

Fauchald K & Jumars P A. The diet of worms: a study of polychaete feeding guilds. *Oceanogr. Mar. Biol. Annu. Rev.* 17:193-284, 1979. [Allan Hancock Foundation, University of Southern California, Los Angeles, CA and Department of Oceanography, University of Washington, Seattle, WA]

"The Diet of Worms" was a successful paper because it gave benthic ecologists a single source of information about feeding in one of the dominant groups of marine invertebrates. It also gave invertebrate zoologists impetus to sort out the many structural and behavioral parameters going into an apparently simple activity such as feeding. [The SC[®] indicates that this paper has been cited in more than 245 publications.]

Diet of Worms

K. Fauchald
Department of Invertebrate Zoology
National Museum of Natural History
Smithsonian Institution
Washington, DC 20560

Polychaetes are present in all marine environments, but are especially common in soft sediments. Benthic ecologists have to account for them, somehow, in synecological studies. Polychaete systematics is very time-consuming and results in long lists of scientific names with little other information content. Anything that can be done to save effort per sample must be explored. Peter A. Jumars suggested looking at food and feeding habits and convinced me to leave systematics long enough to collaborate with him on a model and an overview of worm feeding. "Guild" was a term in vogue about less esoteric organisms (birds) at the time; it became the starting point for our model. We presented our results first at the Baruch Symposium in 1975.¹ Thereafter, I spent half of a sabbatical leave in the Scripps Institution library, trying to put substance behind the model.

Our hope was, rather naively, that each family would have a single feeding mode (i.e., a single combination of how, what, and where). For one, worms often do not use the "obvious" feeding mode, or are capable of using more than one mode. In addition, lack of proper morphological means makes no difference to most polychaetes. Two examples will illustrate the point. We accept that sabellids are filter-feeders because of their tentacular crowns, but that nereidids, with muscular eversible pharynges and jaws, might filter-feed is not obvious. They look more like carnivores. That nereidids use their jaws in fighting rather than feeding is another issue. Many worms are considered carnivores because the few specimens examined had empty guts. The literature is full of this inspired guess; never mind that worms are very capable of convulsively voiding

themselves when suddenly plunged into fixative. Despite the problems, we came up with one or a few feeding modes per family, with some exceptions.

For small or poorly known families we made sweeping statements, so much easier when little or no evidence is available. The statements were actually carefully crafted. This was a time when most MS theses had \emptyset -hypotheses tested by chi-square statistics. Our statements were formulated so that any graduate student could turn it into a \emptyset -hypothesis by inserting a "not" at the appropriate spot.

The information behind "The Diet" was limited; food-habits usually were mentioned parenthetically in systematic papers. Feeding experiments tended to demonstrate that polychaetes in aquaria can handle anything. Experiments define a potential diet (including bologna or Swiss cheese); the realized diet is more difficult to find. Gut-content analysis is usually done on material from the hind-gut, similar to determining the diet of a human from colon contents: One can separate a vegetarian from a carnivore, but separating "French" from "Italian" cuisine is tricky.

Interactions among syntopic polychaetes ought to show up as differences in use of available food. It is possible that no competition for food is happening; many may enjoy the same cuisine; thus many feeding modes per taxon.

"The Diet of Worms," the title suggested by Ralph Lewin, has been successful because it is a single source of information about feeding biology, and synecologists could add a new angle to benthic studies. "The Diet" was also successful because it demonstrated the gaps in our information about polychaetes. Jumars and present and past associates have developed several new research directions. They have studied gut passage time, gut structure, and the dynamics of gut functions and have also looked at the consequences of removal of surface sediments by feeding organisms, a behavioral angle to feeding not previously understood.

Many of our conclusions in "The Diet" are outdated. We were wrong, even spectacularly wrong sometimes. We are now in the second "post-diet" generation of papers citing the first "post-diet" generation, and still, sometimes, "The Diet" itself. Second-generation papers sometimes use the terminology Peter and I invented nearly 20 years ago, without quoting source. This is as it should be: "The Diet" is becoming hidden behind layers of investigations with better results and better theory, in part as consequence of its existence.

1. **Jumars P A & Fauchald K.** Between-community contrasts in successful polychaete feeding strategies. (Coull B C, ed.) *Ecology of marine benthos*. Columbia, SC: University of South Carolina Press, 1977. p. 1-15.
Received September 3, 1992