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Dynamics and Community Structure of Zooplankton in the Davis Strait and Northern Labrador Sea

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ABSTRACT. The dynamics and community structure of zooplankton in the Davis Strait and the northern Labrador Sea were studied over an annual cycle (23 April 1977 - 16 May 1978). "Biological spring", defined as the time of year which includes the annual phytoplankton increase and subsequent increases in zooplankton abundance, proceeds in a counterclockwise sense around the region. It is first observed in April near the southern Greenland coast, from where it proceeds north in the Davis Strait, then moves southward in the Baffin Current and along the retreating ice edge before reaching the Hudson Strait in September and October.

Recurrent group analysis was used to identify communities of zooplankton in the region. Distributions of these groups were closely related to the hydrography. The West Greenland Drift is characterized by abundant populations of *Calanus finmarchicus, C. hyperboreus, Oithona similis, Conchoecia obtusata, Metridia longa* and *Microcalanus pygmaeus*. The colder, less saline water of the Baffin Current and the Hudson Strait arctic outflow are characterized by populations of *Calanus glacialis* and the early developmental stages of *Pseudocalanus minutus*. The breeding cycles of the three species of *Calanus* tend to be separated both spatially and temporally.

Key words: Davis Strait, Labrador Sea, zooplankton, zoogeography, arctic, recurrent group analysis, *Calanus*

RÉSUMÉ. Le présent article étudie la dynamique et la structure communautaire du zooplancton dans le détroit de Davis et dans le nord de la mer du Labrador au cours d'un cycle annuel (du 23 avril 1977 au 16 mai 1978). Le "printemps biologique", cette période au cours de laquelle se produit une augmentation du phytoplancton suivie d'une augmentation dans la quantité de zooplancton, voit ces activités s'effectuer dans le sens inverse des aiguilles d'une montre. La première manifestation est observée en avril près de la côte sud du Groenland, d'où elle se poursuit au nord dans le détroit de Davis, puis vers le sud dans le courant de Baffin et suivant les contours reculants de la banquise pour arriver au détroit d'Hudson en septembre et en octobre.

Des analyses périodiques de groupes ont permis d'identifier les communautés de zooplancton dans la région. La distribution de ces groupes est liée de près à l'hydrographie. La dérive ouest-groenlandaise est caractérisée par d'abondantes populations de *Calanus finmarchicus, C. hyperboreus, Oithona similis, Conchoecia obtusata, Metridia longa* et *Microcalanus pygmaeus*. L'eau plus froide et moins saline du courant de Baffin et de l'écoulement arctique du détroit d'Hudson est caractérisée par des populations de *Calanus glacialis* et des premiers stades de développement de *Pseudocalanus minutus*. Les cycles de reproduction pour les trois espèces de *Calanus* ont tendance à être indépendants selon leur nature spatiale et temporelle.

Mots clés: détroit de Davis, mer du Labrador, zooplancton, zoogéographie, arctique, analyse périodique de groupes, *Calanus*

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INTRODUCTION

Little is known of the dynamics and community structure of zooplankton in the western Davis Strait and Labrador Sea, where ice covers the surface much of the year. Studies conducted in this region (Fontaine, 1955; Grainger, 1961, 1962, 1963) have not been comparable in scope to analogous studies in the southern Labrador Sea (Kielhorn, 1952) or the eastern Davis Strait (Pavshtiks, 1968; Bainbridge and Corlett, 1968).

The region of the western Davis Strait and the northern Labrador Sea is well suited to the study of zooplankton ecology and distribution for several reasons. First, the zooplankton biomass is dominated by a small number of species (compared to tropical and temperate pelagic communities). Second, the region is one of considerable hydrodynamic complexity, where water masses of both the Arctic and Atlantic oceans interact (Fig. 1, inset); advective processes strongly influence the distribution and ecology of the zooplankton. Third, the species of zooplankton have strong seasonal cycles which provide clues to the interactions of physics and biology.

The zooplankton biomass in the Davis Strait is dominated by a small number of species, but their distributions are not known in detail. Previous studies in the area indicate that the calanoid copepods *Calanus finmarchicus, C. glacialis* and *C.*

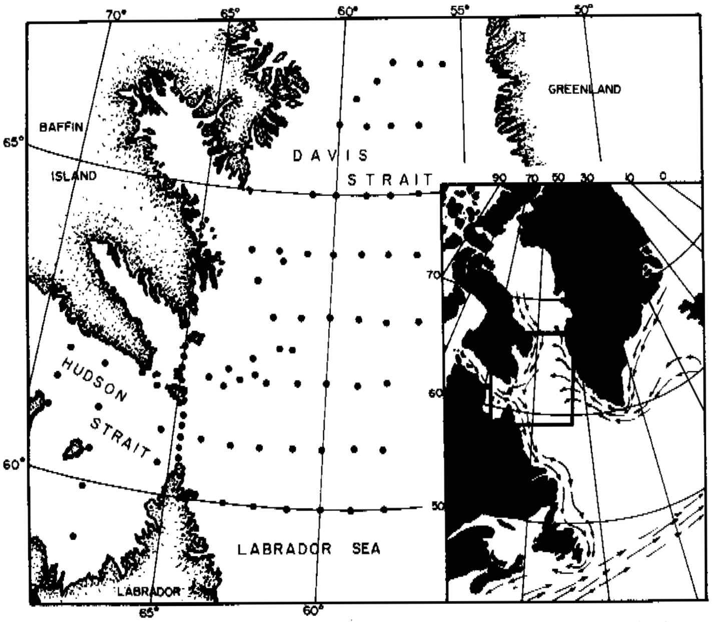

FIG. 1. The Davis Strait and the northern Labrador Sea, showing zooplankton sampling stations visited on six cruises in the period from April 1977 to May 1978. Inset shows the current patterns in the immediate and surrounding areas, based on the descriptions of Smith *et al.* (1937), Lazier (1973) and our own physical observations.

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hyperboreus, and the cyclopoid *Oithona similis*, are the most abundant species (Pavshitiks, 1968; Bainbridge and Corlett, 1968). Grainger (1961, 1963) suggested that the three species of *Calanus* were representative of distinct water masses. Fleminger and Hulsemann (1977) reviewed the geographical distributions of *C. finmarchicus* and *C. glacialis*, and concluded that their geographical boundaries occur in the region we studied. They indicated that the northern distributional boundary of *C. finmarchicus*, a North Atlantic species, "appears to extend deeply into the Hudson and Davis Straits" but questioned its ability to reproduce successfully in this region. Similarly, Fleminger and Hulsemann (1977) regard *C. glacialis*, a polar species, to be reproductively expatriate south of the Labrador Sea. The detailed distributions of these species at their geographical boundaries have not been studied.

The dominant feature of planktonic life at high latitudes is the pronounced seasonality, exemplified by the phenomenon of "biological spring". Generally, zooplankton reproduction either coincides with or immediately follows a brief but intense phytoplankton bloom (Conover, 1979), and the young stages feed in surface waters (Grainger, 1959). The advent of biological spring in the eastern Davis Strait has been studied (Pavshtiks, 1968), but seasonal dynamics have remained largely ignored. In this paper we present new information on the seasonal dynamics of zooplankton in the western Davis Strait and Labrador Sea.

To analyze our data we sought a technique which might concisely define the zooplankton community structure. We chose the method of recurrent group analysis (Fager, 1957). Although this technique has not, to our knowledge, previously been used to examine the zooplankton of the Davis Strait and Labrador Sea, it has been used to analyze other pelagic zooplankton communities (e.g. Fager and McGowan, 1963; McGowan and Walker, 1979). We find that groups of co-occurring zooplankton are associated with principal hydrographic features of the eastern Canadian Arctic. The recurrent group analysis facilitated explanation of the distributions of individual species on the basis of their large-scale geographic affinities.

METHODS

Data Collection

The study area is shown in Figure 1. Data were collected on seven cruises aboard the M.V. *Lady Johnson II* from 23 April 1977 to 16 May 1978. Station locations and dates sampled are given in the Appendix (Table A-1). Collections were made by the personnel of MacLaren Plansearch Limited of Dartmouth, Nova Scotia as part of a baseline definition program for Esso Resources Canada Ltd., Aquitaine Co. of Canada Ltd., and Canada Cities Service Ltd.

Temperature and salinity were measured at standard intervals to a depth of 200 m or more at each station, depth of the water column permitting. These measurements were made with a Guildline CTD (model #8400) or with reversing thermometers and 5-L Niskin bottles. Results from the CTD were routinely checked with independent measurements of salinity.

Zooplankton samples were collected with a 233-μm mesh, 1-m diameter Bongo net fitted with a General Oceanics flowmeter. Because of ice, Hudson Strait and the coastal waters of Baffin Island are accessible only in late summer and early fall, and the ice edge poses a challenge to sampling methods at all times. In open water an oblique tow was made from 200 m to the surface. However, where ice cover was extensive a vertical haul was made from the same depth to avoid breaking the towing wire. We preserved zooplankton samples in 10% buffered formalin.

Zooplankton were identified at least to the genus level, and usually to species. For copepods, adult males, adult females and copepodites were enumerated. All copepodite stages of *Calanus finmarchicus, C. glacialis* and *C. hyperboreus* were identified. Icthyoplankton were also counted and identified. Counts of all plankton were converted to numbers per m^3 using the flowmeter readings.

Displacement volumes of zooplankton, which provide an adequate estimate of zooplankton biomass (Bé *et al.*, 1971), were also measured and converted to units of ml per m^3 using flowmeter readings.

Data Analysis

The data have been analyzed on two levels. First, we considered the distribution and seasonal dynamics of each of the zooplankton separately. This approach highlights the differences between individual species.

On the second level of data analysis we wished to emphasize the similarities among the zooplankton. Thus we asked two questions: "What zooplankton occur together, constituting a community?" and "How are these communities distributed in space and time, and relative to one another?" We considered the characteristics of the data set before deciding upon a method of analysis. First, abundances of a given organism were not strictly comparable between stations since samples were collected at all times of the day and night. Thus the low abundance, or even absence, of a given organism at a given station can be real, or it can result from temporary vertical migration out of the upper 200 m. Second, plankton tows do not give either a precise or an accurate estimate of abundance (Cassie, 1963; Wiebe, 1972), and plankton data usually are not normally distributed.

The use of parametric techniques involving correlation coefficients is inappropriate under such circumstances. Even the use of rank correlation cannot entirely overcome the inherent problems, since it also depends on a measure of abundance. For two organisms which are a constant part of one another's environment, a correlation coefficient will fail to show a relationship unless there is also a close relationship between their relative abundances.

Under these circumstances we chose a technique employing only presence/absence information to establish which zooplankton occur together. We selected the method of recurrent group identification devised by Fager (1957; Fager and Mc-

Gowan, 1963). He quantified co-occurrence by an index between pairs of species (a,b):

$$A\,(a,b) \;=\; \frac{J}{\sqrt{N_a N_b}} - \frac{1}{2\sqrt{N_b}}$$

where N_a and N_b are the numbers of occurrences of a and b, respectively (labelling so that $N_a \leq N_b$), and J is the number of joint occurrences of a and b. Calculations of A(a,b) are made for all pairs of species in the data set. Then the recurrent group procedure is applied. This extracts the largest possible set of species in which all pairs have A(a,b) greater than some criterion value. When two sets of the same size are extracted, that with the highest total is chosen for the affinity indices. The procedure next extracts the largest such set from the remaining list, and so on.

In our data set the probability of A(a,b) exceeding 0.58 from strictly chance co-occurrence was 0.025, and of exceeding 0.52 was 0.05. We tried both of these criterion values of A(a,b), following Fager's (1957) suggestion that species should be significantly associated to be grouped together. This is not a statistically rigorous significance, but it allows us to establish groups of zooplankton that are nearly constant parts of one another's environment. Pairs of species placed by recurrent grouping in different groups can nevertheless have high affinity, exceeding the criterion selected. The frequency of these high values as a fraction of such possible pairings is a measure of the "closeness" of the groups.

In our analysis we considered each copepodite stage of the three *Calanus* species as a separate entity, and thus treated them as Fager (1957) would have treated separate species. Similarly, for other copepod species we considered adults and copedites to be two separate entities. The validity of this approach is borne out by the results of the recurrent group analysis, which sometimes placed different copepodite stages of the same species in different groups due to their spatial or temporal separation.

Some modifications were made in the data table before the recurrent grouping procedure was applied. First, zooplankton tows made to depths other than 200 m were eliminated. A total of 111 samples remained, including 122 zooplankton species or developmental stages (together referred to as "entities"). Second, although the analysis is based on presence/absence data, we did not ignore abundance information. We found that the occurrence of usually important entities at very low abundance can obscure the major temporal and spatial patterns. Therefore, we considered an entity to be "absent" when its abundance was $<20\%$ of its median abundance; this is often done in recurrent group procedure (McGowan and Walker, 1979). We believe it is justified, since the rare occurrence of an abundant entity does not contribute much to the overall community structure. Furthermore, this procedure retains for consideration the occurrences of entities with low overall abundance, which can nonetheless be consistent, ecologically significant members of the community.

Some of the entities in our data set were too infrequent to be a frequent part of any assemblage, and these were eliminated by the grouping procedure such that only 40 of the original 122 entities remained after the analysis. The total number of entities was the same, regardless of whether the 0.025 or the 0.05 significance level was used. However, the results of the analysis at the 0.025 level are presented here, since it increased the number of groups by two. This permitted a finer discrimination of the groupings, but did not change the essential patterns yielded by the analysis at the 0.05 significance level. Although the recurrent grouping procedure eliminated some of the rarer zooplankton species, our analysis of individual species (see Appendix) retained some of these for consideration.

Following the grouping procedure we examined the temporal and spatial distributions of the resulting groups. This analysis confirms and concisely describes patterns which were suggested by the distribution of individual species (see Appendix); furthermore, it elucidates some relationships which were not so obvious.

RESULTS

Surface Circulation

The general pattern of water circulation in Davis Strait and the Labrador Sea is shown in Figure 1 (inset). We found three basic water types in the region: 1) West Greenland Drift water originating from the northward-moving West Greenland Current; 2) the Baffin Current, which flows southward from Baffin Bay along the Canadian side of Davis Strait; and 3) the arctic outflow from Hudson Strait, which joins the Baffin Current and ultimately flows south as the coastal branch of the Labrador Current. Our physical observations confirm previous findings in the area (Smith *et al.*, 1937; Lazier, 1973).

The West Greenland Current has a profound influence on the Canadian side of the Davis Strait and the northern Labrador Sea. The depth profiles of temperature at representative stations within the sampling grid (Fig. 2) demonstrate that the warmer, saline waters of the West Greenland Current

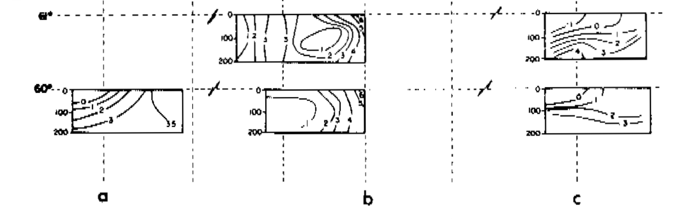

FIG. 2. Depth profiles of temperature isotherms at selected stations in the Davis Strait region. (a) April-May 1977; (b) October-November 1977; (c) April 1978. Cold surface waters on the western side represent the Baffin Current; deeper warm water and warm water to the east are indicative of the West Greenland Drift.

may lie only 100 m beneath the Baffin Current. Toward Baffin Island to the west the thickness of the Baffin Current increased, but even at 200 m (the depth of most zooplankton tows) West Greenland water was often detected. It is therefore clear that zooplankton tows to 200 m may have passed through both water masses, especially on the western side of Davis Strait.

Zooplankton Biomass

Zooplankton displacement volumes, used here as a measure of biomass, were greatest (>0.5 ml·m^{-3}) in late April and early May (1977) at stations in the easternmost section of the sampling area (Fig. 3a), the area most affected by the West Greenland Drift. By June the entire central region of Davis Strait supported doubly large standing stocks; low values occurred only at the mouth of the Hudson Strait (Fig. 3b). In August, however, Hudson Strait outflow had the largest biomass (Fig. 3c). By the following April and May (Fig. 3e,f) the highest biomasses were once again found in the easternmost section of the study area.

Distribution and Abundance of Individual Species

In total, at least 67 species from nine phyla were identified from samples taken on 107 days of cruises between April 1977 and May 1978 (Appendix Table A-2). Of these, 30 species accounted for 96.5% of the total zooplankton abundance, taking

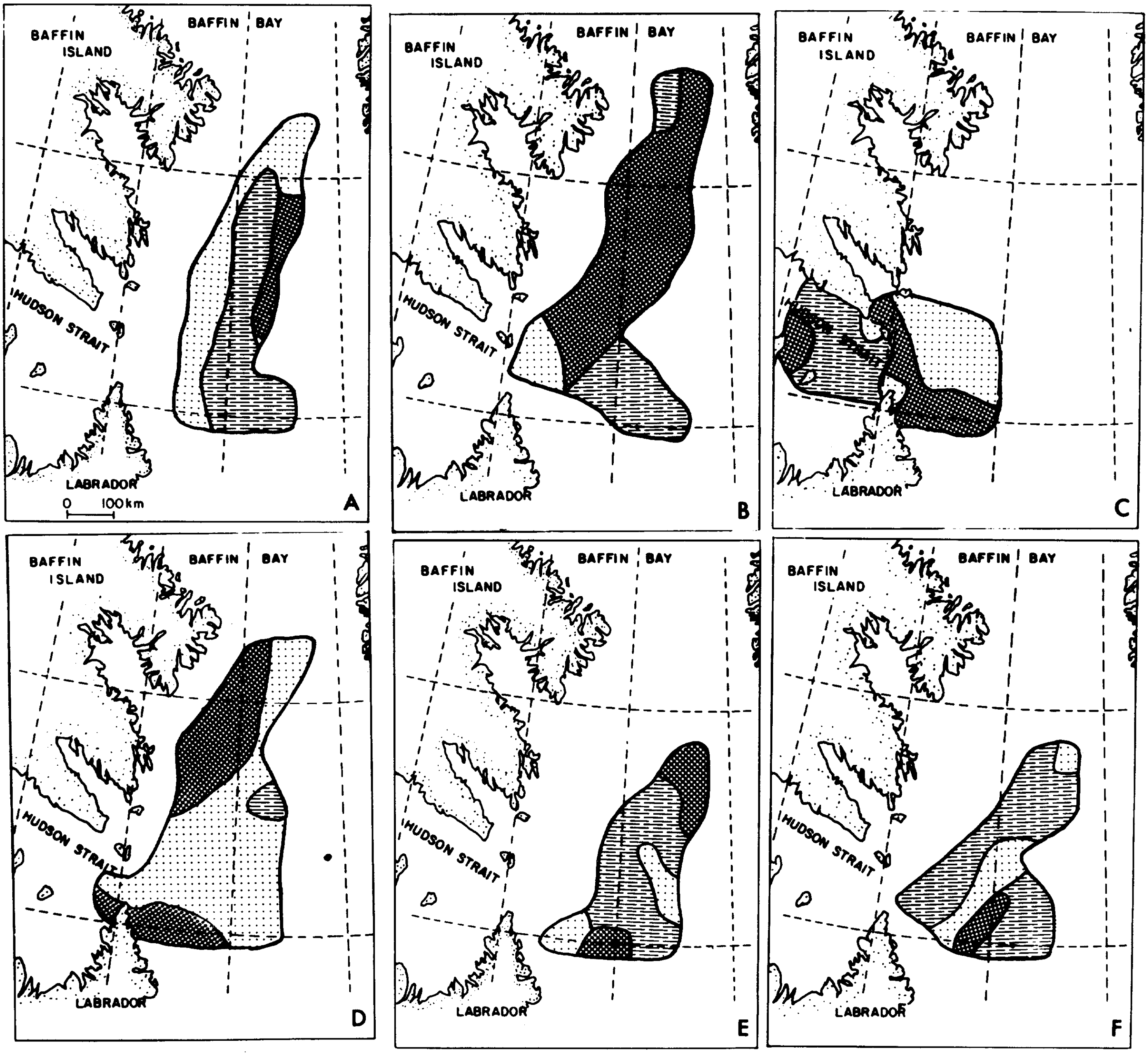

FIG. 3. Distribution of zooplankton displacement volumes during the study. Lightly stippled area: 0.2 ml·m^{-3}; hatched area: 0.2-0.5 ml·m^{-3}; darkly stippled area: 0.5 ml·m^{-3}. Distributions shown are for April-May 1977 (a); June 1977 (b); August-September 1977 (c); October-November 1977 (d); April 1978 (e); and May 1978 (f).

TABLE 1. Mean relative abundance (%) of taxa in the zooplankton community. Averages are calculated for entire cruises and also for the entire set of cruises.

	Cruise date						
Taxa	4/27-5/15	6/6-6/25	8/1-9/9	10/13-11/2	4/16-4/27	5/5-5/15	Mean
Copepods	92.3	92.2	92.7	83.2	83.7	83.9	88.00
Conchoecia obtusata	1.3	3.8	0.3	2.9	7.2	7.4	3.82
Euphausiids	1.2	0.7	0.1	1.4	3.2	1.1	1.28
Parathemisto spp.	0.2	0.1	0.2	1.2	0.5	2.3	0.75
Limacina retroversa	0.1	0.1	2.8	1.0	0.1	0.1	0.70
Cirripede nauplii	0.4	0.1	0.6	0.1	1.9	0.6	0.62
Eukhronia hamata	0.3	0.7	0.1	0.3	0.5	1.6	0.58
Aglantha digitale	0.1	0.3	0.1	2.3	0.2	0.4	0.57
Beröe cucumis	0.1	0.1	0.1	0.2	0.1	0.1	0.12
Mertensia ovum	0.1	0.1	0.1	0.2	0.1	0.1	0.12
Tomopteris septentrionalis	0.1	0.1	0.1	0.1	0.1	0.2	0.12
Pleurobrachia pileus	0	0.1	0.1	0.1	0.1	0.1	0.08
Subtotal	95.8	98.1	97.0	92.9	97.5	97.7	96.50
Other zooplankton	4.2	1.9	3.0	7.1	2.5	2.3	3.50

TABLE 2. Mean relative abundance (%) of copepod species in the zooplankton community. Averages are calculated for entire cruises and also for the entire set of cruises. Species are ranked by overall mean abundance.

	Cruise date						
Species	4/27-5/15	6/6-6/25	8/1-9/9	10/13-11/2	4/16-4/27	5/5-5/15	Mean
Calanus finmarchicus	34.2	64.4	27.9	24.2	44.4	17.9	35.5
Oithona similis	38.4	4.9	11.5	19.9	16.1	28.7	19.9
Pseudocalanus minutus	3.3	3.4	29.5	25.0	5.2	2.8	11.5
Calanus glacialis	1.8	8.9	14.6	2.9	1.3	0.6	5.0
Metridia longa	3.7	0.9	3.1	6.5	2.6	2.9	3.3
Calanus hyperboreus	2.0	8.2	2.1	0.1	0.4	4.8	2.9
Scolecithricella minor	1.6	0.4	1.8	1.9	3.7	4.8	2.4
Microcalanus pygmaeus	1.7	≤0.1	1.8	0.2	2.8	7.1	2.2
Oithona spinirostris	2.3	≤0.1	0.1	0.3	7.0	8.6	2.1
Euchaeta norvegica	3.1	0.8	0.1	0.6	2.5	3.4	1.8
Oncaea borealis	0	0	0	0	0.1	0.4	0.2
Acartia longiremis	0	0	0	0.8	0	0	0.1
Acartia clausii	0	0	0.1	0	0	0	≤0.1
Scolecithricella ovata	0	0	0	0	≤0.1	0.6	≤0.1
Gaidius tenuispinus	≤0.1	≤0.1	≤0.1	0.4	≤0.1	≤0.1	≤0.1
Heterorhabdus norvegicus	0.2	≤0.1	≤0.1	0.1	≤0.1	0.1	≤0.1
Euchaeta glacialis	0	≤0.1	≤0.1	≤0.1	0	0	≤0.1
Paracalanus parvus	≤0.1	≤0.1	0	0	0	0	≤0.1
Aetidius armatus	≤0.1	0	0	0	≤0.1	0	≤0.1

an average over abundances from six cruises (Table 1). Copepods dominated the zooplankton; 19 species of copepods accounted for 88% of the total zooplankton abundance, with nine of these being consistently numerous (Table 2).

The ten most abundant species were *Calanus finmarchicus* (35.5%), *Oithona similis* (19.9%), *Pseudocalanus minutus* (11.5%), *Calanus glacialis* (5.0%), *Conchoecia obtusata* (3.8%), *Metridia longa* (3.3%), *Calanus hyperboreus* (2.9%), *Scolecithricella minor* (2.4%), *Microcalanus pygmaeus* (2.2%) and *Oithona spinirostris* (2.1%). All but one of these species, *C. obtusata*, belongs to the Copepoda.

Detailed maps of the distributions of selected zooplankton species and stages are presented in the Appendix (Figs. A-1 to A-11). Our observations are summarized here, species by species.

1. *Calanus finmarchicus*: This species was usually most abundant in the eastern Davis Strait, where it accounted for more than 80% of the total zooplankton abundance from late winter to early summer. The highest concentration (15 400 copepodites·m^{-3}) was observed at 62°N, 59°W in mid-June 1977. Although *C. finmarchicus* was also observed in the western Davis Strait, its development there was delayed and it was not as abundant. Its reproductive period followed the spatial pattern of bloom development described in part by Pavshtiks (1968), beginning in April and May in the southern portion of the West Greenland Drift and moving counterclockwise to the Davis Strait, the Baffin Current and finally, in early fall, to the mouth of the Hudson Strait. The presence of stage I and II copepodites in the central Labrador Sea in October and November suggests that there may be a second breeding period in late summer or early fall.

2. *Calanus glacialis*: This copepod was most abundant on the western side of Davis Strait, and was often absent from samples taken in the West Greenland Drift. However, where it was present its reproductive period was similar to that of *C. finmarchicus*, first occurring in the Baffin Current and then moving southward to the mouth of Hudson Strait. Unlike *C. finmarchicus*, it does not appear to have a second breeding period later in the year.

3. *Calanus hyperboreus*: This was the largest, but the least abundant, of the three species of *Calanus*. Greatest concentrations were observed in summer. The absence of this species from samples in October and November may signal the ontogenetic descent of the population to deeper waters, where it overwinters (Grainger, 1963). The development of copepodite stages followed the same pattern as that of the other species of *Calanus*, first occurring in the central Davis Strait and then further south. Details of the similarities and differences between species of *Calanus* are discussed in light of the recurrent group analysis.

4. *Pseudocalanus minutus*: This species was most abundant in summer to fall along the coast of Baffin Island and in the Hudson Strait. Its maximum abundance (68 300 copepodites·m^{-3}) was observed at 60°N, 61°W in mid-October 1977. Its neritic distribution and its association with Baffin Current waters are consistent with earlier descriptions (Corkett and McLaren, 1968).

5. *Oithona similis*: This cyclopoid species and its congener, *O. spinirostris*, were most abundant in April and May, when together they accounted for approximately 40% of the total copepod abundance (Table 2). Since our collecting methods (233 μm mesh net) did not quantitatively capture copepodites of these species, we have probably underestimated their abundances. *Oithona similis* was most abundant in the eastern and central Davis Strait.

6. *Conchoecia obtusata*: Four species of ostracods occurred in our collections, but only this one was found in significant numbers. It was most abundant in the central Labrador Sea.

7. *Aglantha digitale*: The only cnidarian which occurred consistently in the region, *A. digitale* was present in low abundances throughout the year. Its peak abundance occurred in October and November in the central Davis Strait, lagging behind the period of maximum copepod abundances (Table 1). Two species of ctenophores, *Beröe cucumis* and *Mertensia ovum*, had similar cycles of abundance but were not as ubiquitous as *A. digitale*.

8. *Eukhronia hamata*: Although two other species of chaetognaths were collected (*Sagitta maxima* and *S. elegans*), this species was by far the most abundant. Greatest numbers were observed in May and June at the southernmost stations. Abundances were lowest in the Hudson Strait region.

9. Other species: Euphausiids were represented primarily by *Thysanöessa longicaudata*, which Kielhorn (1952) considered an important species in the southern Labrador Sea. Five other species of euphausiids were collected sporadically in the region. The predatory polychaete, *Tomopteris septentrionalis*, was present in low concentrations (Table 1), and occurred primarily in central Davis Strait. The pelagic gastropod, *Limacian retroversa*, reached its peak abundance in June (Table 1). Cirripede nauplii occurred off the coast of Baffin Island from April to June.

Zooplankton Communities and their Distribution: Recurrent Group Analysis

It is apparent from the above discussion of individual species that certain species tended to occur together in space and time while others did not. The recurrent grouping procedure we used enabled us to systematically differentiate between these groups.

The eight groups formed at the 0.025 significance level and the rank abundances of their component organisms are shown in Table 3. The numerical definitions of the abundance ranking are: "very abundant" (VA: 100-1000·m^{-3}), "abundant" (A: 10-100·m^{-3}), "common" (C: 1-10·m^{-3}) and "rare" (R: <1·m^{-3}). The frequency distribution of entity abundance was: 6 very abundant entities, 8 abundant entities, 19 common entities and 7 rare entities. Note that the recurrent group analysis considered development stages of some species to be

TABLE 3. Recurrent group analysis: composition of the 8 groups of zooplankton determined using an affinity index of 0.58 (97.5% confidence level). Also shown are mean abundance levels: Very abundant (VA: 100-1000·m^{-3}); Abundant (A: 10-100·m^{-3}); Common (C: 1-10·m^{-3}); and Rare (R: $<$1·m^{-3}).

ENTITY	ABUNDANCE
WEST GREENLAND DRIFT ASSEMBLAGE	
GROUP I	
Calanus finmarchicus CVI ♀	A
C. finmarchicus CVI ♂*	R
C. finmarchicus CV	VA
C. finmarchicus CIV	A
C. hyperboreus CVI ♀	R
C. hyperboreus CV	C
Metridia longa CVI ♀	A
M. longa copepodites	A
Pseudocalanus minutus CVI ♀	A
Euchaeta norvegica copepodites	A
Scolecithricella minor copepodites	C
Aglantha digitale	C
Conchoecia obtusata	A
Eukhronia hamata	C
Sagitta maxima	R
Tomopteris septentrionalis	R
Thysanöessa longicaudata	R
GROUP III	
Calanus finmarchicus CII	VA
C. finmarchicus CI	VA
Oithona similis	VA
GROUP IV	
Scolecithricella minor CVI ♀	R
Oithona spinirostris	C
Bathylagus euryops	C
GROUP V	
Calanus hyperboreus CII	C
C. hyperboreus CI	C
Parathemisto	C
GROUP VII	
Conchoecia elegans	C
Euchaeta norvegica CVI ♀	R
Scolecithricella minor CVI ♀*	C
*Microalanus pygmaeus**	A
GROUP VIII	
Calanus hyperboreus CIV	C
C. hyperboreus CIII	C
BAFFIN CURRENT ASSEMBLAGE	
GROUP II	
Calanus glacialis CVI ♀*	C
C. glacialis CV	C
C. glacialis CIV	C
C. glacialis CIII	C
C. finmarchicus CIII	VA
Pseudocalanus minutus copepodites	VA
GROUP VI	
Calanus glacialis CII	C
C. glacialis CI	C

*group associate

individual components of the groups, and thus we refer to these individual components as "entities". As expected, the recurrent grouping procedure emphasized the importance of certain rare entities which, in our consideration of individual species, we did not find to be important.

Figure 4 shows the connections of the recurrent groups with one another. Values on the interconnecting lines indicate the percentage of possible associations between pairs of entities that exceeded the criterion value of the affinity index. These percentages are a measure of the "closeness" of the groups.

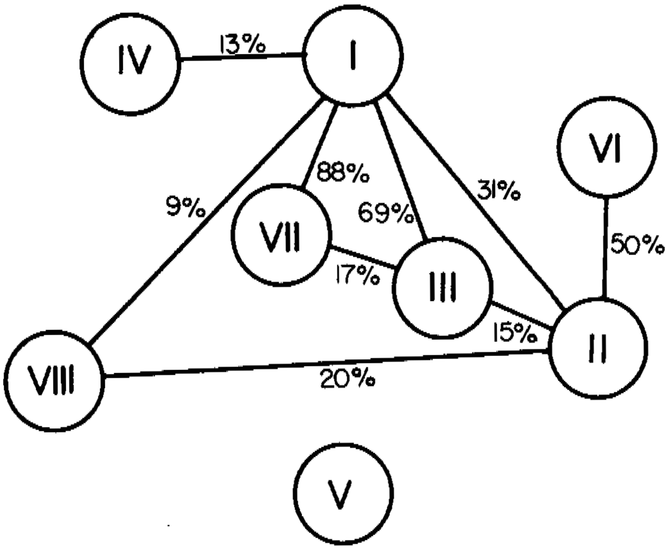

FIG. 4. Trellis diagram showing the percentage of affinity between zooplankton groups (Table 3), as determined by recurrent group analysis. Numbers shown represent the percentage of all possible affinities realized between two entities of connected groups.

Group I is best characterized as the "*Calanus finmarchicus/Calanus hyperboreus* late-stage group". It included copepodite stages CIV, CV and CVI of the former species, and stages CV and CVI of the latter species; together, these made up approximately 30% of the entities in the group. Group I is strongly connected (88%) to Group II, the "*Conchoecia/Euchaeta* group". Group I is also strongly connected to Group III (69%), which is composed of three very abundant entities: stage CI and CII copepodites of *Calanus finmarchicus*, and *Oithona similis*.

Group II, the "*Calanus glacialis* late-stage group", contains copepodite stages CIII, CIV and CV of the species, and the adult female is an associate. It also contains CIII *Calanus finmarchicus* and copepodites of *Pseudocalanus minutus*. It is most strongly connected (50%) to Group VI, which contains the earlier copepodite stages (CI-CII) of *C. glacialis*. There is also a connection (31%) to Group I.

Group III, the "*Calanus finmarchicus* early-stage group", is most strongly connected to Group I (69%). The remaining groups are small. Group IV consists of *Oithona spinirostris*, adult males of *Scolecithricella minor* and larvae of the goitre blacksmelt, *Bathylagus euryops*. This is the only group which contains a larval fish, although nine species of larval fish were present in the original list of 122 entities.

Group V contains the CI and CII copepodites of *Calanus hyperboreus* as well as juvenile stages of the amphipod, *Parathemisto*, of which three species were recorded in the area. Group VI contains only the early copepodite stages (CI-CII) of *Calanus glacialis*, and is connected to the *C. glacialis* late-stage group, Group II. Group VI, the *Conchoecia/Euchaeta* group, is strongly connected to Group I. The final group, Group VIII, contains only the middle copepodite stages (CII-CIV) of *Calanus hyperboreus*.

The most striking aspect of the group formations is that they are dominated by relationships between the three species of *Calanus*. This would not have been expected on the basis of their abundances alone, since they are ranked only as the first, fourth and seventh most important species. Groups containing the late stages of all three species (Groups I and II) are connected (31%), but there are distinct separations between younger and older stages of all *Calanus* species. Differences in the timing and location of development between the three species are reflected by the lack of connections between the groups containing stage CI and CII copepodites of each species (Groups III, V and VI).

Geographical Distributions of Communities

Distributions of each of the eight groups fall clearly into either one of two areas: the West Greenland Drift waters on the eastern side of Davis Strait and the Labrador Sea, or the Baffin Current-Hudson Strait waters on the western side of Davis Strait. We refer to these regional associations as the West Greenland and Baffin Current assemblages, respectively.

The dominant species of the West Greenland assemblage are *Calanus finmarchicus* and *C. hyperboreus* (Groups I, III, V and VIII). Other numerically-important species in the West Greenland assemblage are *Metridia longa*, *Pseudocalanus minutus* adults, *Conchoecia obtusata* (Group I), *Oithona similis* (Group III), *O. spinirostris* (Group IV) and *Microcalanus pygmaeus* (Group VII).

The Baffin Current assemblage, by contrast, is dominated by *Calanus glacialis* of all stages (Groups II and VI), and also contains copepodites of *Pseudocalanus minutus* (Group II).

The strong similarities and differences in the geographical distributions of the groups make it possible to distinguish regional assemblages. Figure 5a shows the geographical distributions of a West Greenland group (I) and a Baffin Current group (II). Although there is marginal overlap of their distributions, the *Calanus finmarchicus/Calanus hyperboreus* late-stage group (I) is restricted to the eastern waters of the Labrador Sea and Davis Strait, whereas the *Calanus glacialis* late-stage group is confined to the colder arctic waters of the western strait. The area of overlap is greatest in the vicinity of the mouth of the Hudson Strait and extends to the north; this is an area of mixing of West Greenland and Baffin currents.

Figure 5b shows the distributions of two West Greenland groups (I and VII), which are 88% connected (see Fig. 4). These groups, the *Calanus finmarchicus/Calanus hyperboreus* late-stage group and the *Conchoecia/Euchaeta* group, coincide very closely in their geographical ranges.

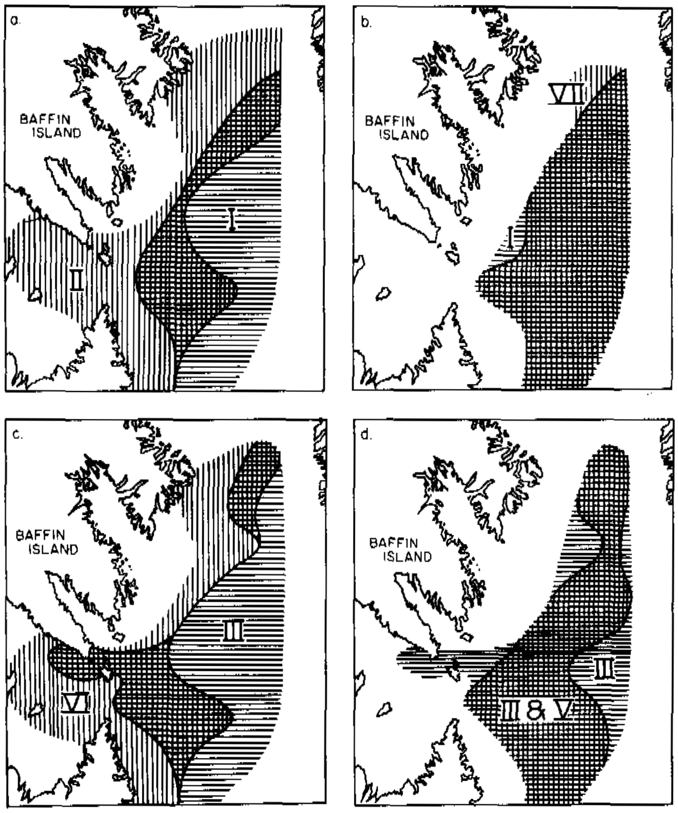

FIG. 5. Geographical distribution of recurrent groups. (a) Distributions of the *Calanus finmarchicus/Calanus hyperboreus* late-stage group (I) and the *Calanus glacialis* late-stage group (II); (b) Distributions of the *Calanus finmarchicus/Calanus hyperboreus* late-stage group (I) and the *Conchoecia/Euchaeta* group (VII); (c) Distributions of the *Calanus finmarchicus* early-stage group (III) and the *Calanus glacialis* early-stage group (VI); (d) Distributions of the early-stage groups of *Calanus finmarchicus* (III) and *Calanus hyperboreus* (V).

Groups with overlapping geographical ranges do not necessarily co-occur. Figure 5c shows the distributions of two such groups (III and VI). Although the stage CI and CII copepodites of *Calanus finmarchicus* (Group III) and *C. glacialis* (Group VI) apparently occupy the same region near the mouth of Hudson Strait, the recurrent grouping procedure showed that they had no affinity (Fig. 4). Even more striking is the relationship between the young stages of *C. finmarchicus* (Group III) and those of *C. hyperboreus* (Group V), shown in Figure 5d. Although these two groups overlap completely in their distribution, and although they both belong to the West Greenland assemblage, the recurrent grouping procedure showed that they had no affinities (Fig. 4). This apparent paradox occurs because the groups are temporally separated, as will be shown clearly below.

Yet another method of distinguishing between the West Greenland and Baffin Current assemblages is to examine the physical characteristics of the waters in which representative groups occurred. We plotted the occurrences of the *Calanus finmarchicus* groups (I and III) and the *C. glacialis* groups (II and VI) according to the temperature and salinity of the waters in which they occurred (Fig. 6). There is a great difference between the groups. The *C. finmarchicus* complex falls along a line which corresponds closely to the T-S curve indicative of the West Greenland Current, which Lazier (1973) described as "virtually straight, passing through 3°C at 34‰ and 5.5°C at 35‰". The *C. glacialis* complex is distributed about a line which represents the T-S characteristics of the Baffin Current. (Although the two complexes occurred over almost the same temperature range, *C. glacialis* was associated with lower salinity (<33‰) than was *C. finmarchicus*.

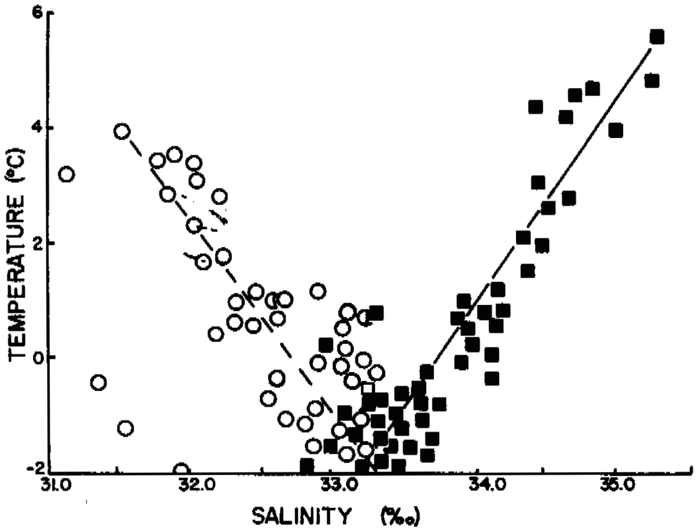

FIG. 6. Temperature-salinity-plankton (T-S-P) diagram, showing the temperature-salinity coordinates at which the *Calanus glacialis* complex (Groups II and VI) and the *Calanus finmarchicus* complex (Groups I and III) occurred. Lines were fitted by eye. T-S lines correspond to Baffin Current waters for *C. glacialis* (open circles) and to West Greenland Drift water for *C. finmarchicus* (solid squares).

Temporal Distributions of Communities

The geographical distributions of the early copepodite stages of the three *Calanus* were shown to overlap; however, according to the recurrent group analysis their respective groups had no affinities. We suggest that the breeding periods of the three species differ, and that they are separated in time.

Figure 7 shows the envelopes of time and temperature which encompassed the distributions of *Calanus* spp. early stages (Groups II, V and VI). Also shown is the envelope for the *Calanus finmarchicus/Calanus hyperboreus* late-stage group (Group I). The young stages of *C. finmarchicus* and *C. glacialis* overlap in their geographical distributions (Fig. 5c). They also overlap in time; *C. finmarchicus* young stages are present from May through November, and *C. glacialis* young stages occur from June to September. However, the early stages of these species tend not to occur simultaneously in the same time *and* space. *Calanus glacialis* young stages occupy colder waters (<3°C) at the time when *C. finmarchicus* occupy warmer waters (up to 6.5°C). The distributions of the young stages of both species follow the retreat of the ice edge into Hudson Strait as the summer wears on and the water warms, but at any given time the edge of the *C. finmarchicus* distribution occurs further east of the ice edge than that of *C. glacialis*.

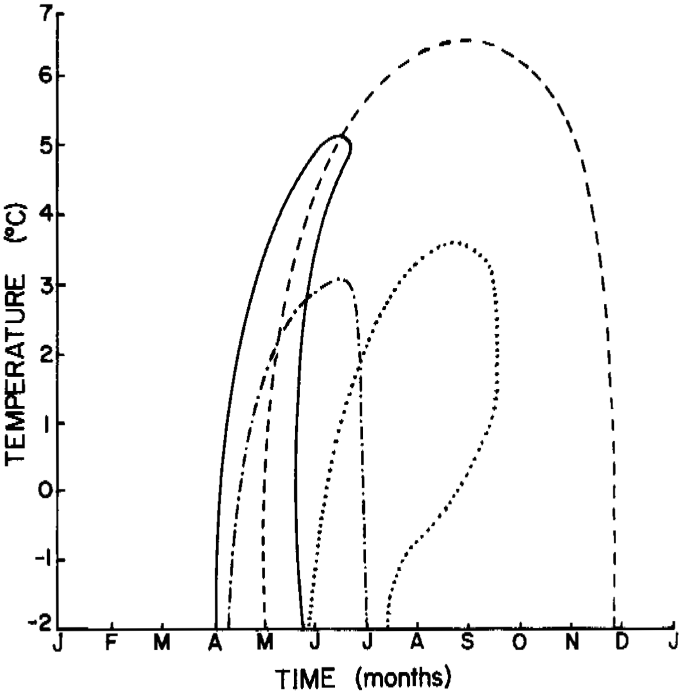

FIG. 7. Time-temperature-plankton (T-T-P) diagram, showing the envelopes of time and maximum surface temperature at stations where four recurrent groups of zooplankton occurred during an annual cycle. Shown are Group I, the *Calanus finmarchicus/Calanus hyperboreus* late-stage group (————); Group III, the *Calanus finmarchicus* early-stage group (- - - -); Group V, the *Calanus hyperboreus* early-stage group (-·-·-·-); and Group VI, the *Calanus glacialis* early-stage group (········).

Early copepodite stages of *Calanus finmarchicus* and *C. hyperboreus* overlap even more in both geographical distribution (Fig. 5d) and in time (Fig. 7). However, as in the previous example, these groups have no affinities (Group III and V, Fig. 4), and tend not to occur in the same time *and* place. Early stages of *C. hyperboreus* appearing in April occur in waters with surface temperatures <3°C, whereas *C. finmarchicus* early stages occur at temperatures up to 6.5°C. This separation continues through time, with *C. hyperboreus* CI and CII copepodites tending to occupy the colder regions of the West Greenland Drift.

DISCUSSION

The results of this study elucidate the seasonal dynamics of zooplankton communities on the western side of Davis Strait and the Labrador Sea, and contribute to what is known of the seasonal distributions of several zooplankton species.

We conclude that 'biological spring" more or less follows the retreating ice edge on the western side of Davis Strait and the Labrador Sea. It develops in the northern Davis Strait in May and moves south and westward in June. It then appears, in September and October, in Hudson Strait and Ungava Bay. Our conclusions are based on a number of observations. First, increases in zooplankton biomass (which result from consumption of the spring phytoplankton bloom), proceed in a counterclockwise sense around the region as time passes. Biological spring began in April on the Greenland side, moved to the Canadian side in June, and finally appeared in the Hudson Strait in September. Second, the appearance of early developmental stages of several zooplankton species followed the same pattern. The appearance of *Calanus finmarchicus* early copepodites followed the same spatial sequence as the zooplankton biomass, first appearing along the coast of Baffin Island, and then in Hudson Strait. This was also true of cirripede nauplii and early copepodites of *C. glacialis*. Increases in the abundances of *Eukhronia hamata* and *Tomopteris septentrionalis*, both carnivores, lagged in time behind the copepod abundances, but followed the same spatial pattern set by the spring phytoplankton bloom and subsequent increases in zooplankton biomass.

Our interpretation of the progression of biological spring in Davis Strait differs slightly from that given by Pavshtiks (1968). Although he indicated that biological spring first occurred on the Greenland side of the region and then moved to the Canadian side in August and September, he concluded that it occurred even earlier in Hudson Strait — in July. We agree that biological spring moves from the Greenland side to the Canadian side of Davis Strait, but we find that it follows the ice edge and thus occurs *latest* — in September and October — in Hudson Strait.

Recurrent group analysis defined zooplankton assemblages whose distributions were closely related to the hydrography of the region. One group, dominated by *Calanus glacialis*, was associated with the Baffin Current and Hudson Strait. The second assemblage, dominated by *C. finmarchicus* and *C. hyperboreus*, and containing the rarer species *Eukhronia hamata, Sagitta maxima, Tomopteris septentrionalis* and *Thysanöessa longicaudata*, was associated with waters of the West Greenland Drift. Previous investigations in the region have identified associations of zooplankton and have related their distributions to the general circulation, but have used no statistical techniques to do so (e.g. Kielhorn, 1952; Grainger, 1961, 1963; Pavshtiks, 1968; Bainbridge and Corlett, 1968). By using the recurrent group procedure of Fager (1957), we have been able to define these associations more closely.

Previous reports indicate that the geographical ranges of *Calanus finmarchicus* and *C. glacialis* overlap greatly; the former species may occur as far north and west as Baffin Bay and Hudson Strait, whereas the latter species may occur as far south as the Newfoundland Grand Banks (Grainger, 1961; Jaschnov, 1970; Fleminger and Hulsemann, 1977). Our raw data (Appendix Figs. A-1 to A-4) is not inconsistent with these observations.

However, zoogeographical distributions based upon raw data alone do not necessarily provide a meaningful definition of different habitats. Without benefit of statistical techniques, Fleminger and Hulsemann (1977) concluded that *C. finmarchicus* does not reproduce successfully in the Hudson and Davis Straits (i.e. the Baffin Current) although it can occur there. Likewise, they considered *C. glacialis* to be expatriate south of the Labrador Sea.

The recurrent grouping procedure devised by Fager (1957) is well suited to the analysis of zooplankton distributions. Unlike correlative parametric techniques, it is not affected by a measure of abundance, nor by a non-normal distribution of data. Fager (1957:593-594) defined his technique as a "method for grouping together species which are frequent components of each other's environment" and stated that, by using the technique, one could "compare groups found in different habitats or at different times and localities". Provided that basic requirements are satisfied, the groups formed have, according to Fager, "ecological unity in the sense of intragroup agreement on what constitues a good or bad habitat".

Thus, by using the recurrent grouping procedure, we were able to identify zooplankton habitats in the sense of Fager (1957). We found the habitats of *Calanus finmarchicus* and *C. glacialis* to correspond spatially to the West Greenland and Baffin currents, respectively. The association of *C. hyperboreus* with *C. finmarchicus* was surprising; a previous report (Grainger, 1965) describes *C. hyperboreus* as a surface form in the Arctic, and thus we expected it to be associated with *C. glacialis*.

Our results add to what is known of the reproductive cycles of the three species of *Calanus* in the Davis Strait and Labrador Sea. *C. finmarchicus* produces two generations annually in the southern central Labrador Sea, with the second generation being much smaller (Kielhorn, 1952). Matthews (1968) observed that development of this species was twice as fast in the central Labrador Sea as in the Baffin Current. Our results support the conclusions of Matthews (1968). Furthermore, we find that only one generation is produced annually on the western side of Davis Strait. Early copepodite stages (CI and CII) appeared in the central Labrador Sea in October and November, suggesting the development of a second generation, but there is no direct evidence that these survived the winter.

Breeding schedules of the three *Calanus* species were separated in space and time. Although the early copepodite stages of *C. finmarchicus* and *C. hyperboreus* occurred in the same region, the *C. hyperboreus* appeared earlier, and disappeared later, than the *C. finmarchicus*. Furthermore, *C. finmarchicus* occurred in waters of higher temperature. The stage CI and CII copepodites of *C. glacialis* appeared as the ice edge retreated; they were separated spatially and temporally from the other *Calanus* species. Unlike the other two species, *C. glacialis* was associated with the Baffin Current and the Hudson Strait outflow; its development was delayed relative to that of the two calanid species in the West Greenland Drift.

The temporal and spatial separation of the three *Calanus* species provides some insight into how they may occupy the same oceanic region without being forced to compete for the same resources. Though the species differ in size they are morphologically similar, and all feed on the same types and sizes of phytoplankton (Mullin, 1963; Huntley, 1981). However, by having evolved different breeding cycles and by having achieved spatial separation, they have effectively partitioned the food resources of the region.

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APPENDIX

TABLE A-1. Locations of stations in the Davis Strait and Labrador Sea, and dates sampled

LATITUDE (°N±05′)	LONGITUDE (°W±05′)	DATES SAMPLED						
59°	67°30′			08/05/77				
60°	58°	04/27/77	06/08/77			11/02/77	04/19/78	05/15/78
60°	59°	04/27/77	06/08/77		09/07/77	11/02/77	04/18/78	05/15/78
60°	60°	04/28/77	06/09/77		09/07/77	11/02/77	04/18/78	05/15/78
60°	61°	04/28/77	06/09/77		09/07/77	11/02/77	04/18/78	
60°	62°				09/08/77	11/02/77	04/16/78	
60°	63°				09/08/77	11/01/77		
60°	64°			08/30/77				
60°	67°30′			08/05/77				
60°30′	67°30′			08/06/77				
61°	58°		06/11/77			11/24/77	04/19/78	05/14/78
61°	59°	05/02/77	06/11/77			10/25/77	04/19/78	05/14/78
61°	60°	05/02/77	06/11/77			10/26/77		05/14/78
61°	61°	04/30/77	06/10/77		09/07/77	10/26/77	04/21/78	05/13/78
61°	62°		06/10/77		09/06/77	10/26/77		
61°	63°		06/10/77		09/06/77	10/27/77		
61°	64°		06/10/77		09/06/77	10/27/77		
61°	65°				09/05/77	10/28/77		
61°	66°			08/02/77				
61°15′	67°30′			08/06/77				
61°40′	65°40′			08/06/77				
61°40′	69°			08/04/77				
62°	58°	05/05/77	06/11/77				04/23/78	
62°	59°	05/05/77	06/12/77				04/23/78	
62°	60°	05/04/77	06/12/77		09/04/77		04/22/78	
62°	60°30′							05/09/78
62°	61°	05/04/77	06/13/77	08/01/77	09/04/77			
62°	61°30′	05/03/77						
62°	62°		06/13/77	08/01/77	09/05/77			
62°	63°		06/13/77	08/02/77	09/05/77			
62°	63°30′		06/14/77					
62°	64°			08/03/77	09/05/77			
62°	65°			08/03/77	09/09/77			
62°	66°			08/03/77	09/08/77			
62°	67°30′			08/03/77				
62°	69°			08/04/77				
63°	57°	05/07/77	06/16/77				04/24/78	05/06/78
63°	58°	05/07/77	06/17/77				04/24/78	05/06/78
63°	59°	05/07/77	06/16/77			10/13/77	04/26/78	05/06/78
63°	60°	05/07/77	06/16/77			10/13/77		05/07/78
63°	61°	05/06/77	06/16/77					
63°	61°30′	05/06/77		08/22/77				
63°	62°					10/22/77		
64°	57°	05/11/77	06/17/77		09/22/77	10/24/77	04/27/78	05/04/78
64°	58°	05/11/77	06/17/77		09/22/77	10/24/77		05/04/77
64°	59°	05/11/77	06/18/77			10/22/77		
64°	60°	05/12/77	06/18/77		09/22/77	10/23/77		
64°	60°30′	05/12/77						
64°	61°					10/23/77		
64°	62°				09/22/77			
64°	63°				09/22/77			
65°	57°	05/13/77	06/21/77					
65°	58°	05/13/77	06/21/77					
65°	59°	05/14/77	06/20/77					
65°	60°	05/15/77						
66°	57°		06/21/77	08/19/77		10/16/77		
66°	58°		06/22/77	08/19/77		10/10/77		
66°	59°			08/19/77		10/16/77		
66°	60°			08/18/77				
66°20′	59°30′		06/22/77					
66°40′	58°30′		06/22/77					
67°	56°		06/22/77					
67°	57°		06/22/77					

TABLE A-2. Mean abundances of zooplankton collected in the Davis Strait and Labrador Sea from April 1977 to May 1978

TAXON	MEAN ABUNDANCE (No.·100 m^{-3})
Cnidaria	
Aglantha digitale	277.89
Bougainvillea superciliaris	0.03
Dimophyes arctica	0.97
Lensia conoidea	2.88
Nanomia cara	0.40
Sarsia princeps	+
Sulceolaria biloba	0.02
Ctenophora	
Boröe cucumis	6.15
B. gracilis	0.17
Mertensia ovum	102.98
Pleurobrachia pileus	0.23
Gastropoda	
Clione limacina	47.88
Limacina helicina	7652.50
L. helicoides	101.52
L. retroversa	2909.80
Polychaeta	
Pelagobia longicirrata	0.09
Tomopteris helgolandica	0.07
T. septentrionalis	18.11
Cephalopoda	
Gonatus fabricii	0.02
Ostracoda	
Conchoecia borealis	14.20
C. elegans	254.46
C. haddoni	44.97
C. obtusata	1007.00
Amphipoda	
Hyperia galba	0.01
Orchomonella pinguis	0.33
Parathemisto abyssorum	11.97
P. gaudichaudi	66.33
P. libellula	107.33
Copepoda	
Acartia clausi	14.10
A. longiremis	14.37
Aetidius armatus	0.70
Calanus finmarchicus	70 884.50
C. glacialis	3706.00
C. hyperboreus	2484.40
Candacia armata	+
Euchaeta glacialis	3.77
E. norvegica	657.68
Gaidius tenuispinus	12.36
Heterorhabdus norvegicus	9.69
Metridia longa	6783.10
Microcalanus pygmaeus	1259.00
Oithona similis	41 641.40
O. spinirostris	666.70
Oncaea borealis	53.11
Paracalanus parvus	+
Pseudocalanus minutus	75 411.50
Scolecithricella minor	587.38
S. ovata	4.54
Euphausiacea	
Euphausia khronii	+
Meganyctiphanes norvegica	0.03
Thysanöessa inermis	0.25
T. longicaudata	92.84
T. raschii	0.18
Thysanopoda acutifrons	0.11
Chaetognatha	
Eukhronia hamata	217.37
Sagitta elegans	390.53
S. maxima	29.77
Appendicularia	
Oikopleura dioica	153.30
O. labradoriensis	704.01
O. vanhoeffeni	10.71
Other	
Asteroidea post-larvae	2.30
Ophiopluteus larvae	9.70
Bivalve post-larvae	2184.60
Cirripede nauplii	166.93
Isopoda	0.60
Mysidacea	0.02
Copepoda:Harpactiocoida	24.70

+: <0.01·100 m^{-3}

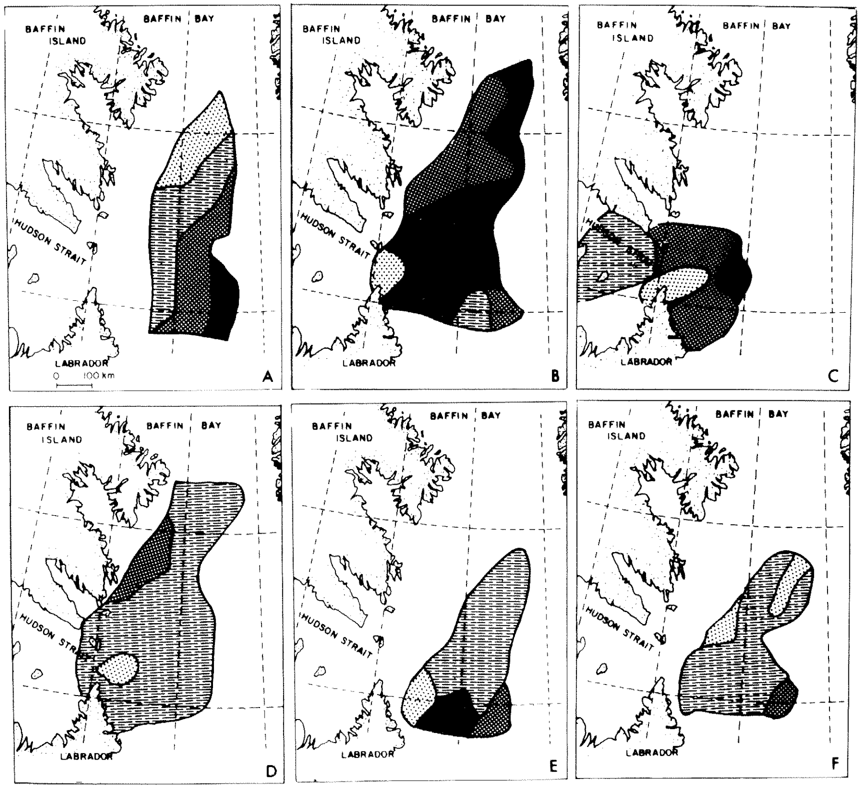

FIG. A-1. Geographical distribution of *Calanus finmarchicus* abundance (no·m^{-3}) in Apr.-May 1977 (a); June 1977 (b); Aug.-Sept. 1977 (c); Oct.-Nov. 1977 (d); Apr. 1978 (e); and May 1978 (f). Lightly stippled area: $\leq 20 \cdot m^{-3}$; hatched area: $20\text{-}100 \cdot m^{-3}$; darkly stippled area: $100\text{-}500 \cdot m^{-3}$; solid area: $\geq 500 \cdot m^{-3}$.

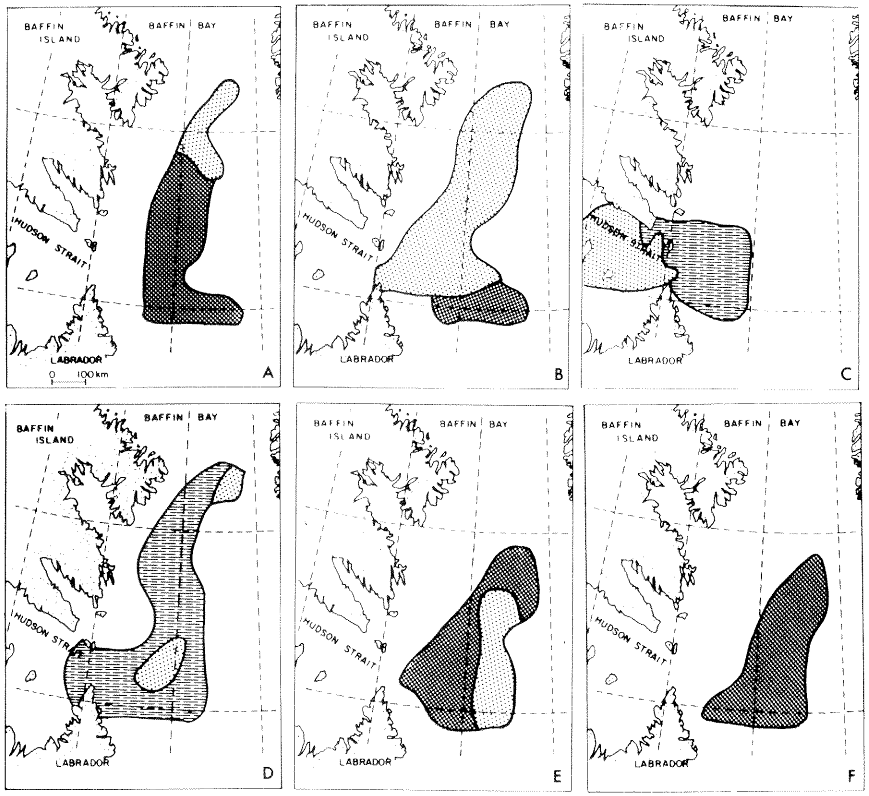

FIG. A-2. Geographical distributions of the dominant copepodite stages of *Calanus finmarchicus*. The dominant stages are those which comprised the largest portion of the population by percentage (%). Time of distribution is the same as for Figure A-1. Lightly stippled area: CI-III; hatched area: CIV-V; darkly stippled area: CVI.

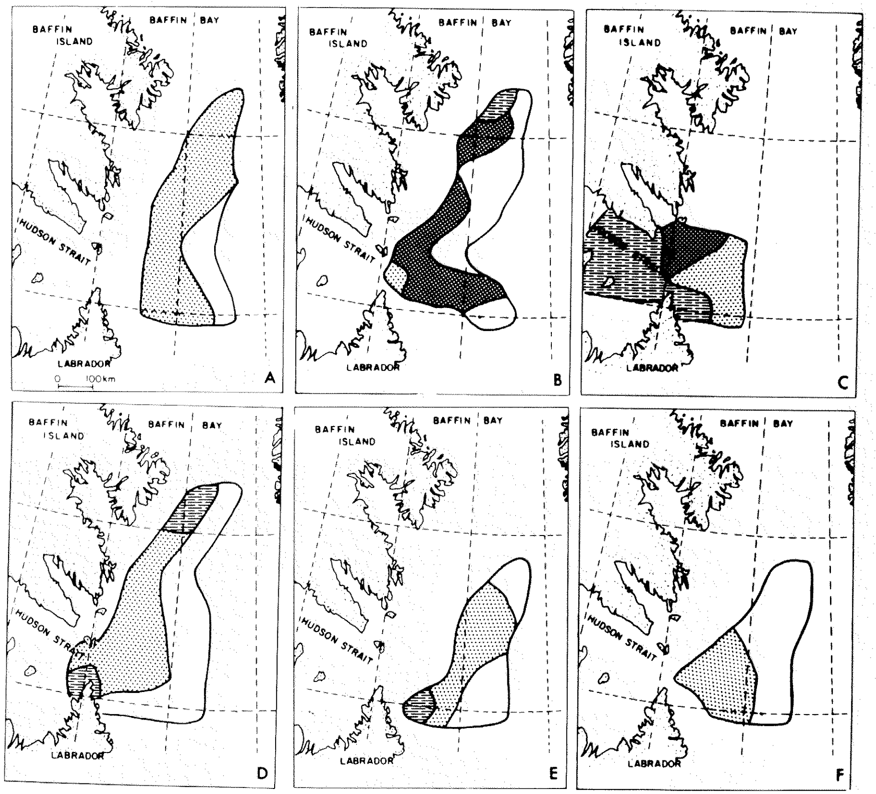

FIG. A-3. Geographical distribution of *Calanus glacialis* abundance (no·m^{-3}). Time of distribution is the same as for Figure A-1. Unshaded: 0; lightly stippled area: 1-20·m^{-3}; hatched area: 20-100·m^{-3}; darkly stippled area ≥ 100·m^{-3}.

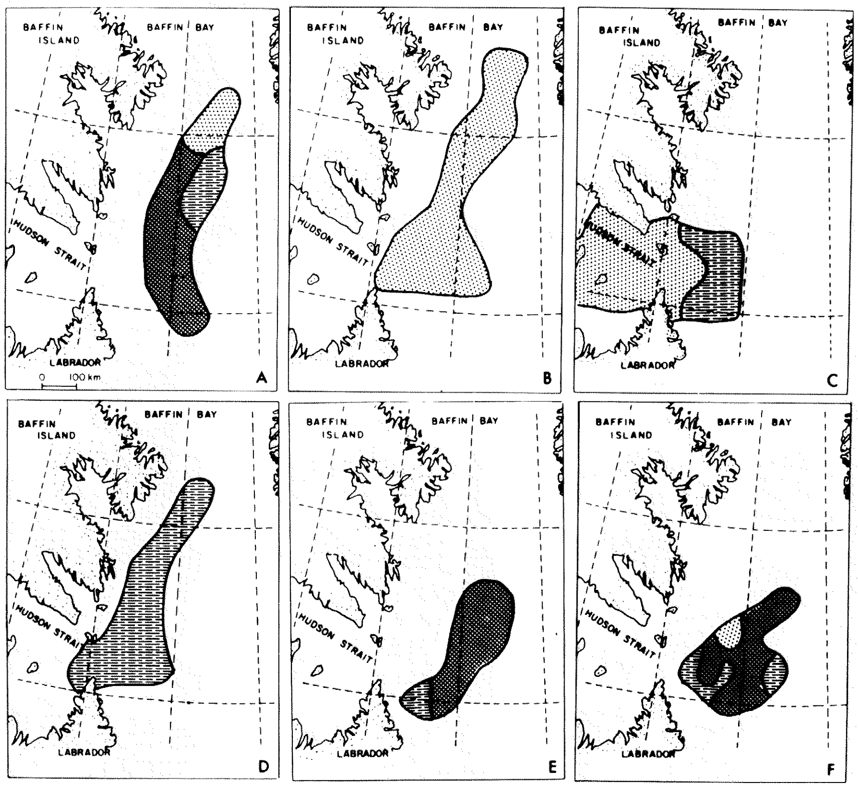

FIG. A-4. Geographical distributions of the dominant copepodite stages of *Calanus glacialis*. Time of distribution is the same as for Figure A-1. Lightly stippled area: CI-III; hatched area: CIV-V; darkly stippled area: CVI.

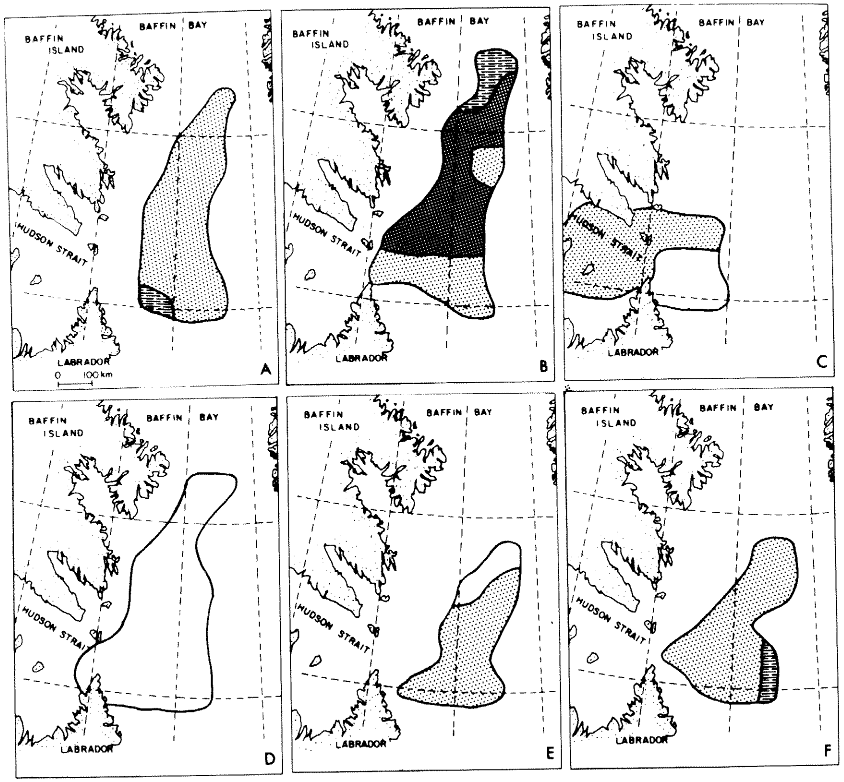

FIG. A-5. Geographical distribution of *Calanus hyperboreus* abundance (no·m^{-3}). Time of distribution is the same as for Figure A-1. Unshaded: 0; lightly stippled area: 1-20·m^{-3}; hatched area: 20-100·m^{-3}; darkly stippled area: ≥100·m^{-3}.

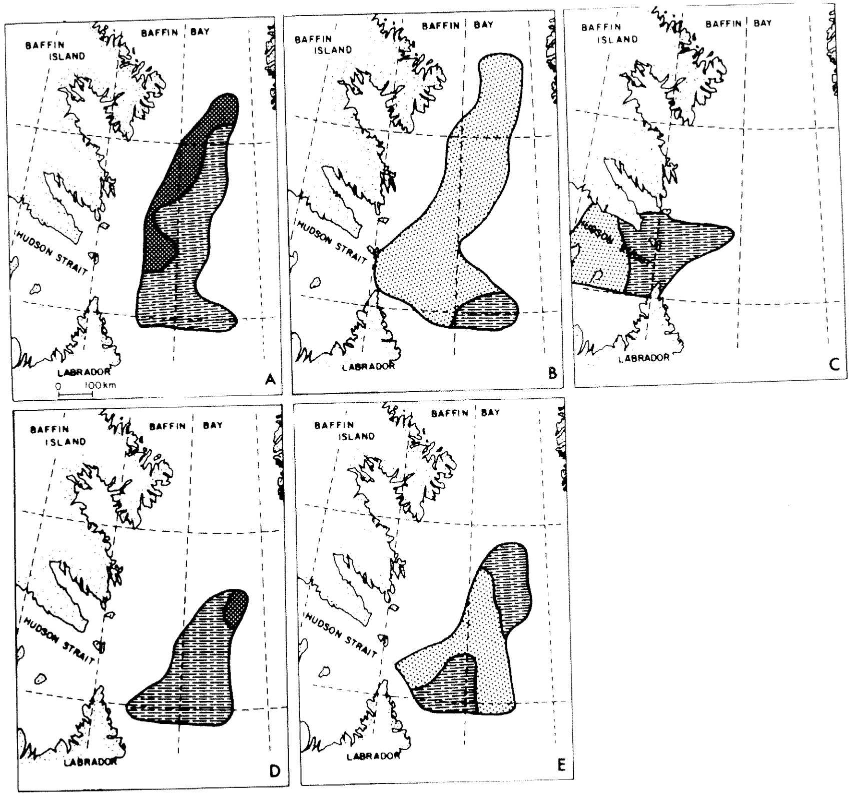

FIG. A-6. Geographical distribution of the dominant copepodite stages of *Calanus hyperboreus*. Time of distribution is the same as for Figure A-1, except not recorded in August 1977. Lightly stippled area: CI-III; hatched area: CIV-V; darkly stippled area: CVI.

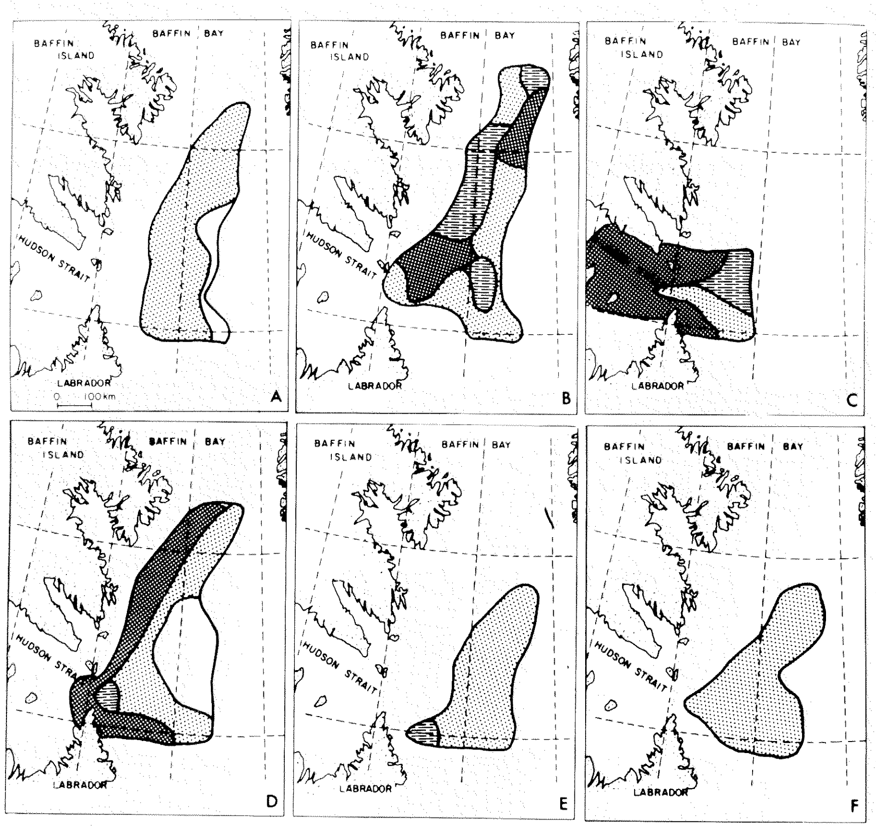

FIG. A-7. Geographical distribution of *Pseudocalanus minutus* abundance (no·m^{-3}). Time of distribution is the same as for Figure A-1. Unshaded: 0; lightly stippled area: 1-20·m^{-3}; hatched area: 20-100·m^{-3}; darkly stippled area: ≥ 100·m^{-3}.

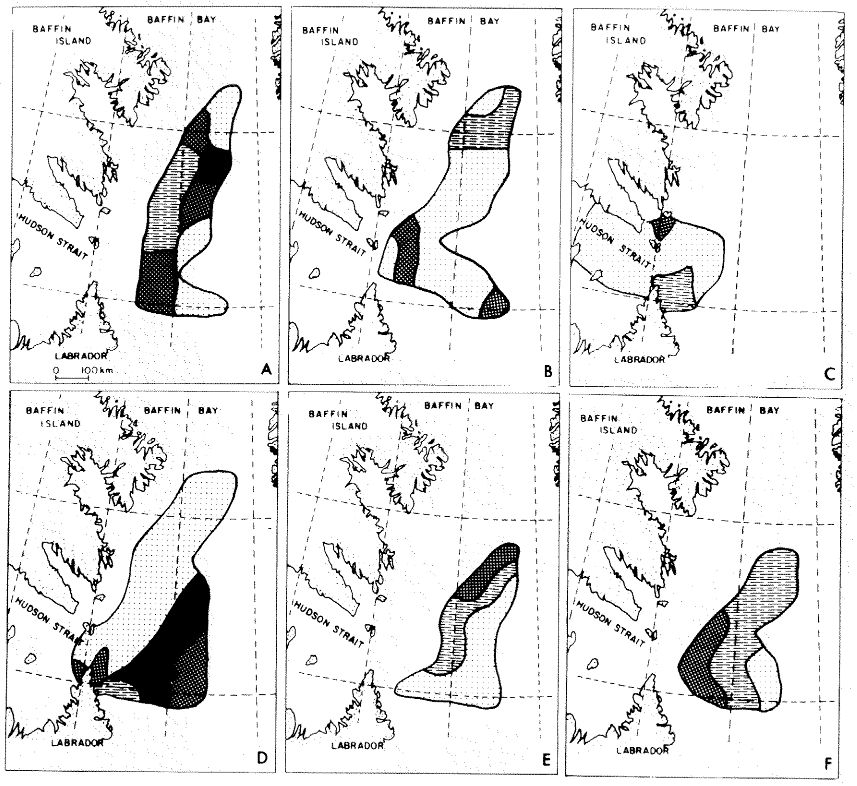

FIG. A-8. Geographical distribution of *Oithona similis* abundance (no·m^{-3}). Time of distribution is the same as for Figure A-1. Lightly stippled area: ≤20·m^{-3}; hatched area: 20-100·m^{-3}; darkly stippled area: 100-500·m^{-3}; solid area: ≥500·m^{-3}.

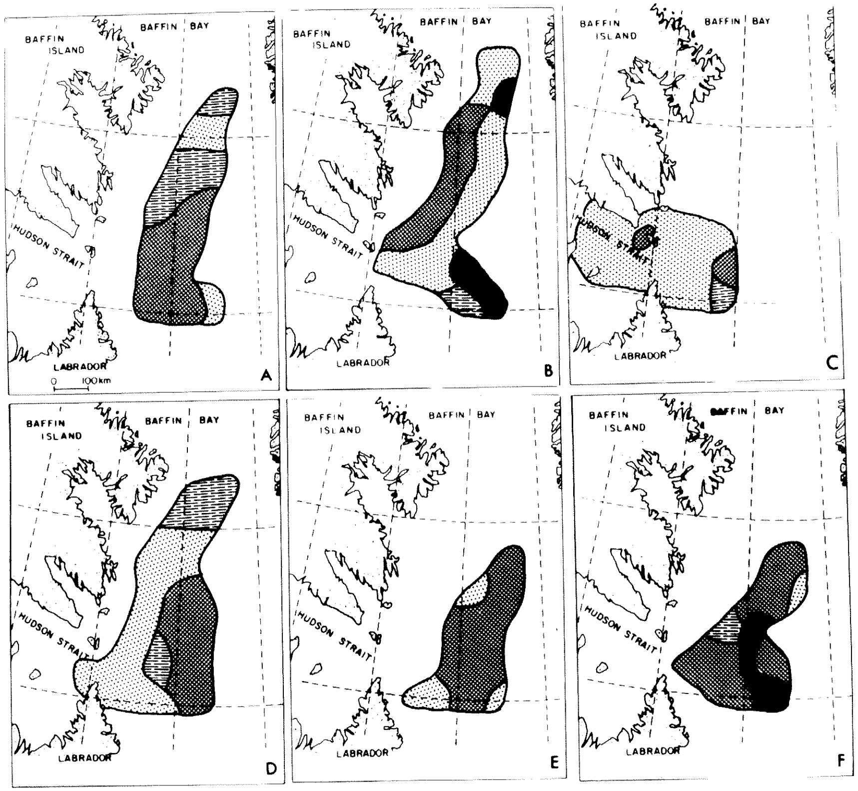

FIG. A-9. Geographical distribution of *Conchoecia obtusata* abundance (no·m^{-3}). Time of distribution is the same as for Figure A-1. Lightly stippled area: $\leq 1 \cdot m^{-3}$; hatched area: $1\text{-}5 \cdot m^{-3}$; darkly stippled area: $5\text{-}20 \cdot m^{-3}$; solid area: $\geq 20 \cdot m^{-3}$.

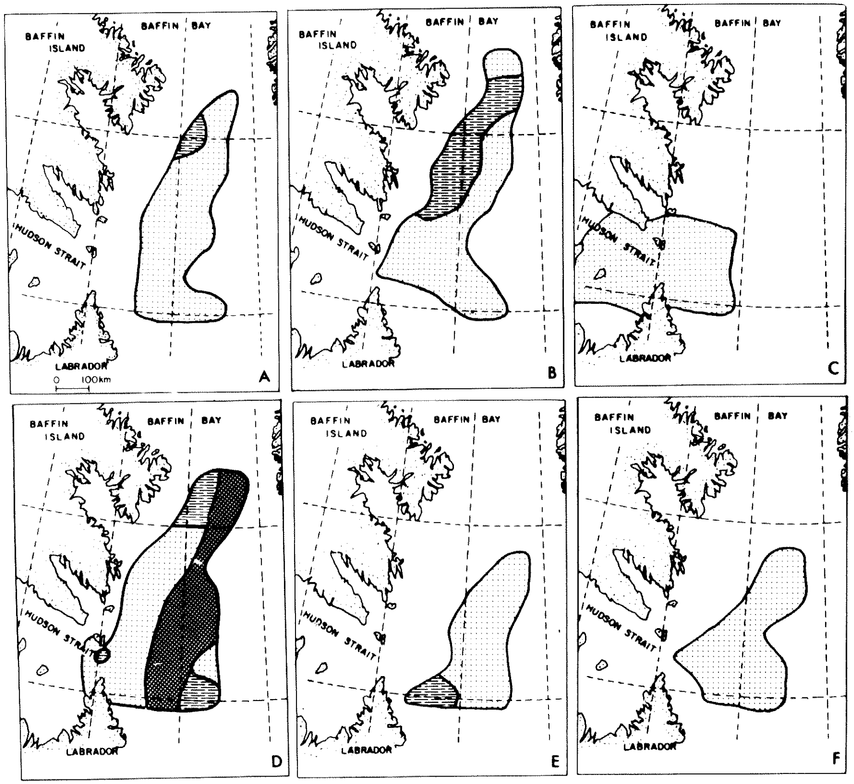

FIG. A-10. Geographical distribution of *Aglantha digitale* abundance (no·m^{-3}). Time of distribution is same as for Figure A-1. Lightly stippled area: $\leq 1 \cdot m^{-3}$; hatched area: $1\text{-}5 \cdot m^{-1}$; darkly stippled area: $\geq 5 \cdot m^{-3}$.

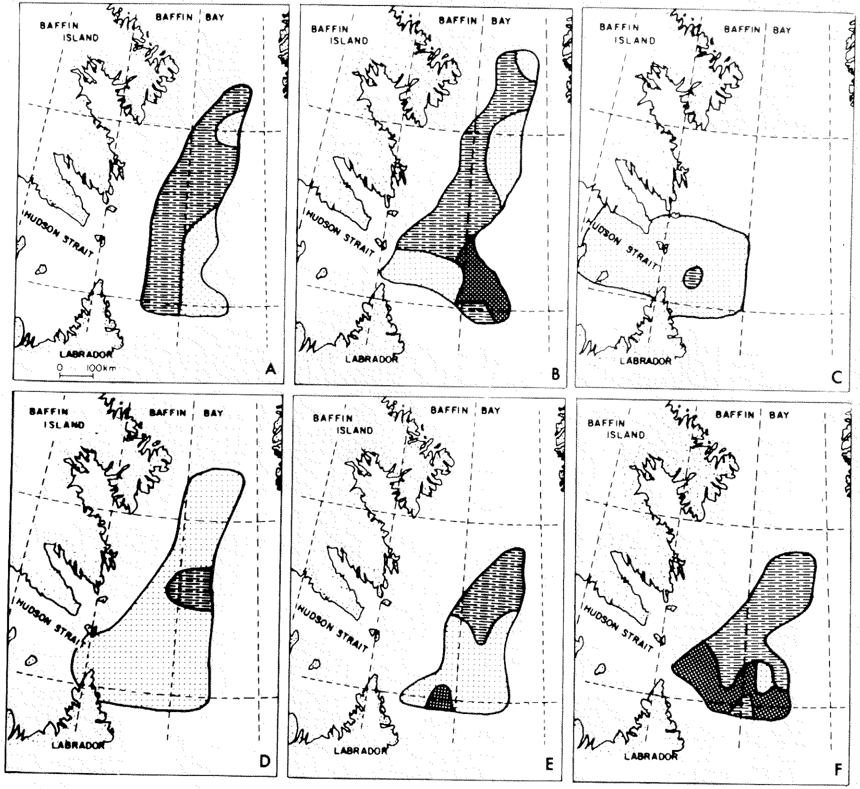

FIG. A-11. Geographical distribution of *Eukhronia hamata* abundance (no·m^{-3}). Time of distribution is the same as for Figure A-1. Lightly stippled area: ≤ 1·m^{-3}; hatched area: 1-5·m^{-3}; darkly stippled area: ≥ 5·m^{-3}.