EEOS 630 Benthic Boundaries Chapter 1 Class 2: 9/4/08 Th Revised: 9/4/08 ©2008 E. D. Gallagher

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BENTHIC FEEDING GUILDS AND FUNCTIONAL GROUPS

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Assignment

Τορις

What are the fundamental biological units of benthic ecology? Are they species, functional groups, guilds or combinations of these categories?

REQUIRED

- Cammen, L. M. 1980. Ingestion rate: an empirical model for aquatic deposit feeders and detritivores. Oecologia (Berlin) 44: 303-310.
- Jumars, P. A. and K. Fauchald. 1977. Between-community contrasts in successful polychaete feeding strategies. Pp. 1-20 *in* B. C. Coull, *ed.*, Ecology of marine benthos. University of South Carolina Press, Columbia. *[This paper introduced the guild classification scheme used later in the comprehensive Fauchald & Jumars Diet of Worms.]*

SUPPLEMENTAL

Boudreau, B. P. 1994. Is burial velocity a master parameter for bioturbation? Geochim. Cosmochim. Acta. 58: 1243-1249. $[D_b \propto flux \ of \ organic \ matter; \ flux \ of \ organic \ matter \ \propto burial \ velocity.$ Mixing depth is $9.8 \pm 4.5 cm$]



- Boudreau, B. P. 1998. Mean mixed depth of sediments: the wherefore and the why. Limnol. Oceanogr. 43: 524-526. [Mixed layer depth has an mean depth of 9.8 cm [documented in Boudreau 1994; BPB's model predicts 9.7 cm.]
- Fauchald, K. and P. A. Jumars. 1979. The diet of worms: a study of polychaete feeding guilds. Oceanogr. Mar. Biol. Ann. Rev. 17: 193-284. [Read the Introduction (2 pp), the section on spionids, and the theoretical framework and description of their guild classification (p. 256-277).]
- Jaksic, F. M. 1981. Abuse and misuse of the term "guild" in ecological studies. Oikos 37: 397-400. [Guilds should be recognized by quantitative, non a priori methods,..., and their relationship with deterministic processes such as competition should be evaluated rather than assumed.]
- Miller, C. B. 2004. Biological Oceanography. Blackwell Science, Malden MA. 402 pp. Chapter 12.
- Woodin, S. A. and J. B. C. Jackson. 1979. Interphyletic competition among marine benthos. Amer. Zool. 19: 1029-1043. [They classify 'functional groups' as: 'A functional group includes all organisms which use and affect their environment in approximately similar ways. (This is rather different from the concept of a guild [Root, 1967] which is defined solely on the basis of modes of exploitation of resources). We define functional groups of benthos by the ways in which they exploit their substratum environment and the nature of their effects on the substratum. Criteria used to define functional groups in sediments and hard substrata differ according to apparent differences in the ways such organisms compete.(p. 1030)' Woodin proposes 5 functional categories for the soft-bottom benthos.]

Comments on Guilds

E. O. Wilson (1992) made the case in his book "The Diversity of Life" that species are the fundamental units of ecology and evolutionary biology. He discounts the role of functional groups, guilds, trophic classifications based on energy flow and the like. Benthic ecologists need to assess whether the biological species is the fundamental unit with which to analyze community structure and the effects of the infauna on benthic geochemistry. **Warwick (1988)**, the British benthic ecologist, argues that the effects of pollution are evident at the familial and generic levels. Species identifications aren't necessary. Could it be that functional groups, or feeding guild classifications, are all that are needed to assess the role of benthos in interdisciplinary studies of the benthos? I think not, but feeding guilds and functional groups play an important role in understanding benthic communities.

'PIGEON HOLES' FOR SOFT-BOTTOM BENTHIC FEEDING

An important early stage in any science is the development of conventionalist theories, or effective "pigeon holes" for classifying observations. In soft-bottom benthic ecology, there are a variety of pigeon holes for benthic organisms:

- I. Early attempts at classification, old but still accepted dichotomies:
 - Meiofauna vs Macrofauna
 - 1. Meiofauna:

А.

a. Permanent.

-The mesopsammon or interstitial fauna are a subset of the permanent meiofauna.





- b. Temporary: most juvenile stages of the macrofauna start life as members of the meiofauna.
- 2. Macrofauna
 - a. Infauna
 - (1) microphages (feed on many food items simultaneously. In the older literature detritivore was used to describe both surface and subsurface deposit feeders)
 - (a) surface-deposit feeders
 - (b) subsurface deposit feeding=burrower
 - (c) suspension feeders
 - (d) interface feeders (switch readily from surface deposit feeding and suspension feeding)
 - (2) macrophages (feed on one food item at a time)
 - (a) scavengers
 - (b) predators
 - (c) herbivores
 - (d) omnivores
 - b. Epifauna
 - (1) mobile
 - (a) scavengers
 - (b) predators
 - (c) deposit feeders
 - (2) sedentary
- B. Sedentary vs. mobile (The polychaete families used to be divided into the functional groups Sedentaria and Errantia, but this dichotomy does not correspond to the known morphological or molecular phylogenies.)
- II. The Fauchald & Jumars guild classification for polychaetes:
 - A. Macrophage vs. microphage
 - macrophages take particles one at a time.
 - a. plant
 - b. animal
 - c. carrion
 - 2. Microphages handle food particles in bulk:
 - a. suspension = filter feeders
 - (1) tentaculate feeders
 - (2) mucous web feeders.
 - b. surface deposit feeders take food from the surface
 - c. subsurface deposit feeders = burrowers.
 - d. subgroups of each
 - (1) jawed
 - (2) unarmed eversible pharynges
 - (3) tentaculate structures.
 - B. Motility

1.

1. Sessile: Throughout their life span do not move sufficiently to feed in an area different from that in which they settled as larvae



- 2. Discretely motile: capable of moving between bouts of feeding.
- 3. Motile: move independently of feeding, or in which efficient use of the feeding apparatus requires locomotion

THE GUILD CONCEPT IN BENTHIC ECOLOGY

The primary definition of guild from a dictionary is: 'An organization of persons with related goals and interests.' **Root (1967)**, in a study of bird feeding, introduced the term 'guild' to ecology:

"[A guild is] a group of species that exploit the same class of environmental resources in a similar way. This term groups together species, without regard to taxonomic positions, that overlap significantly in their niche requirements."

Terborgh & Robinson (1986) and **Hawkins & MacMahon (1989)** provide nice reviews of the applications of the guild concept in ecology in general. Most applications of the guild concept follow **Root (1967)** and restrict the usage to taxon-guilds, or members of the same higher taxon which utilize resources in similar ways.

Fauchald & Jumars' Polychaete Guilds

The concept was first applied to polychaetes by **Jumars & Fauchald in 1977** and in expanded form in their 1979 *magnum opus* on polychaete feeding biology, **'The Diet of Worms'**. One major difference between **Fauchald & Jumars' (1979)** guilds and others is that Fauchald & Jumars do not include the presence of a tube as an important character. The Jumars-Fauchald feeding classification is cited often, but there have only been a few explicit applications of the scheme at the community level. **Maurer** *et al.* (1981) applied the Fauchald-Jumars scheme to the analysis of the effects of drilling fluids on marine benthos (he didn't see much of an effect). **Trueblood (1985)** applied a slightly modified version of the Fauchald-Jumars scheme to the analysis of the recruitment of tropical polychaetes around worm tubes in a Puerto Rican Bay.

Tables 1 and 2 show the classification of common Boston Harbor and Massachusetts Bay families and genera using **Fauchald & Jumars' (1979)** feeding guilds. I have added a few new categories to include the abundant molluscan and crustacean fauna in the feeding guild scheme. Surface deposit feeders are defined as deposit feeders that obtain their food at the sediment-water interface; these organisms can live within the sediments. Subsurface deposit feeders feed on bulk sediments located beneath the sediment-water interface.



Table 1 Fauchald & Jumars' (1979) microphagousfeeding guilds. Feeding guilds not found in Fauchald &Jumars are listed in italics. Common Boston Harbor taxa		Мотіліту			
listed. ∅ indicates a classification containing no Boston Harbor taxa. Shading indicates groups responsible for bioturbation.			Motile	Discretely Motile	Sessile
		Jaws or maxillae	Dorvilleidae Eunicidae Glyceridae Hesionidae Lumbrineridae Nephtyidae	Ø	Ø
	Subsurface Deposit Feeders	Unarmed eversible pharynges	Capitellidae Cossuridae Cossura Opheliidae Orbiniidae Pectinaridae Phyllodocidae Scallibregmidae <i>Oligochaetes</i>	Capitellidae	Maldanidae
		Tentacles, palp proboscides	Spionidae Nuculanidae Nucula Yoldia	Ø	Ø
Microphages (Handle Food	Surface Deposit Feeders	Jaws, <i>radula</i> e	Dorvilleidae Lumbrineridae Gastropods	Nereidae Onuphidae	Ø
ITEMS IN BULK)		Unarmed eversible pharynges, Inhalant siphons	Capitellidae Capitella Paraonidae Aricidea Protodrilidae <i>Oligochaeta</i>	Arenicolidae Tellinid bivalves	Ø
		Tentacles or antennae	Cirratulidae Flabelligeridae	Cirratulidae Flabelligeridae Magelonidae Oweniidae Sabellidae Spionidae Terrebellidae <i>Amphipods</i>	Ø
	Mucous webs, Lamellibranch Feeders Tentacles	Ø	Mya spat	Mya adults	
		Tentacles	Ø	Sabellids Spionids	Sabellids



Table 2 Fauchald & Jumars' (1979) macrophagous feeding guilds. Feeding guilds not found in Fauchald & Jumars are listed in italics. Common Boston Harbor taxa listed. ∅ indicates a classification containing no Boston Harbor taxa. Shading indicates groups responsible for bioturbation.		Μοτιλιτγ			
		Motile	Discretely Motile	Sessile	
	Herbivores	Jaws or <i>Maxillae</i>	Dorvilleidae Lumbrineridae Lumbrineris Nereidae Nereis Syllidae Harpacticoid copepods Isopods Cyathura Ostracods	Eunicidae Onuphidae <i>Amphipods</i>	Ø
Macrophages (Handle Food		Non-Jawed	Paraonidae	Ø	Ø
ITEMS ONE AT A TIME)	Carnivores –	Jaws, maxillae, radulae	Dorvilleidae Eunicidae Hesionidae Lumbrineridae Nereidae Onuphidae Syllidae Shrimp Crangon Gastropods Acteocina	Eunicidae Glyceridae Goniadidae Lumbrineridae Nereidae Onuphidae Polynoidae	Ø
		Non-Jawed	Phyllodocidae Eteone	Ø	Ø

Criticism of Fauchald & Jumars' polychaete feeding guilds

Fauchald & Jumars (1977, 1979) based their feeding guilds on observations of thousands of polychaete worms and reviews of the entire polychaete feeding biology literature, but their classification system was designed to be applied *a priori*. Jaksic (1981), without referring specifically to Jumars & Fauchald, said that this was abusing the guild concept. He argued that guilds could only be identified after the study of the groups in their natural environment to determine if they were utilizing the same resource. Fauchald & Jumars devote too much emphansis on morphological features that may not correspond to differences in the resource utilized.

Pianka (1980) argued that guilds were arenas for competition. **Terborgh & Robinson (1986)** defined guilds as species deriving sustenance from shared resources and argued that guilds could be used to compare the functional similarity of communities that shared no species. It is the shared resource that defines members of the guild, not the mouthparts or other morphological features used to acquire the resource. **Brown et al. (1986)** applied the guild concept to their studies of competition between seed-gathering rodents and ants. This interphyletic competition could not have been inferred from the body plans of these organisms, as **Fauchald & Jumars (1979)** described guilds. They discovered that by increasing rodent density, ant density declined



(and vice versa) and that the growth rate of both rodents and ants was affected by the supply of their shared scarce resource, seeds.

Alternatives and extensions to Fauchald-Jumars guilds

Conveyor-belt feeders

There are some viable alternatives to the **Fauchald & Jumars (1979)** guild classification. Rhoads in a series of papers described the action of stabilizing and destabilizing deposit feeders. A subset of the latter group is made up of conveyor-belt species, species which feed at depth and defecate at the surface. **Jumars & Fauchald (1977)** made the bold assertion that virtually all polychaetes that feed at depth defecate near the surface, so all subsurface deposit feeders might be conveyor-belt species. Their observation is now known to be false. Subsurface and surface deposit feeders can defecate at depth. One of the characteristic features of this group is that they produce feeding cavities at depth, so they are in some ways different from (and probably a subset of) **Fauchald & Jumars' (1979)** burrower guild. **Powell (1977)** divided deposit feeders into surface feeders, funnel feeders and conveyor-belt feeders. Funnel feeders often live in U- or J-shaped burrows with a funnel extending to the surface. Typical examples include pectinarid and arenicolid polychaetes. **Cadee (1979) & Robbins (1986)** introduced another category, deposit feeders that defecate at depth. Some capitellids may defecate at depth.





Reverse conveyor-belt feeders



Figure 1 Schäfer's (1972) drawing of Polydora ciliata. This spionid feeds primarily as a surface deposit feeder, but functional groups with guilds: can act as a subsurface deposit feeder, especially when excavating its burrows. Taghon et al. 1980 showed that members of this polychaete family can also feed as suspension feeders by dangling their coiled, mucouscovered ciliated palps in the near-bed flow to capture suspended particles.

Reverse conveyor-belt feeders are organisms that pick up particles at the surface and rapidly move them deep below the sedimentwater interface. This feeding could entail organisms that feed at the surface and defecate at depth, or those that transport particles from the surface to deep feeding voids for later ingestion. These are sometimes called subductive feeders, but I don't care for that term. Subduction carries with it the plate-tectonics connotation of slabs of sediment being moved to depth. Reverse conveyor-belt feeding could be just a worm picking up a particle at the surface and moving it to the base of its tube.. Figure 1 shows reverse conveyor-belt feeding by the spionid polychaete *Polydora*. The spionid polychaete might transport particles to depth simply to keep its surface feeding area clear of recently ingested sediments. Jumars et al. (1990) proposed that surface deposit feeders may create subsurface food caches, particularly if the food resources are patchy and in short supply.

Functional groups

Woodin & Jackson (1979) contrasted their

"A functional group includes all organisms which use and affect their environment in approximately similar ways. (This is rather different from the concept of a guild **[Root**, **1967** which is defined solely on the basis of

modes of exploitation of resources). We define functional groups of benthos by the ways in which they exploit their substratum environment and the nature of their effects on the substratum.(p. 1030)"

Woodin & Jackson (1979) divided the soft-bottom benthos into five functional groups:

I. Mobile burrowing organisms, a.k.a. Thayer's (1979) bulldozers





- II. Destabilizing sedentary organisms (*e.g.*, *Molpadia oolitica*, described in Rhoads & Young (1971)). Rhoads' (1974) conveyor-belt species would fall in this category.
- III. Sedentary organisms which project above and below the sediment surface (*e.g.*, sea grasses).
- IV. Tube builders
- V. Sedentary organisms which don't destabilize or stabilize.

This five-part classification is an elaboration of **Woodin's (1976)** tube-builder, burrower, suspension-feeder triad.

DISTRIBUTION OF FEEDING GUILDS IN NATURE

Jumars & Fauchald (1977) shows how deposit feeding guilds are distributed along the depth gradient off Southern California. The ratio of motile to sessile species reaches a mid-depth peak due to the interaction of two depth-related variables: sediment mobility and organic matter flux to the sediments. Sessile strategies are relatively infrequent in shallow water sediments, where wave action can move sediments to depths of about 100m. There is a strong selective advantage to being able to move. The sessile strategy increases in frequency to about 1000 m, where it again declines. At deeper depths, the input of organic matter to the sediments from the overlying water is low and variable. There is a strong selective advantage to being able to move to new areas to feed.

One of the surprises in the **Jumars & Fauchald (1977)** analysis is the nearly equal abundance of surface and subsurface deposit feeders in the deep sea. Except for hydrothermal vent areas, the food input to deep sea communities will be from the overlying water column. On the large abyssal plains in the deep sea, the organic matter input is low. How then can subsurface deposit feeders survive? Wouldn't the food be consumed long before it could be buried to depth. Food caching, which was first demonstrated by **Graf (1989)** and proposed as a deep sea feeding strategy by **Jumars et al. (1990)** might provide the answer. **Graf (1989)** observed that the Chl *a* from the sedimenting spring bloom did not remain at the sediment surface in the deep sea. It was quickly buried. Since the sedimentation rates are very low in the deep sea (millimeters per hundred or thousand years), the benthic infauna must be responsible. **Jumars et al. (1990)** proposed that surface deposit feeders in the deep sea may transport organic material from the sediment surface to the subsurface. This behavior may involve feeding behavior similar to that shown in Fig. 1 above.

Jack Word (1978, 1979a, 1979b, 1979c) incorporated the Fauchald & Jumars (1979) feeding guild classification in his Infaunal Trophic Index. This index was designed to assess the effects of pollution on benthic communities. Areas near sewer outfalls are dominated by shallow surface deposit feeders. Subsurface deposit feeders tend to occur in areas of lower organic carbon input. While it is true that organic enrichment does affect the types of infaunal organisms present and does change the relative contribution of feeding modes, Word's index is severely flawed. Word misclassified many of the dominant species, turning surface deposit feeders into suspension feeders in order to make the index work. Anyone who has





a copy of **Fauchald & Jumars (1979)** will recognize the errors in Word's classifications. I mention Word's index because it did play a role in Boston Harbor benthic studies. The MDC proposed to the EPA to use Word's Infaunal Trophic Index in their monitoring plan to assess the effects of their proposed MA Bay sewer outfall on MA Bay benthos.

OPTIMAL FORAGING DEPOSIT FEEDERS

Chemical reactor theory was used to explain the functional morphology of deposit feeder guts by Penry and Jumars (1986, 1987, 1990, Jumars & Penry 1989). They also extended their analysis to explain digestion in calanoid copepods and a variety of other organisms. Natural selection will tend to favor those organisms that maximize the acquisition of energy or essential nutrients per unit time. Penry & Jumars proposed that evolution follows some of the same design principles used in designing industrial chemical reactors. One of the major predictions from this body of theory is that inefficient animal guts have produce higher rates of assimilation than efficient ones. Jumars *et al.* (1989) applied chemical reactor theory to zooplankton grazing, predicting that inefficient zooplankton guts are a major source of the dissolved organic carbon fueling the microbial loop. Jumars *et al.* (1990) applied chemical reactor and optimal foraging theory to deep-sea deposit feeding.

Outlines

ASSIGNED & SUPPLEMENTAL

Cammen, L. M. 1980. Ingestion rate: an empirical model for aquatic deposit feeders and detritivores. Oecologia (Berlin) 44: 303-310.

Fauchald, K. and P. A. Jumars. 1979. The diet of worms: a study of polychaete feeding guilds. Oceanogr. Mar. Biol. Ann. Rev. 17: 193-284. [5, 6, 8, 10, 11]

I. Introduction

II. The feeding biology of some selected polychaetes [I'll tabulate species that are found locally]

FAMILY	SPECIES	FEEDING GUILD	PAGE & REF
Cirratulidae	Chaetozone	{Surface} deposit feeders <i>C. setosa</i> may be selective	207-208
Hesionidae	Microphthalmus aberrans	Diatom feeder	216-217, Westheide 1967, Wolff 1973
Lumbrineridae	Lumbrineris	-Carnivores or carrion feeders -herbivores -deposit feeder	218
	Ninoe nigripes	selective surface deposit feeder	218, Sanders et al. (1962)



FAMILY	SPECIES	FEEDING GUILD	PAGE & REF
Nephtyidae	Nephtys incisa	-mobile carnivores -motile subsurface deposit feeder in Buzzards Bay & LIS (Sanders)	222-224, Sanders (1956, 1960)

Jumars, P. A. and K. Fauchald. 1977. Between-community contrasts in successful polychaete feeding strategies. Pp. 1-20 *in* B. C. Coull, *ed.*, Ecology of marine benthos. University of South Carolina Press, Columbia.[5, 8, 10]

- Data set: Olga Hartman's orange-peel grab
- II. Results

I.

- A. Shallow-water
 - 1. Increasing proportion of motile species with depth to approximately 400 m, followed by a decreasing proportion
 - 2. Ratio of sessile individuals to discretely motile reaches peak at less than 1000 m.
 - -Explanation is the interaction of two depth-related variables:
 - (1) Sediment stability
 - (a) shallow sediments far more susceptible to erosion and deposition.
 - (b) storm events felt beyond 100 m
 - (c) sessile individuals increase with depth during the first 100 m.
 - (2) flux of food to the benthos.
 - (a) lower flux of food to depth
 - (b) lower community respiration
 - 3. Filter feeders are relatively rare in shallow-water as elsewhere.
- B. Deep-sea samples, Figure 6
 - 1. General lack of sessile species (Figure 6, left)
 - 2. Almost complete lack of filter feeders (Figure 6, right)
 - 3. proportion of subsurface deposit feeders is less at abyssal depths than on the outer shelf and slope.

Web Resources

URL	NAME	DESCRIPTION
http://imagequestmarine.com/stock/index.htm	ImageQuest Marine	Wonderful photographs
http://www.mbayaq.org/efc/living_species/defa ult.asp?hOri=1&group=2	Monterey Bay Aquarium Invertebrates	Wonderful photographs
http://biodiversity.uno.edu/%7Eworms/annelid .html	Annelid Resources	Annelid resources
http://www.tmbl.gu.se/libdb/taxon/taxa.html	North East Atlantic Taxa	Just lists
http://tolweb.org/tree?group=Annelida&contgr oup=Bilateria	Rouse <i>et al.</i> (2003) Annelida tree of life page	Taxonomy & photos



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URL	NAME	DESCRIPTION
http://depts.washington.edu/fhl/zoo432/falseba y/fbspecies/fbspecies.htm	False Bay Fauna	Species that thrive in False Bay, on San Juan Island, WA (near the UW Friday Harbor Lab)

References

ON GUILDS

- Adams, L. J. 1985. The definition and interpretation of guild structure in ecological communities. J. Anim. Ecology 54: 43-60.
- Brown, J. H. D. W. Davidson, J C. Munger and R. S. Inouye. 1986. Experimental community ecology: the desert granivore system. Pp. 41-61 in J. Diamond and T. J. Case, eds., Community Ecology. Harper and Row, New York. [One of the nicest applications of the guild concept. Brown <u>et al</u>. (in various permutations) have published over a dozen papers on the desert granivore guild. Seed gathering rodents and ants are members of the same guild.] {7}
- Fauchald, K. and P. A. Jumars. 1979. The diet of worms: a study of polychaete feeding guilds. Oceanogr. Mar. Biol. Ann. Rev. 17: 193-284. [The article is divided into two parts: 1) all that was known about polychaete feeding was catalogued by Family, and 2) the theoretical justification and application of guilds are discussed] {5, 6, 8, 10, 11}
- Grant, P. and D. Schluter. 1984. Interspecific competition inferred from patterns of guild structure. Pp. 201-233 in D. R. Strong, D. Simberloff, L. G. Abele, and A. B. Thistle, eds. Ecological communities: conceptual issues and the evidence. Princeton University Press, Princeton New Jersey. [Members of bird guilds, sometimes recognized by PCA, are less likely to occur together in accordance with naive competition theory]
- Hawkins, C. P., J. P. MacMahon. 1989. Guilds: the multiple meanings of a concept. Ann. Rev. Entomol. 34: 423-451.[5]

- Jaksic, F. M. 1981. Abuse and misuse of the term "guild" in ecological studies. Oikos 37: 397-400. [Guilds should be recognized by quantitative, non <u>a priori</u> methods,..., and their relationship with deterministic processes such as competition should be evaluated rather than assumed.] {7}
- Jaksic, F. M. and R. G. Medel. 1990. Objective recognition of guilds: testing for statistically significant species. clusters. Oecologia 82: 87-92. [An excellent paper. Overlaps calculated with Pianka's index. UPGMA clustering used with bootstrapping to estimate significant cluster membership]
- MaNully, R. C. and J. M. Doolan. 1986. An empirical approach to guild structure: habitat relationships in nine species of eastern-Australian cicadas. Oikos 47: 33-46. [Guilds recognized by PCA]
- Pianka, E. R. 1980. Guild structure in desert lizards. Oikos 35: 194-201. ["Guilds constitute arenas of intense interspecific competition."] {7}
- Root, R. B. 1967. The niche exploitation pattern of the blue-gray gnatcatcher. Ecol. Monogr. 37: 317-350. [The paper that coined the term][5, 9, 16]
- Schoener, T. W. 1986. Overview: kinds of ecological communities ecology becomes pluralistic. Pp. 467-479 *in* J. Diamond and T. J. Case, *eds*.
 Community Ecology. Harper and Row, New York. *[Taxon-guilds are subsets of true guilds.]*
- Shorrocks, B and J. Rosewall 1986. Guild size in drosophilids. J. Anim. Ecol. 55: 527-541. [A superb paper. Shorrocks briefly discusses his subjective determination of guilds, and applies a competition model, incorporating spatial aggregation, to predict guild size.]





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- Simberloff, D. and T. Dayan. 1991. The guild concept and the structure of ecological communities. Ann. Rev. Ecol. Syst. 22 115-143.
- Terborgh, J and S. Robinson. 1986. Guilds and their utility in ecology. Pp. 65-90 in J. Kikkawa and D. J. Anderson, eds., Community Ecology: Pattern and Process. Blackwell Scientific Publications, Melbourne. [Reviews several important applications of the guild concept. For example, guilds can be used to compare the structure of communities that share no species][5, 7]
- Winemiller, K. O. and E. R. Pianka. 1990. Organization in natural assemblages of desert lizards and tropical fishes. Ecol. Monogr. 60: 27-55. [Numerical techniques are used to objectively define guild membership. Resource use similarity calculated using the symmetric niche overlap coefficient. Null-model communities created and their average niche overlap compared to real communities. Single linkage clustering used to define guilds.]

APPLICATIONS OF THE FAUCHALD-JUMARS POLYCHAETE GUILD CONCEPT

- Dauer, D. M. 1984. The use of polychaete feeding guilds as biological variables. Mar. Pollut. Bull. 15: 301-305.
- Maurer, D, L. Watling, W. Leathem, and P. Kinner. 1979. Seasonal changes in feeding types of estuarine benthic invertebrates from Delaware Bay. J. exp. Mar. Biol. Ecol. 36: 125-155.
- Maurer, D., W. Leathem, and C. Menzie. 1981. The impact of drilling fluid and well cuttings on polychaete feeding guilds from the US northeastern continental shelf. Marine Pollution Bulletin 12: 342-347. [A straightforward application of the Fauchald-Jumars scheme.][5]

Maurer, D. and S. Williams. 1988. Deep-sea polychaetous annelids from Central America to the Antarctic Peninsula and South Sandwich Islands. Int. Revue ges. Hydrobiol. 73: 659-701. [Application of feeding guild classifications] Trueblood, D. D. 1985. Small scale dispersion and shortterm successional patterns of a tropical softbottom polychaete population in Phosphorescent Bay, Puerto Rico. M.Sc. dissertation, University of Puerto Rico, Mayaguez. [Grieg-Smith's blocked ANOVA approach and Fauchald & Jumars fielding guilds used to analyze spatial patterns in a tropical subtidal sandy area][5]

GUILDS, FUNCTIONAL GROUPS, AND OTHER BENTHIC 'PIGEON-HOLES'

- Brenchley, G. A. 1981. Disturbance and community structure: an experimental study of bioturbation in marine soft-bottom environments. J. Mar.
 Res. 39: 767-790. [This is a refined version of Woodin (1976) and Rhoads' (1974) classification scheme. 'bioturbators' [what an awful word] include both deposit feeders and suspension feeders. She advocates a guild concept based more on motility than trophic type.]
- Cadee, G. C. 1979. Sediment reworking by the polychaete Heteromastus filiformis on a tidal flat in the Dutch Wadden Sea. Neth. J. Sea Res 13: 441-456. [Feeds at the surface and defecates at depth. Cited by Robbins 1986][8]
- McCall, P. L. 1977. Community patterns and adaptive strategies of the infaunal benthos of Long Island Sound. J. Mar. Res. 35: 221-266. [Peter Law McCall introduced the Type I, II and III classification later used extensively by Rhoads (Rhoads et al. 1978, Rhoads & Boyer 1982, Rhoads & Germano 1986.]
- Powell, E. N. 1977. Particle size selection and sediment reworking in a funnel feeder, *Leptosynapta brevis* (Holothuroidea, Synaptidae). Int. Revue ges. Hydrobiol. 62: 385-408.[8]
- Rhoads, D. C. 1974. Organism-sediment relations on the muddy sea floor. Oceanogr. Mar. Biol. Ann. Rev. 12: 263-300. [Rhoads introduced the concept of a 'conveyor-belt feeder' for a deposit feeder that feeds at depth and defecates at the surface.][10]
- Rhoads, D. C. and D. K. Young. 1970. The influence of deposit-feeding organisms on sediment stability and community trophic structure. J. Mar. Res. 28: 150-178. [They introduced 'trophic group amensalism', which is the exclusion of suspension feeders by destabilizing deposit



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feeders.][15]

- Rhoads, D. C. and D. K. Young. 1971. Animal-sediment relations in Cape Cod Bay, Massachusetts. II. Reworking by *Molpadia oolitica* (Holothuroidea). Marine Biology 11: 255-261. [Molpadia, a holothuroid echinoderm, is a classic conveyor-belt species, whose fecal mounds are often colonized by other organisms, especially the suspension-feeding sabellid feather duster worm Euchone incolor] **{10**}
- Rhoads, D. C. and J. D. Germano. 1986. Interpreting long-term changes in benthic community structure: a new protocol. Hydrobiologia 142: 291-308. [The OSI index, based on REMOTS™-TM photographs is proposed, and the BRAT index is reviewed.]
- Robbins, J. A. 1986. A model for particle-selective transport of tracers in sediments with conveyorbelt deposit feeders. J. Geophys. Res. 91: 8542-8558. [Reviews the literature on functional groups of zoobenthos. Replaces the Goldberg-Koide approach with realistic equations for conveyor-belt feeding][8, 14]
- Sanders, H. L. 1958. Benthic studies in Buzzards Bay. I. Animal-sediment relationships. Limnol. Oceanogr. 3: 245-258. [Detailed descriptions of the feeding modes of the infauna]
- Sanders, H. L. 1960. Benthic studies in Buzzards Bay III. The structure of the soft-bottom community. Limnol. Oceanogr. 5: 138-153. [Howard uses gut content analysis to divide the Buzzards Bay fauna into suspension feeders, carnivores, and detritus feeders; the latter category is divided into selective and non-selective.]
- Schwinghamer, P. 1983. Generating ecological hypotheses from biomass spectra using causal analysis: a benthic example. Mar. Ecol. Prog. Ser. 13: 151-166. [Schwinghamer's guilds are based primarily on size, but he does distinguish meiofaunal taxa from juvenile macrofauna.]
- Stanley, S. M. 1970. Relation of shell form to life habits of Bivalvia (Mollusca). Geol. Soc. Amer. Mem. 125 (the entire volume). [Stanley analyzes the relationship between shell shape and ornamentation to bivalve feeding mode and burrowing abilities.]

- Thayer, C. W. 1979. Biological bulldozers and the evolution of marine benthic communities. Science 203: 456-461. [Thayer divides the fauna into several groups including ISOSS (infaunal suspension feeders living on the surface of soft substrata) and bulldozers. Many species of the former group went extinct upon the appearance of the latter group. This is the Rhoads & Young (1970) trophic group amensalism hypothesis, usually applied to kmscale spatial and short-term temporal patterns, applied to geological time scales. Modern examples of bulldozers are malocostracan crustacea (e.g., Horseshoe crabs), irregular echinoids and holothuroids (sea cucumbers). Modern descendants of the ISOSS taxa survive in 4 refugia: 1) articulate brachiopods moved to hard surfaces, 2) mobile taxa (e.g., gastropods) were relatively unaffected by bulldozers, 3) crinoids survive in the deep sea where bioturbation is low, and 4) some members of the ISOSS apparently survive by growing to large size.][9]
- Whitlatch, R. B. 1980. Patterns of resource utilization and coexistence in marine intertidal deposit-feeding communities. J. Mar. Res. 38: 743-765.
 [Whitlatch groups deposit feeders into surface feeders and burrowers, but then further divides them into their position in the sediments and the distribution of particle sizes in their guts. This paper goes far towards defining guilds as Jaksic would have them defined.]
- Woodin, S. A. 1976. Adult-larval interactions in dense infaunal assemblages: patterns of abundance. J. Mar. Res. 34: 25-41. [Woodin classifies 'dense' infaunal assemblages as dominated by tube builders, burrowers or suspension feeders and describes processes which maintain them. This is a highly speculative paper [<u>i.e.</u>, I don't believe a lot of it][10]
- Woodin, S. A. 1979. Settlement phenomena: the significance of functional groups. Pp. 99-106 in S. Stancyk, ed., Belle W. Baruch Symposium Vol. 9. [Woodin predicts that tube builders may settle preferentially around other tube builders (the response should not be species specific). Thus, 'tube builder' may be a valid category in describing recruitment phenomena]



Woodin, S. A. and J. B. C. Jackson. 1979. Interphyletic competition among marine benthos. Amer. Zool. 19: 1029-1043. [They classify the 'functional groups' of marine organisms, defined as: 'A functional group includes all organisms which use and affect their environment in approximately similar ways. (This is rather different from the concept of a guild [Root, **1967**] which is defined solely on the basis of modes of exploitation of resources). We define functional groups of benthos by the ways in which they exploit their substratum environment and the nature of their effects on the substratum. Criteria sued to define functional groups in sediments and hard substrata differ according to apparent differences in the ways such organisms compete.(p. 1030)' They propose 5 functional categories for the soft-bottom benthos.][9]

- Word, J. Q. 1978. The infaunal trophic index. Pp. 19-39 in 1978 SCCWRP Annual report. [Word divides benthic feeding modes into Types I, II and III][10]
- Word, J. Q. 1979a. Extension of the infaunal trophic index to a depth of 800 m. Pp. 95-101 *in* SCCWRP Annual Report.[10]
- Word, J. Q. 1979b. Classification of benthic invertebrates into infaunal trophic index feeding groups. Pp. 103-121 in SCCWRP Annual Report. [Compare Word's Fig. 2 with Fauchald and Jumars Figure 1. The only thing Word failed to plagiarize was Pete Jumars' initials and the proper feeding mode classification and species identification.] [10]
- Word, J. Q. 1979c. Effects of screen size and replication on the infaunal trophic index. Pp. 123-130 in SCCWRP annual report. [The report includes the following statement in the introduction, 'We have found that single benthic samples, properly taken and sieved through a 1.0-mm screen, are entirely adequate for one type of evaluation of benthic organisms (Infaunal Trophic Index)...This means that properly taken samples need not be replicated for Infaunal Trophic Index Measurements.' This statement is nonsense! [EDG]] [10]
- Word, J. Q., B. L. Myers and A. J. Mearns. 1977.Animals that are indicators of marine pollution.Pp. 199-206 *in* 1977 SCCWRP Annual Report.

GRAZING, PRIMARILY ON BENTHIC DIATOMS

"Grazers are usually lumped into the larger category of deposit feeders, or occasionally as 'selective surface deposit feeders'. Sometimes they are called herbivores. However, many benthic species are either facultative or even obligate predators of the microphytobenthos. Grazers in the Fauchald-Jumars scheme might be termed microphagous surface-feeding herbivores."

- Admiraal, W. L. A. Bouwman, L. Hoeckstra, and K. Romeyn. 1983. Qualitative and quantitative interactions between microphytobenthos and herbivorous meiofauna on a brackish intertidal mudflat. Int. Rev. ges. Hydrobiol. 68: 175-192. [This is one of the best general discussions of the quantitative importance of diatoms to grazers (large) and grazers to microphytobenthic production (relatively modest).] {?}
- Alongi, D. M. 1988. Microbial-meiofaunal interrelationships in some tropical intertidal sediments. J. Mar. Res. 46: 349-365.
- Asmus, H. and R. Asmus. 1985. The importance of grazing food chain for energy flow and production in three intertidal sand bottom communities of the northern Wadden Sea. Helg. wiss. 39: 273-301. [The primary and secondary production of 3 areas (<u>Nereis-Corophium</u> belt, seagrass bed, and <u>Arenicola</u> flat) is measured by oxygen flux and change in specific biomass, respectively. The grazer food-chain on benthic diatoms (dominated by <u>Hydrobia ulvae</u>) is the key carbon source for all three areas.]
- Bianchi, T. S. and J. S. Levinton. 1984. The importance of microalgae, bacteria and particulate organic matter in the somatic growth of *Hydrobia totteni*. J. Mar. Res. 42: 431-443. [Diatoms are important; bacteria are not.] {?}
- Bianchi, T. S. and D. L. Rice. 1988. Feeding ecology of *Leitoscoloplos fragilis* II. Effects of worm density on benthic diatom production. Marine Biology 99: 123-131.
- Bianchi, T. S., R. Dawson, and P. Sawangwong. 1988. The effects of macrobenthic deposit-feeding on the degradation of chloropigments in sandy sediments. J. exp. Mar. Biol. Ecol. *122*: 243-255.



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Blanchard, G. F. 1991. Measurement of meiofauna grazing rates on microphytobenthos: is primary production a limiting factor. J. exp. Mar. Biol. Ecol. *147*: 37-46.

Bouwman, L. A., K. Romeijn, and W. Admiraal. 1984. On the ecology of meiofauna in an organically polluted estuarine mudflat. Est. Coastal and Shelf Science 19: 633-653.

Cammen, L. M. 1980. The significance of microbial carbon in the nutrition of the deposit-feeding polychaete *Nereis succinea*. Marine Biology *61*: 9-20.

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- Carman, K. R. 1990. Mechanisms of uptake of radioactive labels by meiobenthic copepods during grazing experiments. Mar. Ecol. Prog. Ser. 68: 71-83.
- Carman, K. R 1990. Radioactive labeling of a natural assemblage of marine sedimentary bacteria and microalgae for trophic studies: an autoradiographic study. Microbial Ecology 19: 279-290. [¹⁴C-HCO₃ added, little dark uptake observed, slurry method compared to direct injection]
- Carman, K. R. and D. Thistle. 1985. Microbial food partitioning by three species of benthic copepods. Marine Biology 88: 143-148.

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Connor, M. S., J. M. Teal, and I. Valiella. 1982. The effects of feeding by mud snails, *Ilyanassa obsoleta* (Say) on the structure and metabolism of a laboratory benthic algal community. J. exp. Mar. Biol. Ecol. 65: 29-45.

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- D'Amours, D. 1988. Temperature beat on a tidal flat: potential cue for harpacticoid bloom. Neth. J. Sea Res. 22: 301-305. [The harpacticoid bloom occurs when water temperature is colder than air temperature at low tide]
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- Decho, A. W. 1986. Water-cover influence on diatom ingestion rates by meiobenthic harpacticoids. Mar. Ecol. Prog. Ser. 45: 263-270.
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- Forbes, V. E. and G. R. Lopez. 1986. Changes in feeding and crawling rates of *Hydrobia truncata* (Prosobranchia: Hydrobiidae) in response to sedimentary chlorophyll <u>a</u> and recently egested sediment. Mar. Ecol. Prog. Ser. 33: 287-294.

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 Prog. Ser. 229: 33-42. [It is not a useful marker in this Scottish intertidal system with <u>Arenicola</u> <u>Hydrobia ulvae</u> and <u>Corophium</u>]
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- Rieper, M. 1985. Some lower food web organisms in the nutrition of marine harpacticoid copepods: an experimental study. Helg. wiss. 39: 357-366. [Rieper studies an odd mix of harpacticoids and food sources. Little evidence is provided that the food sources are appropriate for the copepods in the field. Growth on bacteria, 2 ciliate species and <u>Skeletonema costatum</u> are compared.]
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- Sommer, U. 1997. Selectivity of *Iothea chlipes* (Crustacea: Isopoda) grazing on benthic micoalgae. Limnol. Oceanogr. 42: 1622-1628. [*The specific grazing rates of different* periphyton on microscope slides. Small single diatoms eaten more readily than other groups]
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- White, D. C., R. H. Findlay, S. D. Fazio, R. J. Bobbie, J. S. Nickels, W. M. Davis, G. A. Smith, and R. F. Mertz. 1980. Effects of bioturbation and predation by *Mellita quinquiesperforata* on sedimentary microbial community structure. Pp. 163-171 in V. S. Kennedy, ed., Estuarine Perspectives. Academic Press, New York.

DEPOSIT FEEDERS

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- Brown, S. C. 1969. The structure and function of the digestive system of the mud snail *Nassarius* obsoletus (Say). Malacologia 9: 447-500. [Contains enzymes to digest algae and marsh grass polysacharides]
- Cammen, L. M. 1980. The significance of microbial carbon in the nutrition of the deposit-feeding polychaete *Nereis succinea*. Marine Biology 61: 9-20.[This worm can't live on mud alone. They must be eating the microbes & meiofauna too]
- Connor, M. S. and R. K. Edgar. 1982. Selective grazing by the mudsnail *Ilyanassa obsoleta*. Oecologia 53: 271-275. [I. obsoleta is highly selective.]
- Daro, M. H. and P. Polk. 1973. The autecology of *Polydora ciliata* along the Belgian coast. Neth. J. Sea Res. 6: 130-140.
- Dauer, D. M. 1983. Functional morphology and feeding behavior of *Scolelepis squamata* (Polychaeta: spionidae). Marine Biology 77: 279-285. [This species is adapted for feeding in the swash zone of beaches. It does not usually surface deposit feed, but rather feeds only when there is current. Its gut contents usually contain the recruits of other infaunal species.]
- Dauer, D. M. 1985. Functional morphology and feeding behavior of *Paraprionospio pinnata* (Polychaeta: spionidae). Marine Biology 85: 143-151.



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OPTIMAL FORAGING THEORY

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Combined with the 3 major functional responses are 3 numerical responses: direct, inverse, & none][?]

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MISCELLANEOUS

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