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SHORT COMMUNICATION

The formation of the twin resting cysts in the dinoflagellate *Dissodinium pseudolunula*, a parasite of copepod eggs

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The dinoflagellate *Dissodinium pseudolunula* is the most common and widespread ectoparasite of copepod eggs in neritic waters. When the host is absent, the species survives with a distinctive pair of twin resting cysts described as *Pyrocystis margalefii*. Based on live samples, the formation of the twin resting cysts is illustrated here for the first time. The gymnodinioid infective cells did not form overwintering cysts under unfavourable conditions. These are formed inside the secondary lunulate sporangium.

KEYWORDS: Dinophyceae; life cycle; overwintering cyst; parasitism; resting spores

Copepods are the most abundant metazoans in the sea and represent a key trophic link in pelagic food webs (Mauchline, 1998). Numerous parasites have been shown to influence the mortality and fecundity of copepod populations (Théodoridès, 1989). The lipid-rich copepod eggs are the target of several specialized parasites (Cachon and

Cachon, 1987; Coats, 1999). The parasitic dinoflagellate *Dissodinium pseudolunula* has a world-wide distribution in marine neritic habitats. This species has been known since the beginning of plankton studies (Pouchet, 1885), but the parasitic stage of *Dissodinium* upon copepod eggs was not discovered until 1978 (Drebes, 1978). The gymnodinioid

dinospores infest planktonic crustacean eggs, absorb the host contents and form two successive sporangia (a globular primary sporangium followed by eight crescent lunate secondary sporangia which develop from the former) that produce new infective gymnodinioid dinospores (Drebes, 1978). The species survives the host-free season as resting cysts. Drebes (Drebes, 1981) was able to germinate a dinoflagellate resting cyst, known as *Pycnostis margalefi*, in culture and he observed that the gymnodinioid dinospores were identical to those of *Dissodinium pseudohunula*. However, he was unable to verify whether the dinospores were able

to infect copepod eggs. These distinctive pairs of twin resting cysts are widely distributed in the plankton of the eastern North Atlantic and North Sea with a peak in numbers in August and September (John and Reid, 1983). Molecular phylogeny has revealed that *Dissodinium* and *Chytriodinium*, both ectoparasites of crustacean eggs, are close relatives within the group of *Gymnodinium sensu stricto* (Gómez *et al.*, 2009).

Drebes (Drebes, 1981) demonstrated that the infective dinospores that emerged from the twin resting cyst resemble those of *Dissodinium pseudohunula*. However, the stage of

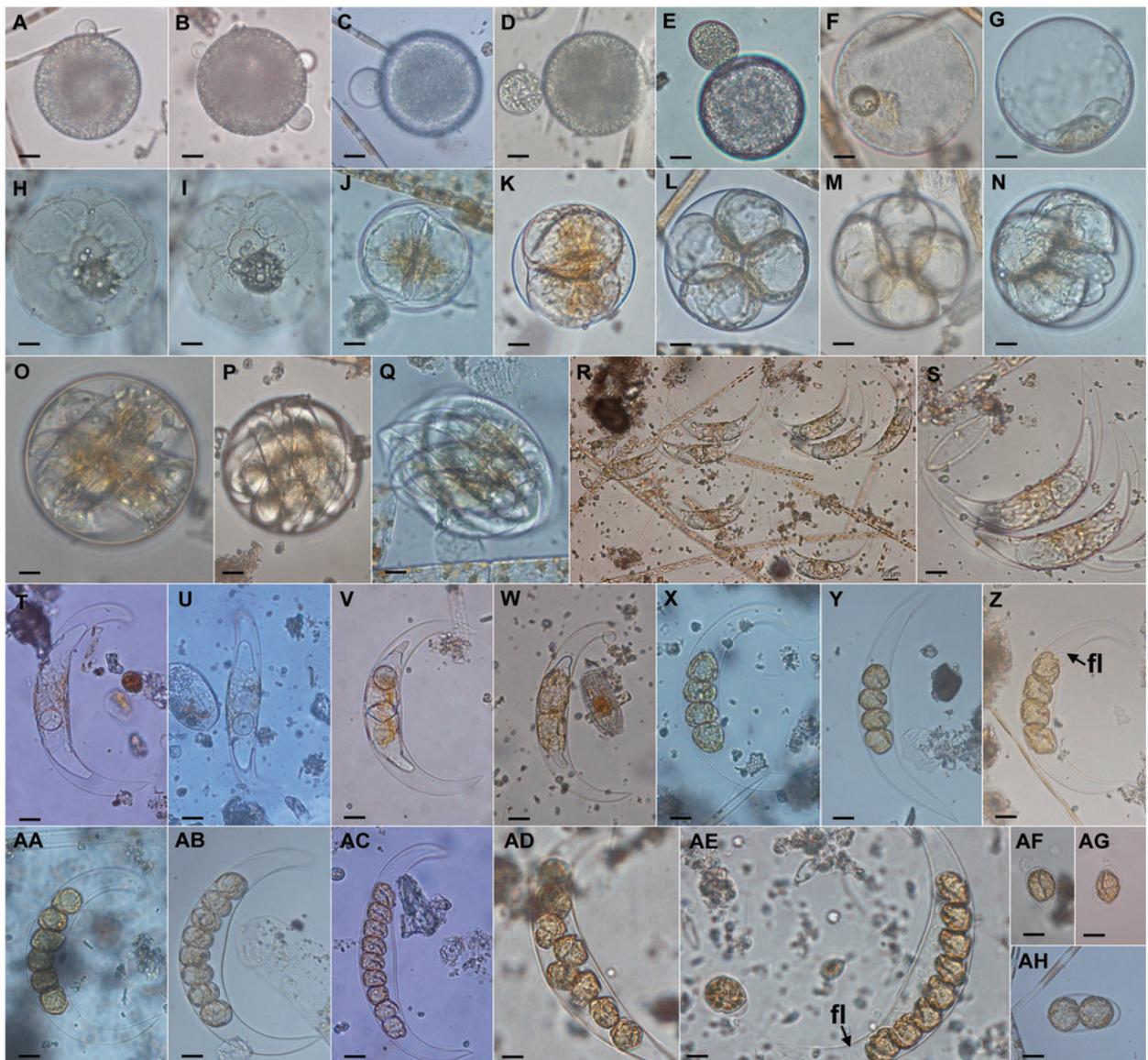


Fig. 1. Light micrographs of life stages of live specimens of *Dissodinium pseudohunula* collected in the coastal NE English Channel in 2010 and 2011. (A–E) Infected copepod eggs. (F–Q) Developmental stages of the globular primary sporangia. (R–AE) Developmental stages of the lunate secondary sporangia. (AE–AH) Infective dinospore enclosed in an outer hyaline membrane. fl, flagellum. Scale bar: 10 µm. See online supplementary data for a colour version of this figure.

the life cycle of *Dissodinium* in which the resting cysts are formed remains unknown. This fact also represents a way to confirm the relationship between the twin resting cyst and *Dissodinium*. The most intuitive explanation is that the infective dinospore forms a resting cyst under unfavourable conditions (when it is unable to find the host). In fact, the infective dinospore forms an outer membrane (Drebes, 1981). However, this corresponds to a temporary cyst which differs from the twin resting cysts of *Dissodinium* in size, shape and cell content. The present study identifies the missing link between the known life stages of *Dissodinium* and its overwintering resting cyst.

Live phytoplankton samples were collected weekly with a 20 μm mesh net in 2010 and 2011 in coastal waters of the NE English Channel (off Wimereux, France), which are characterized by recurrent blooms of diatoms and the haptophyte *Phaeocystis globosa*. Daily sampling was also

performed in a large pool (~ 50 m diameter, ~ 1 m depth) that formed during low tide along the shore at Wimereux. In addition, intertidal surface sediments at Wimereux were examined following the sampling procedure described by Gómez *et al.* (Gómez *et al.*, 2011). Plankton and benthos live samples were settled in Utermöhl chambers and examined with an inverted microscope (Nikon Eclipse TE2000-S) equipped with a Nikon Digital Sight DS-2M camera.

Infected eggs and globular and lunate sporangia of *D. pseudolunula* were common in live samples from April to September, with more specimens in June (Fig. 1). The fast-swimming gymnodinioid dinospores were difficult to record, and the micrographs were taken when they were enclosed inside a thin hyaline outer membrane (Fig. 1AE–AG). Only 10 pairs of twin resting cysts were observed between July and September in 2010 and 2011

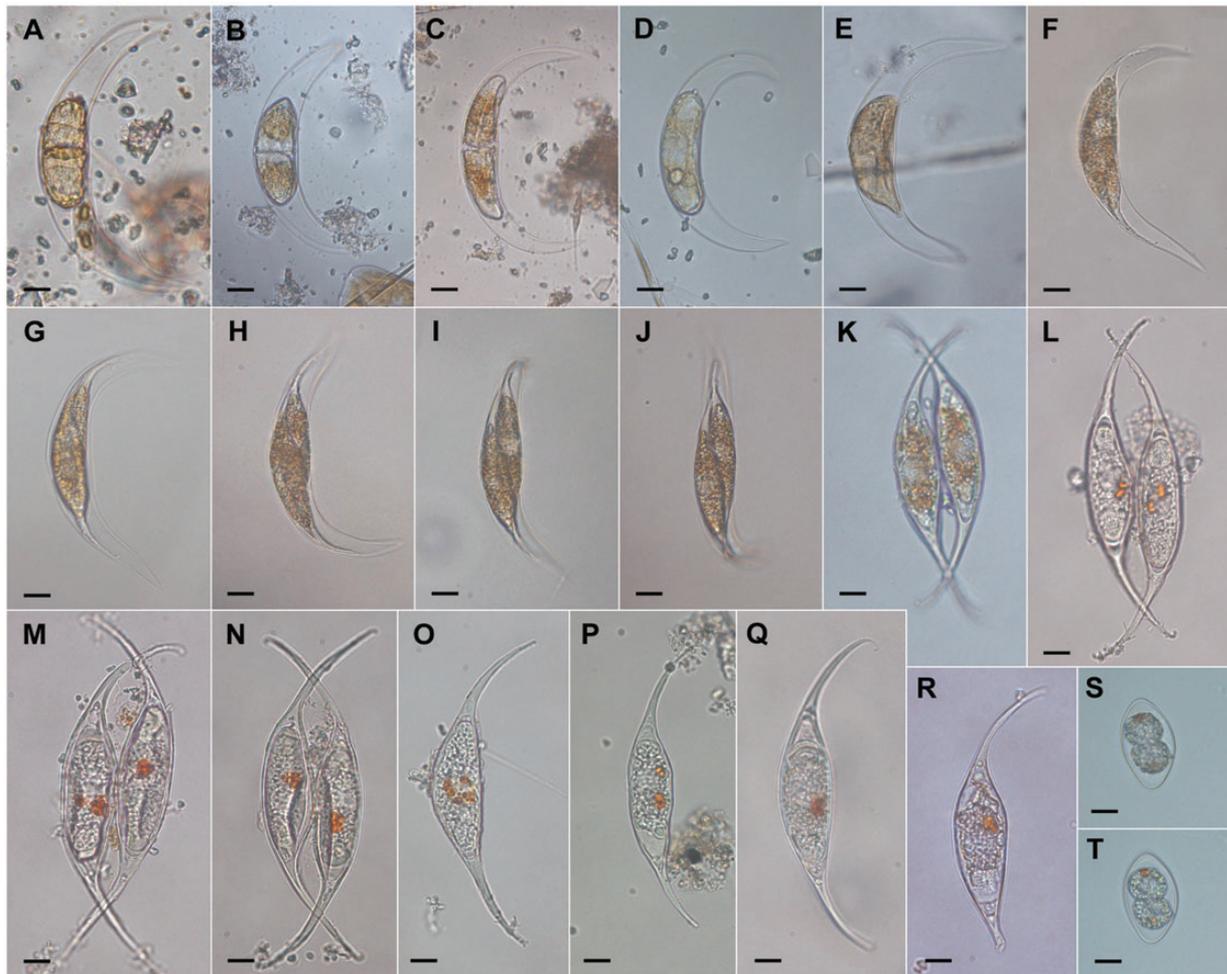


Fig. 2. Light micrographs of the lunate sporangium and the resting cyst of live specimens of *Dissodinium pseudolunula* collected in the coastal NE English Channel in 2010 and 2011. (A–E) Lunate secondary sporangia. (F–J) Formation of a pair of twin resting cysts inside a lunate sporangium. (K–N) Pairs of twin resting cysts. (O–R) Single resting cyst. (S–T) Pairs of cells with the appearance of the resting cyst. Scale bar: 10 μm

egg. A host infection could provide 8 lunate sporangia and the subsequent 8 pairs (16 cells) of resting cysts. Drebes (Drebes, 1981) observed that the cells that germinated to form the twin resting cysts were eventually able to divide. This may be the case in the specimens illustrated in Fig. 2S–T. Consequently, each infected egg may provide 32 new infective dinospores for the following spring (Figs 1 and 2).

Intuitively, one might suggest that the factor that triggers the formation of the twin resting cysts is the absence of copepod eggs. However, the secondary lunate sporangium may be unable to directly sense the presence of hosts in the surrounding waters. It is uncertain whether the decrease in the size or quality of the eggs induces the formation of the resting cysts as a mechanism to avoid the failure of the next generation of infective dinospores. Another possibility would be that the twin resting cyst is produced at a constant rate throughout the year, in order to provide a permanent seeding bank. However, the active *Dissodinium* form is common in April and May, while the resting cysts were mainly observed in July–September (John and Reid, 1983). The twin resting cysts are preferentially formed in the host-free season.

This study provides new insights into the life strategies of this important parasite group (Fig. 3). The production of cysts has been reported in parasites of tintinnid ciliates (Coats *et al.*, 2010). However, we know little about the overwintering cysts in parasitic dinoflagellates. *Dissodinium* and other parasites on copepod eggs may be a contributory factor to the large year-to-year variability in the standing stock of copepods. It is important to understand their life cycles as a first step and to include parasitism in the models of secondary production in the ocean.

SUPPLEMENTARY DATA

Supplementary data can be found online at <http://plankt.oxfordjournals.org>.

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