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Effects of warm water intrusions on populations of macrozooplankton on Georges Bank, Northwest Atlantic

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Abstract

As part of the Georges Bank/North West Atlantic GLOBEC (Global Ocean Ecosystems Dynamics) Program, macrozooplankton and microneuston were collected on 30 Broad Scale Survey Cruises between January–June, 1995–1999, using a 10 m² MOCNESS (3 mm mesh). The objective of this study is to examine the effects of warm water intrusions on populations of macrozooplankton, namely *Salpa* spp., *Phronima* spp., *Neomysis americana*, and *Crangon septemspinosa*, on Georges Bank. *Salpa* spp. and *Phronima* spp. showed a large degree of horizontal co-occurrence, being found predominantly in Upper Slope/Gulf Stream Water and Georges Bank/Gulf of Maine Water. Abundances of these taxa showed striking interannual variability, and were only abundant on the southern flank and in the Northeast Channel in late spring/early summer of 1995 and 1999, periods during which AVHRR imagery and hydrographic data showed the presence of warm water intrusions. These intrusions seemed to have little effect on the distribution of other macrozooplankton (e.g., *N. americana* and *C. septemspinosa*). Warm water intrusions can directly affect *Salpa* spp. and *Phronima* spp. populations by advecting them onto Georges Bank, although other, more resident populations, especially those inside the 100 m isobath, seem to be little affected by such intrusions.

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1. Introduction

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Georges Bank is a submarine bank that lies between Cape Cod, Massachusetts and Cape Sable, Nova Scotia in the Northwest Atlantic. It is one of the most productive seamount ecosystems in the world (Cohen and Grosslein, 1987) and the

site of important commercial fisheries (Bigelow, 1926; Backus and Bourne, 1987). The Global Ocean Ecosystems Dynamics (GLOBEC) Georges Bank Program is charged with investigating the physical and biological oceanographic processes that affect four target species: the copepods *Calanus finmarchicus* and *Pseudocalanus* spp. and the larval stages of cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) (GLOBEC, 1992). As part of the GLOBEC Broad Scale Survey sampling, the macrozooplankton and micronekton of Georges Bank were sampled in January–June 1995–1999. Although designed to target juvenile fishes and predators of the GLOBEC target species, these collections included many thousands of specimens of the pelagic tunicate *Salpa* spp., the hyperid amphipod *Phronima* spp., the decapod shrimp *Crangon septemspinosa*, and the mysid shrimp *Neomysis americana*, which will be the focus of this paper.

Intrusion of slope water onto the southern flank of the bank can be caused by Gulf Stream meander crests that pinch off to form warm core rings (Ryan et al., 2001). Cornillon et al. (1994) estimated that approximately 8 warm core rings are seen in the Northwest Atlantic each year, although few of these rings move beyond the 200 m isobath onto the southern flank of Georges Bank. These intrusions can have important biological consequences, including impacts on phytoplankton (Flierl and Davis, 1993), copepods (Ashjian et al., 2001) and larval fishes (Wroblewski and Cheney, 1984; Flierl and Wroblewski, 1985). However, the effects of these slope water intrusions on the ecology of macrozooplankton and micronekton of Georges Bank have not previously been reported.

The objective of this study is to examine the effects of warm water intrusions on the distribution and abundance of populations of *Salpa* spp., *Phronima* spp., *C. septemspinosa*, and *N. americana*, on Georges Bank. These 4 taxa were chosen because of their contrasting patterns of occurrence on the bank. *Salpa* spp. and *Phronima* spp. are only rarely present, but can occasionally achieve very high abundances, whereas *C. septemspinosa* and *N. americana* are far more common on the bank, especially inside the 100 m isobath (Whitely, 1948).

2. Study site

Georges Bank, defined by the 200 m isobath (Fig. 1), is approximately 150 km wide and 280 km long, and shoals to as little as 30 m. The dominant circulation pattern is one of a permanent anticyclonic gyre around the bank (Limeburner and Beardsley, 1996). Butman and Beardsley (1987) divide the bank region into four physical regions based on water properties and the spatial structure of the currents—the northern flank (50–200 m); the bank crest (≤ 60 m); the shallower southern flank (60–150 m); and the deeper southern flank (> 150 m) on the northern side of the shelf-water/slope-water front, which can be strongly influenced by warm-core rings. There is a relatively constant flow of upper Slope Water in the Northeastern Channel below 100 m (Ramp et al., 1985).

3. Methods

The Georges Bank region was sampled monthly during the period of February–July, 1995 and January–June, 1996–1999 as a part of the GLOBEC Georges Bank Broad Scale Surveys. A cruise track consisting of ca. 40 sampling stations was occupied each month (Fig. 1; <http://globec.whoi.edu>). Sampling of macrozooplankton and micronekton was undertaken at as many stations as possible on each cruise, allowing for problems with weather and equipment (Table 1).

A 10 m² Multiple Opening/Closing Net and Environmental Sampling System (MOC10) (Wiebe et al., 1985b) was used for sampling. The MOC10 consists of a 10 m² frame and five 3 mm mesh nets. The MOC10 allows for sampling in discrete depth strata by opening and closing the nets remotely from the ship. The MOC10 was towed in a double oblique manner (1 net down, ≤ 4 nets up) with a goal of sampling 5000 m³ of water per net. The nets were opened and closed at predetermined depths (nominally, 100, 40, 15, and 0 m) during the ascent of the tow. The MOC10 was also equipped with Conductivity, Temperature, and Depth (CTD) sensors. The overall survey design (e.g. stations, depths and seasons to be sampled) was intended to target juvenile fishes and invertebrate

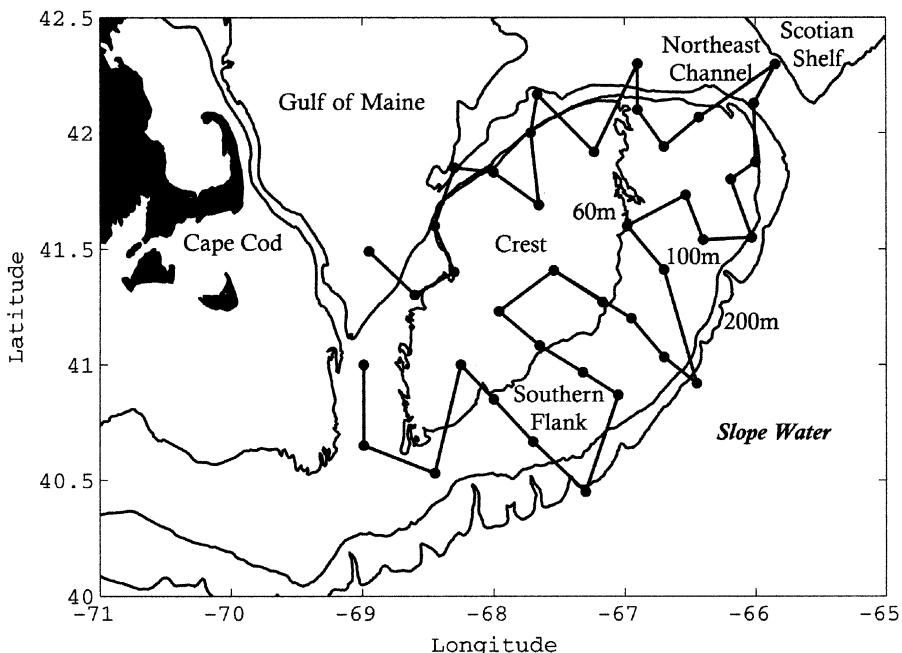


Fig. 1. Cruise Track and station locations (filled dots) for the Georges Bank GLOBEC Broad Scale Surveys (1995–1999), including bathymetry (60, 100, 200 m) and regions of note.

predators (GLOBEC, 1992), although, as will be seen below, many other macrozooplankton were also commonly collected.

Once on board, the nets were rinsed to remove all animals, and the contents of the cod ends were placed in jars and preserved in 5–10% formalin. The samples were analyzed in the laboratory and all specimens were identified to the lowest practicable taxon using taxonomic descriptions provided in Tattersall and Tattersall (1951), Gosner (1971), Bowman and Gruner (1973), and Williams (1984). Individuals within the genus *Salpa* were not identified to the species level nor as solitary or aggregate generation. Both *Salpa aspera* and *Salpa fusiformis* were found in the samples, but were grouped under the single category of *Salpa* spp. for the data set as a whole. Individuals within the genus *Phronima* were not identified to species. Shih (1969) stated that the geographic distributions of *Phronima sedentaria* and *Phronima atlantica* include the northwest Atlantic, and we therefore assume (but can not be certain) that both species were present in our collections. *C. septemspinosa*

and *N. americana* were identified to species. All individuals within each taxonomic group were enumerated and the first 50 individuals within each group were measured in length to the nearest millimeter. Damaged animals were enumerated, but not measured. After the samples were analyzed they were represerved in 5–10% formalin.

The presence of each species was plotted in Temperature–Salinity (T–S) space, using the average T–S values from each depth stratum sampled. The T–S space of three different water masses, Scotian Shelf Water (SSW), Georges Bank/Gulf of Maine Water (GBW) and Upper Slope/Gulf Stream Water (USW), were derived from Flagg (1987).

Sea surface temperatures (SST), derived from the National Oceanic and Atmospheric Administration Advanced Very High Resolution Radiometer (NOAA AVHRR) data, were analyzed using MATLAB® to estimate the percent cover of slope water within the 200 m isobath of the Georges Bank region. Because each MOC10 survey occurred over a period of about two weeks,

Table 1

Dates of GLOBEC Broad-Scale Survey Cruises with number of stations sampled with the MOC10

Dates of Cruise	Number of stations sampled
February 10–20, 1995	5
March 13–24, 1995	3
April 11–22, 1995	6
May 9–18, 1995	16
June 5–15, 1995	23
July 10–20, 1995	27
January 10–22, 1996	2
February 13–25, 1996	9
March 11–22, 1996	12
April 8–20, 1996	5
May 6–17, 1996	12
June 3–13, 1996	38
January 13–20, 1997	8
February 11–23, 1997	8
March 16–28, 1997	13
April 22–May 2, 1997	14
May 19–27, 1997	20
June 18–28, 1997	32
January 7–19, 1998	16
February 7–17, 1998	13
March 15–27, 1998	13
April 15–27, 1998	20
May 11–23, 1998	21
June 16–26, 1998	32
January 11–24, 1999	15
February 11–23, 1999	11
March 10–23, 1999	1
April 16–28, 1999	19
May 19–27, 1999	19
June 14–24, 1999	32

we selected AVHRR data from three consecutive dates in the middle of each cruise to provide a representative estimate of the amount of slope water cover. A warmest pixel composite was made from all available data for these three days from each cruise in order to improve data retrieval due to clouds or fog. Georges Bank was defined by the 200 m isobath, except for the northwest section where the 150 m isobath was used to bisect the Great South Channel. Percent cover of slope water was determined within that area by calculating the percent of data (pixels) that represented sea-surface temperatures of 16 °C (slope water lower threshold) or higher.

The software package Minitab® 12 was used for all statistical analyses. Mann-Whitney U-tests (with Bonferroni Adjustment for multiple comparisons) were used to compare interannual abundances of each of the four species, and chi-square tests were used to test for differences in the presence/absence of each of the species between different water masses. Finally, the abundances of each species were tested for correlation (Pearson product moment) with the percent cover of slope water on the bank.

4. Results

From 1995–1999, thirty broad-scale cruises were undertaken at Georges Bank, and 465 tows were made with the MOC10, yielding 1388 discrete samples. Over 1.3 million individuals were identified and enumerated, representing 426 distinct taxa. A complete discussion and analysis of this larger dataset will be reported elsewhere. In this paper we report only on *N. americana*, *Salpa* spp., *C. septemspinosa*, and *Phronima* spp., the 2nd, 3rd, 8th and 22nd most abundant taxa, respectively, which collectively comprised 291,110 specimens, or about 21% of the total number of organisms sampled. The mean total water column abundances, standard errors, and maximum total water column abundances are shown in Table 2.

The seasonal and interannual abundances of each of these species can be seen in Fig. 2. While *Salpa* spp. and *Phronima* spp. are virtually absent in 1996, 1997, and 1998, they occur in high numbers in both 1995 and 1999. Mann-Whitney U-tests (with Bonferroni Adjustment for multiple comparisons) were performed to compare the interannual abundances of each of the four taxa (Table 3). For both *Salpa* spp. and *Phronima* spp. the abundances in 1995 and 1999 are significantly different from those in 1996, 1997, and 1998. For both *N. americana* and *C. septemspinosa*, however, there were fewer instances of statistically significant interannual differences in abundance, and no clear, consistent pattern between years (Table 3).

The broad scale horizontal distributions of *Salpa* spp. and *Phronima* spp. were similar. Both species begin to show up in April 1995 in the

Table 2

Mean total water column (TWC) abundances (#/1000 m³), standard error of the mean, and the maximum TWC abundances (with corresponding month) for *Salpa* spp., *Phronima* spp., *C. septemspinosa*, and *N. americana*

Species	Mean TWC abundance	Standard error	Maximum abundance found	Month of maximum abundance
<i>Salpa</i> spp.	21.61	14.08	6406.18	June 1999
<i>Phronima</i> spp.	0.87	0.22	56.99	May 1995
<i>C. septemspinosa</i>	5.69	1.15	313.98	May 1998
<i>N. americana</i>	93.83	67.15	30547.97	May 1996

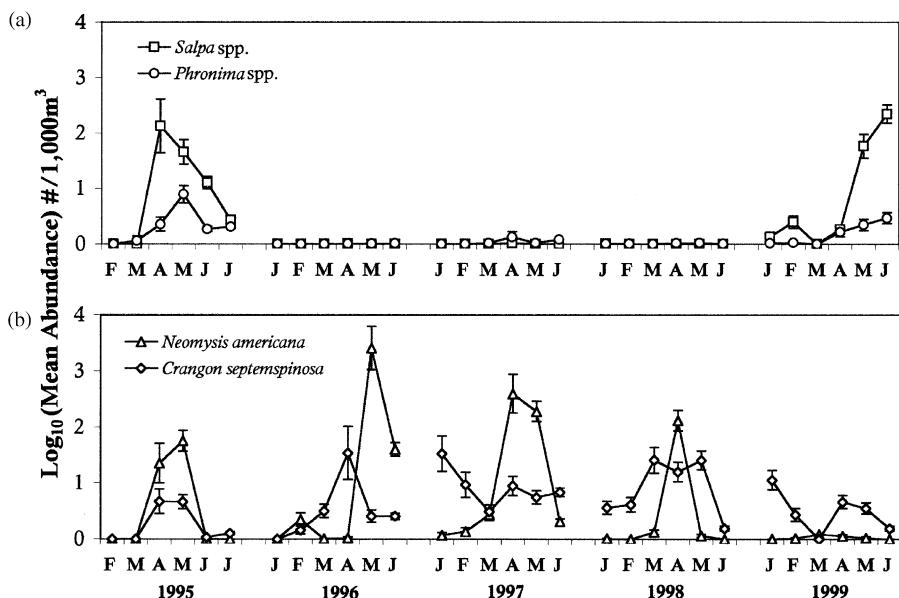


Fig. 2. (a) Log-transformed abundance [((#/1000 m³) + 1) mean ± SE] of *Salpa* spp. and *Phronima* spp., (b) *C. septemspinosa*, and *N. americana* on Georges Bank (1995–1999).

Northeast Channel (data not shown), with the abundance of salps being much higher than that of the phronimids. By May the majority of organisms were found on the Southern Flank, and then slightly off-bank in June (Fig. 3a). In April 1999 *Phronima* spp. began to appear in high numbers in the Northeast Channel, but there was a much lower number of salps at that time. The numbers of both taxa increased in the Northeast Channel in May along with high abundances on the Southern Flank, and persisted on the Southern Flank in June 1999 (Fig. 3b). Broad scale horizontal distributions for 1996, 1997, and 1998 are not shown due to the virtual absence of these

organisms in those years. In contrast, *N. americana* and *C. septemspinosa* were always concentrated inside the 100 m isobath, and often inside the 60 m isobath. This broadscale distribution pattern was similar during all years and seasons, although only May and June of 1995 and April, May and June of 1999 are shown (Fig. 3c and d), for ease of comparison with *Salpa* spp. and *Phronima* spp. distributions (Fig. 3a and b).

Intrusions of warm water into the Georges Bank region can be seen in AVHRR imagery (Fig. 4). Images from the middle of May, 1995–1999, show the interannual variation in sea-surface temperatures on Georges Bank. In 1995 and 1999 warm

Table 3
Results of the Mann–Whitney U-tests with Bonferroni Adjustment on the interannual differences in abundances

<i>Salpa</i> spp.				<i>Phronima</i> spp.			
1995	1996	1997	1998	1995	1996	1997	1998
1996 **				1996 **			
1997 **				1997 **			
1998 **				1998 **			
1999 ** ** **				1999 ** ** **			

<i>C. septemspinosa</i>				<i>N. americana</i>			
1995	1996	1997	1998	1995	1996	1997	1998
1996				1996			
1997 **				1997 *			
1998 *				1998		*	
1999 *				1999 *		**	

Significance levels, * $P \leq 0.05$, ** $P \leq 0.01$.

water ($\geq 16^{\circ}\text{C}$) can be seen intruding inside the 200 m isobath on the southern flank of Georges Bank, while no such intrusions are seen in 1996, 1997 or 1998. The abundances of *Salpa* spp., *Phronima* spp., *N. americana* and *C. septemspinosa* inside the 200 m isobath were compared to the percent of warm water within the 200 m isobath of Georges Bank (Fig. 5). Although we sampled on 30 dates, only 19 and 20 sampling dates yielded non-zero data for *Salpa* spp. and *Phronima* spp., respectively. Using only the non-zero data, the abundance of *Salpa* spp. is significantly correlated to the percent cover of warm water on the bank ($r = 0.787$, $P < 0.001$). When we consider all 20 non-zero data points for the abundance of *Phronima* spp., there is a significant correlation with percent warm water cover ($r = 0.621$, $P < 0.001$). In contrast to *Salpa* spp. and *Phronima* spp., there was no significant relationship between percent cover of warm water on the bank and abundance of *N. americana* ($r = -0.057$, $P = 0.77$) or *C. septemspinosa* ($r = -0.167$, $P = 0.38$) (Fig. 5).

This interannual variability in slope water intrusions can also be seen in the MOC10 CTD data plotted from Standard Station 3 (40.53 N Lat, -68.99° W Long) on the southern flank of Georges Bank for May of each year, 1995–1999 (Fig. 6).

The temperature profiles show two warm water intrusions, one in 1995 and another in 1999. The 1995 profile shows a deep warm water intrusion, while the 1999 profile shows an intrusion that can be seen throughout the entire water column.

The presence of all four taxa was plotted in T–S space, including the delineation of three different water masses (Fig. 7). Both *Salpa* spp. and *Phronima* spp. showed highly statistically significant different patterns of presence/absence between water masses (*Phronima* spp.: $X^2 = 107.010$, $P < 0.001$; *Salpa* spp.: $X^2 = 60.946$, $P < 0.001$), being found predominantly in the Upper Slope/Gulf Stream Water and Georges Bank/Gulf of Maine Water. In contrast, *N. americana* and *C. septemspinosa* were almost exclusively associated with Georges Bank/Gulf of Maine water (*N. americana*: $X^2 = 14.154$, $P < 0.01$; *C. septemspinosa*: $X^2 = 8.334$, $P < 0.05$).

5. Discussion

Advection of water and biota on and off Georges Bank can be caused by entrainment/detrainment events along the periphery of rotating warm-core rings as they pass the bank, as well as by slope water crossovers onto the bank. The effects of these types of events on phytoplankton and larval fish have been previously studied. For instance, Flierl and Davis (1993) showed that these events can cause upwelling that significantly impacts phytoplankton populations. Flierl and Wroblewski (1985) and Wroblewski and Cheney (1984) showed that entrainment events associated with warm core rings can advect larval fish off the bank and advect warm water fish onto the bank. The question then is how do these events affect the macrozooplankton and microneuston of the Georges Bank region? Here a brief review of the life histories of our four taxa of interest is relevant.

Salps can be an abundant and important component of pelagic ecosystems (Andersen, 1998). As a result of their asexual reproduction, their population growth rate is one of the fastest among multicellular animals (Andersen and Nival, 1986; Madin and Deibel, 1988), which in turn can lead to rapid blooms (e.g. Menard et al., 1994).

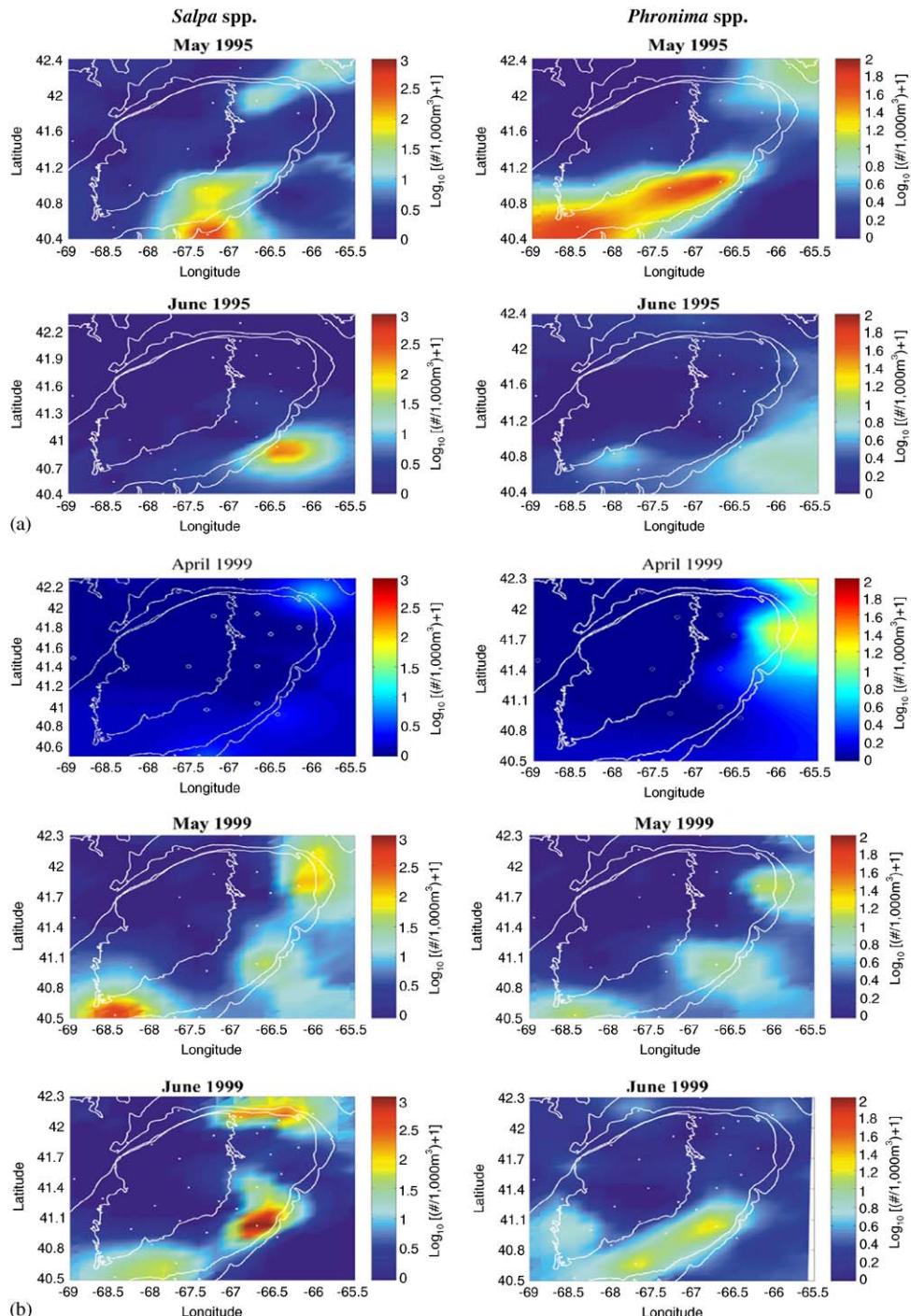


Fig. 3. Broad scale horizontal distributions of *Salpa* spp. and *Phronima* spp., *C. septimspinosa*, and *N. americana* using log-transformed water column total abundances [$\#/\text{1000 m}^3 + 1$] for May and June 1995 and April, May and June of 1999. Distributions of *Salpa* spp. and *Phronima* spp. are shown for (a) May and June of 1995 and (b) April, May and June of 1999. Distributions of *C. septimspinosa* and *N. americana* are, also, shown for (c) May and June of 1995 and (d) April, May and June of 1999. Each plot represents data for a single broad scale survey, with vertically stratified samples summed to yield water column total abundance at a given station. Note the different scales for *Salpa* spp. and *Phronima* spp.

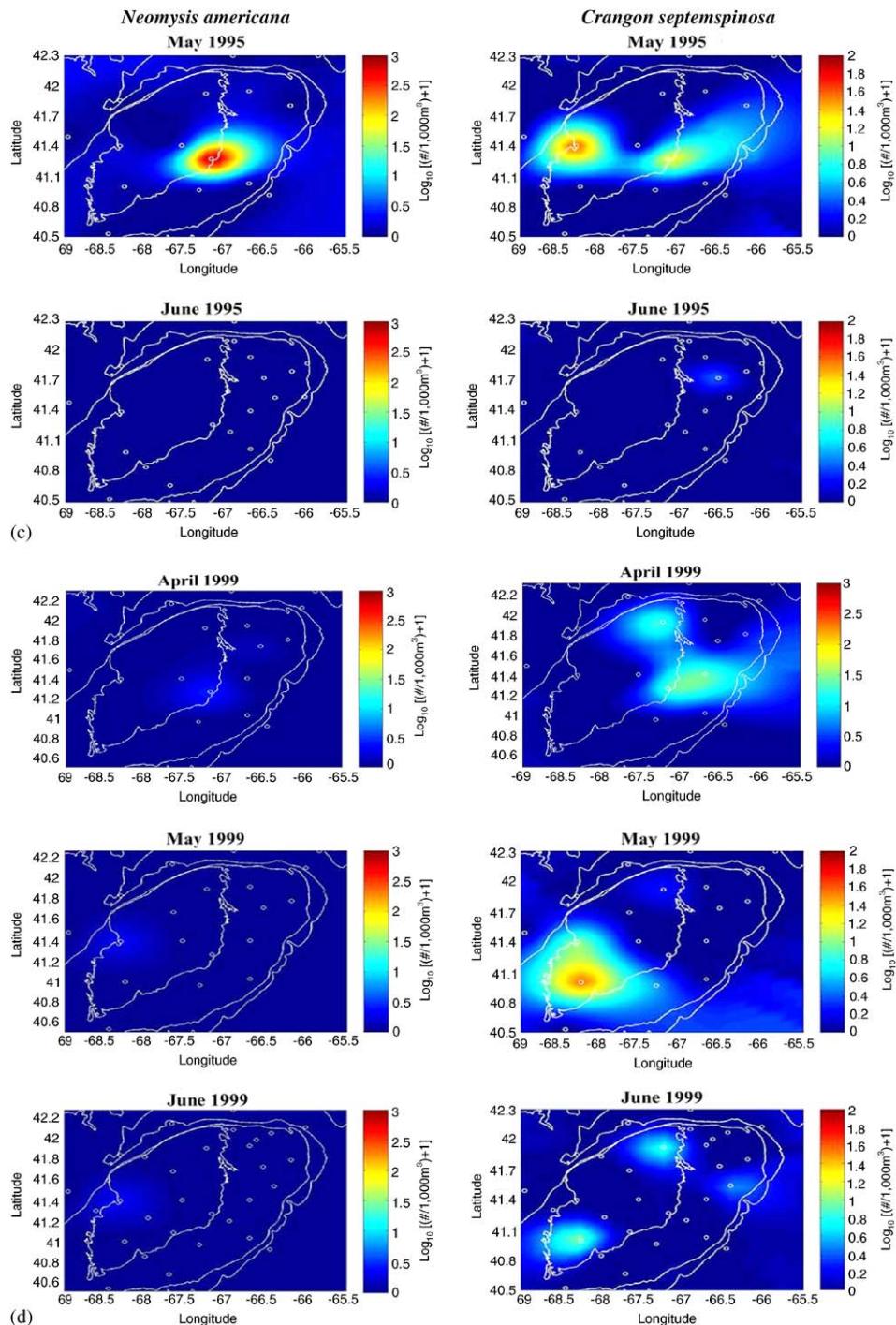


Fig. 3. (Continued)

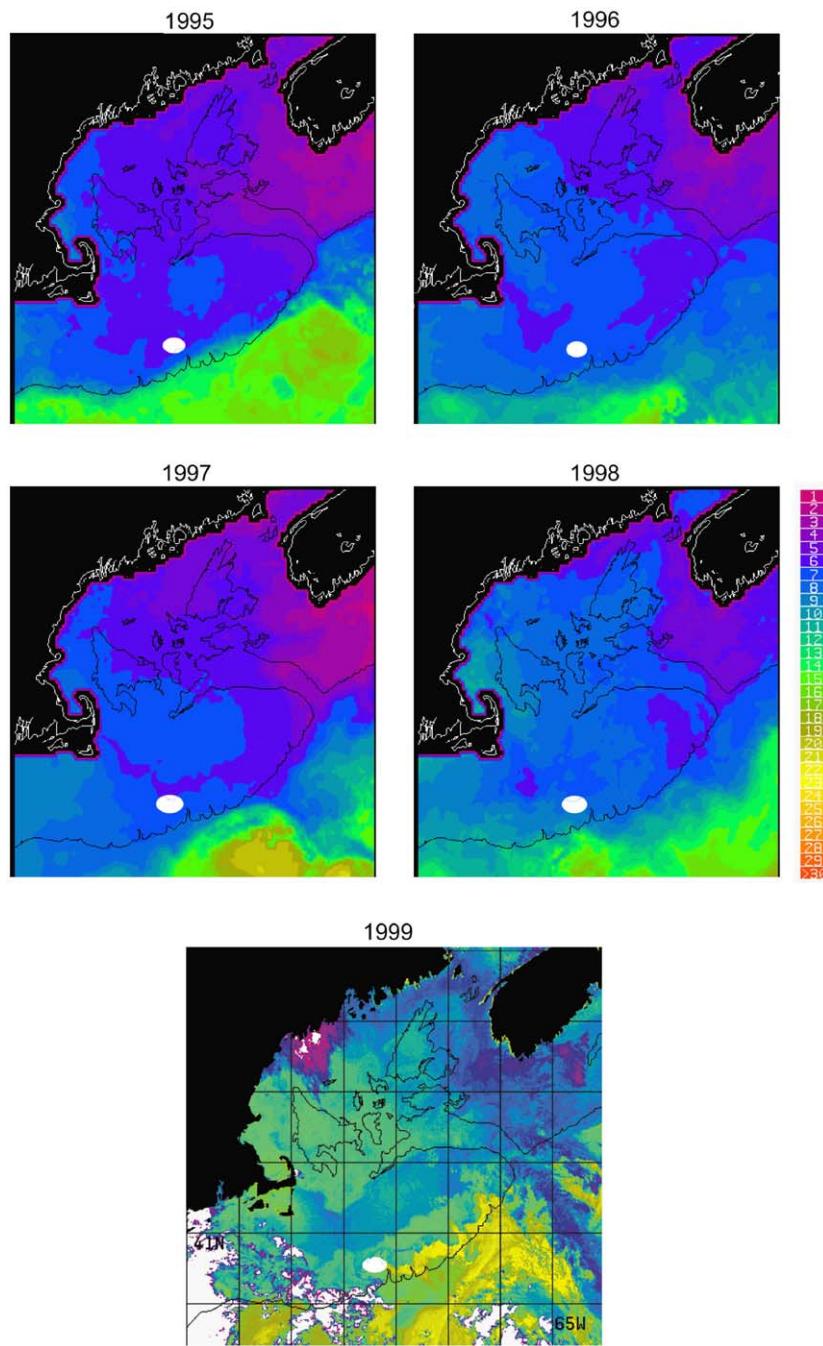


Fig. 4. Satellite-derived sea surface temperature images from May 1995–1999. The images for 1995–1998 are 3-day optimally interpolated images. The 1999 image is not optimally interpolated, as that image was not yet available. The white ovals point out the location of Standard Station 3, where the temperature profiles used in Fig. 6 were obtained.

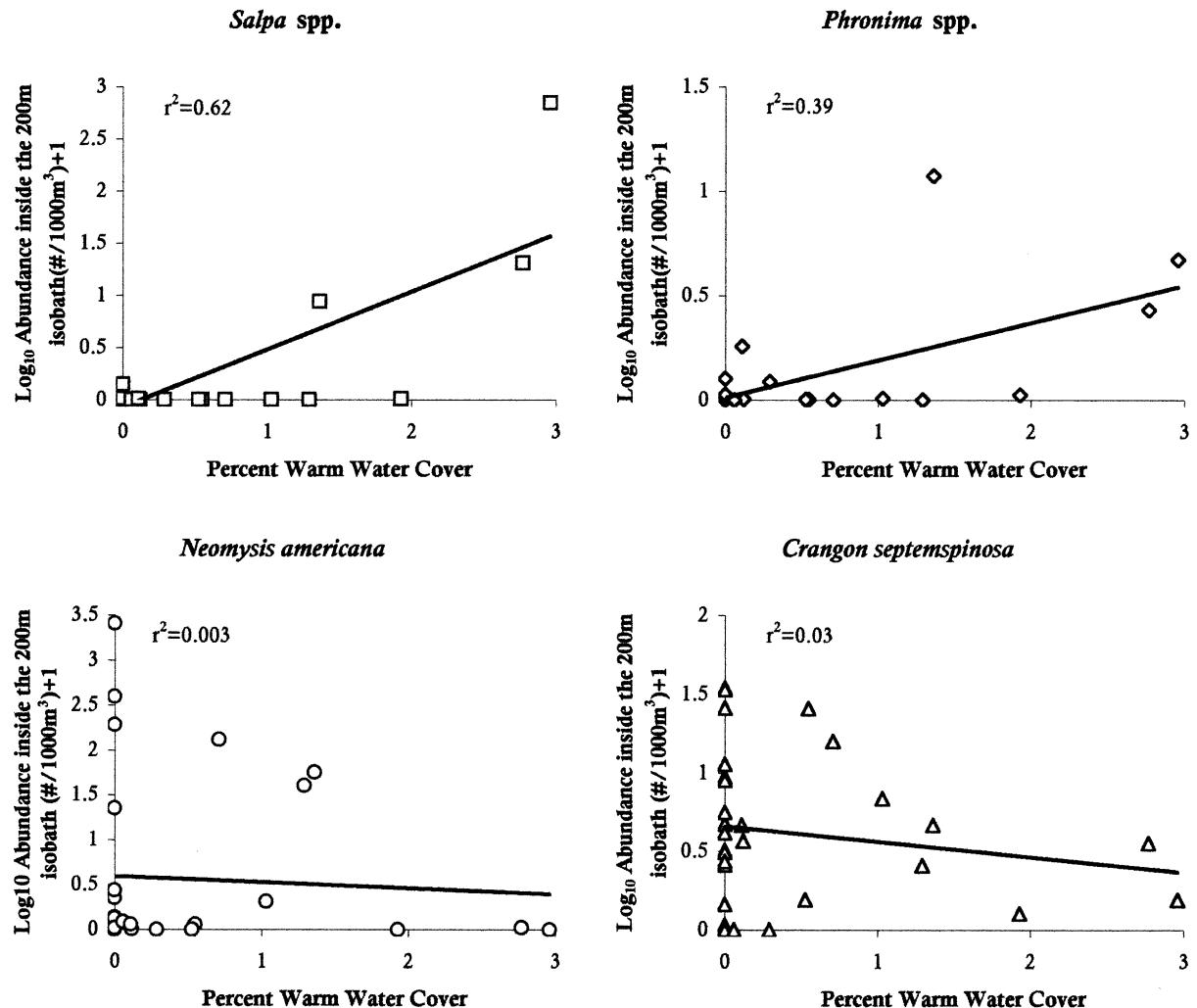


Fig. 5. Scatter plot of the log transformed abundance data for *Salpa* spp. and *Phronima* spp. inside the 200 m isobath versus the percent cover of warm water within the 200 m isobath of the Georges Bank region, 1995–1999. *P* values: *Salpa* spp. <0.01; *Phronima* spp. <0.01; *N. americana*=0.77; *C. septemspinosa*=0.38.

Phronima is a circumglobal genus that inhabits the tropical water of the world's oceans. Although Vinogradov et al. (1996) state that *Phronima* only very rarely cross the limits of the subtropical convergences, Madin (pers. comm.) states that *P. sedentaria* and *P. atlantica* are common in the slope water south of Georges Bank. *Phronima* have an unusual and interesting symbiotic relationship with *Salpa*. Both male and female *Phronima* make a “barrel” out of the body of a salp by eating away the internal organs and

leaving a barrel-shaped portion of the non-cellular salp test. Both sexes occupy these barrels, although it is more common for females, which keep their brood of young within the barrel until they are developed enough to swim and survive independently (Davenport, 1994). This barrel-making behavior appears to be an obligate relationship for *Phronima*, although salps are not the sole source of the barrels. *Phronima* also prey upon pyrosomes and siphonophores (Laval, 1978). Thus *Salpa* spp. and *Phronima* spp. would be expected

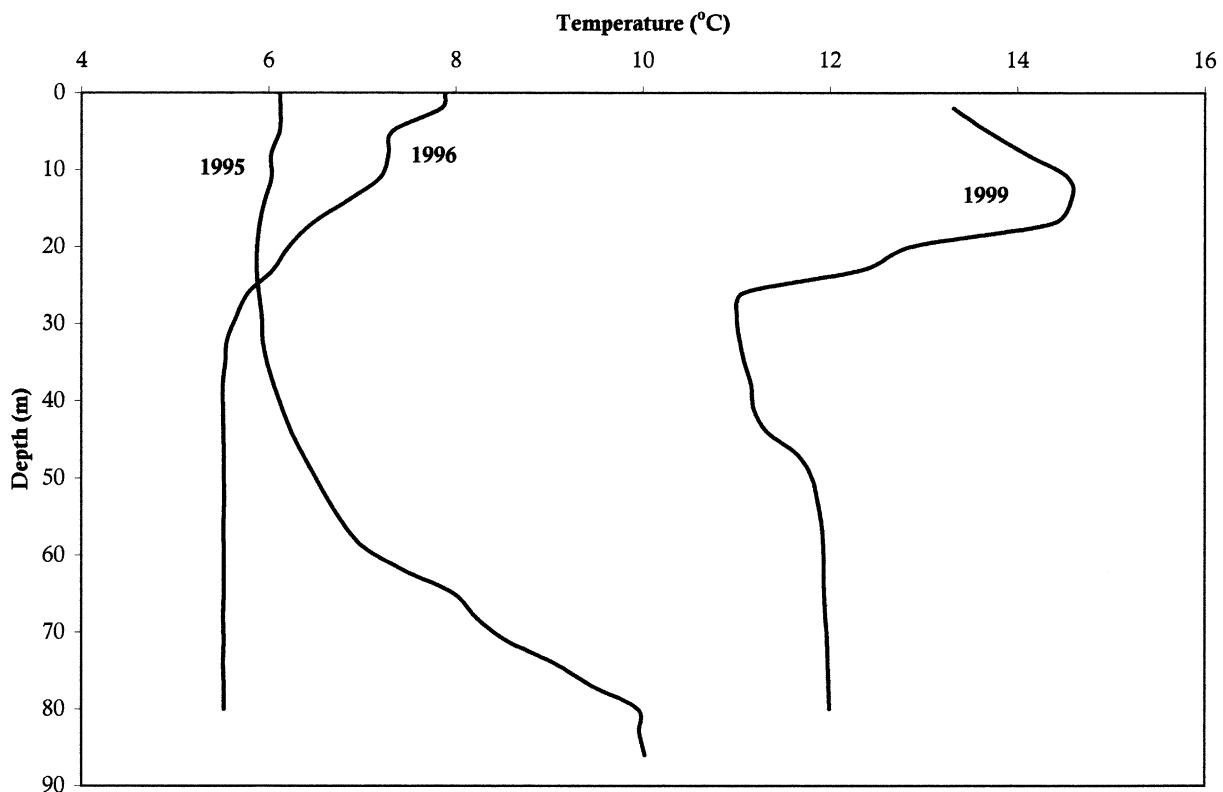


Fig. 6. Temperature profiles from Standard Station 3 (40.53 N Lat, -68.99 W Long) on the southern flank of Georges Bank from May 1995, 1996 (representative of a non-intrusion year) and 1999. The lines are 3 m averaged MOC10 CTD data. The profiles show the warm water intrusions of 1995 and 1999, with the 1995 intrusion being deeper and the 1999 intrusion being seen throughout the entire water column.

to co-occur, especially in the slope waters south of Georges Bank.

N. americana is the most common marine mysid in the shallow coastal waters of the Northwest Atlantic Ocean (Wigley and Burns, 1971; Williams et al., 1974; Hoffmeyer, 1990). In the Georges Bank region it is most commonly reported inside the 60 m isobath and was not found outside the 100 m isobath (Whitely, 1948). *N. americana* is a euryhaline species (Pezzack and Corey, 1979) and is found in water temperatures from 0 to >25 °C (Wigley and Burns, 1971). The decapod shrimp *C. septemspinosa* is common in estuaries in the Northwest Atlantic and is found from the Gulf of St. Lawrence to Florida (Haefner, 1969a). Adults leave the estuarine shallows when the water temperature drops below 20 °C and move to deeper water, but return when the water warms

(Corey, 1987; Modlin, 1980). *C. septemspinosa* are found in water temperatures ranging from 3–25 °C and are effective osmoregulators able to tolerate salinities up to 36 for males and 39 for females (Haefner, 1969a,b). Whitely (1948) reported an extended spring spawn of *C. septemspinosa* on Georges Bank, but rarely observed individuals outside the 100 m isobath.

During our sampling on Georges Bank the presence of *Salpa* spp. and *Phronima* spp. was a conspicuous biological correlate of the slope water intrusions in 1995 and 1999, and contrasted with their total absence in 1996–1998. It may also be contrasted with the presence of the two other macrozooplanktonic species, the mysid *N. americana* and the decapod shrimp *C. septemspinosa*. Both these species occurred typically within the 100 m isobath of Georges Bank, and although

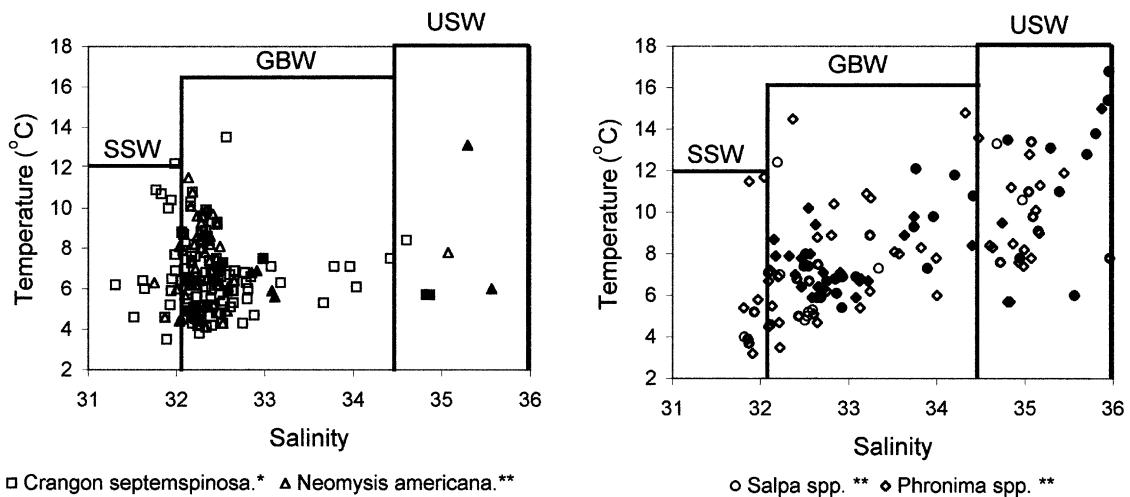


Fig. 7. Presence of *Salpa* spp. and *Phronima* spp., *C. septemspinosa* and *N. americana* in T-S space. The boxes indicate the three water masses—Scotian Shelf Water (SSW), Georges Bank/Gulf of Maine Water (GBW), and Upper Slope/Gulf Stream Water (USW) from Flagg (1987). Solid symbols indicate samples taken during May and June of 1995 and 1999. Differences between water masses in the presence/absence of each species were tested using chi-square distribution ** = $P \leq 0.01$, * = $P \leq 0.05$.

there were interannual variations in their abundances, there was no correlation with warm water intrusions (Fig. 5). More generally though, warm core rings are known to contain distinct assemblages of macrozooplankton and microneuston that are transported along with the water mass (Wiebe et al., 1985a; Young, 1989).

The distribution of *Salpa* spp. and *Phronima* spp. within T-S space showed significant differences between the three defined water regimes (Fig. 7). The broad distribution of the two taxa across the different water regimes was somewhat surprising, as we expected that these taxa would be found predominantly in the Upper Slope/Gulf Stream Water (USW). They were found almost as often in Georges Bank/Gulf of Maine Water (GBW) as in USW, but seldom in the Scotian Shelf Water (SSW). Their presence in GBW can be seen as an indication of the extent of mixing of these species during the warm water intrusion events. In fact, 51.6 and 49.4% of the occurrences of *Salpa* spp. and *Phronima* spp., respectively, in GBW occurred in May or June of 1995 or 1999, periods during which warm core rings occurred and these organisms were presumably mixed from USW to GBW. That is, if organisms move between two different water masses that are moving in different direc-

tions or at different speeds, this would increase their dispersion. In this way, vertical migration of *Phronima* between USW and GBW in May of 1995 (data not shown) may be an additional source of (active) mixing. Our finding that *N. americana* and *C. septemspinosa* were almost exclusively associated with Georges Bank/Gulf of Maine water is consistent with the more qualitative observations of Whitely (1948). Both *N. americana* and *C. septemspinosa* may use bottom-dwelling as a strategy to avoid displacement when flows become strong (Lawrie et al., 1999) or when temperatures increase (Jeffery and Revill, 2002), such as would be the case with warm water intrusions.

In addition to these direct effects on distribution and abundance, warm water intrusions may affect *Salpa* spp. and *Phronima* spp. in more indirect and subtle ways related to their association or symbiosis. Previous studies on the relationship between salps and phronimids have primarily focused only on the use of the salp barrel by the phronimid, with little else said about their co-occurrence or life history dynamics. Sardou et al. (1996) did point out that *P. sedentaria* showed a maximum abundance when *S. fusiformes* were also abundant, namely the spring, in the Mediterra-

nean Sea. Because salps are part of the phronimid diet and the barrels are used for protection and rearing of the offspring, the phronimids are reliant on the salps at certain points of their life cycle. It is important to note, however, that the relationship between these two species is not obligatory. Moreover, *Phronima* spp. do not need these barrels throughout their entire life cycle. Most of the phronimids in our samples were found without a barrel, although it is possible that they were dislodged from the barrels during sampling.

Looking at the horizontal broad-scale distribution of *Salpa* spp. and *Phronima* spp. on Georges Bank in May and June of 1995 and 1999, considerable overlap is evident, but there are also a few locations where salps are abundant and the phronimids are completely absent (Fig. 3). Because of the ability of salps to reproduce quickly and produce blooms (Andersen and Nival, 1986, Madin and Deibel, 1988, Menard et al., 1994), it is not surprising that their abundance is at times much higher than that of the *Phronima* spp.

In summary, we found striking seasonal and interannual variability in the abundance of *Salpa* spp. and *Phronima* spp. on Georges Bank. The broad scale distribution of *Salpa* spp. and *Phronima* spp. was positively linked to slope water intrusions, as determined by both satellite derived sea-surface temperature and subsurface hydrography. This was not the case for *N. americana* and *C. septemspinosa*, whose abundance on the bank was much less variable, especially inside the 60 m isobath, and seemed not to be affected to any significant degree by slope water intrusions. Thus warm water intrusions can directly affect some macrozooplankton (e.g., *Salpa* spp. and *Phronima* spp.) by advecting them onto the bank, and may also have indirect effects as a consequence of trophic interactions (e.g., salps have high filtration rates on phytoplankton (Madin, 1974) and can be a source of food for fishes such as cod and tuna (Silver, 1975)), although this was beyond the scope of the present study. Other taxa (e.g., *N. americana* and *C. septemspinosa*) that are resident on the bank seem little affected by warm water intrusions. The overall consequence of these intrusion events on the Georges Bank food web remains to be determined, but can be expected to vary between species.

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