

Ocean surface characteristics influence recruitment variability of populations of northern shrimp (*Pandalus borealis*) in the Northwest Atlantic

Patrick Ouellet^{1*}, César Fuentes-Yaco⁴, Louise Savard¹, Trevor Platt², Shubha Sathyendranath², Peter Koeller⁴, David Orr³, and Helle Siegstad⁵

¹Fisheries and Oceans Canada, Maurice Lamontagne Institute, 850 route de la Mer, Mont-Joli, QC, Canada G5H 3Z4

²Plymouth Marine Laboratory, Prospect Place, PL1 3DH, Plymouth, UK

³Fisheries and Oceans Canada, Northwest Atlantic Fisheries Center, PO Box 5667, St John's, NL, Canada A1C 5X1

⁴Fisheries and Oceans Canada, Bedford Institute of Oceanography, PO Box 1006, Dartmouth, NS, Canada B2Y 4A2

⁵Greenland Institute of Natural Resources, PO Box 570, 3900 Nuuk, Greenland

*Corresponding Author: tel: +1 418 775 0675; fax: +1 418 775 0546; e-mail: patrick.ouellet@dfo-mpo.gc.ca.

Ouellet, P., Fuentes-Yaco, C., Savard, L., Platt, T., Sathyendranath, S., Koeller, P., Orr, D., and Siegstad, H. 2011. Ocean surface characteristics influence recruitment variability of populations of northern shrimp (*Pandalus borealis*) in the Northwest Atlantic. – ICES Journal of Marine Science, 68: 737–744.

Received 31 May 2010; accepted 4 October 2010; advance access publication 17 December 2010.

Remotely sensed data were used to derive simple ecosystem indicators for four regions of the Northwest Atlantic to test the hypothesis that sea surface temperatures (SSTs) and spring phytoplankton bloom characteristics (initiation, timing, intensity, and duration) have a significant influence on larval survival and recruitment of northern shrimp (*Pandalus borealis*). For all years (1998–2007) and regions, hatching was after the initiation of the bloom and before or after the bloom reached its maximum intensity. The results suggest that the best survival of larvae is associated with high warming rates of SST following hatching, but in very cold environments, warm temperatures at hatching seem to be important for larval survival. The analyses also indicate that larval survival is supported by an early, long phytoplankton bloom which attains high concentrations of chlorophyll *a*. The results demonstrate the potential of remotely sensed data for deriving simple population-specific ecosystem indicators for potential use in building operational recruitment models for predicting changes in northern shrimp abundance.

Keywords: northern shrimp, phytoplankton bloom, recruitment, remote sensing, SST.

Introduction

Studies of the natural feeding of northern shrimp (*Pandalus borealis*) larvae at sea have revealed omnivorous diets for the first larval stages where phytoplankton cells, especially diatoms, can represent a significant contribution (Stickney and Perkins, 1981; Pedersen and Storm, 2002; Hobbs, 2008; Ariza and Ouellet, 2009). In addition, laboratory experiments have proven that selection of phytoplankton cells by larvae declines and that the contribution of various developmental stages of zooplankton species increases in the diet with successive larval stages (Rasmussen *et al.*, 2000; Harvey and Morrier, 2003; Hobbs, 2008). Therefore, it is likely that a match between the hatching of northern shrimp larvae and the development and timing of the plankton production cycle in spring is important for the success of a cohort.

In the North Atlantic, the northern shrimp reproductive cycle has adapted to local bottom temperature, such that, under average conditions, larval emergence dates match those of the spring phytoplankton bloom (Koeller *et al.*, 2009), conforming with the match–mismatch hypothesis on recruitment regulation in marine populations (Cushing, 1990). Consequently, year-on-year variability in the characteristics of the phytoplankton

spring bloom, including its timing, intensity, and duration, should influence the survival of the shrimp larvae and subsequent recruitment to the adult population. However, upper-water-column temperature conditions seem to be another significant factor in determining larval survival and recruitment success, probably by influencing the production rate of the plankton community and the development and growth of shrimp larvae (Ouellet *et al.*, 2007). From this perspective, remote-sensing data may provide the basis for relevant ecosystem indicators and a better understanding of shrimp recruitment processes, and help anticipate possible impacts of a changing oceanic environment.

Recruitment can be influenced by multiple factors. Oceanographic processes over a wide range of temporal and spatial scales, and various hypotheses implying differential survival of the early developmental stages, have been advanced to explain recruitment variability of marine organisms (Leggett and Deblois, 1994; Houde, 2008). However, identification of the dominant factor(s) involved requires tools that survey the environment at the temporal and spatial scales relevant to the entire population (Platt *et al.*, 2007; Leggett and Frank, 2008). Remote sensing of sea surface temperature (SST) and chlorophyll *a* (Chl *a*) concentration

offers the opportunity to develop such tools by providing synoptic-scale data on the characteristics of the phytoplankton spring bloom (Platt *et al.*, 2007).

Empirical studies have rarely revealed simple stock–recruitment relationships in pandalid shrimps (Bergström, 2000), with the possible exceptions of Barents Sea shrimp (*P. borealis*; Aschan and Ingvaldsen, 2009) and Pacific pink shrimp (*P. jordani*) populations (Hannah, 1999), further suggesting that environmental factors mainly determine recruitment. Therefore, the objective of this study was to test the hypothesis that surface ocean characteristics (e.g. Chl *a* and SST) at the time larvae hatch in spring have a significant influence on the survival of northern shrimp larvae.

Material and methods

The relationships between the survival of northern shrimp larvae and ocean surface characteristics were investigated for four regions of the Northwest Atlantic: (i) the northwest Gulf of St Lawrence (NWGSL), (ii) the northeast Gulf of St Lawrence (NEGSL), (iii) northern shrimp fishing area 6 (SFA6) offshore of Newfoundland and Labrador, and (iv) West Greenland (WG) in Davis Strait (Figure 1). These regions support northern shrimp populations and have well-established fisheries that are assessed and managed as separate units. Monitoring data from commercial sampling and research survey programmes are available for all areas, in some instances since the 1980s. Although SFA6 may be a subpopulation linked to a larger band of northern shrimp extending south from Baffin Island to the Grand Banks (a decline in the survival of shrimp larvae in the north could affect recruitment in the south), these populations are currently considered to be production units for management purposes.

Ocean surface characteristics: SST and phytoplankton bloom indices

The SSTs and ecological indices associated with phytoplankton blooms were derived from satellite images for the study areas from 1998 to 2007. SSTs were determined with a nominal spatial resolution of 4 km × 4 km per pixel, and combined to represent a period of 8 d, using data from NOAA/NASA AVHRR

Pathfinder missions (Pathfinder v5.0 SST dataset, JPLPO.DAAC Product #216). The spectral radiometric data (visible spectral reflectance) are from the SeaWiFS programme and interpreted as concentrations of Chl *a* (mg m⁻³). The images used come from the reprocessing 5.2, Level 3 binned datasets (Giovanni project), with a nominal spatial resolution of 9 km × 9 km per pixel, and grouped into 8-d periods (Acker and Leptoukh, 2007; Feldman and McClain, 2007), a similar time-scale as for SST.

The phytoplankton bloom time was limited to a period between day of year (DoY) 65 and 241 for each year. The general pattern of the spring-bloom curve is controlled by various physical and biological factors that result in an asymmetrical structure of the curve about the maximum. Therefore, the bloom period was separated into two sections (before and after the maximum biomass value). The data for individual years and areas were fitted separately using this approach (Koeller *et al.*, 2009), and the curves were then combined to determine the ecological indices associated with phytoplankton blooms. These indices were (i) the intensity (mg m⁻³) or amplitude of Chl *a* concentration (an estimator of the phytoplankton biomass), (ii) the DoY of bloom initiation, when the slope of the concentration curve first exceeds the inflection point, (iii) the timing or DoY at the amplitude of phytoplankton concentration, and (iv) the duration from initiation to when the slope of the descending portion of the biomass curve reaches the inflection point.

Northern shrimp larval hatching time and survival index

Protocols for determining larval hatching dates and the larval-survival index have been detailed in Ouellet *et al.* (2007) and Koeller *et al.* (2009). Briefly, hatching dates are determined from commercial fishery samples collected regularly during the fishing season. The hatching date corresponds to the DoY when half the reproductive females (time at 50% hatching) no longer bear eggs, because the larvae have hatched. The larval-survival index equals the number of recruits divided by the spawning-stock biomass, which, for northern shrimp, is usually taken as the biomass of reproductive females. Estimates of the abundance of recruits and female biomass were obtained from annual research surveys conducted in each region.

For NWGSL, NEGSL, and SFA6, it was possible to estimate the hatching date for all years of the study (1998–2007), except in 2004 for SFA6 and 2005 for NEGSL. For WG, data were available from 1994 to 2001 only where the dates of larval hatching varied from DoY 118 to 139, with a mean of 127 ± 1 week (s.d. = 7.39 d). Therefore, after 2001, the mean DoY (i.e. 127) was used for WG to set larval emergence relative to bloom timing and to determine the time for the estimation of weekly mean SST at 50% hatching.

For NWGSL, NEGSL, and SFA6, the recruitment index was the number of 1-year-old juveniles estimated during the summer or autumn research surveys (Savard and Bourdages, 2010; D. Orr, pers. comm.). However, the estimated total number of age 1 shrimp was not available for WG, so the index was derived from the estimated total abundance of age 2 shrimp (Ziemer and Siegstad, 2008). Female biomass was estimated from the same surveys. Data are available for the 1998–2007 year classes for all regions. For NWGSL, NEGSL, and SFA6, a lag of –1 year was applied to the survey data to obtain the recruitment index for a given year class, whereas a lag of –2 years was applied to WG data. For spawning-stock biomass, a lag of +1 year was applied

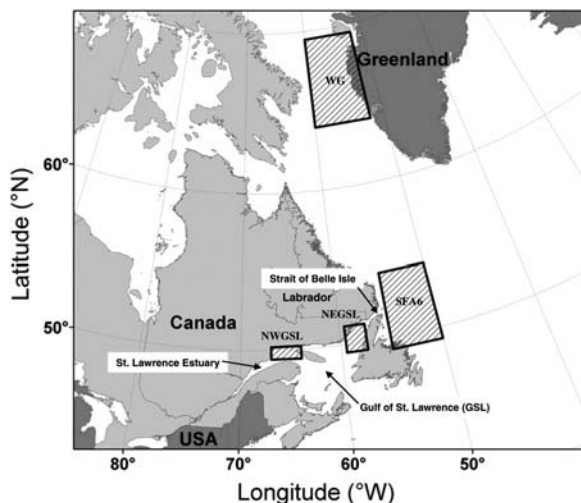


Figure 1. The four regions of the Northwest Atlantic used to study the influence of ocean surface characteristics on survival of northern shrimp larvae and recruitment variability.

to the survey estimates of females for all areas. For comparison, the survival indices were rescaled by dividing the annual values for a region by the maximum for that region.

Statistical analyses

Because of the very short (10 years) and large fluctuations in the time-series within each region, the relationships between the selected environmental variables and the larval-survival index were tested by non-parametric Spearman's correlations. In contrast to the other regions, the survival index time-series in WG demonstrated a strong monotonic decreasing trend, for unknown reasons. A first-order-difference transformation was applied to remove this trend, but the results for the original series are also presented and discussed. A second approach to testing the influence of the selected environmental variables was to compare the values for years of below- and above-average larval survival. That is, for each region, the individual larval-survival index was coded as above or below the series average to create two groups for comparison with the environmental variables using a one-factor ANOVA or the Kruskal–Wallis non-parametric ANOVA when Levene's test indicated non-homogeneity of variance among groups. All tests were executed with SYSTAT 11 software (Cranes Software International, Chicago, IL, USA) or routines implemented in data analysis software OriginPro 8 (OriginLab Corporation, Northampton, MA, USA).

Results

Bloom characteristics and SST correlations with larval survival

For all four regions, the spring phytoplankton bloom was initiated during the first weeks of April (Table 1, Figure 2). Although the hatching dates of larvae varied from one region to another, with SFA6 the earliest and NWGSL the latest, the mean hatching dates fell well within the spring phytoplankton bloom periods (Figure 2). For all years and regions for which there are data, hatching occurred after bloom initiation and, depending on the region and the year, was recorded before or after the phytoplankton bloom peaked (Figure 2).

The sea surface characteristics observed at the time of hatching varied significantly between regions (ANOVA, d.f. = 3, $p < 0.05$). In NWGSL, where hatching was latest, the SST at hatching was the warmest and the warming rate the highest (Table 1); there, however, the spring phytoplankton bloom was short, but very intense. The NEGSL had the lowest SST at the time of larval

hatching, but relatively high SST warming rates and low-intensity blooms (Table 1). In SFA6, where hatching was much earlier, SST was among the coldest, the SST warming rate was low, and the bloom duration was long, but of lowest intensity (Table 1). The second-warmest SST and second-highest bloom intensity at the time of larval hatching were in WG, but similar to SFA6, this region exhibits slow warming rates in spring (Table 1).

The larval-survival index indicates large fluctuations in NWGSL, NEGSL, and SFA6 regions over years, but less so in WG, possibly because we used the age 2 abundance for the index (Figure 2). The survival indices for the two GSL regions exhibited some similarities: strong survival in 1999 and 2006, and very poor survival in 1998, 2003, and 2005 (Figure 2a and b). The larval-survival indices indicated a declining trend between 1998 and 2000 in the other two regions of the Northwest Atlantic, but continued to decline in WG, whereas it increased in 2001/2002 and 2004/2005 in SFA6. In both areas, the highest index was that of 1998 (Figure 2c and d). However, the detrended survival index series in WG exhibits low amplitude interannual fluctuations and a slight increasing slope over time (Figure 2d).

Rank correlations were used to investigate the relationships between SST, spring phytoplankton-bloom characteristics, and larval-survival indices. Overall, just one correlation is significant at the *a priori* probability value of 0.05 (Table 2). The rank correlation analysis indicates opposing relationships between the survival indices and SST conditions during hatching. For the three regions (NWGSL, SFA6, and WG) where the survival index is negatively related to SST, the relationships with the SST warming rate are positive. In contrast, in NEGSL where the surface temperature at hatching is the coldest, the survival index was positively related to temperature, but negatively related to the warming rate. After first-order-difference transformation of the WG survival-index series, the correlation with SST was positive, as for NEGSL (Table 2). Overall, the results suggest that high warming rates following hatching favour larval survival, and that, in very cold environments such as NEGSL, warm temperatures at hatching also favour survival.

The survival indices are negatively related to the phytoplankton bloom initiation DoY, except in NWGSL, where there is no relationship (i.e. $r_s = 0.000$; Table 2). For all regions, larval survival is positively associated with the duration of the bloom and with bloom intensity (except in WG for intensity, although larval survival was positively related to this factor when the first-order-difference series was used). Overall, this suggests that

Table 1. Summary of ocean surface characteristics at the time of northern shrimp larval hatching (week at 50% hatching) for four regions in the Gulf of St Lawrence and the Northwest Atlantic.

Parameter	Region	Weekly mean SST			Spring phytoplankton bloom		
		Hatching (DoY)	50% hatch (°C)	Warming rate (°C d ⁻¹)	Bloom maximum (mg m ⁻³)	Initiation (DoY)	Duration (d)
Mean	NWGSL	131.1	3.840	0.161	7.740	100.2	57.6
s.e.		1.5	0.557	0.007	0.427	2.969	5.439
Mean	NEGSL	117.9	−0.193	0.128	3.323	96.2	62.4
s.e.		3.1	0.133	0.013	0.261	2.215	6.618
Mean	SFA6	112.8	0.151	0.064	2.392	97.8	82.4
s.e.		1.5	0.222	0.008	0.243	3.66	5.067
Mean	WG	127.0	0.374	0.064	4.855	97.5	64.8
s.e.		2.6	0.130	0.007	0.32	2.779	4.983

DoY, day of year.

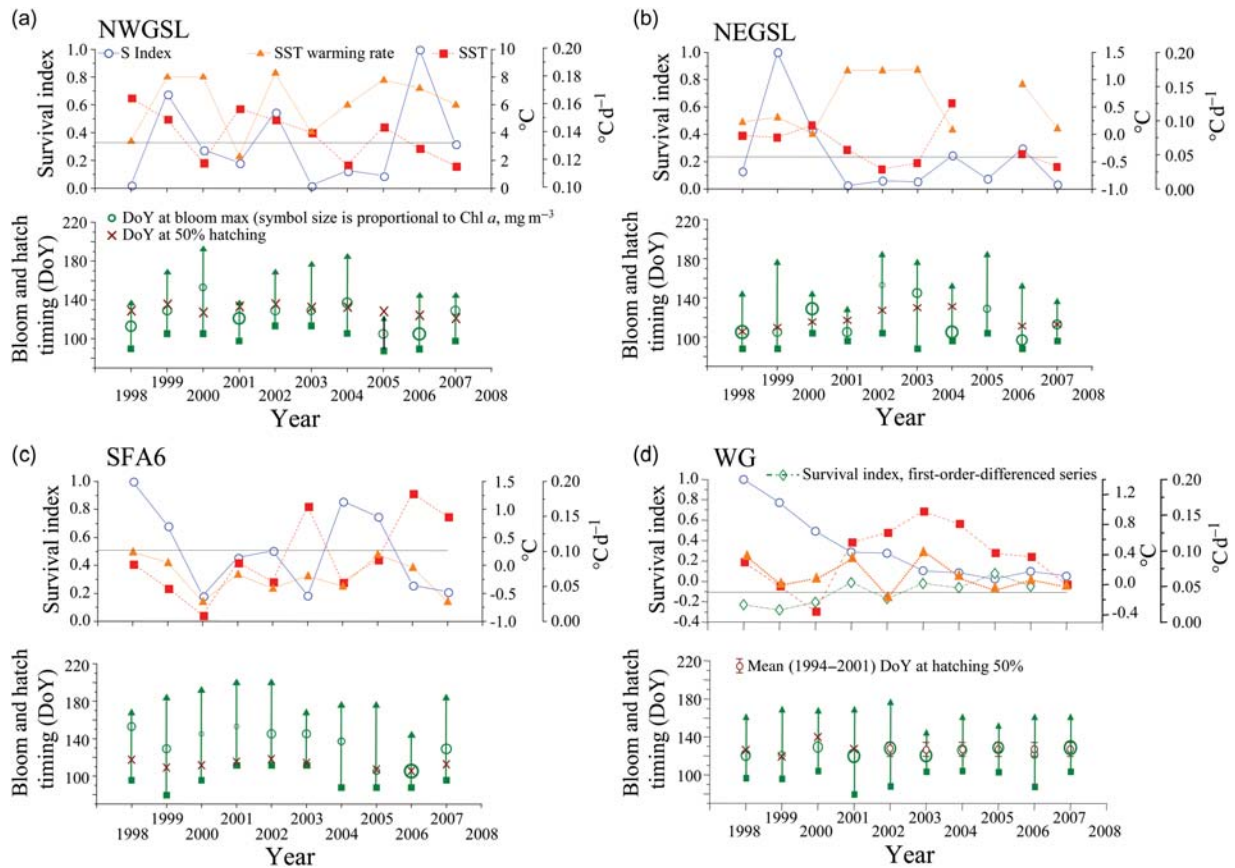


Figure 2. For each region, the upper panel illustrates the larval-survival index, the weekly mean SST at larval hatching, and the mean SST warming rate for 30 d following the date at 50% hatching. The horizontal line on the larval-survival index graph indicates the series average (for WG, the average was calculated for the first-order difference series). The lower panel for each region illustrates the position of the mean larval hatching date (DoY; crosses) relative to the initiation (squares), time at maximum (open circles), and the end (triangles) of the phytoplankton spring bloom. NWGSL, northwest Gulf of St Lawrence; NEGSL, northeast Gulf of St Lawrence; SFA 6, Shrimp Fishing Area 6 on Newfoundland–Labrador Shelf; WG, West Greenland.

Table 2. Rank correlation analysis between ocean surface characteristics and the larval-survival index for the four regions of the study.

Region	Spearman correlation	Weekly mean SST		Spring phytoplankton bloom		
		50% hatch (°C)	Warming rate (°C d ⁻¹)	Bloom max (mg m ⁻³)	Initiation (DoY)	Duration (d)
NWGSL	r_s	-0.164	0.579	0.236	0.000	0.147
	p	0.651	0.079	0.511	1.000	0.688
NEGSL	r_s	0.533	-0.498	0.285	-0.167	0.288
	p	0.139	0.143	0.425	0.645	0.419
SFA6	r_s	-0.224	0.650	0.030	-0.397	0.019
	p	0.533	0.042	0.934	0.257	0.957
WG	r_s	-0.370	0.394	-0.285	-0.250	0.491
	p	0.293	0.260	0.425	0.486	0.150
WG-FD	r_s	0.567	0.067	0.583	-0.134	-0.183
	p	0.112	0.865	0.099	0.731	0.637

WG-FD, correlation coefficients after first-order difference of the survival index time-series. DoY, day of year.

good survival of larvae is favoured by a phytoplankton bloom that begins early, has a long duration, and reaches high intensities.

Conditions for good or poor survival of larvae

Larval-survival indices were divided into high and low categories (meaning good or poor survival), based on the comparison of the annual index with the series mean for each region

(Figure 2). Comparisons of the ocean surface characteristics between above- and below-average larval survival allowed identification of the variables contributing significantly to survival, and resulted in similar conclusions to those made from the correlation analyses (Table 3). For NWGSL, one variable displayed a near-significant difference between the years of good and poor survival; SST warming rates were higher during the years of good survival.

Table 3. Comparison of ocean surface characteristics between years of below average (B) and above average (A) larval-survival index (Surlnd) in each region.

Region	Group	Dependent variable	ANOVA <i>F</i> , <i>p</i>	Kruskal–Wallis χ^2 , <i>p</i>	<i>t</i> -test, <i>t</i> -test <i>p</i>	Conclusion B(avg) vs. A(avg)
NWGSL	Surlnd	SST (°C)	0.202, 0.665	–	–	–
		Wrate (°C d ^{−1})	3.499, 0.098	3.365, 0.066	1.870, 0.098	B(0.154) < A(0.178)
		Chl <i>a</i> (mg m ^{−3})	0.452, 0.520	–	–	–
		Init (DoY)	0.202, 0.665	–	–	–
		Duration (d)	0.015, 0.907	0.211, 0.645	–	–
NEGSL	Surlnd	SST (°C)	5.186, 0.057	–	2.277, 0.057	B(−0.411) < A(0.081)
		Wrate (°C d ^{−1})	2.136, 0.162	–	–	–
		Chl <i>a</i> (mg m ^{−3})	1.758, 0.221	–	–	–
		Init (DoY)	0.178, 0.684	–	–	–
		Duration (d)	0.002, 0.964	–	–	–
SFA6	Surlnd	SST (°C)	1.194, 0.306	1.136, 0.286	–	–
		Wrate (°C d ^{−1})	4.693, 0.062	–	−2.166, 0.062	B(0.052) < A(0.082)
		Chl <i>a</i> (mg m ^{−3})	0.245, 0.634	–	–	–
		Init (DoY)	5.957, 0.041	–	2.441, 0.041	B(103.6) > A(89)
		Duration (d)	0.796, 0.398	–	–	–
WG-FD	Surlnd	SST (°C)	4.026, 0.085	–	2.007, 0.085	B(0.152) < A(0.626)
		Wrate (°C d ^{−1})	0.556, 0.480	–	–	–
		Chl <i>a</i> (mg m ^{−3})	0.533, 0.489	–	–	–
		Init (DoY)	0.009, 0.925	–	–	–
		Duration (d)	0.902, 0.374	–	–	–

For cases where the Levene's test *p* was <0.05, the results of the Kruskal–Wallis non-parametric ANOVA are also presented. For important differences between groups (ANOVA, *p* < 0.1, d.f. = 1), comparisons of the dependent variable means are presented. Wrate, SST warming rate; Init, bloom initiation date.

For NEGSL, SST was significantly higher during the years of good survival. For SFA6, the SST warming rate and the initiation DoY were significantly different between the years of good and poor survival; good survival is associated with early bloom initiation and high warming rates. For WG, good survival at the beginning of the series coincided with cold surface water, but for the detrended series, SSTs were significantly higher when survival was above average (Figure 2d, Table 3).

Spearman's rank correlation analyses between SST and phytoplankton bloom characteristics demonstrated that SST measured at the time of hatching was negatively related to bloom duration and positively to bloom intensity, in all regions (Table 4). The SST warming rate is positively related to bloom duration and negatively related to intensity in the two areas within the Gulf of St Lawrence (GSL), although these relationships are reversed in the other two areas of the Northwest Atlantic. This suggests that warm SST measured at the time of hatching, which is after the initiation of the bloom, is associated with a short, but intense, bloom in all regions. However, a high SST warming rate is associated with longer, but less intense, blooms in the GSL, whereas it is the opposite elsewhere in the NW Atlantic.

Coherence in survival and sea surface characteristics among regions

Comparison among regions of annual deviations of the standardized survival index revealed synchronized events in 1999, 2001, 2003, and 2007 (Figure 3a). All regional indices were above their means in 1999 and below them in 2001, 2003, and 2007. However, survival in WG was opposite to that in other regions in 1999, 2001, and 2003 (Figure 3b) for the detrended series. The same exercise with ocean surface characteristics revealed that, in 1999, when all regional survival indices were above average, all bloom durations were also above average (Figure 4). However, in 2001, 2003, and 2007, when all regions experienced

Table 4. Spearman rank correlation coefficients (upper) and critical *p*-value (lower; emboldened characters indicate statistical significance at *p* ≤ 0.05) between the selected oceanographic variables.

Physical forcing	Biological	NWGSL	NEGSL	SFA6	WG
SST	Bloom initiation	−0.156	−0.044	0.182	−0.061
		0.666	0.909	0.614	0.867
	Bloom duration	−0.416	−0.262	−0.804	−0.200
		0.232	0.496	0.005	0.579
	Chl <i>a</i> maximum	0.285	0.683	0.442	0.309
Warming rate	Bloom initiation	0.425	0.042	0.200	0.384
		0.330	−0.219	−0.385	0.152
	Bloom duration	0.351	0.543	0.272	0.674
		0.357	0.446	−0.260	−0.176
	Chl <i>a</i> maximum	0.311	0.196	0.468	0.627
		−0.488	−0.638	0.030	0.030
		0.153	0.047	0.934	0.934

below-average larval survival, concordant ocean surface characteristics were more obscure, except in 2007, when SSTs were near or below the mean and bloom duration was shorter in all regions (Figure 4).

Discussion

This study has presented evidence that relatively simple ecosystem indicators derived from remote sensing of ocean surface characteristics, seen as proxies for food abundance and conditions for larval growth and development, can help explain the interannual fluctuations in survival of northern shrimp larvae and subsequent recruitment to the adult populations. There were stronger and statistically significant relationships between the larval-survival and SST-derived indices for the four study regions. This is indicative of the important role played by higher or increasing spring

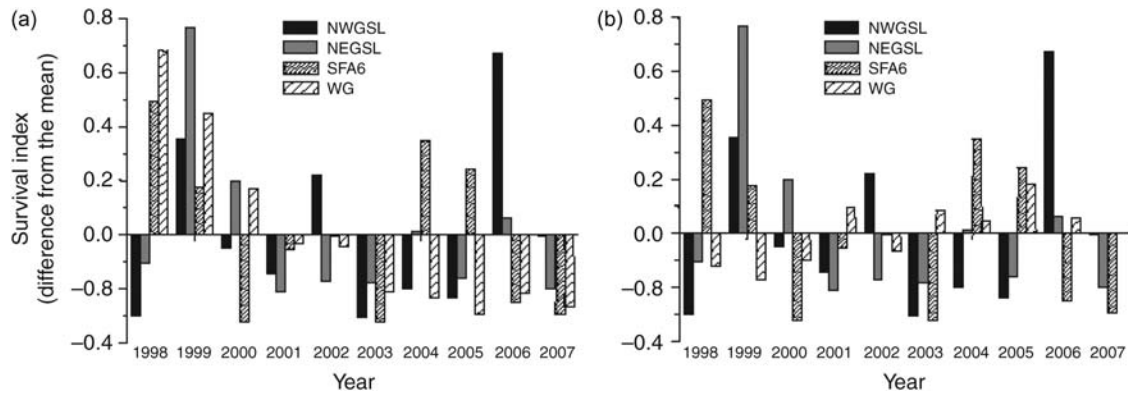


Figure 3. Annual deviation from the mean larval-survival index for each of the four regions: (a) the observed annual survival index and (b) the same index after first-order-difference transformation of the series for WG. NWGSL, northwest Gulf of St Lawrence; NEGSL, northeast Gulf of St Lawrence; SFA6, Shrimp Fishing Area 6 on Newfoundland–Labrador Shelf; WG, West Greenland.

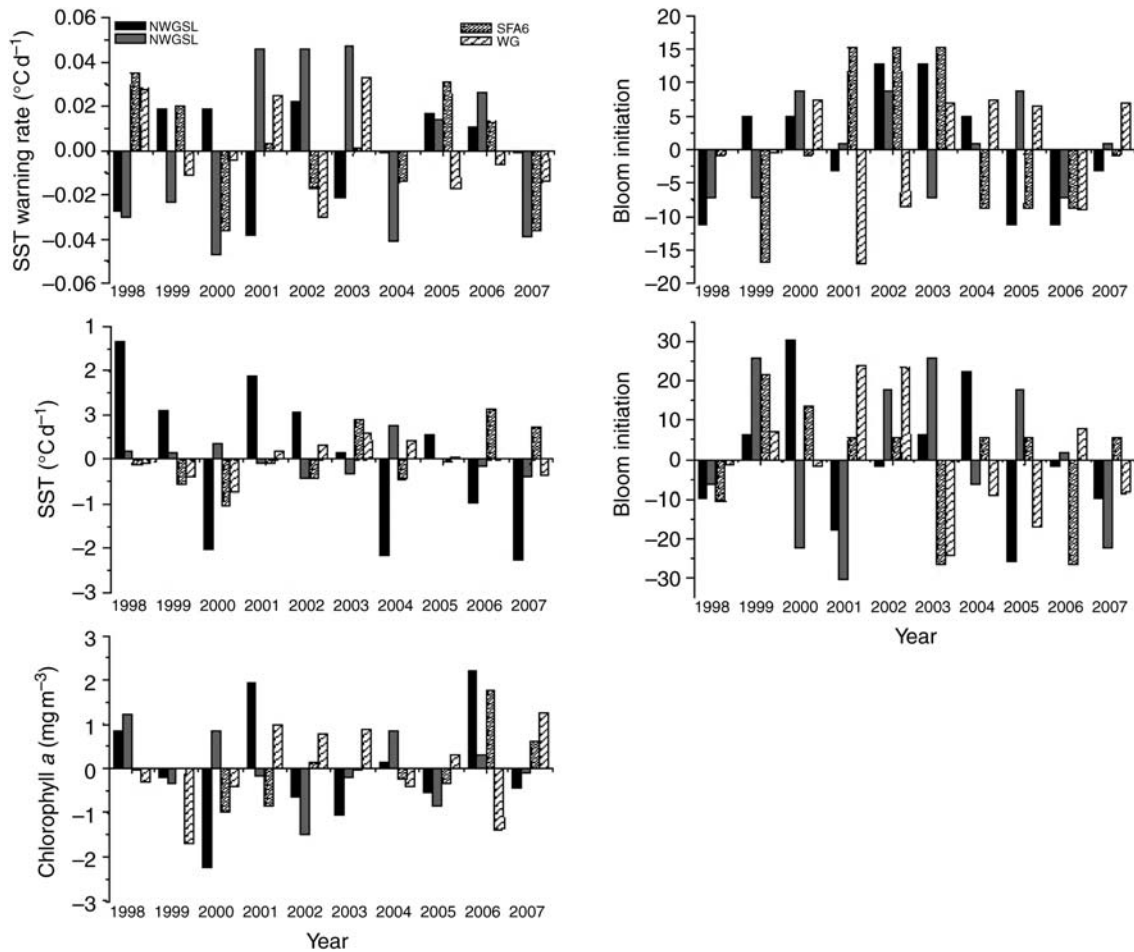


Figure 4. Annual deviations from the mean of the surface characteristics for the four study regions.

water temperatures for successful development and growth of larvae (Rasmussen and Tande, 1995; Ouellet and Chabot, 2005), as well as for the secondary production (e.g. zooplankton eggs, nauplii; Plourde *et al.*, 2009) that provides food for larger (older) larvae. For all regions and years, northern shrimp larvae always hatched after the initiation of the spring phytoplankton bloom. Although not statistically significant, the positive

relationships observed for all regions between larval survival and bloom duration and intensity supports the match–mismatch hypothesis (see Cushing, 1990) as an explanation for interannual fluctuations in recruitment of northern shrimp. Moreover, the negative relationships between larval survival and bloom initiation indicate that survival is more likely if suitable conditions for growth and development are established before hatching.

The match–mismatch hypothesis has been notoriously difficult to prove; unequivocal empirical demonstrations are rare (Leggett and Deblois, 1994). Despite evidence of an existing overlap between the seasonal food-production cycle and larval hatching (Koeller *et al.*, 2009; this study), links to recruitment have generally been indirect (Leggett and Deblois, 1994). Nonetheless, match–mismatch is expected to influence strongly species with short spawning or larval release periods (Mertz and Myers, 1994), as seems to be the case for northern shrimp (Ouellet *et al.*, 2007; Koeller *et al.*, 2009). Moreover, a temporal match between larval hatching and the peak in the plankton production cycle is only one aspect of the hypothesis; developments that are more recent have established the importance of considering total food abundance. Indeed, an abundance of adequate food can offset the negative effects of a mismatch on recruitment (Durant *et al.*, 2005). In our study, we observed good matches between larval hatching dates and spring phytoplankton blooms in all regions and years. However, the sea surface Chl *a* concentrations should be seen only as an indirect indicator of diet for larval stages of northern shrimp. Only the first two larval stages may select phytoplankton cells preferably, and it was estimated that phytoplankton might contribute only a small proportion of the organic energy needs of first-stage larvae (Ariza and Ouellet, 2009). Moreover, pelagic development proceeds through five moult stages and can last more than 2 months (Ouellet and Allard, 2006), so the timing and production of abundant zooplankton as food (Harvey and Morrier, 2003) become important in supporting successful development up to larval settlement in deep waters. In this context, perhaps the oceanographic conditions identified here affect the survival of northern shrimp larvae via their influence on the development of the zooplankton community and the production of adequate food for growth and development.

In addition to a good match between larval hatching and the biological production cycle, we propose that favourable temperature conditions in the upper layer of the water column are key to the survival of northern shrimp larvae and subsequent recruitment success. In the western region of the Gulf of St Lawrence (NWGSL), the phytoplankton bloom is intense, but short. Although SSTs are already high when the larvae hatch, increasing water temperatures apparently promote acceleration of their development and growth, possibly to match the shorter production cycle. In contrast, in the eastern region of the Gulf (NEGSL), SSTs are very low at the time of larval hatching. Although the phytoplankton bloom is longer there, water temperature may be the dominant limiting factor for good survival of larvae in such very cold environments. On the Atlantic side, water temperatures in SFA6 are also cold at the time of hatching, but not as cold as in NEGSL; increasing SST proved to be the factor most favouring survival during the less intense, but longer, phytoplankton blooms. For the WG detrended series, SSTs and Chl *a* concentrations were positively related to the larval-survival index. Water temperatures are again relatively cold ($<1^{\circ}\text{C}$) at larval hatching, but not as low as in NEGSL or SFA6; there, intense spring blooms apparently favour the survival of larvae. Future investigations need to evaluate these scenarios with comparative modelling studies among regions.

We were also interested in determining whether the observed coherence in larval-survival indices among the four regions in some years resulted from common large-scale environmental forcing. For all regions, winter ice retreat and spring melt appear to be determinant factors in the timing of the phytoplankton

bloom (Le Fouest *et al.*, 2005; Heide-Jørgensen *et al.*, 2007; Wu *et al.*, 2007). However, those regions have very different oceanographic environments in terms of physical characteristics and production dynamics (Devred *et al.*, 2007). The NWGSL is a relatively small area at the western limit of the GSL (Figure 1), where the main oceanographic feature is a quasi-permanent anticyclonic gyre (Saucier *et al.*, 2003) that may favour larval retention. Winter ice is advected to the southeast in spring, and the region is ice-free in early April (Saucier *et al.*, 2003; Galbraith *et al.*, 2009). On average, winter ice retreat is ~ 3 weeks later in the NEGSL (Galbraith *et al.*, 2009), and the dominant oceanographic feature is interannual variation in the influx of cold Labrador Shelf waters through the Strait of Belle Isle, which defines the characteristics of the water column (Galbraith, 2006). SFA6 is located off the Labrador Coast and is under the influence of seasonal and inter-annual fluctuations in the strength of the Labrador Current, which runs south along the shelf break and upper continental slope (the shelf edge Labrador Current) and along the coasts (the inshore Labrador Current; Han *et al.*, 2008). Therefore, inter-annual variability of advective transport of larvae can be an important additional factor in shrimp recruitment fluctuations there. WG is under the influence of the West Greenland Current running northwards, but modelling studies have revealed a complex circulation pattern, including permanent anticyclonic eddies over banks that can be important for the larval retention of various species, including northern shrimp (Ribergaard *et al.*, 2004). In short, although spring SST and bloom characteristics are undoubtedly important, the suite of interactions and processes controlling the survival of northern shrimp larvae are likely specific to each region. In this study, no common set of environmental conditions (constituting relatively few, simple variables) was sufficient to explain the years of common good or poor survival among the regions. It is therefore possible that favourable spring conditions for larval survival are the result of complex interactions between ocean surface variables. For example, for a given year, one very favourable variable could compensate for the weakness of others; e.g. in 1999, when an above-average bloom duration may have compensated for the only average Chl *a* concentration (Figure 4), producing above-average survival.

Although our analyses were not successful in revealing the significant empirical relationships that would be required to build regional operational models of recruitment mechanisms in northern shrimp, the analyses establish clearly the potential of remotely sensed data for deriving ocean surface characteristics specific to shrimp production units, and to crucial moments in larval development, including hatching. However, it is also possible that the uncertainties associated with the estimates of year-class strength, spawning-stock biomass, and larval hatching dates introduced additional variability, precluding the identification of significant relationships with environmental conditions. Therefore, it is important to continue monitoring the development of shrimp population and environmental indices to develop regional models that could be used to anticipate changes in abundance of northern shrimp and to assess the potential impacts of fishing and climate change on the populations.

Acknowledgements

We thank all those in each region who through several years dedicated themselves to collecting quality samples and data on northern shrimp during research vessel surveys and commercial fishing activities. We also thank the editors of the special issue of the *ICES*

Journal of Marine Science for their invitation and support to present the paper at the international symposium on Remote Sensing and Fisheries. Laure Devine's editing and comments improved the manuscript. We also thank an anonymous referee whose comments helped to improve an earlier version of the manuscript.

References

- Acker, J. G., and Leptoukh, G. 2007. Online analysis enhances use of NASA earth science data. EOS, Transaction of the American Geophysical Union, 88: 14, 17.
- Ariza, P., and Ouellet, P. 2009. Diet composition of northern shrimp *Pandalus borealis* first stage larvae in the northwest Gulf of St Lawrence. *Journal of Crustacean Biology*, 29: 532–543.
- Aschan, M., and Ingvaldsen, R. 2009. Recruitment of shrimp (*Pandalus borealis*) in the Barents Sea related to spawning stock and environment. *Deep Sea Research II*, 56: 2012–2022.
- Bergström, B. I. 2000. The biology of *Pandalus*. *Advances in Marine Biology*, 38: 1–245.
- Cushing, D. 1990. Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. *Advances in Marine Biology*, 26: 249–293.
- Devred, E., Sathyendranath, S., and Platt, T. 2007. Delineation of ecological provinces using ocean colour radiometry. *Marine Ecology Progress Series*, 346: 1–13.
- Durant, J. M., Hjermann, D. Ø., Anker-Nilssen, T., Beaugrand, G., Mysterud, A., Pettorelli, N., and Stenseth, N. Ch. 2005. Timing and abundance as key mechanisms affecting trophic interactions in variable environments. *Ecology Letters*, 8: 952–958.
- Feldman, G. C., and McClain, C. R. 2007. Ocean color web, SeaWiFS reprocessing 5.2. NASA Goddard Space Flight Center, Greenbelt, MD.
- Galbraith, P. 2006. Winter water masses in the Gulf of St Lawrence. *Journal of Geophysical Research*, 111, doi: 10.1029/2005/JC003159.
- Galbraith, P. S., Pettipas, R. G., Chassé, J., Gilbert, D., Larouche, P., Pettigrew, B., Gosselin, A., et al. 2009. Physical oceanographic conditions in the Gulf of St Lawrence in 2008. Canadian Science Advisory Secretariat Research Document, 2009/14.
- Han, G., Lu, Z., Wang, Z., Helbig, J., Chen, N., and de Young, B. 2008. Seasonal variability of the Labrador Current and shelf circulation off Newfoundland. *Journal of Geophysical Research*, 113, doi: 10.1029/2007/JC004376.
- Hannah, R. W. 1999. A new method for indexing spawning stock and recruitment in ocean shrimp, *Pandalus jordani*, and preliminary evidence for a stock–recruitment relationship. *Fishery Bulletin US*, 97: 482–494.
- Harvey, M., and Morrier, G. 2003. Laboratory feeding experiments on zoea of northern shrimp *Pandalus borealis* fed with natural zooplankton. *Marine Ecology Progress Series*, 265: 165–174.
- Heide-Jørgensen, M. P., Laidre, K. L., Logsdon, M. L., and Nielsen, T. G. 2007. Springtime coupling between chlorophyll *a*, sea ice and sea surface temperature in Disko Bay, West Greenland. *Progress in Oceanography*, 73: 79–95.
- Hobbs, E. B. 2008. Distribution and feeding behaviour of early life stages of the northern shrimp, *Pandalus borealis*, in relation to the spring phytoplankton bloom in the western Gulf of Maine. Master's thesis, University of New Hampshire, Durham, NH. 66 pp.
- Houde, E. D. 2008. Emerging from Hjort's shadow. *Journal of Northwest Atlantic Fishery Science*, 41: 53–70.
- Koeller, P., Fuentes-Yaco, C., Platt, T., Sathyendranath, S., Richards, A., Ouellet, P., Orr, D., et al. 2009. Basin-scale coherence in phenology of shrimps and phytoplankton in the North Atlantic Ocean. *Science*, 324: 791–793.
- Le Fouest, V., Zakardjian, B., Saucier, F. J., and Starr, M. 2005. Seasonal versus synoptic variability in planktonic production in a high-latitude marginal sea: the Gulf of St Lawrence (Canada). *Journal of Geophysical Research*, 110, doi: 10.1029/2007/C002423.
- Leggett, W. G., and Deblois, E. 1994. Recruitment in marine fishes: is it regulated by starvation and predation in the egg and larvae stages? *Netherlands Journal of Sea Research*, 32: 119–134.
- Leggett, W. G., and Frank, K. T. 2008. Paradigms in fisheries oceanography. *Oceanography and Marine Biology: an Annual Review*, 46: 331–363.
- Mertz, G., and Myers, R. A. 1994. Match/mismatch predictions of spawning duration versus recruitment variability. *Fisheries Oceanography*, 3: 236–245.
- Ouellet, P., and Allard, J.-P. 2006. Vertical distribution and behaviour of shrimp *Pandalus borealis* larval stages in thermally stratified water columns: laboratory experiments and field observations. *Fisheries Oceanography*, 15: 373–389.
- Ouellet, P., and Chabot, D. 2005. Rearing *Pandalus borealis* (Krøyer) larvae in the laboratory. 1. Development and growth at three temperatures. *Marine Biology*, 147: 869–880.
- Ouellet, P., Savard, L., and Larouche, P. 2007. Spring oceanographic conditions and northern shrimp *Pandalus borealis* recruitment success in the north-western Gulf of St Lawrence. *Marine Ecology Progress Series*, 339: 229–241.
- Pedersen, S., and Storm, L. 2002. Northern shrimp (*Pandalus borealis*) recruitment in West Greenland waters. 2. Lipid classes and fatty acids in *Pandalus* shrimp larvae: implications for survival expectations and trophic relationships. *Journal of Northwest Atlantic Fishery Science*, 30: 47–60.
- Platt, T., Sathyendranath, S., and Fuentes-Yaco, C. 2007. Biological oceanography and fisheries management: perspective after 10 years. *ICES Journal of Marine Science*, 64: 863–869.
- Plourde, S., Pepin, P., and Head, E. J. H. 2009. Long-term seasonal and spatial patterns in mortality and survival of *Calanus finmarchicus* across the Atlantic Zone Monitoring Programme region, Northwest Atlantic. *ICES Journal of Marine Science*, 66: 1942–1958.
- Rasmussen, T., Aschan, M., and Christiansen, J. S. 2000. The implementation of laboratory studies to shrimp recruitment modelling—a brief review of experimental procedures. *ICES Document CM 2000/R: 07*.
- Rasmussen, T., and Tande, K. 1995. Temperature-dependent development, growth and mortality in larvae of the deep-water prawn *Pandalus borealis* reared in the laboratory. *Marine Ecology Progress Series*, 118: 149–157.
- Ribergaard, M. H., Pedersen, S. A., Ådlandsvik, B., and Kliem, N. 2004. Modelling the ocean circulation on the West Greenland shelf with special emphasis on northern shrimp recruitment. *Continental Shelf Research*, 24: 1505–1519.
- Saucier, F. J., Roy, F., and Gilbert, D. 2003. Modeling the formation and circulation processes of water masses and sea ice in the Gulf of St Lawrence, Canada. *Journal of Geophysical Research*, 108, doi: 10.1029/2000JC000686.
- Savard, L., and Bourdages, H. 2010. Estimation of northern shrimp *Pandalus borealis* biomass and abundance from the multidisciplinary annual survey in the Estuary and the northern Gulf of St Lawrence between 1990 and 2009. Canadian Science Advisory Secretariat Research Document, 2010/061.
- Stickney, A., 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.
- Wu, Y., Peterson, I. K., Tang, C. C. L., Platt, T., Sathyendranath, S., and Fuentes-Yaco, C. 2007. The impact of sea ice on the initiation of the spring bloom on the Newfoundland and Labrador Shelf. *Journal of Plankton Research*, 29: 509–514.
- Ziemer, N., and Siegstad, H. 2008. Results of the Greenland bottom trawl survey for northern shrimp (*Pandalus borealis*) off West Greenland (NAFO Sub area I and Division OA), 1988–2008. NAFO Scientific Council Research Document, 08/71.