

## VARIABLE INGESTION RATE AND ITS ROLE IN OPTIMAL FORAGING BEHAVIOR OF MARINE DEPOSIT FEEDERS<sup>1</sup>

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**Abstract.** Tests of optimal foraging theory have focused generally on food item selection by mobile, high-trophic-level predators. Deposit-feeding invertebrates are aquatic organisms with limited mobility and hence limited ability to forage actively for food-rich patches. In addition, there is little evidence for a major role of behaviorally mediated food item choice in these animals, and growing evidence of mechanical limitations in food particle choice. Given such limited food-selection ability, varying ingestion rate in response to changes in food value is likely to be an important animal response affecting feeding energetics. A previously developed optimal foraging model predicted that ingestion rate and food value should covary positively in order to maximize net time rate of energy gain. To test this general prediction, we fed three species of deposit-feeding polychaetes artificial sediments which varied only in protein content (food value); other physical and chemical properties which might affect ingestion rate were kept constant. In support of the model, ingestion rates increased as protein levels increased.

*Key words:* deposit feeding; ingestion rate; optimal foraging theory; polychaetes.

*Feeding is such a universal and commonplace business that we are inclined to forget its importance. The primary driving force of all animals is the necessity of finding the right kind of food and enough of it.*

C. Elton

### INTRODUCTION

In recent years, ecologists interested in feeding behavior have concentrated on the factors that determine what Elton (1927) called "the right kind of food" and on how animals find "enough of it." One approach began with the theoretical work of Emlen (1966) and MacArthur and Pianka (1966), which focused on predicting the kinds of food items animals eat and on how animals exploit an environment containing patchily distributed food items. These and many subsequent theoretical and empirical studies have assumed that animals seek out and eat those food items which result in the maximum net time rate of energy gain to the forager. Because of the energy-maximization criterion and the further assumption that an animal maximizing its net time rate of energy gain will also maximize its fitness (cf. Maynard Smith 1978), this approach to predicting and explaining food and food patch choice by animals is referred to as optimal foraging theory.

Schoener (1971) and Pyke et al. (1977) reviewed feeding behavior of (mostly) terrestrial animals from the optimal foraging viewpoint, while Hughes (1980) reviewed the marine literature in this context. Most studies have dealt with mobile animals that are assumed to evaluate, by some usually unspecified mechanism, the rate of energy gain from the potential food items they encounter as they move through their en-

vironments. Based on the resultant ranking of food items by net energy yield per time spent foraging and on the abundances of the various food items, the optimally foraging animal chooses those that will maximize its net rate of energy gain or minimize its time spent foraging (Schoener 1971).

Deposit- and suspension-feeding benthic invertebrates range from those fairly limited in mobility to those which are sessile. They are thus unable to sample their environments and hence to choose among food items to the degree that highly mobile predators can. Suspension feeders depend to a large extent on water motion to supply food items, while deposit feeders utilize material supplied by lateral and vertical advection (e.g., Taghon et al. 1980) and by microbial regeneration within the sediment (e.g., Levinton and Lopez 1977, Newell 1979). Optimal foraging models that predict food item choice have been developed for planktonic suspension feeders (Lam and Frost 1976, Lehman 1976) and for deposit feeders (Taghon et al. 1978). However, experiments on particle selection by some deposit feeders show that the observed trends fit only qualitatively the optimal foraging theory predictions, and suggest that the behaviorally mediated ability of these animals to select among food items is not great (Taghon 1982). Food particle selection by some deposit feeders may be modeled most accurately as a stochastic process (Jumars et al. 1981) and explained in terms of a mechanistic model (Jumars et al. 1982). Although optimal foraging theory has concentrated on choice of food items, natural selection is also expected to operate on other components of an animal's feeding biology (Taghon 1982). Thus, for an animal that does not forage widely and whose food selection abilities may be limited, regulation of ingestive and digestive processes may be an especially important component of a strategy to optimize feeding energetics.

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A recently developed model (Taghon 1981a) predicts that, in order to maximize the net time rate of energy gain, ingestion rate will increase as the energetic value of the food increases. This prediction (and the underlying energy maximization assumption) has proven difficult to test rigorously, in part due to the unknown effects on ingestion rate of uncontrolled, confounding variables which often can be correlated with food value (see Taghon 1981a for a brief review). In addition, recent studies show that some traditional measurements of the food value of detritus and sediments, such as nitrogen content, may give ambiguous measures of nutritional value because the nitrogen accumulates in refractory, digestion-resistant compounds (Odum et al. 1979, Rice 1982). Studies in which various food parameters are manipulated individually to separate their cumulative effects on consumer feeding dynamics and energetics have been lacking.

In this paper we describe laboratory experiments that examined the effect of food value on ingestion rates in three species of marine, deposit-feeding polychaetes. The use of artificial sediments as food allowed a selected variable (viz. protein content, our measure of food value) to be modified and controlled independently of all other variables, facilitating experiments to test the model of Taghon (1981a). The results supported the model prediction that ingestion rate should increase with food value.

## MATERIALS AND METHODS

### *Preparation of artificial sediments*

Protein was bonded covalently to solid glass microbeads (13–44  $\mu\text{m}$  or 44–62  $\mu\text{m}$  diameter, 2.42 specific gravity from Cataphote Division, Ferro Corporation, Jackson, Mississippi, USA) to produce artificial sediments of known protein content. Beads were soaked in a hot solution of laboratory glassware detergent, rinsed thoroughly, boiled in one change of distilled water, rinsed with acetone, and finally rinsed with distilled water. The beads were aspirated to a damp cake and then air dried. Covalent attachment of protein to the surface of the glass beads involves a two-step process resulting in formation of a peptide bond. In the first step an amino group is attached to the glass surface using methods adapted from Brotherton et al. (1976). Specifically, 100 g of dry, clean beads was weighed into a 500-mL round-bottomed flask. Aminopropyltriethoxysilane (Aldrich Chemical Company, Milwaukee, Wisconsin) was added (100 mL of a 2% solution in distilled water), a condenser was attached to the flask, and the mixture was refluxed for 4 h. The beads were washed subsequently with several changes of distilled water, rinsed with acetone, and rinsed with more distilled water, after which they were again aspirated to a damp cake and air dried. Bovine serum albumin (BSA) (Sigma Chemical Company, St. Louis, Missouri) was the protein used in all feeding experiments because

it is readily available in a highly purified form (purified Fraction V component of Cohn et al. [1947]). The basic procedure was modified from Lappi et al. (1976) as follows: first, 25 g of beads from the first step was weighed into a flask, then 100 mL of a BSA solution in 0.1 mol/L phosphate buffer, pH 7.0, was added. To vary the amount of protein bound to the beads, and hence their food value to the animals, BSA concentrations of 0.01, 0.1, 1.0, and 5.0 mg/mL were used. The formation of peptide bonds between carboxyl groups in the protein and the amino groups on the glass surface is promoted by a carbodiimide condensing agent (Bauminger and Wilchek (1980). Enough 1-ethyl-3-(3-dimethylaminopropyl)-carbodiimide hydrochloride (Sigma Chemical Company) was added so that it produced twice the concentration, in milligrams per millilitre, of the BSA solution. The bead-protein mixture was incubated at 4°C for 1 h, during which time the flask was swirled periodically. After incubation, the beads were washed with distilled water. The beads were then soaked in one change of 1 mol/L NaCl (300 mL each) to remove noncovalently bound protein, after which they were again rinsed with distilled water and then frozen with a small volume of buffer until use. The amount of BSA actually bound to the beads was determined by a modified Lowry method (Lowry et al. 1951) as described by Brotherton et al. (1976).

### *Ingestion rate experiments*

Adults of three species of tentaculate, surface-deposit-feeding polychaetes were used: the ampharetids *Amphiteis scaphobranchiata* and *Hobsonia florida* and the spionid *Pseudopolydora kempji japonica* (whose feeding behaviors are described by Taghon 1982). *H. florida* were collected from the intertidal zone of Skagit Bay (48°21'N, 122°28'W) in northern Puget Sound, Washington, USA, and *P. kempji japonica* were collected from the intertidal of False Bay (48°29'N, 123°04'W), San Juan Island, Washington. At both of these sand flats animals were collected at low tide by sieving sediment through a 500- $\mu\text{m}$  mesh screen. *A. scaphobranchiata* were collected with a bottom dredge in Massacre Bay (48°38'N, 122°59'W), Orcas Island, Washington, from a depth of 18 m. The sediment at this site is a very cohesive mud which was sieved through a 5-mm mesh to obtain worms in their agglutinated mud tubes. All worms were transported to the Friday Harbor Laboratories and kept in aquaria under running seawater (9°–14° during these experiments). *H. florida* and *P. kempji japonica* were kept in 500- $\mu\text{m}$ -sieved sand from their collection sites, and *A. scaphobranchiata* were kept in mud, dredged up during collection, which was not otherwise treated. *P. kempji japonica* were fed glass beads that were 44–62  $\mu\text{m}$  in diameter, and *H. florida* and *A. scaphobranchiata* were fed 13–44  $\mu\text{m}$  diameter beads. These species ingest readily these sizes of beads (Taghon 1982). In a separate series of experiments, *A. scaphobranchiata* were

fed 44–62  $\mu\text{m}$  diameter beads in order to investigate the sensitivity of ingestion rate to particle size.

Four protein levels (treatments) were offered to each species. Because the polychaetes used in these experiments are surface deposit feeders, dispensing a several-millimetre-thick layer of glass beads over the natural sediment surface assured that only the experimental food was being ingested during a feeding experiment. Each treatment began at approximately the same time of day and lasted 5 h. Between treatments (periods of from 1 to 2 d for *A. scaphobranchiata* and *P. kempji japonica* and from 1 to 20 d for *H. florida*) the worms fed on natural sediment from their collection sites. We randomized the order of treatments to reduce the possibility of bias due to laboratory artifacts. A separate series of experiments was conducted using *P. kempji japonica* to test explicitly the possibility that laboratory conditions affected ingestion rates over time, as well as to monitor, as a function of protein content, the proportion of time the worms fed. In these experiments, worms were offered beads with a low, high, and again low level of BSA, respectively, in 5-h feeding experiments on three consecutive days. Worms were censused every 15 min to determine if they were feeding.

#### Data analysis

Each worm's ingestion rate (henceforth referred to as "mean  $IR$ ") was calculated as the volume of feces, composed of glass beads, that was produced during and after a feeding experiment (when the worms were again feeding on natural sediment) normalized to the duration of the experiment:

$$\text{mean } IR \left( \frac{\text{mm}^3}{\text{min}} \right) = \frac{\text{volume of feces (mm}^3\text{)}}{300 \text{ min}}. \quad (1)$$

Lengths and widths of fecal pellets were measured using a dissecting microscope with an ocular micrometer, and pellet volumes calculated assuming they were cylinders, the approximate shape of all three species' pellets.

It is useful (see Discussion) to compare an individual's mean  $IR$ , over the 5-h feeding period, with an estimate of its initial, "instantaneous" ingestion rate (henceforth referred to as "initial  $IR$ "):

$$\text{initial } IR \left( \frac{\text{mm}^3}{\text{min}} \right) = \frac{\text{gut volume (mm}^3\text{)}}{\text{gut passage time (min)}}. \quad (2)$$

The gut passage time in each experiment was calculated as the time elapsed between initial ingestion of glass beads and the first appearance of beads in a fecal pellet. Pellets composed of natural sediment egested while the animal's gut was filling with glass beads were measured. Assuming that the gut was filled initially with natural sediment before an animal began ingesting glass beads, the sum of the natural-sediment pellet volumes was used as an estimate of gut volume. The median of several (1 to 6, usually 3) gut volume estimates

made on each individual was used in Eq. 2. Gut passage times from feeding experiments described in this paper and elsewhere (Taghon 1981b) were used to calculate the initial  $IR$  for each worm in a given feeding experiment. The difference between the longer term, mean  $IR$  and the initial  $IR$  was expressed as the residual ingestion rate:

$$\text{residual } IR \left( \frac{\text{mm}^3}{\text{min}} \right) = \text{mean } IR \left( \frac{\text{mm}^3}{\text{min}} \right) - \text{initial } IR \left( \frac{\text{mm}^3}{\text{min}} \right). \quad (3)$$

Residual vs. initial ingestion rates were graphed as scatterplots, in which positive residuals indicate an accelerating feeding rate during the experiment, while negative residuals show a decelerating rate.

The data from the ingestion rate experiments were used to test the null hypothesis

$$H_0: IR_1 \geq IR_2 \geq IR_3 \geq IR_4$$

against the alternative hypothesis

$$H_1: IR_1 < IR_2 < IR_3 < IR_4,$$

where  $IR_1$  is the ingestion rate on the lowest protein level beads and  $IR_4$  is the ingestion rate on the highest protein level beads. The form of the alternative hypothesis follows from the optimal ingestion rate model. The data were analyzed using a nonparametric test of predicted order (Sarris and Wilkening 1977). This test uses more of the information contained in the original data than do other rank correlation tests (such as Spearman's rho or Kendall's concordance) because the matched nature of the data is preserved. In addition, this test is extremely conservative because all the inequalities in the alternative hypothesis are strict.

#### Natural sediment ingestion rates

Ingestion rates of *A. scaphobranchiata* and *P. kempji japonica* feeding on natural sediments were measured to compare magnitude and variability with the rates on glass beads under otherwise similar laboratory conditions. Worms which had been maintained on sediment from their collection site for several days were divided into two groups. At time 0, all fecal material around group 1 animals' tubes was removed, and a layer of new sediment added. Sizes of pellets produced during the next 5 h were measured and ingestion rates computed as above. Two days later, this procedure was repeated with the second group of animals.

## RESULTS

In all experiments, mean ingestion rate increased significantly with protein level of the beads. Table 1 gives the results for *Pseudopolydora kempji japonica*. The columns are arranged to present ingestion rates on beads with increasing protein levels, from left to right. Within each row, an individual's ingestion rates are ranked. A rank order of 1-2-3-4 from left to right is

TABLE 1. *Pseudopolydora kempii japonica* feeding experiment. Protein was applied to glass beads as bovine serum albumin. Ranking of ingestion rates (IR) of individual worms in parentheses. Highest rank indicates highest IR.  $H_0$  was tested using a nonparametric test of predicted order (Sarris and Wilkening 1977). Dash indicates the individual did not feed during the experiment.

Worm	Protein level on beads ( $\mu\text{g/g}$ of beads)			
	15 (15 Oct)	37 (18 Oct)	61 (19 Oct)	86 (16 Oct)
	Mean bead IR ( $10^{-3}$ mm <sup>3</sup> /min)			
A	16.86 (3)	13.17 (2)	10.93 (1)	20.72 (4)
B	0.85 (1)	5.57 (2)	8.62 (3)	10.23 (4)
C	5.03 (2)	3.33 (1)	12.32 (4)	7.05 (3)
D	4.60 (2)	7.48 (4)	2.58 (1)	5.59 (3)
E	1.82 (2)	5.33 (4)	1.56 (1)	5.06 (3)
F	4.51 (4)	3.27 (1)	4.28 (3)	4.07 (2)
G	1.98 (1)	6.38 (4)	2.62 (2)	5.57 (3)
H	3.04 (1)	5.10 (2)	6.68 (3)	9.00 (4)
I	3.99 (1)	...	...	7.61 (2)
J	5.70 (2)	1.89 (1)	8.00 (3)	10.23 (4)
K	4.11 (1)	7.02 (3)	4.52 (2)	11.73 (4)
L	6.80 (1)	8.08 (3)	...	7.88 (2)
M	3.17 (1)	6.16 (2)	10.78 (3)	14.05 (4)
Mean	4.80	6.06	6.63	9.14
	$H_0: IR_{15} \geq IR_{37} \geq IR_{61} \geq IR_{86}$			
	$H_1: IR_{15} < IR_{37} < IR_{61} < IR_{86}$			
	$P = .0093$			

consistent with the alternative hypothesis of increased ingestion rate on beads of higher protein content. Because there were four experiments there are 4! or 24 possible rank orderings, and the probability of observ-

TABLE 2. *Pseudopolydora kempii japonica* feeding experiment. Protein was applied to glass beads as bovine serum albumin. Ranking of ingestion rates (IR) of individual worms in parentheses. Highest rank indicates highest IR. Dash indicates the individual did not feed during the experiment.

Worm	Protein level on beads ( $\mu\text{g/g}$ of beads)				
	19 (11 Mar)	76 (12 Mar)	35 (13 Mar)	76 (12 Mar)	35 (13 Mar)
	Mean bead IR ( $10^{-3}$ mm <sup>3</sup> /min)		% time feeding		
N	2.40 (1)	4.05 (3)	3.50 (2)	20	10
O	4.16 (1)	7.32 (3)	5.22 (2)	40	20
P	6.08 (3)	5.14 (2)	2.01 (1)	40	30
Q	5.23 (2)	...	2.29 (1)	...	...
R	4.54 (1)	8.50 (3)	7.22 (2)	35	10
S	5.32 (1)	12.81 (3)	7.42 (2)	55	25
T	2.01 (2)	9.40 (3)	1.14 (1)	20	0
U	6.71 (2)	10.23 (3)	6.17 (1)	45	10
V	2.66 (2)	6.28 (3)	2.42 (1)	30	0
W	0.48 (1)	2.12 (2)	4.98 (3)	40	15
X	2.49 (2)	1.36 (1)	5.56 (3)	50	25
Y	9.76 (3)	7.52 (1)	9.05 (2)	40	45
Z	4.76 (1)	8.76 (3)	6.19 (2)	50	20
AA	4.62 (1)	10.64 (3)	9.47 (2)	15	20
Mean	4.37	7.24	5.19	37	18
	$H_0: IR_{19} \geq IR_{35} \geq IR_{76}$		$H_0: \%_{35} \geq \%_{76}$		
	$H_1: IR_{19} < IR_{35} < IR_{76}$		$H_1: \%_{35} < \%_{76}$		
	$P = .0126$		$P = .0015$		

ing the specific rank order 1-2-3-4 is therefore 1/24, assuming all rank orderings are equally probable. Of the 11 individuals that ingested beads in all four experiments, 3 (B, H, M) fit the rank order predicted by the alternative hypothesis. From the binomial theorem, the probability of observing these results by chance alone, if the null hypothesis of no effect of protein level on ingestion rate were true, is thus  $P[X \geq 3, H_0: B(p = 1/24, N = 11)] = 0.0093$  (Sarris and Wilkening 1977 as corrected by Hsu 1979). Therefore, we reject the null hypothesis and conclude that mean ingestion rate of *P. kempii japonica* increases with food value.

Table 2 shows the results of ingestion rate experiments when *P. kempii japonica* were offered beads of low, high, and again low BSA content on three consecutive days, and gives the percentage of time individual worms fed actively during two of the experiments, based on 20 censuses made during each experiment. (These worms were different individuals than those in Table 1.) Columns are arranged left to right in order of feeding, rather than order of food value as in Table 1, to highlight any possible trends in ingestion rate due to laboratory conditions. If worms were merely becoming acclimated to the laboratory environment and ingestion rate were independent of food value, we might expect ingestion rate to increase over time between treatments, leading to a rank order of 1-2-3. Only 1 of 13 individuals feeding in all experiments (W) displayed this trend, a nonsignificant result ( $P = .907$ ). On the other hand, if worms were becoming moribund, we might expect a rank order of 3-2-1, also seen for only 1 individual (P). The rank order predicted by the alternative hypothesis is 1-3-2. Six individuals (N, O, R, S, Z, and AA) gave this rank order, a result which would occur by chance alone with a probability of 0.0126. We again reject the null hypothesis in favor of the alternative. Worms spent significantly more time feeding on higher protein level beads than on low BSA-level beads (Table 2;  $P = .0015$ , Wilcoxon matched-pairs signed-ranks test [Siegel 1956]).

Of the four *Hobsonia florida* that fed in all experiments (Table 3), two (D and H) showed the 1-2-3-4 rank order for ingestion rates predicted by the alternative hypothesis, enabling the null hypothesis to be rejected at the 0.0098 probability level. The four *Ampiphteis scaphobranchiata* feeding on 13-44  $\mu\text{m}$  diameter beads in all four experiments (Table 4) showed a 1-2-3-4 rank order of ingestion rates. The null hypothesis can be rejected at the 0.000003 probability level. In experiments with the same worms feeding on 44-62  $\mu\text{m}$  diameter beads (Table 5), two of the seven worms that fed in all experiments (C and G) had a 1-2-3-4 rank order of ingestion rates, significant in the predicted direction at the 0.0317 probability level.

Ingestion rates of *A. scaphobranchiata* on 13-44  $\mu\text{m}$  diameter beads vs. 44-62  $\mu\text{m}$  diameter beads of comparable amounts of protein per unit mass (or volume)

TABLE 3. *Hobsonia florida* feeding experiment. Ranking of ingestion rates in parentheses. Symbolism as in Table 1. Dash indicates the individual did not feed during the experiment.

Worm	Protein level on beads ( $\mu\text{g/g}$ of beads)			
	31 (30 Sep)	52 (21 Oct)	123 (22 Oct)	143 (1 Oct)
	Mean bead IR ( $10^{-3} \text{ mm}^3/\text{min}$ )			
A	...	2.20 (1)	4.27 (2)	...
B	...	0.63 (1)	1.48 (2)	...
C	...	5.89 (2)	5.28 (1)	...
D	0.15 (1)	0.32 (2)	0.49 (3)	1.30 (4)
E	0.33 (3)	0.65 (4)	0.32 (2)	0.17 (1)
F	0.65 (1)	4.95 (4)	2.77 (3)	1.96 (2)
G	...	0.15 (1)	2.27 (3)	0.88 (2)
H	0.35 (1)	0.36 (2)	0.42 (3)	2.68 (4)
Mean	0.37	1.89	2.16	1.40

$H_0: IR_{31} \geq IR_{52} \geq IR_{123} \geq IR_{143}$   
 $H_1: IR_{31} < IR_{52} < IR_{123} < IR_{143}$   
 $P = .0098$

of particles were not significantly different ( $P > .05$ , Wilcoxon matched-pairs signed-ranks test).

During these experiments, gut passage times ranged from 58 min (*P. kempii japonica*), 70 min (*A. scaphobranchiata*), and 75 min (*H. florida*) to  $>5$  h in all species (in some treatments animals had not produced pellets with glass beads before the end of the feeding period). Gut passage times generally mirrored the trends in mean ingestion rates; combining all experiments, passage times  $>5$  h occurred in 38% of the worms offered the lowest protein level beads, but in only 17% of worms offered the highest protein beads.

When residual ingestion rates (Eq. 3) are compared with initial rates (Eq. 2) for *P. kempii japonica* (Fig. 1A), the residuals are biased slightly positively up to an initial IR of  $\approx 0.01 \text{ mm}^3/\text{min}$ . At higher initial IR, residuals tend to be negative. The overall correlation between the residual and initial ingestion rates is negative and statistically significant (Pearson's  $r = -0.41$ ,  $P < .001$ ), suggesting that the higher the initial feeding rate, the greater the deceleration in feeding rate over 5 h.

Fig. 1B is a similar scatterplot of the data for *H. florida*. In this case, the residuals cluster about 0 up to an initial IR of  $\approx 0.004 \text{ mm}^3/\text{min}$  and are consistently negative at greater initial IR. Again, the correlation is negative and statistically significant ( $r = -0.81$ ,  $P < .001$ ).

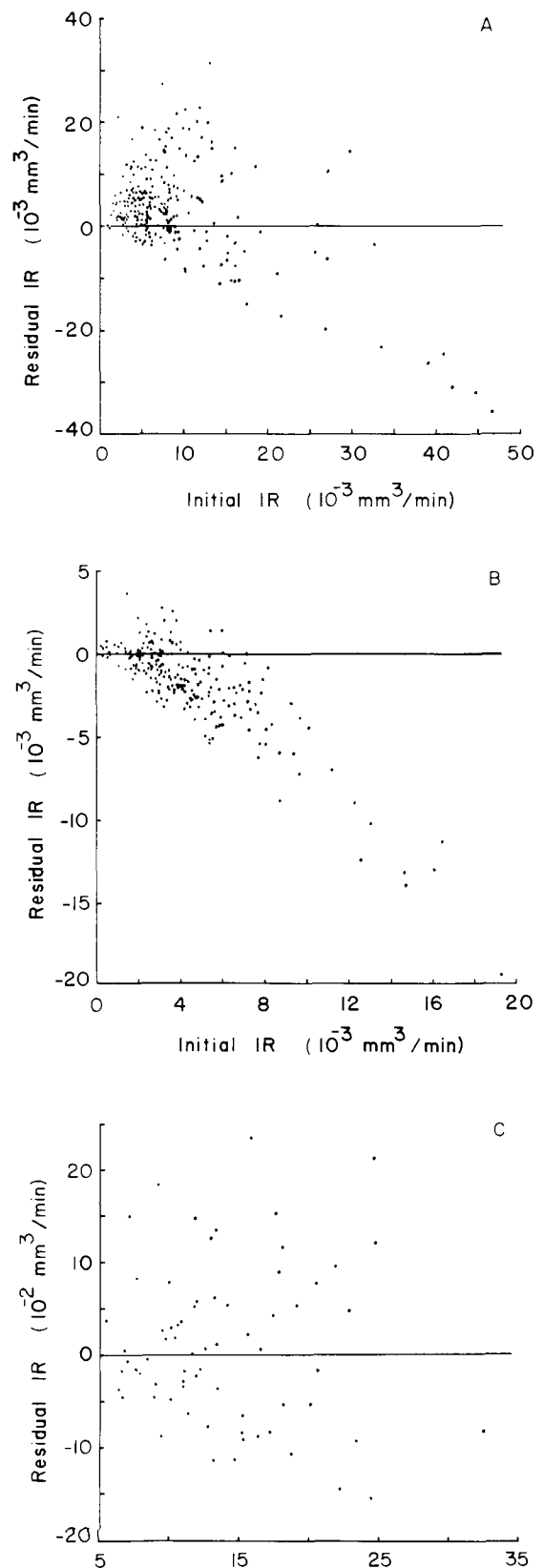


FIG. 1. Scatterplot of residual ingestion rate (Eq. 3) vs. initial ingestion rate (Eq. 2) for: (A) *Pseudopolydora kempii japonica*,  $n = 258$ ; (B) *Hobsonia florida*,  $n = 209$ ; and (C) *Amphiteis scaphobranchiata*,  $n = 69$ . Note the change of scale for *A. scaphobranchiata*. The horizontal line represents 0 residual ingestion rate; that is, no difference between mean, long-term ingestion rate and the initial ingestion rate based

TABLE 4. *Amphitecis scaphobranchiata* feeding experiment, 13–44  $\mu\text{m}$  diameter beads. Ranking of ingestion rates in parentheses. Symbolism as in Table 1. Dash indicates the individual did not feed during the experiment.

Worm	Protein level on beads ( $\mu\text{g/g}$ of beads)			
	42 (10 Sep)	55 (13 Sep)	81 (14 Sep)	119 (11 Sep)
	Mean bead IR ( $10^{-2}$ mm <sup>3</sup> /min)			
A	...	1.73 (1)	2.66 (2)	4.83 (3)
B	4.89 (1)	11.41 (2)	13.20 (3)	28.19 (4)
C	2.56 (1)	5.99 (2)	10.62 (3)	14.67 (4)
D	5.20 (1)	6.24 (2)	12.68 (3)	14.44 (4)
E	...	2.60 (2)	5.81 (3)	1.82 (1)
F	...	9.61 (2)	8.74 (1)	24.25 (3)
G	2.07 (1)	7.28 (2)	11.73 (3)	19.33 (4)
H	...	8.83 (2)	8.04 (1)	13.95 (3)
Mean	3.68	6.71	9.18	15.18
	$H_0: IR_{42} \geq IR_{55} \geq IR_{81} \geq IR_{119}$			
	$H_1: IR_{42} < IR_{55} < IR_{81} < IR_{119}$			
	$P = 0.000003014$			

For *A. scaphobranchiata*, the residuals remain distributed fairly evenly about 0 over the entire range of initial IR (Fig. 1C). This visual impression is supported by the nonsignificant correlation between the residual and initial ingestion rates ( $r = -0.10$ ,  $P = .39$ ).

The procedure used to calculate initial IR accounts for much of the scatter in Fig. 1. In these animals, a single fecal ejection represents about one-third of the gut contents by volume. There is thus a natural variation in the estimate of gut passage time used to calculate the initial IR, because material is held in the posterior-most part of the intestine until enough accumulates to form a pellet. (No mixing of beads and natural sediments was observed; discrete boundaries occurred within fecal pellets.) The method for estimating gut volumes for Eq. 2 assumes that the gut is always full, an obvious simplification in light of the actual pellet production process. Although usually at

TABLE 5. *Amphitecis scaphobranchiata* feeding experiment, 44–62  $\mu\text{m}$  diameter beads. Ranking of ingestion rates in parentheses. Symbolism as in Table 1.

Worm	Protein level on beads ( $\mu\text{g/g}$ of beads)			
	32 (8 Oct)	48 (12 Oct)	53 (11 Oct)	127 (10 Oct)
	Mean IR ( $10^{-2}$ mm <sup>3</sup> /min)			
A	4.29 (2)	5.78 (3)	0.60 (1)	7.51 (4)
B	12.04 (3)	8.58 (1)	9.78 (2)	17.07 (4)
C	9.25 (1)	13.76 (2)	14.33 (3)	17.84 (4)
D	4.95 (2)	12.18 (3)	3.26 (1)	19.43 (4)
F	5.52 (1)	7.47 (2)	7.92 (4)	7.66 (3)
G	7.90 (1)	15.94 (2)	16.99 (3)	25.52 (4)
H	2.25 (1)	17.74 (4)	6.70 (3)	5.20 (2)
Mean	6.60	11.64	8.51	14.32
	$H_0: IR_{32} \geq IR_{48} \geq IR_{53} \geq IR_{127}$			
	$H_1: IR_{32} < IR_{48} < IR_{53} < IR_{127}$			
	$P = .0317$			

least several estimates of gut volume were made on each individual, the coefficient of variation was 10.9% for the most precise data for a *P. kempi japonica* individual, 12.8% for *A. scaphobranchiata*, and 21.5% for *H. florida*. These sources of imprecision are due to modeling a more or less continuous process (ingestion) by a discrete process (egestion). Nonetheless, no consistent bias (inaccuracy) would be expected.

The results of the natural-sediment ingestion rate experiments are given in Table 6.

## DISCUSSION

Three species of deposit-feeding polychaetes increased their ingestion rates as food protein content increased. These results follow the predictions of a simple ingestion rate model based on optimal foraging theory assumptions (Taghon 1981a). The results, over the range of protein levels used, do not support the null hypothesis of no effect of food value on ingestion rate or of an inverse relation between food value and ingestion rate. Before considering these results and their implications for deposit-feeding strategies, some discussion of the experimental protocol is desirable.

Energy budget calculations or growth rate determinations were not the goal of these experiments; rather, we sought to test as unambiguously and directly as possible whether animals would respond to food value in the predicted manner. We chose protein content as the measure of food value for two reasons: techniques were available both for preparing monospecific-protein-labeled sediments and for accurately quantifying their protein content, and protein or protein-nitrogen has been strongly implicated as a limiting substance for detritivores (Hylleberg-Kristensen 1972, Tenore 1977, Martin et al. 1980, 1981). Therefore, it seemed

TABLE 6. Ingestion rates (IR) of *Pseudopolydora kempi japonica* and *Amphitecis scaphobranchiata* individuals feeding on natural sediment. Measurements on group 2 animals taken 2 d after group 1 measurements.  $\bar{X}$  = mean, cv = coefficient of variation.

	<i>P. kempi japonica</i> IR ( $10^{-3}$ mm <sup>3</sup> /min)		<i>A. scaphobranchiata</i> IR ( $10^{-2}$ mm <sup>3</sup> /min)	
	Group 1	Group 2	Group 1	Group 2
		5.46	4.26	10.43
	6.71	9.69	11.02	19.59
	8.90	11.00	11.48	21.18
	10.20	16.52	24.35	24.69
	10.94	18.41		39.23
	13.01	21.56		
	13.56	22.77		
	14.97	22.92		
	15.78	26.09		
	15.91	26.59		
	15.95	30.68		
	24.04	38.07		
$\bar{X}$	12.95	20.71	$\bar{X}$	14.32
cv	39%	46%	cv	47%
				34%

reasonable that deposit feeders might respond most readily to variations in sediment protein content. The time animals were exposed to the experimental diet was kept purposely relatively short in order to allow continuous, direct measurement of ingestion rates.

In these experiments, protein levels ranged between 0.0014–0.014% on a dry mass basis. Nitrogen ranged from 0.0002–0.002%, since BSA has a 16.1% nitrogen content (Brand 1946). These values are not atypical when compared to the organic matter levels found in some natural sediments (e.g., Hartwig 1976, 0.06–0.2% carbon; Hannan 1980, 0.04–0.2% carbon; Ernst 1977, 0.003–0.3% nitrogen). Although other studies have found higher sediment organic contents, all total organic measures also include refractory materials and thus overestimate the digestively available (e.g., protein) components (George 1964, Buchanan and Longbottom 1970, Odum et al. 1979, Rice 1982).

Finally, no unusual feeding behavior was detected during the experiments. For *Amphiteis scaphobranchiata* and *Pseudopolydora kempji japonica*, the average ingestion rates on glass beads were lower than ingestion rates on natural sediments (Table 6), but the ranges were similar. As shown by the data in Tables 1–5, there was much variability in ingestion rates among individuals in any one treatment. The demonstration of statistically significant trends in the face of such variability strengthens the case for optimal foraging. Its causes, nonetheless, are of obvious interest in the foraging context. One possibility is that variations in animal sizes were responsible. However, all animals, within a species, were chosen during collection to be of similar size to minimize this source of variability. As a check, the data were normalized to body volume (determined by displacement for *A. scaphobranchiata* and from regressions of microscopically measured characteristic lengths vs. estimated volumes (Self and Jumars 1978) for *Hobsonia florida* and *P. kempji japonica*). Table 7 compares the coefficients of variation for the untransformed and size-normalized ingestion rates; their similarity implies that size differences did not account for the variability. Ingestion rates on natural sediments show similar coefficients of variation (Table 6). Such variability probably represents real differences among individuals' nutritional physiologies, as has been found for some copepods (Hassett and Landry 1982). We are currently investigating this possibility in deposit feeders.

#### *Animal-sediment interactions*

Ingestion rate dynamics of *P. kempji japonica* and *H. florida* (intertidal) and *A. scaphobranchiata* (subtidal) may be affected in different ways by different food supply patterns to their respective environments. Fig. 1 provides estimates of ingestion rate constancy ("constancy" defined as maintenance of the same, food-value-dependent ingestion rate on a given food type as long as it is available). The initial *IR* (Eq. 2) is based

TABLE 7. Coefficients of variation (%) for untransformed and body size-normalized ingestion rates.

		<i>P. kempji japonica</i>							
		15 Oct	16 Oct	18 Oct	19 Oct	11 Mar	12 Mar	13 Mar	
Untransformed		83	49	48	57	53	46	51	
Size-normalized		62	54	50	79	50	43	41	
		<i>H. florida</i>							
		30 Sep	1 Oct	21 Oct	22 Oct				
Untransformed		56	69	120	86				
Size-normalized		71	69	131	86				
		<i>A. scaphobranchiata</i>							
		10 Sep	11 Sep	13 Sep	14 Sep	8 Oct	10 Oct	11 Oct	12 Oct
Untransformed		43	59	50	40	50	53	68	39
Size-normalized		48	60	50	44	52	54	71	30

on the gut passage time when an animal first began feeding on an experimental food. If an animal maintains this initial ingestion rate throughout a feeding experiment, its residual *IR* (Eq. 3) will be 0. *A. scaphobranchiata*'s ingestion rate does appear to be maintained at the level set at the beginning of an experiment (Fig. 1C). The other ampharetid polychaete, *H. florida* (Fig. 1B) and the spionid *P. kempji japonica* (Fig. 1A) also show residuals distributed about zero at lower initial ingestion rates, but at higher initial rates the residuals are consistently negative. The longer term ingestion rates are lower than rates based on initial gut passage time. This suggests that *H. florida* and *P. kempji japonica* individuals showing the highest initial feeding rates later reduced their feeding rates; similar behavior is seen in other organisms. Herbivorous zooplankton feed at elevated rates after a starvation period (e.g., Frost 1972, Runge 1980). McCullough et al. (1979) found rapid initial feeding by a stream detritivore after food was first made available. Some intertidal suspension feeders feed at initially high rates when the tide returns, later resuming lower, "normal" feeding rates (Newell 1979). Because worms in this study were always maintained on natural sediment between experiments, it is unlikely that the responses of *H. florida* and *P. kempji japonica* were due to satiation following a "starvation response." Their behaviors may reflect an adaptation to pulsed inputs of food into intertidal habitats. Anderson (1980) documented the increased suspended matter content of the floodwater initially traversing a tidal flat. *H. florida* and *P. kempji japonica* may feed rapidly when this "fresh" material becomes available, then return to some lower ingestion rate. In its subtidal environment, *A. scaphobranchiata* may not experience such regularly pulsed inputs of variable-quality food. Instead, this species appears to maintain a more regulated ingestion rate (Fig. 1C), determined by the available food's quality, which may change over

longer time scales in the subtidal. Clearly, experiments over longer time scales with additional species from more varied environments would be required to test this hypothesis.

#### *Feeding behavior and optimal foraging strategies*

While the present results support strongly the ingestion rate model's prediction (Taghon 1981a), they do not exclude the possibility that the increasing ingestion rates on higher protein beads were due, not to active control by the worms, but to these beads' adhering more readily to the worms' tentacles. The protein coating on the glass surface appears to enhance the adhesion between the beads and the mucus these worms secrete from their tentacles (Jumars et al. 1982, Taghon 1982). Thus, more high-protein heads might adhere to the feeding tentacles and lead to an increased ingestion rate. However, since *P. kempji japonica* spent more time feeding on high-protein beads (Table 2), we conclude that active, not passive, processes were responsible for at least part of the increased ingestion rates on these beads. Further support for this conclusion comes from the qualitative impression that all three species fed more avidly on high-protein beads.

It has been suggested that, as food value continues to increase, ingestion rate should eventually decline, due to the balance between gain of some food component from an increased consumption rate and the decreased absorption efficiency expected to accompany faster feeding rates (Slansky and Feeny 1977). While some animals show such an ingestion rate-absorption efficiency correlation, it is by no means universal (e.g., Conover 1978). Certainly it is too early to make valid generalizations for marine deposit feeders. For annelids in particular, little is known about digestive enzyme kinetics (Jeuniaux 1969). There was no evidence of declining ingestion rate at high food value in the present experiments, but it could be argued that the critical food value had not been reached. The short-term nature of our experiments might also be a factor. We stress that, ideally, long-term studies (on the order of the species' generation time) of animals fed on well-defined food sources are needed.

The underlying assumption of optimal foraging theory is that animals seek to maximize net rate of gain of some food component, most often net rate of energy gain. The idea that rate is the important concept in animal feeding energetics and production, and that rate increases will be favored by natural selection, can be traced to Lotka (1922). Since then, this premise has been furthered by Odum and Pinkerton (1955) and Wittenberger (1970), who argued that rate increases should be selected for even at the expense of lowered efficiency. Calow (1977), on the other hand, argued that increased rate will not always be at a premium, but that efficiency or homeostatic ability as well can be adjusted to maximize useful output, that is, transmission of genetic information. Sweeping generalizations

appear neither likely nor advisable. There is ample evidence that different species have become essentially obligate efficiency maximizers or feeding rate maximizers over evolutionary time (e.g., Bell 1971, Milton 1981). Our results from a small number of deposit-feeding polychaetes support a model which predicts that food energy content and ingestion rate should be related positively to maximize the rate of energy gain. Calow's (1977:55) statement is germane: "There is a surprising diversity of physiological strategies and it is only by considering these in the context of where 'metabolic machines' work that they can be understood in terms of selection." Feeding strategies are influenced by factors other than food abundance or value, such as life cycle strategies (Calow et al. 1981). Many organisms must maintain more or less inflexible development schedules (Calow 1977), such as insect larvae developing synchronously with the emergence of their plant food (Feeny 1970). In such organisms, maintaining a "constant" rate may be more advantageous than maximizing the net rate of energy gain. Although thought-provoking compilations of past, mixed-species data (e.g., Cammen 1980) suggest that they may be found, the results of analogous constraints for aquatic deposit feeders await demonstration via carefully controlled laboratory or field experiments. Present data on particle selection (Jumars et al. 1982, Taghon 1982) and ingestion rates are insufficient to reject a simple energy rate maximization model.

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