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Changes in recruitment, growth, and stock size of northern shrimp (*Pandalus borealis*) at West Greenland: temperature and density-dependent effects at released predation pressure

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Stock size of northern shrimp (*Pandalus borealis*) in West Greenland waters has been fairly stable from the late 1980s to the mid-1990s. Thereafter, survey estimates of biomass increased substantially, and the exploitation rate declined slightly in the most recent years. The present analysis was carried out on a spatially disaggregated basis in order to account for the latitudinal differences in bottom temperature and shrimp density. Changes in recruitment and, with a lag of 2 years, in stock biomass were most pronounced in the northern part of its distributional range, while bottom temperature increased in all survey regions since the mid-1990s. Length-at-age was positively correlated with temperature in general, but a trend towards slower growth was observed in areas with the highest stock densities in the most recent years. It is concluded that the moderate increase in temperature above a lower threshold of the optimal range in the northern regions has extended the distributional area that is most favourable for northern shrimp. This, together with a decreasing rate of exploitation and a continuous low predation pressure, resulted in an increase of the stock to a level at which density-dependent effects have become prominent in parts of study area.

Keywords: density-dependence, growth, length-at-age, northern shrimp, *Pandalus borealis*, recruitment, stock biomass, temperature dependence.

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Introduction

Northern shrimp (*Pandalus borealis*) is a protandric hermaphrodite with a circumpolar distribution in the northern hemisphere (Shumway *et al.*, 1985; Bergstrøm, 2000). Its distribution extends from 59°30′ to 72°30′N at West Greenland and covers soft sediments at depths from 150 to 600 m where bottom temperature ranges from −1°C in the north to 6°C in the south (Wieland and Kanneworff, 2002). Transition to the female stage occurs in West Greenland waters on average at carapace lengths between 22 and 26 mm after 5–6 years as male (Horsted and Smidt, 1956; Wieland, 2004a), and the maximum age attained by the females is more than 8 years (Savard *et al.*, 1994). Mating and spawning occur during summer (July to September), the egg-bearing period lasts about 10 months until the larvae hatch in the next spring (April to June), and migration of egg-carrying females into shallower waters in connection with egg hatching has been observed (Horsted and Smidt, 1956; Horsted, 1978). The pelagic larvae are transported in general from south to north, with the prevailing currents, until settling in autumn on the West Greenland Shelf (Ribergaard *et al.*, 2004), and the juveniles migrate from shallow to deeper water (Smidt, 1981).

Stock size of northern shrimp in West Greenland waters has been fairly stable from the late 1980s to the mid-1990s. Thereafter, survey estimates of biomass increased from less than 300 000 t in 1998 to about 650 000 t in 2003 and 2004 (Wieland *et al.*, 2004). Biomass of cod (*Gadus morhua*) and other demersal fish species, which are important predators of northern shrimp, decreased drastically in the beginning of the 1990s, with no signs of a substantial recovery since then (Rätz and Stransky, 2004; Storr-Paulsen and Jørgensen, 2004). When the cod stock collapsed, an expanding fishery for northern shrimp in West Greenland waters became economically most important (Hamilton *et al.*, 2003). The

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catches of northern shrimp varied between 80 000 and 105 000 t in the 1990s and reached about 130 000 and 140 000 t in 2003 and 2004 (Hvingel, 2004). The fishery takes mainly individuals greater than 17-mm carapace length, which consists of males and females aged 3 years and older. Despite increasing catches, exploitation rates have declined in the most recent years (Hvingel, 2004).

The present paper compares trends in bottom temperature and recruitment, and investigates effects of stock density on length-at-age and growth of northern shrimp for five regions in West Greenland waters in the period 1993–2004.

Material and methods

Bottom-trawl surveys for northern shrimp have been conducted annually since 1988 in West Greenland waters between 150- and 600-m depth (Carlsson *et al.*, 2000). The survey follows a stratified random design, with stratification based on geographic region and depth. Different vessels were involved, and area coverage was extended during the first 3 years of the survey. Temperature measurements at trawl stations were introduced in 1990, and the survey has been carried out solely with RV "Paamiut" since 1991. In 1993, the mesh size of the codend liner was reduced from 44 to 20 mm, and the survey area was extended again. The main purpose of the survey is to provide indices of overall stock biomass, and the relative standard error of these estimates has been between 12% and 20%. A description of the current survey design, fishing practice, and catch analysis is given in Wieland *et al.* (2004).

For the purpose of the present study, the original sampling strata of the survey were combined into one inshore and four offshore regions (Figure 1), and the latitudinal limits of the offshore regions were defined by differences in the temperature conditions, which were on average about 1 °C between adjacent offshore regions.

Temperature was measured until 1994 with a Seabird CTD just before or after trawling, and the recordings from the maximum depths of the profiles were interpreted as bottom temperatures. A Seamon temperature sensor mounted on one of the trawl doors with a sampling interval of 30–60 s and an accuracy of 0.05 °C has been used since 1995, and for each station the recordings were averaged along the trawl track. About 175–225 stations at depths between 150 and 600 m were covered in each year, from which annual mean summer (July to September, Table 1) bottom temperatures weighted for the area of the original sampling strata were calculated and combined according to the five regions of the survey area.

From each survey catch, random subsamples of northern shrimp were sorted into males, primiparous females, and multiparous females based on their sexual characteristics defined by Allen (1959) and McCrary (1971). Oblique carapace length (CL) was measured to the nearest 0.1 mm using slide callipers. Swept-area estimates of the total number by sexual group and original sampling stratum were grouped in 0.5-mm-CL intervals and aggregated corresponding to the five regions of the survey area. Modal analysis of the regional length frequencies for juveniles and males was conducted using the MIX 3.1A software (MacDonald and Pitcher, 1979; MacDonald and Green, 1988; release of MIX version 3.1A by Ichthus Data Systems in 1993). No smoothing was applied prior to analysis, and initial estimates of the modes and the number of age groups to be considered were obtained by visual inspection of the length frequencies. The present study does not include males beyond age 4 and females owing to difficulties concerning the separation of overlapping modes with sufficient confidence. A constant coefficient of variation for length-at-age was used in the MIX analysis during a first run. However, varying coefficients of variation were used in final runs because the first age group was not well represented in many of the samples because of low catchability (Wieland, 2004b), and a part of the larger males had already changed sex, and differences in growth between cohorts were likely. Values of mean length, which had to be kept fixed in the modal analysis, were discarded from further evaluation of length-at-age and growth. The original length frequencies by year and region with the fitted Gaussian components as well as details on the estimates of mean length and abundance at age are given in Wieland (2004b). Comparative sampling with fine-meshed (6 mm) bags has shown that estimates of mean length from the 20-mm codend liner were biased for age 1 but not for age 2 (Wieland, 2002). Hence, data for age 1 as well as the years before 1993, in which an even wider codend liner was used, were not considered in the present analysis.

Pearson product moment correlation coefficients (Sokal and Rohlf, 1995) were computed for the relation between bottom temperature and recruitment at age 2 on one hand and recruitment and fishable biomass on the other. In both cases, time-lags of 2 years were used.

Average values of bottom temperature and stock density, which included the current year as well as 2–4 preceding years in order to cover the period from the year of settling to the year of catch, were used to study their possible effects on lengths at ages 2, 3, and 4 using Spearman rank correlation analysis. This non-parametric method avoids the assumption that the underlying relationship is linear and reduces a possible effect of outliers (Sokal and Rohlf, 1995).

Relative growth rates (RG, %) were calculated from mean carapace length (L, mm) at age i in the first and second year as $RG = ((L_{2,i+1} - L_{1,i})/(t_2 - t_1))/L_{1,i}$, where $(t_2 - t_1)$ is the difference between the sampling dates (Table 1). Correspondingly, average values of bottom temperature and stock density in the first and the second year were used to examine the effect of these variables on the length increments at age 2 and age 3 by Spearman rank correlation analysis.

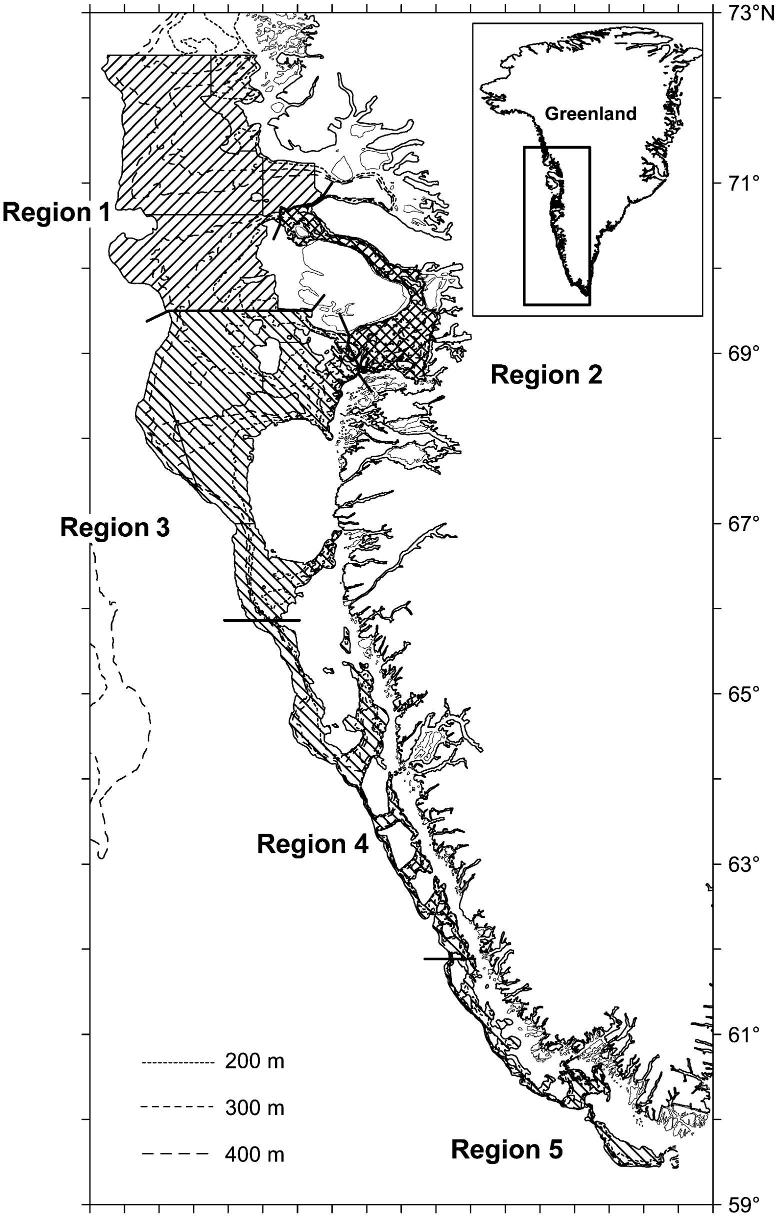

Figure 1. Survey regions and stratification in the West Greenland bottom-trawl survey for northern shrimp in 2004 [the division of survey area into regions was the same for the previous years, whereas survey stratification differed slightly (Wieland *et al.*, 2004)].

Results

The annual mean summer bottom temperatures (Figure 2) showed a substantial increase during the second half of the 1990s, but with some delay in the northernmost regions. The bottom temperatures in regions 1 and 2 were very similar, ranging between 1.1°C and 1.4°C in 1991–1996 and between 2.1°C and 2.9°C thereafter. Bottom temperatures between 2.8°C and 4.4°C were observed in regions 3 and 4 after 1997 and 1995, respectively. In region 5, which was covered first in 1993, the bottom temperature decreased in 1995 to 3.2°C, but ranged between 4.4°C and 5.6°C in all other years.

Survey estimates of northern shrimp recruitment at age 2 and fishable biomass (biomass of all individuals with a carapace length ≥ 17 mm) are shown in Figure 3. Recruitment was fairly stable during the 1990s except for an exceptionally high value recorded in 1996. Recruitment increased continuously from a relatively low level in 1997 to a record high value in 2001. Thereafter, recruitment

Table 1. Mean sampling dates in the five survey regions.

	Region				
Year	1	2	3	4	5
1993	8 Aug	10 Aug	7 Aug	10 Aug	21 Sep
1994	12 Aug	22 Aug	7 Aug	14 Jul	5 Sep
1995	27 Jul	3 Aug	31 Jul	20 Jul	28 Aug
1996	29 Jul	9 Aug	1 Aug	14 Jul	27 Aug
1997	22 Aug	16 Aug	26 Jul	10 Jul	10 Sep
1998	23 Aug	29 Aug	7 Aug	14 Aug	9 Sep
1999	21 Aug	26 Aug	2 Aug	9 Aug	6 Sep
2000	19 Aug	24 Aug	3 Aug	11 Aug	8 Sep
2001	7 Aug	11 Aug	22 Jul	29 Jul	2 Sep
2002	6 Aug	2 Aug	17 Jul	21 Jul	17 Aug
2003	30 Jul	24 Jul	23 Jul	19 Jul	20 Aug
2004	31 Jul	26 Jul	28 Jul	26 Jul	22 Aug

decreased steadily to below the long-term average in 2003 and 2004. Total fishable biomass fluctuated without a trend between 185 000 and 260 000 t before 2000, then increased steadily to about 580 000 t in 2003 and 2004. Pronounced regional differences were observed in both recruitment and fishable biomass. Regions 3 and 4 provided a large contribution to the overall recruitment in all years, but in particular before 1996 with proportions between 22−67% and 30−66%, respectively. Region 2, which constitutes only 8% of the survey area, became increasingly important since the mid-1990s with a contribution between 30% and 44% to the aggregated recruitment index in the years 1996−2002. In addition, recruitment became substantial in region 1 after 1998, but was almost negligible in region 5 in all years. The changes in recruitment were significantly correlated with the bottom temperature 2 years before, i.e. the year in which settling occurred, for regions 1, 2, and 3 (Table 2). The increase in fishable biomass was also most pronounced in regions 1, 2, and 3, i.e. in the northern parts of the survey area, for which significant correlations with the recruitment 2 years before were found (Table 2). Region 5 contributed on average 12% to the total fishable biomass, although only rather small proportions of recruits ($<1\%$) were found in this region in all years.

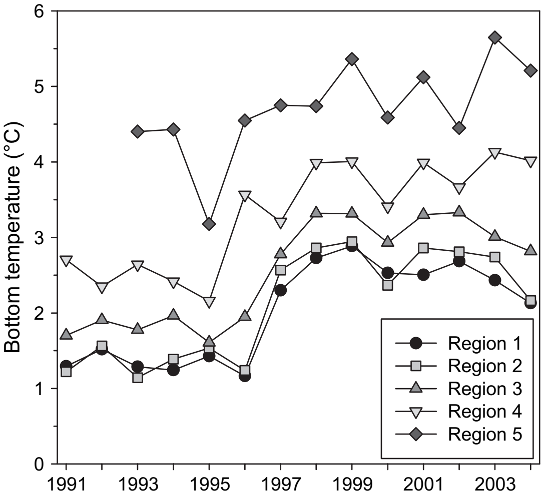

Figure 2. Area weighted mean annual summer (July to September) bottom temperature in the different survey regions, 1991−2004 (no data for region 5 prior to 1993).

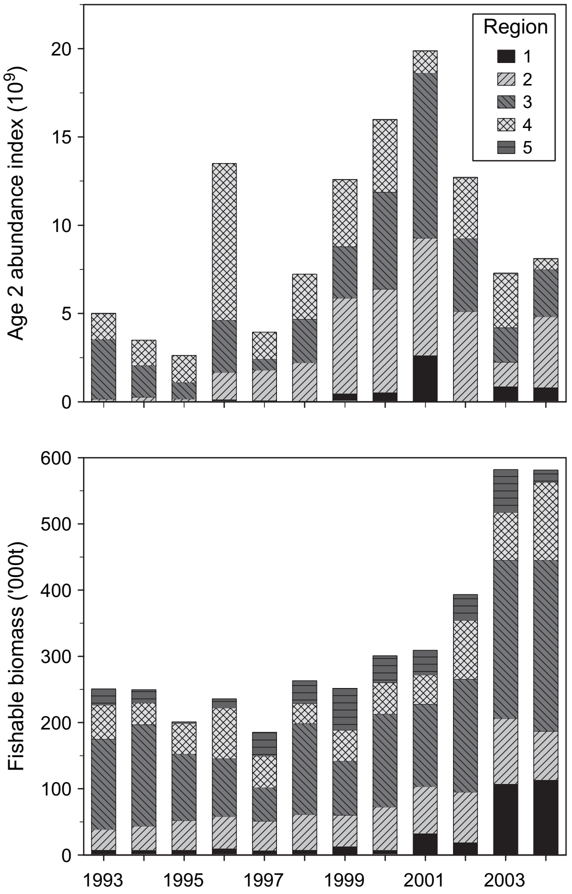

Figure 3. Indices of abundance at age 2 and fishable biomass of northern shrimp in the different survey regions, 1992−2004 (no data on abundance at age 2 for the years before 1993 because of a change in the mesh-size of the trawl's codend, incomplete coverage of region 1 in 2002).

Despite a generally positive trend, pronounced regional differences in stock density (Figure 4) resulted from the changes in biomass. Stock density was comparatively low in region 1 throughout the entire study period, with values between 0.2 and 1.0 g m^{-2} prior to 2003 but about 2.5 g m^{-2} in the last 2 years. Density was highest in almost all years in region 2, and increased steadily from 3.6 g m^{-2} in 1993 to 12.5 g m^{-2} until 2003. In the other regions, densities were at intermediate levels, with a positive trend in regions 3 and 4 since 1999 and 1998, respectively, and exceptionally high

Table 2. Pearson product moment correlation coefficients for the relationship between abundance at age 2 and bottom temperature 2 years before (a), and between abundance at age 2 and fishable biomass 2 years later (b). Number of observations given in parenthesis (region 1 without age 2 abundance in 2002 owing to incomplete sampling of that area in this year).

	Region 1	Region 2	Region 3	Region 4	Region 5	Regions 1–5 aggregated
(a)	0.76*** (11)	0.78** (12)	0.58* (12)	−0.11 n.s. (12)	0.49 n.s. (10)	0.61 n.s. (10)
(b)	0.99*** (9)	0.94*** (10)	0.79** (10)	−0.20 n.s. (10)	−0.23 n.s. (10)	0.78** (10)

*p < 0.05; **p < 0.01; ***p < 0.001; n.s., not significant.

values occurred in region 5 in 1999 and 2003. In 2004, stock density declined in regions 2, 4, and 5, while it was stable in region 1 and decreased in region 2.

In general, mean length-at-age was lower in the north than in the south, and annual differences in the mean length-at-age among the five regions were as large as 3.3-mm CL for age 2, 3.9-mm CL for age 3, and 4.1-mm CL for age 4 (Figure 5). The magnitude of latitudinal differences in length-at-age was similar to the length increments of the subsequent ages of the corresponding year classes. Length-at-age 2 was closely correlated ($p < 0.001$) with that of age 3 a year later, and the same was found for length-at-age 3 in one year and age 4 in the following year. In regions 1, 2, and 3, mean lengths at ages 2, 3, and 4 increased during the second half of the 1990s and decreased again in the most recent years, whereas such clear changes were not observed in regions 4 and 5. Spearman rank correlation analysis revealed a highly significant ($p < 0.001$) positive effect of bottom temperature on length-at-age 2, but with a considerable variation and without a further increase in length at bottom temperatures above 2.5°C (Figure 6). Similar results were obtained for ages 3 and 4. No overall impact of stock density on mean length-at-age was apparent. However, a significant ($p < 0.05$) trend towards decreasing mean length is indicated

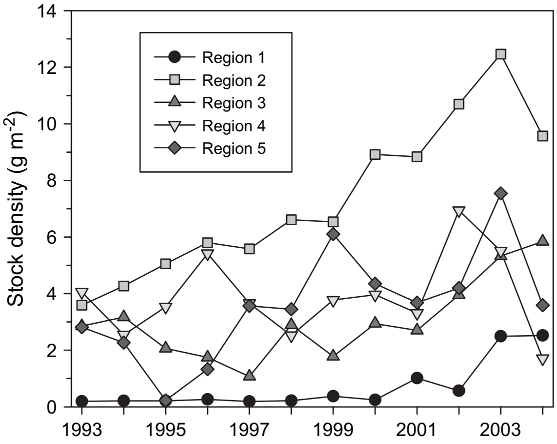

Figure 4. Stock density of northern shrimp in the different survey regions, 1993–2004.

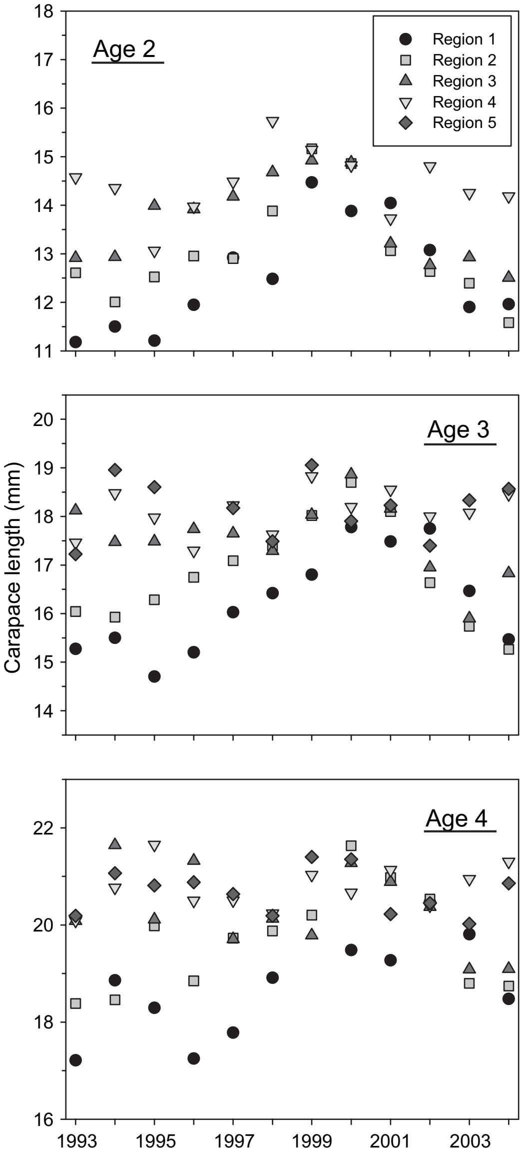

Figure 5. Mean length of northern shrimp at ages 2, 3, and 4, 1993–2004 (no data for age 2 in region 5 owing to insufficient numbers caught).

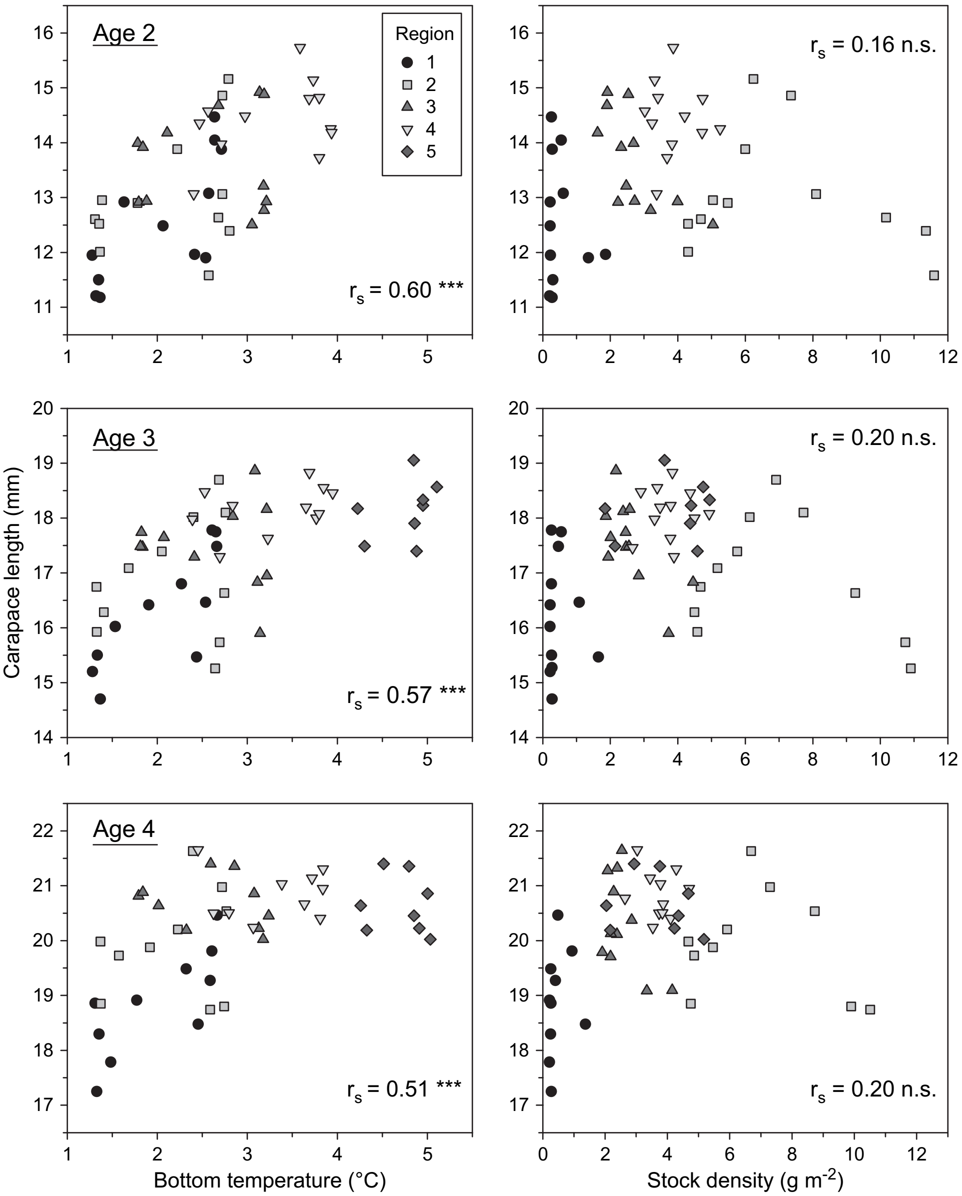

Figure 6. Mean length of northern shrimp at ages 2, 3, and 4 related to bottom temperature and stock density, 1993–2004 (no data for age 2 in region 5 owing to insufficient numbers caught; r_s: Spearman rank correlation coefficient, ***: $p < 0.001$, n.s.: not significant; bottom temperature and stock density: average of the current and the 2, 3, or 4 preceding years for ages 2, 3, and 4, respectively).

for all of the three ages at stock densities above 6 g m^{-2} in region 2 (Figure 6).

On average, relative growth rates for age 2 and age 3 declined during the end of the 1990s, but increased again in the most recent years (Figure 7). However, the annual length increments from ages 2 and 3 and from age 3 to age 4 showed a considerable variability between regions and years, ranging from about 3- to 5-mm CL per year at age 2 and from about 2- to 4-mm CL per year at age 3. No significant overall impact of bottom temperature or stock density on growth was detected by Spearman rank correlation analysis, except for a significant ($p < 0.01$) negative effect of stock density above 6 g m^{-2} on the length increments at age 2 in region 2 since 1995.

Discussion

Northern shrimp at West Greenland experienced a pronounced increase in temperature within a few years in the

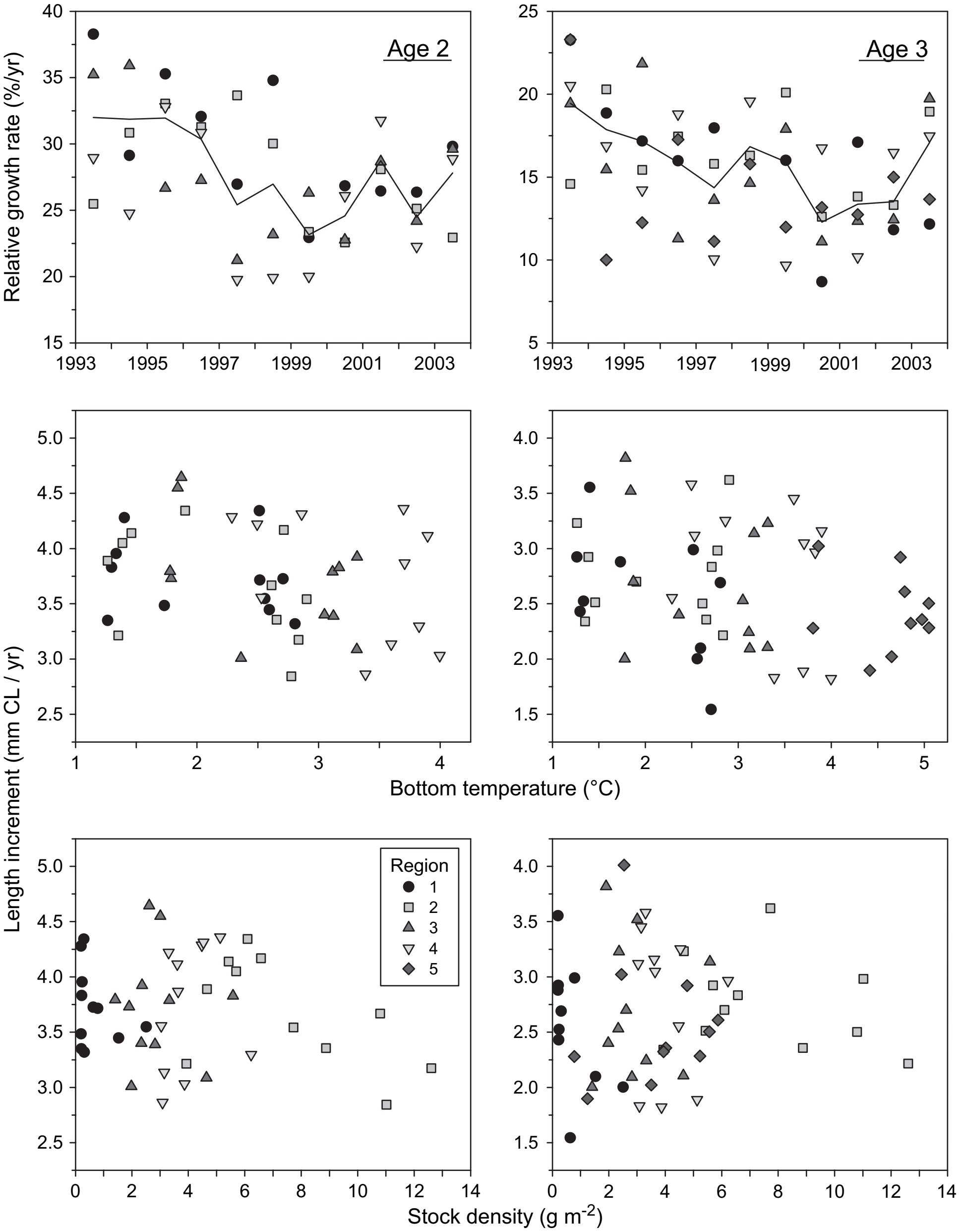

Figure 7. Relative growth rates of northern shrimp at age 2 and age 3 in the different survey regions, 1993−2004 (solid lines refer to mean values), and annual length increments related to average bottom temperature and stock density in the first and the second year (no data for age 2 in region 5 owing to insufficient numbers caught).

mid-1990s, but not above the level that is assumed to be optimum for this cold-water species (1−6°C; Shumway *et al.*, 1985). Recruitment increased 2 years after the change in temperature, and after another 2 years fishable biomass increased significantly. The time-lags of 2 years are plausible in both cases as they correspond to the difference between the year of settling and the year of recruitment in the first case, and to the difference in age between the recruits and the bulk of the fishable biomass (Wieland, 2004b) in the latter. The changes in recruitment and their subsequent effects on the overall fishable biomass were most pronounced in the northern parts of the study area, and it is concluded that the increase in temperature leads to enhanced conditions for survival, in particular during the larval and early juvenile period in this area. This interpretation, however, is based on non-parametric correlation analyses without adjustment for possible autocorrelation, and it should be kept in mind that the obtained levels of significance might be overestimated (Pyper and Peterman, 1998).

Annual mean bottom temperatures recorded in summer have been used in this study as proxy for the temperature regime encountered by northern shrimp. These temperatures may differ from average ambient conditions because they do not account for vertical migration, and probably more important, for seasonal changes and horizontal migration. However, the duration of the egg incubation period depends strongly on temperature (Bergstrøm, 2000), which can explain the observed latitudinal differences in length-at-age in general. Furthermore, the increase in temperature from 1 °C to 3 °C in the northern part of the study area during the mid-1990s would correspond to a decrease in the egg-bearing period of 1.6 months (Figure 8). Thus, earlier hatch and, consequently, an extension of the growth period during the larval and early juvenile stages in the warmer years has likely contributed to the increase in length-at-age 2 until the end of the 1990s. Length at sex transition (Wieland, 2004a) and mean length of the females (Wieland, 2004c) have decreased since the end of the 1990s and the decline of length-at-age 2 in the most recent years could have been due to a smaller size of larvae hatched from smaller eggs despite the extended growth period at the continuous warm regime.

The decrease in annual growth increments during the 1990s might be explained by negative effects of the substantial increase in stock density, because temperature accelerates growth only if food is not limiting, but may reduce it if it is. Detailed information on the productivity of the various regions used in this study is not available, but differences in carrying capacity might explain that no consistent effect of stock density was found. However, the significant correlations between length-at-age as well as growth at age 2 and stock density in a part of the study area suggest that the role of density-dependence, probably attributable to intra-specific competition for food, has become prominent. Such effects on the size of northern shrimp have recently been noted for the Newfoundland and Labrador Shelf area (P. Koeller, pers. comm.) and have previously been reported for Pavlof Bay, Alaska, by Anderson (1991). The joint effects of temperature and stock density on growth in the case of northern shrimp at West Greenland, however, warrant further investigation, preferably when data covering more years have become available.

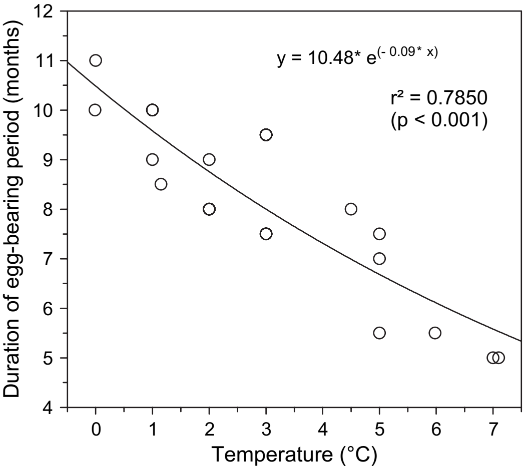

Figure 8. Duration of the egg-bearing period of northern shrimp in relation to temperature [Data from different stocks of northern shrimp, as compiled by Bergstrøm (2000)].

For the Gulf of Maine, where northern shrimp are at their southern limit, Richards *et al.* (1996) found an inverse relationship between recruitment and spring temperature, and Clark *et al.* (2000) described a collapse of the fishery in the mid-1950s related to a period with temperatures above normal. On the other hand, Colbourne *et al.* (2002) reported a significant correlation between sea–ice cover and commercial catch per unit effort of northern shrimp with a lag of 6 years, and pointed out that, in particular, extremely cold ocean temperatures in the waters of the Newfoundland Shelf during the late 1980s and early 1990s coincided with the appearance of large year classes of northern shrimp. Here, however, the effect of temperature in the 1990s has probably been confounded, at least to some extent, by a release of predation pressure caused by the collapse of the cod stock (Lilly *et al.*, 2000). In contrast to the above-mentioned studies, Worm and Myers (2003) found no significant relationship between northern shrimp biomass and ocean temperature. Furthermore, Worm and Myers (2003) rejected the "regime-shift" hypothesis of Anderson and Piatt (1999) that the inverse trends in cod and northern shrimp biomass may be caused by opposite responses to a change in temperature. Nonetheless, it should not be neglected that for northern cod stocks, recruitment is favoured by increasing temperatures (Planque and Frédou, 1999), and warm periods can therefore be associated with a high predation on northern shrimp.

The cod spawning stock at West Greenland collapsed at the end of the 1960s, which coincided with decreasing water temperatures (Buch *et al.*, 1994). Thereafter, recruitment depended mainly on larval drift from Iceland, and cod disappeared almost completely from West Greenland offshore waters in the beginning of the 1990s (ICES, 2004; Storr-Paulsen *et al.*, 2004). The recent surge in northern shrimp biomass can hardly be explained by a release from cod predation pressure owing to the time-lag of more than 10 years, and because the most pronounced increase in northern shrimp recruitment and biomass was recorded in the northern parts of the area in which cod catches (and thus presumably also abundance) have been negligible for a number of years (Horsted, 2000). Exploitation rate for the northern shrimp stock decreased since the mid-1990s, despite a considerable increase in the catches (Hvingel, 2004), and it appears that the favourable temperature regime was the major reason for the increase in stock biomass in the most recent years.

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