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Limnology and Oceanography, Vol. 26, No. 6 (Nov., 1981), 1062-1073.

Stable URL:
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Limnology and Oceanography is currently published by American Society of Limnology and Oceanography.

Limnol. Oceanogr., 26(6), 1981, 1062–1073

Copepod feeding currents: Food capture at low Reynolds number[1]

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Abstract

High-speed motion pictures of dye streams around feeding calanoid copepods revealed that these important planktonic herbivores do not strain algae out of the water as previously described. Rather, a copepod flaps four pairs of feeding appendages to propel water past itself and uses its second maxillae to actively capture parcels of that water containing food particles. The feeding appendages of *Eucalanus pileatus* operate at Reynolds numbers of only 10^{-2} to 10^{-1}. In the viscous world of a feeding copepod, water flow is laminar, bristled appendages behave as solid paddles rather then open rakes, particles can neither be scooped up nor left behind because appendages have thick layers of water adhering to them, and water and particle movement stops immediately when an animal stops beating its appendages.

Calanoid copepods are abundant planktonic crustaceans that play a major role in the transfer of energy through marine food chains. Copepods are selective feeders, exhibit a plasticity of feeding behavior (e.g. Poulet 1974; Richman et al. 1977, 1980; Cowles 1979; Donaghay and Small 1979; Runge 1980; Skiver 1980), and can markedly influence the composition of phytoplankton populations (e.g. Porter 1973; Poulet 1973; McCauley and Briand 1979). In spite of the ecological importance of copepod feeding, the mechanisms by which these animals capture particles (such as diatoms and flagellates) have been poorly understood due to the technical difficulties involved in observing feeding appendages only fractions of a millimeter long that are moving at rates of 20–80 Hz.

Until now, descriptions of copepod feeding have been based on careful microscope observations of currents produced by copepods in drops of water (e.g. Cannon 1928; Storch 1929; Marshall and Orr 1955). The "textbook description" (e.g. Russell-Hunter 1979; Barnes 1980) of copepod feeding based on such observations is basically as follows: The beating of the feeding appendages (labeled in Fig. 1A) pushes water postero-laterally, forming a large swirl on each side of the animal (Fig. 1B). Some of this swirling water is sucked antero-medially by the outward swing of the maxillipeds. The inward swing of the maxillipeds then pushes water between the setae and setules (bristles on the setae) of the second maxillae, which sieve particles out of the water. The filtered water is then expelled anteriorly by the first maxillae, and the captured food is transferred to the mouth by the endites of the first maxillae. We suspected that the recirculating swirls were artifacts of the small volume of water in which the observed copepods were immersed. Furthermore, we were puzzled by water flowing between the closely spaced setae and setules of the stationary second maxillae rather than flowing around them along the paths of least resistance.

Attempts to analyze the feeding behavior of calanoid copepods have been based on the concept that they feed by sieving, as described above. For example, several analyses of size-selective feeding by copepods have focused on the spacing of the setules on the setae of the second

[1] This work was supported by grants from the Natural Sciences and Engineering Research Council of Canada, the National Science Foundation (OCE76-01142), and the University of California, Berkeley (Committee on Research).

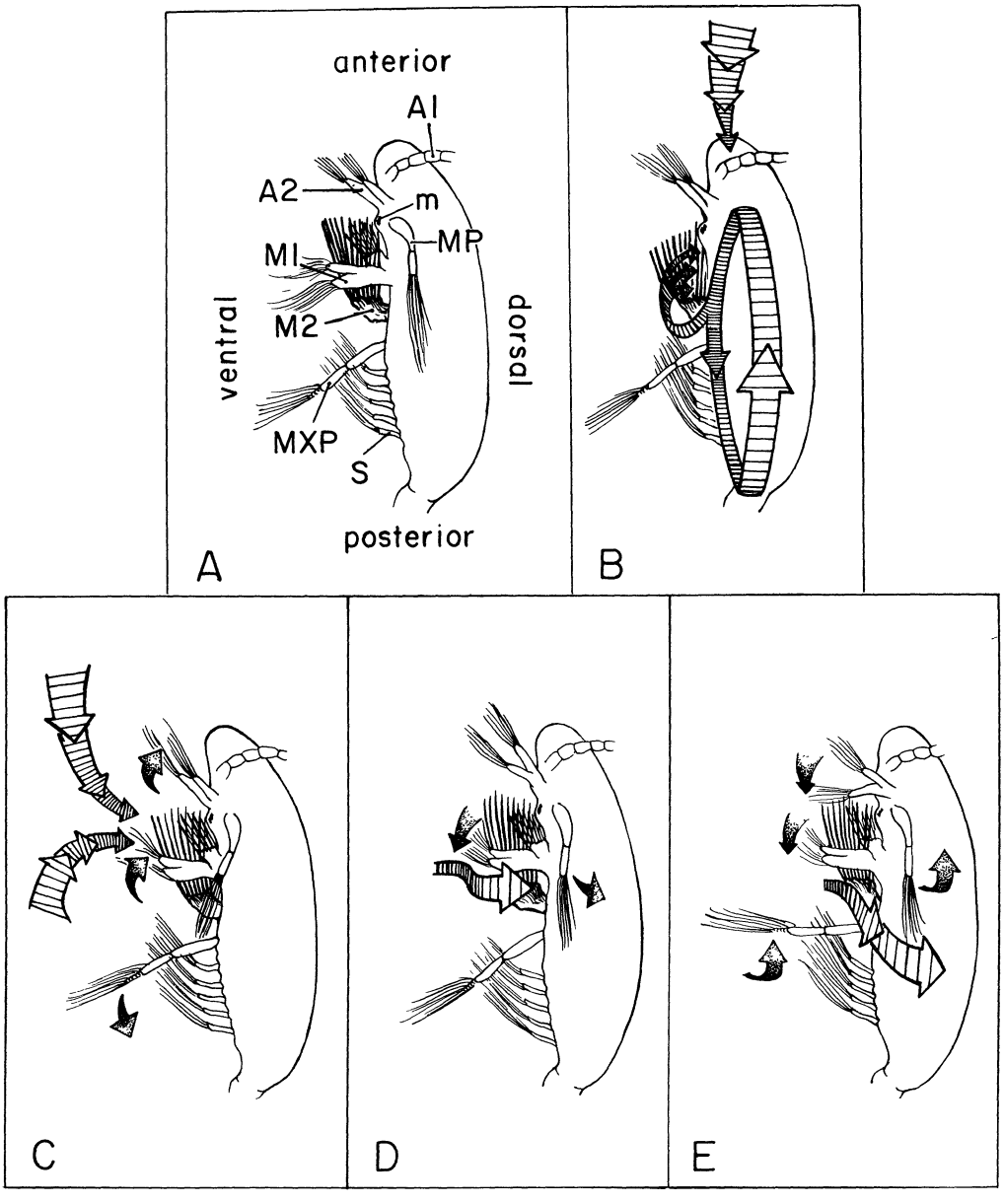

Fig. 1. *Eucalanus pileatus*. A. Diagram of an animal in typical feeding position viewed from its left side. Only left appendage of each pair is shown. Feeding appendages are: A2—second antenna; MP—mandibular palp; M1—first maxilla; M2—second maxilla; MXP—maxilliped. Other structures labeled are: A1—first antenna; S—swimming legs; m—mouth. Structure of appendages has been grossly simplified for clarity. B. Diagram of "textbook version" of copepod feeding currents (wide arrows) drawn from information presented elsewhere (Cannon 1928; Lowndes 1935; Marshall and Orr 1955; Russell-Hunter 1979; Barnes 1980). C–E. Diagrams of feeding appendage movements (stippled arrows) and water currents (striped arrows) they produce as revealed by our films. An arrow with a narrow shaft and wide head indicates lateral movement out of the plane of the page toward the reader; an arrow with a wide shaft and narrow head indicates medial movement away from the reader. C. Outward movements of second antennae and maxillipeds sucks water toward copepod's maxillae. D. Postero-medial movement of the first maxillae and dorso-lateral movement of mandibular palps sucks water laterally. E. Inward movements of second antennae and maxillipeds coupled with dorso-lateral movement of mandibular palps shoves water postero-laterally.

maxillae (e.g. Boyd 1976; Nival and Nival 1976; Frost 1977). Similarly, models of copepod foraging have been based on the assumption that when an animal is feeding, water is passed continuously through its maxillary filter (Lam and Frost 1976; Lehman 1976).

Recent use of high-speed microcinematography to study copepod feeding has revealed the complexity of appendage movements that create water currents which carry food toward the second maxillae (Alcaraz et al. 1980). This study showed that the second maxillae are not always held stationary, but rather periodically actively capture parcels of water containing algal cells, which are then pushed into the mouth by the endites of the first maxillae. The high-speed films also revealed that algal cells are usually redirected without actually being touched by the feeding appendages.

We thank G.-A. Paffenhöfer and T. J. Cowles for discussion and encouragement, and for providing us with healthy copepods tethered in cuvettes with the appropriate algae. We also thank L. Cahoon, D. Crenshaw, T. Daniels, M. Denny, M. LaBarbera, P. Pressley, W. Sousa, and three reviewers for comments, and P. Thompson for help with illustrations.

Methods

Movies at 500 frames·s^{-1} with a resolution of 5 μm were made of calanoid copepod feeding appendages by using the optical apparatus described by Alcaraz et al. (1980). Information presented here was gathered from 27 movies (30.5 m each) of four adult females of *Eucalanus pileatus* and of two adult females of *Centropages typicus*. The copepods were kept and filmed in seawater at 20°C ± 1° and fed dinoflagellates (either *Gymnodinium nelsoni*, 50–53 μm long, or *Prorocentrum micans*, 36–37 μm long) or diatoms (*Thalassiosira weissflogii*, 10–14 μm long). Cultures of these algae were kept in log-phase growth in f/2 medium (Guillard and Ryther 1962) under a 12L:12D photoperiod. During filming, an animal was tethered (Haury 1976) in an optical glass cuvette containing 120 ml of filtered seawater to which algae had been added; an animal was about eight body lengths from the nearest wall of the cuvette. Food concentrations, determined with a model B Coulter Counter, are reported in Table 1. Copepods were conditioned for at least 2 h before filming by placing them in vessels of filtered seawater to which the appropriate species of algae had been added. Animals to which tethers had been glued continued to show normal swimming and feeding behavior until we preserved them several days after filming.

To study water motion produced by feeding appendages, we marked water with India ink released from a micropipette positioned by a micromanipulator at various locations about 5 mm from tethered *E. pileatus*.

Frame-by-frame analyses of the movies were made with a LW photo-optical data analyzer (model 224-A). Length measurements were made with vernier calipers. Algal cells in the plane of focus were used for length scales and distinctive nonmotile features of the copepods' bodies were used as reference points. Velocities of appendages were determined by measuring the displacement of recognizable points on the appendages that were in focus in successive frames of the films. Current velocities were determined by measuring the displacement of particles or dye blobs in the water that were in focus in successive frames. The component of velocity normal to the plane of the film is not detected by this technique; however, since the depth of focus of the films was about 0.2 mm, the maximum amount by which our measured velocities (v, mm·s^{-1}) could be underestimates of the true velocities is only of the order of $[(v^2 + 0.04)^{-2} - v]$mm·s^{-1}.

To determine the degree to which the flow patterns we made visible with ink deviated from those produced by untethered copepods, we also made high-speed (250 frames·s^{-1}) movies of freely swimming copepods and freely sinking ink streams in seawater at 20°C by the technique described by Strickler (1977). Velocities were determined by measuring

Table 1. Some representative values of velocity, Re, and δ of copepod feeding appendages (first number in parentheses is 1 SD; second is number of measurements).

Appendage	Movement type	Species [individual]	Max v (mm·s^{-1})	Re	Boundary layer (μm)*	Half-max spacing between setae (μm)*	Beat frequency (Hz)†	Species	Max v (mm·s^{-1})	Re
2nd maxilla, distal region of large seta	Noncapture	*Eucalanus pileatus* [R]	7 (1.3,5)	2×10^{-2} (3×10^{-3},5)	23 (3.0,5)	18 (6.9,5)	24 (0.5,5)	*C. typicus* [G]	(remains stationary)	
	Outward fling of algal capture	[R]	16 (9.1,4)	6×10^{-2} (19×10^{-3},4)	20 (4.1,4)	25 (13.4,4)	24 (1.0,5)	[G]	317 (12.5,2)	1 (0.7,2)
	Inward sweep of algal capture	[R]	22 (11.3,32)	8×10^{-2} (56×10^{-3},32)	14 (3,32)	18 (8.4,16)	24 (1.0,5)	[G]	319 (4.7,2)	1 (0.8,2)
	Outward movement of rejection	*E. pileatus* [T]	47 (15.6,6)	2×10^{-1} (5×10^{-2},6)	9 (1.8,6)	25 (7.6,6)	15 (3.5,5)	[G]	53 (13.0,3)	2×10^{-1} (13×10^{-2},3)
	Inward movement after injection	[T]	56 (7.0,6)	2×10^{-1} (2×10^{-2},6)	8 (0.5,6)	15 (4.9,6)	15 (3.5,5)	[G]	76 (25.0,3)	3×10^{-1} (16×10^{-2},3)
Maxilliped, middle of seta on distal segment	Regular flapping	*E. pileatus* [M]	24 (5.1,5)	1×10^{-1} (2×10^{-2},5)	15 (2.2,5)	13 (2.8,4)	19 (0,5)	[G]	39	2×10^{-1}
1st maxilla, middle of seta on distal segment	Regular flapping	[M]	15 (0.2,3)	7×10^{-2} (10×10^{-3},3)	19 (1.2,3)	12 (1.5,3)	19 (0,5)			
Maxilliped, middle of seta on distal segment	Regular flapping	*Centropages typicus* [G]	39 (0.6,4)	2×10^{-1} (2×10^{-2},4)	12 (0.8,4)	13 (5.1,4)	51 (2.3,6)			

* "Spacing" refers to distance between two setae in a plane normal to direction of movement. Spacings of setae of 2nd maxillae were measured on "head-on view" films (as in Fig. 2B, D, F). Spacing between setae on 2nd maxillae changes during a cycle of movement, hence we measured maximum spacing during portion of a cycle corresponding to portion for which velocity was measured. First maxillae and maxillipeds change orientation during a cycle of flapping, but not intersetal spacing. We therefore measure intersetal spacings when setae were in the plane of the film and velocities when they were perpendicular to it.

† Larger individuals flapped at lower frequencies. For example, maxilliped of individual M was 17% longer than that of individual R. All animals were feeding in water containing *G. nelsoni* (100 cells·ml^{-1}, 4 ppm by volume) except M and R, which were feeding in water containing *P. micans* (120 cells·ml^{-1}, 1 ppm by volume). δ values were not calculated for *C. typicus* 2nd maxillae because they would likely be gross underestimates since setules on large setae of these appendages are of the order of 40 μm long. *Centropages typicus* [G] beat her appendages at a frequency of 51 Hz (2·3,6).

the displacement of a copepod or ink from frame to frame of the film. Calipers photographed in the frame were used as reference points as well as for length scale. Dye sank at a velocity of 0.6 $mm \cdot s^{-1}$ (SD = 0.06, n = 13), considerably slower than the velocities at which water was moved by copepod appendages (*see below*). *Eucalanus pileatus* flapping its feeding appendages moved upward at velocities of only 1.6 $mm \cdot s^{-1}$ (SD = 0.18, n = 17), hence a small posteriorly directed component of water velocity of 1.6 $mm \cdot s^{-1}$ should be added to the velocity vectors we observed around tethered animals to obtain a picture of the flow around an unrestrained copepod.

Results and discussion

Appendage and water movements—The water currents produced by feeding appendage movements of *E. pileatus*, as revealed by our movies of dye streams, are diagramed in Fig. 1C–E. Note that water is not pumped through the second maxillae when they are held nearly still (Fig. 2A, B; Fig. 3A, B). Rather, the flapping of the other feeding appendages (second antennae, mandibular palps, first maxillae, and maxillipeds) produces a pulsing stream of water past the copepod. The mean of the maximum current velocities we have measured within 150 μm of the nearly stationary second maxillae of *E. pileatus* is 10 $mm \cdot s^{-1}$ (SD = 3, n = 6). A simple calculation further illustrates that these copepods do not push through the second maxillae all of the water that they scan for food: *E. pileatus* can sweep as much as 300 ml of water clear of algae in 24 h (adult females feeding at 20°C on large algal cells, 20–60-μm diameter, 1–5 $cells \cdot ml^{-1}$: Paffenhöfer and Knowles 1978). By assuming that these copepods pump water continuously through the second maxillae, that filtered water is not reprocessed, and that the second maxillae retain all the particles they encounter, we calculate that a pair of second maxillae with a 10 $mm \cdot s^{-1}$ current passing through them would have to be at least 3×10^{-1} mm^2 in area (six times larger than they actually are!) to filter 300 ml of water in a day.

Our dye streams also revealed the water motion produced by the algae-capturing movements of the second maxillae, which have been described by Alcaraz et al. (1980). When an alga is carried into the vicinity of the copepod, the feeding appendages listed above that move water past the animal beat asymmetrically, redirecting the incoming current so as to draw in water preferentially from the direction of the alga. If the copepod were not tethered, this asymmetrical flapping would turn the animal toward the alga. Paffenhöfer and Knowles (1978) have observed that *E. pileatus* can reorient itself with respect to algal chains before ingesting the chains. As the alga nears the second maxillae, they fling apart at high speed (Table 1) in a manner analogous to the vortex-creating "fling" of insect wings (Weis-Fogh 1973). This fling creates a gap between the second maxillae which is filled by inrushing water (Fig. 2C, D, Fig. 3C, D). The water carries the alga at a mean velocity of 32 $mm \cdot s^{-1}$ (SD = 7.0, n = 3) within the basket formed by the second maxillae, which then rapidly (Table 1) close in over the alga and water. Sometimes more than one fling is required to capture the parcel of water containing the alga. 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. 2E, F, Fig. 3E). Water does not escape anteriorly from the second maxillae because the second antennae and first maxillae are pushing water posteriorly at the second maxillae while they are closing. Thus, these copepods appear to scan the large volume of water that is propelled by their feeding appendages, but to force through the second maxillae only that small volume of water surrounding food particles.

We saw *E. pileatus* reject captured material by pushing the second maxillae anteriorly between the material and the body surface, by then shoving the mate-

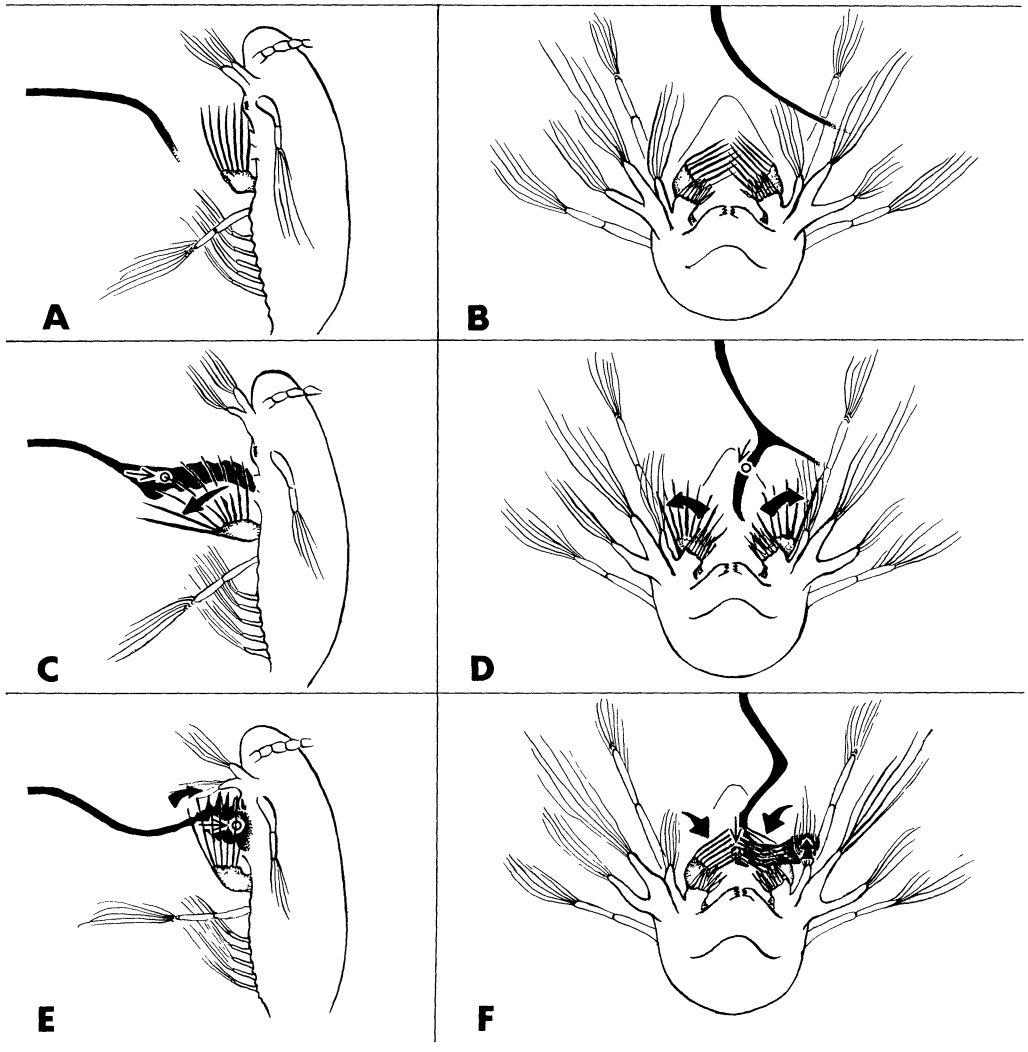

Fig. 2. Diagrams traced from high-speed films of a feeding *Eucalanus pileatus*. Black streaks are dye streams from micropipette. Heavy arrows indicate movements of second maxillae (and of a first maxilla in F). Circles represent positions of and fine arrows indicate movements of algae observed during similar appendage motions in other frames of films. In first column, copepod is viewed from its left side and first maxilla has been left off for clarity. In second column, animal is viewed from its anterior end. Feeding currents bypass second maxillae (A–B) until an alga nears them. Alga is captured by an outward fling (C–D) and an inward sweep (E–F) of second maxillae as described in text.

rial away from the body surface on closely spaced medially located setae of the second maxillae (Fig. 4A), and by then "detaching" the rejected material from the second maxillae by spreading these medial maxillary setae and expelling water between them as they rapidly move inward (Fig. 4B).

Variations of the basic pattern of scanning and capturing movements described above seem to be characteristic of different species of copepods. For example, the setae of *C. typicus* second maxillae move nearly 20 times faster than do those of *E. pileatus* during the capture fling (Table 1). Furthermore, the swimming

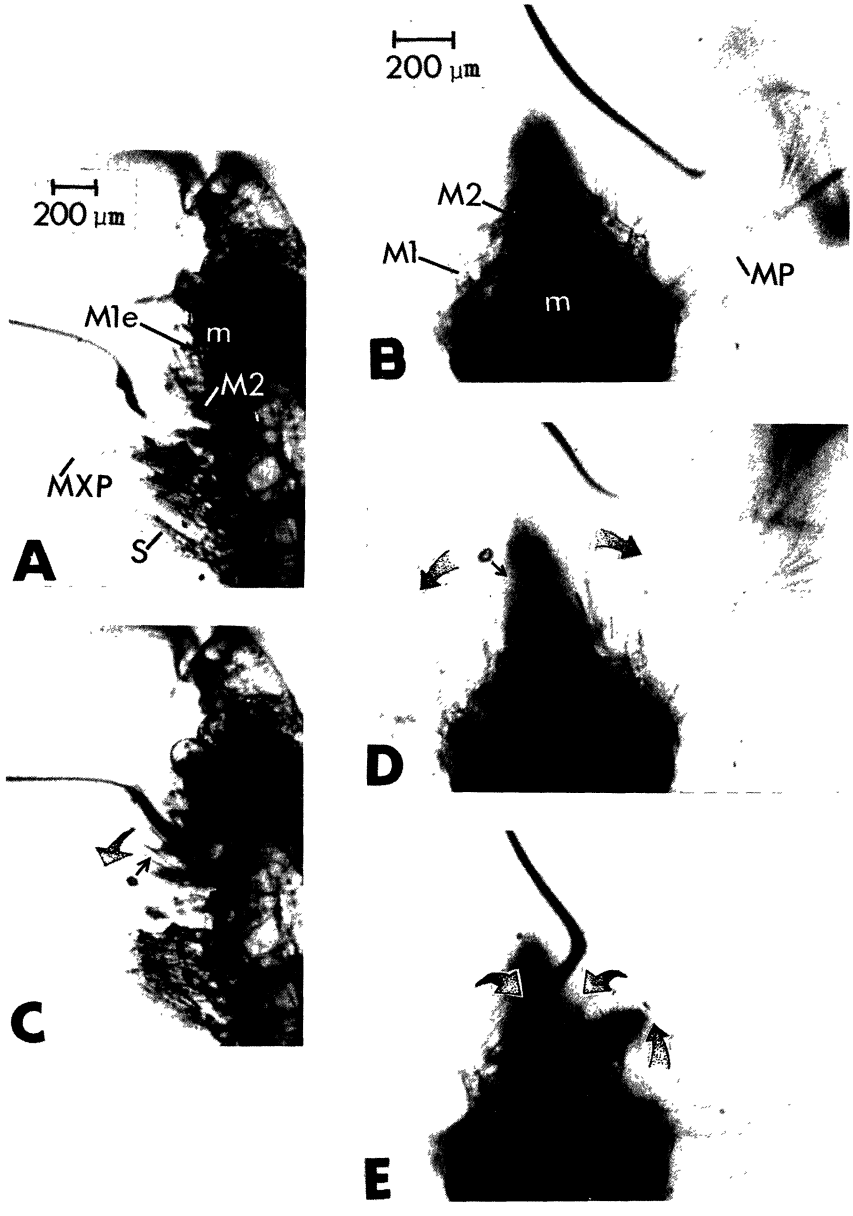

Fig. 3. Photographs made from single frames of high-speed films of feeding *Eucalanus pileatus*. Labeled structures are: m—mouth; Mle—endite of first maxilla; M1—first maxilla; M2—second maxilla; MP—mandibular palp; MXP—maxilliped; S—swimming leg. Black streaks are dye streams from micropipette. Heavy arrows indicate movements of second maxillae (and of a first maxilla in E); fine arrows indicate movements of algae (*Gymnodinium nelsoni*). In first column, animal is viewed from its left side; in second column, from its anterior end. Note narrow depth of focus referred to in methods section. We were able to analyze appendage and water movements diagramed in Figs. 1 and 2 because appendages moved into and out of plane of focus, and because plane of focus was set on different parts of the animals in different films.

Feeding currents bypass second maxillae (A–B) until an alga nears them. Alga is captured by an outward fling (C–D) and inward sweep (E) of second maxillae as described in text. Note in C that both dye and alga are in same medial plane with respect to animal and both are sucked between second maxillae during the fling, whereas in D the alga is approaching from left side of the animal and is sucked between second maxillae while the more medially located dye stream is not. First maxilla on right in E is pushing dye posteriorly.

legs of *C. typicus* and *E. pileatus* move slightly rearward at the beginning of a scanning bout and then remain stationary, whereas the swimming legs of *Acartia clausii* seem to participate in creating feeding currents (Rosenberg 1980). The feeding movements of an individual copepod also seem to be modified under different food conditions. Current work indicates that copepods apportion their time differently between various activities (e.g. scanning, resting) (Cowles and Strickler unpubl.) and move their second maxillae differently (Price and Paffenhöfer unpubl.) when presented with different sizes and concentrations of food particles.

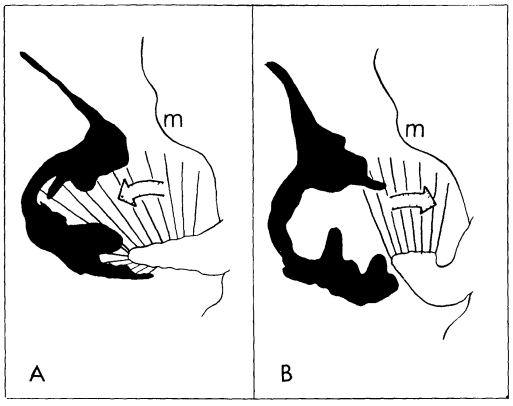

Fig. 4. Tracings of frames of a film of rejection shove (*see text*) of second maxillae. Animal is viewed from its left side. Black area is dye.

Low Reynolds number—We can better comprehend the feeding mechanisms of copepods if we consider them within the context of their physical world. Because copepods are small (1–10 mm long), 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 viscous forces are more important. The ratio of inertial to viscous forces for a flow situation is the Reynolds number (Re),

$$\mathrm{Re} = \frac{\rho v L}{\mu}$$

where v is the relative velocity of a fluid across a solid object, L is a linear dimension of the object, and ρ is the density and μ the dynamic viscosity of the fluid. Flow is laminar when Re is low (i.e. the fluid moves smoothly around the body and can be considered as moving in layers between which there is no significant mixing); flow is turbulent when Re is high (e.g. Shapiro 1961; Happel and Brenner 1965; Blake and Sleigh 1974).

The Reynolds numbers calculated for maximum velocities attained by distal setae on various copepod appendages under different circumstances are presented in Table 1. Reynolds numbers were calculated with the highest velocities measured during a cycle of limb movement, the diameters of the setae at the point for which velocities were measured, and the density (1.025×10^3 $kg \cdot m^{-3}$) and viscosity (1.1×10^{-3} $kg \cdot m^{-1} \cdot s^{-1}$) of seawater (salinity 33‰) at 20°C. Even these maximum Re values are very low, indicating that inertial forces are relatively unimportant to feeding copepods. Although it has been suggested that copepod feeding may be a low Re phenomenon (e.g. Lehman 1976; Lam and Frost 1976; Rubenstein and Koehl 1977), and although some of the implications of low Re have been pointed out for ciliary suspension feeders (e.g. Strathmann 1971; Fenchel 1980), we would like to mention several features of low Re flow that should be kept in mind when copepod feeding is analyzed.

In the viscous low Re world of a copepod, water flow is laminar. By repositioning our micropipette with respect to the tethered copepods, we have shown that water streams from different locations are moved around the copepods' feeding structures along discrete, smooth paths. The dye is not mixed into the surrounding water by beating copepod appendages as it would be in a turbulent, high Re flow situation. One likely consequence of such laminar flow is that a copepod's flapping will not stir the water and thus will not confuse the direction from which chemical signals in the water are coming.

Fluid in contact with the surface of an

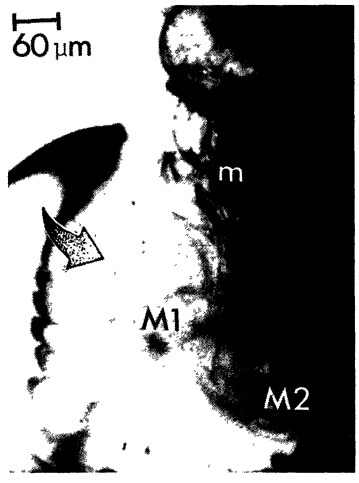

Fig. 5. Photograph of a frame of a film of a first maxilla pushing dye toward reader. Note that dye does not flow between setae.

object does not slip relative to that object. Thus, a layer of fluid along the surface of a body is deformed in shear when the body moves relative to the surrounding fluid. At low Re this boundary layer of fluid adhering to an object is thick relative to the dimensions of the object. Furthermore, at low Re 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 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 (Fig. 5). These appendages, like the bristled wings of very small insects (Ellington 1975), behave more like solid paddles than open rakes. This phenomenon can be illustrated by noting that half the distance between two neighboring setae is generally smaller than the thickness of the boundary layer (δ; order of magnitude calculated: Fung 1969; Ellington 1975) surrounding an isolated seta (Table 1). Exceptions to this are the rapid (the more rapid the movement of a body relative to a fluid, the thinner the boundary layer), wide sweepings of setae of the second maxillae during algal capture and rejection. 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 alga, for example, water is squeezed out between the setae (Fig. 2E, F, Fig. 3E).

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, are probably functionally wide and smooth rather than comblike. Rees (1975) has found corrugated insect wings to be functionally smooth in this way. Although the second maxillae are not used as stationary sieves, and although the setules may well be hidden in the boundary layer, setule length and spacing surely play a role in determining which algae are retained within the basket of the closing second maxillae. Setules should affect the 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 (Rubenstein and Koehl 1977). 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.

Since a copepod's appendage operating at low Re influences a thick layer of water around itself, particles move away when the appendage flaps toward them (Fig. 6A). Thus, a copepod appendage cannot strain an alga out of water as we might catch a ball using a scoop net; rather copepods must maneuver particles by moving the water surrounding the particles. A copepod appendage can, however, grab a particle with the tips of the setae (the "chopsticks" method: Alcaraz et al. 1980).

When moving at low Re, it is difficult to leave water behind. For example, a copepod's appendage moving away from an alga drags the alga along (Fig. 6B). This reversibility of flow at low Re accounts for the pulsing nature of the flow produced by the feeding appendages as they move back and forth. If these appendages

simply flapped back and forth symmetrically, water would be moved back and forth along the same path rather than being pushed in some net direction (*see* Purcell 1977). The complex, asymmetrical paths traced by copepod feeding appendages overcome this problem.

Since water sticks to the appendages of copepods operating at low Re, getting captured algae "unstuck" from the second maxillae and into the mouth is no small feat. The short, stocky endites of the first maxillae perform this function by combing the setae of the second maxillae (Alcaraz et al. 1980). An analogous task for a human might be removing crumbs from the fingers of one hand by combing it with the other hand while both are immersed in molasses. Because we have observed that copepods in the act of combing do not attempt to capture other algae that are brought within their reach (Alcaraz et al. 1980), we believe that combing time (which no doubt depends on particle size and shape) should be incorporated into models of copepod foraging.

The small particles on which copepods feed swim or sink slowly (Eppley et al. 1967) and thus also are surrounded by boundary layers of water that are thick relative to their dimensions. Since phytoplankton exude a range of organic compounds, it is likely that they are surrounded by a volume of odor much larger than themsleves. Furthermore, the distance relative to their dimensions at which objects (such as copepods and algae) affect the flow fields around other objects increases with decreasing Reynolds number (e.g. Zaret 1980).

Copepods feed intermittently (e.g. Lowndes 1935; Rosenberg 1980). If a copepod stops flapping where inertial effects are small, the flow around it stops almost immediately. For example, dye spots ($n = 4$) which had been carried in feeding currents (mean velocity = 8 $mm \cdot s^{-1}$) "coasted" only 46 μm (SD = 14) to a halt within 31 ms (SD = 12) of the time copepods stopped beating their appendages. Nonmotile algal cells have also been seen to halt almost immediately when copepods stop flapping (Alcaraz et al. 1980). A consequence of this effect of viscosity is that a copepod can stop flapping (perhaps to rest, or to sense nearby chemical or mechanical cues in its environment) and nonmotile particles in the water around it will stay put or slowly sink until the animal resumes flapping. Untethered nonflapping *E. pileatus* and *C. typicus* sank at velocities of 1.3 $mm \cdot s^{-1}$ (SD = 0.05, $n = 6$) and 1.6 $mm \cdot s^{-1}$ (SD = 0.08, $n = 5$).

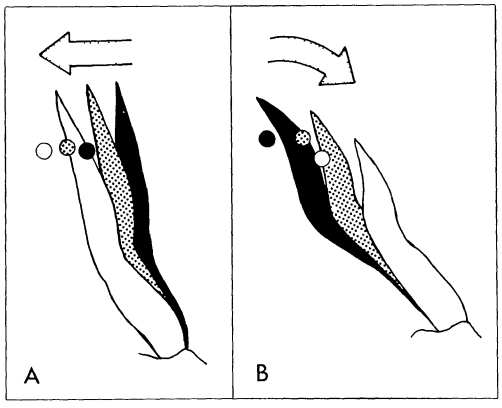

Fig. 6. Tracings of frames of a film of a maxilliped and an alga. Time interval between successive tracings is 6 ms. Black alga corresponds to black appendage, and so on. A. An alga being "pushed" by maxilliped. B. An alga "following" maxilliped.

In summary, high-speed films of water movement near feeding calanoid copepods show that these animals propel water past themselves by flapping their feeding appendages and actively capture small parcels of that water that contain food particles by flinging and closing their second maxillae. Copepods capture food particles in a world governed by viscous forces. The rules of existence at low Re are not intuitively obvious to us who live under high Re conditions but nonetheless are critical to our understanding of copepod feeding.

Selective feeding—Based on our observations of how copepods feed, we can suggest several factors on which the selective feeding of copepods might depend: the mechanical or chemical cues that stimulate copepods to flap asymmet-

rically or to fling their second maxillae, the physical characteristics of the particles retained within the basket of the closing second maxillae, or the chemical or physical features of captured particles that are ingested rather than rejected.

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Submitted: 8 October 1980
Accepted: 7 May 1981