The trophic roles of microzooplankton in marine systems

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Calbet, A. 2008. The trophic roles of microzooplankton in marine systems. – ICES Journal of Marine Science, 65: 325–331.

Microzooplankton (here defined as <200 μm grazers) are key components of marine foodwebs. Their grazing significantly affects primary producers and usually exceeds that of mesozooplankton. However, our knowledge of the detailed roles that microzooplankton taxa play in marine ecosystems is surprisingly limited. Here, I identify the main protists responsible for most of the grazing impact on phytoplankton in two contrasting marine ecosystems: oligotrophic waters and productive waters, such as upwelling systems, spring blooms, and other blooms in nearshore and estuarine systems. Evidence indicates that pico- and nano-sized flagellates, which are routinely included with the microzooplankton size class of protists, appear to be the main grazers of phytoplankton in oligotrophic habitats, whereas heterotrophic and mixotrophic dinoflagellates are candidates for the dominant grazing impact in upwelling and other productive ecosystems. Microzooplankton are also important contributors to mesozooplankton diet, especially in oligotrophic areas, although the strength of the mesozooplankton–microzooplankton link is traditionally overlooked in plankton studies. As a final remark, this review emphasizes the need to develop suitable methods for studying the role of microbial grazers in the dynamics of marine ecosystems.

Keywords: grazing, herbivory, microzooplankton, oligotrophy, primary production, upwelling.

Received 11 July 2007; accepted 3 January 2008; advance access publication 5 March 2008.

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Background

According to the classification of Sieburth *et al.* (1978), microzooplankton are a group of heterotrophic and mixotrophic organisms 20–200 μm in size, which include many protists, such as ciliates, dinoflagellates, and foraminiferans, as well as small metazoans, such as copepod nauplii and some copepodites, and some meroplanktonic larvae. Traditionally, microzooplankton have been relegated to the ranks of secondary contributors when describing the dynamics of marine ecosystems, especially those of productive waters. Furthermore, their complete relevance is not yet reflected in many conceptual and predictive foodweb models (e.g. Barber and Hiscock, 2006; Rothstein *et al.*, 2006). However, increasing evidence indicates that this group is one of the most important, along with phytoplankton and bacteria, in marine geochemical cycles of bioactive elements (Sherr and Sherr, 2002; Calbet and Landry, 2004). They occupy a key position in marine foodwebs as major consumers of primary production (Calbet and Landry, 2004), as intermediaries between primary producers and copepods (Gifford, 1991; Calbet and Saiz, 2005), and as key components of the microbial loop (Azam *et al.*, 1983; Sherr and Sherr, 2002). Indeed, only a small part of the organic matter produced by autotrophs takes the "fast lane" to upper trophic levels, to be grazed directly by large metazoans (e.g. copepods). In fact, most primary production circulates through different trophic levels, including microzooplankton, and is eventually respired within the microbial loop (Azam *et al.*, 1983; Sherr *et al.*, 1986).

A recent review of the grazing activity of microzooplankton assessed by the dilution technique (Landry and Hassett, 1982) revealed microzooplankton as the main predator of phytoplankton in tropical and subtropical oligotrophic waters. On average, their consumption is 75% of particulate primary production and about half of the phytoplankton biomass per day (Figure 1; Calbet and Landry, 2004). Most of the remaining production is grazed by mesozooplankton (Calbet, 2001), resulting in little or no export production, as expected for this sort of recycling-based system (Wassmann, 1998). The role of microzooplankton as grazers is also evident in other types of ecosystems. For instance, in temperate climates, the daily grazing activity of microzooplankton accounts for ca. 60% of the primary production and half of the phytoplankton biomass per day. This picture extends to Antarctic waters, where daily microzooplankton grazing during the light season also accounts for 60% of the primary production, although this equates to only 20% of their biomass (Calbet and Landry, 2004). However, the few data available from the Arctic Ocean seem to reflect less microzooplankton grazing control on primary producers (Sherr *et al.*, in press).

Regarding the trophic characteristics of the system, it is interesting that even in very productive areas, such as estuaries and upwellings, the grazing impact of microzooplankton on phytoplankton is high, an average of 60% of primary production being consumed per day (Figure 1; Calbet and Landry, 2004). This value contrasts with the small overall impact of mesozooplankton (on average, 10% of the primary production consumed daily; Calbet, 2001). The modest average contribution of mesozooplankton to total community grazing in upwellings and very productive systems, even if variable (Dagg and Turner, 1982; Dubischar and Bathman, 1997; Barquero *et al.*, 1998; González *et al.*, 2000), diverges from the traditional view of these ecosystems, which are presented as the archetype of a classical herbivorous food chain (diatoms–copepods–fish). We should consider,

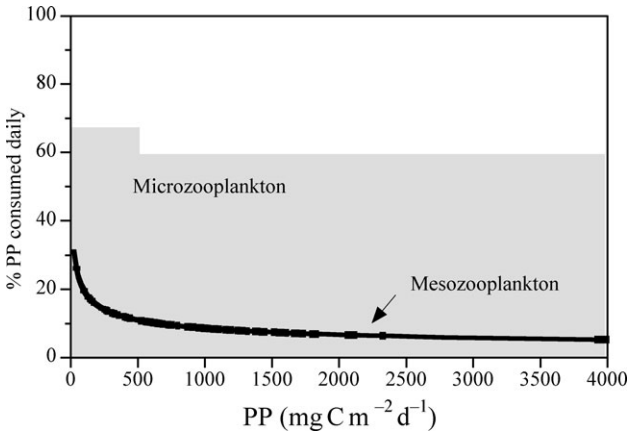

Figure 1. Schematic approximation to the global mean grazing impact on autotrophic production. Percentage of phytoplankton primary production (PP, mg C m^{-2} d^{-1}) consumed daily by microzooplankton (shaded area) and mesozooplankton (line) as a function of autotrophic production (mg C m^{-2} d^{-1}). Data from Calbet (2001) and Calbet and Landry (2004). Microzooplankton grazing impact has been adjusted assuming the PP of the open ocean areas to be $<$500 mg C m^{-2} d^{-1} and coastal and estuary areas $>$500 mg C m^{-2} d^{-1}.

however, that copepods and large metazoans need longer (weeks to months) developmental times than microzooplankton (days), and it is quite likely that, in many instances, they cannot cope with the strong fluctuations in food supply, which is a characteristic feature of many upwelling systems (match–mismatch hypothesis; Cushing 1975). The evidence favouring a revision of the classical paradigm is further reinforced when we examine closely the communities of primary producers, mostly composed of long-chain spiny diatoms. Many mesozooplankters, even if able to feed on these algae, will not do it efficiently (Berggreen *et al.*, 1988).

An overall higher relevance of microzooplankton as a control factor of phytoplankton populations does not mean that large mesozooplankton are not important components of marine foodwebs. Even if their grazing impact is generally lower than that of microzooplankton, they are still important agents for structuring pelagic foodwebs (Gifford, 1991; Nielsen and Hansen, 1995; Pakhomov and Perissinotto, 1997; Roman and Gauzens, 1997; Gowen *et al.*, 1999), and they remain a crucial link between autotrophs and fish (Park *et al.*, 1973; Cushing, 1989). In addition, we cannot disregard episodes of high mesozooplankton grazing on primary producers and indirect effects on phytoplankton by predation on microzooplanktonic grazers (Nejstgaard *et al.*, 2001).

However, we must be aware that, similar to the way that copepods were dealt with in the 1970s and early 1980s until the "black box" was slowly opened, our knowledge of the functional diversity of microzooplankton is scarce, and they are typically considered to be a single homogenous group. This is partly a consequence of the standard method for estimating microzooplankton grazing, the dilution technique (Landry and Hassett, 1982), which does not discriminate between different types and sizes of grazers, and includes not only micro-sized zooplankton (*sensu* Sieburth *et al.*, 1978) but also pico- and nanoheterotrophs. Here, I will attempt to open the black box of microzooplankton and try to identify the major grazers in each ecosystem. This exercise will help to solve the paradox of such strong and similar impacts of microzooplankton in very contrasting ecosystems. This will be useful, not only to satisfy our curiosity, but to understand the dynamics of the system and to establish the complexity of the foodweb. In terms of efficiency of the circulation of matter and energy, and for the overall economy of the system, it is necessary to identify the trophic level at which most of the carbon from autotrophic production enters the foodweb. As an example, I will detail the role of the different groups of microzooplankton on the foodweb dynamics of two trophically distinct ecosystems: oligotrophic oceans and highly productive areas.

Main grazers in oligotrophic ecosystems

It seems conceptually proper to identify small flagellates as the main grazers of low-production ecosystems, where prokaryotic cells and pico-sized autotrophs are the dominant primary producers (Campbell *et al.*, 1994; Worden *et al.*, 2004; Sherr *et al.*, 2005; Not *et al.*, 2007). This is corroborated by the relative biomass distribution patterns of nanoflagellates and large microzooplankton in very oligotrophic areas. For instance, during August 1989 and March/April 1990, near the JGOFS time-series station near Bermuda (Sargasso Sea), 2–5 μm nanoflagellates comprised, on average, 24–30% of the total heterotrophic biomass, whereas 5–200 μm microzooplankton (mostly ciliates and dinoflagellates) only comprised 6–8% of the biomass (Roman *et al.*, 1995). Furthermore, in a seasonal study in the Arabian Sea when the chlorophyll concentration was lowest, the biomass of heterotrophic nanoflagellates was approximately five times higher than that of heterotrophic ciliates and dinoflagellates together, whereas during periods of maximum concentration of chlorophyll, the biomasses of both groups were similar (Garrison *et al.*, 2000). Although biomass distribution patterns may be indicative of trophic pathways, they are mere snapshots of the system and are not conclusive without knowledge of the community's previous history, the turnover rates, and direct evidence of grazing. In this regard, in a study investigating trophic coupling in the subtropical North Pacific using size fractionation to truncate the foodweb at various predator sizes, the growth dynamics of combined autotrophic and heterotrophic prokaryotes was significantly influenced by a three-step predatory chain compressed within the $<$5 μm size fraction. Flagellates $<$2 μm in size were feeding directly on prokaryotes, while 2–3 μm flagellates were feeding on them, and in turn, they were the prey of 3–5 μm flagellates (Calbet *et al.*, 2001). Interestingly, despite the relative constancy of the standing stocks of prokaryotes and protists, which characterizes oligotrophic oceanic areas (Campbell *et al.*, 1997), microbial community interactions varied markedly among experiments, indicating an alternation between resource and predatory control. This intrinsic variability in foodweb dynamics is not always identified in dilution experiments, where negative values are not always reported (Dolan and McKeon, 2005). The study of Calbet *et al.* (2001) identified the main grazers of the small primary producers of oligotrophic waters of the subtropical Pacific, but did not provide an estimate of grazing impact. On the other hand, using a similar methodology (size fractionation of the community) in the northern Baltic Sea, Kuosa (1991) obtained daily impacts of flagellate grazers on phytoplankton of ca. 40% of primary production during autumn (when the production was low), which was in contrast to the small impact (ca. 5%) in spring, coinciding with peaks in production.

Another interesting approach would be to merge size fractionation with the dilution technique to address the impact of flagellates on the primary production of oligotrophic areas. By

conducting dilution experiments with previously size-fractionated natural water, we can estimate the potential grazing activity of each size fraction (Reckermann and Veldhuis, 1997). Thus, we can better identify the most relevant fraction of grazers in the community. Previous studies with this approach using a 20-μm size fraction (Reckermann and Veldhuis, 1997; Lessard and Murrel, 1998) did not result in a significantly different impact on primary producers from that obtained in <200 μm (standard) treatments. This was because most microzooplanktonic predators passed through the 20-μm mesh netting. However, smaller size fractions rendered very interesting results. In the coastal northwest Mediterranean, Calbet *et al.* (2008) conducted a series of experiments where the results of standard dilutions with unfiltered water were compared with those obtained with 10-μm reverse-filtered natural water. The phytoplankton grazing mortality rates obtained for the <10-μm experiment were very high, especially during the warmer months in which most primary producers were <10 μm. At times (August and September 2006), the impact of <10 μm grazers on the standing stock of chlorophyll *a* surpassed that obtained by standard dilutions with unscreened water (Figure 2). This can only be understood if large microzooplankton control the abundance of the main grazers (pico- and nano-sized protists) of the small dominant primary producers. The idea is certainly not new (see, for instance, Sherr and Sherr, 1992), but I think it needs to be emphasized because it is not unusual to find in the literature studies that use the abundance of ciliate protozoa as a proxy for microzooplankton community grazing estimates across varying ocean habitats (including oligotrophic regions; e.g. Dolan and McKeon, 2005).

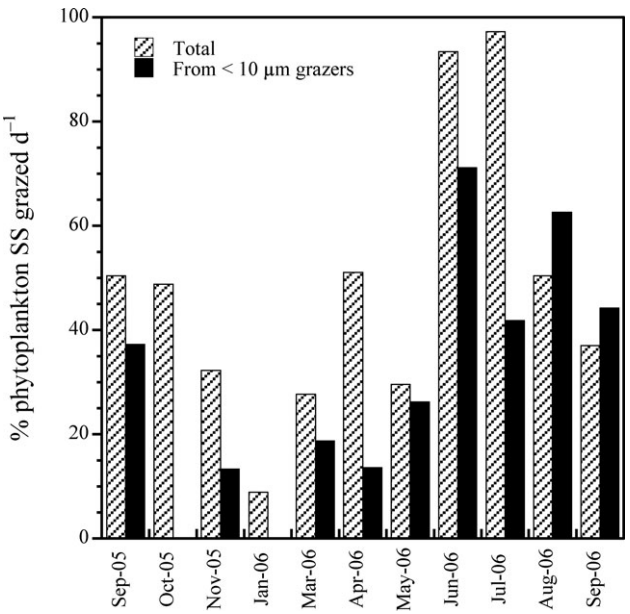

Figure 2. Comparison of the total phytoplankton standing stock (SS) daily consumed in northwest Mediterranean coastal waters by the whole community of grazers (Total, from standard dilution experiments with unfiltered water) and their equivalent for <10-μm prefiltered water treatments. These have been derived from the impact obtained in <10-μm experiments and the contribution of <10-μm chlorophyll *a* to total chlorophyll *a*. Note that this is an extrapolation of a situation without predatory pressure by larger predators on nanograzers, and it is not representative of the actual natural contribution of nanograzers to total community grazing. Data from Calbet *et al.* (2008).

Main grazers in upwelling systems and other productive areas

To affect a dense phytoplankton bloom significantly, a given organism must satisfy several requirements: it must be abundant, it must coincide with algae both in time and in space, and it must be able to feed on them efficiently. When thinking about microzooplankton, ciliates immediately come to mind. However, ciliates, even if very relevant in many ecosystems, are poor candidates to explain the high grazing rates obtained in upwellings. The phytoplankton of these areas are usually dominated by large diatom chains, which are not suitable prey for ciliates, which feed mostly on smaller organisms (Fenchel, 1980; Gifford, 1985; Jonsson, 1986), with some exceptions (Aberle *et al.*, 2007). On the other hand, another group of protists are potential candidates for such a trophic role: the heterotrophic (and perhaps mixotrophic as well) dinoflagellates (Strom and Strom, 1996; Stelfox-Widdicombe *et al.*, 2004; Jeong *et al.*, 2005a, 2005b; Saito *et al.*, 2006; Sherr and Sherr, 2007). The feeding plasticity of this group allows them to ingest prey ranging in size from ca. 1 μm (Strom, 1991; Jeong *et al.*, 2005a) to several times their body size (Figure 3; Lessard, 1991; Hansen, 1992; Strom and Strom, 1996; Saito *et al.*, 2006; Sherr and Sherr, 2007). This is accomplished through three main feeding strategies: direct engulfment, pallium feeding, and tube feeding (Hansen and Calado, 1999).

The clearance rates of heterotrophic dinoflagellates on natural algae are similar to, and even higher for gymnodinoids than,

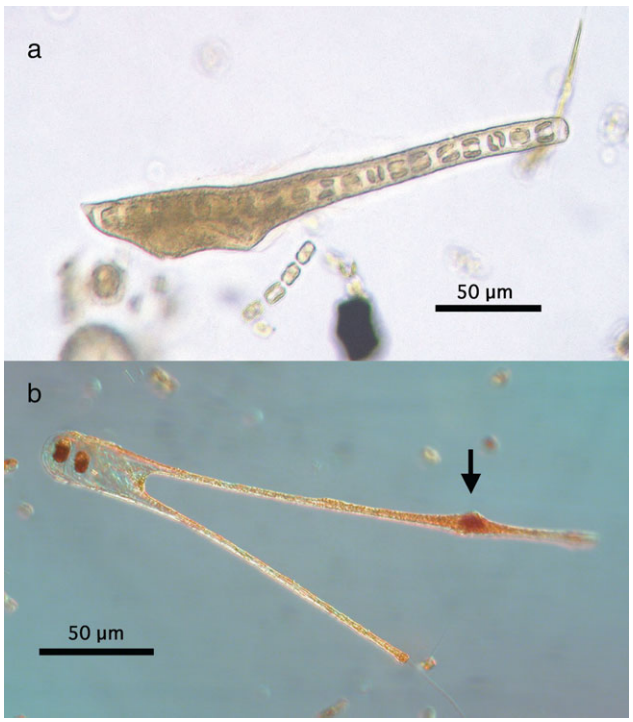

Figure 3. *Gyrodinium* sp. ingesting *Thalassiosira* sp. (a) and *Chaetoceros* sp. (b) several times larger than its body length. Photo (a) courtesy of E. B. Sherr and B. F. Sherr; Photo (b) courtesy of H. Saito. The arrow shows the location of the dinoflagellate.

that of ciliates, as reported by Neuer and Cowles (1995) in coastal waters off Oregon. They also seem to coincide in time with the seasonal blooms of phytoplankton in many coastal areas. Clear examples, among others, are the southern Kattegat during the spring phytoplankton bloom (Hansen, 1991) and the Gulf of Trieste during the winter diatom bloom (Umani and Beran, 2003), in which heterotrophic dinoflagellates peak with the algae (Figure 4). The biomasses reached by this group of protozoans when blooming usually exceed that of ciliates (Jeong, 1999; Sherr and Sherr, 2007), further suggesting a role as main grazers of phytoplankton during diatom blooms.

This feeding relationship has been suggested several times, based on direct microscopic observations and potential impacts obtained from laboratory experiments (see reviews by Jeong, 1999; Sherr and Sherr, 2007). However, on very few occasions has the impact of grazing by heterotrophic dinoflagellates on diatom blooms actually been assessed. Perhaps one of the clearest and most elegant examples was reported by Archer *et al.* (1996) during a diatom bloom in East Antarctic waters (January–February 1994). Using a modification of the technique proposed by Lessard and Swift (1985), measuring uptake rates of ^{14}C by heterotrophic dinoflagellates, the authors reported consumptions of up to 28% of the primary production per day (Figure 5). The end of the diatom bloom occurred at the same time that heterotrophic dinoflagellates biomass was ca. 50% of that of autotrophs. Also, Saito *et al.* (2006), using mathematical simulations, demonstrated that, in the western Subarctic Pacific, most of the carbon fixed by diatoms during an iron enrichment experiment could be respired by the dinoflagellate *Gyrodinium* spp.

Dinoflagellates can exert their influence not only on diatoms, but also on dense populations of harmful algae. For instance, the heterotrophic *Stoeckeria algicida* can feed efficiently on the toxic *Heterosigma akashiwo*, and when these feeding rates are scaled to natural abundances, *S. algicida* can have a severe impact on the algae (Jeong *et al.*, 2005c). This role as grazers of phytoplankton also extends to other prey, such as other protozoans and metazoans (Jeong, 1999). For example, the mixotrophic dinoflagellate *Ceratium furca* removed, on average, 67% of the *Strobilidium* spp. population per day in lower Chesapeake Bay (Smalley and Coats, 2002). Another curious example relates to *Noctiluca miliaris*, which can clear up to 50% of the copepod eggs in the southern North Sea (Daan, 1987).

Phagotrophic dinoflagellates and ciliates are not always the sole microzooplankton grazers for large phytoplankton. There are other poorly studied groups that, at times, can be very relevant to the dynamics of the ecosystem. For instance, during an *Alexandrium minutum* bloom in northwest Mediterranean coastal waters, the rotifer *Synchaeta triophthalma* removed ca. 45% of the daily production of algae, heterotrophic dinoflagellates removed 30%, and ciliates removed the remaining 25% (Calbet *et al.*, 2003). It is worth mentioning that the impact of the co-occurring copepods was not significant. This is likely because microzooplankton have shorter developmental times, which allow not only the fast increase in biomass to cope with algae, but also, in the specific case of toxic prey, the quick selection of resistant species or genotypes.

Microzooplankton as prey for larger organisms

It is now clear that microzooplankton are relevant contributors to the diet of copepods (see reviews by Calbet and Saiz, 2005; Sherr and Sherr, 2007). In a recent analysis of the importance of ciliates as carbon sources for copepods, Calbet and Saiz (2005) concluded that, although phytoplankton represent globally a far larger biomass than ciliates, the consumption of the latter comprise, on average, 30% of copepod daily carbon rations (ciliates+phytoplankton) (Figure 6). The relative importance of ciliate consumption by copepods depends on the trophic state of the system. In oligotrophic ecosystems (most of the world's oceans), the ciliate-associated carbon supply for copepods equals that of

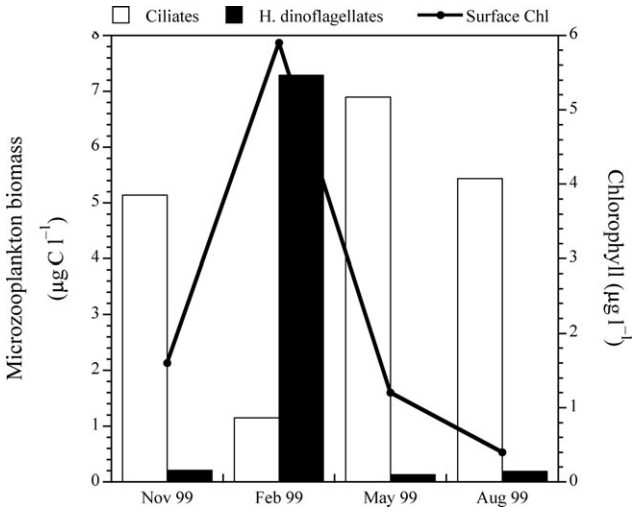

Figure 4. Biomass distribution of ciliates, heterotrophic dinoflagellates, and chlorophyll in November–August 1999 in the Gulf of Trieste (northern Adriatic Sea). The peak of chlorophyll in February corresponds to a diatom bloom. Data from Umani and Beran (2003).

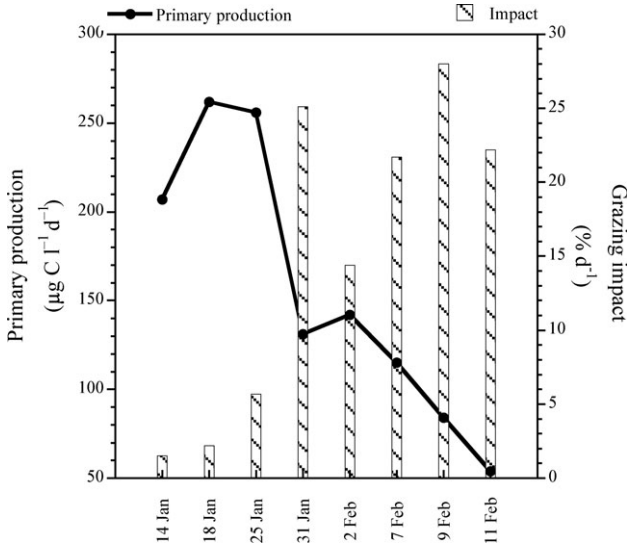

Figure 5. Primary production and grazing impact as percentage of the primary production consumed daily by heterotrophic dinoflagellates during a diatom bloom in coastal waters of East Antarctica. The increasing rate of consumption of primary production with time coincides with an increase in the abundance of heterotrophic dinoflagellates (see text). Data from Archer *et al.* (1996).

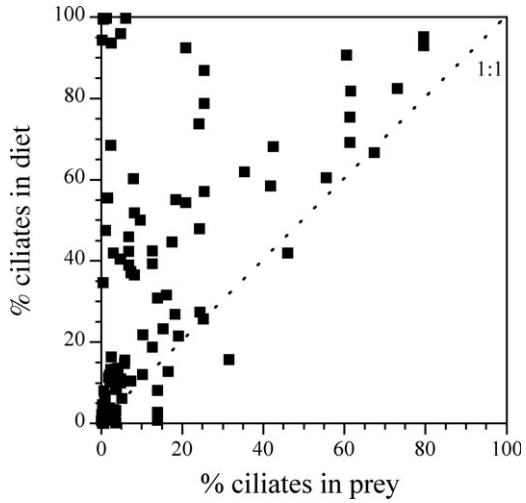

Figure 6. Scatterplot of the relative presence (in terms of carbon) of ciliates in the diet of copepods as a function of its relative availability in different marine systems ($n = 109$). Data above the 1:1 line indicate positive selection for ciliates. Data from Calber and Saiz (2005).

phytoplankton, and this value declines in more productive environments, where ciliates account for ca. 25% of the diet.

Heterotrophic dinoflagellates are also a significant food source for mesozooplankton (Sherr and Sherr, 2007), which are, at times, cleared at higher rates than ciliates (Suzuki *et al*., 1999; Liu *et al*., 2005). Therefore, the combined contribution of heterotrophic ciliates and dinoflagellates (as well as other microzooplankters) to the mesozooplankton diet may surpass that of phytoplankton in certain systems. It seems that this preference for microzooplankton is caused by a combination of different factors: optimal size (Berggreen *et al*., 1988), nutritional composition (Stoecker and Capuzzo, 1990; Wickham, 1995; Broglio *et al*., 2003), and swimming behaviour (Jonsson and Tiselius, 1990; Kiørboe and Visser, 1999), with the relative relevance of these being unresolved.

The derivation of energy and matter from the microbial loop towards upper trophic levels confirms the strength and importance of the heterotrophic link between the microbial foodweb and the classical food chain (Sherr *et al*., 1986). Based on these, the flux of carbon from microzooplankton should definitely be considered in oceanic biogeochemical cycles and pelagic foodweb models.

Concluding remarks

In light of the evidence summarized here, it appears certain that microzooplankton (in a wide sense, including also all grazers <200 μm) are key components of marine foodwebs. It is also clear that they are diverse, with each taxonomic group (and perhaps each species) playing very distinct roles in the ecosystem. Not only are ciliates important, but other groups, often ignored and poorly sampled, can play a crucial role in the foodweb. Among them, heterotrophic and mixotrophic small flagellates and dinoflagellates seem to be very important, but it is likely that rotifera (Mallin *et al*., 1995; Calbet *et al*., 2003), radiolaria (Gowing, 1989; Anderson, 1993; Matsuoka, 2007), foraminifera (Anderson, 1993), meroplanktonic larvae (Turner and Anderson, 1983), copepod nauplii (Turner, 2004), etc., also play significant roles. Therefore, we must go one step further and try to open the microzooplankton black box. By depicting the role of each group, the dynamics of the foodwebs will be better understood, and more precise plankton models will be built (Bruggeman and Kooijman, 2007). However, this can only be accomplished if techniques and methodologies are robust. Unfortunately, for the study of fragile microbial grazers, we lack optimal techniques. In the era of molecular biology, we do not even have a trustworthy way of preserving samples without losing a significant (and unknown) number of protists (Klein Breteler, 1985; Stoecker *et al*., 1994; Gifford and Caron, 2000; Broglio *et al*., 2004). Maybe it is time for the application of new technologies to conduct detailed and conclusive cross-ecosystem studies on specific losses from live to preserved natural samples of micro- and nanoplankton when using different fixatives. In the same way, we should not abandon the idea of testing new fixatives, perhaps taking advantage of well-established disciplines such as cytology and histology. Ideally, our goal should be to create a fixative that is easy to use, that does not damage organisms, and that allows for identification at the species level without masking the chlorophyll signal under epifluorescence microscopy. Only with efficient methods in hand can we explore the role of microzooplankton in the oceans in detail.

Acknowledgements

This work was supported by grant CTM2004–02575/MAR from the Spanish Ministry of Education and Science. I thank E. Saiz, M. Alcaraz, E. B. Sherr, and one anonymous reviewer for helpful comments to early versions of the manuscript. I also thank H. Saito, E. B. Sherr, and B. F. Sherr for providing the pictures in Figure 3.

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doi:10.1093/icesjms/fsn013