



Environmental factors affecting recruitment of northern shrimp *Pandalus borealis* in West Greenland waters

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ABSTRACT: Survey estimates of northern shrimp *Pandalus borealis* biomass in West Greenland waters increased from about 178 000 t in 1998 to about 598 000 t in 2003. The increase in stock size was preceded by several consecutive years in which recruitment was substantially above average. Recruitment has been poor since then despite record high levels of female stock biomass. Ricker-type stock-recruitment functions did not indicate that the variability in recruitment was related to female biomass. Multiple regression analysis revealed that mean female length, ambient bottom temperature and biomass of Greenland halibut *Reinhardtius hippoglossoides* had the most important effect on the variations of the 'recruit per female biomass' time series for the years 1993 to 2011. Variables which did not contribute significantly to the model included biomass of Atlantic cod *Gadus morhua*. This can be explained by the low stock size of Atlantic cod throughout the major part of the study period. The final model explained 83 % of the variation in the recruit per female biomass index. However, the observations for 5 out of the 19 years considered in the present study were outside the 95 % confidence interval of the fitted model, possibly due to a mismatch between the timing of larval hatch and the timing of the phytoplankton bloom, which could not adequately be addressed due to data limitations.

KEY WORDS: Pandalid shrimp · Stock–recruitment relationship · Recruitment success · Temperature · Predation · Maternal effects · Subarctic seas

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INTRODUCTION

Northern shrimp *Pandalus borealis* feeds on phytoplankton, detritus and small zooplankton (Horsted & Smidt 1956), and serves in turn as important prey for several fish species including Atlantic cod *Gadus morhua* and Greenland halibut *Reinhardtius hippoglossoides* (Parsons 2005a,b). In relation to its trophic level, responses of shrimp abundance to bottom-up and top-down processes have been documented (Fuentes-Yaco et al. 2007, Lilly et al. 2000). The reproductive cycle of northern shrimp has adapted to local temperature conditions so that, under average conditions, the timing of larval hatch matches

that of the spring phytoplankton bloom (Koeller et al. 2009). Moreover, upper water column temperature has been identified as a significant factor determining recruitment success of northern shrimp in the North-west Atlantic (Ouellet et al. 2007, 2011). On the other hand, linkages between population size of Atlantic cod and northern shrimp have been reported for various parts of the North Atlantic (Worm & Myers 2003). Hence, simple stock–recruitment relationships have usually not been found for northern shrimp (Aschan & Ingvaldsen 2009) or other pandalid shrimp species (Hannah 1993, Bergström 2000).

Northern shrimp is a protandric hermaphrodite with a circumpolar distribution in the northern hemi-

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sphere (Shumway et al. 1985, Bergström 2000). In West Greenland waters, the juveniles mature as males at about 3 yr of age, undergo transition to female at an age of 5 to 6 yr (Horsted & Smidt 1956, Wieland 2004), and may attain a maximum age, as female, of more than 8 yr (Savard et al. 1994). Mating and spawning occur during July to September, the egg-bearing period lasts 8 to 10 mo, depending on the temperature in the bottom water, and the larvae hatch in April to June of the following year (Shumway et al. 1985, Bergström 2000). The pelagic larvae undergo a 60 to 90 d development period with 6 stages (Rasmussen & Aschan 2011) and attain a carapace length of about 3.5 mm during summer (Storm & Pedersen 2003) before finally settling at the bottom as postlarvae in autumn where they reach a carapace length of 8 to 9 mm at age 1 in the following summer in West Greenland waters (Wieland 2005).

The fishery for northern shrimp off West Greenland started in the 1970s in Disko Bay (Fig. 1) and an offshore fishery developed thereafter with annual landings of up to 150 000 t. In the offshore areas, the fishery is conducted in all seasons (Hammeken Arboe & Kingsley 2010), and egg-bearing females are subject to the fishery during the winter (Fig. 2). Pronounced fluctuations in female biomass and recruitment of northern shrimp have been reported for the past 2 decades. At the same time, temperature conditions and the latitudinal distribution of northern shrimp changed considerably (Wieland et al. 2007). The present study compares Ricker-type stock-recruitment functions with multiple regression models that include environmental variability in order to identify the most important factors influencing the recruitment of northern shrimp off West Greenland in the years 1993 to 2011.

MATERIALS AND METHODS

The analysis was based on 2 bottom trawl survey series for monitoring fish and shrimp resources and 1 time series of routine observations of the oceanographic conditions off West Greenland. These were a Greenland survey for shrimp and fish carried out annually in summer since 1988 by the Greenland Institute of Natural Resources (GINR) in Nuuk and a German groundfish survey conducted annually in autumn since 1982 by the Institute of Sea Fisheries in Hamburg (ISH). Both surveys follow a stratified-random design. The routine observations of the oceanographic conditions off West Greenland are conducted by the Danish Meteorological Institute (DMI)

and provide mean surface layer (0 to 40 m) temperatures based on measurements in mid-June at a standard station on Fylla Bank (Fig. 1) which are considered to represent the general conditions on the West Greenland shelf (Ribergaard 2011).

The GINR survey for shrimp and demersal fish covers the West Greenland shelf between 72° 30' and 59° 30' N down to 600 m depth (Fig. 1). The survey area has been expanded and stratification has changed through time but adjustments for these changes, in particular for the missing coverage of the inshore area (Disko Bay and Vaigat) in 1988 to 1990, have been adopted (Kingsley et al. 2011). The fishing

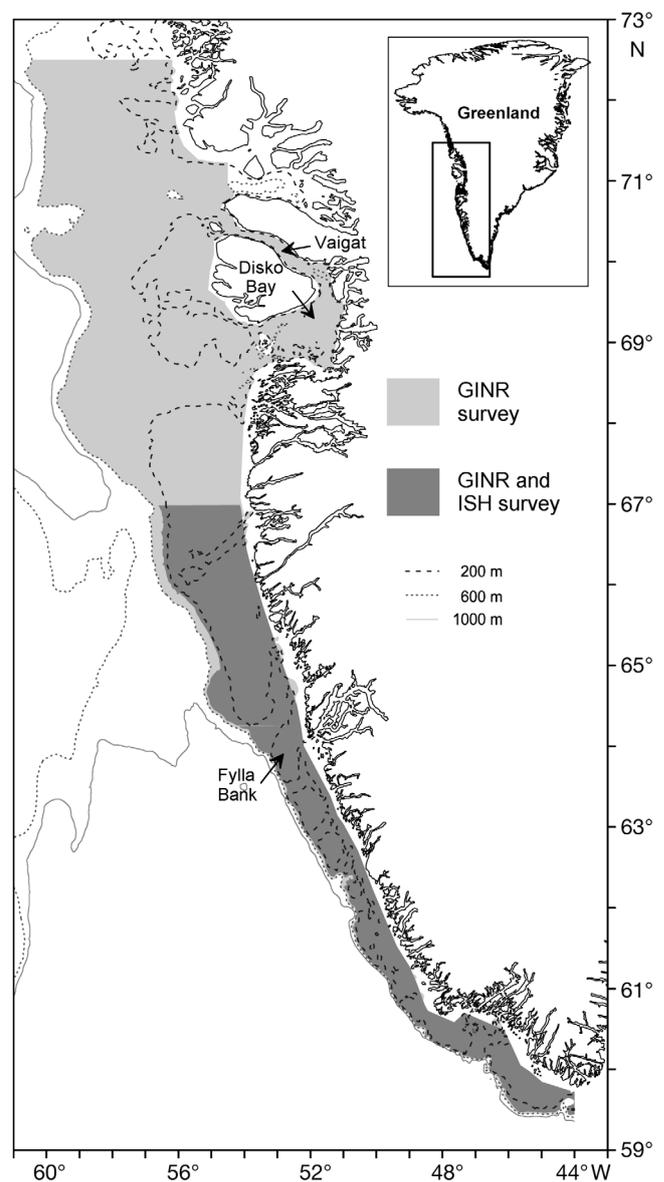


Fig. 1. Area coverage of the Greenland (GINR) and German (ISH) bottom trawl surveys, and location of the oceanographic standard station on Fylla Bank

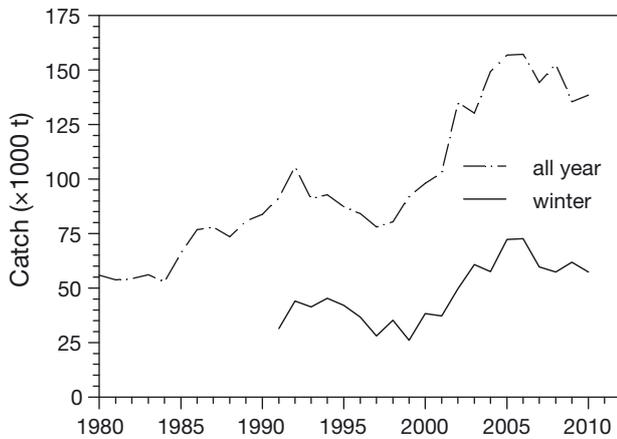


Fig. 2. *Pandalus borealis*. Annual northern shrimp total catch (1980 to 2010) and catch taken during the winter (October to March, 1991 to 2010) off West Greenland (based on Hammeken Arboe & Kingsley 2010)

gear used has a high vertical opening (ca. 14 m), which is essential for catching northern shrimp, and the towing speed is about 2.5 knots. The trawl was changed in 2005 and due to the change in the ground rope from a bobbin chain to a rubber disc rockhopper gear, higher catch rates were observed, particularly of small demersal fish. The survey results were adjusted for the gear change based on a calibration experiment (Kingsley et al. 2008, Nygaard & Jørgensen 2011). The mesh size of the trawl's codend was 44 mm in the early years but a 20 mm codend liner has been used since 1993. Fine meshed (6 mm) juvenile bags were used in only 2 years with full coverage of the survey area and the results indicated that northern shrimp smaller than about 9 mm carapace length (age 1 and younger) are not well retained in the main trawl (Wieland 2002). The primary objective of the GINR survey is to provide an estimate of the fishable biomass and recruitment at age 2 of northern shrimp, and it is considered to be less efficient for Atlantic cod, in particular for the years prior to 2005. Due to the maximum depth of 600 m, the survey catches of Greenland halibut consists mainly of juveniles (<40 cm total length; Nygaard & Jørgensen 2011) as the adults occur predominantly at greater depths and in areas other than that covered by this survey (Jørgensen 1997, Orr & Bowering 1997). The GINR survey provides further area-specific mean bottom temperatures based on measurements logged along the tow path since 1990 (Kingsley et al. 2011). The bottom temperatures were weighted by the density of northern shrimp in the various geographical survey strata to obtain a time series of ambient bottom temperatures during summer.

The ISH survey covers the shelf area outside the 3 nautical mile limit and the continental slope down to a depth of 400 m between 67° 00' and 59° 30' N (Fig. 1) off West Greenland. The fishing gear used is a groundfish trawl with a low vertical opening (ca. 4 m) and a fine meshed (10 mm) liner inside the codend, and the towing speed is 4 knots. The ISH survey was originally designed for Atlantic cod, and does not adequately cover the distributional range of northern shrimp and Greenland halibut.

According to the survey specifications, the data for northern shrimp and Greenland halibut were taken from the GINR survey (Kingsley et al. 2011, Nygaard & Jørgensen 2011) and the data for Atlantic cod were based on the ISH survey (Retzel 2011). Both surveys use measurements of swept area to convert catch rates to estimates of abundance and biomass. However, the efficiency of the survey gear and hence the survey catchability is not precisely known and thus the survey estimates should be considered as indices rather than as absolute values.

Relationships between parental stock size (P) expressed as female biomass and recruitment (R) represented by abundance at age 2 for northern shrimp were fitted to the original Ricker model (Ricker 1954):

$$R = \alpha \times P \times \exp(-\beta \times P) \quad (1)$$

where α and β are the coefficients of the density-independent and the density-dependent terms, respectively, and to a modified version which allowed for a non-zero intercept (Frank & Brickman 2000):

$$R = \alpha \times (P - \gamma) \times \exp(-\beta \times (P - \gamma)) \quad (2)$$

where γ is the stock level associated with absolute recruitment failure. A lag of 3 yr between female biomass and abundance at age 2 was applied to take into account that the females found in a summer survey produce offspring that emerge as larvae in the following spring and are first caught in survey 3 yr later, at age 2.

Environmental and ecological variables were added to the linearized form of the standard Ricker function, similar to the approach of Stocker et al. (1985):

$$\ln(R/P) = \ln(\alpha) - \beta \times P + \chi \times L + \delta \times S + \phi \times A + \eta \times C + \varphi \times G + \kappa \times E \quad (3)$$

or

$$\ln(R/P) = \ln(\alpha) - \beta \times P + \chi \times L + \delta \times A + \phi \times (S - A) + \eta \times C + \varphi \times G + \kappa \times E \quad (4)$$

where L is the mean carapace length of northern shrimp females, S and A are surface layer and ambient bottom temperatures respectively, C and G are survey estimates of Atlantic cod and Greenland halibut biomass respectively, E is the catch of northern shrimp during winter (October to March) relative to female biomass in the preceding summer, and χ , δ , ϕ , η , φ and κ are coefficients of the environmental and ecological variables. Female carapace length was lagged by 3 yr with respect to the year in which the recruitment was measured in order to represent the average size of the egg-bearing females in the year of spawning. Surface layer and ambient bottom temperature were lagged by 2 yr so that they correspond to the year in which the larvae hatched and settled. The difference between surface layer and ambient bottom temperature ($S-A$) lagged by 2 yr was included in the analysis to reflect variations in the match between the timing of larval hatch, which depends on the conditions in the bottom water, and those of the phytoplankton bloom, which depends on the conditions in the surface layer. A time lag of 1 yr was applied for Atlantic cod and Greenland halibut biomass indices representing predation on juvenile northern shrimp at age 1. The biomass indices for Atlantic cod and Greenland halibut were adjusted for the spatial overlap of the distribution of each predator with that of northern shrimp, based on an index of collocation. The index of collocation is a geostatistical tool developed by Bez & Rivoirard (2000) for pelagic species and its application for demersal fish and shellfish is described in Hendrickson & Vázquez (2005), Wieland et al. (2007) and Woillez et al. (2007). Estimates of effective biomass for the 2 predators were obtained by multiplying the original biomass indices with the respective index of collocation. The catch of northern shrimp during winter relative to female biomass in the preceding summer was lagged by 2 yr and used as an indicator for a potential effect of the removal of egg-bearing females in the time period between spawning and larval hatch. The impact of surface layer temperature (S , Eq. 3) and the difference between surface layer and ambient bottom temperature ($S - A$, Eq. 4) were studied separately because a significant correlation between the 2 variables was found (Shapiro-Wilks normality tests passed with $p = 0.637$ and $p = 0.928$, Pearson product moment correlation: $r = 0.657$, $p < 0.01$). Non-significant variables at the 5% level were removed from models (3) and (4) by stepwise (both directions) multiple regression. The residuals were tested for deviation from normality, trends and autocorrelation. Furthermore, the robustness of the final model was

investigated using model runs in which single years were sequentially excluded from the analysis and in which the first 3 yr of the recruit per female biomass index were excluded due to concerns about the consistency of the female biomass estimates related to the reduced area coverage of the survey in the early years. The statistical analyses were performed with S-Plus Version 6.1 and SigmaPlot Version 10.2.

RESULTS

Survey estimates of total and female biomass of northern shrimp were fairly stable until the end of the 1990s, increased to record high levels within a few years, and declined subsequently towards average (Fig. 3a). The increase in stock size was preceded by a couple of years with high recruitment (Fig. 3b) and the high values of the abundance at age 2 per female biomass index indicate exceptionally high survival of the pre-recruits in this period (Fig. 3c). At the same time, the mean size of females declined remarkably over a decade and a reversal of this trend has only been evident in the past 5 yr (Fig. 3d). Average bottom temperature for the entire area covered by the GINR survey increased during the end of the 1990s from 1.8 to 3.2°C and remained at this relatively high level thereafter. Surface layer temperature at Fylla Bank also increased during the mid-1990s but colder conditions were recorded for several years thereafter as well (Fig. 3e). Spatial overlap between northern shrimp and Atlantic cod was lower than for northern shrimp and Greenland halibut in all years, in particular for the years 2005 to 2008 (Fig. 3f). The occurrence of Atlantic cod in West Greenland offshore waters has been sporadic (Fig. 3g), and in the period 2005 to 2010 most of its biomass was distributed outside the area inhabited by northern shrimp. The biomass index of Greenland halibut increased steadily from 1990 to 2004 (Fig. 3h) and showed much lower year to year changes than those for Atlantic cod (Figs. 3g,h). The mean latitude of the northern shrimp survey biomass indicates a southward shift of the centre of the distribution during the late 1990s (Fig. 4a). Conversely, in the past 5 yr, northern shrimp has almost disappeared from the southern area where average bottom temperatures regularly exceeded 4°C after the mid 1990s and the mean latitude of the survey biomass increased from 66°N in 2003 to about 68°N from 2005. The ambient bottom temperature during summer reflects this change in distribution with a value of 4.2°C in 1999 decreasing to 2.6°C in 2010 (Fig. 4b). No change in the seasonal pattern of the fishery has been obvi-

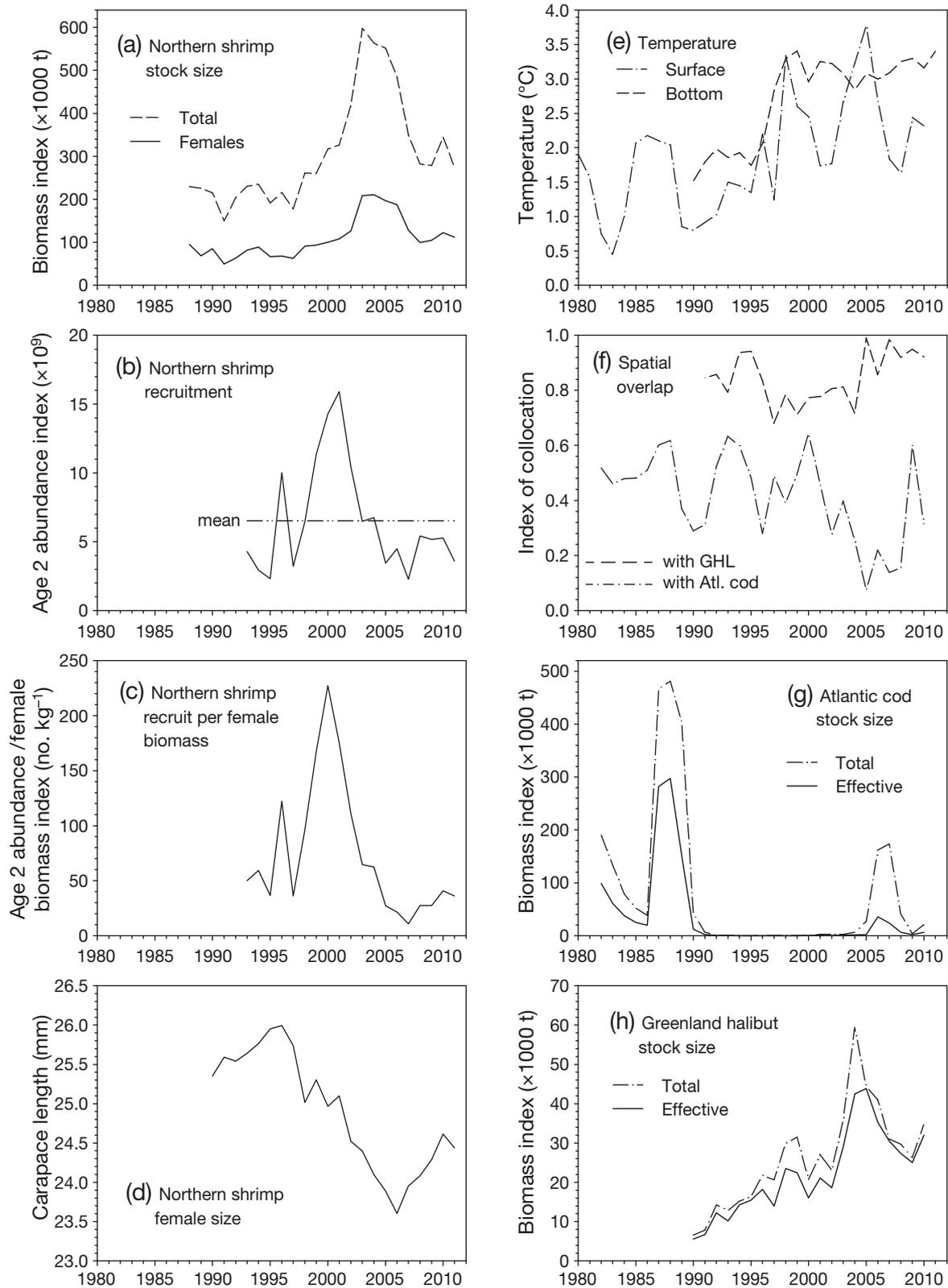


Fig. 3. *Pandalus borealis*. Time series of northern shrimp (a) stock size, (b) recruitment at age 2, (c) recruit per female biomass, (d) mean female length, (e) surface layer and bottom temperature, (f) spatial overlap between northern shrimp and Atlantic cod or Greenland halibut (GHL), and stock size of (g) Atlantic cod and (h) Greenland halibut off West Greenland

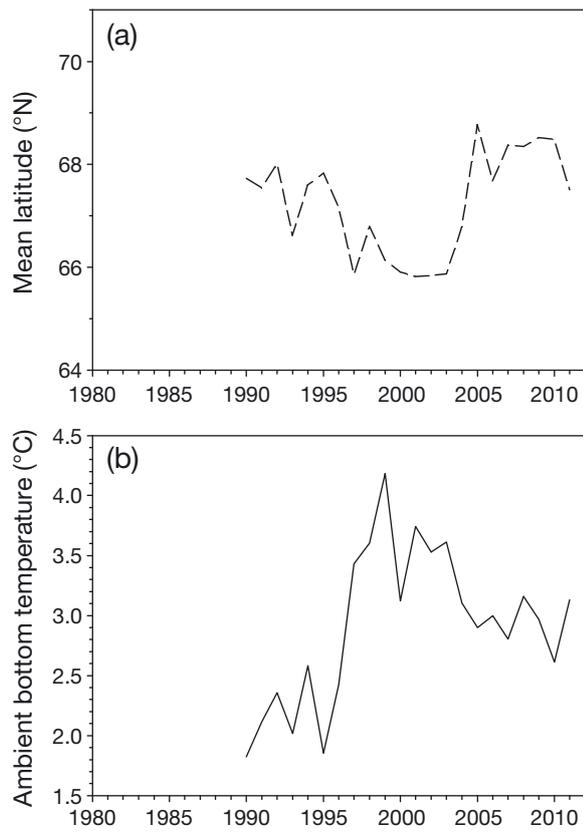


Fig. 4. *Pandalus borealis*. Changes in (a) the latitudinal distribution of northern shrimp and (b) ambient bottom temperature during summer off West Greenland, 1990 to 2011

ous (Fig. 1). However, the catch taken by the commercial fishery during winter (October to March) relative to the female biomass index from the survey in the preceding summer was highest in 1991, declined steadily until 2003 and increased slightly again thereafter (Fig. 5), possibly due to annual variation in the proportion of egg-bearing females removed by the fishery.

Female biomass of northern shrimp ranged from about 50 000 to 210 000 t, and highest abundance indices at age 2 were observed at female biomasses between 60 000 and 90 000 t whereas no strong year classes emerged when female biomass was highest (Fig. 6). Standard and modified Ricker functions explained less than 15% of the recruitment variability (Table 1). Only the density-dependent term (β) of the Ricker functions was significant ($p < 0.05$) in both models; neither the density-independent term (α) nor the offset for the female biomass (γ) were significant in the modified version (Table 1).

Variables that contributed significantly to the final multiple regression model were mean female length in the year of spawning, ambient bottom temperature

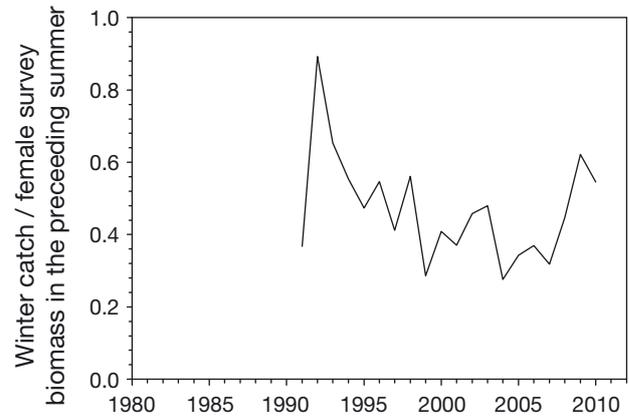


Fig. 5. *Pandalus borealis*. Catch of northern shrimp during winter relative to the female biomass index from the GINR survey in the preceding summer off West Greenland, 1990 to 2010

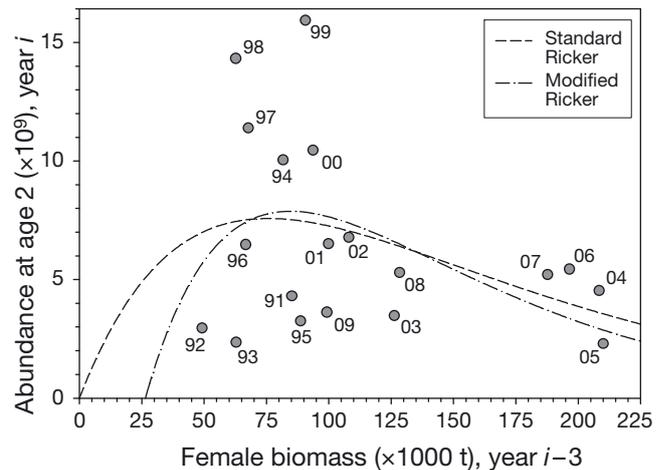


Fig. 6. *Pandalus borealis*. Stock–recruitment plot with fitted Ricker functions for northern shrimp off West Greenland (number at symbol denotes year class)

Table 1. Parameter estimates of the standard and modified Ricker stock–recruitment model for northern shrimp off West Greenland ($n = 19$; standard Ricker: $r^2 = 0.137$, adjusted $r^2 = 0.086$, $p = 0.119$; modified Ricker: $r^2 = 0.147$, adjusted $r^2 = 0.040$, $p = 0.281$)

	Parameter	Coefficient	SE	p
Standard Ricker	α	0.272	0.102	0.016
	β	0.013	0.004	0.002
Modified Ricker	α	0.368	0.194	0.076
	β	0.017	0.007	0.033
	γ	26.382	29.578	0.386

in the year of larval hatch and settling, and Greenland halibut biomass (Table 2). This was the case irrespective of whether the analysis started with

Table 2. Parameter estimates for the environmental variables in the final multiple regression model for northern shrimp recruitment off West Greenland (n = 19, multiple r² = 0.830, adjusted r² = 0.796, p < 0.001, residual SE = 0.3638 at df = 15; VIF: variance inflation factor)

Variable	Coefficient	SE	VIF	p
(Intercept)	-11.208	3.859	-	0.011
Northern shrimp female length, 3 yr lag	0.550	0.147	1.763	0.002
Ambient bottom temperature, 2 yr lag	0.801	0.147	1.182	< 0.001
Greenland halibut biomass, 1 yr lag	-0.038	0.012	1.965	0.007

model (3) or (4). The multiple r² value for the final regression model with 19 yr of observations amounted to 0.830 (p < 0.001, adjusted r² = 0.796). The residuals did not exhibit trends (Fig. 7), did not

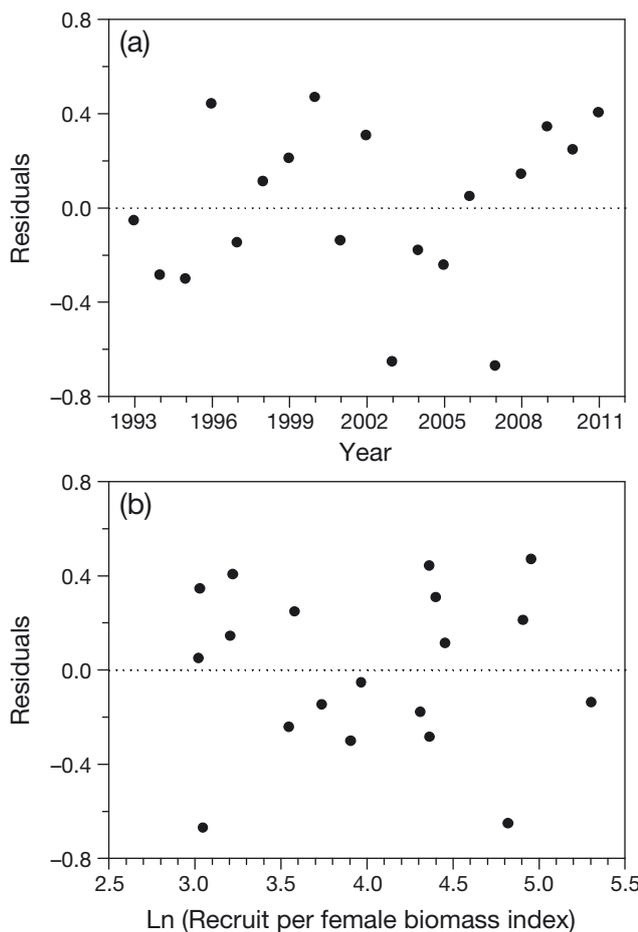


Fig. 7. *Pandalus borealis*. Residuals from the final multiple regression model for northern shrimp recruitment off West Greenland plotted versus (a) year and (b) estimated recruit per female biomass index

deviate significantly from normality (Shapiro-Wilks test passed with p = 0.298) and were not significantly autocorrelated (Pearson product moment correlations with time lags up to 4 yr, p > 0.05). The variance inflation factors for the significant variables (Table 2) were below the value beyond which collinearity may cause difficulties in the parameter estimation (Zuur et al. 2010). The coefficient for mean female length was positive, indicating that pre-recruit survival is higher when the offspring are produced by larger females. The coefficient for Greenland halibut biomass lagged by 1 yr was negative and this would represent predation on the pre-recruits of northern shrimp. Excluding single years from the analysis changed neither the selection of the significant variables (r² between 0.809 and 0.874, p < 0.001 in all cases, adjusted r² between 0.767 and 0.846) nor the signs of the estimated coefficients. Similarly, the exclusion of the first 3 years of the time series did not change the structure of the final model (r² = 0.854, p < 0.001, adjusted r² = 0.817). However, 5 observations were outside the 95% confidence interval associated with the model fit for all available years included, and in particular the high pre-recruit survival in 1996 and the low observed values in 2003 and 2007 were not well represented by the model (Fig. 8).

DISCUSSION

The results of the present study do not support the existence of a classical stock–recruitment relationship for northern shrimp off West Greenland. Egg

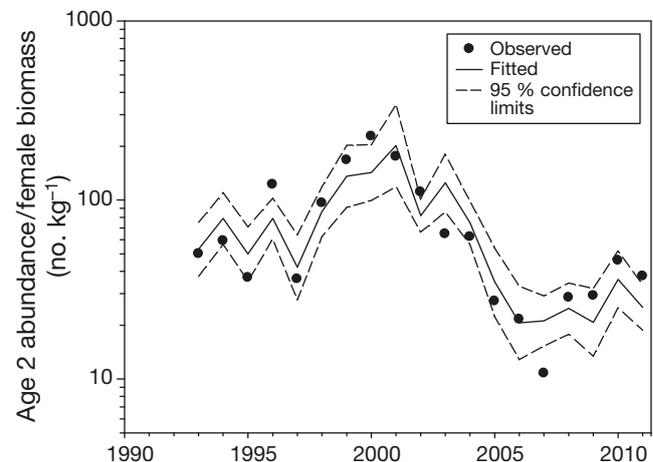


Fig. 8. *Pandalus borealis*. Comparison of the observed recruit per female biomass index with the estimate from the final multiple regression model for northern shrimp off West Greenland

mortality during the egg-bearing period may be due to natural causes such as unfavourable temperature conditions or predation as well as the removal of egg-bearing females from the stock by the fishery in winter. This mortality may result in egg production falling below some threshold level required for the production of a measurable number of recruits. However, using a modified Ricker function, which allows for a non-zero intercept, did not improve the fit, and hence the relevance of such a possible effect could not be demonstrated here.

Both the standard and the modified Ricker models suggested the presence of density-dependence, which justified including female biomass in the initial multiple regression analysis. Female biomass, however, was not significant in the final multiple regression model, which indicates that the low pre-recruit survival at high female biomass was related to unfavourable environmental conditions rather than to density-dependent mechanisms such as limitation of suitable settling areas or cannibalism.

Koeller et al. (2007) reported that decreasing length of northern shrimp off Newfoundland and Labrador was mainly caused by high water temperatures and the fishery could have an accelerating effect through selection of the largest individuals from the population. Off West Greenland, a transition from cold to warm conditions in the late 1990s was related to a decrease in length at sex transition (Wieland 2004). This and the high pre-recruit survival at the same time have likely caused the decline in mean female length observed since the end of the 1990s. Fecundity of northern shrimp is positively correlated with size (Shumway et al. 1985) but changes in mean female length are accommodated when using female biomass instead of abundance as a measure of parental stock size. However, the significance of female length in the multiple regression model on pre-recruit survival suggests that the proportion of large repeat spawners may have an important effect, through egg size and quality, on recruitment success of northern shrimp, as has been postulated for other decapod crustaceans (Moland et al. 2010, Sato & Suzuki 2010).

Warm conditions in the surface layer reduce larval development time and mortality, and will enhance larval growth if food is not limiting (Rasmussen & Tande 1995, Storm & Pedersen 2003). High temperatures shorten the duration of the egg-bearing period but could cause a lower larval size at hatch (Brillon et al. 2005) and a considerably earlier hatching time (Koeller et al. 2009), which may not necessarily match with the timing of the plankton bloom (Ouellet

et al. 2007). However, direct observations on the timing of larval hatch and the onset of the phytoplankton bloom on appropriate spatial scales are sparse and have not provided conclusive results for the West Greenland shelf (Ouellet et al. 2011). The timing and succession of the plankton bloom in high latitude areas does not simply depend on temperature alone due to its link to the actual ice conditions (Heide-Jørgensen et al. 2007, Dünweber et al. 2010). The difference between a surface layer temperature measured at a single standard oceanographic station and an overall ambient bottom temperature at 150 to 600 m depth for the entire shelf between 59° 30' and 72° 30' N, as used in the present study, may not be the most representative indicator for a match or mismatch of the timing of larval hatch of northern shrimp off West Greenland.

Above and below average recruitment levels of northern shrimp were recorded in the absence of Atlantic cod off West Greenland in the period 1992 to 2004, but strong recruitment was not seen in the presence of Atlantic cod, i.e. in the years 2005 to 2009. Similarly, pre-recruit survival of northern shrimp declined when Greenland halibut biomass increased. Northern shrimp has been identified as an important food item in the diet of Greenland halibut at sizes below 60 cm total length in the Davis Strait (Orr & Bowering 1997) and northern shrimp at sizes down to 6 mm carapace length have been found in Greenland halibut stomachs off West Greenland (Pedersen & Riget 1993). It appears therefore reasonable to conclude that the negative coefficient for the Greenland halibut biomass index lagged by 1 yr in the final multiple regression model represents predation on northern shrimp juveniles at age 1. Feeding on juvenile northern shrimp of 4 to 13 mm carapace length has also been reported for Atlantic cod off Newfoundland and Labrador (Parsons et al. 1986). However, in contrast to Greenland halibut, no significant effect of Atlantic cod predation on northern shrimp recruitment was found, which may be explained by the absence or low abundance of Atlantic cod in West Greenland water during the years considered in the present analysis. However, the impact of Atlantic cod may rapidly become important if its biomass and the spatial overlap with northern shrimp increase as was the case until the beginning of the 1990s when the stock dynamics of the 2 species were linked (Wieland et al. 2007).

So far, modelling results on the advection of northern shrimp larvae off West Greenland have not provided conclusive results on the spatial structure of the stock, and the link between Disko Bay and the

adjacent offshore area with respect to larval transport or migration of adults is poorly known (Storm & Pedersen 2003, Ribergaard et al. 2004). Exceptionally high abundance of northern shrimp at age 2 was observed in 1996 and during 1999 to 2002. In 1996, most of these recruits were found in the offshore area between 62° and 66° N, whereas the offshore area between 66° and 69° N and in particular the Disko Bay and Vaigat area contributed the majority of the recruits in the other years (Wieland 2005). The relevant factors for pre-recruit survival may differ between these areas, but spatial effects are at present difficult to incorporate in studies of the processes determining recruitment success of northern shrimp off West Greenland.

Acknowledgements. J. Appel and H. Fock (ISH) provided geo-referenced data for Atlantic cod from the German groundfish survey, and K. Sünksen (previously GINR) did the calculations of spatial overlap between Atlantic cod or Greenland halibut and northern shrimp. Five anonymous reviewers provided valuable comments. The study was supported by the ESSAS (Ecosystem Studies of Sub-Arctic Seas) program.

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Submitted: October 28, 2011; Accepted: May 2, 2012

Proofs received from author(s): August 2, 2012