Effects of turbulence on the feeding rate of a pelagic predator: the planktonic hydroid Clytia gracilis

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ABSTRACT

Relatively little is known about the role of turbulence in a predator - prey system where the predator is a passive, pelagic forager. The Campanulariid hydroid Clytia gracilis (Cnidaria, Hydrozoa) is unusual because it occurs as planktonic colonies and is reported to forage passively in the water column on Georges Bank, Massachusetts, USA. In this study we investigated the role of various turbulence conditions on the feeding rate of C. gracilis colonies in laboratory experiments. We found a positive relationship between turbulence velocities and feeding rates up to a turbulent energy dissipation rate of ca 1 $cm^2 s^{-3}$. Beyond this threshold feeding rate decreased slightly, indicating a dome-shaped relationship. Additionally, a negative relationship was found between feeding efficiency and hydroid colony size under lower turbulent velocities, but this trend was not significant under higher turbulence regimes.

Key Words: turbulent mixing, small-scale turbulence, Hydrozoa, functional response

INTRODUCTION

The predatory effect of cnidarians on either fish larvae or their pelagic eggs, or their competition with fish larvae for prey can be substantial (for review see Purcell & Arai 2001, CIESM 2001). However, this effect refers almost exclusively to the pelagic sexual phase ("jellyfish") of their life cycle. So far, very few hydrozoan species have been reported to be holoplanktonic (Boero 1984). Typically, the asexual phase lives as a sessile benthic colony, attached to rocks, algae or other hard substrates. However, colonies of *Clytia* hydroids occur abundantly, suspended in the water column on Georges Bank, a region east of Cape Cod, Massachusetts that is characterized by shallow, well-mixed water with vertical upwelling, (Fraser 1915, Gallager et al. 1996, Madin et al. 1996, Ashjian et al. 2001, Concelman et al. 2001). The suspended hydroids were found to function as planktonic predators and have sealed stolons, fully extended tentacles and planktonic food in their gut cavities all of which indicate that they might function as fully holoplanktonic organisms (Madin et al. 1996, Madin et al. 1997, Sullivan et al. 1997). Moreover, repeated observations of suspended hydroid colonies over a time period of several decades (Concelman et al. 2001) suggest that their occurrence is not purely ephemeral but that they are a stable component of the planktonic predatory community. The very high seasonal densities of hydroid colonies and their overlapping distribution with larval fish favor this species as both an important competitor and predator of fish larvae in this historically important fishery area (Madin et al. 1996, Klein-MacPhee et al. 1997, Madin et al. 1997, Sullivan et al. 1997, Bollens et al. 2001, Concelman et al. 2001). Shipboard feeding experiments showed that at the density of 10,000 hydranths m^{-3} the hydroids would consume nearly half of the daily production of copepod eggs and about quarter of the daily production of copepod nauplii (Madin et al. 1996). Norrbin et al. (1996) reported an inverse relationship between copepod nauplii and hydroid abundance thereby providing another important source of evidence for the predatory impact of hydroids on Georges Bank. Whether the pelagic hydroids are detached from the benthos by storm action, fish trawling or other disturbance or whether they undergo their entire life cycle in pelagic form remains unanswered. However, the high degree of mixing in the shallow water column, together with both adjacent benthic source regions (Concelman et al. 2001) and abundant small zooplankton prey probably enable the hydroid colonies to flourish in pelagic form. Thus, it is crucial to understand how the environmental conditions of Georges Bank influence the biology of this unusual predator.

Rothschild & Osborn (1988) highlighted the role of turbulence as a factor enhancing a predator's probability of encountering prey. This is due to the random nature of turbulence, which increases uncorrelated velocities between predator and prey and may lead to higher encounter rates than those found in non-turbulent conditions. A number of studies on copepods have documented an increase in feeding rates under turbulent conditions (reviewed by Peters & Marrasé 2000). Although, as many authors (MacKenzie et al. 1994, Dower et al. 1997, Peters & Marrasé 2000) have recently pointed out, an increased encounter rate does not necessarily mean a higher ingestion rate. This suggests that other factors such as the behavioral, sensory or morphological constraints of the animal, must be taken into account. Still less is known about the nature of a predatory system in which the pelagic predator is a passive forager. Such a system is represented by the above described unusual life history of the colonial hydroid Clytia gracilis (Cnidaria, Hydrozoa).

The objective of this paper is to investigate how turbulence influences the feeding ecology of Clytia gracilis by examining the effects of experimentally induced turbulence on feeding rate, feeding efficiency, and behavior. Elucidating this question is key to understanding how this species benefits from the well-mixed conditions found on Georges Bank and in turn provides insight into the dynamics of a passive, pelagic predator.

METHODS

Pelagic colonies of the hydroid Clytia gracilis were originally obtained from Georges Bank (41° 16´ N, 67° 10´ W) during the US GLOBEC program and were cultured at the Environmental Systems Laboratory, Woods Hole Oceanographic Institution, Woods Hole, MA, USA. The nominal C. gracilis appears to represent a multiple cryptic species; whether the Georges Bank form represents the true species is unknown because we did not have material from the type locality. The cultures were kept in the dark in seawater filtered to 1μm at a constant temperature of 15°C, and fed regularly 2-3 times per week with newly hatched Artemia nauplii. Continuous aeration kept hydroids in suspension.

To avoid possible bias due to high prey densities (Johnson & Shanks 1997), before beginning the experiments on feeding rates under various turbulent regimes we constructed a functional response curve relating feeding rate to prey density in still water. In this experiment we used a fixed predator density (1 colony with 10 hydranths l^{-1}) and 6 prey concentrations (10, 15, 20, 40, 60, 80 Artemia nauplii l^{-1}), each with six replicates. All Artemiia nauplii were used 24 hours after hatching. In each trial the hydroid feeding rates were estimated after 24 hours by counting the remaining Artemia nauplii, following the no-mixing procedure of Bollens et al. (2001). Based on the resulting functional curve (see Fig. 1) and data about natural copepod densities on Georges Bank, which ranges from 5 to 50 individuals l^{-1} (Incze et al. 1996, Lough et al. 1996), a density of 33 Artemia l^{-1} was selected for the turbulence experiments. This is the approximate median abundance value for naupliar prey on Georges Bank and is below the saturation level for C. gracilis. Because the natural densities of hydroids on Georges Bank vary considerably in time and space, a concentration of 3.3 hydranths l^{-1} was chosen as a conservative value. This approximates mean densities across various sites and more specifically higher densities of the "Crest" site of Georges Bank (Concelman et al. 2001). Prior to the experiment, colonies with an average number of 5 hydranths (polyp diameter ~1 mm, colony length < 10 mm) each were chosen from our hydroid cultures.

To study the effect of turbulence on feeding rates, doubled-walled 30-liter (33 cm diameter, 66 cm deep) plastic bags were used. These bags were nested in a large, insulated opaque tank with a continuous flow of 15°C seawater. Under each plastic bag three pipes (diameters: 2.8 cm, 1 cm, 1 cm with a bubbling stone at the end) supplying air were affixed to the tank bottom providing control over aeration intensity. Turbulence was induced inside the plastic bags by the bubbles impacting the walls of the plastic bags as described in detail by Von Herbing & Gallager (2000). Variation in the size and number of bubbles afforded the simulation of different turbulence levels in the different experiments. All experiments were run in the dark in order to avoid possible bias due to Artemia nauplii phototaxis.

A 10 MHz acoustic Doppler velocimeter (ADV) was used to quantify water velocities. In steady flow with isotropic, fully-developed turbulence, kinetic energy cascades from large eddies to smaller eddies, which finally dissipate through viscosity. Under these conditions, the turbulent dissipation rate can be estimated by the magnitude of the wavenumber spectrum in the inertial subrange. The inertial dissipation method is used to determine turbulent kinetic energy dissipation:

$$S = \alpha \varepsilon^{2/3} \kappa^{-5/3} \qquad (1)$$

where S is the wavenumber spectrum of the vertical velocity, w, $\kappa = 2\pi f / V$ is the wavenumber, f is the frequency, V is kinematic viscosity, and α is Kolmogorov's empirical constant of 0.52.

Measurements of the dissipation rate, ε, were made in the experimental apparatus using an ADV and Equation 1 for the inertial subrange of the kinetic energy spectrum. The ADV sampled the three components of water velocity at 25 Hz 15 cm below the air-water surface. The frequency spectra were measured and corrected for pulse averaging by dividing the measured frequency spectra by the factor $[\sin(\pi f \Delta t)/\pi f \Delta t]^2$. Assuming Taylor's hypothesis of frozen turbulence, the frequency spectra were then converted to wavenumber space by $\kappa = 2\pi f / V$ and ε is calculated directly from Equation 1 (Frisch 1995). A safe lower bound of the inertial range for this data was determined to be 20 rad m^{-1} according to the criterion $kz > 5$, where z is depth of the container. A reasonable upper bound was determined to be 80 rad m^{-1} according to the criterion $kL < 1$, where L is the length scale of the sample volume (1 cm).

Both the vertical and horizontal components of the velocities were sampled at a rate of 25 Hz for a period of 5 minutes. This was chosen as an appropriate time interval because velocity estimates taken at longer time intervals showed no difference (paired t-test, $t = 1.09$, $P = 0.34$, Fig. 2). Prior to recording any data for a given trial the velocity range for each bag was verified separately.

Experiments in each plastic bag ran for 20 hours following the introduction of known numbers of hydroid colonies and Artemia nauplii. Overall, 17 experiments were performed at turbulent energy dissipation rates ranging from 1.9×10^{-2} cm^2 s^{-3} in the lowest flow regime up to rates of 5.68×10^{1} cm^2 s^{-3}. Reaching levels of turbulent energy dissipation rates lower than 10^{-2} cm^2 s^{-3} was difficult without artifacts in the energy spectra because the size of the plastic bags restricted the decomposition of energy to smaller scales. On the other hand, it is possible to generate high ε in the laboratory system to examine the potential impact of storm-generated events on feeding behavior. To estimate predation rate, following the termination of each experiment the water was filtered and the remaining Artemia nauplii were counted.

The hypothesis that a trade-off exists between colony size and the probability that a given hydranth within a given colony will encounter prey was addressed. Assuming a random distribution of prey the probability of encountering prey should be the same for all hydroids present within a given system (assuming that colony size doesn't influence the vertical position of the hydranth in suspension). Following this assumption we may suppose that the per colony prey capture rates (feeding efficiency) will decrease with increasing colony size. To test this hypothesis we ran additional experiments with a wide range of colony sizes under two turbulence conditions (ε = 10 cm^2s^{-3} and 1 $cm^2 s^{-3}$) with a density of 100 Artemia l^{-1} for a period of 30 min. This is sufficient time for the hydranths to catch and start ingesting prey. After terminating treatment we noted the number of successful captures within a given colony. The "colony feeding effectiveness" was expressed as the proportion of feeding hydranths to the total number of fully differentiated hydranths present in a given colony. Data were analyzed using regression analysis and where appropriate the arcsine transformation was used for proportions to normalize the data.

To confirm that hydroids were indeed still feeding under very high turbulence conditions (ε = 2 - 20 cm^2s^{-3}, and ε = 100 - 200 cm^2s^{-3}), observations on feeding behavior were obtained using a miniaturized Video Plankton Recorder (mVPR; Davis et al. 1992). In addition, a high-speed CMOS camera was used to observe hydroid feeding behavior under high turbulence conditions. Four 6-minute video sequences recorded on S-VHS tape allowed for a detailed frame-by-frame view of hydranths continuing to feed under high turbulence.

RESULTS

A positive relationship was found between turbulence energy dissipation rates and hydroid feeding rates up to an ε of 1 cm^2s^{-3} (Fig. 3). At higher ε values, feeding rate decreased slightly suggesting a domed-shaped relationship, overall. A second-order polynomial regression fitted to the data was significant ($y = 0.59256 + 0.06843x - 0.04846x^2$, $R^2 = 0.42$, $F_{2,14} = 6.83$, $P < 0.01$, first order regression coefficient $t = 3.36$, $P < 0.01$, second order regression coefficient $t = -2.38$, $P = 0.03$, Fig. 3) supporting the idea of a dome-shaped relationship. Active feeding at the highest ε (5.68×10^1 $cm^2 s^{-3}$) was confirmed by observations with the mVPR: Hydroids kept their tentacles fully open even under the highest turbulence levels.

In the second experiment on colony size and feeding efficiency the data show that under lower turbulence conditions colony feeding effectiveness decreased as the colony size increased (ε = 1 cm^2s^{-3}; $y = 0.51 - 0.02x$; $R^2 = 0.14$, $F_{1,35} = 6.71$, $P < 0.01$); however, this trend was not significant under the higher turbulence regime (ε = 10 $cm^2 s^{-3}$; $y = 0.45 - 0.01x$; $R^2 = 0.06$, $F_{1,35} = 2.31$, $P = 0.14$, Fig. 4).

DISCUSSION

What little is known suggests that hydroid diet and feeding ecology can vary greatly from species to species (e.g. Lasker et al. 1982, Barange 1988, Coma et al. 1995, Gili & Hughes 1995, Gili et al. 1996, Gili & Coma 1998, Ribes et al. 1999, Orejas et al. 2000, Orejas et al. 2001). In line with this, fewer studies have focused on the role of turbulence in hydrozoan feeding ecology. Boero (1984) pointed to the role of water movement as a positive factor in hydrozoan life by proposing that water movement increases food and oxygen supply. The present study confirms the predictions about the enhanced feeding rates under higher turbulence made by Rothschild & Osborn (1988). Feeding rates increased up to a level of ca 1 cm^2 s^{-3} (10^{-4} W kg^{-1}) and then dropped slightly beyond this threshold. The dome-shaped relationship between turbulence energy dissipation rates and the feeding rates of hydroids is similar to that predicted by MacKenzie et al. (1994) for ingestion and turbulence in fish larvae. Their model anticipated a decrease in capture (or ingestion) rates at higher turbulence levels.

In our study turbulence levels fell within a higher range than those usually occurring under natural non-storm conditions. On Georges Bank the average energy dissipation rates reach values of around 10^{-2} cm^2 s^{-3} at depth 9-39 m, which are at the lower end of dissipation rates used in this study (Horne et al. 1996). Our highest turbulence level represents conditions that may occur during storms, near the surface or near the bottom of the Bank (Yoshida & Oakey 1996, Sanford 1997, Gallager et al. 2004). However, turbulence levels reported on Georges Bank are typical for summer months when relatively calm weather conditions prevail. Peters and Redondo (1997) pointed out that due to logistical constraints, most field measurements of turbulence have been taken under relatively calm conditions thus biasing average oceanic turbulence levels toward the lower end. It is quite surprising that hydroids continued feeding even in such highly turbulent regimes. In previous studies much lower turbulence levels were sufficient to decrease predators' feeding rates (e.g. Lough & Mountain 1996, review by Peters & Marrasé 2000). This difference is likely to be a consequence of the feeding mechanism employed by the hydroids, which are passive foragers, while sensory mechanisms play a dominant role in prey capture for other species (e.g. fish, copepods). Moreover, observations using the mVPR suggest that hydroid feeding rates at very high turbulence energy dissipation rates were influenced by mechanical disruption rather than tentacle contraction. Concelman et al. (2001) have suggested that the high numbers of hydroids on Georges Bank are maintained when detached from the benthos by storm action or other disturbance, advected clockwise with the mean residual circulation, and concentrated and retained in the central, low-advective region of the Bank. The present study shows that hydroids can directly benefit from a high turbulence regime through enhanced feeding rates. Moreover, this benefit may be greater for the pelagic hydroids than for other species relying on sensory mechanisms for capturing prey. Unfortunately, there is an absence of comparable experimental data on other pelagic hydroids and their feeding responses to turbulence. Turbulent conditions have been shown to enhance prey capture performance in several cnidarian taxa, however, this evidence is only of observational nature (Puce et al. 2002 and references therein). Therefore, we cannot draw any broad conclusions of whether our findings hold in general for other pelagic hydroids. The abundant literature on copepod feeding rates suggests, that several factors need to be controlled for when making inferences to other species. For example, even when controlling for the size of the studied species, sensory mechanisms can cause opposing results from the theoretical expectations (Saiz et al. 2003). In conclusion, our results are in line with the earlier findings on ambush copepods and fish larvae where turbulence-dependent foraging pattern has been observed (see Saiz et al. 2003 for review).

Bollens et al. (2001) did not find evidence for enhanced feeding rates of planktonic C. gracilis colonies in turbulent conditions (ca. $9x10^{-1}$ cm^2 s^{-3}) when compared to their low turbulence condition. This may have been because they used concentrations of Artemia naupii (80 and 160 nauplii l^{-1}), which when inferred from our functional response curve, would have been above feeding saturation (Fig. 1). If the hydroids in the Bollens et al (2001) study were saturated, it would explain the lack of evidence in their study for a positive effect of turbulence. Nevertheless, they found that turbulent mixing had a positive effect on colony growth, which is consistent with the notion of turbulence-induced elevated ingestion rates. Both Bollens et al. (2001) and the present study support the idea that because of their apparently unique life history, planktonic C. gracilis colonies are favored as important predators in the well-mixed Georges Bank ecosystem (Madin et al. 1996).

One important aspect of colonial life is the trade-off between the benefits of larger colony size and the probability that all hydranths within a given colony will catch prey. Water movement has been suggested to be one of the main factors shaping this trade-off in colony morphology. In general, small hydroid species are found in water with intense water movement, while large species are found in calm areas (Riedl 1971, Boero 1984, Gili & Hughes 1995). In addition, a recent study on a Mediterranean hydroid Eudendrium racemosum shows that water movement can induce changes in the hydroid morphology, which leads to a change in its feeding strategy (Puce et al. 2002). Our data suggest that with increasing colony size the overall number of captured prey per hydranth will decrease. However, this seems to be true only in conditions of low turbulence, where the probability of encountering prey is lower than under the higher turbulent condition we tested. This finding is consistent with that of Hunter (1989), who also found that feeding effectiveness was a function of flow velocity and colony size in a closely related, but benthic hydroid Obelia longissima. Because of the ephemeral distribution of high turbulence conditions, small colonies with a few hydranths would appear more advantageous because of their higher feeding efficiency. This may not be true when increased storm-induced mixing persists over extended periods of time. Additional field data will be necessary to test this hypothesis.

ACKNOWLEDGEMENTS

We would like to express our thanks to N. Bucy, M. McElroy, A. Kukulya, S. Sweeney and N. Trowbridge for their valuable help during various stages of this project. The valuable comments by N. Boero, S. Puce and an anonymous referee helped to improve the previous versions of the manuscript. P. Adamík received support from the WHOI Academic Programs Office via the 2002 Summer Student Fellowship and while writing this paper from the Ministry of Education of the Czech Republic (MSM 6198959212 and MSM 153100012).

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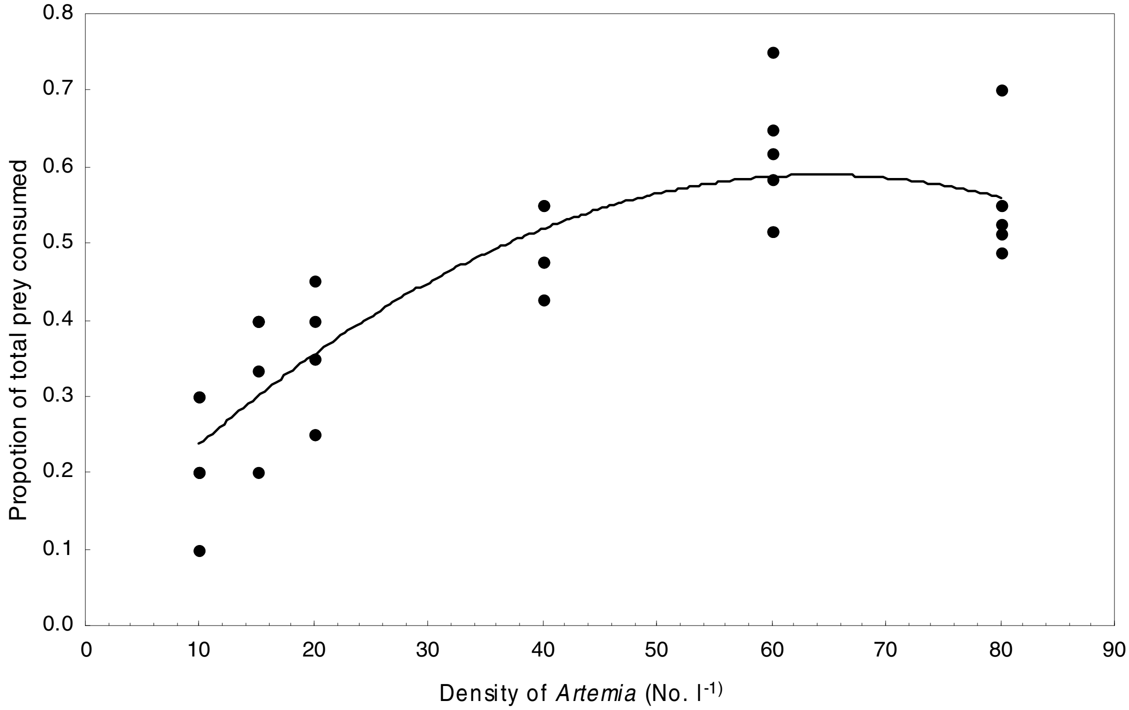
Figure legends:

Figure 1. Effect of prey density (*Artemia*) on consumption rate by Clytia gracilis in still water. Experiment performed with an initial predator density (10 hydranths l^{-1}). Solid line: best-fit second-order polynomial regression (R^2 = 0.74, $F_{2,31}$ = 47.91, P< 0.001). Note: points of equal values overlap.

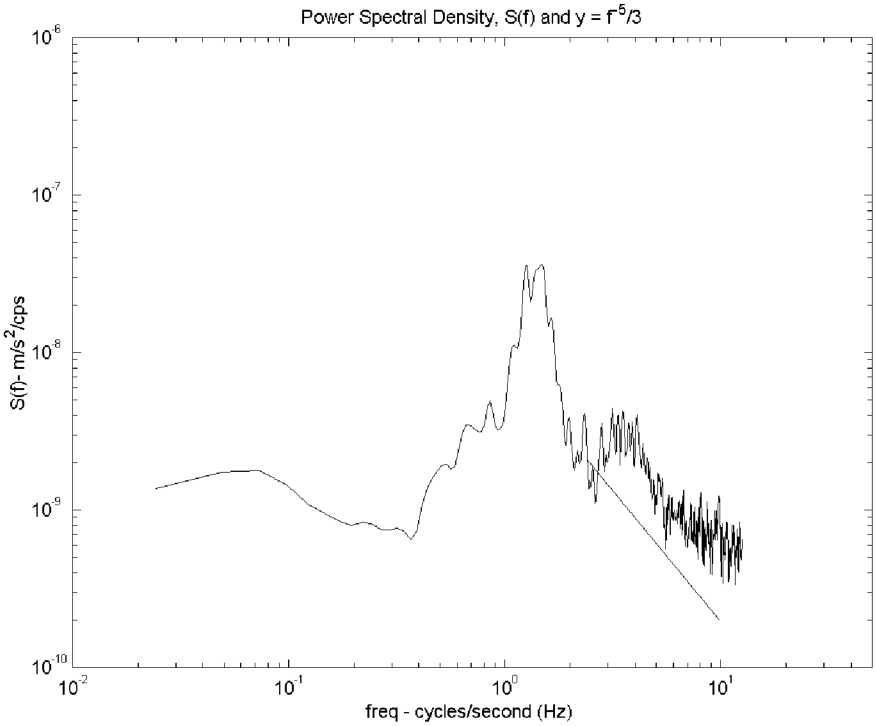
Figure 2. Representative frequency spectra for the recorded velocities measured in 30-L bags. The inertial dissipation subrange in the spectra shown coincident with theoretical –5/3 turbulent decay (solid line).

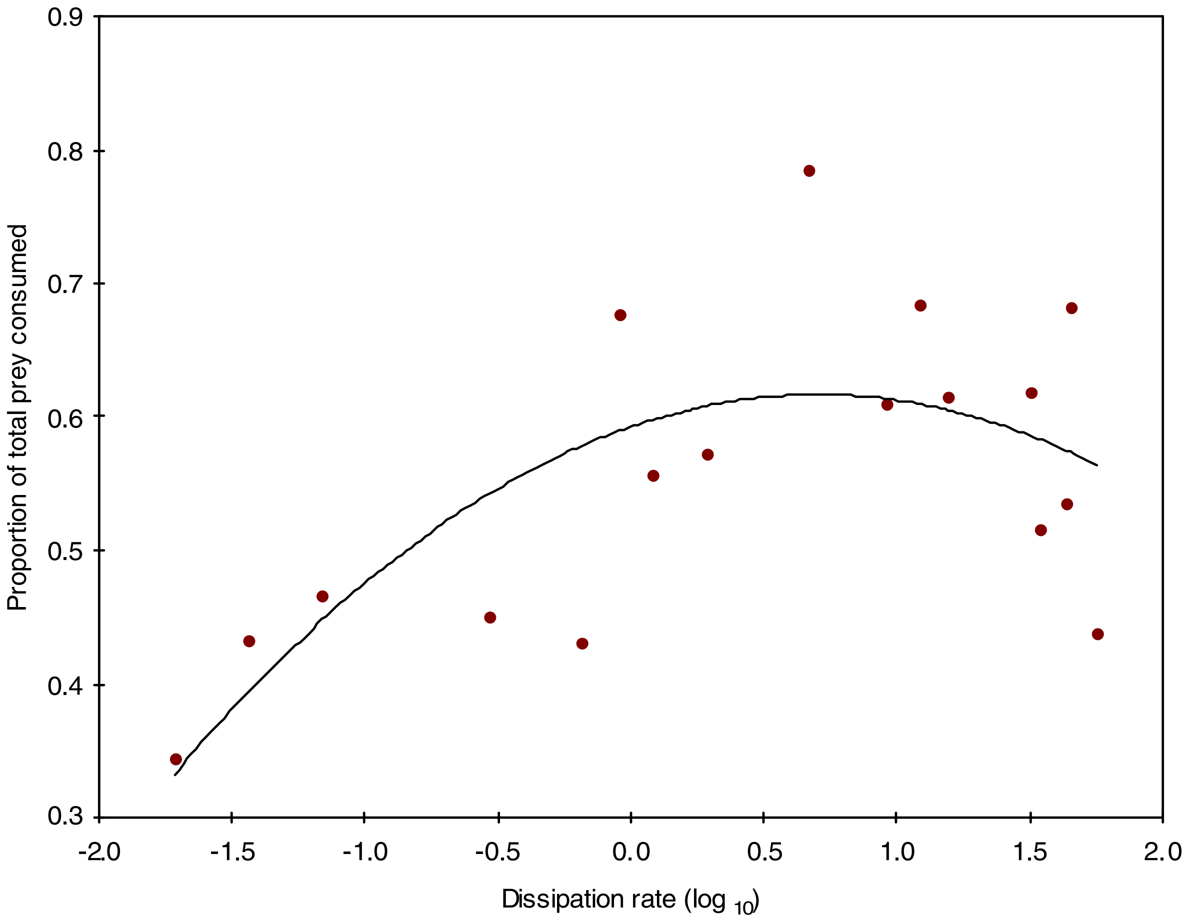
Figure 3. The relationship between turbulence energy dissipation and feeding rate (proportion of *Artemia* nauplii consumed) for the hydroid Clytia gracilis.

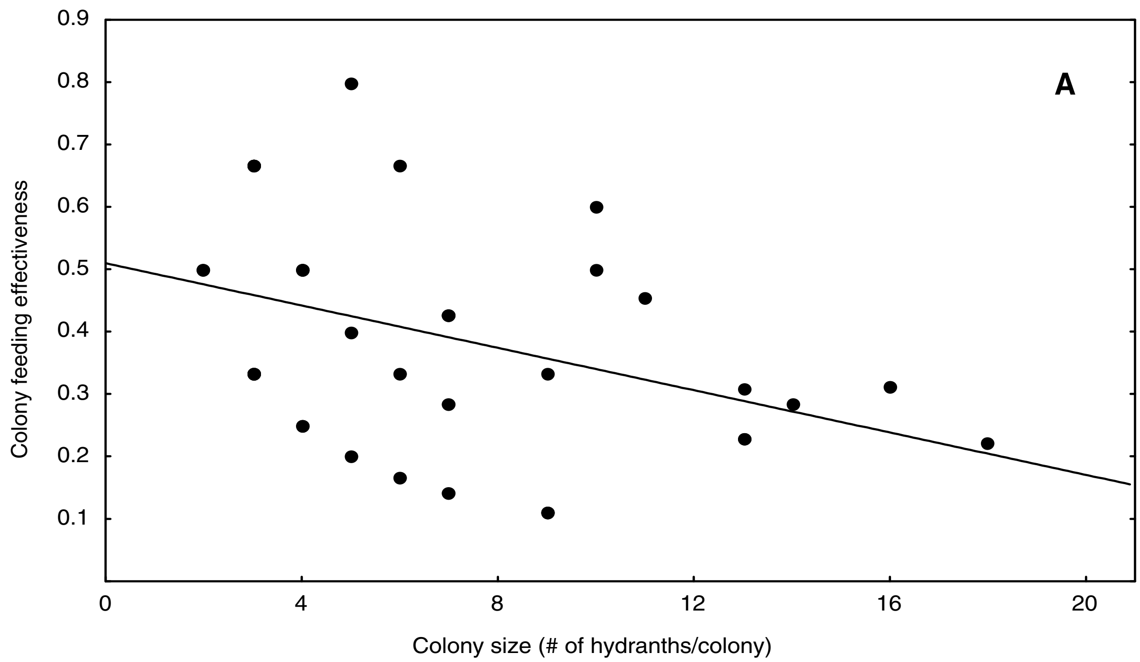
Figure 4. Colony feeding effectiveness as a function of colony size. (**A**) Lower turbulence regime: $\varepsilon = 1$ cm^2 s^{-3}h; (**B**) higher turbulence regime: $\varepsilon = 10$ cm^2 s^{-3}. Colony feeding effectiveness defined as proportion of feeding hydranths to the total number of fully differentiated hydranths within a given colony. Note: points of equal values overlap.

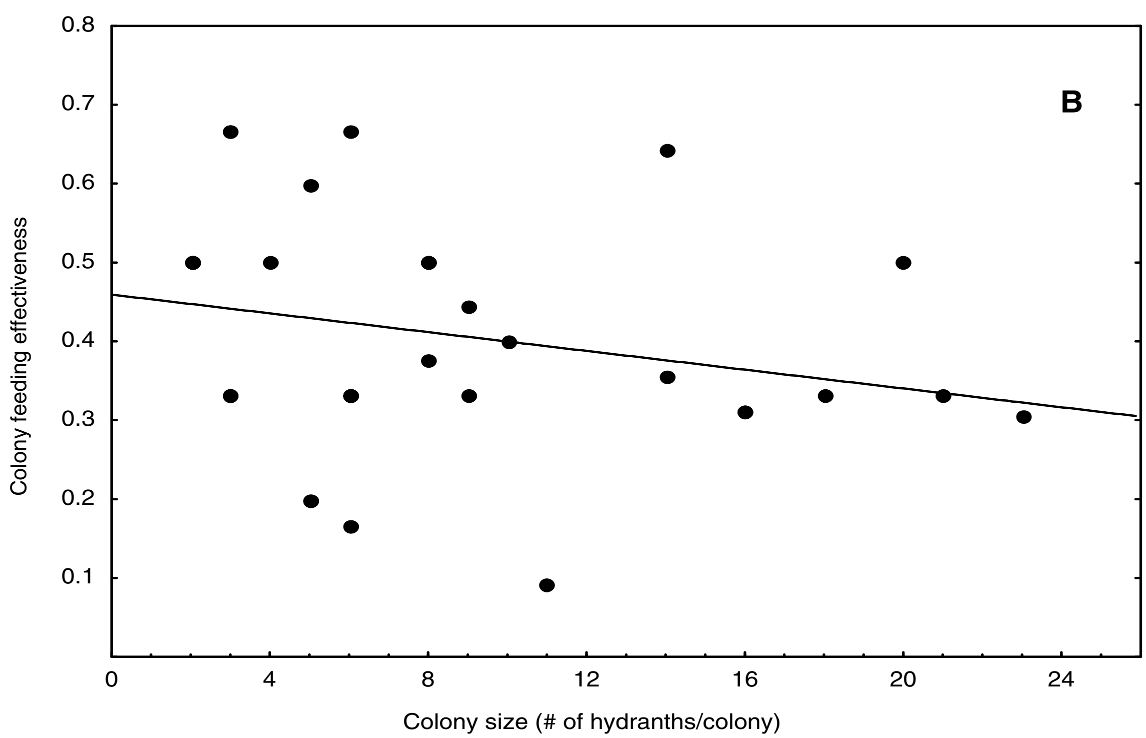


Propotion of total prey consumed
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0
10
20
30
40
50
60
70
80
90
Density of Artemia (No. l-1)


Power Spectral Density, S(f) and y = f-5/3
S(f)- m/s2/cps
10-6
10-7
10-8
10-9
10-10
10-2
10-1
100
101
freq - cycles/second (Hz)


0.9
0.8
0.7
0.6
0.5
0.4
0.3
Proportion of total prey consumed
-2.0
-1.5
-1.0
-0.5
0.0
0.5
1.0
1.5
2.0
Dissipation rate (log 10)


A
Colony feeding effectiveness
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
4
8
12
16
20
Colony size (# of hydranths/colony)


B
Colony feeding effectiveness
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
4
8
12
16
20
24
Colony size (# of hydranths/colony)