



# Migrating zooids allow the dispersal of *Fredericella sultana* (Bryozoa) to escape from unfavourable conditions and further spreading of *Tetracapsuloides bryosalmonae*



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## ABSTRACT

*Fredericella sultana* (Bryozoa: Phylactolaemata) is a primary host in the two-host life cycle of the myxozoan parasite *Tetracapsuloides bryosalmonae*, the etiological agent of Proliferative Kidney Disease (PKD) in salmonids. Overtly infected *F. sultana* colonies were collected from River Kamp (Lower Austria), following the first PKD outbreak affecting autochthonous brown trout (*Salmo trutta*) in Austria. Zooids cultured under unfavourable conditions, e.g. hypertrophication or sudden temperature changes, disconnected their funiculus from the bottom of the body wall, contracted their retractor muscle and packed all organs into a pear-shaped capsule. Migrating zooids dislocated from larger dying branches by separating from the degenerating zooecial tube. After attaching to a new substrate, a new colony could grow rapidly, similar to newly hatched zooids from statoblasts. This is the first observation of an adaptive dispersal mechanism undertaken by adult viable bryozoan zooids to escape from colony deterioration upon adverse summer-like conditions. The evidence of migrating zooids for *F. sultana* colonization of new habitats increases their intrinsic capacity of spreading infective *T. bryosalmonae* malacospores.

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## 1. Introduction

Freshwater bryozoans are benthic invertebrates living as sessile, filter-feeding, branching colonies composed of individual zooids (Massard and Geimer, 2008; Ryland, 2005; Wood, 2001). They occur in nearly all types of lentic or lotic environments, dominating littoral communities and significantly contributing to freshwater fouling, water pipes clogging and causing operating problems in industrial water cooling systems. Bryozoans also play a relevant role in nutrient cycles, represent a food source for many aquatic species and provide microhabitats and refuge for smaller invertebrates. Known as “moss animals”, they interact with sympatric fish populations creating a dynamic ecosystem. Freshwater bryozoans are particularly vulnerable to environmental changes, thus affecting multiple levels of the biological organization (Hartikainen et al., 2009; Ryland, 2005).

*Fredericella sultana* [Blumenbach, 1779] (Phylum Bryozoa: Class Phylactolaemata) is one of the few freshwater bryozoan species with a truly cosmopolitan distribution (Massard and Geimer,

2008) and is a primary host for the endoparasite *Tetracapsuloides bryosalmonae* [Canning et al., 2002] (Phylum Myxozoa: Class Malacosporea) (Okamura and Wood, 2002). *T. bryosalmonae* maintains a two-host life cycle between invertebrate bryozoans and salmonid fish (Feist et al., 2001; Longshaw et al., 2002; Morris and Adams, 2006). Infected fredericellids release mature *T. bryosalmonae* malacospores during overt infections, when large spore sacs are freely floating within their coelomic cavity (Canning et al., 2000; Morris and Adams, 2007). The alternation between covert and overt *T. bryosalmonae* infections allows the persistence throughout the year in *F. sultana* populations (Hill and Okamura, 2007; Morris and Adams, 2006). Seasonal infestations can lead to Proliferative Kidney Disease (PKD) in susceptible fish species, elevating their mortality rate. PKD prevalence is expected to expand its geographic range due to the global climate change. Higher average summer temperatures promote overt infections by accelerating *T. bryosalmonae* sporulation in susceptible fredericellids (Tops et al., 2009). Exacerbated PKD pathology, characterised by a marked dysregulation of the host immune system response (Gorgoglione et al., 2013), impaired aerobic performance and thermal tolerance (Bruneaux et al., 2016), is also predicted to further decrease host survival. It is currently impossible to decrease sporulation rate to prevent PKD outbreaks, or to control

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PKD pathogenesis. PKD represents a health issue for farmed and wild salmonid species in Europe and North America (Henderson and Okamura, 2004; Skovgaard and Buchmann, 2012; Sterud et al., 2007); an efficient vaccination strategy is still not available.

Bryozoan dispersal strategies include passive, upon colony fragmentation and statoblast dispersal, or active mechanisms in the free-swimming larval stage. Both sexual and asexual reproductive strategies are known for fredericellid bryozoans (Rogick, 1945; Wood, 2001). Bryozoans can successfully germinate following unfavourable environmental conditions by production of dormant stages, the statoblasts (piptoblast type for *F. sultana*) (Bushnell and Rao, 1974; Hengherr and Schill, 2011), thus surviving prohibitive winter conditions even when infected with *T. bryosalmonae* (Abd-Elfattah et al., 2014). Displacement of viable zooids allows passive dispersal and colonization of new water bodies. Colony fragmentation is a well-known phenomenon leading to new colony formation and differentiation (astogeny) (Ryland, 2005). Fragmented branches are dispersed in water currents, movement of infected hosts, or can be vector-mediated by attaching to plants or birds (Bilton et al., 2001; Hallett et al., 2015). Environmental changes, such as cooling water currents for the free-living marine Gymnolaemata bryozoan *Cupuladria exfragminis*, can induce colony auto-fragmentation followed by regenerative growth along the fractured margins (O'Dea, 2006).

This study describes the discovery of a novel adaptive dispersal mechanism for Phylactolaemata bryozoans by migrating zooids. The encapsulation and tight packing of polypide organs observed in *F. sultana* is not previously reported for any other Bryozoa species. Importantly, this adaptive dispersal mechanism occurs even in *T. bryosalmonae*-parasitized colonies, which suggests a role in the spreading of PKD.

## 2. Materials and methods

### 2.1. Retrieval of *T. bryosalmonae*-parasitized *F. sultana*

*F. sultana* colonies overtly infected with *T. bryosalmonae* were collected from a restocking farming facility in Rosenberg (Lower Austria) where a PKD outbreak occurred during the summer of 2014. This was the first recorded PKD outbreak in Austria, with the full two-host life cycle determined to be in place (Gorgoglione et al., 2016). *T. bryosalmonae* was observed in histological sections using light microscopy and detected by PCR using primers *T.b.18S\_F* and *R* (Gorgoglione et al., 2013) from kidneys and spleen of infected autochthonous brown trout (*Salmo trutta*) (isolate "AT14Kamp" in GenBank: acc number [KT943757](#)). Several locations upstream of the farming facility were inspected along the River Kamp for the presence of viable bryozoans and *F. sultana* specimens were collected from side-creeks. Bryozoans were

scraped from submerged substrates, including dead wood, cobblestones or directly from underground metal pipeline (Gorgoglione et al., 2016).

### 2.2. Keeping *F. sultana* colonies under lab-controlled conditions

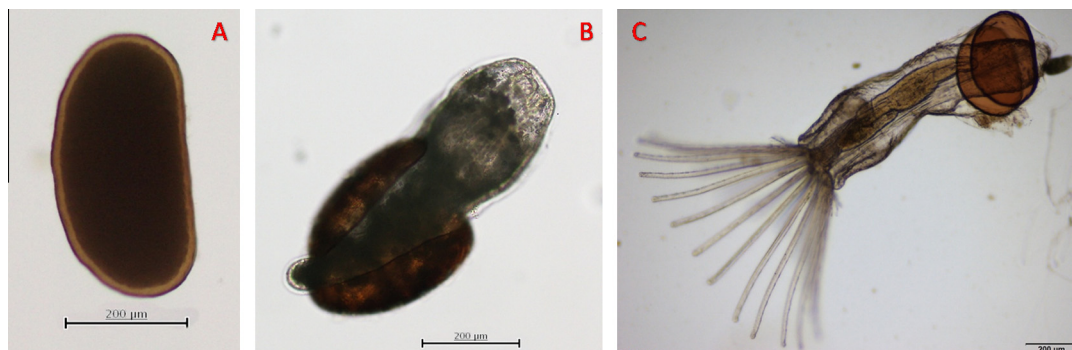
*F. sultana* colonies were held under controlled laboratory conditions. Actively feeding zooids were attached to plastic 10 cm Petri dishes (Corning) and maintained in continuous cultures (Wood, 2005). Colonies were fed a mixture of algae, including *Cryptomonas ovata*, *Synechococcus rubescens* and *S. leopoliensis* as previously described (Grabner and El-Matbouli, 2008; McGurk, 2005). *F. sultana* were maintained at 16–18 °C in 10 L water in plastic buckets with continuous aeration. Statoblasts retrieved from wild colonies were stored at 1 °C until they were incubated to induce hatching to obtain new colonies (Fig. 1) (Kumar et al., 2013).

Detached and fragmented *F. sultana* branches were recovered, including those with overt *T. bryosalmonae* infection. To allow attachment onto a new plate, colonies were incubated on a bench at 19–21 °C with ~10 ml of dechlorinated water and fed daily by adding a few drops of algae mixture. Plates with *F. sultana* branches firmly attached to the surfaces were returned to their buckets. Detached and fragmented *F. sultana* branches were also individually incubated in 12-well plates (Sarstedt) and fed daily with one drop of algae mixture. Water in each well was changed weekly.

## 3. Results

### 3.1. Collection of degenerating *F. sultana* branches

*F. sultana* specimens, including fragmented colonies infected with *T. bryosalmonae* or viable piptoblasts, were collected during the weekly cleaning and water replacement in buckets. Degenerating fragmented branches were observed to occur together with viable growing zooids. Water changes happened in incubating plates due to the occurrence of the feeding-induced hypertrophication and lower oxygenation. Higher light intensity and sudden temperature changes during stereomicroscopic observations may have further contributed to establish unfavourable micro-conditions for growth. Stalked peritrichs protozoans (e.g. *Vorticella* sp. and *Cothurnia* sp.) and bdelloid rotifers (e.g. *Rotifer* sp.) grew within and around the tubular ectocyst. During more advanced colony degeneration, fungal hyphae grew from dead branch extremities. Surviving zooids were observed within the viable extremity of the branch, showing active feeding by extruding their lophophores (retractable crown of tentacles lined with cilia).



**Fig. 1.** Development of *Fredericella sultana* from a statoblast. (A) Dormant statoblast (piptoblast type); (B) Recently hatched zooid, at 3 days post-hatch; (C) mature zooid at 12 days post-hatch, with lophophore tentacles extended for active feeding.

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