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Roberts *et al.* – Feeding in *Oxyrrhis marina*

**Feeding in the dinoflagellate *Oxyrrhis marina*: linking behaviour with mechanisms.**

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## ABSTRACT

Protists are major consumers of phytoplankton and bacterioplankton in the marine environment, playing a key role in carbon cycling and nutrient regeneration. Consequently, the feeding activities of planktonic protists have been intensively studied. In particular, the dinoflagellate, *Oxyrrhis marina*, has been used extensively as a model predator in laboratory-based feeding studies. This is predominately because it is easy to culture and manipulate but also because its plasticity in feeding behaviour allows it to represent a broad range of free-living heterotrophic protists. Prey preferences of this versatile, but selective, predator have been well documented. However, our ability to determine the factors driving prey selectivity is limited by a poor understanding of the detailed mechanisms underlying *O. marina* feeding. Within this study, we explore known aspects of *O. marina* feeding behaviour and highlight areas that require further research to exploit this species as an effective model protist predator.

Key Words: Feeding, Grazing, Ingestion, Phagocytosis, *Oxyrrhis*, Flagellate, Dinoflagellate

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## THE CHALLENGE

“*Oxyrrhis marina* Dujardin, the common dinoflagellate of the brackish supra-littoral, is extremely easy to culture and offers a challenge to all interested in phagotrophy.” (Droop, 1953).

Since the publication of this quote, the scientific community has made extensive use of this adaptable dinoflagellate in feeding studies. To what extent, however, have we risen to the challenge of understanding phagotrophy in this species? Within this paper, we provide critical answers to this question, highlighting that nearly 60 years on from Droop’s paper, there is still much we need to learn about feeding in this model planktonic protist grazer.

## INTRODUCTION

It is now recognised that protists dominate grazing activities in aquatic microbial food webs (Sherr and Sherr, 2002; Sherr and Sherr, 2007) and are the main source of phytoplankton mortality in marine ecosystems, typically accounting for 60 to 70% of daily phytoplankton consumption (Calbet and Landry, 2004). Thus, there has been an impetus to understand factors controlling feeding by planktonic protists and interpret their environmental consequences (e.g. Davidson *et al.*, this issue). Although field-based feeding experiments provide valuable estimates of in situ grazing (e.g. Calbet and Landry, 2004), the extent to which feeding behaviour can be interpreted using this approach is limited by the difficulties associated with low cell concentrations, the presence of multiple species, and the control of other variables (Montagnes *et al.*, 2008). Consequently, many aspects of protist feeding have used laboratory-based studies on model species (see Montagnes *et al.*, 2008).

The heterotrophic dinoflagellate, *Oxyrrhis marina* (15-40  $\mu\text{m}$ ) is the most frequently used marine protist predator in laboratory-based feeding experiments. Since the initial observations of Kent (1880), Barker (1935), and Droop (1953), *O. marina* has been employed

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2  
3 extensively in feeding experiments due to its ease of culture, wide distribution, and tolerance  
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5 to a range of environmental conditions (Lowe *et al.*, this issue-b). Although it is not typically  
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7 found in open waters (Watts *et al.*, this issue), *O. marina* is both a raptorial and intercept  
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9 feeder (see below) and is, therefore, representative in its feeding behaviour of many  
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11 planktonic protists. Thus, *O. marina* has been used as a model to develop new methodologies  
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13 to study feeding, including the use of live fluorescently-stained prey (Premke and Arndt,  
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15 2000; Martin-Cereceda *et al.*, 2008), dual radioisotope-labelled prey (Lessard and Swift,  
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17 1985), acidotrophic probes (Carvalho and Graneli, 2006), fatty acid biomarkers and  
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19 compound-specific stable isotope techniques (Pond *et al.*, 2006). Other studies incorporating  
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21 *O. marina* have enabled interpretation of the relevance of chemoattractants, chemorepellents,  
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23 and chemical defence within aquatic food webs (e.g. Strom *et al.*, 2003a,b; Adolf *et al.*, 2007;  
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25 Tillmann *et al.*, 2008). The effect of physical factors on feeding, including temperature,  
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27 turbulence, and light have also been investigated (Havskum, 2003; Jakobsen and Strom,  
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29 2004; Lowe *et al.*, 2005; Kimmance *et al.*, 2006; Hartz, 2010). Finally, *O. marina* has been  
30  
31 used extensively as a model predator to investigate selective feeding on different prey species  
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33 (e.g. Goldman *et al.*, 1989; Flynn *et al.*, 1996; Hansen *et al.*, 1996; Davidson *et al.*, 2005) and  
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35 on prey of varying nutritional quality (e.g. Flynn and Davidson, 1993; Flynn *et al.*, 2006).  
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43 Despite *O. marina* being a popular model organism (Montagnes *et al.*, this issue),  
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45 there remains a poor understanding of the mechanisms involved in its feeding behaviour.  
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47 Here we examine ‘what’ *O. marina* feeds on and ‘how’ it feeds. We then provide directions  
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49 for future studies to link observed behaviour with feeding mechanisms, specifically to  
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51 interpret the underlying factors driving prey selectivity.  
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## 58 **‘WHAT’ OXYRRHIS MARINA FEEDS ON**

### 59 **Types of prey**

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*Oxyrrhis marina* demonstrates remarkable versatility in its prey preferences (Droop, 1966; Dodge and Crawford, 1974). At the lower end of the size spectrum *O. marina* can grow on bacteria (<1 µm) and small algae, including *Nannochloris oculata* (2-4 µm) and *Micromonas pusilla* (1-2 µm) (Flynn *et al.*, 1996; Hansen *et al.*, 1996; Jeong *et al.*, 2008). However, *O. marina* feeds optimally and achieves higher growth rates on small flagellates  $\geq 4$  µm (Goldman *et al.*, 1989; Hansen *et al.*, 1996; Jeong *et al.*, 2001; Jeong *et al.*, 2003). Although research has often focussed on ‘herbivorous’ grazing activities (e.g. Goldman *et al.*, 1989), *O. marina* also feeds on heterotrophic flagellates including *Cafeteria* sp. (3-4 µm), *Goniomonas amphinema* (4-5 µm), *Pfiesteria piscicida* (7-14 µm), and *Stoekeria algicida* (11-17 µm) (Jeong *et al.*, 2007a,b; Martin-Cereceda *et al.*, 2008) in addition to photosynthetic flagellates such as *Isochrysis galbana* (4-5 µm) and *Dunaliella primolecta* (6-8 µm) (Flynn *et al.*, 1996; Wootton *et al.*, 2007). At the larger end of the prey size spectrum, *O. marina* can feed on protist species as large as itself; e.g. *Cricosphaera elongata* (20-30 µm) (Droop, 1966; Dodge and Crawford, 1971) and is a well documented cannibal (Martel and Flynn, 2008). *Oxyrrhis marina* has even been observed “attacking” amphipods that are moulting or have just moulted (Gaines and Elbrächter, 1987). Although *O. marina* can feed on cells >20 µm, in contrast to other naked dinoflagellates such as *Gyrodinium spirale*, its optimum prey size is smaller than that of itself (Hansen, 1992; Hansen *et al.*, 1996; Davidson *et al.*, this issue). Finally, in addition to nutrition obtained through phagotrophy, *O. marina* can survive through the uptake of dissolved organic molecules in the laboratory and may be able to use this mechanism in saprobic environments (see Lowe *et al.*, this issue-b). The diverse diet of *O. marina* allows researchers to use this species as a versatile model.

### Functional response

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Like many grazers, *O. marina* exhibits a typical type II functional response (see Turchin, 2003) that can be represented by Eq. 1

$$I = \frac{I_{\max} \times p}{k + p} \quad (1)$$

where  $I$  is ingestion rate,  $I_{\max}$  is the maximum ingestion rate,  $k$  is the half saturation constant, and  $p$  is the prey concentration. A number of studies have determined functional responses for *O. marina*, and here we provide a brief summary of these responses (Fig. 1, Table 1). The shape of responses and the maximum ingestion rate may vary depending on prey species, but also between different studies of the same species (possibly due to different experimental conditions such as acclimation of the predator to prey concentrations; e.g. Tarran, 1991).

Carbon:chlorophyll  $a$  ratios are known to be quite variable (Davidson *et al.*, 1991; Montagnes *et al.*, 1994). However, if we assume an ‘average’ value of 50 (Sherr and Sherr, 2010) we find that much of the data presented in Fig. 1 are at chlorophyll  $a$  concentrations  $>20$  mg chlorophyll  $a$   $m^{-3}$  ( $1000$  ng C  $ml^{-1}$ ). These chlorophyll concentrations would be typical of a dense phytoplankton bloom and hence there is a need to better determine functional responses at prey concentrations more representative of in situ abundances, if researchers are concerned with how *O. marina* behaves under conditions typical of open waters (note though that *O. marina* may rarely experience such conditions as it is not typically found in open waters, Watts *et al.* this issue).

Davidson *et al.* (this issue) review the use of functional responses in mathematical models. They report that *O. marina* is typically represented by a type II functional response, which may be modified to account for other abiotic and biotic factors such as temperature and prey quality. Often, *O. marina* ingests its prey to near extinction (Fig. 1, Table 1). However, significant prey thresholds may occur for some species of microzooplankton; e.g. Goldman *et al.* (1989) and Flynn and Davidson (1993) report prey thresholds of  $\sim 1 \times 10^5$  cells  $ml^{-1}$  for *I. galbana* being ingested by *O. marina*. Furthermore, Davidson *et al.* (1995a)

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found it necessary to use a modified type II response to account for such thresholds (see Table 2 in Davidson *et al.*, this issue). There is, therefore, a need to better understand the existence of factors governing prey thresholds and to improve our parameterization of the functional response at lower prey concentrations.

## SELECTIVE FEEDING BY *OXYRRHIS MARINA*

Although *O. marina* consumes a variety of prey, it has distinct feeding preferences. Here we shall consider the implication of experiments examining prey selectivity in this species.

### Selective feeding on artificial particles

Using artificial particles, *O. marina* has been shown to discriminate between prey, based on size, biochemical composition, and charge (Hammer *et al.*, 1999, 2001; Wootton *et al.*, 2007). For instance, ingestion rate is up to four times higher on 4  $\mu\text{m}$  beads compared to 1  $\mu\text{m}$  beads (Hammer *et al.*, 1999; although identical abundances of 4  $\mu\text{m}$  and 1  $\mu\text{m}$  beads were used, increasing encounter probability with 4  $\mu\text{m}$  beads). *Oxyrrhis marina* can also discriminate against artificial particles with a high surface charge, including carboxylate and silicate beads (Hammer *et al.*, 1999) and can distinguish between beads with different surface biochemical composition, showing a significant preference for beads coated with mannose-BSA over N-acetylgalactosamine-BSA (Wootton *et al.*, 2007). Although *O. marina* ingests artificial particles, it prefers live prey (Hammer *et al.*, 1999; Wootton *et al.*, 2007).

Therefore, even though artificial prey provides a useful tool to elucidate some aspects of feeding behaviour, there are still unrecognised signals that live prey supply to induce capture.

### Prey selectivity between species

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3 Numerous studies have investigated prey selectivity of *O. marina* grazing on other protists  
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5 (e.g. Sieburth, 1960; Barlow *et al.*, 1988; Goldman *et al.*, 1989; Flynn *et al.*, 1996; Hansen *et*  
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7 *al.*, 1996). Comparison between these studies is difficult due to differences in experimental  
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9 design, including variations in incubation condition and duration (Goldman *et al.*, 1989;  
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11 Flynn *et al.*, 1996; Hansen *et al.*, 1996). Differences in the initial prey and predator  
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13 abundance, biovolume, and biomass, further complicate comparisons. For example, the  
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15 majority of feeding experiments presented in Hansen *et al.* (1996) used different biovolumes  
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17 of prey mixtures and relatively short incubation times (48 h), with high predator  
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19 concentrations. Hansen *et al.* (1996) accounted for differences in prey concentration by  
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21 applying the Chesson-index, as described by Chesson (1983) for use in selection experiments  
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23 with changing prey densities. They concluded that *O. marina* grazes selectively on larger  
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25 prey species such as *Rhodomonas* sp. and *Tetraselmis suecica* (with equivalent spherical  
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27 diameters >7 µm), relative to smaller species including *Emiliana huxleyi*, *Isochrysis*  
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29 *galbana*, *Micromonas pusilla*, and *Nannochloris* sp. (with equivalent spherical diameter of 1-  
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31 5 µm). Selection for the larger cells within each species was also observed. In contrast,  
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33 Goldman *et al.* (1989) noted that selective feeding occurred on *Phaeodactylum tricorutum*,  
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35 *I. galbana*, and *Dunaliella tertiolecta* by monitoring cell abundance, carbon, and nitrogen  
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37 over longer time periods (10 d). Maximum ingestion rates based on abundance varied  
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39 between prey species, with higher ingestion rates on *P. tricorutum* and *I. galbana*, relative to  
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41 the larger species *D. tertiolecta*. However, on a cell nitrogen basis similar ingestion rates  
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43 occurred for all three prey species. Prey selectivity experiments conducted by Flynn *et al.*  
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45 (1996) measured changes in abundance and biovolumes of *O. marina* and the prey *D.*  
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47 *primolecta*, *I. galbana*, and *M. pusilla* over 22 d, starting with low initial predator and prey  
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49 concentrations. They assessed selective grazing on the basis of ‘equivalent encounter  
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51 distance’, which is the distance an average sized predator would have to swim to encounter a  
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3 biovolume of prey equal to its own cell volume (Flynn *et al.*, 1996). When confronted with  
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5 all three prey species, *O. marina* fed preferentially on *D. primolecta* but did not discriminate  
6  
7 between *I. galbana* and *M. pusilla*. Comparison of these studies illustrates the difficulty of  
8  
9 drawing general conclusions regarding prey selectivity and highlights the need for  
10  
11 coordinated studies with comparable methodologies in future.  
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15 In studies of prey selectivity between species, it is difficult to determine the prey  
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17 parameters that underpin selective feeding. Prey size, motility, cell surface properties, and  
18  
19 the release of dissolved chemical cues (including chemoattractants, chemorepellents, and  
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21 toxins) vary between different prey species. Experimentally controlling and manipulating  
22  
23 these variables is challenging, and, at this point, it is difficult to interpret how prey  
24  
25 parameters affect feeding preference of heterotrophic protists in general. However, given the  
26  
27 tractability of *O. marina* as an experimental organism (Lowe *et al.*, this issue-b), there is  
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29 clearly a good opportunity to progress our understanding of prey selectivity mechanisms  
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31 based on studies of this species.  
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### 39 **Prey selectivity within species**

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41 In addition to selecting between prey species, *O. marina* discriminates between individuals of  
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43 the same species with different properties. For example, *O. marina* preferentially selects  
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45 virus-infected over healthy *E. huxleyi* when presented together at equal densities (Evans and  
46  
47 Wilson, 2008). The underlying mechanisms behind this selection are not fully known.  
48  
49 However, prey parameters that vary between healthy and virus infected prey and hence  
50  
51 potentially influence feeding selectivity include prey cell size, prey cell surface properties,  
52  
53 the release of dissolved infochemicals, and dimethylsulphoniopropionate (DMSP) lyase  
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55 activity (Brussaard *et al.*, 2001; Evans *et al.*, 2006; Evans *et al.*, 2007; Evans and Wilson,  
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57 2008). Other studies have investigated the ability of *O. marina* to discriminate between *E.*  
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*huxleyi* strains with different DMSP lyase activity (Wolfe *et al.*, 1997; Strom *et al.*, 2003a). For example, Wolfe *et al.* (1997) found that although *O. marina* could tolerate high DMSP lyase-activity *E. huxleyi* strains, it avoided them when presented with both low and high activity strains (Wolfe *et al.*, 1997). The enzyme DMSP-lyase cleaves DMSP to yield dimethyl sulphide (DMS) and acrylate, with the latter having potent antimicrobial activities (Sieburth, 1960), and this potentially induces prey rejection. For a detailed review on the chemoreception associated with both of these examples of *E. huxleyi* intra-prey selectivity, the reader is directed to Breckels *et al.* (this issue).

Another well documented example of intra-species prey preference involves *I. galbana* as prey. When *O. marina* is grown in dense cultures of *I. galbana*, grazing ceases as prey become nitrogen limited, although grazing continues if the prey carbon:nitrogen ratio remains low (Flynn and Davidson, 1993; Flynn *et al.*, 1996). These results have been applied, to test various mechanistic mathematical model formulations that use prey carbon:nitrogen ratio as an index for prey quality (Davidson *et al.*, 1995b; Mitra *et al.*, 2003; Mitra and Flynn, 2005) and the application of the models are further discussed by Davidson *et al.* (this issue). It has been suggested that this rejection of nitrogen deplete *I. galbana* by *O. marina* may be due to the build up of an inhibitor within predator cells or a change in prey recognition by the predator (Flynn *et al.*, 1996; Martel, 2009). Without further experimental evidence, however, these suggestions remain speculative.

Although investigating prey preference within species is a promising approach to assess factors affecting prey selectivity, as it enables better control of certain prey variables, the main factors driving selection remain poorly understood. Clearly, we need to recognise how prey parameters including size, motility, cell surface properties, and dissolved chemical cues vary between and within different prey species. It is also essential to have a detailed

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2  
3 understanding of the feeding mechanisms used by *O. marina* to search, capture, and ingest  
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5 their prey (see Montagnes *et al.*, 2008).  
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## 10 **‘HOW’ OXYRRHIS MARINA FEEDS**

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12 In common with other naked dinoflagellates, including *Gyrodinium spirale* and *Noctiluca*  
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14 *scintillans*, *O. marina* feeds by direct engulfment, completely ingesting prey through a non-  
15  
16 permanent cytostome (Elbrächter, 1991; Höhfeld and Melkonian, 1998), consisting of a  
17  
18 subsurface “microtubular basket” (Gaines and Elbrächter, 1987). To assess feeding  
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20 mechanisms used by *O. marina* we will consider the individual feeding stages employed by  
21  
22 this species: i.e. searching, contact, capture, processing, and ingestion (see Montagnes *et al.*  
23  
24 2008 for a synopsis of protist feeding stages, and note that digestion will not be covered  
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26 within our work, which focuses on feeding per se). In particular, we highlight, as a priority  
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28 for future study, the feeding stages that are least understood (Fig. 2).  
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### 38 **Searching**

39 Prey searching by motile protists is influenced by swimming speed and changes in direction  
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41 and frequency of turning (Montagnes *et al.*, 2008). For a detailed assessment of swimming  
42  
43 behaviour in *O. marina*, including discussion on helical paths in a three-dimensional  
44  
45 environment, see Boakes *et al.* (this issue). In brief, *O. marina* swims in a helix, with an  
46  
47 increase in the helical path as prey concentrations decrease (Bartumeus *et al.*, 2003). Similar  
48  
49 patterns are observed for other protists, such as some ciliates (e.g. Fenchel and Jonsson,  
50  
51 1988). Changes in the helical motion are controlled by flagellar movement, and when prey  
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53 concentrations are high ( $\sim 10^4$ - $10^5$  cells ml<sup>-1</sup>), *O. marina* invests more energy in using the  
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55 longitudinal flagellum relative to the transverse flagellum, resulting in a helical path that is  
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57 nearly linear, due to the low amplitude and frequency of gyres (Bartumeus *et al.*, 2003). In  
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3 contrast, at medium to low prey concentrations ( $\sim 10^1$ - $10^3$  cells ml<sup>-1</sup>), *O. marina* invests more  
4  
5 energy in movement using the transverse flagellum, which results in an increase in the helical  
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7 trajectories (Bartumeus *et al.*, 2003). Bartumeus *et al.* (2003) suggested that these “helical  
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9 walks” optimize random searching in three-dimensional environments with low prey  
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11 densities.  
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15 Although changes in *O. marina* swimming behaviour are well documented, we lack  
16  
17 an understanding of the mechanisms underpinning these changes (Boakes *et al.*, this issue;  
18  
19 Breckels *et al.*, this issue). However, there is now strong evidence that *O. marina* exhibits a  
20  
21 positive motile response towards chemical cues released by their prey. Furthermore, prey  
22  
23 exudates and specific infochemicals (including certain amino acids and DMSP) can act as  
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25 chemical cues (Martel, 2006; Menden-Deuer and Grünbaum, 2006; Breckels *et al.*, this  
26  
27 issue). The motile response of protists to chemical cues is often initiated by the binding of a  
28  
29 dissolved chemoattractant molecule to a specific cell surface receptor (Bell *et al.*, 2007;  
30  
31 Bagorda and Parent, 2008). Specifically, in *O. marina*, receptors involved in the motile  
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33 response towards chemoattractants have not been identified, although a study involving cell  
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35 signalling inhibitors has provided preliminary evidence that G-proteins, G-protein coupled  
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37 receptors (GPCR), and protein kinases may be involved in the signalling pathways initiating  
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39 motile behaviour (Hartz *et al.*, 2008). As highlighted in Breckels *et al.* (this issue), there is  
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41 still much to learn about the involvement of dissolved chemoattractants in prey searching.  
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3 In addition to dissolved chemical cues, light also appears to be an important  
4 environmental stimulus used in prey searching. *O. marina* exhibits positive phototaxis  
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6 (Droop, 1954; Hartz, 2010) and a pronounced diel cycle, with increased feeding and growth  
7 rates during the day (Jakobsen and Strom, 2004). This species possesses a number of  
8  
9 rhodopsins (Zhang *et al.*, 2007) and inhibition of these receptors significantly decreases its  
10 phototactic response (Hartz, 2010). Preliminary experimental evidence indicates that *O.*  
11  
12 *marina* may use rhodopsins to detect algal prey based on chlorophyll *a* autofluorescence  
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14 (Hartz, 2010).  
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### 24 **Contact, capture, and processing**

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26 Studying the feeding behaviour of *O. marina* remains challenging due to its relatively rapid  
27 swimming speeds (up to 700  $\mu\text{m s}^{-1}$ ) and engulfment (<15 s) of prey (Cosson *et al.*, 1988;  
28  
29 Öpik and Flynn, 1989). Consequently, despite *O. marina* being a popular model predator,  
30  
31 used extensively in feeding studies, we lack detailed understanding of the mechanisms used  
32  
33 to contact, capture, and process prey by this dinoflagellate.  
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39 For bacterial prey, *O. marina* uses mainly the transverse flagellum to generate feeding  
40 currents that carry bacteria towards its cingular depression (Fig. 3). Within the cingular  
41 depression the bacteria are then carried in a spiral or linear path prior to being engulfed  
42  
43 (Jeong *et al.*, 2008). Thus, Jeong *et al.* (2008) considered *O. marina* to be an intercept feeder  
44  
45 of bacteria, in that it produces a feeding current and directly intercepts food particles.  
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50 In contrast, when protists are prey, *O. marina* is raptorial, actively searching for prey  
51 (Jeong *et al.*, 2008). In these cases, it swims at high speeds in narrow circles around the prey  
52  
53 (Barker, 1935; Goldman *et al.*, 1989; Höhfeld and Melkonian, 1998), and initial contact is  
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55 made by the cell apex, the longitudinal flagellum (Höhfeld and Melkonian, 1998), or the  
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57 transverse flagellum (Dodge and Crawford, 1971, 1974). Reports on the initial contact of the  
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predator and prey are not consistent, with contact being noted both prior to (Höhfeld and Melkonian, 1998) and following (Barker, 1935; Goldman *et al.*, 1989) the encircling of prey. There are also contradictions regarding the use of trichocysts in prey capture (Fig. 2, 3). Although their presence, distribution, and ultrastructure in *O. marina* have been appreciated for some time (Dradesco, 1952; Dradesco and Hollande, 1965; Hausmann, 1973; Clarke and Pennick, 1976), we still lack detailed knowledge of their function in this species. *Oxyrrhis marina* appears to attach to its prey (Öpik and Flynn, 1989) and catch prey >3 µm using trichocysts (Jeong *et al.*, 2008) and may use filament-assisted prey capture (Jacobson and Anderson, 1986; Goldman *et al.*, 1989). Serial section analysis (by TEM), however, has failed to indicate discharged trichocysts during the early stages of phagocytosis, suggesting that they are not involved in prey capture (Höhfeld and Melkonian, 1998). Despite the well documented involvement of trichocysts and filaments in prey capture by other alveolate species (e.g. Jacobson and Anderson, 1986; Hansen and Calado, 1999; Jeong, 1999; Jakobsen *et al.*, 2006), their function in *O. marina* evidently requires further elucidation.

Following prey capture, *O. marina* may reject certain food types during the prey processing stage (Flynn and Davidson, 1993; Wolf *et al.*, 1997). Prey types observed to have been rejected include nitrogen deplete *I. galbana* and *E. huxleyi* strains with high-activity DMSP lyase (Flynn and Davidson, 1993; Wolf *et al.*, 1997). Again, the mechanisms underlying this process are unknown.

### Ingestion

Following contact, capture, and processing, prey are ingested by phagocytosis. For this to occur, the predator must first adhere to the prey (Bozzaro *et al.*, 2008; Cosson and Soldati, 2008). In other phagocytic cells, adherence commonly involves receptors on the phagocytic cell binding to specific ligands on the cell surface of their prey (Ofek *et al.*, 1995; Stahl and

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3 Ezekowitz, 1998; Bozzaro *et al.*, 2008). Lectins, carbohydrate binding-proteins that  
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5 agglutinate cells, commonly function as phagocytic receptors (Venkataraman *et al.*, 1997; Lis  
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7 and Sharon, 1998; Stahl and Ezekowitz, 1998; Roberts *et al.*, 2006). Experimental evidence  
8  
9 indicates the potential involvement of a mannose-binding lectin in prey adhesion and  
10  
11 recognition by *O. marina* (Wootton *et al.*, 2007). However, it is unlikely that this is the only  
12  
13 receptor involved in phagocytosis, as microbial recognition by phagocytic cells often  
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15 involves numerous interacting receptors (Cambi and Figdor, 2005; Cambi *et al.*, 2005).  
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18 *Oxyrrhis marina* appears to possess multiple cell membrane prey-binding proteins (Roberts,  
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20 unpublished data); however, further characterisation and functional work is required to  
21  
22 determine their role in feeding. Once the prey has bound to the cell surface of *O. marina*,  
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24 phagocytosis is initiated through signal transduction pathways. Using cell signalling  
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26 inhibitors, Hartz *et al.* (2008) provided initial evidence that protein kinase signalling  
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28 pathways may be involved in phagocytosis.  
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34 In *O. marina*, phagocytosis takes place at the non-permanent cytostome, which is  
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36 located at the right ventral surface of the cell between the groove of the longitudinal  
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38 flagellum and the ventral ridge microtubules (Fig. 3; Höhfeld and Melkonian, 1998). It  
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40 involves the rearrangement of the microtubular cytoskeleton, an aspect of particular interest  
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42 in dinoflagellates that feed by direct engulfment of large prey (Höhfeld and Melkonian, 1998;  
43  
44 Hansen and Calado, 1999). During phagocytosis, the anterior microtubular bands near the  
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46 ventral surface of the cell are 'lifted' towards the ventral ridge microtubules (Höhfeld and  
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48 Melkonian, 1998). This reversible rearrangement of the cytoskeleton enables uptake of a  
49  
50 wide size-spectrum of prey (see Types of prey, above). Following engulfment, the  
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52 microtubular bands relocate to their original position within minutes. This organization of  
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54 the microtubular cytoskeleton, forming two opposite focal points, has provided  
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60 dinoflagellates with the flexibility required to evolve numerous feeding types, including the

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ability to directly engulf large prey particles (Höhfeld and Melkonian, 1998). Thus, although *O. marina* is not necessarily a typical dinoflagellate (Lowe *et al.*, this issue-a), it may act as a model for certain aspects of dinoflagellate feeding.

## THE CHALLENGE IN PERSPECTIVE: LINKING FEEDING BEHAVIOUR WITH MECHANISMS

Although we have an in depth understanding of the type of prey that *O. marina* ingests, and the factors that affect grazing, knowledge of the underlying feeding mechanisms is incomplete and failure to understand these mechanisms may impinge on our ability to use it as a model species, in a wider context. For instance, there are still large gaps in our knowledge regarding the use of trichocysts in prey capture and the types of receptors employed to detect dissolved and cell surface prey cues. Gaining a more comprehensive understanding of the mechanisms underlying feeding behaviour in *O. marina* will be challenging, and if findings from laboratory-based experiments are to be applied to natural planktonic assemblages as a whole, careful consideration must be given as to whether this species is an appropriate environmental model. High swimming speeds in *O. marina* make swimming behaviour difficult to observe. However, rapid swimming is characteristic of many planktonic species (see Jeong *et al.*, 1999, 2004), suggesting that, although difficult, this is an appropriate avenue of research to pursue (see Boakes *et al.*, this issue). From a molecular perspective, feeding mechanisms used by *O. marina* are poorly understood relative to other model protists, in particular *Dictyostelium discoïdium*. In contrast to *O. marina*, *D. discoïdium* receptors involved in chemotaxis and phagocytosis have been well characterized (Cornillon *et al.*, 2006; Bagorda and Parent, 2008). Also, the complete genome of *O. marina* has not yet been sequenced and given the immense genomes typical of dinoflagellates (Hackett *et al.*, 2005), potentially including *O. marina* (Sano and Kato, 2009), this remains a

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3 significant challenge that deserves pursuing (see Slamovits and Keeling, this issue). In  
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5 addition, methods for generating large libraries of mutants, an approach used extensively with  
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7 *D. discoïdium* (Annesley and Fisher, 2009; <http://dictybase.org>), are currently unavailable for  
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9 *O. marina*, although the many strains now available (see Lowe *et al.*, this issue-a; Watts *et*  
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11 *al.*, this issue) may provide a valuable resource to this end. In contrast to other marine protist  
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13 predators, however, the ease of maintaining *O. marina* in axenic and monoxenic culture  
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15 (Lowe *et al.*, this issue-b) provides an advantage for developing molecular approaches that  
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17 can then be applied to a broader range of environmentally relevant species. Thus, we see  
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19 great potential for the continued use of *O. marina* in this context.  
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25         Interpreting how underlying mechanisms drive feeding efficiency and selectivity in  
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27 planktonic protists is a challenging task. Currently, however, for many protist species we  
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29 only have a limited knowledge of feeding mechanisms, and consequently lack fundamental  
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31 information regarding how protist predators recognise prey and feed. As a result we  
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33 experience difficulties in interpreting isolated laboratory feeding experiments and applying  
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35 the findings to natural assemblages as a whole. Although care must be taken when  
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37 generalizing from one protist predator to another, we recommend *O. marina* as a model  
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39 predator to investigate and build a thorough understanding of feeding mechanisms, providing  
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41 a methodological framework that can then be applied to other environmentally relevant  
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43 protists. We consider that pursuing this approach would enable increased understanding of  
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45 the functional elements that play such a fundamental role in driving and structuring aquatic  
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47 microbial foodwebs.  
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## FIGURE LEGENDS

**Fig. 1.** A comparison of functional responses of *Oxyrrhis marina* feeding on different prey, over a range of prey biomass, all conducted at either 20 or 21 °C. Responses are for *Amphidinium carterae* (Jeong *et al.*, 2001); *Heterosigma akashiwo* (Jeong *et al.*, 2003); *Cafeteria* sp. (Jeong *et al.*, 2007b); *Pfiesteria piscicida*, *Stoeckeria algicida*, *Luciella masanensis*, (Jeong *et al.*, 2007a); mixed natural bacteria (Jeong *et al.*, 2008); *Dunaliella primolecta*, *Chlamydomonas spreta*, *Brachiomonas submarina*, *Nanochloropsis oculata* (Fuller, 1990); *Isochrysis galbana* (Kimmance *et al.*, 2006); *Dunaliella primolecta\**, *Dunaliella primolecta\*\** (unpublished data, Yang and Montagnes, using two strains of *O. marina* as predators, \*351\_FAR01, \*\*45\_BOG01, Univ. Liverpool cultures of *O. marina*). Note, responses derived for *O. marina* with *Dunaliella primolecta\**, *Dunaliella primolecta\*\** were performed on predator cultures that had been acclimated to prey levels for several days, which may explain the different shape of the responses, compared to other studies that tend to not acclimate or acclimate for a relatively short period. Note also that all responses, except those by Fuller (1990) follow Eq. 1 (see text); Fuller (1990) included a threshold prey level, where feeding stops and Eq. 1 is modified as  $I = I_{\max} \times (p-T)/(k+p-T)$ , where  $T$  is the threshold level (ng C ml<sup>-1</sup>).

**Fig. 2.** Linking protist feeding steps with *Oxyrrhis marina* specific feeding mechanisms and influential prey parameters.

**Fig. 3.** *Oxyrrhis marina* with ingested prey. A-C Sections through *O. marina* containing ingested *Isochrysis* from the ventral (A) to the dorsal (C) view of the cell. D-F Sections through a cannibalistic *O. marina* from the dorsal (D) to the ventral (F) view of the cell. G-H Cannibalistic *O. marina*. I *O. marina* with discharged trichocysts. a = anterior, p = posterior, t

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3 = tentacle, vr = approximate position of the ventral ridge, ph = region of phagocytosis, cd =  
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5 cingular depression, tf = transverse flagellum, lf = longitudinal flagellum, n = nucleus, iso =  
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8 ingested *Isochrysis galbana*, c ox = cannibalised *O. marina*. Scale bar = 15  $\mu\text{m}$ .  
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Table 1. Parameters for the functional responses depicted in Fig. 1. See Fig. 1 legend for an explanation of the parameters and sources of the data.

$I_{\max}$ (ng C d <sup>-1</sup> )	$T$ (ng C ml <sup>-1</sup> )	$k$ (ng C ml <sup>-1</sup> )	Prey
1.25		704	<i>Heterosigma akashiwo</i>
2.80		90	<i>Amphidinium carterae</i>
0.29		455	<i>Cafeteria</i> sp.
0.33		83	<i>Pfiesteria piscicida</i>
0.14		89	<i>Stoeckeria algicida</i>
0.07		132	<i>Luciella masanensis</i>
0.07		44	Bacteria
1.10	19.5	127	<i>Dunaliella primolecta</i>
1.97	12.4	388	<i>Chlamydomonas spreta</i>
1.29	41.8	146	<i>Brachiomonas submarina</i>
1.37	-0.77	182	<i>Nanochloropsis oculata</i>
1.43		781	<i>Isochrysis galbana</i>
1.22		4538	<i>Dunaliella primolecta</i> *
2.30		19300	<i>Dunaliella primolecta</i> **

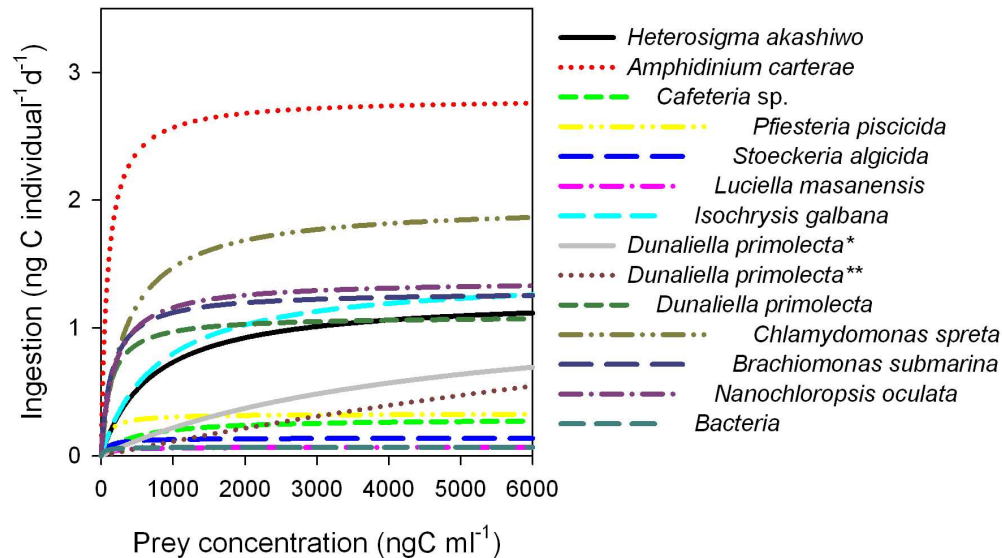
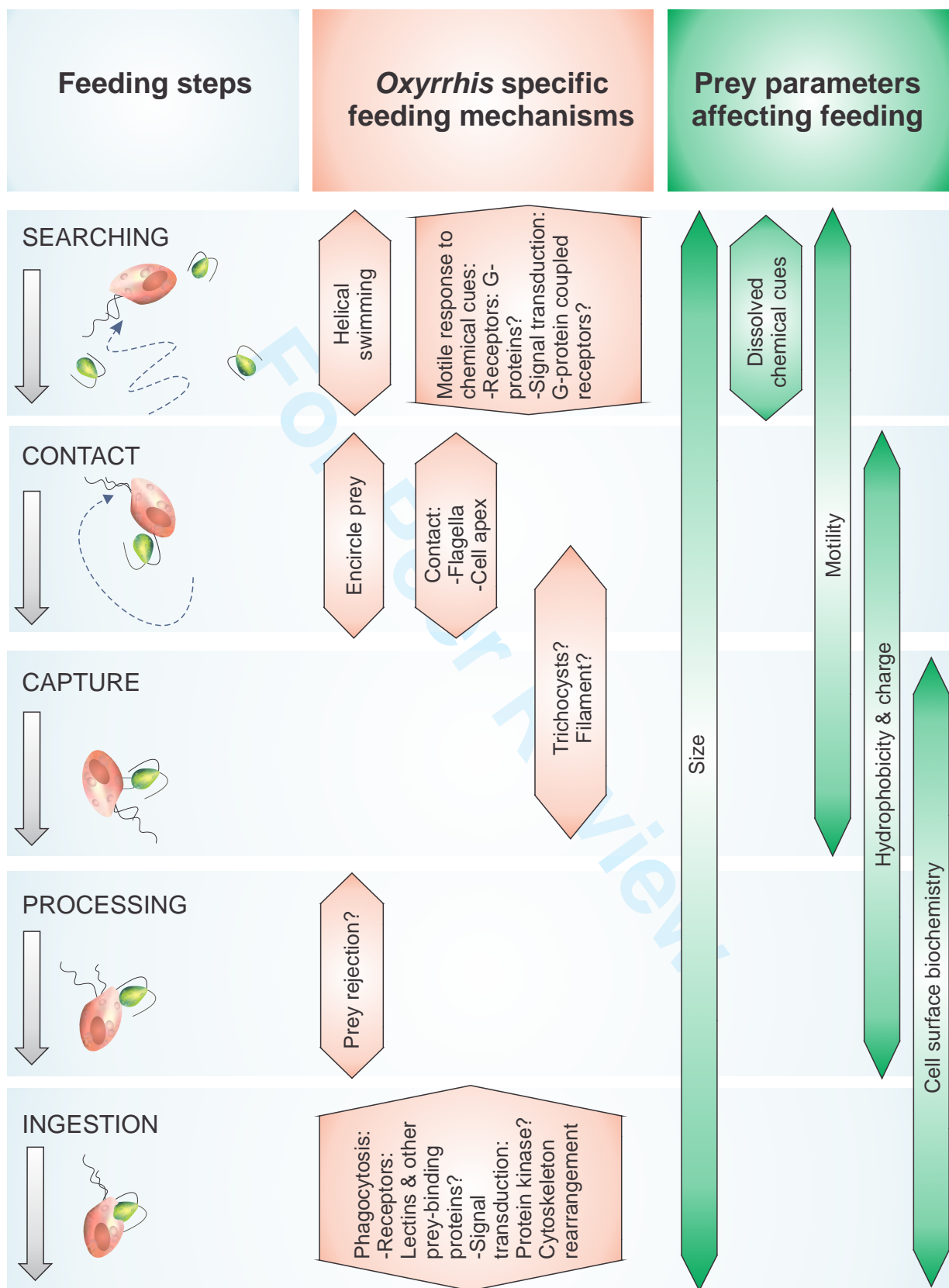


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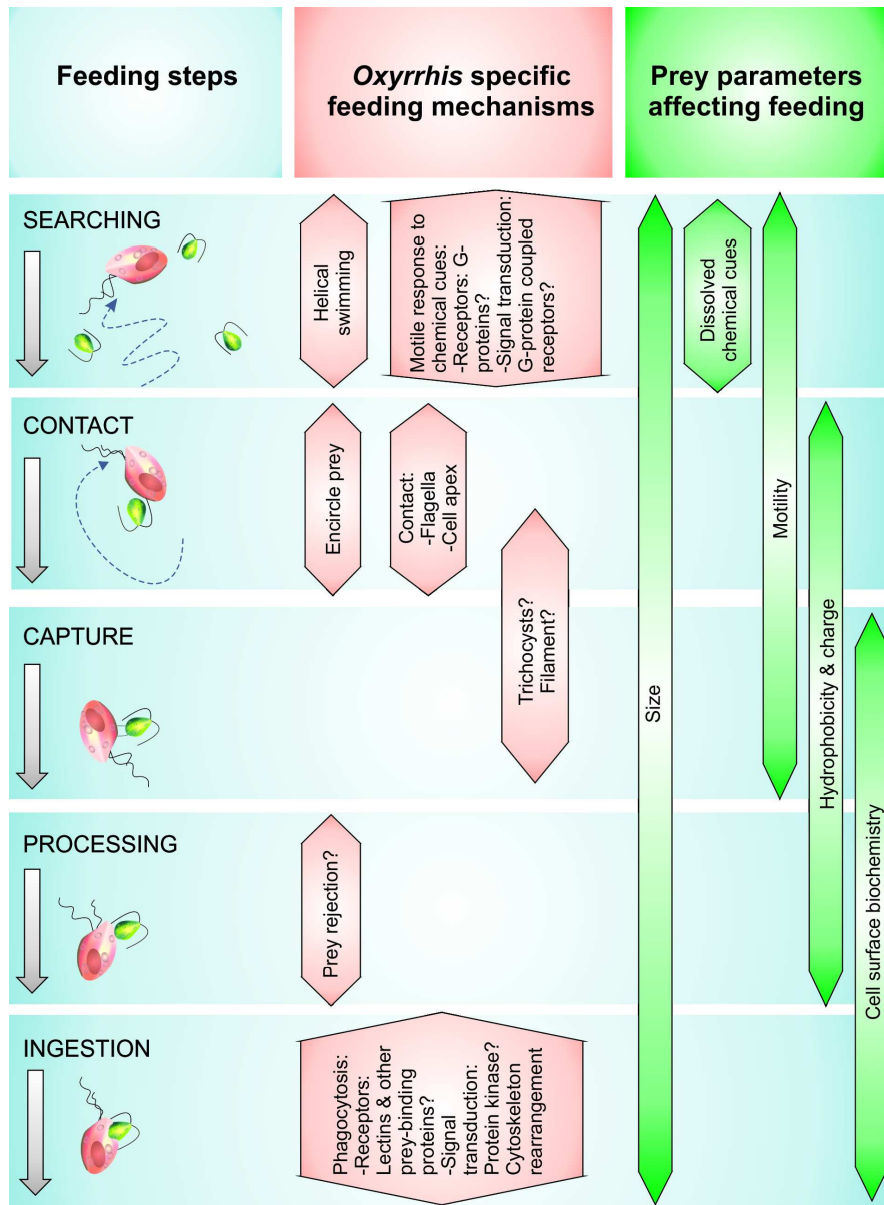
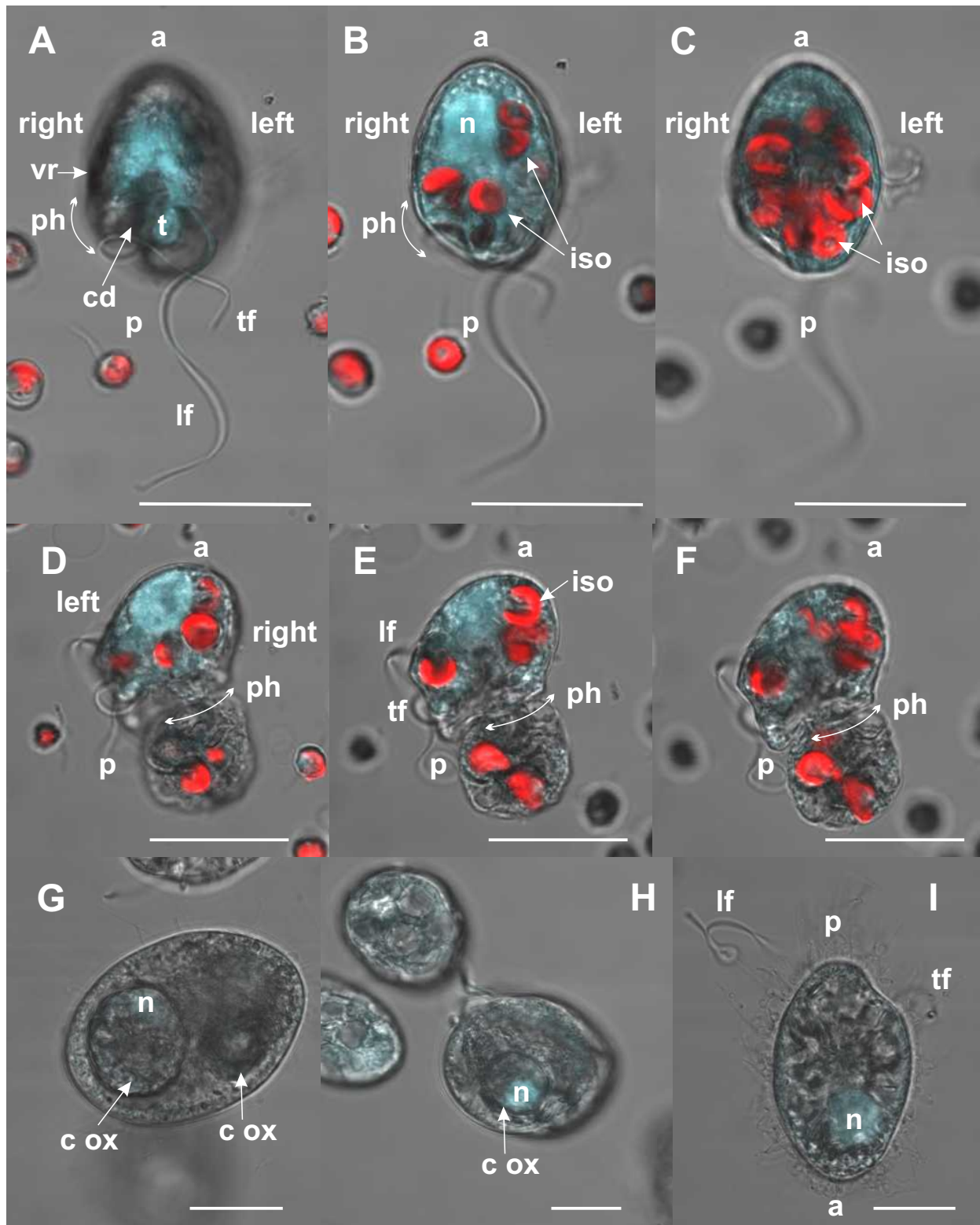


Fig. 2. Linking protist feeding steps with *Oxyrrhis marina* specific feeding mechanisms and influential prey parameters.  
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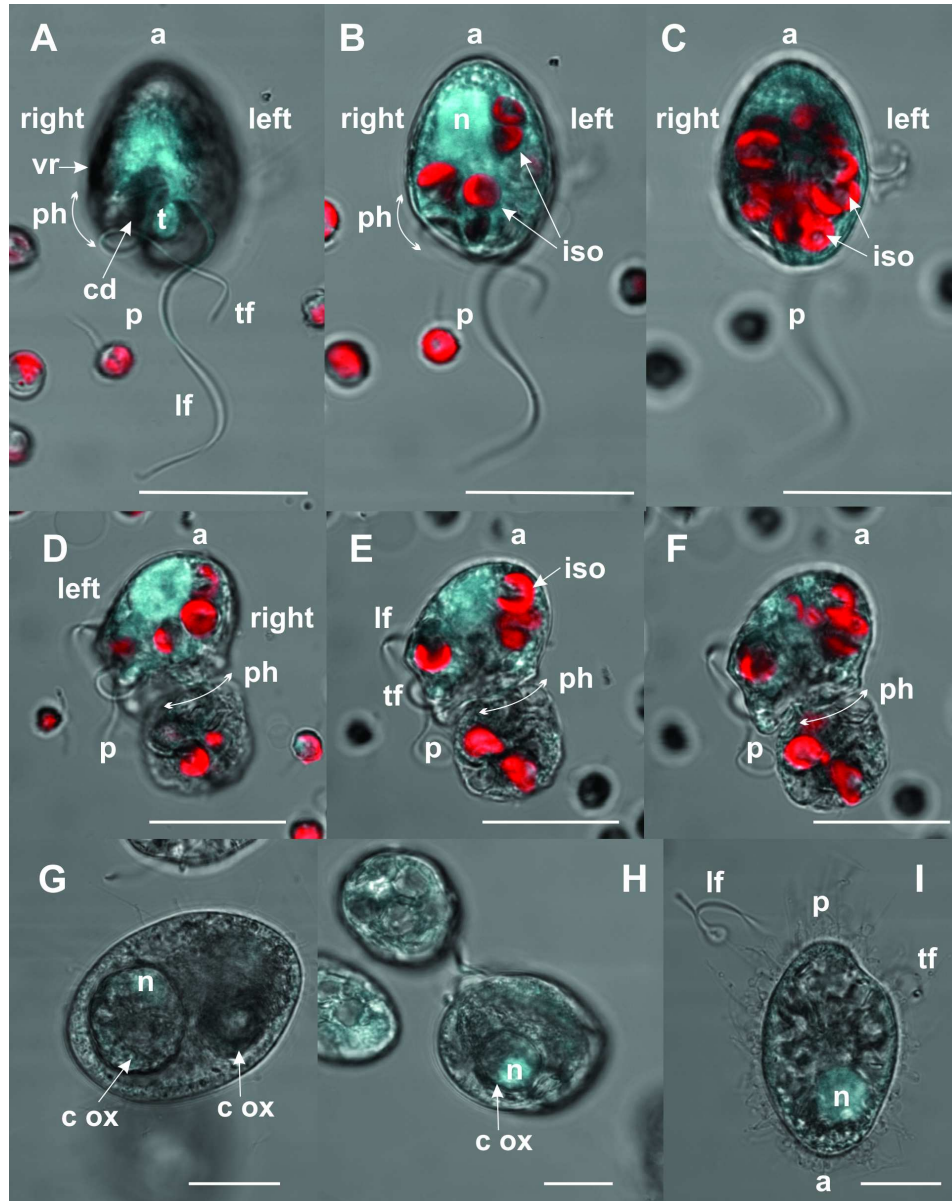


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