Vol. 538: 53–65, 2015
doi: 10.3354/meps11454

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published October 28

An experimental approach for understanding the process of wood fragmentation by marine wood borers in shallow temperate waters

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ABSTRACT: Wood-boring activities by various invertebrates control the availability of food and space in marine sunken wood communities. We investigated the individual stages of wood fragmentation through a 4 yr colonization experiment. We placed Japanese cedar logs on the sea bed ~2 m below the surface of Tanabe Bay, Japan. A cluster analysis showed 6 successive stages (plus 1 alternative second stage) in the development of the wood borer's assemblage. Individuals of the bivalve families Teredinidae and Pholadidae and the isopod family Limnoriidae settled on the logs within 2 mo (Stage 1). After rapidly fragmenting the inside of the logs (Stage 2), most of the teredinids died during the first year, leaving numerous empty tunnels reinforced by calcium carbonate linings (Stage 3). Because of this reinforcement, as well as due to the fact that the tunnels never crossed each other, the resulting honeycombed structure remained stable for about 3 yr, allowing for the ongoing development of the sunken wood community. Large-scale fragmentation finally continued with the limnoriids intensively disintegrating the logs from the surface (Stage 4). As the fragmentation process drew to a close, the pholadids disappeared from the assemblage before the limnoriids (Stage 5), the latter persisting until the log had been turned entirely into small particles (Stage 6). This rapid and dynamic fragmentation process is not universal in the sea, but serves as a useful framework for comparing the wood-boring activities across various conditions. Those comparisons will help to evaluate the role of coarse woody debris in marine ecosystems.

KEY WORDS: Coarse woody debris · Sunken wood · Wood fall · Limnoriidae · Pholadidae · Teredinidae · *Zoothamnium niveum* · Allochthonous inputs

INTRODUCTION

Vascular plants are the most abundant organic material on Earth (570 Pg C), and through degradation and transport, they form an important part of the global carbon cycle (Bianchi 2011). Coarse woody debris is frequently washed out from terrestrial habitats and ultimately transported to sea, where it forms a substrate for various wood-boring invertebrates (Maser & Sedell 1994). These borers physically break apart the wood using file-like sculpture or tough jaws (Turner 1966, Borges et al. 2008), and chemically digest some of the woody constituents (Griffin et al. 1987, Distel et al. 2002, King et al. 2010, O'Connor et al. 2014). These semi-digested wooden particles are scattered into the surrounding sediment, and there the microbial activity results in the final decomposition of all the remaining woody constituents (Palacios

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et al. 2006, Dupont et al. 2009, Fagervold et al. 2012). Through this degradation process, coarse woody debris primarily serves as a food source for various invertebrates in continental shelf settings (Nishimoto et al. 2009), whereas it can harbor a dense and diverse assemblage (i.e. a sunken wood community) in mangrove swamps (Laurent et al. 2013) and deep seas (Wolff 1979, Pailleret et al. 2007, Bienhold et al. 2013).

Wood-boring invertebrates accelerate the degradation of wood and control the availability of food and space for various organisms in sunken wood communities (Turner 1973, Maser & Sedell 1994, McClain & Barry 2014) by (1) becoming themselves prey through predator–prey interactions (Russell 1997, Nishimoto et al. 2009), (2) carving out cavities that are used as shelters by other organisms (Wolff 1979), (3) facilitating the build-up of degradation-related hydrogen sulfide (Yücel et al. 2013), (4) promoting secondary production in the surrounding sediment (Findlay & Tenore 1982, Bernardino et al. 2010), and (5) increasing the surface/volume ratio of the wood, which in turn accelerates the leaching of labile components (Camilleri & Ribi 1986) such as proteins, tannins and terpenoids (Umezawa 2000). In shallow waters, members of the molluscan bivalve families Teredinidae and Pholadidae and the crustacean isopod family Limnoriidae play key roles in wood fragmentation (Miller 1926, Edmondson 1955, Nair & Saraswathy 1971, Southwell & Bultman 1971, Borges 2014, Borges et al. 2014). While teredinids are obligate xylophagous wood borers and create deep tunnels with a calcareous lining (Turner 1966, Turner & Johnson 1971, Evans 1999), pholadids are filter-feeders that rely on wood primarily for shelter (Haga & Kase 2011) and produce short, tear-drop shaped burrows which fragment the wood, especially near its surface (Turner & Johnson 1971, Evans 1999). In contrast, limnoriids typically produce interconnecting tunnels below the surface of the wood and are able to move freely both within these tunnels and between different pieces of debris (Thiel 2003). This freedom of movement eliminates the need for permanent shelter, enabling limnoriids to utilize small and/or fragile pieces of wood unsuitable for the sedentary teredinids and pholadids. We hypothesized that such differences in boring strategies make it likely that wood borer's assemblages are not static, but are dominated by different wood-boring organisms as the fragmentation process progresses.

Previous studies used wooden test panels to record 'snapshots' of sunken wood communities at particular stages of fragmentation (in shallow water: Edmondson 1955, Southwell & Bultman 1971, Tsunoda & Nishimoto 1972, 1976, 1978; in deep water: Muraoka 1965, 1966, 1967, 1970, Turner 1973, 1977, Eaton et al. 1989, Tyler et al. 2007, Borges 2014), but the question of how the fragmentation process itself progresses with time has not yet been answered. To address this gap in knowledge, we carried out a long-term (4 yr long) field experiment based on logs artificially deployed in a temperate shallow marine environment. To the best of our knowledge, our study is the first to report the entire process of wood fragmentation by marine invertebrates, from the initial stage of colonization to complete fragmentation, and includes regularly and frequently sampled species abundance data.

MATERIALS AND METHODS

Experimental design

We used Japanese cedar *Cryptomeria japonica*, which accounts for ~18% of the national forest cover (Ministry of Agriculture, Forestry and Fisheries of Japan 2002) and therefore naturally contributes a large amount of debris to Japanese waters. To achieve a detailed and complete record of fragmentation, we used 54 relatively large logs with non-cork bark (~10 cm in diameter and ~20 cm in length) instead of the small wooden panels used in earlier studies (Southwell & Bultman 1971, Tyler et al. 2007). The logs were deployed at a depth of ~2 m, on the muddy bottom of Tanabe Bay (Shirahama, Wakayama Prefecture) on the Pacific side of central Honshu, Japan (33° 40′ 46.80″ N, 135° 21′ 46.00″ E) (Fig. 1). The site of the experiment was located in the inner part of the bay, which was largely sheltered from storms. In August and September, typhoons often hit mainland Japan and transport large amounts of woody debris to the coast. To synchronize our experiment with this natural cycle, the cedars were cut down in August 2008 and deployed the following month. To prevent them from being washed away, the logs were fixed to the top of a polypropylene net that had been anchored to the sea floor (see Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m538p053_supp.pdf).

Following the start of the experiment, we randomly collected 3 log samples every 2 mo for the first 16 mo, and every 4 mo thereafter for a total of 48 mo, resulting in a total of 45 samples (the remaining 3 samples were fully fragmented and lost in the field) (see Table S1 in the Supplement). Once collected, the

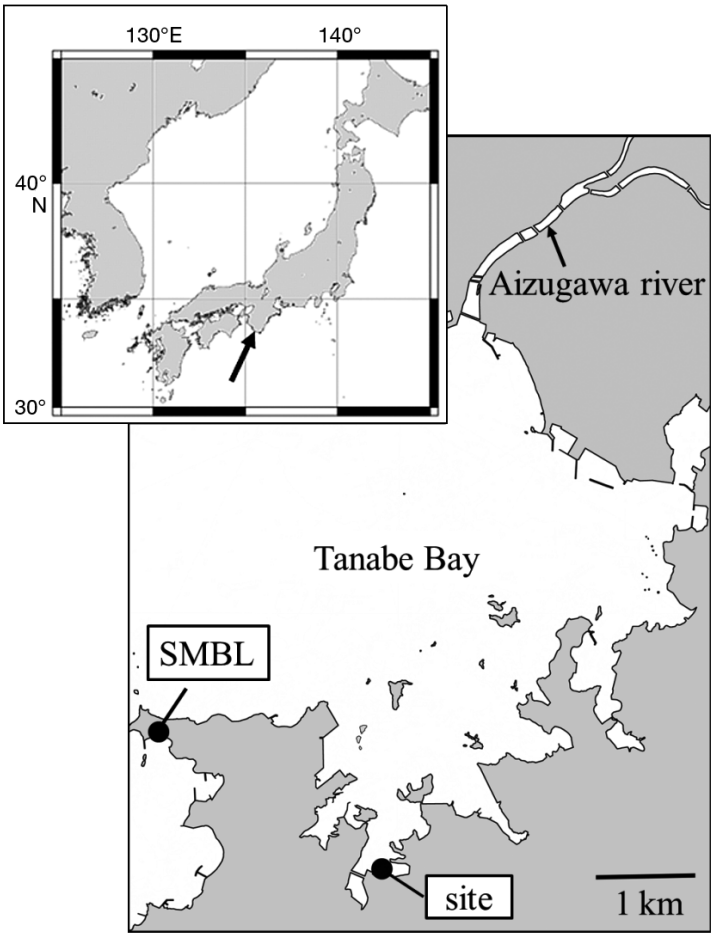

Fig. 1. Experimental site in the inner part of Tanabe Bay, Wakayama Prefecture, on the Pacific coast of central Honshu, Japan. SMBL: Seto Marine Biological Laboratory, Kyoto University

sampled logs were manually broken into small pieces to recover any resident wood-boring organisms. Because of the long, worm-like bodies of teredinids, it was often difficult to recover them in an intact condition, and in some cases, the pallet, a key character for species identification (see Fig. S2 in the Supplement) (Turner 1966), was lost. When this occurred, the specimen in question was treated as 'unidentified'. In the case of teredinids, we counted both live individuals and pairs of empty valves. Because teredinids bore deeply into the log, the empty valves left behind by dead individuals are generally dislodged from their tunnels only by subsequent wood-boring activities. The abundance of empty valves can thus be interpreted as an indicator of the degree of wood fragmentation. In contrast, we did not count pairs of empty pholadid valves, because small and ball-shaped dead shells just beneath the wood surface are lost even in the absence of further wood-boring activities, and are easily dissolved into the water.

Statistical analyses

For each sample, we counted the number of individuals in each family (Teredinidae, Pholadidae and Limnoriidae) and pairs of empty teredinid valves, and transformed all data by taking the 4th root. All 45 samples were then subjected to cluster analysis using a Bray-Curtis similarity matrix and average linkage. We defined sample groups from the dendrogram and tested for differences between them using one-way analyses of similarities (ANOSIM) and following pairwise tests. Similarity percentage (SIMPER) procedures were used to examine the contribution of each taxonomic group to the within-group similarity. All of these analyses were conducted using the software PRIMER v5 (Clarke & Gorley 2001).

Prior to deploying the logs on the sea floor, we measured the wet weight (wet wt) of each one. Following sample recovery and separation of all organisms, we dried the residues for 2 d at 80°C and then measured their dry weight (dry wt). Calcareous linings of the teredinids were not completely removed from the residues, but their weight is relatively small in comparison to that of wood itself. Three logs recovered 2 mo after the start of the experiment were almost intact, and thus could be used to calculate the baseline water content (Wc) of the test logs as:

$$Wc = 1 - \text{dry wt}_{2\text{mo}} / \text{wet wt}_{2\text{mo}} \quad (1)$$

With this information, we were then able to calculate the wood fragmentation ratio (Fr) as:

$$Fr = \left(1 - \frac{\text{dry wt}}{\text{wet wt} \times (1 - Wc)}\right) \times 100(\%) \quad (2)$$

Based on the result of SIMPER procedure, we divided our samples into 2 groups based on the taxon dominating each assemblage, i.e. bivalves (Group B) and isopods (Group I). After confirming the normality of both groups based on a Shapiro-Wilk test, we examined whether the 2 groups were associated with different wood fragmentation speeds by using a homogeneity test (ANCOVA). Both tests were conducted in R v2.13.1 (R Development Core Team 2011).

RESULTS

Long-term observations

As expected, the assemblage of wood borers comprised teredinids, pholadids and limnoriids (Table 1), which together disintegrated the test logs over a period of ~4 yr (see Fig. S3 in the Supplement). Two months after initiating the study, the teredinids had already started to settle on the logs (number of individuals of wood borers, *M*: mean ± SD = 29.0 ± 20.1) (Fig. 2; see also Table S2 in the Supplement). The largest number of individuals was recovered in the following spring (*M* = 111 ± 91.7), but most of the animals died within 1 yr. Teredinid abundance peaked in May every year, but the absolute number of individuals decreased over time (*M* = 29 ± 42.5 in 2010, 17.3 ± 10.0 in 2011, 9.33 ± 10.1 in 2012) (Fig. 2). Except for one test log (No. 9) recovered in the final sampling, teredinids were continuously collected throughout the experiment (see Table S2 in the Supplement). Pairs of empty valves were abundant between November 2009 and May 2011, followed by a sharp decline in September 2011 (Fig. 2).

Most of the live teredinid individuals (77.3%) were identified to species level and comprised 7 taxa (Table 1; see also Fig. S2 in the Supplement): 3 long-term larviparous species (release pediveliger larvae) (Calloway & Turner 1988), *Teredo bartschi* Clapp, 1923, *T. clappi* Bartsch, 1923, and *Lyrodus pedicellatus* Quatrefages, 1849 settled on the logs within 2 mo and actively bored into the logs in the 1st year, but decreased after the 2nd year (Fig. 3). Their abundance reached up to 60% of all recorded teredinid individuals (Table 1). One short-term larviparous species (release straight-hinge veliger) (Calloway & Turner 1988), *T. navalis* Linnaeus, 1758 was first collected 6 mo after the start of the experiment, but became the most abundant teredinid species in this experiment. After the 2nd year,

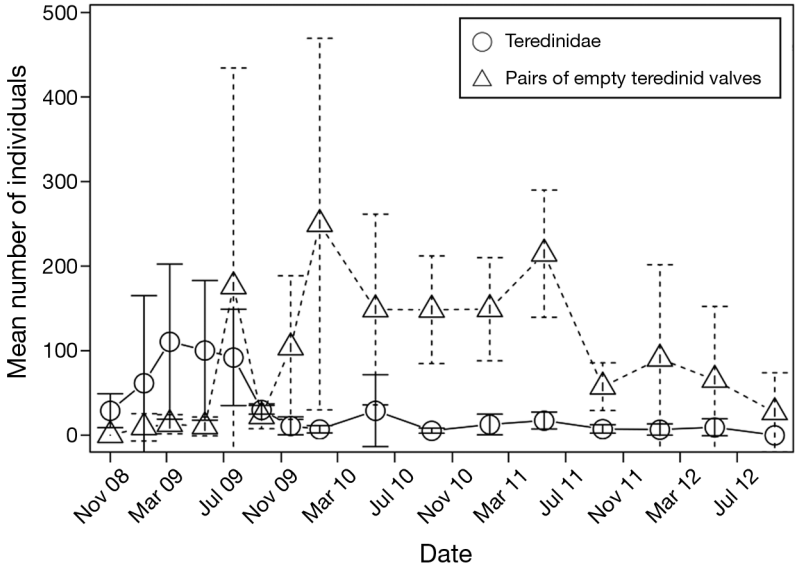

Fig. 2. Long-term changes in the teredinid assemblage collected from cedar logs (n = 3), shown as mean number of individuals (circles) and pairs of empty valves (triangles). Error bars: SD

Table 1. Composition and reproductive mode of the wood-boring community that formed on the test logs. *Psiloteredo megotara* is assumed to be an oviparous species because there are no records of *Psiloteredo* brooding larvae

Phylum	Family	Species	Reproductive methods	Total no. of individuals	
				Alive	Dead
Mollusca	Teredinidae	*Teredo navalis*	Short-term Larviparous[a]	484	–
		Teredo bartschi	Long-term Larviparous[a]	267	–
		Teredo clappi	Long-term Larviparous[a]	210	–
		Lyrodus pedicellatus	Long-term Larviparous[a]	249	–
		Teredothyra matocotana	Oviparous[b]	8	–
		Bankia carinata	Oviparous[b]	2	–
		Psiloteredo megotara	Oviparous	4	–
		Unidentified		364	4455
	Pholadidae	*Martesia striata*	Oviparous[c]	799	–
Crustacea	Limnoriidae	*Limnoria* spp.	Direct development (Brooding)	98 614	–

Data on the reproductive mode of some species are from Calloway & Turner (1988)[a], MacIntosh et al. (2012)[b] and Turner (1971)[c]

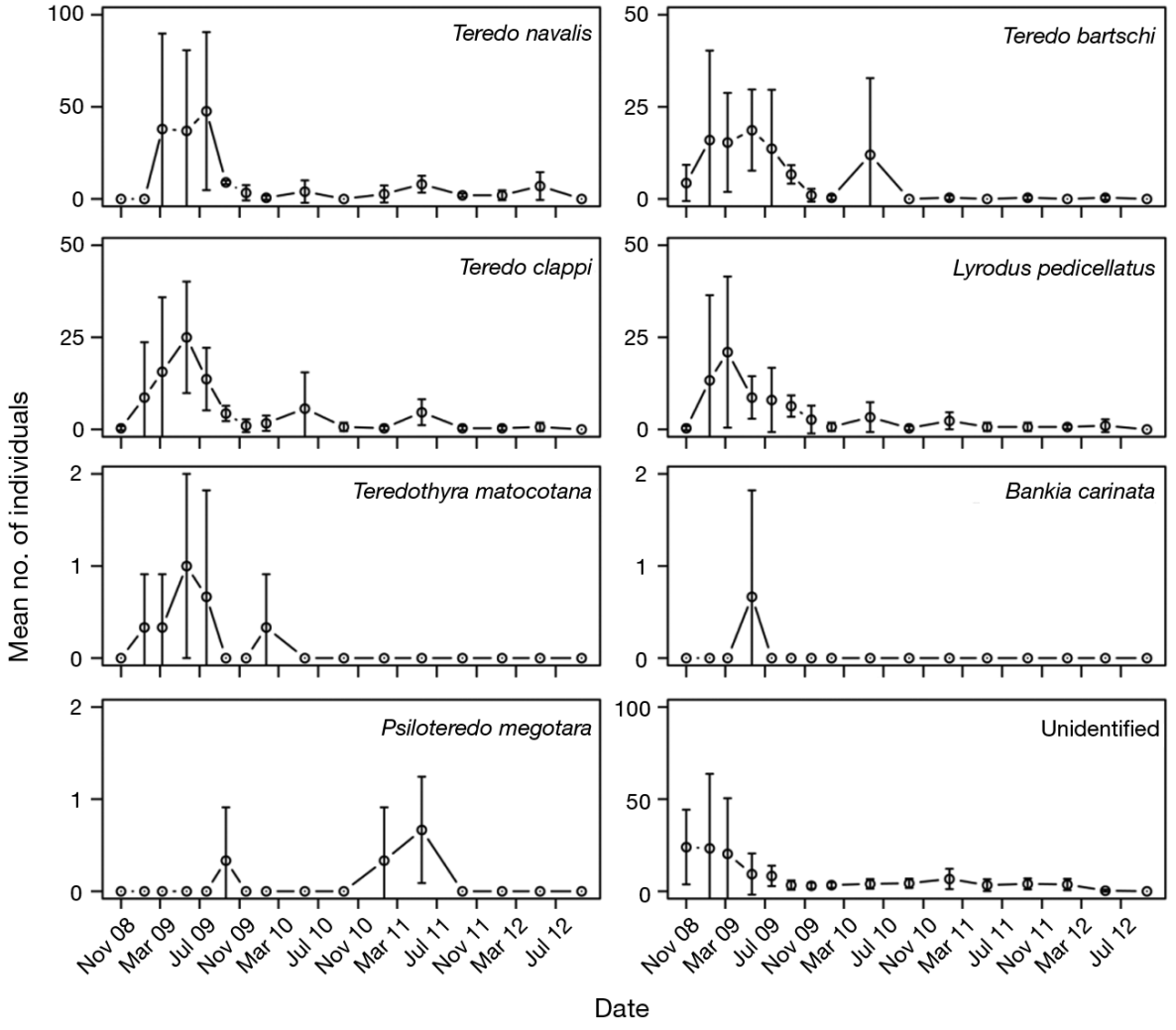

Fig. 3. Long-term change in the mean number of individuals of each teredinid species collected from the cedar logs (n = 3). Error bars: SD. Note the large differences in species abundance

this species also decreased, but its peak in May every year was clearly distinguishable (Fig. 3). The remaining 3 spawning species *Teredothyra matocotana* Bartsch, 1927, *Bankia carinata* Gray, 1827 and *Psiloteredo megotara* Hanley, 1848 were relatively rare (Table 1), with the former 2 settling on the logs only during the first 2 yr of the experiment (see Table S2 in the Supplement). There were no obvious changes in teredinid species composition as wood fragmentation progressed (Fig. 3).

The pholadid *Martesia striata* Linnaeus, 1758 settled on the logs within 2 mo after the start of the experiment (M = 13.3 ± 5.03) and suddenly increased in number between May 2010 (M = 3.33 ± 4.16) and September 2010 (M = 85.0 ± 54.7) (Fig. 4). This was followed by a sharp decline in January 2011 (M = 11.0 ± 13.0), following which *M. striata* occurred only rarely. Overall, the number of the pholadids was significantly lower than that of the teredinids in this experimental setting (paired t-test, $p < 0.05$).

Only a few individuals of the limnoriid *Limnoria* spp., including *L. tuberculata* Sowinsky, 1884 and *L. saseboensis* Menzies, 1957 (Nunomura & Shimomura 2012), started to bore into the logs after 2 mo (M = 1.33 ± 0.88). Limnoriid numbers remained low during the early phase of the experiment, but then increased exponentially and finally peaked in September 2011 ($M = 6.20 \times 10^3 \pm 1.96 \times 10^3$) (Fig. 5). This was followed by a sharp decline in January 2012 ($M = 1.05 \times 10^3 \pm 1.20 \times 10^3$), but individuals of both *L. tuberculata* and *L. saseboensis* continued to be collected until the logs were completely disintegrated.

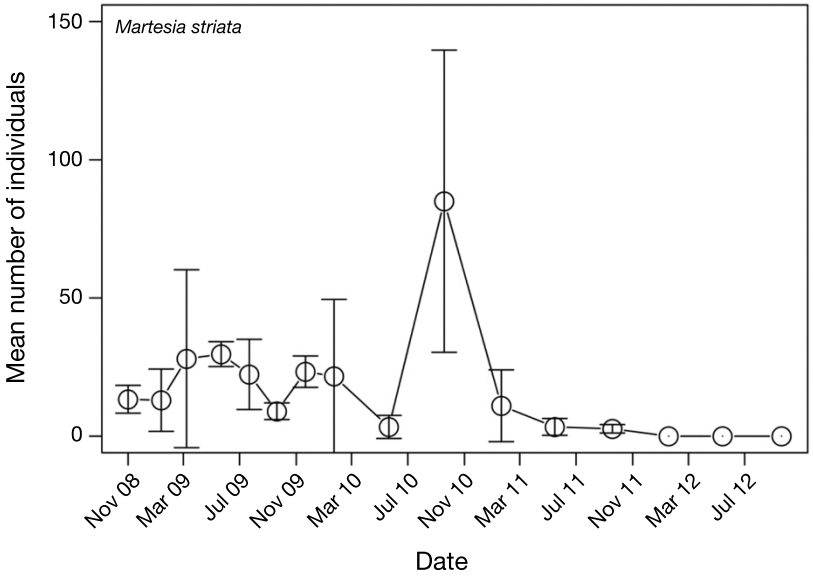

Fig. 4. Long-term change in the mean number of individuals of the pholadid *Martesia striata* collected from the cedar logs (n = 3). Error bars: SD. The mass settlement of *M. striata* in September 2010 was also observed in another unrelated experiment (A. Nishimoto unpubl. data) and is therefore not related to the degree of wood fragmentation

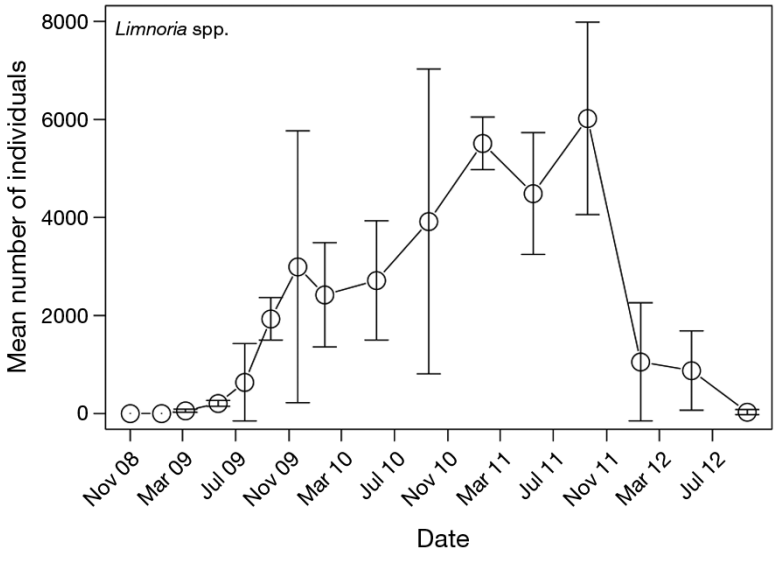

Fig. 5. Long-term change in the mean number of individuals of the limnoriid *Limnoria* spp. (including *L. tuberculata* and *L. saseboensis*) collected from the cedar logs (n = 3). Error bars: SD

Cluster analysis

The dendrogram revealed 3 Clusters (I–III) defined by varying community structures and periods of submersion (Fig. 6, Table 2), with Cluster II further divided into 5 Subclusters (II-a to II-e). There were significant differences (one-way ANOSIM; global R = 0.837, $p < 0.001$) between all pairs of clusters and subclusters ($p < 0.05$, pairwise R values range: 0.633 to 1). Wood samples from Cluster I were characterized by the early settlement of wood borers, all of which (except for some specimens of the pholadids) started to bore into the logs from the cut ends (Fig. 7). In Subcluster II-a, the logs remained intact externally, but their interiors were rapidly fragmented by large numbers of teredinids. The opposite situation was observed in Subcluster II-e, where the logs remained mostly intact internally, but their cut ends were intensively attacked by limnoriids (Fig. 7). After fragmenting the inside of the logs, most of the teredinids disappeared in Subcluster II-b. At the same time, the limnoriids proceeded to excavate the wood from the cut end and destroyed some of the empty tunnels left behind by the teredinids (Fig. 7). In only one test log (No. 53), filamentous bacteria formed a mat harboring the symbiotic ciliate *Zoothamnium niveum* (Rinke et al. 2006) around the openings of some of the empty teredinid tunnels (Fig. 8).

In all the stages distinguished by the 4 previous clusters and subclusters, the bark was still attached to the logs and the external surface remained largely intact. However, once the tree bark had been peeled off, the limnoriids started to attack the logs from all sides (Subcluster II-c), exposing many of the empty teredinid tunnels in the process (Fig. 7). This, in turn, allowed the limnoriids to enter those tunnels and bore further into the log, which led to advanced disintegration and the loss of many empty teredinid valves (Subcluster II-d). This process culminated in the complete break-up and loss of the test log, which occurred after 44 (log No. 51) and 48 mo (Nos. 10 and 42). The remaining samples were generally reduced to fragments buried almost entirely by sediment (Cluster III), with the exception of log No. 48, which was recovered nearly intact after 16 mo. Statistically, this sample fell into Subcluster II-d owing to the absence of pholadids; however, the condition of the log was similar to those of logs in Subcluster II-e.

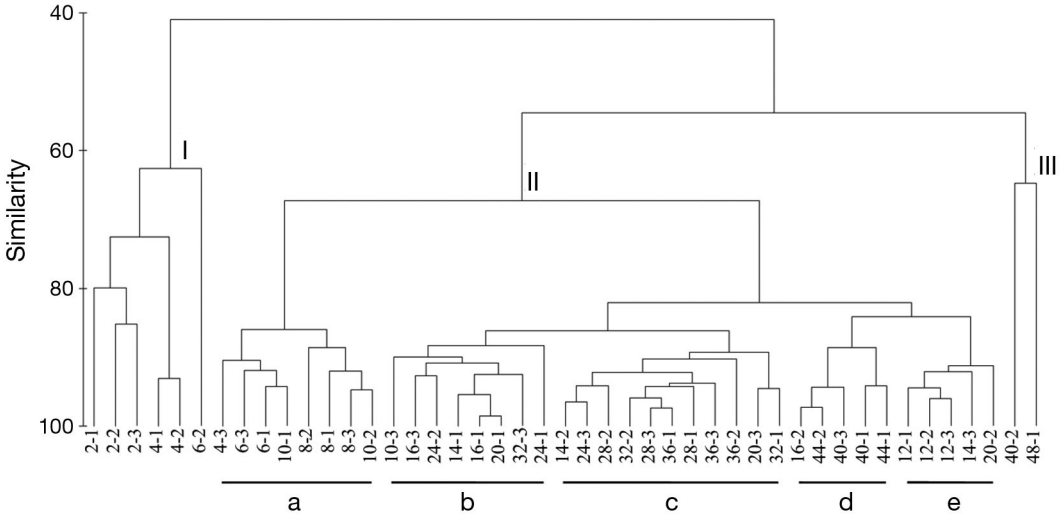

Fig. 6. Cluster dendrogram of the assemblage of wood borers collected from the cedar logs. The 45 samples were divided into 3 Clusters (I–III); Cluster II was further divided into 5 Subclusters (II-a to II-e). Sample labels record submergence time in months, followed by the number of the sample (1 to 3)

Wood fragmentation ratio

The water content (*W*c) value was calculated to be 0.364 (±0.0294), and was applied in Eq. (2) to obtain the wood fragmentation ratio. The wood-boring organisms dominating our samples clearly changed over the 4 yr that they took to break apart the test logs, from bivalves in Clusters I and II-a (Group B), to limnoriid isopods in the remaining clusters (Group I) (Fig. 7, Table 2). Regressions of the wood fragmentation ratios of these 2 groups against time revealed faster rates of fragmentation in Group B than in Group I (Fig. 9). However, the slopes of the regression lines were not significantly different between these 2 groups (homogeneity test; $p = 0.0535$).

DISCUSSION

Biological wood fragmentation dynamics

Wood fragmentation in the ocean depends on several factors, such as the tree species, water depth, salinity, the geographical location and wood boring species present at the site (Southwell & Bultman 1971, Tyler et al. 2007, Laurent et al. 2013). Tree species differ in their natural resistance to wood-boring organisms; abrasiveness, hardness, density and extractives confer their durability in a variety of ways (Edmondson 1955, Southwell & Bultman 1971, Borges et al. 2008). As shown by wood borer's rapid colonization, none of these attributes seem to apply

Table 2. Number of individuals (and % contribution) per fragmentation stage and taxonomic group based on the SIMPER procedure. EV = empty valves. –: taxonomic group was not shared by all samples belonging to the stage

Stage: (Sub) Cluster	Immersion period (mo)	Characters	Dominant taxonomic group No. of individuals (% contribution) 1st	2nd	3rd	4th
Stage 1: Cluster I	2–6	Early settlement of wood bores	Pholadidae 9.17 (50.1)	Teredinidae 16.0 (44.1)	Limnoriidae 11.0 (5.79)	– –
Stage 2 — case 1: Subcluster II-a	4–10	High-density settlement of wood-boring bivalves	Teredinidae 132 (32.3)	Limnoriidae 140 (26.8)	Pholadidae 28.4 (22.3)	Teredinidae – EV 19.0 (18.6)
Stage 2 — case 2: Subcluster II-e	12–20	Low-density settlement of wood-boring bivalves	Limnoriidae 1.65×10^3 (50.7)	Teredinidae 38.2 (19.2)	Teredinidae – EV 28.6 (17.4)	Pholadidae 9.20 (12.6)
Stage 3: Subcluster II-b	10–24	Honeycombed wood logs	Limnoriidae 2.53×10^3 (47.6)	Teredinidae – EV 288 (28.1)	Pholadidae 40.8 (14.4)	Teredinidae 9.25 (9.88)
Stage 4: Subcluster II-c	14–36	Intensive attack to the wood surface by the limnoriids	Limnoriidae 5.61×10^3 (61.1)	Teredinidae – EV 116 (21.6)	Teredinidae 9.91 (11.0)	Pholadidae 13.2 (6.35)
Stage 5: Subcluster II-d	40–44 (16, 40–44)	Collapse of the woods from the surface	Limnoriidae 1.42×10^3 (57.1)	Teredinidae – EV 99.8 (26.1)	Teredinidae 11.8 (16.9)	– –
Stage 6: Cluster III	40–48	Disappearance of the woods	Limnoriidae 52.0 (58.2)	Teredinidae – EV 42.5 (41.8)	– –	– –

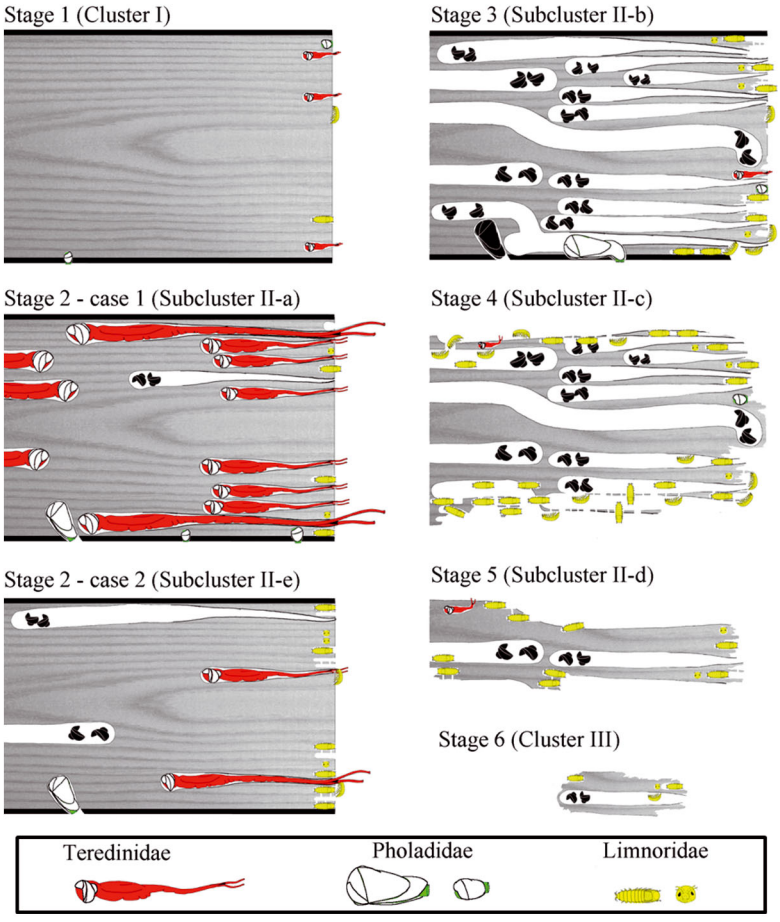

Fig. 7. Schematic illustration of the wood fragmentation process. Samples are shown in a longitudinal section; Thick black lines are tree bark. Empty valves are black

Fig. 8. Bacterial mat growing on the cut end of one of the cedar logs collected 10 mo after the start of the experiment. Inset: *Zoothamnium niveum*

in the case of the Japanese cedar *Cryptomeria japonica*. Even under the same experimental settings, the recruitment of wood borers varies with time, as shown in the case of the pholadidae (Fig. 4). At this site, however, pholadids seem to react negatively to high levels of suspended sediment loads, which may explain the death of a large number of individuals during the winter of 2010/2011 (Fig. 4). Where sedimentary input is low, the recruitment of pholadids will facilitate the rapid disintegration of the wood owing to their relatively large size and destructive burrowing technique.

In light of such variation, standardizing the wood fragmentation process across different environments possesses a serious challenge. However, the results of our study provide a useful framework within which different phases of fragmentation can be described. Specifically, the clusters revealed by our analyses hint at 6 successive stages in the wood fragmentation process: Stages 1 (Cluster I), 2 (Subclusters II-a and II-e), and 3 (Subcluster II-b), during which the wood is fragmented primarily internally; and Stages 4 (Subcluster II-c), 5 (Subcluster II-d), and 6 (Cluster III), in which the wood collapses and ultimately disintegrates (Table 2, Fig. 7). During Stage 1, the test logs were immediately invaded by species of all 3 major wood-boring taxa (Teredinidae, Pholadidae, and Limnoriidae), irrespective of their different dispersal abilities (Table 1). In the case of the sedentary teredinids and pholadids, the instant colonization was likely due to the dispersal of pelagic larvae (Turner 1966, Calloway & Turner 1988, MacIntosh et al. 2012). By contrast, limnoriids undergo direct development and disperse mainly through occasional movements of free-swimming individuals (Thiel 2003). However, limnoriids are not considered active swimmers (Johnson 1935, Quayle 1992), and their rapid recruitment probably resulted from the abundance of coarse woody debris near the experimental site. Following initial settlement during Stage 1, further development of the samples took one of 2 alternative paths: (1) where larval recruitment was high, the inside of the log was rapidly fragmented by teredinids (Stage 2—case 1), and (2) if

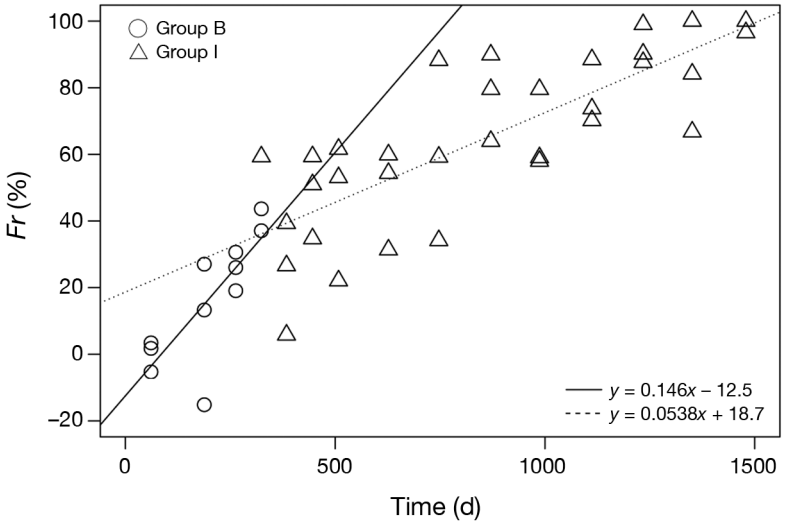

Fig. 9. Scatter plot showing the wood fragmentation ratio (*Fr*) of each sample. Group B: bivalves in Clusters I and II-a; Group I: limnoriid isopods in the remaining clusters. We excluded samples collected after 4 mo because some woody particles were lost during sorting. Some samples had negative *Fr* values because their water contents (*Wc*) were lower than the standard *Wc* value. The *Fr* of samples that completely disintegrated in the field is assumed to be 100%

larval recruitment was low, fouling animals formed a tight mat on the surface of test logs and prevented wood-boring bivalves from further recruiting (Nair & Saraswathy 1971, Southwell & Bultman 1971), thus keeping the inside of the log largely intact (Stage 2 — case 2). However, once the limnoriids settle on the wood surface, such a tight mat cannot prevent them from fragmenting the surface of the wood because their brooding larvae excavate from parental burrows (Southwell & Bultman 1971, Thiel 2003).

The internal fragmentation of the logs by the teredinids initially did not lead to their collapse even after the animals themselves had died (Fig. 7, 9) (Stage 3). This is because the teredinid tunnels (1) never crossed each other, and (2) were reinforced with a lining of calcium carbonate (Turner 1966). In addition, the absence of large-scale collapse means that the log maintained a relatively low surface/volume ratio, which in turn limited microbial decay (Camilleri & Ribi 1986). Marked disintegration (Stage 4) set in only after the tree bark was finally detached from the underlying wood, and the newly exposed surface was rapidly colonized by wood-boring organisms. This process was primarily driven by the limnoriids, whose abundance — unlike that of the teredinids — rapidly increased as a result of this drastic change of substratum (Figs. 2, 5, 7). The greater success and more destructive effect of limnoriids at this stage likely resulted from their particular boring behavior, which includes the creation of holes for respiration (Eltringham 1965) and channels connecting different tunnels (Thiel 2003) (Fig. 7). When fragmentation of the wood neared completion, the sedentary pholadids were the first to disappear from the assemblage of wood borers (Stage 5) because their destructive boring habits rapidly reduced the physical strength of the log. In contrast, the mobile limnoriids were able to utilize a range of ever-smaller fragments, unless the fragments were completely buried by sediment (Stage 6). While the disintegration by the limnoriids progressed slowly, sedentary teredinids were also able to settle on the small and fragile pieces of wood.

Adaptations of wood borers to transient substrates

This study clearly demonstrates that wood fragmentation in temperate shallow water is sometimes considerably faster than that on land (Harmon et al. 1986, Stokland 2001, Stokland et al. 2012) or in rivers (Anderson et al. 1984, Ward & Aumen 1986, Díez et al. 2002) (Figs. 7, 9). Given the rapid disintegration of woody debris in shallow temperate waters, wood-boring organisms need efficient strategies to make use of the relatively short window of opportunity each piece of debris provides (MacIntosh et al. 2012) and to cope with marked differences in the availability of wood across different regions (Hinojosa et al. 2011). Our study showed 3 ways in which different animals have adapted to these challenges: (1) fast development (our Figs. 2, 9; MacIntosh et al. 2014) and a reduction in body size, as exemplified by the teredinid *Teredo navalis*, which matures in only 6 wk at a body length of 15 to 20 mm (Grave 1937, Bulatov 1941), thus enabling it to settle and feed on even small pieces of debris (Figs. 2, 7, see Table S2 in the Supplement); (2) specialized boring abilities, as in the case of the pholadid *Martesia striata*. Unlike teredinids and limnoriids, *M. striata* can bore through non-cork bark, which may provide them with an advantage in the competition for woody substrates (Fig. 7); and (3) specialized modes of reproduction

(Calloway & Turner 1988, MacIntosh et al. 2012). The composition of the relatively diverse teredinid fauna was clearly dominated by larviparous forms, with 99% of all recorded individuals falling into this category (our Fig. 3, Table 1; MacIntosh et al. 2012). Their larviparous mode of reproduction limits the ability of these animals to disperse (Lebour 1946, Calloway & Turner 1988) and may represent an adaptation to living in semi-enclosed coastal areas where woody debris is likely to accumulate. By contrast, oviparous species are able to disperse widely (Turner 1966), and hence are more likely to be found on isolated pieces of woody debris that have been washed out to sea. Moreover, long-term larviparous species dominated the teredinid fauna at this experimental site (Table 1), unlike the results in MacIntosh et al. (2012) where short-term larviparous species dominated the fauna. The abundance of teredinids with specific reproductive methods might therefore indicate the historical background of wood in the sea, i.e. from where the wooden materials were transported.

The variability of microhabitats generated by wood borers

Most organisms cannot feed on coarse woody debris directly (but see Becker et al. 2009, Hoyoux et al. 2009, Zbinden et al. 2010). Through its degradation process, i.e. leaching, physical fragmentation and decay (Harmon et al. 1986), it becomes possible for various invertebrates to use organic materials derived from coarse woody debris as their food source (Nishimoto et al. 2009). It is wood-boring invertebrates that play an important role in facilitating the degradation of wood in the sea (Turner 1973). In earlier studies, boring rate (mm d^{-1}) or fecal pellet production rate (number of fecal pellets d^{-1}) for each individual were measured (Manyak 1982, Borges et al. 2008), but the wood fragmentation speed itself has not been quantitatively measured. Using the weight reduction ratio of wood (*Fr*), we clearly demonstrate that teredinids rapidly excrete their fecal pellets around the wood logs, and the resulting honeycombed structure remains stable in the sea (Fig. 9). Coarse woody debris, therefore, simultaneously serves as both food source and shelter for various organisms, allowing the ongoing development of the sunken wood community in the sea.

The availability of food and space for the species forming part of a sunken wood community varies considerably between successive stages of the fragmentation process (Fig. 7), with each stage potentially harboring a unique assemblage of marine invertebrates (Bienhold et al. 2013, Laurent et al. 2013). For example, predatory polychaetes (e.g. Chrysopetalidae, Nereididae, and Amphinomidae) have been recorded in the tunnels of wood-boring bivalves (from sunken wood: Pettibone 1985, Russell 1997, Nishimoto et al. 2009, Borda et al. 2012; from rafting wood: Thiel & Gutow 2005), and relied on the bivalves as their major food source (Nishimoto et al. 2009). In shallow water, however, teredinids rapidly decreased in number as fragmentation progressed and were replaced by limnoriids as the dominant wood borer (Table 2). Limnoriids are considerably smaller than teredinids, and hence only serve as a minor food source for fish (Fabi et al. 2006) and other species in sunken wood communities.

In addition to this heterotrophic food chain, chemosynthetic bacteria are known to provide an additional source of food in the deep sea (Lorion et al. 2010, Bienhold et al. 2013) and tropical mangrove swamps (Laurent et al. 2009, 2013). The sulfide contents around the surface of *Rhizophora mangle* and *Cocos nucifera* are at their maximum several days after the logs have been immersed in the mangrove swamps, and the high concentration of hydrogen sulfide is sustained only for a few months (Laurent et al. 2009, 2013). Also regarding *Cryptomeria japonica*, bacterial mats covered the cut end around its heartwood 1 mo after the experimental start. This sulfidic condition is expected to be attributed to the decay of woody extractives. In the case of *Pseudotsuga menziesii* deployed in the Eastern Mediterranean deep sea, Bienhold et al. (2013) assumes that the chemosynthetic symbioses will be formed after the wood-boring activities.

In this study, we reported for the first time *Zoothamnium niveum*, an indicator of chemosynthetic conditions, from a wood log in temperate shallow water (Fig. 8). Thus, chemosynthetic habitat around wood logs is not peculiar to the deep sea and mangrove swamps, and is expected to be common in the sea. In the case of *Cryptomeria japonica*, it took 10 mo before *Z. niveum* was observed on one cedar log, and after the sampling, *Z. niveum* was no longer observed (Fig. 8). The cedar sample (No. 53) belonged to Stage 3, and the teredinids dead remains were rotting in their bore-holes after predation by Amphinomidae. The honeycombed structure leads to water stagnation in the cavities, and facilitates the build-up of hydrogen sulfide (Yücel et al. 2013). From these facts, it can be concluded that (1) the amount of cedar extractives is so small that chemosynthetic symbioses are not produced in response to their degradation,

even in the cavities, and (2) chemosynthetic conditions arise from the dead remains of teredinids, which on decay give off hydrogen sulfide. That is, whether the sulfidic condition is formed with or without the mediation of wood borer depends on the tree species involved. In the case of tree species like Japanese cedar, not only wood borer recruitment (Romey & Bullock 1991, Tyler et al. 2007), but also predator–prey interactions will control the concentration of hydrogen sulfide around the wood logs. The remains of teredinids are, however, rapidly consumed by various scavengers or predators (Pettibone 1985, Russell 1997, Nishimoto et al. 2009), and the resulting sulfidic condition might not last so long in the sea.

This rapid and dynamic wood fragmentation process and associated microhabitat is not universal in the sea (Southwell & Bultman 1971). In future studies, however, the present study will play a role as a useful framework for comparing wood-boring activities across various conditions. Those comparisons will help to evaluate the roles of coarse woody debris in marine ecosystems.

Acknowledgements. We thank Keita Harada (Seto Marine Biological Laboratory) and Go Suzuki (Seikai National Fisheries Research Institute, Fisheries Research Agency) for their assistance with the experiment, Felix G. Marx (JSPS Postdoctoral Research Fellow, National Museum of Nature and Science) for his help in preparing the manuscript, and Michitaka Shimomura (Kitakyushu Museum of Natural History & Human History) for his assistance in the species identification of the limnoriids. This study was funded by a Grant-in-Aid for JSPS fellows to A.N. (#222580) and to T.H. (#237855).

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Editorial responsibility: Erik Kristensen, Odense, Denmark

Submitted: January 5, 2015; Accepted: August 11, 2015
Proofs received from author(s): October 10, 2015