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The role of Oxyrrhis marina as a model prey: current work and future directions

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The role of *Oxyrrhis marina* as a model prey: current work and future directions

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ABSTRACT

Protozoa hold a key trophic position in pelagic food webs. Primary and bacterial production is consumed by them; their role as consumers is well established. Not as fully explored is their fate, by predation from upper trophic levels and through viral lyses. Impacts of this are: reduced trophic transfer efficiency; nutrient recycling; and increased respiration (CO_2 generation). Studies that examine loss of protozooplankton via predation often employ model species in lab-based experiments, rather than attempting to follow populations in natural samples. Such model species are rarely ideal representatives of natural systems, but various attributes (e.g. easy of culture and manipulation) facilitate experimentation and, in many cases, provide more precise data. *Oxyrrhis marina* is one such model. Most studies on the fate of *O. marina* are incidental, using it as a convenient prey and not focusing on it as a model to assess general questions or recognising the breadth of its application. We have assembled the dispersed works that uses *O. marina* as prey and synthesised their findings to assess its utility as a model; our premise is that *O. marina* is a versatile and useful model prey that should be adopted in future planktonic studies, ranging from those that examine nutrition to feeding behaviour. To this end, we provide guidance for future work. However, we also recognised that *O. marina* is a valuable food for maintaining laboratory species and have augmented our study with a brief assessment of the pragmatic nature of using it to help maintain its predators.

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INTRODUCTION

There is now, and has been for some time, compelling evidence that protozoa hold a key position and are an essential link in pelagic food webs (Conover, 1982). A high portion of primary and bacterial production is consumed by these "protozooplankton", and their role as consumers has been well established through field and laboratory studies (e.g. Calbet, 2008). Possibly not as fully appreciated or understood is their fate, by predation from upper trophic levels and through viral lyses (Fig. 1), although there has been, and continues to be, a growing emphasis on this link (e.g. Hansen, 1991a; Sanders and Wickham, 1993; Pesan *et al*., 1994; Jakobsen, 2002; Irigoien *et al*., 2003; Fileman *et al*., 2010; Montagnes *et al.,* 2010).

One typical approach to examine the loss of protozooplankton via predation is to employ model species in lab-based experiments, rather than attempting to follow populations in natural samples. Inevitably, such model species are rarely ideal representatives of natural systems, but various attributes (e.g. easy of culture and manipulation) facilitate experimentation and thus, in many cases, provide more precise, if not more accurate, data. For instance, the ciliate *Strombidium sulcatum* has been extensively used as model for the planktonic ciliates, which are often the dominant protozooplankton. Studies on this one species include consumption by zooplankton (e.g. Wiadnyana and Rassoulzadegan, 1989; Bamstedt, 1990; Broglio *et al*., 2003), swimming and trophic behaviour (e.g. Fenchel and Jonsson, 1988), and nutrient recycling and processing (e.g. Allali *et al*., 1994; Dolan and Simek, 1997). *Strombidium sulcatum*, however, is more epibethic than planktonic and is not generally found in the open water column; rather it has been isolated from shallow waters and

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tide pools (e.g. Fenchel and Jonsson, 1988; Montagnes *et al*., 1990; Modeo *et al*., 2003). Nonetheless, because of its morphological and behavioural similarities to other plankters and its ease of maintenance, *S. sulcatum* has provided invaluable data. Such data (e.g. growth and grazing responses) may then be used to stimulate and direct field-based studies, encourage researchers to attempt to culture more representative taxa, and in many cases, may be used directly in ecosystem models, as proxies for more common taxa that are impossible or difficult to study. Here we examine the use of another, easily maintained model species, a heterotrophic dinoflagellate (the other dominant group of protozooplankton; Jeong, 1999) and suggest it can, and should be, used as suitable model in predation studies.

The heterotrophic dinoflagellate *Oxyrrhis marina* is planktonic, *sensu stricto*, in that it remains in the water column, is moved by currents, is the same size as many planktonic species (15-40 µm), and generally behaves like many planktonic protozoa. Furthermore, similarly sized heterotrophic gymnodinoid dinoflagellates and a host of 10-30 µm mixotrophic dinoflagellates occur in planktonic samples (e.g. Kim and Jeong, 2004); thus, *O. marina* might act as a useful proxy for these planktonic taxa that are less tractable to culture. However *O. marina* is rarely found in coastal waters and virtually never occurs in the open ocean. Rather, *O. marina* thrives in shallow waters and littoral and supralittoral pools (Scott, 1987; Johnson, 2000; Kimmance *et al*., 2006), 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} (Fenchel *et al*., 1995; Johnson *et al*., 2003; Begun *et al*., 2004; Jeong *et al*., 2004). Thus, occasionally *O. marina* may be trophically important as a grazer

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and prey for other organisms, but in terms of large-scale plankton dynamics, assessing the specific importance of *O. marina* in natural systems is probably a moot point.

In contrast, there are significant benefits associated with examining *O. marina* as a representative of other planktonic protozoa. It is easy to obtain from natural samples, identify, maintain in culture, and manipulate in experiments. Furthermore, there is a long history of research on this species, including extensive work that has examined its growth and feeding (e.g. Droop, 1953; Montagnes *et al*., this issue).

At present, however, many of the studies on the fate of *O. marina*, are incidental, using it as a convenient prey and not focusing on it as a model to assess general questions regarding predation on protozooplankton. Consequently, as an aid to continued research on this species, we consider it timely to evaluate the dispersed works that uses *O. marina* as prey and synthesise their findings to assess its general utility. Our premise, throughout the review, is that *O. marina* is a versatile and extremely useful model prey that should be adopted in future planktonic studies, ranging from those that examine nutrition to feeding behaviour. In conducting this review, however, we recognised a further point: *O. marina* appears to be a valuable food for maintaining many laboratory species. We, therefore, have augmented our study with a brief assessment of the pragmatic nature of using this species to help maintain its predators.

CONSUMPTION WITHIN THE MICROBIAL FOOD WEB

There is a growing recognition that predation occurs within the microbial food web, at

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a variety of levels (Fig. 1). Potential impacts of predation are a reduction in the trophic transfer efficiency towards upper levels, such as copepods and ultimately fish; recycling of nutrients within the smaller sized fraction of the food web; and increased pelagic food web respiration (CO_2 generation) due to added heterotrophic activity. One such link is "group-cannibalism", a term applied to describe when protozoa eat other protozoa (Weisse, 1990); *O. marina* may be used to help assess this process. For instance, *O. marina* is be preyed upon by the planktonic ciliate *Strombidinopsis jeokjo* (Jeong *et al*., 2004; Fig. 2). To our knowledge, however, there have been no other empirical studies on the feeding by heterotrophic protists on *O. marina*, although Montagnes *et al*. (2008) have incorporated an *O. marina*-ciliate link into a model of toxic dinoflagellate bloom control. There is, without doubt, scope here to use *O. marina* in further experiments to assess group-cannibalism within the microbial food web.

In contrast to group-cannibalism, true cannibalism also occur within protozoan, and specifically dinoflagellate, populations, generally as a survival strategy to cope with food limitation (Jeong and Latz, 1994; Latz and Jeong, 1996; Hausmann *et al*., 2003). Again, *O. marina* may act as a model, as it has long been known to be cannibalistic (Öpik and Flynn, 1989; Davidson *et al*., 1995; Flynn *et al*., 1996). Recently, Martel and Flynn (2008) reviewed cannibalism for *O. marina*, obviating the need for us to do so in detail. In short, a small proportion of a population (~ 2% or fewer) are cannibals, and this number seems to depend on prey availability and the nutritional state of *O. marina*. However, unlike some other protozoa (e.g. the freshwater ciliate *Blepharisma*, where some cells become cannibalistic "monsters" when food is depleted, Giese, 1973), when *O. marina* is starved all cells decrease in size and

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there appears to be a decrease in cannibalism. These findings suggest that multiple cannibal-strategies occur within the protozoa (and even within the dinoflagellates), which should stimulate further research, possibly using *O. marina* as a useful representative for comparison. Furthermore, the indication that cannibalism is relatively rare in cultures should provide solace to those researchers who use *O. marina* to examine population dynamics, either in the laboratory or in models. Likely, in laboratory work cannibalism can be ignored as a confounding factor, and as Martel and Flynn (2008) suggest loss can be considered (if at all) to be a constant in population models, rather than having to apply more complex population dependent relationships.

Possibly the most unexpected microbial-predator of *O. marina* can be, paradoxically, its prey. Although in most cases, *O. marina* engulfs prey, there is one case where the roles become reversed, and the prey ingest *O. marina*. Specifically, the mixotrophic flagellate *Prymnesium parvum* consumes *O. marina* under some conditions (Tillmann, 1998, 2003): when *P. parvum* is not nutrient-stressed it is a suitable prey for *O. marina*, eliciting growth and grazing responses similar to those produced by other suitable prey. However, when exposed to toxin producing *P. parvum* cultures (induced through nutrient stress), *O. marina* loses its motility, becomes rounded, hyaline, and finally lyses. Under these conditions, individual *O. marina* are consumed, sometimes by several *P. parvum* at a time.

A wide range of protozoa are detrimentally influenced by this toxin producer (Tillmann, 2003, and references within), and it is well accepted that protozoan grazing (similar to that exhibited by *O. marina*) may prevent algal blooms (e.g. Tillmann, 2004).

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Consequently, this reversal in roles, by reducing grazing pressure on *P. parvum*, may allow the latter to bloom. In this case, *O. marina* has acted as a model to assess trophic role-reversal, a process that has been recognised for some time (e.g. Hansen, 1991b) and may be more prevalent than expected. We suggest that further studies on other mixotrophic prey be conducted on *O. marina*, to assess the extent of role-reversal.

Finally, no recent review of "microbial predation" on protozooplankton would be complete without including viruses, as although they are parasitic, they result in the demise of their host, and thus from the hosts perspective and in terms of nutrient recycling the consequence remains the same. Some of the earliest work linking viruses into the microbial food web used *O. marina* as a convenient model to indicate that viral-like particles reduce growth rate of protozoa (Pesan *et al*., 1994). Since the early 1990s there has been a substantial amount of research on how viruses will alter planktonic populations and trophodynamics (the reader is directed to the review by Suttle, 2007, as a good starting place on this topic). Given the interest in viruses, it is surprising that there appears to have been little further research conducted on *O. marina* and viruses, or more importantly on viruses and any other planktonic protozoa. We, therefore, propose that, given the ease of conducting experiments with *O. marina*, it be reemployed to investigate viral infection on protozoa, using new methodologies developed over the last 15 years (see Suttle, 2007).

CONSUMPTION BY METAZOOPLANKTON

A range of planktonic invertebrates consume and grow on *O. marina*, including rotifers and

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copepods. Furthermore, especially in the context of mesozooplankton, but also for other invertebrates, *O. marina* has been used as both a dietary-staple and as a prey in a wide range of experiments (Table 1). By assembling these studies, we hope to illuminate the versatility of this species as a prey for invertebrates, and in the next two sections we suggest how such versatility might be exploited.

However, our review of the literature has also recognized that some planktonic vertebrates (i.e. fish larvae) may also consume *O. marina*. Such a "protozooplankton-ichthyoplankton trophic link" could be important for larval survival, and there is a long history of protozoa being used as food for larval fish, in aquaculture and the tropical fish trade (for a recent review on this subject see Montagnes *et al.,* 2010). Although *O. marina* has been successfully used to rear young stages of larval black porgy, *Mylio macrocephalus*, supplemented the diet of larval lemonpeel angelfish, *Centropyge flavissimus*, and, anecdotally, used to raise grey mullet larvae (Kasahara *et al*., 1960; Nash and Kuo, 1975; Olivotto *et al*., 2006), there is limited research into its use, in this respect. Given the ease of growing *O. marina* to high abundances, its potential nutritional quality (see below), and its appropriate size for small fish larvae (May, 1970), *O. marina* may prove to be useful. We propose that feeding it to fish larvae is a direction for aquaculture-based research and laboratory-exploration of the role of protozoa as food for larval fish in natural waters.

ASPECTS OF *OXYRRHIS MARINA* ACTING AS A NUTRITIONAL-MODEL

Evidence suggests that protozoa, in general, are nutritious for a range of organisms (Sanders

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and Wickham, 1993). Specifically, Table 1 indicates that *O. marina* is a suitable food source for a broad taxonomic range of organisms, and it is an appropriate prey size for many protists and invertebrates such as large (~100 µm) ciliates, rotifers, and many copepods (Hansen *et al*., 1994).

Like other protozoa, the composition of *O. marina*, and hence its potential nutritional quality, is in part determined by its diet (typically microalgae but also bacteria), but *O. marina* synthesises a range of compounds that do not occur in its prey. Thus, feed-cultures containing *O. marina* and microalgae may enhance the growth of higher order predators. For instance, *O. marina* grown on the autotrophic flagellate *Dunaliella* sp., produces long-chain fatty acids and sterols that are not abundant in *Dunaliella* sp.; the combined diet of *O. marina* and *Dunaliella* sp. then allows the copepods *Temora longicornis* and *Pseudocalanus elongatus*, to grow successfully, whereas they do not survive well on *Dunaliella* sp. alone (Klein Breteler *et al*., 1999). Lund *et al*. (2008) have also indicated that *O. marina* does not simply elongate and desaturate fatty acid precursors from its prey to produce long chain fatty acids but produces these *de novo*. In a similar study on fatty acids and amino acids Kleppel *et al*. (1998) indicated that the copepod *Acartia tonsa* grew better when fed mixed cultures containing *O. marina*, again suggesting a trophic upgrade by *O. marina*. Furthermore, Scott (1987) indicated that *O. marina* provides a needed source of tryptophan to rotifers that was lacking in the algal prey. Finally, in a recent work, Malzahn *et al*. (2010) indicated that when Acar*tia tonsa* was fed *O. marina* that had been maintained on low-quality autotrophic flagellates (*Rhodomonas salina*) the copepod was not affected, but when the copepod fed

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directly on the low-quality primary producers, their respiration rates were higher and development rate was lower; thus, *O. marina* was used to examine the general principle that an intermediate step in the food chain may ultimately improve upper level productivity when primary producers are of low nutritional quality. These studies above not only use *O. marina* but also include other model plankters (e.g. *Dunaliella, Rhodomonas, Acartia, Temora, Pseudocalanus*) illustrating the utility of model systems and the versatility of *O. marina*.

Heterotrophic dinoflagellates are argued to play a unique role within the microzooplankton, being able to produce key nutritional substances (Klein Breteler *et al*., 1999). If this is so, then it seems *O. marina* may act as a useful model to pursue such research. However, of equal interest, in some cases predators consume *O. marina* but are unable to reproduce on this diet (e.g. Scott, 1987), indicating that it can fail to provide all the essential dietary nutrients to predators. One promising direction for future study is to establish which nutrients occur and which are missing in *O. marina* and then assess if those that are missing can be provided by trophic upgrading; i.e. providing *O. marina* with a defined, complete diet. In this sense, we may be able to use *O. marina* to better understand fundamental processes of survival of heterotrophic dinoflagellates in natural systems. Such work will be facilitated by research that now indicates *O. marina* can easily be grown axenically and on heat-killed bacteria (Droop, 1953; C. D. Lowe, pers. comm.).

FUTURE DIRECTIONS

Given that *O. marina* is a suitably sized, nutritious prey for a wide range of organisms, it is

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not surprising that, over the years, numerous experiment have used it (Table 1). Below, we briefly expand on these types of experiments, suggesting how continued use of the *O. marina* might be appropriate.

Much of the experimental work on *O. marina* has been directed towards assessing why it is such a good supplement or sole diet for grazers and how this influences the growth and reproduction of the grazers (Table 1). This work has focused on several calanoid copepods commonly used to elucidate plankton dynamics. Furthermore, the work has focused on how *O. marina* provides essential fatty acids and sterols to its predator and how these improve their development and egg production. It is, therefore, surprising that comparable studies have not been conducted on the nutritional benefits obtained through group-cannibalism (i.e. between protozoa eating protozoa). Given the evidence that *O. marina* is nutritious and may act as a trophic-upgrader (see the previous section), using this species to investigate the potential importance of group-cannibalism seems a logical future direction of study.

There are also surprisingly few studies of grazing and growth rates of predators fed on *O. marina*; those that do so describe a classic Holling type-II response (Fig. 2). Grazing experiments using *O. marina* and *Gymnodinium dominans* (a similarly sized heterotrophic dinoflagellate) as prey for the large ciliate *Strombidinopsis jeokjo* suggest that predator growth rate is similar when fed these two species, but grazing rates differ (Fig. 2a,b). Noting the difference in these responses, Jeong *et al*. (2004) postulated that *O. marina* may yield a higher gross growth efficiency than *G. dominans*. Two other data sets that examine predation rates on *O. marina* both use the calanoid copepod genus *Acartia* (Fig. 2c); these data suggest

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similar rates of ingestion, although there are study- and predator-differences. Finally, there are only two studies that assess the bioenergetics of copepods (in both cases using the *Acartia tonsa*) when provided with *O. marina*: one examines faecal pellet production (Feinberg and Dam, 1998), while the other is more extensive and examines how food concentration alters feeding, egestion, and ultimately assimilation efficiency (Besiktepe and Dam, 2002). Clearly, if *O. marina* is to be included in food web models (e.g. Lee *et al*., 2003; Montagnes *et al*., 2008), then there is a need to better parameterise these responses in the future, using other predators.

There is a growing recognition that mesozooplankton, and specifically copepod swimming behaviour may play an important role in pelagic ecosystems (e.g. Kiørboe, 2008). To this end, *O. marina* has been used in a model that assess mesozooplankton swimming and feeding (e.g. Mariani *et al*., 2008). Unfortunately, though, there has been little work on the behavioural changes of zooplankton, when feeding on *O. marina*. Schmitt and Seuront (2001) examined the three-dimensional swimming of *Temora longicornis* and noted changes in behaviour when it was fed *O. marina* and the smaller flagellate *Nannochloropsis occulata*. Furthermore, unpublished data (M. Steinke, pers. comm.) indicate that the feeding history of *O. marina* may affect dimethyl sulphide (DMS) production, and this, in turn, influences copepod swimming behaviour (*Centropages hamatus, Acartia tonsa*); thus, indirectly, the prey may alter the predator. These few, and disparate, studies suggest there is substantial scope for future work using *O. marina* as a prey, directed at paramaterising models such as the one developed by Mariani *et al*. (2008).

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Finally, *O. marina* has played a role in multi-trophic level laboratory microcosm studies and computer models (e.g. Hansen, 1993; Montagnes *et al*., 2008; Mariani *et al*., 2008; Malzahn *et al*., 2010) and may continue to do so given its extensive use as a model (Montagnes *et al*., this issue). It thus would seem appropriate that further work focuses on a range of behaviours associated with grazers on *O. marina*, to better understand and model predator-prey dynamics.

A BRIEF NOTE ON MAINTAINING PREDATORS

Although *O. marina* may act to help model predator-prey dynamics and behaviours, possibly its most pragmatic use has been simply as food, for maintaining stock and experimental cultures of laboratory organisms. For most applications, *O. marina* is mixed with other smaller organisms, to provide a composite diet for an upper level grazer. For instance many studies on copepods indicate that a combined diet of *O. marina* plus autotrophic flagellates provides a better diet than either prey alone, and similar findings have been obtained for feeding *O. marina* to rotifers (Table 1). In addition, benthic bryozoa have been successfully grown on a prey mixture of *O. marina* and yeast (Kitamura and Hirayama, 1984). All of these cases illustrate that there is a general improvement in predator growth when they are supplemented with *O. marina*.

From purely empirical observations, we might then suggest that this species should be a recommended food for planktivorous proto- and metazoa that have proven difficult to rear in the lab, and researchers conducting studies on such organisms should maintain stocks of *O.*

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marina. Given that it is simple to establish *O. marina* cultures (e.g. Lowe *et al.*, 2005), and strains are available from commercial culture collections (the CCMP, CCAP) or can be obtained from colleagues, it would seem sensible for researchers to consider this species as a routine stock prey item.

CONCLUSIONS

What then makes *O. marina* so special? It is a robust experimental protozoa that acts as a proxy for many of the more common, but difficult to culture, planktonic species. Furthermore, this review indicates that *O. marina* has the capability to be used to examine many aspects of predation associated with the microbial food web (Fig. 1), from viral infection through to group- and real cannibalism, trophic role-reversal, and ultimately to predation by mesozooplankton and possibly larval fish. Finally, *O. marina* provides either all the dietary needs or supplements the diet of many predators and can be used to reveal processes associated with trophic-upgrading. Thus, *O. marina* acts as a useful, if not ideal, model in this sense, and we recommend its use in future experiments.

We do provide the caveats that: 1) *O. marina* is not found in open waters and therefore does not necessarily act as ideal representative of planktonic systems; 2) almost by definition, as *O. marina* is a weed (i.e. easy to grow), it is robust and, therefore, not representative of many planktonic protozoa; and finally, 3) recent work indicates that there are many strains of *O. marina* (e.g. Lowe *et al*., 2005, 2010) that can have different ecophysiological responses to salinity (Lowe *et al*., 2005) and to temperature and prey types (Montagnes, unpublished data).

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Therefore, there is a need for researchers to work on defined, well characterised strains of *O. marina* (note this concern is, undoubtedly applies to many model species).

Thus, after reviewing the literature, we recommend the following directions: 1) establish more functional and numerical responses of predators (viral, proto-, and metazoan) feeding on *O. marina*; 2) further examine predator behavior associated with the presence of *O. marina* (e.g. swimming, prey rejection); and 3) compare 1 and 2 (above) to other non-toxic, similar sized dinoflagellate prey, to establish *O. marina*'s appropriateness as a model organism. Finally, there is a growing potential for the use of dinoflagellates to produce nutraceuticals for human and agricultural consumption (e.g. Mansour *et al*., 2003); possibly *O. marina*, with its ability to trophically upgrade the quality of fatty acids could be a focus for investigating commercial products, extending the range of predators to ourselves.

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FIGURE LEGENDS

Fig. 1 An illustration of the potential links by predation within and extending from the microbial food web: c, cannibalism; f, larval fish; g, "group-cannibalism"; mz, micro-metozooplankton; v, viral, z mesozooplankton. The illustration is liberally modified from a food web presented by Conover (1982) using information from a range of sources (Stoecker and Capuzzo, 1990; Gifford, 1991; Sanders and Wickham, 1993; Pesan *et al*., 1994; Irigoien *et al*., 2003; Tillmann, 2003; Jeong, *et al*., 2004; Figueiredo *et al*., 2007; Martel and Flynn, 2008)

Fig. 2. A comparison of grazing and growth rates on *Oxyrrhis marina*. a. grazing by the ciliate *Strombidinopsis jeokjo* on *O. marina* (solid line) and the similarly sized heterotrophic dinoflagellate *Gyrodinium dominans* (dotted line). b. specific growth rate of *Strombidinopsis jeokjo* on *O. marina* (solid line) and *Gyrodinium dominans* (dotted line). c. Grazing rate on *O. marina* from two copepod-studies: *Acartia* spp. (*A. omorii* and *A. hongi*) (solid line) and *A. tonsa* (dotted line). Data on *Strombidinopsis jeokjo* are from Jeong *et al*. (2004); data on *Acartia* spp. are from Jeong *et al*. (2001); data on *A. tonsa* are from Besiktepe and Dam (2002). Where necessary *O. marina* volume was converted to carbon following the equation for heterotrophic dinoflagellates presented in Menden-Deuer and Lessard (2000) and volume estimates presented in Jeong *et al*. (2004).

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Table 1. Predators on *Oxyrrhis marina*, indicating the type of grazer and type of study(ies), a brief indication of the scope of the study(ies), and the authors of the studies.

Type of study/grazer	Direction of study	Source
Animal husbandry		
Bryozoa: *Bugula avicularia, B. neritina, B. stolonifera, Bowerbankia gracilis, Conopeum reticulurn*, *Conopeurn seurati*, *Electra monostachys*, *Electra pilosa, Farella repens*, *Farrella repens*, *Tanganella appendiculata*, *Tanganella mulleri*, *Victorella pseudoarachnidia*	Supplement to diet of alga and yeast	Jebram, 1970; Jebram and Everitt, 1982; Kitamura and Hirayama, 1984 and references therein
Copepod: *Acartia clausi*, *Acartia tonsa, Calanus finmarchicus, Centropages hamatus, Centropages typicus, Pseudocalanus elongatus, Pseudocalanus sp., Temora longicornis, Tisbe holothuriae*	Supplement to diet of alga	Klein Breteler *et al*., 1982; 1994; 2004; Klein Breteler and Gonzalez, 1982; 1986; Fryd *et al*., 1991; Klein Breteler and Schogt, 1994; Kirchner and Guérin, 1995; Klein Breteler and Koski, 2003; van Duren *et al*., 2003; Besiktepe and Dam, 2002; Koski and Riser, 2006; Koski *et al*., 2006
Fish larvae: *Centropyge flavissimus*, *Mylio macrocephalzis*, *Mugil cephalus*, *Mugilidae sp.*	Diet of first feeding	(Morris, 1956; Kasahara *et al*., 1960; May, 1970; Nash and Kuo, 1975; Olivotto *et al*., 2006)
Nutrition, food quality, and trophic upgrade		
Acartia longiremis (copepod)	Fatty acid content effect on egg production and hatching success	Augustin, 2006
Acartia tonsa (copepod)	Amino and fatty acids regulation of egg production	Kleppel *et al*., 1998
Acartia tonsa (copepod)	Establishing a trophic upgrade index	Tang and Taal, 2005
Acartia tonsa (copepod)	Trophic modification of essential fatty acids	Veloza *et al*., 2006
Acartia tonsa (copepod)	3 and 4 trophic-level interactions	Malzahn *et al*., 2010
Calanus glacialis (copepod)	Production of polyunsaturated fatty acids	Stevens *et al*., 2004
Pseudocalanus elongatus, Temora longicornis (copepod)	Production of unsaturated fatty acids and sterols	Klein Breteler *et al*., 1999
Encentrum linnhei (rotifer)	Trophic transfer of tryptophan	Scott, 1987
No specific predator	Production of long-chain n-3 essential fatty acids and sterols	Chu *et al*., 2008a
No specific predator	The kinetics and efficiency of sterol production and bioconversion of phytosterols	Chu *et al*., 2008b
Reproduction, development, and growth		
Acartia clause, *Centropages hamatus*, *Temora longicornis* (copepod)	Breeding success and population characteristics	Klein Breteler, 1980
Acartia longiremis (copepod)	Effect of fatty acid content on egg production rate and egg hatching success	Augustin, 2006
Acartia tonsa (copepod)	Egg production	Kleppel *et al*., 1998
Acartia tonsa (copepod)	Egg production and hatching success	Kleppel and Burkart, 1995
Acartia tonsa (copepod)	Egg production rate and egg hatching success	Tang and Taal, 2005
Pseudocalanus elongatus, *Temora longicornis*	Development from young nauplius	Klein Breteler *et al*., 1999

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(copepod)	larvae to maturity	
Pseudocalanus elongatus, *Temora longicornis* (copepod)	Body size in the adult stage and rate of development	Klein Breteler *et al*., 1990
Pseudocalanus elongatus (copepod)	Rate of development from egg to adult	Klein Breteler *et al*., 1995
Pseudocalanus elongatus, *Temora longicornis* (copepod)	Prosome length and biomass	Klein Breteler and Gonzalez, 1988
Temora stylifera (copepod)	Postembryonic development	Carotenuto *et al*., 2002
Tisbe holothuriae (copepod)	Population dynamics	Guérin *et al*., 2001
Behaviour		
Oithona davisae (copepod)	Impact of turbulence on feeding	Mariani *et al*., 2008
Oxyrrhis marina	Cannibalism in protozoa	Martel and Flynn, 2008
Temora longicornis (copepod)	Swimming behaviour	Schmitt and Seuront, 2001
Bioenergetics		
Acartia tonsa (copepod)	Diet effect on faecal pellet production, grazing rate, and assimilation efficiency	Besiktepe and Dam, 2002
Acartia tonsa (copepod)	Diet effect on faecal pellet characteristics	Feinberg and Dam, 1998
Ecotoxicology		
Oithona davisae (copepod)	Subleathal/lethal bioassay and toxin transfer in food chain	Saiz *et al*., 2009
Grazing and ingestion		
Acartia omorii, *Acartia hongi* (copepod)	Ingestion rates	Jeong *et al*., 2001
Acartia tonsa (copepod)	*O. marina* used as non fluorescing particle to assess gut clearance	Kiørboe and Tiselius, 1987
Acartia tonsa (copepod)	Establishing functional response	Besiktepe and Dam, 2002
Pseudocalanus eiongatus, *Temora longkornis* (copepod)	Weight-specific ingestion	Klein Breteler *et al*., 1990
Strombidinopsis jeokjo (ciliate)	Grazing impact on populations	Jeong *et al*., 2004
Food web dynamics		
Acartia spp. (copepod)	Toxic dinoflagellates bloom dynamics	Jeong *et al*., 2001
Acartia tonsa (copepod)	Food chain stoichiometry, review	Boersma *et al*., 2008
Calanoid copepods (various life stages)	Microcosm manipulation	Ptacnik *et al*., 2004
Temora longicornis (copepod)	Laboratory study of trophic cascade	Hansen *et al*., 1993
Virtual (i.e. models)		
Oithona davisae (copepod)	Impact of turbulence on feeding	Mariani *et al*., 2008
Strombidinopsis multiauris (ciliate)	Parasite control of toxic algal blooms	Montagnes *et al*., 2008
Interaction		
Prymnesium parvum (alga)	Mixotrophic prey eat *O. marina*	Tillmann, 1998; 2003

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Fig. 1

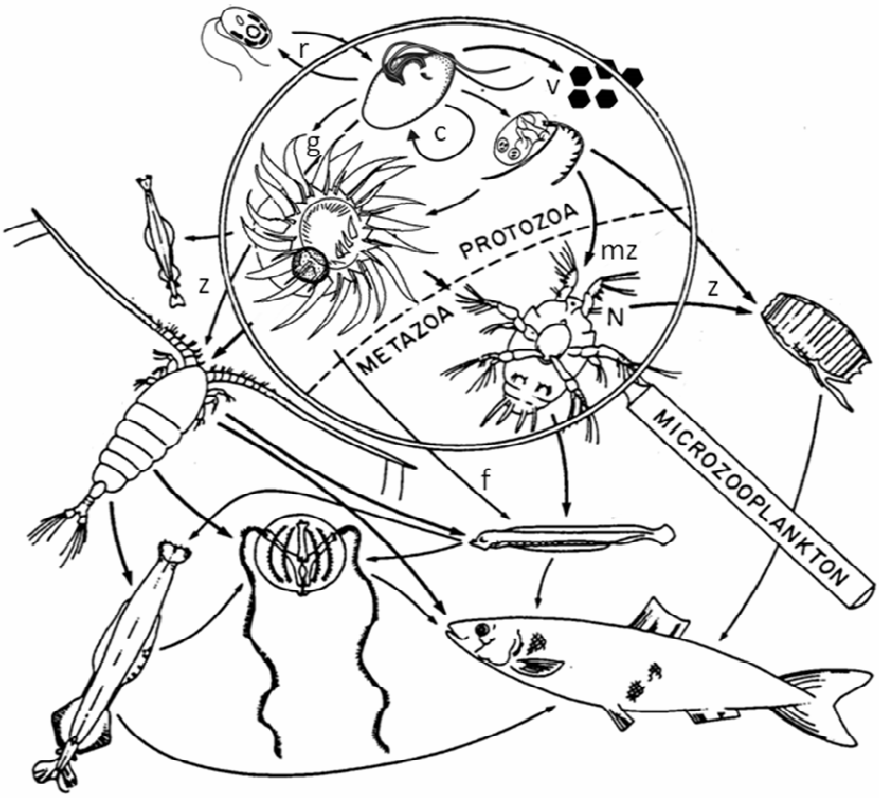
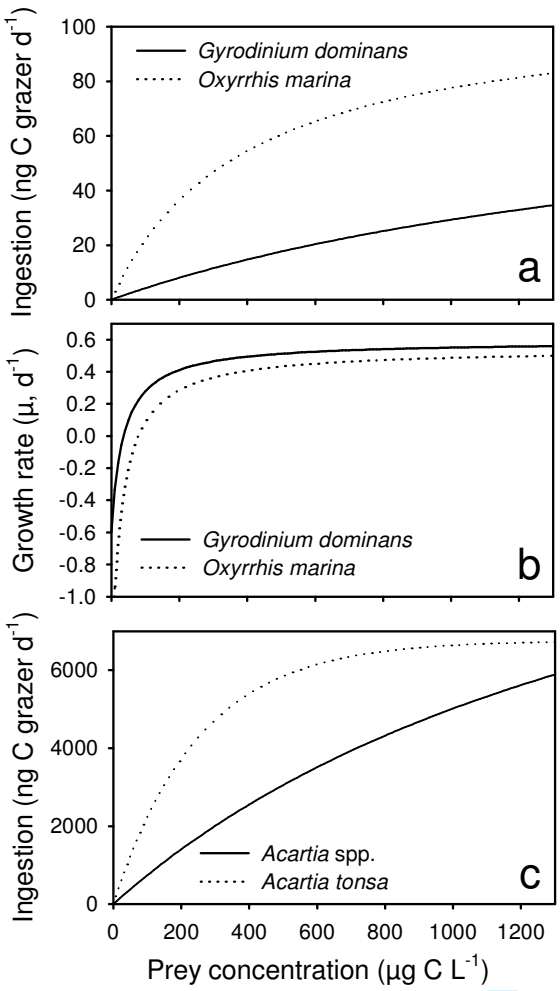


Fig. 2


Ingestion (ng C grazer d-1)
100
80
60
40
20
0
Gyrodinium dominans
Oxyrrhis marina
a
Growth rate (μ, d-1)
0.6
0.4
0.2
0.0
-0.2
-0.4
-0.6
-0.8
-1.0
Gyrodinium dominans
Oxyrrhis marina
b
Ingestion (ng C grazer d-1)
6000
4000
2000
0
Acartia spp.
Acartia tonsa
c
0
200
400
600
800
1000
1200
Prey concentration (μg C L-1)