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Effect of flavor and size on selection of food by suspension-feeding plutei¹

Abstract—Plutei ingested plastic spheres previously incubated with algal cells at higher rates than plastic spheres incubated with filtered seawater. The attractive factor overrode or modified preferential ingestion of spheres of different sizes. The cultured algae were centrifuged and resuspended before the plastic spheres were exposed to the algal cells, so it is probable that natural materials associated with the algal cells were transferred to the plastic spheres and triggered the selective ingestion of particles. Capture on the basis of flavor could be especially important for those suspension feeders that actively respond to particles in order to capture them; if they concentrate only nutritious particles, then they avoid subsequent problems of sorting and handling. Preconditioning plutei by feeding with algal cells of one of two sizes does not increase preference for untreated spheres of the algal size.

Suspension feeders cope with formidable problems. Their food is small, dispersed, not much denser than the surrounding water (see Sournia 1982), and mixed with non-nutritious or toxic particles of the same size. The best controlled studies of selective capture or ingestion of particles have emphasized physical properties such as size (Donaghay and Small 1979), surface charge (LaBarbera 1978), or wettability (Gerritsen and Porter 1982), but these properties are not necessarily correlated with nutritional quality. Chemical cues, or flavor, could give more specific information on nutritional quality (Poulet and Marsot 1978). We have transferred an attractive factor from cultured algal cells to plastic spheres and tested its effect on ingestion rates of echinoid larvae of two species in reciprocal experiments. The algal factor can override effects of size.

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Preferential ingestion of particles in the most abundant size class has been examined for copepods and tintinnids (Poulet 1974; Rassoulzadegan and Etienne 1981). To ensure that preferential ingestion of treated and untreated spheres of different sizes was not affected by the presence of algal cells, we tested for the effect of previous and continuing presence of algae of one size on the preferential ingestion of untreated spheres of two sizes.

In one series of experiments we used larvae of the clypeasteroid echinoid *Dendroster excentricus* as the suspension feeder, polystyrene DVB spheres of about 2-, 5-, or 10- μm diameter for test particles, and the diatom *Thalassiosira weissflogii* as a source of an attractive substance. There was no reason to expect this alga to be particularly attractive. Plutei eat it and a culture was available. Algal culture medium was removed by centrifuging the cells and resuspending them in seawater filtered through a 0.45- μm filter. Spheres were incubated overnight at 14°C with the algal cells or with filtered seawater as a control. They were then resuspended without washing, counted, and diluted with seawater to form suspensions of mixed sizes, each at a known concentration. If differential clumping of spheres occurred in experimental and control treatments, the suspension was discarded. At 400 \times magnification (without staining) we could see no material transferred to the spheres as a result of treatment. During feeding, the 400-ml suspension was mechanically stirred to prevent settling of spheres and held at about 13°C. We added four- or six-armed plutei to the suspension and then fixed them after about 10 min of feeding, before any spheres could be defecated. We counted only spheres in the stomach and intestine because these cannot be regurgitated during handling. Significance

Table 1. Effect of flavor associated with a diatom on selective ingestion of plastic spheres. Proportions are for the smaller spheres. The tests are pooled G for significant differences between proportion in the pluteus guts and first proportion in suspension and then proportion in guts in the reciprocal experiment.

Sphere diam (μm)	Prefed alga (μm)	Proportion small in		Against suspension (P)	Against gut in reciprocal (P)	Spheres eaten	Spheres \cdot ml $^{-1}$	No. plutei counted	Stage of plutei*
		suspension	guts						
5†, 10	—	0.50	0.60	<0.005	<0.005	587	10,000	56	6
5, 10†	—	0.54	0.36	<0.005	<0.005	635	11,000	35	6
2†, 10	—	0.83	0.50	<0.005	<0.025	145	30,000	79	4
2, 10†	—	0.83	0.40	<0.005	<0.005	270	30,000	69	4
2†, 10	—	0.83	0.48	<0.005	<0.005	1,700	30,000	26	6
2, 10†	—	0.83	0.36	<0.005	<0.005	1,591	30,000	26	6
2, 10	—	0.83	0.52	<0.005		344	30,000	34	4
2, 10	—	0.50	0.08	<0.005		171	10,000	45	4
5, 10	4	0.50	0.69	<0.005	<0.05	964	10,000	45	6
5, 10	10	0.50	0.66	<0.005	<0.05	990	10,000	33	6
5, 10	4	0.77	0.81	<0.025	>0.10	483	6,500	50	6
5, 10	10	0.77	0.83	<0.025	>0.10	549	6,500	53	6

* Four armed or six armed.

† Spheres previously incubated with the diatom.

of departures from expected frequencies of capture was tested with the G -test (Sokal and Rohlf 1969).

Potentially confounding variables, such as differential settling of spheres, were well controlled by reciprocal experiments in which either the large or the small spheres were incubated with the diatoms. Within each experiment the plutei were of the same stage, parents, and nutritional history, and the spheres were of the same material. We did not control the number of algal cells carried with the spheres into the feeding trials. Separate experiments (discussed below) testing the effects of the size and presence of algal cells on preferential ingestion of spheres showed that this could not produce changes of the magnitude observed with pretreated spheres. We removed algal medium by centrifuging and resuspending algal cells in filtered seawater; although we did not incubate spheres in dilute algal medium as an additional control, we doubt that the highly diluted remaining Tris buffer, EDTA, vitamins, trace metals, phosphate, and nitrate were the attractive factor and for brevity have referred to the attractive factor as a flavor associated with the algal cells.

Results are summarized in Table 1. In three experiments spheres of one size were soaked with cells of *T. weissflogii* before they were offered to plutei, and spheres of the other size were soaked only in seawater.

Numbers of spheres ingested were compared with the proportion of the two sizes in suspension and with the proportion in pluteus guts from the reciprocal treatment. Treatment with cells of *T. weissflogii* reversed preferential ingestion of the 5- and 10- μm spheres (Table 1, rows 1 and 2). Treatment with the diatom did not reverse preferential ingestion of 10- μm relative to 2- μm spheres, but did increase ingestion of the treated spheres relative to the untreated spheres (Table 1, rows 3–6). Thus there is a transferable factor from the alga that increases ingestion rates of particles.

To test for the effect of size alone we offered untreated spheres to plutei. Plutei ingested untreated spheres of 2- μm diameter at much lower rates than untreated spheres of 10- μm diameter (Table 1, rows 7 and 8). Plutei ingested untreated spheres of 5- μm diameter at slightly higher rates than untreated spheres of 10- μm diameter (Table 1, rows 9–12). Spheres of 5- μm diameter are therefore near the optimum size for ingestion.

The experiments with untreated 5- and 10- μm spheres also tested the hypothesis that plutei preferentially ingest spheres of the same size as the algae present in suspension. In these experiments plutei were fed either *T. weissflogii* (about 10 μm in diameter) or *Thalassiosira pseudonana* (about 4 μm in diameter) for 3 h and then in addition offered a mixture of untreated

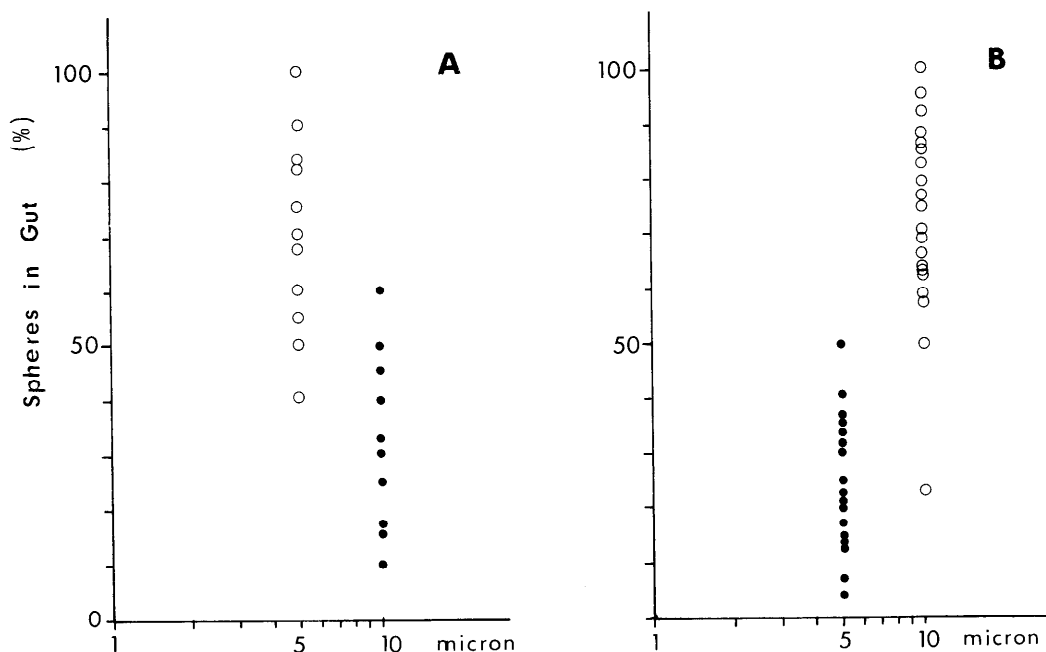


Fig. 1. Percent of 5- and 10- μ m plastic spheres in guts of plutei of *Paracentrotus lividus*. Spheres treated with homogenate of *Hymenomonas elongata*—O; untreated spheres—●.

spheres of 10- and 5- μ m diameter for 10 min. Prior and continuing exposure to algae of one size had little or no effect on the frequency with which spheres were ingested (Table 1, rows 9–12). These two experiments reinforce the conclusion that it is the transferred flavor rather than experience with an abundant size class of particles that is influencing selective ingestion by the plutei.

Our estimated ingestion rates are low because we did not count particles that were captured and in the esophagus but not yet swallowed. Also, plutei are disturbed by the transfer into the suspension and may require some time to recover and begin capturing particles at high rates.

These results confirm preliminary experiments with other species of plutei (family Echinidae) and other algae (flagellates), with slightly differing methods. In these experiments seawater filtered through a 0.22- μ m membrane filter was used to rinse algae by centrifugation and to incubate beads. Algae were not intact at all stages of the experiment. Spheres and algae were separated by

filtration, and, to eliminate solid material from the treated spheres, the spheres were sonicated in filtered seawater. In two experiments with plutei of *Paracentrotus lividus*, treatment of 10- μ m spheres with the alga *Hymenomonas elongata* increased ingestion rates on 10- μ m spheres relative to rates with untreated 10- μ m spheres in separate flasks. The ratios of ingestion of treated to untreated spheres were 1.9 and 2.3. Treatment of spheres with *H. elongata* also increased ingestion rates in reciprocal comparisons of ingestion of 5- and 10- μ m spheres from a mixture (Fig. 1). Prefeeding plutei of *Psammechinus miliaris* with large (near 10 μ m) or small (near 5 μ m) algal cells did not significantly affect relative ingestion rates of untreated 5- and 10- μ m spheres. This experiment included prefeeding plutei for 1 or 2 days with *Dunaliella tertiolecta* or *Cricosphaera carterae* (about 10 μ m) in contrast to prefeeding with *Isochrysis galbana* or *Pavlova lutheri* (about 5 μ m). There is therefore no reason to think that the results are peculiar to one species of pluteus or alga.

Actively responding suspension feeders with a mechanism of particle capture similar to that of plutei include members of the Echinodermata, Hemichordata, Bryozoa, Brachiopoda, and Phoronida (Strathmann 1982). Previous experiments with natural foods showed that plutei selectively ingest particles (Rassoulzadegan and Fenaux 1979) but that work did not separately test for effects of size, shape, flavor, and other physical properties. Plutei are actively responding suspension feeders because they must respond to each captured particle by a reversal of beat in order to capture it (Strathmann et al. 1972). It is also ciliary reversal that causes subsequent rejection of particles (Strathmann 1971). For actively responding suspension feeders, flavor could affect either initial capture of a particle or later rejection. Either failure to capture (no stimulation of a ciliary reversal) or subsequent rejection (stimulation of a ciliary reversal) would affect ingestion rates, but it would be more efficient to make no response to unnutritious particles and thus not capture them in the first place. In these experiments we did not determine whether differential capture or differential rejection causes the observed effect of flavor on ingestion rate. In either case, our results imply that presence or absence of a chemical stimulus from a particle does affect the response of cilia of plutei.

Crustacea also includes actively responding suspension feeders (Koehl and Strickler 1981; Paffenhöfer et al. 1982). Our results are in general agreement with those of Poullet and Marsot (1978), who demonstrated that copepods preferentially ingest semi-permeable nylon capsules filled with algal homogenates over similar capsules filled with albumin molecules too large to pass out of the capsules. Our simpler method can provide better controls and clearer results because it avoids the complication of fragmented large particles and does not depend on cell homogenates.

Direct application of physical theories of filtration to suspension feeders requires that the animals do not respond to individual particles in order to capture them. If the animal does respond to particles on the basis of flavor, then treatments altering physical properties, such as surface charge or

wettability, may affect ingestion not only because of the change in charge or wettability but also because of changes in flavor associated with the treatment. Without information on the method of particle capture, application of theories of filtration to experimental and field conditions can be misleading. Of course the reverse is also true: the attractive factor associated with algae could affect the physical properties of the beads.

To our knowledge this is the first observation that an attractive factor associated with intact planktonic algae, separate from a particular size, shape, hardness, or toughness, can affect ingestion of particles. This attractive property can be transferred from cultured algal cells to other particles, and this transferable property can modify or override the effect of size on preferential ingestion of particles. The method should be applicable to experiments with varied materials and suspension feeders.

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Effect of food acclimation on assimilation efficiency of *Calanus pacificus*¹

Abstract—A technique, based on quantitative conversion of chlorophyll *a* to pheophorbide during digestion, is described for determination of assimilation efficiencies of particle-feeding zooplankton. *Calanus pacificus* had assimilation efficiencies ranging from 68.5 to 85.4% for carbon and 73.9 to 92.5% for nitrogen. Assimilation efficiencies for copepods first acclimated to different food concentrations of *Thalassiosira weissflogii* and then fed at the same food level varied systematically, with animals acclimated to low food having higher efficiencies than animals acclimated to high food.

Assimilation efficiency is defined as the percentage of ingested material that is absorbed across the gut wall of an animal. Efficiency of assimilation is central to budgeting for the utilization of matter and energy by planktonic animals because it represents the proportion of ingested food actually available for metabolism and growth. Assimilation efficiency is equally important in

assessing the rate of flux of particulate matter and associated chemicals from the euphotic zone to depth via fecal pellet transport since it is the differential absorption of chemicals in the digestive process of zooplankton that determines the nutritional value and chemical composition of the resulting defecated material.

Conover (1966a) introduced a method for determining the assimilation efficiency of particle-feeding zooplankton which assumed that the inorganic fraction of ingested material would be unaffected by the digestive process. Thus, the efficiency of absorption of the organic fraction could be quantified by comparing the ratios of organic to inorganic material in the food and in fecal pellets. Subsequent studies demonstrated that a substantial portion of the inorganic fraction is assimilated during digestion (Forster and Gabbott 1971; Lasenby and Langford 1973). A gravimetric method has been shown to be superior to the Conover approach for predatory animals that consume and defecate their prey in discrete pellets (e.g. Coper and Reeve 1975; Dagg 1976). However, difficulty with quantitative recovery of fecal material

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