
Munidopsis cf. *antonii*	-	-	-	-	5.3e-03 ± 9.3e-04	5.6e-03 ± 2.3e-03	3.3e-04 ± 1.9e-04	2.6e-03 ± 1.7e-03
Munidopsis cf. *lignaria*	-	-	-	-	4.4e-04 ± 2.9e-04	3.6e-04 ± 3.6e-04	1.5e-03 ± 8.5e-04	5.2e-04 ± 2.7e-04
ISOPODA								
Eurycopinae sp. A	-	-	-	6.0e-04 ± 6.0e-04	3.8e-03 ± 1.3e-03	3.7e-02 ± 2.2e-02	8.7e-04 ± 7.1e-04	1.4e-02 ± 1.2e-02
Eurycopinae sp. B	-	-	-	-	-	1.8e-04 ± 1.8e-04	-	-
Ilyarachna profunda	1.1e-04 ± 1.1e-04	8.0e-04 ± 6.8e-04	-	1.5e-04 ± 1.5e-04	-	0.0e+00 ± 1.1e-04	1.2e-03 ± 4.7e-04	3.1e-03 ± 1.2e-03
Ischnomesid sp. A	-	-	-	-	-	-	-	-
Isopod sp. H	-	-	-	-	-	-	-	-

Table S2.7 (Continued) Density (individuals per cm^3 substrate) of fauna collected from BoWLs landers. Values are averages ± SE (n = 3).

PHYLUM, CLASS/ORDER, FAMILY, Morphospecies	N-1600		S-1600		N-2800		S-2800	
	W	B	W	B	W	B	W	B
Isopod sp. J	-	-	-	8.0e-05 ± 8.0e-05	-	-	-	-
Isopod sp. K	-	-	-	-	-	-	-	-
Janirid sp.	-	-	-	-	-	0.0e+00 ± 1.1e-04	6.5e-04 ± 5.0e-04	3.3e-04 ± 1.7e-04
MYSIDA								
Mysid sp. A	-	-	-	-	-	-	-	-
NEBALIIDAE								
Nebalia sp. A	3.3e-04 ± 3.3e-04	5.1e-04 ± 4.0e-04	-	-	-	-	-	-
Nebalia sp. B	-	-	-	-	5.4e-04 ± 2.9e-04	-	-	-
TANAIDACEA								
Tanaid sp. A	-	-	-	-	6.5e-04 ± 3.8e-04	-	1.1e-04 ± 1.1e-04	-
Tanaid sp. B	-	8.3e-05 ± 8.3e-05	-	-	-	-	-	-

Table S2.7 (Continued) Density (individuals per cm^3 substrate) of fauna collected from BoWLs landers. Values are averages ± SE (n = 3).

PHYLUM, CLASS/ORDER, FAMILY, Morphospecies	N-1600		S-1600		N-2800		S-2800	
	W	B	W	B	W	B	W	B
Tanaid sp. C	-	-	-	1.5e-04 ± 1.5e-04	-	-	-	-
Tanaid sp. D	-	-	-	-	-	-	-	-
Tanaid sp. E	-	-	-	-	-	-	-	-
Tanaid sp. F	-	-	-	-	1.1e-04 ± 1.1e-04	-	1.1e-04 ± 1.1e-04	7.2e-05 ± 7.2e-05
PYCNOGONIDA								
Pycnogonid sp. A	-	-	-	-	-	-	7.6e-04 ± 7.6e-04	-
CHORDATA								
ACTINOPTERYGII								
Zoarcid sp. A	-	-	-	-	-	-	-	-
CNIDARIA								
ACTINARIA								
Actinarian sp.	2.2e-04 ± 1.1e-04	-	-	-	1.1e-03 ± 2.9e-04	5.3e-04 ± 2.5e-04	5.4e-04 ± 2.9e-04	2.7e-04 ± 1.8e-04

Table S2.7 (Continued) Density (individuals per cm^3 substrate) of fauna collected from BoWLs landers. Values are averages ± SE (n = 3).

PHYLUM, CLASS/ORDER, FAMILY, Morphospecies	N-1600		S-1600		N-2800		S-2800	
	W	B	W	B	W	B	W	B
ECHINODERMATA								
GORGONOCEPHALA								
Gorgonocephalan sp. A	-	8.3e-05 ± 8.3e-05	-	-	-	-	-	-
OPHIUROIDEA								
Ophiophthalmus normani	4.4e-04 ± 2.9e-04	7.4e-04 ± 3.8e-04	-	-	-	-	-	-
Ophiuroid sp. B	-	-	-	1.5e-04 ± 1.5e-04	-	-	-	-
Ophiuroid sp. C	-	-	-	-	-	-	-	-
MOLLUSCA								
APLACOPHORA								
Aplacophoran sp. A	1.1e-03 ± 1.1e-03	8.0e-04 ± 6.8e-04	-	-	-	-	-	-
BIVALVIA								
Bathypecten sp. A	-	-	3.3e-04 ± 1.9e-04	1.5e-04 ± 1.5e-04	-	9.0e-05 ± 9.0e-05	1.1e-04 ± 1.1e-04	-
Bivalve sp. B	6.2e-03 ± 1.5e-03	5.3e-03 ± 1.3e-03	1.1e-04 ± 1.1e-04	-	-	-	-	-

Table S2.7 (Continued) Density (individuals per cm^3 substrate) of fauna collected from BoWLs landers. Values are averages ± SE (n = 3).

PHYLUM, CLASS/ORDER, FAMILY, Morphospecies	N-1600		S-1600		N-2800		S-2800	
	W	B	W	B	W	B	W	B
Bivalve sp. E	1.1e-04 ± 1.1e-04	1.1e-03 ± 9.7e-04	-	2.1e-04 ± 2.1e-04	1.1e-04 ± 1.1e-04	-	-	-
Bivalve sp. F	4.4e-04 ± 4.4e-04	1.7e-04 ± 1.7e-04	3.3e-04 ± 3.3e-04	1.6e-04 ± 1.6e-04	-	-	-	-
Bivalve sp. G	-	4.7e-04 ± 2.9e-04	-	1.9e-04 ± 9.5e-05	-	1.8e-04 ± 1.8e-04	-	-
Bivalve sp. H	-	-	-	-	1.1e-04 ± 1.1e-04	-	-	-
Bivalve sp. I	-	-	-	-	-	-	-	-
Idas washingtonius	4.2e-03 ± 9.8e-04	3.1e-03 ± 9.5e-04	2.4e-03 ± 1.1e-03	3.8e-03 ± 2.6e-03	8.7e-04 ± 8.7e-04	8.8e-04 ± 4.6e-04	-	3.7e-04 ± 3.7e-04
Xylonora corona	-	-	-	-	3.9e-02 ± 2.1e-02	-	-	-
Xylophaga microchira	3.3e-04 ± 3.3e-04	-	1.1e-04 ± 1.1e-04	-	-	-	-	-
Xylonora muraokai	-	-	-	-	2.4e-01 ± 2.3e-01	-	-	-
Xylophaga oregona	9.0e-01 ± 1.8e-01	-	8.3e-03 ± 1.1e-03	-	-	-	-	-

Table S2.7 (Continued) Density (individuals per cm^3 substrate) of fauna collected from BoWLs landers. Values are averages ± SE (n = 3).

PHYLUM, CLASS/ORDER, FAMILY, Morphospecies	N-1600		S-1600		N-2800		S-2800	
	W	B	W	B	W	B	W	B
Xylonora zierenbergi	-	-	-	-	4.2e-01 ± 1.3e-01	-	-	-
Xylopholas crooki	-	-	-	-	3.7e-03 ± 1.1e-03	-	-	-
GASTROPODA								
cf *Laeviphitus* sp.	-	-	-	-	2.2e-03 ± 1.4e-03	1.7e-02 ± 7.3e-03	1.1e-04 ± 1.1e-04	7.6e-04 ± 4.9e-04
Dillwynella sp. A	1.1e-04 ± 1.1e-04	-	-	8.0e-05 ± 8.0e-05	6.5e-04 ± 5.0e-04	1.8e-04 ± 1.6e-03	5.6e-03 ± 3.2e-04	3.7e-04 ± 3.7e-04
Eulimid sp. A	1.1e-04 ± 1.1e-04	1.7e-04 ± 1.7e-04	-	-	-	-	-	-
Gastropod sp. H	-	-	1.1e-04 ± 1.1e-04	-	1.1e-04 ± 1.1e-04	-	-	-
Gastropod sp. I	-	-	-	-	-	-	-	-
Gastropod sp. J	-	-	3.3e-04 ± 3.3e-04	-	-	-	-	-
Gastropod sp. K	-	-	-	-	1.1e-04 ± 1.1e-04	-	-	-
Gastropod sp. L	-	-	4.4e-04 ± 1.1e-04	-	-	-	-	-

Table S2.7 (Continued) Density (individuals per cm^3 substrate) of fauna collected from BoWLs landers. Values are averages ± SE (n = 3).

PHYLUM, CLASS/ORDER, FAMILY, Morphospecies	N-1600		S-1600		N-2800		S-2800	
	W	B	W	B	W	B	W	B
Gastropod sp. M	-	-	-	-	-	-	-	-
Gastropod sp. N	-	-	-	-	-	-	-	-
Hyalogyrina sp. A	1.3e-03 ± 8.2e-04	1.4e-02 ± 4.5e-03	1.1e-04 ± 1.1e-04	4.0e-03 ± 2.6e-03	-	-	-	3.2e-04 ± 1.9e-04
Provanna cf. *macleani*	-	-	-	-	1.3e-03 ± 6.5e-04	7.0e-04 ± 4.9e-04	-	-
LIMPET								
Limpet sp. A	2.2e-04 ± 2.2e-04	-	8.0e-03 ± 6.1e-03	3.0e-04 ± 3.0e-04	2.2e-04 ± 2.2e-04	-	-	-
Limpet sp. B	-	-	1.1e-04 ± 1.1e-04	-	-	8.6e-05 ± 0.0e+00	-	-
NUDIBRANCH								
Ziminella abyssa	-	-	3.3e-04 ± 3.3e-04	-	-	-	-	-
OCTOPODIDAE								
Graneledone pacifica	-	-	-	-	-	-	-	-

Table S2.7 (Continued) Density (individuals per cm^3 substrate) of fauna collected from BoWLs landers. Values are averages ± SE (n = 3).

PHYLUM, CLASS/ORDER, FAMILY, Morphospecies	N-1600		S-1600		N-2800		S-2800	
	W	B	W	B	W	B	W	B
NEMERTEA								
Nemertean sp.	-	-	2.2e-04 ± 2.2e-04	-	5.4e-04 ± 2.9e-04	1.8e-04 ± 1.8e-04	5.4e-04 ± 5.4e-04	2.6e-04 ± 1.6e-04
PLATYHELMINTHES								
Triclad sp. A	2.7e-01 ± 9.0e-02	1.0e-03 ± 7.9e-04	1.9e-02 ± 1.1e-02	-	-	-	-	-
Polyclad sp. A	-	-	-	-	5.7e-03 ± 9.5e-04	-	-	-

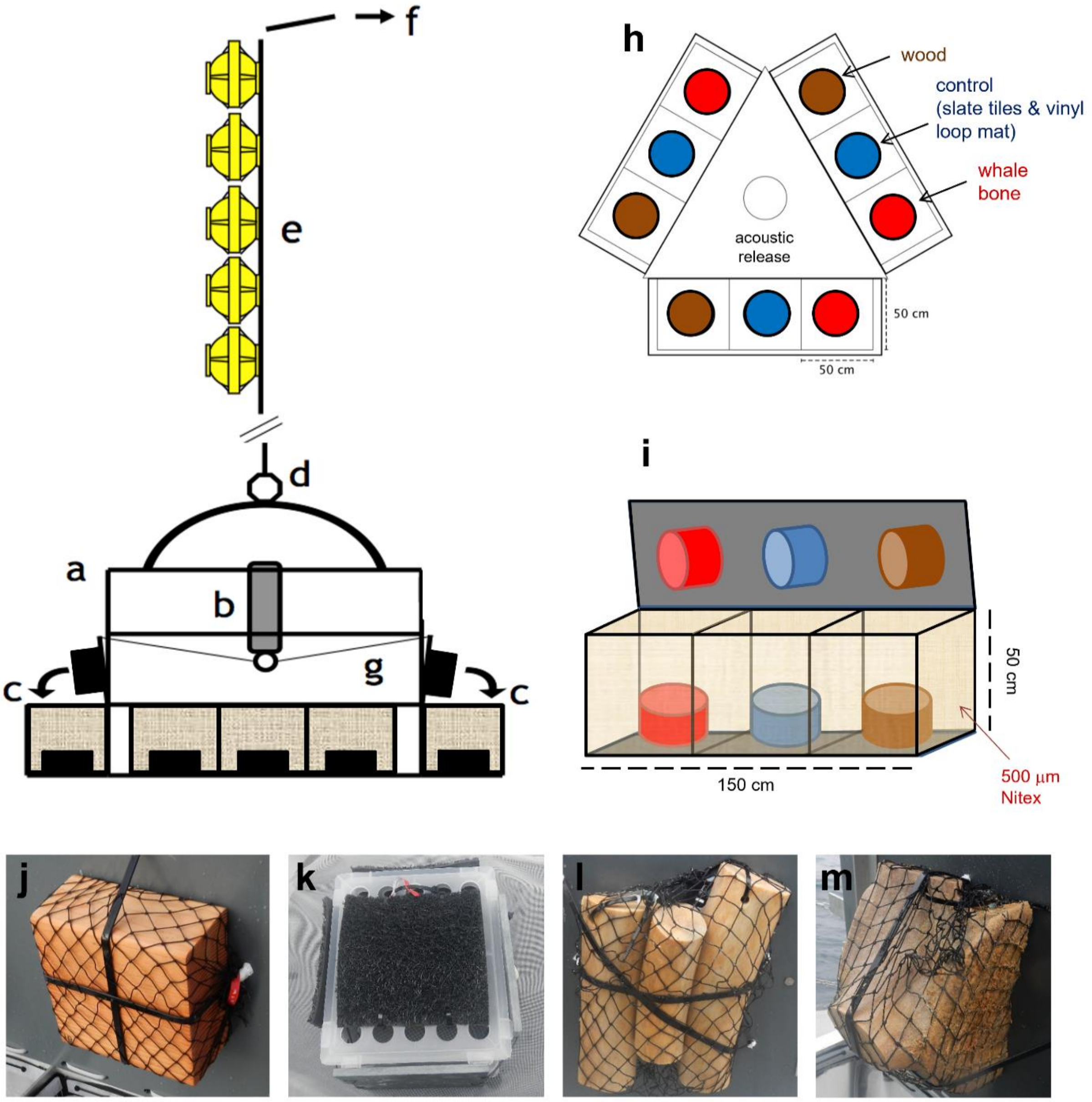

Figure S2.1 (a) Side view of a BoWL at the seafloor with bins open and substrates exposed. (b) Acoustic release, which will release bin doors (c,g) and drop the free-vehicle ballast weight (not shown) on an acoustic signal. (d) Flotation line and (e) glass flotation. (f) Attachment point for radio beacon 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. (j) Douglas fir wood substrate. (k) Control substrate, consisting of an upturned plastic crate with three 15 × 15 cm squares of vinyl loop mat and two 15 × 15 cm slate tiles attached. (l) Humpback whale rib bone packages. (m) Humpback whale vertebral half.

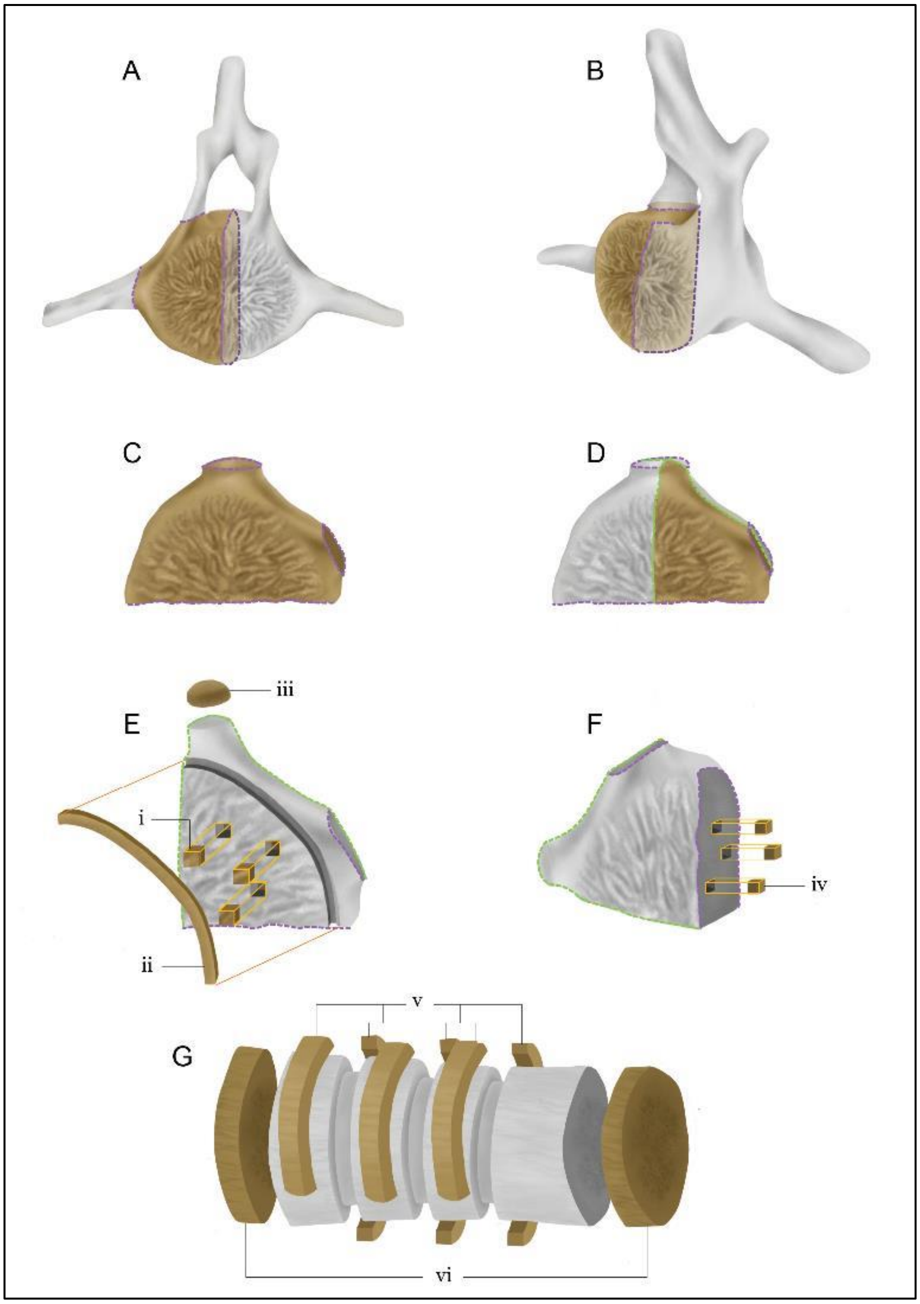

Figure S2.2 Whale bone subsampling schematic. (A, B) Lumbar vertebra of a humpback whale. Prior to deployment, transverse and spinous processes were removed and the remaining vertebral body was cut in half along the vertical axis. Cut locations are indicated by purple dashed lines. (C) Halved vertebral body. Vertebral bodies were attached to landers with the cut side in contact with the bottom of the mesh bins. (D) Subsample of vertebral body halves. After recovery, vertebral body halves were cut into four quarters (green dashed lines). (E, F) Vertebral eighth with transverse process oriented dorsally (E) and laterally (F). Subsampling of vertebral eighths involved extracting and sorting: (i) 3 × 1 cm^3 blocks from the vertebral body surface, (ii) the outer edge of the vertebral body, 1 cm2 around the perimeter, (iii) a 1 cm-thick slice of the exposed surface at the base of the transverse process, and (iv) 3 × 1 cm^3 blocks from the cut surface in contact with the bottom of the mesh bin. (G) Rib sections. Subsampling of rib sections involved extracting and sorting: (v) 3 × 1-cm-wide and 1-cm-deep bands, and (vi) 1-cm-thick slices from the cut edges.

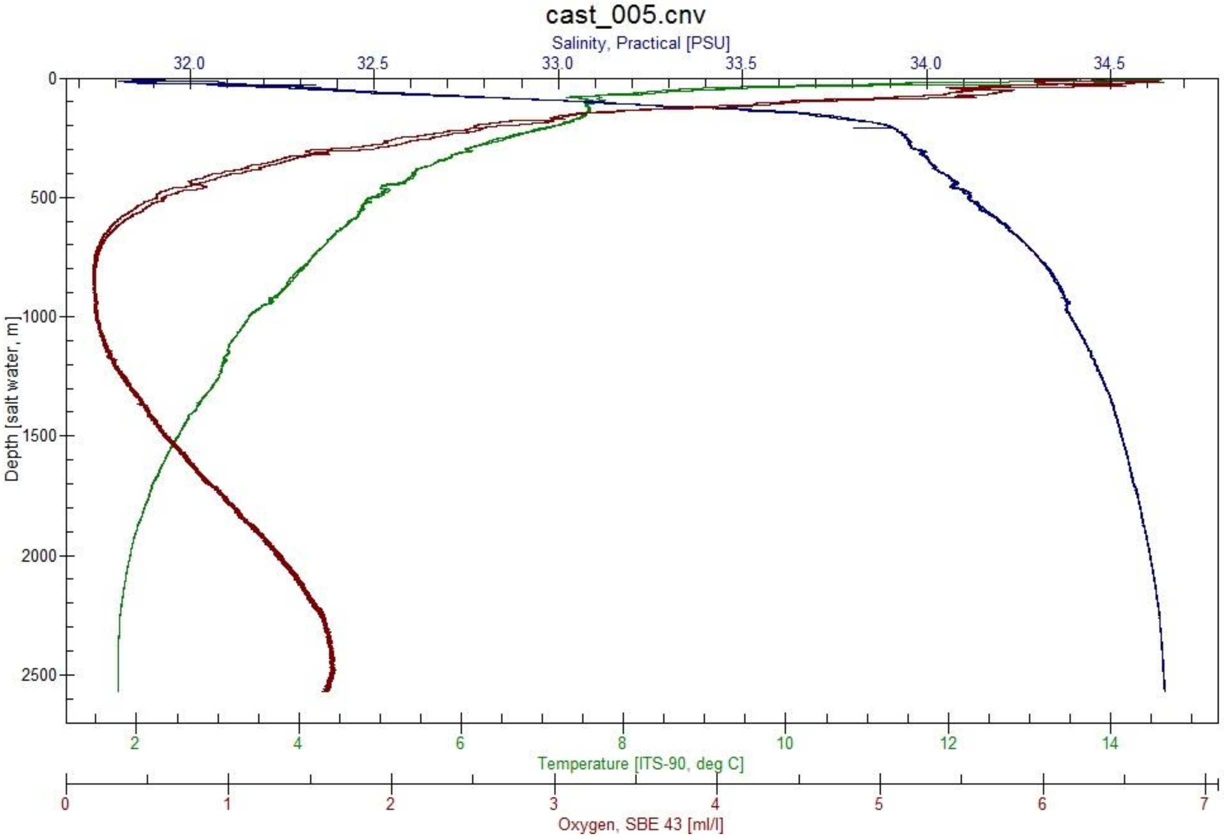

Figure S2.3 Typical salinity, temperature and oxygen profile measured on the Washington-Oregon margin during deployment cruise.

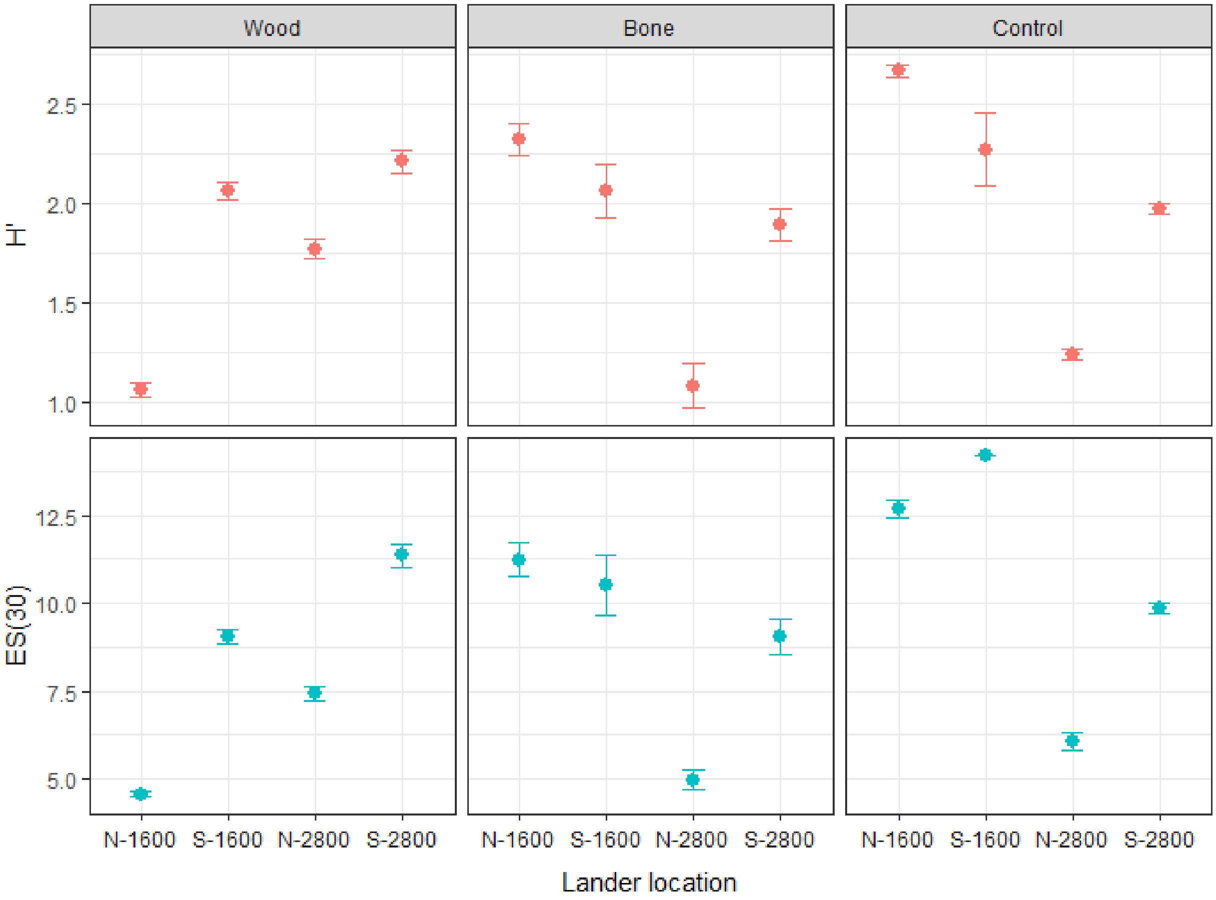

Figure S2.4 Shannon diversity, *H'*, and expected species richness rarefied to 30 individuals, ES(30), by substrate type and lander location. Plotted as mean (n = 3) ± SE.

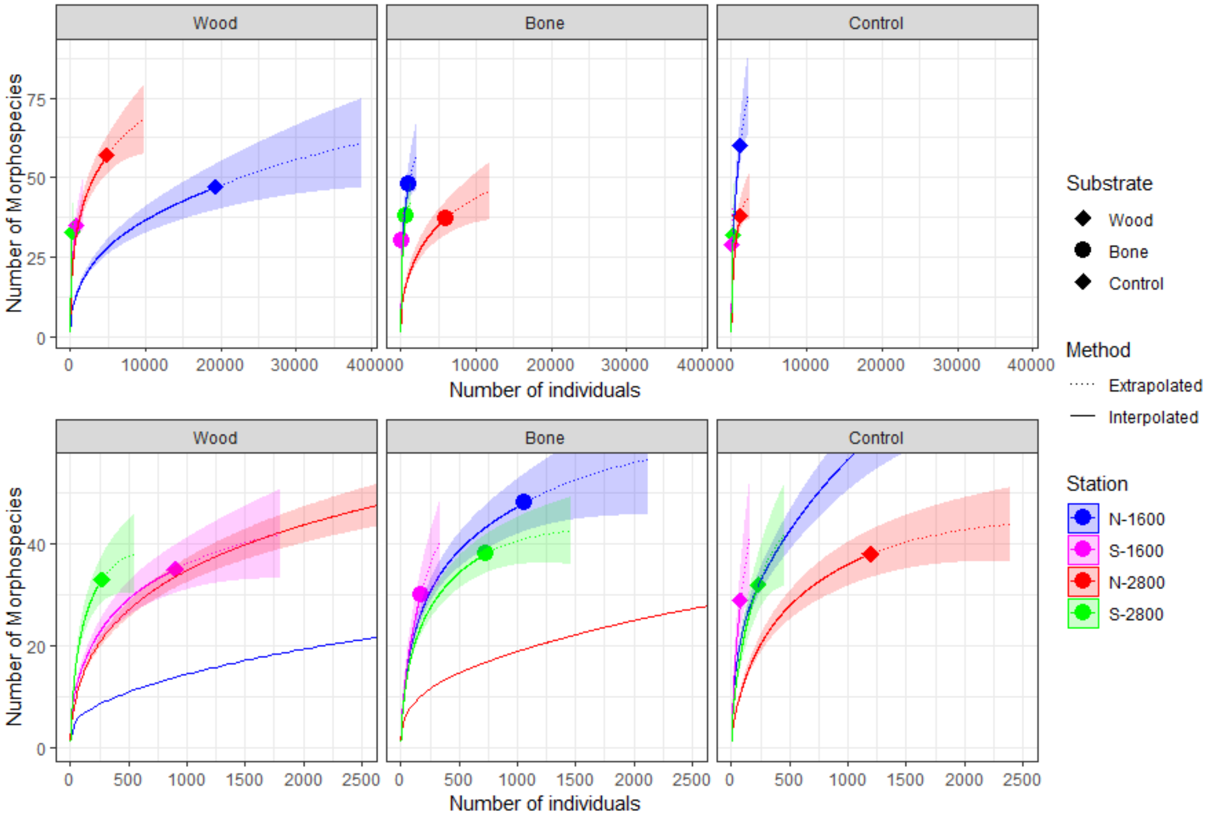

Figure S2.5 Rarefaction curves of assemblages, plotted by station and substrate type. Endpoints are double the sample size.

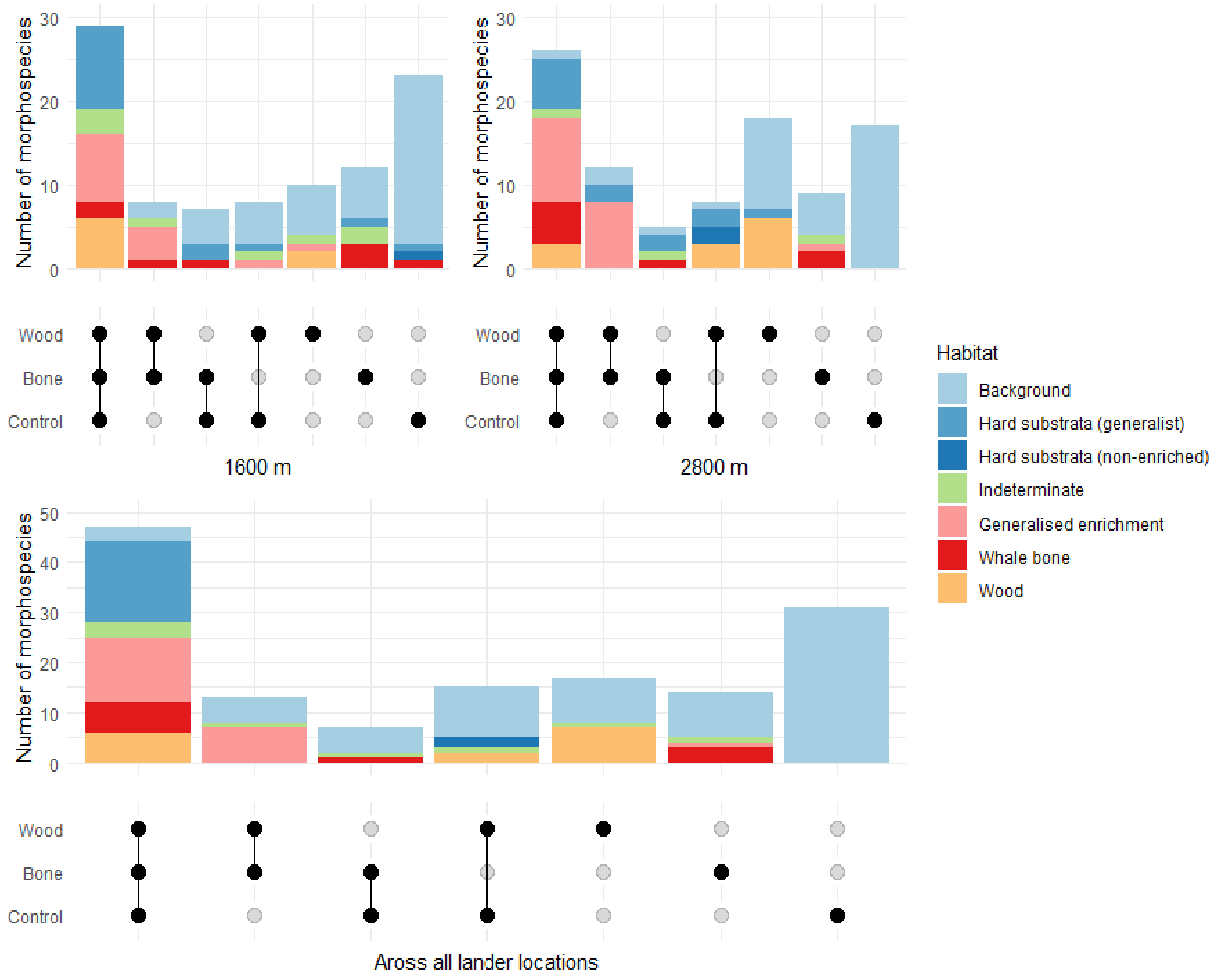

Figure S2.6 UpSet plots of (a) 1600 m deployments, (b) 2800 m deployments and (c) all lander locations.

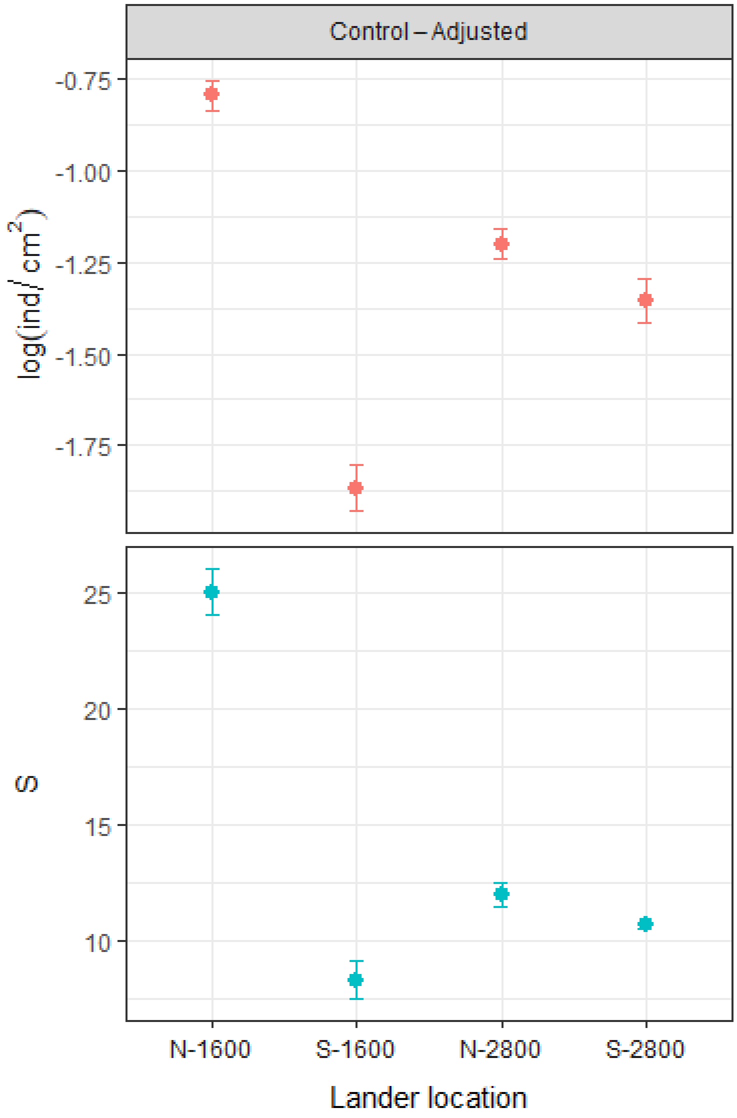

Figure S2.7 Faunal density (log(individuals per cm^2 substrate surface area)) and species richness (S) of adjusted control assemblages by lander location. Control assemblages were adjusted to account for mass effects by removing organic-enrichment, wood specialists and whale bone specialists (Table S2.2).

SUPPLEMENTARY MATERIAL FOR CHAPTER 3

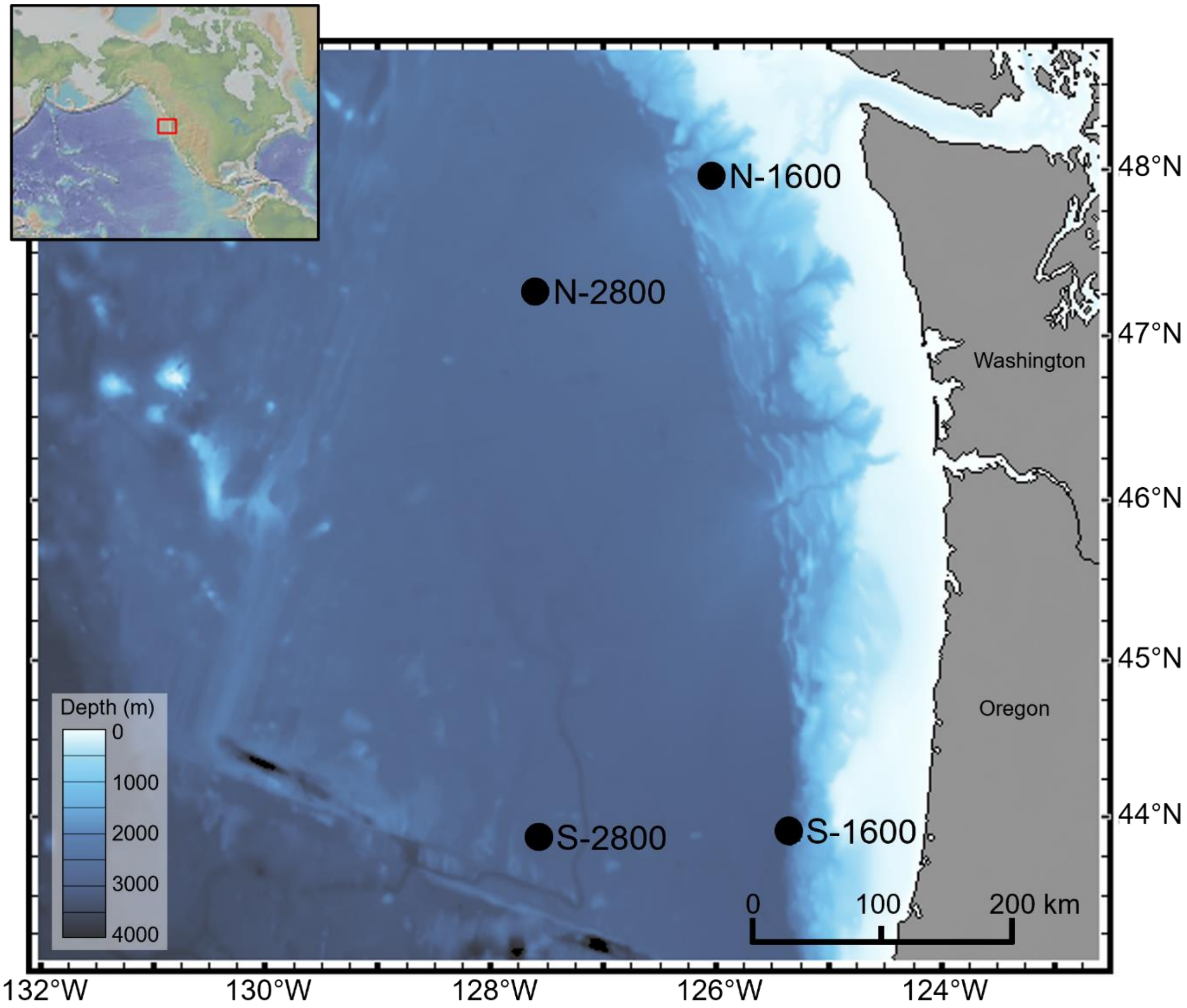

Figure S3.1 Positions of bone and wood landers on the Washington-Oregon margin, NE Pacific. Station names reflects position (North, N, and South, S) and approximate depth (1600 or 2800 m).

Table S3.1 AFDW (g) of wood-fall taxa. Asterisks (*) indicate unmeasurable biomass, with the number of individuals presented in parentheses.

		N-2800 Lid			N-2800 Bin			N-1600 Lid			S-1600 Lid		
Phylum, Family	Species/Morphospecies	W27	W18	W35	W1	W26	W28	W36	W15	W32	W30	W23	W22
Annelida													
	Annelid fragments	-	-	-	0.0076	7.00E-04	0.0085	0.0068	-	-	-	-	-
Ampharetidae	Ampharetid sp. 22	-	-	-	-	*(1)	-	*(1)	6.00E-04	2.00E-04	0.0011	4.00E-04	0.0014
	Decemunciger sp. A	-	-	-	*(1)	2.00E-04	5.00E-04	0.0314	0.0315	0.019	0.0169	0.0177	0.0255
	Ampharetid fragments	-	-	-	-	-	-	-	0.0045	0.0035	0.0044	0.0015	0.015
Capitellidae	*Capitella* cf. *capitata*	-	-	-	0.004	0.0198	0.0096	*(1)	-	-	0.0158	0.0439	0.0712
	Capitellid fragments	-	-	-	-	-	-	-	-	-	0.0133	-	0.0085
Cirratulidae	*Chaetozone* sp. B	-	-	-	*(2)	-	-	-	-	-	-	-	-
Ctenodrilidae	Ctenodrillid sp. 2	-	-	-	-	-	-	-	-	2.00E-04	-	-	-
Dorvilleidae	Dorvilleid sp. 15	-	-	-	-	3.00E-04	*(5)	-	-	-	-	-	-
	Dorvilleid sp. 32	-	-	-	-	-	-	-	*(1)	-	-	-	-
	Dorvilleid sp. 54	-	-	-	-	-	-	-	-	-	-	-	*(4)
	Dorvilleid sp. 55	-	-	-	0.0021	0.0017	0.001	-	-	-	-	-	-
	Ophryotrocha langstrumpae	-	-	-	6.00E-04	-	4.00E-04	0.0119	0.0265	0.0168	0.0306	0.0169	0.1081
	Ophryotrocha batillus	-	-	-	0.0019	0.0018	9.00E-04	4.00E-04	2.00E-04	*(2)	*(5)	*(2)	*(8)
	Dorvilleid fragments	-	*	-	-	-	-	-	0.0052	0.0039	0.0061	0.0022	0.0304
Flabelligeridae	Flabelligerid sp. A	-	-	-	-	-	-	-	-	-	-	-	0.0015
Hesionidae	*Sirsoe* cf. *hessleri*	-	-	-	-	-	-	-	-	-	-	-	*(3)
Nereididae	Nereidid sp. 6	-	-	-	-	-	-	*(1)	-	-	*(1)	-	*(2)
Protodrilidae	Protodrilid sp. 1	-	-	-	-	-	-	-	-	-	-	-	*(2)
Spionidae	*Laonice* sp. A	-	-	-	-	-	-	-	-	-	*(2)	-	*(1)
Syllidae	*Sphaerosyllis* sp. A	-	-	-	-	*(1)	*(1)	-	-	-	-	-	*(1)

Table S3.1 (Continued) AFDW (g) of wood-fall taxa. Asterisks (*) indicate unmeasurable biomass, with the number of individuals presented in parentheses.

		N-2800 Lid			N-2800 Bin			N-1600 Lid			S-1600 Lid		
Phylum, Family	Species/ Morphospecies	W27	W18	W35	W1	W26	W28	W36	W15	W32	W30	W23	W22
Arthropoda													
Amphipoda	*Accedomoera* sp. A	-	-	*(2)	-	-	-	-	-	-	-	-	-
	Lysianassid sp. A	-	-	*(1)	-	-	7.00E-04	0.0026	*(1)	-	-	-	-
	Sebidae sp. A	-	-	-	-	3.00E-04	-	*(4)	*(1)	-	-	-	*(2)
Isopoda	Limnoriid sp. A	-	-	-	-	-	-	-	-	-	-	-	*(1)
Tanaidacea	Tanaid sp. A	-	-	-	*(1)	-	-	-	-	-	-	-	-
Cnidaria													
Actinaria	Actinarian sp. A	-	-	-	-	-	-	*(1)	*(1)	-	-	-	-
Mollusca													
Bivalvia	*Idas washingtonius*	-	-	-	-	*(2)	-	-	-	-	*(1)	-	*(1)
	Abditoconus heterosiphon	-	-	-	-	-	-	-	*(1)	-	-	-	-
	Xylonora muraokai	0.005	-	0.0018	0.2313	-	0.0142	-	-	-	-	-	-
	Xylonora zierenbergi	-	-	0.6108	1.117	1.0419	0.9526	-	-	-	-	-	-
	Xylophaga corona	-	-	-	0.0058	0.0013	0.0214	-	-	-	-	-	-
	Xylophaga microchira	-	-	-	-	-	-	0.0065	0.0056	0.0038	0.001	3.00E-04	0.0014
	Xylophaga oregona	-	-	-	-	-	-	0.542	2.7046	3.4835	3.506	3.6006	3.6269
	Xylopholas crooki	-	-	-	*(3)	*(4)	-	-	-	-	-	-	-
	Xylopahgaid fragments	-	-	-	0.4	0.4823	0.8589	0.3713	0.2264	0.3271	0.5076	0.2026	0.3741
Gastropoda	*Dillwynella* sp. A	-	-	-	-	-	*(1)	-	-	-	-	-	-
Platyhelminthes													
	Triclad sp. A	-	-	-	-	-	-	0.0286	0.0208	0.0123	0.0085	7.00E-04	0.0364
	Triclad fragments	-	-	-	-	-	-	0.011	0.0016	0.0103	0.0032	-	0.0108

Table S3.1 (Continued) AFDW (g) of wood-fall taxa. Asterisks (*) indicate unmeasurable biomass, with the number of individuals presented in parentheses.

		N-2800 Lid			N-2800 Bin			N-1600 Lid			S-1600 Lid		
Phylum, Family	Species/Morphospecies	W27	W18	W35	W1	W26	W28	W36	W15	W32	W30	W23	W22
	Total AFDW (g)	**0.005**	**0**	**1.2216**	**1.7703**	**1.5503**	**1.8687**	**1.0125**	**3.0275**	**3.8806**	**4.1145**	**3.8868**	**4.3112**
	Mean ± SD g AFDW	0.4089 ± 0.7039			1.7298 ± 0.1630			2.6402 ± 1.4728			4.1042 ± 0.2124		
	Mean ± SD inds cm3	0.0005 ± 0.0009			0.0023 ± 0.0002			0.0035 ± 0.0019			0.0054 ± 0.0003		

Table S3.2 Counts (individuals per quarter wood block) of wood-fall taxa.

		N-2800 Lid			N-2800 Bin			N-1600 Lid			S-1600 Lid		
Phylum, Family	Species/Morphospecies	W27	W18	W35	W1	W26	W28	W36	W15	W32	W30	W23	W22
Annelida													
Ampharetidae	Ampharetid sp. 22	-	-	-	-	1	-	1	30	10	22	9	27
	Decemunciger sp. A	-	-	-	1	4	11	77	79	56	52	39	49
Capitellidae	*Capitella* cf. *capitata*	-	-	-	3	1	5	1	-	-	19	25	35
Cirratulidae	*Chaetozone* sp. B	-	-	-	2	-	-	-	-	-	-	-	-
Ctenodrilidae	Ctenodrillid sp. 2	-	-	-	-	-	-	-	-	4	-	-	-
Dorvilleidae	Dorvilleid sp. 15	-	-	-	-	9	5	-	-	-	-	-	-
	Dorvilleid sp. 32	-	-	-	-	-	-	-	1	-	-	-	-
	Dorvilleid sp. 54	-	-	-	-	-	-	-	-	-	-	-	4
	Dorvilleid sp. 55	-	-	-	24	11	33	-	-	-	-	-	-
	Ophryotrocha langstrumpae	-	-	-	29	-	21	801	2160	1304	3115	1098	7943
	Ophryotrocha batillus	-	-	-	149	44	72	4	9	2	5	2	8
Flabelligeridae	Flabelligerid sp. A	-	-	-	-	-	-	-	-	-	-	-	1
Hesionidae	*Sirsoe* cf. *hessleri*	-	-	-	-	-	-	-	-	-	-	-	3
Nereididae	Nereidid sp. 6	-	-	-	-	-	-	1	-	-	1	-	2
Protodrilidae	Protodrilid sp. 1	-	-	-	-	-	-	-	-	-	-	-	2
Spionidae	*Laonice* sp. A	-	-	-	-	-	-	-	-	-	2	-	1
Syllidae	*Sphaerosyllis* sp. A	-	-	-	-	1	1	-	-	-	-	-	1

Table S3.2 (Continued) Counts (individuals per quarter wood block) of wood-fall taxa.

		N-2800 Lid			N-2800 Bin			N-1600 Lid			S-1600 Lid		
Phylum, Family	Species/Morphospecies	W27	W18	W35	W1	W26	W28	W36	W15	W32	W30	W23	W22
Arthropoda													
Amphipoda	*Accedomoera* sp. A	-	-	2	-	-	-	-	-	-	-	-	-
	Lysianassid sp. A	-	-	1	-	-	2	10	1	-	-	-	-
	Sebidae sp. A	-	-	-	-	1	-	4	1	-	-	-	2
Isopoda	Limnoriid sp. A	-	-	-	-	-	-	-	-	-	-	-	1
Tanaidacea	Tanaid sp. A	-	-	-	1	-	-	-	-	-	-	-	-
Cnidaria													
Actinaria	Actinarian sp. A	-	-	-	-	-	-	1	1	-	-	-	-
Mollusca													
Bivalvia	*Idas washingtonius*	-	-	-	-	2	-	-	-	-	1	-	1
	Abditoconus heterosiphon	-	-	-	-	-	-	-	1	-	-	-	-
	Xylonora muraokai	2		4	542	-	11	-	-	-	-	-	-
	Xylonora zierenbergi	-	-	45	518	158	250	-	-	-	-	-	-
	Xylophaga corona	-	-	-	24	4	60	-	-	-	-	-	-
	Xylophaga microchira	-	-	-	-	-	-	29	28	9	4	1	3
	Xylophaga oregona	-	-	-	-	-	-	313	1062	720	1035	944	982
	Xylopholas crooki	-	-	-	3	4	-	-	-	-	-	-	-
Gastropoda	*Dillwynella* sp. A	-	-	-	-	-	1	-	-	-	-	-	-
Platyhelminthes													
	Triclad sp. A	-	-	-	-	-	-	308	296	241	113	7	237

Table S3.3 Densities (individuals per cm^3 wood) of wood-fall taxa.

Phylum, Family	Species/Morphospecies	N-2800-Lid			N-2800-Bin			N-1600-Lid			S-1600-Lid		
		W27	W18	W35	W1	W26	W28	W36	W15	W32	W30	W23	W22
Annelida													
Ampharetidae	Ampharetid sp. 22	-	-	-	-	0.0013	-	0.0013	0.039	0.013	0.0286	0.0117	0.0351
	Decemunciger sp. A	-	-	-	0.0013	0.00519	0.0143	0.1	0.103	0.0727	0.0675	0.0506	0.0636
Capitellidae	*Capitella* cf. *capitata*	-	-	-	0.0039	0.0013	0.00649	0.0013	-	-	0.0247	0.0325	0.0455
Cirratulidae	*Chaetozone* sp. B	-	-	-	0.0026	-	-	-	-	-	-	-	-
Ctenodrilidae	Ctenodrillid sp. 2	-	-	-	-	-	-	-	-	0.00519	-	-	-
Dorvilleidae	Dorvilleid sp. 15	-	-	-	-	0.0117	0.00649	-	-	-	-	-	-
	Dorvilleid sp. 32	-	-	-	-	-	-	-	0.0013	-	-	-	-
	Dorvilleid sp. 54	-	-	-	-	-	-	-	-	-	-	-	0.00519
	Dorvilleid sp. 55	-	-	-	0.0312	0.0143	0.0429	-	-	-	-	-	-
	Ophryotrocha langstrumpae	-	-	-	0.0377		0.0273	1.04	2.81	1.69	4.05	1.43	10.3
	Ophryotrocha batillus	-	-	-	0.194	0.0571	0.0935	0.00519	0.0117	0.0026	0.00649	0.0026	0.0104
Flabelligeridae	Flabelligerid sp. A	-	-	-	-	-	-	-	-	-	-	-	0.0013
Hesionidae	*Sirsoe* cf. *hessleri*	-	-	-	-	-	-	-	-	-	-	-	0.0039
Nereididae	Nereidid sp. 6	-	-	-	-	-	-	0.0013	-	-	0.0013	-	0.0026
Protodrilidae	Protodrilid sp. 1	-	-	-	-	-	-	-	-	-	-	-	0.0026
Spionidae	*Laonice* sp. A	-	-	-	-	-	-	-	-	-	0.0026	-	0.0013
Syllidae	*Sphaerosyllis* sp. A	-	-	-	-	0.0013	0.0013	-	-	-	-	-	0.0013

Table S3.3 (Continued) Densities (individuals per cm^3 wood) of wood-fall taxa.

		N-2800-Lid			N-2800-Bin			N-1600-Lid			S-1600-Lid		
Phylum, Family	Species/ Morphospecies	W27	W18	W35	W1	W26	W28	W36	W15	W32	W30	W23	W22
Arthropoda													
Amphipoda	*Accedomoera* sp. A	-	-	0.0026	-	-	-	-	-	-	-	-	-
	Lysianassid sp. A	-	-	0.0013	-	-	0.0026	0.013	0.0013	-	-	-	-
	Sebidae sp. A	-	-	-	-	0.0013	-	0.00519	0.0013	-	-	-	0.0026
Isopoda	Limnoriid sp. A	-	-	-	-	-	-	-	-	-	-	-	0.0013
Tanaidacea	Tanaid sp. A	-	-	-	0.0013	-	-	-	-	-	-	-	-
Cnidaria													
Actinaria	Actinarian sp. A	-	-	-	-	-	-	0.0013	0.0013	-	-	-	-
Mollusca													
Bivalvia	*Idas washingtonius*	-	-	-	-	0.0026	-	-	-	-	0.0013	-	0.0013
	Abditoconus heterosiphon	-	-	-	-	-	-	-	0.0013	-	-	-	-
	Xylonora muraokai	0.0026	-	0.00519	0.704		0.0143	-	-	-	-	-	-
	Xylonora zierenbergi	-	-	0.0584	0.673	0.205	0.325	-	-	-	-	-	-
	Xylophaga corona	-	-	-	0.0312	0.00519	0.0779	-	-	-	-	-	-
	Xylophaga microchira	-	-	-	-	-	-	0.0377	0.0364	0.0117	0.00519	0.0013	0.0039
	Xylophaga oregona	-	-	-	-	-	-	0.406	1.38	0.935	1.34	1.23	1.28
	Xylopholas crooki	-	-	-	0.0039	0.00519	-	-	-	-	-	-	-
Gastropoda	*Dillwynella* sp. A	-	-	-	-	-	0.0013	-	-	-	-	-	-
Platyhelminthes													
	Triclad sp. A	-	-	-	-	-	-	0.4	0.384	0.313	0.147	0.00909	0.308

Table S3.4 Estimated net xylophagaid production.

Lander/Position	Net xylophagaid production per liter of wood (mean ± SE) (g AFDW L^{-1} yr^{-1})	Net xylophagaid production per m^2 of exposed wood surface area (mean ± SE) (g AFDW m^{-2} yr^{-1})
N-2800-Lid	0.2 ± 0.4	6.7 ± 6.7
N-2800-Bin	1.8 ± 0.2	55.9 ± 3.1
N-1600-Lid	2.7 ± 1.6	83.6 ± 28.0
S-1600-Lid	4.2 ± 0.1	128.6 ± 2.2

SUPPLEMENTARY MATERIAL FOR CHAPTER 4

Table S4.1 Isotopic signatures and C/N ratios of taxa used in this study.

Taxa	**Substrate**	**Replicate**	**Preservative**	**Batch**	**n**	**δ^{13}C (‰)**	**δ^{15}N (‰)**	**C/N**	**δ^{13}C (‰) Post et al. 2007**
Amphipoda sp. K	Bone	V12A	Etoh, Acidified	3	1	-16.8	20.2	4.6	-15.6
Capitella cf. *capitata*	Bone	R4A	F -> E	3	6	-21.4	10.1	4.4	-20.4
Capitella cf. *capitata*	Bone	V4A	F -> E	3	1	-22.4	7.5	4.3	-21.5
Capitella cf. *capitata*	Bone	V4A	F -> E	3	1	-21.3	8.2	3.8	-20.9
Capitella cf. *capitata*	Bone	V4A	F -> E	3	1	-20.9	8.4	3.8	-20.5
Capitella cf. *capitata*	Bone	V4A	F -> E	3	1	-20.8	8	3.8	-20.4
Capitella cf. *capitata*	Bone	V4A	F -> E	3	1	-20.8	10	3.9	-20.3
Capitella cf. *capitata*	Bone	V4A	F -> E	3	1	-19.9	9.7	4	-19.3
Capitella cf. *ovincola*	Bone	R4A	F -> E	3	4	-21.5	10.1	4.2	-20.7
Dillwynella sp. A	Bone	V4A	F -> E, Acidified	3	1	-21.9	11.3	3.7	-21.6
Eurycopinae sp. A	Bone	R4A	F -> E, Acidified	3	4	-21	12.9	3.9	-20.5
Hyalogyrina sp. A	Bone	V12A	F -> E	3	3	-20.4	10.2	3.6	-20.2
Hyalogyrina sp. A	Bone	V12A	F -> E	3	5	-19.5	9	3.7	-19.2
Hyalogyrina sp. A	Bone	V12A	F -> E	3	4	-19.3	9.3	3.7	-19
Hyalogyrina sp. A	Bone	R4A	F -> E, Acidified	3	2	-20.7	7.5	3.9	-20.2
Hyalogyrina sp. A	Bone	R4A	F -> E, Acidified	3	1	-20.1	8.4	3.8	-19.7
Hyalogyrina sp. A	Bone	V4A	F -> E, Acidified	3	1	-19.5	8.5	3.8	-19.1
Laonice sp. A	Bone	V12A	F -> E	3	1	-23.8	7.4	3.7	-23.5
Laonice sp. A	Bone	V4A	F -> E	3	1	-23.4	7.3	3.6	-23.2
Ophiuroid sp. A	Bone	R4A	Etoh, Acidified	3	1	-21.7	15.3	5.7	-19.4
Ophryotrocha batillus	Bone	V4A	F -> E	3	3	-22.6	11	4.4	-21.6
Osedax rubiplumus	Bone	V1a	Frozen fresh	1	1	-17.5	10.2	4.5	-16.4

Table S4.1 (Continued) Isotopic signatures and C/N ratios of taxa used in this study.

Taxa	Substrate	Replicate	Preservative	Batch	n	δ^{13}C (‰)	δ^{15}N (‰)	C/N	δ^{13}C (‰) Post et al. 2007
Osedax rubiplumus	Bone	V1a	Frozen fresh	1	1	-14.9	12.5	5.3	-13
Osedax rubiplumus	Bone	V1a	Frozen fresh	1	1	-16	13.4	6.6	-12.8
Osedax rubiplumus	Bone	V9b	Frozen fresh	1	1	-17.6	8.3	6.6	-14.4
Ampharetid sp. 22	Wood	W30	Etoh	3	1	-22.7	6.8	4.3	-21.8
Capitella cf. *capitata*	Wood	W30	Frozen fresh	1	2	-22.5	2.2	5.4	-20.5
Capitella cf. *capitata*	Wood	W30	Frozen fresh	1	2	-21.3	2.8	4.6	-20.1
Capitella cf. *capitata*	Wood	W30	Frozen fresh	1	3	-22.3	2.6	6.2	-19.5
Capitella cf. *capitata*	Wood	W30	Frozen fresh	1	3	-23.5	2.6	7.8	-19.1
Capitella cf. *capitata*	Wood	W30	Frozen fresh	1	2	-24.2	2	9	-18.6
Capitella cf. *capitata*	Wood	W30	F -> E	2	1	-21.7	2	3.9	-21.2
Capitella cf. *capitata*	Wood	W30	F -> E	2	1	-21.6	2.9	4.1	-20.9
Capitella cf. *capitata*	Wood	W30	F -> E	2	1	-21.3	0.8	3.9	-20.8
Capitella cf. *capitata*	Wood	W30	F -> E	2	1	-21.3	2.8	4	-20.7
Capitella cf. *capitata*	Wood	W30	F -> E	2	1	-21.1	3.1	4	-20.5
Capitella cf. *capitata*	Wood	W30	Formalin	2	1	-24.7	1.8	6.5	-21.6
Capitella cf. *capitata*	Wood	W30	Formalin	2	1	-24.9	1.6	7.2	-21.1
Capitella cf. *capitata*	Wood	W30	Formalin	2	1	-23.8	3.1	6.2	-21
Capitella cf. *capitata*	Wood	W30	Formalin	2	1	-25.1	-0.4	8.9	-19.6
Capitella cf. *capitata*	Wood	W30	Formalin	2	1	-24.6	3.2	8.9	-19.1
Decemunciger sp. A	Wood	W30	F -> E	2	2	-22.9	-0.1	4.1	-22.2
Decemunciger sp. A	Wood	W30	F -> E	2	1	-23.1	0.7	4.3	-22.2
Decemunciger sp. A	Wood	W30	F -> E	2	2	-23.2	4.1	4.6	-22
Dorvilleid sp. 54	Wood	W30	F -> E	3	1	-20.9	8.3	3.8	-20.5
Flabelligerid sp. A	Wood	W19	F -> E	3	1	-21.8	4.1	3.6	-21.6
Laonice sp. A	Wood	W25	Frozen fresh	1	1	-22.7	3.7	4.6	-21.5
Laonice sp. A	Wood	W30	Frozen fresh	1	1	-22.6	0	5.4	-20.6

Table S4.1 (Continued) Isotopic signatures and C/N ratios of taxa used in this study.

Taxa	Substrate	Replicate	Preservative	Batch	n	δ^{13}C (‰)	δ^{15}N (‰)	C/N	δ^{13}C (‰) Post et al. 2007
Laonice sp. A	Wood	W30	Etoh	3	1	-22.1	-0.9	3.8	-21.7
Laonice sp. A	Wood	W6	Frozen fresh	1	1	-21.4	4	4	-20.8
Laonice sp. A	Wood	W30	F -> E	3	1	-22.6	-0.5	3.8	-22.2
Limpet sp. A	Wood	W19	F -> E, Acidified	3	11	-22.8	3.8	4.4	-21.8
Nemertean sp. A	Wood	W30	F -> E	3	1	-20	19.7	4.2	-19.2
Ophryotrocha batillus	Wood	W25	F -> E	3	13	-22.1	5.6	3.9	-21.6
Ophryotrocha langstrumpae	Wood	W30	F -> E	2	11	-22	2.5	3.9	-21.5
Ophryotrocha langstrumpae	Wood	W30	F -> E	2	15	-22	3.3	4	-21.4
Ophryotrocha langstrumpae	Wood	W30	F -> E	2	14	-21.9	3.5	4.1	-21.2
Ophryotrocha langstrumpae	Wood	W30	F -> E	2	12	-21.9	3.5	4.2	-21.1
Ophryotrocha langstrumpae	Wood	W30	F -> E	2	16	-21.9	3.6	4.3	-21
Ophryotrocha langstrumpae	Wood	W30	Formalin	2	11	-23.9	3.5	5.2	-22.1
Ophryotrocha langstrumpae	Wood	W30	Formalin	2	20	-23.5	2.2	5.2	-21.7
Ophryotrocha langstrumpae	Wood	W30	Formalin	2	10	-23.5	3.7	5.3	-21.6
Ophryotrocha langstrumpae	Wood	W30	Formalin	2	21	-23.7	1.9	5.5	-21.6
Ophryotrocha langstrumpae	Wood	W30	Formalin	2	17	-23.9	3	6.1	-21.2
Polynoid sp. A	Wood	W6	F -> E	3	1	-21.7	10.5	3.7	-21.4
Sirsoe cf. *hessleri*	Wood	W25	F -> E	3	1	-21.9	6.4	3.7	-21.6
Sirsoe cf. *hessleri*	Wood	W25	F -> E	3	1	-21.8	6.4	3.7	-21.5
Triclad sp. A	Wood	W30	F -> E	2	2	-22.2	2.2	3.8	-21.8
Triclad sp. A	Wood	W30	F -> E	2	2	-22.3	1.7	3.9	-21.8
Triclad sp. A	Wood	W30	F -> E	2	2	-22.1	1.8	4	-21.5
Triclad sp. A	Wood	W30	F -> E	2	1	-21.7	2.1	3.8	-21.3
Triclad sp. A	Wood	W30	F -> E	2	2	-21.8	5.8	3.9	-21.3
Triclad sp. A	Wood	W30	Formalin	2	2	-23.6	1.9	4.7	-22.3

Table S4.1 (Continued) Isotopic signatures and C/N ratios of taxa used in this study.

Taxa	Substrate	Replicate	Preservative	Batch	n	δ^{13}C (‰)	δ^{15}N (‰)	C/N	δ^{13}C (‰) Post et al. 2007
Triclad sp. A	Wood	W30	Formalin	2	2	-24	1.8	5.2	-22.2
Triclad sp. A	Wood	W30	Formalin	2	2	-23.6	2.6	5	-22
Triclad sp. A	Wood	W30	Formalin	2	2	-23.9	1.9	5.5	-21.8
Xylophaga oregona	Wood	W30	Frozen fresh	1	1	-22.6	-0.2	4	-22
Xylophaga oregona	Wood	W30	Frozen fresh	1	1	-22.9	-0.2	4.4	-21.9
Xylophaga oregona	Wood	W30	Frozen fresh	1	1	-22.6	0	4.5	-21.5
Xylophaga oregona	Wood	W30	F -> E	2	1	-23.2	-0.4	4.8	-21.8
Xylophaga oregona	Wood	W30	F -> E	2	1	-22.8	-0.2	4.2	-22
Xylophaga oregona	Wood	W30	F -> E	2	1	-23.2	-0.2	4.6	-22
Xylophaga oregona	Wood	W30	F -> E	2	1	-23.5	1.6	6.3	-20.6
Xylophaga oregona	Wood	W30	Formalin	2	1	-24.5	-1.1	4.6	-23.3
Xylophaga oregona	Wood	W30	Formalin	2	1	-24.8	-0.5	5.8	-22.4
Xylophaga oregona	Wood	W30	Formalin	2	1	-24.2	-0.3	4.6	-23
Xylophaga oregona	Wood	W30	Formalin	2	1	-24.1	0.2	5.1	-22.4
Xylophaga oregona	Wood	W30	Formalin	2	1	-23.8	0.3	4.8	-22.4
Xylophaga oregona	Wood	W30	Formalin	2	1	-24.6	0.6	5.8	-22.2
Xylophaga oregona	Wood	W30	Frozen	2	1	-23	-0.5	6.1	-20.3
Xylophaga oregona	Wood	W30	Frozen	2	1	-23.8	0.9	5.4	-21.8

Table S4.2 Isotopic signatures and C/N ratios of sources used in this study.

Source	**Replicate**	**Preservative**	**Batch**	**n**	**δ^{13}C (‰)**	**δ^{15}N (‰)**	**C/N**
Surface plankton	ST3 to 2	Frozen fresh	1	1	-23.2	8.0	NA
Surface plankton	Station 6	Frozen fresh	1	1	-23.9	9.3	7.5
Surface plankton	Station 6	Frozen fresh	1	1	-23.7	9.7	9.4
Whale bone	Outer leg C S-1600	Frozen fresh	1	1	-15.9	12.1	3.9
Whale bone	Outer leg C S-1600	Frozen fresh	1	1	-14.9	11.6	3.6
Whale bone	Outer leg C S-1600	Frozen fresh	1	1	-14.5	12.3	3.4
Whale bone	V4b S-2800	Frozen fresh	1	1	-18.5	11.7	5.8
Whale bone	V8b N-2800	Frozen fresh	1	1	-15.7	12.9	3.6
Whale bone	V8b N-2800	Frozen fresh	1	1	-14.2	12.0	3.2
Whale bone bacteria - SCB 99 - Mat	NA	Frozen	NA	NA	-21.2	7.39	NA
Whale bone bacteria - SCB 99 - Mat	NA	Frozen	NA	NA	-21.3	-2.78	NA
Whale bone bacteria - SCB 99 - Mat	NA	Frozen	NA	NA	-20.2	-0.66	NA
Whale bone bacteria - SCB91 *Beggiatoa* sp.	NA	Frozen	NA	NA	-23.4	7.8	NA
Whale bone bacteria - SCB91 *Beggiatoa* sp.	NA	Frozen	NA	NA	-21	6.9	NA
Wood	W30	Frozen	2	1	-24.4	-3.3	314.7
Wood	W30	Frozen	2	1	-25.0	-2.5	310.8
Wood	W30	Frozen	2	1	-25.0	-3.4	306.2
Wood	W30	Frozen	2	1	-24.6	-2.0	285.4
Wood	W30	Frozen	2	1	-25.6	-2.4	271.0
Xylophagaid fecal material	W30	F -> E	2	1	-25.2	-0.7	181.6
Xylophagaid fecal material	W30	F -> E	2	1	-25.2	-0.5	67.8
Xylophagaid fecal material	W30	F -> E	2	1	-25.7	-1.2	64.7
Xylophagaid fecal material	W30	Formalin	2	1	-26.5	-1.6	94.8
Xylophagaid fecal material	W30	Formalin	2	1	-26.6	-2.6	57.5
Xylophagaid fecal material	W30	Formalin	2	1	-26.4	-3.0	48.1
Xylophagaid fecal material	W30	Formalin	2	1	-28.2	-2.8	21.3

Table S4.2 (Continued) Isotopic signatures and C/N ratios of sources used in this study.

Source	**Replicate**	**Preservative**	**Batch**	**n**	**δ^{13}C (‰)**	**δ^{15}N (‰)**	**C/N**
Xylophagaid fecal material	W30	Formalin	2	1	-28.2	-2.6	20.7
Xylophagaid fecal material	W30	Frozen	2	1	-25.0	-1.5	89.2
Xylophagaid fecal material	W30	Frozen	2	1	-25.4	-5.3	78.0
Xylophagaid fecal material	W30	Frozen	2	1	-25.0	-2.5	49.7
Xylophagaid fecal material	W30	Frozen	2	1	-25.4	-2.8	41.2
Xylophagaid fecal material	W30	Frozen	2	1	-25.4	-2.3	40.0

Table S4.3 Dietary proportions for whale-bone and wood fall taxa, determined by MixSIAR modelling, when all taxa are supplied all food sources. Values are means ± standard deviations, calculated from Bayesian posterior distributions.

Substrate	**Functional group**	**Taxa**	Wood (combined)	Whale bone	Bone bacteria	Surface plankton
Bone	Bone specialist	*Osedax rubiplumus*	0.06 ± 0.04	0.86 ± 0.07	0.04 ± 0.05	0.04 ± 0.03
	Deposit feeder	*Laonice* sp. A	0.38 ± 0.13	0.14 ± 0.07	0.11 ± 0.12	0.37 ± 0.16
		Capitella cf. *capitata*	0.27 ± 0.07	0.37 ± 0.06	0.13 ± 0.09	0.24 ± 0.08
		Capitella cf. *ovincola*	0.20 ± 0.11	0.35 ± 0.13	0.14 ± 0.15	0.31 ± 0.18
	Microbial grazer	*Hyalogyrina* sp. A	0.28 ± 0.08	0.45 ± 0.06	0.13 ± 0.11	0.14 ± 0.08
		Dillwynella sp. A	0.15 ± 0.10	0.26 ± 0.13	0.14 ± 0.16	0.45 ± 0.21
	Omnivore	*Ophryotrocha batillus*	0.18 ± 0.11	0.25 ± 0.14	0.24 ± 0.8	0.33 ± 0.20
	Mobile generalists	Ophiuroid sp. A	0.03 ± 0.04	0.64 ± 0.23	0.19 ± 0.22	0.13 ± 0.15
		Amphipoda sp. K	0.03 ± 0.03	0.68 ± 0.20	0.20 ± 0.21	0.09 ± 0.08
		Eurycopinae sp. A	0.06 ± 0.07	0.51 ± 0.23	0.23 ± 0.23	0.20 ± 0.20
Wood	Wood Specialist	*Xylophaga oregona*	0.77 ± 0.06	0.22 ± 0.06	-	0.01 ± 0.01
	Deposit feeder	*Laonice* sp. A	0.71 ± 0.07	0.28 ± 0.07	-	0.02 ± 0.02
		Capitella cf. *capitata*	0.62 ± 0.07	0.37 ± 0.06	-	0.01 ± 0.01
		Decemunciger sp. A	0.76 ± 0.07	0.22 ± 0.06	-	0.02 ± 0.03
		Ampharetid sp. 22	0.68 ± 0.07	0.31 ± 0.07	-	0.02 ± 0.02
		Flabelligerid sp. A	0.69 ± 0.10	0.28 ± 0.09	-	0.03 ± 0.06
	Microbial grazer	Limpet sp. A	0.71 ± 0.09	0.26 ± 0.08	-	0.03 ± 0.05
	Omnivore	*Ophryotrocha batillus*	0.55 ± 0.14	0.32 ± 0.08	-	0.13 ± 0.16
		Ophryotrocha langstrumpae	0.62 ± 0.10	0.34 ± 0.09	-	0.04 ± 0.04
		Dorvilleid sp. 54	0.46 ± 0.09	0.44 ± 0.07	-	0.11 ± 0.10
	Carnivore	Triclad sp. A	0.61 ± 0.05	0.34 ± 0.03	-	0.05 ± 0.05
		Polynoid sp. A	0.46 ± 0.16	0.36 ± 0.07	-	0.19 ± 0.20
		Sirsoe cf. *hessleri*	0.50 ± 0.14	0.34 ± 0.05	-	0.15 ± 0.17
		Nemertean sp. A	0.31 ± 0.09	0.58 ± 0.06	-	0.11 ± 0.09

Table S4.4 Dietary proportions for whale-bone and wood fall taxa, determined by MixSIAR modelling, when all taxa are supplied all food sources. Values are medians, and 2.5% and 97.% confidence intervals calculated from Bayesian posterior distributions.

Substrate	**Functional group**	**Taxa**	Wood (combined)	Whale bone	Bone bacteria	Surface plankton
Bone	Bone specialist	*Osedax rubiplumus*	0.05 (0.01, 0.16)	0.87 (0.7, 0.96)	0.03 (0, 0.19)	0.03 (0, 0.11)
	Deposit feeder	*Laonice* sp. A	0.38 (0.1, 0.63)	0.12 (0.03, 0.32)	0.08 (0, 0.42)	0.38 (0.05, 0.68)
		Capitella cf. *capitata*	0.27 (0.12, 0.39)	0.37 (0.26, 0.48)	0.11 (0.01, 0.34)	0.24 (0.08, 0.41)
		Capitella cf. *ovincola*	0.2 (0.03, 0.44)	0.34 (0.1, 0.6)	0.09 (0, 0.58)	0.3 (0.03, 0.68)
	Microbial grazer	*Hyalogyrina* sp. A	0.29 (0.08, 0.41)	0.46 (0.32, 0.57)	0.1 (0, 0.4)	0.14 (0.02, 0.31)
		Dillwynella sp. A	0.13 (0.02, 0.4)	0.25 (0.05, 0.58)	0.08 (0, 0.6)	0.47 (0.04, 0.8)
	Omnivore	*Ophryotrocha batillus*	0.17 (0.01, 0.43)	0.24 (0.02, 0.56)	0.2 (0.01, 0.66)	0.32 (0.02, 0.74)
	Mobile generalists	Ophiuroid sp. A	0.02 (0, 0.16)	0.68 (0.11, 0.97)	0.1 (0, 0.79)	0.07 (0, 0.53)
		Amphipoda sp. K	0.02 (0, 0.1)	0.74 (0.16, 0.93)	0.11 (0, 0.73)	0.07 (0, 0.29)
		Eurycopinae sp. A	0.03 (0, 0.24)	0.5 (0.08, 0.94)	0.15 (0, 0.81)	0.13 (0, 0.69)
Wood	Wood Specialist	*Xylophaga oregona*	0.76 (0.67, 0.93)	0.24 (0.06, 0.31)		0 (0, 0.05)
	Deposit feeder	*Laonice* sp. A	0.7 (0.59, 0.88)	0.29 (0.1, 0.38)		0.01 (0, 0.08)
		Capitella cf. *capitata*	0.61 (0.52, 0.8)	0.38 (0.19, 0.47)		0.01 (0, 0.04)
		Decemunciger sp. A	0.75 (0.62, 0.89)	0.23 (0.09, 0.33)		0.01 (0, 0.12)
		Ampharetid sp. 22	0.68 (0.53, 0.81)	0.3 (0.18, 0.44)		0.01 (0, 0.09)
		Flabelligerid sp. A	0.69 (0.5, 0.89)	0.29 (0.1, 0.44)		0.01 (0, 0.19)
	Microbial grazer	Limpet sp. A	0.71 (0.53, 0.89)	0.27 (0.09, 0.42)		0.01 (0, 0.17)
	Omnivore	*Ophryotrocha batillus*	0.58 (0.15, 0.74)	0.33 (0.13, 0.44)		0.07 (0, 0.6)
		Ophryotrocha langstrumpae	0.61 (0.48, 0.88)	0.36 (0.07, 0.43)		0.03 (0, 0.16)
		Dorvilleid sp. 54	0.47 (0.24, 0.6)	0.44 (0.27, 0.56)		0.07 (0, 0.38)
	Carnivore	Triclad sp. A	0.62 (0.5, 0.69)	0.34 (0.27, 0.4)		0.04 (0, 0.17)
		Polynoid sp. A	0.5 (0.06, 0.67)	0.36 (0.22, 0.48)		0.11 (0, 0.69)
		Sirsoe cf. *hessleri*	0.54 (0.14, 0.67)	0.35 (0.23, 0.44)		0.09 (0, 0.61)
		Nemertean sp. A	0.32 (0.12, 0.46)	0.58 (0.46, 0.7)		0.09 (0, 0.34)

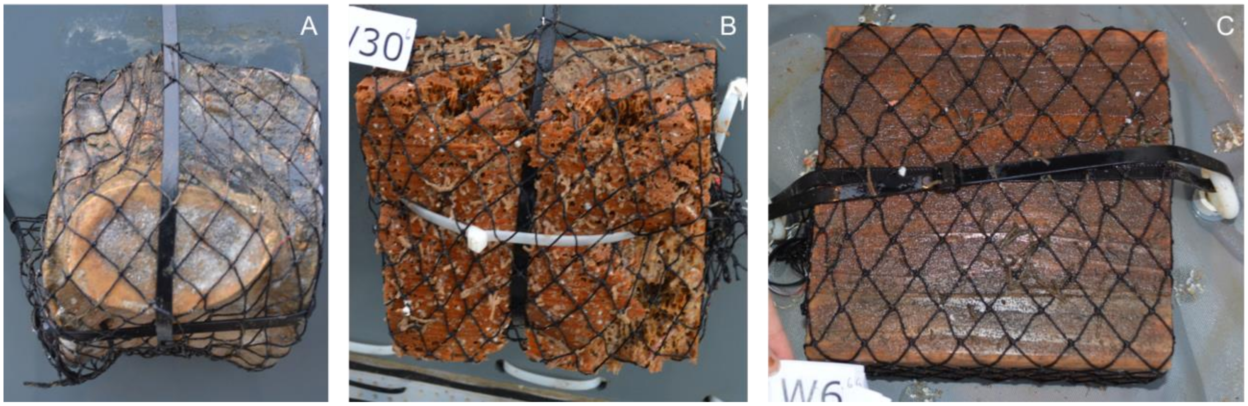

Figure S4.1 Photos of organic-fall substrates upon lander recovery. A) whale vertebra V2a, B) lid-attached wood block W30, C) bin-attached wood block W6

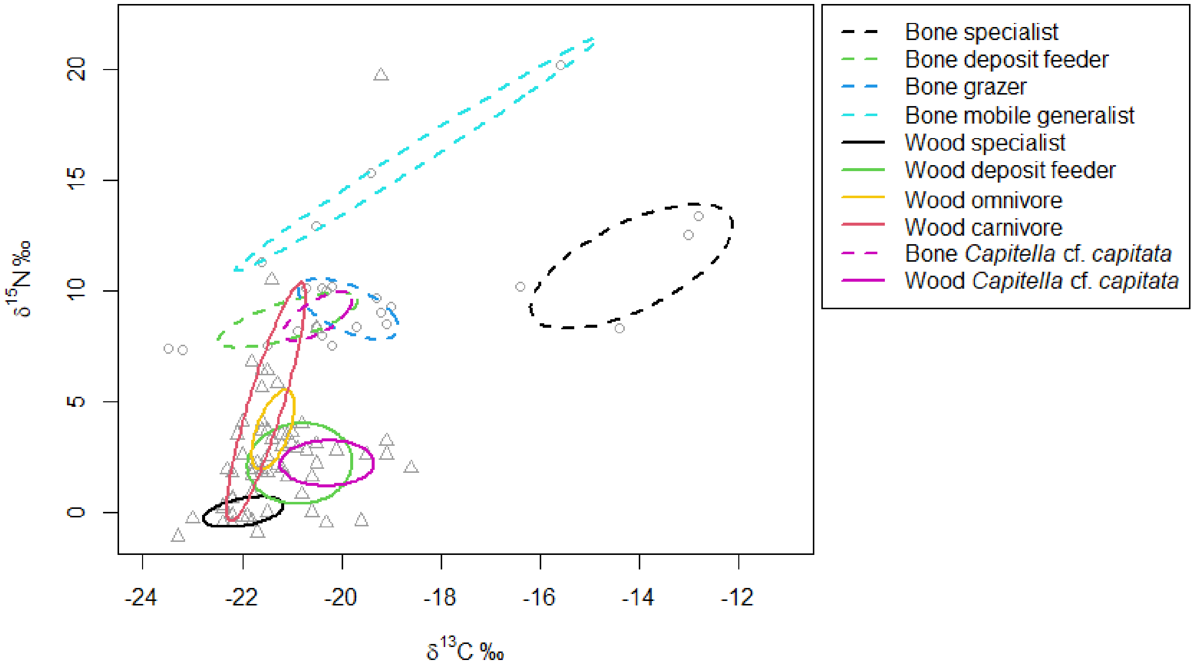

Figure S4.2 SEA$_C$ ellipses of whale-bone and wood functional groups, as well as *Capitella* cf. *capitata*. Open circles are individual bone samples, open triangles are individual wood samples.

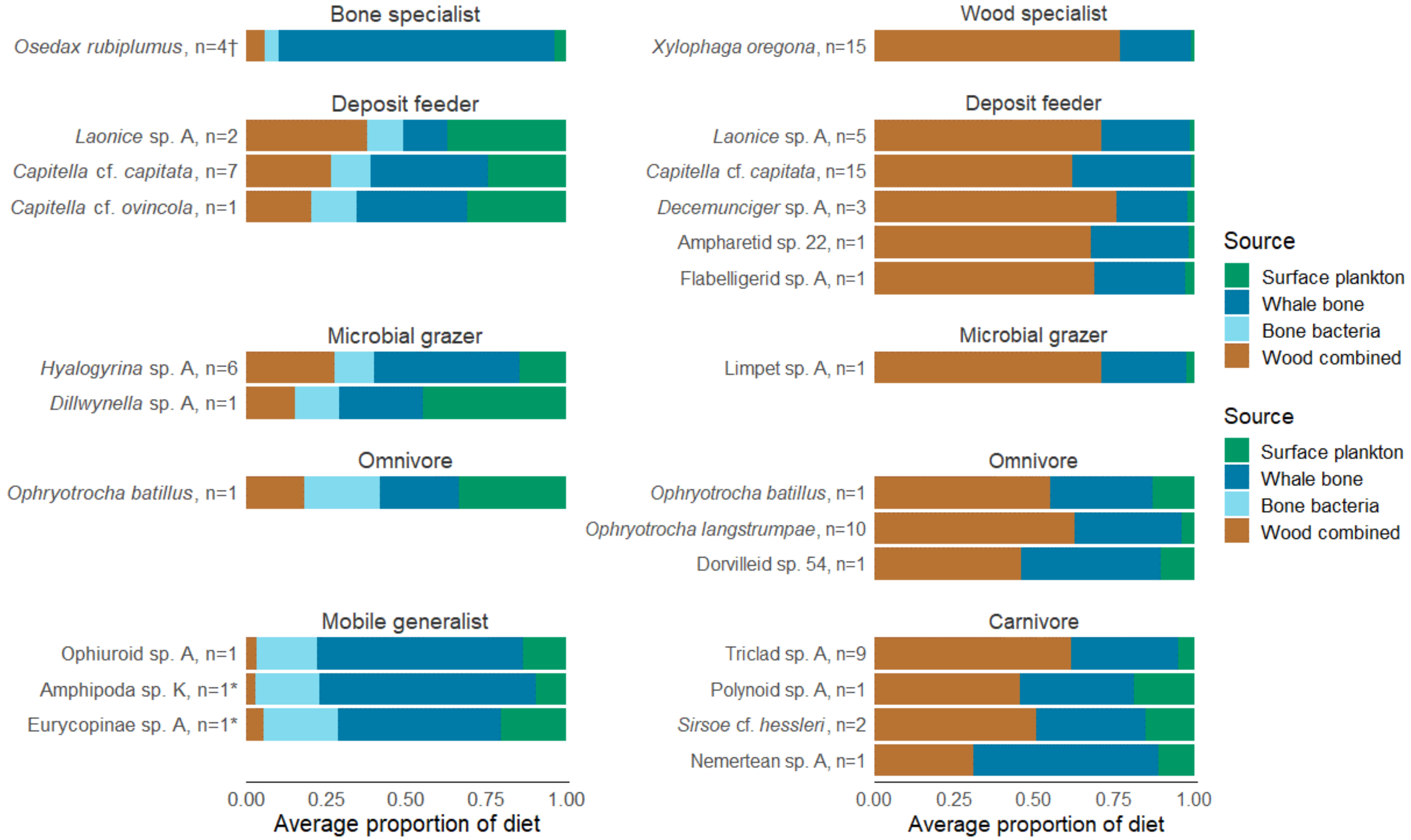

Figure S4.3 Average dietary proportions for whale-bone and wood fall taxa, determined by MixSIAR modelling, when all taxa are supplied all food sources. *Isotopic signature outside of mixing polygon. † n = 1 isotopic signature outside of mixing polygon.

SUPPLEMENTARY MATERIAL FOR CHAPTER 5

Figure S5.1 Whale rib bones attached to outside of BoWL lander (in contact with surrounding sediments) at S-1600.

REFERENCES

Alfaro-Lucas JM, Shimabukuro M, Ferreira GD, Kitazato H, Fujiwara Y, Sumida PY (2017) Bone-eating *Osedax* worms (Annelida: Siboglinidae) regulate biodiversity of deep-sea whale-fall communities. Deep Sea Research Part II: Topical Studies in Oceanography 146:4–12

Alfaro-Lucas JM, Shimabukuro M, Ogata, IV, Fujiwara Y, Sumida PY (2018) Trophic structure and chemosynthesis contributions to heterotrophic fauna inhabiting an abyssal whale carcass. Marine Ecology Progress Series 596:1–12

Allen GH, Pavelsky TM (2018) Global extent of rivers and streams. Science 361:585–88

Allison PA, Smith CR, Kukert H, Deming JW, Bennett BA (1991) Deep-water taphonomy of vertebrate carcasses: a whale skeleton in the bathyal Santa Catalina Basin. Paleobiology 17:78–79

Altabet MA, Pilskaln C, Thunell R, Pride C, Sigman D, Chavez F, Francois R (1999) The nitrogen isotope biogeochemistry of sinking particles from the margin of the Eastern North Pacific. Deep Sea Research Part I: Oceanographic Research Papers 46:655–79

Amon DJ, Copley JT, Dahlgren TG, Horton T, Kemp KM, Rogers AD, Glover AG (2017a) Observations of fauna attending wood and bone deployments from two seamounts on the Southwest Indian Ridge. Deep Sea Research Part II: Topical Studies in Oceanography 136:122–32

Amon DJ, Glover, AG, Wiklund H, Marsh L, Linse K, Rogers AD, Copley JT (2013) The discovery of a natural whale fall in the Antarctic deep sea. Deep Sea Research Part II: Topical Studies in Oceanography 92:87–96

Amon DJ, Hilario A, Arbizu PM, Smith CR (2017b) Observations of organic falls from the abyssal Clarion-Clipperton Zone in the tropical eastern Pacific Ocean. Marine Biodiversity 47:311–21

Amon DJ, Sykes D, Ahmed F, Copley JT, KEMP KM, Tyler PA, Young CM, Glover AG (2015) Burrow forms, growth rates and feeding rates of wood-boring Xylophagaidae bivalves revealed by microcomputed tomography. Frontiers in Marine Science 2:10

Anderson MJ (2001) A new method for non-parametric multivariate analysis of variance. Austral Ecology 26:32–46

Anderson MJ, Gorley RN, Clarke RK (2008) PERMANOVA+ for Primer: Guide to software and statistical methods.PRIMER-E Ltd. Plymouth

Åström EK, Carroll ML, Sen A, Niemann H, Ambrose WG, Lehmann MF, Carroll J (2019) Chemosynthesis influences food web and community structure in high-Arctic benthos. Marine Ecology Progress Series 629:19–42

Baco AR, Smith CR (2003) High species richness in deep-sea chemoautotrophic whale skeleton communities. Marine Ecology Progress Series 260:109–14

Baco-Taylor AR (2002) Food-web structure, succession and phylogenetics on deep-sea whale skeletons, University of Hawaii at Manoa

Barlow J, Forney KA (2007) Abundance and population density of cetaceans in the California Current ecosystem. Fishery Bulletin 105:509–26

Barton PS, Cunningham SA, Lindenmayer DB, Manning AD (2013) The role of carrion in maintaining biodiversity and ecological processes in terrestrial ecosystems. Oecologia 171:761–72

Bates D, Mächler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67

Bennett BA, Smith CR, Glaser B, Maybaum HL (1994) Faunal community structure of a chemoautotrophic assemblage on whale bones in the deep northeast Pacific Ocean. Marine Ecology Progress Series 108:205–23

Bergmann M, Dannheim J, Bauerfeind E, Klages M (2009) Trophic relationships along a bathymetric gradient at the deep-sea observatory HAUSGARTEN. Deep Sea Research Part I: Oceanographic Research Papers 56:408–24

Bernardino AF, Smith CR, Baco A, Altamira I, Sumida PY (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 Part I: Oceanographic Research Papers 57:708–23

Bienhold C, Pop Ristova P, Wenzhöfer F, Dittmar T, Boetius A (2013) How deep-sea wood falls sustain chemosynthetic life. PloS one 8:e53590

Björdal CG (2012) Evaluation of microbial degradation of shipwrecks in the Baltic Sea. International Biodeterioration & Biodegradation 70:126–40

Blake JA (2006) New species and records of deep-water Cirratulidae (Polychaeta) from off Northern California. Scientia Marina 70:45–57

Borchert E, García-Moyano A, Sanchez-Carrillo S, Dahlgren TG, Slaby BM, Bjerga GEK, Ferrer M, Franzenburg S, Hentschel U (2021) Deciphering a marine bone-degrading microbiome reveals a complex community effort. mSystems 6

Borges LMS, Merckelbach LM, Cragg SM (2014) Biogeography of wood-boring crustaceans (Isopoda: Limnoriidae) established in European coastal waters. PloS one 9:e109593

Bousfield EL, Hendrycks EA (1997) The amphipod superfamily Eusiroidea in the North American Pacific region. II. Family Calliopiidae. Systematics and distributional ecology. Amphipacifica 2:3–66

Bowman TE (1974) The "sea flea" *Dolobrotus mardeni* n. gen. n. sp., a deep-water American lobster bait scavenger (Amphipoda: Eusiridae). Proceedings of the Biological Society of Washington 87:129–38

Braby CE, Rouse GW, Johnson SB, Jones WJ, Vrijenhoek RC (2007) Bathymetric and temporal variation among *Osedax* boneworms and associated megafauna on whale-falls in Monterey Bay, California. Deep-sea Research. Part I, Oceanographic Research Papers 54:1773–91

Brauns M, Boëchat IG, Carvalho APC de, Graeber D, Gücker B, Mehner T, Schiller D von (2018) Consumer-resource stoichiometry as a predictor of trophic discrimination (Δ 13 C, Δ 15 N) in aquatic invertebrates. Freshwater Biology 63:1240–49

Brazier RE, Puttock A, Graham HA, Auster RE, Davies KH, Brown CML (2021) Beaver: Nature's ecosystem engineers. WIREs. Water 8:e1494

Bryant SRD, Nunnally C, Hanks G, McClain CR (2022) The macrofaunal metropolis in the sediments around the first-ever deep-sea alligator fall. Marine Ecology 43

Bucher VVC, Hyde KD, Pointing SB, Reddy CA (2004) Production of wood decay enzymes, mass loss and lignin solubilization in wood by marine ascomycetes and their anamorphs. Fungal Diversity 15:1–14

Butman CA, Carlton JT, Palumbi SR (1995) Whaling effects on deep-sea biodiversity. Conservation Biology 2:462–64

Cadien DB (2015) Amphipoda of the Northeast Pacific (Equator to Aleutians, intertidal to abyss): XXVIII. Ampeliscoidea - an updated review.: Southern California Association of Marine Invertebrate Taxonomists (SCAMIT). Available from Amphipoda of the Northeast Pacific. Ampeliscoidea [accessed 20 Feb. 2020]

Calambokidis J, Steiger GH (1997) Abundance and population structure of humpback whales in the North Pacific Basin.

Calambokidis J, Steiger GH, Rasmussen K, Urbán JR, Balcomb KC, Ladrón de Guevara, P P, Salinas M Z, Jacobsen JK, Baker CS, Herman LM, Cerchio S, Darling JD (2000) Migratory destinations of humpback whales that feed off California, Oregon and Washington. Marine ecology progress series 192:295–304

Carney RS (2005) Zonation of deep biota on continental margins. Oceanography and Marine Biology: An Annual Review:211–78

Carpenter EJ, Harvey H, Fry B, Capone DG (1997) Biogeochemical tracers of the marine cyanobacterium *Trichodesmium*. Deep Sea Research Part I: Oceanographic Research Papers 44:27–38

Carretta JV, Forney KA, Oleson EM, Weller DW, Baker J, Muto, M. (Marcia), Hanson B, Orr AJ, Lynch D, Moore JE, Barlow J, Lowry MS, Huber HR, Brownell RL, Carswell L (2020) US Pacific Marine Mammal Stock Assessments: 2019. Washington, DC

Chao A (1984) Non-parametric estimation of the number of classes in a population. Scandinavian Journal of Statistics 11:265–70

Clarke KR, Gorley RN (2015a) PRIMER v7: user manual/tutorial.PRIMER-E. Plymouth

Clarke KR, Somerfield PJ, Gorley RN (2008) Testing of null hypotheses in exploratory community analyses: similarity profiles and biota-environment linkage. Journal of Experimental Marine Biology and Ecology 366:56–69

Clarke R, Gorley RN (2015b) PRIMER v6: User Manual/Tutorial.PRIMER-E. Plymouth.

Cunha MR, Matos FL, Génio L, Hilário A, Moura CJ, Ravara A, Rodrigues CF (2013) Are organic falls bridging reduced environments in the deep sea? - results from colonization experiments in the Gulf of Cádiz. PloS one 8:e76688

Dell R (1987) Mollusca of the Family Mytilidae (Bivalvia) associated with organic remains from deep water off New Zealand, with revisions of the genera *Adipicola* Dautzenborg, 1927 and Idasola Iredale, 1915. National Museum of New Zealand Records 3:17–36

Delwiche CC, Steyn PL (1970) Nitrogen isotope fractionation in soils and microbial reactions. Environmental Science and Technology 4:929–35

Deming JW, Reysenbach A-L, Macko SA, Smith CR (1997) Evidence for the microbial basis of a chemoautotrophic invertebrate community at a whale fall on the deep seafloor: Bone-colonizing bacteria and invertebrate endosymbionts. Microscopy Research and Technique 37:162–70

Deniro MJ, Epstein S (1981) Influence of diet on the distribution of nitrogen isotopes in animals. Geochimica et Cosmochimica Acta 45:341–51

Distel DL, Baco AR, Chuang E, Morrill W, Cavanaugh C, Smith CR (2000) Do mussels take wooden steps to deep-sea vents? Nature 403:725–26

Distel DL, Roberts SJ (1997) Bacterial endosymbionts in the gills of the deep-sea wood-boring bivalves *Xylophaga atlantica* and *Xylophaga washingtona*. The Biological bulletin 192:253–61

Dore WH, Miller RC (1923) The digestion of wood by *Teredo navalis*. University of California Publications in Zoology 22:383–400

Duperron S, Halary S, Lorion J, Sibuet M, Gaill F (2008) Unexpected co-occurrence of six bacterial symbionts in the gills of the cold seep mussel *Idas* sp. (Bivalvia: Mytilidae). Environmental microbiology 10:433–45

Dupont J, Magnin S, Rousseau F, Zbinden M, Frebourg G, Samadi S, Forges BR de, Jones EBG (2009) Molecular and ultrastructural characterization of two ascomycetes found on sunken wood off Vanuatu Islands in the deep Pacific Ocean. Mycological research 113:1351–64

Eilertsen MH, Kongsrud JA, Alvestad T, Stiller J, Rouse GW, Rapp HT (2017) Do ampharetids take sedimented steps between vents and seeps? Phylogeny and habitat-use of Ampharetidae (Annelida, Terebelliformia) in chemosynthesis-based ecosystems. BMC evolutionary biology 17:222

Emmett R, Llansó R, Newton J, Thom R, Hornberger M, Morgan C, Levings C, Copping A, Fishman P (2000) Geographic signatures of North American West coast estuaries. Estuaries 23:765–92

Enríquez S, Duarte CM, Sand-Jensen K (1993) Patterns in decomposition rates among photosynthetic organisms: the importance of detritus C:N:P content. Oecologia 94:457–71

Fagervold SK, Galand PE, Zbinden M, Gaill F, Lebaron P, Palacios C (2012) Sunken woods on the ocean floor provide diverse specialized habitats for microorganisms. FEMS microbiology ecology 82:616–28

Fagervold SK, Romano C, Kalenitchenko D, Borowski C, Nunes-Jorge A, Martin D, Galand PE (2014) Microbial communities in sunken wood are structured by wood-boring bivalves and location in a submarine canyon. PloS one 9:e96248

Fanelli E, Cartes JE, Papiol V, Rumolo P, Sprovieri M (2010) Effects of preservation on the δ13C and δ15N values of deep sea macrofauna. Journal of Experimental Marine Biology and Ecology 395:93–97

Fauchald K, Hancock DR (1981) Deep-water polychaetes from a transect off central Oregon no. 11

Fojutowski A, Wróblewska H, Komorowicz M, Kropacz A, Noskowiak A, Pomian I (2014) Changes in the properties of English oak wood (*Quercus robur* L.) as a result of remaining submerged in Baltic Sea waters for two years. International Biodeterioration & Biodegradation 86:122–28

Forney KA (2007) Preliminary estimates of cetacean abundance along the U.S. west coast and within four National Marine Sanctuaries during 2005. Washington, DC

Fox J (2003) Effect displays in R for general linear models. Journal of Statistical Software 8:1–27

Fox J, Weisberg S (2019) An R companion to applied regression.SAGE Publications. Los Angeles, California

Fujiwara Y, Kawato M, Yamamoto T, Yamanaka T, Sato-Okoshi W, Noda C, Tsuchida S, Komai T, Cubelio SS, Sasaki T, Jacobsen K, Kubokawa K, Fujikura K, Maruyama T, Furushima Y, Okoshi K, Miyake H, Miyazaki M, Nogi Y, Yatabe A, Okutani T (2007) Three-year investigations into sperm whale-fall ecosystems in Japan. Marine Ecology 28:219–32

Fukasawa Y, Matsukura K (2021) Decay stages of wood and associated fungal communities characterise diversity-decomposition relationships. Scientific reports 11:8972

Gaudron SM, Haga T, Wang H, Laming S, Duperron S (2016) Plasticity in reproduction and nutrition in woodboring bivalves (*Xylophaga atlantica*) from the Mid-Atlantic Ridge. Marine biology 163

Gaudron SM, Pradillon F, Pailleret M, Duperron S, Le Bris N, Gaill F (2010) Colonization of organic substrates deployed in deep-sea reducing habitats by symbiotic species and associated fauna. Marine environmental research 70:1–12

Gessner MO (2005) Proximate lignin and cellulose.: A Practical Guide. In: Graça MAS, Bärlocher F, Gessner MO (eds) Methods to Study Litter Decomposition: A Practical Guide: Springer Dordrecht, p 115–120

Gibbs PE (1987) A new species of *Phascolosoma* (Sipuncula) associated with a decaying whale's skull trawled at 880 m depth in the South-west Pacific. New Zealand Journal of Zoology 14:135–37

Glover AG, Wiklund H, Taboada S, Avila C, Cristobo J, Smith CR, Kemp KM, Jamieson AJ, Dahlgren TG (2013) Bone-eating worms from the Antarctic: the contrasting fate of whale and wood remains on the Southern Ocean seafloor. Proceedings. Biological sciences 280:20131390

Goffredi SK, Johnson SB, Vrijenhoek RC (2007) Genetic diversity and potential function of microbial symbionts associated with newly discovered species of *Osedax* polychaete worms. Applied and environmental microbiology 73:2314–23

Goffredi SK, Orphan VJ, Rouse GW, Jahnke L, Embaye T, Turk K, Lee R, Vrijenhoek RC (2005) Evolutionary innovation: a bone-eating marine symbiosis. Environmental microbiology 7:1369–78

Grassle J, Morse-Porteous LS (1987) Macrofaunal colonization of disturbed deep-sea environments and the structure of deep-sea benthic communities. Deep-sea Research. Part I, Oceanographic Research Papers 34:1911–50

Grassle JF, Mackiolek NJ (1992) Deep-sea species richness: Regional and local diversity estimates from quantitative bottom samples. The American Naturalist 139:313–41

Green GA, Bruggeman JJ, Grotefendt RA, Bowlby CE (1995) Offshore distances of gray whales migrating along the Oregon and Washington coasts, 1990. Northwest Science 69:223–27

Hannides CCS, Popp BN, Choy CA, Drazen JC (2013) Midwater zooplankton and suspended particle dynamics in the North Pacific Subtropical Gyre: A stable isotope perspective. Limnology and Oceanography 58:1931–46

Harbour RP, Smith CR, Fernandes TF, Sweetman AK (2021a) Trophic ecology surrounding kelp and wood falls in deep Norwegian fjords. Deep Sea Research Part I: Oceanographic Research Papers 173:103553

Harbour RP, Smith CR, Simon-Nutbrown C, Cecchetto M, Young E, Coral C, Sweetman AK (2021b) Biodiversity, community structure and ecosystem function on kelp and wood falls in the Norwegian deep sea. Marine Ecology Progress Series 657:73–91

Harris PT, Whiteway Y (2011) Global distribution of large submarine canyons: geomorphic differences between active and passive continental margins. Marine geology 285:69–86

Haszprunar G, Wendler SYC, Jöst AB, Ruthensteiner B, Heß M (2022) 3D-anatomy and systematics of cocculinid-like limpets (Gastropoda: Cocculiniformia): more data, some corrections, but still an enigma. Zoomorphology 141:151–71

Hautala SL, Paul Johnson H, Hammond DE (2009) Bottom water circulation in Cascadia Basin. Deep-sea Research. Part I, Oceanographic Research Papers 56:1688–707

Hendy IW, Michie L, Taylor BW (2014) Habitat creation and biodiversity maintenance in mangrove forests: teredinid bivalves as ecosystem engineers. PeerJ 2:e591

Higgs ND, Gates AR, Jones DOB (2014) Fish food in the deep sea: revisiting the role of large food-falls. PloS one 9:e96016

Higgs ND, Glover AG, Dahlgren TG, Little CTS (2011a) Bone-boring worms: characterizing the morphology, rate, and method of bioerosion by *Osedax mucofloris* (Annelida, Siboglinidae). The Biological bulletin 221:307–16

Higgs ND, Little CTS, Glover AG (2011b) Bones as biofuel: a review of whale bone composition with implications for deep-sea biology and palaeoanthropology. Proceedings. Biological sciences 278:9–17

Hilario A, Cunha MR, Génio L, Marçal AR, Ravara A, Rodrigues CF, Wiklund H (2015) First clues on the ecology of whale falls in the deep Atlantic Ocean: results from an experiment using cow carcasses. Marine Ecology 36:82–90

Hoeinghaus DJ, Zeug SC (2008) Can stable isotope ratios provide for community-wide measures of trophic structure? Comment. Ecology 89:2353-7; discussion 2358-9

Hoering TC, Ford HT (1960) The isotope effect in the fixation of nitrogen by *Azotobacter*. Journal of the American Chemical Society 82:376–78

Hoving HJT, Bush SL, Haddock SHD, Robison BH (2017) Bathyal feasting: post-spawning squid as a source of carbon for deep-sea benthic communities. Proceedings. Biological sciences 284

Jackson AL, Inger R, Parnell AC, Bearhop S (2011) Comparing isotopic niche widths among and within communities: SIBER - Stable Isotope Bayesian Ellipses in R. Journal of Animal Ecology 80:595–602

Johnson CE, Siccama TG, Denny EG, Koppers MM, Vogt DJ (2014) In situ decomposition of northern hardwood tree boles: decay rates and nutrient dynamics in wood and bark. Canadian Journal of Forest Research 44:1515–24

Johnson CM, Reisinger RR, Palacios DM, Friedlaender AS, Zerbini AN, Willson A, Lancaster M, Battle J, Graham A, Cosandey-Godin A, Jacob T, Felix F, Grilly E, Shahid U, Houtman N, Alberini A, Montecinos Y, Najera E, Kelez S (2022) Protecting Blue Corridors - Challenges and solutions for migratory whales navigating national and international seas.Zenodo

Jones CG, Lawton JH, Shachak M (1994) Organisms as ecosystem engineers. Oikos 69:373–86

Jones CG, Lawton JH, Shachak M (1997) Positive and negative effects of organisms as physical ecosystem engineers. Ecology 78:1946–57

Jones WJ, Johnson SB, Rouse GW, Vrijenhoek RC (2008) Marine worms (genus *Osedax*) colonize cow bones. Proceedings. Biological sciences 275:387–91

Judge J, Barry JP (2016) Macroinvertebrate community assembly on deep-sea wood falls in Monterey Bay is strongly influenced by wood type. Ecology 97:3031–43

Jumars PA, Dorgan KM, Lindsay SM (2015) Diet of worms emended: an update of polychaete feeding guilds. Annual review of marine science 7:497–520

Kalenitchenko D, Dupraz M, Le Bris N, Petetin C, Rose C, West NJ, Galand PE (2016) Ecological succession leads to chemosynthesis in mats colonizing wood in sea water. The ISME journal 10:2246–58

Kalenitchenko D, Fagervold SK, Pruski AM, Vétion G, Yücel M, Le Bris N, Galand PE (2015) Temporal and spatial constraints on community assembly during microbial colonization of wood in seawater. The ISME journal 9:2657–70

Kalenitchenko D, Le Bris N, Dadaglio L, Peru E, Besserer A, Galand PE (2018a) Bacteria alone establish the chemical basis of the wood-fall chemosynthetic ecosystem in the deep-sea. The ISME journal 12:367–79

Kalenitchenko D, Péru E, Contreira Pereira L, Petetin C, Galand PE, Le Bris N (2018b) The early conversion of deep-sea wood falls into chemosynthetic hotspots revealed by in situ monitoring. Scientific reports 8:907

Kallmeyer J, Ferdelman TG, Weber A, Fossing H, Jørgensen BB (2004) A cold chromium distillation procedure for radiolabeled sulfide applied to sulfate reduction measurements. Limnology and Oceanography: Methods 2:171–80

Kastner M, Kvenvolden KA, Lorenson TD (1998) Chemistry, isotopic composition, and origin of a methane-hydrogen sulfide hydrate at the Cascadia subduction zone. Earth and Planetary Science Letters 156:173–83

Keil RG, Nuwer JM, Strand SE (2010) Burial of agricultural byproducts in the deep sea as a form of carbon sequestration: A preliminary experiment. Marine Chemistry 122:91–95

Kim SL, Thewissen JGM, Churchill MM, Suydam RS, Ketten DR, Clementz MT (2014) Unique biochemical and mineral composition of whale ear bones. Physiological and biochemical zoology PBZ 87:576–84

Kohlmeyer J (1977) New genera and species of higher fungi from the deep sea (1615-5315m). Revue de mycologie 41:189–206

Kokubu Y, Rothäusler E, Filippi J-B, Durieux EDH, Komatsu T (2019) Revealing the deposition of macrophytes transported offshore: Evidence of their long-distance dispersal and seasonal aggregation to the deep sea. Scientific reports 9:4331

Krassowski M (2020) krassowski/complex-upset: R Package.Zenodo

Kussakin OG, Malyutina MV (1989) A new species of deep-sea marine borer of the family Limnoriidae (Isopoda, Flabellifera) from the Okhotsk Sea. Crustacea 56:8–13

Kuznetsova A, Brockhoff P, Christensen R (2017) lmerTest package: Tests in linear mixed effects models. Journal of Statistical Software 82:1–26

Lamlom SH, Savidge RA (2003) A reassessment of carbon content in wood: variation within and between 41 North American species. Biomass and Bioenergy 25:381–88

Larsen K, Krapp-Schickel T (2007) Amphipoda (Crustacea: Peracarida) from chemically reduced habitats; the hydrothermal vent system of the north-east Pacific. Part II. Melitidae and Eusiridae. Journal of the Marine Biological Association of the United Kingdom 87:1207–17

Layman CA, Arrington DA, Montaña CG, Post DM (2007) Can stable isotope ratios provide for community-wide measures of trophic structure? Ecology 88:42-48

Lebreton L, Slat B, Ferrari F, Sainte-Rose B, Aitken J, Marthouse R, Hajbane S, Cunsolo S, Schwarz A, Levivier A, Noble K, Debeljak P, Maral H, Schoeneich-Argent R, Brambini R, Reisser J (2018) Evidence that the Great Pacific Garbage Patch is rapidly accumulating plastic. Scientific reports 8:4666

Leibold MA, Holyoak M, Mouquet N, Amarasekare P, Chase JM, Hoopes MF, Holt RD, Shurin JB, Law R, Tilman D, Loreau M, Gonzalez A (2004) The metacommunity concept: a framework for multi-scale community ecology. Ecology Letters 7:601–13

Lesicki A (2009) Checklist of gastropod species referred to the order Cocculiniformia Haszprunar, 1987 (Gastropoda: Cocculiniformia et Lepetelloidea) with some remarks on their food preferences. Folia Malacologica 6:47–62

Levin LA (2003) Oxygen minimum zone benthos: adaptation and community response to hypoxia. Oceanography and Marine Biology: An Annual Review 41:1–45

Levin LA, Dayton PK (2009) Ecological theory and continental margins: where shallow meets deep. Trends in ecology & evolution 24:606–17

Levin LA, Etter RJ, Rex MA, Gooday AJ, Smith CR, Pineda J, Stuart CT, Hessler RR, Pawson D (2001) Environmental influences on regional deep-sea species diversity. Annual Review of Ecology and Systematics 32:51–93

Levin LA, Mendoza GF, Konotchick T, Lee RW (2009) Macrobenthos community structure and trophic relationships within active and inactive Pacific hydrothermal sediments. Deep Sea Research Part II: Topical Studies in Oceanography 56:1632–48

Levin LA, Sibuet M (2012) Understanding continental margin biodiversity: a new imperative. Annual review of marine science 4:79–112

Levin LA, Ziebis W, F. Mendoza G, Bertics VJ, Washington T, Gonzalez J, Thurber AR, Ebbe B, Lee RW (2013) Ecological release and niche partitioning under stress: Lessons from dorvilleid polychaetes in sulfidic sediments at methane seeps. Deep Sea Research Part II: Topical Studies in Oceanography 92:214–33

Lex A, Gehlenborg N, Strobelt H, Vuillemot R, Pfister H (2014) UpSet: Visualization of intersecting sets. IEEE transactions on visualization and computer graphics 20:1983–92

Limén H, Levesque C, Kim Juniper S (2007) POM in macro-/meiofaunal food webs associated with three flow regimes at deep-sea hydrothermal vents on Axial Volcano, Juan de Fuca Ridge. Marine Biology 153:129–39

Loader NJ, Robertson I, McCarroll D (2003) Comparison of stable carbon isotope ratios in the whole wood, cellulose and lignin of oak tree-rings. Palaeogeography, Palaeoclimatology, Palaeoecology 196:395–407

Lorion J, Duperron S, Gros O, Cruaud C, Samadi S (2009) Several deep-sea mussels and their associated symbionts are able to live both on wood and on whale falls. Proceedings. Biological sciences 276:177–85

Lorion J, Kiel S, Faure B, Kawato M, Ho SYW, Marshall B, Tsuchida S, Miyazaki J-I, Fujiwara Y (2013) Adaptive radiation of chemosymbiotic deep-sea mussels. Proceedings. Biological sciences 280:20131243

Lundsten L, Paull CK, Schlining KL, McGann M, Ussler W (2010a) Biological characterization of a whale-fall near Vancouver Island, British Columbia, Canada. Deep-sea Research. Part I, Oceanographic Research Papers 57:918–22

Lundsten L, Schlining KL, Frasier K, Johnson SB, Kuhnz LA, Harvey JB, Clague G, Vrijenhoek RC (2010b) Time-series analysis of six whale-fall communities in Monterey Canyon, California, USA. Deep-sea Research. Part I, Oceanographic Research Papers 57:1573–84

Lustenhouwer N, Maynard DS, Bradford MA, Lindner DL, Oberle B, Zanne AE, Crowther TW (2020) A trait-based understanding of wood decomposition by fungi. Proceedings of the National Academy of Sciences of the United States of America 117:11551–58

Lutz MJ, Caldeira K, Dunbar RB, Behrenfeld MJ (2007) Seasonal rhythms of net primary production and particulate organic carbon flux to depth describe the efficiency of biological pump in the global ocean. Journal of Geophysical Research 112:C10011

MacIntosh H, Nys R de, Whalan S (2012) Shipworms as a model for competition and coexistence in specialized habitats. Marine Ecology Progress Series 461:95–105

Macko SA, Fogel ML, Hare PE, Hoering TC (1987) Isotopic fractionation of nitrogen and carbon in the synthesis of amino acids by microorganisms. Chemical Geology: Isotope Geoscience section 65:79–92

Marshall BA (1985) Recent and Tertiary Cocculinidae and Pseudococculinidae (Mollusca: Gastropoda) from New Zealand and New South Wales. New Zealand Journal of Zoology 12:505–46

Marshall BA (1987) Osteopeltidae (Mollusca: Gastropoda): a new family of limepts associated with whale bone in the deep-sea. Journal of Molluscan Studies 53:121–27

Marshall BA (1988) Skeneidae, Vitrinellidae and Orbitestellidae (Mollusca: Gastropoda) associated with biogenic substrata from bathyal depths off New Zealand and New South Wales. Journal of Natural History 22:949–1004

Maser, Sedell (1994) From the forest to the sea: The ecology of wood in streams, rivers, estuaries and oceans.St. Lucie Press. Delray Beach

Mason WT, Lewis PA, Weber CI (1983) An evaluation of benthic macroinvertebrate biomass methodology. Environmental Monitoring and Assessment 3:29–44

McClain C, Barry J (2014) Beta-diversity on deep-sea wood falls reflects gradients in energy availability. Biology letters 10:20140129

McClain CR, Barry JP, Eernisse D, Horton T, Judge J, Kakui K, Mah C, Warén A (2016) Multiple processes generate productivity-diversity relationships in experimental wood-fall communities. Ecology 97:885–98

McClain CR, Barry JP, Webb TJ (2018) Increased energy differentially increases richness and abundance of optimal body sizes in deep-sea wood falls. Ecology 99:184–95

McLean JH (1992) Cocculiniform lipets (Cocculinidae and Pyropeltidae) living on whale bone in the deep sea off California. Journal of Molluscan Studies 58:401–14

Menge BA, Lubchenco J, Bracken MES, Chan F, Foley MM, Freidenburg TL, Gaines SD, Hudson G, Krenz C, Leslie H, Menge DNL, Russell R, Webster MS (2003) Coastal oceanography sets the pace of rocky intertidal community dynamics. Proceedings of the National Academy of Sciences of the United States of America 100:12229–34

Menge BA, Sanford E, Daley BA, Freidenburg TL, Hudson G, Lubchenco J (2002) Inter-hemispheric comparison of bottom-up effects on community structure: Insights revealed using the comparative-experimental approach. Ecological Research 17:1–16

Miller TW, Brodeur RD, Rau G, Omori K (2010) Prey dominance shapes trophic structure of the northern California Current pelagic food web: evidence from stable isotopes and diet analysis. Marine Ecology Progress Series 420:15–26

Minagawa M, Wada E (1986) Nitrogen isotope ratios of red tide organisms in the East China Sea: A characterization of biological nitrogen fixation. Marine Chemistry 19:245–59

Mintenbeck K, Jacob U, Knust R, Arntz WE, Brey T (2007) Depth-dependence in stable isotope ratio δ15N of benthic POM consumers: The role of particle dynamics and organism trophic guild. Deep Sea Research Part I: Oceanographic Research Papers 54:1015–23

Moggioli G, Panossian B, Sun Y, Thiel D, Martín-Zamora FM, Tran M, Clifford AM, Goffredi SK, Rimskaya-Korsakova N, Jékelly G, Tresguerres M, Qian P-Y, Qiu J-W, Rouse GW, Henry LM, Martín-Durán JM (2022) The hologenome of *Osedax frankpressi* reveals the genetic interplay for the symbiotic digestion of vertebrate bone

Moore JW, Semmens BX (2008) Incorporating uncertainty and prior information into stable isotope mixing models. Ecology letters 11:470–80

Nagano Y, Fujiwara Y, Nishimoto A, Haga T, Fujikura K (2019) Deep-sea endemic fungi? The discovery of *Alisea longicolla* from artificially immersed wood in deep sea off the Nansei Islands, Japan. Mycoscience 60:228–31

Nishimoto A, Haga T, Asakura A, Shirayama Y (2015) An experimental approach for understanding the process of wood fragmentation by marine wood borers in shallow temperate waters. Marine Ecology Progress Series 538:53–65

Nishimoto A, Mito S, Shirayama Y (2009) Organic carbon and nitrogen source of sunken wood communities on continental shelves around Japan inferred from stable isotope ratios. Deep Sea Research Part II: Topical Studies in Oceanography 56:1683–88

Ohta Y, Nishi S, Haga T, Tsubouchi T, Hasegawa R, Konishi M, Nagano Y, Tsuruwaka Y, Shimane Y, Mori K, Usui K, Suda E, Tsutsui K, Nishimoto A, Fujiwara Y, Maruyama T, Hatada Y (2012) Screening and phylogenetic analysis of deep-sea bacteria capable of metabolizing lignin-derived aromatic compounds. Open Journal of Marine Science 02:177–87

Onishi Y, Shimamura S, Yamanaka T, Nakayama R, Ozaki K-I, Miyazaki M, Tsunogai U, Fujiwara Y (2018) Variation of geochemical environments associated with whale-fall biomass mineralization processes in the sediment during the mobile scavenger, enrichment opportunist, and sulfophilic stages. Marine Biology 165

Onishi Y, Yamanaka T, Ozaki KI, Nakayama R, Shimamura S, Itami R, Fukushima A, Miyamoto M, Fujiwara Y (2020) Relationship between geochemical environments, nutritional resources, and faunal succession in whale-fall ecosystems. Marine Ecology Progress Series 636:35–46

Paavo B, Bailey-Brock JH, Åkesson B, Nylund A (2000) Morphology and life history of *Ophryotrocha adherens* sp. nov. (Polychaeta, Dorvilleidae). Sarsia 85:251–64

Pailleret M, Haga T, Petit P, Privé-Gill C, Saedlou N, Gaill F, Zbinden M (2007) Sunken wood from the Vanuatu Islands: identification of wood substrates and preliminary description of associated fauna. Marine Ecology 28:233–41

Palacios C, Zbinden M, Baco AR, Treude T, Smith CR, Gaill F, Lebaron P, Boetius A (2006) Microbial ecology of deep-sea sunken wood: quantitative measurements of bacterial biomass and cellulolytic activities. Cahiers de Biologie Marine 47:415–20

Palacios C, Zbinden M, Pailleret M, Gaill F, Lebaron P (2009) Highly similar prokaryotic communities of sunken wood at shallow and deep-sea sites across the oceans. Microbial ecology 58:737–52

Paxton H, Davey A (2010) A new species of *Ophryotrocha* (Annelida: Dorvilleidae) associated with fish farming at Macquarie Harbour, Tasmania, Australia. Zootaxa 2509:53–61

Pearson M, Gage JD (1984) Diets of some deep-sea brittle stars in the Rockall Trough. Marine biology 82:247–58

Pearson TH, Rosenberg R (1978) Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. Oceanography and Marine Biology: An Annual Review 16:229–311

Pereira OS, Gonzalez J, Mendoza G, Le J, McNeill M, Ontiveros J, Lee RW, Rouse GW, Cortés J, Levin LA (2022) Does substrate matter in the deep sea? A comparison of bone, wood, and carbonate rock colonizers. PloS one 17:e0271635

Pesante G (2018) Physiology and enzymology of lignocellulose digestion in the shipworm *Lyrodus pedicellatus*. PhD, University of York

Peterson BJ, Fry B (1987) Stable isotopes in ecosystem studies. Annual Review of Ecology and Systematics 18:293–320

Pop Ristova P, Bienhold C, Wenzhöfer F, Rossel PE, Boetius A (2017) Temporal and spatial variations of bacterial and faunal communities associated with deep-sea wood falls. PloS one 12:e0169906

Portail M, Olu K, Dubois SF, Escobar-Briones E, Gelinas Y, Menot L, Sarrazin J (2016) Food-web complexity in Guaymas Basin hydrothermal vents and cold seeps. PloS one 11:e0162263

Post DM, Layman CA, Arrington DA, Takimoto G, Quattrochi J, Montaña CG (2007) Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analyses. Oecologia 152:179–89

Potapov AM, Tiunov AV, Scheu S, Larsen T, Pollierer MM (2019) Combining bulk and amino acid stable isotope analyses to quantify trophic level and basal resources of detritivores: a case study on earthworms. Oecologia 189:447–60

Purchon RD (1941) On the biology and relationships of the lamellibranch *Xylophaga dorsalis* (Turton). Journal of the Marine Biological Association of the United Kingdom 25:1–39

Quiroga SY, BolaÑos MD, Litvatis MK (2006) First description of deep-sea polyclad flatworms from the North Pacific: *Anocellidus* n. gen. *profundus* n. sp. (Anocellidae, n. fam.) and *Oligocladus voightae* n. sp. (Euryleptidae). Zootaxa 1317:1–19

R Core Team (2020) R: A language and environment for statistical computing.R Foundation for Statistical Computing. Vienna, Austria

R Core Team (2021) R: A language and environment for statistical computing.R Foundation for Statistical Computing. Vienna, Austria

Ravara A, Wiklund H, Cunha MR (2021) Four new species and further records of Dorvilleidae (Annelida, Polychaeta) from deep-sea organic substrata, NE Atlantic. European Journal of Taxonomy:44–81

Rex MA, Etter RJ (2010) Deep-sea biodiversity: Pattern and scale.Harvard University Press. Cambridge, Mass.

Rex MA, Etter RJ, Morris JS, Crouse J, McClain CR, Johnson NA, Stuart CT, Deming JW, Thies R, Avery R (2006) Global bathymetric patterns of standing stock and body size in the deep-sea benthos. Marine Ecology Progress Series 317:1–8

Ricart AM, Krause-Jensen D, Hancke K, Price NN, Masqué P, Duarte CM (2022) Sinking seaweed in the deep ocean for carbon neutrality is ahead of science and beyond the ethics. Environmental Research Letters 17:81003

Romano C, Voight JR, Company JB, Plyuscheva M, Martin D (2013) Submarine canyons as the preferred habitat for wood-boring species of *Xylophaga* (Mollusca, Bivalvia). Progress in Oceanography 118:175–87

Rouse GW, Goffredi SK, Johnson SB, Vrijenhoek RC (2011) Not whale-fall specialists, *Osedax* worms also consume fishbones. Biology letters 7:736–39

Rouse GW, Goffredi SK, Vrijenhoek RC (2004) *Osedax*: bone-eating marine worms with dwarf males. Science 305:668–71

Ruby EG, Jannasch HW, Deuser WG (1987) Fractionation of stable carbon isotopes during chemoautotrophic growth of sulfur-oxidizing bacteria. Applied and environmental microbiology 53:1940–43

Saeedi H, Bernardino AF, Shimabukuro M, Falchetto G, Sumida PY (2019) Macrofaunal community structure and biodiversity patterns based on a wood-fall experiment in the deep South-west Atlantic. Deep-sea Research. Part I, Oceanographic Research Papers 145:73–82

Saino T, Hattori A (1980) ^{15}N natural abundance in oceanic suspended particulate matter. Nature 283:752–54

Schander C, Rapp HT, Halanych KM, Kongsrud JA, Sneli J-A (2010) A case of co-occurrence between *Sclerolinum pogonophoran* (Siboglinidae: Annelida) and *Xylophaga* (Bivalvia) from a north-east Atlantic wood-fall. Marine Biodiversity Records 3

Scheipl F, Greven S, Kuechenhoff H (2008) Size and power of tests for a zero random effect variance or polynomial regression in additive and linear mixed models. Computational Statistics & Data Analysis 52:3283–99

Schotte M (1989) Two new species of wood-boring *Limnoria* (Crustacea: Isopoda) from New Zealand, *L. hicksi* and *L. reniculus*. Proceedings of the Biological Society of Washington 102:716–25

Schowalter TD, Morrell JJ (2002) Nutritional quality of Douglas-fir wood: effect of vertical and horizontal position on nutrient levels. Wood Fiber Science 34:158–64

Schuller D, Kadko D, Smith CR (2004) Use of ^{210}Pb/^{226}Ra disequilibria in the dating of deep-sea whale falls. Earth and Planetary Science Letters 218:277–89

Schwabe E, Bartsch I, Błażewicz-Paszkowycz M, Brenke N, Chernyshev AV, Elsner NO, Fischer V, Jażdżewska A, Malyutina MV, Miljutin D, Miljutina M, Kamenev GM, Karanovic I, Maiorova A, Würzberg L (2015) Wood-associated fauna collected during the KuramBio expedition in the North West Pacific. Deep Sea Research Part II: Topical Studies in Oceanography 111:376–88

Shimabukuro M, Couto DM, Bernardino AF, Souza BH, Carrerette O, Pellizari VH, Sumida PY (2022) Whale bone communities in the deep Southwest Atlantic Ocean. Deep Sea Research Part I: Oceanographic Research Papers 190:103916

Shimabukuro M, Sumida PYG (2019) Diversity of bone-eating *Osedax* worms on the deep Atlantic whale falls—bathymetric variation and inter-basin distributions. Marine Biodiversity 49:2587–99

Silva CF, Shimabukuro M, Alfaro-Lucas JM, Fujiwara Y, Sumida PY, Amaral AC (2016) A new *Capitella* polychaete worm (Annelida: Capitellidae) living inside whale bones in the abyssal South Atlantic. Deep Sea Research Part I: Oceanographic Research Papers 108:23–31

Sluys R (1989) A monograph of the marine triclads. Routledge.Rotterdam: CRC Press LLC

Smith CR Bigger is better: the role of whales as detritus in marine ecosystems. In: Whales, whaling, and ocean ecosystems, p 286–300

Smith CR (1985) Food for the deep sea: utilization, dispersal, and flux of nekton falls at the Santa Catalina basin floor. Deep-sea Research. Part I, Oceanographic Research Papers 32:417–42

Smith CR (2007) Bigger is better: The role of whales as detritus in marine ecosystems. In: Estes JA, DeMasterm D. P, Doak DF, Williams TM, Brownell RL (eds) Whales, Whaling, and Ocean Ecosystems: University of California Press, Berkeley, p 286–300

Smith CR, Amon DJ, Higgs ND, Glover AG, Young EL (2017) Data are inadequate to test whale falls as chemosynthetic stepping-stones using network analysis: faunal overlaps do support a stepping-stone role. Proceedings of the Royal Society B 284:20171281

Smith CR, Baco AR (2003) Ecology of whale falls at the deep-sea floor. Oceanography and Marine Biology: An Annual Review 41:311–94

Smith CR, Bernardino AF, Baco AR, Hannides A, Altamira I (2014) Seven-year enrichment: macrofaunal succession in deep-sea sediments around a 30 tonne whale fall in the Northeast Pacific. Marine Ecology Progress Series 515:133–49

Smith CR, Glover AG, Treude T, Higgs ND, Amon DJ (2015) Whale-fall ecosystems: recent insights into ecology, paleoecology, and evolution. Annual review of marine science 7:571–96

Smith CR, Kukert H, Wheatcroft RA, Jumars PA, Deming JW (1989) Vent fauna on whale remains. Nature 341:27–28

Smith CR, Leo FC de, Bernardino AF, Sweetman AK, Arbizu PM (2008) Abyssal food limitation, ecosystem structure and climate change. Trends in ecology & evolution 23:518–28

Smith CR, Roman J, Nation JB (2019) A metapopulation model for whale-fall specialists: The largest whales are essential to prevent species extinctions. Journal of Marine Research 77:283–302

Smith JA, Mazumder D, Suthers IM, Taylor MD (2013) To fit or not to fit: evaluating stable isotope mixing models using simulated mixing polygons. Methods in Ecology and Evolution 4:612–18

Smith KL, Ruhl HA, Huffard CL, Messié M, Kahru M (2018) Episodic organic carbon fluxes from surface ocean to abyssal depths during long-term monitoring in NE Pacific. Proceedings of the National Academy of Sciences of the United States of America 115:12235–40

Stock BC, Jackson AL, Ward EJ, Parnell AC, Phillips DL, Semmens BX (2018) Analyzing mixing systems using a new generation of Bayesian tracer mixing models. PeerJ 6:e5096

Stock BC, Semmens BX (2016) MixSIAR GUI User Manual

Stokland JN, Siitonen J, Jonsson BG (2012) Biodiversity in dead wood.Cambridge University Press. Cambridge

Stott AW, Evershed RP, Tuross N (1997) Compound-specific approach to the δ^{13}C analysis of cholesterol in fossil bones. Organic Geochemistry 26:99–103

Strand SE, Benford G (2009) Ocean sequestration of crop residue carbon: recycling fossil fuel carbon back to deep sediments. Environmental science & technology 43:1000–07

Suess E (1985) Biological communities at vent sites along the subduction zone off Oregon. Biol Soc Wash Bull 6:474–84

Sumida PYG, Alfaro-Lucas JM, Shimabukuro M, Kitazato H, Perez JAA, Soares-Gomes A, Toyofuku T, Lima AOS, Ara K, Fujiwara Y (2016) Deep-sea whale fall fauna from the Atlantic resembles that of the Pacific Ocean. Scientific reports 6:22139

Sweetman AK, Chapman A (2011) First observations of jelly-falls at the seafloor in a deep-sea fjord. Deep-sea Research. Part I, Oceanographic Research Papers 58:1206–11

Sweetman AK, Thurber AR, Stiller J, Levin LA, Mora C, Wei C-L, Gooday AJ, Jones DOB, Rex M, Yasuhara M, Ingels J, Ruhl HA, Frieder CA, Danovaro R, Würzberg L, Baco AR, Grupe BM, Pasulka A, Meyer KS, Dunlop KM, Henry L-A, Roberts JM (2017) Major impacts of climate change on deep-sea benthic ecosystems. Elementa: Science of the Anthropocene 5

Thiel M, Kruse I (2001) Status of the Nemertea as predators in marine ecosystems. Hydrobiologia 456:21–32

Thubaut J, Puillandre N, Faure B, Cruaud C, Samadi S (2013) The contrasted evolutionary fates of deep-sea chemosynthetic mussels (Bivalvia, Bathymodiolinae). Ecology and evolution 3:4748–66

Thurber AR, Kröger K, Neira C, Wiklund H, Levin LA (2010) Stable isotope signatures and methane use by New Zealand cold seep benthos. Marine Geology 272:260–69

Tresguerres M, Katz S, Rouse GW (2013) How to get into bones: proton pump and carbonic anhydrase in *Osedax* boneworms. Proceedings. Biological sciences 280:20130625

Treude T, Smith CR, Wenzhöfer F, Carney E, Bernardino AF, Hannides AK, Krüger M, Boetius A (2009) Biogeochemistry of a deep-sea whale fall: sulfate reduction, sulfide efflux and methanogenesis. Marine Ecology Progress Series 382:1–21

Turner RD (1973) Wood-boring bivalves, opportunistic species in the deep sea. Science 180:1377–79

Turner RD (1977) Wood, mollusks, and deep-sea food chains. Bulletin of the American Malacological Union:13–19

Turner RD (2002) On the subfamily Xylophagainae. Bulletin of the Museum of Comparative Zoology 157:223–307

Tyler PA, Young CM, Dove F (2007) Settlement, growth and reproduction in the deep-sea wood-boring bivalve mollusc *Xylophaga depalmai*. Marine Ecology Progress Series 343:151–59

Voight JR (2007) Experimental deep-sea deployments reveal diverse Northeast Pacific wood-boring bivalves of Xylophagainae (Myoida: Pholadidae). Journal of Molluscan Studies 73:377–91

Voight JR (2009) Diversity and reproduction of near-shore vs offshore wood-boring bivalves (Pholadidae: Xylophagainae) of the deep eastern Pacific ocean, with three new species. Journal of Molluscan Studies 75:167–74

Voight JR (2015) Xylotrophic bivalves: aspects of their biology and the impacts of humans. Journal of Molluscan Studies 81:175–86

Voight JR, Cooper JC, Lee RW (2020) Stable isotopic evidence of mixotrophy in Xylophagaids, deep-sea wood-boring bivalves. Frontiers in Marine Science 7

Voight JR, Marshall BA, Judge J, Halanych KM, Li Y, Bernardino AF, Grewe F, Maddox JD (2019) Life in wood: preliminary phylogeny of deep-sea wood-boring bivalves (Xylophagaidae), with descriptions of three new genera and one new species. Journal of Molluscan Studies 85:232–43

Warén A, Carozza F, Rocchini R (1996) Description of two new species of Hyalogyrinidae (Gastropoda, Heterobranchia) from the Mediterranean. Bollettino Malacologico 32:57–66

Wei C-L, Rowe GT, Hubbard GF, Scheltema AH, Wilson GD, Petrescu I, Foster JM, Wicksten MK, Chen M, Davenport R, Soliman Y, Wang Y (2010) Bathymetric zonation of deep-sea macrofauna in relation to export of surface phytoplankton production. Marine Ecology Progress Series 399:1–14

West AJ, Lin C-W, Lin T-C, Hilton RG, Liu S-H, Chang C-T, Lin K-C, Galy A, Sparkes RB, Hovius N (2011) Mobilization and transport of coarse woody debris to the oceans triggered by an extreme tropical storm. Limnology and Oceanography 56:77–85

Wiklund H, Altamira I, Glover AG, Stiller J, Baco AR, Dahlgren TG (2012) Systematics and biodiversity of *Ophryotrocha* (Annelida, Dorvilleidae) with descriptions of six new species from deep-sea whale-fall and wood-fall habitats in the north-east Pacific. Systematics and Biodiversity 10:243–59

Wiklund H, Glover AG, Dahlgren TG (2009) Three new species of *Ophryotrocha* (Annelida: Dorvilleidae) from a whale-fall in the North-East Atlantic. Zootaxa:43–56

Wohl E (2014) A legacy of absence: Wood removal in US rivers. Progress in Physical Geography: Earth and Environment 38:637–63

Wolff T (1962) The systematics and biology of bathyal and abyssal Isopoda Asellota. Galathea Reports 6:1–320

Wolff T (1976) Utilization of seagrass in the deep sea. Aquatic Botany 2:161–74

Wolff T (1979) Macrofaunal utilization of plant remains in the deep. Sarsia 64:117–36

Yang LH, Bastow JL, Spence KO, Wright AN (2008) What can we learn from resource pulses? Ecology 89:621–34

Yang LH, Edwards KF, Byrnes JE, Bastow JL, Wright AN, Spence KO (2010) A meta-analysis of resource pulse–consumer interactions. Ecological Monographs 80:125–51

Young EL, Halanych KM, Amon DJ, Altamira I, Voight, JR, Higgs ND, Smith CR (2022) Depth and substrate type influence community structure and diversity of wood and whale-bone habitats on the deep NE Pacific margin. Marine Ecology Progress Series 687:23–42

Yücel M, Galand PE, Fagervold SK, Contreira-Pereira L, Le Bris N (2013) Sulfide production and consumption in degrading wood in the marine environment. Chemosphere 90:403–09

Zbinden M, Pailleret M, Ravaux J, Gaudron SM, Hoyoux C, Lambourdière J, Warén A, Lorion J, Halary S, Duperron S (2010) Bacterial communities associated with the wood-feeding gastropod *Pectinodonta* sp. (Patellogastropoda, Mollusca). FEMS microbiology ecology 74:450–63

Zeng N (2008) Carbon sequestration via wood burial. Carbon balance and management 3:1

Zottoli R (1982) Two new genera of deep-sea polychaete worms of the family Ampharetidae and the role of one species in deep-sea ecosystems. Proceedings of the Biological Society of Washington 95:48–57

Zuur AF, Ieno EN, Elphick CS (2010) A protocol for data exploration to avoid common statistical problems. Methods in Ecology and Evolution 1:3–14

Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) Mixed effects models and extensions in ecology with R.Springer. New York, N.Y.