AN ABSTRACT OF THE THESIS OF

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Title: The Swimming Behavior of the Copepod *Calanus marshallae* under Various

Food Conditions

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Abstract approved:

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How certain aspects of the swimming behavior of the copepod Calanus

marshallae vary as a function of different food conditions of Thalassiosira weissflogii

was examined. A two video camera recording and controlled food environment

aquaria system were used to record long-term swimming behavior and to determine 3-

dimensional swimming paths during 24-hour and 4-hour experiments. The 24-hour

experiments examined how diel activity level varied with and without food. The 4-

hour experiments examined the following specific behavioral aspects: level of activity,

time allocation between swimming modes, periodicity within modes, and swimming

velocity.

Swimming activity followed a diel pattern when food was available and remained

relatively constant over a 24-hour period when food was not available. Swimming

activity was intermittent, and active intervals consisted primarily of two distinct

swimming modes: rise/sink and looping. A seasonal, or collection date, effect on

swimming activity level and mode existed, and may have been related to the onset of diapause.

Calanus marshallae modified two aspects of swimming behavior in response to exposure to food. First, non-feeding individuals did not exhibit looping behavior. Second, non-feeding individuals had higher rise swimming velocity compared to feeding individuals. However, none of the examined aspects of swimming behavior varied significantly among the different food conditions, independent of strong individual variation. Looping was more periodic and had significantly higher velocity than rise/sink swimming, yet both modes were effective methods of remaining in a favorable food patch. The absence of food condition effects suggest that swimming speed and duration alone may not reflect the food encounter process.

The Swimming Behavior of the Copepod <u>Calanus</u> <u>marshallae</u>
under Various Food Conditions

by

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Date thesis is presented_____January 24, 1991_____

Typed by Kevin P. Krefft for____Kevin P. Krefft_____

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INTRODUCTION

Copepods are the most abundant group of macrozooplankton (Raymont, 1983). As such, they form major energy pathways in marine food webs, and their feeding behavior may define the structure and dynamics of these food webs. Most copepods are thought to be omnivorous suspension feeders, whose ingestion varies with a diel rhythm (Raymont, 1983). They feed by moving their cephalic appendages at high frequencies in order to create water currents which direct suspended particles towards them (Koehl and Strickler, 1981). Potential food items in the suspension (e.g. phytoplankton and microzooplankton) are detected by mechanical and chemical receptors on the cephalic appendages (Strickler and Bal, 1973; Friedman and Strickler, 1975). Once detected, food items may be captured, and then either ingested or rejected with the cephalic appendages.

In addition to food capture, the cephalic appendage motion provides propulsion for swimming, and so there is a direct relationship between ingestion and swimming behavior. Calanoid copepods must move their cephalic appendages to capture food, and those appendage movements result in body translation though the water. In this study I used video recording methods to test the hypothesis that copepod swimming behavior varies as a function of experimental food conditions. In testing this hypothesis, I recorded the swimming behavior of female Calanus marshallae, a neritic calaniod copepod, under different food conditions. Calanus marshallae was chosen for

this study because it is a dominant zooplankter in the Oregon upwelling zone (Peterson, 1980), and the ingestion response of a congener, C. pacificus, is well known (Frost, 1972; Frost, 1975; Frost, 1977; Runge, 1980).

Background

Copepods are constantly moving, whether by passive sinking or active swimming, through a complex and dynamic environment. Vertically migrating copepods remain at depth during the day and then swim upward at night to feed on plankton populations near the surface. With plankton distributed in patches of various size and structure (e.g. Steele, 1978), it is likely that migrating copepods encounter diverse and unpredictable feeding environments. How they actually exploit the food in their environment and ingest specific items has been the focus of an extensive body of research.

Copepod Ingestion

Field studies of zooplankton have identified complex and diverse patterns of ingestion behavior. Feeding may have a diel rhythm (Dam, 1986; Head and Harris, 1987), it can respond to the specific food spectrum available (Richman et al., 1977), and large scale patterns of distribution influenced by behavior have strong effects on the diet (Boyd, et al., 1980).

Attempts have been made through laboratory investigation to understand the factors regulating food selection and ingestion rate in copepods. Two general relationships have emerged. First, ingestion rates increase as food concentration increases, leveling off when a "saturation" concentration is reached (e.g. Frost, 1972; Mullin et al., 1975). Second, ingestion rates at a given concentration increase with increasing food size (e.g. Frost, 1977). In addition, feeding history and food quality influence the rate of ingestion. Calanus pacificus, when starved (Runge, 1980), or acclimated to low food concentrations (Hasset and Landry, 1983), feeds at higher rates under most food concentrations than do well-fed individuals, or individuals acclimated to high food levels. More recent evidence indicates that food quality, defined by cellular nitrogen content of algal cells, also affects ingestion rate. Cowles et al. (1988) found that Acartia tonsa feed at higher rates, regardless of acclimation conditions, on fast-growing, high-nitrogen content populations of the diatom Thalassisira weissfloggi than on cells with lower nitrogen content.

Copepod Behavior

Direct observation of behavioral movements provide us with data to interpret copepod's response to environmental stimuli. These observations have taken several forms, from unaided, in-situ, observation (Hardy and Bainbridge, 1954), to video observations of swimming patterns in the laboratory (Buskey, 1984; Williamson, 1981; Wong and Sprules, 1986; Wong, 1988), to microcinematographic observations of

cephalic appendage movements (Alcarez et al., 1980; Paffenhofer et al., 1982; Cowles and Strickler, 1983; Price and Paffenhofer, 1984). These observations have provided important insights into copepod feeding and swimming behavior.

Microcinematography of Appendage Movement

Our understanding of feeding mechanics and behavior was significantly altered with the advent of microcinematographic observation methods. Microcinematography permits direct observation of how copepods search for, react to, and handle food items in a low Reynolds number environment where viscous rather than inertial forces dominate. High-speed microcinematographic observation by Koehl and Strickler (1981) indicated that the cephalic appendages of the copepod Eucalanus pileatus function more like paddles than food particle sieves during food capture. They also found that the flow field around the cephalic appendages could be altered to redirect and capture particles in response to some stimuli provided by the approaching food item. Subsequent research by Price et al. (1983) supported these findings and found that the mode of capture differed for large and small cells. There is also direct observational evidence that copepods can learn from acclimation experience. Price and Paffenhofer (1984) found for "experienced" Eucalanus pileatus that both increased ability to detect algal cells and decreased rejection rate contributed to higher ingestion rates. Similar active behavioral responses were observed by Cowles and Strickler (1983) using slow-speed microcinematographic techniques. They found that the

duration of periodic intervals of cephalic appendage activity depends on the available food species and concentrations.

Laboratory Observations of Swimming Behavior

Direct observations of free-swimming copepods, via video recording, enable us to measure the various aspects of swimming that define foraging behavior (e.g. velocity, directional orientation, turning frequency, pause frequency, activity level, and periodicity). Short-term (3-10 minutes), 2-dimensional video observations have documented species specific swimming behavior and have focused on how swimming velocity, turning frequency, and pause frequency are affected by food conditions.

Williamson (1981) found by this method that turning frequency increased at high food densities, and he concluded that it was an adaptive strategy to maintain the copepod in a concentrated food patch. Turning behavior was quantified by Buskey (1984) as the ratio between the net and gross swimming displacement, or NGDR. He found that NGDR remained relatively constant for Pseudocalanus minutus, yet it decreased swimming velocity and increased the number of "pauses" in the presence of either food or mechanical stimuli. Wong and Sprules (1986) found that swimming modes differed between copepods. For example, some species swam smoothly, predominantly in a horizontal plane, while others swam in an intermittently and vertically.

At present, no data exist which quantify specific aspects of copepod swimming behavior over time intervals greater than 10 minutes. Consequently, little is known about how swimming behavior changes as a function of food conditions over time scales of hours. In this study, I investigated swimming behavior over long periods to examine how swimming behavior varies as a function of food conditions. My specific objectives were to monitor activity level, swimming modes, and velocity over periods of hours. I incorporated several experimental design modifications to achieve this goal. First, while past research recorded swimming in 2-dimensions, I used two video cameras to determine 3-dimensional swimming paths and velocity. Second, since swimming activity and ingestion may vary over time, I recorded and monitored each copepod's activity in 4-hour experiments. Third, a large aquarium was used to minimize the copepod's contact with surfaces and other copepods while swimming.

METHODS

Field Collections

Calanus marshallae were collected 10 to 15 kilometers offshore of Newport, Oregon, aboard the R/V Sacajawea. A station was routinely occupied at 0900 hours, and a series of oblique tows were made through the 80 meter water column using a 1 m diameter, 0.333 μm mesh net. A 9.5 liter cod-end was used to minimize crowding and damage to the zooplankton. The cod-end contents were presorted with a 2000 μm mesh screen to exclude large gelatinous zooplankton. The smaller size fraction was then gently poured into several 8 liter, insulated containers, and diluted with surface water to reduce animal densities. Surface seawater was collected in 40 liter carboys for algal cultures, acclimation beakers, and experiments. The containers were transported to the College of Oceanography in Corvallis, Oregon within three hours of collection.

At the laboratory, the containers were placed in a 10 °C cold room and aerated. Healthy, adult, female C. marshallae were identified using a dissecting microscope and pipetted into 1 liter beakers (10 to 15 copepods per beaker) with the acclimation algal concentrations. Approximately 100 copepods were sorted and placed in a 10 °C cold room. Healthy, active copepods were transferred into fresh media each day. All seawater used in the cultures, acclimation beakers, and experiments was filtered through a 0.2 μm Ultipor DFA filter and stored at 10 °C.

Algal Cultures

The food source in all experiments was the centric diatom <u>Thalassiosira</u> <u>weissflogii</u>. It was grown in batch cultures of F/2 media (Guillard and Ryther, 1962) under two light intensities. Fast growth cultures (μ = 0.86/day) were grown under 250 μE/meter/sec at 10 °C, while slow growth (μ = 0.21/day) cultures were grown under 32 μE/meter/sec at 19 °C. Growth rates were determined from cell counts obtained daily with a ZBI Model D Coulter Counter fitted with a 100 μm aperture.

Temperature Controlled Aquarium

I required an unobtrusive video recording system and a controlled environment. This was achieved with a two camera system and an aquarium (Fig. 1) consisting of two parts, the "stage" and the "sleeve". Both were constructed of 0.25 inch, clear plexiglass. The stage, or inner container holding the copepods, was 20 X 20 X 20 cm (8.5 liters), the largest dimensions throughout which individual copepods could be resolved by the video cameras. The 30 X 30 X 30 cm sleeve functioned as a temperature regulating waterbath for the stage. The stage was mounted on pedestals in the sleeve and covered with clear plexiglass affixed with double-sided, foam tape. The stage was then immersed in 10 °C distilled water, chilled and recirculated by a refrigerator (Neslab Coolflow Model CFT-33).

Figure 1   The dual chambered aquarium and video recording system used in the experiments. The aquarium (aquaria) and the video cameras oriented at 90 degrees to each other are viewed from above. Video signals were synchronized with the sync stripper (Sync) and then split by a data insertion generator (Splitter). The split screen signal was displayed on the monitor and recorded on the VCR. The black circle shown in the aquaria represents an object which appears in the split screen images.

Figure 1
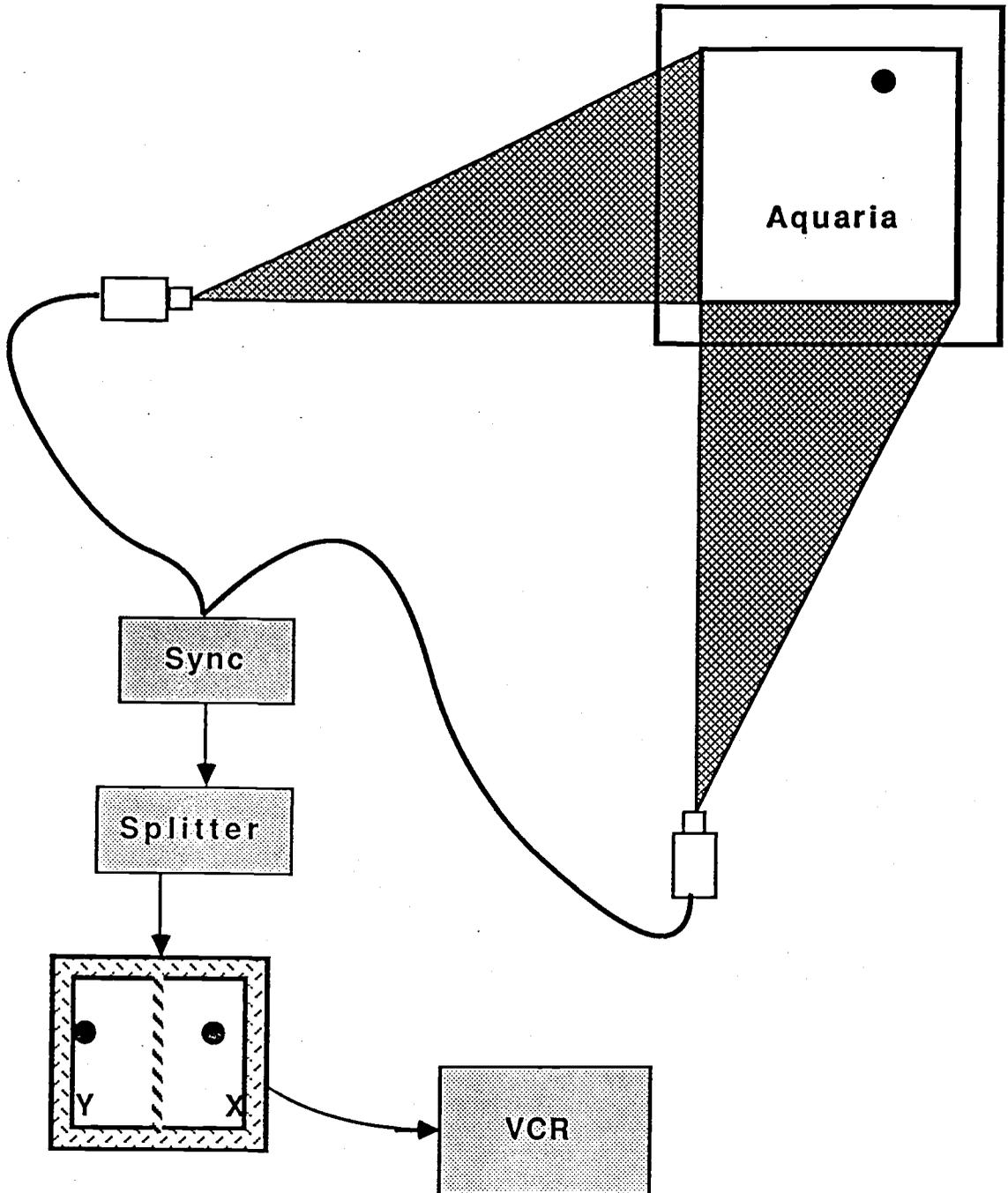
The recirculation inflow and outflow ports were on opposite corners of the sleeve aquarium. An airtrap in the inflow tubing removed air bubbles and provided a temperature monitoring point. All internal surfaces of the sleeve, except those between the cameras and the stage, were painted flat black to provide a uniform, nonreflective background.

Diatom Sinking Experiment

Diatom sinking is typically counteracted in ingestion experiments by some method of resuspension. Observation of undisturbed movement precluded resuspension of the algal food supply, so it was necessary to evaluate the importance of diatom sinking during a filming experiment. I tested the hypothesis that diatom concentration remained homogeneous in the stage aquarium over a 24 hour period. The diatom sinking experiment simulated a 24-hour video experiment and allowed precise water sample extraction for algal concentration determinations. An array of 9 glass tubes was mounted in a 20 X 20 cm, clear plexiglass sheet used to cover the stage aquarium. The glass tube ends were fixed at 3 depths (4,10,18 cm) in the stage aquarium, each depth was replicated 3 times with the resulting 3 X 3 matrix randomized. Water samples were collected from each glass tube at 3 hour intervals, in addition to samples collected after the first hour. The diatom suspension was sampled by inserting a 10 ml syringe into a short rubber tube affixed to each glass tube, withdrawing and discarding a 2 ml flushing volume, and then slowly extracting a 5 ml sample which

was preserved with 10% formalin. Cell concentrations for all 81 samples were determined using an electronic particle counter and compared in an ANOVA of randomized block design (Peterson, 1985). The null hypothesis that the cell concentration means at the three depths were equal was not rejected, and therefore the video experiments were conducted assuming a homogeneous distribution of diatoms in the stage aquarium.

Video Recording System

The video system was two Panasonic WV1350A video cameras with wide angle lenses (Cosmocar C815ES) oriented at 90 degrees to each other. Each camera centered 43 cm from the nearest corner of the sleeve aquarium, which placed a full view of the sleeve on half of the video image. Video signals at 60 fields sec^{-1} were synchronized with a sync stripper (Colorado Video Model 302-2), and then split by a data insertion generator (Colorado Video Model 603). The resulting split screen signal was displayed on a monitor (Panasonic Model WV5350) and recorded on a GYRR Time Lapse Recorder with Maxell P/I Plus T120 VHS tape. The right half of the split screen image corresponded to the X-Z plane of motion viewed by camera A, and the left half to the Y-Z plane viewed by camera B. Recording periodicity in the 24-hour experiments was controlled by a ChronTrol Model CD-4S timer.

The filming experiments were conducted in a photographic dark room, which significantly reduced light and sound disturbance. A single light source, a 400 watt

lamp 0.5 meters above the stage aquarium, provided light for dark field video recording. Stearns and Forward (1984) found that the calanoid copepod <u>Acartia</u> <u>tonsa</u> was primarily sensitive to light of 453 to 620 nm wavelength. So, to eliminate possible phototropic behavior the light was passed through a 15 X 15 cm Kodak Wratten Gel #70 filter, which excluded wavelengths less than 660 nm. In addition, the aquaria and cameras were shrouded with black cloth and plastic to further ensure that only far-red, downward-directed light illuminated the stage.

Experimental Design

Diel Swimming Activity

24-Hour Experiments

While the swimming response to food conditions was the primary focus of this study, I initially conducted 24-hour experiments to see how diel swimming activity varied with and without food (Table 1). The design of these experiments consisted of two food condition treatments replicated twice, with five individuals per experiment. The first treatment (1000-1000) had an acclimation food concentration of 1000 cells/ml and an experimental food concentration of 1000 cells/ml, while the second treatment (1000-FSW) had 1000 cells/ml acclimation condition with filtered seawater (FSW) for the experimental condition.

Table 1   Experimental design used to examine diel swimming activity. All experiments utilized _Thalassiosira weissflogii_ as the food source for the adult _Calanus marshallae_ females.

Acclimation	Experiment	Collect Date	Expt. Date	Start Time	# Copepod
(cells/ml)					
1000	1000	9/9/86	9/10-11	1600	5
		11/5/86	11/6-7	1900	5
1000	FSW	2/6/87	2/7-8	1600	5
		8/13/87	8/14-15	1700	5

Generally recording commenced at 1600 hours. The starting time for the 6 November 1000-1000 experiment was offset to 1900 hours to determine the effect on activity patterns of "handling" prior to the experiment. Recording of these 24-hour experiments was periodic (half-hour on / half-hour off), producing 12 hours of discontinuous record from each experiment.

Swimming Behavior

4-Hour Experiments

The 4-hour experiments consisted of four food condition treatments (Table 2). Initially, the goal was to document and digitize the swimming of 10 individuals per treatment with equal replication of treatments and of digitized individuals per treatment. However, as the experiments progressed it became apparent that equal replication was not possible because of strong individual variation. In some experiments one or more individuals were inactive or limited their activity near surfaces in the stage aquarium where digitization was impossible. At other times, air bubbles not vented by the air trap collected on the tank surfaces and significantly restricted digitization of active individuals. Therefore, in order to increase the probability of digitizing one or more copepods, the number of individuals per experiment was increased in the later experiments (see Table 2).

Table 2   Experimental design used to examine how aspects of swimming behavior varied as a function on food conditions. All experiments utilized <u>Thalassiosira</u> <u>weissfloggi</u> as the food source. <u>T.</u> <u>weissfloggi</u> used in the 2500+ experiment (+ indicates high-nitrogen content) were grown under low light conditions. The number of individuals providing digitized swimming sequences per experiment, or (# Dig), did not always equal the number of individuals per experiment, or (# Copepods). The number of swimming sequences digitized per experiment is expressed as (N).

Acclimation (cells/ml)	Experiment	Collection Date	Expt. Date	# Copepods	# Dig	N
1000	1000	9/21/86	9/22/86	3	3	18
		10/5/86	10/6/86	4	4	6
		11/5/86	11/6/86	5	2	3
1000	2500	10/5/86	10/8/86	4	4	12
		10/5/86	10/10/86	4	1	2
		11/5/86	11/9/86	4	1	19
		3/14/87	3/15/87	4	4	6
FSW	2500	8/13/87	8/16/87	10	4	12
			8/20/87	10	6	20
1000	2500+		8/18/87	10	5	16
			8/19/87	10	4	15
1000	FSW		8/14-15/87	5	1?	5*
				68	38	129

? - Sequences digitized from several half-hour time intervals in 24-hour experiments.
* - 24-hour experiment.

I recorded the behavior of 68 copepods in 11 experiments, and 129 sequences were digitized from 38 of these individuals. The 129 digitized sequences varied in duration from 15.0 to 76.9 seconds (mean = 42.3 seconds/sequence), and the duration digitized per copepod ranged from 16.4 to 891.8 seconds (mean = 143.6 seconds digitized/copepod). The 129 digitized sequences equaled 90.9 minutes of swimming path and velocity data, or one percent of the total copepod-minutes recorded during the 11 4-hour experiments. An additional 5 sequences were digitized from individual(s) in the August 14-15 1000-FSW 24-hour experiment as a control for non ingestion related swimming behavior.

Experimental Protocol

I established a consistent procedure for preparation and culmination of the 4-hour and 24-hour experiments. The copepods acclimated first for 24 hours in the appropriate algal concentrations at 10 °C. The stage and sleeve aquaria were cleaned with dilute detergent, rinsed thoroughly with distilled water, and stored in the cold room. Twenty liters of distilled water were cooled to 10 °C by the Neslab recirculator. Thalassiosira weissfloggii batch culture and filtered seawater were combined to yield 8.5 liters of the desired algal concentration, and a sample was extracted for Coulter Counter verification of the concentration.

The aquarium and video system were set up less than 30 minutes prior to video recording. First, the selected number of copepods were isolated from the acclimation

beakers in the 10 °C cold room. The aquaria were mounted in place, then the stage was filled with 8 liters of food media, and its walls were cleared of air bubbles. The copepods were then pipetted into the stage and the cover was sealed. Next, the sleeve was flooded and the light source, gel filter, and incident light shrouds were put in position. After recording the water temperature at the air trap, video tape recording was initiated.

The dark room was left undisturbed during video recording, except to switch video tapes, in order to minimize external disturbances which could affect copepod behavior. Tape switching in the 4-hour experiments occurred before the first 2-hour tape ended, which prevented gaps in observation. Recording in the 24-hour experiments was on a half hour on / half hour off cycle, so tapes were switched every 4 hours. Water temperature was recorded at each tape exchange. The copepods were collected and preserved in 10% formalin at the end of each experiment.

Videotape Analysis

Videotape analysis consisted of swimming activity documentation and the digitization of selected swimming sequences. Activity was defined simply as any swimming in which an individual avoided repeated contact with the stage aquarium surfaces, primarily the bottom. Swimming activity was documented differently in the 4-hour and 24-hour experiments. In the 24-hour experiments, the recording discontinuity prohibited construction of individual activity profiles longer than 30

minutes, so within each half hour segment I counted how many individuals were active each minute and then summed to yield active minutes per half hour. For example, one copepod active for 20 minutes during a half hour segment was equivalent to two copepods active for 10 minutes (i.e. 20 active minutes). In the 4-hour experiments detailed individual activity profiles were constructed. An activity profile consisted of a minute by minute determination of each copepod's activity level (i.e. active or inactive) and swimming mode (rise/sink, looping, or directed swimming).

The tapes were digitized by replaying a swimming sequence through the data insertion generator and a X-Y Digitizer (Colorado Model 622), which digitized (with 8 bit resolution and at 60 fields per second) the brightest pixel in the video field and sent the pixel coordinates to a data acquisition board in an Apple II+ microcomputer. The video signal was masked with the data insertion generator, except for the area adjacent to the selected individual, because the digitizer was limited to tracking one pixel per video field, which always contained multiple bright images (e.g. air bubbles, other copepods, stage edges). The X-Z and Y-Z coordinates of each sequence were digitized separately from the split screen video tape. The data were stored on diskette, then transferred to an IBM PC/XT for data processing and analysis.

Processing the "raw", 60 Hz, X-Z and Y-Z data pairs to produce "clean", 30 Hz X-Y-Z data involved four steps; (1) bad data (improbable moves) were identified and interpolated, (2) data pairs were synchronized, then (3) combined, and (4) field distortion due to lateral offset of the camera was corrected. In step (1) erroneous coordinate data pairs were identified by comparing pixel brightness levels against a

threshold detection value, or by noting the occurrence of multiple bright pixels per field. Bad sequences shorter than 0.3 seconds were assigned interpolated values based upon preceding and succeeding positions. On completion of this process the X-Z and Y-Z pairs were combined as X-Z-Z-Y data strings.

Synchronization of the X-Z and Y-Z data pairs was necessary since each coordinate pair was digitized separately. The GYRR video recorder had time/date display and a digital tape counter, and both time and count were noted at the start and finish of each selected sequence. Since the time display was electronically masked during digtization, the tape count served as the reference starting point for digitization of both planes of motion. The tape counter lacked precision, so offset of 1 to 2 seconds between the X-Z and Y-Z data pairs was common. The data pairs shared a common Z coordinate, so the synchronization was determined by locating the offset at which the sum of squared differences (SSD) between the two Z coordinate data strings was minimized. The data strings were incrementally offset, or lagged, relative to each other up to 500 times in both directions. At each lag the SSD was computed, and the minimum SSD was chosen as the most likely synchronization point of the data strings. The offset was corrected and one of the shared Z coordinates was dropped, resulting in a synchronized 60 Hz X-Y-Z data time series. The 60 field per second digitization alternated between even and odd numbered video fields, so the 60 Hz XYZ data were reduced to 30 Hz to remove this high frequency noise.

The image distortion caused by the projection of three dimensions onto two dimensions was corrected by manually digitizing the pixel coordinates of the stage

aquarium corners. The vertical and horizontal pixel displacements were then corrected using these coordinates and the true XYZ position was calculated. The velocity components (e.g. positive velocity = upward motion, negative velocity = downward motion) were then calculated from the successive XYZ distances in units of centimeters per second (cm/sec). A velocity resolution of 0.007 cm/sec was estimated by dividing the pixel diameter (0.2 cm) by the sampling rate (30 Hz). The 30 Hz velocity data were then smoothed with a 7-point running-average filter for time domain analysis, and with a 7-point Bingham cosine filter for frequency domain analysis (Bendat and Piersol, 1966). The spectral density of velocity was calculated using the Fast Fourier Transform method, and these spectral estimates were band averaged to yield 10 degrees of freedom (Bendat and Piersol, 1966).

RESULTS

Diel Swimming Activity

Activity during each half hour segment of the 24-hour experiments was standardized as a percentage of the total possible active minutes, or percent time active (PTA). Two general trends in PTA emerged: 1) PTA in all experiments was low, (means were 3.6, 4.1, 6.3, and 12.3), and 2) when food was available activity followed a diel pattern. The log transformed PTA was compared among experiments using the T-method for equal sample size (Sokal and Rohlf, 1981). Only the Feb. 7-8 experiment differed significantly from the others (Fig. 2). In both experiments with food the PTA was highest from approximately 1900 to 0300 hours and lowest from 0400 to 1400 hours, while activity was relatively constant among individuals in the FSW experiments. In order to determine if there was a diel activity pattern, I compared the PTA during the first 12 hours (1600-0400) (which included the peak activity hours) of the experiments to the PTA over the last 12 hours of the experiments (0400-1600) (T-method). The PTA during the nighttime hours was significantly greater than during the daytime hours when food was available, yet did not differ significantly when food was not available (Fig. 3). These results indicated that nighttime recording of behavior would result in the highest activity levels.
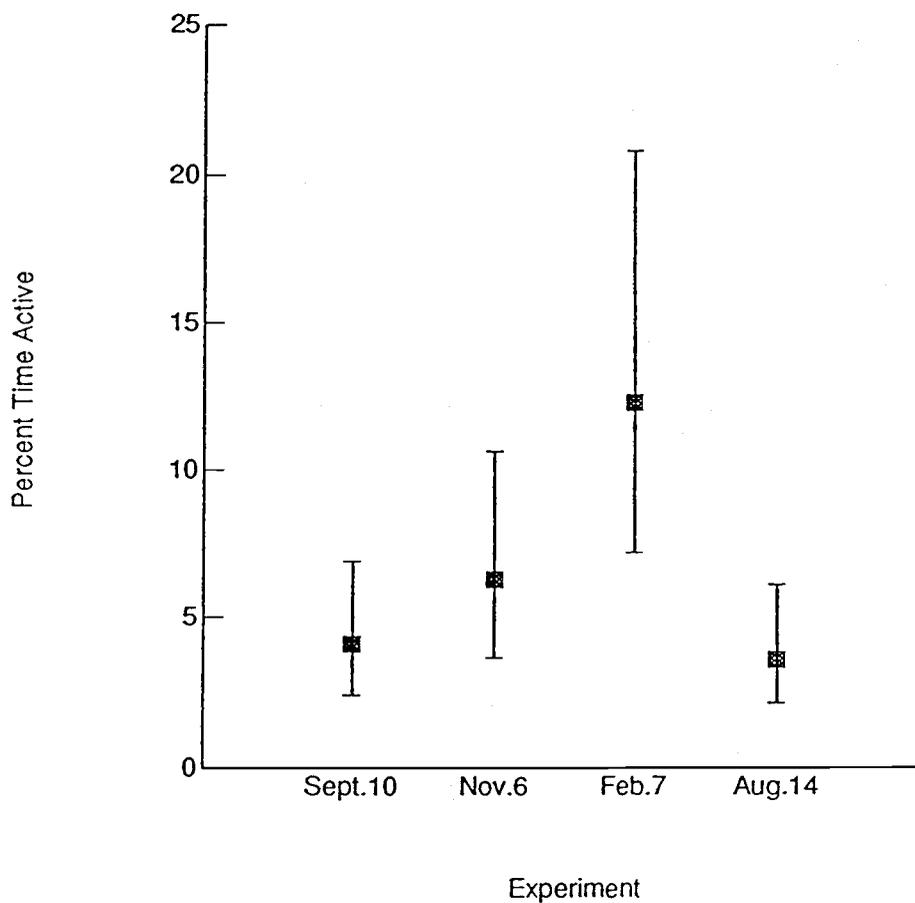
Figure 2   Comparison of activity level among the 24-hour experiments: the T-method. 95% comparison intervals plotted for log transformed percent time active (PTA) from the September 10, 1986 and November 6, 1986 1000-1000 24-hour experiments, and the February 7, 1987 and August 14, 1987 1000-FSW 24-hour experiments. Means whose intervals do not overlap are significantly different.
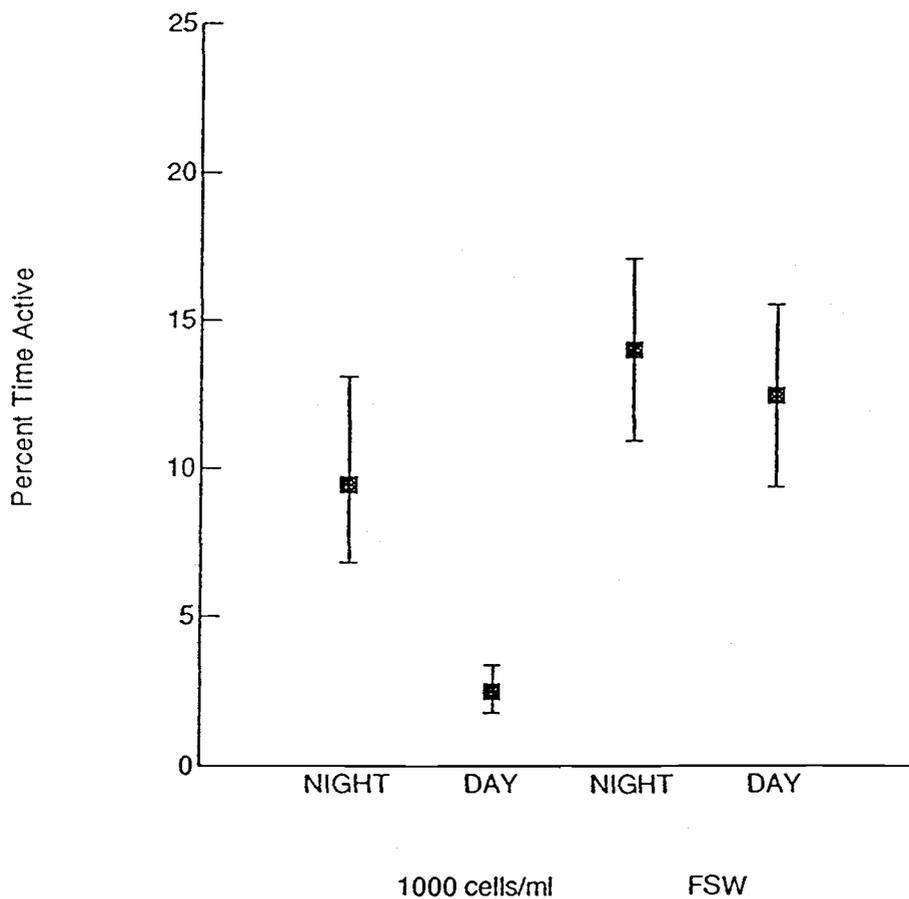
Figure 3   Comparison of activity level between nighttime and daytime: the T-method. 95% comparison intervals plotted for percent time active (PTA) for: (NIGHT) the first 12 hours of the 1000-1000 24-hour experiments; (DAY) the last 12 hours of the 1000-1000 24-hour experiments; (NIGHT) the first 12 hours of the 1000-FSW 24-hour experiments; (DAY) the last 12 hours of the 1000-FSW 24-hour experiments. Means whose intervals do not overlap are significantly different.

General Swimming Behavior

Calanus marshallae generated swimming motions almost solely by the cephalic appendages. The larger thoracic appendages (swimming legs) were used only for brief flight in response to contact with the stage aquaria surfaces, other individuals, or in rare, seemingly unprovoked, jumps. Swimming was intermittent, as individuals alternated between distinct active and inactive periods. An actively swimming individual infrequently contacted the stage aquarium surfaces. When contact was made with a surface, an active copepod either moved away in a startled, fast response, or slowly resumed swimming. If the encounter was with the bottom, an active individual occasionally remained there for up to several minutes before resuming active swimming. Inactive copepods were closely associated with the stage bottom, either lying on the bottom or, more commonly, "tail-hopping". Tail-hopping copepods were oriented with the urosome down. They passively sank until the caudal setae contacted the bottom, and then they swam slowly up several body lengths, only to passively sink and repeat the process. While tail hopping copepods were swimming with the cephalic appendages, it seemed that the appendage motion was in response to contact with the bottom and not hunger.

Active C. marshallae predominantly swam in two modes: rise/sink and looping. These swimming modes were readily distinguishable, yet shared several basic characteristics: vertical orientation, apparent periodicity, and low net to gross displacement ratio. Rise/sink was essentially a mid-water version of tail hopping. The

main body axis was nearly vertical with urosome down. Cephalic appendage movement produced upward swimming (rise), then cessation of appendage movement resulted in sinking (Fig. 4). Looping, in contrast, was produced by continuous appendage motion, and the copepod's path described a series of vertically oriented loops (with ventral surface outward) (Fig 5). Interestingly, copepods in the 24-hour 1000-FSW experiments never exhibited looping behavior, which suggested that looping was a feeding- dependent swimming mode.

Of the 129 digitized sequences, 62 were rise/sink sequences from 21 copepods that spent most of their active time in rise/sink behavior. Another 15 were looping sequences from 12 copepods that generally divided their active time more equally between the two swimming modes. Each of the remaining 52 sequences contained both rise/sink and looping behavior from the 5 remaining copepods.
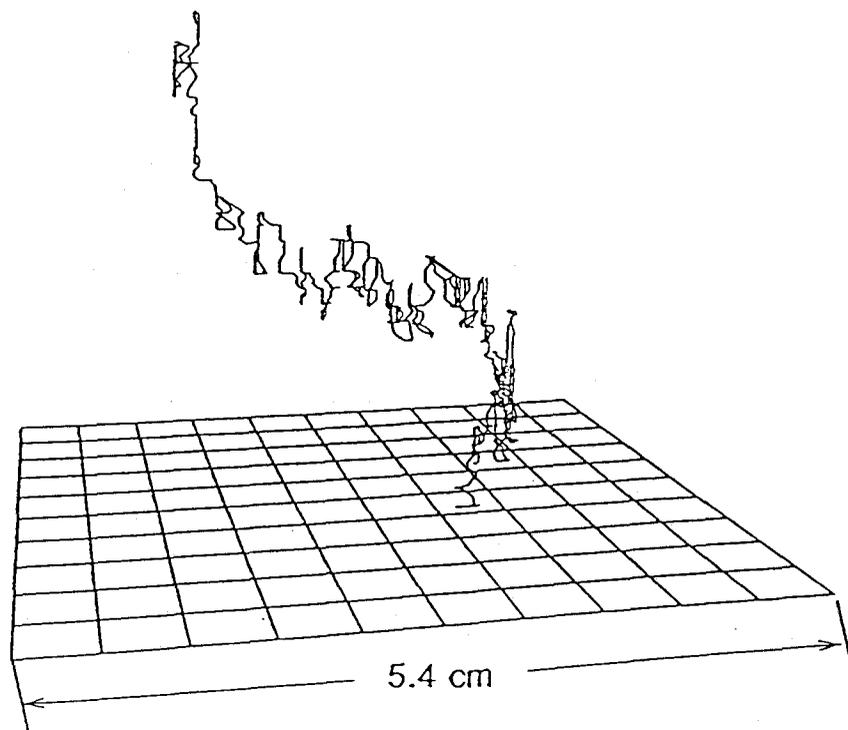
Figure 4   A typical path described during rise/sink swimming. The path shown was traversed in 52.1 seconds. Note distance scale below swimming path.

11.0 cm
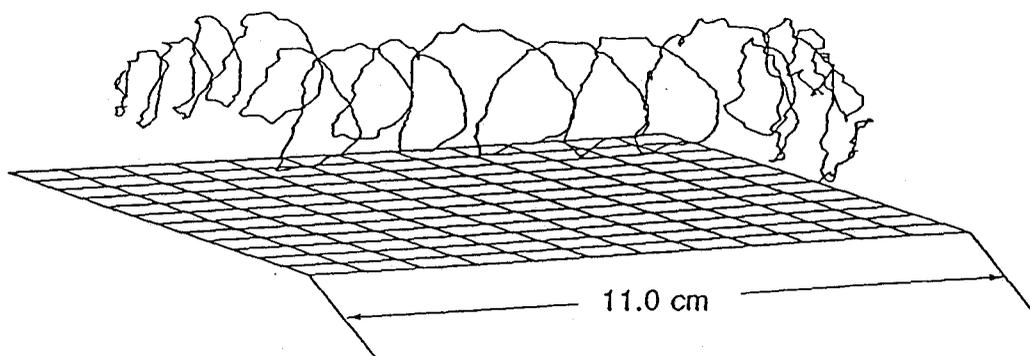
Figure 5   A typical path described during looping swimming. The path shown
was traversed in 73.9 seconds. Note distance scale below swimming
path.

Swimming Activity

Each copepod's active time was standardized as a percentage of the experiment duration, or percent time active (PTA). The PTA among the 68 individuals was extremely variable: mean = 25.1, standard deviation = 27.86 (Fig. 6). The experimental PTA variances were heterogeneous ($P < 0.005$; Bartlett's test; Sokal and Rohlf, 1981), and remained so after arcsine transformation ($P < 0.01$). Given this heterogeneity, I examined the activity trends with non-parametric statistical methods. PTA differed significantly among treatments ($P < 0.01$; Kruskal and Wallis test; Sokal and Rohlf, 1981) and experiments ($P < 0.005$) when all experiments were considered. The October 6 and October 8 experiments, however, had very high PTA (means = 70.5 and 89.3 respectively) and differed significantly from all other experiments ($P < 0.01$; Wilcoxon two-sample test; Sokal and Rohlf, 1981). When the statistical comparisons were recalculated with the October 6 and October 8 experiments omitted, the PTA did not differ significantly among treatments.

As stated in the Methods section, swimming sequences of 38 individuals were digitized. The 30 other copepods recorded but not digitized were mostly individuals with reduced activity (mean PTA = 8.7, standard deviation = 14.94), while the 38 digitized individuals were more active; mean PTA = 37.9, standard deviation = 29.04 (Fig. 7). The experimental PTA variances among the 38 individuals were also heterogeneous ($P < 0.01$) and arcsine transformation failed to reduced the heterogeneity ($P < 0.005$).

Figure 6   Percent time active (PTA) plotted for the 68 individuals in the 11 4-hour experiments.   The 68 individuals are grouped according to experimental date and food condition treatment.   Mean PTA = 25.1, standard deviation = 27.86.
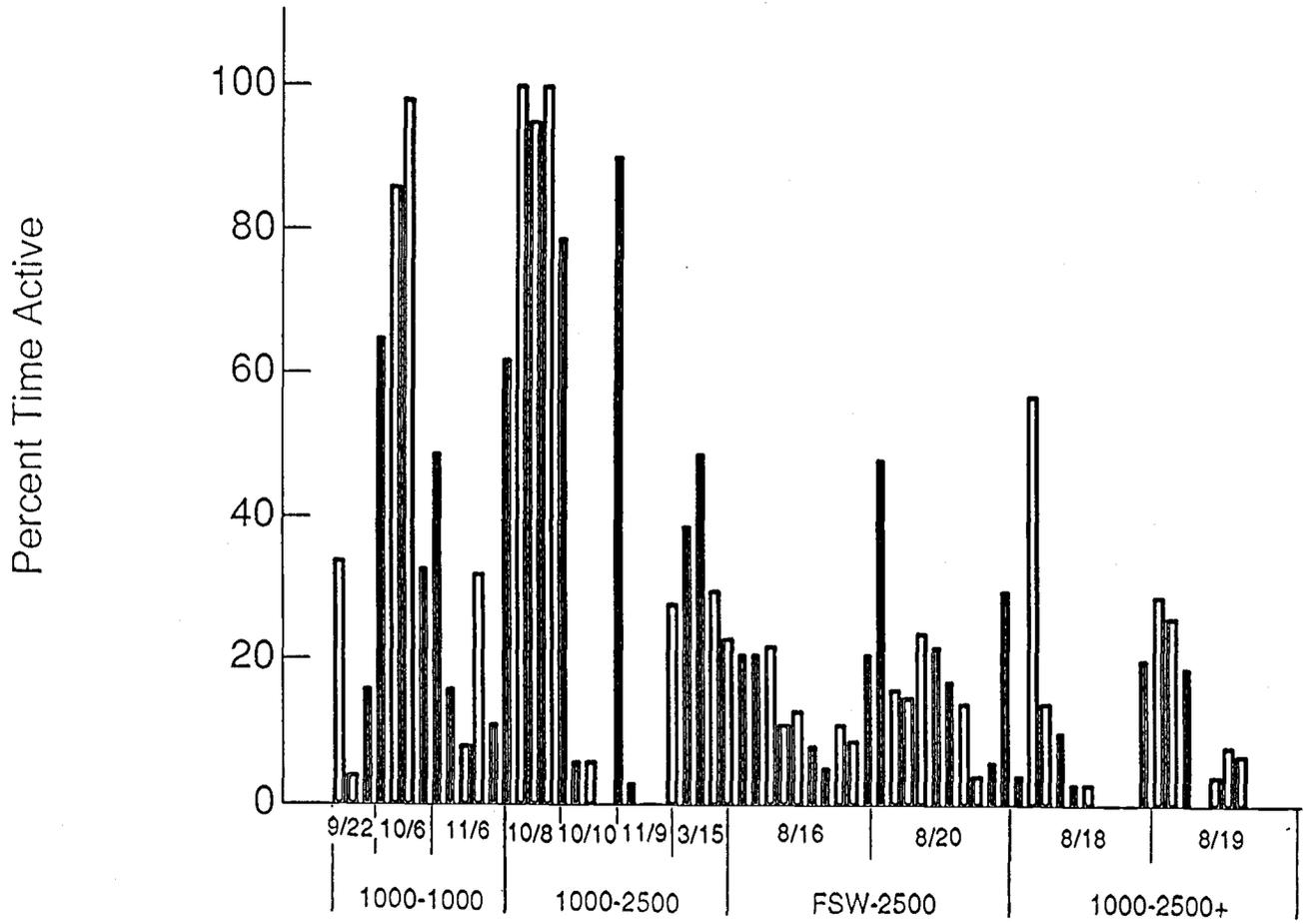
Figure 6

Figure 7   Percent time active (PTA) for the 38 digitized individuals from the 11 4-hour experiments plotted as stacked bars. Precent time active spent rise/sinking (open bars) and looping (shaded bars) plotted for each individual. The 38 individuals are grouped according to experimental date and food condition treatment. Mean PTA = 37.9, Standard deviation = 29.04.
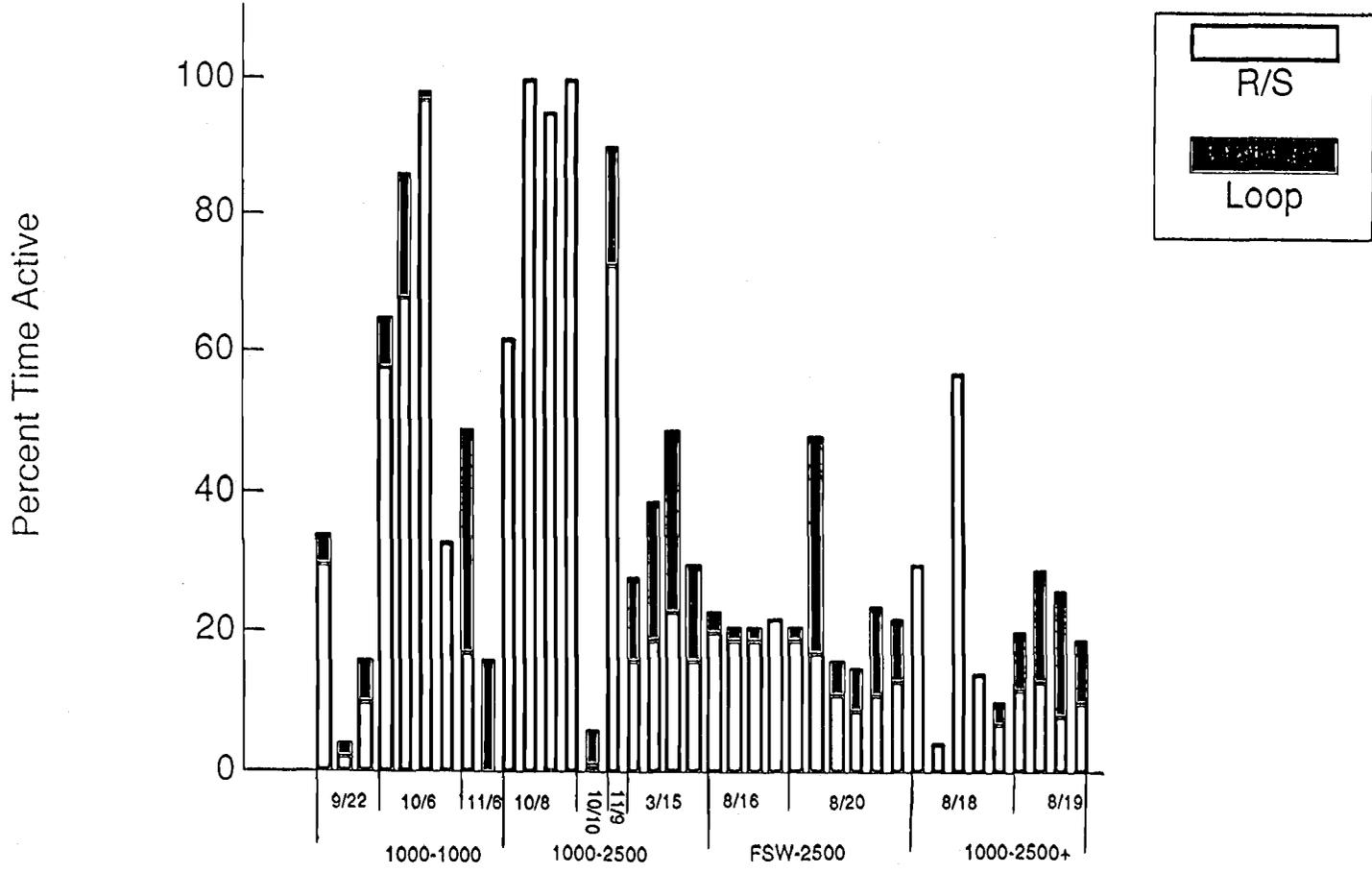
Figure 7

The PTA of the 38 digitized individuals differed significantly among experiments ($P < 0.005$) and treatments ($P < 0.01$), and again the October 6 and 8 experiments differed significantly ($P < 0.01$) from all other experiments. The significant differences among treatments disappeared when these October experiments were omitted from the analysis.

Swimming Mode

Time spent in rise/sink and/or looping behavior by each digitized copepod was standardized as a percentage of the total active time. Generally, the rise/sink mode was used more often (mean = 70.8%) than the looping mode (mean = 29.2%), but time spent in both modes was highly variable (Fig. 7). The experimental variances were extremely heterogenous even after arcsine transformation ($P < 0.005$). Time allocation between the two modes was not affected by food conditions, but differed significantly between experiments (Kruskal and Wallis test; $P < 0.005$). The percentage of active time spent in rise/sink behavior was very high in the October 6 and 8, and August 16 and 18 experiments (means = 91.8, 100, 90.8, 94.6 respectively), differing significantly from the other experiments ($P < 0.01$).

Spectral analysis of the velocity time series revealed that some rise/sink and all looping sequences were strongly periodic, as evidenced by the significant peaks of spectral density (Fig. 8). Typically, periodic rise/sink's duty cycle (i.e. the time duration of consecutive rise and sink events) was approximately 2 seconds, while

Figure 8   Spectral density plots of representative rise/sink and looping velocity
time series. Plotted as log of the spectral density (i.e. variance) versus
log of frequency (Hz). (a) non-periodic rise/sink mode in 1000-FSW;
(b) periodic (2 second period) rise/sink mode in 1000-1000; (c) periodic
(4 second period) looping in 1000-2500; (d) periodic (5 second period)
looping in 1000-1000.

Figure 8
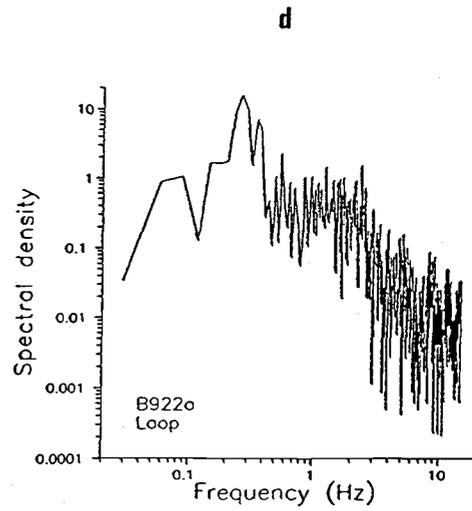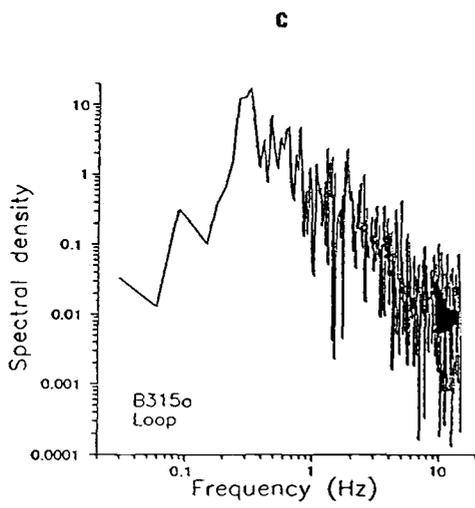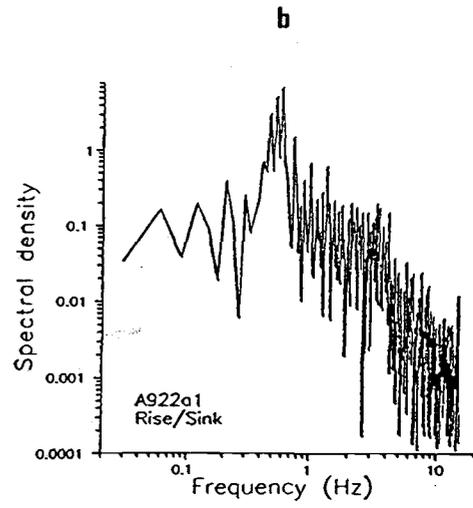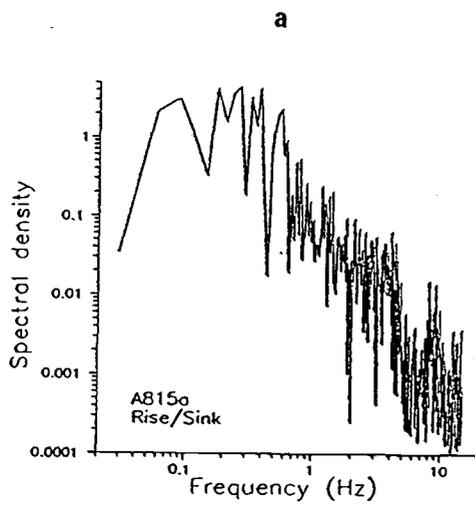
looping had a longer period of 4 to 5 seconds. Many rise/sink sequences were not strongly periodic, which suggested that the duty cycle was variable, and at times more random.

Given that many of the rise/sink sequences were not strongly periodic, I examined duty cycle variation among the 62 rise/sink sequences (from 21 individuals) by comparing the frequency distributions of rise interval and sink interval durations (Fig. 9). The rise and sink duration data posed two analysis problems that prevented rigorous statistical interpretation. First, the 62 rise/sink sequences did not provide sufficient replication of experiments. Second, the non-parametric analysis could not identify the sources of significant variation. The results indicated that the duty cycle differed significantly between individuals (Table 3, Wilcoxon test; $P < 0.05$). For example, the frequency distribution of rise interval duration for the individual in Figure 9b shows a duration mode of 1.4 seconds, while the duration mode for individual in Figure 9d was 0.9 seconds. In addition, rise duration tended to be more similar within an experiment than between experiments.

Rise/sink behavior was also characterized by a particular orientation in swimming direction. Generally, rise and sink directions were nearly vertical, but varied significantly among individuals (Fig. 10), but with no distinct trends attributable to experiments or treatments (Table 4, Wilcoxon test; $P < 0.05$).

Figure 9   Frequency distributions of rise event duration and sink event duration. Duration bin intervals equal 0.25 seconds. Sink event durations represented on X-axis by negative (-) time intervals. Rise event durations represented on X-axis by positive time intervals. (a) individual from 1000-FSW; (b) individual a922 from 1000-1000; (c) individual d818 from 1000-2500+; (d) individual b816 from FSW-2500.

Figure 9

(a)

(b)

(c)

(d)

Table 3   Wilcoxon Test matrix for comparisons of rise event and sink event duration from the 62 rise/sink sequences from 21 individuals. Sequences for the three individuals in the October 6 experiment were pooled. The symbol (X) at the intersection of two individuals indicates that those individuals event durations differ significantly ($P < 0.05$). (a) Rise duration comparisons; (b) Sink duration comparisons.

Table 3

1000-1000	9-22	A922	A922	B922	A106	A108	B108	C108	D108	A119	A816	B816	C816	D816	A818	B818	C818	D818	E818	A819	FSW
1000-1000	9-22	A922	╲	x		x	x	x	x		x	x	x		x	x	x	x	x	x	
1000-1000		B922	x	╲	x	x	x	x	x	x				x	x		x				x
1000-1000	10-6	A106		x	╲	x	x	x	x		x	x	x		x	x	x	x	x	x	x
1000-2500	10-8	A108	x	x	x	╲				x	x	x	x	x	x	x	x	x	x	x	x
1000-2500		B108	x	x	x		╲			x	x	x	x	x	x	x	x	x	x	x	x
1000-2500		C108	x	x	x			╲		x	x	x	x	x	x	x	x	x	x	x	x
1000-2500		D108	x	x	x				╲	x		x		x		x					x
1000-2500	11-9	A119		x		x	x	x	x	╲		x	x		x	x	x	x	x	x	
FSW-2500	8-16	A816	x		x	x	x	x			╲			x	x		x				x
FSW-2500		B816	x		x	x	x	x	x	x		╲		x	x		x	x	x		x
FSW-2500		C816	x		x	x	x	x		x			╲	x	x		x				x
FSW-2500		D816		x		x	x	x	x		x	x	x	╲	x	x	x	x	x	x	
1000-2500+	8-18	A818	x	x	x	x	x	x	x	x	x	x	x	x	╲		x				x
1000-2500+		B818	x		x	x	x	x	x	x				x	x	╲	x	x	x		x
1000-2500+		C818	x	x	x	x	x	x		x	x	x	x	x		x	╲				x
1000-2500+		D818	x		x	x	x	x		x			x		x		x	╲			x
1000-2500+		E818	x		x	x	x	x		x			x		x		x		╲		x
1000-2500+	8-19	A819	x		x	x	x	x	x					x						╲	x
FSW		FSW		x	x	x	x	x	x		x	x	x		x	x	x	x	x	x	╲

(second matrix, same row/column layout)

1000-1000	9-22	A922	A922	B922	A106	A108	B108	C108	D108	A119	A816	B816	C816	D816	A818	B818	C818	D818	E818	A819	FSW
1000-1000	9-22	A922	╲		x	x	x	x						x	x	x		x	x	x	x	x
1000-1000		B922		╲	x	x										x		x		x		x
1000-1000	10-6	A106	x	x	╲	x	x	x		x	x	x	x		x	x	x	x	x	x	
1000-2500	10-8	A108	x	x	x	╲		x		x	x	x	x		x		x				x
1000-2500		B108	x		x	x	╲						x	x	x		x		x		x
1000-2500		C108	x		x			╲	x	x		x		x		x					x
1000-2500		D108				x		x	╲				x		x		x	x	x	x		
1000-2500	11-9	A119			x	x		x		╲		x	x	x		x	x	x	x	x	x
FSW-2500	8-16	A816			x	x					╲			x		x		x		x	x
FSW-2500		B816			x	x		x				╲	x	x	x		x	x	x		x
FSW-2500		C816	x		x				x	x			╲	x		x		x		x	x
FSW-2500		D816	x			x	x	x		x		x	x	╲	x	x	x	x	x	x	x
1000-2500+	8-18	A818	x	x	x		x		x	x	x	x	x	x	╲	x		x			x
1000-2500+		B818			x	x								x	x	╲	x		x		x
1000-2500+		C818	x	x	x		x	x	x	x	x	x	x	x		x	╲	x	x		x
1000-2500+		D818	x		x				x	x		x			x		x	╲	x		x
1000-2500+		E818	x	x	x		x		x	x	x	x	x	x		x	x	x	╲		x
1000-2500+	8-19	A819	x		x				x	x		x		x						╲	x
FSW		FSW	x	x		x	x	x		x	x	x	x	x	x	x	x	x	x		╲

Figure 10   Frequency distributions of rise event direction and sink event direction. Direction bin intervals equal 0.26 radians, and expressed as Phi, the angle subtended from the vertical Z-axis. Vertical up = 0.0 radians; Vertical down = 3.14 radians. (a) individual from 1000-FSW; (b) individual a922 from 1000-1000; (c) individual d818 from 1000-2500+; (d) individual b816 from FSW-2500.
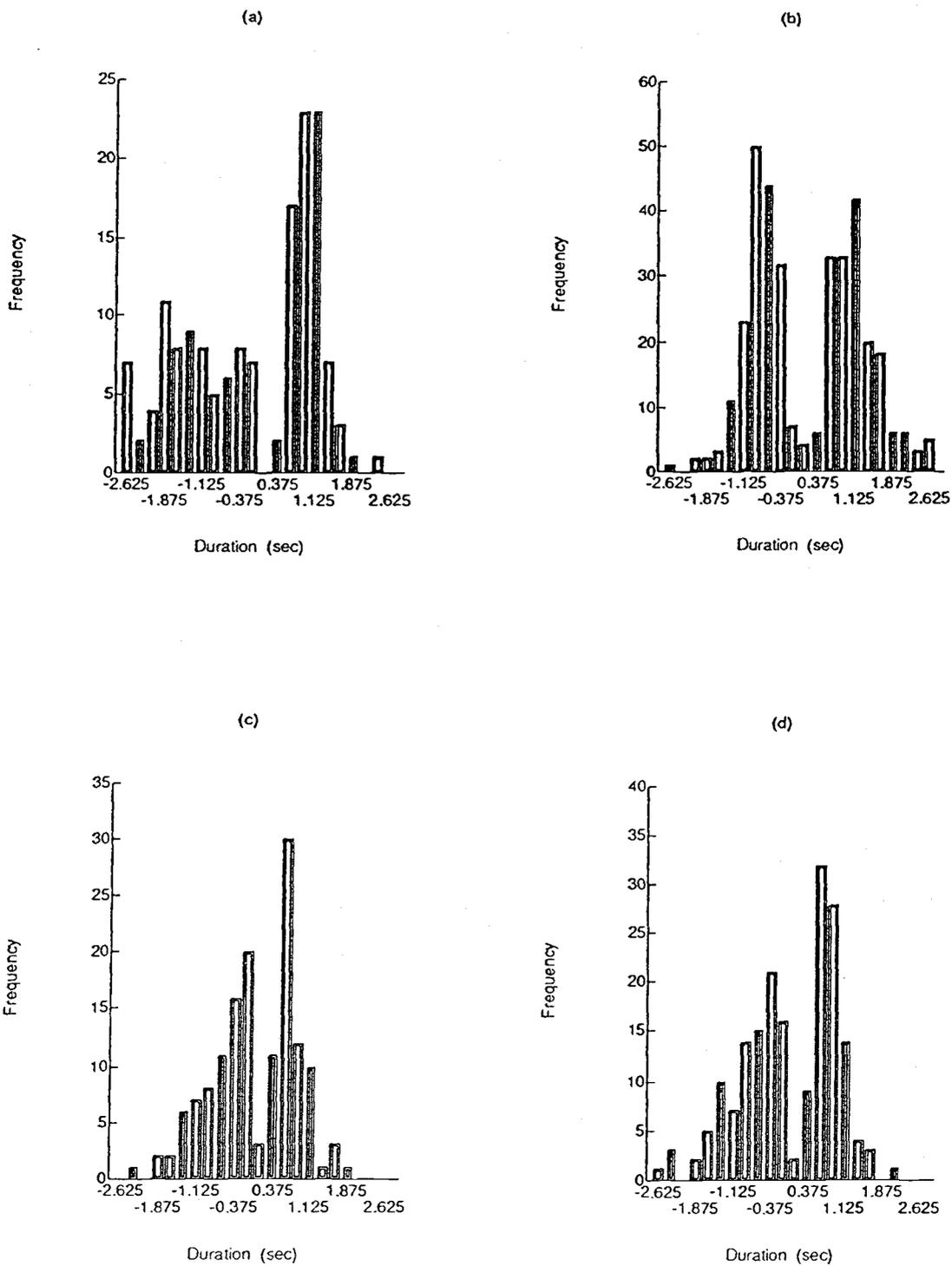
Figure 10

(a)

(b)

(c)

(d)

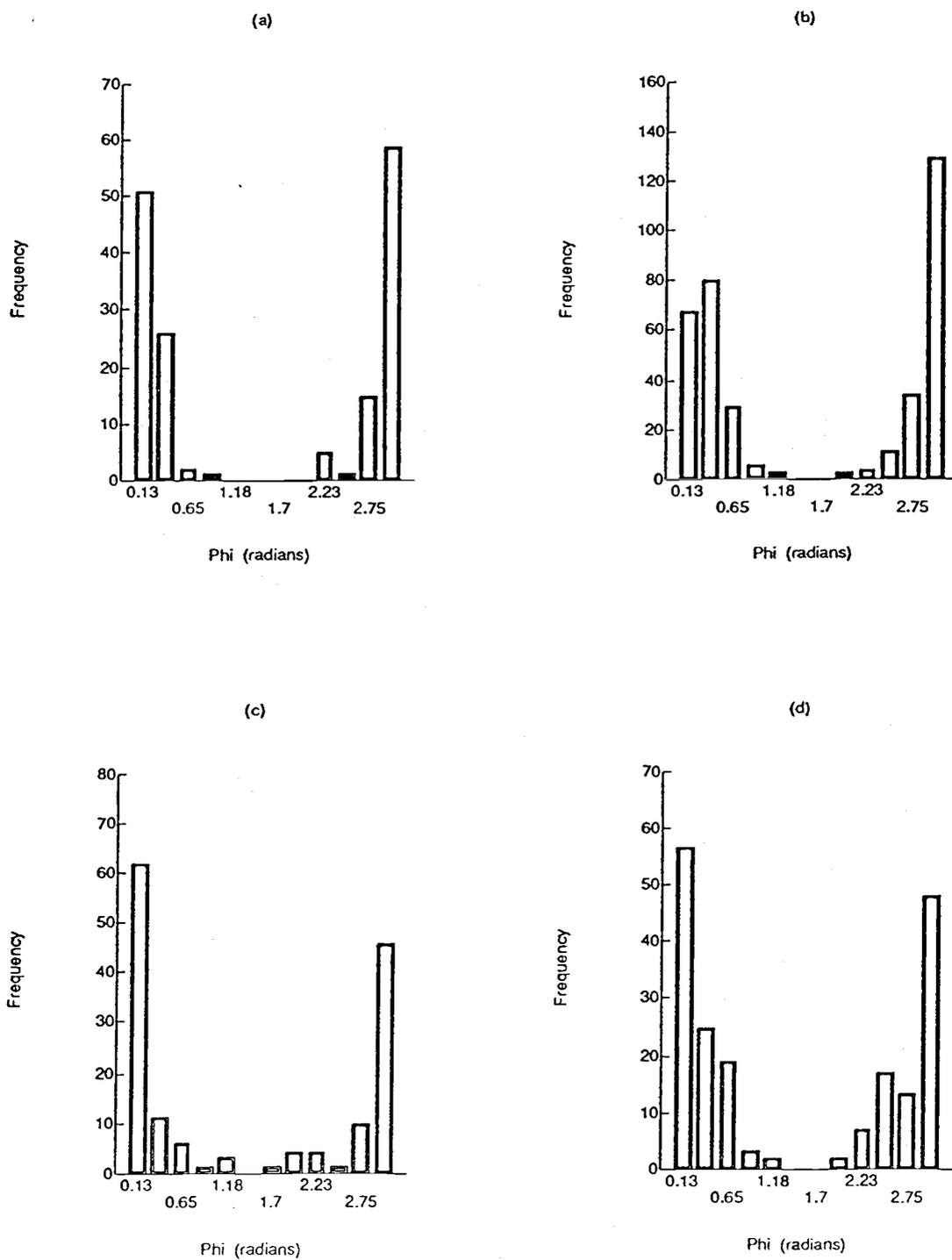Table 4   Wilcoxon Test matrix for comparisons of rise event and sink event direction from the 62 rise/sink sequences from 21 individuals. Sequences for the three individuals in the October 6 experiment were pooled. The symbol (X) at the intersection of two individuals indicates that those individuals event directions differ significantly ($P < 0.05$). (a) Rise direction comparisons; (b) Sink direction comparisons.

Table 4

			A922	B922	A106	A108	B108	C108	D108	A119	A816	B816	C816	D816	A818	B818	C818	D818	E818	A819	FSW
1000-1000	9-22	A922	/		x	x				x	x	x	x	x		x		x			x
		B922		/							x		x			x					
	10-6	A106	x		/	x			x	x	x					x				x	
1000-2500	10-8	A108	x		x	/	x	x	x	x	x	x	x	x	x	x	x	x	x		x
		B108				x	/				x		x			x		x			
		C108				x		/			x		x			x		x			
		D108		x		x			/		x	x	x	x		x					
	11-9	A119	x		x	x				/	x		x	x		x		x	x		x
FSW-2500	8-16	A816	x	x	x	x	x	x	x	x	/		x	x	x	x	x	x	x	x	x
		B816	x		x				x		x	/	x			x		x	x		
		C816	x	x		x	x	x	x	x	x		/	x	x	x	x		x		x
		D816	x			x		x	x	x	x		x	/	x	x	x		x		x
1000-2500+	8-18	A818				x					x		x	x	/	x		x	x		x
		B818	x	x	x	x	x	x	x	x	x	x	x	x	x	/	x	x	x		x
		C818				x					x		x	x		x	/	x	x		x
		D818	x			x	x	x	x	x	x	x			x	x	x	/	x		x
		E818		x	x	x				x	x	x	x	x	x	x	x	x	/		x
	8-19	A819									x									/	
FSW		FSW	x			x			x	x	x		x		x	x	x	x	x		/

|			A922	B922	A106	A108	B108	C108	D108	A119	A816	B816	C816	D816	A818	B818	C818	D818	E818	A819	FSW
1000-1000	9-22	A922	/	x		x					x	x			x	x	x		x	x	
		B922	x	/	x	x	x	x	x	x		x	x	x	x	x	x	x	x	x	x
	10-6	A106		x	/	x					x				x	x	x		x	x	
1000-2500	10-8	A108	x		x	/	x	x	x	x	x	x	x	x		x		x		x	x
		B108		x		x	/				x					x			x	x	
		C108		x		x		/			x					x			x	x	
		D108		x		x			/		x					x			x	x	
	11-9	A119		x		x				/	x		x		x	x	x		x	x	
FSW-2500	8-16	A816	x		x	x	x	x	x	x	/		x	x	x	x	x	x	x		x
		B816	x	x		x					x	/	x	x		x			x	x	
		C816		x		x			x		x	x	/		x	x	x		x	x	
		D816		x		x					x			/	x	x	x		x	x	
1000-2500+	8-18	A818	x	x	x					x	x		x	x	/	x		x		x	x
		B818	x	x	x	x	x	x	x	x	x	x	x	x	x	/	x	x	x	x	x
		C818	x	x	x	x				x	x		x	x		x	/	x	x	x	x
		D818		x		x					x				x	x	x	/		x	
		E818	x	x				x	x	x	x	x	x	x		x	x	x	/	x	x
	8-19	A819	x	x	x	x	x	x	x	x		x	x	x	x	x	x	x	x	/	x
FSW		FSW		x		x					x				x	x	x		x	x	/

Swimming Velocity

Swimming velocity appeared on inspection to differ between rise/sink and looping behavior (Fig. 11). A periodic time series is not random on all time scales, and therefore does not fullfil the assumption of analysis of variance that the sampled variable is from a randomly distributed population. Some time series of swimming velocity obtained in this study were strongly periodic (see Fig. 8), and therefore each velocity time series was reduced to its component means (i.e. mean absolute swimming speed, mean upward velocity, mean downward velocity).

I tested for differences in absolute swimming speed among treatments (1000-FSW, 1000-1000, 1000-2500, FSW-2500, 1000-2500+), and among experiments by the GT2-method for unequal sample size (Sokal and Rohlf, 1981). I did not differentiate between the swimming modes and included all of the sequences. Swimming speed did not differ significantly between treatments, as mean speed varied from 0.68 to 0.84 cm/sec (Fig. 12). Similar comparisons were made for just the 62 rise/sink and just the 15 looping sequences to examine whether the speed differed with swimming mode and whether it differed as a function of food condition (Fig. 13). Looping speeds (means ranged from 1.08 to 1.22 cm/second) were significantly faster than the rise/sink speeds (means ranged from 0.50 to 0.72 cm/second) in all treatments. There was no significant treatment effect on either rise/sink or looping speeds.

Figure 11   Swimming speed frequency distributions of representative rise/sink and looping time series. The top panel (rise/sink behavior) and bottom panel (looping behavior) show frequency distributions of upward (positive) and downward (negative) swimming speed during typical sequences.

Figure 11

Swimming Speed
Rise/Sink behavior

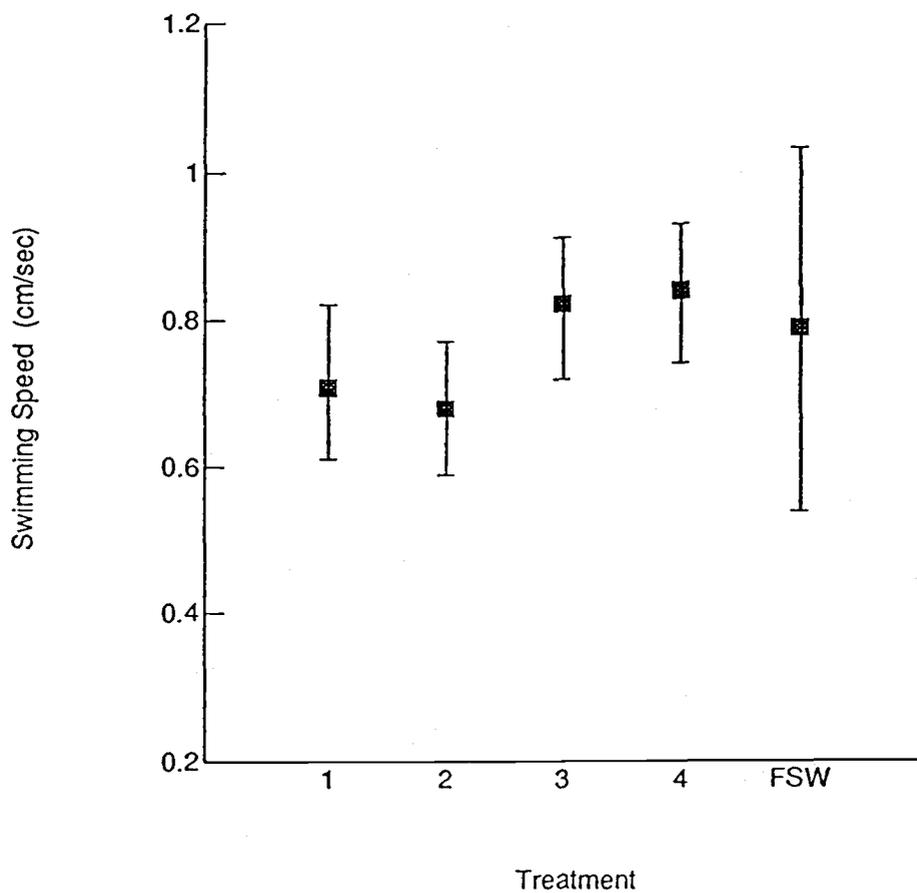## Swimming Speed
Looping behavior
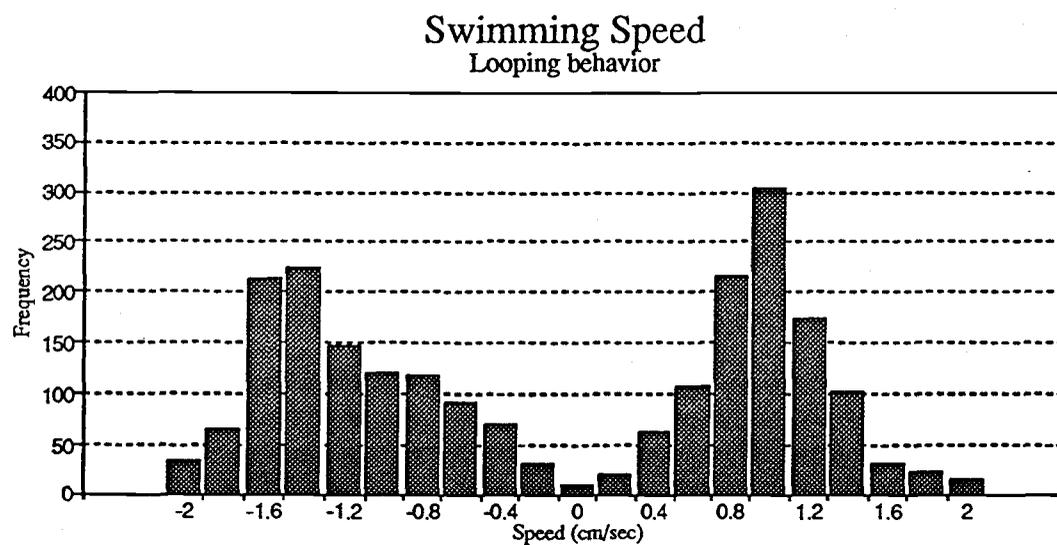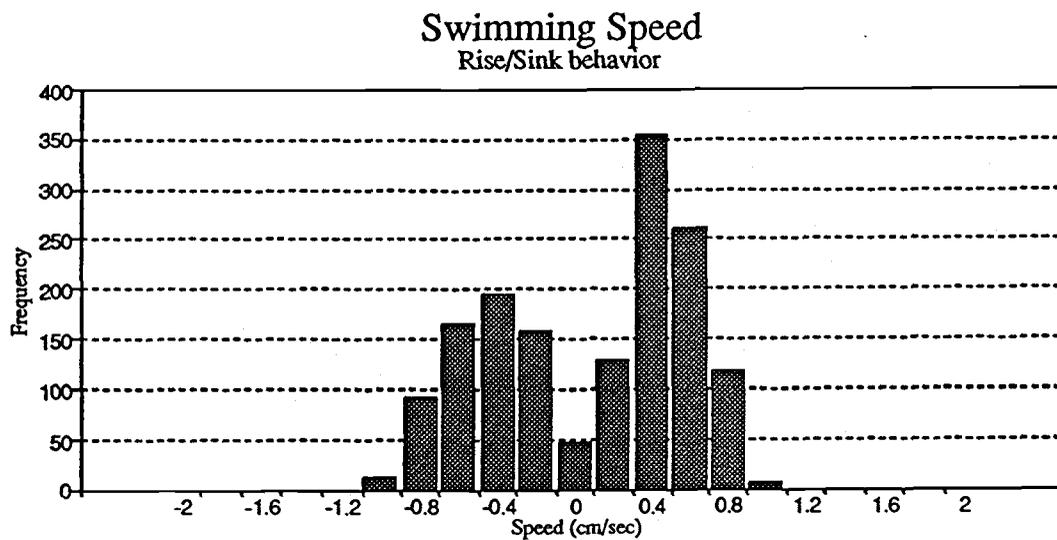
Figure 12   Comparison of means with unequal sample size: the GT2-method. 95% comparison intervals for swimming speed in 134 swimming sequences from the 4 food condition treatments and the 1000-FSW treatment. Treatments: (1) 1000-1000; (2) 1000-2500; (3) FSW-2500; (4) 1000-2500+; (FSW) 1000-FSW. Means whose intervals do not overlap are significantly different.
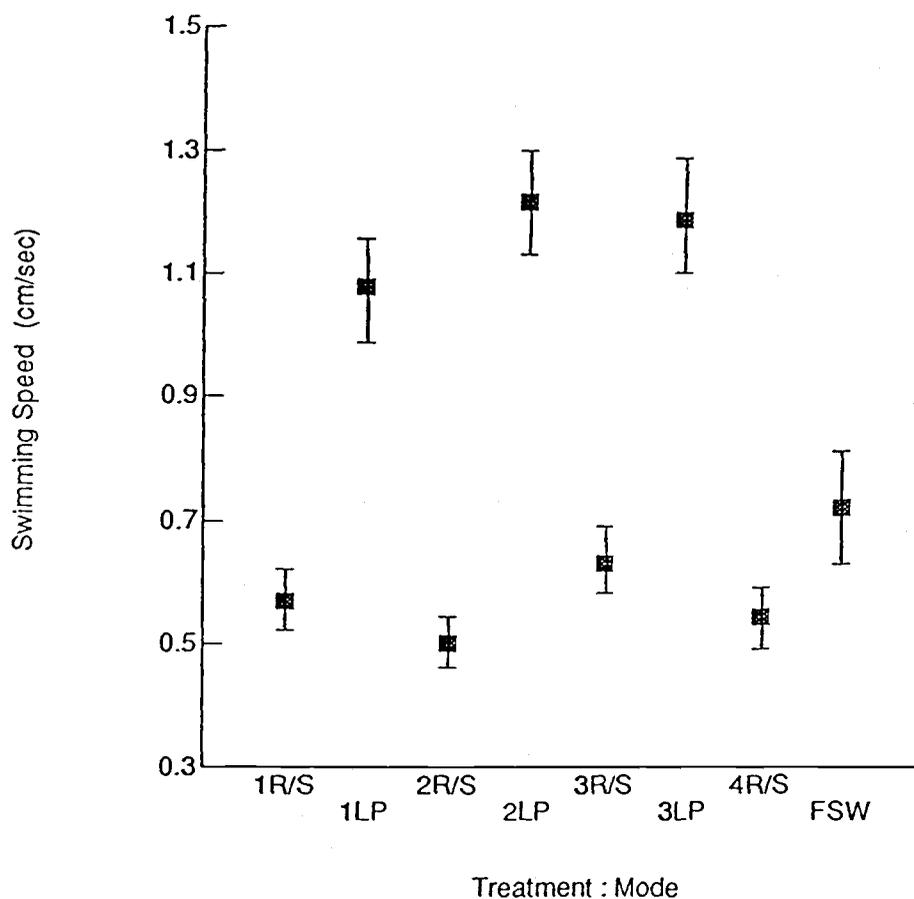
Figure 13   Comparison of means with unequal sample size: the GT2-method. 95% comparison intervals for swimming speed in the 62 rise/sink sequences and 15 looping sequences from the 4 food condition treatments and the 1000-FSW treatment. Treatments: (1) 1000-1000; (2) 1000-2500; (3) FSW-2500; (4) 1000-2500+; (FSW) 1000-FSW. Mode: (R/S) rise/sink; (LP) looping. Means whose intervals do not overlap are significantly different.

In all of these observations, downward velocity during rise/sink behavior was essentially the non-swimming sinking rate for the individual. The upward velocity appeared on inspection to have been ingestion rate dependent, as did the positive and negative looping velocities. This observation was tested in two steps. First, I compared rise and sink velocities to each other and positive and negative looping velocities to each other by the T-method. The 62 rise and 62 sink velocity means and 15 positive and 15 negative looping velocity means were grouped according to treatment in order to increase the sample size for the comparisons. Negative looping velocities were significantly greater than positive looping velocities in all treatments (Fig. 14). Rise velocity did not differ significantly from sink velocity in three treatments, but differed significantly in the 1000-2500 and 1000-FSW treatments (P < 0.05) (Fig. 15). Rise velocity during the 1000-2500 treatment was significantly slower than sink velocity, attributable mainly to the November 9 experiment that included only one individual. In the 1000-FSW treatment, the rise velocity was significantly faster than the sinking velocity. Second, I compared rise velocity among treatments by the GT2-method (Fig. 16). It was significantly faster in FSW than in any of the food conditions. Rise velocities did not differ significantly among the food conditions, except for the 1000-2500 treatment which was again due to the November 9 experiment (i.e. one individual).
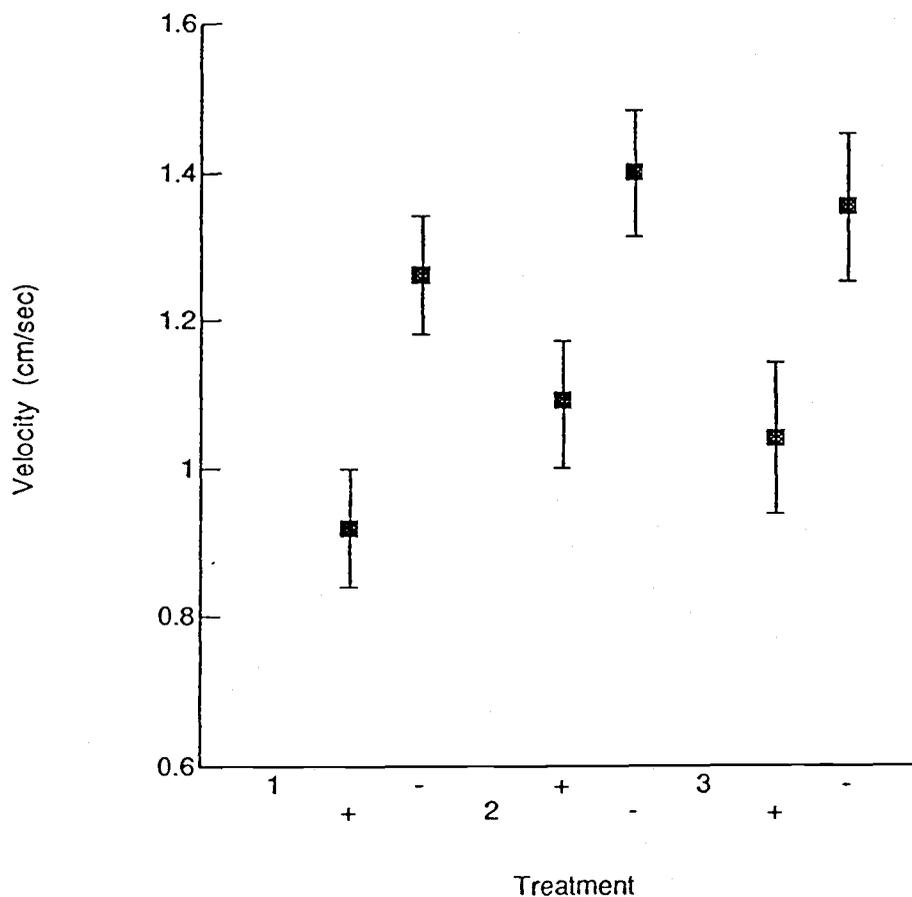
Figure 14   Comparison of means with equal sample size: the T-method. 95% comparison intervals for positive and negative looping velocity from 3 food condition treatments. Comparisons valid only between positive (+) and negative (-) velocity within the same treatment. Treatments: (1) 1000-1000; (2) 1000-2500; (3) FSW-2500. Means whose intervals do not overlap are significantly different.
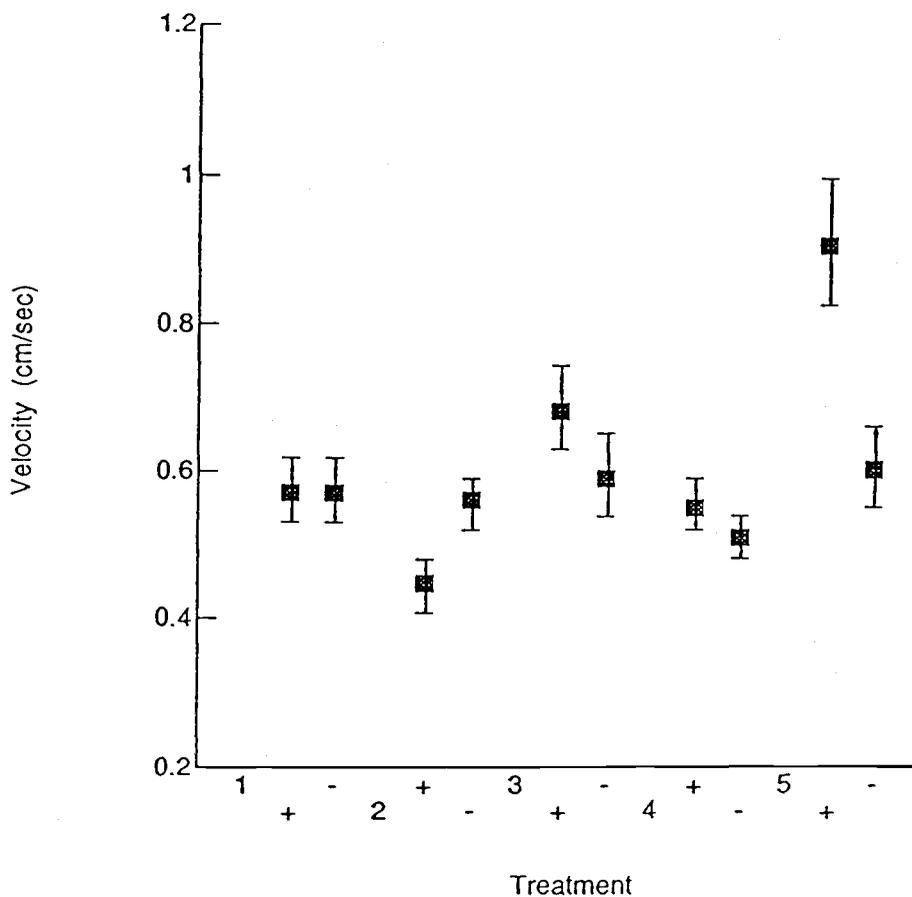
Figure 15   Comparison of means with equal sample size: the T-method. 95% comparison intervals for positive and negative rise/sink velocity from the 4 food condition treatments and the 1000-FSW treatment. Comparisons valid only between positive (+) and negative (-) velocity within the same treatment. Treatments: (1) 1000-1000; (2) 1000-2500; (3) FSW-2500; (4) 1000-2500+; (5) 1000-FSW. Means whose intervals do not overlap are significantly different.
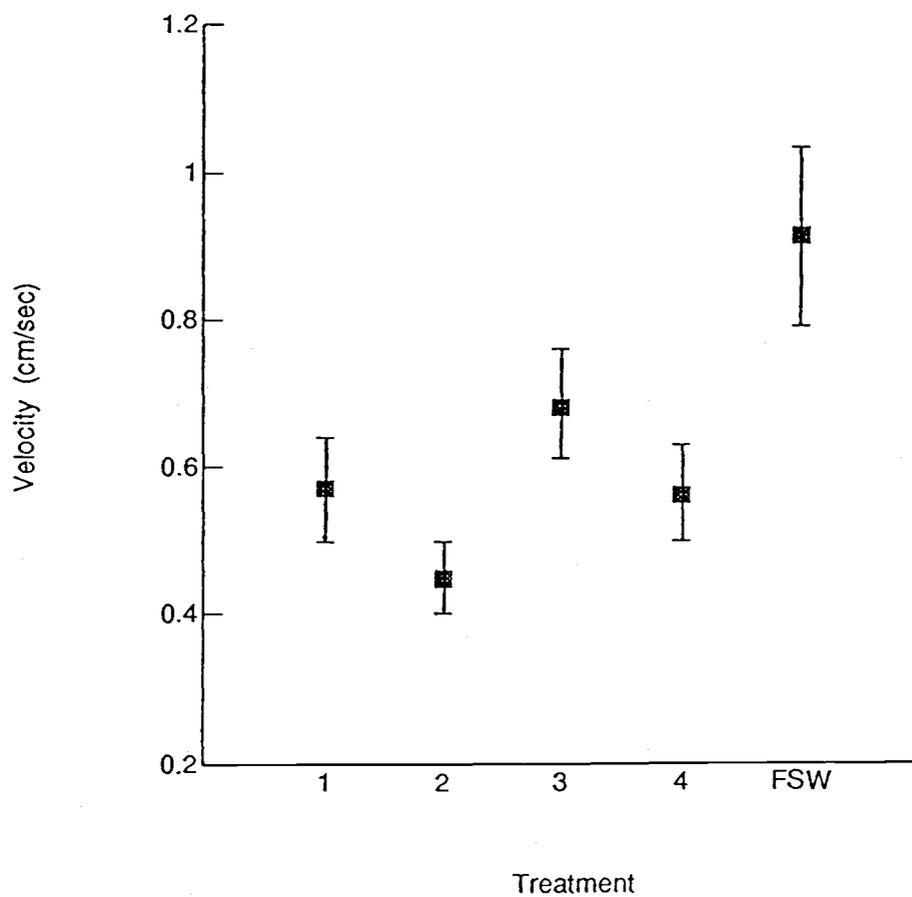
Figure 16   Comparison of means with unequal sample size: the GT2-method. 95% comparison intervals for rise swimming velocity from the 4 food condition treatments and the 1000-FSW treatment. Treatments: (1) 1000-1000; (2) 1000-2500; (3) FSW-2500; (4) 1000-2500+; (5) 1000-FSW. Means whose intervals do not overlap are significantly different.

DISCUSSION

The goal of this study was to examine changes in the swimming behavior of Calanus marshallae in response to differences in food conditions. Specific behavioral characteristics examined were levels of activity, swimming modes (rise/sink and looping), time allocation among and within modes, and patterns of swimming velocity. The results reveal several levels of complexity of copepod swimming behavior, each of which displays considerable variability among individual copepods. In this section of the thesis, I discuss the variability of each aspect of swimming behavior, the interplay between the different aspects of behavior, and how combinations of behavioral characteristics may be used to evaluate behavioral responses.

Swimming activity of Calanus marshallae in 24-hour experiments followed a diel pattern when food was available (i.e. high activity at night, low activity during the daytime), and remained relatively constant over a 24-hour period when food was not available. These results are consistent with previous results. Diel feeding and migration rhythms are commonly observed among copepods (e.g. Dam, 1986; Head and Harris, 1987). Peterson et al. (1979) found that C. marshallae females migrate to the surface waters at night to feed and lay eggs, then descend for the day. The swimming activity patterns that I observed, a diel rhythm in the presence of food and none without food, were consistent with Mackus and Burn's (1986) evidence that gut fullness and swimming activity level are positively correlated.

Aspects of the swimming of copepods in the October 6 and 8 experiments differed significantly from swimming in other experiments. October collections were on the same date, October 5. The copepods were extremely active, and almost exclusively exhibited rise/sink behavior. On October 8, they limited their activity to the upper portion of the stage aquarium. Perhaps these October experimental, or collection date, effects relate to the onset of diapause. Peterson (1980) found that the development and reproduction cycle of C. marshallae coincide with the seasonal upwelling circulation off Oregon. By October and November Peterson found population number significantly reduced, and he speculated that only the fifth copepodites entered diapause and remained at depth off the shelf until the following spring (i.e. February). Some copepod species diapause as females (Miller and Clemons, 1988), so perhaps some C. marshallae do so as well. Perhaps the unusual behavior was due to seasonal variation in feeding behavior (e.g. Runge, 1980). The high activity levels of October individuals, however, were contrary to reduced activity levels observed in copepods in diapause (Alldredge, et al. 1984). Since the unique swimming behavior seen on October 6 and 8 may have been a function of collection date, I will omit it when discussing variation of swimming behavior as a function of food conditions.

Calanus marshallae modified two aspects of swimming behavior in response to exposure to food. First, the non-feeding individuals in the 1000-FSW, 24-hour experiments did not display looping behavior, and had higher swimming velocities compared to feeding individuals. They were relatively active, yet exhibited only

rise/sink behavior, while individuals from the same collection date exhibited looping behavior when exposed to food (Fig. 7). These results were consistent with the findings of Williamson (1981) and Wong (1988), that non-feeding copepods exhibited less looping behavior than feeding copepods. In this case, non-feeding C. marshallae were never observed to loop. Second, rise velocities of non-feeding copepods were significantly greater than those of feeding copepods (Fig. 15). Similar results were found for Pseudocalanus minutus (Buskey, 1984), which reduced its swimming speed in the presence of algal exudate and inert particles (i.e. plastic spheres) relative to its swimming speed in filtered seawater. Wong (1988) observed the same response by Metridia pacificus when feeding on algae. Reduced swimming velocity in the presence of food may reflect the copepod's increased effort devoted to "handling" food items.

When feeding, regardless of the food conditions, none of the aspects of swimming behavior examined varied significantly, apart from individual variation. Swimming activity of Calanus pacificus was extremely variable in all food conditions. Mackus and Burns (1986), in the only published paper examining long-term swimming activity, found that activity level was extremely variable for C. pacificus. Their conclusions, based on time series of gut fullness in relation to swimming activity level at the time of capture, were that gut fullness and swimming activity were positively correlated and were modulated on time scales of 1 hour. Calanus marshallae has been shown to have similar gut-evacuation time scales (Ellis and Small, 1988), and yet my data showed no apparent patterns of activity level on these time scales, even when starved individuals were introduced to food.

Time allocated to looping behavior by C. marshallae was independent of food conditions. Williamson (1981) found similarly that the freshwater copepod Mesocyclops edax exhibited a relatively constant looping effort (i.e. number loops/minute) under various food conditions. Another similar characteristic was that individual loops were uniform in size. Calanus marshallae looping activity, once engaged, appeared to be relatively fixed, with successive loops at similar velocity and duration.

Rise/sink swimming, in contrast, was more variable. At times it was periodic, which may have been indicative of feeding intensity. Cowles and Strickler (1983) found that cephalic appendage activity of Centropages typicus became less random (i.e. more periodic) as food concentration increased. Often, however, rise/sink swimming was not significantly periodic, and these more random duty cycles varied considerably among individuals. Random duty cycles may have reflected lower feeding intensity, and, interestingly, the non-feeding (FSW) individuals had the most random distribution of sink duration (Fig 9a.).

Swimming velocity of C. marshallae was not affected by food conditions. Swimming speeds of Metridia pacifica (Wong, 1988) and Mesocyclops edax (Williamson, 1981) also did not differ significantly between different food conditions. Mesocyclops edax had extremely variable swimming speed among individuals, and speed did not differ significantly between food conditions. Swimming speed of M. pacificus in the presence of Artemia nauplii and Thalassiosira weissfloggi was slightly, but not significantly, reduced relative to speeds during exposure to Artemia nauplii

alone. Copepod swimming speeds, however, can be affected by chemical and mechanical stimuli. Buskey (1984) found that swimming speed of <u>Pseudocalanus</u> <u>minutus</u> depended on whether the copepod was exposed to plastic spheres and/or filtered seawater conditioned with phytoplankton exudate. It's response to these stimuli, however, may not be indicative of it's swimming speed when actually feeding.

The relatively uniform swimming behavior observed in the different food conditions may be explained by examining how the various swimming behaviors contribute to the regulation of the ingestion process. Holling (1966) modeled ingestion rate as a function of four independent sequential events: 1) the food item encounter rate, 2) the percent of the items encountered which are attacked, 3) the percent attacked which are then captured, and 4) the percent captured which are eaten. Given the uniform food environments used in this study, swimming velocity and duration would have a direct influence on the encounter aspect of the ingestion process. So, I expected that swimming speed and/or swimming duration would change as a function of food conditions. These behaviors did not change, and there may be several reasons.

Food item encounter rate is not simply a function of the swimming speed, food item detection radius, or food concentration, because copepods can move their cephalic appendages in various patterns to generate diverse flow fields. Strickler (1982) found that the copepod <u>Eucalanus</u> <u>crassus</u> alternates between "swimming" and "feeding" modes, distinguishable by their flow-field characteristics and the swimming direction. The "feeding" flow field consisted of doubly sheared feeding and swimming currents, while the "swimming" flow-field consisted only of the swimming current. Feeding

current velocities can be quite high. Constant, 55 Hz cephalic appendage motion of a tethered (i.e. restrained) <u>Centropages</u> <u>typicus</u> produced feeding current velocities of 1 to 2 cm/sec, while modified motion during food capture increased the feeding current velocities to 12 cm/sec (Cowles and Strickler, 1983). Similar changes of cephalic appendage beat frequency and amplitude in response to different food conditions have been observed for other copepods (Poulet and Gill, 1988). Paffenhofer and Lewis (1990) found that the feeding current flux for <u>Eucalanus</u> <u>pileatus</u> remained relatively constant even when the swimming speed doubled. These results suggest that swimming speed alone may underestimate the food item encounter rate, and that swimming and feeding current speeds may not be correlated.

Even though swimming velocity alone may not accurately reflect the food item encounter rate, increasing swimming velocity would increase the probability for encounter of favorable food conditions in a patchy environment (Pyke, 1984). <u>Calanus</u> <u>marshallae</u> exhibited such a response when going from non-feeding conditions to feeding conditions. As different food conditions are encountered, a forager may increase the food encounter rate by altering it's swimming speed and/or movement patterns (Pyke, 1984). There is evidence, however, from a model (Gerritsen and Strickler 1977) that in a randomly distributed food environment encounter rate is optimized only in a narrow range of swimming speeds. The model also indicated that encounter rate depends more on the detection radius than on swimming speed. There is evidence that copepods (e.g. <u>Eucalanus</u> <u>pileatus</u>) have the ability to increase the detection radius, which contributes to higher ingestion rates (Price and Paffenhofer,

1984). This may explain why rise/sink and looping velocities were relatively constant in all food conditions.

The data presented in this thesis suggest that the measured aspects of the swimming behavior of C. marshallae did not vary as a function of food conditions. They do suggest, however, which aspects may be of interest in future swimming behavior research, and how experimental and individual variability may be reduced. Experimental variability could be reduced by conducting the experiments over a relatively short time interval (i.e. several weeks), and thus avoiding seasonal variability in ingestion behavior. Individual variability may be more difficult to reduce. However, certain aspects of swimming (e.g. activity level) exhibited more individual variability than other aspects (e.g. velocity, duty cycle duration), so one may reduce individual variability by examining only those less variable aspects. Future research should focus on how rise/sink duty cycles and looping event durations vary as a function of food conditions. Food conditions should be chosen to elicit a broader range of ingestion rates than elicited in this study. These data would provide useful insights on ingestion behavior, since they provide the most direct information about cephalic appendage behavior. With this approach, video recording of swimming behavior and microcinematography of the cephalic appendages can more effectively compliment one another, thus enhancing our understanding of copepod swimming behavior.

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