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1 **Sources partitioning in the diet of the shipworm *Bankia carinata* (J.E. Gray, 1827): an**
2 **experimental study based on stable isotopes**

3

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18

19 **Abstract**

20 Adaptations that allow teredinids to maintain and thrive on wood, a nutritionally unbalanced food, make
21 these marine bivalves remarkable. Capable of filter-feeding, shipworms house endosymbiotic bacteria
22 synthesizing cellulolytic enzymes for digestion of wood carbohydrates and providing nitrogen to their
23 host through nitrogen fixation. To what extent each of these nutrition modes contributes to the
24 shipworm's metabolism remains an open question. In this experimental study, we estimated source
25 partitioning through the determination of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in original biological samples. For this
26 purpose, pieces of common alder (*Alnus glutinosa*) were immersed at a coastal station of the north-
27 western Mediterranean Sea. The shipworm *Bankia carinata* infected wood logs and stable isotope
28 mixing models suggested it got most of the carbon and nitrogen it needs from separate sources. From
29 71 to 77% of the carbon was derived from the digestion of wood carbohydrates, whereas between 42
30 and 82% of the nitrogen originated from N_2 fixation. These first semi-quantitative estimations suggest
31 that the contribution of N_2 fixers to nitrogen requirements of this shipworm species is far from incidental.

32

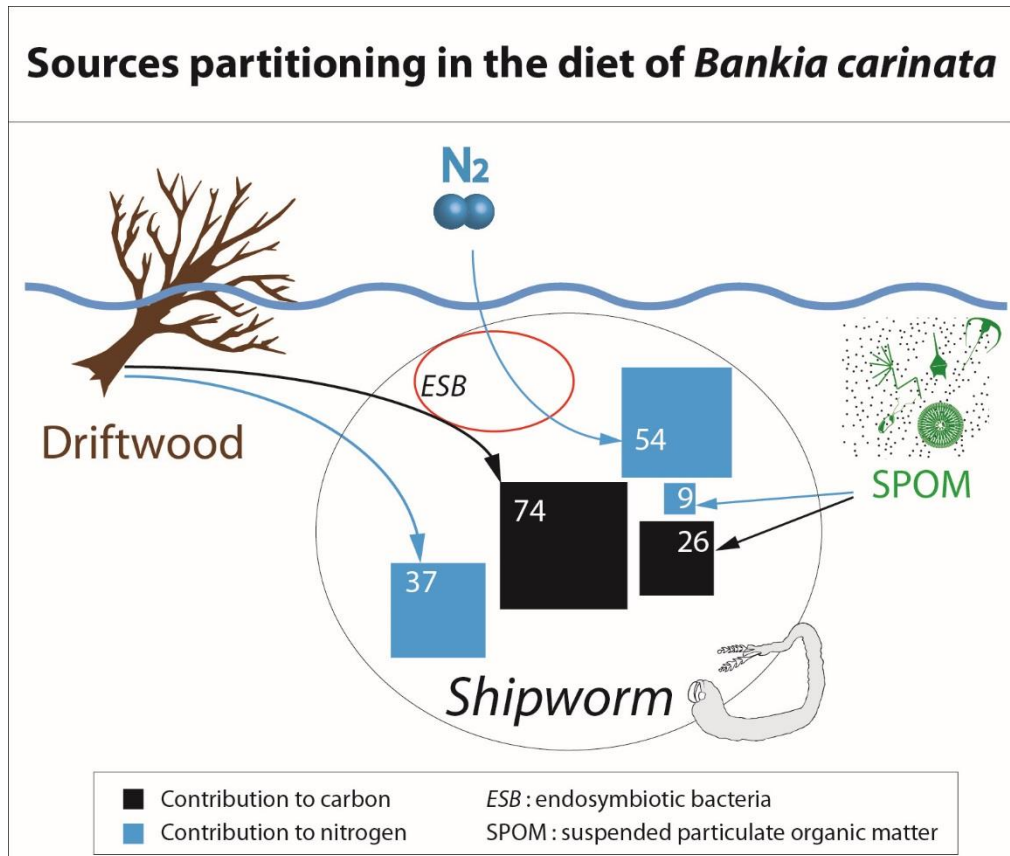
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34 **Keywords:** Teredinidae, Trophic ecology, Stable isotope, *in situ* experiment, Mediterranean Sea

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37 Graphical Abstract



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43 **Highlights:**

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- Nearly all tereidinid mollusks are obligate wood eaters.
- Food sources partitioning in the diet of *Bankia carinata* was investigated based on stable isotope analysis.
- The shipworms get the carbon and nitrogen they need from separate sources.
- $\delta^{13}\text{C}$ values strongly suggest that most carbon is derived from wood.
- Stable isotope mixing models indicate that N₂ fixed by endosymbionts provides at least half of the nitrogen content of the bivalves.

52 1. Introduction

53 Wood-boring teredinid bivalves occur on wood scattered at sea. In spite of being pests for all
54 kinds of maritime wooden structures, these mollusks, commonly known as shipworms, are one of the
55 finest examples of adaptation within the tree of life (Cragg et al., 2015). The strategy that enables these
56 bivalves to digest wood and supplement a nutritionally imbalanced diet has been debated for over a
57 century. While it was shown some time ago that shipworms were able to digest carbohydrates from
58 wood (Dore and Miller, 1923; Miller and Boynton, 1926), the coverage of nitrogen requirements has
59 remained under discussion (Carpenter and Culliney, 1975; Greenfield, 1952; Lasker and Lane, 1953;
60 Nishimoto et al., 2009; Pechenik et al., 1979; Yamanaka et al., 2015) to explain how some species
61 (Gallager et al., 1981) possess the ability to maintain and thrive in the absence of any other food source
62 than wood.

63 Rather than taking advantage of an association with its gut microflora which otherwise is scarce
64 (Betcher et al., 2012), shipworms produce endogenous lignocellulolytic enzymes (Sabbadin et al.,
65 2018), but also rely on dense populations of intracellular bacterial symbionts hosted in the gland of
66 Deshayes, a cluster of bacteriocytes located within the gills (Popham and Dickson, 1973). The many
67 types of bacteria housed in these eukaryotic cells can both digest wood carbohydrates and fix nitrogen
68 gas (Distel et al., 2002; Waterbury et al., 1983). It has been demonstrated that wood-degrading enzymes
69 produced by the endosymbionts were selectively translocated from the gills to the gut of the host
70 (O'Connor et al., 2014), and that dissolved nitrogen fixed by the intracellular bacterial symbionts within
71 the bacteriocytes could further be used for host metabolism (Lechene et al., 2007). All this makes
72 teredinids a unique model in animal endosymbiosis (Lechene et al., 2007) and may explain how
73 shipworms are able to use wood as a primary food source.

74 Marine wood-boring bivalves are indeed remarkable consumers in that the number of potential
75 feeding sources differs according to whether one considers their carbon or nitrogen requirement. With
76 regard to carbon sources, teredinids can rely on wood but also, as filter-feeding bivalves, on suspended
77 particulate organic matter from sea water. Regarding nitrogen sources, wood content is seemingly
78 inadequate to meet shipworms' requirements (Lasker and Lane, 1953; Carpenter and Culliney, 1975),
79 but nitrogen incorporation from this source cannot be excluded (Greenfield, 1952; Yamanaka et al.,
80 2015). Suspended organic particles are also sources of nitrogen but may remain incidental (Gallager et
81 al., 1981) because the ability to filter feed in most shipworm species is reduced by the shortening of gill
82 lamellae (Turner, 1966, Distel et al., 2011). Nitrogen fixation by endosymbionts (Lechene et al., 2007)
83 is one further source. Even though the routes of C and N are known and common among shipworm
84 species, the relative contribution of these routes to the shipworms' metabolism remains controversial
85 particularly with respect to nitrogen.

86 Stable isotope compositions of marine organic matter, terrestrial plants and N₂ dissolved in
87 seawater are different (Peterson and Fry, 1987), and can therefore help in deciphering the composition
88 of the shipworm's diet. To our knowledge, the few studies published on this topic were not conclusive
89 about source partitioning (Nishimoto et al., 2009; Paalvast and van der Velde, 2013; Yamanaka et al.,
90 2015). In this context, the aim of the present study was thus to investigate carbon and nitrogen source

91 partitioning by shipworms via an *in situ* experimental approach and through the use of stable isotopes
92 ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$).

93

94 **2. Material and methods**

95 2.1 Experimental design

96 The experiment was performed from June 6 to October 24, 2016 in the Bay of Banyuls-sur-Mer,
97 in the north-western Mediterranean Sea, France. Twelve 15 cm long sections were sawn from, a branch
98 of a common alder tree, *Alnus glutinosa* (L.) Gaertner, a widespread tree species along the banks of La
99 Massane, a local river which drains a small forested basin on the foothills of the French Pyrenees
100 mountains. The bark-intact small logs were air-dried indoors for a full year before being arranged into
101 packs and deployed at a coastal station (26 m depth; 42°29'302 N; 03°08'700 E). Each pack consisted
102 of four 2.5 to 5.5 cm cross-section wooden pieces tied together with a Colson™ collar. Two packs were
103 installed in June and an additional one on August 20. Wood packs were attached at one end to an
104 anchor and at the other end to a polyethylene buoy in such a way that the wood blocks remained
105 suspended between 1 and 1.5 m above the seabed (Fig. S1).

106

107 2.2 Sampling and preparation for stable isotope analyses

108 Potential food sources, namely alder wood within the experimental wood packs and suspended
109 particulate organic matter (SPOM) from the surrounding sea water, were sampled on several occasions
110 during the experiment. Alder wood was sampled on June 6, at the time of deployment of the first wood
111 packs, and on October 24 after time intervals of nearly 2 and 4.5 months from submersion. SPOM was
112 sampled when installing the experiment, at two intermediate dates, July 7th and September 8th, and at
113 the end of the experiment. Consumers, namely animals present either on (i.e. *Mytilus galloprovincialis*,
114 *Hiatella arctica*, *Musculus subpictus*, *Serpula vermicularis*, *Spirobranchus triqueter*, *Ascidia conchilega*)
115 or inside (*Bankia carinata*) the wood logs, were sampled once, on October 24.

116 Three water samples were collected for SPOM near the submerged wood with a Niskin bottle
117 (10 L) and pre-filtered through a 200 μm mesh to remove large zooplankton and detritus. SPOM was
118 then recovered by filtration on pre-combusted Whatman GF/F filters, 25 mm in diameter, 0.7 μm pore
119 size. The filters were then placed in individual petri dishes and dried in an oven at 50°C overnight. Dry
120 filters were kept away from light in a desiccator until analysis.

121 Invertebrate species present at the surface of the wood packs were collected manually. Wood
122 logs were then cut with a chisel for the collection of wood samples and shipworms. All the animals
123 present were kept alive for 24h in filtered sea water to allow evacuation of the gut contents and, if
124 necessary, were then dissected to separate flesh from the shells. Wood chips and animal tissues were
125 rinsed with deionised water and stored in aluminium foil at -20°C until analysis. Freeze-dried tissues and
126 wood samples were ground into a fine powder using a ball mill (MM 400, Retsch) and a sander (R3000,
127 Dremel), respectively. These samples were then weighed into tin capsules (ca. 0.3 to 0.4 mg for all
128 sample tissue and wood carbon analysis, and ca. 4 to 5 mg for wood nitrogen analysis).

129 SPOM samples may contain carbonates that are more enriched in ^{13}C than plant and animal
130 tissues (DeNiro and Epstein, 1978). Accordingly, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were analysed separately. For

131 measurements of $\delta^{13}\text{C}$ values, one half of each filter was acidified for 4 h with 37 % HCl acid vapours
132 under moderate vacuum in a glass desiccator to remove carbonates (Malet et al., 2007). For
133 measurements of $\delta^{15}\text{N}$ values, the remaining half of each filter was analysed without any pre-treatment,
134 as acidification may alter nitrogen isotope composition (Bunn et al., 1995; Kennedy et al., 2005). The
135 two sets of sub-samples (i.e. acidified half-filters and non-acidified half-filters) were packed separately
136 into individual tin capsules.

137 138 2.3 Stable isotope ratio measurements

139 Carbon and nitrogen isotope composition was determined using an elemental analyser (Flash
140 EA 1112, Thermo Scientific, Milan, Italy) coupled to a continuous-flow isotope-ratio mass spectrometer
141 (Delta V Advantage with a Conflo IV interface, Thermo Scientific, Bremen Germany). Analyses were
142 conducted at the LIENSs stable isotope facility at the University of La Rochelle, France. Data are
143 expressed in the δ notation (in ‰) as deviations from international standards (Vienna Pee Dee
144 Belemnite for $\delta^{13}\text{C}$ and N_2 in air for $\delta^{15}\text{N}$) following the formula: $\delta X = [(R_{\text{sample}} / R_{\text{reference}}) - 1] \times$
145 10^3 , with $R = {}^{13}\text{C}/{}^{12}\text{C}$ for carbon and ${}^{15}\text{N}/{}^{14}\text{N}$ for nitrogen. Calibration was done using reference materials
146 (USGS-24, IAEA-CH6, IAEA-600 for carbon; IAEA-N2, IAEA-NO-3, IAEA-600 for nitrogen). Analytical
147 precision was 0.15 ‰ for both C and N isotope analyses based on the analyses of acetanilide (Thermo
148 Scientific) and peptone (Sigma-Aldrich) used as internal laboratory standards.

149 150 2.4 Data analysis and statistical treatment

151 All statistics were performed using R, released by the R Foundation for Statistical Computing
152 (R Core Team, 2013). First, from the R commander package (Fox and Vialat, 2017), non-parametric
153 Mann-Whitney U tests were run for testing the hypothesis that the distribution of data was the same
154 between groups. In this context, data accounted for either δ values or C/N ratio; groups for exposure
155 intervals to seawater (2 vs 4.5 months), food sources (wood vs SPOM), or feeding modes (suspension-
156 feeding vs xylophagy).

157 The Bayesian mixing model SIAR (Stable Isotope Analysis in R; Parnell et al., 2010) was used
158 to infer the feasible contributions of carbon and nitrogen sources to the diet of the shipworms. Models
159 were run for 200,000 iterations and the first 50,000 iterations were discarded. For SIAR calculations, *A.*
160 *glutinosa* wood and SPOM were considered as potential sources of carbon while *A. glutinosa*, SPOM
161 and dissolved N_2 were considered as potential sources of nitrogen. Isotope compositions of SPOM and
162 wood used as end-members into mixing models were averages of values measured all along the study
163 to account for potential temporal variations of their isotope compositions. Trophic fractionation factors
164 used in mixing models were $0.30 \pm 0.21\text{‰}$ for $\delta^{13}\text{C}$ values and $2.5 \pm 0.25\text{‰}$ for $\delta^{15}\text{N}$ values,
165 corresponding to values for invertebrate species (whole body) as reviewed by Caut et al. (2009).
166 Concerning the specific utilization of dissolved N_2 by the bivalves, we thus used the $\delta^{15}\text{N}$ of 0.6‰ given
167 by Sigman et al. (2009) for the marine dissolved N_2 and a fractionation of -1‰ as suggested by these
168 authors for the fixed N input to the ocean from N_2 fixation. No fractionation was expected between the
169 endosymbionts and their host (Conway et al., 1989).

170 171 3. Results

172 3.1 Stable isotope compositions

173 $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of alder wood remained in narrow ranges around mean values of -2.2‰
 174 and -29.2‰ for N and C isotopes, respectively (Table 1, Figure 1). Ranges of SPOM isotope
 175 compositions were slightly wider around mean time-integrated values of 3.4‰ and -23.8‰ for $\delta^{15}\text{N}$ and
 176 $\delta^{13}\text{C}$ values, respectively. Alder wood was significantly more ^{15}N depleted and ^{13}C depleted than SPOM
 177 and contained two orders less nitrogen relative to its carbon content compared to SPOM (one-sided
 178 Mann-Whitney U-test, $p = 1$ in all cases).

179 The number of animals present either on or inside the wood logs increased with exposure time
 180 intervals. Only one species of shipworm (Table 2), namely, *Bankia carinata* (J.E. Gray 1827), was
 181 observed. Most other taxonomic groups consisted of suspension-feeding species. As no significant
 182 difference for both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values was observed between the two exposure intervals to seawater
 183 (two-sided Mann-Whitney U test, $p = 0.09$, $p = 0.10$), *B. carinata* was considered a homogenous group.
 184 The average $\delta^{15}\text{N}$ value of the shipworm bodies was close to 0‰ and their content was highly depleted
 185 in ^{13}C with a mean $\delta^{13}\text{C}$ value of -27.5‰. Shipworms were much more ^{15}N and ^{13}C depleted than known
 186 strict seston feeders such as *M. galloprovincialis*, *H. arctica*, *M. subpictus*, *S. vermicularis*, *S. triqueter*
 187 or *A. conchilega* (one-sided Mann-Whitney U-tests, $p = 1$ for all cases). Higher C/N ratios were observed
 188 in shipworms (one-sided Mann-Whitney U-tests, $p = 1$) due to higher carbon ($39.9 \pm 1.9\%$ versus 34.9
 189 $\pm 3.3\%$) and lower nitrogen contents ($5.2 \pm 1.6\%$ versus $8.4 \pm 1.6\%$) than in other consumers. The
 190 addition of trophic fractionation factors to alder wood isotope compositions demonstrates a slight shift
 191 between expected and measured of $\delta^{13}\text{C}$ values in shipworms (Figure 1).

192

193 3.2 Stable isotope mixing models

194 Based on 95% Bayesian credible intervals, wood and SPOM proportions to shipworms carbon
 195 diet ranged from 71 to 77% (mode = 74%), and 23 to 29% (mode = 26%), respectively (Figure 2A). As
 196 a result, alder wood contributed to most of the carbon assimilated by the shipworms during the
 197 experiment as compared to local SPOM. Among the three nitrogen sources (Figure 2B), the Bayesian
 198 mixing model suggested a major contribution from N_2 fixation (ranging from 42 to 82%, mode = 54%)
 199 and from *A. glutinosa* (from 9% to 51%, mode = 37%), much higher than contribution of SPOM (7 to
 200 13%, mode = 9%).

201

202 4. Discussion

203 *Bankia carinata* resorted to all the pathways of carbon and nitrogen acquisition described in
 204 shipworms. The approach permitted us to determine estimates of nitrogen source contribution, even
 205 though the number of sources was too large to get a unique solution from standard linear mixing models.
 206 As expected, the conversion of isotope compositions into contributions to the shipworm diet confirmed
 207 that wood was the main source of carbon, but it primarily revealed the significant contribution of nitrogen
 208 fixation pathways to the nitrogen content.

209

210 4.1 Source partitioning in the diet of *B. carinata*

211 *Bankia carinata* possesses a large caecum storing wood particles and all features associated
212 with xylophagy in shipworms, including the presence of dense populations of endosymbiotic bacteria
213 within the large interlamellar space of the single demibranch gills (Distel et al., 2011). In European
214 waters, this shipworm has only been reported in the Mediterranean Sea (Turner, 1966) probably
215 because of a preference for hypersaline conditions (Borges et al., 2014). *Bankia carinata* is a broadcast
216 spawning species that releases fertilized eggs into the water for long periods of development, increasing
217 larval dispersion. Growth in the genus *Bankia* is generally fast and produces adults of large size
218 (Haderlie and Mellor, 1973; MacIntosh et al., 2014). This species is reported in the studied area together
219 with *Lyrodus pedicellatus*, *Teredo navalis* and *Nototeredo norvagica* (Charles et al., 2018). As
220 population dynamics patterns depend on reproductive modes, differences must be expected in food
221 source partitioning between shipworm species according to the level of exhaustion of the wood resource.

222 The measurement of isotope ratios on the whole body of the borers corresponded to the isotopic
223 signature of the flesh of the shipworms including those of the bacteria from the digestive tract and the
224 endosymbionts from the gills. The digestive tract, however, contains relatively few bacteria (Betcher et
225 al, 2012) and endosymbiont bacteria represent a negligible amount of matter compared to the tissues
226 of the shipworm. Thence, it is reasonable to assume that the measurements made on the shipworms
227 were essentially the values of the isotopic ratios in the tissues of the host.

228 The differences of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values between *B. carinata* and SPOM highlighted that,
229 despite being able to capture organic particles from water, *B. carinata* food resources drastically differ
230 from those of strict filter feeders living in the same trophic conditions (Figure 1). Accordingly, from these
231 results, most of the carbon in shipworms is clearly derived from the consumption of alder wood (Figure
232 2a). The carbon isotope mixing model suggested that SPOM could seemingly represent 25% of
233 shipworm's diet. Structural tissues of wood mainly consist of carbohydrates and lignin but shipworms
234 only digest carbohydrates (Dore and Miller, 1923; Miller and Boynton, 1926; Sabbadin et al., 2018).
235 Carbohydrates are more enriched in ^{13}C than lignin (Benner et al., 1987), and this gives whole wood a
236 $\delta^{13}\text{C}$ value which probably led to underestimate the contribution of wood source. This was further
237 suggested by the outputs of the mixing models based on $\delta^{15}\text{N}$ values. High carbon content in the
238 shipworms reflects the accumulation of large amounts of glycogen (Greenfield, 1952; Potts, 1923) which
239 serves as an energy store in bivalves (De Zwaan and Zandee, 1972) and has been shown to be
240 exclusively derived from digestion of wood carbohydrates in the shipworm *Lyrodus pedicellatus* (Lane
241 et al., 1952).

242 According to the SIAR mixing model, SPOM contributed about 10% in average of the nitrogen
243 of the shipworms. Out of the two other potential sources, the mixing model suggested that nitrogen
244 coming from endosymbiosis contributed to the nitrogen pool of the shipworm tissues at an equal or even
245 greater level than alder wood. From the C/N ratio, it appears that *B. carinata* had reduced nitrogen
246 requirements relative to other bivalves but a nitrogen content 20 times higher than that of alder wood.
247 Shipworms can rely on wood to acquire their nitrogen (Lasker and Lane, 1953; Yamanaka et al., 2015)
248 but also through the association with the N_2 -fixing endosymbionts hosted in their gills (Lechene et al.,
249 2007). Even though, by minimizing excretory losses, shipworms are extremely conservative with respect
250 to nitrogen (Gallager et al., 1981), wood source alone can barely cover all their nitrogen needs. Together

251 with recycling mechanisms, a polytrophic capacity is probably the best feeding strategy for balancing
252 requirements in poor-nitrogen environments (Muscatine and Porter, 1977). Intracellular bacteria
253 populations from the gland of *Deshayes* produce cellulolytic enzymes which presumably in combination
254 with enzymes produced endogenously (Sabbadin et al., 2018) allow shipworms to digest efficiently large
255 amounts of wood carbohydrates. Endosymbiotic bacteria probably fulfill their N₂ fixing function with an
256 equal efficiency to the benefit of their host. Accordingly, the conversion of dissolved nitrogen gas into
257 shipworm biomass is likely far from being incidental as suggested by the present study.

258

259 4.2 Carbon and nitrogen sources: scope of the study

260 The $\delta^{15}\text{N}$ value of marine dissolved N₂ was not measured but dissolved N₂ in equilibrium with
261 atmospheric N₂ in the surface ocean has a $\delta^{15}\text{N}$ value that does not vary greatly from 0.6‰ (Sigman et
262 al., 2009). Molecular nitrogen fixation commonly results in weak, slightly negative isotope fractionation
263 (Wada and Hattori, 1979) and no fractionation between endosymbionts and their host was expected
264 (Conway et al., 1989). As a result, the $\delta^{15}\text{N}$ value of dissolved gas nitrogen and fractionation factor
265 implemented into the mixing model must be relatively close to the actual values. The slight ¹⁵N
266 enrichment of shipworm tissue relative to dinitrogen suggests that N₂ fixation through endosymbiotic
267 interaction contributed significantly to the nitrogen content of the shipworm. The contribution of other
268 pathways of dinitrogen-fixing (i.g., ingestion of planktonic diazotrophs or wood particles from nitrogen-
269 fixing tree species) would imply trophic enrichment factors and that would have led to the higher ¹⁵N
270 enrichment of the shipworm.

271 Regarding wood source, *Alnus glutinosa* is a common tree species on the banks of European
272 rivers. Alder wood, therefore, has good chance to end up at sea after events of river flooding. During
273 this study, the characteristics of wood which was initially introduced dry into the water changed very
274 little. $\delta^{13}\text{C}$ values and C/N ratios were representative of most terrestrial C₃ primary producers and in the
275 range of those found in the literature for tree wood (Nishimoto et al 2009; Paalvast and van der Velde
276 2013, Yamaka et al., 2015). $\delta^{15}\text{N}$ values of wood are more variable, showing particularly negative values
277 as previously reported at this site by Carlier et al. (2007) or for terrestrial plants (Fogel et al., 2008;
278 Zapata-Hernandez et al., 2016), including alder tree species (Chambers et al., 2004). Nitrogen
279 incorporation pathways differ among tree species. Alder, which grows on poor quality soils is, for
280 instance, able to supplement its needs through an association with nitrogen-fixing bacteria hosted in its
281 roots (Hooker and Wheeler, 1987). *Alnus incana* is known to derive almost all its nitrogen from the
282 atmosphere (Chambers et al., 2004). This assigned to the wood source a trophic position which probably
283 led us to overestimate its contribution to the nitrogen content of the shipworm, at the expense of the
284 other sources. It, therefore, should be kept in mind that the scope of this study concerns a nitrogen-
285 fixing tree species.

286 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of SPOM were consistent with previous measurements at the studied site
287 (Carlier et al., 2007; Nahon et al., 2012) with ranges of temporal changes of nearly 2‰ for both elements.
288 Marine SPOM is a mixture of living and dead particles (Fry, 1988) of which the total amount and the
289 individual contribution changed according to the seasons and weather conditions. For instance, particles
290 collected in July, when the weather was calm, had δ values and C/N ratio representative of what is

291 reported for plankton (Peterson et al., 1986), while low $\delta^{13}\text{C}$ values and high C/N ratio measured in June
292 and October were characteristic at the studied site of surficial sediment resuspended after windy
293 weather conditions (Charles et al., 2012). On these occasions, debris of vascular plants could be
294 observed in the water samples and most photosynthetic pigments were degraded (data not shown). The
295 sampling approach allowed thus to produce average values of δ and C/N that best reflected the food
296 source for the shipworms and the co-occurring common filter-feeding species over the study period. It,
297 however, should be noted that sampled SPOM particles ranged from 0.7 to 200 μm , and there is
298 considerable heterogeneity in natural abundances of ^{13}C and ^{15}N among the discrete size classes of
299 SPOM (Rau et al., 1990). $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of the smallest size fractions of SPOM can be as low as
300 -25.3‰ and -0.5‰ , respectively (Rau et al., 1990). At the study site, the contribution of
301 picophytoplankton is maximal at periods of low total chlorophyll *a* biomass, that is to say in summer and
302 fall, with contribution reaching more than 60% in September (Charles et al 2005). This, according to the
303 findings of Rau et al. (1990), may to some extents explain the depletion in heavy isotopes measured in
304 the SPOM fraction during the sampling, and so the gap between the bulk SPOM value and strict-filter
305 feeding consumers which retain, sort and select particles differentially according to their size and
306 nutritional quality (Dubois and Colombo, 2014, Cresson et al., 2016). As a consequence, even though
307 this cannot dramatically change the general scheme of food source contributions, the comparison of
308 particle sorting efficiency needs to be investigated to further understand interspecific variations in trophic
309 niches among shipworm species (Cresson et al., 2016, Paalvast and van der Velde, 2013).

310

311 **5. Conclusion**

312 This study, involving alder wood, provides a first quantitative estimate of the contribution of food
313 sources to the diet of *B. carinata*. Most of the assimilated carbon originated from the wood and N_2 fixers
314 contributed significantly to nitrogen requirements of the shipworm. However, it must be stressed that in
315 a previous study conducted on *Teredo navalis* (Paalvast and van der Velde 2013), the overwhelming
316 amount of carbon and nitrogen was derived from SPOM rather than from the wood source. Availability
317 of food sources may change over time and space between studies, but stable isotope composition of
318 wood also varies according to tree species and each species of teredinids has its own traits of life. As a
319 consequence, the relative importance of the symbiotic association could then be better appreciated by
320 testing, on the one hand, several tree and shipworm species, and, on the other hand, by performing ^{13}C
321 and ^{15}N labelling experiments to quantitatively estimate the C and N pathways within the different
322 potential components of the shipworms diet.

323

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333

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Tables and figures' captions

Table 1. Stable isotope compositions and C/N ratios of potential food sources; n, number of samples. SPOM: Suspended particulate organic matter, SD: Standard deviation.

Table 2. Stable isotope compositions and C/N ratios of consumers. Feeding modes are: Xylo, xylotrophy, SF, suspension-feeding; n, number of individuals; SD: Standard deviation.

Fig. 1. Carbon and nitrogen isotope compositions of potential food sources and consumers. The broken line indicates the $\delta^{15}\text{N}$ average value expected for products resulting from the fixation of atmospheric nitrogen. The ellipse indicates the range of theoretical expected $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values for consumers of alder wood, considering trophic enrichments of 0.30‰ and 2.5‰ for $\delta^{13}\text{C}$ for $\delta^{15}\text{N}$, respectively. Dotted lines account for trophic shift of carbon and nitrogen.

Fig. 2. Bayesian mixing model dietary analyses for carbon (A) and nitrogen (B). Boxplots with 50 (in dark gray), 75 (in medium gray) and 95% (in light gray) credible intervals representing the proportion of *Alnus glutinosa*: Wood, suspended particulate organic matter: SPOM, and dissolved nitrogen: N_2 in the diet of the shipworm *Bankia carinata*.

Figure S1: Experimental setup. Image of the alder wood packs at the study site within the Bay of Banyuls-sur-Mer, Mediterranean Sea, France.

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Table 1. Stable isotope compositions and C/N ratios of potential food sources; n, number of samples.
SPOM: Suspended particulate organic matter, SD: Standard deviation.

Sources	Date or exposure duration in months	n	$\delta^{15}\text{N}$ (‰)	$\delta^{13}\text{C}$ (‰)	C/N
SPOM	June 9	3	2.4 ± 0.1	-24.5 ± 0.1	6.5 ± 0.2
	July 11	4	4.8 ± 0.5	-22.6 ± 0.1	5.8 ± 0.6
	Sept 12	3	3.9 ± 0.5	-23.7 ± 0.1	6.2 ± 0.8
	Oct 24	4	2.6 ± 0.3	-24.3 ± 0.7	9.6 ± 2.7
	Time integrated		3.4 ± 1.1	-23.8 ± 0.8	7.0 ± 1.7
Alder	0	5	-2.8 ± 0.7	-28.8 ± 0.5	158 ± 9
	2	4	-2.7 ± 0.1	-29.8 ± 0.1	195 ± 11
	4.5	4	-1.3 ± 0.5	-29.8 ± 0.3	157 ± 11
	Time integrated		-2.2 ± 0.8	-29.3 ± 0.5	170 ± 22

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523 Table 2. Stable isotope compositions and C/N ratios of consumers. Feeding modes are: Xylo,
 524 xylophagy, SF, suspension-feeding; n, number of individuals; SD: Standard deviation.

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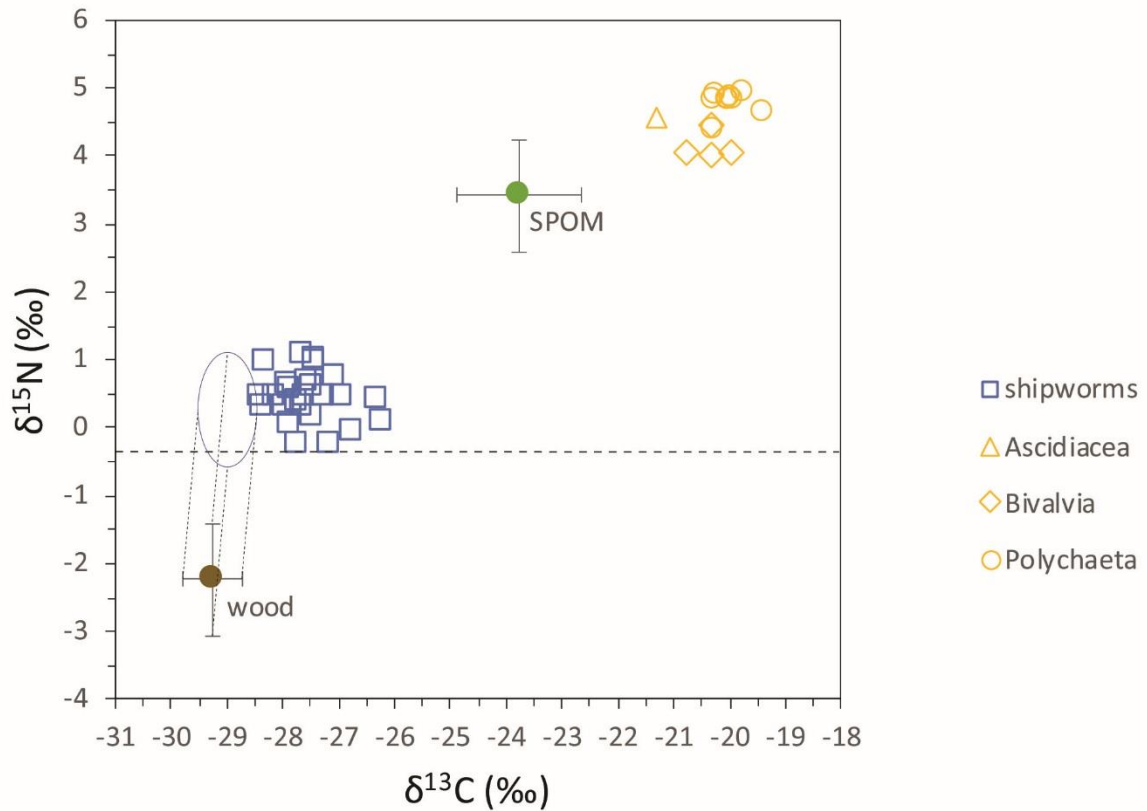
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Class <i>species</i>	Feeding type	n	$\delta^{15}\text{N}$ (‰)	$\delta^{13}\text{C}$ (‰)	C/N
Bivalvia					
<i>Bankia carinata</i>	Xylo/SF	25	0.5 ± 0.4	-27.5 ± 0.6	8.3 ± 2.5
<i>Mytilus galloprovincialis</i>	SF	1	4.4 ± n.d.	-20.3	3.5 ± n.d.
<i>Hiatella arctica</i>	SF	2	4.0 ± 0.07	-20.1 ± 0.2	3.8 ± 0.2
<i>Musculus subpictus</i>	SF	1	4.1 ± n.d.	-20.8	4.0 ± n.d.
Polychaeta					
<i>Serpula vermicularis</i>	SF	4	4.9 ± 0.1	-20.1 ± 0.3	3.9 ± 0.1
<i>Spirobranchus triqueter</i>	SF	4	4.84 ± 0.2	-19.8 ± 0.2	3.9 ± 0.1
Ascidiacea					
<i>Ascidia conchilega</i>	SF	1	4.6 ± n.d.	-21.3 ± n.d.	4.9 ± n.d.

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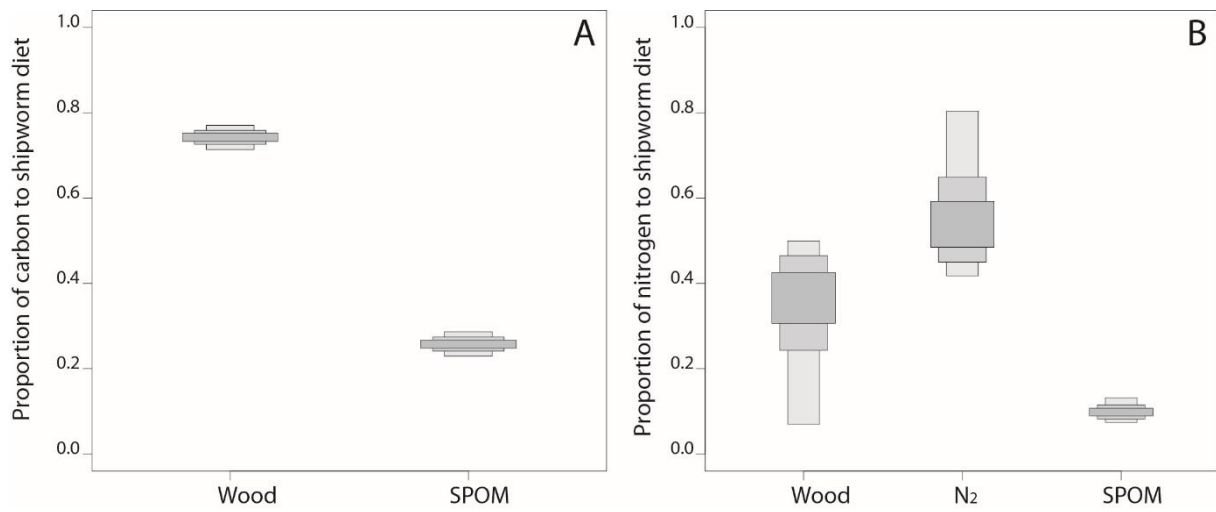
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532 Fig. 1. Carbon and nitrogen isotope compositions of potential food sources and consumers. The broken
 533 line indicates the $\delta^{15}\text{N}$ average value expected for products resulting from the fixation of atmospheric
 534 nitrogen. The ellipse indicates the range of theoretical expected $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values for consumers of
 535 alder wood, considering trophic enrichments of 0.30‰ and 2.5‰ for $\delta^{13}\text{C}$ for $\delta^{15}\text{N}$, respectively. Dotted
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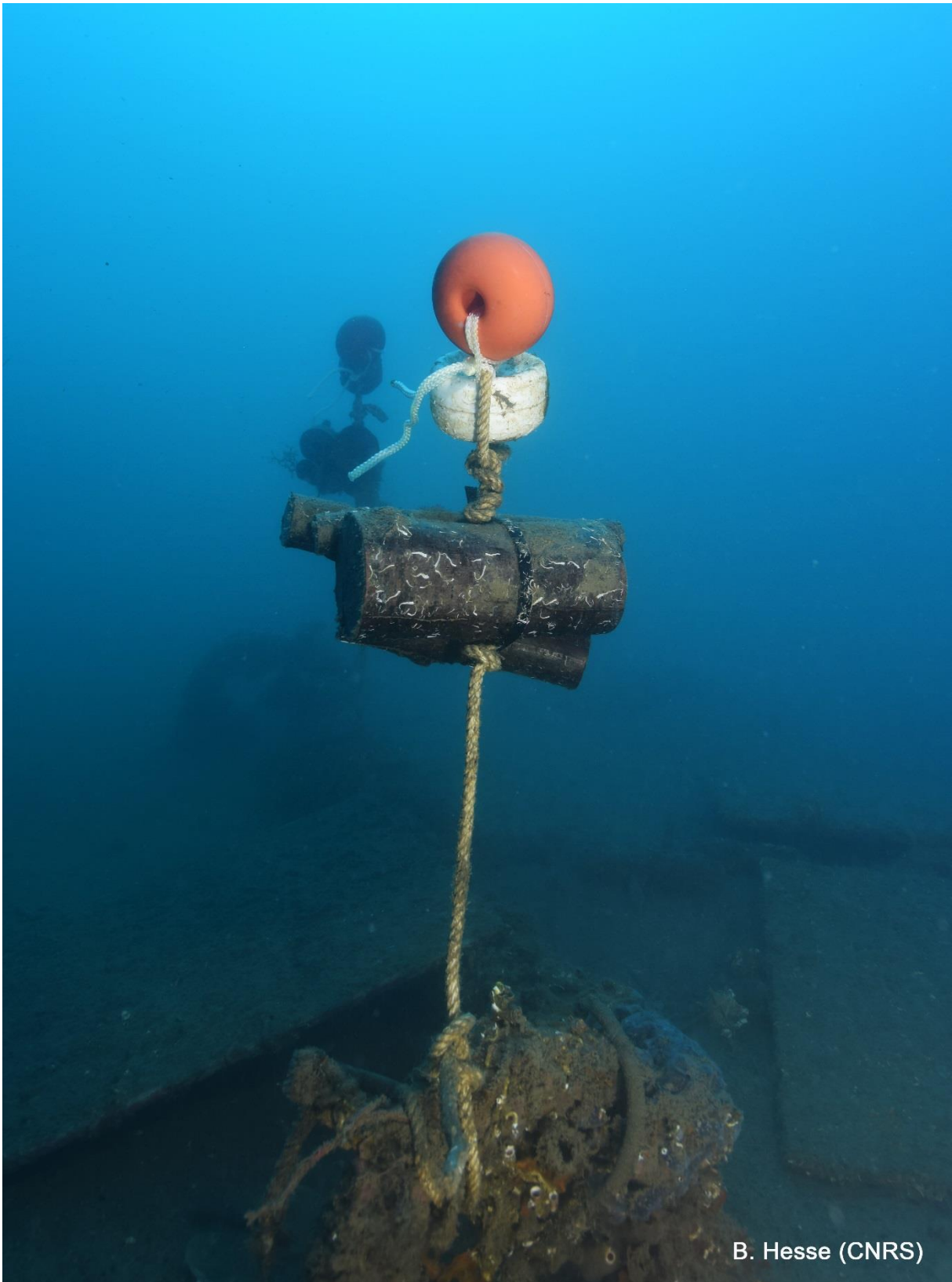
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Fig. 2. Bayesian mixing model dietary analyses for carbon (A) and nitrogen (B). Boxplots with 50 (in dark gray), 75 (in medium gray) and 95% (in light gray) credible intervals representing the proportion of *Alnus glutinosa*: Wood, suspended particulate organic matter: SPOM, and dissolved nitrogen: N₂ in the diet of the shipworm *Bankia carinata*.



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