Selectivity in suspension feeders: food quality and the cost of being selective

By Michael E. Sierszen and Thomas M. Frost

Center for Limnology, University of Wisconsin, Madison, WI 53706, USA

With 4 figures in the text

Abstract

There is considerable variety in both the selective behavior of suspension feeders and the quality of food available to them. We incorporate this variability into a simple model of particle selection in order to examine the relationship between the degree of selectivity exercised, the value of food items available, and the potential consequences of feeding selectively. If particle values differ greatly, selectivity is favored; if toxic particles occur, a high degree of selectivity may be required for survival. Greater similarity of particle values leads to a lower profitability of selection, with decreased selectivity favored at low availability of preferred items. To offset costs associated with the selective process, enhanced returns through highly discriminatory feeding and necessary. When particle toxicity is a hazard, costs are easily outweighed by enhanced diet quality. Use of this approach may aid in understanding patterns of individual feeding behavior and the relative success of different feeding strategies under various environmental conditions.

Introduction

Aquatic suspension feeders are presented with a diversity of potential food items. Their resources vary in size, shape, texture, abundance, chemical content, and nutritional characteristics (e.g. Burbank 1942; Parsons et al. 1961; Arnold 1971; Porter 1977; Pechenik & Fisher 1979; Infante & Litt 1985). In such an environment, the degree to which an organism could select among food resources could have strong consequences; food quality has been shown to affect respiration (Porter & McDonough 1984), lipid reserves (Holm & Shapiro 1984), survivorship (Arnold 1971; Porter & Orcutt 1980; Lampert 1981; Holm & Shapiro 1984) and reproduction (Arnold 1971; Starkweather 1981). Under conditions of varied food quality, selective feeding could improve the overall quality of food ingested (e.g. Pyke 1984).

A broad range of feeding strategies has been observed among suspension feeders. Selective feeding has been documented in many groups, including bivalves (Ten Winkela & Davids 1982; Kjorboe et al. 1980), freshwater sponges...
Frost 1980 a, b), echinoderm larvae (Rassoulzadeh et al. 1984), rotifers (Gilbert & Bogdan 1981, 1984; Bogdan & Gilbert 1984), copepods (Poulet & Marsot 1978; Bogdan & Gilbert 1984; Paffenhofer & Van Sant 1985; DeMott 1986; Huntley et al. 1986) and members of the cladoceran genus Bosmina (DeMott 1982; DeMott & Kerfoot 1982). However, other suspension feeders, notably the cladoceran Daphnia and its close relatives, are generally nonselective (Lampert 1974, 1987; DeMott 1982, 1986; Bogdan & Gilbert 1984). Nonselectively feeding cladocerans have been shown to be inhibited by inorganic suspended particles while rotifers, which selected phytoplankton over inorganic particles, were not (Kirk 1991).

Although the general advantages of selectivity under extreme feeding conditions may be obvious, the costs and benefits of the various feeding strategies implemented are less clear. Variability in the quality of available food may make a given degree of feeding selectivity more or less beneficial, depending upon local or current conditions. Here we incorporate variability in food quality and feeding selectivity into a simple model that quantifies the energetic consequences of different selective behaviors. We then contrast the estimated benefits of selective feeding with the costs.

Particle selection model

Previous models of suspension feeding behavior (Lam & Frost 1976; Lehman 1976; Taghan 1981) have focused on predicting optimal rates of feeding, with relatively little attention given to the question of when to be selective. In this paper we quantitatively examine the consequences of varied degrees of selectivity on different food particle assemblages. To examine the relationship between selection, feeding conditions, and feeding success we vary, within realistic bounds, the quality of food available and the degree of selectivity exercised. In our analyses we use a scale of values from −10 to +10 points per particle. These points may be interpreted as net energy content or food value. Beneficial food items have positive values, and detrimental foods (digestion-resistant and, more severely, toxic items) have negative values. The range of this scale, while arbitrary, is nonetheless conservative in view of the considerable range in the food quality of suspended particles (e.g. Parsons et al. 1961; Arnold 1971; Porter 1977; Infante & Litt 1985). The continuity of the scale, with nutrition and toxicity along the same axis, is a simplification. There is evidence that nutritional content and toxicity are distinct factors in algae (Porter & Orcutt 1980) as well as terrestrial plants (e.g. Bryant & Kurzfat 1980). Rather than consider these two factors separately, we believe that the combination of them into a single currency was a reasonable simplification for the purposes of our model. Separate currencies may be warranted for toxins.
causing immediate mortality, but our single currency is sufficient to simulate a
graded response to varying degrees of toxicity (below).

We use the selectivity coefficient $W_i$ ('VANDERPLOEG & SCAVIA 1979) as an
index of selective feeding behavior. Feeding rate in suspension feeders is ex-
pressed as clearance rate, the volume of water cleared of food per unit time, e.g.
ml animal$^{-1}$ hour$^{-1}$. $W_i$ (which, for simplicity, we will refer to simply as $W$)
is calculated by dividing the clearance rate on an item by the highest clearance
rate obtained on any particle in that feeding trial. Large differences between
these clearance rates would result in $W$ values near zero and indicate a high
degree of selectivity. Consistently similar clearance rates on a variety of par-
icles would result in a narrower range of $W$ values, nearer to 1.0, and would
indicate nonselective feeding. Our model quantifies selection by varying $W$ as
the conditional probability that feeding will occur upon encounter of item, (VANDERPLOEG & SCAVIA 1979). Animals in our model eat particles according to
assigned ingestion probabilities ($I_i$), regardless of the relative abundance of the
particles. Under this scheme an absolutely nonselective feeder would have
equal ingestion probabilities for all items, and those items would be eaten in di-
rect proportion to their occurrence. Selective feeders have greater differences
between ingestion probabilities for different items, with high $I_i$’s for high value
items and lower $I_i$’s for less desirable items. The degree of selectivity exercised
by a feeder in our model corresponds to the maximum difference in clearance
rates on different particle types (i.e. maximum particle discrimination) and
thus is indicated by the minimum observed $W$ ($= I_{min}/I_{max}$).

While some foods may be selected by size (e.g. RICHMAN & ROGERS 1969;
FROST 1977; VANDERPLOEG 1981), a growing body of work shows that, as in our
model, selectivity is linked to food quality. Zooplankton have been shown to
select between flavored and unflavored artificial particles (POULET & MARSOET
1978; DEMOTT 1986), among algae and algal-flavored spheres of the same size
(STARKEWEATHER 1980; DEMOTT 1988) and between live and dead algae of the
same species (STARKEWEATHER & BODGAN 1980; Paffenröper & VAN SANT 1985).
The copepod Eudiaptomus selects for particles of high nutritional quality, and
rejects low-quality particles when high-quality food is abundant (DEMOTT
1989).

Our model feeders may be somewhat unrealistic because they are behav-
iorally inflexible with respect to food abundance and proportion. Although
some freshwater copepods may be inflexible in their selection of particle sizes
(VANDERPLOEG & Paffenröper 1985), recent work indicates that copepods can
change their selectivity in response to food abundance (VANDERPLOEG et al.
1988; DEMOTT 1989). However, there remains disagreement about the patterns
of those changes and the mechanisms governing them (cf. VANDERPLOEG et al.
1988; DEMOTT 1989). There is also evidence that some aquatic consumers alter
their selectivity in response to the relative abundance of food items (LAWTON et
al. 1974; Landry 1981). While our model does not provide predictions on changes in selectivity in response to abundance, it can be used to predict when it would be adaptive to change selectivity in response to relative abundance. For example, the point at which the intake rate of one feeder becomes lower than that of another designates the conditions under which the first feeder should alter its behavior (i.e. change its ingestion probabilities).

In our treatment here, suspension feeders with a range of selectivities are presented with mixtures of two particles. The overall quality of the feeding suspension is manipulated by varying the values and relative proportions of the particles. The feeders consume particles according to their ingestion probabilities and accumulate food as arbitrary units over time. The intake rate of each subject is then

\[ R = \frac{\sum_i V_i A_i h}{T} \]

where

- \( R \) = Intake rate, points animal\(^{-1}\) h\(^{-1}\)
- \( I_i \) = Ingestion probability for particle \( i (i = 1, \ldots , n; \text{here } n = 2) \)
- \( V_i \) = Point value of particle \( i \)
- \( A_i \) = Abundance of particle \( i \)
  \# = Total particles encountered per animal
- \( P_i \) = Proportion of particle \( i \) in suspension
  \( h = (\text{Total particle concentration, particles ml}^{-1}) \) (Water Processing rate, ml animal\(^{-1}\) h\(^{-1}\)) (Duration of feeding bout, h)
- \( T \) = Duration of feeding bout, h

This model is similar to Schoener’s (1971, p. 380) cost-benefit function, especially when the cost of selection is considered (below). The most important differences lie in approach and application. The aim of Schoener’s (1971) model was to predict the optimal diet, given a potentially high degree of selectivity, whereas we attempt to quantify the consequences of different degrees of selectivity, given particular feeding conditions.

In all model simulations, total particle concentration was set at 10\(^6\) particles ml\(^{-1}\), water processing rate of all suspension feeders was 1.0 ml animal\(^{-1}\) h\(^{-1}\), and the feeding bout was 6 h. The ingestion probabilities \( I_1, I_2 \) used for the most selective to nonselective feeders, respectively, are \( (9, .1); (.8, .2); (.7, .3); (.6, .4); (.5, .5) \). The selectivities \( W = I_2/I_1 \) are thus 0.11, 0.25, 0.43, 0.67, and 1.0. We have set \( I_1 + I_2 = 1.0 \) for all feeders because intake \( R \) increases with the total probability of particle ingestion (EI). For example, two equally nonselective \( W = 1.0 \) feeders could have ingestion probabilities of \( (.5, .5) \) and \( (.8, .8) \). The latter feeder would have a higher ingestion rate, and a higher \( R \), than the former regardless of the feeding suspension. Because our objective was to analyze the effects of selectivity \( W \) on \( R \), we chose to equalize the total probability of particle ingestion for all feeders. Similarly, be-
cause we focus on the question of when to be selective, rather than on optimal rates of feeding, our treatment is different than that of most optimal foraging models. In optimal foraging models (e.g. Lehman 1976), food handling and digestion limit the maximum ingestion rates. We have set water processing rates equal for all feeders so that we can test for differences in R due to selectivity, not feeding rates.

Model results

Effects of food quality and selectivity

To analyze the roles of food quality and selectivity in the nutrition of suspension feeders, we must consider the relative nutritional value of the particles, their proportions in suspension, and the degree of selectivity exercised. When there is a substantial difference between the values of food particles available, animals selectively feeding on higher value particles have higher intake rates (R) than nonselectors, even at very low proportions of high-value particles (Fig. 1 A). For example, when there is a tenfold difference in particle values [values = (10,1)] and 10% of the suspension is higher value particle (P1 = .10) the intake rate of the most selective feeder is 4% higher than that of the nonselector. With higher proportions of more valuable particles, selectors enjoy considerably higher food value intake rates than nonselectors, with the highest intake rates attained by the most selective animals. When 50% of the suspension is higher value particle (P1 = .50) the intake rate R of the most selective feeder (W = 0.11) is 40% higher than that of the nonselector (W = 1.0).

With less disparate values, selectivity becomes less profitable, with a higher proportion of more valuable particles required for selectors to have higher rates than nonselectors (Fig. 1 B). Further, at very low proportions of the preferred particle, selective feeders are actually at a disadvantage compared to nonselectors. While the intake rate of nonselectors has risen in response to the higher average particle value, selectors suffer from a low availability of the particle upon which they specialize. If these selective feeders are truly inflexible and unable to adjust selectivities, they would remain at a disadvantage under these conditions. For a behaviorally flexible feeder, enhanced ingestion of less valuable items would be adaptive. When the more valuable particle is sufficiently abundant, however, such inclusion of less valuable particles decreases the intake rate. With a twofold difference in particle values (10,5) and P1 = .10, the intake rate of the most selective feeder is 51% lower than that of the nonselector. When P1 = .50, the intake rate of the most selective feeder is 20% higher than that of the nonselector (Fig. 1 B), compared to 40% higher at the more disparate food values (Fig. 1 A).

When the two different particle types in suspension have equal values (10, 10), nonselective feeders have intake rates that are constant across all relative
proportions of the particles (Fig. 1 C). While one would expect uniform ingestion for selective animals also, Fig. 1 C shows that with equal particle values and \( P_1 = .10 \), the intake rate of the most selective feeder is 64% lower than that of the nonelector. This happens because our behaviorally inflexible selective feeders maintain low ingestion probabilities on “particle 2” — which is defined in the model as being the lower quality particle — regardless of the actual particle values. While this “perception” of particle 2 as being lower in value than particle 1 is in fact an artifact of the model, it is not unrealistic. This may happen if, through inexperience with novel items or preconditioning to specif-
ic particle types, selectors are specialized for taking one particle over another in spite of the availability of alternate high quality food. Clearly, such specialization would be advantageous as long as the “preferred” particle were more abundant than the alternate item, but if the opposite were true it would be adaptive to learn to handle or recognize the alternate item (i.e., adjust selectivities). The situation presented here may also be considered analogous to that of cryptic prey, which resemble inedible or low-quality items (cf. Hughes 1979; Ericsson et al. 1980). The distance between lines for the nonselector and selectors at P < .05 in Fig. 1 C could be interpreted as the energetic loss to a predator as a result of successful cryptis.

The occurrence of toxic algae in aquatic systems can present a hazard to the health of suspension feeders. To examine the effects of toxic algae (negative-value particles) we adjusted model parameters to approximate the results of Lampert’s (1981) experiments in which Daphnia, a nonselective feeder, was fed mixtures of the green alga Scenedesmus and the toxic blue-green Microcystis aeruginosa. In that study, when Microcystis comprised 9% of the food, growth of the daphnids was reduced to 67.6% of the control (100% Scenedesmus). A 17% suspension of Microcystis decreased growth to 19.9% of control, and when 33% and 50% of the suspension was Microcystis most animals died within 4 d. Model results of 9% and 17% “toxic” particle in suspension resulted in intake rates of 61.0% and 26.3% of control for nonselective feeders (Fig. 2). In each case, the effects of “toxic” particles were ameliorated by increased degrees of selectivity. Suspensions of 33% “toxic” particle resulted in negative intake rates for all feeders with lower selectivities than approximately W = 0.62; higher degrees of selectivity (W < 0.62) had positive intake rates. When the model suspension consisted of 50% “toxic” particle, a degree of selectivity of W < 0.30 was required for positive intake rates.

The degree of selectivity required for positive intake rates with 33% toxic particles in suspension has occasionally been reported for generalized filter-feeding Cladocera like Daphnia (Bogdan & Gilbert 1984; Knisely & Geller 1986). Although daphnids are apparently capable of chemically-mediated particle rejection (Porter & Orcutt 1980) most studies have shown them to be relatively nonselective (Lampert 1974; DeMott 1982, 1986; DeMott & Kerfoot 1982; Bogdan & Gilbert 1984; Lampert & Taylor 1985). Lampert (1981) concluded that Daphnia ingested Scenedesmus and toxic Microcystis with equal efficiency. These results suggest that cladocerans such as Daphnia may be more susceptible to algal toxicity than suspension feeders that have been shown to be highly discriminatory, such as copepods (Poulet & Marsot 1978; Bogdan & Gilbert 1984; Paffenbrocker & Van Sant 1985; DeMott 1986; Huntley et al. 1986) rotifers (Gilbert & Bogdan 1981, 1984; Bogdan & Gilbert 1984) and bivalves (Morton 1969; Ten Winke & Davids 1982). The level of selectivity required to have a positive intake rate with 50% toxic
Fig. 2. Intake rates (R, $10^4$ points h$^{-1}$) versus proportion high value particle in suspension. X's: Lamprey's (1981) results for Microcystis proportions of 0.0, 0.09, and 0.17 (= 1.0, 0.91, and 0.87 proportion high value particle, respectively). Greater proportions used in the experiments caused mortality and are not presented. Line: Model results of nonselector ($W = 1.0$) fitted to Lamprey's (1981) results. Dots: Intake rates of selectors ($W = 0.67$ to 0.11) at 50% high value particle; triangles: Intake rates of same at 67% high value particles (33% toxic particle).

particles in suspension ($W = 0.30$) may be beyond the capabilities of many Cladocera.

Costs of selectivity

It is clear that in an environment which offers food of highly variable quality, the ability to actively select food items would be advantageous. At the same time, there may be costs associated with selective feeding. For example, the selection process may decrease the overall rate of food collection, and the construction and maintenance of the selection mechanism (chemoreceptors, mechanoreceptors, appendages) may require additional energetic expenditures. Unfortunately, there is very little information available with which to evaluate the costs of selectivity in suspension feeders.

A detailed study of the feeding efficiencies of two freshwater zooplankters under a range of feeding conditions, by Richman & Dodson (1983), provides excellent information with which to examine selection costs. They calculated feeding efficiencies for the cladoceran Daphnia pulex and the copepod Diaptomus siciloides as the ratio of ingestion rate to respiration rate. When offered mixtures dominated by high quality food, Daphnia had a higher feeding efficiency than Diaptomus, largely because of higher feeding rates. Under the best food conditions (100% high quality food) the feeding efficiency of Diaptomus
was 37% lower than that of *Daphnia*. Thus, under conditions that would not appear to require selection, the selective feeder was at a disadvantage of approximately 37%. However, in suspensions dominated by lower quality food the disadvantages of a lower feeding rate in the copepod were outweighed by the advantages of greater particle sorting capabilities. Under the poorest food conditions (100% low quality food) the feeding efficiency of *Daphnia* was 72% lower than that of *Diatomus*. These results support the idea that there are costs associated with the ability to select, but that under certain conditions those costs are compensated for by higher nutritional returns.

The specific nature of selection costs addressed here is somewhat different than that found in most optimal foraging models (e.g., Schoener 1971; Lehman 1978), where the energy invested in handling or processing food items is lost when those items are rejected after collection by a selective feeder. Recent work on suspension-feeding copepods shows that handling time is negligible and should not constitute a substantial energetic investment (Paffenröper et al. 1982; Paffenröper & Van Sant 1985; DeMott 1989). Instead, our selection costs represent the foregone energy contained in food items not collected because of a slower feeding rate in selective feeders than in nonselective feeders in high-quality feeding suspensions (Richman & Dodson 1983). Ingestion rates of selectivity feeding copepods (Richman & Dodson 1983) and rotifers (Kirk 1991) are relatively constant regardless of the quality of the feeding suspension, while those of nonselective cladocerans increase substantially in high-quality food suspensions (Richman & Dodson 1983; Kirk 1991). This cost could have been incorporated in the model by assigning selectors a lower Water Processing rate or lower $\Sigma_i$, but it would have made the separate analysis of selection costs less clear.

Additional quantification of selection costs are difficult to draw from previous studies. Estimation of selection cost requires that feeding efficiency be measured over a range of feeding conditions, and ideally would include direct comparisons of different species under similar conditions. Further, the measure of efficiency used must be insensitive to, or corrected for, differences in species-specific factors such as rate of feeding or metabolism. Richman & Dodson’s (1983) ratios of simultaneously determined ingestion and respiration rates meet these requirements admirably, and more such determinations would be very useful.

The model we present here provides additional insight into the costs of selection. Our approach involves determining when, under reasonable conditions, costs nullify the advantages gained by feeding selectively. If the animal is feeding selectively, we may deduct selection costs as simply a percentage of the total points ingested. If we consider conditions from Fig. 1 B, with a 1:1 mixture of particles valued at 10 and 5, we can see how costs affect the intake rates of a range of selectors. With increasing cost deductions (i.e., an increasing per-
Fig. 3. Plot of intake rates ($R$, $10^4$ points h$^{-1}$) at different levels of selectivity versus percent cost deducted. Lines labelled with respective $W$ index; values = (10.5); $P_1 = 0.5$. The horizontal line indicates intake rate of nonselective feeder, with no costs deducted for selection.

percentage of R is deducted) the intake rates of all selectors decrease until even the most selective has a rate below that of the nonselector, which pays no cost (Fig. 3).

Model simulations using the estimate of 37% cost to selectors, derived from Ruchman & Dodson (1983), yield intake rate plots (Fig. 4 A, B, C) that indicate the conditions under which costs and benefits are balanced; that is, when the intake rate of a selector equals that of a nonselective feeder. With particles valued 10 and 1 (Fig. 4 A) the line showing net intake of the $W = 0.25$ selector nearly coincides with that of the nonselector. The lines of the most selective feeder ($W = 0.11$) and the nonselector intersect at 40% high value particle ($P_1 = 0.40$, Fig. 4 A). In contrast, the corresponding point of intersection without selection cost deductions was at only $P_1 = 0.09$ (Fig. 1 A). Similarly, their point of intersection with particles valued 10 and 5 is at $P_1 = 0.77$ (Fig. 4 B), up from 0.34 (Fig. 1 B). In general, disparity of particle values and higher proportions of preferred higher value particle help to balance the cost of selection. In addition, when the preferred item is sufficiently abundant, intake rates are maximized by maximizing the degree of selectivity. When the particles have equal value, the $W = 0.11$ feeder does not outcompete the nonselector until “preferred” particle abundance exceeds 87% (Fig. 4 C). Without selection cost deductions, the point of equal intake was at 50% abundance. Clearly, when an animal pays the cost of operating selection processes, misapplied discrimination is highly disadvantageous (see also Hughes 1979; Ericsson et al. 1980).

In contrast to the marked effects that selection costs may have under conditions of varied, but positive, food quality, those costs have little effect under
the life-and-death conditions of particle toxicity. To survive (have non-negative intake rates) with 33% toxic particles, a 0.05 increase in degree of selectivity (from 0.62 to 0.57) is required to offset selection costs. With 50% toxic particles, $W = 0.28$ is needed, compared to 0.30 without charging costs. Thus, when conditions are severe, only slight increases in selectivity are necessary to offset costs.

**Discussion**

There is considerable variability in both the quality of food in suspension and the degree of selectivity employed by suspension feeders. Our model uses these two sources of variability to quantify the consequences of different feed-
ing strategies under various feeding conditions. One apparent shortcoming of our treatment is that only two particles were considered at any time. Although more particles of different values could have been used in the model, we felt that the two particle situation led to the clearest presentation of the costs and benefits of selection. A second shortcoming is our use of a simple currency, i.e., "energy content" or "food value". This does not allow us to consider the contributions made by items that, as part of a mixed diet, are much more valuable than those items would be alone ("complementary resources", LEON & TUMSON 1975). However, our model may easily be expanded to incorporate a greater variety of food types, values, and selectivities to address these and other specific situations.

Application of this approach may help us to understand community and individual feeding patterns. If the nature of selection costs is such that they are with an animal continuously, perhaps as a consequence of maintaining a behavioral repertoire (including maintenance of receptors, appendages, etc.), we may be able to predict the relative success of species with different levels of selective capability. If the quality of available food items is similar, selection costs may outweigh any advantages of selective feeding, favoring the success of nonselectors. Conversely, high variability in the value of food items available would favor selective feeding, particularly when the food assemblage includes toxic particles. As an alternative to continuous selection costs, those costs may only be operative during active selection. If so, we may be able to predict when an animal that can switch feeding models, such as Eucalanus pileatus (PRICE et al. 1983) or Bosmina (DEMOTT & KERFOOT 1982), would do so. We would expect such an animal to begin active selection only when the value of the particle selected is high enough to overcome the costs of the mode of operation. Studies on the feeding of Bosmina lend support to this prediction; active selection is deemed responsible for enhanced clearance rates only on very desirable items such as Chlamydomonas, flagellates, and Cosmarium (DEMOTT 1982; DEMOTT & KERFOOT 1982; BLEWS & STOKES 1985).

We have focused on the advantages and disadvantages of selectivity as a feeding strategy. Because environmental conditions are not uniform, any given strategy will not always be optimal, and each animal may at times suffer the consequences of its own specialization. The consequences of feeding mode specialization can also be seen in animals adapted to low food availability. The marine cladoceran P. avirostris shows decreased ingestion, survival, and reproduction when held in high concentrations of cultured food (PAFFE-NHOFER & ORCUTT 1986). Salps, which feed using a mucus net, can survive at average (i.e., low) oceanic food concentrations. However, at high food levels the net becomes clogged, leading to decreased ingestion and, eventually, starvation (HARRISON et al. 1986). In general, we should not expect species to be perfectly tuned to their environment. In any organism, the development of selectivity
or any other ability is determined not only by pressures for that ability, but also by evolutionary constraints which may limit its development. Phyletic heritage can place restrictions on architecture and developmental pathways (Gould & Lewontin 1979). Imperfect adaptation to the feeding environment must also occur because of conflicting adaptations. For example, body form may be primarily dictated by locomotory or antipredatory considerations (Kerfoot et al. 1980), and the same appendages used in feeding often must function in swimming or respiratory exchange as well (e.g. mysids, Cannon & Manton 1927).

Our approach offers a framework to quantitatively assess the energetic benefits of different feeding behaviors. While there are tradeoffs involved in any feeding strategy, there are substantial quantitative advantages to selectivity. Variable food quality and particle toxicity are both common conditions in aquatic habitats; under those conditions, the benefits of selectivity are often worth the costs.

Summary

The high variability in the quality of food available to suspension feeders could make the ability to feed selectively advantageous under some conditions. We examine the costs and benefits of selective feeding under conditions of variable food quality, using a model of particle selection by suspension feeders. While varying the relative abundance of food particles differing in net nutritional value, we quantitatively compare the success of suspension feeders operating at different degrees of selectivity. The advantages of selectivity vary with the heterogeneity of the feeding suspension; the greater the difference between particle values, the more selectivity is favored. If the suspension includes toxic particles, a high degree of feeding selectivity may be required in order to survive.

We also consider the costs that may be associated with the ability to feed selectively. Because of slower feeding rates or energetic expenses, selective feeders may be at a competitive disadvantage to nonselectors when the feeding suspension consists of items of similar quality and selective feeding is unnecessary. In contrast, when toxic particles pose a hazard, the costs of selectivity are easily outweighed by the benefits of enhanced diet quality.

We discuss the application of this approach to help our understanding of feeding patterns and community composition. Selective feeding is just one example of a strategy that may be highly advantageous under particular conditions, but suboptimal under others. The flexibility in a species' adaptations to some environmental conditions may be limited by evolutionary constraints or by conflicting adaptations for other functions. To further our understanding through this approach, we suggest the following lines of investigation:

1) Comparisons of efficiency for different feeding strategies under various feeding conditions, such as that performed by Richman & Dodson (1983). This would facilitate measuring costs, and would also provide insights to the nature of those costs.

2) The role of selective feeding or other feeding strategies in the outcome of interspecific interactions. Recent work by Kik (1991) provides an excellent example of a laboratory approach to this problem. Such work should also relate the importance of the
outcome of these interactions to the abundance and distribution of species in natural systems.

Acknowledgements

We thank J. A. Rice and S. W. Hewett for valuable discussions and E. P. Hunt, T. M. Moermond, F. S. Stat, G. L. Taghon, J. D. Yount and an anonymous reviewer for critical comments on the manuscript. This work was supported by U.S. EPA cooperative agreement CR812216-01 with the University of Wisconsin and Trout Lake Station, Center for Limnology, University of Wisconsin-Madison.

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