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Distribution and Lipid Composition of Pandalus Shrimp Larvae in Relation to Hydrography in West Greenland Waters

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Abstract

The abundance and distribution of shrimp larvae were studied along four transects off West Greenland in June–July 1996. Zooplankton samples and vertical profiles of temperature, salinity, and fluorescence were obtained along the transects in order to relate larval distribution to hydrographical and biological characteristics. Eight species of shrimp larvae occurred in the samples; *Pandalus montagui* and *Pandalus borealis* were the most numerous constituting 61 and 29% of the larvae, respectively. Other species of shrimp larvae were, in declining order of abundance, *Sabinea septemcarinata*, *Lebbeus groenlandicus*, *Spirontocaris spinus*, *Eualus galmardi*, *Pontophilus* (*norvegicus*?), and *Argis dentata*. Pandalus shrimp larval density showed a significant positive association with mean fluorescence (5–80 m), but no association with mean temperature, or densities of copepod eggs and nauplii. However, most larvae were caught in water columns with temperatures and salinities of ~2°C. and ~33 psu, respectively. Abundance of *P. montagui* was negatively correlated with mean salinity and the proportion of *P. montagui* was higher in stations closest to the coast. Catches of *P. montagui* and *P. borealis* larvae were positively correlated (r = 0.729).

Analysis for lipid class composition in *P. montagui* and *P. borealis* zoea stage 3 and 4 revealed that phospholipids were the most abundant lipid class (~80% of total lipid weight) followed by triacylglycerols (TAG) (10–15%), and wax esters (3–6%). TAG wet-weight ratios of *P. montagui* and *P. borealis* larvae were used as indices of feeding condition, and showed differences between larval species, zoeal stage, sampling station, and transect. In the same zoeal stage *P. montagui* larvae had higher TAG condition indices than *P. borealis* larvae suggesting that *P. montagui* may have a greater growth and survival potential. The TAG condition indices showed a significant negative association with fluorescence and indices of copepod productivity for stage 4 *P. montagui* larvae and no associations for *P. borealis* stage 3 and 4 larvae. Future studies should investigate lipid condition of the earliest stages of *P. borealis* and *P. montagui* larvae and establish trophic relationships (lipid nutrition) using food web tracer lipids. Such studies could be important to achieve better recruitment predictions for both species.

Key words: abundance, condition, distribution, larvae, lipid, shrimp, W. Greenland

Introduction

During the last 20 years the most important fishery resource in West Greenland waters has been the northern shrimp (*Pandalus borealis*). Annual landings of northern shrimp from West Greenland waters increased from 7 000–8 000 tons in the early-1970s to close to 87 000 tons in 1992, the highest level in the history of this fishery (Anon., 1997). Historically the shrimp fishery at West Greenland has taken place in two main areas (Carlsson, 1997): (1) the inshore shrimp fishery (inside the three-mile limit) at West Greenland, taking place mainly in the Disko Bay, but also in a number of fjords and along the West Greenland coastline, (2) the offshore West Greenland shrimp fishery, outside the three-mile limit. Today the fishing industry as well as the economy in Greenland is mainly dependent on this large northern shrimp fishery, based on stable recruitment of new year-classes to the shrimp stocks (Christensen and Vestergaard, 1993). However, knowledge of recruitment variability and its causes for the shrimp stocks at West Greenland and in other areas is sparse (Hvingel, 1997).

Shrimp stock assessments require information on strength of recruiting year-classes as early as possible. Current forecasts of shrimp stock productivity and potential fishing yields are weak partly due to lack of knowledge of population processes from hatching until first capture in the fishery at about 4 years of age. Shrimp stocks may fluctuate between high and very low stock levels within only a few years (e.g. Gulf of Alaska and Gulf of Maine stocks). Other examples show sudden occurrence of new productive shrimp fishing grounds (e.g. the Flemish Cap fishery). Changes in hydrographical conditions (water temperature) have been described as a main factor for northern shrimp stock fluctuations (Shumway *et al.*, 1985; Tande *et al.*, 1994; Rasmussen and Tande, 1995). Year-class strength of fish and shellfish populations is mainly determined during the early life stages (Cushing, 1995). Fluctuations in both abiotic (e.g. sea temperature, water mass stability, hydrographic fronts) and biotic (e.g. food availability, predation) factors affect growth and survival of fish and shellfish larvae (e.g. Stein and Lloret, 1995; Munk *et al.*, 1995; Ouellet *et al.*, 1995; St. John and Lund, 1996).

According to Ouellet *et al.*, (1992, 1995) a biochemical (lipid-based) condition index can reflect survival potential of *P. borealis* larvae. This may prove to be a powerful tool in assessing ecological factor(s) involved in recruitment processes of *P. borealis* populations. In high latitude areas, total lipid content of *P. borealis*, ranging from 10 to 52 months old, exhibits marked seasonal oscillations which are linked to the highly seasonal pelagic production cycle (Hopkins *et al.*, 1993). In general little is known about the lipid composition and relative energetics of field collected Pandalid shrimp larvae (Clarke, 1979; Hopkins *et al.*, 1993; Ouellet *et al.*, 1995). The objectives of this study were: (1) to describe species, stage, size, and lipid composition of shrimp larvae along four sampling transects off the West Greenland coast, and (2) to relate larval distribution and lipid condition indices to hydrographical and biological characteristics observed along the transects.

Materials and Methods

Study area and sampling

A total of 53 stations spaced at 4, 8 or 12 nautical miles along four transects off West Greenland were sampled from 26 June to 5 July 1996 with the 28 m Greenlandic research vessel *Adolf Jensen* (Fig. 1). Transects were placed across shelf areas where coastal water masses meet water of oceanic origin. The distance between station positions was short where hydrographic fronts might be established, enhancing productivity and larval aggregation (Munk *et al.*, 1995). On all stations zooplankton were sampled using a MIK plankton sampler (2 m diameter ringnet) equipped with a 16 m long black polyfile net of 1 mm mesh size. The basic design of the gear is illustrated in Munk (MS 1993). For stations 30 to 53 (the two southernmost transects) a Bongo plankton sampler (diameter 0.61 m) equipped with 0.5 and 1 mm-mesh monofile nets was also used. Zooplankton samples were obtained using depth integrated oblique tows to about 80 m (or to near the bottom) at a towing speed of about 3 knots. The volume filtered was determined using General Oceanics flowmeters. On each station a Sea-bird 25-01 sea logger CTD was used to obtain vertical profiles of temperature (SBE 3), salinity (SBE 4), and fluorescence (Chelsea). On every second station the density (in number per m^3) of copepod eggs and nauplii in the upper 60 m was obtained from one vertical haul with a ringnet (22.5 cm diameter and 50 µm mesh size) to provide indices of copepod productivity. At 16 stations, fresh *Pandalus* sp. larvae were randomly picked out of the samples and frozen individually in 20 mm glass tubes at -25°C for later determination of lipid contents in the laboratory. Remaining organisms were preserved in 4% buffered formalin. Associations among temperature, salinity, fluorescence, indices of copepod productivity, and shrimp larval density (number per m^2) were investigated by Spearman rank correlations. The number of shrimp larvae caught by the two Bongo nets was compared using Chi-square (χ^2) tests ($p \times q$ contingency tables) (Campbell, 1975).

Species, stage size and abundance of the shrimp larvae

In the laboratory all shrimp larvae were sorted from the MIK and Bongo zooplankton samples. In samples containing more than 200 shrimp larvae, the sample was split so that a minimum of about 100 shrimp larvae were counted and identified to species. Shrimp larvae from most of the MIK hauls and from a few selected Bongo hauls (e.g. station 48 with no MIK sample) were identified to species and zoeal stage. Abundance estimates were standardized to number per square meter of sea surface to a sampling depth of 80 m or to the depth to bottom (over the Banks with depths less than 80 m) (Smith and Richardson, 1977). The fresh and formalin preserved shrimp larvae were measured for

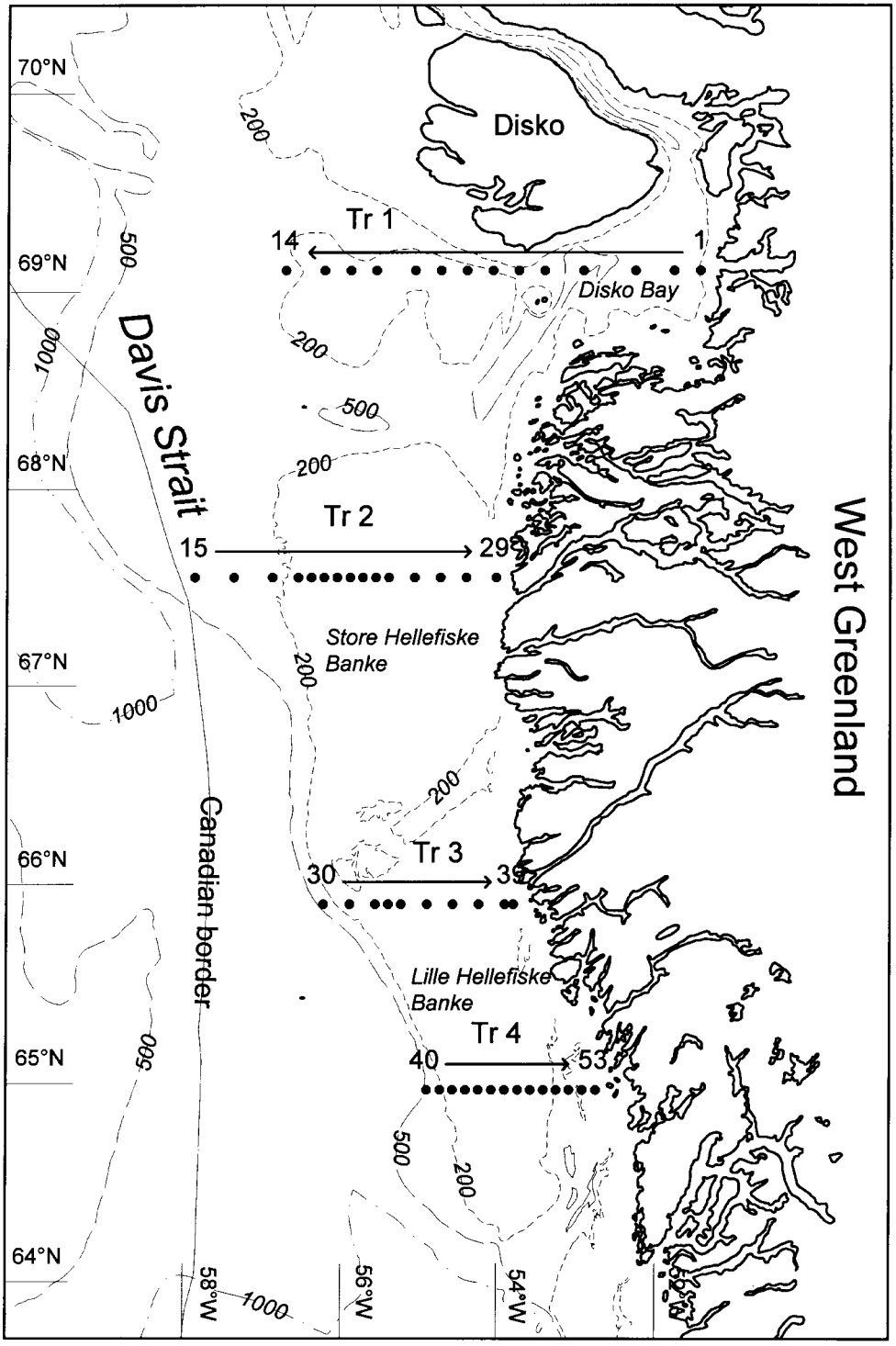

Fig. 1. Map showing transects and stations, direction of sampling, and the major physiographic features.

carapace length (posterior edge of orbit to mid-dorsal posterior margin of carapace) and total length (tip of rostrum to end of telson) under a dissecting microscope with an optical micrometer. Multi-way and one-way analysis of variance (ANOVA) was used to test for differences between stations and

transects in mean size by species and zoeal stage (Anon., 1985; GLM procedure).

Species and stage identifications of the shrimp larvae were based on the following: *Pandalus borealis*, Berkeley (1930), Haynes (1979, 1985), Squires (1993); *Pandalus montagui*, Pike and Williamson (1964), Squires (1993); *Lebbeus groenlandicus*, Haynes (1978), Squires (1993); *Sabinea septemcarinata*, Squires (1993); Other species, Squires (1993).

Biochemical analysis and larvae condition

A total of 162 randomly selected shrimp larvae (*Pandalus borealis* and *P. montagui*) from 12 stations were analyzed for lipid class composition (Table 1). The stations were selected along transects 3 and 4 (coast to offshore) to investigate variation in lipid content of the larvae in relation to changes in the environment (temperature, salinity and abundance of potential larval food). Larvae from one station on transect 2 were also included to test for possible south to north effects on the lipid contents.

Lipid extractions were performed on individual larvae for 2 × 24 hours in 2 × 1 ml chloroform/methanol (2:1 v/v) at -20°C with a known quantity (ca. 45 µg) of Nonadecane added as an internal standard. After extraction the solvent was evaporated under a stream of argon-gas and the lipid extract was resuspended in 50 µl of solvent. 1.4 µl of the sample was then spotted on a SIII–Chromarod for quantification using flame ionization detection with a model MK–5 IATROSCAN TLC/FID analyzer (Iatron, Inc., Japan). The rods were initially developed for 31 min in hexane – ethyl ether – formic acid (82:2.5:0.045, v/v/v, following Ouellet *et al.* 1992) allowing separation of the Nonadecane and the esters. Each rod was then developed for 28 min in hexane – ethyl ether – formic acid (55:29.7:0.075, v/v/v, following Ouellet *et al.*, 1992) for separation of the sterol-ester (WAX), triacylglycerol (TAG), free fatty acid (FFA), and free sterol constituents (CHL). The polar lipids (phospholipids (PHO)) were quantified using an addition of a third chromarods development (25 min in chloroform:methanol:water (70:30:3.5, v/v/v). The quantification of each lipid constituent was based on calibration curves constructed from solutions of standard lipids. For each shrimp larva the analysis for lipids was run twice in order to minimize errors. In general an average of the two calculations of lipid contents was used, however, in a few cases only one of the calculations was within the normal range and reliable. The latter was mainly restricted to phospholipids and due to error in the quantification procedure. Wet weights (WW) and dry weights (DW, freeze-dried for 24 hours using CD52 (HETO)) were measured for each individual larva before and after lipid extractions to the nearest 0.01 and 0.005 mg, respectively. Hence, the dry weights were "lipid free" weight.

TABLE 1. Number of shrimp larvae (N) analysed for lipid content by station. *Pandalus borealis* stage 3 and 4 = Pb-3 and Pb-4; *Pandalus montagui* stage 3 and 4 = Pm-3 and Pm-4.

Station no.	Pb-3	Pb-4	Pm-3	Pm-4	
	N	N	N	N	Sum
23	2				2
31	10	4			14
36	1	1	4	5	11
37	3	3		9	15
39	1	3		16	20
42	6	4			10
43	1	14			15
44	5	6		4	15
46	5	10			15
49	2	9		4	15
50	6	7		2	15
53	2	4	1	8	15
Sum	44	65	5	48	162

Lipid content (WAX, TAG, FFA, CHL and PHO) relative to wet and dry weight of individual larvae was investigated for variation among species, size, stage, sampling station and transect using multi- and one-way analysis of variance (ANOVA) (Anon., 1985; GLM procedure). Associations among fluorescence, indices of copepod productivity, larval density (number per m^2) and TAG condition indices were investigated using Spearman rank correlations (Anon., 1985; CORR procedure).

Results

Hydrography, fluorescence and indices of copepod productivity

Temperature along the four transects showed a general increasing trend from north to south (Fig. 2). Cores of very cold water (below -1°C) were found at depths between 20 and 100 m in the Disko Bay area, on the western most stations close to the edge of the West ice on transect 1, and on the

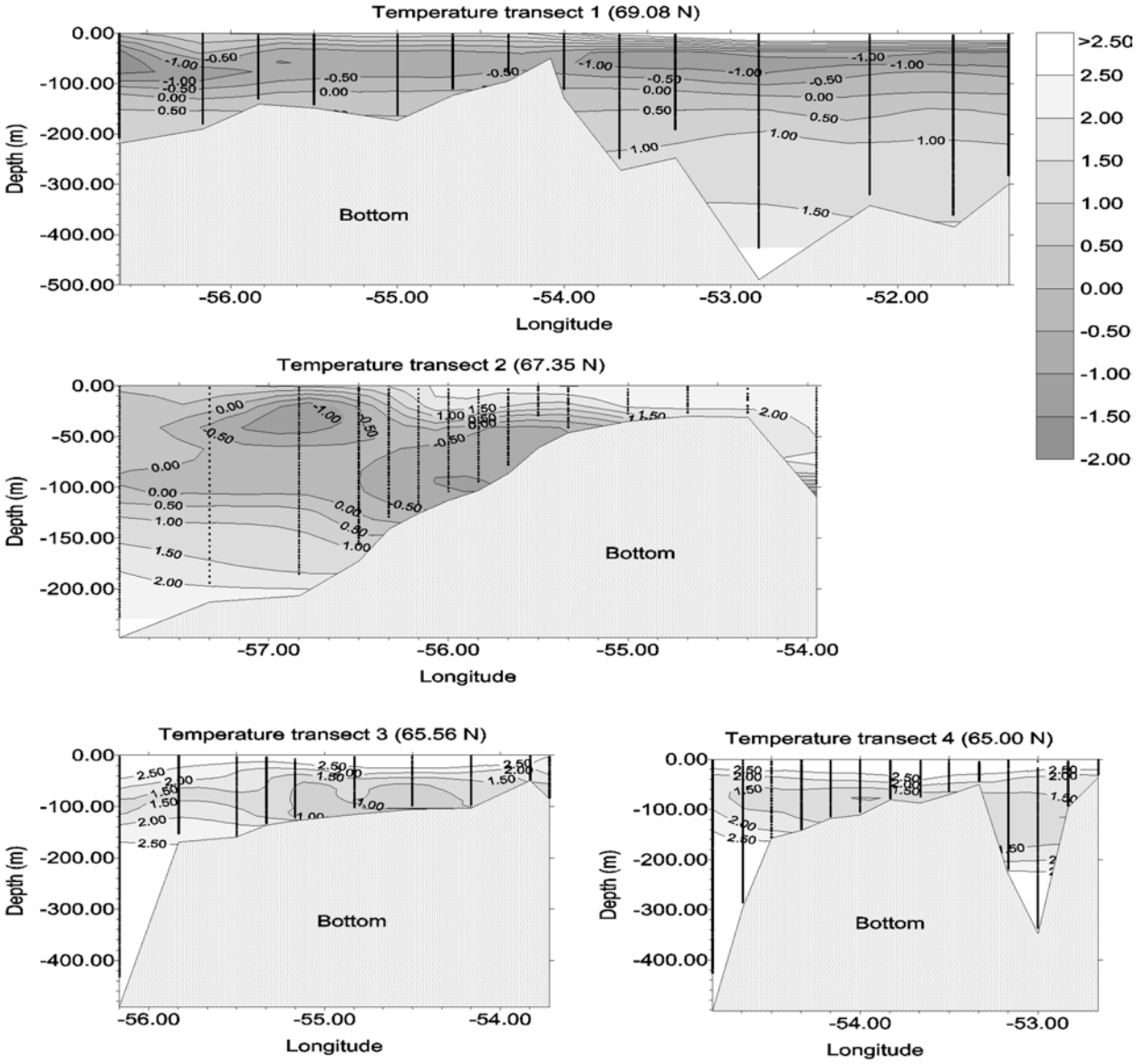

Fig. 2. Vertical sections of temperature (°C) along transects 1–4. Vertical lines indicate sampling stations and depths.

western slope of the shelf on transect 2. On transect 3 and 4 cores of cold water (from below 1 to 1.5°C) were found at depths between 60 and 120 m. The salinities varied from 32.0 to 34.7 psu with the lowest salinity levels in the surface layer of transects 1 and 2 and the highest in the bottom water layer at the western most stations of transect 3 and 4 (Fig. 3). The temperature and salinity profiles along the transects showed no or weak indices (transect 2) of frontal or upwelling zones (Fig. 2 and 3).

The fluorescence data indicate how primary productivity changed along and among the transects (Fig. 4). On transect 1 and 3 there were peaks in the fluorescence at about 40 m (range 20–60 m), whereas the peak was deeper at transect 2 (60 to 120 m), and shallower at transect 4 (0–40 m). The mean fluorescence in the depth range 5–80 m differed significantly between stations and between transects (Fig. 4). Transect 1 generally showed the highest fluorescence although there were variations

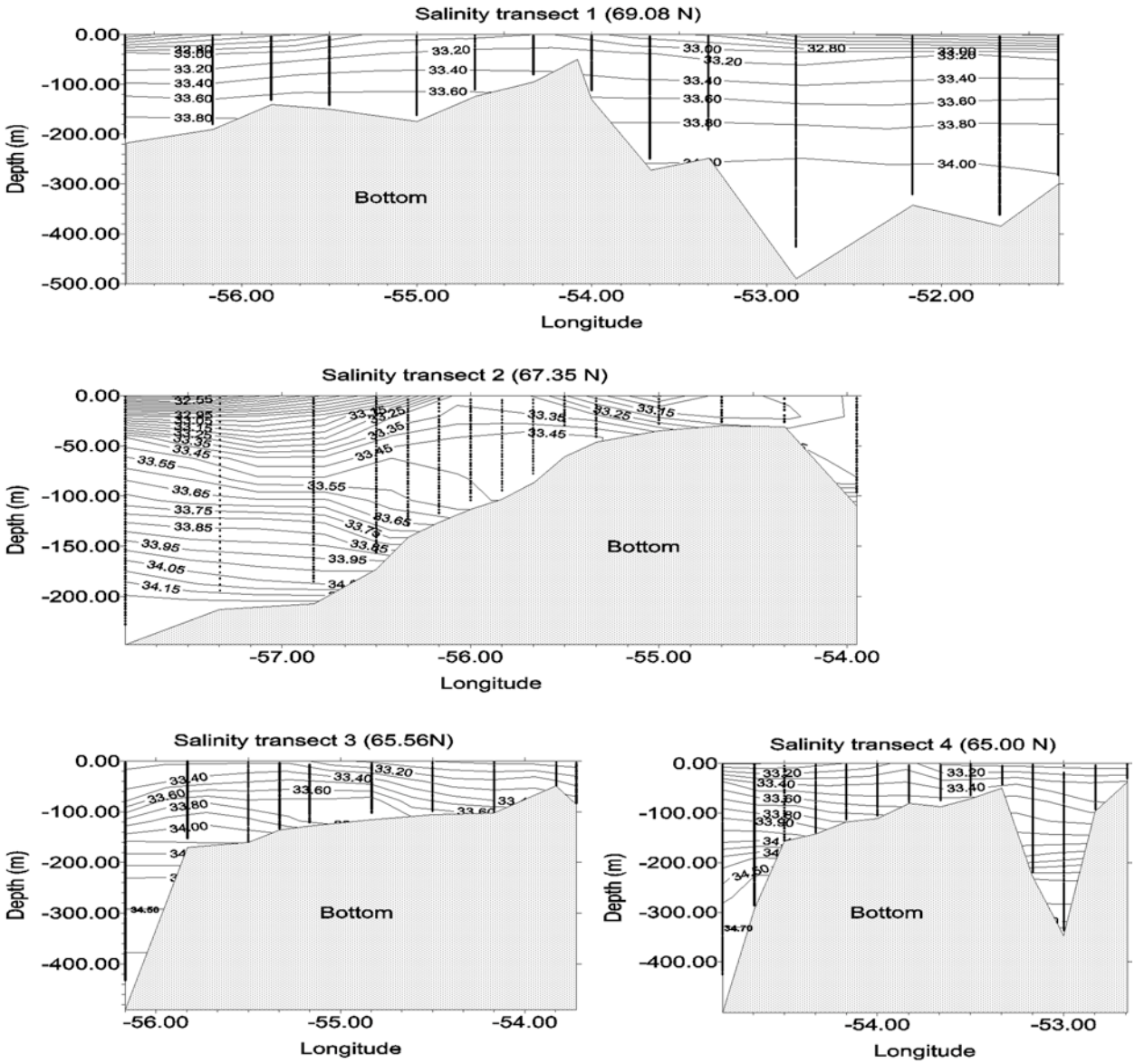

Fig. 3. Vertical sections of salinity (psu) along transects 1–4. Vertical lines indicate sampling stations and depths.

along the transect. Transects 2, 3 and 4 all showed the highest mean fluorescence on the station closest to the coast (Fig. 4). Densities of copepod eggs + nauplii ranged from about 50 to 7500 per m^3 with no clear trend in abundance along or between transects (Peter Munk, unpubl. data). In addition, the ratio egg concentration/nauplii concentration at each sampling station was about 1:1 with no clear trends within or between transects There was no significant correlation between mean fluorescence (5–80 m) and density of copepod eggs + nauplii (n = 26, r = 0.28, p = 0.16).

Shrimp larval catches and abundances

MIK. The estimated total number of shrimp larvae caught with the MIK plankton sampler was 9 737. The highest abundances of shrimp larvae were found on stations 38 and 39 with a total number per haul of 3454 and 4154, respectively. Large catches were also taken on stations 22, 23 and 24 with total numbers per haul of 274, 753 and 248, respectively. The shrimp larvae catches with the MIK sampler recalculated to number of shrimp larvae per m^2 in the upper 80 m of the water column

showed the same relationships (Fig. 4). Shrimp larval abundance was significantly correlated with mean flourescence (5–80 m) on transect 4 ($r = 0.76$, $p = 0.002$), but not on transects 2 and 3. Shrimp larval abundance showed no significant correlation with indices of copepod productivity (number of eggs + nauplii per m^3), mean temperature or mean salinity (5–80 m).

Bongo. The total catch of shrimp larvae in the 24 Bongo hauls with 0.5 mm and 1 mm nets was 2 234 and 3 317, respectively. The largest catches were taken on stations 37, 38 and 39 and the number of shrimp larvae caught was 232, 596, 980 (0.5 mm net), and 576, 883, 1486 (1 mm net), respectively. On transect 3 there was a significant difference ($\chi^2_9 = 31.7$, $p < 0.1$) between the two Bongo nets, the 1.0 mm net catching more shrimp larvae. However, on transect 4 the 0.5 mm net caught significantly ($\chi^2_{13} = 28.6$, $p < 0.1$) more larvae than the 1.0 mm net. Compared with the MIK sampler, the Bongo sampler (both nets) had significantly higher

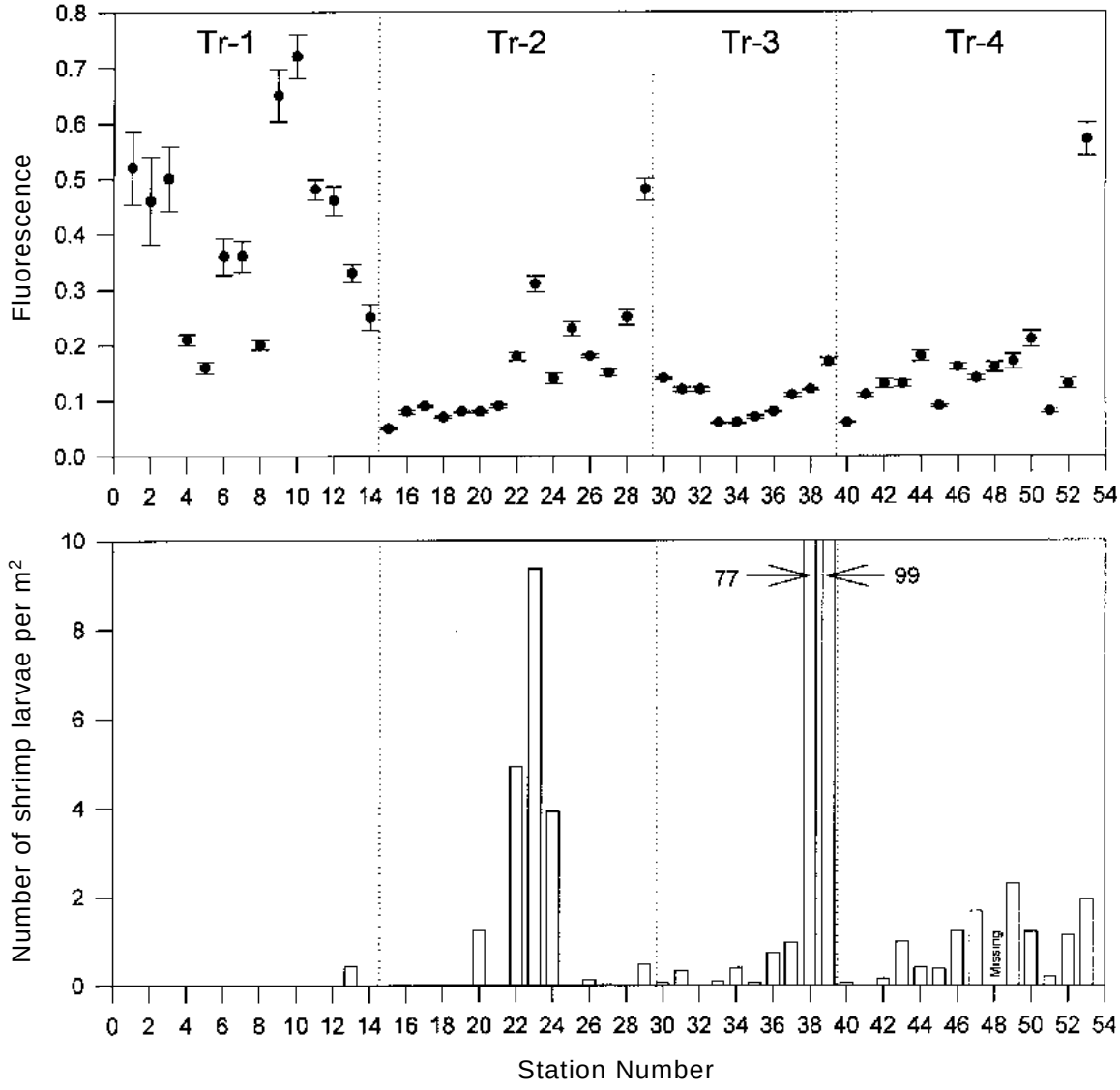

Fig. 4. Mean fluorescence with standard error of the mean (top), and shrimp larvae catches per m^2 by the MIK plankton sampler (bottom) along transects 1–4.

catches of shrimp larvae (on the order of 10 times as many). The difference between the samplers was best illustrated on transect 4 (Fig. 5). However, the catches of Bongo (mean of both nets) and MIK along transect 3 and 4 were significantly correlated (r = 0.88 and r = 0.64, respectively), shows the same trends, and the largest catches by all three net types were taken on the stations closest to the coast.

Species, stages and sizes of the shrimp larvae

Nine species of shrimp larvae were caught with the MIK plankton sampler (Table 2). Pandalid larvae composed over 90% of the catch (n = 1 278 identified larvae). Most Pandalid larvae were in zoeal stages 3 and 4; however, zoeal stages from 2 to 5 were present. Length distributions by stage show two size groups in stages 3 and 4 (Fig. 6). For larvae in zoeal stage 3 there are peaks in the size distribution at carapace length 1.6, 1.8, 2.4 and 2.5 mm. For larvae in zoeal stage 4 there are peaks in the size distribution at carapace length 1.8, 2.0, 2.2 and 3.0 mm. Pandalid larvae less than 2.0 and 2.7 mm carapace length in zoeal stages 3 and 4, respectively, were morphologically identified to *Pandalus montagui*, and the larger larvae to *P. borealis* after the method described by Ouellet *et al*. (1990). There was a north-south trend in the stage distributions of the Pandalid larvae (Fig. 6). The majority of the larvae caught on transect 2 were in stages 2 and 3 whereas the majority of the larvae on transects 3 and 4 were in stage 4. Multi-way ANOVA of larval size (carapace length) showed significant effects of transects, sampling station and type (species and stage) (Table 3). However, most of the variation was explained by transect and type. Mean sizes increased significantly from transect 2 to 4 and size varied significantly among species and stages (Table 3). One-way ANOVA by species and stage showed no significant (p >0.05) effect of transect for either *P. borealis* or *P. montagui* stage 3 larvae (Table 4). However, the *P. montagui* stage 4 larvae were significantly (p <0.001) larger on transect 4 compared to transect 2 and 3. The *P. borealis* stage 4 larvae were significantly (p <0.05) larger on transect 3 compared to transect 4 (Table 4).

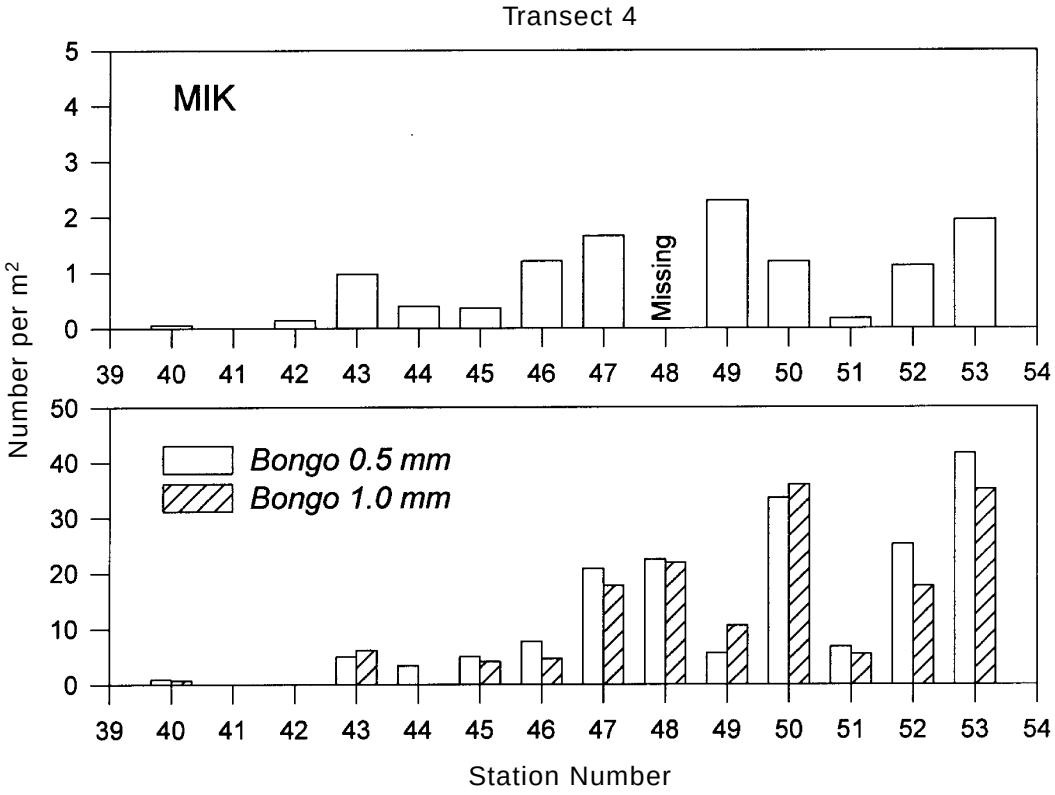

Fig. 5. Comparison of shrimp larvae catches from 3 plankton samplers (MIK, Bongo 0.5 mm, Bongo 1.0 mm) along transect 4.

TABLE 2. Species and stage composition of shrimp larvae caught in 53 hauls with the MIK plankton sampler.

Species	Number caught	% composition	Zoeal stage
Argis dentata	1	1>0.1	2
Crangonidae sp.	1	>0.1	?
Eualus galmardi	18	0.2	3
Lebbeus groenlandicus	302	3.1	2
Pandalus borealis/*P. montagui*	8 866	91.1 (32/68)	2–5
Pontophilus (*norvegicus*?)	3	>0.1	2–3
Sabinea septemcarinata	340	3.5	1–2
Spirontocaris spinus	206	2.1	2–4

There was a significant (p <0.001) relationship between carapace length and total length for both species, but r^2 was relatively low (0.15–0.41) and the linear regression slopes were not significantly different (p >0.05) among species or stages (Fig. 7). However, *P. montagui* stage 4 showed a broad size range and two apparent relationships a linear and a non–linear between carapace and total length. The wide size range in the Pm-4 larvae is also seen in Figure 6.

There was a significant correlation between the log10 transformed catches of *P. montagui* and *P. borealis* larvae (r = 0.729, p <0.01, n = 33). The majority of the larvae were caught in water columns with average temperatures and salinities about 2°C and 33 psu, respectively. The catches of *P. montagui* and *P. borealis* larvae showed no correlation with temperature. However, the catches of *P. montagui* larvae were negatively correlated with salinity (r = -0.447, p <0.01, n = 33), whereas *P. borealis* larvae showed no correlation to salinity. There was an increased proportion of *P. montagui* larvae in catches towards the coast on transect 2 and 3 but not on transect 4 (Fig. 8).

Lipid content and condition indices

Phospholipids (PHO) accounted for the major fraction of the total lipid content in *P. montagui* and *P. borealis* larvae (Fig. 9). The triacylglycerols (TAG) were the most abundant neutral lipid followed by wax esters (WAX), free sterols (CHL), and free fatty acids (FFA) (Fig. 9). The FFA/TAG ratio was low (<0.15) in all larvae indicating high quality of the samples and low lipid degradation before, during, and after the storage period (Christie, 1982).

Both TAG to wet weight and TAG to dry weight ratios were investigated as indices of larval feeding condition. The two indices were strongly correlated (TAG/DW – index = 10.6 x TAG/WW – index, r^2 = 0.93, n = 160). The TAG/WW index was used because it was easier to obtain.

Multi-way ANOVA of TAG to wet weight ratios showed significant effects of transect and species (stage), but no significant effect of sampling station within transect (Table 5). One-way ANOVA by transect, species and stage with station as class variable showed no significant (p >0.05) effect of station and no clear trend along each transect in the mean TAG to wet weight ratios (Fig. 10) or in the mean wet weight ratios of other lipid components. Looking at the mean WAX, TAG and FFA to wet weight ratios for each species, stage and transect the mean lipid contents increase from south to north (transect 4 to 2) (Table 6). However, one-way ANOVA revealed that only mean TAG to wet weight ratios for *P. borealis* stage 4 and mean FFA to wet weight ratios (both species and stages) were significantly (p <0.05) different between transects (Fig. 10 and Table 6).

The neutral lipids (WAX + TAG + FFA + CHL) to wet weight ratios were significantly increasing from transect 4 to 2, from *P. boralis* to *P. montagui* larvae, and on transect 3 and 4 from costal to offshore stations (Table 7). There was a significant (p <0.05) decrease in the contents of neutral lipids from stage 3 to 4 by species, and by stage *P. montagui* larvae were in significantly better lipid condition than *P. borealis* larvae (Table 5–7, Fig. 10). As larval size increased the relative TAG content showed a significant decreasing trend for

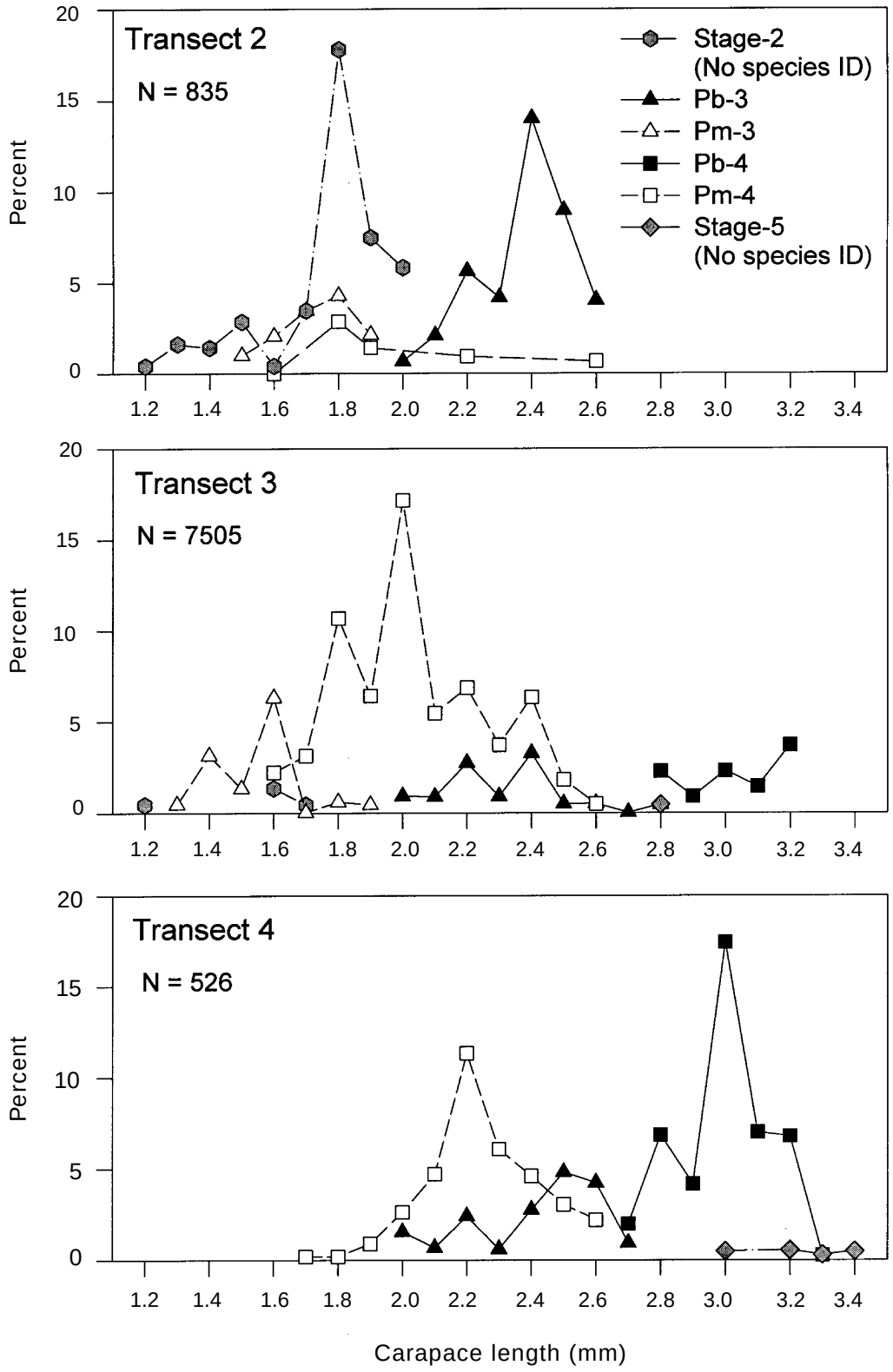

Fig. 6. Size frequency distribution of *Pandalus* larvae caught with the MIK plankton sampler by transect and larval stage.

TABLE 3. Results of a nested multi-way ANOVA of larval carapace length (CPL). Model: CPL = Overall mean + TR + TYPE + ST(TR) + TYPE(TR) + Err, where TR = transect 2–4, TYPE = Pandalid species and stage [*P. borealis* (Pb) or *P. montagui* (Pm) and stage 3 or 4], ST(TR) = sampling station nested within transect, and TYPE(TR) = species and stage nested within transect.

Dependent Variable: CPL

Source	d.f.	Sum of Squares	Mean Square	F Value	Pr > F
Model	33	142	4.3	138	0.0001
Error	798	25	0.03		
Corrected Total	831	168			

R-Square	C.V.	Root MSE	CPL Mean
0.85	7.6	0.2	2.3

Source	d.f.	Type I SS	Mean Square	F Value	Pr > F
TR	2	39.2	19.7	627.5	0.0001
TYPE	3	99.0	33.0	1054.4	0.0001
ST(TR)	23	3.2	0.1	4.4	0.0001
TYPE(TR)	5	1.1	0.2	7.0	0.0001

TABLE 4. Mean carapace length and total length for two stages of *P. borealis* and *P. montagui* larvae by sampling transect.

	P. borealis Stage 3			*P. borealis* Stage 4			*P. montagui* Stage 3			*P. montagui* Stage 4		
Transect	No.	Mean	Std. err.	No.	Mean	Std. err.	No.	Mean	Std. err.	No.	Mean	Std. err.
						Carapace length (mm)						
2	54	2.40	0.02				19	1.71	0.02	9	2.01	0.10
3	68	2.36	0.02	43	3.03	0.02	85	1.66	0.02	235	2.09	0.01
4	74	2.41	0.02	136	2.97	0.01	2	1.82	0.14	107	2.26	0.02
						Total length (mm)						
2	6	9.94	0.35				13	7.50	0.26	2	8.10	1.09
3	46	10.23	0.09	31	12.82	0.15	59	7.28	0.08	173	8.96	0.06
4	28	10.17	0.09	45	12.35	0.11				70	10.13	0.16

larvae stage 3, but no significant relationship for *P. borealis* or *P. montagui* in stage 4 (Fig. 11). The relative WAX content showed a similar decreasing trend with larval size for *P. borealis* larvae stage 3 and no relationship with size for *P. montagui* or *P. borealis* stage 4 (Fig. 11). The relative CHL content showed a weak increasing trend with size only for *P. borealis* stage 4 (Fig. 11).

Rank correlation analyses between the TAG condition indices (Pm-4, Pb-3 and Pb-4) and fluorescence, density of copepod eggs+nauplii, and shrimp larval abundance, respectively, showed significant correlations only between the TAG condition indices of Pm-4 and fluorescence (n = 7, r = -0.82, p = 0.03) and density of copepod eggs + nauplii (n = 4, r = -1.0, p = 0.0001).

Discussion

Abundance and distribution

The proportionate representation of *P. montagui* (68%) and *P. borealis* (32%) larvae in our samples does not correspond to current estimates of adult stock size of the two Pandalid species at West

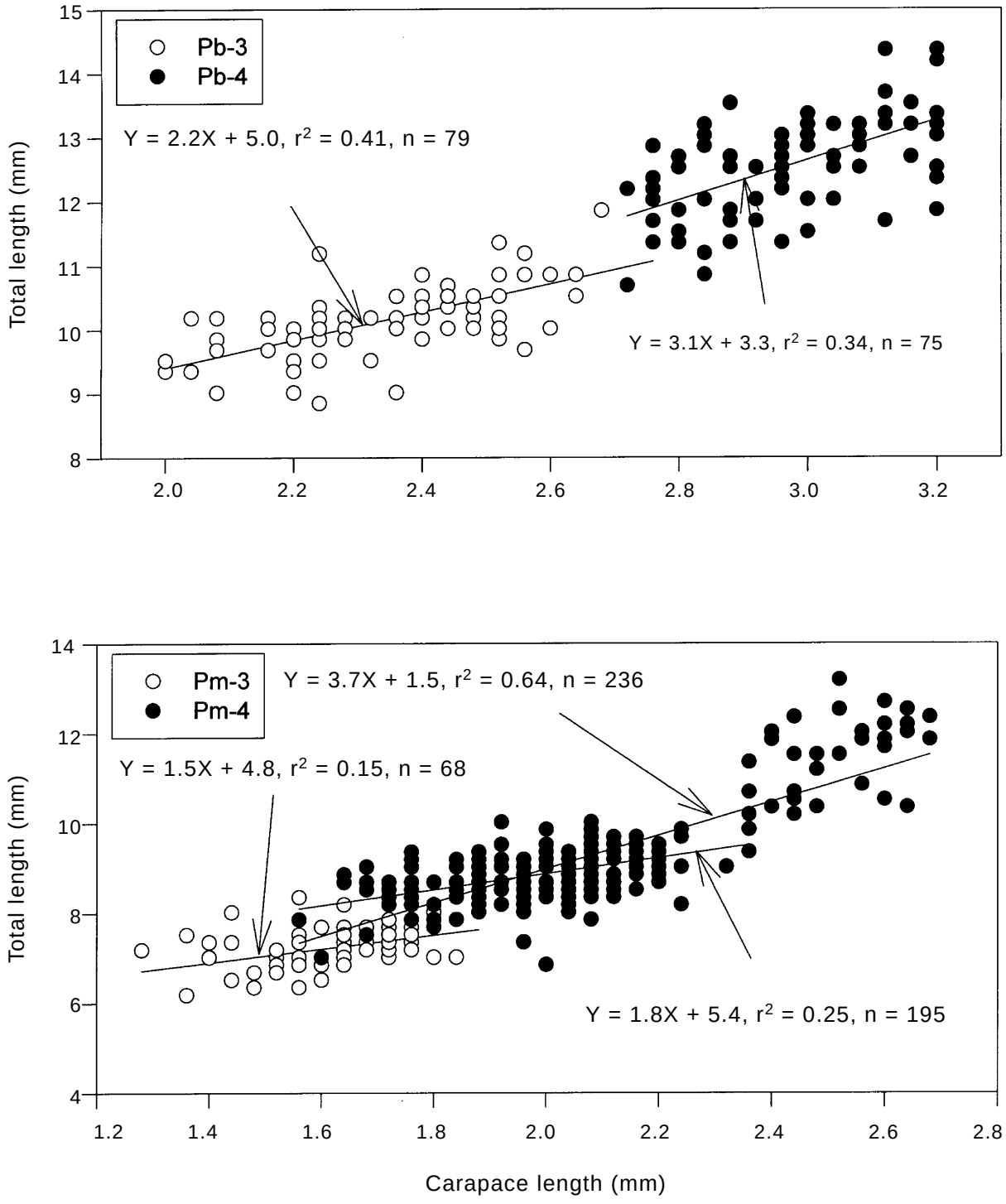

Fig. 7. Carapace length *versus* total length of *P. borealis* (top) and *P. montagui* (bottom) stage 3 and 4 larvae.

Greenland. The stock size of *P. borealis* is far larger as reflected in catch statistics and fishery-independent surveys. However, the Greenlandic fishery for *P. borealis* has observed an increasing amount of *P. montagui* in catches from some fishing grounds in recent years. Biomass indices from the annual Greenlandic shrimp assessment survey off West Greenland indicate a rapid increase in population

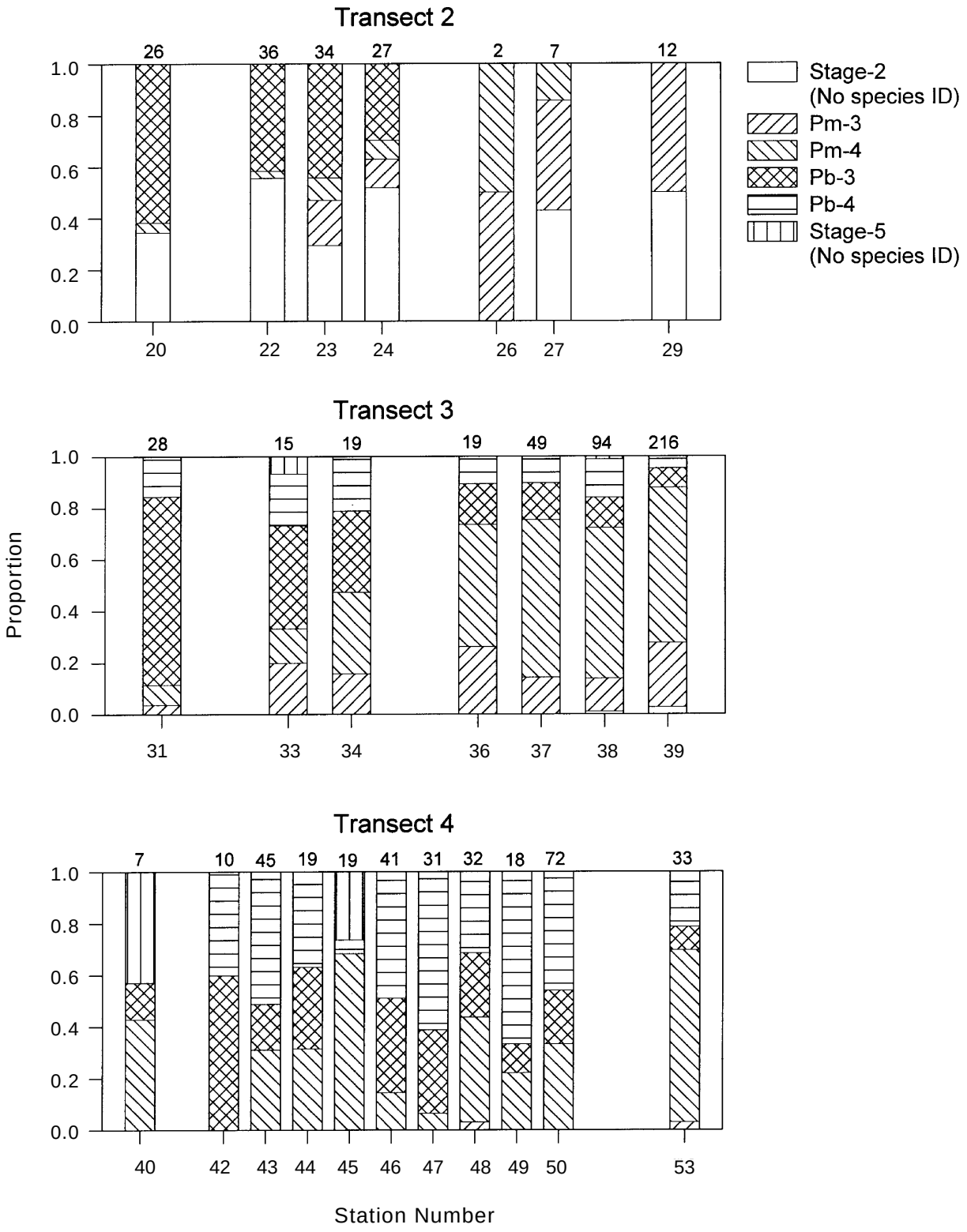

Fig. 8. Proportion of *Pandalus* larvae (species and stages) in the catches by transect and station. Number of larvae identified is given on the top of the columns.

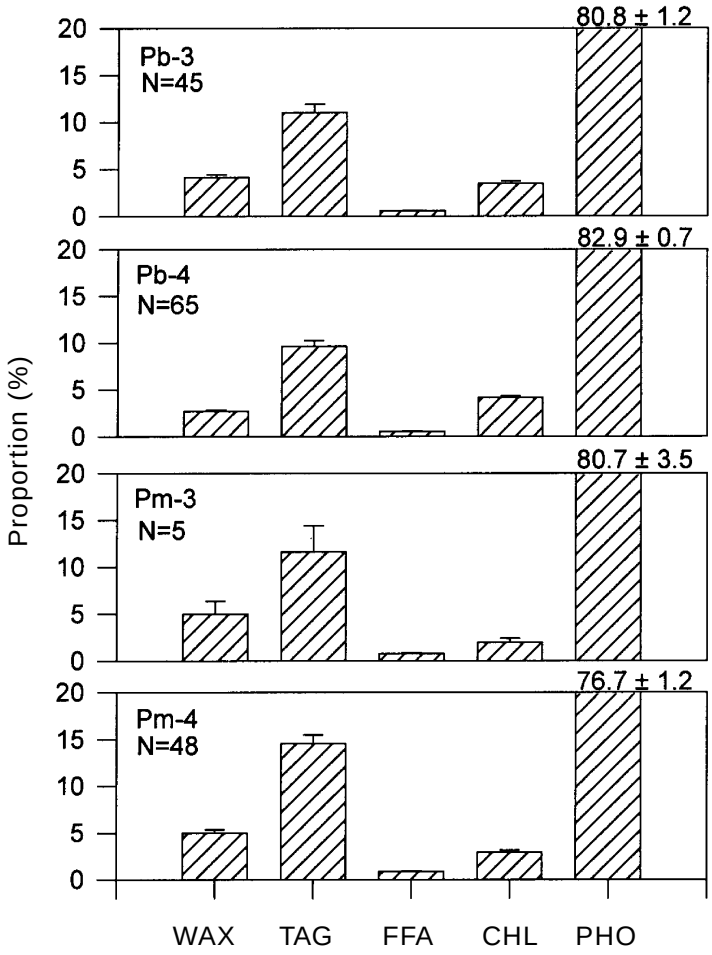

Fig. 9. Percent lipid composition of *P. borealis* and *P. montagui* larvae. 95% confidence interval indicated on columns.

TABLE 5. Results of a nested multi-way ANOVA of TAG to wet weight ratios (TAGI). Model: TAGI = Overall mean + TR + TYPE + ST(TR) + Err, where TR = transect 2–4, TYPE = Pandalid species and stage [*P. borealis* (Pb) or *P. montagui* (Pm) and stage 3 or 4], ST(TR) = sampling station nested within transect.

Dependent Variable: TAGI

Source	d.f.	Sum of Squares	Mean Square	F Value	Pr > F
Model	14	1 349	96.4	5.9	0.0001
Error	148	2 437	16.5		
Corrected Total	162	3 786			

R-Square	C.V.	Root MSE	TAGI Mean
0.36	41.0	4.1	9.9

Source	d.f.	Type I SS	Mean Square	F Value	Pr > F
TR	2	652.7	326.3	19.8	0.0001
TYPE	3	423.7	141.2	8.6	0.0001
ST(TR)	9	273.1	30.4	1.8	0.0650

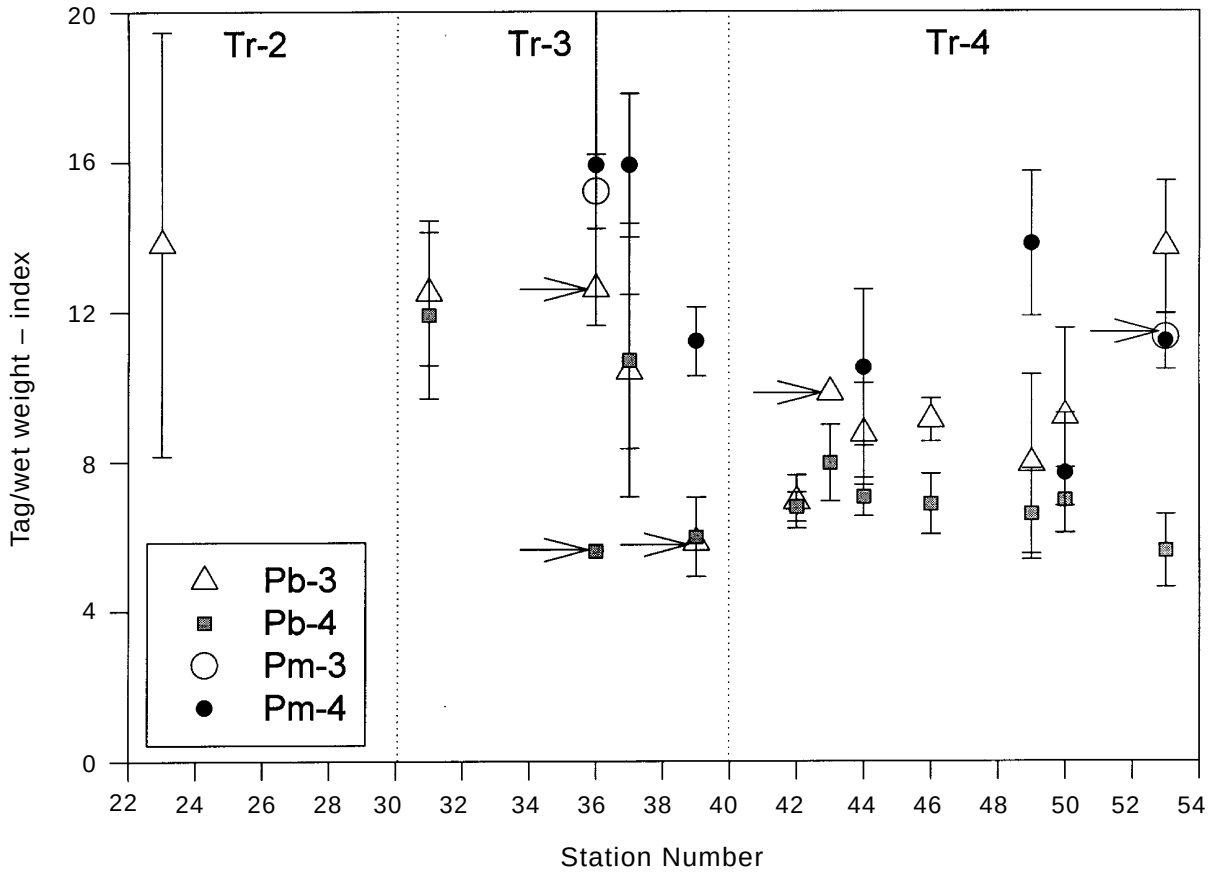

Fig. 10. Mean TAG/wet weight condition index with 95% confidence interval by species, stage, and sampling station. (Arrows indicate points of only one observation).

size of *P. montagui* between 1988 and 1996 (Folmer, MS 1996). No previous records of *P. montagui* larvae exist from West Greenland waters (Stephensen, 1935; Horsted and Smidt, 1956; Horsted *et al.*, MS 1978; Smidt, 1979). The high proportion of *P. montagui* larvae found in this study suggests that the stock of *P. montagui* may continue to increase in the coming years.

Changes in climate can have a considerable impact on the productivity of fisheries resources (Glantz and Feingold, 1992). Research in climatic variability indicates that a future global temperature increase might result in a colder climate and a changed sea environment at Greenland (and in other local areas of the north Atlantic) due to increased melt off from the Greenlandic icecap (Broecker, 1991). In recent years an increasing amount of the annual shrimp catches off West Greenland has been taken in the southern part of the northern shrimp distribution area, and there has been an increase in the catches of less valuable shrimp species, mainly *P. montagui* (Anon., 1997; Folmer, MS 1996). Both of these trends may be indications for a changed and colder sea environment. The latter is supported by a general cooling trend from the late-1960s onwards in the sea temperature time-series from off West Greenland (Stein and Borovkov, 1997).

Larval distribution

P. borealis in West Greenland spawn in offshore waters starting in July and ending in late-August or early-September (Horsted, 1978). The egg mass is carried by females until spring (March–April) when females move to shallow water to release the first pelagic larval stage (Horsted, 1978; Shumway *et al.*, 1985). The planktonic larvae are thought to drift more or less passively during five zoeal stages (approximately 4 months) and settle to the bottom during the sixth (megalopa) stage (Berkeley, 1930; Horsted *et al.*, MS 1978; Shumway *et al.*, 1985).

TABLE 6. Mean wet weight (frozen specimens) and lipid (WAX, TAG, FFA, CHL, and PHO) to wet weight indices for two stages of *P. borealis* and *P. montagui* by sampling transect.

	P. borealis Stage 3			*P. borealis* Stage 4			*P. montagui* Stage 3			*P. montagui* Stage 4		
Transect	No.	Mean	Std. err.	No.	Mean	Std. err.	No.	Mean	Std. err.	No.	Mean	Std. err.
Wet Weight (mg)												
2	2	6.61	0.28									
3	16	7.63	0.39	11	12.09	0.47	4	3.85	0.54	32	6.13	0.19
4	27	7.36	0.29	54	11.83	0.28	1	3.65		18	5.90	0.35
WAX/Wet Weight – Index												
2	2	6.37	0.62									
3	16	4.23	0.37	11	2.79	0.33	4	10.00	4.84	30	4.58	0.43
4	27	3.53	0.36	54	2.13	0.16	1	3.36		18	4.08	0.46
TAG/Wet Weight – Index												
2	2	13.79	5.66									
3	16	11.73	1.42	11	9.40	1.43	4	15.22	0.99	30	13.43	1.07
4	27	8.84	0.67	54	7.03	0.39	1	11.28		18	11.23	0.78
FFA/Wet Weight – Index												
2	2	0.94	0.02									
3	16	0.69	0.05	11	0.66	0.07	4	1.55	0.23	30	0.99	0.04
4	27	0.42	0.04	54	0.38	0.02	1	0.23		18	0.46	0.04
CHL/Wet Weight – Index												
2	2	2.93	0.38									
3	16	2.89	0.11	11	2.96	0.15	4	2.75	0.14	30	2.41	0.07
4	27	3.44	0.41	54	3.26	0.14	1	1.85		18	2.73	0.58
Neutral lipid (WAX + TAG + FFA + CHL)/Wet Weight – Index												
2	2	24.04	6.64									
3	16	19.53	1.63	11	15.81	1.41	4	29.51	4.70	30	21.41	1.10
4	27	16.23	0.94	54	12.80	0.48	1	16.71		18	18.51	0.94
PHO/Wet Weight – Index												
2	2	71.13	11.42									
3	16	88.37	6.65	11	82.41	6.42	4	164.08	43.01	30	90.63	7.57
4	27	88.11	13.06	54	65.94	3.34	1	38.33		18	53.51	4.95

On transects 2 and 3 *P. montagui* larvae dominated at the stations closest to the coast, whereas *P. borealis* dominated offshore. The abundance of *P. montagui* larvae was negatively related to salinity whereas *P. borealis* showed no relation to salinity. Horsted *et al*. (MS 1978) indicated that *P. borealis* larvae were more abundant at depths below 50 m. This difference in larval distribution may be related to differences in the distribution of adults. In the annual Greenlandic shrimp assessment survey off West Greenland covering depths from 50 to 600 m, *P. montagui* have been caught mainly at depths between 200 and 300 m and *P. borealis* mainly at depths between 300 and 400 m (Folmer, MS 1996; Folmer *et al*., MS 1996). In Penobscot Bay (USA), *P. montagui* adults were most common at depths between 20 and 90 m, whereas *P. borealis* most often dominated in deeper water (Stevenson and Pierce, 1985). *P. montagui* is the only Pandalid species which inhabits Arctic waters <1.5°C and it is prevalent in the cold (-1 to 2°C), well-mixed water of Arctic origin which becomes the "cold intermediate layer" in the Northwest Atlantic (Squires, 1966; Hudon *et al*., 1992). *P. borealis* is characteristically found in the deep (150–500 m), warm (2–5°C), stratified layer of Atlantic origin located below the intermediate cold layer (Hudon *et al*., 1992). *P. montagui* differs from *P. borealis* by being more depth, temperature, and salinity tolerant (Hudon *et al*., 1992).

TABLE 7. Results of a nested multi-way ANOVA of neutral lipids to wet weight ratios (NLIPI). Model: NLIPI = Overall mean + TR + TYPE + ST(TR) + Err, where TR = transect 2–4, TYPE = Pandalid species and stage [*P. borealis* (Pb) or *P. montagui* (Pm) and stage 3 or 4], ST(TR) = sampling station nested within transect.

Dependent Variable: NLIPI

Source	d.f.	Sum of Squares	Mean Square	F Value	Pr > F
Model	14	2 840	202.8	8.76	0.0001
Error	148	3 426	23.2		
Corrected Total	162	6 266			

R-Square	C.V.	Root MSE	NLIPI Mean
0.45	28.3	4.8	17.0

Source	d.f.	Type I SS	Mean Square	F Value	Pr > F
TR	2	1308.5	654.3	28.3	0.0001
TYPE	3	1054.4	351.5	15.2	0.0001
ST(TR)	9	476.8	53.0	2.3	0.0197

The general features of the current system and water mass distribution around Greenland have been described by Buch (MS 1994). In the present study there was a trend of older *Pandalus* larvae from north to south. The water temperatures show an analogous increasing trend from north to south. However, larval abundance was not related to temperature for either of the species.

Larvae from transects 2, 3, and 4 are probably not from the same spawning/hatching population. Most of the larvae in stage 2 were identified as *P. borealis* and a higher proportion in stage 4 were *P. montagui*, suggesting that *P. borealis* larvae were hatched later. Eggs and larvae of the West Greenland shrimp populations appear to show a delay in hatching and development from south to north, related to the later warming and onset of primary and secondary production from south to north. A time-series of zooplankton collections off West Greenland (1956–1984) shows that shrimp larvae occur earlier (May–June) in south-west Greenland, than further north in the Disko Bay area (July–August) (Pedersen and Smidt, MS 1995; Pedersen, unpubl. data). Temperature has a strong effect on larval growth and development time of Pandalid larvae (Shumway *et al.*, 1985; Rasmussen, MS 1993; Tande *et al.*, 1994; Rasmussen and Tande, 1995).

P. borealis larvae hatched at south-west Greenland may be transported several hundred naut. miles by the net northward West Greenland current during their planktonic larval life (Horsted *et al.*, MS 1978). The current speed along West Greenland decreases from south to north and also with depth in the northern area. Considering the possibility that current gyres occur in the shrimp area north-west of Store Hellefiske Bank (Fig. 12) it seems likely that the stock in this area is recruited not only from more southerly populations, but possibly to a much greater extent by its own larval source (Horsted *et al.*, MS 1978). These hypothesized larval drift routes assume that larvae can be considered as passive particles in the water mass. In the present study, a weak trend was found of younger larvae from south (majority of stage 4) to north (majority of stage 2 and 3) which does not support the hypothesis of an entirely passive northward drift of larvae hatched in the south.

Lipid composition and larval condition

The structural lipid fraction (i.e. phospholipids) accounted for most of the total lipid in both *P. borealis*, and *P. montagui* larvae. Ouellet *et al.* (1995) similarly found phospholipids to be the most abundant lipid class in *P. borealis* larvae (zoeal stage 1 and 2) from Gulf of St. Lawrence. However, triacylglycerols (TAG) accounted for the major fraction of the total lipid in *P. borealis* from Balsfjord (Hopkins *et al.*, 1993). TAG is the primary storage form (as fat) of organic energy in *P. borealis*, and therefore the TAG to wet weight ratio ((TAG mg/WW mg) $\times$1000)) can be used as

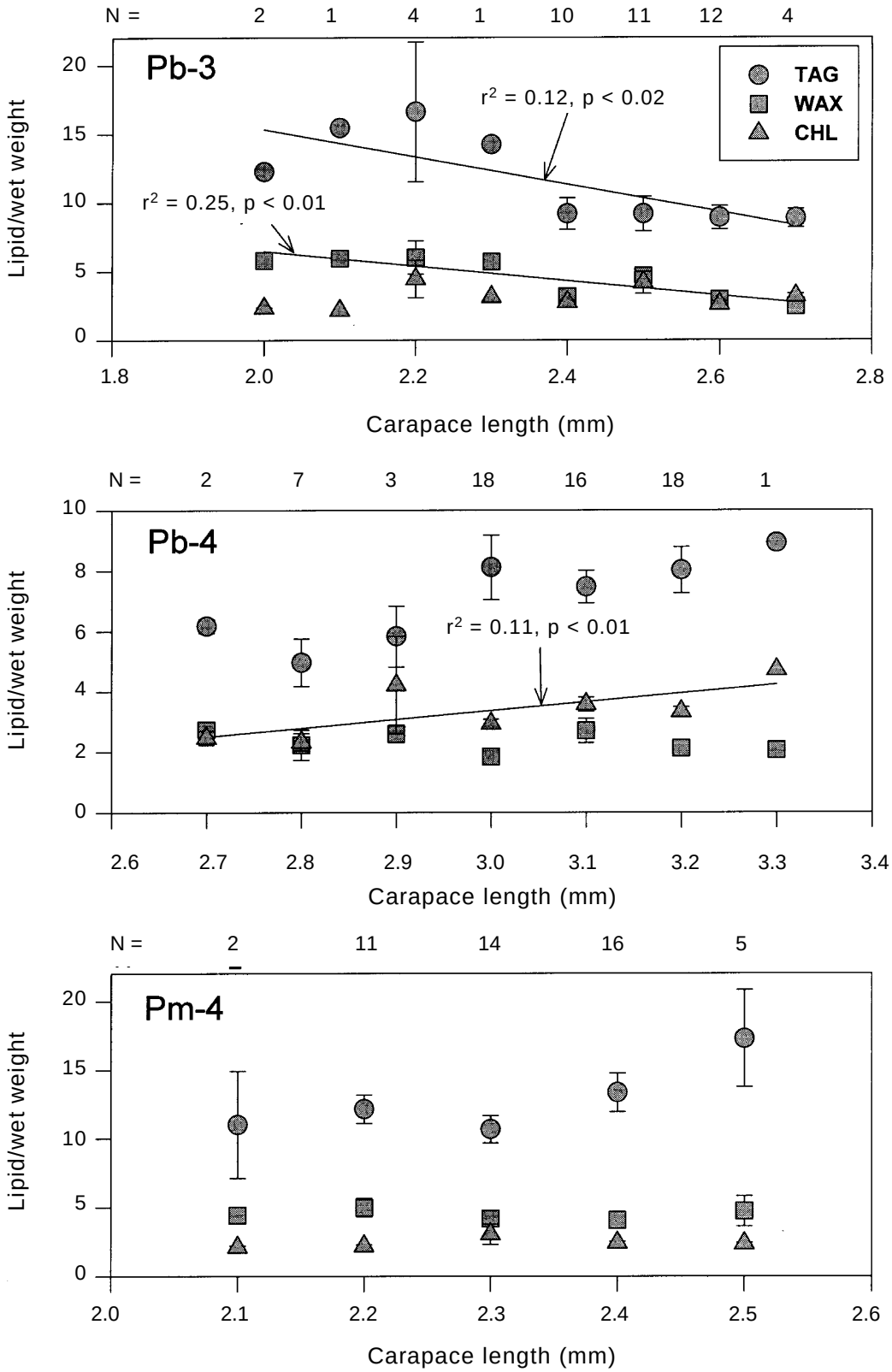

Fig. 11. Mean TAG, WAX and CHL condition indices by size, species, and stage. 95% confidence interval shown. Sample number given on the top of each figure. Fitted lines are shown for significant relationships.

an index for larval feeding condition (Ouellet *et al*., 1992; Hopkins *et al*., 1993). Ouellet *et al*. (1995) found a high content of the diacylglycerols (DAG) in shrimp larvae, which could reflect lipid degradation during storage or metabolic activity. In the present study the second largest lipid fraction was TAG, whereas no DAG was found.

The larvae used for lipid content analyses in this study were randomly picked from catches at selected stations and represent different sizes of *P. borealis* larvae in stages 3 and 4, and *P. montagui* larvae in stage 4. With larval size WAX and TAG contents showed decreasing trends for *P. borealis* larvae stage 3, and no trend for *P. borealis* and *P. montagui* stage 4. This could indicate that the larvae use more lipid than they accumulate in the period before molting from stage 3 to 4. The CHL content showed a weak increasing trend with size only for *P. borealis* stage 4. CHL is used in building cells and is not as accessible for energy use as WAX and TAG.

Ouellet *et al*. (1992, 1995) found a relationship between the proportion of *P. borealis* larvae (zoeal stages 1 and 2) with a TAG condition index below 0.2 and the probability of survival during the next moult. In the present study the larvae were further developed (zoeal stages 3 and 4) and none of them showed a TAG condition index below 0.2. However, the TAG condition indices of the *P. montagui* larvae were generally higher than for the *P. borealis* larvae, suggesting they may have a higher growth and survival potential during their first winter (a catabolic period with drain in the energy budget) (Hopkins *et al*., 1993). The *P. montagui* larvae seem to be in a better feeding condition based on a generally higher content of neutral lipids.

In the Gulf of St. Lawrence, *P. borealis* larvae (zoeal stages 1 and 2) maintained their vertical position in the subsurface chlorophyll *a* and suspended particle concentration maxima during the day but moved towards the surface at night (Ouellet and Lefaivre, 1994). Zoeal stage 2 larvae were larger in weight and length, and showed a higher TAG condition index at sites where developmental stages of calanoid copepods were more abundant (Ouellet *et al*., 1995). Ouellet *et al*. (1995) conclude that secondary production in the water column influences growth, condition, and survival potential of shrimp larvae. They propose that larval survival and recruitment to the fishable stocks are influenced by factors affecting stratification and mixing in the water column (i.e. buoyancy fluxes), and hence phytoplankton and copepod production in the northern Gulf of St. Lawrence. In this study it was not possible to demonstrate similar relationships between TAG condition indices and primary and secondary production. A significant negative association was found between TAG condition indices and both fluorescence and copepod productivity for *P. montagui* stage 4 larvae and no association for *P. borealis* stage 3 and 4 larvae. Hence, the TAG content may not be linked to productivity for stage 3 and 4 larvae. However, the spatial and temporal resolution of the samples in the present study may have been too low to capture a link if it exists. Of immediate interest is whether *P. borealis* larvae are more abundant at depths below 50 m as indicated by Horsted *et al*. (MS 1978).

MIK and Bongo sampling

Our sampling was hindered by large amounts of algae "slime" (algae threads and colonies)

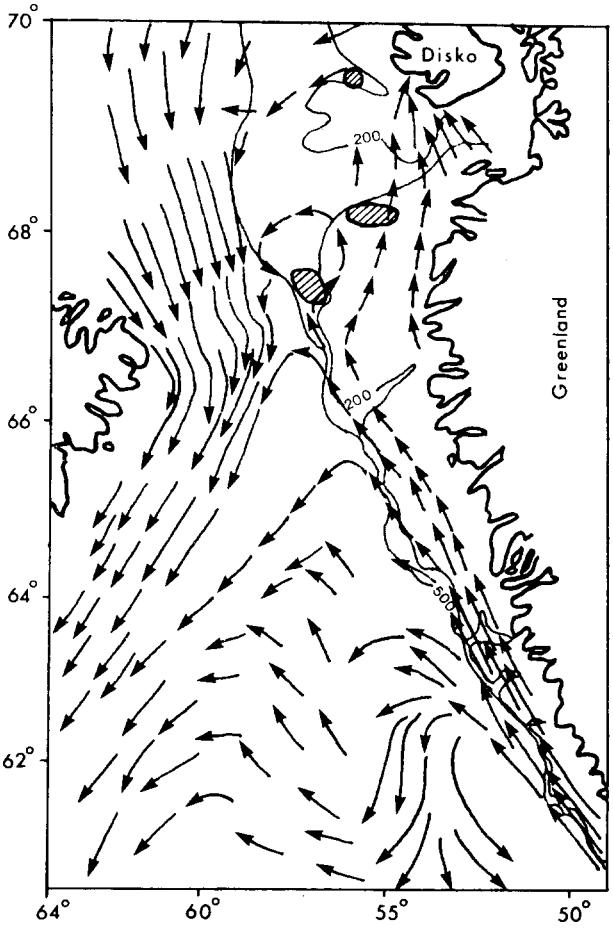

Fig. 12. The areas of near bottom shrimp larvae (stages 4–6) occurrence in August–September off West Greenland (shaded areas) and a scheme of the Davis Strait currents (from Klimenkov *et al*. 1978).

especially in the coastal areas of transects 3 and 4. This was particularly a problem in the MIK sampler, which was very difficult to clean properly between the hauls due to size and net material. The smaller and lighter Bongo nets were easier to handle, wash, and clean. The generally lower shrimp larvae density estimated from the MIK sampler were probably due to greater net clogging and reduced filtration. On transects 1 and 2 there was little algae "slime" in the water and, therefore, little reduction in the MIK sampler filtration.

Species identification

The larvae of *P. montagui* are somewhat smaller but morphologically very similar to *P. borealis*, and the time of hatching and duration of the planktonic phase is also similar (Ouellet *et al*., 1990; Astthorsson and Gislason, 1991). In this study larvae identified to *P. montagui* had yellow pigmentation at the base of the pleopods; this pigmentation was lacking on larvae identified to *P. borealis*. *P. borealis* larvae had red pigmentation on the edge of carapace on most specimens. These pigment patterns were most clearly seen on frozen specimens, but also visible on some formalin preserved specimens. There was correspondance between species identifications based on numbers of setae on the antenna scale (Ouellet *et al*., 1990) and their pigment patterns. In this study, pleopods 2 to 5 on *P. montagui* larvae zoeal stage 3 were biramous and most were more advanced than the stage 3 larvae described by Pike and Williamson (1964), and Squires (1993).

The great size range of *P. montagui* larvae stage 4 found in this study may be explained by misjudgement of large specimens which actually were *P. montagui* larvae in stage 5 or *P. borealis* in stage 3 (or 4). Another less likely explanation is that some large *P. montagui* larvae belong to a different species and were misidentified. However, genetic discrimination and verification of the identified *P. montagui* larvae in this study are desirable. The characteristics and sizes of the *P. borealis* larvae from West Greenland in this study agreed well with descriptions of Haynes (1979) and findings from Ísafjord-deep, north-west Iceland (Astthorsson and Gislason, 1991).

Conclusions

This study was a first attempt to investigate shrimp larvae distribution and lipid composition in relation to hydrography in West Greenland waters. Though I did not find clear relationships, my results suggest that future studies should investigate lipid condition of the earliest stages of *P. borealis* and *P. montagui* larvae and establish trophic relationships (lipid nutrition) using food web tracer lipids (St. John and Lund, 1996). Hence, sampling should take place earlier (end of May) and further to the south compared to transect positions in the present study. Vertical sampling and drift studies of larval patches are needed to study larval distribution, growth and survival in relation to variable hydrographical and biological characteristics of the larval environment. Such studies could be important to achieve better recruitment predictions for both species.

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