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The Biology of Particles in Aquatic Systems

Editor

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1990



CRC Press
Boca Raton Ann Arbor Boston

Chapter 9

FEEDING MECHANISMS AND PARTICLE SELECTION IN
SUSPENSION-FEEDING ZOOPLANKTON

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I. INTRODUCTION

A. SOME INTERESTING NARRATIVES

Landau¹ has pointed out that scientific theories are essentially narratives and that we have certain basic stories, or deep structures, we tell to organize our experiences. Moreover, she showed how narrative analysis was useful to explain competing theories of evolution of man. Feeding, on the one hand, and not being killed in predatory encounters, on the other hand, are two important forces in the survival of individuals and evolution of communities. Our subjects of study, the plankton, are heroes in a narrative of life and death, and we scientists are the storytellers.² Rather than avoiding narratives, Landau¹ suggests scientists use them, as they are used in literature, as a means of discovery and experimentation. Moreover, she notes that recognition of scientific paradigms as narratives or myths is useful because it keeps us from taking them so seriously, thus promoting discovery.

I have begun this chapter on feeding mechanisms of suspension-feeding zooplankton with a reference to narrative because feeding mechanisms have played a central role, and will continue to play a central role, in the ecological stories we tell about aquatic communities. No study of mechanisms is ever free of an ecological context, and the soundness of our ecological stories can be evaluated only by their consistency with observed mechanisms. Some examples of popular narratives for which understanding of feeding mechanisms is essential for evaluation are

1. Suspension-feeding zooplankton are optimal foragers who will track peaks in particle-size spectra; i.e., focus their feeding efforts on the most abundant particles.^{3,4}
2. The dynamics of pelagic ecosystems can largely be described from knowledge of size of their components (algae, zooplankton, and fishes) and food-size preferences.^{5,6}
3. The microbial food web is a "sink" and not "link" to components of the classic food web (large phytoplankton, large zooplankton, fishes) because suspension-feeding metazoans cannot efficiently graze picoplankton (<2 μm).^{7,8}

Other kinds of narratives about food webs we are likely to tell can be motivated by examination of data from the Laurentian Great Lakes. Figure 1 shows that the different Great Lakes exhibit different seasonal patterns of phytoplankton concentration (expressed as chlorophyll *a*), ranging from ultraoligotrophic Lake Superior, which exhibits a stable and low phytoplankton concentration, to eutrophic Lakes Ontario and Erie which exhibit high and wildly fluctuating phytoplankton concentration.⁹⁻¹³ In large part these concentrations reflect the different nutrient supplies to the lakes. In addition, these lakes — all interconnected — have very different food webs. As we move along a gradient of increasing eutrophy, we

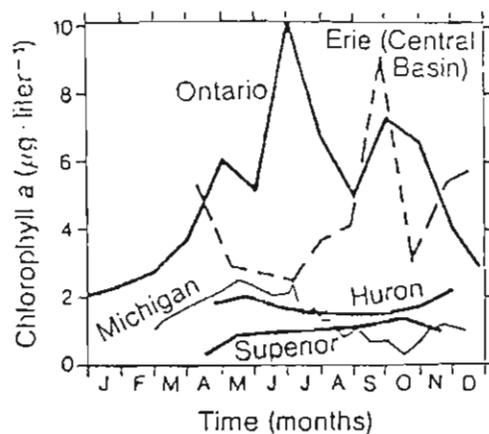


FIGURE 1. Seasonal chlorophyll *a* concentrations in the Great Lakes compiled from survey studies of the early 1970s.⁹⁻¹³ All data are for the epilimnion except the Michigan data, which are integrated over 100 m.

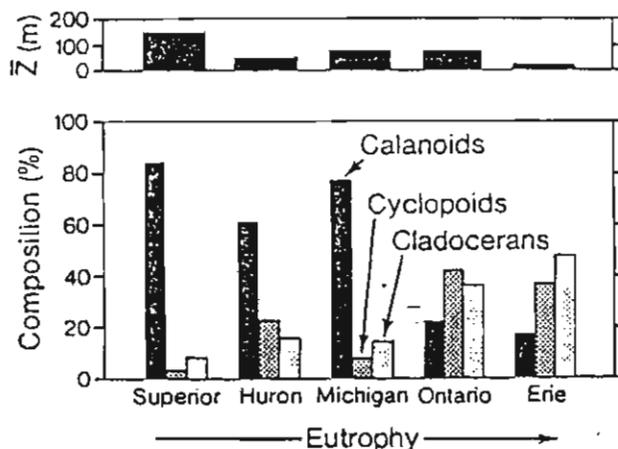


FIGURE 2. Biomass composition of crustacean zooplankton from early spring through late fall from seasonal survey data.¹⁴⁻¹⁶ Dry weights of Hawkins and Evans¹⁷ were used to convert number concentrations to biomass. Upper panel shows mean depths (*Z*) of the lakes.

see that the crustaceans, first dominated by calanoid copepods, become dominated by cladocerans and cyclopoid copepods (Figure 2).¹⁴⁻¹⁷ As we shall see later, feeding mechanisms probably account for this difference. Note especially the very different food webs in Lakes Michigan and Ontario, both of which have the same mean depth (Figure 2) and temperature regimes.

B. MATHEMATICAL FRAMEWORK AND SPECIFIC QUESTIONS

1. Effective Food-Concentration Model

All the narratives described above are just submodels of larger food-web models that incorporate zooplankton-particle interaction. It can be argued that the goal of research on feeding mechanisms is the development of mathematical models that predict the feeding-rate of zooplankton on all the particles in nature. These particles would include not only (1) algae of various morphologies, toxicities, and digestibilities, (2) microzooplankton, and

(3) detritus, but also (4) inert mineral suspensoids such as clay and autogenically precipitated calcite.^{18,19} Ingested inert particles can lower assimilation efficiency of carbon in ingested food, and mineral suspensoids such as resuspended bottom sediments may be a source of toxic chemicals to plankton if these sediments are polluted.^{18,19}

The effective food concentration (EFC) model provides a general framework from which to model ingestion of the different particles in nature, as well as quantitatively express the narratives.^{20,21} This model predicts ingestion-rates of different kinds of food in a mixture from knowledge of food-type (particle) concentrations (X_i) and their selectivity coefficients (W_i'). EFC is the weighted sum of the n food types, where the weighting factors are the selectivity coefficients:

$$EFC = \sum_{i=1}^n W_i' X_i \quad (1)$$

The selectivity coefficient is most easily determined from clearance-rates (F_i) of the different kinds of foods in mixtures from the relation $W_i' = F_i/F_{pref}$, where F_{pref} = clearance-rate (units = ml-animal⁻¹·d⁻¹) on the preferred food. Note this coefficient ranges between 0 and 1 and is equivalent to relative mortality-rate coefficient (m_i) induced by the predator, since m_i is proportional to F_i .²⁰ For a filter feeder, W_i' corresponds to filtration efficiency, assuming all particles collected are ingested. The EFC model states that ingestion-rate (G) of all foods in any mixture of foods is given by a simple functional relation $G = f(EFC)$, where $f(EFC)$ may be any of the relations used to predict ingestion of a single kind of food such as the Michaelis-Menton, linear, or Ivlev.²² For example, substitution of EFC for food concentration in the Michaelis-Menton expression gives the following expression:²⁰

$$G = \frac{G_{max} \cdot (EFC)}{K + EFC} \quad (2)$$

where G_{max} is maximum ingestion-rate, and K is the half-saturation coefficient. Ingestion-rate (G_i) on the i^{th} kind of food is

$$G_i = \frac{G_{max} \cdot W_i' \cdot X_i}{K + EFC} \quad (3)$$

G_{max} and K may be functions of environmental variables such as temperature, as well as physiological condition of the animal that, for example, might change with feeding history or reproductive status of the animal. The basic principle of the EFC model is that Equation 1 converts the quantity of each kind of food to an equivalent amount of the most-preferred food by means of the selectivity coefficient W_i' . Thus $G = f(EFC)$ is the same response for the most-preferred food alone. Vanderploeg and Scavia²⁰ and Vanderploeg et al.²¹ assumed that the W' had to be invariant (not change) with food concentration for the EFC model to be valid. Ambler²³ showed that this assumption could be relaxed. An obvious but important corollary of the EFC model is that $EFC \ll$ total particle concentration, i.e., $\sum_{i=1}^n X_i$. If W' values of the different particle types are low, a suspension feeder can find itself in a high-concentration particle suspension and starve.

Clearance-rates are extremely useful for understanding the interaction of the suspension feeder with its environment. We have already noted that clearance-rates normalized to F_{pref} are selectivity coefficients. Clearance-rate, or volume water swept clear of particles per unit time, is the rate at which suspension feeders address or "search" the environment, since F

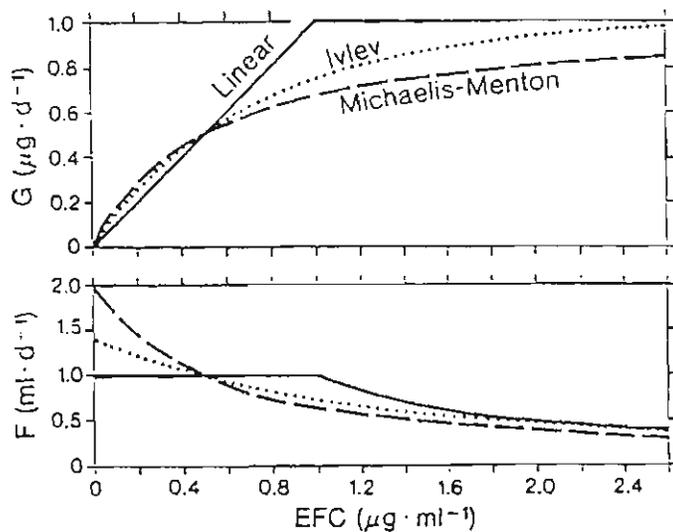


FIGURE 3. Theoretical ingestion-rate (G) and clearance-rate (F) curves as a function of effective food concentration (EFC) for linear, Michaelis-Menton, and Ivlev relations. Curves were drawn so that maximum ingestion rate (G_{max}) = $1.0 \mu\text{g} \cdot \text{d}^{-1}$ for all relations, and all relations have a half maximum G at $\text{EFC} = 0.5 \mu\text{g} \cdot \text{ml}^{-1}$. The incipient limiting concentration, the lowest EFC at which G_{max} is reached for the linear model, is $1.0 \mu\text{g} \cdot \text{ml}^{-1}$.

has the same units as a search-rate. Feeding-rate (G) is the product $F_{pref} \cdot (\text{EFC})$. Figure 3 shows the relationship of G to EFC and F_{pref} to EFC for the three commonly used models. Experimental work shows that not all feeding relationships will fit one, or any, of these models although they often do apply.^{24,25} An important feature of all these models is that at low EFC, clearance-rates are maximal (Figure 3). At low EFC, W' are often approximated from clearance rates determined for individual prey types offered singly using the same relation $W'_i = F_i/F_{pref}$, but here the F_i = clearance-rate of i offered alone.²¹ In this case we are assuming that like the linear model (Figure 3), clearance-rate does not change with EFC at low EFC. This also presumes the suspension feeder is in the same physiological condition in the separate experiments.

Clearance-rates at low EFC represent the maximal rate the organism can address the environment. Therefore, it is of interest to compare weight-specific clearance-rates of different suspension feeders on different particles at low concentrations to determine how well each can address the environment, because relatively low food concentrations may often be the normal situation in aquatic environments. It is also of importance to know weight-specific G_{max} since a high G_{max} identifies organisms adapted to high food environments or identifies opportunistic organisms adapted to take advantage of intermittent high food concentrations. In general, entire G vs. EFC and F_{pref} vs. EFC responses are of interest.

2. Components of Selectivity Approach

W' , W , and E^* are generally considered the preferred variables for quantifying food selection, and are widely used.^{4,20,26-28} I generally prefer using W' over W and E^* , because W and E^* values depend on number of prey species included, and because of the direct connection of selectivity expressed as W' to the EFC model.^{4,20,21,28} To emphasize this point I call W' the selectivity coefficient and W and E^* electivity coefficients.

Another advantage of using W' to express selectivity is that it is possible to break it down into components of selectivity in a fashion analogous to the components of predation approach of Holling.^{20,29} Holling²⁹ broke the feeding process into a sequence of chronological

steps involving different mechanisms. The probability (P_i) that ingestion of the i^{th} kind of prey ultimately occurs is

$$P_i = P_{E_i} \cdot P_{P_i} \cdot P_{C_i} \cdot P_{I_i} \quad (4)$$

where P_E , P_P , P_C , and P_I are, respectively, conditional probabilities of encounter, pursuit, capture, and ingestion. For example, we may think of a pelagic suspension feeder like a copepod that has a volumetric search-rate, i.e., a searching clearance-rate, of ψ . Feeding-rate on the i^{th} prey is

$$G_i = \psi \cdot P_i \cdot X_i \quad (5)$$

Combining Equation 5 and 4

$$G_i = \psi \cdot X_i \cdot P_{E_i} \cdot P_{P_i} \cdot P_{C_i} \cdot P_{I_i} \quad (6)$$

In earlier publications, we wrote Equation 5 as $G_i = \psi W_i' X_i$, where W_i' may be thought of as the conditional probability that the species will be ingested if it occurs in the search volume.^{20,21,26,30} We said "thought of" because the prey with the highest clearance-rates may not necessarily be captured if it is encountered, and because ψ can be an immeasurable quantity if we cannot specify the boundaries of the area the predator sweeps out. Because W' is either this conditional probability or, in the general case, a normalized (scaled to the highest) conditional probability, we can formally break W_i' into components of predation as follows using Equation 4:

$$W_i' = P_i/P_i^* = [P_{E_i} \cdot P_{P_i} \cdot P_{C_i} \cdot P_{I_i}] / P_i^* \quad (7)$$

where P_i^* is the P_i for the most preferred prey, i.e., the maximum P_i for all prey types. We take advantage of Equation 7 and speak of components of selectivity by replacing the chain of conditional probabilities by conditional selectivity coefficients:

$$W_i' = P_i/P_i^* = (W_{E_i} \cdot W_{P_i} \cdot W_{C_i} \cdot W_{I_i}) / W_i^* \quad (8)$$

where W_i^* = the maximum product of the conditional selectivities in the parentheses of Equation 8. Thus, we can break selection into selectivity at each stage of the feeding process. This formalism may not be used for many practical problems; however, it does emphasize the multistep process that ultimately determines selectivity. The studies of Gallager³¹ on filter feeding of bivalve mollusc larvae, Williamson³² on *Diaptomus* preying on rotifers, and Vanderploeg et al.³³ on *Diaptomus* feeding on particles of various food qualities are noteworthy examples of the importance of looking at the whole multistep process. The story does not quite end with ingestion since the ingested food must be digested and utilized. Therefore, it is necessary to consider the suspension feeder's ability to digest and utilize various toxic and digestion-resistant foods; e. g., toxic blue-green algae and dinoflagellates and digestion-resistant, gelatinous, green algae.

In addition, the particles not digested become egested feces. Thus, suspension-feeding zooplankton ingest particles of various sizes and qualities and output particles of different sizes in the form of lower quality fecal pellets or diffuse feces, depending on the taxon.

C. GOALS AND ORGANIZATION

Recently, Price³⁴ organized her review of feeding mechanisms of all major taxa of zooplankton by describing the mechanisms associated with each of the steps, i.e., conditional

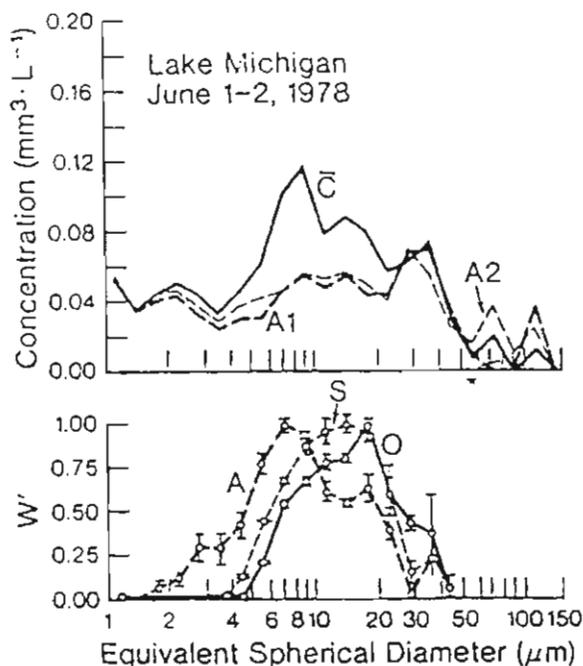


FIGURE 4. A feeding experiment carried out to determine the selectivity of *Diaptomus ashlandi*, *D. sicilis*, and *D. oregonensis* for natural seston in Lake Michigan. The upper panel shows mean concentration of particulate material in control containers (\bar{C}), without zooplankton, and in experimental containers (A1 and A2), containing *D. ashlandi*, after 1 d of feeding. From the difference in these curves, the W' vs. equivalent spherical diameter (ESD) curve for *D. ashlandi* (labeled A) was calculated. The W' vs. ESD curves for *D. sicilis* (labeled S) and *D. oregonensis* (labeled O) in related experiments are also shown. Lengths (prosoma) of *D. ashlandi*, *D. sicilis*, and *D. oregonensis* were, respectively, 0.80, 1.2, and 1.0 mm.

probabilities in Equation 4. Her purpose was to do a survey of the mechanisms. My purpose is to describe selectivities and explicitly connect them to the mechanisms responsible. I will be concerned explicitly about drawing generalizations about feeding types or guilds. Furthermore, the guild or feeding-type orientation is necessary because we cannot, in most cases, describe the actual mechanisms of feeding, but only how the animal functions in an operational sense. Emphasis will be given to size of selected particle and quality since both variables are important. Data will be often presented in the format of W' vs. equivalent spherical diameter (ESD) of the ingested particle, because ESD is a convenient way of expressing size in understandable, easily visualized units. Also, as has been done historically, ESD will be on a logarithmic scale, since particle concentration in volume or mass units is roughly constant across this logarithmic scale.^{33,34} For example, the upper portion of Figure 4 shows the particle-size spectra; i.e., volume of particulate material vs. ESD, in bottles of natural lake seston without and with grazing zooplankton after 1 d of feeding.³⁷ The lower portion shows the W' vs. ESD curve for *Diaptomus ashlandi* determined from these data, as well as W' vs. ESD curves for *Diaptomus sicilis* and *D. oregonensis* in similar, related experiments. The W' vs. ESD curve is the selectivity-size spectrum. Our interest in particle-size spectra and grazing experiments like these can be related to the development of the Coulter Counter® for rapid sizing of particles expressed as ESD and the application of this tool to marine science in the late 1960s and early 1970s.^{33,34,38} It is important to recognize

TABLE 1
Calculation of W' Values for a Set of Three Prey from Two Sets of Two
Prey, Each Having Indicated Clearance-Rates (F) and W' Values

Experiment	Prey type	F (ml d ⁻¹)	W' in each expt.	Combined W'
1	1	5	0.5	0.25
	2	10	1.0	
2	2	15	0.5	0.50
	3	30	1.0	

at the outset that algae come in various shapes other than spheres; therefore, ESD may have more, or less, resemblance to linear dimensions of the algae.

Very often selectivity coefficients are not available for large sets of prey types. In fact, selectivity coefficients were typically available for only pairs of prey types. To estimate W' values of large sets from smaller sets, I used the principle of maintaining proportionality between coefficients defined in smaller sets to build the larger set. An example will help (Table 1). Prey 3 is preferred to prey 2 in experiment 2, and prey 2 is preferred to prey 1 in experiment 1, as indicated by the F and W' values for the separate experiments. Clearly, prey 3 is the preferred prey; thus, we assign it an overall value of 1.0. The proportional relationships between prey 3 and prey 2 in experiment 2 is maintained by assigning prey 2 a value of 0.5. The proportional relationships between coefficients in experiment 1 is maintained by calculating an overall value of 0.25 for prey 1. This approach is most suitable for low concentrations of prey because W' does not vary with relative proportions of prey or concentrations at low prey concentrations (as discussed below).

This chapter will be limited to those taxa that are suspension feeders throughout their lives and are dominant grazers in the oceans or freshwater lakes: calanoid copepods, cladocerans, rotifers, pelagic tunicates, and ciliates (Protozoa). I am using the expression "suspension feeder" in its broadest context to include all zooplankton that feed on small particles. Paffenhöfer et al.³⁹ were the first that I am aware of to apply this expanded definition when they described as suspension feeders copepods that use remote detection to locate particles. Previously the definition was synonymous with filter feeding, and copepods, themselves, were thought to be filter feeders. The suspended particles we are concerned about are in the submicrometer to approximately 200- μ m size range, the size range typically measured by the Coulter Counter[®]. By this expanded definition some suspension feeders themselves are not much bigger than the particles they feed on, and they too would be in the size range counted by the Coulter Counter[®]. All suspension feeders discussed in this chapter, because of their small size and relatively low current velocities they create, live in a viscous environment in which flow is laminar.

The review is not intended to be an exhaustive treatise on mechanisms but an essay on the relation of feeding mechanisms to feeding ecology with emphasis on recent ideas, especially those concerned with food quality and how selectivity for different particles may change as their abundance changes. Another issue is whether zooplankton have sensory systems that can detect particles before touching them. I start the review with copepods because they exhibit a broad range of behaviors and mechanisms that encompass most of those of the other groups. Because of this, and the long history of study of this taxon, generalizations made here will be useful models for understanding other groups. In addition, the review is largely restricted to feeding behavior in a homogeneous environment because we do not have enough information — because of experimental difficulties — on how these suspension feeders might locate and take advantage of patches.

II. CALANOID COPEPODS: BEHAVIORALLY FLEXIBLE OMNIVORES

A. HISTORY

Much of the impetus for studying feeding mechanisms in planktonic suspension feeders can be traced to the first application of high-speed microcinematography by Strickler and colleagues³⁹⁻⁴¹ in the late 1970s and early 1980s to directly observe feeding mechanisms of marine calanoid copepods. Before these observations herbivorous calanoid copepods were thought to be filter feeders, and selection for particles was largely thought to be a function of the size distributions of holes in the copepod's filter, the second maxillae.⁴²⁻⁴⁷ Moreover, the most developed form of this model, called the leaky-sieve model, argued that the cumulative frequency distribution of holes (intersestule and intersestal spaces) in the second maxillae defined the W' curve of the copepod.^{30,44,46-48} The observations of Strickler and colleagues showed that calanoid copepods created a scanning current of water that focused water near the animal's body and that the copepod responded by coordinated movements of the mouthparts to bring in a large alga it detected closer to the body and ultimately ingest it.^{40,41,49,50} At the time, olfaction was hypothesized to be the stimulus for capture. Also, it was discovered that copepods preferentially ingest algae over plastic microspheres, and algal-flavored microcapsules over unflavored microcapsules.^{51,52} These observations were made during a period of intense debate as to whether copepods tracked peaks in the particle-size spectrum.^{3,4,51,53-56} For example in Figure 4 this question was rephrased as: Does the peak in the W' vs. ESD curve match that of the peak in the particle-size spectrum (the C curve), and does the W' vs. ESD curve change from one experiment to another as the shape of the particle-size spectrum changes? If the W' curve, or selectivity spectrum, does not change from experiment to experiment this is concentration-invariant, or "invariant" selection; if it does, this is concentrations-variable, or "variable", selection.^{4,20,26} It was recognized that the leaky-sieve model (or passive, mechanical selection) was one way of obtaining invariant selection and, implicitly, invariant selection became equated with passive mechanical selection; therefore, the idea of invariance fell into disfavor.^{4,20,21,26} The peak-tracking question is basically an optimal foraging question of whether the animal will focus its efforts on the most abundant food and thereby elevate its food intake. This question was important then, and it still motivates research. A lot of confusion in answering this invariance question arose out of three serious problems:^{4,21} (1) improper methods of quantifying selection; (2) zooplankton feces production confusing what was actually ingested (i.e., particles removed) since the Coulter Counter[®] cannot distinguish between egested feces and uneaten particles, and (3) the Coulter Counter[®] does not distinguish quality of the particles. The first problem was solved by the invention of W' (and W and E^*), and the second and third by using methods such as microscopic counting or radiotracer methods that clearly allowed measurement of ingestion and the nature of the particles ingested. The idea of the particle-size spectrum is nevertheless useful, because size is an important variable. We can start attacking this problem by looking at mechanisms responsible for the selection of high-quality food of different sizes.

B. SELECTIVITY, FEEDING RATES, AND MECHANISMS

1. Selection of High-Quality Food

Diaptomus will serve as an example to start the discussion because it is one of the four copepods intensively studied by high-speed microcinematography (Figure 5), and because selectivity and feeding-rate have been explicitly related to feeding mechanisms.^{2,21,25,41,57,58} The W' vs. ESD for *Diaptomus* is shown for easily ingested high-quality algae and an easily ingested soft-bodied slowly moving rotifer in Figure 6. Selectivity increases with increasing size of alga or rotifer. For comparison the W' curve predicted from the leaky-sieve model

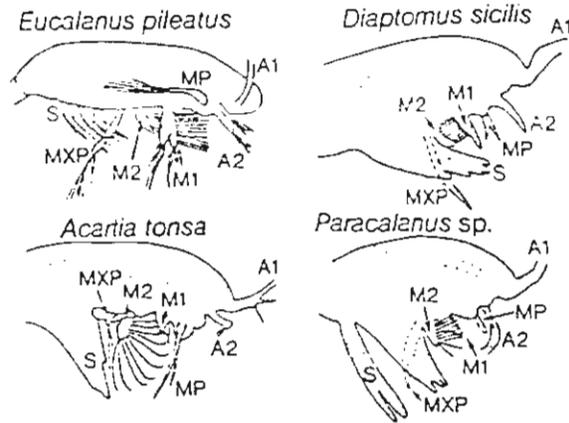


FIGURE 5. Lateral views of the anterior portion of the bodies of copepods studied by high-speed microcinematography. Figures were redrawn from Koehl and Stueckler,⁴¹ Vanderploeg and Paffenhöfer,³⁷ and Paffenhöfer and Stearns.²³ The appendages labeled are A1, first antenna, A2, second antenna, MP, mandibular palp, M1, first maxilla, MXP, maxilliped, and S, swimming feet.

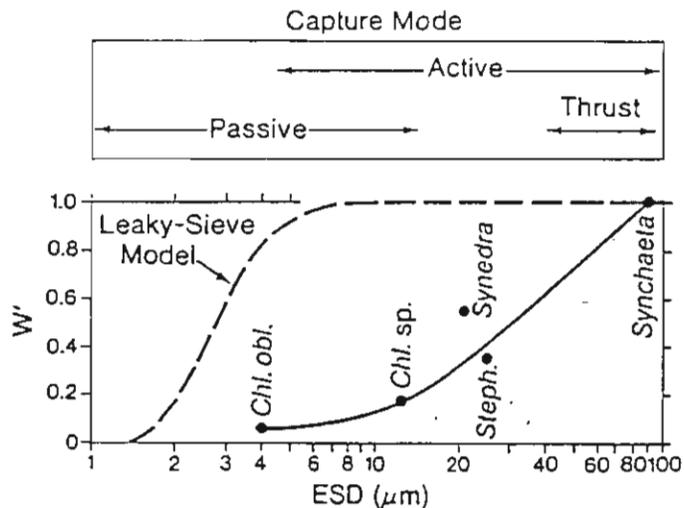


FIGURE 6. The W' vs. equivalent spherical diameter (ESD) curve for *Diaptomus* feeding on high-quality food (solid line). This curve is a composite of results from experiments of Vanderploeg, Paffenhöfer and Liebig² for *D. sicilis* feeding on the algae *Chlamydomonas* sp., *C. oblonga*, *Stephanodiscus niagarae*, and *Synedra* sp., as well as results from Williamson and Vanderploeg⁴² for *D. pallidus* feeding on the rotifer *Synchaeta oblonga*. For comparison, the prediction of the leaky-sieve model is shown. Capture modes for the particles are shown above the curves.

is shown.⁴⁸ Clearly, the leaky-sieve model is a poor predictor of the empirically determined W' curve shown in Figure 6. Above the monotonically increasing W' vs. ESD curve are shown the capture modes used to capture the particles. Very small particles are captured passively without detection by the copepod. The passively captured small particles, carried in the double shear (focused flow in both lateral and vertical direction of body axis) scanning current, flow undetected between the gap in the paired second maxillae or between the

spaces between setae (the projections on M2 in Figure 5) and are funneled toward the mouth.^{57,59} Theoretically speaking, this is interesting because calculated boundary layer thicknesses around the setae should prevent particles from flowing between the setae under these conditions of laminar flow.⁵⁹

As particles get larger, an increasing proportion of them are captured actively, i.e., they are detected in the laminar double-shear scanning current, and coordinated motions of the mouthparts are used to bring the particle between the second maxillae. The fling and clap motion described by Koehl and Strickler⁴¹ is used to squeeze out the water to get the particle between the second maxillae. As algal size gets larger and larger, a greater proportion is captured actively, and the larger particles are detected at greater distance.^{57,60} For example, in the case of *Diaptomus sicilis* the fling and clap motion of the second maxillae (M2 in Figure 5) are used to capture algae nearby and the maxillipeds (MXP in Figure 5) come to aid capture for particles at distances from the body. The proportion the maxilliped-aided capture increases with algal size. Thus, there is a perceptual bias for large algae. *Synchaeta*, the most preferred of all *Diaptomus*' prey, was captured actively like the algae or with a thrust response that has only been observed for capture of microzooplankton. The thrust response involves a sweeping back of the first antennae (A1 in Figure 5) and a vigorous thrust of the swimming feet (S in Figure 5) to pounce on the prey. This vigorous thrust response is probably not just an enthusiastic response to a distantly perceived large particle but probably represents a directed attack toward a target that *Diaptomus* recognizes as animal prey.⁵⁸ Such a directed attack is necessary for capturing microzooplankton since many microzooplankton detect the copepod's scanning current and have well-developed escape capabilities.⁵⁸

2. Effect of Food Quality

Typically, food quality of a particle is regarded as its nutritional content for the predator; e.g., a nutritious particle would be one that was nontoxic, digestible, and contained a balanced composition of proteins, lipids, carbohydrates, and micronutrients to allow growth and reproduction of the suspension feeder. Along with nutritional quality, it is necessary to include any factors that would diminish the suspension feeder's ability to detect, capture, and ingest a particle. These non-nutritional factors would include, e.g., size and other qualities as they affect detection of 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 the selectivity coefficients.

a. Nutritional Quality

So far we have argued that there is a perceptual bias for capture of large algae and microplankton and that olfaction of the alga was hypothesized by Strickler and colleagues to be the cue used by the copepods.^{40,41,49,50,61} According to this view, expressed in a physical model by Andrews,⁶¹ the calanoid copepod creates a laminar double-shear scanning current, and algal exudates become elongated in this field to form an active space that arrives at the copepod's chemosensors before the alga. Legier-Visser et al.⁶² suggested that pressure waves created by particles entrained in this same flow could provide signals for detection. Recent observations of Vanderploeg et al.³³ show that large microspheres (>14 μm) can be actively captured. Preliminary results also suggest that medium-sized (11 μm) microspheres will not be captured actively unless they have been presoaked by the method of DeMott⁶³ in a high concentration of algae to give the microspheres an algal scent. These results argue that physical cues alone may be sufficient for eliciting active capture of large particles, but possibly not smaller particles. Details of how this combination of physical and chemical cues is used need to be worked out.

Thus, biochemical or nutritional quality affects perception of a particle by the cloud of

TABLE 2
W' of *Eucalanus pileatus* for Particles of Different Equivalent Spherical
 Diameters (ESD) and Nutritional Quality⁶⁶

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

exudates around it. Biochemical composition also affects selectivity after capture of the particle because contact chemoreceptors near the mouth are used to taste the particle before ingestion.⁶⁴ Observations of the rejection process give clues how this taste process operates. Large algae or particles like fecal pellets are usually ingested or rejected very soon after being brought to the mouth, whereas small algae or plastic microspheres captured passively are ingested or rejected, as a group, after several have accumulated near the mouth.^{33,57,65,66} Small particles of low nutritional quality can be hidden among a larger mass of high-quality food and be ingested.⁶⁶

The combination of physical and olfactory cues for distance perception and taste before ingestion implies the copepod has a sophisticated two-step process that encourages ingestion of large, high-quality food. At first glance this capture of large, inert particles would seem maladaptive; however, there are few large, inert particles (minerals, sediments, or refractory detritus) in open lake or marine environments.^{18,19,33} These big particles could be fecal material whose scent is disguised by an enclosing (peritrophic) membrane (see below) or could be microzooplankton that would escape if *Diaptomus* delayed while obtaining or processing a chemical signal.³³ The sensitivity and possible operation of this two-step system can be appreciated from a closer look at Paffenhöfer and Van Sant's⁶⁶ results (Table 2). The dead *Rhizosolenia alata* and fecal pellets, both about the same size as live *R. alata* were captured at lower rates. The fecal pellets had a selectivity about the same as the small alga, *Thalassiosira weissflogii*. Also, 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*. The lower active capture proportion for fecal pellets may be caused by a smaller olfactory cue arising from it, or possibly its smaller size, particularly length (see below).

Both lack of active captures and post-capture rejection were responsible for the complete lack of ingestion of 20- μm microspheres offered alone in the experiments of Paffenhöfer and Van Sant.⁶⁶ Very few beads were captured and only one of fifteen observed captures was apparently an active capture. Lack of active captures is not surprising since a 20- μm microsphere is small relative to the large size of *Eucalanus*. None of the captured microspheres were ingested. In a mixture of *T. weissflogii* and beads 42% of the captured beads were ingested. Thus, inert particles are passively captured and ingested incidentally with the algae. This explains the low, but non-zero, *W'* for beads in Table 2.

Other studies of the effect of nutritional quality parallel those of Paffenhöfer and Van Sant.⁶⁶ In their tabulation of previous work Paffenhöfer and Van Sant noted that *W'* for dead algae was between 0.52 and 0.90 relative to that of live algae, with a mean of 0.63; *W'* for fecal pellets was 0.43 to 0.90 relative to living algae. DeMott⁶⁷ also showed that dead algae were less preferred than live algae; however, in addition, he showed that colonization of the dead algae by bacteria improved selectivity. Cowles et al.⁶⁸ and Butler et al.⁶⁹ showed that copepods preferentially select rapidly growing, N-sufficient algae over slowly growing, N-deficient algae.

TABLE 3
Selectivity (W') of *Eudiaptomus* for the Less-Preferred Alga in Indicated Pairs of Algae of Different Food Quality⁶⁷

Food pair	ESD (μm)	Food quality	W'		
			Alone	Low	High
1. <i>Scenedesmus</i>	5	H	0.67	0.79	0.72
<i>Chlamydomonas</i>	12	H			
2. <i>Microcystis</i>	5	T	0.60	0.18	0.15
<i>Monoraphidium</i>	3.5	H			
3. <i>Planktosphaeria</i>	23	G	0.32	0.54	0.16
<i>Chlamydomonas</i>	12	H			

Note: H = high, T = toxic, G = gelatinous sheath, offered at high and low food concentrations. W' is given only for the less-preferred alga in a pair: by definition, W' of a preferred alga = 1. Concentrations of each alga offered alone, or in pairs, at the low concentration were each $0.125 \text{ mm}^3 \text{ l}^{-1}$. The concentration of algae offered in pairs at the high concentration were each $1.0 \text{ mm}^3 \text{ l}^{-1}$.

Selection for algae of different species varies with nutritional quality. Results of DeMott⁶⁷ with *Eudiaptomus* (a close relative of *Diaptomus sicilis*) show that algae with gelatinous sheaths, which may inhibit digestion, have lower selectivities than high-quality algae (Table 3). As can be seen in Table 3, selectivity for toxic blue-green algae is very low. Similar results were reported by Fulton⁷⁰ and Vanderploeg et al.³³ Vanderploeg et al.³³ showed that toxic blue-green algae filaments are readily captured actively, but that they are almost always rejected after they are brought to the mouth. Presumably, the toxic substance or some associated chemical is the "taste" responsible for rejection. Marine calanoid copepods appear not to be able to taste toxins associated with toxic dinoflagellates, the major group of toxic algae in the oceans, since the rejection mechanism appears to be regurgitation, and feeding-rate on both toxic and nontoxic algae in mixtures is reduced drastically.⁷¹

Possibly both taste and perceptual bias play a role in the lower selectivity of the large (23 μm) gelatinous alga *Planktophaeria* compared with *Chlamydomonas* (Table 3). The gelatinous sheath, which protects at least some species of green algae from digestion,⁷² may inhibit ingestion since, once captured, the sheath may inhibit the taste from coming through, or possibly the sheath itself may not have a good taste. Notice in Table 3 that selectivity for the gelatinous alga decreased at high algal concentration. DeMott⁶⁷ described this concentration-variable selectivity as an optimal-foraging strategy. This issue will be discussed below.

DeMott^{63,73} used the microspheres flavored by algal exudate, after the technique of Rassoulzadegan et al.,⁷⁴ as a tool to evaluate and classify selective abilities of different zooplankton taxa by offering them mixtures of unflavored microspheres, microspheres flavored with algal exudate by soaking them for ~1 d in a high concentration of algae, and the algae themselves. If taste is not a factor in food selection, then algae and flavored and unflavored microspheres of the same size would have the same selectivities. These experiments are relevant, first, because of the potential power of the technique to rapidly classify the different species' selective abilities by adding microspheres and algae to bottles of water containing the natural assemblage of zooplankton. Second, flavored microspheres may represent an analogue of suspended or resuspended mineral particles in nature more closely than do unflavored microspheres. These particles may pick up algal exudates in the water column or when they reside on the lake bottom or sea floor before resuspension.

Table 4, calculated from results of DeMott,⁶⁷ shows the following order of selectivity: *Chlamydomonas reinhardtii* (ESD = 6 μm) \gg flavored microspheres \gg unflavored microspheres. In addition, there is a preference for small microspheres to large microspheres:

TABLE 4
W' Relative to *Chlamydomonas reinhardtii*
 of *Eudiaptomus* for Unflavored
 Microspheres and Microspheres Flavored
 with Exudate of *C. reinhardtii*⁷³

Flavoring	Diameter (μm)	<i>W'</i>
Flavored	6	0.19
Unflavored	6	0.025
Flavored	12	0.071
Unflavored	12	0.0061

Note: Microspheres were flavored by soaking them in a suspension of 5×10^4 cells ml^{-1} for ~1 d. Results are for mixture experiments with a low concentration (1000 cells ml^{-1}) of algae. Percent standard errors of the mean for all *W'* data are approximately 25%.

flavored 6- μm microspheres were preferred to 12- μm flavored microspheres, and unflavored 6- μm microspheres were preferred over unflavored 12- μm microspheres. The cinematographic observations of Paffenhöfer and Van Sant⁶⁶ and Vanderploeg et al.³³ reveal the mechanisms behind these results. Vanderploeg et al.³³ showed that unflavored 11- μm microspheres are captured passively like most of the 6- μm *C. reinhardtii*. Preliminary results suggest some flavored 11- μm microspheres may be captured actively. More research is required to clarify this last point. Small microspheres are less likely to be rejected because they can hide among an accumulated mass of *Chlamydomonas* and not be detected as low-quality food, whereas a captured large microsphere or microspheres are more likely to be detected as low-quality food.

b. Size, Shape, and Motility

As seen in Figure 6, there is a perceptual bias for larger targets. Physical shape of the target may affect the copepod's ability to detect an alga. Notice that the *W'* of *Synedra* in Figure 6 is larger than that of *Stephanodiscus*, which has a larger ESD. *Stephanodiscus* is a pill-shaped diatom whose width and height are about the same as its ESD, whereas the elongated *Synedra*, with an ESD of 21 μm has a length of 125 μm . Vanderploeg et al.² hypothesized that rotation of (randomly oriented) elongated algae, as they become aligned in the double-shear scanning current of the copepod, creates a noise that the copepod could respond to. Ultimately, as seen in Figure 4; as particle size increased relative to the copepod, it becomes too large for ingestion. Round algae may become too large to fit in the mouth, and algal colonies elongated in two dimensions — like the stellate colonies of *Asterionella* — cannot be handled for ingestion if their dimensions are greater than those of the mouth parts used to handle them.² Copepods can ingest very long algal filaments (on the order of 1 mm) by orienting the filament perpendicular to the body axis and their pushing it into the mouth.^{2,39}

Rotifers use morphological and escape tactics to foil predation by *Diaptomus*.^{32,51} *Synchaeta*, the most preferred prey of *Diaptomus*, (Figure 6) is a slowly moving soft-bodied rotifer without effective defense mechanisms. The highly palatable soft-bodied *Polyarthra* escapes ingestion by being able to sense the current field of *Diaptomus* and then tumble away quickly (280 body lengths s^{-1}) using its four triplets of paddles. *Keratella* exhibits no escape response to *Diaptomus* but once captured it is manipulated, pressed up against the mandibles, and ultimately rejected. The hard lorica (body surface) and spine of *Keratella* probably foils ingestion.

3. Concentration-Variable Selectivity

There has been much interest in the question of concentration-variable selectivity because it may imply an optimal-foraging strategy to maximize consumption of an abundant high-quality or easily handled food. Vanderploeg et al.^{2,33} demonstrated that W' of *Diaptomus* for a small (4 μm) species of *Chlamydomonas*, which is captured passively, remained constant at about 0.3 relative to a large (12 μm) species of *Chlamydomonas*, which can be actively captured, over a broad range of concentrations with different ratios of the two species. Both Paffenhöfer²⁵ and Vanderploeg et al.² showed that selectivity of elongated algae, which must go through a complicated handling sequence before ingestion, drops at high algal concentrations. The data of DeMott⁶⁷ for "low-quality" *Planktosphaeria* (Table 3), as well as other algae, show a similar pattern.

These drops in selectivity suggest optimal foraging because selectivity for the "less-desirable" alga drops at high food concentrations; however, Vanderploeg et al.^{2,33} argue that it does not conform to optimal foraging in that selectivity for the "less-desirable" alga drops as its concentration is increased relative to the high-quality or easily handled food. Vanderploeg et al.^{2,33} argue that this is a satiation-driven behavior that results from the organism being placed in a food-rich environment for which it was not designed. In these high-concentration situations *Diaptomus* continues to actively and passively capture algae and then reject much of what it has captured. Thus, the broad pattern of lower selectivity for the less-desired particle conforms to optimal foraging; however, it occurs while the organism is behaving in a nonoptimal way of catching and throwing away captured particles of high nutritional value. Vanderploeg et al.^{2,33} note that these behaviors can be explained by simple behavioral (ethological) mechanisms affected by motivation. We cannot expect organisms to behave optimally in all situations, since optimality must operate through sensory and motor pathways that are not infinitely flexible but have certain rules of their own. Moreover, selection pressures also constrain the organism to a certain region where it can operate in an efficient way. Finding these behavioral rules is more likely to lead to models of greater generality and accuracy than optimal foraging narratives that we articulate *a priori*. Studying these mechanisms may also lead to new unsuspected optimality principles. No concentration-variable selectivity has ever been reported for low algal concentrations; however, this is not to say that this phenomenon does not occur in certain species. Such a possibility is suggested by Price and Paffenhöfer's⁷⁶ observation that *Eucalanus* initiated second maxillae vibration to enhance capture of small cells when they became abundant.

4. Generic Calanoid Copepod

For a long while we have believed in the idea of a single generic calanoid copepod; i.e., if we understand *Diaptomus* or *Eucalanus* we understand all copepods. However, cinematographic observations have shown there are significant differences even among those species that have been regarded as omnivores with strong herbivorous tendencies, namely *Diaptomus*, *Eucalanus*, *Paracalanus*, and *Acartia* (Figure 5). *Diaptomus*, *Eucalanus*, and *Paracalanus* are alike in that they use their mouthparts, including the maxillipeds, to create a double-shear scanning current. In contrast, *Acartia* (Figure 5) has reduced maxillipeds and does not create a scanning current, but instead uses seining motions of its second maxillae to capture prey.²⁵ In the estuary, where *Acartia* lives, a scanning current could be less useful for locating the prey because turbulence typically found there could disrupt the scanning current.²⁵ This seining is effective in the food-rich environment of the estuary but not in offshore waters, where food concentration is low.²⁵

Paracalanus and *Diaptomus* look very similar, use their appendages the same way, and probably have very similar selectivity patterns, although it has not been documented that *Paracalanus* can capture microzooplankton.^{2,25,57} The lack of well-developed swimming feet on *Eucalanus* may imply that it is not adapted to capture microzooplankton. More predacious

copepods cruise rather than scan, and they use mechanoreception to detect motile prey.^{49,77,78} The different feeding mechanisms can be correlated with different feeding-rate vs. food-concentration curves. e.g., *Acartia* exhibits threshold feeding behavior, i.e., clearance-rate drops at low levels at low particle concentrations.²² This response may be an appropriate energy-conserving mechanism for its feeding method and environment.²⁵ Thus, there is more than one generic copepod. The degrees to which chemoreception and mechanoreception play important roles need to be worked out for more species. The work to date serves as a foundation on which to build.

Related to the generic copepod problem is that copepods go through six naupliar and five copepodite stages before becoming adults. Most work on feeding and mechanisms has focused on adult females, as I have done in this chapter. Morphology, appendage use, and feeding mechanisms vary with stage of the copepod; e.g., nauplii create a feeding current and capture large cells actively. They cannot capture cells passively because they do not have the appendages to do this. As a result nauplii, relative to their size, capture large particles, even elongated (500 μm) algae like *Rhizosolenia*.⁷⁹ The ontogeny of appendage use, sensory mechanisms, and behavior is an area deserving further study, especially in view of the abundance and grazing impact of the juvenile stages.⁷⁹

III. CILIATES AND ROTIFERS: DIVERSE GENERALISTS AND SPECIALISTS

A. Interesting Analogies

Although ciliates — found in both marine and fresh waters — are protozoans, and rotifers — found primarily in fresh water — are metazoans, we are discussing these taxa together because many of them have analogous feeding strategies, and we could put some species from each taxon in the same feeding guilds. Both taxa are small, ciliates typically 20 to 100 μm long and rotifers typically 100 to 500 μm . Both taxa include species exhibiting polyphagy and extreme stenophagy. Not only may they feed on the same food, they — as recent work shows — are favored prey of freshwater and marine calanoid copepods.^{80,81}

B. CILIATES

1. Filter-Feeding Ciliates

Fenchel⁸² reviewed the possible mechanisms of suspension feeding by ciliates — inertial forces, diffusion, gravity, direct interception (which equals raptorial feeding in the sense that he thought that ciliates bumped into food), and sieving. He concluded that sieving and raptorial feeding were the major mechanisms,⁸³ and gave a detailed account of the hydrodynamics of filter feeding of different groups of ciliates. The size of particles collected by the ciliary filter is closely correlated with spacing between cilia, and the ciliate has little capacity to select particles of different nutritional quality. Many filter-feeding ciliates are adapted for feeding on bacteria and other picoplankton (<2 μm). The broad principles of his analyses of feeding mechanisms will probably remain intact, although recent work has questioned certain details. Sanders⁸⁴ showed that surface effects (charge) can affect the accumulation of large bacteria-sized (0.9 μm) particles, but not small (0.6 μm) particles. Monger and Landry⁸⁵ have argued that geometric model of Fenchel⁸² must be modified to include surface interactive forces, at least when used to describe the feeding of very small protozoans.

Fenchel⁸² showed that ciliates having greater distances between cilia generally have higher clearance-rates, and that bacterivorous ciliates — which must have very small spacing between cilia to capture bacteria — are usually found only in eutrophic environments where food concentrations are high enough to compensate for their lower clearance-rates. Water transport to the ciliate is assumed to be independent of particle concentration, and maximum

feeding-rate is limited by food vacuole formation-rate.^{82,86} Ingestion-rate follows Michaelis-Menton kinetics.⁸⁶ Since food vacuole formation is less efficient for large particles, maximum feeding-rate is affected by the proportion of large particles in the mixture.

2. Raptorial Ciliates

The raptorial ciliates feed on algae and other microzooplankton and are often specialists on particular organisms.⁸⁷⁻⁹⁰ The raptorial ciliates prefer large particles. Tintinnids ingest particles that are up to 45% of their body diameter, and oligotrichs commonly ingest algae almost as large and even larger than themselves.⁹¹⁻⁹⁵ We will be concerned with the phytophagous taxa because they are important grazers in waters of varying trophic in both marine and fresh water;^{87,96,97} for example, in both the eutrophic and oligotrophic Great Lakes, ciliate biomass rivals crustacean biomass.^{96,97} Given their high respiratory demands, ciliate grazing impact should be greater than that of crustacean zooplankton.

The phytophagous ciliates can be highly selective. *Favella ehrenbergii* requires dinoflagellates for growth, and only small amounts of other algae in the proper size range are consumed.⁸⁷ Chemical cues were suggested as the mechanism for selection because dinoflagellates, regardless of type of body wall, were ingested. Freshwater *Coleps* can survive only on flagellates.⁸⁸ *Nassula* is specialized to feed on filamentous blue-green algae and will not feed on green algae, diatoms, or nonfilamentous blue-green algae.⁸⁹ *Nassula* uses its specialized cytopharyngeal basket to grasp, fold in half, and coil the filament into its body.⁹⁸

It is possible that ciliates must ingest particular algae because of certain specific biochemical requirements, digestibilities, and factors associated with handling. It is also possible that certain algae, like the dinoflagellates in the *Favella* example, have exudates that act as very specific chemical signals to the ciliate. This latter possibility is strongly suggested by Taniguchi and Takeda,⁹⁹ who observed with high-speed videography that the capture response to a favored food was initiated before the food made contact with the oral membrane of the ciliate. Similarly, unfavorable foods were rejected before or at contact with the oral membrane. Unfavored cells, which were accidentally captured, were rejected from the peristomal cavity.

The selection process in ciliates is far from understood. A curious example is the selective feeding of *Favella* sp. in paired mixtures of live algae, dead algae, and microspheres of various kinds.⁹⁹ Results of these paired experiments were combined to give the overall W' result in Figure 7. Certain microspheres were preferred even over live algae. Live algae were preferred to dead algae and other types of microspheres. Surface properties, either chemical or physical (e.g., charge) must be responsible for this result.

The only experiment to see if the selectivity of a ciliate changes with relative concentration of food was done with *Balanion* sp. feeding on a mixture of the dinoflagellate *Heterocapsa* and the green alga *Dunaliella*.¹⁰⁰ The results of this experiment are redrawn and analyzed in Figure 8, because their form of presentation gave the impression of variable selectivity. Data were presented as the proportion (r) of *Heterocapsa* in the diet as a function of proportion (p) available. If selection for each algal species were the same, then the data points would fall on the straight line labeled $W'_H = W'_D = 1$. The r values fell to the upper left, indicating a strong preference for *Heterocapsa*. The variable r values do not imply variable selectivity, because the curved line predicted by a constant W' value of 0.05 for *Dunaliella* fit the r vs. p data very well.

C. ROTIFERS: GENERALISTS AND SPECIALISTS

The feeding habits of rotifers are related to the morphology of the ciliary corona, which produces the feeding current, and the mastax, which grasps, and in some cases grinds, the food before swallowing.¹⁰¹ Little is known about the hydrodynamics of swimming and feeding or the function of the feeding organs, because high-speed cinematography or videography,

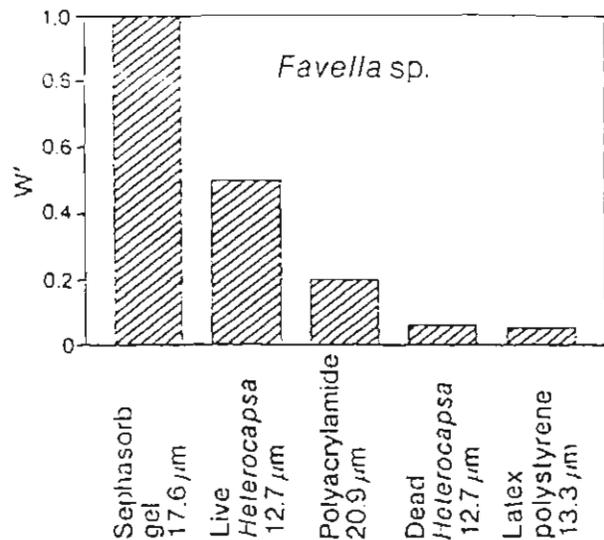


FIGURE 7. Selectivity (W') of the ciliate *Favella* sp. for different particles in the experiments of Stoecker.⁹⁹ This set of W' values was deduced from her sets of paired experiments.

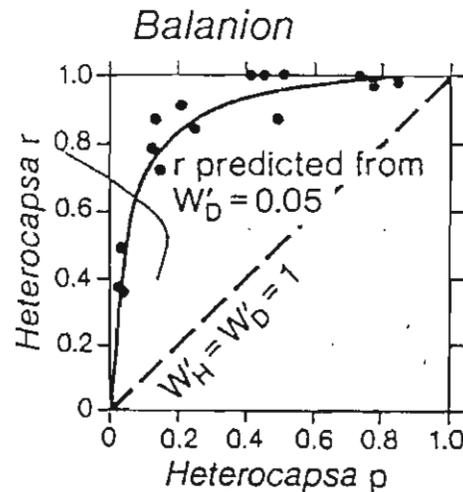


FIGURE 8. The proportion (r) of the dinoflagellate *Heterocapsa* in the diet of the ciliate *Balanion* sp. as a function of proportion (p) of *Heterocapsa* available in mixtures of *Heterocapsa* and an alternate prey, the green alga *Dunaliella*. Results from Stoecker et al.¹⁰⁰ redrawn with the r curve predicted from W' of *Dunaliella* equal to a constant value of 0.05. The line $W'_H = W'_D = 1$ is the line along which all data would fall if W' values of both algae were equal.

which is necessary for observation, has not often been applied.¹⁰² Gilbert and Bogdan¹⁰³ classified rotifers as generalists or specialists depending on the functional morphology of the coronae. The selectivities of generalist and specialist rotifers are shown in Figure 9 and were calculated from raw data on filtering-rates in their experiments. Presentation of results is very similar to theirs, except that W' is used instead of the selectivity index D . The generalists — *Keratella*, *Conochilus*, and *Kellicottia* — have a bell-shaped W' vs. ESD

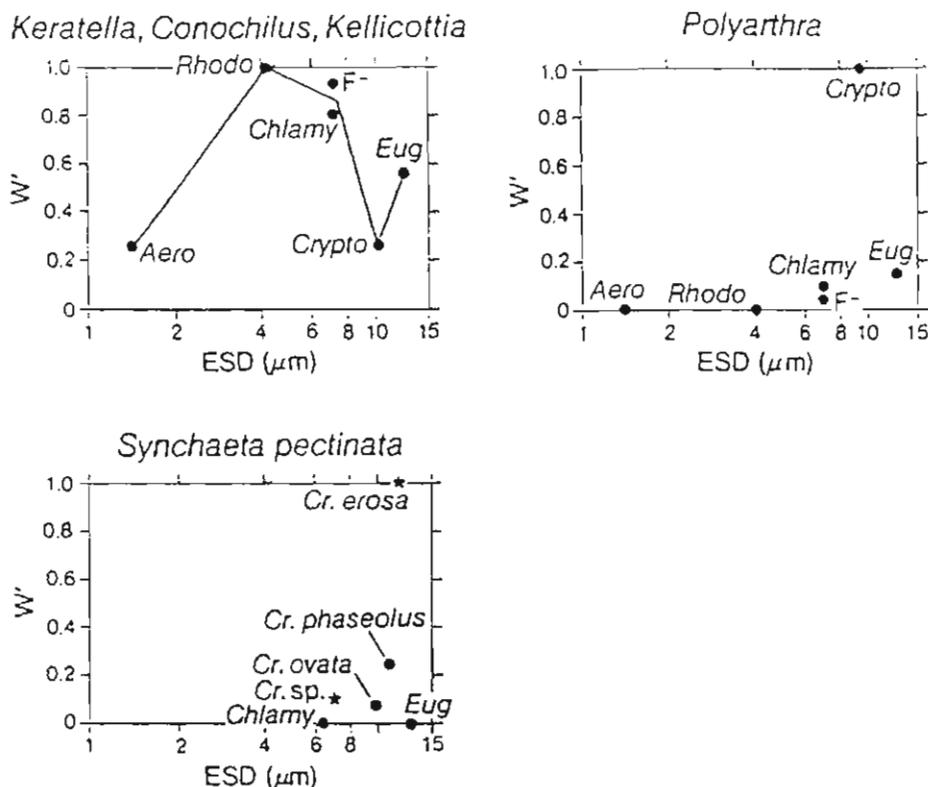


FIGURE 9. W' vs. equivalent spherical diameter curves for generalist rotifers (*Keratella*, *Conochilus*, and *Kellicottia* (in upper left) and specialist rotifers *Polyarthra* (upper right) and *Synchaeta pectinata* (lower left) from study of Gilbert and Bogdan.¹⁰³ The species of algae or bacteria used in the experiments are indicated by their abbreviations Aero (*Aerobacter*), (Chlamy *Chlamydomonas*), F- (*Chlamydomonas* without flagellum), Crypto (*Cryptomonas*), Eug. (*Euglena*), Rhodo (*Rhodomonas*), and Cr. (*Cryptomonas* with indicated species names).

curve showing preference for intermediate-sized particles. *Polyarthra*, a specialist, showed preference for flagellated algae, especially *Cryptomonas*. The specialist *Synchaeta* strongly specialized on *Cryptomonas* and preferred *C. erosa*, the larger of two species on which it was cultured. All the generalists have extensive, finely ciliated buccal fields in which a wide variety of particles may be transposed to the mouth. The coronae of the specialist rotifers are more sparsely ciliated. They seem designed for capture of individual particles. Presumably, these specialists, like the raptorial ciliates, detect their prey before or at contact by physical or chemical means.

Other rotifers exhibit stenophagy.¹⁰¹ One of the more interesting examples is *Notholca squamula*, whose abundance is closely correlated with that of the diatom *Asterionella formosa*.¹⁰⁴ This 120- μm -long rotifer feeds by biting the ends off the cells ($\sim 75 \mu\text{m}$ long) in the stellate colonies (diameter $\sim 150 \mu\text{m}$) with strong crushing action of its well-developed trophi. Remember, the stellate colonies of *Asterionella* offered protection against grazing by *Diatomus*. Algae other than *Asterionella* were rejected by *Notholca*. This selection and the close coupling of *Notholca* abundance to that of its prey, which is reminiscent of the ciliate/dinoflagellate coupling, suggest *Notholca* is keying in on very specific chemical information to make its choice of prey.

In experiments with algal-exudate-flavored and unflavored microspheres, *Branchionus* fed nonselectively, *Filinia* fed preferentially on 6- μm flavored spheres and *Polyarthra*, *Synchaeta*, *Notholca*, and *Keratella* ingested few flavored or unflavored spheres.⁶³ The lack

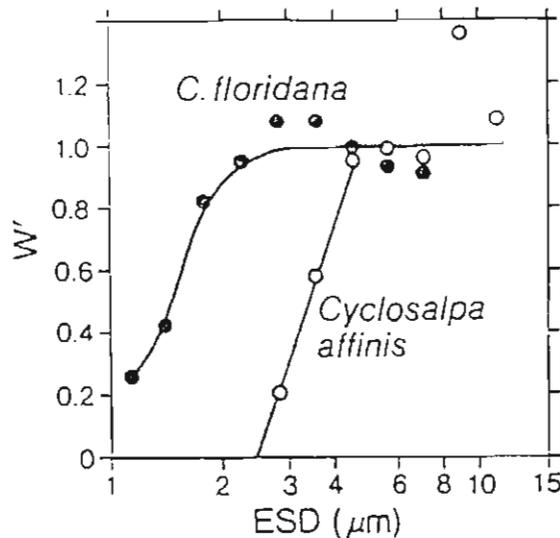


FIGURE 10. W' vs. equivalent spherical diameter (ESD) curves for largest species (*Cyclosalpa affinis*) and smallest species (*C. floridana*) of salps in study of Haribson and McAllister.¹¹³ Figure was redrawn from original figures.

Deibel and Paffenhöfer,¹¹⁴ using high-speed microcinematography, were able to describe special mechanisms necessary to handle large particles and certain aspects of fluid dynamics of particle capture. This appears to be a fruitful area of research, especially since the fluid mechanics of filters like these have already been worked out by Silvester.¹¹⁵

2. Appendicularia

The mechanisms of filtration in pelagic appendicularians have recently been reevaluated by Deibel¹¹⁶⁻¹¹⁹ in his studies of *Oikopleura vanhoeffeni*, a neritic, cold-water species. Appendicularians feed within a complex set of mucopolysaccharide filters known as the house. The animal drives water through coarse incurrent mesh by beats of its tail, and suspended food is concentrated in a food-concentrating filter of very fine pore width ($\sim 0.2 \mu\text{m}$). The concentrated food suspension is then forced through the pharyngeal filter, and the pharyngeal filter removes particles from suspension by sieving and adhesion. Until recently, it was believed that the pore size of the food-concentrating filter, formerly called the food-collection filter, determined the particle retention efficiency. The pore-size distribution of the pharyngeal filter is much coarser, suggesting that 50% efficiency is obtained only for particles $3 \mu\text{m}$ in size. There have been no measurements of particle-size selection to test whether actual filtering efficiency matches that predicted by the pore-size distribution. *Oikopleura*, by adjusting its mouth opening, can reject part or all of the concentrated food suspension. *Oikopleura* can lower its clearance rate in high concentrations of food by intermittent pumping, thereby preventing the capture of excess food.

C. CLADOCERA

1. Single-Mode and Dual-Mode Feeders

When discussing the filter-feeding Cladocera (as opposed to the predacious Cladocera), it is necessary to distinguish between two feeding groups. The first, the single-mode feeders (Sididae and Daphniidae), collect a broad size range of particles with relatively homogeneous filter combs, whereas, the second utilize dual feeding modes: a raptorial mode and filter-feeding mode.^{120,121} These groups have different size-selectivity patterns and responses to

of feeding on spheres by the specialists (*Polyarthra*, *Synchaeta*, *Notholca*) is not surprising, but the results for *Keratella*, a generalist, are surprising, especially in view of the fact that *Keratella* and *Branchionus* belong to the same family. As DeMott⁹³ noted, further work on feeding mechanisms is required to explain these differences.

In addition to ingesting a wide variety of particles, *Branchionus* has a selectivity for the toxic blue-green alga *Anabaena flos-aquae* equal to that of high-quality algae (*Chlamydomonas*), and can utilize this toxic alga as a sole or supplementary food source.^{70,105}

IV. TUNICATES AND CLADOCERANS: METAZOAN FILTER FEEDERS

A. MORPHOLOGICAL DIFFERENCES AND FUNCTIONAL SIMILARITIES

Although pelagic tunicates (Phylum Chordata) — which are restricted to marine systems — and Cladocera (Phylum Arthropoda, Class Crustacea) — which are largely restricted to fresh waters — are very different in both taxonomic and morphological terms, most function as opportunistic filter feeders that can compete successfully with calanoid copepods. They typically filter by sieving and other physical mechanisms (see below) a broad range of particle sizes including picoplankton (<2 μm) and accept or reject a collected mass of particles as a unit. This implies that there is little capacity to select particles on the basis of nutritional quality. Typically, selection is a concentration-invariant function of particle size or in some cases particle size and surface properties (charge).¹⁰⁶⁻¹⁰⁸ Many members of both groups have high weight-specific clearance-rates and/or high G_{max} values, and — unlike the copepods, which must reproduce sexually — they have reproductive strategies that can rapidly turn ingested food into new individuals to exploit temporarily high food concentrations.^{109,110}

B. PELAGIC TUNICATES

1. Salps and Doliolids

Salps and doliolids feed by straining particulate material through a continuously produced conical mucous net that fills much of the pharyngeal cavity.^{109,111-114} This plankton net is wound up and continuously ingested. Salps, which use circumferential muscle bands for both locomotion and for forcing water through the net, have higher filtering-rates and can be larger than the doliolids, which use ciliary action to drive water through the nets.¹⁰⁹ Because of the evanescent and fragile nature of these nets, the pore-size distribution of the net is not known; however, the filtering efficiency (W') vs. particle-size curves have been determined for salps from feeding experiments using natural seston counted and sized with a Coulter Counter[®].¹¹² As can be seen from in Figure 10, showing results from the largest and smallest species studied by Harbison and McAlister,¹¹² some salps are quite efficient at removing small particles, even down to 1 μm . Observed differences in the W' curves among and within species are related to animal size: smaller salps retain smaller particles. Cinematographic observations on the feeding mechanism of the neritic doliolid *Doliolum nationalis* suggest its filter is quite coarse, having a particle retention efficiency on the order of 50% for 4- μm particles.¹¹⁴

The oceanic salp *Pegea confoederata* is able to survive on extremely low concentrations of food found in oceanic central water masses. When it is exposed to higher particle concentrations typically found in neritic areas, feeding is disrupted because the mucous net becomes overloaded with food and breaks.¹¹³ This breakage is thought to be a factor excluding these animals from neritic areas. This is a clear-cut example showing that the optimal-foraging narrative does not apply to all ranges of particle concentration presented by the investigator or some environments; i.e., there are "design" constraints that limit optimal behavior to certain environments.

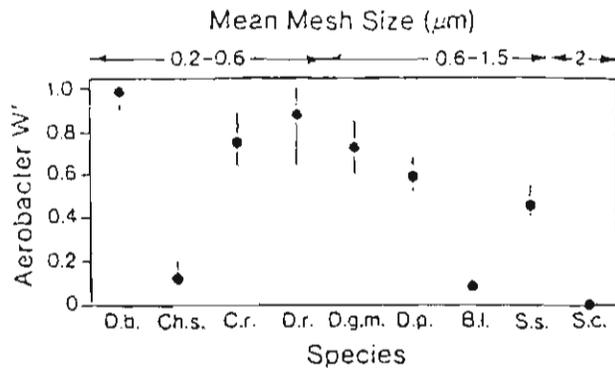


FIGURE 11. The W' for the bacterium *Aerobacter* by different freshwater Cladocera arranged in order of increasing filter mesh width (redrawn from De Mott¹²⁴). The three size-range categories shown above the figure represent from left to right: high-efficiency bacteria feeders, low-efficiency bacteria feeders, and macrofiltrators. The dual-mode feeders are *Chydorus sphaericus* (Ch.s.) and *Bosmina longirostris* (B.l.). The single-mode feeders are *Diaphanosoma brachyurum* (D.b.), *Ceriodaphnia reticulata* (C.r.), *Simocephalus serrulatus* (S.s.), *Sida crystallina* (S.c.), *Daphnia rosea* (D.r.), *D. galeata mendotae* (D.g.m.), and *D. pulicaria* (D.p.).

other aspects of food quality; therefore, special emphasis will be made in contrasting the selectivity patterns of these two groups and relating them to their feeding mechanisms. Cladocerans are the most studied members of the freshwater zooplankton, and we know more about their feeding biology than other freshwater zooplankton and, probably, most marine zooplankton. The filter-feeding approach of this successful group stands in marked contrast to the selective feeding of the copepods. The reasons for the dominance of one group over another in different aquatic systems have been of great interest to limnologists and probably relates, in part, to the success of these different feeding strategies in different systems.¹¹⁰

2. Food Quality

a. Small-Particle Capture Efficiency

For the single-mode feeders, selectivity for particles of different sizes is at least approximately related to the intersetule distances on the filter combs:¹²²⁻¹²⁴ anything greater than the intersetule distances is retained as long as it is not larger than the filtration apparatus can handle. Figure 11, redrawn from DeMott,¹²⁴ shows that W' of the 1 to 2 μm -long bacterium *Aerobacter* (relative to the 6- μm -diameter *Chlamydomonas*) is related to the mesh size of the filter combs of all the single-mode feeders, but not to the dual-mode feeders, *Bosmina* and *Chydorus*. Despite this correlation, the direct observations of Gerritsen et al.¹⁰⁸ suggest the sieving model of water passing through the filter combs is not correct, since they saw no introduced dye pass through most of the surface of the filter combs. They did not argue that sieving does not occur, but that it is not the major mechanism. Gerritsen et al.¹⁰⁸ argued that this correlation can be explained by the increase of surface area for small particles to stick to as the intersetule distances decrease. These particles stick as they flow tangentially across the filter combs. They defined sticking broadly, in that it could include particles entrained in the boundary layer around setae and setules, but not actually touch them. Sticking, along with particle interception and sieving of the larger particles at the distal ends of the comb setae, explain the whole filtering process. These results are consistent with Gerritsen and Porter's¹⁰⁶ work showing that charge and wettability of particles close to the mesh size affected the efficiency of particle retention. This observation on surface

properties has relevance to the ability of the filter to retain very small particles of different types, because electrophoretic mobility — a measure of a particle (and particle-filter) repulsion — varies among algae, cyanobacteria, and bacteria; moreover, electrophoretic mobility changes with pH of the water and dissolved organic carbon concentration.¹⁰⁷ (See also Chapter 4.)

Why do different single-mode filter feeders have different mesh sizes? In addition to the correlation between mesh size and the size of particle captured, there is evidence that the coarse-mesh filter-feeding cladocerans have higher weight-specific clearance-rates.^{123,124} Brendelberger¹²³ notes this is analogous to Fenchel's⁸⁶ observations that coarse-meshed filter-feeding ciliates have higher weight-specific clearance-rates than those having fine meshes. Perhaps there is a penalty to pay for possession of fine meshes in the form of an increased pressure drop across the "filter" system. Perhaps significantly more energy is required to push water through a system with fine meshes. This question cannot be answered now because we cannot specify the energy costs of the filtering system of cladocerans.¹⁰⁸ However, this will not stop me from making some speculations later in the discussion.

The dual-mode feeders *Bosmina* and *Chydorus* have their first two pairs of appendages modified for grasping individual large particles. As particle size increases, W' continues to increase in *Bosmina*, e.g., the clearance rate on *Cosmarium* ($26 \times 16 \times 11 \mu\text{m}$) is six times higher than that for *Chlorella* ($5 \mu\text{m}$).¹²⁵ DeMott and Kerfoot¹²¹ speculated that the continuous horizontal swimming of *Bosmina* may be coupled to a remote detection system for capture of large particles.

b. Nutritional Quality of Particles

Like filter feeders in general, the single-mode feeders have limited capacity to reject individual particles. In the single-mode feeders filtered particles travel up to the food groove to form a bolus under the labrum that is worked over and tasted prior to ingestion.^{108,126} Rejection is accomplished by the first two limbs, which are not used for filtering. Gerritsen et al.¹⁰⁸ noted that some individual large particles could be ingested or rejected from boluses containing many particles. Excess food and colonies or filaments that clog the filtering apparatus are rejected by the abdominal claw.^{72,127} Excess cells not packed in a bolus can also be flushed out of the carapace by "outwashing".¹²⁸ Carapace gape may be decreased somewhat to prevent entry of filaments into the filter chamber.¹²⁹

Selectivity patterns of the single-mode feeders are consistent with the limited capacity of these rejection mechanisms to regulate nutritional quality of ingested food. Selectivities for 6- μm flavored and unflavored microspheres were identical.⁶¹ Single-mode feeders were only partially successful in selecting against the filamentous and toxic blue-green alga *Anabaena flos-aquae* when paired with 6- μm *Chlamydomonas reinhardtii*.⁷⁰ Pairing *Anabaena* with *Chlamydomonas* lowered feeding rate on *Chlamydomonas*, either through toxic effects or inefficient rejection mechanisms that rejected *Chlamydomonas* as well. In contrast, when the filamentous diatom *Melosira* was paired with *C. reinhardtii*, *Melosira* was preferred. Fulton and Paerl¹³⁰ showed that in mixtures of unicellular toxic *Microcystis* ($4 \mu\text{m}$) and *C. reinhardtii* there was no evidence of discrimination against *Microcystis*. Prior exposure to *Microcystis* did not alter selectivity but, through its toxic effects, did lower filtering rates.

The dual-mode *Bosmina* can use chemosensory abilities to select particles but does not avoid ingesting toxic bluegreen algae. DeMott⁶³ showed that the W' of unflavored 6- μm spheres was 0.6 relative to *Chlamydomonas reinhardtii* of the same size. Fulton observed W' values of 0.75 for *C. reinhardtii* relative to toxic unicellular *Microcystis* and 0.59 relative to toxic *Anabaena*. *Bosmina* is resistant to the toxins of these algae, although it does not reproduce if either of these algae is the sole food source.¹³¹

c. Size, Shape, and Motility

Once a particle is captured by a filter-feeding cladoceran it must be handled before

ingestion. Many of the problems described above for copepods handling large particles of varying shapes apply here. *Diaphanosoma brachyurum*, which is a high-efficiency bacteria feeder, is incapable of ingesting filamentous algae. *Daphnia* readily ingests the filamentous diatom *Melosira italica*, but not *M. italica tenuissima* because the cells of the latter cannot be separated easily by *Daphnia* for ingestion.¹³² The colonial diatoms *Asterionella* and *Fragilaria* also offer difficulty for some *Daphnia* spp.¹³² The dual-mode feeder *Bosmina* has very much higher selectivities for filamentous algae than for *Chlamydomonas reinhardtii*.⁷⁰ Its first two appendages, modified for grasping large particles, undoubtedly are important in this high selectivity.

Motile microzooplankton prey like *Polyarthra*, which have vigorous escape responses elicited by cladoceran flow fields, will escape capture.¹³³

3. Concentration-Variable Selectivity

As might be expected from the largely passive and mechanical selection of the single-mode feeders, selectivity for large and small particles of varying nutritional qualities does not change with particle abundance.^{134, 67, 73} It is a different story, however, for *Bosmina* feeding on mixtures of 6- μm *Chlamydomonas* and 1 to 2- μm *Aerobacter*. When *Chlamydomonas*:*Aerobacter* concentrations were 2.5:0.25 and 0.25:2.5 $\mu\text{g} \cdot \text{ml}^{-1}$ dry weight, respective W' values of *Aerobacter* were 0.36 and 0.073. The higher selectivity for *Aerobacter* at the higher *Chlamydomonas* concentration was a result of the clearance-rate for *Aerobacter* remaining the same but that of *Chlamydomonas* dropping. This is a satiation-driven response for the raptorial feeding mode, which we could probably term an active feeding mode, since — like the copepods — response to remotely detected particles is probable. It would be of interest to know what aspect of the behavioral chain leading to ingestion is affected. Is it searching behavior or some aspect of handling?

V. DISCUSSION: SOME INTERESTING NARRATIVES

A. OLD NARRATIVES

1. Zooplankton Are Not Peak Trackers

I have shown that copepods, cladocerans, and ciliates do not focus their efforts on the most available prey. When concentration-variable selectivity has occurred, it was satiation driven and a drop in selectivity for a difficult to handle or less-desirable food was observed. In the case of the less-desirable food, there may not be enough of a stimulus to trigger the ingestion response when the animal is satiated. Ecologists often argue that as the animal gets hungrier it includes more prey items in its diet and gets less selective.² This assumes the implicit frame of reference of the well-fed animal.³³ The more appropriate frame of reference may be the hungry animal. More focus should be put on studying the animal's feeding behavior at very low food concentrations. As has been argued above, an appropriate perspective is to recognize that selection is a multistep process that can be affected by motivation at each step. This mechanistic perspective presumably provides the framework for making observations useful for development of predictive models. After we understand the mechanisms, we can ask if they have adaptive value relative to our narratives concerning optimal foraging.

2. Dynamics of Ecosystems Cannot Be Described By the Size of Their Components

Size is an important variable in terms of its effect on rates of various physiological processes, including metabolic-rate and feeding-rate. Also, if closely related species are of different sizes but have the same food collection systems — as, for example, the *Diaptomus* spp. in Figure 4 — allometry of the food detection, collection, and ingestion organs will lead to size-related patterns in selectivity. The W' -ESD spectrum of *D. ashlandi* is shifted to the left of the other two species because it is a much smaller species.

However, when we start comparing organisms that are not closely related, generalizations about feeding based on size become tenuous, especially when the species belong to different feeding guilds. In this latter case different responses to other aspects of food quality, such as motility, toxicity, shape, and biochemical composition, will confound predictions based on size. Copepods and Cladocera, which overlap in size, do not function in the same way in ecosystems. Likewise, generalist rotifers and ciliates do not function the same way that specialist rotifers and ciliates do.

If we are going to truly understand aquatic ecosystems, we have to study the feeding mechanisms of their major components and not rely on the easy verities of size arguments. If we were studying feeding behavior of lions on the plains of Africa, we would follow them around watching their behavior through binoculars or recording results on video or film. We must do the same with the zooplankton: we must enter their world and follow them around. Recent advances in cinematography and videography make at least some aspects of this direct observation possible.¹³⁵

3. Certain Metazoan Filter Feeders Can Ingest Picoplankton

Certain pelagic tunicates and cladocerans can ingest picoplankton, including bacteria. Probably more work is necessary to identify pelagic tunicates that have this ability. Clearly, only some of the Cladocera can do this. An interesting question is: Why are not more metazoan filter feeders capable of ingesting bacteria? Are there filter-design or energetic constraints that prevent their efficiently filtering bacteria? I will touch on the subject briefly below when I discuss temperature and water viscosity.

B. A GREAT LAKES NARRATIVE: THE IMPORTANCE OF VISCOSITY

Armed with our new information on feeding mechanisms, it is possible to tell a number of new stories about the plankton in the Great Lakes. I choose to focus on one story, the story about viscosity, because viscosity plays an important but generally unappreciated role in the evolution of aquatic communities.⁵⁰ In Figure 2 we have seen that as we move from oligotrophic to the eutrophic Great Lakes, dominance of the grazing community by calanoid copepods shifts to Cladocera. This shift in the annual average community structure is caused by the explosive parthenogenic reproduction of cladocerans during the warmer months in the eutrophic lakes. This result is consistent with Muck and Lampert's¹¹⁰ observations that *Diatomus* has a higher filtering-rate than *Daphnia* at low food concentrations, but that *Daphnia* has a higher maximum ingestion rate, G_{max} . The higher G_{max} is turned into high production of parthenogenic offspring in the higher particle concentrations found in eutrophic lakes.

Of course, this response depends on the size and kind of food available. Geller and Müller¹³⁶ developed a scheme to explain the seasonal succession of zooplankton on the basis of food size. Geller and Müller¹³⁶ subdivided cladocerans into three groups on the basis of filter mesh size: (1) high-efficiency bacteria feeders (0.24 to 0.64- μm mesh size), low-efficiency bacteria feeders (1.0 to 1.6 μm), and macrofiltrators (>2.0 μm). Copepods were thrown into the macrofiltrator category because there are few cladoceran macrofiltrators. In oligotrophic lakes macrofiltrators in the form of copepods dominate throughout the year. In mesotrophic and eutrophic lakes copepods dominate throughout winter. In mesotrophic lakes medium-mesh cladocerans dominate during spring through autumn. In eutrophic lakes medium-mesh species dominate during spring and autumn, while fine-mesh species dominate during summer. Geller and Müller¹³⁶ argued this succession was driven by increasing importance of bacterial food, especially in the eutrophic lakes.

It seems to me that an important additional force behind Geller and Müller's¹³⁶ successional pattern could be the impact of temperature-driven changes in viscosity on the food-collection system of the copepods and cladocerans. In going from 25° to 1°C, viscosity

increases by a factor of two. Pressure drop across a filter is proportional to viscosity (μ).¹¹⁵ Also boundary-layer thickness around filter elements is proportional to $\mu^{1/2}$ and inversely proportional to $U^{1/2}$, where U is flow-rate through the filter.¹¹⁷ Boundary-layer thickness may have a detrimental effect on filter function. Thus, in summer, when viscosity is less likely to be a problem, the fine-meshed cladocerans can dominate. *Diaptomus* spp. generally reproduce during winter and spring. The scanning system of copepods may be especially efficient at low temperatures. I am not aware of any experiments on cladoceran feeding at low temperatures that could be used to test these ideas. Many cladocerans escape winter by producing resting eggs. Perhaps this is their way of escaping the rigors of high viscosity. The low temperatures of Lake Superior may present a year-round barrier to Cladoceran domination: average surface temperature in July is 7°C. I wonder if the seasonal and latitudinal distribution of metazoan filter feeders, in general, may be caused by temperature-related viscosity constraints operating on their filtration systems.

ACKNOWLEDGMENTS

I thank W. R. DeMott and D. Scavia for reviewing the manuscript and G. Laird Pernie for providing unpublished data on Lake Michigan zooplankton. I also thank Springer-Verlag for permission to reprint Table 2. This is GLERL Contribution No. 685.

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