REVIEW ARTICLE

Xylotrophic bivalves: aspects of their biology and the impacts of humans

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ABSTRACT

Bivalves of the families Teredinidae and Xylophagaidae bore into and eat wood in shallow water and the deep sea, respectively. After an introduction to these sister taxa, I consider how they bore, focussing on the evolution of the cephalic hood in teredinids, which could contribute to the depth separation between the families. If the hood serves as a counter pressure to the foot, it may be vital in allowing teredinids to bore wood that contains air. The availability of wood has been suggested to determine the distribution of these animals. Mangrove habitats with abundant wood sustain the highest diversity, about one-third of all known teredinids. The open ocean, where wood is all but nonexistent, presents a nearly impassable barrier to most wood borers. Only after wooden sailing ships transported teredinids between ports did introduced species become problematic. Despite the rarity of wood in the open ocean, some xylophagaids live there as, it is hypothesized, do a limited number of teredinids; wood in the open ocean is predicted to be large because large size enhances buoyancy. The life history of open-ocean species may differ fundamentally from that of nearshore species. Physical stressors of temperature, salinity and desiccation appear to affect teredinids minimally; xylophagaids on the seafloor do not experience these variables. How biotic interactions such as competition and predation affect wood borers is yet to be thoroughly studied, but their impact may be greater than has been recognized, especially among teredinids. Although humans regard teredinids as pests that destroy wooden structures, and attempt to eradicate them from some areas, these animals play vital ecological roles. Teredinids make the energy and nutrients locked into wood available to the local community. Xylophagaids are nearly unique in breaking down cellulose and are analogous to primary producers in sustaining the diverse deep-sea wood-fall communities. The survival of borers requires wood to be present. The reduction of trees near water courses, removal of driftwood from navigable rivers and the destruction and fragmentation of the world's mangrove habitats all threaten the predictable supply of wood in the sea and may seriously threaten the survival of these molluscs.

INTRODUCTION

Two families of bivalves, the Teredinidae and the Xylophagaidae, require wood or other vegetation such as the rhizomes of eelgrass on which to settle; they then undergo metamorphosis and begin to bore into and eat the wood. Although Turner (1968: 46) considered the two groups to be "a study in contrasts", they are now recognized as sister families (Distel *et al.*, 2011). Their morphological synapomorphies are hypothesized to include wood-boring, the wood-storing cecum, the loss of the outer gill and symbiotic bacteria on the gills (Distel *et al.*, 2011). This review approaches them as a single entity, highlighting their many similarities, identifying common constraints on their distribution and evolution and considering their depth separation. Whereas previous reviews (Turner, 1966; Nair & Saraswathy, 1971; Nair,

1988) have treated shallow-water teredinids as pests due to their destruction of wooden structures such as docks, boats and piers (Fig. 1), I consider the impacts of humans on these borers. The huge economic cost of damage done by teredinids to waterfront structures means that far more is known of their biology than that of the relatively inaccessible deep-sea xylophagaids. The recent resurgence of interest in these animals and their habitats, as evidenced by the publication dates of references cited herein, indicate that a review is timely.

A recent molecular phylogenetic study found the teredinids and xylophagaids to be monophyletic sister taxa, with the Pholadidae being their nearest outgroup (Distel *et al.*, 2011). Previously, the deep-sea wood borers had been classified as a subfamily within pholadids, and the teredinids as a distinct family. Turner (1968) supported this classification, arguing that

Figure 1. Destruction in the San Francisco Bay area attributed to *Teredo navalis* in three historical photographs. Photo: Union Oil Co. from Hill & Kofoid (1927).

only superficial similarities (mostly in shell morphology) united the teredinids and xylophagaids; she felt that the anatomically distinct teredinids required family-level recognition while the 'more typical' xylophagaids did not. Anatomical studies of the two groups led Purchon (1941) to view the deep-sea species as a distinct family, the Xylophagaidae, closely related to the Teredinidae. Following Haga & Kase (2013), and the congruent anatomical (Purchon, 1941) and molecular (Distel *et al.*, 2011) data, I treat the deep-sea wood borers as the Xylophagaidae, composed of the genera *Xylophaga*, *Xylopholas* and *Xyloredo*. I follow Turner's (1966) taxonomy and synonymies of the Teredinidae.

I focus on the teredinids and xylophagaids that not only bore into wood (or other vegetation), but ingest and then digest the wood with the aid of symbiotic bacteria living on the gills (Distel & Roberts, 1997; Sipe, Wilbur & Cary, 2000; Distel, Beaudoin & Morrill, 2002a; Distel *et al.*, 2002b; Luyten *et al.*, 2006). I omit the pholadid genus *Martesia*, which bores into, but does not ingest wood, the teredinid genus *Kuphus* that apparently bores into marine sediments (Distel *et al.*, 2011) and an unnamed mudstone-boring form attributed to *Spathoteredo* (Lozouet & Plaziat, 2008: 54, pl. 10). Details of nutrition, such as how the bacteria-generated proteins are transported from the gills to the host's gut (which remain to be resolved; O'Connor *et al.*, 2014) and whether wood boring sustains the animals throughout their lives (Paalvast & van der Velde, 2013), are not pursued here.

GENERAL MORPHOLOGY AND IDENTIFICATION

Teredinids and xylophagaids can co-occur. Externally their valves can appear so similar that correctly identifying them can be difficult. Both families have markedly asymmetric valves that are covered anteriorly by rows of toothed denticles (Fig. 2A); anteroventrally the valves gape, exposing the discoid foot. The rows of denticles define the anterior slope (Fig. 2B, C) (Turner, 1966), while to the posterior is the generally smooth disc. The posterior slope may be expanded to form an ear-shaped lobe or auricle that carries the posterior adductor (Fig. 3A; Turner, 1966: fig. 16A–E). The anterior adductor inserts on the medial anterio-dorsal part of the valve. The most prominent feature of the inner teredinid valve is the styloid apophysis (Fig. 3A; often damaged in shell specimens), the attachment of the pedal retractor muscle.

The valves of intact teredinids are conspicuously small relative to the body and siphon. The animal secretes a calcareous tube that lines its borehole (Fig. 4). The siphons, which contain the gills and parts of the digestive system, extend the length of the tube (Fig. 4). Just proximal to the siphonal openings at the posterior end of the calcareous tube is the pair of paddle-shaped pallets (Fig. 4), one of the unique features of the Teredinidae (Turner, 1966). Muscles that insert on the blade-like bases of the pallets move them in and out of the borehole; closure can be so effective that the borehole is functionally sealed.

The pallets are critical in species identification (Fig. 5), but can become unreliable once dry. In addition, ontogenetic change, physical impacts, wear, chemical dissolution and overcrowding can affect their appearance (Turner, 1966; Leonel, De Moraes & Lopes, 2006; Borges *et al.*, 2012). Additional characters need to be explored to define species boundaries more effectively. Laboratory observation of the duration of larval brooding by Calloway & Turner (1983) distinguished *Lyrodus pedicellatus* (Quatrefages, 1849) from *L. floridana* (Bartsch, 1922). Three additional cryptic-species pairs identified by the same criterion (Turner & Calloway, 1987) have yet to be assessed further. So far, molecular methods have rarely been applied to wood borers; examples for teredinids include studies by Santos *et al.* (2005), Borges *et al.* (2012, 2014) and Shipway *et al.* (2014). Despite their inclusion of few species, the molecular phylogenetic analysis of Distel *et al.* (2011) questioned the monophyly of several genera.

Xylophagaid valves (Fig. 3B) lack the styloid apophysis; instead, the pedal retractor inserts on the inner surface of the valve. The posterior slope is continuous with the disc, and the anterior adductor inserts on the umbonal reflection. The paired accessory plates form the highly variable mesoplax, which covers the anterior adductor dorsally. In contrast to teredinids, the bodies of xylophagaids lie within their valves and the siphon can be fully withdrawn in some, although not all, taxa. Among xylophagaids, calcareous tubes surround the siphons only in the genus *Xyloredo* (best documented by Haga & Kase, 2008). In a few species of *Xylophaga*, periostracal cones cover the siphons, e.g. *X. gerda* Turner, 2002 and *X. heterosiphon* Voight, 2007. Species descriptions are based on morphology of both soft and hard parts; DNA sequence data have been helpful in reconstructing higher level relationships (Distel *et al.*, 2011) and in demonstrating within-species morphological variation in *Xylophaga* (Romano *et al.*, 2014).

BORING MECHANISM

How these bivalves bore into wood had long been debated (Nair & Ansell, 1968), until Miller (1924) replaced a small section of the borehole wall of a *Teredo* with glass to watch it *in situ*. After acclimating, the teredinid resumed what appeared to be normal boring. Based on his review of teredinid anatomy and limited observations of live animals *in situ*, Miller (1924) concluded, as
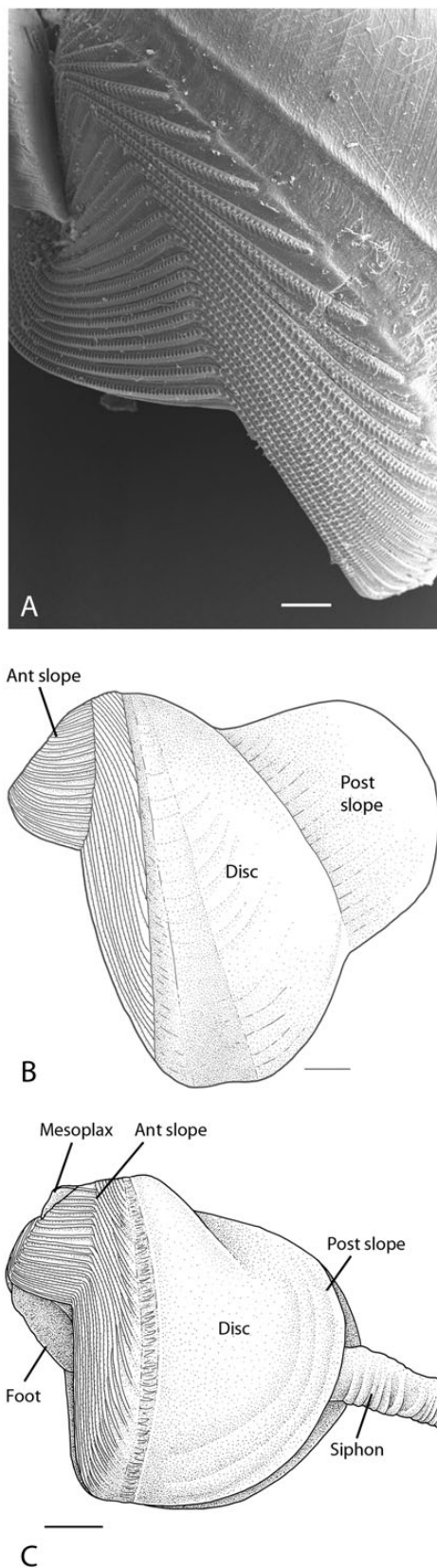
Figure 2. A. SEM of denticles on anterior slope of *Xylophaga multichela*. **B.** Exterior of a teredinid valve (FMNH 312232) collected without pallets. Note denticles on anterior slope. **C.** Exterior of *Xylophaga oregona* valve. Note denticles on anterior slope. Abbreviations: Ant slope, anterior slope; Post slope, posterior slope. scale bars: A = 100 μm; **B**–**C** = 1 mm.

had von Baumhauer (1878), that the denticles on the dorsolateral anterior slope scraped the wood. Heavily worn denticles on this area of the valve of *Xylophaga oregona* Voight, 2007 (Fig. 6) support the same hypothesis for xylophagaids, although acidic conditions in the borehole may enhance the apparent wear. Miller's (1924) report outlines the following steps in boring. The exceptionally mobile foot attaches firmly to the blind end of the borehole. The cephalic hood becomes distended, firmly securing the teredinid in the borehole and directing wood scrapings to the mouth. As the posterior adductor contracts, abducting the denticle-covered anterior slope, the denticles scrape the blind end of the borehole. Contraction of the anterior adductor provides the recovery stroke. Opposing contractions of the anterior and posterior adductors cause the bivalve to pivot about its dorsoventral axis (Ansell & Nair, 1969). Ligaments at the dorsal knobs (chondrophores) and at the ventral condyles help to stabilize the animal (Miller, 1924).

Miller (1924) mentioned distension of the cephalic hood almost incidentally, but Board (1970) suggested that it is vital to the boring mechanism of teredinids and represents a key innovation in their evolution. To appreciate its importance, some background is required. Wood is composed of tracheids and, in angiosperms, vessels that conduct fluids vertically in living plants; they are also conduits in dead wood. These structures form the wood grain, along which teredinids typically bore (e.g. Thompson, 1847; Knudsen, 1961; Voight, 2008). Board (1970) argued that because teredinids bore with the wood grain, they follow the path of water movement; this is in contrast to xylophagaids, which bore across the grain (e.g. Thompson, 1847; Knudsen, 1961; Voight, 2008) In Board's (1970: 196) view, distention of the teredinid's cephalic hood by hydrostatic pressure from the mantle, coupled with the closure of the siphons, allows a teredinid "to act as a plunger within its tunnel and force water into the unlined wood at the blind end". He argued that forcing water into the unlined wood softens it, dissipates heat and flushes bits of substrate from the cutting surface. However, I suggest that the increased pressure generated by the distention of the cephalic hood and the closure of the siphons addresses a more fundamental issue: the presence of air in a fluid system. Air is problematic because, in contrast to water, its volume changes with ambient pressure. Teredinids had to overcome this problem to be able to bore wood containing air.

In boring bivalves, the paired pedal retractor muscles form most of the foot; the pedal haemocoel is replaced by loosely arranged connective tissue (Ansell & Nair, 1969). Nair & Ansell (1968) outlined the steps in boring that reveal why this is significant. After the foot contacts the blind end of the borehole, its margins extend. If the margins of the foot firmly adhere to the wood, when the pedal retractors contract to pull the shell to the blind end of the borehole (and maximize its contact with the wood), the medial foot must be placed under tension. With the margin of the foot firmly sealed to the wood, tension on the medial foot will reduce the pressure beneath it. If the tracheids and vessels under the foot are air-filled, under reduced pressure the air will expand, potentially undermining the foot's attachment to the wood. The cephalic hood in teredinids (Fig. 4) may act as a counter pressure to the foot, generating enough pressure to prevent bubble formation in dry wood. Ansell & Nair (1969: 127) suggested that an area of connective tissue "surrounding the anterior adductor muscle in the anterior dorsal region of the mantle" (apparently near the mesoplax in *Xylophaga*; Fig. 2C) serves this role in *Martesia* and *Xylophaga*. The cephalic hood in teredinids may be an evolutionary elaboration of this tissue, which permitted them to bore into floating, air-filled wood. In contrast, xylophagaids generally bore into sunken (and therefore airless) wood, while pholads bore into subtidal rock and sediment; neither group requires a mechanism to bore in the presence of air. If teredinids are unique in tolerating air in the wood
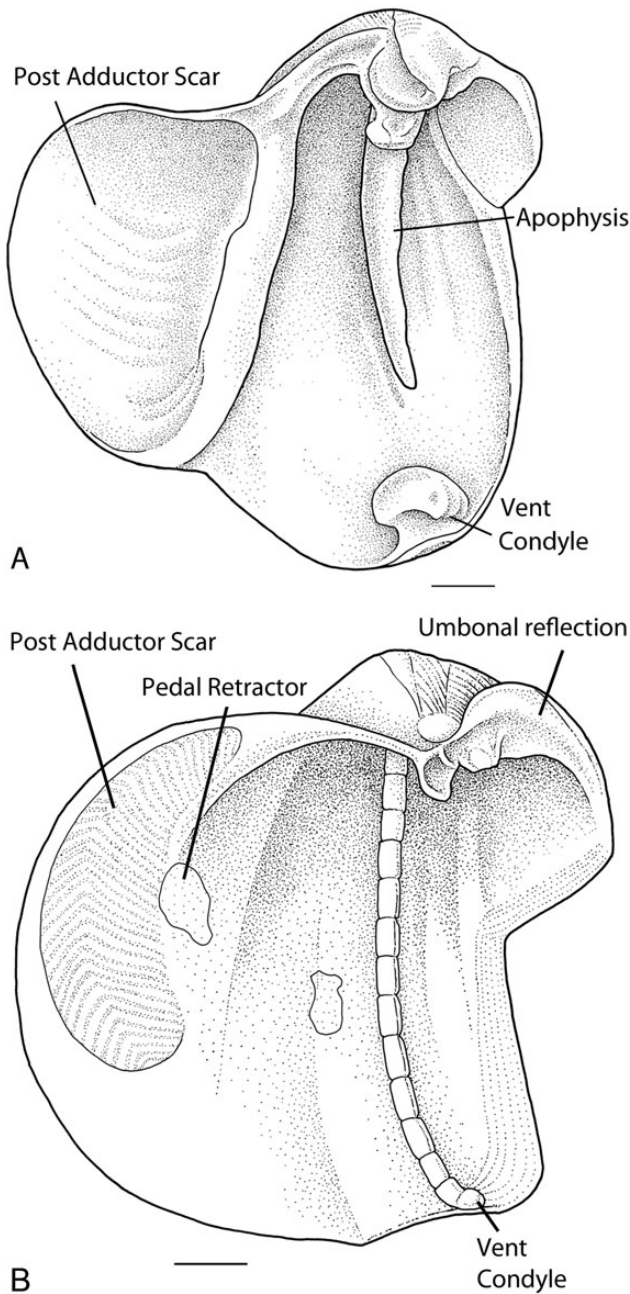
Figure 3. A. Inner teredinid valve (FMNH 312232) collected without pallets. B. Interior of *Xylophaga oregona* valve. Scale bars: **A, B** = 1 mm.

they bore, this may at least partially contribute to the depth separation of the families. Modern microtechniques offer the possibility to test this hypothesis.

GEOGRAPHICAL DISTRIBUTION

Over 125 species of wood-boring bivalves (68 teredinids and 59 xylophagaids) are currently recognized from the world's oceans. In a global perspective, teredinids appear to thrive in the tropics (Hoagland & Turner, 1981) and are absent only from high latitudes (Turner, 1966; 1968; Nair & Saraswathy, 1971). Xylophagaids range into the Arctic (Wilander, 2008). Based on the absence of xylophagaids from two deployments, Glover *et al.* (2013) argued that they are absent from Antarctic seas largely because wood is essentially absent.

The Northern Hemisphere has been home to most studies of wood borers. Those of the Southern Hemisphere are poorly documented despite work in New Zealand (McKoy, 1980), Queensland, Australia (MacIntosh, De Nys & Whalan, 2012), Brazil (Leonel, Lopes & Aversari, 2002; Santos *et al.*, 2005) and the southern Indian Ocean (Amon, 2013).

Teredinids occupy floating, fixed and sunken wood in shallow (typically <200 m deep) water. Some species tolerate salinity ranges from fully marine to nearly fresh (Southwell & Bultman, 1972; Rayner, 1978, 1983). Although Turner (1966) considered depths over 200 m to impair teredinid reproduction, Hoagland & Turner (1981) extended that depth to 250 m. Deployments of wood at 267 m depth near the Bahamas, however, were recovered with two teredinids (Heise *et al.*, 2011); others at 276 m depth were recovered from the Nansei Shoto Trench (associated with the Ryukyu Islands in the western Pacific) with *Coeloteredo mindanensis* (Bartsch, 1923) (T. Haga, pers. comm.). Living teredinids have been collected from far greater depths, e.g. in the Gulf of Mexico from over 610 m depth (Field Museum of Natural History, Chicago: lots FMNH 307787, 318538). These individuals may have colonized wood at shallower depths and moved down with it, for example if it sank, or the records may reflect the species' normal range. The former is supported by Bartsch's (1927) record of five species from 200 fathoms (365 m) or below, of which three are now known to occur typically on driftwood (Edmondson, 1962; Chambers, 2008).

Xylophagaids usually occur in sunken wood on the seafloor, although *Xylophaga dorsalis* is reported to occur as shallowly as the intertidal zone (Turton, 1822). Typically species occur at shallower depths in higher latitudes (e.g. Santhakumaran, 1980). Knudsen (1961) reported xylophagaids from depths over 5,000 m in oceanic trenches but, as in teredinids, collection depth may not always reflect normal habitat depth. The type localities of only three xylophagaid species (Knudsen, 1961; Kudinova-Pasternak, 1975) lie south of the Tropic of Capricorn; I suggest this is more likely due to a lack of collecting effort than a lack of
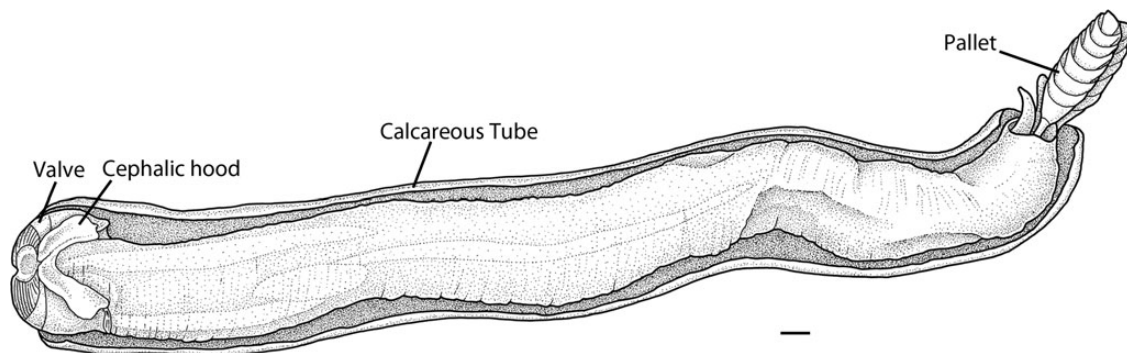

Figure 4. *Bankia gouldi in situ* in dorsal view (FMNH 17205). Scale bar = 10 mm.
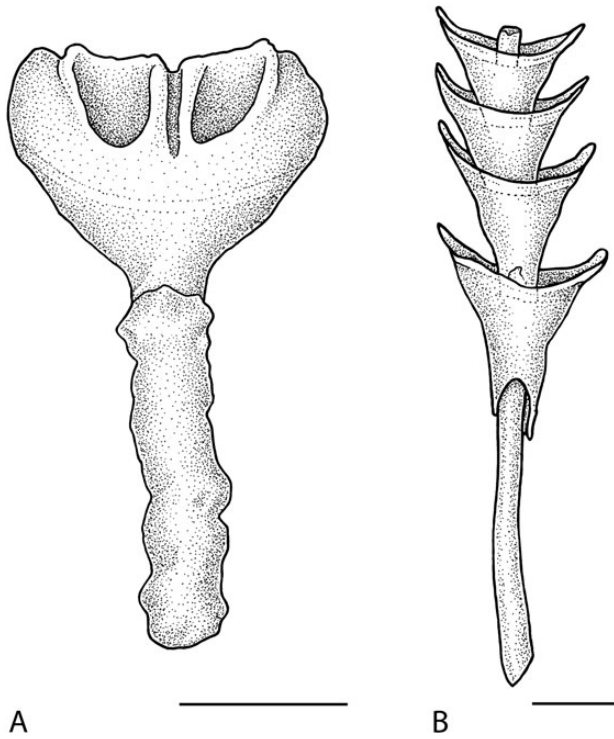
Figure 5. A. Unsegmented pallet, represented by *Teredothyra*, similar to pallets of genera *Lyrodus* and *Teredo*. **B.** Segmented teredinid pallet, genus *Bankia*, similar to pallets of genus *Nausitora*. Scale bars = 1 mm.

Figure 6. SEM of worn denticles on the anterior slope of a valve of *Xylophaga oregona*. Scale bar = 100 μm.

species. Amon (2013) reported new collections from the Southwest Indian Ridge off Southern Africa and collections are being made off Brazil (P. Sumida, A. Fraga Bernardino, pers. comm.). New species continue to be described (e.g. Romano *et al.*, 2014) and many more likely remain to be collected.

Teredinids violate the generality that species with planktonic larvae have significantly larger species ranges than do those with brooded young (Jablonski & Lutz, 1983). Hoagland & Turner (1981) detected no significant relationship between areal range and development, whether range was estimated by the number of ocean basins or latitudinal zones occupied. Species with both planktonic young and with brooded young have circumtropical distributions (Cragg, 2007). In temperate and tropical seas, repeated introductions of alien species have likely obscured the original ranges of many teredinids; *Teredo navalis* Linnaeus, 1758

appears to have been so widely introduced that its original range cannot be determined (Kerckhof, Haelters & Gollasch, 2007). Introductions may also have muddled the relationship between larval mode and species range.

Most xylophagaid species are known only from the type locality, so species ranges cannot yet be discussed.

WOOD AVAILABILITY

In the marine ream, wood is most abundant in mangrove habitats, and nearly a third of the recognized teredinids occur in these habitats (Table 1), despite the small area of the marine realm that mangroves occupy (Giri *et al.*, 2011). The number of sympatric teredinids reported from mangroves ranges from one in Brazil (Filho, Tagliaro & Beasley, 2008), to 14 in Queensland (MacIntosh *et al.*, 2012) and 23 on the east coast of India (Nair & Saraswathy, 1971). Where multiple species co-occur, one typically dominates and the others are rare (Roonwal, 1964; Rayner, 1983; Varotto & Barreto, 1998; Leonel, Lopes & Aversari, 2002; Brearley, Chalermwat & Kakhai, 2003; MacIntosh *et al.*, 2012).

If the availability of wood promotes wood-borer diversity, then the open ocean, well away from land where wood and other vegetation are produced, should be nearly uninhabitable and impassable for teredinids. Two lines of evidence support this prediction. First, the distribution of teredinid larvae is consistent with that of sedentary, coastal bivalves; they become rarer with increasing distance from land (Scheltema, 1971). Second, only after humans sailed wooden ships to foreign seas and brought back exotic teredinids in the ships' timbers did teredinids cause havoc in Europe, suggesting that teredinids did not cross ocean basins without human assistance.

Teredinids were not absent from Europe before the Age of Exploration; ancient Greek and Roman texts reported teredinids in the Mediterranean (see review by Kofoid & Miller, 1927), but they did not pose the same threat as introduced species. A drought in The Netherlands in 1731 appears to reveal the introduction of a new teredinid species. The drought raised the salinity of inland waters and the population of the introduced *Teredo navalis* exploded; it apparently tolerated low salinities better than did the native species. The borings of *T. navalis* caused catastrophic failure of wooden dykes, followed by economic crisis (Sellius, 1733, cited by Kofoid & Miller, 1927). This series of events was repeated in inland areas of San Francisco Bay in 1919 (Hill & Kofoid, 1927). *Teredo navalis* was first reported from the area a few years before; when drought increased the salinity of inland waters, its full impact was felt (Fig. 1). Human-mediated introductions of wood borers continue to this day; although the exact mechanisms of introduction are unknown, teredinid larvae are present in ships' ballast water (Borges *et al.*, 2012, 2014; Shipway *et al.*, 2014).

Although wood is rare far from shore, deep-sea xylophagaids are known from abyssal plains far from the coast (Harvey, 1996; Voight & Segonzac, 2012). If xylophagaids exist on abyssal plains where one would think wood is extremely limited, some teredinids could also be reasonably expected to occur at sea. It is difficult to assess this prediction, because collections of pelagic animals from the open ocean are extremely rare and because the floating wood into which teredinids bore is mobile, so that its collection site is not necessarily where the animal lived. Nevertheless, Edmondson (1962) hypothesized that three teredinids live in the open Pacific. He found the hard parts of *Teredo gregoryi* Dall, Bartsch & Rehder, 1938 [now *Teredora princesae* (Sivickis, 1928)] in logs of Douglas fir (apparently from northwestern North America) stranded on beaches in the Hawaiian archipelago. The associated boreholes were up to 0.6 m long and the shells were up to 19 mm tall. Shells and pallets of *Uperotus clava* (Gmelin, 1791) were collected only from the seed cases of *Xylocarpus* mangroves and

Table 1. Teredinidae from mangrove habitats, based on Turner (1966) and Rayner (1983).

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*_Bactronophorus thoracites_ (Gould, 1856)

Bankia bipennata (Turton, 1819)

Bankia campanellata Moll & Roch, 1931

Bankia carinata (J. E. Gray, 1827)

Bankia fimbriatula Moll & Roch, 1931

Bankia nordi Moll, 1935

Bankia rochi Moll, 1931

*_Dicyathifer manni_ (Wright, 1866)

[†]_Lyrodus massa_ (Lamy, 1923)

[†]_Lyrodus pedicellatus_ (Quatrefages, 1849)

Nausitora dryas (Dall, 1909)

Nausitora dunlopei Wright, 1864

Nausitora excolpa (Bartsch, 1922)

Nausitora fusticula (Jeffreys, 1860)

Nausitora hedleyi Schepman, 1919

Nausitora oahuensis (Edmondson, 1942)

Nausitora saulii Wright, 1866

Neoteredo reynei (Bartsch, 1920)

Psiloteredo healdi (Bartsch, 1931)

[†]_Teredo bartschi_ Clapp, 1923

[†]_Teredo fulleri_ Clapp, 1924

[†]_Teredo furcifera_ Martens, 1894

[†]_Teredo mindanensis_ Bartsch, 1923

[†]_Teredo poculifer_ Iredale, 1936

The proportion of larviparous species is statistically identical to that in the family as a whole (_G_-test: $G = 0.401$; $P > 0.05$).

*The two mangrove-specialist species.

[†]The seven larviparous species (whether larvae are released at straight-hinge or pediveliger stage).

Figure 7. Lateral view of an autonomously boring individual of _Xylopholas scrippsorum_ with numerous dwarf males on proximal ventral siphon and with a chitinous cover over siphon tip. Abbreviation: M, dwarf males. Scale bar = 1 mm.

coconuts, which often float just under the surface for long distances (Tomizawa _et al._, 2012). The third species, _Teredo_ (_Teredothyra_) _palauensis_ Edmondson, 1959 [now _Teredothyra excavata_ (Jeffreys, 1860)], was named from abundant shells and pallets that were only collected from beach-cast driftwood. Soft parts were consistently absent for all three species and they were collected only from driftwood and seeds, despite concerted efforts to document the Pacific wood-boring fauna (Edmondson, 1942, 1946, 1959, 1962). Edmondson (1962) termed these species 'ocean travellers'.

The 'ocean traveller' hypothesis does not appear to have been widely embraced. Turner (1966) only briefly mentioned Edmondson's (1962) 'ocean travellers' and did not suggest where these taxa might live. She noted that all records of _Uperotus_ were from wood cast up on beaches or dredged, but considered it unlikely to be an intertidal group (Turner, 1966: 76). Any reservations Turner may have had about open-ocean specialists among the teredinids seems odd, because she had identified the wood-boring (but not wood-eating) pholad _Martesia fragilis_ Verrill & Bush, 1898 as "a pelagic species with only occasional specimens being taken from fixed structures" (Turner, 1955: 101). Perhaps she used 'pelagic' to mean floating and the word has only later come to indicate open ocean. Hoagland & Turner (1981) listed 'open-ocean in floating wood' among the habitats of wood borers. Two lines of evidence provide additional support for the existence of the open-ocean wood-boring guild. First, McKoy (1980) examined teredinids from 1,500 pieces of driftwood collected around New Zealand and considered that only three had originated elsewhere; all three had been bored by _Teredora princesae_, one of Edmondson's ocean travellers. Second, among xylophagaids, two almost entirely distinct faunas exist in the northeastern Pacific, separated by distance from shore (Voight, 2009).
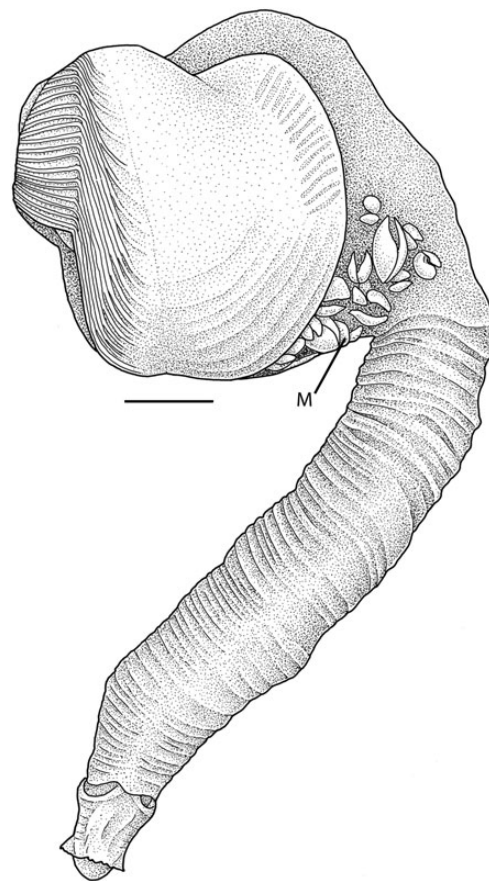
How did these groups of teredinids and xylophagaids evolve to colonize the open ocean, an otherwise nearly impenetrable barrier to most wood borers? Voight (2009) found differences in reproductive mode among the xylophagaids present nearshore and offshore. What are now recognized as dwarf males (Fig. 7; see below) were significantly more common among nearshore than offshore species. Haga & Kase (2013) reported the opposite, that dwarf males are more common in species from greater depths, but reanalysis of their data with a contingency table and a _G_-test fails to find the association to be statistically significant ($G = 2.86$; $df = 7$; $P > 0.05$). Voight (2009) attributed this difference between the groups to the increased abundance and predictability of wood near land. However, mangrove habitats reliably offer abundant wood, but lack a concomitant change in reproductive mode. One difference between wood in the open ocean and that nearshore is that the former is likely to be large.

Häggblom (1982) addressed factors that affect wood's buoyancy. In conifers, buoyancy depends on wood volume; larger logs float for longer than do small ones. Buoyancy of deciduous trees is also affected by variables such as moisture content of the wood, presence of cracks, amount of decay and the condition of the outer layers (Callin, 1945, cited by Häggblom, 1982). Depending on taxon, wood may float for 6 to 17 months or more (Häggblom, 1982). All things being equal, only large pieces of wood are likely to float for long enough to reach the open ocean. Tests of the hypothesis that the wood available nearshore differs in size from that available at sea are limited, although wood can be readily determined to be available in small packets nearshore (e.g. De Leo _et al._, 2012). Like plastic and macroalgal debris

(e.g. Galgani, Souplet & Cadiou, 1996; Vetter & Dayton, 1999; Barnes *et al.*, 2009), sunken wood accumulates in topographically complex areas, such as canyons (Romano *et al.*, 2013; Schlining *et al.*, 2013). Documenting the distribution of what are predicted to be rare logs floating or sunken beneath the open ocean is not currently possible.

In addition to the physical determinants of wood buoyancy, borers themselves impact floating wood. The teredinid *Neoteredo reynei* (Bartsch, 1920) was found living in significantly fewer small than large pieces of driftwood (Filho *et al.*, 2008). It was argued that the relatively greater surface areas of small pieces of driftwood absorb more water and carry more biofilm than larger pieces. These factors may ease penetration by teredinids and attract their larvae, respectively; they also increase the wood's weight, an increase that is more significant for small pieces of wood than for larger ones. Teredinid colonization and boring are key steps in the process of wood destruction (Filho *et al.*, 2008). Smaller pieces of wood thus sink faster. Smaller sticks are broken down significantly faster than are larger ones (Webster *et al.*, 1999). Sinking in shallow water is likely not catastrophic for teredinids, but sinking in depths over 200 m may cause reproductive failure (Turner, 1966). I argue that the increase in the size of floating wood with distance from the coast can lead to differentiation of wood-boring species and to differences in reproductive mode.

Open-ocean species occur in a habitat in which wood is rare but, when present, it occurs in immense volumes. Open-ocean wood borers are under strong selection to find the diminishingly rare wood available. When they do, they consume it with abandon. In contrast, nearshore species occur in a habitat with relatively abundant wood, but its volume is often limited. As teredinids spend their entire lives within one piece of wood, resource conservation becomes vital. Overcrowded wood borers can become stenomorphic or dwarfed; while stenomorphs may complete full life-cycles, their fecundity is size-limited (Bartsch, 1923; Romey, Bullock & DeAlteris, 1994). Dwarf males offer a dioecious strategy that minimizes crowding and resource consumption, as recognized in the eelgrass-rhizome-boring teredinid *Zachsia zenkewitschi* Bulatoff & Rjabtschikoff, 1933 (Turner & Yakovlev, 1983) and in other bivalves (Ó Foighil, 1985). Because dwarf xylophagaid males lack denticles on their shells (Ockelmann & Dinesen, 2011; Haga, 2013; Haga & Kase 2013), they cannot bore. The increase in dwarf males among nearshore species is consistent with a strategy of resource conservation.

PHYSIOLOGICAL STRESSORS

Teredinids in driftwood risk being carried out to sea, or being beached at high tide. Being beached threatens teredinids with desiccation, and extreme salinities and temperatures. The animals, being tolerant of anoxia, retract their siphons and tightly seal their outer calcium carbonate tube with their pallets (Lane, 1959: for *Teredo* sp.). Kofoid & Miller (1927: 206) said that animals of *Teredo navalis* "… live indefinitely in salinities of from 5 parts per 1000 to 60 parts per 1000 (nearly twice that of normal sea water), and … survive for long periods of time in an almost complete absence of oxygen". *Nototeredo knoxi* (Bartsch, 1917) can survive for at least 72 h in air (Omena, Junqueira & Silva, 1990, cited by Filho *et al.*, 2008). In inhospitable conditions, *T. navalis* reportedly withdraws its siphons entirely for up to 6 weeks, to extend them again when placed in water of normal salinity (Roch, 1931, cited by Greenfield, 1952). Some teredinids not only tolerate exposure to hydrogen sulphide, but apparently settle in its presence (Muraoka, 1973). Turner (1966) reported that they can survive freezing temperatures.

Mangrove teredinids face similar risks during tidal emergence. Species of *Nausitora* are so adapted to low salinities that their larvae are hypothesized to be killed by exposure to full marine salinity (Turner, 1966), as supported by experimental work (Saraswathy & Nair, 1974), although questioned by Rayner (1978). Turner (1966) hypothesized that adults of the genus disperse inside wood; Haga (2006) showed such transport to be effective in members of *Zachsia*, which bore into eelgrass rhizomes. The monotypic genera *Bactronophorus*, *Dicyathifer* and *Neoteredo* may also be restricted to estuarine and mangrove habitats (Turner, 1966; Rayner, 1983).

PHYSICAL AND BIOTIC ENVIRONMENT

Research on teredinids in mangrove habitats has largely focused on documenting the species present and their habitat use (Rayner, 1983; Nair, 1994; Leonel *et al.*, 2002; Brearley *et al.*, 2003; Leonel *et al.*, 2006; Filho *et al.*, 2008; Hendy, 2012; MacIntosh *et al.*, 2012; Nayak, Behera & Das, 2012). Whether the distribution of teredinids in mangroves follows physical factors, such as salinity gradients and thermal stress (correlated with tidal level), or follows preferred plants has rarely been directly assessed. For instance, if most members of a species bore into one mangrove species, the teredinid might be concluded to prefer its wood, however, if that mangrove is numerically dominant where sampling was carried out, the apparent preference might be better attributed to a sampling artefact. Leonel *et al.* (2006) suggested that teredinids prefer the same salinity range as the mangrove species into which they bore most often.

Xylophagaids in the physically stable deep sea are seemingly spared such challenges; however, substrate limitation may be a significant problem to these animals. Xylophagaids have attempted to bore into telegraph cable covers (Purchon, 1941), acrylic, plastic, jute and electrical insulation tape (Muraoka, 1965, 1966a,b). Although most xylophagaids may lack the opportunity, or perhaps the ability, to select substrates, recruitment can be uneven. Comparison of boreholes in panels of Douglas fir and white oak, deployed side-by-side at 2,200 to 3,200 m depth, showed far fewer boreholes in the oak than in the fir (Voight, 2007). Xylophagaid larvae might be argued to prefer the softer, lower-tannin fir (among the dominant trees of the adjacent land), but the possible influence of predators (see below) must also be considered. An alternative explanation may be that xylophagaids bore dense wood more slowly (Tipper, 1968); since an exposed xylophagaid is vulnerable to predation, larvae boring into dense wood likely suffer higher mortality. Romey *et al.* (1994) reported that at 100 and 200 m depth in the Atlantic, larvae of *Xylophaga atlantica* Richards, 1942 prefer oak to pine, a pattern attributed to the oak's rougher surface. Their recovery method did not allow predators to be detected.

High densities of potential predators of wood borers, including two taxa of polyclad turbellarian flatworms (a class previously unknown in the deep sea, Herring, 2002) and asteroids of the genus *Xyloplax*, were collected from xylophagaid-colonized wood in the deep sea (Voight, 2007). Shallow-water polyclads are notorious predators of bivalve spat; in oyster farms they can reduce settlement by over 90% (e.g. Loosanoff, 1956; Woelke, 1956; Provenzano, 1959); Hyman (1944) named the Hawaiian polyclad discussed by Edmondson (1942) *Taenioplana teredini* to indicate its preferred prey. Polyclads may be underestimated because they can waft away during recovery of colonized wood, especially during trawl collections of natural wood falls and, without special attention, preservation can render them virtually unrecognizable. Other potential predators include the asteroids *Xyloplax* (which are only known from sunken deep-sea wood; Voight, 2005) and *Caymanostella*; the stomach of the latter, however, reportedly contains wood (Wolff, 1979). Other potential predators include the mussel *Idas argenteus* (Ockelmann & Dinesen, 2011), asellota isopods, and the polynoid and other polychaetes that can occur in high densities at wood falls (Wolff, 1979; Samadi *et al.* 2010; Ockelmann & Dinesen, 2011; Amon, 2013).

Predators reduce population density and minimize competition (Chase *et al.*, 2002). Interspecific competition may also be moderated by the wood's temporal and spatial unpredictability (e.g. Horn & MacArthur, 1972; Hanski, 1981). Competitive interactions do not appear to limit the distributions of wood borers. Teredinids and xylophagaids can bore into the same piece of wood (Hoagland & Turner, 1981; Voight, pers. obs.). An obvious difference between the families is, as noted above, that they tend to bore at 90° to each other: teredinids along the wood grain and xylophagaids across it. Diverse mechanisms have been suggested to moderate competition among microsympatric species. Hoagland & Turner (1981) argued that although competition among teredinid species may be important in a given piece of wood, staggered settlement periods, the stochastic availability of wood and different modes of larval dispersal allow coexistence, as different species dominate adjacent pieces of wood.

Different teredinid species settle at different times of the year, as has been repeatedly documented. What has been rarely reported is that some teredinids show preferences in where they settle. Larvae of the mangrove species, *Bactronophorus thoracites* (Gould, 1856) and *Dicyathifer manni* (Wright, 1866), are reported to actively avoid fresh wood deployments, being at most only rarely found in them (Turner, 1971 cited by Brearley *et al.*, 2003; Brearley *et al.*, 2003). However, larvae of *Teredo bartschi* Clapp, 1923 in nuclear-plant cooling ponds prefer new, uncolonized wood to wood with established borers (Hoagland & Crockett, 1982). If larvae exhibit such selectivity, it would suggest that more desirable wood should be available.

Apparent preferences for either fresh or previously bored wood hint that teredinids partition the resource temporally, as Voight (2007) hypothesized to occur among northeastern Pacific xylophagaids. Early colonists were considered to be specialized for rapid colonization, to have high fecundity, minimal antipredator defences and short life-cycles. Later colonists were hypothesized to be slower-growing with antipredator devices such as covers on the siphonal tips, as in *Xylopholas* (Fig. 7). Heavy predation appears to moderate consumption by early colonists, leaving resources for later colonists.

Teredinids are often studied by the periodic deployment and recovery of wooden panels that often document what species recruits when. Unfortunately, these provide insight only over short time scales. The impact of species interactions and predation on teredinid communities may become apparent only over longer time scales. Asynchronous settlement of different teredinids could itself have evolved as a means to overwhelm and then starve predators. Examining the siphon tips of teredinids for damage caused by predation, such as the truncated siphons seen in xylophagaids collected with abundant predators (Voight, 2007), might test this hypothesis.

REPRODUCTION

The unpredictable habitat and risk of high mortality facing wood borers likely select for high fecundity. Kofoid (1921, cited by Nair & Saraswathy, 1971) reported that a single *Teredo navalis* could produce two million eggs and larvae. Sigerfoos (1907) found that a large female *Teredo dilatata* Stimpson, 1851 [now *Psiloteredo megotara* (Hanley in Forbes & Hanley, 1848)] could produce 100 million eggs in a single spawning event. Teredinids can be sexually mature at less than 20 mm length (Coe, 1933; Edmondson, 1942) and some species can exceed 1.8 m in length (Müller & Lana, 2004 cited by Filho *et al.*, 2008).

Considerable research has focused on teredinid larval morphology and the evolution of larval brooding. Because the larvae are considered the most vulnerable stage of the life cycle, most of these studies pertain to teredinid control. The major evolutionary change from segmented to unsegmented pallets (Fig. 5) has been hypothesized to relate to the origin of brooded young. The genera *Teredo* and *Lyrodus* have comparatively simple, unsegmented pallets (Fig. 5A) and are larviparous, brooding young on their gills until either the straight-line hinge veliger or pediveliger stage (Turner & Johnson, 1971). These two genera form a clade in the phylogeny of Distel *et al.* (2011). In contrast, basal teredinids are oviparous and have segmented pallets (Fig. 5B). Distel *et al.* (2011) argued that unsegmented pallets minimize retention of newly-released larvae. Evidence that segmented pallets are a threat to larvae comes from *Bankia neztalia* Turner & McKoy, 1979; between segments of its pallets were found what appeared to be newly released young, measuring 69 by 81 μm (McKoy, 1980). The straight-line hinge veligers released by some teredinids are virtually indistinguishable from non-brooded larvae of other species and the later swimming stages can be identical (Turner & Johnson, 1971).

Reproduction in xylophagaids remains largely unknown. To my knowledge, only one study (Culliney & Turner, 1976) has succeeded in rearing xylophagaid larvae, but these young of *Xylophaga atlantica* did not settle successfully. In some species small individuals are found attached to autonomously boring larger xylophagaids; these were initially described as brooded young, but have recently been recognized to be sexually mature, dwarf males (Ockelmann & Dinesen, 2011; Haga, 2013; Haga & Kase, 2013). These dwarf male xylophagaids have shells indistinguishable in size from the protoconchs of autonomously boring conspecifics. Xylophagaids likely do not brood young.

Protandry has been widely assumed to be common in both families (Sigerfoos, 1907; Purchon, 1941; Lane, 1959; Turner, 1968; Turner & Johnson, 1971; Eckelbarger & Reish, 1972; Morton, 1978; Cragg, 2007 and references therein). Histological study of six large individuals of *Xylophaga supplicata* Knudsen, 1961 demonstrated protandry in that species (Haga & Kase, 2013). However, Tyler, Young & Dove (2007) documented dioecy in a population of *Xylophaga depalmai* Turner, 2002, with only a few individuals being simultaneous hermaphrodites; their re-analysis of Purchon's (1941) data suggested that *X. dorsalis* (Turton, 1819) also follows this pattern. These two species share an incomplete siphon, ear-shaped mesoplax (Turner, 2002) and generally occur in shallow water (Voight, 2008), so they are likely members of the same clade. Because dioecy seemingly requires at least two conspecific individuals in close proximity for successful reproduction, it does not guarantee successful reproduction. Among bivalves, however, intra-family diversity in reproductive systems appears to be considerable despite having received minimal study (Collin, 2013).

Views on where xylophagaid larvae occur have changed. At one time, the larvae were thought to colonize only floating wood (Turton, 1822; Purchon, 1941; Turner, 1955). Subsequently, it was observed that sunken wood was heavily colonized where it contacted the sediment (Muraoka 1966a, cited by Turner, 2002; Tipper, 1968), leading to the hypothesis that the larvae did not rise more than 3 to 8 m above the sea floor (Tipper, 1968). Turner (2002) stated that xylophagaids colonize only sunken wood, which could be resuspended and cast onto beaches, as apparently occurred with the type material of *X. dorsalis* and *X. washingtona* Bartsch, 1921. Nevertheless, at least some xylophagaids colonize wood above the sediment surface. Wood suspended 20 m above the substrate at 900 to 1,500 m depth was colonized by three xylophagaid species in the western Mediterranean, although densities were lower than seen in wood on the sea floor (Romano *et al.*, 2013). In addition, *X. depalmai* colonized wood suspended up to 90 m above a 500 m deep bottom (Turner, 2002). Conceivably the ability to colonize submerged, floating wood could expand the species' range. However, once wood begins to sink, there is no mechanism that would allow it to regain sufficient buoyancy to float above the sea floor.

HUMAN IMPACTS

Wood availability has been repeatedly recognized as limiting for wood borers (Kofoid & Hill 1927; Turner, 1966; McKoy, 1980). Humans likely have their greatest negative impact on wood borers by restricting the volume of wood that enters the oceans, a strategy advocated as the best means to control the animals (Turner, 1966; Tsunoda & Nishimoto, 1978). Most wood in the sea derives from trees near riverbanks or on the coast (Häggblom, 1982); waterfront development, by reducing the number of trees in close proximity to waterways, may be a severe threat to the wood supply. Overall, deforestation impacts a greater number of trees, but because most trees in an inland forest never reach the ocean, it will have a lesser impact on wood supply to marine borers.

Perhaps the greatest human threat to wood borers is the removal of wood from rivers near the sea, done to ease navigation and reduce maintenance costs. Every year, an estimated 100,000 m^3 of floating debris (including 90% of the driftwood) is removed from the Fraser River, British Columbia (Hales, 2000, cited by Ham, 2005; Thonon, 2006). In addition, flood control measures that reduce the volume of and energy contained in floods may also reduce the volume of wood swept into the ocean.

Mangrove teredinids (Table 1) apparently evolved in an environment with an abundant supply of wood. Nearly one-third of all teredinid species occur in mangroves; it is not known how recent fragmentation and destruction of mangrove habitats (Valiela, Bowen & York, 2001; Duke et al., 2007) might affect them. Teredinids are vital to this ecosystem, freeing nutrients from fallen wood by processing more than 50% of the wood that is produced (Cragg, 2007; Hendy et al., 2013); they thus enhance coastal productivity. In addition, their boreholes increase habitat complexity and provide vital refugia for vulnerable juveniles of other taxa (Hendy, 2012). The connectivity of mangrove habitats along a coast may be important in maintaining teredinid diversity. To determine the impacts of mangrove fragmentation, species diversity in fragmented habitats needs to be contrasted with that in relatively pristine, continuous mangrove habitats. Most at risk may be species, such as those of *Nausitora*, that appear to be intolerant of full marine salinity.

Xylophagaids form the basis of deep-sea ecosystems dependent on wood. Together with their symbiotic bacteria they break down otherwise indigestable cellulose. In the energy-poor deep sea, this frees the energy and nutrients locked in the wood and makes xylophagaids analogous to primary producers. Deep-sea wood falls can sustain extraordinary densities and diversities of other animals, at least some of which are unique to the wood-fall habitat (Wolff, 1979; Samadi et al., 2010), including polyplacophoran (Sigwart & Sirenko, 2012) and gastropod molluscs (Marshall, 1988), echinoderms (Mah, 2006), sipunculans and a species of tanaid crustacean (Larsen, 2006). We know so little of the ecology of the abyssal plain that the impact of relatively small, discrete deposits of terrigenous energy and nutrients can only be imagined. It appears certain, however, that xylophagaids are as vital in making the energy and nutrients in wood available to the broader deep-sea community as teredinids are in mangroves.

Potential support for the argument that wood availability impacts borer diversity derives from the comparison of xylophagaids off the east and west coasts of the USA. Thirteen species of xylophagaids occur between Vancouver Island and southern California (Voight, 2007, 2009), but only four in the northwestern Atlantic north of Florida (data from Turner, 2002). Marine biodiversity in the northern Pacific is often higher than that in the Atlantic and many explanations have been proposed (see review by Vermeij, 1991), but the removal of more than half the forest cover in New England states between about 1650 and 1850 (Thompson et al., 2013) must have impacted the wood borers in the northwestern Atlantic. This remains speculative until we have more data on species diversity in other ocean basins.

Given the association of predictable wood abundance and wood-borer diversity, human-mediated changes in the availability of wood may seriously impact these animals. What we perceive to be stochastically-distributed transient habitats are to wood borers sufficiently predictable to sustain generations of the animals. In doing so, they sustain not only themselves but a suite of other taxa dependent on them to free the energy trapped in the wood that enters the marine realm.

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REFERENCES

AMON, D.J. 2013. *Bone-eating worms and wood-eating bivalves: characterising the ecology of deep-sea organic falls from multiple ocean basins.* PhD thesis, University of Southampton. http://eprints.soton.ac.uk/361854/1.hasCoversheetVersion/Amon,%20Diva_PhD.pdf.

ANSELL, A.D. & NAIR, N.B. 1969. The mechanisms of boring in *Martesia striata* Linné (Bivalvia: Pholadidae) and *Xylophaga dorsalis* Turton (Bivalvia: Xylophaginidae). *Proceedings of the Royal Society, London, Series B*, **174**: 123–133.

BARNES, D.K.A., GALGANI, F., THOMPSON, R.C. & BARLAZ, M. 2009. Accumulation and fragmentation of plastic debris in global environments. *Philosophical Transactions of the Royal Society, Series B*, **364**: 1985–1998.

BARTSCH, P. 1923. Additions to our knowledge of shipworms. *Proceedings of the Biological Society of Washington*, **36**: 95–102.

BARTSCH, P. 1927. The shipworms of the Philippine Islands. *Bulletin of the United States National Museum*, **27**: 533–563.

BOARD, P.A. 1970. Some observations on the tunnelling of shipworms. *Journal of Zoology, London*, **161**: 193–201.

BORGES, L.M.S., MERCKELBACH, L.M., SAMPAIO, I. & CRAGG, S.M. 2014. Diversity, environmental requirements, and biogeography of bivalve wood-borers (Teredinidae) in European coastal waters. *Frontiers in Zoology*, **11**: 13.

BORGES, L.M.S., SIVRIKAYA, H., LE ROUX, A., SHIPWAY, J.R., CRAGG, S.M. & COSTA, F.O. 2012. Investigating the taxonomy and systematics of marine wood borers (Bivalvia: Teredinidae) combining evidence from morphology, DNA barcodes and nuclear locus sequences. *Invertebrate Systematics*, **26**: 572–582.

BREARLEY, A., CHALERMWAT, K. & KAKHAI, N. 2003. Pholadidae and Teredinidae (Mollusca: Bivalvia) collected from mangrove habitats on the Burrup Peninsula, Western Australia. In: *The marine flora and fauna of Dampier, Western Australia* (F.E. Wells, D.I. Walker & D.S. Jones, eds), pp. 345–361. Western Australian Museum, Perth.

CALLIN, G. 1945. Syrfällning och randbarkning av björkkolved. *Norrlands Skogsvårdsföreningen Tidskrift*, **II-45**.

CALLOWAY, C.B. & TURNER, R.D. 1983. Documentation and implications of rapid successive gametogenic cycles and broods in the shipworm *Lyrodus floridanus* (Bartsch) (Bivalvia, Teredinidae). *Journal of Shellfish Research*, **3**: 65–69.

CHAMBERS, P. 2008. *Channel Island marine molluscs: an illustrated guide to the seashells of Jersey, Guernsey, Alderney, Sark and Herm.* Charonia Media, Devon.

CHASE, J.M., ABRAMS, P.A., GROVER, J.P., DIEHL, S., CHESSON, P., HOLT, R.D., RICHARDS, S.A., NISBET, R.M. & CASE, T.J. 2002. The interaction between predation and competition: a review and synthesis. *Ecology Letters*, **5**: 302–315.

COE, W.R. 1933. Sexual phases in *Teredo*. *Biological Bulletin*, **65**: 283–303.

COLLIN, R. 2013. Phylogenetic patterns and phenotypic plasticity of molluscan sexual systems. *Integrative and Comparative Biology*, **53**: 723–735.

CRAGG, S.M. 2007. Marine wood-boring invertebrates of New Guinea and its surrounding waters. In: *The ecology of Papua*. Part 1 (A.J. Marshall & B.M. Beehler, eds), pp. 539–563. Periplus Editions, Singapore.

CULLINEY, J.L. & TURNER, R.D. 1976. Larval development of the deep-water wood-boring bivalve, *Xylophaga atlantica* Richards (Mollusca, Bivalvia, Pholadidae). *Ophelia*, **15**: 149–161.

DE LEO, F.C., DRAZEN, J.C., VETTER, E.W., ROWDEN, A.A. & SMITH, C.R. 2012. The effects of submarine canyons and the oxygen minimum zone of deep-sea fish assemblages off Hawai'i. *Deep-sea Research I*, **64**: 54–70.

DISTEL, D.L., AMIN, M., BURGOYNE, A., LINTON, E., MAMANGKEY, G., MORRILL, W., NOVE, J., WOOD, N. & YANG, J. 2011. Molecular phylogeny of Pholadoidea Lamarck, 1809 supports a single origin for xylotrophy (wood feeding) and xylotrophic bacterial endosymbiosis in Bivalvia. *Molecular Phylogenetics and Evolution*, **61**: 245–254.

DISTEL, D.L., BEAUDOIN, D.J. & MORRILL, W. 2002a. Coexistence of multiple proteobacterial endosymbionts in the gills of the wood-boring bivalve *Lyrodus pedicellatus* (Bivalvia: Teredinidae). *Applied and Environmental Microbiology*, **68**: 6292–6299.

DISTEL, D.L., MORRILL, W., MACLAREN-TOUSSAINT, N., FRANKS, D. & WATERBURY, J. 2002b. *Teredinibacter turnerae* gen. nov., sp. nov., a dinitrogen-fixing, cellulolytic, endosymbiotic gamma-proteobacterium isolated from the gills of wood-boring molluscs (Bivalvia: Teredinidae). *International Journal of Systematic Evolutionary Microbiology*, **52**: 2261–2269.

DISTEL, D.L. & ROBERTS, S.J. 1997. Bacterial endosymbionts in the gills of the deep-sea wood-boring bivalves *Xylophaga atlantica* and *Xylophaga washingtona*. *Biological Bulletin*, **192**: 253–261.

DUKE, N.C., MEYNECKE, J.-O., DITTMANN, S., ELLISON, A.M., ANGER, K., BERGER, U., CANNICCI, S., DIELE, K., EWEL, K.C., FIELD, C.D., KOEDAM, N., LEE, S.Y., MARCHAND, C., NORDHAUS, I. & DAHDOUH-GUEBAS, F. 2007. A world without mangroves? *Science*, **317**: 41.

ECKELBARGER, K.J. & REISH, D.J. 1972. A first report of self-fertilization in the wood-boring family Teredinidae (Mollusca: Bivalvia). *Bulletin of the Southern California Academy of Sciences*, **71**: 48–50.

EDMONDSON, C.H. 1942. Teredinidae of Hawaii. *Occasional Papers of the Bernice Bishop Museum*, **17**: 97–150.

EDMONDSON, C.H. 1946. Dispersal of shipworms among Central Pacific Islands, with descriptions of new species. *Occasional Papers of the Bernice Bishop Museum*, **18**: 211–224.

EDMONDSON, C.H. 1959. Two new species of *Teredo*, subgenus *Teredothyra*, from the Western Pacific. *Occasional Papers of the Bernice Bishop Museum*, **22**: 203–206.

EDMONDSON, C.H. 1962. Teredinidae, ocean travelers. *Occasional Papers of the Bernice Bishop Museum*, **23**: 45–59.

FILHO, C.S., TAGLIARO, C.H. & BEASLEY, C.R. 2008. Seasonal abundance of the shipworm *Neoteredo reynei* (Bivalvia, Teredinidae) in mangrove driftwood from a northern Brazilian beach. *Iheringia, Série Zoologia*, **98**: 17–23.

FORBES, E. & HANLEY, S.C. 1848. *A history of British Mollusca and their shells*. van Voorst, London.

GALGANI, F., SOUPLET, A. & CADIOU, Y. 1996. Accumulation of debris on the deep sea floor off the French Mediterranean coast. *Marine Ecology Progress Series*, **142**: 225–234.

GIRI, C., OCHIENG, E., TIESZEN, L.L., ZHU, Z., SINGH, A., LOVELAND, T., MASEK, J. & DUKE, N. 2011. Status and distribution of mangrove forests of the world using earth observation satellite data. *Global Ecology and Biogeography*, **20**: 154–159.

GLOVER, A.G., WIKLUND, H., TABOADA, S., AVILA, C., CRISTOBO, J., SMITH, C.R., KEMP, K.M., JAMIESON, A.J. & DAHLGREN, T.G. 2013. Bone-eating worms from the Antarctic: the contrasting fate of whale and wood remains on the Southern Ocean seafloor. *Proceedings of the Royal Society*, **B 280**: 20131390. doi:10.1098/rspb.2013.1390.

GREENFIELD, L.J. 1952. The distribution of marine borers in the Miami area in relation to ecological conditions. *Bulletin of Marine Science*, **2**: 448–464.

HAGA, T. 2006. The rhizome-boring shipworm *Zachsia zenkewitschi* (Bivalvia: Teredinidae) in drifted eelgrass. *Venus*, **65**: 263–266.

HAGA, T. 2013. Juvenile, or a male? The reproductive pattern of deep-sea wood-boring bivalve Xylophagaidae. *Umiushi-Tushin*, **78**: 7–9. (in Japanese)

HAGA, T. & KASE, T. 2008. Redescription of the deep-sea wood borer *Neoxylophaga teramachii* Taki & Habe, 1950 and its assignment to the genus *Xyloredo* (Bivalvia: Myoida: Pholadoidea) with comments on fossil Pholadoidae. *Veliger*, **50**: 107–119.

HAGA, T. & KASE, T. 2013. Progenetic dwarf males in the deep-sea wood-boring genus *Xylophaga* (Bivalvia: Pholadoidea). *Journal of Molluscan Studies*, **79**: 90–94.

HÄGGBLOM, A. 1982. Driftwood in Svalbard as an indicator of sea ice conditions. *Geografiska Annaler Series A*, **64**: 81–94.

HALES, W.J. 2000. *The impact of human activity on deltaic sedimentation, marshes of the Fraser River Delta, British Columbia*. PhD thesis, University of British Columbia, Vancouver.

HAM, D.G. 2005. *Morphodynamics and sediment transport in a wandering gravel-bed channel: Fraser River, British Columbia*. PhD thesis, University of British Columbia, Vancouver.

HANSKI, I. 1981. Coexistence of competitors in patchy environment with and without predation. *Oikos*, **37**: 306–312.

HARVEY, R. 1996. Deep water Xylophagaidae (Pelecypoda: Pholadacea) from the North Atlantic with descriptions of three new species. *Journal of Conchology*, **35**: 473–481.

HEISE, E.A., RAYMOND, A., PARSONS-HUBBARD, K., WALKER, S.E., STAFF, G., POWELL, E.A., BRETT, C. & ASHTON-ALCOX, K.A. 2011. Wood taphonomy in a tropical marine carbonate environment: experimental results from Lee Stocking Island, Bahamas. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **312**: 363–379.

HENDY, I. 2012. *Habitat creation for animals by teredinid bivalves in Indonesian mangrove ecosystems*. PhD thesis, University of Portsmouth.

HENDY, I.W., EME, J., DABRUZZI, T.F., CONNOLLY, H.F., NEMBHARD, R., CRAGG, S.M. & BENNETT, W.A. 2013. Dartfish use teredinid tunnels in fallen mangrove wood as a low-tide refuge. *Marine Ecology Progress Series*, **486**: 237–245.

HERRING, P. 2002. *The biology of the deep ocean*. Oxford University Press, Oxford.

HILL, C.L. & KOFOID, C.A. 1927. *Marine borers and their relation to marine construction on the Pacific coast. Final report of IHR San Francisco Bay Marine Piling Committee*. San Francisco Bay Marine Piling Committee, San Francisco.

HOAGLAND, E. & CROCKETT, L. 1982. *Ecological studies of wood-boring bivalves in the vicinity of the Oyster Creek Nuclear Generating Station. Progress Report June–August 1981*. NUREG, CR-1939 4: 1–44.

HOAGLAND, K.E. & TURNER, R.D. 1981. Evolution and adaptive radiation of wood-boring bivalves (Pholadacea). *Malacologia*, **21**: 111–148.

HORN, H.S. & MACARTHUR, R.H. 1972. Competition among fugitive species in a harlequin environment. *Ecology*, **53**: 749–752.

HYMAN, L.H. 1944. A new Hawaiian polyclad flatworm associated with *Teredo*. *Occasional Papers of the Bernice Bishop Museum*, **18**: 73–75.

JABLONSKI, D. & LUTZ, R.A. 1983. Larval ecology of marine benthic invertebrates: paleobiological implications. *Biological Reviews*, **58**: 21–89.

KERCKHOF, F., HAELTERS, J. & GOLLASCH, S. 2007. Alien species in the marine and brackish ecosystem: the situation in Belgian waters. *Aquatic Invasions*, **2**: 243–257.

KNUDSEN, J. 1961. The bathyal and abyssal *Xylophaga* (Pholadidae, Bivalvia). *Galathea Report*, **5**: 163–209.

KOFOID, C.A. 1921. The marine borers of San Francisco Bay region. *Proceedings of the American Wood Preservation Association*, **12**: 209–247, 301–325.

KOFOID, C.A. & MILLER, R.C. 1927. Biological aspects of the marine borer problem. In: *Marine borers and their relation to marine construction on the Pacific Coast. Final report of IHR San Francisco Bay Marine Piling Committee* (C.L. Hill & C.A. Kofoid, eds), pp. 188–193. San Francisco Bay Marine Piling Committee, San Francisco.

KUDINOVA-PASTERNAK, R.K. 1975. Xylophaga *mollusks (Bivalvia, Pholadidae) found in a Scotia Sea shipwreck*. Institute of Oceanology Research Publication, **103**: 179–180.

LANE, C.E. 1959. Some aspects of the general biology of *Teredo*. In: *Marine boring and fouling organisms* (D.L. Ray, ed.), pp. 137–156. University of Washington Press, Seattle.

LARSEN, K. 2006. Tanaidacea (Crustacea; Peracarida) from chemically reduced habitats—the hydrothermal vent system of the Juan de Fuca Ridge, Escabana Trough and Gorda Ridge, northeast Pacific. *Zootaxa*, **1164**: 1–33.

LEONEL, R.M.V., DE MORAES, D.T. & LOPES, S.G.B.C. 2006. A new method of analysis of the periostracum in pallets of *Bankia* Gray, 1842 (Bivalvia: Teredinidae). *Journal of Molluscan Studies*, **72**: 117.

LEONEL, R.M.V., LOPES, S.G.B.C. & AVERSARI, M. 2002. Distribution of wood-boring bivalves in the Mamanguape River estuary, Paraíba, Brazil. *Journal of the Marine Biological Association of the United Kingdom*, **82**: 1039–1040.

LOOSANOFF, V.L. 1956. Two obscure oyster enemies in New England waters. *Science*, **123**: 1119–1120.

LOZOUET, P. & PLAZIAT, J.-C. 2008. *Mangrove environments and molluscs: Abatan River, Bohol and Panglao Islands, Central Philippines*. Conch Books, Hackenheim, Germany.

LUYTEN, Y.A., THOMPSON, J.R., MORRILL, W., POLZ, M.F. & DISTEL, D.L. 2006. Extensive variation in intracellular symbiont community composition among members of a single population of the wood-boring bivalve *Lyrodus pedicellatus* (Bivalvia:Teredinidae). *Applied Environmental Microbiology*, **72**: 412–17.

MCKOY, J.L. 1980. Distribution of shipworms (Bivalvia: Teredinidae) in the New Zealand region. *New Zealand Journal of Marine and Freshwater Research*, **14**: 263–275.

MACINTOSH, H., DE NYS, R. & WHALAN, S. 2012. Shipworms as a model for competition and coexistence in specialized habitats. *Marine Ecology Progress Series*, **461**: 95–105.

MAH, C.L. 2006. A new species of *Xyloplax* (Echinodermata: Asteroidea: Concentricycloidea) from the northeast Pacific: comparative morphology and a reassessment of phylogeny. *Invertebrate Biology*, **125**: 136–153.

MARSHALL, B. 1988. Skeneidae, Vitrinellidae and Orbitestellidae (Mollusca: Gastropoda) associated with biogenic substrata from bathyal depths off New Zealand and New South Wales. *Journal of Natural History*, **22**: 949–1004.

MILLER, R.C. 1924. The boring mechanism of *Teredo*. *University of California Publications in Zoology*, **26**: 41–80.

MORTON, B. 1978. Feeding and digestion in shipworms. *Oceanography and Marine Biology Annual Reviews*, **16**: 107–144.

MÜLLER, A.C.P. & LANA, P.C. 2004. *Manual de identificação de moluscos bivalves da família dos teredinídeos encontrados no litoral brasileiro*. Universidade Federal do Paraná, Curitiba.

MURAOKA, J.S. 1965. Deep-ocean biodeterioration of materials – Part II. Six months at 2,340 feet. *Technical Report U. S. Naval Civil Engineering Laboratory, Port Hueneme, California*, R 393: 1–42.

MURAOKA, J.S. 1966a. Deep-ocean biodeterioration of materials – Part IV. One year at 6,800 feet. *Technical Report U. S. Naval Civil Engineering Laboratory, Port Hueneme, California*, R 456: 1–45.

MURAOKA, J.S. 1966b. Deep-ocean biodeterioration of materials – Part V. Two years at 5640 feet. *Technical Report U. S. Naval Civil Engineering Laboratory, Port Hueneme, California*, R 495: 1–46.

MURAOKA, J.S. 1973. Effect of bottom sediment continuing hydrogen sulfide on materials. Part I. *Technical Note U. S. Naval Civil Engineering Laboratory, Port Hueneme, California*, N 1263: 1–18.

NAIR, N.B. 1988. The problem of biodeterioration along the Indian coasts and its impact on fisheries. *Proceedings of the Indian National Science Academy B*, **54**: 7–23.

NAIR, N.B. 1994. Biodeterioration of cellulose materials in estuarine and insular biotopes. *Proceedings of the Indian National Science Academy B*, **60**: 217–228.

NAIR, N.B. & ANSELL, A.D. 1968. The mechanism of boring in *Zirphaea crispata* (L.) (Bivalvia: Pholadidae). *Proceedings of the Royal Society, Series B*, **170**: 155–173.

NAIR, N.B. & SARASWATHY, M. 1971. The biology of wood-boring teredinid molluscs. *Advances in Marine Biology*, **9**: 335–509.

NAYAK, L., BEHERA, D.P. & DAS, S. 2012. Molluscan wood-borers of Chilika Lagoon, east coast of India and their control measures. *Current Research Journal Biological Science*, **4**: 186–191.

OCKELMANN, K.W. & DINESEN, G.E. 2011. Life on wood—the carnivorous deep-sea mussel *Idas argenteus* (Bathymodiolinae, Mytilidae, Bivalvia). *Marine Biology Research*, **7**: 71–84.

O'CONNOR, R.M., FUNG, J.M., SHARP, K.H., BENNER, J.S., MCCLUNG, C., CUSHING, S., LAMKIN, E.R., FOMENKOV, A.I., HENRISSAT, B., LONDER, Y.Y., SCHOLZ, M.B., POSFAI, J., MALFATTI, S., TRINGE, S.G., WOYKE, T., MALMSTROM, R.R., COLEMAN-DERR, D., ALTAMIA, M.A., DEDRICK, S., KALUZIAK, S.T., HAYGOOD, M.G. & DISTEL, D.L. 2014. Gill bacteria enable a novel digestive strategy in a wood-feeding mollusk. *Proceedings of the National Academy of Sciences of the USA*, **111**: E5096–E5104. doi:10.1073/pnas.1413110111.

Ó FOIGHIL, D. 1985. Form, function and origin of temporary dwarf males in *Pseudopythina rugifera* (Bivalvia: Galeommatacea). *Veliger*, **27**: 72–80.

OMENA, E.P., JUNQUEIRA, A.O.R. & SILVA, S.H.G. 1990. Resistência de Teredinidae Rafinesque, 1815 (Mollusca: Bivalvia) a diferentes períodos de exposição ao ar. *Revista Brasileira de Biologia*, **50**: 701–707.

PAALVAST, P. & VAN DER VELDE, G. 2013. What is the main food source of the shipworm (*Teredo navalis*)? A stable isotope approach. *Journal of Sea Research*, **80**: 58–60.

PROVENZANO, A.J. 1959. Effects of the flatworm *Stylochus ellipticus* (Girard) on oyster spat in two salt water ponds in Massachusetts. *Proceedings of the National Shellfisheries Association*, **50**: 83–88.

PURCHON, R.D. 1941. On the biology and relationships of the lamellibranch *Xylophaga dorsalis* (Turton). *Journal of the Marine Biological Association of the United Kingdom*, **25**: 1–39.

RAYNER, S.M. 1978. Comparison of the salinity range tolerated by teredinids (Mollusca: Teredinidae) under controlled conditions with that observed in an estuary in Papua New Guinea. *Australian Journal of Marine and Freshwater Research*, **30**: 521–533.

RAYNER, S.M. 1983. Distribution of teredinids (Mollusca: Teredinidae) in Papua New Guinea. *Records of the Australian Museum*, **35**: 61–76.

ROCH, F. 1931. Die Terediniden der Skandinavischen Museums-sammlungen (Stockholm, Gothenburg, Kopenhagen, Oslo, Nidaros und Tromso). *Archiv für Zoologie*, **22A**: 1–29.

ROMANO, C., VOIGHT, J.R., COMPANY, J.B., PLYUSCHEVA, M. & MARTIN, D. 2013. Submarine canyons as a habitat preferred for wood-boring species *Xylophaga* (Mollusca: Bivalvia). *Progress in Oceanography*, **118**: 175–187.

ROMANO, C., VOIGHT, J.R., PEREZ-PORTELA, R. & MARTIN, D. 2014. Morphological and genetic diversity of the wood-boring *Xylophaga* (Mollusca, Bivalvia): new species and records from deep-sea Iberian canyons. *PLoS One*, **9**: e102887. doi:10.1371/journal.pone.0102887.

ROMEY, W.L., BULLOCK, R.C. & DEALTERIS, J.T. 1994. Rapid growth of a deep-sea wood-boring bivalve. *Continental Shelf Research*, **14**: 1349–1359.

ROONWAL, M.L. 1964. Wood-boring teredinid shipworms (Mollusca) of mangroves in Sundarbans, West Bengal. *Symposium on Scientific Problems of the Humid Tropical Zone Deltas and their Implications*. UNESCO/NS/NR/55 Paper no. 6. http://unesdoc.unesco.org/images/0015/001539/153955eb.pdf (accessed Feb. 2014).

SAMADI, S., CORBARI, L., LORION, J., HOURDEZ, S., HAGA, T., DUPONT, J., BOISSELIER, M-C. & RICHER DE FORGES, B. 2010. Biodiversity of deep-sea organisms associated with

sunken-wood or other organic remains sampled in the tropical Indo-Pacific. *Cahiers de Biologie Marine*, **51**: 459–466.

SANTHAKUMARAN, L.N. 1980. Two new species of *Xylophaga* from Trondheimsfjorden, western Norway. *Sarsia*, **65**: 269–272.

SANTOS, S.M.L., TAGLIARO, C.H., BEASLEY, C.R., SCHNEIDER, H., SAMPAIO, I., FILHO, C.S. & MÜLLER, A.C.D.P. 2005. Taxonomic implications of molecular studies on northern Brazilian Teredinidae (Mollusca: Bivalvia) specimens. *Genetics and Molecular Biology*, **28**: 175–179.

SARASWATHY, M. & NAIR, N.B. 1974. The influence of salinity on a tropical estuarine shipworm *Nausitora hedleyi* Schepman (Bivalvia - Teredinidae). *Hydrobiologia*, **44**: 397–411.

SCHELTEMA, R.S. 1971. Dispersal of phytoplanktotrophic shipworm larvae (Bivalia: Teredinidae) over long distances by ocean currents. *Marine Biology*, **11**: 5–11.

SCHLINING, K., VON THUN, S., KUHNZ, L., SCHLINING, B., LUNDSTEN, L., JACOBSEN STOUT, N., CHANEY, L. & CONNOR, J. 2013. Debris in the deep: using a 22-year video annotation database to survey marine litter in Monterey Canyon, central California, USA. *Deep-Sea Research I*, **79**: 96–105.

SELLIUS, G. 1733. *Historia naturalis teredinis seu xylophagi marini tubulo-conchoidis speciatum*. Belgici, Trajecti ad Rhenum.

SHIPWAY, J.R., BORGES, L.M.S., MÜLLER, J. & CRAGG, S.M. 2014. The broadcast spawning Caribbean shipworm, *Teredothyra dominicensis* (Bivalvia, Teredinidae), has invaded and become established in the eastern Mediterranean Sea. *Biological Invasions*, **16**: 2037–2048.

SIGERFOOS, C.P. 1907. Natural history, organization, and late development of the Teredinidae, or ship-worms. *Bulletin of the Bureau of Fisheries*, **27**: 193–231.

SIGWART, J.D. & SIRENKO, B.I. 2012. Deep-sea chitons from sunken wood in the West Pacific (Mollusca: Polyplacophora: Lepidopleurida): taxonomy, distribution, and seven new species. *Zootaxa*, **3195**: 1–38.

SIPE, A.R., WILBUR, A.E. & CARY, S.C. 2000. Bacterial symbiont transmission in the wood-boring shipworm *Bankia setacea* (Bivalvia: Teredinidae). Applied Environmental *Microbiology*, **66**: 1685–1691.

SOUTHWELL, C.R. & BULTMAN, J.D. 1972. Marine borer resistance of untreated woods over long periods of immersion in tropical waters. *Biotropica*, **3**: 81–107.

THOMPSON, J.R., CARPENTER, D.N., COGBILL, C.V. & FOSTER, D.R. 2013. Four centuries of change in northeastern United States forests. *PLoS One*, **8**: e72540.

THOMPSON, W. 1847. Note on the *Teredo norvegica* (*T. navalis*, Turton, not Linn.), *Xylophaga dorsalis*, *Limnoria terebrans* and *Cheluda terebrans*, combined in destroying the submerged wood-work at the harbor of Ardrossan on the coast of Ayrshire. *Annals and Magazine of Natural History*, **20**: 157–164.

THONON, I. 2006. The Fraser River debris trap: a cost benefit analysis. Report for the Fraser River Debris Operating Committee. http://www.fraserbasin.bc.ca/_Library/Water/report_debris_trap_2006.pdf (accessed Feb. 2014).

TIPPER, R.C. 1968. *Ecological aspects of two wood-boring molluscs from the continental terrace off Oregon*. PhD thesis, Oregon State University.

TOMIZAWA, Y., TAKAYAMA, K., SUNGKAEW, S., SALEH, M.N.B., ASAKAWAL, T., ADJIE, B., ARDLI, E.R., SOE, M.K.K., SHAN, W.K., TUNG, N.X., MALEKAL, N.B., ONRIZAL, YLLANO, O.B., MEENAKSHISUNDARAM, S.H., SALMO, S.G., III, WATANO, Y., BABA, S., TATEISHI, Y. & KAJITA, T. 2012. Phylogeography of *Xylocarpus granatum*. In: *Proceedings of the International Conference Meeting on Mangrove Ecology, Functioning and Management – MMM3′, Galle, Sri Lanka, 2–6 July 2012* (F. Dahdouh-Guebas & B. Satyanarayana, eds), Vlaams Instituut voor de Zee (VLIZ) Special Publication 5, Oostende.

TSUNODA, K. & NISHIMOTO, K. 1978. Studies on the shipworms III. Pattern of vertical settlement of shipworms. *Wood Research: Bulletin of the Wood Research Institute, Kyoto University*, **64**: 1–8.

TURNER, R.D. 1955. The family Pholadidae in the western Atlantic and the eastern Pacific, Part II: Martesiinae, Jouannetiinae and Xylophagainae. *Johnsonia*, **3**: 65–160.

TURNER, R.D. 1966. *A survey and illustrated catalogue of the Teredinidae*. Museum of Comparative Zoology, Cambridge, MA.

TURNER, R.D. 1968. The Xylophagainae and Teredinidae—a study in contrasts. *Annual Reports of the American Malacological Union*, **1967**: 46–48.

TURNER, R.D. 1971. Australian shipworms. *Australian Natural History*, **1971**: 139–146.

TURNER, R.D. 2002. On the subfamily Xylophagainae (Family Pholadidae, Bivalvia, Mollusca). *Bulletin of the Museum of Comparative Zoology*, **157**: 223–307.

TURNER, R.D. & CALLOWAY, C.B. 1987. Species pairs in the Teredinidae. *American Malacological Union Annual Meeting Program*, p. 44 (Abstract).

TURNER, R.D. & JOHNSON, A.C. 1971. Biology of marine wood-boring molluscs. In: *Marine borers, fungi and fouling organisms of wood* (E.B.G. Jones & S.K. Eltringham, eds), pp. 259–301. Organization for Economic Cooperation and Development, Paris.

TURNER, R.D. & MCKOY, J.L. 1979. *Bankia neztalia* n. sp. (Bivalvia: Teredinidae) from Australia-New Zealand, and its relationships. *Journal of the Royal Society of New Zealand*, **9**: 465–473.

TURNER, R.D. & YAKOVLEV, Y.M. 1983. Dwarf males in the Teredinidae (Bivalvia, Pholadacea). *Science*, **219**: 1077–1078.

TURTON, W. 1822. *Conchylia Insularum Britanicarum. The shells of the British Islands*. J. Booth, London.

TYLER, P.A., YOUNG, C.M. & DOVE, F. 2007. Settlement, growth and reproduction in the deep-sea wood-boring bivalve mollusc, *Xylophaga*. *Marine Ecology Progress Series*, **343**: 151–159.

VALIELA, I., BOWEN, J.L. & YORK, J.K. 2001. Mangrove forests: one of the world's threatened major tropical environments. *BioScience*, **51**: 807–815.

VAROTTO, R.S. & BARRETO, C.C. 1998. Colonization of artificial substrata by teredinid larvae released from a previously infested focus at Ilha Grande Bay, RJ. *Brazilian Archives of Biology and Technology*, **41**. English translation at doi:10.1590/S1516–89131998000400002.

VERMEIJ, G.J. 1991. Anatomy of an invasion: the trans-Arctic interchange. *Paleobiology*, **17**: 281–307.

VETTER, E.W. & DAYTON, P.K. 1999. Organic enrichment by macrophyte detritus, and abundance patterns of megafaunal populations in submarine canyons. *Marine Ecology Progress Series*, **186**: 137–148.

VOIGHT, J.R. 2005. First report of the enigmatic echinoderm, *Xyloplax* from the North Pacific. *Biological Bulletin*, **208**: 77–80.

VOIGHT, J.R. 2007. Experimental deep-sea deployments reveal diverse Northeast Pacific wood-boring bivalves of Xylophagainae (Myoida: Pholadidae). *Journal of Molluscan Studies*, **73**: 377–391.

VOIGHT, J.R. 2008. Deep-sea wood-boring bivalves of *Xylophaga* (Myoida: Pholadidae) on the continental shelf. *Journal of the Marine Biological Association of the United Kingdom*, **88**: 1467–1472.

VOIGHT, J.R. 2009. Near-shore and offshore wood-boring bivalves (Myoida: Pholadidae: Xylophagainae) of the deep Eastern Pacific Ocean: diversity and reproduction. *Journal of Molluscan Studies*, **75**: 167–174.

VOIGHT, J.R. & SEGONZAC, M. 2012. At the bottom of the deep blue sea: a new wood-boring bivalve (Mollusca: Pholadidae: *Xylophaga*) from the Cape Verde abyssal plain (subtropical Atlantic). *Zoosystema*, **34**: 171–180.

VON BAUMHAUER, E.H. 1878. The Teredo and its depredations. *Popular Science Monthly*, **13**: 400–410.

WEBSTER, J.R., BENFIELD, E.F., EHRMAN, T.P., SCHAEFFER, M.A., TANK, J.L., HUTCHENS, J.J. & D'ANGELO, D.J. 1999. What happens to allochthonous material that falls into streams? A synthesis of new and published information from Coweeta. *Freshwater Biology*, **41**: 687–705.

WILANDER, P.B. 2008. *Xyloredo* sp(p). in Norway. Abstract in: *J. Knudsen: 60+ years in malacology, global imprints and foresight in taxonomy*. Zoological Museum, University of Copenhagen, Denmark.

WOELKE, C.E. 1956. The flatworm *Pseudostylochus ostreophagus* Hyman, a predator of oysters. *Proceedings of the National Shellfisheries Association*, **47**: 62–67.

WOLFF, T. 1979. Macrofaunal utilization of plant remains in the deep sea. *Sarsia*, **64**: 117–136.