

Life cycle and distribution of *Calanus finmarchicus* in deep basins on the Nova Scotia shelf and seasonal changes in *Calanus* spp.

D. D. Sameoto¹, A. W. Herman²

¹ Biological Sciences Branch, Department of Fisheries and Oceans, Bedford Institute of Oceanography, PO Box 1006, Dartmouth, Nova Scotia, Canada B2Y 4A2

² Physical/Chemical Sciences Branch, Department of Fisheries and Oceans, Bedford Institute of Oceanography, PO Box 1006, Dartmouth, Nova Scotia, Canada B2Y 4A2

ABSTRACT: The deep basins on the Nova Scotia shelf contain high concentrations of *Calanus finmarchicus*, *C. glacialis*, and *C. hyperboreus* at depths below 200 m. From May to late fall these were as high as 20 000 m⁻³. The dominant species by numbers was *C. finmarchicus*; however, its biomass was equalled or exceeded by *C. hyperboreus*. The life cycle of *C. finmarchicus* in the region of 2 of the largest basins showed that breeding started late in winter with a peak in April. High concentrations of *Calanus* suggested that the basins had higher levels of *C. finmarchicus* production than the adjacent shelf with mean depths less than 100 m. All 3 species of *Calanus* started to accumulate below 200 m in May as Stages CIV and CV. *C. glacialis* and *C. hyperboreus* did not reproduce in significant numbers on the NW half of the shelf but did accumulate in the basins as they were advected from the NE shelf region. Resting stages of *Calanus* resided at depths below 200 m in water at between 8.5 and 11 °C for an estimated 7 to 8 mo. The fate of these copepods is uncertain, but evidence suggested that a large proportion were preyed on by euphausiids in the deep regions of the basin. The deep basins on the shelf make it possible for *C. finmarchicus* populations to dominate the Nova Scotia shelf zooplankton community for most of the year; without the basins the shelf zooplankton would probably resemble that of the Grand Banks which has no deep basins, and is dominated by microzooplankton.

INTRODUCTION

Deep basins are not common features on most continental shelves and their influences on the distribution and production of zooplankton and fish populations on shelves is unknown. The Nova Scotian shelf contains a large number of basins greater than 200 m depth that make up ca 5 % of the total area of the shelf. Two of the largest basins, Emerald and La Have, are known to contain large populations of silver hake *Merluccius bilinearis* that feed principally on the euphausiid *Meganyctiphanes norvegica* (Koeller et al. in press), and acoustic data (Sameoto & Cochrane 1985) have shown the presence of a large euphausiid population in Emerald Basin. Herman (1988) reported an increase in zooplankton concentrations below a depth of 200 m during the fall in Emerald Basin and Louisbourg basins (Fig. 1). Concentrations of zooplankton deep in Emerald Basin were dominated by the copepod *Calanus finmarchicus*, whereas in Louisbourg Basin 3

species of *Calanus*, *C. finmarchicus*, *C. glacialis* and *C. hyperboreus*, were present in similar concentrations (Lewis & Sameoto 1989).

Calanus finmarchicus, *C. glacialis* and *C. hyperboreus* are oceanic species which have life cycles that include a seasonal vertical migration (Ostvedt 1955, Conover 1988). Copepodite Stages IV and V migrate from the surface to depths between 400 and 1000 m in the open ocean every summer and fall, where they remain until the spring when as mature females they return to the surface waters to reproduce. This pattern is found in all open ocean regions where these species occur, with differences in the timing of the reproductive period occurring in different geographic regions (Conover 1988).

Calanus finmarchicus, *C. glacialis* and *C. hyperboreus* are all common expatriates from oceanic regions on the Nova Scotia shelf, with *C. finmarchicus* dominating the zooplankton community during the spring and early summer period (Sameoto 1982, 1984,

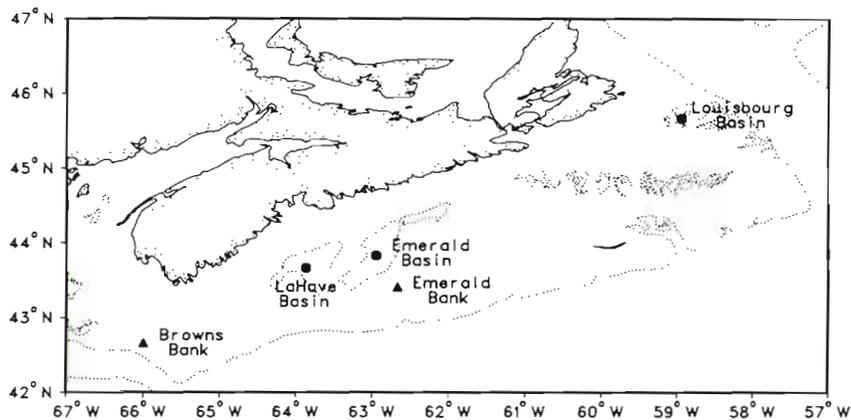


Fig. 1. Positions of zooplankton stations and locations of the deep basins and banks on the Nova Scotia shelf. Dotted lines represent the 200 m contour of the shelf edge and basins

Tremblay & Roff 1983). Little is known about the vertical distribution of *Calanus* in the basins of the Scotian shelf at different times of the year, nor is anything known about the importance of these high concentrations of copepods in the deep regions of the basins to the total zooplankton community on the shelf. Earlier studies on zooplankton production and distribution (Tremblay & Roff 1983, O'Boyle et al. 1984, McLaren et al. 1989) were based on data collected in the top 200 m of the water column and therefore missed the concentrations of zooplankton in the deep basins. This study describes seasonal changes in the *Calanus* community of Emerald and other basins and compares the production of *C. finmarchicus* in Emerald Basin to its estimated production on Emerald Bank (McLaren et al. 1989).

METHODS

The study area, sampled between 1984 and 1988, included the major basins on the Scotian shelf (Fig. 1) and stations on the shallow plains and banks. Mesozooplankton samples were taken with the Bedford Institute of Oceanography Net and Environment Sensing System (BIONESS), an opening and closing net sampler with 10 nets of 1 m² mouth opening each with a mesh size of 243 μ m (Sameoto et al. 1980). The BIONESS also continuously measured temperature and salinity during tows by means of a Guildline Instruments digital conductivity, temperature and depth instrument (CTD). The flow through the nets was monitored with external and internal flowmeters. The BIONESS was towed at a speed of 3 knots as it was slowly lowered along an oblique path to the desired depth where the nets were opened and closed on command from the ship. Each net filtered between 30 and 150 m³ of water per sample. Samples were taken every 5 to 10 m depth stratum in the region from the surface to the thermocline, and at ca 10 to 20 m intervals below the thermocline.

Samples were also taken with an unmetred 0.75 m diameter opening and closing ring net, with a 246 μ m mesh, towed vertically at 1.5 m s⁻¹. This sampler was used on ships of opportunity that were unable to operate the BIONESS and enabled us to obtain a time series of zooplankton vertical structure at a single station in Emerald Basin. The volume of water filtered by the ring net was estimated by multiplying the vertical distance it was towed by its mouth area. Because the net did not take into account the effect of currents or the ship's drift it probably underestimated water filtered and overestimated the numbers of zooplankton m⁻³ by between 20 and 30%. However, because the exact degree of overestimation is unknown, no corrections were made to these data.

In situ zooplankton concentration and sizes were also measured using an optical zooplankton counter (Herman 1988). This instrument counted and sized particles between 0.5 and 20 mm in spherical diameter. It was mounted on the side of the BIONESS with a rectangular collecting net (8.5 \times 30 cm) in front of the sampler mouth. It provided in situ data of the zooplankton concentration during the profiles. The counter gave information on the vertical distribution of zooplankton with an effective resolution of ca 30 cm. The counter's accuracy decreased with increased zooplankton density due to coincident counts. At concentrations greater than 4000 m⁻³ a coincidence correction is required (Herman 1988). The optical counter also measured light attenuation and thereby indirectly provided an approximate depth for the chlorophyll maximum (Herman et al. in press).

The zooplankton samples were preserved in a 5% formalin seawater solution buffered with sodium borate and strontium chloride. All samples were sorted for macrozooplankton (animals > 1 cm in length) and ichthyoplankton that were removed, identified, and weighed wet after excess water was removed by blotting. The remaining mesozooplankton sample was filtered over a 50 μ m screen under vacuum to remove the

water until water ceased to drip from the filter and was then weighed to obtain a wet biomass. The sample was then split to obtain a subsample of about 400 animals using a Motoda splitter (Motoda 1959); these animals were identified to species and the *Calanus* spp. staged. The maturity stages of female *C. finmarchicus* were determined and classified into the following 3 categories:

- (1) Developing females; ovaries formed, oviducts lightly colored, developing a few small pale eggs, abundant oil and the copepod in good condition.
- (2) Gravid females; oviduct and body very dark and full of mature sized eggs, copepods in good condition.
- (3) Spent females; oil in body depleted, oviducts with very little contents, female in poor condition and pale.

Oxygen concentrations in the total water column of Emerald Basin were determined from triplicate water samples collected at various depths with a rosette sampler or measured by means of an oxygen electrode mounted on a CTD.

RESULTS

Physical oceanography of basins

Deep regions of Emerald and La Have Basins differ from the shallow regions of the shelf during all seasons. Below ca 100 m, the basins contain slope water with temperature and salinity much higher than found in the upper 100 m for most of the year (Fig. 2). The warm

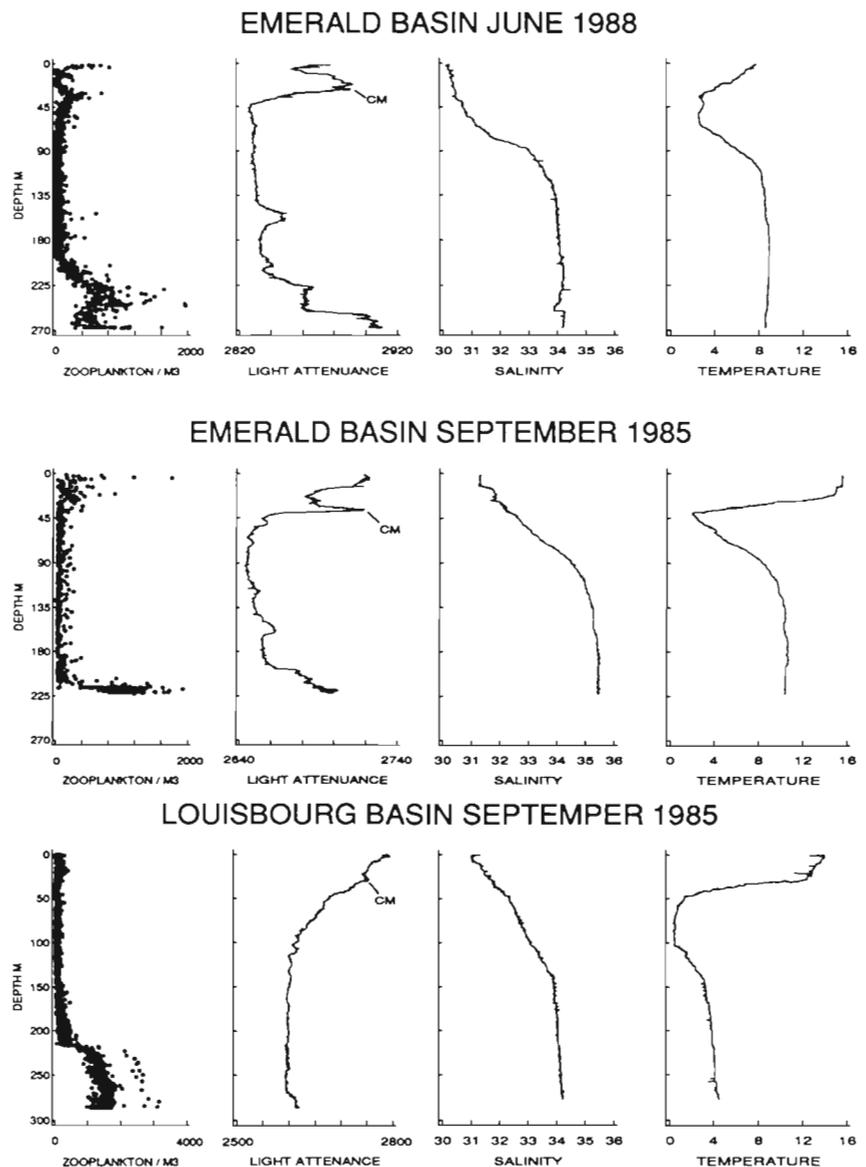


Fig. 2. Profiles of temperature, salinity, relative light attenuation and in situ optical zooplankton concentration profiles for Emerald Basin during June and September, and profiles for Louisbourg Basin in September. Bottom depths: Emerald Basin 272 m, Louisbourg Basin 285 m. CM: chlorophyll maximum

saline layer is a permanent feature (Drinkwater & Taylor 1982, Drinkwater & Trites 1987). These 2 basins are flushed by slope water intrusions several times during winter displacing the lower density basin water (Herman et al. in press). The mean upwelling velocity was estimated to be only 0.1 mm s^{-1} , thereby presenting little or no displacement for the zooplankton resident in the deep regions of the basins. The basins on the NE shelf are not influenced by an inflow of warm slope water and the waters in the deeper regions of these basins are colder and less saline during all seasons of the year (Rowell et al. 1985, Drinkwater & Trites 1987) (Fig. 2).

The light attenuation profiles in Emerald and La Have Basins during June and September generally showed a decrease from the surface to the depth of the chlorophyll maximum where a sharp increase occurred (Fig. 2). Below the chlorophyll maximum attenuation decreased sharply. From 50 to 160 m light attenuation remained relatively stable to 160 m where an increase occurred for a short depth interval and then a decrease at about 180 m. Below 200 m the light attenuation increased to bottom.

The light attenuation in Louisbourg Basin during the fall was different from that of Emerald Basin in that there was little change in attenuation with depth below 100 m. The large increase in attenuation below 200 m in Emerald Basin was not present and there was only a slight increase in attenuation in the bottom 20 m (Fig. 2).

Distribution of zooplankton measured by optical counter

Profiles of the concentrations of zooplankton m^{-3} made with the optical counter showed that the variability of concentration at successive depths was very small, generally less than twice the mean value (Fig. 2). The data suggest small localized areas with higher concentrations of zooplankton. The counter had a horizontal resolution of 2 cm, the thickness of the detector light beam, and a vertical resolution of 30 cm, the vertical dimension of the collecting net in front of the optical counter (Herman 1988).

The vertical pattern of zooplankton concentration

was similar in all the basins during June and October, generally showing high concentrations in the upper 40 m and low concentrations from 40 to about 200 m (Fig. 2). Below 200 m there was a rapid increase in concentration to between 1300 and 4000 m^{-3} .

There was a positive relationship between sharp increases in light attenuation and in concentration of zooplankton m^{-3} in the upper 40 m in the Emerald Basin profiles. No relationship between zooplankton concentration and light attenuation was seen in Louisbourg Basin (Fig. 2). Particles in the water responsible for the increased light attenuation between 20 and 40 m were believed to be phytoplankton cells, because Herman (1988) showed a close relationship between the chlorophyll maximum layer and an increase in light attenuation at these depths. Below the euphotic zone, chlorophyll concentrations were $< 0.1 \text{ mg m}^{-3}$ (Herman et al. in press) and, therefore, the increased light attenuation below 140 m was probably detrital material with very little if any chlorophyll.

The concentrations of zooplankton did not show any obvious relationship with temperature or salinity in any of the zooplankton profiles. There was little change in the temperature and salinity below 200 m in all the basins, but yet in all of the profiles there was an increase in the concentrations of the copepods (Fig. 2).

The oxygen concentration of the slope water in Emerald Basin gradually decreased to ca 5 mg l^{-1} near the bottom during all months with no evidence of oxygen depletion near the bottom (Fig. 3). Oxygen levels in the basins on the northeastern end of the shelf were not measured.

Season vertical distribution and abundance of *Calanus* spp.

Calanus finmarchicus was the most abundant copepod in Emerald and La Have Basins during all sampling periods. Between February and October, *C. finmarchicus* represented up to 70% of the all mesozooplankton in the water column and *C. glacialis* and *C. hyperboreus* accounted for 1 to 27% of the total (Table 1). The main concentration was found in the deep part of Emerald Basin during all months except

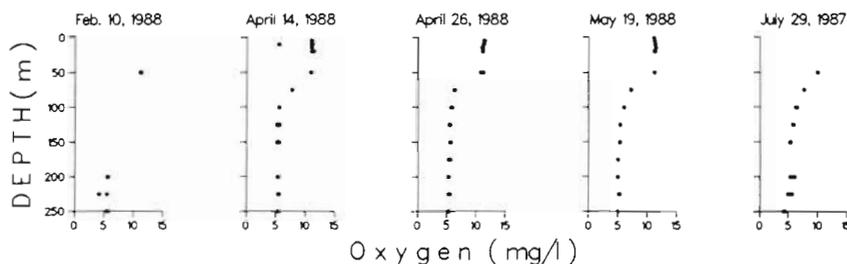


Fig. 3. Distribution of oxygen in Emerald Basin during different seasons

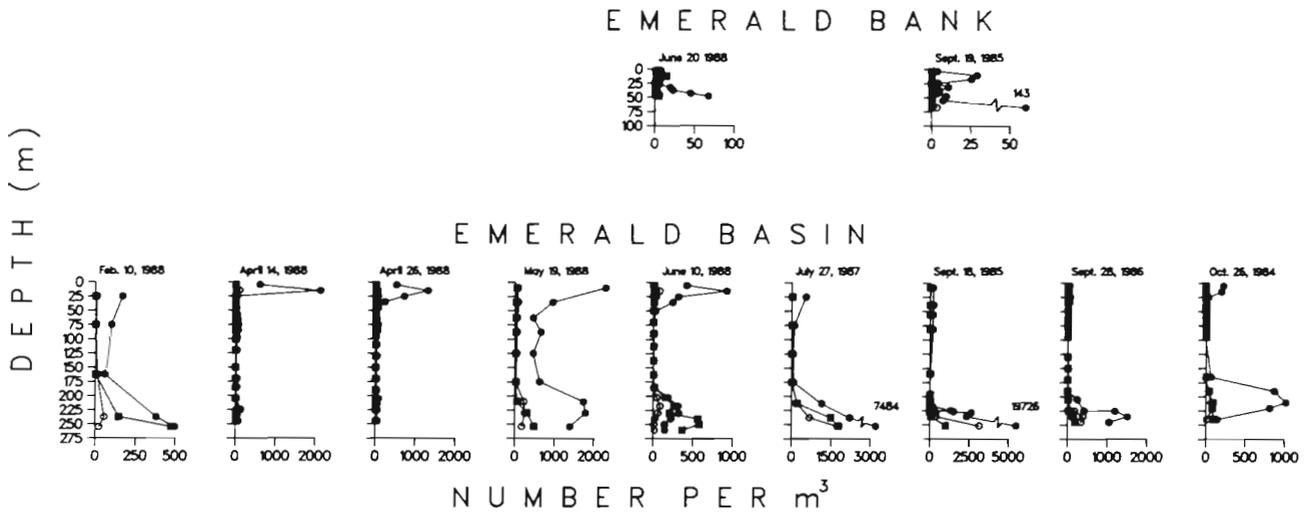


Fig. 4. *Calanus* spp. Vertical distribution in Emerald Basin during different months. (●) *C. finmarchicus*; (■) *C. hyperboreus*; (○) *C. glacialis*. Note different scales for numbers

and La Have Basins. In October the 3 *Calanus* species in Louisbourg Basin had similar concentrations m^{-2} (Table 2).

The basins in the NE half of the shelf were only sampled in June and October, but they showed similar vertical distribution patterns to Emerald and La Have Basins on these dates. The primary difference between

the 2 regions was the higher concentrations of *Calanus hyperboreus* and *C. glacialis* in the NE and evidence of an accumulation in June of *C. hyperboreus* and *C. glacialis* but not *C. finmarchicus* in the deeper part of Louisbourg Basin during June (Fig. 5). It is possible that *C. hyperboreus* and *C. glacialis* developed to Stage IV earlier than *C. finmarchicus* or else underwent sea-

Table 2. *Calanus* spp. Concentrations m^{-2} and estimated percentage of *Calanus* volume of each species in deep regions (> 200 m) of the basins

Date	Depth range (m)	<i>Calanus</i> species								
		<i>C. finmarchicus</i>			<i>C. glacialis</i>			<i>C. hyperboreus</i>		
		No. m^{-2}	Percent of total <i>Calanus</i> population	Percent of total <i>Calanus</i> biomass	No. m^{-2}	Percent of total <i>Calanus</i> population	Percent of total <i>Calanus</i> biomass	No. m^{-2}	Percent of total <i>Calanus</i> population	Percent of total <i>Calanus</i> biomass
Emerald Basin										
Feb 10, '88	225-260	17 140	63	36	1 584	6	3	8 610	31	60
Apr 14, '88	190-250	3 586	63	20	454	8	3	1 635	29	77
Apr 26, '88	200-268	3 398	71	25	316	7	2	1 073	22	73
May 19, '88 ^a	200-268	109 688	75	32	14 828	10	4	20 968	14	64
Jun 07, '87	195-250	14 410	29	13	10 021	20	9	24 695	50	79
Jun 10, '88	195-265	14 305	37	14	2 930	8	3	21 240	55	84
Jul 06, '87	195-250	13 981	29	15	9 614	20	11	24 191	51	74
Jul 27, '87 ^a	200-255	125 620	60	41	31 110	15	10	51 605	25	49
Sep 03, '87 ^a	200-230	38 010	85	63	2 730	6	4	3 990	9	33
Sep 18, '85	220-257	259 297	83	77	41 384	13	12	12 239	4	10
Sep 28, '86	200-250	44 310	75	51	10 280	17	11	4 540	8	38
Oct 26, '84	200-240	40 230	72	49	3 930	7	5	10 338	21	46
La Have Basin										
Jul 30, '87	175-235	61 555	32	15	29 960	16	7	100 185	52	78
Oct 28, '84	200-230	28 247	69	45	4 612	11	7	8 015	20	48
Louisbourg Basin										
Sep 21, '85	200-285	134 225	37	22	137 745	38	23	88 650	25	55

^a Samples taken with ring net

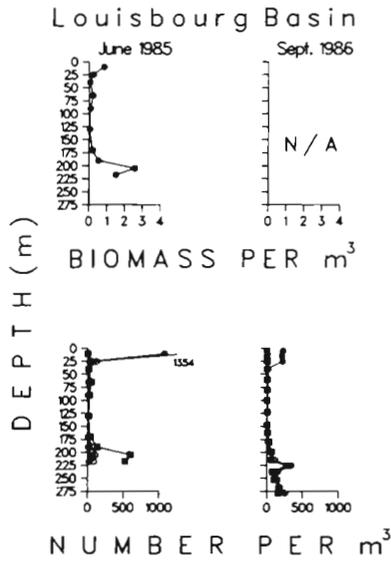


Fig. 5. Vertical distributions of concentration of *Calanus* spp. and of total zooplankton biomass g m^{-3} in Louisbourg Basin. (●) *C. finmarchicus*; (■) *C. hyperboreus*; (○) *C. glacialis*; N/A: data lost

sonal vertical migration earlier or were remnants of an overwintering population.

Day/night differences

Calanus finmarchicus, *C. hyperboreus* and *C. glacialis* did not show any evidence of diurnal vertical migration from below 200 m (Fig. 6).

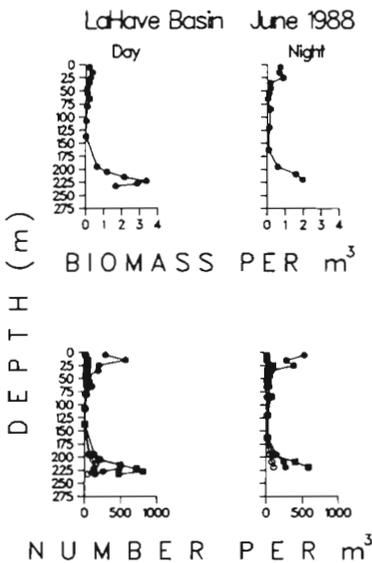


Fig. 6. Day/night vertical distribution of total numbers m^{-3} of *Calanus* spp. and total zooplankton biomass g m^{-3} in La Have Basin. (●) *C. finmarchicus*; (■) *C. hyperboreus*; (○) *C. glacialis*

Table 3. *Calanus* spp. Percentages of copepodite stages below 200 m in Emerald Basin

Date	Copepodite stage						
	Male	Female	CVI	CV	CIV	CIII	CII
<i>C. finmarchicus</i>							
Feb 10, '88	3	17	63	15	1		
Apr 14, '88	8	8	69	10	4	1	
Apr 26, '88	27	12	48	10	2	0.5	
May 19, '88	7	5	38	20	16	9	
Jun 10, '88	8	2	85	3	1	0.5	
Jul 27, '87	0.4	4	92	3			
Sep 03, '87	0.5	4	93	3			
Oct 26, '84	1	2	97	1			
<i>C. glacialis</i>							
Feb 10, '88				100			
Apr 14, '88		1	47	50	2	0.5	
Apr 26, '88			92	7	1		
May 19, '88		18	71	12	7	7	
Jun 10, '88			67	33			
Jul 27, '87			51	49			
Sep 03, '87			53	47			
Oct 26, '84			87	13			
<i>C. hyperboreus</i>							
Feb 10, '88		1		95	4		
Apr 14, '88	0.5	2	49	44	3		
Apr 26, '88		2	43	48	7	0.3	
May 19, '88			22	72	5		
Jun 10, '88		0.2	10	88	1		
Jul 27, '87			3	85	11		
Sep 03, '87				100			
Oct 26, '84			10	90			

There were no major differences in the vertical day/night profiles of total zooplankton biomass or concentrations of *Calanus* spp. below 80 m. Above 80 m there was a slight increase in biomass at night due to the upward migration of euphausiids (Fig. 6). *Calanus* spp. below 80 m were mainly resting stage individuals that probably remained at these depths until the following spring.

Vertical distribution of *Calanus* spp. stages

Calanus finmarchicus concentrations between 50 and 200 m from June to October were usually $< 50 \text{ m}^{-3}$ during both day and night. The copepodites in this depth range were primarily CIV and CV, with CV dominating. However, small numbers of CIII and CII were found below 200 m during April and June (Table 3). Copepodite Stages CI to CIII were concentrated in the upper 40 m during all sample periods. Below 200 m during February to June *C. finmarchicus* males and females were common indicating that some individuals were reproducing. After June the percentage of males and females dropped, primarily because of increased CVs of the new generation.

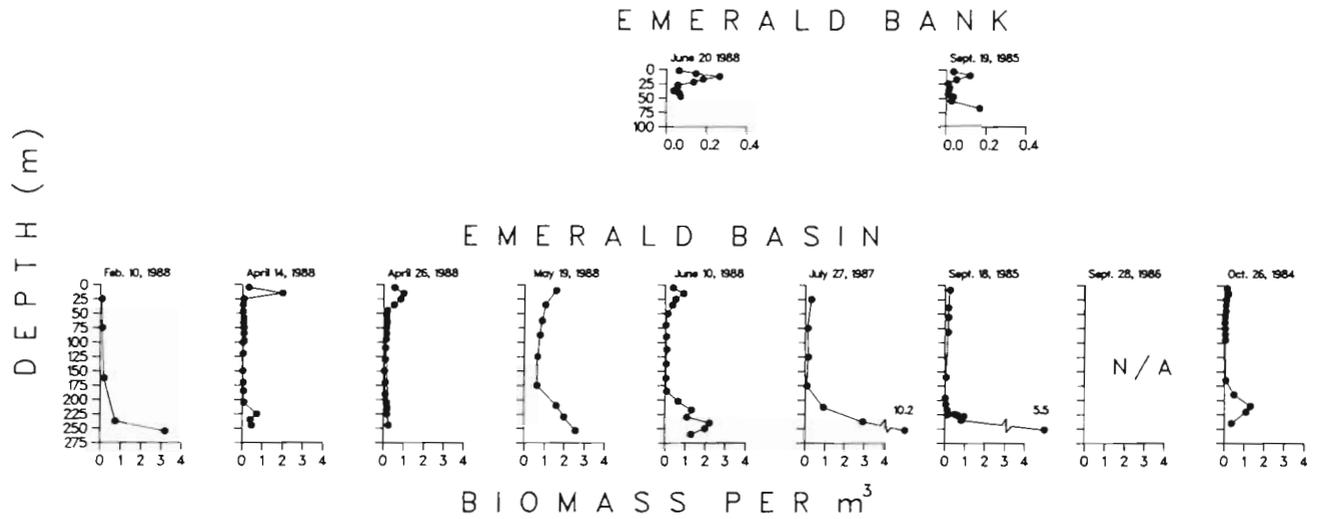


Fig. 7. Vertical distribution of total zooplankton biomass (g m^{-3}) for Emerald Basin through the year and Emerald Bank for June and September

Calanus glacialis CV was the only stage of this species found below 200 m during February, whereas Stages CIV and CV were dominant between April and September. In October CV was the dominant stage of *C. glacialis*. No males were found and only a small number of females were seen in early April (Table 3), suggesting that *C. glacialis* did not breed in the Emerald Basin area.

Copepodite CIV was the most common stage of *C. hyperboreus* during all months but April. In April CIII, CIV, CV, and male and female CVI were present (Table 3).

Seasonal distribution of copepod biomass

Depth profiles of the total zooplankton biomass (g m^{-3}) in Emerald Basin showed a biomass maximum between 230 and 250 m during May to October (Fig. 7) with the highest concentration m^{-3} found in July. The lowest total biomass (g m^{-2}) occurred during February and the highest in May (Table 4). No samples were collected between November and February, so it is unknown if the biomass m^{-2} continued to increase or decreased after October.

The biomass m^{-3} in the upper 50 m of Emerald Basin

Table 4. Total zooplankton and euphausiid wet biomass m^{-2} (g m^{-2})

Date	Total zooplankton biomass in entire water column	Total zooplankton in bottom 100 m	Euphausiid biomass in entire water column	Percentage of total water column biomass in bottom 100 m
Emerald Basin				
Feb 10, '88	34.4	30.9	0.4	90
Apr 14, '88	47.4	20.4	3.1	27
Apr 26, '88	55.0	17.5	3.2	32
May 19, '88	308	141	14.6	46
Jun 07, '87	72.5	59.6	0.9	82
Jun 10, '88	92	63.2	8.0	69
Jul 27, '87	178	157	2.0	88
Sep 18, '85	94.5	76.9	1.0	81
Oct 26, '84	66.3	58.1	6.2	88
La Have Basin				
Apr 14, '88	179	89	25.2	50
Jun 08, '88	110	79	29.5	72
Jul 30, '87	518	481	1.0	93
Oct 28, '84	46.8	31.6	1.6	68
Louisbourg Basin				
Sep 28, '85	228	212	1.3	93

was about 5 times greater than it was at the same depths on Emerald Bank during June. During September the values were similar in the basin and on the bank (Fig. 7). Data from the optical zooplankton counter towed on a Batfish over transects across Emerald Basin and Bank at the same times as the BIONESS sampling confirmed the large differences seen in zooplankton concentrations with the BIONESS (Herman pers. comm.).

Copepods represented up to 90% of the total zooplankton biomass below 200 m in the basins with the euphausiids, primarily *Meganyctiphanes norvegica*, the second most important group, making up between 1 and 27% of the biomass. No other single group of animals made up more than 1% of the total biomass in the deep regions of the basins.

The body volumes of *Calanus hyperboreus* CIV and CV are 2.8 and 11.7 times the body volume of *C. finmarchicus* CV (Herman 1988). If it is assumed that the specific densities per unit volume of these 2 species are the same, then it is possible to estimate the percentages of the total *Calanus* biomass of each of the species represented in the deep regions of the basins. This was done by taking the total volume of the different stages of each species relative to the volume of *C. finmarchicus* CV, and assuming these volume percentages were equal to weight-based percentages. Based on these assumptions *C. hyperboreus* represented a majority of the *Calanus* biomass in the deep regions of Emerald Basin from February to June and almost equalled the biomass contribution of *C. finmarchicus* for the other months (Table 2). In Louisbourg Basin in October *C. hyperboreus* dominated the biomass and the contribution of *C. glacialis* to the biomass equalled that of *C. finmarchicus*.

DISCUSSION

Emerald Basin acts as an accumulation site for *Calanus finmarchicus*, *C. glacialis* and *C. hyperboreus* that undergo seasonal migration when they reach Copepodite CIV and CV. Such basins probably collect the copepodites that developed in the water immediately over them and also migrating individuals carried into them by currents from shallower regions. This results in a higher concentration of *Calanus* in the deep basins than would be expected from the production in the water column of the basin. The general direction of currents on the Nova Scotia shelf is from NE to SW (Smith & Petrie 1982, Herman et al. in press) which means that some of the copepods in the basins likely originated from the NE regions of the shelf, or from the Gulf of St. Lawrence. Head (unpubl.) found the species composition of *Calanus* in the Strait of Belle Isle region

of the Gulf of St. Lawrence was similar to that of Louisbourg Basin, which may explain how *C. glacialis* and *C. hyperboreus* accumulated in Emerald Basin during the summer when there was no evidence of reproduction in the upper layers. Below 100 m (the sill depth) the basin is a very quiet physical environment with the mean current below 200 m in the spring to fall period only 0.008 m s^{-1} and the low frequency RMS amplitude 0.06 m s^{-1} (Herman et al. in press). These weak currents enable *Calanus* to accumulate below 200 m and remain there for the winter.

Large populations of *Meganyctiphanes norvegica* are found in all the basins whereas few were found on the shallow plains or the banks (Lewis & Sameoto 1988a, b, c, 1989). *M. norvegica* needs high concentrations of copepods to survive and grow (Sameoto 1980, McClathie 1985); therefore the high concentrations of *Calanus* spp. in the deep basin provided a favourable growing environment for the euphausiids the year around. The high concentrations of copepods and euphausiids in Emerald and La Have Basins may also be attractive to juvenile and adult silver hake *Merluccius bilinearis*, in the basin (Cochrane et al. in press), copepods and euphausiids make up a large part of the diet of the silver hake (Koeller et al. 1989).

There was a large decrease in the numbers of the *Calanus* spp. populations in Emerald Basin over the winter. There are 3 likely explanations: (1) that the population of *Calanus* spp. was grazed by predators such as the euphausiids and silver hake; (2) possibly that a large part of the population in the deep water migrated vertically to the upper 50 m prior to February 10, meaning that some individuals started their seasonal migration as early as January; (3) that these copepods cannot survive on their oil reserves at temperatures between 8.5 and 10°C for the period from June to February. Respiration rates of the *Calanus* spp. from the deep water of the basin in June were at levels that would exhaust the oil reserves before the next spring. It is unknown if the rates remained at these levels through the full winter (Head, Bedford Institute of Oceanography, pers. comm.). None of these species feed while in the resting CV stage (Conover 1962, Hiche 1983).

In Emerald Basin females and males were present during all sampling periods (Table 1, Fig. 8), having their highest percentage of the total population in February (Table 5). The highest percentage of gravid females in the population of females occurred at the end of April, whereas the highest percentage of gravid females in the total population in was early in April (Table 5). There was an small increase in the percentage of gravid females in late July and August, when females represented up to 5% of the total population (Table 5). The main reproductive period for *Calanus*

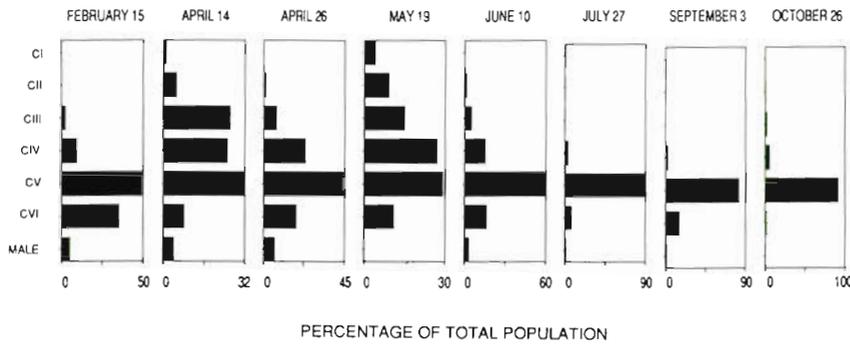


Fig. 8. *Calanus finmarchicus*. Seasonal distributions of copepodites in Emerald Basin as percentages of the total population

finmarchicus was in April with a smaller one occurring in late July. However, when the total numbers of gravid females m^{-2} were compared at different times of the year they suggest that the July and September period may be equal to or more important than spring for reproduction (Table 1). In July and September the percentage of gravid females in the total population is much lower than in spring but the total number m^{-2} is higher due to the much higher total population (Table 1). In July and September the concentration of *C. finmarchicus* in the upper 50 m is much lower than in the spring. This may be the result of the copepods reaching Stage CV faster in 10 to 20°C water than in the 2 to 4°C water in the spring. The slower growth in the spring would cause the population of younger copepodites to accumulate in the upper 50 m resulting in a large population.

There were large numbers of CV and CVI copepods below 200 m in February that probably reproduced later in the year. Few *Calanus finmarchicus* were found below 200 m on April 14, suggesting that the overwintering population (G_0) had migrated to the surface waters to reproduce. Therefore, the main breeding period was probably between mid-February and mid-April. The copepods that started to accumulate below

200 m in May were likely CIV and CV of the first new generation (G_1) produced from eggs laid in mid-February. A large part of the total population remained in the surface waters from May to early July. These could have been G_1 copepods from late breeding G_0 individuals or they could have been G_2 or G_3 copepods that breed without going into a resting stage.

McLaren & Corkett (1986) reported that *Calanus finmarchicus* collected from Emerald and Brown's Bank, south and southwest of Emerald and La Have Basins (Fig. 1), produced 2 generations per year, a large one in spring and a much smaller generation in late summer.

Estimates of the number of days it took *Calanus finmarchicus* to reach maturity at different temperatures were made using Corkett et al. (1986) Belehradek's temperature function

$$D = a(T - 10.6)^{-2.05}$$

where $a = 17\,477$; T = water temperature; D = days to reach maturity from hatching for *C. finmarchicus*.

Gravid females made up 2% of the total population during January and February (Table 5). If it is assumed that *Calanus finmarchicus* started to lay eggs on February 10 – not an unreasonable assumption since 4% of

Table 5. Percentages of gravid females in total copepodite VI and total *Calanus finmarchicus* populations

Date	Percentage of female CVI in total <i>C. finmarchicus</i> population	Percentage of gravid females in total CVI population	Percentage of gravid females in total population
Jan 10, '85 ^a	21	8	2
Feb 10, '81	57	4	2
Feb 10, '88	47	11	5
Apr 14, '88	29	40	32
Apr 26, '88	17	37	8
Jun 10, '88	14	33	5
Jun 07, '87	10	5	0.5
Jul 06, '87	11	6	0.6
Jul 27, '87	14	35	5
Aug 27, '76	35	10	3.5
Sep 28, '86	10	10	1
Oct 26, '84	13	3	0.4

^a Samples taken with 0.75 m ring net towed from bottom to surface

Table 6. *Calanus finmarchicus*. Estimated number of generations using Belehradek's growth equation (Corkett & McLaren's (1986). Generation G_4 reaches Stage CV in 22.7 d or Day 256 when it is assumed to migrate into deep water and goes into a resting stage

Parent generation	Day of the year they reproduce	Date they reproduce	Water temperature ($^{\circ}\text{C}$)	No. of days from egg to Stage CVI	New generation
G_0	46	Feb 10	2	97	G_1
G_1	143	May 18	6	55	G_2
G_2	198	July 12	10	35	G_3
G_3	233	Aug 18	12	29	G_4

the female CVI were spent on this date (Table 1) – an estimated 4 generations could be produced by September if each generation omitted the resting stage (Table 6). These calculations of the number of generations are obviously much too simple, since they do not consider other environmental factors besides temperature, but the above data suggests that more than 2 generations are possible.

If there are only 2 generations as suggested by McLaren et al. (1989), then how do we explain the presence of gravid females during all months sampled from January to October? Possibly a small number of females laid eggs in January and February that developed into Stage CIV or CV copepodites that migrated into the deep water during May and remained in the resting stage until the next winter. A second possibility is that they may remain in the deep water for only a short time before maturing and returning to the surface to reproduce the late summer generation. The presence of large numbers of gravid and developing females below 200 m from June to September suggests that this may happen. If this is so then the life cycle of *Calanus finmarchicus* is not as simple as suggested by McLaren et al. (1989).

McLaren et al. (1989) estimated yearly production and turnover rate of *Calanus finmarchicus* on Emerald Bank, an area about 60 km south of Emerald Basin. They assumed 2 generations per year, with the second generation overwintering as CV. They also assumed that all females plus one-half the copepodites of each generation survived to reproduce 250 eggs each. The size of the cohort of the overwintering population in February was estimated to be 22.6 m^{-3} and this cohort (G_0) produced the first new generation (G_1). The size of the G_1 breeding cohort in early June was estimated to be between 8.0 and 7.8 m^{-3} which produced generation G_2 . The size of the reproducing cohort G_2 in early August was 1.7 m^{-3} . The assumptions McLaren et al. (1989) made were also made in estimating production of *C. finmarchicus* in Emerald Basin. To estimate cohorts it was assumed that only copepods in the upper 50 m were potential breeders. This overcame the problem of the large numbers of resting individuals that accumulated in the deep water of the basin. In the

present study the estimated size of the cohort for G_0 was 121 m^{-3} in February, 133 m^{-3} for G_1 in early June and 196 m^{-3} for G_2 in late July. These cohort values are 5.3 to 115 times larger than the cohorts on Emerald Bank found by McLaren et al. (1989), which suggests that *C. finmarchicus* production within basins was probably between 1 and 2 orders of magnitude greater than that on Emerald Bank, which was estimated at $122 \text{ mg dry wt m}^{-3}$ (McLaren et al. 1989). We could not calculate with any more confidence the production of *C. finmarchicus* in Emerald Basin for 3 reasons. First, we lacked an adequate time series of samples. Second, with the accumulation of CV and CIV copepodites in the deep water there was no way of telling if these individuals all originated from the basin region, or if they were advected from some other area. Third, the percentage of generation G_1 which migrated into deep water and the percentage that produced generation G_2 are unknown.

The high estimated yearly production of *Calanus finmarchicus* combined with the accumulation of very high concentrations of *Calanus* spp. below 200 m make Emerald and the other basins regions of exceptionally high biological activity. Different regions of the shelf probably have different *C. finmarchicus* production levels depending on the size of the initial breeding population and the size of the basins. Therefore it is not possible to extrapolate the results from a small region to the entire shelf or parts of the shelf.

The low concentrations of *Calanus finmarchicus* between 50 and 200 m during day and night between May and October may be due to a slow downward migration of Stages CIV and CV rather than a single mass migration. If so, then there may be a continuum of ages of CIV and CV in the layers below 200 m that may reproduce at different times in the late winter and spring. *C. glacialis* and *C. hyperboreus* accumulated in the basin possibly by being carried to the basin by advection from the coastal Scotia Current, which contains concentrations of *C. hyperboreus* CIV and CV that conceivably originated from the Gulf of St. Lawrence (Herman et al. in press) or from Labrador Current water that is advected on to the shelf.

The vertical distribution of *Calanus* spp. in Emerald

Basin was similar from May to October. Concentrations increased below 200 m and continued to increase until about 240 to 250 m, after which depth there was generally a decrease near the bottom. This decrease near the bottom may have been due to predation by high concentrations of *Meganycitiphanes norvegica* on the bottom. Photographic and video observations showed the bottom 2 m to have high concentrations of euphausiids and chaetognaths (Cochrane et al. in press). During the day there is also a large population of juvenile silver hake and sandlance *Ammodytes americanus* on the bottom (J. Nielson, Department of Fisheries and Oceans, St. Andrews, N.B., pers. comm.). All of these species are potential predators of *Calanus* spp. near the bottom.

This study has shown that the basins on the Nova Scotia shelf are distinctly different from the shallow plains and banks. The accumulation of *Calanus* spp. in the deep water may provide the food base for larger macrozooplankton and fish. Basins greater than 200 m depth make up only about 5% of the shelf area, but in the fall the biomass of zooplankton in the basins was estimated to be up to 50% of the total zooplankton biomass on the shelf (Lewis & Sameoto 1988a, b, c, 1989). The fall *Calanus* population below 200 m in the basins represented 56% of the total *Calanus* population on the shelf. This estimate was based on an autumn concentration of *Calanus* in the upper 200 m of the entire shelf of 10 450 m⁻² and a concentration of 301 920 m⁻² below 200 m in the basins (Sameoto unpubl.).

The deep basins on the Nova Scotia shelf influence the composition of the zooplankton community of the shelf. If the basins did not exist it is likely the Nova Scotia shelf zooplankton would resemble that of the the Grand Banks which is dominated by microzooplankton and gelatinous zooplankton, with *Calanus* spp. a minor component advected on to the edge of the bank from the slope water (Anderson & Gardner 1986). Krause & Trahms (1983) discussed the origins of *C. finmarchicus* on the North Sea shelf, which has no deep basins, and came to the conclusion that the population is replenished each spring by transport from the deep waters from the shelf edge, since the absence of deep basins on the North Sea shelf resulted in *C. finmarchicus* being advected off the shelf each year. Clearly, to understand the production of the Nova Scotia shelf we must have a better understanding of the production in the basin regions and the physical processes that cause copepods to accumulate and remain in them.

Acknowledgements. We would like to express our appreciation to Drs A. Longhurst and R. J. Conover for their thoughtful reviews of the manuscript, to Ms M. K. Lewis and Mr B. Fraser for their able technical assistance during the cruises and in data analysis, and the officers and crew of the CSS 'Dawson' for their help during the many cruises.

LITERATURE CITED

- Anderson, J. T., Gardner, G. A. (1986). Plankton communities and physical oceanography observed on the southeast shoal region, Grand Bank of Newfoundland. *J. Plankton Res.* 8: 1111–1135
- Cochrane, N. A., Sameoto, D. D., Herman, A. W., Nielson, J. (in press). Multiple frequency acoustic backscattering and zooplankton aggregations in the inner Scotian shelf basins. *Can. J. Fish. Aquat. Sci.*
- Conover, R. J. (1962). Metabolism and growth in *Calanus hyperboreus* in relation to its life cycle. *Rapp. P.-v. Réun. Cons. perm. int. Explor. Mer* 153: 190–197
- Conover, R. J. (1988). Comparative life histories in the genera *Calanus* and *Neocalanus* in high latitudes of the northern hemisphere. *Hydrobiologia* 167: 127–142
- Corkett, C. J., McLaren, I. A., Sevigny, J.-M. (1986). The rearing of the marine calanoid *Calanus finmarchicus* (Gunnerus), *C. glacialis* Jaschnov and *C. hyperboreus* Kroyer with comment on the equiproportional rule (Copepoda). *Proc. Second Internat. Conf. on Copepoda in Syllogeus*. *Natn. Mus. Canada* 58: 539–546
- Drinkwater, K., Taylor, G. (1982). Monthly means of the temperature, salinity and density along the Halifax section. *Can. Tech. Rep. Fish. Aquat. Sci.* 1093: 1–67
- Drinkwater, K. F., Trites, R. W. (1987). Monthly temperature and salinity in the Scotian shelf region. *Can. Tech. Rep. Fish. Aquat. Sci.* 1539: 1–101
- Herman, A. W. (1988). Simultaneous measurement of zooplankton and light attenuation with a new optical plankton counter. *Cont. Shelf Res.* 8: 205–221
- Herman, A. W., Sameoto, D. D., Chen Shunnian, Mitchell, M. R., Petrie, B., Cochrane, N. (in press). Sources of zooplankton on the Nova Scotia shelf and their aggregations within deep shelf basins. *Cont. Shelf Res.*
- Hirche, H. J. (1983). Overwintering *Calanus finmarchicus* and *Calanus helgolandicus*. *Mar. Ecol. Prog. Ser.* 11: 281–290
- Koeller, P., Coates-Markle, L., Nielson, J. D. (1989). Feeding ecology of juvenile (0-group silver hake) *Merluccius bilinearis* on the Scotian Shelf. *Can. J. Fish. Aquat. Sci.* 46: 1762–1768
- Krause, M., Trahms, J. (1983). Zooplankton dynamics during FLEX '76. In: Sundermann, J., Lenz, W. (eds.) *North Sea dynamics*. Springer-Verlag, New York, p. 632–661
- Lewis, M. K., Sameoto, D. D. (1988a). The vertical distribution of zooplankton on the Nova Scotia slope – April 1983. *Can. Data Rep. Can. J. Fish. Aquat. Sci.* 682: 1–46
- Lewis, M. K., Sameoto, D. D. (1988b). The vertical distribution of zooplankton and ichthyoplankton on the Nova Scotia shelf – October 1981. *Can. Data Rep. Can. J. Fish. Aquat. Sci.* 684: 1–106
- Lewis, M. K., Sameoto, D. D. (1988c). The vertical distribution of zooplankton and ichthyoplankton on the Nova Scotia shelf – April 1984. *Can. Data Rep. Can. J. Fish. Aquat. Sci.* 717: 1–64
- Lewis, M. K., Sameoto, D. D. (1989). The vertical distribution of zooplankton and ichthyoplankton on the Nova Scotia shelf – October 1984. *Can. Data Rep. Fish. Aquat. Sci.* 731: 1–80
- McClatchie, S. (1985). Feeding behavior in *Meganycitiphanes norvegica* (M. Sars) (Crustacea: Euphausiacea). *J. exp. mar. Biol. Ecol.* 86: 271–284
- McLaren, I. A., Corkett, C. J. (1986). Life cycles and production of two copepods on the Scotian shelf, eastern Canada. *Proc. Second Internat. Conf. on Copepoda in Syllogeus*. *Natn. Mus. Can.* 58: 362–368
- McLaren, I. A., Tremblay, M. J., Corkett, C. J., Roff, J. C.

- (1989). Copepod production on the Scotian shelf based on life-history analyses and laboratory rearings. *Can. J. Fish. Aquat. Sci.* 46: 560–583
- Motoda, S. (1959). Devices of simple plankton apparatus. *Mem. Fac. Fish. Hokkaido Univ.* 7: 73–94
- O'Boyle, R. N., Sinclair, M., Conover, R. J., Mann, K. H., Kohler, A. C. (1984). Temporal and spatial distribution of ichthyoplankton communities of the Scotian Shelf in relation to biological, hydrological and physiographic features. *Rapp. P.-v. Réun. Cons. perm. int. Explor. Mer* 183: 27–40
- Ostvedt, O.-J. (1955). Zooplankton investigations from weather ship M in the Norwegian Sea, 1948–49. *Havsforsk Inst. Skr.*, Helsingf. 40: 1–93
- Rowell, T. W., Young, J. H., Poulard, J. C., Robin, J. P. (1985). Changes in distribution and biological characteristics of *Illex illecebrosus* on the Scotian shelf, 1980–83. *NAFO Sci. Coun. Studies* 9: 11–26
- Sameoto, D. D. (1980). Relationships between stomach contents and vertical migration in *Meganyctiphanes norvegica*, *Thysanoessa rashii* and *T. inermis* (Crustacea, Euphausiacea). *J. Plankton Res.* 2: 129–143
- Sameoto, D. D. (1982). Zooplankton and micronekton abundance in acoustic scattering layers on the Nova Scotian slope. *Can. J. Fish. Aquat. Sci.* 39: 760–777
- Sameoto, D. D. (1984). Environmental factors influencing diurnal distribution of zooplankton and ichthyoplankton. *J. Plankton Res.* 6: 767–792
- Sameoto, D. D., Cochrane, N. A., Herman, A. W. (1985). Response of biological acoustic backscattering to ship's lights. *Can. J. Fish. Aquat. Sci.* 42: 1535–1543
- Sameoto, D. D., Herman, A., Longhurst, A. (1986). Relations between the thermocline meso- and microzooplankton, chlorophyll *a* and primary production distribution in Lancaster Sound. *Polar Biol.* 6: 53–61
- Sameoto, D. D., Jaroszynski, L. O., Fraser, W. B. (1980). BIO-NESS, a new design in multiple net zooplankton samplers. *Can. J. Fish. Aquat. Sci.* 37: 722–724
- Smith, P. C., Petrie, B. D. (1982). Low-frequency circulation at the edge of the Scotian shelf. *J. phys. Oceanogr.* 12: 28–46
- Tremblay, M. J., Roff, J. C. (1983). Community gradients in the Scotian Shelf zooplankton. *Can. J. Fish. Aquat. Sci.* 40: 598–611

This article was submitted to the editor

Manuscript first received: January 16, 1990

Revised version accepted: May 29, 1990