

Variations in Overwintering Depth Distributions of *Calanus finmarchicus* in the Slope Waters of the NW Atlantic Continental Shelf and the Labrador Sea

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Abstract

Vertical depth distributions of *Calanus finmarchicus* were examined in autumn and winter (2001–2003) for the slope and offshore waters of the Canadian Atlantic continental shelf from the south Labrador Shelf in the north to the southwestern tip of the Scotian Shelf in the south as well as along sections across the Labrador Sea and in Cabot Strait. A total of 324 samples were collected at 53 stations that ranged over ~19 degrees of latitude and ~17 degrees of longitude.

Calanus finmarchicus populations in the subsurface layers (depths >100 or 200 m) were dominated (>90%) by CV copepodites off the western Scotian Shelf, in Cabot Strait, the central Newfoundland slope waters and the Labrador Sea. Along the slope between Flemish Pass and the eastern Scotian Shelf CVs made up 60–80% of the population in autumn and 80–86% in winter, with accompanying CIVs being replaced by CVs and adults between autumn and winter. CVs were deepest off the Greenland Shelf (70% below 1 000 m) and shallowest in Cabot Strait (80% in the 100–300 m interval; bottom depth ~450 m). Overwintering depth intervals were generally broad and covered large ranges of temperature and salinity.

There were relatively high concentrations (>15 m⁻³) of late stage (CIV–CVI) *C. finmarchicus* in the surface layers in the Cabot Strait region in autumn (2003) and in the slope waters off St. Pierre Bank (south Newfoundland Shelf) in winter (2003). These were probably the result of late seasonal production in the Gulf of St. Lawrence and Cabot Strait region, or on the Newfoundland Shelf where vertical ring net tows indicated high numbers (>10 000 m⁻²) of *C. finmarchicus* at stations upstream of the St. Pierre Bank sampling area.

The vertical distribution data from winter 2003 suggest that transport of overwintering animals around the Tail of the Grand Bank where water depths are >1 000 m and southwestwards along the Scotian shelf break was limited, and that populations along the slope between the NW Grand Bank and the eastern Scotian Shelf had important local sources. There was also evidence of northeasterly transport of overwintering CVs from the western Scotian Shelf to the central Scotian Shelf slope waters between October and December 2003.

Keywords: *Calanus*, Labrador, NW Atlantic, overwinter, plankton, Scotia Shelf, vertical distribution.

Introduction

The copepod *Calanus finmarchicus* provides an important food source for larval groundfish and pelagic fish

on the NW Atlantic continental shelf, where it can constitute 70% or more of the zooplankton biomass. The life cycle is annual over much of its range (Conover, 1988), which includes the North Atlantic waters north of the

Gulf Stream from Georges Bank and the Gulf of Maine in the southwest to the Norwegian Sea and Barents Sea in the northeast. *Calanus finmarchicus* reproduces before and during the spring phytoplankton bloom (e.g. Norwegian Sea, Niehoff *et al.*, 1999; Labrador Sea, Head *et al.*, 2000; Scotian Shelf, McLaren *et al.*, 2001) and the offspring develop in the surface layers in spring/summer. During summer and autumn, most of the new generation migrate downwards, mainly as stage CV pre-adult copepodites, to enter a period of dormancy, often referred to as diapause (e.g. Scotian Shelf, Sameoto and Herman, 1990; McLaren *et al.*, 2001). On the Scotian Shelf some individuals do not descend, but mature to produce a second generation that contributes to the following year's adult spawning population (McLaren *et al.*, 2001). Nevertheless, the seasonal descent of most of the population means that *C. finmarchicus* are largely absent from shelf regions in winter, which must be re-populated in spring from nearby deep waters. The deep waters adjacent to the NW Atlantic continental shelf to the east of the Tail of the Grand Bank comprise the southeasterly flowing western margin of the sub-polar NW Atlantic gyre (Loder *et al.*, 1998, Fig. 1). The sub-polar gyre includes the Labrador and Irminger Seas and is bounded on its southern side by the North Atlantic Current. To the west of the Tail of the Bank the waters adjacent to the shelf comprise the westerly flowing northern boundary of a re-circulation gyre, henceforward referred to as the Slope Water gyre. The Slope Water gyre is bounded on its southern side by the north wall of the Gulf Stream, with easterly and westerly limits at the Tail of the Grand Bank and Cape Hatteras, respectively. Wiebe (2001) suggested that these gyres, together with the NE Atlantic Norwegian Sea gyre, form three distinct retention areas and distribution centres for *C. finmarchicus* overwintering in the N. Atlantic. Head *et al.* (2003) reported high concentrations of *C. finmarchicus* in the near surface waters of the Labrador Slope and central Labrador Sea (*i.e.* the sub-polar gyre) in spring, which included large numbers of overwintered CVs and females (Head *et al.*, 2000), supporting the idea that the sub-polar gyre can provide a springtime source to the Labrador and Newfoundland Shelves. In addition, Head *et al.* (1999) reported high springtime levels of *C. finmarchicus* along the central and western Scotian shelf-break, consistent with the idea of a Slope Water gyre source for these regions of the Scotian Shelf.

From the Labrador Shelf to the Gulf of Maine, the NW Atlantic continental shelf is an advective system, with equatorward flow over the shelf and in the slope waters (Loder *et al.*, 1998, Fig. 1). In spring and summer *C. finmarchicus* are advected southwards over the shelves in the surface layers, while in autumn and winter

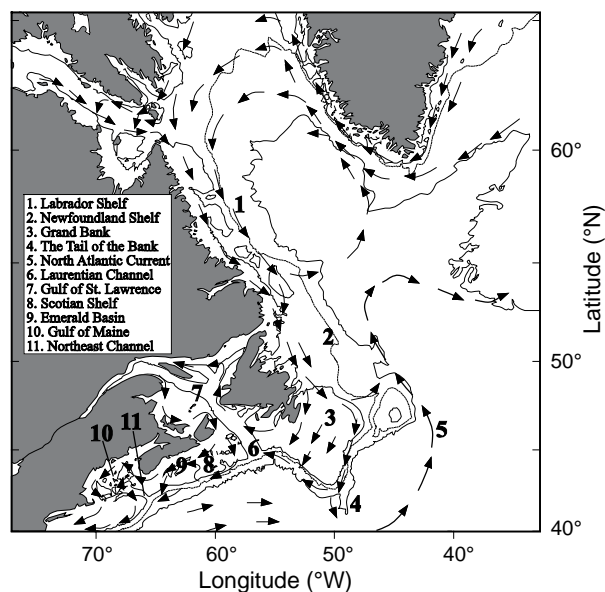


Fig. 1. Major currents of the NW Atlantic shelf and Labrador Sea region (re-drawn from Head and Sameoto, in press, after Loder *et al.*, 1998).

southward transport of overwintering *C. finmarchicus* at depth can occur in the slope waters. Flow around the Tail of the Bank can connect the NW Atlantic sub-polar and Slope Water gyres, although generally much of the flow is deflected to the northeast to join the North Atlantic Current.

Zakardjian *et al.* (2003) developed a biophysical model that supports the idea that the Slope Water gyre may indeed retain overwintering *C. finmarchicus* exported from the Scotian Shelf and the Laurentian Channel, which can return to the shelf the following season. Speirs *et al.* (2006) developed a basin-scale biophysical model for *C. finmarchicus* for the entire North Atlantic, which suggests connectivity throughout the entire domain, although it predicts that advective transport has little effect on the population dynamics of *C. finmarchicus* within the NW Atlantic sub-polar and Norwegian Sea gyres. These models do, however, show that transport is important for shelf regions and at the limits of the geographic range of *C. finmarchicus*, and indicate that the population in the Gulf of St. Lawrence is self-sustaining.

Existing reports of overwintering depths of *C. finmarchicus* in the North Atlantic show that they vary from 300–1 500 m, with most populations west of Iceland occurring in waters of $\sim 4^{\circ}\text{C}$, while most populations east of Iceland occur in waters between -1 – 2°C (Halvorsen *et al.*, 2003; Heath *et al.*, 2004). Off Rockall Bank and in the Norwegian Trench, however, *C. finmarchicus*

overwinter at 7–8°C (Heath *et al.*, 2004) and overwintering temperatures of up to 11°C have been reported for Emerald Basin (on the Scotian Shelf) and west of the British Isles (Kaartvedt, 1996). Most overwintering *C. finmarchicus* occur at salinities of ~34.9‰. Heath *et al.*'s (2004) summary of data from many contributors was rich in observations east of Greenland but provided only a brief summary of data from the Labrador Sea and there were no data from the Northwest Atlantic (Newfoundland to the southern Scotian Shelf).

In this paper we present detailed observations of hydrography and the vertical distribution of *C. finmarchicus* in autumn and/or winter in the Labrador Sea, the slope waters from the south Labrador Shelf in the north to the western tip of the Scotian Shelf in the south, the Slope Water gyre and the Cabot Strait region. No such observations have been reported before for these regions of the NW Atlantic, which cover ~19 degrees of latitude and ~17 degrees of longitude. Our observations have enabled us to examine the winter-time connectivity of populations among regions, and the importance of different sources to different slope water regions. In addition, we present observations on the distribution of *C. finmarchicus* on the shelves in 2001 and 2003, which show that the species is not completely dormant in October–December.

Materials and Methods

Sampling was conducted either as part of regional oceanographic surveys coordinated by the Atlantic Zone Monitoring Program (AZMP; Therriault *et al.*, 1998) or as part of directed studies, some of which have been ongoing for many years (*e.g.* Labrador Sea AR7W line). Samples from AZMP surveys were collected using a multiple net system at the deepest stations of the fixed transects. Other sampling sites, such as those to the West of the Southeast Shoals (SPB, GBL1 and GBL2 lines, Fig. 2), were chosen to provide observations for previously under-represented regions. Hydrographic, water and plankton sampling in the autumn was conducted at stations on the Newfoundland Shelf and in the slope waters east of the Tail of the Grand Bank and south of the Labrador Shelf between 15–24 November 2001 (Fig. 2, Tables 1 and 3). Similar sampling in autumn at stations west of the Tail of the Bank (west of the SEGB line), on the Scotian Shelf and in the slope waters, was between 19–31 October 2003. Winter cruises included sampling at stations along a section across the Labrador Sea between 3–9 December 2002 and at stations in the slope waters to the west of the Tail of the Grand Bank between 11–21 December 2003.

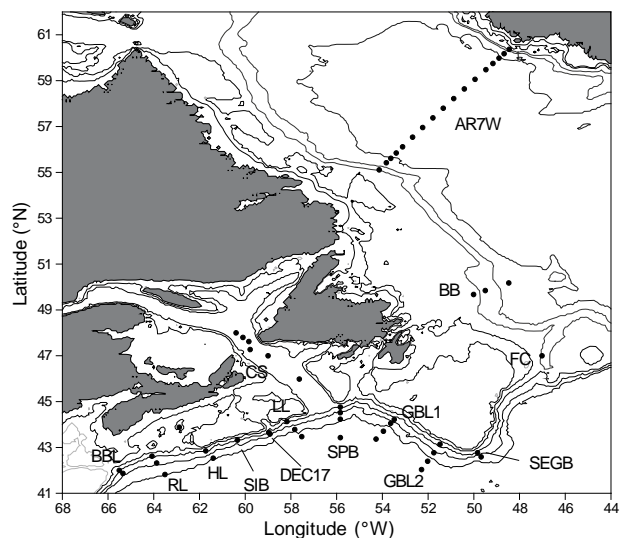


Fig. 2. Stations where vertically stratified Multi-net tows were performed. The lines are from northeast to southwest: AR7W, Atlantic Repeat Section 7 West (of the WOCE programme); BB, Bonavista Bay Line; FC, Flemish Cap Line; SEGB, Southeast Grand Bank Line; GBL2, Grand Bank Line 2; GBL1, Grand Bank Line 1; SPB, St Pierre Bank; CS, Cabot Strait region (includes all stations in the Laurentian Channel); LL, Louisbourg Line; DEC17, stations occupied on December 17; SIB, Sable Island Bank; HL, Halifax Line; RL, Roseway Line; BBL, Browns Bank Line. The lines denote 100, 200, 1 000, 2 000 and 3 000 m contours.

Hydrographic measurements and water sampling

Temperature and salinity profiles were collected at all sampling stations using a Seabird Model SBE 25 sensor on cruises in autumn 2003 and winter 2002 and 2003 or a SBE911 sensor in autumn of 2001, mounted on a CTD rosette. Water samples were collected in the 0–100 m depth interval at eight fixed depths (5, 10, 20, 30, 40, 50, 75, 100 m) in autumn 2001 and at nine fixed depths (0, 10, 20, 30, 40, 50, 60, 80, 100 m) in autumn 2003 and winter 2002. Water samples (100 ml) were filtered on to Whatman GF/F glass fibre filters and chlorophyll concentrations were measured after ~24 h extraction in 90% acetone at -20°C using a Turner designs fluorometer and the Holm-Hansen *et al.* (1965) method, except in the case of the autumn 2001 cruise, when the Welshmeyer (1994) method was used.

Zooplankton sampling

Vertically stratified tows were made using a 0.5 × 0.5 m square-mouthed Hydro-bios Multi-net sampler in water depths of >400 m (Fig. 2, Table 1). The

TABLE 1. Stations where vertically stratified net tow were made using the Multi-net in autumn (A) and winter (W) 2001, 2002 and 2003. Stations are listed with lines in order from the north east to the southwest, and stations seaward from Canada. Stations not identifiable in the Fig. 2 figure legend are in the Cabot Strait region: LH1-3, Laurentian Hole Stations 1-3 (numbered proceeding up the Laurentian Channel); CSL4, Cabot Strait Line Station 4; LCN, Laurentian Channel North (a little south of Cabot Strait); LCL4, Laurentian Channel Line Station 4 (mid-way between Cabot Strait and the shelf-break).

Station name	Latitude (Decimal Degrees)	Longitude	Nominal depth	Sample season/year (m)	Maximum tow depth (m)	Surface tow depth	No. of nets
AR7W-08	55.12	54.13	960	W, 2002	840	0-200	5
AR7W-10	55.42	53.82	2 700	W, 2002	1 500	0-200	7
AR7W-11	55.61	53.63	2 900	W, 2002	1 000	0-200	5
AR7W-12	55.85	53.40	3 160	W, 2002	1 000	0-200	5
AR7W-13	56.11	53.12	3 340	W, 2002	2 000	0-200	9
AR7W-14	56.55	52.68	3 500	W, 2002	1 000	0-200	5
AR7W-16	57.37	51.80	3 560	W, 2002	2 000	0-200	9
AR7W-18	58.22	50.88	3 570	W, 2002	1 000	0-200	5
AR7W-19	58.63	50.42	3 540	W, 2002	2 000	0-200	9
AR7W-20	59.07	49.95	3 490	W, 2002	1 000	0-200	5
AR7W-21	59.48	49.47	3 410	W, 2002	2 000	0-200	9
AR7W-22	59.75	49.17	3 270	W, 2002	1 000	0-200	5
AR7W-23	59.99	48.90	3 040	W, 2002	1 000	0-200	5
AR7W-24	60.18	48.68	2 880	W, 2002	2 000	0-200	9
AR7W-26	60.37	48.50	2 740	W, 2002	540	0-100	5
BB-11	49.67	50.01	607	A, 2001	580	0-100	5
BB-12	49.85	49.50	1 372	A, 2001	1 300	0-200	5
BB-14	50.18	48.47	2 349	A, 2001	2 000	0-200	9
FC-17	47.00	47.02	1 130	A, 2001	1 130	0-200	5
SEGB-16	42.77	49.84	1 485	A, 2001	1 480	0-200	5
SEGB-17	42.59	49.68	2 500	A, 2001	2 200	0-300	5
GBL2-3	43.14	51.48	1 000	W, 2003	900	0-200	5
GBL2-4	42.77	51.75	2 270	W, 2003	2 000	0-200	9
GBL2-5	42.40	52.02	3 400	W, 2003	1 000	0-200	5
GBL2-6	42.03	52.29	4 300	W, 2003	1 000	0-200	5
GBL1-3.5	44.22	53.48	1 300	W, 2003	1 250	0-200	5
GBL1-4	44.05	53.64	2 380	W, 2003	2 000	0-200	9
GBL1-5	43.71	53.95	3 786	W, 2003	1 000	0-200	5
GBL1-6	43.37	54.28	4 206	W, 2003	1 000	0-200	5
SPB08	44.76	55.84	1 072	W, 2003	1 030	0-200	5
SPB09	44.52	55.84	2 260	A, 2003	1 000	0-200	5
SPB10	44.23	55.84	2 923	A+W, 2003	1 000	0-200	5
SPB12	43.43	55.84	3 057	W, 2003	1 000	0-200	5
LH3	48.00	60.40	486	A, 2003	478	0-100	5
LH2	47.80	60.10	508	A, 2003	508	0-100	5
LH1	47.62	59.84	534	A, 2003	524	0-100	5
CSL4	47.27	59.78	473	A, 2003	454	0-100	5
LCN	47.00	59.00	449	A, 2003	435	0-100	5
LCL4	45.98	57.63	490	A, 2003	481	0-100	5
LL7	44.13	58.18	960	A, 2003	925	0-200	5
LL8	43.78	57.83	>2 500	A, 2003	1 000	0-200	5
LL9	43.47	57.43	>3 500	A, 2003	1 000	0-200	5
DEC17-1	43.65	58.97	1 390	W, 2003	1 200	0-200	5
DEC17-2	43.59	58.92	1 890	W, 2003	1 800	0-200	5
SIB6	43.32	60.34	1 400	A, 2003	1 000	0-200	5
HL3	43.88	62.88	276	W, 2003	270	0-50	3
HL6	42.85	61.73	1 056	W, 2003	1 030	0-200	5
HL7	42.53	61.40	2 750	A+W, 2003	1 000	0-200	5
RL5	42.62	64.08	900	A+W, 2003	850(A), 930(W)	0-200	5(A),5(W)
RL6	42.32	63.87	1 880	A+W, 2003	1 000(A), 1 875(W)	0-200	5(A),9(W)
RL7	41.82	63.51	3 050	A, 2003	1 000	0-200	5
BBL6	42.00	65.51	1 000	A+W, 2003	946(A), 43(W)	0-200	5(A), 5(W)
BBL7	41.35	65.35	1 850	A+W, 2003	1 000	0-200	5

TABLE 2. Stations where ring net tows were made in autumn (A) and winter (W) 2001, 2002 and 2003. Stations are listed with lines in order from the north east to the southwest, and stations seaward from Canada. Samples were collected between the bottom and the surface, or 1 000 m and the surface at stations deeper than 1 000 m. Stations not identifiable in the Fig. 2 figure legend are stations 1-5 of the Cabot Strait region: CSL1-5, across Cabot Strait, numbered from Nova Scotia to Newfoundland.

Station name	Latitude (Decimal Degrees)	Longitude	Nominal depth (m)	Sample season/year	Station name	Latitude (Decimal Degrees)	Longitude	Nominal depth (m)	Sample season/year
BB-01	48.73	52.97	98	A, 2001	SEGB-10	44.36	51.10	73	A, 2001
BB-03	48.83	52.65	256	A, 2001	SEGB-11	44.00	50.81	73	A, 2001
BB-04	48.92	52.40	352	A, 2001	SEGB-12	43.63	50.52	66	A, 2001
BB-05	49.03	52.07	290	A, 2001	SEGB-13	43.20	50.17	67	A, 2001
BB-06	49.10	51.83	298	A, 2001	SEGB-15	42.85	49.89	389	A, 2001
BB-07	49.19	51.54	312	A, 2001	SEGB-16	42.77	49.84	1 485	A, 2001
BB-08	49.28	51.28	323	A, 2001	SEGB-17	42.59	49.68	2 500	A, 2001
BB-09	49.37	51.02	340	A, 2001	SEGB-19	42.08	49.27	3 000	A, 2001
BB-10	49.52	50.53	332	A, 2001	GBL2-1	43.50	51.20	76	W, 2003
BB-11	49.67	50.01	607	A, 2001	GBL2-2	43.31	51.34	130	W, 2003
BB-12	49.85	49.50	1 372	A, 2001	GBL1-1	44.56	53.16	101	W, 2003
BB-13	50.00	49.00	1 866	A, 2001	GBL1-2.5	44.47	53.24	125	W, 2003
BB-14	50.18	48.47	2 349	A, 2001	SPB5A	45.05	55.95	73	W, 2003
BB-15	50.33	47.95	2 624	A, 2001	SPB6	44.93	55.84	154	W, 2003
FC-01	47.00	52.83	107	A, 2001	CSL1	46.96	60.22	77	A, 2003
FC-02	47.00	52.71	188	A, 2001	CSL2	47.02	60.12	180	A, 2003
FC-03	47.00	52.58	159	A, 2001	CSL3	47.10	59.99	330	A, 2003
FC-04	47.00	52.32	126	A, 2001	CSL4	47.27	59.78	473	A, 2003
FC-05	47.00	52.03	140	A, 2001	CSL5	47.43	59.56	475	A, 2003
FC-06	47.00	51.49	101	A, 2001	CSL6	47.58	59.34	265	A, 2003
FC-07	47.00	51.00	106	A, 2001	LL1	45.83	59.85	90	A, 2003
FC-09	47.00	50.00	85	A, 2001	LL2	45.66	59.70	130	A, 2003
FC-10	47.00	49.12	82	A, 2001	LL3	45.49	59.52	130	A, 2003
FC-12	47.00	48.12	136	A, 2001	LL4	45.16	59.18	102	A, 2003
FC-14	47.00	47.50	218	A, 2001	LL5	44.82	58.85	215	A, 2003
FC-15	47.00	47.25	535	A, 2001	LL6	44.48	58.51	66	A, 2003
FC-17	47.00	47.02	1 130	A, 2001	LL7	44.13	58.18	960	A, 2003
FC-18	47.00	46.83	1 172	A, 2001	LL8	43.78	57.83	>2 500	A, 2003
FC-20	47.00	46.48	350	A, 2001	HL1	44.40	63.45	85	A, 2003
FC-21	47.00	46.02	304	A, 2001	HL2	44.27	63.32	150	A, 2003
FC-24	47.00	45.21	170	A, 2001	HL3	43.88	62.88	270	A, 2003
FC-26	47.00	44.77	150	A, 2001	HL4	43.48	62.45	81	A, 2003
FC-29	47.00	44.23	276	A, 2001	HL5	43.18	62.10	95	A, 2003
FC-31	47.00	43.83	557	A, 2001	HL6	42.85	61.73	1 056	A, 2003
FC-33	47.00	43.40	1 236	A, 2001	HL7	42.53	61.40	2 750	A, 2003
FC-35	47.00	43.00	3 550	A, 2001	BBL1	43.25	65.48	70	A, 2003
SEGB-01	46.58	52.93	53	A, 2001	BBL2	43.00	65.48	115	A, 2003
SEGB-03	46.35	52.73	173	A, 2001	BBL3	42.76	65.48	100	A, 2003
SEGB-05	46.07	52.50	92	A, 2001	BBL4	42.45	65.48	100	A, 2003
SEGB-06	45.79	52.27	85	A, 2001	BBL5	42.13	65.48	200	A, 2003
SEGB-07	45.46	52.00	82	A, 2001	BBL6	42.00	65.48	1 000	A, 2003
SEGB-08	45.10	51.70	73	A, 2001	BBL7	41.87	65.35	1 850	A, 2003
SEGB-09	44.73	51.40	71	A, 2001					

Multi-net was deployed vertically and collected samples from up to five depth intervals while being towed upwards. At some stations of >1 000 m depth two separate hauls were performed and up to nine depth intervals were sampled. At a station in Emerald Basin (HL3) only three depth intervals were sampled in a water depth of 270 m (Table 1). The volume of water sampled (m³) over each depth interval was estimated as 0.25 m² × the towed

depth (m). On the continental shelves, zooplankton samples were also collected in vertical ring net hauls between the bottom and the surface, or 1 000 m and the surface for depths >1 000 m, with the net rigged in such a way that it towed only on the way up (Table 2). Data from these samples were used to provide a perspective of the abundance of *C. finmarchicus* on and off the continental shelves during the overwintering period. The volume of

TABLE 3. Water column abundances of *Calanus finmarchicus* (individuals m^{-2}) in the Multi-net tows summed over all the depth intervals sampled. At stations in the Labrador Sea, denoted with an asterisk, due to the poor condition of some samples, it was not possible to differentiate CI, CII and CIII *C. finmarchicus* stages; instead the sum of CI-CIII is shown in the column for CII. Stations not identifiable in the Fig. 2 figure legend are in the Cabot Strait region: LH1-3, Laurentian Hole Stations 1-3 (numbered proceeding up the Laurentian Channel); CSL4, Cabot Strait Line Station 4; LCN, Laurentian Channel North (a little south of Cabot Strait); LCL4, Laurentian Channel Line Station 4 (mid-way between Cabot Strait and the shelf-break).

Station name	CI	CII	CIII	CIV	CV	CVI	Total
AR7W-08(W)*		–		400	19 960	1 040	21 400
AR7W-10(W)*		–		440	13 440	720	14 600
AR7W-11(W)*		–		440	15 720	840	17 000
AR7W-12(W)*		160		520	14 920	1 200	16 800
AR7W-13(W)*		40		240	12 920	760	13 960
AR7W-14(W)*		360		520	11 720	720	13 320
AR7W-16(W)*		40		–	14 880	640	15 560
AR7W-18(W)*		–		80	13 320	560	13 960
AR7W-19(W)*		–		480	12 000	680	13 160
AR7W-20(W)*		40		760	15 480	360	16 640
AR7W-21(W)*		–		320	11 840	600	12 760
AR7W-22(W)*		160		200	15 120	600	16 080
AR7W-23(W)*	–	–		80	8 760	560	9 400
AR7W-24(W)*	–	–		880	18 160	640	19 680
AR7W-26(W)*		2 520		600	2 360	200	5 680
BB-11(A)	96	96	96	608	14 944	1 088	16 928
BB-12(A)	64	64	112	376	29 760	2 264	32 640
BB-14(A)	768	448	800	935	12 872	790	16 612
FC-17(A)	–	–	–	13 060	24 975	861	38 896
SEGB16(A)	128	–	320	7 552	37 952	2 496	48 448
SEGB17(A)	32	–	–	7 680	31 840	704	40 256
GBL2-3(W)	2 880	6 120	3 760	1 720	5 600	120	20 200
GBL2-4(W)	–	80	200	1 520	23 720	2 680	28 200
GBL2-5(W)	200	80	120	1 280	10 640	1 240	13 560
GBL2-6(W)	–	–	–	400	2 240	280	2 920
GBL1-3.5(W)	80	120	200	2 400	9 800	1 280	13 880
GBL1-4(W)	–	–	–	720	4 660	532	5 912
GBL1-5(W)	–	–	–	160	2 208	180	2 548
GBL1-6(W)	–	40	–	216	1 808	260	2 324
SPB08(W)	–	–	164	682	8 056	864	9 766
SPB09(A)	–	–	–	444	1 324	216	1 984
SPB10(A)	–	–	–	612	2 120	284	3 016
SPB10(W)	–	–	–	388	3 520	348	4 256
SPB12(W)	–	–	–	176	2 364	152	2 692
LH3(A)	–	360	540	2 120	16 140	220	19 380
LH2(A)	–	1 760	640	3 200	22 080	600	28 280
LH1(A)	–	–	100	1 700	16 720	440	18 960
CSL4(A)	–	1 280	2 080	9 480	45 520	1 000	59 360
LCN(A)	–	160	240	3 080	26 692	340	30 512
LCL4(A)	–	240	160	1 032	4 114	296	5 842
LL7(A)	–	200	620	872	6 116	472	8 280
LL8(A)	–	–	–	456	2 116	184	2 756
LL9(A)	–	160	84	460	2 812	152	3 668
DEC17-1(W)	1 440	1 360	80	388	3 284	528	7 080
DEC17-2(W)	480	80	80	356	3 160	248	4 404
SIB6(A)	–	–	–	212	3 012	192	3 416
HL3(W)	–	–	4	56	17 344	912	18 316
HL6(W)	–	–	–	200	2 236	212	2 648
HL7(A)	–	–	–	32	864	80	976
HL7(W)	–	–	–	182	2 024	76	2 282
RL5(A)	–	600	400	1 204	17 252	1 808	21 264
RL5(W)	–	–	–	88	1 872	192	2 152
RL6(A)	–	–	–	368	6 784	200	7 352
RL6(W)	–	–	–	64	2 976	84	3 124
RL7(A)	–	–	–	116	3 228	176	3 520
BBL6(A)	840	720	256	592	9 584	308	12 300
BBL6(W)	–	–	–	204	9 036	536	9 776
BBL7(A)	–	–	–	296	11 288	408	11 992
BBL7(W)	–	–	–	156	3 644	248	4 048

water sampled (m^3) was assumed to be the cross-sectional area of the mouth of the net (m^2) \times the towed depth (m). Both net systems were fitted with 200 μm mesh nets and retrieved at $\sim 1 m s^{-1}$. Zooplankton samples were preserved in 5% buffered formalin for subsequent identification and enumeration.

Results

Areal distributions in autumn (2001, 2003) and winter (2002, 2003) in Multi-net tows

Calanus finmarchicus populations below the surface sampling layer were assumed to be in an overwintering state. At most stations, the surface sampling layer was 0–200 m, but off the Tail of the Grand Bank (SEGB-17) it was 0–300 m, in the Cabot Strait region and at some shallow stations it was 0–100 m, and in Emerald Basin it was 0–50 m (Table 1). *Calanus finmarchicus* in slope waters consisted mainly of stage CV copepodites (Fig. 3) although 12–34% of animals were CIV copepodites between Flemish Pass (FC-17) and the Eastern Scotian Slope (ESS) in autumn. In winter the CIV contribution dropped to <10% in these areas. Less than 10% of animals were adults in both autumn and winter.

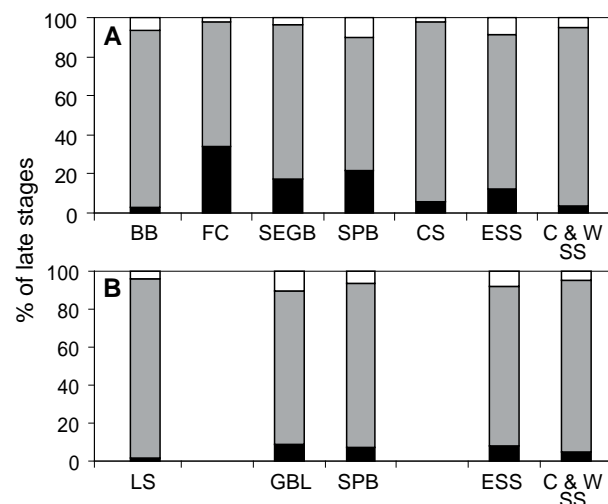


Fig. 3. Relative stage composition (%) of CIV (black), CV (grey) and adult (white) *C. finmarchicus* in the sub-surface layers of the NW Atlantic slope waters and Labrador Sea in Multi-net tows in (A) autumn and (B) winter. Results are averaged over stations in different regions: BB, Bonavista Bay Line; FC, Flemish Cap Line; SEGB, South East Grand Bank Line; SPB, St Pierre Bank Line; CS, Cabot Strait region; ESS, Eastern Scotian Slope (east of and including DEC-17); C & W SS, Central and Western Scotian Slope Water (west of and including SIB); LS, Labrador Sea; GBL, Grand Bank Lines (GBL1 and GBL2).

In autumn, the areal concentrations (number m^{-2}) of late stage *C. finmarchicus* (CIV-CVI) in the subsurface layers (depths >100 or 200 m) were highest at stations in the Cabot Strait region (CSR) and east of the Tail of the Grand Bank (Fig. 4, Table 3). There were moderate concentrations off the Western Scotian Shelf (WSS), and lower concentrations off St. Pierre Bank (SPB) and the ESS. Concentrations of late stages in the surface layers were high only in the CSR. In winter, subsurface concentrations of late stages were highest in the Labrador Sea, on the GBL2 line and in Emerald Basin (Fig. 5, Table 3). Surface layer concentrations were highest on the Western Grand Bank lines (GBL1 and GBL2) and near SPB. Young (CI–CIII) stage *C. finmarchicus* copepodites were abundant in the surface layers in the CSR in autumn and on GBL2 in winter (Fig. 6, Table 3).

Relationship between CV distributions and hydrographic properties (T and S) in autumn (2001, 2003) and winter (2002, 2003)

Subsurface temperature and salinity ranges varied little to the east of the Tail of the Grand Bank and temperature varied more than salinity in the slope waters farther west. In the CSR there were large changes in both temperature and salinity with depth. High concentrations of CV *C. finmarchicus* (m^{-3}) occurred over a wide range of temperatures and salinities throughout the

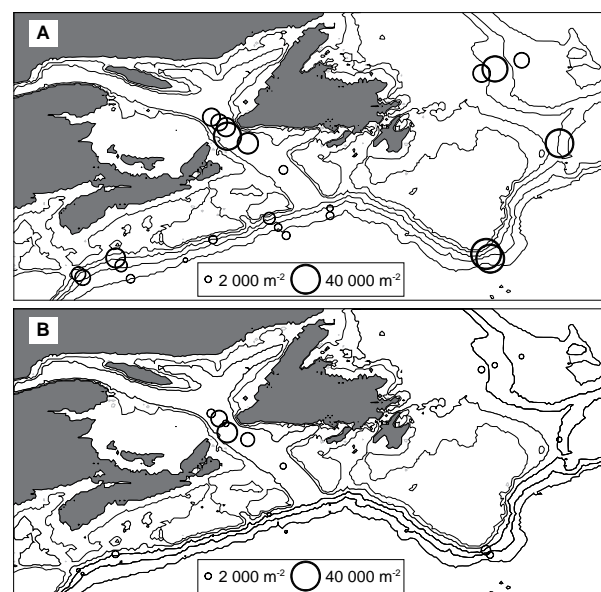


Fig. 4. Areal concentrations of stage CIV-CVI *C. finmarchicus* in autumn 2001 (East of the Tail of the Grand Bank) or 2003 (West of the Tail of the Bank) in the (A) sub-surface (>100 or 200 m) layers to the bottom or 1000 m and (B) surface (<100 or 200 m) layers.

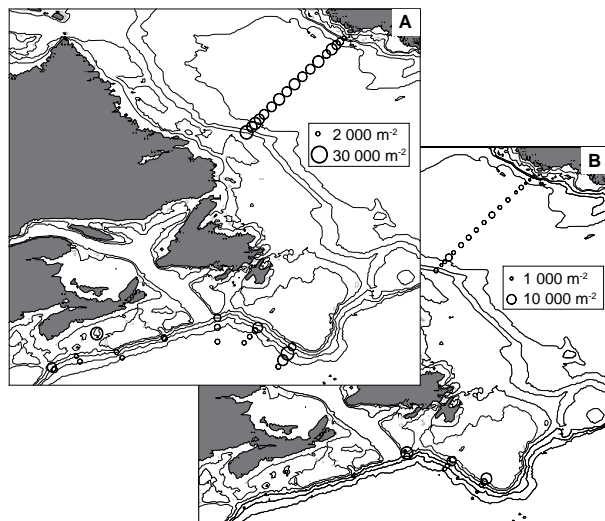


Fig. 5. Areal concentrations of stage CIV-CVI *C. finmarchicus* in winter 2002 (Labrador Sea) or 2003 (West of the Tail of the Grand Bank) in the sub-surface layers (>200 m or >50 m in Emerald Basin, mid-Scotian Shelf) to (A) the bottom or 1000 m and surface layers (B) <200 m or <50 m in Emerald Basin. Note that the surface layer data also includes stations sampled by ring net from bottom to surface for the SPB, GBL1 and GBL2 lines.

entire sampling area (Fig. 7). The highest concentrations were in waters of low (<2°C, <33.5 PSU) and intermediate (~5°C, ~35 PSU) average temperature and salinity in the CSR, and in Emerald Basin, where the average temperature and salinity were both high (>9°C, >35 PSU).

Vertical distributions of CV *C. finmarchicus*

The Labrador Sea section (winter 2002). The highest concentrations of CVs on the AR7W section across the Labrador Sea in winter 2002 were in the Labrador Slope waters (AR7W-08) at depths >600 m (Fig. 8). In the western Labrador Sea CV concentrations peaked in the 200–400 m depth interval, with few individuals below 1 000 m. Farther east, larger proportions of CVs were at greater depths, and near the Greenland Shelf (AR7W-24) 70% of the CVs were below 1 000 m. At station AR7W-26 the Multi-net tow was to <600 m and CVs were much less abundant than elsewhere. Water temperatures below 200 m were ~4°C and uniform with depth in the west (AR7W-08 to AR7W-16) but increased at depths <400 m in the east (AR7W-21, AR7W-24). Salinities below 200 m were relatively uniform. In western and central regions there were appreciable numbers of CVs in the near-surface layer (0–200 m). Integrated abundances of CVs, omitting AR7W-26, ranged from a low of ~9 000 m⁻² at station AR7W-23 to a high of ~20 000 m⁻² at AR7W-08

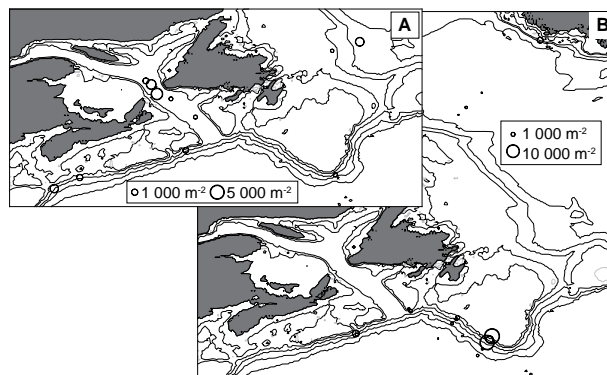


Fig. 6. Areal concentrations of stage CI-CIII *C. finmarchicus* in the surface layers (<100 or 200 m) in (A) autumn 2001 (East of the Tail of the Grand Bank) or 2003 (West of the Tail of the Bank), and (B) winter 2002 (Labrador Sea) or 2003 (West of the Tail of the Bank). Note that the surface layer data also includes stations sampled by ring net from bottom to surface for the SPB, GBL1 and GBL2 lines.

(Table 3). At AR7W-23 (not shown in Fig. 8) the Multi-net tow was only to 1 000 m, however. If the vertical distribution of CVs had been the same at AR7W-24, then the total number here would have been higher by a factor of ~3. The average concentration of CVs over all stations (Tables 1 and 2), omitting AR7W-26, was ~14 000 m⁻².

The Newfoundland Shelf, Flemish Pass and Tail of the Grand Bank, autumn 2001.

For the three stations across the Newfoundland Slope on the Bonavista Bay line (BB) the vertical distribution patterns were somewhat similar to those seen farther north on the western end of the AR7W section, in that the CV *C. finmarchicus* were deeper at the stations nearer the shelf (BB-11 and BB-12) than at the offshore station (BB-14), where the peak abundance was at 200–400 m (Fig. 9). On the other hand, the abundance peak at BB-12 was shallower than at AR7W-08. Farther south in Flemish Pass (FC-17) and at SEGB-16 the CVs were somewhat deeper than at BB-11 and BB-12, but farther offshore at SEGB-17 there was a relatively large number of CV *C. finmarchicus* at 300–600 m, similar to the pattern at BB-14. Total water column concentrations of CVs at stations of ~1 000 m depth (BB-12, FC-17, SEB-16; 25 000–37 000 m⁻², Table 3) and at SEGB-17 (depth 2 500 m, 31 000 m⁻²) were amongst the highest seen in the study.

Temperature and salinity profiles below ~300 m were relatively uniform (Figs. 7 and 9). Near surface layers were warmer and fresher with a thermocline/halocline within the top 200 m for stations on the Newfoundland Shelf and in Flemish Pass (FC-17). At SEGB-16 and 17,

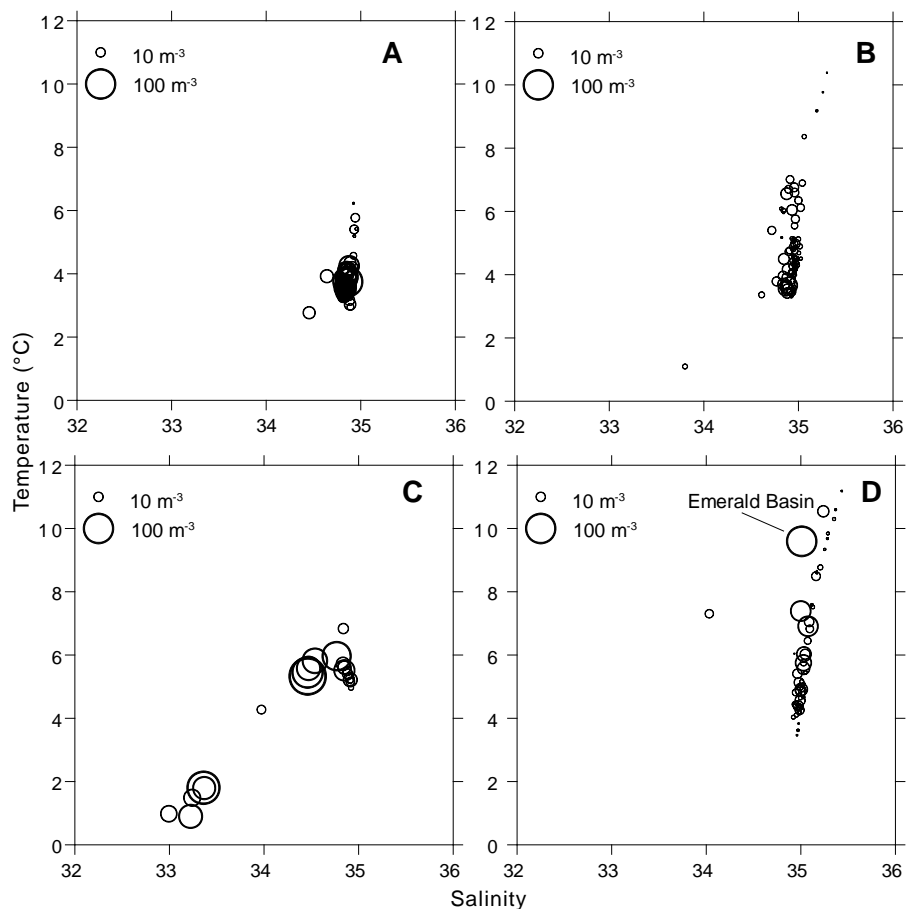


Fig. 7. Concentrations of CV *C. finmarchicus* (m^{-3}) in relation to temperature and salinity averaged over the capture depth intervals for different regions in autumn and winter: (A) East of the Tail of the Grand Bank (LS to SEGB), (B) Eastern slope waters (GBL2 to DEC-17), (C) Cabot Strait Region and (D) Central and Western Scotian Slope waters (SIB to BBL).

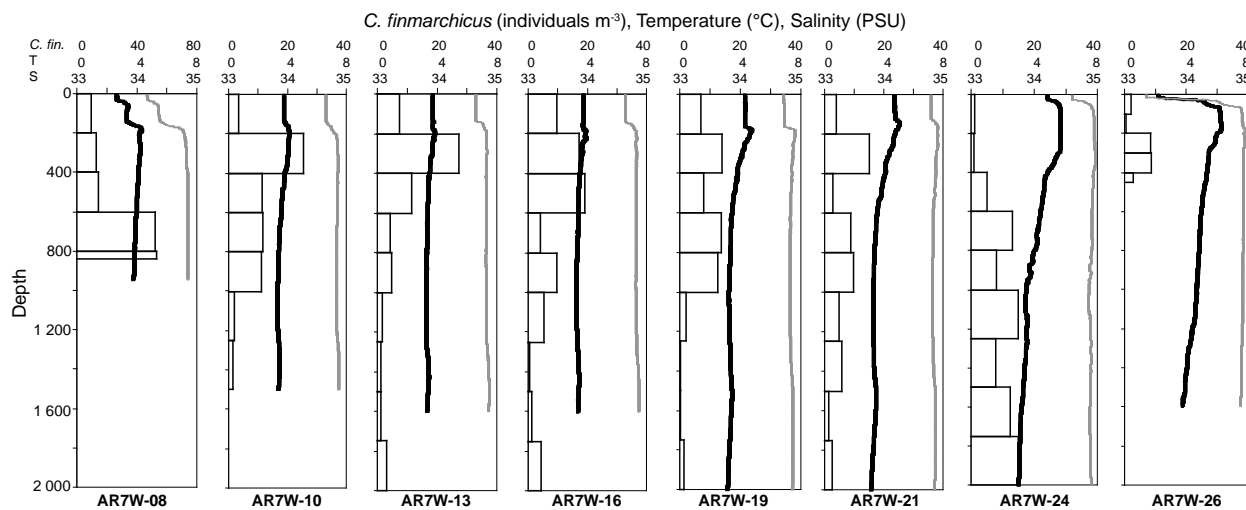


Fig.8. Vertical distribution of CV *C. finmarchicus* (individuals m^{-3}), temperature ($^{\circ}C$, black line) and salinity (PSU, grey line) at selected stations of the AR7W line across the Labrador Sea in winter 2002.

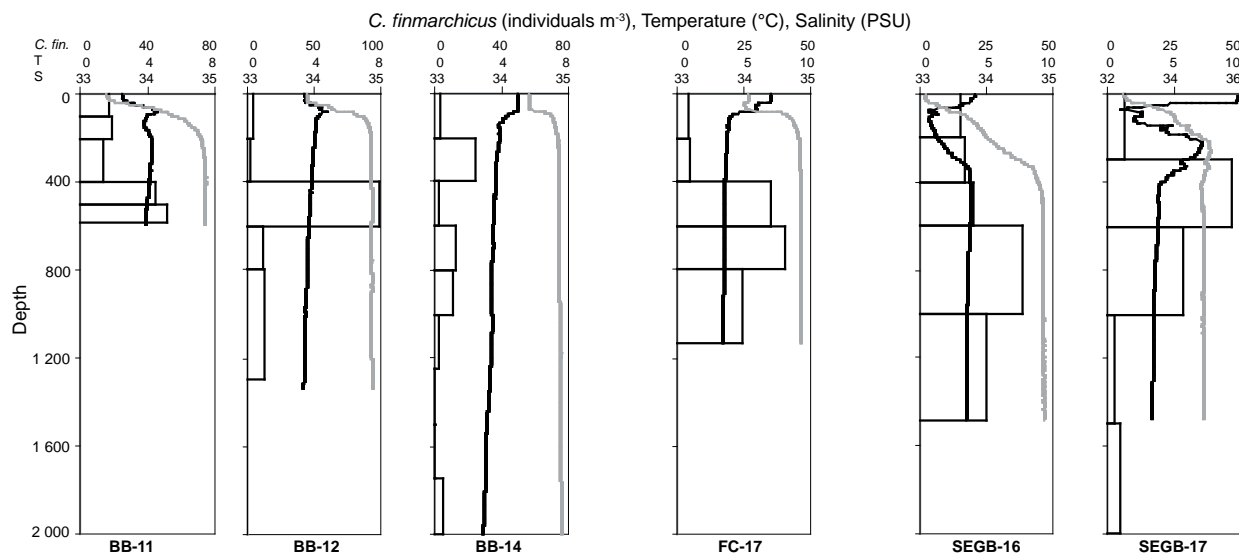


Fig. 9. Vertical distribution of CV *C. finmarchicus* (individuals m^{-3}), temperature ($^{\circ}C$, black line) and salinity (PSU, grey line) at stations on the Bonavista Bay (BB), Flemish Cap (FC) and Southeast Grand Bank (SEGB) Lines in November 2001.

there was evidence of a cold intermediate layer between 100 and 300 m (100–200 m at SEGB-17), but surface temperatures were higher at SEGB-17 due to the proximity of the western boundary of the Gulf Stream.

Slope waters west of the Tail of the Grand Bank (winter 2003). In winter 2003, on the most easterly line sampled (GBL2), CVs were most concentrated at depths close to 1 000 m, although the vertical distributions were broad and there were some CVs in the surface layer (Fig. 10). At GBL2-4 CVs were abundant below 1 000 m, but this was the only station west of the Tail of the Grand Bank where this was observed. At GBL1 peak abundances were shallower than at GBL2, with CVs broadly distributed from the surface to 1 000 m at GBL1-3.5 and mostly above 400 m at GBL1-4. At both GBL1-3.5 and GBL1-4 there were appreciable numbers of CVs in the surface layer. At the SPB line there was a distinct difference between vertical distributions at the 1 000 and the ~3 000 m contours. At SPB08 CVs were most concentrated at the surface, whereas at SPB10 the peak was at 400–600 m (Fig. 10). At the DEC17 stations, peak abundance was at 200–400 m, and there were appreciable numbers in the surface layer at DEC17-1. At stations of the Roseway and Halifax lines (RL and HL) peak abundance was at 400–600 m, and vertical distributions were narrower than farther east with few CVs in the surface layers. At BBL6 CVs showed a broad distribution peak between 400 and 800 m, while at BBL7 the peak concentration was at 200–400 m. Total water column concentrations were highest at GBL2-4 (24 000 m^{-2}) and otherwise generally higher (average 5 500 m^{-2})

to the east of the Laurentian Channel than to the west (average 2 500 m^{-2}), with the exception of BBL6 (9 000 m^{-2}) (Table 3).

Temperature and salinity profiles at GBL2-3 showed a cool fresh layer at much the same depth interval (50–300 m) as was observed at SEGB-16. At all of the stations from the GBL2 line to the ESS there were cool subsurface layers, with salinities fresher above this layer than beneath. The subsurface layer was coolest and deepest at SPB08 (reaching $-0.9^{\circ}C$ at 100 m). Farther west there were no cool subsurface layers and temperatures and salinities were lowest near the surface, below which there were warm, salty layers between ~100 and 500 m.

Slope waters between St. Pierre Bank and Browns Bank (autumn 2003). Peak abundance of CV *C. finmarchicus* was at 400–600 m at most stations at both the 1 000 and 2 000 m isobaths between SPB and Browns Bank (Fig. 11), which is north of the BBL stations shown in Fig. 2. One exception was at the 1 000 m contour off the ESS (LL7), where the peak was at 200–400 m. A second was at the 1 000 m contour on the Roseway Line (RL), although here the peak abundance was over a range (300–500 m) that overlapped the 400–600 m interval sampled elsewhere. Total water column concentrations were highest off the WSS (BBL and RL) ranging between ~7 000 m^{-2} (RL6) and ~17 000 m^{-2} (RL5) (Table 3). Farther east total water column concentrations were higher at the 1 000 m contour ($\geq 3 000 m^{-2}$) than farther offshore ($\leq 2 000 m^{-2}$).

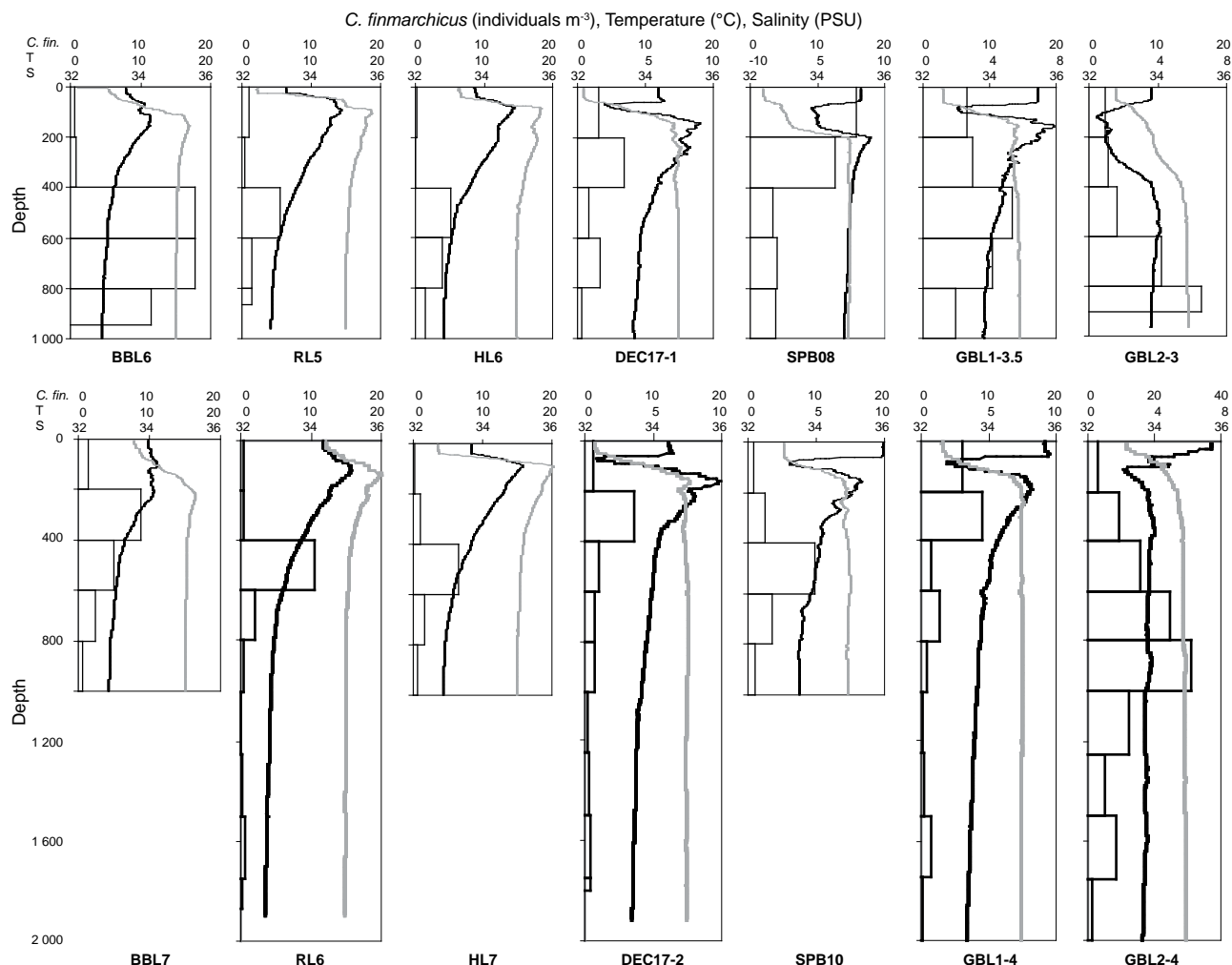


Fig. 10. Vertical distribution of CV *C. finmarchicus* (individuals m^{-3}), temperature ($^{\circ}C$, black line) and salinity (PSU, grey line) at stations along off the western (BBL, RL), central (HL) and eastern (DEC17) Scotian Shelf and off St. Pierre Bank (SPB) and the SW Grand Bank (GBL1 and GBL2) in December 2003. The upper panels correspond to the $\sim 1\,000$ m isobath and the lower panels to the $\sim 2\,000$ m isobath, except for SPB10, where the depth was $\sim 2\,900$ m.

Temperatures were generally maximal at the surface and at all stations, except HL7, there was a cool subsurface layer (generally 50–100 m), beneath which was a warm layer extending to ~ 600 m. Salinities were minimal at the surface and maximal in the subsurface warm layer. At HL7 the maximum temperature and minimum salinity were at the surface, with a gradual decline below the mixed layer (50 m) and slight interleaving of warmer and cooler layers between 50 and 100 m.

Cabot Strait region and off the Western Scotian Shelf, autumn 2003 and Emerald Basin and off the south Newfoundland Shelf and Western Grand Bank (winter 2003). In the CSR, concentrations of CV *C. finmarchicus* generally peaked at depths of 200–300 m, and at some stations there were large numbers at shallower depths (Fig. 12). The highest total water column

concentration ($46\,000\,m^{-2}$) was at CSL4 and the lowest ($4\,000\,m^{-2}$) at LCL4 (Table 3). Temperature and salinity profiles from CSL4 into the Gulf of St. Lawrence were similar. The surface water was warm and fresh; there was an underlying cool fresh layer (50–200 m) and warmer saltier water from 200 m to the bottom. The patterns at LCN and LCL4 were similar to the others, but were distinguished by having water of $<0^{\circ}C$ in their subsurface cool layers and at LCN the surface water was especially fresh (salinity <32 PSU). The concentration of CV *C. finmarchicus* in Emerald Basin was highest in the deepest layer (100–260 m), coincident with the highest temperatures and salinities (Figs. 7 and 12).

Concentrations of CV *C. finmarchicus* peaked at 400–600 m at most stations beyond the 2 000 m isobath (Fig. 12). At LL9, however, the peak was at 200–400 m,

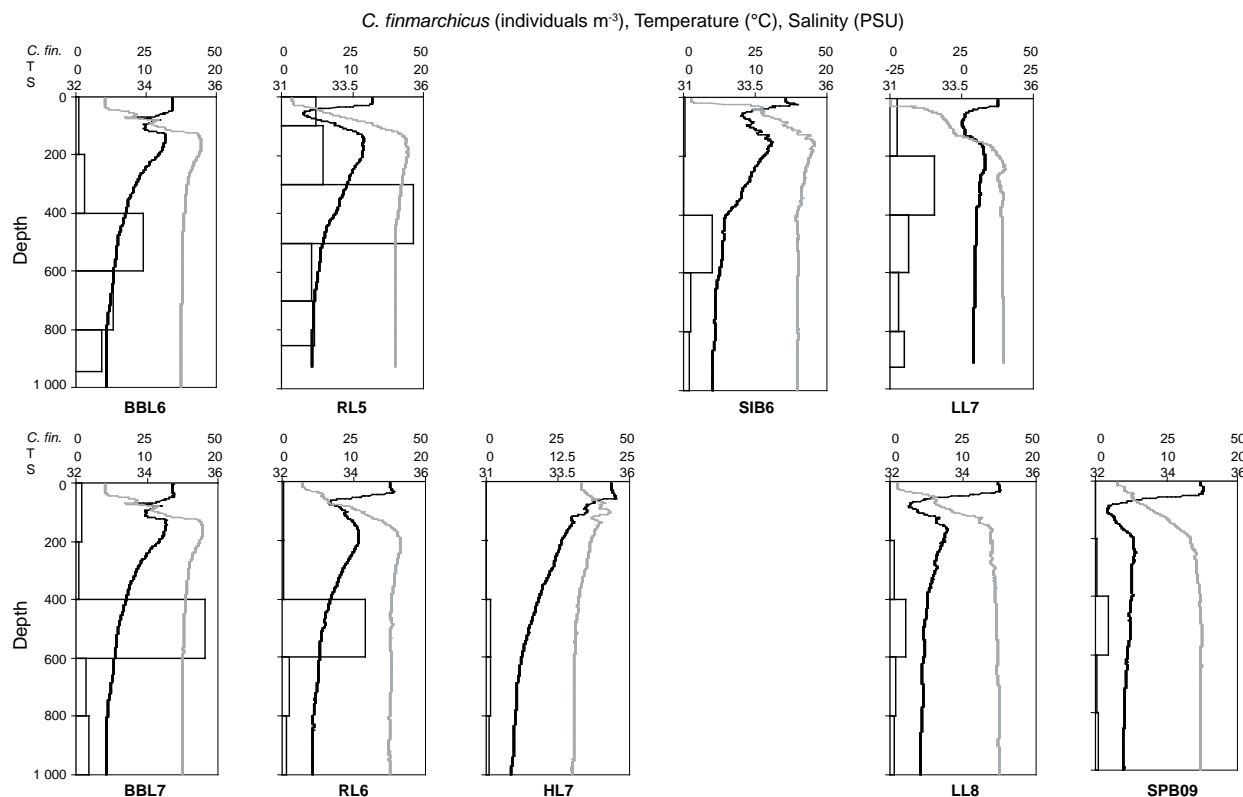


Fig. 11. Vertical distribution of CV *C. finmarchicus* (individuals m⁻³), temperature (°C, black line) and salinity (PSU, grey line) at stations off the western (BBL and RL) central (HL) and eastern (SIB, LL) Scotian Shelf and off St. Pierre Bank (SPB) in October 2003. The upper panels correspond to the ~1 000 m isobath and the lower panels to the ~2 000 m isobath.

while at GBL2-5 CVs were equally abundant from 400–1 000 m. For the latter station it is likely that the population extended below 1 000 m, as it did at GBL2-4, so that the total water column abundance was underestimated. Even so, the total concentration was much higher at GBL2-4 than at the other offshore stations to the west of the Tail of the Grand Bank (11 000 m⁻² versus an average of 2 400 m⁻²).

All stations showed a surface mixed layer of relatively freshwater overlying warmer (GBL1-6, GBL2-5, GBL2-6) or cooler (LL-9, SPB12, GBL1-5) layers. Surface temperatures were highest in the west (RL7) and lower at stations closer to the shelf-break for a given line (e.g. GBL1-5 versus GBL1-6 and GBL2-5 versus GBL2-6). Maximum concentrations of CVs were generally associated with water that was relatively cool and relatively salty.

Ring net stations on the Newfoundland and Scotian Shelves and in the Cabot Strait region. During the autumn 2001 cruise to the Newfoundland Shelf and Grand Bank and the autumn 2003 cruise to the Scotian

Shelf and Cabot Strait, ring net tows were made as part of the Atlantic Zone Monitoring Programme (AZMP, Therriault *et al.*, 1998). Off Newfoundland, abundances of late stage (CIV–CVI) *C. finmarchicus* at a station inshore and to the north of the Grand Bank on the Flemish Cap Line (FC-06) and at another on Flemish Cap (FC-31) were >100 000 m⁻², the highest seen anywhere in this study, while at most stations deeper than 90 m on the Newfoundland Shelf abundances were >10 000 m⁻² (Fig. 13, Tables 3 and 4). On the Scotian Shelf, late stages were abundant (>10 000 m⁻²) on the Halifax Line between Emerald Basin and Halifax and at most stations of the Browns Bank Line. In Cabot Strait, late stages were very abundant (>25 000 m⁻²) at every station, except at the relatively shallow CSL1. Young stages (CI–CIII) of *C. finmarchicus* were generally less abundant than late stages in all regions (Fig. 13, Table 4). The maximum abundance of young stages on the Newfoundland Shelf was 6 000 m⁻² at FC-06, and while there were several stations with concentrations of 1 000–4 000 m⁻², there were also several with effectively no young stages. On the Scotian Shelf and in Cabot Strait, concentrations of young stages were 1 000–4 000 m⁻² or

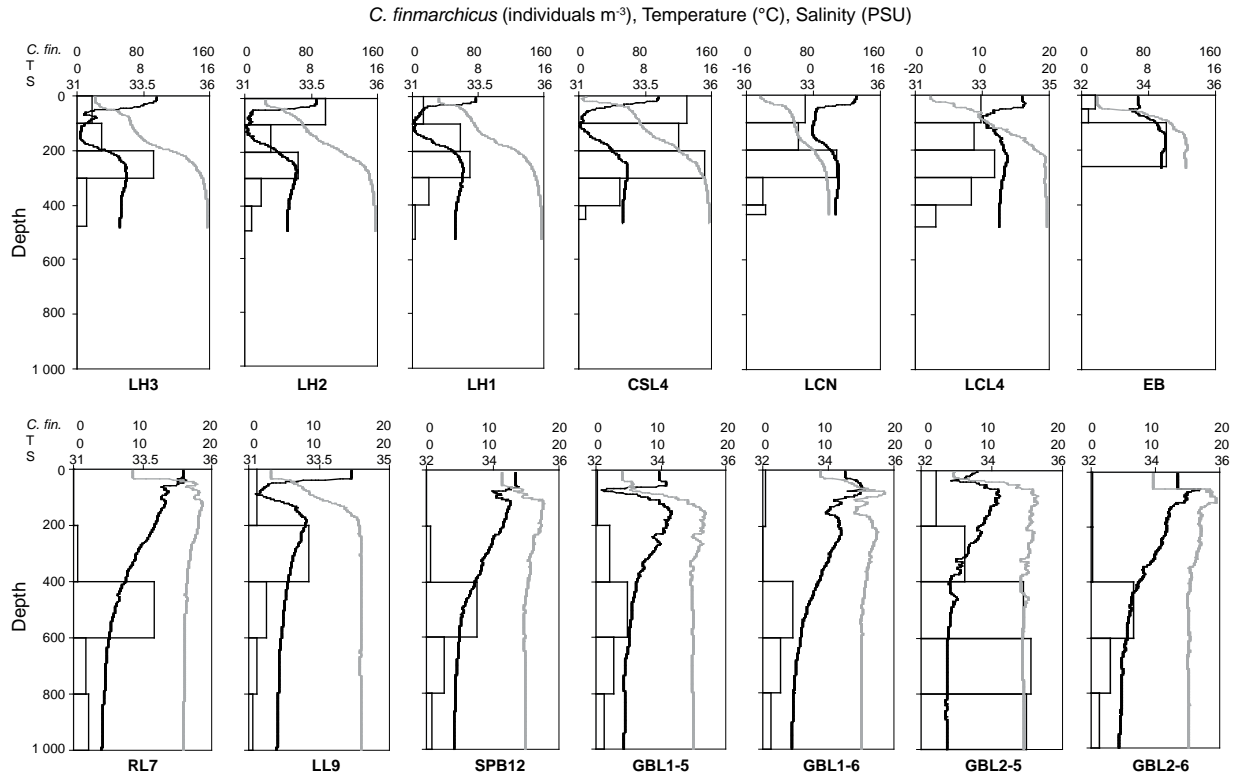


Fig. 12. Vertical distribution of CV *C. finmarchicus* (individuals m⁻³), temperature (°C, black line) and salinity (PSU, grey line) at stations in the Cabot Strait Region (LH3, LH2, LH1, CSL4, LCN, LCL4) in autumn 2003 and in Emerald Basin (EB) in winter 2003 (upper panel) and beyond the 2000 m contour off the western (RL7) and eastern (LL9) Scotian Shelf in autumn 2003 and the south Newfoundland Shelf (SPB) and western Grand Bank (GBL1 and GBL2) in winter 2003 (lower panel).

less, except at BBL4 and BBL3, where they were much higher (108 000 and 7 000 m⁻², respectively). In winter 2003, ring net tows were made at two stations near the shelf-break on each of the SPB, GBL1 and GBL2 lines. Abundances of late stage *C. finmarchicus* for these stations were 5 000–17 000 m⁻² (Fig. 5, Table 4), except at SPB5A where there were only ~400 m⁻². Young stage *C. finmarchicus* were abundant at the ring net stations of the GBL2 line, but not elsewhere (Fig. 6, Table 4).

Discussion

In this study we have shown substantial variations in autumn/winter vertical depth distributions of *C. finmarchicus* over a large geographic area of the Northwest Atlantic. The mean depth distribution of *C. finmarchicus* was shallowest in Emerald Basin (100–270 m), in Cabot Strait (100–300 m) and off the Eastern Scotian Shelf (200–400 m), while animals were generally found deepest in waters off the Western Scotian Shelf (400–950 m), Eastern and Southern Newfoundland (400–1 500 m) and west of Greenland (600–2 000 m). There was consider-

able variability in the mean depth of *C. finmarchicus* in the Labrador Sea, with animals generally being found at greater depths near the continental shelves than in the central basin.

Interpreting spatial patterns of *C. finmarchicus* areal abundance

In autumn, late stage *C. finmarchicus* were most abundant in the subsurface layers at stations in the slope waters east of the Tail of the Grand Bank, off the WSS and in the CSR (Fig. 4, Table 3). These high concentrations probably reflected production in the regions from which these individuals originated, which the circulation indicates would be the Newfoundland Shelf, the Scotian Shelf and the Gulf of St. Lawrence, respectively (Fig. 1). In winter, subsurface late stage abundances were high at all stations of the AR7W transect across the Labrador Sea, in the slope waters of the GBL2 line and in Emerald Basin (Fig. 5, Table 2). For the Labrador Sea, the abundance of *C. finmarchicus* probably reflected production within the region, although the slope waters may be the areas of highest production with subsequent trans-

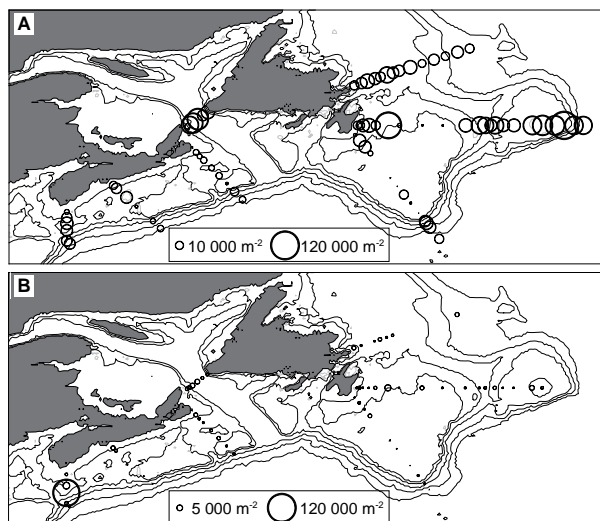


Fig. 13. Areal concentrations of (A) stage CIV-CVI and (B) CI-III. *C. finmarchicus* determined by ring net tows from the bottom to the surface on the Bonavista Bay (BB), Flemish Cap (FC) and Southeast Grand Bank (SEGB) Lines in autumn (November) 2001 and on the Cabot Strait (CS), Louisbourg (LL), Halifax (HL) and Browns Bank (BBL) Lines in autumn (October) 2003.

port to the central Labrador Sea (Head *et al.*, 2000), and there could have been input to eastern regions from the Irminger Sea. For the southwest Grand Bank (GBL2) the high levels probably resulted from advection around the Tail of the Grand Bank (*cf.* Figs. 9 and 10). For Emerald Basin, the levels likely reflected the production of the ESS, including advective input from the CSR and Gulf of St. Lawrence.

Abundances of *C. finmarchicus* overwintering in the Labrador Sea (9 000–20 000 m^{-2}) were similar to those reported for the Irminger Basin (7 000–30 000 m^{-2} ; Gislason and Astthorsson 2000) and for the northern Norwegian Sea (4 000–37 000 m^{-2} ; Dale *et al.*, 1999). They were lower, however, than those reported for the Faroe-Shetland Channel (35 000–50 000 m^{-2} ; Heath *et al.*, 2000) and for some retentive areas southwest of Tromsøflaket off northern Norway (up to 150 000 m^{-2} ; Halvorsen *et al.*, 2003). The abundances of *C. finmarchicus* in the slope waters of the WSS (Table 3, RL and BBL, 4 000–21 000 m^{-2}) were similar to those reported by Miller *et al.* (1991) for the slope waters downstream off Georges Bank (5 000–10 000 m^{-2}). The high concentrations in the central Labrador Sea are consistent with the idea that this area is a distribution centre for *C. finmarchicus* for the NW Atlantic (*sensu* Wiebe, 2001). By contrast, the low concentrations (<4 000 m^{-2}) of late stage *C. finmarchicus* beyond the 2 000 m isobath west of the Tail of the Grand

Bank (Fig. 12, Table 3) do not support the idea (Wiebe, 2001) that the central Slope Water gyre is an important overwintering area.

Late stage (CIV-VI) *C. finmarchicus* were abundant in the surface layers in the CSR in Multi-net tows, and there were also >1 000 m^{-2} young stages (CI-III) at CSL4 and LH2, and in the ring net tows (bottom to surface tows) at all Cabot Strait Line stations. Plourde and Runge (1993) measured egg production rates for *C. finmarchicus* in the Lower St. Lawrence Estuary between June and August and found relatively high rates in late August when their sampling ended. Thus, the seasonal cycle of production may not have finished by October 2003 in the CSR. In October 2003 chlorophyll concentrations were >1 $mg\ m^{-3}$ near the surface at all stations in the CSR, which should have been sufficient for phytoplankton alone to fuel egg production and development of copepodites at *in situ* surface temperatures (~8°C; Campbell *et al.*, 2001).

Young stage (CI-III) *C. finmarchicus* were found at levels of >1 000 m^{-2} at a number of stations throughout the region (Figs. 6 and 13, Tables 2 and 4) in autumn (12 stations on the Newfoundland Shelf, seven stations in CSR, eight stations on the Scotian Shelf, one off the ESS and two off the WSS) and winter (one station in the Labrador Sea, three near the SEGB and one off the ESS). Maximum chlorophyll concentrations were >1 $mg\ m^{-3}$ in autumn at five stations on the Newfoundland Shelf, at four CSR stations, at seven Scotian Shelf stations, and at the two stations off the WSS, and in winter at the station off the ESS in and at the SEGB stations. Although young stages were very abundant (>100 000 m^{-2}) at BBL4 in autumn, chlorophyll concentrations were not especially high there (maximum 1.25 $mg\ m^{-3}$). The young stage copepodites that we observed would have derived from eggs laid 2–3 weeks previously. Thus, our observations of chlorophyll concentrations *in situ* do not allow us to determine whether there is some threshold of phytoplankton concentration needed to induce reproduction and the development through the naupliar stages, although it is likely that this is the case.

Our results suggest that in parts of our study area the production cycles for *C. finmarchicus* may extend later in the year than is seen elsewhere. In fact, at Stn. 27 (46° 33' N 52° 35' W), a station on the inner Newfoundland Shelf that is sampled monthly as part of the AZMP programme (Therriault *et al.*, 1998), appreciable concentrations (>5 000 m^{-2}) of young stage (CI-III) *C. finmarchicus* have been seen at least once in every month of the year except March and April over seven years of sampling (1999–2005), suggesting that the population

TABLE 4. Water column abundances of *Calanus finmarchicus* (individuals m⁻²) in the ring net tows. BB stands for Bonavista Bay Line; FC, for Flemish Cap Line; SEGB, for South East Grand Bank Line.

Station name	CI	CII	CIII	CIV	CV	CVI	Total	Station name	CI	CII	CIII	CIV	CV	CVI	Total
BB-01	580	1 449	580	1 159	10 577	724	15 069	SEGB-10	9	27	9	14	9	5	72
BB-03	–	290	290	2 318	15 069	1 739	19 706	SEGB-11	–	–	–	3 767	8 694	145	12 606
BB-04	–	–	–	3 478	26 081	1 739	31 298	SEGB-12	–	–	9	290	380	18	697
BB-05	–	–	290	2 898	17 967	1 159	22 314	SEGB-13	72	299	245	63	9	–	688
BB-06	–	–	2 029	4 926	7 824	1 739	16 518	SEGB-15	–	–	290	1 449	16 808	1 159	19 706
BB-07	–	–	580	1 159	35 355	2 318	39 412	SEGB-16	72	–	181	4 274	21 481	1 413	27 422
BB-08	290	580	–	2 898	15 649	1 739	21 155	SEGB-17	18	–	–	4 347	18 021	398	22 785
BB-09	–	–	–	2 608	15 359	1 449	19 416	SEGB-19	–	–	–	1 739	10 867	145	12 751
BB-10	–	–	–	2 318	22 024	3 478	27 820	GBL2-1	904	3 390	9 492	7 006	6 102	452	27 346
BB-11	54	54	54	344	8 458	616	9 581	GBL2-2	170	1 130	1 978	1 921	2 656	113	7 967
BB-12	36	36	63	213	16 844	1 281	18 474	GBL1-2	–	509	452	1 243	2 995	283	5 481
BB-13	–	–	145	–	9 708	1 159	11 012	GBL1-2.5	–	57	452	2 204	6 554	396	9 831
BB-14	1 159	398	1 032	1 544	19 321	883	24 338	SPB5A	45	158	158	136	249	23	768
BB-15	–	–	–	1 304	11 012	–	12 316	SPB6	–	226	565	1 243	14 238	1 017	17 741
FC-01	–	145	435	724	8 404	1 739	11 447	CSL1	129	345	1 638	3 880	862	–	6 855
FC-02	–	290	435	869	9 418	435	11 447	CSL2	–	302	2 113	9 054	35 010	604	47 083
FC-03	–	–	290	1 159	21 734	1 449	24 632	CSL3	–	1 191	2 383	10 722	48 251	596	63 143
FC-04	–	290	–	3 478	24 053	1 159	28 979	CSL4	–	596	2 978	17 275	48 846	596	70 291
FC-05	145	724	724	724	11 881	435	14 635	CSL5	362	543	362	4 346	12 676	543	18 833
FC-06	–	3 478	2 318	16 228	83 460	3 478	108 962	CSL6	453	226	679	7 244	19 920	679	29 200
FC-07	–	109	181	580	1 775	254	2 898	LL1	113	792	1 471	2 490	2 660	57	7 583
FC-09	688	1 051	761	326	36	–	2 862	LL2	–	176	654	1 258	2 289	151	4 527
FC-10	27	217	154	235	91	–	724	LL3	–	121	362	2 051	4 101	80	6 714
FC-12	–	290	290	4 057	22 604	290	27 530	LL4	–	262	872	2 224	2 791	87	6 237
FC-14	–	–	580	1 159	44 048	–	45 787	LL5	50	352	1 509	4 628	1 710	–	8 250
FC-15	580	–	580	4 637	28 979	5 216	39 991	LL6	70	70	457	773	141	–	1 511
FC-17	–	–	–	7 417	14 164	489	22 069	LL7	272	362	272	2 173	8 783	272	12 133
FC-18	–	580	1 159	12 171	31 298	–	45 208	LL8	–	–	–	1 250	5 088	302	6 640
FC-20	–	–	290	1 449	22 604	–	24 343	HL1	247	741	1 646	1 975	7 243	823	12 676
FC-21	–	–	290	2 898	21 445	580	25 212	HL2	113	214	1 023	3 810	11 511	1 237	17 908
FC-24	2 318	–	1 159	580	49 265	1 739	55 060	HL3	–	–	–	2 716	16 411	2 377	21 504
FC-26	1 159	–	–	–	58 538	1 739	61 436	HL4	–	–	–	550	550	157	1 258
FC-29	–	–	–	1 739	53 901	580	56 220	HL5	–	23	–	23	158	–	204
FC-31	–	–	–	4 637	110 121	–	114 758	HL6	30	–	–	392	3 803	151	4 376
FC-33	–	–	–	8 694	40 571	580	49 844	HL7	–	–	–	373	5 699	320	6 391
FC-35	–	–	–	11 012	35 934	1 159	48 105	BBL1	198	283	594	1 811	1 528	283	4 697
SEGB-01	–	–	36	109	1 286	109	1 540	BBL2	–	91	181	1 268	14 034	453	16 026
SEGB-03	290	–	869	4 347	17 098	1 449	24 053	BBL3	328	2 460	4 101	15 091	8 365	–	30 345
SEGB-05	–	–	290	3 478	15 069	4 057	22 894	BBL4	24 447	46 177	37 123	10 865	4 527	4 527	127 666
SEGB-06	72	290	1 739	2 536	1 014	145	5 796	BBL5	91	68	23	–	23	–	204
SEGB-07	9	63	104	136	36	–	349	BBL6	1 132	679	113	1 019	16 072	453	19 467
SEGB-08	5	68	136	131	18	5	362	BBL7	792	–	–	453	17 203	453	18 901
SEGB-09	14	41	54	23	9	–	140								

as a whole is only inactive for a rather short period of the year (Pepin *et al.*, MS 2006). Numbers of young stages found in the CSR on autumn AZMP cruises are variable (500–30 000 m⁻², 1998–2005, E. Head, unpublished data), suggesting that there the production season sometimes extends until October. Female *C. finmarchicus* are actively laying eggs in the CSR in April (Campbell and Head, 2000), suggesting that here too the period of dormancy is sometimes short. Durbin *et al.* (1997)

found late autumn-early winter recruitment of *C. finmarchicus* on Georges Bank, but concluded it was due to early arousal from overwintering, rather than prolonged spring/summer production. It is unclear whether our observations on the WSS represent production by individuals that awoke early or by a portion of the population that never entered dormancy. A detailed discussion of the variations in seasonal cycles of *C. finmarchicus* in different regions of the NW Atlantic and how they vary

from year to year is beyond the scope of this paper, but it is clear that the persistence of *C. finmarchicus* on the Newfoundland Shelf into the autumn and winter, which occurs every year, will influence its distribution in the slope waters downstream. Advection from the shelf can be of late stages (e.g. at the GBL or SPB lines) or young stages, the latter being produced when near-surface, perhaps semi-dormant, late stage *C. finmarchicus* respond to autumn/winter phytoplankton blooms, or a portion of the population may rely more heavily on omnivory during periods of limited primary production.

Inferring inter-regional connectivity from vertical distributions of CV, hydrography and circulation

For the purposes of this discussion, we will assume that we have an effectively synoptic determination of the vertical distribution of CV *C. finmarchicus* and hydrography throughout the sampling region. This is a reasonable assumption because adjacent areas sampled at different times showed limited variability (e.g. Scotian Shelf sampled in October and December). The Labrador and Newfoundland slope waters had very similar TS properties below 200 m, which is where most of the CV *C. finmarchicus* were found (Figs. 7–9). The more inshore stations (e.g. AR7W-08, BB-11, BB-12) showed a greater influence of relatively cool, fresh shelf water at the surface than stations farther offshore (AR7W-10, BB-14) and concentrations of CVs were higher closer to the shelf, suggesting that the shelf could be a source to the slope waters (Figs. 8 and 9, Table 3). Nevertheless, surface concentrations were low and the number of late stage *C. finmarchicus* on the shelf on the BB line was low in November (Fig. 13), so that at this time the main flow of CVs would have been along the slope and not from the shelf to the offshore.

The TS properties below 300 m in Flemish Pass and off the SE Grand Bank were similar to those farther north on the BB and AR7W lines (Figs. 7–9), but off the SE Grand Bank (SEGB16) there was a cool fresh layer (ca 100–300 m), with TS properties characteristic of the shallow Labrador Slope water that can sometimes penetrate along the slope to the Scotian Shelf (e.g. Greene *et al.*, 2003). This layer was not seen farther upstream because the sampling stations were too far offshore, but it was seen on the SW Grand Bank line (GBL2-3) in December 2003 (Fig. 10), although not farther downstream at the GBL1 line. It was unimportant in the transport of CV *C. finmarchicus*, which were not abundant in this layer. The TS properties and vertical distribution of CVs were both consistent with transport of overwintering *C. finmarchicus* from the Newfoundland slope waters to the SE Grand Bank and around the Tail of the Grand

Bank to the GB2 line. Downstream at the GBL1 line, however, there were relatively high levels of CVs in the near surface layers, which were probably derived from the adjacent shallower waters (Fig. 5, Tables 2 and 4). According to a particle tracking study (Luo *et al.*, 2006), these shallow shelf-edge individuals could have been transported here from the outer shelf on the Flemish Cap line and western Flemish Pass, where concentrations were quite high (Fig. 13, Table 4). Individuals arriving in the surface layers of the slope waters probably migrate down as they leave the shelf, so that any flow of organisms from the GBL2 stations at depth is likely to be augmented by the shelf contribution at GBL1.

It is possible that there is input to the offshore SPB stations from upstream at GBL1 (*cf.* Figs. 10–12). At station SPB08, however, there were large numbers of CVs in the surface layer, in association with a subsurface layer of very cold fresh water that extended to ca 200 m (Fig. 10) that was most likely derived from Haddock Channel, which runs north-south off the shelf to the east of SPB. The particle tracking study of Luo *et al.* (2006) suggests that the likely source to Haddock Channel is the inshore branch of the Labrador Current, *i.e.* the western end of the Flemish Cap line. This latter area had high CV abundance levels (Fig. 13, Table 4) and was the likely source to SPB08. Farther offshore at SPB10, at the 2 900 m isobath, there was little sign of this surface population. West of SPB the flow along the slope diverges with some entering the Laurentian Channel and some continuing southwest. It is possible that this was the source of the very cold water seen at stations in Laurentian Channel offshore from Cabot Strait (LCN and LCL4) in autumn 2003 (Fig. 12), although at both stations the *Calanus* populations probably derive mainly from the CSR. This is concluded not only because *C. finmarchicus* were more abundant at these stations relative to SPB08 in winter and SPB09 in autumn (Figs. 10 and 11, Table 3), but more obviously because *Calanus hyperboreus*, which are abundant in the Gulf of St. Lawrence, were as numerous as *C. finmarchicus* at all of the CSR stations, including these two, whereas they were ten times less abundant than *C. finmarchicus* at stations off SPB (E. Head, unpublished data).

Calanus finmarchicus found off the Eastern Scotian Shelf (LL line) probably represent a mixture of animals coming along the slope from southern Newfoundland, and from the Gulf of St. Lawrence through Cabot Strait. Stage CV *C. finmarchicus* at stations in the CSR in autumn 2003 were most concentrated above 300 m (Fig. 12), which was consistent with this being a source to the 0–400 m layer at LL7 off the ESS (Fig. 11). The TS properties are also consistent with this view, as was

the observation that *C. hyperboreus* were nearly as abundant as *C. finmarchicus*. The relatively low numbers of CV *C. finmarchicus* below 400 m at LL7 could, however, have been derived from the slope water current, *i.e.* from off SPB. At the 2 000 m isobath (LL8), there was no sign of the shallow CSR population, six times fewer *C. hyperboreus* than *C. finmarchicus* and the CVs were at the same depth as those at SPB09 (Fig. 11). Yet farther offshore, at LL9, the CVs were shallow again, and *C. hyperboreus* were three times less abundant than *C. finmarchicus* (Fig. 12). To the west of the LL line, at the DEC17 stations, CV *C. finmarchicus* were again relatively shallow, consistent with their being derived from the CSR, but *C. hyperboreus* were 4–7 times less abundant than *C. finmarchicus*. Farther downstream at SIB06, *C. hyperboreus* were 10 times less abundant than *C. finmarchicus* and the CVs were at the same depth as at SPB09 (Fig. 11). Off the central and western Scotian Shelf CV *C. finmarchicus* were generally below 400 m (Figs. 10–12). At HL6 in winter *C. hyperboreus* were half as abundant as *C. finmarchicus*, and on and west of the central Scotian Shelf they were 5–20 times less abundant.

The TS properties of the slope waters in which the CVs were found west of SIB06 were generally a little warmer than those between the GBL2 and DEC-17 lines, due to a greater contribution of warm water from the south, and this is consistent with the relative levels of the two *Calanus* species and the diminishing influence of the outflow from the CSR. This interpretation is also consistent with the accepted circulation pattern (Fig. 1), which indicates flow is generally from northeast to southwest. Reversals in direction of this flow have been observed in records collected by current meters deployed off the central Scotian Shelf, however. These reversals are thought to be associated with the presence of meso-scale anti-cyclonic eddies, which can impinge on the shelf-break. In fact, the direction of flow between July and November 2003 near HL6 was apparently from southwest to northeast (J.W. Loder, unpublished data) and interestingly, high abundances of *C. finmarchicus* off the WSS decreased (RL5, RL6, BBL7), while the low abundance of *C. finmarchicus* at HL7 increased, between October and December (Table 3). Whether the change in flow direction was responsible for the changes in abundance cannot be proven, but the fact that reversals can occur suggests that *C. finmarchicus* can sometimes be transported from southwest to northeast.

A high degree of inter-regional connectivity was implied for *C. finmarchicus* populations in the NW Atlantic by the coupled physical-biological model of

Speirs *et al.* (2006), such that inoculating a small area of the sub-polar gyre (centred at ~55° N 50° W) with *C. finmarchicus* led to dispersal of individuals throughout the sub-polar and Slope Water gyres over six years. Our observations do not contradict this result, but they suggest that the data and assumptions used in the model may have been inadequate. Firstly, it was assumed that *C. finmarchicus* populations are dormant in autumn and winter, which is apparently not the case everywhere in the NW Atlantic, and which could certainly influence model results in some areas. Secondly, no data on overwintering depth distributions for *C. finmarchicus* in the slope waters off the Newfoundland and Scotian shelves were used, which could affect the modelled degrees of retention within the sub-polar or Slope Water gyres. It will be interesting to see how this and any other models respond to these new data inputs.

Variations in vertical distribution of overwintering *C. finmarchicus* in different regions: can they be explained?

In our observations, overwintering *C. finmarchicus* were found in the slope waters over a range of TS conditions. The highest concentrations of overwintering CV *C. finmarchicus* (>100 m⁻³) were found in waters of low (~3°C, Newfoundland slope), intermediate (~5°C, Cabot Strait) and high (~9°C, Emerald Basin) temperatures at depths of 400–600, 200–300 and 100–260 m, respectively (Figs. 7–12). High concentrations were also associated with temperatures of <2°C (100–200 m) in Cabot Strait, although when sampling depth intervals were chosen to isolate the cold intermediate layer in October 2006, it was found to have 5–10 times fewer *C. finmarchicus* than the layers above and beneath it (E. Head, unpublished data), so that the occurrence of high overwintering concentrations at very low temperatures in 2003 was probably apparent, rather than real. Whether the populations overwintering at relatively high temperatures suffer high mortality because of high metabolic costs or losses to predators is not clear, but populations in both Emerald Basin and Cabot Strait would likely be subject to heavy predation by fish and invertebrates (see below).

Several suggestions have been made as to why *C. finmarchicus* overwinter at particular depths in different areas, but none of them can readily explain the differences seen throughout our NW Atlantic sampling area. One suggestion is that *C. finmarchicus* migrate to a depth with a fixed daytime light intensity (Miller *et al.*, 1991). In such a scenario overwintering individuals should be deepest at the most southerly latitudes. In our study, however, where bottom depths were not limiting, there was no relationship between overwintering depth

and latitude; the deepest overwintering population was in fact at one of the most northerly stations, in the Greenland Slope waters at $>60^{\circ}$ N (AR7W-24).

Another suggestion is that overwintering depths are selected to avoid predators (Kaartvedt, 1996). Dale *et al.* (1999) reported that in the Norwegian Sea *C. finmarchicus* were distributed deepest in areas where Atlantic water was dominant and shallower in Arctic waters and they attributed this to differences in the abundance of mesopelagic fish in the water masses. In the Labrador Sea, the distribution pattern was somewhat similar to that in the Norwegian Sea, in that individuals were deepest in the waters having the highest Atlantic water contribution (*i.e.* the Greenland Slope) and shallower farther west, where the Arctic water influence was greater (as indicated by the lower salinities). On the other hand, Dale *et al.* (1999) sampled only to 1 000 m, which seems to have included the bulk of the *C. finmarchicus* population, while in the Greenland Slope waters the depth distribution was substantially deeper, as was also the case in the Irminger Basin (Gislason and Astthorsson, 2000). The dominant mesopelagic fish species, the myctophid *Benthosema glaciale*, is confined to the upper 1 000 m in the northern Labrador Sea (Sameoto, 1989), so that *C. finmarchicus* in the Greenland Slope waters seem to be migrating to excessive depths, if they are trying to avoid mesopelagic fish predation. Sameoto (1989) also observed that the daytime peak in the vertical distribution of the *B. glaciale* in the northern Labrador Sea/Baffin Bay in August 1983 was at 400–600 m, coincident with one of the highest concentrations ($\sim 100 \text{ m}^{-3}$) of overwintering *C. finmarchicus* seen in this study, in the Newfoundland slope waters (BB-12, Fig. 9). Recent observations in the western Labrador Sea have shown that the mean depth at which *C. finmarchicus* overwinters corresponds closely to the depth of the deep scattering layer determined in June–September 2006, which consisted principally of *B. glaciale* (P. Pepin, unpublished data) and that late stage *C. finmarchicus* and *C. glacialis* were in fact numerically the most important prey item found in *B. glaciale* stomachs (P. Pepin, unpublished data). Mesopelagic fish are not the only potential predators of *C. finmarchicus* overwintering in the Labrador Sea, however. Sameoto (1987) reported that chaetognaths are major predators on copepods in the northern Labrador Sea and Baffin Bay and that in summer substantial levels of chaetognath biomass extend to depths of 1 000 m. In addition, we have observed large decapods in deep tows in the Labrador Sea, at concentrations such that their biomass sometimes exceeds that of the copepods in some depth intervals (E. Head, personal observation). Farther south, in the relatively shallow waters of Cabot

Strait, overwintering *C. finmarchicus* were most abundant in the 200–300 m interval and not very abundant in the near-bottom layers. This might relate to predator avoidance, since some near-bottom living fish species (*e.g.* redfish) are quite abundant there (data from the Marine Fish Division Virtual Data Centre (MFDVDC) held at the Bedford Institute of Oceanography). In Emerald Basin silver hake are abundant (MFDVDC) and *C. finmarchicus* concentrations are lower near the bottom than at slightly shallower depths (Sameoto *et al.*, 1994). In both areas the carnivorous euphausiid *Meganyctiphanes norvegica* is also abundant in the near-bottom layer during the daytime (Sameoto *et al.*, 1994; E. Head, personal observation). Overall, we cannot say whether predator avoidance is a major determinant of *C. finmarchicus* overwintering depth distribution.

Heath and Jónasdóttir (1999) investigated the vertical distribution of *C. finmarchicus* in the Faroe-Shetland channel and found that the overwintering population was associated with the Arctic water near the bottom of the channel, and that these individuals had a high fat content relative to those overwintering in nearby waters. Visser and Jónasdóttir (1999) showed in a modelling study that the fat body inside overwintering *C. finmarchicus* varies in density with pressure (*i.e.* depth) and temperature, such as to change the overall density of the animal, so that individuals with different fat content may be neutrally buoyant at different depths, with salinity also having an influence via its effect on water density. Assuming that overwintering *C. finmarchicus* are neutrally buoyant, Heath *et al.* (2004) developed this idea to calculate the implied fat content for *C. finmarchicus* overwintering in several regions of the North Atlantic: this analysis included the Labrador Sea data presented here. When we calculated the implied fat content of overwintering *C. finmarchicus* in the Labrador Sea, we found that below 200 m it was, in fact, essentially constant with depth and over all stations ($\pm 2\%$), because fat density is more dependent on temperature than on pressure, and temperatures varied very little, and because salinities were also relatively constant (Fig. 7). Thus, in the Labrador Sea differences in fat content and density are not likely to be responsible for variations in the vertical distribution of overwintering *C. finmarchicus*.

Visser and Jónasdóttir (1999) suggested that *C. finmarchicus* should become positively buoyant as they start to leave their overwintering depths to return to the surface, which would enable them to conserve energy reserves during their ascent. In several of the areas where we sampled, however, *C. finmarchicus* leaving their overwintering depths will encounter water that is both cooler

and fresher as they ascend so that their fat bodies will become denser and they will become negatively buoyant and will have to swim up actively. Backhaus *et al.* (2003) suggested that overwintering copepods might save energy during ascent by being brought to the surface during deep water column convection in late winter. For this to be effective he suggested that overwintering should be at depths near to, but below, the depth of convection (J. O. Backhaus, Pers. Comm.). Irigoien (2004) also suggested that overwintering should occur below the depth of convection. He hypothesised that overwintering depth selection is a heritable trait that is related to lipid content and its effect on buoyancy and that individuals that do not overwinter below the depth of winter convection will not survive and will be selected against genetically. The behaviour of the Labrador Sea *C. finmarchicus* population does not support these hypotheses: the western/central Labrador Sea is one of the world's deep convection areas with convection depths generally reaching 1 000 m, but in central and western regions *C. finmarchicus* overwinter at depths of <1 000 m, and large numbers of overwintered individuals apparently survive through to the spring (Head *et al.*, 2003).

Conclusions

Our observations of the vertical distribution and abundance of *C. finmarchicus* and of hydrography in the slope waters of the NW Atlantic are consistent with the accepted pattern of circulation and connectivity of overwintering *C. finmarchicus* populations between adjacent regions. Transport around the Tail of the Grand Bank seems to be limited, with most of the southwesterly flow along the SE Grand Bank being deflected to join the northeasterly flowing North Atlantic Current, and there is flow into and out from the Laurentian Channel, so that the system is clearly not a simple continuum. One novel and confounding finding is that *C. finmarchicus* on the Newfoundland Shelf, in the Cabot Strait region and in some areas of the Scotian Shelf may have prolonged production seasons, so that the slope water populations can receive important inputs from these sources in autumn and winter. These probable effects of local secondary production are unlikely to have been included in current coupled transport/population dynamics models. As well, we note that there are periodic reversals of the southwesterly flow along the Scotian Shelf, which could cause northwesterly transport of *C. finmarchicus* from western to central regions, contrary to the expected direction of flow. Finally, our results suggest that the vertical distribution of overwintering *C. finmarchicus* is not constrained in extent by temperature or salinity in the NW Atlantic

and we have found no one explanation that can account for the broad range of overwintering depths observed in this study.

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