PERGAMON

Deep-Sea Research II 48 (2001) 645–658

DEEP-SEA RESEARCH
PART II

www.elsevier.com/locate/dsr2

Distribution, abundance and benthic-pelagic coupling of suspended hydroids on Georges Bank☆,☆☆

Stephanie Concelman[a,b,*], Stephen M. Bollens[a], Barbara K. Sullivan[c], Laurence P. Madin[d], Erich Horgan[d], Mari Butler[a,d], Donna van Keuren[c]

[a]*Romberg Tiburon Center for Environmental Studies, San Francisco State University, 1600 Holloway, CA, USA*
[b]*Department of Biology, San Francisco State University, San Francisco, CA 94132, USA*
[c]*Graduate School of Oceanography, University of Rhode Island, Narragansett, RI 02882-1197, USA*
[d]*Biology Department, Woods Hole Oceanographic Institution, Woods Hole, MA 02543, USA*

Received 4 February 1999; received in revised form 10 August 1999; accepted 22 December 1999

Abstract

Clytia spp. hydroids (Phylum Cnidaria), typically attached to a substrate during their asexual, polyp stage, have been found in significant numbers within the mesozooplankton on Georges Bank, North Atlantic Ocean. We examined unpublished historical records of the 1939–1941 cruises of the R/V *Atlantis* and obtained samples at four-study sites on Georges Bank in June/July 1995 in an attempt to (1) quantify the planktonic and benthic distributions of hydroids on Georges Bank, and (2) determine the coupling between benthic and pelagic habitats of this population. We found that planktonic hydroids have a patchy distribution, varying both spatially and temporally (most abundant in summer months, absent in winter). In 1939–1941 the planktonic hydroids were most broadly distributed following a spring (1940) with strong wind events; hydroids were absent from all samples in 1941. In 1995 we found the highest abundance of planktonic *Clytia* spp. hydroids (6213.5 $\pm$ 1343.6 hydranths m^{-3}) in the central crest of the bank, "downstream" in the Georges Bank circulation pattern from sites along the northeast peak of the Bank where large populations of benthic *Clytia* spp. hydroids were found (up to 6465 hydranths m^{-2}). Our plankton sampling did not show significant numbers of hydroids in the water column at the Northeast peak sites, indicating that large numbers of planktonic hydroids are not being introduced into the Bank's circulation patterns from off-Bank sites to the northeast (e.g. Scotian shelf). The source population for planktonic hydroids found in the central region of the Bank is most likely the benthic habitats on the northeast peak of the Bank. We hypothesize, and our limited data suggest, that hydroids are 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.

☆We dedicate this manuscript to Mary Landsteiner, a good friend and excellent scientist, whose constant good humor and positive outlook on life will continue to serve as an inspiration for all of us.

☆☆Paper published in December 2000.

* Corresponding author. Current mailing address: P.O. Box 976, Kemah, TX 77565, USA.
E-mail address: stephanie.concelman@mindspring.com (S. Concelman).

0967-0645/01/$ - see front matter
PII: S0967-0645(00)00091-6

1. Introduction

Georges Bank is a large, shallow submarine plateau located east of Cape Cod, Massachusetts, along the southeast side of the Gulf of Maine, lying between 40°N and 42°N latitude and 66°W and 69°W longitude. The Bank measures approximately 241 km long by 160 km wide. Depth varies between 200 m at the edge of the bank to 5 m on Georges Shoal in the northwest section, with the majority of the Bank having a depth ranging between 40 and 100 m. Georges Bank has long been important economically to the New England and Canadian fisheries due to its high level of productivity.

Research conducted under the Global Ocean Ecosystem Dynamics (GLOBEC) research project studying key animal species and physical processes on Georges Bank (US GLOBEC, 1992) found large numbers of suspended hydroid polyps (*Clytia* spp., including *Clytia gracilis* and *Clytia cylindrica*) in the water column (Madin et al., 1996). Although there are a few genera of holoplanktonic hydroids (*Velella, Porpita, Margelopsis*) (Boero, 1984), the asexual polyps of *Clytia* spp. are typically found attached to substrates (Fraser, 1944). However, the suspended *Clytia* spp. found on Georges Bank appear to be healthy, generating both asexual feeding polyps and sexual gonangia polyps, and functioning well as a planktonic predator.

Hydranth density on Georges Bank has been measured as high as 2.5×10^4 hydranths m^{-3}. Feeding experiments performed with planktonic *Clytia* spp. indicate that with a density of 10,000 hydranths m^{-3}, planktonic hydroid consumption rates are close to the daily hatching rate of copepod nauplii (Madin et al., 1996). Larval cod (*Gadus morhua*) feed primarily on copepods (Bainbridge and McKay, 1968; Last, 1978) and an abundant supply is necessary for larval cod growth (Meeren and Naess, 1993), suggesting that larval cod and hydroids are likely competing for the same food. Norrbin et al. (1996) reported an inverse relationship between the abundance of hydroids and copepod nauplii on Georges Bank and suggested that the reduced naupliar abundance may be due directly to a high concentration of hydroids in the water column. Feeding experiments with larval cod and planktonic hydroids also showed that the hydroids were able to consume larval fish (Madin et al., 1996; Klein-MacPhee et al., 1997). Undoubtedly the planktonic hydroids will feed on other prey in addition to copepod nauplii and larval fishes, and thus are an important predator in the dynamics of the Georges Bank ecosystem.

Planktonic *Clytia* spp. hydroids were reported on Georges Bank as early as 1913 (Fraser, 1915) and more recently by Madin et al. (1996, 1997), Norrbin et al. (1996) and Sullivan et al. (1997). *Clytia* spp. also have been described in the planktonic community of the Atlantic Ocean off western Africa. In that location, hydroids, described as *Clytia hemisphaerica*, often had basal discs containing a sand grain, indicating a recent benthic origin (Cornelius, 1982, and references therein). However, the pelagic hydroids of Georges Bank were described as not exhibiting evidence of recent benthic attachment. These colonies often had multiple hydranths (# of feeding polyps > 5) and were spherical in shape, suggesting an extended life span in the pelagic state (Fraser, 1915; Madin et al., 1996; Norrbin et al., 1996; Sullivan et al., 1997). Although various aspects of the pelagic ecology of *Clytia gracilis* on Georges Bank have been studied recently, including feeding and growth (Madin et al., 1996; Bollens et al., 2001a), sinking (Sullivan et al., 1997) and predation by fish (Avent et al., 2001), no attempt has yet been made to study the benthic/pelagic coupling of this population.

In order to determine historical presence of planktonic hydroids on Georges Bank, we examined unpublished records of the cruises of the R/V *Atlantis* from 1939 to 1941. To study the more recent

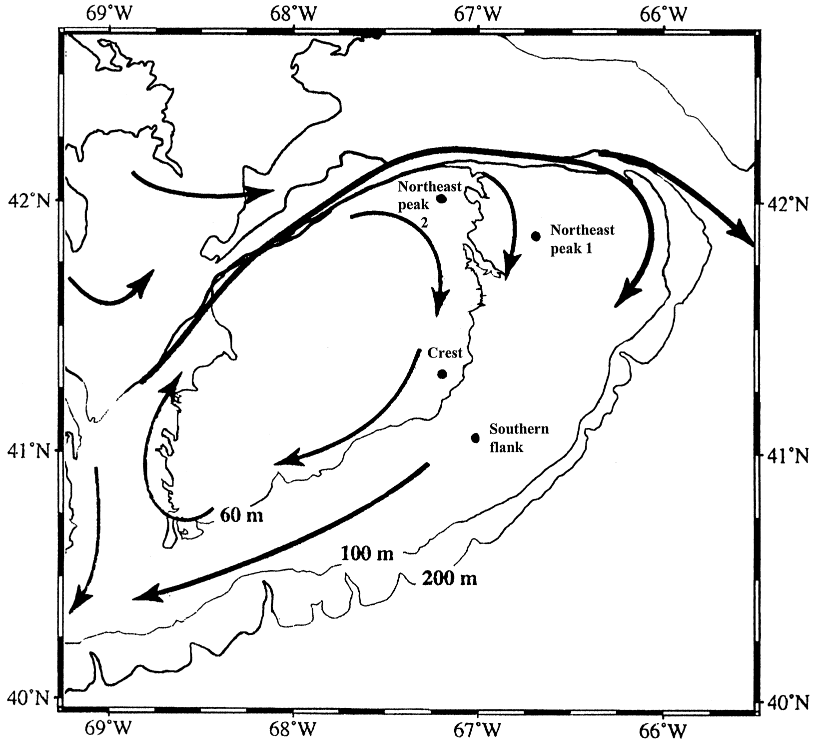

Fig. 1. A stylized representation of the mean-residual circulation on Georges Bank redrawn from Bigelow (1927), with supporting data from Butman et al. (1987) and Limeburner and Beardsley (1996). Study sites from the 1995 cruise are identified.

distribution and abundance patterns of planktonic and benthic hydroids, we sampled four sites on Georges Bank in June/July 1995 during cruise EN268 of the R/V *Endeavor*. We included sites "upstream" in the circulation pattern of the Bank from locations where planktonic hydroids are known to occur (Bank crest) in hopes of finding the benthic source population. The circulation pattern of Georges Bank (Fig. 1), as described by Bigelow (1927), Butman et al. (1987) and Limeburner and Beardsley (1996), is a clockwise circulation pattern with a relatively low-advective region in the central, shallower area of Georges Bank. We wanted to test the hypothesis that a benthic source population exists on or close to Georges Bank in such a location that as hydroid colonies become detached from the bottom substrate due to storm action or other disturbance, they enter the circulation pattern and are at least partially retained on Georges Bank.

2. Materials and methods

2.1. Historical data, 1939–1941

Zooplankton samples were collected on Georges Bank during 1939–1941 from the R/V *Atlantis*. Details of the sampling protocol are given in Clarke et al. (1943), and results for the major taxonomic groups are presented and discussed in Bollens et al. (2001b). Briefly, samples were collected with a flow-metered Clarke-Bumpus plankton sampler (Clarke and Bumpus, 1940) with 12.7 cm diameter mouth opening and ~ 250 mm mesh netting. Samples were collected from near-bottom to the surface at 21–52 stations on each of 11 cruises between September 1939 and June 1941. All samples were analyzed for species composition but, in the case of hydroids, only "presence" or "absence" of "hydroid material" was noted. The data sheets from these cruises were only recently discovered in the Woods Hole Oceanographic Institution archives and have since been entered into computer files. The samples apparently were discarded some years ago. Although nearly a half-century old, these hydroid data have never before been published.

Contemporary wind data from Nantucket airport were collected and analyzed as described in Bollens et al. (2001b). For the present analysis, three measures of storminess were computed for the 30 days preceding the May 1940 and May 1941 cruises of R/V *Atlantis:* (1) average daily wind speed ($\mathrm{m\,s^{-1}}$), (2) maximum daily wind speed ($\mathrm{m\,s^{-1}}$), and (3) number of "storm" events (daily wind speed greater than $9\,\mathrm{m^{-1}}$).

2.2. 1995 Sample sites

We obtained samples at four sites on Georges Bank between June 29 and July 5, 1995. The choice of study sites on Georges Bank was based on two criteria: (1) the presence or absence of temperature stratification within the water column; and (2) bottom composition. The Southern flank site, characterized by water column temperature stratification throughout the year, was located on the Bank's southern flank at 41°03.9′N, 67°03.9′W (depth = 73.4 m). The Crest site lacked a stratified water column and was located on the crest of the Bank at 41°16.5′N, 67°16.7′W (depth = 53.5 m). This site was strongly influenced by tidal currents and surface winds that allowed for complete mixing within the water column and was near locations where earlier studies found planktonic hydroid colonies to be very abundant (Madin et al., 1996; Sullivan et al., 1997). The remaining two study sites, the Northeast peak sites, were chosen due to bottom composition and their location upstream in the Georges Bank circulation pattern from the Crest and Southern flank sites. Geological maps (Valentine et al., 1993) indicated the Northeast peak sites had a cobble bottom, a likely substrate for attached benthic source populations for the suspended hydroid colonies found downstream on the Bank. Northeast peak 1 site was located at 41°53.1′N, 66°47.4′W (depth = 65 m), and Northeast peak 2 site at 41°59.9′N, 67°15.2′W (depth = 50.1 m).

2.3. 1.0 m^2 MOCNESS samples

A $1.0\,\mathrm{m}^2$ multiple opening and closing net and environmental sensing system (MOCNESS) (Wiebe et al., 1985) was used to sample the water column at each site in multiple 5–10 m strata from the surface to within 10–15 m above the bottom. Multiple tows were made at each site except the Northeast peak 1 site where adverse weather conditions limited us to a single tow. At the Southern flank and Crest sites, the samples were equally partitioned between day and night. All samples were preserved with 5% formalin for examination ashore in the laboratory.

Samples were sorted to remove all organisms greater than 1 cm in length and subsampled using a Folsom Plankton Splitter to provide approximately 200 hydroid colonies. Number of individual hydranths and gonangia per unit volume of sample were counted using a dissecting microscope.

When samples were too concentrated to split, they were diluted with filtered (20 μm) seawater and stirred vigorously while subsampling with a Stempel pipette.

2.4. Video transects

We made video transects at each of the four study sites using a Phantom S2 Remote Operated Vehicle (ROV) equipped with a Sony Hi-8 video camera. We used methods described by Auster et al. (1989) for video transect data collection and data analysis. A weight was attached to the ROV's tether 50 m from the ROV, and each video transect followed a course heading from the weight 50 m out to the end of the tether. Multiple transects, oriented 90° from each other, were done with two fields of view, wide angle (0.39 m^2 per screen) and high magnification (0.0275 m^2). Two wide-angle transects and two high-magnification transects were made at each of the Southern flank and Crest sites. Due to strong current conditions, only one wide-angle and one high-magnification transect were possible at each of the Northeast peak sites.

A non-overlapping screen-by-screen count was made of all visible organisms for each transect. The observed area of each screen was then multiplied by the total number of non-overlapping screens in each transect to obtain a total area surveyed. The video transects also were used to assess the bottom substrate composition.

2.5. Water column suction samples

The ROV also enabled us to sample water near the bottom, a region we could not sample with the MOCNESS. Using the ROV's suction sampler, we collected near-bottom planktonic samples at 1 and 3 m off bottom, with the samples being equally distributed between day and night.

Each suction sample pumped 1892.5 l of seawater through a 333 μm mesh filter during ten minutes. Upon the ROV's return to the surface, the filters were removed and the organisms preserved in 5% formalin-filtered seawater solution. In the laboratory, the preserved samples were filtered with a 300 μm mesh filter and the hydroid colonies were separated and counted, as were other zooplankton.

2.6. Van Veen Grab samples

Twelve bottom samples were taken with a Van Veen sampler lowered from the deck of the ship. The sample area of each grab was 0.043 m^2. After each deployment, the sampler was retrieved to the surface, the contents rinsed from the sampler and preserved with 5% formalin-filtered seawater solution and returned to shore for examination in the laboratory.

Each sample was filtered with a 300 μm mesh filter, and the hydroid colonies were counted. All non-sand substrate was removed and examined for attached hydroid colonies. The sand substrate was divided into subsamples of 0.4 l and examined for hydroids as follows: each subsample was spread into an examination tray where filtered water was slowly added until it covered the substrate to a depth of approximately 2 cm. The tray was then gently agitated to allow hydroid colonies to float out of the sand. The water was then filtered with a 300 μm mesh filter, and all hydroid colonies were counted. This procedure was repeated twice for each 0.4 l subsample and effectively removed all hydroids from the sample.

3. Results

3.1. Historical data, 1939–1941

In our examination of the presence/absence data from 1939 to 1941, planktonic hydroids were patchily distributed in both time and space on Georges Bank (Fig. 2), with seasonal and inter-annual differences being particularly striking. Planktonic hydroids were absent from September 1939 through March 1940. They first appeared in April 1940, although at only one shallow station. By May 1940 they were much more broadly distributed (19 stations), and remained so through late June, although they were almost entirely confined to inside the 100 m isobath. Hydroids were completely absent during the four sampling periods between March and June, 1941.

Wind patterns for the spring of 1940 and the spring of 1941 differed greatly. In the 30 days preceding May 1940, the average daily wind speed was 5.6 m s^{-1}, while for the same time period in 1941 the average daily wind speed was 3.4 m s^{-1}. Likewise, the maximum daily wind speed for the thirty days preceding May 1940 exceeded that for the same time period in 1941 (11.7 m s^{-1} in 1940; 6.4 m s^{-1} in 1941). The number of "storm" events, measured as daily wind speed greater than 9 m s^{-1}, was higher in the 30 days preceding May 1940 (3 events) than the same time period in 1941 (0 events).

3.2. 1.0 m^2 MOCNESS samples

Our 1.0 m^2 MOCNESS samples showed highest abundance of planktonic hydroids close to the bottom at all sites (Fig. 3). At the Crest site, however, this pattern was not as pronounced (842 hydranths m^{-3} at 5 m, increasing to 2783 hydranths m^{-3} at 40 m) and hydroids were found in abundance higher than 1000 m^{-3} throughout most of the water column. A higher concentration of planktonic *Clytia* spp. was found at the Northeast peak 1 site (226 hydranths m^{-3} at 55 m) than at the Northeast peak 2 site (22.8 hydranths m^{-3} at 40 m). Hydroids were also found in low abundance at the Southern flank site (94.6 hydranths m^{-3} at 60 m) (Fig. 3).

3.3. Video transects

As shown in Table 1, the community composition varied significantly between the four sites. The Crest site had a sandy bottom with sand ridges measuring 1–5 m in height. The Southern flank site also had a sandy bottom, but lacked the ridges and was level with a thin (approx. 1 cm) layer of algal detritus on top of the sand. Both Northeast peak sites had a relatively level bottom of cobble and gravel lying over sand (Table 1). Sand dollars were the dominant benthic organism visible at the Crest site (67.2% of organisms seen in wide-angle frames and 91.8% of organisms seen in high-magnification frames), while sea anemones were less abundant (31.5% of organisms seen in wide angle frames and 7.7% of organisms seen in high-magnification frames). Sea anemones were dominant at the Southern flank site (68.8% of organisms seen in wide-angle frames and 73% of organisms seen in high-magnification frames), with a low abundance of sand dollars (2.2% of organisms seen in wide-angle frames and 1.8% of organisms seen in high-magnification frames). The cobble bottom at both Northeast peak sites provided attachment sites for colonies of the hydroid *Obelia* and they formed the dominant group at both sites (Northeast peak 1 site: 52% of

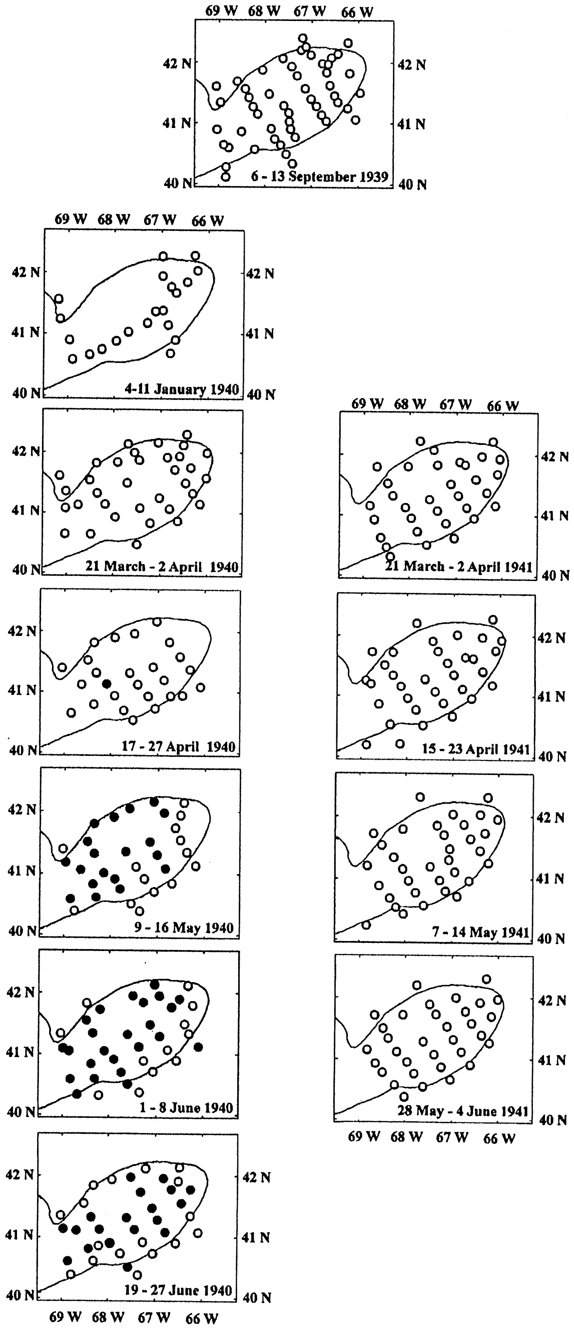

Fig. 2. Presence (filled circles) and absence (open circles) of planktonic "hydroid material" during 11 cruises of the R/V *Atlantis* from September, 1939–June, 1941. Solid line is the 100 m isobath.

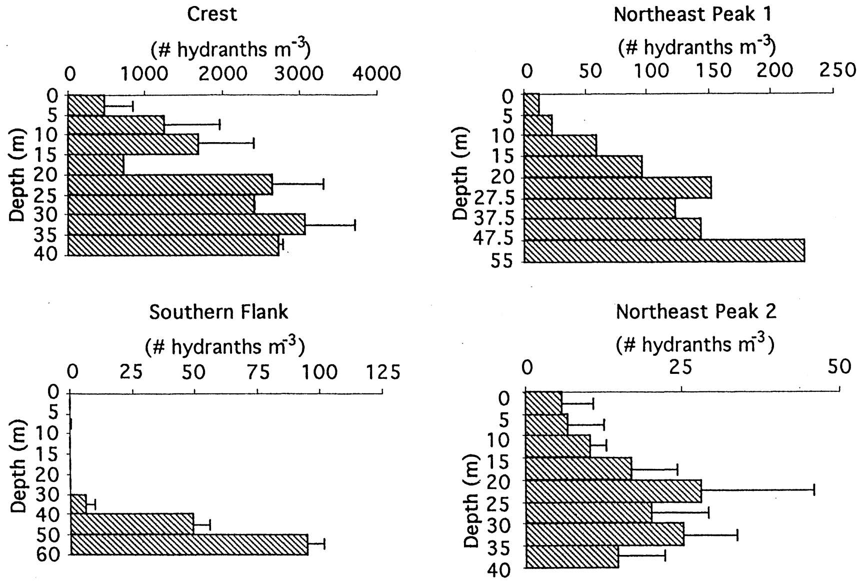

Fig. 3. Vertical distribution of planktonic hydroids (hydranths m^{-3}) obtained with a 1.0 m^2 MOCNESS at each of four sites. Each horizontal bar is the mean ($\pm$ standard error) of two samples except for the Northeast peak 1 site where only a single tow was made.

organisms seen in wide-angle frames and 77% of organisms seen in high-magnification frames; Northeast peak 2 site: 68.4% of organisms seen in wide angle frames and 77% of organisms seen in high-magnification frames).

3.4. Water column suction samples

The water column suction samples taken with the ROV showed that planktonic *Clytia* spp. hydroids were significantly ($p = 0.002$) more abundant at the Crest site (6213.5 ± 1343.6 hydranths m^{-3}) than any of the other study sites (Southern flank = 110.5 ± 21.9 hydranths m^{-3}; Northeast peak 1 = 476.6 ± 129.3 hydranths m^{-3}; and Northeast peak 2 = 39.6 ± 5.6 hydranths m^{-3}) (Fig. 4). Hydroids were the dominant group (hydranths = 86.9% of the total mesozooplankton) at the Crest site, compared to 15.2% at the Southern flank site, 7.6% at the Northeast peak 2 site and 61.4% at the Northeast peak 1 site (Table 2).

3.5. Van Veen Grab samples

The Van Veen grab samples showed the highest abundance of *Clytia* spp. hydroids attached to substrate at the Northeast peak sites (Northeast peak 1 = 6465 hydranths m^{-2}; Northeast peak 2 = 2465 hydranths m^{-2}) (Fig. 4). Grab samples from the Crest site also showed relatively high abundance of hydroids (4692 ± 2142 hydranths m^{-2}); however, only one hydroid colony at the Crest site was found actually attached to a sand grain. The majority of colonies found in the grab samples at the Crest site did not have broken stolons and had 3–4 feeding polyps per colony

Table 1
Study site characterization and benthic community composition as determined by video transects using the ROV. Hydroid colonies are the larger *Obelia* spp., not *Clytia* spp. Percentages are shown in number of organisms. Predominant group is shown in bold.

STUDY SITE	DEPTH	BOTTOM TYPE	TEMPERATURE	ROV VIEW	TOTAL AREA SURVEYED	NUMBER OF ORGANISMS ENCOUNTERED	BENTHIC COMMUNITY COMPOSITION BY GROUP						
							Hydroid Colonies	Sea Anemones	Sea Stars	Crabs	Sand Dollars	Fishes	Other
CREST	53.5 m	Sandy bottom with sand ridges common, varying in height from 1 - 5 m.	10.5° C day	Wide Angle	37.1 m^2	2482	0.0%	31.5%	0.2%	0.7%	**67.2%**	0.1%	0.3%
			11.4° C night	High Mag.	7.0 m^2	1514	0.0%	7.7%	0.0%	0.2%	**91.8%**	0.1%	0.2%
SOUTHERN FLANK	73.4 m	Sandy, level bottom with layer of algal detritus approx 1 cm deep resting on top of bottom surface.	7.6° C day	Wide Angle	35.1 m^2	530	3.9%	**68.8%**	11.6%	8.7%	2.2%	0.4%	4.4%
			7.5° C night	High Mag.	7.6 m^2	741	6.2%	**73.0%**	6.1%	6.0%	1.8%	0.1%	6.8%
NORTHEAST PEAK 1	65.0 m	Cobble, gravel and pebble bottom over sand.	9.8° C day	Wide Angle	17.6 m^2	180	**52.0%**	0.0%	1.1%	42.4%	0.0%	2.3%	2.2%
			10.1° C night	High Mag.	3.7 m^2	282	**77.0%**	7.8%	0.7%	14.5%	0.0%	0.0%	0.0%
NORTHEAST PEAK 2	50.1 m	Cobble, gravel and pebble bottom over sand.	10.4° C day	Wide Angle	17.6 m^2	59	**68.4%**	0.0%	3.5%	22.8%	0.0%	1.8%	3.5%
			11.0° C night	High Mag.	1.5 m^2	74	**77.0%**	6.8%	0.0%	16.2%	0.0%	0.0%	0.0%

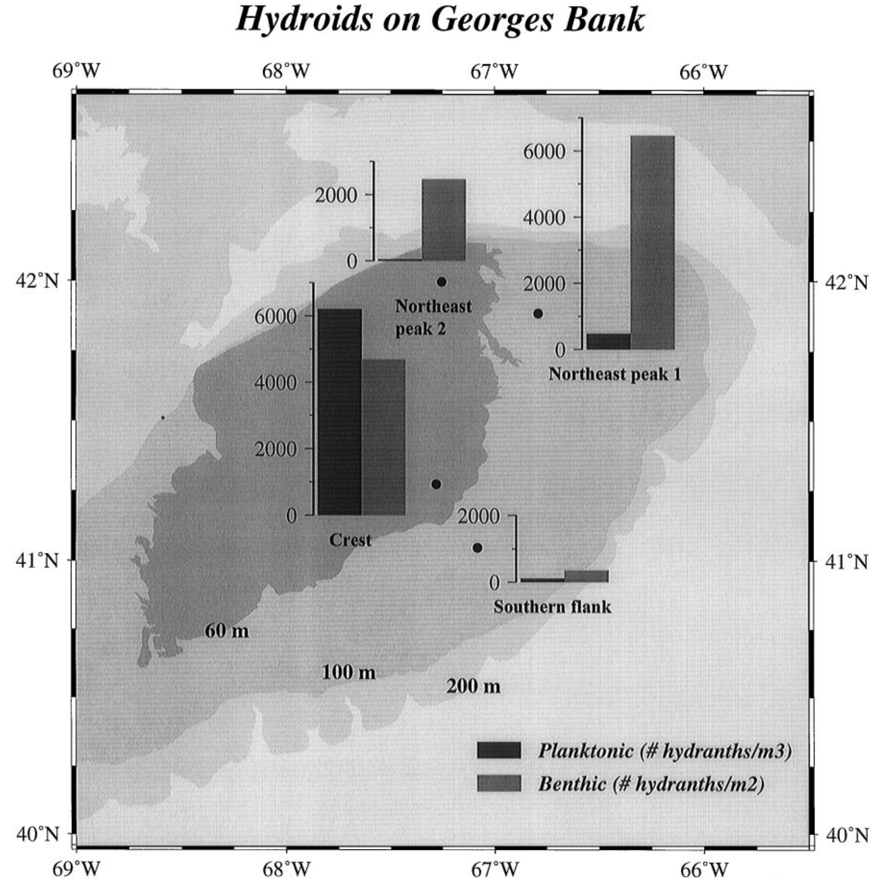

Fig. 4. Distribution of hydroids at four study sites on Georges Bank obtained with: (1) a ROV suction samples (plankton) (hydranths m^{-3}; $n = 32$) and (2) a Van Veen Grab (benthos) (hydranths m^{-2}; $n = 12$). The hatched bar represents the abundances of near-bottom planktonic hydroids: Northeast peak 1 site, 6465 hydranths m^{-2}; Northeast peak 2 site, 2465 hydranths m^{-2}; Southern flank site, 357 ± 109 hydranths m^{-2}; Crest site, 4692 ± 2142 hydranths m^{-2}. The solid bar represents benthic hydroids with abundances of: Northeast peak 1 site, 476.6 ± 129.3 hydranths m^{-3}; Northeast peak 2 site, 39.6 ± 5.6 hydranths m^{-3}; Southern flank site, 110.5 ± 21.9 hydranths m^{-3}; Crest site, 6213.5 ± 1343.6 hydranths m^{-3}.

(mean = 3.84), consistent with the appearance of planktonic colonies suspended near, or settled onto, the bottom, rather than attached benthic colonies. There were far fewer benthic *Clytia* spp. colonies found at the Southern flank site (357 ± 109 hydranths m^{-2}) than the other three sites and these were primarily found attached to shells or other hard substrates.

4. Discussion

It is clear from the 1939 to 1941 data that planktonic hydroid distribution on Georges Bank is patchy in both time and space, with higher concentrations in the well mixed, central area and

Table 2
Composition (% of total zooplankton numbers) of the near-bottom (1–3 m) plankton community as determined by ROV pump samples ($n = 8$ at each site). Percentages are shown in number of organisms

STUDY SITE	PLANKTONIC COMMUNITY COMPOSITION				
	Hydranths	Chaetognaths	Copepods	Other Crustacea	Other
Crest	86.9%	1.7%	6.6%	4.0%	0.8%
Southern flank	15.2%	16.0%	62.3%	6.3%	0.2%
Northeast Peak 1	61.4%	4.8%	25.4%	7.8%	0.6%
Northeast Peak 2	7.6%	1.8%	44.8%	44.2%	1.5%

greatest abundances in late spring to early summer. The temporal pattern may be influenced by wind strength. Using all three measures of "storminess", spring 1940, when planktonic hydroids were broadly distributed on the central Bank, was a much stormier period than spring 1941, when hydroids were absent from the Bank. Also, it is important to note that the only other published report of planktonic hydroid abundance (Madin et al., 1996) showed higher abundances of planktonic hydroids in May 1994 compared to June/July 1995, as reported here; interestingly wind anomalies were much higher in March and April of 1994 than in 1995 (Manning, 1999). This lends further support to the hypothesis that storm activity could introduce hydroids into the plankton. The relative importance of storms versus other disturbances (e.g., bottom trawling) in introducing hydroids into the water column is impossible for us to assess, but warrants further study.

Through the use of the video camera and instrumentation on the ROV, it was possible to describe the bottom characteristics and benthic community at each study site more completely than through deck sampling alone. We originally hoped to use the ROV video transects to survey benthic *Clytia* spp. abundance; however, this proved impossible with the magnification and resolution of the video equipment. ROV transects can be quite accurate for larger organisms (Michalopoulos et al., 1993); but the colonies of *Clytia* spp. were too small (< 3 mm) to be reliably counted on video, even at high magnification. The ROV video was useful for identifying larger hydroid colonies such as *Obelia*, which may be a proxy measure for suitable habitat for other hydroids, and the layer of algal detritus on the sand at the Southern flank site. The vehicle also proved to be a very useful tool for sampling near-bottom plankton, enabling us to quantify planktonic hydroids in an area where we were unable to use the MOCNESS.

The combination of MOCNESS and ROV sampling enabled us to examine the vertical distribution of hydroids from the surface to within 1 m of the bottom. The highest abundance of planktonic hydroids was found throughout the water column at the Crest site (Figs. 3 and 4), consistent with earlier sampling by Madin et al. (1996) and Norrbin et al. (1996). The lowest abundance of planktonic hydroids was at the Northeast peak 2 site, with higher numbers at the Northeast peak 1 site. At the Southern flank site, no hydroids were found above 30 m and the overall abundance was low (Figs. 3 and 4).

As expected, the abundance of attached, benthic hydroids appeared to be related to bottom substrate. The benthic hydroid abundance was high at both Northeast peak sites, where the bottom was composed of cobble (Table 1, Fig. 4). The Crest site also had a high abundance of benthic hydroids (4692 hydranths m^{-2}), but the presence of closed stolens and small colony size suggests these colonies had settled onto the bottom, or were suspended just above it, as opposed to actually being attached to the bottom substrate (sand). The lowest benthic abundance of hydroids (357 hydranths m^{-2}) was at the Southern flank site.

The circulation pattern on Georges Bank (Fig. 1) would appear to be an important factor linking the benthic and planktonic distribution of hydroids. Our limited data indicate that the highest abundance of benthic hydroids occurs upstream of the highest abundance of planktonic hydroids, suggesting the former may be a source of the latter. While it is possible that some planktonic hydroids may be entering the Georges Bank system from off the Bank (e.g. Scotian shelf), the scarcity of hydroids in the water column at the most upstream station (Northeast peak 2) would argue against a primary source population off the Bank. We think it more likely that hydroids attached to the bottom in the northeast peak areas enter the water column after being separated from, or broken off, their substrates by storms or other disturbances. Results from the ROV suction sampling show the density of suspended hydroids is lowest at the Northeast peak 2 site (40 ± 6 hydranths m^{-3}), but their numbers increase markedly at the Northeast peak 1 site (477 ± 129 hydranths m^{-3}). By the time the water reaches the Crest site, hydroids make up the bulk of the mesozooplankton population, present in the water column at a concentration of 6214 ± 1344 hydranths m^{-3}. At this point, the planktonic hydroids are likely being retained in the well-mixed, but weakly advective circulation on the peak of the Bank (Figs. 1 and 4). The low abundance of near-bottom planktonic hydroids at the Southern flank site (111 ± 22 hydranths m^{-3}) may be explained by that site's position near the southern edge of the Bank. It might receive fewer suspended hydroids from the upstream northeast peak areas, and strong along-Bank currents outside of the 60 m isobath could rapidly sweep water and suspended hydroids off the Bank (Werner et al., 1993; Limeburner and Beardsley, 1996; Sullivan et al., 1997). While bottom type is an important factor in benthic hydroid distribution (Calder, 1991), it has no obvious direct connection with distribution of planktonic hydroids. Instead, the physical processes of horizontal advection and water stratification appear to be the main forces determining planktonic *Clytia* spp. distribution on Georges Bank. Once introduced to the crest area, rapid growth and development may occur because of the food-rich and turbulent planktonic environment of that region (Bollens et al., 2001a).

In summary, the historical data from 1939 to 1941 show that hydroids were present in relatively shallow (< 100 m) water in the late spring-early summer following a "stormy" spring (1940), but absent the following year after a calmer spring. Our field sampling in 1995 showed planktonic hydroids to be most abundant on the central crest, but abundances of benthic colonies were highest at the northeast peak. Our results suggest that planktonic hydroids found on the crest are not entering the Georges Bank circulation from off-bank; instead, the benthic source population for the planktonic hydroids likely lies along the northeast peak area of the Bank itself. We hypothesize that the circulation system of Georges Bank traps these suspended hydroids in the central area of the Bank. Given that hydroids can be found in high abundance during at least some years, and are apparently both competitors with and predators on larval gadoids (Madin et al., 1996, 1997), further studies of potential sources (e.g. the northeast peak), mechanisms of retention and loss, and trophic-dynamics of hydroids (e.g. Avent et al., 2001), are warranted. Finally, we recommend that coupled biological/physical models be used to integrate all of these processes and to look at their relative importance in the ecology of planktonic hydroids on Georges Bank.

Acknowledgements

We would like to thank Dale Calder for taxonomic identifications, Susan Drapeau, Paul Donaldson and the crews of the R/V *Endeavor* and R/V *Albatross* for assistance in the field, Sean Avent and Harmon Brown for assistance with graphics, and Cabell Davis for advice and encouragement on analysis of historical data. This research was supported through National Oceanic and Atmospheric Administration grant NA66GP0356 (to L. Madin and S.M. Bollens) and grant NA66GP0357 (to B. Sullivan and G. Klein-MacPhee), NSF grants OCE9617209 (to S.M. Bollens) and OCE9632738 (to A. Solow and S.M. Bollens), the National Underwater Research Program Grant # UCAP-95-04 (to L. Madin, S.M. Bollens, B. Sullivan and G. Klein-MacPhee), an Office of Naval Research Young Investigator Award (N00014-94-1-0495) to S.M. Bollens, and a Woods Hole Oceanographic Institution Summer Student Fellowship to S. Concelman. This is contribution #154 of the US GLOBEC/Georges Bank Program and no. 10 323 of the Woods Hole Oceanographic Institution.

References

Auster, P.J., Stewart, L.L., Sprunk, H., 1989. Scientific imaging with ROVs: tools and techniques. MTS Journal 23, 16–20.

Avent, S., Bollens, S.M., Butler, M., Horgan, E., Rountree, R., 2001. Planktonic hydroids on Georges Bank: ingestion and selection by predatory fishes. Deep-Sea Research II 48, 673–684.

Bainbridge, V., McKay, B.J., 1968. The feeding of cod and redfish larvae. Special Publications in the Commn. NW Atlantic Fish 7, 187–217.

Bigelow, H.B., 1927. Physical oceanography of the Gulf of Maine. Bulletin of the U.S. Bureau of Fisheries 40, 1–567.

Boero, F., 1984. The ecology of marine hydroids and effects of environmental factors: a review. P.S.Z.N.I. Marine Ecology 5, 93–118.

Bollens, S.M., Horgan, E., Concelman, S., Madin, L.P., Gallager, S.M., Butler, M., 2001a. Planktonic hydroids on Georges Bank: effects of mixing and food supply on feeding and growth. Deep-Sea Research II 48, 659–672.

Bollens, S.M., Landsteiner, M.C., Davis, C.S., Solow, A.R., 2001b. Three-dimensional distribution and abundance of zooplankton on Georges Bank, 1939–1941, with comments on the effects of storm events. Deep-Sea Research II, submitted for publication.

Butman, B., Loder, J.W., Beardsley, R.C., 1987. The seasonal mean circulation: observation and theory. In: Backus, R.H. (Ed.), Georges Bank. MIT Press, Cambridge, MA, pp. 125–138.

Calder, D.R., 1991. Associations between hydroid species assemblages and substrate types in the mangal at Twin Cays, Belize. Canadian Journal of Zoology 69, 2067–2074.

Clarke, G.L., Bumpus, D.F., 1940. The plankton sampler — an instrument for quantitative plankton investigations. Limnology Society of America Special Publication 5, 1–8.

Clarke, G.L., Pierce, E.L., Bumpus, D.F., 1943. The distribution and reproduction of *Sagitta elegans* on Georges Bank in relation to hydrographical conditions. Biological Bulletin 85, 201–226.

Cornelius, P.F.S., 1982. Hydroids and medusae of the family Campanulariidae recorded from the eastern North Atlantic, with a world synopsis of genera. Bulletin of the British Museum of Natural History (Zoology) 42, 37–148.

Fraser, C.M., 1915. Pelagic hydroids in Exploration of the coast water between Nova Scotia and Chesapeake Bay, July and August, 1913, by the U.S. Fisheries schooner *Grampus*. Oceanography and Plankton. Bulletin of the Museum of Comparative Zoology 59, 306–314.

Fraser, C.M., 1944. Hydroids of the Atlantic Coast of North America. University of Toronto Press, Toronto, pp. 451.

Klein-MacPhee, G., Sullivan, B.K., Van Keuren, D., Horgan, E., Klos, E., 1997. Mortality of larval cod related to predation by the hydropid *Clytia gracilis* on Georges Bank. ICES 1997 Annual Science Conference, ICES CM 1997/T:03.

Last, J.M., 1978. The food of three species of gadoid larvae in the eastern English Channel and southern North Sea. Marine Biology 48, 377–386.

Limeburner, R., Beardsley, R.C., 1996. Near-surface recirculation over Georges Bank. Deep-Sea Research II 43, 1547–1574.

Madin, L.P., Bollens, S.M., Horgan, E., Butler, M., Runge, J., Sullivan, B.K., Klein-MacPhee, G., Durbin, E., Durbin, A., Van Keuren, D., Plourde, S., Bucklin, A., Clarke, M., 1996. Voracious planktonic hydroids: unexpected predatory impact on a coastal marine ecosystem. Deep-Sea Research II 43, 1823–1829.

Madin L.P., Horgan, E., Sullivan, B.K., Klein-MacPhee, G., Bollens, S.M., Butler, M., 1997. Estimating the impact of invertebrate predation on target species of copepods on Georges Bank. ICES 1997 Annual Science Conference, ICES CM 1997/T:16.

Manning, J., 1999. Anomalous Wind Stress. WWW site. HTTP://www.wh.whoi.edu/ ~ jmanning/wind/allbwsa.gif.

Meeren, T., Naess, T., 1993. How does cod (*Gadus morhua*) cope with variability in feeding conditions during early larval stages? Marine Biology 116, 637–647.

Michalopoulos, C., Auster, P.J., Malatesta, R.J., 1993. A comparison of transect and species-time counts for assessing faunal abundance from video surveys. MTS Journal 26, 27–31.

Norrbin, M.F., Davis, C.S., Gallagher, S.M., 1996. Differences in fine-scale structure and composition of zooplankton between mixed and stratified regions of Georges Bank. Deep-Sea Research II 43, 1905–1924.

Sullivan, B., Williams, J., Van Keuren, D., 1997. Abundance and distribution of planktonic hydroids with respect to larval fish and hydrographic features on Georges Bank. ICES 1997 Annual Science Conference, ICES CM 1997/T:02.

U. S. GLOBEC, 1992. Northwest Atlantic Implementation Plan. U.S. Global Ocean Ecosystems Dynamics, Report No. 6, University of California, Davis.

Valentine, P.C., Strom, E.W., Lough, R.G., Brown, C.L., 1993. Maps showing the sedimentary environment of eastern Georges Bank. U.S. Geological Service. MAP I-2279-B.

Werner, F.E., Page, F.H., Lynch, D.R., Loder, J.W., Lough, R.G., Perry, R.I., Greenberg, D.A., Sinclair, M.M., 1993. Influences of mean advection and simple behavior on the distribution of cod and haddock early life stages on Georges Bank. Fisheries Oceanography 2, 43–64.

Wiebe, P.H., Morton, A.W., Bradley, A.M., Backus, R.H., Craddock, R.J., Barber, V., Cowles, T.J., Flierl, G.R., 1985. New developments in the MOCNESS, an apparatus for sampling zooplankton and micronekton. Marine Biology 87, 313–323.