

Shrimp (*Pandalus borealis*) growth and timing of the spring phytoplankton bloom on the Newfoundland–Labrador Shelf

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ABSTRACT

We examined latitudinal and temporal changes in the availability of food for young shrimp (*Pandalus borealis*) on the Newfoundland–Labrador Shelf, using a suite of quantitative characteristics of the spring phytoplankton bloom determined from satellite ocean colour data, including bloom initiation time, maximum chlorophyll concentration, timing of the maximum, and bloom duration. We found significant correlations between bloom intensity, timing, and the size of young shrimp. The results are discussed in relation to the observation that, since the early 1990s, carapace lengths of shrimp have been decreasing in many Northwest Atlantic stocks.

Key words: growth, Labrador, Newfoundland, Northwest Atlantic, ocean colour, *Pandalus borealis*, phytoplankton, remote sensing, SeaWiFS, shrimp, spring bloom

INTRODUCTION

In a companion paper, Koeller *et al.* (2006) used scientific survey and commercial sampling data to describe the decrease in shrimp (*Pandalus borealis*) size and growth rates off Newfoundland and Labrador since the early 1990s. Similar decreases have been observed in other stocks, including the West Greenland (Wieland, 2004), the Gulf of Maine (Joseph Idoine, National Marine Fisheries Service, Woods Hole, MA, personal communication), the

Scotian Shelf (Koeller *et al.*, 2004) and the Gulf of St Lawrence (Savard and Bouchard, 2004) stocks. In addition to the temporal decrease in the size of all shrimp life-history stages and size at sex reversal, the Newfoundland–Labrador Shelf area also exhibits a strong and persistent latitudinal size trend (Koeller *et al.*, 2006), specifically an increase in carapace lengths with latitude that may be due to the decreased growth rate and increased longevity often found in more northern stocks (Shumway *et al.*, 1985; Nilssen and Hopkins, 1991). Parsons *et al.* (1989) inferred an increase in longevity from 6 to 8 yr from the southern Newfoundland–Labrador Shelf to Davis Strait.

Changes in shrimp growth could be forced by a number of factors. Under food limitation, which apparently occurs for shrimp on the Newfoundland Shelf (Koeller *et al.*, 2006), an increase in temperature would increase metabolic requirements and decrease growth in cold-blooded animals. Similarly, an increase in shrimp abundance would tend to decrease growth rates as the per-capita food intake decreases. Increasing temperatures, increasing population size, and decreasing food supply would therefore be expected to act synergistically to decrease growth rates. Wieland (2004) and Koeller *et al.* (2006) suggested that the widespread increasing water temperatures and shrimp populations during the 1990s probably contributed to the decrease in shrimp sizes off West Greenland and on the Newfoundland–Labrador Shelf respectively. In this study, we examine changes in food availability (over and above density-dependent effects), determined from remotely sensed ocean colour data, as a possible contributing cause of the temporal decrease in carapace lengths of *P. borealis* on the Newfoundland–Labrador Shelf.

The sea-viewing Wide Field-of-view Sensor (SeaWiFS) measures chlorophyll-*a* concentration (an index of phytoplankton biomass) related to the surface water transparency or more precisely, to the first optical depth (an optical depth is that depth at which irradiance is reduced to 1/*e* of its value at the surface). *Pandalus borealis* larvae are known to eat significant amounts of phytoplankton (Stickney and Perkins, 1981; Pedersen and Storm, 2002), especially during

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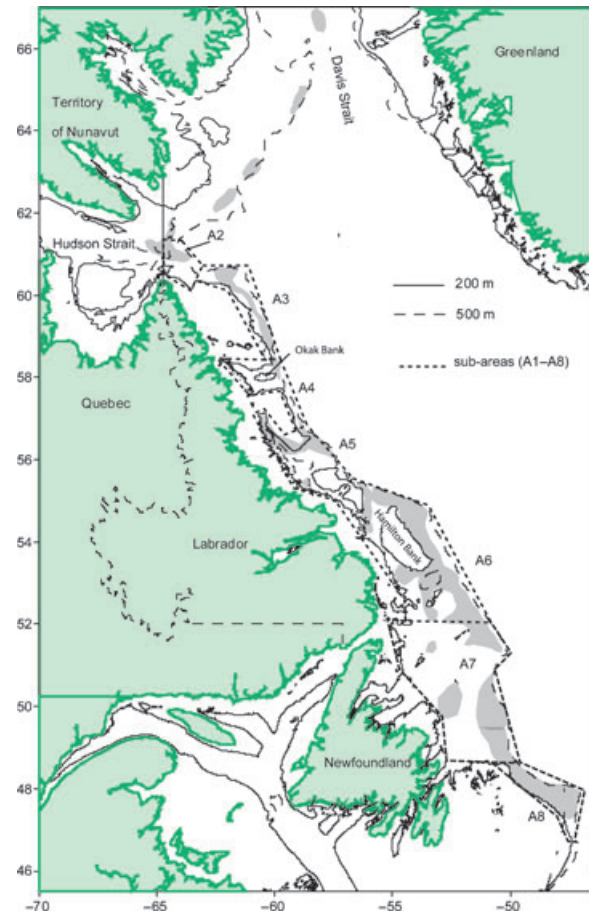
the larval stage which is several months long and occurs in shallow (<50 m) water. As shrimp grow they spend more time near or on the bottom. Adults are mainly benthic, but males migrate to surface layers to eat during the night. Consequently, detritus, much of which is derived from the decomposition of phytoplankton, is an important food source for later stages (Hopkins *et al.*, 1993; Ramseier *et al.*, 2000). Copepod eggs and nauplii appear to be the main prey items for early larval stages and larger copepodites are the main food source of older shrimp (Hopkins *et al.*, 1993; Harvey and Morrier, 2003). As the seasonal timing and abundance of copepod grazers is closely tied to phytoplankton production dynamics, changes in phytoplankton abundance and availability can be expected to influence shrimp growth at all stages and in the same year that these changes occur (Ouellet and Lefaivre, 1994; Bergström, 2000). Platt *et al.* (2003) linked the timing of the spring bloom determined from remotely sensed ocean colour data to recruitment success of a commercially important demersal fish species. Remotely sensed data have also been applied in ecological studies of other commercial species including shrimp (Lindner and Bailey, 1968; Ramseier *et al.*, 2000; Stein, 2000). However, we believe ours is the first attempt to link satellite observations of ocean colour to the growth (as opposed to the biomass or abundance) of a commercially important marine species (e.g. Platt *et al.*, 2003).

METHODS

Shrimp data

The mean sizes of various life-history stages were determined as described in Koeller *et al.* (2006). Briefly, samples of shrimp were obtained for analysis during fall multispecies research vessel surveys and at various times of year during commercial shrimp fishing. The research surveys were designed to provide abundance estimates for a variety of commercially important species, including shrimp. A stratified random design covered all depths and habitats where shrimp are known to occur. Survey coverage started in 1995. However, the coverage in northern areas is limited (Fig. 1): although some information is available in areas north of A6, most survey samples were collected in the areas south of A5. Commercial samples have been collected since 1990, including relatively large numbers from the northern areas. Commercial samples therefore have a wider latitudinal coverage than surveys, and they are concentrated in the main shrimp fishing areas,

Figure 1. Study area with place names used in the text, and location of the main shrimp fishing areas (grey).



which tend to be in the deeper, seaward boundaries of the defined subareas.

For each sample, the carapace lengths of the smallest male and largest female shrimp were determined. The quantities L_{\min} and L_{\max} were then calculated as the average of the smallest and largest shrimp for all samples per year and area. Similarly, the mean size of males and females was determined for each sample and averaged for all samples per year and area. For commercial samples, L_{50} , the size at which half of the individuals in the sample were female was determined per sample from a sigmoid curve fitted to the maturity ogive. Size calculations for survey samples were restricted to samples in which there were at least 200 shrimp and in which both males and females were present. Observer samples always contained more than 200 shrimp.

Shrimp egg extrusion times in the fall, and incubation and hatching times in the spring, were determined from commercial observer samples collected

throughout the year. The presence or absence of eggs on the abdomen for each shrimp was routinely recorded. Extrusion was usually completed within 1 month and was characterized by steep, well-defined ascending limbs in the area plot between 0% and nearly 100 % ovigerous. The initiation of hatching was less well defined in some areas because of significant winter egg loss. However, the completion of hatching from about 40% to 0% ovigerous did have well-defined descending limbs for most areas and years. The plot of percentage ovigerous versus sample collection time was smoothed with Friedman's supersmoother, and hatching/extrusion times interpolated from the predicted values as the dates on which 75% of the females were ovigerous or non-ovigerous respectively. Egg incubation times were then estimated as the length in days between the summer-fall extrusion and hatching the following spring.

Satellite data

Remotely sensed data were derived from all available SeaWiFS on OrbView-2 satellite for the North-West Atlantic covering the area 39°N to 62.5°N and 42°W to 71°W. Data were captured in real time at the receiving station of the Bedford Institute of Oceanography. NASA's protocol for SeaWiFS data processing is based on the ratios of water-leaving radiance in different spectral bands that are used in empirical algorithms to retrieve chlorophyll concentration (O'Reilly *et al.*, 2000). The software used for conventional retrieval is the SeaWiFS Data Analysis System (SeaDAS) (<http://seadas.gsfc.nasa.gov/>). In this study the images were processed in-house to obtain chlorophyll-*a* concentration, from the Level 0 NASA data with SeaDAS version 4.5 and an improved atmospheric correction, satellite zenith angle and cloud albedo threshold as described in Fuentes-Yaco *et al.* (2005). The catalogue of processed data consists of daily images between February and September from 1998 to 2003. Weekly composite images were calculated using spatial resolution of about 1.5 km per pixel. During winter, most of the shrimp fishing area is covered with ice, which affects the remotely sensed retrievals because SeaWiFS is not able to penetrate the ice cover. However, the software provided by NASA (SeaDAS) and our own improvements (Fuentes-Yaco *et al.*, 2005) to estimate chlorophyll *a* prevent the use of pixels flagged as ice. This procedure is a robust method to remove errors due to ice cover in single images. Furthermore, the compositing procedure also includes steps to verify that ice-covered pixels are eliminated from the computation.

Spring phytoplankton bloom characteristics

The development of objective indices allows the characterization of the phytoplankton spring bloom (Platt *et al.*, 2003). These indices are: the maximum observed chlorophyll *a* (an index of phytoplankton biomass) referred to as the intensity; the weeks elapsed since beginning of February when the biomass first exceeded 20% of the maximum (bloom initiation); the weeks elapsed when the maximum intensity occurred (bloom timing); and the period during which the biomass remained above the 20% threshold (bloom duration). All these properties were established without losing the spatial structure of the phytoplankton fields because the indices were calculated for each pixel. The analysis is not compromised by any potential systematic errors in the chlorophyll-retrieval algorithms as the use of only relative values renders the indices independent of absolute chlorophyll concentration estimates. The analysis was repeated for every year to compute the climatology for the 6 yr of available satellite data (1998–2003). The annual values were compared with temporal and latitudinal data on shrimp size in the same years. The number of pixels per image by shrimp fishing areas was distributed as follows: A2 = 3852, A3 = 11069, A4 = 9051, A5 = 13040, A6 = 39588, A7 = 40412 and A8 = 7202.

RESULTS

Average carapace length estimates for L_{\min} , males, L_{50} , females and L_{\max} for all areas and years and the corresponding estimates for spring bloom initiation, time of the chlorophyll maximum, bloom duration and the chlorophyll concentration at the maximum are given for commercial data in Tables 1 and 2 and for survey data in Tables 3 and 4. Figure 2 shows bloom characteristics plotted by area (*a*) and year (*b*). Also shown are carapace lengths by area (*c*) and year (*d*) for commercial samples for years in which bloom characteristic data are available. Survey data are not shown here but display similar temporal and spatial trends in carapace lengths as the commercial data (Koeller *et al.*, 2006). Analysis of variance with phytoplankton bloom characteristics as the dependent variable and area and year as independent factors (fixed effects) showed that all characteristics were significantly different between areas (F , $P < 0.02$), but a significant year effect was present only for the initiation and timing characteristics. The same model using carapace lengths from commercial samples versus area and year, using only years with corresponding bloom characteristic data (1998–2002), showed highly significant

Table 1. Shrimp carapace length statistics (mm) from samples collected by observers during commercial shrimp fishing trips averaged by year and area, and the corresponding spring phytoplankton bloom characteristics [in weeks for initiation, timing (from February 1) and duration, and in mg m^{-3} chlorophyll for intensity]. The carapace length data shown are for all observer samples regardless of time of year or tonnage class.

Area	Year	N	L_{\min}	Male	L_{50}	Female	L_{\max}	Intensity	Initiation	Timing	Duration
A2	1998	174	16.53	20.64	22.88	25.40	29.72	3.37	16.98	18.46	7.68
A2	1999	140	17.35	20.85	23.29	25.32	29.40	2.96	19.68	22.89	8.44
A2	2000	131	16.45	20.68	22.97	25.14	28.82	2.97	20.94	25.47	8.91
A2	2001	154	15.92	20.30	22.69	24.99	28.59	3.55	19.09	21.37	7.05
A2	2002	158	15.86	20.36	22.72	24.74	28.35	3.13	20.70	26.22	8.02
A3	1998	240	17.99	21.06	21.59	25.09	29.58	3.24	18.44	24.06	8.66
A3	1999	216	18.53	21.44	22.03	25.17	29.30	2.84	18.93	23.46	9.25
A3	2000	233	18.17	21.37	22.21	24.87	28.58	2.98	20.72	26.41	9.46
A3	2001	146	17.08	20.84	22.40	24.72	28.33	3.09	19.47	21.43	9.43
A3	2002	152	17.41	20.99	22.44	24.72	28.37	4.35	19.78	23.80	9.41
A4	1998	36	16.47	19.34	20.66	23.81	27.78	1.88	15.80	20.72	9.65
A4	1999	31	17.19	20.05	21.00	23.89	27.63	1.38	12.26	23.46	13.30
A4	2000	44	16.72	20.07	21.18	24.03	27.81	2.40	18.46	25.75	10.67
A4	2001	25	16.36	19.59	21.20	23.71	27.34	2.72	18.78	21.30	10.03
A4	2002	43	16.23	19.65	21.14	23.58	27.40	2.06	16.63	26.67	12.90
A5	1998	70	13.68	18.27	20.73	23.19	27.11	2.06	16.54	18.30	7.61
A5	1999	119	13.90	18.65	21.29	23.30	26.84	1.89	16.52	21.77	9.72
A5	2000	121	13.55	18.57	21.16	23.23	26.69	1.98	17.81	19.97	9.99
A5	2001	78	14.81	19.02	21.51	23.55	26.90	2.85	18.55	19.86	6.74
A5	2002	87	13.72	18.51	21.14	23.24	26.82	1.53	16.50	24.64	12.71
A6	1998	852	14.14	18.26	20.77	23.60	27.86	3.35	13.66	16.69	5.62
A6	1999	796	14.23	18.37	20.61	23.33	27.56	3.40	14.51	17.28	6.44
A6	2000	1110	14.04	18.11	20.47	23.25	27.31	2.26	13.42	19.26	10.28
A6	2001	834	13.49	17.77	20.34	23.15	27.06	2.72	13.70	19.23	7.64
A6	2002	766	13.55	17.58	20.02	22.93	27.05	2.87	15.12	21.25	10.04
A7	1998	1	12.00	17.19	20.55	23.44	29.50	3.07	9.29	14.89	7.94
A7	1999	4	13.38	18.52	22.23	23.47	27.25	3.26	8.69	12.31	8.58
A7	2000	182	11.40	17.16	20.91	22.83	26.43	2.99	10.55	15.10	8.98
A7	2001	18	12.33	17.39	20.72	22.31	26.06	2.04	7.18	15.98	11.31
A7	2002	97	11.77	17.46	21.00	23.30	27.07	4.30	12.85	15.87	5.59
A8	2000	39	14.69	18.94	21.60	23.97	27.64	3.97	9.96	12.85	5.96
A8	2001	93	14.09	18.44	20.87	23.27	27.23	1.50	5.20	14.90	12.95
A8	2002	87	14.99	18.74	20.81	23.31	27.49	5.52	12.03	14.85	4.64

($P < 0.00001$) area differences for all five size categories and significant ($P < 0.05$) year effects for all size categories except L_{50} . Survey data also showed highly significant ($P < 0.0007$) area effects for all size categories, but a significant year effect ($P < 0.04$) was found only for females.

It is apparent from the above analysis and Fig. 2a that the most significant trend in bloom characteristics is a progressive delay in initiation and timing of the peak with latitude. The climatology of both spring bloom initiation (Fig. 3a) and timing of the peak chlorophyll concentration (Fig. 4a) clearly show their latitudinal development. Peak chlorophyll concentrations in the southernmost areas occur in May, whereas

those in the northernmost areas tend to occur in July, a difference of 3 months. The relationship between L_{\min} and initiation and that between mean male length and timing of the chlorophyll maximum are shown in Figs 3b and 4b respectively. Figure 2a also shows that bloom duration tends to increase with latitude and can last as much as a month longer in the north (A4) than in the south (A8). Only bloom intensity shows a bimodal trend (Fig. 2a), with chlorophyll concentrations attaining the highest values in the north and south, and relatively low levels in the mid-shelf areas, A4 and A5 (Fig. 5a). The relatively high phytoplankton production on the northern Newfoundland Shelf is well known and attributed to

Table 2. Pearson's correlation coefficients for the data in Table 1 (7277 samples) and for the data filtered to include only samples collected in the second half of the year from vessels over 500 mt (2960 samples).

	L_{\min}	Male	L_{50}	Female	L_{\max}
All samples (7277)					
Intensity	0.0464	0.1081	0.2634	0.2661	0.3080
Initiation	0.6738**	0.7253**	0.5588**	0.6708**	0.4389*
Timing	0.6897**	0.6834**	0.3710*	0.5241**	0.3233
Duration	0.1629	0.1067	-0.1111	-0.1265	-0.2041
Vessels >500 mt July–December (2960 samples)					
Intensity	0.4966**	0.5984**	0.6609**	0.6076**	0.5625**
Initiation	0.3982*	0.6225**	0.7426**	0.6323**	0.4244*
Timing	0.3607	0.460*	0.2873	0.3569	0.2486
Duration	-0.0363	-0.1050	-0.3440	-0.2392	-0.2545

*Significant at $P < 0.01$.**Significant at $P < 0.001$.**Table 3.** Shrimp carapace length statistics (mm) from samples collected during scientific surveys averaged by year and area, and the corresponding spring phytoplankton bloom characteristics (in weeks for initiation), timing (from February 1) and duration, and in mg m^{-3} chlorophyll for intensity. The carapace length data shown are for all samples from the fall multispecies survey series.

Area	Year	N	L_{\min}	Male	Female	L_{\max}	Intensity	Initiation	Timing	Duration
A2	1999	2	13.00	19.87	24.00	26.00	2.96	19.68	22.89	8.44
A3	1998	11	15.09	19.46	22.77	25.14	3.24	18.44	24.06	8.66
A3	1999	27	16.31	20.22	23.66	26.41	2.84	18.93	23.46	9.25
A4	1998	9	14.28	18.70	23.05	26.17	1.88	15.80	20.72	9.65
A4	1999	9	13.28	18.50	23.11	24.94	1.38	12.26	23.46	13.30
A4	2001	4	14.50	18.27	21.77	25.13	2.72	18.78	21.30	10.03
A5	1998	38	12.96	17.51	22.83	25.68	2.06	16.54	18.30	7.61
A5	1999	33	11.65	17.54	23.15	26.09	1.89	16.52	21.77	9.72
A5	2000	1	8.50	15.47	22.90	25.00	1.98	17.81	19.97	9.99
A5	2001	22	12.30	17.23	22.16	24.93	2.85	18.55	19.86	6.74
A5	2002	2	12.75	17.54	21.56	24.00	1.53	16.50	24.64	12.71
A5	2003	1	12.00	16.52	21.00	25.00	2.40	16.69	19.46	7.61
A6	1998	93	12.16	17.83	22.63	26.03	3.35	13.66	16.69	5.62
A6	1999	89	10.94	17.17	22.45	25.97	3.40	14.51	17.28	6.44
A6	2000	73	10.40	17.11	22.54	25.53	2.26	13.42	19.26	10.28
A6	2001	87	11.11	16.78	22.29	25.63	2.72	13.70	19.23	7.64
A6	2002	89	10.96	16.63	21.75	25.49	2.87	15.12	21.25	10.04
A6	2003	64	11.70	16.96	21.81	25.56	4.66	15.67	17.01	4.56
A7	1998	104	8.92	16.68	22.04	25.71	3.07	9.29	14.89	7.94
A7	1999	117	9.38	16.45	22.19	25.93	3.26	8.69	12.31	8.58
A7	2000	101	9.41	16.78	22.35	25.71	2.99	10.55	15.10	8.98
A7	2001	111	9.98	16.69	22.19	25.80	2.04	7.18	15.98	11.31
A7	2002	100	9.75	16.40	21.92	25.65	4.30	12.85	15.87	5.59
A7	2003	103	9.67	16.33	21.85	25.40	2.72	13.06	15.60	5.96
A8	1998	17	10.94	18.29	23.08	25.47	5.11	9.68	12.77	4.93
A8	1999	18	12.31	18.24	22.90	26.17	4.34	7.75	8.63	4.08
A8	2000	13	10.92	17.99	22.35	26.04	3.97	9.96	12.85	5.96
A8	2001	18	12.31	18.25	22.84	25.97	1.50	5.20	14.90	12.95
A8	2003	16	10.50	18.70	22.61	26.09	2.38	10.93	14.75	6.99

Table 4. Pearson's correlation coefficients for the data in Table 3 (1372 samples) and for the data filtered to include only samples with more than 200 shrimp containing both males and females (1114 samples).

	L_{\min}	Male	Female	L_{\max}
All samples (1372)				
Intensity	-0.1551	0.0005	-0.0668	0.2548
Initiation	0.5066**	0.2140	0.0801	-0.3297
Timing	0.5633**	0.2964	0.1323	-0.4418*
Duration	0.1959	0.0899	0.0945	-0.3237
Samples with >200 shrimp, males and females present (1114)				
Intensity	-0.2867	-0.0566	-0.0697	-0.0606
Initiation	0.5083**	0.3997*	0.2919	0.1973
Timing	0.6082**	0.3564	0.2169	0.1190
Duration	0.3055	0.0801	0.0313	-0.0277

*Significant at $P < 0.01$.

**Significant at $P < 0.001$.

mixing processes in the vicinity of, and nutrient input from, Hudson Strait (Drinkwater and Harding, 2001). The most significant trend in carapace lengths of all stages is also latitudinal, with increasing carapace lengths further north, most clearly seen in the smaller stages (Fig. 2c). Commercial data also revealed a positive correlation between bloom intensity and the carapace lengths of all size categories (Fig. 5b).

Temporal trends in bloom characteristics for particular areas include a tendency towards later bloom initiation and timing of the peak during the study period (Fig. 2b). Peak chlorophyll concentration decreased during the first 4 yr, but increased thereafter. This was mirrored by bloom duration, which increased to 2001, and decreased thereafter. Shrimp carapace sizes continued to decrease during the study period, but not nearly to the extent prior to 1998 (Fig. 2d). Decreases in all size categories were less than a millimetre after 1998, compared with decreases of up to 3 mm from 1992 to 1997 (Koeller *et al.*, 2006).

Tables 2 and 4 give Pearson correlation coefficients between all bloom characteristics and carapace length categories for survey and commercial data, for all areas and years. Two sets of correlation analyses were run for each data set (data shown in Tables 1 and 3), one including all available commercial and survey data and a second filtered according to more stringent criteria: for commercial data this involved selecting data from vessels larger than 500 mt that were fishing in the second half of the year. Individual sample size is not a problem with this subset of commercial data as all have sufficient numbers of male and female shrimp

(>200) to allow accurate size determinations; survey data were filtered to include only samples with at least 200 shrimp and with both males and females present. Both filtered and unfiltered data for survey and commercial samples show a significant positive relationship between bloom initiation, timing, and carapace lengths, reflecting the strong latitudinal changes in these variables seen in Fig. 2. For commercial data, these correlations were significant for all length categories but tended to be stronger for the smaller categories. For survey data, correlations were significant only for the smallest categories (L_{\min} and males). Only a single negative correlation was significant in the unfiltered survey data (Table 4).

Temporal influences of bloom characteristics on carapace lengths were investigated using linear regression (Table 5) of characteristics versus the smallest categories (L_{\min} and males) because the youngest shrimp are more dependent upon the bloom events on which they are being regressed. Lagged regressions were not attempted because of the short time series available. Up to 5 yr for commercial, and 6 yr for survey, data were available for comparison with the 6 yr of bloom-characteristic data, except for northern areas where survey coverage was limited. Consequently, some regressions had as few as 3 data pairs (1 degree of freedom) from a limited number of samples (N in Tables 1 & 3), such that these particular results should be interpreted cautiously. Eight significant coefficients were found among the 96 regressions, a result which can be expected from chance alone. Similarly, about half of the coefficients were positive, also to be expected from chance alone. The discussion here focuses on those relationships that were also significant in the pooled data, Tables 2 and 4.

The most consistent temporal trend was the significant negative relationship between mean male size and bloom timing in area A6, for both commercial and survey data. This area is well sampled for both data sources including 60% of all commercial samples and 36% of all survey samples (Tables 1 & 3). Figure 6a shows the anomalies (difference = year-climatology) of the bloom timing in A6 during the study period. Figure 6b illustrates the negative relationships between timing and male carapace lengths in A6 for both commercial and survey data. The negative slope reveals a correspondence between early maximum intensity of spring blooms with longer male shrimp carapaces. The shrimp carapace lengths at ages 1 and 2 shown in Koeller *et al.* (2006) also suggest the analogous effect of early/late spring bloom arrival on the shrimp growth. A similar observation (Platt *et al.*,

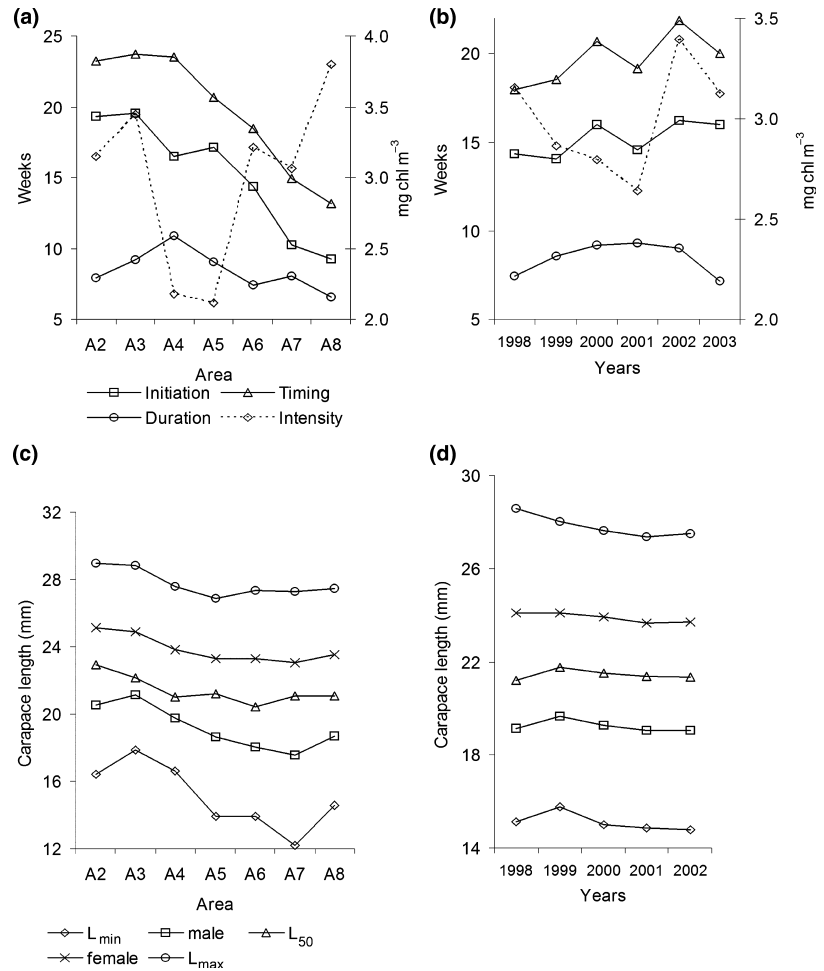


Figure 2. Phytoplankton spring bloom characteristics: averages of all areas (a) and years (b) for spring bloom initiation (□), time of the chlorophyll maximum (△), bloom duration (○) and the chlorophyll concentration at the maximum (◇). Means of carapace length by area (c) and year (d) for L_{min} (◇), males (□), females (X), L_{50} (△) and L_{max} (○) in which bloom characteristic data are available. Units are mm for shrimp carapace, weeks for times (from first week of February until last week of September) and mg of chlorophyll m^{-3} for intensity.

2003) with the recruitment of haddock (*Melanogrammus aeglefinnus*) larvae on the Scotian Shelf stresses the ecological importance of spring bloom onset. Within areas, an early spring bloom may enhance early growth compared with that in years when the spring bloom occurs later. The significant negative temporal relationships are in contrast to the stronger positive latitudinal pattern.

Estimates of shrimp egg hatching time by area and year (Tables 6 and 7) show that hatching dates in the northern areas where this can be calculated (A3, A4) are similar to hatching dates in the two southernmost areas (A7 and A8) on the Newfoundland–Labrador Shelf, i.e. mid to late April. Similarly, the lengths of the ovigerous periods in A3 and A4 are similar, or shorter than, in A7 and A8. Hatching times appear to be somewhat later, and the ovigerous period longer in the two mid-shelf areas (A5 and A6). Data pooled for all areas show no clear temporal trend in hatching times and length of the ovigerous period, although there is a tendency for shorter ovigerous periods after 1997. Hatching times were quite similar both latitudinally and temporally, and occurred within 1 month of each other in all areas. This is remarkable considering that much of the difference must be the result of variability in the data used in the estimates. It is, however, not unexpected as egg incubation and hatching times are determined mainly by temperature (Stickney and Perkins, 1981) which is quite similar in all areas at depths where incubation occurs (Koeller *et al.*, 2006). The similarity in hatching times is in contrast to the large latitudinal differences in timing of the spring bloom. Figure 7 shows that the time of hatching and the spring bloom coincide only in the three southern areas (A6–A8), whereas in the north (A2 and A3) the end of the hatch (75% completion estimate) precedes peak chlorophyll concentrations by as much as 3 months.

DISCUSSION

Previous authors inferred that the large decrease in shrimp carapace lengths during the 1990s off West Greenland (Wieland, 2004) and on the Newfoundland

Figure 3. (a) Climatology (1998–2003) of initiation of the bloom with units in weeks from the first week of February, as defined in Fig. 2. The polygons represent shrimp fishing areas from north (A2) to south (A8). (b) Relationship of initiation of the bloom with L_{\min} (average of the smallest shrimp for all samples per year and area) for both commercial (●) and survey (○) data. Lines represent linear regressions.

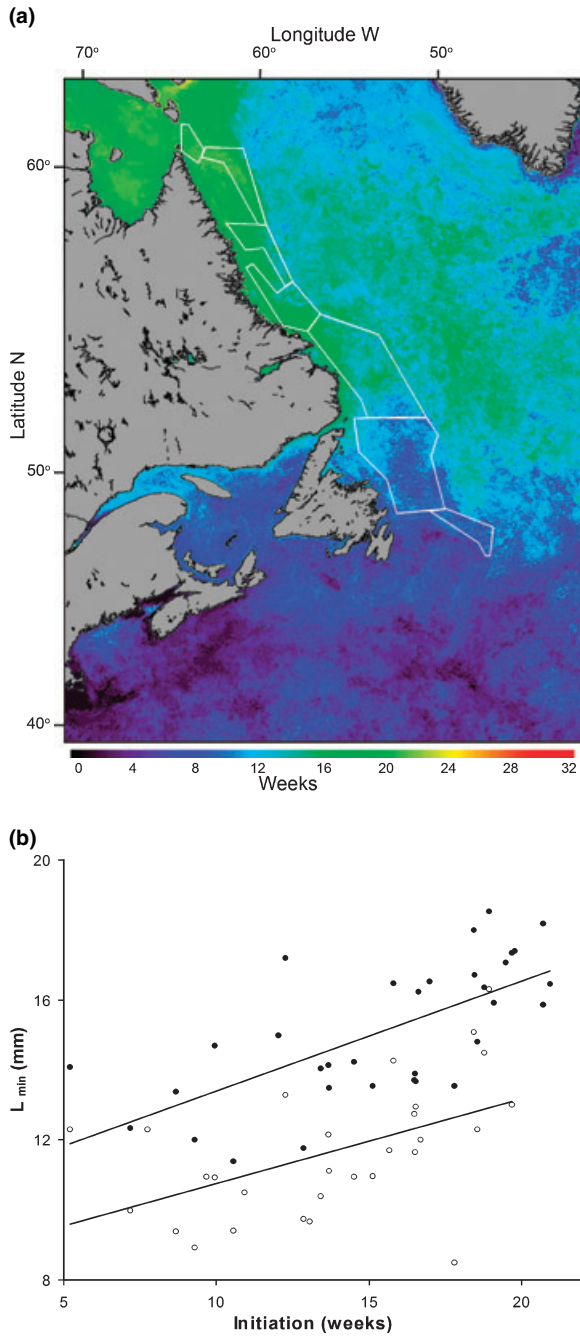
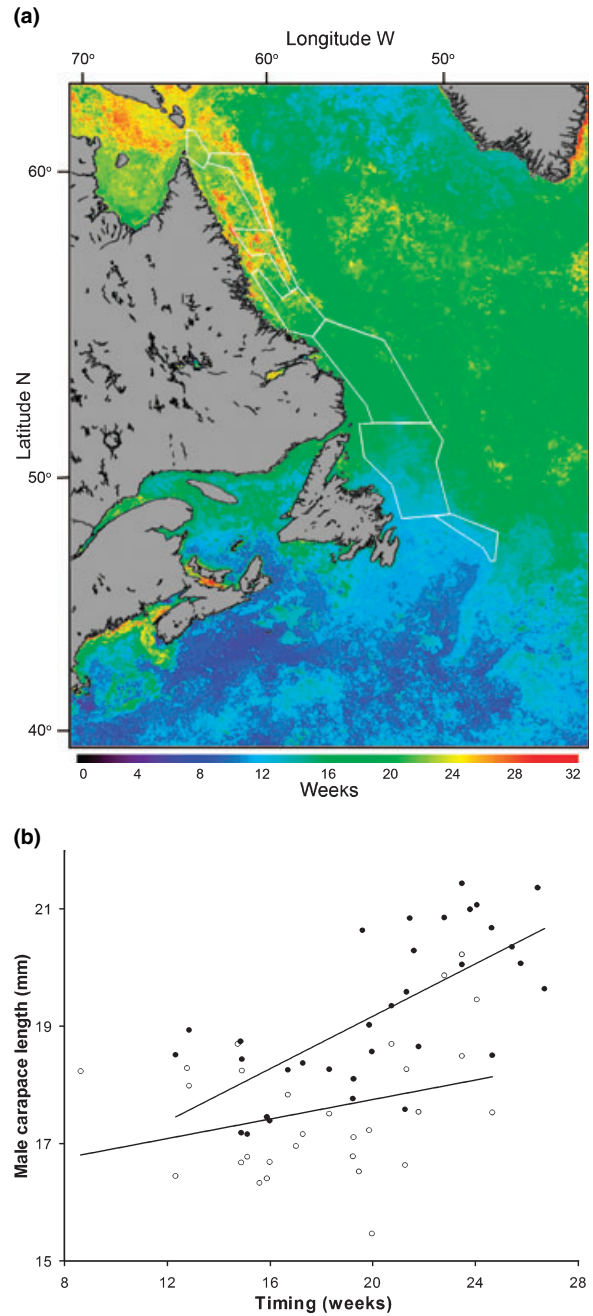


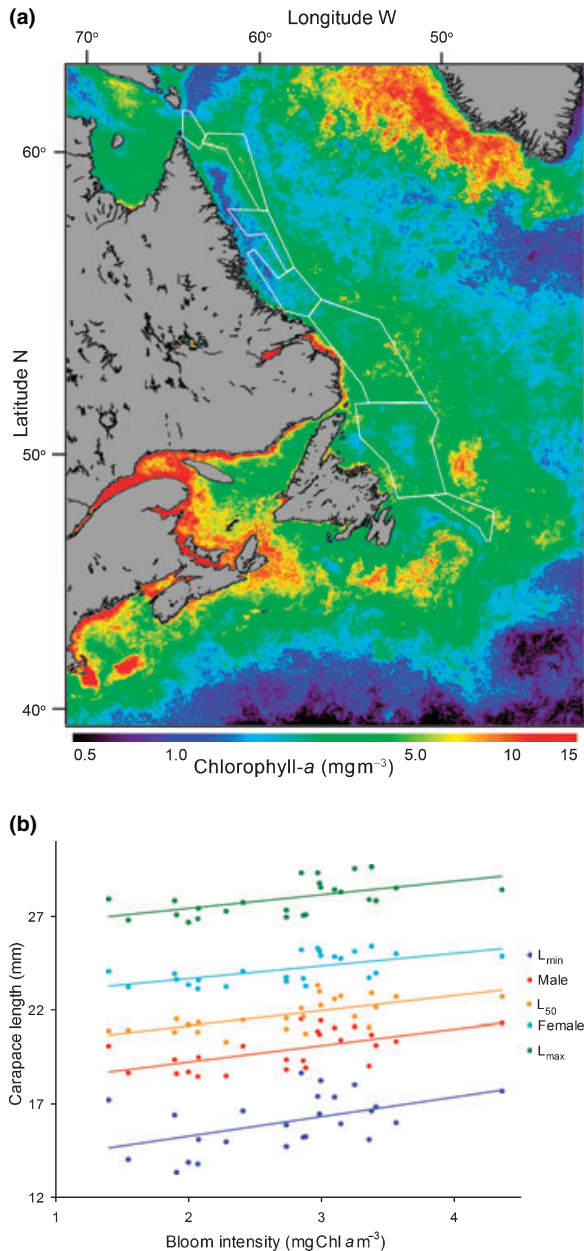
Figure 4. (a) Climatology (1998–2003) of timing of maximum bloom intensity with units in weeks from the first week of February, as defined in Fig. 2. (b) Relationship of timing of maximum bloom intensity with male shrimp. The average size of carapace lengths for commercial = 19.2 mm and survey = 17.6 mm. Symbols and units are as in Fig. 3. Lines represent linear regressions.



land–Labrador Shelf (Koeller *et al.*, 2006) was due to decreasing growth rates from the higher metabolic requirements of the warmer temperatures during this

period, and concurrent lower per-capita food availability caused indirectly by increasing shrimp population densities. In this paper we explore the possibility of a

Figure 5. (a) Climatology (1998–2003) of maximum intensity of the bloom with units in mg of chlorophyll m^{-3} . (b) Relationship of maximum intensity of the bloom with carapace length for L_{\min} (dark blue), males (red), L_{50} (orange), females (light blue), and L_{\max} (green). Lines represent linear regressions.



direct link between remotely sensed changes in food availability and changes in shrimp growth on the Newfoundland-Labrador Shelf.

Our data sets have spatial and temporal limitations and our conclusions must be framed within appropriate caveats. The most notable limitations include the

scarcity of shrimp data in the northern areas and the absence of ocean colour data prior to 1998, when the largest decreases in carapace lengths occurred (Koeller *et al.*, 2006) and the strongest temporal correlation between spring bloom characteristics and growth would have been expected. In addition, the uncertainties associated with shrimp age determination make it difficult to establish whether differences in carapace lengths are due to faster growth, or slower growth but higher longevity, or vice versa. Consequently, the relationships we have found between spring bloom characteristics and carapace lengths can have different, even conflicting explanations, resulting in alternative hypotheses as discussed below. These problems are beyond the scope of this paper and can be resolved only with wider survey coverage, continued ocean colour measurements, improved age-determination techniques and consistent growth models.

In the first hypothesis, we assume that the increasing carapace lengths with latitude are due to the generally accepted cause, i.e. that shrimp in northern areas are larger because they grow slower but have increased longevity in colder water, an observation supported by Parsons *et al.* (1986, 1989) for the Newfoundland-Labrador Shelf. Similar bottom temperatures throughout the shelf at depths where shrimp spend most of their life (Colbourne and Mertz, 1998; Koeller *et al.*, 2006) indicate that in this area temperature probably has less influence on growth than food availability. From this we infer that the larger shrimp in the northern areas grow more slowly because food is less available there. This is supported by our results, which show that the phytoplankton bloom and shrimp egg hatching coincide only in the south, and that hatching precedes peak chlorophyll concentrations by as much as 3 months in the north. Under this hypothesis, the much larger minimum sizes (L_{\min} , Fig. 2) of shrimp first entering survey and commercial nets in the north (Koeller *et al.*, 2006) are due to increased longevity of pelagic larval, and early benthic juvenile, stages. The delay of up to 3 months between hatching and spring bloom peak corresponds approximately with the length of the pelagic larval phase. Juveniles may be too small when they descend to the bottom, passing through nets without detection, or may descend at a larger size after a delay of 1 yr. We cannot rule out, however, that in addition to food availability, colder surface-water temperatures for longer periods also contribute to slower growth of northern larvae during the pelagic phase. A key finding by Koeller *et al.* (2006) was the significantly greater temporal decrease of shrimp carapace lengths in all size categories in the northern areas under the

Table 5. R^2 for linear regressions between spring bloom characteristics and the smallest shrimp size categories, L_{\min} and average male size, in each area for all years with a minimum number (3) of paired annual averages. The sign before R^2 is that of the regression coefficient.

Area L_{\min}	Commercial				Survey			
	Intensity	Initiation	Timing	Duration	Intensity	Initiation	Timing	Duration
A2	-0.3198	-0.0199	-0.0399	0.2540	-	-	-	-
A3	-0.2613	-0.0149	0.3525	-0.0821	-	-	-	-
A4	-0.4091	-0.4885	-0.0000	0.1644	-0.9851	-0.9943*	0.5322	0.6375
A5	0.7347	0.4519	-0.0217	-0.3579	-0.0116	-0.0885	-0.2709	-0.0539
A6	0.1697	-0.0699	-0.6265	-0.2122	0.8974*	0.3329	-0.4749	-0.8777*
A7	-0.0251	-0.3167	-0.6167	0.0470	0.1344	-0.0685	0.0000	0.0563
A8	0.9966*	0.9989*	-0.0440	-0.9661	-0.4019	-0.7765*	0.0295	0.6313
<i>Male</i>								
A2	-0.4621	-0.0057	-0.0117	0.4764	-	-	-	-
A3	-0.2368	0.0331	0.4280	0.0026	-	-	-	-
A4	-0.0382	-0.0506	0.3255	0.2801	0.3773	0.2009	0.0438	0.0107
A5	0.4996	0.5960	0.0034	-0.1059	0.0764	-0.0100	-0.6271	-0.4462
A6	0.2029	-0.1542	-0.8161*	-0.3784	0.0730	-0.1147	-0.7140*	-0.3070
A7	0.0209	-0.0767	-0.8208	-0.0062	-0.0000	-0.3400	-0.0022	0.3063
A8	0.4845	0.5764	-0.6651	-0.7206	-0.1128	0.3072	0.2978	0.0008

*Indicates significance of the regression coefficient (not shown) at $P < 0.01$.

influence of Hudson Strait run-off (subareas A2 and A3) during the mid-1990s. Under this first hypothesis, we would conclude that the greater sensitivity of shrimp growth to food availability in these areas resulted in a greater decrease in growth due to a greater decrease in food availability at this time. Such circumstances could have occurred as the warmer atmospheric temperatures of the mid-1990s increased freshwater run-off and water-column stability, thereby decreasing nutrient flux into the euphotic zone, leading to a decrease in production in the usually productive areas directly under the influence of Hudson Strait run-off (Koeller *et al.*, 2006). The enhanced production on the northern Newfoundland shelf caused by nutrient input from complex mixing processes in and near Hudson Strait has also been demonstrated previously (Sutcliffe *et al.*, 1983; Drinkwater and Harding, 2001). Drinkwater and Harding (2001) also noted enhanced primary production on the southern shelf probably due to local upwelling around Hamilton Bank, resulting in a production minimum in the mid-shelf region.

Our second hypothesis assumes that the generally accepted view on the relationship between latitude and growth does not hold for the Newfoundland–Labrador Shelf, and that northern shrimp grow faster and larger in the more productive northern areas. The strong positive relationship between shrimp carapace lengths of all stages and bloom intensity in the filtered commercial data supports this. In this

hypothesis, pelagic larvae subsist for several months prior to bloom onset, grow quickly during the intense northern blooms, descend to the bottom as larger juveniles, and begin to enter nets at a larger minimum size in the same year. However, this does not explain the smaller size of shrimp in the southern areas which have the advantage of hatching concurrently with spring blooms having intensities comparable with those experienced in the north. Other influences on growth must be involved in this scenario, for example, lower per capita food availability from higher population densities, although there is no clear evidence for this. Our explanation for the significantly greater decreases in carapace lengths in the areas directly under the influence of Hudson Strait run-off would be the same as under the first hypothesis.

A further complication is the strong positive correlation between bloom initiation/timing and carapace lengths driven by latitudinal trends versus the significant negative temporal correlations in the same parameters. Under the first hypothesis, this could have occurred if decreased growth and larger sizes (and longevity) in the north occur only after prolonged periods of relatively stable environmental conditions and growth, or if geographical differences in growth rates and longevity are genetically determined. In the short term, decreased growth at any particular location would result in decreased sizes without concurrent changes in longevity. Under our second hypothesis

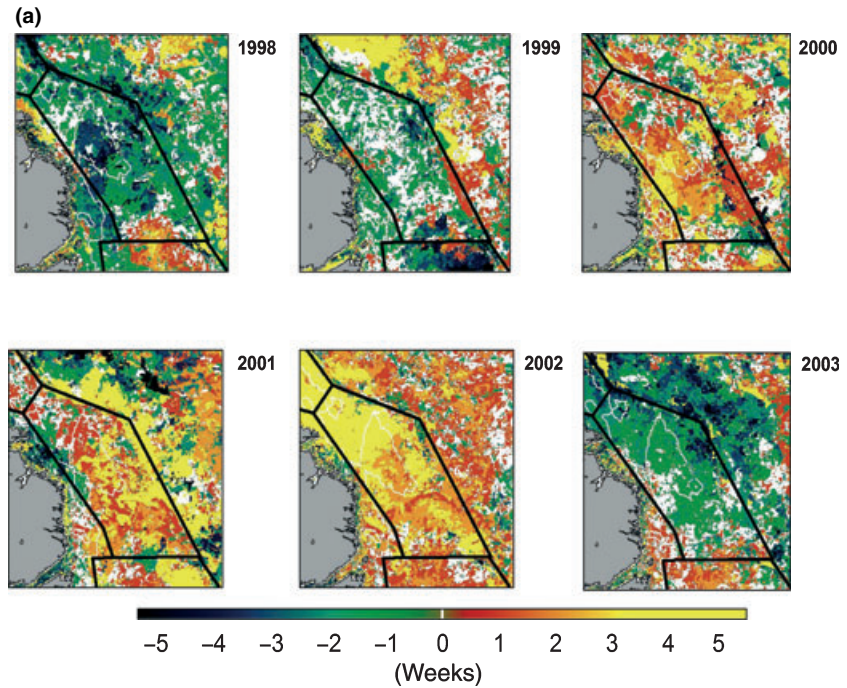
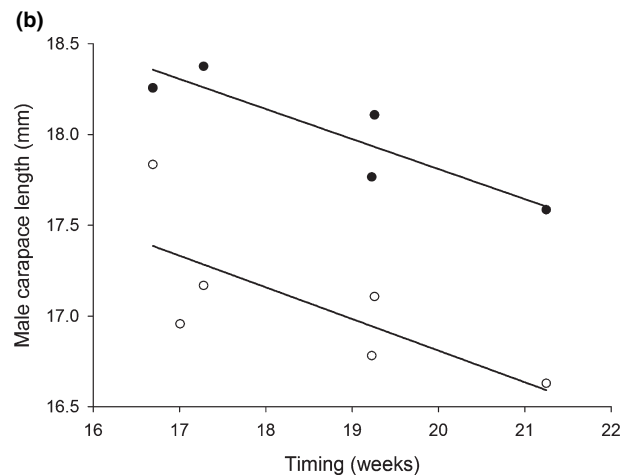


Figure 6. (a) Anomalies (difference = year – climatology) of the time for the maximum pigment concentration in A6 during the period of study. Negative (positive) values indicate earlier (later) bloom time than the climatology. (b) Relationship between timing and male carapace lengths in A6 for both commercial (●) and survey (○) data. Symbols and units are as in Fig. 3. Numbers indicate years.



longevities would have to be similar in all areas and shrimp size would be directly and positively related to growth rate. It is less likely that size decreases since 1998 were due to density-dependent effects as the large increase in shrimp abundances occurred prior to this (Koeller *et al.*, 2006). The final resolution to this problem awaits the development of a definitive growth model for Pandalids.

The exact functional relationship between our correlations of remotely sensed phytoplankton data and shrimp growth needs clarification because of the uncertainties surrounding the proportions of food types consumed by different shrimp life-history stages in the wild (e.g. phytoplankton, detritus, copepods, etc.). In particular, the importance of

phytoplankton detrital material in shrimp diet may have been underestimated in previous studies because of the difficulties of its quantitative determination in gut analysis. The importance of this food source has been demonstrated indirectly by the strong affinity of older shrimp for areas of high particulate organic carbon deposition (Ramseier *et al.*, 2000) and bottom types with a high organic content (Koeller, 2000). The importance of small zooplanktonic prey directly dependent on phytoplankton production appears to be well established, however, and this in itself could account for our correlations considering the well-established small-scale temporal and spatial linkages between zooplankton and primary production.

Table 6. Egg hatching, incubation (length of ovigerous period) and extrusion statistics calculated from all available commercial samples. Spring hatching is given as the date when 75% of the females had released their eggs, and fall extrusion as the dates when 25%, 50% and 75% of females had extruded their eggs (i.e. were ovigerous) for each area, all years combined. Also given are the lengths of the extrusion, non-ovigerous, and ovigerous periods.

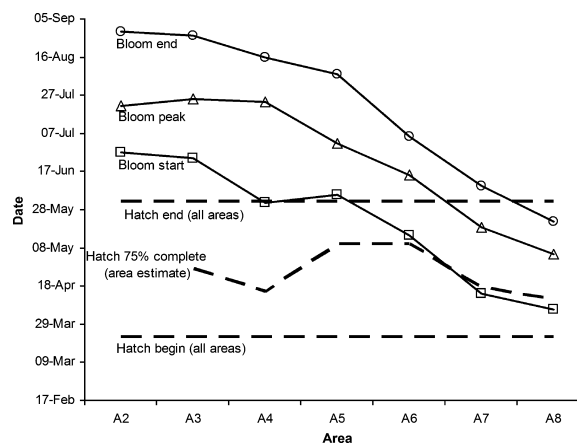
	% compl.	A2	A3	A4	A5	A6	A7	A8	Mean	Range (days)
Hatch	75	No data	27 April	15 April	10 May	17 April	17 April	11 April	25 April	29
Extrusion	25	25 April	3 September	2 September	4 August	18 August	10 August	7 August	17 August	30
Extrusion	50	6 September	11 September	18 September	17 August	29 August	21 August	18 August	29 August	32
Extrusion	75	16 September	19 September	2 October	1 September	13 September	8 September	1 September	12 September	31
Extrusion (days)		22	16	30	28	26	29	25	26	14
Non-ovigerous (days)		No data	145	170	114	126	144	143	140	56
Ovigerous (days)		No data	220	195	251	239	221	222	225	56

Table 7. Annual estimates for hatching and extrusion and the length of the ovigerous period (all areas pooled).

Year	Hatching	Extrusion	Ovigerous
1990	10 May	10 October	212
1991	N/D	1 October	N/D
1992	16 May	15 October	213
1993	5 May	4 October	213
1994	6 May	1 October	217
1995	4 May	2 October	214
1996	23 April	18 September	226
1997	27 April	17 September	222
1998	6 May	9 October	209
1999	1 May	27 October	186
2000	9 May	2 October	219
2001	30 April	4 October	208
2002	4 May	11 October	205
2003	26 April	12 September	226
Mean	4 May	3 October	213
Range (days)	20	45	40

N/D, not determined.

Figure 7. Estimates of shrimp egg hatching time by area and year. Temporal evolution of phytoplankton bloom lies on top showing the start (□), peak (△) and end (○) of the bloom.



In conclusion, our demonstrated link between remotely sensed ocean colour data and shrimp growth has allowed us to frame two plausible hypotheses about latitudinal differences and temporal changes in shrimp carapace lengths and growth which include, arguably, the most important factor contributing to growth – the availability of food. While not providing definitive conclusions because of data limitations, we have demonstrated that large-scale and long-term changes in the food sources of important commercial marine

species can be measured and, given suitably long time series, hypotheses involving changes in these measurements and the resource itself can be tested.

In this paper we focused on growth, but linkages to shrimp recruitment success have not yet been investigated. We have also not considered the effects of larval advection to the south on shrimp growth and length frequency patterns. Our preliminary results and other works in high-latitude areas using satellite-derived ocean colour data have shown the important role of ice variability in the development of the spring phytoplankton bloom (Arrigo and van Dijken, 2004; Stramska, 2005). Marginal ice regions are zones of high primary production and phytoplankton biomass which support rich pelagic or benthic food webs (Smith *et al.*, 1987; Stead and Thompson, 2003), including the Newfoundland–Labrador Shelf shrimp populations (Parsons and Colbourne, 2000; Ramseier *et al.*, 2000). A detailed analyses of ice and phytoplankton production dynamics using remote sensing is beyond the scope of the present study. Still, our results and those presented in Koeller *et al.* (2006) are of relevance to current issues facing the shrimp industry. Clearly, environmental changes have significantly influenced the shrimp size decrease of the 1990s – it seems unlikely that lowering exploitation rates would have mitigated this decrease. Much additional work is necessary, but remotely sensed data could be of immediate interest as ancillary information in stock assessments as such issues arise. In long-term fisheries research, remotely sensed chlorophyll data could be useful in identifying ‘hot spots’ (e.g. Hudson Strait) for future study of shrimp population dynamics and in the design of field programmes.

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REFERENCES

- Arrigo, K.R. and van Dijken, G.L. (2004) Annual cycles of sea ice and phytoplankton in Cape Bathurst polynya, south-eastern Beaufort Sea, Canadian Arctic. *Geophys. Res. Lett.* **31**:doi:10.1029/2003GL018978.
- Bergström, B.I. (2000) The biology of *Pandalus*. *Adv. Mar. Biol.* **38**:55–245.
- 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., Devred, E., Sathyendranath, S. *et al.* (2005) Comparison of *in situ* and remotely-sensed (SeaWiFS) chlorophyll-*a* in the Northwest Atlantic. *Indian J. Mar. Sci.* **34**:341–355.
- Harvey, M. and Morrier, G. (2003) Laboratory feeding experiments on zoea of northern shrimp *Pandalus borealis* fed with natural zooplankton. *Mar. Ecol. Prog. Ser.* **265**:165–174.
- Hopkins, C.C.E., Sargent, J.R. and Nilssen, E.M. (1993) Total lipid content, and lipid and fatty acid composition of the deep-water prawn *Pandalus borealis* from Balsfjord, northern Norway: growth and feeding relationships. *Mar. Ecol. Prog. Ser.* **96**:217–228.
- Koeller, P.A. (2000) Relative importance of abiotic and biotic factors to the management of the northern shrimp (*Pandalus borealis*) fishery on the Scotian Shelf. *J. Northw. Atl. Fish. Sci.* **27**:21–33.
- Koeller, P., Covey, M. and King, M. (2004) *An Assessment of the Eastern Scotian Shelf Shrimp Stock and Fishery for 2003 and Outlook to 2004*. Canadian Science Advisory Secretariat Research Document 2004/01, 50 pp.
- Koeller, P., Fuentes-Yaco, C. and Platt, T. (2006) Decreasing shrimp sizes off Newfoundland and Labrador – environment or fishing? *Fish. Oceanogr.* doi:10.1111/j.1365-2419.2006.00403.x.
- Lindner, M.J. and Bailey, J.S. (1968) Distribution of brown shrimp (*Penaeus aztecus aztecus* Ives) as related to turbid water photographed from space. *Fish. Bull.* **72**:289–293.
- 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.
- O’Reilly, J., *et al.* (2000) Ocean color chlorophyll *a* algorithms for SeaWiFS, OC2 and OC4: version 4. In: *SeaWiFS Technical Report Series*. S.B. Hooker & E.R. Firestone (eds) NASA Tech. Memo. 2000-206892 **11**:8–22.
- Ouellet, P. and Lefaivre, D. (1994) Vertical distribution of northern shrimp (*Pandalus borealis*) larvae in the Gulf of St. Lawrence; implications for trophic interactions and transport. *Can. J. Fish. Aquat. Sci.* **51**:123–132.
- Parsons, D.G. and Colbourne, E.B. (2000) Forecasting fishery performance for northern shrimp (*Pandalus borealis*) on the Labrador Shelf (NAFO Divisions 2HJ). *J. Northw. Atl. Fish. Sci.* **27**:11–20.
- Parsons, D.G., Lilly, G.R. and Chaput, G.J. (1986) Age and growth of northern shrimp *Pandalus borealis* off Northeastern Newfoundland and Southern Labrador. *Trans. Am. Fish. Soc.* **115**:872–881.
- Parsons, D.G., Mercer, V.L. and Veitch, P.J. (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.
- Pedersen, S.A. and Storm, L. (2002) Northern shrimp (*Pandalus borealis*) recruitment in West Greenland waters. Part II. Lipid classes and fatty acids in *Pandalus* shrimp larvae: implications for survival expectations and trophic relationships. *J. Northw. Atl. Fish. Sci.* **30**:47–60.

- Platt, T., Fuentes-Yaco, C. and Frank, K.T. (2003) Spring algal bloom and larval fish survival. *Nature* **423**:398–399.
- Ramseier, R.O., Garrity, C., Parson, D.G. and Koeller, P. (2000) Influence of particulate organic carbon sedimentation within the seasonal sea-ice regime on the catch distribution of the northern shrimp (*Pandalus borealis*). *J. Northw. Atl. Fish. Sci.* **27**:35–44.
- Savard, L. and Bouchard, H. (2004) *Estuary and Gulf of St. Lawrence shrimp (Pandalus borealis) stock status in 2003*. DFO Canadian Science Advisory Secretariat Research Document 2004/091. http://www.dfo-mpo.gc.ca/csas/csas/DocREC/2004/RES2004_091_B.pdf.
- 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. NOAA Technical Report NMFS 30, US Department of Commerce, Springfield, VA.
- Smith, W.O., Baumann, M.E.M., Wilson, D.L. and Aletsee, L. (1987) Phytoplankton biomass and productivity in the marginal ice zone of the Fram Strait during summer 1984. *J. Geophys. Res.* **92**:6777–6786.
- Stead, R.A. and Thompson, R.J. (2003) The effect of the sinking spring diatom bloom on digestive processes of the cold-water protobranch *Yoldia hyperborea*. *Limnol. Oceanogr.* **48**:157–167.
- 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**:63–67.
- Stickney, A.P. and Perkins, H.C. (1981) Observations on the food of the larvae of the northern shrimp, *Pandalus borealis* Krøyer (Decapoda, Caridea). *Crustaceana* **40**:36–49.
- Stramska, M. (2005) Interannual variability of seasonal phytoplankton blooms in the north polar Atlantic in response to atmospheric forcing. *J. Geophys. Res.* **110**:doi:10.29/2004JC002457.
- 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.