

# Decreasing shrimp (*Pandalus borealis*) sizes off Newfoundland and Labrador – environment or fishing?

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## ABSTRACT

During the 1990s, carapace length statistics including minimum size caught ( $L_{\min}$ ), mean male and female lengths, size at sex transition ( $L_{50}$ ) and maximum size ( $L_{\max}$ ) of northern shrimp (*Pandalus borealis*) decreased in commercial and survey catches off Newfoundland and Labrador. Decreased growth rates caused by decreases in per-capita food availability due to large population increases, exacerbated by increased metabolic demands from higher water temperatures in the mid-1990s, appear to be the main cause of the size decrease. Fishing could have had an accelerating effect on environmentally driven decreases in shrimp growth and size by ‘cropping’ the largest shrimp from the population. The greatest decreases in shrimp size occurred in Hudson Strait and the adjacent northern shelf, the area which also has the highest densities and largest shrimp. We hypothesize that the greater size decrease here resulted from decreased primary production from decreased nutrient flux into the euphotic zone, caused by increased atmospheric warming, freshwater runoff and stratification during the warming trend of the 1990s.

**Key words:** density dependence, environment, fishing, growth, *Pandalus borealis*, shrimp

## INTRODUCTION

The mean size of females caught in the shrimp (*Pandalus borealis*) fishery off Newfoundland has been

decreasing for over a decade (Orr *et al.*, 2003). This is of concern for a number of reasons. The fishery for northern shrimp off the east coast of Canada is one of the largest in the world. In 2001 it accounted for 34% of the landed value and 28% of the total landed weight of all species in Newfoundland, and it has become an important part of that province’s economy. Market prices are closely tied to shrimp size, and the shift in size composition has contributed to a repositioning of shrimp in the market place from a luxury item to a lower-priced commodity (Anon., 2004). During 2001, the fishery experienced a voluntary closure during the summer months, partly due to low prices caused by large catches of small shrimp.

Biologically, a decrease in the mean size of female shrimp could have a significant effect on the population’s reproductive capacity, as size is directly related to fecundity (Shumway *et al.*, 1985). Decreased size at transition from male to female for this protandric shrimp hermaphrodite has been hypothesized to be a response to fishing (Charnov, 1981), but it has also been attributed to environmentally-caused or density-dependent changes in growth rate (Koeller *et al.*, 2000, 2003). The latter is a plausible explanation for the Newfoundland stock, which has been increasing in biomass for a number of years due to release of predation pressure and/or a favourable physical environment (Lilly *et al.*, 2000). The extraordinarily high population densities of shrimp attained on the Newfoundland–Labrador Shelf during the 1990s may have resulted in decreased per-capita food availability and decreased growth rates.

In the *Pandalus* literature, higher temperatures are often associated with faster growth rates, younger and smaller size at maturation, a smaller maximum size and a shorter longevity (e.g. Shumway *et al.*, 1985; Parsons *et al.*, 1989; Nilssen and Hopkins, 1991). The fastest growth rates and shortest life spans generally occur in warmer southern areas (e.g. Gulf of Maine and Scotia Shelf: 4–5 yr) and the slowest growth rates and longest life spans in the colder northern areas (e.g. Newfoundland–Labrador Shelf, east Greenland stocks: 6–8 yr). Assuming that the other important factor determining growth (per-capita food availability) remained unchanged, temperature changes during the

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study period should be considered as a possible cause of the declining shrimp lengths off Newfoundland and Labrador.

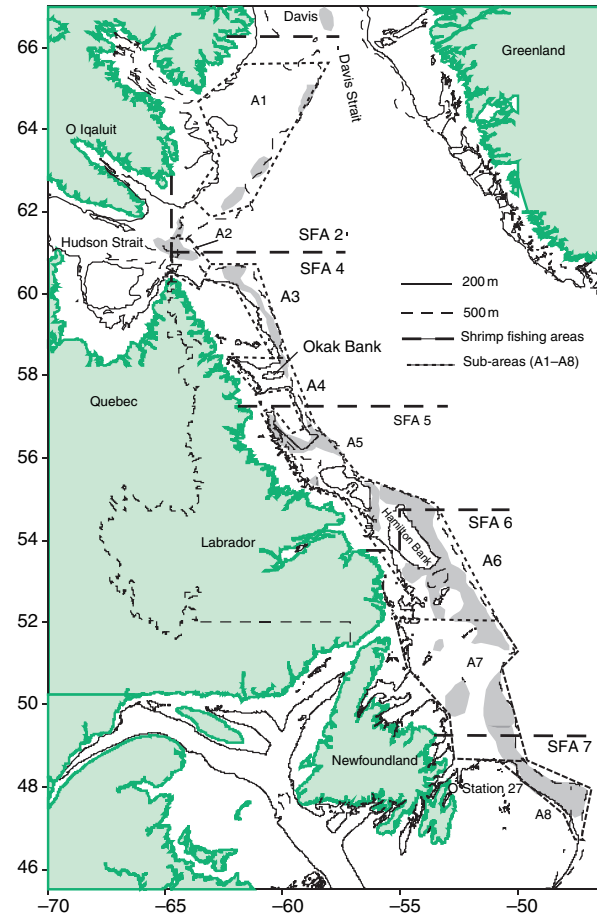
Finding the real cause of the observed temporal decreases in mean size of females in commercial catches off Newfoundland and Labrador is imperative – if fishing is the main causative factor it could be mitigated by decreasing fishing effort. It is noteworthy and further cause for concern that the collapse of many groundfish stocks in the Northwest Atlantic has been associated with a decrease in average fish size and condition, which probably affected reproductive capacity. Although decreased condition has been widely attributed to environmental causes, the actual collapses themselves probably resulted from the combined effects of fishing and unfavourable environmental conditions. In this paper we examine the available length-frequency data from survey and commercial samples in relation to environmental information and fishery statistics with the objective of determining the cause of the decline of shrimp sizes in commercial catches off Newfoundland and Labrador.

## METHODS

The study area, including place names, statistical shrimp fishing areas (SFAs), and the main shrimp fishing grounds are given in Fig. 1. Catch and effort statistics, in particular catch weight, date, tow duration, location and tonnage class, were obtained since 1992 from fishing vessel logbook records. Only statistics from vessels >500 metric tons (mt) were used because these vessels ranged over the entire area throughout the study period and used relatively similar fishing gears and methods. For summary statistics, e.g. SFAs (Fig. 1) by year, catch-per-unit-effort (CPUE) was standardized to account for variations in vessel fishing power, year, month and area as described in Orr *et al.* (2003). Standardized commercial CPUE is considered to be representative of abundance change, but because the fishery occurs in an area smaller than the overall distribution of shrimp, i.e. in the areas where shrimp concentrate, it is more accurate to consider CPUEs as indices of population density (hereafter simply called density) on these grounds. Note that fishing in SFA 7 only began in 2000 by small inshore vessels and since then has only accounted for 4–8% of total landings. This fishery has not been assessed and was excluded from analyses involving summary fisheries statistics by SFA.

Carapace lengths of shrimp by sex were obtained to the nearest 0.1 mm from samples collected by observers from commercial catches or from samples

**Figure 1.** Study area with place names used in the text, location of the main shrimp fishing grounds (shaded), shrimp fishing areas (SFAs) used to report fishery statistics and subareas (A1–A8) for analyses involving smaller geographical units.



taken from research vessel survey catches and summarized by 0.5-mm intervals. Nearly 14 000 individual samples collected since 1992 representing about 7 000 000 individual shrimp measurements from all SFAs off Newfoundland–Labrador were available for analysis from the observer database. The majority of these were from large offshore vessels (>500 mt) – samples collected only by these vessels were used to minimize differences in gear or fishing practices between the inshore (<500 mt) and offshore (>500 mt) fleet. About one-tenth that number of samples and individual measurements were available from surveys conducted since 1995. Length statistics were calculated for each sample for comparisons involving individual catches per tow. Commercial samples, although not as widespread geographically within SFAs, have a wider overall geographical range, i.e.

they sample all SFAs. Also, they have many more samples per SFA and year from within the main shrimp concentrations. Minimum cod-end mesh size for the commercial fleet is 40 mm. Survey coverage began in 1995 but decreases with increasing latitude – the best being in SFA 6, and no coverage in SFA 2. These ‘multispecies’ surveys were designed to provide abundance estimates for a variety of commercially important species, not just shrimp (Brodie, 1996). Consequently the depth-stratified random design covered all depths and habitats (Bishop, 1994). A minimum of two 15-min sets were sampled within each depth stratum using the standard Campelen survey trawl (cod-end mesh size: 40 mm with a 12.7-mm liner). Bottom water temperatures were determined from CTD recorders deployed at all survey stations (Model SBE-19, Seabird Electronic Inc., Bellevue, WA, USA).

Note that while survey set lengths are short and constant at 15 min, commercial tow lengths vary and can last for many hours. It is known for survey trawls in general (Gunderson, 1993) and for shrimp surveys in particular (Koeller *et al.*, 1996) that shorter tows produce larger catches per unit time. Shrimp trawls fish more efficiently when nearly empty – as the net fills, cod-end meshes in front of the catch expand and allow more small shrimp to escape. Consequently, tow length will have some effect on selectivity, but opposite to the density-dependent effect described in this paper.

Growth during the first and second years of life can be determined with modal analysis because the first and often the second modes are relatively easy to distinguish in survey samples. Commercial trawl gear selects for larger shrimp and is usually unsuitable for early growth determinations, which mainly involves shrimp <15 mm in length. Visual inspection showed that survey length frequencies in SFA 6 offered the most consistent opportunity to discriminate between the first and second modes. The second mode was never easily distinguished from combined length frequencies in SFA 5, and the first mode often had too few shrimp to provide a reliable estimate of mean size. Spatial and temporal coverage was limited in other SFAs. Consequently, modal analysis was conducted only on the combined survey samples of SFA 6. Modal analysis was conducted using the MIX computer program (MacDonald and Pitcher, 1979).

The statistic  $L_{50}$  was estimated by fitting a sigmoid curve to a cumulative percent (female) length-frequency (maturity) ogive and estimating the length at which 50% of the shrimp were females, according to the method described in Skúladóttir (1998). For commercial samples,  $L_{50}$  was estimated for each

sample and area/year estimates obtained by averaging the sample values. Because of random sampling, many survey samples did not have enough shrimp to determine  $L_{50}$  accurately (minimum 200 shrimp), so this statistic was not calculated for this data source. The statistics  $L_{\min}$  and  $L_{\max}$  were calculated as the smallest and largest shrimp measured in each sample, averaged (arithmetic mean) for all samples in each area and year. Mean male and female lengths were calculated for individual samples and these were averaged (unweighted) by year and SFA.

An estimate of the effect that the fishery could have had on mean female size was obtained by subtracting the female catch at length for each year from an estimate of the population at length obtained from the survey the same year. Only females were used as these are fully recruited to both commercial and survey gear and less likely than males to be affected by differences in selectivities associated with different commercial trawls. Mean female sizes were calculated for the population estimate before and after subtracting the catch at length to obtain an estimate of the difference in mean female length due to the fishery. Catch-at-length was estimated by applying weighted (by catch) length frequencies from observer samples to the total catch in SFA 6 using a length–weight relationship. Female survey population at length was estimated from survey catches and corresponding sample length–frequency relationships using the swept area method (Halliday and Koeller, 1981). We adjusted the total survey population estimate at length so that the resulting exploitation rates (number of females in catch/number of females in survey population estimate) encompassed those given for SFA 6 in Orr *et al.* (2003). As expected, the change in the mean size of females before and after removals of the catch at length was highly sensitive to exploitation rates. Note that survey abundance estimates are usually considered to be indices only; consequently our results must be interpreted cautiously. Usually, they are considered to be minimum estimates because of trawl catchability problems, so our results on fishery effects are likely to be overestimated. In addition, commercial samples were collected throughout the year, whereas survey data were collected near year end, i.e. shrimp caught in the year-end survey generally had more time to grow than those caught commercially throughout the year. This would also tend to overestimate the effect of the fishery on female size.

To examine changes in shrimp sizes on a geographical scale finer than SFAs, the study area was divided into eight subareas (A1–A8 in Fig. 1). These subareas represent major shrimp concentrations as

determined by the distribution of commercial catches. In addition to separating these concentrations latitudinally, each subarea also encompassed the peripheral shrimp population associated with it, as determined from the distribution of survey catches. Both commercial and survey catches show that most of the stock is found between 200 and 500 m; consequently the areas were defined by including the surface area between these depth contours.

## RESULTS

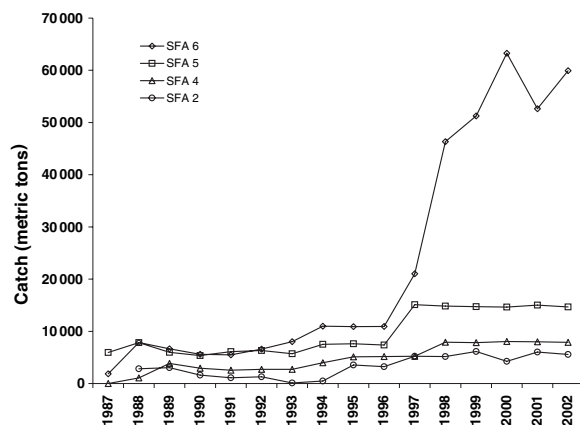
### *Fishery and resource statistics*

Catches were relatively low in all areas during the 1980s (Fig. 2). They began to increase during the early 1990s, with the largest increases occurring in the two southern SFAs, in 1997 for SFA 5 and from 1997 to 2000 in SFA 6. Annual catches in each SFA decrease with increasing latitude, so that the southernmost SFA tends to have the highest and the northernmost SFA the lowest annual catches throughout the history of the fishery.

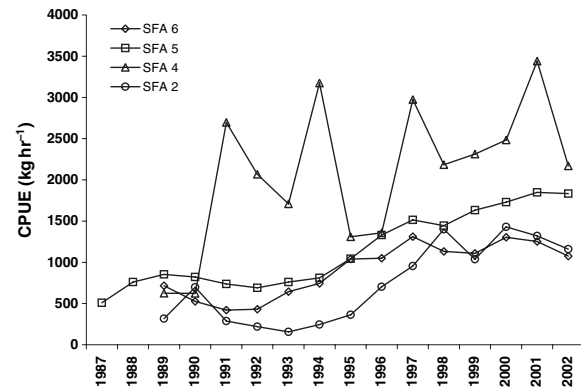
Catch-per-unit-effort, and hence density, on the shrimp grounds in SFAs 2, 5, and 6, began to increase during the early 1990s with the most significant increases occurring between 1994 and 1997 (Fig. 3). CPUE appeared to level off at a high level in SFAs 2 and 6 in 1998, and it continued to increase at a lower rate in SFA 5. SFA 4 showed by far the highest catch rates of all SFAs except for the first 2 yr of the series. CPUEs in this SFA are also more variable, and the increasing trend, while present, is not as well defined as in other SFAs.

Exploitation indices can be calculated for years when surveys occurred (Fig. 4). These indicate that

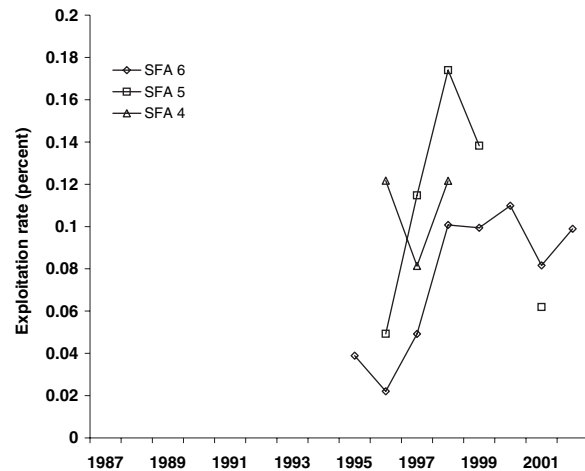
**Figure 2.** Total catches from shrimp fishing areas (SFAs) 2, 4, 5 and 6 off Newfoundland and Labrador, 1987–2002.



**Figure 3.** Standardized (to a reference vessel) shrimp catch-per-unit-effort (CPUE) from large vessels (>500 metric tons) for shrimp fishing areas (SFAs) 2, 4, 5 and 6, 1987–2002.



**Figure 4.** Exploitation rates (commercial catch/survey biomass) for years when surveys were conducted in shrimp fishing areas (SFAs) 4, 5 and 6. Survey data are not available from SFA 2.

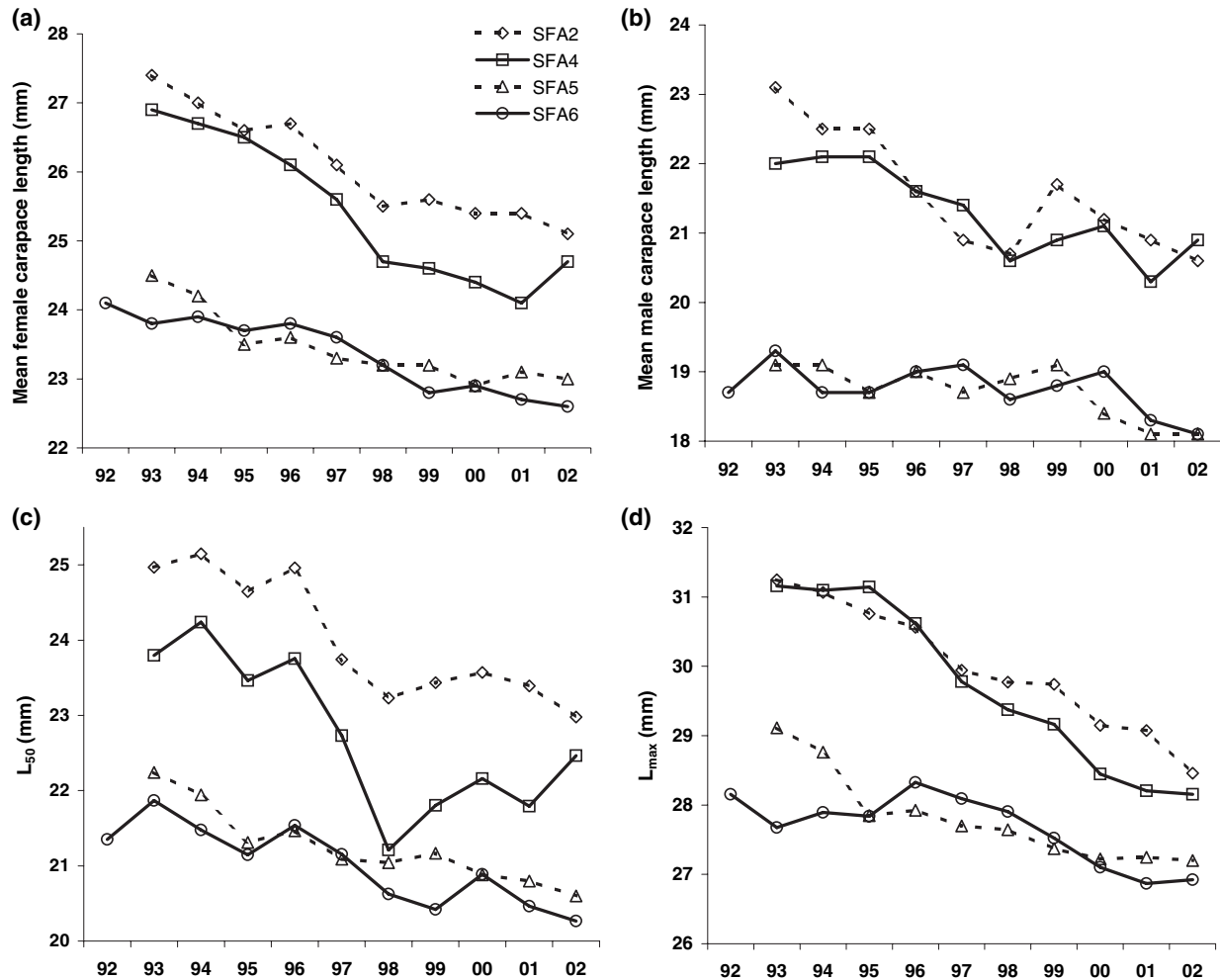


although SFA 6 has returned the highest total catches (Fig. 2), it has the lowest exploitation rates because of high biomasses. Exploitation of the female population (number of females in catch/survey female population), was in the order of 10–20% and 10–15% in SFAs 5 and 6, respectively, during recent years (Orr *et al.*, 2003).

### *Temporal and latitudinal changes in carapace length*

The mean sizes of males, females, size at sex transition ( $L_{50}$ ) and maximum size ( $L_{max}$ ) in the two northern areas (SFAs 2 and 4) are significantly (ANOVA,  $P < 0.001$ ) larger than in the two southern areas (Fig. 5). The size decrease for all categories in the two northern areas was larger than in the south. In the short

**Figure 5.** Changes in the mean size of females (a), males (b), size at sex transition ( $L_{50}$ ) (c) and maximum size ( $L_{max}$ ) (d) in the commercial fishery off Newfoundland Labrador by shrimp fishing area (SFA), from commercial fishery samples.

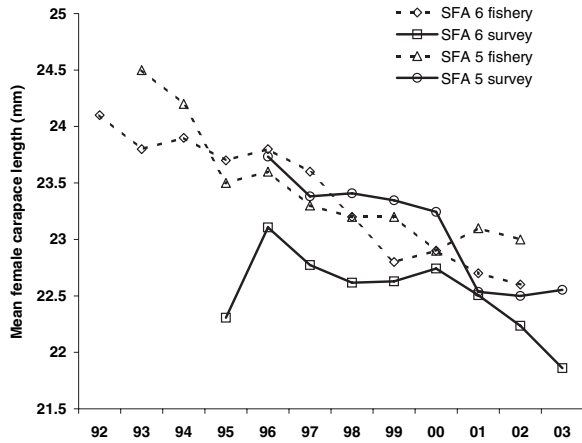


term, northern females showed a relatively rapid decrease from 1995 to 1998 (Fig. 5a). A similar pattern was seen in one of the southern areas (SFA 6, Fig. 5a). Only SFA 5 did not show a period of more rapid decrease during the mid-to-late 1990s. Size decreases in the smaller males were similar to females (Fig. 5b). The temporal trends in  $L_{50}$  and  $L_{max}$  are broadly similar to changes observed in mean male and female carapace lengths, i.e. there was a decrease in size at sex change and maximum size in all areas, greater changes were observed in the two northern areas, and an accelerated decrease occurred during the mid-to-late 1990s which appeared to be more pronounced in the northern areas (Fig. 5c, d). The period of more rapid decline in shrimp sizes in most areas corresponds to the time period when catches, CPUE and, at least in SFA 6, exploitation, increased significantly.

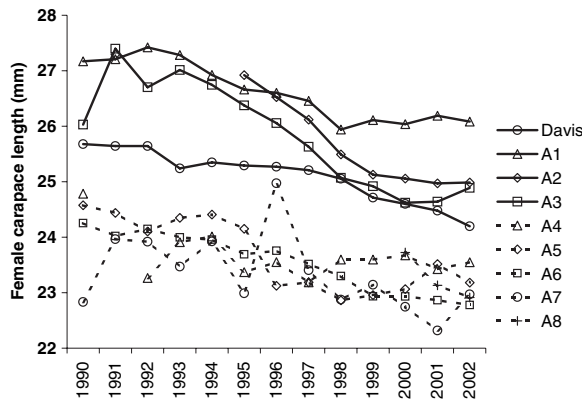
Survey coverage is more limited geographically and has a shorter time series, but in general the data show the same decreasing trend in carapace lengths as the commercial data (Fig. 6).

Temporal changes in female commercial carapace lengths by subareas (Fig. 7) reveal that the large differences in carapace lengths between the northern and southern SFAs shown in Fig. 5 are due to a pronounced latitudinal increase in length between areas A4 and A3. This occurs mainly in the vicinity of Okak Bank (latitude 58°N) rather than being a gradual cline from the northernmost to the southernmost areas. On average the decrease in carapace length from A3 to A4 is 2.2 mm, about the same as the largest temporal change observed in the north, and considerably more than the temporal changes in the south (approx. 1 mm). Clearly, spatial (latitudinal) factors on the

**Figure 6.** Mean female carapace lengths from survey and commercial fishery samples in shrimp fishing areas (SFAs) 5 and 6.



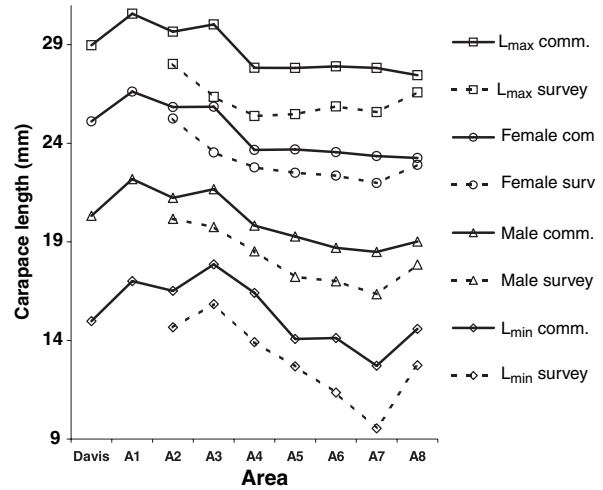
**Figure 7.** Mean female carapace lengths (mm) for subareas identified in Fig. 1 from commercial samples.



Newfoundland shelf have at least as strong an influence on shrimp growth as do temporal factors. Temporal trends in mean carapace lengths for the southern areas (A4–A8) were difficult to discern individually but showed a gradual decrease when combined. In contrast, the northern areas showed clear latitudinal and temporal differences. Shrimp in A3 were consistently smaller than in the area immediately to the north (A2). Particularly noteworthy is that shrimp in A2 and A3 showed a much larger temporal decrease than the northernmost area (A1). A commercial concentration north of A1 (labelled ‘Davis’ in Fig. 1) had significantly smaller shrimp than those in the other northern areas and showed the more gradual temporal decline exhibited in A1 and the southern areas (A4–A8).

As with the temporal trends shown in Fig. 6, the latitudinal trends in the commercial and survey

**Figure 8.** Average carapace lengths (mm) for  $L_{max}$ , females, males and  $L_{min}$  by subareas for commercial and survey data (all years combined).

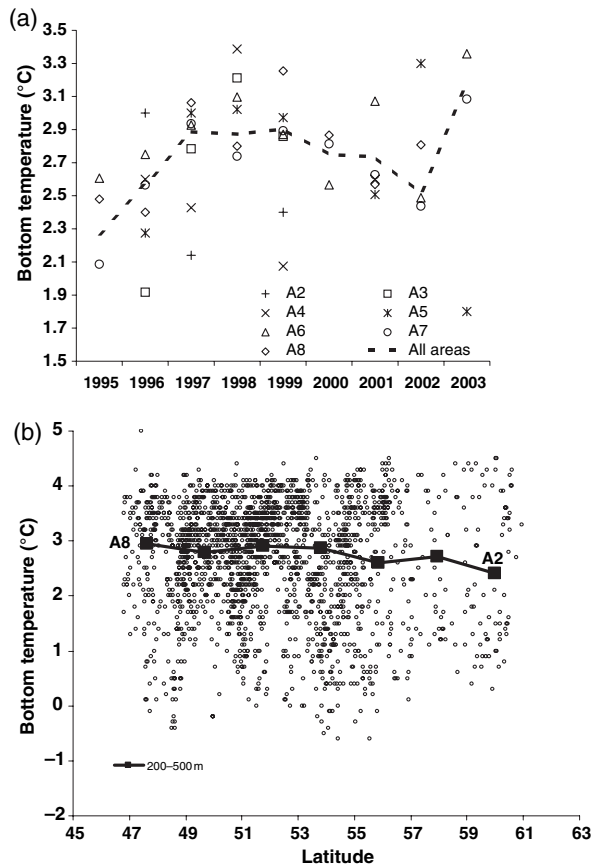


samples are broadly similar (Fig. 8). Both data sets show the rapid increase in carapace lengths north of A4 for females and  $L_{max}$ , although the increase is more gradual for survey males. Also, survey samples for  $L_{max}$  showed minimum sizes in the mid-shelf areas (A4, A5), with larger sizes in the areas to the north and south. Males, females, and  $L_{max}$  are always smaller in survey samples because commercial trawlers actively seek the largest shrimp, which tend to be found in deeper water, and they use larger cod-end mesh sizes. Survey samples cover the entire area and depth range of distribution and therefore give a better indication of population size characteristics and trends.

*Temporal and latitudinal changes in temperature*

Long-term water temperature trends on the Newfoundland–Labrador Shelf are associated with the North Atlantic Oscillation (NAO) which influences atmospheric and water temperatures over a large part of the North Atlantic. For example, increasing temperatures (150-m depth) at an oceanographical transect on Hamilton Bank and at Station 27 during the mid-1990s (Colbourne, 2003) were also observed in bottom water temperatures during shrimp surveys off West Greenland (Wieland, 2004) and have been reported elsewhere in the literature (e.g. Stein, 2000). This signal was apparent in our survey bottom-temperature data at depths where shrimp are found (Fig. 9a). Clearly shrimp on the Newfoundland–Labrador Shelf were subjected to increasing water temperatures of about 1–1.5°C during the mid-1990s.

**Figure 9.** (a) Average bottom water temperatures (200–500 m) by subarea on the Newfoundland–Labrador Shelf from multispecies surveys 1995–2003. (b) All bottom water temperatures (200–500 m) collected during multispecies surveys plotted against latitude. The solid line shows average temperatures by area (all years).



Available survey temperature data show that during fall, bottom water temperatures (all depths) increase with latitude on the Newfoundland Shelf by about half a degree (from about 4 to 4.5°C) for the deepest water (Fig. 9b). Average bottom water temperatures (all years) by subarea in the depths where shrimp are found (200–500 m) do suggest some decrease with latitude; however, the difference between A7 and A3 is <math>0.1^{\circ}\text{C}</math>, and none of the area averages differ significantly from each other (ANOVA,  $P > 0.01$ ). There was a significant year effect ( $P < 0.001$ ) for years in which all areas have observations (1996–99), indicating that annual changes occur in all areas. These data indicate that on average shrimp in all areas on the Newfoundland–Labrador Shelf experience similar bottom-temperature regimes.

### Carapace lengths and density

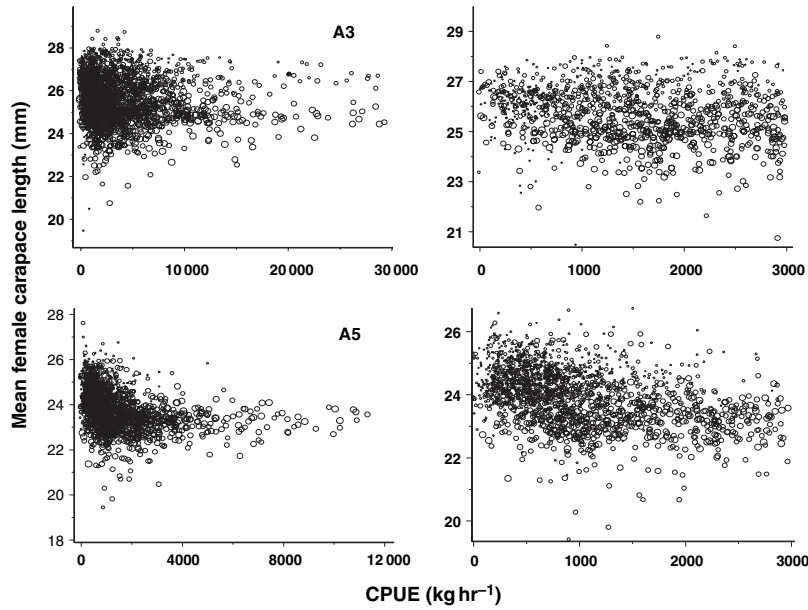
The relationships between density and female carapace length in areas A3 and A5 are shown in Fig. 10 as representative of shrimp length in the northern and southern areas. In A5 there is a negative linear relationship with densities below  $1500 \text{ kg h}^{-1}$ . Above this density the relationship tends to level off, although the range in mean carapace lengths continues to narrow, probably because these highest densities represent exceptional year classes. The regression at densities  $< 1500 \text{ kg h}^{-1}$  is highly significant (Table 1) and represents a decrease in carapace length of about 1.5 mm from the lowest to the highest densities, about the same as the overall temporal decrease in this area. In contrast, A3 displays less narrowing of the range of female sizes with increasing densities – the pattern is ‘dome’ shaped as opposed to ‘triangular’ in A5, because there are fewer prominent year classes in A5 and more uniformly large year classes in A3 (note the difference in scales between the left panels in Fig. 10). A negative relationship between density and female size was significant ( $P < 0.0001$ ) in five of the nine areas for which data were available, suggesting that growth was limited by per-capita food availability in these areas (Table 1). Female size in A3, A4 and A8 showed no significant decrease with density and A7, although significant, showed a positive slope.

### Growth

Modal analysis of survey samples showed that length at age 1 increased from 1995 to 1998 and decreased thereafter in SFA 6 (Fig. 11). Except for 1999, length at age 2 decreased throughout the period between 1995 and 2002. The increment between age 1 and age 2 decreased from a maximum of 5.2 mm in 1995 to 2.1 mm in 2002, a difference of over 3 mm, which was greater than the decrease experienced by males or females as determined from commercial samples in this area (Fig. 5a, b). We were unable to determine early growth for northern areas due to limited survey sampling and difficulties in distinguishing modes in these areas; consequently, it was not possible to directly determine if the observed increases in size with latitude were due to increased growth rates or decreased growth rates and increased longevity.

### The effect of fisheries removals on population carapace lengths

The difference between population (survey) mean female carapace length before and after fishery removals (catch-at-length) was positive for all years in SFA 6, indicating that the mean size of females removed by



**Figure 10.** Density (catch-per-unit-effort; CPUE) versus mean female carapace length for commercial observer samples from subareas A3 and A5, 1990–2002. Symbol sizes increase with years. The panels on the left include all CPUEs, those on the right only CPUEs <3000 kg h<sup>-1</sup>.

**Table 1.** Statistics by subarea for linear regressions of mean female carapace lengths versus density [commercial catch-per-unit-effort (CPUE)] for CPUEs <1500 kg h<sup>-1</sup>.

Area	R <sup>2</sup>	Slope	P
Davis	0.0559	-0.3439	0.0000 **
A1	0.0275	-0.1417	0.0000 **
A2	0.0213	-0.1817	0.0002 **
A3	0.0034	-0.0846	0.1446 NS
A4	0.0076	-0.1829	0.4170 NS
A5	0.0545	-0.3068	0.0000 **
A6	0.0262	-0.2306	0.0001 **
A7	0.0161	0.1611	0.0018 *
A8	0.0082	0.0777	0.3543 NS

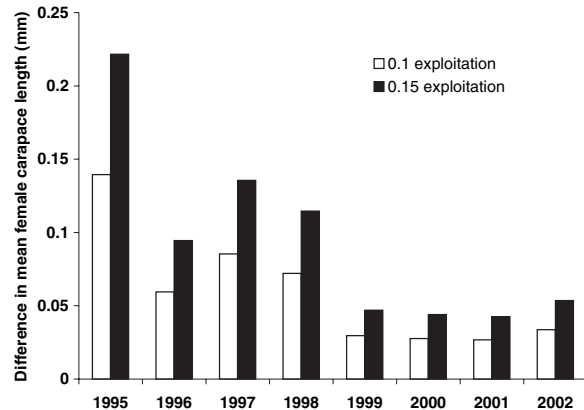
\*\*P < 0.001; \*P < 0.01.

**Figure 11.** Annual average length at age 1 and age 2 from modal analysis of the combined length frequencies from surveys in shrimp fishing area (SFA) 6.



the fishery was always larger than the mean of those sampled by the survey (Fig. 12). This is expected since the fishery actively seeks larger females (see also Fig. 8). The differences were greater during the earlier years (1995–98), probably because the fishery was more successful at finding and removing accumulated larger females from the population. As expected, the difference in carapace length is highly sensitive to exploitation rates – the two rates used in the calculations (10% and 15%) represent the range for SFA 6 females in recent years given in Orr *et al.* (2003). Recent exploitation rates were probably the highest experienced during the period. Note that exploitation rates are considered relative indices only – given that

**Figure 12.** Differences in population (survey) mean female carapace length before and after fishery removals in shrimp fishing area (SFA) 6, estimated for two exploitation rates.



**Table 2.** Coefficients ( $r$ ) for correlations between carapace length statistics (commercial samples) and abundance [commercial catch-per-unit-effort (CPUE)], commercial shrimp catch, air temperatures at Iqaluit, and water temperatures (Station 27, 175 m).

	CPUE	Catch	Iq. air	Stn 27(175 m)
$L_{\min}$	-0.0474	-0.3429	-0.1384	-0.2378
Male	-0.4416	-0.7002**	-0.5219	-0.5864*
$L_{50}$	-0.7311**	-0.9083**	-0.7672**	-0.8028**
Female	-0.7774**	-0.9370**	-0.8125**	-0.8255**
$L_{\max}$	-0.7104**	-0.9037**	-0.7315**	-0.7253**

\*\* $P < 0.001$ ; \* $P < 0.01$ .

abundance estimates are considered to be minimal, the true rates may have been considerably lower, and those for earlier years, lower still. Accepting, however, an exploitation rate for SFA 6 of 10%, the difference in carapace lengths before and after the fishery in 1995 was about 0.25 mm, about the same as the annual rate of decrease observed for females before 1996 (Fig. 5d). After 1996, the difference was less than 0.1 mm, yet between 1996 and 1999 carapace lengths dropped by nearly a millimetre in this area.

Correlation coefficients between commercial-sample carapace-length statistics and shrimp abundance (commercial CPUE) and catches in SFA 6, water temperature anomalies representative of the southern Newfoundland Shelf (Station 27, 175 m), and annual mean air temperature anomalies at Iqaluit are shown in Table 2. Significant ( $P < 0.001$ ) negative correlations were found between the three largest length categories ( $L_{50}$ , females and  $L_{\max}$ ) and the other variables, i.e. catch, abundance, and the two temperature series.

## DISCUSSION

### *The case for fishery-induced changes in shrimp size*

Limited survey data restrict a comparison of exploitation rates and size decreases between areas, but some conclusions can still be drawn. The catches were highest by far in SFA 6, but the exploitation rates there were lowest because the biomass there was highest – consequently one would expect any fishery impact on mean female size to be less pronounced than in other areas. However, there is no significant difference in the long-term (1992–2002) rate of length decrease between SFA 6 and the more heavily fished (indexed by exploitation rate) SFA 5. Exploitation rates for the northern areas are only available for SFA 4 for 1996–98. These appear to be roughly the same as the other areas. Assuming exploitation rates in the two northern areas to be about the

same as those in southern areas, and assuming the cause of the size decrease to be mainly fishery induced, one would expect the rate of size decrease to be about the same in the north as in the south. However, the rate of size decrease was considerably greater in the north, suggesting that this difference was due to factors other than fishing.

Assuming again that size decreases were at least partly due to fishing, one would expect an acceleration of this decline when exploitation rates increased. This was indeed the case in SFA 6 – exploitation rates increased sharply from 1996 to 1998 due to quota increases and mean female size began a 3-yr decline beginning the same year. In fact, three of the four fishing areas (SFAs 2, 4 and 6) had their greatest decline in mean female size during years when quotas and catches increased significantly. Accelerated declines in  $L_{50}$  and mean male sizes were also observed at about the same time. Charnov (1981) presented evidence for fishery-induced decreases in  $L_{50}$  and theorized that this was a response to decreased female densities and egg production. However, in Newfoundland, female densities increased during the time of decreasing  $L_{50}$ , such that Charnov's (1981) theoretical mechanism is unlikely to be the cause of the length declines off Newfoundland. Size decreases also occurred in males, before sex transition. The largest density increases occurred at the time of the greatest size decreases, suggesting that growth was decreasing due to decreasing per-capita food availability. Modal analysis confirmed that growth rates of the smallest shrimp (ages 1 and 2) were decreasing during the late 1990s. Removal of the catch at length from the survey population estimate at length did suggest that the fishery could have had an impact on mean female carapace length during earlier years when the fishery was removing accumulated large females. However, the calculated impact of the fishery was less than that observed during the period of rapid decline, indicating that other factors were involved. The large decrease in early growth in SFA 6 from modal analysis of survey data cannot have been caused by fishing since these small sizes have not recruited to the commercial gear and only small numbers are caught. Since temporal decreases in carapace lengths were apparent at all sizes (males, females,  $L_{50}$  and  $L_{\max}$ ) including those which had not yet or only partially been recruited to the fishery, we conclude that fishing was not the main cause of these decreases, although it probably contributed to them, as suggested by Fig. 12 and by the strong correlation between carapace lengths and shrimp catches (Table 2).

### *The case for the environment*

Wieland (2004) concluded that a decrease in shrimp sizes off West Greenland during the mid-1990s was due to decreased growth caused by increased bottom water temperatures and their associated higher metabolic requirements, coupled with increased biomasses and densities caused in part by decreased predation pressure (cod stock collapse) and the resulting lower per-capita food availability. We have shown that a similar situation existed on the Newfoundland–Labrador Shelf during the same time period. The increase in bottom water temperatures of the mid-1990s was also observed on the Newfoundland shelf, although it averaged only about 1°C versus about 2°C off Greenland (Wieland, 2004). The increased shrimp abundances on the Newfoundland shelf during the 1990s have also been attributed, at least in part, to the release of predation pressure caused by the collapse of the northern cod stock (Lilly *et al.*, 2000). As in West Greenland, negative relationships between density and shrimp size suggest that growth is food limited over much of the Newfoundland Shelf. We conclude that the concurrent decrease in shrimp sizes on the Newfoundland–Labrador Shelf and off West Greenland was caused by similar mechanisms, i.e. increased shrimp biomass and densities from decreased predation by cod resulted in lower per-capita food availability, and the resultant slower growth was exacerbated by the increased metabolic demand of higher temperatures. This is supported by the strong negative correlation between carapace length statistics, abundance, and water temperatures.

We have shown that colder temperatures are not necessarily the cause of the assumed slower growth, increased longevity, and larger sizes (e.g. Parsons *et al.*, 1989) of shrimp on the northern Newfoundland–Labrador Shelf – shrimp in all areas of the shelf experienced similar bottom water temperatures. In fact, during much of the summer growing season bottom water temperatures tend to increase with latitude in this area (Colbourne and Mertz, 1998). The similar bottom water temperature conditions experienced by shrimp on the Newfoundland–Labrador Shelf between latitudes 48°N and 65°N (<1°C) stand in sharp contrast to the latitudinal temperature gradient of about 5°C experienced by the West Greenland stock between 60°N and 73°N (Wieland, 2004). If temperature differences are not the main cause of the observed latitudinal changes in shrimp growth and size, then they may result from differences in food availability. The significant negative relationships between shrimp

size and density confirm that food is growth limiting on much of the shelf.

It is particularly noteworthy that the areas at the mouth and immediately to the south of Hudson Strait (A2–A3), which have the largest shrimp on the Newfoundland Shelf, also experienced the greatest temporal size decrease during the mid-1990s. We hypothesize that shrimp here are larger because of greater food availability from enhanced primary production, in turn caused by complex mixing processes and higher nutrient concentrations in these areas (Sutcliffe *et al.*, 1983; Drinkwater and Harding, 2001). We further hypothesize that the factors and mechanisms resulting in larger shrimp here were also responsible for the greater size decreases in these areas. Increased freshwater runoff during the warming period of the mid-1990s, evidenced by the increased air temperatures at Iqaluit, could have led to increased stratification of the water column and decreased mixing of nutrients into the euphotic zone. This effect would have been more pronounced near the main freshwater source for the Newfoundland Shelf, i.e. Hudson Strait. In a companion paper (Fuentes-Yaco *et al.*, 2006) we explore in detail the possibility that latitudinal and temporal changes in phytoplankton production dynamics, as revealed by satellite ocean-colour analysis, could help explain the changing shrimp growth patterns, both temporally and spatially, on the Newfoundland–Labrador Shelf.

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### REFERENCES

- Anon. (2004) *Proceedings of the International Coldwater Prawn Forum 2004*. London: Shellfish Association of Great Britain, Fishmonger's Hall (available on CD).
- Bishop, C.A. (1994) Revisions and additions to stratification schemes used during research vessel surveys in NAFO Sub-areas 2 and 3. *NAFO SCR Doc 94/43*, 23 pp.
- Brodie, W. (1996) A description of the 1995 fall groundfish survey in Division 2J3KLMNO. *NAFO SCR Doc 96/27*, 7 pp.
- Charnov, E.L. (1981) Sex reversal in *Pandalis borealis*: effect of a shrimp fishery? *Mar. Biol. Lett.* 2:53–57.

- Colbourne, E.B. (2003) Physical oceanographic conditions on the Newfoundland and Labrador shelf during 2002. *Canadian Science Advisory Secretariat Research Document* 2003/020, 52 pp.
- Colbourne, E.B. and Mertz, G. (1998) Spatial and temporal variability of ocean temperature over the Labrador Shelf. *Atmosphere-Ocean* **36**:299–317.
- Drinkwater, K.F. and Harding, G.C. (2001) Effects of the Hudson Strait outflow on the biology of the Labrador Shelf. *Can. J. Fish. Aquat. Sci.* **58**:171–184.
- Fuentes-Yaco, C., Koeller, P., Sathyendranath, S. and Platt, T. (2006) Shrimp (*Pandalus borealis*) growth and timing of the spring phytoplankton bloom on the Newfoundland–Labrador Shelf. *Fish. Oceanogr.* doi:10.1111/j.1365-2419.2006.00402.x.
- Gunderson, D.R. (1993) *Surveys for Fisheries Resources*. New York: John Wiley and Sons, 248 pp.
- Halliday, R.G. and Koeller, P.A. (1981) A history of Canadian groundfish trawling surveys and data usage in ICNAF Divisions 4TVWX. In: W.G. Doubleday and D. Rivard (eds) *Bottom Trawl Surveys*. *Can. Spec. Publ. Fish. Aquat. Sci.* **58**: 273 pp.
- Koeller, P., Covey, M. and King, M. (1996) The Scotian Shelf shrimp (*Pandalus borealis*) fishery in 1996. *DFO Atlantic Fisheries Research Document* 96/128, 54 pp.
- Koeller, P., Mohn, R. and Etter, M. (2000) Density dependent sex-reversal in pink shrimp, *Pandalus borealis*, on the Scotian Shelf. *J. Northw. Atl. Fish. Sci.* **27**:107–118.
- Koeller, P., Covey, M. and King, M. (2003) Is size at sex transition an indicator of growth or abundance in pandalid shrimp? *Fish. Res.* **65**:217–230.
- Lilly, G.R., Parsons, D.G. and Kulka, D.W. (2000) Was the increase in shrimp biomass on the northeast Newfoundland shelf a consequence of a release in predation pressure from cod? *J. Northw. Atl. Fish. Sci.* **27**:45–61.
- MacDonald, P.D.M. and Pitcher, T.J. (1979) Age-groups from size-frequency data: a versatile and efficient method of analysing distribution mixtures. *J. Fish. Res. Board Can.* **36**:987–1011.
- Nilssen, E.M. and Hopkins, C.C.E. (1991) Population parameters and life histories of the deep-water prawn *Pandalus borealis* from different regions. *ICES CM* 1991/K:2, 19 pp.
- Orr, D.C., Veitch, P.J. and Sullivan, D.J. (2003) Northern shrimp (*Pandalus borealis*) off Baffin Island, Labrador and northeastern Newfoundland. *DFO Canadian Science Advisory Secretariat Research Document* 2003/050, 65 pp. Available at: [http://www.dfo-mpo.gc.ca/csas/Csas/DocREC/2003/RES2003\\_050\\_E.pdf](http://www.dfo-mpo.gc.ca/csas/Csas/DocREC/2003/RES2003_050_E.pdf).
- Parsons, D.G., Lilly, G.R. and Veitch, V.L. (1989) A comparison of the growth of northern shrimp (*Pandalus borealis*) from four regions of the Northwest Atlantic. *J. Northw. Atl. Fish. Sci.* **9**:123–131.
- Shumway, S.E., Perkins, H.C., Schick, D.F. and Stickney, A.P. (1985) Synopsis of biological data on the pink shrimp, *Pandalus borealis* Krøyer, 1838. *FAO Fish. Synop.* **144**:57.
- Skúladóttir, U. (1998) Size at sexual maturity of female northern shrimp (*Pandalus borealis*) in the Denmark Strait 1985–93 and a comparison with the nearest Icelandic shrimp populations. *J. Northw. Atl. Fish. Sci.* **24**:27–37.
- Stein, M. (2000) Hydrographic and atmospheric conditions off east Greenland – their potential effect on the distribution of shrimp (*Pandalus borealis*). *J. Northw. Atl. Fish. Sci.* **27**:63–76.
- Sutcliffe, W.H., Jr, Loucks, R.H., Drinkwater, K.F. and Coote, A.R. (1983) Nutrient flux onto the Labrador Shelf from Hudson Strait and its biological consequences. *Can. J. Fish. Aquat. Sci.* **40**:1692–1701.
- Wieland, K. (2004) Length at sex transition in northern shrimp (*Pandalus borealis*) off West Greenland in relation to changes in temperature and stock size. *Fish. Res.* **69**:49–56.