Degree of taste discrimination among suspension-feeding cladocerans and copepods: Implications for detritivory and herbivory

W. Charles Kerfoot

Lake Superior Ecosystem Research Center and Department of Biological Sciences, Michigan Technological University, Houghton 49931,
University of Michigan Biological Station, Pellston 49769, and
School of Natural Resources, University of Michigan, Ann Arbor 48109

Kevin L. Kirk

Lake Superior Ecosystem Research Center and Department of Biological Sciences, Michigan Technological University, and
University of Michigan Biological Station

Abstract

We used the Rassoulzadegan-DeMott bead bioassay to evaluate the ability of various pelagic microcrustaceans to discriminate between particles on the basis of taste and size. The test examined zooplankton reactions to fresh algal exudates adsorbed onto polystyrene microspheres. The investigation shows that there is a marked dichotomy between certain large-bodied freshwater microcrustaceans in how they respond to small particles; it confirms that large daphnid cladocerans exhibit no taste discrimination for small beads, whereas calanoid copepods continually appraise resource quality of both small and large particles with a fine degree of discrimination.

In contrast, smaller bodied daphnids and other cladocerans show some degree of taste and acute size discrimination, the former presumably related to processing large particles one at a time and to the individual peculiarities of the filtering mechanisms. Based on the findings from taste discrimination tests, we suggest that the degree of taste discrimination is often related to particle size. Moreover, we assert that many cladocerans are categorized more appropriately as detritivores than as herbivores, although they exhibit modest, size-related taste discrimination.

In pelagic environments, suspension feeders frequently encounter high-quality resources such as algae mixed with particles of lower food value, such as silt and detritus (Porter 1977; Kirk 1991). Even among algal and detrital groups there is considerable variation in resource quality (Kerfoot et al. 1988; Butler et al. 1989). How suspension-feeding organisms respond to both the quantity and quality of suspended particles is fundamental to an understanding of the ecological niche of each species and its role in the cycling of materials.

Organic detritus, in particular, can be very abundant both in epilimnetic and hypolimnetic waters, varying seasonally with phytoplankton production and physical mixing. Organic detritus often dominates particu-

late organic C (POC) in the open ocean and in coastal waters (Riley 1970). For example, the percentage of detritus relative to total POC varied from 50 to 90% over a year in two Canadian bays (Sutcliffe 1972) and averaged 80% in Mediterranean waters (Rassoulzadegan 1979). In freshwaters as well, particulate detritus can occur in concentrations equal to or greater than living phytoplankton cells (Mann 1988).

Equally important, the quality of detritus as a zooplankton food resource varies considerably, ranging from fresh bacterial or algal exudates to highly refractory lignin (Decho and Moriarty 1990; Moran et al. 1988). Given the abundance of detritus in the water column, it seems curious that detritivory is considered relatively rare in pelagic environments (Schoener 1989). We believe that this notion is based on an ill-informed interpretation of suspension feeders and would like to present an alternative view.

Despite decades of research, the interaction of suspension feeders with various par-

ticle types is unclear. Early studies of particle discrimination were restricted to casual observations of grazer guts, fecal pellets, and feeding habits. Ingestion of substantial amounts of inert particles by certain taxa prompted the use of carmine, fine sand, and polystyrene spheres to study particle-size selection in both freshwater and marine zooplankton (*see* Vanderploeg 1990). The original intent of the inert-particle work was important and ambitious, i.e. to measure the fraction of available resources grazed by both the entire community and individual species on a size-specific basis (e.g. Gliwicz 1969, 1977), An untested assumption of the particle-size methods was that selection depended primarily on particle size and not flavor, hardness, or features like charge.

The observation that small cyclopoid copepods rarely ingest inert particles, while consuming diatoms and other living algae, led Fryer (1957) to speculate that these animals must be able to perceive tastes or odors associated with algal particles. For certain species of zooplankton, chemical cues now seem to be important in both distance detection of algal patches and in determining whether captured particles are ingested or rejected (Poulet and Marsot 1978; Rassoulzadegan et al. 1984; DeMott 1986).

In particular, the DeMott (1986) study suggested major differences between cladocerans and copepods in the way that they react to suspended particles. Here we expand the Rassoulzadegan-DeMott test to examine simultaneously size and taste selection in various freshwater suspension feeders. The protocol utilizes freshly produced algal exudates adsorbed onto polystyrene spheres; hence the test evaluates reaction to freshly produced, high-quality algal detritus. The ability of pelagic cladocerans and copepods to discriminate between exudate-coated spheres and uncoated spheres is quantified for assemblages. Novel aspects of techniques include detailed statistical examination of methods, incorporation of ontogenetic checks, and introduction of dual-flavor tests.

More importantly, we attempt to relate the laboratory test results to the field environment. In so doing, we argue that the dichotomy between most cladocerans and copepods is a fundamental distinction suggesting that many cladocerans are functioning more as detritivores than as herbivores in the strict sense.

Methods

Evaluations of taste discrimination utilized the adsorption of algal exudates onto the surfaces of polystyrene spheres—a technique first developed by Rassoulzadegan et al. (1984) and DeMott (1986). The basic experimental design featured reciprocal flavoring of small (6-μm diam) and large (12 μm) polystyrene divinylbenzene microspheres (Duke Scientific Corp). The source and sizes of experimental beads were chosen specifically to duplicate the design of DeMott (1986). These sizes fall within the modal peak of particle size distributions in many lakes (e.g. Richman et al. 1980) and in many zooplankton guts (Gliwicz 1969, 1977).

By reciprocal we mean that each experiment consisted of a treatment that paired small, flavored beads with large, unflavored beads and the reverse treatment that paired large, flavored beads with small, unflavored beads. To evaluate the ability of grazers to discriminate between particles coated with different flavors, we extended the basic design by flavoring small and large beads with algal exudates from two different algal species. The experimental design thus allowed a simultaneous test of taste and size discrimination among co-occuring suspension feeders.

The flavoring treatment produced the equivalent of uniformly sized particles of fresh algal exudate detritus. The adsorbed algal exudates came from stock cultures of algae, grown in batch culture in Percival environmental chambers (12:L/D cycle; unbuffered WC medium, Guillard 1975). Coated spheres were prepared by incubation with 5×10^5 algal cells ml^{-1} for 24 h in 25-ml flasks. The algae were log-phase cells of either *Chlamydomonas reinhardii* (a flagellated green, UTEX 796, 6-μm diam) or *Cyclotella meneghiniana* (a centric diatom, CYOH2, 5×15 μm, obtained from S. S. Kilham). Uncoated spheres were incubated with culture medium alone.

Incubation duration was fixed at 24 h, well within safe margins, because prior bio-

assay tests had indicated sufficient adsorption of extracellular exudates by 9 h for maximal discrimination (DeMott 1988*b*). Longer incubations were not used in order to prevent the beads from adhering to each other. Agitation and gentle sonication, if necessary, were used to ensure dispersion of particles in flavoring treatments. Immediately before grazing tests, concentrations of spheres and stock algae were determined by hemocytometer counts and adjusted to achieve a combined $1:1:1$ ratio (6-μm spheres: 12-μm spheres: algae) in the final, introduced mixture.

Zooplankton were collected before experiments, split into approximately equal density groups, and transferred to 250-ml Falcon tissue-culture flasks that contained filtered lake water. Field samples came from three sources: Thurston Pond and Third Sister Lake (Washtenaw County) and Douglas Lake (Cheboygan County), Michigan. At least 1 h before the addition of spheres, flasks were filled with filtered lake water and pretreatment food (three standard pretreatments: no food, 5×10^3 cells ml^{-1} *C. reinhardii*, or 5×10^3 cells ml^{-1} *C. meneghiniana*). After preconditioning, zooplankters were fed for 20 min on the $1:1$ mixture of flavored and unflavored spheres in the presence of an equivalent concentration of *Chlamydomonas* or *Cyclotella*. In the dual-flavoring experiments, small and large spheres were incubated for 24 h with either *Chlamydomonas* or *Cyclotella* exudate. These flavors were offered in a $1:1$ ratio.

During grazing experiments, settling of plastic spheres was not considered a major problem; according to Stokes' law, 6- and 12-μm spheres (sp gr, 1.02 g cm^3) have maximal settling velocities of only 0.35 and 1.4 cm h^{-1}. In any case, to guard against differential settling, we rotated flasks every 2–5 min to ensure uniform suspension of spheres. At the end of the 20-min feeding period, all zooplankters were anesthetized with carbonated water, then preserved in a sucrose-Formalin mixture for later removal and mounting. Preservation in the original test vessel allowed several important a posteriori checks (relative ratio of beads, absolute concentration of beads, preservation of all experimental grazers).

In the laboratory, zooplankton were picked individually from flasks and mounted for counting in groups of 20–30 between slide and coverslip (50% glycerin-water medium). Animals were classified by species and body size. Lengths of cladocerans were measured from the base of the carapace to the top of the head, along a line that passed through the eye. Copepods were measured from the anterior of the cephalothorax to the base of the caudal furca. Beads were counted in guts under $400\times$ magnification (Fig. 1, Leitz and Zeiss Universal compound microscopes). Because of the refractive index of the beads relative to body tissues, beads in the gut could be highlighted by increasing direct illumination to the point where other structures were washed out. For difficult cases (e.g. spring lipid-laden copepods), we found that an alcohol extraction (24 h in 50% ethanol, 24 h in 95% ethanol), followed by mounting in clove oil or creosote, helped clear even the most strongly colored individuals. Most cladocerans and immature copepods were clear enough, however, so that additional treatment was unnecessary.

Analysis of data concentrated on two basic plots: number of small beads vs. large beads in individual guts ($1:1$ expected ratio), and calculation of Chesson's selectivity index (α, Chesson 1983) for beads ingested by different-size individuals. Bias in the total number of small to large beads ingested was also examined. Chesson's selectively index (α_{small}, selectivity for small beads) is

$$\alpha_{small} = \frac{r_{small}/m_{small}}{(r_{small}/m_{small}) + (r_{large}/m_{large})} \quad (1)$$

where r is the number of beads in the gut and m the number of beads in the environment. In the case of a simple binary choice, where the numbers of small and large beads are equal and in sufficient numbers that consumption does not change the number of beads in the environment, the above equation reduces to

$$\alpha_{small} = r_{small}/(r_{small} + r_{large}). \quad (2)$$

Under these conditions, a value of zero would indicate that no small beads were eaten, a value of 0.50 would indicate non-
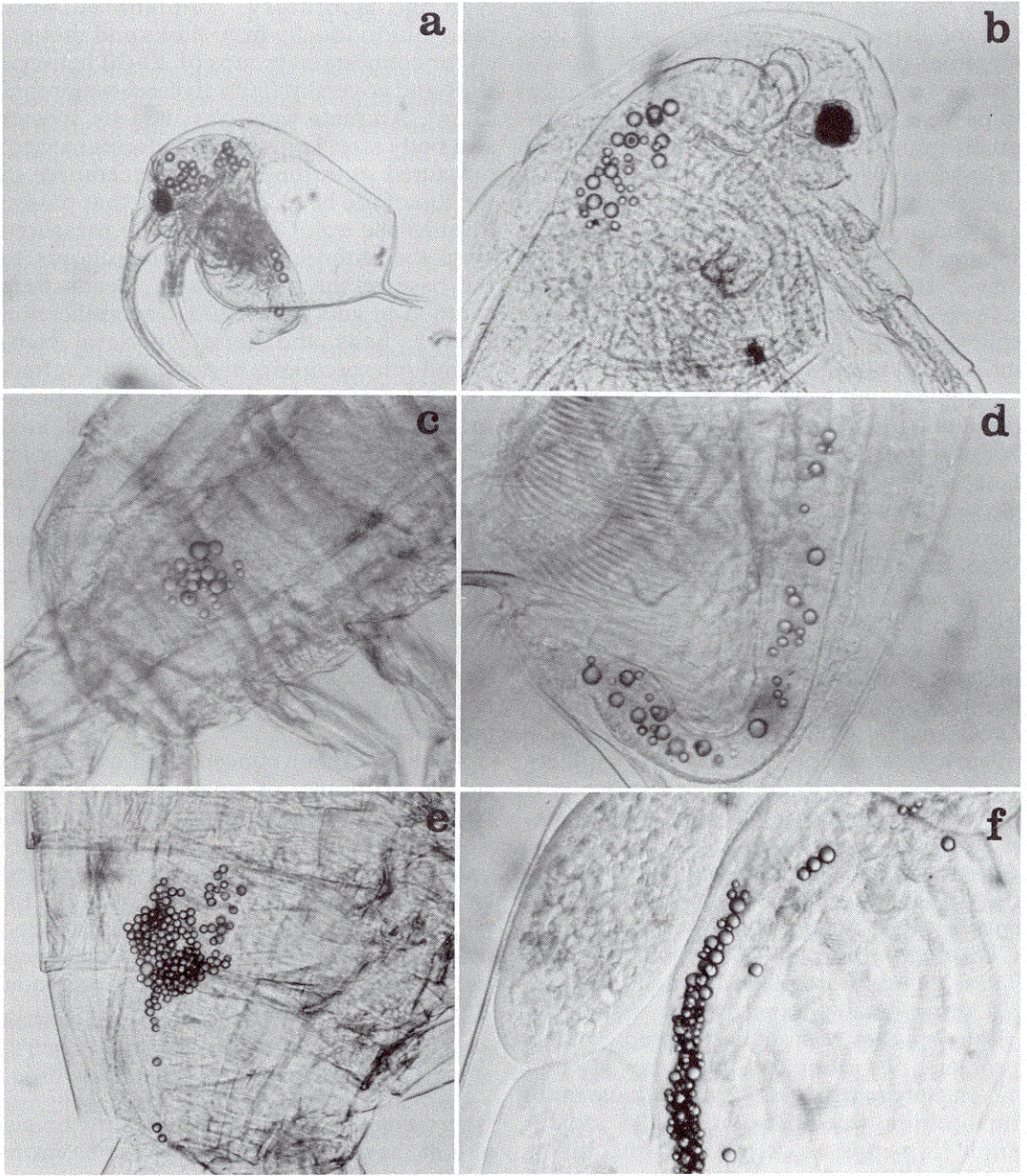
Fig. 1.   Light micrographs showing polystyrene beads in the guts of various suspension-feeding zooplankton. a—*Bosmina longirostris*; b—*Daphnia ambigua* foregut; c—*Skistodiaptomus oregonensis*; d—*D. ambigua* hindgut; e—*Onychodiaptomus sanguineus*; f—*Diaphanosoma birgei*.

selective feeding, and a value of 1.0 would indicate that only small beads were eaten. In order to assess ontogenetic changes in taste preferences, we regressed the selectivity index against zooplankton body length.

Certain statistical properties of comparisons were examined in some detail. A model 2 regression was fitted to the plot of selectivity index vs. body size because α_{small} could be viewed as a dependent variable predicted by size. The same was done for plots of small vs. large bead ingestion. Yet

one could question the appropriateness of model 2 regressions applied to ingestion plots because the choice of x- and y-axis is arbitrary and both variables have experimental variance, hence formal designation of a dependent and independent variable is not possible. Consequently, we compared model 2 linear regression fits, which utilize least-squares minimization along the y-axis, with linear regressions based on principal components solutions, which utilize orthogonal minimization, and treat both variables as dependent (Sokal and Rohlf 1981).

We also examined the observed sampling scatter of α_{small} against expected values, simplified here by the close correspondence to a simple proportion (e.g. $1:1$ in the null model). The expected 95% confidence limits of the binomial distribution were calculated from

$$p = \frac{f}{n} \pm a \left[\frac{\frac{f}{n}\left(1 - \frac{f}{n}\right)}{n} \right]^{1/2} . \qquad (3)$$

Here f is the number of small beads, n the total number of beads, f/n the frequency of small beads (0.50), p the expected proportion of small beads, and a the limits of a normal curve under which $k\%$ of the area lies ($a = 1.960$ for the 95% C.L.).

Selective feeding was evaluated with t-tests to compare α_{small} to the value expected given nonselective feeding, 0.5 in this case. Taste discrimination was tested by examining for significant differences in α_{small} values between reciprocal flavor treatments with t-tests; α_{small} values were arcsine-square-root transformed before statistical analysis to normalize the proportions (Sokal and Rohlf 1981). All statistical tests were conducted with the SYSTAT statistical package.

We summarized the overall degree of taste and size discrimination of each species by comparing α values from reciprocal treatments. The higher the degree of taste selectivity, the larger the difference between α_{small} values in reciprocal treatments. Thus, an index of taste discrimination was calculated as: α_{small} when small beads flavored $- \alpha_{small}$

when large beads flavored. Similarly, an index of size discrimination was calculated as: $\alpha_{flavored}$ when small beads flavored $- \alpha_{flavored}$ when large beads flavored.

Results

Expected patterns — Because the experimental design is so simple, we expect certain scatter patterns and variance relationships for the null model (i.e. no size and no taste discrimination). Bias in choice will depart from the null pattern in distinctive ways, depending on the sensitivity of experimental animals to size or taste (Fig. 2). For example, species that show neither taste nor size discrimination are expected to ingest beads in proportions found in the environment with no difference between reciprocal flavor treatments (Fig. 2C). These species are also expected to exhibit no significant regression between α_{small} and body length.

Bias toward either size or taste will be expressed in various ways. Size-discriminating species will most often experience difficulty ingesting larger beads. Thus species with size, but not taste, bias are expected to ingest higher than $1:1$ ratios of small:large beads yet exhibit no difference between reciprocal taste treatments (Fig. 2A). These species should also show significant negative regressions of α_{small} on body length. Taste-discriminating species are expected to show major divergence from a $1:1$ ratio and major differences between reciprocal treatments, because the test produces divergence in different directions with the strength of the response (Fig. 2D). Species that discriminate on the basis of both taste and size should show departures from the $1:1$ ratio and divergence between reciprocal treatments (Fig. 2B).

Because beads are presented to grazers as binary choices, stochastic variation in α_{small} (equivalent to the proportion of small beads) is very sensitive to sample size (i.e. the absolute number of ingested beads). For a binomially distributed variate, the relationship of the sampling variance to the sample size is well known (*see methods*). Expected confidence intervals for the null model (i.e. no taste or size discrimination) are superimposed in Fig. 3 over the actual experimental values for α_{small}. As expected, the
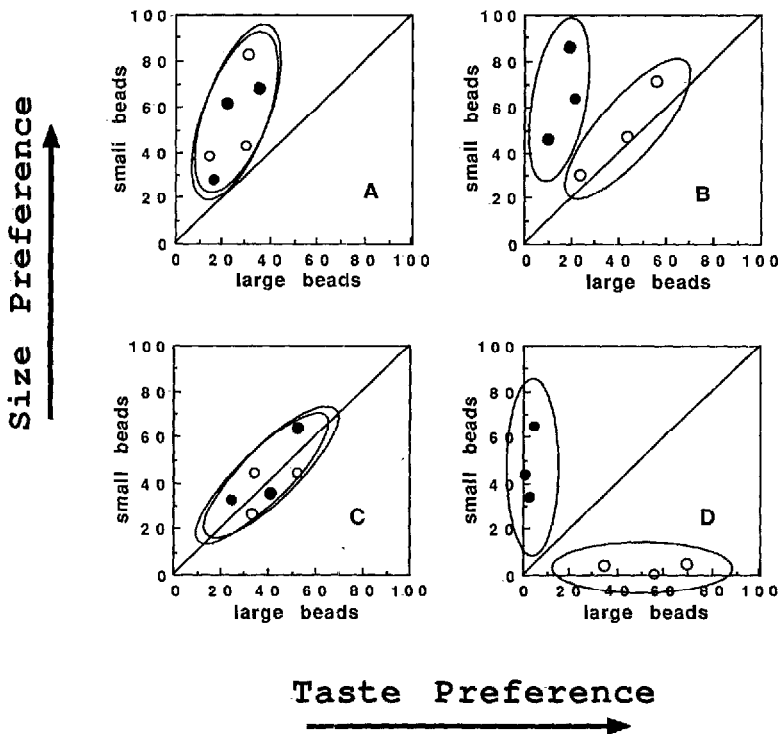
Fig. 2.   Expected patterns of bead ingestion in animals with varying degrees of taste and size discrimination. Treatments in which small beads are flavored—● treatments in which large beads are flavored—O. A. Size preference (for small beads) with no taste preference. B. Moderate preference on the basis of both size and taste. C. No taste preference and no size preference. D. Taste preference with no size preference.

smaller the absolute number of ingested beads, the greater the scatter of α_{small}. Scatter also declines dramatically as the absolute number of beads increases. Here agreement between expected and observed values was also close. Slight departure from the expected 0.5 mean value caused some deviation from the null model, however, as the total number of beads became large.

Taxa that approximate the null model— Genera in the family Daphnidae (*Daphnia, Ceriodaphnia*) corresponded most closely to the null model (Table 1). Species ranged widely in mean body length, from a minimum of 0.50 mm (*Daphnia ambigua, Ceriodaphnia quadrangula*) to a maximum of 0.92 mm (*Daphnia pulicaria*). The number of beads ingested was positively correlated with body length (Pearson *r* range = 0.14–0.70, $\bar{x}$ = 0.40, *n* = 21) raised to a power of 2.0–2.4. Within the genus *Daphnia*, the mean number of beads counted per indi-

vidual varied from 10 (*D. ambigua*) to 227 (*D. galeata*). The mean number of beads counted per sample was 3,194 (range = 644–8,396).

In general, plots of bead ingestion patterns and calculations of α_{small} indicated that most larger bodied *Daphnia* species (*D. pulicaria, D. galeata mendotae, D. retrocurva,* Douglas Lake *D. ambigua*) conformed very closely to the null model, i.e. nonsize and nontaste discrimination (Fig. 4, Table 1). Coefficients of determination for regression lines fitted to small vs. large bead plots were very high (r^2 = 0.78–0.99, Table 1), indicating fairly precise determination of patterns. Regression slopes were very similar and ranged between 0.73 and 1.22 ($\bar{x}$ = 0.89, SD = 0.15, *n* = 18), reflecting two properties: a slight statistical artifact produced by fit of a type 2 regression model to data where both *x* and *y* show equal variance, and a real, slight bias by juvenile instars against

larger beads. Chesson's selectivity index, which is not subject to the slight statistical correction, was very close to the null model. α_{small} ranged between 0.46 and 0.61 ($\bar{x}$ = 0.51, SD = 0.04, n = 18), indicating no bias at all for small or large beads in species of moderate-to-large body length. Within the Daphnidae, and especially within the genus *Daphnia*, flavored and unflavored bead pairings produced the same results as dual-flavor pairings (Fig. 4). The other moderate-sized genus, *Ceriodaphnia*, also showed no discrimination in size or taste (α_{small} = 0.50, Table 1).

Regression equations fitted by the type 2 model vs. the principal-components ordination (Table 2) for two species of large cladocerans are very similar, but notice the modest increase in slope when the dependent nature of both variables is recognized. Regression slopes are still significantly different from 1.00, but closer to the expected value.

A slight yet important exception to the patterns is found in the smallest body-size species of the Daphnidae. *Daphnia parvula* (0.71 mm) and especially *D. ambigua* (0.50–0.74 mm) showed slight, but significant, departures in both size and taste discrimination from the null model (Fig. 5, Table 1). Some young instars had difficulty ingesting 12-μm beads, whereas those that ingested beads showed slight taste discrimination.

Strongly size-selective, but only weakly taste-selective, cladocerans—Certain smaller bodied cladocerans (*Diaphanosoma, Chydorus*) fall in the category of strongly size selective, but only weakly taste selective. Both *Diaphanosoma* and *Chydorus* ingested fewer total beads per individual than daphnids (*Diaphanosoma*, mean ranged between 73 and 99 beads ind.$^{-1}$; *Chydorus* between 3 and 51 beads ind.$^{-1}$). Plots of large vs. small ingested beads illustrate modest to strong preferences for small beads (Fig. 6), although coefficients of determination are lower than those for daphnids (*Chydorus*, 0.41–0.79; *Diaphanosoma*, 0.12–0.61) (Table 1).

Chesson's index is much closer to the null model for *Chydorus* (mean body length = 0.27–0.37 mm; mean α_{small} = 0.47–0.61) than for *Diaphanosoma* (body length =

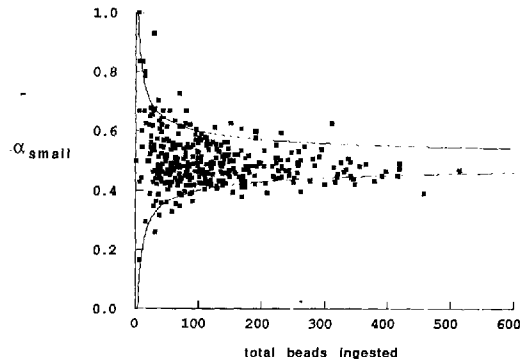Fig. 3. Expected vs. observed variation in Chesson's selectivity index for small beads (α_{small}) with sample size (No. of beads ingested). Data from the large-bodied, nonselective cladocerans *Daphnia retrocurva* and *Daphnia galeata mendotae*. Lines are expected 95% C.I. for the null model, assuming a binomial distribution and no selectivity (mean α_{small} = 0.5).

0.49–0.72 mm; α_{small} = 0.70–0.96), despite the larger body size of *Diaphanosoma*. *Chydorus* showed a significant size preference in only one sample, whereas *Diaphanosoma* exhibited a highly significant preference for smaller beads in all samples (Fig. 6, Table 1). In *Diaphanosoma*, the strong small-bead bias ranged from nearly complete ingestion of 6-μm beads by all instars to a nearly 1 : 1 null pattern in very large adults during one experiment. Two samples of *Diaphanosoma* also showed significant indications of taste sensitivity (Fig. 6, Table 1).

Taste-selective cladocerans—Whereas small daphnids and a few *Diaphanosoma* samples seemed to have a slight taste sensitivity, only one cladoceran had a clear taste bias, the small-bodied *Bosmina longirostris* (mean body length, 0.26–0.37 mm). Coefficients of determination for small- vs. large-bead ingestion regressions were lower than for daphnids (0.10–0.38), largely because fewer beads were ingested per individual (5–25 beads ind.$^{-1}$). *Bosmina* showed a strong age and size preference, as first instars fed almost exclusively on 6-μm beads, whereas adults showed modest taste responses (Fig. 6); t-test comparisons of α_{small} with both the null model and between taste treatments showed significant to highly significant differences between treatment responses (Table 1).

Strongly taste-selective copepods—Cal-

Table 1. Results from bead ingestion experiments. Treatment abbreviations: Ch—*Chlamydomonas*-flavored beads; Cy—*Cyclotella*-flavored beads; nf—nonflavored beads. n—Number of individuals. Number of beads counted per treatment; mean number of beads counted per individual given in parentheses. Regression equation for number of large vs. small beads ingested where X = No. large beads ingested, Y = No. of small beads ingested, and C = Y-intercept; 95% C.I. given for slope. Mean selectivity index for small beads (α_{small}); P-value symbols for t-tests comparing α_{small} to 0.5, the value expected if animals fed nonselectively. Taste selection P-value symbols for t-tests comparing α_{small} values between two reciprocal treatments. Correlation of α_{small} vs. body length (mm) shows checks for ontogenetic shifts in selectivity; correlation coefficient and P-value for significance of correlation. Asterisks: $P > 0.05$; *—$P < 0.05$; **—$P < 0.01$; ***—$P < 0.001$; ns—not significant.

Location and date	Treatment (small/large beads)	n	Body length (mm) mean (range)	No. beads counted	Regression of large vs. small beads ingested		$\alpha_{small} \pm$ SE	Taste selection	Correlation of α_{small} vs. length r
					r^2	Y = slope ($\pm$C.I.) $X + C$			
Daphnia ambigua									
Third Sister Lake, 8 May	Ch/nf	89	0.50 (0.33–1.17)	2,749(31)	0.21	0.71($\pm$0.29)X + 15.99	0.73±02***	*	−0.27*
10 May	nf/Ch	153		1,596(10)	0.55	0.93($\pm$0.13)X + 2.21	0.64±0.02***		−0.42***
Douglas Lake, 10 Aug	Cy/nf	10	0.74 (0.55–0.88)	1,146(115)	0.95	1.09($\pm$0.19)X + 8.67	0.55±0.01**	*	0.15ns
10 Aug	nf/Cy	16		1,753(110)	0.93	0.84($\pm$0.13)X + 2.01	0.49±0.02ns		−0.46ns
14 Aug	Ch/Cy	33	0.65 (0.49–0.85)	1,613(49)	0.88	0.79($\pm$0.11)X + 2.35	0.48±0.03ns	ns	0.23ns
14 Aug	Cy/Ch	31		1,730(56)	0.81	0.85($\pm$0.16)X + 3.78	0.50±0.03ns		0.16ns
Daphnia galeata mendotae									
Douglas Lake, 10 Aug	Cy/nf	37	0.81 (0.41–1.29)	8,396(227)	0.88	0.73($\pm$0.10)X + 19.00	0.48±0.01ns	ns	−0.22ns
10 Aug	nf/Cy	42		8,270(197)	0.92	0.80($\pm$0.08)X + 14.35	0.52±0.02ns		−0.26ns
14 Aug	Ch/Cy	44	0.80 (0.46–1.73)	4,236(96)	0.91	0.79($\pm$0.08)X + 7.10	0.49±0.01ns	ns	−0.10ns
14 Aug	Cy/Ch	35		3,791(108)	0.90	0.83($\pm$0.10)X + 6.08	0.50±0.01ns		−0.17ns
Daphnia parvula									
Third Sister Lake, 8 May	Ch/nf	31	0.71 (0.38–1.25)	2,093(68)	0.87	1.16($\pm$0.17)X + 5.95	0.61±0.04*	*	−0.46**
10 May	nf/Ch	131		2,401(18)	0.90	0.94($\pm$0.06)X + 1.20	0.51±0.02ns		−0.18*
Daphnia pulicaria									
Third Sister Lake, 8 May	Ch/nf	16	0.92 (0.52–1.63)	1,617(101)	0.95	1.22($\pm$0.15)X − 1.08	058±0.05ns	*	−0.62*
10 May	nf/Ch	10		2,140(214)	0.99	0.83($\pm$0.07)X + 4.33	0.46±0.02ns		−0.01ns
Daphnia retrocurva									
Douglas Lake, 23 Jul	Ch/nf	12	0.81 (0.51–1.25)	757(63)	0.92	0.95($\pm$0.19)X + 1.58	0.49±0.03ns	ns	−0.43ns
23 Jul	nf/Ch	6		644(107)	0.78	0.65($\pm$0.44)X + 16.98	0.51±0.04ns		−0.05ns
10 Aug	Cy/nf	51	0.79 (0.38–1.06)	6,438(126)	0.87	0.92($\pm$0.10)X + 3.33	0.50±0.01ns	ns	−0.23ns
10 Aug	nf/Cy	40		3,744(94)	0.85	0.80($\pm$0.11)X + 5.27	0.50±0.02ns		−0.13ns
14 Aug	Ch/Cy	36	0.79 (0.41–1.10)	3,260(91)	0.90	0.88($\pm$0.10)X + 4.05	0.50±0.01ns	ns	−0.08ns
14 Aug	Cy/Ch	84		7,356(88)	0.86	0.86($\pm$0.08)X + 3.62	0.49±0.01ns		−0.01ns

Table 1. Continued.

| Location and date	Treatment (small/large beads)	n	Body length (mm) mean (range)	No. beads counted	Regression of large vs. small beads ingested		α_small ± SE	Taste selection	Correlation of α_small vs. length r
					r^2	$Y = \text{slope} (\pm\text{C.I.}) X + C$			
Ceriodaphnia quadrangula									
Douglas Lake, 14 Aug	Ch/Cy	26	0.50 (0.31–0.61)	1,639(63)	0.79	0.80(±0.17)X + 5.73	0.50±0.02ns	ns	0.003ns
14 Aug	Cy/Ch	27		2,025(75)	0.91	0.89(±0.11)X + 3.32	0.50±0.03ns		−0.15ns
Chydorus sphaericus									
Third Sister Lake, 8 May	Ch/nf	24	0.37 (0.23–0.55)	1,225(51)	0.75	0.54(±0.14)X + 5.29	0.51±0.04ns	ns	−0.47ns
10 May	nf/Ch	28		78(3)	0.47	0.42(±0.18)X + 0.40	0.47±0.08ns		−0.18ns
Douglas Lake, 23 Jul	Ch/nf	24	0.27 (0.18–0.38)	415(17)	0.41	0.42(±0.22)X + 5.50	0.61±0.05*	ns	−0.66***
23 Jul	nf/Ch	17		260(15)	0.79	0.79(±0.22)X + 2.57	0.60±0.05ns		−0.38ns
Diaphanosoma birgei									
Douglas Lake, 23 Jul	Ch/nf	54	0.68 (0.39–0.97)	3,794(70)	0.39	0.69(±0.24)X + 28.55	0.70±0.02***	ns	−0.79***
23 Jul	nf/Ch	73		5,513(76)	0.37	0.75(±0.23)X + 36.48	0.75±0.02***		−0.61***
10 Aug	Cy/nf	52	0.49 (0.30–0.86)	3,255(63)	0.41	1.32(±0.45)X + 38.40	0.89±0.02***	**	−0.72***
10 Aug	nf/Cy	79		4,168(53)	0.58	3.00(±0.58)X + 38.37	0.96±0.01***		−0.83***
14 Aug	Ch/Cy	26	0.72 (0.51–1.16)	1,903(73)	0.61	2.29(±0.77)X + 44.74	0.90±0.02***	***	−0.04ns
14 Aug	Cy/Ch	44		3,274(74)	0.24	1.41(±0.78)X + 38.77	0.80±0.02***		−0.04ns
Bosmina longirostris									
Third Sister Lake, 8 May	Ch/nf	9	0.37 (0.21–0.57)	229(25)	0.19	2.67(±4.77)X + 11.99	0.78±0.07**	*	−0.30ns
10 May	nf/Ch	63		334(5)	0.38	0.34(±0.11)X + 1.07	0.52±0.05ns		−0.24ns
Douglas Lake, 23 Jul	Ch/nf	120	0.26 (0.20–0.43)	2,244(19)	0.15	0.65(±0.28)X + 13.67	0.88±0.01***	**	−0.69***
23 Jul	nf/Ch	145		1,625(11)	0.10	0.31(±0.15)X + 6.76	0.78±0.02***		−0.50***
Skistodiaptomus oregonensis									
Third Sister Lake, 10 Jul	Ch/nf	43	0.55 (0.21–0.73)	2,881(67)	0.40	38.77(±14.88)X + 53.13	1.00±0.00***	***	−0.21ns
11 Jul	nf/Ch	12		69(6)	0.11	0.12(±0.26)X + 0.59	0.21±0.05**		−0.36ns
Douglas Lake, 10 Aug	Cy/nf	140	0.96 (0.57–1.17)	7,387(53)	0.16	5.78(±2.25)X + 41.58	0.97±0.00***	***	−0.33***
10 Aug	nf/Cy	111		2,034(18)	0.45	0.27(±0.06)X + 5.12	0.53±0.02ns		−0.16ns
14 Aug	Ch/Cy	52	0.91 (0.55–1.13)	1,420(27)	0.33	7.00(±2.83)X + 16.84	0.95±0.01***	***	−0.35*
14 Aug	Cy/Ch	60		1,292(22)	0.43	1.40(±0.42)X + 7.47	0.73±0.03***		0.06ns
Onychodiaptomus sanguineus									
Thurston Pond, 10 Jul	Ch/nf	34	1.01 (0.79–1.35)	4,712(139)	0.05	12.96(±21.00)X + 121.35	0.99±0.00***	***	−0.07ns
11 Jul	nf/Ch	34		1,481(44)	0.02	0.01(±0.02)X + 1.78	0.08±0.02***		−0.15ns
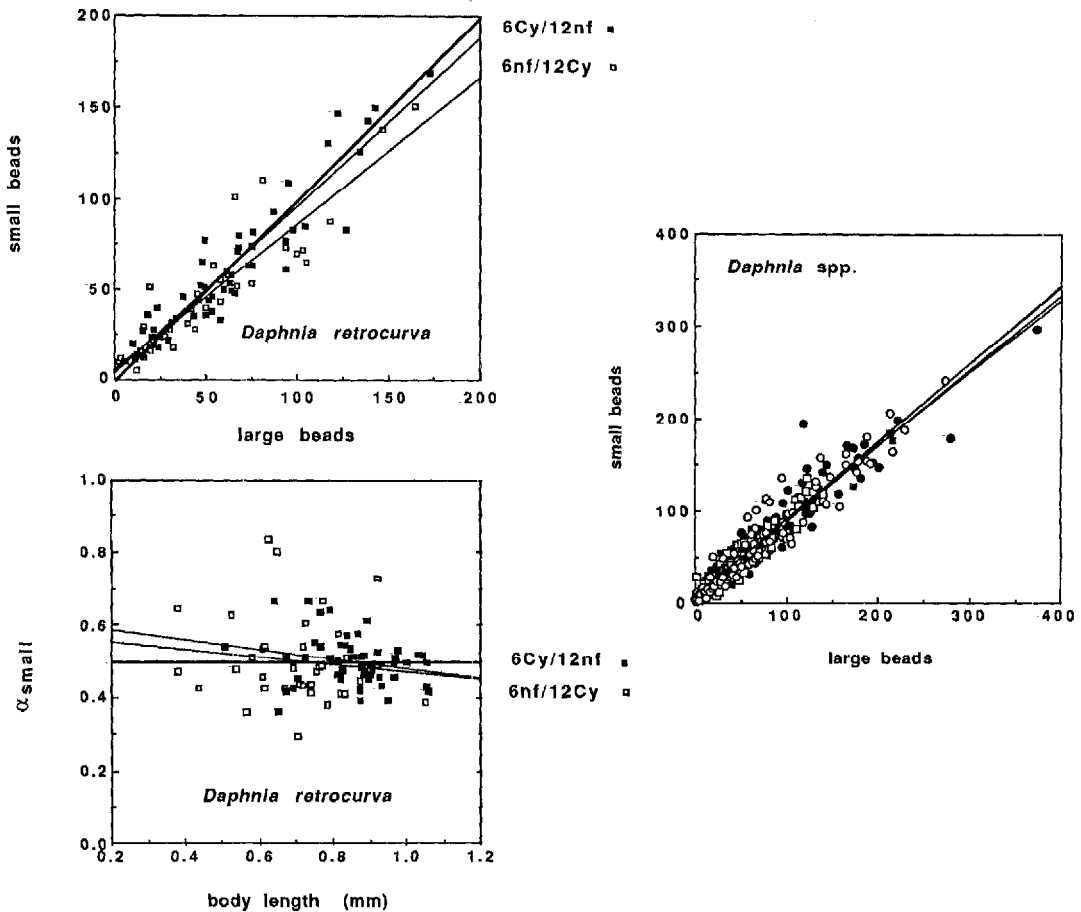
Fig. 4. Patterns of bead ingestion by nonselective, large-bodied daphnid cladocerans. Numbers of large and small beads ingested by individuals shown for *D. retrocurva* (with *Cyclotella*-flavored beads); closed symbols— treatments in which small beads are flavored; open symbols—treatments in which large beads are flavored. 6Cy/ 12nf indicates a treatment in which small (6 μm) beads were flavored with *Cyclotella* exudates and large (12 μm) beads were not flavored. Regression lines were fitted to data from each treatment. The plot of α_{small} vs. body length for *D. retrocurva* shows a lack of ontogenetic shifts in selectivity. Also shown are patterns of large- and small-bead ingestion for *D. retrocurva* and *Daphnia galeata mendotae* combined, from experiments pairing *Cyclotella*-favored vs. unflavored beads (circles) and *Cyclotella*-flavored vs. *Chlamydomonas*-flavored beads (squares).

anoid copepods were reluctant to ingest exudate-coated beads early in the year, when high-quality food resources were abundant and their energy reserves were high. For example, during taste tests run between 8 and 10 May on 152 individuals (mean body length, 0.74–1.16 mm), only 0.5–2.0 beads ind.$^{-1}$ were ingested, too few for accurate preference checks. During July and August, however, when lipid reserves appeared lower and when algal resource quality and quantity seemed lower (dominance by cy-

anobacteria), ingestion rates were high enough (18–139 beads ind.$^{-1}$) for taste discrimination tests. In these late-season experiments, species spanned the same body lengths as daphnids, 0.55–1.01 mm, yet rates of bead ingestion were usually lower than those of cladocerans. The number of beads ingested was positively correlated with body length (Pearson r range = 0.31–0.67, $\bar{x}$ = 0.45, n = 8) raised to a power of 2.0–2.2.

One might suppose that willingness to ingest coated, otherwise inert particles would

Table 2. Comparison of model 2 and principal-component regression fits on data for *Daphnia* small- vs. large-bead ingestion. Treatment abbreviations as in Table 1.

Treatment	Model 2 regression (95% C.I. of slope)	Principal-component regression (95% C.I. of slope)
10 Aug 89		
Cy/nf	$Y = 0.78(\pm 0.06)X + 13.30$	$Y = 0.82(\pm 0.06)X + 10.00$
nf/Cy	$Y = 0.83(\pm 0.05)X + 7.02$	$Y = 0.87(\pm 0.05)X + 4.59$
14 Aug 89		
Ch/Cy	$Y = 0.83(\pm 0.05)X + 4.33$	$Y = 0.87(\pm 0.05)X + 2.87$
Cy/Ch	$Y = 0.85(\pm 0.05)X + 4.20$	$Y = 0.90(\pm 0.05)X + 1.97$

go hand in hand with poor taste discrimination. Such was not the case, as *Skistodiaptomus oregonensis* and *Onychodiaptomus sanguineus* were highly taste selective and moderately size selective. The moderate size preference was evident in higher ingestion rates when small beads were labeled (~3–10-fold difference, Table 1), with the interesting exception of the dual-label experiments. The taste preference was dramatic, as copepods clearly chose small beads when they were flavored and large beads when they were flavored (Fig. 7). In the Thurston Pond and Third Sister Lake experiments, α_{small} ranged as high as 0.99–1.00 when small beads were flavored to as low as 0.05–0.21 when large beads were flavored (Table 1). *S. oregonensis* from Douglas Lake was also excellent at picking out small beads when they were flavored ($\alpha_{small} = 0.97$), but were poorer at sorting large beads from small beads when the large beads were flavored ($\alpha_{small} = 0.44$).

Dual-flavor tests run on Douglas Lake animals showed that *S. oregonensis* not only was sensitive to flavor vs. nonflavor treatments, but also responded differently to *Chlamydomonas*- or *Cyclotella*-flavored beads, so that all four treatments produced distinctive results (Fig. 7). If calanoid copepods were responding solely to the presence or absence of organic compounds, and not the kind of compound, then dual-flavor treatment regressions should overlap. They clearly do not. The selectivity coefficient for small beads was 0.95 when small beads were flavored with *Chlamydomonas* and declined to 0.78 when small beads were flavored with *Cyclotella* (Table 1), indicating a slight preference for *Chlamydomonas*-flavored beads.

Discussion

The exudate-coated bead tests are viewed as conservative yet powerful indicators of taste discrimination in that differences are based solely on adsorbed organic compounds, with most other particle properties
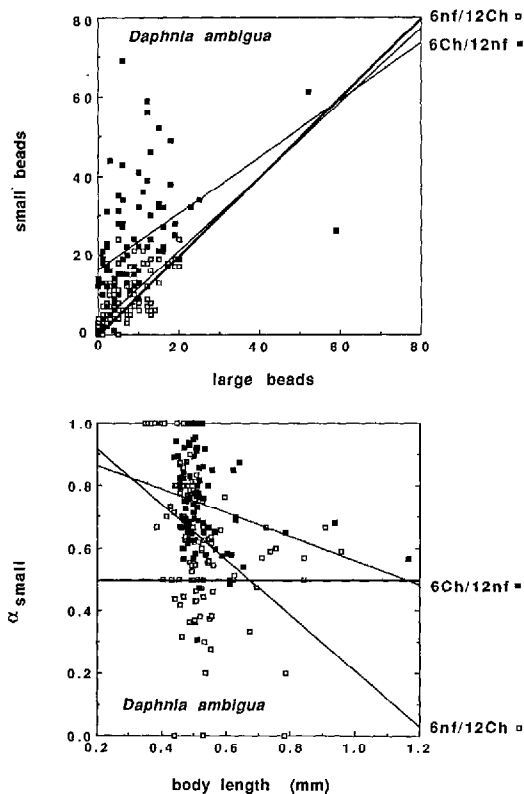

Fig. 5. Pattern of bead ingestion by *D. ambigua.* Symbols as in Fig. 4. Ch indicates beads flavored with *Chlamydomonas* exudates. *D. ambigua* shows clear size selectivity and modest taste selectivity (upper graph). There is also an ontogenetic pattern to its size selectivity—a significant negative correlation between body length and α_{small} (Table 1).
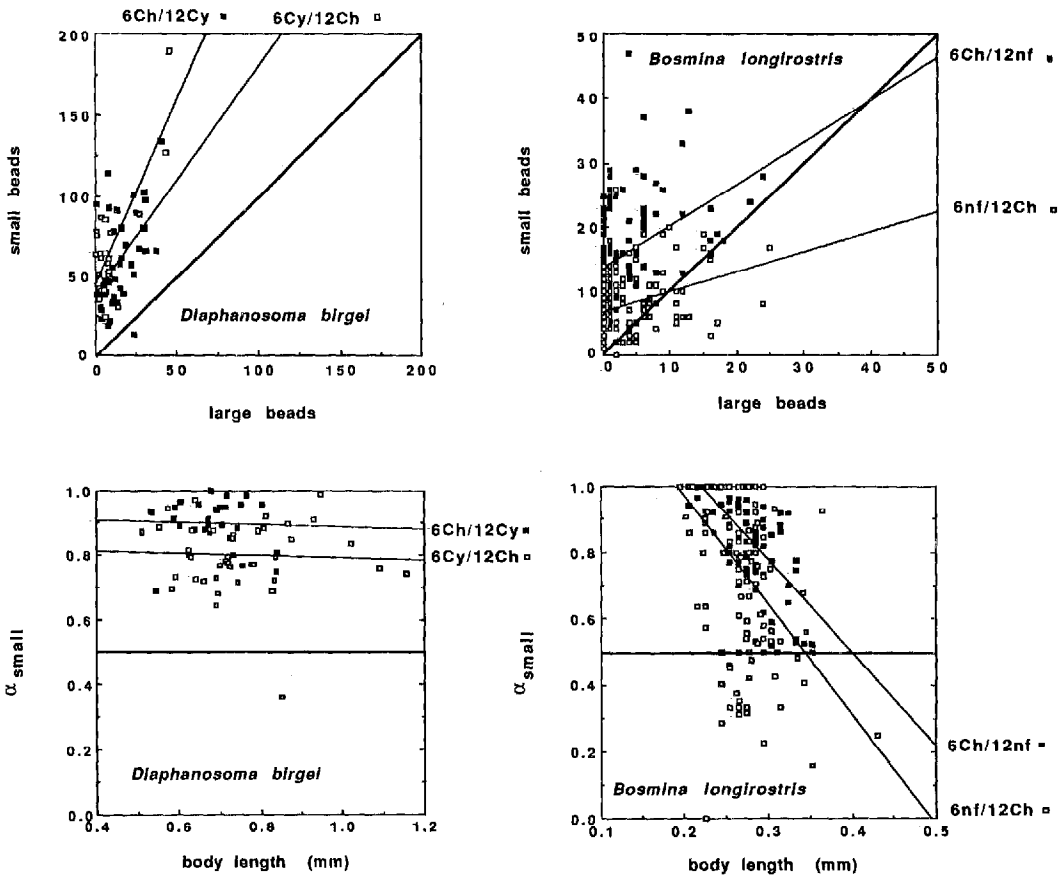
Fig. 6. Patterns of bead ingestion by the small-bodied cladocerans *D. birgei* and *B. longirostris.* Symbols as in Fig. 4. Both genera show a strong preference for small beads, with a strong ontogenetic correlation in all *Bosmina* cases and some other *Diaphanosoma* cases (Table 1). Preference for large beads in *Bosmina* is seen only when large beads are flavored (taste preference) and is more pronounced in adults. Interpretation of the pattern in *Diaphanosoma* is more complicated (*see text*).

held constant. Although somewhat artificial, this design possesses an advantage over bead vs. living algal pairings (DeMott 1986, 1989; Bern 1990a). In the latter experiments, properties of living cells other than taste (e.g. motility, pliability) could influence preference.

Given the simplicity of the laboratory tests, the contrast between how large-bodied cladocerans and copepods react to small beads is striking (Fig. 8) and certainly confirms the original findings of DeMott (1986). The dichotomy between copepods and cladocerans is clear. On the index scale from 0 to 1.0 (difference between reciprocal treatments), all copepods had differences >0.4, while most cladocerans (including weakly

discriminating *Daphnia* and *Diaphanosoma*) had taste discrimination values <0.2. Only the cladoceran genera *Bosmina* and *Eubosmina* had differences >0.2 (range 0.3–0.6). Moreover, the large grouping of points at the origin (no taste or size discrimination) is made up of several large daphnid, *Ceriodaphnia,* and *Chydorus* species.

With regard to handling of small particles, large-bodied cladocerans and calanoid copepods fall at the extremes of a continuum. Large-bodied species in the family Daphnidae seem to be generalized fine-particle suspension feeders, capable of clearing water of a broad range of small particle sizes. There was no indication that taste made any difference in bead ingestion patterns,
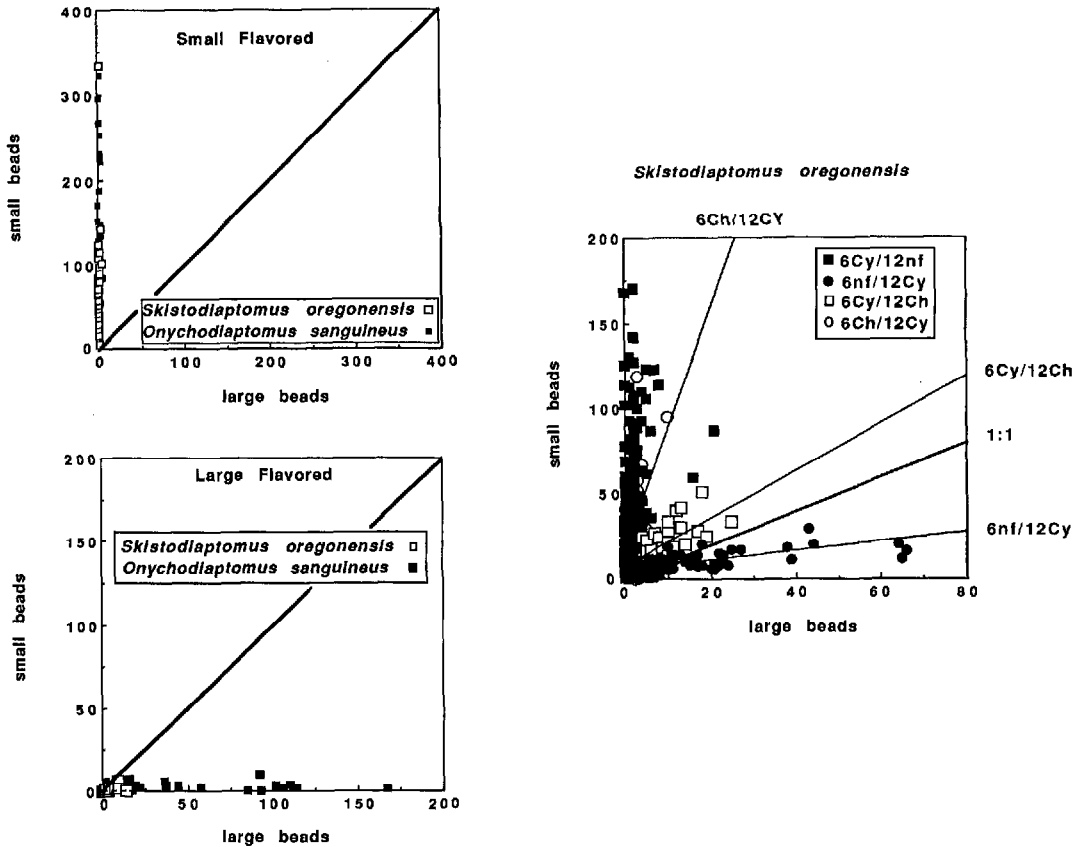
Fig. 7. Patterns of bead ingestion by two species of calanoid copepods. Symbols as in Fig. 4. Strong taste discrimination is exhibited by both *S. oregonensis* and *O. sanguineus*. Both species ingest flavored beads almost exclusively, irrespective of bead size. *S. oregonensis* could distinguish between *Chlamydomonas*-flavored and *Cyclotella*-flavored beads when both were offered simultaneously, showing a slight preference for *Chlamydomonas*-flavored beads.

either for flavored vs. unflavored or for dual-flavor tests. The latter is understandable, for if *Daphnia* show no (to only weak) sensitivity to a flavored vs. unflavored pairing, they should be relatively insensitive to dual-flavor treatments. Indeed, many large-bodied taxa appear to have evolved toward fine filtration and bulk processing, expending large quantities of energy continuously pumping water in order to extract small particles. Agglutination of fine food particles as they pass through the gnathobase setae toward the mandibles contributes to this generalized gathering mode. Individual particles are relatively small, leading individuals either to accept or to reject the entire bolus with the postabdominal claw rather than to reject individual particles. Because of their relative insensitivity to small-particle quality, most cladocerans could just as likely be termed detritivores as herbivores.

The fundamental difference in bead-handling tactics suggests broader implications for biotic interactions, beyond minimal energy levels for maintaining suspension feeding (Richman and Dodson 1983; Muck and Lampert 1984). Although the strategy of a generalized, rapid bulk feeder may be detrimental when suspended paritcles are predominantly inorganic (Kirk 1991), the same tactic may have merit with mixtures of algae and relatively high-quality organic detritus. Under the circumstances of high absolute abundance of fresh detritus, *Daphnia* may extract enough energy to resist starvation between algal pulses. For example, the rel-
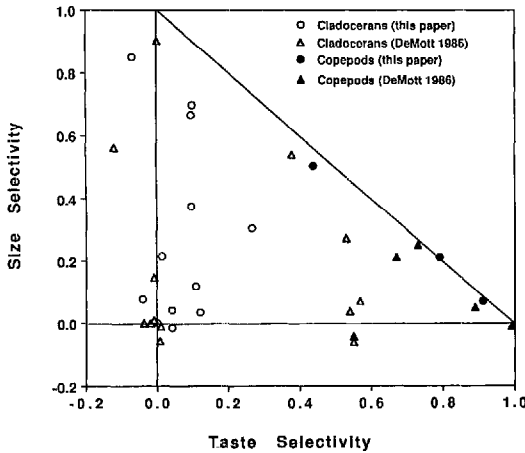
Fig. 8. Overall patterns of taste and size selectivity. Index of taste selectivity = α_{small} when small beads are flavored − α_{small} when large beads are flavored. Index of size selectivity = $\alpha_{flavored}$ when small beads are flavored − $\alpha_{flavored}$ when large beads are flavored. Data are from this paper and from DeMott (1986). Taste and size selectivities in the region above the diagonal line cannot be resolved with this method. All cladocerans with taste selectivities >0.2 are *Bosmina* or *Eubosmina*.

atively high absolute amounts of detrital particles present in epilimnetic and hypolimnetic waters in summer or early fall can run 4–6× more abundant than living algae (Mann 1988). Under these circumstances, even if detrital particles contain only 17–25% of the energetic content of living algae, on a bulk basis they might contribute more than half of the consumer's energetic requirements.

Moreover, the vertical position of large cladocerans in the water column may have additional ecosystem repercussions. A generalized detritivore may be able to capitalize on sinking algae and small organic detrital particles that accumulate along the top of the thermocline. Under these conditions, large-bodied cladocerans would constitute the functional aquatic analog of the earthworm, reworking organic debris through generalized ingestion, while their poorly consolidated defecation broadcasts detritus for further reworking. These cladocerans would then represent an important detritivore feature of recycling in epilimnetic waters.

In contrast to the findings of DeMott (1986), our experiments revealed discriminatory powers in small-bodied daphnids and other cladocerans. Size discrimination was evident in most of these small cladocerans and we suspect that it is tied to taste discrimination. For example, *Diaphanosoma* clearly had a preference for fine particles, confirming filter mesh and bead studies by others (Geller and Müller 1981; DeMott 1985), where *D. ambigua* and *Bosmina* were also very sensitive to particle size. The situation with *Diaphanosoma* remains especially interesting because the degree of size and taste selection varied with the experiment. Evidently, this genus has a way of regulating acceptance of large beads. One could speculate that the mechanism is the gape aperture mechanism proposed by Gliwicz (1977), but we suspect that the weak-to-modest discriminatory powers in small-bodied *Daphnia* and *Diaphanosoma* indicate an important point about relative particle size. In cladocerans this small, the beads may be processed one at a time, allowing single particle rejection at the mandibles. Indeed, these observations lend credibility to several recent tests that suggest selective acceptance of especially nutritious algae and rejection of relatively large, noxious particles by *Daphnia* (e.g. Butler et al. 1989; Bern 1990b).

Bern (1990b) in particular has suggested that taste discrimination within *Daphnia cucullata* and *Bosmina* could be related to particle size. Moreover, relative particle size could explain some puzzling observations. For example, DeMott (1990) discussed small-bead experiments (2- and 6-μm polystyrene spheres) with *Diaphanosoma* in which selectivity was biased toward small beads and invariant over a body size range of 0.3–1.2 mm. As mentioned earlier, our own results show surprising variability between experiments. Clearly there is a behavioral mechanism here that requires further study.

We believe that nontaste discrimination of small particles and taste-discriminating collection of relatively large particles may be widespread. Size-dependent shifts from nontaste selective to taste-selective feeding have important implications for the evolution of plant-herbivore interactions. It is

easy to conceive of the evolution of unpalatability in phytoplankton as a defense against grazers, if those grazers are capable of taste discrimination and rejection of noxious particles. Unpalatability as an algal defense against nondiscriminatory foragers, however, presents real challenges.

The contrast between *Chydorus* and *Bosmina* also remains interesting. Although similar in body length, *Chydorus* does not exhibit taste discrimination, whereas *Bosmina* adults clearly are sensitive to taste. *Bosmina* juveniles are also strongly sensitive to particle size, a feature that complicates precise determination of taste selectivity with our particular experimental design. The strong taste discrimination may relate to *Bosmina*'s unique dual-option feeding mechanism (DeMott and Kerfoot 1982; DeMott 1985, 1986; Bleiwas and Stokes 1985; Bern 1990*b*). Differential taste discrimination may occur in the anterior thoracic-appendage region, whereas nondiscrimination may occur in the posterior filtration-mesh portion of the dual-option feeding mechanism (DeMott and Kerfoot 1982; DeMott 1985; Bern 1990*b*).

In contrast to most cladocerans, calanoid copepods showed extreme sensitivity to taste. These results clearly confirm the initial findings of DeMott (1986, 1988*b*) and underscore the ability of copepods to examine items individually (Vanderploeg 1990). Moreover, the response was clearly influenced by the nutritional environment. In the energy-rich environment of May and early June, copepods would hardly ingest beads at all. In simultaneous experiments, copepods ingested small *Cyclotella,* which indicates preference for living cells over exudate-coated beads. In the energy-poor environment of July and August, however, copepods ingested beads and were highly selective about which beads they ate. The relatively high discriminatory ability during periods of resource shortage at first appears counterintuitive. If copepods are hungry enough to accept polystyrene beads, we might expect them to be less discriminatory to flavor.

Yet the fact that the beads are coated with fresh algal exudate may explain the dilemma. As mentioned earlier, in late summer detritus is much more abundant than living phytoplankton. Taste discrimination may have evolved partly in order to allow calanoid copepods to assess the nutritional quality of detritus, in addition to distinguishing between phytoplankton, detritus, and inorganic particles. Calanoid copepods are known to show strong preference for living cells over detritus (DeMott 1988*a*). Applying the clear laboratory responses to field conditions involves another dilemma. Rather than concentrating in regions of higher food quantity and quality (e.g. highly productive epilimnetic waters), calanoid copepods are broadly distributed throughout the water column. For example, in the Great Lakes, calanoid copepods occur in epilimnetic waters and in cool hypolimnetic regions of low productivity and low particle quality, whereas cladocerans seem more restricted to warm, productive environments. We suspect that the acute ability of calanoid copepods to assay food quality provides a key benefit in detritus-rich waters. Selective suspension feeders may dominate deep and offshore waters because they can bypass low-quality detritus or suspended clay particles and concentrate on settling algae, larger and more nutritionally rich detrital particles, and perhaps small animals (omnivory). Taste discrimination may be more closely allied with the ability to avoid low-quality detritus in detritus-rich waters than with discrimination between living taxa of algae. As opposed to large-bodied cladocerans, calanoid copepods are facultative detritivores, concentrating their foraging on high-quality detrital particles when average particle quality becomes low.

These laboratory experiments are consistent with observations by others. For example, diaptomids and other calanoid copepods are able to detect algae, moving toward odors (Poulet and Ouellet 1982). These organisms can utilize high-speed manipulation of currents and particles to capture large algae or to separate clumps of algae from inert particles (Vanderploeg 1990). The ability of diaptomids to discriminate so well between flavored and unflavored beads in our experiments indicates great sensitivity at the individual-item level through capture, handling, and ingestion.

The degree to which diaptomids can discriminate among small algae and flavored and unflavored microspheres (DeMott 1986, 1989) suggests that these copepods are continually appraising resource quality in nature.

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