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► **To cite this version:**

M. R. Landry, A. Calbet. Reality checks on microbial food web interactions in dilution experiments: Responses to the comments of Dolan and McKeon. *Ocean Science Discussions*, 2004, 1 (1), pp.65-76. hal-00298365

HAL Id: hal-00298365

<https://hal.science/hal-00298365>

Submitted on 18 Jun 2008

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Reality checks on microbial food web interactions in dilution experiments: Responses to the comments of Dolan and McKeon

M. R. Landry¹ and A. Calbet²

¹Integrative Oceanography Division, Scripps Institution of Oceanography, University of California at San Diego, 9500 Gilman Dr., La Jolla, California 92093-0227, USA

²Institut de Ciències del Mar, CMIMA (CSIC), P. Marítim de la Barceloneta 37–49, 08003 Barcelona, Spain

Received: 13 December 2004 – Accepted: 27 December 2004 – Published: 29 December 2004

Correspondence to: M. R. Landry (mlandry@ucsd.edu)

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Abstract

Microzooplankton grazing rate estimates by the dilution approach have recently been criticized as systematically biased in the direction of being overestimates of actual rates in nature, and particularly in the open oceans. This argument is based on observed mortality responses of ciliated protozoa to reduced food in several coastal experiments and a global extrapolation which assumes that all grazing in all ocean systems scales to the abundance of ciliates. We suggest that these conclusions are unrealistic on several counts: they do not account for community differences in open ocean and coastal systems; they ignore experimental direct evidence supporting dilution rate estimates in the open oceans, and they discount dilution effects on mortality as well as growth in multi-layered, open-ocean food webs. High microzooplankton grazing rates in open-ocean systems are consistent with current views on export fluxes and trophic transfers. More importantly, significantly lower rates would fail to account for the efficient nutrient recycling requirements of these resource-limited and rapid-turnover communities.

1. Introduction

It has long been speculated that the gradient of food availability in dilution experiments could lead to treatment differences in the population growth rates of microzooplankton grazers (Landry and Hassett, 1982; Gallegos et al., 1989; Landry, 1993; Landry et al., 1995). This, in fact, should be the case whenever ambient concentrations of food resources are insufficient to sustain maximal rates of food intake and growth. Dolan et al. (2000) and Dolan and McKeon (2004) have now demonstrated additional caveats for such experiments; ciliated protozoa may not only grow slower, but may, in fact, decline precipitously in seawater diluted to low percentages (10%) of natural food concentration. This observation is important to those who use the technique to assess the microzooplankton grazing impacts on phytoplankton stocks and production rates. Whether it means that dilution experiments yield systematically inflated estimates of microzoo-

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plankton grazing is, however, quite another matter. In the interest of promoting a useful discussion of this point, we therefore respond to the main conceptual issues raised by Dolan and McKeon (2004) as well as several inaccuracies and misconceptions in that critique.

2. General premise

In order to frame the microzooplankton grazing issue for discussion, we will first consider what the Calbet and Landry (2004) synthesis of dilution results actually reported on the matter and how that relates to our understanding of microbial trophic interactions and organic matter cycling and fluxes in the oceans. Calbet and Landry (2004), for instance, did not point to the relative invariance or “near-constancy” of grazing losses, as one might be led to believe by Dolan and McKeon (2004). In fact, the analyzed data were marked by extraordinary variability, from zero to several-fold contemporaneous estimates of phytoplankton growth, as evident in the accompanying figures and the web-accessible table. This variability is presumably as it should be for individual experiments that capture communities in varying states of phytoplankton increase, decline or near-steady state. We did however find that, within relatively broad categories of marine habitats and regions, the “mean” fractions of daily phytoplankton production removed by microzooplankton grazers varied modestly, from about 60 to 75% of primary production (PP). As potentially applied to a global ocean average, the grand data mean of 64% of PP could even be an underestimate because open-ocean experiments, providing the highest mean rate estimates, were under represented in the data set relative to their contributions to ocean productivity on an areal basis.

Is 64%, or presumably some slightly higher fraction, of global ocean primary production too much grazing for microherbivores? The general premise of Dolan and McKeon (2004) is that “there would be little left” for carbon export or higher level food webs. This argument does not however consider the reusable fluxes associated with trophic transfers. For instance, if 70% of PP were directly consumed by micrograzers,

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only about half of that would be actually lost to respiration by the primary consumers (Fenchel and Finlay 1983, Verity 1985), and the remainder would be available as heterotrophic biomass and as small particulate debris for further utilization and transfer. If each level of intermediate consumer in a protistan predatory chain of 2–3 links (n) had a gross growth efficiency (GGE) of 0.3 (Straile et al., 1997), 32 to 36% of PP would ultimately be available to mesozooplankton (net available for transfer = $30\% \text{ ungrazed PP} + 70\% \cdot 0.3^n$; where $n=2$ or 3). Such an amount would be quite adequate to support the relatively low rates of POC export in the central open oceans (e.g. 5–10% of PP; Karl, 1999; Landry et al., 1997). Moreover, this simple calculation does not consider the trophic fluxes associated with protist utilization of bacterial production ($\sim 15\%$ of PP; Anderson and Ducklow, 2001) or the possible trophic fates of small particulate egesta. High microzooplankton grazing impacts are therefore not inherently at odds with what we know about ocean export fluxes.

Indeed, as a “reality check”, one might contemplate the difficulties that would arise in explaining open-ocean equilibrium conditions in the absence of high microherbivore grazing. For this thought problem, one should note that microzooplankton grazing rates from dilution experiments are measured relative to the net realized rates of phytoplankton cell growth, not the gross rates of primary carbon production, the latter being partially offset by losses to phytoplankton respiration, DOC production and bacterial uptake, viral lysis, etc. Thus, observed cell growth rates of one doubling day⁻¹ or more for phytoplankton of the central tropical/subtropical oceans actually demand loss terms of comparable magnitude to maintain quasi-steady state. The candidate loss processes are: 1) micrograzers, 2) larger mesozooplankton grazers, and 3) direct cell sinking to export.

There is little evidence to support massive and temporally persistent export of chlorophyll-rich material in the central open-oceans, and both the tiny size of the dominant phytoplankton (*Prochlorococcus*, *Synechococcus*) and the nutrient recycling needs for sustainable productivity provide strong arguments against such a possibility. Most mesozooplankton also cannot directly exploit tiny phytoplankton. Experimenten-

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tal assessments of mesozooplankton grazing impact in such regions typically range on the order of 5–10% of daily PP (Bautista and Harris, 1992; Dagg, 1993; Dam et al., 1993, 1995; Rollwagen-Bollens and Landry, 2000) and one must typically invoke a strong predatory link through heterotrophic protists to account even for the basic metabolic requirements of these consumers (Stoecker and Capuzzo, 1990; Roman and Gauzens, 1997). These considerations leave microzooplankton grazing therefore as the most likely loss process for the vast majority of phytoplankton biomass growth, which is consistent with measurements by the dilution technique. To make this argument another way, if microzooplankton grazing impact in the open oceans are as low as suggested by Dolan and McKeon (2004), ~50% of PP, and if losses to export flux and to mesozooplankton grazers are both of order 5–10% of PP, about 30 to 40% of daily PP would have no obvious mechanism for its direct utilization within the food web and for the efficient return of remineralized nutrients to phytoplankton.

In extending the above thoughts about trophic interactions and fluxes for the open oceans to more coastal environments, or even among different open-ocean regions, one also needs to consider that similar rates of microzooplankton herbivory can have very different implications in a food web context. For instance, if 60% of PP is consumed by micrograzers, and these, in turn, are “directly” consumed by mesozooplankton, then the POC pool for direct particle export or mesozooplankton consumption can be as high as 70% of PP, or about double that of the example above, since only 30% of PP would be lost to microherbivore respiration. A more efficient transfer of bacterial secondary production to mesozooplankton might also occur in such a system, pushing this POC pool even higher. Different ocean regions clearly may have substantially different characteristics with respect to mesozooplankton secondary production and export flux, even while appearing to have reasonably similar rates of microherbivory. The important difference is the mean length of the protistan predatory chain to higher-level consumers. In Landry and Calbet (2004), we provide a more detailed discussion of the implications of differing food-web scenarios for microzooplankton secondary production and trophic transfers.

3. Methodological issues and insights

The heart of the Dolan and McKeon (2004) commentary is its critique of the dilution methodology. We welcome such discussion as an important part of the evolution of scientific methodology, and hope that it ultimately leads to new or improved approaches.

5 What we offer in this section is therefore not a “defense” of the method or how it is applied in different circumstances by various users. We do, however, wish to clarify certain points that we believe to be inaccurately or incompletely represented by Dolan and McKeon (2004), and to provide a few relevant insights of our own.

10 One problem with the Dolan and McKeon (2004) critique is the characterization of insignificant dilution regression statistics as experimental “failures”. According to the method, the regression slope provides an estimate of instantaneous grazing rate. An insignificant regression slope therefore provides a result of “zero” grazing. A high incidence of such results, as Dolan and McKeon (2004) claim, is therefore directly contradictory to their claim that dilution experiments “are unlikely to furnish evidence of low grazing rates”. In this regard, Calbet and Landry (2004) discarded very few experimental results from the literature as problematic and averaged zero values with all of the other estimates. Moreover, all of the ratio data were arctan transformed so as not to exaggerate the relative importance of grazing values far in excess of 100% PP.

20 A second arguable issue in the Dolan and McKeon (2004) critique is that they cite both Dolan et al. (2000) and Gallegos (1989) as providing supporting evidence for over-estimated grazing rates. While the former is accurate, the latter is at best misleading. The main point of the Gallegos (1989) paper was the observation of saturated protistan grazing kinetics under high food conditions, which led to “underestimates” of grazing impact in dilution experiments conducted. What is interesting about the Gallegos (1989) and Dolan et al (2000) papers is that they both involved experiments in the Rhode River Estuary (Maryland, USA), one leading to underestimates of grazing, the other to overestimates. Apparently, even in a given system, it is difficult to make an unambiguous case for systematic biases.

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Be that as it may, it is undeniable (Dolan et al., 2000) that protist growth rates decline with reduced food concentrations in the dilution series, and that should have some effect on the outcome of the regression analyses for grazing rates. In an open-ocean study in the equatorial Pacific, Landry et al. (1995) addressed this uncertainty in a round-about manner using fluorescently labeled bacteria (FLB) as a grazing probe, the notion being that the regression relationship could be based on actual rates of relative grazing in the different dilution treatments (FLB disappearance) rather than initial dilution estimates of the grazer community. The results of these experiments yielded essentially identical grazing rates estimates to the standard dilution regressions. Moreover, FLB disappearance rates were entirely consistent with the estimated grazing rates on a similarly sized natural prey (*Synechococcus*), indicating a clear grazer-mediated effect. Thus, while Dolan and McKeon (2004) speculate about dilution effects on grazer activity in the open oceans, there are techniques available and experimental results that support the published rate estimates. How then do we reconcile the expected dilution effect on population growth rate with the demonstrated negligible impact on rate estimates?

As in any natural system, the dynamics of populations in the dilution incubations are not determined by growth rates alone, but by imbalances in growth and mortality losses. In subtropical waters off Hawaii, Calbet and Landry (1999) and Calbet et al. (2001) have demonstrated multiple levels of intermediate consumers between the size range of dominant bacterial and small eukaryotic prey and the nominal size of small ciliates. It is therefore fair to say that oligotrophic open-ocean communities of this type are complex in the sense of having a strong predator hierarchy or network of interacting populations. In addition, strategies such as mixotrophy (i.e. photosynthetic phagotrophs) are relatively widespread and may isolate at least some populations from serious starvation responses to reduced food concentrations. We hypothesize that such complexities lend themselves well to dilution manipulation. For instance, if we can assume that the bioenergetics of small flagellates are such that they grow in proportion to their food intake (e.g. Fenchel and Findlay, 1983), then diluting their food will

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result in a proportional decrease in growth rate. Simultaneously, however, their direct predators, and thus the mortality impact on them, will also have been diluted by the same factor. These counteracting effects may or may not precisely offset one another in practice, but it is important to recognize that they exist and may help to explain a quasi-constancy of grazer populations, and grazing activity, when complex microbial communities are serially diluted. Problems could clearly arise, however, at the level of the top consumer, which presumably would suffer all of the disadvantages of having its food reduced without a corresponding relative reduction in losses to predators. At least in principle, the presence of small starvation-resistant metazoan consumers (e.g. *Oithona*, *Oncaea* spp.) can provide top-consumer stability to protistan populations in open-ocean dilution incubations. Because such organisms appear to have little direct impact on the dynamics of phytoplankton and Chl *a* (Calbet and Landry, 1999), it can do more harm than good to pre-screen them from such experiments.

4. Ciliates as community grazing proxies

Dolan and McKeon (2004) advance the notion that the abundance of ciliated protozoa can be used as a proxy to test the “reliability” of microzooplankton community grazing estimates across varying ocean habitats. If so, then zooplankton ecologists should be able to scale total mesozooplankton grazing to the abundance of copepods. Ciliates, as copepods, vary enormously in their sizes, discriminations and activities. Ciliates, as copepods, are just parts of grazer assemblages that vary in relative abundance and impact with physically associated shifts in the dominance structure of phytoplankton prey. Other factors, e.g. environmental temperatures, should also be relevant in comparing rate estimates from the tropics to polar systems. What Dolan and McKeon (2004) most clearly show in their data syntheses are: 1) that the abundances of important categories of grazers, nano- and dinoflagellates, are poorly correlated with and poorly predicted by ciliates, and 2) that grazing rates, particularly in low chlorophyll regions of the ocean, cannot be adequately explained by ciliates alone. The fact that

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their grazing analysis leaves unexplained residuals does not, in and of itself, constitute evidence that the rate estimates are systematically biased. What is systematically biased is the inadequacy of their underlying assumption, which does not account for the changed community composition and function in low-chlorophyll systems. One potentially important point in this regard is that small heterotrophic flagellates may feed principally on heterotrophic bacteria in richer coastal systems, and their grazing there would be largely irrelevant to and not even measured in chlorophyll-based dilution experiments. In the low chlorophyll regions of the open oceans, however, similarly sized flagellates would feed directly on the dominant phytoplankton (photosynthetic bacteria). Thus, similar concentrations of heterotrophic flagellates in different regions of the oceans could reasonably have very different implications with regard to grazing on phytoplankton.

Dolan and McKeon (2004) use their ciliate-proxy analysis to focus principally on potential inadequacies in grazing rate estimates from open-ocean systems. For richer, e.g. coastal, systems the apparent reasonableness of rate estimates relative to ciliates present would seem to suggest that they are “acceptable”. While the latter inference would be welcomed news, we wonder whether this is really the case. From our perspective, as presented above, we would predict that food-web complexities and longer trophic path lengths of open-ocean (low chlorophyll) systems should make community grazing estimates from dilution experiments more reliable there than those from systems in which ciliates represent both the dominant grazers and the top microbial consumer. These richer systems are the very places where dilution-reduced food effects on growth might not be counterbalanced by reduced predation mortality. They are consequently the places where the starvation and growth rate effects described by Dolan et al. (2000) might be most important. It therefore could be the case that microzooplankton grazing impacts in coastal and open-ocean habitats may not be as similar as the available data presently suggests (e.g. Calbet and Landry, 2004). This remains to be determined.

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5. Concluding comments

Dolan et al. (2000) and Dolan and McKeon (2004) have shown that coastal ciliate populations can respond adversely to dilution of their food resources and that this can lead to overestimates of their grazing rates by the dilution technique. Previous work (Galle-
gos, 1989) has demonstrated that grazing rates can be underestimated when ambient
food conditions exceed those that saturate ingestion rates of the microzooplankton
consumers. Careful work therefore needs to be done to test for either of these effects
in applications of the dilution technique and to account for them in experimental rate
interpretations. In our opinion, where Dolan and McKeon (2004) critique goes wrong
is in extrapolating their results with one class of grazer under one set of circumstances
(coastal food limitation) to all experimental studies in open-ocean ecosystems, and
more importantly in drawing from that conclusions about systematic biases in global
grazing estimates. We certainly do not contend that dilution rate estimates are per-
fect in every, or perhaps even any, regard, or that all applications of the technique are
done equally well. We do, however, suggest that there is reasonable cause to believe,
in particular, the rate estimate from open-ocean (low chlorophyll) regions. Although
Dolan and McKeon (2004) see grazing biases and artifacts whenever measured rates
cannot be explained by the number of ciliates present, this notion simply does not
pass several reality checks. First, the community compositions in low-chlorophyll re-
gions of the open ocean are clearly different from coastal ecosystems, and ciliates
are much less important on both a standing stock and functional basis (as grazers
of Chl *a*). Second, there is direct experimental evidence from fluorescently labeled
grazing probes in low-chlorophyll, open-ocean waters that support rate estimates and
interpretations of dilution experiments. Third, the dominant grazers in such systems,
namely small flagellates, are deeply embedded in the size hierarchy of protistan con-
sumers where dilution is accompanied by compensatory growth and mortality effects.
Lastly, the general premise of the Dolan and McKeon (2004) critique does reflect cur-
rent views of open-ocean plankton dynamics. High microzooplankton grazing rates

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in low-chlorophyll open-ocean systems are entirely consistent with the export fluxes, trophic transfers and efficient nutrient recycling requirements of these resource-limited, self-sustaining and rapid-turnover communities.

Acknowledgements. This work was supported by National Science Foundation Grants OCE-9908808, -9911765, and -034666 (MRL) and CTM2004-02575/MAR, Program Ramón y Cajal from the Ministry of Education and Science of Spain (AC). This is a contribution of the US JGOFS Program.

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