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DIAPTOMUS VS. NET PHYTOPLANKTON: EFFECTS OF ALGAL SIZE AND MORPHOLOGY ON SELECTIVITY OF A BEHAVIORALLY FLEXIBLE, OMNIVOROUS COPEPOD

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ABSTRACT

Effects of algal size, colony form, and morphology on selection by *Diaptomus sicilis* and *D. ashlandi* were determined for certain net diatoms commonly found in the pelagic regions in lakes. Mechanisms of capture, observed by high-speed microcinematography, were correlated with selectivity results from traditional feeding experiments with mixtures of algae. The attribute of elongation (up to 365 μm) in one dimension possessed by *Synedra* spp. was not useful for avoiding grazing. In fact, at low concentrations, selectivities for *Synedra* were much higher than for *Chlamydomonas* of equal cell volume. This suggests a perceptual bias for capture of elongated algae. Films showed that *D. sicilis* could even bite off sections of 700-μm-long *Melosira* colonies. However, long fragments of *Synedra* and *Melosira* were often left behind after attacks by *Diaptomus*. Elongation in two dimensions, an attribute possessed by the stellate colonies of *Asterionella formosa* was extremely effective for avoiding grazing once more than six to eight cells per colony was reached. This results may explain the abundance of the eight-cell form in nature. Selectivity of *Diaptomus* changed with concentration in mixtures of a 12-μm-diameter spherical green alga and a 240-μm-long *Synedra*. In these same experiments, the proportion of attacked *Synedra* that were only partially ingested—i.e., the proportion rejected after partial ingestion—increased linearly with attack rate on *Synedra*, and was not correlated with attack rate on *Chlamydomonas* or on the sum of both algal species. These and other data demonstrate that this concentration-variable selectivity is not an optimal-foraging strategy. We assert these observations can be properly viewed within the classical ethological framework of motivation and excitability of different motor patterns used to capture, handle, and ingest different kinds of algae.

Diatoms of the net plankton (>45 μm; Throndsen, 1978) like *Stephanodiscus, Asterionella, Fragilaria, Melosira, Synedra,* and *Tabellaria* are an important part of the algal community in fresh water. In Lake Michigan (Bowers, 1980; tables 3 and 4), for example, the annual mean percent of total chlorophyll retained on a 53-μm screen was 45 (range 14–65). Because of their large size, abundance, and distinctive morphologies—all but *Stephanodiscus* are elongated in one or two dimensions—net plankton are the first algae identified by students of limnology. Despite their familiarity, little is known about their vulnerability to grazing, especially to *Diaptomus* spp. (Horn, 1985; Infante and Litt, 1985; Knisely and Geller, 1986), the most important calanoid copepod grazers in fresh water. The conspicuous presence of these algae and their relatively slow growth rates, due to their large size, argues for low vulnerability to grazing. Elongation of algae in one or two dimensions may be a compromise balancing a hypothetical minimization of grazing loss with increased costs of loss due to increased sinking rate and lowered growth rate. The costs from sinking and lowered growth rate have been quantified for algae of different morphologies, colony forms, and sizes (Reynolds, 1984). Elongation in one or two dimensions, rather than three, somewhat mitigates these costs through possession of high form resistance to sinking and through high surface area to volume ratios necessary for maintenance of reasonable growth rates. Obviously, to understand the ubiquitousness of these algae we must quantify

the release from grazing pressure their size and morphology give them. Moreover, grazing experiments employing the size-fractionated chlorophyll technique showed that *Diaptomus sicilis*, a large species, fed heavily on net plankton (>53 μm), whereas *D. ashlandi*, a small species, did not (Bowers, 1980). Understanding the feeding biology and population dynamics of *Diaptomus*, therefore, requires knowledge of their interactions with net diatoms.

In addition to the sparse information available on grazing of net phytoplankton, the only direct microcinematographic observations on mechanisms of capture of net plankton by either freshwater or marine calanoids are those for *Eucalanus* capturing and ingesting *Rhizosolenia indica* and *Lauderia borealis* (Paffenhöfer et al., 1982; Price and Paffenhöfer, 1986). Further observations on other zooplankton and phytoplankton are necessary to reveal mechanisms needed to interpret selectivity results obtained from traditional feeding experiments (Vanderploeg and Paffenhöfer, 1985).

Matrices of selectivity coefficients, W′ (Vanderploeg and Scavia, 1979; Vanderploeg et al., 1984), derived from traditional feeding experiments are being used to predict grazing by different zooplankton on their phytoplankton prey in models that predict seasonal succession of algae in marine and freshwater systems (Reynolds et al., 1982; Ambler, 1986; Knisely and Geller, 1986; Scavia et al., 1988). An important simplification in the use of selectivity coefficients for *Diaptomus* and other freshwater zooplankton is their invariance under conditions of varying availability of phytoplankton of different sizes (Vanderploeg et al., 1984; Horn, 1985; Knisely and Geller, 1986). This simplification is only a first-order approximation for the marine calanoid copepod *Paracalanus* (Paffenhöfer, 1984: figs. 8, 9, 10; Ambler, 1986), since selectivity changed somewhat with concentration of algae in mixtures containing the net diatom *Rhizosolenia* (150–260 μm long). We thought similar variable selectivity may have not been seen by other investigators (Frost, 1977; Bartram, 1981; Vanderploeg, 1981; Vanderploeg et al., 1984; Horn, 1985; Knisely and Geller, 1986) because they did not include net plankton like *Rhizosolenia* that requires considerable handling before ingestion (Paffenhöfer et al., 1982). When prey are difficult to handle, the optimal-foraging paradigm dictates concentration-varying selectivity (Hughes, 1980).

One goal of our study was to do traditional feeding experiments (Vanderploeg et al., 1984) to determine the selectivity of *Diaptomus* for algae having different lengths in one, two, or three dimensions (Fig. 1). Selectivity on *Synedra* spp. of various lengths and widths (Fig. 1) was examined to determine the effect of algal length in one dimension on grazing vulnerability. Experiments with *Asterionella formosa* (Fig. 1) allowed determination of advantages gained by forming colonies that are elongated in two dimensions. Experiments with *Stephanodiscus niagarae* (Fig. 1) revealed advantages of being a large pill-shaped centric diatom. Since size of the alga relative to the copepod may be the important factor, experiments were done with adult females of a large and small species of *Diaptomus*, *D. sicilis* ($\bar{x}$ ± SD prosome length = 1.18 ± 0.03 mm) and *D. ashlandi* ($\bar{x}$ ± SD prosome length = 0.79 ± 0.03 mm). Experiments with mixtures of *Chlamydomonas* sp. and the large *Synedra*, *S. delicatissima* v. *angustissima* (Fig. 1), at different concentrations allowed us to determine whether *Diaptomus'* selectivity varies with concentration of a large net phytoplanker.

The other goal of this study was to directly observe with high-speed microcinematography capture and handling of the different net phytoplankton to gain insight into the mechanisms behind the observed selectivity patterns. We therefore made high-speed motion pictures of *D. sicilis* capturing and handling all species of algae used in the traditional feeding experiments. Films were also made of *D. sicilis*

handling very long (>500 μm) colonies of *Melosira italica* to gain insight into problems with handling very long algae.

METHODS

Traditional Feeding Experiments.—All diatoms (*Synedra*, *Asterionella*, and *Stephanodiscus*) were isolated from Lake Michigan or Huron except *Synedra* sp., which was obtained from the Starr collection (UTEX 2392). Except for a few cases noted in the results, the algae were used within a few months of isolation to avoid changes in size and morphology. *Chlamydomonas* sp. and *C. oblonga* were also obtained from the Starr collection (UTEX 796 and 219). Dimensions of the algae and their equivalent spherical diameters are given in Figure 1. All algae were cultured in unbuffered WC medium (Guillard and Lorenzen, 1972) as described by Vanderploeg et al. (1984). None of these algae produce toxins, and all are high quality food. Zooplankton and lake water used in this study were collected 1 day before the experiments from offshore Lake Michigan (Vanderploeg et al., 1984).

Selectivity experiments, quantified by use of W' (Vanderploeg and Scavia, 1979; Vanderploeg, 1981; Vanderploeg et al., 1984), were conducted with mixtures of exponential-phase algae suspended in filtered lake water using the methods of Vanderploeg et al. (1984). These methods include a 1-d-duration prefeeding period followed by a 1-d-duration feeding experiment with two initial, two control, and four 300-ml experimental bottles, containing adult female copepods. All bottles were rotated at 0.5 revolutions·min^{-1} at 10°C in dim light (4–8 μEinst·m^{-2}·s^{-1}) set to a 12:12 L:D cycle. *Chlamydomonas* sp. was included in all mixtures as a reference alga to facilitate comparisons with different mixtures. Algae were preserved in a 1% Lugol solution and counts were made of entire settling chambers on the inverted microscope. At least two settling chambers were settled for each bottle, and usually enough algal suspension was settled down to obtain a minimum count of 400 per chamber of each of the different species of solitary algae or colony types (see below) for the colonial algae. Equations of Frost (1972) were used to determine clearance rates and average concentrations of algae available to the zooplankton during the feeding experiment.

Asterionella formosa forms stellate colonies (Fig. 1) that are strongly glued together at the center. In one experiment with a mixture containing *Asterionella*, we determined clearance rate on colonies for colonies of different cell number and on cells within those same colonies. We did this by recording for each colony we counted the number of cells it contained and the number that were broken off by the zooplankton during feeding. A colony was considered attacked if any of its cells were broken. This method assumes that if *Diaptomus* cannot ingest the whole colony it will leave behind the inner portion of the colony intact with the exterior parts of the successfully attacked cells bitten off, thus allowing us to recognize the number of live cells originally present and the number of live cells remaining. Our observations of many colonies containing some cells with the exterior portions of the cells bitten off support this conclusion.

In experiments with the larger species of *Synedra*, we noticed during our counts of the algae that cells were often not completely ingested. Typically the broken cells had one end of the cell broken off with 50 to 95% of the algal length remaining. By counting these fragments, we obtained a clearance rate for those cells for which more than 50% of the cell was ingested. This clearance rate for "successful ingestions" was significantly lower than the clearance rate obtained from counting intact cells, which give the clearance rate for breaking or killing the cells. Moreover, we were interested in knowing if the proportion of incomplete ingestions was related to algal concentration or satiation of *Diaptomus*. To do this, we determined the proportion of attacked cells with one end bitten off. This portion, P, was estimated by:

$$P = N/(C - Z), \quad (1)$$

where N = concentration of cells with one end of the cell remaining, C = concentration of intact cells in the control containers, and Z = concentration of intact cells in the experimental container containing zooplankton. Equation (1) is a reasonable approximation since there was little or no growth of algae in the control containers.

Microcinematographic Observations.—All filming was done at the Great Lakes Environmental Research Laboratory on a microcinematography apparatus identical to that described in Alcaraz et al. (1980). To maintain temperature control during filming, the apparatus was situated in an environmental room controllable to ±0.1°C within the temperature range of 0 to 30°C. Unless specifically noted all filming was done at 19°C. Adult female *D. sicilis* used for filming were tethered as described by Vanderploeg and Paffenhöfer (1985). A total of 4,200 m of film were exposed to get observations on 25 individual animals.

Because of the large size of the net plankton, there is a relatively low number concentration of cells for solitary forms or of colonies for colonial forms for each unit of volume concentration. Number concentrations will be particularly low in nature, where total volumetric concentration of seston is

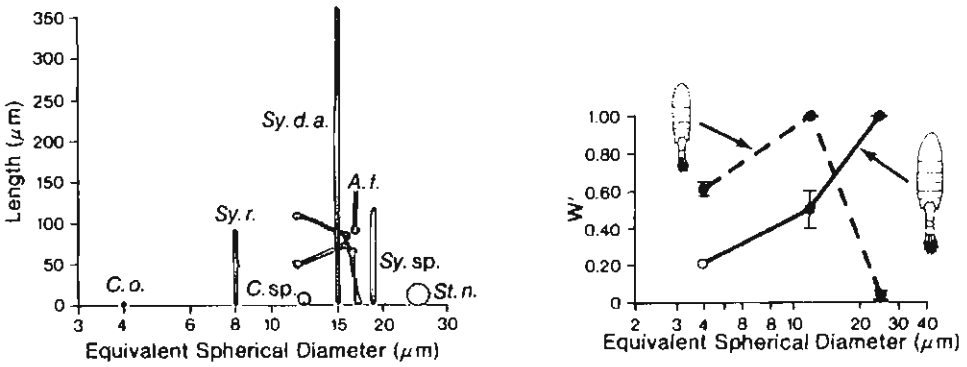

Figure 1. Dimensions of interest: lengths and equivalent spherical diameters of algae used in this study. Green algae used were *Chlamydomonas* sp. (*C.* sp.), *C. oblonga* (*C. o.*); diatoms, shown in valve view, were *Asterionella formosa* (*A. f.*), *Synedra* sp. (*Sy.* sp.), *S. radians* (*Sy. r.*), *S. delicatissima* v. *angustissima* (*Sy. d. a.*) and *Stephanodiscus niagarae* (*St. n.*).

Figure 2. Selectivity (W') of *Diaptomus sicilis* (large body outline) and *D. ashlandi* (small body outline) for a mixture of spherical or pill-shaped algae: *Chlamydomonas* sp. (12 μm), *C. oblonga* (4 μm) and *Stephanodiscus niagarae* (25 μm). The W' of *D. sicilis* for *C. oblonga* (open circle) was determined from W' values given by Vanderploeg et al. (1984) for *Chlamydomonas* sp. and *C. oblonga*. Body outlines of *Diaptomus* were redrawn from Torke (1974).

about 1 $mm^3 \cdot liter^{-1}$ (e.g., Lake Michigan: Vanderploeg, 1981; Vanderploeg et al., 1984). This complicates high-speed filming because few if any interactions between a tethered copepod and the algae at natural concentrations will be seen during the 8 s of viewing offered by the typically-used, 30.5-m-long roll run at 500 frames·s^{-1}. To get around this problem, we starved a tethered animal for 1 d and then positioned it into the filming cuvette containing filtered lake water. Then, enough algae were gently pipetted into the cuvette using a large-bore serological pipette to give a concentration of 1–5 $mm^3 \cdot liter^{-1}$. After the turbulence in the cuvette subsided and the copepod's current field dominated the flow (about 20 s), the camera was turned on at usually 500 frames·s^{-1}. One or more 30.5-m-long rolls of film were then shot. Removing a roll of film from the camera and loading a new one took about 5 min. Experience showed that after we made two or three films, the animals did not attempt to capture and ingest as many algae or that the rejection rate of captured cells increased dramatically. Therefore, we began shooting one 122-m-long roll of film at 500 frames·s^{-1} to observe captures for a full 32 s subsequent of the turbulence settling down.

With this approach, we recognize there is the danger that a starved animal may not respond to the introduced algae in the same way a preconditioned animal may respond to an alga present at a low concentration typical of that for the natural environment. However, our primary interest with the net plankton was the handling of the alga by *Diaptomus* after capture, because previous work had shown that large algae were captured actively (Paffenhöfer et al., 1982; Price and Paffenhöfer, 1985; Vanderploeg and Paffenhöfer, 1985). The possibility that the starved, tethered copepod would not accept the introduced algae (Paffenhöfer et al., 1982) was ruled out by the observation of gradual filling of the gut over a period of about 20 min when the animal was presented with edible algae. Also, the captures and attempts at ingestion described in the results show that the copepods were motivated to feed.

In a few later experiments, a binocular scope was mounted above the aquarium with the animal positioned ventral or dorsal side up. Since the animal was illuminated from the side for filming, the binocular scope gave us a dark-field, low power view of the current field in front of the animal. By filming at low temperatures—1 or 4°C—we were able to slow the current field enough so that we could turn on the camera when an alga appeared to be on a favorable trajectory for capture, and then turn off the camera when nothing of interest was happening. We used this approach with some success for filming sequences of capture of long colonies of *Melosira italica* at the relatively low concentration of 1 $mm^3 \cdot liter^{-1}$. Sequences were usually filmed immediately after turbulence settled down following addition of algae to the cuvette.

Results and Discussion

Large Size in Three Dimensions.—When we think of particle selection by copepods, we usually imagine copepods feeding on good-tasting spheres or pill-shaped

Table 1. Mean clearance rates, F (±SE, N = 4), and selectivity, W', of *Diaptomus sicilis* feeding on a mixture of *Chlamydomonas* sp. and *Synedra* spp. of various sizes. See Figure 1 for dimensions of algae

Species and attack success	Concentration (mm³·liter⁻¹) Initial	Concentration (mm³·liter⁻¹) Average	F (ml·animal⁻¹·d⁻¹)	W'
Chlamydomonas sp.	0.046	0.031	13.7 ± 0.70	0.330
Synedra radians	0.045	0.023	25.0 ± 0.09	0.602
Synedra sp.	0.027	0.010	41.5 ± 1.49	1.00
Synedra delicatissima v. *angustissima*:	0.030	0.018		
Broken*			20.3 ± 0.74	0.489
Successful ingestions†			11.1 ± 0.56	0.267

* Clearance rates determined from concentrations of unbroken cells in the bottles.
† Clearance rates determined from sum of concentrations of live cells plus number of cells with one end bitten off (5 to 50% removed) plus cells with two ends bitten off with the central portion of the cell intact. 86% of broken cells had only one end bitten off.

particles of different sizes. Figure 2 shows selectivity for such ideal particles by *Diaptomus ashlandi* and *D. sicilis*. The gradual monotonic increase of W' of *D. sicilis* with increasing particle size results from increasing probability of active capture as well as increasing retention efficiency of particles with increasing particle size (Vanderploeg and Paffenhöfer, 1985). In *D. ashlandi*, the relatively high W' for the smallest alga (Fig. 2) reflects the greater ability of small copepods to individually detect and actively handle small cells (Price and Paffenhöfer, 1985). The very low W' of *D. ashlandi* for the largest alga probably results from its inability to swallow it or get it between the mandibles for crushing. Microcinematographic verification of this last point has not been possible because details of ingestion were obscured by the first maxillae of *Diaptomus*.

The W' vs. size results for round algae (Fig. 2) serve as a useful starting point for viewing interactions between *Diaptomus* and net plankton. First of all, we would expect these large algae to be mostly captured actively, because of their large size. As a working hypothesis, we expect as a first-order approximation that a copepod's ability to detect these algae is a function of the cell or colony's equivalent spherical diameter (ESD). This would seem a reasonable approximation in view of the very similar concentrations of protein, carbohydrate, and lipids in different algal taxa grown under similar conditions (Parsons et al., 1984). Since many of these net diatoms are very large, even in terms of ESD, we expect them to be detected with approximately the same efficiency, because efficiency of detection appears to level off once a certain minimum large equivalent spherical diameter is reached (Price and Paffenhöfer, 1985; Vanderploeg and Paffenhöfer, 1985). Because all algae used were high-quality food any large decrease from high selectivity for net diatoms would result from the copepod having difficulty handling and ingesting them.

Elongation in One Dimension—Feeding Results.—We investigated the importance of algal length by examining selectivity of *D. sicilis* in a mixture of *Chlamydomonas* sp. and all three species of *Synedra* shown in Figure 1. Length does not appear to be an effective defense to greatly minimize grazing mortality from *Diaptomus*, at least for algae up to 365 μm in length (Table 1). *Synedra* sp., the alga of largest ESD, was clearly the preferred alga, with a W' three times higher than that of *Chlamydomonas* sp. Interestingly, all species of *Synedra*—even the very long *S. delicatissima* v. *angustissima*—were preferred to *Chlamydomonas*. In the case of *S. delicatissima*, the rate of cell killing, or breakage, was much

Table 2. Selectivities of *Diaptomus sicilis* for *Synedra* spp. of different lengths and equivalent spherical diameters (ESD) expressed as clearance rates relative to *Chlamydomonas* sp. (ESD = 12.4 μm). Data were extracted from low concentration (total concentration <0.1 $mm^3 \cdot liter^{-1}$) experiments or treatments (Tables 1 and 5)

Alga	Length (μm)	ESD (μm)	Selectivity
S. radians	89	8.1	1.84 ± 0.10 (4)
Synedra sp.	125	20.8	3.03 ± 0.08 (4)
S. delicatissima v. *angustissima*	236	13.2	1.64 ± 0.06 (8)
S. delicatissima v. *angustissima*	362	15.2	1.48 ± 0.03 (4)

higher than for "successful" (see METHODS) ingestions. The proportion of attacked cells with one end bitten off was 0.26 ± 0.01(4).

We can combine all low-concentration experiments (total concentration <0.1 $mm^3 \cdot liter^{-1}$) with *Synedra* and *Chlamydomonas* sp. (Table 2) to evaluate the importance of algal length to selectivity by *Diaptomus sicilis* without the potential influence of concentration-varying selectivity that occurs at high concentrations (see below). At low concentrations, only *Diaptomus'* ability to detect and ingest a good-tasting alga determines its selectivity. It is noteworthy that all *Synedra* spp. are preferred to 12-μm-diameter *Chlamydomonas* sp., even the very small *Synedra radians* which has an equivalent spherid diameter of 8 μm. This probably means that elongated algae are detected at a greater distance than spherical algae of the same ESD. We could imagine that surface area and length of a long alga could create a phycosphere (sensu Strickler, 1984) of odor more readily detected by the zooplankton. If mechanical cues are important (Légier-Visser et al., 1986), an elongated alga perhaps creates a greater deformation in the copepod's flow field than a sphere, especially before it becomes aligned with the direction of flow. Also, a detectable signal (change in pressure) might be generated by a randomly oriented long alga as it swings during alignment in the flow field. Interestingly, the most preferred alga, *Synedra* sp., has the maximum ESD and is of intermediate length. Possibly there is some minimum target thickness that is desirable for detection. Selectivities of the thin species of *Synedra, S. radius* and the long and short forms of *D. delicatissima,* are about the same (1.48–1.84). That the longest *Synedra* have somewhat lower selectivities may imply that handling difficulties prevent ingestion of some cells or that *Diaptomus* perceives some of them to be too large for ingestion.

Cinematography.—Cinematographic observations showed that short species of *Synedra, Synedra* sp. and *S. radians,* can be actively captured, and the capture method is the same as that described by Vanderploeg and Paffenhöfer (1985) for large *Chlamydomonas* spp. That is, flapping of swimming legs, occasionally aided by the maxillipeds, and flapping of the second maxillae accelerate the alga between second maxillae toward the mouth. We cannot say more about handling after this because our view of the algae was lost once they got between the first maxillae.

For algae like *Synedra delicatissima,* which do not fully fit between the maxillae or within the space bounded by the body and swimming feet, complicated handling behavior was required to maneuver the alga for ingestion. A few films were tried with *S. delicatissima,* but details of handling were difficult to see because of the extreme thinness of the alga. For this reason, we focused our efforts on the much thicker and longer colonial diatom, *Melosira italica.* In this case, full details of handling, including ingestion could be observed. Since *M. italica* filaments were

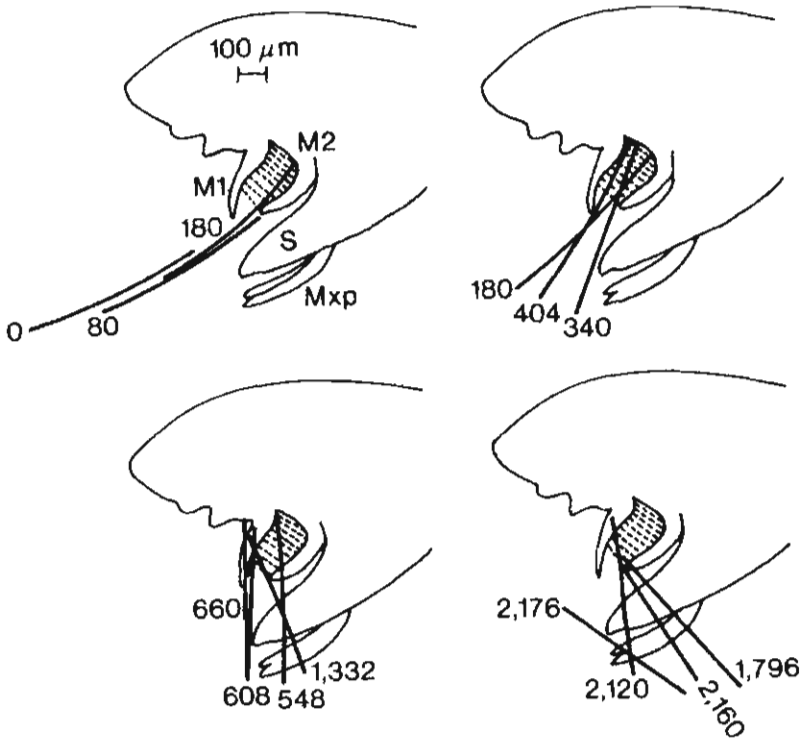

Figure 3. Capture, handling, ingestion, and loss of a *Melosira italica* colony by *Diaptomus sicilis* shown by plotting position of the colony at different times (ms) indicated by the numbers next to the colony. Positions of all appendages shown are those observed at time = 0. Film was made at 250 frames·s^{-1} at 1°C. Appendages other than the first maxillae (M1), second maxillae (M2), maxillipeds (Mxp), and thoracopods (S) have been omitted to improve clarity. To follow the sequence, view the drawings in the following order: upper left, upper right, lower left, and lower right.

very long (Fig. 3), we were able to gain insight into additional difficulties *Diaptomus* might have with very long forms.

A complete sequence of capture, ingestion, and loss of a *Melosira* filament is shown in Figure 3. This sequence is typical of the many others viewed except in two minor respects. First, we could say with complete certainty that *D. sicilis* ingested a portion of the colony. This is the reason for showing the sequence. Second, the alga was on a perfect trajectory for passive capture, so that large amplitude flaps of the second maxillae were not necessary to bring it between the maxillae (times 0–404 ms in Fig. 3). After the initial passive capture, all other aspects of handling were similar to those for actively captured filaments. Positions at 548–660 ms show passage of the filament forward by the first maxillae and insertion of the colony into the mouth at 660 ms. Large amplitude flapping of the thoracopods, maxillipeds, and second maxillae that started at the time of insertion persisted until 1,256 ms (not shown). An idea of the extreme contortions the animal went through to insert and handle the colony can be seen from the photomicrograph made at time = 916 ms (Fig. 4) showing the extremely open position of the thoracopods and the high and bent position of the maxillipeds appearing posterior of the colony. By 1,332 ms, one end of the colony has lost contact with the mouth, and the other end in the absence of large amplitude flaps

Figure 4. Contortions used by *Diaptomus sicilis* to ingest a part of the *Melosira italica* colony shown hanging vertically from the mouth. This frame was photographed at 916 ms in of the sequence shown in Figure 3 (by arrow). Note the extremely open position of the thoracopods and the bent maxilliped just posterior of the colony.

contact with the mouth, and the other end in the absence of large amplitude flaps has been pulled backwards by the normal feeding current field around the animal (Vanderploeg and Paffenhöfer, 1985: fig. 1). Positions at 1,796–2,176 ms document recapture (1,796–2,120 ms), reingestion of a portion of the colony, and loss (2,160–2,176 ms). The alga was inserted in the mouth at 2,128 ms (not shown). The alga was pushed away at 2,176 ms because the animal jumped by flapping its thoracopods. During this entire 2.2 s sequence, it managed to ingest a 120-μm-long section of the 710-μm-long filament.

The handling described here after initial capture by the second maxillae was characteristic of all ingestions or ingestion attempts on *S. delicatissima* and *Melosira italica*. Not all captures resulted in successful ingestions of a length of colony. Colonies once captured were not always successfully maneuvered into the position normal to the body axis required for ingestion. Also some actively captured colonies were observed to be held for periods of 10 s to more than a minute between the second maxillae without attempts to position the colony in the position necessary for ingestion. During these periods, normal low-amplitude vibrations of the mouth parts created the usual current field around the animal. A few observations—unaided by camera—of free-swimming animals in small cuvette using a binocular scope showed that free-swimming animals orient the

Table 3. Clearance rates, F (±SE, N = 4), and selectivity coefficients, W', for *Diaptomus ashlandi* and *D. sicilis* feeding on mixtures of the listed algae. Average cell number per colony for *Asterionella formosa* was 3.5. See Figure 1 for dimensions of algae

Alga	Zooplankton	Algal concentration (mm^3 liter $^{-1}$) Initial	Average	F (ml·animal $^{-1}$·d $^{-1}$)	W'
Chlamydomonas sp.	*D. ashlandi*	0.095	0.082	5.05 ± 0.13	1.00
	D. sicilis	0.094	0.072	5.36 ± 0.62	0.376
Synedra radians	*D. ashlandi*	0.076	0.041	3.54 ± 0.22	0.701
	D. sicilis	0.066	0.060	2.02 ± 0.15	0.142
Asterionella formosa	*D. ashlandi*	0.185	0.089	4.60 ± 0.28	0.911
	D. sicilis	0.168	0.097	14.27 ± 0.52	1.00

filaments to the position normal to the body axis, and that it takes time periods on the order of a few to several seconds to ingest or attempt to ingest small sections of the colonies. The orientation of filaments normal to the long axis of the body for insertion into the mouth was also a feature observed for *Eucalanus* (Paffenhöfer et al., 1982).

The great amount of broken *S. delicatissima* left behind by *Diaptomus sicilis* during feeding (Table 1) can be explained by the cinematographic observations. Long filaments oriented perpendicular to the body axis are pushed forward by the first maxillae to the mouth. Vigorous active motions of the mouthparts then appear to drive in a small length of the filament and a piece is bitten off. The alga must then be recaptured and the whole process repeated again. For very long filaments the animal may not always be successful getting every piece. This capture sequence appears to be at least superficially similar to that described for *Eucalanus* feeding on *Rhizosolenia*; however, *Eucalanus* was always successful in ingesting the entire cell (Paffenhöfer et al., 1982; Price and Paffenhöfer, 1986).

Elongation in Two Dimensions: Asterionella.—In the experiment shown in Table 3, *Asterionella*'s colonial form, having an average of 3.5 cells per colony, did not give it any protection from grazing. It was clearly the preferred food of *D. sicilis*. *D. ashlandi* had nearly equal selectivities for all three species of algae. *S. radians* was used in the mixture as an analogue for single *Asterionella* cells since they are about the same size. From *D. ashlandi*'s perspective, all three species represent easily handled large algae, since selectivities were about the same.

This view on the vulnerability of *Asterionella* radically changes when average cells per colony increases to 6.2 (Table 4). Clearance rate and W' for *D. ashlandi* feeding on *Asterionella* of 6.2 cells per colony were extremely low (W' = 0.093). For *D. sicilis*, clear preference (W' = 1.0) for the colonies of 3.5 cells per colony (Table 3) becomes a second place preference (W' = 0.871) for the colonies of 6.2 cells per colony (Table 4).

Further insight is gained by reexamining the *Asterionella* results for *D. sicilis* in Table 2 for each of the 16 colony-size categories (Fig. 5). W' for colonies and cells within colonies is highest for colony sizes of 2 to 6 cells. The increase in W' in going from 1-cell to 2-cell colonies is probably a result of *D. sicilis* being able to more easily detect the 2-cell colonies. After 6 cells per colony, there are precipitous drops in W' for both colonies and cells within colonies as colony size increases. The more precipitous drop in W' for cells within colonies than for colonies reflects *D. sicilis*' ability to get only some of the cells in the larger colonies it attacks. Clearly there is an advantage to minimizing grazing loss by forming

Table 4. Clearance rates, F (±SE, N = 4), and selectivity coefficients, W', for *Diaptomus ashlandi* and *D. sicilis* feeding on mixtures of the listed algae. Average cell number per colony for *Asterionella formosa* was 6.2. See Figure 1 for dimensions of algae

Alga	Zooplankton	Algal concentration ($mm^3 \cdot liter^{-1}$) Initial	Average	F (ml animal·d^{-1})	W'
Chlamydomonas sp.	*D. ashlandi*	0.171	0.075	4.57 ± 0.27	1.00
	D. sicilis	0.211	0.159	5.34 ± 0.42	1.00
Synedra radians	*D. ashlandi*	0.174	0.096	3.38 ± 0.21	0.740
	D. sicilis	0.157	0.138	3.01 ± 0.42	0.564
Asterionella formosa	*D. ashlandi*	0.297	0.272	0.423 ± 0.106	0.093
	D. sicilis	0.370	0.289	4.65 ± 0.23	0.871

large colonies. Most of the advantage to avoidance of grazing by *D. sicilis* occurs by reaching a colony size of 7 or 8 cells.

Cinematographic results show that *Asterionella* colonies of all sizes are captured by *D. sicilis* actively similar to large *Chlamydomonas* cells (Vanderploeg and Paffenhöfer, 1985). The difficulty in handling must occur after their reaching the first maxillae. Unfortunately, we were not able to see what happens after they reach there because they—like most algae observed—disappear from sight. Observations of rejected colonies suggest that they are not pulled apart or broken at the center.

Concentration, Selectivity, Cell Breakage, and Optimal Foraging.—The selectivities of *Chlamydomonas* sp. and *Synedra delicatissima* change with concentration of the algae (Table 5). Selectivity expressed as the ratio of clearance rates (Vanderploeg et al., 1984) remained independent of relative concentration of the two species of algae at the low concentration treatments (Table 5). However, selectivity for *Chlamydomonas* was higher in the high concentration treatments than in the low concentration treatments. Also, selectivity increased for *Chlamydomonas* sp. as its relative concentration decreased in the high concentration treatments. These results may be directly contrasted with a similar analysis done by Vanderploeg et al. (1984: fig. 8b) for mixtures of *Chlamydomonas* sp. and *C. oblonga* (ESD = 4 μm). In this case, selectivity for the algae remained invariant of both relative and absolute abundance of the two species of algae.

At this juncture, the variable selectivity observed would usually be described as evidence for optimal foraging (Vanderploeg et al., 1984). Our data are of especial relevance because the trends are statistically significant (Table 5) and are free of artifacts of experiment design—notably particle production—that have compromised many experiments of this kind (Vanderploeg et al., 1984). Interestingly, Paffenhöfer (1984) used the optimal foraging paradigm to explain concentration-variable selectivity in *Paracalanus* in an experiment having some resemblance to ours. At high concentrations, the 12-μm-diameter *Thalassiosira weissflogii* was preferred to *Rhizosolenia alata* (150–260 μm long); at the low concentration treatment, *R. alata* was preferred to *T. weissflogii* (his figs. 8, 9, 10). Our results show even a more dramatic change in selectivity than his. Paffenhöfer noted that *R. alata* had a lower N content than *T. weissflogii*, and suggested that it would be advantageous to select against *R. alata* at the high concentrations since more time and/or energy would be expended for each unit of energy ingested. He further noted this pattern is analogous to the diet broadening that optimal foraging predicts at low food concentrations (Pyke et al., 1977).

We will show by closer examination of our and other data that *Diaptomus* is

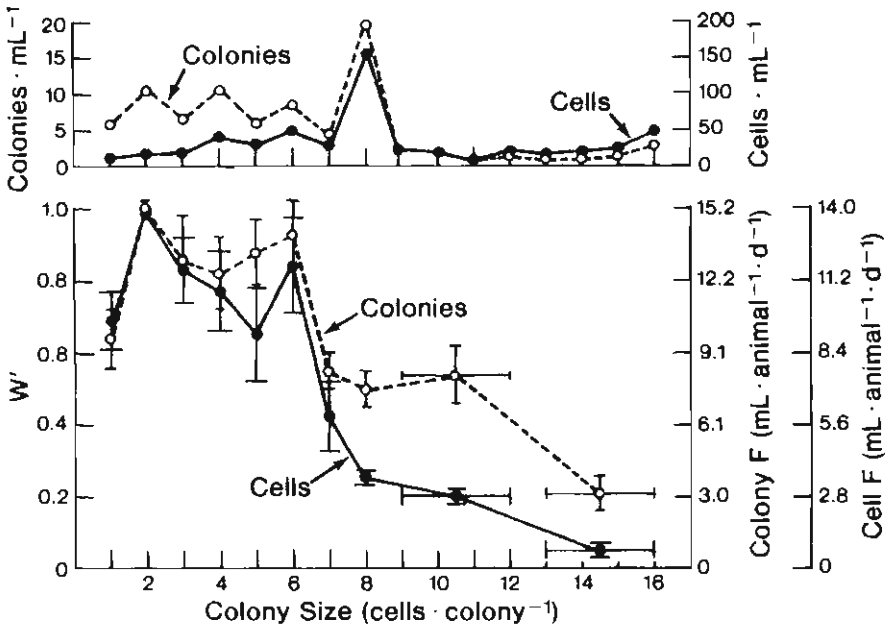

Figure 5. Upper panel: Concentration of colonies and cells in the 16 colony-size categories in the control bottles. Lower panel: Selectivities (W') and clearance rates (F) for colonies and for cells within the colony-size categories. The horizontal bars indicate that data from colonies in size categories 9–12 and in 13–16 were combined to get a sufficient number of colonies to get statistically acceptable results. A total of approximately 6,000 colonies was examined to obtain these results.

not an optimal forager (energy maximizer) and that her concentration-variable selectivity is not an energy maximization strategy. Moreover, we propose a new hypothesis to explain these results. This hypothesis draws heavily on classical ethological concepts of motivation (Tugendhat, 1960; Gardner, 1964; Lorenz, 1981) and limited excitability of the fixed motor patterns of instinctive behavior (Lorenz, 1981). Whether or not our specific hypothesis is correct, it has obvious heuristic value in that it demonstrates the necessity of viewing selectivity in terms of classical ethological concepts that have been largely ignored by optimal-foraging proponents.

Under conditions of satiating food concentration, motivation to complete a behavioral chain of motor patterns leading to ingestion fluctuates (Tugendhat, 1960). We will argue that the instinctive fixed motor patterns associated with handling and ingestion of an elongated alga are less excitable than the fixed motor patterns for handling and ingestion of a spherical alga; that is, as motivation fluctuates the more excitable motor pattern recovers more quickly as satiation wanes. Our hypothesis draws on two behavioral generalizations. First, under satiating conditions, the probability of completing each behavior in a sequence leading to ingestion is lower than the initial behavior or behaviors (Tugendhat, 1960; Gardner, 1964; Leyhausen, 1973; Lorenz, 1981). Second, the excitability of a motor pattern is related to the frequency at which it is called forth by the animal (Lorenz, 1981).

Let us start by describing an excitable motor pattern in this sequence that clearly violates the energy maximization principle of optimal foraging. At high food concentrations (>1 mm^3·liter^{-1}) of monospecific cultures of *Chlamydomonas* sp. or *C. proteus*, *D. sicilis* rejected a great proportion (0.3–0.4) of both actively and

Table 5. Clearance rates (F ± SE, N = 4), selectivities (F_c/F_s) expressed as clearance rate of *Chlamydomonas* sp. (ESD = 12.4 μm) relative to that of *Synedra delicatissima* v. *angustissima* (x ± SD length = 236 ± 31, ESD = 13.2 μm) in mixtures of these algae, and proportion (P) of incomplete ingestions of *Synedra* as a function of the ratio (X_c/X_s) of *Chlamydomonas* to *Synedra* concentration at high and low concentration treatments. Grouping denoted by different letters indicates statistically different (5% level) F_c/F_s ratios by ANOVA

Treatment/species	Average concentration (mm³ liter⁻¹)	X_c/X_s	F (ml animal⁻¹ d⁻¹)	F_c/F_s	P	Grouping*
Low conc., $X_c > X_s$:		10.20		0.603 ± 0.020		A
Chlamydomonas sp.	0.051		21.04 ± 2.12			
S. delicatissima	0.005		34.87 ± 3.27		0.184 ± 0.046	
Low conc., $X_c < X_s$:		0.517		0.628 ± 0.041		A
Chlamydomonas sp.	0.015		18.68 ± 0.76			
S. delicatissima	0.029		30.10 ± 2.03		0.340 ± 0.035	
High conc., $X_c > X_s$:		6.05		1.34 ± 0.03		B
Chlamydomonas sp.	0.551		9.42 ± 0.57			
S. delicatissima	0.091		7.05 ± 0.41		0.319 ± 0.035	
High conc., $X_c < X_s$:		0.413		2.05 ± 0.12		C
Chlamydomonas sp.	0.163		10.51 ± 0.50			
S. delicatissima	0.395		5.14 ± 0.12		0.608 ± 0.013	

* ANOVA using the Boniferroni multiple *t*-test procedure and the Duncan's multiple-range procedure gave these identical results. Because ANOVA can be influenced by inhomogenous variance that can occur in ratio data, we also did ANOVA on rank-transformed data (Conover, 1980). Identical groupings were obtained with rank transformed data.

passively captured cells (Vanderploeg and Paffenhöfer, 1985). Obviously, the active capture motor pattern is both excitable and energy wasting, since captures exceeded ingestions. This description of *Diaptomus* is analogous to the behavior of Leyhansen's (1973) cat released into a room full of mice (cited in Lorenz, 1981). The cat first captured, killed, and at a half dozen of the mice, and then killed a few more without eating them. Then the cat playfully captured a few more without eating them. Then the cat playfully captured a few more without delivering the killing bite. Finally the cat sat in ambush of mice across the room while ignoring mice crawling over its paws. Lorenz (1981: 134–135) emphasized the excitability principle by stating: "The number of performances after which each of these motor patterns proved to be exhausted corresponds exactly to the frequency with which each of them is in 'demand'." Analogous behavior has been reported for fish (Tugendhat, 1960) and for hunting spiders (Gardner, 1964).

Our hypothesis, which we will call the "differential excitability hypothesis," is consistent with the correlation between proportion (P) of *Synedra* cells partially ingested with feeding rate in the mixture experiments with *Chlamydomonas* and *Synedra* (Table 5, Fig. 6). That this rejection rate P (=partial ingestion rate) on *Synedra* is well correlated with attack rate (cells partially or fully ingested) on *Synedra* and not well correlated with attack rate on *Chlamydomonas* or the sum of *Chlamydomonas* and *Synedra* is evidence for limited excitability of the motor pattern associated with handling required for ingestion of *Synedra*. Note the energy maximization principle would predict a good correlation between P and attack rate on *Chlamydomonas* or between P and the sum of both algal species, since we would expect some energy gain to accrue from rejecting the more difficult-to-handle *Synedra* as *Chlamydomonas* availability and ingestion increased. Also note (Table 5) that selectivity for *Chlamydomonas* in the high concentration treatments was higher when *Synedra* concentration was higher. This runs counter to the optimal foraging prediction of specialization on the easier handled alga as its concentration increases, and is consistent with our hypothesis. Thus both selectivity and rejection data support our hypothesis.

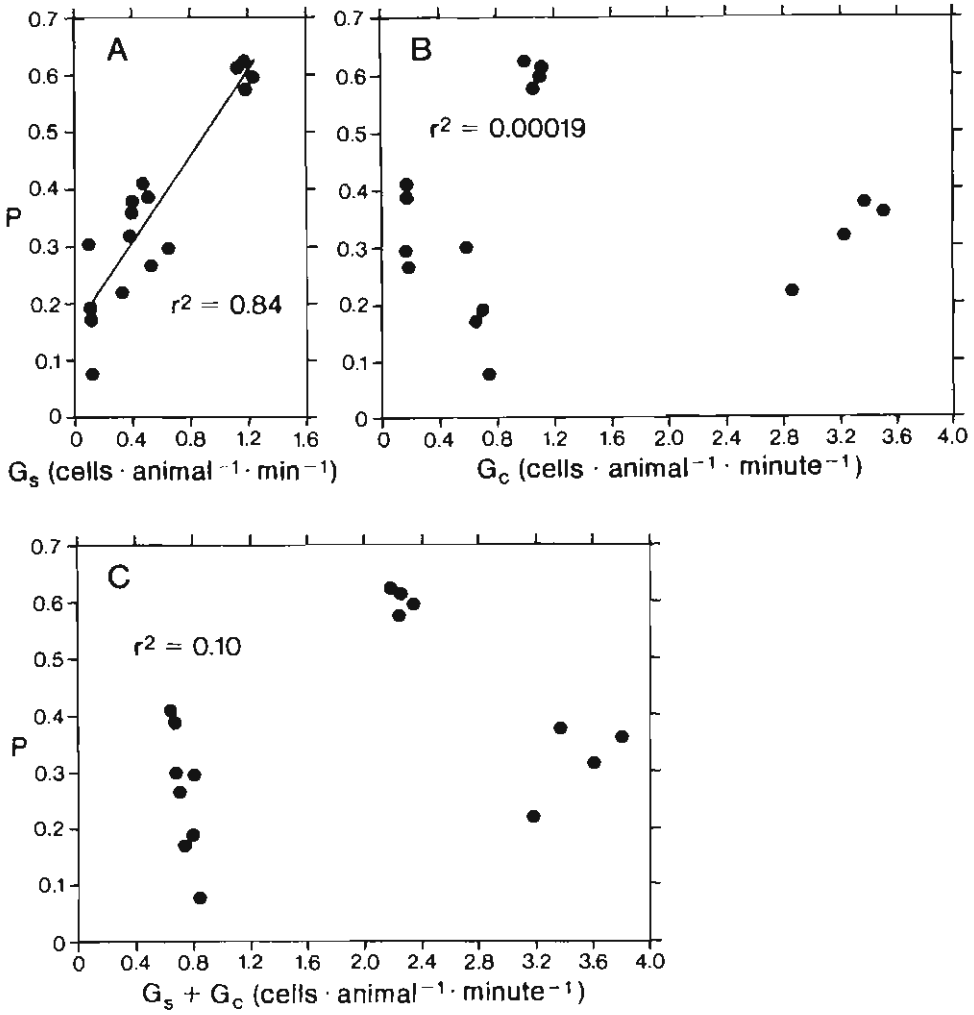

Figure 6. Proportion (P) of *Synedra delicatissima* only partially (less than half) ingested by *Diaptomus sicilis* in mixtures of *S. delicatissima* and *Chlamydomonas* sp. as a function of attack rate (G) on: (A) *S. delicatissima* (G_s); (B) *Chlamydomonas* sp. (G_c); and (C) sum of *S. delicatissima* and *Chlamydomonas* sp. ($G_s + G_c$). Only the regression in (A) was significant at the 5% level.

Basically, we are asserting that in the natural environment *Diaptomus* has become programmed by evolution to use the motor pattern for ingestion of a large spherical alga (*Chlamydomonas* sp.) more frequently than the more complicated motor patterns required for handling and ingestion of an elongated alga like *Synedra*. This interpretation is given further strength by the fact that both small particles captured passively (by "filtering") and larger spherical particles captured actively would be ingested by the same simple coordinated movements of the first maxillae and mandibles (Paffenhöfer et al., 1982; Price and Paffenhöfer, 1983; Vanderploeg and Paffenhöfer, 1985). Although we cannot precisely say at what rate *Diaptomus* encounter elongated net plankton relative to other cells (because we do not know their abundance in nature), it seems reasonable to assume fewer interactions with elongated algae since large algae are not as numerically

abundant as small algae, and because the passive mode of feeding is an important mode of feeding in *Diaptomus* (Vanderploeg and Paffenhöfer, 1985).

Another possible interpretation for the correlation between P and attack rate on *Synedra* is that handling time for ingestion of a *Synedra* cell is very long, on the order of a minute. We suggest handling time of this length because P increased from a low value (0.2) at an attack rate on *Synedra* of 0.1 cell·min^{-1} to a very high value (0.6) at 1.2 cells·min^{-1} (Fig. 6). This interpretation assumes that the capture of a *Synedra* cell and subsequent handling and ingestion attempts would interfere with handling and ingestion of a *Synedra* cell already captured. The few films we have of *Diaptomus* feeding on *Synedra* show that a *Synedra* cell can be captured and handled even while another cell is in position for ingestion. Unfortunately, we do not have films at a low enough *Synedra* concentration to see how or how quickly a hungry *Diaptomus* would handle them. A hungry animal must be observed since handling time—like duration of other feeding responses (Tugendhat, 1960)—may increase with satiation. Note that handling times of double cells of *Rhizosolenia alata* (cell length = 450 μm) by *Eucalanus elongatus* is only 1.3 s (Price and Paffenhöfer, 1986). If *Diaptomus* is as adept at handling long cells as *Eucalanus*, then our hypothesis and not handling time is the likely explanation for the variable selectivity.

Ecological Implications: A General Discussion.—Little previous information existed on grazing of *Diaptomus* and other calanoid copepods on net diatoms (Paffenhöfer et al., 1982; Paffenhöfer, 1984; Horn, 1985). This lack follows in part because net diatoms are not usually available from culture collections: the algae get smaller with time in culture, and some like *Stephanodiscus* do not last long in culture, presumably because some required nutrient is absent. No previous systematic examination of morphology of net plankton as a mechanism of reducing grazing mortality from *Diaptomus* has ever been done.

Elongation in one dimension does not appear to be a useful attribute for avoiding grazing by *Diaptomus*, at least for algae shorter than 365 μm. *Diaptomus* showed remarkable flexibility for handling and even ingesting small segments off of *Melosira* colonies 700 μm long (Fig. 3). It will be of great interest to determine clearance and ingestion rates of colonies this long. *Melosira* also has an advantage over *Synedra* because of its colonial form. If a segment of a colony is bitten off, a few cells die rather than the whole unicellular unit as in *Synedra*.

The stellate colonial form of *Asterionella formosa* appears to be an extremely effective attribute for minimizing grazing by *Diaptomus*. The change in average cell number per colony from 3.5 to 6.2 grossly depressed grazing in the smaller copepod, *D. ashlandi*. Even the selectivity of *D. sicilis*, a relatively large suspension-feeding copepod, was depressed by colonies having more than eight cells. Some caution must be noted here because of our observation that selectivity for *Synedra* decreased at high concentrations of algae. As can be discerned from the relatively low clearance rates on *Chlamydomonas* in the mixture experiments with *Asterionella*, algal concentrations were saturating. Perhaps if *Diaptomus* were hungrier, it might have had higher selectivities for larger colonies.

Reynolds (1984) argues that the dominance of 8-cell colonies observed in nature results from the dramatic loss of form resistance and consequent increase in sinking rate that occur when colonies contain more than eight to nine cells. Our results suggest that eight-cell colonies offer considerable protection from grazing by *Diaptomus* that is not greatly increased by formation of colonies with still greater cell number. Thus eight-cell colonies may offer considerable protection from grazing while minimizing sinking losses. The abrupt improvement in grazing protection around eight cells per colony may occur because at this number of cells they—

like spokes in a wheel—complete a circle. This circle may act as a solid disc in terms of the copepod's ability to graze on them.

Elongation of an alga in three dimensions is obviously a useful attribute to avoid ingestion by zooplankton. *Stephanodiscus niagarae* was too large to be grazed effectively by *D. ashlandi,* but not by *D. sicilis.* This grazing protection was however accomplished at the cost of a high sinking rate and a low surface area to volume ratio, which results in low growth rates (Reynolds, 1984).

This study and the study of Williamson and Vanderploeg (1988) suggest that we must reassess our view of *Diaptomus* as a small particle specialist (Vanderploeg and Paffenhöfer, 1985). It now appears that *Diaptomus* does very well on small particles, particles elongated in one dimension, and small microzooplankton (Williamson and Butler, 1986). In the latter case, *Diaptomus* exhibits a thrust response—involving a flap of the thoracopods and sweep of the first antennae—to pounce on the microzooplankton (Williamson and Vanderploeg, 1988). Thus, *Diaptomus* is a behaviorally flexible omnivore. In this respect, it is of interest to compare its behavior—particularly the fixed action patterns of its appendages—with those of *Acartia. Eucalanus,* and *Paracalanus,* the species for which we have cinematographic observations (Paffenhöfer et al., 1982; Price and Paffenhöfer, 1983, 1985, 1986). *Diaptomus* is most like *Paracalanus* and *Eucalanus* in that all three species create double-shear scanning currents (Strickler, 1982) with use of their second antennae, first maxillae, and maxillipeds (Paffenhöfer et al., 1982; Strickler, 1984; Vanderploeg and Paffenhöfer, 1985; Paffenhöfer and Stearns, 1988). All of these species except *Acartia* have high clearance rates on elongated algae and are adept at handling them. Curiously, unlike *Diaptomus, Eucalanus* and *Paracalanus* do not flap their thoracopods to help capture algae. In *Acartia,* flapping of the thoracopods is used in conjunction with seining motions of the second maxillae to capture algae and microzooplankton (Paffenhöfer and Stearns, 1988). Thus, *Diaptomus* has behaviors common to all the other species. The thrust response reported for tethered *Diaptomus* attacking rotifers (Williamson and Vanderploeg, 1988) has not been reported for *Eucalanus* and *Paracalanus.* We cannot say this response does not exist in these species, because it has not been looked for; however, the lack of thoracopod flapping in the presence of algae suggests this response may not exist or is weaker. Note that the thrust response is not only useful for prey capture, but also serves the very important function of avoiding predation. Further work is necessary so that useful generalizations will emerge.

The other issue that emerges from this study is the decreased selectivity for the net plankton at high concentrations. We showed that this feeding behavior of *Diaptomus* violated the energy maximization principle of the optimal foraging paradigm. Thus, although *Diaptomus* is behaviorally flexible, its concentration-variable selectivity is not an optimal foraging response. We presented a new hypothesis, the differential excitability hypothesis, that was based on classical ethological theory to explain variable selectivity. A complete behavioral analysis of our hypothesis would require observation of *Diaptomus*' interaction with its prey at all stages of the prey-location, orientation, capture, handling, and ingestion chain. Nevertheless, our partial evaluation of our specific hypothesis served the goal of demonstrating the necessity for viewing foraging within the framework of classic ethological theory.

We are not arguing that energy maximization is not an ultimate goal underlying organism design and behavioral repertoire, but rather that energy maximization and other goals operate through heritable fixed motor patterns which are not always acting in an energy optimizing fashion for every situation the organism finds itself in. This is especially relevant at satiating concentrations, where selec-

tion pressures may be minimal, because satiating food concentrations may not be a frequent occurrence in nature. Thus, in this sense, prey selection determined at high food concentrations could be viewed an artifact created by the experimenter subjecting the predator to conditions for which it was not designed. This points out the danger of drawing conclusions about optimality of foraging from selectivity data at high prey concentrations unless observations on the complete chain of behavior leading to ingestion are made.

Curiously, most ethological studies on feeding predate work by optimal foraging theorists, who largely ignored them. In view of the limited success of optimal foraging as a tool for prediction of prey selection, more emphasis should be placed on careful, old-fashioned ethological observations of foraging behavior. With the new tools of high-speed microcinematography (Alcaraz et al., 1980) and videography (Strickler, 1985), such old-fashioned observations are now possible for zooplankton.

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APPENDIX: DISCUSSION AFTER VANDERPLOEG *ET AL.*

D. Stearns: Did you observe *Diaptomus* breaking large *Asterionella* colonies into smaller colonies?

H. Vanderploeg: No, we did not observe that, although *Diaptomus* did appear to nip off the ends of colonies occasionally, judging from colony debris. The colony seems to be "glued" together very well.

K. Porter: Since particles are typically more abundant in freshwater than marine systems. Do you feel that freshwater species can "afford" to be more selective?

H. Vanderploeg: This raises the interesting question of whether there might be different selective forces operating on grazers in freshwater than in marine systems. The freshwater grazer is confronted with many more species of phytoplankton than grazers in the sea, although I know of no experimental results indicating that freshwater zooplankton are more selective. Your own work has shown that freshwater grazers during summer can encounter many species of both unpalatable algae and undigestable algae. Our work here has emphasized possible effects of algal geometry. Cursory examination of taxonomic treatises would suggest that in addition to a greater taxonomic diversity, there is probably greater morphological diversity of phytoplankton in freshwater. Although particles may be more abundant in freshwater, these particles may present more challenges to the zooplankton in terms of taste, digestibility and morphology.

Having said that freshwater and marine environments are qualitatively different, I can turn now to the question of whether—assuming all things being equal—freshwater species can "afford" to be more selective. Implicit in this question is the optimal foraging idea, that as prey become more abundant, the predator focuses his attention on the preferred prey and that fewer prey species are captured. In our revised manuscript, we emphasized instead the ideas of motivation and excitability of different motor patterns used to capture, handle, and ingest different kinds of prey. We also emphasized that changes in selectivity may be a satiation response, at least for palatable algae. Taking this reasoning to its logical end, we could argue that selectivity will not vary unless the animal is experiencing satiating food concentrations.

Now the question becomes: Are particle concentrations in freshwater typically satiating for copepods? When answering this question, we must know what the effective particle (food) concentation (Vanderploeg *et al.*, 1984) is because many of the particles may not fall within the proper size range or have the proper scent or taste to be detected and ingested. Theoretically, effective particle concentration can be much lower than total particle concentrations; therefore a copepod may not be experiencing satiating feeding conditions in a particle-rich environment.

Unknown: The subjects of zooplankton feeding studies, particularly cinematographic ones, are generally viewed as heroes in a narrative—always doing the "right" thing.

H. Vanderploeg: A recent paper called "Human Evolution as Narrative" by Misia Landau (Am. Sci. 72: 262–268) is especially relevant to zooplankton ecology because of its obsession with optimal foraging. Optimal foraging is basically a particular evolution story with a hero behaving in an ordered, reasoned way in the environment. We are compulsive storytellers, we get paid for telling stories (writing papers), and we love this story. When I was trying to get some of my ideas published on invariant selection, the strong appeal of this story became obvious to me in the negative reviews on my manuscripts. I think a paradigm with such deep psychic appeal can color our perceptions. For a few years now I have kept a card in my desk drawer with the following title for a paper: "Copepod feeding as narrative: *Diaptomus* and the optimal foraging myth." I have not used the title yet, but the idea motivates much of my research.