Reference: *Biol. Bull.* **162:** 290–298. (June, 1982)

THE FEEDING RESPONSE OF *HYDRA VIRIDIS*: EFFECTS OF PREY DENSITY ON CAPTURE RATES

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Abstract

A model of the feeding processes of *Hydra viridis* was developed and used to predict the environmental parameters which maximize feeding.

Feeding was measured by exposing individual hydra to *Artemia salina* nauplii and recording the number ingested. When fed to repletion *H. viridis* resumed feeding after 4.8 hours and ingested significantly fewer *Artemia* during the second feeding. At low prey densities, increasing the exposure time from 15 to 60 minutes increased the number of *Artemia* ingested. However, at higher densities exposure time did not affect the number of *Artemia* ingested. There was a strong correlation between the number of *Artemia* captured and the number ingested. Increased prey capture did not alter the duration of the feeding response but did reduce the time interval between ingestions. Exposure to *Artemia* extract reduced the number of *Artemia* ingested and the duration of the feeding response.

These data indicate that feeding success under conditions of low prey density is limited by the availability of prey. At high prey density the feeding process is itself saturated and prey availability has limited effects on ingestion. *H. viridis* is well suited to high density feeding and ingests more prey when prey density is high even if the total exposure to prey is maintained at a constant level.

Introduction

The manner in which an organism extracts nutrients from its surroundings, feeding, is one of the organism's most basic interactions with the environment. Like other phenotypic characters, feeding can be studied as an adaptation of a species to its environment. Feeding is, however, a function of many parameters and an integrative study can illustrate the manner in which physiological, behavioral, and morphologic characters co-evolve and lead to successful feeding in a given environmental millieu.

Hydra are particularly well suited for a detailed study of feeding since extensive work has already been carried out. Laboratory and field data both indicate that feeding rates are particularly important in regulating *Hydra* population densities. Laboratory studies (Lenhoff and Loomis, 1957; Muscatine, 1961; Muscatine and Lenhoff, 1965) have repeatedly shown that *Hydra* population growth rates are directly related to the frequency of feeding. Slobodkin (1964) has even suggested that *Hydra* population size cannot exceed the number of available food particles. In a field study Cuker and Mozley (1981) showed that *Hydra* population densities closely followed increases in zooplankton abundance, and they experimentally demonstrated that increased feeding by the *Hydra*, when zooplankton were abundant, could account for the observed increase in the *Hydra* population.

The feeding process of *Hydra* has been divided into a series of discrete steps:

Received 5 January 1982; accepted 23 March 1982.

the capture of prey with nematocysts, transport of prey to the mouth, mouth opening, ingestion, digestion, and egestion (Forest, 1962). The steps between the capture of a prey item and its ingestion have been termed the feeding reaction or response (Loomis, 1955; Lenhoff, 1961a) and have been examined in great detail. The response in *Hydra* is triggered by glutathione (Lenhoff, 1961a; Mariscal, 1971), and a wide variety of environmental parameters are known to affect the response (*c.f.* Lenhoff and Boviard, 1959; Lenhoff, 1961b, 1965). However, the effects of stimuli on the feeding rate, *i.e.,* the amount of food ingested, are not known.

In this paper we develop a model of the feeding process in *Hydra viridis*, and discuss how the morphology, physiology, and behavior of *H. viridis* interact to make *H. viridis* an effective feeder in aquatic environments in which prey are concentrated in dense patches.

Materials and Methods

Cultures of *Hydra viridis* (Carolina Biological Supplies strain) were maintained in M solution (Lenhoff and Brown, 1970) at 20 ± 1°C, on a 12 hour light/dark photoperiod at a light intensity of 65 $\mu E \cdot m^{-2} \cdot sec^{-1}$. Hydra were fed every third day with freshly hatched *Artemia salina* nauplii. Hydra used in experiments were starved for two days in mass culture. Only hydra with a single bud were used in experiments. All experiments were conducted in 35 mm petri dishes containing a single hydra in 3 ml of M solution.

Satiation of feeding was examined by allowing 10 individual hydra to feed to repletion on an excess of *Artemia* nauplii. *Artemia* were then presented to the hydra every 30 min until feeding resumed. The number of *Artemia* ingested by each hydra during both feedings, as well as the time to resumption of feeding, was recorded for each hydra.

The density of prey available to *H. viridis* when fed to repletion probably exceeds natural prey densities. To examine the effects of prey density and exposure time on ingestion 10 individual hydra were exposed to 1.7, 3.3, 6.7 or 13.3 *Artemia* $\cdot ml^{-1}$ and allowed to feed for 15 or 60 minutes. The number of *Artemia* ingested was determined by counting the number of nauplii remaining in the petri dish at the conclusion of the experiment.

Effects of chemical stimulation on feeding were examined by treating hydra with *Artemia* extract. *Artemia* were ground with a mortar and pestle, filtered, and the filtrate then used as a chemical stimulus. Twenty individual hydra were treated with one drop of *Artemia* extract either for 1, 5, 10, or 30 min. Hydra were then rinsed with fresh M solution and immediately fed an excess of *Artemia*. The number of *Artemia* captured, the time required for each ingestion, the number of prey ingested, and the duration of the feeding response were recorded for each hydra.

To examine whether *H. viridis* ingests more prey when exposed to prey at high density for short periods rather than at lower prey densities for longer time periods, groups of 20 individual hydra were exposed to different combinations of prey density and exposure time and allowed to feed. In all cases prey exposure (prey density × exposure time) remained constant. Cultures were checked regularly and density maintained by replacing all non-swimming or ingested *Artemia*. The number of *Artemia* ingested was determined by counting the number remaining in the petri dish at the conclusion of the experiment.

Results

Observations made during the experiments are in close agreement with previous descriptions of the feeding sequence in hydra (Loomis, 1955; Lenhoff 1961a).

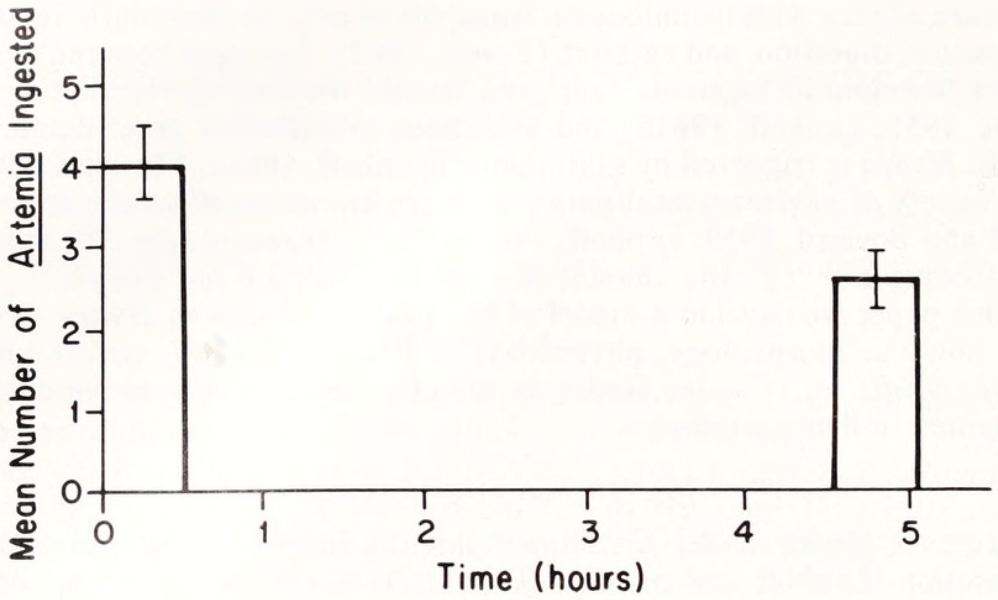

FIGURE 1. Mean number of *Artemia* nauplii ingested/hydra of 10 individual *H. viridis* fed to repletion. Hydra were offered *Artemia* every 30 min after the initial feeding until feeding resumed. Bars denote standard errors.

Nauplii, which swam about in a seemingly random fashion, would strike a single tentacle which usually resulted in the capture of a nauplius. The captured nauplius was then transported to the mouth and ingested. After a period of time (always less than 30 minutes) captured nauplii not yet ingested fell off the tentacles. Nauplii striking the tentacles at this time were sometimes captured but never ingested.

The effects of the feeding sequence on the number of prey ingested are illustrated in Figure 1, which presents the results of the satiation feeding experiments. During their initial exposure to prey *H. viridis* captured an average of 4.0 *Artemia*, but individual hydra ingested significantly different numbers of *Artemia* ($P < 0.01$, analysis of variance [ANOVA]; $F = 16.9$; $df = 1, 9$). Subsequent exposures to prey did not elicit any ingestions until at least 3.5 h had elapsed at which time a second feeding bout occurred. The length of time between feeding bouts was independent of the number of prey ingested during the first feeding bout ($r = 0.25$, $P < 0.05$). The average time between feeding bouts was 4.8 h. Feeding during the first feeding bout was greater than during the second ($P < 0.01$, ANOVA).

Both the density of *Artemia* nauplii and the length of exposure to prey affected ingestion rates (Fig. 2). Increasing *Artemia* density increased the number of prey ingested (ANOVA, $F = 21.7$; $df = 3, 72$; $P = 0.001$). Increased exposure time also enhanced the number of prey ingested (ANOVA, $F = 8.35$; $df = 1, 72$; $P = 0.005$). *A posteriori* *t*-tests indicate, however, that increased exposure time did not significantly affect ingestions at the high densities. This suggests that at high prey density *H. viridis* captured all of its prey within 15 min.

A more detailed analysis of feeding can be developed from an examination of the detailed observations of hydra fed to repletion (Table I). There was considerable variability in all components of the feeding sequence in these experiments. These data reveal that hydra regularly captured more prey than were actually ingested. There is, however, a positive correlation between the number of *Artemia* captured and the number ingested ($r = 0.87$, $P < 0.001$). Regression analysis indicates, however, that as the number of prey captured increased, percent prey captured actually decreased. (The slope of the regression [0.49] is less than 1.0 [$t = 4.45$, $P < 0.001$].) *Artemia* which were not ingested fell off the tentacles after the last ingestion.

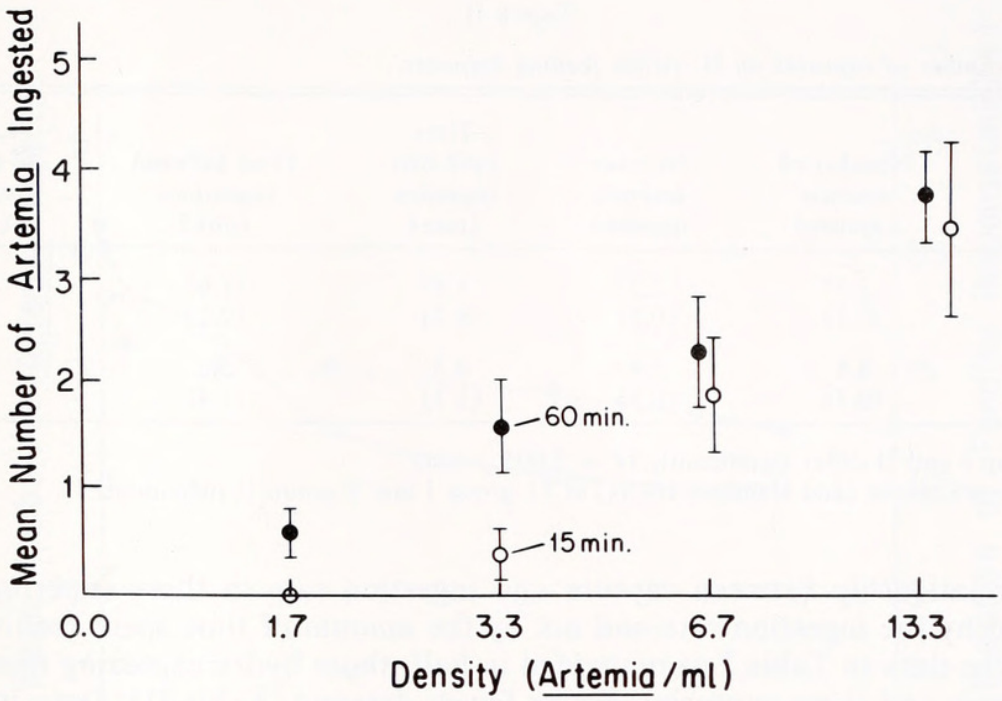

FIGURE 2. Effects of prey density and exposure time on the mean number of *Artemia* ingested by 10 individual *H. viridis* polyps fed for 15 min (○) or 60 min (●). Bars denote standard errors.

TABLE I

Results of feeding an excess of Artemia *nauplii to individual* Hydra viridis.

			TIME INTO EXPERIMENT (MIN)		
	Number of Artemia Captured	Number of Artemia Ingested	First Ingestion	Second Ingestion	End of Feeding
	3	2	6	30	30
	2	2	4	19	19
	3	2	6	15	15
	2	2	9	19	19
	3	3	3	21	21
	4	2	6	21	21
	5	3	5	12	24
	4	2	3	20	20
	4	3	7	11	26
	8	3	5	10	30
	6	2	17	30	30
	10	4	8	16	22
	8	5	6	15	23
	7	3	10	13	15
	10	7	6	9	20
	11	6	5	8	26
	14	7	4	5	28
	9	6	3	10	17
	8	4	2	15	15
	6	4	3	5	14
Mean	6.4	3.6	5.9	15.2	21.8
Standard Error	0.7	0.4	0.8	1.6	1.2

TABLE II

Effects of number of captures on H. viridis *feeding response.*

	Number of artemia captured	Number artemia ingested	Time until first ingestion (min)	Time between ingestions (min)	Length of feeding response (min)
GROUP I	3.3* (0.3)	2.3* (0.2)	5.4* (0.7)	11.6* (2.2)	21.0 (1.6)
GROUP II	8.8 (0.7)	4.6 (0.5)	6.3 (1.3)	5.6 (1.4)	21.8 (1.8)

* Group I and II differ significantly ($P < 0.005$, t-test).
Values are means (and standard errors) of 11 group I and 9 group II individuals.

The relationship between capture and ingestion rate in these experiments is controlled by the ingestion rate and not by the amount of time spent feeding. For analysis the data in Table I were divided in half, those hydra capturing more than five *Artemia* and those capturing five or fewer *Artemia* (Table II). Data in Table II indicate that hydra which captured larger numbers of prey spent as much time feeding as those hydra capturing lower numbers of nauplii, ($P > 0.1$, t-test). Hydra which captured large numbers of prey ingested nauplii at a greater rate and ingested a greater total number of nauplii ($P < 0.005$, t-test). Increased prey capture increased the number of prey ingested by decreasing the time interval between ingestions ($P < 0.005$, t-test).

The effects of *Artemia* extract on the number of prey ingested and the duration of the feeding response are depicted in Figure 3. The presence of the extract significantly reduced the duration of the feeding response ($P = 0.0016$, ANOVA, $F = 4.30$, df = 5, 88) and also reduced the number of *Artemia* ingested ($P = 0.003$, ANOVA, $F = 3.85$, df = 5, 88). The duration of the feeding response among untreated hydra was significantly greater than that of treated hydra ($P < 0.05$, least significant difference test). Treatments which differed only in the length of exposure to extract did not differ significantly from each other, but there was a significant negative correlation between duration of the feeding response and exposure to extract ($r = 0.35$, $P < 0.01$, $n = 94$). A comparison of the number of *Artemia* ingested among the treatments indicated that no single treatment differed significantly from all other treatments. However, ingestions among both untreated and 1 min treated hydra differ from the 10, 20, and 30 min treated hydra. A significant negative correlation was also observed between ingestion and exposure to extract ($r = 0.37$, $P < 0.01$, $n = 94$).

The effects of manipulating the length of time exposed to the prey and prey density are depicted in Figure 4. In each of the three experiments the total exposure to prey (*i.e.*, the probability of an *Artemia* striking a hydra) was kept constant. However, ingestion rates were significantly different ($P < 0.001$, ANOVA, $F = 18.8$, df = 2, 57) and steadily decreased with decreasing prey density ($P < 0.05$, least significant difference).

DISCUSSION

H. viridis' response to prey is modified by the feeding process itself. Therefore the response of *H. viridis* to prey cannot be modelled as a simple impact–capture–

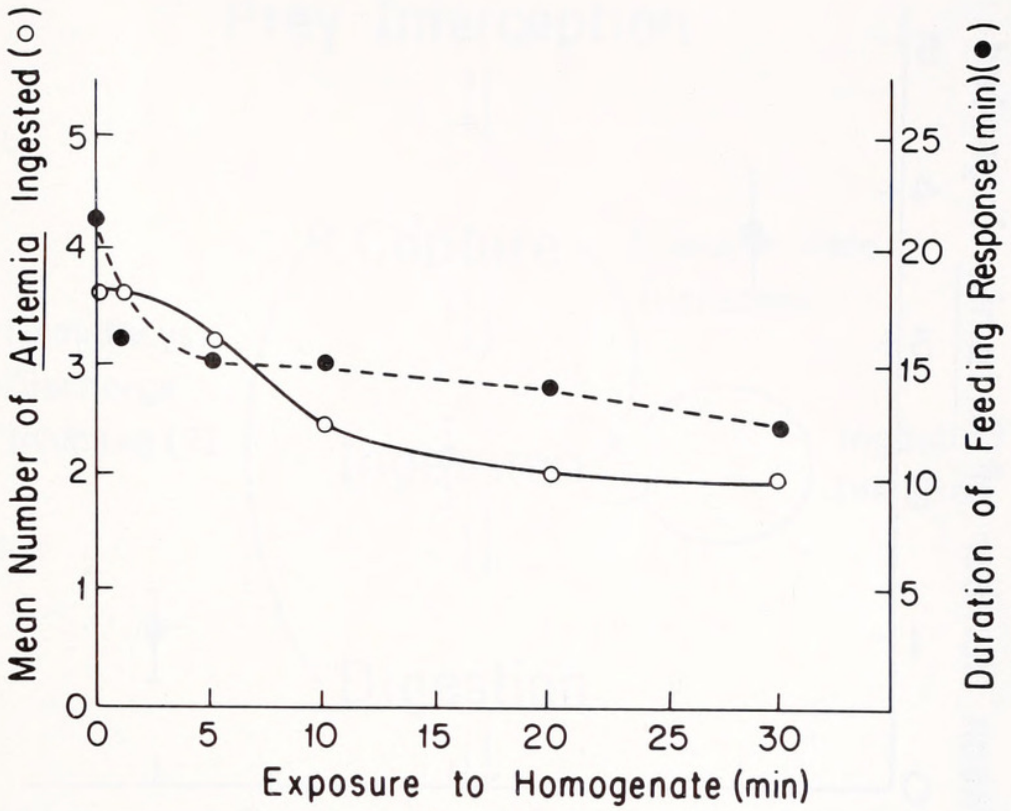

FIGURE 3. The effect of *Artemia* extract on the mean number of *Artemia* ingested (○) and duration of the feeding response (●) of 20 individual *H. viridis*.

ingestion sequence in which the probabilities of prey capture and ingestion are static. The probability of a zooplankter striking a tentacle and then being captured and ingested depends on the timing of the occurrence relative to previous feeding events. This effect is evident in Figure 5, which presents a model of feeding by *H. viridis*. The model incorporates many well known aspects of *Hydra* feeding (see Linstedt, 1971; Lenhoff, 1974) as well as the variations in feeding observed in this study.

The first step of the feeding process is the impact of a prey item with a tentacle. Tentacle movements prior to impact appear random with respect to prey movement and the rate of impacts is probably a function of prey density and prey behavior.

Following impact, nematocysts in the tentacle discharge leading to capture of the prey. Nematocyst discharge decreases when there is food in the gastrovascular cavity (Burnett *et al.*, 1960; Hand, 1961). In our experiments *H. viridis* continued to capture *Artemia* nauplii even after ingestion had ceased. However, observations of fed hydra revealed instances of nauplii swimming away after striking tentacles. Such occurrences almost never occurred at the start of feeding experiments. The ability to capture prey also appeared to decrease during the course of the 4 h digestion period.

The chemical stimulation provided by *Artemia* extract reduced the length of the feeding response (Fig. 3) suggesting that chemical stimulation of the feeding response is in some fashion time limited. However, chemical stimulation of 30 min reduced the feeding response by only 12 min which indicates that the feeding response is not controlled by chemical stimuli alone. Although the size of the gut ultimately limits the amount of food ingested, hydra frequently stopped feeding after only a single nauplius had been ingested. Thus, extension of the gut alone did not control the shutdown of the feeding response either.

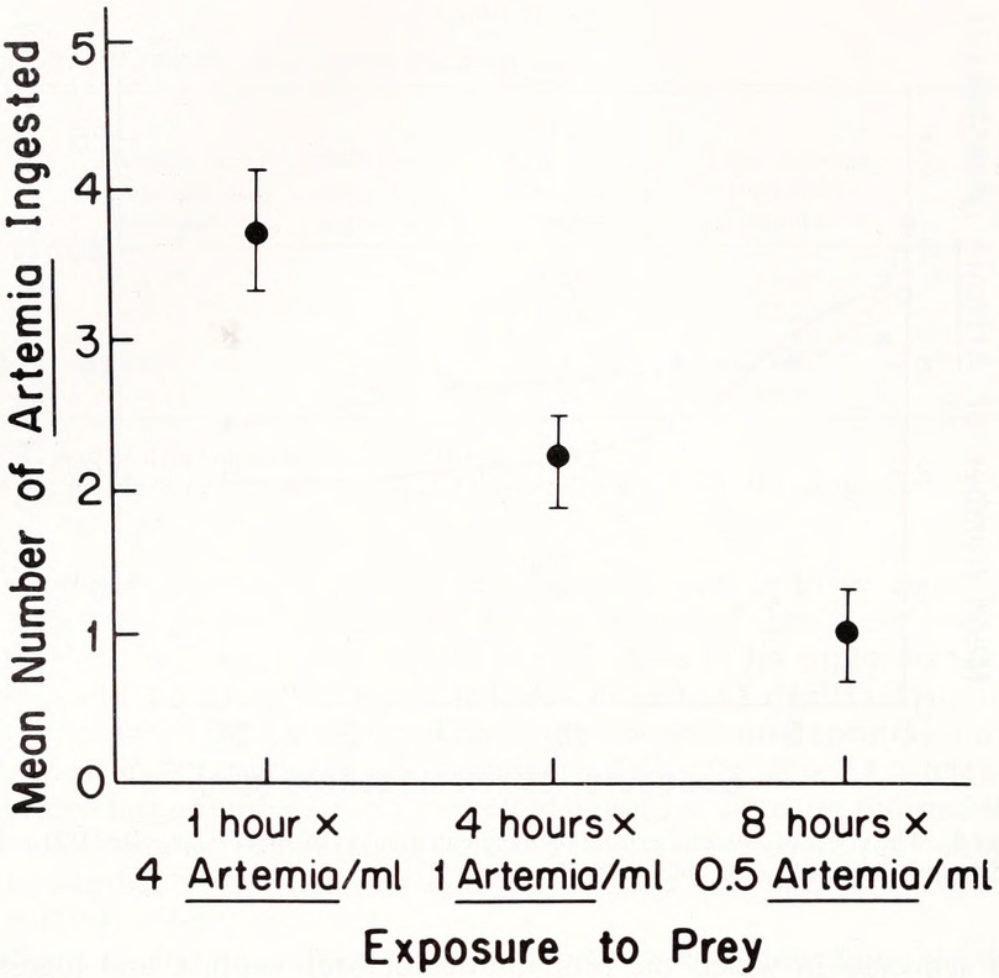

FIGURE 4. Effects of prey density and exposure time on the mean number of *Artemia* ingested/hydra by 20 individual *H. viridis* polyps. Prey exposure (*Artemia* density × exposure time) is identical in all instances. Bars denote standard errors.

Prey density affects the number of prey ingested through the ingestion rate. When large numbers of prey are captured the rate at which prey are ingested increases (Table II). Consequently, a larger number of prey are consumed during the fixed period of the feeding response.

Implicit in the model of feeding is the constraint on feeding imposed by *Hydra's* simple gut. Food must be ingested, digested, and egested in discrete batches. Consequently, *H. viridis* captures and ingests prey during short feeding bouts followed by longer periods of digestion. The time spent digesting prey limits the amount of food consumed, since prey are not captured while there is food in the gut.

The feeding sequence modelled in Figure 5 controls *H. viridis'* functional response to prey (*sensu* Holling, 1959), and the model can be used to predict the conditions in which *H. viridis* is most effective as a predator. Where prey are present in low densities, *H. viridis* are unlikely to catch and ingest more than a single zooplankter during an ingestion–digestion sequence. This limits feeding success to only a single prey every 3–5 hours regardless of the number of prey striking tentacles during the period in which ingestion is inhibited. This is evident in Figure 4 in which *H. viridis* exposed to 0.5 *Artemia* · ml^{-1} for 8 hours captured significantly fewer prey than *H. viridis* exposed to greater densities for less time. The number of prey consumed is lower than expected on the basis of hydra-prey encounters. Under these circumstances the feeding process exhibited by *H. viridis* appears to be particularly disadvantageous.

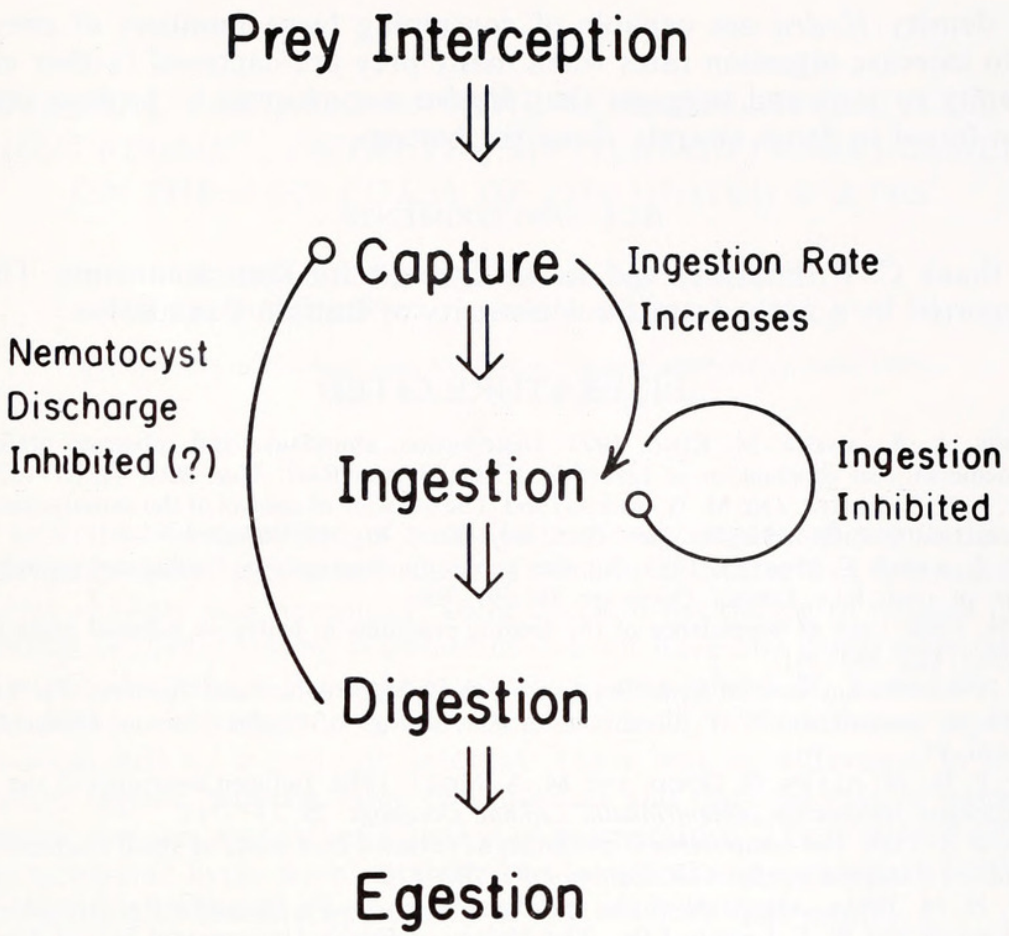

FIGURE 5. Generalized model of feeding showing effects of ingested prey on feeding. → indicates a stimulatory effect and ⊖ indicates an inhibitory effect.

As evident from Figure 4, at high prey densities *H. viridis* is capable of multiple captures, and an increase in the rate at which it ingests captured prey enables *H. viridis* to increase the number of prey consumed during a single capture–ingestion–digestion sequence.

The response of *H. viridis* to prey at different densities indicates that it is best suited to feeding on densely distributed prey. The enhanced ingestion rates reported here were observed at prey densities of 4,000 *Artemia*·l^{-1}, while crustacean densities in lakes are usually in the range of 5–50·l^{-1} (Wetzel, 1975). Denser concentrations, however, do occur and may be a regular feature of aquatic environments. In a study of a dense *Hydra* population in Toolik Lake, Alaska, Cuker and Mozley (1981) captured up to 14,000 *Bosmina* per day in 0.125 m^2 emergence traps. They report that the *Bosmina* were found in dense swarms and cite one example of *B. longirositis* swarms of up to 27,000·l^{-1}. Swarming has also been observed in *Heterocope septentrionalis* (Herbert, *et al.*, 1980) and is frequently observed in marine zooplankton which concentrate at the bottom during the day (Alldredge and King, 1977). As predicted, in the presence of plankton swarms *Hydra* are effective predators. Cuker and Mozley (1981) regularly found *Hydra* with 5–7 prey per gut and report one case of a *Hydra* with 23 carapaces in its gut. (The species Cuker and Mozley [1981] studies is much larger than *H. viridis*, which can hold only 5–7 *Artemia* in its gut.)

At low prey densities the simple gut and the feeding sequence exhibited by *Hydra* reduce their capability to consume prey. However, when prey are present

in high density *Hydra* are capable of consuming large numbers of prey. Their ability to increase ingestion rates when many prey are captured further enhances their ability to feed and suggests that *Hydra* are adapted to feeding upon zooplankton found in dense swarms along the bottom.

ACKNOWLEDGMENTS

We thank C. R. Fourtner and K. M. Stewart for their comments. This work was supported by a grant from the University of Buffalo Foundation.

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