JOURNAL OF PLANKTON RESEARCH | VOLUME 33 | NUMBER 4 | PAGES 549–554 | 2011

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

DAVID J. S. MONTAGNES[1]*, CHRIS D. LOWE[1], EMILY C. ROBERTS[2], MARK N. BRECKELS[3], DAN E. BOAKES[3], KEITH DAVIDSON[4], PATRICK J. KEELING[5], CLAUDIO H. SLAMOVITS[6], MICHAEL STEINKE[3], ZHOU YANG[7] AND PHILLIP C. WATTS[1]

[1]SCHOOL OF BIOLOGICAL SCIENCES, UNIVERSITY OF LIVERPOOL, BIOSCIENCES BUILDING, LIVERPOOL L69 7ZB, UK, [2]PURE AND APPLIED ECOLOGY, SWANSEA UNIVERSITY, SINGLETON PARK, SWANSEA SA2 8PP, UK, [3]DEPARTMENT OF BIOLOGICAL SCIENCES, UNIVERSITY OF ESSEX, COLCHESTER CO4 3SQ, UK, [4]SCOTTISH ASSOCIATION FOR MARINE SCIENCE, SCOTTISH MARINE INSTITUTE, OBAN, ARGYLL PA37 1QA, UK, [5]DEPARTMENT OF BOTANY, UNIVERSITY OF BRITISH COLUMBIA, 3529-6270 UNIVERSITY BOULEVARD, VANCOUVER, BC, CANADA V6T 1Z4, [6]DEPARTMENT OF BIOCHEMISTRY AND MOLECULAR BIOLOGY, DALHOUSIE UNIVERSITY, HALIFAX, NOVA SCOTIA, CANADA AND [7]JIANGSU PROVINCE KEY LABORATORY FOR BIODIVERSITY AND BIOTECHNOLOGY, SCHOOL OF BIOLOGICAL SCIENCES, NANJING NORMAL UNIVERSITY, NANJING 210046, CHINA

*CORRESPONDING AUTHOR: dmontag@liv.ac.uk

Received May 12, 2010; accepted in principle August 9, 2010; accepted for publication August 18, 2010

Corresponding editor: John Dolan

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 Being written by experts in their respective fields, the authors have included unpublished data and in all cases have offered a synthesis of data and ideas.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, emphasizing 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 recognize *O. marina* as a model in three distinct disciplines: ecology, evolution/genomics and biogeography. Of possibly greater importance, we recognize that if *O. marina* continues to be studied at an escalating rate, there will be a concomitant increase in realized and potential synergies across these fields.

KEYWORDS: *Oxyrrhis marina*; review; dinoflagellate; experimental design

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* (Fig. 1), but given the current interest and the rapidly increasing amount of the literature on this taxon (Fig. 2), 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, emphasizing and stimulating the interdisciplinary nature

doi:10.1093/plankt/fbq121, available online at www.plankt.oxfordjournals.org. Advance Access publication October 7, 2010

Fig. 1. *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 coloration (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).

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

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

There can be no defined set of attributes to describe an ideal "lab rat" that provides a solution to all questions. However, there are general traits that we might consider as useful (Table I). Furthermore, each field of research will inevitably impose unique criteria when selecting models, and organisms are thus often chosen for a specific need (see Bahls *et al*., 2003); although in some cases there appears to be some intellectual inertia, as a model originally used for one purpose is adopted for others, at times with serendipitous consequences (e.g. *Drosophila melanogaster*, Roberts, 2006). It is, therefore, not our intention to suggest that the heterotrophic dinoflagellate, *O. marina*, can act as a model in an absolute sense; instead, we address its general and specific versatility.

Oxyrrhis marina has been routinely used in experiments for over 100 years, and its application appears to be rising exponentially across a number of fields (Fig. 2a). Certainly, citations related to *O. marina*-related research are increasing rapidly (Fig. 2b), reflecting its widespread distribution, small size, utility in addressing ecological issues and crucially its experimental tractability. Thus,

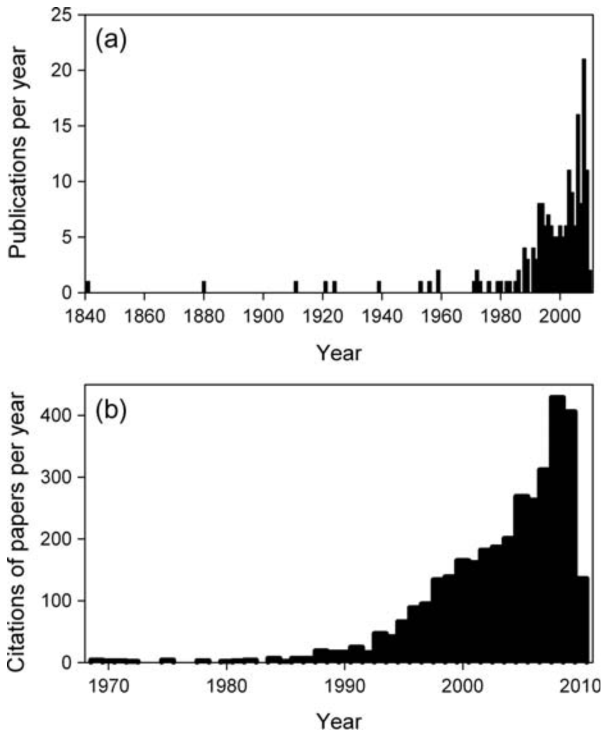

Fig. 2. Publications (books and journal articles) per year on *Oxyrrhis marina*, dating from its description. Data were obtained from the Web of Knowledge and augmented by sources that we have found elsewhere.

we suggest that *O. marina* is an "emerging model organism". In the following sections, we reflect on the broad appeal of *O. marina* to address a range of questions across a hierarchical scale, from genetic processes to aut- and synecological issues. 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 I 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 recognized *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.*, 2011), it has been used as a proxy for a range of fundamental processes that relate to marine planktonic protozoa, which are recognized 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.*, 2011a,b; Montagnes *et al.*, 2011), *O. marina* has been extensively characterized in terms of its growth, feeding, swimming behaviour and response to chemical stimuli (Boakes *et al.*, 2011; Breckels *et al.*, 2011; Montagnes *et al.*, 2011; Roberts *et al.*, 2011). Furthermore, *O. marina* is consumed by a number of planktivores (Yang *et al.*, 2011), 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.*, 2011). Davidson *et al.* (Davidson *et al.*, 2011) 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, 2011); this research has been facilitated by its ease of maintenance and near-global availability (Lowe *et al.*, 2011a,b; Watts *et al.*, 2011). *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,

Table I: 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 *O. marina* possesses this trait: Positive	Negative	Paper in the special
Easier to study than the target it is modelling	Generally this seems to be so		
Relevant: • Ecologically • Economically • Evolutionarily • Genetically • Behaviourally	• Mimics pelagic species • Can shed light on the biology of toxic (human health, fisheries) and parasitic dinoflagellates • Can help understand aspects of the biology and evolution of apicomplexans • Economic potential as a food supplement in fin-fish aquaculture • Novel phylogenetic position; thus useful to model evolutionary divergence between apicomplexans and dinoflagellates • Unusual genetic and genomic architecture; thus, interesting as a an example of novel/non-typical eukaryotic genome organization • Highly adaptable feeding behaviour and broad diet range—useful to explore a wide range of feeding and swimming mechanisms	• Rare in open water; thus not a true plankton representative • Limited direct economic applications • Unusual and, therefore, unlikely to represent a useful model of wider taxonomic groups • Genome is potentially large and repetitive, and thus large scale sequencing is likely to be challenging	Boakes *et al.*, 2011; Breckels *et al.*, 2011; Davidson *et al.*, 2011; Slamovits and Keeling, 2011; Lowe *et al.*, 2011a; Roberts *et al.*, 2011; Watts *et al.*, 2011; Yang *et al.*, 2011
Small	Big enough to see and isolate under a dissection microscope	Motile thus requires practice needed to isolate single cells	
Inexpensive to obtain, maintain and practical to use	Can be collected all over the world, and cultures established with ease	Poorly characterized strain variation; not all strains are easy to maintain in culture	Lowe *et al.*, 2011b
Not rare or threatened	Given the wide distribution and abundance, it appears not to be rare or threatened		Watts *et al.*, 2011
Easy to identify	Distinctive morphology	Several clades that may be distinct (cryptic) species	Lowe *et al.*, 2011b
Easy to culture	• Can be grown on a wide range of food under a wide range of conditions • Individual strains have been maintained in culture collections for decades		Lowe *et al.*, 2011b; Montagnes *et al.*, 2011
Easy to manipulate in experiments (e.g. robust to manipulation)	• Individual can be transferred easily • Withstands sorting in flow cytometers		Lowe *et al.*, 2011b; Montagnes *et al.*, 2011
Able to survive storage (e.g. cryopreservation)	For many strains, cultures can be virtually ignored for weeks	Has yet to be successfully cryopreserved	Lowe *et al.*, 2011b
Fecund, with rapid generation times	Up to ~2 divisions per day, which is reasonably rapid for protozoa of its size	Life cycle poorly understood	Montagnes *et al.*, 2011
Able to produce clonal lines (to separate environmental from genetic effects)	This has been well established		Lowe *et al.*, 2011b
Stable in characteristics over many generations		This has yet to be rigorously tested	
Genetically/physiological variable (where appropriate)	Appears to do so across local and global scales		Lowe *et al.*, 2011b

Continued

Table I: Continued

A model species should be:	Level to which *O. marina* possesses this trait		Paper in the special
	Positive	Negative	
Useful for interdisciplinary (e.g. molecular–ecological–numerical modelling) use	• There have been a few such studies, and there is great potential for future ones • Has been used to parameterize a range of functional response relationships and mathematical models	Limited data sets exist with which to test model predications	Lowe *et al*., 2011b; Roberts *et al*., 2011; Davidson *et al*., 2011
Long-standing, with a history of use and substantial background	There is over 100 years of research on it	There are differences in strain responses, making interpretation of past, unqualified, studies difficult	Lowe *et al*., 2011a; Montagnes *et al*., 2011; Roberts *et al*., 2011
Unemotive (e.g. not being a target for animal rights)	Protists do not tend to elicit emotive responses		

2011; Lowe *et al*., 2011a). 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 dinoflagellates and the development of derived "*Oxyrrhis*" characteristics (Lowe *et al*., 2010; 2011a). Advances in culturing strategies to allow axenic maintenance of *O. marina* (Lowe *et al*., 2011b) 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*., 2011). 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 (i) the relative influences of evolutionary processes such as selection, dispersal and genetic drift on the distribution of functional and neutral diversity and (ii) 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*. (Lowe *et al*., 2005) have examined how *O. marina* ecophysiology and distribution may be related; Lowe *et al*. (Lowe *et al*., 2010) have explored the extent of biogeographical distributions of distinct *O. marina* clades; the Roberts-group are adapting methods developed for metazoan phagocytic blood cells to investigate prey recognition by *O. marina* (e.g. Wootton *et al*., 2007); Keeling and Slamovits have uncovered exciting genetic patterns (Slamovits and Keeling, 2008, 2011) and together with Watts, Lowe and Montagnes (Lowe *et al*., unpublished data) are producing a range of genomic resources (sequence data, EST libraries) that may have wide ecological and evolutionary applicability. Clearly, if *O. marina* continues to be studied at an escalating rate (Fig. 1), there will be a concomitant increase in both realized and potential synergies.

A survey of 36 papers, since 1990, that mention *O. marina* in the title indicated ~55% were aut- or synecologically based, ~40% examined some aspect related to evolutionary or genetic biology and ~5% were associated with distributional patterns; few of these ~5–10%, however, displayed any form of rigorous cross-disciplinary evaluation. There is thus scope to study many aspects of *O. marina* biology (Table I), and there is clearly potential for cross-disciplinary studies. Consequently, it appears that this species may eventually become a robust model, following in the footsteps (pseudopodial streaks?) of such protists as *Amoeba*, *Dictyostelium* and *Paramecium*. The remainder of this special issue sets the stage for such exploration and then reviews and explores means by which *O. marina* can and cannot act as a model to address questions.

ACKNOWLEDGEMENTS

The Authors would like to thank Emma Wootton and Fiona Hobden for their constructive comments on this manuscript. We would also like to thank Susanne Menden-Deuer and two anonymous reviewers for their constructive suggestions. Finally, we wish to recognize the outstanding editorial efforts made by John Dolan and Roger Harris in the production of this special issue.

FUNDING

This work was, in part, supported by a UK NERC grant (NE/F005237/1) awarded to P.C.W., C.D.L. and D.J.S.M.; UK NERC grants NE/C519438/1 and NE/G010374/1 awarded to E.C.R. and E. Dudley; SAMS/NERC Oceans 2025 programme supporting K.D.; grants from the Tula Foundation and the Canadian Institute for Advanced Research, awarded to C.S.; and a Project of International Cooperation and Exchanges from the National Natural Science Foundation of China (30970500) awarded to Y.Z.

REFERENCES

Bahls, C., Weitzman, J. and Gallagher, R. (2003) Biology's models. *Scientist*, **17**, 5.

Behringer, R. R., Johnson, A. D., Krumlauf, R. E. *et al.* (2009) *Emerging Model Organisms: v. 1: A Laboratory Manual*. Cold Spring Harbor Laboratory Press.

Boakes, D. E., Codling, E. A., Thorn, G. J. *et al.* (2011) Analysis and modelling of swimming behaviour in *Oxyrrhis marina*. *J. Plankton Res.*, **33**, 641–649.

Breckels, M. N., Roberts, E. C., Archer, S. D. *et al.* (2011) The role of dissolved infochemicals in mediating predator–prey interactions in the heterotrophic dinoflagellate *Oxyrrhis marina*. *J. Plankton Res.*, **33**, 629–639.

Davidson, K., Sayegh, F. and Montagnes, D. J. S. (2011) *Oxyrrhis marina*-based mathematical models as a tool to interpret protozoan population dynamics. *J. Plankton Res.*, **33**, 651–663.

Hedges, S. B. (2002) The origin and evolution of model species. *Nat. Rev. Gen.*, **3**, 838–849.

Krebs, H. A. (1975) The August Krogh principle: for many problems there is an animal on which it can be most conveniently studied. *J. Exp. Zool.*, **194**, 221–226.

Lowe, C. D., Keeling, P. J., Martin, L. E. *et al.* (2011a) Who is *Oxyrrhis marina*? Morphological and phylogenetic studies on an unusual dinoflagellate. *J. Plankton Res.*, **33**, 555–567.

Lowe, C. D., Martin, L. E., Roberts, E. C. *et al.* (2011b) Collection, isolation and culturing strategies for *Oxyrrhis marina*. *J. Plankton Res.*, **33**, 569–578.

Lowe, C. D., Kemp, S. J., Bates, A. D. *et al.* (2005) There are high levels of functional and genetic diversity on *Oxyrrhis marina*. *J. Euk. Microbiol.*, **52**, 250–257.

Lowe, C. D., Montagnes, D. J. S., Martin, L. E. *et al.* (2010) Patterns of genetic diversity in the marine heterotrophic flagellate *Oxyrrhis marina* (Alveolata: Dinophyceae). *Protist*, **161**, 212–221.

Montagnes, D. J. S., Lowe, C. D., Martin, L. E. *et al.* (2011) *Oxyrrhis marina* growth, sex and reproduction. *J. Plankton Res.*, **33**, 615–627.

Nanney, D. L. (1980) *Experimental Ciliatology: an Introduction to Genetic and Developmental Analysis in Ciliates*. John Wiley & Sons, New Jersey.

Roberts, D. B. (2006) *Drosophila melanogaster*: the model organism. *Entomol. Exp. App.*, **121**, 93–103.

Roberts, E. C., Wooton, E. C., Davidson, K. *et al.* (2011) Feeding in the dinoflagellate *Oxyrrhis marina*: linking behaviour with mechanisms. *J. Plankton Res.*, **33**, 603–614.

Saldarriaga, J. F., McEwan, M. L., Fast, N. M. *et al.* (2003) Multiple protein phylogenies show that *Oxyrrhis marina* and *Perkinsus marinus* are early branches of the dinoflagellate lineage. *Int. J. Syst. Evol. Microbiol.*, **53**, 355–365.

Sherr, E. B. and Sherr, B. F. (2002) Significance of predation by protists in aquatic microbial food webs. *Anton. Leeuw. Int. J. G.*, **81**, 293–308.

Slamovits, C. H. and Keeling, P. J. (2011) Contributions of *Oxyrrhis marina* to molecular biology, genomics and organelle evolution of dinoflagellates. *J. Plankton Res.*, **33**, 591–602.

Slamovits, C. H. and Keeling, P. J. (2008) Plastid-derived genes in the nonphotosynthetic alveolate *Oxyrrhis marina*. *Mol. Biol. Evol.*, **25**, 1297–1306.

Slamovits, C. H., Saldarriaga, J. F., Larocque, A. *et al.* (2007) The highly reduced and fragmented mitochondrial genome of the early-branching dinoflagellate *Oxyrrhis marina* shares characteristics with both apicomplexan and dinoflagellate mitochondrial genomes. *J. Mol. Biol.*, **372**, 356–368.

Watts, P. C., Martin, L. E., Kimmance, S. A. *et al.* (2011) The distribution of *Oxyrrhis marina*: a global wanderer or poorly characterized endemic? *J. Plankton Res.*, **33**, 579–589.

Wootton, E. C., Zubkov, M. V., Jones, D. H. *et al.* (2007) Biochemical prey recognition by planktonic protozoa. *Environ. Microbiol.*, **9**, 216–222.

Yang, Z., Jeong, H. J. and Montagnes, D. J. S. (2011) The role of *Oxyrrhis marina* as a model prey: current work and future directions. *J. Plankton Res.*, **33**, 665–675.