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Ingestion Selectivity of Sedimentary Organic Matter by the Deposit-Feeder *Nucula annulata* (Bivalvia: Nuculidae)*

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ABSTRACT: Methods are described that allow a quantitative estimation of selective ingestion of sedimentary organic matter by deposit-feeding animals. The estimation can be made independently of any information of possible modes of selection. Animals need not be starved for a feeding trial, as is usual in other electivity studies. In the example presented, the protobranch bivalve *Nucula annulata,* when offered silt-clay sediment in which it was living, ingested sedimentary organic matter non-selectively.

INTRODUCTION

In order to obtain sufficient food, deposit-feeders must process – that is, swallow or sort through – large volumes of sediment. One widespread adaptation that increases the rate of sediment processing is selective ingestion of food-rich particles. In many studies of deposit-feeding, selective ingestion usually refers to particle-size selection, partly because it is relatively simple to measure the size distribution of sediment particles, but mainly because of the general assumption that food richness is controlled by particle size, or more properly, by particle surface area (e.g. Sanders, 1958; Hylleberg and Gallucci, 1975; Taghon et al., 1978). It is clear that many deposit-feeders do select finer sediment particles, but there are several modes of selective ingestion other than selection of fine particles. Some species may select by particle shape, preferring the larger, more angular particles (Whitlatch, 1974). Other species select by surface texture or specific gravity (Hylleberg and Gallucci, 1975; Self and Jumars, 1978). Some animals may be attracted to areas of enhanced microbial activity within the sediment (Gerlach, 1977; Reise, 1979), others may even create such patches by 'microbial gardening' (Hylleberg, 1975; Riemann and Schrage, 1978; Lopez et al., 1979). Certain species, perhaps especially those closely related to carnivores, have highly developed chemoreceptory abilities for finding food-rich patches of sediment, resulting in a close coupling of food quality and feeding behavior. The fiddler crab *Uca pugilator* displays such refined chemoreceptory abilities (Robertson et al., 1980), as does the deposit-feeding neogastropod *Ilyanassa obsoleta* (Crisp, 1969; Lopez, 1980).

Although it is obvious that deposit-feeding animals may select food-rich particles in a number of different ways, our knowledge of the various modes of selection is very limited (e.g. Fauchald and Jumars, 1979), and it is safe to conclude that a number of modes of selection are yet to be analyzed. The recently described epipsammic browsing of hydrobiid snails is an example of a previously unknown mode of selective ingestion (Lopez and Kofoed, 1980). Examination of the various modes of selective ingestion may increase understanding of functional morphology of deposit-feeders, but this modal approach will never allow a characterization of the feeding behavior of an animal, because we can never be certain that all possible modes have been examined. Rather than attempting to determine selective ingestion by examining possible modes of selection, it may be more valuable to develop methods of estimating the magnitude of selective ingestion without explicit information on feeding modes.

The approach described here is based on the electivity coefficient $E_i = (r_i - p_i)/(r_i + p_i)$, where r_i, p_i = proportions of food type i in ingested food and offered

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sediment, respectively (Ivlev, 1961). E_i can be calculated if proportions by weight of a potential food in ingested material and offered sediment are estimated. In the experiment described below, ingestion selectivity of the organic fraction of sediment by the protobranch bivalve *Nucula annulata* was estimated.

MATERIALS AND METHODS

Sediment and animals were collected from the seawater holding tank at the Flax Pond laboratory, which is located on a salt marsh on the north shore of Long Island, New York. The sediment, a rich silt-clay, was sieved through an 88 μm sieve to remove other macrofauna and larger pieces of detritus. The organic fraction of the sediment was labelled with ^{14}C-formaldehyde by incubating 20 ml of sediment slurry with 50 μCi ^{14}C-formaldehyde (Lopez and Crenshaw, 1982). Following ^{14}C labelling, ^{51}Cr was added to the sediment slurry (300 μCi $^{51}CrCl_2$ in 0.1 N HCl), the mixture being neutralized with 0.1 N NaOH. Under these conditions, Cr adsorbs to particle surfaces (Calow and Fletcher, 1972). After 24 h, the sediment, now labelled with ^{14}C and ^{51}Cr, was centrifuged and rinsed.

Adult *Nucula annulata* (5.5–6.5 mm shell length) were placed singly in fingerbowls (5 cm diameter) with a 3 mm layer of unlabelled sediment. When an individual was observed to be feeding, unlabelled sediment immediately around the individual was replaced with labelled sediment, which was added as a thick slurry. The individual was observed until feeding ensued on the labelled sediment. *N. annulata* were allowed to feed for 30 min; gut passage time of individuals of this size class is approximately 40 min. A separate group of *A. annulata* was allowed to feed on sediment for approximately 12 h, then the fecal pellets produced were collected.

Analytical methods followed Cammen (1980); samples were counted both in gamma and liquid scintillation counters, and DPM of each isotope was estimated. Preparation of samples for liquid scintillation counting differed from Cammen (1980) in the use of an organic scintillant, resulting in higher counting efficiency and reduced chemiluminescence. Also, a truncated ^{14}C channel was used in liquid scintillation counting to reduce interference from ^{51}Cr.

RESULTS AND DISCUSSION

Nucula annulata fed non-selectively on the organic fraction of the offered sediment (Table 1, Col. 7). There was very good consistency in E_{org} values for individuals, even though the amount of material ingested (Table 1, Columns 1 and 2) varied considerably. It is not known whether differences in amount ingested

Table 1. *Nucula annulata*. Ingestion selectivity of organic matter

Individual No.	(1) DPM ^{51}Cr ingested	(2) DPM ^{14}C ingested	(3) mg of org. ingested	(4) mg of inorg. ingested	(5) mg total ingested	(6) $r_{org.}$	(7) $E_{org.}$
1	2,009	166	.0023	.0172	.0195	.1178	+.063
2	2,176	144	.0020	.0186	.0206	.0971	−.034
3	1,763	110	.0015	.0151	.0166	.0904	−.069
4	2,601	183	.0025	.0223	.0248	.1008	−.015
5	2,659	187	.0025	.0228	.0253	.0988	−.025
6	1,344	91	.0013	.0115	.0128	.1016	−.011
7	3,555	318	.0044	.0305	.0349	.1261	+.097
8	5,506	374	.0052	.0472	.0524	.0992	−.023
9	5,708	352	.0049	.0489	.0538	.0991	−.066

1 ^{51}Cr DPM: estimated from gamma counts
2 ^{14}C DPM: estimated from liquid scintillation counts
3 mg of organic matter ingested = ^{14}C DPM ind.$^{-1}$ ÷ ^{14}C DPM mg^{-1} organic matter in sediment, where ^{14}C DPM mg^{-1} organic matter = ^{14}C mg' dry wt ÷ mg organic mg^{-1} dry wt. For this sediment: 7,517 ± 791 ^{14}C–DPM mg^{-1} dry wt (n = 5); .1039 ± 0.0041 mg org mg^{-1} dry wt (n = 4)
4 mg inorganic matter ingested = ^{51}Cr–DPM ingested ÷ (^{51}Cr–DPM mg^{-1} dry wt of pellet) × (mg ash mg^{-1} dry wt of pellet). For this sedimet: 104,533 ± 8,387 ^{51}Cr–DPM mg^{-1} dry wt pellet (n = 4); .8961 ± 0.0041 mg ash mg^{-1} dry wt pellet (n = 4). Assumptions: No. ^{51}Cr absorbed, no inorganic matter absorbed. (Note: measured ^{51}Cr absorption < 3 %)
5 = (3) + (4)
6 = (3) / (5)
7 $E_{org} = \frac{(r-p)}{(r+p)}$; r = proportion of organic matter ingested (6); p = proportion of organic matter in sediment, for this sediment = 0.1039. For this experiment E_{org} mean and ± s.d. = −.009 ± .055

was due to variation in ingestion rate or in time spent feeding.

We hesitate to make general comments on the feeding behavior of *Nucula annulata*. In other trials of this experiment, in which individuals were conditioned and handled differently, positive slection of the organic fraction was sometimes noted. For a given study, care must be taken so test animals are not traumatized before or during the feeding trial. Some species are rather robust (e.g. *Hydrobia* spp.), while others, like *Nucula* spp., respond to even slight disturbances (i.e. picking up the fingerbowl). Workers must be sensitive to such problems before attempting comparative studies.

Even though *Nucula annulata* appeared to feed non-selectively upon the organic fraction of sediment, it is probably not fair to characterize a species as a selective or non-selective deposit-feeders. Selectivity is more a function of a given animal-sediment combination than it is a species characteristic, though some species (or size classes within a species) may always feed more selectively upon a given sediment than another species.

Use of ^{51}Cr labelling allows the estimation of mineral grain ingestion without the need for prior starvation or direct recovery of ingested sediment. This calculation is based on the assumption that neither ^{51}Cr or mineral grains are absorbed by the animals, or if absorbed, they are taken up equally. This assumption is not likely to lead to serious problems in estimation of ingestion selectivity, though this should be further investigated.

Ivlev's index of electivity allows a reasonable intuitive feel for how selectively an animal has fed (E_i of -1: perfect rejection, E_i of $+1$: perfect selection), but statistical analysis is precluded. This is generally the case for electivity measures (e.g. Jacobs, 1974), and greater effort should be made to develop statistics for electivity measures (Gabriel, 1978). This problem is under investigation (Cerrato and Lopez, in prep.).

The main purpose of this study was to develop a protocol for estimating ingestion selectivity of deposit-feeding animals. The example presented here describes how to estimate selectivity of sedimentary organics, but with suitable modifications in labelling, other potential foods could also be investigated. In fact, the use of combined $^{14}C:^{51}Cr$ labelling also allows the estimation of assimilation efficiency of potential foods, provided certain conditions are met (Calow and Fletcher, 1972; Cammen, 1980). It is now possible to estimate simultaneously ingestion rate, ingestion selectivity, and assimilation efficiency for several potential food types in a sediment (Lopez, in prep.). The methods are based on a combination of those described here with those previously described for assimilation studies (Calow and Fletcher, 1972). These methods will allow a better characterization of the feeding behavior of deposit-feeders.

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