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Planktonic hydroids on Georges Bank: effects of mixing and food supply on feeding and growth☆

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Abstract

Huge numbers of hydroids (principally *Clytia gracilis*) were recently reported suspended in the plankton over the shallow, well-mixed region of Georges Bank, where preliminary feeding experiments suggested that these planktonic predators could have a potentially devastating effect on their zooplankton prey (Madin et al., 1996). Based on these initial findings we undertook a more extensive set of laboratory experiments examining the effects of particulate food concentration and mixing (turbulence) intensity on the feeding and growth of suspended hydroids. Not surprisingly, we found a clear effect of particulate food concentration on the growth of hydroid colonies. After 7 days at 15°C, both colony size (number of hydranths colony^{-1}) and specific growth rate (hydranth hydranth^{-1} day^{-1}) were significantly greater in well-fed (80–160 *Artemia* nauplii L^{-1}) versus starved treatments. More interesting was the additional significant effect of turbulent mixing ($\varepsilon = 9 \times 10^{-5}$ W kg^{-1}) on hydroid growth. Consumption rates (4.5 *Artemia* nauplii hydranth^{-1} day^{-1}) were not significantly different between mixing vs. non-mixing treatments, indicating that the enhanced growth rate in the mixing treatments could not have been due to turbulence-enhanced predator–prey contact rates. An alternative hypothesis for the apparent advantage that mixing seemed to confer on hydroid growth is that reduced boundary layer thickness around the hydroids served to replenish the local supply of DOM and oxygen and/or remove waste products. This study indicates that growth rate of planktonic hydroids is dependent on both food concentration and mixing intensity, a finding that helps explain why these organisms are vastly more abundant in the central, shallow, well-mixed region of Georges Bank compared to the stratified flanks of the Bank.

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1. Introduction

Georges Bank in the northwest Atlantic Ocean is the site of an extremely productive and historically important commercial fishery for the United States and Canada (Backus, 1987). As part of the continued interest in the ecology and oceanography of Georges Bank, the US GLOBEC (Global Ocean Ecosystem Dynamics) Program is conducting a multi-year, multi-disciplinary study of the population biology of four target species of organisms on the Bank — the copepods *Calanus finmarchicus* and *Pseudocalanus* spp., and larval cod, *Gadus morhua*, and larval haddock, *Melanogrammus aeglefinus* (US GLOBEC, 1992). Among the many biological and physical processes identified for study under GLOBEC, predation was one of the key processes thought to affect the population dynamics of GLOBEC target species on Georges Bank. However, the recent "discovery" (Madin et al., 1996) of planktonic hydroids, principally *Clytia gracilis*, as an abundant and voracious predator in the Georges Bank ecosystem came as a great surprise.

Marine hydrozoans (Phylum Cnidaria) typically have a life history consisting of an alternation of generations in which the sessile, asexual hydroid phase is attached to rocks, seaweeds or benthic animals, and the sexual medusa (or "jellyfish") phase is released and dispersed as part of the plankton. Although a few genera of hydroids do not possess a sessile life phase (Boero, 1984; Mills, 1987), species of *Clytia* normally have attached hydroid stages. Cornelius (1982) noted that *Clytia hemisphaerica* has been reported to form floating hydroid colonies in the North Sea and along much of the west coast of Africa, but that these colonies often contain sand grains in its basal discs, suggesting a benthic origin. In contrast, the suspended *Clytia* on Georges Bank (Gallager et al., 1996; Madin et al., 1996, 1997; Sullivan et al., 1997) had sealed stolons (stems), fully extended feeding tentacles, and planktonic food in their gut cavities, indicating success as truly planktonic organisms. Earlier reports of *Clytia* hydroids being a conspicuous part of the plankton community on Georges Bank date as far back as 1915 (Fraser, 1915), although their abundance and trophic importance within the ecosystem had not been assessed previously.

It is now known that planktonic hydroids can play an important role in the trophic dynamics of the Georges Bank ecosystem. Preliminary laboratory feeding studies indicated that these organisms could exert a significant impact on their prey. At densities of up to 25 hydranths l^{-1} and the ability to consume up to several prey items hydranth^{-1} day^{-1}, planktonic hydroids could remove anywhere from 25% to more than 100% of the standing stock of copepod nauplii per day on the central, well-mixed region of Georges Bank (Madin et al., 1996, 1997). Predation by planktonic hydroids on larval fish, while more difficult to assess in the field, has been demonstrated in the laboratory (Madin et al., 1996) and in experimental mesocosms (Klein-MacPhee et al., 1997), and most likely occurs in nature as well (Sullivan et al., 1997).

The distribution of planktonic hydroids on Georges Bank seems to be limited to the central, well-mixed region of Georges Bank, where they are usually found only inside the 60 m isobath, and almost never outside the 100 m isobath (Madin et al., 1996, 1997; Sullivan et al., 1997; Concelman et al., 2000). The central, shallow ($\leqslant 60$ m) region of the bank is continuously mixed from surface to the bottom due to tidal activity (e.g., Horne et al., 1996; Mountain and Taylor, 1996; Werner et al., 1996), which probably helps keep the hydroids suspended (Oakey and Elliot, 1992; Sanford, 1997). In contrast, Sullivan et al. (1997) reported sinking rates of 0.03–0.3 cm s^{-1} for planktonic hydroids in an unmixed experimental water column. Yet the most likely food for planktonic hydroids, copepod nauplii, are usually less abundant in the well-mixed region compared to the stratified

flanks (bottom depth $\geqslant 60$ m) of the bank (e.g., Incze et al., 1996; Lough et al., 1996; Norrbin et al., 1996). How then do the planktonic hydroids achieve their good condition and high numerical abundance in the well-mixed region of the bank, but not the adjacent stratified regions ?

The objective of the present study was to test experimentally for the separate and combined effects of food concentration and mixing (turbulence) on the feeding and growth of the planktonic hydroid *Clytia gracilis*.

2. Materials and methods

Suspended hydroid colonies (*Clytia* spp.) were collected at the well-mixed study site (41°10′N; 67°35′W) on Georges Bank in May through July 1995 and returned to the Woods Hole Oceanographic Institution. The colonies were maintained in suspension by an air bubbler and kept in a constant temperature environment (15°C). The colonies were transferred to fresh filtered seawater and fed *Artemia* spp. nauplii daily. After experimentation with various culturing techniques (Horgan et al., in preparation), we conducted two laboratory experiments between July and October 1995 designed to investigate the effects of food concentration and mixing (turbulence) on the feeding and growth of suspended hydroid colonies (food × mixing experiments).

For both of the food × mixing experiments, a number of large colonies of 20–40 feeding hydranths were carefully divided into small colonies of 4–10 hydranths each. This size is more typical of colonies seen in the field (Madin et al., 1996; Norrbin et al., 1996), although we found that colonies of 30–40 hydranths each could be readily grown and maintained in laboratory cultures (Madin et al., 1996; Horgan et al., in preparation). These smaller colonies were fed *Artemia* spp. nauplii replete for five days. At the beginning of each experiment, the number of feeding hydranths were counted on 24 colonies and each colony was placed into a 1-l jar of filtered (1 μm) seawater (35 PSU). We then established the following 2×2 factorial design of four experimental treatments: (1) mixing, food; (2) mixing, no food; (3) no mixing, food; and (4) no mixing, no food. Twelve of the jars (colonies) received constant aeration (mixing) while 12 received no aeration (no mixing); six of each of these 1-l jars received food while six did not. Each colony was randomly assigned to one of the four treatments. Thus, four treatments of six 1-l jars each were established.

The food concentration and mixing intensities used were meant to represent extremes for environmental conditions that might be experienced by planktonic hydroids on Georges Bank. The food treatments consisted of 80 *Artemia* nauplii l^{-1} for the first food × mixing experiment and 160 *Artemia* l^{-1} for the second food x mixing experiment. Concentrations of copepod nauplii on Georges Bank are usually in the range of 5–50 l^{-1} (Lough and Mountain, 1996; Lough et al., 1996), and only very rarely reach a density of 80–160 l^{-1} (Incze et al., 1996).

The mixing treatment consisted of a bubbling rate of ca. 500 bubbles min^{-1} through a pipette bore of 1.25-mm internal diameter. Turbulence dissipation rates in the experimental jars were quantified using particle imaging velocimetry (PIV) similar to the approach used by Willert and Gharib (1991). Fluid tracers (30-μm polystyrene beads) were tracked at 5 ms intervals using a high-speed CCD camera (field rate 200 Hz) synchronized with a strobe-generated light sheet. Image dimensions were $2.0 \times 2.0 \times 0.2$ cm. Component velocities in the x and z coordinates (u and w) were calculated from particle paths with the aid of a Motion Analysis VP110 system. Fluctuating root-mean-square (rms) turbulence velocities ($u'x$ and $w'z$) were calculated after ensemble-averaging

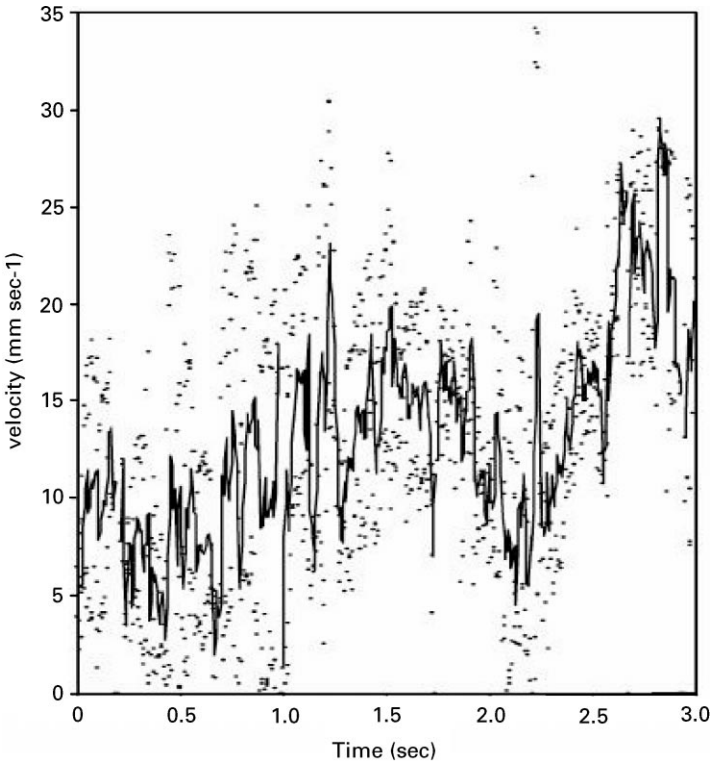

Fig. 1. Three second record of the mean (solid line) $\pm$ rms (dots) velocity in the *xz* plane at a bubble rate of 490 bubbles min^{-1} in the center of a 1-l jar.

particle displacements within each 5 ms time interval. The integral length scale *l*, corresponding to the largest eddy size in the container, was calculated as the product of the integral of the velocity autocorrelation function through the first zero crossing and rms velocity. An approximation to the energy dissipation rate, epsilon, is then $\varepsilon = (u'x)^2 w'z/l$ assuming horizontal isotropy. For comparison with the literature, units of $cm^2\ s^{-3}$ were converted to $W\ kg^{-1}$ using $W\,kg^{-1} = 10^4\,cm^2\,s^{-3}$.

Since turbulence velocities varied considerably over both time and location within the jar, measurements were taken over 3-min periods with the vertical image plane located on the jar's axis and the horizontal image plane at three locations: near surface, center and near bottom. To establish an appropriate mixing rate in the experimental jars, dissipation was estimated at air bubbling rates between 0 and 650 bubbles min^{-1} (bpm). Bubble rates were quantified by synchronizing the position of the rising bubbles with the illumination from a strobe tachometer. To approximate the average local environment of a hydroid colony as it was carried around the experimental jar, dissipation rates estimated at near surface, center, and near bottom were averaged. The considerable temporal fluctuations in mean and rms velocities (Fig. 1) shows why it was important to take measurements over relatively long periods of time.

Temporally - and spatially -averaged energy dissipation rates increased from $1.7 \times 10^{-7}\,W\,kg^{-1}$ with the bubbler turned off, to a maximum of $1.2 \times 10^{-4}\,W\,kg^{-1}$ at a bubble rate of 650 bpm. Thus

even without aeration, convective currents in the jar produced shear which translated into measurable dissipation. We were interested in using a dissipation rate which was similar to the highest rates found in the well-mixed area of Georges Bank under non-storm conditions (e.g., observations by Yoshida and Oakey, 1996, Horne et al., 1996; model results by Werner et al., 1996). Therefore a bubbling rate of ca. 500 bpm was chosen, which translated into an energy dissipation rate of ca. $9 \times 10^{-5}\,\mathrm{W\,kg^{-1}}$. At this level of mixing hydranths remained fully extended and in predatory mode, just as they have been observed in nature (Madin et al., 1996).

It is important to realize that the local environment around the hydroids in nature will be considerably different than the mean or bulk flow reported here. Natural turbulence is sporadic, ephemeral, and occurs over considerably different time and space scales than can be reproduced in a 1-l jar. Because of the spatial constraints set by the container, turbulence does not decompose to smaller and smaller scales at the theoretical rate of $-5/3$, but at a much reduced rate (i.e., the turbulence spectrum is very flat). Therefore, the hydroids were exposed to only a small portion of the upper end of the energy spectrum. This means that the relative energy contained in turbulent eddies of a given size were much greater than would be found in nature. We do not know how this artifact of the laboratory may have influenced the physiology of the hydroids.

All colonies in all treatments were kept in a constant temperature environment (15°C). To obviate surface swarming or other positive phototactic behavior on the part of the *Artemia*, all experiments were run in the dark, except for approximately 1 h $\mathrm{day^{-1}}$ of low light for maintenance and counting of hydroids. On each day of each experiment we counted the number of "feeding" (fully developed with tentacles extended) hydranths and "budding" (or partially-formed) hydranths. Each colony was transferred to fresh, filtered (1 μm) seawater (35 PSU) daily and the feeding treatments received new food each day. The day-old seawater was filtered through a 45-μm mesh in order to determine the number of *Artemia* spp. nauplii consumed during the previous 24-h period.

In all experiments we used the number of feeding hydranths (colony size) over time as a simple and convenient measure of hydroid growth. We calculated a specific growth rate

$$r = \ln[N_t/N_0]/t,$$

where N_t is number of hydranths at time t, N_0 is numbers of hydranths at time zero, and t is time in days; units of r are hydranth hydranth^{-1} $\mathrm{day^{-1}}$ for each colony at the end of each experiment. This is an imperfect measure of colony growth, however, because of potential resorption of older hydranths at one location within a colony to form new hydranths elsewhere on the colony, as has been noted in *Obelia* and *Campanularia* (e.g., Berill, 1949; Crowell, 1953). Moreover, growth in hydroid colonies also can include production of medusae and/or leakage of dissolved organic material, two processes not quantified in our study. Thus our estimates of hydroid growth, based on change in colony size (number of feeding hydranths) over time, are conservative and meant to serve merely as an indicator of relative growth in the different treatments and experiments.

We analyzed the resulting data by analysis of variance (ANOVA). In the mixing × food experiments, a two-way ANOVA examining the effects of mixing, food, and food × mixing interactions was performed on colony size (or number of hydranths per colony) data from the last day of each experiment. Similar two-way ANOVAs were run on the specific growth rate (r) data from the last day of each experiment.

An alternative approach to statistical analysis could have been a three-way, repeated measures ANOVA, where food and mixing were the two between-subjects factors, and time the within-

subject (or repeated measure) factor (e.g., Zar, 1996), but this would not have been appropriate given that we established the subjects (hydroid colonies) to be of equal size at the beginning of each experiment and that the potential effects of the treatments (mixing and food) on colony size were expected to take some time to occur. In other words, the prescribed similarity of colony size at the beginning of the experiment would have diluted the effects of the treatments if we had analyzed the entire data set (with respect to time) together. Thus we examined only the data from the final day of each experiment. Similarly, in the case of consumption rate data (*Artemia* consumed hydranth^{-1} day^{-1}), we ran a one-way ANOVA testing for an effect of mixing on the last day of each experiment. In all cases we log-transformed the data prior to running the ANOVA in order to normalize the variance.

3. Results and discussion

Over the seven-day period of the first mixing × food experiment, hydroid colonies in the treatment receiving both food and mixing attained the largest size (Fig. 2) and highest specific growth rate (mean $r = 0.24\,\text{day}^{-1}$). Colonies in the no mixing/food treatment achieved the next largest size (Fig. 2) and growth rate (mean $r = 0.18\,\text{day}^{-1}$), followed by the mixing/no food treatment (Fig. 2; mean $r = -0.01\,\text{day}^{-1}$), and finally the no mixing/no food treatment (Fig. 2; mean $r = -0.07\,\text{day}^{-1}$). Statistical analysis of the colony size data from this experiment showed a very highly significant effect due to food ($p < 0.001$), an additional highly significant effect due to mixing ($p < 0.01$), but no significant interaction effect (Table 1). Very similar statistical results were obtained when examining the specific growth rate data from this experiment.

Results from the second mixing × food experiment showed the exact same ranking of treatments: mixing/food > no mixing/food > mixing/no food > no mixing/no food. This was true for both colony size and specific growth rate data. Statistical results were also virtually identical to those of

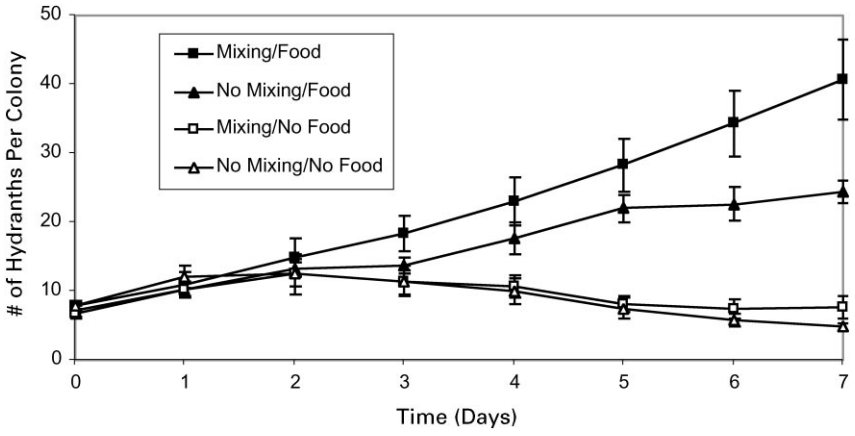

Fig. 2. Effects of mixing intensity and food concentration (2 × 2 factorial design) on the growth (colony size) of planktonic hydroids as determined in the laboratory. Data points are means (± one standard error) of six replicates ($n = 6$) for each treatment. See Table 1 for results of statistical analysis of data from the last day of the experiment.

Table 1
Two-way ANOVA table summarizing the effects of food and mixing on hydroid growth, measured as colony size (log-transformed number of hydranths per colony) from the last day of experiment 1

Source of variation	df	SS	MS	F
Food	1	3.205	3.205	129.915[a]
Mixing	1	0.203	0.203	8.236[b]
Mixing × food	1	0.0017	0.0017	0.796 ns
Error	20	0.493	0.025	
Total	23			

[a] Probability that observed F value occurred by chance is < 0.001.
Other F value is not significant (ns, $p > 0.05$).
[b] Probability that observed F value occurred by chance is < 0.01.

Table 2
Two-way ANOVA table summarizing the effects of food and mixing on hydroid growth, measured as colony size (log-transformed number of hydranths per colony) from the last day of experiment 2

Source of variation	df	SS	MS	F
Food	1	1.365	1.365	21.014[a]
Mixing	1	0.621	0.621	9.558[b]
Mixing × food	1	0.105	0.105	1.610 ns
Error	20	1.299	0.065	
Total	23	3.390	0.147	

[a] Probability that observed F value occurred by chance is < 0.001.
[b] Probability that observed F value occurred by chance is < 0.01.
Other F value is not significant (ns, $p > 0.05$).

the first mixing × food experiment, showing a very highly significant effect due to food ($p < 0.001$), an additional highly significant effect due to mixing ($p < 0.01$), but no significant interaction effect (Table 2).

The dramatic effect of food on growth was not surprising; starved animals tended to decrease in size and animals fed sufficient food grew. Far more interesting, however, was the positive effect of turbulent mixing on growth. Initially we interpreted our results as evidence for a role of turbulence in enhancing contact rates between planktonic predator (hydroids) and prey (*Artemia* nauplii), leading to increased feeding success and growth. This phenomenon has been extensively studied in planktonic predator–prey dynamics (Rothschild and Osborn, 1988; Sundby and Fossum, 1990;

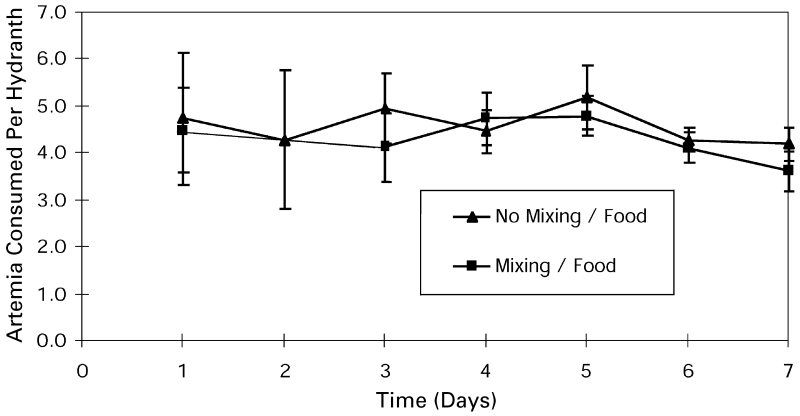

Fig. 3. Effect of mixing intensity on the consumption rate (*Artemia* nauplii consumed hydranth^{-1} day^{-1}) of planktonic hydroids as determined in the laboratory. Data points are means ($\pm$ one standard error) of six replicates ($n = 6$) for each treatment. See Table 3 for results of statistical analysis of data from the last day of the experiment.

Table 3
One-way ANOVA table summarizing the effect of mixing on hydroid feeding rate (No. of *Artemia* nauplii consumed hydranth^{-1} day^{-1}; log-transformed) from the last day of experiment 1

Source of variation	df	SS	MS	*F*
Between groups	1	0.014	0.014	1.398 ns[a]
Within groups	10	1.102	1.019	
Total	11			

[a]ns indicates *F* value is not significant ($p > 0.05$).

MacKenzie and Leggett, 1991; 1993; Muelbert et al., 1994), including recent work on Georges Bank (Incze et al., 1996; Lough and Mountain, 1996; Werner et al., 1996). In general, a 2–5-fold increase in contact rate between planktonic predator and prey is predicted in "turbulent" versus "non-turbulent" conditions.

We tested the hypothesis that mixing enhanced hydroid feeding by statistically analyzing data on their feeding rates in our experiments. These results clearly showed that the expected increase in ingestion with mixing did not occur (Fig. 3; $p > 0.05$, Table 3). The hydroids maintained a relatively constant rate of consumption of approximately 4.5 *Artemia* nauplii hydranth^{-1} day^{-1}, irrespective of mixing. A virtually identical result was found in our second food × mixing experiment ($p > 0.05$, Table 4). Moreover, enhancement of predator–prey contact rates would not explain the apparent advantage of mixing in the absence of food, i.e., the difference between the mixing/no food and no mixing/no food treatments (Fig. 2; Tables 1 and 2 for the significant effect of mixing, but non-significant interaction between mixing and food). How then could hydroid growth increase in

Table 4
One-way ANOVA table summarizing the effect of mixing on hydroid feeding rate (No. of *Artemia* nauplii consumed hydranth^{-1} day^{-1}; log-transformed) from the last day of experiment 2

Source of variation	df	SS	MS	*F*
Between groups	1	0.329	0.329	2.936 ns[a]
Within groups	10	1.122	0.112	
Total	11			

[a]ns indicates *F* value is not significant ($p > 0.05$).

the presence of mixing but in the absence of any apparent increase in consumption of particulate food ?

Increased turbulence could be reasonably expected to reduce the boundary layer thickness around the hydroid colonies, which might enhance transfer of dissolved nutrients or oxygen from the water to the hydroids. This suggests a possible role for dissolved organic material (DOM). The uptake of DOM (i.e., amino acids and sugars) has been shown for a wide variety of soft-bodied marine invertebrates (e.g., Stewart, 1981; Manahan, 1990; Jaeckle and Manahan, 1992; Shilling et al., 1996), including a number of different cnidarians, even those lacking endosymbionts (Hammett, 1943; Schick, 1975; Ferguson, 1988). For instance, Hammett (1943) cited a large body of experimental work with *Obelia* (later identified as *Campanularia* [Crowell, 1957]) showing that "amino acids added to the surrounding seawater are taken in by oral ingestion." Ferguson (1988) studied seven cnidarian species, including the small hydrozoan medusa *Liriope exiqua*, and found amino acid uptake to be particularly high in the tentacles. Leaving aside for the moment the issue of whether such uptake is mediated by attached or free-living microorganisms, these studies strongly suggest a role for DOM in the nutrition of soft-bodied marine invertebrates generally and hydrozoans in particular.

Thus we hypothesize that DOM might become depleted in the boundary layer around the hydroid colony in the absence of turbulent mixing, but be continuously resupplied to the colony in the presence of such mixing. We attempted to test this hypothesis experimentally by incubating replicate hydroid colonies in autoclaved seawater, in vigorously mixed jars (as described above), and subjecting them to one of two treatments: (1) supplemental DOM (1 μM glucose and 1 μM amino acids, consisting of 62.5 nM each of 16 amino acids, as described by Jaeckle and Manahan [1992]), and (2) no supplemental DOM. The number of feeding hydranths per colony in the two treatments was not significantly different ($p > 0.05$), although the trend after three days was toward a greater number of feeding hydranths in the presence of supplemental DOM. When the same colonies were examined for the number of budding hydranths (i.e., hydranths that were not yet fully developed but clearly on their way to becoming feeding hydranths), there were significantly greater numbers of budding hydranths in the DOM supplement treatment as compared to the unsupplemented treatment ($p < 0.05$). Unfortunately, the experiment had to be terminated after only three days because of a fungal infection of the colonies. The inconclusive results do not allow us to distinguish between the direct uptake of DOM by the hydroids, and uptake and increased growth

of bacteria and/or protozoa that are then consumed by the hydroids. Alternatively, DOM-enhanced bacterial growth need not be beneficial to hydroid growth, and may actually be a detriment. For instance, Fulton (1959) attributed an inhibition effect on hydroid regeneration to bacterial metabolites. Thus our DOM hypothesis remains to be fully tested with more sophisticated experiments using radioisotope techniques and axenic culture methods.

Two other possible benefits of reduced boundary layer thickness around the hydroid colonies include improved supply of oxygen and removal of waste products. We measured oxygen concentration in the mixed and unmixed jars and found no significant difference between treatments ($p > 0.05$). However, a more subtle deficiency of oxygen in the boundary layer immediately surrounding the colonies was beyond our means to evaluate and therefore cannot be ruled out. The second possibility of a build-up of waste products within the boundary layers of the colonies also could not be measured in these experiments.

Yet another interpretation of the effect of mixing in our experiments is that the bubbling caused formation of particulate organic matter (POM) as a result of DOM being adsorbed onto bubbles as they passed through the seawater, and that this enhanced the concentration of POM available to the hydroids. Formation of POM by bubbling of seawater has been well documented in laboratory experiments (e.g., Sutcliffe et al., 1963) as well as on Georges Bank (Kepkay et al., 1990). Indeed, POM generated by bubbling of seawater has been shown experimentally to provide a source of nutrition for at least one planktonic suspension feeder (Baylor and Sutcliffe, 1963) and has been speculated to have far-ranging consequences for detritus-based pelagic food webs more generally (e.g., Riley, 1970; Mann, 1988). Although we did not measure either DOM or non-prey POM in our experiments, POM formed by bubbling could have provided significant amounts of material in the no food treatments (e.g., DOC in coastal waters generally occurs at concentrations of 1–5 mg C l^{-1} (Sharp et al., 1993), which if multiplied by a factor of 19% for DOM conversion to POM by bubbling (Alber and Valiela, 1994) yields a POC concentration of 0.2–1.0 mg C l^{-1}. However, in the food treatments, in which we had 80–160 *Artemia* nauplii l^{-1}, conditions were almost certainly food-saturated and thus any additional POM generated by bubbling should not have increased ingestion, but we cannot exclude this possibility.

Whatever the mechanism, the present results show a clear benefit of increased mixing to planktonic hydroid growth. We think the most likely mechanism for this is reduced boundary layer thickness around the hydroid colonies, and not increased predator–prey contact rates due to turbulence. We therefore recommend that the interactions between mixing, boundary layer thickness, and concentrations of DOM, oxygen and waste products be examined experimentally in hydroids. The interaction between bubble formation, DOM and particulate food for hydroids should also be further investigated. Only then will we know the exact mechanisms by which turbulent mixing enhances planktonic hydroid growth.

Our results help explain why planktonic hydroids are vastly more abundant in the central, shallow, well-mixed region of Georges Bank compared to the stratified flanks of the Bank (Madin et al., 1996, 1997; Norrbin et al., 1996; Sullivan et al., 1997; Concelman et al., 2001). First is the issue of remaining suspended. Energy dissipation rates at 500 bpm were more than sufficient to keep the hydroids in suspension in our experimental containers (in contrast, hydroid colonies in the no mixing treatments eventually sunk to the bottom of the jar). In fact, if we use the maximum sinking velocity of 0.03 m s^{-1} reported by Sullivan et al. (1997), turbulence velocities required for continuous suspension would be $u_{rms} = 0.03\,\mathrm{m\,s^{-1}}$, which translates into a dissipation rate of

2.5×10^{-5} W kg^{-1}. This apparently occurs near bottom 100% of the time but reaches into the water column only on maximum tidal current speeds (i.e., every 6 h) and during storms. Therefore, one would expect some sinking (and concomitant change in concentration) to occur on tidal frequencies.

But perhaps more important is the positive effect of turbulent mixing on the growth of planktonic hydroids. In a recent review of hydroid ecology, Boero (1984) notes the importance of water movement as a means of providing greater oxygen and food supply, while also reducing sedimentation on the colony. Although Boero's comments refer to benthic colonies, our results with *C. gracilis* suggest that the same may be true for planktonic hydroids, especially if "food" is interpreted broadly to include dissolved material. Boero (1984) states that the Campanulariidae, which includes the genera *Clytia* and *Obelia*, are adapted to a wide range of environmental conditions, and are often cosmopolitan and able to colonize very different habitats. In the case of *C. gracilis*, this includes the turbulent water column on the crest of Georges Bank.

One of the most interesting and important observations about planktonic hydroid colonies on the crest of Georges Bank (Madin et al., 1996; Norrbin et al., 1996) was that their stolons were sealed (implying that they were not recently torn off the bottom), that they were actively feeding, and apparently were growing in situ. Our experimental results confirm that hydroids are capable of very high growth rates ($r \geqslant 0.25$ day^{-1}) under planktonic conditions of abundant food and strong mixing, and need not be associated with the bottom to thrive. However, we do not yet know if *Clytia gracilis* can pass through its entire life cycle suspended in the plankton. Boero (1984) made the point that some hydroids (e.g., *Velella*, *Porpita*, and *Margelopsis*) are able to reduce or avoid any sessile phase in their life cycles by producing planktonic polyps. Mills (1987 and references therein) makes the similar point about *Pelagohydra*, *Climacocodon*, and *Eirene hexanemalis*. At the very least it seems clear that *Clytia gracilis* possesses an extended planktonic phase, including the planktonic medusa and the suspended hydroid phase studied here.

Preliminary evidence suggests that the impact of planktonic hydroids as predators in the pelagic ecosystem of Georges Bank can be considerable, especially on copepod nauplii, and perhaps also on larval fish (Madin et al., 1996, 1997; Sullivan et al., 1997). To understand fully the impact of this predator, however, will require much more knowledge about the life history and ecology of both the planktonic and benthic stages of this organism, a point made recently by Marcus and Boero (1998) about coastal marine organisms generally. To date, studies of hydroids on Georges Bank include reports on distribution and abundance (Madin et al., 1996, 1997; Sullivan et al., 1997; Concelman et al., 2001), feeding (Madin et al., 1996; Klein-MacPhee et al., 1997; this study), sinking (Sullivan et al., 1997), and predation from fishes (Avent et al., 2001), but have focused primarily on planktonic stages. Ultimately, models which couple the biology and physics of Georges Bank, such as those recently developed as part of the GLOBEC program (Werner et al., 1993, 1996, Lynch et al., 1998), will need to include the complex life history of hydroids so that we can fully evaluate their role in the Georges Bank ecosystem.

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