

Original papers

Gut architecture, digestive constraints and feeding ecology of deposit-feeding and carnivorous polychaetes

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Summary. We analyze gut architectures of 42 species of marine polychaetes in terms of their anatomically distinct compartments, and quantify differences among guts in terms of ratios of body volume to gut volume, relative compartmental volumes, total gut aspect ratios and compartmental aspect ratios. We use multivariate techniques to classify these polychaetes into 4 groups: carnivores with tubular guts; deposit feeders with tubular guts; deposit feeders with 3 gut compartments; and deposit feeders with 4 or 5 gut compartments. Tubular guts, morphological expressions of plug flow, are common among deposit feeders and may allow relatively rapid ingestion rates and short throughput times. Median gut volume per unit of body volume in deposit feeders (31%) is twice that of carnivores (15%) and ranges up to 83% in one deep-sea species. Deep-sea deposit feeders tend to have relatively larger and longer guts than closely-related nearshore and shelf species. Guts of a number of deep-sea deposit feeders and nearshore and shelf deposit feeders from muddy environments are relatively longer and narrower as body size increases, suggesting that digestive diffusion limitations may be important. Gut volume scales as (body volume)¹ while ingestion rate scales as (body volume)^{0.7}. If diet and the chemical kinetics of digestion do not change appreciably, throughput time and thus the extent of digestion of given dietary components therefore must increase as a deposit feeder grows. Digestive processing constraints may be most important in juveniles of species (especially those species with plug-flow guts) that are deposit feeders as adults.

Key words: Digestion – Gut morphology – Polychaetes – Deposit feeders – Carnivores

Once food is acquired digestive processing determines an animal's rate and extent of gain of energy and nutrients. Because volume limits throughput, kinematics of digestive processing are expressed statically in gut morphologies. Thus, given an understanding of gut kinematics, comparative descriptions of gut morphologies can be used to infer digestive constraints and aspects of animals' feeding ecologies. Optimal digestion theory (Penry and Jumars 1986, 1987) provides one basis for such inference. It postulates two basic models for digestive reaction kinetics, the Michaelis-Menten model for enzymatic reactions and an autocatalytic model for microbially mediated, fermentative digestion. It then shows that, in general, when enzymatic digestion is the most important component of an animal's digestive strategy its gut should function as a plug-flow reactor. When, additionally, microbially mediated fermentation is an important component of a digestive strategy, and throughput time is not long, an animal's gut should function as a mixing reactor/plug-flow reactor series (foregut fermentation) or a plug-flow reactor/mixing reactor series (hindgut fermentation). Animals using enzymatic digestion have more-or-less simple, tubular guts. In contrast the guts of animals using digestive fermentation are often characterized by expanded chambers that allow mixing and extend mean particle residence times.

Within the framework of digestion theory we analyze gut morphologies of deposit-feeding and carnivorous polychaete worms from intertidal, shallow subtidal, continental shelf and bathyal environments and infer potential constraints on digestion and foraging. We choose one major class of animals to minimize issues of between-phyllum variability. Since our goal is to model polychaete guts in terms of reactor components and infer general characteristics of digestive processes and foraging strategies, we describe guts in terms of anatomically-distinct, not necessarily histologically-distinct or embryologically-distinct, compartments. We quantify differences in guts and gut compartments among individuals and species in basic engineering terms: ratios of body volume to gut volume and relative volumes of compartments, total gut aspect ratios (total gut length to mean diameter) and compartmental aspect ratios (compartment length to mean diameter). Such descriptions allow us to examine scalings of body and gut parameters within and among species and to test explicit predictions about interrelationships among gut morphologies, digestive constraints and food resources.

Predictions

Metabolic requirements generally scale as body mass or volume to the 0.7 power (Calder 1984). Ingestion rate (mass or volume time⁻¹) for animals in general (Calder 1984) and deposit feeders in particular (Cammen 1980; Forbes and Lopez 1987) follows this pattern. If throughput time remains constant as animals increase in size, gut volume in these animals should scale as body volume to the 0.7 power. If throughput time decreases as animals increase in size, gut volume should scale as body volume to some

power less than 0.7, and if throughput time increases as animals increase in size, gut volume should scale as body volume to some power greater than 0.7. If, within a polychaete species, ingestion rate scales as body volume to the 0.7 power, but gut volume scales as a function of body volume to a power different from 0.7, ontogenetic changes in digestive kinematics must occur and may indicate ontogenetic changes in diet.

Diet quality (as characterized by energetic and nutritional composition of food and its susceptibility to digestive reactions) decreases as body size increases in herbivorous mammals, presumably because larger animals are unable to obtain sufficient quantities of higher-quality but relatively rare food items (Parra 1978; Sibly 1981). Gut volume in herbivorous mammals generally scales as body mass or volume to a power of one or greater (Calder 1984), and the resulting increase in throughput time with increasing body size may be a digestive adaptation to a lower-quality diet. Self and Jumars (1988) have shown that among shallow-water, marine polychaete species larger worms tend to be less selective for particle size, a physical parameter that, in most sediments, is inversely correlated with microbial biomass, an important food resource for deposit feeders (ZoBell 1938; Dale 1974; DeFlaun and Mayer 1983; Yamamoto and Lopez 1985). If ontogenetic changes in diet quality occur within polychaete species, we predict that changes will be in the same directions as those observed for mammals: diet quality should decrease as body volume increases, and gut volume should scale as body volume to a power greater than 0.7 – more specifically, to a power greater than or equal to 1.0. In other words, gut volume should scale at least linearly with body volume in polychaetes as it does in other animals. In the extreme, switches from strict carnivory or herbivory to deposit feeding would be expected as juveniles grow into adults. Analogous patterns of diet and body size have been observed among reptiles: small species of lizards tend to be insectivorous while larger species tend to be herbivorous, and hatchlings of herbivorous species tend to be insectivorous until they reach some critical body mass (Pough 1973).

Among-species patterns in gut morphology and diet quality parallel within-species patterns. Sibly (1981) predicted that animals eating poorer-quality diets should have larger gut volumes than similarly sized animals eating higher-quality food. This prediction is borne out in herbivorous birds and mammals (Sibly 1981; Hume 1982). If it holds among polychaetes, deposit-feeding species should have larger gut volumes than similarly sized carnivorous species. Among the deposit feeders, deep-sea species (species from a relatively food-poor environment) should have proportionally more gut volume than nearshore and shelf species (species from relatively food-rich environments). If the pattern of increased relative gut volume with decreased relative diet quality is expressed anatomically in deposit-feeding polychaetes as it is in some birds (Savory and Gentle 1976; Al-Joborae 1980), deep-sea deposit feeders should have relatively longer guts than nearshore and shelf species – a trend that already has been observed among six species of deposit-feeding tellinid bivalves (Allen and Sanders 1966).

Diffusive limitations (of enzymes to substrates or products to the gut wall; Penry and Jumars 1987) may be additional, important digestive constraints in deposit feeders. If digestion is limited by diffusion we expect such limita-

tions to be more important in individuals with greater gut diameters and in species ingesting relatively less permeable sediments. We predict ontogenetic changes in gut morphology with larger individuals having relatively longer, narrower guts; species ingesting relatively less permeable sediments should be more likely to show such changes.

Methods

Species of polychaetes known to be deposit feeders or carnivores were used in this study and were chosen to represent as many different families and, among the deposit feeders, as many different feeding guilds (Fauchald and Jumars 1979) as possible. Species were selected from three environments: intertidal and shallow subtidal areas of Puget Sound, Washington; the continental shelf off Cape Hatteras, North Carolina; and the bathyal basins of southern California (Santa Catalina Basin and San Diego Trough). Specimens from Puget Sound, Washington, were collected specifically for this study; specimens from the North Carolina shelf and the basins of southern California were obtained from archived collections of two earlier studies (Jumars 1974; Weston 1983, 1988). All worms were fixed in formalin and then preserved in alcohol. No relaxants were used because polychaetes continue to move material through their guts while in a relaxant bath (Jumars, pers. obs.), and thus relaxation before fixation would exchange one potential set of artifacts for another. Whole individuals were rehydrated in de-ionized water before dissection.

A total of 429 individuals of 42 species was dissected (Table 1). Gut volume, gut length and mean gut radius were calculated for each worm from a longitudinal cross-section of the gut (dorsal view) drawn using a dissecting microscope with a camera lucida. Gross anatomical features were used to distinguish regions of the gut (e.g., anterior, middle and posterior regions, gut caeca), and each region was drawn and analyzed separately (see Penry 1988 for species-by-species descriptions of gut anatomy). Our use of terms such as foregut, midgut and hindgut do not necessarily have embryological connotations. Pharynges of carnivorous polychaetes were not considered to be digestive structures and were not included in gut measurements. Types, locations and numbers of gut caeca (e.g., in Arenicolidae and Opheliidae) were noted but were not included in analyses. Body volumes of small worms (less than about 30 mm³) were calculated from longitudinal cross-sections. Body volumes of large worms were measured by displacement; tentacles, large branchiae (e.g., in Terebellidae) and everted pharynges were removed before measurement. Locations and volumes of sediment in guts were recorded, and sediment composition was described qualitatively (i.e., sand, muddy sand, sandy mud, mud).

The longitudinal, cross-sectional outlines of bodies and guts were digitized using a video system (Motion Analysis Corporation, Santa Rosa, California) and described as a series of x and y coordinates of pixels. Given the assumption that each worm was cylindrical in transverse cross-section, a radius, r_i , was calculated at each point, x_i , along the axis of the longitudinal cross section ($i=1$ to n , where n is the total number of pixels along the axis of the longitudinal cross-section and represents the number of transverse cross-sections into which any given longitudinal outline can be divided). The volume, v_i , of each transverse cross section

Table 1. List of species and collection locations (n=number of specimens analyzed). CA=California; NC=North Carolina; WA=Washington

Species	n	Collection location	Species	n	Collection location
Ampharetidae			Nereidae		
<i>Amphicteis scaphobranchiata</i>	16	Puget Sound, WA	<i>Ceratocephale pacifica</i>	10	San Diego Trough, CA
<i>Ampharete acutifrons</i>	10	Cape Hatteras, NC	Opheliidae		
<i>Ampharete americana</i>	10	Cape Hatteras, NC	<i>Armandia agilis</i>	9	Cape Hatteras, NC
<i>Anobothrus</i> sp. A	9	San Diego Trough, CA	<i>A. maculata</i>	10	Cape Hatteras, NC
<i>Ecamphicteis elongata</i>	6	San Diego Trough, CA	<i>Ophelina acuminata</i>	6	Puget Sound, WA
Arenicolidae			<i>Travisia foetida</i>	12	Abyssal plain off Baja, CA
<i>Abarenicola pacifica</i>	23	Puget Sound, WA	Paraonidae		
<i>A. vagabunda</i>	14	Puget Sound, WA	<i>Levinsenia oculata</i>	10	Santa Catalina Basin, CA
Capitellidae			Polynoidae		
<i>Capitella</i> cf. <i>capitata</i>	10	Puget Sound, WA	<i>Harmothoe extenuata</i>	10	Cape Hatteras, NC
Cirratulidae			Scalibregmatidae		
<i>Cirratulus cirratus</i>	10	Puget Sound, WA	<i>Scalibregma inflatum</i>	23	Puget Sound, WA
<i>Tharyx multifilis</i>	10	Puget Sound, WA	<i>S. inflatum</i>	10	Cape Hatteras, NC
<i>T. luticastellus</i>	9	San Diego Trough, CA	Spionidae		
<i>Chaetozone</i> cf. <i>setosa</i>	11	Santa Catalina Basin, CA	<i>Pseudopolydora kempii japonica</i>	10	Puget Sound, WA
Fauveliopsidae			<i>Paraprionospio pinnata</i>	10	Cape Hatteras, NC
<i>Fauveliopsis glabra</i>	10	San Diego Trough, CA	<i>Spiophanes</i> cf. <i>bombyx</i>	10	San Diego Trough, CA
Glyceridae			Sternaspidae		
<i>Glycera americana</i>	7	Cape Hatteras, NC	<i>Sternaspis fossor</i>	6	Santa Catalina Basin, CA
<i>G. dibranchiata</i>	4	Cape Hatteras, NC	<i>S. scutata</i>	13	Puget Sound, WA
Hesionidae			Terebellidae		
<i>Ophiodromus pugettensis</i>	10	Puget Sound, WA	<i>Artacamella hancocki</i>	8	San Diego Trough, CA
Maldanidae			<i>Eupolyornia heterobranchia</i>	12	Puget Sound, WA
<i>Euclymene reticulata</i>	20	Santa Catalina Basin, CA	<i>Neoamphitrite robusta</i>	6	Puget Sound, WA
Nephtyidae			<i>Polycirrus eximius</i>	10	Cape Hatteras, NC
<i>Nephtys caeca</i>	2	Puget Sound, WA	<i>Thelepus crispus</i>	9	Puget Sound, WA
<i>N. caecoides</i>	16	Puget Sound, WA	Trichobranchidae		
<i>N. picta</i>	10	Cape Hatteras, NC	<i>Terebellides stroemi</i>	12	Cape Hatteras, NC
<i>Aglaophamus paucilamellata</i>	6	San Diego Trough, CA	<i>Terebellides</i> cf. <i>stroemi</i>	10	San Diego Trough, CA

was estimated as the volume of a cylinder of radius, r_i (pixels), and height of one pixel; total volume was calculated as the sum of all volumes, v_i , for $i=1$ to n . Measurements in pixels were converted to millimeters using digitized reference scales.

The two assumptions central to the video method for determining volumes are that the body or gut axis is parallel to the x axis of the video-digitizing system and that the body or gut is circular in transverse cross section. The sensitivity of results to violations of these assumptions was tested by comparing volumes measured by displacement with volumes calculated from digitized longitudinal outlines (Penry 1988). Deviations of the body or gut axis from orientations parallel to the video axis were found to be a lesser source of error in the volume estimates than were deviations from the assumption that the body or gut is circular in transverse cross section. This second source of error was most important in computations of body volume and was mitigated by assuming an elliptical transverse cross section for species

that were obviously not circular. Major and minor axes of an elliptical cross section were defined, respectively, by the mean radii of a dorsal, longitudinal cross section and a lateral, longitudinal cross section.

Classification (Wishart 1975) and discriminant analysis (Nie et al. 1975) were used to identify and analyze groupings of individuals based on body and gut descriptors. Two divergent classification methods were used in parallel in an attempt to eliminate analytical artifacts. The dissimilarity measure in the first ("Euclidean" method) was squared Euclidean distance with Ward's method of sorting. The dissimilarity measure in the second ("Canberra" method) was the Canberra metric coefficient with the average-linkage method of sorting. To identify between-group differences, direct discriminant analysis was used when the number of variables was small ($m=4$). Stepwise discriminant analysis (minimization of Wilks lambda) was used when the number of variables was large ($m=16$) to identify more easily the subset of variables with discriminating power.

Results

Analyses of a priori species groups

Two groups, deposit feeders ($n=354$) and carnivores ($n=75$), were identified a priori (i.e., before analysis as part of the study design) and were analyzed using direct discrimination. Each individual was treated as a separate case described by four measures, body volume (B), gut volume (G), gut length (L) and mean gut radius (R). Since body volumes and gut volumes ranged over five orders of magnitude, natural log transformations of B and G were used in all multivariate analyses. The ratio B/G, body volume to gut volume, distinguishes deposit feeders from carnivores: median B/G for deposit feeders is 3 (95% C.L. of the median = 3 to 4; range = 1 to 10); median B/G for carnivores is 7.5 (95% C.L. of the median = 5 to 11; range = 4 to 21).

Among the deposit feeders some of the intraspecific variation in B/G can be attributed to variations in gut fullness (volume of sediment in the gut). In 6 of the 11 species exhibiting the greatest intraspecific variations in B/G (i.e., B/G range ≥ 4) there is a significant trend in increasing B/G with decreasing percent gut fullness calculated as the ratio of measured sediment volume to measured gut volume (Kendall's τ ; $\alpha=0.05$ for each test); the combination of probabilities for all 11 tests is also significant ($P=0.001$, Fisher's method for combining independent probabilities, Fisher 1970).


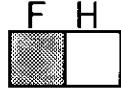
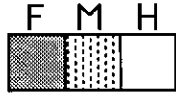



Deposit feeders can be assigned to groups based on any number of single criteria or combinations of criteria: for example, they can be grouped by functional guilds (e.g., surface or subsurface deposit feeders, motile or sedentary species), by characteristics of sediment in their guts (sand, muddy sand, sandy mud, mud), or by environments (e.g., nearshore, shelf, deep sea). Two groups of deposit feeders, surface ($n=204$) and subsurface ($n=150$), were examined using discriminant analysis (direct method: variables = $\ln(B)$, $\ln(G)$, L, R) and could not be distinguished reliably using these general body and gut parameters. Since it was not obvious, a priori, if or how these two groups should be subdivided further, classification analyses were used a posteriori to identify species groups for subsequent discriminant analyses.

A posteriori identification and analysis of species groups

In these analyses each species, described by median values of gut parameters, was treated as a separate case ($n=41$; *Nephtys caeca* and *N. caecoides* were combined as *Nephtys* spp.) to avoid weighting species in proportion to the number of individuals dissected. The set of variables was expanded to include ratios of body volume to gut volume (B/G) and total gut aspect ratio (TAR), gut compartment aspect ratios, and gut compartment volumes expressed as percentages of total gut volume. These standardized variables were used because initial results showed that species tended to cluster on the basis of absolute body and gut volumes. As few as one and as many as 5 anatomically-distinct gut compartments were identified in the species examined (Table 2). A matrix of 41 species by 16 gut parameters was generated in which each species was described by the overall gut parameters B/G and TAR and some subset of the remaining 14 gut compartment parameters.

We then identified the species that clustered together

Table 2. Anatomical definitions of the gut compartments used to classify species

Definition	Key to Figure 1
I. <i>Species with one gut compartment</i> Fore- and midgut not anatomically distinct from hindgut. Entire gut was coded as "hindgut" (H) in classification analyses.	
II. <i>Species with two gut compartments</i> Anatomically-distinct foregut (F) and hindgut (H).	
III. <i>Species with three gut compartments</i> Anatomically-distinct fore- (F), mid- (M), and hindgut (H).	
IV. <i>Species with four or five gut compartments</i>	
A. Midgut subdivided into two anatomically-distinct subregions: a nonmuscular, anterior subregion (AM) and a nonmuscular, posterior subregion analogous to the single midgut compartment (M) defined in III above.	
B. Midgut subdivided into two anatomically-distinct subregions: a nonmuscular, anterior subregion (AM) and a muscular, posterior subregion (PM).	
C. Midgut and hindgut each subdivided into two anatomically-distinct subregions: Midgut: anterior subregion (AM) and posterior, muscular subregion (PM). Hindgut: anterior subregion (AH) and posterior subregion (PH).	

consistently in *both* classification analyses (Table 3). A subset of 26 species falling into 4 groups was thus selected and examined using stepwise discriminant analysis. The biological interpretation of these results is quite clear: these 26 species are grouped on the basis of general feeding strategy (carnivores vs deposit feeders as distinguished by B/G) and gut architecture (numbers and types of gut compartments identified using gross anatomical characteristics). The four groups are (Fig. 1): (1) carnivores; (2) deposit feeders with more or less simple, tubular guts, i.e. species with only 1 or 2 anatomically-distinct gut compartments; (3) deposit feeders with 3 gut compartments, i.e. species with anatomically-distinct fore-, mid-, and hindguts; and (3) deposit feeders with 4 or 5 gut compartments, i.e. species in which the midgut and/or hindgut can be further subdivided into anatomically-distinct subregions.

We changed the groups assignments of 3 of the 26 species when the results of discriminant analysis suggested that they were misclassified initially. *Abarenicola pacifica* was reassigned to group 3; *Armandia agilis* and *Faweliopsis glabra* were both reassigned to group 2. We then assigned the remaining 15 species to the four groups on the basis of affinities in the classification analyses that were used to select the initial subset of 26 species (Table 3). These

Table 3. Four groups of species defined on the basis of similarities in feeding strategies and gut architectures, and the results of within-species regressions of gut volume, G (mm³), versus body volume, B (mm³), and mean gut diameter, D (mm), versus gut length, L (mm). The 26 species that clustered together in both classification analyses and the groups to which they were assigned initially are indicated by the numbers in parentheses (see text for explanations of subsequent reassignments). PS=Puget Sound, NC=North Carolina, and SDT=San Diego Trough. Sediment in the gut was described qualitatively: S=sand; MS=muddy sand; SM=sandy mud; M=mud. B/G is the median ratio of body volume to gut volume, and TAR is the median ratio of gut length to gut diameter. Median gut volumes are given in Fig. 1. Regressions were performed using natural log transformations of the variables. See Table 1 for the number of individuals in each sample. The regression coefficient is *m* with its standard error (SE), and the regression constant is *ln(b)* with its standard error (SE). The F ratio, with associated probability, *P*, was used to test the significance of each regression ($H_0: m=0$; $H_a: m \neq 0$). Probabilities: * = 0.01 < *P* ≤ 0.05; ** = 0.001 < *P* ≤ 0.01; *** = *P* ≤ 0.001

Species	Sedi- ment in gut	B/G	TAR	Body Volume (mm ³)		Regression of ln(G) vs ln(B): ln(G) = m[ln(B)] + ln(b)			Regression of ln(D) vs ln(L): ln(D) = m[ln(L)] + ln(b)		
				Median	Range	<i>P</i>	<i>m</i> (SE)	ln(<i>b</i>) (SE)	<i>P</i>	<i>m</i> (SE)	ln(<i>b</i>) (SE)
GROUP 1: Carnivores											
<i>Nephtys</i> spp. (1)	–	11.7	84	800	450–21000	***	1.1 (0.10)	–3.0 (0.70)	***	0.9 (0.12)	–3.9 (0.52)
<i>Glycera dibranchiata</i> (1)	–	6.5	82	65	10–170	*	0.9 (0.12)	–1.8 (0.47)	0.14	1.7 (0.71)	–7.0 (2.6)
<i>Glycera americana</i>	–	9.8	99	100	40–200	**	1.1 (0.20)	–2.5 (0.92)	0.17	0.7 (0.44)	–3.3 (1.7)
<i>Ophiodromus pugettensis</i> (2)	–	6.5	16	42	25–92	***	1.2 (0.18)	–2.8 (0.69)	***	0.5 (0.10)	–1.6 (0.25)
<i>Nephtys picta</i> (1)	–	6.6	85	12	4–50	***	0.8 (0.12)	–1.6 (0.34)	**	0.4 (0.10)	–2.5 (0.32)
<i>Harmothoe extenuata</i>	–	12.9	21	2	0.3–10	***	1.0 (0.06)	–2.8 (0.08)	***	0.8 (0.05)	–2.8 (0.08)
<i>Ceratocephale pacifica</i> (2)	–	4.7	57	3	0.2–9	***	1.0 (0.05)	–1.6 (0.07)	***	0.6 (0.04)	–3.1 (0.10)
<i>Aglaophamus paucilamellata</i> (2)	–	6.4	15	0.3	0.2–2	***	1.1 (0.08)	–1.8 (0.10)	*	0.8 (0.21)	–2.4 (0.19)
GROUP 2: Deposit feeders with simple, tubular guts											
<i>Capitella</i> cf. <i>capitata</i> (2)	M	5.5	48	20	2–300	***	1.1 (0.05)	–1.7 (0.18)	*	0.5 (0.20)	–2.2 (0.66)
<i>Euclymene reticulata</i>	M	3.8	76	7	2–40	***	1.2 (0.07)	–1.6 (0.14)	***	0.8 (0.07)	–3.7 (0.23)
<i>Armandia agilis</i> (3)	S	2.7	36	11	0.1–40	***	1.1 (0.03)	–1.4 (0.09)	***	1.0 (0.06)	–3.5 (0.16)
<i>Armandia maculata</i> (2)	S	2.9	26	2	0.1–30	***	1.1 (0.07)	–1.4 (0.13)	***	1.0 (0.09)	–3.4 (0.19)
<i>Tharyx multifilis</i> (2)	M	2.5	32	14	4–25	***	1.0 (0.07)	–0.8 (0.19)	0.52	0.2 (0.29)	–1.0 (0.86)
<i>Paraprionospio pinnata</i>	M	4.3	87	14	8–20	*	0.9 (0.35)	–1.1 (0.92)	0.06	0.5 (0.23)	–2.7 (0.80)
<i>Cirratulus cirratus</i>	M	1.9	18	2	1–14	***	1.1 (0.10)	–1.3 (0.13)	*	0.4 (0.18)	–1.9 (0.36)
<i>Pseudopolydora kempii japonica</i> (2)	S	2.4	29	4	2–8	**	1.0 (0.26)	–0.8 (0.39)	0.33	0.2 (0.18)	1.3 (0.42)
<i>Tharyx luticastellus</i>	M	1.2	40	5	3–8	***	1.0 (0.13)	–0.5 (0.23)	0.33	0.2 (0.20)	–1.4 (0.58)
<i>Chaetozone</i> cf. <i>setosa</i>	M	4.0	65	2	0.1–3	***	0.8 (0.06)	–1.4 (0.06)	***	0.6 (0.12)	–3.2 (0.30)
<i>Fauvelopsis glabra</i> (3)	M	5.1	23	0.1	0.1–3	***	1.0 (0.05)	–1.4 (0.09)	**	0.5 (0.12)	–2.3 (0.16)
<i>Spiophanes</i> cf. <i>bombyx</i>	M	4.0	31	0.2	0.2–2	***	0.7 (0.12)	–1.9 (0.16)	*	0.4 (0.14)	–2.7 (0.22)
<i>Levinsenia oculata</i> (2)	M	2.4	83	0.6	0.3–1	***	1.0 (0.14)	–0.9 (0.08)	0.52	0.1 (0.19)	–2.2 (0.51)
GROUP 3: Deposit feeders with three anatomically-distinct gut compartments											
<i>Abarenicola pacifica</i> (2)	S	2.8	43	200	10–1550	***	0.9 (0.05)	–0.7 (0.25)	***	1.0 (0.06)	–3.4 (0.25)
<i>Sternaspis scutata</i>	M	2.7	72	110	15–280	***	1.0 (0.04)	–1.2 (0.20)	***	0.5 (0.06)	–2.4 (0.26)
<i>Amphicteis scaphobranchiata</i> (3)	M	3.8	30	85	10–250	***	1.0 (0.06)	–1.3 (0.29)	***	0.8 (0.09)	–2.7 (0.33)
<i>Ophelina acuminata</i>	M	3.2	37	65	50–170	*	1.0 (0.26)	–1.5 (1.1)	*	0.8 (0.22)	–2.9 (0.75)
<i>Artacamella hancocki</i> (3)	M	2.0	30	4	1–100	***	1.0 (0.08)	–1.1 (0.19)	***	0.8 (0.08)	–3.0 (0.22)
<i>Scalibregma inflatum</i> (from PS) (3)	M	1.9	19	30	20–70	***	1.0 (0.09)	–0.7 (0.30)	**	0.5 (0.15)	–1.4 (0.44)
<i>Ampharete acutifrons</i> (3)	M	3.9	24	18	0.4–40	***	1.0 (0.05)	–1.5 (0.14)	***	0.9 (0.07)	–2.7 (0.18)
<i>Ampharete americana</i> (3)	M	4.3	24	2	1–20	***	0.9 (0.04)	–1.5 (0.05)	***	0.8 (0.16)	–2.9 (0.33)
<i>Scalibregma inflatum</i> (from NC) (3)	S	4.4	26	5	2–16	***	1.2 (0.19)	–1.9 (0.30)	0.06	0.6 (0.25)	–2.4 (0.59)
<i>Sternaspis fossor</i> (2)	M	3.8	142	6	4–12	*	0.7 (0.23)	–0.8 (0.46)	*	0.6 (0.14)	–3.4 (0.49)
<i>Ecampicteis elongata</i> (3)	M	3.2	45	4	1–6	**	0.8 (0.13)	–0.9 (0.17)	0.08	0.5 (0.23)	–2.5 (0.60)
<i>Anobothrus</i> sp. A (3)	M	3.6	24	0.4	0.1–1	***	0.9 (0.06)	–1.3 (0.09)	**	0.3 (0.07)	–2.3 (0.11)

Table 3 (continued)

Species	Sedi- ment in gut	B/G	TAR	Body Volume (mm ³)		Regression of ln(G) vs ln(B): ln(G) = m[ln(B)] + ln(b)			Regression of ln(D) vs ln(L): ln(D) = m[ln(L)] + ln(b)		
				Median	Range	P	m (SE)	ln(b) (SE)	P	m (SE)	ln(b) (SE)
GROUP 4: Deposit feeders with four or five anatomically-distinct gut compartments											
<i>Neoamphitrite robusta</i> (4)	M	4.4	65	22000	15000–24000	*	0.6 (0.23)	2.2 (2.3)	0.99	0.01 (0.46)	1.5 (2.6)
<i>Abarenicola vagabunda</i>	S	3.1	35	5000	2000–20000	***	1.0 (0.06)	−1.4 (0.53)	***	1.0 (0.09)	−3.2 (0.42)
<i>Thelepus crispus</i>	SM	3.9	40	4900	3500–5600	**	0.9 (0.27)	−0.9 (2.3)	0.94	−0.04 (0.45)	1.4 (2.2)
<i>Travista foetida</i>	M	2.4	23	870	4–4000	***	1.0 (0.02)	−1.3 (0.15)	***	0.9 (0.11)	−2.7 (0.44)
<i>Eupolymnia heterobranchia</i> (4)	S	3.3	28	780	400–2200	***	1.0 (0.10)	−1.3 (0.68)	**	0.6 (0.14)	−1.7 (0.58)
<i>Terebellides cf. stroemi</i> (SDT) (4)	M	2.8	44	2	0.3–70	***	1.1 (0.07)	−1.2 (0.15)	***	0.8 (0.14)	−3.3 (0.38)
<i>Polycirrus eximius</i>	MS	3.0	32	7	1–38	***	1.0 (0.05)	−1.0 (0.12)	***	1.1 (0.16)	−4.0 (0.44)
<i>Terebellides stroemi</i> (from NC)	MS	3.7	31	3	1–12	***	0.9 (0.04)	−1.2 (0.06)	***	0.8 (0.15)	−2.8 (0.33)

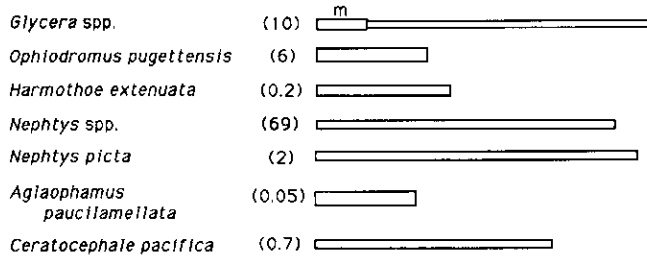
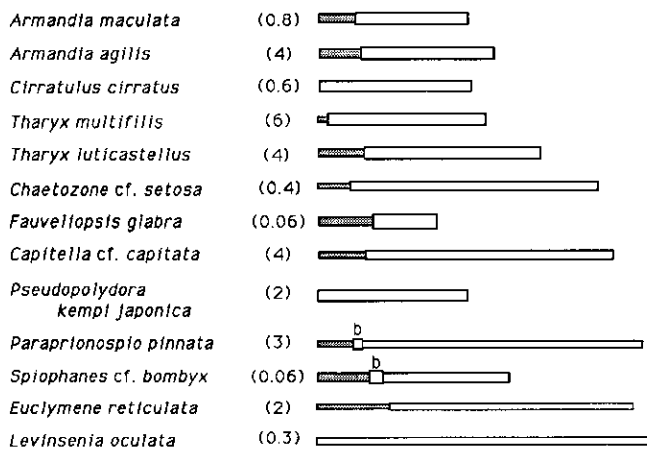
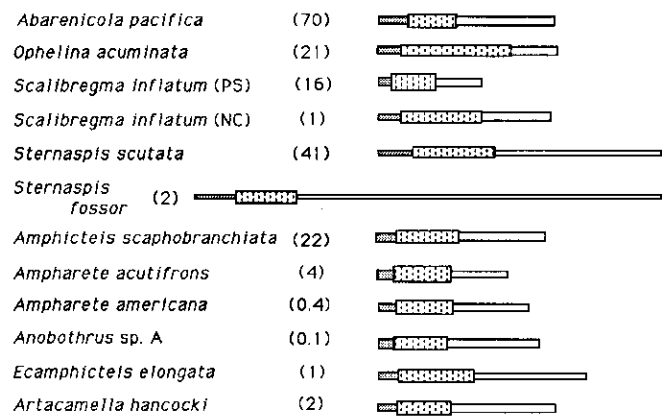
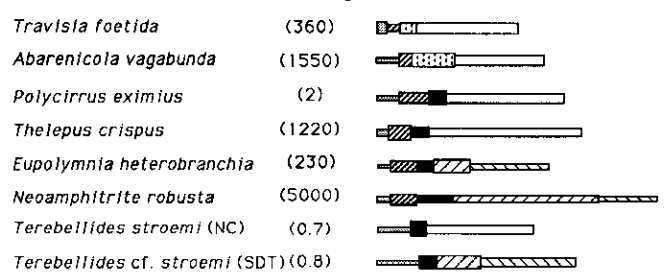
Carnivores**Deposit feeders with simple, tubular guts****Deposit feeders with 3 gut compartments****Deposit feeders with 4 or 5 gut compartments**

Fig. 1. Gut schematic showing anatomical compartmentalization. To facilitate visual comparisons of relative gut and compartmental lengths and diameters these gut schematics are normalized to gut volumes. Median gut volumes (mm³) are given in parentheses to provide absolute size references. Relative diameters are exaggerated by a factor of 2, i.e. the ratio of the vertical (gut diameter) scale to the horizontal (gut length) scale is 2:1. See Table 2 for definitions of gut compartments and a key to symbols. *Glycera* spp. = *G. dibranchiata* and *G. americana*; *Nephtys* spp. = *N. caecoides* and *N. caeca*. m = thick-walled, muscular region immediately posterior to the pharyngeal sheath in *Glycera* spp. b = muscular bulb seen in 2 of the 3 spionids examined. PS = Puget Sound, Washington; NC = North Carolina; SDT = San Diego Trough, California

final 4 groups ($n=41$ species) were examined using stepwise discriminant analysis (Table 4).

For 4 species the final group assignments determined using classification differed from the group assignments that we would have predicted based on our knowledge of their feeding strategies and gut morphologies. The carni-

vores, *Aglaophamus paucilamellata*, *Ceratocephale pacifica*, and *Ophiodromus pugettensis*, were assigned to group 2 when we would have predicted that they would be assigned to group 1, and the deposit feeder, *Sternaspis fossor*, was assigned to group 2 when we would have predicted it would be assigned to group 3. We thus ran the discriminant analy-

Table 4. Results of the discriminant analysis of 41 species assigned to four groups: carnivores (group 1), deposit feeders with tubular guts (group 2), deposit feeders with three gut compartments (group 3), and deposit feeders with four or five gut compartments (group 4). See Table 2 for definitions of gut compartments and Table 3 for the species in each group. The discriminant functions classify correctly 100% of the species

	Discriminant function			
	I	II	III	
A. Discriminating power of the variables				
Wilks lambda		0.0008	0.020	0.261
Chi-square probability		≤0.0001	≤0.0001	≤0.0001
B. Discriminant functions				
Eigenvalue	25	12	2.8	
Discriminating variables and coefficients				
Ratio of body volume to gut volume	-0.29	-0.07	0.87	
Total gut aspect ratio (TAR)	0.26	-0.45	0.25	
Aspect ratio of foregut (F)	0.13	0.42	-0.62	
Aspect ratio of anterior subregion of midgut (AM)	0.85	1.32	0.24	
Aspect ratio of posterior subregion of midgut (PM)	-0.21	0.70	-0.30	
Volume of foregut (F)	0.04	-0.68	-0.34	
Volume of midgut (M)	1.32	0.12	0.22	
Volume of anterior subregion of midgut (AM)	-0.58	0.47	0.02	
Volume of posterior subregion of midgut (PM)	0.85	1.23	0.40	
Volume of posterior subregion of hindgut (PH)	0.44	0.43	0.35	
C. Group means				
Discriminating variables				
Ratio of body volume to gut volume	8.1	3.3	3.3	3.3
Total gut aspect ratio (TAR)	57.4	45.7	43.0	37.2
Aspect ratio of foregut (F)	0	9.0	6.8	7.8
Aspect ratio of anterior subregion of midgut (AM)	0	0	0	0.6
Aspect ratio of posterior subregion of midgut (PM)	0	0.3*	0	2.8
Volume of foregut (F)	0	8.2	7.6	4.5
Volume of midgut (M)	0	0	61.2	16.8
Volume of anterior subregion of midgut (AM)	0	0	0	2.5
Volume of posterior subregion of midgut (PM)	0	1.0*	0	12.0
Volume of posterior subregion of hindgut (PH)	0	0	0	9.5

* The presence of small, muscular gut bulbs in 2 spionids, *Paraprionospio pinnata* and *Spiophanes cf. bombyx* (see Fig. 1), results in these non-zero values

sis twice, once using the classification assignments for these 4 species and once using our predicted assignments. The results were essentially identical. One additional discriminating variable, the volume of the anterior subregion of the midgut identified in worms in group 4 (see Table 2), was identified when the predicted assignments were used, but in both analyses all 41 species were classified correctly

Table 5. Comparisons of ratios of body volume to gut volume (B/G) and median standard gut lengths (SL): deep-sea species versus nearshore and shelf species

H₀: B/G's of deep-sea species ≥ B/G's of nearshore and shelf species.

H_a: B/G's of deep-sea species < B/G's of nearshore and shelf species.

H₀: SL's of deep-sea species ≤ SL's of nearshore and shelf species.

H_a: SL's of deep-sea species > SL's of nearshore and shelf species.

Species	B/G	Pairwise comparisons	SL	Pairwise comparisons
Deposit feeders with tubular guts				
Cirratulidae				
Deep sea				
<i>Tharyx luticastellus</i>	1.2	-, -	64	+, +
<i>Chaetozone cf. setosa</i>	4.0	+, +	84	+, +
Nearshore				
<i>Tharyx multifilis</i>	2.5		49	
<i>Cirratulus cirratus</i>	1.9		45	
Spionidae				
Deep sea				
<i>Spiophanes cf. bombyx</i>	4.0	+, -	58	+, -
Nearshore and shelf				
<i>Pseudopolydora kempji japonica</i>	2.4		45	
<i>Paraprionospio pinnata</i>	4.3		97	
Deposit feeders with three gut compartments				
Ampharetidae and Terebellidae				
Deep sea				
<i>Anobothrus sp. A</i>	3.6	-, -, -	49	-, +, +
<i>Ecampichteis elongata</i>	3.2	-, -, -	65	+, +, +
<i>Artacamella hancocki</i>	2.0	-, -, -	54	+, +, +
Nearshore and shelf				
<i>Amphichteis scaphobranchiata</i>	3.8		51	
<i>Ampharete acutifrons</i>	3.9		39	
<i>Ampharete americana</i>	4.3		46	
Sternaspidae				
Deep sea				
<i>Sternaspis fossor</i>	3.8	+	149	+
Nearshore				
<i>Sternaspis scutata</i>	2.7		91	
Deposit feeders with four or five gut compartments				
Terebellidae and Trichobranchidae				
Deep sea				
<i>Terebellides cf. stroemi</i>	2.8	-, -, -, -, -	58	+, -, -, +, +
Nearshore and shelf				
<i>Eupolymnia heterobranchia</i>	3.3		51	
<i>Neoamphitrite robusta</i>	4.4		85	
<i>Thelepus crispus</i>	3.9		61	
<i>Polycirrus eximius</i>	3.0		55	
<i>Terebellides stroemi</i> (NC)	3.7		31	
Binomial Test	17(-), 4(+)		17(+), 4(-)	
	<i>P</i> = 0.025		<i>P</i> = 0.025	

by the discriminant functions. Since they make more sense to us biologically, we have chosen to present in Table 4 the results obtained when our predicted assignments for these four species are used.

Interspecific patterns in body and gut parameters

We expected that deep-sea deposit feeders would have proportionally larger guts and relatively longer guts (i.e., smaller B/G's and greater standard gut lengths, a relative measure of gut length scaled to a constant body volume to eliminate differences in body size) than nearshore or shelf deposit feeders. Tests of this hypothesis must be limited to comparisons of closely-related taxa within groups defined on the basis of similarities in gut architecture. Comparisons thus are possible among the cirratulids, spionids, sternaspids, the ampharetids and terebellids in group 3, and the terebellids and trichobranchids in group 4, but not, for example, among the opheliids because the 4 species fall into three different gut-architecture groups. Median values of B/G and standard gut length were used for each species (Table 5). These comparisons suggest that the deep-sea species do tend to have proportionally larger guts and relatively longer guts than nearshore or shelf species.

Intraspecific patterns in body and gut parameters

Morphometric relationships between body volume and gut volume and between mean gut diameter and total gut length were examined for each species using parametric regression with natural log transformations of the variables (Nie et al. 1975). Body volume and gut length were chosen as the independent variables since they could be estimated with less error than gut volume and mean gut diameter. Regressions of the natural log of gut volume versus the natural log of body volume ($\ln G = m(\ln B) + \ln(b)$, where m is the regression coefficient, and $\ln(b)$ is the regression constant) are significant in all cases: Gut volume can be expressed as some positive power of body volume, $G = b B^m$, (overall F 's for regressions: $P \leq 0.05$) (Table 3). Gut volume scales as body volume to some power greater than 0.7 and not significantly different from 1.0 in 21 of 33 deposit feeders and 5 of 8 carnivores (95% C.L.'s on regression coefficients do not include 0.7 but do include 1.0). In the remaining species the 95% confidence limits on the regression coefficients include both 0.7 and 1.0, but in 4 of these species, all deposit feeders, 0.7 is the lower limit. Unlike the results of comparisons of herbivorous and carnivorous mammals (Calder 1984) there appears to be no difference in the scaling of gut volume with body volume between deposit-feeding and carnivorous polychaetes. The relatively small number of carnivorous species analyzed (8 spp.) and the relatively small numbers of individuals examined within each carnivorous species (about 10 individuals per species), however, limit our ability to detect differences in scaling if they exist.

Regressions of the natural log of mean gut diameter versus the natural log of gut length ($\ln D = m(\ln L) + \ln(b)$) are significant in 33 species: Mean gut diameter can be expressed as some positive power of gut length, $D = b L^m$ (overall F 's for regressions: $P \leq 0.05$) (Table 3). The regression coefficient, m , is less than 1.0 in 17 of these 33 species ($H_0: m \geq 1.0$, and $H_a: m < 1.0$; one-tailed t -test, $\alpha = 0.05$) indicating that total gut aspect ratio tends to increase as gut length increases in each of the 17 species. These 17 species include 4 of 8 carnivores, 7 of 12 deep-sea deposit feeders and 6 nearshore and shelf deposit feeders from muddy environments.

Discussion

Gut architecture and diet quality

All carnivorous polychaetes examined have very simple guts while deposit feeders may have more elaborate, compartmentalized guts. As we predicted, carnivorous polychaetes have significantly less gut volume per unit of body volume than do deposit-feeding polychaetes, a difference that can be attributed directly to diet quality. Diets of carnivorous polychaetes obviously contain greater proportions of high-quality foods (i.e., higher in protein, lower in ratios of carbon to nitrogen, probably more rapid digestion kinetics) than diets of deposit feeders. We suggest that polychaete species with simple, tubular guts and relatively large ratios of body volume to gut volume ($B/G > 7$) are more likely to be carnivores than deposit feeders.

Polychaetes exhibit the same general patterns in gut architecture that are seen among other animal groups. Among mammals, for example, carnivores have simple guts while herbivores have more elaborate guts, and relative gut volume decreases with increasing diet quality (Hume 1982). Gut masses in mammalian carnivores tend to be smaller than gut masses in similarly-sized ruminants (Calder 1984), and, among the ruminants, the weight of the reticulo-rumen and contents (together about 80% of the total weight of the gut and contents) decreases relative to body weight as diet quality increases (Hoppe 1977).

In the context of digestion theory we can generalize observed relationships between gut architecture and diet quality and modify Sibly's prediction of increasing relative gut volume with decreasing food quality as applied to similarly sized animals. An increase in gut volume that results in an increase in throughput time should occur when food quantity becomes limiting, i.e., an animal should increase extent of digestion (Jumars and Penry 1988). An increase in gut volume with no corresponding increase in throughput time should occur when food quality is limiting, i.e., an animal should maximize production rate of digestive products. This latter response has been observed in laboratory experiments with birds (Savory and Gentle 1979; Al-Joborae 1980).

Food quality rather than quantity is likely to be limiting for deposit feeders, and deep-sea deposit feeders are thought to have, on average, diets lower in quality than nearshore and shelf deposit feeders (Carney 1989 and references therein). They have more gut volume per unit of body volume and relatively longer guts than nearshore and shelf deposit feeders when comparisons are restricted to closely-related species within a gut-architecture group (to make it more likely that the species compared have similar digestive kinematics). Based on the arguments above and those of Dade et al. (in press), we would predict that deep-sea deposit feeders should have throughput times similar to those of nearshore and shelf species and should digest and absorb ingested organic matter to the same or relatively greater extents. As Carney (1989) emphasizes, however, measurements of the types of sedimentary organic matter utilized by deposit feeders and the pathways, rates and extents of utilization are essentially nonexistent. Deposit feeders may not be constrained by average food quality but may key in on pulses of relatively higher-quality organic matter (e.g., Khripounoff and Sibuet 1980; Smith and Baldwin 1984; Gooday 1988; Jumars et al. 1989; Lochte and Turley 1988).

Even at this relatively general level of comparison, deep-sea versus nearshore and shelf deposit feeders, the current inability to quantify food resources and digestive kinematics limits understanding.

Gut architecture and digestive and foraging constraints

Digestion theory allows us to suggest reasonable digestive kinematics and foraging constraints for deposit-feeding polychaetes with simple, tubular guts, a gut architecture that is very common among deposit feeders. We predict and have so far found that the guts of these species operate as plug-flow reactors (no axial or radial mixing of sediment particles within the gut; Penry and Jumars 1986, 1987; Penry 1989). Advantages of a simple gut for a deposit feeder are that it may be relatively inexpensive to construct and maintain, and rapid growth and reproduction may be characteristics of many of these polychaetes (e.g., *Armandia* spp., Woodin 1974; *Capitella capitata*, Grassle and Grassle 1974; *Streblospio benedicti* (Spionidae), Levin et al. 1987).

Among mammals simple guts indicate short throughput times and relatively high-quality diets (Hume 1982). A simple, tubular gut similarly may allow deposit-feeding polychaetes to process rapidly large amounts of material, but may limit these worms to exploiting relatively higher-quality foods – to feeding on surface flocs, inhabiting areas of organic enrichment, or having feeding strategies that incorporate significant degrees of carnivory or herbivory. Several species that we examined, *Capitella* cf. *capitata*, *Tharyx multifilis*, *Cirratulus cirratus*, *Chaetozone* cf. *setosa*, *Paraprionospio pinnata*, *Levinsenia oculata*, are characteristic of areas of organic enrichment or have been shown to respond rapidly to organic enrichment (Pearson and Rosenberg 1978; Fauchald and Jumars 1979; Smith 1986; Weston, pers. comm.). In fact, many “opportunistic” deposit feeders belong to three polychaete families, Capitellidae, Cirratulidae and Spionidae (Pearson and Rosenberg 1978), that are characterized by simple, tubular guts. There is evidence that carnivory may be important in the feeding strategies of at least two of the “deposit-feeding” species that we examined (*Levinsenia oculata*, Fauchald and Jumars 1979; *Euclymene reticulata*, Penry, pers. obs.). Nearly nothing is known about the ecology of two sessile, deep-sea deposit feeders with tubular guts, *Tharyx luticastellus* and *Fauveliopsis glabra*; *T. luticastellus* is a surface deposit feeder, and *F. glabra* probably is. *T. luticastellus* lives in an elaborate mud concretion that may induce local deposition on the sediment surface (Jumars 1975), and bacterial standing stocks are enhanced around those concretions that are occupied by worms (Thistle and Eckman 1990). It is further distinguished as having by far the highest fraction of body volume occupied by gut of any polychaete we have examined so far and thus may achieve a relatively high throughput time with a relatively high throughput rate. We suspect that *Fauveliopsis* will be found to have an unusual feeding ecology, perhaps supplementing its apparent sediment diet with richer foods.

The potential limitations imposed by relatively short throughput times and the need to ingest relatively high-quality foods are not necessarily the only, or even the most important, constraints on foraging and digestion in all deposit feeders with simple, tubular guts. Our results suggest that there may be an upper limit on body size in deposit-

feeding polychaetes with such simple, tubular guts (Table 3). It may reflect general, evolutionary body size constraints resulting from selection for relatively rapid growth and reproduction, or it may reflect digestive constraints. Smaller individuals have a digestive diffusion advantage and can obtain digestive products at greater rates (Dade et al. 1990). As we have noted (Penry and Jumars 1987) small deposit feeders with simple, tubular, plug-flow guts dominate areas of organic enrichment and the relatively food-poor deep sea – environments characterized by sediments of low permeability (i.e., muds). Additional digestive limitations imposed by the permeability of ingested sediments on diffusion of enzymes and digestive products may also have constrained polychaetes that ingest mud to decrease gut diameter relative to gut length (i.e., to increase gut aspect ratio) while maintaining similar proportions of gut volume to body volume as they grow.

It is difficult to suggest general digestive constraints for deposit feeders with compartmentalized guts. Similarities in gut architecture do not necessitate similarities in digestive processes. We know, for example, that axial mixing is important in the guts of two ampharetids, *Hobsonia florida* and *Amphicteis scaphobranchiata* (Self and Jumars 1978; Penry 1989). They and other terebellimorphs (Dales 1955) have compartmentalized guts that can be modeled as mixing reactor/plug-flow reactor series (Penry 1989). *Abarenicola pacifica* and *A. vagabunda* also have compartmentalized guts, but they operate as plug-flow reactors (Penry and Jumars 1987; Plante et al. 1989). *Travisia foetida* has an elaborate and unusual gut (Penry 1988), and we suspect that microbial fermentation may be important in its digestive strategy – an hypothesis also suggested by the characteristic smell of the species that is reflected in its name. Experimental descriptions of digestive kinematics (e.g., Penry 1989) are necessary prerequisites to identification of foraging and digestive constraints among deposit feeders with compartmentalized guts.

Ontogenetic changes in gut architecture

Within-species analyses of gut parameters are less likely to be affected by our lack of knowledge of gut kinematics. In the majority of the species we examined gut volume remains a constant proportion of body volume as body volume increases. Gut volume is a linear function of body volume – rather than a power function of body volume with an exponent less than one as suggested by Forbes and Lopez (1987) for *Capitella* sp. I. They, however, inferred trends in gut volume from patterns of gut fullness instead of measuring gut volume directly. Degrees of gut fullness affect gut volume estimates since polychaete guts are very distensible, and worms with relatively less full guts do not necessarily have relatively less gut volume as Forbes and Lopez implicitly assume.

In general the scaling of throughput rate with body volume (or mass) parallels the scaling of metabolic rate with body volume (or mass). Both rates scale as power functions of body volume with exponents less than one – generally between 0.67 and 0.75 (Calder 1984). Forbes and Lopez (1987) found that egestion rate scales as body volume to the 0.70 power for *Capitella* sp. I, and in an among-species comparison of ingestion rates of deposit feeders Cammen (1980) found that ingestion rate scales as body mass to

the 0.77 power when the fraction of organic matter in the food is removed as a covariable. Since gut volume scales as body volume to a power greater than 0.7 – it, in fact, scales as body volume to a power of one – throughput time must increase as body size increases. Extent of digestion is completely determined by throughput time (Penry and Jumars 1987), and thus extent of digestion must increase with body size in deposit feeders (if diet and digestive reaction kinetics remain more or less constant).

These relationships suggest that digestive processing constraints may be more important in small individuals of deposit-feeding species than they are in large individuals. Supply-side optimization arguments applied to metabolism suggest that smaller individuals have higher weight-specific metabolic demands because they have higher weight-specific rates of metabolic gain (Dade et al., in press). The diffusion advantage of small individuals may yield greater absorptive rates of digestive products, but they may also have relatively shorter throughput times and lower digestive conversions. Thus, if digestive kinetics remain constant, small individuals require relatively high-quality food resources to achieve their relatively high weight-specific rates of metabolic gain. Hatchling and juvenile iguanas have the same digestive capacities (same B/G's) as adults, but have a mean gut residence time that is about one-half that of adults and select foods higher in protein (Troyer 1984).

We suggest that availability of adequate food resources for juveniles may be important in determining distributions of deposit-feeding species, especially those species with simple, tubular guts. Juvenile *Hobsonia florida* (Ampharetidae) appear to be highly dependent upon the availability of benthic diatoms and compete strongly for them with oligochaetes (Gallagher et al., in press). Most research on deposit feeders, however, has focused on adults, and juveniles cannot be viewed simply as smaller versions of adults. Juvenile *Capitella* sp. I, for example, have ingestion rates that are significantly higher than would be expected by extrapolating ingestion rates observed in larger worms (Forbes 1989). Theory and observation thus suggest that studies of the ecology of juveniles of species that are deposit-feeders as adults are sorely needed.

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