

**Effects of Warm Water Intrusions on Populations of Macrozooplankton on
Georges Bank, Northwest Atlantic**

Harmon Brown^{1*}, Stephen M. Bollens^{1},
Laurence P. Madin² and Erich F. Horgan²**

¹Romberg Tiburon Center for Environmental Studies and Department of Biology, San
Francisco State University, 3152 Paradise Drive, Tiburon, CA, 94920, USA

²Biology Department, Woods Hole Oceanographic Institution, Woods Hole, MA
02543, USA

*Corresponding author: Current address: Coastal Fisheries Institute, Department of
Oceanography and Coastal Sciences, Louisiana State University, Baton Rouge, LA,
70803, USA

** Current address: School of Biological Sciences, Washington State University Vancouver,
4204 NE Salmon Creek Avenue, Vancouver, WA, 98686, USA

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Abstract

As part of the Georges Bank/North West Atlantic GLOBEC (Global Ocean Ecosystems Dynamics) Program, macrozooplankton and micronekton were collected on 30 Broad Scale Survey Cruises between January – June, 1995 –1999, using a 10 m² MOCNESS (3mm 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., *Neomysis americana* and *Crangon 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 100m isobath, seem to be little affected by such intrusions.

Keywords

Macrozooplankton; distribution; abundance; warm water intrusions; slope water; Northwest Atlantic; Georges Bank

Introduction

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*, *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 hyperiid 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 200m 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., *Crangon septemspinosa*, and *Neomysis 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 *Crangon septemspinosa* and *Neomysis americana* are far more common on the bank, especially inside then 100m isobath (Whiteley 1948).

Study Site

Georges Bank, defined by the 200m isobath (Figure 1), is approximately 150 km wide and 280 km long, and shoals to as little as 30m. 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 – 200m); the bank crest (≤ 60 m); the shallower southern flank (60-150m); 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 100m (Ramp et al., 1985).

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 (Figure 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 10m² frame and five 3mm 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, \leq 4 nets up) with a goal of sampling 5,000 m³ of water per net. The nets were opened and closed at predetermined depths (nominally, 100, 40, 15 and 0m) 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 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. *Crangon septemspinosus* and *Neomysis 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 200m isobath of the Georges Bank region. Because each MOC10 survey occurred over a period of about two weeks, 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 200m isobath, except for the northwest section where the 150m 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.

Results

From 1995-1999, thirty broad-scale cruises were undertaken to Georges Bank, and 465 tows were made with the MOC10, yielding 1,388 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 *Neomysis americana*, *Salpa* spp., *Crangon 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 Figure 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 *Neomysis americana* and *Crangon 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 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 (Figure 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 (Figure 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, *Neomysis americana* and *Crangon Septemspinosa* were always concentrated inside the 100m isobath, and often inside the 60m 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 (Figure 3c and 3d), for ease of comparison with *Salpa* spp. and *Phronima* spp. distributions (Figure 3 a and 3b).

Intrusions of warm water into the Georges Bank region can be seen in AVHRR imagery (Figure 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 water

($\geq 16^{\circ}\text{C}$) can be seen intruding inside the 200m 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., *Neomysis americana* and *Crangon septemspinosus* inside the 200m isobath were compared to the percent of warm water within the 200m isobath of Georges Bank (Figure 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 *Neomysis americana* ($r=-0.057$, $P=0.77$) or *Crangon septemspinosus* ($r=-0.167$, $P=0.38$) (Figure 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 (Figure 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 (Figure 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, *Neomysis americana* and *Crangon septemspinosus* were almost exclusively associated with Georges Bank/Gulf of Maine water (*N.americana*: $X^2=14.154$, $P < 0.01$; *C. septemspinosus*: $X^2=8.334$, $P < 0.05$).

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

Neomysis 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 60m isobath and was not found outside the 100m isobath (Whiteley, 1948). *N. americana* is a euryhaline species (Pezzack and Corey, 1982) and is found in water temperatures from 0 - >25°C (Wigley and Burns, 1971). The decapod shrimp *Crangon septemspinosus* is common in estuaries in the Northwest Atlantic and is found from the Gulf of St. Lawrence to Florida (Haefner, 1979). 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, 1981, Modlin, 1980). *C. septemspinosus* 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). Whiteley (1948) reported an extended spring spawn of *C. septemspinosus* on Georges Bank, but rarely observed individuals outside the 100m 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 *Neomysis americana* and the decapod shrimp *Crangon septemspinosa*. Both these species occurred typically within the 100m isobath of Georges Bank, and although there were interannual variations in their abundances, there was no correlation with warm water intrusions (Figure 5). More generally though, warm core rings are known to contain distinct assemblages of macrozooplankton and micronekton 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 (Figure 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 directions 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 *Neomysis americana* and *Crangon septemspinosus* were almost exclusively associated with Georges Bank/Gulf of Maine water is consistent with the more qualitative observations of Whiteley (1948). Both *N. americana* and *C. septemspinosus* may use bottom-dwelling as a strategy to avoid displacement when flows become strong (Lawrie et al., 1999) or when temperatures increase (Jeffery and Reville, 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 *Phronima sedentaria* showed a maximum abundance when *Salpa fusiformes* were also abundant, namely the spring, in the Mediterranean 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 (Figure 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 *Neomysis americana* and *Crangon septemspinosa*, whose abundance on the bank was much less variable, especially inside the 60m 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., *Neomysis americana* and *Crangon 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.

Literature Cited

- Andersen, V. (1998) Salp and pyrosomid blooms and their importance in biogeochemical cycles. In: Bone Q (ed.) *The biology of pelagic tunicates*. Oxford University Press, Oxford pp. 125-138.
- Andersen, V. and Nival, P. (1986) A model of the population dynamics of salps in coastal waters of the Ligurian Sea. *J. Plankton Res.*, **8**, 1091-1110.
- Ashjian, C.J., Davis, C.S., Gallagher, S.M. and Alatalo, P. (2001) Distribution of plankton, particles, and hydrographic features across Georges Bank described using the Video Plankton Recorder. *Deep Sea Res. II*, **48**, 245-282.
- Backus, R.H. and Bourne, D.A. (eds.) (1987) *Georges Bank*. MIT Press, Cambridge, MA.
- Bigelow, H.B. (1926) Plankton of the offshore waters of the Gulf of Maine. *Bull. US Bur. Fish.*, **40**, 1-509.
- Bowman, T.E. and Gruner, H.-E. (1973) *The Families and Genera of Hyperiidea (Crustacea: Amphipoda)*. Smithsonian Institution Press, Washington, DC.
- Butman, B. and Beardsley, R.C. (1987) Physical Oceanography. In: Backus, R.H. and Bourne, D.A. (eds.) *Georges Bank*. MIT Press, Cambridge, MA, pp. 88-98.
- Cohen, E.B. and Grosslein, M.D. (1987) Production on Georges Bank compared with other shelf ecosystems. In: Backus, R.H. and Bourne, D.A. (eds.) *Georges Bank*. MIT Press, Cambridge, MA, pp. 383-391.
- Corey, S. (1987) Reproductive strategies and comparative fecundity of *Crangon septemspinosa* Say (Decapoda, Caridea), *Crustaceana*, **52**, 25-28.
- Cornillon, P., Lee, T. and Fall, G. (1994) On the probability that a Gulf Stream

- meander crest detaches to form a warm core ring. *J. Phys. Oceanogr.*, **24**, 159-171.
- Davenport, J. (1994) Observations on the locomotion and buoyancy of *Phronima sedentaria* (Forsk., 1775) (Crustacea: Amphipoda: Hyperiidia). *J. Nat. Hist.*, **28**, 787-793.
- Flagg, C.N. (1987) Hydrographic structure and variability. In: Backus, R.H. and Bourne, D.A. (eds.) *Georges Bank*. MIT Press, Cambridge, MA, pp. 108-124.
- Flierl, G.R. and Davis, C.S. (1993) Biological effects of Gulf Stream meandering. *J. Mar. Res.*, **51**, 529-560.
- Flierl, G.R. and Wroblewski, J.S. (1985) The possible influence of warm core Gulf Stream rings upon shelf water larval fish distribution. *Fish. Bull.*, **83**, 313-330.
- GLOBEC (1992) *Northwest Atlantic Implementation Plan*. US Global Ocean Ecosystems Dynamics Report Number 6.
- Gosner, K.L. (1971) *Guide to Identification of Marine and Estuarine Invertebrates: Cape Hatteras to the Bay of Fundy*. Wiley-Interscience, New York.
- Haefner, P.A. (1969a) Temperature and salinity tolerance of the sand shrimp *Crangon septemspinosa* Say. *Physiol Zool.* **42**, 388-397.
- Haefner, P.A. (1969b) Osmoregulation of *Crangon septemspinosa* Say (Crustacea: Caridae). *Biol Bull.* **42**, 438-446.
- Hoffmeyer, M.S. (1990) The occurrence of *Neomysis americana* in two new localities of the South American Coast (Mysidacea). *Crustaceana* **58**, 186-192.
- Jeffery, S. and Revill, A. (2002) The vertical distribution of southern North Sea *Crangon crangon* (brown shrimp) in relation to towed fishing gears as

- influenced by water temperature. *Fish. Res.* **55**, 319 – 323.
- Laval, P. (1978) The barrel of the pelagic amphipod *Phronima sedentaria* (Forsk.) (Crustacea: Hyperiidia). *J. Exp. Mar. Biol. Ecol.*, **33**, 187-211.
- Lawrie, S.M., Speirs, D.C., Rafaelli, D.G., Gurney, W.S.C., Paterson, D.M., and Ford, R. (1999) The swimming behavior and distribution of *Neomysis integer* in relation to tidal flow. *J. Exp. Mar. Biol. Ecol.* **242**, 95 – 106.
- Limeburner, R. and Beardsley, R.C. (1996) Near surface recirculation over Georges Bank. *Deep Sea Res. II*, **43**, 1547-1574.
- Madin, L.P. (1974) Field observations on the feeding behavior of salps (Tunicata: Thaliacea). *Mar. Biol.*, **25**, 143-147.
- Madin, L.P. and Deibel, D. (1998) Feeding and energetics of Thaliacea. In: Bone Q (ed.) *The biology of pelagic tunicates*. Oxford University Press, Oxford pp. 81-104.
- Menard, F., Dallot, S., Thomas, G. and Braconnot, J.-C. (1994) Temporary fluctuations of two Mediterranean salp populations from 1967 to 1990. Analysis of the influence of environmental variables using a Markov chain model. *Mar. Ecol. Prog. Ser.*, **104**, 139-152.
- Modlin, R.F. (1980) The life cycle and recruitment of the sand shrimp, *Crangon septemspinosa*, in the Mystic River Estuary, Connecticut, *Estuaries*, **3**, 1-10.
- Pezzack, D.S. and Corey, S. (1979) The life history and distribution of *Neomysis americana* (Smith) (Crustacea: Mysidacea) in Passamaquoddy Bay. *Can J Zool*, **57**, 785-793.
- Ramp, S.R., Schlitz, R. and Wright, W.R. (1985) On the deep transport of mass, heat and nutrients through northeast channel, Gulf of Maine. *J. Phys.*

- Oceanogr.*, **15**, 1790-1808.
- Ryan, J.P., Yoder, J.A. and Townsend, D.A. (2001) Influence of a Gulf Stream warm-core ring on water mass and chlorophyll distributions along the southern flank of Georges Bank. *Deep Sea Res. II*, **48**, 159-178.
- Sardou, J., Etienne, M. and Andersen, V. (1996) Seasonal abundance and vertical distributions of macroplankton and micronekton in the Northwest Mediterranean Sea. *Oceanol. Acta*, **19**, 645-656.
- Shih, C. (1969) *The systematics and biology of the family Phronimidae (Crustacea: Amphipoda)*. Dana Report No. 74.
- Silver, M.W. (1975) The habitat of *Salpa fusiformis* in the California Current as defined by indicator assemblages. *Limnol. Oceanogr.*, **20**, 230-237.
- Tattersall, W.M., Tattersall, O.S. (1951) *The British Mysidacea*. The Ray Society, London
- Vinogradov, M.E., Volkov, A.F. and Demenova, T.N. (1996) *Hyperid Amphipods (Amphipoda, Hyperideida) of the World Oceans*. Science Publishers, Lebanon, NH.
- Whitely, G.C. Jr. (1948) The distribution of larger planktonic crustacea on Georges Bank, *Ecol. Monogr.* **18**, 233-264.
- Wiebe, P.H., Flierl, G.R., Davis, C.S., Barber, V. and Boyd, S.H. (1985a) Macrozooplankton biomass in Gulf Stream warm-core rings: spatial distribution and temporal changes. *J. Geophys. Res.*, **90**, 8885-8901.
- Wiebe, P.H., Morton, A.W., Bradley, A.M., Backus, R.H., Craddock, J.E., Barber, V., Cowles, T.J. and Flierl, G.R. (1985b) New developments in the MOCNESS, an apparatus for sampling zooplankton and micronekton. *Mar.*

- Biol.*, **85**, 313-323.
- Wigley, R.L. and Burns, B.R. (1971) Distribution and biology of mysids (Crustacea, Mysidacea) from the Atlantic coast of the United States in the NMFS Woods Hole Collection. *US Fish Wildlife Serv Fish Bull.* **69**, 717-746.
- Williams, A.B. (1984) *Shrimps, Lobsters, and Crabs of the Atlantic Coast of the eastern United States, Maine to Florida*. Smithsonian Institution Press, Washington, DC
- Williams, A.B., Bowman, T.E., Damkaer, M.N. (1974) Distribution, variation, and supplemental description of the opossum shrimp, *Neomysis americana* (Crustacea: Mysidacea). *US Fish Wildlife Serv Fish Bull* **72**, 835-842
- Wroblewski, J.S. and Cheney, J. (1984) Ichthyoplankton associated with a warm core ring off the Scotian Shelf. *Can. J. Fish. Aquat. Sci.*, **41**, 294-303.
- Young, J.W. (1989) The distribution of hyperiid amphipods (Crustacea: Pericarida) in relation to warm-core eddy J in the Tasman Sea. *J. Plankton Res.*, **11**, 711-728.

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

Table 1. Dates of GLOBEC Broad-Scale Survey Cruises with number of stations sampled with the MOC10.

Species	Mean TWC abundance	Standard Error	Maximum abundance found	Month of maximum abundance
<i>Salpa</i> spp.	21.61	14.08	6,406.18	June 1999
<i>Phronima</i> spp.	0.87	0.22	56.99	May 1995
<i>Crangon septemspinosus</i>	5.69	1.15	313.98	May 1998
<i>Neomysis americana</i>	93.83	67.15	30,547.97	May 1996

Table 2. Mean total water column (TWC) abundances (#/1,000 m³), standard error of the mean, and the maximum TWC abundances (with corresponding month) for *Salpa* spp., *Phronima* spp, *Crangon septemspinosus*, and *Neomysis americana*.

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

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

<i>Crangon septemspinosa</i>				
	1995	1996	1997	1998
1996				
1997	**			
1998	*			
1999	*			

<i>Neomysis americana</i>				
	1995	1996	1997	1998
1996				
1997	*			
1998			*	
1999		*	**	

Table 3. Results of the Mann-Whitney U-tests with Bonferroni Adjustment on the interannual differences in abundances. (Significance levels, * $P \leq 0.05$, ** $P \leq 0.01$)

Figure Captions

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

Figure 2. Log-transformed abundance [$((\#/1000\text{m}^3)+1)$ mean \pm SE] of *Salpa* spp. and *Phronima* spp., *Crangon septimspinosa*, and *Neomysis americana* on Georges Bank (1995-1999).

Figure 3. Broad scale horizontal distributions of *Salpa* spp. and *Phronima* spp., *Crangon septimspinosa*, and *Neomysis americana* using log-transformed water column total abundances [$(\#/1000\text{m}^3) + 1$] 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 *Crangon septimspinosa* and *Neomysis 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.

Figure 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 Figure 6 were obtained.

Figure 5. Scatter plot of the log transformed abundance data for *Salpa* spp. and *Phronima* spp. inside the 200m isobath versus the percent cover of warm water within the 200m isobath of the Georges Bank region, 1995-1999. Bracket indicates outlier data point removed in test for correlation.

Figure 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 3m 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.

Figure 7. Presence of *Salpa* spp. and *Phronima* spp., *Crangon septemspinosa* and *Neomysis 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 (**= $P \leq 0.01$, *= $P \leq 0.05$).

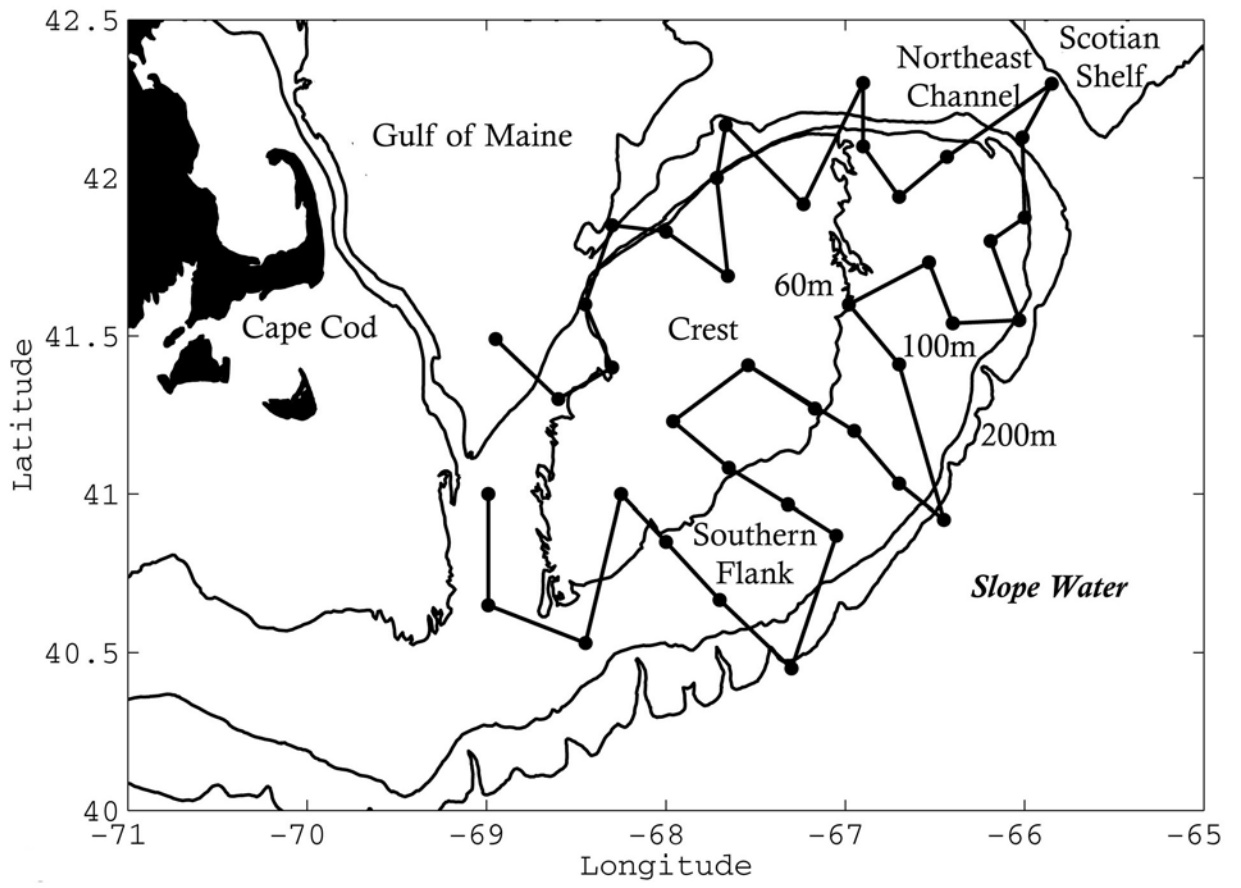


Figure 1

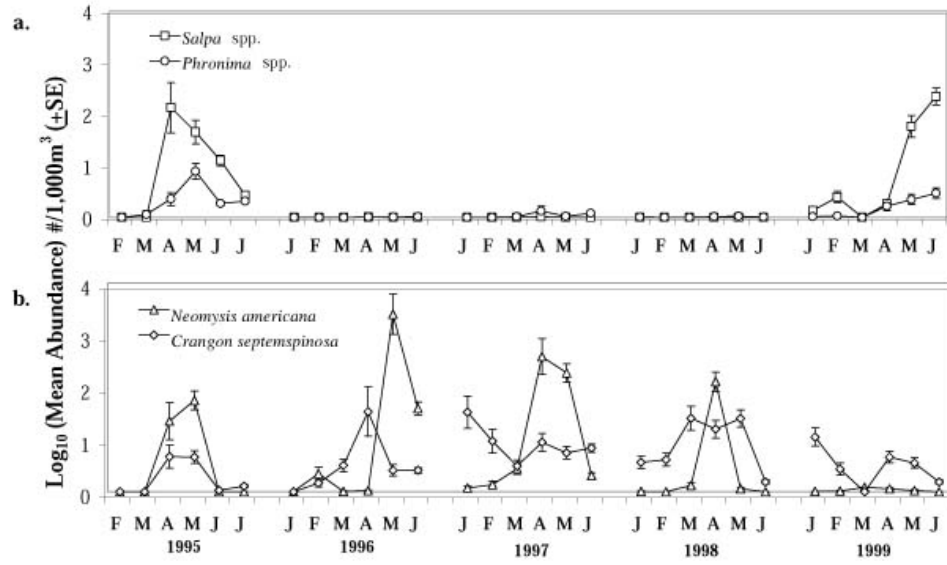


Figure 2

Salpa spp.

Phronima spp.

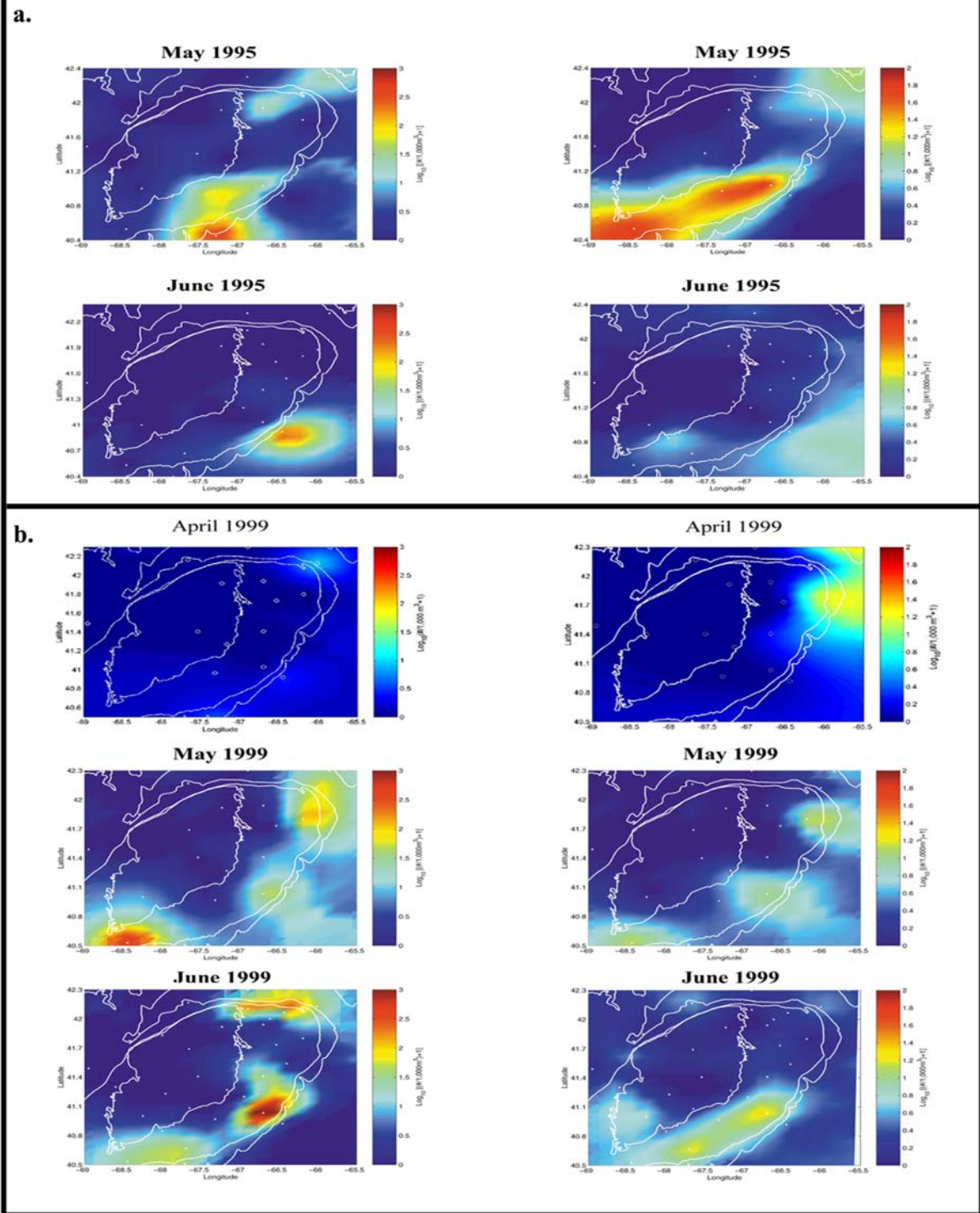
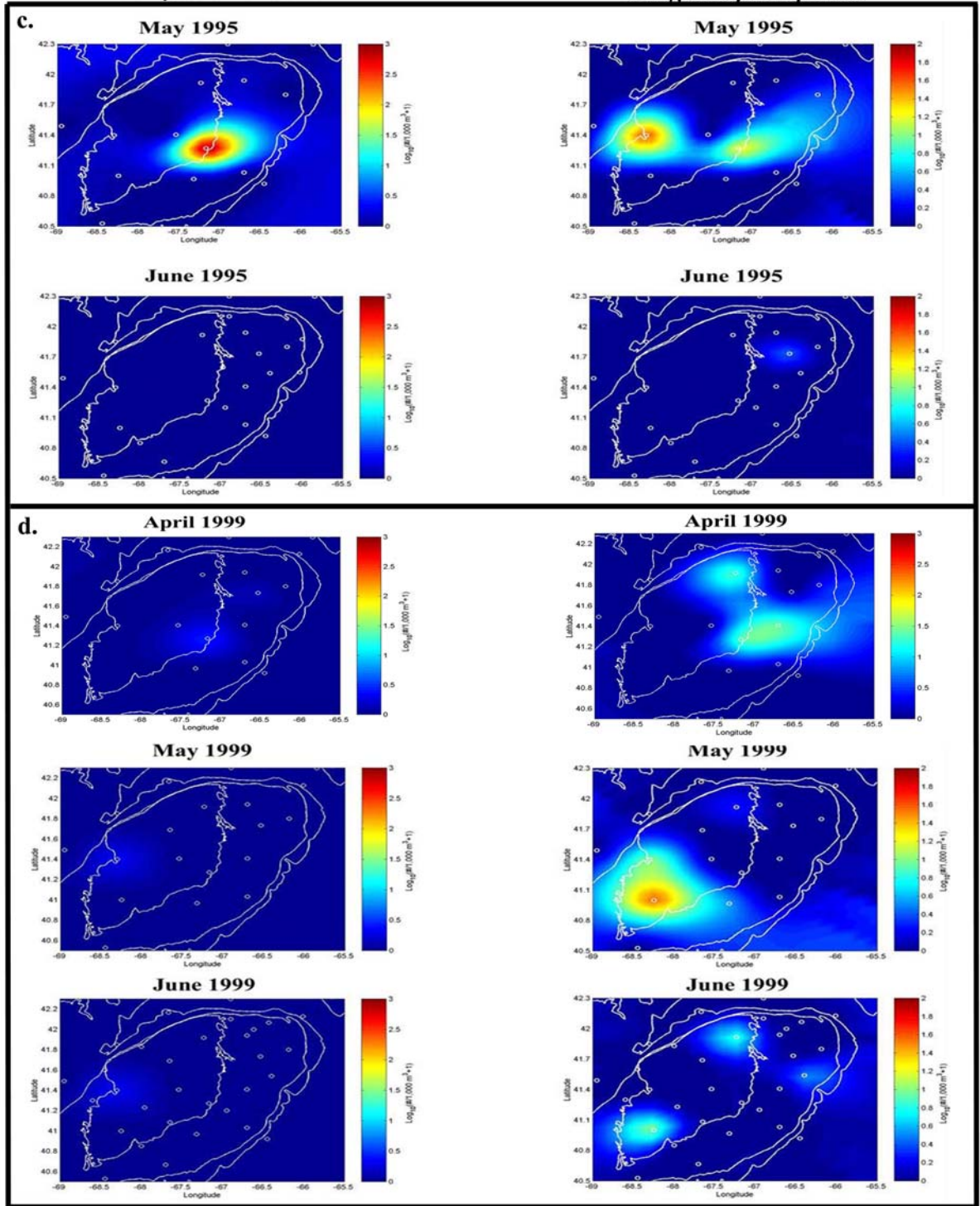


Figure 3

Neomysis americana

Crangon septemspinosa



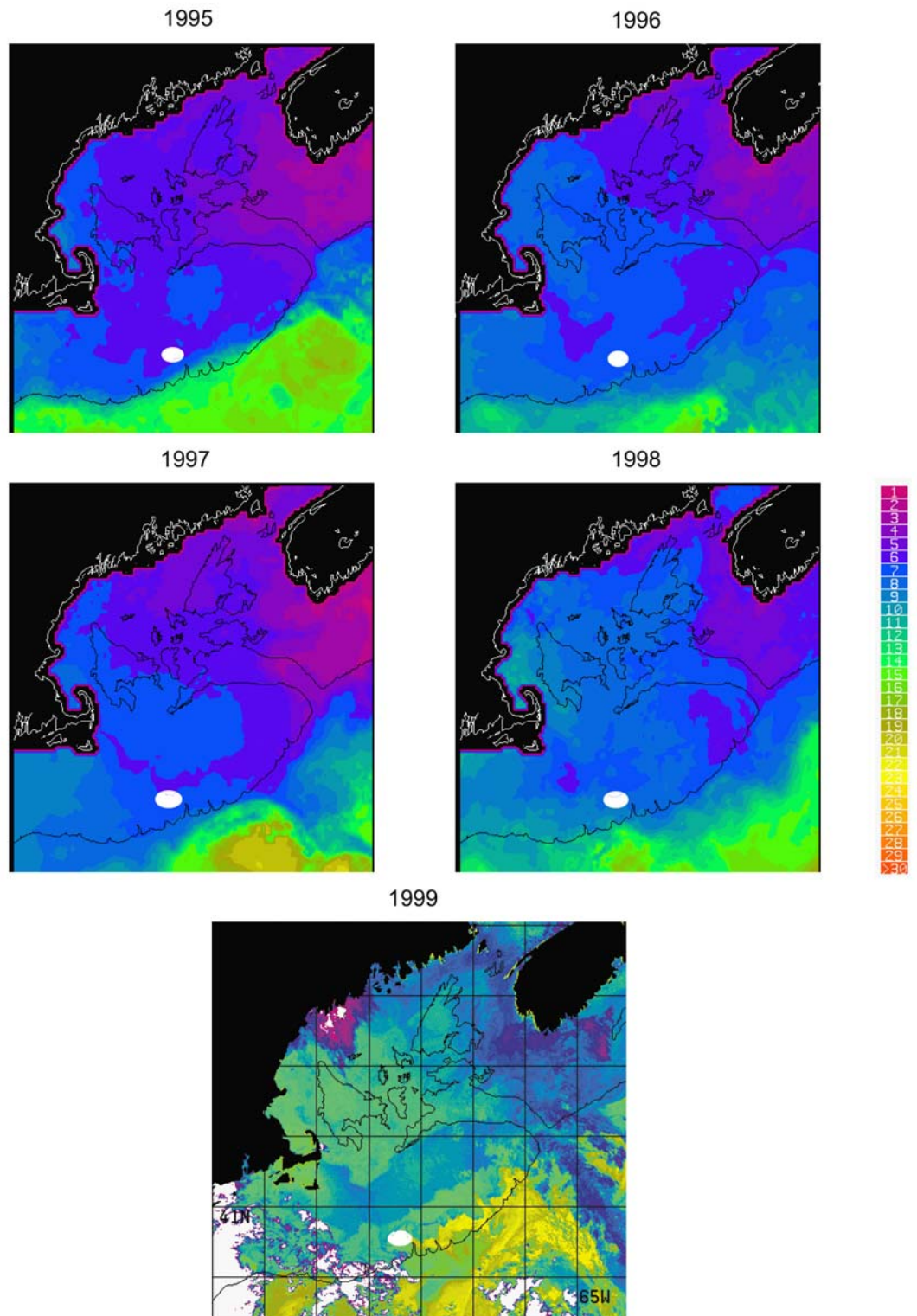


Figure 4

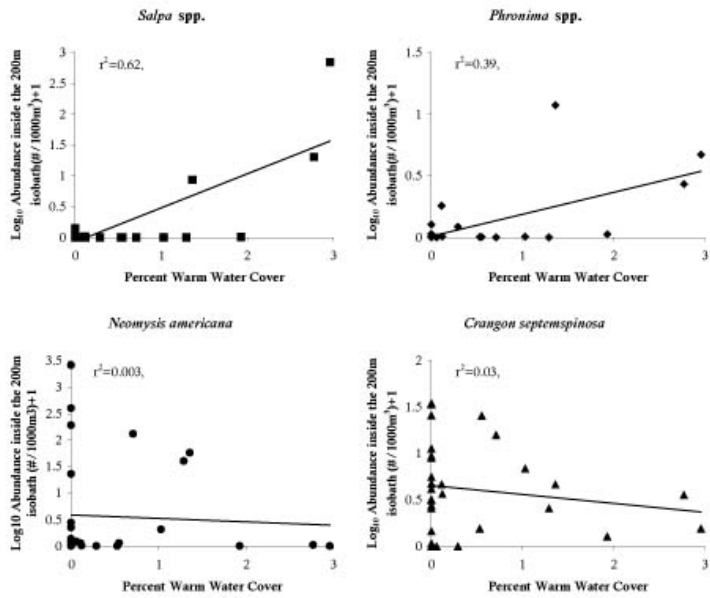


Figure 5

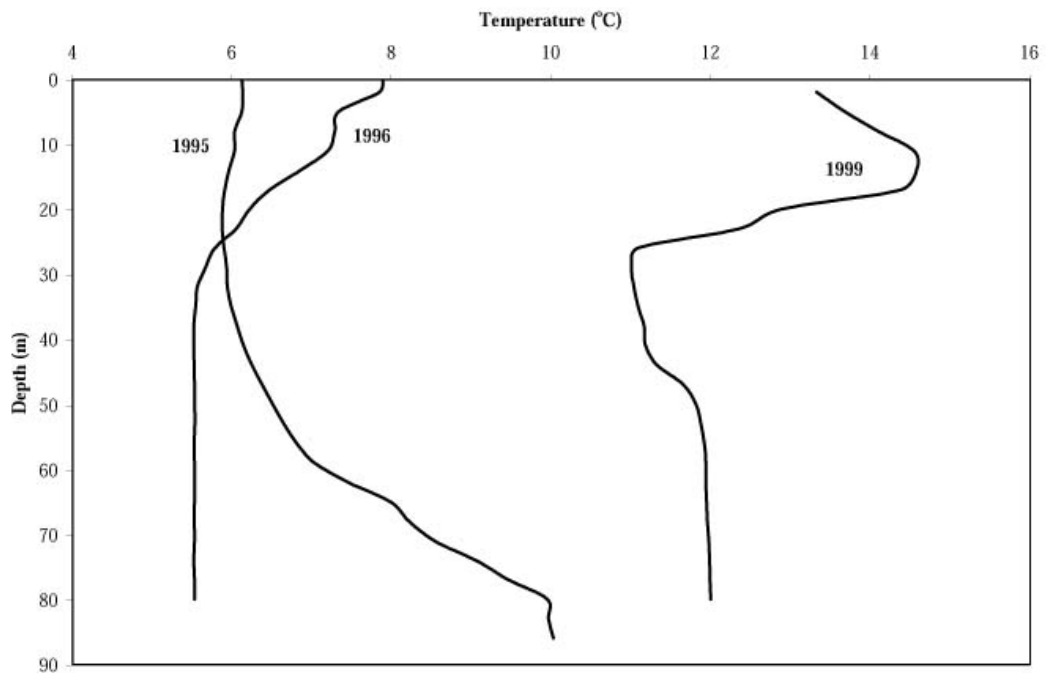


Figure 6

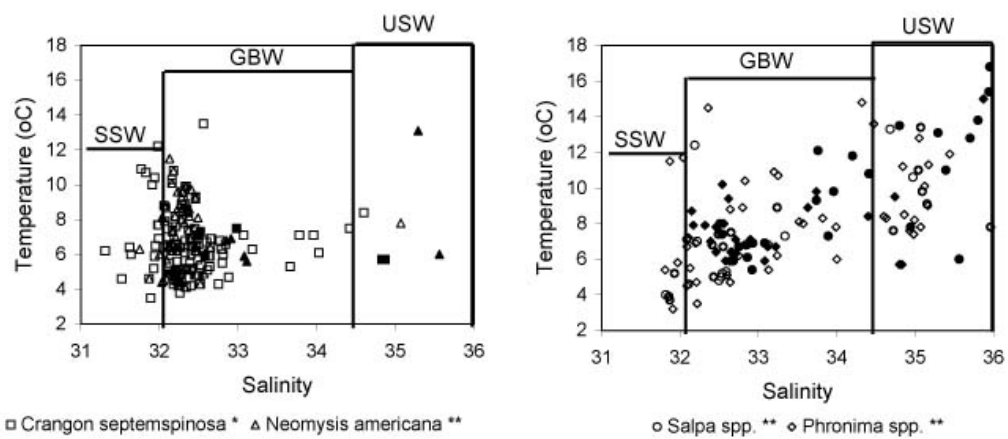


Figure 7

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