

Modeling the Effects of Satiation on the Feeding Rate of a Colonial Suspension Feeder, *Acanthogorgia vegae*, in a Circulating System under Lab Conditions

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Ming-Chao Lin, Chung-Min Liao and Chang-Feng Dai (2002) Modeling the effects of satiation on the feeding rate of a colonial suspension feeder, *Acanthogorgia vegae*, in a circulating system under lab conditions. *Zoological Studies* 41(4): 355-365. We developed a mathematical model, based on observations relating to feeding behavior of the gorgonian *Acanthogorgia vegae*, to characterize the feeding rates of colonial suspension feeders in a circulating system. We found that simultaneously none of all the polyps belonging to the same colony of *A. vegae* showed a feeding response after capturing a certain amount of *Artemia* nauplii. Equations in terms of the satiation factor were derived to predict feeding rates of colonial suspension feeders. Flume experiments were conducted under different ambient flow regimes to test the application of the equations. Good agreement between the results of the experiments and the predictions was evident. The results of this study show that satiation is an important factor influencing the feeding rate of colonial suspension feeders with an abundant food supply and a closed system of water. Furthermore, our study shows that the feeding rate of colonial suspension feeders in a circulating system can easily be calculated from the residual number of prey items at various times, even when the initial numbers of prey items and feeding animals are unknown. Our model is useful as a good methodological tool to estimate the feeding rate of colonial suspension feeders in the laboratory or aquacultural environments. <http://www.sinica.edu.tw/zool/zoolstud/41.4/355.pdf>

Key words: Colonial suspension feeder, Feeding, Gorgonian, Mathematical modeling, Satiation.

Two national marine museums are under construction in Taiwan. Legislation concerning marine protected areas, mainly marine parks and preserves, is being developed in order to conserve endangered species. Techniques for culturing colonial suspension feeders, such as sponges, sea pens, corals, bryozoans, and ascidians, have become important.

Traditional aquaculture for growing colonial suspension feeders was based only on empirical methods, but these methods have proven not to be accurate enough. Culturing takes place under unpredictable and often suboptimal conditions. An adequate supply of food seems to be the key to

successful suspension feeder cultures: lack of food will produce animals in poor health; too much food can pollute the aquacultural environment. When designing a culture system, it is important to quantitatively determine the food demands of the cultivated species. A well-defined feeding rate of the cultivated species is desirable.

Feeding rates of colonial suspension feeders are controlled by both behavioral and physiological mechanisms (Shimeta and Koehl 1997). Physiological reactions, such as satiation, can influence the feeding behavior. Patterson (1991b) showed that the feeding rate of suspension feeders is not simply proportional to the number of

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prey items available; he suggested that satiation is an important factor affecting the feeding of colonial suspension feeders. Williams (1982), LaBarbera (1984), and Shimeta and Jumars (1991) among others have presented mathematical models to estimate the influences of behavioral and physiological reactions on feeding rates of suspension feeders, but they did not consider the fact that animals may become satiated after continuous feeding.

Colonial suspension feeders depend on ambient currents to drive particle-laden fluids within reach of their feeding structures (LaBarbera 1984, Hunter 1989, Sponaugle 1991). Feeding rates of organisms, such as scleractinian corals (Helmuth and Sebens 1993), alcyonacean corals (Patterson 1984 1991a,b), sea pens (Best 1988), gorgonians (Leversee 1976, Lasker 1981, Sponaugle and LaBarbera 1991, Dai and Lin 1993), and bryozoans (Okamura 1984 1985 1987 1990), have been extensively examined. A common finding of these studies is that flow velocity is an important factor affecting the feeding rates of colonial suspension feeders. However, the feeding rates at various velocities have seldom been investigated using mathematical models.

Traditionally, the feeding rate of a suspension feeder at a given flow velocity is calculated from the observed decrease in prey items. Coughlan (1969) reviewed the use of exponential models for calculating the feeding rates of suspension feeders; he suggested that the feeding rate of an individual animal can be represented mathematically as,

$$R = \frac{\ln P_0 - \ln P_T}{nT}, \quad (1)$$

or

$$P_T = P_0 e^{-RnT}, \quad (2)$$

where R is the feeding rate of an individual animal ($\text{no.}^{-1} \text{h}^{-1}$); P_0 is the initial number of prey items (no.); P_T is the number of prey items (no.) after the feeding time T (h); and n is the total number of animals. (no.)

Although Williams (1982) pointed out that this equation was a misinterpretation because it wrongly considers feeding rate as pumping rate and is not valid for feeding efficiency less than 100%, this equation is still used as a basic assumption for many other equations (Williams 1982, Patterson 1991b, Anthony 1997). Since the number of animals in equation (1) is assumed to be constant,

the model fails to consider the effect of satiation.

Ribes (1998) demonstrated that satiation is an important factor influencing the feeding rate of hydrozoans, primarily *Hydra* spp. However, satiation effects in cnidarians are little known. This study was designed to investigate the effects of satiation on feeding behavior and feeding rates of a gorgonian, *Acanthogorgia vegae*. First, a mathematical model in which the effect of satiation is incorporated was developed to estimate feeding rates. The feeding behavior of polyps was then observed, and the number of prey items that led to satiation was measured. Flume experiments were conducted to quantify feeding rates under different ambient flow regimes, in order to expand the model to encompass variability in flow velocity.

MATERIALS AND METHODS

Mathematical modeling

Colonial suspension feeders are animals that form aggregate structures with organic connections between individual members (Hughes 1989). It is reasonable to consider such a colony as a single organism with many mouths rather than an assemblage of many individuals (Murdock 1978). Thus, the feeding rate is related to the number of prey items required to satiate the colony, but is not related to the total number of polyps on the colony.

To develop a mathematical model, we hypothetically used "the number of feeding units (N)" to replace "the total number of animals (n)" (equations (2) and (3)). A feeding unit was defined as a group of polyps that together is satiated when the group has ingested a combined total of 1 prey item. The number of feeding units (N) is equal to the prey items required to satiate the colony. The ratio of the number of feeding units (N) and the total number of polyps on a colony (n) was defined as the satiation efficiency (E), i.e., $E = N/n$. For example, for a colony with 500 polyps ($n = 500$) and a single polyp which can be satiated by 2 prey items ($E = 2$), the number of feeding units is 1000 ($N = 1000$); or if a colony has 500 polyps ($n = 500$) and the number of feeding units is 250 ($N = 250$), then the satiation efficiency is 0.5 ($E = 0.5$). Based on these assumptions, the feeding rate of feeding units (F) is equal to the ratio of the feeding rate of an individual animal (R) and its satiation efficiency (E), i.e., $F = R/E$.

The number of feeding units (N) is a function of time (being equal at any moment to the number

of prey required to reach satiation), while the number of animals (n) is a constant. This means that E ($= N/n$) is a function of time, and thus R ($= F \times E$) is also a function of time. On the other hand, F is a constant ($= R/E$), even though N decreases with time at the same rate as R decreases.

The residual number of prey items can be expressed as a function of the initial number of prey items, the initial number of feeding units, the feeding rate, and the feeding time:

$$P_T = \frac{P_0 - N_0}{1 - \frac{N_0}{P_0} e^{-F(P_0 - N_0)T}}, \quad (3)$$

where P_T is the number of prey items (no.) after the feeding time T (h); P_0 is the initial number of prey items (no.); N_0 is the initial number of feeding units (no.); and F is the feeding rate (no.⁻¹ h⁻¹). The model formulations and analytical solutions are described in detail in Appendix A. A description of variables is given in Appendix B.

The underlying process represented by the model is that the number of available prey items (no.) decreases to a constant value when the colony is satiated and feeding ceases. Thus the final, constant number of residual prey items is equal to the initial number of prey minus the number required for satiation. Equation (3) is simply a statement that at T_0 , the residual prey items $P_T = P_0$ (the initial number of prey items), while at T_∞ , $P_T = P_0 - N_0$, where N_0 is the initial number of prey required to satiate the colony.

The advantage of parameterizing satiation in this way is that the equation can be manipulated to express residual prey as a function of only 1 variable: time. Therefore, it is easy to apply the model to simple measurements of prey depletion over time, and it allows calculation of a single number (F) to represent the feeding rate, despite the fact that the colony is steadily becoming satiated over time.

Specimen collection and acclimation

Acanthogorgia vegae Aurivillus (Gorgonacea: Octocorallia: Anthozoa) is a colonial suspension feeder (Dai and Lin 1993); it usually grows on the lateral sides of blocks or reef fronts with its fan-shaped colonies oriented perpendicular to the prevailing current (Chen and Chang 1991, Dai and Lin 1993). For use in feeding studies, colonies of *A. vegae*, each about 15 cm high and 15 cm wide, were collected from Nanwan Bay, southern Taiwan (120°44'E, 21°57'N). Only colonies with no

branches located downstream of another branch were selected. These colonies were then transferred to an acclimation tank (60 cm long, 30 cm wide, 30 cm high) in which the temperature was controlled at 24°C. The acclimation tank was equipped with 2 current generators that create constant flow. Organisms were acclimated for 1 week before the experiments. During this period, colonies were fed *Artemia* nauplii, but were starved 24 h prior to beginning the experiments.

Feeding behavior

Because it was difficult to observe the feeding behavior of *Acanthogorgia vegae* in any detail in the acclimation tank, we conducted the feeding behavior experiment in a petri dish under a dissecting microscope (Olympus SZH). A coral colony, starved for 24 h, was placed on a petri dish in an acclimation tank (Fig. 1). The colony was allowed to acclimate for a further 3 h in the tank before the feeding behavior experiment began. The petri dish with the colony was removed from the tank and then placed under the dissecting microscope. The colony was fed with live *Artemia* nauplii, using a pipette to release seawater containing *Artemia* nauplii toward the polyps at a flow speed of 5-10 cm s⁻¹. The direction of the current was oriented perpendicular to the colony. The feeding behavior of polyps was observed and photographed. The handling time of 10 polyps was measured for each coral colony. Three replicate colonies were examined.

Flume experiments

A circulating flow tank (Fig. 1) of 75-L capacity (320 cm long, 15 cm wide, 20 cm high) was made according to Leversee (1976). The tank was filled with 69 L of filtered seawater, which was filtered using a 200-μm plankton net and then stored in the dark for more than 2 wk before the experiment. A laboratory stirrer (Her-Cheng SC-VS35W) with a propeller (14 cm in diameter) was used to generate water flow. The flow velocity was regulated by a solid-state motor control and was measured with an electromagnetic current meter (Kenek, VM-401H). The detector (sensor part φ 8 × 30 mm) of the current meter was placed 15 cm upstream of the colony. An acrylic laminator was placed 30 cm upstream of the colony to maintain reasonably laminar flow.

A colony, starved for 24 h, was transferred to

the circulating flow tank and oriented perpendicular to the flow direction. The colony was fastened onto a base, which consisted of a combination of a silicone cylinder with upright stainless steel nails. The colony was allowed to further acclimate to the flow tank for 3 h before the feeding experiments began. The feeding experiments were conducted in the range of flow velocities in which the gorgonian expands its polyps. Living *Artemia* nauplii were harvested from a culture 24 h after hatching in seawater. In total, 2800 *Artemia* nauplii were

counted with the naked eye using a 10-ml pipette and added to 1 L of seawater. The seawater containing *Artemia* nauplii was then poured evenly into the flow tank. During the following 6 h, the number of *Artemia* nauplii in the tank was determined at hourly intervals in 1-L samples drawn from the tank. Water samples were poured through a plankton net (200 μm), and the *Artemia* nauplii on the net were counted. The *Artemia* nauplii were returned to the flow tank along with the filtered seawater after counting.

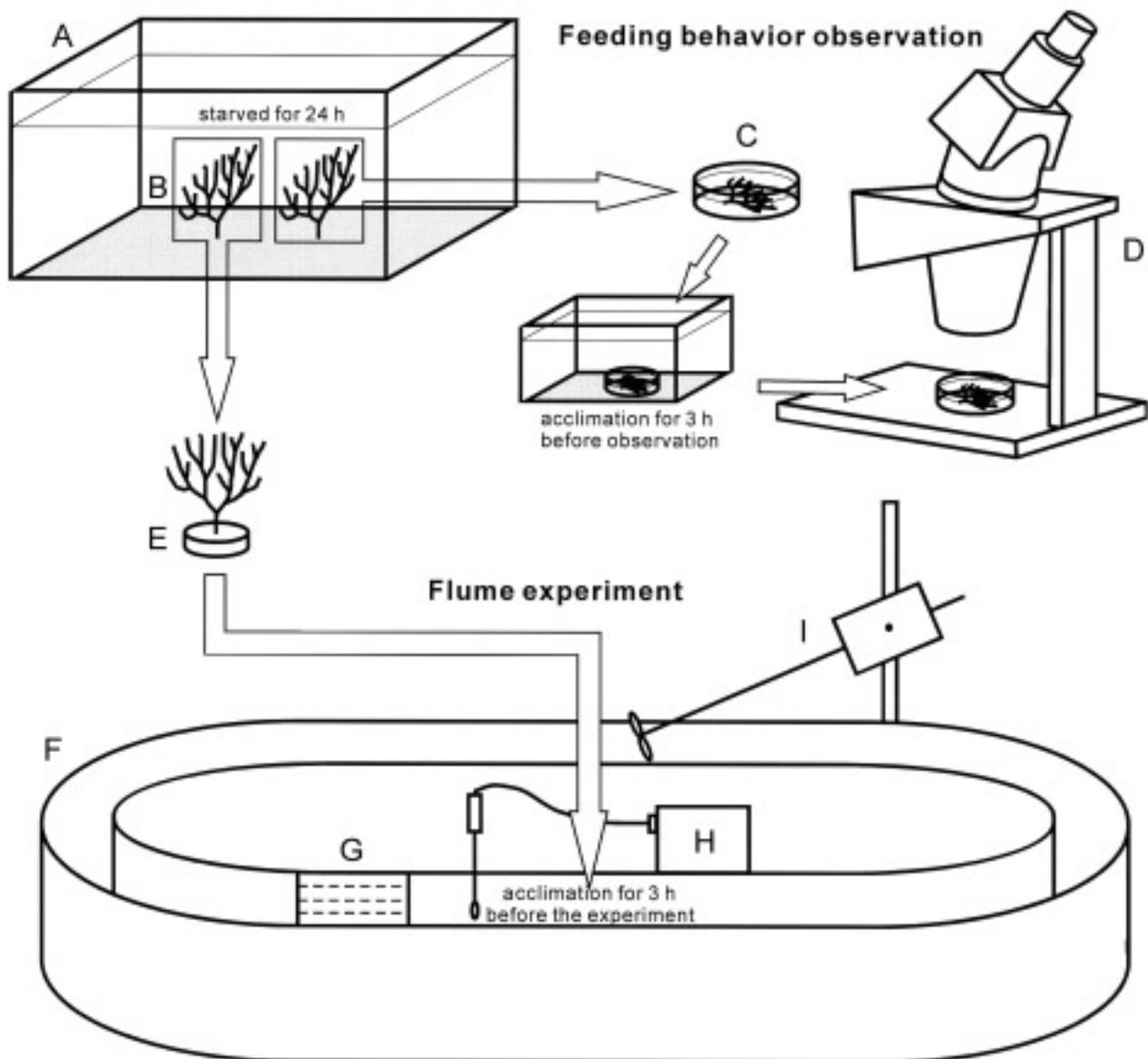


Fig. 1. Scheme for feeding behavior observations and flume experiments. (A) acclimation tank; (B) coral colony; (C) petri dish; (D) dissecting microscope; (E) colony base; (F) circulating flow tank; (G) acrylic laminar; (H) electromagnetic current meter; (I) laboratory stirrer with propeller.

During the experiments, two replicate colonies were examined, and the feeding rates at various flow velocities were determined by counting the residual number of *Artemia* nauplii. To detect the natural mortality and precipitation of the nauplii during the experiment, blank tests were conducted at various flow velocities without coral colonies.

The feeding data were fitted to the developed mathematical models using an iterative, nonlinear, least-squares curve-fitting technique (Statgraphics IV, STSC). Estimates from the mathematical models were compared. The applicability of the best-fitting equation and Coughlan equation (equation (2)) were further examined by comparing the estimates obtained from the 2 equations with empirical data at a velocity of the maximum feeding rate.

RESULTS

Feeding behavior

During the 24-h period when food was withheld from the acclimation tank, the coral polyps were fully expanded in search of food. No retraction was detected.

Observations of the feeding behavior of *Acanthogorgia vegae* showed that the feeding behavior of polyps could be classified into 5 consecutive steps: (1) the expanded tentacles cap-

tured an *Artemia* nauplius; (2) the tentacles contacting the nauplius gradually retracted; (3) the adjacent tentacles gradually retracted, keeping the nauplius in a central position on the oral disk; (4) the polyp ingested the nauplius into the coelenteron; and (5) the tentacles re-expanded in reverse order (Fig. 2). The time a polyp required to move the 1st nauplius it captured to the central position of the oral disk was 2.1 ± 0.9 s ($n = 30$). Gradual withdrawal of adjacent tentacles took 11.4 ± 1.2 s ($n = 30$). Ingesting the nauplius into the coelenteron of the polyp took 22.5 ± 4.1 s ($n = 30$). Re-expansion of the feeding tentacles took 50.0 ± 8.9 s ($n = 30$). Thus, the time to complete a feeding cycle was 86.3 ± 9.1 s ($n = 30$). When a polyp successively captured the 2nd *Artemia* nauplius with repeated feeding, the step-by-step handling times were about doubled (4.4 ± 1.8 s, $n = 30$; 22.7 ± 5.3 s, $n = 30$; 50.5 ± 8.6 s, $n = 30$; 93.2 ± 8.0 s, $n = 30$; and 170.8 ± 12.1 s, $n = 30$, respectively).

The entire colony stopped feeding after capturing 0.54 ± 0.22 shrimp polyp⁻¹ ($n = 30$); no feeding response was observed even when the polyps were fully expanded. On the other hand, if no food was added, the colony continued to exhibit feeding behavior for more than 6 h.

Flume experiments

The result of the blank tests showed that

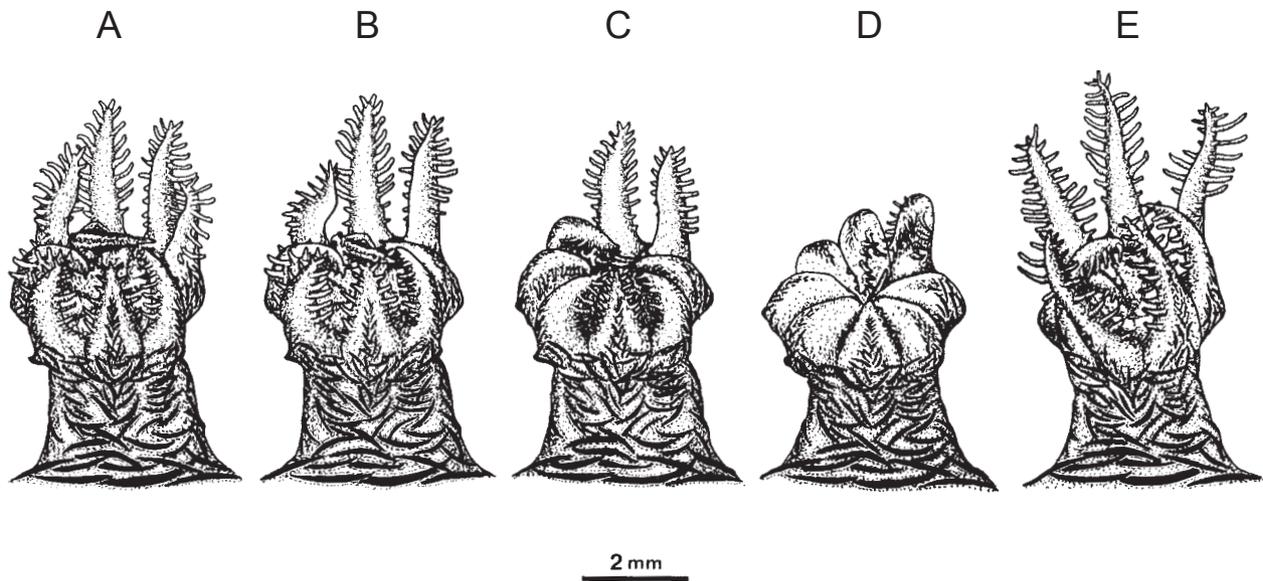


Fig. 2. Feeding steps of *Acanthogorgia vegae*. (A) the tentacles capture an *Artemia* nauplius; (B) the tentacles contacting the nauplius gradually retract; (C) the adjacent tentacles gradually retract, keeping the nauplius in a central position on the oral disk; (D) the polyp ingests the nauplius into the coelenteron; (E) the tentacles re-expand in reverse order.

there was no significant change in the number of *Artemia* nauplii during the 6-h experimental period. The regression slope did not significantly differ from 0 ($F = 0.32, n = 35, p > 0.05$ at 8 cm s^{-1} ; $F = 0.18, n = 35, p > 0.05$ at 24 cm s^{-1}). This showed that *Artemia* nauplii were not damaged while traveling through the stirrer propeller; so the natural mortality and precipitation of *Artemia* nauplii during the experiment period can be neglected.

The *A. vegae* colony expanded its polyps at flow velocities ranging from 0 to 24 cm s^{-1} , but could only capture *Artemia* nauplii from 2 to 22 cm s^{-1} (Fig. 3). Higher feeding rates of the colony were found at flow velocities ranging from 6 to 10 cm s^{-1} with the highest at 8 cm s^{-1} . The residual number of *Artemia* nauplii in the flow tank decreased most rapidly during the 1st h of feeding (Fig. 4A). The residual number of *Artemia* nauplii with time of feeding can be described by the equation (Richards 1959):

$$P_T = A(1 - Be^{-CT})^{\frac{1}{1-K}}, \quad (4)$$

where P_T is the residual number of *Artemia* nauplii (no.) after feeding time T (h); while $A, B, C,$ and K are fitting parameters.

The nonlinear least squares curve-fitting technique (Statgraphics IV, STSC) was used to fit the

feeding data to equation (4). The result shows that the value of K in equation (4) is approximately equal to 2 (2.003 ± 0.004); thus equation (4) can be rewritten as

$$P_T = \frac{A}{1 - Be^{-CT}}. \quad (5)$$

The residual number of *Artemia* nauplii at var-

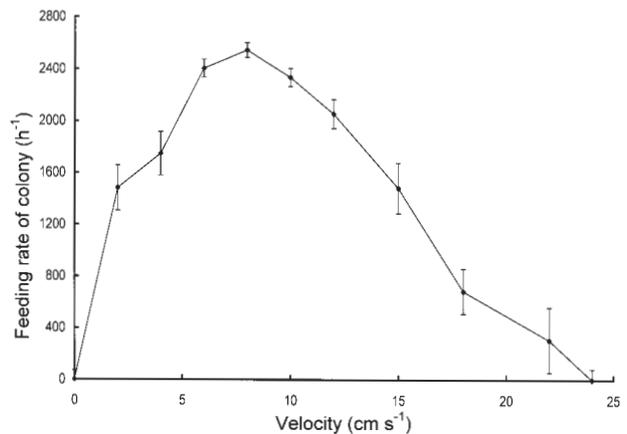


Fig. 3. Feeding rate (number of *Artemia* nauplii captured by a colony in 1 h) of the colony of *Acanthogorgia vegae* during the 1st hour of exposure to *Artemia* nauplii at flow velocities ranging from 0 to 24 cm s^{-1} .

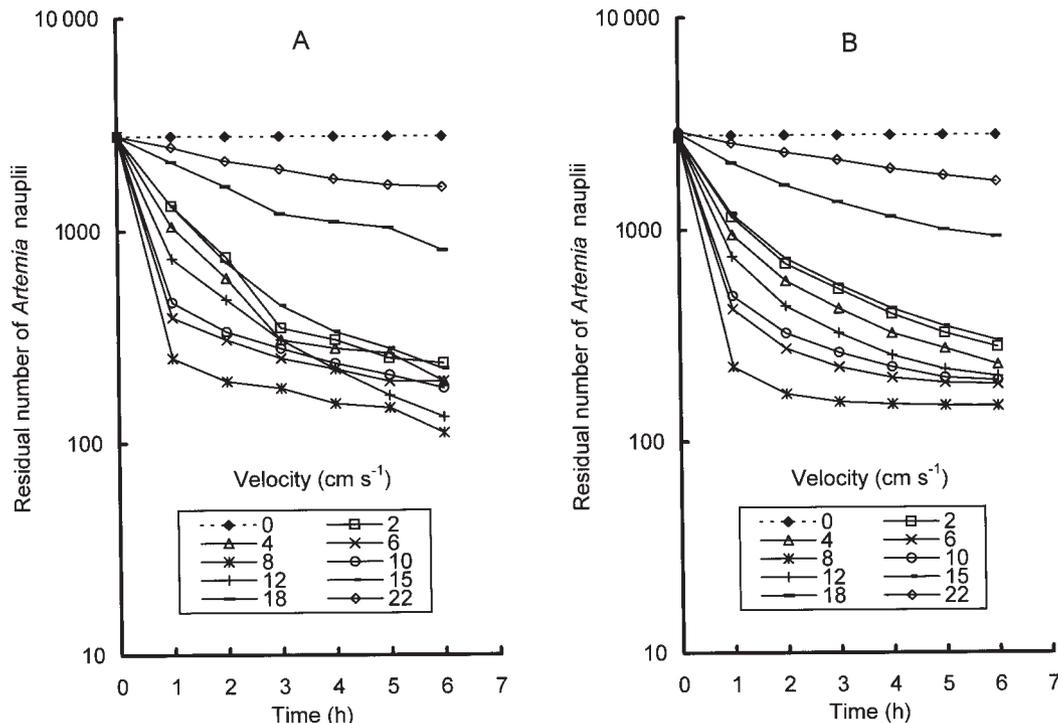


Fig. 4. Residual number of *Artemia* nauplii in the 6-h period of the flume experiment for *Acanthogorgia vegae* at various flow velocities: (A) empirical data; (B) data calculated from $P_T = A/(1 - Be^{-CT})$.

ious flow velocities after a 6-h feeding period was calculated according to equation (5) and is shown in figure 4B. Table 1 shows that equation (5) is suitable to describe changes in feeding rates of *A. vegae* ($R^2 = 0.87-0.99$, $n = 21$, $p > 0.05$).

The applicability of equation (5) and the Coughlan equation (equation (2)) was examined at a flow velocity of 8 cm s^{-1} . Figure 5 shows that the empirical data fit the estimates obtained from equation (5) ($R^2 = 0.87-0.99$, $n = 21$, $p > 0.05$) better than the estimates obtained from the Coughlan equation ($R^2 = 0.17-0.23$, $n = 21$, $p < 0.05$).

DISCUSSION

Observations of the feeding behavior of *Acanthogorgia vegae* showed that the feeding responses were elicited only by contact with *Artemia* nauplii. Tactile stimuli seem to be the major factor inducing the feeding reactions. Lewis and Price (1975) reported that there are 3 feeding strategies observed in corals: (1) feeding by tentacle capture only, (2) feeding entanglement with mucus filaments, and (3) feeding by a combination of tentacle capture and mucus filament entanglement. The entire feeding behavior of *A. vegae* consists of the 1st strategy.

Utilization of food sources by suspension feeders is largely dependent upon the amount of prey and the successful capture of prey from the surrounding waters (Lawn and McFarlane 1991). Water flow determines the amount of prey arriving at colonial suspension feeders (Best 1988,

Sponaugle 1991, Dai and Lin 1993). For slow currents, the volume of flow increases with flow velocity, as does the encounter rate (Best 1988). When the current speed is too extreme to allow efficient feeding, a colony will retract its polyps (Sebens 1984, Dai and Lin 1993). Many authors have reported that the efficiency of food retention, which is inversely related to drag force, affects the feeding rate of a suspension feeder (e.g., Rubenstein and Koehl 1977, Okamura 1984 1985, Patterson 1984, Dai and Lin 1993).

Acanthogorgia vegae expanded its polyps and fed at flow velocities ranging from 0 to 24 cm s^{-1} . However, we still find colonies in the field that do not always simultaneously expand their polyps when they encounter the suitable velocity range. This phenomenon can also be found in other gorgonians, such as *Melithaea ochracea* and *Subergorgia suberosa*. Even when different coral colonies from the same species live on the same reef with similar microhabitats, they may show different feeding responses: some have the polyps fully expanded, while others have the polyps fully retracted. It seems that some colonies become satiated and retract their polyps, while others are still capturing food from the ambient water.

Handling time is also a constraint affecting the feeding rate (Patterson 1991b, Shimeta and Koehl 1997). Observations of feeding behavior of *A. vegae* showed that the feeding rate of a polyp slows down with repeated feeding. Leverage (1976) reported a similar phenomenon for the gorgonian *Leptogorgia*, and as did Reimer (1971) for the zoanthid *Palythoa psammophyllia*. Furthermore, Leverage (1976) described a great range of individual polyp responses: some polyps fed repeatedly; some polyps fed once and stopped feeding; and some polyps evidently did not feed at all. In our study, the entire colony stopped feeding after capturing a certain amount of *Artemia* nauplii. This implies that satiation is an important factor influencing the feeding rate of colonial suspension feeders. Additional research in this field must consider satiation, because it affects feeding behavior, feeding rates, and feeding periodicity.

From our study, we suggest using equation (5) to estimate the feeding rates of colonial suspension feeders, because it takes into account the satiation effect. Estimates obtained from equation (5) fit very well with the empirical data; more than 85% of variation in feeding rates of *A. vegae* could be explained by the residual number of *Artemia* nauplii and the feeding time. On the other hand, estimates from the Coughlan equation (equation

Table 1. Values of the 3 fitting parameters, *A*, *B*, and *C*, from the equation $P_T = A/(1 - Be^{-CT})$ during a 6-h period of experimental feeding of *Acanthogorgia vegae* at various flow velocities (cm s^{-1})

Velocity	<i>A</i>	<i>B</i>	<i>C</i>	R^2
2	20.5±9.8 ^a	0.99±0.00	0.02±0.08	0.97
4	75.9±137.0	0.97±0.05	0.06±0.21	0.98
6	181.0±24.5	0.94±0.01	0.52±0.13	0.99
8	147.2±20.3	0.95±0.01	0.77±0.26	0.99
10	194.1±32.0	0.93±0.00	0.45±0.13	0.99
12	73.5±92.8	0.97±0.02	0.08±0.12	0.99
15	56.8±66.3	0.98±0.12	0.03±0.44	0.98
18	29.0±2.5	0.99±0.00	0.00±0.00	0.93
22	29.5±1.3	0.99±0.00	0.00±0.00	0.87

^aMean ± SE.

(2)) failed to depict the empirical data when the effect of satiation became evident. The equation that considers satiation makes far better predictions than the equation that does not account for satiation, so it is clear that satiation indeed does have a strong effect on the feeding of suspension feeders. Equation (5) is valid to depict the feeding rate of colonial suspension feeders if satiation exists.

In view of equations (3) and (5), the 3 fitting parameters of A , B , and C can be expressed as

$$A = P_0 - N_0, B = \frac{N_0}{P_0}, \text{ and } C = F(P_0 - N_0). \quad (6)$$

The feeding rate, F , can be calculated by dividing parameter C by parameter A (Table 1),

$$F = \frac{C}{A}. \quad (7)$$

A plot of F values of feeding units against

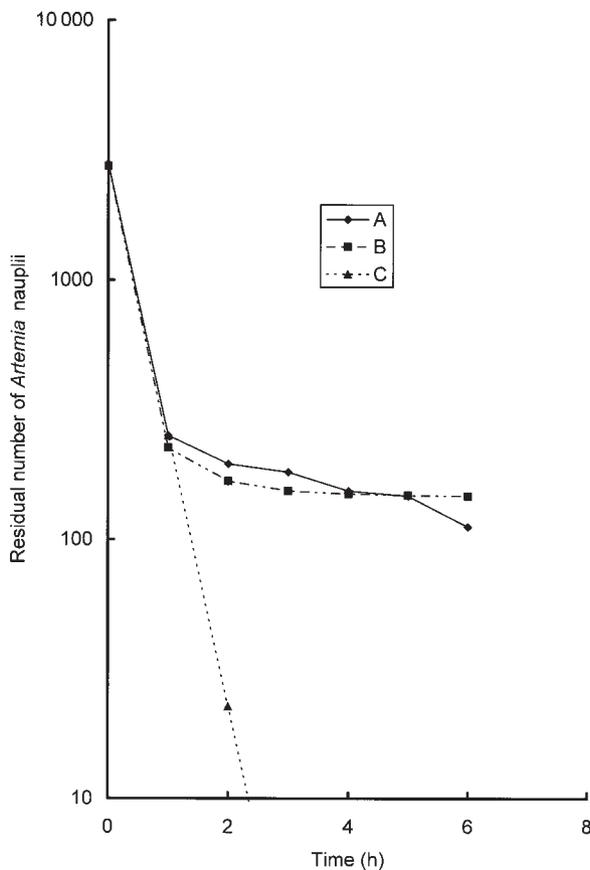


Fig. 5. Residual number of *Artemia* nauplii in the 6-h period of the feeding experiment for *Acanthogorgia vegae* at 8 cm s^{-1} . (A) empirical data; (B) data calculated from $P_T = A/(1 - Be^{-CT})$ with satiation; (C) data calculated from the Coughlan equation, ignoring the satiation factor.

velocity calculated from equations (5) and (7) is shown in figure 6. The feeding unit of *A. vegae* shows higher feeding rates at flow velocities ranging from 6 to 10 cm s^{-1} with the highest at 8 cm s^{-1} . At low flow speeds, feeding rates are limited by the supply of prey, while at high flow, capture is inhibited by interference of the high current speeds (Dai and Lin 1993). The feeding unit shows a similar tendency to the feeding rates of the colony, therefore the method of using “the feeding rate of feeding units” to describe “the feeding rate of a colony” is a meaningful and useful approach for colonial suspension feeders.

The model states that $P_0 - N_0$, equal to the fitting parameter A , is a constant with respect to time, yet the flume data show that $P_0 - N_0$ changes with velocity, with higher values at flow velocities ranging from 6 to 10 cm s^{-1} . Probably because under those optimal flow velocities the feeding units have higher feeding rates (Fig. 6), it thus takes less energy and handling time to satiate the colony. At other flow velocities, the colony needs more time to reach satiation, and so some feeding units may begin to capture food again after digestion. However, the difference between 2 A values under varied flow velocities (0.5-164.6) can be neglected because the P_0 value is high (2800), while B values (the ratios of P_0 and N_0) show that P_0 and N_0 values are similar.

The result of feeding behavior observations in petri dishes showed that the value of satiation efficiency (E) of the colonies of *A. vegae* under a flow of $5\text{-}10 \text{ cm s}^{-1}$ is 0.54 ± 0.22 . The average num-

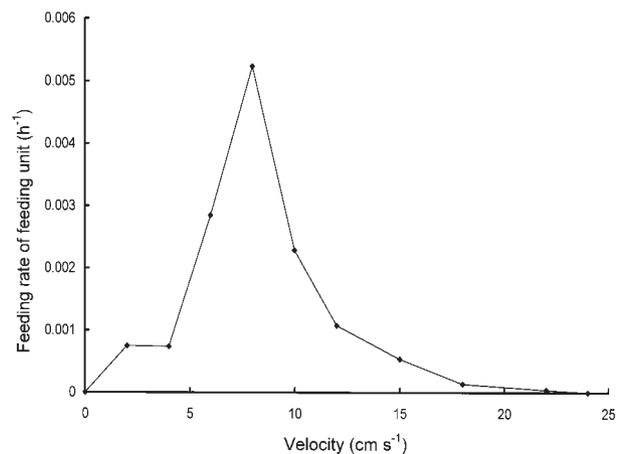


Fig. 6. Feeding rate (number of *Artemia* nauplii captured by a feeding unit in 1 h) of the feeding unit of *Acanthogorgia vegae* during the 1st hour of exposure to *Artemia* nauplii at flow velocities ranging from 0 to 24 cm s^{-1} . Data are calculated from the equations, $P_T = A/(1 - Be^{-CT})$ and $F = C/A$.

ber of polyps (n) on the colonies was 4801 ± 244 (Dai and Lin 1993). This means that a colony needs to capture about 2592 *Artemia* nauplii to reach satiation (N_0). This value is very close to the average amount (2541 ± 307) of *Artemia* nauplii captured by a colony of *A. vegae* after 1 h of exposure to *Artemia* nauplii in the circulating flow tank under a flow of 6-10 cm s⁻¹, while the colony was nearly satiated.

According to directly measured data and equation (6), the difference between the number of prey items ($P_0 = 2800$) and the number of feeding units ($N_0 = 2592$) is 208 (A). This value is close to the value of fitting parameter A (174.1 ± 24.2) calculated from equation (5), based on data from the flume experiments under a flow of 6-10 cm s⁻¹. In addition, the B values calculated from directly measured data (0.93) and model-fitting data (0.94 ± 0.01) are also similar. This shows that the estimates obtained from equation (5) fit the empirical data very well. Thus, equations (5) and (6) are dependable for predicting the feeding rate of feeding units.

While calculating the feeding rate of an individual animal (R), the number of prey items it takes to satiate the colony (N) and the satiation efficiency (E) must be examined. Therefore, we recommend using the residual number of prey items at various times to predict the feeding rate of colonial suspension feeders with equation (5), even when the initial numbers of prey items and feeding polyps are unknown.

Shimeta (1993), Ribes et al. (1998 1999a,b), and Fabricius and Dommissse (2000) reported that suspended particles are important food resources for suspension feeders. The particles may contribute to 1/2 of the carbon and 1/3 of the nitrogen required for tissue growth of corals (Anthony 1999). In Nanwan Bay, the concentration of natural zooplankton is 2.92 ± 1.8 individuals L⁻¹ (Huang 1993), which is about only 1/7 of the initial concentration of *Artemia* nauplii (20 individuals L⁻¹) we used for the flume experiments. Under natural conditions, *Acanthogorgia vegae* is unlikely to encounter zooplankton prey in such high concentrations, as those used in laboratory rearing experiments. The model presented in this paper based on laboratory results provides a good method for predicting the feeding rates of colonial suspension feeders, especially when the food concentration is high in an aquacultural environment.

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Appendix A: The Derivation of Equation (3)

When a colony has a certain number of polyps (n , a constant), their feeding rate (R) declines over time as the colony approaches satiation. We introduce derived variables, however, to produce the converse relation: feeding rate is a constant (F , feeding rate of feeding units), whereas the number of effective feeding units (N) decreases over time.

The number of feeding units decreases with the number of prey items captured during the process of feeding, and thus the decreasing rate of P and N can be considered to be equal, i.e., $dP/dT = dN/dT$. The equation for feeding rate may be written as,

$$\frac{dP}{dT} = -PNF, \quad (A1a)$$

or

$$\frac{dN}{dT} = -PNF, \quad (A1b)$$

where P is the number of prey items available (no.); N is the number of feeding units (no.) equal to the number of prey items that satiates the colony; F is the feeding rate (no.⁻¹ h⁻¹); and T is the feeding time (h).

We introduce a constant, D , to be the difference between the number of prey items and the number of feeding units,

$$D = P - N = P_0 - N_0. \quad (A2)$$

Substituting equation (A2) with $dP/dT = dN/dT$ into equation (A1b), we obtain

$$\frac{dN}{dT} = -(N+D)NF. \quad (A3)$$

Rearranging equation (A3) yields

$$\begin{aligned} -FdT &= \frac{1}{N(N+D)} dN \\ &= \frac{1}{D} \left(\frac{1}{N} - \frac{1}{N+D} \right) dN. \end{aligned} \quad (A4)$$

Integrating equation (A4) from 0 to T , we obtain

$$-\int_0^T FdT = \frac{1}{D} \int_0^T \left(\frac{1}{N} - \frac{1}{N+D} \right) dN. \quad (A5)$$

Rearranging equation (A5) yields

$$\int_0^T \frac{1}{N} dN - \int_0^T \frac{1}{N+D} dN = -D \int_0^T FdT. \quad (A6)$$

The feeding rate (F) therefore could be derived from equation (A6) as,

$$\begin{aligned} F &= \frac{\ln(N+D)|_0^T - \ln N|_0^T}{DT} \\ &= \frac{(\ln P_T - \ln P_0) - (\ln N_T - \ln N_0)}{DT} \\ &= \frac{(\ln N_0 - \ln N_T) - (\ln P_0 - \ln P_T)}{DT} \\ &= \frac{(\ln N_0 - \ln N_T) - (\ln P_0 - \ln P_T)}{(P_0 - N_0)T}. \end{aligned} \quad (A7)$$

Equation (A7) is suggested to estimate the feeding rate while incorporating the satiation effect.

Equation (A7) can also be rewritten as,

$$\ln \left(\frac{N_0 P_T}{N_T P_0} \right) = FDT, \quad (A8a)$$

or

$$\frac{N_0 P_T}{N_T P_0} = e^{FDT}. \quad (A8b)$$

In view of equation (A8b), the residual numbers of feeding units (N_T) and prey items (P_T) after the feeding time T can be expressed respectively as follows,

$$N_T = N_0 \frac{P_T}{P_0} e^{-FDT}, \quad (\text{A9a})$$

or

$$P_T = P_0 \frac{N_T}{N_0} e^{FDT}. \quad (\text{A9b})$$

Equation (A9a) can be modified according to the relation of $N_T = P_T - D$ as

$$P_T - D = N_0 \frac{P_T}{P_0} e^{-FDT}. \quad (\text{A10})$$

Rearranging equation (A10) yields

$$\frac{P_T - D}{P_T} = 1 - \frac{D}{P_T} = \frac{N_0}{P_0} e^{-FDT}. \quad (\text{A11})$$

The final expression of P_T can then be described as

$$P_T = \frac{D}{P_0 - N_0 e^{-FDT}} = \frac{P_0 - N_0}{1 - \frac{N_0}{P_0} e^{-F(P_0 - N_0)T}}. \quad (\text{A12})$$

Appendix B: List of Variables

D	difference between the number of prey items and the number of feeding units. (no.)
E	satiation efficiency. (no. no. ⁻¹)
F	feeding rate. (no. ⁻¹ h ⁻¹)
n	number of feeding animals. (no.)
N	number of feeding units. (no.)
N_0	initial number of feeding units. (no.)
N_T	number of prey items after feeding time T . (no.)
P	number of prey items. (no.)
P_0	initial number of prey items. (no.)
P_T	number of prey items after feeding time T . (no.)
R	feeding rate of an individual animal. (no. ⁻¹ h ⁻¹)
T	feeding time. (h)

模擬飽食效應對群體型懸浮物攝食生物於實驗室循環水系統環境下攝食效率的影響——以星棘柳珊瑚 (*Acanthogorgia vegae*) 為例

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本研究根據星棘柳珊瑚 (*Acanthogorgia vegae*) 的攝食行為發展出一套數學模式，用來模擬群體型懸浮物攝食生物於實驗室循環水系統中的攝食效率。研究中發現，星棘柳珊瑚在持續餵食豐年蝦幼生的情況下，一旦珊瑚群體捕獲某特定數量豐年蝦後，群體上的所有珊瑚蟲都會停止攝食。根據此一觀察結果，我們發展出了考慮飽食因子的數學模式，用來推算懸浮物攝食生物的攝食效率。根據不同流速下的測試，發現實驗所得的數據和模式推估結果相近，顯示飽食是影響攝食效率的重要因子，尤其在食物供給充分的閉鎖式循環系統內，其影響更是顯著。另外，本研究也發現，即使在攝食生物和獵物初始數量未知的情形下，只要根據獵物殘存量和攝食時間，便能簡易地計算出生物的攝食效率。因此，本研究發展出的模式可用來推算群體型懸浮物攝食生物的攝食效率，尤其在實驗室和養殖環境下更是適用。

關鍵詞：群體型懸浮物攝食生物，攝食，柳珊瑚，數學模擬，飽食。

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