



Oxyrrhis marina based models as a tool to interpret protozoan population dynamics

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**Oxyrrhis marina based models as a tool to interpret
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ABSTRACT

Oxyrrhis marina based experiments have frequently been used to underpin the construction and, or, parameterization of protozoan mathematical models. Initially, we examine the suitability and limitations of *O. marina* for this task. Subsequently, we summarise the range of aut- and synecological modelling studies based on *O. marina*, examining the questions asked and conclusions drawn from these, along with the range of processes and functions employed within the models. Finally, we discuss future modelling directions based on studies of *O. marina*.

Key Words: review, dinoflagellate, experimental design

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23 INTRODUCTION

24 With improved understanding of the pivotal role that protozoa play within microbial food webs (Azam
25 *et al.*, 1983; Pomeroy *et al.*, 2007), an increasing body of experimental work has investigated their
26 response to a range of environmental conditions. Knowledge of the functional relationships that
27 underpin protozoan growth and grazing, in turn, allows us to derive mathematical models that represent
28 their behaviour. Such protozoa-specific modelling studies provide a means of understanding predator-
29 prey interactions than could not be achieved from observation alone. Furthermore, the specific
30 inclusion of protozoa within more general population and ecosystem models allows us to assess their
31 role in the natural environment. Finally, as protozoa exhibit rapid generation times and are easily
32 manipulated, they are an excellent tool for population dynamic studies and model parameter generation
33 in general. Protozoa have, therefore, for a considerable time been used as the basis for mathematical
34 models of population growth (e.g. Gause, 1936; Painting *et al.*, 1993; Fenton *et al.*, 2010). Inevitably,
35 such models are derived for the species that we can grow in the laboratory, and for planktonic protozoa
36 these have proven to be few. This paper is about one such species, *Oxyrrhis marina*, that can act as a
37 model for others and the insights that have been obtained from mathematical models based on its study.

38 The heterotrophic flagellate *O. marina* is an ideal candidate organism for the experimental
39 study and modelling of the natural and theoretical population dynamics of protozoan predators. It is
40 easy to find, isolate, maintain in culture and manipulate in the laboratory and has been maintained in
41 culture for over 50 years in a number of culture collections (see Montagnes *et al.*, this issue-a).
42 *Oxyrrhis marina* is, therefore, often a natural choice as a model organism and is extensively used for
43 experimental studies, some of which have been employed to develop or parameterise mathematical
44 models. Within this paper we review the literature to: 1) examine the limitation of using *O. marina* as
45 a model organism; 2) indicate the breadth of responses and functions that are available for its use, and

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thus facilitates mathematical model development; 3) summarize modelling studies that have been conducted with *O. marina*, and briefly review the questions asked and conclusions drawn from these; and finally 4) discuss continued directions of research for modelling studies using *O. marina*.

TO WHAT EXTENT IS OXYRRHIS MARINA A REPRESENTATIVE MODEL ORGANISM?

Meta analysis studies (e.g. Hansen *et al.*, 1997) suggest that *O. marina* is representative of the dinoflagellates. However, phagotrophic protozoa are diverse and abundant organisms in aquatic environments, including taxa typically with a size range of 2-200 μm (Montagnes *et al.*, 2008a). Hence, no single species or even genus will be representative of the functional group, and championing *O. marina* as a representative of the heterotrophic dinoflagellates or even heterotrophic protists *en mass* raises some reservations. Therefore, we first consider factors that may limit the general applicability of *O. marina* based results to phagotrophic protozoa.

Mode of nutrition

Oxyrrhis marina is a raptorial feeder that directly engulfs its prey. Although protozoa exhibit a range of nutritional modes (Montagnes *et al.*, 2008a), many, and possibly most, of the protozoa in aquatic pelagic ecosystems (e.g. ciliates, flagellates) also engulf their prey, and thus *O. marina* might be considered directly comparable to these. Furthermore, anecdotal data suggest that *O. marina* ingests prey between 1 - 12 μm , indicating that its predator:prey size ratio includes, but also exceeds, the approximate 10:1 ratio predicted by others (e.g. Azam *et al.*, 1983). Thus, as a first approximation we support the use of *O. marina* as a model organism in this sense.

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Habitat

Oxyrrhis marina is rarely seen in pelagic samples, although “red-tide” blooms occur in large bays, reaching up to 10^5 cells ml^{-1} , and it can regularly be found in some estuaries at abundances of 10 - 100 ml^{-1} (Johnson *et al.*, 2003; Begun *et al.*, 2004; Jeong *et al.*, 2004). In contrast, *O. marina* is typically found in shallow waters associated with the shoreline, such as splash pools and tide pools, (Johnson, 2000; Kimmance *et al.*, 2006). Still, *O. marina* is planktonic, not benthic, and in mixed cultures remains well distributed (Davidson, Montagnes, unpublished data), although it may accumulate at mid-water column interfaces (Menden-Deuer and Grünbaum, 2006). Thus, again, in this sense it seems an appropriate model organism for planktonic processes. Furthermore, using protists associated with very shallow waters to model planktonic systems is not uncommon; much of the earlier work on protozoa, used to obtain rate processes and conversion factors for pelagic ecosystem models, has been obtained from semi-benthic species (e.g. Capriulo, 1990). Examples of such an approach include the semi-benthic rock pool dwelling *Stombidium sulcatum* (= *S. inclinatum*; see Modeo *et al.*, 2003) that has been extensively used to represent planktonic ciliates and the frequently studied mixotrophic chrysophyte *Ochromonas danica*, which was originally isolated from an acidic moor (Pringsheim, 1955). There is, thus, considerable precedence for using taxa like *O. marina* as model pelagic organisms, mainly because they are easy to grow, maintain, and collect, as indicated above. We, therefore again, support the past and continued use of the *O. marina*, with the codicil that it is not necessarily typical of open water taxa and should, ultimately, be compared to them.

Taxonomy

Oxyrrhis marina is unlikely to be a single species, and there are strain-differences in eco-physiological responses (Lowe *et al.*, 2005; Lowe *et al.*, 2010). There are serious implications regarding this point,

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related to population studies. For instance, the growth response of *O. marina* strains differs based on responses to: salinity (Lowe *et al.*, 2005a), prey concentration and type, and temperature (Montagnes, unpublished data). However, such strain-specific responses are far from unique to *O. marina*; e.g. similar strain-specific differences occur in a model freshwater ciliate, *Urotrichia* (Weisse and Montagnes, 1998). Thus, modellers must simply be aware of these differences and consider them when interpreting results. In fact, as strain differences are becoming topical in ecological research (see Weisse and Montagnes, 1998); this “problem” can become an asset, and modellers will undoubtedly begin to use the responses of the various strains to examine potential strain-succession, as we are at present doing (Yang *et al.*, submitted). Finally, modelling studies based on *O. marina* typically use defined strains, and we are exceptionally fortunate with *O. marina* that several commercial and personal culture collections have maintained these (Lowe *et al.*, this issue). Hence, notwithstanding the caveats highlighted above, and the recognition that further comparative studies of the behaviour of *O. marina* and other planktonic protozoa are required, *O. marina* seems fit for purpose as a representative protozoan, from which mathematical models can be derived.

OXYRRHIS MARINA BASED MATHEMATICAL MODELS

We, therefore, now turn to those studies that have derived or parameterised mathematical models based on *O. marina*. Broadly, these fall into two categories: 1) autecological studies that specifically simulate response of *O. marina* to a set of physical, biological, or chemical conditions and 2) synecological studies that embed *O. marina* based responses within food web simulations, to study the wider role of ecosystem processes. These models are reviewed, grouped in relation to the hypotheses tested, below with the mathematical responses that underpin them summarised (Table 1).

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Autecological models

Functional and numerical responses

Functional and numerical response relationships are often central to population models (Turchin, 2003), typically characterised by a rectangular hyperbolae or a “type II Holling” response. Such rectangular hyperbolic responses are used extensively to characterise the behaviour of protozoa (e.g. Taylor, 1978; Montagnes, 1996; Jeong *et al.*, 2004; Fenton *et al.*, 2010). Their suitability to simulate ingestion and growth of *O. marina* has been supported by a number of studies (Table 1, Eq. 1-2) on a range of prey species (for further details beyond the scope of this modelling based review, see Lowe *et al.*, this issue; Montagnes *et al.*, this issue-b; Roberts *et al.*, this issue). Modifications of these two responses (Table 1) are also fundamental to a number of the mathematical models that we review; e.g. Eq. 3 (Table 1) is a modified version of Eq. 2 (Table 1), where the numerical response is recognised to be negative below a threshold (p') abundance of prey (Fenton *et al.*, 2010). It is also important to note that, to our knowledge, for *O. marina* there are no data that suggest inhibition of growth or grazing rates at elevated prey concentrations, as has been indicated for other protozoa (e.g. Montagnes and Lessard, 1999), although see *Prey inhibition of grazing*, below.

The influence of abiotic factors

Various abiotic factors will modify protist (and specifically *O. marina*) population dynamics; e.g. salinity (Droop, 1959; Samuelsson *et al.*, 1996), turbulence (Peters and Marrasé, 2000), temperature (Montagnes *et al.*, 2003; Kimmance *et al.*, 2006), and pH (Droop, 1959; Pedersen and Hansen, 2003). Two *O. marina* modeling based studies have specifically sought to investigate the role of such abiotic factors.

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Temperature

Trends of increasing water temperature have the potential to influence the productivity and biodiversity of marine phytoplankton (Bresnan *et al.*, 2009). Understanding the temperature response of protozoa is equally important, as any temperature induced mismatch between predators and prey in pelagic communities could have significant implications for trophic transfer (Montagnes *et al.*, 2008a; Koeller *et al.*, 2009). Using *O. marina*, Kimmance *et al.* (2006) demonstrated the need for an adequate representation of temperature response by making a range of rate parameters within an *O. marina* model a (experimentally determined) function of temperature and prey density (Table 1, Eq. 4, 5). Furthermore, recognising that both prey abundance and temperature will alter cell volume, Kimmance *et al.* (2006) established a relationship between these and *O. marina* volume (Table 1, Eq. 6), allowing models to determine production in terms of carbon (assuming a relation between volume and carbon content; Menden-Deuer and Lessard, 2000). Application of these functions within a mathematical model demonstrated different dynamics when the full temperature-prey response was incorporated, in comparison to the more commonly used Q_{10} based function (see Montagnes *et al.*, 2003). The potential of these functions to improve model predictions, suggests that they should now be incorporated into larger ecosystem models.

Physical influences on the distribution of protozoan population

Protozoa may be locally and globally distributed by abiotic factors such as currents and wind driven aerosols. Models that assess such factors in governing distributions are potentially useful not only for protozoa but also for small metazoa, such as invertebrate larvae.

An example of abiotic influence is that of tidal action on coastal *O. marina* populations.

Johnson (2000) developed a simple mathematical model to study this phenomenon and specifically to

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test the hypothesis that *O. marina* has a competitive advantage that makes it prevalent in rock pool shoreline environments. The model simulated cell abundance in rock pools using a simple difference equation (Table 1, Eq. 8) to determine population size, based on the intrinsic population growth rate and the carrying capacity of the environment. The influence of flushing and the effects of extreme conditions on the upper shore were included in the model by making growth rate a function of pool location in relation to tidal height. The model predicted that *O. marina* distribution was influenced by both rock pool height on the shore and tidal cycle and that it differs from other protozoa in the pools, in that it is more stress tolerant. The stress tolerance of *O. marina* is consistent with its success in the rock pool habitat and its success in the (presumed somewhat stressful) conditions of laboratory culture. However, it also indicates that mathematical models based on *O. marina* are most appropriate for other stress tolerant protozoa, and observations of this species should be view in this light.

Other abiotic factors

Clearly, there is scope to extend modeling work on *O. marina* to examine other physical factors. There are data in the literature that would potentially allow a relationship between growth rate and salinity to be established (Droop 1959; Lowe *et al.*, 2005a); possibly assuming growth rate is quadratic function of salinity (Lowe *et al.*, 2005b). Similarly, the data of Droop (1959) and Pedersen and Hansen (2003) could be used to establish a growth response to pH, which superficially appears to be either sigmoidal or rectangular hyperbolic in shape. We have also conducted preliminary experiments to parameterize the influence of turbulence on growth of *O. marina* (Montagnes, unpublished data), following similar work on the autotrophic flagellate *Isochrysis galbana* (Downes-Tettmar and Montagnes, 2008), and it appears that only the level of turbulence generated by heavy wave action in rock pools will reduce *O. marina* growth rate. We, therefore, recommend that 1) further experimental data are collected on these

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physical parameters and 2) existing data are used to parameterize new functions for incorporation into models.

Swimming behaviour and aggregation

Study of *O. marina* to characterise the swimming behaviour of protists, is dealt with in a separate study (Boakes *et al.* this issue), and representation of *O. marina* searching trajectories using Lévy walk or other similar encounter statistics is discussed by Bartumeus *et al.* (2003) and Reynolds (2008). In a more general sense, modelling-based interpretation of *O. marina* foraging in response to prey aggregations was conducted by Menden-Deuer and Grünbaum (2006) who characterised the availability of patchy prey by means of the Frost number, a composite parameter based on forager speed, turning interval, distance between prey patches, and patch longevity. In addition, *O. marina* has also been used in models that assess mesozooplankton swimming and feeding (e.g. Mariani *et al.*, 2008). Thus, we see the potential for this species to be incorporated into multi-level behavioural models in the future.

Feeding behaviour

Protozoa can discriminate between prey types, with selective grazing, on the basis of prey quantity or quality, now being recognised as a key issue in the functioning of microbial food webs (Montagnes *et al.*, 2008a). A range of factors such as morphology, chemical defence, and nutritional quality may govern the selectivity of prey items by protozoa (Montagnes *et al.*, 2008a). The *O. marina*-based studies that have experimentally addressed these factors are not germane to our work, but the interested reader is directed to (Roberts *et al.*, this issue); here we specifically review how models have addressed feeding behaviour.

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207 *Modelling re-ingestion of faecal material*

208 Coprophagy is a well-recognised process in planktonic systems that may have considerable impact on

209 food web dynamics. For instance, low chlorophyll:phaeopigment ratios have been proposed to indicate

210 high levels of mesozooplankton coprophagy, but given the importance of microzooplankton in food

211 webs (e.g. Azam *et al.*, 1983; Davidson, 1996), it may be that they too are important in this process.

212 To this end, Strom (1993) developed a mathematical model to test the hypothesis that re-ingestion of

213 faecal material by protozoa could account for the observed variation in the conversion of chlorophyll to

214 phaeopigment. In this model, which was applied to her experiments on *Strombidium* and

215 *Gymnodinium* and to the *O. marina*-based data of Klein *et al.* (1986), protozoa preyed on

216 phytoplankton and faecal particles (with which phaeopigment was associated). Protozoan growth was

217 made a function of phytoplankton prey (Table 1, Eq. 1), with a selection factor for phytoplankton cells

218 or faecal particles that allowed the determination of an ingestion rate for faecal particles (Table 1, Eq.

219 9) and hence, by subtraction from the functional response, an ingestion rate for phytoplankton cells.

220 Although the model did not lend support to the notion that re-ingestion governed phaeopigment

221 distributions, it demonstrated that the re-ingestion of faecal material by protozoa was a plausible

222 trophic pathway that may have significant implications for energy flow within the microbial loop.

223

224 *Multi prey selectivity*

225 Following Strom's (1993) model-based demonstration of discrimination between live and dead food by

226 protozoa, the selection of alternative live prey by *O. marina* was addressed by Flynn *et al.* (1996) who

227 presented a theoretical relationship for the distance travelled by a raptorial predator to encounter a

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volume of prey equal its own volume (δ , Table 1, Eq. 10). To illustrate how such simulations are developed, below we use this model as an example.

The model was developed by first determining that the cross sectional area (S_p) of the encounter path for the predator and a given prey (p) species is $S_p = \pi(r_{pred} + r_p)^2$, where r_{pred} and r_p are the radius of the predator and prey cells, respectively. The rate of prey encounters per predator (E) was then given by $E = S_p \cdot N_p \cdot \sqrt{C_p^2 + C_{pred}^2}$, where predator and prey are speeds are C_{pred} and C_p , respectively, and N_p is the number of prey. The number of prey cells equivalent, in terms of biovolume, to one predator (N_{eq}) was then determined from $N_{eq} = V_{pred} \cdot V_p^{-1}$, where V_{pred} and V_p are mean predator and prey cell volumes, respectively. This allow the calculation of the encounter distance $\delta = N_{eq} \times \alpha \times (S_p \times p)^{-1}$, where $\alpha = C_{pred} \cdot \left(\sqrt{C_p^2 + C_{pred}^2} \right)^{-1}$.

If predation of a particular prey type continues when δ is greater than that of alternative prey, then the predator is deemed to select the former item. This concept was applied to a set of laboratory experiments in which *O. marina* ingested three differently sized prey species. The analysis demonstrated the occurrence of selection of live cells and suggested that selective grazing in microbial communities may be complex and dependent on both prey size and prey quality, both of which may change with time, rather than simple random encounter. Clearly, in this case, *O. marina* acted as a model organism to test general issues associated with selection.

Prey inhibition of grazing

The role of selective grazing in governing the temporal changes of both prey and predator was further studied by Davidson *et al.* (1995a) through simulation of two independent data sets: the *I. galbana*-*O.*

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249 *marina* study of Flynn and Davidson (1993b) and the multi prey-*O. marina* experiments of Flynn *et al.*

250 (1996).

251 Flynn and Davidson (1993b) suggested that *O. marina* initially ingested but then rejected the

252 flagellate prey, but Davidson *et al.* (1995a) found that no parameterization of a standard type II

253 functional response (Table 1, Eq. 1) generated adequate simulations of their data. Instead, qualitatively

254 better simulations were achieved if the maximum ingestion rate was made to decrease with continued

255 prey ingestion (Table 1, Eq. 11), a factor that was attributed to the build up of an inhibitor within *O.*

256 *marina* through the ingestion of the prey. The same model structure was also able to simulate the *O.*

257 *marina*-multiple prey data of Flynn *et al.* (1996). Thus, this *O. marina*-based model quantitatively

258 demonstrated that the quality of a prey item as well as its abundance or size may govern its suitability

259 as a prey item for protozoa. Given the tractability of using *O. marina* for grazing experiments (e.g.

260 Kimmance *et al.*, 2006), it would now seem appropriate to test these model predictions with empirical

261 data.

263 *Prey quality governing predator functional response*

264 The role of prey quality was further explored by Mitra *et al.* (2003) who hypothesized that it could

265 influence predation through modulation of either 1) the rate of ingestion (Table 1, Eq. 11), with “*a*” in

266 Eq. 11 being a variable rather than a constant or 2) the efficiency of assimilation of this ingested

267 material. The study examined the relative importance of these processes through a model that related

268 both maximum rate of predation and assimilation efficiency to prey quality (defined as its C:N ratio) in

269 a range of different functional forms. By making the maximum predation rate a function of prey

270 quality the model simulated experimentally observed phenomena exhibited by *O. marina* of “surge

271 feeding” (Öpik and Flynn, 1989) and prey rejection (Flynn *et al.*, 1996). In particular, this study

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indicated that while different functional formulations for ingestion and assimilation of prey caused the model to predicted similar trophic transfer of carbon, this occurred on very different timescales; demonstrating that such physiological responses of protozoa could influence the temporal availability of organic matter for trophic transfer. However, it is important to note that this response has yet to be documented for *O. marina*, and again we suggest that experiments in this direction are needed.

Prey quantity governing predator assimilation response

While Mitra *et al.* (2003) focused on the effect of prey quality on assimilation rate, Fenton *et al.* (2010) have explored the relationship between prey abundance and protozoan assimilation efficiency; they indicate that many protozoa, including *O. marina*, exhibit a decreasing assimilation efficiency with increasing prey concentration. Then, by comparing simple Rosenzweig-MacArthur-based predator - prey models (using *O. marina* and *I. galbana* parameters, derived from Kimmance *et al.*, 2006) with either a constant or variable assimilation efficiency, Fenton *et al.* (2010) indicate that prey carbon production may be increased by >65% when a variable assimilation efficiency is applied. Thus, using *O. marina* as a model, they conclude that, from an applied perspective, such as examining biomass productivity for food web dynamics or examining the recycling of nutrients within an ecosystem, including prey abundance-dependent assimilation efficiency leads to very different quantitative predictions from those given following commonly applied models.

Stoichiometry and selectivity

Mitra and Flynn (2005) continued to study the influence of stoichiometrically driven ingestion and assimilation, using a model that was optimized by fitting to the *I. galbana*-*O. marina* based data of Flynn and Davidson (1993b). The authors reached similar conclusions to Davidson *et al.* (1995a), with

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best simulations being obtained with “negative modulation” of ingestion; i.e. a decrease in ingestion rate on the flagellate in response to non optimal quality of this prey (Table 1, Eq. 11). However, when this analysis was extended to mesozooplankton-based data sets (Jones *et al.*, 2002), simulation required assimilation of non-optimal prey to also be linked to the prey quality. This difference was related to *O. marina*’s (and other protists’) lack of a gut and hence the greater likelihood of modulation at the point of capture and ingestion rather than digestion in protozoa.

Mitra (2006) extended the above work through the derivation of a generic multi-nutrient zooplankton model that included specific representation of both ingestion and assimilation, both of which were functions of prey nutrient stoichiometry, which she termed “stoichiometric modulation of predation”. This model was again fitted to the experimental data of Flynn and Davidson (1993b), with similar conclusions to those reached above; i.e. it is necessary to decrease ingestion rate for poor quality prey to obtain a fit of the model to the data.

In the most recent of their suite of *O. marina*-related publications Mitra and Flynn (2006) studied the influence of two alternative modeling formulations to represent predator selectivity. They incorporated either a ratio-based function (Fasham *et al.*, 1990, Table 1, Eq. 12) governed by the relative abundance of different prey types or made prey capture a function of prey availability and a capture rate parameter (Table 1, Eq. 13), that could take a range of functional forms based on prey quality (or other factors). Again, the model response was compared to the data of Flynn *et al.* (1996) and Flynn and Davidson (1993b). The new prey capture function (Eq. 13) was found to be most appropriate, albeit with the caveat that further modulation of ingestion based on prey quantity and quality was necessary to optimize the fit, a finding that is consistent with the models above.

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318 *The quantitative importance of nutrient regeneration and cycling*

319 While mathematical models are often used in predictive mode, an equally important application is the
320 analysis of processes that cannot be easily understood by simple observation. One of the most
321 important of these for microbial community population dynamics is the regeneration of inorganic
322 nutrients by protozoa, and their subsequent use by phytoplankton (Goldman *et al.*, 1987). This process
323 maintains the stoichiometric balance of nutrients within the predator and fuels further growth of the
324 prey (Caron, 1991).

325 To this end, Davidson *et al.* (1995b) studied nutrient regeneration using a predator-prey model
326 that included *O. marina* and *I. galbana*, to assess the response of different nitrogen (N) regeneration
327 equations. The model incorporated the phytoplankton growth model of Davidson *et al.* (1993) that
328 simulates both carbon (C) and N dynamics of *I. galbana* during unbalanced growth, allowing
329 simulation of experiments in which prey exhibit active growth. Again, as an example of how such
330 models are developed, we provide the relevant equations.

331 The equation for the rate of change of *I. galbana* N is give by

$$\frac{dI_{s_N}}{dt} = -E_{Is} \cdot Is - \left(\frac{Is_N}{Is} \right) \cdot I \cdot Ox,$$

333 and the rate of change of *O. marina* N was simulated by

$$\frac{dOx_N}{dt} = \left(\frac{Is_N}{Is} \right) \cdot I \cdot Ox - E_{Ox} \cdot Ox,$$

335 where Ox , Is , Ox_N , and Is_N represent the number and N-content of *O. marina* and *I. galbana*,
336 respectively; I is the ingestion rate of *O. marina*; and E_{Is} and E_{Ox} are the N-regeneration rates of *I.*
337 *galbana* and *O. marina*, respectively. Within the equations, N-regeneration by *O. marina* was
338 simulated either as a constant or on the basis of an “optimal” *O. marina* C:N ratio, using a range of N
339 regeneration models.

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340 The study demonstrated a need to include N-regeneration in protozoan based models to
341 adequately simulate experimental data. This model observation is consistent with many mathematical
342 models of microbial communities. However, such models often simulate this process in an
343 unsophisticated manner, making regeneration a constant amount of nutrient, independent of prey or
344 predator physiology or composition (Davidson, 1996). Using *O. marina*, Davidson *et al.*'s (1995b)
345 model lent support to arguments about protozoa made by Goldman *et al.* (1985) by indicating that a
346 dynamic (Table 1, Eq. 14, 15), rather than constant, regeneration rate must be applied to protozoan
347 nutrient cycling, indicating the utility of an *O. marina*-based model to provide more general insights. It
348 may now be possible to use developing methods, such as stable isotope labeling, to assess nutrient
349 cycling and assess empirically if *O. marina* behaves according to model predictions.

351 *Summary of autecological work*

352 Four main insights are clear from the above review of autecological models: 1) *O. marina* is useful as a
353 “model organism”; 2) there are *O. marina* experimental data in the literature that could be used to more
354 fully parameterize its numerical and functional response; 3) notwithstanding the previous point, we
355 need to collect more data to extend and improve upon the responses that need parameterization (e.g.
356 given concerns of ocean acidification, to pH); and 4) we need to extend our empirical testing of
357 predictions that have been obtained from *O. marina* based models.

359 **Synecological *Oxyrrhis marina* based models**

360 Above, our review has revealed an extensive range of autecological models associated with *O. marina*;
361 these provide an understanding of its behavior and how it can be used to assess key ecological
362 processes. Therefore it may be surprising that application of such *O. marina*-based models to study the

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influence of protozoa in food webs is, to date, relatively limited. To indicate how *O. marina* might be incorporated into larger models, we examine case studies, below.

Parameterising microplankton models

Lee *et al.* (2003) developed a carbon-nitrogen based model of the phytoplankton, bacterial, and protozoan components of a planktonic food web, which was embedded in a three layer physical framework. The protozoan model was developed as a single compartment with constant C:N ratio consistent with experimental and modeling results discussed above. *Oxyrrhis marina* parameters, from Fuller (1990), were used to parameterize the protozoan component of the model. Given the substantial increase in parameter estimates for *O. marina* over the past 15 years (Table 1) since Fuller (1990), it may be appropriate to revisit such models.

Control of toxic dinoflagellate blooms by microzooplankton and parasites

Montagnes *et al.* (2008b) incorporated *O. marina* parameters into a model that examined the relative role of microzooplankton grazing (by large ciliates) and protozoan parasites in the control of dinoflagellate blooms. *O. marina* was included as a representative grazer of nanoflagellates and zoospores, the dispersal stage of the parasite. The conclusion of this model was that parasites, not microzooplankton, could control dinoflagellate blooms, even when the dispersal stages can be reduced by top-down control from *O. marina*-like predators.

The influence of N regeneration on a food web

The role of protozoan N-regeneration was assessed in a microbial food web model (Davidson *et al.*, 2005); this was an extension of the model by Fasham *et al.* (1990) that included a multiple currency of

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C and N, and hence variation in the C:N ratio of both phytoplankton and their protozoan predators.

The protozoan compartment of the model was parameterized from laboratory experiments on *O. marina*. Nutrient regeneration was related to the relative C:N ratios of prey and predator using three alternative functions all capable of representing, to some degree, the N regeneration efficiency of *O. marina*: a constant nitrogen regeneration efficiency (NRE); a stepwise switching function between low and high NRE, termed threshold elemental ratio (TER), (Table 1, Eq. 16); and a dynamic nutrient regeneration equation (Caron and Goldman, 1988), (Table 1, Eq. 15).

Simulations demonstrated quantitative differences between the output generated by the different models, particularly between the switching and dynamic models and the constant NRE model in terms of the density of phytoplankton blooms. Differences in C:N ratio of model components were also evident with only the dynamic model predicting a stoichiometrically balanced zooplankton C:N ratio close to 6.6, the Redfield value, similar to the values that experimental estimates suggests that protozoa, including *O. marina*, maintain (Goldman and Dennett, 1992; Nakano, 1994; Davidson *et al.*, 1995a). Such *O. marina*-derived results have important implications for the formulation of the multiple functional type models that are now being formulated to better understand the global C cycle (e.g. le Quéré *et al.*, 2005).

Summary of synecological work.

Considering the importance of protozoa within marine ecosystems and the relative wealth of data, response relationships and models based on *O. marina* (Table 1), it is unclear why so few synecological modelling studies have drawn on this resource, to date. Clearly, considerable scope exists to develop and improve existing models, and to produce alternative formulation for comparison, as illustrated above (*The influence of N regeneration on a food web*). Moreover, the now recognised diversity of *O.*

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marina (e.g. Lowe *et al.*, 2005a, 2010), offers the potential to produce data sets that will allow an “organism sensitivity analysis” to better quantify biologically reasonable ranges of model parameter values. It may also be possible to examine spatial distributions using the framework established by Johnson (2000) and the physical-biological functions outlined above; perhaps allowing the assessment of large scale patterns.

FUTURE DIRECTIONS OF *O. MARINA*-BASED MODELLING

Better parameterisation

Response relationships such as those presented in Table 1 are increasingly being derived for *O. marina*, and these studies provide a valuable resource for model construction. Modellers need to be made aware of the existing data sets for *O. marina*, which have yet to be fully exploited for model parameterization (e.g. Fuller, 1990; Jeong *et al.* 2001, 2004; Kimmance *et al.*, 2006). Hopefully this paper has helped fulfil that role. However, many of the existing studies have been related to the grazing impact on harmful or aquaculture-relevant prey species (e.g. Jeong *et al.*, 2001), and we suggest that further study of cosmopolitan and benign prey and the role of abiotic factors in modulating these relationships are required.

Independent time-series for comparison

Models also require test data, independent to the observations on which they are derived. Considering the number of studies conducted using *O. marina*, surprisingly few have proved to be amenable for this purpose. For example, studies that analyse the selective grazing properties of *O. marina* are particularly prominent in the works we have reviewed. However, a disproportionately high fraction of these have applied their model to the data of Flynn and Davidson (1993b). Further time course

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experiments following *O. marina* and one, or more, prey items in differing environmental conditions
are, therefore, required to better validate these and future models. As guidance, we present an example
of such a data set for model comparison (Fig. 1). This represents a subset of numerous time course
experiments beginning at many initial predator and prey concentrations. Such an approach, while
generating time-course data, may minimize the bottle effects (e.g. accumulation of toxins and fouling
on surfaces) that can bias long-term incubations. Population models, independently derived from *O.*
marina functional and numerical response and prey growth data may be tested using the resultant
phase-plot data.

One of the reasons that the *O. marina*-*I. galbana* data set of Flynn and Davidson (1993b) has
been so often used as a comparison with simulations is the availability of a robust model that predicts
prey growth in non-steady state conditions (Davidson *et al.*, 1993; Davidson and Cunningham, 1996).
Hence, the experimental study and modelling of *O. marina* in particular, and protozoa in general must
be conducted in parallel with that of their prey, to allow both trophic levels to be simulated to the same
level of complexity. This requires experimental studies to measure a sufficient array of parameters
including numbers, biomass, ingestion, grazing, respiration, and nutrient cycling rates to allow
appropriate model parameterization and testing, to minimise the need to “fit” free model parameters.

Improving model structure, using *O. marina*

Doney (1999) highlighted the need for succinct but realistic mathematical models capable of simulating
the cycling of multiple nutrients within microbial food webs. These are necessary to simulate the
transfer of production to higher trophic levels and the export flux of C to the ocean floor. Within this
context parameterisation of zooplankton or microzooplankton response in a range of different model

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structures is increasingly a topic of debate. To this end, below, we provide an indication of how *O. marina* might be used in a range of models to help resolve this debate.

Nutrient-phytoplankton-zooplankton models

In general the classical nutrient-phytoplankton-zooplankton (NPZ) models, (e.g. the widely used model of Fasham *et al.*, 1990) use a simple closure term to represent grazing. The potential deficiency in this approach was highlighted by Mitra (2009) who discussed the difference between the theoretical response of NPZ models that employ generic “closure” functions and those that include specific representation of carnivory and cannibalism, finding that these generated differences in simulated primary production and f-ratio. In a similar vein Gentleman *et al.* (2003) comprehensively reviews the mathematical formulation and use of a range of different multiple resource functional response relationships for zooplankton. Again, her comparison of response was based on theoretical simulations. Hence, while studies such as these highlight the potential pitfalls for modellers from an erroneous choice of functional response, experimental verification of the most appropriate functions is still required.

Considering the relative wealth of information on *O. marina* revealed in this review, it seems a very suitable organism with which to test the suitability of alternative functional relationships to represent grazing processes. For example, *Isochrysis galbana*, the prey species on which much of the *O. marina* based predator-prey modelling is based, becomes smaller during N-deprivation (Davidson *et al.*, 1992; Flynn *et al.*, 1994). However, other phytoplankters, e.g. *Nannochloropsis oculata*, increase in size under such conditions Flynn *et al.* (1993). Understanding and modelling the response of microzooplankton grazers to alternative prey, following simple changes in environmental conditions will be a necessary step to the development of robust models in the future.

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478 *Plankton functional type models*

479 Plankton functional type (PFT) models are increasingly being employed in ocean biogeochemistry, and
480 here again using *O. marina* may be instructive. The use of PFT models is somewhat controversial,
481 with some authors (e.g. Anderson, 2005) suggesting that their application may be premature. However,
482 notwithstanding this debate, there is consensus that better model parameterization is required. This is
483 particularly pertinent at the microzooplankton level. For example, the dynamic green ocean model (Le
484 Quéré *et al.*, 2005) contains five separate autotrophic functional types, but only a single composite,
485 protozooplankton compartment to represent heterotrophic flagellates and ciliates. While this is
486 understandable in terms of model tractability, the parameterisation of the equations used to represent
487 this “functional group” requires deeper consideration in the light of the wealth of behaviour that
488 different species and genera are capable of (Montagnes *et al.*, 2008) and observations of temporal
489 succession of different micro-zooplankton groups (Davidson *et al.*, 2007).

490 Analysis of the functional response of *O. marina* in comparison with other heterotrophic marine
491 micro- or dinoflagellates, expanding on initial studies such as those of Jeong *et al.* (2008), and with
492 multiple prey items (John and Davidson, 2001), would add confidence to single functional group
493 parameterisation, or provide definitive evidence that multiple micro-zooplankton functional groups are
494 required in models. The application of developing techniques such as lectin labelling Wootton *et al.*
495 (2007), flow cytometric separation of prey and predators (Montagnes *et al.*, 2008), the analysis of
496 stable isotope signatures (Flynn and Davidson, 1993a), or stable isotope probing (Radajewski *et al.*,
497 1999), will hopefully provide the data sets from which to progress this field.

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Individual based models

Individual based models (IBMs) provide an alternative modelling strategy to those that seek to represent the ecosystem as a whole, and *O. marina* is an ideal candidate for these. IBMs calculate biological variables while following individual (or meta-) particles in space. These models may then be of particular use for the study of advective populations and/or species that form only a small fraction of the biomass of a trophic level but are important for other reasons. A number of important biotoxin producing phytoplankton species such as the advective *Dinophysis* spp. (Hart *et al.*, 2007) or the low-biomass high-toxicity dinoflagellate *Alexandrium tamarense* (Touzet *et al.*, 2010) fit these criteria. As *O. marina* ingests biotoxin producing dinoflagellates (Jeong *et al.*, 2001; Jeong *et al.* 2003) it may be a suitable candidate organism for developing grazing terms within such models. Furthermore, in rare cases it forms large blooms of up to 10^5 cells ml⁻¹ (Begun *et al.*, 2004) and thus own its own may be important in short-term rapid fluxes of nutrients in some ecosystems. Thus, *O. marina*-IBMs may too be justified in the future.

SUMMARY

What has *O. marina* modelling delivered to the scientific community? Of the autoecological models reviewed, the majority deal with some aspect of prey selectivity; the combined body of work in this area is particularly useful in demonstrating that prey selectivity by micro-heterotrophs is, indeed, capable of influencing the trophic transfer of phytoplankton biomass (e.g. Strom, 1993; Flynn *et al.*, 1996; Davidson *et al.*, 1995a,b) and that functional form used to simulate this selectivity will influence model results (Mitra *et al.*, 2003; Mitra, 2006; Mitra and Flynn, 2006). In this light, there is a somewhat surprising relative lack of more basic combined experimental-modelling studies based around *O. marina* that specifically seek to model the response to particular environmental drivers (an

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exception being the temperature based study of Kimmance *et al.*, 2006). This is an obvious area for
further fruitful study. The relative lack of synecological studies employing *O. marina* based model
parameterisation perhaps reflects this need, with the more sophisticated models of prey selectivity
requiring a fundamental underpinning prior to their wider application.

In conclusion, as *O. marina* is not often abundant in open water samples, it might not be the
organism of first choice to parameterize the protozoan component of such models. However, as
indicated above, available evidence suggests its use is appropriate, and the relative wealth of *O. marina*
studies makes it a pragmatic choice. Furthermore, there are ecosystems where *O. marina* may be
abundant, and in these regions using *O. marina*-derived parameters would be entirely appropriate.
Therefore, we support its continued use as a model organism to parameterize simple and more complex
population models.

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740 **FIGURE LEGENDS**

741 **Fig 1.** An indication of how further population dynamics might be obtained for comparison with model
742 output: abundance of *Oxyrrhis marina* and the prey flagellate *Dunaliella primolecta*, grown at 16 °C in
743 32 PSU seawater enriched with f/2 media (Sigma). Panels a-c are 18 d time-course incubations of
744 predator (○) and prey (●) in triplicate flasks. Panels d and e are phase plots: d is a plot of the three
745 18-d time course incubations (a-c); e is a plot of a series of short (5-11 d) incubations, indicating a
746 semblance of population cycling.

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Davidson *et al.* 10. *Oxyrrhis marina* based models748 Table 1. Studies that determine or apply *O. marina* based equations and their functional forms.

Equation type and number	Equation (see caption for symbols)	Selected works that employ the function
1. Functional response	$I = \frac{I_{\max} \times p}{k_I + p}$	Kimmanse <i>et al.</i> (2006) Strom (1993)
2. Numerical response	$r = \frac{r_{\max} \times p}{k_r + p}$	Jeong <i>et al.</i> (2008)
3. Numerical response with threshold prey level (p') included.	$r = \frac{r_{\max} \times (p - p')}{k_r + (p - p')}$	Kimmanse <i>et al.</i> (2006) Strom (1993)
4. Functional response modified by ambient temperature	$I = \frac{I_{\max} \times p}{k_I + p} \times a(T - b)^c$	Kimmanse <i>et al.</i> (2006)
5. Numerical response modified by ambient temperature	$r = \frac{r_{\max} \times (p - p')}{k_r + (p - p')} \times aT$	Kimmanse <i>et al.</i> (2006)
6. <i>O. marina</i> volume as a function of prey abundance	$v = \frac{v_{\max} \times p}{k_v + p} + v'$	Kimmanse <i>et al.</i> (2006)
7. <i>O. marina</i> volume response modulated by temperature	$v = \left[\frac{v_{\max} \times p}{k_v + p} + v' \right] \times a(T - b)^c$	Kimmanse <i>et al.</i> (2006)
8. Difference equation for <i>O. marina</i> increase in abundance	$N_{t+1} = \frac{r \times N_t}{1 + a \times N_t}$	Johnson (2000)
9. Ingestion of detrital particles modulated by a selection factor (SF)	$Re = I \times \left[\frac{D}{D + p} \times SF \right]$	Strom (1993)

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10. distance a predator has Flynn *et al.* (1996)

to travel to encounter a $\delta = N_{eq} \times \alpha \times (S_p \times p)^{-1}$
volume of prey equal to
its own volume

11. Functional response Davidson *et al.* (1995a)

modified (decreased) $I = \frac{I_{\max}(a) \times p}{k_I + p}$ Mitra *et al.* (2003)

by the influence of Mitra and Flynn (2005)

inhibitor (*a*) obtained

from ingestion of non

optimal prey

12. Ratio based selectivity Fasham *et al.* (1990)

function for multiple $I = \frac{I_{\max} \times e_i \times p_i^2}{k_I \times (e_1 \times p_1 + e_2 \times p_2 + \dots) + e_1 \times p_1^2 + e_2 \times p_2^2 + \dots}$ Mitra and Flynn (2006)

prey

13. Rate of prey capture Mitra and Flynn (2006)

related to a selectivity

function f_i that defines

the relationship with a

specific prey (p_i)

concentration

14. Nitrogen regeneration Davidson *et al.* (1995b)

as a function of

predator N content and

protozoan C:N ratio

15. Nitrogen regeneration as Caron and Goldman (1998)

a function of Davidson *et al.* (1995b)

respiration, gross Davidson *et al.* (2005)

growth efficiency and

prey and predator C:N

ratios

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16. Nitrogen regeneration

Davidson *et al.* (2005)

as a stepwise function $\text{if } \theta > a \quad E = b, \quad \text{else } E = c$
of protozoan C:N ratio

a, b, c are constants; I = ingestion rate; I_{\max} = maximum ingestion rate; *p* = prey abundance; k_I = half saturation constant of the ingestion curve; *r* = specific growth rate; r_{\max} = maximum specific growth rate; p' = threshold prey abundance (at which $r = 0$); k_r = a constant ($k_r - p'$ = half saturation constant of the growth curve); *T* = temperature; *v* = volume; v_{\max} = maximum volume; k_v = half saturation constant of the volume curve; v' = the volume at zero food abundance; *N* = *O. marina* concentration; *Re* = re-ingestion of faecal particles; *D* = concentration of faecal particles; *SF* = selection factor; N_{eq} = number of prey cells equivalent to one predator in terms of biovolume; α = variable related to the swimming speed of prey and predator; S_p = cross section of encounter party of predator and a given prey species; e_i = preference for different prey types; C_i = capture rate of specific prey species; f_i = capture rate parameter; *E* = nitrogen excretion rate; *n* = *O. marina* nitrogen content; θ_i = C:N ratio of prey or predator; *R* = respiration rate, *S* = gross growth efficiency.

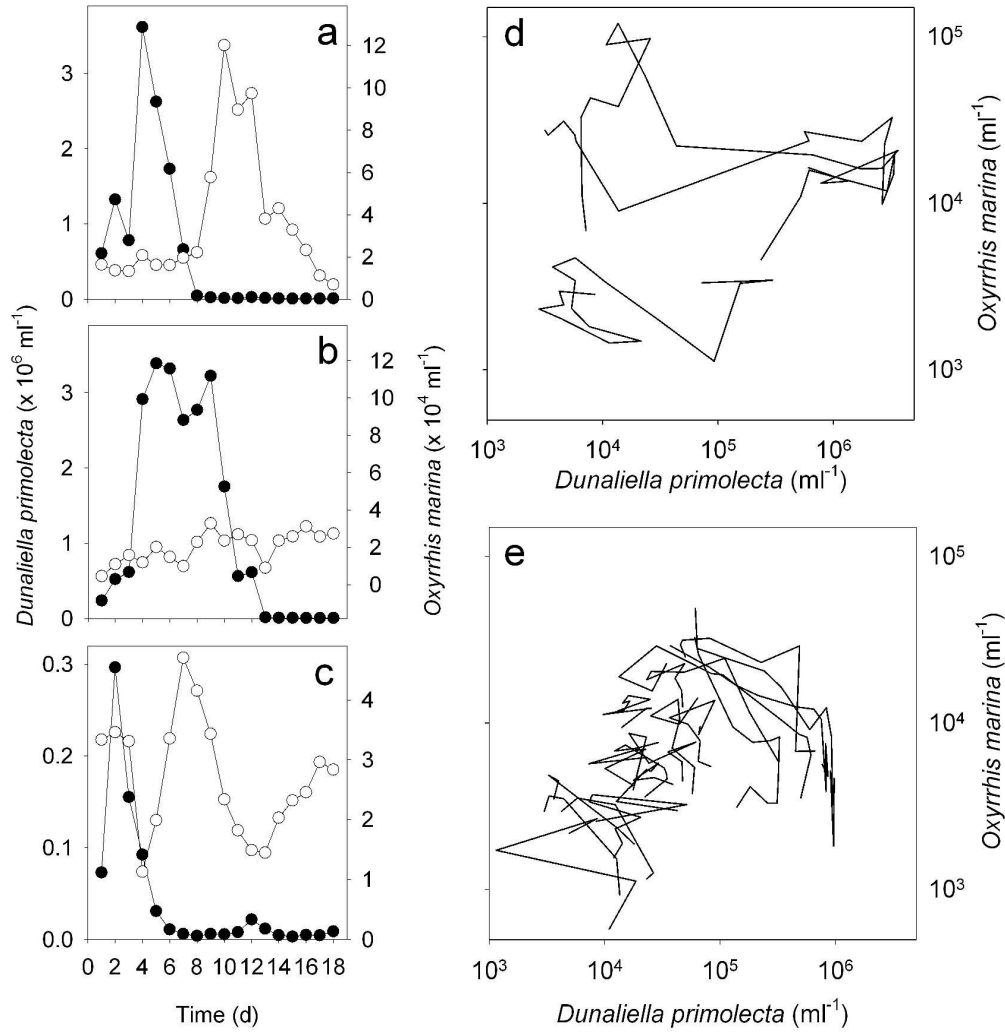


Fig 1. An indication of how further population dynamics might be obtained for comparison with model output: abundance of *Oxyrrhis marina* and the prey flagellate *Dunaliella primolecta*, grown at 16 °C in 32 PSU seawater enriched with f/2 media (Sigma). Panels a-c are 18 d time-course incubations of predator (○) and prey (●) in triplicate flasks. Panels d and e are phase plots: d is a plot of the three 18-d time course incubations (a-c); e is a plot of a series of short (5-11 d) incubations, indicating a semblance of population cycling.