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FEEDING AT LOW REYNOLDS NUMBER BY COPEPODS

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ABSTRACT. Calanoid copepods are small planktonic crustacens that are extremely abundant in oceans and lakes. Many of these shrimp-like animals eat unicellular algae and thus play a major role in the transfer of energy through marine food chains. In spite of the ecological importance of copepod feeding, the mechanisms by which these animals capture particles such as algal cells has been poorly understood. Analysis of high-speed movies of feeding copepods has revealed how these tiny creatures move water to capture food. Because copepods are small, their physical world is dominated by viscous forces rather than the inertial forces that large organisms encounter when moving through fluids. In the viscous world of a copepod, water flow is laminar, bristled appendages behave as solid paddles rather than open rakes, particles can neither be scooped up or left behind because appendages have thick layers of water stuck to them, and water and particle movements stop immediately when an animal stops moving its appendages. This study of copepod feeding illustrates the importance of considering the physical forces that are most important at the size scale of the organisms being studied. A number of unsolved problems about copepod feeding that are ripe for mathematical analysis are presented.

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INTRODUCTION

Why Study Copepod Feeding?

Calanoid copepods (Fig. 1) are planktonic crustaceans that are extremely abundant in oceans and lakes. These small (usually a few millimeters long) shrimp-like animals are a very important link in marine food chains (see Russell-Hunter, 1970; Cushing, 1975). Many copepods feed on unicellular plants such as diatoms and dinoflagellates. These copepods are in turn eaten by carnivorous zooplankton and small fish. Thus copepod feeding is ecologically important in a number of ways. Copepods can markedly influence not only the abundance, but also the size- and species-composition, of the phytoplankton by grazing on some species of these small plants more heavily than on others (e.g. Porter, 1977; Richman _et al._, 1977; McCauley and Briand, 1979). Conversely, the abundance and composition of the phytoplankton can have important effects on the growth or

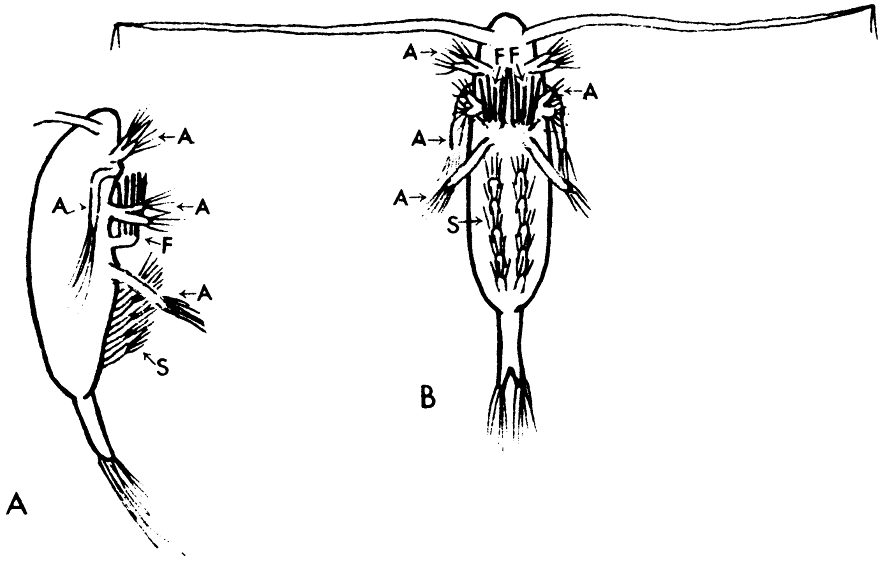


Fig. 1. Side (A) and ventral (B) views of a calanoid copepod. The filters are indicated by "f", the feeding appendages by "a" and the swimming legs by "s".

decline of populations of various species of copepods (e.g. Mullin and Brooks, 1970; Harris and Paffenhöffer, 1976; Daag, 1977; Checkley, 1980) which in turn affect the animals of higher links in the food chain. Furthermore, copepod feeding is of ecological importance because copepods remove from the water not only phytoplankton, but also particulate matter such as detritus, fecal pellets, and spilled oil (e.g. Paffenhöfer and Strickland, 1970; Conover, 1971).

The Copepod Feeding Controversy

In spite of the tremendous ecological importance of copepod feeding, the mechanisms by which these animals capture particles are 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 20 to 80 Hz, and due in part to the non-intuitive nature of viscous water flow around small objects.

Until recently, information about copepod feeding came mainly from microscope observations of feeding currents produced by copepods in drops of water and from laboratory experiments in which the rates at which copepods removed food particles from volumes of water was determined. A copepod was thought to flap four pairs of legs ("feeding appendages", Fig. 1) to create a current of water, part of which was shoved continuously through the bristles on another pair of legs ("filters", Figs. 1 and 2) that were held stationary over the mouth. Copepods tend to graze on large particles more heavily than small ones (e.g. Marshall, 1973; Frost, 1977); it has been suggested that such "size-selective" feeding is due to the spacing of barbs ("setules") on the bristles ("setae") of the filters, which act like passive sieves (e.g. Nival and Nival, 1976; Boyd, 1976). However, copepods show a plasticity of selective feeding behavior that is difficult to explain if they simply sieve particles out of the water (e.g. Poulet and Marsot, 1978; Cowles, 1979; Donaghay and Small, 1979; Richman *et al.*, 1980). Therefore, a controversy exists in the literature as to whether copepod selective feeding is due to the physical properties of the animals' sieve-like filters, or rather is due to active choice by the animal (see, for example, "The Copepod Filter-Feeding Controversy" in Kerfoot, 1980).

A Plea to Theoreticians

In this symposium on mathematical questions in biology, I would like as a biologist to pose a number of questions about copepod feeding to mathematicians. I will first describe the new picture we are now working out about how copepods feed, and I will then mention some of the physical constraints on feeding by such small animals. I will point out a number of problems about copepod feeding that need theoretical work. My hope is that some mathematicians will find these problems amusing enough to tackle.

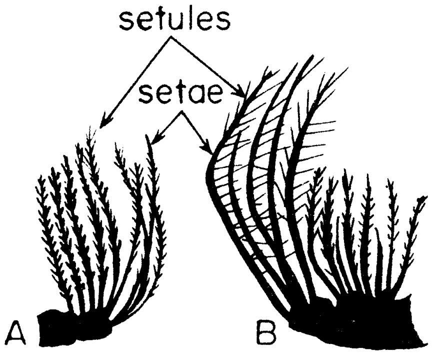


Fig. 2. Sketches of filters from two different species of copepods that can feed on algal particles.

KINEMATICS OF COPEPOD FEEDING

It has recently become possible to make high-speed (500 frames$\cdot$s^{-1}) close-up (resolution of 5 μm) movies of copepods in relatively large vessels (120 ml) of water, where artefacts in flow patterns due to confining the animals in small drops of water can be minimized (Alcaraz et al., 1980; Koehl and Strickler, 1981). A copepod in a large vessel can be kept in the field of view of the microscope for filming by holding the animal on a "leash" (i.e. gluing the animal to a fine hair that can be positioned by a micromanipulator). Such films of feeding copepods show the complexity of the appendage movements that create water currents that carry food towards the filters. The films also reveal that the filters are not always held stationary, but rather periodically actively capture parcels of water containing food particles.

To study the water motion produced by the feeding appendages of one species of copepod, Eucalanus pileatus, we marked water near feeding animals with dye released from a micropipette (Koehl and Strickler, 1981). The kinematics of copepod flapping and water movement was worked out by frame-by-frame analysis of high-speed movies of the appendage and dye stream positions. The sequence of events during one cycle of flapping is diagrammed in Fig. 3. Note that water is not pumped through the filters when they are held still. Rather, the flapping of the four pairs of feeding appendages produces a stream of water that moves past the copepod. Low-magnification high-speed movies of untethered copepods showed that they move upwards (anteriorly) at velocities of about 1.5mm$\cdot$s^{-1} when they flap their feeding appendages.

Our movies of dye streams also revealed the water motion produced by particle-capturing movements of the filters (Fig. 4). When an alga is carried into the vicinity of the copepod, the feeding appendages beat assymetrically, redirecting the incoming current so as to draw in water preferentially from the direction of the alga. (If the copepod were not on a leash, this assymetrical flapping would turn the animal towards the alga.) As the alga nears the filters, they fling apart in a manner similar to the vortex-creating "fling" of insect wings (Weis-Fogh, 1973). This fling creates a gap between the filters that is filled by inrushing water (Fig. 4,A and B). This water carries the alga within the basket formed by the filters, which then rapidly close over the alga and water. While the filters are closing, the water (having no other escape route) is squeezed out between the setae of these appendages. Water does not escape out the front of the filters as they close because certain of the feeding legs located in front of the filters are pushing rearward while the filters close. Captured particles are scraped off the filters and shoved into

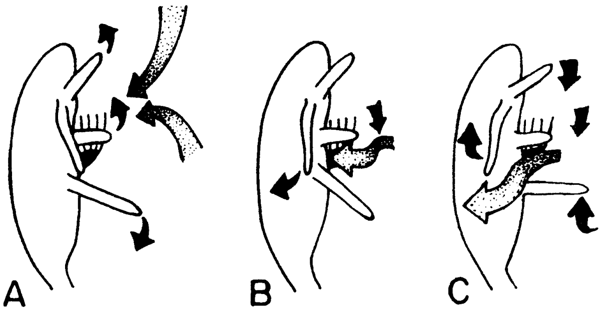


Fig. 3. Diagrams of feeding appendage movements of a copepod (black arrows) and the water currents (stippled arrows) they produce as revealed by high-speed movies of dye streams around feeding *Eucalanus pileatus*. An arrow with a narrow shaft and wide head indicates lateral movement out of the plane of the page towards the reader; an arrow with a wide shaft and narrow head indicates medial movement away from the reader. The filter is shown in black. (A) Outward movements of the indicated appendages suck water towards the copepod's filter. (B) Postero-medial movements and dorsal-lateral movement of the indicated appendages suck water laterally. (C) Inward movements of three pairs of appendages coupled with dorso-lateral movement of the fourth pair shove water postero-laterally.

the mouth by special comb-like structures on one of the pairs of feeding appendages.

Thus, high-speed films of water movement near feeding copepods reveal that these important herbivores propel water past themselves by flapping their feeding appendages ("scanning"), and actively capture small parcels of that water that contain food particles by flinging and closing their filters. The films also reveal that copepods stop scanning from time to time to go through an elaborate procedure of cleaning their feeding appendages, and that copepods regularly stop moving all their appendages and sink at velocities of 1 to 2 $mm \cdot s^{-1}$ (Koehl and Strickler, 1981).

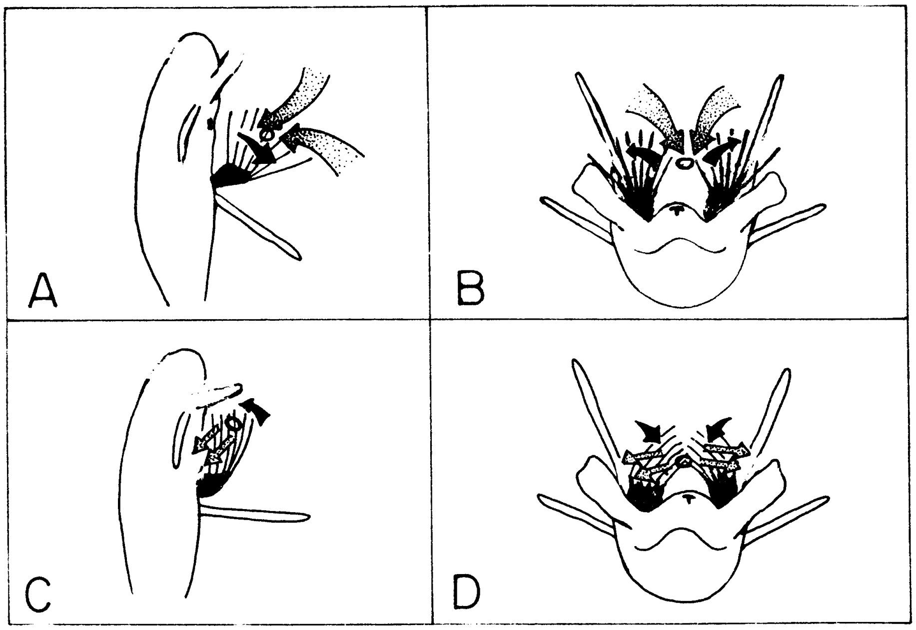


Fig. 4. Diagrams of the filter movements (black arrows) of a copepod and the water currents (stippled arrows) they produce. The filters are shown in black; the pair of feeding appendages just anterior to the filters have been omitted for clarity. The circle indicates the position of a particle being captured. The animal is viewed from its right side in A and C, and from its head end in B and D. The alga is captured by an outward fling (A and B) and inward sweep (C and D) of the filter, as described in the text.

COPEPODS LIVE IN A STICKY WORLD

In order to analyze the feeding of copepods, one must consider what the physical world is like for an organism that small. What sorts of forces are most important to a copepod trying to flap its feeding appendages?

A copepod's appendages are solid objects moving through water. Consider the basic Navier-Stokes equation describing the forces (F) affecting the motion of a Newtonian viscous fluid,

$$F_{\text{pressure}} + F_{\text{viscous}} = F_{\text{inertial}},$$

or

$$-\frac{\partial p}{\partial x} + \mu \frac{\partial^2 v}{\partial y^2} = \rho \frac{\partial v}{\partial t} + v \frac{\partial v}{\partial x},$$

where p is pressure, μ is the viscosity and ρ is the density of the fluid, and v is velocity in the x direction. If this equation is put into dimensionsless form by letting $x' = x/L$, $y' = y/L$, $v' = v/V$, $t' = Vt/L$, and $p' = p/\rho V^2$, then

$$-\frac{\partial p'}{\partial x'} + \frac{1}{Re}\left(\frac{\partial^2 v'}{\partial y'^2}\right) = \frac{\partial v'}{\partial t'} + v' \frac{\partial v'}{\partial x'},$$

where L and V are characteristic length and velocity respectively, and

$$Re = \frac{\rho V L}{\mu}.$$

This physical parameter Re, known as the "Reynolds number", represents the ratio of inertial to viscous forces for a particular flow situation. If a disturbance is produced in a stream of fluid, it will tend to persist if inertial forces predominate. Thus, for organisms operating at high Reynolds numbers (i.e. for large, rapidly-moving organisms) the world is a turbulent place. In contrast, at low Reynolds numbers any disturbance in the fluid tends to be damped out by the viscous resistance of the fluid to undergoing shear deformation. Hence, flow around small, slowly-moving organisms tends to be laminar (i.e. the fluid movies smoothly around the body and can be considered as moving in layers between which there is no significant mixing.)

Are copepod feeding appendages and filters small enough to be operating at low Reynolds numbers?

The Reynolds numbers calculated for maximum velocities attained by distal setae on various feeding appendages and on the filter during its fling range between 10^{-2} and 10^{-1} for E. pileatus (Koehl and Strickler, 1981). Even these maximum Reynolds numbers are very low, indicating that inertial forces are relatively unimportant to these copepods when they are feeding. To get a feeling for what the world might be like for a feeding copepod, imagine trying to remove crumbs from olive oil using forks moving no faster than half a millimeter per second -- also a flow situation with a Reynolds number of 10^{-2}. The constraints that such viscous flow put on copepod feeding are not intuitively obvious to us high Reynolds number humans.

A number of features of low Reynolds number flow, which have been considered quantitatively (e.g. Happel and Brenner, 1965; White, 1974; Weinbaum, this symposium), and which have been described qualitatively for copepods (Koehl and Strickler, 1981), should be kept in mind when copepod feeding is analyzed.

Laminar Flow

In the viscous, low Reynolds number world of a copepod, water flow is laminar. By repositioning our dye-releasing micropipette with respect to tethered copepods, we have shown that water streams from different locations are moved around the copepod along different discrete smooth paths. 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 should not mix together the water around it and thus should not confuse the direction from which chemical signals in the water are coming.

Water Flow Around Setae

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 surrounding the object and subject to shear deformation is thick relative to the dimensions of the object. Furthermore, at low Reynolds numbers when inertial effects can be ignored, the resistance to the motion of water between two objects depends upon the rate at which the water is deformed in shear; the closer together the objects are, the greater the shear deformation rate (and therefore the resistance) will be of water forced to move between them at a given flow rate. Thus, although copepod appendages with their long setae (Fig. 1) look like open rakes, perhaps they behave more like solid paddles through which water does not flow.

A rough estimate of whether or not water is likely to flow through the gaps between setae of a copepod appendage can be made by comparing half the distance between two neighboring setae (s) with the thickness of the boundary layer that would form around a solitary seta. Ellington (1975) has used this approach for bristled insect wings. The thickness of the boundary layer (δ) around a cylindrical seta can be estimated by

$$\delta = O\left(\frac{d}{(Re)^{1/2}}\right)$$

where d is the diameter and Re the Reynolds number of the cylinder. When copepod feeding appendages flap to create the scanning currents, δ>s (Koehl and Strickler, 1981). This is consistent with our observations that little water moves through the gaps between setae on these appendages (Fig. 5). Similarly, δ>s for the setae of the stationary filters when the feeding appendages flap and produce a water stream over the filters. Remember that dye is observed to bypass rather than flow through the stationary filters (Fig. 3). However, when the filters actively capture algae, δ is the same as or slightly lower than s (Koehl and Strickler, 1981). The capturing motions of the filters are more rapid (δ becomes thinner as velocity is increased) and the s's are greater than they are for the setae of the feeding appendages.

Of course water can be forced to move through the narrow gaps between setae if given no other escape route. For example, when the setae of the filters rapidly close over a parcel of water that they have actively captured, water is observed to be squeezed out between the setae (Fig. 4, C and D). Since the closely-spaced setae of the filters should offer a great deal of resistance to flow, such a motion might be metabolically costly. Therefore, it makes sense for an animal only to force water through the filters when an algal cell is there, as they do.

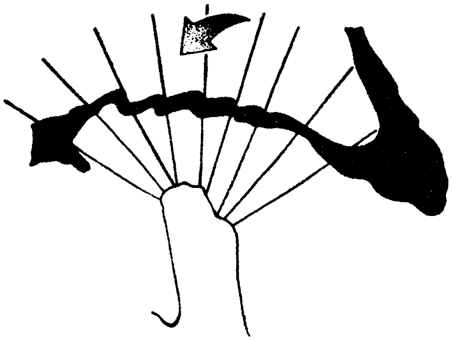


Fig. 5. Diagram of a feeding appendage moving towards the reader as indicated by the arrow. Note that the black dye stream does not flow between the setae.

PROBLEM: What is the cost of driving water through the filters of a copepod? How does this vary with changes in the morphology and kinematics of the filters? The metabolic cost (energy per time) for an animal to drive water through its filters should be a function of the resistance those filters offer to the flow of water. Resistance is the pressure drop (Δp) across a filter for a given flow rate (Q, volume per time) of water through the filter. Various theoretical and empirical approaches have been used to determine the resistance of filters composed of cylindrical fibers to the flow of fluid through them (for example, see reviews by Fuchs, 1964; Pich, 1966; Davies, 1973). The problem is more complicated in copepods because: a) the tips of the setae (fibers) of the filters move more rapidly than do their attached ends, b) the gaps between setae are greater at their distal than at their proximal ends, and c) the gaps between setae change with time (they become smaller as the setae close over the captured water).

The structure of copepod filters varies from species to species (Fig. 2) and also changes as animals grow and mature. How do changes in the length, diameter, and spacing of setae affect costs of driving water through the filters?

Members of different species of copepods move their filters at different velocities. For example, filter setae of *Eucalanus pileatus* close over captured water at maximum velocities of about 20 $\text{mm}\cdot\text{s}^{-1}$ ($Re = 8 \times 10^{-2}$), whereas those of *Centropages typicus* do so at about 300 $\text{mm}\cdot\text{s}^{-1}$ ($Re = 1$) (Koehl and Strickler (1981). For which copepods is this motion more expensive? It should be pointed out that for filters operating at low Reynolds numbers in purely viscous flow, $\Delta p/Q$ is constant, whereas for filters operating at intermediate Reynolds numbers (of the order of 10^{-1} to 10^{1}) where flow is laminar but inertial effects cannot be ignored, $\Delta p/Q$ rises as Q rises (Davies, 1973).

How do the setules (barbs) on the filter setae (Fig. 2) affect the resistance of the filter? As a first approximation, can they be considered as simply increasing the effective diameter of the setae?

Water Flow Around Setules

Biologists have thought that water flows between the setules on the setae of copepod filters and that particles larger than the gap between the setules are sieved out of the water. However, water no doubt resists flowing between these closely-spaced setules on setae. The setae of copepod filters, covered with rows of setules and the water stuck to them, may well be functionally wide and smooth rather than comb-like. Rees (1975) has found that the corrugated wings of insects operating at low Reynolds numbers are functionally thick and smooth in this way.

PROBLEM: What is the flow field like at low Reynolds numbers around a cylinder (a seta) with smaller cylinders (setules) sticking out of it? How is the flow field affected by: a) the position and number of the setules relative to the flow direction (Fig. 6); b) the diameter and length of the setules relative to the diameter of a seta; c) the spacing of setules along the length of a seta; and d) the proximity of other similar setae bearing setules?

Fig. 6. Cross-section of a seta (O) with setules (▮). The arrow indicates flow direction. Some examples of possible setule arrangements are shown.

The "Sphere of Influence" of a Food Particle

We have observed copepods to flap assymetrically the appendages that create the scanning current, thereby drawing in water preferentially from the direction from which an alga is arriving (i.e. turning towards the alga). We have also observed copepods to fling apart their filters when an alga is a distance of a few hundred micrometers from them. Do copepods use mechanical or chemical cues to perceive food particles?

PROBLEM: 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, 1975b; Strickler and Bal, 1973), and feeding experiments reveal that copepods can capture inert particles (e.g. Wilson, 1973; Poulet, 1976). Furthermore, behavioral studies indicate that various small planktonic animals feel the presence of walls and other zooplankton in the water around them (Lillelund and Lasker, 1971; Strickler, 1975b; Kerfoot *et al.*, 1980; Zaret, 1980). At low Reynolds numbers objects affect the movement of fluid many diameters away from themselves (e.g. Happel and Brenner, 1965; White, 1974; Weinbaum, this symposium). How would the flow field produced by a copepod (which can be described empirically) be distorted by particles of a) different sizes moving at b) different velocities at c) different distances from the animal?

PROBLEM: Can copepods smell nearby food particles? The algal cells and other small particles on which copepods feed swim or sink (Eppley *et al.*, 1967) slowly through the water at Reynolds numbers of the order of 10^{-5} to 10^{-3}. Therefore these particles are no doubt surrounded by relatively thick boundary layers of water. If the food particles exude chemicals into the water around them, it is likely that they are surrounded by spheres of odor much larger than themselves. What is the distribution of concentrations of a chemical leaked by and diffusing away from an algal cell as it sinks or swims through the water? How is the shape of such a field of odor distorted as it moves through the flow field created by a copepod?

Morphological studies indicate that copepods have chemoreceptors (e.g. Fleminger, 1973; Friedman and Strickler, 1975). Chemosensation has been demonstrated in other crustaceans (e.g. Ache, 1972; Hamner and Hamner, 1977) and does appear to be involved in copepod mate-finding (e.g. Griffiths and Frost, 1976; Blades and Youngblath, 1980). Some feeding experiments indicate that copepods can preferentially feed on certain particles on the basis of their smell (e.g. Mullin, 1963; Poulet and Marsot, 1978), although it has not yet been demonstrated whether such selective feeding is due only to rejection of certain particles after they have been captured, or is due also to preferential capture of particular food.

Do scanning currents increase the amount of chemical information a copepod can receive from its environment? If diffusion of molecules is considered in the x direction only, the rate of change of concentration of molecules with time at a fixed distance from the source of the molecules is

$$\frac{\partial c}{\partial t} = D \frac{\partial^2 c}{\partial x^2} ,$$

where c is the concentration of the molecules and D is the diffusion coefficient (D is generally of the order of $10^{-5} m^2 \cdot s^{-1}$ for molecules diffusing in water). Thus the time required for a molecule to diffuse a distance (a) through water is roughly $a^2/D = a^2 \times 10^5$, whereas the time to transport a molecule that distance by moving the water in which it sits is roughly a/v, where v is the velocity at which the water is moving (Purcell, 1977). Thus, at the velocities of scanning currents created by flapping copepods (about 10 $mm \cdot s^{-1}$ in the vicinity of the animal (Koehl and Strickler, 1981)), flapping should allow them to smell things at distances of 0.1 μm or greater sooner than they would if they held still and waited for molecules to diffuse to them. For example, it takes about 100x longer for a molecule to diffuse to a copepod that is holding still from a distance of 100 μm as it does for that molecule to be transported to the animal when it is flapping.

Can a flapping copepod receive chemical information about the location of food particles in the water around it? Recall that streamlines around a scanning copepod are not mixed together. For a copepod creating a scanning current of 10 $mm \cdot s^{-1}$, I estimate that molecules might diffuse only about 4 μm out of a streamline while the water moved a distance of 200 μm past the animal. Thus, chemoreceptors on the appendages of a copepod closer to that particular streamline might well receive more molecules from a food particle in that streamline than would chemoreceptors on the other side of the animal. These crude estimates indicate that it might be possible for a copepod to receive chemical information about the location of a food particle, but a more rigorous analysis is needed.

Theoretical approaches have been used to analyze chemoreception by organisms such as bacteria (Berg and Purcell, 1977) and moths (Murray, 1978). Mathematical analyses could also shed light on questions of copepod chemoreception.

Producing Water and Particle Movement at Low Reynolds Number

Since an appendage on a copepod operating at low Reynolds number influences a thick layer of water around itself, particles move away when the appendage moves towards them (Fig. 7, A). Thus, a copepod appendage cannot strain a particle out of the water as we might catch a ball using a scoop net. Copepods, rather, must maneuver particles by moving the water surrounding the particles, as they do during the capture "fling" of the filters (Fig. 4, A and B). Furthermore, when moving at low Reynolds number, it is difficult to leave water behind. For example, a copepod appendage moving away from an alga drags the alga along (Fig. 7, B).

Since inertial effects are small at low Reynolds number, when a copepod stops flapping its feeding appendages, the flow around it stops almost immediately. For example, dye spots carried in scanning currents "coasted" only 40 to 50 μm to a halt within about 30 ms of the time copepods stopped flapping their feeding appendages (Koehl and Strickler, 1981). At very low Reynolds numbers, when inertia can be ignored and when things don't coast, an organism that simply flapped its appendages back and forth symmetrically with a fast "power stroke" and a slow "recovery stroke" would move water back and forth along the same path rather than pushing it in some net direction (Purcell, 1977). How do copepods, whose feeding currents only coast very slightly, overcome this near reversibility of flow in

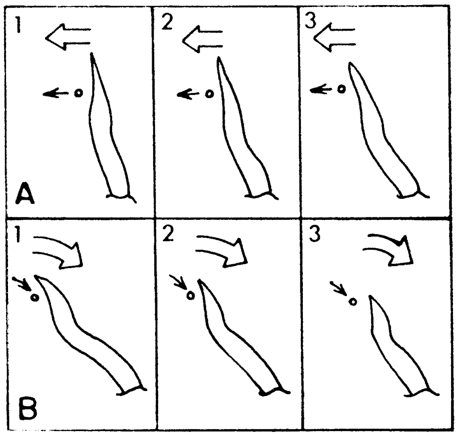


Fig. 7. Tracings of frames of a film of a copepod appendage and an alga. The time interval between pictures is 6 ms. A. An alga being "pushed" by the appendage. B. An alga "following" the appendage.

space and time and propel water past themselves in some net direction? Copepod feeding appendages follow complex, assymetrical paths such as figure-eights when they flap. Furthermore, appendages can change their shape during a cycle of movement. For example, the setae on some appendages are more flexible in certain directions than in others so that at particular points during a flap they are straightened and spread out, whereas at others they are collapsed and bent over. In addition to these complexities of behavior of individual appendages, the various pairs of feeding appendages flap in different planes. Although these appendages flap at the same frequency, they flap out of phase with each other, thereby sucking water in and then pushing it out from between them (Fig. 3). Clearly the qualitative description given above of how copepods produce scanning currents should be replaced by a quantitative analysis of the fluid dynamics of this process.

PROBLEM: What are the mechanisms by which the movements of copepod feeding appendages produce the water flow patterns we observe? Is circulation set up around a copepod appendage as it is around the wing of a tiny insect (Weis-Fogh, 1973)? How do the feeding appendage movements together produce the net scanning current we observe? Are the mechanisms used to propel water by larger, faster copepods for whom inertial effects are more important likely to be different from those used by smaller copepods? How do the size and velocity of the filters during the capture fling affect the distance over which they capture water?

PROBLEM: What is the cost for a copepod of creating the scanning current? As mentioned above, a scanning copepod in the orientation depicted in Fig. 3 moves upwards slowly; when it stops scanning, it sinks slowly. Scanning is therefore somewhat analogous to hovering flight. Perhaps the theoretical approaches that have been used to analyze the flow around and power requirements of a small hovering insect (e.g. Ellington, 1978) could be usefully applied to a scanning copepod.

PARTICLE CAPTURE BY THE FILTERS

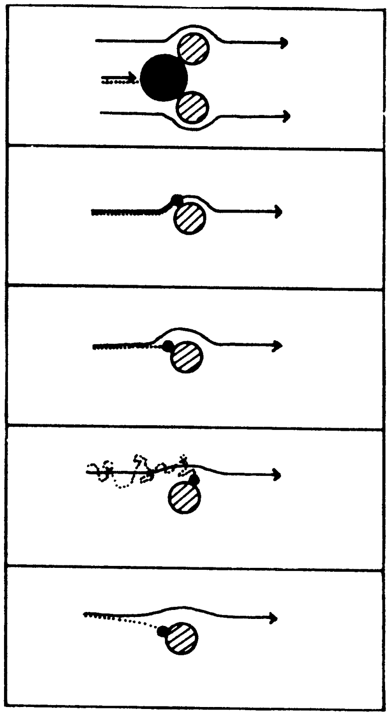
Although there has been considerable speculation in the literature about the processes by which the selective feeding of copepods occurs, the actual mechanisms involved have not been demonstrated. Based on our new understanding of how copepods feed, it can be suggested that selective feeding could depend upon the chemical or mechanical cues for which a copepod flaps assymetrically or flings its filters, as discussed above. Copepod selective feeding could also depend upon the physical characteristics of particles retained within the basket formed by the filters as they close over a parcel of captured water. Correlations have been noted between the types of food selectively eaten by various species of copepods and the morphology of their filters (e.g. Itoh, 1970; Boyd, 1976; Nival and Nival, 1976; Richman et al., 1980); it has therefore been suggested that copepods capture only particles bigger than the gaps between setules on the setae of their filters (e.g. Boyd, 1976).

Filters are Not Just Sieves

The physical mechanisms by which filter feeding organisms remove particles from the surrounding water are poorly understood. Biologists generally assume that filters act as sieves that only capture particles larger than the spaces between neighboring fibers composing the filter. Rubenstein and Koehl (1977) have applied to biological filters the theoretical analysis of filtration developed by engineers (for reviews, see Fuchs, 1964; Dorman, 1966; Pich, 1966; Davies, 1973); 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 screens (Sheldon and Sutcliffe, 1969) and copepod filters (Friedman, 1980) have been reported to retain particles from natural waters that are smaller that the "pore size" of the filters. Furthermore, experimental studies indicate that this filtration theory is applicable to other particle-capturing organisms such as brittle stars (LaBarbera, 1978), sea anemones (Koehl, unpubl. data), and protozoans (Fenchel, 1980). Murray (1978) 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).

PROBLEM: How do the morphology and kinematics of copepod filters affect the types of particles they selectively capture? The mechanisms by which filters capture particles are described by Rubenstein and Koehl (1977) and are illustrated in Fig. 8: sieving, direct interception, inertial impaction, gravitational sedimentation, and motile-particle or diffusion deposition. One can predict using certain physical characteristics of a filter, particles, and fluid flow, which of these mechanisms of particle capture are operative for a given filtration situation (see 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 sedimentation, 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



sieving

direct interception: $N_I = d_p/d_f$

inertial impaction:

$$N_I = [(\rho_m)d_p^2 V_o] /18\mu d_f$$

diffusion or motile-particle deposition:

$$N_M = \frac{KT}{d_p} \frac{1}{3\pi\mu V_o d_f}$$

gravitational sedimentation: $N_G = v_g/Vo$,

where $v_g = [d_p^2 g(\rho_p - \rho_m)] /18\mu$

Fig. 8. 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. (Reprinted from D. I. Rubenstein and M. A. R. Koehl, Amer. Natur., 1977, Vol.111, pp. 981-984, by permission of the University of Chicago Press. © 1977 by the University of Chicago. All rights reserved.)

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_o = upstream velocity of the fluid relative to the 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

which the efficiency of capture by the simultaneous action of all mechanisms reaches a minimum. ("Filtering efficiency" is defined as the ratio of the number of particles striking a fiber in a filter to the number that would strike it if the flow streamlines were not diverted by it (Dorman, 1966).) 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.

As mentioned above, the morphology (see Fig. 2) and kinematics of copepod filters can vary considerably from species to species of copepod. A model of copepod filters that would allow particle selectivity to be predicted from the structure and movement of such filters would be extremely useful to biologists.

PROBLEM: How can a copepod change the size of particles on which it selectively feeds? Feeding experiments indicate that copepods can alter the size range of particles that they preferentially capture (e.g. Cowles, 1979). If a copepod's second maxillae are considered only as sieves, it appears that the animal can change the size of particles on which it feeds only by changing the spacing between the fibers of these filters. Copepod setules are fixed structures whose spacing on setae cannot be actively altered (and which may well be hidden in the boundary layer around setae). Filtration theory indicates several other means by which a copepod might alter its diet. For example, by changing the velocity of water passing through the filters, or by altering the diameter or adhesiveness (with mucus?) of the setae, the range of particle sizes that can be captured most efficiently by the filter can be shifted. Price and Paffenhöfer (pers. comm.) have noted that copepods move their filters differently when feeding on very small (<7 μm) algae than they do when feeding on larger algae. It would be useful to be able to predict how such differences in movement would affect the size range of particles most efficiently captured by a copepod's filters.

PROBLEM: How do the morphology and movement of copepod filters affect their effective filter area? The area of a filter through which water actually passes should decrease as the variability of the spacing between fibers in the filter increases (because water tends to flow through the wider spaces and to avoid the narrower ones). The spacing between and velocity of copepod setae both increase along the length of the setae from base to tip, as does the length and density of setules on the setae. How do these features interact to affect the volume flow rates of water through different areas of filters of various species of copepods?

OPTIMAL FORAGING MODELS FOR COPEPODS

Several optimal foraging models have been proposed to predict the size-selective feeding behavior of copepods (e.g. Lam and Frost, 1976; Lehman, 1976). Those models are based on the assumption that copepods are simple on-off filter feeders (i.e. when they flap their feeding appendages, they continuously drive water through their sieve-like filters). Now that we know the complex repertoire of behaviors used by feeding copepods, new foraging models should be developed based on more realistic assumptions. Copepods create scanning currents ("search"), fling and close their filters ("capture"), comb particles from the filters into the mouth ("handle"), and cease flapping and thus sink ("rest"). Copepods can also rapidly locomote through the water be flapping their swimming legs (Fig. 1) (Vlyman, 1970; Strickler, 1975a; Lehman, 1977). Both sinking and swimming may be involved in predator avoidance and both behaviors may also move copepods to new food envirionments. If reasonable estimates of the power requirements (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 food conditions could be assessed (as Cowles and Strickler (pers. comm.) and Price and Paffenhöfer (pers. comm.) are now doing empirically), then more realistic foraging models could be developed. Before the complexity of copepod behavior had been directly observed, Haurey and Weihs (1976) used such an approach to model how a copepod should apportion its time between sinking and swimming to maintain a position in the water column at minimum cost.

CONCLUSIONS

Although copepod feeding is extremely important ecologically, the mechanisms by which it occurs are poorly understood. Controversies rage in the literature about how copepods feed selectively. Now that we can use high-speed microcinematography to work out the kinematics of copepod feeding, and now that we are aware of the non-intuitive nature of low Reynolds number water flow around these tiny animals, we can pose a number of questions about copepod feeding mechanisms that require mathematical analyses. This field of biological research would certainly be advanced at this stage by the contributions of theoreticians.

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