



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 prodissoconch I shell with or without a small amount of prodissoconch 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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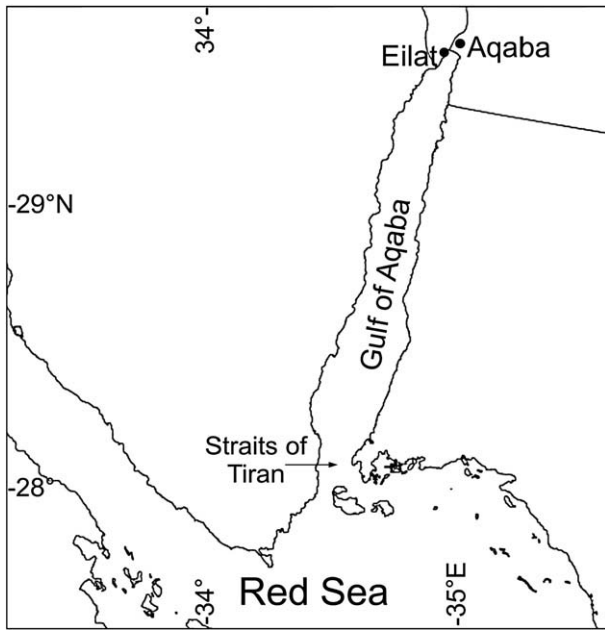


Fig. 1. Location of Gulf of Aqaba in relation to the Red Sea. The coastline plot with national boundaries shown extending from the northern end of the Gulf was obtained from the Coastline Extractor hosted by the US National Geophysical Data Center at <http://rimmer.ngdc.noaa.gov/> and is not subject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

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