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The Morphology and Performance of Suspension-feeding Appendages

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Many aquatic animals feed on small particles that they remove from the surrounding water using suspension-feeding appendages. Calanoid copepods are an ecologically important group of particle-feeding animals whose diverse second maxillae provide an ideal system for investigating how the structure and behavior of suspension-feeding appendages affect their performance. Questions about the selective particle capture and the cost of movement of such appendages are outlined, and theoretical approaches that might point to answers are suggested in this paper.

Introduction

Many aquatic animals feed on small organisms or particles suspended in the water (see Jørgensen, 1966, 1975, for reviews), and a large number of these animals collect the particles by moving suspension-feeding appendages through the water. The mechanisms by which such appendages capture particles are still poorly understood, hence the functional consequences of differences in the morphology and behavior of such suspension-feeding structures are not known.

Calanoid copepods are small (of the order of millimeters in length) planktonic crustaceans that can be extremely abundant in oceans and lakes. Many of these planktonic copepods feed on unicellular algae and other suspended particulate matter. Copepods form a major link in many marine food chains, and their feeding can alter both the abundance and composition of phytoplankton. The size, shape, and movement of the particle-catching appendages varies from species to species of copepod, as well as from one developmental stage to the next. Furthermore, the spectrum of particles removed from the water by different copepods varies (see Koehl, 1983, for a review). Therefore, calanoid copepods are an ecologocally important group of animals that can be used to explore basic questions about how

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the performance of biological particle-collectors depends on their structure and behavior.

The Kinematics and Morphology of Copepod Feeding Appendages

With the development of high-speed microcinematographic techniques (Alcaraz, Paffanenhöfer & Strickler, 1980), we have recently been able to work out the movements of copepod appendages and of water when the

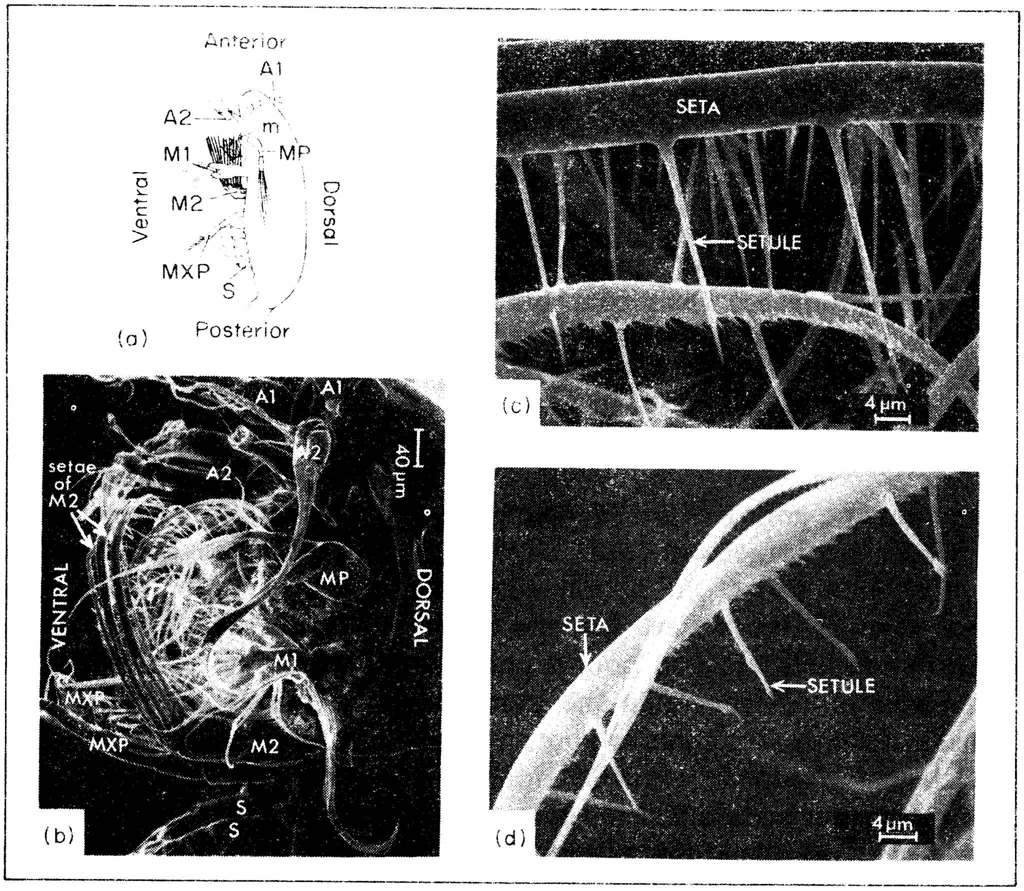

FIG. 1. Diagram of a calanoid copepod viewed from its left side. Only the left appendage of each pair is shown. The appendages that create the scanning current are the second antennae (A2), mandibular palps (MP), first maxillae (M1), and maxillipeds (MXP). Other appendages shown are the particle-catching second maxillae (M2), the sensory first antennae (A1), and the swimming legs (S). The position of the mouth (m) is also shown. (Reprinted from Koehl & Strickler, 1981, p. 1063, with permission of the American Society of Limnology and Oceanography). (b) Scanning electron micrograph of the anterior end of a *Centropages hamatus* viewed from its left side. Labels and orientation are as in A. Only the left MP, M1, and M2 are visible, whereas both left and right A1's, A2's, MXP's, and S's can be seen. Note the long setae of the M2. (c) Scanning electron micrograph of seta and setules of a second maxilla of a *Centropages hamatus*. (d) Scanning electron micrograph of seta and setules of a second maxilla of a *Pleuromamma borealis*.

animals feed (Koehl & Strickler, 1981). A feeding copepod propels a current of water past itself by flapping four pairs of appendages; this is the "scanning current". When a parcel of water containing a food particle nears a copepod, the animal actively captures that water and particle using another pair of appendages, the second maxillae. The second maxillae (Fig. 1) are short appendages bearing long bristles, called "setae". The setae are studded with barbs, called "setules". During a capture motion (Fig. 2),

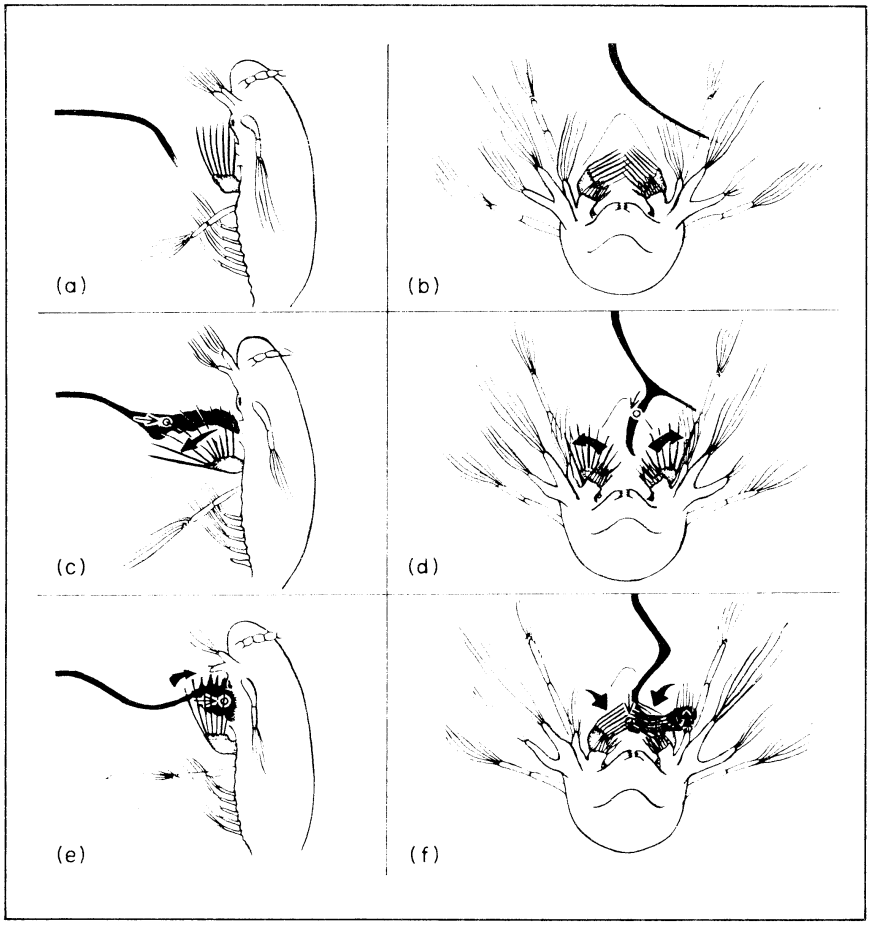

FIG. 2. Diagrams traced from high-speed films of feeding *Eucalanus pileatus*. Black streaks are dye streams from a micropipette. Heavy arrows indicate the movements of the second maxillae (and of a first maxilla as well in (f)). Circles represent the positions of and fine arrows the movements of algae observed during similar appendage movements 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. Scanning currents bypass the second maxillae (a) and (b) until an alga nears them. The alga is captured by an outward fling (c) and (d) and inward sweep (e) and (f) of the second maxillae, as described in the text. (Reprinted from Koehl & Strickler, 1981, p. 1067, with permission of the American Society of Limnology and Oceanography).

the second maxillae fling apart, thereby sucking water between them, and then squeeze back together again over that water. During the squeeze, the only escape route for the water is between the setae of the second maxillae (see Koehl & Strickler, 1981). Particles retained within the basket formed by the squeezing second maxillae are then combed into the mouth by another pair of appendages.

The morphology of the second maxillae varies considerably from species to species. Copepods differ in the length, diameter, and curvature of the setae of their second maxillae, as well as in the size, spacing, and orientation of the setules (Fig. 1). Correlations have been noted between the morphology of second maxillae and the types and sizes of particles captured by copepods (for a review, see Koehl, 1983).

The movements of the second maxillae also vary. For example, during the capture fling, the setae of a *Centropages typicus* move at about 320 mm/sec, whereas those of *Eucalanus pileatus* go at only about 20 mm/sec when feeding on the same types of particles (Koehl & Strickler, 1981). The motions executed by an individual animal also vary under different conditions (Paffenhöfer, Strickler & Alcaraz, 1982; Cowles & Strickler, 1983; Price, Paffenhöfer & Strickler, 1983). For example, when in water containing only small algae (<7 μm), *Eucalanus* move their second maxillae many times in a row at much lower amplitude than during the single fling-and-squeeze motion (described above) that they use to catch larger algae (Price, *et al.*, 1983).

The ratio of inertial to viscous forces for a flow situation is the Reynolds number ($Re = \rho VL/\mu$, where V is the relative velocity of fluid across the object, ρ is the density and μ the viscosity of the fluid, and L is a linear dimension of the object). If one considers the flow of water around setae of a copepod's second maxillae during the capture motion (using setal diameter for L) the Res are of the order of 10^{-2} to 1, depending on species (Koehl & Strickler, 1981). If one considers the movement of water around entire appendages (using the length of a second maxilla for L) the Res are of the order of 10^{-1} to 10. Therefore, viscosity is very important in copepod feeding motions, and even when Re is high enough that inertia cannot be ignored, water flow around a feeding copepod is nearly laminar (i.e. the water moves smoothly around the animal and can be considered as moving in layers between which there is no significant mixing). Various consequences of low Re flow for feeding copepods are discussed by Koehl (1981, 1983) and by Koehl & Strickler (1981). One feature of low Re flow that should be mentioned here is that the boundary layer of fluid (in which the shear gradient exists between the surface of a moving body and the surrounding fluid) is thick relative to the dimensions of the body.

A number of problems concerning the mechanisms and strategies of copepod foraging that are ripe for theoretical analyses have been outlined (Koehl, 1981). In this paper I would like to focus on one unsolved problem in more detail: How do the morphology and kinematics of copepod second maxillae affect their performance? The aspects of performance I will stress are selective particle capture and energetic costs of movement.

The Capture Fling

When the second maxillae of a copepod fling apart, the gap between them is filled by inrushing water. This motion appears to be somewhat analogous to the vortex-creating fling of insect wings, as described by Weis-Fogh (1973). It appears that little fluid moves between the bristles on small insect wings (Ellington, 1975) or between the setae on copepod appendages (Koehl & Strickler, 1981) during this motion, hence the wings and second maxillae can be treated as solid plates as a first approximation. The non-steady-state aerodynamics of insect hovering has received some theoretical attention (e.g. Weis-Fogh, 1973; Lighthill, 1973, 1974, 1975; Ellington, 1978, 1980; Maxworthy, 1981). Although these analyses have focused on the performance of wings in terms of generating lift, they also provide information about flow patterns as well as about power requirements. Perhaps a similar approach could shed light on questions about the performance of copepod second maxillae during the capture fling.

Several aspects of the performance of copepod second maxillae during the capture fling should be addressed:

CAPTURE RANGE

What is the size and shape of the parcel of water that will be sucked between the second maxillae when they fling apart? How does this capture range vary with the velocity at which the fling occurs? with the amplitude of the fling? with the size of the second maxillae? with the shape of the second maxillae? Might we expect animals whose second maxillae have small capture ranges to have the ability to create stronger scanning currents to bring particles closer to themselves? Might we expect those animals whose second maxillae have large capture ranges to have more sensitive or sophisticated sensory apparati to perceive the location of particles at greater distances from their bodies? One thing we do know now about the capture range of second maxillae is that a few species initiate the fling when particles (35–55 μm) are of the order of hundreds of micrometers away from those appendages (Koehl, 1983).

WATER VELOCITY

What is the velocity of the inrushing water during a capture fling, and how does this depend on the velocity, amplitude of motion, size, and shape of the second maxillae? Many species of copepods are omnivorous and can capture small animals as well as particulate food. What morphological and kinematic criteria must be met by the second maxillae during a fling for the inrushing water to move more rapidly than a prey item can swim away? (Note that some species of copepods are carnivorous and only eat other animals; carnivorous copepods tend to have large, coarse raptorial second maxillae. It would be interesting to consider the parameter space in which an animal's second maxillae can catch both particles and animals, can catch only particles, or can catch only animals. For such an analysis, one would have to consider the capure squeeze (discussed below) as well as the fling.)

COST

What is the work required to execute a fling, and how does that vary with the velocity, amplitude of motion, size, and shape of the second maxillae? Does the work per fling differ when a single fling is made vs. when many flings are made in a row? Perhaps a consideration of the induced power (the increase in energy of the water flow per unit time) produced by a fling can address these questions (for example, see Ellington, 1980). Data is not yet available on the efficiency of copepod muscles, or on the frictional energy losses at their joints, hence the total energy requirement (see Casey, 1981) for the copepod to execute a fling would not be revealed by this approach, although the *relative* costs of different motions by various morphologies could be explored.

The Capture Squeeze

After a parcel of water and the particles it contains have been sucked between the second maxillae, these appendages close down over that water. The water, having no other escape route, is squeezed out between the setae of the second maxillae during this motion, leaving the particles behind. The water that is squeezed out is pushed away by another pair of appendages, and the retained particles are combed into the mouth. Perhaps the theoretical analyses of flow through and particle retention by filters can shed light on questions about the performance of copepod second maxillae during the squeese.

Several aspects of the performance of the second maxillae during the squeeze should be addressed:

SELECTIVE CAPTURE OF PARTICLES

What are the mechanisms by which particles are retained within the basket formed by the closing second maxillae, and how does the particle-selectivity of these appendages depend on their morphology and kinematics?

Many "black box" studies have been conducted of the rates at which various species of copepods remove particulate food from the water (reviewed by Koehl, 1983). Some investigations have shown that these animals can be size-selective feeders, while others indicate that factors such as particle smell or shape can also affect the selectivity of copepod feeding, and that copepods display plasticity in their selective feeding behavior. A controversy has existed in the literature as to whether copepod selective feeding is due to the physical properties of the second maxillae (which were thought to act as sieves), or rather is due to active choice by the animals (see, for example, "The Copepod Feeding Controversy" section in Kerfoot, 1980).

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, it can be suggested that selective feeding could depend on (1) the chemical or mechanical cues for which a copepod flings its second maxillae, (2) the physical characteristics of particles retained by the closing second maxillae during the squeeze, or (3) the chemical or mechanical features of particles that are ingested rather then rejected. In this paper I will focus on suggestion number two.

As mentioned above, the physical mechanisms by which biological filters separate particles from the surrounding fluid are poorly understood. Biologists generally assume that filters act as sieves that can only capture particles larger than the spaces between the fibers composing the filter. Rubenstein & Koehl (1977) have applied to biological filters the theoretical analyses of filtration developed by engineers (for reviews, see Fuchs, 1964; Dorman, 1966; Pich, 1966; Davies, 1973; Spielman, 1977); we suggested that mechanisms other than sieving (direct interception, inertial impaction, gravitational deposition, and motile-particle or diffusion deposition) may also be used by biological filters to capture particles. The efficiency of a filter is defined as the ratio of the number of particles striking a filter to the number that would strike it if the streamlines were not diverted by it (Dorman, 1966). Filtration theory describes how the efficiency of a fiber at capturing particles of various sizes, densities, and surface properties varies with the velocity of the flow past the fiber as well as with the diameter and surface properties of the fiber. Copepod setae may be such filtering fibers. Empirical studies indicate that this filtration theory is applicable to other particle-capturing organisms (e.g. LaBarbera, 1978; Fenchel, 1980). Similar theoretical approaches have been used to work out the capture of pheromone molecules by moth antennae (Murray, 1976), and to predict the deposition of particles in the human respiratory tract (e.g. Taulbee & Yu, 1975; Savilonis & Lee, 1977).

Engineering filtration theory could be used to explore how the efficiency of capture of particles of various physical characteristics by setae of copepod second maxillae during the squeeze varies with the velocity of setal movement. As mentioned above, not only are there interspecies differences in the velocities the second maxillae move, but there are differences in the speed that one individual moves its setae when exposed to different types of particles.

Filtration theory could also be used to investigate how selective particle retention during the squeeze depends on the morphology of the second maxillae. At the low *Re*s at which the setae of copepod second maxillae operate, water no doubt resists flowing between the closely-spaced setules on the setae. Perhaps a seta with rows of setules and the water stuck between them is functionally a smooth cylinder of larger diameter. One might replace the fiber diameter (d_f) in the filtration theory equations with effective fiber diameter (d_f'), the latter being a function of velocity. Certainly among the most striking differences in the morphology of copepod second maxillae are the size and spacing of setules on the setae. An interesting fluid dynamics problem might be to explore the flow fields around cylinders covered with barbs of various lengths, spacings, and arrangements. At what range of velocities and setule lengths or spacings does water flow between setules? The problem becomes more challenging if one considers an array of such setulated setae with the spacing between them decreasing with time, as it does during the squeeze.

Filtration theory assumes the fibers of a filter are adhesive and considers a particle as caught if it contacts a fiber. When a particle *in water* approaches a fiber, whether or not it actually contacts the fiber is determined by factors such as surface charge and van der Waals forces, therefore these factors are included in filtration theories for water (e.g. Spielman, 1977). Perhaps these factors can be ignored in models of the copepod squeeze since a particle need not actually contact a seta to be captured—any particle that merely fails to move past a seta during the closing motion of the second maxillae is retained. It should be pointed out, however, that ophiuroids

(LaBarbera, 1978) and cladocerans (Gerritsen & Porter, 1982) capture charged particles at greater rates than uncharged.

COST

Since water resists moving through narrow gaps, the squeezing motion of the second maxillae may well be energetically expensive. If so, it makes sense that copepods engage in this motion only when particles are between the second maxillae, rather than continuously strain water through these appendages (as copepods were previously thought to do).

What is the energetic cost of executing a squeeze? If one could plot the force on setae versus the distance they move during a squeeze, the area under such a curve should indicate the amount of work required for the movement. (Note, as mentioned above, that this approach does not indicate the total cost to the copepod to make the motion since muscle efficiency, etc., are not considered; it does, however, allow relative costs for motions of different velocities by different structures to be compared.) Various approaches to calculating the resistance to the movement of a fluid through an array of cylinders are reviewed by Fuchs (1964), Pich (1966), Davies (1973) and Spielman (1977). Note that the problem is complicated for copepods by the fact that intersetal spacing is greater near the tips than the bases of setae, and also varies with time. It is interesting to note that the ratio of pressure difference across an array of fibers to the volume flow rate through the array is constant at low *Re*s, but increases as flow rate increases at *Re*s of 0·05 to 20 (Davies, 1973). There are copepods whose setae operate in each of these *Re* ranges. Should we expect to find differences in their strategies for moving the second maxillae?

Conclusions and Further Questions

Many animals move small bristled appendages through water to capture food particles. The second maxillae of the ecologically-important calanoid copepods provide a system for investigating how the morphology and kinematics of such appendages affect their performance, both in terms of selective particle capture, and in terms of cost of movement. The theoretical approaches that have been used to investigate insect flight and man-made filters can probably be applied to this problem. Answers to the questions outlined above would not only give us insights about the design of suspension-feeding appendages, but also could lead into explorations of various aspects of the behavior, ecology, or evolution of copepods. For example, if the costs of various motions were known, then how copepods of different morphologies should partition their time between various behaviors to maximize net energy gain under different ambient food conditions (see Koehl, 1981, 1983) could be addressed. Similarly, if the capture range and water velocity of the fling were known, then we could explore strategies in scanning behavior by omnivorous and carnivorous copepods of different morphologies (e.g. should the animal scan vigorously or gently, or should it hold still and sink, to minimize the chance that prey outside the capture range will feel its presence and escape?). Examples of other question that might also be pursued include: Can the same feeding performance be generated by second maxillae of different morphologies? For effective particle capture, must certain features of second maxillae be accompanied by particular characteristics of the appendages that create the scanning current, or by particular sensory capabilities? Are various species of copepods constrained by their morphologies to only certain foraging strategies? Which suites of morphological and kinematic features of feeding appendages characterize food generalists as opposed to specialists?

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