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Northern Shrimp (*Pandalus borealis*) Recruitment in West Greenland Waters
Part I. Distribution of *Pandalus* Shrimp Larvae in Relation to Hydrography and Plankton

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Abstract

Plankton samples and oceanographic data were obtained during transect studies across fishing banks over the West Greenland shelf areas in June 1999, May, and July 2000. The hypothesis that larval shrimp are linked to the behaviour of hydrographic fronts was tested by determining whether larval shrimp abundance was linked to plankton distributions, species composition and primary productivity. We found six pelagic developmental stages (ZI–ZVI) in two species of *Pandalus* larvae. *P. borealis* was the most abundant species in all stages from ZII to ZVI. The smaller *P. montagui* larvae were slightly more advanced in development than *P. borealis*, suggesting later hatching or longer development time for *P. borealis* larvae. In May, high concentrations of newly hatched ZI larvae were caught near the coast and at fjord stations. In June and July, larvae in development stage ZIV dominated the catches. The two species showed minor differences in larval distribution across banks and between transects, indicating a wide larval dispersal and a relatively short hatching period. We found no relationship between indices of larval shrimp abundance and the T–S characteristics of water masses, chlorophyll *a* concentrations or zooplankton abundance (species, groups or sizes classes). Data from two satellite tracked SVP buoys was used to calculate a net northward drift of about 3.1 km d^{-1} or 200–400 km during the pelagic life of a larval cohort. Difference in year-class strength was attributed to differences in the environmental conditions and the larval transport patterns. We suggest that coupled physical-biological models should be developed to investigate the climatic impact on distribution and recruitment variability of northern shrimp in West Greenland waters.

Key words: distribution, Greenland, larval shrimp, *Pandalus*, plankton, recruitment

Introduction

During the last part of the 20th century the fishery for northern shrimp (*Pandalus borealis* Krøyer, 1838) has been the most important fishery off Greenland. Although subjected to a large fishery, the West Greenland shrimp population has shown increasing growth and recruitment since 1997 (Carlsson and Kanneworff, MS 1999; Siegstad, MS 2000). Year-class strength of shrimps is most likely established during the pelagic larval life driven by environmental changes (Shumway *et al*., 1985; Tande *et al*., 1994; Rasmussen and Tande, 1995; Parsons and Colbourne, 2000; Anderson, 2000). In a study of northern shrimp in the Gulf of St. Lawrence, Ouellet *et al*. (1995) proposed that larval survival and recruitment to the shrimp stocks are influenced by factors affecting stratification and mixing in the water column, i.e. buoyancy fluxes, through control of phytoplankton and copepod production. In general the hydrographic and biological processes behind observed variability in recruitment to shrimp stocks in West Greenland are poorly understood (Hvingel and Savard, 1997; Pedersen, 1998). More studies are required to identify the nursery grounds and ontogenetic movements of the shrimp found on each of the fishing grounds in the northwest Atlantic (Lilly *et al.*, 1998). The increase in the shrimp biomass in recent years can most likely not be attributed solely to changes in climate (Pedersen and Rice, 2002). Drastic declines in the West Greenland fish stocks have reduced shrimp predation, and by-catch of fish in the shrimp fishery have contributed to keep the predator pressure on the shrimp population low (Buch *et al.*, 2002).

Hydrographic conditions along the west coast of Greenland are determined by the mixture of water from the East Greenland Polar Current and Atlantic water from the Irminger Current forming the West Greenland Current. The exchange of water between the polar and temperate regions affects the marine productivity in the shelf areas, and changes in the global circulation system have major impacts on species distributions and fisheries yield (Pedersen and Smidt, 2000; Pedersen and Rice, 2002; Buch *et al*., 2002). Historic observations show relationships between climate variability and changes in the West Greenland fisheries, which should allow the incorporation of environmental information in prediction models for fish stock recruitment and abundance (Buch *et al*., 2002). Successful predictive modelling requires a comprehensive understanding of the processes involved. Understanding the links between hydrographic features and the marine pelagic food web during the productive period are keys to understand changes in recruitment of fish and shellfish in marine ecosystems (e.g. Cushing, 1989; Kiørboe, 1993; Mann and Lazier, 1996; Horwood *et al*., 2000; Anderson, 2000; Hansen *et al.*, 2002).

Hydrographic fronts (e.g. regions of transition between mixed and stratified water masses) surrounding banks may have profound effects on plankton distribution patterns, and larval fish and shrimp recruitment (e.g. Taggart *et al*., 1989; Franks, 1992; Munk *et al*., 1995; Lochmann *et al*., 1997; Reiss *et al*., 2000; Lough and Manning, 2001). Associations between abundances of various fish and shrimp larvae, and hydrographic gradients over the West Greenland shelf area between 1950–1984, indicate that it may be possible to relate interannual variation in larval abundance and subsequent recruitment of year classes to the distribution of water masses with varying characteristics (Pedersen and Rice, 2002).

We collected plankton and hydrographic data from the West Greenland shelf in June 1999, May and July 2000 in order to describe the marine pelagic food web, its structure and dependence upon hydrographic fronts at and around the shelf banks. The present paper reports on (1) distribution and abundance indices of larval shrimp development stages, (2) larval distribution in relation to hydrography and biological habitat characteristics, and (3) current tracking, hydrographic features, and possible plankton drift. A companion paper, Pedersen and Storm (2002), reports on lipid content and trophic relationships of the shrimp larvae.

Materials and Methods

Study area and sampling

Sampling for *Pandalus* spp. shrimp larvae was carried out in June 1999, May 2000, and July 2000 between 63°50'N and 66°50'N on the West Greenland shelf with the Greenlandic research vessels *Adolf Jensen* and *Paamiut* (Fig. 1; Table 1). Stations were spaced at approximately 4, 8 and 15 km along transects across shelf areas. The distance between stations was less where hydrographic fronts enhancing productivity and larval aggregation are likely to occur. In May and June, sampling was performed at stations along transects crossing Fyllas- and Sukkertop Bank. In July, sampling was carried further north to include stations along transects crossing Lille- and Store Hellefisk Bank using the two research vessels at the same time. A large number of off-transect stations were sampled in June and July, and 6 coast/fjord stations were sampled in May in the inshore Nuuk-area (Fig. 1; Fig. 2a,b).

The sampling gear used was: (1) MIK plankton sampler (2 m diameter) equipped with a 16 m long nylon monofile net of 1 mm mesh size (Munk, MS 1993), and (2) Bongo plankton sampler (0.61 m diameter) equipped with two 0.5 mm nylon monofil nets (Table 1). At every station larval shrimp samples were obtained between 8 and 21 o'clock (local time) using depth integrated oblique (diagonal) tows to near the bottom or to a maximum of 200 m at a towing speed of 3 knots. The towing time was ~30 minutes for tows to the maximum depth, 200 m. However, during the cruise with *Paamiut* in July most tows were performed at night and the maximum towing depth was 90 m. The volume filtered was determined using General Oceanics flowmeters.

On each station vertical profiles of temperature, salinity, and density were obtained with a Sea-bird

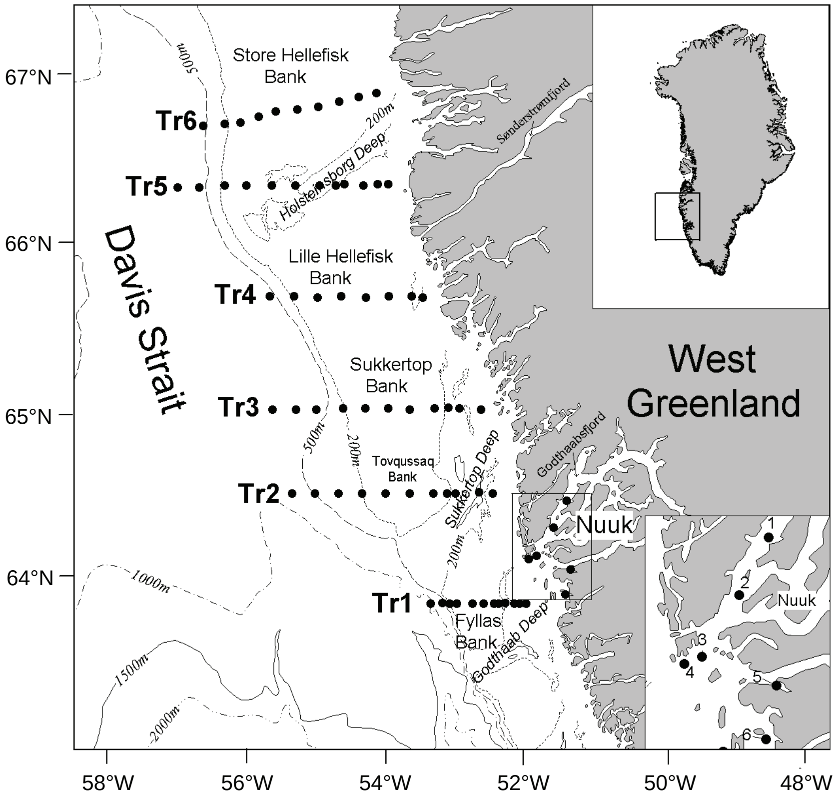

Fig. 1. Bathymetric chart of the West Greenland Shelf study area, with indication of sampling stations along 6 cross-shelf transects (Tr1–Tr6). Transects were sampled as follows: Tr1 and Tr3 in May 2000, Tr2–Tr3 in June 1999, Tr1–Tr6 in July 2000. Six inshore sampling stations were sampled in May 2000, only.

TABLE 1. Sampling data from the four cruises. May and July sampling was conducted in 2000, whereas June sampling was conducted in 1999.

Period	Reseach Vessel	Transect	Gear (Diameter; mesh size)
12–21 May 2000	RV *Adolf Jensen*	1, 3	Bongo (0.6m; 500µm)
21–30 June 1999	RV *Adolf Jensen*	2, 3	MIK (2m; 1000µm)
11–23 July 2000	RV *Adolf Jensen*	1, 4, 5	MIK (2m; 1000µm)
12–27 July 2000	RV *Paamiut*	2, 3, 6, 7, 8	Bongo (0.6m; 500µm)

SBE 9-011 sealogger CTD. Fluorescence was measured with a HydroScat2 fluorometer from HOBI-Labs, except during the cruise with *Paamiut* in July. The fluorescence was calibrated against fluorometrically determined chlorophyll *a* content in water samples collected on selected stations in May and June (Poulsen and Reuss, 2002). The chlorophyll *a* concentrations were used as indices of phytoplankton biomass.

Depth integrated micro- and mesozooplankton samples of the upper 100 m (or 2 m above bottom at shallower stations) were obtained on at least every second station. In June and in July with *Paamiut*, these samples were collected from one vertical haul with a WP-2 net (0.58 m diameter and 50 μm mesh size) retrieved at 10 m min^{-1} assuming 100% filtration efficiency. In May and in July with *Adolf Jensen*, samples were collected using a submersible pump (900 l min^{-1}, HOMA-H500, DIFRES-design) equipped with a conical net of 50 μm mesh size. The pump was lowered to max sampling depth of the MIK or Bongo plankton sampler (100 m in May; 200 m in June and July with *Adolf Jensen*) started and retrieved to the surface at 10 m min^{-1}. All zooplankton samples (MIK, Bongo, WP-2 and pump) were preserved in 4–8 % buffered formalin in seawater.

Species, stage, size, and abundance of larval shrimp and zooplankton

Pandalus shrimp larvae were sorted from the MIK and Bongo zooplankton samples in the laboratory. Samples containing more than 400 shrimp larvae were split in order to count a minimum of about 200 larvae. From each sample a subsample of about 40 shrimp larvae were identified to zoeal stage and their carapace length (cl) measured (posterior edge of orbit to mid-dorsal posterior margin of carapace) under a dissecting microscope with an optical micrometer.

Stage identifications of the shrimp larvae were based on Rasmussen (MS 1993) and T. Rasmussen, SEA ECO, Harstad, Norway, pers. comm. Two species of *Pandalus* shrimp larvae and six zoeal larval stages (ZI–ZVI) were identified for both species: *Pandalus borealis* (Berkeley, 1930; Haynes, 1979,1985; Squires, 1993; Rasmussen, MS 1993), and *Pandalus montagui* (Pike and Williamson, 1964; Squires, 1993; Schultze and Anger, 1997). It is difficult to discriminate between these two species morphologically, especially formalin preserved larvae whose pigmentation has disappeared (Pedersen, 1998). However, in the same zoeal stage *P. borealis* (Pb) are larger than *P. montagui* (Pm). Based on Pedersen (1998) and length-frequency

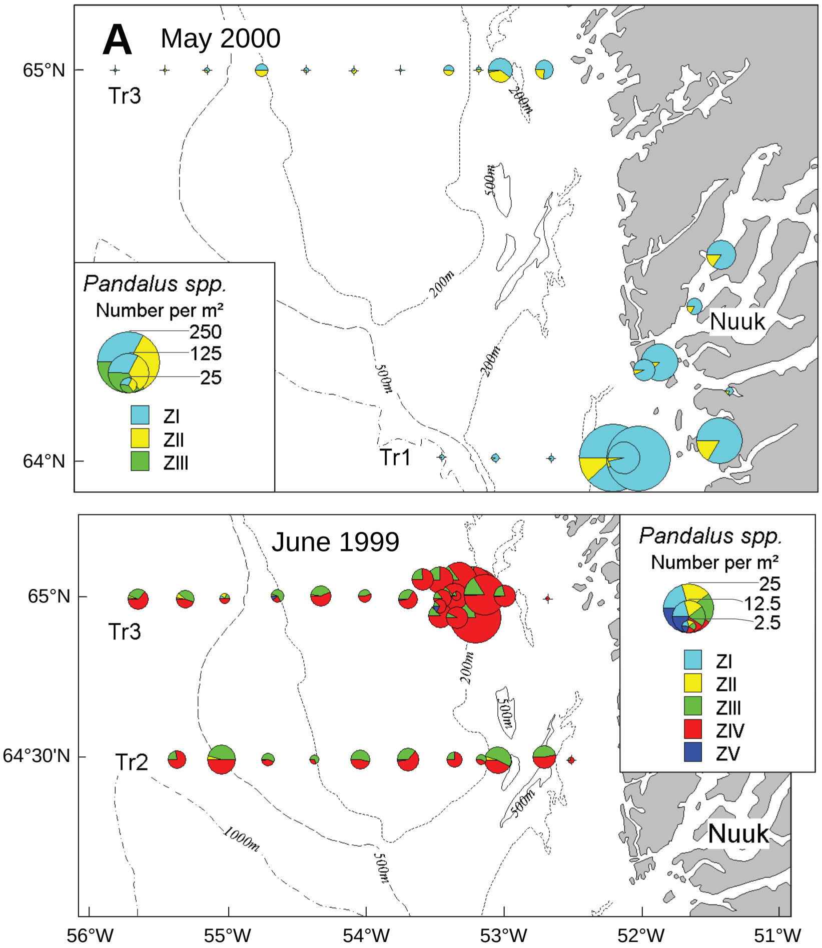

Fig. 2a. Distribution and abundance of larval *Pandalus* development stages in May 2000 and June 1999. Transects and off transect stations shown. Dot sizes are graduated by square root.

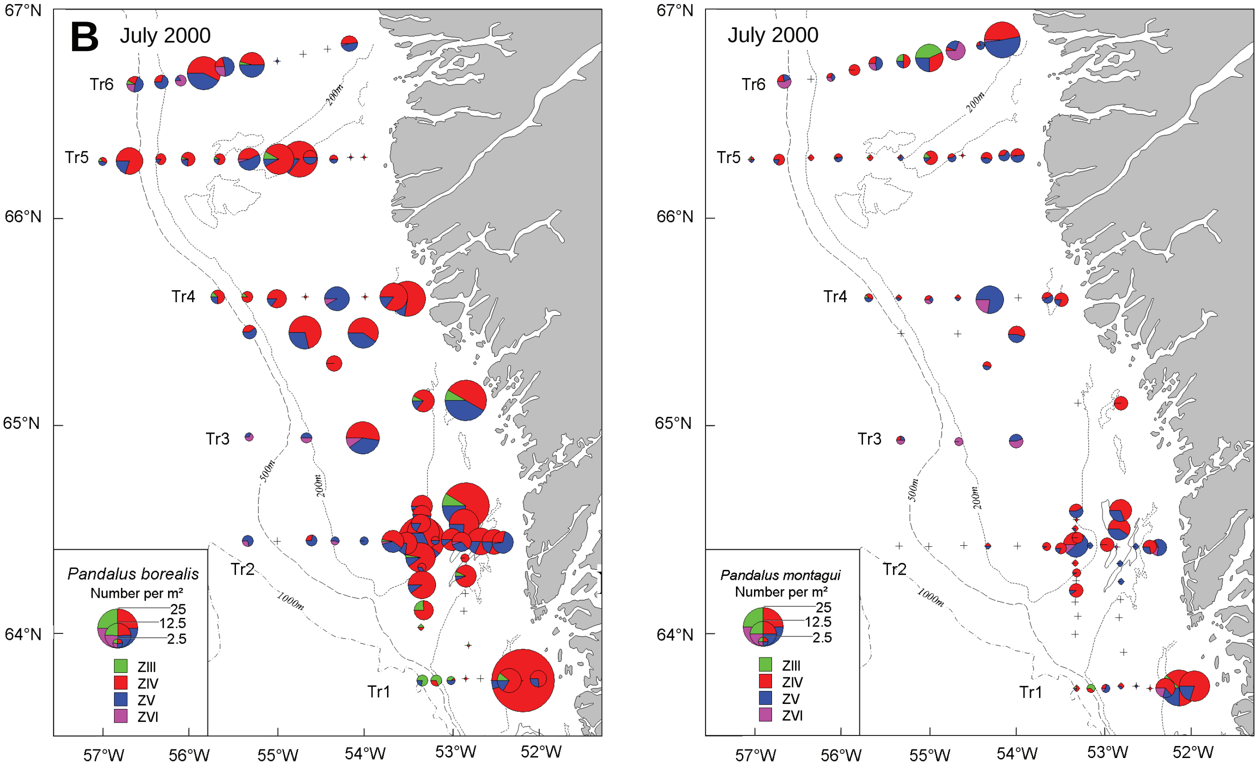

Fig. 2b. Distribution and abundance of larval *Pandalus* development stages in July 2000. Transects and off transect stations shown. Dot sizes are graduated by square root.

diagrams by stage and station from this study the following size criteria by stage were found to identify and separate the smaller *P. montagui* larvae: Stage ZI: no discrimination; Pm stage ZII: cl <1.5 mm; Pm stage ZIII: cl <2.0 mm; Pm stage ZIV: cl <2.7 mm; Pm stage ZV: cl <3.0 mm; Pm stage ZVI: cl <3.5 mm. Discrimination between the two species based on fixed size criteria is questionable as different sizes at stage could be caused by genetic or temperature differences during larval development (ecophenotypic effects). However, no genetic differences in *P. borealis* populations from West Greenland have been found. Furthermore laboratory experiments found no significant difference in carapace length, at the same stage, from the effect of different rearing temperatures (Shumway *et al.*, 1985). Therefore, we assume that the size criteria discriminated the two *Pandalus* species although overlap in the size frequency distributions was seen at some stations (see discussion in Pedersen, 1998).

To identify biotic habitats and abundances of potential food sources of *Pandalus* larvae, subsamples of micro- and mesozooplankton were sorted and identified to the lowest possible taxon in the laboratory. Each species or taxonomic category was enumerated and length measured. Within each copepodite stage up to 10 specimens were length measured (prosome length). Abundance and length information was used to estimate the copepod biomass as total carbon within taxonomic categories at each sampling station. Length-weight relationships (ash-free dry weight) were obtained from the literature: *Calanus* (all three species) and *Metridia longa* from Hirche and Mumm (1992), *Acartia* spp. and all nauplii from Berggreen *et al*. (1988), *Pseudocalanus* sp. from Klein Bretler *et al*. (1982), while for the smaller taxons *Oithona* spp., *Microcalanus* spp., *Oncaea* spp. and *Microsetella* spp. the relationship for *Oithona* spp. in Sabatini and Kiørboe (1994) was used. The carbon content of *Calanus* spp. stages I to III and the smaller taxons were assumed to be 50% of dry weight, while a conversion factor of 60% was used for older stages (Hansen *et al*., 1994). The shrimp larval biomass as carbon content was estimated from total lipid contents (Pedersen and Storm, 2002) using a relation for brachyuran larvae (Anger and Harms, 1990).

Abundance and biomass estimates of shrimp larvae and other taxa were standardized to number m^{-2} of sea surface to sampling depth (e.g. Smith and Richardson, 1977).

Ocean stability and current tracking

The potential energy (P) of the upper part of the water column was calculated as a measure of the stability of the water column, i.e. the energy input needed to break down stability and homogenise the water column (Pedersen, 1986):

$$P(z) = -g\int_0^z (\rho_{\text{hom}} - \rho(z))z\,dz\ (J\ m^{-2})$$

where g is the gravitational acceleration (9.82 m s^{-2}), ρ_{hom} is the density (σ_t) of the homogenised water column and $\rho(z)$ is the density measured at depth z.

Two satellite tracked SVP drift buoys (Techno-ocean, Inc) with drogues of 3.4 m^2 at 30 m were deployed east and west of Fyllas Bank during the May cruise. Positions of the buoys obtained approximately every three hours from the two drifters were used to give information on velocities of prevailing ocean currents and possible plankton drift in the study area. Data from the meteorological station at Nuuk on wind speed and directions every three hours during the study periods were compared to the observed patterns of hydrography and ocean drift.

Data analysis

Tests for differences between stations and transects of larval shrimp development stages and sizes were performed using multi- and one-way analysis of variance (ANOVA) (SAS, 1985 – GLM procedure). Associations among temperature, salinity, phytoplankton (chlorophyll *a*), abundance of copepods, egg, nauplii (indices of copepod productivity), invertebrate larvae, and larval shrimp abundance were tested using Spearman rank correlations.

Results

Larval *Pandalus* distributions, stage development, and sizes

In May, highest larval concentrations (30–300 individuals per m^{-2}) were found at the coastal stations of Tr1 and Tr3 and at stations within the fjords (Fig. 2a). *Pandalus* larvae were also caught at stations crossing the banks westward, with fewer larvae on the bank in Tr3 and a slight increase offshore after crossing the bank. The majority of the larvae caught in May were ZI larvae with a trend of higher proportion of ZII larvae on Tr3 (Fig. 2a). We were unable to separate stage ZI larvae in *P. borealis* and *P. montagui*. At the fjord stations many ZI larvae were small and apparently newly hatched. Of all ZII larvae 27% were identified to *P. borealis*, indicating that *P. borealis* lagged behind in development compared to *P. montagui*.

In June, highest larval concentrations (~20 individuals per m^{-2}) were found just east of Sukkertop Bank on Tr3 and at a few off transect stations (Fig. 2a). At other stations of Tr2 and Tr3 larval concentrations were below 10 individuals per m^{-2} with lowest concentrations at the 2 easternmost transect stations. Most larvae were in ZIII and ZIV, with ZIV generally dominating, especially at stations with highest larval concentrations (Fig. 2a). Of all *Pandalus* larvae caught 68% were identified as *P. borealis*. The highest proportions of *P. montagui* were observed on stations closest to the coast and over the shallower parts of the banks. On westernmost stations of Tr2 and Tr3 small proportions of ZII larvae were found. Of the ZII larvae 95% were identified to *P. borealis*, indicating that *P. montagui* was more advanced in development compared to *P. borealis*.

In July, highest larval concentrations (10–35 m^{-2}) were found over the banks and in the deep channels between the banks and the coast (Fig. 2b). On the two northern transects, Tr5 and Tr6, high concentrations were also found at stations west of Store Hellefisk Bank. The species proportion of all *Pandalus* larvae caught was 71% *P. borealis* and 29% *P. montagui*. The larvae were in stages ZIII to ZVI, ZIV larvae being dominant in both species. Generally *P. borealis* and *P. montagui* in stages ZIV to ZVI showed similar distribution (Fig. 2b, Appendix Fig. 1 and 2). However, along Tr6 *P. borealis* larvae were most abundant on the western deeper stations and *P. montagui* were most abundant on the eastern shallower stations over the bank (Fig. 2b, Appendix / Fig. 1 and 2).

Multi-way ANOVA of zoeal stage by month showed significant ($p<0.05$) effects of species, station and transect in June and July. There were no clear trends in stage composition (mean stage) between or along transects in either June or July. The mean stage duration was estimated to be about 20 days for both species, assuming peaks in hatching and larval appearance in the plankton in the beginning of May (Fig. 3). Assuming linear growth, the larvae caught in June 1999 appeared to be more advanced in

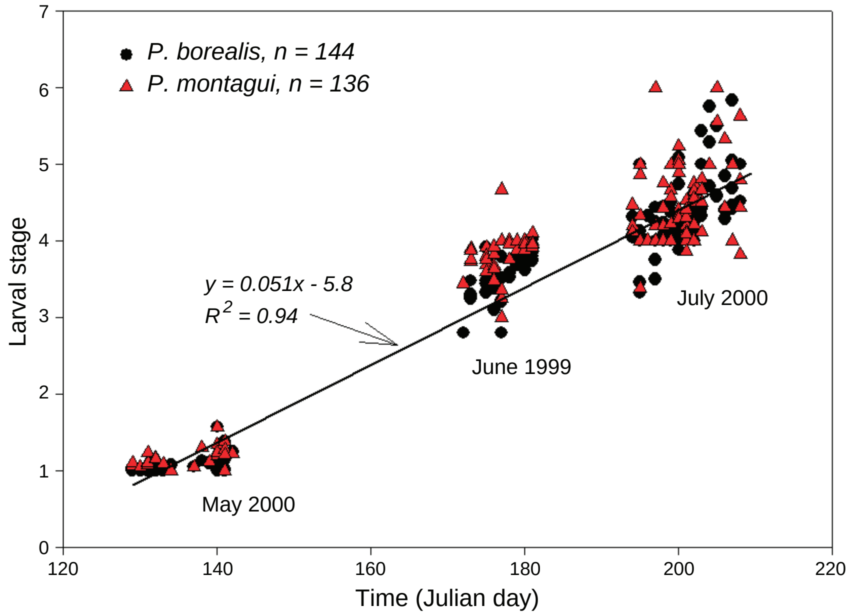

Fig. 3. Mean zoeal stage by station and species as a function of time. All stations May 2000, June 1999, and July 2000.

development compared to the July 2000 larvae. In June 1999, the stage composition of the smaller *P. montagui* larvae was skewed to slightly more developed larvae compared to *P. borealis*.

In May, ZI and ZII larvae were larger on Tr1 and Tr3 compared to larvae from inshore (fjord and coastal) stations (Table 2a). Although multi-way ANOVA of larval size by species, and stage showed significant ($p<0.05$) effects of station, and transect, there was no clear trends in mean size (carapace length) between or along transects either in June or July. However, the mean size of *P. montagui* larvae in stage ZIV and ZV showed large variations e.g. ZV larvae from TR1, 5, and 6 in July being significantly smaller than ZIV larvae from Tr2, 3, and 4 (Table 2b). This was partly caused by uncertainty in the determination of larvae to stage/species (e.g. during moulting; moulting larvae occurred at some stations), and partly because exceptional small stage ZIV and ZV larvae occurred at a few stations, these might belong to a different species, *Dichelopandalus leptocerus* (see remarks p. 276 in Pike and Williamson, 1964).

Hydrography and biological habitats

From May to July, temperatures in the upper 200 m of the water column over the southwest Greenland shelf Banks (Tr1-3) increased from below zero to above 5°C (Fig. 4). During this period thermoclines developed in the upper 50 m and salinity dropped from 33.6 to below 33.2 psu. The lowest salinities was found in the upper water column at the nearshore stations in May (Tr1 and 3), June (Tr3), and July (Tr1, 4, and 5). On Tr3 in June 1999, relative warm and low saline water was found east and on top of Sukkertop Bank, whereas a core of cold water (<–0.5°C) was seen west of the bank at depths between 25 and 125m. In July 2000, cold water (<0°C) was distributed at intermediate depths between 50 and 150m over the shelf, and salinity showed an increasing trend from south to north (Tr1 to 6) (Fig. 4). Density clines (σ_t) varied between 25.6 and 28.4 and followed the salinity clines (data not shown). The integrated potential energy (P) showed generally low water stability in the upper 50 m ($P<500\ J\ m^{-2}$). Exceptions were the offshore stations of Tr3 in June and the nearshore stations of Tr1, 4, and 5 which were influenced by freshwater runoff from the large West Greenland fjords. There were no significant correlations (or visual relationships) between larval shrimp abundance and mean (5–90 m) temperature or salinity. In May, shrimp larvae were caught in temperatures from -1 to 1.5°C, and salinities from 33 to 34.2 psu. In June, from -1 to 3.5°C, and 32.4 to 34 psu. In July, from 0 to 4.5°C, and 32.4 to 33.8 psu.

Copepods dominated the zooplankton. The following species were identified: *Calanus finmarchicus, Calanus hyperboreus, Calanus glacialis, Metridia longa, Acartia longiremis, Microcalanus*

TABLE 2a. Mean carapace length (mm) by species, stage, transect, and month.

Transect	*Pandalus* sp. Stage ZI			*P. borealis* Stage ZII			*P. montagui* Stage ZII		
	No.	Mean	Std. err.	No.	Mean	Std. err.	No.	Mean	Std. err
Inshore May 2000	511	0.92	0.01	3	1.57	0.03	72	0.96	0.02
Trl May 2000	322	1.07	0.01	11	1.67	0.10	18	1.17	0.05
Tr3 May 2000	397	1.12	0.01	64	1.65	0.02	118	1.21	0.02
Tr2 June 1999	–	–	–	22	1.92	0.03	–	–	–
Tr3 June 1999	14	1.11	0.03	40	1.69	0.01	3	1.30	0.00

TABLE 2b. Mean carapace length (mm) by species, stage, transect, and month.

Transect	Stage ZIII			Stage ZIV			Stage ZV			Stage ZVI		
	No.	Mean	Std. err.	No.	Mean	Std. err.	No.	Mean	Std. err.	No.	Mean	Std. err.
P. borealis												
Tr3 May 2000	1	2.00	-	-	-	-	-	-	-	-	-	-
Tr2 June 1999	565	2.37	0.01	503	3.02	0.01	4	3.15	0.10	-	-	-
Tr3 June 1999	572	2.35	0.01	985	2.95	0.01	22	3.28	0.04	-	-	-
Tr1 July 2000	34	2.34	0.04	51	3.00	0.02	24	3.05	0.02	-	-	-
Tr2 July 2000	1	2.30	-	210	2.94	0.01	113	3.27	0.02	12	3.78	0.05
Tr3 July 2000	4	2.58	0.21	53	3.03	0.02	30	3.38	0.04	8	3.68	0.05
Tr4 July 2000	5	2.22	0.07	128	2.95	0.02	35	3.25	0.04	1	3.70	-
Tr5 July 2000	11	2.23	0.04	193	2.98	0.01	78	3.20	0.02	5	3.72	0.06
Tr6 July 2000	2	2.10	0	47	2.99	0.03	61	3.49	0.03	13	3.75	0.05
P. montagui												
Tr3 May 2000	4	1.75	0.09	-	-	-	-	-	-	-	-	-
Tr2 June 1999	98	1.75	0.01	289	2.28	0.01	4	2.80	0.06	-	-	-
Tr3 June 1999	20	1.79	0.02	623	2.31	0.01	8	2.58	0.10	-	-	-
Tr1 July 2000	7	1.83	0.03	69	2.19	0.03	26	2.29	0.08	7	2.87	0.13
Tr2 July 2000	-	-	-	58	2.47	0.02	38	2.47	0.09	8	2.98	0.2
Tr3 July 2000	-	-	-	4	2.43	0.14	5	2.02	0.20	7	3.09	0.09
Tr4 July 2000	1	1.90	-	25	2.48	0.03	28	2.64	0.05	7	2.91	0.11
Tr5 July 2000	4	1.83	0.07	98	2.13	0.04	85	2.22	0.05	6	2.53	0.36
Tr6 July 2000	42	1.37	0.02	84	2.04	0.03	72	2.32	0.04	20	3.01	0.07

pusillus, *Microsetella norvegica*, *Oithona similis*, *Oncaea borealis*, and *Pseudocalanus elongatus*. The latter six species were grouped by genus, together with unidentified species of these taxa. A few specimens of *Euchaeta norvegica*, *Temora longicornis*, *Centropages hamatus*, and *Pleuromamma robusta* were identified; but these were excluded from the distribution maps in Fig. 5.

The larger *Calanus* copepodites (CI–CVI) showed an increasing abundance from May to July (Fig. 5). *C. glacialis* and *C. hyperboreus* dominated in May, whereas *C. finmarchicus* dominated in June and July. Abundance was highest over deep water east and west of the banks in May and July. Abundance was low at the fjord stations sampled in May. The small copepod community consisted predominantly of, *Oithona*

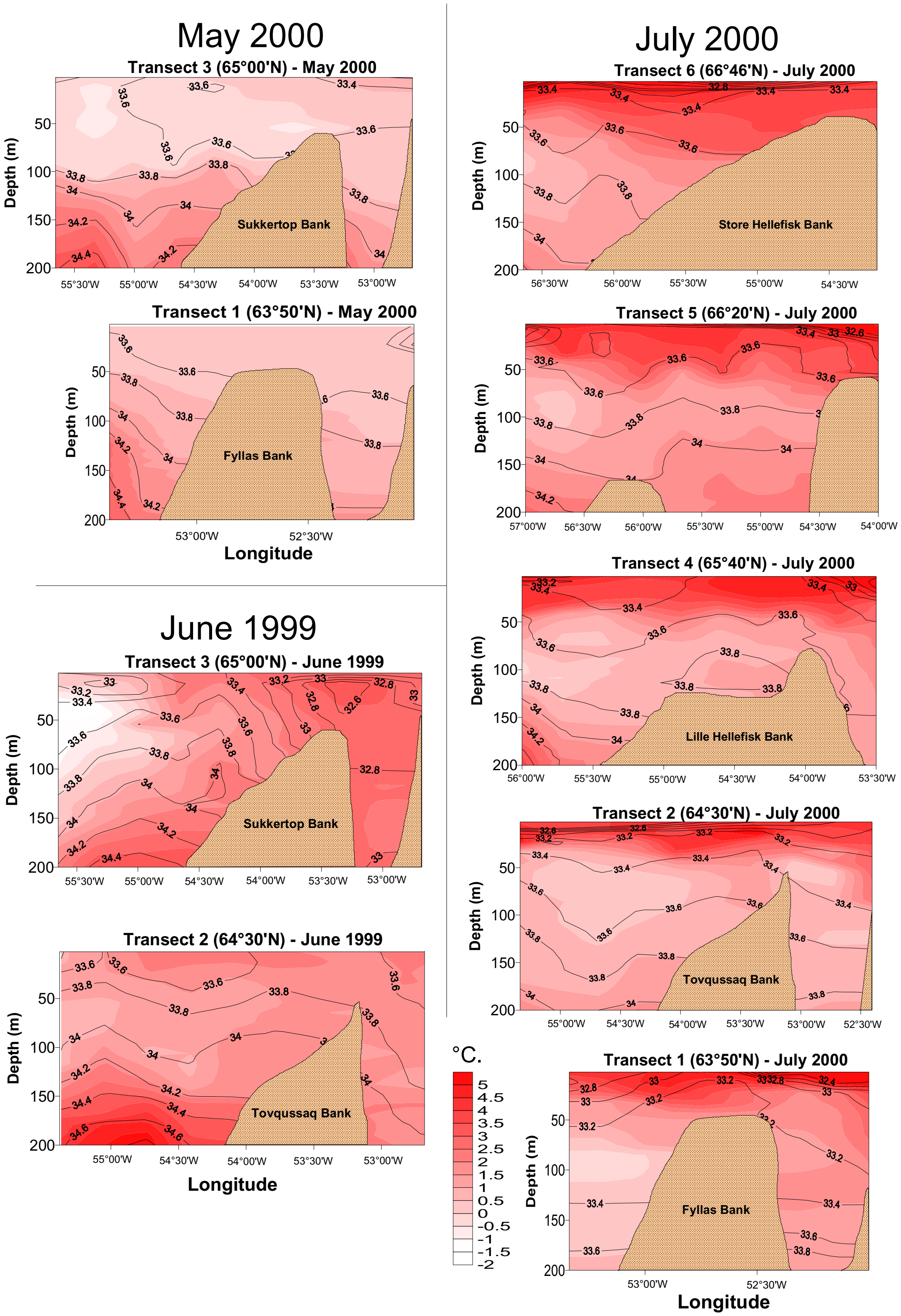

Fig. 4. Vertical sections of temperature (°C), and salinity (psu) along transects 1–6. Temperature is illustrated by different intensity of shading and denoted by inserted bar.

similes and Microsetella norvegica during all sampling times. Total abundances were at similar low levels in May and June, and highest in July. In May the fjord stations were dominated by *Microsetella* spp., and *Pseudocalanus elongatus*. *Microcalanus* spp. was dominant at one station on Tr3 in May. *Pseudocalanus* spp. occurred in high abundance at the two shallow stations nearest to shore of Tr6 in July. The abundance of both large and small copepods was exceptionally high over deep water east and west of the bank on Tr2 in July (Fig. 5).

In order to relate shrimp larvae distributions and potential food availability, profiles of chlorophyll *a*, biomass of copepods, abundance of copepod egg, nauplii, and invertebrate larvae were compared to the distribution of shrimp larvae biomass along transects (Fig. 6a–c). Chlorophyll *a* concentrations were highest during the spring bloom in May with peaks (4–6 µg l^{-1}) over the shallow parts of Fyllas- and Sukkertop Bank (Fig. 6a–b), with similar high levels at most fjord stations, except at station 5 with much lower chlorophyll *a* values (<0.7 µg l^{-1}). In June, a post-bloom situation prevailed resulting in low autotrophic biomass and low chlorophyll *a* values over Sukkertop Bank, but peak chlorophyll *a* values (1 µg l^{-1}) in the upper water column were seen at the westernmost stations of Tr3 (Fig. 6b). In July, subsurface blooms with chlorophyll *a* peaks (1–2 µg l^{-1}) at water depths of about 30 m were seen along Tr1, 4, and 5 (Fig. 6a and 6c).

The large *Calanus* spp. copepodites by far dominated the plankton community structure, with *Pseudocalanus* spp., *Metridia longa*, and *Oithona* spp. comprising most of the remaining copepod biomass (Fig. 6a–d). Visual inspections of Figs. 6a–d indicated generally higher biomasses of copepods, and higher abundance of copepod egg, nauplii, and invertebrate larvae at stations with higher concentrations of chlorophyll *a*. Exceptions were on top of Fyllas and Sukkertop Bank in May with high chlorophyll *a* concentrations but low copepod biomass and at the inshore stations with very low biomass of *Calanus*. Shrimp larval biomass was generally insignificant compared to the copepod biomass. However, at one station at Tr1 (May) and on most fjord stations the shrimp larvae biomass was relatively high compared to the copepod biomass. The exception was station 5 (Fig. 6d) with low chlorophyll *a* values. The shrimp larvae abundance seemed to be related to areas of high chlorophyll *a* concentrations at the fjord stations in May and on Tr1 in July, however there were no such relationships on other transects in June and July. There were no correlations ($p>0.05$) or visual patterns between abundances of larval shrimp and individual zooplankton species, species groups (individual or combined) or size classes (50–100, 100–1000, and ≥1000 µm) at any time (Fig. 6a–d). Shrimp larvae were abundant over deep water in the channels east of banks and over the banks.

Current tracking

The two SVP buoys deployed east and west of Fyllas Bank on May 12 and 13 both showed a net northward drift (Fig. 7). The trajectories of the drifters intersected several times and showed meandering paths. Occasionally eddies and gyres trapped the buoys for periods of 2–3 weeks. Overall drift distances and mean velocities differed between the two buoys (Fig. 7, Table 3). Based on data from both buoys the overall mean net northbound current was estimated to about 3.1 km d^{-1} for the period from deployment (12–13 May) to 31 July.

During most of May 2000, winds blowing from a northerly direction and in periods after deployment relatively strong northerly wind (8–15 m s^{-1}) prevailed (Fig. 8). Although northerly winds, the two buoys drifted northward into the *Sukkertop Deep* at a mean speed of 10–12 km d^{-1} until they were trapped in eddies on 22 May. After 23 May both buoys drifted west and buoy No.3378 became trapped in a new eddy, while bouy No. 3377 followed a cyclonic circulation before being trapped in an eddy at the southern edge of Tovqussaq Bank (Fig. 7).

In June and July 2000, wind speeds were generally below 5 m s^{-1} and seldom exceeded 10 m s^{-1} (Fig. 8). However, from 25 July to 8 August strong winds (15–28 m s^{-1}) from the south dominated the wind field. For a period of July the drift patterns of the buoys showed daily tidal induced anticyclonic circulation of about 5 km in diameter, with drift speeds often exceeding 1.8 km h^{-1} (0.5 m s^{-1}) (Fig. 7). At about 67°N, buoy No. 3378 maintained circulation around the shallow Store Hellefisk Bank (<30 m) for seven weeks from 31 July to 19 September. Thereafter it drifted north along the same route as buoy No. 3377 until it came aground on coast south of Disko Bay on 17 November. Buoy No. 3377 maintained anticyclonic circulation over Disko Bank from mid September to mid October before drifting north and before it was forced south by the developing winter "West ice" in mid December (Fig. 7).

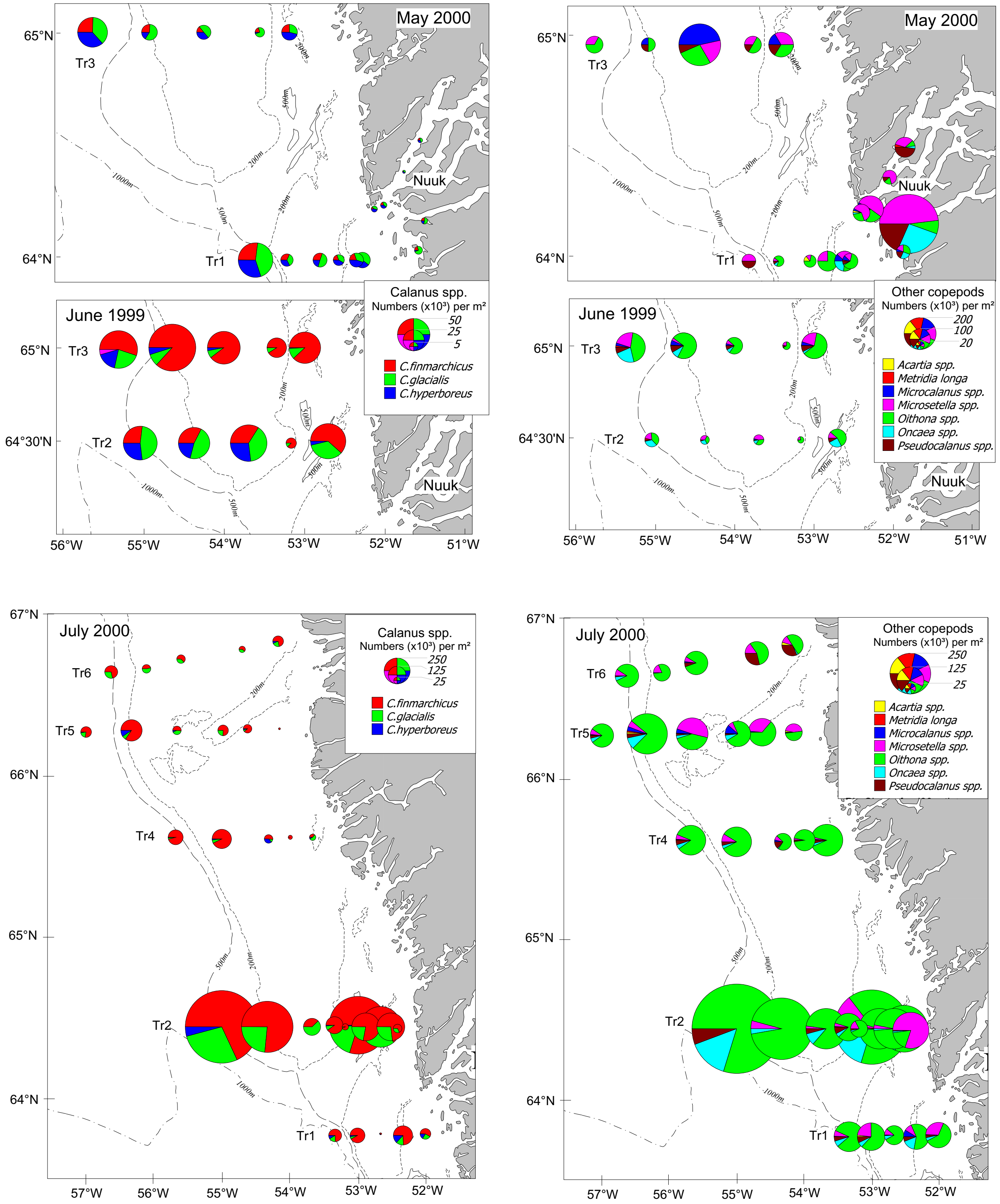

Fig. 5. Distribution, and abundance of *Calanus* spp. (left panels) and other copepods (right panels) in May 2000, June 1999, and July 2000. Dot sizes are graduated by square root. Note different scales between left and right panel.

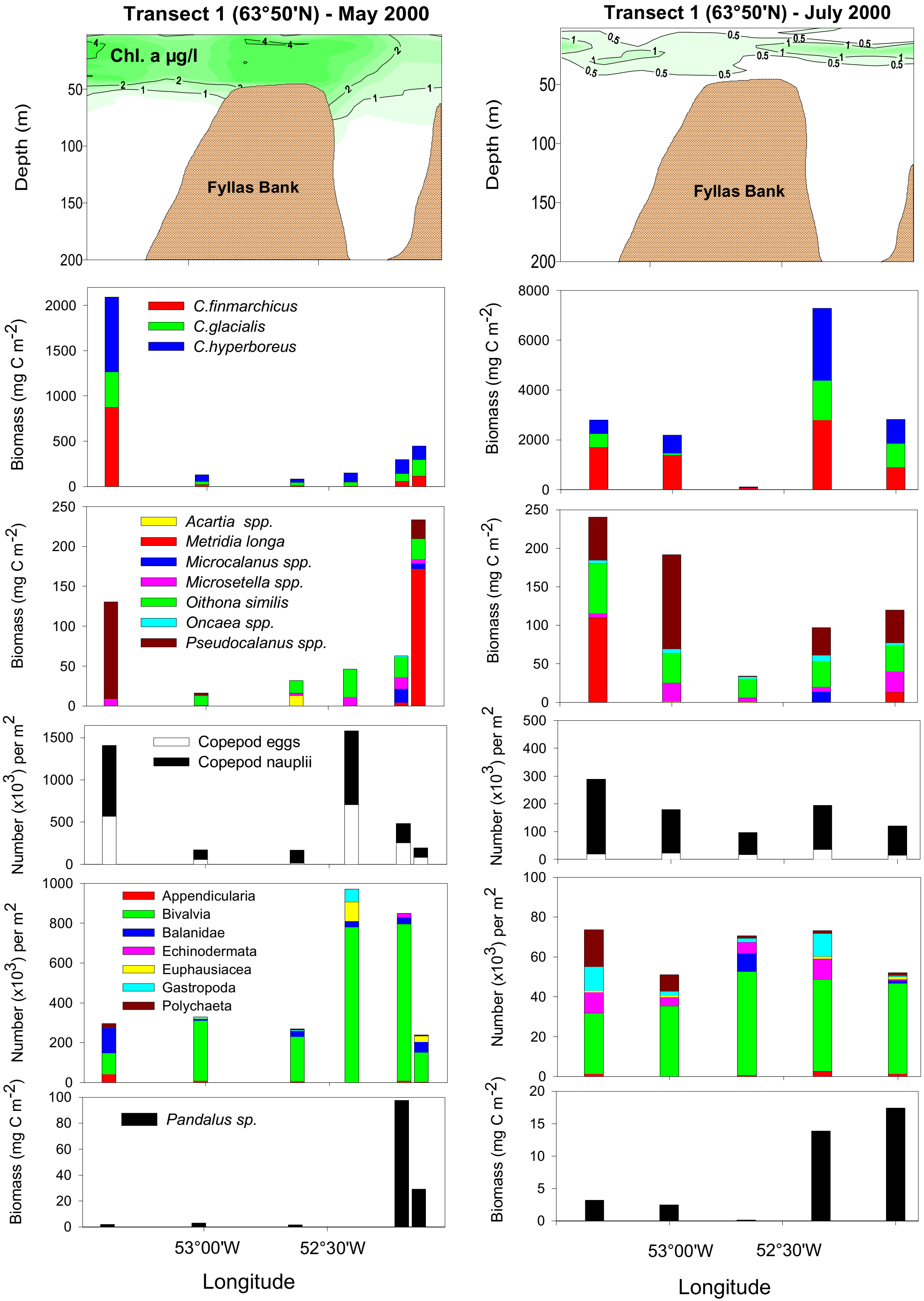

Fig. 6a. Distribution of *Pandalus* larvae biomass (mg C m^{-2}) related to: vertical section of chlorophyll *a* concentration in µg l^{-1}, composition of *Calanus* spp. and other copepod biomass (mg C m^{-2}), number of copepod eggs, nauplii, and other invertebrate larvae (×10^3 m^{-2}) along transect 1 in May 2000 (left panels), and July 2000 (right panels).

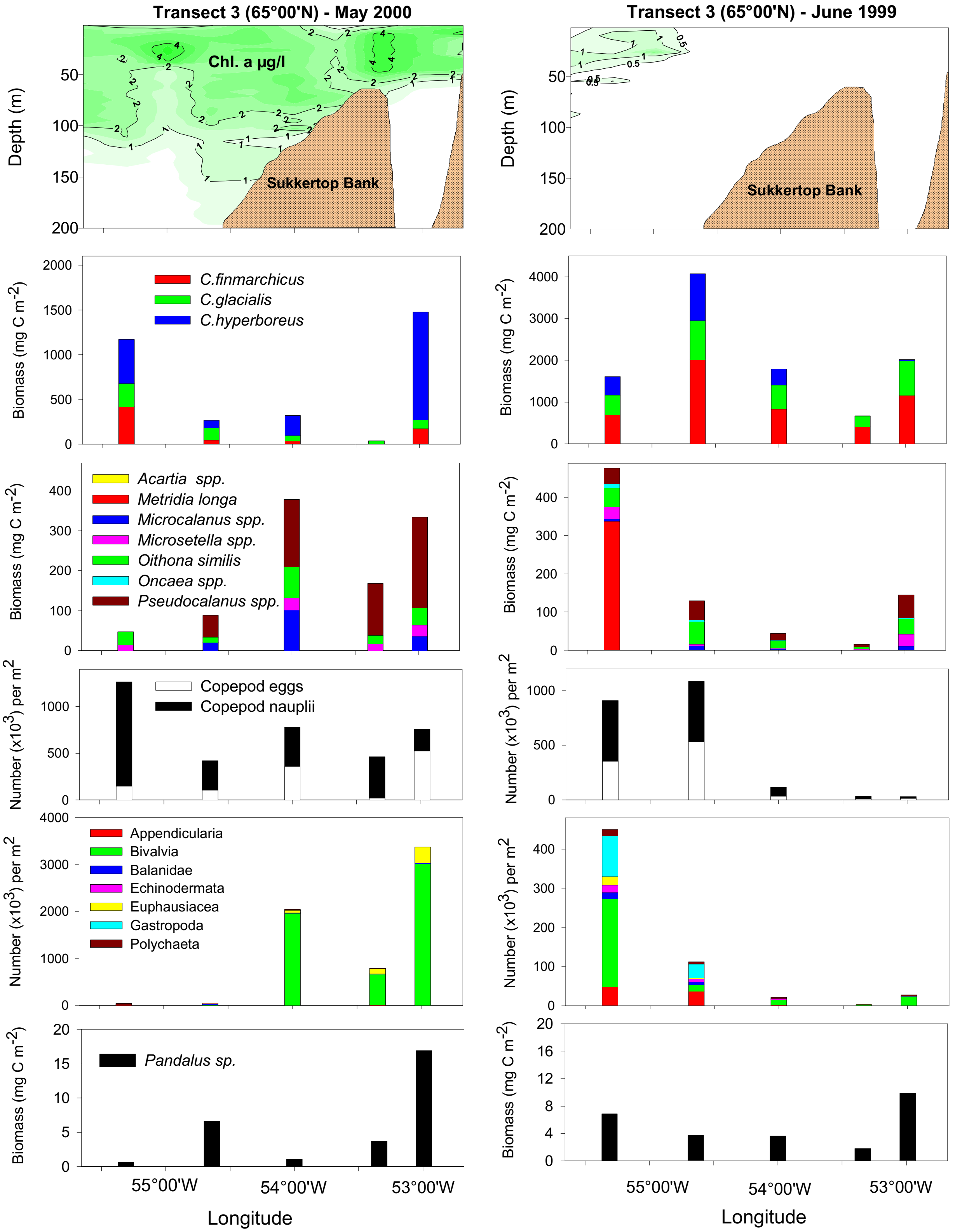

Fig. 6b. Distribution of *Pandalus* larvae biomass (mg C m^{-2}) related to: vertical section of chlorophyll *a* concentration in µg l^{-1}, composition of *Calanus* spp. And other copepod biomass (mg C m^{-2}), number of copepod eggs, nauplii, and other invertebrate larvae (×10^{3} m^{-2}) along transect 3 in May 2000 (left panels), and June 1999 (right panels).

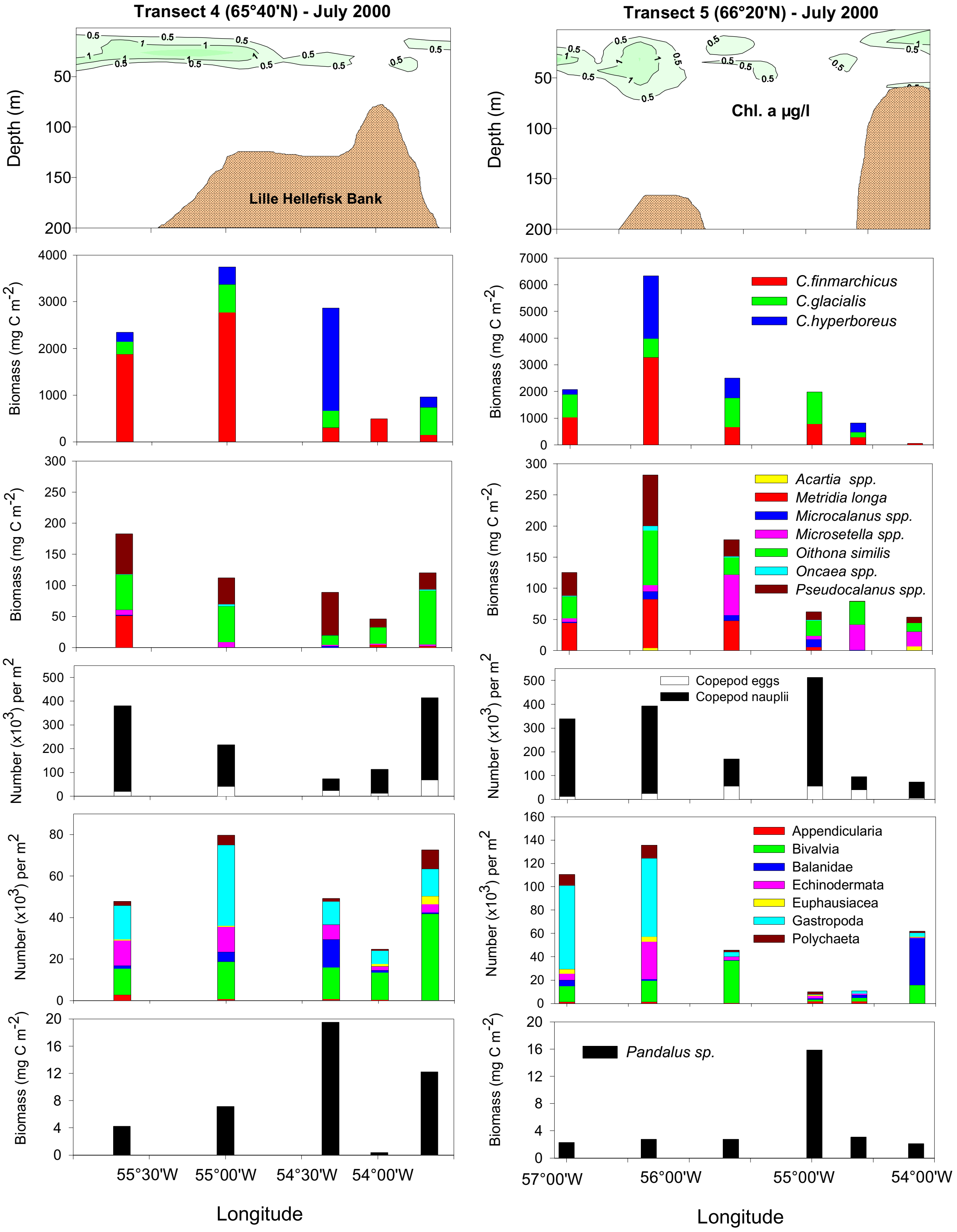

Fig. 6c. Distribution of *Pandalus* larvae biomass (mg C m^{-2}) related to: vertical section of chlorophyll *a* density in µg l^{-1}, composition of *Calanus* spp. and other copepod biomass (mg C m^{-2}), number of copepod eggs, nauplii, and other invertebrate larvae (x10^3 m^{-2}) along transect 4 in July 2000 (left panels), and transect 5 July 2000 (right panels).

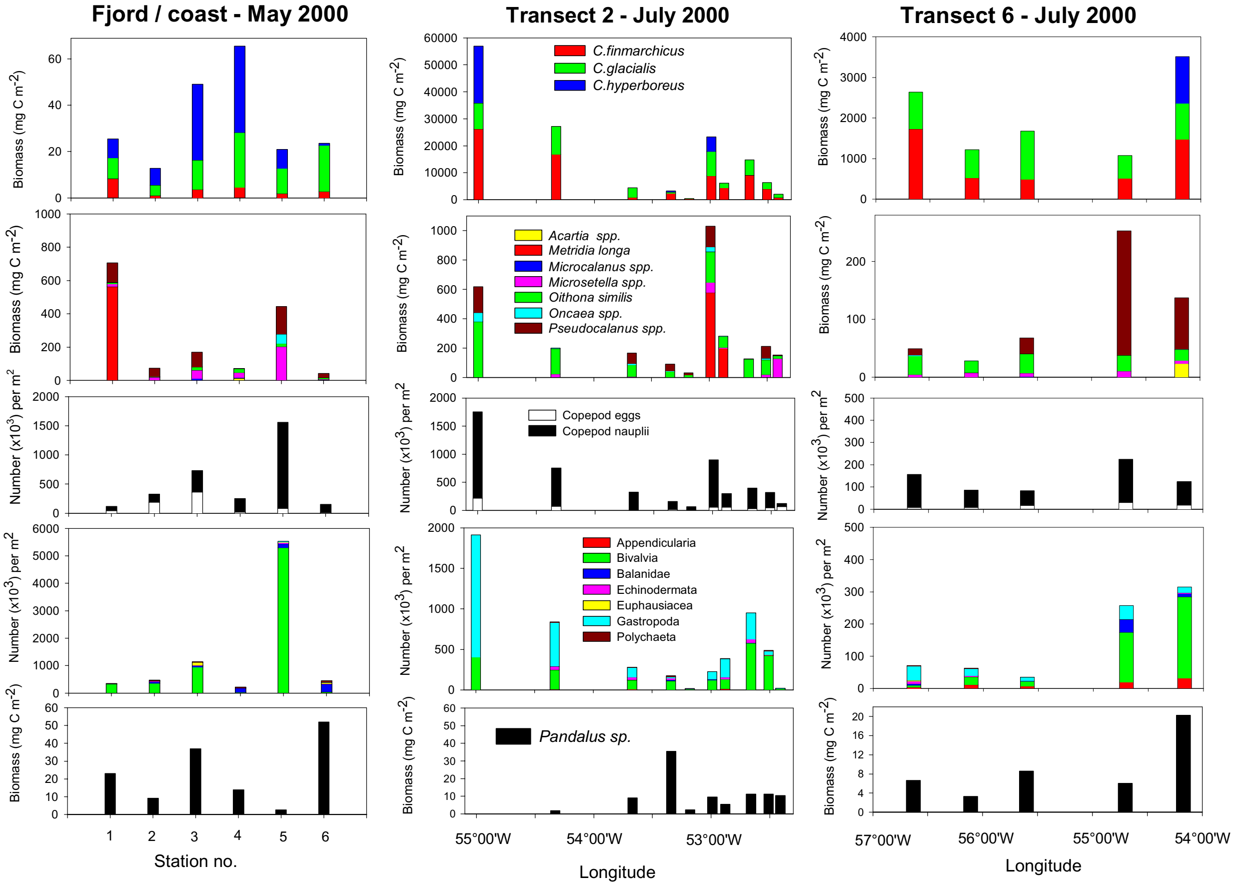

Fig. 6d. Distribution of *Pandalus* larvae biomass (mg C m^{-2}) related to: composition of *Calanus* spp. and other copepod biomass (mg C m^{-2}), number of copepod eggs, nauplii, and other invertebrate larvae (×10^{3} m^{-2}) on six inshore stations in May 2000 (left panels), along transect 2 in July 2000 (mid panels), and transect 6 July 2000 (right panels).

Discussion

Larval *Pandalus* distribution, abundance, and stage development

We found six pelagic development stages in two species of *Pandalus* larvae. The larger *P. borealis* larvae were slightly less developed than *P. montagui*, suggesting later hatching or slower development time of *P. borealis* larvae. The larval distribution, abundance, and proportion of ZIII and ZIV along Tr3 in June 1999 were similar to findings in early July 1996 (Pedersen, 1998).

In West Greenland *P. borealis* spawns (extrudes eggs) in offshore waters beginning in July and ending in late August or early September (Horsted, 1978). The egg mass is carried by females until spring (March–April) when they move to shallow water to release the first pelagic larval stage (Shumway *et al.*, 1985). The exact time of hatching is directly related to water temperature, warmer water resulting in earlier hatching and a shorter pelagic larval phase (Shumway *et al.*, 1985). The planktonic larvae are thought to drift more or less passively during five zoeal stages and settle to the bottom during the sixth (megalopa) stage (Berkeley, 1930; Horsted *et al.*, MS 1978; Shumway *et al.*, 1985). According to Horsted and Smidt (1956) planktonic larval influx into Disko Bay and many fjords in West Greenland may be critical to recruitment of *P. borealis* in those areas. During the May 2000 cruise, *Pandalus* larvae concentrated east of Fyllas Bank near the coast, and at fjord stations in the Nuuk area. Most larvae were ZI and probably newly hatched. Previous plankton studies from West Greenland did not catch Pandalid larvae earlier than May (Horsted and Smidt, 1956; Smidt, 1979), therefore hatching probably occurred in late April and early

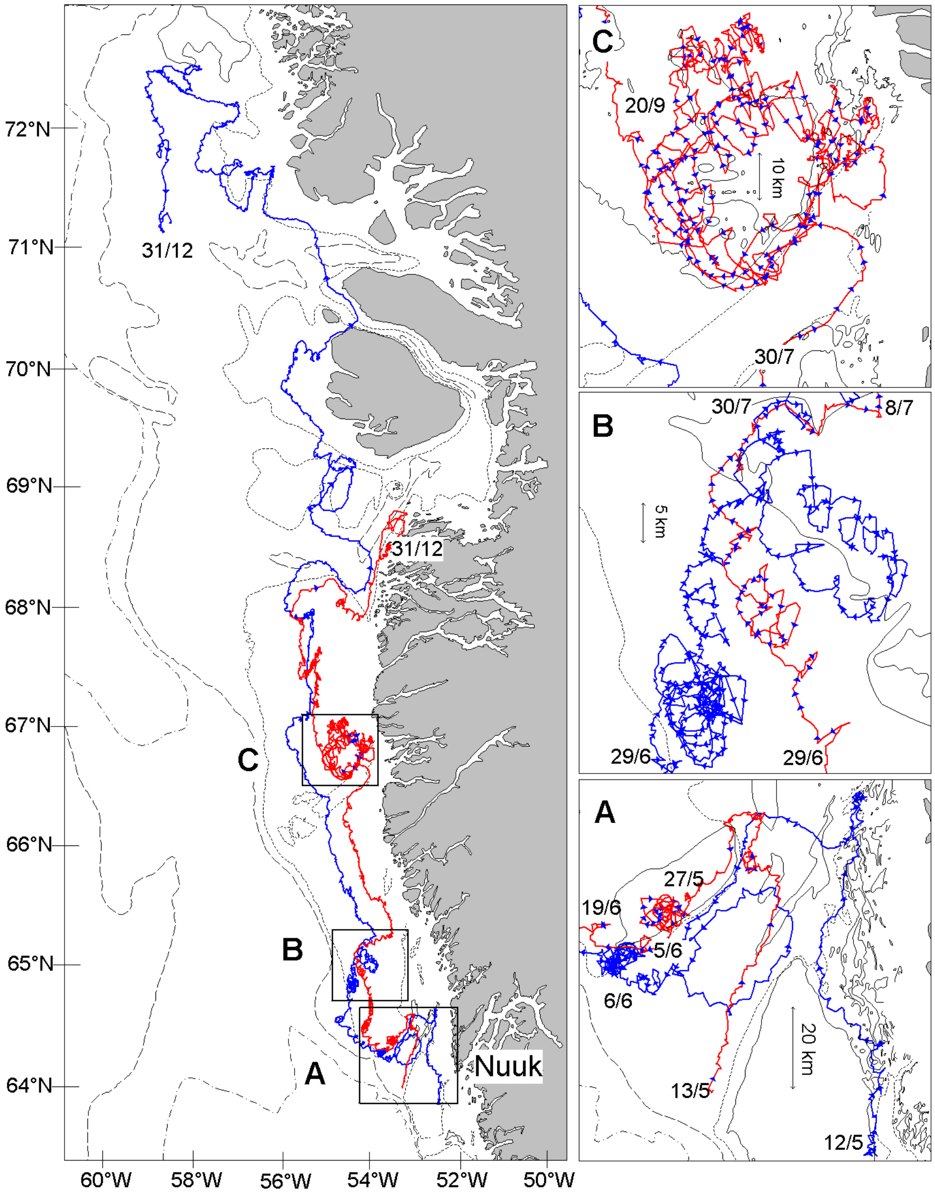

Fig. 7. Drift of the two satellite tracked SVP buoys (drogue at 30 m), No. 3377 (blue line), 12/5–31/12, 2000 and No. 3378 (red line), 13/5–31/12, 2000. **A**: following the bottom topography (No. 3377: 12/5–19/6; No. 3378: 13/5–6/6). B: daily tidal induced clockwise circulation of about 5 km in diameter (No. 3377: 29/6–30/7; No. 3378: 29/6–8/7). **C**: anticyclonic circulation around bank (No. 3378: 30/7–20/9).

May. Progressively later stage larvae were caught during June 1999 and July 2000. Although ZIV dominated, ZV and ZVI larvae were also present in July. This indicated a somewhat slower stage development and longer duration of the planktonic larval phase in waters of West Greenland compared to *P. borealis* populations in the Barents Sea and around Iceland. In the former ZVI larvae were present already in late-June and early July (Lysy, 1983), while at the same time period ZIV or early ZV larvae were present in waters northwest of Iceland (Astthorsson and Gislason, 1991). We estimate the planktonic phase

TABLE 3. Northern drift distances of the two satellite tracked SVP drifting buoys (drouge at 30 m), 12–13 May–31 July 2000.

	12/13 - 31 May		1 - 30 June		1 -31 July		12/13 May - 31 July	
Buoy	Distance (km)	Mean velocity (km/day)	Distance (km)	Mean velocity (km/day)	Distance (km)	Mean velocity (km/day)	Distance (km)	Mean velocity (km/day)
ID no. 3377	50	2.6	80	2.6	50	1.6	181	2.3
ID no. 3378	45	2.4	64	2.1	200	6.5	311	3.9
Mean	47.5	2.5	72	2.4	125	4.1	246	3.1

of *P. borealis* in West Greenland to be ~4 months which is similar to larval development in West Murman coastal waters (Lysy, MS 1981). Differences in sea-temperature are likely to be responsible for the slower development time. Temperature and so called "thermal increase enhancement" have a direct effect on *P. borealis* larvae by increasing growth and reducing mortality and development time (Shumway *et al*., 1985; Rasmussen, MS 1993; Tande *et al*., 1994; Rasmussen and Tande, 1995). However, periods of starvation or restricted food availability may prolong stage duration and increase mortality (T. Rasmussen, pers. comm.).

The depth-integrated plankton hauls presented in this study provided no information on vertical distribution of different stages, migrations, or time and stage of settling. Ouellet and Lefaivre (1994) found that ZI and ZII *P. borealis* larvae concentrated in the upper layers (<30 m) above the permanent pycnocline and coincident with subsurface chlorophyll *a* and suspended particle concentration maxima. During the cruise in May, plankton pump samples at different depths showed deeper and wider vertical distributions of ZI and ZII larvae (S. A. Pedersen, unpublished data). According to Rasmussen *et al*. (MS 2000), newly hatched *P. borealis* are positively phototactic, while ZIII the larvae tend to actively seek deeper water. The ZV is considered to be semi benthic (Rasmussen *et al*., MS 2000). In a study of temperature and salinity preference, Rasmussen *et al*. (MS 2000) found that all stages of larval *P. borealis* seek the highest available temperature (4.6°C). ZI and ZII larvae preferred a salinity of 28 psu, whereas ZIII and ZIV preferred higher salinities. Activity was reduced when exposed to low temperatures (0°C), but no mortality was observed (Rasmussen *et al*., MS 2000). The pelagic occurrence of ZV and ZVI in our studies may be due to avoidance of the cold intermediate water at depths of about 50 m, buoyancy effects of hydrographic features or vertical migration in search for food. Vertical distribution and planktonic occurrence of ZV and ZVI larvae may vary between areas and times due to differences in hydrographic features, food availability and biochemical larval condition.

The larval distribution patterns and lack of clear differences in the proportion of stages across banks and between transects, indicates wide larval dispersal and a relatively short period of hatching. According to Anderson (2000) larval emergence and recruitment success in *P. borealis* seems to be timed to and favoured by relatively late zooplankton peak abundance observed during a cold ecosystem regime.

Hydrography and biological habitat characteristics

The upper 200 m during May, June, and July were dominated by Polar water, which is characterised by temperatures below 0°C (increasing to 3–5°C in the surface layer during summer) and salinities below 34.4 psu (Buch, 2000). A hydrographic frontal zone between cold Polar water and warmer mixed shelf water over the bank was most clearly seen in June on the western part of Tr3 (Fig. 4). In May and July, fronts were difficult to identify across transects. Vertical clines were clearly seen between warmer and less saline water in the surface layers and near the coast due to freshwater runoff. The coarse spatial and temporal resolution of hydrographical data measurements makes detection of frontal processes difficult. Fronts may only occur periodically within the sampled areas. We found no relationship between larval shrimp abundance and water mass characteristics. This is similar to findings in Gulf of St. Lawrence and West Greenland (Ouellet *et al*., 1990; Pedersen and Rice, 2002).

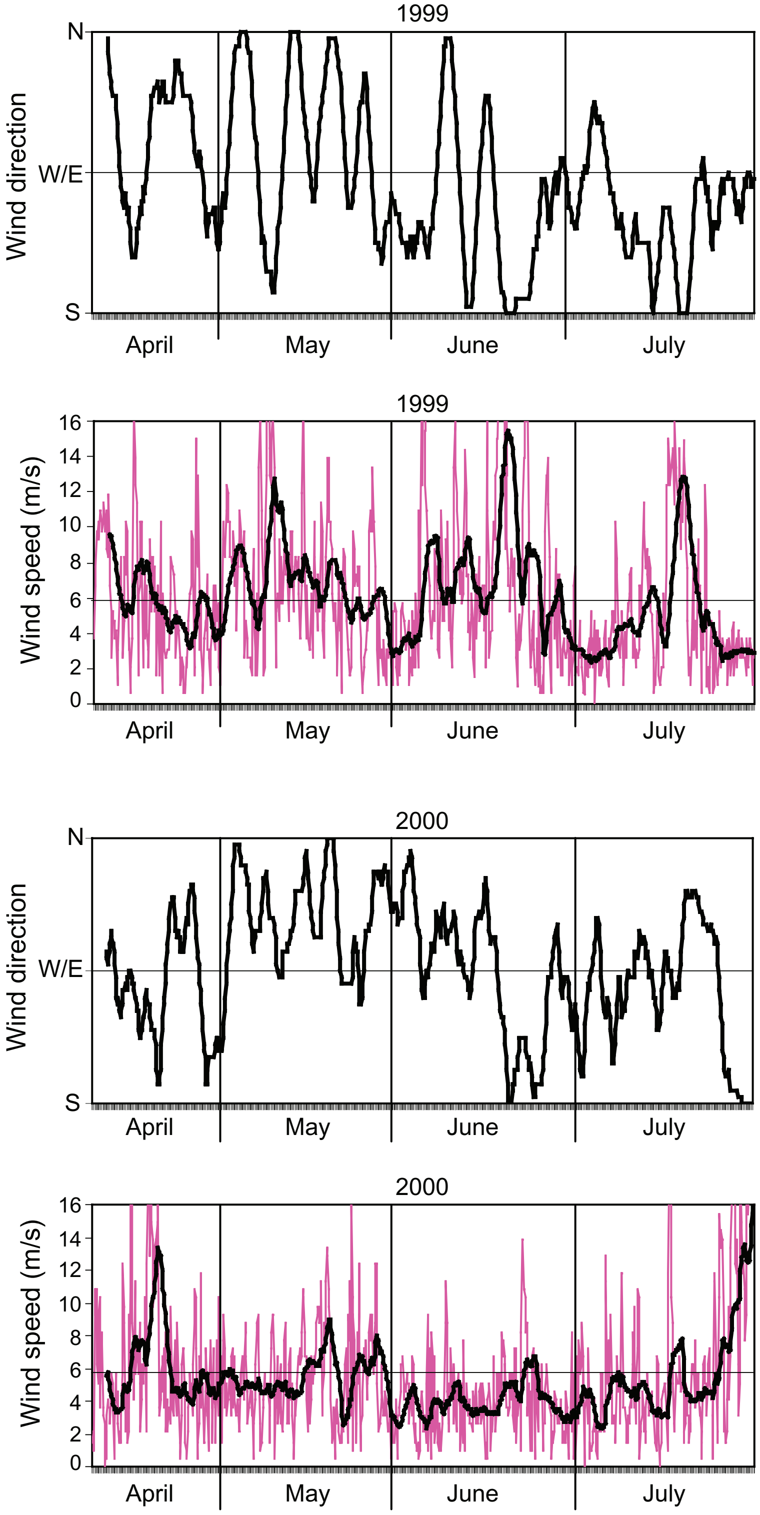

Fig. 8. Temporal variation in wind direction and speed in 1999 and 2000. Solid line is moving average. Data: from the Nuuk meteorological station, West Greenland.

In May and June, chlorophyll *a* was concentrated in the relatively cold Polar water mass (Fig. 6a,b). During the spring bloom in May the phytoplankton biomass (92 ± 45 mg C m^{-3}) was dominated by diatoms of *Thalassiosira* spp. and *Chaetoceros* spp. (Poulsen and Reuss, 2002). Fjord station 4 (Fig. 1) deviated from the spring-bloom stations with lower phytoplankton standing stock (30 mg C m^{-3}). In June, a post-bloom situation prevailed on most of Tr3 resulting in a very low phytoplankton biomass (2 ± 1 mg C m^{-3}) (Poulsen and Reuss, 2002). Peak phytoplankton biomasses (30 mg C m^{-3}) were found at the western part of Tr3 where diatoms of *Chaetoceros* spp. dominated. In July pronounced subsurface concentrations of chlorophyll *a* were observed in the upper 50 m of the water column on Tr1, Tr4, and Tr5 (Fig. 6a,c). The phytoplankton composition of these subsurface blooms was not investigated, but diatoms probably dominated (Nielsen and Hansen, 1999).

The mesozooplankton community over the West Greenland shelf in May, June, and July was dominated by copepods. The three species of large copepods *Calanus finmarchicus*, *C. glacialis*, and *C. hyperboreus* were dominating in terms of biomass. In terms of number the smaller copepods, *Oithona* spp. and *Microsetella* spp., dominated. Other studies have described the distribution and dominance of *Calanus* spp. in West Greenland plankton communities (MacLellan, 1967; Nielsen and Hansen, 1995; Pedersen *et al.*, 1999; Hansen *et al.*, 1999; Pedersen and Smidt, 2000; Madsen *et al.*, 2001). The biomasses of large and small copepods in the present study were in the same range as found in other studies conducted in the same areas in July (Pedersen *et al.*, 1999). An exception was the unusual high abundance and biomass of copepods and invertebrates at stations over deep water on Tr2 in July 2000 (Fig. 6d), which was an order of magnitude higher than other transects. The area crossed by Tr2 is an important summer feeding area for baleen whales, mainly humpback whale (*Megaptera novaeangliae*), which supports the findings of exceptional high plankton densities here (Finn Larsen, DIFRES, Charlottenlund, Denmark, pers. comm.). Special hydrographical features in this area may cause plankton aggregations. As the northward drifting *West Greenland Current* meets Sukkertop Deep and pass west of Tovqussaq- and Sukkertop Bank it produces complex gyres and circulation patterns in Sukkertop Deep and along the bank slopes which may aggregate zooplankton (Fig. 7).

We did not find relationships between larval shrimp abundance and either chlorophyll *a* concentrations or zooplankton abundance (species, groups or sizes classes). According to Stickney and Perkins (1981) the food of larval *P. borealis* is predominately diatoms taken through chance encounter, but also zooplankton is eaten when it is abundant. It may become more important than phytoplankton as the larvae grow during spring (Stickney and Perkins, 1981). Their laboratory observations showed that larvae could capture particles from 100µm to 1 mm efficiently, with efficiency dropping off above and below these limits, and cannibalism was not uncommon. Rasmussen *et al*. (MS 2000) investigated food preferences of shrimp larvae in laboratory experiments and they found ZI and ZII had higher clearance rates for alge than for other food items offered, while ZIII lost interest in planktonic algae. Shrimp larvae in ZIII to ZVI actively chased and ate smaller capelin and cod larvae when these were introduced (Rasmussen *et al*., MS 2000).

During laboratory studies of food concentration and shrimp larval survival, Stickney and Perkins (1981) found the following concentrations necessary for high survival: 400–1000 diatoms l^{-1} (at 4°C), 1 000 copepod nauplii l^{-1} or 500 copepodites l^{-1} (at 6°C). They also found that the concentrations of phyto- and zooplankton required for survival in laboratory experiments was far greater than would normally be found in the wild. Concentrations of the dominant diatoms were in the range 450–1220 cells l^{-1} along Tr1 and Tr3 in May (Poulsen and Reuss, 2002). We calculated the average (depth-integrated) concentrations of potential shrimp larvae food to be in the range of 1–100 zooplankton particles l^{-1} in June 1999 and July 2000. Actual food concentrations are likely to be higher because the particles are probably not evenly distributed in the water column. However, Pedersen and Storm (2002) found that most larvae in July exhibited low lipid condition, indicating generally low food availability. Temperatures were lower in the present study than during the observations by Stickney and Perkins (1981). The food particle concentrations, either phyto- or zooplankton, necessary to meet the requirements of shrimp larvae will depend on many factors e.g. larval shrimp size, temperature, the food value of the particle (species, size, energy content, etc.), predator and prey movements/activity, turbulence, and encounter rates (Savenkoff *et al.*, MS 1995; Rasmussen *et al*., MS 2000; MacKenzie, 2000; Incze *et al.*, 2001; Werner *et al.*, 2001). Werner *et al*. (2001) have investigated coupled models to explore the relative importance of biological and physical variables on the growth and survival of larval cod and haddock on Georges Bank. These model studies are relevant for studies of shrimp and fish recruitment in West Greenland waters. Although, modelling of shrimp recruitment differs by e.g. the omnivorous nature of the larvae and the presumably less important size specific predator-prey interactions. According to MacKenzie (2000), an important question to answer for future studies of fish stock recruitment is: Are the surviving individuals of a larval fish (or shrimp) cohort a subset of offspring which have experienced some optimal level of turbulence that enabled high growth or survival rates?

Larval drift

Hydrographic features, fronts and eddies may function as barriers to larval shrimp transport, or contribute to larval retention (Ivanov, 1967; Horsted *et al.*, MS 1978; Iles and Sinclair, 1982; Sinclair, 1988). In West Greenland larval drift by surface currents is assumed to be essential for the recruitment to downstream fishing areas and fjords, whereas larval retention may dominate in other areas. According to Horsted *et al*. (MS 1978) it is likely that current gyres occur in the shrimp area northwest of Store Hellefisk Bank and that the stock in this area is recruited mainly by local spawning. However, recruitment to some of the fishing grounds in Disko Bay appears to be dependant on drift from offshore shrimp populations. Larvae hatched in the bay itself may contribute to the local stock but some may also drift (through the Vaigat northeast of Disko) to more northerly offshore shrimp distribution areas. Knowledge of larval drift paths and hence links between subpopulations is important to develop management strategies, which take spatial variation of the recruitment process into account.

SVP drift buoy data indicated a net northward drift of about 3.1 km d^{-1} for the period from deployment (12–13 May) to 31 July. If we assume a shrimp cohort drifts in a similar fashion we can expect a net northward larval transport of 200–400 km during the pelagic larval life of ~4 months. This drift distance is somewhat less than previously assumed by Horsted *et al*. (MS 1978) due to the many gyres and circulations entrapping the buoys in this study. Wind fields and tidal motions are important in the generation of water mass transport e.g. up- and downwelling, tidal-front entrainment, advection and retention of plankton over the West Greenland shelf as elsewhere (Cushing, 1990; Lochmann *et al.*, 1997; Blanton *et al.*, 1999; Incze and Naimie, 2000; Lough and Manning, 2001). Observations on the Scotian Shelf indicated that physically driven retention, not differential mortality, was responsible for high abundances of cod larvae at a convergent front (Lochmann *et al.*, 1997). After deployment in May the buoys drifted north- and coastward. Northerly winds prevailed during this period and offshore Ekman drift in the upper layer replaced by upward-moving water from below may have forced the buoys (and newly hatched larval shrimp) north- and coastward. During June and July the buoys may have followed currents along wind and tidally induced gyres and hydrographic fronts. However, better spatial and temporal coverage will be required to confirm this and its biological implications.

Recruitment and year-class strength

The distribution of juvenile shrimp during the annual shrimp survey in 2000 and 2001 showed highest abundances in the deeps between the banks of southwest Greenland between 62°N and 65°N, north of Store Hellefisk Bank and in Disko Bay (Fig. 9; Kanneworff and Wieland, MS 2001; Wieland and Carlsson, MS 2001). Lilly *et al*. (1998) reported a wide spatial distribution of age-0 *P. borealis* whereas older juveniles were found primarily in shallow water and with increasing size, shrimp moved into deeper water (300–500 m). In West Greenland, analyses indicated that small males occur first in several relative small and isolated areas and extend over a wider region with increasing size and age (Wieland and Carlsson, MS 2001). During the 1990s the offshore West Greenland shrimp fishery moved southward, which may indicate stock migrations towards preferable habitat temperatures due to the changes in the ocean climate (Hvingel, MS 2001; Buch *et al.*, 2002). High fishing pressure on the shrimp population at Southwest Greenland may reduce future recruitment in this region but also in the areas further north.

In the Barents Sea, M. Aschan, Norwegian Institute of Fisheries and Aquaculture, Tromsø, Norway, pers. comm., found strong correlations between total egg production, number of spawning females, and recruitment index for age-1 shrimps. According to M. Aschan (pers. comm.), this indicates that natural mortality of shrimp larvae in the Barents Sea is constant the first year. Also in the Barent Sea, Pedersen *et al*. (2002) found larval shrimp transport patterns to vary between years, with the effect of annually different dispersion pattern of larval shrimp settlements. According to Pedersen *et al*. (2002) the

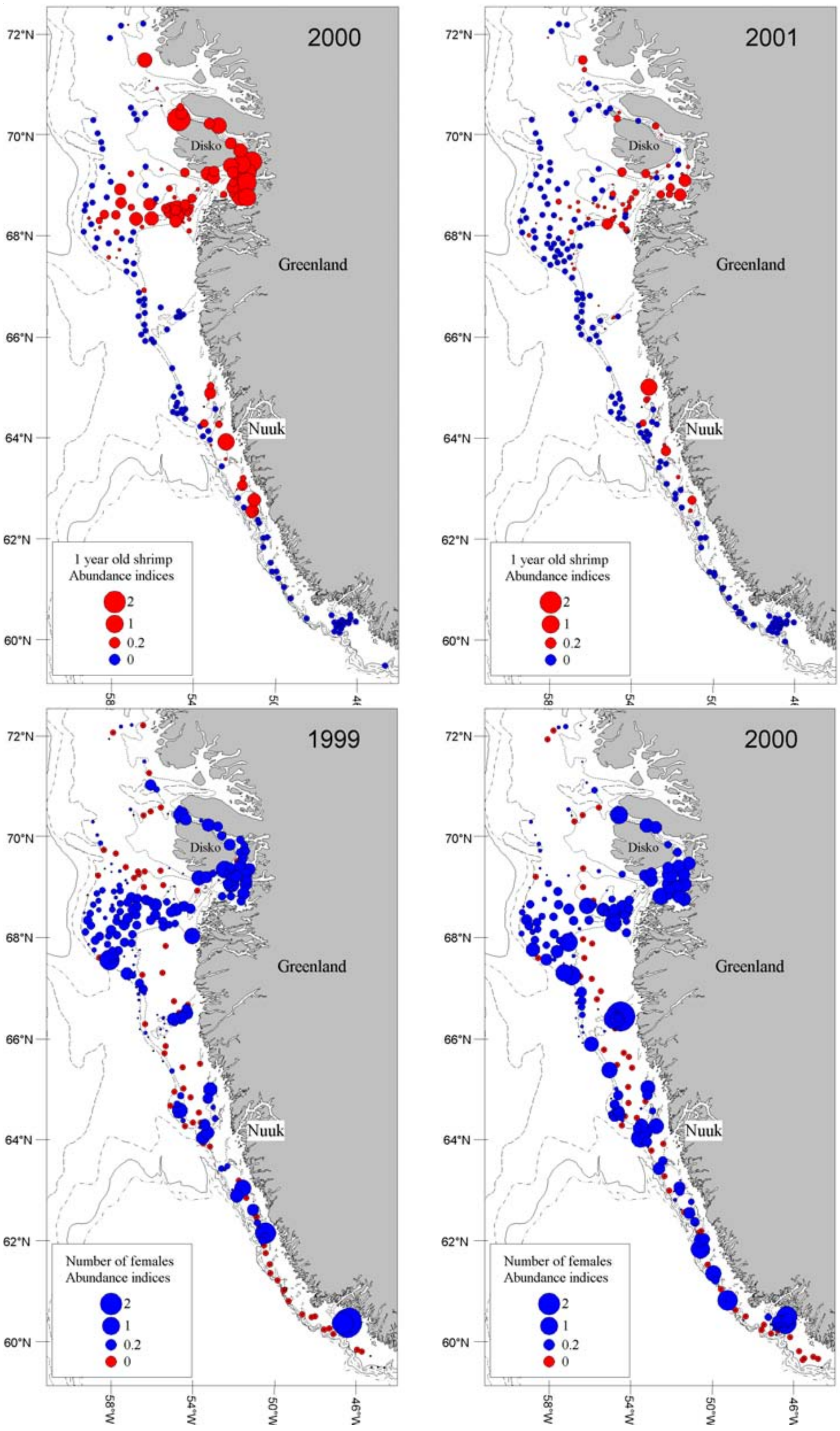

Fig. 9. Distribution and abundance indices (number m^{-2}) of juveniles (age 1) in 2000 and 2001 (top panels), and females in 1999 and 2000 (bottom panels). Data of age 1 abundance indices was provided by D. M. Carlsson (Greenland Institute of Natural Resources, Nuuk, Greenland, pers. comm.) and data of female abundance indices was provided by K. Wieland (Greenland Institute of Natural Resources, Nuuk, Greenland, pers. comm.).

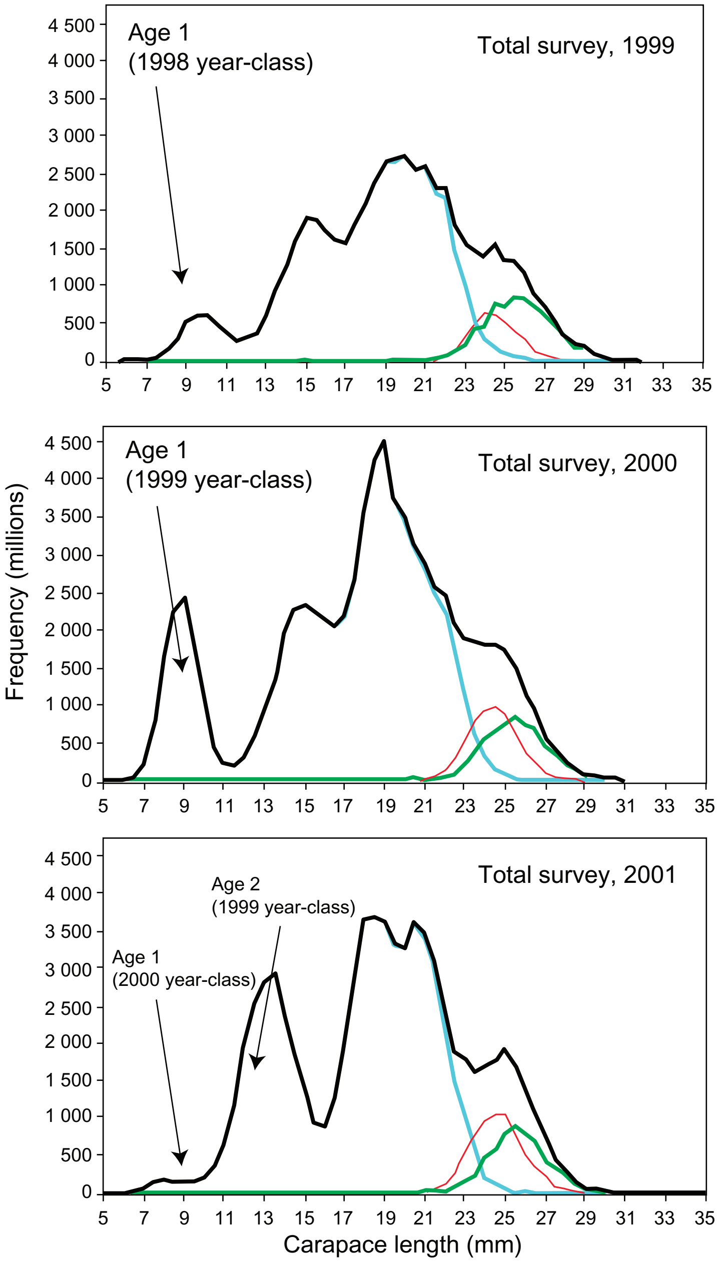

Fig. 10. Number of shrimp by length group in total survey area (offshore and Disko combined) 1999–2001. Modified from Kanneworff and Wieland, MS 2001. Blue line = males, red line = primiparous females, green line = multiparous females, and black = total.

shrimp in the Barents Sea should be considered as one stock, where female shrimp produce settling larvae in the whole distribution area. Pedersen *et al.* (2002) found a good agreement between the spatial distribution of modeled settled larvae and the abundance of 1 year old juveniles obtained from trawl surveys. For shrimp populations where no female stock-recruitment relationship is found particle tracking combined with biological models of pelagic larval development to settling may prove to be useful in detection of environmental impacts on recruitment success (Pedersen *et al*., 2002).

In West Greenland there is large variability in year-class strength as age-1, and no female stock – recruitment relationship have been found (Kanneworff and Wieland, MS 2001). For example the 1999 year-class being at least 10 times larger than the 2000 year-class is indicated in the size distributions of the annual West Greenland shrimp survey (Fig. 9 and 10). Differences between the two years in the environmental conditions and transport patterns of larvae during development are likely the main reason for this difference in year-class strength. Pedersen and Storm (2002) found shrimp larvae in better lipid condition in 1999 compared to 2000. The wind fields were different between the two years. In April–July 1999 wind speeds were higher and southerly winds occurred more frequently compared to 2000. According to MacKenzie (2000), resolving how larval growth rates vary with exposure to turbulence may be a suitable topic for both experimental and field evaluation.

We suggest that differences in climatological conditions between years and their effects on larval shrimp and plankton transport patterns, the physical environment (e.g. turbulence and encounter between larvae and their food), larval lipid condition indices, and larval survival should be investigated with coupled physical-biological models. Hence, future studies of shrimp recruitment in West Greenland should investigate and couple models of:

- climate change.
- physical flow field determining larval shrimp transport or retention.
- larval behaviour, e.g. vertical migrations.
- energy requirements of the shrimp larvae during development.
- food concentrations and production in the dynamic pelagic food web necessary for survival.
- effect of turbulence and prey encounter.
- match/mismatch hypothesis (Cushing, 1990).
- species interactions, e.g. to what extent do larval shrimp eat fish larvae and *vice versa*.
- regional nursery grounds, ontogenetic growth and movements to fishing grounds.
- top down effects e.g. effects of the shrimp fishery, increase in shrimp predators.

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Appendix 1: Figures shows *Pandalus* sp. Abundance

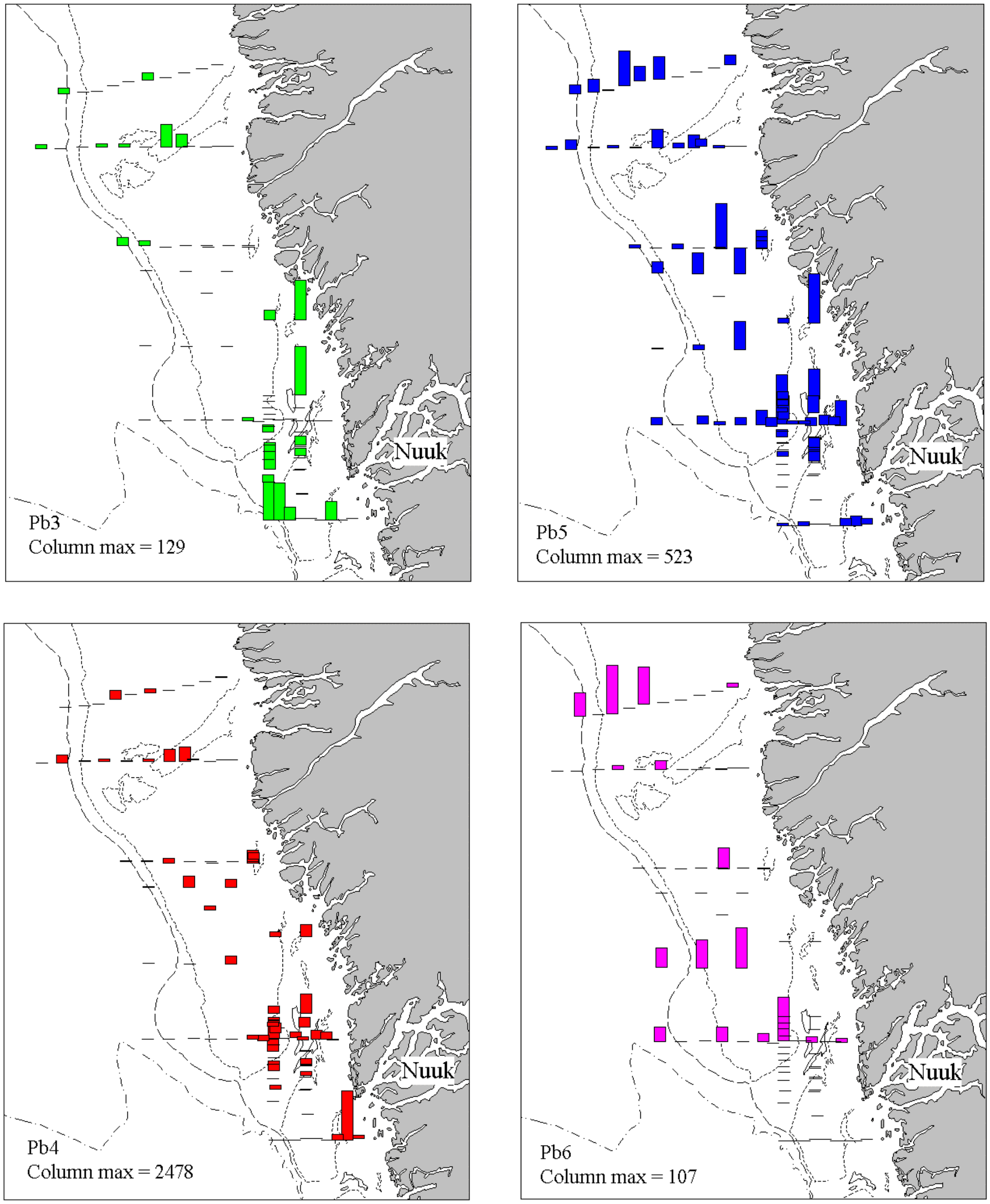

Fig. 1. Abundance indices of *P. borealis* larvae (number per 100 m^2) zoeal stage 3 to 6 (Pb3 to Pb6), July 2000.

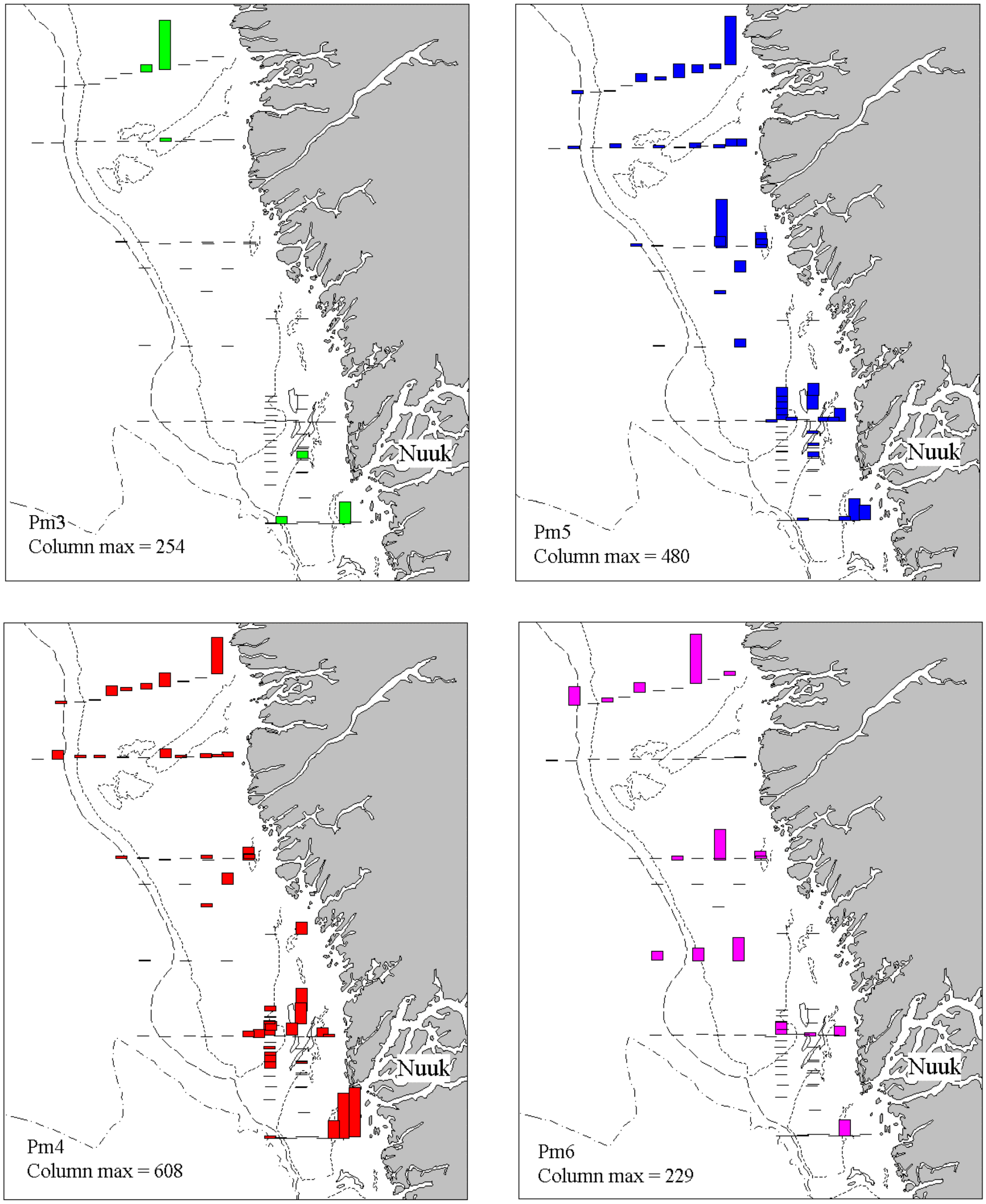

Fig. 2. Abundance indices of *P. montagui* larvae (number per 100 m^2) zoeal stage 3 to 6 (Pm3 to Pm6), July 2000.