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Contrasting life histories in shipworms: Growth, reproductive development and fecundity

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ABSTRACT

Trade-offs are implicit in life history strategies, and contribute to the coexistence of competing species. Shipworms, a family of obligate wood-feeding marine bivalves (Teredinidae), form communities where larval-brooding species are ten-fold more abundant than free-spawning species. Shipworm metacommunities are shaped solely by interactions between and amongst shipworm species, making this group ideal for examining the follow-on effects of life history on recruitment success and community structure. Using timber recruitment panels, tropical Australian shipworms were collected over a 12 month period, and the growth, reproductive development and fecundities of brooding and spawning species were quantified. Life histories of both brooding and spawning species reflected the ephemeral nature of wood habitats, with rapid growth, precocious development and high reproductive output. Spawning species (23.13 ± 0.63 mm average length) were significantly larger than brooding species (11.94 ± 0.09 mm). Both species reached sexual maturity within 2 months, at body lengths of 2–4 mm. Fecundities were similar for both species in individuals under 40 mm in length, after which spawners were more fecund by over a factor of ten, reaching a clutch size of 3×10^6 eggs by 100 mm in length. Results show that growth, reproductive development and fecundity are not sufficient to explain patterns of recruitment success for tropical shipworms, and rather that the brooding of larvae conveys the most substantive advantage in colonizing new habitat and defining population structure.

1. Introduction

Marine invertebrates possess a broad diversity of life histories, with extensive variation in body size (Blueweiss et al., 1978; Woodward et al., 2005), reproductive mode (Giangrande et al., 1994) and degree of parental investment in offspring (Marshall et al., 2007; Ramirez-Llodra, 2002). There has been a wealth of research investigating the ramifications of life-history characteristics under competitive conditions, with effects ranging from individual fitness to the structure of whole communities (Eckman, 1996; Foggo et al., 2007; Giangrande et al., 1994; Marshall and Morgan, 2011; McGill et al., 2006). Shipworms are an excellent candidate for investigating life history ecology, as their diverse communities are made up of species with differing reproductive modes. The diversity in reproductive mode between brooders and spawners constitutes a range of trade-offs between investment in offspring, fecundity and larval dispersal, and can play a significant role in structuring shipworm metacommunities (Cragg et al., 2009; MacIntosh et al., 2012).

Shipworms (Family Teredinidae) are a diverse and globally distributed family of marine bivalves with a highly specialized wood-feeding niche. As obligate wood-feeders, shipworms bore into woody plant tissue, which serves as both a habitat and food source. As shipworms are sessile, each of these wood habitats constitutes an independent community, often with an abundant and diverse species composition (Cragg, 2007). The growth and feeding of shipworms steadily destroy the host timber, making these communities short lived and highly competitive. Therefore, rapid breeding and larval dispersal are essential to establish communities in new wood habitats, which are often patchily distributed in the marine environment (Alix, 2005; Hinojosa et al., 2011). On a broader scale, numerous shipworm communities linked by larval dispersal form a diverse metacommunity (MacIntosh et al., 2012), with life history playing a significant role in species' ability to compete and colonize new habitats (Cragg et al., 2009; MacIntosh et al., 2012).

The life histories of shipworms reflect the patchiness and short life span of their habitats, and shipworms can be broadly categorized into one of several reproductive modes. The majority of shipworms, including the genus *Bankia* are oviparous, broadcasting gametes or fertilized eggs into the water column for a lengthy planktotrophic development upward of 20 days (Culliney, 1975; Nair and Saraswathy, 1971).

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A few genera, such as *Teredo*, are larviparous, in which eggs are fertilized within the mantle cavity and brooded in modified gill chambers before release. The duration of the brooding period varies from species to species, which in turn determines the form in which larvae are released (Calloway and Turner, 1988). Short term brooders incubate larvae for 5 to 8 days, releasing straight-hinge veligers which develop for a further for a 10 to 15 days in the water column (Calloway and Turner, 1988; Culliney, 1975). Long term brooders retain and provision larvae until fully developed, releasing competent, non-feeding pediveligers (Calloway and Turner, 1988; Karande and Pensey, 1969).

The majority of research on shipworms has had an economic focus, with an aim to prevent or mitigate the severe damage shipworms can cause to marine wood structures (Cookson, 1990, 1996; Cookson and Scown, 1999; Haderlie, 1983). The systematics of the family were comprehensively established by Turner (1966) and an excellent overview of shipworm biology compiled by Nair and Saraswathy (1971), but large knowledge gaps in the taxonomy, biology and ecology of shipworms remain. The life histories and physiologies are well known for some common species (e.g. *Teredo navalis, Lyrodus pedicellatus* and *Bankia setacea*) but poorly understood for many others (Nair and Saraswathy, 1971). Promisingly, recent work has begun to examine shipworms from a broader ecological perspective, and identifies that the level of coexistence within their patchy, specialized habitats makes them a useful model taxon for examining recruitment dynamics and competitive strategies of other invertebrate groups (Cragg et al., 2009; MacIntosh et al., 2012).

As part of recent work investigating shipworm demographics (MacIntosh et al., 2012), a large population sample of shipworms was collected from experimental recruitment panels in northern Queensland documenting 12 months of recruitment and growth for 19 species. This provides an excellent opportunity for generating detailed life histories for tropical shipworms, comparing and contrasting life history strategies, and incorporating this knowledge into a broader ecological context. The larval brooding *Teredo parksi* and the free-spawning *Bankia carinata* were selected because they are abundant year-round (MacIntosh et al., 2012) and their different reproductive modes typify the competing life history strategies in shipworm communities. The goal of this research was to record the life history characteristics of these ecologically dominant species, and importantly understand how brooding and spawning strategies both constitute adaptations to shipworms' unique ephemeral niche. More specifically, the size, reproductive development and fecundity of *T. parksi* and *B. carinata* were quantified and compared to construct a picture of contrasting successful life histories and reproductive efforts.

2. Materials and methods

2.1. Collection

Wooden panels were used to quantify the abundance, size, reproduction and diversity of regional shipworms, as per the methods of MacIntosh et al. (2012). In brief, panels comprised six separate 2 mm thick layers of radiata pine (*Pinus radiata*), bolted together between two 170 mm × 120 mm Perspex sheets. The final dimensions of panels were 220 × 150 × 12 mm, with a total surface area of 340.8 cm^2 available for recruitment and a total volume of 396 cm^3 of wood habitat. This panel design allowed larvae to recruit and provide for unimpeded growth by adults. The separate layers of wood in the panels enable easy deconstruction and facilitated the removal of intact individuals.

Specimens were collected from White Lady Bay in Magnetic Island, northern Queensland (19°06′29.85″ S, 146°51′73″ E) (Fig. 1). Starting in the Austral winter, July 2007, panels were collected and replaced every 2 months (destructive time series sampling). 6 panels were hung from floating long lines at depths of 1.5 m, spaced 4 m apart along the long line. Water depth ranged from 3 to 10 m with a soft sediment benthos. The surrounding coastal habitat was dry tropical forest, with fringing mangroves.

Panels collected from each time point were gently cleaned to remove light external fouling, fixed with 5% formalin in seawater for 2 weeks and subsequently stored in 70% ethanol pending analysis. Each panel was then opened and all shipworms were removed. Based on abundances recorded in previous research (MacIntosh et al., 2012),

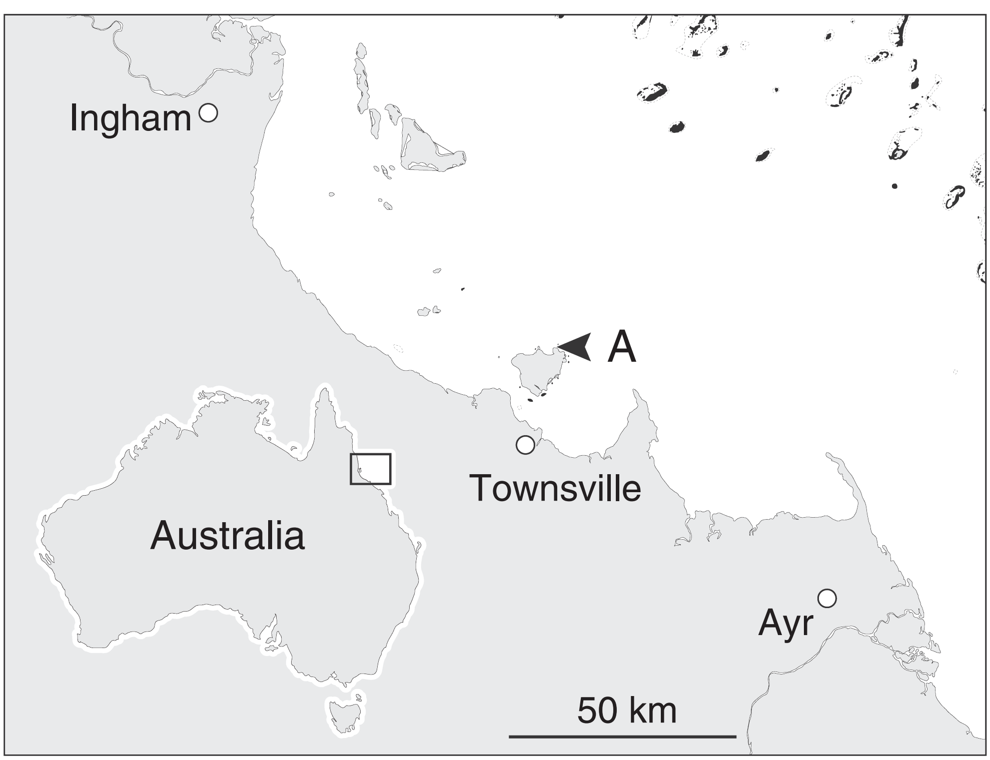

Fig. 1. Map of study site in North Queensland, Australia. White Lady Bay, Magnetic Island (A; 19°06′29.85″ S, 146°51′73″ E).