CONCENTRATION-VARIABLE INTERACTIONS BETWEEN CALANOID COPEPODS AND PARTICLES OF DIFFERENT FOOD QUALITY: OBSERVATIONS AND HYPOTHESES*

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Introduction

The two major issues of research in feeding behavior of calanoid copepods and, indeed, in all research on zooplankton feeding have been concentration-variable selection and food quality (Vanderploeg in press). The concentration-variable selectivity hypotheses in its earliest form stated that copepods would track peaks in natural particle-size spectra, that is, focus their efforts on the most abundant food (Vanderploeg 1981a; Vanderploeg et al. 1984). The counter hypothesis is that selectivity, when expressed as W' or other appropriate measures, remains invariant no matter what the relative proportions or total concentration of the various food types (Vanderploeg and Scavia 1979a,b; Vanderploeg 1981a; Vanderploeg et al. 1984).

The direct observations of Strickler and colleagues (e.g., Alcaraz et al. 1980; Koehl and Strickler 1981; Strickler 1982; Paffenhöfer et al. 1982), using the newly developed technique of high-speed microcinematography, showed that certain calanoid copepods can create a double-shear scanning current that focuses water near their bodies, and that they respond with coordinated movements of their mouthparts to capture large algae they detect in this current. At this time, olfaction was described as the stimulus (Andrews 1983), and this is still the accepted paradigm, although mechanoreception has been also hypothesized (Legier- Visser et al. 1986). Invariant selectivity became identified with the passive-mechanical selection of filtering since this was one obvious means of obtaining invariant selection (Vanderploeg 1981a; Vanderploeg et al. 1984). At the same time, a number of studies showed that copepods preferentially ingest algae over plastic microspheres and algal-exudate-flavored

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microcapsules over unflavored microcapsules (e.g., Poulet and Marsot 1978; Donaghay 1980) and that copepods have numerous mechanoreceptors and chemoreceptors on the mouth parts to make choices (e.g., Friedman 1980). These cinematographic observations and ability of copepods to select particles on the basis of a particle's nutritional value ushered in a new era zooplankton feeding biology emphasizing the importance of nutritional value of particles and the optional foraging narrative, since peak tracking is one facet of the optional foraging story (Pyke et al. 1977; Hughes 1980; Vanderploeg et al. 1984, 1988).

Our goals in this paper are to present new observations and hypotheses on the food selection mechanisms of calanoid copepods and relate these mechanisms to the many new observations on involving food quality (e.g., DeMott 1986, 1988, 1989; Fulton 1988; Fulton and Paerl 1988). We will focus our efforts on *Diaptomus*, a freshwater copepod that creates a scanning current. *Diaptomus* and other scanners like the marine copepods *Paracalanus* and *Eucalanus* are dominant grazers in lakes and in coastal and offshore waters (Vanderploeg and Paffenhöfer 1985; Paffenhöfer and Stearns 1988).

The Current Paradigm on Mechanisms

Selection for High Quality Food -- The current paradigm of feeding mechanisms and its connection to selectivity in calanoid copepods come in large part from high-speed microcinematography of tethered copepods feeding on live algae and microzooplankton of various sizes (e.g., Alcaraz et al. 1980; Koehl and Strickler 1981; Paffenhöfer et al. 1982; Price et al. 1983; Price and Paffenhöfer 1985; Vanderploeg and Paffenhöfer 1985; Vanderploeg et al. 1988; Williamson and Vanderploeg 1988). Figure 1 summarizes our present knowledge on capture modes of *Diaptomus* and their relation to selectivity from experiments with easily ingested high-quality algae and an easily ingested soft bodied rotifer. Selectivity is expressed here as $W_i'=F_i/F_{pref} = m_i/m_{pref}$, where F_i and F_{pref} are, respectively, clearance rates on prey i and the preferred prey, and m_i and m_{pref} are respective mortality rate coefficients (Vanderploeg and Scavia 1979a). That is, W' is just the clearance rate or mortality rate normalized to that of the preferred prey. We prefer the selectivity coefficient, W', to Vanderploeg and Scavia's (1979b) electivity indices W(=α of Chesson 1983), which is proportional to W', and E* because the values of W and E* depend on number of kinds of prey, and because W' is the coefficient used in the effective food concentration model (Vanderploeg and Scavia 1979a; Vanderploeg et al. 1984). Moreover, W' can be

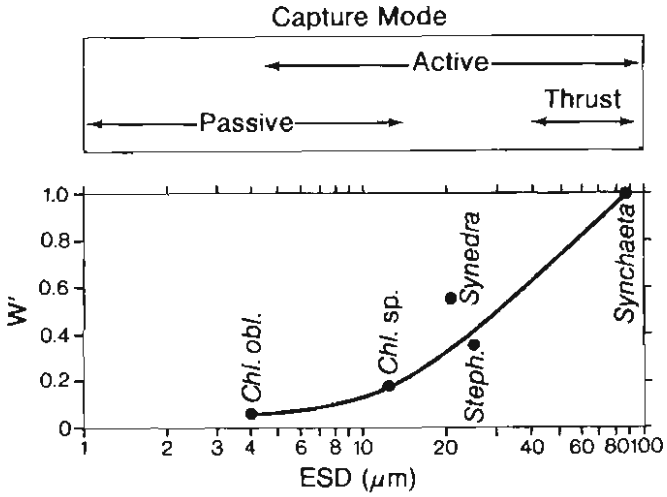

Figure 1. Lower panel: The selectivity (W') vs. equivalent spherical diameter (ESD) curve for *Diaptomus* feeding on high quality food. The curve is a composite of results from experiments of *D. sicilis* feeding on the algae *Chlamydomonas* sp., *C. oblonga*, *Stephanodiscus niagare*, and *Synedra* sp. (Vanderploeg et al. 1984; Vanderploeg et al. 1988) as well as those for *D. pallidus* feeding on the rotifer *Synchaeta oblonga* (Williamson and Butler 1986). Upper panel: The capture modes used for these prey (Vanderploeg and Paffenhöfer 1985; Vanderploeg et al. 1988; Williamson and Vanderploeg 1988).

broken down into a sequence of conditional selectivities at each step of the behavioral chain leading to ingestion in a fashion analogous to Holling's (1966) conditional probabilities for his components-of-predation approach (Vanderploeg in press).

The selectivity curve shown in Figure 1 represents the perceptual bias of *Diaptomus* for the different prey. We can say this because factors including handling and taste that affect the rest of the behavioral chain leading to ingestion do not apply to this high quality food at the low food concentrations at which these experiments were performed. As seen in Figure 1, there is an overlap in size range over which the various capture modes operate. Small particles are captured passively without detection by the copepod. These passively captured particles carried in the scanning current flow in undetected between the feeding appendages, and are funneled toward the mouth (Vanderploeg and Paffenhöfer 1985; Price and Paffenhöfer 1986). As particles get larger an increasing proportion of them are captured actively, that is, they are detected in the scanning current, and coordinated motions of the mouthparts are used to bring the particle toward the median and ultimately ingest it (Koehl and Strickler 1981). As algal size increases, it is probable that the algae are also

sensed at greater distances (Vanderploeg and Paffenhöfer 1985). Thus the perceptual bias explains the increasing selectivity with increase in algal size (Price and Paffenhöfer 1985; Vanderploeg and Paffenhöfer 1985) .

The rotifer *Synchaeta*, the most preferred of *Diaptomus*' prey, was captured actively like the algae or with a thrust response that has only been observed for microzooplankton. The thrust response is a vigorous pouncing motion created by a sweeping back of the antennae and thrust of the swimming feet (Williamson and Vanderploeg 1988). This vigorous thrust response is thought not just to be an enthusiastic response to a distantly perceived large particle but probably a directed attack at potentially highly mobile prey that *Diaptomus* recognizes as animal prey (Williamson and Vanderploeg 1988).

In feeding experiments with mixtures of the passively captured alga *Chlamydomonas oblonga* (diameter = 4 μm) and the actively captured *Chlamydomonas* sp. (12 μm), Vanderploeg et al. (1984) showed that selectivity (W') for the small alga remained at approximately 0.3 relative to the large alga no matter what the relative proportions or total concentrations of the algae offered. In contrast, Vanderploeg et al. (1988) showed that at high concentrations of *Synedra* sp. (a rod 240 μm long) in mixtures with *Chlamydomonas* sp., selectivity for *Chlamydomonas* increased (Table 1). They argued that this concentration-variable selectivity could be viewed properly in the classical ethological framework of motivation and excitability of different motor patterns used to capture, handle, and ingest different kinds of algae. Specifically they

Table 1. A summary of *Diaptomus sicilis* clearance rate ratios (F_c/F_s), a measure of selectivity, and proportion (Pr) of attacked *Synedra* only partially ingested (<50%) as a function of relative concentrations (X_c/X_s) and total concentrations of *Chlamydomnas* (C) and *Synedra* (S) in experiments of Vanderploeg et al. (1988).[a]

Total conc.	X_c/X_s	F_c/F_s	Pr	Grouping[b]
Low conc.[c]	10.2	21/35=0.60±0.02	0.18	A
Low conc.[c]	0.52	19/30=0.63±0.04	0.34	A
High conc.[d]	6.0	9.4/7.0=1.3±0.03	0.32	B
High conc.[d]	0.41	10.5/5.1=2.0±0.12	0.61	C

[a] See Vanderploeg et al. for full statistical details.
[b] A different letter indicates a statistically different result.
[c] Total concentration = 0.04-0.06 $mm^3 \cdot liter^{-1}$.
[d] Total concentration = 0.6 $mm^3 \cdot liter^{-1}$.

argued that the complex motor patterns required to handle and ingest *Synedra* were less excitable than the simpler patterns used to ingest small spherical algae. More will be said about the utility of the behavioral approach for understanding food selection below.

Mechanisms and Food Quality - Typically food quality of a particle has been regarded as its nutritional content for the predator. A nutritious particle would be one that was non-toxic, digestible, and contained a balanced composition of proteins, lipids, carbohydrates, and micronutrients to allow growth and reproduction of the suspension feeder. Also, it is necessary to include any factors that would diminish the predator's ability to detect, capture, and ingest a particle. Non-nutritional factors would include, for example: size and other qualities as they affect detection and "filtering efficiency", size and shape as they affect handling and ingestion, and escape abilities of motile prey. For copepods, both nutritional and non-nutritional factors are reflected in their selectivity coefficients. We are emphasizing nutritional quality in this paper because of the strong linkage between selectivity and nutritional quality. The current paradigm argues that the combination of olfaction for distance perception and short-range olfaction, or taste, before ingestion implies the copepod has a sophisticated two-step process that encourages ingestion of large high-quality food.

The sensitivity and possible operation of this two-step olfactory system can be appreciated from the study of Paffenhöfer and Van Sant (1985) on *Eucalanus* feeding on particles of varying nutritional quality. It is the only study in which directly observed feeding mechanisms have been coupled to selectivity data derived from traditional feeding experiments. Results of their separate experiments run with only one or two particle types at a time were combined (Vanderploeg in press) to produce these overall results shown in Table 2. The dead *Rhizosolenia alata* and fecal pellets, which are the same size or nearly the same size as live *R. alata*, had lower selectivities. The fecal pellets had a selectivity about the same as the small alga, *Thalassiosira weissflogii*. The percentage of captures that were active captures for pellets and *T. weissflogii* were 66 and 63, values less than the ~100% observed for *R. alata*. They argued that these results are consistent with a smaller long-range olfactory cue arising from this lower quality food. Moreover, they argued that lack of both long-range and short-range olfactory cues were responsible for the complete lack of ingestion of microspheres when offered alone. Very few microspheres were captured and only 1 of 15 observed captures was an active capture. None of the

Table 2. Selectivity (W') of the marine calanoid copepod *Eucalanus pileatus* in experiments of Paffenhöfer and Van Sant (1985) for particles of different nutritional quality and equivalent spherical diameter (ESD).

Particle	ESD (μm)	Active Capture (%)	W'	
			Offered alone	Offered in pairs
Rhizosolenia alata (live)	59	~100	1.0	1.0
R. alata (dead, heat killed)	59	-	0.63	0.83
Thalassiosira weissflogii (live)	14	63	0.36	0.30
Fecal pellets	51	66	0.43	0.44
Polystyrene spheres	20	7	0	0.02

captured beads was ingested. In a mixtures of *T. weissflogii* and microspheres, 42% of the captured microspheres were ingested incidentally with the algae.

How the incidental ingestion occurs is available from observations of the rejection process. Large algae or large particles like fecal pellets are usually ingested or rejected very soon after being brought to the mouth (Price et al. 1983; Paffenhöfer and Van Sant 1985; Vanderploeg and Paffenhöfer 1985), whereas small algae or plastic microspheres captured passively are ingested or rejected as a group after several have accumulated near the mouth. Small particles of low nutritional quality can be hidden among a larger mass of high quality food and be ingested (Paffenhöfer and Van Sant 1985). Thus, incidental ingestion explains the low but non-zero W' for microspheres offered with algae (Table 2).

Specific Questions

Recent experimental work has raised questions about selection and nutritional quality that were not answered by Paffenhöfer and Van Sant's (1985) study since only inert microspheres and fecal pellets were used as the less preferred foods. Experiments of Fulton (1988), Fulton and Pearl (1988), and DeMott (1989) show that selectivity for toxic bluegreen algae is very low. Where in the behavioral chain leading to ingestion or rejection is it that bluegreen algae are

rejected? Also, we were intrigued by the experiments of DeMott (1986, 1988) with mixtures of algae, microspheres, and algal-exudate flavored microspheres. A summary of his results for the low concentration experiments are shown in Table 3. Notice there is a range of selectivities for microspheres depending on whether they are flavored and on their size. What are the reasons for this? This question is relevant because *Diaptomus*, although cabable of very selective feeding, can ingest significant quantities of inert suspensoids like calcite in nature (Vanderploeg et al 1987). In addition we wondered whether olfaction was the complete explanation for perceptual bias for larger prey. We came to suspect physical cues (distortion of the flow field caused by a particle in the double shear scanning current) suggested by Legier-Visser et al. (1986) because the elongated alga *Synedra* was always preferred to spherical algae of the same equivalent spherical diameter (1988), as can be seen for one example in Figure 1. We hypothesized that an elongated alga creates a greater deformation in the flow field than a sphere, especially before it becomes aligned in the scanning current (Vanderploeg et al. 1988). We thought also that a detectable signal (change in pressure) might be generated by a randomly oriented alga as it swings to alignment in the current field (Vanderploeg et al. 1988). Also, Barrientos Chacon (1980) showed that the first antennae, the organs thought responsible for distance perception of large particles, have both mechano- and chemoreceptors. Scanners like *Diaptomus* have a greater proportion of

Table 3. Selectivity (W) of *Eudiaptomus* in experiments of DeMott (1988) for algae, microspheres, and algal-exudate-flavored microspheres.[a]

Particle	Diameter (μm)	W
Chlamydomonas reinhardti	6	1.00
Flavored microsphere	6	0.19
Unflavored microsphere	6	0.025
Flavored microsphere	12	0.071
Unflavored microsphere	12	0.0061

[a]Data from Tables 1 and 3 of DeMott (1988) were combined by the technique of Vanderploeg (in press) to produce these results. Results are for mixture experiments with a low concentration of algae (≤ 1000 cells·ml^{-1}). Percent standard errors of the mean for the W data for microspheres are approximately 25%. Standard error of W of *C. reinhardti* is zero since it was always the preferred particle.

chemoreceptors than the estuarine copepod *Acartia*, which does not create a scanning current.

We attempted to answer all these questions by using high-speed microcinematography to make direct observations on the entire behavioral sequences from capture to rejection or ingestion for particles of different kinds: (1) toxic and non-toxic bluegreen algae, (2) algae and flavored and unflavored microspheres of various sizes, and (3) large nylon rods (13x200 μm). We also discuss the utility of classic ethological approaches for understanding concentration-variable selectivity that DeMott (1989) has reported for mixtures of particles of high and low nutritional quality, as for example the *Planktosphaeria* vs. *Chlamydomonas* pair and the dead vs. live *Scenedesmus* pair shown here in Table 4. His results for particles of low nutritional quality parallel ours for the difficult to handle *Synedra* (Vanderploeg et al. 1988).

Table 4. Selectivity (W) of *Eudiaptomus* for the less preferred alga in indicated pairs of algae of different food quality (H=High, T=Toxic, G=Gelatinous sheath) offered alone and at high and low concentrations in experiments of DeMott (1989).[a]

Food Pair	ESD (μm)	Food quality	W Alone	W Low	W High
1. *Scenedesmus*	5	H	0.67	0.79	0.72
Chlamydomonas	12	H			
2. *Microcystis*	5	T	0.060	0.18	0.15
Monoraphidium	5	H			
3. *Planktosphaeria*	23	G	0.82	0.54	0.16**
Chlamydomonas	12	H			
4. Dead (sterile) vs.			0.025	0.014	0.011
Live *Staurastrum*	16	H			
5. Dead (sterile) vs.			0.27	0.45	0.19**
Live *Scenedesmus*	5	H			

[a]W is given only for less preferred alga in pair; by definition, W of the preferred alga = 1. Concentrations of each alga offered alone or in pairs at the low concentration were each 0.125 $mm^3 \cdot liter^{-1}$. The concentration of algae offered in pairs at the high concentration were each 1.0 $mm^3 \cdot liter^{-1}$. Standard errors of the mean of the W data are on the order of 5%.
**Indicates highly significant differences between low and high concentration results.

Methods

Filming Techniques -- All filming was done at the Great Lakes Environmental Research Laboratory using a microcinematography apparatus identical to the one described by Alcaraz et al. (1980). All films were made at rates between 250 and 500 frames·s^{-1}. Adult female *Diaptomus sicilis* were used, and they were tethered to a fine cat hair (Vanderploeg and Paffenhöfer 1985; Vanderploeg et al. 1988) to hold the animal in place inside of the 35-ml aquarium of 2.1-cm-W x 4.0-cm-L x 4.2-cm-H dimensions. Films were made through the width of the aquarium to observe a lateral view of the animal. Recently, an addition was made to the system to allow an experimental feeding suspension to be replaced with filtered lake water with the animal still in the aquarium. A small glass inlet tube connected with rubber tubing to a reservoir (2 l) of water and a small glass outlet tube were used to flush out the cuvette with filtered lake water. This flow-through system keeps the animal under water while purging the system of particles. A clamp turns the flow on and off and gravity controls the rate. The flow rate (25-50 ml·s·min^{-1}) is slow enough so the animal is not harmed, yet fast enough to purge the system in 6 to 15 min using a total water volume of 300-500 ml. This makes it possible to film the same animal in many different feeding suspensions in the same day without having to remove the animal. Removing and replacing the animal is difficult, time consuming, and potentially harmful to the animal. In the past we often used different animals for each suspension. The flow aquarium allows us to minimize problems associated with individual variation as well. During the purging process the animal behaves normally: it continues to scan and does not try to escape. It will even ingest food if food is captured.

Toxic Blue-green Algae -- Non-toxic (UTEX 1444) and toxic (UTEX 2383) strains of the filamentous colonial blue-green alga *Anabaena flos-aquae* were used in the filming experiments to clearly contrast the effect of toxicity with nontoxicity on the feeding behavior; these species have a very similar gross morphology (Fulton 1988). Experiments of DeMott (unpublished) showed that the non-toxic strain is readily ingested, and Fulton (1988) showed that the toxic strain is strongly selected against in mixtures with *Chlamydomonas*. Both algae were cultured in WC medium at 15°C using general methods described by Vanderploeg et al. (1984). For the filming, exponentially growing cultures of the *A. flos-aquae* strains were screened with a 20-µm sieve and resuspended in 0.22-µm-filtered lake water. The cultures were also screened with a 200-µm

screen to remove very long colonies. Colonies used in filming generally fell in the size range 300-500 μm.

We preconditioned the animal to a low concentration (0.05 $mm^3 \cdot liter^{-1}$) of the toxic and non-toxic *Anabaena* for 1 h. The suspension was then flushed out of the cuvette with 0.22-μm-filtered lake water, and 1 h later the filming was started. The following film sequences were made of *D. sicilis* in 3000 colonies$\cdot ml^{-1}$ *Anabaena* suspensions: non-toxic *Anabaena* (1.0 $mm^3 \cdot liter^{-1}$) 45 s after addition of algae, non-toxic *Anabaena* 7.5 min after addition, toxic *Anabaena* (1.4 $mm^3 \cdot liter^{-1}$) 45 sec after addition, and toxic *Anabaena* 12.2 min after addition. The animal was in filtered lake water for approximately 25 min between the non-toxic and toxic suspension. The temperature during filming was 14°C.

These films, run at 300 frames-s^{-1}, allowed 53 s of observation for a 122-m-long roll, the longest roll taken by the camera. Filming is expensive, about $130 per roll; therefore, we chose a high *Anabaena* concentration to maximize events on film. Films shot before this experiment showed that toxic *Anabaena* was always rejected, but that non- toxic *Anabaena* was sometimes rejected in films we made after waiting a few minutes after the introduction of the algae. We suspected satiation was responsible for the result (Vanderploeg et al. 1988). Therefore, we chose to make the first films 45 s after introduction of the algae to minimize satiation-driven rejections.

Preliminary Experiments with Flavored and Unflavored 11-μm Microspheres -- The particles used in the feeding suspension were 11-μm polystyrene microspheres (Duke Scientific). The treated microspheres were flavored with *Chlamydomonas reinhardti* (4.5 μm) following the method of DeMott (1986). Our *C. reinhardti* was smaller than his so we adjusted the concentration of algae used to flavor the microspheres upward to match his volumetric concentration of algae used to flavor his microspheres. *D. sicilis* was acclimated to a mixture containing the complete array of *Chlamydomonas* and microspheres (flavored and unflavored), each at a low concentration of 0.05 $mm^3 s \cdot liter^{-1}$ for 1 h before filming. Films of *D. sicilis* were made at 20 min intervals using six experimental treatments: control beads at 20,000 ml^{-1}, control beads and *C. reinhardti* (4.5 μm) at 20,000 ml^{-1} each, flavored beads at 20,000 ml^{-1}, flavored beads and *C. reinhardti* at 20,000 ml^{-1} each, flavored beads at 3564 ml^{-1} (3 $mm^3 \cdot liter$-1) and *Chlamydomonas* sp. (11-μm) at 3564 ml^{-1} (3 $mm^3 \cdot liter^{-1}$).

Experiments with Large Rods and Spheres -- At the end of the feeding

experiment with toxic and non-toxic Anabaena we added enough 13x200-μm nylon rods to make 1400 rod·ml^{-1} suspension. Rods were made by microtoming bundles of nylon yarn as described by Vanderploeg (1981b) for evaluating Coulter counter function. About 4 h before the experiment, a concentrated stock suspension of rods was made by adding filtered lake water to the microtomed bundles of yarn and sonifying them to separate them. No surfactant was added to separate the rods. The flow aquarium was purged, and 1 min after mixing in the rods, a film as made.

A few days later, after viewing the films from the rod experiments, we made films of the same tethered *Diaptomus* in suspensions of large spheres. On the morning of each of the two experiments with the spheres, *Diaptomus* was fed a moderate concentration (< 1 mm^3 liter^{-1}) of *Chlamydomonas* sp. After purging the system and waiting 2 h, the first film was made. Each polystyrene microsphere (Duke Scientific) feeding suspension (1400 ml^{-1}) was made by pipetting a measured amount of a microsphere working stock into the filming cuvette containing filtered lake water and the animal. The working stock was made by placing a number of drops of the original microsphere solution into a measured volume (20 or 25 ml) of 0.22-μm-filtered lake water and sonifying the suspension to separate the microspheres. The number of drops added was determined by Coulter Counter measurement of the concentration of the microspheres. Five different sizes of microspheres, having diameters of 14, 29, 42, 48 and 102 μm, were used. Filming was started about 2 minutes after mixing in the microspheres. The cuvette was purged of microspheres immediately after the completion of each film, and there was a 20-minute waiting period between films.

To determine if there was an effect of any odors associated with the microspheres, another film was made a few days later of 48-μm-diameter microspheres which were thoroughly rinsed. These microspheres were rinsed four times in distilled water and left in distilled water overnight. They were then resuspended in 0.22-μm-filtered lake water and prepared for filming as above. Similar results were obtained for these washed microspheres.

Results

Toxic and Non-Toxic Anabaena -- The summary of results in Table 5 shows that both toxic and non-toxic *Anabaena* are actively captured, indicating that *Diaptomus* did not use long-range olfactory cues to distinguish between toxic

Table 5. Number of active and passive captures, rejections, and times between capture and rejection per 53-s film sequence by *Diaptomus sicilis* for non-toxic (UTEX 1444) and toxic (UTEX 2383) strains of *Anabaena flos-aquae* offered at 3000 colonies·ml^{-1}.

Strain	Time after addition (min)	No. of captures		No. of rejections	Rejection response time (ms)
		Active	Passive		
Non-toxic	0.8	6	0	1	367
Non-toxic	7.5	11	0	8	207 ±49(7)
Toxic	0.8	10	2[a]	12	138 ±40(7)
Toxic	12.2	6	0	5	186 ±101(5)

[a]Rejected before entering maxillae by flap of swimming feet.

and non-toxic strains. However, 2 toxic *Anabaena* colonies entering on a perfect line for passive capture were avoided before entry into the second maxillae. All captured colonies of the toxic strain in these films and in all other films made were rejected. In the case of the non-toxic strain, 5 out of 6 captures resulted in ingestion during the first film, but 8 of 11 were rejected in the second film. This demonstrates the tendency of *Diaptomus* to capture more prey than it ingests when prey are abundant. In all cases here, rejections occurred relatively quickly after capture for both toxic and non-toxic strains.

Experiments with Flavored and Unflavored Microspheres -- Some of the algal-exudate flavored spheres were captured actively. The 11-μm spheres when offered alone were definitely only captured passively (Table 6). In all cases the microspheres appeared to be rejected after capture. We cannot make quantitative statements beyond this because captures and rejections were hard to evaluate at the high concentration of microspheres used.

Large Nylon Rods and Spheres -- Unmistakable, vigorous active captures like those reported for algae (Vanderploeg and Paffenhöfer 1985) were made for both nylon rods and large microspheres. Flaps of the maxillipeds and swimming feet often aided the second maxillae in a manner similar to patterns observed for large algae (Vanderploeg and Paffenhöfer 1985). These experi-

Table 6. Number of passive and active captures per film sequence by *Diaptomus sicilis* for inert particles of various shapes and sizes. Each entry represents one film sequence of the indicated length for the same animal. The nylon-rod results are for 15°C, and those for microspheres are for 10°C. Concentrations were always 1400 particles·ml^{-1} except for the 11-µm micropheres of June 21 offered at 20,000·ml^{-1}.

Date	Particle		Sequence length (s)	Number of Captures	
	Type	Dimensions (µm)		Passive	Active
June 21	Microsphere	11	64	Many	0
June 22	Nylon rod	13x200	53	0	25
June 28	Microsphere	48	13	1	6
June 28	Microsphere	102	13	0	5
June 29	Microsphere	14	13	1	2
June 29	Microsphere	29	13	0	6
June 29	Microsphere	42	13	0	6
July 6	Microsphere	48	13	0	10

ments confirm the hypothesis of Legier-Visser et al. (1986) that suspension-feeding copepods can use physical cues to detect and capture large particles. A particle of about 14 µm in diameter is apparently the smallest that *Diaptomus* can detect by mechanoreception (Table 6).

Once captured, the typical behavioral sequence for handling large algae was followed until rejection at or near the mouth. We could clearly see the spheres being passed from the first maxillae to the labial palp area, where rejection occurred. Many of the spheres were too large (> 30 µm) to be ingested. An exception to this sequence was results for the 102-µm microspheres: they were too large to fit well between the second maxillae and were not passed forward efficiently. They were usually rejected while still in the second maxillae. Ingestion of an elongated alga requires complicated manipulation of the alga so that it can be inserted into the mouth perpendicular to the long axis of the body (Paffenhöfer et al. 1982; Vanderploeg et al. 1988). Typically the captured nylon rods were handled by this same sequence and inserted into the mouth, where

rejection occurred. There are contact chemoreceptors on all the appendages used for handling the spheres and rods (Friedman 1980). Apparently, they were not used to reject these large inert particles.

Discussion: New Paradigms

Importance of Mechanical and Chemical Cues -- Once particles get larger than some threshold size, they can be detected by mechanoreception and captured actively. The capture response for the 102-µm microspheres appeared not to be as enthusiastic and appeared to occur at a shorter distance. Perhaps *Diaptomus* recognized this particle was too large to ingest.

What are the relative contributions of mechano- and chemoperception to the W vs. equivalent spherical diameter curve (Figure 1)? *Diaptomus* can capture live *Chlamydomonas* as small as 5 µm. Flavored 11-µm microspheres can be actively captured, but not unflavored microspheres. Paffenhöfer and Van Sant (1985) observed a high proportion (63%) of active captures with a 14-µm diatom (*T. weissflogii*) but only 7% (1 of 15) with 20-µm microspheres for *Eucalanus pileatus* (Table 2). *E. pileatus* (prosome length = 1.9 mm) being larger than *D. sicilis* (prosome length = 1.2 mm) may explain why it did not actively capture more 20-µm microspheres. All of these results lead to this hypothesis: With increasing particle (algal) size, chemoperception by the calanoid increases up to a point; with further increases in size chemoperception does not increase, but mechanoperception does. The relative contributions of mechano- and chemoperception to the W vs. equivalent spherical diameter curve (Figure 1) need to be worked out.

There are probably many interesting synergies of chemical and mechanical cues related to capture of particles. In the studies of Williamson and Vanderploeg (1988), the thrust response was often used to capture small microzooplankton (rotifers). We have not seen this pouncing behavior with algae or any of the large inert spheres or rods. Perhaps both chemical and mechanical cues are necessary to elicit this response. Another possibility is that the prey's movement may inform *Diaptomus* that there is a microzooplankter nearby; however, Williamson and Vanderploeg (1988) discount this possibility because they observed thrust responses for non-moving (non-escaping) rotifers. We cannot rule out the possibility that hydrodynamic signals produced by moving prey in the very far field alerted *Diaptomus* of their presence.

It would appear at first glance that use of mechanoreception for the

capture of large particles is maladaptive. However, consider that large inert particles like nylon rods or plastic microspheres are not common in nature. Large mineral particles do not stay suspended for long. Objects like fecal pellets may have some nutritional value, yet not give off much of a scent because of the membrane that surrounds them. The remaining large objects are algae and microzooplankton. Perhaps the mechanosensory system can perceive large objects at greater distances than the chemosensory system. Perhaps it is faster responding, which would be important for capture of microzooplankton with high escape abilities.

Sensory Modes and Nutritional Quality -- The cinematographic observations on toxic and non-toxic strains of Anabaena help explain the low selectivities observed in *Diaptomus* by Fulton (1988) for the same toxic strain of *Anabaena* used here and by Fulton and Pearl (1988) and DeMott (1989; results shown here in Table 4) for *Microcystis*. With both *Anabaena* and *Microcystis*, post-capture rejection is the explanation. It is possible that, like the nylon rods, both toxic and non-toxic strains are captured in response to mechanical cues. Fulton (1988) showed that the presence of *Anabaena* in mixtures with *Chlamydomonas reinhardti* (6 mm) did not depress clearance rates on *C. reinhardti*. This is explained by the immediate rejection of *Anabaena* that we observed in our films. In two cases, this rejection occurred before entry into the second maxillae.

Our collective experience (Paffenhöfer et al. 1982; Price and Paffenhöfer 1985; Vanderploeg and Paffenhöfer 1985; Vanderploeg et al. 1988) can be used to generate hypotheses that explain *Diaptomus*' selectivities for non-toxic particles of low nutritional quality (Tables 3 and 4). We hypothesize that the probability of ingestion a single particle or group of particles collected at the mouth depends on the strength of the appropriate chemical signal given off per unit volume (or area) for the particle or group of particles being tasted. This implies there is an interaction between selection and size of the low-quality particle, because a small low-quality particle, captured passively, can be hidden in a mass of high quality particles at time of tasting, as suggested by Paffenhöfer and Van Sant's (1985) data. This explanation clearly applies to DeMott's (1988) results for *Chlamydomonas* and flavored and unflavored microspheres shown here in Table 3: the selectivities for flavored and unflavored large microspheres (12 μm) are lower than respective selectivities for flavored and unflavored small (6 μm) microspheres.

We believe the same signal-strength argument applies to DeMott's (1989)

results for algae of varying nutritional quality, as for example, food pairs 3, 4, and 5 in Table 4. In the case of pairs 4 and 5, the dead *Staurastrum* would be selected against more stringently than the dead *Scenedesmus* because of the former's larger size. Distance olfaction could also play a role in the case of *Staurastrum* since less algal exudate associated with the dead cells could lead to a smaller perceptive volume for *Diaptomus* scanning for food. In the case of food pair 3, the *Planktosphaeria* by virtue of its large size could result in a large perceptive volume caused by mechanoreception. Its gelatinous sheath, however, could inhibit signal strength and hence lower selection for this large cell.

In algal pairs 3 and 5 in Table 4, selectivity for the lower quality food dropped as food concentration increased. We believe this is a satiation-driven motivational response. At high food concentrations, where captures typically greatly exceed ingestions (Vanderploeg and Paffenhöfer 1985; Vanderploeg et al. 1988), low motivation may require greater signal strength to initiate the ingestion reflex. Like Leyhausen's (1973) cat in a room full of mice, *Diaptomus* will capture, handle, and even partially ingest more particles than it can ingest. For example, at high concetrations of Synedra, 61% of the (obviously) attacked *Synedra* were only partially ingested (Table 1). Motivation will be fluctuating in high concentrations, and if a high-strength chemical cue is available as motivation is increasing the ingestion response will be triggered. This explanation is analogous to the motivation argument we presented for the difficult-to-handle *Synedra* (Table 1) that follows the same concentration- variable selectivity pattern (Vanderploeg et al. 1988). This result for low-nutritional-quality food is also consistent with another aspect of signal strength: As the proportion of low quality particles increases, the proportion of low quality particles increases in the group of particles to be tasted at the mouth, resulting in a higher probability of rejection. This argument would be most relevant for small particles.

Summary

Direct high-speed microcinematographic observations of the suspension-feeding copepod *Diaptomus* showed that it uses mechanoreception in addition to olfaction to detect particles in its scanning current. Mechanoreception may explain part of the reason for the increase in selectivity that occurs with increasing particle size. Much of the selection for particles of varying nutritional quality is determined by taste at the mouth. Particles of low nutritional quality

as well as toxic blue-green algae are rejected after capture. Concentration-variable selection of particles of low nutritional quality is a satiation-driven response that can be understood from classical ethological principles.

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