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## An introduction to the special issue: *Oxyrrhis marina*, a model organism?



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**An introduction to the special issue: *Oxyrrhis marina*, a model organism?**

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## ABSTRACT

Many “model” protists are maintained in culture and used, experimentally, to answer questions associated with planktonic processes. Given the current interest and rapidly increasing amount of literature on the heterotrophic dinoflagellate *Oxyrrhis marina*, we present in this special issue a series of focused, interlinked research articles. Being written by experts in their respective fields, the authors have included unpublished data and in all cases have offered a synthesis of data and ideas. Furthermore, we have encouraged cross-paper discourse, emphasising the interdisciplinary nature of our work and the utility of *O. marina* to this end; we also offer guidance, both practical and intellectual, on how future research related to *O. marina* might progress. In this introduction, however, we raise the wider issue of which criteria are required to consider a taxon as a “model species”. We then assess the extent to which *O. marina* can fill this role. In general, we recognise *O. marina* as a model in three distinct disciplines: ecology, evolution/genomics, and biogeography. Of possibly greater importance, we recognise that if *O. marina* continues to be studied at an escalating rate, there will be a concomitant increase in realised and potential synergies across these fields.

Key Words: *Oxyrrhis marina*, review, dinoflagellate, experimental design

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## PREFACE FOR THE SPECIAL ISSUE

Many protists (unicellular eukaryotes) are maintained in culture and used, experimentally, to answer questions associated with planktonic (and other) processes, ranging from ecological to evolutionary relevance. Many of these taxa have been reviewed in detail, usually in book chapters or, indeed, in dedicated books. We now considered it timely to provide a similar synthesis on the heterotrophic dinoflagellate *Oxyrrhis marina*, but given the current interest and the rapidly increasing amount of literature on this taxon (Fig. 1), we have chosen to present our work as a series of focused, interlinked research articles, in this special issue. All of our papers provide a review of the literature, often stretching back decades (and in some cases over a century), but they progress beyond a summary of extant data. Being written by experts in their respective fields, the authors have, in places, included previously unpublished data, and in all cases they have offered a synthesis of data and ideas. Furthermore, while developing this issue, we have encouraged cross-paper discourse, emphasising and stimulating the interdisciplinary nature of our work and the utility of *O. marina* to this end. Finally, the papers in this special issue offer guidance, both practical and intellectual, on how future research related to *O. marina* might progress.

## INTRODUCTION

Nanny (1980), when discussing experiments with ciliates, referred to a group of select genera as “the chosen few”, as these protists, notably ones like *Paramecium*, have long acted as successful experimental tools. This contention reflects Krogh's principle that “for such a large number of problems there will be some animal of choice, or a few such animals, on which it can be most conveniently studied.” (see Krebs, 1975). Clearly, many such organisms have been chosen for their ability to address questions related to a particular

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4 discipline, with an emphasis on a handful of taxa; e.g. these extend from the prokaryote  
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7 *Escherichia coli*, to the fungus *Sacchromyces cerevisiae*, to the invertebrates *Drosophila*  
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9 *melanogaster* and *Caenorhabditis elegans*, and to the vertebrates *Mus musculus* and *Rattus*  
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11 *norvegicus*, the last providing a strain of that gave rise to the vernacular “lab-“ or “white-rat”.  
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14 Indeed, various model organisms have been adopted across countless biological fields, and  
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16 like any model, they are chosen to amalgamate levels of simplicity and complexity needed to  
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18 address specific questions within a particular discipline (e.g. Hedges, 2002; Behringer *et al.*,  
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21 2009).

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24 There can be no defined set of attributes to describes an ideal “lab rat” that provides a  
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26 solution to all questions. However, there are general traits that we might consider as useful  
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28 (Table 1). Furthermore, each field of research will inevitably impose unique criteria when  
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30 selecting models, and organisms are thus often chosen for a specific need (see Bahls *et al.*,  
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32 2003); although in some cases there appears to be some intellectual inertia, as a model  
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34 originally used for one purpose is adopted for others, at times with serendipitous  
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36 consequences (e.g. *Drosophila melanogaster*, Roberts, 2006). It is, therefore, not our  
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38 intention to suggest that the heterotrophic dinoflagellate, *O. marina*, can act as a model in an  
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40 absolute sense; instead, we address its general and specific versatility.  
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45 *Oxyrrhis marina* has been routinely used in experiments for over 100 years, and its  
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47 application appears to be rising exponentially across a number of fields (Fig. 1a). Certainly,  
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49 citations related to *O. marina*-related research are increasing rapidly (Fig. 1b), reflecting its  
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51 widespread distribution, small size, utility in addressing ecological issues, and crucially its  
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53 experimental tractability. Thus, we suggest that *O. marina* is an “emerging model organism”.  
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56 In the following sections, we reflect on the broad appeal of *O. marina* to address a range of  
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58 questions across a hierarchical scale, from genetic processes to aut- and synecological issues.  
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Our review of the literature (see papers in this special issue) suggest that this protozoa (i.e. heterotrophic protist) appears to be joining the ranks of such unicellular “lab rats” as *Paramecium*, *Tetrahymena*, *Amoeba*, and *Dictyostelium*, not simply based on its historical application but on its appropriateness to answer specific questions, following the Krogh principle (Krebs, 1975).

### IS OXYRRHIS MARINA A USEFUL MODEL?

Although no one species can provide a model for all studies or questions, a convenient attribute is to fulfil the needs of many disciplines. This is not simply because of the practical benefits associated with the economy of size (e.g. availability, ease of routine maintenance, development of standard protocols) but more critically, that being able to answer many types of questions using a single species stimulates synergistic, interdisciplinary studies. Table 1 briefly explores the benefits and disadvantages of *O. marina* to answer questions and guides the reader to the papers in this special issue. In general though, by preparing this special issue we have recognised *O. marina* emerging as a model in three distinct disciplines: ecology, evolution, and biogeography.

#### An ecological model

Several of the papers in this special issue explore the utility of *O. marina* in aut- and synecological contexts. Although *O. marina* is rarely pelagic and is virtually never found in open ocean waters (Watts *et al.*, this issue), it has been used as a proxy for a range of fundamental processes that relate to marine planktonic protozoa, which are recognised as a key component of pelagic food web dynamics (e.g. Sherr and Sherr, 2002). Mainly because this taxon is easy to obtain, identify, and rear in the laboratory (Lowe *et al.*, this issue-a,b;

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Montagnes *et al.*, this issue), *O. marina* has been extensively characterised in terms of its growth, feeding, swimming behaviour, and response to chemical stimuli (Boakes *et al.*, this issue; Breckels *et al.*, this issue; Montagnes *et al.*, this issue; Roberts *et al.*, this issue). Furthermore, *O. marina* is consumed by a number of planktivores (Yang *et al.*, this issue), and some data are available for predation rates upon it. In turn, *O. marina*-based responses have been embedded into various numeric models to assess a range of ecological processes (Davidson *et al.*, this issue). Davidson *et al.* (this issue) provide a detailed consideration of the pros and cons of using *O. marina* as an ecological model, and we refer the reader to this work, but in general, there is a clear indication that, although it is far from perfect, *O. marina* is and will continue to be used as an ecological model organism.

### **An evolutionary model**

Because of its phylogenetic position, *O. marina* constitutes an increasingly useful model to understand the origin and evolution of a range of unusual cellular and molecular features within the alveolates, particularly dinoflagellates (Slamovits and Keeling, this issue); this research has been facilitated by its ease of maintenance and near-global availability (Lowe *et al.*, this issue-a,b; Watts *et al.*, this issue). *Oxyrrhis marina* seems to have diverged very early in the branch leading to the dinoflagellate lineage, close to the time that dinoflagellates diverged from apicomplexans (Saldarriaga *et al.*, 2003; Slamovits *et al.*, 2007).

Consequently, it possesses morphological, cytological, and genetic features common with its near phylogenetic neighbours as well as exhibiting interesting taxon-specific characteristics (Slamovits and Keeling, this issue; Lowe *et al.*, this issue-a). In addition the recognition of several genetically diverse lineages within the *O. marina* morphospecies represents a useful pool of genomic variation to elucidate processes that occurred during the evolution of the



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dinoflagellates and the development of derived “*Oxyrrhis*” characteristics (Lowe *et al.*, 2010; this issue-a). Advances in culturing strategies to allow axenic maintenance of *O. marina* (Lowe *et al.*, this issue-b) combined with the increasing availability of low-cost high-throughput sequencing mean that *O. marina* is likely to continue to represent an important model for evolution and comparative genomics of alveolates in the coming decades.

### **A model for biogeography**

A further benefit of its wide geographic range is that *O. marina* can be a useful model to examine hypotheses concerning factors that affect distribution and dispersal of protists (Watts *et al.*, this issue). In addition, an increasing pool of intraspecific genetic diversity within *O. marina* has been uncovered, and there is some indication that this genetic variation is spatially structured (Lowe *et al.*, 2010). Thus, although an area of research in its infancy, the pattern and distribution of *O. marina* clades appear to represent a useful model to examine both 1) the relative influences of evolutionary processes such as selection, dispersal, and genetic drift on the distribution of functional and neutral diversity and 2) the influences of historical contingency and anthropogenic transport in shaping patterns of biodiversity among populations of free-living marine protists.

### **Synergism**

Combining the potential of *O. marina* to act as an ecological, evolutionary, and biogeographic model offers opportunity for synergism. Here we present a few examples of such works, based on our own research: Lowe *et al.* (2005) have examined how *O. marina* ecophysiology and distribution may be related; Lowe *et al.* (2010) have explored the extent of biogeographical distributions of distinct *O. marina* clades; the Roberts-group are adapting

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4 methods developed for metazoan phagocytic blood cells to investigate prey recognition by *O.*  
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7 *marina* (e.g. Wootton *et al.*, 2007); Keeling and Slamovits have uncovered exciting genetic  
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9 patterns (Slamovits and Keeling, 2008; Slamovits and Keeling, this issue) and together with  
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11 Watts, Lowe, and Montagnes (Lowe *et al.*, unpublished data) are producing a range of  
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13 genomic resources (sequence data, EST libraries) that may have wide ecological and  
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15 evolutionary applicability. Clearly, if *O. marina* continues to be studied at an escalating rate  
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17 (Fig. 1), there will be a concomitant increase in both realised and potential synergies.  
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21 A survey of 36 papers, since 1990, that mention *O. marina* in the title indicated ~55%  
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23 were aut- or synecologically based, ~40% examined some aspect related to evolutionary or  
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25 genetic biology, and ~5% were associated with distributional patterns; few of these ~5-10%,  
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27 however, displayed any form of rigorous cross-disciplinary evaluation. There is thus scope to  
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29 study many aspects of *O. marina* biology (Table 1), and there is clearly potential for cross-  
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31 disciplinary studies. Consequently, it appears that this species may eventually become a  
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33 robust model, following in the footsteps (pseudopodial streaks?) of such protists as *Amoeba*,  
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35 *Dictyostelium*, and *Paramecium*. The remainder of this special issue sets the stage for such  
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37 exploration and then reviews and explores means by which *O. marina* can and cannot act as a  
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39 model to address questions.  
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57 special issue.  
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For Peer Review

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## FIGURE LEGENDS

**Fig. 1.** Publications (books and journal articles) per year on *Oxyrrhis marina*, dating from its description. Data were obtained from the Web of Knowledge and augmented by sources that we have found elsewhere.

**Fig. 2.** *Oxyrrhis marina*. a. a bloom of *O. marina* in an intertidal pool on the Isle of Man (courtesy of T. Shammon). b. *O. marina* in culture. c. *O. marina* membrane proteins, showing the distinctive pink colouration (which it exhibits even when raised on a diet of heat killed bacteria lacking any pink pigmentation), characteristic of this species (courtesy of E. C. Wootton).

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Table 1 Characteristics of a model species, partially obtained from Bahls *et al.* (2003), an indication of how well *Oxyrrhis marina* fits these, and a guide to relevant papers in this special issue.

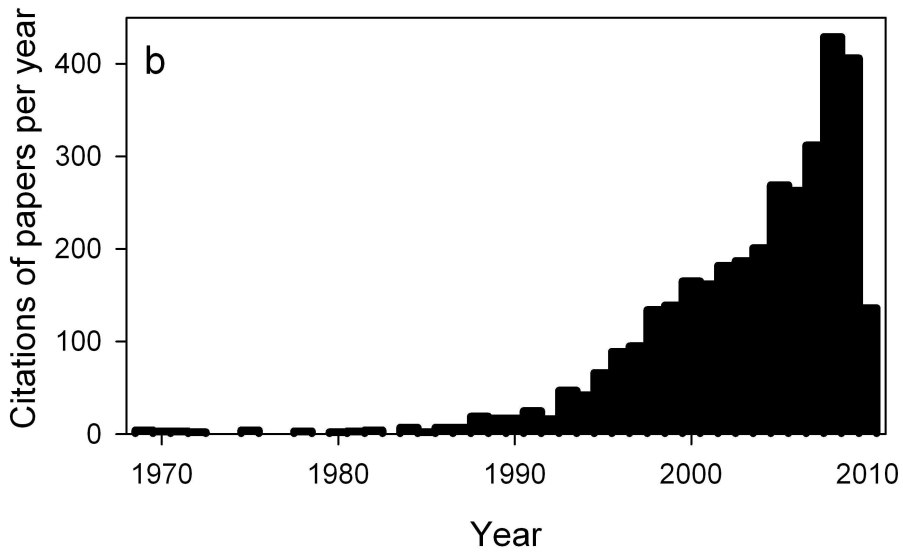
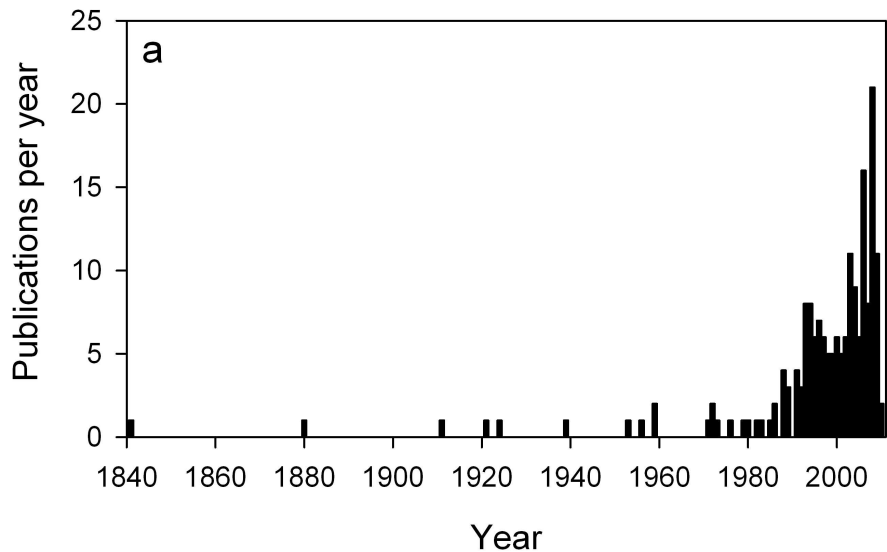
A model species should be:	Level to which <i>O. marina</i> possesses this trait		Paper in the special
	Positive	Negative	
easier to study than the target it is modelling	<ul style="list-style-type: none"> <li>Generally this seems to be so</li> </ul>		
relevant: <ul style="list-style-type: none"> <li>ecologically</li> <li>economically</li> <li>evolutionarily</li> <li>genetically</li> <li>behaviourally</li> </ul>	<ul style="list-style-type: none"> <li>Mimics pelagic species</li> <li>Can shed light on the biology of toxic (human health, fisheries) and parasitic dinoflagellates</li> <li>Can help understand aspects of the biology and evolution of apicomplexans</li> <li>Economic potential as a food supplement in fin-fish aquaculture</li> <li>Novel phylogenetic position; thus useful to model evolutionary divergence between apicomplexans and dinoflagellates</li> <li>Unusual genetic and genomic architecture; thus, interesting as an example of novel/non-typical eukaryotic genome organisation</li> <li>Highly adaptable feeding behaviour and broad diet range – useful to explore a wide range of feeding and swimming mechanisms</li> </ul>	<ul style="list-style-type: none"> <li>Rare in open water; thus not a true plankton representative</li> <li>Limited direct economic applications</li> <li>Unusual and, therefore, unlikely to represent a useful model of wider taxonomic groups</li> <li>Genome is potentially large and repetitive, and thus large scale sequencing is likely to be challenging</li> </ul>	Boakes <i>et al.</i> (this issue) Breckels <i>et al.</i> (this issue) Davidson <i>et al.</i> (this issue) Slamovits & Keeling (this issue) Lowe <i>et al.</i> (this issue-a) Roberts <i>et al.</i> (this issue) Watts <i>et al.</i> (this issue) Yang <i>et al.</i> (this issue)
small	<ul style="list-style-type: none"> <li>Big enough to see and isolate under a dissection microscope</li> </ul>	<ul style="list-style-type: none"> <li>Motile thus requires practice needed to isolate single cells</li> </ul>	
inexpensive to obtain, maintain, and practical to use	<ul style="list-style-type: none"> <li>Can be collected all over the world, and cultures established with ease</li> </ul>	<ul style="list-style-type: none"> <li>Poorly characterised strain variation; not all strains are easy to maintain in culture</li> </ul>	Lowe <i>et al.</i> (this issue-b)
not rare or threatened	<ul style="list-style-type: none"> <li>Given the wide distribution and abundance, it appears not to be rare or threatened</li> </ul>		Watts <i>et al.</i> (this issue)
easy to identify	<ul style="list-style-type: none"> <li>Distinctive morphology</li> </ul>	<ul style="list-style-type: none"> <li>Several clades that may be distinct (cryptic) species</li> </ul>	Lowe <i>et al.</i> (this issue-b)
easy to culture	<ul style="list-style-type: none"> <li>Can be grown on a wide range of food under a wide range of conditions</li> <li>Individual strains have been maintained in culture collections for decades</li> </ul>		Lowe <i>et al.</i> (this issue-b) Montagnes <i>et al.</i> (this issue)



Montagnes *et al.* 1. Introduction to the *Oxyrrhis marina* special issue

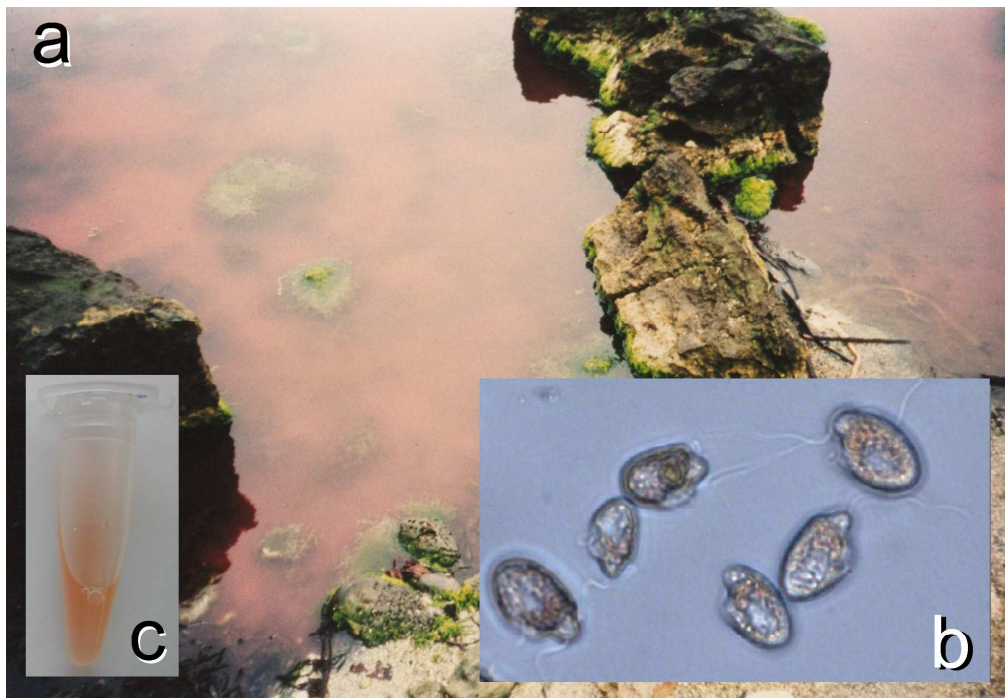
easy to manipulate in experiments (e.g. robust to manipulation)	<ul style="list-style-type: none"> <li>Individual can be transferred easily</li> <li>Withstands sorting in flow cytometers</li> </ul>		Lowe <i>et al.</i> (this issue-b) Montagnes <i>et al.</i> (this issue)
able to survive storage (e.g. cryopreservation)	<ul style="list-style-type: none"> <li>For many strains, cultures can be virtually ignored for weeks</li> </ul>	<ul style="list-style-type: none"> <li>Has yet to be successfully cryopreserved</li> </ul>	Lowe <i>et al.</i> (this issue-b)
fecund, with rapid generation times	<ul style="list-style-type: none"> <li>Up to ~ 2 divisions per day, which is reasonably rapid for protozoa of its size</li> </ul>	<ul style="list-style-type: none"> <li>Life cycle poorly understood</li> </ul>	Montagnes <i>et al.</i> (this issue)
able to produce clonal lines (to separate environmental from genetic effects)	<ul style="list-style-type: none"> <li>This has been well established</li> </ul>		Lowe <i>et al.</i> (this issue-b)
stable in characteristics over many generations		<ul style="list-style-type: none"> <li>This has yet to be rigorously tested</li> </ul>	
genetically/physiological variable (where appropriate)	<ul style="list-style-type: none"> <li>Appears to do so across local and global scales</li> </ul>		Lowe <i>et al.</i> (this issue-b)
useful for interdisciplinary (e.g. molecular-ecological-numeric modelling) use	<ul style="list-style-type: none"> <li>There have been a few such studies, and there is great potential for future ones</li> <li>Has been used to parameterise a range of functional response relationships and mathematical models</li> </ul>	<ul style="list-style-type: none"> <li>limited data sets exist with which to test model predications</li> </ul>	Lowe <i>et al.</i> (this issue-b) Roberts <i>et al.</i> (this issue) Davidson <i>et al.</i> (this issue)
long-standing, with a history of use and substantial background	<ul style="list-style-type: none"> <li>There is over 100 years of research on it</li> </ul>	<ul style="list-style-type: none"> <li>There are differences in strain responses, making interpretation of past, unqualified, studies difficult</li> </ul>	Lowe <i>et al.</i> (this issue-a) Montagnes <i>et al.</i> (this issue) Roberts <i>et al.</i> (this issue)
unemotive (e.g. not being a target for animal rights)	<ul style="list-style-type: none"> <li>Protists do not tend to elicit emotive responses</li> </ul>		

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Review