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6. Mechanisms of Particle Capture by Copepods at Low Reynolds Numbers: Possible Modes of Selective Feeding

Abstract

Calanoid copepods play an important role in many aquatic food webs, hence their feeding has been studied extensively. Even though a large body of information has been gathered on copepod feeding rates, the mechanims by which these animals capture food particles are poorly understood. This paper summarizes recent organismal-level research on calanoid copepod feeding and points out in light of these studies possible mechanisms by which copepods feed selectively.

High-speed movies of water movement near feeding calanoid copepods reveal that the copepods propel water past themselves by flapping their second antennae, mandibular palps, first maxillae, and maxillipeds, and that the animals actively capture with their second maxillae parcels of that water that contain food particles. Copepods are not simple on-off filtering machines, but rather have a repertoire of behaviors associated with feeding: they can create scanning currents, fling and close their second maxillae to capture individual large particles, repeatedly flap their second maxillae to feed on small particles, reorient and comb particles from the second maxillae into the mouth, and groom their feeding appendages.

Feeding studies have shown that calanoid copepods graze on some types of food particles at greater rates than they do on other types of particles. Although there has been considerable speculation in the literature about the processes by which the selective feeding of copepods occurs the actual mechanisms involved have not been demonstrated. Based on our new understanding of how copepods feed, it can be suggested that selective feeding could depend on the chemical or mechanical cues for which a copepod flaps

asymetrically or for which it flings its second maxillae, on the physical characteristics of the particles retained within the basket of the closing second maxillae, or on the chemical or physical features of captured particles that are ingested rather than rejected.

Introduction

Calanoid copepods are abundant planktonic crustaceans that play a major role in the transfer of energy through marine food chains and that can be important members of freshwater zooplankton communities. Thus, a large body of information has been gathered on the rates at which various herbivorous and omnivorous copepods remove particulate food (such as diatoms and dinoflagellates) from the water (e.g. Fuller 1937; Gauld 1953; Bemer 1962; Mullin 1963; Adams and Steele 1966; Mullin and Brooks 1967; Richman and Rogers, 1969; Haney 1971; Ikeda, 1971; Paffenhofer, 1971; 1976a; 1976b; Frost 1972; 1975; 1977; Taguchi and Ishii 1972; Marshall 1973; Poulet 1973; 1974; 1976; 1977; 1978; Gaudy 1974; Poulet and Chanut 1975; Boyd 1976; Nival and Nival 1976; 1979; Allan et al. 1977; Hargis 1977; Paffenhoffer and Knowles 1978; Poulet and Marsot 1978; Cowles 1979; Donaghay and Small 1979; Schnack 1979; Dagg and Grill 1980; Donaghay 1980; Landry 1980).

Such feeding studies have revealed that calanoid copepods graze on some types of particles at greater rates than they do on other types of particles (but, see Huntley 1981). Copepods have been described as "size-selective" feeders (e.g. Harvey 1937; Gauld 1953; Mullin 1963; Conover 1966; Mullin and Brooks 1967; Richman and Rogers 1969; Hargrave and Geen 1970; McQueen 1970; Paffenhofer 1971; Frost 1972; 1977; Marshall 1973; Poulet 1973; 1974; Boyd 1976; Lam and Frost 1976; Lehman 1976; Nival and Nival 1976; Huntley 1980; Vanderploeg 1981; Harris 1982). However, there is evidence that factors other than particle size (such as particle smell or shape) also affect the selectivity of copepod feeding, and that copepods display plasticity in their selective feeding behavior (e.g. Martin 1970; Haney 1971; Esias and Curl 1972; Poulet 1973; 1974; 1977; 1978; Wilson 1974; Poulet and Chanut 1975; O'Connor _et_ _al_. 1976; Allan _et_ _al_. 1977; Fernandez 1979; Richman _et_ _al_. 1977; Poulet and Marsot 1978; 1980; Cowles 1979; Donaghay and Small 1979; Schnack 1979; Bartram 1980; Dagg and Grill 1980; Donaghay 1980; Richman _et_ _al_. 1980; Runge 1980; Skiver 1980). A controversy exists in the literature as to whether copepod selective feeding is due to the physical properties of the animals' food-capturing sieves, or rather is due to active choice by the animals (see, for example, "The Copepod Filter-Feeding Controversy" section in Kerfoot 1980).

Selective feeding by copepods can have important effects on planktonic communities. For example, zooplankton can markedly influence the composition of the phytoplankton by grazing more heavily on some species of algae than on others (Hargrave and Geen 1970; Martin 1970; Porter 1973; 1977; Poulet 1973; Wilson 1974; Berman and Richman 1974; Steele 1974; Lehman 1976; Nival and Nival 1976; Richman et al. 1977; McCauley and Briand 1979) as well as by changing nutrient concentrations (and therefore phytoplankton growth rates) in the water with their excretory products (e.g. Lehman 1980; this volume). Conversely, the size- and species-composition of phytoplankton may have important effects on the growth or decline of populations of various species of copepods (Mullin and Brooks 1970a; 1970b; Nassogne 1970; Parsons and LeBrasseur 1970; Harris and Paffenhofer 1976a; 1976b; Paffenhofer and Harris 1976; Dagg 1977; Gamble 1977; Cooney and Gehrs 1979; Checkley 1980a; 1980b; Cummings 1980; Lehman 1980). Perhaps selective feeding plays a role in permitting the coexistence of several species of copepods in planktonic communities (Markarewicz and Likens 1975; Paffenhofer and Knowles 1978; Boyd et al. 1980; Richman et al. 1980, Skiver 1980).

Most studies of copepod feeding have treated copepods as "black boxes" that remove particles from the water. Although those studies have led to insights about the dynamics of planktonic communities, a number of investigators have pointed out ways in which a lack of appreciation of what copepods actually do during grazing experiments can lead to various artefacts and erroneous interpretations (Anraku 1964; Paffenhofer 1971; 1976; Poulet 1974; O'Conners et al. 1976; Allan et al. 1977; Ikeda 1977; Richman et al. 1977; Poulet and Marsot 1978; Donaghay and Small 1979; Schnack 1979; Deason 1980; Harbison and McAlister 1980; Richman et al. 1980; Roman and Rublee 1980; Paffenhofer, this volume).

The purpose of this paper is to summarize recent organismal-level studies of calanoid copepod feeding and to point out in light of these studies possible mechanisms by which copepods might feed selectively. I hope that the information about feeding mechanisms that I will present here will enhance the ability of investigators working at the population, community, or ecosystem level to design meaningful experiments and models, and to interpret their data realistically.

Mechanisms of Feeding by Copepods

In spite of the tremendous ecological importance of copepod feeding, the mechanisms by which these animals

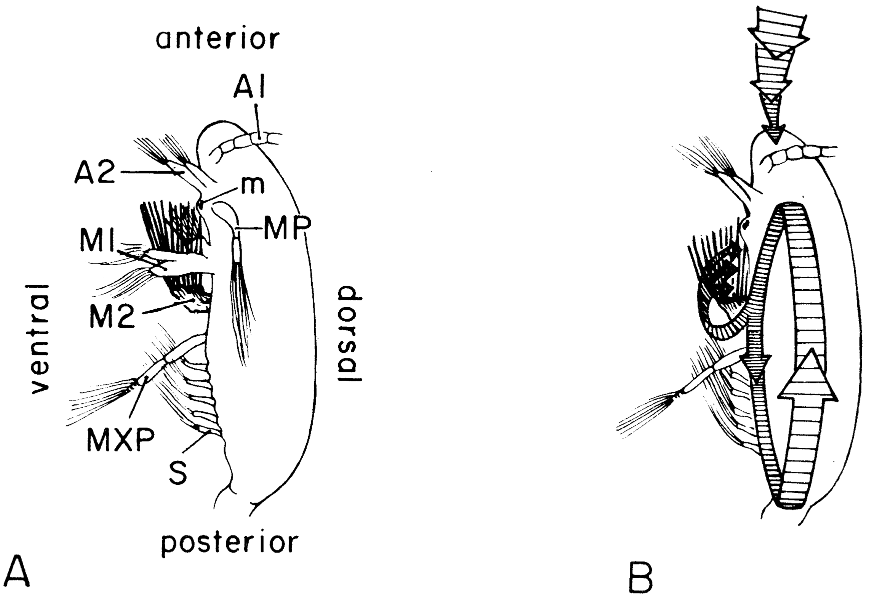


Figure 1. Diagram of a calanoid copepod such as *Eucalanus pileatus* in the typical feeding position viewed from its left side. Only the left appendage of each pair is shown.
A. The feeding appendages are: A2 = second antenna, MP = mandibular palp, M1 = first maxilla, M2 = second maxilla, and MXP = maxilliped. Other structures labeled are: A1 = first antenna, S = swimming legs, and M = mouth.
B. Diagram of the "textbook version" of copepod feeding currents (wide arrows) drawn from information presented in Cannon (1928), Lowndes (1935), Marshal and Orr (1955), Russell-Hunter (1979), and Barnes (1980). The beating of the feeding appendages (other than the stationary second maxillae) was thought to push water postero-laterally, forming a large swirl on each side of the animal. Some of this swirling water was thought to be sucked antero-medially by the outward sweep of the maxillipeds. The inward swing of the maxillipeds was thought to then push water between the setae and setules (Fig. 2) of the stationary second maxillae, which were believed to sieve particles out of the water. The filtered water was described as then being expelled anteriorly by the first maxillae. Reprinted from Koehl and Strickler (1981: p.1063) with permission of the American Society of Limnology and Oceanography.

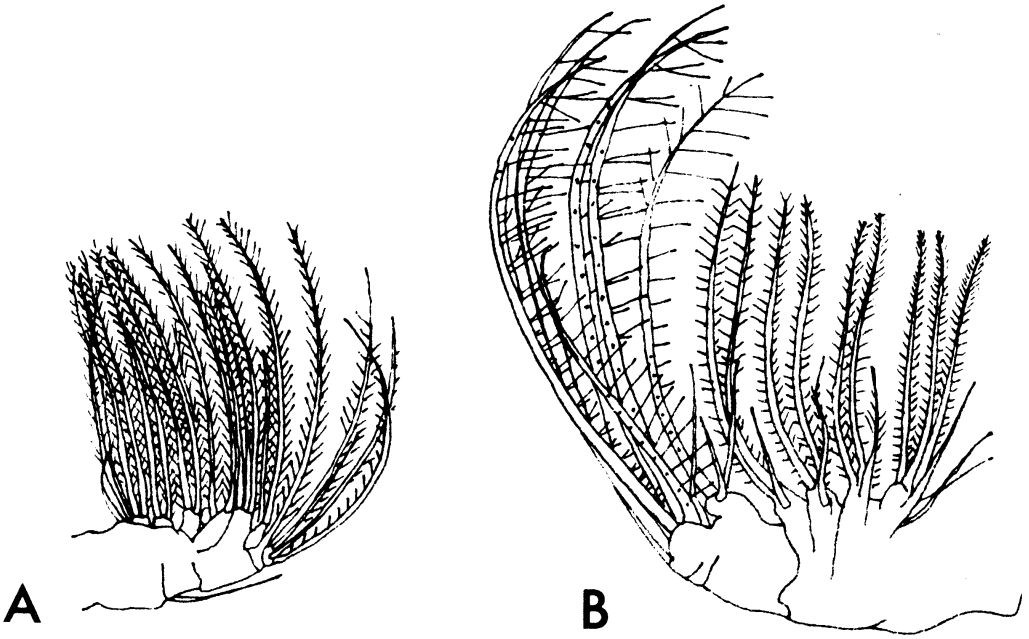


Figure 2. Diagrams of the second maxillae of two species of calanoid copepods. The large bristles are the "setae", and the smaller barbs on those setae are the "setules". A. *Calanus pacificus*. Redrawn from Frost (1977: p. 481) with permission of the American Society of Limnology and Oceanography. B. *Centropages typicus*. Redrawn from Lawson and Grice (1970: p. 204) with permission of E.J. Brill.

capture particles have been poorly understood, due in part to the technical difficulties involved in observing feeding appendages only fractions of a millimeter long that are moving at rates of the order of 20 to 100 Hz, and due in part to the non-intuitive nature of viscous water flow around small objects.

Until recently, descriptions of copepod feeding have been based on careful microscope observations of currents produced by copepods in drops of water (Esterly 1916; Cannon 1928; Storch 1929; Lowndes 1935; Marshall and Orr 1955; Gauld 1966). The "textbook description" (see, for example, figures in Russell-Hunter 1979, and in Barnes 1980) of copepod feeding based on such observations is illustrated in Fig. 1. It has been thought that the beating of the feeding appendages (labeled in Fig. 1,A) forces water continuously between the setae and setules of the stationary second maxillae (Fig. 2), which sieves particles out of the water. The second maxillae of carnivorous copepods actively capture prey (e.g. Landry), but there have only been a few mentions in the literature that the second maxillae of copepods feeding on phytoplankton may be active (Lowndes 1935; Conover 1966; Frost 1977; Richman and Rogers 1969).

Many attempts to analyze the feeding behavior of calanoid copepods have been based on the assumption that they feed by sieving, as described above. For example, a number of people have suggested that the particle-size selectivity of copepods is due to the physical properties of the second maxillae as passive sieves (Marshall and Orr 1955; Frost 1972; 1977; Marshall 1973; Boyd 1976; Lam and Forst 1976; Lehman 1976; Nival and Nival 1976; 1979). Similarly, models of copepod foraging have been based on the assumption that when an animal is creating feeding currents, water is passed continuously through its maxillary filter (Lam and Frost 1976; Lehman 1976), and that only the abundance and size of particles in the water affects the rates at which copepods consume them (Steele and Mullin 1977; Conover and Huntley 1980).

Recent use of high-speed microcinematography to study copepod feeding has revealed the complexity of appendage movements that create water currents that carry food towards the second maxillae (Alcaraz et al. 1980; Price and Paffenhofer 1980; Rosenberg 1980; Koehl and Strickler 1981; Paffenhofer et al. 1982; Cowles and Strickler, in press; Strickler, this volume). These studies showed that the second maxillae are not always held stationary, but rather periodically actively capture algal cells, which are then pushed into the mouth by the endites of the first maxillae.

They also revealed that algal cells are usually redirected without actually being touched by the feeding appendages.

The water currents produced by the feeding appendage movements of copepods have recently been revealed by high-speed movies of dye streams around feeding animals (Koehl and Strickler 1981). These appendage and water motions are diagrammed in Figs. 3 and 4. Note that water is <u>not</u> pumped through the second maxillae when they are held nearly still (Fig. 3; Fig. 4, A and B). Rather, the flapping of feeding appendages produces a pulsing stream of water past the copepod. The dye streams also revealed the water motion produced by the algae-capturing movements of the second maxillae. When an alga is carried into the vicinity of the copepod, the feeding appendages (second antennae, mandibular palps, first maxillae, and maxillipeds) beat asymetrically, redirecting the incoming current so as to draw in water preferentially from the direction of the alga. (Each copepod was tethered for filming; if it had been swimming freely, this assymetrical flapping would have turned the animal towards the alga (Paffenhofer <u>et</u> <u>al</u>. 1982)). As the alga nears the second maxillae, these two appendages fling apart at high speed (mid-setal velocities of about 10 to 300 $mm.s^{-1}$, depending on species (Koehl and Strickler 1981)) in a manner analogous to the vortex-creating "fling" of insect wings (Weis-Fogh 1973; Ellington 1980; Maxworthy 1981).

This fling creates a gap between the second maxillae that is filled by inrushing water (Fig. 4, C and D). This water carries the alga within the basket formed by the second maxillae, which then rapidly close over the alga and water. While the second maxillae are closing, the water (having no other escape route) is squeezed out between the setae of these appendages and is pushed posteriorly by the first maxillae (Fig. 3, E and F). Water does not escape anteriorly from the second maxillae because the second antennae are pushing water posteriorly at the second maxillae while they are closing. Thus, we have shown (Koehl and Strickler 1981) that copepods are not filter feeders as they have been described, but rather appear to scan the large volume of water that is propelled by their feeding appendages, and to force through the second maxillae only that small volume of water surrounding food particles.

Note that this new description of copepod feeding currents applies to animals feeding on algal cells that are 10um to 53 um in their longest dimension (Koehl and Strickler 1981). Similar appendage motions appear to be involved in the capture of large algae, although more motions of the second maxillae are required to position the food for ingestion

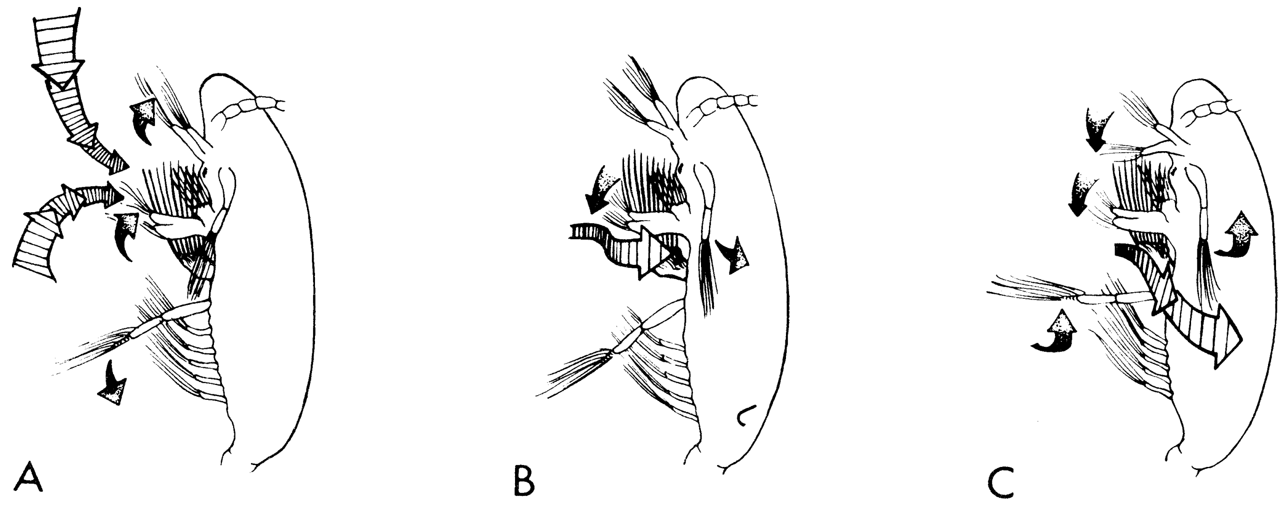


Figure 3. Diagrams of feeding appendage movements of a copepod (stippled arrows) and the water currents (striped arrows) they produce as revealed by high-speed movies of dye streams around feeding Eucalanus pileatus. An arrow with a narrow shaft and wide head indicates lateral movement out of the plane of the page towards the reader; an arrow with a wide shaft and narrow head indicates medial movement away from the reader. A. Outward movements of the second antennae and maxillipeds suck water towards the copepod's maxillae. B. Postero-medial movement of the first maxillae and dorso-lateral movement of the mandibular palps suck water laterally. C. Inward movements of the second antennae and maxillipeds coupled with dorso-lateral movement of the mandibular palps shove water postero-laterally. Reprinted from Koehl and Strickler (1981: p. 1063) with permission of the American Society of Limnology and Oceanography.

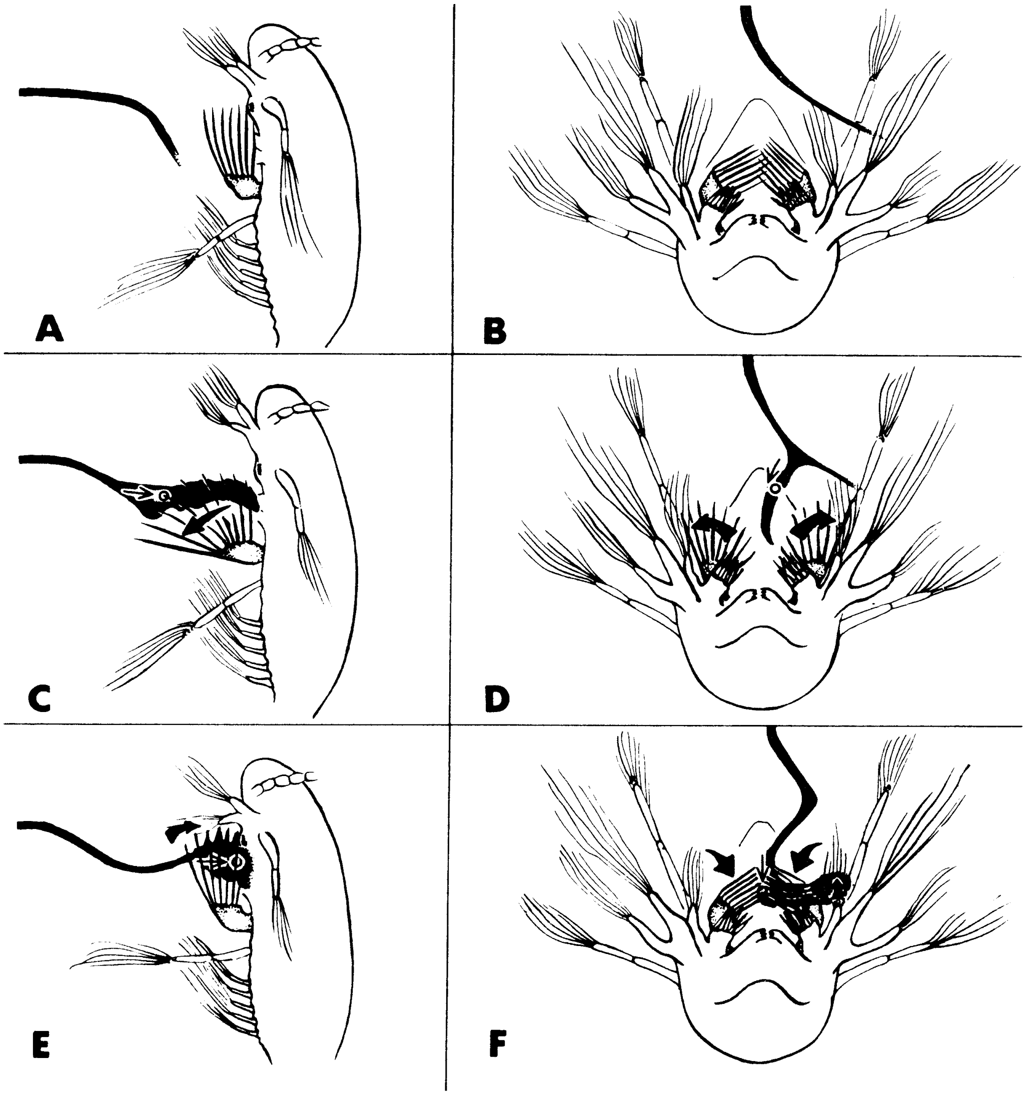


Figure 4. Diagrams traced from high-speed films of feeding Eucalanus pileatus. Black streaks are dye streams from a micropipette. Heavy arrows indicate the movements of the second maxillae (and of a first maxilla in F). Circles represent the positions of and fine arrows the movements of algae observed during similar appendage movtions in other frames of the films. In the first column the copepod is viewed from its left side and the first maxilla has been left off for clarity. In the second column the animal is viewed from its anterior end. Feeding currents bypass the second maxillae (A-B) until an alga nears them. The alga is captured by an outward fling (C-D) and inward sweep (E-F) of the second maxillae as described in the text. Reprinted from Koehl and Strickler (1981: p. 1067) with permission of the American Society of Limnology and Oceanography.

(Paffenhofer _et_ _al_. 1982). However, when copepods feed on very small cells (¼ 7 um for _Eucalanus_ spp.), they flap their second maxillae many times in a row at low amplitude (Price and Paffenhofer 1980). We do not yet know how the water moves when copepods feed on very large and very small particles, hence the mechanisms of particle capture and manipulation are still unknown.

Copepods Live in a Viscous World

We can better comprehend the feeding mechanisms of copepods if we consider them within the context of their physical world. Because copepods are small (generally 1 to 10mm in length), their physical world is dominated by viscous forces rather than the inertial forces that large organisms like humans encounter when moving through fluids. If an irregularity is produced in a stream of fluid, it will persist if inertial forces predominate, but will be damped out if viscuous forces are more important. The ratio of inertial to viscuous forces for a flow situation is the Reynolds number (Re),

$$Re = \frac{o\ V\ L}{u}$$

where V is the relative velocity of a fluid across a solid object, L is a linear dimension of the object, and [illegible] is the density and u the viscosity of the fluid. Flow is laminar when Reynolds number is low (i.e. the fluid moves smoothly around the body and can be considered as moving in layers between which there is not significant mixing); flow is turbulent when Reynolds number is high (see Shapiro 1961; Happel and Brenner 1965; Purcell 1977; Vogel 1981).

A number of investigators have pointed out that small planktonic crustaceans such as copepods no doubt operate at low Reynolds numbers (Vlyman 1970; 1977; Strickler 1975a; 1975b; 1977; this volume; Strickler and Twombly 1975; Lehman 1976; 1977; Enright 1977; Lochead 1977; Rubenstein and Koehl 1977; Alcaraz _et_ _al_. 1980; Kerfoot _et_ _al_. 1980; Zaret 1980a; 1980b; Zaret and Kerfoot 1980; Koehl and Strickler 1981; Paffenhofer _et_ _al_. 1982; Strickler, this volume). Koehl and Strickler (1981) have found that the Reynolds numbers for the setae of various feeding appendages of _Eucalanus_ _pileatus_ are of the order of 10^{-1} to 10^{-2}. Such low Reynolds numbers indicate that the effects of viscosity are much more important to these copepods when feeding than are the effects of inertia. Koehl and Strickler (1981; Koehl 1981; Strickler, this volume) have described a number of non-intuitive features of low Reynolds number flow that are important in copepod feeding, and some of the implications of such viscous flow have also been pointed out for ciliary suspension feeders (e.g. Strathmann 1971; 1973; Strathmann et al. 1972; Fenchel 1980).

Possible Modes of Selective Feeding

The mechanisms copepods use to feed selectively on different sorts of particles are not yet known. However, in light of our new knowledge of the kinematics of copepod feeding, a number of possible mechanisms of selective feeding can be proposed. In considering these various mechanisms, the physical constraints of low Reynolds number flow as well as the evidence from feeding studies on copepods must be kept in mind.

The Second Maxillae as Size-Selective Filters

Correlations have been noted between the types of food selectively eaten by various species of copepods and the morphology of the feeding appendages, especially the second maxillae (Ussing 1938; Marshall and Orr 1955; Anraku and Omori 1963; Gauld 1966; Arshkevich 1969; Itoh 1970; Nival and Nival 1976; 1979; Boyd 1976; Friedman 1977; 1980; Robertson and Frost 1977; Poulet 1978; Poulet and Marsot 1980; Bartram 1980; Richman et al. 1980; but, Vanderploeg and Ondricek, 1982). It has therefore been suggested that the sizes of particles captured by a copepod are determined by the spacings of the setules on the setae of the second maxillae. How can this interpretation be reconciled with the observed ability of copepods to change the selectivity of their feeding? In order to evaluate the role of the morphology of the second maxillae in determining the selective capture of particles by copepods, we must consider the behavior of water and particles around fibers at low Reynolds numbers.

Water Flow Around Setae and Setules. Fluid in contact with the surface of an object does not slip relative to that object. Thus, a layer of fluid along the surface of a body undergoes shear deformation when the body moves relative to the surrounding fluid. At low Reynolds number this boundary layer of fluid stuck to an object and subjected to shear deformation is thick relative to the dimensions of the object. Furthermore, at low Reynolds number when inertial effects can be ignored, the resistance to the motion of water between two objects is proportional to the rate at which the water is deformed in shear; the closer together the two objects are, the greater the shear deformation rate will be of water forced to move between them at a given flow rate.

It is not surprising, therefore, that little water moves through the narrow gaps between setae on copepod appendages (Koehl and Strickler 1981; Koehl 1981). These appendages, like the wings of tiny insects (Ellington 1975) behave more like solid paddles than open rakes. Water can, of course, be forced to move through very narrow gaps when given no other escape route. During the closing of the second maxillae over an algae, for example, water is squeezed out between the setae (Fig. 3, E and F). This motion may well be energetically expensive (see Tamada and Fujikawa 1957, Fuchs 1964, or Spielman 1977, for accounts of how the resistance to the movement of a fluid through an array of cylinders increase as the spacing between the cylinders decreases at low Reynolds numbers).

Water no doubt also resists flowing between closely-spaced setules on setae. Second maxillary setae, with rows of setules and the water stuck to them may well be functionally wide and smooth rather than comb-like. Rees (1975) found that corrugated insect wings operating at low Reynolds number are functionally smooth in this way. Although the second maxillae are not used as stationary sieves, and although water may well not flow between setules, setule length and spacing no doubt play a role in determining which algae are retained within the basket of the closing second maxillae. The presence of setules probably affects water flow patterns around the setae during basket closure; these flow patterns should affect which physical types of particles are most likely to bump into the second maxillae, as will be explained in the next section. Setule length, spacing, and stiffness should also affect which of the particles that bump into the filter will be retained, and which will be washed away as water is squeezed between the setae.

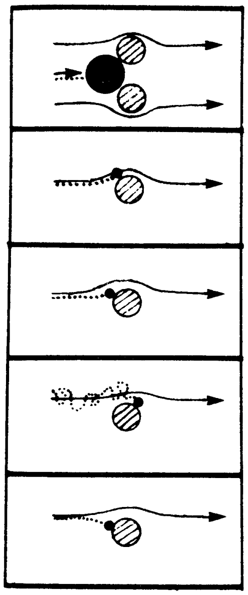
<u>Filters Are Not Just Sieves</u>. The physical mechanisms by which filter-feeding organisms remove particles from the surrounding fluid are poorly understood. Biologists generally assume that filters that act as sieves can only capture particles larger than the space between the fibers composing the filter. Rubenstein and Koehl (1977) have applied to biological filters the theoretical analysis of filtration developed by engineers (see Ranz and Wong 1952; Fuchs 1964; Dorman 1966; Pich 1966; Spielman and Goren 1968; Davies 1973; Spielman 1977); we have suggested that there are several mechanisms other than sieving by which a filter can capture particles, and that particles smaller than the interfiber spacing of a filter can be caught. Both man-made filters and screens (Sheldon and Sutcliffe 1969) and copepod second maxillae (Friedman 1980) have been found to retain particles from natural waters that are smaller than the "pore

size" of the filters. Furthermore, experimental studies indicate that this filtration theory is applicable to other particle-capturing organisms such as ophiuroids (LaBarbera 1978, sea anemones (Koehl, unpublished data), and protozoans (Fenchel 1980). Murray (1976) has used a similar analysis to work out the capture of pheromone molecules by moth antennae, and a number of other investigators have used this approach to predict the deposition of particles in the human respiratory tract (e.g. Taulbee and Yu 1975; Savilonis and Lee 1977).

The mechanisms of particle capture, which are described by Rubenstein and Koehl (1977) and illustrated in Fig. 5, are direct interception, inertial impaction, gravitational deposition, and motile-particle or diffusion deposition. Using filtration theory, one can predict using certain physical characteristics of a filter, particles, and water current, which of these mechanisms of particle capture are operative for a given filtration situation (Ranz and Wong 1952; Pich 1966).

One of the consequences of the ability of a filter to capture particles by a number of mechanisms is that the filter differentially captures particles of different sizes. As particle size is increased, a filtering element's ability to collect particles by inertial impaction, gravitational deposition, and direct interception is improved. As particle size is reduced, collection by diffusion deposition is enhanced. As a result, there is an intermediate range of particle sizes for which the efficiency of capture by the simultaneous action of all mechanisms reaches a minimum. (Filtering efficiency is defined by engineers as the ratio of the number of particles striking a filtering element to the number that would strike it if the streamlines were not diverted by it (Dorman 1966), that is, the ratio of particles captured to particles available.) The efficiency minimum occurs at smaller particle sizes as velocity is increased and as fiber diameter is decreased (Pich 1966). Therefore, physical features of a filter other than just its inter-fiber spacing determine the size range of particles the filter is most efficient at capturing.

When a particle in water approaches a filtering element, factors such as surface charge and van der Waals forces determine whether or not the particle actually contacts the fiber (e.g. Spielman 1977). LaBarbara (1978) and Gerritsen and Porter (1982) have found ophiuroids and cladocerans, respectively, capture charged particles at greater rates than uncharged particles. Although such differential capture is most likely due to enhanced adhesion of charged particles to



Sieving

Direct Interception: $d_p/d_f = N_R$*

Inertial Impaction: $\frac{d_p^2(\rho_p - \rho_m)V_0}{18\mu d_f} = N_I$

Diffusion or
Motile-Particle Deposition: $\frac{KT}{d_p}\left(\frac{1}{3\pi\mu V_0 d_f}\right) = N_M$

Gravitational Deposition: $v_g/V_0 = N_G$
where $v_g = [d_p^2 g(\rho_p - \rho_m)]/18\mu$

Figure 5. Diagrams of the mechanisms of particle capture by a fiber and the dimensionless indices (N's) indicating the intensity of particle capture by each mechanism. Redrawn from Rubenstein and Koehl (1977: p. 983) with permission of the University of Chicago Press.

d_f = diameter of a fiber
d_p = diameter of a particle
g = acceleration due to gravity
K = Boltzmann's constant
m = mass of particle
N_G = index of gravitational deposition
N_I = index of inertial impaction
N_M = index of motile-particle or diffusion deposition
N_R = index of direct interception
T = absolute temperature
V_0 = upstream velocity of the fluid relative to fiber
v_g = settling velocity of the particle
μ = viscosity. of the fluid
ρ_m = density of the fluid
ρ_p = density of the particle
▨ = crossection of fiber
● = particle
⟶ = streamline of fluid relative to fiber
······ = path of particle .

*Note that for particles being captured from water by a fiber that is very large relative to them, capture intensity depends less on particle size than this classical filtration theory predicts, and depends inversely on flow rate (see Spielman, 1977).

filters, the possibility that charge may correlate with particle flavor has not been ruled out. Furthermore, it should be pointed out that a particle need not actually contact the seta of a copepod's second maxilla to be captured -- any particle that merely fails to move past a seta during the closing motion of the second maxillae is retained.

If a copepod's second maxillae are considered only as sieves, it appears that the beast can change the size of particles on which it feeds only by changing the spacing between the fibers of these filters. Filtration theory reveals several other mechanism by which a copepod might alter its diet. For example, by changing the velocity of water passing through the second maxillae, or by altering the diameter or adhesiveness (with mucus?) of the filtering fibers, the range of particle sizes that can be captured most efficiently by the filter can be shifted. Price and Paffenhofer (1980) have noted that copepods move their second maxillae differently when feeding on algal cells smaller than 7u than they do when feeding on larger cells. It is not yet known whether such differences in movement affect the size range of particles most efficiently captured by the second maxillae.

The morphology (see Fig. 2) and kinematics of the second maxillae can vary considerably from species to species of copepod. For example, the coarse setae of _Centropages typicus_ second maxillae move nearly twenty times faster than do the fine setae of _Eucalanus pileatus_ during the capture fling and closure (Koehl and Strickler 1981). _C_. _typicus_ second maxillae operate at Reynolds numbers of the order of one; although flow is laminar at such Reynolds numbers, inertia cannot be ignored as it can for smaller, slower second maxillae. The consequences of such differences in structure and motion both to particle selectivity of the second maxillae and to costs of moving these appendages are not yet known.

Thus, the morphology and kinematics of the second maxillae may play an important role in determining which particles are retained by these appendages as they close over captured parcels of water. However, there are other stages in the feeding process at which particle selection also could occur.

Chemo- and Mechanoreception

Based on our new understanding of how copepods feed, it can be suggested that selective feeding might depend upon; 1) the chemical or mechanical cues for which a copepod asymetrically flaps the appendages that create the scanning current, or for which it flings the second maxillae, and 2) the chemical or physical features of captured particles that are ingested rather than rejected.

Flinging and Asymetrical Flapping. Copepods have been observed to flap asymetrically the appendages that create the scanning current, thereby drawing in water preferentially from the direction in which an alga is arriving (i.e. turning towards the alga) (Koehl and Strickler 1981; Paffenhofer et al. 1982; Strickler, this volume). How far away is an alga when the scanning appendages react to it? By tracing the positions of these appendages on movies (500 frames.s^{-1}) of tethered animals for many cycles of flapping, I observed that they moved along the same paths over and over when they produced the scanning current (also, see Fig. 3 in Strickler, this volume). Such tracings allowed me to note the point in time (within 2 to 4ms) when the movement of a feeding appendage deviated from this pattern (i.e. when assymetrical flapping began). The distance of an alga from the nearest seta of the appendage was measured for that frame of the film. (Note that I could not measure the distance between an alga and seta in the direction normal to the plane of the film. Therefore, unless both the alga and seta were in sharp focus, such a measure was an underestimate of the distance between them.) Which appendages beat asymetrically before a particular capture depended on the direction from which the alga was arriving: second antennae responded to particles arriving antero-laterally, first maxillae to those arriving laterally, and maxillipods to those arriving postero-laterally. The amplitude and direction of an appendage's response also depended on the direction of the alga. I found that adult female Eucalanus pileatus, when they flapped asymetrically, changed the motion of these appendages a mean of 20ms (S.D. = 24, n = 8) before the second maxillae began their capture fling (data for three individuals feeding on Gymnodinium nelsoni, 50-53um long, 100 cells.ml^{-1}, or Prorocentrum micans, 36-37 um long, 120 cells.ml^{-1}). The algae were a mean distance from the appendages of 136 um (S.D. = 72, n = 5, four were underestimates). Strickler (1982) reported that an untethered E. pileatus changed its behavior 430ms before an alga reached its "capture area"; the alga was 1250 um away when the animal responded.

Copepods fling their second maxillae apart to capture the parcel of water containing an alga (Koehl and Strickler 1981; Koehl 1981; Strickler, this volume). I measured for the E. pileatus described above that the algae were a mean distance of 365 um (S.D. = 324, n = 7, four were underestimates) from the second maxillae within 2ms of the time that its capture fling began. For Centropages typicus, the second-maxillary fling began when algae were a mean distance of 137 um away (S.D. = 93, n = 2, one was an underestimate; data for one adult female feeding on G. nelsoni, 100 cells.ml^{-1}).

Although the measurements reported above do not tell us the distance at which copepods can perceive particles, they do show that copepods react to particles as they are carried near the animal in the scanning current. Do copepods use mechanical or chemical signals to perceive food particles? Does selective feeding depend upon the nature of the mechanical and/or chemical features of food particles that trigger the assymetrical flapping and second-maxillary flinging by copepods?

At low Reynolds numbers, objects affect the movement of water many body lengths away from themselves (e.g. Happel and Brenner 1965; White 1974; Zaret 1980a; Weinbaum 1981). Can a flapping copepod feel distortions in the flow field it is producing caused by the presence of sinking or swimming food particles? Morphological studies suggest that copepods have mechanoreceptors (Strickler and Bal 1973; Friedman and Strickler 1975; Strickler 1975b), and feeding experiments reveal that copepods can capture inert(?) particles such as plastic beads (e.g. Wilson 1973). Furthermore, behavioral studies indicate that various small zooplanktonic animals feel the presence of walls and other zooplankton in the water around them (Lillelund and Lasker 1971; Strickler 1975a; Kerfoot 1978; Kerfoot et al. 1980; Zaret and Kerfoot 1980; Haurey et al. 1980; Landry 1980; Zaret 1980a; 1980b). The role of mechanoreception in the perception and selection of food particles by copepods needs to be investigated.

The algal cells and other small particles on which copepods feed, swim or sink (Eppley et al. 1967) slowly through the water at Reynolds of the order of 10^{-3}. Therefore these particles are no doubt surrounded by relatively thick boundary layers of water. It has been suggested that if food particles exude chemicals into the water around them, they are probably surrounded by zones of odor much larger than themselves (Koehl and Strickler 1981; Koehl 1981; Strickler 1982; this volume).

In the viscuous low Reynolds number world of a copepod, water flow is laminar. By repositioning a dye-releasing micropipette with respect to tethered feeding copepods, we have shown that water streams from different locations are moved around the copepods along different discrete, predictable paths (Koehl and Strickler 1981). The dye is not mixed into the surrounding water by beating copepod appendages as it would be in a turbulent, high Reynolds number flow situation. One likely consequence of such laminar flow is that a copepod's flapping will not stir up the water and thereby confuse the direction from which chemical signals in the water are coming.

Although it has been suggested that chemical cues may be used by copepods to locate the approaching food to which they respond (e.g. Koehl and Strickler 1981; Koehl 1981; Paffenhofer et al. 1982; Strickler 1982; this volume), this has not yet been demonstrated. Morphological studies suggest that copepods have chemoreceptors (Ong 1969; Elofsson 1971; Fleminger 1973; Strickler and Bal 1973; Friedman and Strickler 1975; Friedman 1977). Chemosensation has been demonstrated in other crustaceans (e.g. Ache 1972; 1978; Laverack 1975; Hamner and Hamner 1977), and does appear to be involved in copepod mating behavior (Katonia 1973; Griffiths and Frost 1976; Blades and Youngbluth 1980). Some feeding experiments indicate that copepods can select food particles on the basis of their smell (Mullin 1963; Poulet and Chanut 1975; Poulet and Marsot 1978; 1980; Donaghay and Small 1979), but we do not yet know whether this selectivity is due to preferential capture of certain types of particles as well as to rejection of other types of particles after they have been caught.

Rejection. Copepods have been observed to reject captured particles (Conover 1966; Frost 1977; Poulet and Marsot 1978; 1980; Donaghay and Small 1979; Donaghay 1980; Alcaraz et al. 1980; Runge 190; Koehl and Strickler 1981; Paffenhofer et al. 1982; Cowles and Strickler, in press; Strickler, this volume). Copepod mouthparts are covered with chemoreceptors (Ong 1969; Friedman and Strickler 1975; Friedman 1977), hence, it seems likely that chemical cues are used to determine whether a particle should be ingested or thrown away. Strickler (this volume) has observed a copepod to manipulate glass particles too big to ingest in the presence of chemical signals from a micropipette, but to discard them when the flow of the chemicals was shut off. Whether or not copepods pick up mechanical information about the size and shape of particles as they handle them and use such information to determine whether or not to ingest the particle is not yet known.

Foraging Behavior Patterns

We now realize that copepods are not simple on-off filtering machines, but rather have a repertoire of behaviors associated with feeding (such as scanning, capturing, and grooming). Whether or not the ways in which copepods apportion their time between these various activities affects which particles are selectively captured is not yet known.

Scanning and Sinking. As described above, copepods propel water past themselves by flapping their second antennae, mandibular palps, first maxillae, and maxillipeds; I will refer to such behavior as "scanning". When copepods scan, they slowly move anteriorly (generally upwards) (at velocities of about 1.5 $mm.s^{-1}$ for E. pileatus (Koehl and Strickler 1981) and of 1.75 $mm.s^{-1}$ for E. crassus (Strickler 1982), for example). Copepods also stop flapping these appendages for periods of time during which they sink (at velocities of 1 to 2 $mm.s^{-1}$ for E. pileatus and C. typicus (Koehl and Strickler 1981), for example). Cowles and Strickler (in press) have found that C. typicus spends longer periods of time taking "breaks" (i.e. sinking) when food is sparse than they do when food is plentiful. Can a copepod mechanically sense distortions in the flow field around it as it sinks produced by swimming or sinking algal particles? Can a copepod use chemical cues to perceive whether or not it has sunk into a patch of water containing more or different algal cells? Cowles and Strickler (in press) have found that the duration of a break for C. typicus depends on the type as well as the concentration of algae present. Do local chemical or mechanical cues trigger the onset of scanning or sinking, or does a copepod's apportionment of time to these two behaviors depend on the recent history of particle ingestion by the animal? What are the energetic costs of scanning as compared to sinking (i.e. how much energy does a copepod save by taking breaks)? Before the complexity of copepod behavior had been directly observed, Haurey and Weihs (1976) modeled how a copepod should apportion its time between sinking and swimming to maintain a position in the water column at a minimum cost.

Capture. Although it seems reasonable to suggest that chemical and/or mechanical cues may trigger copepods to turn toward a food item and to fling their second maxillae to capture it, recent work indicates that copepods do not always individually capture each food particle in this way. Price and Paffenhofer (1980) have found that several species of calanoid copepods (that do capture large algal cells individually as described above) when in the presence of algal cells smaller the 7 um flap their second maxillae repeatedly and then comb into their mouth whatever cells have been caught. Are such little algae too small to be chemically or mechanically perceived by a copepod for individual capture? That sensory perception by the first antennae is not required for the capture of small algal cells has been demonstrated by Landry (1980); he found that removal of their first antennae from omnivorous copepods drastically reduced their rate of raptorial feeding on nauplii but not their rate of feeding on small algal cells. The cues that cause a copepod to switch its second-maxillary movements from the "individual fling" mode of capture used in the presence of large algal cells to the "multiple flap" mode of capture used in the presence of small algal cells are not yet known. Furthermore, although Price and Paffenhofer (1980) have proposed an energetic model to predict when a copepod should switch its capture mode, the costs of the two types of capture movements are not yet known.

Handling. Since water sticks to the appendages of copepods operating at low Reynolds numbers, getting captured algae "unstuck" from the second maxillae and into the mouth is no small feat. As mentioned above, the short, stocky endites of the first maxillae perform this function by combing the setae of the second maxillae (Alcaraz et al. 1982; Koehl and Strickler 1981; Paffenhofer et al. 1982; Cowles and Strickler, in press; Strickler, this volume). By considering an analogous low Reynolds number task for a human -- using a fork to comb crumbs off another fork when both are immersed in honey -- one might suggest that the amount of time required would depend on particle size and shape. Indeed, Price and Paffenhofer (1980) have found that the duration of a copepod's combing is only 100 to 300ms for large spherical algal cells, but is 400 to 800ms for small algae. When feeding on small algae, the animals appear to let a number of cells accumulate under the second maxillae before ingesting them (Paffenhofer et al. 1982). In contrast, large elongate cells or chains must be oriented end-on rather than broadside to the mouth to be ingested. Paffenhofer et al. (1982) described the motions of the second maxillae that reorient these long algae and reported the handling time was longer than that for smaller, more-nearly spherical cells.

Although copepods in the act of combing continue to create scanning currents, they do not attempt to capture other algae carried past them in these currents (Alcaraz et al. 1980; Koehl and Strickler 1981). However, Strickler (this volume) observed a copepod to catch an algal even though it was already handling glass particles with its second maxillae. Handling time should be incorporated into models of copepod foraging once we know more about its duration for different sorts of particles as well as about the conditions under which handling interferes with subsequent captures.

Grooming. In the viscous, low Reynolds number world of a copepod, particles of various sorts become stuck to appendages other than just the second maxillae. High-speed movies of feeding copepods reveal that they stop scanning from time to time and go through an elaborate procedure of scraping their first antennae and feeding appendages (Strickler, this volume). The conditions under which such "grooming" behavior might vary in frequency or duration have not yet been worked out, although one might expect more grooming when animals are in water containing high concentrations of particles.

Optimal Foraging Models. Several optimal foraging models have been proposed to predict the size-selective feeding of copepods (Lam and Frost 1976; Lehman 1976). Those models are based on the assumption that copepods are on-off filter feeders. Now that we know the complex repertoire of behaviors used by feeding copepods, new foraging models can be developed based on more realistic assumptions. Copepods can create scanning currents, fling and close their second maxillae to capture individual large particles, repeatedly flap their second maxillae to feed on small particles, reorient and comb particles from the second maxillae into the mouth, and groom their feeding appendages. Furthermore, Strickler (1982) reported that E. crassus can use its feeding appendages for "cruising" as well as for "feeding", the flow fields in the two situations being different. Copepods can also cease flapping and thus sink, and can rapidly locomote using their swimming legs (Fig. 1) (Strickler 1975a; this volume); both these behaviors may be involved in predator avoidance, and both behaviors may also move copepods to new food environments. If reasonable estimates of the energetic costs per time of these various activities could be made using fluid dynamic analyses, and if the ways in which copepods apportion their time between these activities under different conditions could be assessed (as Cowles and Strickler, in press, and Price and Paffenhofer (1980) have begun to do), then more realistic foraging models could be developed to predict the grazing behavior of copepods.

Summary

High-speed films of water movement near feeding calanoid copepods reveal that these important planktonic herbivores propel water past themselves by flapping their second antennae, mandibular palps, first maxillae, and maxillipeds, and that copepods actively capture parcels of that water that contain food particles by flinging and closing their second maxillae. Although there has been considerable speculation in the literature about the processes by which the selective feeding of copepods occurs, the actual mechanisms involved have not been demonstrated. Based on our new understanding of how copepods feed, it can be suggested that selective feeding could depend on the chemical or mechanical cues for which a copepod flaps asymetrically or for which it flings its second maxillae, on the physical characteristics of the particles retained within the basket of the closing second maxillae, or on the chemical or physical features of captured particles that are ingested rather than rejected.

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