Available online at www.sciencedirect.com

ScienceDirect

European Journal of Protistology 66 (2018) 68–76

European Journal of PROTISTOLOGY

www.elsevier.com/locate/ejop

REVIEW

The Villefranche *Strombidium sulcatum*: A review

John R. Dolan*

Sorbonne Université, CNRS, Laboratoire d'Océanographie de Villefranche-sur-Mer, Station Zoologique, Villefranche-sur-Mer 06230, France

Received 21 June 2018; received in revised form 3 August 2018; accepted 9 August 2018
Available online 15 August 2018

Abstract

The marine oligotrich ciliate *Strombidium sulcatum*, the best known marine oligotrich of the marine microozoplankton, was first cultured in Villefranche-sur-Mer 35 years ago. Cultures were maintained from 1983 to 2003 and used in 22 studies investigating a very wide variety of questions. Here we review the major findings of these studies and underline their contributions to our knowledge of planktonic ciliate ecology and microbial ecology in general. We conclude with the observation that while ecophysiology has apparently fallen out of fashion, culture work will likely return as an invaluable resource in our present 'omics' era.

Keywords: Culture; Ecological physiology; Marine microzooplankton; Model species; Oligotrich ciliates; Plankton

Introduction

The oligotrich ciliate *Strombidium sulcatum* has been the subject of many studies. A quick search in Google Scholar for publications containing the term "Strombidium sulcatum" yields over 500 titles. The species was described by Claparède and Lachmann from the Fjord of Bergen (Norway) in 1858 as the type species for the genus (Claparède and Lachmann 1858); it is then one of the longest-known oligotrich ciliates and is apparently cosmopolitan (Agatha 2011). It was subsequently found in the Bay of Kiel (Bütschli 1873). In the Mediterranean, it was found first in the Gulf of Naples by Entz (1884) and then in the port of Bastia in Corsica (Gourret and Roeser 1888). The first detailed observations made on *S. sulcatum* were by Fauré-Fremiet who examined cells from the marshes of Croisic, on the Atlantic coast of France (Fauré-Fremiet 1911, 1912). However, *S. sulcatum* was not brought into culture until 1983 when Dave Brownlee, established cultures in Villefranche-sur-Mer. From 1983 to 2003, *S. sulcatum* was maintained in wheat grain culture providing the raw material for the 22 laboratory studies reviewed here (for a complete chronological list please Supplemental material).

The studies using the Villefranche culture of *Strombidium sulcatum* involved a quite large range of topics as indicated by the 'word cloud' in Fig. 1 created from the titles of the publications. It should be noted firstly, that the species called *S. sulcatum* in the experiments reviewed here has been described as *S. inclinatum* (Montagnes et al. 1990; Granda and Montagnes 2003). However, some researchers consider that *S. sulcatum* and *S. inclinatum* are likely synonymous (Song et al. 2000). Loss of all biological samples of *S. sulcatum* culture material prevents us from ever knowing with certainty the molecular identity of the ciliate cultured in Villefranche-sur-Mer. Secondly, while there have been many important studies using cultures of ciliates described as *S. sulcatum* isolated from other local-

*Corresponding author.
E-mail address: dolan@obs-vlfr.fr

https://doi.org/10.1016/j.ejop.2018.08.002
0932-4739/

Fig. 1. Word cloud made of the 75 most frequently occurring words in the titles of the 22 publications, which appeared between 1985 and 2004, reporting work done using the Villefranche culture of *Strombidium sulcatum*. The size of a word reflects its relative frequency of occurrence. The complete list of publications is provided in the Supplementary material.

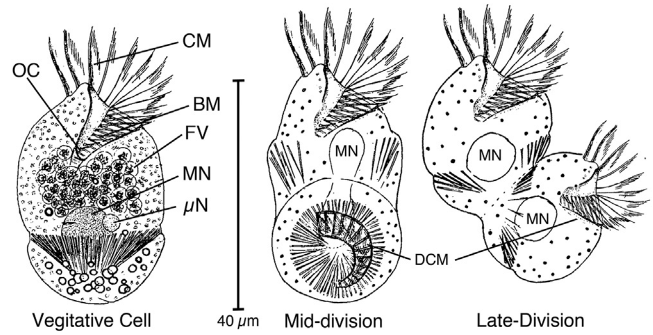

Fig. 2. Gross anatomy and cell division stages of *Strombidium sulcatum*. Beating of the Collar Membranelles (CM) moves the cell and brings potential food items to the Buccal Membranelles for transport into the Oral Cavity (OC). In the Oral Cavity ingested food items are enveloped inside Food Vacuoles (FV) inside which digestion occurs within the ciliate cell. The Macronucleus (MN) is the somatic nucleus and the Micronucleus (MN) contains chromosomes replicated during sexual reproduction. During asexual cell division, the Daughter Cell Mouth (DCM) develops in the anterior portion of the cell; the mouth of the parental cell remains functional. The Macronucleus is partitioned between the two cells. In the late division stage the two mouths are functional shortly before cell separation.
Adapted from Fauré-Fremiet (1912).

ities (e.g. Klein Breteler et al. 2004; Kiørboe et al. 2009; Saiz et al. 2014; Chen et al. 2015), they are not considered here. Our goal in this review is to illustrate the myriad results that can be derived from a single ciliate culture.

Strombidium sulcatum is a heterotrophic oligotrich, about 40 μm in length, and in the laboratory feeds on bacteria, small algae and heterotrophic nanoflagellates. In common with many free-living protists, it generally reproduces asexually via binary fission or cell division. Cyst production has not been reported but can not be excluded. Among oligotrich ciliates, the dividing cell develops a new mouth for the daughter cell and the original mouth does not degrade or become dis-organized thus the dividing cell continues to swim and possibly ingest prey while dividing. Basic morphological features and stages of cell division in *S. sulcatum* are shown in Fig. 2.

The numerical response, changes in growth rate or rate of cell division as a function of food concentration, has been examined in *Strombidium sulcatum*. The numerical responses can be considered as the net result of feeding. Following Montagnes (2013), feeding and processing of food items can be broken down into individual steps. Here we will focus of the steps of swimming/encounter, prey capture, digestion and excretion because each of these steps has been examined in *S. sulcatum* in some detail. We will first briefly review, in sequence, knowledge about these steps based on work done using cultures of the Villefranche *S. sulcatum*, before consideration of the numerical responses. Following then the sections summarizing work on as *S. sulcatum* as prey consumer, nutrient recycler, and biomass producer, its role as prey for copepods will be reviewed. As stated above, our general goal is to summarize the rich results that have been obtained from a single ciliate culture but also specifically to point out that the considerable knowledge of *S. sulcatum* supports its use in establishing reference sequence databases in our 'omics' era.

Swimming

For a planktonic consumer, swimming rate and pattern largely determine the rate of encountering prey. Swimming in *Strombidium sulcatum* is characterized by movement in a helical pattern interrupted by occasional 'tumbles' resulting in a change of direction (Fenchel and Jonsson 1988), as shown schematically in Fig. 3. The average linear displacement is about 0.1 cm s^{-1}, which translates into a possible distance travelled of about 100 m in 24 h if the linear displacement was consistently in a single direction. Swimming speed and pattern can vary markedly. Tumbles increase in presence of aggregates of prey and results in the ciliate remaining near the prey (Fenchel and Jonsson 1988). In contrast, ciliates that have been starved swim in a tight helical pattern, an apparently maladaptive behavior (Fenchel and Jonsson 1988). The study of Fenchel and Jonsson elucidated the mechanism behind ciliate chemotaxis and the variability in swimming behavior with physiological state. Later, a study examining the effects of small-scale turbulence found that swimming speeds might be lower when ciliates are subject to high levels of small-scale turbulence (such as in rough seas) resulting in lower ingestion and growth rates (Dolan et al. 2003).

Prey capture

Feeding in *Strombidium sulcatum*, and other oligotrichs, involves first the capture of the prey item between the Col-