

Mullin M M. Some factors affecting the feeding of marine copepods of the genus *Calanus*. *Limnol. Oceanogr.* 8:239-50, 1963.
[Biological Laboratories, Harvard University, Cambridge, MA]

Grazing rates by *Calanus* varied inversely with the concentration of phytoplankton cells and the duration of the experiment. In mixtures, *Calanus* generally removed large cells at higher rates than small, and this tendency was most pronounced in the largest species of *Calanus* tested. [The SCJ® indicates that this paper has been cited in over 135 publications since 1963.]

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"The research was conducted at Scripps Institution of Oceanography, Woods Hole Oceanographic Institution, and Harvard University. Freedom to move between institutions while I was still a graduate student was provided by a National Science Foundation predoctoral fellowship and advisers who held loose reins. This migration was broadening, since Woods Hole was dominated by the 'food chain dynamics' approach to pelagic ecology, while at Scripps, statistical community ecology was being superimposed on a strong base of biogeography.

"It was (and still is) convenient to assume that the grazing of unicellular phytoplankton by 'herbivorous' planktonic copepods is a simple, constant, and unselective filtration, though experiments by Harvey¹ in the year I was born (1937) had indicated some selectivity in the process. Marine zooplankton had proved difficult to maintain in the laboratory, and experimental measurements of rates were benevolently dominated by the 'grandparents,' Sheina Marshall and A.P. Orr.² At the rates of feeding they and others had measured, it was difficult to see how copepods could make a living in the open ocean. Conversely, some calculations of the grazing necessary to balance the growth

rate of phytoplankton resulted in rates which seemed impossibly high on morphological grounds.

"I was also much impressed by the lucid essays of G.E. Hutchinson (see, for example, 'The paradox of plankton'³) on how, in a turbulent environment with few physical structures, many species could coexist while seemingly competing for a few, generalized sources of nutrition. Demonstration that copepods not only fed selectively, but that different species selected different food, would suggest a resolution to the 'paradox of the plankton.'

"On a less cerebral level, my enjoyment in working with living, aesthetically pleasing, but esoteric aquatic animals was undoubtedly a strong motivation. The research was possible because of extensive collections of cultured phytoplankton at both Scripps and Woods Hole, and the availability of the first generation of machines which could count suspended particles in seawater by size category.

"One referee was unimpressed by the resulting manuscript, but the editor must have given the benefit of the doubt to a graduate student author. I attribute the paper's citation to timing, since oceanic ecology experienced rapid growth in the subsequent decade for reasons which were probably as much political as intellectual. None of the basic questions were fully resolved (they still aren't), but the paper helped inject an awareness of the complexities of interactions between particular species into the 'trophic level' approach taken in global models of oceanic ecology.

"Through high-speed cinematography we can now see how a copepod feeds,⁴ rather than drawing indirect conclusions from what it removes from suspension and its gross morphology, though as yet this visualization has not increased our ability to predict what and how much a copepod will eat in nature. Though the electronic particle counters are so easy to use that they have sometimes been employed uncritically, the fundamental importance of particle size in planktonic trophic relations continues to be recognized. A recent review of feeding by marine zooplankton is by Conover.⁵

1. Harvey H W. Note on selective feeding by *Calanus*. *J. Mar. Biol. Ass. UK* 22:97-100, 1937.
2. Marshall S M & Orr A P. *The biology of a marine copepod, Calanus finmarchicus (Gunnerus)*. Edinburgh: Oliver & Boyd, 1955. 188 p.
3. Hutchinson G E. The paradox of plankton. *Amer. Naturalist* 95:137-47, 1961.
4. Paffenhofer G A, Strickler J R & Alcaraz M. Suspension-feeding by herbivorous calanoid copepods: a cinematographic study. *Mar. Biol.* 67:193-9, 1982.
5. Conover R J. Nutritional strategies for feeding on small suspended particles. (Loughurst A R, ed.) *Analysis of marine ecosystems*. New York: Academic Press, 1981. p. 363-95.