

1 **Submarine canyons as the preferred habitat for wood-boring species of**
2 ***Xylophaga* (Mollusca, Bivalvia)**
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30 *an essential habitat"*
31

32 **Abstract**

33 Submarine canyons are often viewed as natural “debris concentrators” on seafloor.
34 Organic substrates may be more abundant inside than outside canyon walls. To
35 determine the effects of the presence these substrates in the Blanes submarine canyon
36 (NW Mediterranean) and its adjacent western open slope, we deployed wood to study
37 colonizing organisms. Three replicate pine and oak cubes (i.e. most common trees
38 inland) were moored at 900, 1200, 1500 and 1800 m depth and collected after 3, 9 and
39 12 months. Wood from inside the canyon was significantly more heavily colonized by
40 the five morphotypes of wood-boring bivalves than was wood on the adjacent open
41 slope. *Xylophaga* sp. A dominated all wood types and locations, with peak abundance at
42 900 and 1200 m depth. Its growth rate was highest (0.070 mm d^{-1}) during the first three
43 months and was faster (or recruits earlier) in pine than in oak. Size distribution showed
44 that several recruitment events may have occurred from summer to winter. *Xylophaga*
45 sp. B, appeared first after 9 months and clearly preferred pine over oak. As the
46 immersion time was the same, this strongly supported a specific association between
47 recruiters and type of substrate. Three morphotypes, pooled as *Xylophaga* spp. C, were
48 rare and seemed to colonize preferentially oak inside the canyon and pine in the
49 adjacent open slope. Individuals of *Xylophaga* were more abundant inside the canyon
50 than in nearby off-canyon locations. Blanes Canyon may serve as a long-term
51 concentrator of land-derived vegetal fragments and as a consequence sustain more
52 animals.

53

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

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59 **Introduction**

60 Life in the deep sea generally depends on the constant rain of particles produced in the
61 photic zone and/or exported from the continental shelf (Gage et al., 1991).
62 Allochthonous organic matter might sustain deep-sea oligotrophic systems and create
63 patchy distributions of organic substrata and benthos (Gooday and Turley, 1990). Shelf-
64 basin exchanges are particularly enhanced by the presence of submarine canyons,
65 especially where they are preferential conduits driving materials down-margin (Martín
66 et al., 2006; De Stigter et al., 2007). Matter transport from shelf waters to the abyssal
67 plains may be strongly enhanced during the "dense shelf water cascading" events,
68 which carry huge amounts of organic and inorganic substances that scour the shelf and
69 slope seafloor and sink to the deep basin through the main NW Mediterranean
70 submarine canyons (Canals et al., 2010). Research on sedimentological and
71 hydrological processes in submarine canyons is increasing significantly (Durrieu de
72 Madron et al., 2008; Zúñiga et al., 2009; De Stigter et al., 2011; Lastras et al., 2011),
73 but our understanding of faunal patterns and processes in these environments remains
74 marginal. Previous studies showed that the abundance and biomass of macro- and
75 meiobenthic fauna inside the canyons are enhanced compared with equally deep stations
76 in the slopes (Ingels et al., 2009; Cunha et al., 2011). However, many exceptions are
77 reported due to the high heterogeneity and environment variability inside canyons
78 (McClain and Barry, 2010; Romano et al., this volume).
79 Submarine canyons may concentrate large organic falls, like terrestrial debris, sunken
80 wood and whale falls from a large area. These organic substrates create "islands" on the
81 deep-sea canyon floor, which by supporting high species richness, increase deep-sea
82 diversity (Snelgrove and Smith, 2002; Bernardino et al., 2010; De Leo et al., 2010).
83 Despite its general oligotrophic environment, the deep Mediterranean has local areas
84 such as submarine canyons, cold seep and mud volcanoes (Olu-Le Roy et al., 2004;
85 Vanreusel et al., 2009; Ritt et al., 2011) with high productivity which allows them to
86 function as biodiversity and biomass hotspots, characterized by specific benthic fauna.
87 For instance, organic matter accumulation can dramatically enhance the populations of
88 both opportunistic and sulphophilic species, such as wood-boring bivalves, capitellid
89 and dorvilleid polychaetes, leptostracans, and cumaceans (Turner, 1977; Smith, 1986;
90 Grassle and Morse-Porteous, 1987; Snelgrove et al., 1994; Smith et al., 2002; Smith and
91 Baco, 2003; Gaudron et al., 2010). Canyons may also function as recruitment areas for

92 demersal and benthic faunal species (Stefanescu et al., 1994; Sardà et al., 2009; Cartes
93 et al., 2010), many of which are of commercial interest.

94 Land-derived vegetation such as woody plant material transported to the ocean,
95 especially after heavy precipitation, storms or hurricanes, is not rare on the seafloor at
96 all depths (Wolff, 1979; Pailleret et al., 2007). Wood may be an important source of
97 organic material on the deep-sea floor where it creates unique ecosystems as it
98 undergoes decay, sometimes creating anaerobic conditions with production of hydrogen
99 sulphur and possibly methane (Duperron et al., 2008; Yücel et al., 2013). The
100 functioning of these ecosystems is poorly described worldwide and has rarely been
101 studied in the deep Mediterranean, except for the wood degrading microbial
102 communities, which are the starting point of the community succession (Palacios et al.,
103 2006; Fagervold et al., 2012; Bienhold et al., 2013; Fagervold et al., this issue).

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

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

114 Nevertheless, the Xylophagainae play a key role in the succession of degrading wood
115 falls. Their bacterial endosymbionts allow them to convert the refractory cellulose from
116 wood and other plant remains to a form available to other deep-sea organisms (Turner,
117 1973; Waterbury et al., 1983; Distel & Roberts, 1997, Distel et al., 2002). Also, the
118 "burrows" of some species are filled with partially digested wood that harbor unique
119 microbial communities (Besette et al., in press) and the large quantities of organic-rich
120 faecal matter produced (Turner, 2002) may attract some detritivorous invertebrates,
121 which may grow at a fairly rapid rate (Gaudron et al., 2010).

122 Despite our knowledge on the Mediterranean species is better than that in any other
123 ocean, much remains to be understood, especially about the biodiversity of deep-sea
124 ecosystems and their vulnerability to anthropogenic pressure (Coll et al., 2010;
125 Danovaro et al., 2010; Ramirez-Llodra et al., 2010). Furthermore, the taxonomy,

126 biology and ecology of benthic deep-sea macrofauna, and their connection to the land or
127 shallower environments, remain poorly known, including that on xylophagain bivalves
128 inhabiting NW Mediterranean canyon systems.

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

133 We sought to specifically assess the following questions:

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

139

140 **Material and methods**

141 Description of the area, deployments and sampling

142 Blanes Canyon (BC) is located at the Catalan continental margin and constitutes one of
143 the most important cross-slope structures in the NW Mediterranean shelf (Fig. 1). BC
144 cuts the continental shelf in a N-S direction. Its head is 60 m deep and is located at 4 km
145 from the coast, near the Tordera River mouth. The river has a typically Mediterranean
146 torrential regime. The mean water discharge is of $7.2 \text{ m}^3 \text{ s}^{-1}$, with maximum peaks
147 higher than $1800 \text{ m}^3 \cdot \text{s}^{-1}$ and suspended sediment concentrations ranging from 10 to 300
148 $\text{mg} \cdot \text{l}^{-1}$ (Austen et al., 2002).

149 Six mooring lines were deployed along two transects (three along BC axes and three
150 along the western open continental slope), at different depths (BC 900, 1200 and 1500
151 m; open slope 1200, 1500 and 1800 m) (moorings are fully described in López-
152 Fernández et al., this issue). Each mooring line was equipped with an experimental trap
153 suspended 20 m above the seafloor containing three replicate cubes (8 cm long) of pine
154 and oak (the most common trees on adjacent inland watersheds). At 1200 m deep inside
155 BC, an additional experimental trap containing two pine and two oak cubes was
156 deployed directly on the sea floor (BC1200_bottom). Deployment periods were 3, 9 and
157 12 months (Table 1). The traps were recovered with the mooring lines by an acoustic

158 release that dropped the anchor weight, allowing the traps to be carried to the surface by
159 floating buoys. During ascent, epifauna on the wood may have been lost.

160 A total of fifty cubes were recovered. Immediately after collection, two cubes from
161 1200 and 1500 m depth were preserved in 96 % ethanol; all others were fixed in 4%
162 buffered formaldehyde-seawater solution.

163

164 Laboratory analysis

165 **Density.** In the laboratory, all wood cubes were photographed and carefully dissected
166 by hand; all wood-boring bivalves were stored in 70% ethanol for taxonomic
167 identification. To ensure that recently settled individuals were included, extraction was
168 performed with the aid of a magnifier (2x) or a dissecting microscope. All specimens of
169 wood-boring bivalves were sorted by morphotype and counted. Identification was
170 carried out with reference to relevant literature (e.g. Turner, 2000, Voight, 2007, Voight
171 2008). Density was expressed as number of individuals per dm^{-3} .

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

174 **Biomass estimates.** Dry (DW in g) and ash free dry weights (AFDW in g) were
175 estimated for a series of specimens that included the greatest range of SL possible. For
176 these sub-samples, specimens were dried to a constant weight at 105°C for about 48 h
177 (DW) and then burned at 500°C for 4 h to obtain total AFDW to the nearest 0.1 mg. The
178 relationships of SL with DW and AFDW were calculated for each species by using
179 exponential curves $\text{DW} = a \cdot \text{SL}^b$ and $\text{AFDW} = a_1 \cdot \text{SL}^{b_1}$; where a (intercept) and b
180 (slope) are allometric coefficients corresponding respectively to the initial growth
181 coefficient and the relative growth rate of the variable (Gould, 1966; LaBarbera, 1989).
182 Data were then transformed to natural logarithms and fitted to the allometric regression
183 model ($\log \text{DW} = \log a + b \log \text{SL}$). The estimated regressions were used to calculate
184 AFDW of all specimens and total biomass in the samples.

185 **Size frequency distribution.** SL frequency distributions in 1-mm size class intervals
186 were developed from pooled replicate cubes for each wood type, depth and time.
187 Cohorts were identified from each size-frequency distribution using Bhattacharya's
188 method and the specific routine in FISAT II package (FAO 2002). The separation index
189 (SI) was used to measure the goodness of the modal separation: $\text{SI} = (\text{SL}_{i+1} - \text{SL}_i) /$
190 $((\text{std}_{i+1} + \text{std}_i)/2)$, where SL_i is the mean SL of the distribution i , SL_{i+1} is the mean

191 length of distribution $i+1$, and std is standard deviation of the distributions. Values of SI
192 >2 were considered as successfully separated by definition. Overall, mean SL (total
193 mean SL) was calculated for each size-frequency distribution and mean SL , standard
194 deviations and SI were calculated for each of the identified cohorts.

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

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

$$201 \quad L_t = L_\infty [1 - e^{-K(t-t_0)}]$$

202 where L_∞ is the mean asymptotic shell height (maximum length) in mm, K is the Brody
203 growth coefficient, t the age in months, and t_0 the theoretical age at which shell height
204 equals zero. Lacking any firm data, we assumed that the first larvae settled on the wood
205 15 days after its deployment.

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

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

213

214 Data analysis

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

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

224 900 and 1500 m in BC; 1500 and 1800 m in the open slope) and Wood (two levels: pine
225 and oak) as fixed factors. Cochran's test was used prior to the ANOVA to test the
226 assumption of homogeneity of variances (Underwood 1997). The Student-Newman-
227 Keuls test (SNK test) was used to compare the means of the different treatments.
228 PRIMER v6 & PERMANOVA+ software (Clarke and Gorley, 2006, Anderson 2006)
229 was used for multivariate analyses. For these analyses, density data were organized into
230 a matrix of sample vs *Xylophaga* morphotypes. Non-metric multi-dimensional scaling
231 (MDS) ordination was performed using the Bray–Curtis similarity coefficient, after
232 square root transformation of data to show similarities among samples. A
233 PERMANOVA (McArdle and Anderson, 2001) design was created based on two
234 factors: Location (two levels, BC vs Open Slope) and wood type (crossed, two levels,
235 Pine vs Oak). SIMPER analysis (Similarity Percentages–species contributions) was
236 performed to indicate the percentage contributions of each species of *Xylophaga* to the
237 similarity within and dissimilarity between groups of samples.
238 Non-parametric Kolmogorov-Smirnov test (KS-test) was performed to compare shell-
239 length distributions (Sokal and Rohlf, 1995).

240

241 **Results**

242 Abundance of wood-borer bivalves

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

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

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

257 $\pm 56 \text{ ind. dm}^{-3}$ in pine, 187 ± 16 vs $60 \pm 7 \text{ ind. dm}^{-3}$ in oak, t-test, $p < 0.01$) and pine was
258 more heavily colonized than oak (t-test, $p < 0.05$). To the contrary, differences in total
259 abundance between the three- and nine-month deployments were not significant on the
260 adjacent slope (9.1 ± 4.5 vs $9.8 \pm 3.9 \text{ ind. dm}^{-3}$ in pine, 4.6 ± 2 vs $3.9 \pm 1 \text{ ind. dm}^{-3}$ in
261 oak). The burrows of the largest specimens extended across the whole 8 cm cube (Fig.
262 4). The exterior of wood in the most densely colonized BC samples appeared solid, but
263 its interior was more or less hollow and it crumbled on handling. All *Xylophaga*
264 burrows were filled by soft, compacted faecal matter that formed a chimney lining the
265 bored tunnels (Fig. 4C).

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

272 The twelve-month pine cubes from 900 m depth in BC (BC900_pine) were so
273 extensively bored that they partly crumbled and some large specimens of *Xylophaga*
274 likely were lost (Fig 2). Furthermore, *Xylophaga* sp. A was significantly more abundant
275 in shallower than in the deeper twelve-month cubes, both in BC and the adjacent open
276 slope (900 and 1500 m depth, respectively) regardless of wood type (ANOVA, Table
277 2). *Xylophaga* sp. B was significantly more abundant in pine than in oak, both in BC
278 and on the adjacent open slope (ANOVA, $p < 0.01$, Table 2). It occurred in oak only
279 from inside BC at 1500 m depth (2 specimens) and in one cube deployed on seafloor at
280 1200 m.

281 Considering all cubes, *Xylophaga* sp. A was significantly more abundant at the shallow
282 deployments of 900 and 1200 m depth than the deeper ones at 1500 and 1800 m. The
283 morphotypes grouped as *Xylophaga* spp. C were rare, appearing first after nine months
284 at 1200 m depth in oak inside BC and in pine in the adjacent slope (3.9 ± 3.3 and $0.7 \pm$
285 1.1 ind. dm^{-3} , respectively).

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

291 0.020 to 3.917 g AFDW dm⁻³ in these two deployments, respectively. In the twelve-
292 month old cubes, pooled biomass ranged from 0.116 to 3.947 g AFDW dm⁻³ in oak in
293 the adjacent open slope at 1800m deep (OS_1800_oak) and in pine in BC at 900 m deep
294 (BC_900_pine), respectively.

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

301

302 Other fauna

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

309

310 Length-Weight relationships

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

315

316 Demography and Growth

317 Individuals of *Xylophaga* sp. A presented a large size-range (1.8-15.1 mm SL, Fig. 7,
318 Table 5). In BC, the size-frequency distributions significantly differed among locations,
319 recovery times and wood type (KS-test, p< 0.05,). Many samples presented bimodal
320 distributions, suggestive of distinct age groups (Table 5 and Fig. 7). The mean SL of
321 *Xylophaga* sp. A in three-month pine cubes (6.1 ± 1.5 mm in BC1200_Pine_3M) was
322 significantly lower (t-test, p <0.05) than that in nine-month cubes (7.96 ± 1.9 mm in
323 BC1200_Pine_9M). Although when the animals recruited cannot be exactly determined,

324 the large animals (e.g. up to 8-10 mm in pine) in the three-month cubes are suggested to
325 have recruited soon after deployment. In the twelve-month cubes, the overall mean SL
326 slightly decreased at 900 m depth (due to the presence of a second, smaller cohort) and
327 slightly increased in the 1200 m depth cubes. In BC oak cubes, mean SL markedly
328 increased between the three and nine month cubes; between the nine- and twelve-month
329 cubes, a second smaller cohort limited the size of the increase in overall mean SL.
330 In the open slope, the size-frequency distributions in pine and oak, although slightly
331 increased, did not significantly differ between three- and nine-month cubes (KS-test, p
332 > 0.05). Conversely, SL was significantly higher in the twelve-month cubes both for
333 pine and oak (KS-test, $p < 0.05$).

334 The modes of each of the two cohorts in the BC twelve-month cubes were 6.5 and 11
335 mm, and 6 and 9 mm in pine and oak, respectively. Based on cohort analysis, the
336 average growth rates in BC pine cubes were estimated as $2.09 \text{ mm} \cdot \text{month}^{-1}$ (0 to 3
337 months), $0.47 \text{ mm} \cdot \text{month}^{-1}$ (3 to 9), and $0.64\text{-}0.73 \text{ mm} \cdot \text{month}^{-1}$ (9 to 12). In oak cubes,
338 the estimated average growth rates were $1.63 \text{ mm} \cdot \text{month}^{-1}$ (0 to 3 months), 0.47
339 $\text{mm} \cdot \text{month}^{-1}$ (3 to 9), and $0.43 \text{ mm} \cdot \text{month}^{-1}$ from (9 to 12). In the open slope, the
340 number of specimens was too low to estimate the average growth rates.

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

346 Specimens of *Xylophaga* sp. B ranged from 1.6 mm to 9.3 mm in SL and the size-
347 distributions were unimodal (Fig 9). In BC, overall mean SL did not differ significantly
348 between nine- and twelve-month cubes, despite being slightly higher (5.2 ± 1.0 mm) in
349 the 12-month BC 1500 cohort than in the other cohorts (4.3 ± 1.3 and 3.45 ± 1.4 in BC
350 1200_9M and BC_900_12M, respectively). Mean SL in the 12-month cubes in the open
351 slope (7.27 mm) was higher than in BC.

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

355

356 **Discussion**

357 Mediterranean wood-boring bivalves

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

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

383 Despite having our experimental cubes suspended 20 m above the sediment, they were
384 heavily colonized by the wood-boring bivalves, and the variety of morphotypes was
385 higher than in bottom samples. This result refutes previous postulates that xylophagains
386 recruit at the sediment surface and do not occur in floating wood (Turner, 2002) and
387 supports their long-distance dispersal capacity. Anyway, colonization was faster and
388 recruitment was higher on sessile cubes, which were either completely consumed after
389 nine months (pine) or more consumed than the corresponding suspended ones (oak).
390 However, when recovered, the abundance of live *Xylophaga* was lower, and their mean

391 size was significantly smaller in sessile than in suspended cubes. These differences may
392 be due to factors other than intra-specific competition. For instance, predation may be
393 higher on the sediment, as confirmed by the higher colonization of Gammaridea,
394 Leptostraca and Polychaeta compared to suspended samples (Table 3). Mobile macro-
395 and megabenthic organisms present in BC, such as decapod crustaceans (e.g. *Aristeus*
396 *antennatus*, *Geryon longipes*) or echinoderms (e.g. *Ceramaster grenadensis*, *Molpadia*
397 *musculus*, *Bathypolypus sponsalis*) (Tecchio et al., this issue) may also potentially
398 predate on the wood fauna when directly deployed on the bottom, especially when the
399 substrate is highly consumed.

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

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

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

424 their largest sizes (14-16 mm in SL); the mean SL of *Xylophaga* sp. B on the slope was
425 also higher than in BC.

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

434 Demography and growth

435 If individuals smaller than 2 mm SL indicate recent settlement, our results suggest two
436 distinct autumnal and winter settling events. However, the bimodal distributions in the
437 nine-month and twelve-month cubes suggest that recruitment events occurred several
438 times a year. In the nine-month BC pine cubes, the two cohorts measured 5.89 ± 1.7 and
439 9.09 ± 1.5 mm mean SL, respectively. Based on our estimated growth rates (Fig. 9), we
440 calculate that settling took place two to three months before recovery (i.e. August-
441 September). The largest cohort (11 mm in mean SL) in the twelve-month cubes may
442 indicate an even earlier settlement, likely during summer. Settlement in late summer
443 may be consistent with spring runoff and later transport offshore and sinking of wood
444 onto the deep-sea floor and thus the arrival (or availability) of food/substrate potentially
445 acting as a cue to attract new recruitments. More wild wood was found during
446 experimental trawling in spring in the whole BC area (including the open slope) than in
447 autumn (1.02 vs 0.13 kg km⁻² respectively). Our results suggest that *Xylophaga* sp. A
448 has a "pulsing" recruitment strategy (*sensu* Todd, 1998) with planktonic larvae released
449 several times during the year. Previous studies at shallower sites reported continuous
450 recruitment for *Xylophaga atlantica* (Romey et al., 1994), *X. washingtonia* (Haderlie,
451 1983), and *X. depalmai* (Tyler et al., 2007). Conversely, the absence of planktonic
452 larvae of *Xylophaga* in June and the presence of newly settled specimens in September
453 suggested a cyclic reproduction with a potential seasonal settlement in August (Turner
454 1973), but also in late fall or winter for *X. dorsalis* in Scotland (Turner and Johnson,
455 1971) as well as for *X. atlantica* in the USA eastern continental shelf (max depth 234
456 m), with gonad ripening correlated to water temperatures higher than 10 °C (Berg et al.,

457 1987). Spawning in the deep Mediterranean is unlikely to be affected by temperature,
458 which at all our stations ranged only from 13.0 to 13.3 °C (Tecchio et al. this issue).
459 Anyway, very little information is available about the reproductive biology of these
460 deep-water organisms, particularly in the Mediterranean Sea.

461 Our experimental design (which included different deployment durations) forced us to
462 assume that growth did not change with depth or time of the year before estimating
463 growth rates. Despite this over-simplification, our unique data provide a reasonable
464 approach to be tested by further studies. Taking this into account, our data suggest that
465 average growth rate of *Xylophaga* sp. A was higher (0.070 mm d⁻¹) during the first
466 three-four months after colonization of wood cubes, followed by slower rate (0.021-
467 0.016 mm d⁻¹) over the next eight months (Fig. 10). Also, the growth rates were higher
468 in pine than in oak (Fig. 9) or, alternatively, recruitment occurred earlier. The only
469 comparable data reported: 1) early growth rates of 0.015 mm d⁻¹ for *X. atlantica*, higher
470 in oak than in pine, as were maximum sizes, but four months later the situation reversed
471 and growth rates increased up to 0.133 mm d⁻¹ in pine (Romey et al., 1994), and 2)
472 mean growth rates of 0.03 mm d⁻¹ for *X. depalmai* after three and six months (in line
473 with ours), which did not differ between spruce and oak (Tyler et al., 2007). Such a
474 rapid growth is rare in the deep sea (Gage and Tyler, 1991), leading qualify these
475 organisms as opportunists (Turner, 1973).

476 Length-weight allometric relationships provide information on the physiological and
477 trophic conditions in bivalves through the variations of “b” (the equilibrium constant),
478 which represents the growth in weight with respect to that in length (Ramesha et al.,
479 2009). In many bivalves (e.g. mussels, oysters and clams) deviation in b revealed to be
480 correlated with physiological and environmental conditions, for instance it is density-
481 dependent (Seed, 1968; Chinzei et al., 1982; Cigarría and Fernández, 1998; Alunno-
482 Bruscia et al., 2001), while in hydrothermal vent mytilids, allometric relationships were
483 affected by the presence of symbiotic polynoid polychaetes that live inside the bivalve
484 (Britayev et al., 2007). Values of “b” range between 2.4 and 4.5 in most bivalves
485 (Wilbur and Owen, 1964), but no previous information was available for *Xylophaga*
486 species. Both *Xylophaga* sp. A and B showed b coefficients between 2.7 and 2.9, which
487 indicate biometrical relationships similar to those in other bivalves and close to the
488 allometric threshold (b=3, (LaBarbera, 1989). An exception was *Teredo pedicellata*, a
489 shallow water wood-boring bivalve, which showed a nearly linear relationship (b = 1)
490 (Isham et al. 1951). Regardless, it would be interesting to compare the BC and adjacent

491 open slope populations, but the low density of *Xylophaga* in the later prevented us to
492 estimate the corresponding allometric relationships.

493

494 Driving factors affecting allochthonous wood inputs into deep sea?

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

502 The NW margin is the most densely incised part of the entire Mediterranean basin;
503 active transport of continental vegetation to the deep-sea floor may occur frequently on
504 the narrow continental shelf off the Catalan coast. The urban development of Catalonia
505 from the 1950s to the 1980s dramatically affected river discharges (Sala and Inbar
506 1992). The subsequent modification of the watershed of Catalan rivers lead to increased
507 total runoff and peak flows that shortened the lag time in the rainfall draining from the
508 land (Liquete et al, 2009; Sala and Farguell, 2002).

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

519 Our experiments are the first to examine wood-fall associated fauna in Mediterranean
520 canyons to enhance our understanding of both the deep-sea Mediterranean biodiversity
521 and how allochthonous materials may enhance local biota. Our results confirm that BC
522 presents a heightened abundance and biomass of wood-boring bivalves, thus acting as a
523 highly localized biomass hot spot, with a large potential to store and process carbon

524 from allochthonous vegetational debris. Consequently, this essential habitat, and the
525 species it harbors (such as deep-sea wood-boring organisms), may be particularly
526 sensitive to global climate change impacts, pointing on the relevance of developing
527 adequate sustainable management and conservation strategies.
528 Knowledge on the distribution and life history of deep-sea macrofauna, given its
529 importance in the diet of many valuable bathyal species (e.g. macrurids, the red shrimp
530 *Aristeus antennatus*), may be relevant for the conservation of deep-sea resources
531 (Cartes, 1994; Madurell and Cartes, 2006; Cartes et al., 2010). More specifically,
532 further studies are needed to assess the connectivity among and within canyons, and to
533 evaluate the role of sunken wood in deep-sea biodiversity as stepping stones to other
534 fragmented ecosystems like hydrothermal vents (Distel et al. 2000).
535 Our results confirm that the studied *Xylophaga* species behave as opportunists, showing
536 long-distance dispersal capacity, high settlement rate, and fast growth. In summary,
537 these taxa are equipped with an efficient capability to exploit and persist in the
538 ephemeral and fragmented habitats represented by wood falls. They are keystone
539 species in wood falls habitats that are critical to facilitate the establishment of other
540 benthic species and, thus, to maintain or even enhance the overall biodiversity of deep-
541 sea ecosystems.

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- 559 Alunno-Bruscia, M., Edwin Bourget, Fréchette, M., 2001. Shell allometry and length-
560 mass-density relationship for *Mytilus edulis* in an experimental food-regulated
561 situation. *Mar Ecol Prog Ser*.
- 562 Arellano, S.M., Young, C.M., 2009. Spawning, development, and the duration of larval
563 life in a deep-sea cold-seep mussel. *Biological Bulletin*, 216, 149-162.
- 564 Austen, M.C., Lambshead, P.J.D., Hutchings, P.A., Boucher, G., Snelgrove, P.V.R.,
565 Heip, C., King, G., Koike, I., Smith, C., 2002. Biodiversity links above and below
566 the marine sediment–water interface that may influence community stability.
567 *Biodiversity and Conservation*, 11, 113-136.
- 568 Berg, C.J., Bradford, B., Early, J., Turner, E.J., 1987. Seasonal Recruitment of Marine
569 Invertebrates to Hard Substrates on Georges Bank and the Eastern Continental Shelf
570 of the United States. *Nautilus*, 101, 19-24.
- 571 Bessette S., Fagervold S., Romano C., Martin D., Le Bris N., Galand P. E.. in press.
572 Diversity of bacterial communities on sunken woods in the Mediterranean Sea.
573 *Journal Marine Science and Technology*.
- 574 Bienhold, C., Pop Ristova, P., Wenzhöfer, F., Dittmar, T., Boetius, A., 2013. How
575 Deep-Sea Wood Falls Sustain Chemosynthetic Life. *PLoS ONE*, 8.
- 576 Canals, M., Danovaro, R., Heussner, S., Lykousis, V., Puig, P., Trincardi, F., Calafat,
577 A.M., de Madron, X.D., Palanques, A., Sánchez-Vidal, A., 2010. Cascades in
578 mediterranean submarine grand canyons. *Oceanography*, 22, 26-43.
- 579 Chinzei, K., Savazzi, E., Seilacher, A., 1982. Adaptational strategies of bivalves living
580 as infaunal secondary soft bottom dwellers. *Neues Jahrbuch fuer Geologie und*
581 *Palaeontologie Abhandlungen*, 164, 229-244.
- 582 Cigarría, J., Fernández, J., 1998. Manila clam (*Ruditapes philippinarum*) culture in
583 oyster bags: Influence of density on survival, growth and biometric relationships.
584 *Journal of the Marine Biological Association of the United Kingdom*, 78, 551-560.
- 585 Coll, M., Piroddi, C., Steenbeek, J., Kaschner, K., Ben Rais Lasram, F., Aguzzi, J.,
586 Ballesteros, E., Bianchi, C.N., Corbera, J., Dailianis, T., Danovaro, R., Estrada, M.,
587 Frogli, C., Galil, B.S., Gasol, J.M., Gertwagen, R., Gil, J., Guilhaumon, F., Kesner-
588 Reyes, K., Kitsos, M.-S., Koukouras, A., Lampadariou, N., Laxamana, E., López-Fé
589 de la Cuadra, C.M., Lotze, H.K., Martin, D., Mouillot, D., Oro, D., Raicevich, S.,
590 Rius-Barile, J., Saiz-Salinas, J.I., San Vicente, C., Somot, S., Templado, J., Turón,
591 X., Vafidis, D., Villanueva, R., Voultsiadou, E., 2010. The biodiversity of the
592 Mediterranean Sea: Estimates, patterns and trends *PLoS ONE*, 5, e11842.
- 593 Company, J.B., Puig, P., Sardà, F., Palanques, A., Latasa, M., Scharek, R., 2008.
594 Climate Influence on Deep Sea Populations. *PLoS ONE*, 3, e1431.
- 595 Cunha, M.R., Paterson, G.L.J., Amaro, T., Blackbird, S., de Stigter, H.C., Ferreira, C.,
596 Glover, A., Hilário, A., Kiriakoulakis, K., Neal, L., Ravara, A., Rodrigues, C.F.,
597 Tiago, A., Billett, D.S.M., 2011. Biodiversity of macrofaunal assemblages from
598 three Portuguese submarine canyons (NE Atlantic). *Deep-Sea Research Part II:*
599 *Topical Studies in Oceanography*, 58, 2433–2447.
- 600 Danovaro, R., Company, J.B., Corinaldesi, C., D'Onghia, G., Galil, B., Gambi, C.,
601 Gooday, A.J., Lampadariou, N., Luna, G.M., Morigi, C., Olu, K., Polymenakou, P.,
602 Ramirez-Llodra, E., Sabbatini, A., Sardà, F., Sibuet, M., Tselepides, A., 2010.
603 Deep-sea biodiversity in the Mediterranean Sea: The known, the unknown, and the
604 unknowable. *PLoS ONE*, 5, 1-25.

605 De Leo, F.C., Smith, C.R., Rowden, A.A., Bowden, D.A., Clark, M.R., 2010.
606 Submarine canyons: Hotspots of benthic biomass and productivity in the deep sea.
607 Proceedings of the Royal Society B: Biological Sciences, 277, 2783-2792.

608 De Stigter, H.C., Jesus, C.C., Boer, W., Richter, T.O., Costa, A., van Weering, T.C.E.,
609 2011. Recent sediment transport and deposition in the Lisbon–Setúbal and Cascais
610 submarine canyons, Portuguese continental margin. Deep Sea Research Part II:
611 Topical Studies in Oceanography, 58, 2321-2344.

612 Durrieu de Madron, X., Wiberg, P.L., Puig, P., 2008. Sediment dynamics in the Gulf of
613 Lions: The impact of extreme events. Continental Shelf Research, 28, 1867-1876.

614 Fagervold, S.K., P. E. Galand, M. Zbinden, F. Gaill, P. Lebaron, Palacios, C., 2012.
615 Sunken woods on the ocean floor provide diverse specialized habitats for microbes.
616 Fems Microbiology Ecology.

617 Fagervold S. K., Bessette S., Romano C., Martin D., Plyuscheva M., LeBris N and
618 Galand P. E. accepted. Microbial communities associated with the degradation of
619 oak wood in the Blanes submarine canyon and its adjacent open slope (NW
620 Mediterranean). Progress in Oceanography. this issue.

621 Gaudron, S.M., Demoyencourt, E., Duperron, S., 2012. Reproductive traits of the cold-
622 seep symbiotic mussel *Idas modiolaeformis*: Gametogenesis and larval biology.
623 Biological Bulletin, 222, 6-16.

624 Gaudron, S.M., Pradillon, F., Pailleret, M., Duperron, S., Le Bris, N., Gaill, F., 2010.
625 Colonization of organic substrates deployed in deep-sea reducing habitats by
626 symbiotic species and associated fauna. Marine Environmental Research, 70, 1-12.

627 Gooday, A.J., Turley, C.M., 1990. Responses by benthic organisms to inputs of organic
628 material to the ocean floor: a review. Philosophical Transactions of the Royal
629 Society of London A Mathematical and Physical Sciences, 331, 119-138.

630 Gould, S.J., 1966. Allometry and size in ontogeny and phylogeny. Biological Reviews,
631 41, 587-640.

632 Haderlie, E.C., 1983. Depth Distribution and settlement times of the Molluscan wood
633 borers *Bankia setacea* (Tryon, 1863) and *Xylophaga washingtona* Bartsch, 1921 in
634 Monterey Bay. The Veliger, 25, 339-343.

635 Haga, T., Kase, T., 2013. Progenetic dwarf males in the deep-sea wood-boring genus
636 *Xylophaga* (Bivalvia: Pholadoidea). Journal of Molluscan Studies, 79, 90-94.

637 Ingels, J., Kiriakoulakis, K., Wolff, G.A., Vanreusel, A., 2009. Nematode diversity and
638 its relation to the quantity and quality of sedimentary organic matter in the deep
639 Nazaré Canyon, Western Iberian Margin. Deep-Sea Research Part I: Oceanographic
640 Research Papers, 56, 1521-1539.

641 Koho, K.A., Garcia, R., de Stigter, H.C., Epping, E., Koning, E., Kouwenhoven, T.J.,
642 van der Zwaan, G.J., 2008. Sedimentary labile organic carbon and pore water redox
643 control on species distribution of benthic foraminifera: a case study from Lisbon-
644 Setubal Canyon (southern Portugal). Progress In Oceanography, 79, 55-82.

645 LaBarbera, M., 1989. Analyzing body size as a factor in ecology and evolution. Annual
646 Review of Ecology and Systematics, 20, 97-117.

647 Lastras, G., Canals, M., Amblas, D., Lavoie, C., Church, I., De Mol, B., Duran, R.,
648 Calafat, A.M., Hughes-Clarke, J.E., Smith, C.J., Heussner, S., 2011. Understanding
649 sediment dynamics of two large submarine valleys from seafloor data: Blanes and
650 La Fonera canyons, northwestern Mediterranean Sea. Marine Geology, 280, 20-39.

651 Mateo, M Á; Garcia-Rubies, A; Alcoverro, T; Ballesteros, E; Becerro, M; Bonaviri, C;
652 Cebrian, E; Coma, R; Company, J B; De Caralt, S; Diaz, D; Dimitriadis, C; Farina,
653 S; Garcia, M; Garrabou, J; Gera, A; Gordoia, A; Hereu, B; Uriz, M J; Jiménez, J A;
654 Jordana, E; Lázaro, P; Linares, C; Lorente, Á; Losada, I; Macpherson, E; M, M;
655 Martin, D; Méndez, F; Navarro, L; Pagès, J; Pérez, M; Pinedo, S; Ribes, M; Roca,

656 G; Romano, C; Romero, J; Tomás, A; Satta, M P; Segura, M; Serrano, E; Teixidó,
657 N; Torras, X; Villamor, A; Weitzman, B; Zabala, M 2012. Assessment of the
658 ecological impact of the extreme storm of Sant Esteve's Day (26 December 2008)
659 on the littoral ecosystems of the north Mediterranean Spanish coasts. Final Report
660 (PIEC 200430E599). Centro de Estudios Avanzados de Blanes, Consejo Superior
661 de Investigaciones Científicas, Blanes.
662 http://www2.ceab.csic.es/GAME/Sant_Esteve_Storm/HOME.html

663 McArdle, B.H., Anderson, M.J., 2001. Fitting multivariate models to community data:
664 A comment on distance-based redundancy analysis. *Ecology* (Washington D C), 82,
665 290-297.

666 McClain, C.R., Barry, J.P., 2010. Habitat heterogeneity, disturbance, and productivity
667 work in concert to regulate biodiversity in deep submarine canyons. *Ecology*, 91,
668 964-976.

669 Olu-Le Roy, K., Sibuet, M., Fiala-Médioni, A., Gofas, S., Salas, C., Mariotti, A.,
670 Foucher, J.-P., Woodside, J., 2004. Cold seep communities in the deep eastern
671 Mediterranean Sea: composition, symbiosis and spatial distribution on mud
672 volcanoes. *Deep Sea Research Part I: Oceanographic Research Papers*, 51, 1915-
673 1936.

674 Palacios, C., Zbinden, M., Baco, A.R., Treude, T., Smith, C.R., Gaill, F., Lebaron, P.,
675 Boetius, A., 2006. Microbial ecology of deep-sea sunken wood: Quantitative
676 measurements of bacterial biomass and cellulolytic activities. *Cahiers de Biologie
677 Marine*, 47, 415-420.

678 Ramesha, M.M.a., Seetharamaiah, Thippeswamy, 2009. Allometry and condition index
679 in the freshwater bivalve *Parreysia corrugata* (Muller) from river Kempuhole, India.
680 *Asian Fisheries Science*, 203-214.

681 Ramirez-Llodra, E., Brandt, A., Danovaro, R., De Mol, B., Escobar, E., German, C.R.,
682 Levin, L.A., Martinez Arbizu, P., Menot, L., Buhl-Mortensen, P., Narayanaswamy,
683 B.E., Smith, C.R., Tittensor, D.P., Tyler, P.A., Vanreusel, A., Vecchione, M., 2010.
684 Deep, diverse and definitely different: unique attributes of the world's largest
685 ecosystem. *Biogeosciences*, 7, 2851-2899.

686 Ritt, B., Pierre, C., Gauthier, O., Wenzhofer, F., Boetius, A., Sarrazin, J., 2011.
687 Diversity and distribution of cold-seep fauna associated with different geological
688 and environmental settings at mud volcanoes and pockmarks of the Nile Deep-Sea
689 Fan. *Marine Biology*, 158, 1187-1210.

690 Romano C., Coenjaerts J., Flexas M. M., Zúñiga D., Vanreusel A., Company J. B.,
691 Martin D., in press. Spatial and temporal variability of meiobenthic density in the
692 Blanes submarine canyon (NW Mediterranean). *Progress in Oceanography*. This
693 issue.

694 Romey, W.L., Bullock, R.C., DeAlteris, J.T., 1994. Rapid growth of a deep-sea wood-
695 boring bivalve. *Continental Shelf Research*, 14, 1349-1359.

696 Sala, M., Inbar, M., 1992. Some hydrologic effects of urbanization in Catalan rivers
697 *Catena*, 19, 363-378.

698 Sanchez-Vidal, A., Canals, M., Calafat, A.M., Lastras, G., Pedrosa-Pàmies, R.,
699 Menéndez, M., Medina, R., Company, J.B., Hereu, B., Romero, J., Alcoverro, T.,
700 2012. Impacts on the Deep-Sea Ecosystem by a Severe Coastal Storm. *PLoS ONE*,
701 7, e30395.

702 Seed, R., 1968. Factors Influencing Shell Shape in the Mussel *Mytilus Edulis*. *Journal
703 of the Marine Biological Association of the United Kingdom*, 48, 561-584.

704 Sokal, R.R., Rohlf, F.J., 1995. *Biometry: the principles and practice of statistics in
705 biological research*. Third edition.

706 Tecchio S., Ramírez-Llodra, E., Aguzzi, J., Sanchez-Vidal, A., Flexas, M. M., ; Sardà
 707 F., Company, J. B. in press. Seasonal fluctuations of deep megabenthos: finding the
 708 evidences of standing stock accumulation in a flux-rich continental slope. Progress
 709 In Oceanography. this issue
 710 Tudela, S., Sarda, F., Maynou, F., Demestre, M., 2003. Influence of submarine canyons
 711 on the distribution of the deep-water shrimp *Aristeus antennatus* (Risso 1816) in the
 712 NW Mediterranean. *Crustaceana* (Leiden), 76, 217-225.
 713 Tyler, P.A., Young, C.M., Dove, F., 2007. Settlement, growth and reproduction in the
 714 deep-sea wood-boring bivalve mollusc *Xylophaga depalmai*. *Marine Ecology-*
 715 *Progress Series*, 343, 151-159.
 716 Vanreusel, A., Andersen, A.C., Boetius, A., Connelly, D., Cunha, M.R., Decker, C.,
 717 Hilario, A., Kormas, K.A., Maignien, L., Olu, K., Pachiadaki, M., Ritt, B.,
 718 Rodrigues, C., Sarrazin, J., Tyler, P., Van Gaever, S., Vanneste, H., 2009.
 719 Biodiversity of cold seep ecosystems along the European margins. *Oceanography*,
 720 22, 110-127.
 721 Vetter, E.W., Smith, C.R., De Leo, F.C., 2010. Hawaiian hotspots: Enhanced
 722 megafaunal abundance and diversity in submarine canyons on the oceanic islands of
 723 Hawaii. *Marine Ecology*, 31, 183-199.
 724 Voight, J.R., 2007. Experimental deep-sea deployments reveal diverse Northeast Pacific
 725 wood-boring bivalves of *Xylophaginae* (Myoida : Pholadidae). *Journal of*
 726 *Molluscan Studies*, 73, 377-391.
 727 Wolff, T., 1979. Macrofaunal utilization of plant remains in the deep-sea. *Sarsia*, 64,
 728 117-135.
 729 Yücel, M., Galand, P.E., Fagervold, S.K., Contreira-Pereira, L., Bris, N.L., 2013.
 730 Sulfide production and consumption in degrading wood in the marine environment.
 731 *Chemosphere*, 90, 403-409.
 732 Zenetos, A., 1996. Fauna graeciae VII: The Marine Bivalvia (Mollusca) of Greece.
 733 Hellenic Zoological Society and NCMR.
 734 Zúñiga, D., Flexas, M.M., Sanchez-Vidal, A., Coenjaerts, J., Calafat, A., Jordà, G.,
 735 García-Orellana, J., Puigdefàbregas, J., Canals, M., Espino, M., Sardà, F., Company,
 736 J.B., 2009. Particle fluxes dynamics in Blanes submarine canyon (Northwestern
 737 Mediterranean). *Progress In Oceanography*, 82, 239-251.
 738
 739
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 741

742 Table 1.

743 Location and deployment time of the experimental traps in the Blanes Canyon (BC) and

744 in the adjacent slope (OS)

Trap	Seafloor depth (m)	Latitude	Longitude	Drop date	Sampling date	Duration (months)
BC 900	894	41° 34' 12,72"	2° 54' 19,14"	November 2008	November 2009	12
BC 1200	1195	41° 31' 15,06"	2° 50' 49,26"	November 2008	February 2009	3
BC 1200 and BC 1200 bottom	1195	41° 31' 15,06"	2° 50' 49,26"	February 2009	November 2009	9
BC 1500	1468	41°27' 28,80"	2° 52' 58"	November 2008	November 2009	12
OS 1200	1184	41° 13' 8,99"	2° 48' 54,6"	November 2008	February 2009	3
OS 1200	1184	41° 13' 8,99"	2° 48' 54,6"	February 2009	November 2009	9
OS 1500	1497	41° 09' 0,59"	2° 53' 48"	November 2008	November 2009	12
OS 1800	1806	41° 04' 52,19"	2° 58' 9"	November 2008	November 2009	12

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Table 2.

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Results of ANOVA carried out on *Xylophaga* sp. A and sp.B abundance data from

751

samples collected after 12 months duration. SNK test= The Student-Newman-Keuls

752

test. Bold values denote $p < 0.05$

753

Source	df	Blanes Canyon						Open Slope					
		<i>Xylophaga</i> A			<i>Xylophaga</i> B			<i>Xylophaga</i> A			<i>Xylophaga</i> B		
		MS	F	<i>P</i>	MS	F	<i>P</i>	MS	F	<i>P</i>	MS	F	<i>P</i>
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		

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758 **Table 4.**759 Deployments harboring taxa other than *Xylophaga* spp. (densities per dm³)

760

Taxa	BC 1200_bottom Oak (n=2)	BC 900 Pine (n =2)	BC 900 Oak n=1
Polychaeta			
Capitellidae <i>Capitella</i> complex	28.3	24.9	2.0
Dorvilleidae <i>Ophryotrocha</i> sp.	1.0	2.0	
Euphosinidae n. id.	1.0		
Spionidae <i>Prionospio</i> sp.	2.0		
Spionidae <i>Spiohanes</i> sp.	3.9	4.4	
Terebellidae <i>Neoamphitrite</i> 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 <i>Seba aloe</i>	100.6		
Leptostraca	20.5		
Mollusca			
Cocculinoidea n. id.	1.0		
Mitylidae <i>Idas</i> sp.	1.0		

761

762

763

764 **Table 3.**
765 PERMANOVA results for differences among locations (BC vs OS) and between pine
766 and oak. Bold and underlined values indicate $p < 0.01$
767

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				

768

769

770 **Table 5.**
771 Average and range of shell lengths (SL, mm) from *Xylophaga* sp. A by deployment. Parameters of the
772 cohort components of the length-frequency distribution estimated by Bhattacharya's method. BC=Blanes
773 Canyon, OS= Open Slope, 3M, 9M, 12M= 3, 9 and 12 months deployments, SI= Separation Index
774

Sample	MIN SL	MAX SL	Overall average SL	distribution curve type	Bhattacharya analysis		SI
					mean SL I cohort	mean SL II cohort	
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	-	-

775
776

777 **Figure captions**

778

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

781

782

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

785

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

790

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

792

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

798

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

802

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

808

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

813

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

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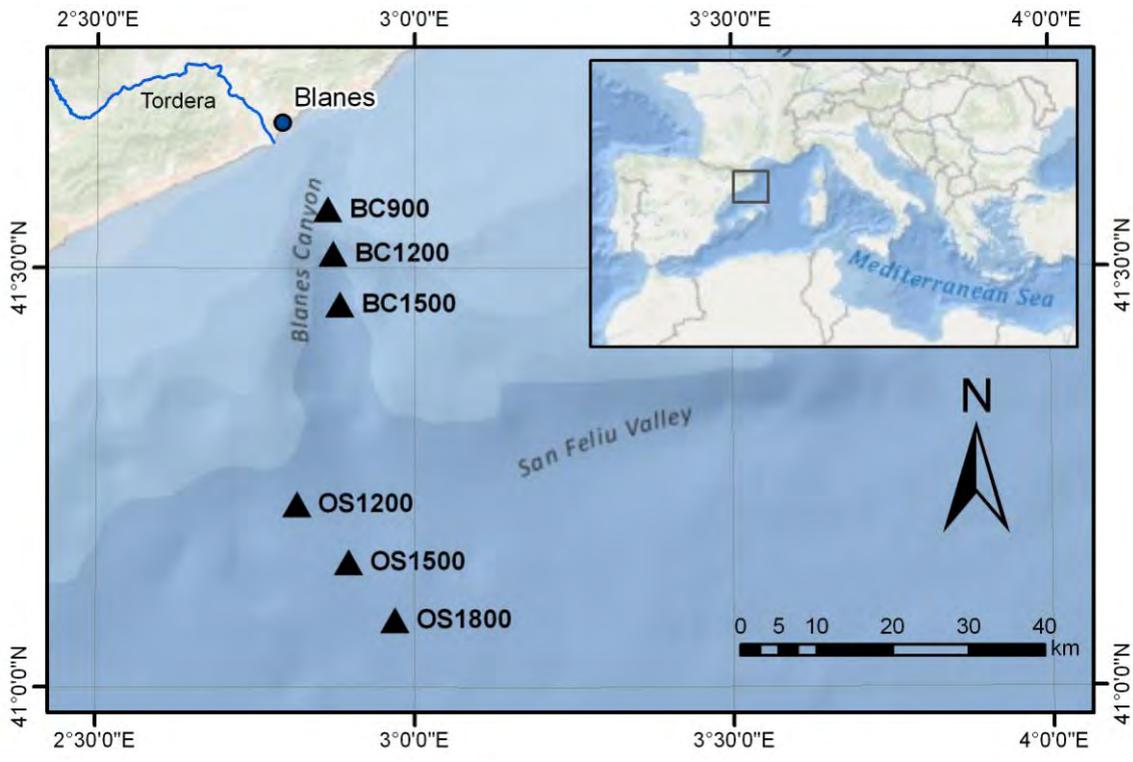


Figure 1

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

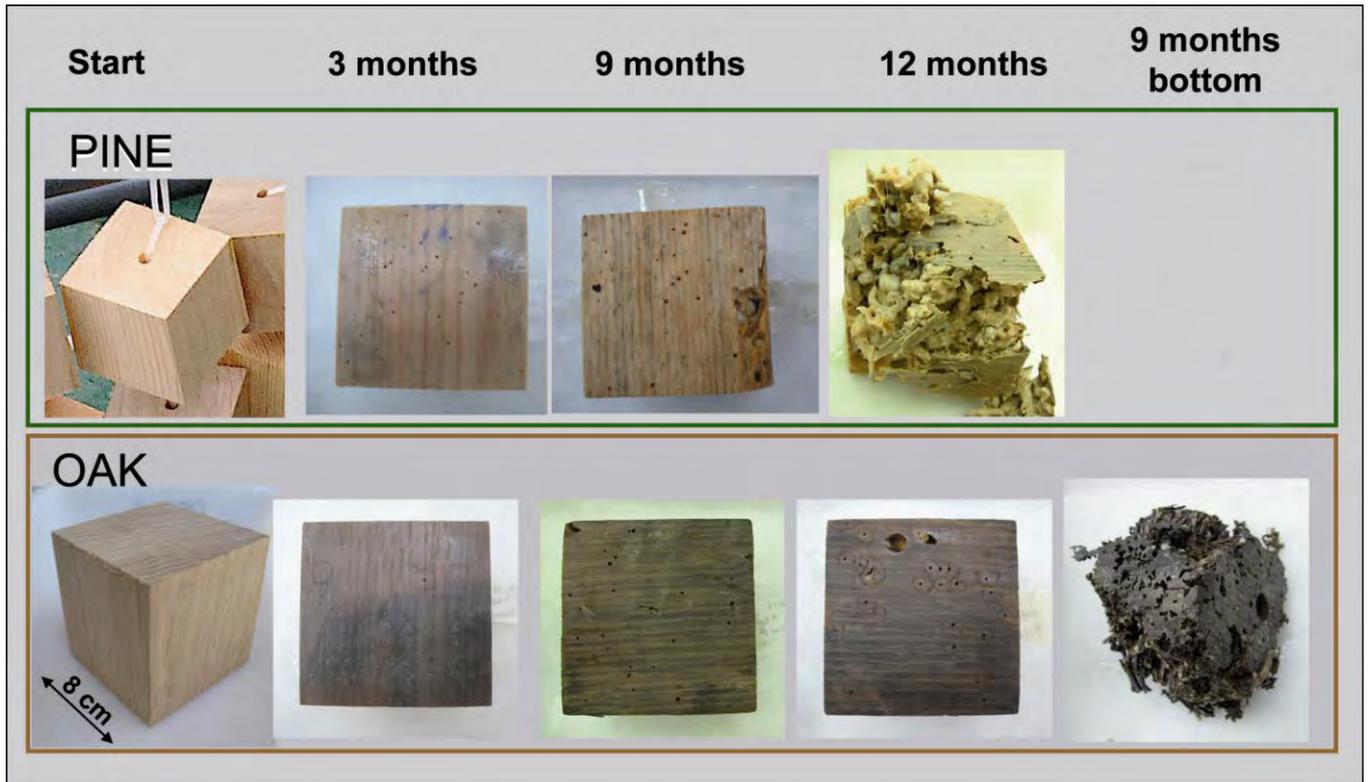
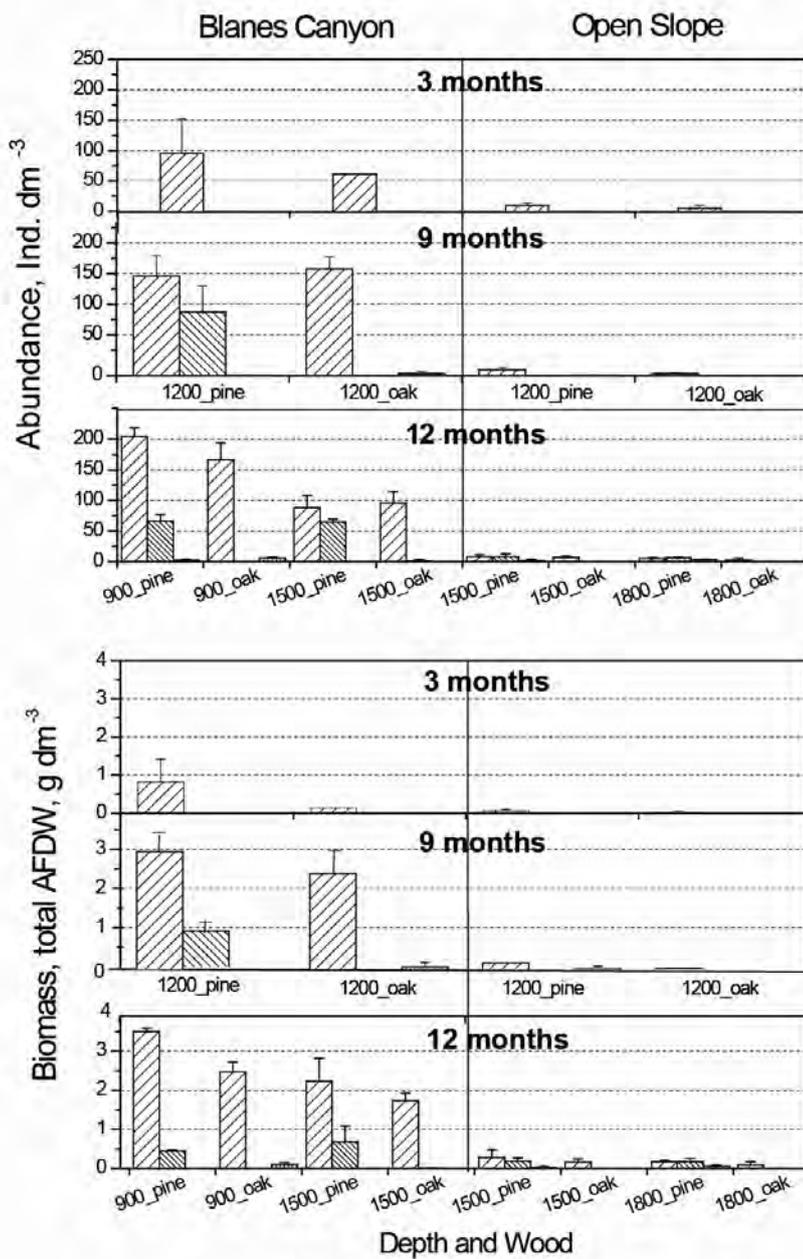


Figure 2

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).



250



200

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.

Y Axis Title

150

100

50

0

900_pine 900_oak 1500_pine 1500_oak 1500_pine 1500_oak 1800_pine 1800_oak

X Axis Title

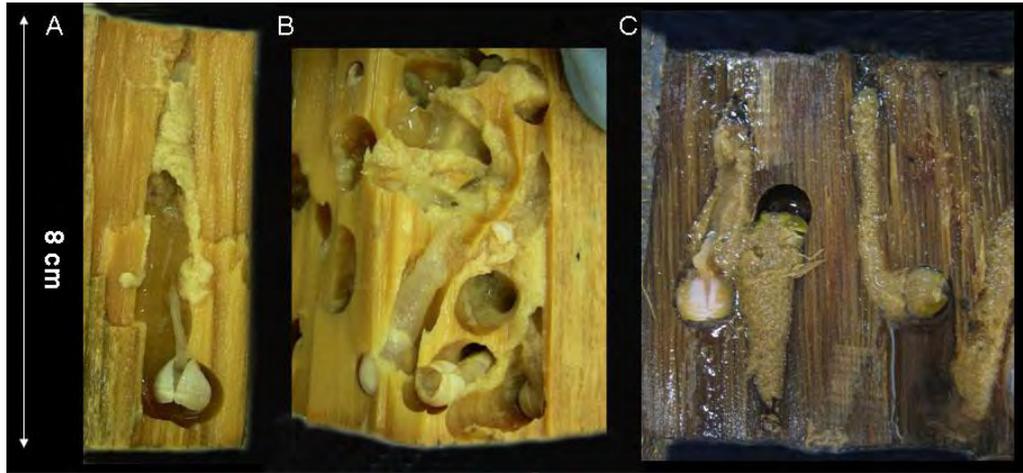


Figure 4
Detail of burrows in pine (A and B) and oak (C)

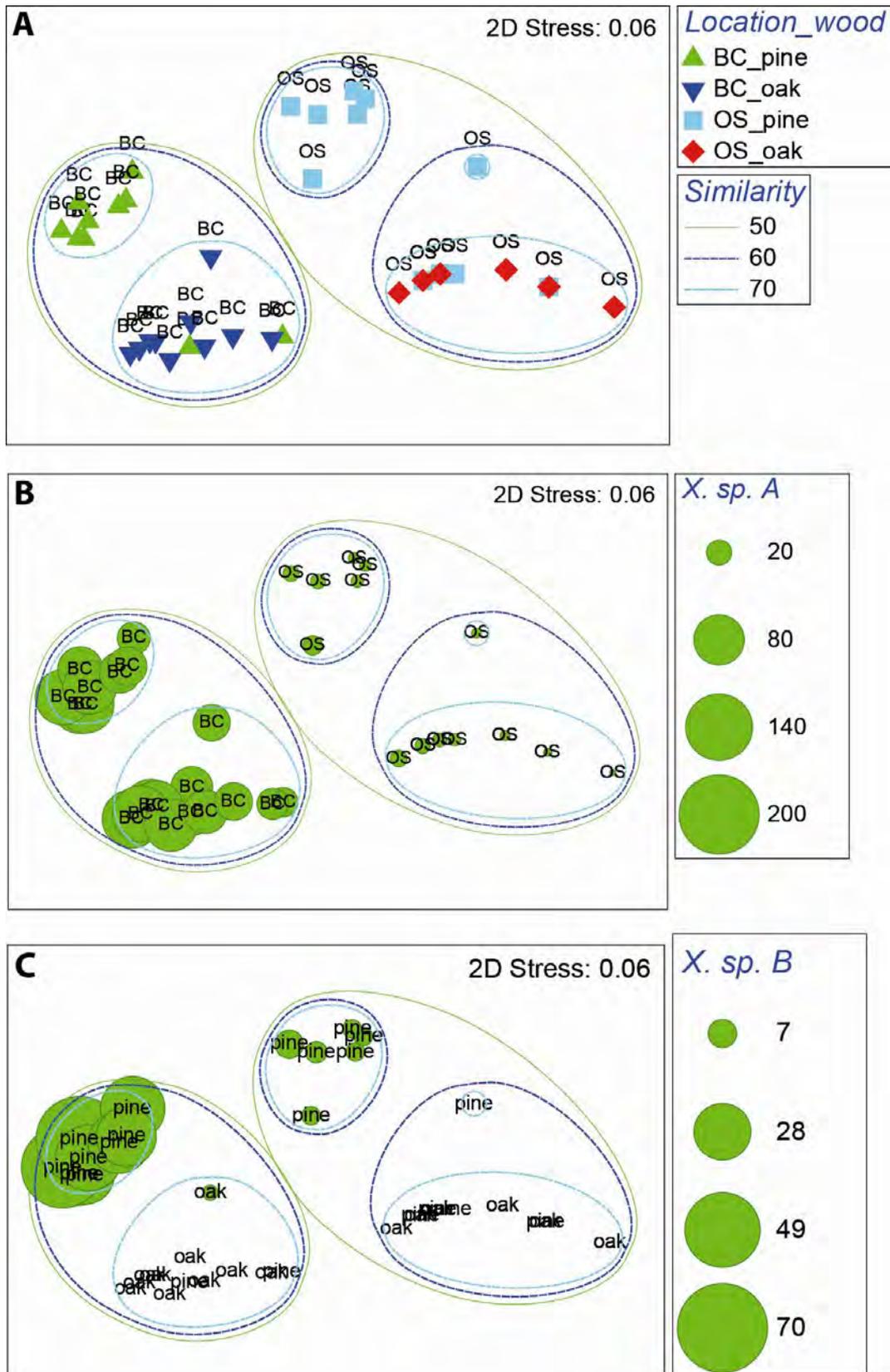


Figure 5

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.

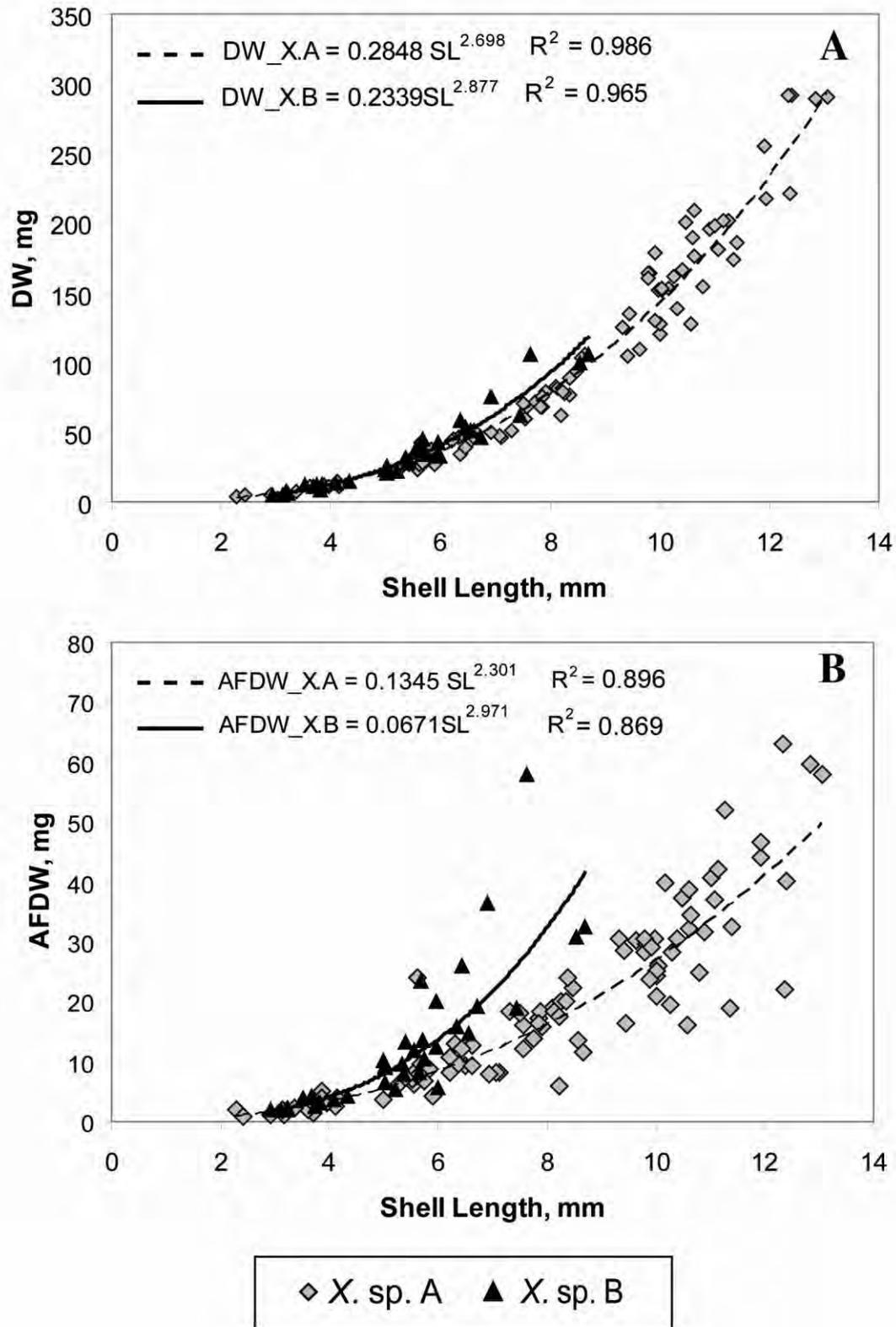


Fig 7

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.

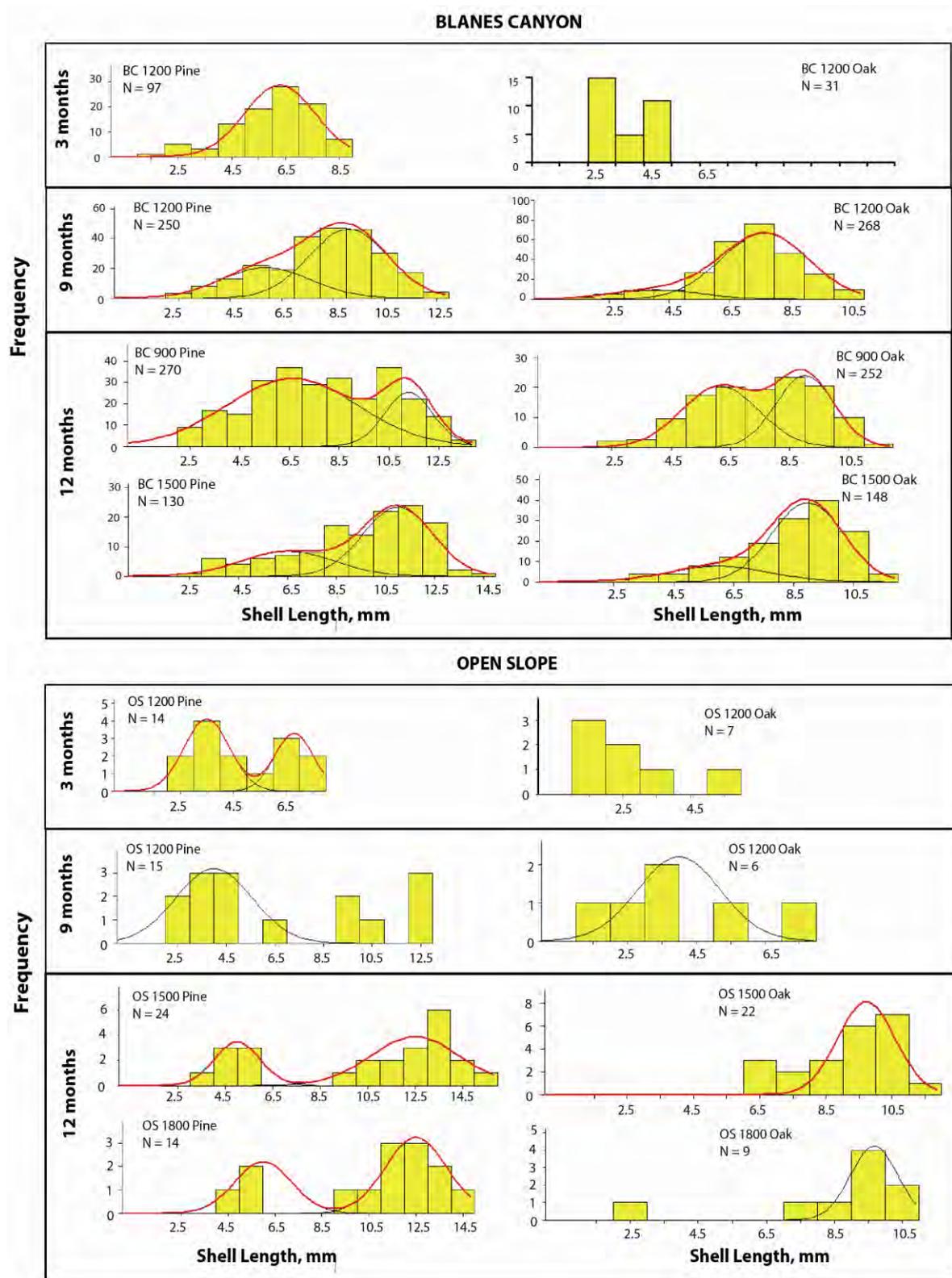


Figure 7

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.

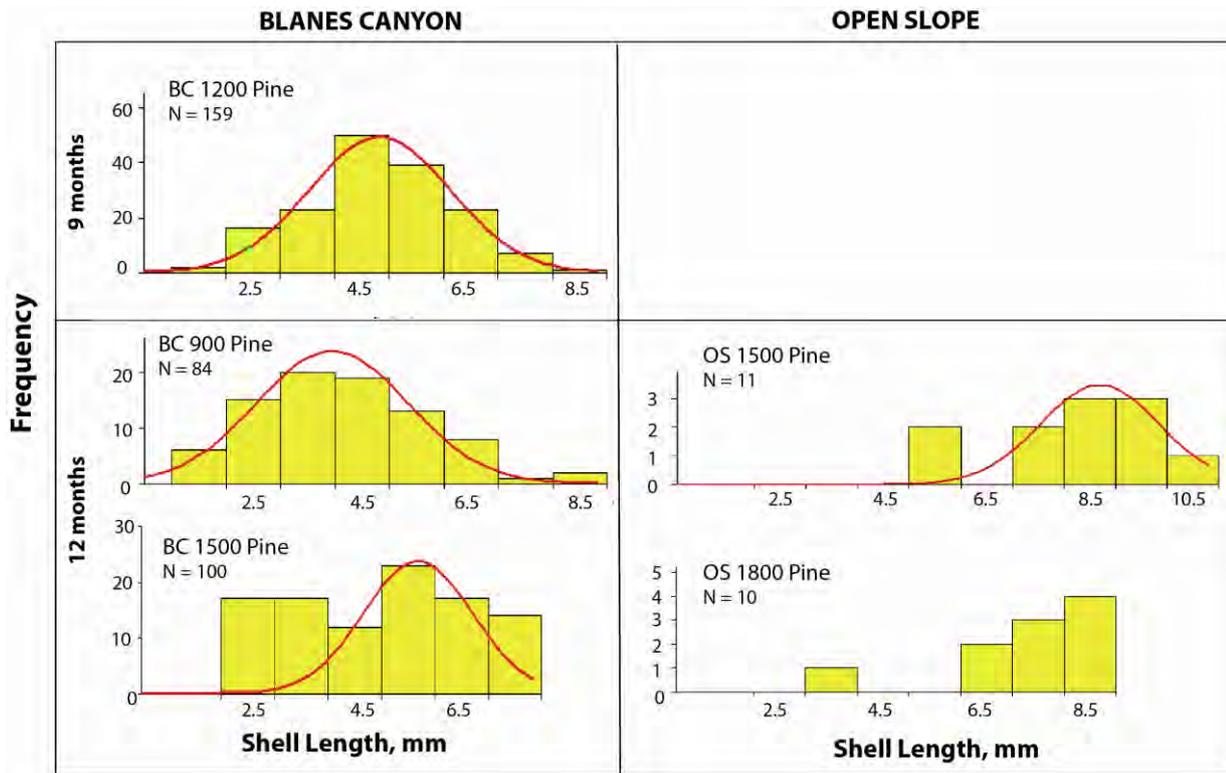


Figure 8

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.

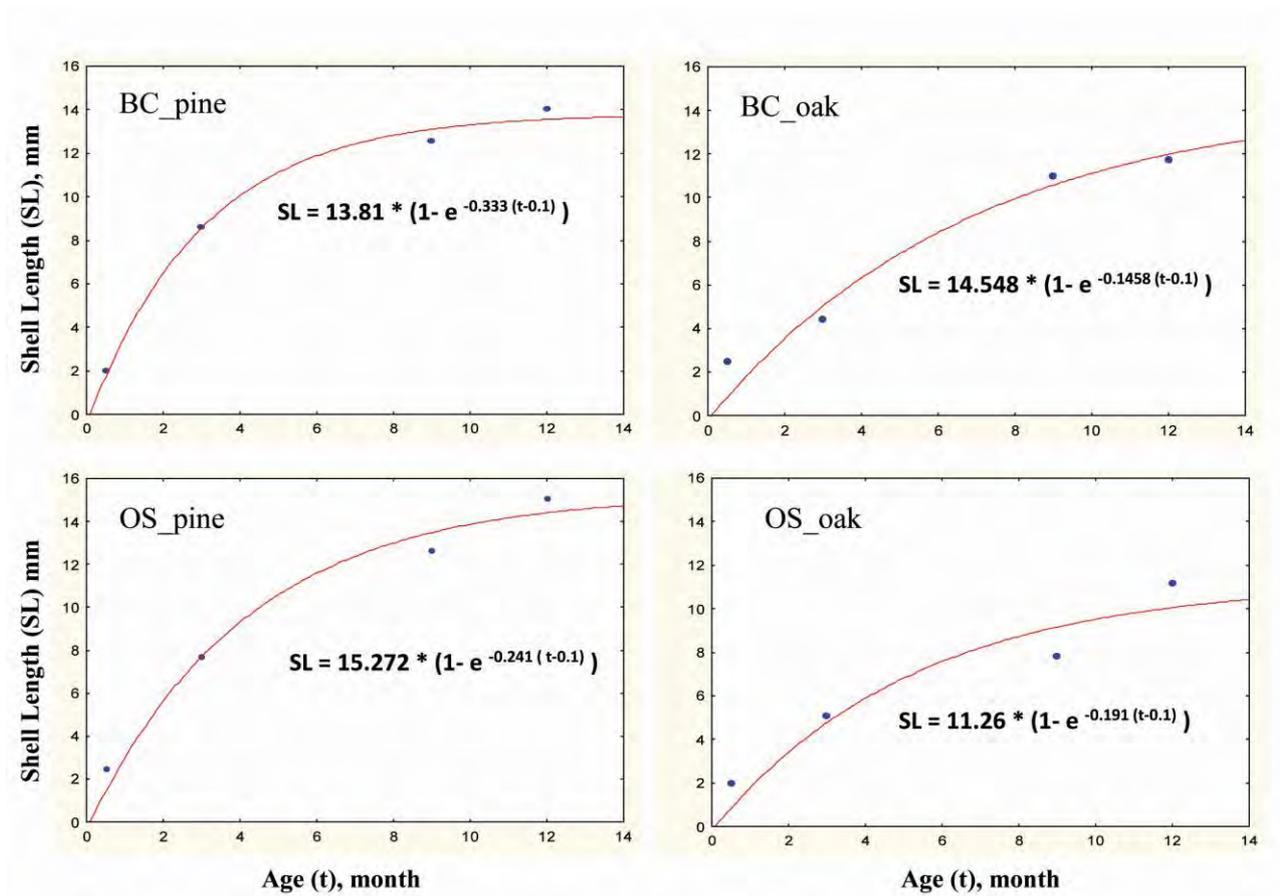


Figure 9

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.