

Role of polychaetes in bioerosion of coral substrates

Pat Hutchings¹

¹ The Australian Museum, Sydney NSW 2010, Australia, (path@austmus.gov.au)

Abstract. Polychaetes are important in the early stages of bioerosion of newly available coral substrate often as a result of coral death by disease, bleaching, Crown-of-Thorns starfish attack etc., and physical destruction during storms. A succession of polychaetes are recruited to the substrate, which it is hypothesised, facilitates subsequent recruitment by sponges, sipunculans and molluscs that are dominant in 'mature' boring communities. Recruitment of boring polychaetes varies according to the type of substrate available, season and geographical location of substrate, and environmental factors such as light, water quality, depth and wave exposure. The mechanisms by which polychaetes bore still require further investigations.

Keywords. Bioerosion, polychaetes, early stages, succession

Introduction

Present day coral reefs are dynamic systems as were fossil reefs (Vogel 1993), resulting from the balance between reef growth and erosion both physical and biological. Biological erosion consists of losses of calcium carbonate by organisms boring into the substrate. It involves a wide variety of borers such as microalgae, fungi, sponges, molluscs, polychaetes and sipunculans (Hutchings 1986), which often results in a honeycombed structure. Then when endolithic algae and fungi are embedded in the substrate (Le Campion-Alsumard et al. 1995), it makes it highly susceptible to grazing by herbivores such as echinoderms, molluscs and certain species of fish (Bellwood and Choat 1990; Conand et al. 1998), which physically remove the substrate containing the algae. This porous structure also makes the substrate more susceptible to physical and chemical erosion, as water is pumped into the borings and buffeted by waves and currents that may cause dislodgement of parts of the coral substrate, especially upright dead coral colonies (Glynn 1997). Water movement facilitates the chemical dissolution of calcium carbonate substrates and while no detailed measurements have been made on the dissolution of reef substrate, a study by Fulton and Bellwood (2005) on rates of dissolution of gypsum (calcium sulfate) in reefal environments found that rates varied significantly with wave motion. While gypsum dissolves faster than calcium carbonate it does provide an indication of the relative rates of dissolution in a variety of reefal environments and that areas of high water movement experience the highest rates of dissolution,

M. Wisshak, L. Tapanila (eds.), *Current Developments in Bioerosion*. Erlangen Earth Conference Series, doi: 10.1007/978-3-540-77598-0_13, © Springer-Verlag Berlin Heidelberg 2008

although relative to biological erosion rates are very small. It is important to stress that these agents of reef destruction, biological, chemical and physical, interact all together and vary between habitats and geographical areas in space and time (Le Campion-Alsumard et al. 1993). All rates of bioerosion will of necessity include a component of chemical and physical erosion, as dissecting out the individual components is not possible.

Once a coral colony dies as a result of various events such as predation, disease or being physically dislodged by storms, it is rapidly colonised by micro-organisms including endolithic algae, viruses (Tribollet et al. 2005) and presumably bacteria, which are attracted to the dying or dead coral tissue. The surface of this dead colony rapidly becomes pale green as algae colonises both the surface and the substrate immediately below the surface (Chazottes et al. 1995).

Recruitment of boring organisms is believed to be entirely via pelagic or benthic larvae which settle on the substrate, metamorphose and rapidly bore into the substrate (Hutchings 1986). As live corals are active carnivores, recruitment onto live coral colonies is difficult or restricted to areas where polyps are damaged or very scarce. In contrast, dead corals or dead parts of live coral colonies and coral substrate are actively bored. Traditionally, only mature bored colonies have been studied, where conspicuous borers include extensive sponge colonies, bivalves and sipunculans (Glynn 1997). However, it is also important to understand the initial stages of bioerosion, and to determine the substrate susceptibility, and to assess if these initial stages have an influence on the development of mature boring communities. In situ studies on massive colonies of *Porites lobata* Dana, 1846 ranging from living colonies to 100% dead colonies in French Polynesia showed that boring rates increased with the time elapsed since the death of the colony, and that the dominant agents of boring also changed with increasing age of the coral structure (Peyrot-Clausade et al. 1992). As coral reefs are becoming increasingly degraded by bleaching events, diseases, Crown-of-Thorns starfish attacks etc. (Wilkinson 2004), it is becoming more and more critical to understand how the balance between reef construction and reef destruction is being altered, and which can lead to loss of reef framework and all the ensuing consequences of this (Glynn 1997; Holmes et al. 2000; Salvat et al. 2001).

To date virtually all the experimental studies have been carried out on massive species of *Porites* Link, 1807, with only one study (Musso 1994) using colonies of *Acropora* Oken, 1815. Preliminary studies on the complete infauna (borers + nestlers) on a range of coral substrates composed of a variety of morphological types of coral at One Tree Island, Great Barrier Reef, found considerable differences between branching, massive and columnar type corals in terms of the biomass and diversity of infauna (Hutchings 1974). The highest biomass and diversity occurred in the substrates composed of the massive species and the least in the samples of dead organ pipe corals. This suggests that borers favour substrates composed of large colonies of dead massive species as these habitats are less vulnerable to physical destruction and provide sufficient space for borers to either become large as in the case of some polychaetes, sipunculans or bivalves,

or form massive colonies such as sponges (Hutchings 1974). Branching thickets of *Acropora* have limited numbers of borers as the physical dimensions of the branches limits large borings from forming (Hutchings et al. unpublished data).

Traditionally, boring sponges, molluscs and sipunculans have been regarded as major bioeroders and, certainly, they are responsible for substantial losses of coral substrate in mature boring communities (Hutchings 1986; Perry 1998). The mechanisms by which these animals bore are reasonably well documented and include both chemical dissolution as well as mechanical abrasion or a combination of both (Lazar and Loya 1991; Mao Che et al. 1996; Schönberg and Wilkinson 2001). These organisms are conspicuous when coral colonies are broken open and as well, they are easily recognised in fossil coral reefs. During the past 20 years using experimental techniques, the initial stages of bioerosion of recently killed coral has been investigated in the Pacific both in relatively pristine and disturbed environments. This review discusses the findings of these studies dealing with polychaete borers. To assist in this review line drawings of the common polychaete borers and the structures which they use to bore are provided in Figures 1 to 3.

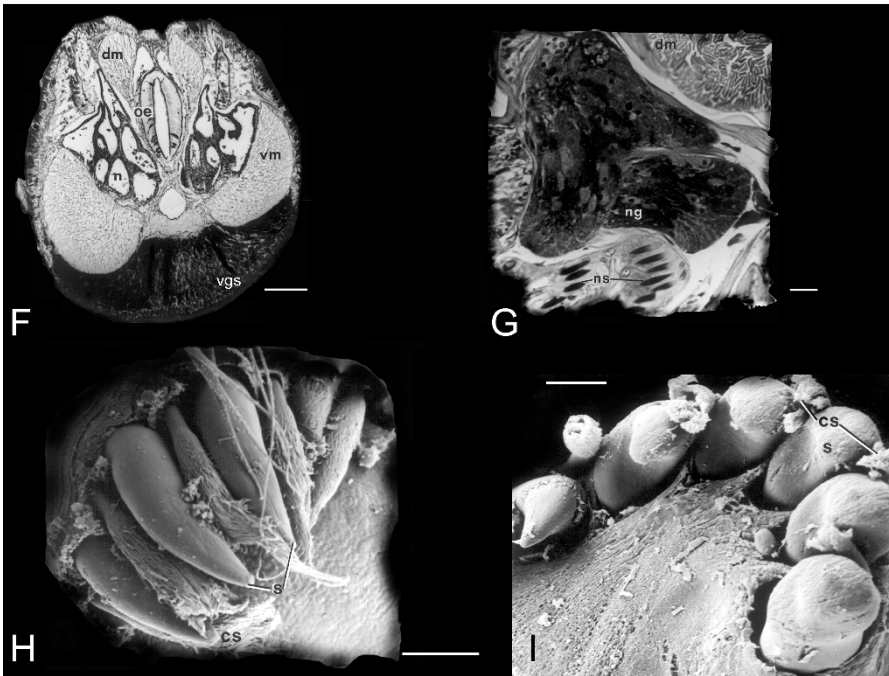
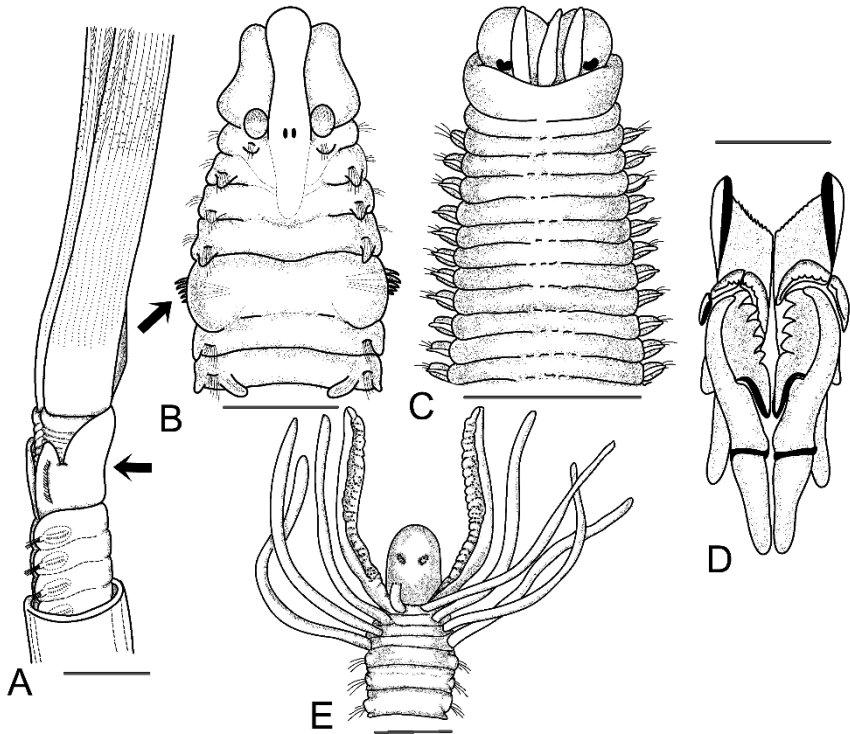
Study techniques

To study the recruitment of the early borers to recently killed coral substrates, colonies of live coral are collected, typically one of the massive species of *Porites*. The layer of live polyps are trimmed off and regular sized blocks are cut using a band saw. Any blocks with signs of boring are discarded. The resultant blocks are then washed, dried and measured and so when the samples are returned to the reef and firmly attached, one is certain that no living organisms are present in them. The blocks (Fig. 2A) are then collected at intervals to document the distribution and abundance of the infauna, over time, allowing the succession of borers to be determined. Early studies used to place the blocks in an acid mixture, to dissolve the calcium carbonate substrate and to extract the animals, which are often small and impossible to extract in any other way (Kiene and Hutchings 1994). Following dissolution, the resultant residue consists of a matrix of endolithic algae and a suite of animals, and it is relatively easy to extract them intact and to sort them to species. More recently, the collected blocks are cut in half, one to be treated as above, the other to be used to determine boring, accretion and grazing rates, and allowing net rates of gains or losses to be calculated (Fig. 2B; Tribollet et al. 2002).

Bioeroders

Distinguishing between nestlers and borers

The polychaetes extracted after acid dissolution include both borers and species that enter the coral substrate after borings have been established to settle inside. The latter are referred to as 'nestlers' or 'opportunistic species' (Hutchings 1983) and separating them from borers can be problematic. However, knowing the morphology and ecology of the groups, as well as examining the species in situ



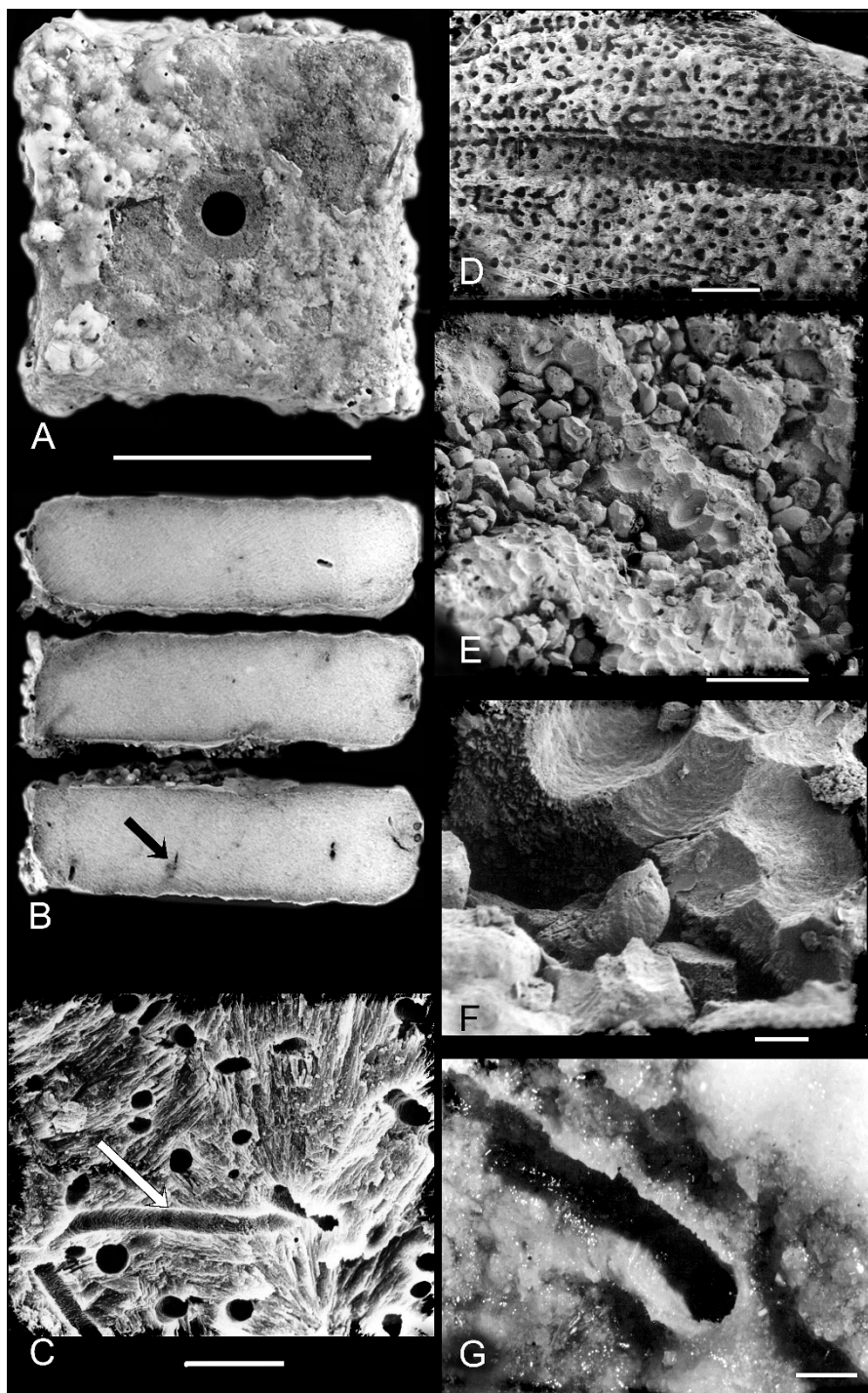
in coral substrate, allows the identification of the real borers, and to characterise their borings. Some of these polychaete borers are also found in other calcareous substrates such as limestone and mollusc shells, especially species of spionids and sabellids. One genus of the polychaete family Sabellidae, *Caobangia* Giard, 1893, are found boring into mollusc shells. They occur in 'blind-ending tear drop-shaped burrows' according to Giard (1893). Later, Jones (1969, 1974) was able to expand these descriptions based on additional material becoming available and moved the genus into a new family Caobangiidae. The genus represented by several species was found in 22 species of molluscs from fast flowing streams in South East Asia and the Philippines at elevations from 800 to 1300 m. This genus appears to be restricted to freshwater and only bores into mollusc shells belonging to several genera. Recent phylogenetic studies have suggested that the family should be placed back within the Sabellidae (Beesley et al. 2000).

Which polychaetes bore?

Polychaetes which dominate the initial stages of colonisation of experimental substrates belong to a wide range of families and species. They have been observed to occupy tight borings, similar to its body width, although sometimes more than twice its body length (Chughtai and Knight-Jones 1988). Those belonging to sedentary species (such that they cannot be extracted from the borings easily) are certainly borers, while those occupying cavernous borings and moving freely are nestlers.

Basically, there are only two options for providing an explanation of how boring species can actually bore into hard substrates. First they can secrete substances to dissolve the substrate or, secondly they can use hard structures such as teeth or spines (Fig. 1D, H-I) to physically erode the substrate. Perhaps a combination of both mechanisms is also possible. Among polychaetes, one of the best known groups of borers are the polydorids, which include several species of Spionidae (e.g., *Polydora* Bosc, 1802 and *Dipolydora* Augener, 1914) having modified chaetae on the 5th chaetiger; Fig. 1B, H-I). Polydorids are known to bore into a wide variety of calcium carbonate substrates including mollusc shells and limestone as well as coral substrates (Blake and Evans 1973; Zottoli and Carriker 1974; Simon et al. 2006). While some polydorids are found in benthic muddy substrates (Wilson 2000), all species occurring in coral substrates are regarded as borers and are always found in tight fitting borings. The exact method of boring is unknown in corals but has been extensively studied in commercial mollusc species (Evans 1969). Thus, it is not surprising that the boring mechanism by these polychaetes has been the

Fig. 1 **A** Anterior end of *Notaulux* sp.; arrow indicates glandular collar; scale 1 mm. **B** Anterior end of *Polydora* sp.; arrow indicates position of modified chaetiger 5; scale 1.5 mm. **C** Anterior end of *Lysidice* Savigny, 1818; scale 2 mm. **D** Dissected jaws of *Lysidice* sp.; scale 0.6 mm. **E** Anterior end of *Dodecaceria* sp.; scale 1 mm. **F** Transverse section of *Notaulux* in thoracic region; Alcian blue / fast red stain; scale 150 μ m. **G** Transverse section of thoracic segment of *Eunice* Cuvier, 1817 showing notopodial gland. **H-I** SEM of spines of *Polydora* sp. from *Porites* spp. at Lizard Island; scale 10 μ m. (dm = dorsal musculature, n = nephridium, ng = notopodial gland, ns = notochaetae, oe = oesophagus, vgs = ventral glandular shield, vm = ventral musculature, s = chaeta, cs = capillary chaeta; Figures A-E: redrawn from Day 1967)



best studied, as their extensive borings reduce the value of the infested shells and, if heavily infested, may be lethal to the molluscs. It was suggested that boring was assisted by the modified chaetae on chaetiger 5 (Fig. 1B, H-I) and that the ventral epithelium and segmental mucus glands produced acid mucopolysaccharides (Dorsett 1961), which may bring about decalcification by acting as chelating agents (Simkiss and Tyler 1957). Nevertheless, *Polydora websteri* Hartman, 1943, could still bore after removing the modified chaetae (Haigler 1969). The same species boring into *Crassostrea* Sacco, 1897 and *Mytilus* Linnaeus, 1758, secretes a viscous fluid, which dissolves interprismatic and interlamellar organic matrices and then dissolves the exposed crystals (Zottoli and Carricker 1974). However, the actual composition of the fluid was not determined. Although this substance has not been further identified, it was suggested that it is secreted along the body of the worm and that it is able to dissolve mollusc shells (Sato-Okoshi and Okoshi 1993). It seems likely that similar processes occur when polydorids bore into coral substrate. These polychaetes are among the earliest colonisers of the experimental substrates and after just 3 months, they may already form dense colonies. Species of *Polydora* may spawn in either summer or spring, while other polydorids deposit egg capsules in winter, which release pelagic larvae in spring (Blake 1969). Recruitment varied between sites, depending on the local composition of the polydorid populations and environmental conditions, which suggests that competent larvae may be available for recruitment throughout much of the year (Hutchings et al. 1992).

Another well represented group are species of *Dodecaceria* Örsted, 1843 (Cirratulidae). After successful recruitment by pelagic larvae, and establishment, these worms can then rapidly build up large populations within a chamber (Figs. 1E, 3E). They use asexual reproduction where adult worms split up into individual segments, and each developing into miniature worms, using the process of fragmentation (Gibson 1977). However, these asexually produced recruits appear unable to produce their own borings (Gibson and Clark 1976). This group of polychaetes is also commonly found boring into calcareous substrates in both temperate and tropical areas. These animals must secrete an acid like secretion, as they have no hard structures capable of eroding the substrate. The flask-shaped chambers are connected to the exterior by a narrow passage and these surface deposit feeding animals protrude their long palps from the chamber to collect fine sediments which are washed into or onto the substrate (Fig. 3E). *Dodecaceria concharum* Örsted, 1843 produces a straight boring in bivalve shells, which tend to expand towards the blind end, but the method by which it bores is not known (Evans 1969). *Dodecaceria* species are present within 3-6 months of exposure in experimental coral blocks and they are abundant in areas where the substrates are subjected to high sediment loads from river run off or from nearby inter reefal areas where regular trawling occurs (Hutchings et al. 2005; Osorno et al. 2005).

Fig. 2 **A** Experimental block of *Porites* collected after 12 months of exposure. **B** Block cut into slices revealing internal borings; arrow indicates worm boring. **C** Longitudinal section along *Notaulux* boring under the SEM; scale 30 µm. **D** Longitudinal section of *Notaulux* under SEM; scale 30 µm. **E** *Lysidice* sp. boring in *Porites* under SEM; scale 30 µm. **F** *Lysidice* sp. boring in *Porites* under SEM; scale 30 µm. **G** *Eunice* sp. in *Porites*; scale 30 µm

Another family which has several boring representatives are the Sabellidae (Chughtai and Knight-Jones 1988), which include species of *Notaulux* Tauber, 1879, *Megalomma* Johansson, 1926, *Pseudopotamilla* Bush, 1904, *Perkinsiana* Knight-Jones, 1983 and *Terebrasabella* Fitzhugh and Rouse, 1999. Common in all experimental coral blocks is a species of *Notaulux*, which has been referred to as *Hypsicomus* Grube, 1870 (see Peyrot-Clausade et al. 1992 and subsequent papers; Fig. 1A). Most species of *Hypsicomus* were transferred to *Notaulux* (see Perkins 1984) and subsequently an additional species of *Notaulux* including an illustration of a longitudinal section of the tube buried deep within *Porites* was described (Nishi and Nishihira 1999). *Notaulux* seems to be very common throughout the Indo-Pacific and typically includes boring species (J. Gil pers. comm.). However, it is still unclear, whether it represents one widely distributed species or several. This group of fan worms are found in tight fitting flask-shaped tubes lined with chitin and, in both experimental and 'natural' habitats, they are found penetrating deep into almost pristine coral, but still maintaining an opening allowing them to expand the branchial crown for filter feeding and respiration (Figs. 2C-D, 3A-B, D). Like *Dodecaceria* they have no hard structures capable of eroding the substrate. Thus, boring by an acid-like secretion must be assumed. Sabellids have well developed glands at the base of the branchial crown, although attempts to identify the nature of the substances extruded by these glands were unsuccessful (Hutchings unpub. data; Fig. 1F). However, this is the most likely secretory area, given that the rest of the body is far less glandular. Studies on species boring into limestone on the Welsh coast strongly indicate that the substrate was removed by chemical dissolution aided by the boring irrigation of the cavity by muscular action and faecal removal by cilia (Chughtai and Knight-Jones 1988). These authors also found that the chaetae rarely exhibited any sign of damage or wear which could have resulted from mechanical boring into hard rock. Another group of sabellids, the fabriciniids, have also been identified as borers (Peyrot-Clausade et al. 1995) but the data supporting this is weak as the animals are very small and about the size of the pores in the coral matrix. While present in the earliest experimental blocks, fabriciniid borings are impossible to distinguish from the coral structure.

The other group of polychaete borers are the eunicids and several species are involved (Fig. 1C). They typically do not occur until several months after the experimental substrates have been exposed and they become more abundant as the boring communities mature. Eunicids (including species of Eunicidae and Dorvilleidae) have well developed, complex jaws (Fig. 1C-D) and occur in well developed borings (Figs. 2G, 3C, F). Detailed examinations of the walls of these borings using SEM reveal gouges resembling tooth marks, and fragments of coral substrate are often found between the numerous teeth which constitute these complex jaws (Hutchings unpubl. data; Fig. 2E-F). Acid secretion may also occur although this has not been documented (Fig. 1G).

In summary the identification of boring species of polychaetes depends on the shape of the boring relative to the animal, the distribution of borings in the substrate both in the experimental substrates as well as in in situ substrates. Polychaete borings

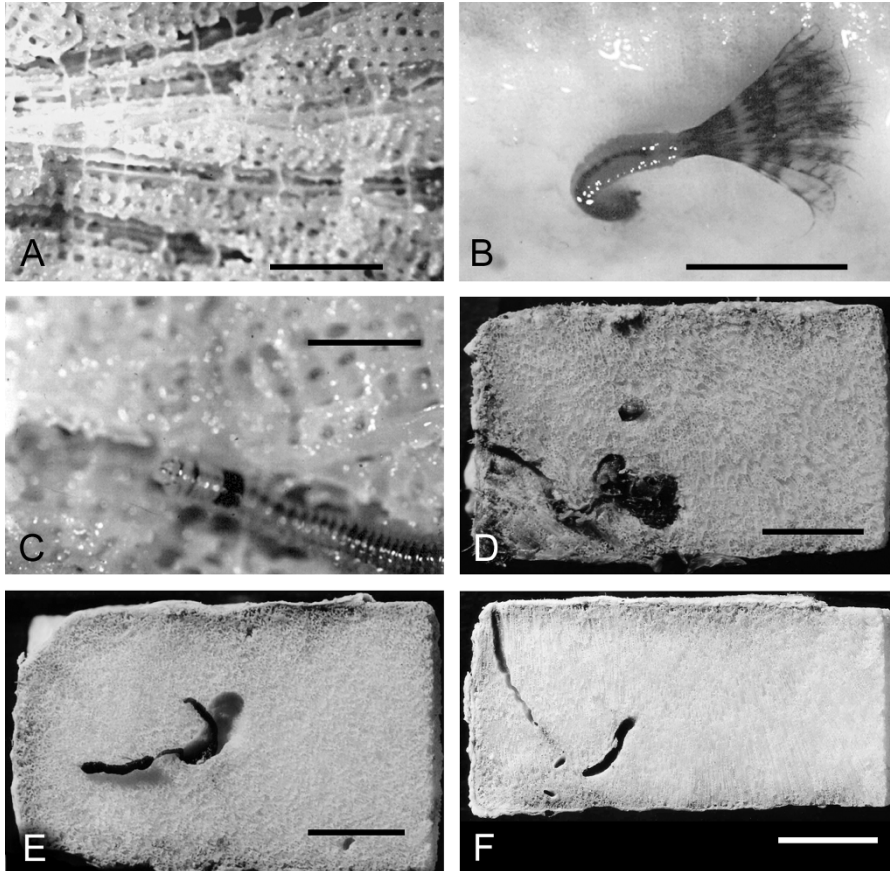


Fig. 3 **A** Boring of *Notaulux* sp.; scale 1 mm. **B** *Notaulux* sp. emerging from boring; scale 1 mm. **C** *Eunice* sp. in boring; scale 1 mm. **D** Sabellid boring in section of experimental block; scale 10 mm. **E** *Dodecaceria* sp. in section of experimental block; scale 10 mm. **F** Eunicid boring in section of experimental block together with a sipunculan tube; scale 10 mm

are characteristic in shape so that examining thin sections of substrate in order to measure rates of loss of calcium carbonate, will allow identification of borings as belonging to polychaete worms rather than to other borers (Hutchings et al. 2005; Fig. 2B-C). More detailed information on the exact mechanism of boring is needed but it is difficult to study these small worms. However, it should be possible now to actually measure the microenvironments within individual borings to detect acid secretion and characterise its composition, although to date this has not been done. The only detailed investigation was undertaken by Zottoli and Carriker (1974) who studied boring in *Polydora* by examining live worms living in artificial preparations of polished shell covered with plastic film. They found that the worms can settle in crevices on the shell surface and they slowly penetrate the shell forming a U- or flask-shaped cavity by secreting a viscous fluid which dissolves the interprismatic and interlamellar organic matrices and then the exposed crystals. SEM of the borings

reveal a complex pattern of internal dissolution. They found no evidence of chaetal abrasion on the shell walls even under high magnification. It seems likely that a similar process of boring would occur in coral substrates.

Succession of borers

Experiments carried out both on the Great Barrier Reef and the Coral Sea as well as in French Polynesia clearly show a succession in the polychaete borers. Newly available substrate is heavily colonised by *Polydora* spp., (Spionidae), *Schistomeringos* Jumars, 1974 (Dorvilleidae belonging to the eunicids) and *Notaulux* (Sabellidae), with initially increasing densities that decline after 12-15 months. With increasing exposure, other eunicids arrive as well as *Dodecaceria* spp. In mature boring communities, large eunicids are common, often reaching many cm in length (Hutchings et al. 1992). The relative densities of the different borers vary according to habitat and location. In the northern Great Barrier Reef, *Polydora* sp., favoured more oceanic sites, whereas *Dodecaceria* sp. preferred more inshore sites with higher levels of turbidity (Osorno et al. 2005). In contrast, in French Polynesia *Polydora* spp. favoured the more polluted sites where turbidity run off levels were high (Hutchings and Peyrot-Clausade 2002). Unfortunately, no long term data were available from the most polluted site at Faaa, as the experimental substrate was completely eroded after only two years of exposure (Pari et al. 1998). At Faaa, the densities of polychaete borers were determined after 6 months of exposure. However, the grazing rate by the echinoid *Echinometra mathaei* Blainville, 1825 which was present in high numbers, was such that the surface of the blocks was being heavily eroded, so that the borers present in the peripheral areas of the experimental substrate were constantly being removed, so the recorded densities of the borers were seriously underestimated. Nevertheless, the presence of *Polydora* and *Dodecaceria* was reported at this highly polluted site (Peyrot-Clausade et al. 1995; Pari et al. 1998; Hutchings and Peyrot-Clausade 2002).

Due to the nature of the boring communities, the substrate must always be destroyed to extract the borers. Thus, while one can document the densities and species composition at a particular point and time, and then compare them with the next sampling time, this may not reflect the real dynamics of the boring community during the period between sampling. Some polychaetes have life cycles ranging from a few weeks to several months, so that it is possible that generations have come and gone between the sampling periods. All studies on early stages of bioerosion have found considerable variation between replicate blocks collected at the same sampling period. However, these differences are less than those found between sites, suggesting that recruitment patterns at the local scale are variable. Certainly, larvae recently settled on the block are extremely vulnerable to predation or they may be easily washed off by local currents (Sebens and Johnson 1991) until they actually bore into the substrate. In fact, the highest density of larvae of boring sabellids occurred around surface concavities, which provides shelter from wave action, but also harbor many predators (Chughtai and Knight Jones 1988). They suggest that, at this stage, larvae are most vulnerable so that a high mortality must be presumed.

Seasonality of recruitment

A distinct seasonality of recruitment has been demonstrated, reflecting that of breeding for many of these polychaete borers (Hutchings and Murray 1982; Hutchings et al. 1992; Hutchings and Peyrot-Clausade 2002). Maximum recruitment occurs during the summer months, with windward and reef flat sites being preferred. Recruitment varies over time at a particular site and patterns of recruitment vary between sites over time (Hutchings and Peyrot-Clausade 2002). However, any newly available substrate is colonised rapidly regardless of the time of year (Hutchings et al. 1992). In addition, at Lizard Island (Great Barrier Reef), significant variations between years occurred at individual sites, likely reflecting variations in larval supply, and / or recruitment success, which in turn will be modified by variations in weather patterns between years (Hutchings et al. 1992). In addition, significant differences occurred between sites over a four-year period at Lizard Island, with a windward slope site at 10 m and the reef flat being the preferred recruitment sites for borers (Kiene and Hutchings 1994). Similar patterns were found over a five-year period, in French Polynesia (Pari et al. 2002).

Rates of boring

The few published rates of worm borings include both polychaetes and sipunculans (Peyrot-Clausade et al. 1992; Kiene and Hutchings 1994; Osorno et al. 2005). However, they are not directly comparable as Osorno et al. (2005) determined rates of loss from examining thin sections and estimating the volume of the boring volumes, whereas the other two studies estimated rates of loss of calcium carbonate by measuring the volume of the worms. The highest rates recorded at Lizard Island (Great Barrier Reef) were 0.104 kg/m² (Kiene and Hutchings 1994), whereas those recorded in French Polynesia were 0.1979 kg/m² (Peyrot-Clausade et al. 1992). But rates which included both polychaetes and sipunculans across the Great Barrier Reef varied from 0.113 ± 0.066 to 0.356 ± 0.243 kg/m² (Osorno et al. 2005). It must be taken into account that all these net rates are almost certainly underestimates, as worm borings in the outer layers of the substrate are habitually being removed by grazers, and the borings of small worms are difficult to identify in thin sections.

Discussion and future areas of research

While polychaetes have been shown to be important colonisers of newly available coral substrate, their importance declines as the boring community ages so that other boring agents tend to become dominant. It has been suggested that the small borings created by the polychaetes and their high rate of turnover facilitates the recruitment of other borers such as sponges, bivalves and sipunculans which are never found in substrates made recently available. However, it seems difficult to actually test this hypothesis, taking into account our knowledge of the actual settlement and larval boring process. An additional problem is to actually measure the polychaete boring rates, as those calculated from thin sectioning of bored substrates by Pari et al. (2002) and Osorno et al. (2005) are almost certainly underestimates. Moreover,

although sipunculans tended to be less numerous than polychaetes, these authors grouped polychaetes and sipunculans together as worm borings. Measuring rates may also be problematic as these early colonising borers occur in the surface layers of the substrate, and this is the region more susceptible to being removed by grazers unless it is protected by heavy layers of silt, which inhibit the development of endolithic algae (Osorno et al. 2005).

Another area requiring urgent attention is the resolution of the species-level taxonomy of the taxa involved. This will reveal whether some boring species are really widely distributed Indo-Pacific species, as currently suggested, or a suite of cryptic species. However, this will require major taxonomic revisions of the groups.

Finally, while this review has by default concentrated on experimental studies in French Polynesia and the Great Barrier Reef (Australia), similar data are required from the eastern Pacific and the Caribbean. Some bioerosion studies have been carried out in Indonesia (e.g., Holmes et al. 2000) but did not look at the polychaetes. In the tropical eastern Pacific, the bioerosion by polychaetes in *Pocillopora* Lamarck, 1816 was investigated, revealing that, although present at all the study sites, were the least important of the bioeroders (Londoño-Cruz et al. 2003).

Most of the experimental work referred to above used blocks of *Porites*. However, one study on *Acropora* has been carried out (Musso 1994). In this case, polychaetes were found to be important early colonisers, suggesting that similar processes would occur in both coral species. As the amount of dead coral continues to increase with increasing reef degradation (Wilkinson 2004), we are witnessing increasing bioerosion rates (Pari et al. 2002), suggesting that the initial colonisation of substrates by polychaetes is important in facilitating the subsequent processes.

Acknowledgements

I should like to thank Alicia Osorno for supplying some of the illustrations on Figures 2 and 3, and Kate Attwood for help in preparing the figures. The paper also benefitted from constructive comments from two reviewers and I would also like to thank the editors for inviting me to contribute this chapter.

References

- Augener H (1914) Polychaeta II, Sedentaria. In: Michaelsen W, Hartmeyer R (eds) Die Fauna Südwest-Australiens. Ergebnisse der Hamburger südwest-australischen Forschungsreise 1905. Fischer, Jena, 5:65-304
- Beesley PL, Ross GJB, Glasby CJ (2000) Polychaetes & Allies: The southern synthesis. Fauna of Australia 4A. Polychaeta, Myzostomida, Pogonophora, Echiura, Sipuncula. CSIRO Publ, Melbourne, 465 pp
- Bellwood DR, Choat JH (1990) A functional analysis of grazing in parrotfishes (family Scaridae): the ecological implications. Environ Biol Fish 28:189-214
- Blainville HM de (1825) Oursins. Dictionnaire Sci Nat 37:59-102
- Blake JA (1969) Systematics and ecology of shell boring polychaetes from New England. Amer Zoologist 9:813-820

- Blake JA, Evans JW (1973) *Polydora* and related genera as borers in mollusk shells and other calcareous substrates. *Veliger* 15:235-250
- Bosc LAG (1802) Histoire naturelle des vers, contenant leur description et leurs moeurs, avec figures dessinées d'après nature. Deterville, Paris, 324 pp
- Bush KJ (1904) Tubicolous annelids of the tribes Sabellides and Serpulides from the Pacific Ocean. *Harriman Alaska Exped* 12:169-355
- Chazottes V, Le Campion-Alsumard T, Peyrot-Clausade M (1995) Bioerosion rates on coral reefs: interaction between macroborers, microborers and grazers (Moorea, French Polynesia). *Palaeogeogr Palaeoclimatol Palaeoecol* 113:189-198
- Chughtai I, Knight-Jones EW (1988) Burrowing into limestone by sabellid polychaetes. *Zool Scripta* 17:231-238
- Conand C, Heeb M, Peyrot-Clausade M, Fontaine MF (1998) Bioerosion by the sea urchin *Echinometra* on La Reunion reefs (Indian Ocean) and comparison with Tiahura reefs (French Polynesia). In: Mooi R, Telford M (eds) *Echinoderms*. Balkema, Rotterdam, pp 609-615
- Cuvier G (1817) Le règne animal distribué d'après son organisation, pour servir de base à l'histoire naturelle des animaux et d'introduction à l'anatomie comparée. Deterville, Paris, vol 2, 532 pp
- Dana JD (1846) Zoophytes. *U S Explor Exped 1838-1842*, 7:1-120 and 709-720
- Day JH (1967) A monograph on the Polychaeta of Southern Africa. Part 1. *Publ Brit Mus Nat Hist London* 656, 458 pp
- Dorsett DA (1961) The behaviour of *Polydora ciliata* (Johnst.). Tube building and burrowing. *J Mar Biol Assoc UK* 56:649-674
- Evans JW (1969) Borers in the shell of the sea scallop, *Placopecten magellanicus*. *Amer Zoologist* 9:775-782
- Fitzhugh K, Rouse GW (1999) A remarkable new genus and species of fan worm (Polychaeta: Sabellidae: Sabellinae) associated with marine gastropods. *Invertebrate Biol* 118:357-390
- Fulton CJ, Bellwood DR (2005) Wave induced water motion and the functional implications for coral reef fish assemblages. *Limnol Oceanogr* 50:255-264
- Giard A (1893) Sur un type nouveau et aberrant de la famille des Sabellides (*Caobangia billeti*). *C R Soc Biol Paris, Ser 9*, 5:473-476
- Gibson PH (1977) Reproduction in the cirratulid polychaetes *Dodecaceria concharum* and *D. pulchra*. *J Zool London* 182:89-102
- Gibson PH, Clark RB (1976) Reproduction of *Dodecaceria caulleryi* (Polychaeta, Cirratulidae). *J Mar Biol Assoc UK* 41:577-590
- Glynn P (1997) Bioerosion and coral-reef growth: A dynamic approach. In: Birkeland C (ed) *Life and death of coral reefs*. Chapman and Hall, New York, pp 68-95
- Grube AE (1870) Bemerkungen über Anneliden des Pariser Museums. *Arch Natgesch Berlin* 36:281-352
- Haigler S (1969) Boring mechanisms of *Polydora websteri* inhabiting *Crassostrea virginica*. *Amer Zoologist* 9:821-828
- Hartman O (1943) Description of *Polydora websteri* n.sp. In: Loosanoff VL, Engle J (ed) *Polydora* in oysters suspended in the water. *Biol Bull* 85:70-72
- Holmes KE, Edinger EN, Hariyadi, Limmon GV, Risk MJ (2000) Bioerosion of live massive corals and branching coral rubble on Indonesian coral reefs. *Mar Poll Bull* 40:606-617
- Hutchings PA (1974) A preliminary report on the density and distribution of invertebrates living in coral reefs. *Proc 2nd Int Coral Reef Symp* 2:285-296
- Hutchings PA (1983) Cryptofaunal communities of coral reefs. In: Barnes DJ (ed) *Perspectives in coral reefs*. AIMS, Townsville, pp 200-208

- Hutchings PA (1986) Biological destruction of coral reefs - A review. *Coral Reefs* 4:239-252
- Hutchings PA, Murray A (1982) The establishment of polychaete populations to coral substrates at Lizard Island, Great Barrier Reef - an experimental approach. *Austral J Mar Freshwater Res* 33:1029-37
- Hutchings PA, Peyrot-Clausade M (2002) The distribution and abundance of boring species of polychaetes and sipunculans in coral substrates in French Polynesia. *J Exper Mar Biol Ecol* 269:101-121
- Hutchings PA, Kiene WE, Cunningham RB, Donnelly C (1992) Experimental investigation of bioerosion at Lizard Island, Great Barrier Reef. Part 1. Patterns in the distribution and extent of non-colonial, boring communities. *Coral Reefs* 11:23-31
- Hutchings PA, Peyrot-Clausade M, Osorno A (2005) Influence of land runoff on rates and agents of bioerosion of coral substrates. *Mar Poll Bull* 51:438-447
- Kiene WE, Hutchings PA (1994) Experimental investigations on patterns in the rates of bioerosion at Lizard Island, Great Barrier Reef. *Coral Reefs* 13:91-98
- Knight-Jones P (1983) Contributions to the taxonomy of Sabellidae (Polychaeta). *Zool J Linn Soc* 79:245-295
- Johansson KE (1926) Bemerkungen über die Kinbergschen Arten der Familien Hermelidae und Sabellidae. *Ark Zool Stockholm* 18A(7):1-28
- Jones ML (1969) Boring of shell by *Caobangia* Giard, 1893 in freshwater snails of southeast Asia. *Amer Zoologist* 9:829-835
- Jones ML (1974) On the Caobangiidae, a new family of the Polychaeta, with a redescription of *Caobangia billeti* Giard. *Smithson Contr Zool* 175:1-55
- Jumars PA (1974) A generic revision of the Dorvilleidae (Polychaeta) with six new species from the deep North Pacific. *J Linn Soc London Zool* 54:101-135
- Lamarck J-B de (1816) Histoire naturelle des animaux sans vertèbres, présentant les caractères généraux et particuliers de ces animaux, leur distribution, leurs classes, leurs familles, leurs genres, et la citation des principales espèces qui s'y rapportent; précédée d'une introduction offrant la détermination des caractères essentiels de l'animal, sa distinction du végétal et des autres corps naturels, enfin, l'exposition des principes fondamentaux de la zoologie. Verdrière, Paris, 3:1-586
- Lazar B, Loya Y (1991) Bioerosion of coral reefs: A chemical approach. *Limnol and Oceanogr* 36:377-383
- Le Campion-Alsumard T, Romano J-C, Peyrot-Clausade M, Le Campion J, Paul L (1993) Influence of some coral reef communities on the calcium carbonate budget of Tiahura reef (Moorea, French Polynesia). *Mar Biol* 115:685-693
- Le Campion-Alsumard T, Golubic S, Priess K (1995) Fungi in corals: symbiosis or disease? Interaction between polyps and fungi causes pearl-like skeleton biomineralization. *Mar Ecol Progr Ser* 117:137-147
- Link HF (1807) Beschreibung der Naturalien-Sammlung der Universität zu Rostock. Adler, Rostock, pp 1-38
- Linnaeus C (1758) *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. Tomus I. Editio decima, reformata. Laurentii Salvii, Holmiae, 824 pp
- Londoño-Cruz E, Cantera JR, Toro-Farmer G, Orozco C (2003) Internal bioerosion by macroborers in *Pocillopora* spp. In the tropical eastern Pacific. *Mar Ecol Progr Ser* 265:289-295
- Mao Che L, Le Campion-Alsumard T, Boury-Esnault N, Payri C, Golubic S, Bezac C (1996) Biodegradation of shells of the black pearly oyster *Pinctada margaritifera* var. *cumingii*, by microborers and sponges of French Polynesia. *Mar Biol* 126: 509-519

- Musso BM (1994) Internal bioerosion of in situ living and dead corals on the Great Barrier reef. James Cook Univ North Queensland, 212 pp
- Nishi E, Nishihira M (1999) Use of annual density banding to estimate longevity of infauna of massive corals. *Fish Sci* 65:48-56
- Oken L (1815) *Oakens Lehrbuch der Naturgeschichte. Dritter Theil. Zoologie. Mit vierzig Kupfertafeln. Erste Abtheilung. Fleischlose Thiere.* Reclam, Leipzig, 850 pp
- Örsted AS (1843) *Annulorum danicorum conspectus fasc. J Maricolae* Copenhagen, 52 pp
- Osorno A, Peyrot-Clausade M, Hutchings PA (2005) Patterns and rates of erosion in dead *Porites* across the Great Barrier Reef, Australia after 2 and 4 years of exposure. *Coral Reefs* 24:292-303
- Pari N, Peyrot-Clausade M, Le Campion-Alsumard T, Hutchings PA, Chazottes V, Golubic S, Le Campion T, Fontaine MF (1998) Bioerosion of experimental substrates on high islands and atoll lagoons (French Polynesia) after 2 years of exposure. *Mar Ecol Progr Ser* 166:119-130
- Pari N, Peyrot-Clausade M, Hutchings PA (2002) Bioerosion of experimental substrates on high islands and atoll lagoons (French Polynesia) during 5 years of exposure. *J Exp Mar Biol Ecol* 276:109-127
- Perkins TH (1984) Revision of *Demonax* Kinberg, *Hypsicomus* Grube, and *Notaulax* Tauber, with a review of *Megalomma* Johansson from Florida (Polychaeta: Sabellidae). *Proc Biol Soc Wash* 97: 285-368
- Perry CT (1998) Macroborers within coral reef framework at Discovery Bay, north Jamaica: species distribution and abundance, and effects on coral preservation. *Coral Reefs* 17:277-287
- Peyrot-Clausade M, Hutchings PA, Richard G (1992) Successional patterns of macroborers in massive *Porites* at different stages of degradation on the barrier reef, Tiahura, Moorea, French Polynesia. *Coral Reefs* 11:161-166
- Peyrot-Clausade M, Le Campion-Alsumard T, Hutchings PA, Le Campion J, Payri C, Fontaine MF (1995) Initial bioerosion of experimental substrates in high islands and atolls lagoons (French Polynesia). *Oceanol Acta* 18:531-541
- Sacco F (1897) *I molluschi dei terreni terziarii del Piemonte e della Liguria. Pt. 23, Ostreidae, Anomiidae, and Dimyidae.* Turin, 66 pp
- Salvat B, Hutchings PA, Aubanel A, Tatarata M, Dauphin C (2001) The status of the coral reefs and marine resources of French Polynesia, New Caledonia. Global Coral Reef Monitoring Network, Fond Nat Polynesia, Papeete, Tahiti
- Sato-Okoshi W, Okoshi K (1993) Microstructure of scallop and oyster shells infested with boring *Polydora*. *Nippon Suisan Gakkaishi* 59:1243-1247
- Savigny JS (1818) Section on Annelida in Lamarck JB de (1818). *Hist Nat Animaux sans Vertèbres* 5, 618 pp
- Schönberg CHL, Wilkinson CR (2001) Induced colonization of corals by a clionid bioeroding sponge. *Coral Reefs* 20:69-76
- Sebens KP, Johnson AS (1991) Effects of water movement on prey capture and distribution of reef corals. *Hydrobiologia* 226:91-102
- Simkiss K, Tyler C (1957) A histochemical study of the organic matrix of hen egg shells. *Quart J Microsc Sci* 98:19-28
- Simon CA, Ludford A, Wynne S (2006) Spionid polychaetes infesting cultured abalone, *Haliotis midae*, in South Africa. *African J Mar Sci* 28:167-171
- Tauber P (1879) *Annulata Danica. En kritisk revision af de i Danmark fundne Annulata, Chaetognatha, Gephyrea, Balanoglossi, Discophorae, Oligochaeta, Gymnocopa og Polychaeta.* Reitzel, Copenhagen, 144 pp

- Tribollet A, Decherf G, Hutchings PA, Peyrot-Clausade M (2002) Spatial large scale variability in bioerosion of experimental coral substrates on the GBR (Australia): Importance of microborers. *Coral Reefs* 21:424-432
- Tribollet A, Langdon C, Golubic S, Atkinson M (2005) Endolithic microflora are major primary producers in dead carbonate substrates of Hawaiian coral reefs. *Coral Reefs* 24:422-434
- Vogel K (1993) Bioeroders in fossil reefs. *Facies* 28:109-114
- Wilkinson C (2004) Status of coral reefs of the world: 2004. Austral Inst Mar Sci, Townsville, 301 pp
- Wilson R (2000) Family Spionidae. In: Beesley PL, Ross GJB, Glasby CJ (eds) *Polychaetes & Allies: The Southern Synthesis. Fauna of Australia 4A. Polychaeta, Myzostomida, Pogonophora, Echiura, Sipuncula*. CSIRO Publ, Melbourne, pp 196-200
- Zottoli RA, Carriker MR (1974) Burrow morphology, tube formation, and microarchitecture of shell dissolution by the spionid polychaete *Polydora websteri*. *Mar Biol* 27:307-316