Interannual variations in hydrography and spring bloom dynamics, and their effect on *Calanus finmarchicus* distribution and reproduction on the Scotian Shelf in the late '90s and 2000

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Abstract

The Eastern Scotian Shelf (ESS) has as its upstream source the Gulf of St. Lawrence, (GSL), whereas the central and western regions are influenced by the Nova Scotia Current and by intrusions of water from beyond the shelf-break that occur in the central region. Both the GSL and the offshore are springtime sources of overwintered Calanus finmarchicus and for central and western regions, the degree of penetration of offshore water and cross-shelf distribution of C. finmarchicus in April appear to be related to the position of the Gulf Stream in March-April of that year. Between 1995 and 2000 concentrations of *C. finmarchicus* were generally higher in central and western regions than in the ESS and copepodites of the current year's generation were dominant. In 1995, 1997 and 1998 C. finmarchicus abundances on the ESS were low and overwintered late stages were dominant. In 1999 the spring bloom occurred unusually early on the ESS and this was co-incident with an early onset of reproduction in the C. finmarchicus population, indicated by the presence of large numbers of young stage copepodites in April. In 2000, the bloom occurred at the same time as in 1998 on the ESS, but water temperatures were warmer than in 1998 or 1999. Concentrations of C. finmarchicus young stages were higher than in 1998, but lower than in 1999. In all years population stage structures were more advanced on the central and western shelf than in the east apparently due to earlier reproduction. Several factors may be involved: an earlier arousal from diapause of the offshore overwintering population; higher water temperatures during development to reproductive maturity; and/or an earlier start of the spring phytoplankton bloom.

Background

The North Atlantic copepod *Calanus finmarchicus* dominates the zooplankton of the Scotian Shelf on an annual basis, although it is present in the near-surface layers for only part of the year (Sameoto and Herman, 1992). One reason for this is that the species requires deep water in which to overwinter. For the Scotian Shelf, potential overwintering areas are: the Gulf of St. Lawrence to the northeast; the deep water beyond the shelf-break to the south (Head et al. 1999); and, the deep basins of the shelf itself, notably Emerald Basin in the mid-central shelf (Fig 1; Sameoto and Herman, 1990). According to our current understanding of the circulation (Han et al. 1997; Hannah et al. 2000), C. finmarchicus derived from the Gulf of St. Lawrence will be brought on to the northeastern shelf via the outflow through Cabot Strait and propagate southwest along the coast in the Nova Scotia Current. By contrast, C. finmarchicus derived from the shelfbreak population will be brought on to the shelf by intrusions of offshore water which occur in the central region to the west of Sable Island, and to a lesser extent through the Gully. Mixing of these populations will occur in the mid-central Scotian Shelf, off Halifax, where a component of the Nova Scotia Current splits from the coast, and it is to this mixture that individuals derived from Emerald Basin might add. From the midcentral shelf there is southwesterly flow towards the western shelf, with off-shelf flow east of Browns Bank.

Hydrographic and biological sampling between 1995 and 2000

During 1995, in 1997 and 1998 as part of the GLOBEC-Canada programme, and since then as part of the Atlantic Zone Monitoring Programme (AZMP), hydrographic

profiles and plankton samples have been collected each spring (April) along sections across western (Browns Bank and Roseway Lines), central (Halifax Line) and eastern (Louisbourg Line) regions of the Scotian Shelf and in Cabot Strait (Cabot Strait Line) (Fig. 1). The *Calanus* spp. results presented here, were from zooplankton samples collected using 200 µm mesh ring nets in vertical tows made from the bottom (if <100 m) or 100 m to the surface. Additional data on sea surface temperature and chlorophyll concentration were obtained using AVHRR and SeaWifs satellite images collected at the Bedford Institute and processed by colleagues from the Biological Oceanography Section to give bi-weekly composite images and bi-weekly average surface chlorophyll concentrations for areas covering the Halifax and Louisbourg Lines.

Abundances of *C. finmarchicus* and *C. hyperboreus* on and around in the Scotian Shelf in April 1995-2000: evidence for suggested sources and transport processes

The distribution of total abundance of *Calanus hyperboreus* is shown in Fig. 2. *C. hyperboreus* is a "cold water" relative of *C. finmarchicus* and it shares several lifehistory traits. For example, *C. hyperboreus* also overwinters in deep water, but in this region only in the Gulf of St. Lawrence in significant numbers, not beyond the shelfbreak. Thus, its distribution reflects the influence of the Gulf outflow on the shelf, so that it is most abundant on the ESS and in the Nova Scotia Current, off Halifax. *Calanus finmarchicus* (Fig. 3) is generally more abundant than *C. hyperboreus*, and generally more abundant in central and western regions of the shelf than in the east (except in 1999). This pattern is consistent with the suggested sources to the different regions, since concentrations of *C. finmarchicus* are low in the outflow from the Gulf of St. Lawrence, while those at or beyond the shelf-break in central and western regions can be quite high.

In 1995 on the Halifax Line, and in 1998 on all 3 lines over the central and western Scotian Shelf, cross-shelf distributions of *C. finmarchicus* showed a gradient in abundance, with low concentrations inshore and increasingly high concentrations towards the shelf-break. By contrast, in 1997, 1999 and 2000, there was a more even cross-shelf distribution, although concentrations in the Nova Scotia Current off Halifax were low in 1997 (and note the missing data at Stn. HL 4, in 1999).

The variations in cross-shelf distribution appear to be related to differences in hydrography, both on the shelf itself and beyond the shelf-break. Thus, for example, satellite images of sea surface temperature (SST) show that during late March (2-4 weeks before field sampling in April), the shelf-slope front (the 8°C isotherm) was noticeably farther south of the shelf-break in central and western regions in 1998, than in 1997, 1999 or 2000 (Fig. 5). In fact, the front abutted the shelf-break in the west in 2000 and in western and central regions in 1999. A comparison between the distribution patterns for C. finmarchicus (Fig. 4) and these images suggests that the offshore population and its offspring, which occupy the slope water north of the shelf-slope front, remain on the outer shelf and beyond when the front is in the south. When the front moves northwards it appears that animals from the offshore are pushed farther on to the shelf. Hydrographic measurements along the Halifax Line are consistent with these ideas. Note also, that the distribution patterns along the Halifax Line are apparently conserved as animals are advected to the west. Another feature shown in the SST images is the increase in temperature in the GSL outflow (Nova Scotia Current), which has been confirmed by field measurements.

<u>Stage compositions of *C. finmarchicus* populations along the Louisbourg and Halifax</u> Lines: interannual differences and implications for the timing of reproduction.

Where C. finmarchicus were abundant (>10,000 m⁻²) on the Halifax and Louisbourg Lines the populations were generally dominated by young-of-the-year copepodites (Fig. 6). The stage structures show that the new year's generation was more developed on the central SS than in the east in all 4 years. Careful examination of distributions on the Halifax Line reveals that the inner shelf stations in the Nova Scotia Current (HL1 and 2) were generally more reflective of their upstream source (the inner eastern SS), with low numbers (mostly overwintered late stages and adults) in 1995, 1997 (HL1 only) and 1998, and higher numbers (mostly very young stages) in 1999. In 2000 and in 1997 (HL2 only), even these inner shelf populations were similar in stage structure to those on the mid- and outer shelf, suggesting the offshore was their source. The mid-(HL3 and 4) and outer (HL 5) shelf regions show the effects of the annually variable intrusions from the offshore, with concentrations highest over the mid-shelf in 1997, 1999 and 2000, and over the outer shelf in 1995 and 1998. Stage compositions showed relatively little variation between mid- and outer shelf stations in a given year, but did vary between years, with populations apparently most developed in 1999, followed by 1997, 1995 and 2000, and least developed in 1998. These interannual variations in stage structure reflect differences in sampling dates (late in 1995 and 1997, early in 1998-2000), temperature (highest in 2000, followed by 1999, 1997, 1998 and 1995) and perhaps food supply in 1999 (see below). There was no indication of significant input of overwintered animals (Stage 5s and adults) from Emerald Basin (HL3) in April.

On the eastern Scotian Shelf (Louisbourg Line) C. finmarchcus young stages (1-3) were most abundant in the mid-shelf area in 1999, less so in 2000 and 1997, and rare in 1995 and 1998. The high numbers in 1999 and 2000 were not due to later sampling, since sampling was in fact earliest in 1999 (April 14-15), followed by 2000 (April 17-18), 1998 (April 19-21), 1997 (April 24-25) and 1995 (April 24-26). Also, the high values in 1999 were not due to the influence of temperature on development rate, since average 0-30 m temperatures on the mid-shelf were highest in 2000, followed by 1998, 1999, 1995 and 1997 (Table 1). Instead, the implication is that reproduction started earlier in 1999 than in the other years. Elsewhere it has been reported that the onset of reproduction in C. finmarchicus is associated with the start of the spring phytoplankton bloom (Plourde and Runge, 1993) or that the time between the final moult to adulthood and the start of egg-laying is dependent on food concentration (Hirche, 1996). Consistent with these ideas, reproduction occurred earlier in 1999 than in other years and, according to SeaWiFS satellite observations (Fig 6), the spring peak in chlorophyll concentration on the ESS Shelf was earlier than in either 1998 or 2000, and high concentrations appeared some 4 weeks earlier (Fig. 6). The linkage between the timing of the spring bloom and that of the onset of reproduction in C. finmarchicus is not altogether straightforward, however. Thus, for example, on the ESS in 1999 development times calculated using a Belehrådek temperature function (after Corkett et al., 1986) suggest that mid-shelf populations started reproducing in mid-February, well before the peak of the spring bloom in early March. The inner shelf populations, however, apparently did not start laying eggs until at least ca. 10 days later, even though the bloom appeared at more-orless the same time on the inner and mid-shelf. Also, in 1998 and 2000, the spring bloom

reached high levels at roughly the same time on the ESS (early-April), but estimates of birth dates for the mid-shelf (calculated as above) indicate that reproduction probably started in early March in 2000 and more than ca. 10 days later in 1998. Finally, for the central SS, stage distributions and temperature dependent development times indicate that reproduction probably started in mid-to-late February in all years. Satellite estimates of chlorophyll concentration for the central SS showed relatively small springtime peaks in all years, with the increase starting in mid-February in 1999, and not before early March in 1998 and late March in 2000. Thus, for 1998 and 2000 the onset of reproduction definitely preceded the bloom. In 1999, however, the early increase in chlorophyll may have accelerated (synchronised) maturation in a population that was probably nearing maturity anyway and caused the overall population structure to have been more advanced in April of 1999 compared with other years (Fig. 5).

An hypothesis to explain spatial and interannual variations in the timing of reproduction in *C. finmarchicus* on the Scotian Shelf.

Based on observations made in the Labrador Sea (Head et al., 2000) we have proposed that the timing of the onset of reproduction in C. finmarchicus depends on the rate at which newly aroused overwintered stage 5s and adults reach maturity. This rate, we suggest, is controlled by temperature and food concentration, and can be greatly accelerated if high food (phytoplankton) concentrations occur. This scheme is consistent with our observations on and around the Scotian Shelf. C. finmarchicus overwintering south of the shelf will experience higher temperatures than those in the Gulf of St. Lawrence throughout maturation, even while at depth (range ca. 3-6°C). Thus, they can attain maturity earlier, even if there is no intense early bloom. If they also awake from diapause earlier than C. finmarchicus overwintering in the Gulf, then they will have an additional "head-start". Since 1997, C. finmarchicus from the Gulf have been experiencing increasingly higher temperatures during maturation in the surface layers (Table 1) and possibly before reaching the surface layers. Thus, they could have started to reproduce earlier in 2000 than in 1998, even though the bloom started at the same time. In 1999, the early bloom greatly accelerated pre-adult maturation rates, leading to an unusually early onset of reproduction on the mid-ESS, but the lower temperatures on the inner shelf meant that the response was not as rapid in those populations.

Concluding remarks

According to CPR data annual average concentrations of *C. finmarchicus* on the ESS have been much lower during the early-mid 90s than they were in either the 60s or 70s. One theory is that the cold temperatures that developed both in the surface layers and at depth in the GSL during the early 90s may have rendered the GSL a less suitable habitat for *C. finmarchicus*. Our analysis suggests that reproduction may have been starting later, giving a shorter growth season, but the availability of deep areas with temperatures suitable for overwintering may have been more important. A reduction in overwintering area might be expected to lead to a decrease in the overwintering stock in the GSL and hence in the springtime flux to the ESS. It remains to be seen if the current increases in temperature that are occurring in the GSL will continue, but if they do we might expect to see concentrations of *C. finmarchicus* on the ESS return to the previous higher levels.

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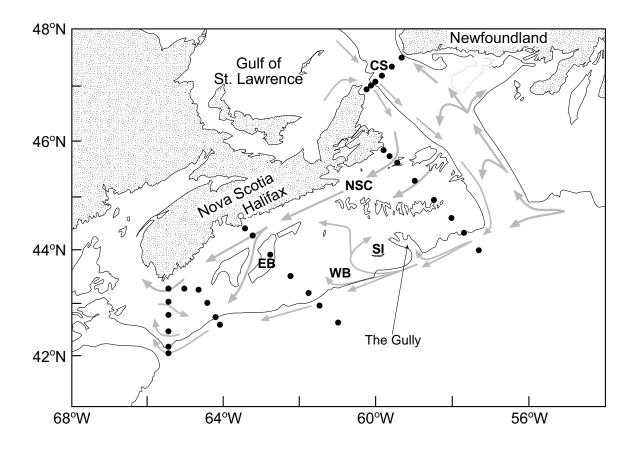


Fig. 1. Surface circulation (grey arrows) and location of various features (EB, Emerald Basin; WB, Western Bank; NSC, Nova Scotia Current; SI, Sable Island; CS, Cabot Strait) and standard sampling stations (circles) along the Browns Bank, Roseway, Halifax, Louisbourg and Cabot Strait Lines (labelled from SW to NE).

ABUNDANCE OF C. HYPERBOREUS IN APRIL

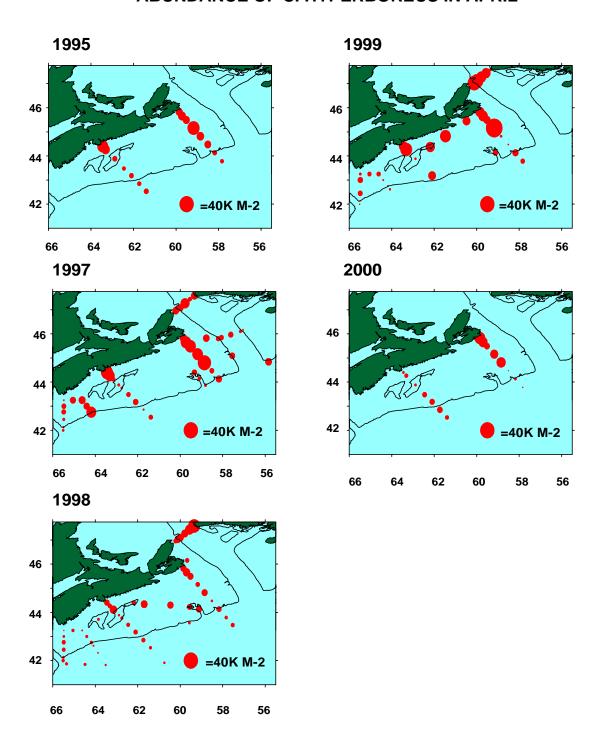


Fig. 2. Abundance of *Calanus hyperboreus* on and around the Scotian Shelf in April between 1995 and 2000

ABUNDANCE OF C.FINMARCHICUS IN APRIL

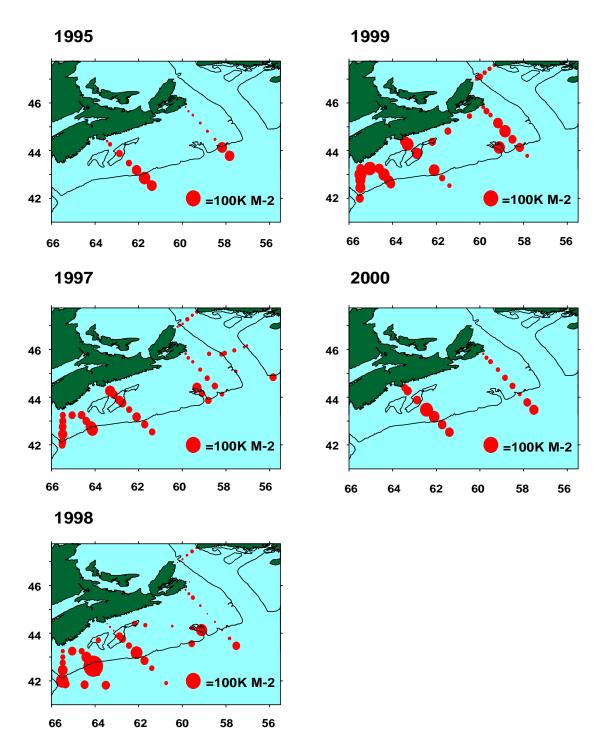


Fig. 3. Abundance of *Calanus finmarchicus* on and around the Scotian Shelf in April between 1995 and 2000

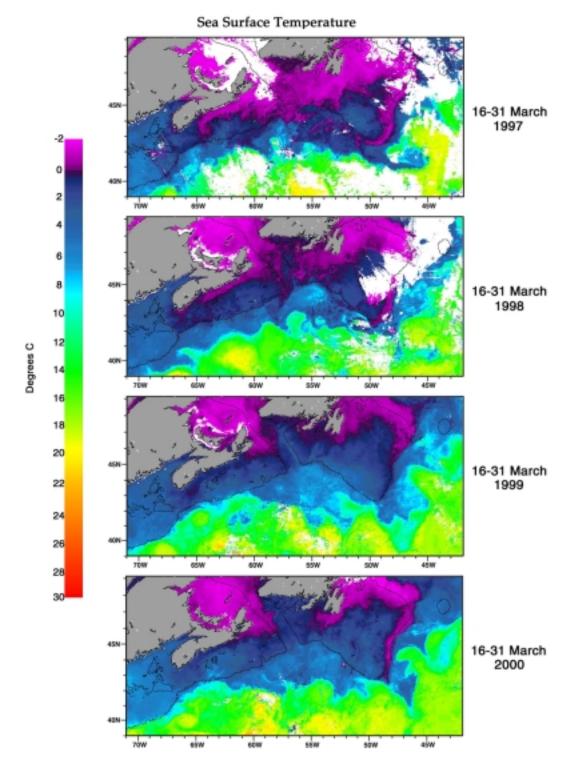


Fig. 4. Composite AVHRR (advanced very high resolution radiometer) images of sea surface temperature collected over March 16-31 of 1997, 1998, 1999 and 2000.

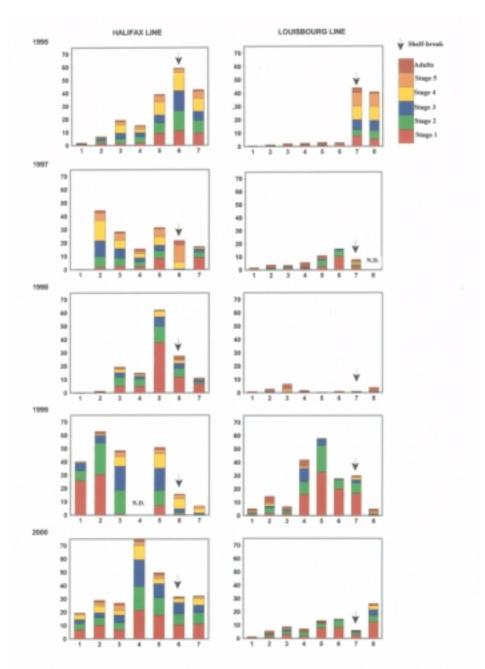
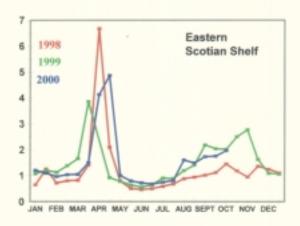


Fig. 5. Stage structure of Calanus finmarchicus populations

 $HL: Inner\ shelf = HL1\ and\ 2;\ Mid-shelf = HL3\ and\ 4;\ Outer\ shelf = HL5;\ Shelf-break = HL6;\ 2000m = HL7$ $LL: Inner\ shelf = LL1,\ 2\ and\ 3;\ Mid-shelf = LL4\ and\ 5;\ Outer\ Shelf = LL6;\ Shelf-break = LL7;\ 2000m = LL8$

SEAWIFS CHLOROPHYLL A CONCENTRATIONS (mg per cubic m)



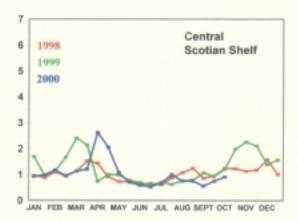


Fig. 6. Average concentrations of sea surface chlorophyll, estimated from Sea WiFS satellite images over bi-weekly periods, for rectangular areas covering the eastern and central Scotian Shelf.

Table 1. Temperatures and development rates for *Calanus*finmarchicus on the Eastern Scotian Shelf

Average temperatures (0-30m)

	1995	1997	1998	1999	2000
Inner shelf	-0.06	-0.20	0.84	0.34	1.95
Mid-shelf	1.13	0.47	1.58	1.29	2.13
Outer shelf	3.28	1.54	2.31	2.26	3.05

Time to reach CI copepodite – calculated using a Belehrádek temperature function

	1995	1997	1998	1999	2000
Inner shelf	52	53	44	48	36
Mid-shelf	41	46	38	40	35
Outer Shelf	31	38	34	34	30