



The life history characteristics of the wood-boring bivalve *Teredo bartschi* are suited to the elevated salinity, oligotrophic circulation in the Gulf of Aqaba, Red Sea

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ABSTRACT

In the Gulf of Aqaba, the slow, unidirectional surface inflow of oligotrophic waters from the Red Sea may limit the dispersal of planktotrophic larvae, thus favouring brooded over planktonic development. A site at the northern end of the Gulf was used to examine recruitment by wood borers of the family Teredinidae (Bivalvia) with brooded or planktotrophic larvae. Wood panels exposed for 4 months at depths from 6 m to 36 m became colonised by the brooding *Teredo bartschi* and a few individuals of the planktotrophic *Bankia carinata*. Driftwood at the site contained *T. bartschi* and the brooding isopod wood-borer *Limnoria tripunctata*. No significant variation in intensity of recruitment with depth was detected. The size distributions of shells within the panels were unimodal, suggesting a single period of recruitment, but shell size was negatively correlated with the degree of crowding. For *T. bartschi*, the length and width of pallets proved to be good predictors of shell diameter. Pallet width also defines the diameter of the siphonal opening. Across the range of animal sizes sampled, this opening tended to be larger in *T. bartschi* than that calculated from reported widths of *Teredo navalis*, a species which grows in more plankton-rich waters. Groups of larval shells, which averaged 66 µm in width, were found on the inner surface of about 7% of all adult shells investigated. They had the characteristic D outline and pitted surface of a prodissococonch I shell with or without a small amount of prodissococonch II growth. These would have resulted from a single spawning event at about the time of year that nutrient-rich waters mix into the upper water column. At Aqaba, a sink population of *T. bartschi* is likely to be maintained by adults rafting from the Red Sea. These observations build a picture of the life history strategy of *T. bartschi*: brooding with maternal rather than egg-derived nutrition; release of a non-feeding pediveliger; limited larval dispersal; rapid development of a synchronous brooding capability; dispersal by rafting as adults.

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1. Introduction

Most adult teredinids (Bivalvia, Teredinidae) are obligate wood consumers with life history strategies that vary considerably between species, particularly with regard to patterns of breeding and of larval development. Some have seasonal breeding, while others undergo rapidly repeated gametogenic and brooding cycles (Calloway and Turner, 1983). Some species are broadcast spawners with planktotrophic larvae (some with the capacity to cross ocean basins during the larval phase (Scheltema, 1971)), others brood before releasing planktotrophic veligers and others still brood larvae right up to the settlement stage, the pediveliger (Calloway and Turner, 1983; Turner, 1966). In tropical waters, several teredinid species may simultaneously occupy the same piece of wood, being able to live in sympatry partly due to distinct life history strategies (Cragg, 2007). Thus the selective advantages of different strategies can be examined within this family.

Comparing the selective benefits of such strategies under field conditions is notoriously challenging, with studies yielding apparently contradictory findings (Lester et al., 2007). Furthermore, the role of larval dispersal in determining connectivity between sessile benthic invertebrates is not clear-cut (Levin, 2006). Small, ephemeral environments impose particularly strong selection pressures on larval development (Metaxas, 2004), favouring an opportunistic life history, as can be seen with organisms exploiting wood in the sea (Turner, 1973). By their tunnelling, teredinids eventually cause the wood in which they live and on which they feed to disintegrate. The surrounding benthic environment cannot support them, so effective dispersal is essential and this is achieved during the larval phase.

One of the difficulties for evaluating the selective advantages of larval development patterns is that conditions on open sea coasts are not sufficiently constant or constrained to permit identification of selection pressures imposed by environmental variables. However, in the Gulf of Aqaba, at the northern end of the Red Sea, there is a stable and predictable circulation of oligotrophic waters (northward at the surface and southward at depth) through a confined deep water body limited by a shallow sill at the Straits of Tiran (Fig. 1) (Klinker et al., 1976; Wolf-Vecht et al., 1992). Development patterns that differ in

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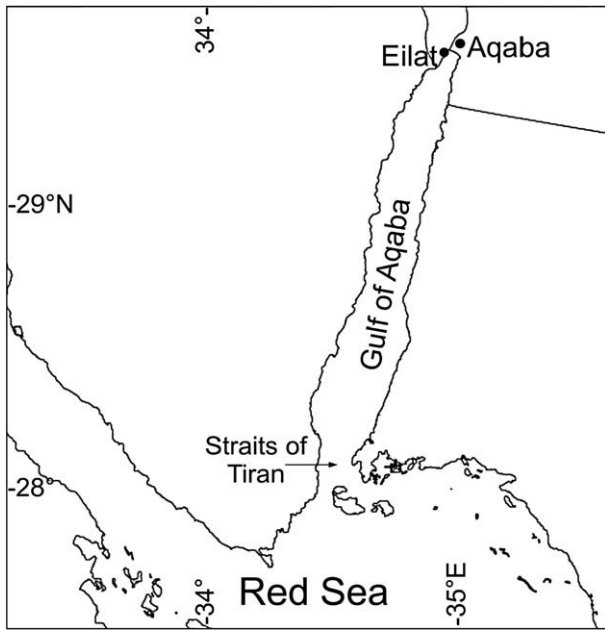


Fig. 1. Location of Gulf of Aqaba in relation to the Red Sea. The coastline plot with national boundaries shown extending from the northern end of the Gulf was obtained from the Coastline Extractor hosted by the US National Geophysical Data Center at <http://rimmer.ngdc.noaa.gov/> and is not subject to copyright protection.

their dispersal potential are likely to be strongly selected for or against by the slow water circulation rates and by the limited availability of food for planktotrophic larvae (Badran et al., 2005; Klinker et al., 1978; Manasrah et al., 2006). Also, dispersal is likely to be affected by the limited availability of substrate for larval settlement. In the Gulf of Aqaba this is mainly driftwood brought in by the thermohaline circulation, as there is little or no riverine input of wood, and mangroves, which are a major niche for adult teredinids (Cragg, 2007), only become extensive further south in the Red Sea (Price et al., 1998).

Sites like Aqaba, with unusual environmental characteristics help us to identify conditions which limit the occurrence of species of teredinids within their range of distribution. Unusual conditions may provide refuges from competition for particularly tolerant species, thus permitting them to live in sympatry elsewhere, where conditions are more generally tolerable. This study set out to focus on the recruitment and growth aspects of the life history strategy, but also generated information regarding brood characteristics and timing of reproduction that permitted consideration of the benefits of brooding. Given the importance of the floating wood substrate at this site, depth of the settlement substrate was identified as a factor that could affect recruitment of species with limited larval dispersal and thus experimental settlement panels were deployed over a range of depths and driftwood was also sampled.

All borers were identified and enumerated to characterise the nature of the wood boring community developing in experimental panels and driftwood. Isopod borers competing with teredinids were recorded. Measurements of teredinid shells and pallets were used to assess life history characteristics such as recruitment, growth, development and potential to dominate the food resource. For most bivalves, shell features are diagnostic, but species of the Teredinidae are mainly distinguished by features of the paired calcareous tunnel stoppers, the pallets (Turner, 1971), which have a stalk with retractor muscles and a calcified blade with a rim of periostracum (Leonel et al., 2006). However, pallet features vary during growth (Fuller et al., 1989; Tan et al., 1993), and may be affected by substrate, environmental conditions and weathering (Miller, 1923; Turner, 1966). Some of the differences in previous reports of pallet appearance are likely to be

due to the extent of degradation of the periostracum (Turner, 1966). There is a high level of synonymy in the Teredinidae, often due to descriptions based on poorly preserved pallets (Turner, 1966). Turner records seven synonyms for *Teredo bartschi* alone. Thus, species identification is more secure if variation in pallet morphology is characterised by measurements of large numbers of pallets. Pallet dimensions also give insights into organism function. When the flat inner faces of the blades are pressed together during pallet retraction, the outer faces form a circular profile that fits tightly into the opening of the tunnel. Pallet width therefore defines the size of the orifice through which the feeding and respiratory current enters the animal, giving a measure of a key constraint on these functions.

2. Materials and methods

Measurements at the site at Aqaba over a number of years show that in the summer, there is a very weak temperature stratification with water temperatures ranging from 25.4 to 25.8 °C between 6 m and 36 m depth. No stratification is evident in the winter, with water temperatures in the range of 21.2–21.4 °C. Salinities at the site in the summer range from 40.4 to 40.5 and in the winter from 40.6 to 40.7. No salinity stratification occurs.

Experimental panels of *Pinus* sp. measuring approximately 50 mm along the wood grain and 30 mm wide by 20 mm thick were exposed close to the Aqaba Marine Science Station at depths of 6, 8, 15, 18, 21, 24, 27, 30, 33 and 36 m. Panels placed at shallower depths were lost during the exposure period. The panels were tethered to ceramic tiles and kept about 20 cm above the sandy substratum by small floats. Four replicate panels were exposed at each depth. The panels were submerged on 27th July 2005 and retrieved on the 22nd November 2005. Driftwood samples were collected from the shore at Aqaba in August 2005.

After retrieval, the panels and driftwood were broken open in the laboratory. The period between removal and examination meant that the tissues of teredinids in the panels were dried out or were lost, but both shells and pallets were retained. Any wood-boring isopods (limnoriids) and all teredinid pallets and shells were extracted. These were counted and measurements were made of maximum dimension of the roughly hemispherical shells (referred to below as diameter). Pallet dimensions were measured from the free end of the stalk to the middle of the line between the tips of the periostracal cap (Fig. 2a) to give total pallet length. The length and width of the broad portion of the pallet, the blade, were also measured. Pallets were examined under reflected and transmitted light to distinguish between the calcareous portion and the periostracal cap. The wood boring organisms were identified using the keys of Turner (1971) for teredinids and Cookson (1991) for limnoriids. When larval shells were noticed associated with dried tissue within some of the adult shells, a large random sample of adult shells was taken and examined in detail for the presence of larval shells.

For SEM examination, adult shells were air dried, placed on conductive adhesive tabs then sputter coated with gold and palladium. Secondary electron images were formed using an acceleration voltage of 15 kV.

The variation between depths in numbers of teredinids was examined using a GLM ANOVA model with depth as a fixed factor and with shell counts square-root-transformed. The effect of crowding on size of shells in panels was examined by regression analysis of square-root-transformed counts of individuals per cm³ of wood and log-transformed shell diameter. The relationship between shell diameter and pallet dimensions was also examined by linear regression.

3. Results

Numerous pallets with a dark brown periostracal cap extended into lateral horns were found in the experimental panels at all depths

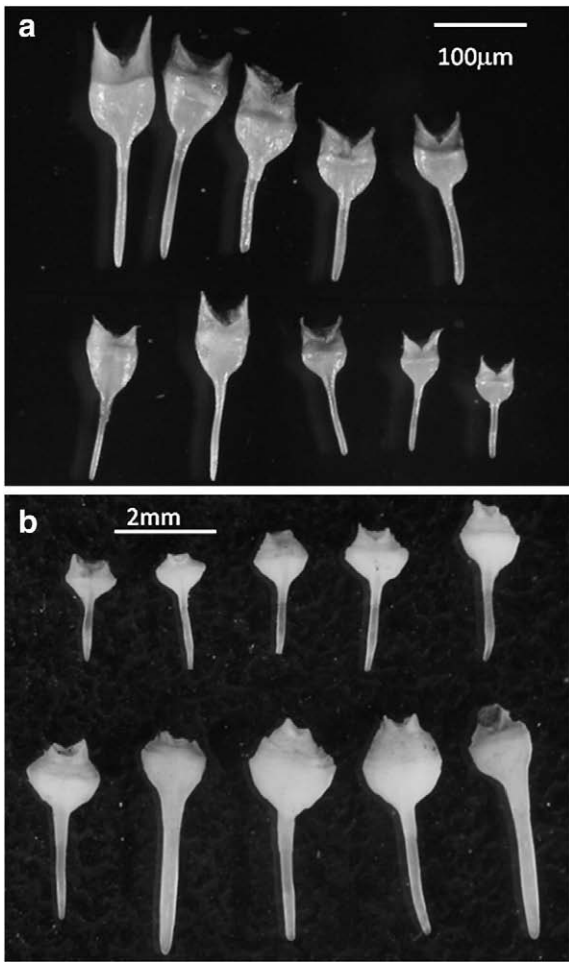


Fig. 2. Pallets of *T. bartschi* a) collected from experimental panels at Aqaba, showing typical sharp horns of undamaged periostracal caps. b) Collected from driftwood at Aqaba, with periostracal caps eroded away.

(Fig. 2a). These matched the description for pallets of *T. bartschi* Clapp by Turner (1966, 1971). A few pallets of *Bankia carinata* Gray were found in experimental panels at some depths. Driftwood samples contained numerous terebinid shells and also pallets, many of which had lost some or all of the periostracum (Fig. 2b shows particularly weathered examples). A comparison of the range of periostracal damage in driftwood pallets with undamaged pallets from experimental panels indicated that the driftwood specimens were also *T. bartschi*. One driftwood sample contained no terebinids, but had extensive superficial limnoriid tunnelling and a number of limnoriids (Isopoda, Limnoriidae), which were identified as *Limnoria tripunctata* Menzies.

While some shells or pallets may have been lost in the extraction process, the agreement between shell and pallet counts in the experimental panels was close, with pallet numbers averaging 96% of the shell count. However, in one panel with exceptionally high numbers of small animals, the pallets recovered represented only two thirds of shell numbers. *T. bartschi* numbers (as estimated from shell counts and the proportion of *T. bartschi* to *B. carinata* pallets) varied with depth, but showed no clear depth-related trend (Fig. 3). Panel-to-panel variation in numbers was high and there was no significant difference between animal densities at the depths sampled (ANOVA, 9 df, $F = 1.8$, $p = 0.109$). *B. carinata* was much less numerous, with a maximum of four individuals in a panel. This species was only found in panels at between 15 and 27 m in depth.

Size/frequency distributions of shells taken from a single panel at each depth were unimodal. Shell diameter varied between the depths

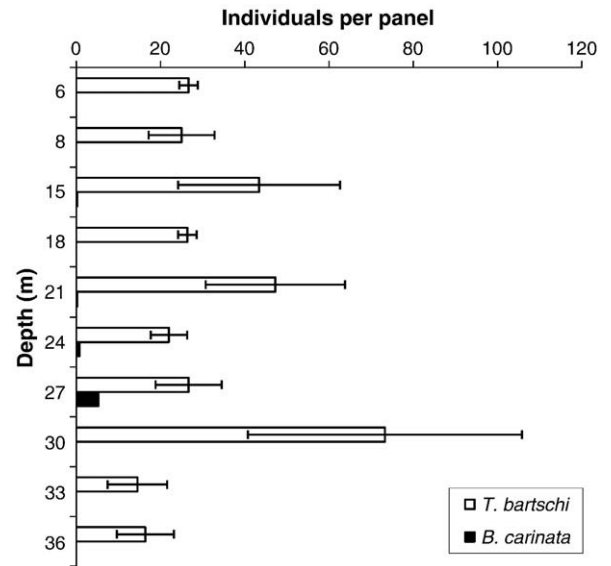


Fig. 3. Variation in numbers of individuals per panel of *T. bartschi* (mean \pm SE) and *B. carinata* (mean only) with depth at Aqaba. Numbers of individuals per species have been estimated from the counts of shells in each panel and the proportion of pallets of the two species in the panel.

sampled, but there was no consistent trend with depth. However, shell size showed a significant negative correlation with degree of crowding of adult terebinids in the panel ($p < 0.0005$, $R^2 = 0.22$) (Fig. 4).

In experimental panels where both pallets and shells from a single individual were extracted, pallet length of *T. bartschi* showed a strong positive correlation with shell diameter as did the width of the pallet blade. Pallet length tended to be slightly larger than shell diameter across the range of sizes collected. This data set is shown in Fig. 5, with published data from *Teredo navalis* for comparison. The blades of the smallest pallets of *T. bartschi*, were roughly as broad as long, but they tended to become more slender as pallet length increased. This trend was evident in pallets from experimental panels and from driftwood. However, the proportion of pallet length composed of blade did not vary significantly over the range of sizes investigated. Blade length was approximately half of total pallet length ($52 \pm 0.4\%$, mean \pm SE). Pallet sizes reached a maximum of 3.6 mm in length in experimental wood, but many driftwood pallets exceeded this size, with the largest being 5.4 mm long.

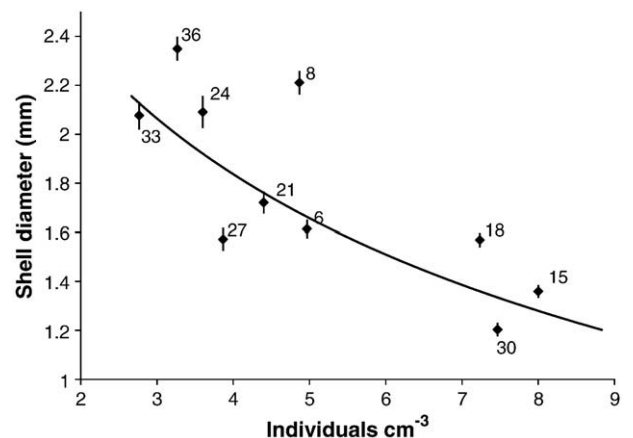


Fig. 4. Variation of shell diameter with degree of crowding of panels (expressed as individuals per cm³ of wood). Numbers by the data points indicate depth (m) of panel. Error bars indicate SE. Trend line derived from regression analysis of square-root transformed counts of shells and natural log transformed shell diameters.

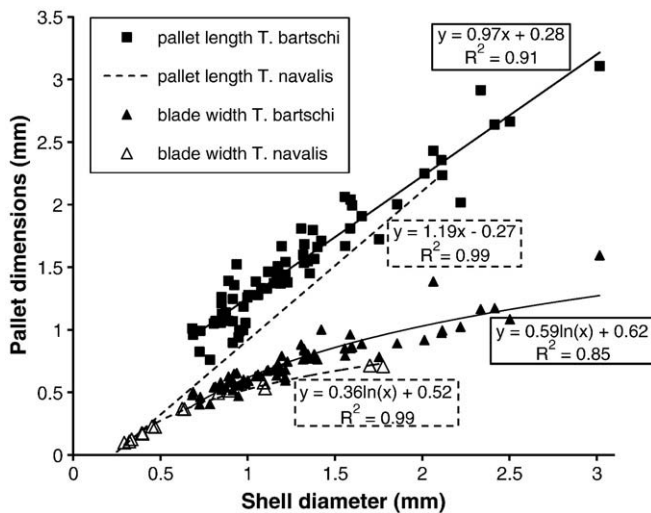


Fig. 5. Relationships of shell diameter to pallet length, and to blade width in *Teredo*. Data for *T. bartschi* derived from experimental panels exposed at Aqaba and for *T. navalis* from Fuller et al. (1989). The blade width data for *T. navalis* were measured from Fig. 12 of that paper.

Groups of D-shaped larval shells were found adhering to the inner surfaces of adult shells (Fig. 6a). The larval shells consisted of prodissoconch I alone (Fig. 6b) or prodissoconch I with only a few micrometers commarginal growth of prodissoconch II from an indistinct boundary line (Fig. 6c). The prodissoconch I surface was pitted. Measurements from SEM images of the width of the prodissoconch I of the larval shells gave a range of 65–70 μm with a mean width of 66.4 μm . Of the 742 adult shells examined, 54 were found to contain larval shells. Adult shells containing larval shells were found in samples from all depths. Larval shells were found within all sizes of adult shells except those less than 0.8 mm in diameter and no relationship between adult shell size and proportion containing larval shells was evident (Fig. 7).

4. Discussion and conclusions

4.1. Larval shell form and mode of larval development

The larval shells found in this study had the D-shaped outline and pitted surface typical of a prodissoconch I shell. They more closely resembled those of planktotrophic larvae, than those of most brooding bivalves, which have large eggs that give rise to a large prodissoconch I with little subsequent prodissoconch II growth and no development of umbones (Jablonski and Lutz, 1980). Indeed, the prodissoconch I shells of brooding teredinids, like those of ostreids, are even small for planktotrophic larvae and much smaller than the 135–230 μm typical of lecithotrophic larvae (Jablonski and Lutz, 1980). A considerable amount of prodissoconch II growth with commarginal striae occurs in the brooding teredinids *T. navalis*, *Teredo furcifera* and *Lyrodus pedicellatus*, and umbones eventually mask the straight hinge line (Turner, 1975). Prodissococonch II growth and umbones are also visible in images of *T. bartschi* larvae in gill brood pouches (Morse and Zardus, 1997). Egg content alone is insufficient to fuel such growth during brooding. While larvae might be able to capture phytoplankton while retained on the gills, larvae of at least one brooding teredinid appear to ingest glycogen-forming cells lining the brood pouches (Calloway, 1982) a process known as matrotrophy that has also been reported for corbiculids (Korniushin and Glaubrecht, 2003).

The fact that all larvae within an adult shell were at the same stage of development indicates that *T. bartschi*, like *Lyrodus floridanus* undertakes synchronous brooding of larvae from a single fertilization

event, rather than sequential brooding of larvae from a series of such events, as occurs in *L. pedicellatus* (Calloway and Turner, 1983).

4.2. Pallet morphology and growth characteristics of adults

Ontogeny of pallets varies between species, so pallet and shell dimensions may assist identification. The ratio of pallet length to shell diameter in *T. bartschi* is distinct from that of *T. navalis* at smaller shell sizes, but the ratio of pallet width to shell diameter becomes more distinct at larger sizes (Fig. 5). Pallet blades of *T. navalis* and *Bankia gouldi* become more slender during juvenile growth (Fuller et al.,

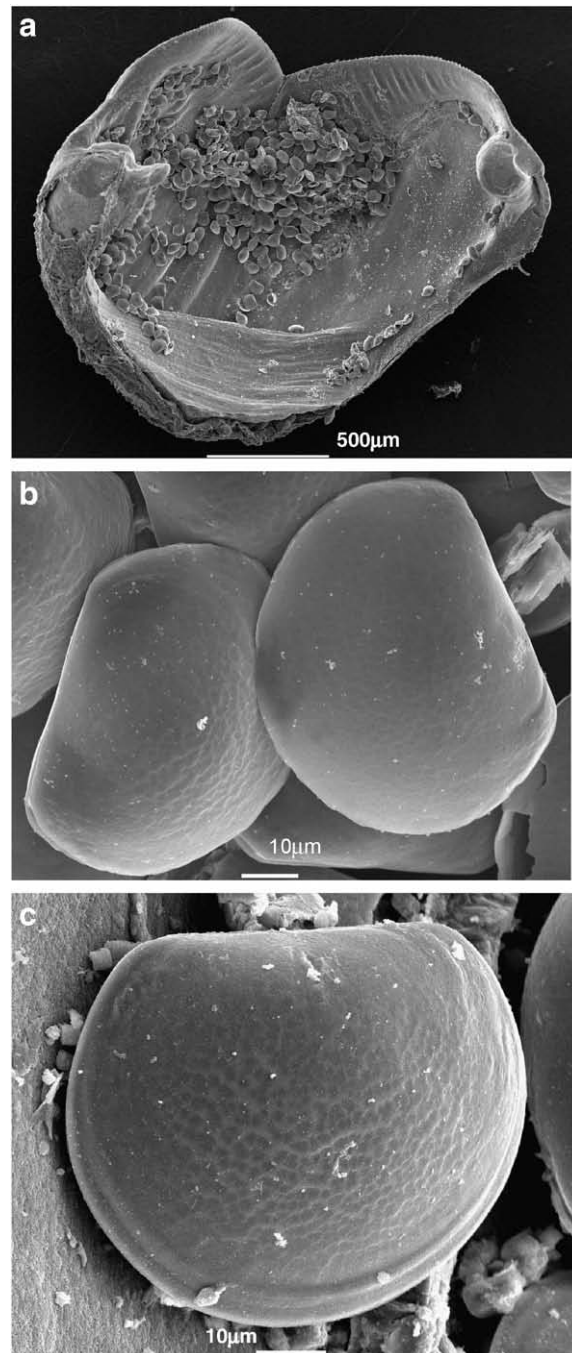


Fig. 6. SEM images of larval shells found within adult shells of *T. bartschi* from panels exposed at Aqaba. a) Adult shell with a mass of larval shells adhering to the inner surface. b) Larval shell consisting only of prodissoconch I. c) Larval shell with first commarginal growth line of prodissoconch II.

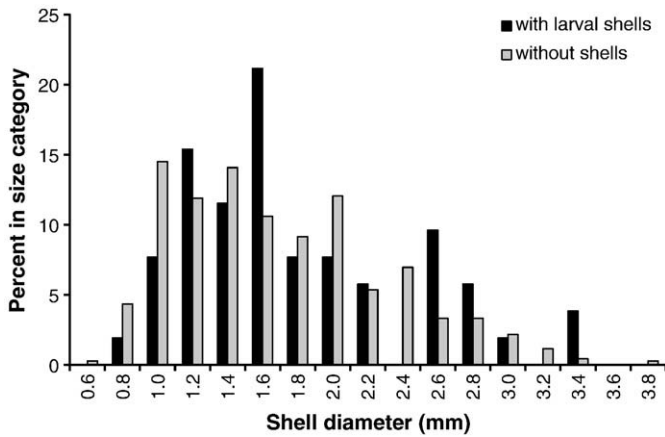


Fig. 7. Size distribution of adult teredinid shells taken from panels exposed at Aqaba and examined for the presence of larval shells on the inner surface, categorised into those with and those without larval shells ($n = 52$ and $n = 689$ respectively).

1989; Tan et al., 1993), as they do in early adult *T. bartschi* (this study). Thus pallet width does not grow as rapidly as shell diameter.

As pallet width defines the opening for the respiratory/feeding water current and shell diameter determines the area of denticulated shell surface that abrades wood particles, these two dimensions can be used in comparisons of the capacity of teredinid species to exploit phytoplankton and wood. However, differences in gill length and wood-storing caecum size should also be considered (Turner, 1966). Estimates from the data in Fig. 5, indicate that *T. bartschi* has an opening over 40% larger than that of *T. navalis* in a 1 mm animal and nearly 70% larger in a 1.5 mm animal. A larger orifice would give a greater capacity to draw in water, thus compensating for the more limited planktonic food at Aqaba than in the continental shelf water used by *T. navalis* (Fuller et al., 1989). Comparisons of shell and pallet dimensions from different sites are needed to determine whether the larger orifice in *T. bartschi* is phenotypic or genotypic.

Pallets dimensions from driftwood indicate that animals at Aqaba can grow markedly larger than they did in the experimental panels during a maximum of 4 months. In Hawaii, the largest *T. bartschi* found during extensive sampling grew to a length of 23 cm over a period of 259 days (Edmondson, 1942), much larger than any found in this study.

4.3. Physical factors affecting recruitment of *T. bartschi* and *B. carinata*

Both *T. bartschi* and *B. carinata* are widely distributed in full-salinity tropical and warm temperate waters (Turner, 1966), but their occurrence at Aqaba shows that within this range, they are capable of recruiting in unusual conditions. This fits the assertion of Hoagland (1986b) that *T. bartschi* has a general purpose genotype with broad physiological tolerance, suiting colonisation of many habitats. This non-specialist genotype may be maintained by inbreeding due to the brooding habit, early maturation and short swimming period of larvae which increase chances of settlement on the parental piece of wood (Hoagland, 1986a).

The strong seasonality in water conditions (Wolf-Vecht et al., 1992) may affect the pattern of teredinid recruitment. In this study, panels were exposed during the period of the summer thermocline, when superficial waters are warm and particularly low in nutrients. The unimodal range in sizes of adults collected from the experimental panels does not suggest settlement of distinct cohorts, but the very similar sizes larval shells within adult shells, indicates almost simultaneous spawning at around the time that the summer thermocline breaks down and more nutrient-rich deep waters mix into the surface layer. A teredinid not found in our panels—*T. furcifera*—also recruited nearby at Eilat during the period of thermocline breakdown (Haderlie, 1983). Breeding of

T. bartschi in response to seasonal fluctuations was also observed in a population of *T. bartschi* outside its natural range near a warm water outfall in Barnegat Bay, eastern USA (Hoagland, 1986b). However, in less seasonal conditions in Florida, this species settles year-round (Hoagland, 1986b).

T. bartschi larvae tolerate water temperatures between 16 °C and 32 °C (Edmondson, 1942; Hoagland, 1986b), so *T. bartschi* larvae at Aqaba are unlikely to be temperature-stressed. They will experience salinities of over 40 PSU which are outside the published tolerance range of both the teredinid species found in this study. *B. carinata* was one of the more stenohaline of the 17 species of teredinid within an estuary in Papua New Guinea (Rayner, 1979), being restricted to the outer estuary where salinities generally fluctuated between 30 and 35 PSU. *T. bartschi* settlement has been reported in estuarine sites (Leonel et al., 2002) and larvae derived from adults from estuarine populations are adversely affected by salinities of over 35 PSU (Hoagland, 1986b), but this species has also been found at full salinity sites (Kohlmeyer et al., 1995; Singh and Sasekumar, 1996; Suhrman and Eaton, 1984).

Most information on the distribution of teredinids is based on wood from intertidal or just subtidal shoreline sites. Few systematic attempts have been made to assess the effect of depth on teredinid recruitment. Increasing teredinid settlement intensity was found from the intertidal zone to the sea bed in shallow water on the Pacific Coast of Canada (Gara et al., 1997) and in Japan (Tsunoda and Nishimoto, 1978), but sharply decreasing settlement from the surface was observed in Sweden (Norman, 1976). No such depth effect was evident at Aqaba. The ready recruitment of *T. bartschi* at up to 36 m at Aqaba from parents probably living in driftwood suggests either that their larvae are capable of significant vertical movement during their free swimming period, which is very short (Lane et al., 1954), or that waterlogged driftwood provides significant amounts of larval inoculum at depth.

The oviparous *Bankia* recruits at greater depths and offshore: at 62 m, 160 km offshore from Bombay (Raveendran and Wagh, 1991); at 38 m in the Gulf of Papua (Cragg, 2007); at 100 m off Fort Lauderdale, Florida (Turner, 1966). *T. bartschi* did not recruit at these offshore, deeper water sites, though they fall within its geographic range. Thus, *B. carinata* can exploit niches that are either not suitable for *T. bartschi* or stand little chance of being colonised by its small broods with low dispersal potential.

4.4. Life history strategy

In the short settlement period sampled at Aqaba, recruitment was dominated by the long-term larviparous (brooding) *T. bartschi* rather than the oviparous *B. carinata* with its planktotrophic larvae. Furthermore, the other teredinids reported from the area—*L. pedicellatus* and *T. furcifera* (Haderlie, 1983)—are also long-term brooders. Though planktotrophic development would seem to offer the greatest dispersal potential, oviparous teredinids are not more widely distributed than brooding teredinids (Hoagland and Turner, 1981). This discrepancy between larval dispersal potential and species distribution has also been noted with brooding prosobranch gastropods, which are found at isolated sites where related planktotrophic species with overlapping geographical ranges do not occur (Johannesson, 1988). Furthermore, brooding species of the bivalve *Lasaea* tend to have a larger geographic range than planktotrophic species. Brooding and self-fertilizing species are well adapted to using rafting for dispersal, as they can establish a population from a single pioneer (O' Foighil, 1989; Thiel and Gutow, 2005), particularly if, like the brooding teredinid *L. pedicellatus*, they are capable of self-fertilization (Eckelbarger and Reish, 1972).

In the slow surface water currents of the Gulf of Aqaba, pediveligers of *T. bartschi* are not likely to be carried far, so the observed heavy recruitment was probably due to larvae derived from local adults that were brought into the area in driftwood, significant quantities of which occur on the shoreline close to the sampling site (Abu-Hilal and Al-Najjar, 2004). Adult

dispersal in flotsam has been reported from other teredinids such as the seagrass borer *Zachisia* (Haga, 2006). This is equivalent to rafting, a mode of dispersal now seen to have biogeographic and evolutionary implications (Thiel and Haye, 2006). Post-metamorphosis dispersal may explain the large range of this species which confounds the predictions of the site colonisation hypothesis for species with larvae with limited dispersal capability (Lester et al., 2007).

Oligotrophic waters at Aqaba limit the food available for planktonic larvae, but brooded larvae may get their nutrition by matrotrophy, a form of feeding that could be driven by parental intake of wood rather than phytoplankton. Furthermore, pediveligers of *T. bartschi*, like those of *L. pedicellatus* (Pechenik et al., 1979), may not require phytoplankton as food before metamorphosis. Adults can survive in oligotrophic conditions as they benefit from the nitrogen fixation capability of their bacterial symbionts (Lechene et al., 2007).

Adults are more severely constrained by the finite quantity of wood available to them. Late arriving or slow maturing individuals run the risk of dying before reproducing, due to exhaustion of their wood resource. In the small wood pieces used in this study, a fast maturing species such as *T. bartschi* will have a selective advantage. Rapid maturation coupled with brooding to the pediveliger stage also enables a species to maximise resource share by building up numbers within the piece of wood by re-colonisation (Calloway and Turner, 1983). The smaller adults in heavily colonised panels (Fig. 4) are probably stunted due to the crowded conditions, a phenomenon also noted with *T. navalis* (Norman, 1977) and with the wood boring pholad, *Xylophaga* (Turner, 1973). Nonetheless, even such small individuals were capable of reproduction (Fig. 7). The quantities of larval shells found suggest a small brood size which fits in with the estimated 10^3 – 10^4 eggs per reproductive event for *T. bartschi* growing on the East Coast of the USA (Hoagland, 1986a). The life history strategy of rapid maturation at small size and production of small batches of ready-to-settle larvae contrasts with the extremely high fecundity and extended planktonic larval development of oviparous teredinid species (Hoagland, 1986a). The fecundity of oviparous teredinids compensates for the hazards of planktonic dispersal, so there is probably a minimum adult size (not yet defined for teredinids) at which sufficient eggs could be produced. *Bankia setacea* can reach nearly a metre in length and 15 mm in diameter (Haderlie and Mellor, 1973) and the mangrove specialists, *Dicyathifer* and *Bactronophorus* also grow to considerable lengths with diameters of up to 20 mm (Rayner, 1979, 1983). *T. bartschi* with a much smaller body size cannot compete in terms of egg production, but maximises offspring survival by extended brooding. The data regarding limnoriid recruitment were insufficient to enable conclusions to be drawn regarding competition between the brooding isopod and teredinids.

5. Conclusions

In view of the surface current regime, *T. bartschi* larvae settling at Aqaba are probably recruits from a sink population established by flotsam-dispersed adults from source populations in the Red Sea. The life-history characteristics of this species—early maturation and synchronous brooding of small numbers pediveligers that only disperse locally—favour rapid exploitation of small, ephemeral habitats, though some of these characteristics are more commonly associated with *K*-selected species. The possibility that a relatively large siphonal opening and matrotrophy are adaptations to limited planktonic food deserves investigation. Teredinids are useful model organisms for comparisons of the selective benefits of different life history strategies due to the range of strategies in this family, to the ease of quantifying recruitment and to the utility of shell and pallet dimensions for revealing population structure.

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