



Use of satellite data to identify critical periods for early life survival of northern shrimp in the Gulf of Maine

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ABSTRACT

The northern shrimp *Pandalus borealis* is at its southern limit in the Gulf of Maine (GOM), and recruitment success is higher in years with relatively cool water temperature. However, the mechanisms for the temperature effect are not clear. We used rolling window analysis of daily satellite data to identify critical periods for early life survival of the 1998–2012 northern shrimp year-classes and to investigate the importance of the phenology of the hatch and bloom. Survival was negatively correlated with sea surface temperature (SST) during a 6-week period around the time of larval emergence (late winter) and during a 4-week period in late summer when SST and stratification reached annual maxima. Survival was negatively correlated with chlorophyll-*a* concentration (chl-*a*) during two 5-week periods centered approximately a month before the hatch midpoint and around the time of settlement to the benthos. A small-magnitude winter bloom occurred around the time of the hatch in many years, but our results did not reveal a link between survival and bloom-hatch phenology. The timing of winter and spring blooms were correlated with SST during the preceding 10 months. A survival model including SST and chl-*a* during the critical periods explained 73% of the variance in survival. Summer SST increased significantly during the study period; the other critical variables showed no trend. The rolling windows approach revealed sensitive periods in early life history that may not have otherwise been hypothesized, providing a foundation for research towards a greater understanding of processes affecting recruitment.

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INTRODUCTION

Fine-scale data from observation systems such as oceanographic buoys and satellites present opportunities for ecological investigations on broader spatial and finer temporal scales than was possible only a few years ago. For example, the long-standing Hjort-Cushing ('match-mismatch') hypothesis (Hjort, 1914; Cushing, 1990) was difficult to test with field data before satellite data became available (Frank and Leggett, 1982; Platt *et al.*, 2003; Koeller *et al.*, 2009). The fine scale and synoptic nature of satellite data invite application of new methods that take advantage of its data richness. In this paper, we describe a novel application of an existing statistical technique to identify critical periods for survival during the early life history of a commercially and ecologically important species, the northern shrimp *Pandalus borealis*.

The northern shrimp (hereafter 'shrimp') is at the southern limit of its distribution in the Gulf of Maine (GOM), where it is thought to be particularly sensitive to temperature (Dow, 1964, 1977; Apollonio *et al.*, 1986; Richards *et al.*, 2012). The GOM shrimp fishery collapsed during a warm period in the 1950s (Dow, 1964, 1977;), and subsequent studies have shown strong temperature effects on growth and reproduction (Stickney and Perkins, 1977; Apollonio *et al.*, 1986; Richards *et al.*, 2012). A recent decline began in 2009 and by 2012 the biomass had plummeted to historic lows (NEFSC 2014), leading to fishery closures during 2014 and 2015. The reasons for the rapid decline are not certain; however, warming trends in the GOM have been steep (Friedland and Hare, 2007; Mills *et al.*, 2013; Pershing *et al.*, 2015), predation pressure has increased (NEFSC, 2014) and a suite of other environmental changes have been observed (Townsend *et al.*, 2010; EcoAP, 2012; Smith *et al.*, 2012;).

Northern shrimp are protandrous hermaphrodites, reproducing in the GOM as males at age 2 and as

females at ages 4 and 5, after which most are thought to die (Shumway *et al.*, 1985; Clark *et al.*, 2000). Females brood embryos externally and migrate to inshore waters to release their larvae during a winter hatch period of about 45 day's duration (Richards, 2012). The pelagic larvae settle as benthic juveniles in late spring to early summer and remain in coastal inshore waters for a year or more before migrating offshore to join the mature stock (Shumway *et al.*, 1985).

The recruitment success of shrimp in the GOM is higher in years with cold water during spring, when the pelagic larvae are developing (Richards *et al.*, 2012). Temperature's most important influence has been hypothesized to be on the phenology of the larval hatch: warmer temperatures may cause the hatch to occur before phytoplankton is available as food for the newly hatched larvae (Stickney and Perkins, 1981). Laboratory experiments (Stickney and Perkins, 1977) and field studies (Richards, 2012) have confirmed an effect of temperature on hatch timing in the GOM but have not investigated the potential link between the timing of the hatch and recruitment success.

Here we use data from satellite observations coupled with information on hatch timing to explore relationships between early life survival and the phenology of temperature and chlorophyll production in shrimp nursery areas in the Gulf of Maine. Rather than attempting to define *a priori* time periods that may be important to larval survival (e.g., temperature during a particular month), we applied a statistical tool borrowed from econometric analysis (rolling window analysis, Zivot and Wang, 2006) to allow the data to reveal conditions associated with variability in survival. Specific questions include: (i) Are there critical time periods in the relationship between temperature or chlorophyll-*a* concentrations and early survival? (ii) Is the match between bloom and hatch timing important to larval survival? and (iii) Do hatch and bloom phenologies respond to temperature in similar ways?

MATERIALS AND METHODS

Ocean color and temperature

Temporal and spatial patterns of sea surface temperature (SST) and surface phytoplankton chlorophyll (chl-*a*) during 1998–2012 in shrimp nursery areas (Fig. 1) were estimated from remotely sensed data. We used daily images at 4 km (SST) and ~1 km (chl-*a*) pixel resolution from the coastline to the 100-m contour from Cape Ann, Massachusetts, U.S.A., to Penobscot Bay, Maine, U.S.A. ($N = 3178$ pixels).

Time series data from each pixel were interpolated and boxcar-smoothed (8-day interval) over time, then all pixels within the study area were averaged for each day. SST data were from AVHRR Pathfinder Version 5.2 (<http://www.nodc.noaa.gov/SatelliteData/pathfinder4km/>). Chl-*a* concentrations were derived from SeaWiFS data (Level 2, R2010.0) for 1998–2007 and MODIS-Aqua (Level 2A, R2012.0 & R2013.1) data for 2008–2012 (<http://oceancolor.gsfc.nasa.gov/>) using the Pan *et al.* (2008, 2010) regional chlorophyll algorithm for both time periods. Chl-*a* was expressed relative to the observed minimum during Jan–Feb each year to account for possible effects of inter-annual variation in near-coast sediment loads that may affect chl-*a* estimation.

Bottom temperature (BT) in the shrimp nursery area was characterized using data from the USA National Oceanic and Atmospheric Administration (NOAA) electronic Monitoring of Lobster Traps (eMOLT) program (<http://www.emolt.org/>), in which sensors attached to lobster pots collected hourly temperature data. We used eight eMOLT locations within the study area at depths ranging from 31 to 99 m that had collected data starting in 2001 (Fig. 1). The number of locations reporting varied seasonally and over the time series; however, the trends in daily mean BT were highly correlated between sites (average Pearson's product moment correlation $r = 0.88$). The difference between the daily SST and the daily BT was taken as an index of stratification of the water column.

Shrimp survival estimates

Early life survival of shrimp was calculated as the number of recruits (age 1.5 yr) per unit population fecundity (see Richards *et al.*, 2012 for full description):

$$S_t = \ln(R_{t+1}) - \ln(E_{t-1}) \quad (1)$$

where $S = \log_e$ year-class survival index, $t = \text{year}$, $R = \text{recruitment index}$ and $E = \text{population fecundity}$ (millions of eggs). Abundance indices and length composition were from fishery-independent shrimp surveys conducted in the western Gulf of Maine each summer since 1984 (Clark, 1989). Recruits were observed in the survey 2 yr subsequent to the observation of the females that produced them. The fecundity-length relation was estimated using data for GOM shrimp from Haynes and Wigley (1969):

$$F_{CL} = -0.198 * CL^2 + 128.81 * CL - 17821 \quad (2)$$

$$r^2 = 0.76$$

where $F = \text{individual fecundity}$ (number of eggs) and $CL = \text{dorsal carapace length}$ (mm).

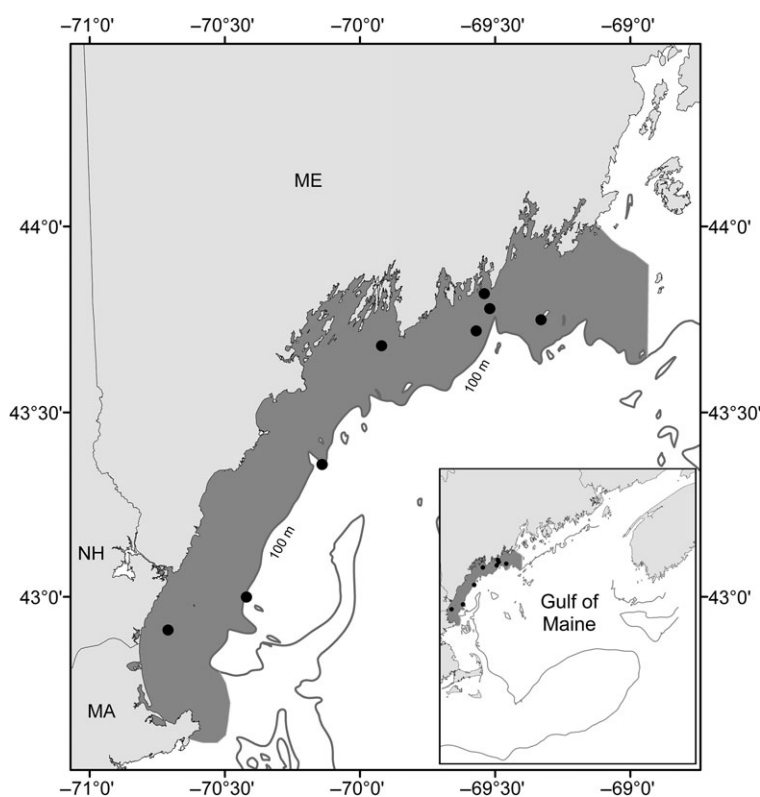


Figure 1. Map of the study area in the Gulf of Maine, northeast US coast. Dots indicate locations where bottom temperature data were collected from sensors on lobster traps. Inset shows entire Gulf of Maine.

Statistical analysis

The technique of rolling window analysis (Zivot and Wang, 2006) was used to identify critical periods in the relationships between shrimp survival, temperature and chl-*a*. Critical periods were defined as those in which shrimp survival was significantly correlated with one of the environmental variables. In our application of rolling window analysis, the mean SST and chl-*a* were calculated for 15-day periods (windows) that were sequentially shifted 1 day forward starting 60 days before the midpoint of the hatch period (H_{50}) to 180 days after H_{50} in each year (Fig. 2a). For each window, the correlation between annual survival and average SST or chl-*a* was estimated across the 15 yr (Fig. 2b). This resulted in a series of time-dependent correlations that extended from approximately 2 months before the median hatch through 6 months after (Fig. 2c), corresponding to the time of late embryonic development through the pelagic larval stages and approximately the first 4 months of the post-settlement benthic juvenile stage. Earlier stages of embryogenesis would have occurred in deeper offshore waters with different conditions, so were not considered here. Windows were indexed by the first day of their 15-day period (e.g., window 10 included days 10 through to 24).

An important aspect of the analysis was centering the data for each year on the midpoint of the hatch period (H_{50} , the estimated day on which 50% of females had hatched their brood) so the windows were relative to hatch timing, not to an arbitrary calendar date (e.g., 1 January). This was done because hatch timing can vary by more than a month between years. For example, H_{50} occurred on yearday 79 in 2005, so the first rolling window (window -60, starting 60 days before H_{50}) began on January 19. In contrast, H_{50} occurred on yearday 44 in 2012, so window -60 started on 15 December 2011. Centering the windows on hatch date aligned them biologically across years so that in each year window 0 represented the time when 50% of larvae would have been released. H_{50} was estimated using probit analysis of the annual proportion of females that had released their brood over time (Richards, 2012).

The rolling correlations have inherent serial autocorrelation. Two types of test were performed to assess the influence of the autocorrelation on identifying critical periods. In one, we calculated the rolling correlations using data centered on 1 January, rather than on the biologically significant dates (e.g., H_{50}). This retained the autocorrelation structure of the data but used a reference date with no biological significance. In the other test, we used randomly-generated data

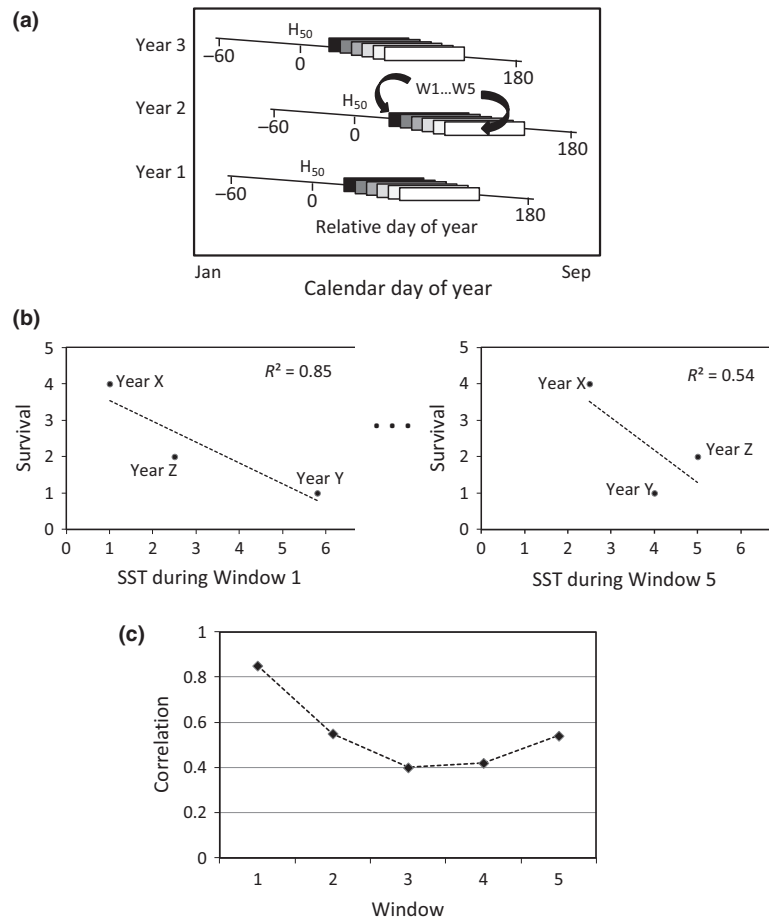


Figure 2. Schematic of method used for rolling correlation analysis. (a) The mean sea surface temperature (SST) and chlorophyll-*a* (chl-*a*) are estimated for each year during rolling windows with start dates from 60 days before H_{50} to 180 days after H_{50} . Only five windows (w1–w5) are shown in the illustration. The first window starts on a different calendar day each year because windows are defined with respect to H_{50} rather than an arbitrary calendar date; (b) For each window, the correlation between survival and mean SST or chl-*a* for that window is estimated using all years of data. (c) the correlations for each window are then plotted as a time series to reveal time periods when SST and chl-*a* are correlated with survival.

within the observed range of temperatures and chl-*a* to evaluate whether the patterns observed were statistical artifacts.

To develop an overall model for shrimp early life survival, we defined critical time periods with respect to SST and chl-*a* as those are the windows during which correlations with survival had $|r| \geq 0.50$ (approximate $P = 0.05$ significance level, Pearson's product moment correlations). We estimated the annual average temperature and chl-*a* during the critical periods and included these in a model of shrimp survival. Principal components analysis (PCA) was used as a data reduction technique for the independent variables, thus, the model was:

$$S_t = \alpha + \beta * PC_{tj} + \epsilon \quad (3)$$

where $S_t = \log_e$ survival, t = year, α and β are regression coefficients, PC = principal component (PC) score from PCA of temperature and chlorophyll variables, j = PC number, and ϵ is a log-normal error term. Terms were included in the model if they were significant at $P < 0.10$.

To investigate phenology of phytoplankton production in relation to temperature, we identified the timing of the peak concentrations of chl-*a* during the winter and spring and correlated these with SST using rolling window analysis. We used bloom peak rather than bloom initiation as our indicator of timing because it was less ambiguous to define. To identify peaks, we used the STARS technique (Rodionov, 2004) to define change points in the rate of increase or decrease of chl-*a*, and then found the yearday on which the chl-*a* reached a maximum within the change points. STARS uses time series analysis with pre-whitening to remove red noise before applying the procedure to identify change points. We then calculated rolling correlations between SST and timing of the winter or spring bloom using 15-day rolling windows during 10 months before to 60 days after the pulse or bloom. This time frame approximated the shrimp annual reproductive cycle, which starts with ovogenesis the previous spring, and is strongly affected by temperature (Stickney and Perkins, 1977; Brillion *et al.*, 2005; Richards, 2012;). The rolling windows

were constructed relative to the yearday of the peak winter or spring chl-*a* concentration in each year. The winter bloom in the western Gulf of Maine is weaker and more variable than the spring bloom (O'Reilly and Zetlin, 1998), and the STARS algorithm did not identify a winter bloom in some years (2003, 2005, 2008 and 2009).

To examine whether bloom and hatch timing respond in similar ways to temperature, we compared the relationships between timing of H_{50} or peak chl-*a* and the average temperature in the preceding 60 days. We chose the 60-day time period because this approximates the time when female shrimp would be present in the inshore nursery grounds.

RESULTS

The time series of annual SST, chl-*a* and shrimp survival estimates that formed the basis for the rolling window analysis are plotted in Figs 3 and 4. The survival index declined significantly during the study period (t -test, $P < 0.05$, Fig. 4). Annual estimates of hatch timing and bloom peak timing are given in Table 1.

SST was negatively correlated ($r < -0.5$) with survival during two time periods (Fig. 5). The first (SST1) spanned H_{50} (windows -16 through to 19,

which included days -16 through 30) and had correlations stronger than -0.60 during windows -2 through to 14 (days -2 to 29). SST1 corresponded to final maturation of embryos through the first few pelagic larval stages, with the strongest correlations during the early larval stages. The duration of SST1 was equivalent to the average duration of the hatch period. The second time period of a negative correlation between SST and survival (SST2) was during windows 147–164 (days 147–178), corresponding on average to mid-summer, approximately 2 months after settlement of juvenile shrimp to the benthos.

Chl-*a* was negatively correlated ($r < -0.5$) with shrimp survival during two time periods (Fig. 5). The first (CHL1) lasted about 5 weeks, centered about 40 days before the median hatch (windows -48 through to -29, days -48 through to -15) and reached a minimum at window -38. The second period (CHL2) occurred around the time of settlement to the benthos (windows 82–105, days 82–119) and lasted for about 4 weeks.

Rolling correlations between temperature and timing of the winter and spring bloom peaks were strong and followed similar patterns offset by approximately 2 months (Fig. 6). The timing of the winter bloom was positively correlated with SST 6.5–10 months earlier but was negatively correlated with SST during the

Figure 3. Timeplots of sea surface temperature (SST) and chlorophyll-*a* (chl-*a*) from remotely sensed data in shrimp nursery areas in the Gulf of Maine. Red circles (estimated hatch midpoint, H_{50}) are scaled to the shrimp survival estimate for each year. The yellow diamond is the estimated peak of the winter bloom.

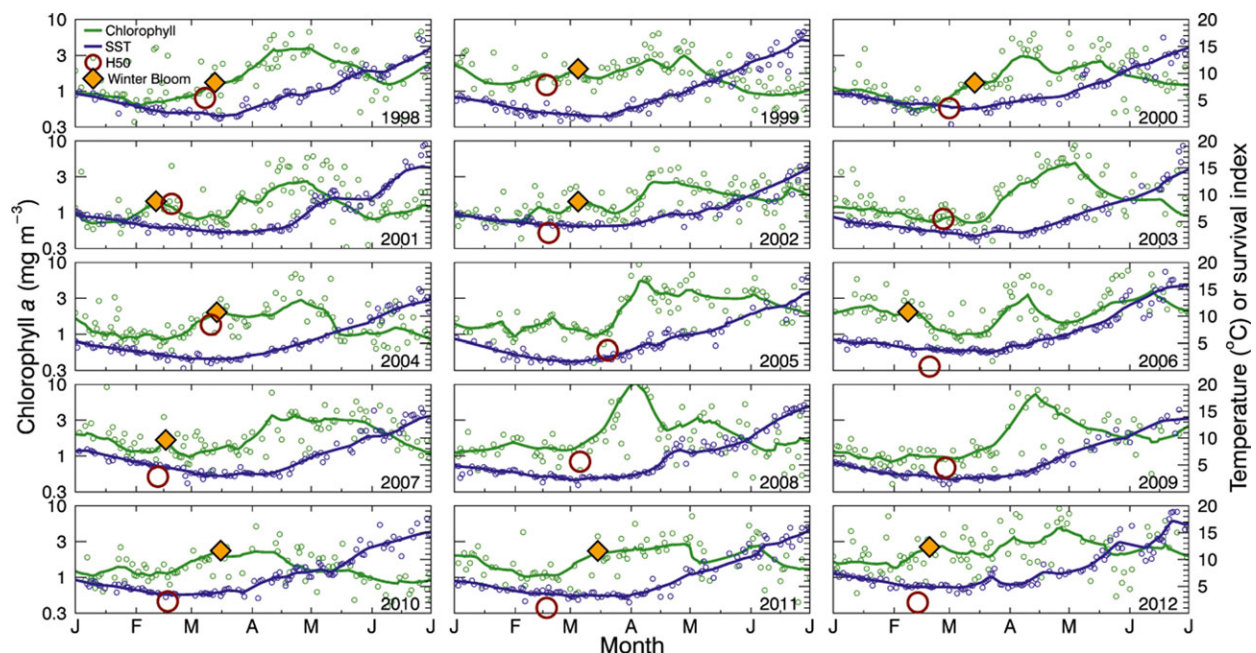


Figure 4. The northern shrimp early life survival index in the Gulf of Maine (GOM), based on number of recruits per million eggs.

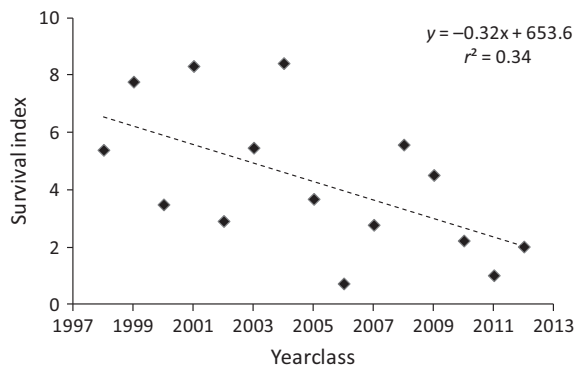


Table 1. Estimated yearday of hatch midpoint (H_{50}) and peak chl-*a* during winter and spring blooms. No winter bloom was observed in some years.

Year	H_{50}	Yearday of	
		Winter bloom	Spring bloom
1998	67	72	120
1999	48	64	118
2000	60	73	98
2001	50	42	119
2002	49	64	103
2003	57		124
2004	70	73	116
2005	79		96
2006	50	39	100
2007	43	47	113
2008	65		93
2009	58		104
2010	48	75	102
2011	48	74	118
2012	44	50	117
Average	56	61	109

6 months preceding the winter bloom. Within about a month after the winter bloom peak, the correlation had returned to a strong positive one. The timing of the spring peak was positively correlated with temperatures 8.5–10 months earlier and was negatively correlated with SST during the 2 to 8 months before the spring bloom. About 2 weeks before the spring bloom peak, the correlation with temperature was again significant and positive.

On average, the winter bloom peaked near H_{50} and the spring bloom peaked about 7 weeks later, near the end of the pelagic larval stage (Table 1). The mismatch in timing of the winter bloom and H_{50} was not

correlated with survival (Fig. 7). Both H_{50} and timing of the winter bloom were correlated with the mean SST during the preceding 60 days (*F*-tests, H_{50} : $P < 0.0001$, adjusted $r^2 = 0.80$; bloom: $P < 0.01$, adjusted $r^2 = 0.63$; Fig. 8a). The slopes did not differ significantly (*F*-test, $P = 0.36$); however, winter bloom timing was not correlated with the mean SST during the 60 days preceding the hatch (*F*-test, $P = 0.15$; Fig. 8b).

Tests using January 1 as a reference date for the rolling window analyses (versus biologically significant dates) produced patterns that showed few significant correlations for any of the variables (Fig. 9). Similarly, using random data resulted in no coherent correlation patterns (Fig. 9).

The average SST and chl-*a* during the critical periods for survival are plotted over time in Fig. 10. SST2 showed a sharp increasing trend (slope = 0.11) over the study period; the other series were highly variable and did not show trends. The univariate correlations between environmental variables and survival ranged from $r^2 = 0.3$ to 0.4 (Fig. 10). The results of the PCA analysis incorporating SST and chl-*a* are shown in Table 2. PC1 explained 51% of the variance, was weighted approximately equally on SST1, CHL1 and CHL3 and did not show a significant time trend (*t*-test, $t_{14} = 1.70$, $P = 0.11$; Fig. 11). PC2 explained 23% of the variance and was weighted most heavily on SST2.

The survival model included only PC1 and was significant at $P < 0.001$ ($F = 39.7$, 14 d.f., adjusted $r^2 = 0.73$) (Fig. 11). The Durbin–Watson *D*-statistic was 2.08, indicating no significant autocorrelation in the residuals. Survival was negatively related to PC1.

DISCUSSION

Rolling window analysis of daily satellite data allowed detailed examination of two important environmental variables without requiring *a priori* hypotheses about which time periods might be relevant to shrimp survival. This yielded some unexpected results as well as some that confirmed expectations. The results have the same limitations as with all correlation analyses – the relationships may or may not be causal. However, our tests with random data indicate that the results are not artifacts but revealed time periods when environmental conditions were significantly correlated with shrimp early life survival. Aligning the data relative to the timing of a biological event (e.g., H_{50}) rather than calendar dates was crucial for revealing the sensitive periods.

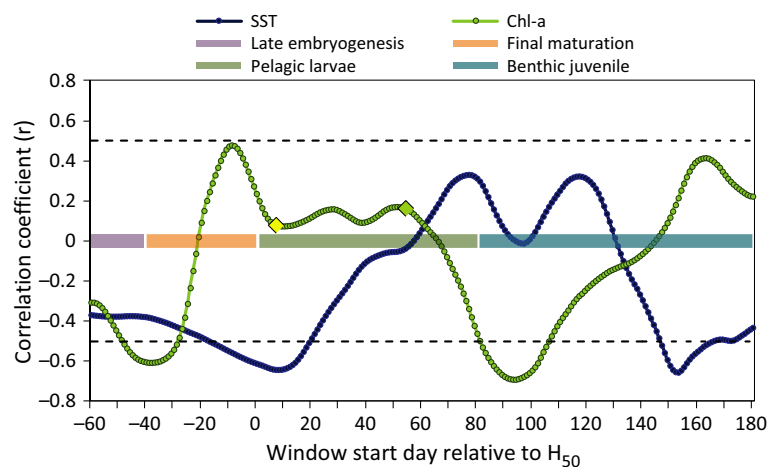


Figure 5. Rolling correlations between shrimp survival and sea surface temperature (SST), and shrimp survival and chlorophyll-*a* (chl-*a*) biomass during windows starting 60 days before hatch through to 180 days after hatch. Yellow and green points represent average year-day (window midpoint) of winter and spring bloom peaks during 1998–2012. Approximate timing of life history stages is shown in shaded bars.

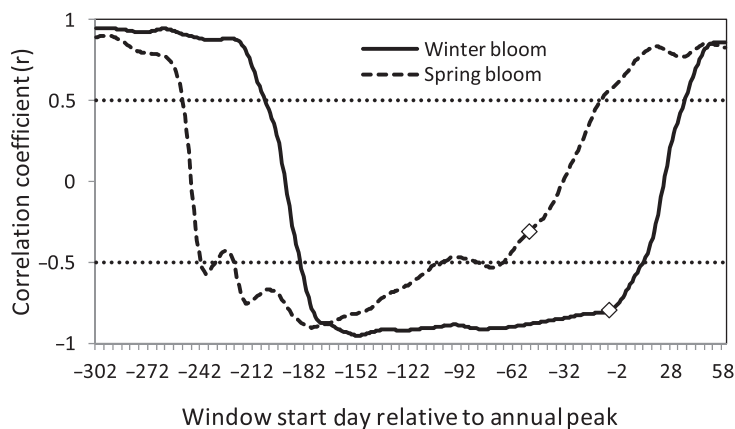


Figure 6. Rolling correlations between sea surface temperature (SST) and winter and spring bloom peak timing during windows starting 302 days (10 months) before each peak through to 60 days after. Window 0 for both series starts on the yearday of the peak chlorophyll-*a* (chl-*a*) for each year. Expanded points represent the DOY (midpoint in window) when the hatch would have occurred on average during 1998–2012 relative to the bloom windows.

Previous studies using temperature data collected shipboard during spring and fall resource surveys showed that spring temperature is linked to recruitment of shrimp in the Gulf of Maine (Richards *et al.*, 1996, 2012). The current study using daily SST from remote sensing shows that the ‘spring’ temperature effect is centered on the time of larval emergence, generally from early February through to mid-March, and thus is more accurately characterized as a winter temperature effect. Having a more precise understanding of timing should facilitate efforts to understand processes driving recruitment variation.

While it makes sense that colder temperatures are favorable for a species at its southern extent, it is not immediately clear why colder temperatures during the coldest time of year should favor higher survival. Temperature effects on the phenology of the hatch and bloom have been hypothesized as an important mechanism (Stickney and Perkins, 1979), given the strong dependence of hatch timing on temperature (Stickney and Perkins, 1977). Several studies support the

hypothesis that a match in phenology of the hatch and the spring bloom are important in shrimp populations (Fuentes-Yaco *et al.*, 2007; Ouellet *et al.*, 2007, 2011; Koeller *et al.*, 2009). However, in a study spanning the North Atlantic, the GOM shrimp population was the only one in which hatch timing did not coincide with the spring bloom (Koeller *et al.*, 2009). Our results show that in GOM shrimp nursery areas, the hatch precedes the spring bloom by almost 2 months, and coincides more closely with the smaller winter bloom. Despite the closer overlap, survival was not correlated with the mismatch in timing of the hatch and winter bloom, and significant positive correlations between survival and chl-*a* biomass were not seen. However, positive correlations approached significance during windows –11 through to 7 (11 days before H_{50} through 21 days after), and further work may shed more light on this relationship. The present results indicate that phytoplankton biomass during larval emergence was not a controlling factor during our study period. The coastal waters of the Gulf of Maine have elevated chl-

Figure 7. Shrimp survival versus mismatch in timing of winter bloom peak and shrimp hatch (H_{50}) for 11 yr during 1998–2012 in which a winter bloom could be identified.

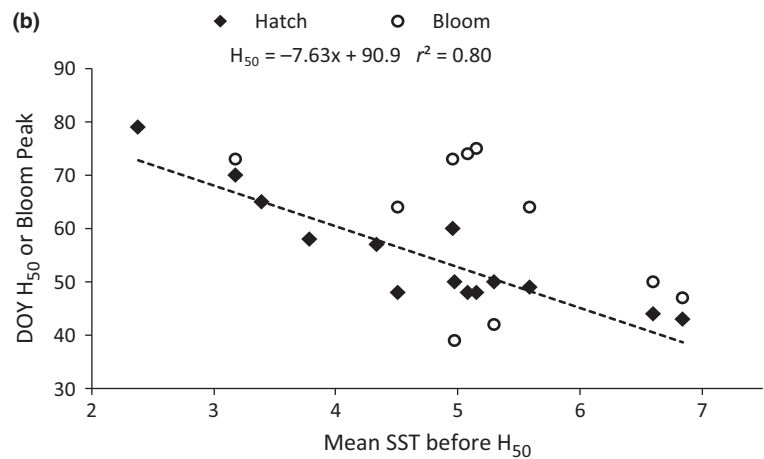
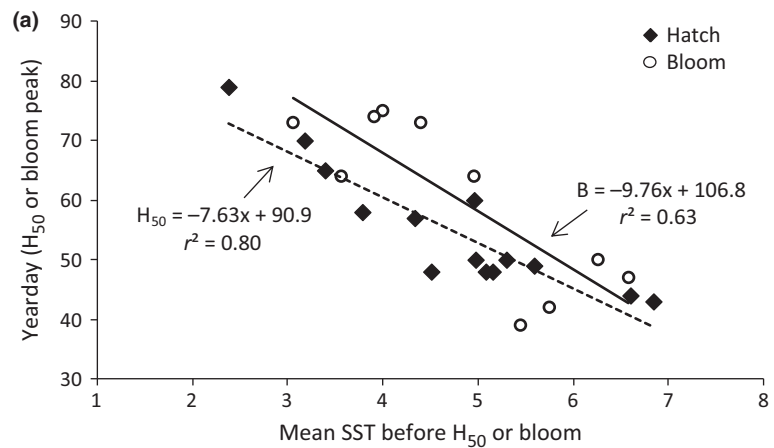
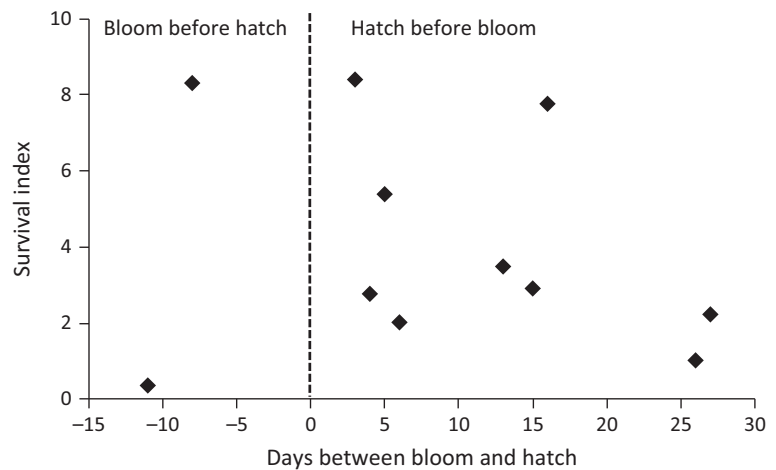
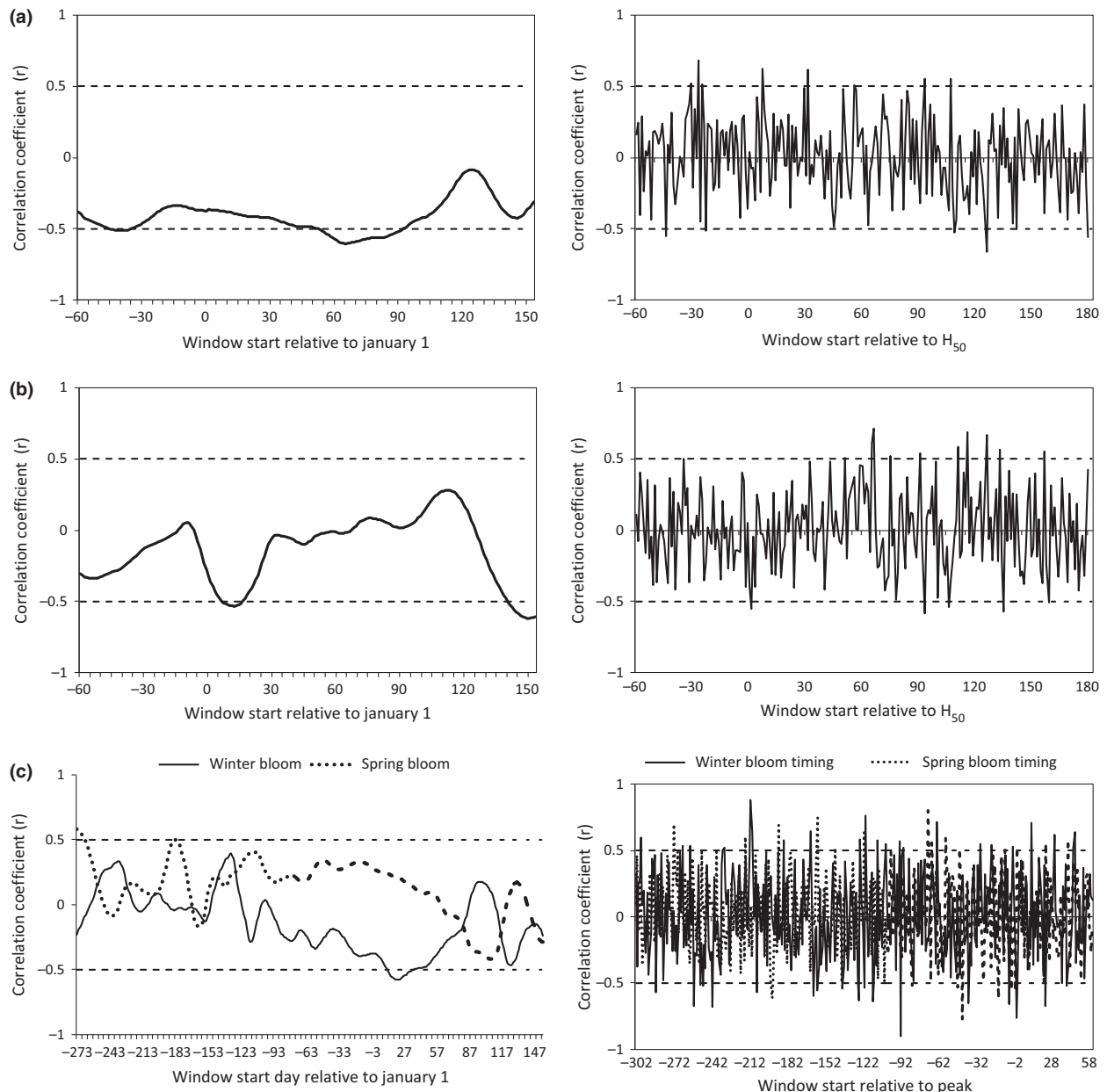


Figure 8. (a) Relationship between H_{50} and mean sea surface temperature (SST) during the 60 days preceding H_{50} , and between timing of the winter bloom peak (B) and SST during the 60 days preceding the winter bloom peak, and (b) relationship between mean SST during the 60 days preceding H_{50} and timing of the hatch and winter bloom. Relationship for bloom timing was not significant.

a levels year round (Thomas *et al.*, 2003). Perhaps these are sufficient to support early larval survival in the absence of a bloom and hypothetically could have provided selective pressure for the evolution of the extensive inshore migration of brooding female shrimp in the GOM.

A second hypothesis for the beneficial effect of cold winter temperature relates to metabolic demand. Ectotherms have evolved to optimize functioning within particular thermal niches (Pörtner and Farrell, 2008) and physiological performance declines well before lethal limits are reached

Figure 9. Rolling correlations using 1 January as a reference date (left column) and using randomly-generated input data (right column) for correlations between (a) survival and sea surface temperature (SST), (b) survival and chlorophyll-*a* (chl-*a*), and (c) timing of phytoplankton blooms and SST. Different random streams were used for each variable.



(Pörtner and Knust, 2007; Pörtner, 2010;). In laboratory experiments with GOM shrimp, both fed and starved larvae had higher survival rates at 4 °C than at 6 °C (Stickney and Perkins, 1977), and oxygen consumption increased exponentially with temperature (range 2.6 to 6.5 °C) (data from Stickney and Perkins, 1979). Similar relations have been seen in experiments with other populations of shrimp (Paul and Nunes, 1983; Chabot and Ouellet, 2005;

Arnberg *et al.*, 2013). The first zoeal stage (lasting about 2 weeks in the GOM; Shumway *et al.*, 1985) appears to be the most sensitive to temperature (Chabot and Ouellet, 2005), consistent with our results showing a critical period for temperature around the time of the hatch. The combination of laboratory and field results suggest the hypothesis that temperature effects on metabolic processes during the first weeks of life may be important for

Figure 10. Time series plots (left column) of mean sea surface temperature (SST) and relative chlorophyll-*a* (chl-*a*) biomass during critical time periods identified by the rolling correlation analysis. Right column, correlations between SST and chl-*a* variables and survival indices for northern shrimp.

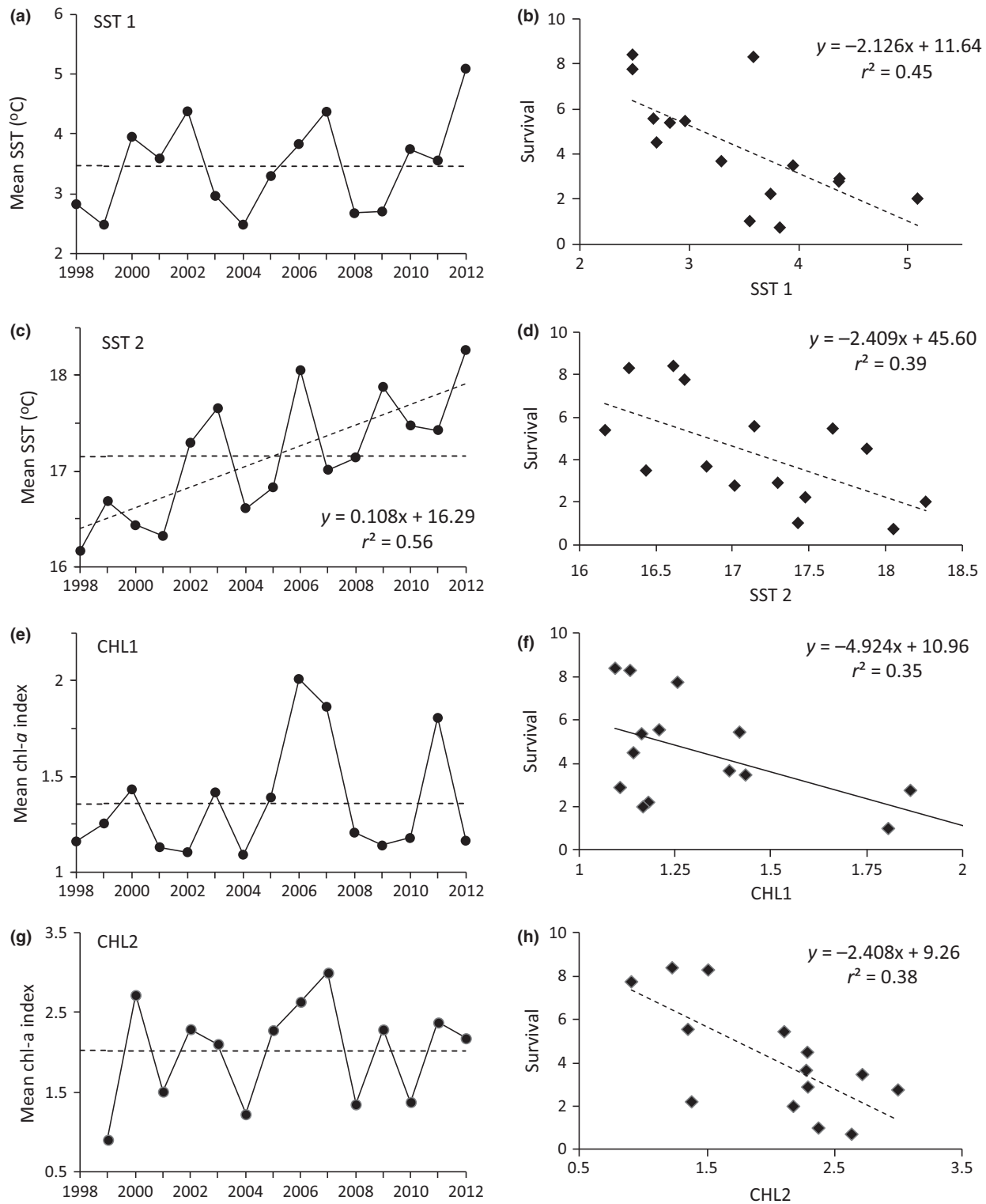


Table 2. Eigenvectors (PC) from principal components analysis of temperature and chlorophyll variables.

Variable	PC 1	PC 2	PC 3	PC 4
SST period 1	0.526	0.257	-0.663	-0.468
SST period 2	0.394	0.769	0.368	0.345
Chl- <i>a</i> period 1	0.519	-0.345	0.617	-0.481
Chl- <i>a</i> period 2	0.547	-0.473	-0.213	0.657
Proportion of variance	0.51	0.23	0.17	0.09
Cumulative variance	0.51	0.74	0.91	1.00

GOM shrimp larvae, even although they emerge near the coldest time of year.

Other studies have suggested more complex processes to explain the beneficial effects of colder water at larval emergence. In the Gulf of St Lawrence, warm temperatures were thought to be detrimental because they could lead to early stratification, rapid depletion of nutrients and a reduced potential for sustained phytoplankton production (Ouellet *et al.*, 2007). This seems less likely to be important in GOM shrimp nursery areas, which are shallower and do not become

thermally stratified until after the hatch period (Fig. 12). A rapid increase in SST after H_{50} also was favorable in the Gulf of St Lawrence and several other Canadian Atlantic populations (Ouellet *et al.*, 2007, 2011) as well as in Norway (Rasmussen and Tande, 1995), but we have not been able to identify a similar effect in the warmer environment of the GOM (Richards *et al.*, 1996; RAR, unpublished data). Clearly there are many avenues for the influence of temperature, and the relative importance of different processes undoubtedly varies among populations and among years.

The second significant period (SST2) for temperature effects on shrimp survival in the GOM occurred during the summer (~mid-July to early September) after juveniles would have settled to the benthos. During this period SST reached its annual peak ($>16^{\circ}\text{C}$), the bottom temperature was as high as $7\text{--}10^{\circ}\text{C}$ and the difference between bottom and surface temperature was at its annual maximum ($\Delta = 7\text{--}9^{\circ}\text{C}$) (Fig. 12). We hypothesize that these warm temperatures reduce the metabolic efficiency and/or limit the

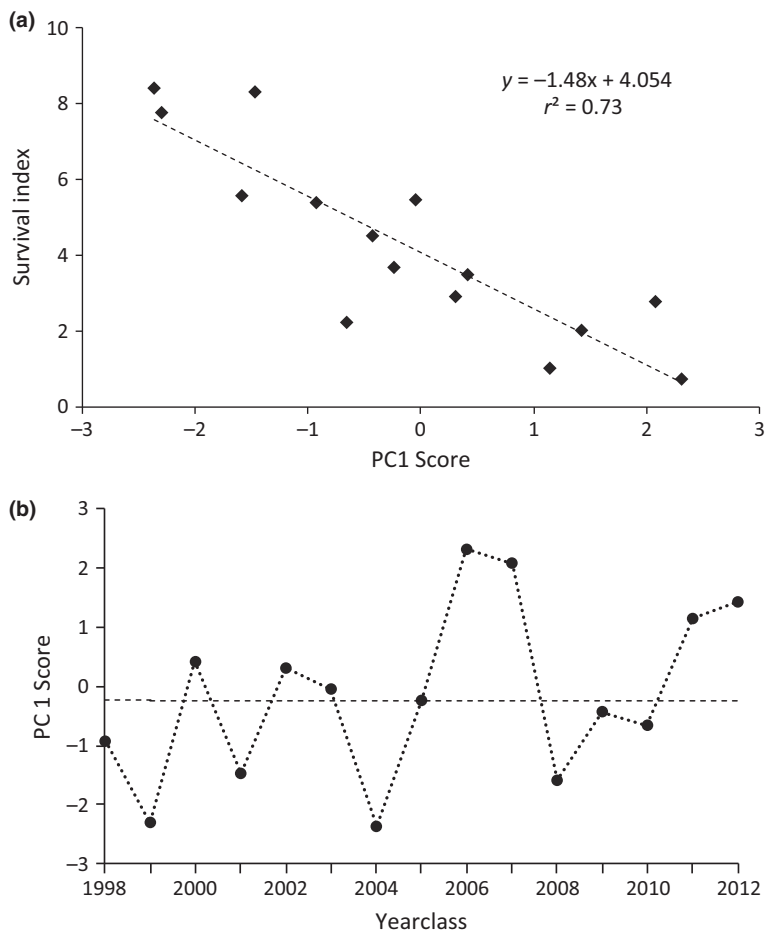
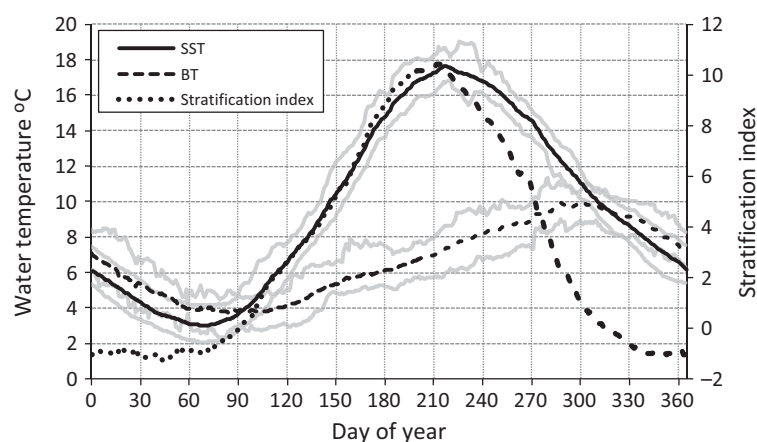
**Figure 11.** (a) Relationship between shrimp survival index and PC1 score, 1998–2012. (b) Time trends in PC1 scores. Dashed line is time series (1998–2012) median.

Figure 12. The mean, 10th and 90th percentile of daily sea surface temperature (SST) (1998–2012) and bottom temperature (BT) (2001–2012), and the stratification index in the study area.



ability to feed. In the laboratory, the growth efficiency of GOM juvenile shrimp declined with increasing temperature in the range 4–10 °C (Stickney and Perkins, 1977). Thermal stress could compromise the condition of juveniles and increase susceptibility to predators or disease (Pörtner, 2010). In addition, summer warming may create a behavioral impediment to feeding. Northern shrimp show pronounced vertical migrations (Barr, 1970; Apollonio *et al.*, 1986) and zooplankton forms an important part of their diet (Wienberg, 1980; Bergström, 2000). However, vertical movements may be limited in strong temperature gradients; field studies in the GOM have shown that shrimp do not cross the thermocline (Apollonio *et al.*, 1986). Reduced access to the foraging habitat coupled with increased metabolic demand may create a survival bottleneck for juvenile shrimp during the summer. A negative effect of summer SST has also been seen in an Icelandic population of northern shrimp (Jónsdóttir *et al.*, 2013), but the bottom temperature was positively correlated with shrimp survival at West Greenland (Wieland and Siegstad, 2012).

Negative correlations between shrimp survival and chl-*a* were observed during two time periods. The earliest (CHL1) was centered about 40 days before the hatch midpoint, corresponding on average to early January through to mid-February. A possible explanation for these negative correlations is a seasonal succession in the plankton community. If chl-*a* increases early relative to H_{50} , the phytoplankton community may evolve to species or size classes that are less suitable as food for young larvae (St. John *et al.*, 2001; Sommer *et al.*, 2012). First and second stage larvae consume relatively small particles, especially diatoms (Stickney and Perkins, 1981; Rasmussen *et al.*, 2000; Harvey and Moirier, 2003), which tend to dominate earlier in the bloom (Kane, 2011; Barton *et al.*, 2013).

Animal food becomes increasingly important for later larval stages (Rasmussen *et al.*, 2000) and certain developmental stages of prey (e.g., copepodites) may be particularly beneficial (Stickney and Perkins, 1977). Thus, an early increase in chl-*a* concentration may lead to a lower availability of high-quality food for some larval stages, and could additionally stimulate production of higher level consumers that prey on shrimp larvae.

A second period with strong negative correlations between chl-*a* and survival was seen around the time of metamorphosis and settlement to the benthos (CHL2, ~mid-May, about a month after the spring bloom peak). An effect of chl-*a* at this time was unexpected because late stage larvae and juveniles do not consume phytoplankton. The correlations may be a proxy for another process affecting shrimp larvae, such as the intensity or depth of stratification during the settlement period, or some other aspect of benthic–pelagic coupling (e.g., Lehtonen and Andersin, 1998). Survival was weakly correlated with the mean stratification index during CHL2 ($r^2 = 0.23$, $P = 0.08$), but including stratification in the survival model did not improve the fit.

The significant correlations between bloom timing and temperature up to 10 months previous are intriguing. Research on conditions triggering phytoplankton blooms historically has focused on proximate factors, but longer-term conditions may also be highly influential (Sommer *et al.*, 2012). The present results suggest this may be true for the study area. However, despite the strong long-term correlations between temperature and bloom timing, the shorter-term relationship between bloom timing and the mean SST during the 2 months prior to H_{50} (versus prior to the bloom) was not significant. This was because the hatch usually occurred after the bloom, and the significant

correlations between temperature and bloom timing deteriorated shortly after the bloom peak. These results imply that even although the phenology of hatch and bloom respond in a similar way to changes in SST (equal slopes), the timing of hatch and bloom still may not match, probably because other factors also influence timing (e.g., light for the bloom).

Regardless of the mechanisms involved, the rolling window analysis allowed us to identify time periods in the shrimp early life history during which environmental variables were strongly correlated with survival in the GOM. Trends in the identified variables suggest that the decline in survival during 1998–2012 was not entirely as a result of a directional change as only summer SST (SST2) showed a clear trend over time. Whether the correlations identified will hold in the future is unknown; however, they provide insight into the recent past and may hold clues to the future. Rolling window analysis is a powerful tool that warrants further development and could be useful in other applications in marine ecology and oceanography as well.

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