



Biodiversity, community structure and ecosystem function on kelp and wood falls in the Norwegian deep sea

Rob P. Harbour^{1,*}, Craig R. Smith², Cornelia Simon-Nutbrown³, Marta Cecchetto¹, Emily Young², Caterina Coral^{1,4}, Andrew K. Sweetman¹

¹Deep-Sea Ecology and Biogeochemistry Research Group, The Lyell Centre for Earth and Marine Science and Technology, Heriot-Watt University, Edinburgh EH14 4AS, UK

²Department of Oceanography, University of Hawai'i at Manoa, Honolulu, Hawai'i 96822, USA

³The Lyell Centre for Earth and Marine Science and Technology, Heriot-Watt University, Edinburgh EH14 4AS, UK

⁴COS and EDS departments, Royal Netherlands Institute for Sea Research and Utrecht University, 1790 AB, Den Burg, Texel, The Netherlands

ABSTRACT: Fjordic systems in temperate and Arctic regions often feature extensive kelp forests at their shallow coastal margins as well as extensive terrestrial forests. Detrital export from these shallow-water and terrestrial ecosystems is an important source of carbon for deep-sea communities in the form of kelp and wood falls. Benthic landers with experimental substrates (wood blocks and kelp parcels) were deployed for 10 mo at a depth of 530 m in a deep Norwegian fjord to investigate and compare macro- and megabenthic community structure, biodiversity and ecosystem functioning on kelp and wood falls. Results revealed that while wood and kelp falls can support a similar number of species and abundance of fauna, they support significantly different faunal communities. Biomass and secondary production on both wood and kelp substrates were significantly greater than in the control samples. Secondary production estimates were similar or higher than those reported from soft-sediment ecosystems at shallower European marine sites. Biological trait analysis showed that macrofaunal assemblages were distinct between the kelp and wood, providing evidence for differences in ecosystem function between the substrates. This case study from a deep-sea fjord in Norway provides clear evidence that while wood and kelp organic falls can support similar abundances of fauna, the associated benthic biodiversity, community structure and ecosystem functioning can be dramatically different between these substrates. The work presented here aims to provide information that is useful in assessing the extent of anthropogenic impacts on deep fjord ecosystems with respect to informing future conservation and management strategies.

KEY WORDS: Deep sea · Organic falls · Fjord · Kelp · Wood · Benthic lander

— Resale or republication not permitted without written consent of the publisher —

1. INTRODUCTION

Sporadic influxes of organic detritus that reach the deep seafloor, including whale and fish carcasses, jellyfish, sunken kelp, wood and other macrophytic detritus, are known to increase localised stocks of

organic carbon in sediments and can be quickly consumed or otherwise exploited by a variety of specialist fauna (Wolff 1979, Gage 2003, Bernardino et al. 2010, Smith et al. 2014, Sweetman et al. 2014, McClain et al. 2016a, Harbour et al. 2020). These 'organic falls' can increase beta diversity relative to

*Corresponding author: r.harbour@hw.ac.uk

[§]The email address for corresponding author was updated after publication.
This corrected version: February 17, 2021

sediments not subjected to organic enrichment (e.g. Vetter & Dayton 1999, West et al. 2011).

Fjordic systems in temperate and Arctic regions often feature extensive kelp forests in the shallow coastal waters at their margins (e.g. in Alaska [USA], Canada, Chile, New Zealand, Norway; Krumhansl et al. 2016). Kelp forests provide primary production and habitat for a large variety of fauna, including important commercial stocks of decapods and fish (Steen et al. 2016). Annual regeneration, along with the dislodging of plants during periods of high wave action, produces a large amount of detritus. Between 3 and 8% of this detritus is thought to be consumed within the kelp forest, while the rest makes its way into adjacent habitats (Norderhaug & Christie 2011, Filbee-Dexter et al. 2018, Wernberg & Filbee-Dexter 2018). Exported kelp detritus can significantly increase secondary production in habitats located 10s to 100s of km from the kelp forest source (Krumhansl & Scheibling 2012). Deep-sea kelp falls support elevated macrofaunal species richness and abundance, particularly of sulphur-tolerant enrichment specialists such as dorvilleid polychaetes and cumaceans, as well as fish, shrimp and amphipods (Wolff 1979, Jeffreys et al. 2010, Bernardino et al. 2010, Renaud et al. 2015, Ramirez-Llodra et al. 2016). Increased microbial respiration in the surrounding sediment and in the kelp detritus itself can also create sulfidic conditions that attract chemosynthetic bacteria and archaea that fix inorganic carbon using sulphide as an electron donor (Bienhold et al. 2013). Furthermore, the deposition of macroalgae detritus is a carbon sequestration pathway, with 90% of this sequestration thought to occur in deep-sea sediments (Krause-Jensen & Duarte 2016).

The remains of terrestrial plant material are common in the deep sea, particularly in fjords and other deep-sea habitats located close to estuaries, which are often surrounded by forests (Wolff 1979, McClain & Barry 2014, Amon et al. 2017). During storm events, millions of tonnes of wood can be washed into the sea (West et al. 2011), where it eventually becomes waterlogged and sinks. For the coniferous woods that are commonly found along fjord margins, waterlogging usually takes 10–17 mo (Hägglblom 1982). Sunken wood has been shown to contribute significantly to deep-sea diversity (McClain et al. 2016b, Saedi et al. 2019). A variety of specialist wood-consuming fauna have been reported from the deep sea, such as xylophagaid bivalves (Turner 1973, Voight et al. 2020), echinoids (Becker et al. 2009), munidopsid lobsters and galatheid crabs (Hoyoux et al. 2009, Macpherson et al. 2014) as well as copepods and isopods

(Amon et al. 2017). Suspension feeders like serpulid polychaetes, poriferans and hydrozoans also use the wood as a hard substrate on which to settle (Amon et al. 2015). The organically enriched sediments created around wood falls and on the wood itself can support a variety of chemosynthetic microbial organisms, as well as fauna dependent on them (Bernardino et al. 2010, McLeod et al. 2010, Bienhold et al. 2013).

The Norwegian sublittoral zone features large stands of the kelp species *Laminaria hyperborea*, which covers an area of >5000 km² growing at densities of 10–15 plants m⁻² (Abdullah et al. 2017). Since 1970, approximately 9500 km² of kelp forests have been lost in Norway, much of which is attributed to catastrophic urchin grazing events and eutrophication as well as the multiple complex stressors associated with climate change (Sivertsen 1997, Steneck et al. 2002, Steen et al. 2016, Christie et al. 2019). In addition, there has been a recent resurgence in kelp harvesting (Steen et al. 2016), with mechanised harvesting removing 130 000–180 000 t wet weight annually (Vea & Ask 2011). The removal of large volumes of kelp material from coastal ecosystems is likely to greatly reduce transport of kelp detritus to the seafloor (Krumhansl & Scheibling 2012, Filbee-Dexter et al. 2018).

In contrast to the loss of kelp forests, the area covered by terrestrial boreal forests in Norway has tripled in the past 100 yr, with several government-sponsored programmes encouraging reforestation and banning land clearing (Amundsen 2014). It is hypothesised here that with such reforestation near the coast, combined with frequent storm and rainfall events, there will be an increase in the transport of wood and other organic forest detritus into deep fjords.

Despite numerous studies investigating the fauna colonising kelp substrates in shallow environments in Norway (e.g. Duggins et al. 1989, Christie et al. 2003, Waage-Nielsen et al. 2003), none have investigated benthic biodiversity and ecosystem functioning on wood and deep-sea kelp falls in Norwegian fjords. While specialist deep-sea wood-consuming fauna are known, wood is thought to be initially inaccessible to most animals due to its refractory compounds, mostly lignin and cellulose—this is likely to affect its availability to colonising fauna compared to kelp, which has a much lower C:N ratio.

In this study, benthic landers were deployed for 10 mo in a deep Norwegian fjord to investigate and compare macro- and megabenthic community structure, biodiversity and ecosystem functioning on kelp and wood falls. Ecosystem function was assessed using

biomass and secondary production. Secondary production estimates, calculated using biomass measurements, describe the energy flow between different trophic levels and are an essential part of the analysis of ecosystem function (Tumbiolo & Downing 1994, Brey 2012). Biological trait analysis (BTA) was used to further investigate functional structure. Benthic macrofauna that express particular traits play important roles in the functioning of benthic ecosystems (Snelgrove 1998), as well as linking benthic and pelagic systems (Bremner et al. 2006). BTA can play an important role in assessing the benthic community response to stressors (Barrio Froján et al. 2011, Paganelli et al. 2012, Bolam et al. 2014).

The work presented here aims to provide information that is useful in assessing the extent of anthropogenic impacts on deep fjord ecosystems with respect to informing future conservation and management strategies. Two hypotheses were tested: (1) wood falls exhibit significantly different community structure and trait assemblages than kelp falls; and (2) wood falls support significantly lower biodiversity, biomass and secondary production than kelp falls.

2. MATERIALS AND METHODS

2.1. Experimental design

Four benthic landers (Fig. 1A), designed and fabricated at University of Hawai'i at Manoa and Friday Harbor Laboratories (University of Washington), were deployed for 10 mo at 530 m depth between May 2017 and March 2018 in Osterfjorden from the RV 'Solvik'. Osterfjorden is located 15 km north of Bergen, Norway, and is 27 km in length and 1–3 km wide (Fig. 2). It features steep rocky sides that drop off to a relatively flat muddy seabed, reaching 639 m at its deepest point.

Lander frameworks were constructed out of aluminium; each lander comprised nine $40 \times 40 \times 40$ cm frames, each retaining Nytex mesh bags (500 μ m), arranged in lines of 3 to create a triangular shape that maximised the possibility that treatments

on each side of the lander were influenced differently by basin water currents (Fig. 1A). Each set of 3 bins had a PVC lid, held open by a releasing mechanism for the duration of the experiment; when the lander was signalled for retrieval, the lid closed so that the contents were protected and not washed out or contaminated with pelagic fauna during the ascent to the surface. Experimental substrates (Fig. 1B–E) of wood and kelp (*Laminaria hyperborea*) were wrapped in 2 cm mesh nylon netting attached by cable ties to the underside of the lid and to the bottom of each bin. Blocks of untreated wood measuring approximately $15 \times 15 \times 15$ cm were cut from a felled pine tree (*Pinus* sp.) found in an area close to the location of the

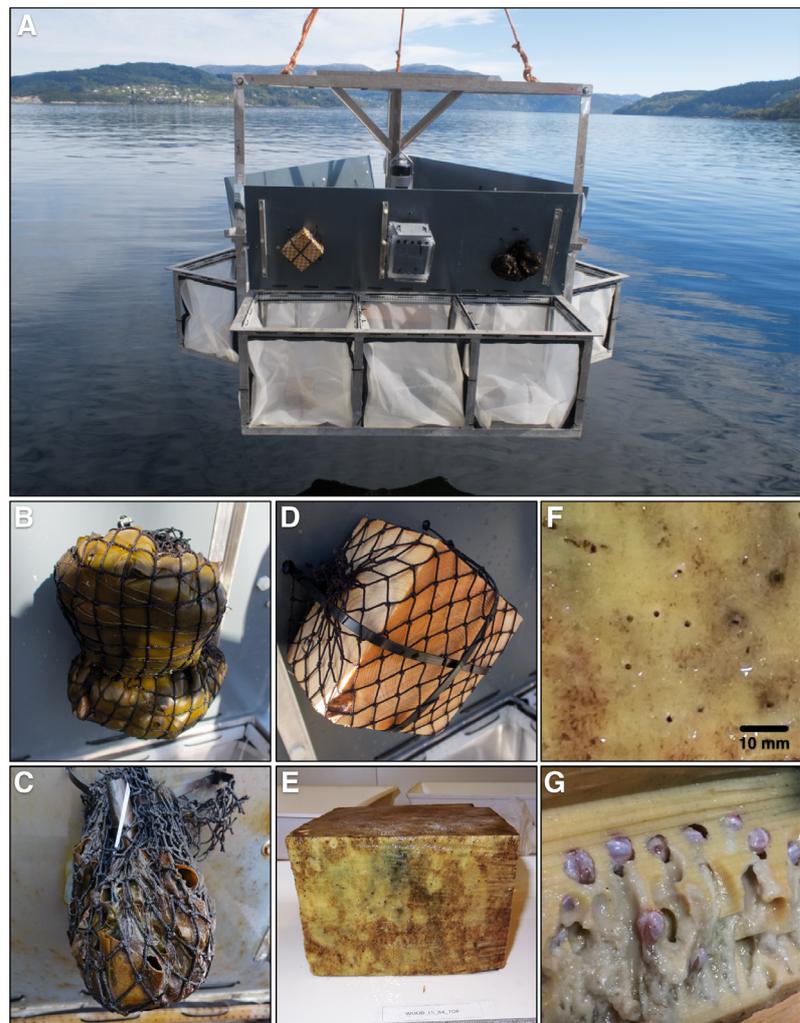


Fig. 1. (A) One of 4 identical benthic landers during deployment in May 2017; each lander consisted of nine $40 \times 40 \times 40$ cm fine-mesh bins, each containing one of 3 types of experimental substrate (wood block, settlement tile control, kelp parcel). (B) Fresh kelp parcel, (C) kelp parcel after deployment, (D) fresh wood block, (E) wood block after deployment, (F) *Xylophaga dorsalis* boreholes in the wood, (G) *X. dorsalis* molluscs and burrows inside the wood block

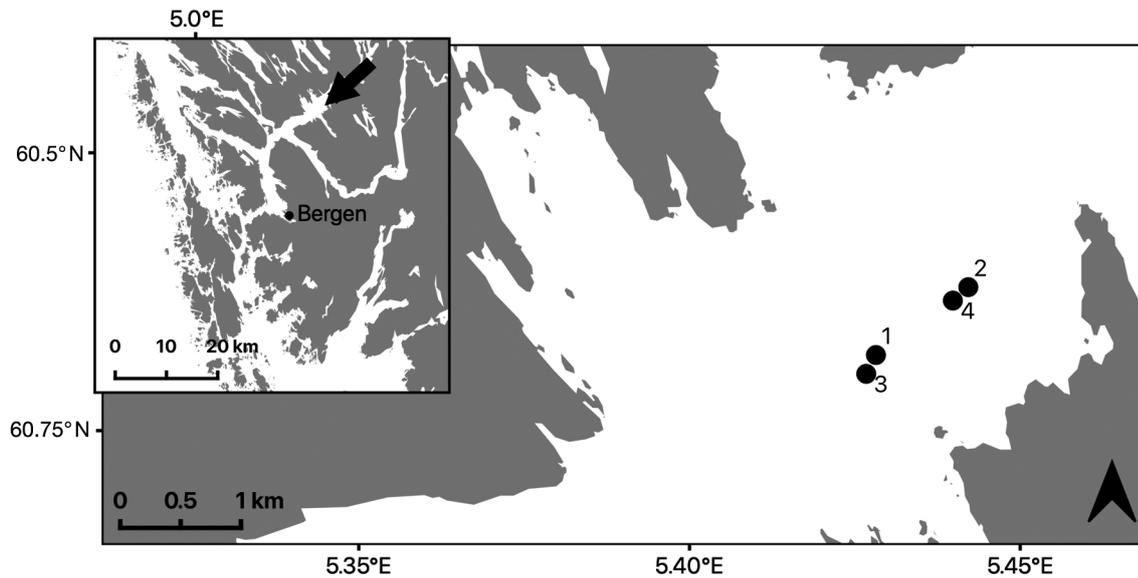


Fig. 2. Positions of the 4 benthic landers in Osterfjorden, Norway

lander deployments. *L. hyperborea* was collected by hand from a depth of approximately 2 m from a rocky outcrop in a fjord close to Bergen, Norway. The stipes were cleaned of epiphytes and cut into ~15 cm lengths, and the kelp blades were separated. Bundles of kelp stipes and blades (15 × 15 × 15 cm) were wet weighed to achieve approximately 2 kg before being attached to the lander.

The wood blocks and kelp parcels were designed to occupy a similar volume when attached to the lander; however, the carbon content of these 2 different substrates was expected to vary. It was not possible to measure this difference and adjust the substrate sizes before deployment of the landers due to time constraints; however, estimates of carbon content were calculated later for comparison. The carbon content of the wood blocks was measured directly using subsamples of the untreated wood that was used in the experiment. Samples were sent to the UC Davis Stable Isotope Facility for analysis with an Elementar Vario EL Cube or Micro Cube elemental analyser (Elementar Analysensysteme) interfaced with an Isoprime VisION (Elementar UK) isotope ratio mass spectrometer (Sercon). The carbon content of the kelp samples was estimated by first converting wet weight to dry weight using conversion factors calculated for *L. hyperborea* in the north-east Atlantic Ocean (Pessarrodona et al. 2018), and then multiplying by a mean carbon percentage of 27.4% measured in *L. hyperborea* plants on the west coast of Norway in March (Sjötun et al. 1996).

Four 15 cm² tiles made from plastic and one of smooth stone attached to the outside of a 15 × 15 ×

15 cm plastic box (Fig. 1A) were also attached to the lander as control substrates (hereafter referred to as 'control samples'). The inclusion of settlement tiles served as an inorganic control so that animals found on all 3 substrates could be designated as hard-substrate colonisers not specifically colonising any one type of organic substrate. The settlement tiles were placed in the central bins on each side of the lander so as to be furthest away from the structural elements of the lander, which might also provide settlement opportunities. Boxes were attached to the underside of the lid and the bottom of each allocated bin, covering a complete range of settlement angles. The wood and kelp were attached inside randomly allocated bins on either side of the control treatment. Once each substrate was attached to the lander, a reference photograph was taken.

2.2. Shipboard processing

After 10 mo on the seafloor, the landers were recalled to the surface by an acoustic signal. Once onboard, the substrates were photographed and placed into buckets of 5 µm filtered, cold seawater for transit to the University of Bergen Espeland Marine Station. The mesh bags were gently washed with cold, 5 µm filtered seawater, their contents washed on a 300 µm sieve and the residue fixed in 4% buffered formalin. In the laboratory, wood blocks were cut into 1 half and 2 quarters with a reciprocating saw. The 2 quarters were frozen, and the remaining half was preserved in 4% borax buffered formaldehyde

seawater. Kelp parcels were rinsed on a 300 μm sieve and the fauna fixed in 4% borax buffered formaldehyde seawater, with the remaining kelp detritus preserved in separate buckets. No visible macrofauna were detected on the settlement tiles under a dissecting microscope at 20 \times magnification—the plates were subsequently discarded, but the contents of the mesh bags were retained.

2.3. Faunal analysis

In the laboratory, formalin-preserved samples were first rinsed of formalin and transferred to a 2% phenoxyethanol solution. Samples were hand-picked under a Leica S8 APO stereo microscope and a Leica DM1000 LED compound microscope with phase-contrast functionality. Approximately 10 000 animals were identified, in the majority of cases to species level, using dichotomous taxonomic keys and through expert consultation (S. Hamilton pers. comm.). A reference collection was created for every individual species found; these samples were labelled accordingly and stored in 99.8% ethanol. Wood-boring molluscs were extracted from the wood blocks by carefully removing small pieces of wood with a hammer and chisel and extracting the molluscs with forceps.

After species identification, samples were dried and weighed for biomass analysis (species collected from a single sample were dried and weighed together). Molluscs were removed from their inorganic shells before weighing. Dry mass (DM) was calculated by weighing the container, placing the wet animal(s) inside, drying them at 60°C for 1 wk (or until their weight remained constant) and re-weighing, before subtracting the weight of the container. A Mettler Toledo microbalance was used for smaller animals (e.g. dorvilleid polychaetes) and for larger animals (e.g. shrimp), a Sartorius QUINTIX analytical balance was used. *Xylophaga dorsalis* was highly abundant in the wood samples, and extracting them from the wood without breaking their shells was impractical. Therefore, 50 molluscs spanning a range of sizes (4–10 mm) from 4 different wood blocks were extracted, carefully removed from their shells and weighed. The resulting weights were normally distributed, so their mean weight was multiplied by the abundance of *X. dorsalis* in each sample to generate *X. dorsalis* biomass estimates.

To calculate secondary production, DM measurements were converted first to grams ash free dry weight (gAFDW) and then to joules (J) using pub-

lished conversion factors at the family or genus level (Brey 2012). Annual production to biomass (P:B) ratio for each taxon in a sample was then calculated (with data on species where available, or closely related taxa where it was not) using the R script 'Benthic Energy Flow v1.0', which accounts for body size, major taxonomic group, life history and water temperature (Andresen & Brey 2018, R Core Team 2019). Production estimates ($\text{kJ substrate}^{-1} \text{yr}^{-1}$) were then produced by multiplying the total mean biomass (kJ) for each substrate sample by these ratios. For thorough explanations of this methodology and model, see Bolam et al. (2010) or Brey (2001).

2.4. BTA

Biological traits were chosen based on the availability of data covering the greatest number of taxa. Biomass data was selected as the 'abundance metric' for this analysis because it better represents the distribution of resources in an ecosystem compared to species abundance data (Cesar & Frid 2009, Bolam & Eggleton 2014). Trait data for all taxa in this study were derived from The Arctic Trait Database (Degen & Faulwetter 2019), with the exception of the species *X. dorsalis*, for which data were derived from publications (e.g. Turner 2002, Tyler et al. 2007, Voight 2009, 2015, Voight et al. 2020). For taxa where no specific trait data were available, trait coding was carried out using their closest taxonomic relative. Each trait was subdivided into categories, referred to as modalities (Bremner et al. 2003); a total of 11 traits, including 50 modalities, were allocated to each taxon (Table 1). Since one taxon may exhibit more than one trait modality, modalities were coded from 0–3 using a 'fuzzy coding' technique, where '3' codes for exclusive affinity and '0' codes for no affinity for a particular modality, to produce a taxon \times trait matrix (Chevenet et al. 1994). Each trait was made up of a varying number of modalities; to account for this, the fuzzy coded (0 to 3) taxon \times trait matrix was first processed with the 'prep.fuzzy.var' function in the 'ADE4' package in R v.3.6 (Dray et al. 2018, R Core Team 2019) so that the modalities of each trait were proportional ($\Sigma = 1$). To produce a sample \times trait matrix representing the biomass (gAFDW) within each trait within a sample, the taxon \times trait matrix was multiplied by a sample \times taxon biomass matrix using standard matrix multiplication techniques. This sample \times trait matrix, weighted by biomass is hereafter referred to as T_{biom} .

Table 1. Traits categories. Reproduced from The Arctic Traits Database (Degen & Faulwetter 2019). Feeding habit 7 and substratum affinity 5 were added specifically for the obligate wood boring mollusc *Xylophaga dorsalis*

Trait	Modality	Description
Body size	S1 Small	<10 mm
	S2 Small–medium	10–50 mm
	S3 Medium	50–100 mm
	S4 Medium–large	100–300 mm
	S5 Large	>300 mm
Body form	BF1 Globulose	Round or oval
	BF2 Vermiform, elongate	Worm-like or thin, elongate body form
	BF3 Dorso-ventral compressed	Species that are flat, or encrusting
	BF4 Laterally compressed	Thin
	BF5 Upright	E.g. coral, basket star, sponge
Skeleton	SK1 Calcareous	Skeleton material aragonite or calcite
	SK2 Siliceous	Skeleton material silicate
	SK3 Chitinous	Skeleton material chitin
	SK4 Cuticle	No skeleton but a protective structure like a cuticle
	SK5 None	No form of protective structure
Reproduction	R1 Asexual	Budding and fission
	R2 Sexual—external	Fertilization external, eggs & sperm deposited on substrate or released into water
	R3 Sexual—internal	Fertilization internal, but no brooding, eggs deposited on substrate, indirect or direct development
	R4 Sexual—brooding	Fertilization internal or external, Eggs or larvae are brooded, indirect or direct development
Larval development	LD1 Pelagic/planktotrophic	High fecundity, larvae feed and grow in water column, generally pelagic for several weeks
	LD2 Pelagic/lecithotrophic	Medium fecundity, larvae with yolk sac, pelagic for short periods
	LD3 Benthic/direct	Larvae have benthic or direct development
Living habit	LH1 Free living	Not limited to any restrictive structure at any time. Able to move freely within and/or on the sediments
	LH2 Crevice dwelling	Adults are typically cryptic, inhabiting spaces made available by coarse/rock substrate and/or biogenic species or algal holdfasts
	LH3 Tube dwelling	Tube may be lined with sand, mucus or calcium carbonate, tube can also be in a burrow
	LH4 Burrowing	Species inhabiting permanent or temporary burrows in the sediment, or are just burrowing in the sediment
	LH5 Epi/endo zoic/phytic	Living on or in other organisms
	LH6 Attached	Adherent to a substratum
Movement	MV1 Sessile/none	No movement as adult
	MV2 Burrower	Movement in the sediment; including tube dwellers.
	MV3 Crawler	An organism that moves along on the substratum via movements of its legs, appendages or muscles (e.g. crab, snail)
	MV4 Swimmer (facultative)	Movement above the sediment
Feeding habit	FH1 Surface deposit feeder	Active removal of detrital material from the sediment surface. Includes species which graze or scrape algal matter from surfaces
	FH2 Subsurface deposit feeder	Removal of detrital material from within the sediment matrix
	FH3 Filter/suspension feeder	Sponge, coral, hydrozoan, bivalves
	FH4 Omnivore/scavenger	An organism that can use different types of food sources/an organism that feeds on dead organic material
	FH5 Predator	An organism that feeds by preying on other living organisms
	FH6 Parasite/commensal/symbiotic	An organism that lives in or on another living organism (the host), from which it obtains food and other requirements; or an organism containing symbionts
	FH7 Xylophagy	Specific trait for <i>Xylophaga dorsalis</i> , wood consuming
Substratum affinity	SA1 Soft	Soft substrata, sand or mud
	SA2 Hard	Hard substrata, rock, gravel
	SA3 Biological	Epizoic or epiphytic lifestyle
	SA4 None	Species is hyper/supra benthic and has no affinity for a certain substrate, but it might prefer one for hunting/scavenging
	SA5 Terrestrial wood	Specific trait for <i>Xylophaga dorsalis</i>
Bioturbation	B1 Diffusive mixing	Surficial movement of sediment and/or particles, resulting from movement or feeding activities on the surface
	B2 Surface deposition	Deposition of particles at the sediment surface resulting from defecation or egestion (pseudofaeces)
	B3 Conveyor belt transport (upward)	Translocation of sediment and/or particulates from depth within the sediment to the surface during subsurface deposit feeding or burrow excavation
	B4 Downward (reverse) conveyor	The subduction of particles from the surface to some depth by feeding or defecation
	B5 None	No bioturbation
Environmental position	EP1 Infauna	Lives in the sediment or inside substrate
	EP2 Epibenthic	Lives on the surface of the seabed
	EP3 Hyper-benthic	Living in the water column, but (primarily/occasionally) feeds on the bottom; benthic-pelagic

2.5. Statistical analysis

Species abundance data were used to calculate species richness (S), number of individuals (N), Shannon-Wiener diversity (H') and Pielou's evenness (J') in PRIMER v7 (Quest Research Limited). The treatments were analysed for significant differences in OriginPro v2020b (OriginLab Corporation). Prior to statistical testing, univariate diversity indices and biomass data were checked for normality and homogeneity of variances using Shapiro-Wilk tests and Levene's tests. Data were then subjected to 1-way ANOVA, with significance assumed at $\alpha < 0.05$. All ANOVA results were corrected for the multiple tests using the sequential Bonferroni-Holm correction. Production versus treatment data were strongly skewed, so $\log(x + 1)$ transformation was applied to achieve normal distribution before 1-way ANOVA was used to assess for significant differences between substrates.

Species accumulation curves were generated using PRIMER v7 to assess whether the community was sufficiently sampled to gain an accurate representation. Differences in biodiversity between treatments were analysed by rarefaction analysis in Primer v7. To check for statistically significant differences between the wood and kelp treatments, 95% confidence limits were calculated around the means for each treatment, with overlapping confidence limits being evidence for non-significance. Differences in community structure were analysed by non-metric multidimensional scaling (nMDS) on non-transformed data in PRIMER v7. Resemblance matrices were produced for multivariate abundance and biomass data using Bray-Curtis similarity, and ANOSIM tests were run to a maximum of 9999 permutations with the Spearman rank correlation method.

BTA was carried out using the 'ADE4' package in R (Dray et al. 2018, R Core Team 2019). The T_{biom} matrix was strongly skewed, so data were transformed using a $\log(x + 1)$ transformation. The transformed T_{biom} matrix was then ordinated with fuzzy correspondence analysis (FCA) and the ordinate scores for the FCA1 and FCA2 axes were analysed, using an independent samples t -test using substrate (wood, kelp) as a factor, in SPSS Statistics v26 (IBM).

3. RESULTS

3.1. General notes

Temperature and oxygen concentrations at the experimental deployment sites were measured from

a sample taken with a Niskin bottle and at the time of retrieval were 8°C and $135 \mu\text{mol l}^{-1}$, respectively.

Prior to deployment, the estimated carbon content for wood samples was 49.0%, with each lander bin estimated to contain a mean (\pm SE) of $902.48 \pm 14.2 \text{ g C}$ ($n = 33$). The nitrogen content for wood was estimated to be 0.85%, with a C:N ratio of 57.5. Kelp samples were estimated to contain $362.57 \pm 7.5 \text{ g C}$ ($n = 33$) per lander bin before deployment. For comparison in this study, a previously measured C:N ratio for kelp from western Norwegian fjords was used (C:N = 9.5; Sjøtun et al. 1996). *Xylophaga dorsalis* pseudofaeces (woody material extracted from the burrow of the mollusc) in the wood blocks after recovery contained 36% carbon and 6.75% nitrogen, with a C:N ratio of 5.39.

Following lander recovery, white filamentous bacterial mats (possibly *Beggiatoa* spp.) were observed coating the wood blocks and kelp bundles, suggesting chemosynthetic activity may have occurred on both types of substrate. Stable isotope analysis of these mats showed depleted $\delta^{13}\text{C}$ signatures (mean \pm SD: $-27.75 \pm 0.3\text{‰}$, $n = 2$) consistent with this observation. The wood blocks looked otherwise intact from the outside, with tiny boreholes ($\sim 1 \text{ mm}$) being the only evidence of xylophagaid presence (Fig. 1E). Inside each block, hundreds of molluscs were found towards the outside of the wood blocks with very few on the side attached to the lander (Fig. 1F). Kelp samples were extensively degraded (Fig. 1B); much of the material from the blades had become small pieces of detritus ($< 1 \text{ cm}$) which littered the bottoms of the mesh bags. The kelp stems were generally completely hollowed out, with just a tube constructed from the thicker outer cell walls remaining.

3.2. Biodiversity and community structure

Mean (\pm SE) S in the kelp (14.45 ± 4.36 , $n = 11$) and wood samples (15.55 ± 4.69 , $n = 11$) ('sample' will hereafter refer to the entire contents of the mesh bags, including wood/kelp substrate itself) was significantly higher than in the control samples (8 ± 2.4 , $n = 11$) (1-way ANOVA, $p < 0.001$), but no significant difference was observed between the kelp and wood samples (Fig. 3). The mean N in kelp (596 ± 180 , $n = 11$) and wood samples (543 ± 163 , $n = 11$) were also significantly higher than in the control samples (21.64 ± 6.52 , $n = 11$) (1-way ANOVA, $p < 0.001$, $n = 33$), but no significant difference was observed between the kelp and wood samples (Fig. 3). Species accumulation curves generated for kelp, wood and

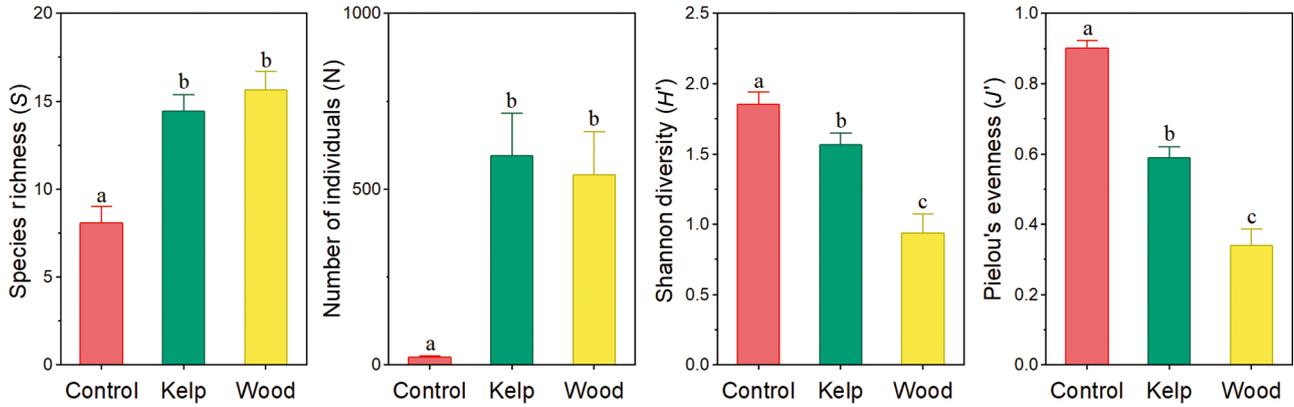


Fig. 3. Comparisons between communities found on each type of experimental substrate for species richness, number of individuals, Shannon diversity index and Pielou's evenness. Data are displayed as means \pm SE. Significant results are shown with a different alphabetical letter (1-way ANOVA, $p < 0.001$ with Bonferroni-Holm correction for multiple tests; $n = 33$)

control samples reached asymptotes after 8–11 samples (Fig. 4), suggesting that adequate sampling took place to provide an accurate indication of the communities associated with each substrate type. Mean rarefaction curves showed S of 10 in both kelp and wood samples when rarefied to 150 individuals, and no significant difference between kelp and wood substrates was observed (Fig. 4). Control samples contained so few individuals that they were excluded from mean rarefaction curve plots.

The kelp, wood and control samples showed significantly different H' indices (1-way ANOVA, $p < 0.001$, $n = 11$). H' values in the control samples were the highest (1.85 ± 0.06 , $n = 11$), kelp values were

slightly lower (1.57 ± 0.05 , $n = 11$) and the lowest were the wood samples (0.94 ± 0.09 , $n = 11$) (Fig. 3). J' values were 0.90 ± 0.01 ($n = 11$) in the control samples, 0.34 ± 0.03 ($n = 11$) in the wood and 0.59 ± 0.02 ($n = 11$) in kelp and were significantly different across all substrates (1-way ANOVA, $p < 0.001$, $n = 33$) (Fig. 3).

Investigations into species overlap based on presence/absence data showed that 70% of species found in wood samples and 78% of species found in kelp samples were also found in the control samples. Sixty percent of species found in wood samples were also found in the kelp samples. However, most species that overlapped were seen in very low abundances in certain types of samples and high

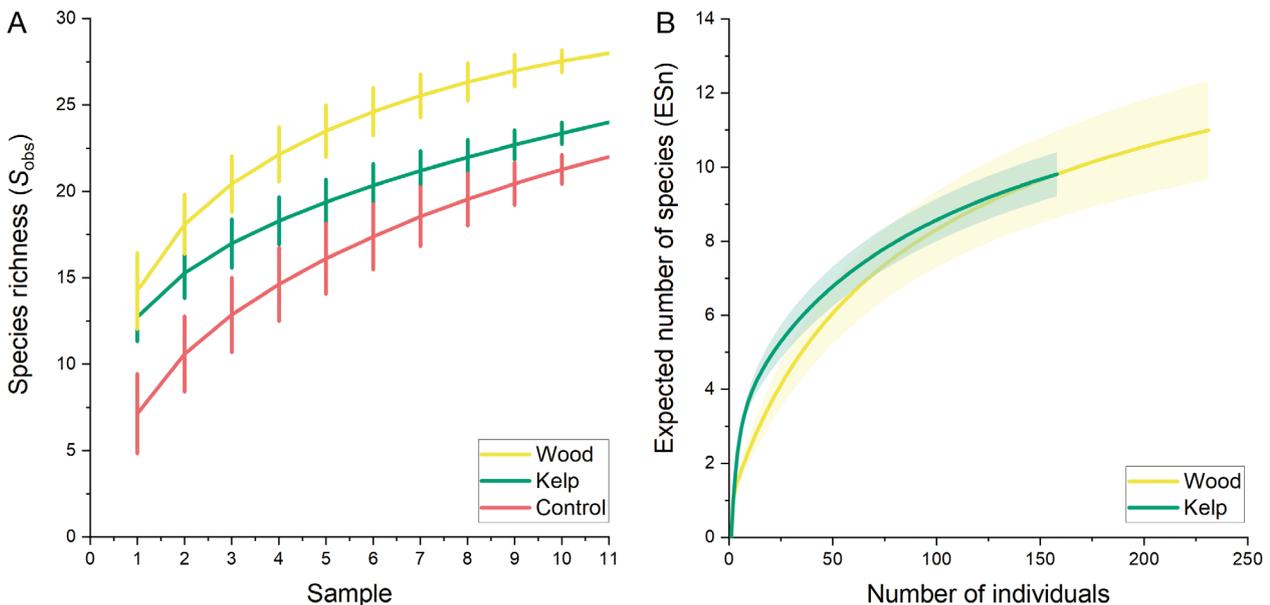


Fig. 4. (A) Species accumulation curves (S_{obs}) for wood ($n = 11$), kelp ($n = 11$) and control ($n = 11$) samples. Data are mean \pm SE. (B) Rarefaction curves for pooled wood ($n = 11$) and pooled kelp samples ($n = 11$) as means \pm 95% confidence intervals

in others (e.g. *Ophryotrocha* sp. had an average abundance of 7 in wood samples and 205 in kelp samples). See Table S1 in the Supplement at www.int-res.com/articles/suppl/m657p073_supp.pdf for more information.

A nMDS using species abundance data showed very clear clustering of communities among substrates (Fig. 5). The communities found in the wood, kelp and control samples were all significantly different (ANOSIM, $Rho = 1.0$, $p < 0.001$), despite 8, 37 and 59% of the total species abundance being highly mobile crustaceans (e.g. shrimps) in the wood, kelp and control samples, respectively. To reduce the influence of highly abundant species on the resemblance matrix, the data were transformed into presence/absence. Following this transformation, the communities on each substrate still formed separate clusters (ordination not shown) and were significantly different, though with a slightly weaker Rho statistic (ANOSIM, $Rho = 0.6$, $p < 0.001$), confirming that the differences seen amongst treatments were related mostly to compositional rather than abundance patterns.

SIMPER analysis showed that overall community similarity within the different treatments was 64.3% for kelp and 66.2% for wood. The highest contributors to the similarity matrix in the kelp samples were *Nebalia strausi* (36.6%), *Ophryotrocha* spp. (32.2%) and *Capitella* sp. (20.9%). In wood samples, *X. dorsalis* contributed almost all of the similarity (86.6%). Kelp and wood communities were 88.4% dissimilar, and the largest contributor to this difference was *X. dorsalis*, which contributed 44.8% to the dissimilarity. *Ophryotrocha* spp. contributed 19.2% and

N. strausi contributed 17.4%. Kelp and wood communities were both 95.0% dissimilar to the control communities, but the species contributing to the dissimilarity were different: 82.5% of the dissimilarity between the control and wood substrates was contributed by *X. dorsalis*, whereas between kelp and the control, *N. strausi* (33.5%), *Ophryotrocha* spp. (32.5%) and *Capitella* sp. (21.6%) were primarily responsible. Though not a large contributor to the overall dissimilarity, there was a significantly higher abundance of the shrimp *Atlantopandalus propinquus* in kelp and wood samples compared to the control samples (1-way ANOVA, $p < 0.05$).

3.3. Biomass and secondary production

Mean (\pm SE) faunal biomass in the kelp samples was 1.18 ± 0.2 gAFDW, of which 80.2% were crustaceans and the remaining 19.8% were polychaetes (Fig. 6). When the polychaetes were divided into families, Capitellidae (60.1%) and Spionidae (33.5%) contributed most to the biomass, with the highly abundant but much smaller Dorvilleidae contributing only 5.3% (Fig. 7). Mean faunal biomass in the wood samples was 3.70 ± 0.6 gAFDW and was significantly higher than the kelp samples (1-way ANOVA, $p < 0.05$, $n = 33$). *X. dorsalis* bivalves contributed the most biomass in the wood samples (79.2%), with crustaceans contributing 20.1%. Polychaetes made up only 0.8% of the biomass (Fig. 6). When polychaetes were divided into families, Spionidae contributed 84.7% of the polychaete biomass in the wood samples (Fig. 7). Mean faunal biomass in



Fig. 5. Community and abundance non-metric multidimensional scaling plot by substrate type (wood, kelp, hard). Similarity lines show less than 20% similarity between substrates illustrating significant community separation (ANOSIM, $Rho = 1.0$, $p < 0.001$, $n = 33$). Generated from a Bray-Curtis resemblance matrix. Data are not transformed

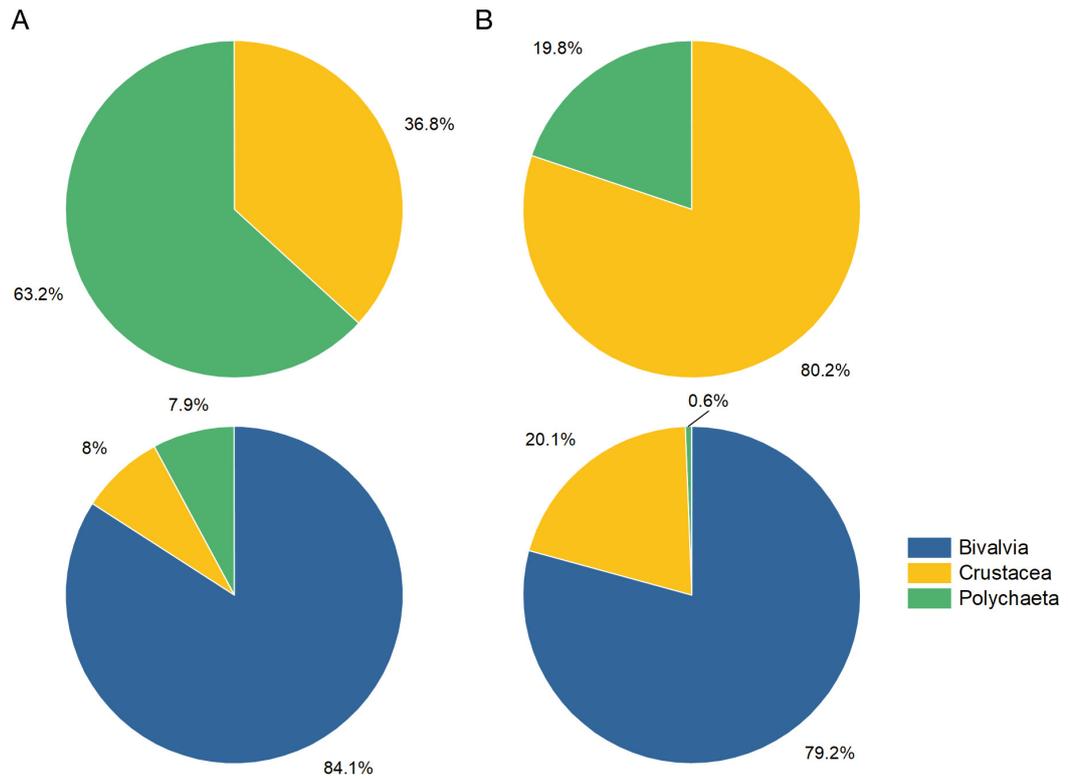


Fig. 6. (A) Relative abundance (ind. substrate⁻¹) and (B) biomass (gAFDW substrate⁻¹) of the macrofaunal classes found on kelp (top) and wood (bottom) samples

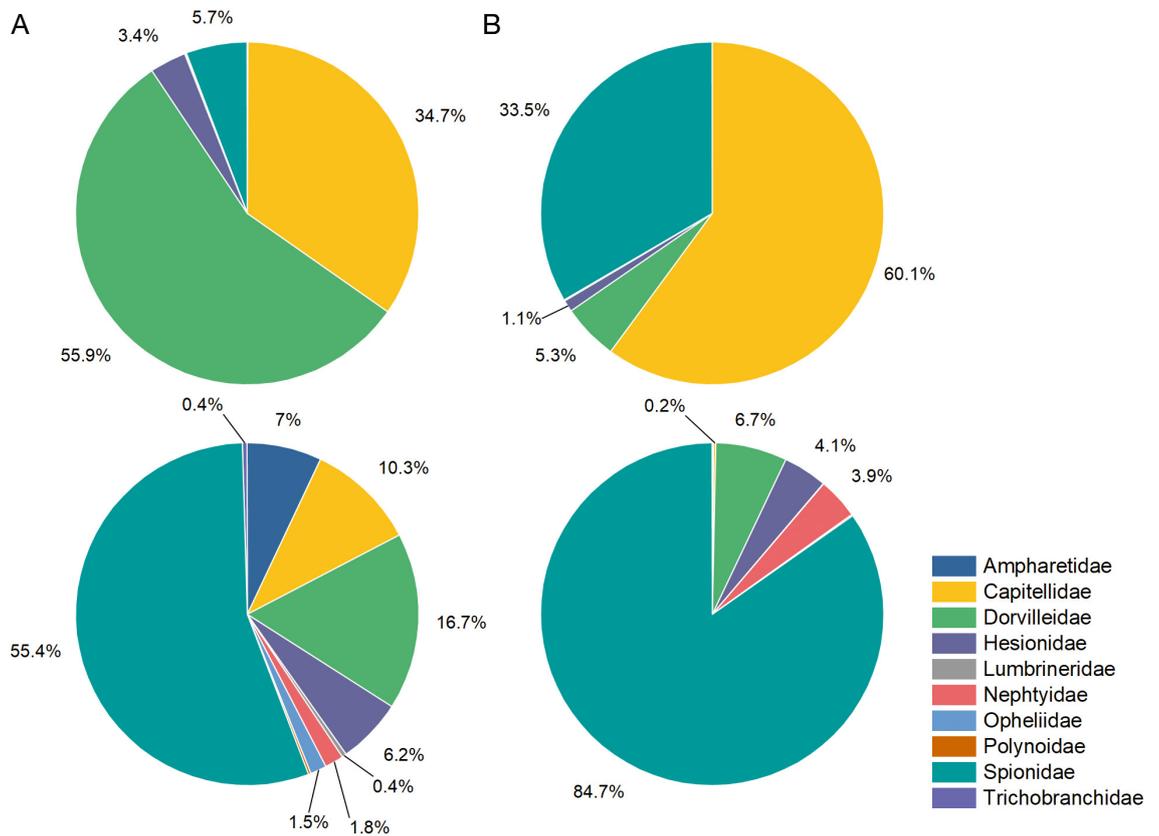


Fig. 7. (A) Relative abundance (ind. substrate⁻¹) and (B) biomass (gAFDW substrate⁻¹) of the major polychaete families found on kelp (top) and wood (bottom) samples

the control samples was 0.38 ± 0.1 gAFDW, of which 58.9% were crustaceans and the remaining 41.1% were polychaetes (data not shown). When the polychaetes were divided into families, Hesionidae (39.8%), Opheliidae (33.5%), Ampharetidae (15.9%) and Spionidae (9.1%) contributed most to the biomass (data not shown). Wood had significantly higher biomass than the control samples (1-way ANOVA, $p < 0.05$, $n = 33$) but no significant biomass difference was found between the kelp and control samples after correcting for multiple tests.

The mean annual P:B ratio was 0.80 ± 0.04 yr⁻¹ ($n = 11$) for kelp samples, 0.87 ± 0.08 yr⁻¹ ($n = 11$) for wood samples and 0.43 ± 0.06 yr⁻¹ for the control samples. Mean annual production estimated for control, kelp and wood samples was significantly different (1-way ANOVA, $p < 0.001$, $n = 33$) (Fig. 8). The highest mean productivity was derived from wood samples (53.83 ± 8.6 kJ substrate⁻¹ yr⁻¹, $n = 11$); kelp was significantly lower (29.63 ± 5.3 kJ sub.⁻¹ yr⁻¹, $n = 11$) (Fig. 8). Production derived from the control samples (5.30 ± 1.1 kJ sub.⁻¹ yr⁻¹, $n = 11$) was significantly lower than both the wood and kelp samples, which correlated with the very low numbers of individual animals found in these samples (Fig. 8).

Significant differences were found between the major taxonomic groups that contributed to the productivity in the control, kelp and wood samples

(2-way ANOVA, $p < 0.001$, $n = 33$) (Fig. 8). Crustaceans and polychaetes in the kelp samples provided significantly more production than in wood samples, with a large part of the production in wood samples being provided by *X. dorsalis* molluscs. The nMDS analysis using community secondary production values showed distinct clustering of the kelp, wood and control samples (ANOSIM, $Rho = 0.968$, $p < 0.001$, $n = 33$) (Fig. 9).

3.4. BTA on kelp and wood samples

The first 2 axes of the FCA explained 85.45% of the variance between the samples (Fig. 10). FCA1 explained 66% of the variance; the most important traits were body form, skeleton and feeding habit, with trait modalities indicating globulose body forms, calcareous shells and xylophagy, respectively (Table 2). FCA2 explained 19.45% of the variance, with the most important contributions being traits for larval development, adult movement and environmental position, with modalities indicating direct larval development, crawling movement and an epibenthic lifestyle, respectively (Table 2). The highest contributors to the variance on FCA2 were trait modalities generally associated with the polychaetes and crustaceans more commonly found on the kelp samples.

The FCA ordination showed a distinct clustering of samples according to substrate type (Fig. 10). On FCA1, all kelp sample ordination scores were positive, and all wood samples were negative. Ordination scores from FCA1 were compared using substrate as the factor and community-trait assemblages were found to be significantly different between substrates (independent samples *t*-test, $p < 0.001$).

Since *X. dorsalis* were so dominant in the relative trait contributions, they were later removed from the FCA in order to more closely explore the 'background' trait assemblages expressed by the rest of the community (Table 3). The first 2 axes of the second FCA explained 77.33% of the variance between the samples, with FCA1 explaining 54.67% and FCA2 explaining 22.66% of the variance (Fig. 10). Ordination scores from FCA1 were compared with substrate as the factor and the community-trait assem-

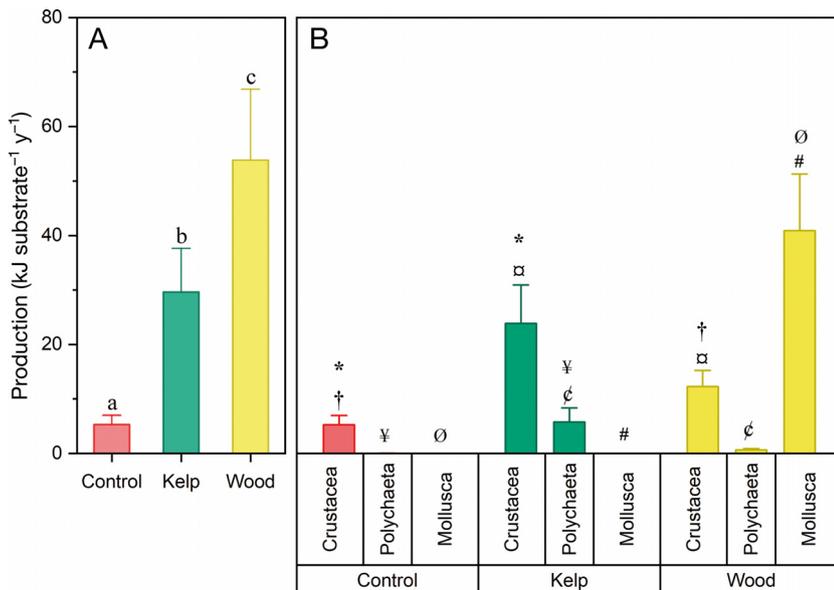


Fig. 8. (A) Mean \pm SE annual production per substrate. A different alphabetical letter shows a significant difference between the groups (ANOVA, $p < 0.01$, $n = 33$). (B) Mean \pm SE annual production by substrate and major taxonomic group. Significantly different major taxa compared between substrate groups are shown with the same symbol (2-way ANOVA, $p < 0.01$, with Bonferroni-Holm correction, $n = 33$)

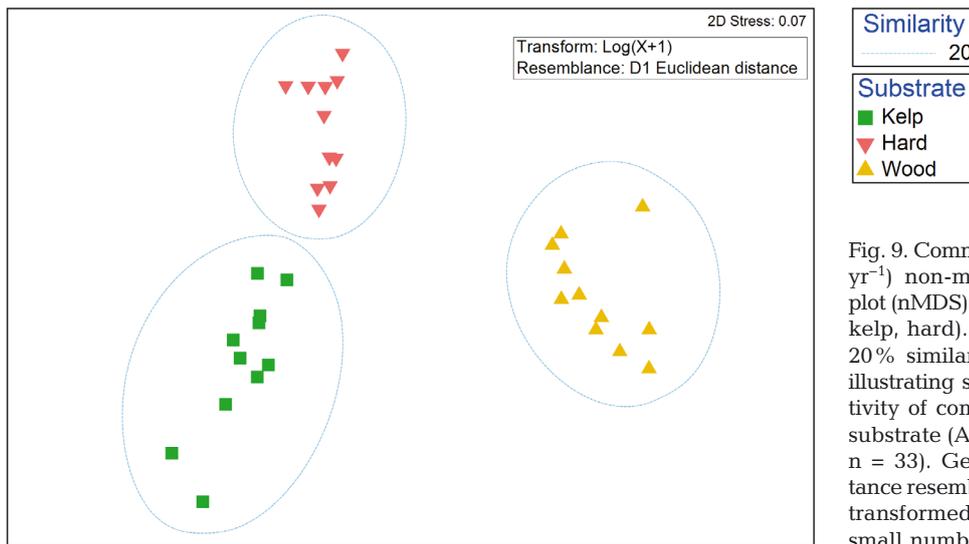


Fig. 9. Community production ($\text{kJ substrate}^{-1} \text{yr}^{-1}$) non-metric multidimensional scaling plot (nMDS) plotted by substrate type (wood, kelp, hard). Similarity lines show less than 20% similarity between substrate groups, illustrating significant separation in productivity of communities associated with each substrate (ANOSIM, $Rho = 0.968$, $p < 0.001$, $n = 33$). Generated from a Euclidean distance resemblance matrix. Data are $\log(x + 1)$ transformed to lessen the influence of a small number of highly productive species

blages between substrates were still found to be significantly different (independent samples t -test, $p < 0.05$).

4. DISCUSSION

4.1. Biodiversity

After 10 mo on the seafloor, S , rarefied S and N in both the wood and kelp samples were not significantly different (Figs. 3 & 4); these results mean that the second hypothesis, that wood falls support signif-

icantly lower biodiversity, biomass and secondary production than kelp falls, is partially rejected. Evidence was found to support the importance of both wood and kelp falls in providing important substrates to benthic fauna in at least one Norwegian deep-sea fjord. Findings here were similar to those from comparable experiments in the North Pacific and South Atlantic oceans, where both wood and kelp falls were shown to support benthic ecosystems by providing colonisation substrate and food (Snelgrove et al. 1994, Bernardino et al. 2010, McClain et al. 2016a, Saeedi et al. 2019).

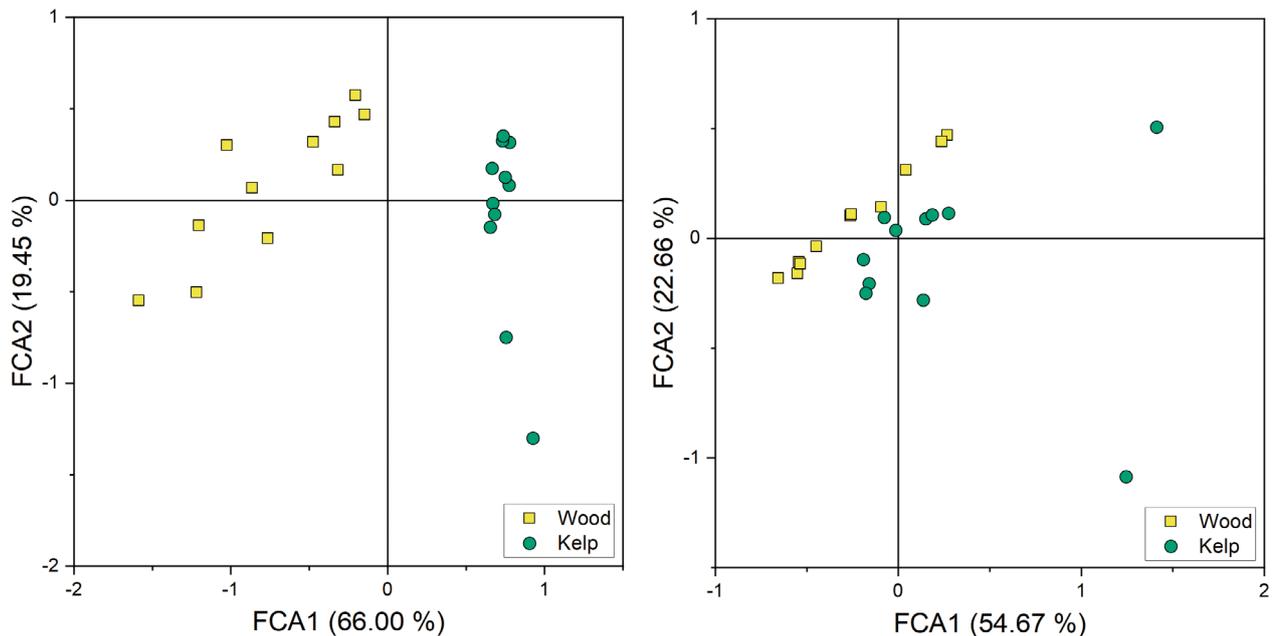


Fig. 10. Fuzzy correspondence analysis (FCA) ordination of biological trait assemblages associated with wood (yellow squares) and kelp (green circles) samples. Top: all trait assemblages; bottom: FCA ordination showing trait assemblages with *Xylophaga dorsalis* removed from the analysis

Table 2. Top 10 trait modality contributions to the variance on FCA1 and FCA2 from the fuzzy correspondence analysis (FCA) of biological trait assemblages

		FCA1 (%)		FCA2 (%)	
Relative inertia		66.00		19.45	
Relative trait modality contributions					
BF1	Globulose	10.6	LD3	Larval — direct/benthic	7.5
SK1	Calcareous	10.6	MV3	Crawler	7.3
FH7	Xylophagy	10.6	EP2	Epibenthic	6.2
SA5	Substrate aff. — wood	10.6	S2	Small/medium	3.6
LH4	Burrowing	9.0	FH2	Subsurface deposit feeder	3.0
R3	Sexual — internal	7.4	FH1	Surface deposit feeder	2.5
S1	Small	7.3	B3	Bioturbation — upward	2.4
MV2	Burrower	7.0	SK5	Skeleton — none	2.2
EP1	Infauna	7.0	B5	Bioturbation — none	2.2
LD1	Larval — pelagic	4.2	FH4	Opportunist/scavenger	2.1

Table 3. Top 10 trait modality contributions to the variance on FCA1 and FCA2 from the fuzzy correspondence analysis (FCA) of biological trait assemblages with the highly dominant *Xylophaga dorsalis* removed

		FCA1 (%)		FCA2 (%)	
Relative inertia		54.67		22.66	
Relative trait modality contributions					
LD3	Larval — direct/benthic	6.9	FH2	Subsurface deposit feeder	13.8
MV3	Crawler	6.7	B3	Bioturbation — upward	8.9
R4	Sexual — brooding	5.7	S4	Medium — large	8.2
EP2	Epibenthic	5.5	SK5	Skeleton — none	7.9
FH2	Subsurface deposit feeder	5.0	MV2	Burrower	7.8
S2	Small/medium	4.8	EP1	Infauna	7.8
LH1	Free living	4.2	LH4	Burrowing	7.6
B5	Bioturbation — none	4.2	B5	Bioturbation — none	4.3
B3	Bioturbation — upward	4.0	FH5	Predator	3.7
MV2	Burrower	4.0	SK3	Chitinous	3.7

The kelp samples exhibited significantly higher H' and J' compared to the wood samples. Very low abundance and a lack any dominant species produced a significantly higher H' in the control samples (Fig. 3). Similarities in S and N between kelp and wood samples were unexpected results but could be related to the carbon content of each substrate and their respective lability. While the kelp parcels and wood blocks provided a similar physical volume of substrate on the landers, the wood samples were estimated to contain 2.5 times more carbon than the kelp samples. However, since carbon in wood is primarily in the form of the refractory structural compounds cellulose and lignin, it is largely inaccessible until specialist ecosystems engineers, i.e. xylophagoids, break down these compounds into more digestible forms. Indeed, *Xylophaga dorsalis* pseudofaeces extracted from the burrow of the mollusc had a considerably

lower C:N ratio (C:N = 5.4) than the wood itself, potentially making this material much more accessible to other fauna. Despite the fact that there was considerably more total carbon in the wood samples, the actual bioavailable carbon to other fauna may well have been similar. The nitrogen content was extremely low in the wood compared to kelp, which had a C:N ratio of 9.5 (measured in *Laminaria hyperborea* on the west coast of Norway by Sjøtun et al. 1996), which may further offset the nutritional usefulness of wood.

Community assemblages were highly significantly different between substrate types, partially supporting the first hypothesis. Much of the similarity that did occur was provided by mobile fauna such as shrimp and leptostracans. Kelp detritus has been shown to quickly attract shrimp and amphipods in Oslofjord, Norway (Ramirez-Llodra et al. 2016). In

the present study, there was a significantly higher abundance of the shrimp *Atlantopandalus propinquus* in the wood and kelp samples compared to the control. This species is highly mobile but appeared to be preferentially attracted to the decaying organic matter. Interestingly, there was no significant difference in the abundance of the other 2 species of shrimp, *Caridion gordonii* and *Lebbeus polaris*, between the wood and kelp samples and the control, potentially pointing to a unique detritus-feeding behaviour exhibited by *A. propinquus*. High numbers of individuals of a few species commonly associated with organic enrichment were found within the kelp samples. The boreal leptostracan crustacean *Nebalia strausi* was the most common species within the kelp samples; *Nebalia* spp. are frequently found in western Norwegian fjords and often associated with decaying organic matter—for example, they have been previously found associated with decaying *Laminaria* sp. (Tzvetlin et al. 1997). Dorvilleid polychaetes of the genus *Ophryotrocha* were also highly abundant in the kelp samples, which is similar to findings on kelp substrates deployed for up to 6 mo in the Santa Cruz Basin (Bernardino et al. 2010). Some of these fauna were identified as *O. craigsmithi*, an organic fall-associated species first discovered on a minke whale carcass in Sweden and also below a fish farm in Norway (Wiklund et al. 2009). *Capitella* sp. was the third most abundant taxon in the kelp samples and is a polychaete commonly used as a bioindicator for organic enrichment (Pearson & Rosenberg 1978, Sweetman et al. 2010, 2014, Silva et al. 2017). Similar species dominance by *Capitella* spp. and *Nebalia* sp. were also found on *Sargassum* substrates that were deployed at 900 m depth in the US Virgin Islands (Snelgrove et al. 1994). Smith et al. (2014) found very high abundances of cumaceans associated with deep-sea kelp and whale falls, an order not seen at all in the current study (Smith et al. 2014). However, cumaceans are sediment-dwelling infauna so their absence may have been a result of the experimental design in the current study—there was no direct access to the lander bins from the sediment interface.

Wood samples were dominated by high abundances of *X. dorsalis*, a wood-boring bivalve mollusc of the family Xylophagaidae. *N. strausi*, *Ophryotrocha* spp. and *Capitella* sp. were also found in wood samples; however, in contrast to the kelp, they were found in much lower numbers, contributing to the dissimilarity between wood and kelp samples. In wood samples, these taxa exhibited greatly reduced body sizes compared to the kelp, which suggests recruitment took place late in the experiment as the

wood became more and more degraded by xylophagaid molluscs (Fig. 1F).

Xylophagoids have toothed ridges on the anterior edge of their shells that they use to bore into terrestrial wood material. Wood chips produced during boring are stored in their caecum where digestion is assisted by symbiotic bacteria thought to produce enzymes such as cellulases, like their shallow-water cousins, the teredinids (Distel & Roberts 1997, Voight 2015). Although the rate of wood degradation by xylophagoids was not measured in this study, degradation looked superficially similar to observations made by Amon et al. (2015) of wood boring by *X. murrayi* in the Indian Ocean. The degradation rate of the wood in this study (Fig. 1C), however, appeared to be much lower than in much warmer water in the Bahamas (Tongue of the Ocean, 10–13°C) at 500 m where wood was largely reduced to pulp within 1 yr (C. M. Young & P. A. Tyler unpubl. data). Lower temperature has previously been linked to reduced wood degradation and may be why comparatively lower degradation was seen in the current study, where water temperature was 8°C (Cunha et al. 2013). Wood degradation by xylophagoids, and the subsequent colonisation of the wood by other fauna, depends on the density of the wood and its texture (Romey et al. 1994, Bernardino et al. 2010, McClain & Barry 2014); in the current study, soft pinewood was used, potentially increasing its recruitment potential. *S*, *N* and *H'*, as well as the number of rare species, have been shown to increase with wood fall size (McClain et al. 2016b). McClain et al. (2016b) suggested that this occurrence is due to higher energy availability associated with larger substrates (a factor that was not tested here), but others have suggested that high diversity at small organic falls is driven by regional diversity (Cunha et al. 2013). In the South Atlantic, xylophagaid colonisation and macrofaunal diversity and biomass was found to vary with depth, with the latter decreasing by 95% between 1500 and 3300 m (Saeedi et al. 2019). All of the landers in the current study were deployed to the same depth in a relatively flat-bottomed fjord, so such comparisons were not possible here; further studies would be needed to explore the effect of depth in comparatively shallow fjord environments. Terrestrial organic C fluxes to the seafloor can be high in western Norwegian fjords due to extensive forests and rain-fall events (Lalande et al. 2020); this may increase the abundance of recruits, and therefore it is possible that wood-falls in Norwegian fjords could support an even higher abundance and biodiversity of fauna with more time. This hypothesis is supported by a study in the Santa Cruz Basin in the north Pacific

Ocean, where a 3 fold increase in macrofaunal abundance was seen on wood blocks over a 5.5 yr period compared to kelp parcels (Bernardino et al. 2010).

The similarity in S , as well as the overlap in the species found between the kelp and the wood samples, may be explained simply by the stochastic movement of highly mobile fauna between nearby sample bins. It is also possible that these results may have been caused by a mass effect produced by the experimental design (Leibold et al. 2004). In addition, wood, kelp and control samples were subject to some substrate cross contamination — a small amount of woody pseudofaeces from xylophagaid molluscs was found in the bottoms of the kelp and control sample bags, and likewise, fine particles of kelp detritus were found in wood and control sample bags — which will have also influenced species overlap.

4.2. Biomass and secondary production

Mean faunal biomass, P:B ratios and secondary production estimates were significantly different between the wood and kelp substrates (Fig. 8). Collectively, these findings show that while biodiversity tends to be lower on wood substrates in deep Norwegian fjords, biomass and secondary production can be higher over 10 mo, and ecosystems developing on the different organic substrates do appear to function differently. This result means that the second hypothesis, that wood falls support significantly lower biodiversity, biomass and secondary production than kelp falls, is partially rejected.

Large crustaceans, such as *A. propinquus*, have greater longevity and resultingly lower mean P:B ratios compared to other fauna found in this study (Vogt 2012), and contributed most to faunal biomass in the kelp samples. These factors could have contributed to the lower secondary production estimates measured in the kelp samples. Both crustaceans and polychaetes, however, contributed significantly more to secondary production in the kelp samples than these same taxa in the wood samples (Fig. 8). Dorvilleids and capitellids are omnivorous polychaetes and were very likely feeding directly on the lower C:N ratio kelp detritus and bacterial mats, as also found on kelp falls by Bernardino et al. (2010).

Most of the biomass in wood samples was provided by *X. dorsalis*; because of the cumulative biomass of this species, secondary production estimates were twice as high in the wood compared to the kelp, and 10 times more secondary production was found on the wood samples compared to the control samples.

Throughout the experiment, *X. dorsalis* were protected inside the wood blocks (Fig. 1D) from predatory macro- and megafauna, so their availability as a food source to predators was limited; this could be a major reason for the significantly higher biomass in the wood samples. Given more time, however, it is likely that the wood blocks would have degraded to the point of collapse, exposing both living and dead molluscs to benthic and demersal predators and scavengers common in Norwegian fjords (Turner 1973, 2002, Bienhold et al. 2013, Sweetman et al. 2014, Dunlop et al. 2018), as well as pathogens.

Bolam & Eggleton (2014) reported mean annual secondary production rates between 19.8 ± 7.1 to 196.6 ± 215.1 $\text{kJ m}^{-2} \text{yr}^{-1}$ for grab-sampled, soft-sediment macrofauna communities (down to approximately 15 cm sediment depth) from around the British Isles down to a depth of 137 m. Mean annual production rates for benthic macrofauna at 150 m depth in the Arctic Sørkjorden was $185 \text{ kJ m}^{-2} \text{ sediment yr}^{-1}$ (Nilsen et al. 2008). Mean annual production estimates calculated for wood and kelp substrates in this study were generally much lower than these results (Fig. 8); however, the comparison is not straightforward as it was only possible to estimate production as $\text{kJ substrate}^{-1} \text{yr}^{-1}$, that is, the mean cumulative energy derived from the taxa found in the bins associated with each substrate. All of the substrates used in this experiment were designed to provide a surface area of a similar size, on which faunal settlement could take place. Assuming the 2 wood blocks and kelp parcels in each bin ($0.15 \times 0.15 \times 0.15$ m) provided a surface area of 0.225 m^2 (10 sides at 0.0225 m^2 each) and were 0.15 m deep, secondary production rates for a 1 m^2 area would be $131.7 \text{ kJ m}^{-2} \text{ kelp yr}^{-1}$ and $239.2 \text{ kJ m}^{-2} \text{ wood yr}^{-1}$. This calculation shows that kelp and wood falls in deep fjords could support similar or higher levels of secondary production per unit area compared to shallow, soft-sediment habitats. However, caution should be observed with this approach, as kelp parcels were not uniform in their exposed surface area, and community production in wood samples was heavily dependent on the action of wood-boring molluscs. Though it has been shown that increased wood fall size can increase S (McClain et al. 2016b), there is no evidence of a direct correlation between wood size and xylophagaid abundance in Norwegian fjords. However, it is hypothesised that large numbers of xylophagaid larvae exist in Norwegian fjords due to the large amount of terrigenous material entering fjords from the land (Schander et al. 2010, Lalande et al. 2020), and as such, these fauna may be able to take advantage of larger wood falls. It is also hypothesised

that given more time, secondary productivity could be even higher at deep-sea wood falls as the substrates become further degraded and more organic material becomes available to a wider variety of fauna (Turner 1973, 2002, Bienhold et al. 2013); this process could potentially enhance secondary production at the seafloor above that which kelp material supports. Further studies will be needed to test this hypothesis.

4.3. BTA

BTA provided evidence that the 2 different organic substrates supported communities with different ecosystem functions (Fig. 10, Table 2), partially supporting the first hypothesis. Community trait assemblages on kelp falls included a larger maximum body size, which has been linked directly to higher productivity (Banse & Mosher 1980, Romero-Wetzel & Gerlach 1991). In the deep Norwegian Sea (1200–1500 m), it was shown that taxa with a larger maximum body size played more important roles in bio-irrigation and vertical particle transport in the sediment (Romero-Wetzel & Gerlach 1991), as also confirmed by Wheatcroft et al. (1990). In kelp samples, there was a higher prevalence of fauna associated with upward conveyor bioturbation; burrowing and feeding behaviour that redistributes sediment, increasing oxygen penetration and altering the rate of organic decomposition (Bertics et al. 2010). Though these traits are associated with sediment and not necessarily useful inside the experimental lander bins, they could become more important ecosystem functions at natural kelp falls. More mobile taxa were attracted to kelp samples. Increased mobility implies a higher metabolic demand (Alexander 2005) and could suggest faster colonisation of substrates by adult fauna that are able to more quickly consume the comparatively nutritious kelp.

The trait modalities such as globulose body form, calcareous shell, xylophagy and an affinity for wood as a substrate were highly dominant in the wood samples, and are all traits associated exclusively with *X. dorsalis* (Table 2). In fact, 9 of the top 10 trait modalities that contributed to the variation on FCA1 were associated with this highly abundant species. Removing this species from a second FCA analysis (Table 3) revealed that *X. dorsalis* appears to play a key role in shaping community trait assemblages — it was the only taxon found in this study that is known to consume and process wood. The results also showed that this newly bioavailable food source attracts not only a different faunal community than that of the kelp samples, but a community that ex-

presses different functional traits and therefore ecosystem functions (Bremner et al. 2003). These results support the hypothesis that in deep-sea wood-fall ecosystems, xylophagoids are key ecosystem engineer organisms that free energy from difficult-to-digest compounds in wood, mostly cellulose and lignin, breaking them down into digestible forms on which other animals are able to feed (Schander et al. 2010, Voight 2015).

The trait assemblages found on wood and kelp samples were most likely influenced by the experimental setup, particularly the fact that animals were not able to enter the sample bins directly from the sediment, which could potentially bias community populations towards pelagic larval development and crawling trait modalities (Smith & Brumsickle 1989, Snelgrove et al. 1994). Indeed, the pelagic larval development modality was the 10th most influential to variation between the samples and was especially associated with the wood samples (Table 2). Crawling behaviour was dominant in both the background fauna of the wood samples and those associated with the kelp samples. If substrates were placed directly onto the sediment, as in a natural fall event, it is hypothesised here that a greater number of burrowing species would be seen in the faunal assemblages (e.g. Smith & Brumsickle 1989, Kukert & Smith 1992).

BTA was used in this study to compare the functional traits of the benthic macrofaunal assemblage on the deployed wood and kelp substrates. However, it should be noted that it only provides part of the overall story. For instance, it was not possible within the scope of this study to assess microbial functional roles in these ecosystems; this group is of considerable importance in respiration and nutrient exchange in deep-sea benthic systems (Sweetman et al. 2019). Microbial communities have been shown to exhibit a high degree of functional redundancy, potentially making them better adapted to benefit from either type of substrate (Franklin & Mills 2006). Fuzzy coding of trait modalities allows for the incorporation of taxa that exhibit more than one aspect of a particular trait, but it does not provide information on whether organisms are actually expressing those modalities within the system (Cesar & Frid 2009).

5. CONCLUSIONS

This 10 mo colonisation experiment revealed that wood and kelp organic falls can support similar levels of *S* and faunal abundances, but significantly different biodiversity in terms of *H'* and *J'*. Benthic com-

munity structure, secondary production and trait diversity was also found to be significantly different between the wood and kelp substrates. Overall, this case study from a deep-sea fjord in Norway provides clear evidence that while wood and kelp organic falls can support similar abundances of fauna, the associated benthic biodiversity, community structure and ecosystem functioning can be dramatically different between these substrates. While extensive harvesting of kelp continues along the shallow coastal waters of Norway, coupled with the enduring effects of anthropogenic climate change-related events, this valuable carbon subsidy will be gradually reduced, depriving deep-sea communities living in Norwegian fjords and possibly further afield. Wood does not appear to act as a like-for-like substitute for kelp detritus, and if there are greater influxes of wood material into deep Norwegian fjords as a result of increased afforestation, this will do little to mitigate the effects of kelp loss in deep-sea communities. Nevertheless, wood falls are an important habitat for a unique community of fauna, including some specialists that depend on them completely e.g. xylophagid molluscs. Furthermore, communities living on wood samples exhibited secondary production estimates twice that of communities living on kelp falls, largely due to high abundances of xylophagid molluscs. When normalised to 1 m², secondary production for both wood and kelp falls was found to be similar or higher than that of shallower, soft-sediment sites in European seas, illustrating the importance of both these substrates in the transfer of energy from primary production in terrestrial and shallow-ocean ecosystems to higher trophic level consumers in deep-sea habitats.

Acknowledgements. We thank Sue Hamilton for her invaluable assistance in the taxonomic identification of the polychaete species in this study, as well as Daniel Harries for his support and introducing us to Sue. Thank you to Alison Palmer of Fugro for her support and advice, and loans of the taxonomic literature we needed to get started. Thank you to Filza Nawaz for her meticulous work in the lab measuring the biomass of the animals in this study. Landers were designed and fabricated by Craig R. Smith and Mario Williamson at the University of Hawaii and Friday Harbor Laboratories, with support from US NSF grant number 1155703 (OCE Biological Oceanography Program) to C.R.S. We thank Iris Altamira, Pavica Srsen, Adrian Glover and Leon Pedersen for assistance in the design and construction of the landers. We thank Leon Pedersen for assisting us in deploying and recovering the landers in Osterfjorden. The research outlined in this paper was funded from the European Union's Horizon 2020 research and innovation programme under grant agreement no. 689518 (Marine Ecosystem Restoration in Changing European Seas - MERCES) to A.K.S.

LITERATURE CITED

- ✦ Abdullah MI, Fredriksen S, Christie H (2017) The impact of the kelp (*Laminaria hyperborea*) forest on the organic matter content in sediment of the west coast of Norway. *Mar Biol Res* 13:151–160
- ✦ Alexander RM (2005) Models and the scaling of energy costs for locomotion. *J Exp Biol* 208:1645–1652
- ✦ Amon DJ, Sykes D, Ahmed F, Copley JT and others (2015) Burrow forms, growth rates and feeding rates of wood-boring Xylophagidae bivalves revealed by micro-computed tomography. *Front Mar Sci* 2:10
- ✦ Amon DJ, Hilario A, Arbizu PM, Smith CR (2017) Observations of organic falls from the abyssal Clarion-Clipperton Zone in the tropical eastern Pacific Ocean. *Mar Biodivers* 47:311–321
- ✦ Amundsen B (2014) Norwegian woods triple since WW2. <https://sciencenorway.no/emiroment-forest-forskningno/norwegian-woods-triple-since-ww2/1409508> (accessed 13 February 2020)
- ✦ Andresen H, Brey T (2018) Benthic energy flow. v1.0, R-package. <https://github.com/HenrikeAndresen/BenthicPro>
- ✦ Banse K, Mosher S (1980) Adult body mass and annual production/biomass relationships of field populations. *Ecol Monogr* 50:355–379
- ✦ Barrio Froján CRS, Cooper KM, Bremner J, Defew EC, Wan Hussin WMR, Paterson DM (2011) Assessing the recovery of functional diversity after sustained sediment screening at an aggregate dredging site in the North Sea. *Estuar Coast Shelf Sci* 92:358–366
- Becker P, Samadi S, Zbinden M, Compère P, De Ridder C (2009) First insights into the gut microflora associated with an echinoid from wood falls environments. *Cah Biol Mar* 50:343–352
- ✦ Bernardino AF, Smith CR, Baco A, Altamira I, Sumida PYG (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
- ✦ Bertics VJ, Sohm JA, Treude T, Chow CET, Capone DG, Fuhrman JA, Ziebis W (2010) Burrowing deeper into benthic nitrogen cycling: the impact of bioturbation on nitrogen fixation coupled to sulfate reduction. *Mar Ecol Prog Ser* 409:1–15
- ✦ Bienhold C, Pop Ristova P, Wenzhöfer F, Dittmar T, Boetius A (2013) How deep-sea wood falls sustain chemosynthetic life. *PLOS ONE* 8:e53590
- ✦ Bolam SG, Eggleton JD (2014) Macrofaunal production and biological traits: spatial relationships along the UK continental shelf. *J Sea Res* 88:47–58
- ✦ Bolam SG, Barrio-Frojan CRS, Eggleton JD (2010) Macrofaunal production along the UK continental shelf. *J Sea Res* 64:166–179
- ✦ Bolam SG, Coggan RC, Eggleton J, Diesing M, Stephens D (2014) Sensitivity of macrobenthic secondary production to trawling in the English sector of the Greater North Sea: a biological trait approach. *J Sea Res* 85:162–177
- ✦ Bremner J, Rogers SI, Frid CLJ (2003) Assessing functional diversity in marine benthic ecosystems: a comparison of approaches. *Mar Ecol Prog Ser* 254:11–25
- ✦ Bremner J, Rogers SI, Frid CLJ (2006) Matching biological traits to environmental conditions in marine benthic ecosystems. *J Mar Syst* 60:302–316
- ✦ Brey T (2001) Population dynamics in marine benthic invertebrates — a virtual handbook. www.thomas-brey.de/

- science/virtualhandbook/navlog/index.html (accessed 29 September 2020)
- Brey T (2012) A multi-parameter artificial neural network model to estimate macrobenthic invertebrate productivity and production. *Limnol Oceanogr Methods* 10:581–589
- Cesar CP, Frid CLJ (2009) Effects of experimental small-scale cockle (*Cerastoderma edule* L.) fishing on ecosystem function. *Mar Ecol* 30:123–137
- Chevenet F, Dolédec S, Chessel D (1994) A fuzzy coding approach for the analysis of long-term ecological data. *Freshw Biol* 31:295–309
- Christie H, Jørgensen NM, Norderhaug KM, Waage-Nielsen E (2003) Species distribution and habitat exploitation of fauna associated with kelp (*Laminaria hyperborea*) along the Norwegian Coast. *J Mar Biol Assoc UK* 83:687–699
- Christie H, Andersen GS, Bekkby T, Fagerli CW, Gitmark JK, Gundersen H, Rinde E (2019) Shifts between sugar kelp and turf algae in Norway: Regime shifts or fluctuations between different opportunistic seaweed species? *Front Mar Sci* 6:72
- 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
- Degen R, Faulwetter S (2019) The Arctic Traits Database—a repository of Arctic benthic invertebrate traits. *Earth Syst Sci Data* 11:301–322
- Distel DL, Roberts SJ (1997) Bacterial endosymbionts in the gills of the deep-sea wood-boring bivalves *Xylophaga atlantica* and *Xylophaga washingtona*. *Biol Bull (Woods Hole)* 192:253–261
- Dray S, Dufour AB, Thioulouse J, Jombart T and others (2018) Ade4: analysis of ecological data: exploratory and Euclidean methods in environmental sciences, v1.7-13. <https://CRAN.R-project.org/package=ade4>
- Duggins DO, Simenstad CA, Estes JA (1989) Magnification of secondary production by kelp detritus in coastal marine ecosystems. *Science* 245:170–173
- Dunlop KM, Jones DOB, Sweetman AK (2018) Scavenging processes on jellyfish carcasses across a fjord depth gradient. *Limnol Oceanogr* 63:1146–1155
- Filbee-Dexter K, Wernberg T, Norderhaug KM, Ramirez-Llodra E, Pedersen MF (2018) Movement of pulsed resource subsidies from kelp forests to deep fjords. *Oecologia* 187:291–304
- Franklin RB, Mills AL (2006) Structural and functional responses of a sewage microbial community to dilution-induced reductions in diversity. *Microb Ecol* 52:280–288
- Gage JD (2003) Food inputs, utilization, carbon flow and energetics In: Tyler PA (ed) *Ecosystems of the deep oceans*. *Ecosystems of the World*, Vol 28. Elsevier, Amsterdam, p 313–380
- Häggblom A (1982) Driftwood in Svalbard as an indicator of sea ice conditions. *Geogr Ann, Ser A* 64:81–94
- Harbour RP, Leitner AB, Ruehleemann C, Vink A, Sweetman AK (2020) Benthic and demersal scavenger biodiversity in the eastern end of the Clarion-Clipperton Zone—an area marked for polymetallic nodule mining. *Front Mar Sci* 7:458
- 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
- Jeffreys RM, Lavaleye MSS, Bergman MJN, Duineveld GCA, Witbaard R, Linley T (2010) Deep-sea macrourid fishes scavenge on plant material: evidence from *in situ* observations. *Deep Sea Res I* 57:621–627
- Krause-Jensen D, Duarte CM (2016) Substantial role of macroalgae in marine carbon sequestration. *Nat Geosci* 9:737–742
- Krumhansl KA, Scheibling RE (2012) Production and fate of kelp detritus. *Mar Ecol Prog Ser* 467:281–302
- Krumhansl KA, Okamoto DK, Rassweiler A, Novak M and others (2016) Global patterns of kelp forest change over the past half-century. *Proc Natl Acad Sci USA* 113:13785–13790
- Kukert H, Smith CR (1992) Disturbance, colonization and succession in a deep-sea sediment community: artificial-mound experiments. *Deep-Sea Res A, Oceanogr Res Pap* 39:1349–1371
- Lalande C, Dunlop K, Renaud PE, Nadaï G, Sweetman AK (2020) Seasonal variations in downward particle fluxes in Norwegian fjords. *Estuar Coast Shelf Sci* 241:106811
- Leibold MA, Holyoak M, Mouquet N, Amarasekare P and others (2004) The metacommunity concept: a framework for multi-scale community ecology. *Ecol Lett* 7:601–613
- 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
- McClain C, Barry J (2014) Beta-diversity on deep-sea wood falls reflects gradients in energy availability. *Biol Lett* 10:20140129
- McClain CR, Barry JP, Eernisse D, Horton T and others (2016a) Multiple processes generate productivity–diversity relationships in experimental wood-fall communities. *Ecology* 97:885–898
- McClain CR, Barry JP, Eernisse D, Horton T and others (2016b) Multiple processes generate productivity–diversity relationships in experimental wood-fall communities. *Ecology* 97:885–898
- McLeod RJ, Wing SR, Skilton JE (2010) High incidence of invertebrate-chemoautotroph symbioses in benthic communities of the New Zealand fjords. *Limnol Oceanogr* 55:2097–2106
- Nilsen M, Pedersen T, Nilssen EM, Fredriksen S (2008) Trophic studies in a high-latitude fjord ecosystem—a comparison of stable isotope analyses ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) and trophic-level estimates from a mass-balance model. *Can J Fish Aquat Sci* 65:2791–2806
- Norderhaug KM, Christie H (2011) Secondary production in a *Laminaria hyperborea* kelp forest and variation according to wave exposure. *Estuar Coast Shelf Sci* 95:135–144
- Paganelli D, Marchini A, Occhipinti-Ambrogi A (2012) Functional structure of marine benthic assemblages using biological traits analysis (BTA): a study along the Emilia-Romagna coastline (Italy, North-West Adriatic Sea). *Estuar Coast Shelf Sci* 96:245–256
- Pearson TH, Rosenberg R (1978) Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. *Oceanogr Mar Biol Ann Rev* 16:229–311
- Pessarrodona A, Moore PJ, Sayer MDJ, Smale DA (2018) Carbon assimilation and transfer through kelp forests in the NE Atlantic is diminished under a warmer ocean climate. *Glob Change Biol* 24:4386–4398
- R Core Team (2019) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

- Ramirez-Llodra E, Rinde E, Gundersen H, Christie H and others (2016) A snap shot of the short-term response of crustaceans to macrophyte detritus in the deep Oslo-fjord. *Sci Rep* 6:23800
- Renaud PE, Løkken TS, Jørgensen LL, Berge J, Johnson BJ (2015) Macroalgal detritus and food-web subsidies along an Arctic fjord depth-gradient. *Front Mar Sci* 2:31
- Romero-Wetzel MB, Gerlach SA (1991) Abundance, biomass, size-distribution and bioturbation potential of deep-sea macrozoobenthos on the Voring Plateau (1200–1500 m, Norwegian Sea). *Meeresforschung* 33:247–265
- Romey WL, Bullock RC, Dealteris JT (1994) Rapid growth of a deep-sea wood-boring bivalve. *Cont Shelf Res* 14: 1349–1359
- Saedi H, Bernardino AF, Shimabukuro M, Falchetto G, Sumida PYG (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
- Schander C, Rapp HT, Halanych KM, Kongsrud JA, Sneli JA (2010) A case of co-occurrence between *Sclerolinum pogonophoran* (Siboglinidae: Annelida) and *Xylophaga* (Bivalvia) from a north-east Atlantic wood-fall. *Mar Biodivers Rec* 3:e43
- Silva CF, Seixas VC, Barroso R, Domenico MD, Amaral ACZ, Paiva PC (2017) Demystifying the *Capitella capitata* complex (Annelida, Capitellidae) diversity by morphological and molecular data along the Brazilian coast. *PLOS ONE* 12:e0177760
- Sivertsen K (1997) Geographic and environmental factors affecting the distribution of kelp beds and barren grounds and changes in biota associated with kelp reduction at sites along the Norwegian coast. *Can J Fish Aquat Sci* 54:2872–2887
- Sjøtun K, Fredriksen S, Rueness J (1996) Seasonal growth and carbon and nitrogen content in canopy and first-year plants of *Laminaria hyperborea* (Laminariales, Phaeophyceae). *Phycologia* 35:1–8
- Smith CR, Brumsickle SJ (1989) The effects of patch size and substrate isolation on colonization modes and rates in an intertidal sediment. *Limnol Oceanogr* 34:1263–1277
- Smith CR, Bernardino AF, Baco A, Hannides A, Altamira I (2014) Seven-year enrichment: macrofaunal succession in deep-sea sediments around a 30 tonne whale fall in the Northeast Pacific. *Mar Ecol Prog Ser* 515:133–149
- Snelgrove PVR (1998) The biodiversity of macrofaunal organisms in marine sediments. *Biodivers Conserv* 7:1123–1132
- Snelgrove PVR, Grassle JF, Petrecca RF (1994) Macrofaunal response to artificial enrichments and depressions in a deep-sea habitat. *J Mar Res* 52:345–369
- Steen H, Moy FE, Bodvin T, Husa V (2016) Regrowth after kelp harvesting in Nord-Trøndelag, Norway. *ICES J Mar Sci* 73:2708–2720
- Steneck RS, Graham MH, Bourque BJ, Corbett D, Erlanson JM, Estes JA, Tegner MJ (2002) Kelp forest ecosystems: biodiversity, stability, resilience and future. *Environ Conserv* 29:436–459
- Sweetman AK, Middelburg JJ, Berle AM, Bernardino AF, Schander C, Demopoulos AWJ, Smith CR (2010) Impacts of exotic mangrove forests and mangrove deforestation on carbon remineralization and ecosystem functioning in marine sediments. *Biogeosciences* 7:2129–2145
- Sweetman AK, Smith CR, Dale T, Jones DOB (2014) Rapid scavenging of jellyfish carcasses reveals the importance of gelatinous material to deep-sea food webs. *Proc R Soc B* 281:20142210
- Sweetman AK, Smith CR, Shulse CN, Maillot B and others (2019) Key role of bacteria in the short-term cycling of carbon at the abyssal seafloor in a low particulate organic carbon flux region of the eastern Pacific Ocean. *Limnol Oceanogr* 64:694–713
- Tumbiolo ML, Downing JA (1994) An empirical model for the prediction of secondary production in marine benthic invertebrate populations. *Mar Ecol Prog Ser* 114:165–174
- Turner RD (1973) Wood-boring bivalves, opportunistic species in the deep sea. *Science* 180:1377–1379
- Turner RD (2002) On the subfamily Xylophaginae (Family Pholadidae, Bivalvia, Mollusca). *Bull Mus Comp Zool* 157:223–307
- Tyler PA, Young CM, Dove F (2007) Settlement, growth and reproduction in the deep-sea wood-boring bivalve mollusc *Xylophaga depalmai*. *Mar Ecol Prog Ser* 343:151–159
- Tzvetlin AB, Mokievsky VO, Melnikov AN, Saphonov MV, Simdyanov TG, Ivanov IE (1997) Fauna associated with detached kelp in different types of subtidal habitats of the White Sea. *Hydrobiologia* 355:91–100
- Veia J, Ask E (2011) Creating a sustainable commercial harvest of *Laminaria hyperborea*, in Norway. *J Appl Phycol* 23:489–494
- Vetter EW, Dayton PK (1999) Organic enrichment by macrophyte detritus, and abundance patterns of megafaunal populations in submarine canyons. *Mar Ecol Prog Ser* 186:137–148
- Vogt G (2012) Ageing and longevity in the Decapoda (Crustacea): a review. *Zool Anz* 251:1–25
- Voight JR (2009) Diversity and reproduction of near-shore vs offshore wood-boring bivalves (Pholadidae: Xylophaginae) of the deep eastern Pacific ocean, with three new species. *J Molluscan Stud* 75:167–174
- Voight JR (2015) Xylotrophic bivalves: aspects of their biology and the impacts of humans. *J Molluscan Stud* 81: 175–186
- Voight JR, Cooper JC, Lee RW (2020) Stable isotopic evidence of mixotrophy in xylophagoids, deep-sea wood-boring bivalves. *Front Mar Sci* 7:50
- Waage-Nielsen E, Christie H, Rinde E (2003) Short-term dispersal of kelp fauna to cleared (kelp-harvested) areas. *Hydrobiologia* 503:77–91
- Wernberg T, Filbee-Dexter K (2018) Grazers extend blue carbon transfer by slowing sinking speeds of kelp detritus. *Sci Rep* 8:17180
- West AJ, Lin CW, Lin TC, Hilton RG and others (2011) Mobilization and transport of coarse woody debris to the oceans triggered by an extreme tropical storm. *Limnol Oceanogr* 56:77–85
- Wheatcroft RA, Jumars PA, Smith CR, Nowell ARM (1990) A mechanistic view of the particulate biodiffusion coefficient: step lengths, rest periods and transport directions. *J Mar Res* 48:177–207
- Wiklund H, Glover AG, Dahlgren TG (2009) Three new species of *Ophryotrocha* (Annelida: Dorvilleidae) from a whale-fall in the North-East Atlantic. *Zootaxa* 2228:43–56
- Wolff T (1979) Macrofaunal utilization of plant remains in the deep sea. *Sarsia* 64:117–143