The role of morphology and ecology in the transmission of actinospore types (Myxozoa) in freshwater ecosystems

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Introduction

It is now recognised that some myxozoans undergo a two-host lifecycle, alternating between a fish host and an invertebrate host (usually an oligochaete). Exceptions to this include members of the myxospore genus *Enteromyxum*, which appear to have a direct lifecycle and malacospores (*Tetracapsuloides* and *Buddenbrockia*), which utilise a bryozoan invertebrate host.

Approximately 170 actinospore morphotypes in 15 collective groups have been described to date from freshwater and marine oligochaetes. This compares with approximately 1400 myxospores in 60 genera, mainly in fish. Of these, approximately 30 lifecycles have been elucidated. Figure 1 shows that there appears to be no clear and consistent pattern in lifecycle links between the actinospore and myxospore forms. For example, different *Myxobolus* spp. have been shown to have hexactinomyxon, triactinomyxon and raabeia forms in oligochaetes, whilst aurantiactinomyxons have been shown to transform into *Henneguya*, *Myxidium*, *Thelohanellus* or *Hoferellus* in different fish hosts. Thus, each actinospore type does not have a unique equivalent myxospore type and *vice versa*, referred to as a lack of congruence between the two lifecycle stages by Xiao and Desser (2000) (*Sys. Parasitol.* **46**: 81-91). The aim of this poster is to draw attention to the importance of considering habitat for understanding biological relationships between myxospore and actinospore types.

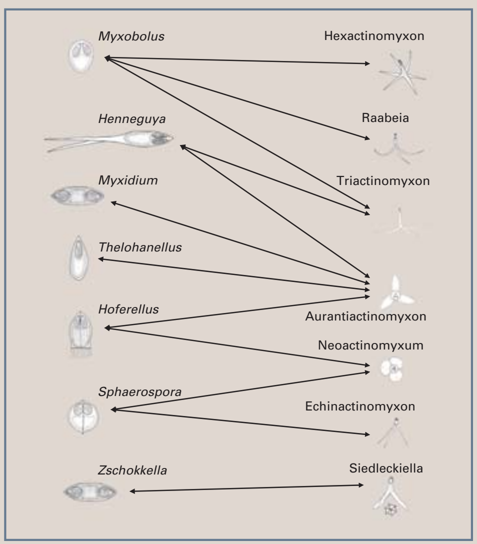

Figure 1: Established links between myxospore and actinospore stages. It is clear that there is a lack of congruence between the two stages.

Methods

Data for all known myxozoan lifecycles were collected from the scientific literature. Information regarding the fish host biology and myxozoan stages, including data on position in water column and water flow was obtained form published sources. All data for actinospore measurements were obtained from published descriptions. Volume of aurantiactinomyxon, neoactinomyxum, echinactinomyxon and raabeia types were calculated from the formula π x (half caudal width at base)^2 x caudal process length. For triactinomyxon types, volume was calculated as [π x (half caudal width at base)^2 x caudal process length] + [π x (half width of style)^2 x style length]. Hexactinomyxon volume was calculated as 3 x [π x (half caudal width at base)^2 x caudal process length] + [π x (half width of style)^2 x style length]. Siedleckiella volume was calculated as 24 x [π x (half caudal width at base)^2 x caudal process length]. In each case it was assumed that each caudal process was approximately a cone and the style, where present, was approximately a cylinder.

Results and Discussion

Based on the published data, it is clear that for those myxospore types occurring in fish either associated with the benthos or occurring in still waters, or both, the volume of the actinospore stage is less than $20000 \mu m^3$ and caudal length is less than 200µm. This includes neoactinomyxum, aurantiactinomyxon and raabeia types. The exception to this is the echinactinomyxon stage of *Sphaerospora truttae*, a parasite of salmonids, which occur in the pelagic zones of riverine systems.

Where actinospore volume exceeds $20000 \mu m^3$ and the maximum caudal process length exceeds 200µm, the myxospore equivalents are characterised by those species that are found in fish that predominate in the pelagic zone of riverine habitats. This includes most triactinomyxon types.

It has been assumed that there must be an evolutionary or phylogenetic basis to link the two stages of the lifecycle and this has been used as an argument to suggest polyphyletic origin of assorted myxospore genera. Whilst this may be true, we would suggest that it is the physical properties of the water body in which actinospore stages are found that determines the actinospore shape.

Thus, actinospores characteristic of still waters with bottom dwelling fish hosts, appear to have short caudal processes, whilst those infecting fish in moving water have larger caudal processes i.e. small forms such as neoactinomyxum and aurantiactinomyxon types predominate in still waters, whilst the larger forms such as triactinomyxons are found associated with riverine habitats. Net forming actinospores may be designed to become entangled in gills, weeds or other suitable substrates to facilitate infections.

The taxonomy of the phylum should be determined by the myxospore stage as there appears to be greater congruence within the myxospore stage. Actinospores are relatively short lived and thus size (or volume) and shape are extremely important to ensure that they have the most efficient transmission to fish host. In comparison myxospores are long lived and their shape outside the fish host is less important in transmission to the oligochaete host.

In evolutionary terms this makes sense, as different life stages will be subjected to different environmental selection pressures which "account for the observed morphological differences that mask phylogenetic relationships" (Xiao and Desser, 2000).

We have made some general statements regarding myxozoan lifecycles and it is clear that not all will conform to such a simplistic model. It is important to consider the importance of a variety of environmental and biological factors that may influence the morphological characteristics of each stage of the lifecycle. Such an approach may provide a predictive capability to link different life stages of myxozoans. In conclusion, we propose that future studies should consider the "normal" environment in which the lifecycle takes place and provide data such as preferred habitat of the fish host.

Table 1: Summary of freshwater myxozoan lifecycles.

Actinospore type	Myxospore genus	Current type in which fish host predominates	Vertical zone in which fish host predominates	Maximum caudal process length (µm)	Maximum actinospore volume (μm^3)
Echinactinomyxon	*Sphaerospora*	River	Pelagic	60	1100
Neoactinomyxum	*Hoferellus, Sphaerospora*	Still	Benthic	20	3000
Aurantiactino-myxon	*Henneguya, Hoferellus, Myxidium, Thelohanellus*	Still	Benthic	60	4000
Raabeia	*Myxobolus*	Mixed	Mixed	120	12000
Raabeia	*Myxobolus*	Still	Benthic	200	16000
Triactinomyxon	*Myxobolus*	Still	Pelagic	130	18000
Hexactinomyxon	*Myxobolus*	Still	Pelagic	150	19000
Triactinomyxon	*Myxobolus*	Mixed	Benthic	250	33000
Triactinomyxon	*Myxobolus*	River	Benthic	190	52000
Triactinomyxon	*Myxobolus*	Mixed	Pelagic	240	56000
Triactinomyxon	*Henneguya, Myxobolus*	River	Pelagic	300	62000
Siedleckiella	*Zschokkella*	River	Pelagic	520	84000