

Investigations on the ecology of *Calanus* spp. in the Labrador Sea. I. Relationship between the phytoplankton bloom and reproduction and development of *Calanus finmarchicus* in spring

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ABSTRACT: During mid-May–early June 1997 observations of hydrography, phytoplankton and nitrate concentrations, and abundance and stage distribution of *Calanus finmarchicus* populations were made in the Labrador Sea and south of Greenland. Egg production rates were also measured for isolated *C. finmarchicus* females. Surface nitrate and integrated phytoplankton concentrations indicated that, in the deep water, the phytoplankton bloom had ended in the north and east, was in progress in the north central Labrador Sea and near the basin margins, and had not yet become established in an area stretching from the central Labrador Sea to the south of Greenland. *C. finmarchicus* egg production rates and stage distributions at stations in the 3 areas designated as early, mid- and late/post-bloom zones, suggested that development rates of the overwintered G0 generation into mature adults (females and males) were probably low before the bloom, but accelerated during its development. Individual and areal rates of egg production were highest in the early bloom zone, whereas nauplii were more abundant in the bloom and late/post-bloom zones. Differences in naupliar abundance may have been related to food limitation, or predation. Following development through to the young copepodite stages (C1–III), which were most abundant in the late/post-bloom zone, mortality rates were apparently lower and growth rates less dependent on high phytoplankton concentrations and perhaps more dependent on temperature. In the Labrador Sea, where the annual growth season is relatively short and *C. finmarchicus* produces only 1 generation per year, the timing of the spring bloom may have a significant impact on recruitment of the new year's generation. In areas where the bloom is early and intense, maturation of the overwintered adults will be rapid and egg-laying will occur when phytoplankton concentrations are high. Subsequent survival success of eggs through to later stages will also probably be relatively high and individuals from the new year's generation will have ample time to reach stages capable of overwintering. By contrast, if the bloom is late or of low intensity, adult maturation will be delayed and egg-laying may occur when phytoplankton concentrations are low. Under these conditions relatively few eggs may survive and individuals that do survive will have a shorter period in which to attain stages which can overwinter.

KEY WORDS: *Calanus finmarchicus* · Reproduction · Spring bloom · Labrador Sea

INTRODUCTION

Detailed studies of ecological and biological processes in the Labrador Sea have been relatively scarce, with the exceptions of the observations of Kielhorn

(1952) of the annual cycle of zooplankton abundance at Ocean Station Bravo (56° 30' N, 51° 00' W), which included information on hydrography and phytoplankton abundance, and the reports of the ICNAF (International Commission for the Northwest Atlantic Fisheries) Norwestlant I–III surveys, which included observations of hydrography, phytoplankton and zooplankton distributions for 3 time periods between late March and July for sections across the Greenland Shelf and in the Irminger and Labrador Seas (ICNAF 1968).

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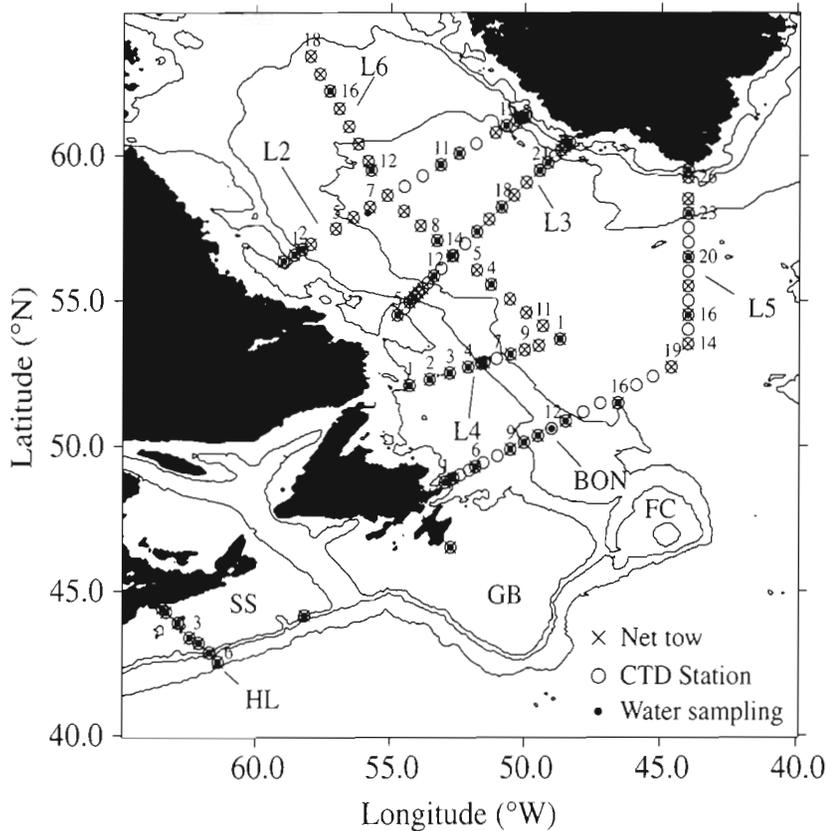


Fig. 1. Hydrographic and biological sampling stations occupied during May–June 1997. BON: Cape Bonavista Line; FC: Flemish Cap; GB: Grand Bank; HL: Halifax Line; SS: Scotian Shelf; L2–L5: Lines 2 to 5. Contours are at 200, 1000 and 3000 m

Additional observations of the distribution of zooplankton abundance, over the entire Labrador Sea (Grainger 1963) or areas within it (Huntley et al. 1983), have also been reported. More recently, the Biological Oceanography group from the Bedford Institute of Oceanography has been extending previous observations in the Labrador Sea during a number of cruises: 3 in spring (May–June: 1994, 1996, 1997); 2 in summer (July: 1995, 1998); and 1 in autumn (Oct.: 1996). During each cruise sampling was carried out along the WOCE (World Ocean Circulation Experiment) AR7/W Section (Fig. 1, L3), which runs from Hamilton Bank (Labrador Shelf) to Cape Desolation (Greenland), and additional lines were run on some cruises. Sampling has generally included measurements of temperature, salinity and nutrient concentrations and observations of the distribution of phytoplankton, zooplankton and bacteria within the near-surface layers (0 to 100 m).

Seasonal and interannual observations of hydrographic conditions and the distributions of phytoplankton and all zooplankton species will be described elsewhere (Head unpubl.), but here we will report on observations made during only one cruise, that of the

spring of 1997, for which the spatial coverage was most extensive (Fig. 1). Furthermore, in this paper we confine our attention to 1 of the 3 *Calanus* species that dominate the zooplankton in the area, namely *C. finmarchicus*, and we will discuss the relationship of reproduction and recruitment in this species to the dynamics of the phytoplankton bloom. The reasons for limiting the discussion to *C. finmarchicus* are 2-fold: firstly, it is arguably the most important copepod in the Labrador Sea (in the central basin at least); and, secondly, this species and variations in its life history throughout its geographic range are subjects of prime interest for current international studies, including GLOBEC (Global Ocean Ecosystem Dynamics) and TASC (Trans Atlantic Study of *Calanus*).

Calanus finmarchicus is distributed throughout the Atlantic, from the New England Shelf (40°N) in the southwest, to the Greenland and Barents Seas (80°N) in the northeast (Planque et al. 1997) and populations in different areas vary with respect to certain life history characteristics, such as the number of generations produced annually. In the west, on Georges

Bank (ca 42°N), it appears that some portion of the *C. finmarchicus* population remains reproductively active throughout most of the year and that several generations may be produced annually (Durbin et al. 1997), while in the east, north of the Faroes (ca 64°N: Gaard 1996), in northern Norway (69°N: Diel & Tande 1992) and the Barents Sea (ca 74°N: Tande et al. 1985), *C. finmarchicus* apparently produces only 1 generation per year. Between these extremes, on the mid- and western regions of the Scotian Shelf (McLaren & Corkett 1986, I. A. McLaren, E. Head, D. D. Sameoto unpubl.), in the waters around Iceland (Longhurst & Williams 1992, Gislason & Astthorsson 1996, 1998) and east of the Faroes (Gaard 1996), there appear to be 2 generations per year, although the second may contribute little to the annual production (e.g. McLaren & Corkett 1986, Gislason & Astthorsson 1998). In the Labrador Sea, at Ocean Station Bravo, Kielhorn (1952) suggested that *C. finmarchicus* produces 2 generations per year. Using the Northwestlant survey data, Matthews (1968) suggested that there is 1 generation per year throughout our study area (Fig. 1). Our recent observations have also suggested that there is only 1

generation produced per year throughout most of the Labrador Sea. Young copepodite stages of a second minor generation are sometimes seen, but it is possible that few of these develop to stages that can successfully overwinter by autumn (Grainger 1963, Head unpubl.).

The arousal from diapause and spring ascent of *Calanus finmarchicus* may be triggered by changes in photoperiod or some internal mechanism (Hirche 1996), but the initiation of reproduction seems to be linked to the start of the spring bloom. There is some controversy as to whether females start producing eggs before (e.g. Diel & Tande 1992, Gisslasson & Astthorsson 1996) or only after (Runge & Plourde 1996) the bloom has actually become established, but there is general agreement that sustained egg production requires that females feed (Marshall & Orr 1952, Plourde & Runge 1993, Hirche et al. 1997) and that egg production rates are generally maximal during the spring bloom (Anderson 1990, Diel & Tande 1992, Gisslasson & Astthorsson 1996). Rates may remain high even after the bloom has ended, however, if alternative food sources are available (Runge & Plourde 1996). According to Matthews (1968), female *C. finmarchicus* throughout our sampling area start to breed in April and, from observations of eggs and nauplii in the water, Anderson (1990) suggested that the peak breeding season for *C. finmarchicus* on and around Flemish Cap (Fig. 1) was mid-April. During our 1997 cruise to the Labrador Sea, which was from mid-May to early June, egg production rates, measured for groups of individual *C. finmarchicus* females (Campbell 1998, Campbell & Head 2000), were generally high. In fact, in the central Labrador Sea and south of Greenland (L5 line, Fig. 1) females had the highest rates ever observed for the species, for the relatively low ambient temperatures. In addition, since adults dominated the population at many stations, it is obvious that reproduction was still important in May and early June.

In this paper, we present data describing: the abundance and stage structure of *Calanus finmarchicus* populations; hydrography; nitrate and phytoplankton concentrations; and areal estimates of egg production rates, for the near surface layers (0 to 100 m) at stations throughout the Labrador Sea, sampled between May 13 and June 9, 1997 (Fig. 1). On the basis of these observations we will attempt to: assess the state of the spring bloom in different areas of the study region; explore the relationship between reproduction in *C. finmarchicus* populations and the state of the spring bloom; and examine the survival success of the newly laid eggs throughout the region, in order to make some suggestions as to factors which might be contributing to egg and naupliar survival and recruitment in the species.

MATERIALS AND METHODS

The sampling operations carried out at each of the sampling stations during the 1997 spring cruise to the Labrador Sea are shown in Fig. 1. Hydrographic and biological sampling was along the Halifax Line (HL) on May 9 and 10; along the Bonavista (BON) and L5 lines between May 13 and 20; along the L3 (the WOCE AR/7 section) and L2 lines between May 21 and June 2; and along the L6 and L4 lines, between June 3 and 9.

Hydrographic measurements and water sampling.

Temperature and salinity profiles were collected throughout the full ocean depth using a Seabird (Model SBE 25) sensor mounted on a CTD rosette, or in the 0 to 100 m depth range using a Seabird (Model SBE 25) sensor mounted on the frame of a biological pump. Both the CTD rosette and the pump frame also carried submersible fluorometers (Chelsea Instruments Aquatrack 3 and Sea Tech Model 304, respectively). Water samples were collected by means of the pump (or occasionally from bottles on the CTD rosette) for the determination of extracted chlorophyll and nutrient concentrations at 10 m intervals in the 0 to 100 m depth range. For extracted chlorophyll determinations, water samples (100 ml) were filtered through GF/F filters, which were immediately placed in 90% acetone and stored at -20°C until analysis, which was between 1 and 3 d after sample collection. Chlorophyll concentrations were measured using a Turner Designs fluorometer according to the method of Holm-Hansen et al. (1965). For the determination of nutrient concentrations, water samples were frozen at -20°C and analysed back in the laboratory using an Alpkem RF-300 autoanalyser.

Continuous monitoring at 5 m. Temperature and salinity data were recorded continuously using Seabird sensors in the intake of the ship's 'clean' under-way pumping system, which collected water ca 5 m depth. A Wetstar 3 (Wetlab) submersible fluorometer was used to monitor fluorescence. The fraction collector from an autoanalyser was used to collect water samples for the determination of nutrient concentrations from a small flow-through reservoir at 15 min intervals. These were frozen at -20°C and analysed as described above. Two or 3 times per day, water samples were taken for the determination of extracted chlorophyll concentration (as described above) to calibrate the fluorometer.

Zooplankton sampling. Zooplankton were collected in vertical net hauls between 100 and 0 m using a 0.75 m diameter ring net fitted with a 200 μm mesh. The cod-end was attached to the weight on the bottom of the hydro-wire and the towing bridle, to a crossbow mounted on the wire at a height above the

weight such that the net was held vertically. In this configuration zooplankton were only collected as the net was towed upwards. The towing speed was ca 0.5 m s^{-1} and the volume of water sampled was assumed to be the volume of the cylinder filtered by the net. Samples were preserved in 2% formalin. Size frequency distributions of sizes-at-stage were constructed at each station and were used to distinguish the early copepodite stages (CI–CII) of *Calanus finmarchicus* from those of *C. glacialis*. There was no size overlap in the later stages (CIII–CVI). Dry weights were determined for groups of individuals belonging to each stage of *C. finmarchicus* at each of the sampling stations. Biomass results (dry weights) based on these are presented without correction for formalin preservation.

RESULTS

Near-surface temperature, salinity, nitrate concentrations and fluorescence from the continuous monitoring system

Areal contour plots of near-surface temperature, salinity, nitrate and fluorescence at ca 5 m were compiled from data collected along the ship's track using the continuous monitoring system (Fig. 2). The absolute values of temperature and salinity (which must be corrected for temperature) were not precise, because the water warmed by 1 to 2°C as it passed through the system, but the spatial trends were real. Thus, areal contour plots of temperature and salinity showed features which are consistent with our under-

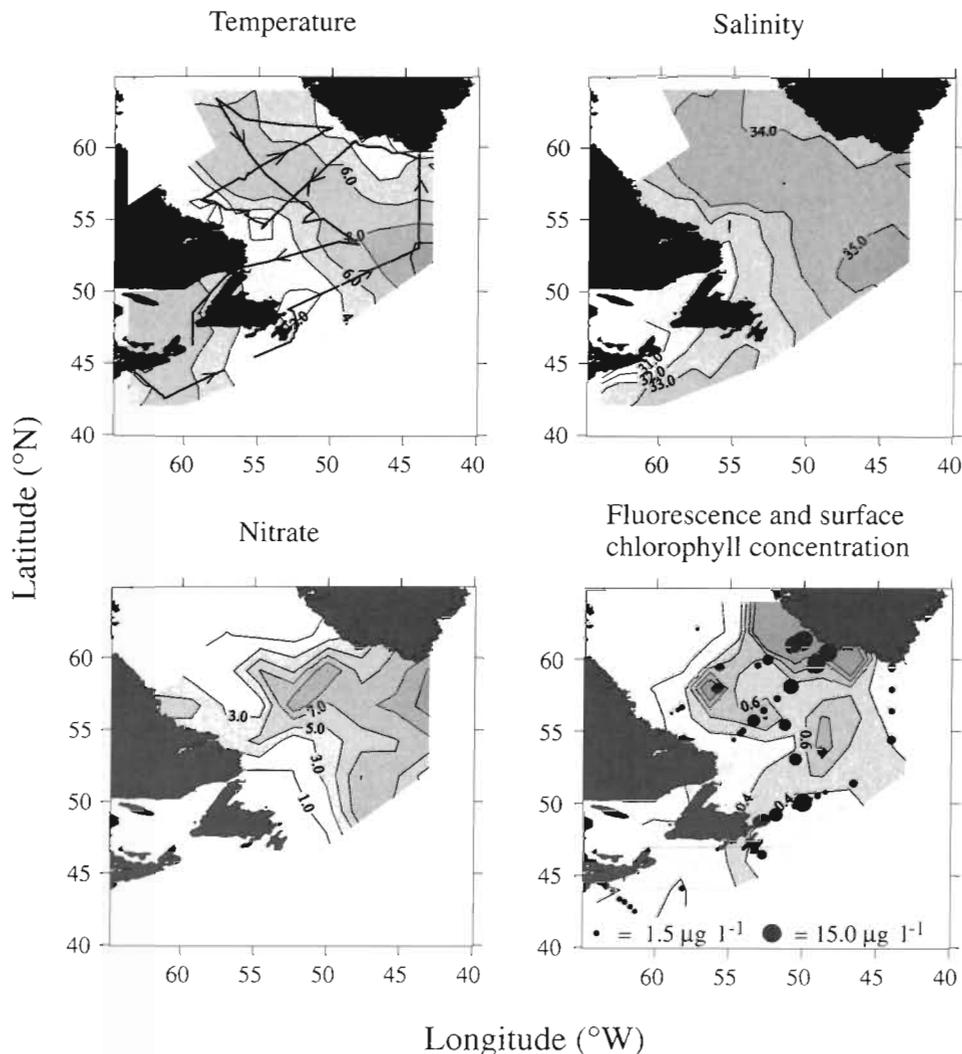


Fig. 2. Contour plots of temperature ($^\circ\text{C}$), salinity, nitrate concentration (μM) and fluorescence (mV) and chlorophyll concentration ($\mu\text{g l}^{-1}$) in the near-surface (5 m) of the sampling region, compiled from data collected by the continuous flow-through system (see 'Materials and methods'). Upper left-hand panel shows the ship's track

standing of the circulation patterns (Fig. 3): near-surface temperatures and salinities were highest ($>8^{\circ}\text{C}$ and >34 , respectively) in the south and east, in areas most influenced by the North Atlantic Current, and relatively warm, salty water extended northwest throughout the central Labrador Sea. The near-surface waters over the shelves were cooler and fresher ($<0^{\circ}\text{C}$ and <33 , respectively), and this cool, fresh water extended south over the eastern Newfoundland Shelf and on to the Grand Bank in the west, while being confined to a narrow band around the southern tip of Greenland in the east. High near-surface nitrate concentrations ($>7\ \mu\text{M}$) were generally associated with the warm salty waters in the south central Labrador Sea and farther to the southeast. The lowest nitrate concentrations were found in the north central Labrador Sea, over the north Greenland Shelf and over the Newfoundland Shelf, Grand Bank and farther to the southwest. On this cruise, although estimates of extracted chlorophyll concentrations co-varied with measurements of fluorescence for water collected by the continuous monitoring system (Fig. 2, lower right-hand panel), the 2 were not well correlated. This was also true for profiles of extracted chlorophyll compared with the fluorometers on the CTD rosette and biological pump, perhaps because of variations in fluorescence yield between different phytoplankton populations. For this reason, fluorescence measurements in Fig. 2 and elsewhere are shown as voltages, rather than as calculated chlorophyll concentrations. Near-surface fluorescence levels and were highest on the Greenland Shelf, where extracted near-surface chlorophyll concentrations were $>10\ \mu\text{g l}^{-1}$, and much lower in the north central region, where extracted near-surface concentrations were $<1\ \mu\text{g l}^{-1}$. Elsewhere, there were patches where fluorescence was high, relative to an intermediate background level.

Profiles of temperature, salinity, nitrate concentrations and fluorescence at fixed stations

Contour plots of profiles (0 to 100 m) of temperature and salinity along the sampling lines (Figs. 4 & 5) show values in the near-surface layer that follow the same spatial trends as those compiled from the continuous monitoring system: highest temperatures and salinities occurred in the offshore regions of lines L4 (6.9°C , 34.8) and BON (8.3°C , 34.9) (Fig. 4) and at the southern ends of lines L5 (7.7°C , 34.9) and L6 (6.9°C , 34.8) (Fig. 5). There were hydrographic fronts along both the Labrador (and Newfoundland) and Greenland shelves (L2, L3, L4, BON, L5), with warm salty water offshore and cool fresh water over the shelves. Along the Labrador Shelf, the frontal zone apparently broadened

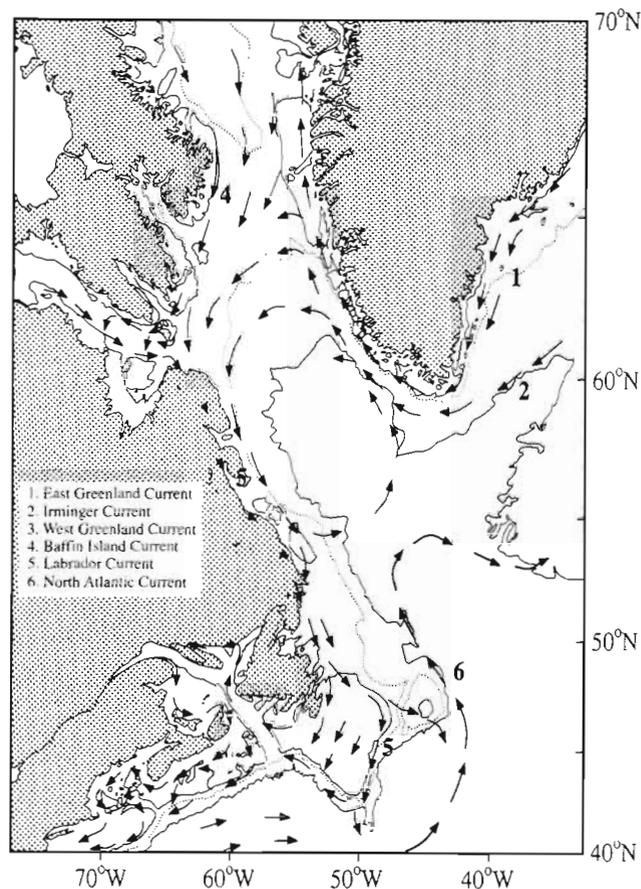


Fig. 3. Near-surface circulation of the main currents in the Labrador Sea sampling region. Contours are at 200, 1000 and 3000 m

from north (ca 20 km wide on the L2 line) to south (ca 80 km wide on the BON line) and there was indication of the advection of near-surface (0 to 30 m) shelf water to the offshore extending offshore ca 50 km beyond the shelf-break at the eastern end of the L2 line and about the same distance beyond the shelf-break at the western end of the L3 line, leading to higher density stratification in those areas. The near-surface waters were slightly warmer (by ca 1°C) than those underlying in some areas of the deep central Labrador Sea (L2, L3, L6), perhaps due to intrusions of Atlantic water, in the areas where the salinity was also higher (e.g. L3 line), or because of local warming. Over the Labrador Shelf on the L4 line, near-surface layers were also warmer than the underlying layers. Solar warming was probably responsible: the line was sampled at the end of the cruise in June and the weather had been generally fine.

The vertical and horizontal resolution of the nutrient data was less than for the other variables. Nevertheless, profiles of nitrate concentration (Figs. 6 & 7) showed near-surface levels which were consistent with the spatial patterns produced by the continuous monitoring sys-

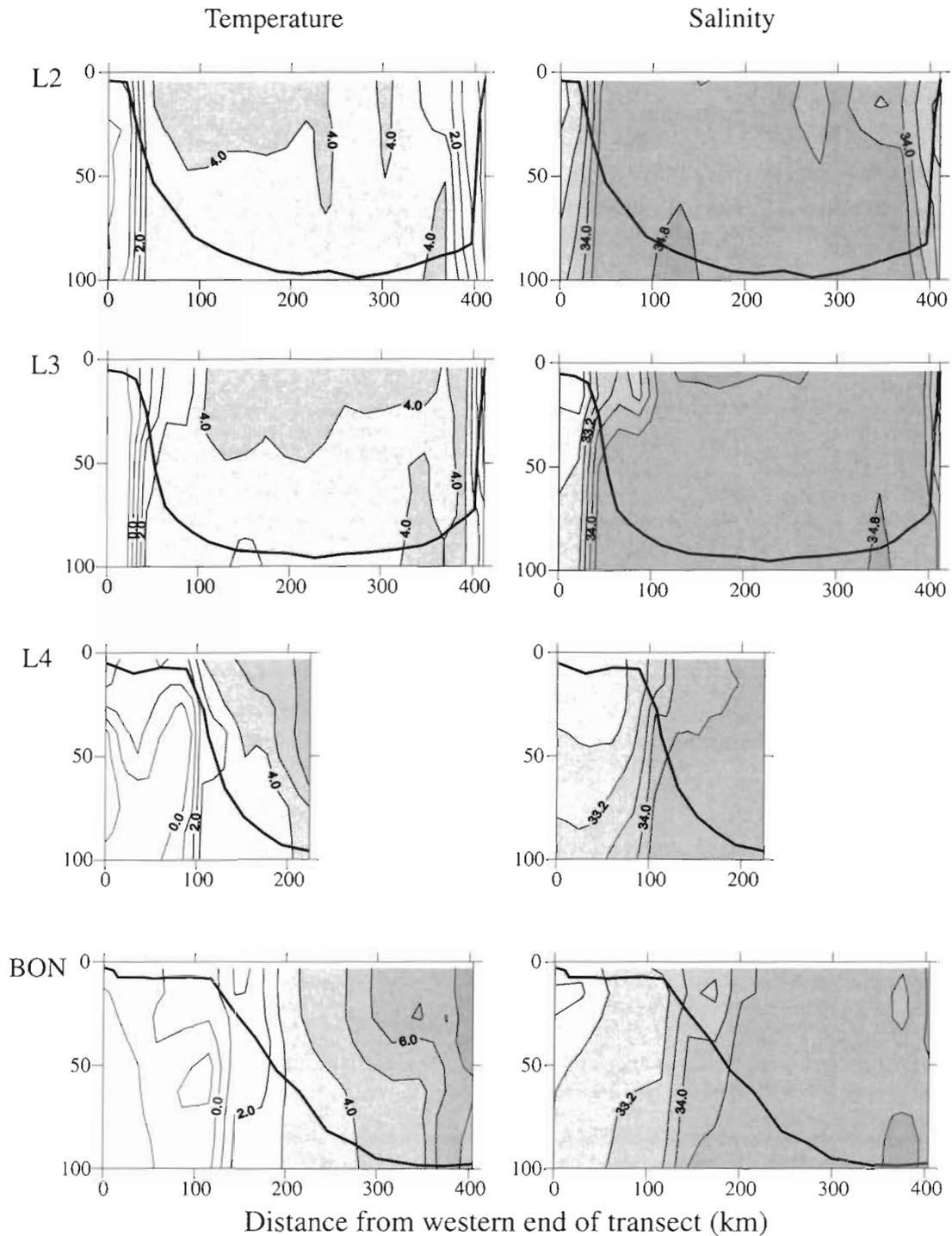


Fig. 4. Contoured profiles of temperature ($^{\circ}\text{C}$) and salinity collected at 1 m depth intervals using the CTD rosette sampler for lines orientated west (left) to east (right). The y-axis is the depth in meters and the heavy line overlays show the bathymetry along each line: the deepest point in each case is >3000 m (not drawn to scale)

tem (Fig. 2). Near-surface concentrations were relatively low ($<3 \mu\text{M}$) in the north central Labrador Sea (L2, L6), over the northern Greenland Shelf (L2), in the frontal shelf-break region of the central Labrador Shelf (L4), and

over the Newfoundland Shelf (L4, BON). They were high ($>7 \mu\text{M}$), however, in some areas of the central Labrador Sea (L3) and at offshore stations in the south (BON) and southeast (L5, L6). At stations where surface

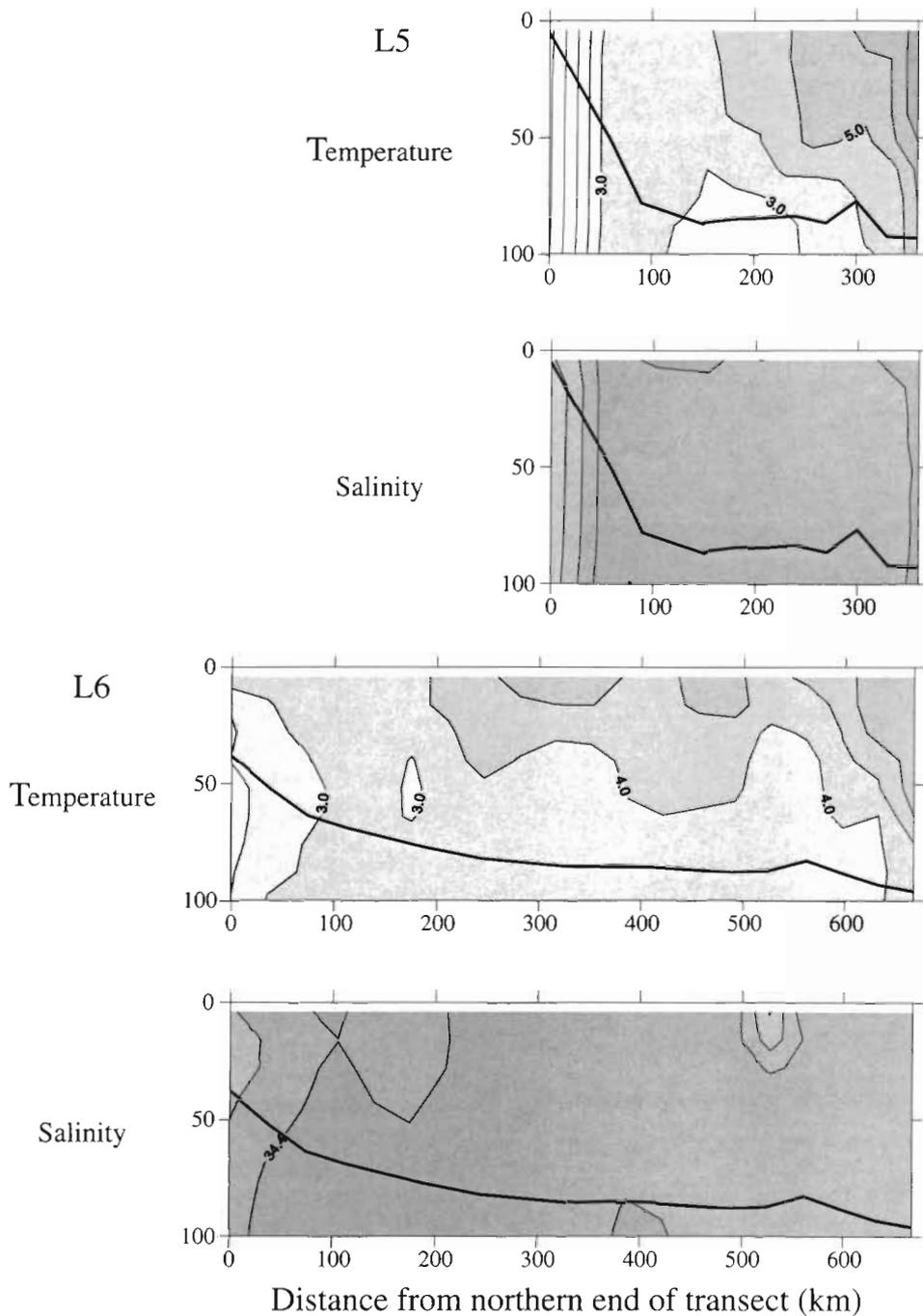


Fig. 5. Contoured profiles of temperature ($^{\circ}\text{C}$) and salinity collected at 1 m depth intervals using the CTD rosette sampler for lines orientated north (left) to south (right). The y-axis is the depth in meters and the heavy line overlays show the bathymetry along each line: the deepest point in each case is >3000 m (not drawn to scale)

nitrate levels were low, concentrations at 50 m were >5 μM , except along the shelf-break on the northern Greenland Shelf (L2), where the nitrate concentration at 50 m was 2.5 μM and at 100 m was still only 3 μM .

The continuous monitoring system showed patches of enhanced fluorescence that were 20 to 50 km wide. The profiles showed that fluorescence was often maximal at the surface or within the 0 to 20 m depth range.

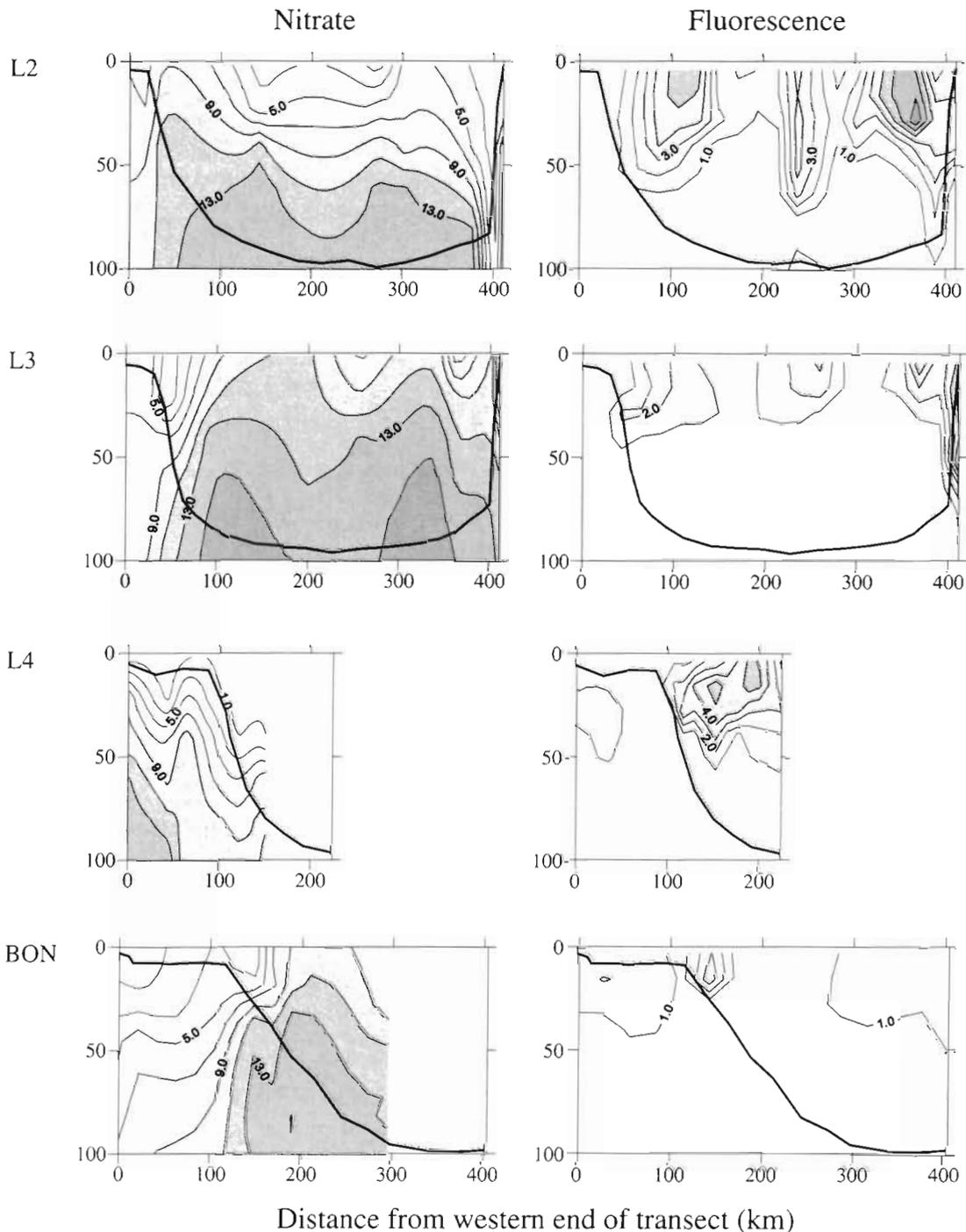


Fig. 6. Contoured profiles of nitrate concentration (μM) collected at 10 m depth intervals using the biological pump and of fluorescence collected at 1 m depth intervals using the CTD rosette sampler. Line orientation and bathymetry as in Fig. 4

Areas of most intense fluorescence were midway along the sections across the northern central and central Labrador Sea (L2, L3), near the western and eastern margins of the central basin (L2, L3, L4) and on the central Greenland Shelf (L2, L3). Profiles of nitrate

concentration and phytoplankton fluorescence were not obviously related, i.e. areas where fluorescence was high did not necessarily correspond to areas where near-surface nitrate levels were low and vice versa.

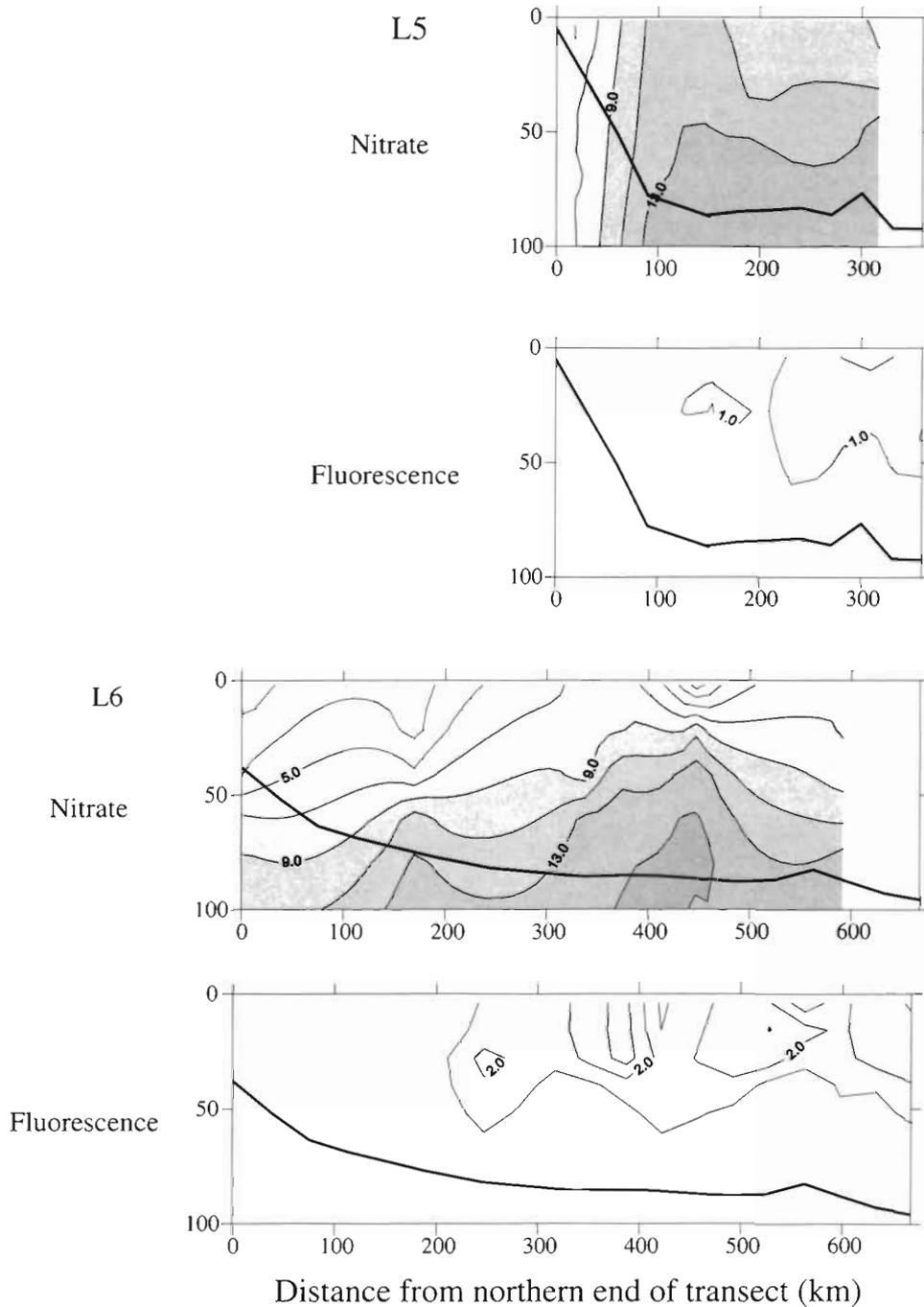


Fig. 7. Contoured profiles of nitrate concentration (μM) collected at 10 m depth intervals using the biological pump and of fluorescence collected at 1 m depth intervals using the CTD rosette sampler. Line orientation and bathymetry as in Fig. 5

Distribution of abundance and biomass of *Calanus finmarchicus* in the Labrador Sea

The early stages (CI–III) dominated the pattern of abundance of *Calanus finmarchicus* copepodites overall, with highest values in the northern Labrador Sea

(L6) and near the margins of the central basin on the L2 line (Fig. 8, Table 1). The CIs were generally the most abundant, showing a maximum value of ca $80\,000\text{ m}^{-2}$ (L2 Stn 14; Table 1). At some stations, however, CIs were outnumbered by CIIs and CIIs (L2 Stns 2, 3 and 6; L6 Stns 13 and 15; Tables 1 & 2) and the highest

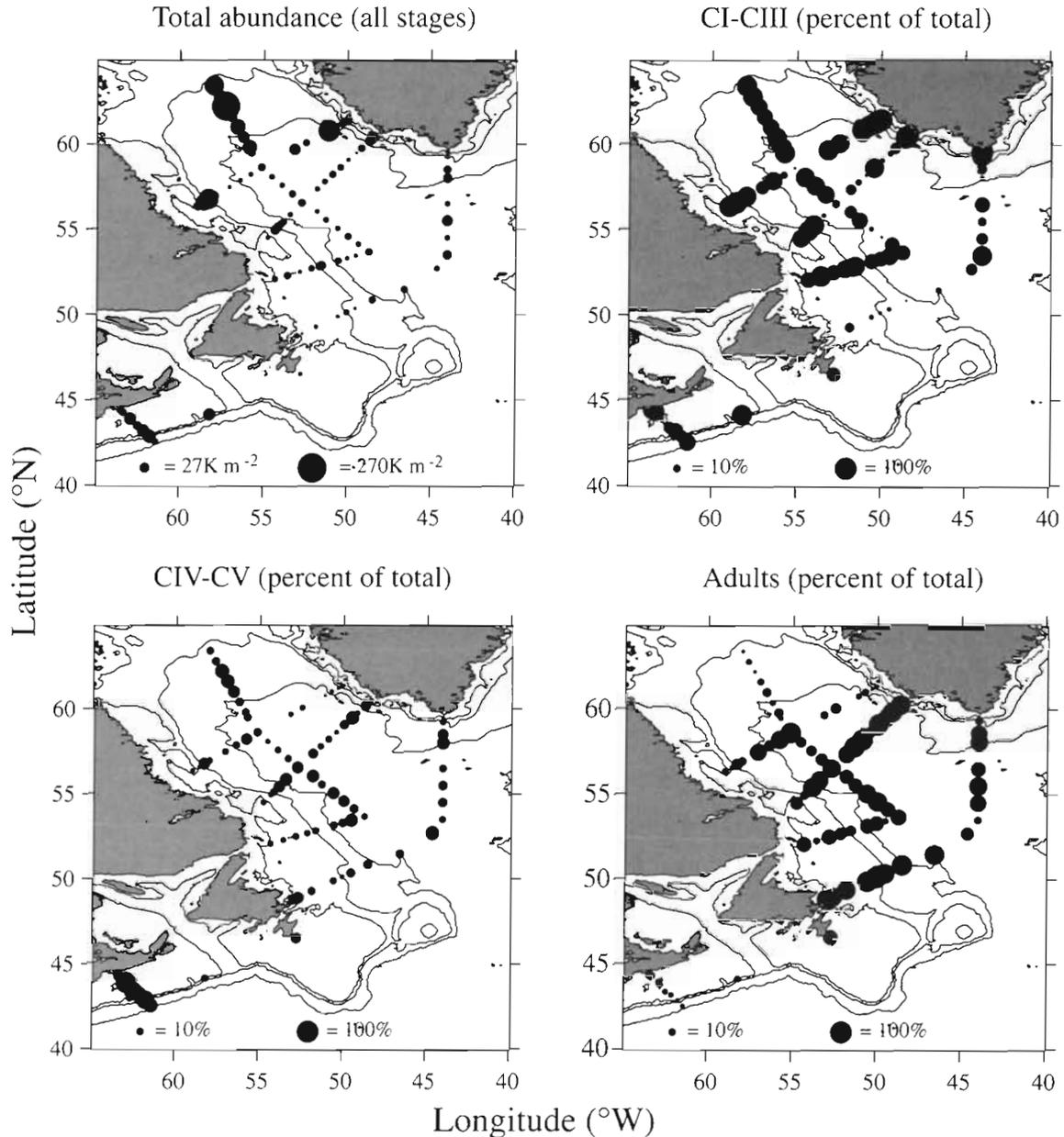


Fig. 8. *Calanus finmarchicus*. Abundance in the Labrador Sea in May–June 1997. The areas of the solid circles are proportional to the number of copepods m^{-2} .

abundance for any individual stage was CIII at ca $131\,000\ m^{-2}$ (L6 Stn 16). In the Labrador Sea, stages CIV and CV were only numerous in the north (L6) and at 1 station at the Labrador shelf-break on the L2 line (L2 Stn 2). Females generally outnumbered males by a factor of 5 or more and were themselves most abundant at the shelf-break station on the L2 line (ca $30\,000\ m^{-2}$; L2 Stn 2), with next highest abundances in the southeast (L5), on the eastern side of the central Labrador Sea (L3) and in the south (BON Stns 13 and

16). Males had their highest abundances at stations on the L5 line and at stations of depth $>3000\ m$ in the central Labrador Sea (Stns L2, L3 and L6) (Tables 1 & 2). Along the HL on the Scotian Shelf, where the spring bloom occurred in April in 1997 (Head unpubl. data), CIVs and CVs were the most abundant stages, followed by CI–CIII, and adults were relatively rare (Fig. 8).

In the Labrador Sea total *Calanus finmarchicus* biomass (Fig. 9) varied between a maximum of ca $20\ g\ dry$

Table 1. *Calanus finmarchicus*. Abundances of individual stages along the latitudinal sections from west to east (no. m⁻²)

Line	Stn	I	II	III	Stage IV	V	VI F	VIM	Total
L2-BO	7	7955	3480	933	461	70	1182	0	14082
L2	1	49946	19585	7442	2054	411	3526	0	82965
L2	2	8136	21696	30510	17628	16950	31866	0	126786
L2	3	2825	12656	7910	1806	588	3770	226	29780
L2	5	610	407	136	90	203	1806	158	3410
L2	6	678	1806	1175	316	271	1220	90	5557
L2	7	298	199	0	75	1342	3232	547	5693
L2	8	90	45	0	181	2068	14012	768	17165
L2	11	18080	10848	3015	1406	588	4371	136	38443
L2	12	4371	3919	1085	158	678	2712	90	13013
L2	14	82363	45541	7051	1116	411	8520	59	145063
L2	15	8136	3616	1299	294	136	1356	0	14837
L2	16	9492	4746	1525	136	45	203	0	16148
L2	17	8136	4974	1299	90	0	68	0	14568
L2	18	8136	4522	1681	339	45	158	0	14882
L2	19	10297	9232	2106	323	25	348	0	22331
L3	5	2260	452	136	45	226	1487	0	4606
L3	6	6780	2486	452	316	181	2531	45	12792
L3	8	15368	4068	1921	859	362	3618	45	26241
L3	9	9718	5650	2170	1731	678	4070	158	24175
L3	10	9492	3315	960	490	264	1469	68	16060
L3	12	136	45	113	775	2441	9038	294	12841
L3	14	113	45	45	723	1469	4068	610	7074
L3	16	158	452	45	407	678	3164	542	5447
L3	17	655	542	249	945	384	3955	249	6979
L3	18	407	181	0	339	249	6780	497	8452
L3	19	0	68	113	226	1087	11752	497	13743
L3	20	90	0	90	475	226	3390	203	4475
L3	21	14	9	27	99	226	438	95	909
L3	22	1806	768	90	136	497	10846	407	14550
L3	24	362	316	226	452	5424	19888	1304	27972
L3	25	4746	1977	438	102	124	933	68	8389
L3	26	22148	12656	2441	271	203	1175	11	38906
L3	27	8362	3955	994	384	136	1469	68	15368
L4	1	2599	1921	712	136	542	4520	181	10611
L4	2	7533	3435	1989	484	423	1268	61	15192
L4	3	1431	301	129	271	90	1731	181	4134
L4	4	4068	1446	960	316	497	2938	136	10362
L4	5	7684	4070	3015	814	814	3315	45	19757
L4	6	8362	6554	2825	407	407	4972	90	23617
L4	8	3164	1957	904	136	1469	5650	271	13551
L4	9	1058	764	181	113	520	1883	90	4608
L4	10	1806	407	23	68	1187	203	45	3738
L4	11	2057	768	226	316	814	2608	339	7128
BON	1	0	0	0	226	678	5876	0	6780
BON	3	0	0	0	75	149	547	99	870
BON	6	755	0	0	226	339	3166	90	4577
BON	9	118	0	0	176	118	2642	59	3112
BON	10	181	0	0	181	226	9492	181	10260
BON	11	68	0	0	271	113	1806	68	2326
BON	13	45	0	0	1175	1085	11300	452	14057
BON	16	158	316	362	113	1883	10396	68	13296
BON	19	181	362	1550	904	2558	2441	362	8357

Table 2. *Calanus finmarchicus*. Abundances of individual stages along the longitudinal sections from north to south (no. m⁻²)

Line	Stn	Stage							Total
		I	II	III	IV	V	VI F	VI M	
L5	27	3618	551	203	45	0	36	7	4461
L5	26	2825	1356	382	169	254	610	23	5619
L5	24	2097	933	617	1333	3173	9695	979	18828
L5	23	181	181	316	2825	5424	13560	2893	25380
L5	20	2260	1058	316	158	707	2133	1130	7763
L5	18	2642	1695	588	823	5141	22916	1351	35157
L5	16	1193	522	398	199	1193	4473	124	8102
L5	14	11752	6328	2983	1742	588	2531	90	26015
L6	18	55402	34119	16814	11049	3098	2170	0	122652
L6	17	25764	10712	4068	3526	3254	3119	0	50443
L6	16	3164	16950	131080	83620	21093	4972	0	260879
L6	15	2441	5650	10848	9944	2967	2967	0	34818
L6	14	12430	17402	11933	18396	2287	10608	0	73057
L6	13	9492	11300	10848	4515	904	2441	181	39681
L6	12	22781	14645	10848	5641	1519	10125	289	65847
L6	11	9284	3810	2859	1243	1094	796	199	19285
L6	9	4371	1731	384	203	203	1681	68	8642
L6	8	3763	994	316	316	271	1356	181	7198
L6	7	3616	2599	2712	588	814	4215	45	14588
L6	5	911	373	174	75	1492	1740	224	4988
L6	4	3763	1085	475	113	1019	3611	158	10224
L6	3	50	50	199	0	2188	4805	348	7639
L6	2	0	45	45	45	3164	9040	497	12837
L6	1	4339	1898	316	127	1012	7087	316	15097

wt m⁻² at the Labrador shelf-break of the L2 line (L2 Stn 2; Table 3) and a minimum of ca 42 mg dry wt m⁻² on the shelf at the southern tip of Greenland (L5-27; Table 4). Adults generally dominated the total biomass, except at stations in the northern Labrador Sea (L6 Stns 14, 15, 16, 17 and 18) and at L2 Stn 2, where CVIs and CVs made important contributions. CIVs and CVs also dominated the biomass at stations of the HL on the Scotian Shelf.

Egg production rates and naupliar abundance versus the state of the spring bloom

In Fig. 10, we have divided the sampling area into 4 different zones based on the concentration of nitrate obtained from the continuous monitoring system (at ca 5 m depth). In the dark grey zone, covering the southeast region and central Labrador Sea, near-surface nitrate levels were >6 µM. In this area, chlorophyll concentrations were generally relatively low and we have designated this an 'early bloom' zone. The actual value (6 µM) was chosen somewhat arbitrarily, and corresponds to a nitrate concentration of roughly

one-half the highest values generally seen in the profiles to 100 m. In the intermediately coloured zone, covering the north central Labrador Sea and the Labrador Shelf, near-surface nitrate concentrations were between 1 and 6 µM. Integrated chlorophyll concentrations were variable, but often high, and we have therefore designated this a 'bloom' zone. In the 2 light grey zones, one in the northern Labrador Sea and the other over the Newfoundland Shelf and to the southwest, near-surface nitrate concentrations were <1 µM. Integrated chlorophyll concentrations were variable and we have designated these 'late' or 'post-bloom' zones. For near-surface water samples from profiles collected in the 3 zones (Table 5), average nitrate concentrations were highest in the early bloom zone, intermediate in the bloom zone and lowest in the late/post-bloom zone (p < 0.001). The average integrated chlorophyll concentration was lower in the early bloom zone than those in either the bloom or late/post-bloom zones.

Egg production rates were measured experimentally as average rates determined for groups of 20 to 30 females from 50 stations which were incubated individually (Campbell 1998, Campbell & Head 2000).

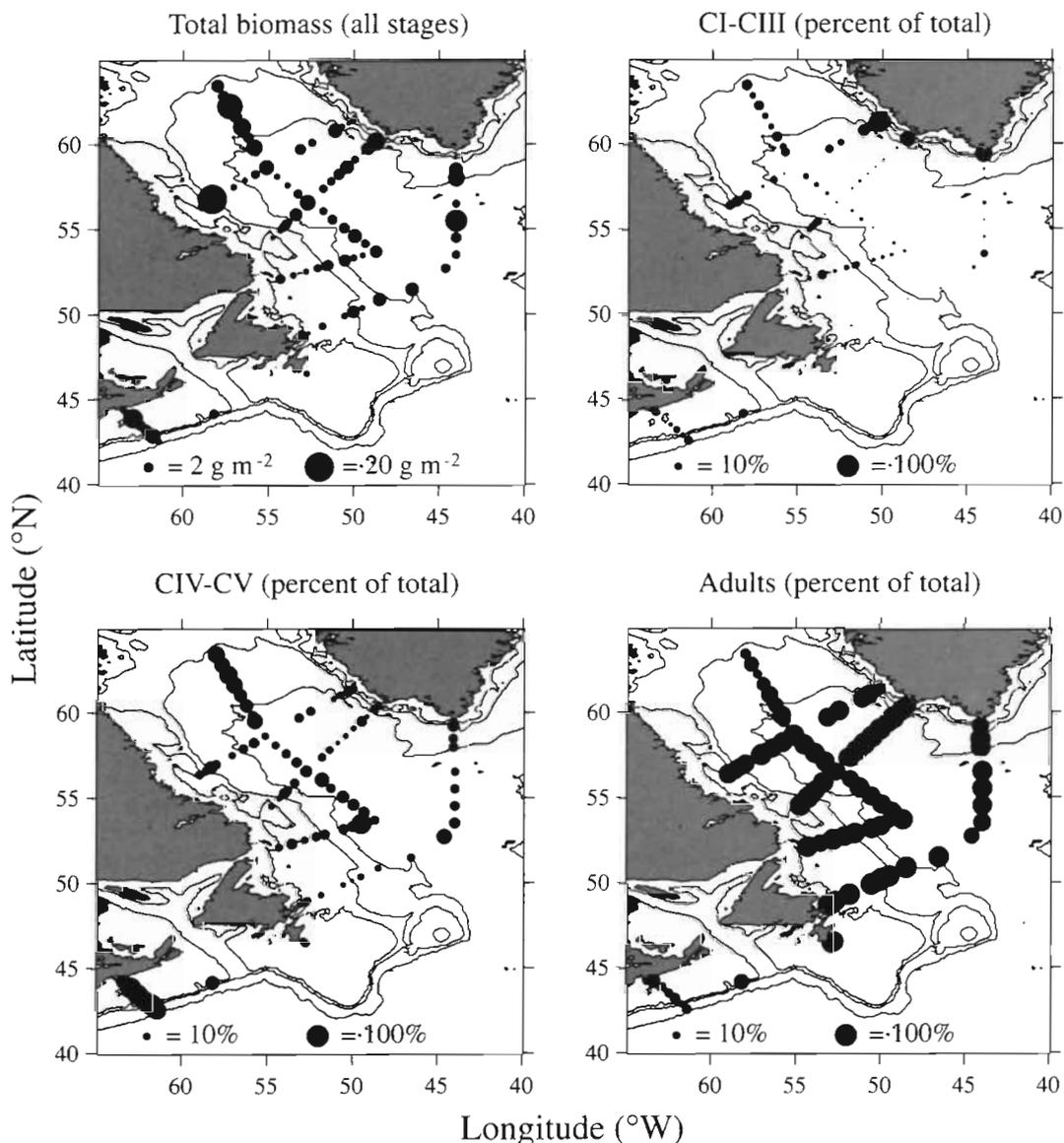


Fig. 9. *Calanus finmarchicus*. Biomass in the Labrador Sea in May–June 1997. The areas of the solid circles are proportional to the dry weight of copepods m^{-2}

When results were grouped by zones (Table 5), the average rate was higher in the early bloom zone than in either the bloom or late/post-bloom zones. Few, if any, eggs were produced at late/post-bloom stations in the northern Labrador Sea (L6 Stns 16 and 18) and at bloom L2 Stn 1 and L2 Stn 2. Average female abundance did not vary significantly between the zones ($p > 0.1$), although it was highest in the early bloom zone, intermediate in the bloom zone and lowest in the late/post-bloom zones (Table 5). Areal estimates of egg production rate followed the same pattern as that of individual egg production

rates: values were significantly higher in the early bloom zone than in either the bloom or late/post-bloom zones. Areal estimates of egg production rate and female abundances were closely correlated ($p < 0.001$; also, cf. Figs. 8 & 10) primarily because while average female egg production rates varied by only a factor of 50 between stations (excluding the zero values), female abundances varied by a factor of $ca 10^3$.

Estimates of relative abundance of *Calanus* spp. nauplii were made for the zooplankton samples collected using a 200 μm mesh net (Fig. 10). Since *C.*

Table 3. *Calanus finmarchicus*. Biomasses of individual stages along the latitudinal sections from west to east (mg dry wt m⁻²)

Line	Stn	Stage							Total
		I	II	III	IV	V	VI F	VI M	
L2-BO	7	20.8	22.4	24.4	47.5	8.6	374.7	0.0	498.3
L2	1	1087	140.1	178.3	173.6	109.6	1296.8	0.0	2007.1
L2	2	22.4	194.4	688.2	1955.4	4470.1	12320.6	0.0	19650.9
L2	3	10.8	153.2	212.9	174.5	163.2	1389.4	64.6	2168.7
L2	5	23	47	3.6	8.1	63.5	715.3	37.7	835.3
L2	6	2.7	19.7	35.9	30.5	76.6	420.1	24.0	609.5
L2	7	1.1	2.7	0.0	8.1	300.8	1086.6	147.4	1546.7
L2	8	0.0	0.5	0.0	14.5	487.5	4261.0	210.4	4973.8
L2	11	75.9	116.2	133.3	189.8	217.6	1761.7	44.5	2539.1
L2	12	15.6	42.9	37.1	18.1	190.5	1013.8	22.6	1340.6
L2	14	298.3	590.5	233.2	122.3	134.0	3064.6	21.7	4464.6
L2	15	32.3	40.5	44.5	25.1	37.3	438.2	0.0	617.9
L2	16	40.5	53.6	47.7	12.4	12.9	65.1	0.0	232.1
L2	17	33.9	68.5	42.3	7.9	0.0	17.9	0.0	170.4
L2	18	48.8	77.3	61.0	29.2	12.0	48.6	0.0	276.9
L2	19	51.5	95.1	53.6	29.6	5.7	87.7	0.0	323.2
L3	5	6.6	2.9	2.5	3.4	34.1	418.3	0.0	467.8
L3	6	19.4	16.0	12.4	23.3	22.4	747.2	8.8	849.5
L3	8	41.1	37.5	59.9	71.6	87.2	1337.9	12.2	1647.5
L3	9	35.7	58.3	68.0	256.3	205.2	1455.4	0.0	2079.0
L3	10	41.6	28.5	35.5	58.5	68.9	571.3	17.6	822.0
L3	12	0.5	0.2	2.5	83.8	495.6	2882.6	84.1	3549.3
L3	14	0.5	0.5	1.1	78.0	323.4	1353.7	171.5	1928.7
L3	16	0.5	3.8	0.9	38.6	142.2	1087.7	131.3	1405.0
L3	17	2.5	6.3	8.4	90.4	61.9	1260.6	64.6	1494.8
L3	18	1.4	1.6	0.0	33.4	36.8	2374.6	139.2	2587.0
L3	19	0.0	0.7	2.9	21.0	185.3	3637.2	118.9	3966.1
L3	20	0.2	0.0	1.8	38.0	36.6	1106.7	49.0	1232.4
L3	21	0.0	0.0	0.0	8.4	31.4	129.3	21.5	190.5
L3	22	7.5	9.0	3.6	10.8	99.7	3595.9	115.9	3842.5
L3	24	1.1	2.3	6.6	42.7	1127.1	5978.6	342.8	7501.2
L3	25	20.6	27.1	12.0	7.2	29.6	254.5	17.9	368.8
L3	26	84.1	164.5	88.1	20.6	41.8	296.3	2.9	698.3
L3	27	35.3	50.9	28.9	29.6	25.5	425.6	12.9	608.6
L4	1	14.0	28.2	26.0	18.8	193.9	1636.9	47.7	1965.5
L4	2	35.3	31.4	65.5	41.8	141.0	471.9	14.9	801.8
L4	3	5.7	3.2	3.6	37.3	29.2	561.6	42.9	683.4
L4	4	19.0	15.4	32.1	59.0	155.0	1038.9	36.8	1356.2
L4	5	25.3	38.6	92.7	75.3	276.6	1337.2	11.8	1857.5
L4	6	33.2	58.3	80.7	39.6	132.9	1983.8	25.3	2353.8
L4	8	12.4	21.0	31.0	15.6	553.5	2417.1	85.2	3135.7
L4	9	45	8.6	7.7	10.2	202.0	742.0	24.9	999.8
L4	10	7.7	3.8	0.7	4.3	515.3	88.6	14.9	635.3
L4	11	7.0	5.2	5.7	24.6	345.8	948.7	147.4	1484.4
BON	1	0.0	0.0	0.0	19.9	116.8	1720.5	0.0	1857.3
BON	3	0.0	0.0	0.0	2.9	36.6	167.7	23.7	231.0
BON	6	3.2	0.0	0.0	19.7	64.0	1040.7	21.5	1149.0
BON	9	0.2	0.0	0.0	19.9	20.6	786.9	14.7	842.3
BON	10	0.2	0.0	0.0	20.8	64.9	3346.2	59.4	3491.5
BON	11	0.0	0.0	0.0	24.2	26.2	572.5	16.5	639.4
BON	13	0.2	0.0	0.0	110.7	195.7	3500.3	126.8	3933.8
BON	16	0.2	1.8	7.7	28.2	469.2	3539.6	15.8	4062.6
BON	19	0.7	2.9	37.1	77.1	735.2	800.7	116.6	1770.3

Table 4. *Calanus finmarchicus*. Biomasses of individual stages along the longitudinal sections from north to south (mg dry wt m⁻²)

Line	Stn	Stage							Total
		I	II	III	IV	V	VI F	VI M	
L5	27	15.6	5.4	5.2	5.7	0.0	9.3	1.1	42.3
L5	26	10.1	11.8	10.3	10.4	57.1	142.2	5.2	46.9
L5	24	6.1	6.8	13.3	119.6	550.3	3262.3	264.9	4223.3
L5	23	0.5	1.1	5.7	251.1	816.5	4381.2	831.9	6288.0
L5	20	7.2	9.7	8.4	14.0	148.7	789.9	303.1	1281.0
L5	18	8.1	16.7	12.7	90.2	1693.9	8754.1	431.4	11007.1
L5	16	3.4	4.1	12.0	18.8	412.2	1855.7	37.5	2343.6
L5	14	24.4	50.6	68.8	151.0	184.9	920.5	24.9	1425.0
L6	18	125.9	153.5	482.1	1019.5	967.5	756.9	0.0	3505.3
L6	17	57.9	55.8	86.3	241.4	1107.4	1215.9	0.0	2764.7
L6	16	5.0	83.6	2548.6	5348.1	4547.3	2121.2	0.0	14653.8
L6	15	7.0	31.2	194.4	942.0	784.2	1236.4	0.0	3195.2
L6	14	33.9	144.6	297.4	1653.6	779.2	4405.2	0.0	7314.0
L6	13	27.6	91.8	330.9	444.1	356.2	57.2	1045.5	2353.1
L6	12	65.1	103.5	360.5	640.7	561.4	4245.2	68.9	6045.3
L6	11	38.2	35.7	81.4	121.1	370.0	293.8	64.0	1004.1
L6	9	18.8	14.5	10.4	17.0	66.0	580.8	21.9	729.3
L6	8	13.3	6.3	7.5	32.3	90.4	558.7	51.1	759.6
L6	7	12.4	19.7	0.0	66.9	279.6	1352.2	9.3	1740.0
L6	5	2.3	2.7	5.7	5.2	515.7	680.9	76.6	1289.1
L6	4	12.9	12.2	14.7	17.6	301.5	1593.5	45.7	1998.1
L6	3	0.0	0.2	5.4	0.0	710.1	1606.2	99.0	2420.9
L6	2	0.0	0.2	0.2	3.8	1181.1	2992.7	124.8	4302.8
L6	1	13.6	16.5	6.8	20.1	497.9	2613.2	123.4	3291.5

finmarchicus was by far the most abundant of the 3 *Calanus* spp. found in the region and was the only one which was reproductively active at this time, it is reasonable to assume that all of the calanoid nauplii collected would have been *C. finmarchicus* nauplii. Hauls using a 200 μ m mesh may have underestimated the abundance of nauplii, because of extrusion of the smaller stages through the net, but we suggest that our values are probably good estimates of relative abundance, because over all stations, while measured naupliar abundances were unrelated to measured abundances of *Oithona* spp. (a fairly ubiquitous and similar-sized, but unrelated organism; $p > 0.5$), they were highly correlated with those of *C. finmarchicus* CIs and CIIIs ($p < 0.001$, in each case). Relative abundances of nauplii were not correlated with female abundances ($p > 0.4$) nor with areal estimates of egg production rate ($p > 0.05$). The highest relative naupliar abundances occurred at stations L3 Stn 26, L2 Stn 1, L2 Stn 15 (124 300, 149 838 and 305 552 m⁻², respectively), which were all within the bloom zone (Fig. 10). Average relative naupliar abundances were higher in bloom and late/post-bloom zones than in the early bloom zone. It should

be noted that we did not include data on naupliar abundances on the Scotian Shelf, since at those stations there were probably other species of calanoid nauplii present.

DISCUSSION

Phytoplankton bloom development in the Labrador Sea

The pattern of bloom development in the Labrador Sea sampling area (late/post-bloom conditions in northern areas; bloom conditions at the middle latitudes; early bloom conditions in the southeast) was consistent with observations made during the 1963, Norwestlant surveys (ICNAF 1968), and with observations of surface chlorophyll concentrations made by satellite during 1998. For example, during the April Norwestlant I survey period, phytoplankton concentrations at 10 m were high along the west coast of Greenland north of 60°N, but low to the south of Greenland and from there to Labrador, in the general area of our L3 line. During the late May–early June Norwestlant II

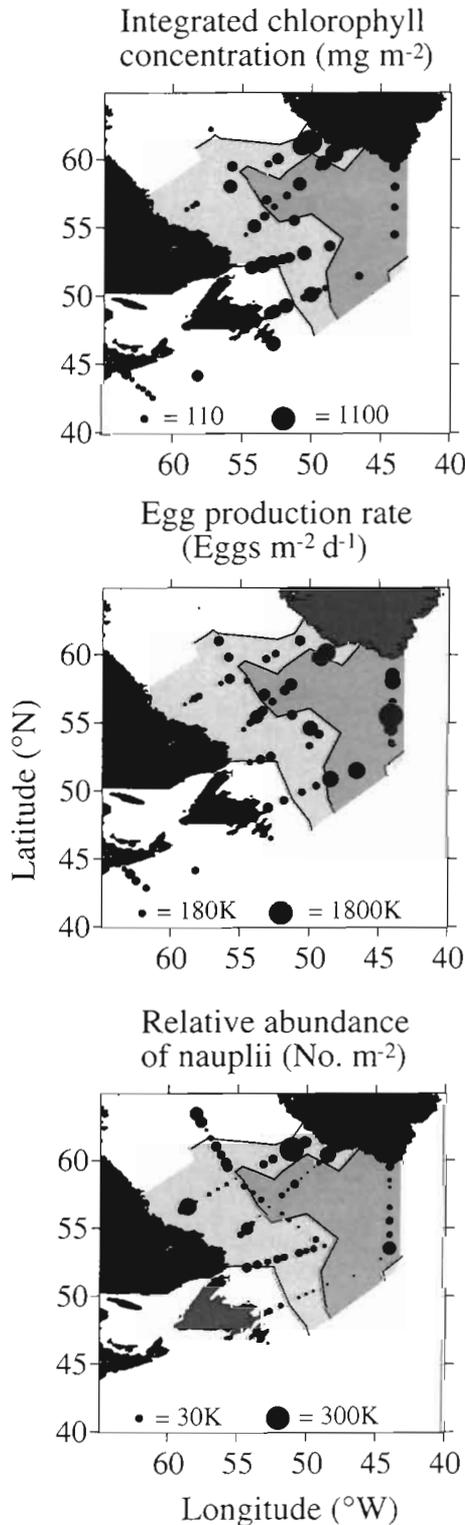


Fig. 10. Areas of the Labrador Sea designated as early bloom (dark grey), bloom (medium grey) and late/post-bloom (light grey) zones, on the basis of the 1 and 6 μM contours of near-surface nitrate concentration. The areas of the solid circles are proportional to: integrated chlorophyll concentration (mg m^{-2} , upper panel), areal egg production rate ($\text{eggs m}^{-2} \text{d}^{-1}$) and relative naupliar abundances (no. m^{-2})

survey period, phytoplankton concentrations were lower than they had been in April north of 60°N , and intermediate or high, but patchy, throughout the Labrador Sea and to the south of Greenland. Similarly, in early April 1998, observations of surface chlorophyll concentrations, compiled from the SeaWiFS satellite images for bi-weekly intervals (L. Payzant & H. Bishop pers. comm.) showed high values over the central Labrador Sea basin north of 60°N and east of 54°W (and from Flemish Cap and the Grand Bank southwest to Georges Bank) and low values to the south of Greenland. Thereafter there was a progression of the bloom southwards into the central Labrador Sea through May, with high values occurring south of Greenland in early June. Thus, it seems that early blooming in the north and east is a regular occurrence. One explanation for this might be the influence of locally melting ice in late winter. In general, in March ice covers the entire Labrador Shelf and the deep water north of a line between ca 60°N , 60°W and 66°N , 55°W (Drinkwater & Mountain 1997). Ice-melt starts in earnest in April, and the prevailing winds are northwesterly with the potential to advect fresh water towards the southeast, causing density stratification that allows the bloom to develop. In fact, in 1998 there was a slight 'greening' in the northern regions in the satellite image for late March, implying that the melt may sometimes start earlier than April. The connection between bloom development and melting ice has been recognised in the Barents Sea (Rey & Loeng 1985), the Greenland Sea (Spies 1987) and other seasonally ice-covered areas (Smith & Nelson 1985).

It is generally accepted that in order for phytoplankton to bloom in spring following deep winter mixing, stratification of the water column is required via the formation of either a pycnocline (as discussed above) or a thermocline (caused by solar warming of the surface layers). Exceptions to this pattern, however, are common in boreal, temperate and polar regions (Colebrook 1979, Townsend et al. 1992, Wassmann et al. 1996), as well as in Norwegian fjords (Wassmann 1991, Eilertsen 1993, Wassmann et al. 1996). Townsend et al. (1992) suggested that for temperate ocean areas the increasing light penetration in spring and the clarity of the post-winter water are sufficient conditions to allow phytoplankton to bloom, if winds are light and vertical mixing is not deep. In contrast, if wind strengths are high and vertical mixing extends to depths below the critical depth, a bloom should not be expected. During our sampling in the Labrador Sea there was little thermal stratification of the water column on any of the lines, with the possible exception of the Labrador Shelf area of the L4 line, where solar warming may have had an influence. There was, however, only slight evidence of elevated chlorophyll concentrations there and these

Table 5. Characteristics of zones designated as 'early bloom', 'bloom' and 'late/post-bloom' zones in the Labrador Sea in May 1997. Values are shown as averages \pm SD and the number of stations contributing is shown in brackets below. EPR: egg production rate; fem.: female

Near-surface nitrate conc. (μM)	Integrated chl. conc. (mg m^{-2})	Female EPR (eggs fem. $^{-1}$ d $^{-1}$)	Female abundance (fem. m $^{-2}$)	Areal EPR (eggs m $^{-2}$ d $^{-1}$)	Relative naupliar abundance (no. m $^{-2}$)	Male abundance (male m $^{-2}$)
Early bloom zone 8.3 \pm 2.6 ^a (11)	149 \pm 100 ^a (11)	71.3 \pm 15.8 ^a (16)	6617 \pm 6034 (24)	548491 \pm 441367 ^a (16)	10150 \pm 17547 ^a (24)	542 \pm 649 ^a (24)
Bloom zone 3.7 \pm 3.0 ^a (25)	304 \pm 282 (25)	47.3 \pm 22.4 (29)	4363 \pm 5302 (44)	186750 \pm 145787 (29)	33642 \pm 51828 (44)	151 \pm 178 (44)
Late/post-bloom zone 0.4 \pm 0.9 ^a (7)	296 \pm 137 (7)	25.9 \pm 21.1 (5)	3060 \pm 1750 (7)	94543 \pm 109995 (5)	31717 \pm 31900 (7)	40 \pm 52 (7)

^aDenotes that the value is statistically different from those in the other 2 zones ($p < 0.05$). We used ANOVA for nitrate concentrations and t -tests for other measurements

only in the subsurface layers, since surface nitrate concentrations had already been depleted (Figs. 3 & 6), probably because of prior surface blooming in association with density stratification caused by melting ice. Elsewhere, at stations near the shelf break of the Greenland (L2) and Labrador (L3, L4) shelves, where there was weak density stratification, there tended to be areas of enhanced phytoplankton concentration. Intense blooms also occurred, however, in some localised areas of the central Labrador Sea which were essentially unstratified (e.g. L2 and L3 lines), but not in others, and chlorophyll concentrations were relatively low in the unstratified waters to the south of Greenland (L5). The phytoplankton species composition, which was examined along the L3 line only, was similar to that reported for other boreal areas in spring (e.g. Spies 1987, Wassmann et al. 1990): *Phaeocystis pouchetii* was the most abundant phytoplankton species at all bloom stations, with diatoms (e.g. *Chaetoceros* and *Thalassiosira* spp.) quite abundant at bloom stations near the Greenland shelf and jointly more abundant than *P. pouchetii* at L3 Stn 22 (W. K. W. Li unpubl. data). One question that arises from our observations is why blooms should have occurred in some unstratified areas and not in others. We suggest that this may have been caused by differences in the extent of vertical mixing. During our cruise to the Labrador Sea, average daily wind speeds were >20 knots on 4 of the 8 d it took to sample the BON and L5 lines, and <15 knots on only 2. By contrast, during the following 18 d spent sampling the L3, L2, L6 and L4 lines, average daily wind speeds were >20 knots on only 2 d and <15 knots on 11 d. Instantaneous shipboard observations of wind speed cannot be used to hindcast the likelihood of encountering of blooms at particular stations, since the past history and duration of local mixing events are

unknown. They do suggest, however, that vertical mixing was generally more extensive on the BON and L5 lines than on lines farther north, which is consistent with our observation that intense blooms had not become established in this area.

Another factor, which might influence the dynamics of the spring bloom, is the timing of the return to the surface layers of populations of mesozooplankton, such as *Calanus finmarchicus*, which overwinter at depth (Bathmann et al. 1990, Wassmann et al. 1996). If their concentrations are high and if their return precedes the initiation of the bloom, then their grazing might be sufficient to delay it or depress its intensity. To examine this possibility we estimated potential daily carbon requirements for the copepods and phytoplankton growth rates using some very simple assumptions. To estimate copepod carbon demands at each station, we took the sum of the dry weights of all 3 *Calanus* spp. (*C. finmarchicus*, *C. glacialis* and *C. hyperboreus*), which constituted $>80\%$ of the herbivorous zooplankton biomass (Head unpubl. data) and assumed a carbon content of 50% and a carbon specific requirement of 30% d $^{-1}$. To estimate phytoplankton growth rates we either used the integrated chlorophyll concentration and assumed a carbon:chlorophyll ratio of 50 and a doubling time of 1 d $^{-1}$ or a maximum value of 2.3 g C m $^{-2}$ d $^{-1}$ (Longhurst 1995), if our calculated value was higher than this. Data was available for 8 stations in the early bloom zone: at 1 (L3 Stn 21), copepod demand for carbon was $<10\%$ of phytoplankton production; at 4 (BON Stn 11, L3 Stn 8, L5 Stn 16, L5 Stn 20), it was between 10 and 22%; and at 3 (BON Stn 16, L3 Stn 22, L5 Stn 23), it was between 40 and 50%. Thus, although copepod grazing might have been affecting bloom development at some early bloom stations, it was probably not important at others.

***Calanus finmarchicus* maturation and spawning in relation to the phytoplankton bloom**

The highest rates of egg-laying by female *Calanus finmarchicus* occurred in the early bloom zone, suggesting that even though chlorophyll concentrations were relatively low, egg production was not limited by food. In fact, however, at most early bloom stations integrated chlorophyll concentrations exceeded 79 mg m^{-2} , which appears to be the concentration below which *C. finmarchicus* egg production rates becomes food limited in the western Atlantic (Campbell 1998, Campbell & Head 2000). This and other observations of egg-laying by *C. finmarchicus* before the development of the spring bloom (Diel & Tande 1992, Gislason & Astthorsson 1996) do not contradict the idea that females need to feed to produce eggs (Marshall & Orr 1952, Plourde & Runge 1993, Hirche et al. 1997), but rather show that relatively low food concentrations, which may occur before the bloom becomes established, are sufficient to allow females to produce eggs at maximal rates.

Egg-laying by *Calanus finmarchicus* was occurring before the bloom had become established in some areas, but the products of reproduction were more abundant in areas showing bloom (nauplii) or late/post-bloom conditions (nauplii and CI–CIII). In fact, at the northern stations of the L6 line, stage distributions suggest that even many of the later stage copepodites (CIVs and CVs) were from the G1 (current year's) generation (Table 2). Also, at L6 Stns 16 and 18, where egg production rates were zero or near zero, most of the females were reproductively immature (Campbell 1998), probably because they also belonged to the G1 generation. At stations slightly farther south (L6 Stns 12 and 14), where egg production rates and the proportion of females with mature gonads were also relatively low, female populations probably consisted of mixtures of the G1 and G0 (overwintered) generations.

According to Matthews (1968), diapausing *Calanus finmarchicus* emerge at the same time throughout our study area. Thus, one question that arises is why there were no or few G0 females at the northerly stations: if G0 females were abundant farther south, they should also have been present in the north. One possible explanation is that although egg production rates in mature females were not generally limited by food, perhaps rates of development from immature to mature egg-laying females were more affected. Thus, if there had been an intense early bloom (March/April) in the northeast Labrador Sea in 1997 (as in other years), females there would have matured and started producing eggs earlier than those farther south, so that they would have become spent and died by the sampling time (early June) after a ca 2 mo spawning

period. In other areas gonad maturation would have been slower and the onset of egg production would have been delayed. Females had apparently attained maturity in areas where the bloom had not yet become established by mid-May, however, since egg production rates in the early bloom zone were very high. Thus, once mature, it appears that females can produce eggs at maximal rates, more-or-less independent of *in situ* food concentration, presumably until they become spent and die. The scheme that we propose is similar to that discussed by Diel & Tande (1992), who compared spawning times of *C. finmarchicus* in Norwegian fjords (early) and in nearby open ocean areas (later) and who concluded, as we have, that temperature differences could not account for differences in maturation rates, and that food supply was also important. The link between female maturation and bloom development has been noted elsewhere (e.g. Marshall & Orr 1952, Tande et al. 1985, Plourde & Runge 1993), although our explanation of the observation that maximal egg production rates may precede the establishment of a delayed bloom is somewhat novel.

Abundances of females did not vary between zones, but abundances of males in the near-surface layers were highest in the early bloom zone and lower in the other 2 zones (Table 5): indeed, males were often absent from stations in the late/post-bloom zone. Previous studies have suggested that adult males tend to appear in the population earlier than females, that they fertilize immature females, possibly while still at overwintering depths (e.g. Tande & Hopkins 1981, Miller et al. 1991), and that they do not live as long as females (Hirche 1996). It is difficult to reconcile these behaviours with our observations, if arousal from diapause was more-or-less synchronous over the study area. Instead, our data suggest that, as for females, maturation of overwintered males was delayed at southern latitudes.

Another possible explanation for our observations of adult abundances is that the arousal of *Calanus finmarchicus* populations was not synchronous everywhere, but occurred earlier at more northerly latitudes. This seems unlikely, however, since there appears to be a reasonably high degree of synchrony in arousal times from 40 to 70°N (Miller et al. 1991) and the suggested triggers (photo-period or internal clock; Hirch 1996) would not lead us to predict early arousal in the north. Yet another suggestion is that adult *C. finmarchicus* to the south of Greenland and in the central Labrador Sea (i.e. early bloom zones) belonged to the G1 generation, derived from members of a population that appear to have an early (January) start to their upward migration in an area south of Newfoundland (Planque et al. 1997). This too seems unlikely: firstly, because the abundances of

young stages were generally lower than those of the adults at these stations; and secondly, because on Flemish Cap and to the southwest of Iceland, it is clear that it is the G0 population which spawns in April and/or May (Anderson 1990, Gislason & Astthorsson 1995).

Overall, our observations suggest that following arousal from diapause, maturation rates for both male and female *Calanus finmarchicus* are low before the development of the spring bloom, but accelerate as phytoplankton levels rise. This scheme appears to provide overwintered *C. finmarchicus* with the ability to respond rapidly to early intense blooms, such as sometimes occur in several areas of its distribution. In general, however, reproduction should be maximal during the bloom, but if the bloom is unusually late or of low intensity in a given year and area, then reproduction of the G0 generation will be delayed and may occur under conditions unfavourable to the development of the new G1 generation (see below).

Development of the G1 generation

The pattern of copepodite distribution that we observed (CI–IIIs dominant in the north, adults farther south) is consistent with previous observations for the region at this time of year. The Norwestlant II (May–June) data show high abundances of CI–IIIs in the north, and much lower total abundances, with higher proportions of adults, at stations to the south of Greenland. In Davis Strait (ca 70°N), Huntley et al. (1983) found concentrations of CI–III *Calanus finmarchicus* increased between April–May and June samplings. In April–May, adults were dominant in western Davis Strait (ca 60 to 68°N), but by June these had been displaced by CI–IIIs. Matthews (1968) interpreted the Norwestlant data as showing progressively decreasing rates of development from south to north, which he attributed to differences in temperature. Close examination of the original data does not support this view for the progression between April and May–June sampling periods, however, and his analysis may also have been confounded by the fact that *C. finmarchicus* was not distinguished from *C. glacialis* in samples from the April survey.

Our observations of *Calanus finmarchicus* relative naupliar abundances and copepodite abundances and stage distributions strongly suggest that development was linked to the progress of the bloom, so that the G1 generation was more advanced in the north. Furthermore, even though egg production rates were very high in our early bloom zone, few nauplii were found. Although it is conceivable that their scarcity was simply due to timing (i.e. egg-laying had started only

within the last 1 to 2 wk), Marshall & Orr (1955) noted that in Loch Striven most *C. finmarchicus* eggs laid before the bloom failed to develop into a new generation and they suggested that this might have been because the smaller, less mobile early life stages need relatively high concentrations of suitable (e.g. small) food items. The small size and lack of mobility of eggs and early stages also suggest another factor that might contribute to their demise: namely, predation. One potential predator might be the female *C. finmarchicus* themselves, which are known to eat their own eggs under experimental conditions (Cabal et al. 1997). If we assume filtration rates ca 2 ml female⁻¹ h⁻¹, then even where the females were most abundant (ca 23 000 m⁻² at L5 Stn 18), and if they had been concentrated over a depth range of only 5 m, they would only have filtered ca 20% of that 5 m water column in a 24 h period. On the basis of this calculation it seems unlikely that cannibalism would have been very important *in situ*. Another potential predator might have been the carnivorous copepod *Euchaeta norvegica*. This species is very abundant throughout the deep water in the entire sampling area and appears to reproduce in January or February (Head & Harris unpubl. data). By May, the dominant stages are IIs, IIIs and IVs, for which *C. finmarchicus* eggs and nauplii would probably be suitable prey. Larval redfish (*Sebastes* spp.) might also have been important predators: they are known to consume *C. finmarchicus* eggs in large numbers (Runge & de Lafontaine 1996). At this time of year, larval redfish occur in the deep waters south and east of Greenland and they are very abundant in the Irminger Sea (ICNAF 1968), although we did not see any in our vertical nets tows. In the presence of high phytoplankton concentrations cannibalism on eggs by females would probably be reduced, since they would easily be able to fulfill their nutritional requirements and *E. norvegica* and fish larvae may be less able to capture their prey: for the latter, which are visual predators, this might be caused by a reduction in under water light intensity.

Once the eggs had developed into the larger nauplii, which would have been sampled relatively efficiently with our 200 µm net, it appears that there was a reduction in the mortality and it became more regular, since naupliar abundances were well correlated with the somewhat lower abundances of CIs and CIIIs. In addition, it appears that high phytoplankton levels per se may not have been important for further development, perhaps because a greater selection of larger food items became available: for example, phytoplankton concentrations were low at the northern stations of the L6 line, but ciliate microzooplankton were very abundant. One might also anticipate that at this stage of development the effect

of temperature on growth rate might become more important, which would tend to bring the northern advanced population into synchrony with the southern retarded population as the summer progresses, as seen during the Norwestlant II and III surveys (Matthews 1968).

Implications for recruitment in *Calanus finmarchicus* in the Labrador Sea

In the Labrador Sea it is possible that the timing of the spring bloom may have an important influence of the level of recruitment to the new year's G1 generation of *Calanus finmarchicus*, since if the bloom is late and eggs are laid before high phytoplankton concentrations prevail, many may not survive. Elsewhere, where there are multiple generations, recruitment to G2 and subsequent generations may be able to make up for a poor G1 recruitment, but in the Labrador Sea, low temperatures and a short growth season probably preclude such a compensatory mechanism.

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LITERATURE CITED

- Anderson JT (1990) Seasonal development of invertebrate zooplankton on Flemish Cap. *Mar Ecol Prog Ser* 67: 127–140
- Bathmann UV, Noji TT, von Bodungen B (1990) Copepod grazing potential in late winter in the Norwegian Sea—a factor in the control of spring phytoplankton growth? *Mar Ecol Prog Ser* 60:225–233
- Cabal J, Harris LR, Head EJH (1997) Egg production rates of *Calanus finmarchicus* in the northwest Atlantic (Labrador Sea). *Can J Fish Aquat Sci* 54:1270–1279
- Campbell RW (1998) Reproduction of *Calanus finmarchicus* in the western North Atlantic: fecundity and hatching success. Master thesis, Dalhousie Univ
- Campbell RW, Head EJH (2000) Egg production rates of *Calanus finmarchicus* in the western North Atlantic: effect of gonad maturity, female size, chlorophyll concentration and temperature. *Can J Fish Aquat Sci* (in press)
- Colebrook JM (1979) Continuous plankton records: seasonal cycles of phytoplankton and copepods in the North Atlantic Ocean and the North Sea. *J Plankton Res* 4: 435–462
- Diel S, Tande K (1992) Does the spawning of *Calanus finmarchicus* in high latitudes follow a reproducible pattern? *Mar Biol* 113:21–31
- Drinkwater KF, Mountain DG (1997) Climate and oceanography, Chap 1. In: Boreman J, Nakashima BS, Wilson JA, Kendall RL (eds) Northwest Atlantic groundfish: a perspective on a fishery collapse. American Fisheries Society, Bethesda, MD, p 3–25
- Durbin EG, Runge JA, Campbell RG, Garrahan PR, Casas MC, Plourde S (1997) Late fall-early winter recruitment of *Calanus finmarchicus* on Georges Bank. *Mar Ecol Prog Ser* 151:103–114
- Eilertsen HC (1993) Spring blooms and stratification. *Nature* 363:24
- Gaard E (1996) Life cycle, abundance and transport of *Calanus finmarchicus* in Faroese waters. *Ophelia* 44: 59–70
- Gislason A, Astthorsson OS (1995) Seasonal cycle of zooplankton southwest of Iceland. *J Plankton Res* 17:1959–1976
- Gislason A, Astthorsson OS (1996) Seasonal development of *Calanus finmarchicus* along an inshore-offshore gradient southwest of Iceland. *Ophelia* 44:71–84
- Gislason A, Astthorsson OS (1998) Seasonal variations in biomass, abundance and composition of zooplankton in the subarctic waters north of Iceland. *Polar Biol* 20:85–94
- Grainger EH (1963) Copepods of the genus *Calanus* as indicators of Eastern Canadian waters. In: Dunbar MJ (ed) Marine distributions. R Soc Can, Special Publ No 5, Univ Toronto Press
- Hirche HJ (1996) The reproductive biology of the marine copepod, *Calanus finmarchicus*—a review. *Ophelia* 44: 111–128
- Hirche HJ, Meyer U, Niehoff B (1997) Egg production of *Calanus finmarchicus*: effect of temperature, food and season. *Mar Biol* 127:609–620
- Holm-Hansen O, Lorenzen CJ, Holmes RW, Strickland JDH (1965) Fluorimetric determinations of chlorophyll. *J Cons Int Explor Mer* 30:3–15
- Huntley M, Strong KW, Dengler AT (1983) Dynamics and community structure of zooplankton in the Davis Strait and Northern Labrador Sea. *Arctic* 36:143–161
- ICNAF Special Report No 7 (1968) Environmental Surveys—Norwestlant 1–3, 1963. Issued from the Headquarters of the Commission, Dartmouth, NS
- Kielhorn WV (1952) The biology of the surface zone zooplankton of a boreo-arctic Atlantic Ocean area. *J Fish Res Board Can* 9:223–264
- Longhurst A (1995) Seasonal cycles of pelagic production and consumption. *Prog Oceanogr* 36:77–167
- Longhurst A, Williams R (1992) Carbon flux by seasonal migrant copepods is a small number. *J Plankton Res* 14: 1495–1509
- Marshall SM, Orr AP (1952) On the biology of *Calanus finmarchicus* VII Factors affecting egg production. *J Mar Biol Assoc UK* 30:527–547
- Marshall SM, Orr AP (1955) The biology of a marine copepod *Calanus finmarchicus* (Gunnerus). Oliver and Boyd, Edinburgh
- Matthews JBL (1968) On the acclimatization of *Calanus finmarchicus* (Crustacea, Copepoda) to different temperature conditions in the north Atlantic. *Sarsia* 34:371–382
- McLaren IA, Corkett CJ (1986) Life cycles and production of two copepods on the Scotian Shelf, eastern Canada. *Sylogeus*. *Nat Mus Can* 58:362–368
- Miller CB, Cowles TJ, Wiebe PH, Copley NJ, Grigg H (1991) Phenology in *Calanus finmarchicus*; hypotheses about control mechanisms. *Mar Ecol Prog Ser* 72:79–91
- Planque B, Hays GC, Ibanez F, Gamble JC (1997) Large scale spatial variations in the seasonal abundance of *Calanus finmarchicus*. *Deep-Sea Res I* 44:315–326
- Plourde S, Runge JA (1993) Reproduction of the planktonic copepod *Calanus finmarchicus* in the lower St. Lawrence

- Estuary: relation to the cycle of phytoplankton production and evidence for a *Calanus* pump. *Mar Ecol Prog Ser* 102: 217–227
- Rey F, Loeng H (1985) The influence of ice and hydrographic conditions on the development of phytoplankton in the Barents Sea. In: Gray J, Christiansen M (eds) *Marine biology of polar regions and effect of stress on marine organisms*. Wiley, Chichester, p 49–63
- Runge JA, de Lafontaine Y (1996) Characterization of the pelagic ecosystem in surface waters of the northern Gulf of St. Lawrence in early summer: the larval redfish-*Calanus*-microplankton interaction. *Fish Oceanogr* 5:21–37
- Runge JA, Plourde S (1996) Fecundity characteristics of *Calanus finmarchicus* in coastal waters of eastern Canada. *Ophelia* 44:171–187
- Smith WO, Nelson DM (1985) Phytoplankton bloom produced by a receding ice edge in the Ross Sea: coherence with the density field. *Science* 227:163–166
- Spies A (1987) Phytoplankton in the marginal ice zone of the Greenland Sea during summer, 1984. *Polar Biol* 7: 195–205
- Tande KS, Hopkins CCE (1981) Ecological investigations of the zooplankton community of Balsfjorden, Northern Norway: the genital system in *Calanus finmarchicus* and the role of gonad development in overwintering strategy. *Mar Biol* 63:159–164
- Tande KS, Hassel A, Slagstad D (1985) Gonad maturation and possible life cycle strategies in *Calanus finmarchicus* and *Calanus glacialis* in the northwestern part of the Barents Sea. In: Gray J, Christiansen M (eds) *Marine biology of polar regions and effect of stress on marine organisms*. Wiley, Chichester, p 141–155
- Townsend DW, Keller MD, Sieracki ME, Ackelson SG (1992) Spring phytoplankton blooms in the absence of vertical water column stratification. *Nature* 360:59–62
- Wassmann P (1991) Dynamics of primary production and sedimentation in shallow fjords and pols of western Norway. *Oceanogr Mar Biol Annu Rev* 29:87–154
- Wassmann P, Vernet M, Mitchell BG, Rey F (1990) Mass sedimentation of *Phaeocystis pouchetii* in the Barents Sea. *Mar Ecol Prog Ser* 66:183–195
- Wassmann P, Andreassen I, Reigstad M, Slagstad D (1996) Pelagic-benthic coupling in the Nordic Seas: the role of episodic events. *PSZN I: Mar Ecol* 17:447–471

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