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

Emily L. Young[1,*], Kenneth M. Halanych[2], Diva J. Amon[3], Iris Altamira[1],
Janet R. Voight[4], Nicholas D. Higgs[5], Craig R. Smith[1]

[1]Department of Oceanography, University of Hawai'i at Mānoa, Honolulu, HI 96822, USA
[2]Center for Marine Science, University of North Carolina Wilmington, Wilmington, NC 28409, USA
[3]SpeSeas D'Abadie, Trinidad and Tobago
[4]Negaunee Integrative Research Center, Field Museum of Natural History, Chicago, IL 60605, USA
[5]Cape Eleuthera Institute, Rock Sound, Eleuthera EL-26029, Bahamas

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 ~84 890 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 hypothesise results partly from lower propagule supply as wood falls decrease in abundance with distance from terrestrial sources of wood. Bone-eating *Osedax* colonised whale bones, but bone degradation was low compared to some NE Pacific whale falls of similar duration; nonetheless, bones exhibited reducing conditions and supported sulphophilic 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.

KEY WORDS: Deep sea · Organic falls · Wood · Whale bone · Community structure · Biodiversity · Continental margin

1. 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 pro-

vision 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,

*Corresponding author: elyoung@hawaii.edu

deep-sea environments creates food-rich oases known as 'organic falls'. Sunken animal carcasses, including those of whales ('whale falls', e.g. Smith & Baco 2003, Fujiwara et al. 2007, Lundsten et al. 2010a), large fish (e.g. 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 ('wood falls', e.g. Turner 1978, 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 2006, 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, 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 faecal material (Turner 1978, 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. 2017). Localised organic enrichment of the surrounding seafloor can sustain generalised 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 (e.g. 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 (e.g. 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 (C. Smith et al. 2008, Rex & Etter 2010, K. 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 (e.g. 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. 2017). 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 whale-bone communities require deployments of inorganic substrata to serve as controls for the provision of hard substrate alone. Bathymetric zonation in substrate-specialised 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 standardised 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 colonisation 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. MATERIALS AND METHODS

2.1. 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 (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m687p023_supp.xlsx), 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. 2021).

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 1, Fig. 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 (Fig. 2; Fig. S1). Replicate colonisation substrates were affixed to the bottom of each bin and to the overlying lid. Colonisation 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

Table 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 (m)	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
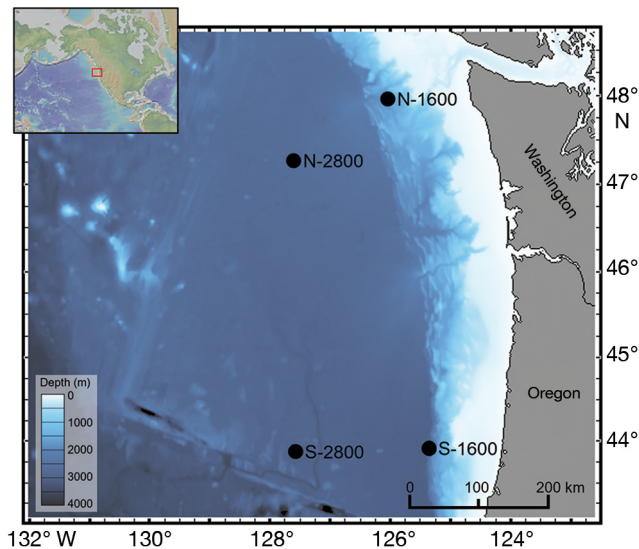
Fig. 1. Positions of bone and wood landers on the Washington–Oregon (USA) margin, NE Pacific. Station names reflect geographic position (N: north; S: south) and approximate depth (1600 or 2800 m). Made with GeoMapApp (www.geomapapp.org)

(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 randomised 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 (Fig. S1).

2.2. Study area

The study sites were located between 43° and 48° N on the Washington–Oregon margin on the Cascadia Plain and the adjacent continental slope of the Cascadia Basin, NE Pacific (Fig. 1, Table 1). In the Cascadia Basin, North Pacific Deep Water flows slowly southward (mean flow of ~1 cm s^{-1}) along the slope at depths of 900–1900 m, and Cascadia Basin Bottom Water flows slowly northward (~1 cm s^{-1}) throughout

the basin at depths greater than 2400 m (Hautala et al. 2009). Mean bottom-water temperature, salinity, and dissolved oxygen concentrations measured from CTD casts at each location during deployment and recovery are included in Table 1. The oxygen minimum zone (<0.5 ml l^{-1} dissolved O$_2$, Levin 2003) was located between depths of ~500 and ~1400 m during the experiment (Fig. S3). Estimates of seafloor POC flux at each location were obtained from Sweetman et al. (2017) who used the model of Lutz et al. (2007) for the period 1998–2010. The Cascadia margin is heavily sedimented and features numerous canyons and channels, as well as areas of methane seepage and gas hydrate deposits (Suess et al. 1985, Kastner et al. 1998). The Washington–Oregon margin lies alongside heavily wooded coastlines with multiple rivers that provide natural sources for sunken wood, and we have observed multiple wood falls along the NE Pacific margin from human- and remotely operated vehicles as well as trawl samples. Multiple resident populations of large cetacean species (Barlow & Forney 2007) combined with annual migrations of humpback and gray whales along the margin (Green et al. 1995, Calambokidis et al. 1997, Roman et al. 2014) provide sources of whale falls in this region (e.g. Lundsten et al. 2010b).

2.3. 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 (molluscs), 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
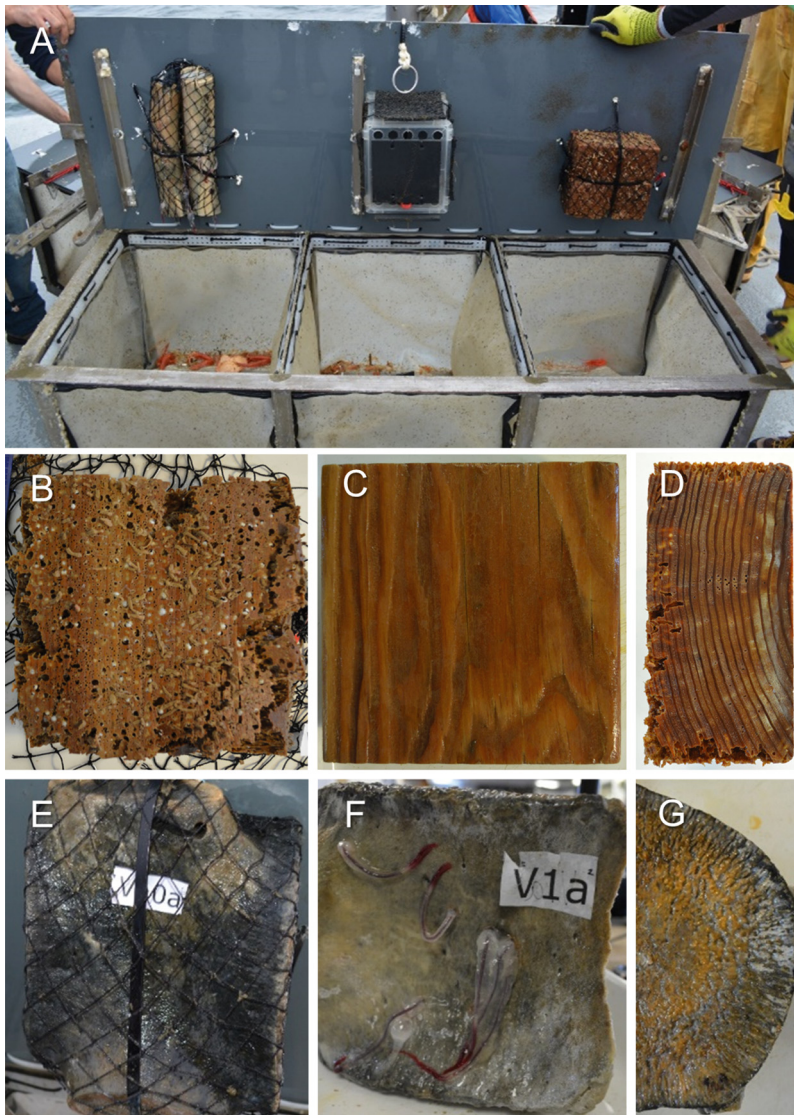
Fig. 2. Substrates following recovery. (A) One side of the N-1600 lander, showing bone (rib package), control, and wood substrates attached to lid. (B) N-1600 wood block, (C) S-2800 wood block, (D) N-2800 wood block, (E) S-1600 whale vertebra, (F) N-1600 whale vertebra with *Osedax rubiplumus*, and (G) N-1600 whale vertebra

the vertebral process (Fig. S2). 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 (Fig. S2). 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 aluminium 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 S1). 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 (generalised-enrichment respondents). Because species responding to organic enrichment generally attain high abundances (e.g. 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 infor-

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 randomised 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 randomised 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

mation suggested otherwise. The remaining unde-scribed 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 S1). 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 S1.

2.4. Statistical analyses

2.4.1. Community structure

Multivariate analyses were used to evaluate community structure of assemblages using PRIMER 7 software (Version 7, Clarke & Gorley 2015). 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 (PERM-ANOVA; 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.

2.4.2. 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 Fig. 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 α = 0.05.

3. RESULTS

3.1. Overall colonisation and condition of substrates

A total of 36 008 individuals and 144 morphospecies were collected and identified across all 4 lander bins.

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 %, Fig. 3A). Annelids were the most species-rich taxon (67 of 144 morphospecies), with Dorvilleidae the most abundant (n =
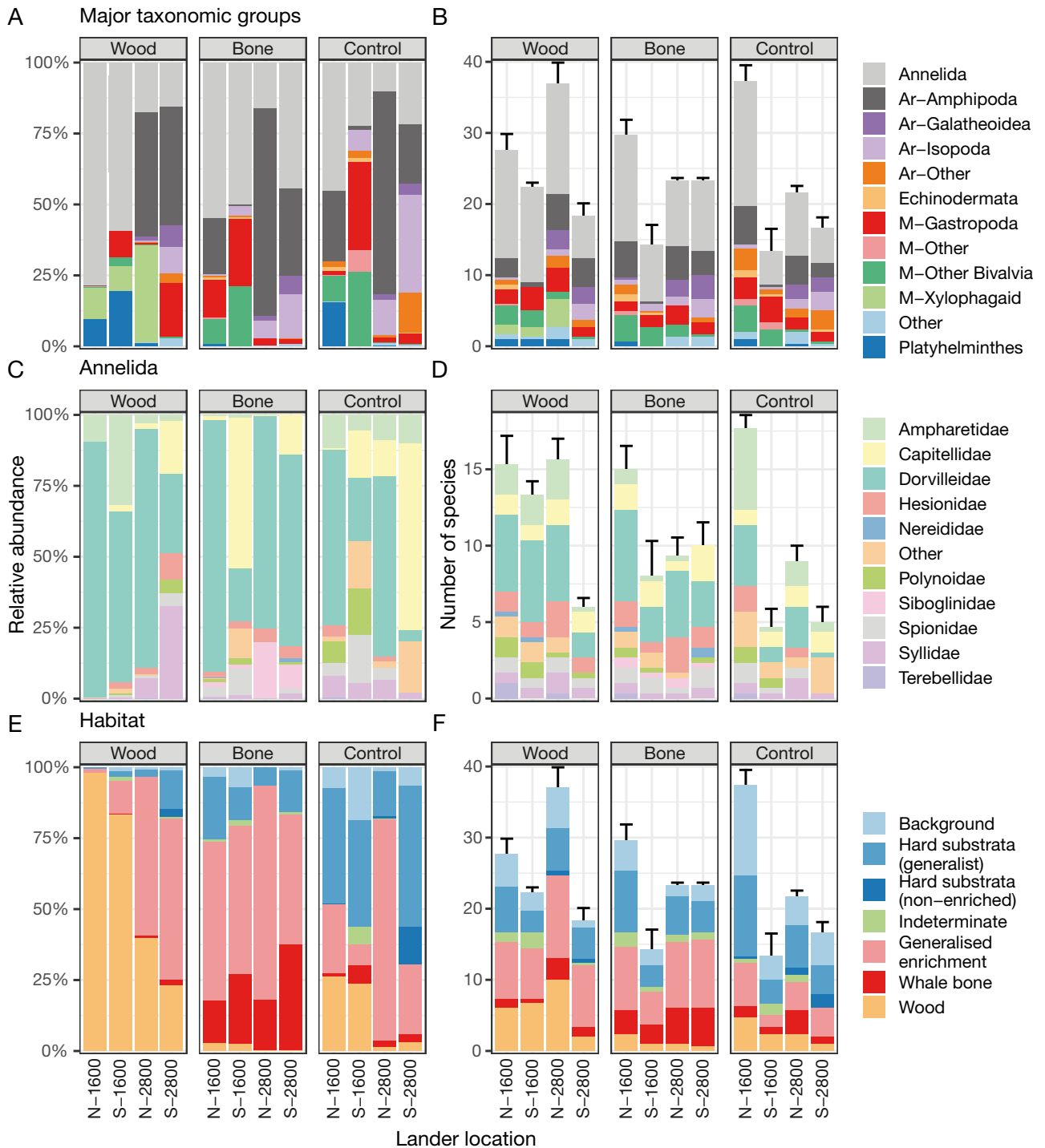

Fig. 3. Taxonomic composition of assemblages. (A,C,E) Relative abundances and (B,D,F) number of species of all fauna by major taxonomic grouping (A,B), by polychaete families (C,D), and by habitat type (E,F). Error bars are SE from n = 3 replicates. Ar: Arthropoda, M: Mollusca

16 635 of 36 008 individuals) and species-rich (S = 13) family overall, and within 9 of the 12 substrate-lander combinations (Fig. 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 S1). Generalised-enrichment respondents, along with wood and whale-bone specialists, dominated abundances and species richness of organic-rich assemblages (Fig. 3E,F). Control assemblages were often dominated by hard substrate (generalist) taxa; however, control assemblages at site N-2800 were dominated by generalised-enrichment respondents. Wood/bone specialists and generalised-enrichment respondents constituted between 30.6 and 81.6% of control as-

semblage abundance across the 4 landers (Fig. 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 (Fig. 4).

3.1.1. Wood

Wood blocks at N-1600 were crumbling upon recovery (Fig. 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
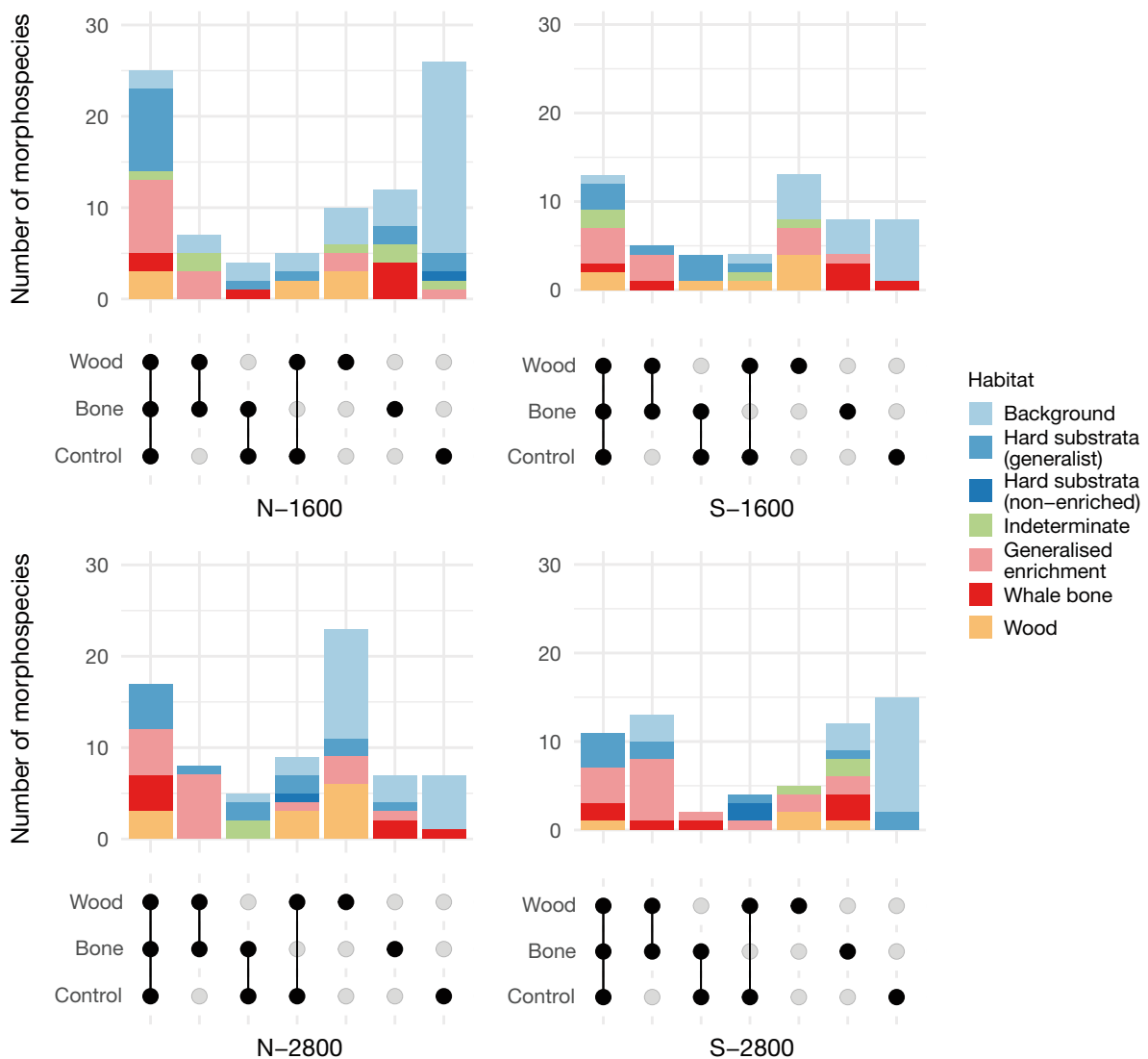

Fig. 4. UpSet plot (Lex et al. 2014, Krassowski 2020) indicating substrate types at which morphospecies were present. Black dots indicate substrate types, or combinations of substrate types when connected. UpSet plots for each depth and for all landers combined are displayed in Fig. S6

faecal 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 colonisation, despite heavy colonisation of wood blocks on the lid directly above. Because the lid wood blocks at S-1600 were heavily colonised 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} (Fig. 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 (Fig. 2C), with occasional empty boreholes ~2 mm in diameter.

Patches of black discolouration 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}).

3.1.2. Bone

Whale bones from all landers displayed black discolouration indicating reducing conditions (Fig. 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. Colonisation 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 whale-falls 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 S1).

3.1.3. Control

Control substrates supported visibly less fauna on substrate surfaces and in bins than did organic-rich substrates (Fig. 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 generalised-enrichment respondents constituted between 30.6 and 81.6 % of control assemblage abundances across the 4 landers (Fig. 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 S1). 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.

3.2. Community structure

The nMDS analysis of morphospecies assemblages shows clustering according to depth, lander location, and substrate type (Fig. 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). 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). 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;
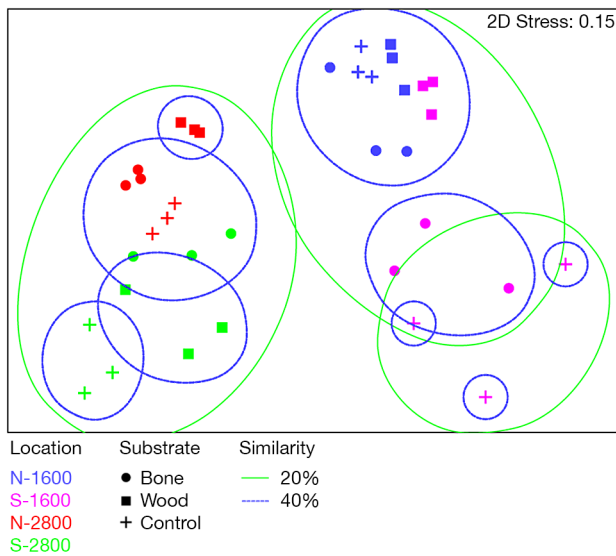
Fig. 5. Nonmetric multidimensional scaling (nMDS) ordinations of wood, control, and bone assemblages from 4 experimental colonisation landers deployed on the Washington–Oregon margin, based on Bray-Curtis dissimilarities of $\log(x + 1)$ transformed abundances

both p < 0.05) are evident in Fig. 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). Bone assemblages were significantly different between depths (pairwise PERMANOVA; Monte Carlo random draws; p < 0.05, Table S2), 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%, Fig. 5) despite the lack of colonisation 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%).

3.3. Abundance and diversity

3.3.1. 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 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 (Fig. 6; however, see Section 4.1 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.

3.3.2. 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

Table 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 3. Generalised linear mixed model summary information. Full mixed model information is included in Table S4. 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^2m: marginal R^2 value; R^2c: conditional R^2 value

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

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 3). Within northern and southern locations, patterns of log(ind. cm⁻²), S, and J with depth were inconsistent across the different substrate types (Fig. 6). Densities of control assemblages had no clear pattern with depth (Fig. 6).

3.3.3. 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 3). There were no consistent patterns of densities or diversity (S, J, or Chao1) across substrate types within individual landers (Fig. 6).

3.3.4. 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 3, Fig. 6). Patterns of H' and ES(30) closely resembled patterns of evenness, J (Fig. S4, Table S3). Rarefaction and extrapolated species richness curves, estimated with Chao1, showed no consistent patterns with location or substrate type (Fig. S5).

4. 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.

4.1. 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
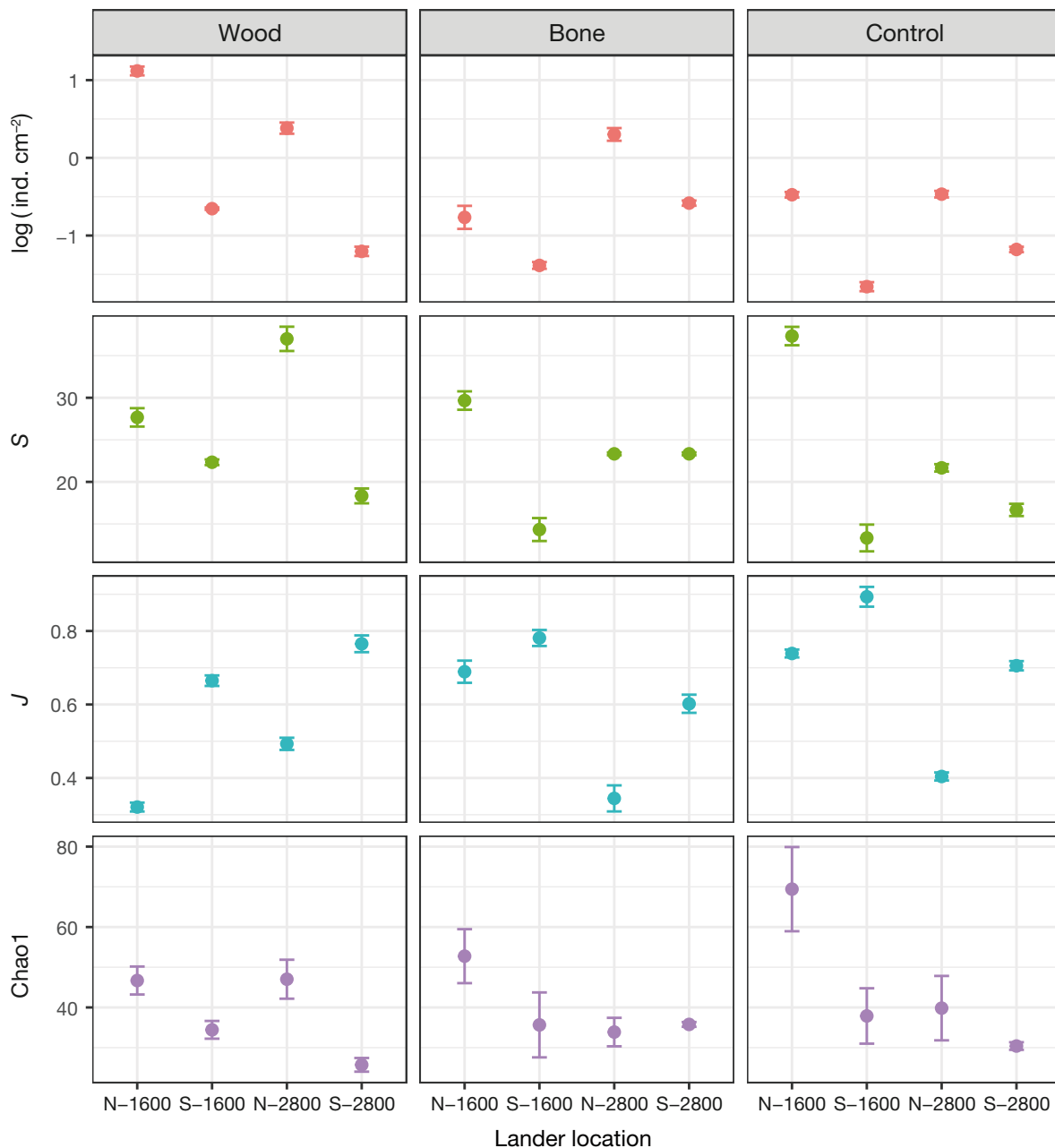
Fig. 6. Faunal density (log(ind. cm⁻² substrate surface area)) and diversity metrics (*S*: species richness; *J*: evenness; Chao1: estimated total species richness) by substrate type and lander location. Plotted as mean ± SE (n = 3). Abundances are estimates based on subsampling of wood and bone substrate infauna

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 colonisa-

tion studies in the deep sea (e.g. Saeedi et al. 2019). Continental margins are characterised 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 colonisation of wood blocks in bins at S-1600; this is surprising given the heavy colonisation 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 localised 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 4.3.2).

4.2. Variability with substrate type — Hypotheses 1 and 2

Wood, bone, and control substrates were colonised by statistically different communities (Table 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.

4.2.1. Wood

Wood blocks in this study were colonised 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 coloniser, *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 spatio-temporal 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 colonisation, 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 (e.g. Gaudron et al. 2010, Bienhold et al. 2013, Romano et al. 2013). Reports of higher xylophagaid densities (e.g. 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, 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, 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 sulphur-oxidising bacteria (Bernardino et al. 2010). *Ophryotrocha* spp. inside xylophagaid-bored wood blocks are likely omnivorous, deriving nutrition from the labile faecal material produced by the xylophagaid bivalves, which also may include sulphur-oxidising bacteria (Harbour et al. 2021). Xylophagaid faecal 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).

4.2.2. Bone

Bone assemblages were often dominated by a few species of mobile crustaceans, contributing to the high abundance and low evenness of bone assem-

blages. Dense populations of the pontogeneid amphipod *Accedomoera* sp. at N-2800 may have been attracted to odour 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 (e.g. 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 utilising whale bones opportunistically as an infaunal habitat at NE Pacific whale falls. Bones also supported mollusc genera known from reducing environments (e.g. *Laeviphitus*, *Hyalogyrina*, and *Idas*), albeit in low densities, which indicates an early reducing, sulphophilic successional stage for our bones (Smith & Baco 2003).

The majority of taxa (by abundance and richness) in our bone assemblages were substrate specialists plus generalised-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,b). 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 (e.g. Bennett et al. 1994, Baco & Smith 2003, Hilário et al. 2015, Smith et al. 2017, Alfaro-Lucas et al. 2017).

4.2.3. 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 generalised 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 unfavourable (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. 2021). 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.

4.2.4. 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 generalised-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 (e.g. Smith & Baco 2003, Amon et al. 2017). The relatively low *I. washingtonius* densities on our bone and wood deployments suggest that sulphidic conditions were low, either because of the small substrate sizes, or because the substrates were in early stages of development after 15 mo.

4.3. Variability with depth — Hypotheses 3 and 4

4.3.1. 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 centred at 1600 m and a lower slope-abyssal fauna centred 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 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 colonised 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.

4.3.2. Abundances

Because POC flux is implicated as an important driver of bathymetric patterns of faunal densities (e.g. 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 generalised-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 (Fig. S7). 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 assem-

blages. 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 colonised more rapidly by the wood-fall fauna than blocks at deeper locations. As indicated earlier, the presence and extent of xylophagaid bivalve colonisation can greatly influence the abundances, species richness, and dominance of wood-fall communities. Our findings of greater xylophagaid colonisation, 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 (Hautala et al. 2009). However, for ~2800 m deployments, xylophagaid densities were much higher on the northern landers (Table S5). We hypothesise 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 hypothesise 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, 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 colonisation of whale skeletons by multiple *Osedax* species in Monterey Bay (Lundsten et al. 2010a), compared to elsewhere in the NE Pacific (e.g. Smith & Baco 2003, Smith et al. 2015, this study). Because *Osedax* can influence the biodiversity (Alfaro-Lucas et al. 2017) and perhaps longevity of juvenile whale-fall habitats (Smith & Baco 2003, Lundsten et al. 2010a, Smith et al. 2015, 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 2006, 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.

4.4. Conclusions

The composition and diversity of faunal assemblages colonising 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 hypothesise 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.

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