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ORIGINAL PAPER

The marine myxosporean *Sigmomyxa sphaerica* (Thélohan, 1895) gen. n., comb. n. (syn. *Myxidium sphaericum*) from garfish (*Belone belone* (L.)) uses the polychaete *Nereis pelagica* L. as invertebrate host

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Abstract *Sigmomyxa sphaerica* (Thélohan, 1892) gen. n. (Myxozoa, Myxosporea) with myxosporean stages in the gall bladder of *Belone belone* (L.) (Teleostei, Belonidae) uses the polychaete *Nereis pelagica* L. (Nereidae) from shallow water in the northern Øresund, Denmark, as invertebrate host. The nearly spherical tetractinomyxon-type actinospores of *S. sphaerica* differ from those of two species of *Ellipsomyxa* which also use *Nereis* spp. as invertebrate host. Pansporocysts of *S. sphaerica* were not seen. *S. sphaerica* is redescribed on the basis of myxospore stages from *B. belone* and actinospores from *N. pelagica*, and the phylogenetic affinities examined on the basis of ribosomal small subunit gene sequences. *S. sphaerica* is closest related to *Ellipsomyxa* spp., and is not congeneric with morphologically similar *Myxidium* spp. from gadids. This is the fifth elucidated two-host life cycle of a marine myxozoan.

Introduction

Only four marine myxozoan life cycles involving polychaete hosts have been elucidated and controlled using DNA analysis. *Ellipsomyxa gobii* Køie, 2003 and *Ellipsomyxa mugilis* (Sitjà-Bobadilla and Alvarez-Pellitero, 1993) use *Nereis* spp. (Nereidae), *Gadimyxa atlantica* Køie et al., 2007 (Parvicapsulidae) uses *Spirorbis* spp. (Spirorbidae) and *Ceratomyxa auerbachi* Kabata, 1962 (Ceratomyxidae) uses *Chone infundibuliformis* Krøyer, 1856 (Sabellidae), as invertebrate hosts (Køie et al. 2004, 2007, 2008; Rangel et al. 2009). Marine actinosporean stages have in addition been found in the polychaetes *Hydroides norvegicus* Gunnerus, 1768 (Serpulidae), in unidentified spionids (Spionidae) and in *Diopatra neapolitana* Delle Chiaje, 1841 (Onuphidae; Køie 2002, 2005; Rangel et al. 2011). In the present study actinospores found in *Nereis pelagica* (L.) are identified with the garfish (*Belone belone* L.) myxosporean *Myxidium sphaericum* on the basis of SSU rDNA sequences. *M. sphaericum* was originally described from *B. belone* from the Mediterranean and Atlantic coasts off France (Thélohan 1895). However, the species has later been identified and described from other hosts such as the gadid *Merlangius merlangus* (L.), widening the species conception. The conspecificity of *M. sphaericum* from belonid and gadid hosts has been questioned (MacKenzie and Kalavati 1995). Here we redescribe *M. sphaericum* from *B. belone* and show that the species does not belong in genus *Myxidium* and is not closely related to *Myxidium* spp. from gadids. Based on the morphological and phylogenetic distinctness from genus *Myxidium* sensu stricto, the novel genus *Sigmomyxa* is proposed for *M. sphaericum*.

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Material and methods

Specimens of the garfish *B. belone* (L.) (Teleostei, Belonidae) were obtained from local fishermen in May to June 2008 and in September 2010. These fish were caught in the northern Øresund, Denmark. Also, an *M. sphaericum*-infected specimen (76 cm) was collected in June

2003, near Misje, western Norway. Fresh smears of parts of the urinary system and bile were examined at high magnification (×1,000), and myxosporean spores and plasmodia were photographed. Measurements were taken from digital images using the software ImageJ 1.43u. Measurements are in micrometres.

About 45 specimens of *N. pelagica* L. (Annelida, Polychaeta, Nereidae) were dredged in the northern Øresund, Denmark at 4–12 m (12–20‰ salinity) during 2008–2010. Most specimens were examined for actinosporean infections immediately upon capture; a few were kept live in aquaria and examined later. Actinosporean measurements were taken from live specimens.

Two infected gall bladders of *B. belone* from Denmark in 2008 (isolates SigBel-1 and 2), from Norway in 2003 (isolate Msph) and pieces of infected *N. pelagica* (isolates Npel-1 and 2) were fixed in absolute ethanol for later DNA extraction. Morphological description is based on material represented by isolate 'Msph' and an infection from Denmark in 2010. Additional sequences for comparison were obtained from two *Myxidium laticurvum* Kabata, 1962-infected *Trachinus draco* L. caught in northern Øresund, Denmark (sequence isolates Mtra and MyFj-1; GenBank Accession No's JN033229-30 respectively), and from a *Myxidium bergense* Auerbach, 1909-infected *Pollachius virens* (L.) from Bodø, Norway (isolate X1; JN033231).

DNA was extracted from myxosporean spores and developmental stages or pieces of polychaetes using the DNeasy® Tissue Kit protocol for animal tissues (Qiagen, Hilden, Germany). The PCR primers used were the forward primers Erib1/Ur-R1, MarF1/RosR2 and MyxF2/Myxgen4R (see Køie et al. 2008), with annealing temperatures 57°C, 60°C and 58°C, respectively. The novel reverse primer Ur-R1 has sequence 5′-AAG AAT TTC ACC TCT CGC CA. The PCR amplifications were performed in a total volume of 50 µl using 2 µl of template DNA and a reaction mixture consisting of 10 µl 5× PCR buffer, 3 µl 25 mM $MgCl_2$,5 µl 10 mM dNTP, 2 µl (10 mM) of the reverse and forward primer, 2 U of thermostable DNA polymerase (GoTaq) and 26 µl dH_2O. The PCR conditions were as previously described (Køie et al. 2008). The PCR products were cleaned with ExoSAP-IT® (Affymetrix Inc.) and then sequenced using the BigDye® Terminator v3.1 Cycle Sequencing Kit. The sequencing was done using the amplification primers. The sequence data were assembled with the Vector NTI 11 software (Invitrogen) and GenBank searches were done with Blast (2.0).

The phylogenetic relationship between *M. sphaericum* and related members of the 'marine clade' (Fiala 2006) was examined using Bayesian inference (MrBayes 3.1.2; 3×10^6 generations), maximum likelihood (ML, Paup 4.0b10; 100 bootstrap replicates) and maximum parsimony (Mega 4.0.2). Sequences were aligned using AlignX (Vector NTI), and manually edited in Genedoc. Hypervariable or ambiguous regions were deleted in order to achieve comparison of homologous positions. The Paup ML analysis used a heuristic search algorithm with 10 random sequence additions and TBR branch swapping. A GTR+Γ+I model of nucleotide substitution was selected (AIC) following the examination of the data set with the program jModeltest (Posada 2008). The model was implemented in Paup (Paup Block) and MrBayes (Invgamma).

Results

Infections in *B. belone* and *N. pelagica*

Myxospores identified as *M. sphaericum* Thelohan were found in the gall bladder of one specimen of *B. belone* in May 2008 and in one in June 2008. The total number of specimens examined in 2008 was about 100. One of 200 gall bladders examined in September 2010 was infected. All caught in the northern Øresund, Denmark. A single *B. belone* caught near Bergen, western Norway was also infected with *M. sphaericum* in the gall bladder. No myxospores were found in the urinary system of the *B. belone* examined in 2008.

None of the about 40 specimens of *N. pelagica* caught in 2008–2010 and examined immediately upon capture were infected with actinospores. In August 2010 six specimens (4–6 cm long) were isolated in glass containers (8°C, 20‰ S) without air supply. Accidentally the temperature increased to about 22°C for about 24 h. During this period one specimen died. When it was examined the following day, it contained hundreds of free actinospores. Most of the internal organs had disappeared and bacteria occurred in the body cavity. The remaining five surviving specimens were not infected.

Description of *M. sphaericum* from *B. belone*

Plasmodia were spherical to irregular (Fig. 1a, b), attached to gall bladder epithelium or free, often with brushy region representing the zone of epitheliar adhesion. Parts of plasmodia with distinct ectoplasm when unsporulated (Fig. 1a), while ectoplasm often not apparent in fully sporulated ones (Fig. 1a, b). Plasmodia contained refractive granules, scattered or in aggregations, increasing in number during sporogony. Mature plasmodia were usually markedly vacuolate (Fig. 1b). Plasmodia were generally disporic, rarely tetrasporic. Sporogony was disporic. Occasionally, plasmodia releasing spores were seen to contain a second sporoblast at an early stage in sporogony. Plasmodia without spores measured up to 36 µm in average diameter (N=16), plasmodia with immature spores 20–30 µm (N=4), and plasmodia with two mature spores 23–37 µm (mean 28 µm, N=11).

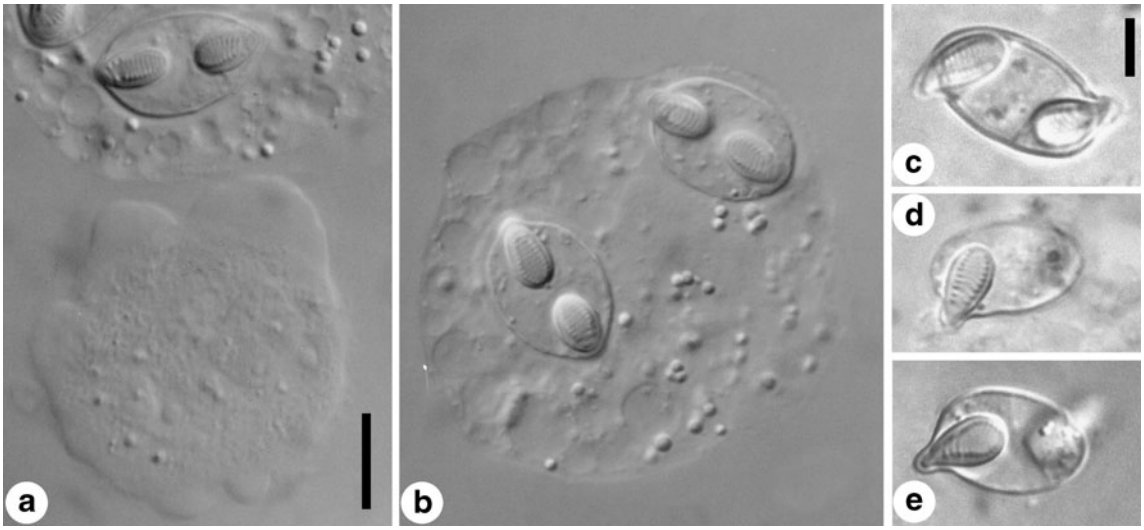

Fig. 1 Plasmodia and myxospores of *S. sphaerica* from the gallbladder of *B. belone*. **a** Plasmodium (flattened) without visible indication of sporogony, showing distinction between ecto- and endoplasm. **b** Sporulated plasmodium (flattened) showing spores in valvular view, vacuolate appearance and refractive granules. Note that any polar capsule lengths taken in valvular view may be erroneously short due to their oblique orientation in the spores. **c** Spore in sutural view. **d**, **e** Spores as seen in the focal plane of one polar capsule, showing polar filament coils and the valvular extensions associated with the protruding part of the capsules. *Scale bars* **a**, **b** 10 μm, **c**, **d** 5 μm

Spore main outline was ellipsoid (Fig. 1c), but valvular protrusions were associated with the tip of the polar capsules (PC), giving a sigmoid appearance in sutural view and spindle shape in valvular view (Fig. 2). Immature spores were occasionally crescent shaped. Valves were smooth, thicker along the ellipsoid outline of the main spore body and thin surrounding the protruding part of the PCs (Fig. 1c, d). Suture was weakly sigmoid, faint and symmetrical (Fig. 2). PCs were terminal, equal, elongate pyriform, PC axis in medial plane in valvular view, but with an angle reaching c. 47° to spore axis in sutural view. Polar filament coils are perpendicular to PC axis, with filament coil diameter averaging 70% of PC diameter. Coils are not present in the protruding part of the PCs (Fig. 1c–e). Polar capsule length to spore length was 1:2.1–2.8 (mean 2.3± 0.2; N=21). Fully extruded polar filaments reach 134–153 μm in length. Sporoplasm was binucleate, filling the barrel-shaped spore cavity between the PC cells. Spore measurements are given in Table 1.

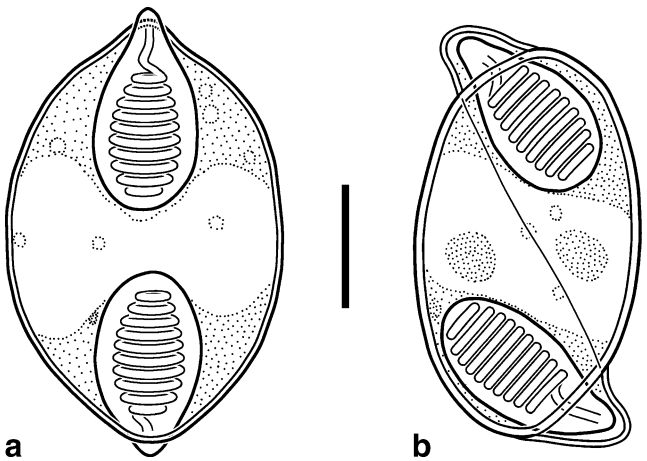

Fig. 2 Line drawings of *S. sphaerica* myxospores from *B. belone*. **a** Valvular view and **b** sutural view. *Scale bar* 5 μm

Description of actinospores from *N. pelagica*

All actinospores were of the tetractinomyxon type (Fig. 3). They all occurred free in the decaying polychaete body. No pansporocysts were found. The thick-walled actinospores were spherical to slightly ellipsoidal, length 7.0–8.0 (mean 7.6; n=10) and diameter 6.0–7.5 (6.7). The actinospores were composed of eight cells most easily identified by the presence of their nuclei; the three nuclei of the shell valve cells appeared as small thickenings internally on the spore wall, the three nuclei of the polar capsules and the two nuclei of the sporoplasm. The diameter of the three identical spherical polar capsules was 2.0–2.3 (2.1). It was not possible to provoke extrusion of the polar filaments.

SSU rDNA sequences

Partial SSU rDNA sequences were obtained from *M. sphaericum*-infected gall bladders of two *B. belone* from Denmark (sequence isolates SigBel-1 and 2, GenBank accession nos. JN033225, JN033226) and the studied infection from Norway (sequence isolate Msph, JN033227). These were identical (1696 nt compared).

Table 1 Measurements (in micrometres) of *S. sphaerica* from *B. belone* in Denmark and Norway (this study) compared with those published previously from *B. belone*

	Thélohan (1895)	Lubat et al. (1989)	Mladineo et al. (2009)	Present study range (mean±SD; *N*)
Plasmodia, diameter	20–22	20–22	44 (in image 1A)	21–37
Plasmodia	Disporic	Disporic	Disporic	Disporic[a]
Spore length	15–20	14–20 (15)	12.95±1.1[b]	16.7–19.4 (18.0±0.8; 22)
Spore width	7–8[c]	7–10 (8)[c]	13.16±2.16	10.2–12.8 (11.7±0.8; 19)
Spore thickness			8.17±1.05	7.9–9.1 (8.2±0.6; 4)
PC length		5	5.89±0.98	6.3–9.3 (7.5±0.7; 41)
PC width		3	2.83±0.52	3.5–4.9 (4.0±0.4; 43)
PC coil dia		–	–	2.4–3.5 (2.9±0.3; 27)
PC windings		–	8–9	9–12 (10.3, mode 10; 27)
PC-PC[d]		–		1.9–4.8 (3.3±0.9; 21)

[a] Plasmodia releasing spores seen to contain a second pansporoblast at an early stage in sporogony

[b] Length less than width; likely erroneous

[c] Width and thickness apparently not distinguished

[d] Valvular view

Two different parts of a *N. pelagica* infected with tetractinomyxon actinospores produced two identical partial SSU sequences (sequence isolates Npel 1 and 2, JN033228) (1696 nt compared). These sequences were identical with the *M. sphaericum* sequences from *B. belone*, apart for four substitutions (99.8 % identity, 1696 nt compared). On this basis the actinosporean infection in *N. pelagica* is identified with the myxosporean *M. sphaericum* infecting *B. belone*.

Blast searches returned *Ellipsomyxa* spp. as most similar to the partial *M. sphaericum* SSU rDNA sequences. Phylogenetic analyses on the basis of the SSU rDNA sequences supported a close relationship between genus *Ellipsomyxa* and *M. sphaericum* (Fig. 4). *Myxidium queenslandicus* Gunter and Adlard, 2008 represent a sister group to *Ellipsomyxa* spp./*M. sphaericum* in these analyses (Fig. 4). The congeneric marine clade members *M. laticurvum*, *Myxidium incurvatum* Thélohan, 1892 *Myxidium gadi* Georgévitch, 1916 and *M. bergense* are not closely related to *M. sphaericum* (Fig. 4). A schematic illustration of the life cycle of *Sigmomyxa sphaerica* (syn. *M. sphaericum*, see below) is shown in Fig. 5.

Discussion

Taxonomy

M. sphaericum was originally described from *B. belone* from the Mediterranean (Banyuls) and Atlantic (Vivier) coasts of France (Thélohan 1895), as producing large (15–20 μm long) spores in disporic plasmodia. Noble (1957) identified the species from the gadid fish *M. merlangus* in Plymouth, and doubted the validity of *M. bergense*, a species described from the gadid *P. virens* by Auerbach (1909) and recorded from other gadids including *M. merlangius* in Norway (Auerbach 1912). Other authors studying the myxosporea of *M. merlangus* accepted this, which resulted in a very wide conception of *M. sphaericum* that has caused much taxonomic confusion. MacKenzie and Kalavati (1995) distinguished between *M. sphaericum* and *M. bergense*, and considered it possible that the parasite from *B. belone* is distinct from *Myxidium* spp. in the gallbladder of gadid hosts. *M. sphaericum* as redescribed

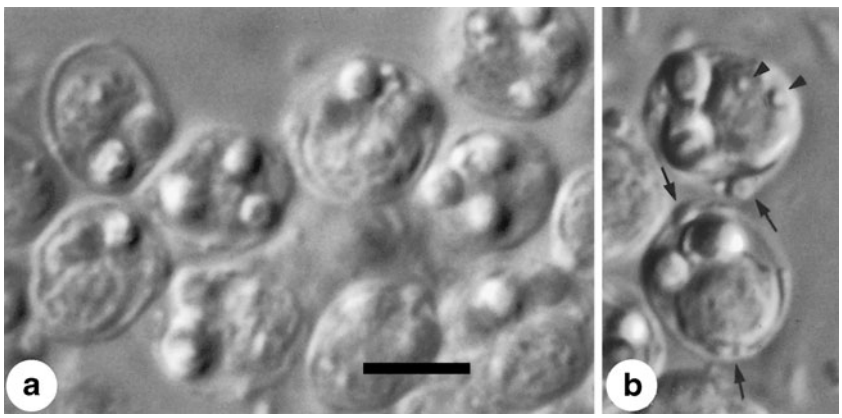

Fig. 3 Actinospores of *S. sphaerica* in naturally infected *N. pelagica* from northern Øresund, Denmark. Interference contrast, to same scale. **a** Apical and lateral views of free actinospores. **b** Lateral views showing the three nuclei of the shell valve cells (*arrows*) and the two nuclei of the sporoplasm cells (*arrowheads*). *Scale bar* 5 μm

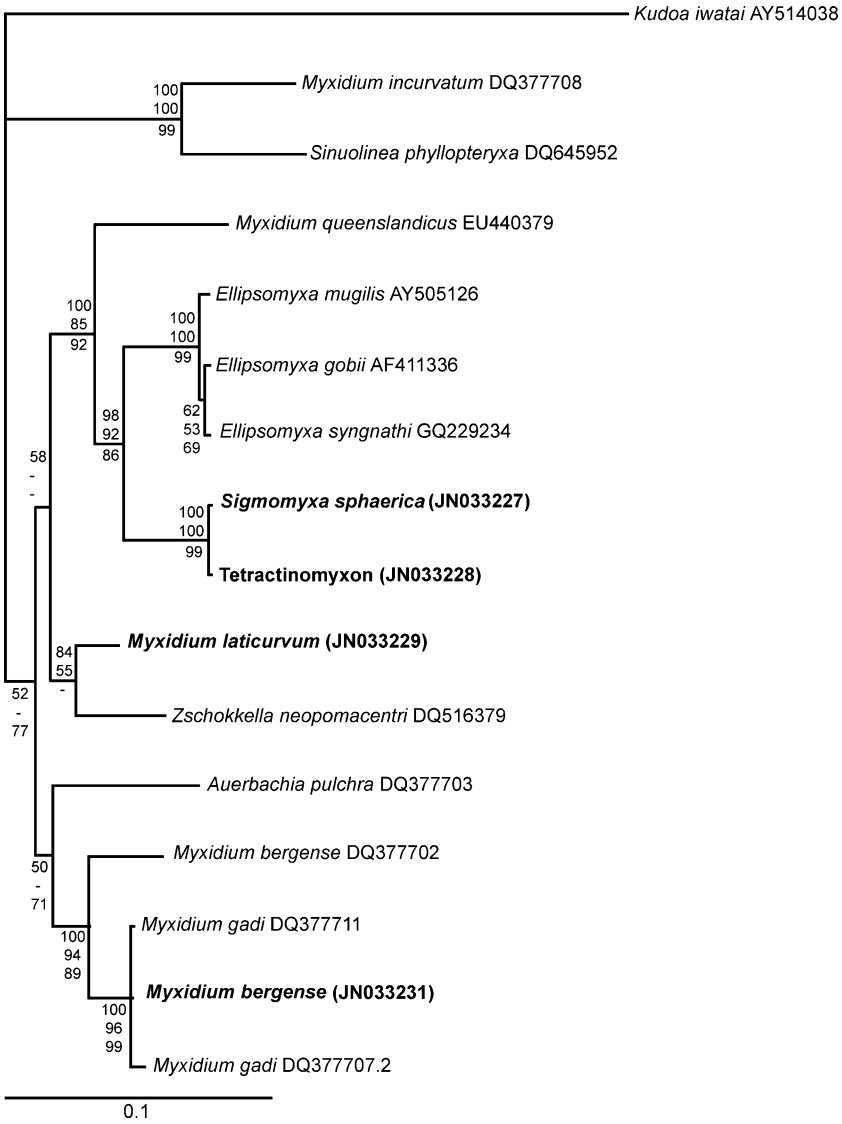

Fig. 4 Phylogenetic affinities of *S. sphaerica* among related members of the marine clade of Myxosporea. *S. sphaerica* is closest related to *Ellipsomyxa* spp., and these two genera represent a sister group to *M. queenslandicus* incertae sedis in a well-supported clade. Other *Myxidium* spp. in the marine clade are not closely related to *S. sphaerica*, including *M. laticurvum* (JN033229, new sequence) and *M. bergense* from the type host *P. virens* in Norway (JN033231, new sequence). All new sequences in *bold*. Clade support values: upper, MrBayes posterior probabilities (in percent); middle, maximum likelihood bootstrap (N=100) support values (Paup); lower, maximum parsimony (Mega)

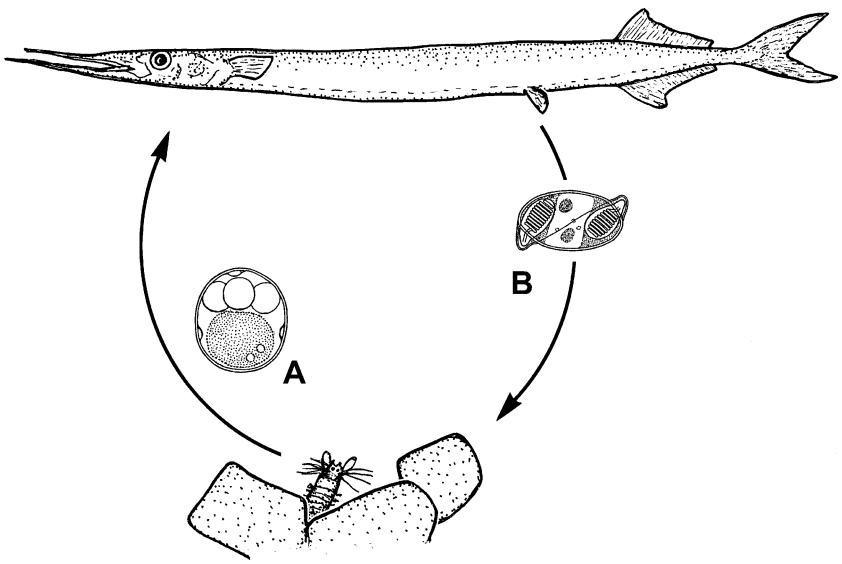

Fig. 5 Schematic illustration of the life cycle of *S. sphaerica*. The polychaete *N. pelagica* acts as the invertebrate hosts and the garfish *B. belone* acts as the fish hosts. **a** Actinospore, **b** myxospore. Not to scale

here is clearly differentiated from all *Myxidium* spp. recorded from gadids in the northeast Atlantic by characters such as the large and elongated polar capsules with a high number of windings, and show phylogenetic affinity to the *Ellipsomyxa* spp. rather than to the *Myxidium* spp. with sigmoid spores recorded from gadids.

Considering only records of *M. sphaericum* from *B. belone*, there are two records subsequent to Thélohan (1895), both from the Adriatic Sea (Lubat et al. 1989; Mladineo et al. 2009). Lubat et al. (1989) provided spore measurements agreeing well with the present. However, Mladineo et al. reported spore lengths shorter than the width, which suggests these may be erroneous. The polar capsule lengths of Lubat et al. (1989) and Mladineo et al. (2009) are less than the present, but similar measurements were obtained by us when taken in valvular view. Such measurements tend to represent polar capsule span and not length, due to the oblique angle of the polar capsule axes relative to the spore main axis. However, while such considerations may account for differing length observations, the polar capsule width measurements also differ significantly, being less in the Adriatic samples. Hence verification of conspecificity of Adriatic *M. sphaericum* isolates with the present through SSU rDNA sequencing would be valuable. The light microscope images of *M. sphaericum* spores and plasmodia presented by Mladineo et al. (2009) compare well with the present material.

The type species in genus *Myxidium*, *Myxidium lieberkuehni* Bütschli, 1882, produce large polysporic plasmodia in the urinary system of pike, *Esox lucius* L., a freshwater fish. Spores develop in disporic pansporoblasts and show striated valves. Phylogenetic analyses on the basis of SSU rDNA sequences place *M. lieberkuehni* in a 'freshwater clade' of Myxosporea, as a member of a '*M. lieberkuehni* clade', representing a sister group to a '*Myxobolus* clade' containing mostly members of the Platysporina (see Fiala 2006; Holzer et al. 2007). *M. sphaericum* is closest related to *Ellipsomyxa* spp. in the 'marine clade' and belongs to the marine '*Myxidium* clade' of Fiala (2006). Sequence similarity in the aligned SSU rDNA sequences of *M. sphaericum* and *M. lieberkuehni* is only 66% (2,057 sites compared). Hence *M. sphaericum* is not congeneric with *M. lieberkuehni* and does not belong in the Myxidiidae typified by that species. We therefore propose a novel genus to encompass *M. sphaericum* and related species.

Sigmomyxa n. gen.

Coelozoic in gallbladder, sporogony disporic, plasmodia are di- to polysporic, spores smooth, spindle shaped in valvular view and sigmoid in sutural view. Valves are ellipsoid in outline, with thin walled protrusions associated with the PC tips. Polar capsules elongate pyriform, with >7 windings. Intercapsular distance is short. Type species is *S. sphaerica* (Thélohan, 1895)

Comments

Myxidium elmatboulii Ali et al., 2006 and *Myxidium maamouni* Abdel-Baki, 2009 are similar to *S. sphaerica* and likely congeners, but molecular data is lacking (cf. Ali et al. 2006; Abdel-Baki 2009). *M. elmatboulii* is transferred to *Sigmomyxa* as *Sigmomyxa elmatboulii* (Ali et al., 2006) comb. n. on the basis of its morphology, the species is so similar to *S. sphaerica* that conspecificity is possible. The host, *Tylosurus choram* (Rüppell, 1837) is also related to *B. belone* (both belonids). The spores of *M. queenslandicus* appear morphologically similar to those of *S. sphaerica*, but these species show only 89% identity in the partial SSU rDNA sequences available. However, expansion segments in the V7 region of *M. queenslandicus* are responsible for the low identity; exclusion of these gives 94% identity with *S. sphaerica*. *M. queenslandicus* is phylogenetically closest related to *S. sphaerica* and *Ellipsomyxa* spp., but inclusion in *Sigmomyxa* appears to render the genus polyphyletic. However plasmodia and sporogony of *M. queenslandicus* are unknown and the species is therefore considered an incertae sedis. *M. laticurvum* Kabata 1962 (syn. *Myxidium trachinorum* Canning et al. 1999, see Karlsbakk 2001) show a protruding polar capsules similar to *S. sphaerica* but differ in containing very prominent capsulogenic cells in mature spores, a convex spore structure and a different organisation of the polar filaments (Kabata 1962; Canning et al. 1999). Our SSU rDNA sequences of *M. laticurvum* confirm that this species is not closely related to *Sigmomyxa* n. gen.

The erection of *Sigmomyxa* n. gen. removes two species from the polyphyletic genus *Myxidium* Bütschli, 1882. Several species in the marine group of Myxosporea and currently assigned to *Myxidium* are not closely related to *Myxidium* sensu stricto or *Sigmomyxa* n. gen. on the basis of their SSU rDNA sequences, but show a related morphology and development. Redescriptions and revisions of these taxa are needed.

Life cycle

The actinosporean infection in *N. pelagica* and the myxosporean *S. sphaerica* in *B. belone* is considered different life cycle stages due to the high SSU sequence similarity. Sequence identity has aided the disclosure of all the marine myxosporean life cycles known so far. We observed that five specimens of *N. pelagica* survived and only the infected specimen died due to stress (high temperature and lack of oxygen). This indicates that an infection with actinosporean stages may affect the survival

of the polychaete host. Other observations on the effects of actinosporeans on the annelid hosts are scarce. Shirakashi and El-Matbouli (2009) found feeding and fecundity of actinosporean-infected *Tubifex tubifex* to be reduced, but did not observe reduced survival.

Apparently only fully developed actinospores of *S. sphaerica* were found in the examined *N. pelagica*. However, the wall of the pansporocysts and younger developmental stages may have disintegrated in the decaying polychaete host.

The present actinospores differ from those of *E. gobii* and *E. mugilis* (as *Zschokkella mugilis*), which also use *Nereis* spp. as polychaete hosts, by being nearly spherical contrary to the elongated actinospores of *Ellipsomyxa* spp. having nearly twice the length (Køie et al. 2004; Rangel et al. 2009).

Nereis diversicolor and *Nereis succinea* from less than 1 metre depth may be infected with actinosporean stages (Køie et al. 2004; Rangel et al. 2009). The *N. pelagica* specimens examined were dredged in among other a shallow sandy bay harbouring *N. diversicolor* and *N. succinea*. These two species were only infected with *E. gobii*, even though specimens of *B. belone* must have spent some time in this bay. Hence it is possible that these myxosporeans display some degree of host specificity to the invertebrate host; *E. gobii* uses two species of *Nereis* as invertebrate hosts (Køie et al. 2004), whereas *S. sphaerica* apparently use one species, *N. pelagica*.

Actinospores of the tetractinomyxon type are the actinosporean stages of myxozoans belonging to at least three clades: the *Ceratomyxa* clade (Køie et al. 2008), the Parvicapsulidae (Bartholomew et al. 2006; Køie et al. 2007) and the *Sigmomyxa*/*Ellipsomyxa* clade. A fourth clade is represented by *Ceratomyxa shasta*, which also show tetractinomyxon actinospores (Bartholomew et al. 1997), but the phylogenetic affinities of *C. shasta* is unclear (see Fiala and Bartosova 2010).

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