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Distribution of zooplankton in the Northeast Water Polynya during summer 1992

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Abstract

The distribution and abundances of zooplankton in the Northeast Water (NEW) Polynya during the summer of 1992 have been determined from samples collected with Bongo (this study) and MOCNESS (earlier analysis) plankton net tows. The initial hypothesis was that the troughs of the Greenland Shelf in the region of the NEW polynya would be conduits for the infusion of zooplankton species of Arctic and North Atlantic origin on to the shelf. Analysis of MOCNESS tows indicated instead that advection of zooplankton onto the shelf in the polynya region was limited, resulting in low abundances of the large herbivores in the polynya.

The distribution of zooplankton determined from the 43 Bongo tows reported here strengthen this finding. Low abundances of the large herbivorous copepods and of other primarily herbivorous zooplankton taxa were observed throughout the ice-free region, in contrast to higher abundances observed further to the east in Westwind Trough or in the south in Belgica Trough. Cluster analysis was used to identify groups of co-occurring zooplankton taxa and groups of stations with similar relative compositions of zooplankton taxa. The community composition of the Belgica Trough was distinctly different from that observed in northern regions, with high abundances of open ocean copepods (*Calanus finmarchicus* and *C. hyperboreus*). Two types of communities were identified in the northern regions: one typical of the eastern basin (Westwind Trough) and one typical of the western basin (Norske Trough) of the northern trough. The relationship between the different zooplankton communities and the water mass characteristics was not conclusive; however, it did appear that zooplankton populations had been advected in the upper water column into the Westwind Trough from north of the study area. The low abundances of herbivorous taxa in the ice free region supported previous estimates that meso–macro zooplankton may not be significant consumers of primary production in the polynya.

Keywords: Arctic; zooplankton; ecology; oceanography; assemblages; polynya

1. Introduction

The Northeast Water Polynya, located at the northeast corner of Greenland, is a recurrent summer polynya that opens annually over the East Greenland Shelf. Polynyas may be of considerable importance

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to the overall fixation, cycling, and storage of carbon in the Arctic ecosystem, since primary and secondary production may be increased in ice-free regions (e.g., Northeast Water Steering Committee, 1993; W.O. Smith, 1995). Furthermore, since the polynya is located over a shelf region, export of carbon from the polynya may be important to shelf–slope exchange and to storage of carbon in the deep water masses of the Greenland Sea (e.g., Harrison et al., 1982; Sambrotto et al., 1984; Sarmiento et al., 1988; Anderson et al., 1990; Northeast Water Steering Committee, 1993).

The polynya is located in a region over the shelf where the topography is dominated by a deep (> 300 m) trough system intersecting shallow (< 60 m) banks (Fig. 1a). Two major troughs intersect the shelf: Westwind Trough in the north and Belgica Trough in the south. Westwind Trough continues to the south and west as Norske Trough; however, it is unclear at the present whether Norske and Belgica troughs are continuous because a semi-permanent ice shelf (Norske Øer Ice Barrier) lies over the troughs (Fig. 1a). A fairly shallow bank, Belgica Bank, lies in the center of the encircling troughs. Shallow banks (e.g., Ob Bank) also bound the region to the north. The polynya usually opens to the north of Norske Øer ice barrier in mid June, with the total extent of the ice-free area varying between years (Parkinson et al., 1987; Minnett et al., 1997-this volume). The ice-free region (Fig. 1) was small during the summer of 1992 compared with previous years (Parkinson et al., 1987; Northeast Water Steering Committee, 1993; Gudmandsen et al., 1995; Böhm et al., 1997-this volume).

The circulation of the region, as described previously, is complex and not entirely resolved (Bourke et al., 1987; Budéus and Schneider, 1995; Johnson and Niebauer, 1995; Bignami and Hopkins, 1997-this volume; T.S. Hopkins, unpubl. data). It is clear, however, that the Belgica and Norske–Westwind trough systems should be considered independent (Budéus and Schneider, 1995; Bignami and Hopkins, 1997-this volume; T.S. Hopkins, unpubl. data). The essential features of the circulation in the upper water column (0–~150 m), based on published descriptions, are presented in Fig. 1a for reference. The water masses in the study region have been variously named in previous publications; the present

study will follow the nomenclature of Bignami and Hopkins (1997-this volume). Belgica Trough is characterized by circulation of Polar Halocline Water (PHW) (also known as Knee Water (KW); e.g., Bourke et al., 1987) and underlying return Atlantic Intermediate Water (rAtIW) (also known as Return Atlantic Water (RAW); e.g., Budéus and Schneider, 1995) intruding from the East Greenland Current (EGC) system. The Norske–Westwind trough system, in contrast, is dominated (surface to approximately 120 m) by a large anticyclonic gyre consisting of locally formed Polynya Intermediate Water (PyIW) (also known as East Greenland Shelf Water; e.g., Budéus and Schneider, 1995) centered over Belgica Bank (Bourke et al., 1987; Budéus and Schneider, 1995; Johnson and Niebauer, 1995; Bignami and Hopkins, 1997-this volume). The PyIW gyre, and circulation, is continuous from the Norske Trough to the Westwind Trough with fairly high current velocities (10–20 cm/sec) in the upper water column over the troughs (Budéus and Schneider, 1995; Johnson and Niebauer, 1995; T.S. Hopkins, unpubl. data). This gyre appears to prevent significant influx of EGC water at the mouth of the Westwind Trough, at least in the upper water column. The thickness of the PyIW is greatest in the center of the gyre, decreasing towards the edges, with the contours approximately following the geostrophic circulation (Budéus and Schneider, 1995; Bignami and Hopkins, 1997-this volume; T.S. Hopkins, unpubl. data).

The zooplankton community of the Northeast Water polynya was hypothesized to consist of species of both Arctic and Atlantic origin (Northeast Water Steering Committee, 1993). Large herbivorous *Calanus* species were hypothesized to be important members of that zooplankton community and to be significant consumers of the primary production in the ice-free region. Our initial findings, based on the zooplankton abundances from the Multiple Opening and Closing Net and Environmental Sensing System (MOCNESS; Wiebe et al., 1976) tows conducted at three locations within the study region during the summer of 1992, suggested that a somewhat different situation existed (Ashjian et al., 1995). Belgica Trough was dominated by the *Calanus* species, especially the North Atlantic species *Calanus finmarchicus*. However, abundances of *C. finmarchicus* and

the Arctic *Calanus* species (*C. hyperboreus* and *C. glacialis*) were considerably reduced in northern regions relative to abundances observed in Belgica Trough and to abundances observed in previous studies in the East Greenland Current. Abundances of adult *C. hyperboreus* and *C. glacialis* were similar

to those observed in the Arctic Basin, rather than to abundances typical of the East Greenland Current (Ashjian et al., 1995 and references therein). Furthermore, early copepodite stages of the *Calanus* species were considerably less abundant in the ice-free region (Norske Trough) than in the Westwind Trough.

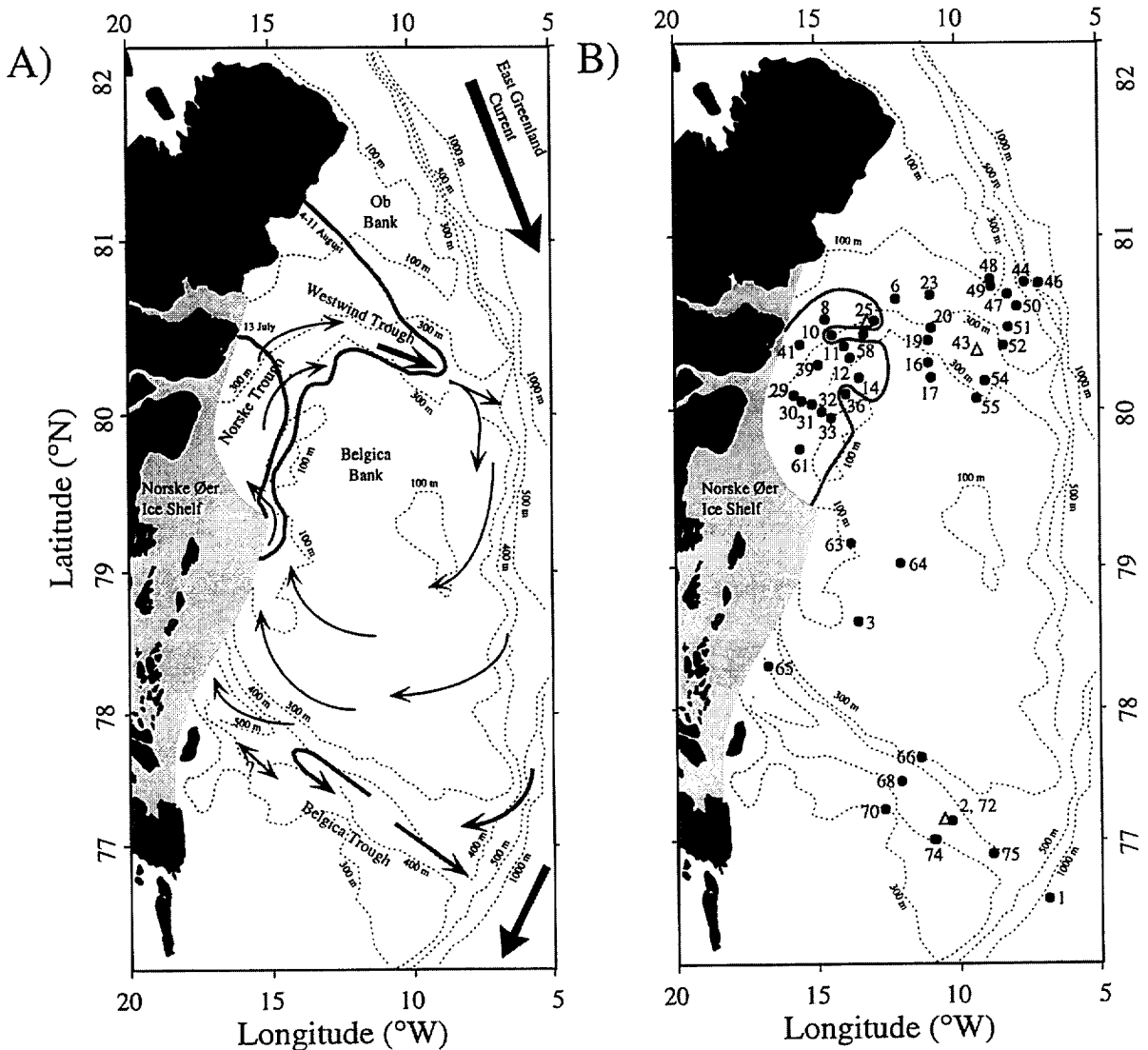


Fig. 1. (a) Shelf topography and prevailing currents in the study area, and area of polynya during the study period. Arrows indicate circulation patterns in the upper water column (upper 150 m). The approximate boundaries of the polynya (0–1/10 ice cover) near the start (July 13) and end (4–11 August) of the study period (15 July–15 August) are indicated by solid lines. Ice cover from maps provided by the Danish Meteorological Institute in Copenhagen. Bathymetry courtesy of M. Johnson. (b) Locations of the Bongo (●) and MOCNESS (Δ) tows considered in this study. Stations to the north of the Norske Øer Ice Shelf and within the solid line were characterized by less than 3/10 ice cover at the time of sampling.

Estimates of potential ingestion as a proportion of daily primary production for the *Calanus* species suggested that utilization of primary production in the polynya by these herbivores may not have been as significant as had been previously hypothesized because of their low abundance (e.g., Hirche et al., 1991; Northeast Water Steering Committee, 1993; Hirche et al., 1994; Ashjian et al., 1995; S.L. Smith, unpubl. data).

Previous conclusions were based on abundances determined from MOCNESS tows conducted at only three locations in the study region. The present study addresses the distribution of zooplankton throughout the region during the summer of 1992 using abundances of zooplankton determined from 43 vertically integrated Bongo tows, with reference to vertical distributions obtained from the vertically discrete MOCNESS tows (Fig. 1b). The locations of the Bongo tows were widely distributed throughout the study region and hence provide an effective means of mapping the distribution of the numerically important taxonomic groups of the zooplankton (Fig. 1b). The goals of the present study were to describe further the distribution of zooplankton taxa, to examine zooplankton community groups on a regional basis and identify groups of stations with similar zooplankton compositions, to compare regional patterns in abundance described using the Bongo samples with those described previously (Ashjian et al., 1995), and to identify associations between the locations of stations within a particular station group with water mass type and regional circulation.

2. Methods

Sampling was conducted on a cruise to the Northeast Water Polynya from July 15, to August 15, 1992, on USCGC *Polar Sea*. Zooplankton samples were collected from the surface to near the bottom with vertical tows using paired Bongo nets, equipped with 153 μm mesh nets, and with oblique tows using a MOCNESS net system that sampled at discrete depths, equipped with 149 μm mesh nets (Fig. 1b). Samples were preserved in 4% formalin seawater immediately following collection and were enumerated at a later date in the laboratory. In total, 58 taxonomic categories were identified. Stations were

numbered consecutively, hence higher numbers indicate locations that were sampled later in the sampling period. Further details concerning the collection and enumeration of the samples may be found in Ashjian et al. (1995) and Lane et al. (1995).

In order to reduce the complexity and number of taxonomic categories for the present analysis, abundances of adjacent life stages of the dominant copepod species (*C. finmarchicus*, *C. hyperboreus*, *C. glacialis*, *M. longa*, and *Pseudocalanus*) were summed and taxa that were not observed consistently were eliminated (reducing the number of categories to 26 from 58). The adjacent life stages to be combined were selected after consideration of both the Spearman rank coefficients between stage abundances within each species (Table 1) and the overall abundance trends of the life stages. In cases where a life stage was not clearly associated with adjacent life stages following consideration of these criteria, the life stage was not combined with others. This conservative approach was used so as not to obscure variations in abundance unique or specific to a given life stage.

Groups of co-occurring zooplankton taxa were identified from abundances determined from the Bongo tows using agglomerative hierarchical cluster analysis with the average distance method in the Statistical Analysis System (SAS; SAS Institute Inc., 1985). Several types of input matrices were considered, including log transformed species' abundances and between-species Spearman rank order coefficients. The Spearman rank order coefficients were modified by subtracting the coefficient from 1 in order to be of the correct sense for the distance algorithm. Total abundances of the taxa varied over several orders of magnitude ($100\text{--}10,000\text{ m}^{-2}$) so that input matrices based on abundances or log (abundances) of all taxa were biased by the abundances of the small sized, extremely numerous taxa (e.g., *Oithona*, *Oncaea* and nauplii). These matrices were not useful. The taxonomic groups ultimately were defined using an 26×26 matrix of modified Spearman coefficients. An additional criterion considered in the selection of a method for identification of groups of stations with similar zooplankton composition was that the method selected should differentiate stations located in Belgica Trough from stations at other locations because the taxonomic com-

position of stations in Belgica Trough were markedly different (e.g., Ashjian et al., 1995; Lane et al., 1995). Groups of stations with similar zooplankton composition were identified using an input matrix (43 stations \times 13 copepod types) of log-transformed abundances of the major copepod types (*Calanus*, *Metridia* and *Pseudocalanus*; life stages summed as described above). Dendrograms from the two cluster analyses were constructed using SAS.

The depths of the abundance maximum for each taxonomic group from six MOCNESS tows (day-

night pair each at stations 25, 43 and 72) were determined to demonstrate the vertical distributions of the taxa (see also Ashjian et al., 1995; Lane et al., 1995).

Temperature and salinity profiles were obtained from each station during the cruise using a Neil Brown Instrument Systems Mark III CTD. From these data, the thickness (in meters) of the characteristic locally formed polynya water mass (Polynya Intermediate Water; core values of -1.7°C , 32.2–32.3 PSU) and the freshwater content (indicative of

Table 1
Spearman rank order coefficients between life stages of five copepod species

Stage	Adult female	Adult male	Copepodite stage				
			V	IV	III (I–III)	II	I
<i>Calanus finmarchicus</i>							
Adult female	1	–					
Copepodite stage V	0.677 ^b	–	1				
Copepodite stage IV	0.278	–	0.349 ^a	1			
Copepodite stage III	0.001	–	0.235	0.352 ^a	1		
Copepodite stage II	–0.153	–	–0.003	0.134	0.252	1	
Copepodite stage I	0.049	–	0.184	0.027	–0.101	0.305 ^a	1
<i>Calanus glacialis</i>							
Adult female	1	–					
Copepodite stage V	0.506 ^a	–	1				
Copepodite stage IV	–0.221	–	0.154	1			
Copepodite stage III	–0.293	–	0.091	0.572 ^b	1		
Copepodite stage II	0.262	–	0.529 ^b	0.053	0.522 ^b	1	
Copepodite stage I	0.326 ^a	–	0.614	0.047	0.448 ^a	0.89 ^b	1
<i>Calanus hyperboreus</i>							
Adult female	1	–					
Copepodite stage V	0.53 ^b	–	1				
Copepodite stage IV	0.3	–	0.428 ^a	1			
Copepodite stage III	0.067	–	0.044	0.146	1		
Copepodite stage II	0.114	–	0.077	0.199	0.711 ^b	1	
Copepodite stage I	0.156	–	0.198	0.097	0.431 ^a	0.745 ^b	1
<i>Metridia longa</i>							
Adult female	1	–					
Adult male	0.599 ^b	1					
Copepodite stage V	0.657 ^b	0.567 ^b	1				
Copepodite stage IV	0.418 ^a	0.577 ^b	0.625 ^b	1			
Copepodite stages I–III	0.424 ^a	0.668 ^b	0.496 ^b	0.387 ^a	1		
<i>Pseudocalanus</i> sp.							
Adult female	1	–					
Copepodite stage V	0.383 ^a	–	1				
Copepodite stage IV	0.178	–	0.423 ^a	1			
Copepodite stages I–III	0.04	–	0.427 ^a	0.304 ^a	1		

Abundances from the 43 Bongo tows were used to calculate the coefficients.

^a Coefficient significant at the $p < 0.05$ level ($n = 43$, two tailed); ^b coefficient significant at the $p < 0.001$ level (Zar, 1984).

Italics = adjacent life stages within a species that were combined on the basis of Spearman rank order coefficients and/or species abundance trends.

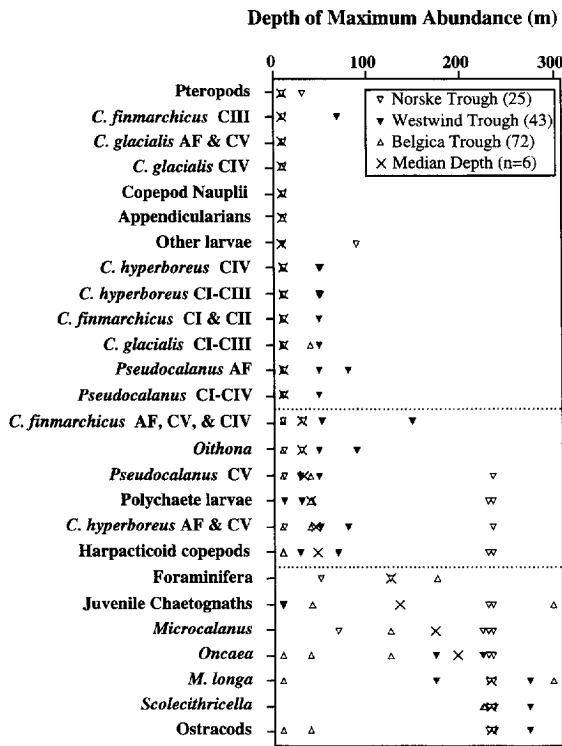


Fig. 2. Vertical distribution of the zooplankton taxa. The depth of maximum abundance for each taxon for each of six MOCNESS tows and the median depth of maximum abundance for the six tows are shown. The MOCNESS tows considered were tows 25A and 25C, 43A and 43D, and 72A and 72C (Ashjian et al., 1995); station numbers for each of the three troughs are indicated. The taxa are ordered by the median depth of maximum abundance. Dashed lines indicate separation between shallow (0–20), intermediate (20–100), and deep (> 100 m) taxa. Depths correspond to selected depth limits sampled during the MOCNESS tows (Ashjian et al., 1995; Lane et al., 1995).

the total freshwater input to the surface layer during the summer) were calculated. (The freshwater content represents the calculated quantity of freshwater,

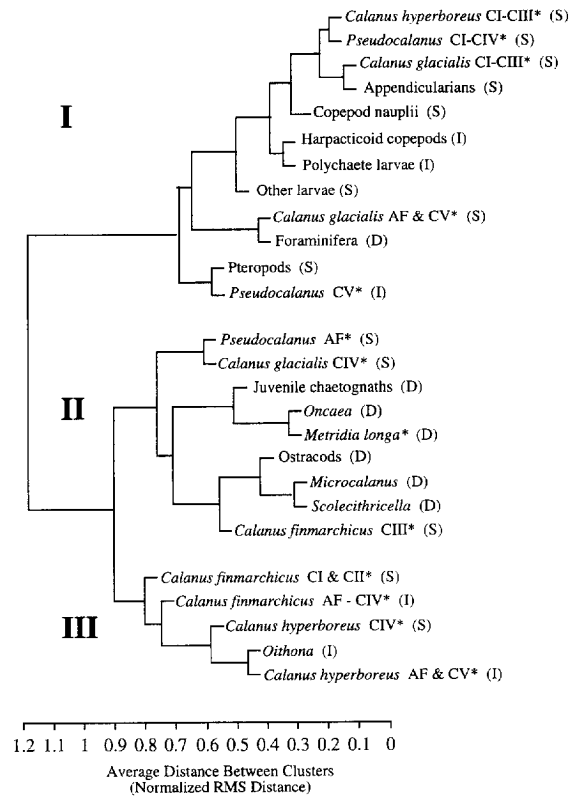
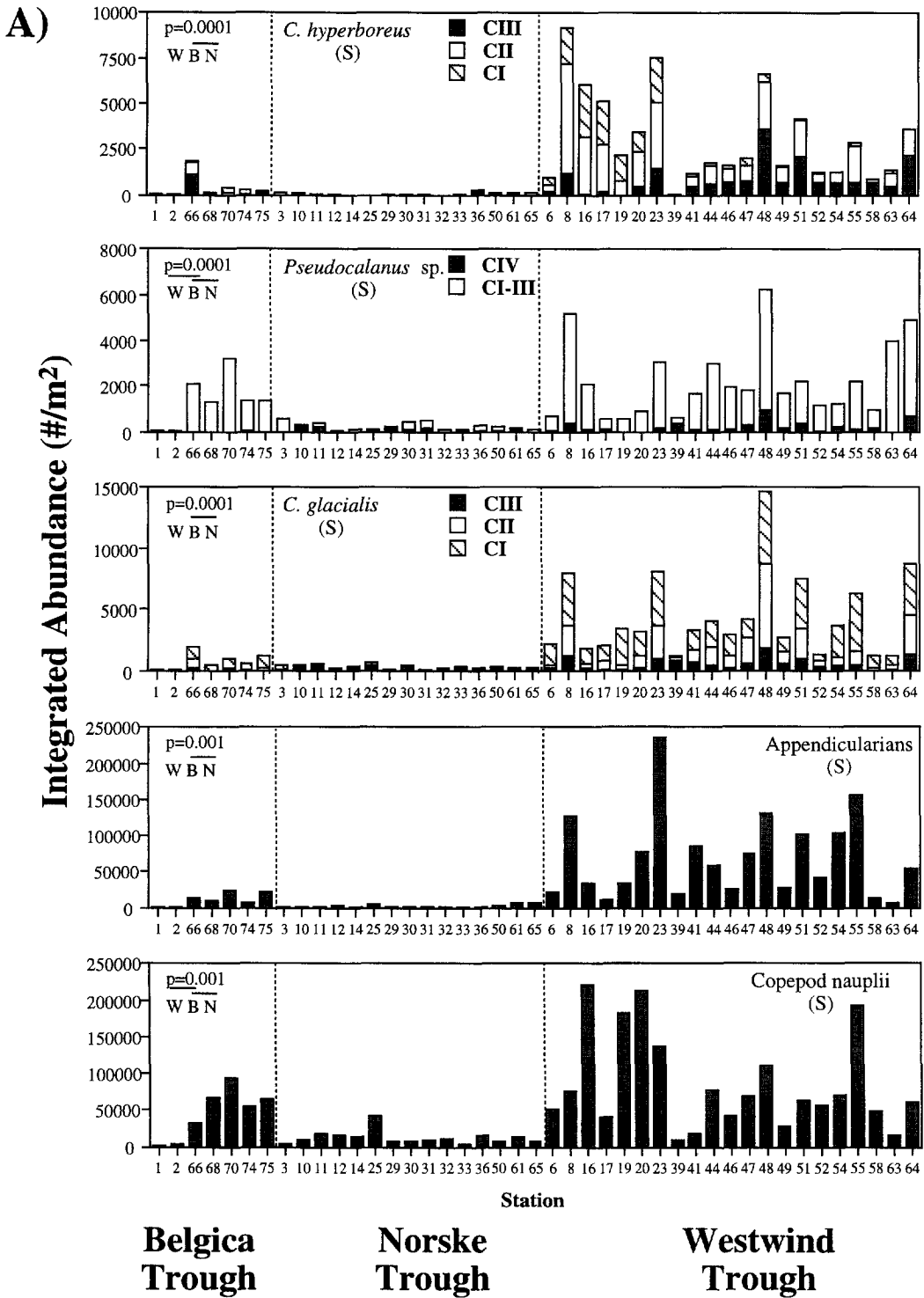
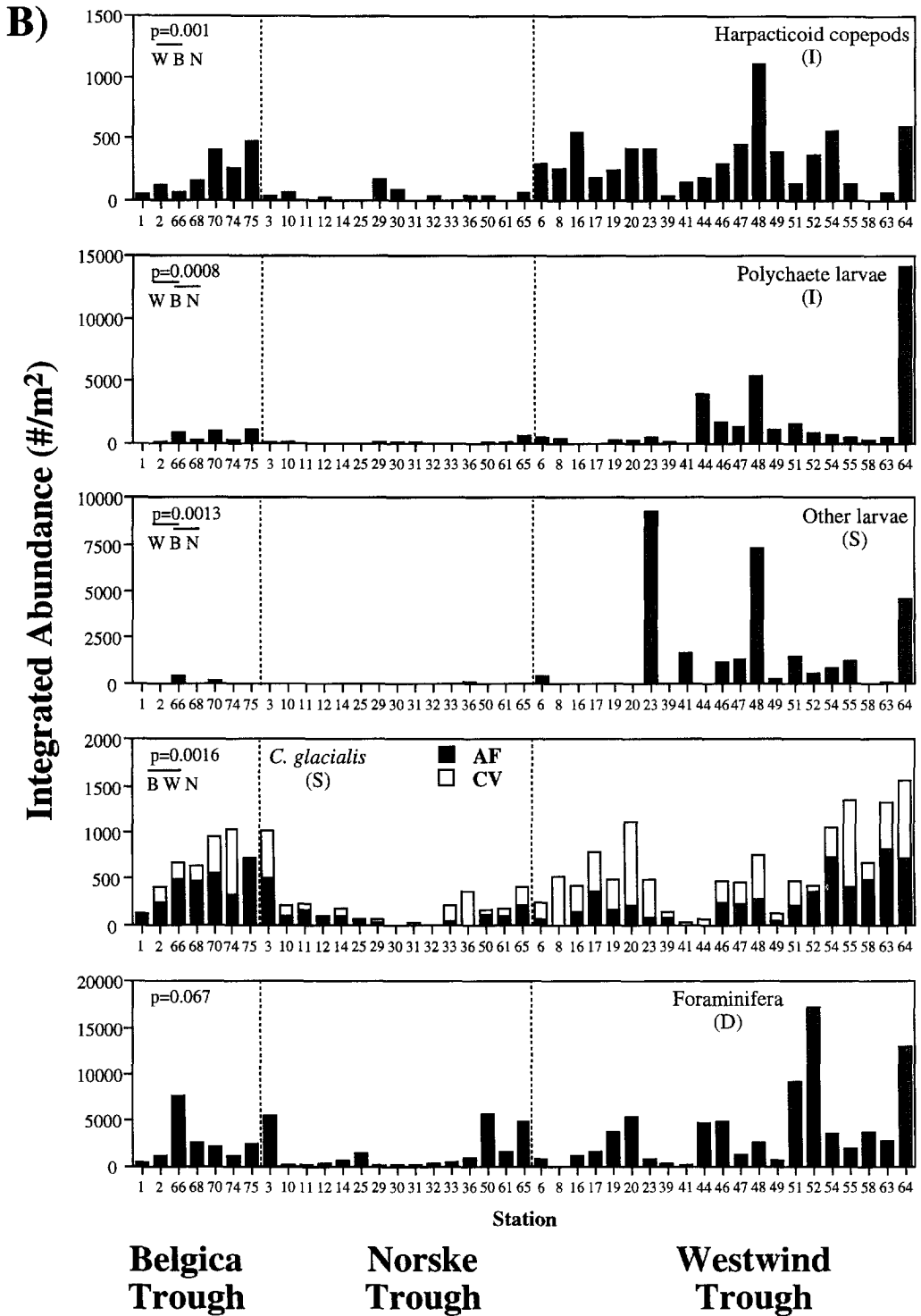


Fig. 3. Dendrogram demonstrating result of cluster analysis of the taxa enumerated in the 43 Bongo tows. Asterisks identify taxa used in subsequent cluster analysis to classify stations on the basis of taxonomic composition. Taxa are identified as having shallow (S), intermediate (I), or deep (D) vertical distributions on the basis of the median depth of maximum abundance from six MOCNESS tows (Fig. 2).

expressed as vertical meters, that diluted the upper water column from the core salinity to the observed salinity (Schneider and Budéus, 1994; Bignami and Hopkins, 1997-this volume)). Further details concerning collection and reduction of these data may

Fig. 4. Integrated abundances of the 26 taxa from the Bongo tows, plotted as a function of station type (Belgica Trough, Norske Trough, or Westwind Trough type). (A)–(C) Taxa from zooplankton Group I. (D) and (E) Taxa from zooplankton Group II. (F) Taxa from zooplankton Group III. Taxa within each zooplankton group are ordered according to their order in the species group dendrogram (Fig. 3). Station number indicated on horizontal axis; stations ordered numerically within each group of stations. Dashed lines indicate station groupings. For taxa where abundances of adjacent life stages were summed, abundances of individual life stages are shown; statistical analyses were performed on total abundances of the adjacent life stages. Results of Kruskal–Wallis test (p) to identify differences in abundance between station groups indicated for each taxon. For taxa with significant differences in abundance between station groups ($p < 0.05$ or better), results of Tukey-type non-parametric multiple comparisons are shown, with the horizontal lines across adjacent symbols indicating station groups with no significant difference in abundances ($p < 0.05$) (W = Westwind, B = Belgica, N = Norske).





be found in Wallace et al. (1995) and Bignami and Hopkins (1997-this volume). Description of the acoustic Doppler current profiler velocities and water mass characteristics may be found in Johnson and Niebauer (1995) and Bignami and Hopkins (1997-this volume).

3. Results

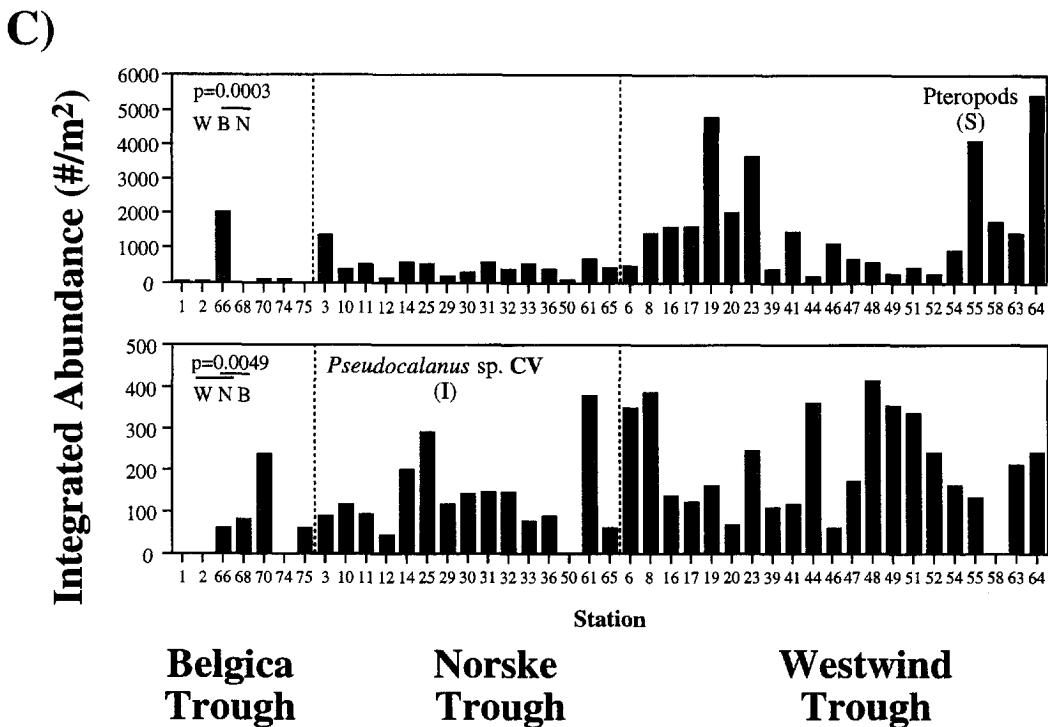
3.1. Vertical distribution of taxa

Three general types of vertical distributions were observed in the MOCNESS data: taxa found primarily at surface depths (0–20 m), taxa found below 100 m and taxa with an intermediate distribution (20–100 m). Depths were selected based on median depth of maximum abundance for six MOCNESS tows (Fig. 2). The younger stages of *Calanus* and *Pseudocalanus* were found in the upper water column, as were the copepod nauplii, appendicularians, pteropods, older stages of *C. glacialis* and *Pseudocalanus*, and all stages of *Oithona*. Of these taxa, some showed strong fidelity to the upper 20 m, while

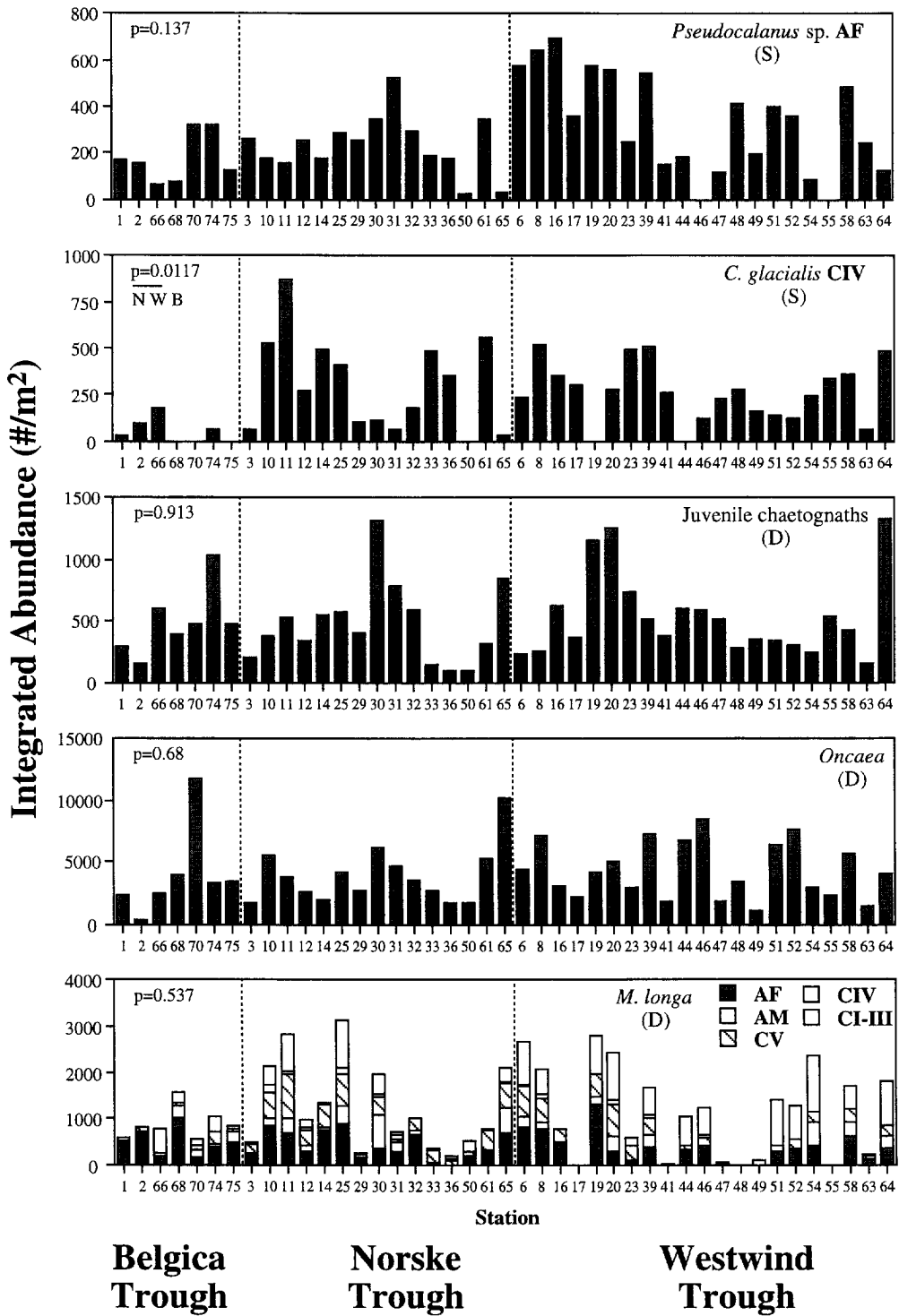
others occasionally had abundance maxima deeper in the water column. Among these taxa were groups that had previously been observed to be associated with the depth of the chlorophyll maximum (e.g., *Calanus* copepodites) (Ashjian et al., 1995). Taxa found deeper in the water column (> 100 m) included all stages of *M. longa*, *Oncaea* and *Microcalanus*, the ostracods, the juvenile chaetognaths, and the foraminifera. Abundance maxima for these species rarely were observed at depths less than 100 m. Taxa demonstrating more variable or intermediate depth distributions (average depths of maximum abundance 50–100 m) included the older life stages of *C. hyperboreus* and *C. finmarchicus* and *Pseudocalanus* CV, as well as harpacticoids and polychaete larvae.

3.2. Groups of co-occurring taxa

Three major groups of co-occurring taxa were defined using cluster analysis (Fig. 3). Notable members of Group I were the younger life stages of the Arctic copepod species *Calanus glacialis*, *C. hyperboreus*, and *Pseudocalanus*, the older stages of *C.*



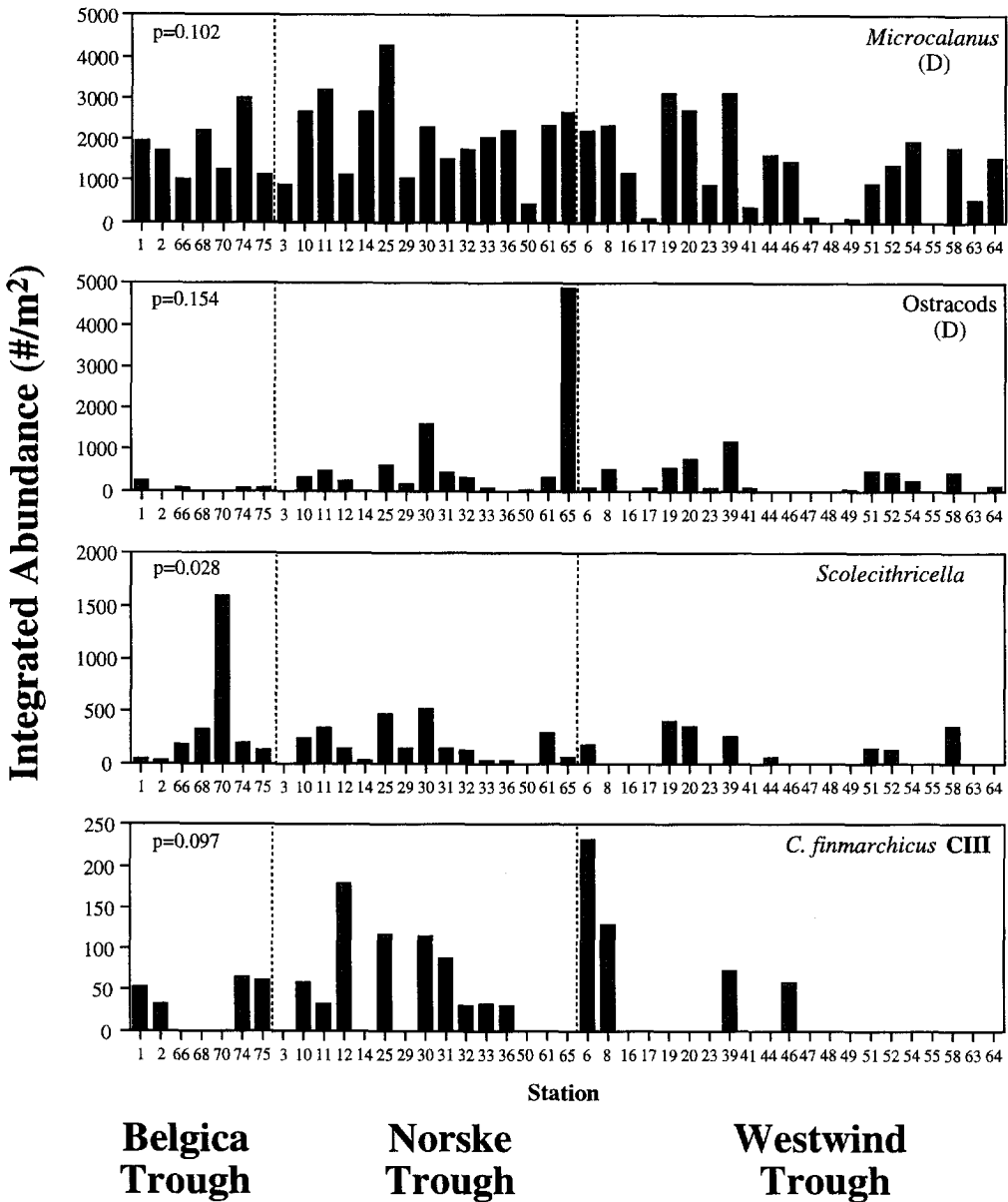
D)



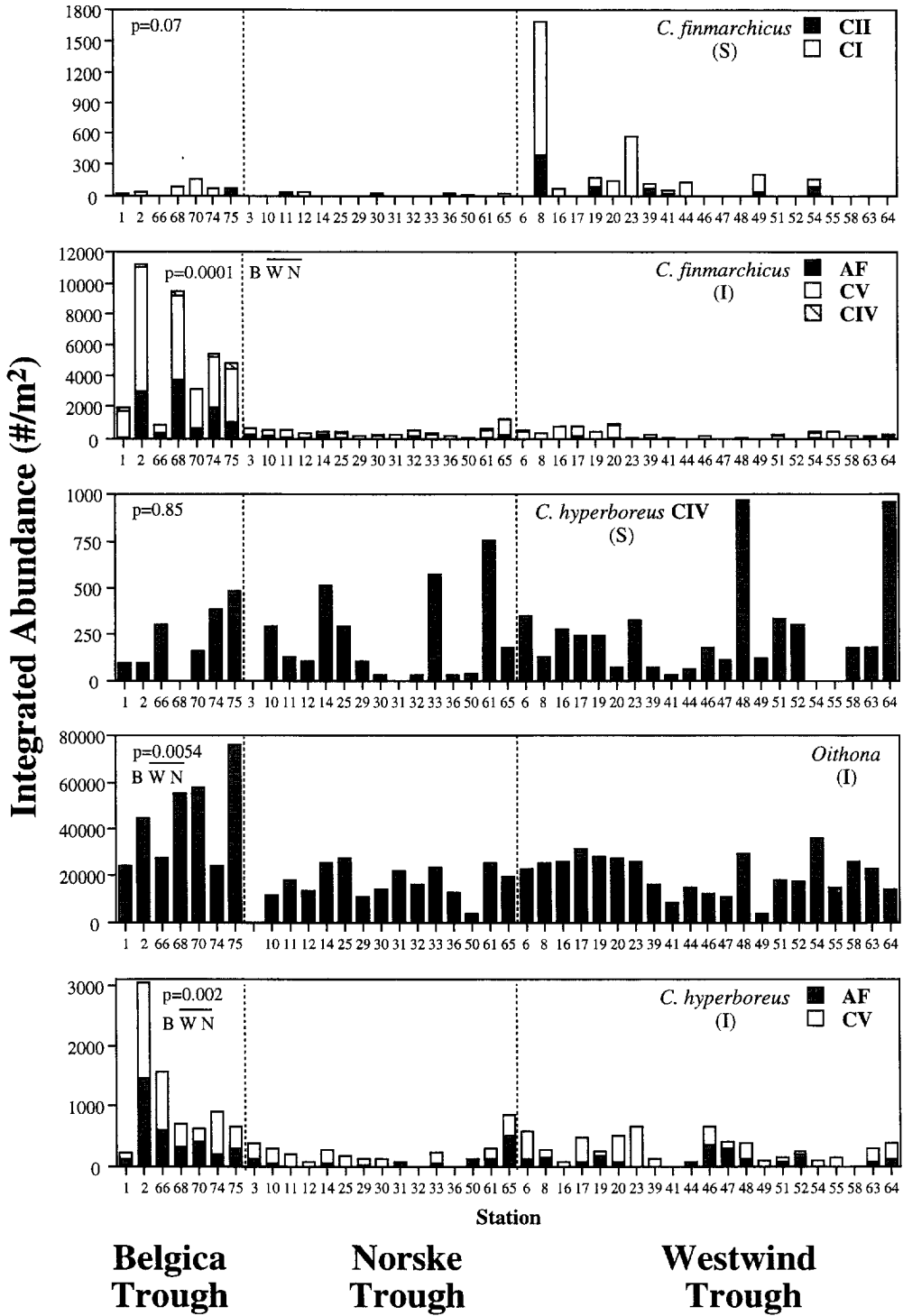
glacialis, and copepod nauplii, appendicularians, and pteropods. Most members of this group (8 of 12) were found in the upper portion (< 50 m) of the water column (Fig. 2) and are primarily herbivorous (e.g., Deibel, 1988; S.L. Smith and Schnack-Schiel, 1990; Deibel and Acuña, 1994). The taxa within the group generally exhibited similar regional abundance

patterns (Fig. 4). Group II was composed mainly (6 of 9) of taxa usually found deeper in the water column (100–150 m) (Fig. 2), many of which are considered to be omnivorous (e.g., Perueva, 1984; Paffenhöfer, 1993). The taxa included in this group that were not found at depth were either only loosely associated (*Pseudocalanus* AF and *C. glacialis* CIV)

E)



F)



or were found in especially low abundance in the samples (Fig. 4). This group did not demonstrate a consistent regional abundance pattern. Group III was composed of life stages of the North Atlantic copepod *C. finmarchicus*, *Oithona*, and older life stages of *C. hyperboreus*. These taxa are both omnivorous and herbivorous (S.L. Smith and Schnack-Schiel, 1990; Paffenhöfer, 1993) and had broad vertical distributions with abundance maxima in the upper 100 m (Fig. 2; Ashjian et al., 1995). Most of these species were abundant only in Belgica Trough (Fig. 4).

3.3. Groups of stations

Three major groups of stations with similar taxonomic compositions were identified from the cluster analysis (Fig. 5): a group with stations located in Belgica Trough; a group with most stations located in Norske Trough but including two locations south of the Norske Øer ice shelf and a single station in the Westwind Trough; and a group with most stations located in Westwind Trough but including four stations located in Norske Trough and two stations located over Belgica Bank. The Norske Trough stations were located in the region where the polynya (ice-free region) had originated and that had been ice-free for the period of the cruise (Fig. 1). The three groups of stations are referred to as the Belgica Trough Group, the Norske Trough Group, and the Westwind Trough Group, respectively, although the groupings are based on similarity in taxonomic compositions between stations and not geographic location.

3.4. Species abundances as a function of location and group

The abundance of most zooplankton taxa (Fig. 4) varied according to the regional location of the sample (identified by the station group; Fig. 5) and the vertical distribution of the taxa under consideration (Fig. 2). Although the groupings of stations with similar taxonomic compositions were determined based on the abundances of only 13 taxonomic groups (the life stages of *Calanus*, *Pseudocalanus*, and *Metridia*), the abundances of most taxa within a particular taxonomic group (Fig. 3) demonstrated

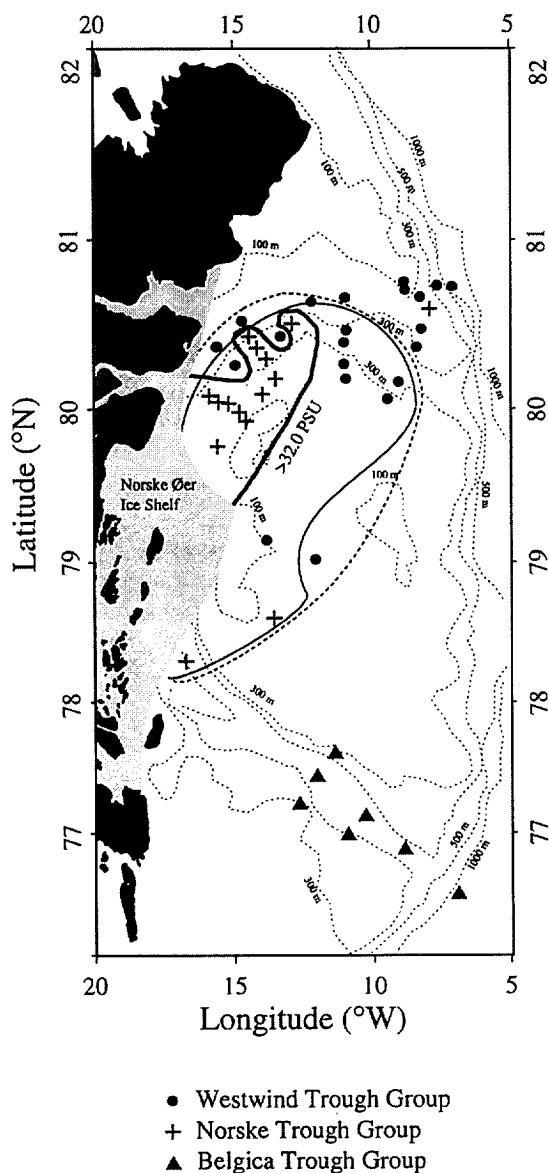


Fig. 5. Geographic locations of the three types of station identified by the cluster analysis on the basis of log transformed abundances of selected taxa, thickness of the Polynya Intermediate Water (PyIW), and surface salinity. Stations were identified as being typical of the Norske Trough (+), Westwind Trough (●), or Belgica Trough (▲). PyIW thickness shown as hand-drawn contours of > 30 m (dashed line) and > 50 m (solid line) thickness. Stations within the heavy line were characterized by surface salinity of greater than 32.00 PSU.

similar regional trends (Fig. 4). Many of the taxa exhibited significant differences in abundance among the three groups of stations (Kruskal–Wallis test; Zar, 1984). There was significant concordance ($p < 0.001$; Kendall's coefficient of concordance (W); Zar, 1984) between ranks of abundances within both Group I and Group III for all taxa exhibiting significant differences in abundance (Kruskal–Wallis results), indicating that taxa within those groups followed similar regional abundance trends.

Group I taxa had high abundances at locations typical of the Westwind Trough. This was especially evident for appendicularians, and the copepodite stages I–III of the Arctic *Calanus* species. Abundances were greatest in Westwind Trough for *C. glacialis* CV and AF, copepod nauplii, and the younger stages of *Pseudocalanus* as well; however, these taxa also were abundant in Belgica Trough. Almost all Group I taxa demonstrated significant differences ($p < 0.05$) in abundance between the three regions, with either Westwind Trough type station being significantly greater in abundance than the locations typical of the other two regions or with the Norske Trough type station being of lower abundance than the other two regions (Tukey-type non-parametric multiple comparison, $p < 0.05$ or better; Zar, 1984) (Fig. 4). With one exception (*Pseudocalanus* CV), all taxa within Group I had very low abundances at those stations typical of Norske Trough.

Group II taxa showed little consistent regional variation in abundance and were generally found in similar abundance at most locations. The abundances of some taxa (*M. longa* and *C. glacialis* CIV) appeared reduced in Belgica Trough relative to other locations (significant for *C. glacialis* CIV).

Group III taxa either had elevated abundances in Belgica Trough (*C. hyperboreus* AF and CV, *C. finmarchicus* CIV–AF and *Oithona*) (Kruskal–Wallis, Tukey-type non-parametric multiple comparison, $p < 0.05$ or better) or showed little regional trend in abundance (*C. hyperboreus* CIV, *C. finmarchicus* CI and CII).

3.5. Associations of the groups of stations and zooplankton taxa with water mass characteristics

The thickness of the Polynya Intermediate Water (PyIW) was utilized as a proxy to describe the

location of the PyIW gyre relative to the geographical locations of the stations in the three groups (Fig. 5). The description and definition of the thickness of the PyIW is discussed in detail in Bignami and Hopkins (1997–this volume); these data are used in the present study only to indicate whether a particular station was located within the locally formed PyIW and to determine whether any correlation existed between the abundances of zooplankton taxa and the PyIW gyre. Belgica Trough locations, which were clearly differentiated from the northern stations in terms of zooplankton taxonomic composition and relative abundance, were outside of the anticyclonic gyre centered on Belgica Bank. A similar distinction between the Norske Trough and Westwind Trough groups of stations was not possible. Most of the Norske Trough type stations were located within the PyIW core. However, Westwind Trough stations were located both inside and outside of the PyIW. Locations over Belgica Bank were identified as being similar to either the Norske or the Westwind type stations (on the basis of taxonomic composition); however, all were within the PyIW core. Station 65 (south of Norske Øer ice barrier) was clearly similar in composition to stations located to the north of the

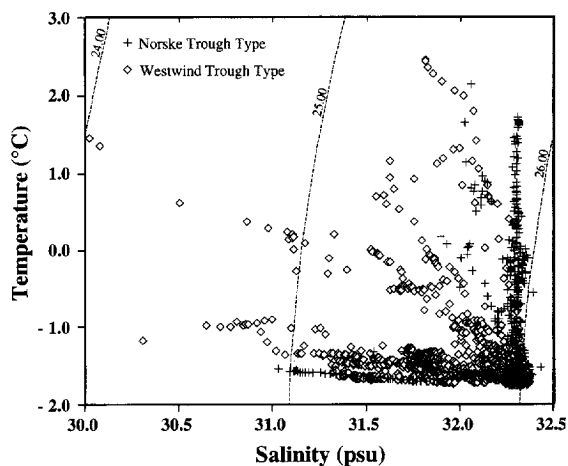


Fig. 6. Temperature/salinity plot for the CTDs conducted at each Bongo station in the northern region. Only data from the upper 50 m are presented. Data from the different station types identified by the two symbols. Constant density lines (sigma-theta units) are shown as dashed lines. Data averaged over 1 m depth intervals, from 2 to 50 m; 49 data points plotted for each CTD.

ice barrier, consistent with the presence of PyIW water south of the ice barrier (established by the physical data; e.g., Budéus and Schneider, 1995; Bignami and Hopkins, 1997-this volume) and suggesting that continuity in circulation existed at some depths along the Norske Trough.

The definitive difference in zooplankton composition between the Norske Trough and Westwind Trough station groups was the elevated abundance of the shallow-living Group 1 taxa (Figs. 2 and 4). Accordingly, the T/S (temperature–salinity) signatures for the upper 50 m of the stations in the northern region were considered (Fig. 6) to identify

different water mass characteristics in that depth interval for the station groups. A distinction between stations characteristic of Westwind Trough and those characteristic of Norske Trough was observed, with a few stations exhibiting intermediate conditions. Most locations exhibited similar T/S characteristics at depth (50 m), which were typical of the PyIW (-1.7°C , 32.2–32.3 PSU) (Bignami and Hopkins, 1997-this volume); significant differences were observed between the two types of stations upper water column (< 50 m). Locations characteristic of Westwind Trough had consistent temperatures (~ -1 to -2°C) but became fresher in the surface layers (with

Table 2

Spearman rank order coefficients between zooplankton taxa abundances and integrated water column chlorophyll (0–100 m) and freshwater content of the upper water column for stations outside of Belgica Trough (Fig. 5) and between zooplankton taxa abundances and the thickness of the PyIW water mass for all stations

Zooplankton taxon	Integrated chlorophyll $n = 29$ (mg/m^2)	Freshwater content $n = 36$ (m)	PyIW thickness $n = 43$ (m)
Group I			
<i>Calanus hyperboreus</i> CI–CIII	0.451 ^a	0.532 ^c	–0.177
<i>Pseudocalanus</i> CI–CIV	0.366	0.471 ^b	–0.321 ^a
<i>Calanus glacialis</i> CI–CIII	0.411 ^a	0.455 ^b	–0.167
Appendicularians	0.439 ^a	0.530 ^c	–0.215
Copepod nauplii	0.455 ^a	0.443 ^b	–0.174
Polychaete larvae	0.018	0.404 ^a	–0.505 ^c
Harpacticoid copepods	0.422 ^a	0.397 ^a	–0.400 ^b
Other larvae	0.387	0.313	–0.334 ^a
<i>Calanus glacialis</i> CV and AF	0.177	0.497 ^c	–0.073
Foraminifera	–0.296	0.516 ^c	–0.205
Pteropods	0.136	0.444 ^b	0.442 ^c
<i>Pseudocalanus</i> CV	0.368	0.182	–0.003
Group II			
<i>Pseudocalanus</i> AF	0.454 ^a	0.164	0.314
<i>Calanus glacialis</i> CIV	0.290	–0.234	0.363 ^a
Juvenile chaetognaths	–0.177	0.114	0.527
<i>Oncaea</i>	–0.129	0.206	–0.031
<i>Metridia longa</i>	–0.040	0.236	0.124
Ostracods	–0.039	0.141	0.262
<i>Microcalanus</i>	–0.144	–0.094	0.178
<i>Scolecithricella</i>	–0.122	–0.180	0.105
<i>Calanus finmarchicus</i> CIII	0.103	–0.237	0.005
Group III			
<i>Calanus finmarchicus</i> CI and CII	0.331	0.175	–0.228
<i>Calanus finmarchicus</i> CIV–AF	–0.191	0.126	0.057
<i>Calanus hyperboreus</i> CIV	–0.136	0.106	–0.075
<i>Oithona</i>	–0.167	0.157	–0.053
<i>Calanus hyperboreus</i> CV and AF	–0.136 ^a	0.299	–0.338 ^a

Zooplankton taxa ordered according to zooplankton group (1–3) and, within each group, according to their order in the species group dendrogram (Fig. 3). Significant correlations indicated by asterisk: $p < 0.05$ (^a), $p < 0.005$ (^b), $p < 0.0001$ (^c).

the exception of a single station, identified as being station 50, geographically located far to the east in the Westwind Trough; Fig. 1b). In contrast, stations characteristic of Norske Trough had constant salinity throughout the upper water column (~ 32.3) but water temperature increased towards the surface. Some locations, particularly those with taxonomic composition typical of Westwind Trough but that were located in Norske Trough, along the northern edge of the study region, or at the boundary of the PyIW (stations 6, 8, 16, 23, 25, 30, 39, 41), exhibited intermediate T/S characteristics. All locations characteristic of the Norske Trough had surface salinities that were equal to or greater than 32 PSU (Fig. 5).

Spearman rank order coefficients were calculated between species abundances and integrated chlorophyll (0–100 m) (W.O. Smith et al., 1995; Wallace et al., 1995), freshwater content (representative of the total freshwater input to the surface layer during the summer), and the thickness of the PyIW (see Bignami and Hopkins (1997-this volume) for the definition and distribution of the latter two variables). Significant negative correlations (Spearman rank order coefficients) were found between abundances of Group 1 taxa and the freshwater content of the surface layer (Table 2) for stations outside of Belgica Trough, demonstrating that increased abundances of those taxa were found at locations that had experienced greater freshwater input. Few significant correlations were found between freshwater content and the abundances of either Group 2 or Group 3 taxa (Table 2). Only 7 taxa showed significant correlations between abundance and the thickness of the PyIW gyre (Table 2). Limited correlation also was observed between integrated chlorophyll and zooplankton abundances: only 7 out of 26 taxa showed significant correlation. For both of the latter comparisons, 5 of the 7 taxa demonstrating significant correlations were members of Group 1.

4. Discussion

Dramatic variations in the abundances of the zooplankton taxa were observed at the 43 locations across the study region. Multiple taxa followed similar regional patterns in abundance. Examination of the vertical distribution of the taxa (from the MOC-

NESS tows) indicated that the depth distribution also influenced the regional abundance trends. Our ability to group the taxa suggested that similar mechanisms may have been acting on the taxa within a group, whether the mechanism be biological, physical, or a combination. The trends in abundance observed among the different regions were consistent with abundances observed previously in MOCNESS tows that had been conducted at a limited number of locations (Ashjian et al., 1995). The present study established that the different regions, with their characteristic zooplankton abundances, were of substantial area.

Markedly different taxonomic compositions and species abundances were observed between the three groups of stations (Fig. 5). The most dramatic pattern was the extremely low abundances of most shallow-living, herbivorous taxa in the ice-free region in Norske Trough, including both adults and younger stages of calanoid copepods. For the older life stages of *Calanus* and *Metridia*, abundances observed in the ice-free region were similar to those in the Arctic Basin rather than to the abundances on other Arctic shelf regions or in the East Greenland Current (S.L. Smith et al., 1985; S.L. Smith, 1988, 1990; Hirche, 1991; Hirche and Mumm, 1992; Richter, 1994). In contrast, high abundances of the younger stages and nauplii of the herbivorous calanoid copepods and other taxa such as appendicularians (Group I) were found in the Westwind Trough. The North Atlantic copepod species *C. finmarchicus*, essentially absent in northern regions, numerically dominated the community in Belgica Trough. The deeper living, omnivorous taxa exhibited relatively consistent abundances throughout the different regions. In particular, because the abundances of these taxa were not reduced in the ice-free region of Norske Trough, they were relatively more abundant in this region.

Initially, it was thought that the different types of station, defined by the species compositions, would correspond to different physical regimes (e.g., PyIW gyre, EGC, PHW, or rAtIW) and that the locally formed PyIW gyre would contain a distinct zooplankton community. Stations characterized as being of the Belgica Trough type were all located outside of the PyIW gyre in the Belgica Trough and stations typical of the Norske Trough were, with one excep-

tion, located within the gyre (Fig. 5). The Norske Trough type stations, therefore, may represent the local 'polynya' community. However, stations of the Westwind Trough type were located both within and outside of the PyIW gyre. The differentiating characteristic between the Norske Trough and Westwind Trough stations was the markedly different abundances of the Group 1 taxa, all of which were found in the upper 20 m of the water column. The lack of consistent correlations between the PyIW thickness and the abundances of Group 1 zooplankton taxa (Table 2) suggested we look to additional mechanisms to explain the distributions of the Group 1 taxa and Westwind Trough type stations.

Elevated abundances of Group 1 taxa may have resulted in response to favorable conditions in the partially ice covered, lower salinity surface layers or from the advection of different zooplankton populations in the upper water column. We were unable to differentiate the dominant mechanism in the present analysis. However, few correlations were observed between zooplankton abundance and integrated water column chlorophyll, suggesting that favorable conditions in situ may not be solely responsible for the observed differences. Furthermore, the close proximity (spatial and temporal) of adjacent stations with different taxonomic compositions and species abundances (e.g., stations 8 and 10; stations 25 and 19), the velocities observed for the PyIW gyre ($\sim 10 \text{ cm s}^{-1}$), and the extended development time at Arctic temperatures for at least some of the taxa (e.g., 2–5 months for *Calanus*; Corkett et al. (1986)) together suggested that the transit time between these adjacent stations would be insufficient for the development of the observed abundance differences.

Associations between (1) the Westwind Trough stations and reduced salinity and (2) abundances of the Group 1 zooplankton taxa and freshwater content of the upper layer were observed (Figs. 5 and 6; Table 2). The two end points in the T/S diagram (constant temperature and constant salinity; Fig. 6) appeared to be discrete water masses, with the two types of stations (Norske Trough and Westwind Trough) each characterized by a different water type. However, the differences in T/S properties were also consistent with in situ modifications, such as heating of the upper water column in the ice-free region (Norske Trough) or dilution of the upper

water column with fresher water (Bignami and Hopkins, 1997-this volume). This dilution may result from in situ melting of sea ice in partially ice-covered regions (e.g., Schneider and Budéus, 1994; Bignami and Hopkins, 1997-this volume; Minnett et al., 1997-this volume), advection from the north of fresher water, both from continental snow melt and riverine water from along the coast (e.g., Schneider and Budéus, 1994; Bignami and Hopkins, 1997-this volume) or from north of Ob Bank (Hopkins, unpubl. data), or a combination of these two mechanisms.

Geostrophic velocities calculated for the summer of 1992 demonstrated that advection of water from the north occurred in the near-surface layers of the water column (0–20 m) both in Westwind Trough and along the northern edge of Norske Trough and that the water at the Westwind Trough type stations had a greater probability of containing water from the north (Hopkins, unpubl. data). For stations located within the boundary of the PyIW, this advection would have occurred over the PyIW in the upper 20 m (surface water depth defined by Bignami and Hopkins, 1997-this volume). The abundances of Group 1 taxa were significantly correlated with increased freshwater input in the upper water column (Table 2), with greatest abundances observed in the freshest water. Hence, the markedly different abundances of the Group 1 zooplankton taxa observed between the Norske Trough type stations and the Westwind Trough type stations may have resulted, in part, from advection of low salinity water and intrinsic zooplankton populations from along the coast and to the north in the upper water column into the Westwind Trough and spreading southward over Belgica Bank in the anticyclonic gyre.

This mechanism elucidates the classification of some locations within the boundary of the PyIW as being the Westwind Trough type (Fig. 5), since the taxa that differentiated the two types of stations were located in the upper 20 m (Fig. 2). Advection of Group 1 taxa south above the PyIW gyre during summer may also have occurred, explaining the presence of two Westwind Trough type stations located far to the south over Belgica Bank (Fig. 5). The presence of the lone Norske Trough type station far to the east near the mouth of Westwind Trough remains unexplained at present.

The regional patterns in abundance of *C. finmarchicus*, *C. glacialis*, and *C. hyperboreus* are of particular interest, both because of their dominance in the zooplankton biomass (e.g., Hirche et al., 1994; Richter, 1994; Ashjian et al., 1995; Hirche and Kwasniewski, 1997-this volume) and also because these species potentially may be useful as indicator species. Both *C. hyperboreus* and *C. glacialis* are considered Arctic species (e.g., Conover, 1988; S.L. Smith and Schnack-Schiel, 1990). *C. glacialis* is predominantly a shelf species (e.g. Conover, 1988; Hirche, 1991) while *C. hyperboreus* is primarily oceanic, with a more extensive distribution, especially southward into subarctic and temperate regions (Conover, 1988). *Calanus finmarchicus* is considered a temperate species, originating in the North Atlantic and advected into the East Greenland Sea and Arctic Ocean via the West Spitzbergen Current (e.g., S.L. Smith and Schnack-Schiel, 1990; Hirche and Mumm, 1992; Richter, 1994). Both *C. finmarchicus* and *C. hyperboreus* are abundant in the East Greenland Current system and the Greenland Sea; *C. glacialis* is present in reduced abundance in the EGC (e.g., S.L. Smith, 1988; Hirche, 1991; Richter, 1994).

The *Calanus* species often have life cycles that span 2 or 3 years, in which they undergo at least one winter of diapause during the life cycle (e.g., Conover, 1988; S.L. Smith and Schnack-Schiel, 1990). It is unknown whether the *Calanus* species are present in any abundance over the East Greenland Shelf during winter. The depths at which the animals overwinter vary with region; however, most populations have been found at deeper than 200 m and to as deep as 2000 m (e.g., Dawson, 1978; Conover, 1988; Sameoto and Herman, 1990; Hirche, 1991; Richter, 1994). Overwintering of *Calanus* on the East Greenland Shelf in the study region should occur only in the deepest portions of the troughs; a situation analogous to that described for *C. finmarchicus* on the Nova Scotia Shelf (Sameoto and Herman, 1990). As a result, limited abundances of these species may remain on the shelf by spring. Significant abundances of these copepods on the shelf during the summer would be largely a result of an annual re-introduction from off the shelf (Hirche et al., 1994; Ashjian et al., 1995).

The relative abundances of the three *Calanus*

species may be examined in the context of these off-shelf re-introductions. The high abundances of *C. finmarchicus* and *C. hyperboreus* in Belgica Trough were consistent with considerable input of Polar Halocline Water (PHW) (Bourke et al., 1987) and underlying return Atlantic Intermediate Water (rAtIW) intruding from the East Greenland Current system (Budéus and Schneider, 1995; Johnson and Niebauer, 1995; Bignami and Hopkins, 1997-this volume), since these species were found in high abundance in these water types. The particularly low abundances of *C. finmarchicus*, and the reduced abundances of *C. hyperboreus* older stages, in northern regions were consistent with little input of PHW/rAtIW water from the EGC system either in the Norske Trough (from the south) or in the Westwind Trough (from the east) (e.g., Bignami and Hopkins, 1997-this volume). Low abundances of all three species were observed in the ice-free region in Norske Trough, where little input of off-shelf water may have occurred (Budéus and Schneider, 1995; Bignami and Hopkins, 1997-this volume).

The regional patterns in abundance supported our previous conclusions regarding the role of the large herbivores in the consumption of primary production in the polynya (Norske Trough) (Ashjian et al., 1995). Estimates of potential ingestion as a proportion of primary production for the low abundances of herbivorous taxa, especially the *Calanus* species and appendicularians, in the ice-free region suggested that these important herbivores may not have been significant consumers of primary production (Ashjian et al., 1995). Because of the low abundances of the shallow-living, primarily herbivorous taxa, the deeper living omnivorous forms (e.g., *Metridia*) may have been relatively more important in the utilization of organic matter in the ice-free region (Fig. 6). However, the extremely high abundances of the shallow-living herbivores, in particular the appendicularians (Deibel, 1988; Deibel and Acuña, 1994), in Westwind Trough strongly suggested that these taxa may have had a significant impact on the utilization and repackaging of organic matter in that region.

Similar conclusions regarding the biomass, abundance, and the importance of the large herbivores on the utilization of primary production in the polynya were described for a study conducted during the summer of 1991 (Hirche et al., 1994). Mesozoo-

plankton biomass in the polynya during that period also was similar to that observed in the Arctic Ocean and the impact of the mesozooplankton on the spring bloom and on primary production in general was thought to be low. Our study and that of Hirche et al. (1994) suggest that a low standing stock of mesozooplankton in the polynya may be typical of the region (but see Hirche and Kwasniewski, 1997-this volume).

In summary, the present analysis identified several taxonomic groups within the study region that exhibited different regional trends in abundance and characteristic depth distributions. The results, expanded to the entire zooplankton community, were consistent with those observed previously at three locations and considering only four copepod species (Ashjian et al., 1995). The exact mechanisms producing the observed patterns remains somewhat elusive: the distribution and abundance of the zooplankton were controlled by a variety of physical circulation patterns operating in tandem with the biological characteristics of the organisms (e.g., life history and vertical distribution). However, both the circulation (geostrophic velocities) and the zooplankton abundance trends are consistent with advection of Arctic shelf water from the north over the PyIW in the upper water column. It is probable that in 1992 the zooplankton communities in the polynya (Norske Trough) were not important consumers and transformers of the primary production, simply because they were present in such low abundance.

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