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THE ALLOMETRY OF DEPOSIT FEEDING IN *CAPITELLA* SPECIES I (POLYCHAETA:CAPITELLIDAE): THE ROLE OF TEMPERATURE AND PELLET WEIGHT IN THE CONTROL OF EGESTION

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ABSTRACT

This study investigates the relationships between egestion rate, body size, and environmental temperature in the opportunistic marine polychaete *Capitella* species I. Measurements were made of (1) fecal pellet weight, (2) pellet production rate, and (3) pellet standing stock within the gut of live worms. Egestion rate experiments were conducted with worms ranging in size from 0.27 mm^3 to 2.62 mm^3 (approx. 1.0–15 mm in length). Pellet production rate measurements were made at 15°, 20°, and 25°C. Individual fecal pellet weight was related to worm body volume to the 0.70 power. Fecal pellet production rate in *Capitella* sp. I was independent of body size. The number of pellets maintained on average within the guts of larger animals is at least equal to that of smaller animals. Fecal pellet production rate increased exponentially with increasing temperature between 15°C and 25°C, with an overall Q_{10} value of 2.49. Power functions relating changes in egestion rate (μg sediment h^{-1}) and size-specific egestion rate [μg dry weight sediment $(mm^3 \text{ worm})^{-1}$ h^{-1}] to body size were fit to the data. These curves show that egestion rate scales as body volume to the 0.70 power, indicating that larger *Capitella* sp. I specimens process relatively less sediment per unit body volume than smaller worms. *Capitella* sp. I individuals thus control sediment processing rate during ontogeny by reducing the relative pellet weight as they grow.

Estimates of the scaling of external surface area in *Capitella* sp. I show that surface area scales as worm size to the 0.77 power, paralleling the scaling of feeding rate to body size. Data on oxygen uptake rates at different temperatures for *Capitella* sp. I (Cammen, 1985) are re-examined in light of our results and the implications for a coherent metabolic strategy (*sensu* Newell, 1980) are discussed. We hypothesize that a physiological surface such as the external respiratory surface or the absorptive area of the gut surface may limit growth and anabolism in *Capitella* species I.

INTRODUCTION

Few studies have addressed the effects of temperature and body size on egestion rates within single species of deposit-feeding invertebrates (Hargrave, 1972; Hylleberg, 1975; Kudenov, 1982). This study was designed to measure changes in feeding rate *versus* body size at different temperatures for small, actively growing *Capitella* species I. This species has been shown to be one of a complex of sibling species, all formerly classified as *Capitella capitata*, each of which exhibits distinctive life history characteristics (Grassle and Grassle, 1976, 1977, 1978; Grassle, 1979). Throughout

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this paper we adopt the convention of referring to the worm by sibling species where it has been determined, and as *Capitella capitata* when referring to studies where the species is unknown.

Capitellid polychaetes typically occur, occasionally in great numbers, in organically enriched nearshore marine environments (*e.g.*, Grassle and Grassle, 1974; McCall, 1977; Pearson and Rosenberg, 1978; Rhoads *et al.*, 1978; Thistle, 1981). The genus *Capitella* has been termed an 'enrichment opportunist' by Pearson and Rosenberg (1978) and laboratory studies have documented that small individuals of *Capitella* sp. I can attain daily weight-specific growth rates as high as 21% (Tenore and Chesney, 1985). These characteristics make *Capitella* sp. I an ideal animal in which to study the allometry of feeding during the period of rapid growth and maturation.

Data on the allometry of feeding or egestion rate among species of deposit feeders indicates that feeding rate increases as a function of body size to a power less than one (Hargrave, 1972; Cammen, 1980). This means that larger animals will process relatively less sediment per unit weight than smaller animals. Hargrave (1972) discovered, in comparisons primarily among species of lacustrine and marine deposit feeders, that feeding rate scaled to approximately the 2/3 power of body weight. In a compilation of data encompassing 19 deposit-feeding species and spanning 3 phyla, Cammen (1980) found that organic matter ingestion was a function of body weight to the 0.74 power. These results suggest that egestion or feeding rate may be related to a physiological surface that scales to body size to approximately the 0.7 to 0.8 power (Pauly, 1981).

Studies of the allometry of egestion rate within a single species of polychaete, [the so-called 'dynamic' or ontogenetic allometry of Calder (1984)] indicate that the allometric exponent of feeding rate *versus* body size can be quite variable (Cadée, 1979; Hobson, 1967; Nichols, 1974; Kudenov, 1982; Dobbs and Scholly, 1986). These differences in the size-scaling of feeding rate may reflect differing metabolic strategies between species of infaunal polychaetes.

Several studies have measured the effect of temperature on feeding rate in polychaetes (Gordon, 1966; Cadée, 1976, 1979; Kudenov, 1982; Dobbs, 1983). Of these most were principally concerned with estimates of sediment reworking rate in the field, and the effect of temperature change was followed seasonally (Cadée, 1976, 1979; Kudenov, 1982). The effect of temperature may have been confounded with changes in food level and/or quality, worm density, and other random variables. Laboratory microcosm studies by Dobbs (1983) and Gordon (1966) have found that egestion rate varied linearly with temperature in *Clymenella torquata* and *Pectinaria gouldii*, respectively.

Polychaetes of the genus *Capitella* are often found in organic-rich environments which frequently have very low to nonexistent interstitial oxygen partial pressures (*e.g.*, Wells and Warren, 1975; Pearson and Rosenberg, 1978 and references therein). This suggests the possibility that *Capitella* species I may at times be limited energetically more by oxygen than by food supply in nature. Thus, an animal's ability to digest and absorb food would be greater than its ability to procure oxygen to efficiently metabolize food. One might also postulate an alternative hypothesis that growth and anabolism in *Capitella* sp. I are limited by food or energy availability (Tenore, 1975, 1977a, b, 1981; Tenore *et al.*, 1979; Tenore and Hanson, 1980). Under this hypothesis, at high food levels, anabolism would ultimately be limited by a surface area such as that of the gut absorptive area or the worm's ability to digest and absorb food or essential nutrients. The hypotheses of food or oxygen limitation need not be mutually exclusive, and indeed, interactions between the two may be important to animals in nature. A critical assumption of this type of analysis is that animals

are built 'reasonably,' and that the evolutionary process will tend to minimize energy expenditure where possible. For example, if *Capitella* sp. I were energetically limited during growth by the allometry of gut or respiratory surface area, then the processing of additional sediment above an amount that could be effectively digested and absorbed, or metabolized by the oxygen reaching the mitochondria, would be an added cost with no additional benefit. One might then expect natural selection to reduce this added cost of feeding as body size increases through an egestion rate that scales in proportion to the relevant physiological surface(s).

We have performed experiments which indicate that egestion rate ($\mu g\ h^{-1}$) in *Capitella* sp. I scales as body size to the 0.70 power and increases exponentially as a function of acute temperature change. Data are also reported which directly measure the size-scaling of one potentially growth-limiting surface, that of external surface area, which scales as body size to the 0.77 power. These results are then compared to studies of respiration as a function of temperature in *Capitella* sp. I and other polychaetes. In addition, we discuss the results in view of the hypothesis that a physiological surface may limit growth or net energy gain in *Capitella* species I.

Materials and Methods

Sediments

The sediment for all egestion rate experiments was obtained on 8 November 1983 from an intertidal mudflat located near the Flax Pond Marine Laboratory, Long Island, New York. The top 1–2 cm of mudflat sediment was sieved to <61 μm on a Nitex screen, thoroughly homogenized, transferred to one pint freezer containers, and frozen at −20°C. Organic content of the sediment was estimated from weight loss on ignition (475°C, 6 h) after drying (60°C, 48 h) to be approximately 10%.

Laboratory culture conditions

Small juvenile and adult *Capitella* species I individuals (obtained from Dr. K. Tenore) were used in all egestion rate experiments. The worms were maintained in mass culture in 720 cm^2 aerated plastic containers layered with 1–3 cm clean fine sand (<300 μm) at 15°C in a recirculating seawater aquarium. Animals were fed a 7 $g\ m^{-2}$ daily ration of Gerbers Mixed Cereal (Tenore, 1981). The cereal was first ground with a mortar and pestle and then stirred into the overlying culture water. Salinity in the mass culture varied between 25‰ and 35‰ . The live worms used for the determination of the number of fecal pellets per gut and the number of fecal pellets per unit animal volume had been maintained in mass culture (28‰ S, 20°C) on Flax Pond silt-clay (<61 μm) surface sediment.

Determination of body-size relationships

To determine the relation between body size and fecal pellet weight, between 200 and 800 fecal pellets (depending on size) were counted and filtered onto preweighed Nuclepore® membrane filters, rinsed with several ml 3% NH_4COOH to remove salts, and dried for 24 hours at 55°C. The filters were then weighed on a Cahn 26 microbalance to ±1 μg to measure pellet dry weight. Thus each point represents a value for several hundred individual pellets. To measure worm dry weight, preserved animals were placed on preweighed Nuclepore® filters, dried for 24 hours (55°C), and weighed to ±1 μg.

Animal volumes for egestion rate experiments (uncorrected for gut lumen) were

measured by drawing the animals with the aid of a camera lucida and assuming a two-dimensional projection of a cylinder (Self and Jumars, 1978). To estimate the number of fecal pellets per unit body volume, live worms were removed from mass culture on silt-clay sediment (20°C) and rapidly transferred to glass petri dishes (4 cm diam.) where they were relaxed in isosmotic $MgCl_2$ solution. The number of fecal pellets in each worm gut is readily determined by flattening the worm under a glass cover slip. Fecal pellets defecated during the relaxation period were added to those counted within the gut. Body volumes of relaxed animals were determined in an analogous manner to those of preserved worms using a video camera mounted on a dissecting microscope. The precision of volume measurement for both preserved and relaxed worms is within 5%. In order to compare live and preserved worms we have assumed that fixation does not alter body volume.

Measurements of the projected area of the worms used in the feeding rate experiments were made by camera lucida drawings of the preserved worms.

Feeding rate versus *temperature experiments*

The worms were removed from mass culture and transferred without food to the experimental temperature (15°, 20°, 25°C) for 24 hours prior to the start of each egestion rate experiment. Thus, the feeding rates measured at 20° and 25°C were based on acute temperature changes. Egestion rate experiments were run for either 6 (I, II, III, V) or 26 (IV) hours. The experimental salinities were 24‰ (III, IV) and 30‰ (I, II, V). Upon completion of each experiment animals were cleaned of adhering debris, fixed in a seawater solution of 20% buffered formaldehyde for 24 hours, and then transferred to 70% ETOH. All animals had a preserved body volume of between 0.27 and 2.62 mm^3. These body volumes correspond to worm lengths of approximately 1.0 to 15 mm. Feeding rate experiments (I through V) were conducted on worms placed singly in small (4 cm diameter) glassware dishes in 2–3 mm of Flax Pond silt-clay sediment. The animals were then allowed to feed undisturbed at the experimental temperature for 6 or 26 hours. None of the animals ever pelletized all of the available sediment. Feeding rate was determined by sieving (85 μm) and counting all fecal pellets defecated by an individual worm over the duration of the feeding experiment. Food density was manipulated by adding a known volume of non-nutritive diluent (clean glass beads) to sediment (1 beads:4 settled sediment, v/v). The glass beads added were in the range of particle diameters (3–85 μm) ingestible by *Capitella* sp. I of experimental size. Feeding rate was expressed as fecal pellets $animal^{-1}\ h^{-1}$.

Body size versus *feeding rate*

A power function was fit to the data to describe the relationship between individual fecal pellet weight and worm volume. Plots of feeding rate (μg sediment processed h^{-1}) and worm volume at the three experimental temperatures were made by multiplying the number of fecal pellets produced by an individual worm times the expected fecal pellet weight calculated from the relation between pellet weight and worm volume. Worm volume-specific [μg dry weight (DW) sediment $(mm^3\ worm)^{-1}\ h^{-1}$] egestion rate plots were made by dividing feeding rate ($\mu g\ h^{-1}$) by worm volume. Geometric mean (GM) regressions were used to construct all functional relationships while an ordinary predictive least-squares regression was used for the relation between preserved animal volume and dry weight (Ricker, 1973; 1984 and references therein).

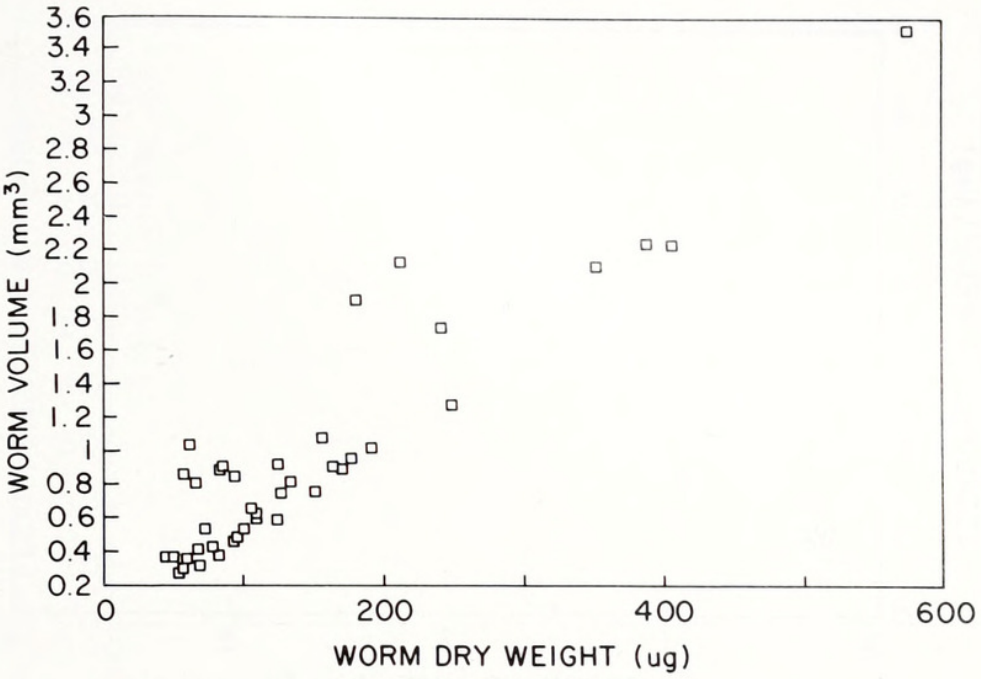

FIGURE 1. Relationship between estimated preserved volume and dry weight for *Capitella* species I. V = 0.127 + 0.006DW, r^2 = 85.1%, n = 40; where V = worm volume (mm^3) and DW = worm dry weight (μg).

RESULTS

Body-size relationships

There is a positive linear relationship between individual worm dry weight and estimated body volume (Fig. 1). Individual fecal pellet weight was allometrically related to worm volume (Fig. 2). Large worms form relatively lighter fecal pellets. The relation between projected area and worm dry weight is shown in Figure 3. GM regression of the data indicates that projected area *Capitella* sp. I scales as dry weight to the 0.77 power. The number of pellets per unit live worm volume was found to decrease exponentially as body size increased (Fig. 4A). However, the relationship between the absolute number of pellets per worm and body volume was positive but nonsignificant (r = .275, $P > 0.05$, n = 21) (Fig. 4B). Thus, the number of pellets maintained on average within the guts of larger animals is at least equal to that of smaller animals. This is true in spite of the fact that the smallest worms measured had approximately ten times more pellets per unit body volume than the largest animals (Fig. 4A). The average number of pellets within the gut over the entire range of worm body sizes was 30.2.

Feeding rate versus *temperature*

The results of egestion rate experiments I through V are given in Table I. Mean egestion rates ranged from approximately 13 pellets $animal^{-1}$ h^{-1} at 15°C to 34 pellets $animal^{-1}$ h^{-1} at 25°C. Egestion rate (pellets $animal^{-1}$ h^{-1}) did not vary with animal size (r = −.109, $P > 0.20$, n = 42). Differences in salinity or duration of the experiment had no influence on mean egestion rate (Table I). Experiments II and V were carried out under identical conditions with the exception that in experiment V the sediment was diluted with a known volume of glass beads. The worms showed no

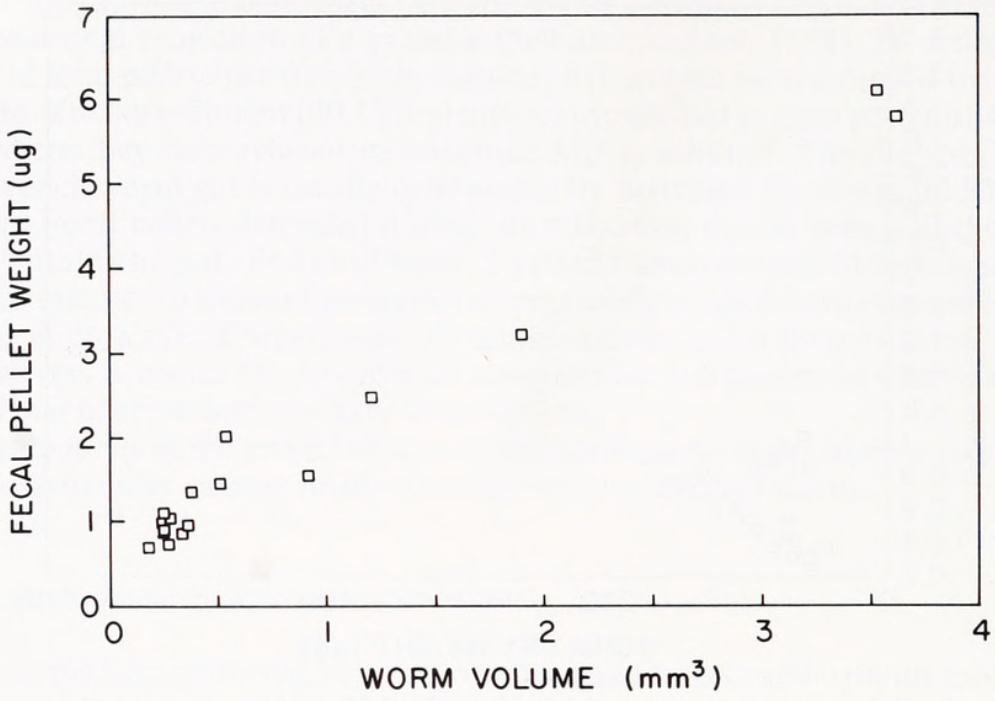

FIGURE 2. Allometric relation between individual fecal pellet weight and preserved *Capitella* sp. I volume. $PW = 2.270V^{0.701}$, $r^2 = 93.1\%$, $n = 17$; where PW = individual pellet weight (μg) and V = worm volume (mm^3).

difference in egestion rate between experiments II and V. Thus, *Capitella* sp. I did not alter its egestion rate in response to changes in food density. An exponential relationship exists between egestion rate and temperature (Fig. 5). The calculated Q_{10} values for egestion rate between 15°C and 20°C and between 20°C and 25°C are 1.52

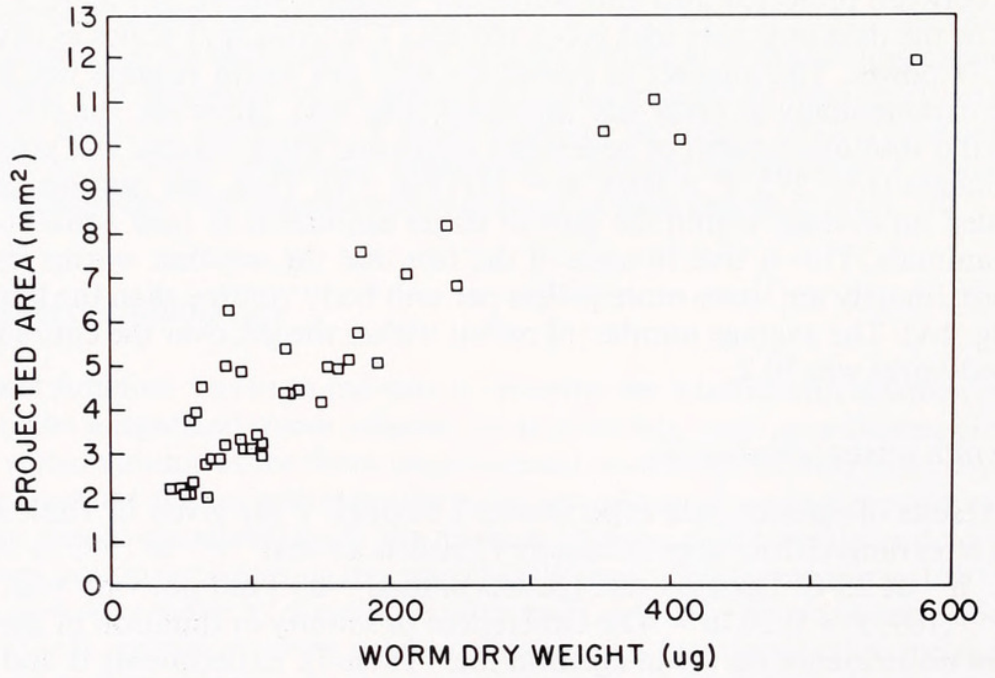

FIGURE 3. Allometric relation between worm projected area and dry weight. $A = 0.109DW^{0.772}$, $r^2 = 78.7\%$, $n = 40$; where A = projected area (mm^2) and DW = worm dry weight (μg).

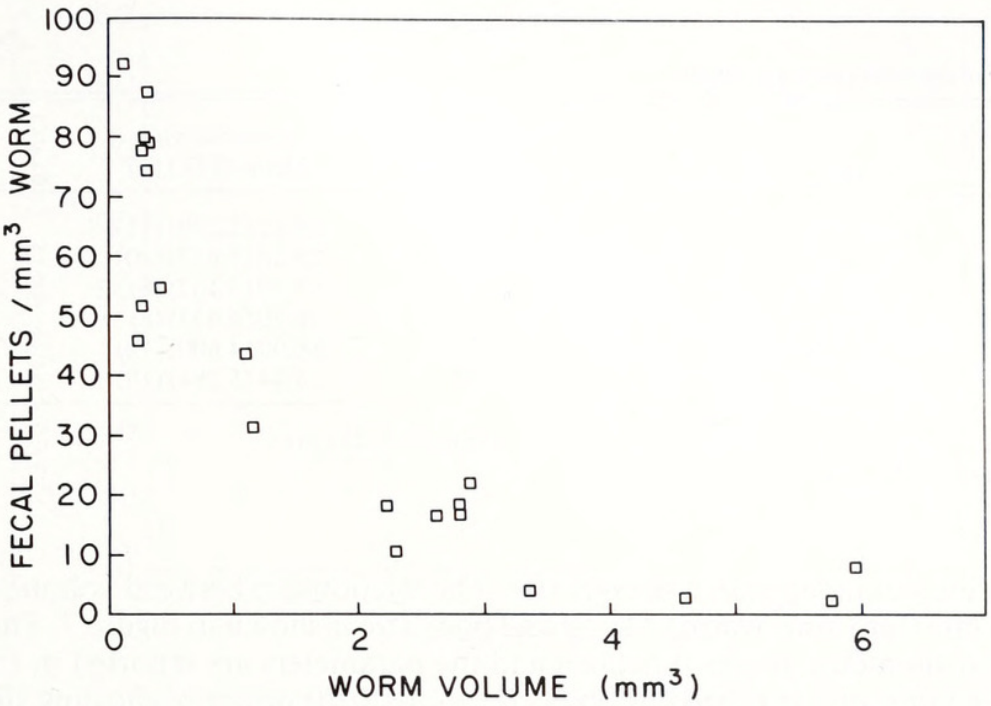

FIGURE 4a. Changes in the number of fecal pellets counted within the gut per unit worm volume of live *Capitella* species I. F = 81.48exp(−0.60V), r^2 = 86.7%, n = 21; where F = FP (mm^3 worm)$^{-1}$, V = worm volume (mm^3).

and 4.07, respectively (Fig. 5). The Q_{10} over the entire temperature range was 2.49. Thus, egestion rate ($\mu g\ h^{-1}$) could be predicted knowing only worm body size and temperature.

Body size versus *feeding rate*

Changes in egestion rate ($\mu g\ h^{-1}$) *versus* body size at the experimental temperatures are given in Figure 6. Estimates could be made in this way because pellet pro-

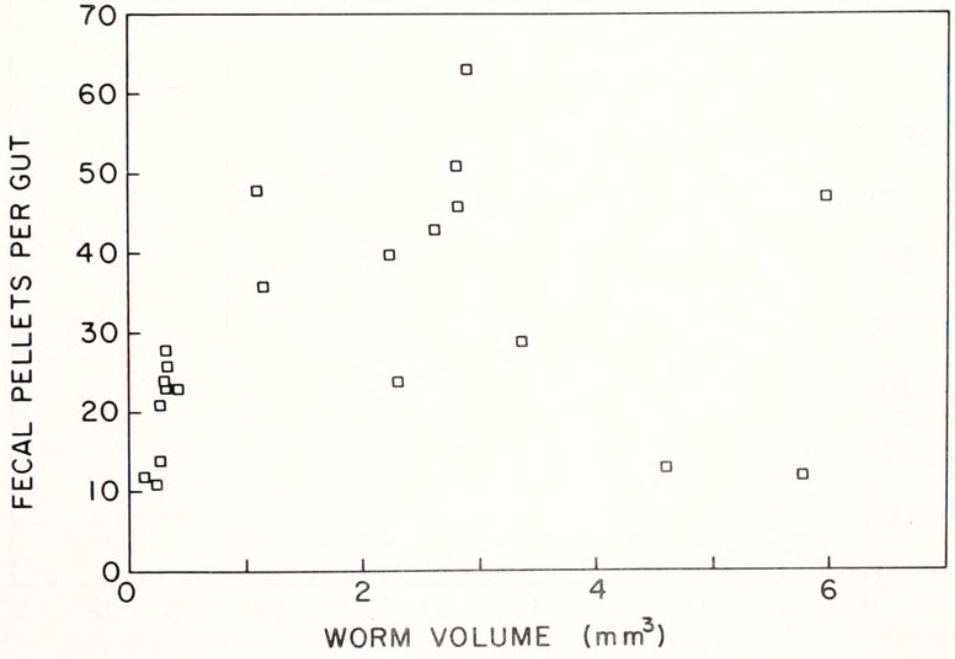

FIGURE 4b. Relationship between worm body volume and the number of fecal pellets counted within the gut (r = 0.275, $P > 0.05$, n = 21).

TABLE I

Summary of egestion rate experiments

Expt.	Date	°C	S‰	*Egestion rate* Mean (S.D.) (n)	Time (h)
I	29 Nov 83	25	30	34.12 (12.99) (11)	6
II	11 Feb 84	15	30	13.50 (7.657) (10)	6
III	27 Sept 83*	20	24	17.10 (5.167) (6)	6
IV	27 Sept 83*	20	24	16.70 (4.433) (6)	26
	27 Sept 83**	20	24	16.90 (4.600) (12)	—
V	19 Nov 83*	15	30	13.94 (5.284) (10)	6

Egestion rates are in fecal pellets per animal hour (mean) (S.D.) (n).
* Glass beads added.
** 27 Sept 83 experiments combined.

duction rate was independent of body size. The relationship between volume-specific egestion rate ([μg (mm^3 worm)$^{-1}$ h^{-1}]) and body size is shown in Figure 7. These data were fit to allometric power functions and the parameters are reported in Figures 6 and 7. Egestion rate is related to body size to the 0.70 power, indicating that large worms feed at a lower rate per unit body volume than small worms (Fig. 7). The fact that all curves for the three experimental temperatures have an identical slope when log-transformed indicates that a large animal has a greater absolute change in egestion rate with increasing temperature whereas a smaller worm has a greater relative change in egestion rate.

DISCUSSION

Body size relationships

Like many other deposit-feeding invertebrates, egestion rate in *Capitella* species I (μg DW sediment h^{-1}) is related to body size by an allometric exponent less than one

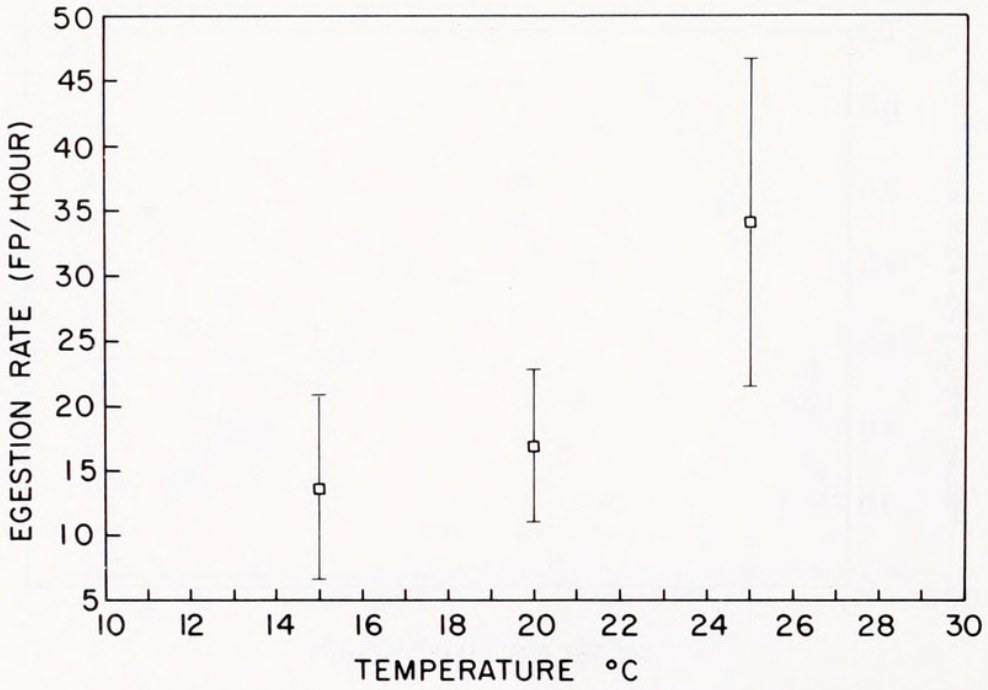

FIGURE 5. Changes in fecal pellet production rate with temperature. FP h^{-1} = 0.94exp(0.15T), r^2 = 33.1%, n = 43; where T = °C. Error bars ± 1 S.D.

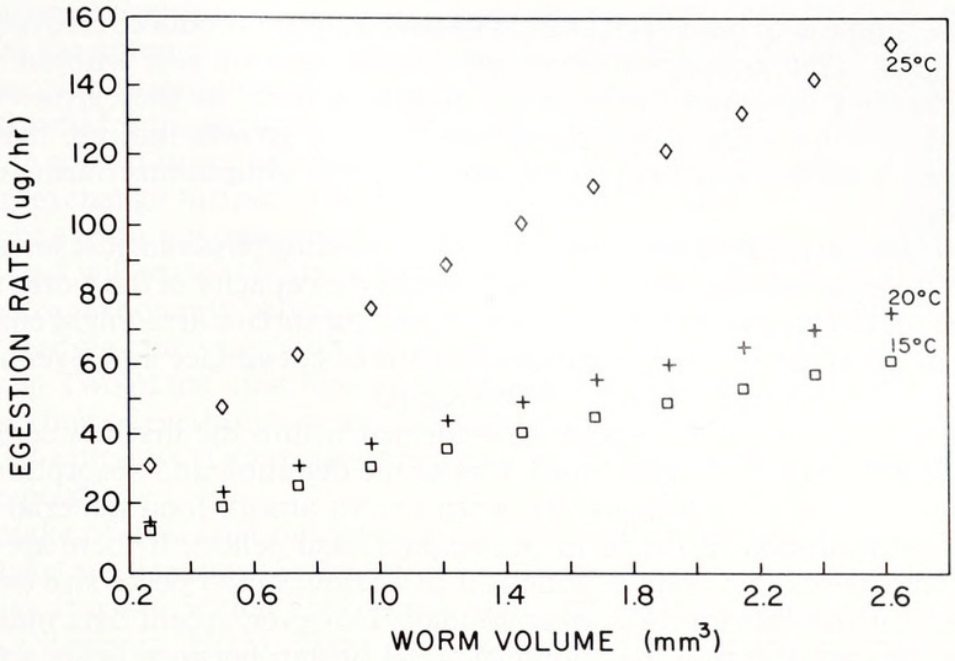

FIGURE 6. Calculated curves showing changes in estimated egestion rate *versus* worm volume at the three experimental temperatures. The parameters for the allometric functional relationships at the three experimental temperatures are a(15) = 31.14; a(20) = 38.36; a(25) = 77.45; b = 0.701. Where μg DW sediment $h^{-1} = a(T)V^b$. V = worm volume (mm^3) and a(T) = temperature dependent constant.

(Hargrave, 1972; Cammen, 1980 and references therein). The change in the specific feeding rate of *Capitella* sp. I [μg DW sediment (mm^3 worm)$^{-1}$ h^{-1}] with body size is due entirely to two observed relationships: (1) Fecal pellet production rate does not

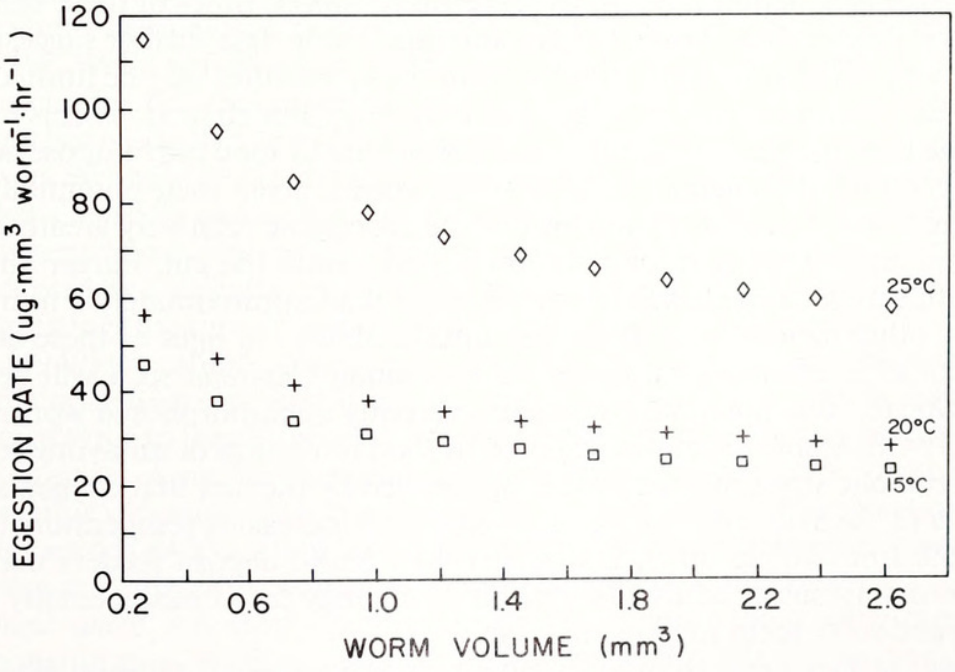

FIGURE 7. Calculated curves showing changes in estimated relative egestion rate with worm volume. The parameters for the allometric functional relationships at the three experimental temperatures are a′(15) = 31.14; a′(20) = 38.36; a′(25) = 77.45; b = −0.299. Where [μg dry weight sediment (mm^3 worm)$^{-1}h^{-1}$] = $a'(T)V^{b'}$. V = worm volume (mm^3) and a′(T) = temperature dependent constant.

change as a function of body size, and (2) smaller animals produce relatively heavier pellets (Fig. 2). This indicates that worms control egestion rate without changing pellet production rate, and therefore gut residence time, as they grow. Measurements made on individual *Capitella* species I during growth indicate that relative pellet weight is altered primarily by changes in pellet dimensions during ontogeny (Ms in prep.).

Gut surface area and volume. One potentially limiting physiological surface is that of the gut. It is possible that gut surface area limits the capacity of the worm to absorb food material. Nothing is presently known of how gut surface area might change with body size in *Capitella* sp. I. Direct measurements of gut surface area over a range of body sizes would be of great interest in this regard.

In *Capitella* species I, fecal pellets are formed within the first few setigers after ingestion of sediment (T. F. pers. obs.). Unless the digestion and absorption process occurs within the first few setigers, the worms must absorb food material from ingested sediment already in the form of compact fecal pellets. If there are physicochemical constraints (*e.g.*, rate of diffusion of enzymes etc.) pellet size (or weight) might reach an absolute limit in larger animals. However, recent data indicate that this is not the case and that the allometric relationship between pellet weight and worm body volume is maintained up to animal volumes of at least 10 mm^3 (Ms in prep.).

If the relative fullness (*i.e.*, fecal pellets/unit volume gut) of the gut of large worms is at least as great as that of small animals, then the exponential decline of relative pellet number with increasing body size (Fig. 4A) indicates that the percentage of the total worm volume occupied by the gut decreases as worms increase in size, meaning that gut volume will be related to total worm volume raised to a power less than one.

Additional data on pellet standing stocks within the gut of worms between the size of metamorphosis and approximately 1 mm^3 would be of great interest. Animals in this size range all have pellet standing stocks below the overall mean of 30 fecal pellets per gut. If this trend is real, and given the constant relationship between body size and pellet production rate, the average gut residence times of these smaller animals will be shorter than those of larger animals. These data further suggest that the growth of very small animals (less than 1 mm^3 body volume) may be limited by their ability to pack sediment into their gut and effectively absorb food. This is important because the time needed for digestion and absorption of food may impose additional constraints on the net energy intake of small worms, given their potentially shorter gut passage times. These small worms may be processing relatively greater amounts of sediment and retaining it for a shorter period within the gut. Larger animals do not show this trend, and growth in worms larger than approximately 1 mm^3 may be limited by other factors, such as oxygen uptake ability. In light of these considerations, absorption efficiency estimates for very small *Capitella* sp. I will be of great interest. Due to these potential constraints, recently metamorphosed worms may be particularly vulnerable to stresses imposed by food limitation or unfavorable temperatures. Metabolic stress may be further aggravated by the fact that oxygen solubility in seawater (35‰ S) decreases quite markedly with increasing temperature (approximately 30% from 10° to 30°C, DeJours, 1981). Small deposit feeders may not be scaled-down versions of adults. Juvenile animals may face fundamentally different problems and solve them in different ways.

External surface area. In order to obtain an estimate of external surface area in *Capitella* sp. I, we have assumed that external or respiratory exchange surface is proportional to worm projected area. In a study of the external surface of the aquatic oligochaete *Tubifex tubifex,* Kaster and Wolff (1982) found the posterior region of

the worm (last 25 segments) to be about three times as surface-rich as the same length of worm at the anterior end. Unfortunately, no attempt was made to determine the size-scaling of this relationship. However, for the present discussion of the allometric arguments, and for the estimation of the scaling of external (respiratory) surface area in *Capitella* sp. I, it is not necessary to assume that the entire surface of the worm is used as an exchange surface, only that the proportion used as an exchange surface does not change during ontogeny. Given these assumptions, external surface area in *Capitella* sp. I will scale as body volume to the 0.77 power (Fig. 3). The similarity of the allometric exponents between the feeding rate and surface area functions indicates that feeding rate is proportional to, and indeed may be constrained by, external surface area. Two of the most likely ways by which external surface area might influence the scaling of egestion rate are through (a) limitation of transepidermal uptake of dissolved nutrients (DOM, vitamins) and/or (b) limitation of oxygen uptake for aerobic respiration.

(a) Uptake of dissolved nutrients. *Capitella capitata* has been shown to possess active uptake mechanisms for the transport of dissolved primary amines from interstitial water at a rate which approaches that calculated for metabolic oxygen consumption (Stephens, 1975). The uptake of dissolved nutrients probably does not amount to a large component of the nutritional strategy of *Capitella* sp. I because the worms shrink and lose weight exponentially when maintained in seawater without sediment (Cammen, 1985; Forbes and Lopez, unpub.). However, the possibility that some essential nutrient or 'vitamin' obtainable only through transepidermal uptake in dissolved form does limit growth or net energy gain, and thereby influences the scaling of feeding rate, cannot be ruled out.

(b) Uptake of dissolved oxygen. External surface area may limit oxygen uptake and therefore anabolism. A relationship of this type may have evolved under conditions of generally high food availability and chronically low oxygen tensions. Mangum (1976) states that "the greatest deprivation . . . that has accrued from the exploitation of the soft bottom was the loss of a microenvironment that remains constant in oxygen and virtually equilibrated to the atmosphere."

The cellular hemoglobin of *C. capitata* has a very high affinity for oxygen (P_{50} = 3 mm Hg; Wells and Warren, 1975) and sulfide has been shown to be a larval settlement cue for *Capitella* species I (Cuomo, 1985). These data indicate that the genus *Capitella* is adapted to exploit organic-rich low oxygen habitats. However, experiments by Warren (1977) and studies reviewed by Pearson and Rosenberg (1978) suggest that *Capitella capitata* is not exceptionally tolerant of low oxygen or high sulfide concentrations. Interstitial oxygen partial pressures from the organic sediments occupied by *Capitella capitata* are very low (8–12 mm Hg; Wells and Warren, 1975), suggesting that tube irrigation may be important in this species.

Wells (1949) was able to simultaneously measure irrigation and proboscideal activity in the polychaete *Arenicola marina* and found an inverse relationship with a periodicity of three to four minutes. That is, animals decreased feeding activity during irrigation episodes. A similar suspension of feeding activity occurs in *Capitella* species I during burrow irrigation (T.F. pers. obs.). These data suggest that cessation of feeding during periods of low ambient O_2 levels may be one mechanism by which decreased oxygen availability could act to suppress growth or anabolism.

Coelomic space. Another potential constraint affecting the feeding rate to body size relationship may be that animals must decrease the relative amount of space occupied by the gut within the coelom as they grow, and thereby decrease the relative pellet weight as they increase in size. This could be due to a demand for coelomic space not related to energy procurement or growth, such as the requirement for the

production and development of eggs. Because sex determination in *Capitella* species I is probably a digametic system, with females as the heterogametic sex, all animals are either potential hermaphrodites or true females (Petraitis, 1985). Therefore, one would expect any constraints on total gut volume or width to operate on all animals, even functioning males, because they retain the potential to become hermaphrodites in the absence of females.

Feeding rate and temperature

The calculated overall Q_{10} value of 2.49 (Fig. 5) for the change in fecal pellet production rate with temperature from 15° to 25°C agrees well with values obtained for oxygen consumption in polychaetes (Coyer and Mangum, 1973) over similar temperature ranges. In general however, the values obtained for active and resting metabolism in polychaetes are quite variable. For example, Coyer and Mangum (1973) found Q_{10} values ranging from 1.81 to 4.56 over 12.5° to 27.5°C for the increase in resting metabolism of *Glycera dibranchiata.*

In a recent study, Cammen (1985) estimated metabolism in *Capitella* species I by a variety of methods (oxygen uptake, weight loss, metabolic carbon loss), over a wide range of body sizes. GM regressions were calculated for experiments performed at 10°, 20°, and 30°C. Allometric coefficients and exponents calculated for each regression were also given (Cammen, 1985; Table I). It is thus possible to calculate, using data from the O_2 uptake method, metabolic carbon loss for a 200 μg individual between 15° and 25°C. This calculated loss will be directly proportional to oxygen uptake. The Q_{10} value calculated from Cammen's data from 15° to 25°C is 2.82. The agreement with the change of feeding rate with temperature calculated in this study (Q_{10} = 2.49) is thus quite close. This is somewhat surprising given the fact that in one study the temperature change was acute (this study) and in the other more gradual acclimation occurred (Cammen, 1985). Increases in metabolic rate with temperature seem to be closely paralleled by concomitant increases in feeding rate. It does not appear [based on calculations made from data in Cammen (1985), for a 200 μg DW worm] that *Capitella* sp. I is able to show a compensatory response in metabolic rate with increases in temperature. That is, metabolic carbon loss increases exponentially with temperature, even in worms acclimated to experimental temperatures for 11 to 16 days. One can also calculate from Cammen's (1985) O_2 uptake data that temperature has a greater effect on the metabolic carbon loss (*i.e.,* metabolism) of smaller worms. The rate-temperature (RT) curves of metabolic carbon loss increase exponentially with increasing temperature for an animal of given size. More interesting, however, is the fact that the rate of increase (*i.e.,* the exponential coefficient of temperature, K) is greater for smaller animals. We have plotted the calculated values of K *versus* body size over a wide range of body sizes in Figure 8. *Capitella* sp. I may thus face an energetic 'bottleneck' during ontogeny due to the fact that the effect of unfavorable temperature or food conditions may have a much greater impact on the small animals. However, under conditions of abundant food, the high metabolic rate of small animals may result in the very high growth rates observed in the laboratory (21% per day for small worms; Tenore and Chesney, 1985).

The inability to adjust metabolic energy expenditure with increasing temperature, particularly evident in small worms, is indicative of an 'exploitative' metabolic strategy (Newell, 1979, 1980). Briefly, species adopting an exploitative strategy are adapted to an abundant food supply, and exhibit high rates of energy turnover and production. Energy conservation brought about by metabolic compensation under conditions of high food availability may not be the most efficient strategy for animals

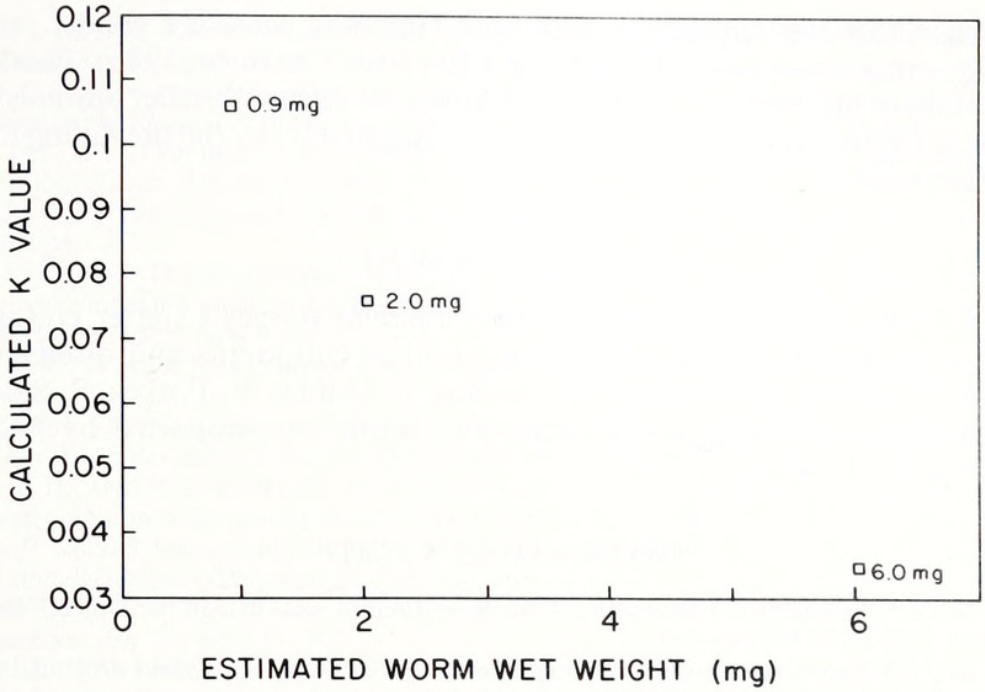

FIGURE 8. Calculated changes in the exponential coefficient K with body size. Where MR = C [exp(KT)]; MR = μg carbon released day^{-1} worm^{-1}, T = temperature °C. C = constant. Data from Cammen, 1985.

tending to grow rapidly and reproduce quickly (Newell, 1979). Animals adapted to exploiting food-rich habitats may be unable to make adjustments in metabolic systems that are designed to make the most out of environmentally favorable situations. Homeostatic changes in such metabolically important parameters as the activities of key enzyme systems, or the number of mitochondria per cell, in response to fluctuating environmental conditions may not be possible for some of the so-called opportunistic or 'weedy' species. Shumway *et al.* (1983) have found that the opportunistic bivalve *Mulinia lateralis* maintains elevated activity even under conditions of anoxia. The clams maintain a high level of metabolism and do not seem capable of adjustment in the face of low oxygen levels. *M. lateralis* appears to be adapted to high levels of food availability, and when food level declines, characteristic mass mortalities may occur (Shumway and Newell, 1984). It may be that species such as *Capitella* sp. I and *Mulinia lateralis,* by adopting physiologies that maximize energy turnover rates at high food levels, are then incapable of adjustment in response to a decrease in food or oxygen supply.

Summary

Egestion rate (μg h^{-1}) in *Capitella* species I scales as body size to a power less than one. This is due entirely to two observed relationships: (1) Fecal pellet production rate does not change as a function of body size, and (2) smaller worms produce relatively heavier pellets. We discuss several hypotheses that may explain why such relationships have evolved. For example, egestion rate may be functionally related to a limiting physiological surface such as: (1) Gut surface area, or (2) external respiratory surface area. Relative pellet size ([μg (mm^{3}worm)$^{-1}$]) also may be limited by the need for coelomic space for the development of the ovary.

Changes in measured egestion rates (fecal pellets h^{-1}) closely parallel those of met-

abolic carbon loss over similar temperatures. However, there is a greater rate of increase with temperature in smaller animals (data from Cammen, 1985). This suggests the possibility of an energetic 'bottleneck' during ontogeny. Smaller animals may be affected to a greater degree (both positively and negatively) by the prevailing food and temperature regime.

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