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Competition and coexistence in tropical Australian shipworms

Thesis submitted by

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For the degree of Doctor of Philosophy
In the school of Marine and Tropical Biology
James Cook University

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Statement on the Contribution of Others

Financial support for this study was provided by the School of Marine and Tropical Biology, James Cook University (JCU). An Endeavour International Postgraduate Research Scholarship and JCU Postgraduate Research Scholarship provided tuition and stipend support.

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Abstract

Shipworms are a fascinating group of marine bivalves (Family Teredinidae) with a highly-specialized wood-feeding niche, and are an engaging topic of research from ecological and economic perspectives. However, the underlying biology of many shipworms remains poorly understood, hindering our understanding of their broader-scale demographics and community ecology. Taking advantage of the abundant shipworm fauna in tropical Australia, the aim of this study was to provide an in-depth investigation of shipworm demographics, diversity and life histories, focusing on recruitment, growth and reproduction. Timber recruitment panels were used to quantify 2, 4, 6 and 12 month abundances of tropical Australian shipworm species, recording 62,075 individuals from 6 genera and 19 species (Chapter 2). Species exhibited differing peak recruitment seasons and reproductive modes, with free-spawning, short-term brooding and long-term brooding occurring. However, despite a higher diversity of spawning species overall (58%), abundance was strongly driven by the lower diversity of short-term brooding species (37%), comprising 95.7% of recruitment. Competition for habitat was high, with up to 1200 individuals per panel (~3 individuals per cm^3), and widespread mortality (40 to 90%) in panels over 4 months old. These results demonstrate that reproductive mode is a key contributor to recruitment success, with the constraints of a patchy, ephemeral habitat favoring a 'middle of the road' strategy of short duration larval brooding, most effectively balancing fecundity, larval retention and dispersive ability.

Life history strategies play a significant role in the competition and coexistence of species, but the life histories of many shipworm species are poorly understood. The life histories of two shipworm species differing in reproductive mode, the larval-brooding *Teredo parksi* and the free-spawning *Bankia carinata* (Chapter 3) were examined and recorded for the first time, comparing size, reproductive development and fecundity. *B. carinata* (26.15 ± 1.00mm average length) were significantly larger than *T. parksi* (16.09 ± 0.25mm). 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. However, after this time spawners were more fecund by over a factor of ten, reaching a clutch size of $3x10^6$ eggs by 100 mm in length providing the major contrast between the two reproductive modes. The rapid growth, precocious development and high fecundity of these two competing species highlight the evolutionary adaptations that allow them to be successful in a specialized ecological niche.

The reproductive strategies of brooding and spawning shipworms both constitute successful adaptation to their shared niche. Incorporating data on maternal provisioning and reproductive effort permits a more complete model of shipworms' life history trade-offs. Therefore, maternal provisioning and reproductive effort were compared for *Teredo parksi* and *Bankia carinata* (Chapter 4). The number and size of larvae and eggs were quantified and coupled with ultimate analysis of body tissue, larvae and eggs, to generate a model of reproductive energy allocation. Results showed that *T. parksi* possessed significantly higher maternal provisioning and reproductive effort than *B. carinata*. Larvae of *T. parksi* contained more energy than the eggs of *B. carinata*, with 3.13×10^{-4} J of energy per larva, and comprise over 30% of both total body mass and energy. This demonstrates that brooding and spawning strategies in shipworms are not simply a number-size trade-off, and that higher overall reproductive investment by brooding species may be responsible for their dominant position in the composition of shipworm communities.

In Chapter 5, a species of shipworm, *Lyrodus turnerae*, is described from specimens in tropical Australia and Papua New Guinea. The new species is characterized by the morphology of the pallets, with a dark periostracal cap sharply descending into a thin calcium cup. New and existing collection records of *L. turnerae* are presented, indicating a distribution range from coastal Papua New Guinea and the Bismarck Archipelago, extending along eastern Australia to New South Wales. An updated key to the genus *Lyrodus* is also presented, incorporating new taxonomic information.

In conclusion, this study provides a novel, in-depth investigation of the demographics, diversity and life histories of tropical Australian shipworms. By quantifying the life histories of competing shipworm species and recording larger scale patterns of recruitment and abundance, this work has established how the biology of shipworms on the individual and species level shape broader processes of community composition and regional diversity.

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Chapter 1

General Introduction

1.1 Shipworms – marine wood borers

Though the vast majority of woody plants are terrestrial, wood inevitably finds its way into the marine environment where it is utilized in a variety of ways (Maser and Sedell 1994). As a hard substrate, wood can provide habitat to benthic organisms; its buoyancy often aiding long distance dispersal via rafting (Thiel and Gutow 2005). Wood is not solely utilized as a habitat; its composition of cellulose and associated structural carbohydrates also makes it an energetic resource (Sjöström 1993). A diverse array of marine microorganisms including bacteria and fungi are associated with the decomposition of wood (Kim and Singh 2000, Jones 2011), but few marine metazoans use wood as a food source. One group of organisms, more than any other taxa, has evolved to exploit this resource, and is primarily responsible for the breakdown of wood in the world's oceans: the shipworms.

Shipworms are an intriguing family of marine bivalve molluscs (Teredinidae) with an unconventional wood-feeding niche. Like their sister taxon the Piddocks (Pholadidae), shipworms are benthic infauna, adapted to burrowing or boring into hard substrates. Shipworms have taken this specialization one step further and exclusively inhabit wood, which they consume as their primary source of nutrition. As a result of this niche shipworms have evolved a remarkable biology, play an important role in marine ecosystems and are costly destructive pests of marine wood structures, making them engaging subjects for research.

1.2 Shipworm biology

1.2.1 Anatomy

Shipworms' wood-feeding niche has given rise to a form that stretches the typical bivalve body plan almost to its limit. As pediveliger larvae searching for wood substrates, shipworms' molluscan ancestry is evident (Young et al. 2006), but after locating suitable habitat and metamorphosing, shipworms become sessile and bore into the wood, their morphology changing strikingly. Continually tunneling further into the wood as they feed, the body becomes long and stretched out, resulting in a wormlike shape that makes their common name apparent (Figure 1.1).

The boring process is accomplished by the shell valves, which are highly reduced and covered in rows of rasping teeth. Worked by powerful adductor muscles and pressed tightly to the substrate by a disc-like foot, the shell valves are flexed and rotated, wearing away the wood and extending the burrow (Board 1970). In this manner shipworms can grow rapidly to lengths of over a meter (Filho et al. 2008) and line their burrow with a hard calcareous secretion (Turner 1966, Manyak et al. 1980).

The only external trace of the shipworm's burrow is a tiny entrance at the wood surface, with two slender extensible siphons at the posterior of the body extending out into the water column. Also at the posterior is a pair of calcareous paddle-like structures known as pallets, which serve to seal the entrance of the burrow against predators or desiccation. These can be solid structures, covered with a thick periostracal layer, or even segmented and highly ornate (Turner and McKoy 1979). The dimensions of shipworms are highly plastic, affected by age, overcrowding and wood hardness (Clapp 1925). As a result, the morphology of the body and shell valves can vary drastically amongst species, and are not reliable identifying characteristics (Turner 1966). The pallets at the posterior, while still subject to some variability, are the most accurate way of identifying shipworms to the genus and species level (Turner 1966, Turner 1971b).

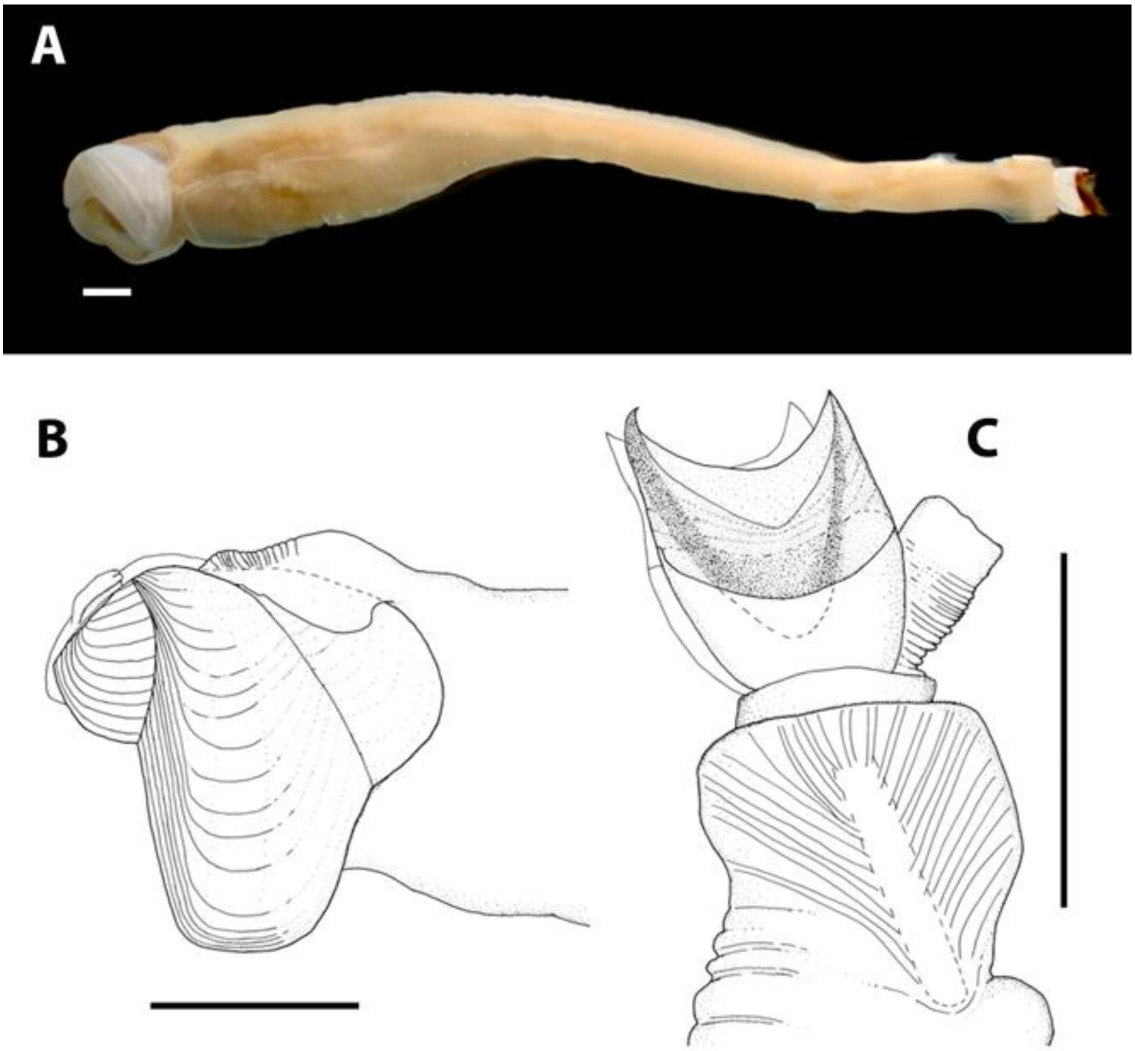

Figure 1.1: Key features of shipworm anatomy. (A) Adult *Lyrodus turnerae*, displaying typical elongated teredinid body plan; (B) anterior of body showing reduced shell valves with rasping surface; (C) posterior with siphon (right) and calcareous pallets. Scale = 1 mm

1.2.2 Feeding and Nutrition

The mechanical action of shipworms' boring creates fine wood fragments, which are ingested and stored within a large gut caecum (Bazylinski and Rosenberg 1983, Lopes et al. 2000). The wood is then broken down into its component sugars by cellulolytic enzymes produced by a suite of symbiotic bacteria (Distel 2003, Betcher et al. 2012). Unique to wood-feeding animals, these symbionts are intracellular and located in the shipworms' gills, their digestive enzymes transported to the digestive tract through as yet unknown means (Betcher et al. 2012).

Wood is rich in carbon, but comparatively nitrogen poor (Sjöström 1993), consequently most shipworm species filter feed to supplement their diets with phytoplankton (Pechenik et al. 1979). However this feeding is facultative as shipworms can thrive in oligotrophic environments (Cragg et al. 2009), incorporating nitrogen into their diets with the aid of nitrogen-fixing bacterial symbionts (Carpenter and Culliney 1975, Gallager et al. 1981, Lechene et al. 2007).

1.2.3 Reproduction and life cycle

The reproduction of shipworms reflects the patchiness and short life span of their host habitat. All species (bar one) are protandrous hermaphrodites (Turner 1966), switching sex from male to female early in their lives (Nair and Saraswathy 1971, McKoy 1980). Interestingly, self fertilization is rare, having only been recorded in a single species (Eckelbarger 1972). The sole exception is the enigmatic species *Zachsia zenkewitschi*, found only in the rhizomes of seagrasses, where dwarf males live within the mantle cavity of females (Turner and Yakovlev 1983, Haga 2006).

Shipworms can be broadly categorized into one of several reproductive modes (Figure 1.2). The majority of shipworm species are oviparous- broadcasting gametes or fertilized eggs into the water column for a lengthy planktotrophic development upward of 20 days (Nair and Saraswathy 1971). Three genera, *Teredo*, *Lyrodus* and *Zachsia* are larviparous, in which eggs are internally fertilized 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 (Culliney 1975, Calloway and Turner 1988). Short term brooders incubate larvae for 5 to 8 days, releasing straight-hinge veligers for a 10 to 15 day planktotrophic development (Culliney 1975, Calloway and Turner 1988). Long term brooders retain larvae until fully developed, releasing competent, non-feeding pediveligers (Karande and Pensey 1969, Calloway and Turner 1988).

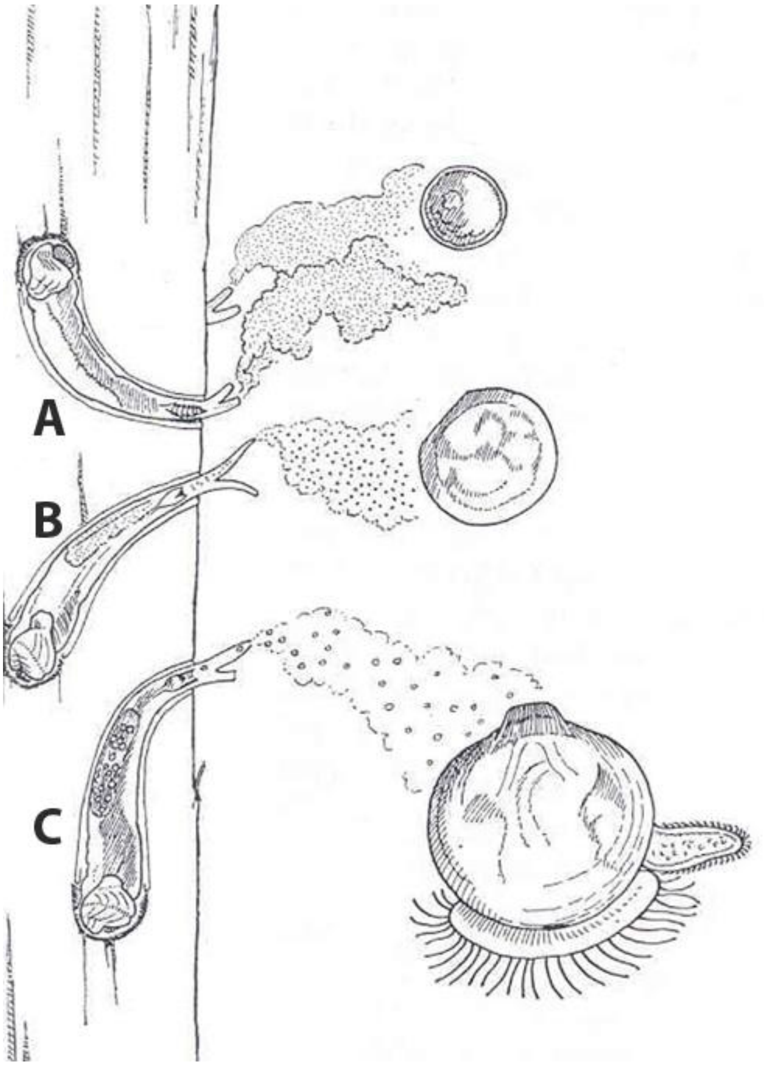

Figure 1.2: Shipworm reproductive modes. (A) Broadcast or free-spawning, releasing eggs and sperm; (B) short term brooding, fertilized eggs retained until straight-hinge stage; (C) long term brooding, offspring released as pediveligers. Eggs/larvae not to scale. Adapted from Turner (1966).

Regardless of reproductive mode, larval development progresses through the typical bivalve stages as trochophores, straight-hinge veligers and pediveligers (Culliney 1975). By the time they are competent to recruit, pediveligers are typically 250-300 µm in size, with a large swimming velum and muscular foot (Nair and Saraswathy 1971). To enable burrowing, the margin of the larval shell develops calcified, toothed ridges; after burrowing into the substrate full metamorphosis occurs, developing the calcareous tube lining, pallets and gills (Isham and Tierney 1953).

1.3 Diversity and ecology

Shipworms are a diverse family, with over 70 species across 15 genera (Turner 1966, Turner and Calloway 1987). They are globally distributed, with the highest biodiversity and abundance occurring in subtropical and tropical waters (Nair and Saraswathy 1971). Recruitment is predominantly in shallow seas (< 100 m), though specimens have occasionally been recovered from wood falls at depths of over 7000 m (Turner 1966). Many species have a cosmopolitan distribution (Turner 1966) and although shipworm larvae have been found to cross oceanic distances (Scheltema 1971), it is unknown if wooden ships with infested hulls have played any role in distributing species around the world.

Shipworms are purely marine and can inhabit wood from the intertidal zone to deep soft sediments, with a wide range of tolerances to salinity, temperature and anoxic conditions (Nair and Saraswathy 1971). Many species readily tolerate brackish conditions (Hoagland 1986, Spicer and Stromberg 2003), and some genera such as *Psiloteredo* and *Nausitora* thrive in salinities as low as 10 ‰ (Rayner 1979). Temperature plays a large role in the demographics of shipworms and in temperate climates, reproduction and recruitment occurs mostly in the warmer months (Ibrahim 1981, McKoy 1981), while in tropical waters favourable conditions permit reproduction and recruitment year-round (Nair and Saraswathy 1971).

Many shipworm species are sympatric and compete for the same wood habitats, particularly in tropical environments (Cragg 2007, MacIntosh et al. 2012). As sessile organisms, each habitat constitutes an independent community, often with a diverse species composition. These communities are shaped primarily by interactions among shipworm species competing for space and resources, as shipworms have few predators or competitors within wood (Nair and Saraswathy 1971).

The combined boring action of shipworms steadily destroys the host timber, making these communities short lived and highly competitive. Larval dispersal is essential to establish communities in new wood habitats, which are often patchily distributed in the marine environment (Alix 2005, Hinojosa et al. 2011). The life histories of shipworms reflect this pressure, with diverse reproductive modes such as larval brooding and free-spawning representing trade-offs in larval dispersal and local retention (MacIntosh et al 2012). On a broader scale, numerous shipworm communities linked by larval dispersal form a diverse metacommunity, with life history characters such as growth rate, reproductive development and fecundity playing a significant role in species' ability to compete and colonize new habitats (Cragg et al. 2009).

1.4 Human impact and research

Over time, the boring activity of shipworms can completely destroy the structural integrity of a timber structure, leaving little external trace of the damage within. Due to this insatiable appetite for wood, shipworms have been a costly menace ever since humans first built wooden vessels or structures in the ocean. The earliest recorded reference to shipworms is from the Greek natural historian Theophrastus (371-287 BCE) in his *Enquiry into plants*, who named them 'Teredon' (τερηδόνος) from the ancient Greek verb "To bore; wear away" (Borror 1960). Other early sources include notable Roman authors Ovid (43 BCE-17 CE) and Pliny (23-79 CE), who both reference the destructive power of shipworms, often poetically- Ovid uses the image of shipworms boring a ship's hull as a simile for the "gnawing of sorrow" in his heart (*Ex Ponto:* I.i.47-74). Considered by ancient and medieval authors to be a type of insect or worm, shipworms were finally identified as bivalve molluscs by Dutch researcher Sellius (1733) and the first genus *Teredo* was established by Linnaeus (1758), who described them in a footnote as *"calamitas navium"*- "the bane of ships".

The majority of research on shipworms has been driven by the economic impacts of their recruitment to wooden marine structures, with an aim to prevent or mitigate their damage (Haderlie 1983, Cookson 1990, Cookson 1996, Cookson and Scown 1999). 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 strong economic focus on shipworms has shaped our current understanding of their biology and while the life histories and physiologies are well known for some key species such as *Teredo navalis, Lyrodus pedicellatus* and *Bankia setacea*, they are poorly understood for many others (Nair and Saraswathy 1971).

Demographics and community ecology of shipworms are also largely unexplored. Research has often relied on the haphazard collection of driftwood or recruitment panels to establish their fundamental ecology, rather than controlled exposure conditions or manipulative experiments (McKoy 1981). 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).

1.5 Aims and chapter summary

The wood-boring niche of shipworms makes them an engaging topic for research, particularly from an ecological perspective. However, the underlying biology of many shipworm species remains poorly understood, hindering our understanding of broader-scale demographics and community ecology. Taking advantage of the abundant shipworm fauna of tropical Australia, the aim of this study is to provide an in-depth examination of shipworm demographics, diversity and life histories, focusing on recruitment, growth and reproduction. The expected outcome of this work is an understanding of the biology of shipworms on both small and large scales, linking processes on the individual scale with community composition and regional diversity.

In Chapter 2, a baseline of recruitment, diversity and seasonality is established for shipworms in tropical North Queensland, using recruitment panels under experimental conditions. The life spans and community compositions are measured, and interspecific competitive strategies are examined. The competition and coexistence of diverse shipworm fauna is examined in a metacommunity context.

In Chapter 3, the life histories of two ecologically significant shipworm species (as determined in Chapter 2) are examined- the larval brooding *Teredo parksi* and the free-spawning *Bankia carinata*. Growth, reproductive development and fecundity are quantified, building a picture of how their life histories have contributed to their success in a highly specialized niche.

In Chapter 4, reproductive investment is quantified and compared for *Teredo parksi* and *Bankia carinata*. The number and size of shipworm body tissue, eggs and larvae is quantified and coupled with ultimate analysis to generate a calorific model of maternal provisioning and reproductive effort.

In Chapter 5, a new species of shipworm, *Lyrodus turnerae* is described. The identifying characteristics and distribution of this species are recorded and illustrated from new and existing collections. Incorporating additional recent information, an updated key to the genus *Lyrodus* is presented.

In Chapter 6, the results of this study are summarized, synthesized with past research, and placed into the broader context of shipworm ecology. Future avenues of research are identified, with the aim of building a more detailed picture of this economically and ecologically significant group.

Chapter 2

Shipworms as a model for competition and coexistence in specialized habitats[1]

2.1 Introduction

Populations of sessile marine organisms often exist in spatially (Levin and Whitfield 1994, Hanski 1999) and temporally (Giesel 1976, McPeek and Holt 1992, Travis and Dytham 1999) heterogeneous environments. While larval dispersal and recruitment are amongst the most important factors determining adult population maintenance (Levin 2006, Cowen and Sponaugle 2009, Pineda et al. 2009), post recruitment competition can also be fundamental to population success (Caley et al. 1996, Marshall and Keough 2009, Burgess and Marshall 2011). Understanding and quantifying competition amongst coexisting species has been a focus for ecologists using both theoretical (Levins and Culver 1971, Hanski 2008, Spencer and Tanner 2008) and empirical approaches (Cadotte et al. 2006, Chadwick and Morrow 2011, Logue et al. 2011).

In the marine environment, inter- and intra-specific competition often manifests in a variety of reproductive modes and larval dispersal behaviours (Kawecki and Stearns 1993, Hadfield and Strathmann 1996, Krug 2001), with larval dispersal occurring over wide (Scheltema 1988) and narrow spatial scales (Swearer et al. 1999). However, despite the advances in our understanding of larval dispersal, recruitment and competition, much of the empirical work to date has focused on individual invertebrate species, in part due to the complexity associated with recruitment dynamics (Pineda et al. 2009). While this single-species approach has been useful in providing information on processes such as larval dispersal (Shanks 1995) and planktonic mortality (Vaughn and Allen 2010), identifying the relative effectiveness of competitive strategies requires either detailed retesting of successive target species, or examining competition between unrelated species. This ‘apples to oranges approach’ risks making inferences

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[1] Chapter 2 is adapted from MacIntosh H, de Nys R & Whalan S (2012). Shipworms as a model for competition and coexistence in specialized habitats. *Marine Ecology Progress Series* 461:

about the competitive strategies of species, when advantage may actually be due, in part, to differing underlying anatomies, physiologies or locations. An ideal approach would be to target a taxon with multiple species or genera that share and compete for the same discrete substrata- allowing for direct comparisons to be made as to the effectiveness of competitive strategies, without confounding by any extraneous biological differences.

Shipworms (Family Teredinidae) are highly derived lamellibranch bivalves that are obligate wood-feeders, and as such are limited to a substratum that is both sparsely distributed and often uncommon in the marine environment (Alix 2005, Hinojosa et al. 2011). The reduced shells and wormlike bodies of the sessile adults facilitate growth, via burrowing, into woody plant tissue. This mechanical action of burrowing by many coexisting individuals and species steadily destroys the host timber, resulting in short-lived and highly competitive populations. The life history and dispersive strategies of shipworms have evolved to exploit these ephemeral habitats, and shipworms can be broadly grouped by reproductive mode. Broadcast-spawning species release gametes or fertilized eggs into the water column for a full, planktotrophic development of 20 to 25 days (Nair and Saraswathy 1971, Culliney 1975). Short-term brooding species hold fertilized eggs in specialized gill pouches for 5 to 8 days, and release swimming, planktotrophic larvae that reach competency in 10 to 15 days (Calloway and Turner 1988). Long-term brooding species release large, non-feeding, highly competent larvae capable of settling in hours to days (Calloway and Turner 1988). Consistent with the literature for other benthic invertebrates (Blueweiss et al. 1978, Strathmann 1978, Strathmann and Strathmann 1982), brooding is correlated with a smaller body size (Cragg et al. 2009) and lower clutch size, compared to free-spawning species (Calloway and Turner 1988), which grow larger (Haderlie and Mellor 1973) and have prodigious fecundities estimated at 10^6 or higher per adult (Scheltema 1971).

Much of the research conducted on shipworms has focused on the economic impacts of their recruitment and growth, and the resistance of various wood species to borer damage (Haderlie 1983, Cookson 1990, Cookson and Woods 1995, Cookson and Scown 1999). However, recent work has begun to examine shipworms from a broader ecological perspective, and identifies that the level of coexistence within the patchy, specialized habitat of shipworms makes them a useful taxon for examining recruitment dynamics and competitive strategies of benthic invertebrates (Cragg et al. 2009). The wood-feeding niche of shipworms means that growth and feeding are synonymous, and the competition faced by shipworm species is directly correlated with their abundance and diversity within wood habitat. Furthermore, shipworms have few known predators (Nair and Saraswathy 1971) or other competitors within wood, so shipworm communities are shaped primarily by environmental effects and interactions among shipworm species.

Tropical Australian waters support a high diversity and abundance of shipworms (Cookson and Scown 1999), making it an ideal location to investigate the biology of co-occurring and competing species, and the mechanisms that enable regional coexistence in the absence of habitat partitioning. The numerous species in the region form a competitive metacommunity, and the scattered habitats available can be viewed as a patch dynamic paradigm in modern metacommunity theory (Leibold et al. 2004). As such, the goals of this research were to quantify patterns of seasonality, recruitment and diversity in tropical Australian shipworm species, to examine modes of inter- and intra-specific competition amongst co-occurring shipworm species, and to explore shipworms as a metacommunity model in understanding patterns of coexistence and the relative contributions of competitive strategies.

2.2 Materials and Methods

Wooden panels were used to quantify larval recruitment abundance, seasonality and adult demographics. Panels comprised 6 separate 2 mm thick layers of radiata pine *Pinus radiata* bolted together between two 170mm x 120mm Perspex sheets, following Manyak (1982) and Junqueira et al. (1991). The final dimensions of panels were 220 × 150 × 12 mm (Figure 2.1), with a total area of 340.8 cm^2 available for recruitment. The use of these panels allowed larvae to settle and for unimpeded growth by adults. The separate layers of wood in the panels allow easy deconstruction, facilitating the removal of intact individuals.

Panels were deployed at three sites in northern Queensland, Australia: the Australian Institute of Marine Science (AIMS), Cape Cleveland (19°16'37.02" S, 147°03'31.46" E); White Lady Bay, Magnetic Island (19°06'29.85" S, 146°51'42.73" E); and Pioneer Bay, Orpheus Island (18°36'14.70" S, 146°29'14.48" E) (Figure 2.2). To record seasonal variation in recruitment, panels were submerged for 1, 2, 4, 6 and 12 months, with 6 replicate panels per month, then collected and replaced (destructive time series sampling) for a 12 month period starting in the Austral winter, July 2007. Because of logistical constraints, 1 month collections were not used at Magnetic Island and

Orpheus Island. At each site, panels were distributed randomly in pairs every 1 meter along floating long lines, with the panels hanging from ropes at depths of 1.5 m. Water depth ranged from 3 to 10 m with a soft sediment benthos. The surrounding coastal habitat was dry tropical forest with fringing mangroves.

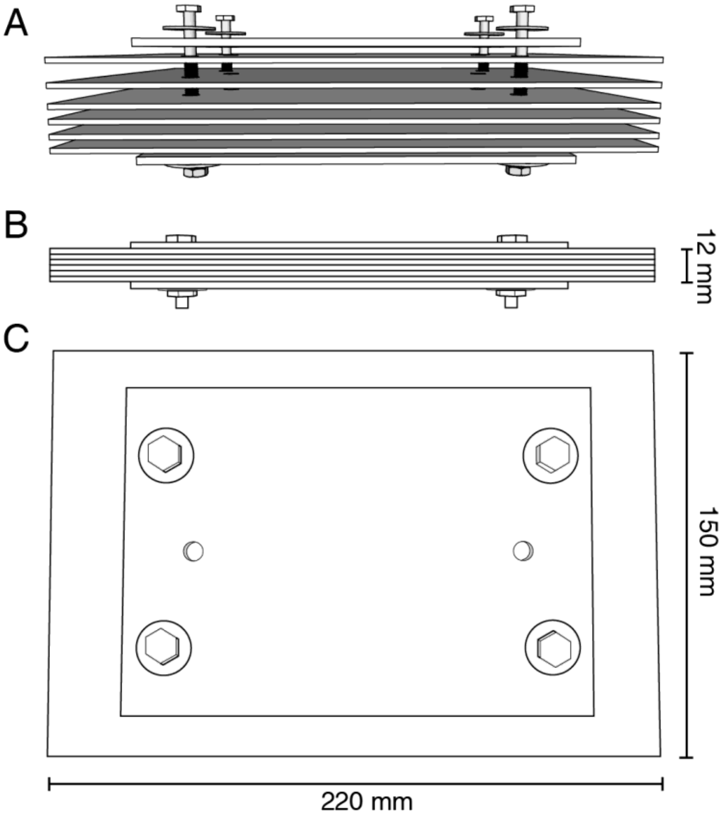


Figure 2.1: Design of recruitment panel. (A) Expanded schematic, showing 6 layers of 2 mm thick radiata pine held together by steel bolts between 2 sheets of plexiglas; (B) side view; (C) face view. Attachment to rope lines facilitated by 2 remaining holes.

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. To quantify recruitment, each panel was then carefully opened and all shipworms were removed. As shipworm identification relies almost exclusively on the morphology of calcareous ‘pallet’ structures at the animal’s posterior (Turner 1966), care was taken to ensure specimens were removed intact. Each shipworm only makes one burrow, and this remains after death, therefore a burrow count provides a value of total recruitment to a panel. Intact individuals provide a value of living adults occupying the panel at time of collection. The difference between these two values represents the total mortality experienced by settled adults. All specimens retrieved were identified to species level, photographed and measured (length and width) using ImageJ analysis software (v. 1.38) (Schneider et al. 2012). Species identifications and their modes of reproduction were verified against collections in the Australian Museum, Sydney.

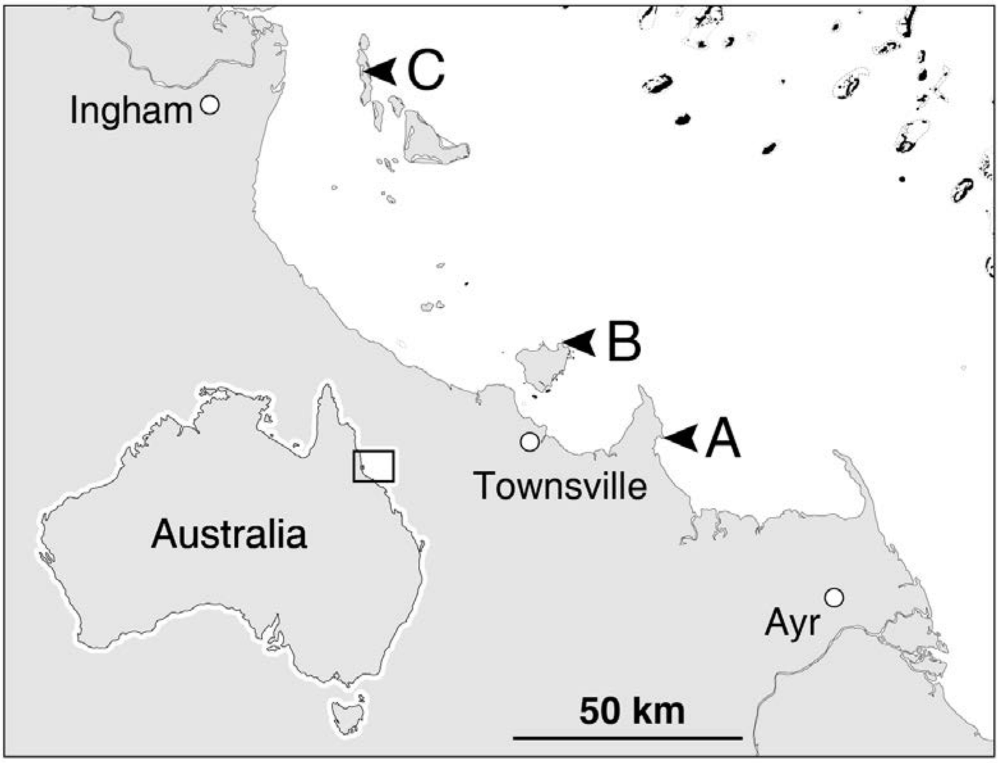


Figure 2.2: Study sites in North Queensland, Australia. (A) Australian Institute of Marine Science (AIMS), Cape Cleveland; (B) White Lady Bay, Magnetic Island; (C) Pioneer bay, Orpheus Island.

Recruitment data were plotted according to the age of the panel, site and time, in order to visualize temporal and spatial recruitment patterns. Further analysis with PRIMER v6 (Clarke and Gorley 2006) consisted of principal component analyses (PCA) to determine species weighting across the sample period, and multivariate analysis of similarities (ANOSIM) to generate pair-wise statistical comparisons between sites and age treatments. To avoid undue weighting by species at extremes of abundance, scarce species were omitted from analysis (see ‘Results’), with the remaining data log transformed.

2.3 Results

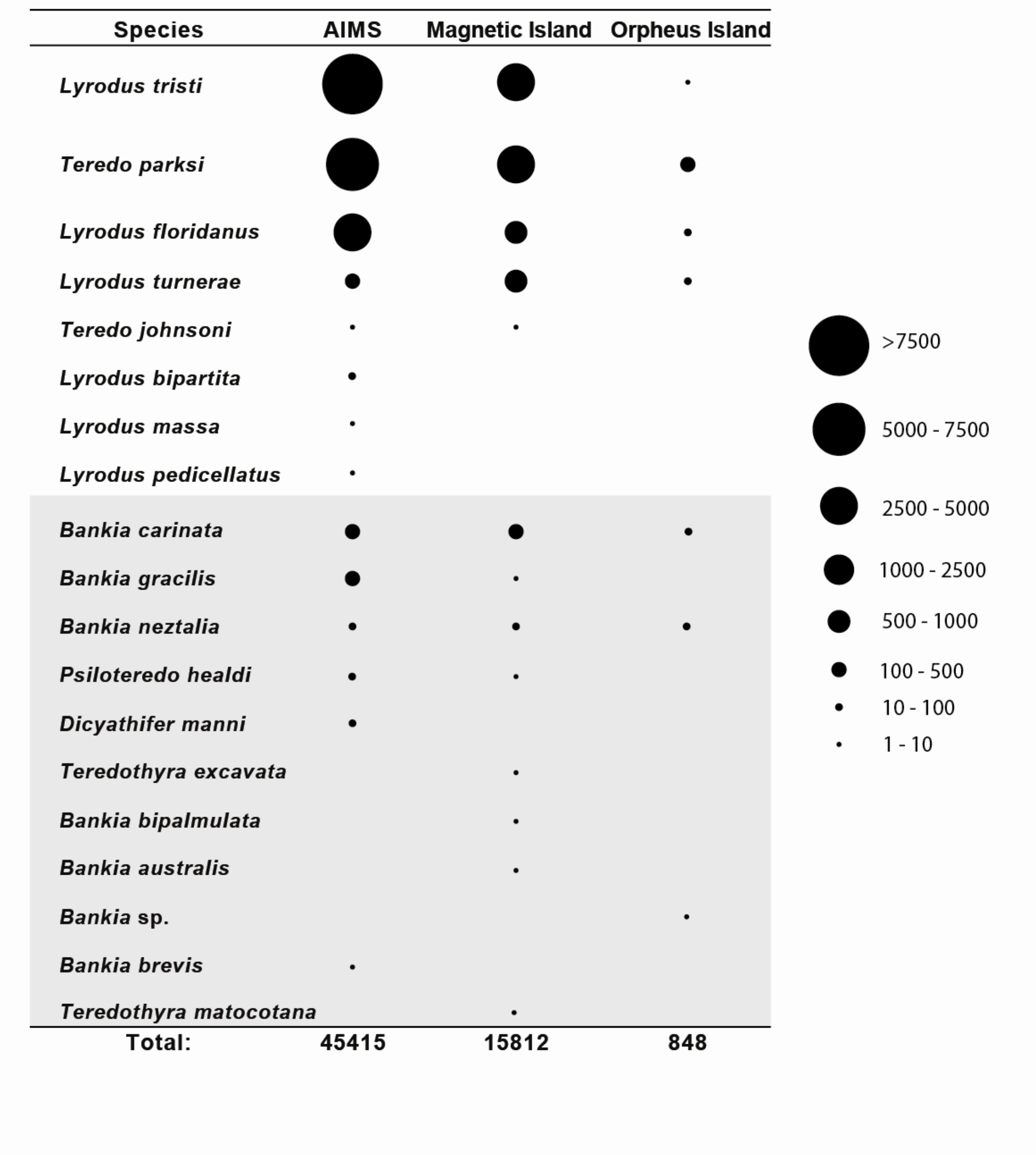
2.3.1 Species diversity

From 6 genera of Teredinidae, 19 species were recorded across all panels (Table 2.1), with a total of 62,075 individuals. Spawning and short-term brooding species were both present, with spawning species comprising 58% of species and short-term brooders comprising 37%. Only one long-term brooding species (*Lyrodus pedicellatus)* was recorded. Of the 19 species, 11 were recorded intermittently across the year or in too low an abundance to make accurate inferences about their seasonality or demographics, other than their relative scarcity. Further analyses examined data for the four most abundant brooding (*L. tristi, Teredo parksi, L. floridanus* and *L. turnerae*) and spawning (*Bankia carinata, B. gracilis, B. neztalia* and *Psiloteredo healdi*) species, totaling 99.7% of all recruitment, with each recorded in at least two sites for at least two sample periods.

2.3.2 Recruitment and abundance

Panels were settled by shipworms year-round, with peak intensities in March and May (Figure 2.3A). At AIMS, 1 month old panels, sampled at a finer resolution, showed similar levels of recruitment to 2 month old panels, indicating that the majority of recruitment in a given panel occurred between 1 and 2 months of age. At AIMS, mean 2 month panel recruitment ranged from 130 (± 42) individual shipworms per panel in the winter and spring months of September and November, to > 1200 (± 132) individuals per panel in the autumn peak of May, before falling sharply again in July (Figure 2.3A). At AIMS, 4 month old panels displayed similar trends but with a later peak, as less frequent sampling expressed May recruitment as part of the final July collection. Adding the total recruitment across all panel ages showed decreased recruitment with panel age, particularly in 4 to 6 month old panels (Figure 2.3B). This was most clearly observed in 12 month old panels, where despite exposure for a year, recruitment was at levels more consistent with the first 4 months of measurement.

Table 2.1: Presence/abundance matrix of shipworm species at study sites (Australian Institute of Marine Science [AIMS], Magnetic Island and Orpheus Island, ranked in decreasing abundance for both larval brooding (unshaded) and free-spawning (shaded) species. Total abundance per site is listed beneath.



Species	AIMS	Magnetic Island	Orpheus Island
Lyrodus tristi	●	●	●
Teredo parksi	●	●	●
Lyrodus floridanus	●	●	●
Lyrodus turnerae	●	●	●
Teredo johnsoni	●	●	
Lyrodus bipartita	●		
Lyrodus massa	●		
Lyrodus pedicellatus	●		
Bankia carinata	●	●	●
Bankia gracilis	●	●	
Bankia neztalia	●	●	●
Psiloteredo healdi	●	●	
Dicyathifer manni	●		
Teredothyra excavata		●	
Bankia bipalmulata		●	
Bankia australis		●	
Bankia sp.			●
Bankia brevis	●		
Teredothyra matocotana		●	
Total:	**45415**	**15812**	**848**

Magnetic Island and Orpheus Island received significantly lower recruitment rates (ANOSIM, $R > 0.7$, $p < 0.001$), but patterns of seasonality and abundance mirrored that of AIMS. At all sites high mortality rates, indicated by empty burrows, were measured in panels 4 months and older, ranging from 40 to 90% (Figure 2.3A). High mortality in a panel reduced the accuracy of ascertaining species composition. Low mortality (0 to 30%) in 2 month old panels again provided a much more accurate representation of seasonal recruitment. Increasing mortality with age occurred at all sites regardless of overall recruitment, suggesting that mortality was driven by the age of the habitat, and is not dependent on density-related competition.

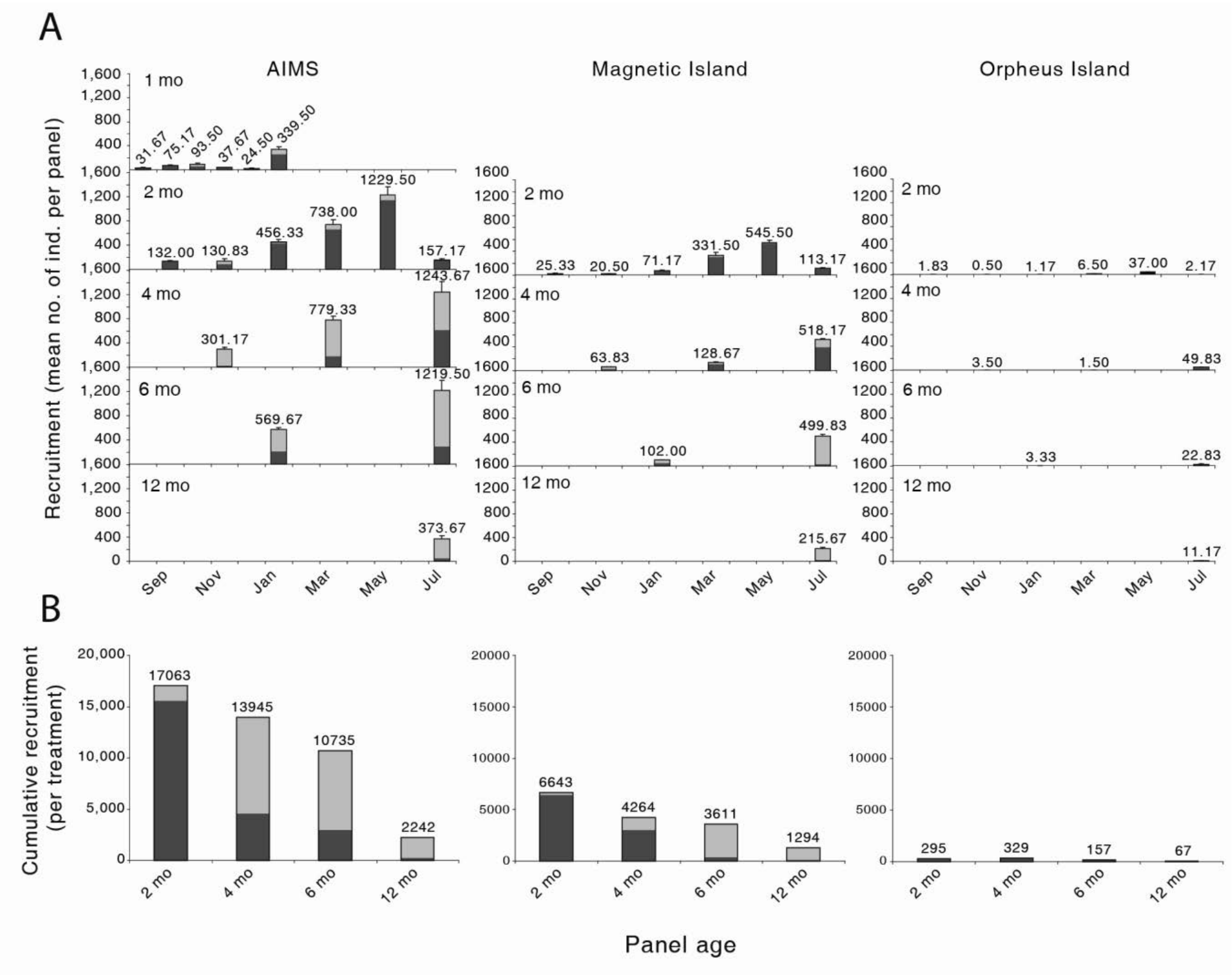


Figure 2.3: (A) Mean monthly recruitment of shipworms (± SE) by age of panel and (B) cumulative recruitment of shipworms to panel age treatments at (a) AIMS, (b) Magnetic Island and (c) Orpheus Island. Recruitment values are located above each bar. Light gray portion of bar represents dead individual. See study sites in Figure 2.2.

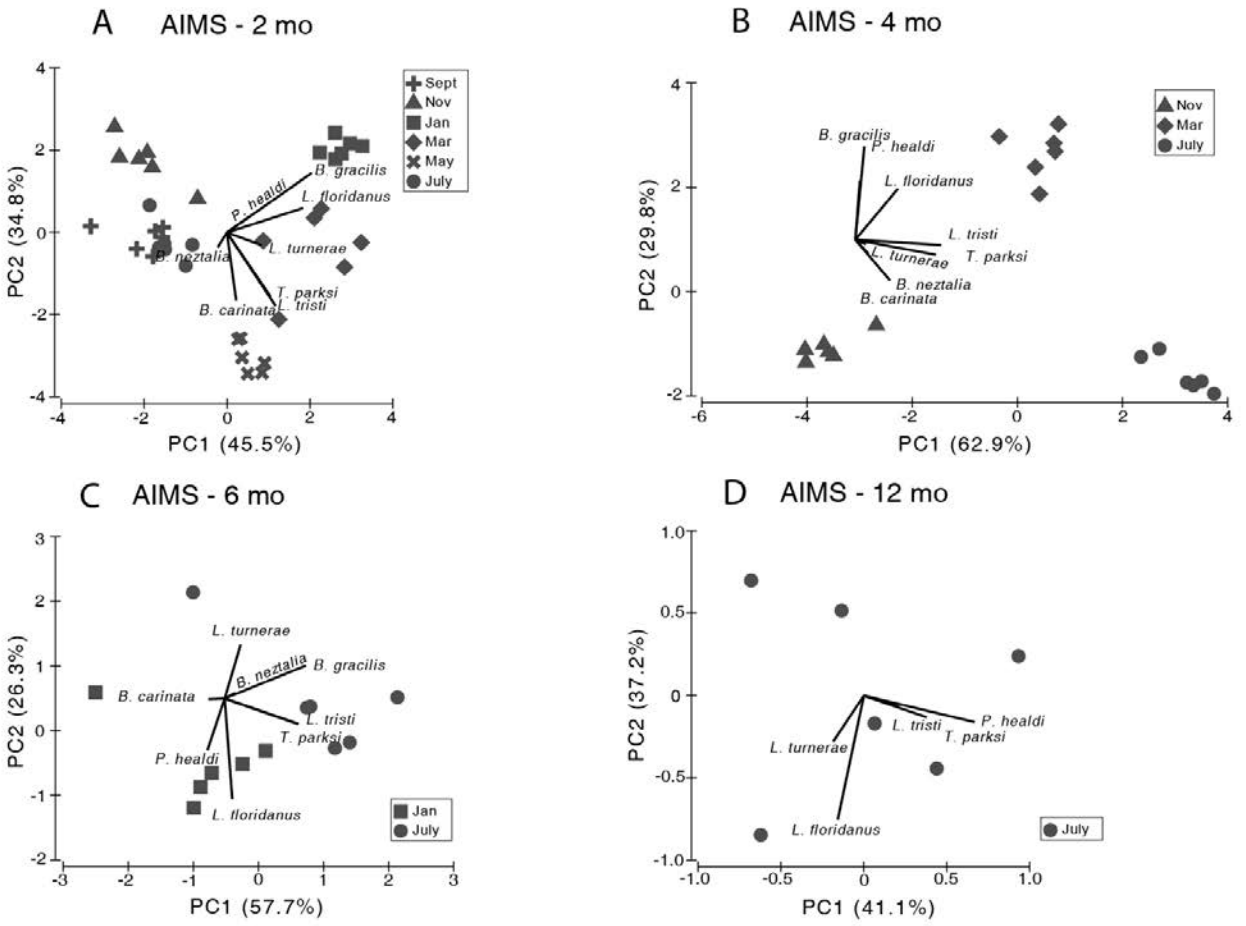


Figure 2.4: Principal component analysis of shipworms (*Lyrodus*, *Teredo*, *Bankia* and *Psiloteredo* spp.) contributing to recruitment across sites and panels ages. Sampling months are indicated. Principal components (PCs) with percentage of variation explained in parentheses. (A–D) AIMS; (E–H) Magnetic Island; (I–L) Orpheus Island. See study sites in Figure 2.2.

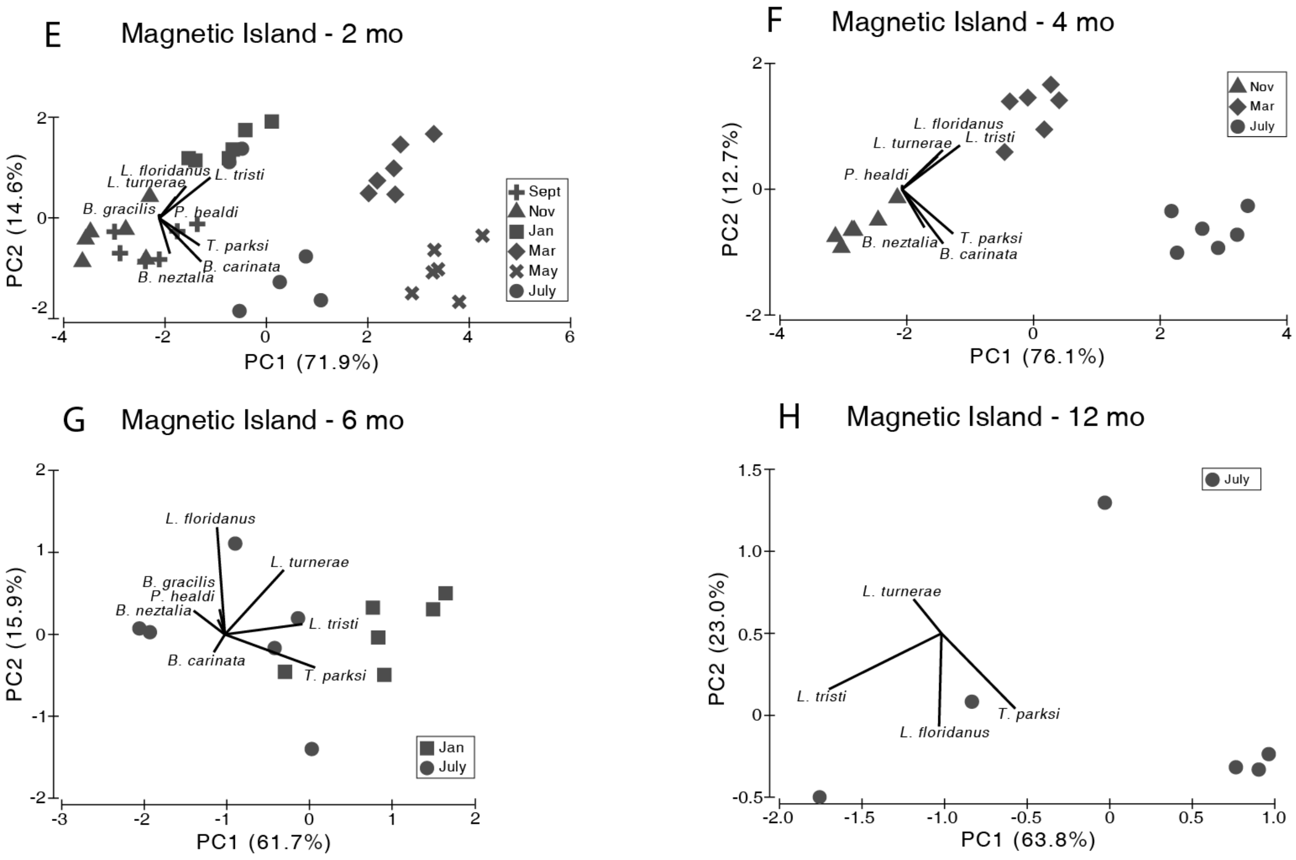


Figure 2.4 (cont.)

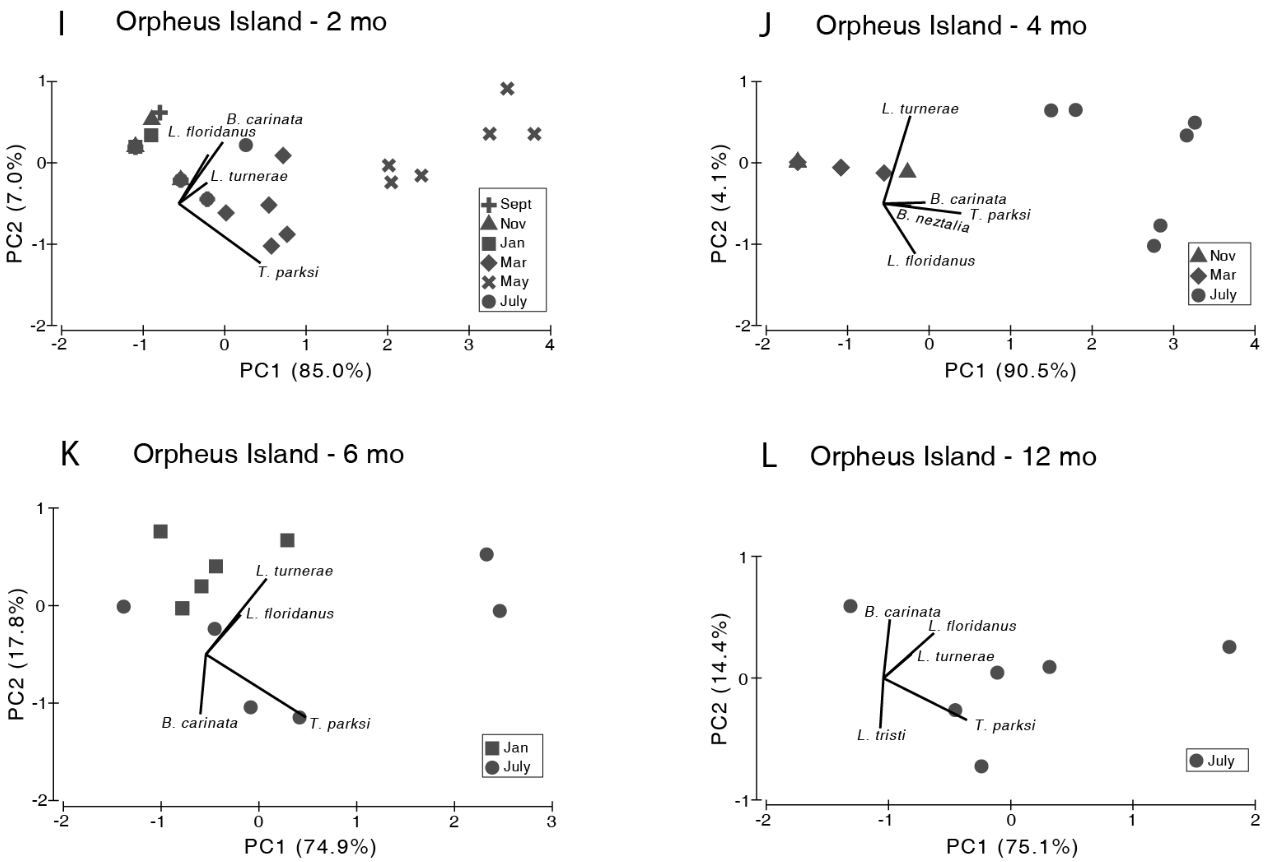


Figure 2.4 (cont.)

PCA demonstrated that different species of shipworms drive recruitment abundance at different times across the year, with a high (> 75%) percentage of variation accounted for by the first 2 principal components in all age treatments and sites (Figures 2.4A–L). In 2 and 4 month old panels, clear separation between months was visible within the ordination, with strong associations by groups of species driving patterns of abundance. In 6 and 12 month old panels, high mortality resulted in less distinct monthly groupings.

At AIMS, 2 and 4 month old panels were driven by 2 groups of species. This is clearly seen in the ordination where the first group, made up of *Lyrodus floridanus* and *Bankia gracilis*, drove the majority of recruitment in January while the second group, made up of *Teredo parksi*, *L. tristi*, *L. turnerae* and *B. carinata,* composed the majority of recruitment abundance in May (Figures 2.4A,B). January and May represent two peaks in recruitment for these species at AIMS. At Magnetic Island, in 2 and 4 month old panels, *L. tristi, L. turnerae* and *L. floridanus* were contributors to a peak in January and March, while *T. parksi, B. carinata* and *B neztalia* were associated with a May peak (Figures 2.4E,F). At Orpheus Island, accurate inferences could not be made, as recruitment by all species was low, resulting in fewer distinct vectors on the ordination (Figures 2.4I–L).

While a PCA quantifies the contributions of different species over time, it is difficult to visualize recruitment patterns on a per-species basis. For direct comparison, the abundance of each species across all sites and times was presented graphically (Figure 2.5). At all three sites, the most abundant species recruit year-round, and peak recruitment occurred between January and May. Matching the PCA results, each species exhibited a peak in recruitment. For example, *Lyrodus floridanus* and *Bankia gracilis* peaked in January and March, *L. tristi, Teredo parksi*, *L. turnerae* and *B. carinata* peaked in March and May, and *B. neztalia* peaked in July. Despite a higher number of spawning species, recruitment by short-term brooding species was notably higher than that of free-spawning species, with brooders comprising 95.7% of recorded abundance. Only one individual of a long-term brooding species (*L. pedicellatus*) was found, with all other brooders being short-term.

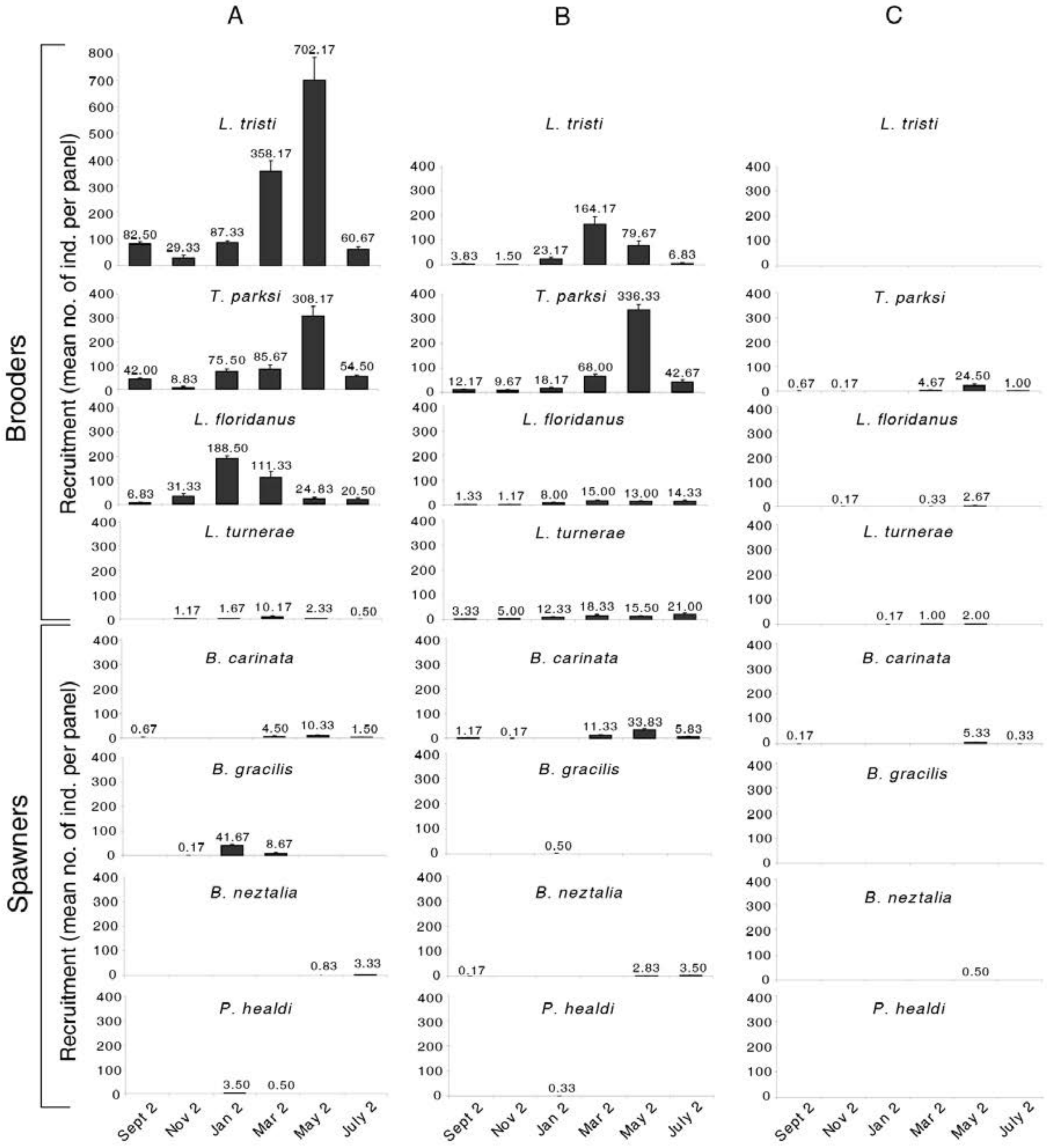


Figure 2.5: Mean abundance (± SE) of shipworms of *Lyrodus*, *Teredo*, *Bankia* and *Psiloteredo* spp. in 2 month old recruitment panels at (A) AIMS; (B) Magnetic Island; and (C) Orpheus Island. Separation into brooding and spawning reproductive modes is noted. See study sites in Figure 2.2

Table 2.2: ANOSIM 1-way pairwise tests of species composition between 2 month old recruitment panels at (A) Australian Institute of Marine Science (AIMS), (B) Magnetic Island and (C) Orpheus Island. ANOSIM R-statistic with p-value in parentheses. Significant results in bold.

(A)	September	November	January	March	May	July
September	-	-	-	-	-	-
November	**0.742** **(0.002)**	-	-	-	-	-
January	**1** **(0.002)**	**0.959** **(0.002)**	-	-	-	-
March	**0.991** **(0.002)**	**0.961** **(0.002)**	**0.806** **(0.002)**	-	-	-
May	**0.991** **(0.002)**	**0.978** **(0.002)**	**1** **(0.002)**	**0.937** **(0.002)**	-	-
July	**0.617** **(0.002)**	**0.820** **(0.002)**	**1** **(0.002)**	**0.988** **(0.002)**	**0.974** **(0.002)**	-

(B)	September	November	January	March	May	July
September	-	-	-	-	-	-
November	0.087 (0.221)	-	-	-	-	-
January	**0.897** **(0.002)**	**0.897** **(0.002)**	-	-	-	-
March	**1** **(0.002)**	**1** **(0.002)**	**0.922** **(0.002)**	-	-	-
May	**1** **(0.002)**	**1** **(0.002)**	**1** **(0.002)**	**0.767** **(0.002)**	-	-
July	**0.981** **(0.002)**	**1** **(0.002)**	**0.693** **(0.006)**	**0.650** **(0.002)**	**0.707** **(0.002)**	-

(C)	September	November	January	March	May	July
September	-	-	-	-	-	-
November	0.019 (0.416)	-	-	-	-	-
January	0.158 (0.106)	0 (1.0)	-	-	-	-
March	**0.293** **(0.006)**	**0.512** **(0.004)**	**0.736** **(0.002)**	-	-	-
May	**0.368** **(0.002)**	**0.510** **(0.002)**	**0.708** **(0.002)**	**0.924** **(0.002)**	-	-
July	–0.100 (1.0)	0.106 (0.242)	0.316 (0.061)	**0.324** **(0.004)**	**0.529** **(0.002)**	-

Two-way nested ANOSIM (Month[Age]) of each site showed significant differences in species composition and abundance between panel ages and over time ($R > 0.3$, $p < 0.001$). One-way ANOSIM-generated pairwise tests of 2 month old panels showed significant differences between all months at AIMS (Table 2.2A) and all but September and November at Magnetic Island (Table 2.2B), demonstrating that the abundance and composition of species assemblages exhibit significant variation. At Orpheus Island there was no significant difference in recruitment for months outside of the March and May peak season (Table 2.2C).

2.4 Discussion

The broad findings of this study highlight the dynamic life history of shipworms, an ecologically and economically important invertebrate group that utilizes a sparsely distributed, highly-specific habitat in the marine environment. Shipworm populations exist as highly competitive metacommunities in patchy, ephemeral habitats, and employ different reproductive modes and seasonality to overcome these limitations and seek competitive advantage. Shipworm diversity can be categorized into broadcast-spawning species and brooding species, and the relative effectiveness of these strategies can be assessed. Despite the higher diversity of broadcast spawning species, abundance at all sites, ages and months was strongly driven by short-term brooding species, indicating that the constraints of shipworms' niche favor a life history strategy balancing fecundity, larval retention and dispersive ability. The different reproductive strategies employed by tropical Australian shipworms represent different levels of investment in colonization ability and dispersal, enabling regional coexistence of species despite a lack of habitat partitioning. This fits the predictions of patch-dynamic paradigms (Levins and Culver 1971) and supports shipworms as a useful model group for examining competition within metacommunities.

The year-round larval recruitment that occurs is consistent with past reports on the reproduction of tropical Australian shipworms (Smith 1963, Ibrahim 1981), with 2 month old panels providing discrete measurements of recruitment across a 12 month period. This perennial reproduction, early maturation and high fecundity (Turner 1966, Nair and Saraswathy 1971) produces constant larval supply, but given the specificity of shipworm habitat, also highlights the competitive stress for these communities. This stress can be spatial, whereby most of a panel is occupied (e.g. > 1200 individuals recruiting to a single panel, resulting in a density of ~3 individuals per cm^3), as well as temporal, with high mortality rates observed in panels over 4 months of age. While these stresses are likely to be dependent on the size of the wood habitat, the ability of shipworm larvae to assess habitat age or size as a function of its quality remains unknown. Our findings show that in addition to using year-round spawning to increase larval supply, faced with high interspecific competition, shipworm species have different peak reproductive seasons, which increase the relative proportion of their larvae returning to wood substrata at different times of the year. In sampling 2 month old panels, *Lyrodus floridanus*, *Bankia gracilis*, and *Psiloteredo healdi* reached peak recruitment in January-March, *L. tristi* and *L. turnerae* in March-May, *Teredo parksi* and *B. carinata* in May, and *B. neztalia* in July. Staggered peak reproductive seasons suggest that even comparatively rare shipworm species such as *B. gracilis* or *B. neztalia* provide a higher proportion of their larvae recruiting to new habitat independently of one another, reducing interspecific competition.

Dead woody plant tissue, as the obligate habitat for shipworms, is extremely patchy in the marine environment, with high variation in the abundance, size and life span of wood debris (Alix 2005, Hinojosa et al. 2011). Due to the limited life span of wood substrata, it is unlikely that philopatric recruitment—larvae returning and recruiting to the same source habitat from which they were released—is advantageous. Indeed, as shipworms gradually destroy their habitat by boring and growing into wood, producing larvae with extended planktonic larval phases is a more plausible scenario, as is often the case for other marine invertebrate larvae (Levin 2006, Cowen and Sponaugle 2009). Nevertheless, the roles endogenous recruitment or larger scale dispersal play in shipworm population maintenance remain unknown. Low habitat permanence and high habitat patchiness are known to strongly influence the recruitment dynamics of organisms (Travis and Dytham 1999), with the benefits of new habitat outweighing the risks associated with planktonic larval dispersal.

Faced with competition for limited habitat resources, and with the need to balance self-recruitment and dispersal, the different reproductive modes of shipworm species reflect ways in which species can become more competitive with regard to fecundity and the size or dispersive ability of larvae. Both numbers of larvae and their dispersal capability may play critical roles in their recruitment success, given the relatively scarce nature of wood in the marine environment. The effectiveness of these strategies can be readily examined, and our results show that despite more species of free-spawners occurring overall, abundance at all sites was clearly driven by short-term brooders in the genera *Lyrodus* and *Teredo*. Broadcast-spawning of gametes hedges on high fecundity and a longer larval period, with dispersal recorded even at oceanic scales (Scheltema 1971), but is often constrained by variable rates of fertilization (Levitan 1995, Yund 2000), high mortality of early embryos (Vaughn and Allen 2010) and poor early swimming ability (Culliney 1975, Koehl and Hadfield 2010). Long-term brooding, by releasing competent, non-feeding larvae, allows for a high chance of local retention and rapid re-recruitment (Strathmann et al. 2002), but risks overcrowding, limits the effective range of larvae dispersal due to limited energy reserves and is more reliant on adult rafting for delivering larvae to new habitats (Highsmith 1985, Cragg et al. 2009). Short-term brooding, however, strikes a balance between lower fecundity and a high rate of fertilization success. This results in developed planktotrophic larvae with a higher chance of being locally retained, but with the ability to survive long dispersal periods in search of new suitable substrata, all characteristics of effective opportunistic species (Grassle and Grassle 1974, Benton and Grant 1999, McMahon 2002). Short-term brooding shipworms, so equipped, outcompete other reproductive modes and are generally the most geographically widespread (Turner 1966). Long-term brooders, limited by short dispersal, are often constrained to rafting or fewer source populations (Cragg et al. 2009). In contrast, broadcast-spawning genera, incorporating the more basal members of the family, are more common in brackish or cold water locations (Turner 1966), deeper offshore wood sinks, or large reservoir habitats such as mangrove swamps (Cragg 2007).

This research shows that shipworms are an ideal model group with which to examine metacommunities inhabiting patchy, ephemeral habitats. Shipworms are a fascinating confluence of recruitment/dispersal trade-offs, the constraints of a sessile lifestyle, and specialized habitat. For shipworms, the ‘middle of the road’ strategy of short-term brooding is most effective at balancing reproductive output, local recruitment, and longer range dispersal, and competition between species can be lessened through different peak spawning seasons. With this work focusing on larval supply and recruitment, further research on this group has the potential to examine the ecological paradigms of r/K selection between reproductive modes, and the carry-on effects of competition and overcrowding on fitness.

Chapter 3

The life histories of tropical shipworms – size, reproductive development and fecundity

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3.1 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 (Ramirez-Llodra 2002, Marshall et al. 2007). 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 (Giangrande et al. 1994, Eckman 1996, McGill et al. 2006, Foggo et al. 2007, Marshall and Morgan 2011). 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 destroys the host timber, making these communities short lived and highly competitive. Therefore, rapid breeding and larval dispersal is 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 (Nair and Saraswathy 1971, Culliney 1975). A few genera, such as *Teredo*, are larviparous, in which eggs are internally fertilized 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 for a 10 to 15 day planktotrophic development (Culliney 1975, Calloway and Turner 1988). Long term brooders retain larvae until fully developed, releasing competent, non-feeding pediveligers (Karande and Pensey 1969, Calloway and Turner 1988).

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 (Haderlie 1983, Cookson 1990, Cookson 1996, Cookson and Scown 1999). 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 the broader ecological context established in Chapter

2. The larval brooding *Teredo parksi* and the free-spawning *Bankia carinata* were selected because they are abundant year-round (Chapter 2) 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.

3.2 Materials and methods

3.2.1 Collection

Wooden panels were used to quantify the recruitment 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 170mm x 120mm Perspex sheets. The final dimensions of panels were 220 x 150 x 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) (Figure 3.1). Starting in the Austral winter, July 2007, panels were collected and replaced every 2 months (destructive time series sampling). At each site 6 panels were hung from floating long lines at depths of 1.5 m. Water depth ranged from 3-10 m with a soft sediment benthos. The surrounding coastal habitat was dry tropical forest, with fringing mangroves.

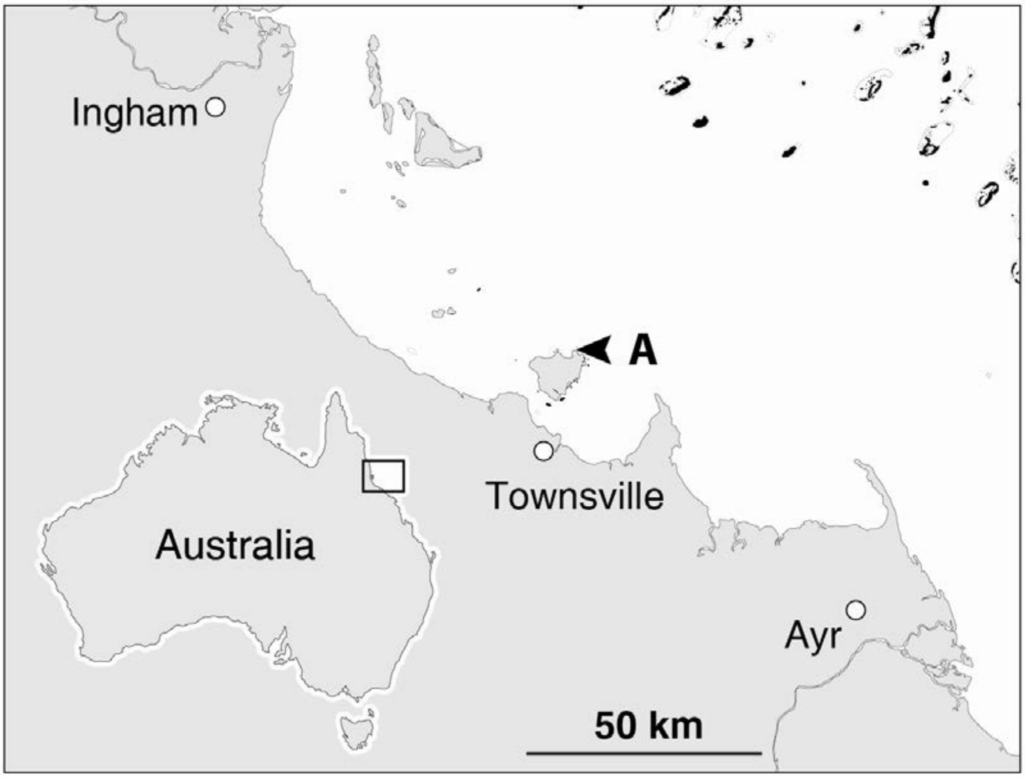


Figure 3.1: Map of study site in North Queensland, Australia. White Lady Bay, Magnetic Island (A; 19°06'29.85" S, 146°51'73" E).

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), *Teredo parksi* and *Bankia carinata* were selected as representative larval-brooding and free-spawning shipworm species, respectively. As shipworm identification relies almost exclusively on the morphology of calcareous 'pallet' structures at the animal's posterior (Turner 1966, Turner 1971b), care was taken to ensure specimens were removed intact.

3.2.2 Size

Both species were identified, photographed then measured using ImageJ analysis software (v. 1.38) (Schneider et al. 2012). Length was measured from the furthest anterior portion of the shell valve to the posterior end of the mantle, and width the widest point across the valves. Species identifications and their modes of reproduction were verified against collections in the Australian Museum, Sydney. To show the distribution of body dimensions, size data were grouped by reproductive mode and plotted as a scatter plot and fitted with regression lines. As an estimation of an individual shipworm's body size, and a proxy for the habitat space it occupies, the volumes of individuals were calculated from length and width data (Figure 3.2). For each collection period, the length, width and volume of *Teredo parksi* and *Bankia carinata* were compared with a permutational multivariate analysis of variance (PERMANOVA) with species as a single fixed factor, using PRIMER v6 statistical software and the PERMANOVA+ v1.0.3 extension (Clarke and Gorley 2006). For this analysis, Euclidean distance measures were used between samples and p-values were calculated using unrestricted permutation of data with 9999 random permutations. All mean data values reported were expressed with standard error as a measure of variation.

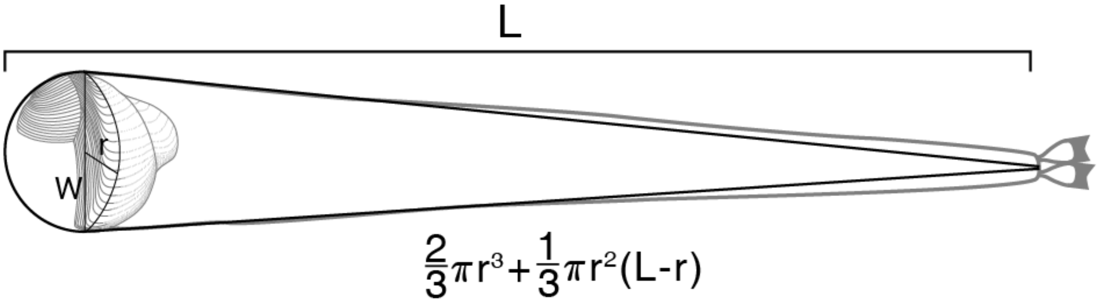


Figure 3.2: Calculation of shipworm volume from length and width measurements. The model consists of a half sphere (anterior portion of valves and burrow) and cone (body portion). Shipworm illustration modified from MacIntosh (2012). Anterior is to left.

3.2.3 Reproductive development

Reproductive development was assessed using histological examination. Specimens of *Teredo parksi* and *Bankia carinata* were selected from a range of size classes (1-100 mm in body length) from the same collection period (March and May 2007). Gonads were dissected out and embedded in paraffin, while small (< 5 mm) specimens were decalcified in 5% formic acid and embedded whole. Samples were sectioned at 5 µm with a rotary microtome, stained with haematoxylin and eosin and mounted as slides. Slides were examined and photographed with a compound microscope (Leica DMLB) with an attached digital camera (Olympus DP25). Body size (length) was recorded and each shipworm was categorized into one of three reproductive development states: the first onset of mature male gametes, the start of female gametogenesis, or a fully reproductive female state.

3.2.4 Fecundity

Fecundity was assessed for both species. To ensure accurate counts of maximum fecundity at a given body size, only gravid females were chosen (branchial cavities holding D-stage veligers for the larval-brooding *Teredo parksi*, and large ripe ovaries for the free-spawning *Bankia carinata*). For *T. parksi*, the gills and branchial cavities were dissected and the larvae removed. Larvae were diluted into 5 mL of 70% ethanol, sub-sampled 20 times in 10 µL volumes and counted under a stereomicroscope. *B. carinata* individuals were dissected to remove the gonads, which were subsequently stripped of mature eggs through gentle agitation in 70% ethanol. Eggs were diluted into 1 mL of 70% ethanol, and counted with a haemocytometer in 8 sub samplings. Larvae and eggs from all specimens were photographed (as above) and measured using ImageJ image analysis software (v.138) (Schneider et al. 2012). The circumference of the eggs was taken, while for larvae, the length (antero-posterior), height (dorso-ventral) and width (lateral) of the shell were measured. From these measurements, the average volume of larvae and eggs were calculated. Fecundity, adult size and offspring volume data were plotted and fitted with regression lines to provide models of growth and fecundity for both species.

3.3 Results

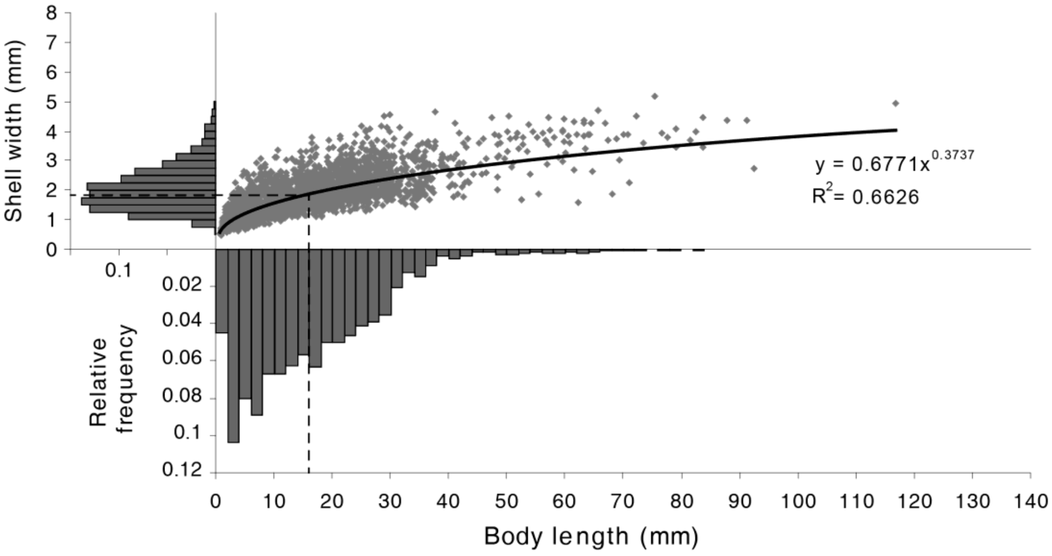
3.3.1 Size

Both species grew rapidly, primarily in body length, in the 2 months following recruitment (Figure 3.3). Body form was varied and highly plastic for both groups, with lengths that ranged from 0.4 mm to 140 mm. The mean size of the broadcast spawning *Bankia carinata* specimens was significantly larger than the brooding *Teredo parksi* in length, width and volume, except for the collection periods of November and January, where not enough specimens were present to make statistical inferences (for detailed results, see Table 3.1). *B. carinata* was on average twice as long (26.15 ± 1.00 mm) as *T. parksi* (16.09 ± 0.25 mm), and significantly wider (2.77 ± 0.06 mm to 1.83 ± 0.01 mm, respectively). Accordingly, *B. carinata* had a significantly higher overall body volume (88.75 ± 8.40 mm^3) than *T. parksi* (26.141 ± 0.92 mm^3, Figure 3.4).

3.3.2 Reproductive development

Both *Teredo parksi* (n = 44) and *Bankia carinata* (n = 20) exhibited protandric hermaphroditism typical of the Teredinidae. After recruitment, male sexual maturity was reached within 2 months, corresponding to lengths less than 4 mm. There was no distinct gradation between male and female gametogenesis, as gonadal tissue began differentiating into oocytes following the start of sperm production (Figure 3.5A-C). For both species, all individuals over 10mm in length had no further traces of sperm, with gonads holding large mature ova, indicating mature females. The brooding *T. parksi* species males became sexually mature at less than 2 mm in length (Figure 3.5A), compared to between 2.5-4 mm for the free-spawning *B. carinata*. *T. parksi* also reached female sexual maturity at a slightly smaller size (6-8 mm in length) than *B. carinata* (8-10 mm).

A - *Teredo parksi*



B - *Bankia carinata*

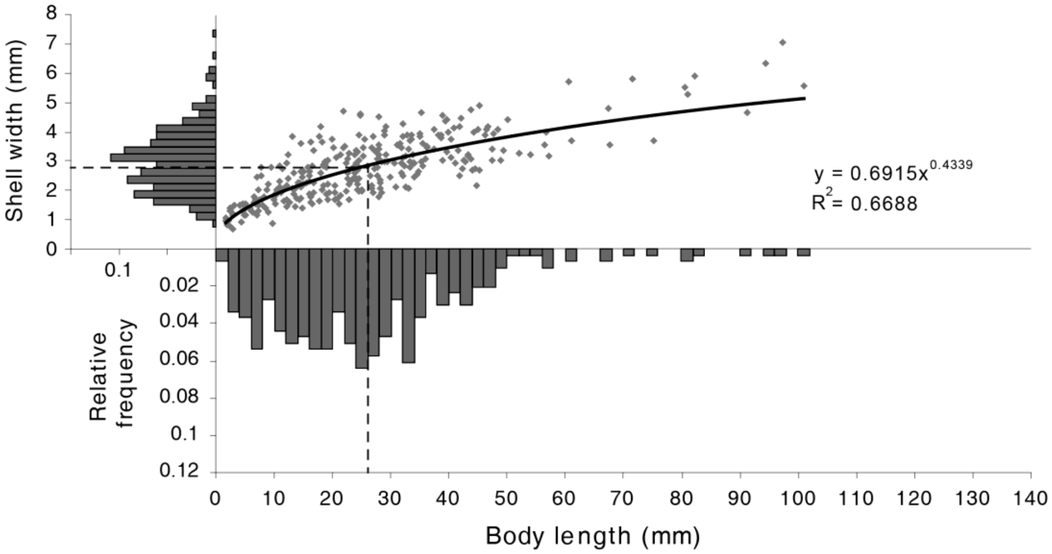


Figure 3.3: Growth parameters (length and width) of *Teredo parksi* (A; n = 2,722); and *Bankia carinata* (B; n = 296) from 2 month old recruitment panels at Magnetic Island, Queensland. Histograms on axes depict relative frequency of data. Dotted lines indicate average values for lengths and width. Regression function and coefficient of determination (R^2) are shown for each.

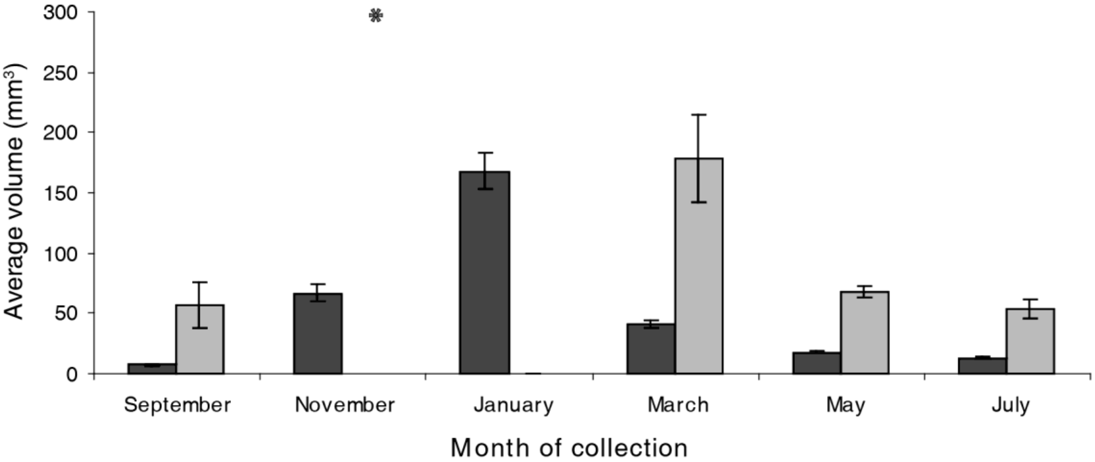


Figure 3.4: Mean volume (± SE) for brooding (*Teredo parksi,* dark, n = 2,722) and spawning (*Bankia carinata,* light, n = 296) shipworms from 2 month old recruitment panels at Magnetic Island, Queensland. Asterisk denotes a single outlying *B. carinata* individual.

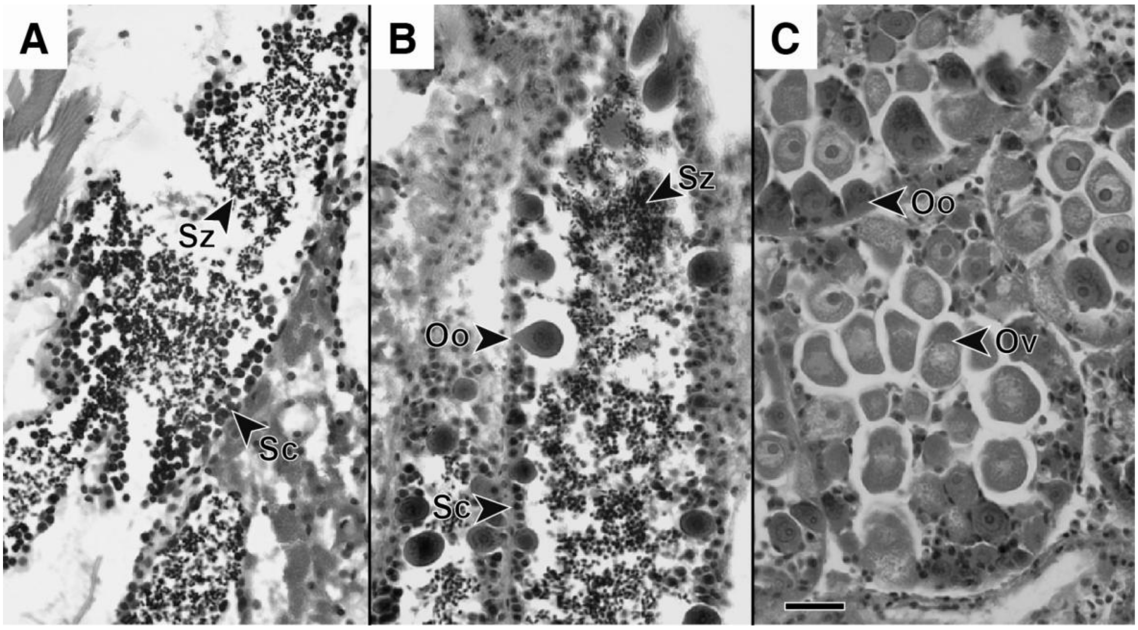


Figure 3.5: Reproductive development of shipworm gonads. (A) Mature male gonad with spermatozoa (*Teredo parksi*, body length 1.86 mm); (B) intermediate stage with developing oocytes and some remaining spermatozoa in follicle (*Bankia carinata,* body length 7.77 mm); (C) mature female gonad with ripe ova and no remaining spermatogenesis (*B. carinata*, body length 17.6 mm). Oo = oocytes; Ov = ova; Sc = spermatocytes; Sz = spermatozoa. Scale bar = 25 µm.

Table 3.1: Single-factor PERMANOVA analysis with significant differences between body size parameters of *Teredo parksi* and *Bankia carinata*, collected from 2 month old recruitment panels at Magnetic Island, Queensland.

		Source	*df*	MS	*F*	*p*
September	Length	Species	1	519.84	55.17	< 0.001
		Residuals	77			
	Width	Species	1	15.42	57.42	< 0.001
		Residuals	77			
	Volume	Species	1	19095	103.70	< 0.001
		Residuals	77			
November	Length	Species	-	-	-	-
		Residuals	-	-	-	-
	Width	Species	-	-	-	-
		Residuals	-	-	-	-
	Volume	Species	-	-	-	-
		Residuals	-	-	-	-
January	Length	Species	-	-	-	-
		Residuals	-	-	-	-
	Width	Species	-	-	-	-
		Residuals	-	-	-	-
	Volume	Species	-	-	-	-
		Residuals	-	-	-	-
March	Length	Species	1	16291	47.42	< 0.001
		Residuals	429			
	Width	Species	1	62.94	64.63	< 0.001
		Residuals	429			
	Volume	Species	1	$9.61\text{x}10^5$	69.158	< 0.001
		Residuals	429			
May	Length	Species	1	15610	159.48	< 0.001
		Residuals	2080			
	Width	Species	1	150.78	347.31	< 0.001
		Residuals	2080			
	Volume	Species	1	$4.42\ \text{x}10^5$	547.82	< 0.001
		Residuals	2080			
July	Length	Species	1	1678.40	41.375	< 0.001
		Residuals	282			
	Width	Species	1	34.10	102.63	< 0.001
		Residuals	282			
	Volume	Species	1	49383	130.96	< 0.001
		Residuals	282			

3.3.3 Fecundity

Upon reaching full female gametogenesis and maturity, both brooding (*Teredo parksi,* n = 19) and spawning (*Bankia carinata,* n = 25) species possessed high fecundities, producing D-stage veliger larvae and eggs, respectively. Initial reproductive output was similar for both species, holding 7,500-15,000 larvae/eggs per individual, with fecundity increasing steadily with body size (Figure 3.6). As body length increased up to 30 mm, both species still had similar fecundities, reaching up to 50,000 larvae/eggs per individual. For body lengths greater than 30 mm, fecundity for *B. carinata* increased at an exponential rate, with adults over 100 mm in length being capable of releasing over 3 million eggs. The fecundity of *T. parksi* increased at a lower rate with a predicted brood size of under 300,000 larvae by 100 mm in size, which is tenfold less than for *B. carinata* of similar size. The size of larvae and eggs were consistent, and did not vary with adult body size. The D-stage veliger larvae of *T. parksi* measured on average 72.1 ± 0.57 μm in length, and the eggs of *B. carinata* 37.5 ± 0.68 μm in diameter.

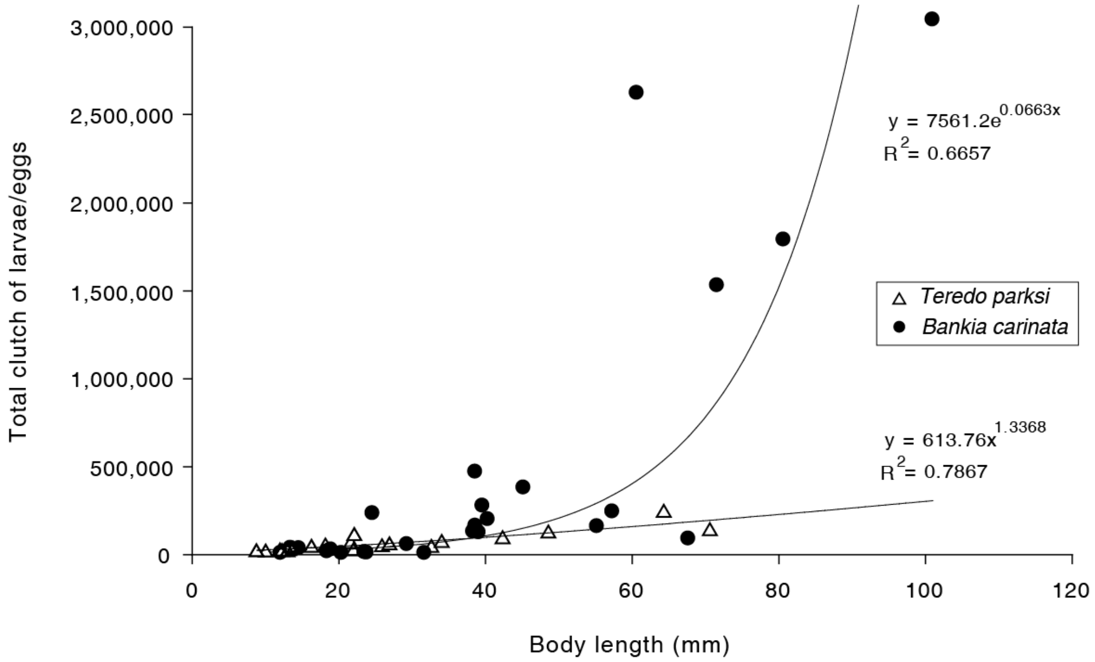


Figure 3.6: Model of fecundity and growth in brooding (*Teredo parksi*; n = 19) and free-spawning (*Bankia carinata;* n = 25) shipworms. Regression function and coefficient of determination (R^2) are shown for each.

3.4 Discussion

This study determined the life history strategies of tropical Australian shipworms, highlighting evolutionary adaptations to their specialized ecological niche. The growth, reproductive development and fecundities of *Teredo parksi* and *Bankia carinata* were quantified for the first time, adding to our understanding of the biology and ecology of shipworms. While differing in reproductive mode, size and fecundity, both species displayed rapid growth, precocious development and high reproductive output. These are key adaptations to shipworms' specialized, ephemeral niche, and enable them to quickly establish themselves in scarce, patchy habitats. Moreover, diverse life history traits are the primary basis for interspecific competition in shipworm communities, enabling regional coexistence and the formation of diverse metacommunities (MacIntosh et al. 2012).

The free-spawning *Bankia carinata* grew significantly longer and wider than the larval brooding *Teredo parksi* in the same time period, resulting in an overall larger body size. These results are consistent with past literature on shipworms, where free-spawners are amongst the largest species (Haderlie and Mellor 1973, Cragg et al. 2009), and also fit widely-observed paradigms of body size and life histories in other taxa (Blueweiss et al. 1978, Strathmann and Strathmann 1982, Ripley and Caswell 2008). Shipworms have a highly plastic body form, shaped by habitat availability (Clapp 1925), which contributes to high variation in lengths and widths. It is important to note that shipworms are sessile, obligate wood-feeders, and therefore growth describes both resource and space consumption. Thus, a larger body size can be expected to confer competitive advantage by way of higher energy intake, reduced habitat availability for co-habitants and ultimately a higher reproductive potential, consistent with our understanding of metabolism and size in ecological theory (Brown et al. 2004, Woodward et al. 2005, Lord and Shanks 2012).

Both *Teredo parksi* and *Bankia carinata* matured within two months of recruitment, reaching male gametogenesis by an average 2-4 mm in body length and were capable of releasing offspring by 6-10 mm. Early maturation is similar to that reported for other tropical shipworms (Karande and Pensey 1969, Nair and Saraswathy 1971). However, this precocious sexual maturity stands in contrast to temperate shipworm species, which typically reach female maturity within 2 months but at a size of 40 mm in length (Coe 1933, Grave 1942, McKoy 1980). The rate at which shipworms sexually develop highlights the intense competitive conditions within these communities, where the ephemeral nature of wood habitats drives strong selective pressure to quickly establish reproductive populations (Kozlowski 1992, Bernardo 1993). Tropical environmental conditions permit year-round reproduction in shipworms (MacIntosh et al. 2012), resulting in a year-round supply of larval recruits. Life histories that encompass short generation time and repeated reproductive events are often characterized as strongly r-selected, a strategy typically associated with high habitat instability (Giangrande et al 1994), and mirrors those of early successor species colonizing newly available habitats (Grassle and Grassle 1974, McMahon 2002).

The fecundity of *Teredo parksi* and *Bankia carinata*, coupled with high growth rates and rapid maturity, results in prodigious reproductive outputs. From the onset of female sexual maturity to body sizes up to 30 mm, both species possessed fecundities of up to 15,000 larvae or eggs. As body size increased, the free-spawning *B. carinata* was exponentially more fecund than *T. parksi*, with 100 mm long individuals reaching clutch sizes of over 3×10^6 eggs, ten times that of similar sized *T. parksi*. Shipworm communities are characterized by a steady decrease in habitat quality as the inhabitants consume space and resources, driving the short life spans of habitat patches. Under these conditions, high fecundity supports a bet-hedging strategy in which large numbers of offspring counterbalance the poor availability and varied distribution of habitat patches (Ramirez-Llodra 2002). This strategy is consistent with the characteristics of r-selection, with high reproductive output widely associated with habitat unpredictability (Giesel 1976, Benton and Grant 1999). Free-spawning of gametes is inherently more prolific than brooding strategies where larvae are retained internally, with limitations in body volume and resources devoted to developing young (Ramirez-Llodra 2002). If viewed purely from a supply-side perspective, the significantly higher fecundities of free-spawning shipworms should translate to a correspondingly high rate of larval recruitment success (Hughes et al. 2000, Cowen and Sponaugle 2009). However, brooded larvae have higher fertilization rates (Levitan 1995, Yund 2000), are more capable of local retention (Strathmann et al. 2002) and are released at a higher competency, enabling a shorter planktonic lifespan subject to less mortality (Vaughn and Allen 2010). This combination suggests that larval brooding shipworms species have a higher overall fitness than free-spawning species and hold a competitive advantage in colonizing newly-available habitats, reflected in the high abundance of brooding species (Chapter 2).

The rapid growth, precocious development and high reproductive output of shipworms all constitute adaptations to a highly specialized ecological niche. With the scarce distribution of new habitats and no ability to assess habitat/patch quality before recruitment, shipworms must ensure reproductive success with the threat of community collapse and mortality seemingly imminent. These selective pressures have pushed the life history characteristics of the family to an extreme, which now approach those of the hypothetical “Darwinian Demon”- breeding early, breeding often and living indefinitely (Law 1979, Klimek et al. 2010). The life histories of brooding and spawning shipworms represent classic trade-offs in growth, fecundity and larval dispersal; coupled with diverse, competitive metacommunities, shipworms are a promising model taxon for investigating life history competition and evolution.

Chapter 4

Maternal provisioning and reproductive effort in tropical shipworms

4.1 Introduction

All organisms exist under some degree of energetic constraint, where finite energy reserves must be carefully allocated between somatic functions (including metabolic maintenance, growth, and energy capture) and reproduction (Kozlowski 1992, Kooijman 2000, van der Meer 2006). This reproductive allocation primarily takes the form of maternal provisioning, the energy invested in individual larvae or eggs (Villinski et al. 2002, McEdward and Miner 2006, Byrne et al. 2008) as well as reproductive effort, the proportion of an organism's total energy devoted to reproduction (Stearns 1992, Caley et al. 2001, Pianka 2011). How this finite reproductive energy is allocated is the basis for the classic trade-off between the number and size of offspring and is one of the most fundamental and far-reaching aspects of an organisms' life history (Vance 1973, Stearns 1992, Bernardo 1996, Marshall and Keough 2008b). Quantifying maternal investment and reproductive effort is a critical step in understanding an organism's ecology, linking reproductive investment at the individual or species level with broader population and community structure. The key measures required for examining maternal investment and reproductive effort are the number of offspring produced by an organism, their mass or energetic content, and a measure of adult size or energy content.

The number and size of eggs is an easily quantifiable measure of maternal provisioning and reproductive effort, with egg size linked to life history characteristics such as fertilization success (Levitan 2006), developmental mode (Moran and McAlister 2009) and post-larval survival (Marshall and Keough 2004). However, egg size alone is not a reliable measure of energy, especially amongst species with planktotrophic larvae (McEdward and Morgan 2001). As planktotrophic larvae feed during their development, their lipid content, and therefore their egg size, are smaller than for species with lecithotrophic larvae (Jaeckle 1995, Young et al. 2006). For this same reason, quantifying lipid content in eggs does not provide an accurate picture of maternal provisioning for planktotrophs as it does for lecithotrophs (Byrne et al. 2008). Instead, techniques such as ultimate analysis permit accurate measurement of organic composition (C, H, O, N and S) of larvae and eggs, and generate a calorific value for the energy invested into them. From here it is possible to compare energetic provisioning at the scale of individual larvae and eggs, and subsequently calculate the relative proportion of an organism's total energy invested in reproduction.

In this research, I examine maternal provisioning and reproductive effort in shipworms, a family of marine bivalves (Teredinidae) with an unusual wood-boring niche. Shipworms are sessile organisms that recruit to, and rapidly consume, wood substrates, forming diverse, short-lived communities which are entirely reliant on planktonic larvae to find new habitat. The previous chapters have explored the demographics of shipworm communities and the life history strategies that enable shipworms to survive in their specialized niche. As detailed in Chapter 3, shipworms can be broadly categorized by reproductive mode into larval brooding and free-spawning species and these competing strategies correspond to significant differences in the characteristics of growth rates and fecundity. More importantly, reproductive mode is a key driver of recruitment success in shipworm communities, with larval-brooding species in tropical Australia exhibiting recruitment up to ten-fold higher than free-spawning species (MacIntosh 2012). Incorporating data on maternal provisioning and reproductive effort will permit a more complete model of shipworms' life-history trade-offs, and provide insight into the role reproductive investment plays in shaping shipworm communities.

The reproductive strategies of larval brooding and free-spawning shipworms both constitute successful adaptations to this niche, raising a key question- are brooding and spawning simply a trade-off on the number and size of offspring, with similar reproductive effort? If not, which of the two strategies results in a higher reproductive effort? Therefore, the aim of this research was to compare maternal provisioning and reproductive effort in the larval brooding *Teredo parksi* and the free-spawning *Bankia carinata*, two commonly occurring species from tropical Australia. The number and size of larvae and eggs were quantified, and coupled with ultimate analysis of adults, larvae and eggs to generate a caloric model of maternal provisioning and reproductive effort.

4.2 Materials and methods

4.2.1 Collection

Shipworm specimens were collected from wooden recruitment panels, as part of a broader investigation into the reproductive ecology of tropical shipworms (for detailed methodology, see MacIntosh et al. 2012). Panels were constructed from layers of radiata pine (*Pinus radiata*), sandwiched between two 170mm x 120mm Perspex sheets. The final dimensions of panels were 220 x 150 x 12 mm, with a total surface area of 340.8 cm^2 and volume of 396 cm^3. This panel design allowed for unimpeded recruitment and growth of shipworms, and permitted easy removal of intact specimens.

Brooding (*Teredo parksi*) and spawning (*Bankia carinata*) shipworm species were collected from the Australian Institute of Marine Science (AIMS) jetty (19°16'37.02" S, 147°03'31.46" E) in Cleveland Bay, northern Queensland, Australia. For consistent measurement of reproductive investment, only gravid females were chosen. For the larval-brooding *Teredo parksi*, this was determined by branchial cavities full of D-stage veligers, and large ripe ovaries for the free-spawning *Bankia carinata*. To provide adequate samples and avoid confounding by seasonal effects, only specimens from the peak reproductive period of March and May were examined. Adults of both species were photographed and their body length measured with ImageJ image analysis software (v. 1.38) (Schneider et al. 2012). Length was measured from the furthest anterior portion of the shell valve to the posterior end of the mantle. Species identifications and their modes of reproduction were verified against collections in the Australian Museum, Sydney.

4.2.2 Fecundity

For the larval brooding *Teredo parksi*, the gills and branchial cavities were dissected and the larvae removed. Larvae were diluted into 5 mL of 70% ethanol, sub-sampled 20 times in 10 µL volumes and counted under a stereomicroscope. *Bankia carinata* specimens were dissected to remove the gonads, which were subsequently stripped of mature eggs through gentle agitation in 70% ethanol. Eggs were diluted into 1 mL of 70% ethanol, and counted with a haemocytometer in 8 sub samplings. Fecundity was plotted by adult body length for each species and fitted with regression lines.

4.2.3 Size of larvae and eggs

Eggs and larvae were photographed with a compound microscope (Leica DMLB) with attached digital camera (Olympus DP25) and measured with ImageJ image analysis software (v. 1.38). Egg diameter was recorded, while for larvae the length (antero-posterior), height (dorso-ventral) and width (lateral) of the shell were measured (Figure 4.1). To illustrate any variation in larval/egg size, larval/egg dimensions were plotted by adult body length.

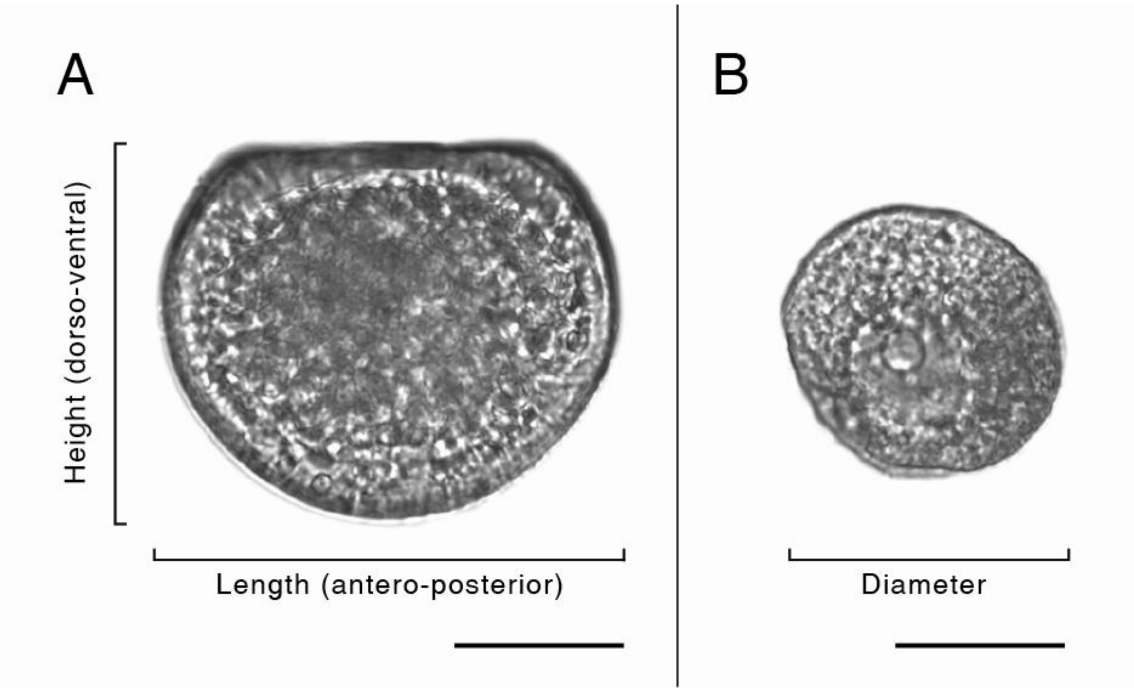


Figure 4.1: Measured dimensions showing size and state of development of (A) *Teredo parksi* veliger and (B) *Bankia carinata* egg. Width (lateral) measurement of *T. parksi* larva not shown. Scale bars = 25 µm.

To measure the relative somatic and reproductive masses of shipworms, body tissue, eggs and larvae were separated and stored in 70% ethanol. To ensure true determination of organic mass in shipworm tissue, the wood-storing gut caecum, calcareous shell valves and pallets were removed from adult samples, as these would increase the proportion of carbon and inorganic material. Body tissue, larvae and egg samples were freeze-dried, homogenized and apportioned into individual weighed silver foil containers. The dry weight of each sample was determined to 0.001 mg accuracy using a microbalance (Perkin-Elmer AD-4). As the number of larvae and eggs in each sample was known, the mass (in µg) per larva or egg was calculated. To compare adult growth between species, the somatic body mass of adult shipworms (body tissue with no larvae or eggs) was measured, and plotted as a function of overall body length. Using the mass of larvae, eggs and body tissue, the relative proportion of total body mass (body tissue plus larvae or eggs) made up by larvae or eggs was also calculated.

To determine the inorganic (ash) content within shipworms, body tissue of both species, larvae and egg samples were weighed (as above), apportioned into silver foil containers and ashed in a muffle furnace at 500°C for 6 hours, then reweighed. The average ash contents in body tissue, larvae and egg were used to determine ash free dry weights in other samples. Samples of radiata pine used to construct the recruitment panels were also weighed and ashed (as above).

4.2.4 Energetics

Samples of body tissue, larvae, eggs and wood were apportioned into tin foil containers, then dried and weighed at which point elemental analysis (CHNS) could be carried out (OEA Labs, UK). Samples were flash combusted at 1800°C in helium with a controlled dosage of oxygen. The resulting combustion gases were then separated and quantified via a gas chromatograph with a thermal conductivity detector. Results were reported as relative percentage (by mass) of carbon, hydrogen, nitrogen and sulphur and ash (as determined above). Oxygen content was calculated by difference, as the remaining organic fraction (Shah et al. 2012).

As the flash combustion occurred at such high temperatures, the inorganic calcium, carbon and oxygen present in the larval shells (present as calcium carbonate, $CaCO_3$) was released and contributed to the overall percentage of carbon and oxygen as determined in the elemental analysis. To correct for this, the percentages of carbon, hydrogen, nitrogen, oxygen and ash in larval samples were multiplied by the total sample mass, providing relative masses of each. The ash mass, comprising the $CaCO_3$ larval shell could be then be separated into calcium, carbon and oxygen using the atomic masses and proportions of the shell's components (40% Ca, 12% C, 48% O). These inorganic carbon and oxygen masses were subtracted from the organic carbon and oxygen masses and the percentages of C, H, O, N and S recalculated using the ash-free dry weight of the sample. To allow for comparison across all samples, the percentages of C, H, O, N and S in body tissue, egg and wood samples were also recalculated using ash-free dry weight, excluding ash mass from all further analysis.

As a measure of total organic energy, the Higher Heating Value (HHV) was calculated for all samples, as per the methods of Channiwala and Parikh (2002), with HHV (J/mg) determined as:

$$\text{HHV (J/mg)} = (0.3491\times C) + (1.1783\times H) - (0.1034\times O) - (0.0151\times N) + (0.1005\times S)$$

where C, H, O, N, S were the relative percentages of carbon, hydrogen, oxygen, nitrogen, and sulphur respectively. As the number of larvae or eggs in each sample was known, the energy per larva or egg was calculated in Joules, as was as the relative proportion of total energy invested in larvae or eggs (offspring energy / body energy + offspring energy).

4.2.5 Statistical analysis

For all of the above analyses, *Teredo parksi* and *Bankia carinata* were statistically compared by permutational multivariate analysis of variance (PERMANOVA) with species as a single fixed factor, using PRIMER v6 statistical software and the PERMANOVA+ v1.0.3 extension (Clarke and Gorley 2006). For this analysis, Euclidean distance measures were used between samples, and p-values were calculated using unrestricted permutation of data with 9999 random permutations. Mean Squares (MS), PERMANOVA pseudo-*F* statistics (*F*) and p value were reported for all statistical analyses (Table 4.2), and all mean data values expressed with standard error as a measure of variation.

4.3 Results

4.3.1 Fecundity

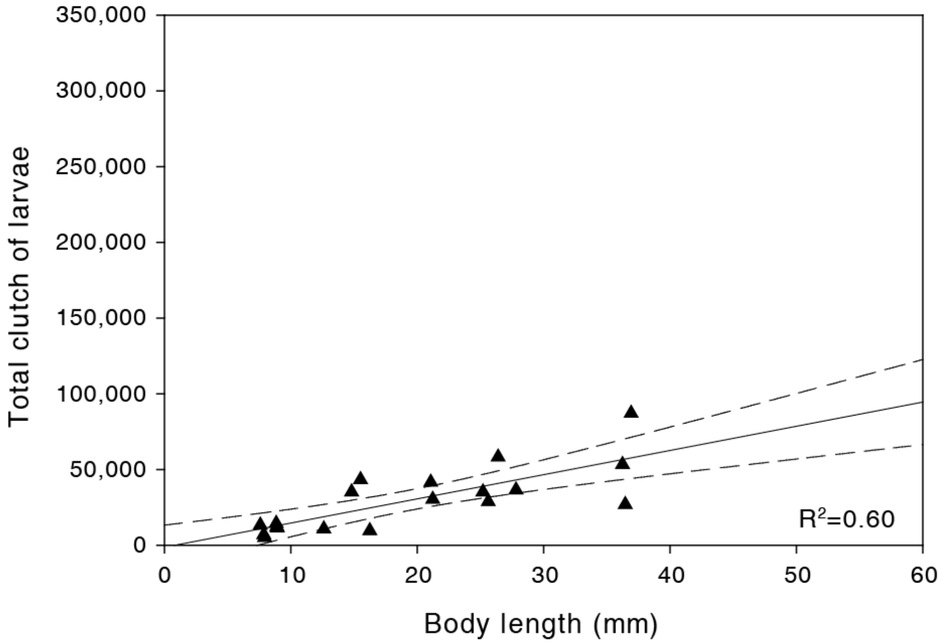
Teredo parksi (n = 19) and *Bankia carinata* (n = 21) were both highly fecund, producing large numbers of D-stage veliger larvae and eggs, respectively. For body lengths of 10-30 mm, fecundities for both species were similar, with up to 50,000 larvae/eggs per individual (Figure 4.2). As body length increased over 30 mm, the fecundity of *B. carinata* increased exponentially, with a predicted fecundity of over 200,000 eggs for individuals 50 mm in length. The fecundity of *T. parksi* increased at a slower, linear rate, with a 50 mm long adult predicted to produce 75,000 larvae.

4.3.2 Size of larvae and eggs

The size of larvae and eggs was consistent for both *Teredo parksi* and *Bankia carinata*, with no significant effect due to adult body length (Figure 4.3). The mean size of D-stage veliger larvae of *T. parksi* measured 71.93 ± 0.54 µm in length (antero-posterior), 57.89 ± 0.62 µm in height (dorso-ventral) and 38.36 ± 0.53 µm in width. The eggs of *B. carinata* were comparatively small, with a mean diameter of 37.07 ± 0.49 µm. The larvae of *T. parksi* were significantly larger in length (MS 13609.00, *F* 2204.10, $p < 0.001$) and height (MS 4854.10, *F* 656.96, $p < 0.001$), but not in width (MS 18.90, *F* 3.18, $p = 0.08$).

The D-stage veliger larvae of *T. parksi* had an mean individual mass of $7.31\times10^{-2} \pm 0.46\times10^{-2}$ µg including the mass of the shell, nearly ten-fold heavier than the eggs of *B. carinata*, which had a mean mass of $0.89\times10^{-2} \pm 0.17\times10^{-2}$ µg. Larvae had an mean ash content of 73.35 ± 6.45%, compared with 5.93 ± 2.58% for eggs. The mean ash-free mass of individual *T. parksi* larvae was $1.95\times10^{-2} \pm 0.12\times10^{-2}$ µg, and significantly heavier than the eggs of *B. carinata*, which has a mean mass of $0.84\times10^{-2} \pm 0.11\times10^{-2}$ µg (MS 1.13×10^{-3}, *F* 46.02, $p < 0.001$) (Figure 4.4).

A - *Teredo parksi*



B - *Bankia carinata*

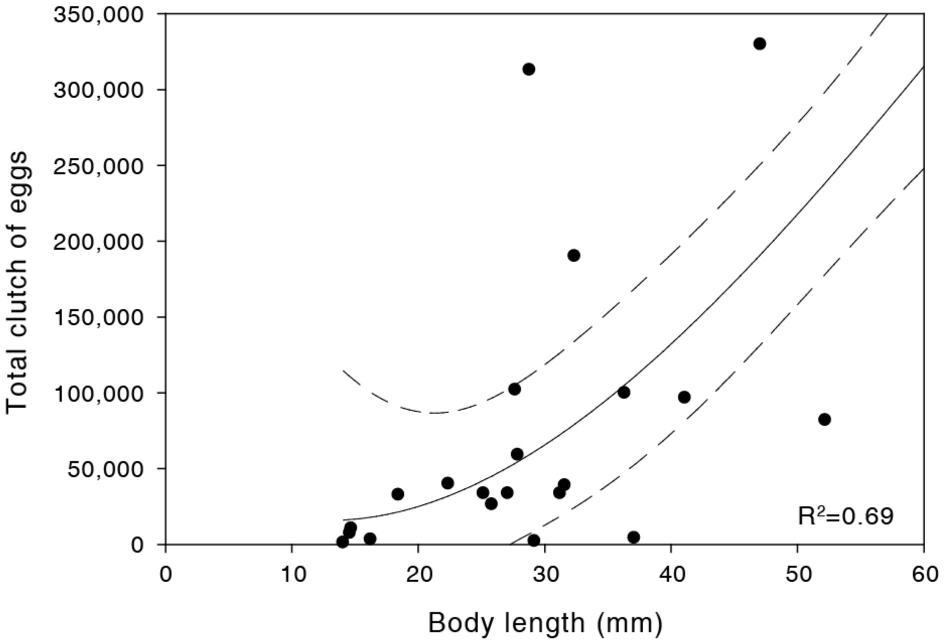
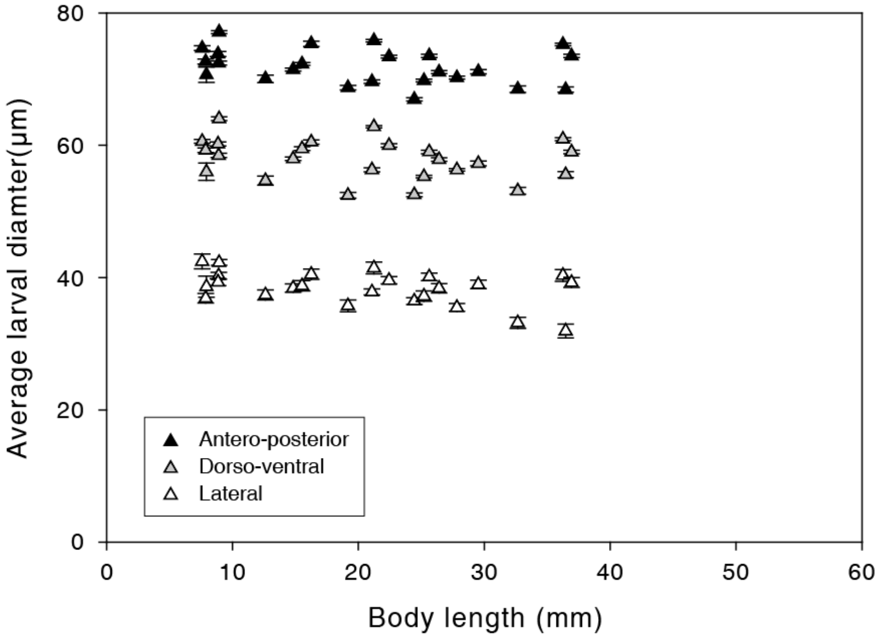


Figure 4.2: Model of fecundity and growth in (A) brooding (*Teredo parksi*; n = 19) and (B) free-spawning (*Bankia carinata*; n = 21) shipworms collected from the Australian Institute of Marine Science between March and May. Regression lines with 95% confidence interval and coefficients of determination (R^2) are shown for each.

A - *Teredo parksi*



B - *Bankia carinata*

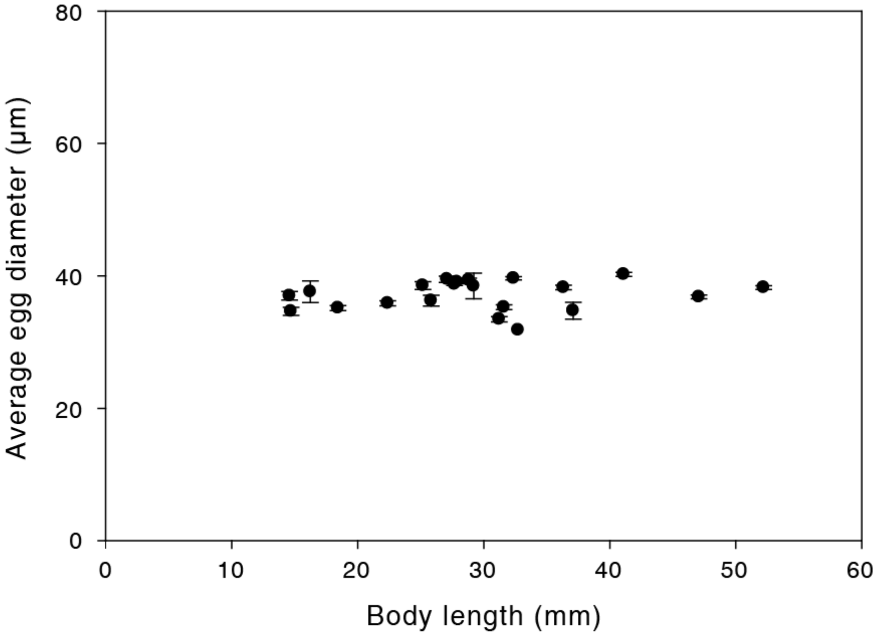


Figure 4.3: Mean diameter (± SE) of larvae and eggs in (A) brooding (*Teredo parksi;* n = 20) and (B) free-spawning (*Bankia carinata;* n = 21) shipworms collected from the Australian Institute of Marine Science between March and May. Larvae were measured in 3 planes (see legend).

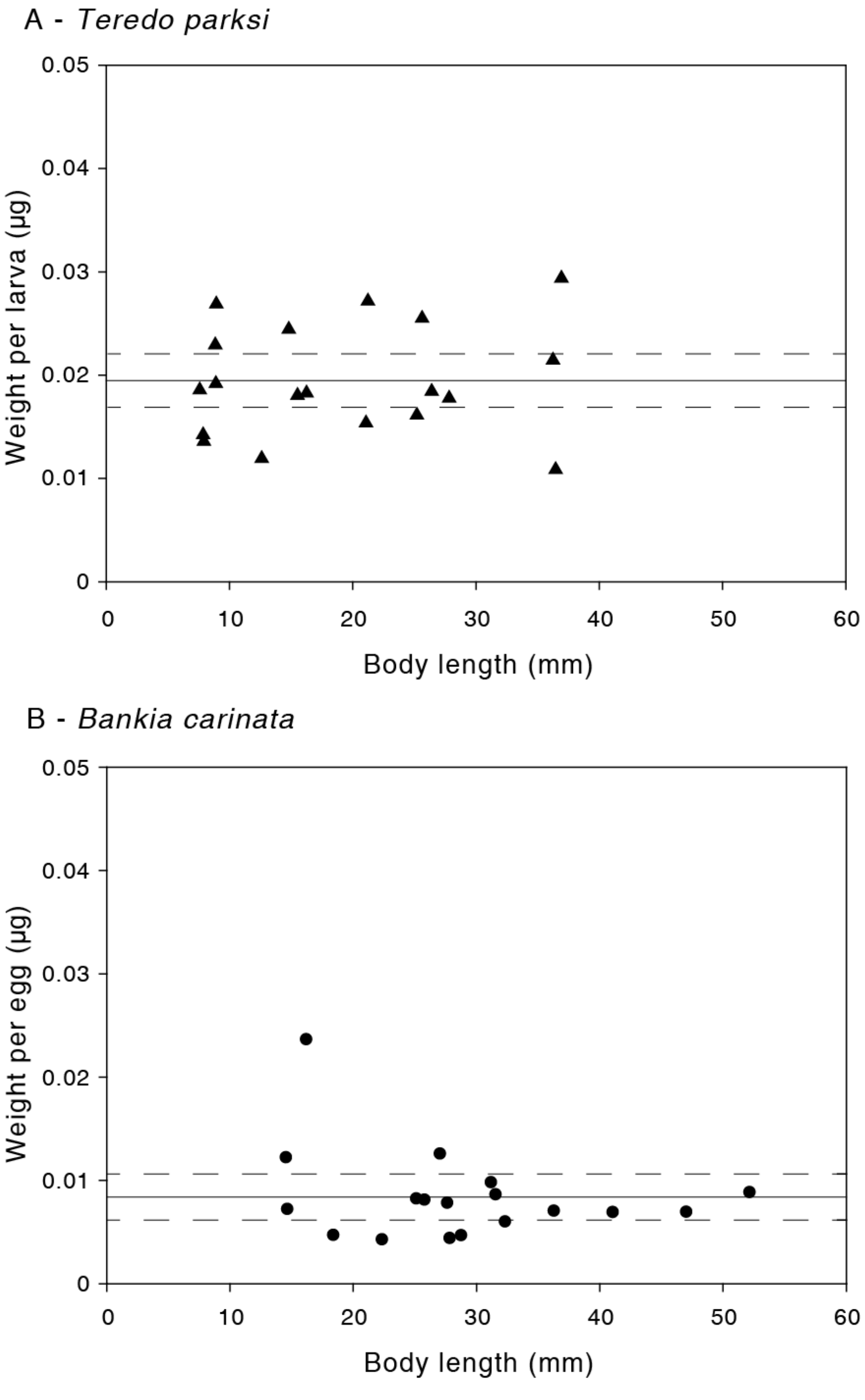


Figure 4.4: Mass per individual larva and egg in (a) brooding (*Teredo parksi;* n = 19) and (B) free-spawning (*Bankia carinata;* n = 18) shipworms collected from the Australian Institute of Marine Science between March and May. Solid line represents mean mass while dotted lines represent 95% confidence interval.

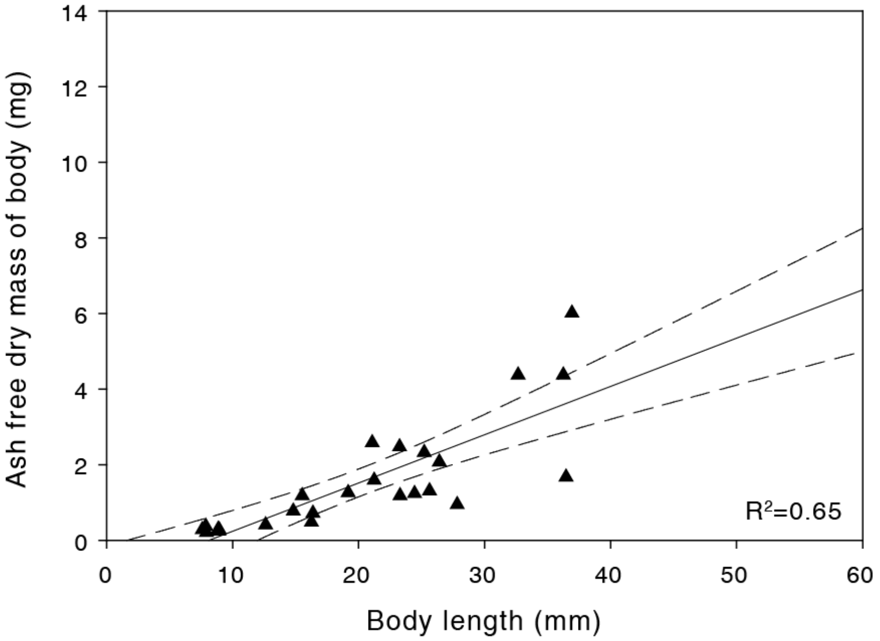
The body mass of both species increased linearly with respect to body length, with *B carinata* possessing significantly higher mass than *T. parksi* (Figure 4.5). Because of this and the higher mass of larvae, *T. parksi* had a significantly higher proportion of body mass devoted to reproduction than *B. carinata* (MS 4013.10, *F* 40.26, $p < 0.001$) with total body mass determined by the ash-free weight of body tissue and eggs/larvae (Figure 4.6). *T. parksi* larvae composed a mean of 32.28 ± 3.00% of of the total adult body mass compared to *B. carinata*, for which eggs composed a mean of 10.44 ± 1.15% of the total adult body mass.

4.3.3 Energy

The organic composition of shipworm body tissue, larvae, eggs and wood was determined through ultimate analysis (for detailed results, see Table 4.1). The elemental (CHONS) composition of *Teredo parksi* and *Bankia carinata* were broadly similar with the only notable difference being a slightly higher percentage of carbon and a lower percentage of oxygen in *B. carinata* body tissue and eggs (Table 4.1). This resulted in a higher energy content (HHV) for *B. carinata*, with a mean of 22.10 ± 1.28 J/mg in body tissue and 22.98 ± 1.44 J/mg in eggs. In contrast, *T. parksi* body tissue had a mean of 19.17 ± 1.42 J/mg, while larvae has a mean of 16.08 ± 1.43 J/mg. Radiata pine contained similar levels of carbon, hydrogen and oxygen to shipworm tissue, but lower levels of nitrogen 0.08 ± 0.01% and sulphur < 0.05%. This did not strongly affect the energetic content of the wood, which had a mean of 20.24 ± 0.05 J/mg. Carbon-nitrogen ratios were similar across all shipworm tissues, between 4.4-4.6:1, but the low nitrogen levels present in radiata pine resulted in a C:N ratio of 617:1.

Based on the number and mass of larvae and eggs, the mean energetic content per egg/larva was calculated (Figure 4.7). *T. parksi* larvae contained a mean of $3.13\times10^{-4} \pm 0.20\times10^{-4}$ J each, significantly higher than the energetic content in *B. carinata* eggs which had a mean of $1.93\times10^{-4} \pm 0.22\times10^{-4}$ J (MS 1.34×10^{-7}, *F* 14.89, $p < 0.001$). For *T. parksi,* the percentage of total body energy (energy content of body tissue plus eggs/larvae) invested in larvae was 30.15 ± 2.74% of total body energy, significantly higher than *B. carinata*, where eggs composed 10.80 ± 1.19% of total body energy (MS 3459.70, *F* 40.39, $p < 0.001$; Figure 4.8).

A - *Teredo parksi*



B - *Bankia carinata*

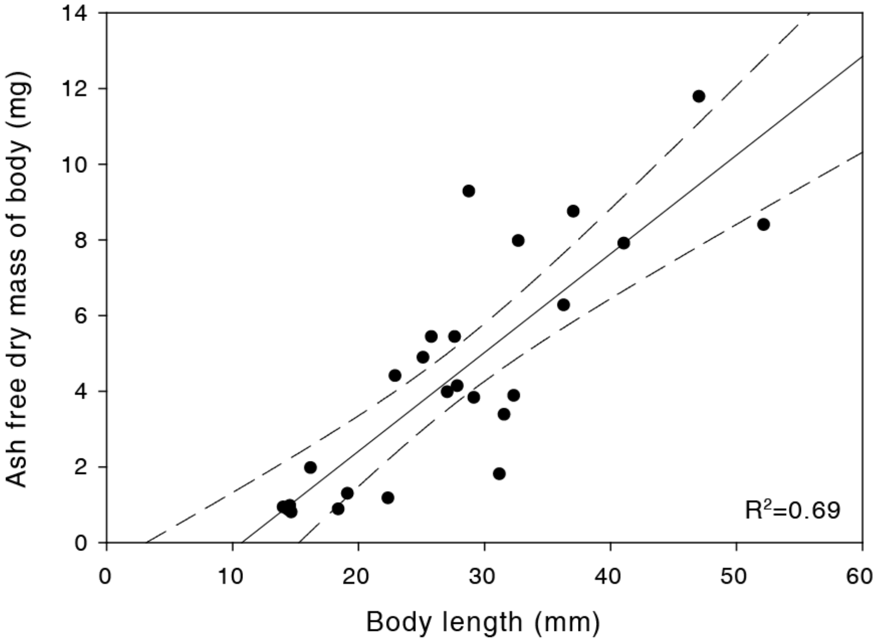
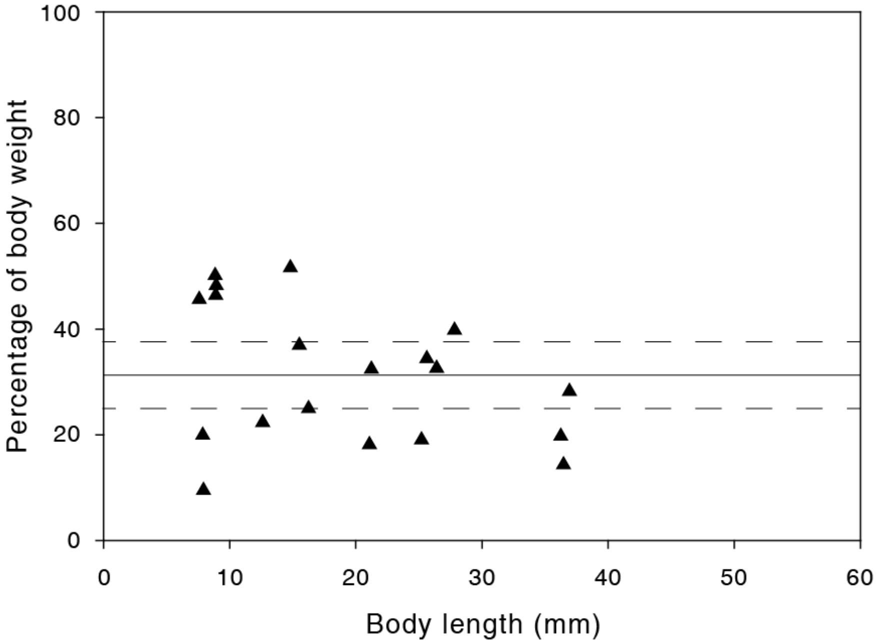


Figure 4.5: Relationship between length and somatic body mass in (A) brooding (*Teredo parksi*; n = 25) and (B) free-spawning (*Bankia carinata*; n = 25) shipworms collected from the Australian Institute of Marine Science between March and May. Regression lines with 95% confidence interval and coefficients of determination (R^2) are shown for each.

A - Teredo parksi



B - Bankia carinata

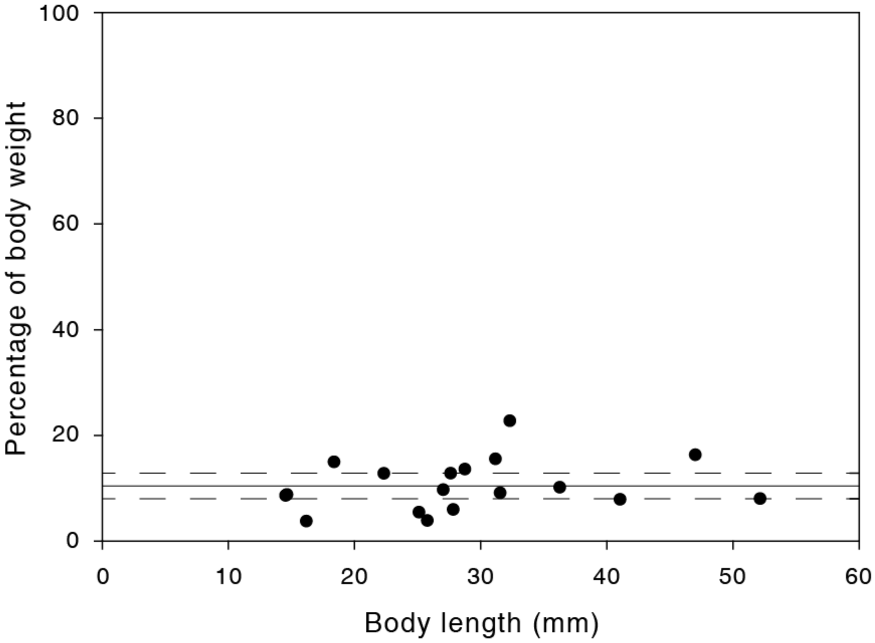


Figure 4.6: Percentage of total ash-free mass (larvae/eggs + body tissue) of larvae and eggs in (A) brooding (Teredo parksi; n = 19) and (B) free-spawning (Bankia carinata; n = 18) shipworms collected the Australian Institute of Marine Science between March and May. Solid line represents mean mass while dotted lines represent 95% confidence interval.

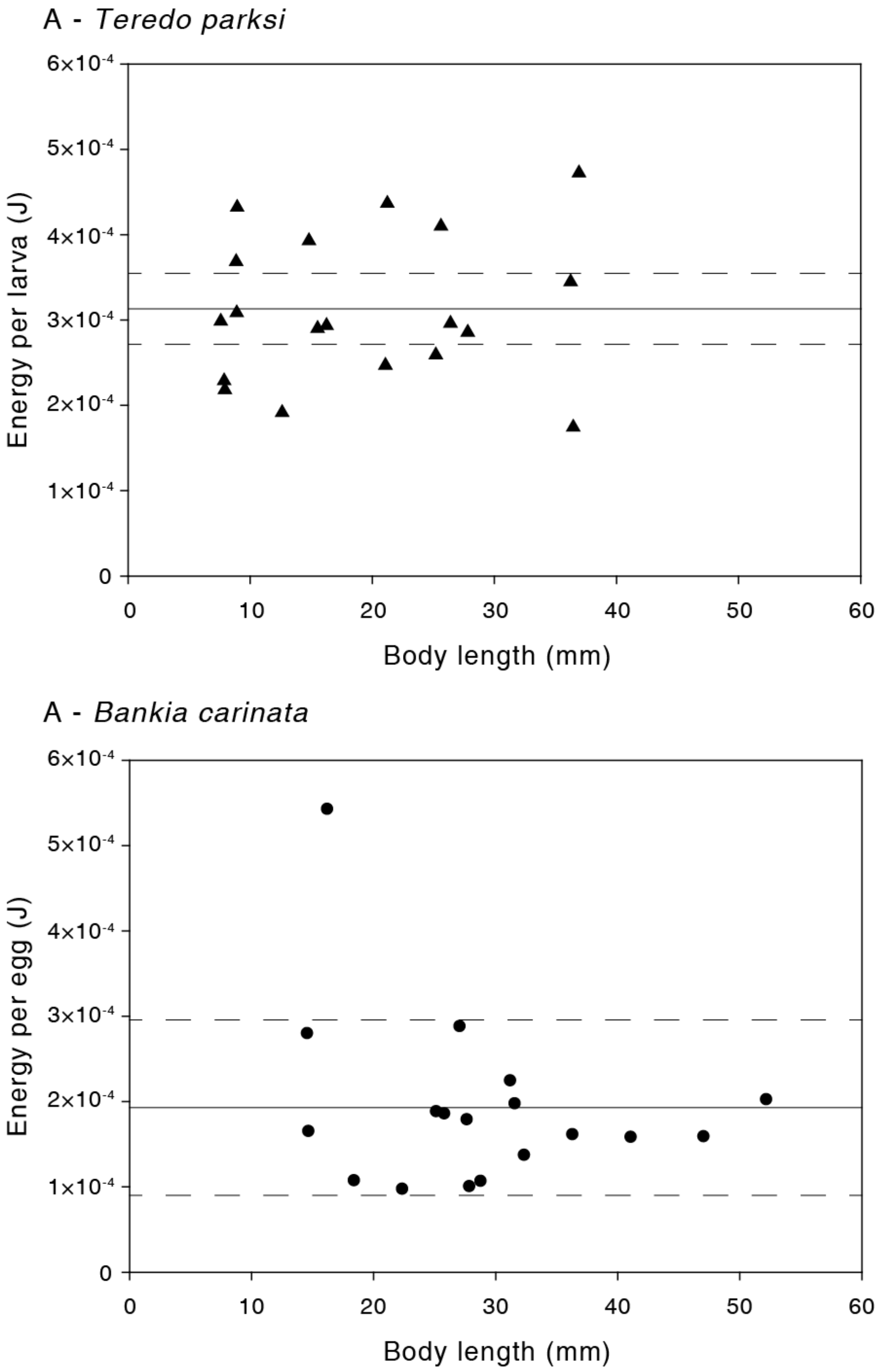
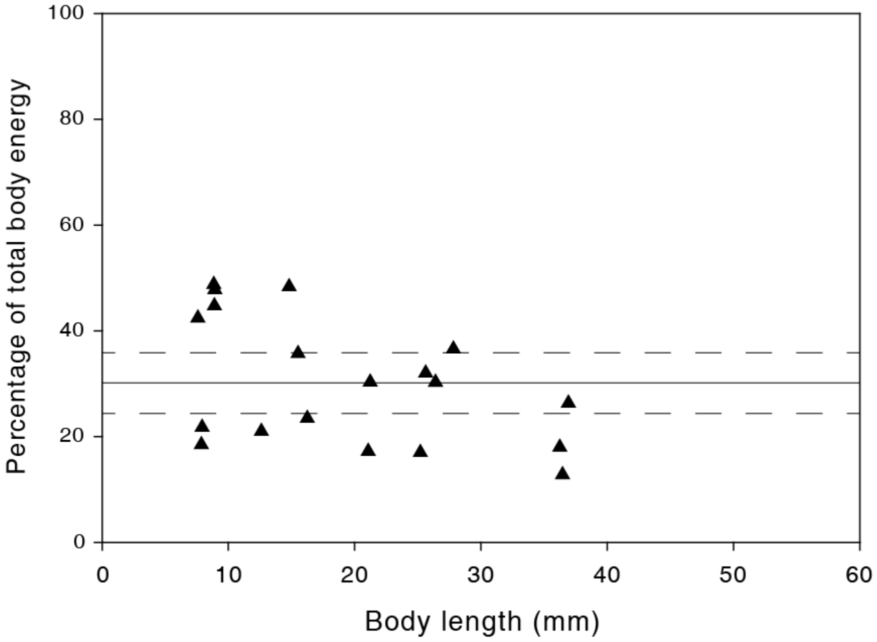


Figure 4.7: Energy per individual larva and egg in (A) brooding (*Teredo parksi;* n = 19) and (B) free-spawning (*Bankia carinata;* n = 18) shipworms collected from the Australian Institute of Marine Science between March and May. Solid line represents mean mass while dotted lines represent 95% confidence interval.

A - *Teredo parksi*



B - *Bankia carinata*

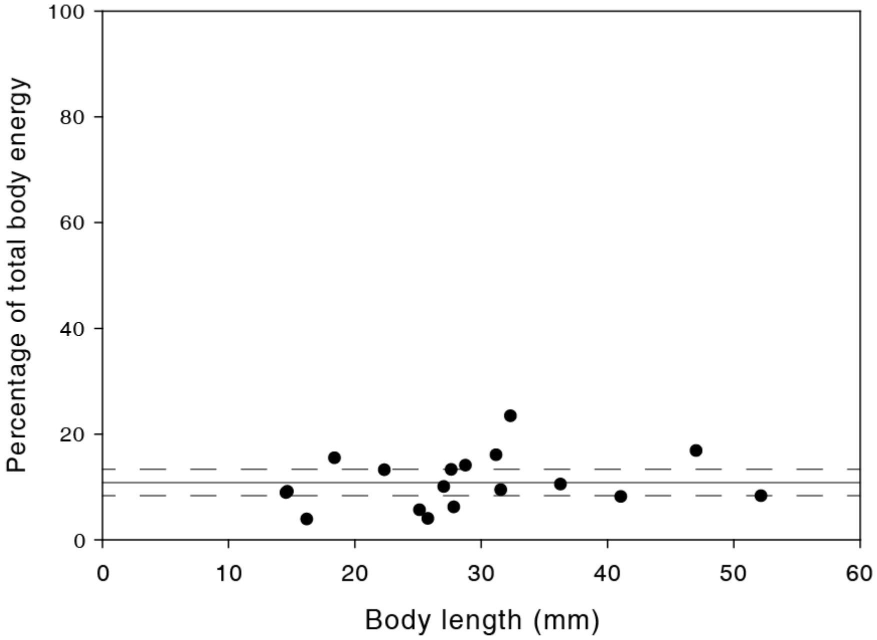


Figure 4.8: Percentage of total energy (larvae/eggs + body tissue) of larvae and eggs in (A) brooding (*Teredo parksi*; n = 19) and (B) free-spawning (*Bankia carinata*; n = 18) shipworms collected the Australian Institute of Marine Science between March and May. Solid line represents mean mass while dotted lines represent 95% confidence interval.

Table 4.1: Organic composition of brooding (*Teredo parksi;* n = 9) and free-spawning (*Bankia carinata*; n = 9) shipworm species and radiata pine (*Pinus radiata;* n = 3) samples. Results expressed as percentage (± SE) of ash-free mass of carbon (C), hydrogen (H), oxygen (O), nitrogen (N) and sulphur (S). Energy content expressed in J/mg as Higher Heating Value (HHV), and ratio of carbon to nitrogen expressed (C:N).

Species	Tissue	% C	% H	% O	% N	% S	HHV (J/mg)	C : O	C : N
Teredo parksi	**Body**	**45.62** ± 2.09	**6.08** ± 0.40	**37.11** ± 2.14	**10.40** ± 0.55	**0.79** ± 0.13	**19.17** ± 1.42	**1.2 : 1**	**4.4 : 1**
	Larvae	**41.02** ± 1.92	**5.50** ± 0.39	**44.45** ± 2.94	**8.87** ± 0.63	**0.17** ± 0.07	**16.08** ± 1.43	**0.9 : 1**	**4.6 : 1**
Bankia carinata	**Body**	**52.45** ± 0.63	**5.82** ± 0.94	**29.02** ± 1.51	**11.62** ± 0.59	**1.09** ± 0.08	**22.10** ± 1.28	**1.8 : 1**	**4.5 : 1**
	Eggs	**52.12** ± 1.61	**6.61** ± 0.85	**28.23** ± 2.14	**12.04** ± 0.51	**1.00** ± 0.06	**22.98** ± 1.44	**1.8 : 1**	**4.3 : 1**
Pinus radiata	**Wood**	**49.38** ± 0.16	**6.39** ± 0.06	**43.81** ± 0.22	**0.08** ± 0.01	**< 0.05**	**20.24** ± 0.05	**1.1 : 1**	**617 : 1**

Table 4.2: Single-factor PERMANOVA analysis with significant differences between larval and egg characters of *Teredo parksi* and *Bankia carinata*.

Test	Source	*df*	MS	*F*	*p*
Larval length vs egg diameter (µm)	Species	1	20846	3341.90	< 0.001
	Residuals	67	6.24		
Larval height vs egg diameter (µm)	Species	1	7672.2	1226.2	< 0.001
	Residuals	67	6.26		
Larval width vs egg diameter (µm)	Species	1	32.11	5.55	0.02
	Residuals	67	5.78		
Mass per larva/egg (µg)	Species	1	1.95×10^{-3}	46.56	< 0.001
	Residuals	59	4.20×10^{-5}		
Proportion of total body weight (%)	Species	1	3850.70	34.75	< 0.001
	Residuals	59	110.81		
Energy per larva/egg (J)	Species	1	2.47×10^{-7}	15.97	< 0.001
	Residuals	59	1.55×10^{-8}		
Proportion of total body energy (%)	Species	1	3181.10	31.03	< 0.001
	Residuals	59	102.53		

4.4 Discussion

In this study the number, size and energetic make up of larvae and eggs were quantified for the shipworm species *Teredo parksi* and *Bankia carinata*, to compare maternal provisioning and reproductive effort. The broad finding of this study was a significantly higher maternal provisioning and reproductive effort by the larval brooding *T. parksi*, with higher energy content per larva, and a higher proportion of overall body energy invested in reproduction. This demonstrates that brooding and spawning strategies of shipworm species are not simply trade-offs between the number and size of offspring, and that higher overall investment into reproduction by brooding species may be responsible for their dominant position in the composition of shipworm communities.

Both *Teredo parksi* and *Bankia carinata* have high fecundities, producing tens to hundreds of thousands of larvae and eggs which increase with body size. The fecundity of both species was similar at body lengths less than 30 mm, with clutch sizes of 15,000 to 50,000 larvae/eggs. As body size increased, the fecundity of *B. carinata* increased at a higher rate than *T. parksi*, with 50 mm long *B. carinata* predicted to produce over 200,000 eggs, a clutch size two and a half times greater than *T. parksi* individuals of the same size. Such high fecundities are typical of shipworm species (Nair and Saraswathy 1971), and these results closely match those of *T. parksi* and *B. carinata* recorded from other locations in tropical Australia (see Chapter 3). Shipworms face high habitat variability, to which high fecundities are a common evolutionary response (Benton and Grant 1999), maximizing the chances of offspring locating new habitat patches (Ramirez-Llodra 2002). The lower fecundity of larval brooders can simply be attributed to the higher size and energy of larvae, which occupy more space and resources than similar numbers of eggs (Ripley and Caswell 2008).

The D-stage veliger larvae brooded by *Teredo parksi* were significantly larger than the eggs of *Bankia carinata*, averaging 72 x 58 x 38 µm in length, width and height, within the typical size range of D-stage veligers produced by short-term brooding shipworms (Nair and Saraswathy 1971, Culliney 1975, Cragg et al. 2009) and indicating that these larvae were nearing release. The eggs produced by *B. carinata* has a mean diameter of 37 µm, similar in size to other shipworm species (Nair and Saraswathy 1971), but significantly smaller than the eggs of many bivalves (Moran 2004, Powell et al. 2011). The small size of these eggs can be understood in the context of shipworms' larval biology- as planktotrophs, eggs require smaller yolk reserves, and as a result are generally smaller than those species with lecithotrophic development (Jaeckle 1995, Young et al. 2006). Small egg size is also known to be an adaptation to adverse habitat conditions and competition, where maternal fitness is maximized by producing more, smaller eggs (Allen et al. 2008).

While shipworms often possess a ‘stenomorphic’, highly plastic body form (Chapter 3, Clapp 1925), the larvae and eggs of *T. parksi* and *B. carinata* displayed little variation in size within clutches and between individuals, with coefficients of variation between 3-6%. Many invertebrate species produce larvae or eggs with high variation in size as a bet-hedging strategy (Marshall et al. 2008), but this low level of variation is typical of those with planktotrophic development (Marshall and Keough 2008a), where lower maternal investment does not influence offspring size as significantly.

The veliger larvae of *T. parksi* were significantly heavier than the eggs of *B. carinata*, with the large calcium carbonate shell constituting over 70% of larval mass, similar to other records of shipworm development (Mann and Gallager 1985). As in many other taxa, free-spawning shipworms are larger than brooding species (Strathmann and Strathmann 1982, Ripley and Caswell 2008, Cragg et al. 2009), with a clear linear relationship between total body length and mass. With a combination of higher mass per offspring and smaller overall body mass, larval brooding shipworms have a significantly higher proportion of their total body mass allocated to reproduction.

The organic elemental compositions of both species were broadly similar, with high proportions of both carbon and oxygen. The higher ratio of carbon to oxygen in the body tissue and eggs of *Bankia carinata* indicates a higher lipid content (Gorokhova and Hansson 2000), and bivalve eggs are characteristically lipid-rich (Honkoop et al. 1999). In *B. carinata,* this represents a yolk reserve (albeit small) to fuel the early development of the larva until planktotrophy can begin, typically within 18 hours (Nair and Saraswathy 1971). The C:N ratios of both species reflect the herbivorous niche of shipworms, matching current models of ecological stoichiometry (Brey et al. 2010). Wood provides almost the entirety of shipworm nutrition (Carpenter and Culliney 1975, Gallager et al. 1981), but is extremely poor in nitrogen (Sjöström 1993, Watkinson et al. 2006), as reflected here in the high carbon-nitrogen ratio. As a result, shipworms can supplement their diet with phytoplankton, but meet the majority of their metabolic nitrogen demands with the use of symbiotic nitrogen-fixing bacteria (Gallager et al. 1981, Lechene et al. 2007).

Energetic content was similar for the body tissue of both species and eggs of *Bankia carinata*, but was noticeably lower in the larvae of *Teredo parksi*. As these larvae are capable of feeding immediately upon release, they do not require large lipid reserves, but instead are known to contain high levels of glycogen (Lane et al. 1952, Mann and Gallager 1985, Beukema 1997), the energetic value of which (~17 J/mg) closely matches that found in *T. parksi* larvae. The energy in these larvae is maternally derived from initial investment in the egg and extraembryonic maternal provisioning in the brood chambers, in the form of glycogen-rich epithelial cells fed to developing young (Calloway 1982, Turner 1984). Though they possessed a lower energy density, the larger size of *T. parksi* veligers translates to significantly higher energy levels per larvae compared with the eggs of *B. carinata*.

Combined with the smaller adult body size, the larvae of *T. parksi* made up a high proportion of total body energy, averaging 30% of the total energy. This is a significantly higher reproductive effort than *B. carinata*, where eggs averaged only 10% of total energy, and demonstrates that the different brooding and spawning life histories of *T. parksi* and *B. carinata* do not embody similar levels of reproductive effort. Reproductive effort exceeding 30% of body energy is commonly observed in marine bivalves (Honkoop et al. 1999, van der Veer et al. 2006, Dame 2011) and indeterminate growth strategies are linked to continually increasing size and reproductive output (Heino and Kaitala 1999, Lord and Shanks 2012). It should be noted that although this study only used a “snapshot” of shipworm reproduction, tropical shipworms exhibit rapid, continuous cycles of reproduction year-round (Calloway and Turner 1983, MacIntosh et al. 2012), making these values a reasonable approximation of reproductive effort over longer periods of time. The effects of age and environmental conditions on shipworm reproductive effort are unknown, and further investigation under controlled conditions would be valuable.

Due to their planktotrophic development and high fecundities, shipworms have both low maternal provisioning and high reproductive effort, devoting large proportions of their metabolism energy to the production of larvae or eggs- adaptations to their patchily distributed habitats and short-lived communities (Giangrande et al. 1994, McMahon 2002, Allen et al. 2008). Larval brooding and free-spawning can both be successful strategies to these conditions, typifying a trade-off in the number and size of larvae. However, although the life histories of larval brooding and free-spawning shipworm species are similar in many of their characteristics (see Chapter 3), this research has shown that they are not equivalent in reproductive effort. Larval brooding shipworms such as *Teredo parksi* invest significantly more energy into their offspring, both in terms of the energy per larva and as a proportion of total metabolism. This reproductive effort, coupled with rapid maturity, similar early fecundities, high fertilization success and a shorter larval period (see Chapter 3) suggests larval brooding shipworms greatly out-compete free-spawners in establishing populations in newly-available habitats, and explains broader patterns of shipworm abundance in tropical waters (MacIntosh et al. 2012).

Chapter 5

Lyrodus turnerae, a new teredinid from eastern Australia and the Coral Sea (Bivalvia: Teredinidae)[2]

5.1 Introduction

Bivalves of the family Teredinidae, or shipworms, are obligate wood-borers, with a high economic impact and worldwide distribution. In a CSIRO survey of Australian wood borers (1970-1972), Turner and Marshall (1972) recorded the occurrence of a new species of *Lyrodus* Gould, 1870 and assigned it the provisional name *Lyrodus* sp. *v*, noting that it was as yet undescribed. Ibrahim (1981) and Rayner (1983), in further work on the distributions of wood borers (in Australia and PNG, respectively), also noted this species but did not describe it further, recording it as *Lyrodus* sp. *v* or *Lyrodus* sp. Apart from its inclusion (under the provisional species designation *Lyrodus* sp. *v*) in literature reviews of teredinid diversity in Australia (Cookson and Scown 1999) and Papua New Guinea (Cragg 2007), no further work has addressed the taxonomy or biology of this species.

In 2008, as part of ongoing research into the ecology and reproduction of tropical Australian shipworms, 835 individuals matching the preliminary description of *Lyrodus* sp. *v* were collected from experimental wood panels at three sites in northern Queensland (AIMS, Magnetic Island and Orpheus Island), along with settlement, growth and reproduction data (MacIntosh, in prep). The addition of new specimens to previous distribution data enables the description of a distinct new species, *Lyrodus turnerae*.

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[2] Chapter 5 is adapted from MacIntosh, H (2012). *Lyrodus turnerae*, a new teredinid from eastern Australia and the Coral Sea. *Molluscan Research* 32(1): 36-42.

5.2 Materials and methods

Animals were collected from wood panels deployed across Australia and PNG, with a focus on northern Queensland. Specimens were removed from the wood, taking care to keep shell valves and pallets intact, and then preserved in 70% ethanol. Photographs were taken with a stereomicroscope (Olympus SZ61) with attached digital camera (Olympus DP25). Line drawings were made with the aid of a stereomicroscope (Leica M125) with a *camera lucida* attachment.

5.2.1 Abbreviations:

AIMS: Australian Institute of Marine Science; AMS: Australian Museum Sydney; CSIRO: Commonwealth Scientific and Industrial Research Organization; JCU: James Cook University, Townsville Queensland; MCZ: Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts USA; MTQ: Museum of Tropical Queensland, Townsville QLD; NSW: New South Wales, Australia; PNG: Papua New Guinea; QLD: Queensland, Australia; QM Queensland Museum, Brisbane QLD; WA: Western Australia.

5.3 Taxonomy

Family TEREDINIDAE Rafinesque, 1815

Genus *Lyrodus* Gould, 1870

Lyrodus Gould, 1870: 33, fig. 360. Type species *Teredo chlorotica* Gould, 1870 (= *Teredo pedicellatus* Quatrefages, 1849), by subsequent designation of Turner, 1966. Type specimens lost (*fide* Johnson, 1964).

5.3.1 Remarks

Because of numerous similarities in shell valve and soft-body anatomy within Teredinidae, the key feature for identifying genera and species is the morphology of the posterior pallets, which are used to seal the entrance of the shipworm's burrow from desiccation or predators (Turner 1966). In *Lyrodus*, these pallets are composed of single, thick calcareous bases which are flat or rounded at the distal ends, capped with large, dark loose-fitting periostracal caps. Internal anatomy is similar to other highly-derived teredinid genera such as *Teredo* (Linnaeus, 1758), with an elongated stomach, large cylindrical caecum and blade or U-shaped gills; siphons are short and separate. Modified gill lamellae form pouches in which larvae are brooded to the straight-hinge or pediveliger stage, depending on the species (Calloway and Turner 1988). Turner (1966) corrected many synonymies in her comprehensive review of the Teredinidae, and produced a key to the family (Turner 1971b), identifying six species- *L. affinis* (Deshayes, 1893)*, L. bipartita* (Jeffreys, 1860)*, L. massa* (Lamy, 1923)*, L medilobata* (Edmondson, 1942)*, L. pedicellatus* (Quatrefages, 1849) and *L. takanoshimensis* (Roch, 1929). Later research demonstrated the presence of cryptic species pairs in *Lyrodus*, with *L. floridanus* (Bartsch, 1922) and *L. singaporeana* (Roch, 1935) morphologically indistinguishable from *L. pedicellatus* and *L. massa,* respectively, differing by the stage to which larvae are brooded (Turner and Calloway 1987).

Lyrodus turnerae n. sp.

Figures 5.1 – 5.4.

Lyrodus sp. *v,* Turner and Marshall 1972: 2

Lyrodus sp. Ibrahim 1981: 597

Lyrodus n.sp. Rayner 1983: 67

5.3.2 Type material

Holotype. (Figure 5.1; MTQ MO40687) with brooded larvae. Length 25.68 mm, Width 2.17 mm. From *Pinus radiata* panel. Deployed 5 March 2008, collected 4 June 2008, White Lady Bay, Magnetic Island QLD, 19°06'29.85"S, 146°51'42.73"E. Specimen fixed in 5% formalin in seawater, stored in 75% ethanol.

Paratypes. MTQ MO40688-MO40694 (7 specimens), AMS C.471002.001-C.471005.001 (4 specimens), MCZ 370214-370217 (4 specimens), QM MO80195-MO80198 (4 specimens). Collected 5 March, 4 June, 2 October 2008, White Lady Bay, Magnetic Island QLD, 19°06’29.85” S, 146°51’42.73” E. Specimens fixed in 5% formalin in seawater, stored in 75% ethanol.

5.3.3 Material examined

Type material: (see above).

Other material: Pioneer Bay, Orpheus Island QLD, 18°36’14.70” S, 146°29’14.48” E, 26 February 2008 (4), 22 May 2008 (6), 11 August 2008 (11), 28 September 2008 (27). Townsville, QLD: Townsville Harbour, 26 March 1971, (AMS, 1); Platypus channel, 26 March 1971, (AMS, 1). Magnetic Island, QLD: Middle Reef, March 1971, (AMS, 1); Nelly Bay, October 1971, (AMS, 1), December 1971 (AMS, 1); White Lady Bay, 19°06’29.85” S, 146°51’42.73” E, 2 October 2007 (colln. H. MacIntosh, JCU, 20), 4 December 2007 (colln. H. MacIntosh, JCU, 45), 5 March 2008 (colln. H. MacIntosh, JCU, 108), 4 June 2008 (colln. H. MacIntosh, JCU, 169), 1 August 2008 (colln. H. MacIntosh, JCU, 92), 2 October 2008 (colln. H. MacIntosh, JCU, 251). AIMS, Cape Cleveland QLD, 19°16’37.02” S, 147°03’31.46” E, 19 November 2007 (colln. H. MacIntosh, JCU, 4), 5 March 2008 (colln. H. MacIntosh, JCU, 15), 26 May 2008 (colln. H. MacIntosh, JCU, 37), 15 August 2008 (colln. H. MacIntosh, JCU, 14), 3 October 2008 (colln. H. MacIntosh, JCU, 12). Brisbane, QLD: Lower Brisbane River, June 1971, (AMS C.397929, 1); Redland Bay, 28 September 1959 (AMS, 1). Sydney Harbour, NSW: Roseville, 21 September 1971, (AMS C.326025, 1); Goat Island, 13 May 1971, (AMS C.326026, 1). Rosedale NSW, 21 November 1970, (AMS C.326024, 1). Carnarvon WA, 5 November 1970 (AMS, 1).

5.3.4 Etymology

This species is named for the late Dr. Ruth Dixon Turner (1914-2000), in recognition of her long and invaluable career on the biology and taxonomy of marine wood borers.

5.3.5 Diagnosis

Pallets with dark periostracal cap infolded into calcareous portion, strengthened, forming clear ‘V’ shape descending into calcareous portion. Straight-hinge larvae brooded in gills.

Figure 5.1: Holotype (MTQ, MO40687) and larvae of *Lyrodus turnerae*. (A) View of whole adult animal showing typical elongated teredinid body. Anterior with shell valves at left, posterior with pallets at right; (B) posterior end, with pallets. Arrow marks strengthened interior portion of periostracum descending into thin calcareous cup; (C) scanning electron micrograph of straight-hinge stage larvae brooded in gill chambers (seen as purple colouration in A, above). Larvae removed from damaged adult individual collected alongside holotype. A, B scale bars = 1 mm, C scale bar = 50 μm.

5.3.6 Description

Shell valves small, globose, anterior face with numerous denticulate ridges, typical of Teredinidae (Figure 5.2). Pallets compact, calcareous portion not descending far onto stalk (Figure 5.3). Calcareous portion formed into cup, with walls thin at distal edges. Outer margin of calcareous portion concave, U- to V-shaped, inner margin concave, U-shaped. Margin of inner calcareous portion sometimes extending distally as a very short, thin blade. Periostracum dark, golden to reddish-brown, with outer and inner distal margins concave, U- to V-shaped, moderately projecting distally and forming small lateral horns (Figures 5.1B and 5.3). Exterior surface of periostracum may have superficial wrinkles or striations. Interior portion of periostracum strengthened and darkly coloured, reddish brown to black, sharply contrasting with outer periostracum. Strengthened portions of periostracum descending sharply into calcareous cup. Effect is strong ‘V’ inside periostracal cap with apex inside calcareous portion and arms extending to ends of lateral horns. Strengthened interior periostracum often visible through thin walls of calcareous cup. Siphons small, separate, pale red spotting distally may be present. Gill filaments modified into brood pouches; larvae are brooded until straight-hinge stage, 75 µm in length (Figure 5.1C).

5.4 Remarks

The shell valves of *Lyrodus turnerae* are typical of the family Teredinidae: small in size, open anteriorly to permit forward projection of the foot, and possessing numerous rows of denticulated ridges on the anterior face to facilitate tunneling into wood. However, as the size and morphology of teredinid shells are highly variable between individuals, based on numerous factors such as overcrowding (Clapp 1925) and the density of the wood substrate (Turner 1966), they cannot serve as reliable characteristics for the identification of species.

Brooding of larvae occurs only in the shipworm genera *Lyrodus*, *Teredo*, and *Zachsia* (Calloway and Turner 1988). In these genera, fertilized ova are released from the gonads and held amongst the interlamellar spaces of the gills until their release as straight-hinge or pediveliger stage larvae (Calloway and Turner 1988). The stage to which larvae are held before release can be used to differentiate between species pairs such as *Lyrodus pedicellatus* and *L. floridanus* (see key in appendix below).

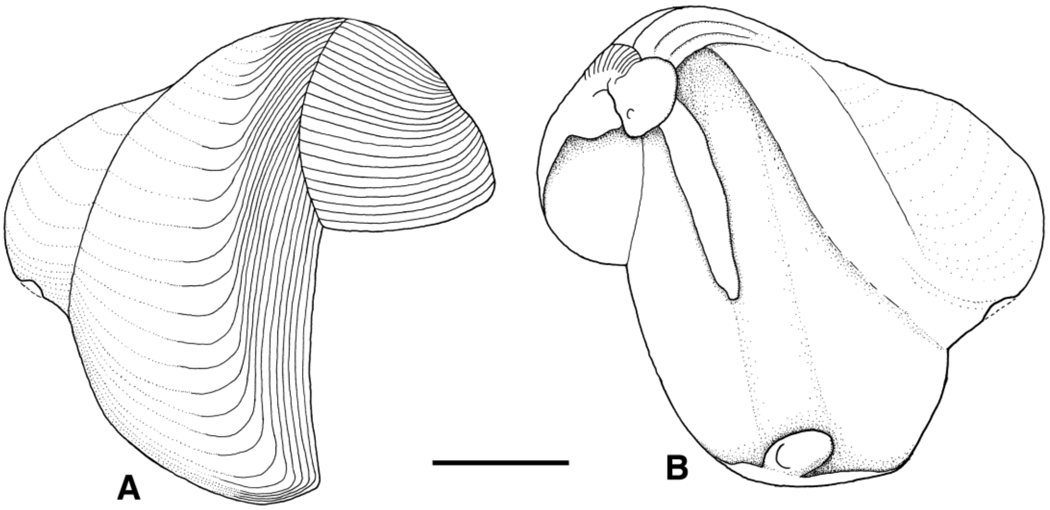


Figure 5.2: Shell valves of paratype 4 (MTQ, MO40691) of *Lyrodus turnerae*. (A) Outer face, anterior to right; (B) inner face, anterior to left. Scale bar = 1 mm.

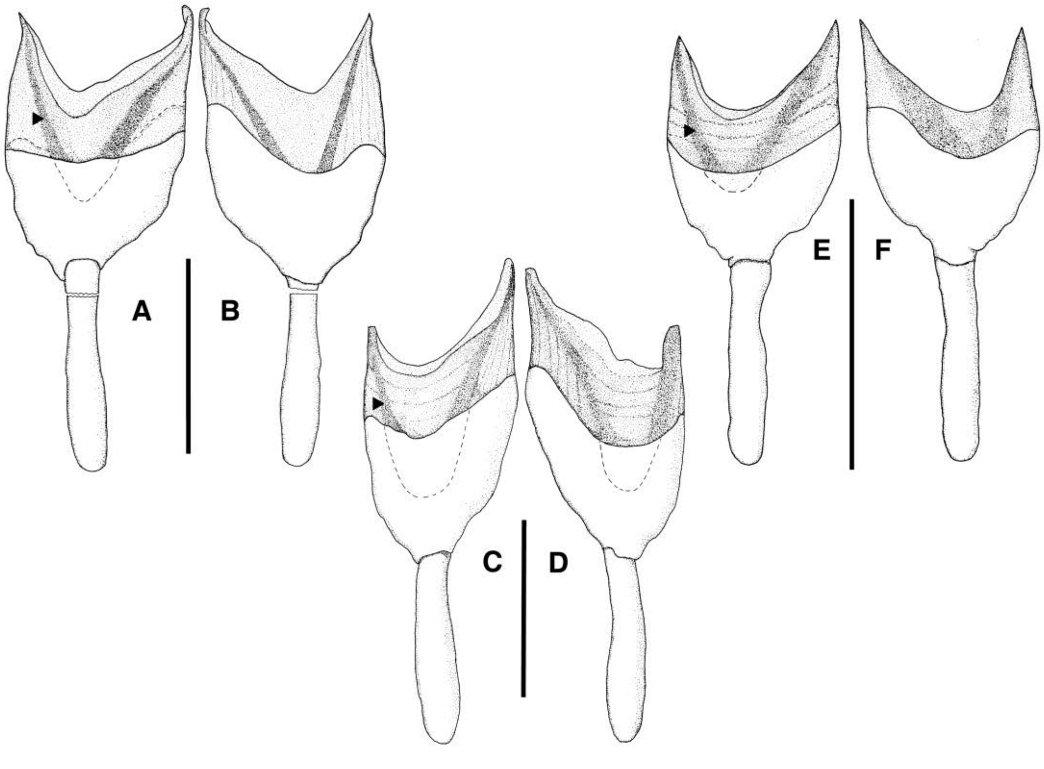


Figure 5.3: Pallets of *Lyrodus turnerae*. (A) Paratype 1 (MTQ MO40688), outer face; (B) paratype 1, inner face; (C) paratype 2 (MTQ MO40689), outer face; (D) paratype 2, inner face; (E) paratype 3 (MTQ MO40690), outer face; (F) paratype 3, inner face. N.B. ▶: strengthened interior of periostracum descending into calcareous cup. Scale bars = 1 mm.

With similarities in shell and soft body morphology, including the brooding of larvae, the genus *Lyrodus* is differentiated from *Teredo* on the basis of pallet morphology, with the latter possessing a thin periostracal lining closely fitting over calcareous projections or elaborations, and not extending distally as a cap.

Lyrodus turnerae can be differentiated from other species in this genus by the compact, hollowed, cup-shaped calcareous portion of its pallets, with a dark periostracal cap contiguous with the calcareous portion, projecting distally and infolding sharply into the calcareous cup. *Lyrodus massa* (Lamy, 1923) possesses similar features, but is differentiated by having a sharp pyramidal shaped calcareous cup instead of the compact, rounded form seen in *L. turnerae*. The dense periostracal portion of *L. massa* forms a separate cup inserted into the calcareous portion and not contiguous with the calcareous portion, whereas the periostracum in *L. turnerae* is contiguous with the margins of the calcareous portion, and extends fully distally while the centre is infolded into the base of the calcareous cup. *Lyrodus singaporeana* (Roch, 1935) exists as cryptic species pair with *L. massa* (Calloway and Turner 1988) with otherwise identical pallet morphology, but is characterized by brooding larvae to the late pediveliger stage. *L. turnerae*, while also brooding larvae, only retains them to the earlier straight-hinge stage (Figure 5.1C).

Other genera of Teredinidae with cup-shaped pallets include *Teredothyra* (Bartsch, 1921), but *Teredothyra* have little or no periostracum on the pallets, and reproduce by free-spawning their gametes (Calloway and Turner 1988), while the presence of a large periostracal cap on the pallets and brooded straight-hinge larvae in the gills establish this species as belonging to the genus *Lyrodus.*

In light of these findings, provided in the appendix is an updated key to the genus *Lyrodus*, incorporating species pairs (Turner and Calloway 1987, Calloway and Turner 1988), and the newly described *Lyrodus turnerae*.

5.5 Discussion

Research into the ecology of tropical teredinids in northern Queensland, Australia (Figure 5.4, ○:(MacIntosh et al. 2012) yielded a large number of specimens of *Lyrodus turnerae* for examination. These new data, combined with previous collection records, offer insight into the distribution of *L. turnerae* in Australia and PNG.

The first recorded collections of *L. turnerae* were made by Turner and Marshall (1972), in a three-year, Australia-wide survey of teredinid diversity (Figure 5.4, ●). In further research stemming from Turner and Marshall's report (1972), Ibrahim (1981) surveyed Australian harbours (Figure 5.4, □), while Rayner (1983) added numerous records from survey sites in PNG and the Bismark Archipelago (Figure 5.4, ▲).

Figure 5.4: Recorded collections of *Lyrodus turnerae* in Australia and Papua New Guinea. N.B. ●: Turner and Marshall 1972; □: Ibrahim 1981; ▲: Rayner 1983; ○: MacIntosh herein.

Specimens of *L. turnerae* were found in highest abundance in PNG and tropical Australian waters (Turner and Marshall 1972), with settlement and reproduction occurring year-round. A small number of *L. turnerae* specimens were also collected from the more temperate regions of southern Queensland and New South Wales. However, the collection periods of these southern samples all coincided with warmer summer months, so it is possible that *L. turnerae* is restricted to warm waters, and that southern populations are transitory. Further to this, no brooded larvae indicating reproduction were observed in examined specimens collected from southern Queensland and New South Wales.

The details of the distribution of this species across northern and western Australia remains uncertain, with only small collections recorded at Port Hedland and Carnarvon, Western Australia (Turner and Marshall 1972). More recent surveys of marine borers in Western Australia did not record any species resembling *L. turnerae* (Brearly et al. 2003). Data on the growth, reproduction, settlement and seasonality of *L. turnerae* will be detailed, alongside other northern Queensland shipworm species, in forthcoming publications (MacIntosh et al 2012).

After extensive collections of Teredinidae in the early 20th century, Turner (1966) published a comprehensive review of the family, synonymizing the majority of species described to date. Due to the high natural variation in shell and body morphology, the morphology of the pallets was established as being the most reliable factor in distinguishing between individual species. However, there still remains confusion in the taxonomy of the Teredinidae, with the discovery of cryptic species pairs with different modes of brooding larvae (Turner and Calloway 1987). A combined review of molecular, physical and geographical data would resolve many unknowns about this family but is beyond the scope of this present paper.

5.6 Appendix – Key to *Lyrodus*.

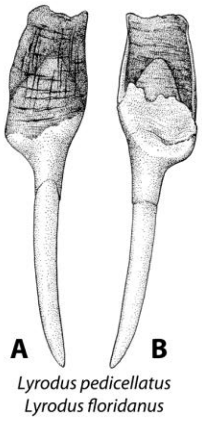
Key to the genus *Lyrodus*, modified from Turner (1971).
All figures except *L. turnerae* are from Turner (1966). (A) Outer face of pallet; (B) inner face of pallet.

Pallet with single, unsegmented calcareous base. Distal half of pallet composed of a large brown to nearly black loose-fitting periostracal cap which overlaps the calcareous portion, or with a dark periostracal cup inserted in a basal calcareous cup. Larvae brooded in water tubes of gills to straight hinge or pediveliger stages..***Lyrodus*** Gould

1a Calcareous portion solid; rounded or conical distally. Periostracal cap enveloping upper outer portion of calcareous base; periostracum colour variable, light golden brown to nearly black...**2**
1b Calcareous portion hollow distally, formed into cup. Periostracum inserted or infolded into calcareous cup; periostracum colour varying from light golden brown to dark red-brown or nearly black..**5**

2a Calcareous portion of pallet conical distally...**3**
2b Calcareous portion rounded to nearly flat distally..**4**

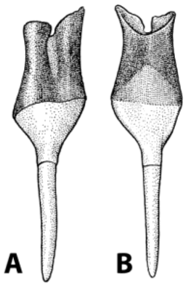
3a Periostracal cap more or less straight sided; distal margin slightly concave to U-shaped, occasionally extending as lateral horns; distal end often eroded so that conical calcareous base protrudes. Colour of cap varying from light brown to nearly black. Larvae brooded to straight hinge stage............................***L. floridanus*** (Bartsch)
Larvae brooded to pediveliger stage................................***L. pedicellatus*** (Quatrefages)



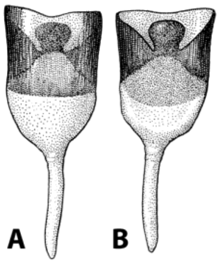
Lyrodus pedicellatus
Lyrodus floridanus

3b Periostracal cap similar to that above, but with deep longitudinal furrow on outer face. Larvae brooded to pediveliger stage.....................................***L. bipartita*** (Jeffreys)

3c Periostracal cap similar to above, distal margin of outer face nearly straight, that of inner face deeply U-shaped with median lobate process. Larvae brooded to pediveliger stage..***L. medilobata*** (Edmondson)

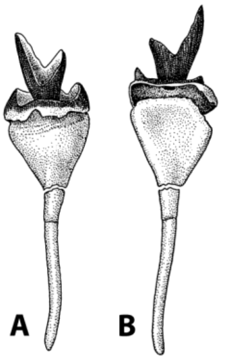


Lyrodus bipartita



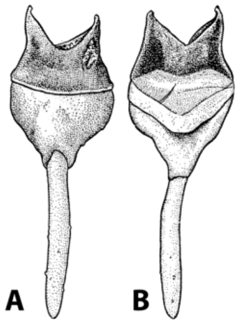
Lyrodus medilobata

4a Calcareous base rounded distally; periostracal cap with long inner cup-like projection set in a shallower outer one, distal margin deeply v-shaped, the outer face more so that the inner, cap a dark red-brown to black....................***L. affinis*** (Deshayes)



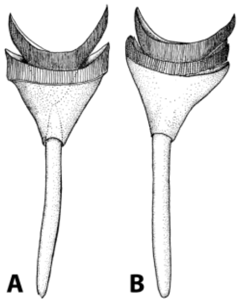
Lyrodus affinis

4b Periostracal cap golden-brown with lateral thickening extending to distal end and projecting slightly; distal margin of inner face U-shaped, of outer face V-shaped. Larvae brooded to straight hinge stage..***L. takanoshimensis*** (Roch)



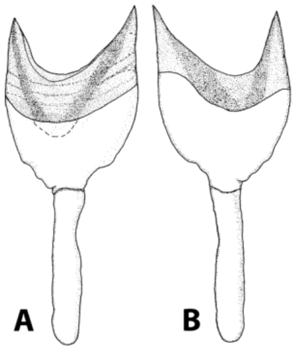
Lyrodus takanoshimensis

5a Calcareous base triangular. Periostracum as separate conical cup, inserted into calcareous base; Periostracum colour varying from light golden brown to dark red-brown or nearly black. Larvae brooded to straight hinge stage.............***L. massa*** (Lamy)
Larvae brooded to pediveliger stage...***L. singaporeana*** (Roch)



Lyrodus massa
Lyrodus singaporeana

5b Calcareous base rounded, compact. Periostracum as cap, contiguous with distal end of calcareous base, with strengthened interior portions, forming clear "V" shape descending into calcareous base. Larvae brooded to straight hinge stage...***L. turnerae*** MacIntosh, n. sp.



Lyrodus turnerae

Chapter 6

Synthesis and Discussion

Shipworms have a highly specialized niche, utilizing wood as both a substrate and food source. These wood habitats are sparse, ephemeral and patchily distributed in the marine environment, and evolutionary adaptation to these conditions is reflected in the unique biology of shipworms. Shipworms are fast growing and highly fecund, enabling them to quickly establish reproductive populations and proliferate in new habitats before the inevitable community collapse. The specificity of shipworms' niche, coupled with high diversity and abundance, particularly in tropical coastal waters, results in widespread competition and coexistence at both local and regional scales. With each wood habitat forming a distinct community, shipworms are an excellent model with which to evaluate life history strategies of competing species and, in turn, how they shape metacommunity composition.

Notably, there is a wealth of literature on the seasonality, abundance and diversity of shipworm recruitment worldwide, largely due to the economic ramifications of their recruitment (Nair and Saraswathy 1971, Tsunoda 1979, McKoy 1981, Tuente et al. 2002, Paalvast and van der Velde 2011). These provide excellent accounts of regional and local shipworm abundance, but unfortunately the methodology of many studies precludes their use in understanding broader-scale shipworm ecology. Techniques such as counting burrow entrances or radiographing the wood, while non-destructive and permitting time-series sampling, do not provide accurate counts or identification of the individuals within (Junqueira et al. 1991). Many studies also rely on haphazard collection of drifting or sunken wood (Rimmer et al. 1983, Gara and Greulich 1995, Brearly et al. 2003, Filho et al. 2008), which can provide a more accurate picture of local diversity (Leonel et al. 2006), but a lack of experimental rigor limits the ability to make comparisons between samples. Elevating shipworm research from the observational to the experimental requires a more in-depth understanding of the biology of shipworms, which is lacking for many species (Turner 1984). Therefore, new research into shipworm demographics and life histories, conducted with an ecological rather than economic mindset, will provide the basis for further exploration of their metacommunity ecology and population structures.

The aims of this study were to provide an in-depth investigation of shipworm demographics, diversity and life history, with a focus on recruitment, growth and reproduction, taking advantage of the abundant shipworm fauna in tropical northern Australia (Cookson and Scown 1999). By establishing this baseline, my goal was to provide insight into shipworm biology on both small and large scales, linking individual processes with community dynamics and regional diversity.

The major findings of this work are:

1. Shipworms form highly competitive metacommunities, and species possess differing peak recruitment seasons and reproductive modes (Chapter 2). The abundance, seasonality and diversity of shipworms were recorded over a year, incorporating 62,075 individuals from 6 genera and 9 species. Most importantly, reproductive mode is a key contributor to recruitment success, with larval brooders contributing to over 95% of total recruitment.

2. Shipworms display rapid growth, precocious maturation and high fecundities as adaptations to their specialized niche (Chapter 3). The larval brooding *Teredo parksi* and free-spawning *Bankia carinata* both reach sexual maturity by 2-4 mm in length, but *B. carinata* is significantly larger and more fecund, growing to lengths of over 100 mm in 2 months, and with clutch sizes of 3×10^6 eggs.

3. The reproductive modes of larval brooding and free-spawning shipworms are not simply a trade-off in the number and size of offspring, with *Teredo parksi* possessing significantly higher maternal provisioning and reproductive effort than *Bankia carinata*. The larvae of *T. parksi* contain more energy than the eggs of *B. carinata*, with 3.13×10^{-4} J per larva, and comprise over 30% of both total body mass and energy.

4. An updated key to the genus *Lyrodus* is presented, incorporating new taxonomic information. A new species of shipworm, *Lyrodus turnerae* is described and named, based on new and existing material.

Australia possesses a diverse and abundant shipworm fauna (Turner 1971a, Cookson and Scown 1999), making it an ideal location for investigating shipworm competition and coexistence. Tropical northern Australia has been particularly well represented in biodiversity surveys (Smith 1963, Turner and Marshall 1972, Ibrahim 1981) but lacks a complete picture of year-round shipworm recruitment and community composition. Therefore, this thesis presents the largest and most in-depth investigation of abundance, seasonality and diversity of tropical shipworms, encompassing 62,075 individuals from 6 genera and 19 species. The use of controlled collection periods enabled the abundance of competing shipworm species to be quantified and compared across sites and seasons, identifying patterns of recruitment success and the effect of habitat age in community composition and mortality.

Results show that shipworms recruit year-round and rapidly establish diverse, highly competitive communities, with up to 1200 individuals in a panel (~3 per cm^3) within 2 months. This rapid recruitment, coupled with shipworms' boring, results in a short life span of these communities, with widespread mortality (40-90%) after only 4 months. Importantly, reproductive mode is a key contributor to recruitment success, with short-term brooding species being more successful in colonizing patchy, ephemeral wood habitats. These findings provide the most detailed picture of shipworm recruitment collected to date, and establish the time frame in which shipworm communities develop. These results are corroborated by previous research, with year-round recruitment recorded in tropical environments (Smith 1963, Ibrahim 1981) and short-term brooding species amongst the most abundant in coastal seas worldwide (Turner 1966).

Notably, early colonization and community formation of shipworms remain poorly understood outside of laboratory experiments, and future research should further examine recruitment to newly available habitat. In addition, the scarcity of free-spawning species may be explained by depth-related habitat partitioning, and recruitment to wood habitats at increasing depths and distances from shore warrants further investigation. However, any such studies must also take into consideration the underlying biology and life histories of shipworm species, and how these shape observed patterns of community composition, distribution and abundance.

As a family, shipworms share a remarkably similar anatomy, and their long, thin bodies, reduced abrading shell valves, wood-storing caeca and posterior calcareous pallets all facilitate burrowing within wooden substrates (Turner 1966). There is a strong background of the general biology of shipworms (Turner 1966, Nair and Saraswathy 1971), but more in-depth biology and life histories have only been recorded for a few species, such as *Teredo navalis*, *Lyrodus pedicellatus* or *Bankia setacea* (Nair and Saraswathy 1971), which are commonly-encountered temperate species with a high economic impact in Europe and North America. Comparatively little is known about the remainder of shipworm species, particularly those in tropical seas (Turner 1984).

This study is the first to characterize the life histories of two abundant tropical shipworm species, *Teredo parksi* and *Bankia carinata*, quantifying their growth/size distribution, reproductive development and fecundity. Both species possess rapid growth rates, precocious maturity and high fecundities typical of opportunistic species adapted to specialized ecological niches (Giangrande et al. 1994, Benton and Grant 1999, McMahon 2002). As a result, these species are amongst the most abundant in tropical Australia (MacIntosh et al. 2012). The free-spawning *B. carinata* has a significantly larger body size and higher fecundity than the larval brooding *T. parksi*, with individuals growing to over 100 mm in length by 2 months post metamorphosis, and producing over $3x10^6$ eggs per clutch. These results are similar to trends in other shipworm species, with free-spawning species often growing up to a meter in length (Nair and Saraswathy 1971, Filho et al. 2008), but also fit widely observed paradigms of body size and reproductive mode in other taxa, wherein brooding is typically associated with smaller body size and lower fecundity (Blueweiss et al. 1978, Strathmann and Strathmann 1982, Ripley and Caswell 2008).

Shipworms' wood-boring niche necessitates destructive sampling to accurately identify and examine individuals, and the methodology of this study produced a "snap shot" view of shipworm communities and the individuals within. Future research into shipworm life histories should endeavor to examine shipworm life histories in situ to record growth rates and fecundity over time, with techniques such as X-ray micro-computed tomography capable of resolving fine details on microscopic scales (Carl et al. 2012). As shipworms bore through wood, their growth is synonymous with feeding and is it likely that constraints on shipworms' size also limit their energy intake. However, it is unknown to what extent factors such as density (overcrowding) or wood hardness or influence the growth or nutrition of shipworms, and if these in turn have negative effects on fitness.

The brooding and spawning reproductive modes of shipworms significantly influence characteristics such as body size, fecundity, and recruitment success, and reflect different energetic investment. However, while previous work has investigated the physiology and nutrition of shipworms and their offspring (Lane et al. 1952, Prusch et al. 1981, Mann and Gallager 1985), there has been no attempt to compare energetic investment between brooding and spawning species. This study presents the first detailed measurements of maternal provisioning and reproductive effort in shipworms, using novel analytical techniques. Contrary to expectations, brooding and spawning in shipworms are not a simple trade-off in the number and size of offspring, with brooders devoting a significantly higher proportion of energy resources to reproduction. Instead, brooding and spawning in shipworms represent a competition-colonization trade-off, with brooding species recruiting in higher numbers across shorter distances, but free-spawning species dispersing across greater distances in search of habitat (Scheltema 1971). Interestingly, this study found little variation in larval/egg size or maternal provisioning within species or individuals, which is unusual compared with many other invertebrate fauna (Phillips 2007, Powell et al. 2011), especially those with high variability in habitat quality (Marshall et al. 2008). Further studies should quantify lifetime reproductive effort for both brooding and spawning shipworm species, and test for the effects of habitat quality on maternal provisioning, as variation in the size or energy of offspring can have significant follow-on effects on fitness (Marshall and Keough 2008b). Incorporating data on reproductive output, larval energetics and dispersal is an excellent way to compare competing species and will allow for modeling of shipworm ecology at a deeper theoretical level, such as the “meta” population and community scales.

Metacommunity theory is a valuable framework with which to examine the broader-scale ecology of competing species (Leibold et al. 2004, Logue et al. 2011). This study is the first to examine shipworm ecology in a metacommunity context, and explain observed patterns of competition and coexistence between shipworm species. With their highly specific niche, shipworms establish scattered communities of varying size wherever suitable habitat can be found. These habitats, linked by larval dispersal, form a true metacommunity, in which shipworm species vary in their ability to colonize and compete within new habitats. Due to the high temporal and spatial heterogeneity of habitats, there is no single Evolutionary Stable Strategy (Cohen and Levin 1991) and no one species can dominate all habitats in the metacommunity, and this fosters the high diversity and coexistence of species in regions such as tropical Australia.

Intellectualizing shipworm ecology within a metacommunity framework is highly appropriate given their discrete habitat patches linked by dispersal and demonstrates that shipworms are a valuable group for modeling and testing life history competition and community ecology in other taxa. Larval dispersal is key to the success of shipworm species, and further research should experimentally test the ability of different shipworm species to colonize new habitats. The connectivity of shipworm populations is also largely unexplored, though many species have recorded distributions across oceans basins or even worldwide (Turner 1966, Nair and Saraswathy 1971, Scheltema 1971). Modern molecular techniques have great potential for investigating the systematics and speciation within the Teredinidae (Santos et al. 2005, Borges et al. 2012), and a critical question that should be answered is what constitutes a “natural” distribution for a given shipworm species, and what role humans have played in introducing shipworms to new regions via wooden vessels.

Any picture of the ecology of shipworms is incomplete without an understanding of their larval biology, as the critical link between abundance, diversity, and reproduction. Larval dispersal is the most crucial step in the life history of shipworms, as the sole means of dispersal to new habitats. While there is a wealth of knowledge on the culture and biology of shipworm larvae (Board and Feaver 1973, Culliney 1973, 1975, Mann and Gallager 1985), research on larval recruitment has focused more on the wood substrates than the larvae themselves, focusing on testing the resistance of different woods to shipworm attack (Cookson 1996). Exploring the larval biology of shipworm was outside the scope of this thesis, and there are numerous unanswered questions that beg research. The size and age of a piece of wood may play significant roles in the fitness and life span of a newly recruiting shipworm, but it is unknown to what extent larvae can assess habitat quality, or modify their recruitment preferences accordingly. Though most shipworm larvae are planktotrophic and can survive for extended periods in the water column, do larvae delay settlement in the presence of poor habitat, weighing the chance of locating more suitable habitat with the likelihood of mortality? As mentioned, certain woods are resistant to shipworms but it remains unclear whether shipworms preferentially avoid these substrates, or if larvae readily settle to all woods, but fail to survive in some due to hardness or the presence of toxic metabolites. It has been demonstrated that wood chemical cues stimulate an immediate settlement response in shipworm larvae (Culliney 1973, Pachu et al. 2012), including from cellulosic material such as ropes, but surprisingly the cues responsible have not been elucidated. Research into the biology and ecology of shipworm larvae would provide critical insight to the mechanics behind their dispersal and recruitment completing our understanding of how shipworm communities form. Furthermore, shipworms are an ideal model taxa for larval dispersal and recruitment in organisms with highly specific, patchy habitats.

Overall, this thesis has provided a novel, in-depth investigation of the demographics, diversity and life history of tropical Australian shipworms. By quantifying the life histories of competing shipworm species as well recording larger scale patterns of recruitment and abundance, this work has established how the biology of shipworms on the individual and species level shape the broader processes of community composition and regional diversity.

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