

2003

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Karen F. Wishner

University of Rhode Island, kwishner@uri.edu

Dian J. Gifford

See next page for additional authors

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Wishner, K.F., D. J. Gifford, B. K. Sullivan, J.J. Bisagni, D. M. Outram, and D. D. Van Keuren. (2003), Biological Signature of Scotian Shelf Water Crossovers on Georges Bank During Spring 1997. *Journal of Geophysical Research*, 108 (C11) 8014, doi: 10.1029/2001JC001266

Available at: <http://dx.doi.org/10.1029/2001JC001266>

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Authors

Karen F. Wishner, Dian J. Gifford, Barbara K. Sullivan, James J. Bisagni, Dawn M. Outram, and Donna E. Van Keuren

Biological signature of Scotian Shelf Water crossovers on Georges Bank during spring 1997

Karen F. Wishner, Dian J. Gifford, and Barbara K. Sullivan

Graduate School of Oceanography, University of Rhode Island, Narragansett, Rhode Island, USA

James J. Bisagni

Physics Department and School for Marine Science and Technology, University of Massachusetts, New Bedford, Massachusetts, USA

Dawn M. Outram and Donna E. Van Keuren

Graduate School of Oceanography, University of Rhode Island, Narragansett, Rhode Island, USA

Received 13 December 2001; revised 9 January 2003; accepted 18 April 2003; published 6 September 2003.

[1] Episodic crossovers of cold low salinity Scotian Shelf Water (SSW) onto the Northeast Peak of Georges Bank are a potentially important mechanism transporting plankton species, including the copepod *Calanus finmarchicus* and its prey and predators, onto the Bank each spring. We provide the first detailed investigation of horizontal and vertical zooplankton distributions in SSW crossovers compared to other onbank locations from three GLOBEC cruises during spring 1997. SSW crossovers are physically and biologically distinct from other Bank locations. In late spring, chlorophyll concentrations and in vivo fluorescence are elevated and light transmission is reduced in SSW, while during early spring, these parameters are more variable. SSW communities do not contain a unique zooplankton assemblage or indicator species but instead show differences in abundance and life history parameters for various taxa compared to other Bank locations. SSW has high abundances of young *C. finmarchicus* life history stages, almost no diel vertical migration of zooplankton, low abundances of invertebrate predators, and low fish egg abundance. Population development of *C. finmarchicus* in SSW lags that in adjacent water. The potential biological impact of SSW crossovers on Georges Bank varies seasonally. In April, density inversions and interleaving of SSW and non-SSW suggest active mixing, resulting in similar community composition of SSW and adjacent non-SSW. SSW crossovers are probably an important source to Georges Bank of young stages of *C. finmarchicus* in early spring. In May, after stratification strengthens, the greater differentiation between SSW plankton and elsewhere indicates that mixing between communities is more limited. **INDEX TERMS:** 4855 Oceanography: Biological and Chemical: Plankton; 4219 Oceanography: General: Continental shelf processes; 4815 Oceanography: Biological and Chemical: Ecosystems, structure and dynamics; 4223 Oceanography: General: Descriptive and regional oceanography; 4227 Oceanography: General: Diurnal, seasonal, and annual cycles; **KEYWORDS:** Georges Bank, Scotian Shelf Water, *Calanus finmarchicus*, GLOBEC, copepods, *Oithona*

Citation: Wishner, K. F., D. J. Gifford, B. K. Sullivan, J. J. Bisagni, D. M. Outram, and D. E. Van Keuren, Biological signature of Scotian Shelf Water crossovers on Georges Bank during spring 1997, *J. Geophys. Res.*, 108(C11), 8014, doi:10.1029/2001JC001266, 2003.

1. Introduction

[2] Georges Bank, located in the northwest Atlantic off Cape Cod, Massachusetts (Figure 1), is historically one of the world's most productive fishery areas. The calanoid copepod, *Calanus finmarchicus* Gunnerus, dominates the copepod biomass of Georges Bank on an annual basis [Davis, 1987]. However, *C. finmarchicus* does not overwinter on the Bank, presumably because the shallow depths and

strong currents there are not appropriate for the overwintering diapause stage characteristic of this species elsewhere in deeper water. Evaluation of potential sources transporting *C. finmarchicus* onto Georges Bank is thus critical to understanding the Bank ecosystem and the population dynamics of this species in the northwest Atlantic.

[3] Much of the springtime inflow of water and plankton onto Georges Bank is believed to originate from the Gulf of Maine and to occur along the northern edge of the Bank [e.g., Davis, 1987; Meise and O'Reilly, 1996; Durbin et al., 1997; Hannah et al., 1998; Lynch et al., 1998]. Additionally, episodic plumes of cold low salinity water moving

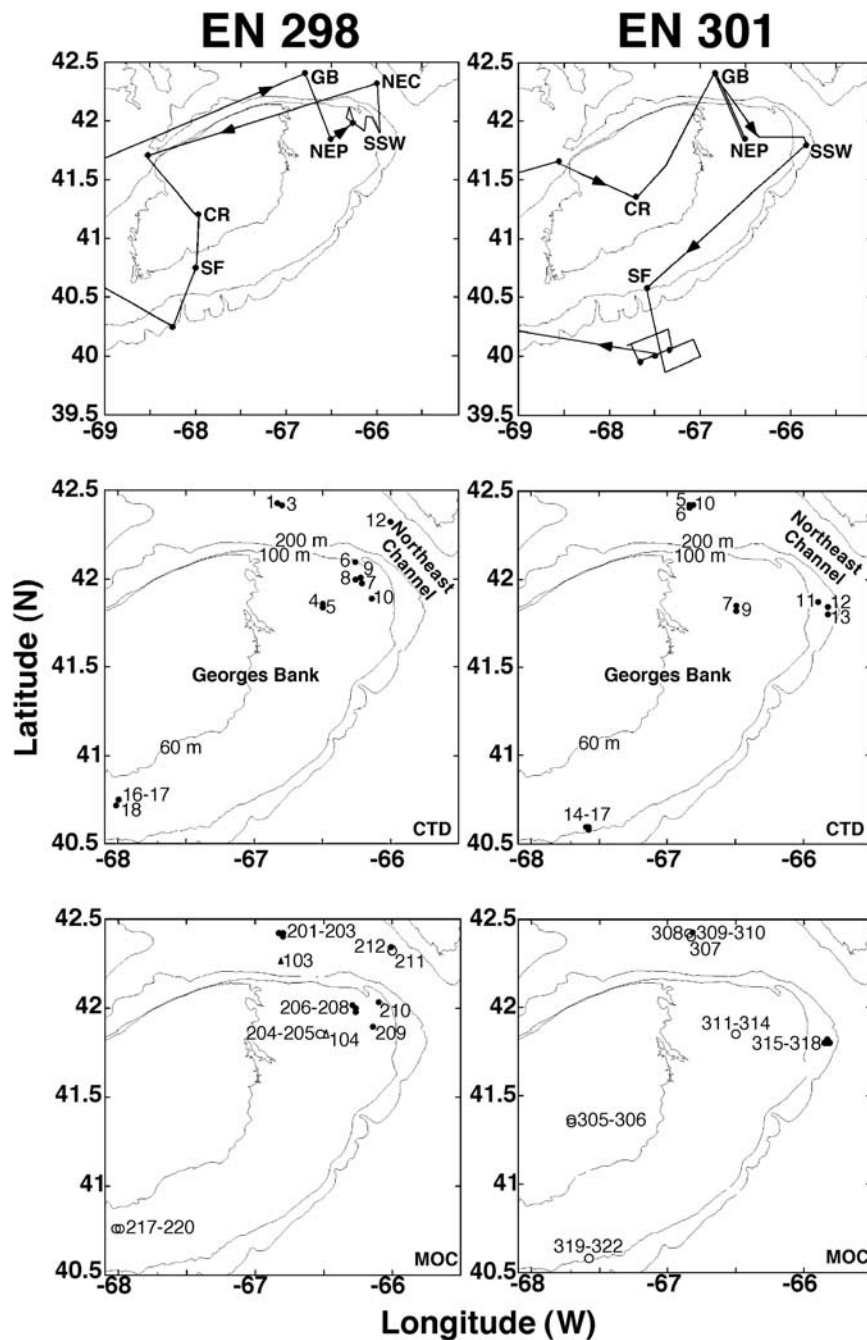


Figure 1. Maps of sampling locations on and near Georges Bank for (left) EN 298 and (right) EN 301. (top) Cruise tracks and site locations (see text for site abbreviations). (middle) CTD casts. (bottom) MOCNESS tows. Solid circles show MOCNESS tows that sampled SSW, while open circles show tows not in SSW. Moc 103 and 104 from EN 296 are also shown on the EN 298 map as triangles.

southwest from the Scotian Shelf toward the Bank have recently been described from satellite images and hydrographic data. Although much of this Scotian Shelf Water (SSW) flows into the Gulf of Maine north of the Bank near Cape Sable and joins the Gulf’s circulation system, some SSW enters the Northeast Channel episodically, where it crosses over directly to the northeast region of the Bank and is also transported southward by the Bank’s anticyclonic mean circulation [Smith et al., 2001, and references therein].

[4] Evidence for crossovers of SSW onto Georges Bank comes from three sources. (1) During early to midspring,

SSW plumes are seen in satellite images and hydrographic data as cold tongues extending along the eastern and southern edges of the Bank [EG&G, 1980; Flagg, 1987; Bisagni et al., 1996; Bisagni and Smith, 1998]. (As the surface water warms in late spring, the surface temperature signal of the plumes disappears from the satellite images.) (2) SSW plumes have been detected and monitored by moorings deployed in the Northeast Channel and on the Northeast Peak of the Bank [Smith et al., 2001, 2003]. (3) Real and modeled drifters released in the region have at times crossed from SSW plumes onto northeastern Georges

Bank [Shore *et al.*, 2000; Smith *et al.*, 2003]. These observations suggest that plankton, as well as water, must be transported episodically onto Georges Bank from the Scotian Shelf. Such crossover events may seed the Bank with new mixtures of plankton species or their life history stages.

[5] As SSW enters the Gulf of Maine during late winter to early spring, it is distinguished from Georges Bank water by its low salinity (<32.00 psu) and low temperature and contributes to the salinity and heat budgets of the region [Bisagni *et al.*, 1996; Bisagni and Smith, 1998; Houghton and Fairbanks, 2001; Smith *et al.*, 2001]. Considerably less is known about the biology of SSW as it crosses onto Georges Bank, although numerous authors have studied the plankton communities and processes of the Scotian Shelf region, the immediate upstream source of SSW observed on the Bank [e.g., Sameoto and Herman, 1992; Head *et al.*, 1999; McLaren *et al.*, 2001]. Townsend and Thomas [2001] observed higher chlorophyll in SSW compared to other northeast peak water in spring 1997.

[6] It has been suggested that SSW is a source of key organisms for Georges Bank. Evaluating this hypothesis is a goal of the U.S. GLOBEC (Global ocean Ecosystems dynamics) Northwest Atlantic program [Wiebe *et al.*, 2002]. The potential for SSW to transport fish eggs and/or larvae to Georges Bank from upstream locations is an important and unresolved issue for fisheries recruitment. High abundances of fish eggs occur on the Northeast Peak in spring, including locations with a surface SSW layer [Sibunka and Weiner, 1997]. However, much of the earlier data were obtained by bongo tows integrating the entire water column, and reports published to date do not specify whether eggs were collected from SSW or the water located below.

[7] The present study is the first to directly target SSW on Georges Bank for intensive replicated depth-stratified zooplankton sampling. Specific objectives are (1) to determine whether SSW is as distinct biologically as it is physically, (2) to evaluate whether SSW functions as a plankton source for Georges Bank, and (3) to examine temporal variation in the potential biological impact of SSW crossovers during spring. Priorities include identifying the zooplankton in SSW, determining whether the SSW community differs from that already present on the Bank, and describing zooplankton behavior, such as diel vertical migration, that would facilitate their incorporation into Bank communities. We focus on the calanoid copepod *C. finmarchicus* and some of its prey and predators and compare plankton communities and distributions in SSW to those in adjacent water on the northeast region of the Bank, at depth immediately below the SSW layer, and downstream at a South Flank location of similar depth.

[8] A major difference between potential physical and biological impacts of SSW crossovers is that biological impacts are likely to vary strongly with the seasonal plankton cycle. A crossover occurring during a quiescent part of the seasonal cycle may have little biological impact while a crossover occurring at another time could have major effects on species, populations, or the community. The growth and development of plankton populations is especially rapid during spring on Georges Bank [e.g., Davis, 1987; Durbin *et al.*, 2000], and temporal changes occurring on timescales of days to weeks have the potential to

influence population structure. Here, we use data from three U.S. GLOBEC cruises in March, April, and May 1997 to examine the changing physical and biological characteristics of Scotian Shelf crossovers during spring.

2. Methods

2.1. Sampling and Data Collection

[9] Three cruises were conducted on the R/V *Endeavor* during spring 1997 as part of Phase II of the U.S. GLOBEC Northwest Atlantic program (Figure 1). Cruise dates were: EN 296 (5–14 March), EN 298 (9–17 April), and EN 301 (23 May to 3 June). During two cruises, EN 298 in April and EN 301 in May, low salinity SSW (<32.00 psu) was encountered repeatedly in the northeast region of the Bank. During EN 296 in March, which was plagued by bad weather, only a single plankton tow (and no CTDs) sampled SSW, so there are limited data from this cruise. In the northeast region of the Bank within and near the crossovers, sampling stations were located at the Northeast Peak (NEP), Georges Basin (GB), the Northeast Channel (NEC), and within SSW (Figure 1). Other Bank stations included the South Flank (SF) and a shallow Crest (CR) station.

[10] Although SSW is identified by its low salinity, it was colder than adjacent surface water during the three cruises and appeared on Advanced Very High Resolution Radiometer (AVHRR) satellite images as a plume of cold water. In order to locate SSW for sampling, near-real time AVHRR declouded images were supplied to the ship for use in coarse positioning. Because the SSW edge was in constant motion due to winds and tides, SSW was re-located from shipboard before each sampling procedure using the underway sea surface temperature and salinity sensors. Typically, there was a sharp, but initially variable, decrease in temperature and salinity at the SSW edge; steaming continued for another 10–15 min to penetrate farther into the feature.

[11] Sampling at each station consisted of a CTD (conductivity, temperature, depth) rosette cast to collect hydrographic information and bulk water for analysis of phytoplankton pigment (Table 1, Figure 1). This was followed by a series of zooplankton collections, consisting of two daytime and two nighttime tows with a 1 m² MOCNESS (Multiple Opening-Closing Net and Environmental Sensing System) [Wiebe *et al.*, 1976] (Table 1, Figure 1).

[12] Hydrographic data were collected on the downcast of the profiling package, consisting of a Sea-Bird Electronics SBE-11 CTD system equipped with a Paro Scientific Digiquartz pressure transducer, redundant pumped conductivity (SBE4) and temperature (SBE3F) sensors, a Sea Tech Flashlamp fluorometer, a Sea Tech 25-cm Path length Deep transmissometer, and a SBE smart rosette mounted with 12 Teflon-lined 10-L Go-flo bottles. Surface water was collected using a bucket. At selected stations, bottles were tripped on the upcast at depths targeted on the basis of hydrographic characteristics (e.g., above, within and below the pycnocline; within and outside of SSW). Triplicate 100-ml samples were collected from each Go-flo bottle for analysis of chlorophyll and phaeopigments [Gifford *et al.*, 1995].

[13] Zooplankton sampling consisted of vertically-stratified day and night tows to within 10 m of the bottom at each

Table 1. Sampling Information for MOCNESS Tows and CTD Casts^a

MOCNESS	Date	Time	Site	SSW, m	CTD	Date	Time	Site	SSW, m
<i>EN 298</i>									
SSW									
MOC 201	4/9	0414	GB	7	CTD 1	4/8	2155	GB	8
(MOC 202)	4/9	0751	GB	9	CTD 3	4/9	1609	GB	6
MOC 203	4/9	1731	GB	21	CTD 4	4/10	1005	NEP	8
MOC 206	4/12	0740	SSW	5	CTD 5	4/11	1100	NEP	3, 9 (2, 4–8)
MOC 207	4/12	1215	SSW	17	CTD 6	4/12	0608	SSW	18
MOC 208	4/12	1426	SSW	20	CTD 7	4/12	0940	SSW	16
MOC 209	4/13	0428	SSW	8	CTD 8	4/12	1117	SSW	2, 10–17 (3–9)
MOC 210	4/13	1815	SSW	17	CTD 9	4/12	2300	SSW	1, 6–11 (2–4)
MOC 212	4/15	0019	NEC	25	CTD 12	4/14	1100	NEC	7
Adjacent									
MOC 204	4/11	0022	NEP		CTD 10	4/13	1114	SSW	
MOC 205	4/11	1224	NEP						
MOC 211	4/14	1306	NEC						
Downstream									
(MOC 217)	4/17	0211	SF		CTD 16	4/17	0140	SF	
MOC 218	4/17	0355	SF		CTD 17	4/17	1108	SF	
MOC 219	4/17	1311	SF		CTD 18	4/17	1733	SF	
(MOC 220)	4/17	1504	SF						
<i>EN 301</i>									
SSW									
MOC 309	5/27	0057	GB	23	CTD 5	5/26	1331	GB	9
MOC 310	5/27	0305	GB	21	CTD 6	5/27	0000	GB	9
MOC 315	5/29	1632	SSW	21	CTD 10	5/28	2229	GB	43
MOC 316	5/29	1824	SSW	27	CTD 11	5/29	1007	SSW	16
MOC 317	5/30	0422	SSW	38	CTD 12	5/29	1200	SSW	38
MOC 318	5/30	0605	SSW	18	CTD 13	5/29	2330	SSW	17
Adjacent									
MOC 307	5/26	1443	GB		CTD 7	5/27	1300	NEP	
MOC 308	5/26	1700	GB		CTD 9	5/28	1300	NEP	
MOC 311	5/27	1416	NEP						
MOC 312	5/27	1528	NEP						
MOC 313	5/28	0106	NEP						
MOC 314	5/28	0230	NEP						
Downstream									
MOC 319	5/31	0326	SF		CTD 14	5/30	1740	SF	
MOC 320	5/31	0500	SF		CTD 15	5/30	2200	SF	
MOC 321	5/31	1224	SF		CTD 16	5/31	1112	SF	
MOC 322	5/31	1356	SF		CTD 17	5/31	1156	SF	
Miscellaneous Tows									
EN296 MOC 103	3/9	0030	GB	61					
EN296 MOC 104	3/10	0148	NEP						
EN301 MOC 305	5/25	1350	CR						
EN301 MOC 306	5/26	0104	CR						

^aDates are 1997 and time is UTC. See text for site abbreviations. The SSW (depth in m) is assumed to begin at the surface unless indicated; blank cells indicate no SSW was present. Depths of density interleaving in CTD data are in parentheses. Parentheses around tow numbers indicate that only the physical data were used from that tow.

station using a 1 m² MOCNESS equipped with 153 μ m mesh nets. Five to 8 strata were sampled during each tow, depending on bottom depth. Near-surface strata usually consisted of 10 m intervals; intervals were thicker at depth in the deepest tows. Environmental instrumentation on the MOCNESS included a Sea-Bird SBE-3S Ocean Thermometer and SBE-4 Conductivity Sensor, a standard MOCNESS pressure sensor, a flowmeter for volume filtered (a modified T.S.K. flowmeter), a Sea Tech fluorometer, and a Sea Tech 25 cm beam transmissometer. MOCNESS environmental information was logged every 4 s. Physical data from only the upward portion of each tow were used because they were collected simultaneously with the plankton.

2.2. Data Processing

[14] Satellite-derived sea surface temperature (SST) images were produced at a resolution of 1.4 km from the AVHRR on the NOAA series of polar-orbiting satellites.

Raw satellite data were remapped to a domain encompassing the Gulf of Maine and Georges Bank [Cornillon *et al.*, 1987]. Despite the potential for twice-daily SST sampling over the region from morning and evening overpasses, a severe space-time constraint is imposed on AVHRR sampling as a result of cloud cover, that causes erroneous SST retrievals and may linger over the region for several days. This constraint is partly overcome by careful inspection of individual SST images and use of “warmest-pixel” compositing techniques, that retain the warmest value from multiple SST images at a given pixel, assuming that cloud-contaminated SST retrievals are always colder than the true SST value at each pixel location. In this study, we use daily, uncomposited SST images whenever possible, but in some instances rely upon warmest pixel techniques to provide a multiday SST composite image.

[15] The continuous conductivity, temperature, light transmission, and fluorescence data from each CTD down-

cast were binned into 1 m depth intervals using the SBE SeaSoft software package. The presence of density inversions, especially during EN 298, complicated the detection and elimination of outlying points. Density inversions in this study were considered to be real if the negative change in density between successive points of the 1-m binned data was $\leq 0.2 \sigma_t$ units/m. Although this criterion is $4\times$ the National Oceanographic Data Center's value of $-0.05 \sigma_t$ units/m for acceptable inversion data, we suggest that it is justified by the dynamic hydrography of eastern Georges Bank and careful examination of the data (M. Taylor and D. Mountain, NOAA, personal communication, 2001).

[16] Hydrographic data were divided into 4 main categories: SSW, adjacent non-SSW in the northeast region of the Bank, deeper water immediately below SSW, and water at a potential downstream location on the SF. SSW included water in the depth range where salinity < 32.00 psu regardless of bottom depth or geographic location. SSW was encountered and sampled when specifically targeted and also during some other casts and tows done in the northeast region of the Bank at the GB and NEC stations (Table 1). Sampling at virtually identical geographic locations could at one time encounter SSW and at another time not find it. "Adjacent non-SSW" was located between 0 and 20 m in casts done at the NEP and NEC stations when SSW was not present. This represents surface water that is immediately adjacent to the SSW surface layer on the northeast part of the Bank and is presumably the zone of first impact should mixing occur from SSW onto the Bank. When SSW and non-SSW were interleaved in the same vertical profile (e.g., CTD casts 5, 8, and 9 in EN 298), each data point was evaluated separately, with the < 32 psu water assigned to the SSW category and the > 32 psu water assigned to a fifth category called "interleaved". "Deeper water" included water located below SSW in the same casts but excluded the deep water of Georges Basin with its complex hydrography. "Downstream" water was located from 0 to 20 m at the SF. The SF station was chosen as a geographically distant comparison because it was comparable in depth to stations located on the northeast part of the Bank and potentially downstream in the Bank's gyral circulation from SSW input. The 0–20 m depth range approximated the median thickness of the SSW layer. Nonparametric Mann-Whitney tests ($P \leq 0.05$) were used to compare SSW with other categories.

[17] Zooplankton wet weight biomass was determined by draining, blotting, and then weighing each entire preserved MOCNESS sample within a few months after collection. Samples with high phytoplankton volume were not weighed. Copepod abundance was determined by splitting samples with a flat-bottomed splitter after removing and enumerating large rare organisms. Three types of split samples were processed. (1) *C. finmarchicus* was counted and staged (copepodite stages C1–C5, adult females, adult males) from a split sample containing ~ 100 individuals of this species. (2) The ratio of calanoid to noncalanoid copepods was determined from a subsample obtained using a Stempel pipette and containing a minimum of 100 copepods in addition to *C. finmarchicus*. (3) Other copepod species were counted and identified in selected samples from another Stempel pipette aliquot containing a minimum of 100 calanoid copepods. Abundances (number/m³) were calculated after adjusting for aliquot size and volume filtered

by each net. Cephalothorax lengths of ~ 70 –100 C4 and C5 *C. finmarchicus* specimens from several nets and tows representative of each regional category during each cruise were measured using a calibrated ocular micrometer. The size of a life history stage is a trait that varies with environmental conditions, especially temperature [Campbell *et al.*, 2001], so size differences provide information about sources of *C. finmarchicus*.

[18] Large invertebrate predators and fish were removed from whole samples prior to splitting, measured, and identified. Smaller taxa were enumerated from split samples with a minimum target count of 100 individuals and identified to lowest possible taxon, size class, and stage. For this study, most taxa were combined into broader groupings. Abundances (number/m³) were calculated after adjusting for split size and volume filtered by each net. Detailed predator counts were done only for EN 301 because previous studies showed predators to be in low abundance until May [Davis, 1987; Sullivan and Meise, 1996].

[19] For zooplankton comparisons among Bank regions, four location and water mass categories were defined, similar to the CTD analyses: samples from SSW, below SSW, adjacent to SSW, and downstream at the SF. Data from the different nets from each tow were grouped according to the environmental parameters measured within the depth interval sampled by each net. Nets filtering within depth intervals where salinity was entirely < 32.00 psu were considered to have sampled SSW. Typically, this included the upper 1–4 nets in locations where SSW was present. Nets from the same tows, but from deeper in the water column where salinity was always higher, were placed in the "below" group. Nets having only a portion of their depth interval with salinity < 32.00 psu were defined as "transitional" and were not included in any group ($N = 8$ transition samples during EN 298 and 6 during EN 301). Deep GB samples were considered separately because of their unique hydrography and diapausing *C. finmarchicus* population. For comparison with nearby non-SSW water of approximately the same depth and also on the northeastern part of Georges Bank, nets sampling from 0–10 and 10–20 m from other tows at the NEP and NEC stations that did not encounter SSW were placed in the "adjacent non-SSW" group. Surface samples from 0–10 m over GB not in SSW were also included in this category. (The next deeper sampling interval in GB, 10–30 m, crossed the thermocline and for that reason was not included in the "adjacent" category.) A "downstream" comparison was done between SSW and SF samples. Nets from all depths were included from the SF to incorporate any changes in vertical distributions of the fauna.

[20] Several statistical approaches were used. For community synthesis, cluster analyses were done using log $(x + 1)$ transformed abundances and the Bray-Curtis method with group averaging. Results were analyzed for similarity and dissimilarity within and between location categories for each cruise and displayed in nonmetric multidimensional scaling (MDS) plots (PRIMER-E, v.5 software [Clarke and Gorley, 2001]). Only *C. finmarchicus* life stages were used for clustering to obtain the broadest synthesis that included all samples from both cruises. For individual taxa, Mann-Whitney tests were done to compare abundances and

relative abundances in SSW with other categories (Statview software). This nonparametric method uses ranked data, thus minimizing the influence of outliers. Only common species, i.e., those occurring in at least four samples from the northeast area and with total counts of at least 50 individuals, were analyzed, with adult and immature stages combined. Diel vertical migration was examined by comparison of day and night abundances in SSW and deep samples (Mann-Whitney tests). To examine environmental associations, nonparametric Spearman correlations were done between *C. finmarchicus* life stage abundances in each net and the average temperature and salinity for the depth interval of that net from the MOCNESS CTD data (Statview software). For all tests, a significance level of $P \leq 0.05$ was used. No corrections were made for multiple testing.

[21] For an ecological perspective, groups of zooplankton species were also compared among regions. The “small copepods” (*Pseudocalanus* spp., *Microcalanus pusillus*) are omnivorous particle-feeding species, likely to compete for food with *C. finmarchicus*. “Large copepods” (*Centropages* spp., *Temora longicornis*, *Metridia lucens*) are more predacious and have been reported to ingest various life history stages of *C. finmarchicus* [Sell et al., 2001]. “Gelatinous predators” included hydroids and medusae. “Crustacean predators” included euphausiids, amphipods, mysids, crab larvae, isopods, and decapods.

3. Results

3.1. Satellite-Derived Sea Surface Temperature (SST)

[22] Satellite-derived SST maps (Figure 2) show a small SSW crossover feature occurring during the first half of cruise EN 296 (5–9 March), with cold ($\sim 3^{\circ}\text{C}$) SSW crossing the NEC and flowing onto the extreme northeastern portion of Georges Bank. This same feature was largely obscured by clouds during the latter part of that cruise (10–14 March). By the time of cruise EN 298 on 11 April, a large pool of very cold ($< 2^{\circ}\text{C}$) SSW was located just inside the NEC and north of the 200-m isobath on eastern Georges Bank. By 16 April, the pool of very cold SSW moved across the NEC and then southeastward across eastern Georges Bank, crossing the 200-m isobath on southern Georges Bank. Generally colder water ($\sim 5^{\circ}\text{C}$) was located along the entire southern flank of the Bank and persisted during EN 298. Despite general warming of SST over the entire region by the time of EN 301 in late May, eastern Georges Bank continued to show some of the coldest SST values, with a pair of cyclonic eddies similar to those described by Bisagni and Smith [1998] located inside the NEC. The eddies had a central core SST of $\sim 8^{\circ}\text{C}$, with colder SSW SST $\sim 6^{\circ}\text{C}$ surrounding each core.

3.2. Physical Characteristics of SSW

[23] The temperature-salinity diagrams derived from CTD/rosette and MOCNESS-CTD sensors during EN 298 and EN 301 show the water masses sampled in April and May (Figure 3). SSW was present both months as the low salinity endpoint but warmed substantially between cruises. The high salinity endpoint was Warm Slope Water in April and both Warm and Labrador (cold) Slope Water in May [Houghton and Fairbanks, 2001]. Statistically, SSW was significantly colder and fresher than water in adjacent,

deeper, or downstream categories during both cruises, with the exception of very cold water located below SSW in May (Table 2). Mean values from CTD casts (Table 2) show that SSW was 0.8°C colder than adjacent northeast water in April and 1.0°C colder than adjacent water in May, but warmed almost 3°C between cruises. Salinity was ~ 0.6 psu lower in SSW than in adjacent water. The deeper water below SSW in the same casts was warmer and saltier than SSW in April but colder and saltier in May. Downstream at the SF, temperatures in the upper 20 m were warmer by about 1.6°C than in SSW in both months, and the water was more saline.

[24] Several of the CTD casts classified as SSW during EN 298 exhibited density inversions (see σ_t plots in Figure 4) in the upper few tens of meters of the water column. The inversions, which were present in CTDs 6, 8, and 9 as strong sub-surface salinity and density minima (Figure 4), persisted for 17 hours on 12 April in repeated casts done at approximately the same location. CTD 7, also done on 12 April, did not exhibit the same inversion structure but did have a nearly isopycnal low-density (low salinity) SSW upper layer. There was also some evidence of density inversions at the non-SSW and SF stations in CTDs 10 and 16–18, respectively, although these features were less robust and located closer to the surface than those observed on the NEP. Density inversions were almost entirely absent from the EN 301 CTDs (Figure 5).

[25] The density inversions observed during EN 298 likely represent real interleaving, i.e., unstable structures related to cross isobath movement of SSW. The proximity of CTDs 6–9 during EN 298 to the leading edge of the cold SSW tongue, located just north of the 200-m isobath in AVHRR imagery on 11 April (Figure 2), supports this idea. Given the unstable nature of the inversions, overturn must eventually take place, returning the water column to a stable or neutrally stable state. Evidence for mixing associated with interleaved SSW and non-SSW can be seen statistically in the CTD data (Table 2). SSW was significantly different from adjacent non-SSW in the northeast in temperature and salinity during both cruises, indicating separation between these water masses. However, only the salinity of SSW differed significantly from the interleaved water in the inversions. The temperature of the interleaved water was similar to that of SSW; both were colder than adjacent non-SSW, indicating that the process of mixing was underway.

[26] The thickness of the SSW layer ranged from 1–43 m in the combined CTD/rosette and MOCNESS CTD data during April and May (Table 1), with a median thickness of 8 m during April (not including interleaving zones) and 21 m during May. Although values of physical variables were not obtained from surface water samples, SSW was assumed to extend to the surface when the shallowest valid data point indicated SSW. During EN 296 in March, a single MOCNESS tow (MOC 103) sampled a 61 m thick SSW layer over GB with a temperature of 3.44°C and salinity of 31.72 psu. The thickness of the SSW layer varied over short distances and times, often between successive tows and casts done nominally at the same location. The SSW edge was usually encountered abruptly but appeared to be convoluted and in motion. Underway sea surface temperature and salinity indicated that the ship entered and left the feature repeatedly. Cruise logistics did not permit further

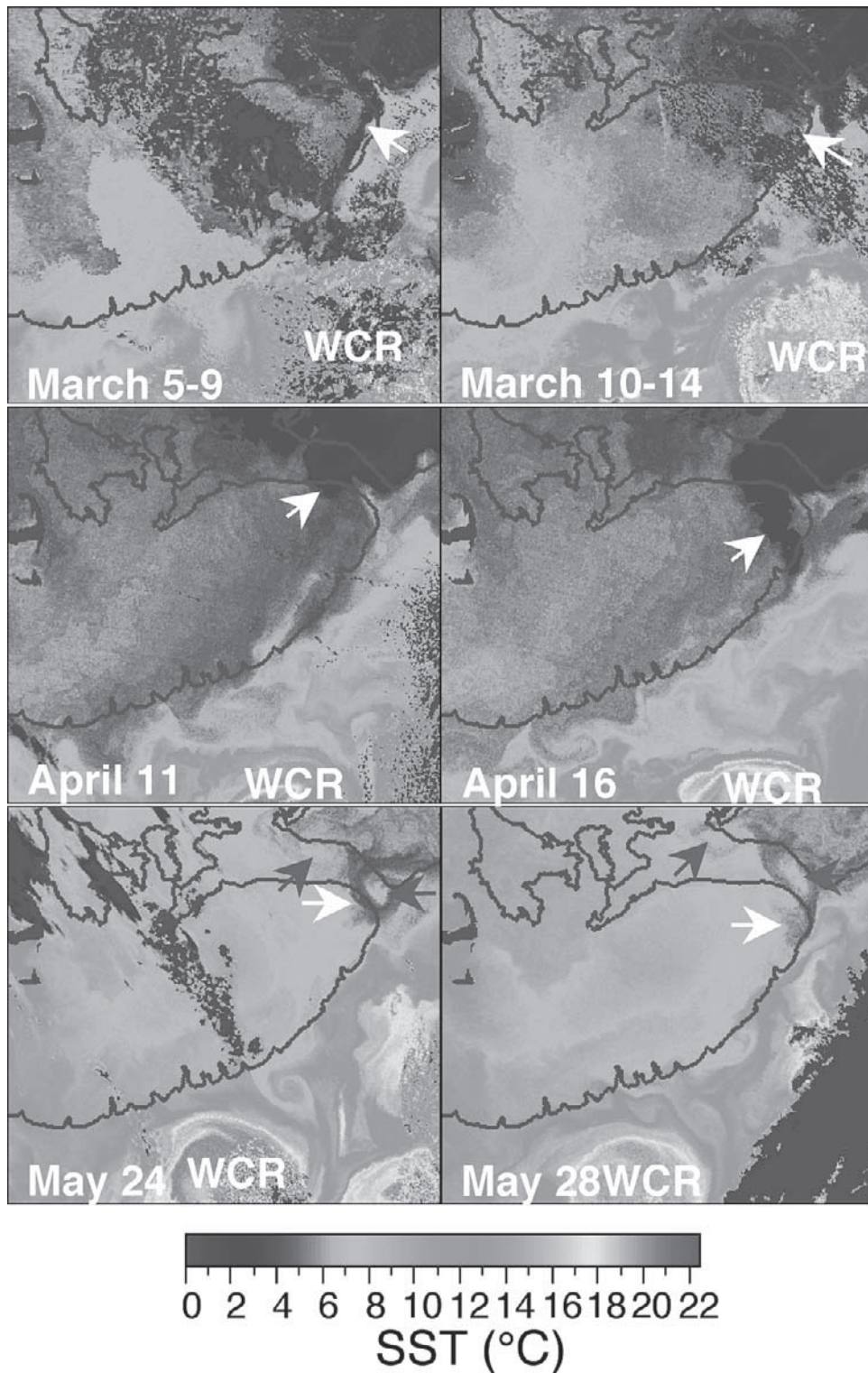


Figure 2. Satellite-derived SST images from spring 1997 corresponding to the EN 296 (March), EN 298 (April), and EN 301 (May–June) cruise periods. SST images with a range of dates are 5-day, warmest-pixel composite images. SST images with single dates are daily images. Also shown is the 200-m isobath (thick purple line), the locations of SSW crossovers (white arrows), the pair of cyclonic eddies (red arrows), and Gulf Stream warm-core rings (WCR). See color version of this figure at back of this issue.

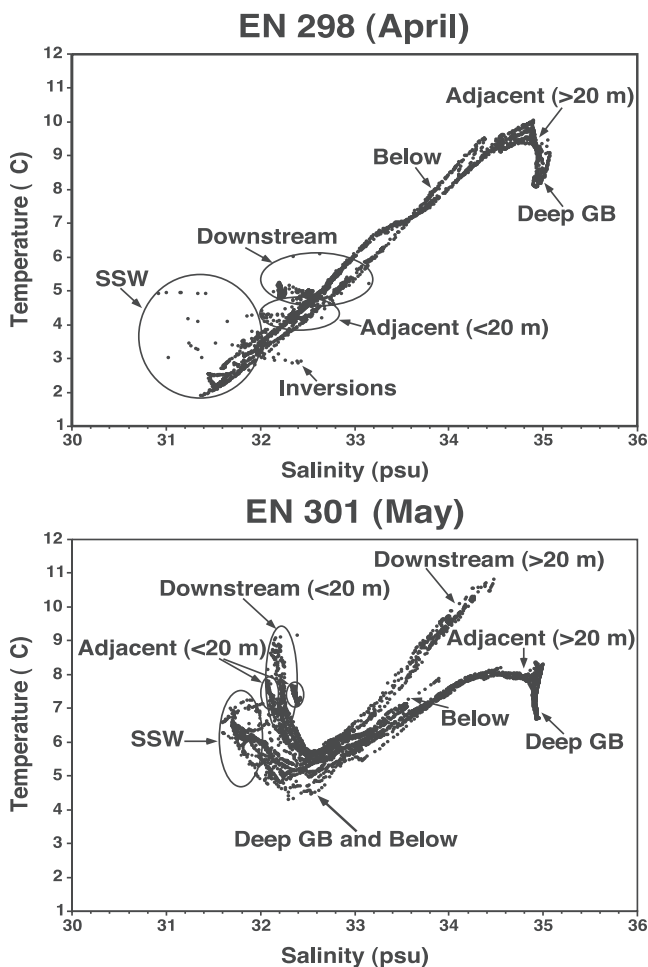


Figure 3. Temperature-salinity diagrams from EN 298 and EN 301 using both CTD and MOCNESS CTD data. Data from each location category are indicated.

upstream sampling to ascertain the spatial extent and gradient of the SSW layer.

3.3. Chlorophyll, in Vivo Fluorescence, and Light Transmission

[27] In vivo fluorescence and light transmission in SSW and adjacent water masses were similar in April and exhibited marked differences in May (Figure 6). In April, the optical characteristics of SSW and water located adjacent to it were similar among all Bank regions sampled (Figures 4 and 6). The concentration of extracted chlorophyll *a* exhibited the same pattern as in vivo fluorescence at all stations (e.g., CTDs 1 and 16: Figure 4). At the GB

stations (e.g., CTD 1: Figure 4), light transmission was similar in SSW and the water located below it. In vivo fluorescence was low at all depths at these stations, but was $\sim 2\times$ higher in the upper water column, including SSW, than at depth. At stations located in the center of the NEP (e.g., CTD 5: Figure 4), there were no differences in light transmission or in vivo fluorescence between the <32 psu SSW and water located immediately above or below it. Three of the four stations located at the edge of the NEP (e.g., CTD 7: Figure 4) exhibited lower light transmission, indicative of higher particle concentration, and higher in vivo fluorescence in SSW than water located immediately above or below it. There was no difference in light transmission between SSW and water located below it at the NEC station (CTD 12: data not shown) where in vivo fluorescence was $\sim 8\times$ higher in the upper water column, including SSW, than at depth. Light transmission and in vivo fluorescence at the SF stations were similar to those observed at the center of the NEP (e.g., CTD 16: Figure 4).

[28] Differences in optical characteristics between SSW and other waters were more marked in May during EN 301 (Figure 6). The concentration of extracted chlorophyll exhibited the same pattern as in vivo fluorescence at all stations (e.g., CTDs 5, 7, 11 and 14: Figure 5). At the GB stations (e.g., CTD 5: Figure 5) and stations located on the edge of the NEP (e.g., CTDs 11 and 12: Figure 5), light transmission was considerably lower, and in vivo fluorescence considerably higher, in SSW versus water located below it. SSW was not present at the NEP-central stations or the SF stations in May. Light transmission at the stations located at the center of the NEP (e.g., CTD 7: Figure 5) was similar to that observed at the SF stations (e.g., CTD 14: Figure 5). In vivo fluorescence was low at the NEP-central stations and high in the upper water column at the SF stations, reflecting the seasonal development of thermal stratification accompanied by development of the sub-surface chlorophyll maximum (detailed data not shown).

[29] In vivo fluorescence, light transmission, and extracted plant pigments of SSW were considerably more variable in April than in May (Figure 6). In April, the highest light transmission, indicating fewer particles, occurred at stations with SSW located at GB. Light transmission was lowest, indicating more particles, in SSW at stations located on the edge of the NEP and in the NEC. Light transmission was intermediate in SSW at stations located in the center of the NEP and on the SF. With the exception of stations located at the edge of the NEP, light transmission in SSW was similar in water located above or below SSW. At the edge of the NEP, light transmission was consistently lower in SSW ($\sim 79\text{--}80\%$) than in water located immediately above or below SSW. In contrast, light transmission in SSW was

Table 2. CTD Data: Means (and Standard Deviations) of Temperature and Salinity for SSW and Other Hydrographic Categories^a

	SSW Mean (SD)	Adjacent Mean (SD)	Interleaved Mean (SD)	Below Mean (SD)	Downstream Mean (SD)
EN 298	(N = 66)	(N = 17)	(N = 16)	(N = 597)	(N = 52)
Temperature (°C)	3.43 (0.60)	4.25 (0.13) ^b	3.49 (0.67)	5.87 (2.15) ^b	5.01 (0.23) ^b
Salinity (psu)	31.712 (0.280)	32.362 (0.150) ^b	32.170 (0.147) ^b	33.142 (1.073) ^b	32.328 (0.173) ^b
EN 301	(N = 119)	(N = 36)	none	(N = 274)	(N = 71)
Temperature (°C)	6.28 (0.45)	7.28 (0.03) ^b		5.92 (0.70) ^b	7.86 (0.70) ^b
Salinity (psu)	31.827 (0.085)	32.419 (0.001) ^b		32.794 (0.448) ^b	32.227 (0.046) ^b

^aN, number of samples.

^bValues significantly different from those in SSW.

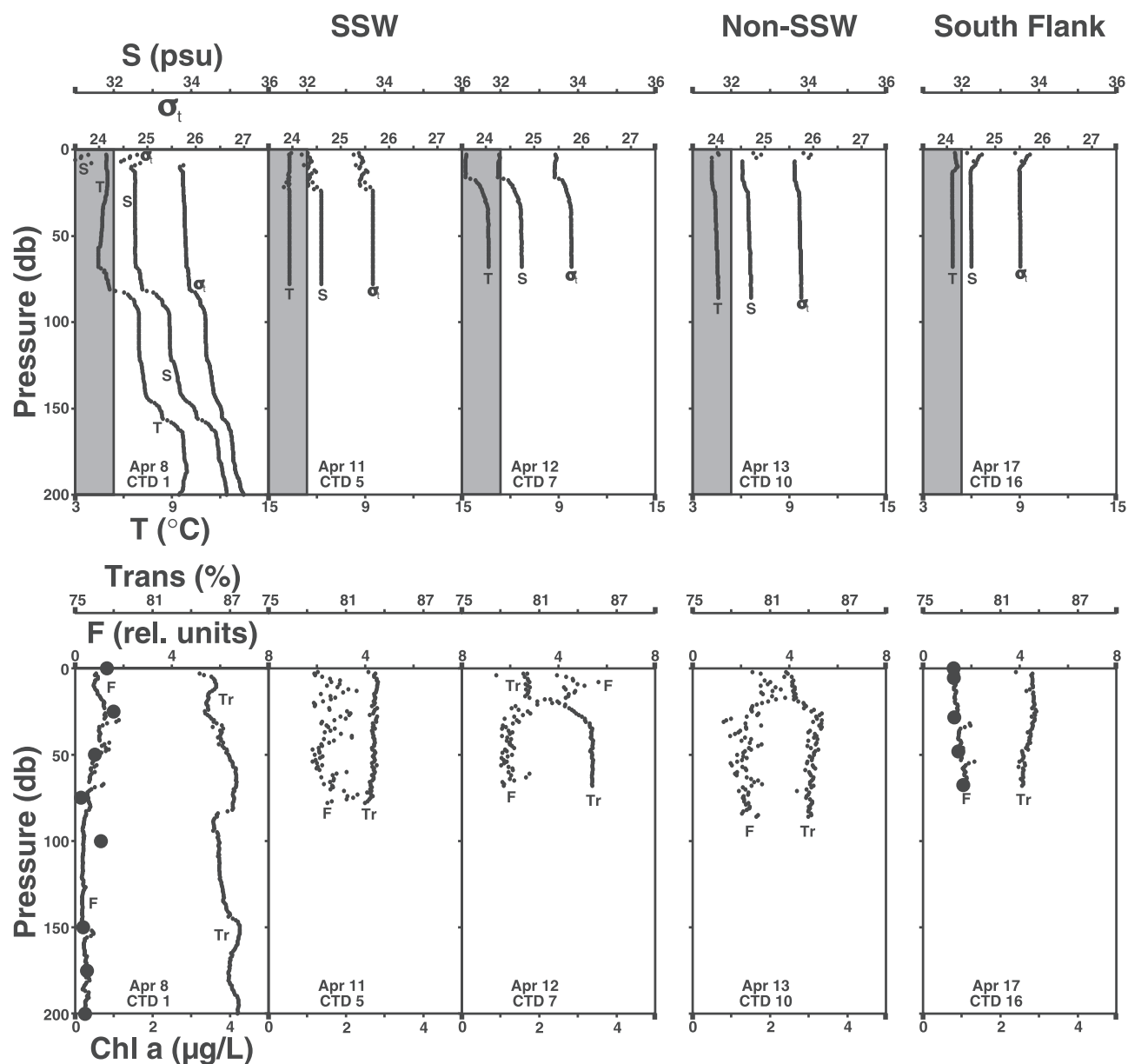


Figure 4. Examples of physical and optical characteristics of the water column during EN 298 in April 1997. SSW is Scotian Shelf Water. S is salinity (psu). T is temperature ($^{\circ}\text{C}$). Trans is light transmission (%). F is in vivo fluorescence (relative units). Solid circles, extracted chlorophyll a ($\mu\text{g/L}$). The shaded area indicates salinity < 32 psu.

consistently lower in May, and in vivo fluorescence was consistently higher, than in water of higher salinity at all stations.

3.4. Zooplankton Distributions: Overall Summary

[30] Consistent features of SSW zooplankton distributions include the following: (1) high abundances of young *C. finmarchicus* life history stages in SSW, especially when compared to deeper and downstream samples, (2) almost no diel vertical migration of zooplankton in or out of SSW, (3) lower abundances of invertebrate predators in SSW than elsewhere (May), (4) low fish egg abundances in SSW during all cruises, and (5) significant relationships of zooplankton abundance and sizes with temperature and salinity. Some characteristics of SSW zooplankton and

relationships to other Bank locations differed between cruises. In April, *C. finmarchicus* abundance in SSW was much lower than in May, and the population structure favored younger stages (Tables 3 and 4 and Figure 7). There was strong similarity between the SSW and adjacent non-SSW communities on the northeast Bank in April but significant differences between these populations in May (Table 5). The SSW community was a tightly clustered entity in May, showing high within-group similarity (Table 5) and a tight array of points in the MDS plot (Figure 8).

3.4.1. Zooplankton: March and April

[31] In April, wet weight biomass was high throughout the northeast part of the Bank (similar in SSW and adjacent non-SSW samples) compared to deeper or downstream samples (Table 3). However, the zooplankton biomass of

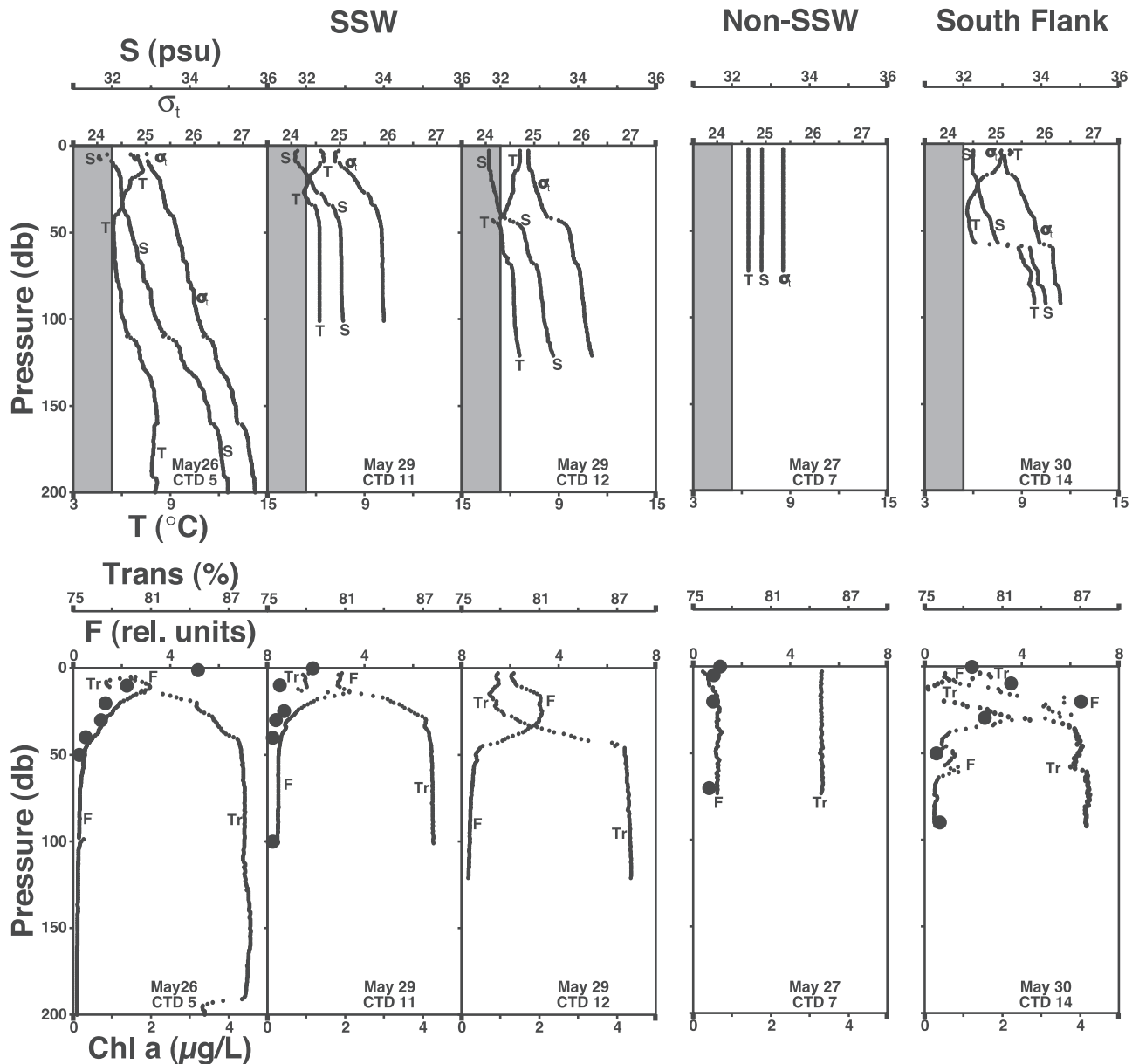


Figure 5. Examples of physical and optical characteristics of the water column during EN 301 in May 1997. Abbreviations and symbols as in Figure 4.

many samples during this cruise could not be determined because of the large amount of phytoplankton caught by the nets (see Table 3 for sample numbers).

[32] Total *C. finmarchicus* abundance was similar for all location categories in April (Table 3). In vertical distributions, the youngest and most common stage, C1, was significantly more abundant in the surface SSW than below in deeper water (by $\sim 3\times$). Peak *C. finmarchicus* abundances also often occurred in or near the transition zone at the lower boundary of SSW (Figure 7). Life history stage abundances were similar for SSW and adjacent non-SSW, with younger stages (C1, C2) dominating the surface water throughout the northeastern part of the Bank. At the SF, proportions of several older stages were higher than in SSW, although abundances were similar. Diel vertical migration was not evident for most stages. There were no significant

differences between day and night abundances within SSW for any stage (except C1); however, females were more abundant at depth during the day than at night. In the one tow (MOC 103) from SSW obtained during EN 296 in March, total *C. finmarchicus* abundance was comparable to that observed in April, with stages C1 and C2 dominant. There were few older stages and very low abundances at depth.

[33] Sizes of *C. finmarchicus* C4s and C5s were similar in SSW and adjacent non-SSW samples, which suggests similar growth conditions in these two water types (Table 6). C4s were significantly larger in SSW than below and downstream, based on nonparametric Mann-Whitney tests. C5s in SSW were similar to those at depth, but significantly larger than those downstream. Size ranges of animals in different water types overlapped, however.

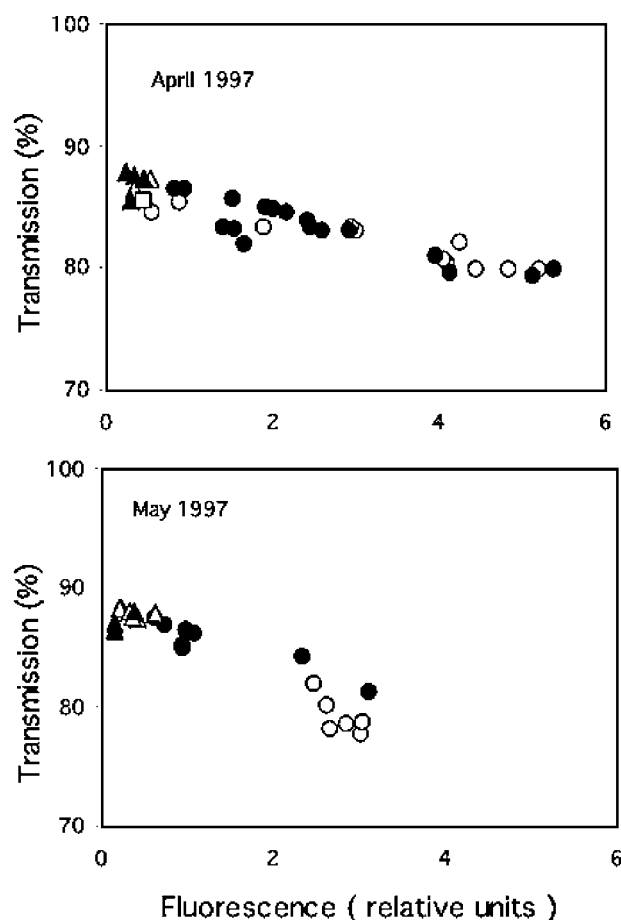


Figure 6. Light transmission (percent) and in vivo fluorescence (relative units) for all stations and depths. Data from CTD-rosette downcasts averaged over 1 psu intervals. Open circles, 31.0–31.9 psu; solid circles, 32.0–32.9 psu; open triangles, 33.0–33.9 psu; solid triangles, 34.0–34.9 psu; open squares, 35.0–35.9 psu.

[34] Other calanoid copepods, including *Metridia lucens*, *Centropages* spp. and *Pseudocalanus* spp., were significantly less abundant in SSW than in adjacent non-SSW samples (Table 3). *M. lucens* and *Microcalanus pusillus* were also more abundant at depth below SSW than in SSW. All of these taxa remained in SSW day and night without migrating in or out of this layer; none showed significant differences in day versus night SSW abundances.

[35] Summarizing by ecological groups (Figure 9), abundances of total *C. finmarchicus* in April were similar at all locations while both large and small calanoid copepods of other species were lower in abundance in SSW compared to adjacent non-SSW samples in the northeast. However, *Oithona* spp. abundance was similar in SSW and non-SSW northeast samples but lower at depth and downstream.

[36] Total *C. finmarchicus* and stages C1–C4 were significantly negatively correlated with both salinity and temperature in April (Spearman correlations, rho range from -0.288 to -0.729) (Figure 10), indicating an association with the cold low salinity SSW. Males were positively correlated with both temperature and salinity, consistent with their occurrence at depth. C5 and female abundances

showed no significant correlations with temperature or salinity, probably because distributions of these stages were related to reproduction or diapause behavior, rather than water mass associations.

[37] SSW was not a source of fish eggs during April. Fish egg abundance in SSW (mean of $1 \pm 0.4/m^3$) was significantly less than in adjacent non-SSW in the northeast region of the Bank (mean of $22 \pm 3/m^3$) (Table 3). During EN 296 in March, there were no fish eggs in two samples from SSW and 1 sample from below the SSW (MOC 103), while low fish egg abundance ($2-3/m^3$) was found in 2 samples from adjacent non-SSW in the northeast region (MOC 104). A few unidentified eggs of other taxa were present in many samples from both cruises.

3.4.2. Zooplankton: May

[38] During EN 301 in May, zooplankton wet weight biomass was almost double that observed in April except at depth (Tables 3 and 4). Zooplankton biomass was significantly higher in SSW than deeper, but was similar to adjacent non-SSW and downstream SF water. Total *C. finmarchicus* was $\sim 23\times$ more abundant in SSW than deeper (Table 4), and all life history stages except males were significantly more abundant in SSW than at depth. Younger life history stages were located almost entirely in the shallow SSW layer. Proportions of younger stages (C1–C3) were significantly higher in SSW than in the deeper water below it, while proportions of older life history stages (C5s, females, males) were significantly lower. The average dissimilarity between the SSW and deep communities was high, with younger stages contributing most of the % dissimilarity (Table 5). Transition nets crossing the lower boundary of the SSW were also zones of high *C. finmarchicus* abundance in vertical profiles (Figure 7).

[39] The northeast region in May was overall a location of high abundance of *C. finmarchicus*, especially younger stages, although the population structure was older in SSW than in adjacent non-SSW (Tables 4 and 5). C1 abundance was significantly higher (by $\sim 4\times$ based on mean abundances) in adjacent non-SSW compared to SSW. C3s and older stages (except males) were significantly more abundant (by $3-5\times$) in SSW than adjacent water. In summary, while the total *C. finmarchicus* abundance was similar in both SSW and non-SSW, there were fewer younger stages and more older stages in SSW than in adjacent non-SSW.

[40] Downstream at the SF, abundances of all life history stages and total *C. finmarchicus* were significantly lower than in SSW (Table 4). Proportions of younger stages (C1–C3) were lower while the proportion of C5s was higher than in SSW. Near the center of the Bank, *C. finmarchicus* abundances at the shallow (~ 30 m) Crest station (MOC 305, 306) were even lower than at the SF (mean of $164 \pm 21/m^3$, $n = 6$) and were dominated by stages C3–C5.

[41] *C. finmarchicus* did not show diel vertical migration into and out of SSW. Day versus night abundances were not significantly different for any life history stage (except SSW females) in either SSW or deeper samples from below SSW.

[42] The sizes of some *C. finmarchicus* life history stages varied with location, suggesting different growth conditions (Table 6). During EN 301, C4s in SSW were significantly smaller than in deeper or adjacent water but similar to those downstream at the SF. C5s in SSW were significantly larger than those in adjacent samples or downstream but smaller

Table 3. Zooplankton Abundances (EN 298, April)^a

EN 298	SSW Mean (SD)	Adjacent Mean (SD)	Below Mean (SD)	Downstream Mean (SD)
<i>C. finmarchicus</i>	(N = 13)	(N = 6)	(N = 28)	(N = 12)
C1	200 (199)	235 (107)	60 (105) ^b	103 (150)
C2	122 (170)	145 (113)	41 (59)	180 (273)
C3	87 (141)	99 (80)	41 (49)	178 (280)
C4	43 (66)	52 (59)	35 (32)	112 (129)
C5	42 (72)	17 (18)	31 (24)	33 (34)
F	57 (169)	6 (3)	25 (36)	7 (7)
M	3 (8)	0.5 (1)	8 (10) ^b	3 (5)
Total <i>C. finmarchicus</i>	564 (679)	568 (362)	253 (231)	629 (855)
Other copepods	(N = 6)	(N = 4)	(N = 22)	(N = 12)
<i>Centropages</i> spp.	6 (4)	56 (36) ^b	15 (15)	138 (113) ^b
<i>Metridia lucens</i>	4 (6)	40 (24) ^b	42 (60) ^b	46 (72)
<i>Microcalanus pusillus</i>	5 (13)	20 (9)	17 (23) ^b	36 (63)
<i>Pseudocalanus</i> spp.	223 (117)	500 (122) ^b	264 (222)	685 (549)
<i>Temora longicornis</i>	70 (30)	128 (33)	41 (48)	42 (42)
<i>Oithona</i> spp.	1366 (825)	692 (210)	705 (881) ^b	635 (505) ^b
Total calanoids	422 (202)	1157 (240) ^b	692 (466)	1578 (904) ^b
Total noncalanoids	1370 (829)	696 (211)	712 (888) ^b	635 (505) ^b
Total copepods	1791 (958)	1853 (326)	1404 (1240)	2214 (1377)
Fish eggs	(N = 3)	(N = 4)	(N = 2)	
	1 (0.4)	22 (3) ^b	1.5 (0.1)	NA
Wet wt biomass (mg/m ³)	(N = 6)	(N = 2)	(N = 17)	(N = 12)
	729 (494)	448 (34)	233 (178) ^b	331 (182) ^b

^aMeans (standard deviations) of abundances (number/m³) of *C. finmarchicus* life history stages, other major copepod species, fish eggs, and wet weight biomass (mg/m³) in the 4 hydrographic categories. N, number of samples. NA, not available.

^bSignificant differences from SSW, based on nonparametric Mann-Whitney tests. No correction was made for multiple testing.

Table 4. Zooplankton Abundances (EN 301, May)^a

	SSW Mean (SD)	Adjacent Mean (SD)	Below Mean (SD)	Downstream Mean (SD)
<i>C. finmarchicus</i>	(N = 13)	(N = 9)	(N = 17)	(N = 32)
C1	290 (221)	1285 (843) ^b	0 (1) ^b	57 (123) ^b
C2	653 (193)	793 (537)	2 (5) ^b	66 (118) ^b
C3	712 (295)	235 (149) ^b	9 (18) ^b	78 (129) ^b
C4	512 (340)	179 (114) ^b	15 (18) ^b	110 (161) ^b
C5	425 (340)	82 (119) ^b	42 (39) ^b	86 (76) ^b
F	154 (107)	34 (23) ^b	46 (59) ^b	10 (12) ^b
M	7 (8)	4 (8)	6 (4)	2 (2) ^b
Total <i>C. finmarchicus</i>	2780 (949)	2631 (1449)	123 (129) ^b	414 (520) ^b
Other copepods	(N = 11)	(N = 3)	(N = 17)	(N = 16)
<i>Centropages</i> spp.	31 (53)	182 (104) ^b	154 (603)	43 (103)
<i>Clausocalanus arcuicornis</i>	37 (38)	0 (0)	6 (7) ^b	96 (177)
<i>Metridia lucens</i>	11 (18)	0 (0)	59 (33) ^b	189 (164) ^b
<i>Microcalanus pusillus</i>	14 (20)	0 (0)	125 (115) ^b	12 (16)
<i>Pseudocalanus</i> spp.	2524 (2711)	3384 (2149)	784 (881) ^b	2088 (3497) ^b
<i>Temora longicornis</i>	119 (161)	617 (727)	15 (45)	374 (718)
<i>Oithona</i> spp.	1163 (848)	7939 (3558) ^b	172 (149) ^b	NA NA
Total calanoids	5512 (2917)	8280 (2281) ^b	1272 (1115) ^b	3193 (4748) ^b
Total noncalanoids	1177 (842)	7939 (3558) ^b	179 (149) ^b	1883 (2664)
Total copepods	6689 (2872)	16219 (5250) ^b	1451 (1162) ^b	5077 (7000)
Predators and other taxa	(N = 11)	(N = 8)	(N = 17)	(N = 16)
Hydroid hydranths	0 (0)	133 (144) ^b	64 (262) ^b	0.03 (0.1)
<i>Obelia</i> sp. medusae	0 (0)	3 (4) ^b	3 (13)	0 (0)
Other Cnidaria	0.04 (0.09)	0.5 (1)	0.3 (0.4) ^b	0.2 (0.5)
Chaetognaths	0.5 (0.5)	33 (32) ^b	4 (13)	51 (79) ^b
Polychaetes	0.05 (0.2)	9 (14) ^b	13 (55)	0.07 (0.3)
<i>Themisto compressa</i>	3 (2)	0.2 (0.4) ^b	2 (4)	33 (45)
Gammarid amphipods	0.009 (0.02)	5 (12)	0.4 (2)	0.2 (0.4)
Euphausiids	0.9 (1)	0.7 (1)	0.3 (0.3)	2 (3)
Crab larvae	0.1 (0.2)	0.3 (0.5)	7 (28)	0.1 (0.3)
Fish	0.02 (0.03)	0.2 (0.2)	0.1 (0.5)	0.2 (0.9)
Fish eggs	0.02 (0.04)	18 (11) ^b	0.4 (2)	0 (0)
Wet wt biomass (mg/m ³)	(N = 13)	(N = 9)	(N = 17)	(N = 32)
	1171 (563)	812 (291)	273 (265) ^b	871 (543)

^aMeans (standard deviations) of abundances (number/m³) of *C. finmarchicus* life history stages, other copepod species, invertebrate predators, fish eggs, and wet weight biomass (mg/m³) in the four areas. N, number of samples. NA, not available.

^bSignificant differences from SSW, based on nonparametric Mann-Whitney tests. No correction was made for multiple testing.

Calanus Abundance

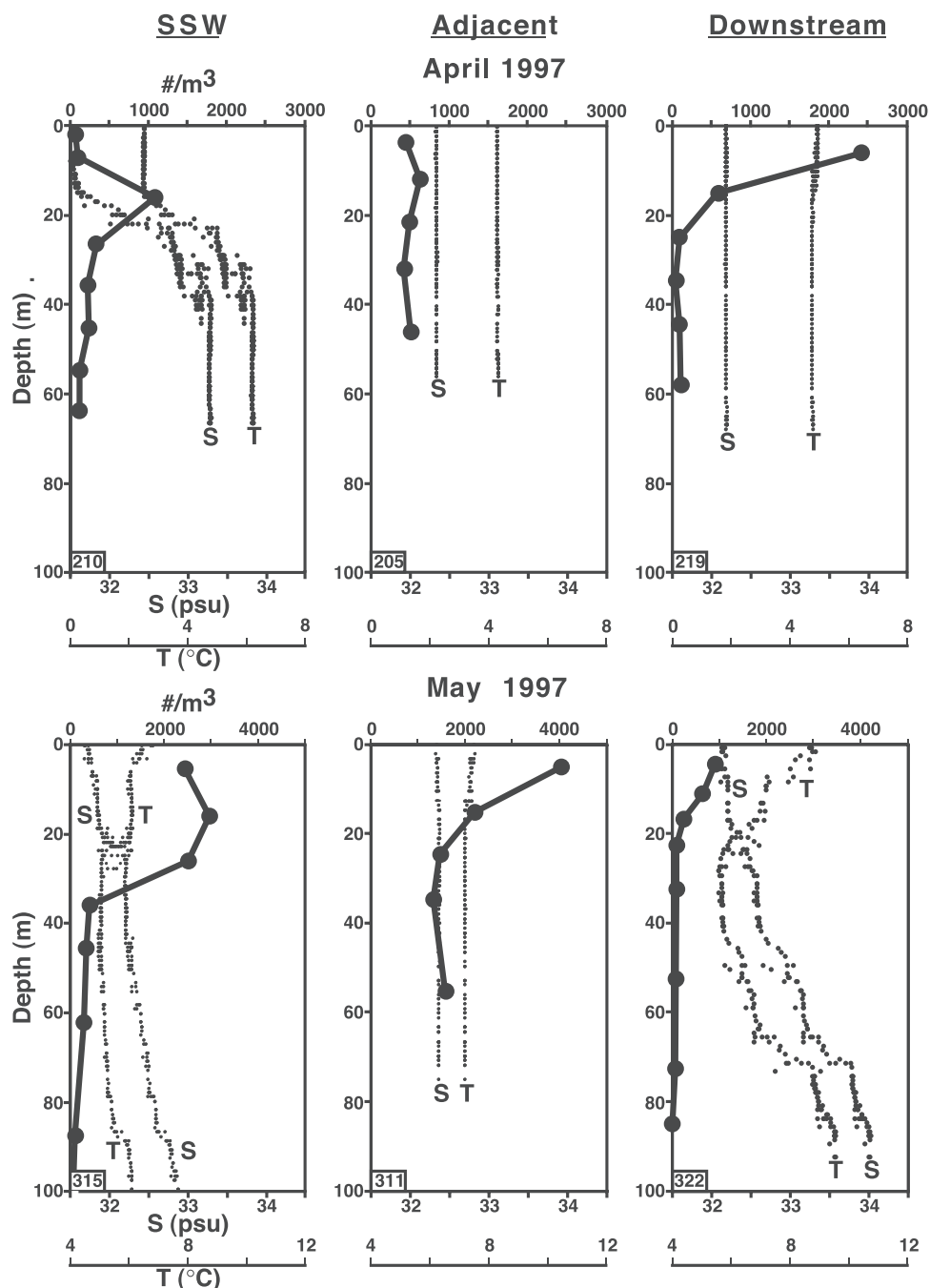


Figure 7. Examples of vertical profiles of the distribution of *C. finmarchicus* relative to temperature (T) and salinity (S) from MOCNESS tows representative of each area during each cruise.

than specimens from depth. As in April, size ranges among populations overlapped.

[43] Distributions of several other common copepods also varied significantly relative to SSW in May (Table 4). *Pseudocalanus* spp., *Clausocalanus* spp., and *Oithona* spp., were significantly more abundant in SSW than in deeper water in the same tows, while *Microcalanus pusillus* and *Metridia lucens* were significantly more abundant at depth. *Oithona* spp. and *Centropages* spp. were significantly less abundant in SSW than in adjacent non-SSW in the northeast region of the Bank. The contrast for *Oithona*

spp. was particularly striking, with abundances $\sim 7\times$ higher outside SSW (means of $7939/m^3$ for adjacent non-SSW northeast samples versus $1163/m^3$ for the SSW). *Pseudocalanus* spp. was abundant in both SSW and adjacent non-SSW in the northeast region, similar to *C. finmarchicus*. Significantly more *Metridia lucens* but fewer *Pseudocalanus* spp. were present at the SF than in SSW. There were no significant differences in day versus night abundances in SSW for any of these species.

[44] SSW was not a major source of invertebrate predators to the Bank at this time (Table 4). Abundances of many

Table 5. Analyses of Similarity in *C. finmarchicus* Life Stage Composition Within Each Area and Dissimilarities in Composition Between SSW and Other Areas for Each Cruise^a

Area	EN 298 (April)			EN 301 (May)		
	Average Similarity	Stage	Cumulative Percent Similarity	Average Similarity	Stage	Cumulative Percent Similarity
SSW	71.48	C1	30.98	90.99	C2	19.15
		C2	50.80		C3	38.18
Adjacent	86.64	C1	26.12	85.25	C4	54.70
		C2	48.54		C1	23.67
		C3	69.42		C2	45.17
Below	63.90	C5	25.49	70.52	C3	63.81
		C4	43.57		C5	35.58
		F	58.93		F	56.90
Downstream	70.49	C2	22.55	62.12	C5	36.07
		C3	42.64		C4	64.57
		C4	62.47			

	EN 298 (April)			EN 301 (May)		
	Average Dissimilarity	Stage	Cumulative Percent Dissimilarity	Average Dissimilarity	Stage	Cumulative Percent Dissimilarity
SSW versus adjacent	23.40	C5	18.56	16.46 ^b	C5	23.30
		C2	36.93		C1	39.28
		C3	54.74		F	53.99
SSW versus below	39.47	C1	20.14	54.59 ^b	C2	23.32
		C2	37.00		C3	44.09
		C3	51.48		C1	63.75
SSW versus downstream	30.51	C5	16.67	42.26 ^b	C2	21.64
		C4	33.16		C3	41.82
		C1	48.88		C1	17.32
		C2	64.43			

^aThe life stages contributing to 50% of the cumulative similarity or dissimilarity are shown. Results (using PRIMER software) are from ANOSIM and SIMPER tests and are based on cluster analysis.

^bAreas that are significantly different based on the R statistic from pairwise tests.

potential predatory taxa in SSW were lower than in adjacent non-SSW in the northeast region of the Bank. Only the amphipod *Themisto compressa* (formerly *T. gaudichaudii*) was significantly more abundant in SSW than in adjacent non-SSW samples. Hydranths of the hydroid *Clytia* spp., a potentially important predator of immature *C. finmarchicus* and fish larvae in the central region of the Bank [Madin et al., 1996], were absent in SSW and significantly more abundant outside it, both in adjacent non-SSW (mean of 133/m³) and deeper (mean of 64/m³) samples. Other predators that were significantly more abundant in adjacent non-SSW included chaetognaths, polychaetes, and the medusa *Obelia*. Chaetognaths were the only predator group that was significantly more abundant downstream at the SF than in SSW. Euphausiids, gammarid amphipods, crab larvae, and fish were other relatively common predators in most samples but similar in abundance between SSW and elsewhere. A variety of other crustacean and gelatinous predators occurred occasionally. The ctenophore *Pleurobrachia pileus*, sometimes abundant at the SF, was rare during this cruise.

[45] There were no significant day versus night differences in abundances of these predators in SSW, indicating no diel vertical migration into or out of SSW. However, in the upper 20 m of adjacent non-SSW in the northeast region of the Bank, *Obelia* sp., isopods, gammarid amphipods, and mysids were all significantly more abundant at night compared to day. This suggests that the presence of the SSW layer inhibited the normal diel vertical migration of these taxa to the surface. The lower abundances of predators in SSW and the possible inhibition of diel vertical migration

of predators into this layer suggest that predation on *C. finmarchicus* in SSW was reduced compared to adjacent non-SSW on the northeast region of the Bank.

[46] Summarizing by ecological groups, in May, SSW and adjacent non-SSW in the northeast region exhibited higher total *C. finmarchicus* and small copepod abundances than water below SSW or downstream. However, large predatory/omnivorous copepods, gelatinous predators, and chaetognaths were more abundant outside SSW in adjacent water than within SSW. Thus SSW at this time appeared to be a refuge from many predators for smaller copepods and *C. finmarchicus*. The small cyclopoid copepod *Oithona* spp., however, was significantly less abundant in SSW than in adjacent non-SSW samples even though there were more predators outside the SSW.

[47] Abundances of total *C. finmarchicus* and stages C1–C5 were significantly negatively correlated with salinity in May (Spearman correlations, rho from –0.361 to –0.644), indicating an association with low salinity SSW. However, in contrast to April, their abundances were not significantly correlated with temperature, probably because deeper water was warmer than SSW in April but colder in May. Female abundance was negatively correlated with both salinity and temperature while male abundance was positively correlated with salinity and negatively correlated with temperature.

[48] SSW was not a source of fish eggs in May, similar to the situation in April. Eggs were significantly more abundant in adjacent non-SSW in the northeast of the Bank, where their mean abundance was 18/m³, compared to 0.02/m³ in SSW (Table 4).

4. Discussion

4.1. Is SSW Distinct Biologically From Nearby Environments?

[49] SSW did not transport a unique assemblage of zooplankton or a characteristic indicator species during either April or May. The most abundant calanoid copepods in SSW, *C. finmarchicus* and *Pseudocalanus* spp., were also the most abundant calanoids in non-SSW on the northeast region of the Bank. Less abundant copepods and other taxa

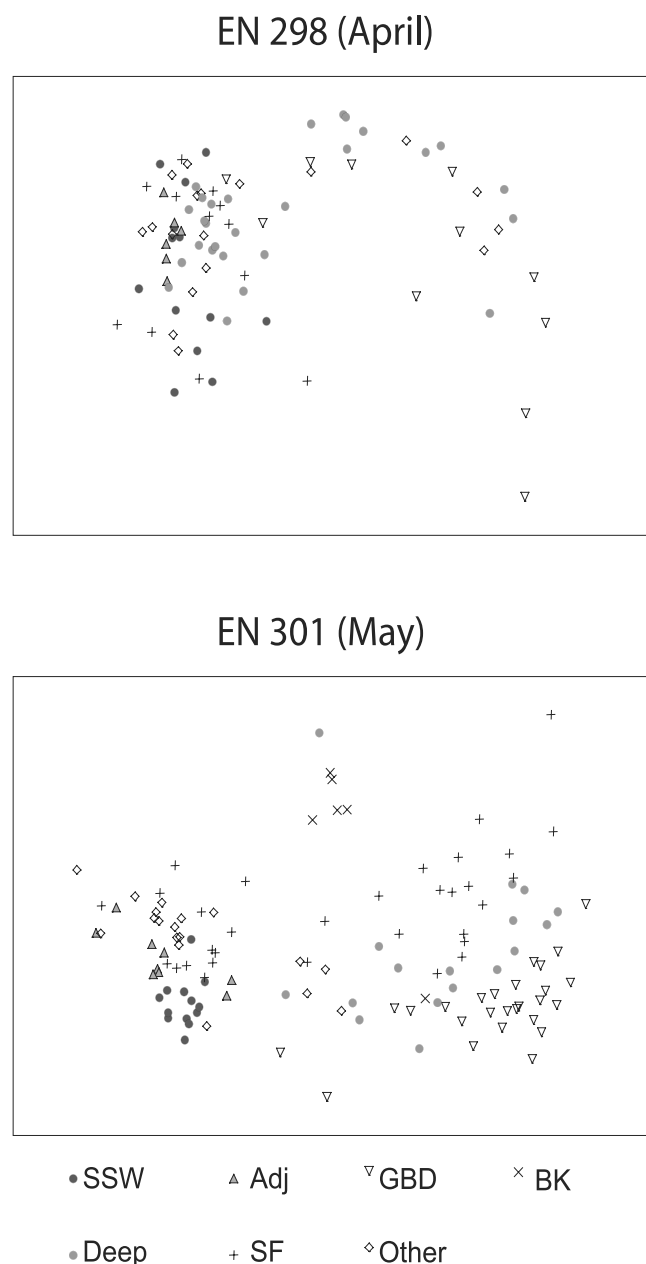


Figure 8. Multidimensional scaling (MDS) plots based on cluster analyses of *C. finmarchicus* life stage abundances. Each point represents a sample, and the distance between points is an indicator of similarity. Stress is 0.07 for each graph. Axes are nondimensional. Point type shows location category. GBD, deep Georges Basin; BK, Bank crest; other abbreviations as in text.

Table 6. Cephalothorax Size of Two *C. finmarchicus* Life Stages From the Different Areas From Each Cruise^a

		Area			
		SSW	Adjacent	Below	Downstream
<i>EN 298</i>					
C4	mean (SD)	1.99 (0.14)	1.96 (0.13)	1.93 (0.12)	1.81 (0.11)
	median (N)	1.98 (77)	1.94 (76)	1.98 ^b (76)	1.82 ^b (80)
C5	mean (SD)	2.51 (0.18)	2.53 (0.15)	2.49 (0.17)	2.30 (0.13)
	median (N)	2.55 (53)	2.51 (76)	2.47 (70)	2.30 ^b (82)
<i>EN 301</i>					
C4	mean (SD)	1.89 (0.18)	1.93 (0.13)	1.99 (0.23)	1.86 (0.13)
	median (N)	1.88 (184)	1.94 ^b (100)	1.94 ^b (102)	1.88 (100)
C5	mean (SD)	2.57 (0.19)	2.46 (0.22)	2.65 (0.23)	2.44 (0.22)
	median (N)	2.56 (184)	2.44 ^b (97)	2.69 ^b (100)	2.44 ^b (90)

^aSize in millimeters. SD, standard deviation. N, number of individuals measured.

^bGroups that were significantly different from SSW, based on non-parametric Mann-Whitney tests.

were generally present at least in low concentration in all locations, although a few species, such as *Centropages* spp. and *Metridia lucens*, tended to be more abundant outside SSW. SSW was notably depauperate in several noncopepod taxa. Fish eggs were rare in SSW during all cruises, and several predator groups were rare or absent in May from SSW. The absence of hydroid hydranths in SSW, compared to their moderate abundance in non-SSW surface and deep samples in the northeast, was a clear difference. There were also subtle differences among locations. SSW had an older *C. finmarchicus* life history stage structure than adjacent non-SSW in May, but was similar in April.

[50] The absence of a unique indicator species for SSW is not surprising. Zooplankton species assemblages on the Scotian Shelf, the proximate upstream source of SSW, are similar to SSW and non-SSW samples on and near Georges Bank. *C. finmarchicus* is the dominant springtime copepod on the Scotian Shelf [Tremblay and Roff, 1983; Corey and Milne, 1987; Sameoto and Herman, 1992; Head et al., 1999; McLaren et al., 2001], similar to Georges Bank. Some apparent differences between Scotian Shelf and SSW crossover fauna are most likely related to differences in sampling techniques and recent taxonomic revisions. For example, *Pseudocalanus* spp., a codominant with *C. finmarchicus* in this study, is now known to consist of the *moultoni/newmani* species complex [Frost, 1989; Bucklin et al., 2001]. In some Scotian Shelf work done before the systematic revision of this genus, *P. minutus* was the only *Pseudocalanus* species mentioned (it was rare in our samples), although later reports documented the other species as well [McLaren et al., 1989]. Bucklin et al. [2001] hypothesized that *P. newmani* was the most likely species to be transported in SSW, and suggested that this input may be essential for its population development on Georges Bank. The Scotian Shelf investigations also reported more species with oceanic affinities, probably because many of their transects extended beyond the shelf to deep water.

[51] Despite geographical proximity, the seasonal development cycle of *C. finmarchicus* populations differed between SSW and adjacent non-SSW on the northeast part of Georges Bank. In April, *C. finmarchicus* had similar population structures (relative abundances of life stages) in these two environments, while in May, the SSW population

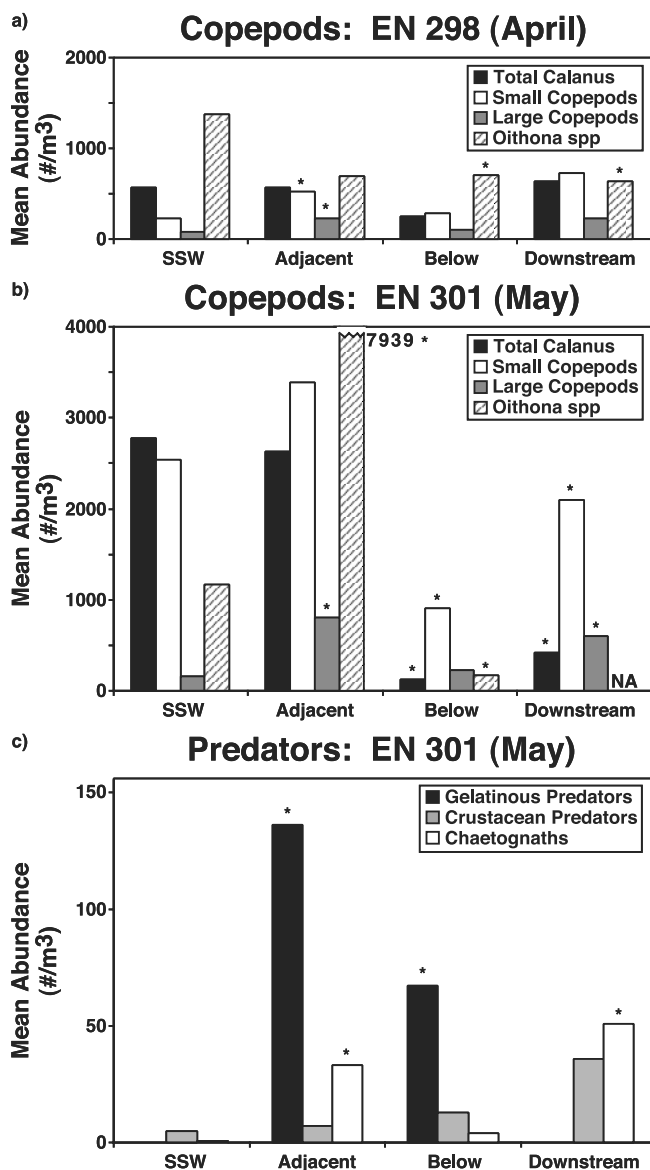


Figure 9. Bar graphs showing mean abundances (number/ m^3) of ecological groups by location category. Asterisks indicate values significantly different from SSW. (a) Copepods from EN 298, (b) copepods from EN 301, (c) invertebrate predators from EN 301. “Total *Calanus*” refers to *C. finmarchicus*.

appeared to be lagging behind the adjacent non-SSW population in its development rate, consistent with the lower SSW temperature. The number of generations per year in this species depends on geographic location. One generation per year occurs in the Labrador Sea [Head et al., 2000], two generations per year on the Scotian Shelf [McLaren et al., 2001], and probably two generations on Georges Bank [Durbin et al., 2000]. During the April cruise, SSW and adjacent non-SSW northeast samples were both dominated by early copepodites of the G1 generation, suggesting that similar environmental conditions were influencing both Georges Bank and the Scotian Shelf. In May, the high abundance of stages C1s and C2s in non-SSW samples was probably due to the appearance of the G2 generation on

Georges Bank [Durbin et al., 2000]. The SSW stage proportions, however, reflected mostly the aging of the earlier G1 generation, as observed on the Scotian Shelf in May [McLaren et al., 2001], although abundances of all stages were higher than in April.

[52] Sizes of some *C. finmarchicus* life history stages differed between SSW and other locations during both April and May, but in different ways. Stage size is an indicator of the water temperature in which development and growth occurred, with larger individuals within a stage characteristic of colder water, assuming sufficient food availability [Campbell et al., 2001]. Thus size differences can be used to characterize populations with different environmental histories. During April, both C4s and C5s in SSW and adjacent non-SSW were about the same size as animals reared in the laboratory at 4°C [Campbell et al., 2001], despite colder temperatures in SSW. Individuals from both environments may have been mixed by the overturning water observed in April, or the temperature difference between the habitats was not sufficient to affect size. During May, SSW C4s were similar in size to laboratory animals at 8°C, while C5s resembled those from 4°C. The older C5s probably spent more time at the cold early spring temperatures on the Scotian Shelf and SSW than the younger C4s. Both C4s and C5s in adjacent non-SSW in the northeast part of the Bank were intermediate in size between individuals grown at 4°C and 8°C, consistent with the warmer temperature of the adjacent non-SSW. The size difference between SSW and adjacent non-SSW populations during May compared to April coincided with a more stable water column structure and increased habitat separation in May. SSW sizes were similar to those of the same stages during spring 1991 on the Scotian Shelf [McLaren et al., 2001].

[53] Invertebrate predator abundances in May were consistent with the long-term pattern of a peak over the center of the Bank out to the SF and comparatively low abundances on the NEP [Sullivan and Meise, 1996]. It was surprising, however, that most predators had lower abundances in SSW compared to adjacent non-SSW, given that all of the predator species except hydroids are commonly found both on Georges Bank and the Scotian Shelf where SSW originates. One clue to their low abundance in SSW is that diel vertical migration to the surface at night appeared to be truncated in SSW areas compared to adjacent non-SSW areas. In SSW, there were no significant day versus night abundance differences for these predators, while in nearby non-SSW areas several predators showed significant day-night differences in abundance in the upper water column. Perhaps the SSW environment is in some way unfavorable for these species or the strong gradients in salinity and temperature at the base of SSW are a barrier to their upward movement. In any case, one consequence of reduced predator abundances in SSW is potentially reduced predation rates on their prey (including *C. finmarchicus*) in SSW. Thus SSW animals may survive longer with a greater proportion reaching older life history stages than in non-SSW. This process could further explain the more abundant older stages found in SSW compared to adjacent non-SSW in May, as well as the very low number of *C. finmarchicus* on the Bank crest.

[54] The high abundance of the small cyclopoid copepod *Oithona* spp. in the adjacent water outside SSW, despite the increased concentration of predators there, may be attributed

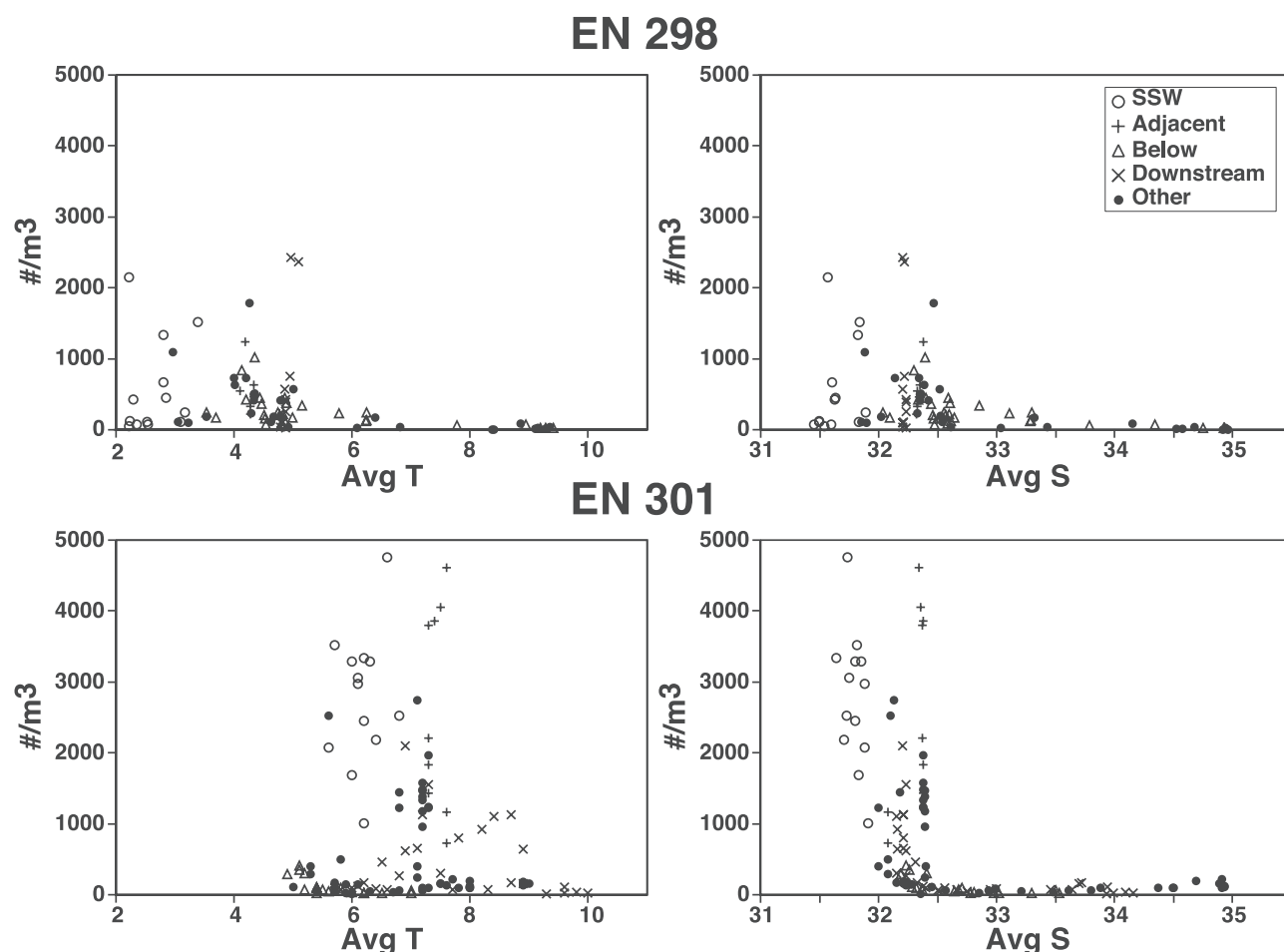


Figure 10. *C. finmarchicus* abundance in each net relative to the average temperature (T) or salinity (S) for the depth interval of that net from the MOCNESS data. All nets from the tows in Table 1 were used. The open circles designate nets from SSW. The “Other” category includes transition nets and nets from deep water in GB and on the NEP.

to its unique biology. *Oithona* spp. swims less actively than many calanoids [Paffenhoffer and Mazzocchi, 2002], reducing its encounter rate with invertebrate predators and thus its vulnerability to predation relative to calanoid species [Costello et al., 1999]. Small size may also provide a refuge from predation for this copepod [Suchman and Sullivan, 1998].

[55] The overall pattern of in vivo fluorescence and chlorophyll distribution is consistent with Bank-wide observations made during the same months in 1997 [Townsend and Thomas, 2001], where near surface chlorophyll began to increase in February, declined by April, then exhibited a secondary bloom during May. The optical characteristics of in vivo fluorescence and light transmission indicate that the particle content of SSW was similar to that of adjacent water masses in April when interleaving and, presumably, mixing of SSW with Bank water occurred (Figure 6). In contrast, in May, when the water column was generally more stable, the optical signatures of SSW were distinct from those of Bank water (Figure 6).

4.2. Is SSW a Source of Plankton for Georges Bank?

[56] The high abundance of *C. finmarchicus* in SSW suggests that mixing between SSW crossovers and Georges

Bank water may be a potentially important source of this species for the Bank. However, the entire northeast region of the Bank is a site of high *C. finmarchicus* concentrations in spring [Meise and O'Reilly, 1996; Durbin et al., 1997, 2000], and total *C. finmarchicus* abundance did not differ significantly between SSW and adjacent non-SSW during the 1997 April or May cruises. The major input of *C. finmarchicus* to Georges Bank is thought to occur at the northern edge of the Bank from the Gulf of Maine [Davis, 1987; Meise and O'Reilly, 1996; Durbin et al., 1997; Hannah et al., 1998; Lynch et al., 1998]. Additional input may come from the Great South Channel to the west, where dense aggregations of *C. finmarchicus* occur each spring [Wishner et al., 1988, 1995]. Presumably, these sources supplied the animals found in our adjacent non-SSW samples on the northeast region of the Bank.

[57] The ultimate origin of the SSW *C. finmarchicus* population is unknown, but is consistent with a Labrador Shelf Water source, similar to that of the low salinity water on Georges Bank in 1997 [Houghton and Fairbanks, 2001; Smith et al., 2001]. Potential sources of the Scotian Shelf population upstream from Georges Bank include development on the Shelf from animals overwintering in deep basins, transport from the Gulf of St. Lawrence in the

coastal Nova Scotia Current, and input from the Labrador Current or slope water at the outer edge of the shelf [Sameoto and Herman, 1990, 1992; Head *et al.*, 1999]. Although the exact scenario is controversial [McLaren *et al.*, 2001], the Gulf of St. Lawrence is not a likely source of *C. finmarchicus* during spring because of the species' late reproductive cycle there, in which peak abundances of young stages do not occur until July [Plourde *et al.*, 2001]. The presence of young *C. finmarchicus* stages in early spring in SSW is consistent with the hypothesis that the Labrador Current and/or deep shelf basins are the distant sources of populations in SSW crossovers on Georges Bank.

[58] The absence of planktonic hydroids in SSW and their abundance in both adjacent and deeper non-SSW samples confirm the hypothesis that they are not being introduced to the Bank from the Scotian Shelf but originate from benthic populations on the northeast peak [Concelman *et al.*, 2001].

[59] Despite reports suggesting that SSW is an important source of fish eggs to the Bank [Sibunka and Weiner, 1997; Townsend and Thomas, 2001], fish egg abundances in SSW were low during our cruises in March, April, and May 1997. SSW was clearly not a major source of fish eggs at these times, regardless of the extent of mixing that may have occurred. Fish egg abundances were significantly higher in adjacent non-SSW on the northeast region of Georges Bank than in SSW during both April and May and were absent from the two March SSW samples. There are several possible explanations for this discrepancy. Reports published to date include data from bongo nets towed to depth through the water column. These reports do not differentiate between eggs found specifically in SSW (the low salinity surface layer) versus those elsewhere in the water column [Sibunka and Weiner, 1997]. It is also possible that fish eggs are more common in SSW at other times or in other years, although 1997 was a typical recent year for haddock eggs and a somewhat high year for cod eggs [Wiebe *et al.*, 2002]. Most of the gadoid egg input occurs earlier in February or March [Wiebe *et al.*, 2002] and may have been missed by our sampling. Analyses of the multiyear GLOBEC broad-scale surveys, that employed stratified MOCNESS sampling monthly at standard stations, are presently underway by other investigators and may help to resolve the bigger picture. Our study, however, is the only GLOBEC process work that specifically targeted SSW crossovers with replicated stratified sampling to address this issue in detail.

4.3. What is the Spatial and Temporal Variation in the Potential Biological Impact of SSW Crossovers During Spring?

[60] SSW crossovers onto the northeast region of Georges Bank showed evidence of mixing and interleaving with adjacent non-SSW early in April 1997, but not later in May. If this pattern is representative of the long term mean seasonal cycle, then early spring is the most likely time for physical and biological mixing to occur and its impact on Georges Bank to be greatest. A spring mixing maximum is consistent with observations that drifters most often cross from SSW onto Georges Bank during February–April [Smith *et al.*, 2003]. The long-term signal of SSW crossovers, i.e., colder temperatures on the northeast peak of Georges Bank, is evident in mean, in situ, near surface

temperature (~1-m depth) from the 11-year MARMAP study [Healey, 2001]. However, both satellite-derived SST data and water property measurements for eastern Georges Bank show strong interannual variability in SSW crossovers [Bisagni *et al.*, 1996; Bisagni and Smith, 1998].

[61] Tidal currents in conjunction with the seasonal increase in stratification may influence the degree of mixing between SSW and Georges Bank water. Interleaving, unstable upper water columns noted during EN 298 occurred on 12 April just 3 days after the spring tide current maximum. This timing calculation, based upon modeled, daily averaged tidal currents for station M9 on the southern flank of Georges Bank, was computed using the M_2 , S_2 , N_2 , O_1 , and K_1 tidal current components of Moody *et al.* [1984]. However, stable upper water columns, noted during EN 301 on 29 May, also occurred close to (4 days after) a spring tidal current maximum. The tidal fronts and tidal mixing occur regardless of the presence of SSW, with the location of the fronts strongly dependent on bathymetry and therefore possibly on tidal phase. Variability observed among closely spaced stations in the northeastern and SF regions of the Bank may have been affected by tidal amplitude and the position of tidal mixing fronts, as well as by SSW.

[62] Plankton contained in water collected on the Bank edge are less likely to mix while plankton collected toward the center are more likely to mix because tidal mixing is strongest on the shallower parts of the Bank. There is a consistent minimum in annual SST variability, indicative of strong tidal mixing, from the 80–100 m isobaths [Bisagni *et al.*, 2001].

[63] Overall, the observed distributions of in vivo fluorescence and plant pigments during both months appear to reflect the seasonal phytoplankton production cycle in specific geographic regions on and around the Bank [O'Reilly *et al.*, 1987]. The high levels of extracted chlorophyll and in vivo fluorescence observed on the NEP in both SSW and non-SSW water in April had declined by May. In GB, where the spring bloom typically occurs later in the season than on Georges Bank [O'Reilly *et al.*, 1987], the relatively low levels of extracted chlorophyll and in vivo fluorescence observed in the upper water column in April achieved bloom concentrations by May. A similar pattern was observed in the NEC (data not shown), which, like GB, is part of the Gulf of Maine region. At the downstream station on the SF, thermal stratification developed between April and late May. The water column of the SF was well mixed in April, and this is reflected in the relatively low pigment and fluorescence values. The deep chlorophyll maximum, characteristic of stratified waters on the SF, developed in May, exhibiting the highest concentrations of chlorophyll and in vivo fluorescence observed at any station in this study.

[64] During May, SSW and non-SSW populations of *C. finmarchicus* were distinguished by traits including size and life history stage structure (proportions of each stage), but during April, most of these characteristics were similar in both groups. The maintenance of differences in May implies that little mixing had occurred between the two groups and that water masses remained separate. The appearance in May of a large population of *Oithona* spp. in adjacent non-SSW compared to SSW also suggests separation between populations and water masses. This is

consistent with the stable water column structure in CTD profiles and also the lack of reported drifter crossovers during May 1999 [Smith *et al.*, 2003].

[65] There are several possible explanations for the similarities observed in April. First, mixing of SSW and non-SSW plankton may have obscured differences among populations. Alternatively, environmental conditions in early spring prior to water column stratification may have been similar enough in SSW and non-SSW that growth and development rates did not vary sufficiently between water masses to produce significant differences in copepod size or life history stage structure at the population level. The colder temperatures in April compared to May would slow growth rates, and animals present in April would also have been exposed to such environmental differences for less time than those of the same generation in May. Both of these factors would reduce the possibility of observing divergence.

[66] Estimating the amount of zooplankton that SSW contributes to the Georges Bank ecosystem is complex. Unlike a river whose entire freshwater flow enters the sea and whose input can be calculated directly, most SSW enters the Gulf of Maine off Cape Sable, Nova Scotia, while the SSW crossovers penetrate Georges Bank at its eastern edge. Thus mixing of the Georges Bank and SSW zooplankton communities would occur only along the borders of this circulation system. As a conceptual approach, there are two components that must be quantified for each time interval: (1) the transport of zooplankton within SSW onto the Bank, and (2) the proportion of those animals that actually become mixed into the Bank community. These variables then need to be integrated temporally over the seasonal cycle. One simplifying factor is that most SSW zooplankton do not show diel vertical migration, meaning that they are likely to remain associated with a water parcel. The first component can be estimated from the volume transport of SSW over Georges Bank (using satellite-derived SST for area and CTD data for thickness) multiplied by the mean concentration of zooplankton in SSW. An estimate of SSW transport onto the Bank was previously derived using an inverse method from heat budget calculations [Bisagni *et al.*, 1996], yielding a result of 0.21 ± 0.06 Sv for a large SSW crossover during spring 1992. The second component, however, is much more difficult to address quantitatively. Detailed dynamics of small-scale mixing processes involving inversions and tidal cycles, such as we observed, are still not well understood and were not modeled for our cruise. A larger scale perspective comes from drifter studies. In 1999, 4% (17%) of drifters released near Brown's Bank in SSW crossed the 60 m (100 m) isobath of Georges Bank with transit times of a few days to almost a month [Smith *et al.*, 2003], so an initial estimate might be that 4–17% of SSW zooplankton mixes onto the Bank, at least during early spring. Since almost all of the low salinity signal on Georges Bank in 1997 came from SSW [Houghton and Fairbanks, 2001; Smith *et al.*, 2001], freshwater river input would not complicate this calculation. Biological and physical results suggest that most of the annual transport of SSW onto the Bank probably occurs as a seasonal peak in winter to early spring. This supports our hypothesis that SSW may be especially important in supplying young life stages of *C. finmarchicus* early in the year to the Georges Bank ecosystem. Once the zooplankton mix, ecological factors

such as competition and predation with a new suite of animals would affect survival.

5. Conclusions

[67] SSW crossovers on Georges Bank are physically and biologically distinct from other Bank locations, based on a 1997 sampling series that specifically targeted these features. Physically, SSW is characterized by low salinity and colder temperatures than adjacent surface water. Biological distinctions are more subtle. In early spring (April), light transmission and *in vivo* fluorescence are highly variable in all regions of the Bank, including SSW. In contrast, in late spring (May), the optical characteristics of SSW differ markedly from those of adjacent surface waters. SSW communities do not contain a unique suite of zooplankton or a specific indicator species but instead show differences in abundance and life history parameters for various taxa compared to other Georges Bank locations. SSW has high abundances of young *C. finmarchicus* life history stages, almost no diel vertical migration of zooplankton into or out of SSW, lower abundances of invertebrate predators in SSW than elsewhere including a complete absence of hydroids, and low fish egg abundances. Population development of *C. finmarchicus* in SSW lags that in adjacent water by late spring (May), and the sizes of some life history stages in SSW differ from those elsewhere.

[68] SSW is probably an important source to Georges Bank of young stages of *C. finmarchicus* in early spring (April), as suggested by their high abundances and the physical evidence for mixing at this time. During our cruises, however, SSW was not a major source to Georges Bank of invertebrate predators or fish eggs, since these taxa had lower abundances in SSW compared to water elsewhere. This might differ at other times and places, however.

[69] The potential biological impact of SSW crossovers on Georges Bank varies with the seasonal cycle and Bank location. In April, density inversions and interleaving of SSW and non-SSW suggested the presence of active mixing. The relatively similar composition of SSW and adjacent non-SSW communities in April probably resulted from such mixing, or alternatively, reflected similar early spring conditions and plankton development processes in each water mass. In May, after stratification strengthened, the greater differentiation between SSW plankton and elsewhere indicated that mixing between communities was more limited. Also, as populations aged, there was more time for contrasting environmental conditions in the various water masses to affect their communities differentially and result in increased divergence among locations. Spatially, mixing of SSW plankton onto Georges Bank is most likely at locations of intermediate depth (80–100 m) because of potential interactions with tidal fronts. Quantifying the mixing of water and plankton between SSW crossovers and Georges Bank, and realistically incorporating spatial and temporal variability, remains a challenging problem for both physical and biological oceanography.

[70] **Acknowledgments.** We would like to thank the following people who helped in the lab or at sea: T. Cucci, M. McManus, P. Donaghay, C. Gelfman, G. Klein-MacPhee, E. Martin, J. Merrell, K. Merrell, D. Nelson, S. Nelson, T. Orvash, M. Rapien, J. Schadlick, M. Sieracki, J. Sullivan, J. Szelag, M. Twardowski, J. Van Keuren, M. Wah, and the captains and crew of the R/V *Endeavor*. This work was supported by the

National Science Foundation and the National Oceanic and Atmospheric Administration by grants OCE9632746 and OCE9806444 to K. Wishner, NOAA/CMER NA87FE0092 and OCE9806376 to J. Bisagni, OCE9632634 and OCE9806375 to D. Gifford, and OCE9632395 and OCE9806594 to B. Sullivan, as well as funding from the University of Rhode Island. This is contribution 382 from the U.S. GLOBEC program.

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J. J. Bisagni, Physics Department and School for Marine Science and Technology, University of Massachusetts, New Bedford, MA 02744, USA.
 D. J. Gifford, B. K. Sullivan, and K. F. Wishner, Graduate School of Oceanography, University of Rhode Island, Narragansett, RI 02882, USA. (kwishner@gso.uri.edu)
 D. M. Outram and D. E. Van Keuren, Graduate School of Oceanography, University of Rhode Island, Narragansett, RI 02882, USA.

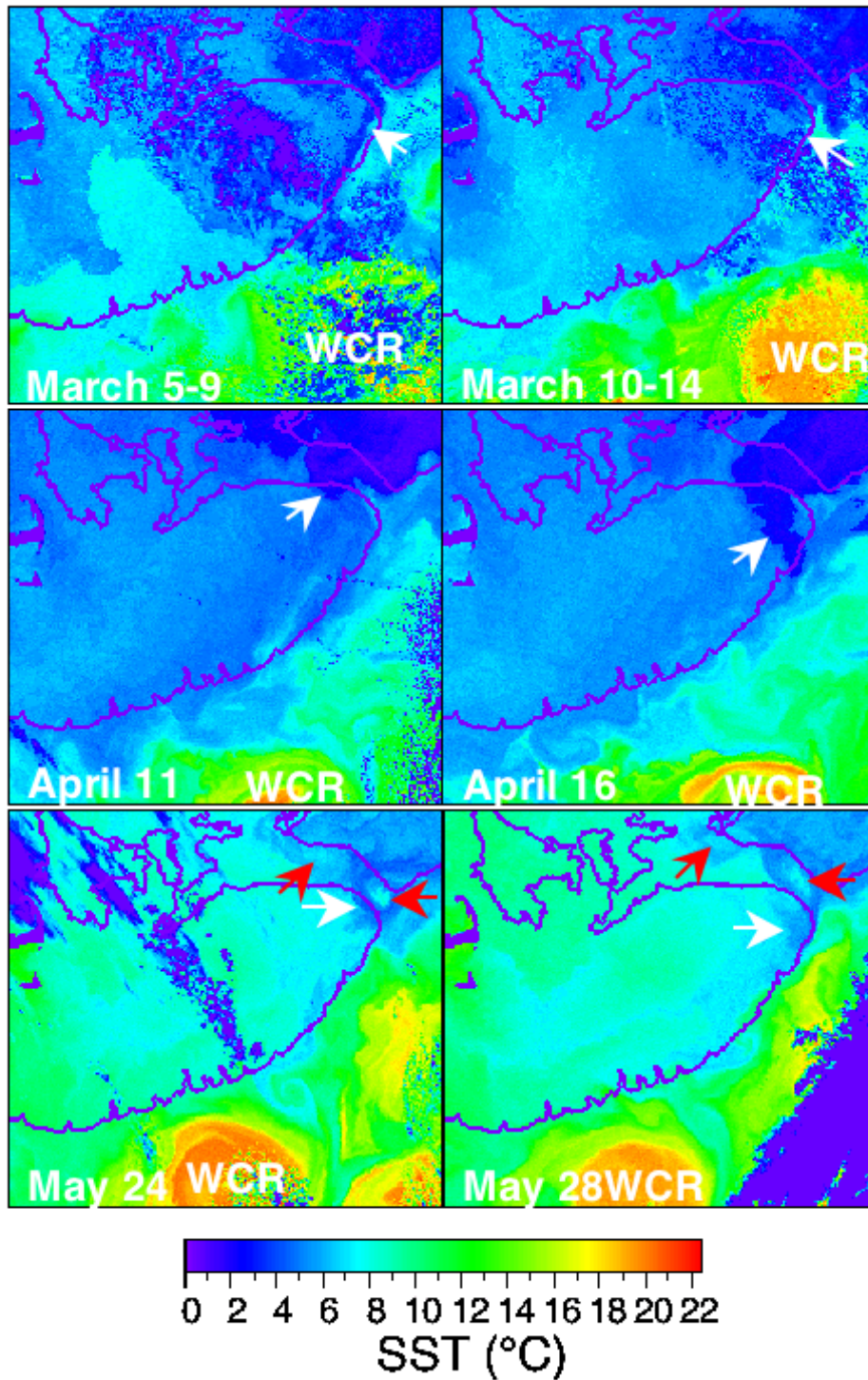


Figure 2. Satellite-derived SST images from spring 1997 corresponding to the EN 296 (March), EN 298 (April), and EN 301 (May–June) cruise periods. SST images with a range of dates are 5-day, warmest-pixel composite images. SST images with single dates are daily images. Also shown is the 200-m isobath (thick purple line), the locations of SSW crossovers (white arrows), the pair of cyclonic eddies (red arrows), and Gulf Stream warm-core rings (WCR).