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Characterization of feeding activity patterns in the planktonic copepod *Centropages typicus* Kroyer under various food conditions[1]

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Abstract

High-speed (500 frames·s^{-1}) cinematography of particle capture by *Centropages typicus* revealed that cells of the dinoflagellate *Gymnodinium nelsoni* were captured via a rapid extension of the second maxillae after particle detection. The capture sequence requires <14 ms, and appendage movement (55 Hz) continues during capture. Slow-speed (20 frames·s^{-1}) cinematographic analysis of the feeding behavior of *C. typicus* showed that the copepod spent at least 95% of its time alternating between periods of rhythmic mouthpart movement and periods of no mouthpart movement. Intervals of activity lasted from 0.1 to 10 s, but the duration of activity was highly dependent on the species and concentration of food available to the copepod. The results suggest considerable plasticity in the temporal partitioning of feeding activity.

Feeding studies with copepods have shown that ingestion rates are a function of several factors, including size of food (Mullin 1963; Harvey 1937; Frost 1972), species composition of the food (Paffenhöfer 1970), and total food concentration (Marshall and Orr 1955; Mullin 1963; Frost 1974; Corner et al. 1976). The above factors interact to create complex feeding responses under natural conditions (Poulet 1974; Richman et al. 1977; Cowles 1979; O'Conners et al. 1980).

The range of feeding responses documented in the copepod literature suggests that food selection by copepods is not easily characterized by stereotyped mechanical responses, but seems to be governed by behavioral responses to particular stimuli. Copepod swimming behavior and activity change in response to light (Strickler 1970; Hardy and Bainbridge 1954) or mechanical stimuli (Strickler 1975; Haury et al. 1980), but little is known about changes in feeding activity in response to changes in food conditions.

We report here results obtained with *Centropages typicus* during filmed observations of its feeding behavior under various food conditions. Specifically, we wished to address the following questions: What appendage movements are involved in food capture? Does the copepod vary the pattern of slow swimming and sinking so often observed? If so, is this variation correlated with changes in food conditions? We found that application of high-speed (500 fps, frames per second) cinematography (Alcaraz et al. 1980) would resolve the details of appendage movement in *C. typicus*, and that 20 fps cinematography would be adequate to describe the temporal patterns of activity under different food conditions.

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Methods

Adult females of *C. typicus* were isolated from shallow plankton tows taken in Cape Cod Bay, Massachusetts. The copepods were kept in insulated thermos

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jugs during transport to the laboratory of J. R. Strickler (Univ. Ottawa). Individual females were then tethered by attaching a short length (1–2 cm) of dog hair to the dorsal surface of the fourth thoracic segment with a cyanoacrylate adhesive. This was accomplished by transferring the copepod from a beaker to a smaller volume (0.5 ml) of water in a large-bore pipette. The drop containing the copepod was touched to a moist piece of filter paper on the stage of a dissecting microscope. A small piece of filter paper was used to dab water away from the dorsal surface of the copepod, at which time the hair, with its drop of adhesive, was touched to the fourth thoracic segment. The adhesive dried within 5 s and the copepod was then gently covered with a large drop of seawater and transferred to the feeding chamber. Clamping forceps were used to hold the free end of the dog hair, and the forceps were mounted above the feeding chamber. If the dog hair was applied successfully, the copepods continued to swim and feed normally, with no apparent ill effects, several days after the series of experiments described below.

The copepods were fed the dinoflagellates *Prorocentrum micans* and *Gymnodinium nelsoni*. The algae were kept in log phase growth in f/2 medium (Guillard and Ryther 1962) under a 12:12 L–D photoperiod. Food concentrations for experiments were determined with a model B Coulter Counter.

Filming methods were similar to those reported by Alcaraz et al. (1980). The tethered copepod was positioned in an optical glass cuvette (ca. 10 × 10 × 2.5 cm) filled with filtered seawater containing the appropriate food for the particular experiment. Laboratory temperature was kept at 20°C ± 1°. The 16-mm films were taken at 500 fps (55 μs exposure·frame^{-1}), providing time resolution of 2 ms between frames, and at 20 fps (1.35 ms exposure·frame^{-1}), providing time resolution of 50 ms between frames. The time resolution in the high-speed films was sufficient to resolve appendage movement frequencies and individual particle captures. Appendage movement events (as described below) were observed in the high-speed films to last for at least 6 cycles for a minimum duration of 100 ms. Therefore a film speed of 20 fps (50 ms time resolution·frame^{-1}) was chosen for analysis of activity patterns. Although food capture events lasted <15 ms, each appendage movement event (slow swimming event) lasted at least 100 ms, with most of the events lasting longer than 250 ms (*see Figs. 6 and 7*). We therefore feel justified in using 20-fps films to elucidate the activity patterns described below.

One-hundred-foot (30 m) rolls of film permitted about 8 s of filming at 500 fps and about 3.4 min of filming at 20 fps. In order to capture a feeding event on film at 500 fps, food densities must be high enough so that the probability of observing a food capture within 8 s is high. Therefore, the high-speed (500 fps) film was made with the *G. nelsoni* as food at 100 cells·ml^{-1}. After processing, each film was analyzed frame by frame with a Vanguard motion analyzer. Appendage movement patterns and food capture movements were derived from the high-speed films, while the activity durations were obtained from the slower speed films. Over 20,000 frames were analyzed to obtain the data presented below.

Results

The results are presented in two sections. First, we describe the appendage movements during slow swimming and food capture, then we present the patterns of feeding activity under different food conditions.

High-speed cinematography: Appendage movement and food capture—The films were taken with *C. typicus* oriented in its usual swimming posture, dorsal surface up with the body sloping obliquely upward. Only lateral views were filmed on this occasion, and thus our analysis is restricted to the major longitudinal movements of the feeding appendages. The depth of field provided by the optical arrangement permitted us to follow the path of the second antenna, the distal endite of the first maxilla, the second maxilla, and the maxilliped. The second antenna,

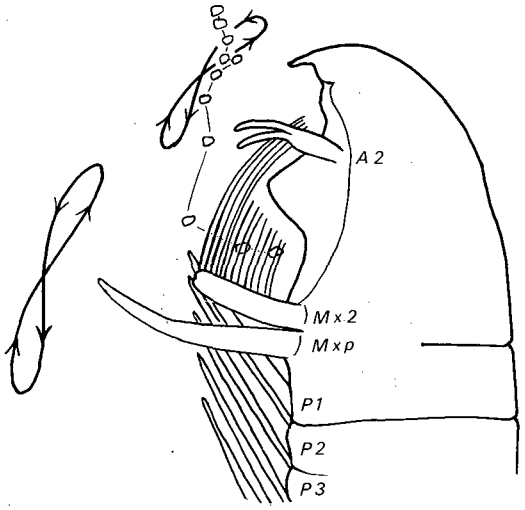

Fig. 1. Schematic diagram from high-speed film of *Centropages typicus*, left lateral view, showing figure-eight paths described by tips of second antenna (A2) and maxilliped (Mxp) during slow swimming. Motions of the A2 and Mxp are 180° out of phase. Second maxilla (Mx2) is shown in its usual configuration during slow swimming and breaks. Particle path is that described by a single *Gymnodinium nelsoni* cell over 11 film frames (22 ms). *See text for description of capture.* P1, P2, P3 are swimming legs. First antennae, mandibles, and first maxillae omitted for clarity.

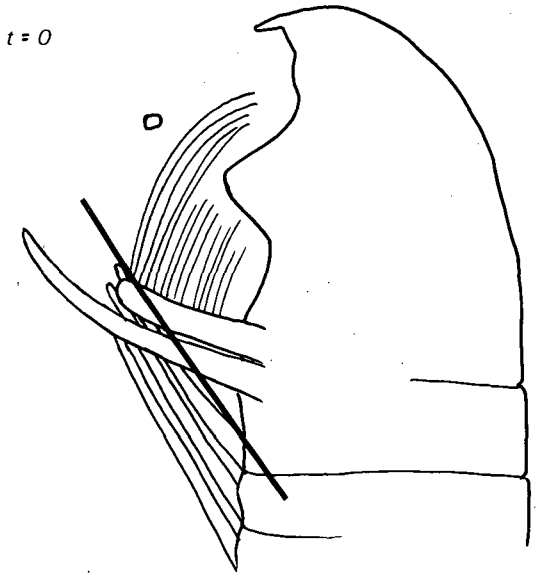

Fig. 2. Position of second maxillae, maxilliped, and swimming legs just before capture of *Gymnodinium nelsoni* cells. $t = 0$. Heavy dark line is for later reference to precapture position of swimming legs.

the first maxilla, and the maxilliped were observed to move at the same frequency, with the maxilliped and second antenna moving toward each other and then apart, almost 180° out of phase. The frequency of appendage movement was 55 Hz when the copepod was feeding on *G. nelsoni* (4.0 ppm). The maxilliped and second antenna described a path which resembled a figure-eight, as illustrated in Fig. 1. Both appendages move from outside to inside during the posteriorly directed power stroke, then move back to the outside and move inside during the recovery stroke. ("Inside" and "outside" are relative to a line parallel to the medial longitudinal axis of the animal.) The particle path shown in Fig. 1 illustrates the track of a single cell before and during capture. Based upon the distance moved by the food particle between frames, the particle speed ranged from 2 $cm \cdot s^{-1}$ before capture to 12 $cm \cdot s^{-1}$ during capture. These values suggest that the copepod is creating fluid velocities of at least 12 $cm \cdot s^{-1}$ near the second maxilla during food capture.

The most striking feature of the food capture process by *C. typicus* is the role played by the second maxillae. This process is illustrated in Figs. 2–5, most of which are schematic diagrams derived from individual film frames of the capture of the single food particle whose path is shown in Fig. 1. While the setation of the second antennae, first maxillae, and maxillipeds is important in generating the overall flow field (Koehl and Strickler 1981), the setae of the second maxillae play the largest role in single particle capture and are therefore emphasized in Figs. 1–5. The capture sequence described is typical of three such sequences we have filmed with *C. typicus* and is thus likely to be representative of large particle capture by this copepod. In Fig. 2, the second maxillae are at rest as a *G. nelsoni* cell is brought near via the flow generated by the movements of the second antennae. Two milliseconds later, the setae of the second maxillae have begun to extend ventrally, with the tips of the

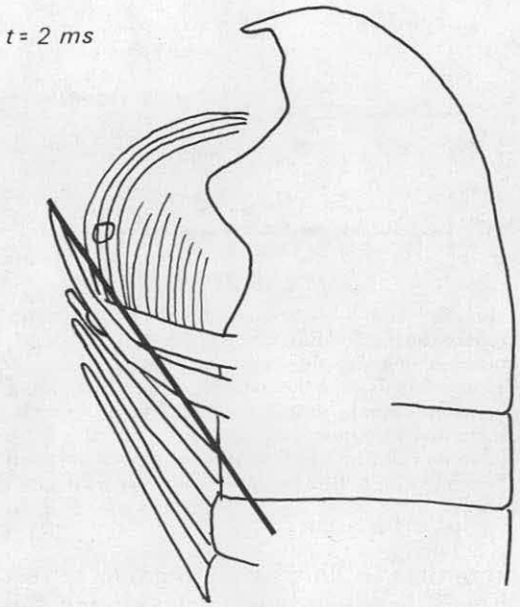

Fig. 3. Position of appendages at $t = 2$ ms. Note curvature of setae on second maxillae and position of swimming legs relative to $t = 0$ swimming leg position (heavy dark line).

setae still at rest as their base accelerates outward (Fig. 3). Within the next 4 ms, the setae of the second maxillae have reached full extension (Fig. 4). Figure 5 shows that the setae have almost returned to a resting position 2 ms later.

The *G. nelsoni* cell appeared to be pushed toward the mouth by the proximal endite of the first maxilla (not shown in the figures) between the film frames shown in Figs. 4 and 5. (Our films did not show the movements made by the mandibles during actual ingestion.) The extension motion of the setae of the second maxillae, coupled with posteriorly directed motion of the swimming legs (cf. Figs. 3, 4, and 5) created a current which drew the *G. nelsoni* cell into the space between the second maxillae. The cell was effectively trapped between the setae as the second maxillae returned to a resting position. Throughout the capture process (10 ms), the second antennae, the first maxillae, and maxillipeds continued to move at 55 Hz, so that the incoming flow of water (ca. 1–2 cm·s^{-1}) was not interrupted.

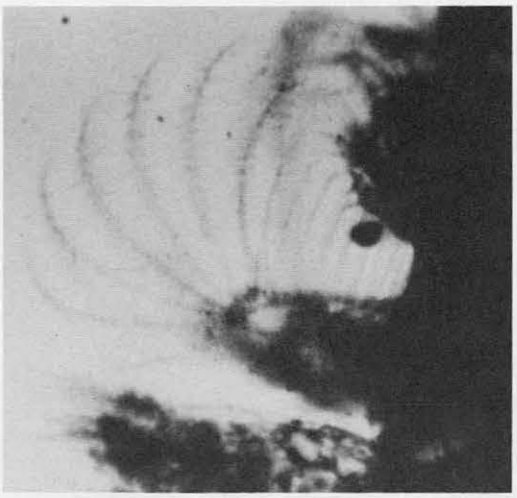

Fig. 4. Photograph from high-speed film, showing extended position of second maxillae at $t = 6$ ms. Note that swimming legs have moved posteriorly to help draw food particle between setae of second maxillae.

Slow-speed cinematography: Activity patterns under different food conditions—Five films (at 20 fps) were made of a single *C. typicus* female acclimated for at least 2 h to each of five food con-

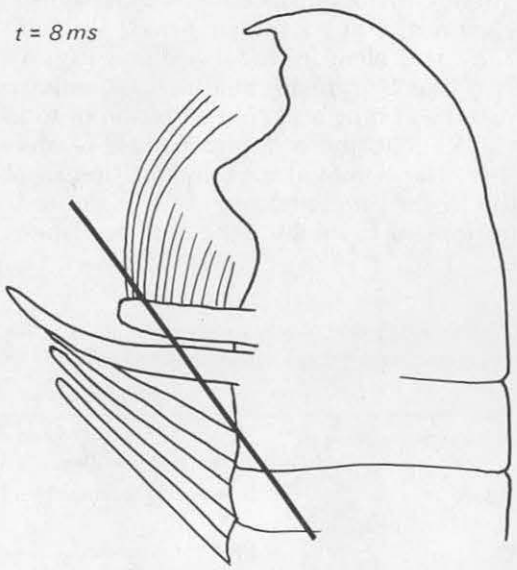

Fig. 5. Position of second maxillae at $t = 8$ ms. Note position of swimming legs relative to $t = 0$ position. Second maxillae is almost at rest. Particle has been ingested.

Table 1. Food conditions for *Centropages typicus* feeding experiments.

Sequence	Species	Food concn Cells·ml^{-1}	Vol (ppm)
2	*Prorocentrum micans*	400	3.50
3	*Prorocentrum micans*	40	0.35
1	*Gymnodinium nelsoni*	100	4.0
4	*Gymnodinium nelsoni*	10	0.4
5	Filtered seawater	0	0

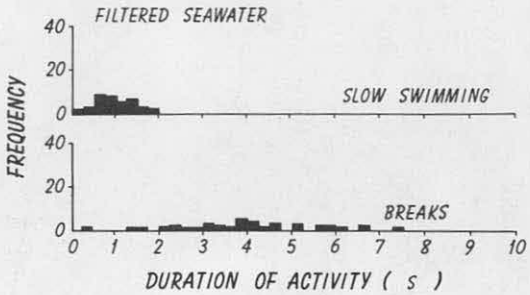

Fig. 6. Activity patterns of female *Centropages typicus* during feeding, showing frequency distribution of activity durations in filtered seawater. Frame analysis gave the patterns of slow swimming events and breaks within the 4,000-frame film. Ordinate gives frequency of occurrence of either type of event or during the film. Abscissa gives duration of each event, with time intervals every 0.25 s (=5 frames).

ditions (Table 1). Frame-by-frame analysis revealed four types of behavior, summarized in Table 2. Slow swimming movements and breaks accounted for >95% of the activity time in all of the films. Food capture events were included in the slow swimming mode, since the filming speed during these experiments was not capable of always resolving the motion of the second maxillae, and since the other appendages were known to keep moving while the second maxillae were capturing a food particle.

Periods of slow swimming alternated with breaks during each of the experiments, with mean durations as shown in Table 3. The data for slow swimming and breaks have also been summarized as frequency histograms of event duration for each of the five food conditions (Figs. 6, 7, 8). It is clear from Table 3 and Figs. 6, 7, 8 that *C. typicus* modified its activity pattern as type and concentration of food varied. With both *P. micans* and *G. nelsoni*, the copepod took longer breaks at the lower concentration. At high concentrations of *P. micans*, the copepod spent more time in slow swimming than at rest (Fig. 7), while at low concentrations, the durations of swimming movements and break events were quite similar. The event durations with *G. nelsoni* as food both support and contradict the results found with *P. micans* as food. At high concentrations of *G. nelsoni*, slow swimming and break durations were roughly equivalent, but at low concentrations, more time was spent in slow swimming than at rest (Fig. 8). In filtered seawater, the copepod spent more time at rest, with a few slow swimming events of short duration (Fig. 6).

The copepod was returned to a high concentration of *G. nelsoni* after the final film in filtered seawater. In films made 30 min later, the pattern of break duration

Table 2. Types of activity observed in *Centropages typicus*.

Activity	Description	Occurrence	Duration of activity
Slow swimming	Rhythmic motion of second antennae, first maxillae, maxillipeds	Often	Variable, 0.2–10 s
Breaks	No appendage movement, animal at rest	Often	Variable, 0.15–7.5 s
Cleaning	First antennae brush across mouthparts, maxillipeds groom maxillae and antennae	Occasional	Variable, 0.15–1.1 s
Rapid swimming	Rhythmic swimming thrusts with swimming legs	Rare	Variable, 0.1–1.5 s

Table 3. Activity durations (s) for *Centropages typicus* ($X \pm 1$ SD; n—number of events observed per film).

Food conditions (cells·ml^{-1})	Slow swimming	Breaks
Prorocentrum micans (400)	2.11±1.80, n=81	0.38±0.07, n=57
P. micans (100)	0.80±0.45, n=119	0.87±0.34, n=115
Filtered seawater	0.98±0.45, n=38	4.08±1.52, n=38
Gymnodinium nelsoni (100)	1.38±1.09, n=76	1.30±0.43, n=68
G. nelsoni (10)	2.59±2.10, n=46	1.75±0.76, n=43

again resembled that shown in Fig. 8, showing that the activity patterns described were not a consequence of a gradual deterioration of the copepod during the filming sequence.

Discussion

High-resolution, high-speed cinematography has provided a new mechanism for observation of the feeding processes of copepods (Alcaraz et al. 1980; Kerfoot 1978; Rosenberg 1980; Koehl and Strickler 1981). Our results, using normal-speed cinematography, indicate that feeding activity is correlated to food conditions and that *C. typicus* spends less time in slow swimming and more time at rest as food concentrations decrease. Two familiar questions emerge from these data. How does the copepod assess food concentration? Why does it then modify its behavior pattern? At least two explanations are possible for the first question. First, the copepod may move its feeding appendages so as to propel itself through the water and eventually encounter the chemical or physical stimulus of a food particle. The frequency of encounter with either the chemical or physical presence of the food could provide the animal with an estimate of food concentration. The interval between stimuli could also influ-

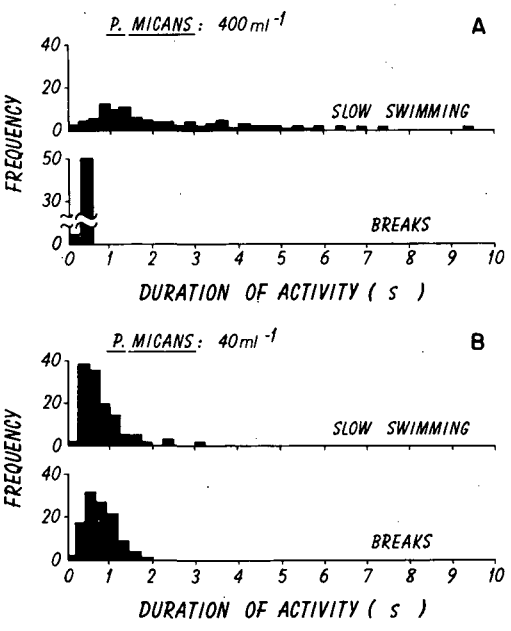

Fig. 7. Activity patterns of female *Centropages typicus* while feeding on *Prorocentrum micans* at (A) 400 cells·ml^{-1} and (B) 40 cells·ml^{-1}. Symbols as in Fig. 6.

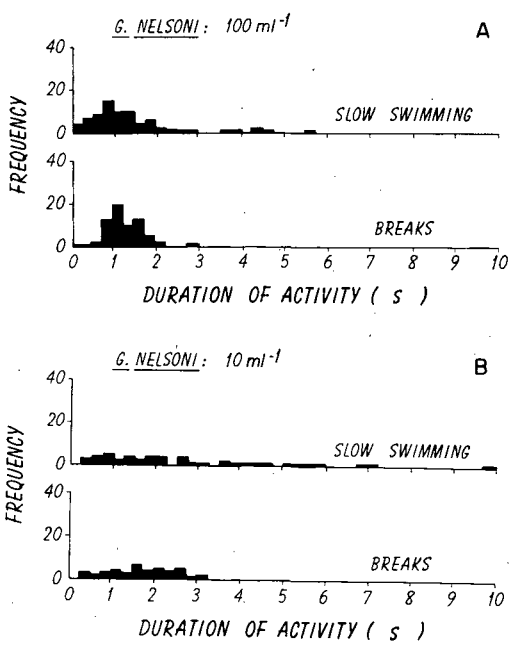

Fig. 8. As Fig. 7, but on *Gymnodinium nelsoni* at (A) 100 cells·ml^{-1} and (B) 10 cells·ml^{-1}. Symbols as in Fig. 6.

ence the duration of particular feeding activities. Alternatively, the physical presence of particles in the mouth or in the gut could provide the stimulus for a particular activity.

Why does the copepod modify its behavior pattern? Again, two possible explanations come to mind. First, the metabolic expense incurred in moving appendages may not be offset by ingestion benefits at low food concentrations. Analysis of fluid motion around copepod mouthparts (Koehl and Strickler 1981) indicates that these appendages are operating at low Reynolds number (0.1–1.0). Viscous drag may therefore impart a higher cost to movement of mouthparts than indicated in the models of Lehman (1976) or Lam and Frost (1976). An alternative explanation for increased break duration at low food concentrations is that the copepod ceases appendage movements so that it sinks *out* of a low food patch and sinks *into* a patch with higher food concentrations. The copepod could thus use the sinking behavior as a mechanism for scanning the fluid for chemical or physical signals.

The food capture process, as illustrated in Figs. 2–5, combined aspects of both traditional filter feeding and raptorial feeding (Conover 1966). The food particles, once detected, are moved close to the second maxillae by the fluid motions generated by the other mouthparts. Actual capture of particles is accomplished through "suction" created by the rapid extension of the setae of the second maxillae and posteriorly directed movements of the swimming legs, similar to the suction-capture method of some planktivorous fish (Drenner et al. 1978). We did not observe any appendages other than the second maxillae to move abruptly. The proximal endites of the first maxillae appear to act as brushes which move at the same frequency as the second antennae and maxillipeds. Our films did not offer a view of the mandibles during appendage movement, but we did observe that the mandibular palps move with the same frequency as the other appendages. In *C. typicus*, the raptorial capture of a particle thus does not interrupt slow swimming movements, and therefore does not interrupt the flow of chemical or mechanical clues which may indicate the presence of prey. Our results are consistent with the data reported by Rosenberg (1980) for *Acartia clausi* in that it appears that intermittent feeding is the rule under a wide range of food conditions, but further studies are certainly required before any quantitative relationship can be developed between activity level and food conditions.

Many investigators have suggested that copepods may have a "feeding threshold," a food concentration below which feeding is curtailed or ceases altogether (Adams and Steele 1966; Parsons et al. 1969; Frost 1975; Reeve and Walter 1977). Although the results of our study can only be applied to one species, earlier workers may have detected changes in activity patterns of copepods, such that feeding threshold behavior was a consequence of increased break duration at low food concentrations. Copepods have both mechanoreceptors and chemoreceptors on the first antennae which have been implicated in the perception of prey (Strickler and Bal 1973; Strickler 1975; Friedman and Strickler 1975; Landry 1980) by either hydrodynamic or chemical stimuli. Although filmed observations of copepod feeding (Alcaraz et al. 1980; Koehl and Strickler 1981) lead us to hypothesize that remote detection of algae is accomplished via chemoreception, conflicting evidence has been presented by Landry (1980) for *Calanus pacificus*; his results indicate that algal capture rates are not affected by amputation of the first antennae but naupliar capture rates are reduced, suggesting that first antennae receptors play a role in distance perception of moving prey, but not in perceiving algal prey. On the other hand, distance perception of algal prey may occur via chemoreceptors on other appendages. Contact chemoreception is the most likely mechanism for particle rejection by copepods (Donaghey 1980) and it is reasonable to expect that copepods possess distance chemoreceptors similar to those

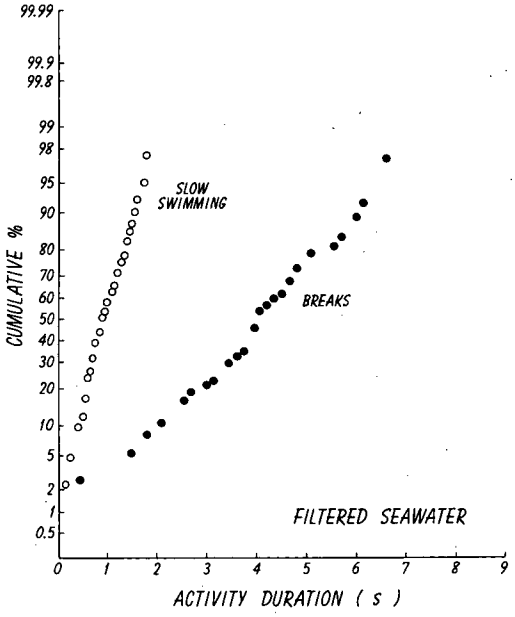

Fig. 9. Distribution of activity duration vs. cumulative percent on a probability scale for *Centropages typicus* in filtered seawater.

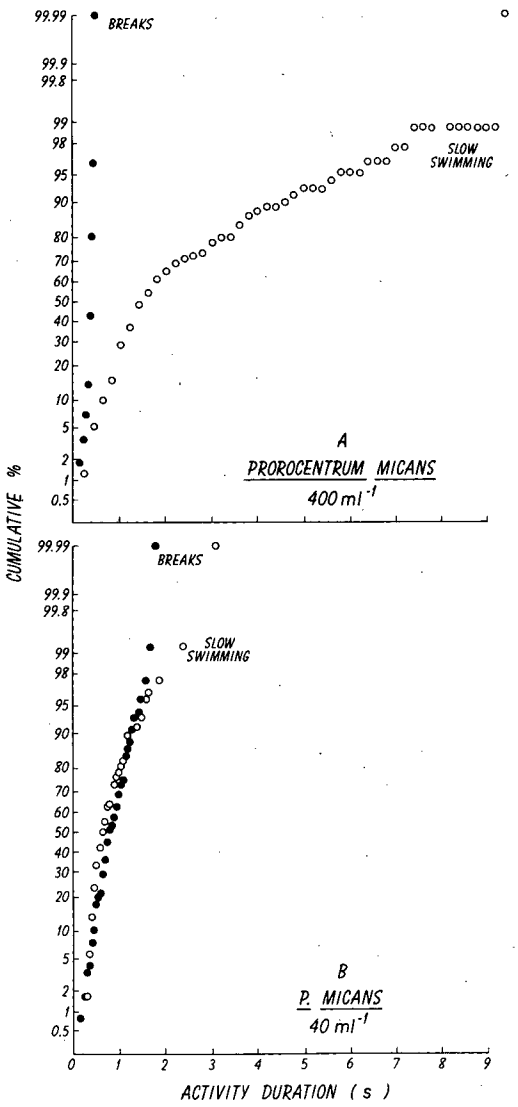

Fig. 10. As Fig. 9, but in *Prorocentrum micans* at (A) 400 cells·ml^{-1} and (B) 40 cells·ml^{-1}.

found in planktonic shrimp (Hamner and Hamner 1977). It is clear from our high-speed films that food capture takes place only during appendage movement, so that slow-speed (20 Hz) films which resolve slow swimming movements are adequate for defining periods when food capture is possible. Only during intervals of slow swimming movements can a *C. typicus* capture a food particle; therefore it is reasonable to hypothesize that the frequency and duration of slow swimming intervals and break intervals would be related to food encounters per unit time. Since feeding rate is in direct proportion to food encounters per unit time, it follows that the activity patterns derived from the films reflect the pattern of food search and capture under various food conditions. It is therefore possible to use these activity patterns to examine whether the copepod samples its environment randomly.

If the search for food involved a random sampling of the fluid environment, it would require slow swimming "events" of random duration occurring at random intervals. The resulting distributions of activity would approximate normal distributions.

The data from each treatment (Table 1) were assigned to four categories: intervals of slow swimming; intervals of breaks; intervals consisting of a slow swimming interval + the succeeding break interval; intervals consisting of a break interval + the succeeding slow swimming interval. The data in each category were judged to fit a normal distri-

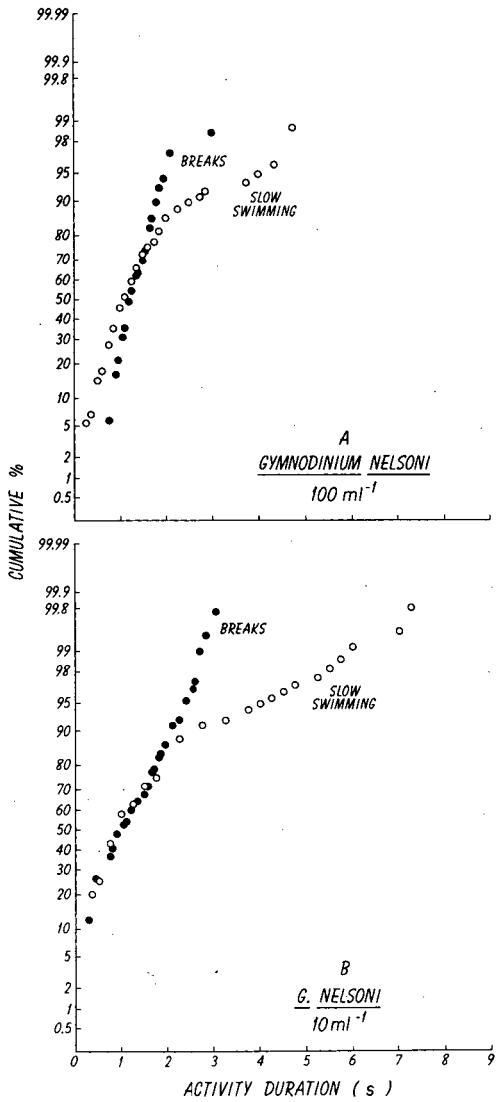

Fig. 11. As Fig. 9, but in *Gymnodinium nelsoni* at (A) 100 cells·ml^{-1} and (B) 10 cells·ml^{-1}.

bution if they approximated a straight line in a normal probability plot.

On the basis of the above criteria, *C. typicus* only demonstrated "random" food search behavior in filtered seawater (Fig. 9). In this treatment all interval categories approximated normal distributions. As food concentrations increased to low levels of *P. micans* or *G. nelsoni*, only the distributions of break intervals remained nearly normal (Figs. 10, 11), while all other categories deviated from a straight line in the probability plot. At the high concentrations of *P. micans* and *G. nelsoni*, none of the interval categories approximated normal distributions (Figs. 10, 11). The above results indicate that the copepod only searches randomly in the absence of food stimuli, i.e. it samples the environment at random times for intervals of random duration. Such a random search pattern may represent the least energetic expenditure for testing or tasting the environment.

As food concentrations increase, the copepod must spend a higher proportion of search time in food capture and handling; thus the distribution of duration of slow swimming intervals is likely to deviate from normal, as is seen in Figs. 10 and 11. Williamson (1981) showed that freshwater copepods increase their turning rate in high food concentrations, thus altering their search pattern. Our observations of *C. typicus* behavior are consistent with this concept of a switch from random to directed search behavior in the presence of sufficient food stimuli. Directed search behavior will deviate from random in both duration of swimming events and duration of intervals between those events (Figs. 10, 11). Thus the activity pattern data reported here support the suggestions in the literature that predator search patterns are modified in response to changes in prey concentration (e.g. Williamson 1981). Further quantitative analysis of zooplankton behavior will shed further light on the underlying mechanisms which control food search, detection, and capture.

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