

A QUANTITATIVE DESCRIPTION OF *MELIBE* FEEDING BEHAVIOR AND ITS MODIFICATION BY PREY DENSITY

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The feeding behavior of the nudibranch *Melibe leonina* is unusual because it lacks a buccal mass. When sufficient prey are present in the water column, rhythmic feeding movements commence. A typical feeding cycle can be divided into 5 phases, beginning with the oral veil opened, and then followed by closing of the oral veil, squeezing and tilting of the head and veil, transfer of food into the mouth, and finally opening of the oral veil. This pattern is then repeated at 0.5-3 cycles/min, depending on the prey concentration. As the feeding rate increases, the duration of each feeding cycle decreases, but the proportion of a cycle occupied by a given phase of the behavior remains the same. When the density of prey are very low, animals will often initiate a feeding cycle and then terminate it just before the tilt and squeeze phase. These data, taken together, suggest that *Melibe* feeding is a fixed action pattern which is modulated by the availability of prey in the water column.

KEY WORDS: *Melibe leonina*, nudibranch, feeding behavior, buccal ganglia, gastropod, prey density.

INTRODUCTION

The feeding strategies used by most gastropods can be categorized as rasping, browsing or hunting (Audesirk and Audesirk, 1985). While the type of prey consumed, and the method used to capture it, differ widely, the buccal mass plays a similar role in most species. Once food is obtained using a radula or proboscis, it is transferred into the buccal mass, where rhythmic movements of the buccal mass musculature and teeth chew it. Subsequently, peristalsis of the esophagus moves food from the buccal mass to the stomach. The focus of this paper is the unusual feeding behavior of the nudibranch, *Melibe leonina*, which lacks a radula, proboscis and buccal mass.

There are 13 different *Melibe* species in the family Tethyidae (Gosliner, 1987). Brief descriptions of the feeding behavior of several species have been presented previously (*Melibe fimbriata*: Elliot, 1902, Thompson and Crampton, 1984; *Melibe*

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bucephala: Schuhmacher, 1973; *Melibe rosea*: Thompson and Crampton, 1984; *Melibe leonina*: Agersborg, 1921; Hurst, 1968; Ajeska and Nybakken 1976; Bickell and Kempf, 1983). All species are carnivorous and capture food by trapping it with the tentacles of the oral veil. Coordinated movements of these tentacles, the oral veil, and the lips surrounding the mouth are used to transfer prey into the esophagus. In *M. leonina* masticatory structures are absent, and therefore food is swallowed whole.

Adult *M. leonina* are benthic hunters (Purchon, 1968), feeding on small free-swimming crustaceans, such as copepods (Agersborg, 1921; Hurst, 1968) as well as a variety of invertebrate larvae (Ajeska and Nybakken, 1976). Juvenile *Melibe* are very sensitive to tactile stimulation, orienting their oral hood towards prey in the water column (Bickell and Kempf, 1983). When a prey item contacts the extended oral hood of an adult *Melibe* it elicits an immediate contraction of the hood, resulting in food capture (Hurst, 1968). However, feeding movements of *Melibe leonina* are probably not solely reflexive because both Ajeska and Nybakken (1976) and Thompson and Crampton (1984) have noted that *Melibe leonina* and *Melibe rosea* carry out feeding movements even in the absence of food. In this paper we present the results of a series of experiments which indicate that the feeding behavior of *Melibe leonina* is a fixed action pattern which is modified by the concentration of prey in the water column.

MATERIALS AND METHODS

Animals

All animals were collected, using SCUBA, from eel grass beds located around the San Juan Archipelago (Washington), and shipped to the University of New Hampshire Coastal Marine Laboratory, Newcastle, N.H.. Animals were maintained in seawater tables which were continuously perfused with filtered seawater from Portsmouth Harbor (6–12° C). Every 3–4 days *Melibe* were fed a small amount of the material which was filtered from the water that passed through seawater system. During the time of our feeding experiments this inflow filtrate consisted primarily of barnacle nauplii.

Analysis of Normal Feeding

Adult *Melibe* were placed in a 15 liter aquarium filled with seawater, containing a prey density of 1500 larvae/Liter. This concentration of prey was chosen because it induced feeding at a rate that was approximately 50% of the maximal rate we were able to obtain in the density experiments (Figure 4). After a period of acclimation (30 min), animals were videotaped for thirty minutes. Tapes were replayed and the duration of each phase of the feeding cycle was measured (3 trials, 4 animals/trial; 750 feeding cycles) and entered into a computer for analysis.

The Influence of Prey Density on Feeding Frequency

Three to five *Melibe* were placed in a 20 liter aquarium containing 12 liters of filtered sea water. The animals were allowed thirty minutes to acclimate before initiating the experiment. Each trial consisted of a ten minute exposure to a specific concentration of prey. The first trial was a control; prey not present in the aquarium. The prey density for subsequent trials was regulated by serially adding known amounts of filtrate. Thus, during each successive 10 minute interval the animals were exposed to incremental concentrations of prey. The concentration of available prey in the experimental chamber was determined by removing 1 ml aliquots, counting the number of animals present, and multiplying by 1000 to yield the concentration in prey/liter. Experiments (n=27) lasted an average of 3 hours. A video camera, positioned 5 ft. above the aquarium was used to record their behavior throughout the experiment.

The tapes obtained during these feeding trials were reviewed to determine the number of feeding cycles which occurred during each 10 minute time interval (feeding frequency). The number of complete vs. prematurely terminated feeding cycles was also noted. In addition to measuring the effect of prey on feeding rate we also determined how the concentration of food influenced the duration of each phase of the feeding cycle.

To determine how changes in feeding rate affected the duration of each phase of the feeding cycle we used data from the prey experiments described above, and performed the following additional calculations. First, we grouped 10 minute feeding sessions during which animals fed with a particular rate, ranging from 1.4 to 3.6 cycles/min (n=90). Then, for each different feeding rate, we calculated the average duration of each phase, and plotted this relationship. In addition, we determined the average percentage of the total duration of each feeding cycle that was occupied by a given phase, and plotted this relationship.

RESULTS

Description of Feeding

Melibe leonina exhibits a variety of feeding behaviors, depending on the water currents and the availability of prey. In calm filtered water they will often use surface tension to float on the surface with their oral veil extended below. Food capture under these conditions is intermittent, and appears to be triggered by contact of prey with the oral veil. If there is detritus on the bottom of the aquarium *Melibe* will also graze on the bottom, spreading their oral veil over the substrate and then carrying out the stereotyped feeding movements described below. Finally, they will attach to a surface (eel grass in their natural habitat) and, when sufficient prey are available, exhibit rhythmic feeding movements.

When searching for prey *Melibe* extends its oral hood, as illustrated in Figures 1A and 2A. If food is present in the water column some occasionally is carried into the oral hood by the ambient currents. A feeding cycle commences when the lateral

edges of the hood start to move forward and close (Figures 1B, 2B). While closing the oral hood, animals also open their mouths (Figure 2B). The closing phase of the behavior takes approximately 4 seconds (Figure 3). Once closed the smaller tentacles lining the inner rim of the oral hood interdigitate, forming a sieve (Figure 2C). Animals then tilt the oral hood postero-dorsally (Figure 2D) while contracting it to reduce the volume of the enclosed pocket of water. This squeezing forces water out through the sieve and causes the larger outer tentacles to extend away from the oral hood (Figure 1D). Prey are filtered from the water by the inner tentacles during this phase of the behavior (Figures 1D, 2D). Typically, the tilt and squeeze phase of a feeding cycle takes 5–6 seconds (Figure 3). When the oral hood is fully contracted the inner tentacles are placed inside the open mouth. The mouth closes around the prey which are caught on the tentacles. As the oral veil is reopened and the tentacles withdrawn, food items are scraped off the tentacles by the lips encircling the mouth. Transfer of the food into the mouth usually requires 4 to 5 seconds. The oral veil then takes approximately 4 seconds to reopen to its original position. If prey are readily available (1500 prey/Liter) the oral hood remains open for between 12 and 13 seconds, and then another feeding cycle commences, when the closing phase of the behavior is repeated.

Effect of Prey Density on Feeding Behavior

Usually, when *Melibe* are held in aquaria containing filtered seawater they consistently, but infrequently, exhibit feeding movements (1 feeding cycle every 2 minutes, 0.5 cycles/min.). However, addition of prey to the aquarium initiates more frequent feeding, and the rate of feeding is a function of the concentration of prey in the water column (Figure 4). The maximum feeding rate we observed, with a prey concentration of 4900 larvae/liter, was 3.2 cycles/min, 6 times the feeding rate in the absence of prey.

An analysis of the duration of each phase of a feeding cycle at different feeding rates showed that every phase, except perhaps the squeeze and tilt, decreases in length proportionally as the rate of feeding increases (Figure 5). This is even more evident, when each phase is expressed as a percentage of the whole feeding cycle (Figure 5). Thus, it appears as if there is little change in the temporal organization of a feeding cycle as the feeding rate increases.

Occasionally, animals terminate a feeding cycle before completing all the phases of the behavior. Typically, they do this during the closing phase; opening their oral veil before proceeding through the tilt and squeeze portion of the feeding cycle. In our experiments the frequency of these incomplete feeding cycles was greater when the density of food was low. This observation suggests that animals were able to sense that they had failed to capture food during the closing phase and thus terminated the feeding cycle before attempting to pass prey to the mouth during the tilt and squeeze portion of the behavior (Figure 6). In fact, it appears as if at low food densities animals periodically sample the water column using the initial phases of a feeding cycle.

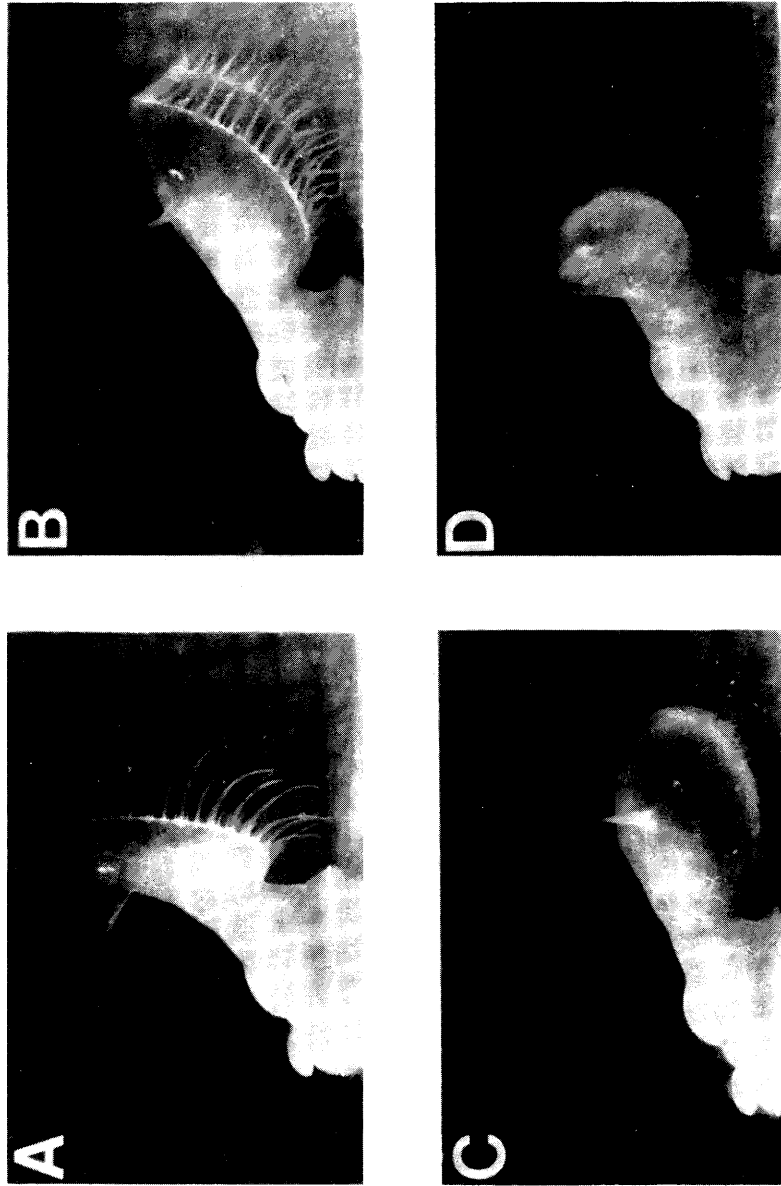


Figure 1 Lateral view of the phases of *Melibe* feeding behavior. A. Oral veil opened. B. Closing. C. Closed. D. Tilt and squeeze. During feeding the animal moves gradually from one phase to the next in the same sequence as illustrated in this figure. Following the tilt and squeeze phase (D), during which food is brought in contact with the mouth, the oral veil opens rapidly and extends to the position shown in A. The animal holds the veil in the open state for several seconds-to minutes (depending on the concentration of food in the water column), before closing the oral veil, as shown in B, and capturing small crustaceans in the water column. The animal pictured in this figure and Figure 2 is approximately 4 inches in length.

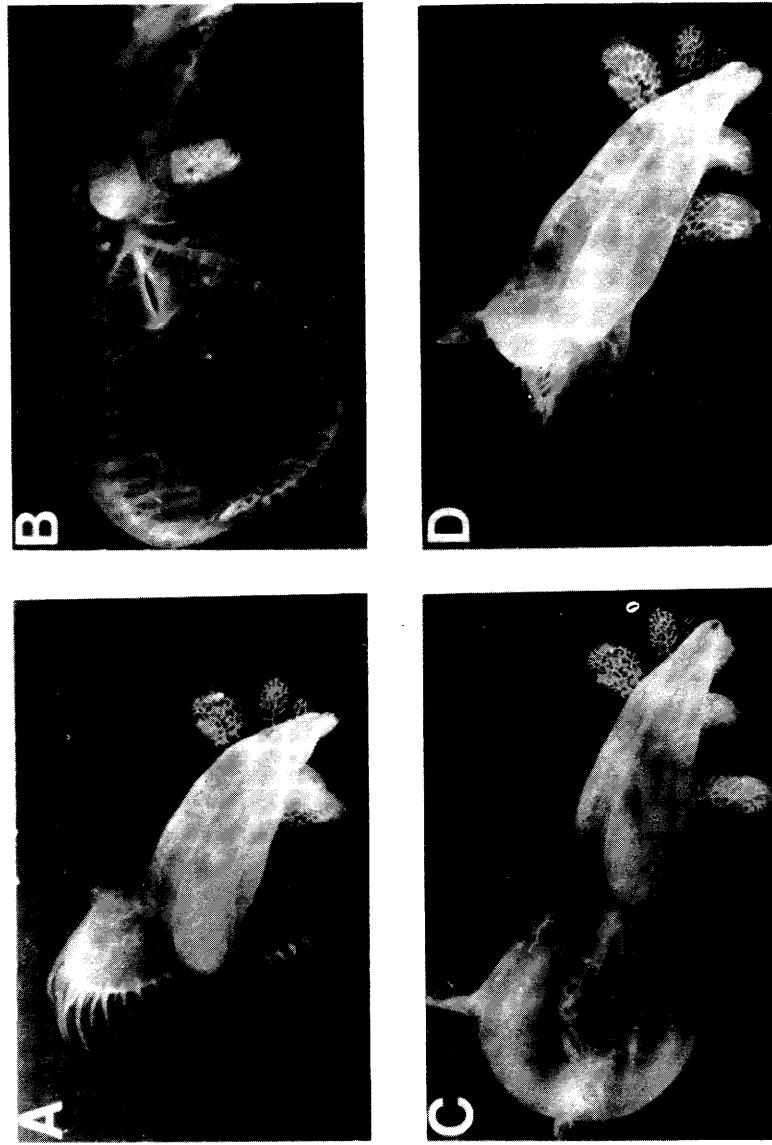


Figure 2 Ventral view of a *Metibe* feeding. This series of photographs illustrates the same 4 phases of feeding shown in Figure 1, from a different perspective. A. Opened. B. Closing. C. Closed. D. Tilt and Squeeze. This view makes it possible to see the mouth, which is a small slit at the base of the oral hood, beginning to open in B. The role of the inner tentacles in filtering small prey from the water is well illustrated in the ventral view shown in C. Both Figure 1D and 2D demonstrate how the head region and oral veil are tilted back while simultaneously contracting the oral veil, reducing its volume, and forcing water out through the sieve formed by the inner tentacles.

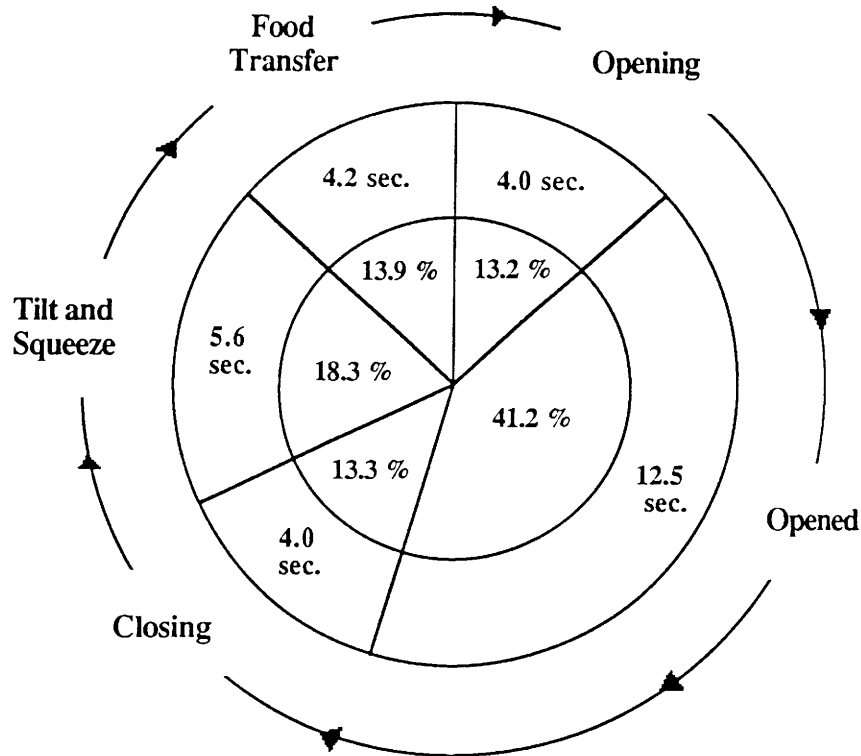


Figure 3 The time course of *Melibe* feeding behavior. The duration of each phase of the feeding behavior of 16 animals was measured during spontaneous feeding in the presence of moderate concentrations of food (1500 prey/Liter). These data were averaged (outer region of the pie diagram, 750 cycles), and also normalized to indicate the percentage of the entire feeding cycle occupied by each phase of the behavior (inner region of the pie diagram). The animals used to generate the data for this figure had feeding cycles lasting approximately 30 sec, or 2 cycles/minute. By far the longest part of the cycle was occupied by the opened phase, when animals hold their oral veil open to provide the maximal surface area for trapping animals moving in the water column.

DISCUSSION

In contrast to most gastropods *Melibe leonina* is devoid of any masticatory apparatus (jaws and stomach plates, Gosliner 1987). As a result, it has a unique form of feeding that combines prey capture, active filtration, and swallowing of prey whole. Brief descriptions of the feeding behavior of 4 of the 13 *Melibe* species indicate that they all use the same basic mechanisms, even though their preferred prey differ; *M. fimbriata* sweeps small crustaceans from the substrate (Thompson and Crampton,

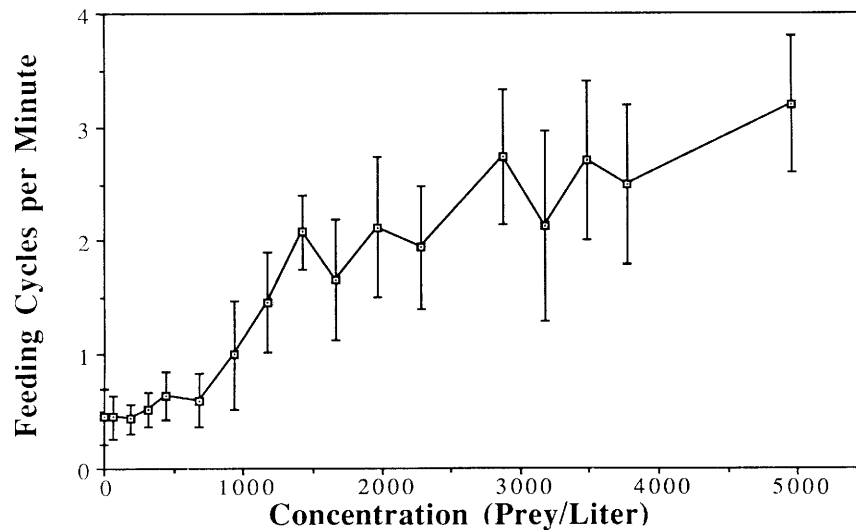


Figure 4 The effect of prey density on the frequency of *Melibe* feeding. Animals ($n=7$) were exposed, for sequential 10 min trial periods, to increasing concentrations of prey, and the number of feeding cycles which occurred in each 10 minute period was measured. In the absence of prey (filtered seawater, conc. = 0), the basal frequency of feeding was 0.5 cycles/min, or one cycle every 2 minutes. However, once the concentration of prey was increased beyond 700 organisms/liter, there was a dramatic increase in the frequency of feeding.

1984), *M. bucephala* strips detritus and associated micro-organisms off algal filaments (Schuhmacher, 1973) and *M. leonina* and *M. rosea* capture small planktonic crustaceans from the water column (Agersborg, 1921; Hurst, 1968; Ajeska and Nybakken, 1976; Thompson and Crampton, 1984). Despite these subtle differences between species, all members of the genus *Melibe* use a unique mode of feeding, at least amongst the gastropods. While Audesirk and Audesirk (1985) and Purchon (1968) categorize *Melibe* as a hunter, under conditions of high prey density and moderate to high currents it more closely resembles a suspension feeder. Thus, perhaps it would be more appropriate to call them facultative pelagic suspension feeders, as well as pelagic hunters.

The descriptions of *Melibe* feeding in the literature indicate that it has characteristics of both reflexes (Hurst, 1968; Bickell and Kempf, 1983) and fixed action patterns (Ajeska and Nybakken, 1976). Our data suggests that the capture of food by *Melibe*, like the feeding behavior of most gastropods, is a fixed action pattern which can be modulated by sensory input. First, when moderate numbers of prey are available, the rhythmic feeding movements have all the temporal and stereotypical characteristics of feeding behaviors that are known to be centrally programmed (Benjamin, 1983). Despite considerable variability in the amount of prey in the vicinity of the open oral hood, and thus the random contact of prey with the hood, we documented very consistent, stereotyped feeding movements with phases of proportional duration between one cycle and the next. This suggests

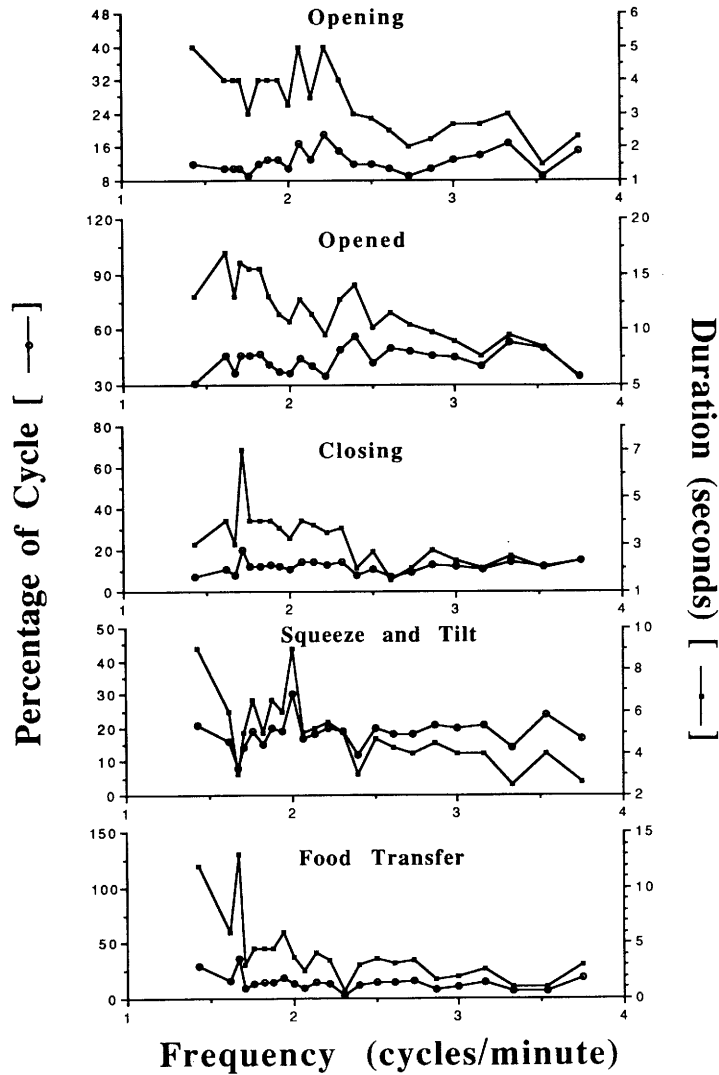


Figure 5 The effect of prey density on the different phases of a feeding cycle. The average duration (sec) of each phase of a feeding cycle was calculated for animals feeding at different rates. In addition, the same data were transformed into the percentage of a feeding cycle occupied by a given phase. This figure shows how these variables change as animals increase their feeding rate. While the duration of any part of the feeding cycle, such as opening, decreases as the animals feed faster, because all the phases are decreasing proportionally, the percentage of the whole feeding cycle occupied by a certain activity changes little, if at all. As a result, the temporal organization of each cycle is maintained.

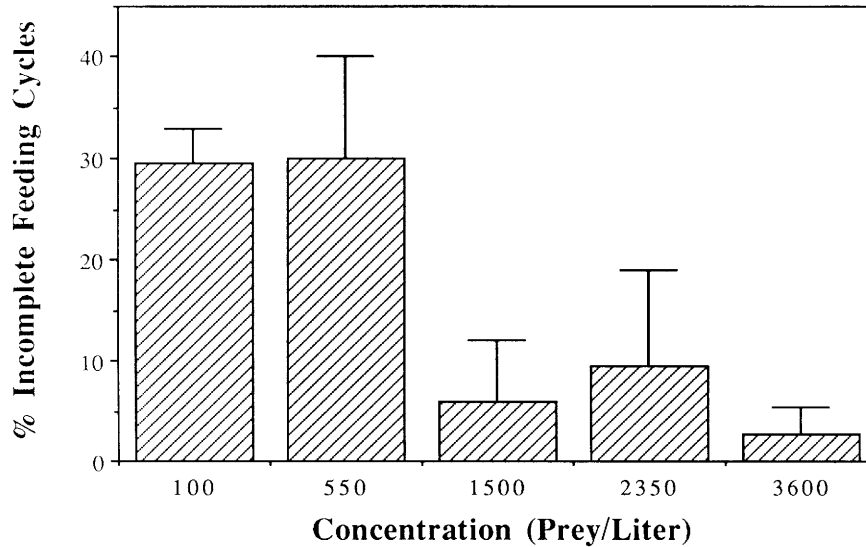


Figure 6 The relationship between prey density and premature termination of a feeding cycle. On occasion animals initiated a feeding cycle yet terminated it just before the tilt and squeeze phase; prematurely reopening their oral veil. We examined the frequency of these prematurely terminated feeding cycles in 27 animals, feeding in aquaria containing concentrations of prey ranging from 100–3600 prey/liter. Premature termination of a feeding cycle took place primarily (30% of the time) at low food densities (less than 1250 prey/liter) and appears to happen when food is not captured during the closing phase of the feeding cycle. Possibly these feeding attempts are used at low food densities to periodically sample the water column and determine food availability.

central timing of the feeding process rather than the triggering of each successive cycle by external stimuli. Second, the behavior occurs in the absence of food stimuli, as noted for *M. rosea* by Thompson and Crampton (1984) and *M. leonina* by Ajeska and Nybakken (1976). If each feeding cycle were triggered by contact of the prey with the oral veil, then under low prey densities one would predict very rare, sporadic feeding cycles. On the contrary, we documented fairly rhythmic (0.5 cycles/min) feeding activity by animals held in filtered seawater. This “vacuum activity”, suggests that there is a central pattern generator which is capable of expressing all of the aspects of the behavior in the absence of sensory input or feedback. Preliminary electrophysiological studies by Hurst (1968) indicate that there are rhythmic neurons in the *Melibe* brain which may be involved in generating rhythmic feeding behavior. Further studies, with all sensory input to the brain eliminated, are needed to determine if the feeding behavior is, in fact, produced by a central pattern generator.

While many features of *Melibe* feeding behavior suggest that a central pattern generator is involved, the following data and observations indicate that sensory input also plays an important role: (1) the oral veil is very sensitive to tactile stimulation

and contact of prey with the oral veil often elicits closure of the veil (Hurst, 1968); (2) if prey are too large and/or covered with sharp processes, they are regurgitated (R. Gillette, personal communication); (3) the frequency of feeding is a function of the concentration of prey in the water (Figure 4); (4) animals often prematurely terminate a feeding cycle when the concentration of prey is low, perhaps because too few have been captured to warrant an attempt to swallow; (5) when large amounts of food are captured in a single oral veil closure, animals extend the duration of the transfer phase, presumably to allow for more complete transfer into the mouth and; (6) preliminary data suggest that both the smell of prey (filtered seawater from a suspension of *Artemia*), and small inert objects in suspension (plastic beads), influence the rate of *Melibe* feeding (Watson and Chester, unpublished data). While these observations indicate the importance of both chemical and mechanical sensory input, they do not detract from the evidence that the basic components of the behavior are probably programmed centrally. In fact, sensory input plays a very similar role in other gastropods which are known to have a centrally programmed feeding behavior (Audesirk and Audesirk, 1985). Studies are presently underway which should help clarify the role of sensory input in the regulation of *Melibe* feeding behavior.

Our experiments demonstrated that as the concentration of prey is increased there is a concomitant increase in the frequency of feeding movements. In addition, the increase in frequency occurs via a proportional increase in all phases of the feeding behavior. These experiments were performed by sequentially adding more and more filtrate to the experimental chamber so that data for animals feeding at higher frequencies may be distorted by the fact that these same animals had been eating for some time prior to exposure to the high concentration of food. If we had exposed different animals to only one concentration of food, and then constructed our graph from such pooled data we might have obtained a curve with a greater slope; presumably because animals exposed to the higher prey concentrations would be just as hungry as those exposed to low prey densities. While this may be true, *Melibe* are known as voracious feeders, and the quantity of food they consumed during our density trials was well below the amount they ate during the lesion experiment described in the accompanying paper (Trimarchi and Watson, this issue). The influence of hunger, and other competing behaviors, such as swimming and mating, on *Melibe* feeding are certainly issues which must be addressed in the future.

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