Submarine canyons as the preferred habitat for wood-boring species of *Xylophaga* (Mollusca, Bivalvia)

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Abstract

Submarine canyons are often viewed as natural “debris concentrators” on seafloor. Organic substrates may be more abundant inside than outside canyon walls. To determine the effects of the presence these substrates in the Blanes submarine canyon (NW Mediterranean) and its adjacent western open slope, we deployed wood to study colonizing organisms. Three replicate pine and oak cubes (i.e. most common trees inland) were moored at 900, 1200, 1500 and 1800 m depth and collected after 3, 9 and 12 months. Wood from inside the canyon was significantly more heavily colonized by the five morphotypes of wood-boring bivalves than was wood on the adjacent open slope. *Xylophaga* sp. A dominated all wood types and locations, with peak abundance at 900 and 1200 m depth. Its growth rate was highest (0.070 mm d^{-1}) during the first three months and was faster (or recruits earlier) in pine than in oak. Size distribution showed that several recruitment events may have occurred from summer to winter. *Xylophaga* sp. B, appeared first after 9 months and clearly preferred pine over oak. As the immersion time was the same, this strongly supported a specific association between recruiters and type of substrate. Three morphotypes, pooled as *Xylophaga* spp. C, were rare and seemed to colonize preferentially oak inside the canyon and pine in the adjacent open slope. Individuals of *Xylophaga* were more abundant inside the canyon than in nearby off-canyon locations. Blanes Canyon may serve as a long-term concentrator of land-derived vegetal fragments and as a consequence sustain more animals.

Keywords: organic falls, wood boring, submarine canyon, sunken wood, *Xylophaga*, Mediterranean Sea.

Introduction

Life in the deep sea generally depends on the constant rain of particles produced in the photic zone and/or exported from the continental shelf (Gage et al., 1991). Allochthonous organic matter might sustain deep-sea oligotrophic systems and create patchy distributions of organic substrata and benthos (Gooday and Turley, 1990). Shelf-basin exchanges are particularly enhanced by the presence of submarine canyons, especially where they are preferential conduits driving materials down-margin (Martín et al., 2006; De Stigter et al., 2007). Matter transport from shelf waters to the abyssal plains may be strongly enhanced during the "dense shelf water cascading" events, which carry huge amounts of organic and inorganic substances that scour the shelf and slope seafloor and sink to the deep basin through the main NW Mediterranean submarine canyons (Canals et al., 2010). Research on sedimentological and hydrological processes in submarine canyons is increasing significantly (Durrieu de Madron et al., 2008; Zúñiga et al., 2009; De Stigter et al., 2011; Lastras et al., 2011), but our understanding of faunal patterns and processes in these environments remains marginal. Previous studies showed that the abundance and biomass of macro- and meiobenthic fauna inside the canyons are enhanced compared with equally deep stations in the slopes (Ingels et al., 2009; Cunha et al., 2011). However, many exceptions are reported due to the high heterogeneity and environment variability inside canyons (McClain and Barry, 2010; Romano et al., this volume).

Submarine canyons may concentrate large organic falls, like terrestrial debris, sunken wood and whale falls from a large area. These organic substrates create “islands” on the deep-sea canyon floor, which by supporting high species richness, increase deep-sea diversity (Snelgrove and Smith, 2002; Bernardino et al., 2010; De Leo et al., 2010). Despite its general oligotrophic environment, the deep Mediterranean has local areas such as submarine canyons, cold seep and mud volcanoes (Olu-Le Roy et al., 2004; Vanreusel et al., 2009; Ritt et al., 2011) with high productivity which allows them to function as biodiversity and biomass hotspots, characterized by specific benthic fauna. For instance, organic matter accumulation can dramatically enhance the populations of both opportunistic and sulphophilic species, such as wood-boring bivalves, capitellid and dorvilleid polychaetes, leptostracans, and cumaceans (Turner, 1977; Smith, 1986; Grassle and Morse-Porteous, 1987; Snelgrove et al., 1994; Smith et al., 2002; Smith and Baco, 2003; Gaudron et al., 2010). Canyons may also function as recruitment areas for demersal and benthic faunal species (Stefanescu et al., 1994; Sardà et al., 2009; Cartes et al., 2010), many of which are of commercial interest.

Land-derived vegetation such as woody plant material transported to the ocean, especially after heavy precipitation, storms or hurricanes, is not rare on the seafloor at all depths (Wolff, 1979; Pailleret et al., 2007). Wood may be an important source of organic material on the deep-sea floor where it creates unique ecosystems as it undergoes decay, sometimes creating anaerobic conditions with production of hydrogen sulphur and possibly methane (Duperron et al., 2008; Yücel et al., 2013). The functioning of these ecosystems is poorly described worldwide and has rarely been studied in the deep Mediterranean, except for the wood degrading microbial communities, which are the starting point of the community succession (Palacios et al., 2006; Fagervold et al., 2012; Bienhold et al., 2013; Fagervold et al., this issue).

After bacteria, the first animals colonizing sunken wood in deep sea are often the Xylophagainae (Pholadidae) that bore into wood using toothed ridges on their anterior shells and ingest wood fragments. Xylophagain bivalves are more common at depths from 150 m to over 7000 m, whereas Teredinidae dominante in floating wood and in shallow waters (intertidal to 100 m) (Turner, 1972).

More than 50 species of Xylophagainae occur worldwide, most known only from one locality. Indeed, all specimens of a given species were often encountered in a single piece of wood and very little is known about species distribution. Species of *Xylophaga* Turton, 1822 are often included in technical reports or checklists (e.g. Zenetos, 1996), but their identifications are rarely verified by expert taxonomists.

Nevertheless, the Xylophagainae play a key role in the succession of degrading wood falls. Their bacterial endosymbionts allow them to convert the refractory cellulose from wood and other plant remains to a form available to other deep-sea organisms (Turner, 1973; Waterbury et al., 1983; Distel & Roberts, 1997, Distel et al., 2002). Also, the "burrows" of some species are filled with partially digested wood that harbor unique microbial communities (Bessette et al., in press) and the large quantities of organic-rich faecal matter produced (Turner, 2002) may attract some detritivorous invertebrates, which may grow at a fairly rapid rate (Gaudron et al., 2010).

Despite our knowledge on the Mediterranean species is better than that in any other ocean, much remains to be understood, especially about the biodiversity of deep-sea ecosystems and their vulnerability to anthropogenic pressure (Coll et al., 2010; Danovaro et al., 2010; Ramirez-Llodra et al., 2010). Furthermore, the taxonomy, biology and ecology of benthic deep-sea macrofauna, and their connection to the land or shallower environments, remain poorly known, including that on xylophagain bivalves inhabiting NW Mediterranean canyon systems.

In this paper, our novel dataset offers information on the spatial and temporal patterns of colonization by wood-boring xylophagain bivalves in experimentally deployed wood at different depths (900-1800 m), both inside Blanes Canyon and on its adjacent western open slope (NW Mediterranean).

We sought to specifically assess the following questions:

1) Are the species richness and abundance of wood–boring bivalves higher inside the canyon than on the adjacent open slope?
2) Do the composition and density of the wood–boring bivalves change with deployment time and depth, as well as on the type of the sunken wood?
3) What is the growth rate of the dominant wood-boring species?

Material and methods

Description of the area, deployments and sampling

Blanes Canyon (BC) is located at the Catalan continental margin and constitutes one of the most important cross-slope structures in the NW Mediterranean shelf (Fig. 1). BC cuts the continental shelf in a N-S direction. Its head is 60 m deep and is located at 4 km from the coast, near the Tordera River mouth. The river has a typically Mediterranean torrential regime. The mean water discharge is of 7.2 $m^3 s^{-1}$, with maximum peaks higher than 1800 $m^3 \cdot s^{-1}$ and suspended sediment concentrations ranging from 10 to 300 $mg \cdot l^{-1}$ (Austen et al., 2002).

Six mooring lines were deployed along two transects (three along BC axes and three along the western open continental slope), at different depths (BC 900, 1200 and 1500 m; open slope 1200, 1500 and 1800 m) (moorings are fully described in López-Fernández et al., this issue). Each mooring line was equipped with an experimental trap suspended 20 m above the seafloor containing three replicate cubes (8 cm long) of pine and oak (the most common trees on adjacent inland watersheds). At 1200 m deep inside BC, an additional experimental trap containing two pine and two oak cubes was deployed directly on the sea floor (BC1200_bottom). Deployment periods were 3, 9 and 12 months (Table 1). The traps were recovered with the mooring lines by an acoustic release that dropped the anchor weight, allowing the traps to be carried to the surface by floating buoys. During ascent, epifauna on the wood may have been lost.

A total of fifty cubes were recovered. Immediately after collection, two cubes from 1200 and 1500 m depth were preserved in 96 % ethanol; all others were fixed in 4% buffered formaldehyde-seawater solution.

Laboratory analysis

Density. In the laboratory, all wood cubes were photographed and carefully dissected by hand; all wood-boring bivalves were stored in 70% ethanol for taxonomic identification. To ensure that recently settled individuals were included, extraction was performed with the aid of a magnifier (2x) or a dissecting microscope. All specimens of wood-boring bivalves were sorted by morphotype and counted. Identification was carried out with reference to relevant literature (e.g. Turner, 2000, Voight, 2007, Voight 2008). Density was expressed as number of individuals per dm^{-3}.

Biometry. Shell length (SL), as well as siphon's length in intact specimens, of *Xylophaga* spp., were measured to the nearest 0.1 mm with digital calipers.

Biomass estimates. Dry (DW in g) and ash free dry weights (AFDW in g) were estimated for a series of specimens that included the greatest range of SL possible. For these sub-samples, specimens were dried to a constant weight at 105°C for about 48 h (DW) and then burned at 500°C for 4 h to obtain total AFDW to the nearest 0.1 mg. The relationships of SL with DW and AFDW were calculated for each species by using exponential curves $DW = a*SL^{b}$ and $AFDW= a1*SL^{b1}$; where a (intercept) and b (slope) are allometric coefficients corresponding respectively to the initial growth coefficient and the relative growth rate of the variable (Gould, 1966; LaBarbera, 1989). Data were then transformed to natural logarithms and fitted to the allometric regression model ($\log DW = \log a + b \log SL$). The estimated regressions were used to calculate AFDW of all specimens and total biomass in the samples.

Size frequency distribution. SL frequency distributions in 1-mm size class intervals were developed from pooled replicate cubes for each wood type, depth and time. Cohorts were identified from each size-frequency distribution using Bhattacharya's method and the specific routine in FISAT II package (FAO 2002). The separation index (SI) was used to measure the goodness of the modal separation: $SI = (SL'i+1 – SL'i) / ((stdi+1 + stdi)/2)$, where SL'i is the mean SL of the distribution i, SL'i+1 is the mean length of distribution i+1, and std is standard deviation of the distributions. Values of SI >2 were considered as successfully separated by definition. Overall, mean SL (total mean SL) was calculated for each size-frequency distribution and mean SL, standard deviations and SI were calculated for each of the identified cohorts.

Growth rate. The average growth rates of *Xylophaga* sp. A were estimated based on the cohort analysis, considering the difference in mean SL between sampling times for BC in pine and oak.

Total growth curves for each wood type (pine, oak) and location (BC, open slope) were calculated by fitting a von Bertalanffy growth function to the resulting size-at-age data pairs using a non-linear iterative Newton algorithm (Brey, 2001):

$$Lt = L_{\infty} [\ 1 - e^{-K(t-t0)}\ ]$$

where L_{∞} is the mean asymptotic shell height (maximum length) in mm, K is the Brody growth coefficient, t the age in months, and t0 the theoretical age at which shell height equals zero. Lacking any firm data, we assumed that the first larvae settled on the wood 15 days after its deployment.

To calculate *Xylophaga* sp A growth rates and curves, we pooled data from all depths, assuming that growth did not change with depth due to the relative isothermal conditions of the Mediterranean deep sea.

Other fauna. The remaining wood fragments and faecal material inside the excavated cavities were sieved with a 250-µm mesh; other macrofaunal organisms were recovered under a dissecting microscope. These species were stored in 70% ethanol, counted and identified to the lowest possible taxonomic level.

Data analysis

Xylophaga sp. A and sp. B, represent a single morphotype each, while three other rare morphotypes were pooled as *Xylophaga* spp. C for statistical purposes. A two-sample t-test was used to test whether the abundance of all *Xylophaga* spp. pooled was statistically different among samples paired by station, depth, recovery time and wood type (n=3).

Twelve-month samples were not available from the same depths for BC and the open slope. Thus, each location had to be considered separately. Both for *Xylophaga* sp. A and for *Xylophaga* sp. B, the differences in abundance among twelve-month samples were analysed by two-way Analysis of Variance (ANOVA) using Depth (two levels:

900 and 1500 m in BC; 1500 and 1800 m in the open slope) and Wood (two levels: pine and oak) as fixed factors. Cochran's test was used prior to the ANOVA to test the assumption of homogeneity of variances (Underwood 1997). The Student-Newman-Keuls test (SNK test) was used to compare the means of the different treatments. PRIMER v6 & PERMANOVA+ software (Clarke and Gorley, 2006, Anderson 2006) was used for multivariate analyses. For these analyses, density data were organized into a matrix of sample *vs* *Xylophaga* morphotypes. Non-metric multi-dimensional scaling (MDS) ordination was performed using the Bray–Curtis similarity coefficient, after square root transformation of data to show similarities among samples. A PERMANOVA (McArdle and Anderson, 2001) design was created based on two factors: Location (two levels, BC *vs* Open Slope) and wood type (crossed, two levels, Pine *vs* Oak). SIMPER analysis (Similarity Percentages–species contributions) was performed to indicate the percentage contributions of each species of *Xylophaga* to the similarity within and dissimilarity between groups of samples.

Non-parametric Kolmogorov-Smirnov test (KS-test) was performed to compare shell-length distributions (Sokal and Rohlf, 1995).

Results

Abundance of wood-borer bivalves

We collected and examined 2,014 wood-boring bivalves. Morphological studies revealed five morphotypes (presumptive species) of *Xylophaga*; *Xylophaga* sp. A and sp. B were dominant (79.5 % and 19 % respectively), while the three rare morphotypes pooled as *Xylophaga* spp. C represented less than 1.5 %.

Wood colonization (and degradation) increased over time (Fig. 2) and the different species of *Xylophaga* colonized the wood at different times (Fig. 3). The three-month cubes from 1200 m depth at BC and the open slope were colonized only by *Xylophaga* sp. A, which colonized the wood in BC 10 times more heavily than the wood outside the canyon. In both locations pine was 1.5-2 times more heavily colonized than oak (Fig. 3).

The nine-month cubes harboured *Xylophaga* spp. A, B and C and were significantly more heavily colonized (t-test, $p< 0.01$) inside BC than in the adjacent open slope (22 and 44 times higher in pine and oak, respectively). In BC, the total abundance of these three groups was significantly higher after nine than after three months (277 ± 30 *vs* 94

± 56 ind. dm^{-3} in pine, 187 ± 16 *vs* 60 ± 7 ind. dm^{-3} in oak, t-test, $p<0.01$) and pine was more heavily colonized than oak (t-test, $p<0.05$). To the contrary, differences in total abundance between the three- and nine-month deployments were not significant on the adjacent slope (9.1 ± 4.5 vs 9.8 ± 3.9 ind. dm^{-3} in pine, 4.6 ± 2 vs 3.9 ± 1 ind. dm^{-3} in oak). The burrows of the largest specimens extended across the whole 8 cm cube (Fig. 4). The exterior of wood in the most densely colonized BC samples appeared solid, but its interior was more or less hollow and it crumbled on handling. All *Xylophaga* burrows were filled by soft, compacted faecal matter that formed a chimney lining the bored tunnels (Fig. 4C).

The BC1200_bottom trap was recovered after nine months containing only two largely consumed oak cubes (Fig. 2); the pine cubes had completely disappeared. The oak cubes harboured many small, empty *Xylophaga* shells; the total abundance of living bivalves was 51 and 23 ind. dm^{-3}. The first cube carried only *Xylophaga* sp. A (maximum SL = 4.5 mm); the second cube also supported *Xylophaga* sp. B (33% of the specimens).

The twelve-month pine cubes from 900 m depth in BC (BC900_pine) were so extensively bored that they partly crumbled and some large specimens of *Xylophaga* likely were lost (Fig 2). Furthermore, *Xylophaga* sp. A was significantly more abundant in shallower than in the deeper twelve-month cubes, both in BC and the adjacent open slope (900 and 1500 m depth, respectively) regardless of wood type (ANOVA, Table 2). *Xylophaga* sp. B was significantly more abundant in pine than in oak, both in BC and on the adjacent open slope (ANOVA, $p<0,01$, Table 2). It occurred in oak only from inside BC at 1500 m depth (2 specimens) and in one cube deployed on seafloor at 1200 m.

Considering all cubes, *Xylophaga* sp. A was significantly more abundant at the shallow deployments of 900 and 1200 m depth than the deeper ones at 1500 and 1800 m. The morphotypes grouped as *Xylophaga* spp. C were rare, appearing first after nine months at 1200 m depth in oak inside BC and in pine in the adjacent slope (3.9 ± 3.3 and 0.7 ± 1.1 ind. dm^{-3}, respectively).

The biomass patterns mirrored those of abundance, increasing with time and differing markedly among locations and between wood types (Fig. 3). In the three-month old cubes, the average biomass of *Xylophaga* sp. A was from 0.008 to 0.820 g AFDW dm^{-3} in oak on the adjacent slope (OS_1200_oak) and in pine in BC (BC_1200_pine), respectively. In the nine-month old cubes, pooled biomass of all *Xylophaga* ranged from

0.020 to 3.917 g AFDW dm^{-3} in these two deployments, respectively. In the twelve-month old cubes, pooled biomass ranged from 0.116 to 3.947 g AFDW dm^{-3} in oak in the adjacent open slope at 1800m deep (OS_1800_oak) and in pine in BC at 900 m deep (BC_900_pine), respectively.

The composition of the *Xylophaga* species assemblages differed significantly depending on location, wood type and their interaction (Fig. 5A and Table 3). The average dissimilarity between BC and the adjacent open slope was 64%. *Xylophaga* sp. A contributed 70% to that dissimilarity, being more abundant in BC than in the open slope (SIMPER, Fig. 5B). The average dissimilarity between pine and oak was 35%; *Xylophaga* sp. B was the main contributor with 47% (SIMPER, Fig 5C).

Other fauna

Species other than *Xylophaga* spp. were recovered from wood only in two deployments (BC900 and BC 1200_bottom) (Table 4). In the two oak samples in contact with the sediment (BC1200_bottom), crustaceans were the most abundant group (~ 540 individuals per dm^{-3}) with polychaetes secondary (~ 55 individuals per dm^{-3}). In the suspended BC900 pine samples only deposit feeding polychaetes were present (*Capitella* sp., *Spiophanes* sp., *Neoamphitrite* spp., and *Ophryoytrocha* sp.).

Length-Weight relationships

SL was significantly correlated with DW and AFDW in *Xylophaga* sp. A and sp. B (Fig. 6). Allometric growth curves for DW and AFDW were similar (Fig. 6). The highest allometric coefficient, b, was that of *Xylophaga* sp. B, particularly for the AFDW, but *Xylophaga* sp. A clearly reached the highest SL and biomass (Fig. 6B).

Demography and Growth

Individuals of *Xylophaga* sp. A presented a large size-range (1.8-15.1 mm SL, Fig. 7, Table 5). In BC, the size-frequency distributions significantly differed among locations, recovery times and wood type (KS-test, $p< 0.05$,). Many samples presented bimodal distributions, suggestive of distinct age groups (Table 5 and Fig. 7). The mean SL of *Xylophaga* sp. A in three-month pine cubes (6.1 ± 1.5 mm in BC1200_Pine_3M) was significantly lower (t-test, $p <0.05$) than that in nine-month cubes (7.96 ± 1.9 mm in BC1200_Pine_9M). Although when the animals recruited cannot be exactly determined, the large animals (e.g. up to 8-10 mm in pine) in the three-month cubes are suggested to have recruited soon after deployment. In the twelve-month cubes, the overall mean SL slightly decreased at 900 m depth (due to the presence of a second, smaller cohort) and slightly increased in the 1200 m depth cubes. In BC oak cubes, mean SL markedly increased between the three and nine month cubes; between the nine- and twelve-month cubes, a second smaller cohort limited the size of the increase in overall mean SL.

In the open slope, the size-frequency distributions in pine and oak, although slightly increased, did not significantly differ between three- and nine–month cubes (KS-test, $p > 0.05$). Conversely, SL was significantly higher in the twelve–month cubes both for pine and oak (KS-test, $p < 0.05$).

The modes of each of the two cohorts in the BC twelve-month cubes were 6.5 and 11 mm, and 6 and 9 mm in pine and oak, respectively. Based on cohort analysis, the average growth rates in BC pine cubes were estimated as 2.09 $\text{mm}\cdot\text{month}^{-1}$ (0 to 3 months), 0.47 $\text{mm}\cdot\text{month}^{-1}$ (3 to 9), and 0.64-0.73 mm month^{-1} (9 to 12). In oak cubes, the estimated average growth rates were 1.63 $\text{mm}\cdot\text{month}^{-1}$ (0 to 3 months), 0.47 $\text{mm}\cdot\text{month}^{-1}$ (3 to 9), and 0.43 $\text{mm}\cdot\text{month}^{-1}$ from (9 to 12). In the open slope, the number of specimens was too low to estimate the average growth rates.

The smallest individuals (i.e. < 2 mm in SL) of *Xylophaga* sp. A were present in three-month pine cubes (February, BC1200_Pine_3M) and nine-month oak cubes (November, BC1200_Oak_9M), representing 29% and 17% of the population, respectively. In the twelve-month samples the largest size classes (14-16 mm) were more abundant in pine on the open slope.

Specimens of *Xylophaga* sp. B ranged from 1.6 mm to 9.3 mm in SL and the size-distributions were unimodal (Fig 9). In BC, overall mean SL did not differ significantly between nine- and twelve-month cubes, despite being slightly higher (5.2 ± 1.0 mm) in the 12-month BC 1500 cohort than in the other cohorts (4.3 ±1.3 and 3.45 ± 1.4 in BC 1200_9M and BC_900_12M, respectively). Mean SL in the 12-month cubes in the open slope (7.27 mm) was higher than in BC.

Assuming that *Xylophaga* sp. A recruited simultaneously in oak and pine, its total growth rate (based on von Bertalanffy) was faster in pine than in oak (Fig. 9) and, among oak samples, faster in BC than on the open slope.

Discussion

Mediterranean wood-boring bivalves

Although only *Xylophaga dorsalis* (Turton, 1819) had been reported from the Mediterranean (Gaudron et al., 2010; Bienhold et al., 2013), we found five morphotypes of wood-boring bivalves in the study area. Xylophagains were more abundant and larger in BC than on the adjacent open slope, consistent with the hypothesis that canyon systems enhance benthic abundance (Koho et al., 2008; Ingels et al., 2009) and may result in biomass hotspots (Vetter et al., 2010; De Leo et al., 2010). The higher abundance of wood-boring bivalves inside BC may be caused by either enhanced larval settlement due to favourable local circulation pattern or by higher food availability (i.e. trapped and concentrated allochtonous vegetation). Experimental trawling carried out in autumn 2009 (Tecchio et al., this issue; Fernádez-Arcaya et al. this issue) allowed us to provide a preliminary support to this hypothesis, as the biomass of naturally sunken wood found in BC exceeded that on the adjacent open slope (0.4 *vs* 0.12 kg km^{-2} respectively) (Romano et al. unpublished results).

The total abundance of *Xylophaga* in BC increased over time, while it was constant from three to nine months in the open slope. Accordingly, we suggest that larval supply may be limiting on the open slope but not in BC, where a second cohort recruited under the same conditions. We cannot assess if the second BC cohort resulted from self-recruitment or from an external larval supply coming from northern-most submarine canyons transported by the predominant Northern Current circulation (Millot, 1999). Planktotrophic larvae of xylophagains may spend extended periods in the water column (e.g. *Xylophaga supplicata* in Haga and Kase, 2013), suggesting long-distance dispersal capacity, as demonstrated in other deep-sea bivalves such as the chemosynthetic mytilds *Bathymodiolus childressi* and *Idas modiolaeformis*, which the larval life span has been estimated up to 13 and 5 months, respectively (Arellano and Young, 2009; Gaudron et al., 2012).

Despite having our experimental cubes suspended 20 m above the sediment, they were heavily colonized by the wood-boring bivalves, and the variety of morphotypes was higher than in bottom samples. This result refutes previous postulates that xylophagains recruit at the sediment surface and do not occur in floating wood (Turner, 2002) and supports their long-distance dispersal capacity. Anyway, colonization was faster and recruitment was higher on sessile cubes, which were either completely consumed after nine months (pine) or more consumed than the corresponding suspended ones (oak). However, when recovered, the abundance of live *Xylophaga* was lower, and their mean size was significantly smaller in sessile than in suspended cubes. These differences may be due to factors other than intra-specific competition. For instance, predation may be higher on the sediment, as confirmed by the higher colonization of Gammaridea, Leptostraca and Polychaeta compared to suspended samples (Table 3). Mobile macro- and megabenthic organisms present in BC, such as decapod crustaceans (e.g. *Aristeus antennatus, Geryon longipes*) or echinoderms (e.g. *Ceramaster grenadensis, Molpadia musculus, Bathypolypus sponsalis*) (Tecchio et al., this issue) may also potentially predate on the wood fauna when directly deployed on the bottom, especially when the substrate is highly consumed.

Different species of *Xylophaga* coexisted in the same experimental wood cube consuming the same resource, as has been noted previously in much larger wood deployments (Voight, 2007). However, different wood types deployed simultaneously at the same depth in the same conditions, were colonized by different species, suggesting that recruiters may actively select their substrate (Fig. 3). This specific association is particularly true for *Xylophaga* sp. B. and pine. Differences in wild wood falls in colonization have been attributed to differences in the wood's chemical composition (Pailleret et al., 2007; El-Shanshoury et al. 1994). However, how long the wood had been on the seafloor was unknown, a major limit to analyses of wild wood falls.

Both pine and oak were certainly consumed. However, all species of *Xylophaga* were less abundant in oak, which as harder wood may be more difficult to bore. Also, *Xylophaga* sp. A reached bigger sizes in pine and we can only postulate a faster growth (Fig. 9) if we assume simultaneous recruitment in both wood types.

Inter-specific interactions may also influence habitat selection. For instance, the morphotypes grouped in *Xylophaga* spp. C were more abundant in oak inside BC but more abundant in pine on the open slope. We hypothesize that when the pine was heavily colonized by the two dominant species inside BC, *Xylophaga* spp. C opted to use the more available resource offered by the oak. On the open slope, where the total abundance of *Xylophaga* was significantly lower (and therefore competition for space and food was reduced), the rarer *Xylophaga* spp. C could choose pine, which perhaps is their preferred substrate. Our results suggest that both inter- and intraspecific competition may affect both the growth and size-frequency distribution of the bivalves. On the open slope, individuals in the less dense populations of *Xylophaga* sp. A reached their largest sizes (14-16 mm in SL); the mean SL of *Xylophaga* sp. B on the slope was also higher than in BC.

In BC, the maximum density of *Xylophaga* spp. in pine was about 290 ind. dm^{-3}, much higher than that reported in sunken wood from Vanuatu islands (Pailleret et al., 2007), where the xylophagains represented less than 6% of the total macrofauna (about 390 ind. dm^{-3}). In the Nile Deep-Sea Fan (E Mediterranean), Douglas fir samples recovered from deep-sea cold seeps carried 525 ind. dm^{-3} of what was identified as monospecific populations of *Xylophaga dorsalis*, while samples of the same wood from a mud volcano in the Norwegian Sea harbored 14,412 ind. dm^{-3} of *Xyloredo ingolfia* (Gaudron et al., 2010).

Demography and growth

If individuals smaller than 2 mm SL indicate recent settlement, our results suggest two distinct autumnal and winter settling events. However, the bimodal distributions in the nine-month and twelve-month cubes suggest that recruitment events occurred several times a year. In the nine-month BC pine cubes, the two cohorts measured 5.89 ± 1.7 and 9.09 ± 1.5 mm mean SL, respectively. Based on our estimated growth rates (Fig. 9), we calculate that settling took place two to three months before recovery (i.e. August-September). The largest cohort (11 mm in mean SL) in the twelve-month cubes may indicate an even earlier settlement, likely during summer. Settlement in late summer may be consistent with spring runoff and later transport offshore and sinking of wood onto the deep-sea floor and thus the arrival (or availability) of food/substrate potentially acting as a cue to attract new recruitments. More wild wood was found during experimental trawling in spring in the whole BC area (including the open slope) than in autumn (1.02 vs 0.13 kg km^{-2} respectively). Our results suggest that *Xylophaga* sp. A has a "pulsing" recruitment strategy (*sensu* Todd, 1998) with planktonic larvae released several times during the year. Previous studies at shallower sites reported continuous recruitment for *Xylophaga atlantica* (Romey et al., 1994), *X. washingtonia* (Haderlie, 1983), and *X. depalmai* (Tyler et al., 2007). Conversely, the absence of planktonic larvae of *Xylophaga* in June and the presence of newly settled specimens in September suggested a cyclic reproduction with a potential seasonal settlement in August (Turner 1973), but also in late fall or winter for *X. dorsalis* in Scotland (Turner and Johnson, 1971) as well as for *X. atlantica* in the USA eastern continental shelf (max depth 234 m), with gonad ripening correlated to water temperatures higher than 10 °C (Berg et al., 1987). Spawning in the deep Mediterranean is unlikely to be affected by temperature, which at all our stations ranged only from 13.0 to 13.3 °C (Tecchio et al. this issue). Anyway, very little information is available about the reproductive biology of these deep-water organisms, particularly in the Mediterranean Sea.

Our experimental design (which included different deployment durations) forced us to assume that growth did not change with depth or time of the year before estimating growth rates. Despite this over-simplification, our unique data provide a reasonable approach to be tested by further studies. Taking this into account, our data suggest that average growth rate of *Xylophaga* sp. A was higher (0.070 mm d^{-1}) during the first three-four months after colonization of wood cubes, followed by slower rate (0.021-0.016 mm d^{-1}) over the next eight months (Fig. 10). Also, the growth rates were higher in pine that in oak (Fig. 9) or, alternatively, recruitment occurred earlier. The only comparable data reported: 1) early growth rates of 0.015 mm d^{-1} for *X. atlantica*, higher in oak than in pine, as were maximum sizes, but four months later the situation reversed and growth rates increased up to 0.133 mm d^{-1} in pine (Romey et al., 1994), and 2) mean growth rates of 0.03 mm d^{-1} for *X. depalmai* after three and six months (in line with ours), which did not differ between spruce and oak (Tyler et al., 2007). Such a rapid growth is rare in the deep sea (Gage and Tyler, 1991), leading qualify these organisms as opportunists (Turner, 1973).

Length-weight allometric relationships provide information on the physiological and trophic conditions in bivalves through the variations of “b” (the equilibrium constant), which represents the growth in weight with respect to that in length (Ramesha et al., 2009). In many bivalves (e.g. mussels, oysters and clams) deviation in b revealed to be correlated with physiological and environmental conditions, for instance it is density-dependent (Seed, 1968; Chinzei et al., 1982; Cigarría and Fernández, 1998; Alunno-Bruscia et al., 2001), while in hydrothermal vent mytilids, allometric relationships were affected by the presence of symbiotic polynoid polychaetes that live inside the bivalve (Britayev et al., 2007). Values of “b” range between 2.4 and 4.5 in most bivalves (Wilbur and Owen, 1964), but no previous information was available for *Xylophaga* species. Both *Xylophaga* sp. A and B showed b coefficients between 2.7 and 2.9, which indicate biometrical relationships similar to those in other bivalves and close to the allometric threshold (b=3, (LaBarbera, 1989). An exception was *Teredo pedicellata*, a shallow water wood-boring bivalve, which showed a nearly linear relationship (b = 1) (Isham et al. 1951). Regardless, it would be interesting to compare the BC and adjacent open slope populations, but the low density of *Xylophaga* in the later prevented us to estimate the corresponding allometric relationships.

Driving factors affecting allochtonous wood inputs into deep sea?

Most records of plant remains in sea basins deal with close coastal waters, often off the mouth of large rivers. However, floating roots and branches may travel long distance before sinking, and strong climatic events (such as big storms or, particularly, hurricanes) may transport plants remains 1,100 km offshore before sinking and settle on the bottom (Wolff, 1979). Turbidity currents, slumping, and cascading events, frequently reported in submarine canyons (Canals et al., 2010), may also be important mechanisms that bring vegetation to great depths.

The NW margin is the most densely incised part of the entire Mediterranean basin; active transport of continental vegetation to the deep-sea floor may occur frequently on the narrow continental shelf off the Catalan coast. The urban development of Catalonia from the 1950s to the 1980s dramatically affected river discharges (Sala and Inbar 1992). The subsequent modification of the watershed of Catalan rivers lead to increased total runoff and peak flows that shortened the lag time in the rainfall draining from the land (Liquete et al, 2009; Sala and Farguell, 2002).

The impact of global climate change on riverine loads is unclear. Daily water discharge, and, carrying capacity could be reduced, but extreme flood events will be more frequent and increase erosional force. For instance, from 1962 to 1988, nine devastating floods occurred in Catalonia causing serious damage and several hundred victims (Sala and Inbar 1992). During our experiments, the most severe storm recorded in the area in the last 60 years hit the Catalan Coast on 26th December 2008 (Mateo et al. 2012; Sanchez-Vidal et al., 2012). Thus, in a changing climate frame, all these extreme events will likely increase transfer of allochthonous material to deep-sea ecosystems, understanding the fate of terrestrial organic materials transferred to deep environments (i.e. whether they will be recycled or so far stored) become a matter of high relevancy.

Our experiments are the first to examine wood-fall associated fauna in Mediterranean canyons to enhance our understanding of both the deep-sea Mediterranean biodiversity and how allochthonous materials may enhance local biota. Our results confirm that BC presents a heightened abundance and biomass of wood-boring bivalves, thus acting as a highly localized biomass hot spot, with a large potential to store and process carbon from allochtonous vegetational debris. Consequently, this essential habitat, and the species it harbors (such as deep-sea wood-boring organisms), may be particularly sensitive to global climate change impacts, pointing on the relevance of developing adequate sustainable management and conservation strategies.

Knowledge on the distribution and life history of deep-sea macrofauna, given its importance in the diet of many valuable bathyal species (e.g. macrurids, the red shrimp *Aristeus antennatus*), may be relevant for the conservation of deep-sea resources (Cartes, 1994; Madurell and Cartes, 2006; Cartes et al., 2010). More specifically, further studies are needed to assess the connectivity among and within canyons, and to evaluate the role of sunken wood in deep-sea biodiversity as stepping stones to other fragmented ecosystems like hydrothermal vents (Distel et al. 2000).

Our results confirm that the studied *Xylophaga* species behave as opportunists, showing long-distance dispersal capacity, high settlement rate, and fast growth. In summary, these taxa are equipped with an efficient capability to exploit and persist in the ephemeral and fragmented habitats represented by wood falls. They are keystone species in wood falls habitats that are critical to facilitate the establishment of other benthic species and, thus, to maintain or even enhance the overall biodiversity of deep-sea ecosystems.

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Table 1.

Location and deployment time of the experimental traps in the Blanes Canyon (BC) and in the adjacent slope (OS)

Trap	Seafloor depth (m)	Latitude	Longitude	Drop date	Sampling date	Duration (months)
BC 900	894	41º 34' 12,72"	2º 54 19,14"	November 2008	November 2009	12
BC 1200	1195	41º 31' 15,06"	2º 50' 49,26"	November 2008	February 2009	3
BC 1200 and BC 1200 bottom	1195	41º 31' 15,06"	2º 50' 49,26"	February 2009	November 2009	9
BC 1500	1468	41º27' 28,80"	2º 52' 58"	November 2008	November 2009	12
OS 1200	1184	41º 13' 8,99"	2º 48' 54,6"	November 2008	February 2009	3
OS 1200	1184	41º 13' 8,99"	2º 48' 54,6"	February 2009	November 2009	9
OS 1500	1497	41º 09' 0,59"	2º 53' 48"	November 2008	November 2009	12
OS 1800	1806	41º 04' 52,19"	2º 58' 9"	November 2008	November 2009	12

Table 2.

Results of ANOVA carried out on *Xylophaga* sp. A and sp.B abundance data from samples collected after 12 months duration. SNK test= The Student-Newman-Keuls test. Bold values denote p<0.05

		Blanes Canyon						Open Slope					
		Xylophaga A			*Xylophaga* B			*Xylophaga* A			*Xylophaga* B		
Source	df	MS	F	*P*	MS	F	*P*	MS	F	*P*	MS	F	*P*
Depth = De	1	8008.3	28.46	***0.0007***	0.33	0.04	*0.8457*	44.08	6.61	***0.0331***	0.03	0.47	*0.5111*
Wood = Wo	1	432.0	1.54	*0.2505*	3400.33	412.16	***0.000***	6.75	1.01	*0.3438*	4.16	67.26	***0.0000***
De X Wo	1	768.0	2.73	*0.1371*	3.00	0.36	*0.5632*	0.75	0.11	*0.7459*	0.03	0.47	*0.5111*
Residuals	8							6.67			0.06		
SNK test		900 m > 1500 m depth			pine > oak			1500 m > 1800 m depth			pine > oak		

Table 4.

Deployments harboring taxa other than *Xylophaga* spp. (densities per dm^3)

Taxa	BC 1200_bottom Oak (n=2)	BC 900 Pine (n =2)	BC 900 Oak n=1
Polychaeta			
Capitellidae *Capitella* complex	28.3	24.9	2.0
Dorvilleidae *Ophryoytrocha* sp.	1.0	2.0	
Euphrosinidae n. id.	1.0		
Spionidae *Prionospio* sp.	2.0		
Spionidae *Spiohanes* sp.	3.9	4.4	
Terebellidae *Neoamphitrite* spp.	18.6	3.9	
Crustacea			
Amphipoda n. id spp.	96.7		
Amphipoda Gammaridae n. id. spp.	232.4		
Amphipoda Gammaridae Lysianassidae spp.	87.9		
Amplipoda Gammaridae *Seba aloe*	100.6		
Leptostraca	20.5		
Mollusca			
Cocculinoidea n. id.	1.0		
Mitylidae *Idas* sp.	1.0		

Table 3.

PERMANOVA results for differences among locations (BC *vs* OS) and between pine and oak. Bold and underlined values indicate p<0.01

Source	df	SS	MS	Pseudo-F	P(perm)	perms
Location = Lo	1	35284	35284	88.523	**<u>0.0001</u>**	9953
wood = wo	1	5562.4	5562.4	13.955	**<u>0.0001</u>**	9954
Lo x wo	1	2877.3	2877.3	7.2189	**<u>0.0007</u>**	9960
Res	39	15545	398.58			
Total	42	59049				

Table 5.

Average and range of shell lengths (SL, mm) from *Xylophaga* sp. A by deployment. Parameters of the cohort components of the length-frequency distribution estimated by Bhattacharya's method. BC=Blanes Canyon, OS= Open Slope, 3M, 9M, 12M= 3, 9 and 12 months deployments, SI= Separation Index

				Bhattacharya analysis			
Sample	MIN SL	MAX SL	Overall average SL	distribution curve type	mean SL I cohort	mean SL II cohort	SI
BC1200_Pine_3M	2.0	8.6	6.1 ± 1.5	unimodal	6.3 ± 1.4	-	-
BC1200_Pine_9M	2.1	12.6	8.2 ± 2.2	bimodal	5.9 ± 1.7	9.1 ± 1.5	9.19
BC900_Pine_12M	2.0	13.3	7.9 ± 2.7	bimodal	6.6 ± 2.6	11.3 ± 1.0	10.00
BC1500_Pine_12M	2.8	14.0	9.5 ± 2.6	bimodal	6.5 ± 1.9	11.0 ±1.4	10.52
BC1200_Oak_3M	2.5	4.4	4.9 ± 1.8	-	-	-	-
BC1200_Oak_9M	1.8	11.0	7.2 ± 1.7	unimodal	4.1 ± 1.5	7.7 ± 1.5	8.01
BC900_Oak_12M	2.8	11.1	7.5 ± 1.9	bimodal	6.1 ± 1.3	9.0 ± 1.0	13.36
BC1500_Oak_12M	2.3	11.8	8.5 ± 1.8	bimodal	6.0 ± 1.7	9.0 ± 1.2	10.35
OS1200_Pine_3M	2.6	7.7	4.9 ± 1.8	bimodal	3.5 ± 0.9	6.8 ± 0.7	13.03
OS1200_Pine_9M	2.5	12.6	7.0 ± 3.7	-	4.0 ± 1.6	-	-
OS1500_Pine_12M	3.2	15.1	10.4 ± 3.9	bimodal	5.0 ± 1.0	13.6 ± 1.4	15.83
OS1800_Pine_12M	4.6	14.8	10.8 ± 3.2	bimodal	6.0 ± 1.2	12.5 ± 1.3	14.74
OS1200_Oak_3M	2.0	5.1	2.8 ± 1.2	-	-	-	-
OS1200_Oak_9M	1.9	7.8	4.4 ± 2.2	-	4.0 ± 1.2	-	-
OS1500_Oak_12M	6.3	11.2	9.1 ± 1.5	-	9.7 ± 0.9	-	-
OS1800_Oak_12M	2.6	10.3	8.5 ± 2.4	-	9.7 ± 0.7	-	-

Figure captions

Figure 1. Map showing the position of the experimental moorings and traps in relation to the Blanes Canyon (BC) and the open slope (OS).

Figure 2. Changes in the two types of wood (pine and oak) with deployment duration. Pine deployed on the seafloor at 1200 m depth disappeared after 9 months.

Figure 3. Abundance and Biomass (Ash free dry weight, AFDW) of *Xylophaga* spp. A, B and C at different depths and deployment durations (3, 9, 12 months) in pine and oak inside Blanes Canyon and on the adjacent Open Slope. Each column represents the mean of three replicates; error bars represent standard deviation.

Figure 4. Detail of burrows in pine (A and B) and oak (C).

Figure 5. nMDS ordination plots for comparison between samples based on square-root transformed *Xylophaga* species relative abundances, A) comparison between location and wood type, showing superimposed 50, 60 and 70 % similarity groups from cluster analysis. Bubbles in B) indicate the abundance of *Xylophaga* sp. A in the samples and in C) the abundance of *Xylophaga* sp. B. BC= Blanes Canyon, OS= Open Slope.

Figure 6. Allometric relationships between A) shell length and total dry weight (DW) and between B) shell length and ash free dry weight (AFDW) for *Xylophaga* sp. A and B at each depth.

Figure 7. Length-frequency distributions showing the shell lengths of all specimens of *Xylophaga* sp. A obtained from the Blanes Canyon and the adjacent open slope in each oak and pine cube deployed for 3, 9, and 12 months . Normal curves represent each detected cohort. The sample name, including its depth, and number of individuals are indicated at top of each histogram.

Figure 8. Length-frequency distribution of all specimens of *Xylophaga* sp. B obtained in the Blanes Canyon and the adjacent open slope in pine cubes deployed for 9 and 12 months. Normal curves represent each detected cohort. The sample name, including depth, and size are indicated at top of each histogram.

Figure 9. Growth rates of *Xylophaga* sp. A for each location (BC= Blanes Canyon, OS= Open Slope) and wood type. A von Bertalanffy growth function is fitted in each graph. The location and wood type are indicated at top of each graph.

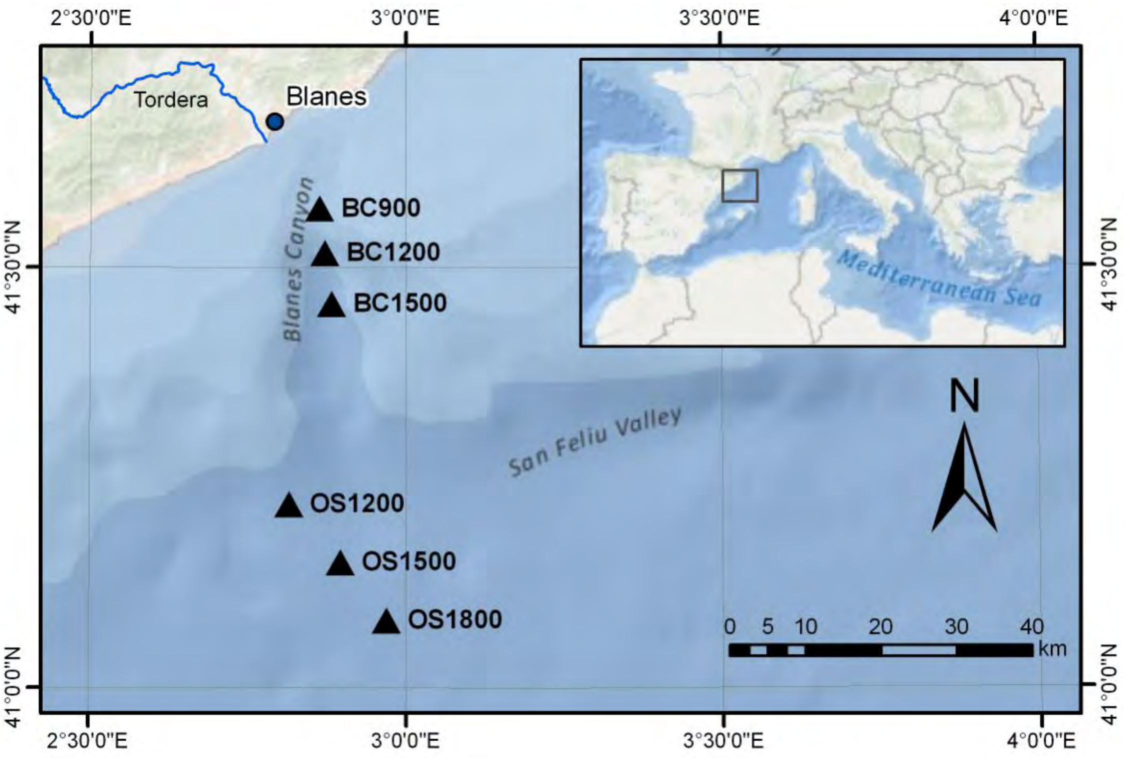


Figure 1

Map showing the position of the experimental moorings and traps in relation to the Blanes canyon (BC) and the open slope (OS).

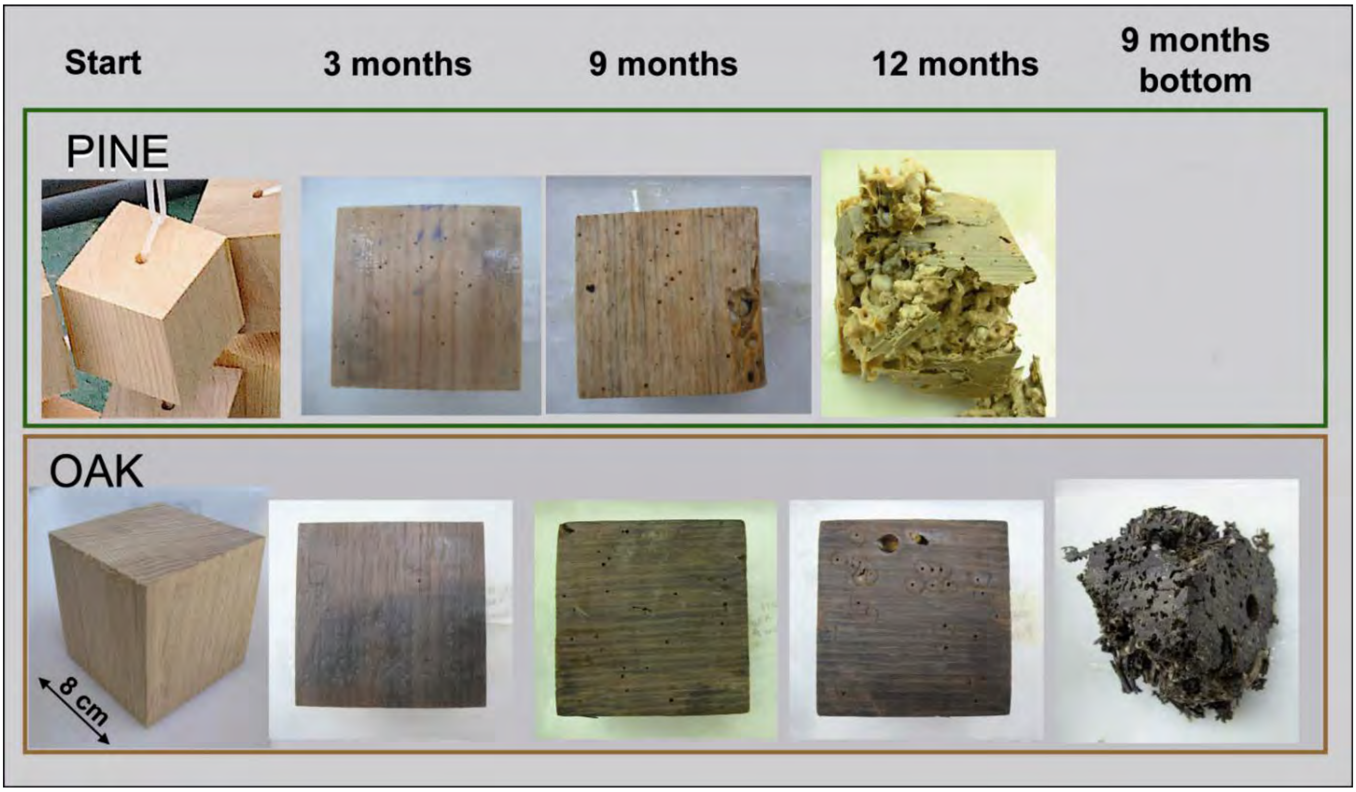


Figure 2

Changes in the two types of wood (pine and oak) with length of deployment. Pine cubes deployed on the seafloor at 1200 m depth disappeared after 9 months (empty square).

Figure

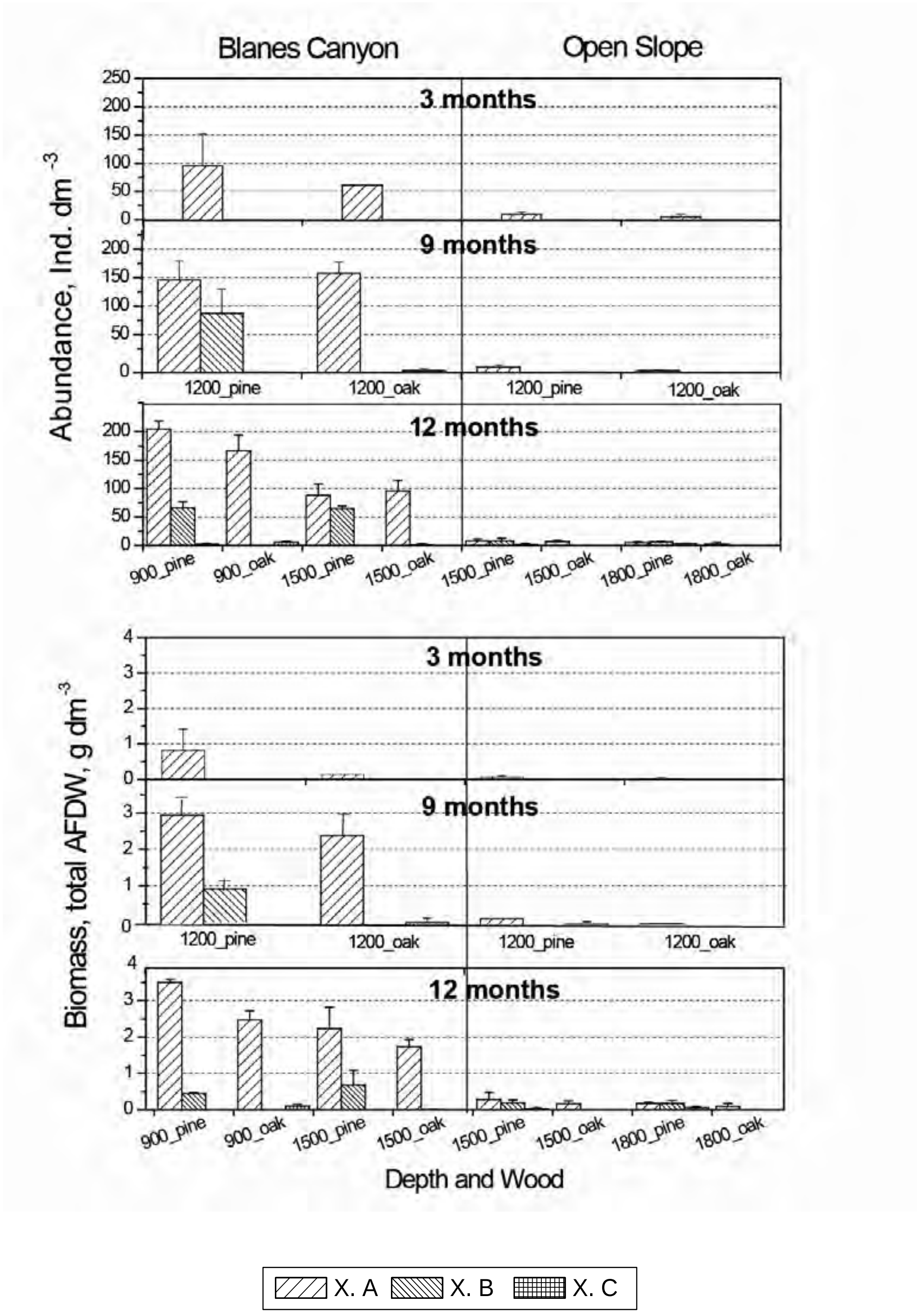
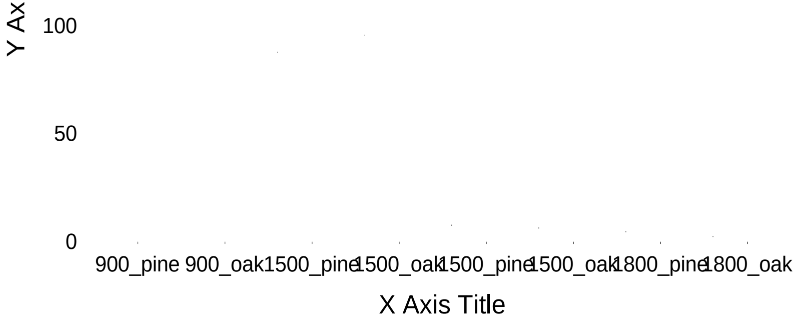


Figure 3

Presence of *Xylophaga* spp. A, B and C at different depths and durations of deployment (3, 9, 12 months) in pine and oak samples inside the Blanes Canyon and in the adjacent Open Slope. Each column represents the mean of three replicates and error bars represents standard deviation.



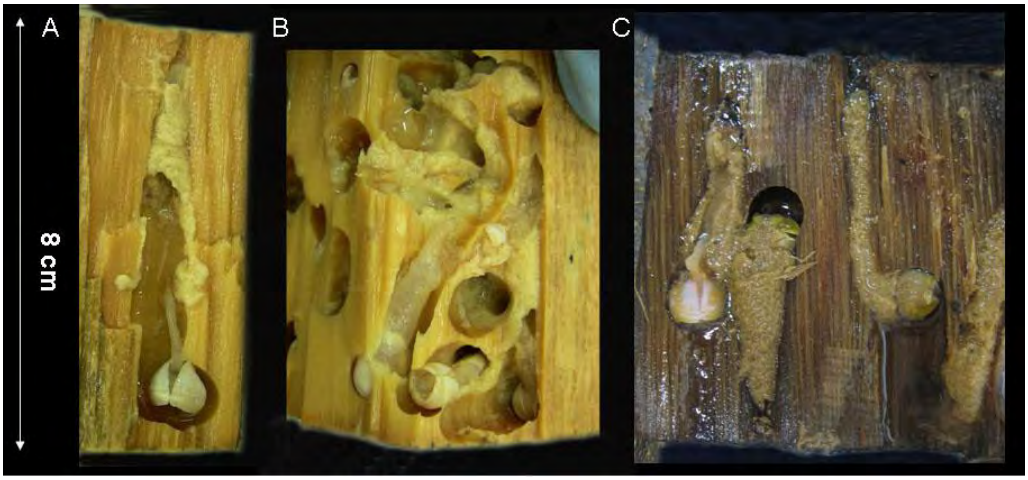


Figure 4
Detail of burrows in pine (A and B) and oak (C)

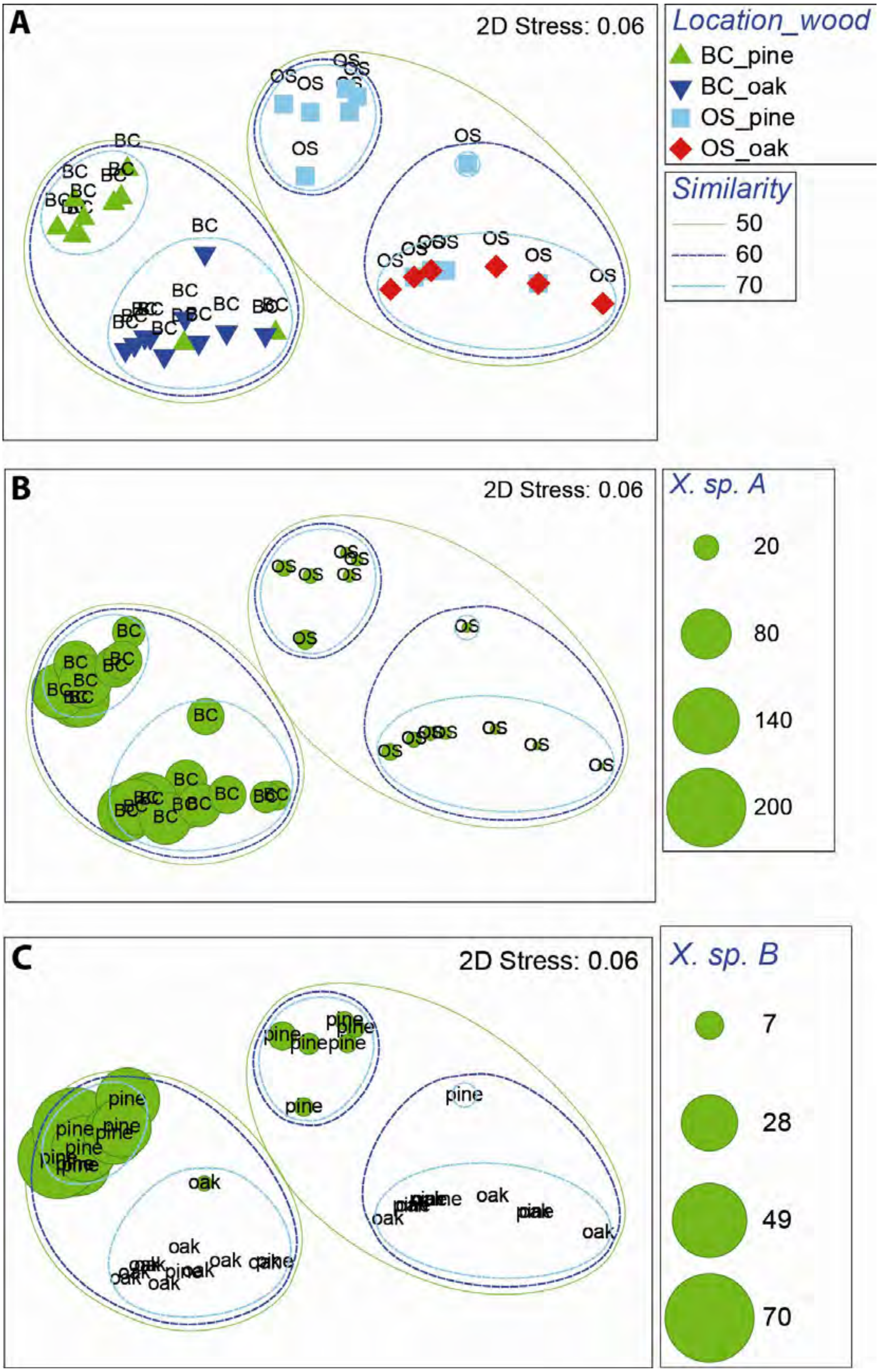


Figure 5

nMDS ordination plots for comparison between samples based on square-root transformed *Xylophaga* species relative abundances, A) comparison between location and type of wood, showing superimposed 50, 60 and 70 % similarity groups from cluster analysis. Bubbles in B) indicate the abundance of *Xylophaga* sp. A and in C) the abundance of *Xylophaga* sp. B. Labels indicated: BC= Blanes Canyon, OS= Open Slope.

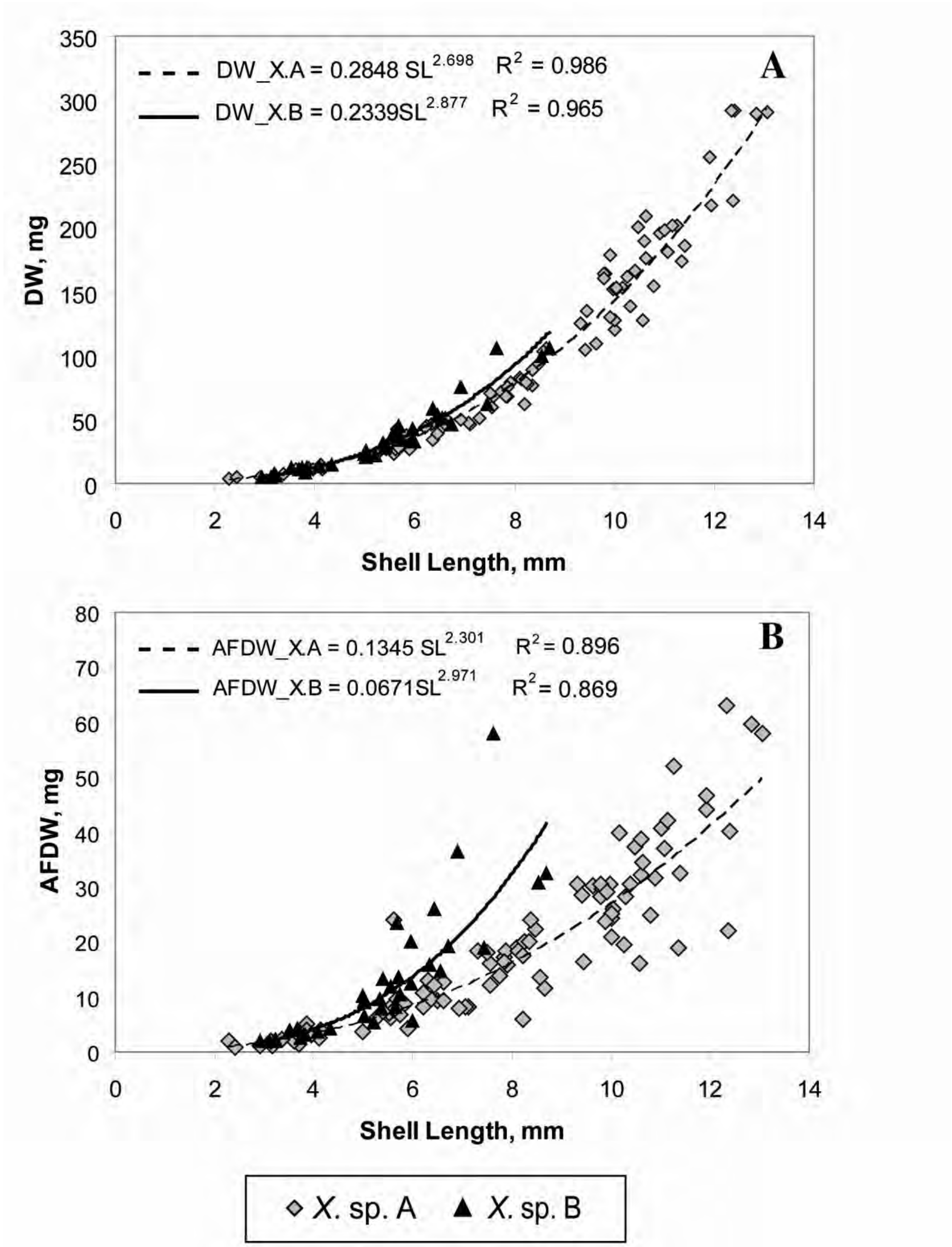


Fig 7

A) Allometric relationships between shell length and total dry weight (DW) and B) between shell length and ash free dry weight (AFDW) for *Xylophaga* sp. A and B at each depth.

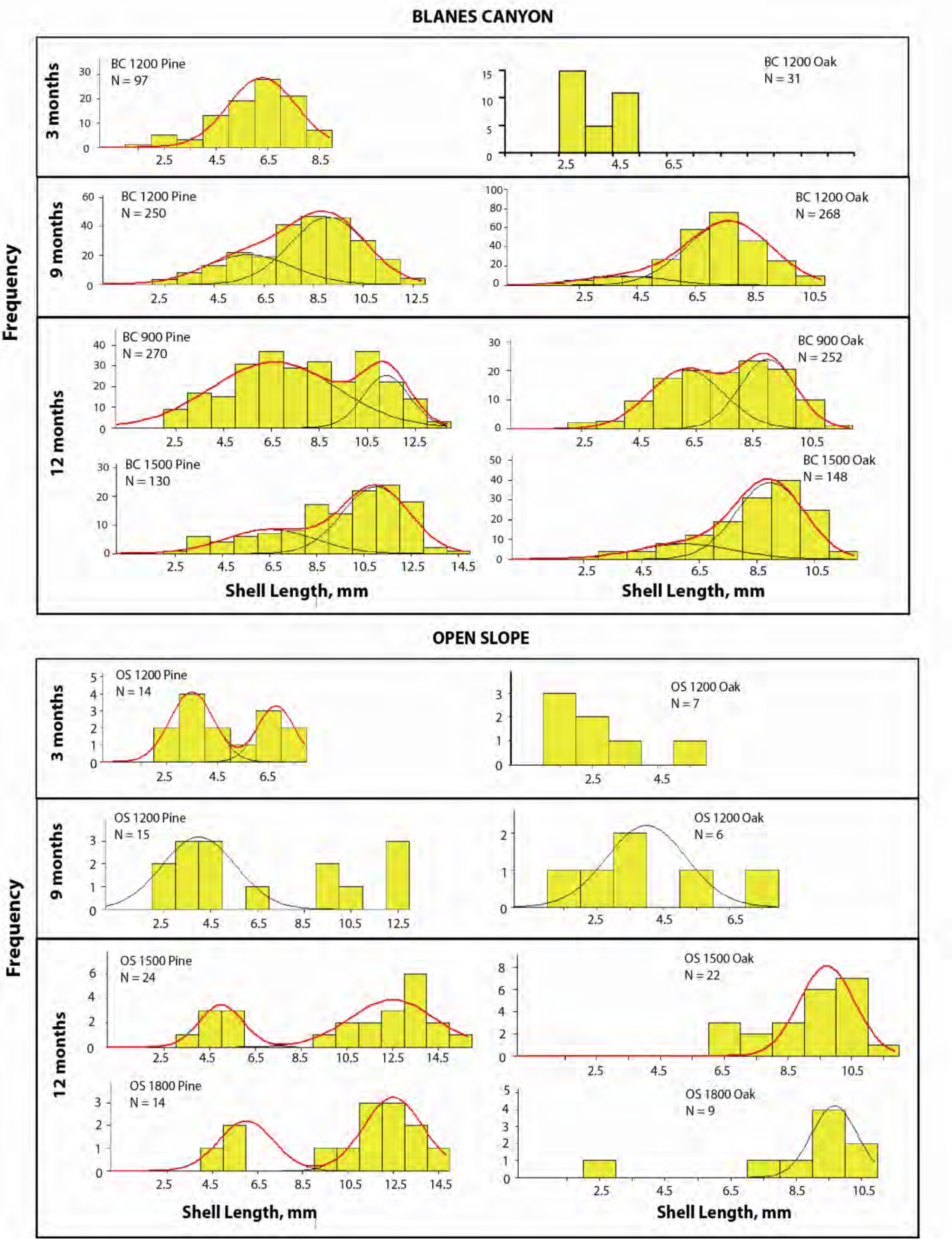


Figure 7

Length-frequency distributions showing the shell lengths of all specimens of *Xylophaga* sp. A obtained from the Blanes Canyon and the adjacent open slope in each oak and pine trap deployed for 3, 9, and 12 months . Normal curves represent each detected cohort. The sample name, including its depth, and number of individuals are indicated at top of each histogram.

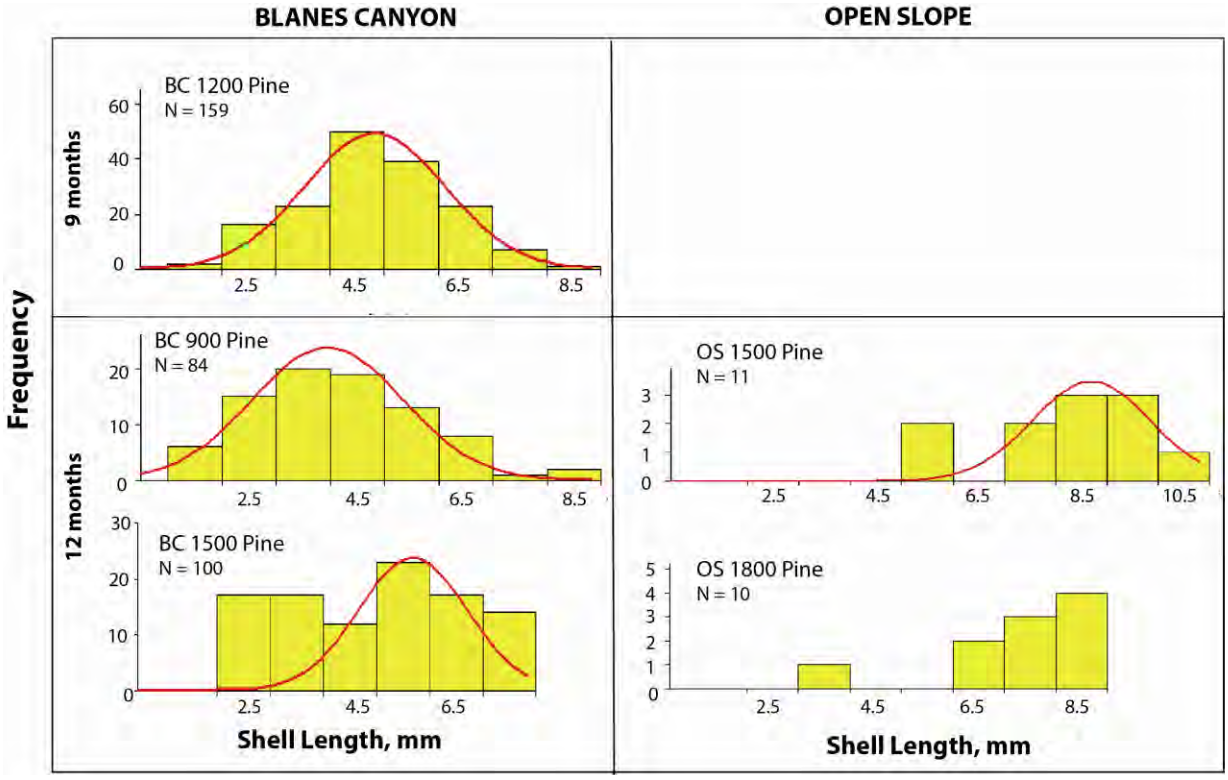


Figure 8

Length-frequency distribution of all specimens of *Xylophaga* sp. B obtained in the Blanes Canyon and the adjacent open slope in pine cubes deployed for 9 and 12 months. Normal curves represent each detected cohort. The sample name, including depth, and size are indicated at top of each histogram.

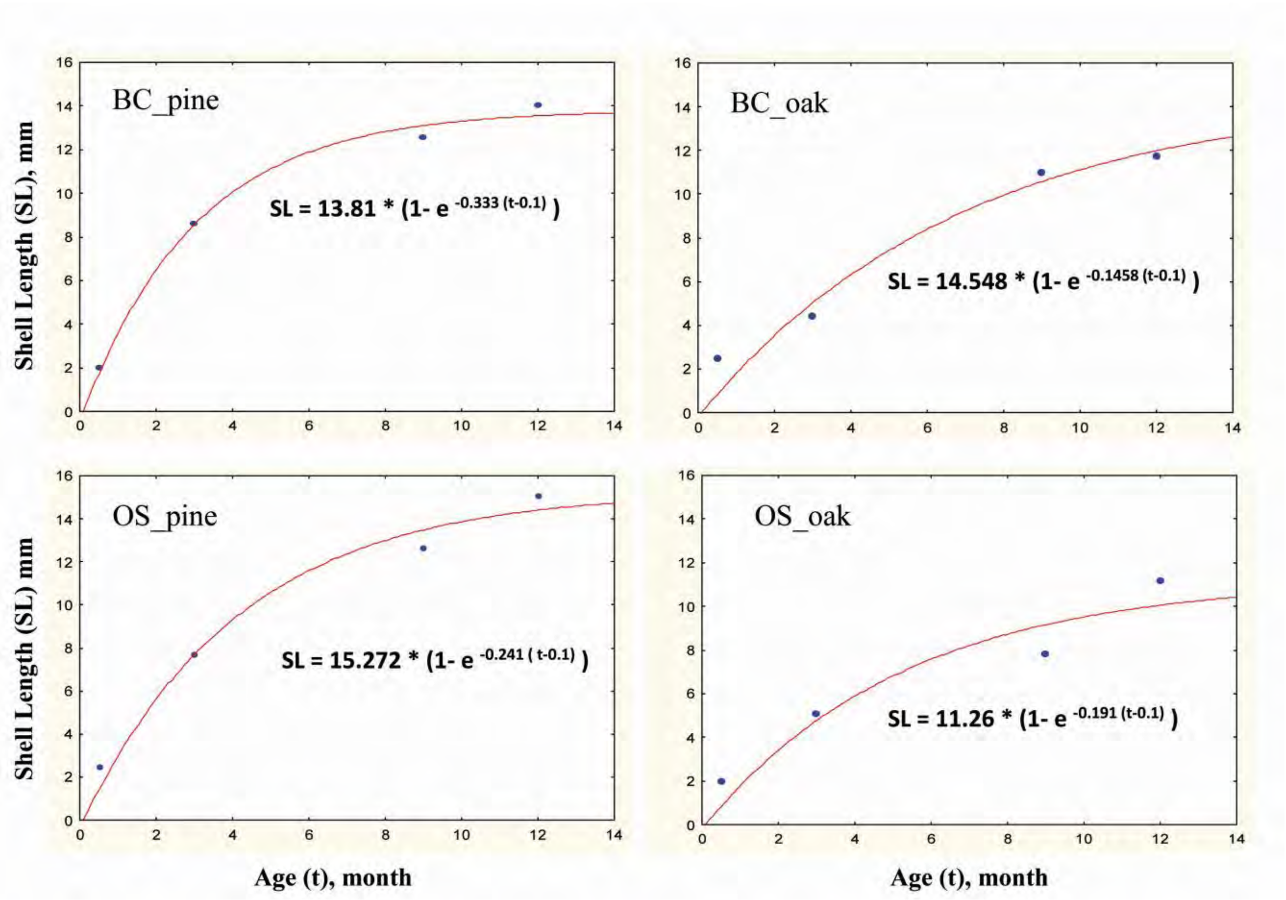


Figure 9

Growth rates of *Xylophaga* sp. A for each location (BC= Blanes Canyon, OS= Open Slope) and wood type. A von Bertalanffy growth function is fitted in each graph. The location and wood type are indicated at top of each graph.