Diet of Worms Emended: An Update of Polychaete Feeding Guilds

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Abstract

Polychaetes are common in most marine habitats and dominate many infaunal communities. Functional guild classification based on taxonomic identity and morphology has linked community structure to ecological function. The functional guilds now include osmotrophic siboglinids as well as sipunculans, echiurans, and myzostomes, which molecular genetic analyses have placed within Annelida. Advances in understanding of encounter mechanisms explicitly relate motility to feeding mode. New analyses of burrowing mechanics explain the prevalence of bilateral symmetry and blur the boundary between surface and subsurface feeding. The dichotomy between microphagous deposit and suspension feeders and macrophagous carnivores, herbivores, and omnivores is further supported by divergent digestive strategies. Deposit feeding appears to be limited largely to worms longer than 1 cm, with juveniles and small worms in general restricted to ingesting highly digestible organic material and larger, rich food items, blurring the macrophage-microphage dichotomy that applies well to larger worms.

Keywords
trophic, stable isotopes, functional morphology, sipunculan, echiuran, myzostome
INTRODUCTION

Until ecological function is resolved, value in species diversity must remain implicit: What and how much an individual does is more important ecologically than its taxonomic identity. The accelerating rate of ecological extinctions (reductions in species’ abundances to the point that their functions are lost to the local community) brings new urgency to measure functional diversity before it is gone. Climate change, ocean acidification, the release of synthesized reactive nitrogen by a human population headed toward eight billion and already appropriating a substantial fraction of Earth’s net primary production, and trawling that rakes the majority of continental shelves more than once each year leave little of the marine biosphere untouched. Yet the ability to predict winners and losers as well as their ecological functions under these changing selective pressures remains rudimentary. One of the dimensions of ecological function that helps to determine winners and losers and to shape the consequences of their respective fates is an individual’s trophic function—what is, and how and where it is, consumed.

Polychaetes have been radiating into marine, freshwater, and terrestrial environments since the Cambrian (Butterfield 2003). Conservatively, $1.3 \times 10^4$ species of polychaetes are accepted as taxonomically valid (Read 2014). Polychaetes dominate marine sedimentary environments and are important components of hard-bottom and pelagic communities as well. As common prey of various fishes, crustaceans, and shorebirds, polychaetes also represent key trophic links in estuarine and marine food webs. Through respiratory irrigation of sediments and suspension and deposit feeding, they greatly alter the redox conditions of sediments and sediment-water fluxes of solutes and seston. They literally gate the entry of organic material and microfossils into deep burial—the only major natural pathway that removes carbon from contact with the active biosphere on geological timescales.

Studying the functional ecology of each of these species individually is clearly impractical. Jumars & Fauchald (1977) and Fauchald & Jumars (1979; hereafter F&J) used the morphology and taxonomic identity (specifically, families or subgroups within families) of polychaetes to group worms into functional guilds (groups of species that utilize the same resources in similar ways). These guilds were based on feeding mode (subsurface deposit feeder, carnivore, filter feeder, herbivore, or surface deposit feeder), motility (motile, discretely motile, or sessile), and feeding structure (jawed, pumping, tentaculate, or other). This guild classification has been widely used (>1,600 citations), largely as a lookup table of trophic function from taxonomic identity. Since F&J, however, a great deal has been learned about polychaete morphology, life habits, and phylogeny. Investigators have described considerable variability in pharynx and gut morphologies and have begun to explore functional differences (e.g., Penry & Jumars 1990, Tzetlin & Purschke 2005), and have also discovered remarkable new taxa and lifestyles. Phylogenetic analyses as well as those new discoveries have broadly expanded the definition of Polychaeta to subsume the previously segregated taxa of Echiura, Sipunculida, and Pogonophora (now Siboglinidae) as well as Clitellata (Struck et al. 2007, Zrzavý et al. 2009), leaving the phylum Annelida with only two classes, Myzostomida and Polychaeta. Although family-level clades remain more stable than other groupings of polychaetes, families have also been reorganized, split, synonymized, and renamed since F&J in an ongoing process.

New taxa and new revisions of old taxa would be reasons enough to revise feeding guilds and their memberships as recognized by F&J, but even more compelling is the accelerating pace of mechanical understanding of animal-sediment interactions, including animal movement through solid media in the contexts of material properties of muds and sands (e.g., Dorgan et al. 2006), particle capture in fluids (Rubenstein & Kochl 1977, Shimeta & Jumars 1991, Riisgård & Larsen 2010), and particle selection from bulk sediments (Jumars et al. 1982, Self & Jumars 1988, Guieb et al. 2004). The relative sizes and complexity of guts have been linked to digestive strategies by the
application of chemical reactor theory (Penry & Jumars 1987). This new understanding demands substantial correction and expansion of F&J’s inferred links between polychaete morphologies and functional guilds.

**FEEDING GUILDS**

F&J characterized guilds as a combination of motility, feeding structures, and feeding mode, noting that some guilds (e.g., motile, jawed carnivores) included representatives of many families, whereas others (e.g., discretely motile, nonjawed surface deposit feeders) were much less common.

Numerous advances in understanding of mechanisms underlying feeding allow us to approach the problem of identifying common guilds—and, more specifically, of identifying syndromes of linked feeding and motility characters—from a more predictive standpoint. We anticipate that, as for F&J, most users will be interested primarily in feeding mode, and our intentions are both to provide more comprehensive and versatile information and to emphasize syndromes of linked characters and functions that collectively characterize a feeding guild. Syndromes emerge because food availability, food quality, sensory structures, digestive structures, organism size, organism motility, and environmental parameters are inextricably linked.

Our revised guild classification subdivides the traits included in F&J into more categories that are organized hierarchically (Figure 1 and the Supplemental Appendix; follow the Supplemental Material link from the Annual Reviews home page at http://www.annualreviews.org). We retain the distinction between microphagous feeding on small particles and macrophagous feeding on larger items. We divide feeding structures to distinguish between the mechanism by which food is encountered or delivered to the mouth and the structure of the pharynx, e.g., muscular versus nonmuscular. We add sensory structures and habitat, as both are associated with feeding modes. These additional traits would result in an overwhelming number of discrete guilds if all potential combinations existed (as they would have in F&J’s guilds). We recognize that phylogenetic history results in covarying traits as well, and so provide information in the Supplemental Appendix, when known, about taxonomic relationships. More rigorous inclusion of a phylogenetic signal in our analysis is precluded by the remaining uncertainty in interfamilial relationships within Annelida (Zrzavý et al. 2009, Struck et al. 2011).

**Osmotrophs**

The largest (now polychaete) osmotrophs, the vestimentiferan tube worms, were discovered around the time of publication of F&J, forcing biologists to understand the energetics and physiologies of relatively large animals that lack digestive tracts. The Siboglinidae family now comprises four distinct morphotypes, three of which use ambient flow, their own pumping, or a combination of the two to deliver inorganic reductants to their symbiotic chemosynthetic autotrophs and oxygen to themselves, similarly to other animals and colonial protists harboring chemosynthetic prokaryotes (Ott et al. 1998). The advection thins diffusive boundary layers, and each morphotype has structures that increase surface area for solute uptake. The fourth morphotype, currently corresponding with the genus *Oseledax*, enhances surface area with its dendritic posterior end and harbors prokaryotic, heterotrophic mutualists that secrete bone-dissolving acids and release organic solutes from whale bones (Tresguerres et al. 2013). The only other polychaetes lacking digestive tracts are the interstitial protodrilids *Astomus* spp., which lack symbionts and appear to rely on epidermal microvilli for the uptake of dissolved organic material and on epidermal vesicles and lysosomes for the uptake of particles (Jouin 1979).
### Habitat

<table>
<thead>
<tr>
<th>Pelagic</th>
<th>Epifaunal</th>
<th>Infaunal</th>
<th>Commensal</th>
</tr>
</thead>
<tbody>
<tr>
<td>• Upper mixed layer</td>
<td>• On sediments</td>
<td>• In sediments</td>
<td>• Internal to another animal</td>
</tr>
<tr>
<td>• Midwater</td>
<td>• On hard bottoms</td>
<td>• In hard bottoms</td>
<td>• External to another animal</td>
</tr>
<tr>
<td>• Bottom boundary layer</td>
<td>• Epiphytic</td>
<td>• Intersitial</td>
<td></td>
</tr>
</tbody>
</table>

### Motility

<table>
<thead>
<tr>
<th>Motile</th>
<th>Discretely motile</th>
<th>Sessile</th>
</tr>
</thead>
<tbody>
<tr>
<td>• Burrowing</td>
<td>• Burrow constructing</td>
<td>• Unlikely to survive if removed from attachment site, tube, or burrow</td>
</tr>
<tr>
<td>• Crawling</td>
<td>• Tube dwelling; able to rebuild or extend tube</td>
<td></td>
</tr>
<tr>
<td>• Swimming</td>
<td>• Tube dwelling; portable tube</td>
<td></td>
</tr>
</tbody>
</table>

### Sensory structures

<table>
<thead>
<tr>
<th>Nuchal organs</th>
<th>Projections</th>
<th>Invaginations</th>
<th>Absent</th>
</tr>
</thead>
<tbody>
<tr>
<td>Anterior structures</td>
<td>Tentacles</td>
<td>Palps</td>
<td>Antennae</td>
</tr>
<tr>
<td>Eyes</td>
<td>Present, anterior, complex</td>
<td>Present, anterior, simple</td>
<td>Present, not on head, simple</td>
</tr>
</tbody>
</table>

### Feeding characteristics

- **Feeding mode**
  - Microphage
    - • Active suspension feeder
    - • Mixed-mode suspension feeder
    - • Passive suspension feeder
    - • Surface deposit feeder
    - • Subsurface deposit feeder
    - • Funnel feeder
    - • Cacher
    - • Scraper
  - Macrophage
    - • Carnivore
    - • Carrion feeder
    - • Parasite
    - • Herbivore on microphagotrophs
    - • Herbivore on macroalgae
    - • Herbivore on angiosperms
  - Omnivore
    - • Simultaneously feeding on more than one type of food
    - • Sequentially feeding on more than one type of food
  - Osmotroph
    - |

- **Mechanism for encountering or delivering food**
  - Tentacles/palps
  - Mucus net
  - Nonmuscular, eversible pharynx
  - Muscular, eversible pharynx
  - Ramified or lamellar surfaces

- **Pharynx structure**
  - Nonmuscular
    - • Ciliated/nonciliated
    - • Axial/ventral
  - Muscular, unarmed
    - • Axial/ventral
  - Muscular, armed
    - • Axial/ventral
    - Armed with:
      - Strongly articulated, multifunctional jaws
      - Opposable fangs or stylets for grasping/holding
      - Unarticulated, opposable, crushing teeth
      - Assorted other teeth (for rasping or puncturing)
  - No pharynx

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**Figure 1**

Guild assignments used in the evaluation of polychaete families and morphotypes.

**Macrophyage Versus Microphyage**

Macrophyages usually encounter, handle, and ingest one item at a time. Their prey or other food items are usually on the order of 0.1 times as long as the ingesting individual. In microphyage, by contrast, multiple simultaneous encounters with food items and handling of several to many at a time are characteristic, and the items are less than (sometimes substantially less than) 0.1 times as long as the ingesting individual. This dichotomy of microphyages versus macrophyages, the history of which was reviewed in F&J, has held up reasonably well for most polychaetes longer than approximately 1 cm, but smaller worms are misfits.

We follow F&J in characterizing macrophyagous feeders as herbivores, which feed on macroalgae or angiosperms, and carnivores, which include carrion feeders and parasites (Figure 1). The distinction between carnivory on motile prey and carnivory on sessile prey has in some cases been blurred since F&J, e.g., with evidence of more active carnivory by Amphinomidae. The
importance of this distinction, however, has been highlighted by a recent study using F&J’s guild classification to test the hypothesis that the Cambrian explosion was linked to the appearance in benthic systems of sufficient oxygen for the evolution of carnivory, defined as feeding on active prey (Sperling et al. 2013). High oxygen demands when capturing and digesting large prey items apply less to predation on sessile invertebrates through rasping mechanisms (e.g., many Amphinoimidae). Another reason to distinguish between motile and sessile prey is the potential for different sensory needs: Mechanosensory capabilities are useless in food acquisition if prey are not motile. Degrees of specialization vary among macrophages, and stable isotope data suggest that some taxa are capable of generalized feeding on rich material, whether on heterotrophic prey or on primary producers (e.g., Lumbrineridae and Nereididae, wherein some taxa will switch to microphagous feeding on rich patches of microalgae or fresh phytodetritus).

Variations in selectivity also occur within microphagous particle feeding, although partial preference is prevalent. Food items with low or no food value (such as glass beads; e.g., Self & Jumars 1988) are often ingested. Such ingestion may enable a greater rate of gain compared with the deployment of elaborate and expensive sensory and handling structures, and it avoids the inflated handling times (and lowered ingestion rates) that selection would require in order to avoid the ingestion of low-value items. Perfection in selection comes with costs in terms of lost opportunities. Adhesive-coated, mechanical mimics of encounter structures without any sensory capabilities do remarkably well at selecting particles for intermediate size, low specific gravity, and the presence of bacterial coatings (Jumars et al. 1982, Guieb et al. 2004).

Microphy: Suspension Feeders More Finely Resolved

Suspension feeding occurs in several families of polychaetes and has clearly evolved multiple times (Table 1). F&J did not resolve suspension feeders into finer categories beyond those that pump and those that use ciliary mechanisms. In the interim, suspension feeding has been reenvisioned through the mechanistic lens of hydrosol filtration theory (Rubenstein & Koehl 1977, Shimeta & Jumars 1991, Riisgård & Larsen 2010). Whereas suspension feeding had been presumed to involve filtering or sieving particles out of solution, with the sizes of the particles captured dependent on the gaps between feeding structures, filtration theory shifted the focus to mechanisms of encounter between particles and feeding structures, of which direct interception and gravitational deposition are the most important for most polychaete suspension feeders. We therefore avoid the term filter feeder.

We also distinguish active from passive and obligate from facultative suspension feeding (Table 1). Active suspension feeders create the greater share of the flow velocities that account for particle flux to their feeding appendages. Passive suspension feeders rely entirely on ambient fluid or particle motion to bring particles within reach of feeding structures. Ciliary feeders use what we term a mixed approach, wherein ciliary motions greatly magnify particle encounter and capture rates but do not in general (except at slack water) produce as high a flux of particles to the vicinity of the animal as does ambient, boundary-layer flow. Indeed, feeding in still water reveals maladaptive traits such as extensive refiltration (Strathmann et al. 1984). Obligate, active suspension feeding may be limited to the basal annelid genus Chaetopterus (Chaetopteridae), which uses a muscular piston pump, and the more derived echiuran genus Urechis (Urechidae), which uses a peristaltic pump; both force water through a fine-meshed mucus bag (Struck et al. 2011, Weigert et al. 2014).

F&J observed that all known holopelagic polychaetes were carnivorous, but since then, pelagic suspension feeders from several families have been discovered. One planktonic, pedomorphic species (Chaetopterus pugaporcinus) encounters sinking aggregates by gravitational deposition onto an external mucus web that is periodically ingested and replaced. This mode of feeding is also...
found in _Poeobius meseres_ (currently Poeobidae, but likely soon to be Flabelligeridae) and possibly in _Buskiella_ spp. (Flabelligeridae) and is reminiscent of suspension feeding in thecosome pteropods. These species are limited largely to midwaters of low turbulence intensity and high vertical particulate fluxes. Swimming Acrocirridae constitute a group with longer tentacles that detect sinking aggregates, likely by mechano- and chemosensing, and can use swimming and tentacles to enhance their encounter rates. They presumably focus on large aggregates whose fluid mechanical and chemical signatures are strong. They occur in more energetic bottom boundary layers and depend on gravitational deposition but may also achieve some particle encounters through turbulent shear.

We omit two potential suspension feeders from Table 1 for lack of information. A protodrilid from a sunlit, anchiline cave has been reported to be holopelagic (Martínez García et al. 2009, figure

**Table 1** Suspension-feeding polychaetes, their pump mechanisms, hydrosol encounter mechanisms, and alternative or simultaneous other feeding modes

<table>
<thead>
<tr>
<th>Active/passive&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Taxa</th>
<th>Pump mechanism</th>
<th>Likely dominant encounter mechanisms</th>
<th>Other feeding mode</th>
<th>Motility</th>
</tr>
</thead>
<tbody>
<tr>
<td>Active</td>
<td>Chaetopterus except <em>C. pugaporcinus</em> (Chaetopteridae)</td>
<td>Parapodial piston</td>
<td>Direct interception with mucus bag</td>
<td>None</td>
<td>Sessile</td>
</tr>
<tr>
<td></td>
<td>Benthic Chaetopteridae except <em>Chaetopterus</em></td>
<td></td>
<td></td>
<td>Passive suspension with coiled palps or surface deposit with palps</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Urechidae</td>
<td>Peristaltic</td>
<td></td>
<td>None</td>
<td>Discretely motile</td>
</tr>
<tr>
<td></td>
<td>Serpulidae, Sabellidae except <em>Myxicola</em></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td></td>
<td><em>Myzioidea</em>, Fabriciidae lacking ventral filamentous appendages</td>
<td></td>
<td>Downstream ciliary entrainment on radioles</td>
<td>Mucus adhesion (surface deposit) to trailing appendages when moving</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Fabriciidae with ventral filamentous appendages</td>
<td>Ciliary</td>
<td></td>
<td>Simultaneous surface deposit with ventral filamentous appendages, mucus adhesion to surface deposits by trailing appendages when moving</td>
<td>Discretely motile</td>
</tr>
<tr>
<td></td>
<td><em>Themiste, Thysanocardia</em> (Golfingiidae); <em>Antilloeoma antillarum</em> (Antillosesomatidae); <em>Sipunculus sp.</em> (Sipunculidae)</td>
<td></td>
<td>Direct interception or ciliary entrainment</td>
<td>Surface deposit with oral tentacles?</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Owenia</em> (Oweniidae)</td>
<td></td>
<td></td>
<td>Surface deposit with dendritic tentacular crown</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Flabelligeridae, Alvinellidae</td>
<td></td>
<td>Mucociliary entrainment in branchial currents</td>
<td>Tentacular surface deposit</td>
<td></td>
</tr>
</tbody>
</table>

*(Continued)*
Table 1 (Continued)

<table>
<thead>
<tr>
<th>Active/passive&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Taxa</th>
<th>Pump mechanism</th>
<th>Likely dominant encounter mechanisms</th>
<th>Other feeding mode</th>
<th>Motility</th>
</tr>
</thead>
<tbody>
<tr>
<td>Passive</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sabellariidae</td>
<td></td>
<td></td>
<td>Direct interception, gravitational deposition, inertial impaction</td>
<td>Surface deposit with palps or tentacles</td>
<td>Sessile</td>
</tr>
<tr>
<td><em>Lanice</em> except <em>L. bidewa</em> (Terebellidae)</td>
<td></td>
<td></td>
<td>Direct interception with tentacles or mucus web</td>
<td>Surface deposit with tentacles</td>
<td></td>
</tr>
<tr>
<td>Many Spionidae</td>
<td></td>
<td>None</td>
<td>Direct interception, inertial impaction</td>
<td>Surface deposit with palps</td>
<td></td>
</tr>
<tr>
<td><em>Praxillura maculata</em> (Maldanidae)</td>
<td></td>
<td></td>
<td>Direct interception with mucus web</td>
<td>Subsurface deposit?</td>
<td>Discretely motile</td>
</tr>
<tr>
<td><em>Chaetopterus pugaporcinus</em> (Chaetopteridae), <em>Pocobidae,</em> <em>Buskiella</em> (Flabelligeridae)</td>
<td></td>
<td></td>
<td>Gravitational deposition onto mucus web</td>
<td>None</td>
<td></td>
</tr>
<tr>
<td>Planktonic Acrocirridae</td>
<td></td>
<td></td>
<td>Mechano- and chemosensing-enhanced gravitational deposition</td>
<td></td>
<td>Motile</td>
</tr>
</tbody>
</table>

<sup>a</sup>Passivity indicates dependence solely on ambient fluid and particle motions.

6b in Wilkens et al. 2009). The species has not yet been described, so we lack basic morphological information, and its food source and mechanics of hydrosol encounter are also unknown. *Longipalpa saltatrix* (Nerillidae), also from an anchiline cave, is capable of extended ciliary swimming, but the extent to which it depends on suspension feeding as opposed to feeding on or in the bottom is unknown (Worsaae et al. 2004). We also note that suspension feeding in *Sipunculus* is based on a single report and that all other known members of the genus (and of the Sipunculidae family) are considered deposit feeders.

Among benthic worms, a common passive suspension-feeding mode entails the deployment of two palps in distally narrowing helical coils up into the lowermost centimeters of the bottom boundary layer, where particles are encountered by direct interception and inertial impaction, perhaps aided by vortical flow induced by the narrowing helix. Coiling is actively controlled and becomes tighter at higher flow velocities, and the direction of narrowing is locally downstream, including under oscillatory flows. No polychaete feeds this way exclusively, but it has been observed frequently in Spionidae and likely occurs in all benthic Chaetopteridae except those in the genus *Chaetopterus*. Most if not all species that use this suspension-feeding mode also surface deposit feed. Factors affecting the shift to suspension feeding include the horizontal flux of particles, flow speed, and suspended food quality (Taghon et al. 1980, Bock & Miller 1996). The payoff from suspension feeding is a dramatic increase in growth rate (Hentschel 2004) resulting from the large increase in the quality of low-density particles winnowed by the flow from the bed (Mayer et al. 1993). Future studies may find members of other families (e.g., Apistobranchidae, Longosomatidae, Poecilochaetidae, Trochochaetidae, and Uncispionidae) that feed in this manner.

Hydrosol filtration theory has also helped to explain suspension feeding in *Lanice* spp. (Terebellidae) that build tubes that branch across tidal currents and support weak tentacles. Experiments
have confirmed appreciable clearance rates in *Lanice conchilega* resulting from a combination of direct interception and induced deposition. *Lanice conchilega* also retains the ability to deposit feed. Suspension feeding does not appear to be possible in other genera of Terebellidae that do not build rigid support structures for their tentacles. *Praxillura maculata* (Maldanidae) has support structures for its mucus web that appear to converge on those of *Lanice* spp., but details are lacking.

Perhaps the largest advance in the understanding of polychaete suspension feeding has come from the identification and analysis of ciliary downstream collecting (Riisgård et al. 2000). Lateral cilia move rapidly enough to catch up with particles passing the radiole or another feeding appendage and reorient the particles along an arc to a feeding groove on the downstream (oral) side. Active, unsteady behavior was not a feature of engineered collectors for which hydrosol filtration theory was first derived (e.g., Pich 1966), and this mechanism is less intuitive than, e.g., direct interception. The reach of the lateral cilia greatly increases particle detection and encounter distances and rates. We consider this mode of suspension feeding to be obligate in suspension-feeding taxa that have radioles and no other feeding appendages. We have observed that serpulids, sabellids, and sabellariids occasionally mop up particles from surrounding surfaces in aquaria, but we do not see this behavior as frequently in the field, where animals have not been cut off from currents and particulate fluxes, and we exclude it from Table 1 because we doubt that it is quantitatively important.

Two groups of suspension feeders are in particular need of additional research. The mechanisms of suspension feeding in Sabellariidae remain to be identified and quantified under suspended loads and flow regimes resembling those in the field. Also lacking are estimates of clearance rates in suspension-feeding sipunculans (of the genera *Trypanostomum* and *Themiste* in Golfingiidae and *Antillesoma antillarum* in Antillesomatidae) or any analyses of their capture mechanisms in a hydrosol filtration context.

**Microphagy: Multiple Adaptive Peaks in the Deposit-Feeding Syndrome**

Over the past few decades, it has become apparent that most deposit feeders (defined as individuals that ingest dilute food whose principal content by weight is mineral material) share several characteristics. They include microphagy, the relatively rapid processing of food, and partial preference in the form of imperfect particle selection. The ciliated ventral gutter at least in some species of Ampharetidae accelerates the departure of particles that enter it, providing a means to increase the input rate of more nutritious particles without increasing gut volume. Ventral gutters in other taxa likely perform similar functions. Deposit feeding appears to require a greater volume of digesta than does feeding on richer foods, with gut volumes of ∼30% of total body volume compared with ∼10% for carnivorous polychaetes (Penry & Jumars 1990).

Publications since F&J have stimulated a reexamination of conventional thinking that smaller grain size is always better for ingestion by deposit feeders. Because there is zero food value inside mineral grains and the organic content is proportional to the grain surface area (Mayer et al. 2004), a given volume of small grains contains more organic material than the same volume of large grains (Taghon et al. 1978). Among polychaetes, Arenicolidae and Opheliidae that ingest intertidal or very-shallow-water sand exhibit the highest ingestion rates, with mean gut residence times for sand grains as short as 4 min (Kemp 1986). The (dry-weight) rates are stunning in terms of body weights of ingesta per day, which are up to 300 in Arenicolidae (Taghon 1988) and 9,000 in smaller Opheliidae (Kemp 1986). Even though sands as low in organic matter as 0.25% by weight are common, their organic coatings are more easily digested than those of muds for two reasons. One is their much smaller surface area for adsorption of surfactants and enzymes. The other is their permeability: It takes less work and time to get digestive reagents to the organic matter.
and to get the digested solutes out. Wave pumping and surge in shallow water quickly renew the value of egested sand because sand is an effective filter for fine particles and for filaments and flakes of organic material. Moreover, sands in dynamic equilibrium with waves and currents are not locations where refractory organic materials that can tie up digestive agents accumulate. In predicting that deposit feeders should always select for fine particles to maximize organic content, Taghon et al. (1978) did not consider the digestive problems of impermeability and adsorptive interference with digestive reagents in these finer sediments.

Among deposit feeders, there appear to be multiple adaptive peaks in particle preferences and ingestion rates. Arenicolidae show only modest selection for particles below the ambient median grain size, which is unsurprising given their rapid feeding rates on sands. The feeding-rate record holders, Opheliidae, nevertheless show a feeding preference based on mineral composition. The basis of this selection has not been determined (Dafoe et al. 2008). Pectinariidae, however, preferentially ingest particles larger than the ambient median grain size. They are obligate inhabitants of heterogeneous, poorly sorted sediments, requiring increasing grain size for tube construction as they grow. However, a majority of surface deposit feeders that use tentacles ingest particles smaller than the median grain size and are biased toward particles low in specific gravity (Ampharetidae, Spionidae, and Terebellidae). In shallow-water species feeding in muds, gut residence times of inert tracer particles are typically 0.5–2 h.

Deposit-feeding Echiuridae may be part of another adaptive peak. Their feeding bouts can be separated by a few days, with gut residence times of >1 d, suggesting the potential for high assimilation efficiency and perhaps selective coprophagy (eating of feces), as is common in small, hindgut-fermenting mammals (Sakaguchi 2003). Some Golfingiidae species show strong evidence of caching, wherein episodically rich surficial deposits, typically resulting from pulses of phytodetritus or fecal pellets of planktonic herbivores, are gathered from the surface but stored below the surface for later ingestion and possible reingestion. Sipunculidae also appear to be highly efficient in extracting organic matter, reducing it to what were in 1978 undetectable levels in feces expelled from the burrow (Hansen 1978). Both sipunculans and echiurans tend to have a mildly alkaline gut pH, further differentiating them from other polychaetes. Higher alkalinity in termite guts desorbs refractory humic material from minerals and breaks down and solubilizes high-molecular-weight compounds (Kappler & Brune 1999). In short, there are hints but few details of a potential echiuran-sipunculan digestive syndrome with high digestive efficiencies, long gut residence times, caching and reingestion, and mildly alkaline gut pH.

F&J were somewhat skeptical about classifying organisms as nonselective deposit feeders. More recent trophic classifications have been even more skeptical (e.g., Macdonald et al. 2010). Ingestion is biased by particle roughness, size, and specific gravity (Self & Jumars 1978, 1988); by nonliving, organic coatings (Taghon 1982); by bacterial coatings (Guieb et al. 2004); and by both large- and small-scale choice of feeding location (Fisk 1983, Kihslinger & Woodin 2000). Selectivity may be active, based on sensory information, or passive, based on unsensed mechanical properties of particles. Larger species energetically can afford to be less selective (Self & Jumars 1988), but even large species such as arenicolids show selectivity, producing lag layers of rejected material (Baumfalk 1979). For all of these reasons, the concept and category of nonselective deposit feeders is problematic and therefore not used in our review. It is a useful null hypothesis for statistical testing but unlikely to be an accurate descriptor for any real animal.

The great majority of deposit feeders whose lumen chemistries have been analyzed contain a mixture of surfactants and enzymes in the midgut region that, like commercial laundry detergents, act quickly to solubilize adsorbed and particulate organic matter (Mayer et al. 2001b). This generalization extends to an omnivorous species of Nereididae when deposit feeding, but that species lacks surfactants when feeding carnivously (Bock & Mayer 1999). The midguts of Arenicolidae
also contain higher concentrations of proteins than could occur if fluids traveled posteriorly at the same speed as sediment grains (Chen & Mayer 1999). Most polychaetes are slightly hyperosmotic at normal salinities. We hypothesize that, especially in deposit feeders, this osmotic imbalance directs an osmotically driven flow, containing digestive products, to absorptive sites. Two adaptive advantages are (a) the possibility of passive uptake of products across the gut lining without the need for active uptake sites and (b) extended gut residence times for solutes (longer than for solids), allowing a longer period for the hydrolysis of solutes too large for active uptake. At least part of the water in this flow is taken up through the anus. We suspect that prior findings of uptake of amino acids and short-chain fatty acids by polychaetes from ambient solution (as described in F&J) may have been associated largely with anal uptake of ambient water. This mode of uptake has recently been documented in a holothuroid (Jaekle & Strathmann 2013) and leads us to hypothesize that dependence on this mode of enhancing digestive efficiency may account for the intolerance of some deposit-feeding taxa to salinity variation (i.e., holothuroids, sipunculans, and echiurans). The distinctive coiling of the hindgut and foregut around each other in sipunculans may provide another effective means to take advantage of osmotic imbalance between the animal and ambient seawater in a perfect geometry for countercurrent exchange of water and solutes. Anal inflow also relieves the oxygen demands produced by bacterial activity in hindgut digesta (Plante et al. 1990).

For Arenicolidae ingesting permeable sands, intraluminal flow can move through the digesta. In Capitella and some other Capitellidae taxa, the packaging of ingesta into pellets may facilitate peripheral liquid flow in an anterior direction around the pellets. This same solution apparently arose independently in Chaeotrocho brunnea (Cirratulidae). Many Echiuridae also pelletize ingesta before they leave the esophagus. Semipermeable peritrophic membranes covering such pellets may allow the diffusion of digestive products outward while maintaining high enzyme concentrations within. Fluid flow in the anterior direction would also enhance retention of digestive enzymes, helping to explain the generally low enzymatic activity found in the feces of deposit feeders (Mayer et al. 2001a). Such countercurrent flow is not included in the simple reactor-theory models of digestion thus far used to make ecosystem-level predictions in marine systems (e.g., Jumars et al. 1989).

The digestive syndrome of deposit feeders—especially the combination of countercurrent fluid flow and surfactants—brings potential sensitivity to environmental contaminants. Surfactants can effectively solubilize hydrophobic pollutants (Voparil & Mayer 2004), and the high concentrations of gut proteins resulting apparently from reflux are effective at solubilizing metals (Chen et al. 2002). Thus, deposit feeders are prime entry points for pollutants into marine food webs.

F&J recognized only two deposit-feeding modes based on feeding stratum—surface and sub-surface deposit feeding. Bearing in mind that the utility of guilds depends on the similarity of both collection sites and collection mechanics, there is now sufficient information to suggest two additional categories. Based primarily on observations in Arenicolidae, we now recognize a third deposit-feeding stratum: funnel feeding, in which animals feed mainly on surficial sediments but do so from below. This subductive feeding mechanism is restricted largely to granular materials with an angle of repose of $<40^\circ$ and depends on both horizontal and vertical separation of feeding and defecation sites. In addition to Arenicolidae, it is found routinely in some Maldanidae and has been reported in Pectinariidae. A second new mode that we recognize is caching, for which the evidence is best developed for some Golfingiidae and some Maldanidae; it is also strongly suspected in some Bonelliidae. Caching is prevalent where deposition of phytodetritus or fecal pellets of plankton is seasonal or episodic and entails its sequestration from shallow-burrowing animals by burial. In Maldanidae, it has been called hoeing because the material is pulled into the animal’s burrow by a hoeing motion of its posterior segments and pygidium.
Microphagous Guild Switching

Dauer et al. (1981) proposed the term interface feeding for animals—such as many Spionidae and Chaetopteridae—that either suspension feed or deposit feed depending on local conditions and their feeding histories. Despite its subsequent popularity, we decline to adopt this terminology because it runs counter to the ecological concept of guild members exploiting the same resources in similar ways. The mechanics of adhesive pickup of surficial sediments by palps are vastly different from the mechanics of hydrosol encounter by those same palps, and suspended food is generally far richer in organic matter (Mayer et al. 1993) and yields much higher growth rates (Hentschel 2004) compared with deposited sediments. It seems much more informative to ask what conditions cause switching (e.g., Miller et al. 1992, Lindsay & Woodin 1995, Riisgård & Kamermans 2001) and what environments favor species that can switch between guilds over specialists within one guild.

Switching between suspension and deposit feeding affords a degree of omnivory, but in Spi-onidae and Chaetopteridae (as opposed to some Fabriciidae), the palps are generally used for only one mode at a time. This omnivory is sequential rather than simultaneous. Obligate suspension feeders have not usually been found to produce surfactant concentrations above the critical micelle concentration, whereas those concentrations are reached in nearly all obligate deposit feeders assayed (Mayer et al. 1997, 2001b). Whether spionids and chaetopterids up- and downregulate surfactant concentrations with changes in diet and feeding mode and how long this regulation takes are unknown.

Behavioral rather than morphological distinctions among deposit-feeding modes, especially for caching, which is most advantageous under highly variable food conditions, make switching among deposit-feeding modes common. Whereas many surface deposit feeders can also suspension feed, we know of no species of subsurface deposit feeders that also suspension feed, with the possible exceptions of Magelonidae and Praxillura maculata (Maldanidae).

Omnivory: Sequential or Simultaneous?

Evidence for broad omnivory (including macrophagous and microphagous feeding) in three families—Eunicidae, Nereididae, and Onuphidae—is especially strong. All three families have jaws that can handle food items larger than their mouths. In Nereididae, at least part of this diet breadth is accommodated by digestive adaptation to the combination of ingested materials. No comparable experiments have been done with Eunicidae or Onuphidae.

Above, we mentioned the disparity in relative gut volumes between carnivorous and deposit-feeding polychaetes; there are also differences in optimal processing times. In general, richer foods (those with food concentrations further above the half-saturation constants for hydrolytic enzymes) should be held longer in the gut because they continue to give higher product formation rates and absorption rates longer than do less concentrated foods. Polychaete carnivores typically have particle residence times (for undigested particles) of approximately 24 h (Vahl 1976), much longer than the residence times of mineral grains in most deposit-feeder guts. Indeed, the very nature of feeding changes between animals such as carnivores taking discrete meals (Zanutto & Staddon 2007) and deposit feeders feeding more or less continuously.

There are also differences in lipid digestion between carnivory and deposit feeding. Digestion in carnivores is associated with large lipid droplet formation (an emulsion), and such droplets do not transport well through fine sediments (Voparil et al. 2008). In Nereididae that can both deposit feed and eat animal flesh, emulsions are formed only in the absence of sediments, and surfactants above critical micellar concentrations occur only in the presence of ingested sediments (Bock &
Mayer 1999, Voparil et al. 2008). It is interesting that mixtures of sand and animal remains are not infrequently reported as gut contents (e.g., Gaston 1987 for Nephtyidae), as sands have sufficiently large pore spaces to allow emulsions to pass.

In vertebrates, some diet changes are accommodated by rapid changes in the volumes of particular gut structures (e.g., Pulliainen & Tunkkari 1983, Starck 1999). No comparable experiments have been done with polychaetes. A great deal remains to be learned about the advantages and disadvantages of omnivory and how the latter are ameliorated.

The Small-Worm Syndrome

Metabolic scaling puts intense selective pressure on small individuals to ingest foods rich in labile organic matter; the gut is too small to yield a high rate of return from rapid throughput because the residence time is too short for enzymatic hydrolysis and absorption from dilute food (Penry & Jumars 1990). Small juveniles of species that deposit feed as adults specialize on rich food items such as diatoms until they grow large enough to eat the more dilute diets of bona fide deposit feeders (Hentschel 1998a,b). As an order-of-magnitude generalization, for a roughly cylindrical worm, the crossover to deposit feeding begins at approximately 1 cm body length or 1 mm³ gut volume.

Although the best experimental evidence available points to the importance of diatoms as food (Gallagher et al. 1990, Hentschel & Jumars 1994), and exclusive feeding on diatoms would make such small worms macrophages, visual observations of feeding in small worms suggest a generally broader diet that includes microbial films that are licked, sucked, rubbed, or scraped from surfaces (Aeolosomatidae, Ctenodrilidae, Dinophilidae, Diurodrilidae, small Dorvilleidae, Parergodrilidae, Protodrilidae, Psammodrilidae, and Saccocirridae). The Saccocirridae family was recently split into two genera, one of which uses a muscular pharynx to feed on bacteria, diatoms, and other algae that it sweeps up with cilia, and the other of which lacks a muscular pharynx and is presumed to be carnivorous (Di Domenico et al. 2014). Polygordiidae also lack a muscular pharynx, but their feeding mode is poorly understood. Whether a muscular pharynx is necessary for scraping labile material is unclear but is especially interesting because we know of no polychaetes with a nonmuscular pharynx that have any tooth-like structures. At least three species of small Ampharetidae use scraping teeth, and we would not be surprised if these teeth were found in small juveniles of other ampharetid species.

This resource mix of macrophagously ingested diatoms and other rich items (other microalgae, fresh phytodetrital aggregates, forams, and other protists) and microphagously ingested films, other detrital fragments, and bacteria arises from the overarching requirement based on digestive constraints to ingest rich food and from the varied packages in which rich food occurs on surfaces and interstitially on scales of these small worms. Species grown in culture have been raised on a wide variety of natural and exotic food materials, providing further evidence of omnivory, with the constraint that the ingested items must be highly labile organic materials that include organic nitrogen (Dinophilidae, Dorvilleidae, Fabriciidae, and Protodrilidae). At this scale, the animal-plant-protist-prokaryote distinction is digestively moot; C:N ratios are all fairly low, and members of the microphytobenthos lack the structural carbohydrates that require modified digestive approaches. A finer resolution of small-worm guilds may be achievable, and there may well be dietary specialists, but the nature of dietary patterns based on taxon or morphology in most cases is not yet evident. Could the prevalence of asexual reproduction in polychaetes be selected for in part by the ability of larger juveniles to avoid or shorten the period when rich resources are needed? Conversely, could the high prevalence of pedomorphy among polychaetes be an evolutionary response to habitats where rich juvenile resources are more prevalent than dilute adult resources?
A rare situation in which food specialization by small polychaetes is clear is in the commensal relationships of polychaetes with other invertebrates. Most notable is the relatively frequent occurrence of Syllidae as internal parasites of reef sponges. Fenchel (1984) clearly described the advantages that benthic bacterivores, especially sponges, have over planktonic ones in bacterivory. By attachment, they have access to relative water motion without paying the costs to produce that motion. On oligotrophic reefs, recent experiments showed that the sponge advantage extends to the uptake of dissolved organic matter (de Goeij et al. 2013). In a striking departure from the classic pelagic microbial loop, the total uptake rate of dissolved organic matter on reefs by sponges exceeds by one to two orders of magnitude the uptake rate by planktonic bacteria, and sponges dominate the delivery of particulate organic matter to the reef (de Goeij et al. 2013). Several polychaete groups have found ways to short-circuit the delivery of this rich detritus source and likely return the favor as sponge mutualists by providing excreted ammonium to cyanobacteria living in sponges. Several Syllidae species can be abundant inside sponges, but before de Goeij et al.’s (2013) work and the identification of the detrital food source, these abundances were difficult to explain. Homochromatic polychaetes externally commensal on sponges may be making the same trade [Chaetozone nr. corona (Cirratulidae) and Spintheridae].

The suggested requirement for labile material and avoidance of the ingestion of diluents among small polychaetes is based on observations and experiments with shallow-water species, however, and yields questions about the diets of deep-sea species. Deep-sea infaunal polychaetes are generally smaller than their shallow-water, confamilial relatives (e.g., Hessler & Jumars 1974), and it is not evident whether small abyssal polychaetes can grow on more dilute foodstuffs by increasing extraction efficiency or decreasing metabolic rates or whether they, too, depend on encountering concentrated, labile foods.

Both the quantity and quality of food supplied to soft-bottom benthos will be impacted by changes in the ocean environment in the coming century (Mora et al. 2013). Predicted declines in primary productivity and particulate organic carbon (POC) flux are especially sobering, and the absolute magnitude of reductions will be greatest in shallower soft-bottom habitats, including those on the continental shelf (Mora et al. 2013). Although absolute reductions in POC flux to deep-sea habitats may be relatively smaller, their impact on species that are already food limited is likely to be profound, reducing not only macrofaunal abundance but also the mixed-layer depth, oxygen consumption by the sediment community, and bioturbation intensity, which are all important components of the ecosystem services provided by abyssal species (Smith et al. 2008). Increased variability in POC flux may benefit species that cache food, and longer digestion times (e.g., in some Echiura) may be favored under reduced POC conditions. Ocean acidification is likely to change the biochemical composition of primary producers and in turn constrain the growth of primary consumers. For example, Rossoll et al. (2012) found that the fatty acid composition of phytoplankton changed in response to acidification, in turn constraining copepod growth.

Among polychaete feeding guilds, we expect that suspension- and deposit-feeding species are more likely to be affected by such changes in nutritional quality. The ability to switch between suspension and deposit feeding may be advantageous with changing hydrodynamics and food supply. For example, Wicking & Kröncke (2001) observed significant increases in spionid polychaetes that can switch feeding modes in the central North Sea following a decade of increasing North Atlantic Oscillation index and accompanying changes in primary productivity. By contrast, El Niño–associated reductions in rainfall and freshwater input reduced benthic invertebrate abundance equally across all feeding groups (suspension feeders, deposit feeders, scavengers, and predators) in an Australian estuary (Currie & Small 2005). Regardless of the habitat, the synergistic effects of changes in temperature, oxygen, nutrients, pH, and food will undoubtedly impact species in different ways.
EMENDING THE DIET OF WORMS: OUR APPROACH

Our revised feeding-guild classification is based on a family-by-family literature review, which grew far too long to include in this article and which we anticipate will be used primarily as a reference, so it has been published as a Supplemental Appendix (follow the Supplemental Material link from the Annual Reviews home page at http://www.annualreviews.org). In this appendix, each family’s information, including references, is relatively short and self-contained. The reference list also grew too long; to overcome that problem, our use of a formal family name (ending in “dae”) above indicates that supporting references are found in the appendix.

Our review focuses on marine species (as it must in this venue), with some extensions into fresh waters and fewer onto land. It also excludes clitellid annelids, despite the ubiquity of marine oligochaetes and leeches and despite the recent molecular genetic finding that Clitellata constitutes a clade within Polychaeta that likely evolved in fresh waters (Struck et al. 2011). Our exclusion is purely pragmatic, reflecting the largely nonoverlapping literatures of “polychaete” and clitellid annelids and our lack of familiarity with the latter. We expand our review to differentiate adult from juvenile diets in the few cases where the literature permits because doing so sheds light on syndromes of feeding characteristics seen in generally small-bodied species that are encountered in a surprisingly large number of polychaete families. Because metamorphosis corresponds with changes in polychaete body plans, habitats, and diets, we completely avoid larval feeding modes and diets. We warn both polychaete specialists and novices that our use of terminology for morphological structures is nonstandard, but unless noted here, it follows that of F&J. Our proposed shifts in terminology have two goals: transparency to nonspecialists and a more deliberate focus on function. Additional studies and new methods have allowed our focus to shift further from potential to realized diets.

F&J relied on records of gut contents, observed behaviors, and inferences from morphology to characterize feeding. Since this review, however, powerful new methods, including stable isotopic analyses and lipid profiles, have been developed to test and advance diet hypotheses. Briefly, differences in δ¹³C and δ¹⁵N between consumers and available foods can be used to identify food sources and trophic levels (Peterson & Fry 1987). Biological processes shift stable isotope ratios in relatively predictable ways at each trophic step (+1‰ for δ¹³C and +2–4‰ for δ¹⁵N). Consistently heavy δ¹⁵N values (compared both with sediment and with other polychaetes sampled) in Glyceridae, Goniadidae, Lumbrineridae, Nephtyidae, and Oenonidae support existing evidence for carnivory, whereas isotope ratios of both C and N that vary substantially within and among different sites support broad omnivory by Nereididae and Onuphidae.

There are some caveats, however, in making inferences of trophic position from isotopic data. First, isotopic baselines of food sources can vary substantially. Phytoplankton, microphytobenthos, total suspended particles, and sediments vary widely in δ¹⁵N because of spatial and temporal differences in pathways and reaction rates within the exceedingly complex nitrogen cycle (e.g., Middelburg & Nieuwenhuize 1998). These baseline values vary with water depth (e.g., Kojima & Ohta 1989, Mintenbeck et al. 2007) and with organic enrichment, e.g., from sewage inputs (Sampaio et al. 2010). This large variance limits the information contained in an absolute value of δ¹⁵N and places greater emphasis on the difference in δ¹⁵N between an organism and its food. Even knowing the baseline δ¹⁵N for bulk food source leaves some uncertainty, as the difference between an organism and the baseline food source depends on its trophic position as well as Δ¹⁵N, the so-called discrimination factor between an organism and its known food. The N discrimination factor varies around a mean of approximately 2.5 when the consumer is an invertebrate or a fish (Caut et al. 2009), but when food is modified by microbial processes, as occurs in virtually all detrital and aquatic systems, interpretation becomes more difficult. Microbial processing can shift
isotopic signatures in bulk sediments, yielding $|\Delta^{15}N| > 5\%$ in 8 d or less (Goedkoop et al. 2006). Although the shift is usually toward higher $^{15}N$ content, the metabolism of some substrates by bacteria can reduce the proportion of $^{15}N$. Macko & Estep (1984) demonstrated substrate-dependent microbial discrimination factors of $-12.9\%$ to $+22.6\%$ for $^{15}N$ and $-5.5\%$ to $+11.1\%$ for $^{13}C$. Physiology can also affect $^{15}N$ discrimination factors. Taxa that excrete ammonia have lower $^{15}N$ discrimination factors than those that excrete uric acid or urea (Vanderklift & Ponsard 2003). Feeding on low-quality food (with high C:N) can increase the $^{15}N$ discrimination factor, possibly owing to the metabolism of stored lipids and proteins (Fantle et al. 1999). Even in the most thoroughly studied benthic communities, interpreting stable isotope data can be challenging (e.g., Middelburg & Nieuwenhuize 1998).

Many studies using stable isotopes to characterize food webs have relied on F&J to assign feeding guilds from taxonomic identity. In many cases, the inferences from stable isotope data were consistent with F&J, but a few interesting exceptions have arisen. Magelonidae, considered surface deposit feeders based on their long tentacles and aquarium observations of feeding on enriched material presented at the sediment surface, have $\delta^{15}N$ values that are consistently heavier than expected. In this case, we suspect that this family has a greater tendency toward carnivory and subsurface feeding than is apparent from other data—more specifically, that positive net growth depends on a more carnivorous diet than is reflected in gut contents. Many subsurface deposit feeders, however, also have very elevated $\delta^{15}N$ values, comparable to those of known carnivores. *Travia* (Scalibregmatidae) is an extreme example, a grub-like, jawless worm with $\delta^{15}N$ values higher even than those of rattail fishes whose gut contents showed clear carnivory (Drazen et al. 2008). In this case, elevated $\delta^{15}N$ appears to be characteristic of deposit feeding deeper in the sediments, where isotopic content may have been modified by microbial activity. Together with even modest natural history data, stable isotope information can be highly informative in providing clues and testing alternative hypotheses about diets. Gut contents clearly indicate what is ingested, whereas stable isotope data provide evidence of the components that are assimilated.

**Motility and Habitat**

F&J identified several links between motility and feeding mode; the authors found no completely sessile macrophagous feeders, observed that the only sessile surface deposit feeders had tentacles to increase their foraging radii, and referred to the subsurface deposit-feeding mode as burrowing (largely to avoid repetition of the term deposit feeding). This link between subsurface feeding and motility is clearly intuitive but has since been supported by theory (Mayer et al. 2001a) and experiments (van Nugteren et al. 2009) indicating that bacteria and animals compete for the detrital resources that form the foundation of the benthic food web. An attached benthic bacterium can do well when enough organic particulate and adsorbed resources are within approximately five cell radii of it (Vetter et al. 1998), whereas worms require much larger, spatially coherent patches of rich material to repay their motility, respiratory, feeding, digestion, and assimilation costs. The value of motility depends on the distribution of distances to—and ephemerality of—resource concentrations (Grübaum 2002). The link between being sessile and having tentacles is also fairly intuitive for surface deposit feeders, and it applies to passive suspension feeders as well: Eating large volumes of food per unit of time requires either movement or appendages to collect food from a relatively large area. Encounter rate theory explains the rarity of effectively sessile, macrophagous polychaetes except for sit-and-wait predators dependent on prey motility (e.g., Acoetidae) and feeders on wrack in areas of high flux (e.g., Onuphidae).

The recent discoveries of several charismatic pelagic species, some of which—e.g., *Chaetopterus pugaporzinus* (Osborn et al. 2007)—evolved from sessile benthic ancestors, illustrate the
benthos-centric definition of motility in F&J and, more important, point to a link between habitat and motility. Is a planktonic polychaete with a balloon-like morphology and no observed locomotory capabilities motile or sessile? From a Lagrangian frame of reference (following a moving water parcel), a neutrally buoyant individual of *Chaetopterus pugatorius* is sessile, but because fluids deform much more easily than solid elements and small changes in buoyancy affect vertical position, less locomotory capacity is necessary to generate movements, and these moderate movements may constitute discrete motility. We attempt to maintain an Eulerian perspective in defining motility for benthic taxa and a Lagrangian perspective in doing so for pelagic taxa, and include habitat information to clarify these perspectives. Similar confusion arises for commensal polychaetes on motile hosts; we characterize many of them as discretely motile based on the assumption that they can move to a new host individual, and our reference frame is that of the host (Lagrangian for mobile hosts).

We retain distinctions among motile, discretely motile, and sessile polychaetes used by F&J but provide additional subcategories that emphasize the linkage between motility and habitat (Figure 1). These distinctions are not merely semantic: Swimming through a fluid and crawling over or burrowing through a solid medium involve different forces (Dorgan 2010, Dorgan et al. 2013). *Armandia brevis* (Opheliidae) uses the same undulatory behavior to burrow and to swim, but the different mechanical responses of the fluid and solid make the resulting movement patterns quite different (Dorgan et al. 2013). Even among infauna, forces can differ qualitatively and quantitatively. Burrow extension in muds occurs by elastic fracture, whereas movement through noncohesive, granular sand requires plastic rearrangement of grains or localized fluidization (Dorgan et al. 2006).

Even distinguishing among motile, discretely motile, and sessile infauna and epifauna can be challenging, in part because of the impossibility of making a clear distinction between a tube and a burrow lining. Structures at one end of the spectrum are obvious: Serpulids secrete, pectinariids and sabellariids cement, and species of *Hyalinoecia* (Onuphidae) and Acoetidae spin tubes. At the other end of the spectrum, a fast burrower in either sand or mud leaves little trace of its passing. On longer timescales, however, mud is poroelastic (Wang 2000). Pressure from the prolonged presence of a worm squeezes water out from the mud nearest the burrow in a manner evident in X-radiographs (e.g., figure 4 from Shull & Yasuda 2001). Whether a semiconsolidated burrow lining remaining on a sieve after sample washing constitutes a tube is a semantic conundrum that we do not resolve here; instead, we attempt to identify cases where a tube or burrow structure plays an integral role in feeding and provides insight into motility. The current understanding of material properties on the temporal and spatial scales of burrowing accommodates some aspects of sediment elasticity (Dorgan et al. 2007), but deformation of sediments to create a permanent burrow has not been considered in burrowing mechanics. We have no doubt that such incorporation will soon prompt further revision of our guild classifications.

Bilateral symmetry in motile, epifaunal, and planktonic polychaetes with coordinated parapodial motion has clear advantages but also some associated subtleties, such as improved traction on surfaces from jointed chaetae (Merz & Edwards 1998). Consideration of elastic fracture mechanics has illuminated the value of bilateral symmetry in animals that burrow in mud (Dorgan et al. 2006). Observations in transparent analogs of mud have revealed that animal shapes differ systematically under the elastic rebound forces in muds from shapes observed in preserved specimens. Rebound of dorsal and ventral walls of the crack-shaped burrow causes dorsoventral compression. *Scalibregma inflatum*, named for its balloon-like shape ex situ, is much more ovoid in cross section in situ (K.M. Dorgan, unpublished data). Cirratulid gills are stretched to fill the lateral crack edges, appearing much more kempt than they do when removed from sediment (Che & Dorgan 2010a). Worm anteriors generally function as wedges, with eversible pharynges or muscular, expansible
antennaries that apply dorsoventral forces to burrow walls (Dorgan et al. 2005, Che & Dorgan 2010a). Frontal horns and palps can aid in fracture by expanding the burrow laterally, frequently through a characteristic side-to-side motion, relieving the need to produce the large forces that propagating a single large crack would require. This same side-to-side motion may allow worms to systematically sample pore waters for dissolved chemical cues. The muscular posterior ends of worms can also function as wedges, allowing backward burrowing (Che & Dorgan 2010b). These ends may be particularly necessary in worms with a large aspect ratio (length/diameter), whose bodies are much more easily pulled than pushed along, analogous to engines at both ends of long trains (Jumars et al. 2007).

**Feeding and Sensory Structures: Relating Form to Function**

Following F&J, we include the morphological structure used in feeding, but draw on advances in particle encounter and selection (Rubenstein & Koehl 1977, Shimeta & Jumars 1991, Riisgård & Larsen 2010) and the comparative morphology research on polychaete pharyngeal structures (Tzetlin & Purschke 2005) to subdivide and organize the categories. We distinguish between morphological structures used to encounter and deliver food to the mouth and the structure of the pharynx (Figure 1). We emphasize, however, that whereas knowledge of morphological form of pharynges has advanced substantially, explicit relationships between form and function remain much more rudimentary. The addition of osmotrophs (Siboglinidae) results in a corresponding additional external feeding structure of ramified or lamellar surfaces used for the uptake of dissolved energy sources and oxidants (Figure 1). Otherwise, our most substantial deviation from the feeding structures defined by F&J is a shift from distinguishing between jaws and an unarmed pharynx to distinguishing between muscular and nonmuscular pharynges. Muscular pharynges may hold jaws or teeth or may be unarmed (in some cases with considerable variability even within families, e.g., Phyllodocidae), and they are often associated with macrophagous feeding. Nonmuscular pharynges may be ciliated (e.g., Orbiniidae) or not (e.g., Capitellidae), with a somewhat speculative distinction and even less clear functional implications between using small currents as opposed to mucus to collect particles. Functional differences between axial and ventral pharynges can be inferred in some cases (e.g., the rasping or scraping buccal organs of some interstitial annelids), but in others (e.g., maldanids) this distinction is not clear even from detailed morphology, and functional importance is elusive. It does appear, however, that few macrophagous feeders have nonmuscular pharynges, and those microphagous feeders with muscular pharynges have tendencies toward omnivory.

Muscular pharynges and introverts may be armed with hard parts that vary considerably in form and function. In the decades since F&J, the terminology of these hard parts has grown ever more specialized and divergent among families. The words tooth and jaw are often used interchangeably. Here and in the Supplemental Appendix, we adopt a more generalized terminology focused on function rather than taxonomic characters, intending to convey something of the mechanics of feeding. First, we use the term jaws only for a pair of rigid structures that through the operation of integral hinges and musculature can bite or chew food, reducing it to smaller sizes or at least altering its mechanical properties. This term clearly applies to the hinged jaws of Eunicida (Paxton 2009). Nereididae and Polynoidae (scaleworms) have strongly articulated, multifunctional jaws, and we tentatively propose that these jaws use a muscle articulation joint similar to that of cephalopod beaks (Uyeno & Kier 2005) to achieve multifunctionality comparable to eunicidan jaws. This cross-phylum similarity is supported by studies in a nereidid (Uyeno 2007). Second, we use the term tooth for any hardened structure in the pharynx or on the introvert. Teeth may be present within a jaw; opposable but only weakly articulated and used primarily for grasping (not a jaw;
e.g., Glyceridae); unarticulated, opposable, and used primarily for crushing (e.g., Nephtyidae); or present as assorted, generally single or unopposed teeth or ridges used primarily for piercing, rasping, or scraping (Figure 1). Teeth can also vary greatly in shape. A fang is a large, inward-curving tooth, presumably used for grasping and holding, as in a canine tooth. Venom secretion through glycerid fangs is well established, as is its function in immobilizing prey (as reviewed in F&J), but glands are also associated with other types of teeth and jaws (e.g., Goniodae, Polynoidae, Acoetidae, and Sigalionidae) and even with toothless Euphasinidae (Wolf 1986, Ward et al. 2003), although the functions of these secretions have not been established. A stylet is a pointed, approximately cylindrical tooth much longer than its diameter, presumably used in piercing (e.g., Syllidae) and, when opposed by another stylet, in holding (e.g., Chrysopetalidae). Many sipunculans and all Sternaspidae have hardened hooks external to the pharynx and mouth that are used in scraping food. We refer to these structures as introvert hooks. Some Goniodae have pharyngeal hooks that point backward when the pharynx is everted and are thus not useful in holding prey but instead are likely used to secure purchase on the tube walls of their prey as an aid to prey extraction. The rarity of kinematic and dynamic analyses of jaw operation alongside bewilderingly detailed jaw descriptions in polychaetes is somewhat depressing.

Substantial advances have been made since F&J in linking mechano- and chemosensory abilities of planktonic organisms (Kiørboe 2008) and benthic decapods (Weissburg & Zimmer-Faust 1993, Koehl et al. 2001) with feeding biology. Understanding of sensory mechanisms that modulate feeding in polychaetes is more rudimentary, but the stimulation and depression of feeding by simple and complex chemical signals has been demonstrated in numerous taxa, including predators and deposit feeders (reviewed in Lindsay 2009). Nuchal organs serve as primary chemoreceptive organs, but other chemosensory structures also exist, including the feeding palps of spionid polychaetes, where the same chemical cues that elicit behavioral responses also activate sensory cells in the palps (Riordan & Lindsay 2002, Lindsay et al. 2004). Preliminary data suggest that nuchal organs coordinate responses to subsurface chemical signals as well (S.M. Lindsay, unpublished data). The morphologies of nuchal organs are known for many polychaetes (Purschke 1997). A general pattern of burrowers tending to have inverted, recessed, or pit-like nuchal organs is consistent with protection from abrasion and may have sensory implications. We anticipate advances in linking the morphologies of sensory appendages and nuchal organs of polychaetes to their functions, and so we here (Supplemental Appendix) include morphological data and tentatively postulate functions and positions within syndromes.

SUMMARY POINTS

1. New taxa, methods, and advances in understanding of mechanisms of feeding and locomotion necessitate a revision of polychaete feeding guilds. Family-by-family descriptions, including habitat, sensory and feeding structures, motility, and feeding, are given in the Supplemental Appendix.

2. Hydrosol filtration theory has refined guild classification among suspension feeders.

3. Deposit feeders show multiple adaptive peaks, with a small subset of species having rapid throughput of sands and a large group having gut residence times largely between 0.5 and 2 h. In addition, there is some evidence of a third peak among sipunculans and echiurans with gut residence times an order of magnitude longer, slightly basic digestive pH, and possible caching.
4. Omnivory leads to digestive conflicts that are more easily overcome by a sequential change of diet rather than simultaneous digestion of mixed diets.

5. Stable isotopic analyses have largely discredited reports of omnivory in some families (Glyceridae, Goniadidae, Lumbrineridae, and Nephtyidae) but have buttressed them in others (Nereididae, Onuphidae, and Eunicidae).

6. Small worms are an exception to the generally robust distinction between microphagy and macrophagy and are limited by small guts to feeding on rich foods of varied sizes.

FUTURE ISSUES

1. Sensory structures in general, and nuchal organs in particular, are in need of functional analysis. How they are deployed and the geometries of the fields sensed are important unknowns.

2. Nocturnal observations have been scarce but revealing and should be expanded.

3. Extraordinarily detailed descriptions of pharyngeal morphology, including teeth and jaws, contrast starkly with a dearth of studies on their mechanical function.

4. Connections between digestion, digesta solute reflux, and water balance in deposit feeders merit additional experiments.

5. The application of hydrosol filtration theory to other suspension feeders (e.g., sipunculans and Owenia) would elucidate feeding mechanisms.

6. Measurement of the variability in mechanical properties of sediments, including inelastic behavior and parameters of poroelasticity, will provide new insights into the mechanics of burrowing.

7. A more complete and stable annelid phylogeny would allow explicit testing of relationships among characters (e.g., motility, morphology, diet) that constitute syndromes.

8. Whether changes in food quality due to changes in ocean biogeochemistry will impact feeding guilds differentially remains to be determined.

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LITERATURE CITED


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