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Long-term trends and drivers of larval phenology and abundance of dominant brachyuran crabs in the Gulf of St. Lawrence (Canada)

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Abstract

Climate change has led to major shifts in the timing of biological events, with many studies demonstrating earlier phenology in response to warming. However, few of these studies have investigated the effects of climate change on the phenology of larvae in marine species. Phenological shifts can result in mismatches between consumers and prey and hence affect growth and survival of individuals, and ultimately population demography. We investigated the temporal changes in phenology and abundance of the larvae of dominant brachyuran crabs in the southern Gulf of St. Lawrence (eastern Canada) based on plankton collections spanning 1982–2012. The Gulf of St. Lawrence has warmed since the early 1990s, and our analyses revealed that larvae of snow crab (*Chionoecetes opilio*) and toad crabs (*Hyas* spp.) exhibited a significant trend towards earlier phenology over the 30-year study period. This shift in phenology appeared to be a consequence of the effect of climate warming on both the timing of hatching and larval development rate. Larval abundance responded differently by crab taxon to climate warming, likely due to differences in thermal tolerance. The warming trend was unfavourable to snow crab, which is the most cold-adapted and stenothermic of the taxa examined in this study. The abundance of snow crab larvae was lower when sea ice retreat occurred earlier than day 110 of the year and sea surface temperature was higher than 8.5°C. On the other hand, larval abundance of rock crab (*Cancer irroratus*), which prefers higher temperatures, was positively related to surface temperature.

KEYWORDS

climate change, larval production, marine larvae, phenology, snow crab, spring bloom, temperature

1 | INTRODUCTION

The dynamics of animal populations can be influenced by events occurring across multiple life stages. However, for most marine fishes and invertebrates with complex life cycles, processes affecting early life history phases (i.e. embryos, larvae and juveniles) are generally the most important drivers of population dynamics (Chambers & Trippel, 1997). The larval phase, in particular, is thought to represent a "critical period" (sensu Hjort, 1914) of the life cycle, as the recruitment success of many marine species, including commercially important ones, appears to be largely determined by processes affecting larval growth, dispersal and survival (Houde, 2016).

The larval life of many marine fishes and invertebrates occurs in the pelagic environment where their planktotrophic larvae must

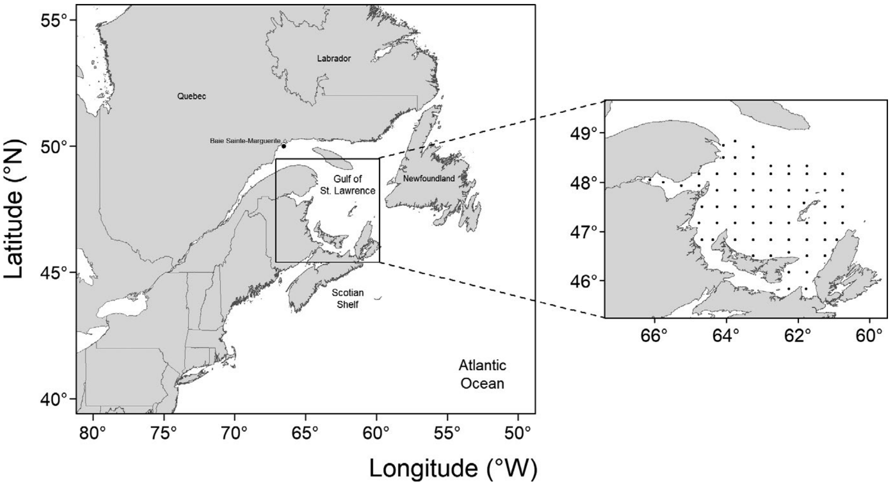

FIGURE 1 Map of the Gulf of St. Lawrence (right) with box indicating the southern Gulf of St. Lawrence, enlarged at left. Black circles represent the stations sampled during the annual mackerel egg survey

find enough food to grow and survive. For these species, larval development rate and survival are strongly dependent upon the timing and magnitude of plankton blooms (Castonguay, Plourde, Robert, Runge, & Fortier, 2008; Starr, Himmelman, & Therriault, 1990; Welker, Pierce, & Wahl, 1994). Synchrony between the larval period and peaks of plankton production can increase the likelihood that larvae encounter sufficient food and thus maximize survival to the juvenile stage (match–mismatch hypothesis; Cushing, 1969, 1990). The observed warming of the oceans has shifted the phenology of plankton blooms, which now occur earlier in the year than they did in the past (Hays, Richardson, & Robinson, 2005; Winder & Sommer, 2012). Few studies to date have explored climate change effects on the phenology of larvae in marine species; however, shifts in phenology have been reported for some fishes (e.g. Asch, 2015; Murphy, Pepin, & Robert, 2018) and invertebrates (e.g. Koeller et al., 2009; Moore, Thompson, & Hawkins, 2011). Consumer species that cannot adjust their phenology to that of plankton may be subject to mismatches with their main food source, potentially leading to lower survival during the larval phase and therefore reduced recruitment (Beaugrand, Brander, Lindley, Souissi, & Reid, 2003; Edwards & Richardson, 2004; Thackeray et al., 2010).

Ocean warming can also have a direct effect on survival of larvae by influencing their metabolic and growth rates. Within their normal temperature range, larvae generally exhibit faster growth and development with increasing temperature (O'Connor et al., 2007). A shortened planktonic phase may be beneficial for larvae as it decreases time spent in the high-risk pelagic environment, thus increasing their probability of survival. However, prolonged exposure to relatively high temperatures may also be deleterious to larvae. Indeed, species tolerance to temperature is typically a dome-shaped relationship, where survival rate increases with temperature up to an optimum and then decreases with further increase in temperature (Pörtner & Peck, 2011). Therefore, the current warming of oceans can potentially generate thermal stress in a wide range of marine organisms at the centre and lower latitudes of their distribution range, particularly in shelf and pelagic zones.

Stenothermic species are expected to be among the most vulnerable to climate change (Beaugrand, 2015; Somero, 2010). The snow crab (*Chionoecetes opilio*), for example, is a marine decapod crustacean that tolerates only a narrow range of cold temperatures in its benthic phase and should thus be very sensitive to warming (Chabot, Guénette, & Stortini, 2013; Dionne, Sainte-Marie, Bourget, & Gilbert, 2003; Foyle, Odor, & Elner, 1989). Snow crab supports one of the most important, but also one of the more variable, commercial fisheries of the north Atlantic and north Pacific (FAO, 2017). In many portions of the snow crab distribution range, populations undergo wide circa-decadal swings in abundance due to highly variable recruitment, and this variability appears to be largely driven by processes that affect the production and survival of the early life stages (Caddy, Wade, Surette, Hebert, & Moriyasu, 2005; Sainte-Marie, Sévigny, Smith, & Lovrich, 1996; Zheng & Kruse, 2006). Over the past 15–30 years, these high-frequency oscillations have become attenuated in some snow crab populations (e.g. Gulf of St. Lawrence, GSL; eastern Bering Sea) and/or progressive or rather sudden declines in the level of recruitment have become apparent (e.g. Newfoundland and Labrador Shelf). These changes have been attributed to a decrease in larval abundance/survival and settlement intensity, presumably due to direct or indirect temperature effects (Émond, Sainte-Marie, Galbraith, & Bêty, 2015; Ernst, Armstrong, Burgos, & Orensanz, 2012; Mullowney, Dawe, Colbourne, & Rose, 2014; Szuwalski & Punt, 2013).

Snow crab larval abundance and supply to benthic habitat could be affected by climate warming in more than one way. Hatching of snow crab larvae occurs in spring (Incze, Armstrong, & Smith, 1987; Sainte-Marie, 1993), seemingly coincident with the phytoplankton and microzooplankton blooms on which *Chionoecetes* larval zoeae feed (Incze & Paul, 1983; Starr, Therriault, Conan, Comeau, & Robichaud, 1994). Climate-induced shifts in plankton phenology could reduce survival of snow crab larvae if hatching no longer occurs synchronously with the plankton bloom (Dawe, Parsons, & Colbourne, 2008; Somerton, 1982; Szuwalski & Punt, 2013). The survival rate may also decrease if surface water temperatures exceed the thermal optimum for zoeae, either from direct physiological stress (Yamamoto, Yamada, Fujimoto, & Hamasaki, 2014) or from malnutrition due to active selection of deeper (colder), but less nutrient-rich waters (Ouellet & Sainte-Marie, 2018). On the other hand, a decrease in larval abundance and settlement may result from reduced overall larval production (Émond et al., 2015) or declining supply of megalopae caused for example by changes in the spatial distribution of larval production and megalopa settlement (Parada, Armstrong, Ernst, Hinckley, & Orensanz, 2010). Warmer than usual conditions in surface waters are also likely to accelerate larval development (Ouellet & Sainte-Marie, 2018; Yamamoto et al., 2014) and possibly reduce the extent of larval drift and supply to some areas (e.g. Quinn, Chassé, & Rochette, 2017).

In this study, we investigated the interannual variability in phenology and abundance of snow crab larvae in the southern GSL, eastern Canada (Figure 1), based on plankton collections spanning 1982 to 2012. Since the early 1990s, the summer surface water temperature in the GSL has warmed by 0.6°C per decade for 1990–2018 and it is expected that climate change will cause further warming over the next century (Galbraith et al., 2019; Long et al., 2016). We assessed whether a change in the phenology and a reduction of the abundance of snow crab larvae occurred from 1982 to 2012 and we investigated the environmental factors that may have driven observed changes. We also examined whether changes occurred in the larval phenology and abundance of toad crabs (*Hyas* spp.) and in the larval abundance of rock crab (*Cancer irroratus*), which along with snow crab, are the dominant brachyurans in the GSL (Chabot et al., 2007). Since toad crabs are also boreo-arctic species (Christiansen, 1982; Squires, 1990), although less stenothermic than snow crab (Sabean, 2007), we expected this taxon to respond to warming similarly to snow crab. Rock crab, on the other hand, is a temperate and eurythermal species (Bigford, 1979; Squires, 1990) and should instead be positively affected by rising temperature.

2 | MATERIAL AND METHODS

2.1 | Study species

2.1.1 | Snow crab

The snow crab is widely distributed in cold coastal and bathyal waters of the northern hemisphere (FAO, 2017). The duration of egg incubation beneath the mother depends on temperature (Webb, Eckert, Shirley, & Tamone, 2007); in eastern Canada, females brood their eggs for approximately 1 year at <0.75–1°C or for about 2 years at >0.75–1°C (Kuhn & Choi, 2011; Moriyasu & Lanteigne, 1998; Sainte-Marie, Gosselin, Sevigny, & Urbani, 2008). Most mature females in the GSL are distributed at depths where they are exposed to water <1°C and thus have a biennial reproductive cycle (Moriyasu & Lanteigne, 1998; Sainte-Marie, 1993). Hatching has been inferred to peak around mid-May in the GSL (Conan et al., 1996; Sainte-Marie, 1993), but may be spread over a period of up to 3 months in at least some Atlantic Canadian regions (Kuhn & Choi, 2011). The larval phase, consisting of 2 zoeal stages and 1 megalopa stage, was reported to last a total of at least 3–5 months in the GSL after which settlement and metamorphosis to the first benthic stage occur (Lovrich, Sainte-Marie, & Smith, 1995; Ouellet & Sainte-Marie, 2018). Water temperature may strongly influence the development and survival rates of larvae. Laboratory studies showed that larval stage duration of snow crab decreased exponentially with increasing temperature (Ouellet & Sainte-Marie, 2018; Yamamoto et al., 2014), and that relative survival was highest at temperatures of about 10.8°C for the zoea I, 9.5°C for the zoea II and 8.7°C for the megalopa (Ouellet & Sainte-Marie, 2018).

2.1.2 | Toad crabs

Toad crabs are widespread on both sides of the North Atlantic Ocean (Pohle, 1991). In the southern GSL, two species of toad crabs coexist, *Hyas araneus* (also known as the spider crab) and *H. coarctatus* (Squires, 1990). Like snow crab, *H. araneus* may brood eggs for 1 or 2 years depending on temperature (Petersen, 1995). Hatching times for toad crabs are not well specified in eastern Canada; however, in northern Europe, *H. araneus* larvae are released in spring and early summer and spend from one to several months in the plankton (Anger, 1983). Larvae go through 2 zoeal stages and 1 megalopa stage before settling on the bottom (Pohle, 1991). Growth and survival of toad crab larvae are also temperature-dependent; stage durations are inversely related to temperature and maximum survival rates occur at temperatures of 6–12°C (Anger, 1983, 1984).

2.1.3 | Rock crab

Rock crab is widely distributed along North America's east coast; its range stretches as far north as Labrador, Canada, and reaches southward to South Carolina, USA (Bigford, 1979; Squires, 1990). One of the reasons for the extensive distribution of rock crab is its tolerance to a wide range of temperatures and salinities (Bigford, 1979). Rock crab is pervasive and abundant in shallow waters of the southern GSL (Robichaud & Frail, 2006). The egg incubation period there lasts approximately 10 months (DFO, 2013). Larvae are released in early summer and go through 5 zoeal stages and 1 megalopa stage before settling to the bottom in mid-September (DFO, 2013; Scarratt & Lowe, 1972). Rock crab larvae are eurythermal and their survival rate in the laboratory was maximized at 15–24°C with appropriate salinity (Johns, 1981; Sastry, 1977).

2.2 | Study area and sampling

Abundance indices of snow crab, toad crab and rock crab larvae were estimated from the annual mackerel egg survey conducted by the Department of Fisheries and Oceans Canada in the southern GSL (Grégoire, Girard, & Boudreau, 2014). Starting in early to late June of each year since 1982, except 1995 and 1997 (no survey), sampling was carried out for 7 to 13 consecutive days over a grid of 66 fixed stations located between longitudes 66°07′ and 60°45′W and latitudes 45°49′ and 48°49′N (Figure 1). However, due to various logistic issues, the number of stations sampled over the study period varied from 46 to 66 annually. Plankton samples were collected at each station using a 61-cm-diameter bongo gear fitted with two 0.333-mm mesh nets and a General Oceanics^{TM} flowmeter to estimate the volume of water filtered. Bongo tows generally lasted 10 min and were made following a saw-tooth pattern between the surface and a maximum depth of 50 m, or down to 5 m from the bottom at shallower stations. This sampling depth range fully encompasses the known vertical distribution of the zoeal stages of snow crab and toad crabs, but only partially covers the vertical distribution of the megalopa stage (Ouellet & Sainte-Marie, 2018). On recovery, the bongo nets were rinsed to the cod end, and plankton samples were immediately preserved in a 4%–5% formalin seawater solution.

Preserved samples were taken to the Maurice Lamontagne Institute, where all larvae of snow crab, toad crabs and rock crab from a fraction (1/512 to 1/2, varied according to a rough estimation of the number of larvae in the samples) or the entirety of each sample were sorted and enumerated using a dissecting microscope. The resulting total number of larvae was 171,991 for snow crab, 33,376 for toad crabs and 46,793 for rock crab. Larvae of each taxon and stage were identified according to the criteria of Roff, Davidson, Pohle, and Dadswell (1984), Davidson and Chin (1991), and Pohle (1991). Our ability to effectively distinguish the similarly looking zoea I of snow crab and toad crabs (Davidson & Chin, 1991; Pohle, 1991) was confirmed by microsatellite analysis of specimens we identified from a mixture of larvae from both taxa (Éric Parent, Maurice Lamontagne Institute, pers. comm.). Toad crabs and rock crab were not sorted in 1983–1985, and the two species of toad crab (*Hyas araneus* and *H. coarctatus*) as well as the various zoea stages of rock crab were never distinguished. Numbers of larvae for each combination taxon-larval stage at each station were standardized to abundance per m^3 of water filtered and then converted into abundance per m^2 considering the maximum sampled depth.

2.3 | Constructing abundance and phenology indices

We interpolated the abundances per m^2 of each combination taxon-larval stage (except for rock crab, see previous section) at each sampling station to the entire study area using local ordinary kriging. For each year, a semivariogram, which describes the variability between pairs of observations as a function of the distance separating these observations, was estimated from the data by the method of moments. Omnidirectional semivariograms were used because no anisotropy was found when we computed experimental semivariograms in four different directions. Exponential and spherical theoretical semivariogram models were fitted to each empirical semivariogram using a weighted least-squares method, and in all cases, the spherical model gave the best fit. The spherical semivariogram models were used to predict the larval abundance per m^2 of snow crab, toad crabs (in both cases: zoea I, zoea II and megalopa separately) and rock crab (zoeae and megalopa separately) in each 3.4 × 4.2 km cell of a grid covering the whole study area using the kriging procedure. Only stations within a distance of 50 km from each grid cell were used for kriging.

In order to examine the interannual variability and longer-term trends in the larval abundance of snow crab, toad crabs and rock crab, we estimated an annual index of abundance by m^2 for each taxon by simply averaging the interpolated total (all stages) larval abundance by taxon in each grid cell. Annual indices of larval abundance of snow crab and toad crabs were also estimated in the same way for zoea I, zoea II and megalopa separately.

A larval phenology index was calculated for snow crab and toad crabs based on the proportions of zoea I by taxon in each year. The proportional contribution of zoea I to abundance of all larvae of snow crab or toad crabs was calculated for each grid cell and averaged over the whole study area to obtain the phenology index. Phenology indices ranged from 0 to 1, with low and high index values indicating, respectively, early or late phenology. No larval phenology index was estimated for rock crab, because individual zoeal stages were not identified.

2.4 | Climate and biotic variables

The explanatory environmental variables used to model variations in the phenology indices of snow crab and toad crabs included the timing of ice retreat (1982–2015) and temperature indices for the cold intermediate water layer (CIL, 1982–2012) and surface water layer (1985–2012). The day of year of ice retreat was estimated by Galbraith et al. (2016) from digitized charts of ice cover obtained from the Canadian Ice Service. The CIL temperature index was developed by Gilbert and Pettigrew (1997) and is defined as the mean of the CIL minimum core temperatures (in °C) observed in the GSL between 1 May and 30 September of each year, adjusted to 15 July. The CIL index was updated by Galbraith et al. (2016) using all available temperature profiles measured within the Gulf between May and September inclusively. We assume this index to be representative of the temperature during late egg incubation before larvae are released, because most ovigerous snow crab and toad crab females in the southern GSL are found at depths corresponding to the CIL (Moriyasu & Lanteigne, 1998; B. Sainte-Marie, pers. comm.). Surface water temperature was calculated by Galbraith et al. (2016) using National Oceanic and Atmospheric Administration Advanced Very High Resolution Radiometer satellite images, available at 1 km resolution from the Maurice Lamontagne Institute remote sensing laboratory. Surface temperatures are representative of the surface mixed layer in which snow crab and toad crabs spend their zoeal life (Ouellet & Sainte-Marie, 2018). Average surface temperatures were calculated for the months of May and June, which is the period of larval development covered in this study.

The explanatory environmental variables used to model variations in the larval abundance indices of snow crab, toad crabs and rock crab were the timing of ice retreat and surface water temperature in

May–June. Additionally, but for snow crab only, we also tested the effects of female spawner abundance on the larval abundance using an index of larval production. Data on female spawner abundance were derived by Hébert et al. (2011) and Hébert, Wade, DeGrâce, and Moriyasu (2015) for the period 1988–2012 (except 1996) from a bottom trawl survey conducted by the Department of Fisheries and Oceans that covers the southern GSL snow crab habitat. Adult females recorded as primiparous during the survey were not included in the estimation of the spawner abundance index as they do not contribute to larval production in the survey year, so we considered only females recorded as multiparous (thus including primiparous females releasing larvae in the survey year). Using the linear regression of fecundity (i.e. number of eggs per brood) on carapace width (CW) estimated by Sainte-Marie (1993) for multiparous females in the northwest GSL ($\log_{10}$ fecundity = 2.616 $\log_{10}$ CW + 0.062), we calculated potential fecundity for one female at the annual mean CW of multiparous females (recorded during the survey) in each year and multiplied the fecundity estimate by the abundance of multiparous females in each year to obtain total female population fecundity. The index of larval production was then obtained by halving total fecundity to reflect the assumed biennial reproductive cycle. Data on female spawner abundance were not available for toad crabs and rock crab.

The timing of ice retreat was used as a proxy for the timing of the spring bloom and for larval food availability (data on the characteristics of the spring bloom in the southern GSL were available only from 1998 to 2015). Studies have shown that the timing of the spring bloom is strongly linked to the timing of ice retreat (Le Fouest, Zakardjian, Saucier, & Starr, 2005; Wu et al., 2007). We found a moderate positive correlation between the timing of ice retreat and the day of start of the spring bloom from 1998 to 2015 in the study area ($r = .61$, $p = .006$; Figure S1a), indicating that an early ice retreat results in an earlier bloom onset. In the GSL, spring bloom magnitude has also been linked to the timing of ice retreat (Le Fouest et al., 2005). We found that the magnitude of the spring bloom in the study area during the 1998–2015 period was negatively correlated with the timing of ice retreat ($r = -.67$, $p = .002$; Figure S1b), indicating that an early ice retreat leads to a more intense bloom, and therefore to a higher availability of food for larvae.

2.5 | Data analysis

Pearson correlation coefficients (r) were calculated between phenology indices of snow crab and toad crabs and also between abundance indices of all three crab taxa. Temporal trends in both phenology and abundance indices were assessed using linear regression models with sampling year as a predictor variable. Median date of sampling (ordinal date) was included in the trend analysis of the phenology indices, because we expected some variation in the phenology index to be associated with differences in sampling time. Likewise, the phenology index was included in the trend analysis of the abundance indices of snow and toad crab larvae to incorporate potential interannual variations in release time and development rate. The regression models were fitted to the data with the ordinary least-squares method, but if the presence of autocorrelated residuals was detected (using a Durbin–Watson test), a generalized least-squares method allowing for correlation among residuals was used instead. The modified Mann–Kendall test for autocorrelated data (Santander Meteorology Group, 2012) was used to detect significant temporal trends in the explanatory variables used in fitting the generalized additive models (see below).

Spectral analysis was performed to detect periodicity in the total larval abundance indices of snow crab, toad crabs and rock crab. Abundance indices were smoothed using locally weighted regression (LOESS) prior to analysis to reduce random noise and make long-term fluctuations stand out more clearly (Ao, 2010). We first calculated the Lomb–Scargle periodogram, which produces better results on unevenly spaced data (i.e. no survey in 1995 and 1997) than the classical Fourier transform method (Ruf, 1999). We then estimated the statistical significance of the periodogram maximum (peak) based on the null hypothesis of an Ornstein–Uhlenbeck state-space process using the peacots R package (Louca & Doebeli, 2015), instead of using the classical white noise null hypothesis. Using white noise as a null hypothesis greatly increases the false cycle detection rate (type I error) and can lead to erroneous conclusions (Louca & Doebeli, 2015).

After an initial data exploration following the protocol outlined in Zuur, Ieno, and Elphick (2010), we ran generalized additive models (GAMs) to identify which variables most closely correlate with larval phenology of snow crab and toad crabs, and with larval abundance. GAMs are a flexible class of statistical models which allow for nonlinear relationships between a set of potential explanatory variables and the dependent variable (Wood, 2006). Thin plate regression splines were used to represent the (possibly) nonlinear effect of the environmental variables. The maximum degree of smoothing allowed was 3 to avoid unrealistic patterns in the explanatory variables and to reduce overfitting. The phenology indices were modelled using a beta distribution with a logit link function, while the abundance indices were modelled using a Gaussian or Gamma distribution and a logarithmic link function.

We used Akaike's information criterion corrected for small sample sizes (AICc) to compare and evaluate a set of candidate GAMs (Burnham & Anderson, 2002). Although variables were selected based on a priori hypotheses, model selection was performed on all possible subsets of the environmental variables described above (Tables S1 and S2). In the case of snow crab only, we tested 3 alternative hypotheses to explain variations in larval abundance: driven by environment only, driven by larval production only, and driven by the additive effect of environment and larval production. Median sampling date was included as a linear term in all the candidate models of phenology indices to account for the differences in sampling time among years. Similarly, to account for the positive influence of phenology on abundance (see results), we included the phenology index as an offset within each candidate model of the larval abundance indices of snow crab and toad crabs. In each candidate model set, the most parsimonious model within 2 AICc units of the lowest AICc score with the highest explained deviance was considered the best model supported by the data (Tables S1 and S2). When timing of ice retreat was selected in the best model, we reran that model using the direct measurements of the spring bloom (i.e. day of start or magnitude for the period 1998–2012) instead of the timing of ice retreat to see if the spring bloom had a significant effect. Because the two models (i.e. with timing of ice retreat or direct measurements of the spring bloom) did not cover the same time period, we reran the model with timing of ice retreat but only for the 1998–2012 period to be able to compare the explanatory power of the variables. All analyses were carried out using R 3.3.1 (R Development Core Team, 2016).

3 | RESULTS

3.1 | Larval phenology and abundance

The larval phenology indices of snow crab and toad crabs in the southern GSL were characterized by great variability during the 30-year study period. The average proportion of zoea I was as low as 0.06 in 2006 for both taxa, and as high as 0.98 in 1987 and 0.97 in 1982 for snow crab and toad crabs, respectively (Figure 2). The phenology indices of snow crab and toad crabs varied similarly over time: the two indices were highly correlated with each other ($r = .86$, $p < .001$) and both exhibited a significant negative trend over the years (Table 1). The average rate of phenological change was also similar between snow crab and toad crabs, as the slope of the relationship between phenology index and year of sampling did not differ between the two taxa ($t = -0.01$, $p = .996$; Table 1). Also, there was a negative relationship between the phenology index and sampling date (Table 1), which is not surprising because later sampling allows more time for larval development, all other things being equal. Megalopae of snow crab were found only in 2006 ($n = 14$) and 2008 ($n = 1$), while megalopae of toad crabs were found in 2006 ($n = 35$), 2007 ($n = 13$), 2008 ($n = 2$), 2010 ($n = 4$) and 2012 ($n = 16$). Megalopae represented <1% of all oregoniid larvae enumerated each year in samples, except in 2006 when they represented 16% and 44% of larvae of snow crab and toad crabs, respectively (sampling in 2006 started later than usual and this was also the year with the warmest surface waters of the time series). Larval phenology indices were low to average in years of megalopae presence (Figure 2). Megalopae of rock crab were found only in 2006 ($n = 22$) and represented <0.7% of rock crab larvae enumerated in that year.

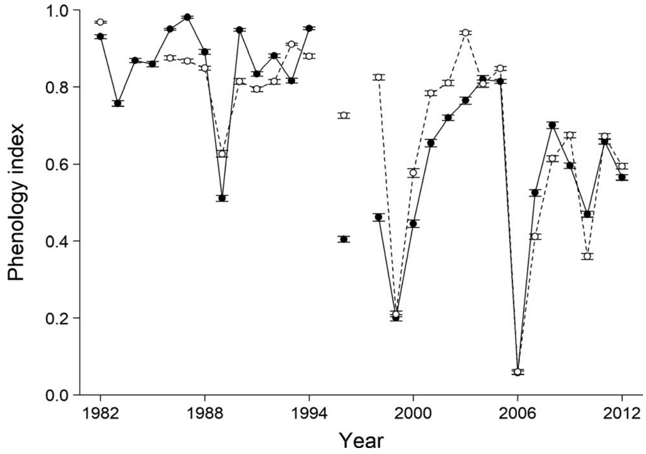

FIGURE 2 Phenology indices of larval snow crab (full line, black circles) and toad crabs (dashed line, white circles) in the southern Gulf of St. Lawrence from 1982 to 2012. Phenology indices were calculated using the proportions of zoea 1 by taxon in each year (see methods) and ranged from 0 to 1, with low and high index values indicating, respectively, late or early phenology. Error bars indicate the 95% confidence interval

The average abundance of larvae over the 1982–2012 time series was 45.8 zoeae per m^2 (zoea I = 33.7/m^2, zoea II = 12.1/m^2 and megalopae = 0.03/m^2) for snow crab, 37.8 zoeae per m^2 (zoea I = 30.6/m^2, zoea II = 7.1/m^2 and megalopae = 0.1/m^2) for toad crabs and 36.7 larvae per m^2 for rock crab (zoea = 36.7 m^2 and megalopae = 0.07 m^2). However, the larval abundance indices of the three crab taxa fluctuated considerably (>80-fold) over the period 1982–2012 (Figure 3). Variation in total larval abundance was positively correlated between snow crab and toad crabs (see Figure 3a,b); however, the relationship was statistically significant only when the exceptionally high 1982 value for toad crabs was excluded ($r = .33$, $p = .097$ with 1982 vs. $r = .76$, $p < .001$ without 1982). Variations in the abundance indices of each zoeal stage were also similar between snow crab and toad crabs, with zoea II ($r = .83$, $p < .001$) being more strongly correlated than zoea I ($r = .39$, $p = .047$ with 1982; $r = .81$, $p < .001$ without 1982). The abundance index of rock crab larvae was not significantly correlated with those of snow crab or toad crab larvae ($r = -.12$ and .05, respectively; $p > .573$; Figure 3c).

Spectral analysis of the smoothed total larval abundance index revealed a significant cycle of ~7.8 years (frequency = 0.13, $p = .023$) in snow crab (Figure 4a,b), while no cycle was found in toad crabs (with or without the 1982 value) and rock crab. Peaks in abundance of snow crab larvae occurred around 1983–1984, 1992–1994, 2000–2002 and 2007–2008 (Figures 3a and 4a). Although we found no statistically significant temporal trend in the larval abundance indices of all three crab taxa, the correlation coefficients had a negative sign for snow crab and toad crabs and a positive sign for rock crab as expected (Table 1). Moreover, the two last peaks of 2000–2002 and 2007–2008 in the total larval abundance index of snow crab were lower than those of 1983–1984 and 1992–1994 (Figures 3a and 4a). We used the criterion of non-overlapping 95% confidence intervals to determine whether there was a statistically significant difference between peaks in the total larval abundance index of snow crab and found that the two last peaks of 2000–2002 and 2007–2008 were significantly different from those of 1983–1984 and 1992–1994 (Figure 3a). Conversely, although the larval abundance index of rock crab did not reveal any significant trend over time, the last peak of abundance (2006–2010) was statistically higher than the previous peaks of 1989–1992 and 1999–2000 (Figure 3c).

TABLE 1 Temporal trends in phenology and abundance indices of larval snow crab, toad crabs and rock crab in the southern Gulf of St. Lawrence from 1982 to 2012

Taxon	Index	Predictor variables	Estimation method	Coefficients (standard error)	*F*	*p*
Snow crab	Phenology	Year	gls	−0.015 (0.006)	7.05	.013
		Sampling date		−0.026 (0.007)	13.57	.001
	Abundance	Year	ols	−0.517 (0.650)	0.63	.434
		Phenology index		43.47 (26.14)	2.75	.109
Toad crabs	Phenology	Year	ols	−0.013 (0.004)	11.40	.003
		Sampling date		−0.026 (0.007)	11.93	.002
	Abundance	Year	ols	−1.355 (1.024)	1.34	.259
		Phenology index		22.18 (33.83)	0.50	.487
Rock crab	Abundance	Year	ols	0.622 (0.547)	1.29	.267

Note: Sampling date represents the median sampling date (day of the year). The models were fitted with generalized least squares (gls) by maximizing the log-likelihood when residuals were serially correlated at a positive lag of 1; otherwise models were fitted with the ordinary least-squares method (ols). Significance level was set to 0.05. A type III (marginal) sum of squares was considered for the *F* tests.

3.2 | Climate and biotic variables

Prior to 1991–1992, timing of ice retreat and surface water temperature were apparently trendless, whereas the CIL was cooling (Figure 5a–c). Afterwards, all three climate variables indicated that the southern GSL was warming. The timing of ice retreat showed a significant negative trend from 1992 on (tau = −0.60, $p < .001$), with ice retreating on average 2 days earlier per year (Figure 5a). For comparison, the actual start of the bloom measured over the period 1998–2012 advanced by an average of 0.5 day per year. The CIL temperature index and surface water temperature also displayed a statistically significant warming trend starting in 1991–1992, with temperatures increasing at an average annual rate of 0.12°C (tau = 0.58, $p < .001$) and 0.06°C (tau = 0.32, $p = .032$), respectively (Figure 5b,c). The timing of ice retreat was negatively correlated with the CIL temperature index ($r = -.61$, $p < .001$) and surface water temperature ($r = -.40$, $p = .035$), while the CIL index and surface temperature were positively correlated with each other ($r = .40$, $p = .037$).

The larval production index of snow crab followed a negative trend over the period 1988–2012 (tau = −0.52, $p < .001$; Figure 5d). Larval production was high during the period 1988–1995, with a maximum reached in 1992, but remained moderately low afterwards with an exceptionally weak value in 2009.

3.3 | GAM analyses

The models best explaining variations in larval phenology, for both snow crab and toad crabs, included the timing of ice retreat and surface water temperature (Table 2). The two variables were highly significant ($p < .002$) and accounted for over 75% of the variation (i.e. deviance) in the phenology indices of both taxa. The phenology of snow crab and toad crabs was positively associated with the timing of ice retreat and negatively associated with surface temperature (Figure 6). We reran the two models for the period 1998 to 2012 after replacing the timing of ice retreat with the timing of the spring bloom. These alternative models accounted for 89.2% and 84.3% of the variation in the larval phenology index of snow crab and toad crabs, respectively (Table S3). Over the period 1998–2012, timing of ice retreat and timing of the spring bloom had similar explanatory power (Tables S3 and S4). As was the case for the timing of ice retreat, spring bloom timing had a significant positive effect on the phenology index of both taxa ($p < .03$; Figure S2). Some of the candidate GAM models that included the CIL temperature index also had a considerable level of empirical support (i.e. ΔAIC < 4, Table S1). In fact, the larval phenology index of snow crab and toad crabs was negatively correlated to the CIL index ($r = -.50$ and −.41, respectively; $p < .03$).

Variation in total abundance of larval snow crab was best explained by the additive effects of climate factors—timing of sea ice retreat and surface water temperature—and larval production; however, only surface temperature was statistically significant at $p < .05$ (Table 3; Table S2). Larval abundance of snow crab increased when ice retreated later than day 110 of the year and decreased at surface temperatures>~8.5°C (Figure 7a,b). Larval production had a positive linear effect on the abundance of snow crab larvae (Figure 7c). After replacing the timing of ice retreat by the magnitude of the spring bloom, the model accounted for 77% of the variation in the abundance index of snow crab larvae over the period 1998–2012 (Table S5). The magnitude of the spring bloom had a significant effect ($p = .050$), with abundance of snow crab larvae increasing at a chlorophyll a concentration>~75 mg/m^2 (Figure S3). Timing of ice retreat and magnitude of the spring bloom had similar levels of explanatory power over the period 1998–2012 (Tables S5 and S6).

The final GAMs for toad crabs and rock crab explained only 18.9%–24.2% of variation in total larval abundance (Table 3), but larval production was not available as an explanatory factor. Only surface water temperature was selected as best explaining the variations in larval abundance of these two taxa (Table 3). However, toad crabs and rock crab responded in opposite ways to variation in temperature: larval abundance of toad crabs followed a pattern similar to that of snow crab and was negatively impacted by surface

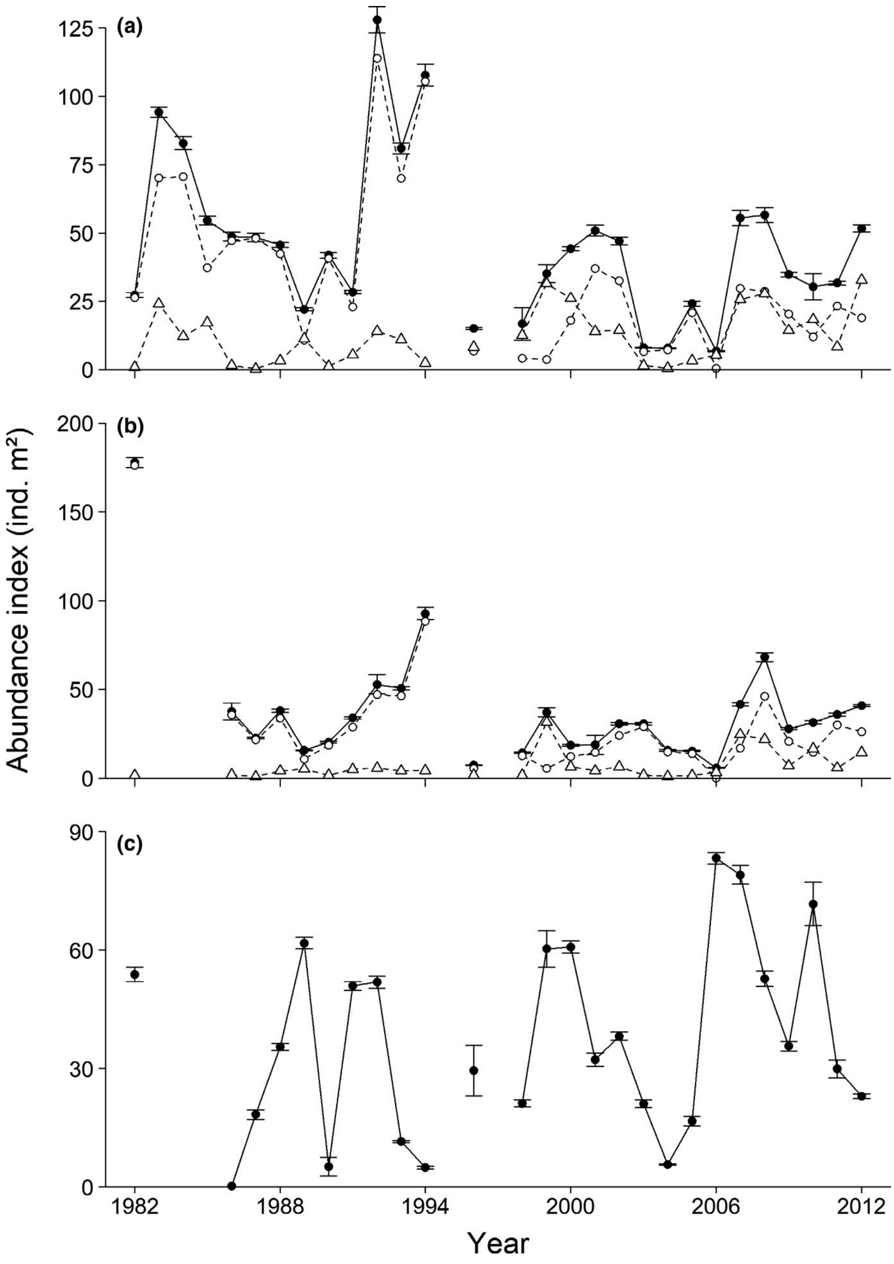

FIGURE 3 Total larval abundance indices (full line, black circles) of snow crab (a), toad crabs (b) and rock crab (c) in the southern Gulf of St. Lawrence from 1982 to 2012. Error bars indicate the 95% confidence interval based on the variance of the estimation of the kriged biomass. Zoea I (dashed line, white circles) and zoea II (dashed line, white triangles) are also shown separately for snow crab and toad crabs

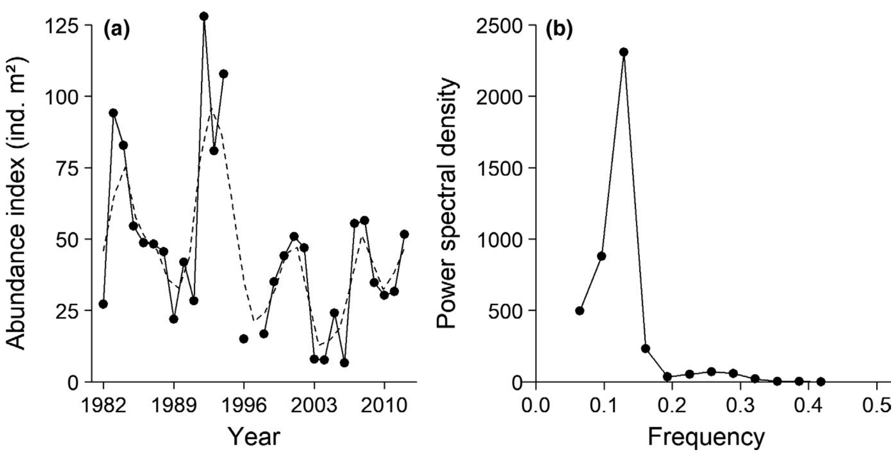

FIGURE 4 (a) Raw (full line) and smoothed (dashed line) total larval abundance index of snow crab in the southern Gulf of St. Lawrence, 1982–2012. (b) Lomb–Scargle periodogram of the smoothed total larval abundance index of snow crab showing a clear peak at a frequency of 0.13 (period = ~7.8 years)

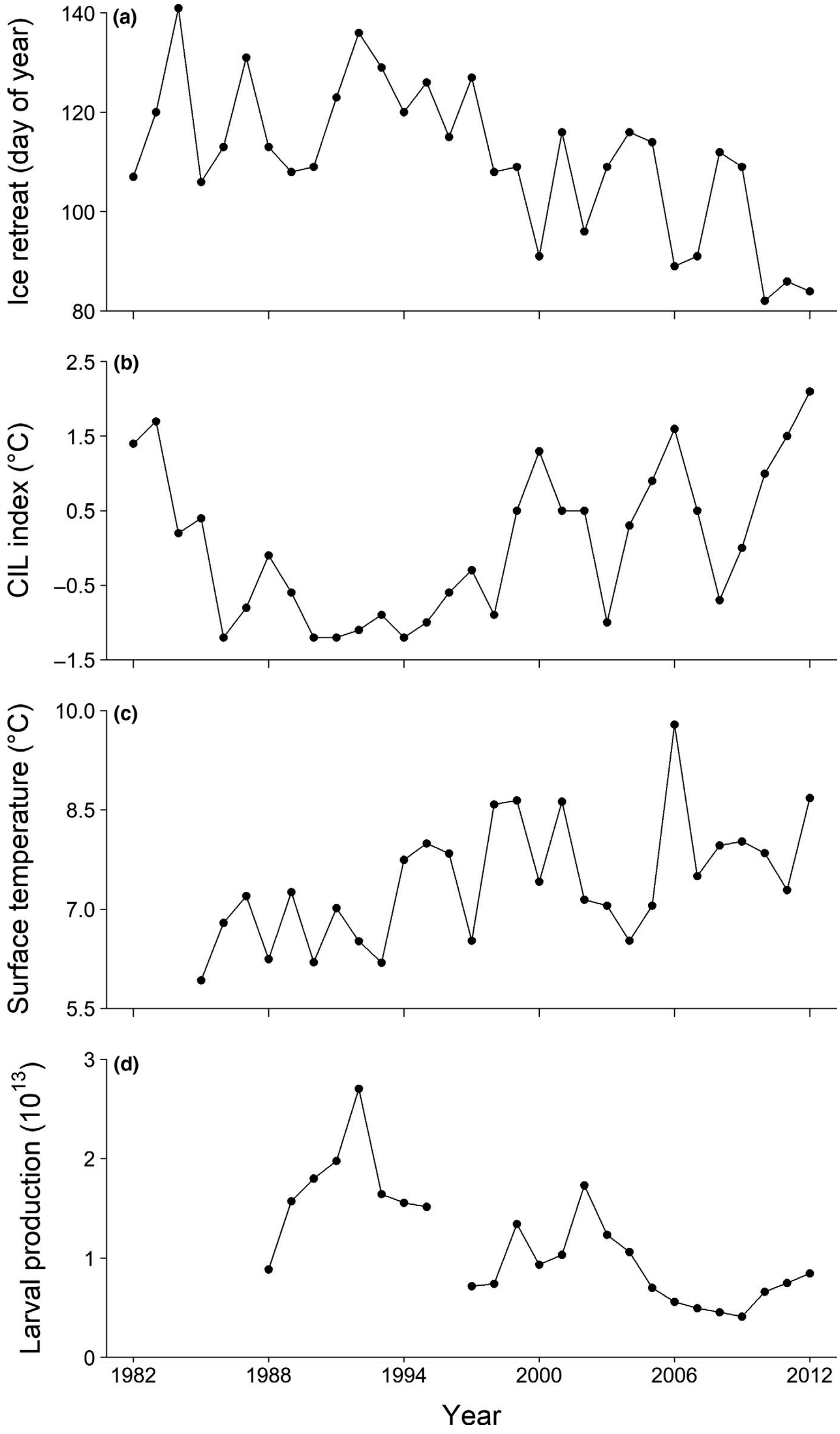

FIGURE 5 Variables used in GAM analysis to explain variation in larval phenology and abundance indices of snow crab, toad crabs and rock crab: (a) the day of year of ice retreat, (b) the CIL temperature index developed by Gilbert and Pettigrew (1997) and updated by Galbraith et al. (2016), (c) the mean surface water temperature in May–June and (d) the index of snow crab larval production

temperatures warmer than ~8.5°C, while larval abundance of rock crab increased linearly with rising temperature (Figure 7d,e).

4 | DISCUSSION

Climate change has caused marine organisms, including decapod crustaceans, to shift towards earlier phenology (Koeller et al., 2009; Lindley & Kirby, 2010; Richards, 2012). Our study revealed a substantial change in the larval phenology of two predominant brachyurans in the southern GSL during the period 1982–2012 (Figure 2). This change was characterized by an increase in the occurrence of late-stage larvae (i.e. zoea II and megalopae) in plankton samples, suggesting that climate warming modified both the timing of hatch and larval development rate. As expected, only the abundance of rock crab larvae, which tolerate a wider range of temperatures, was

TABLE 2 Final generalized additive models describing the phenology of larval snow crab and toad crabs

Parametric terms					Non-parametric (smoothed) terms					
Variable	Estimate	*SE*	*z*	*p*	Variable	edf	Chi^2	*p*	*N*	% Dev
Snow crab										
Intercept	12.951	5.66	2.286	.022	ICE	1	9.78	.002	26	75.6
Date	−0.071	0.033	−2.139	.032	ST	1	24.84	<.0001		
Toad crabs										
Intercept	19.30	5.218	3.699	.0002	ICE	1.477	15.89	.002	25	78.5
Date	−0.108	0.030	−3.531	.0004	ST	1	12.93	.0003		

Note: Estimated coefficients are shown for parametric terms and estimated degrees of freedom are shown for non-parametric (smoothed) terms. % Dev, deviance explained by the model; date, median sampling date; edf, effective degree of freedom; ICE, timing of ice retreat; *SE*, standard error; ST, surface water temperature.

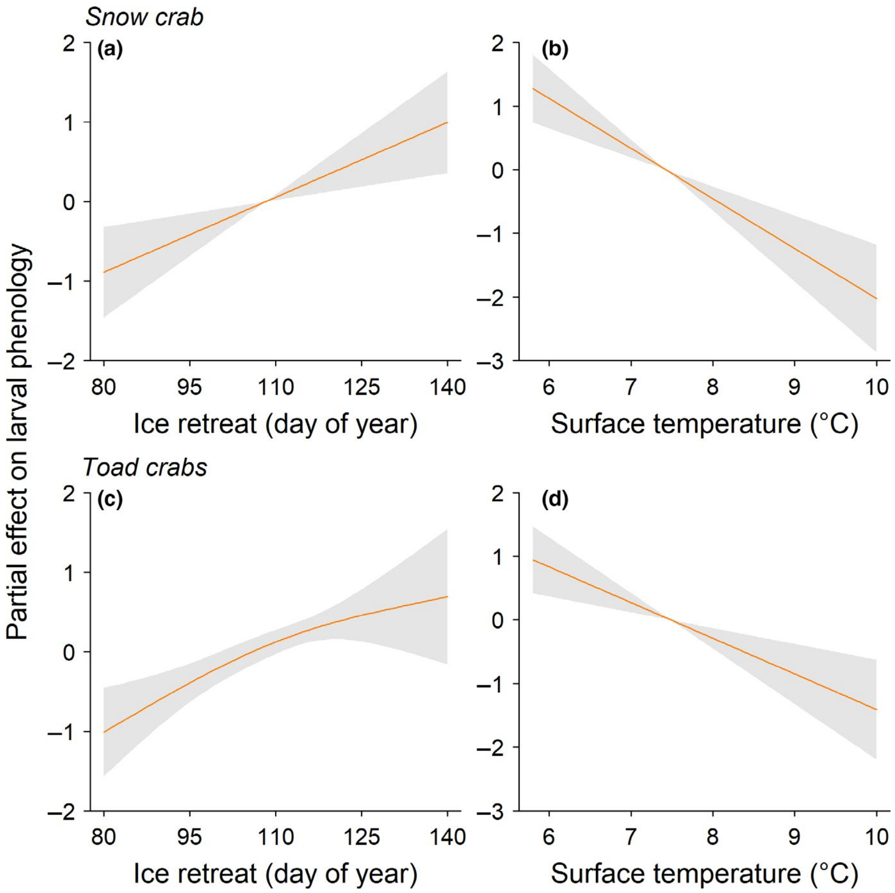

FIGURE 6 Generalized additive model results showing the partial effects of the timing of ice retreat and surface water temperature on the larval phenology index of snow crab (a, b) and toad crabs (c, d). Fitted lines (solid line) and 95% confidence intervals (grey shaded areas) are shown [Colour figure can be viewed at wileyonlinelibrary.com]

positively affected by recent warming, while larval abundance of the stenothermic snow crab and the less stenothermic toad crabs appeared to be negatively affected (Figure 7).

4.1 | Phenology

The larval phenology index of snow crab and toad crabs was positively correlated to the timing of the spring bloom from 1998 to 2012 (Table S3 and Figure S2) and to the timing of ice retreat (a proxy for timing of the spring bloom) over the much longer period 1982–2012 (Table 2, Figure 6). This suggests that the timing of hatch of both taxa is tracking, to some extent, the interannual variability and advancing trend of the spring bloom. The zoea I of *Chionoecetes* and *Hyas* spp. are at least partially dependent for nutrition on microalgae and on the microzooplankton that follows (Incze & Paul, 1983; Meyer-Harms & Harms, 1993), so tracking the spring bloom is likely adaptive. Furthermore, in the case of snow crab, an abundant and high-quality food source may strongly contribute to offset or attenuate the negative effects of GSL surface temperature in May (3.0–7.0°C, Galbraith et al., 2016) during hatch time and initial larval development, which is well below the experimentally determined optimum of 9.1–10.8°C for growth and survival of its zoea I (Ouellet & Sainte-Marie, 2018; Yamamoto, Jinbo, & Hamasaki, 2017).

TABLE 3 Final generalized additive models describing the abundance of larval snow crab, toad crabs and rock crab

Parametric coefficients					Non-parametric (smoothed) terms					
Variable	Estimate	*SE*	*t*	*p*	Variable	edf	*F*	*p*	*N*	% Dev
Snow crab										
Intercept	2.808	0.159	17.66	<.0001	ICE	2.063	2.784	.088	22	73.7
					ST	2.838	4.135	.025		
					LP	1	3.042	.101		
Toad crabs										
Intercept	2.724	0.108	25.24	<.0001	ST	2.694	2.625	.053	25	24.2
Rock crab										
Intercept	3.549	0.135	26.33	<.0001	ST	1	6.101	.021	25	18.9

Note: Estimated coefficients are shown for parametric terms, and estimated degrees of freedom are shown for non-parametric (smoothed) terms. The phenology index was included as an offset within each model.

% Dev, deviance explained by the model; edf, effective degree of freedom; ICE, timing of ice retreat; LP, index of larval production.; SE, standard error; ST, surface temperature.

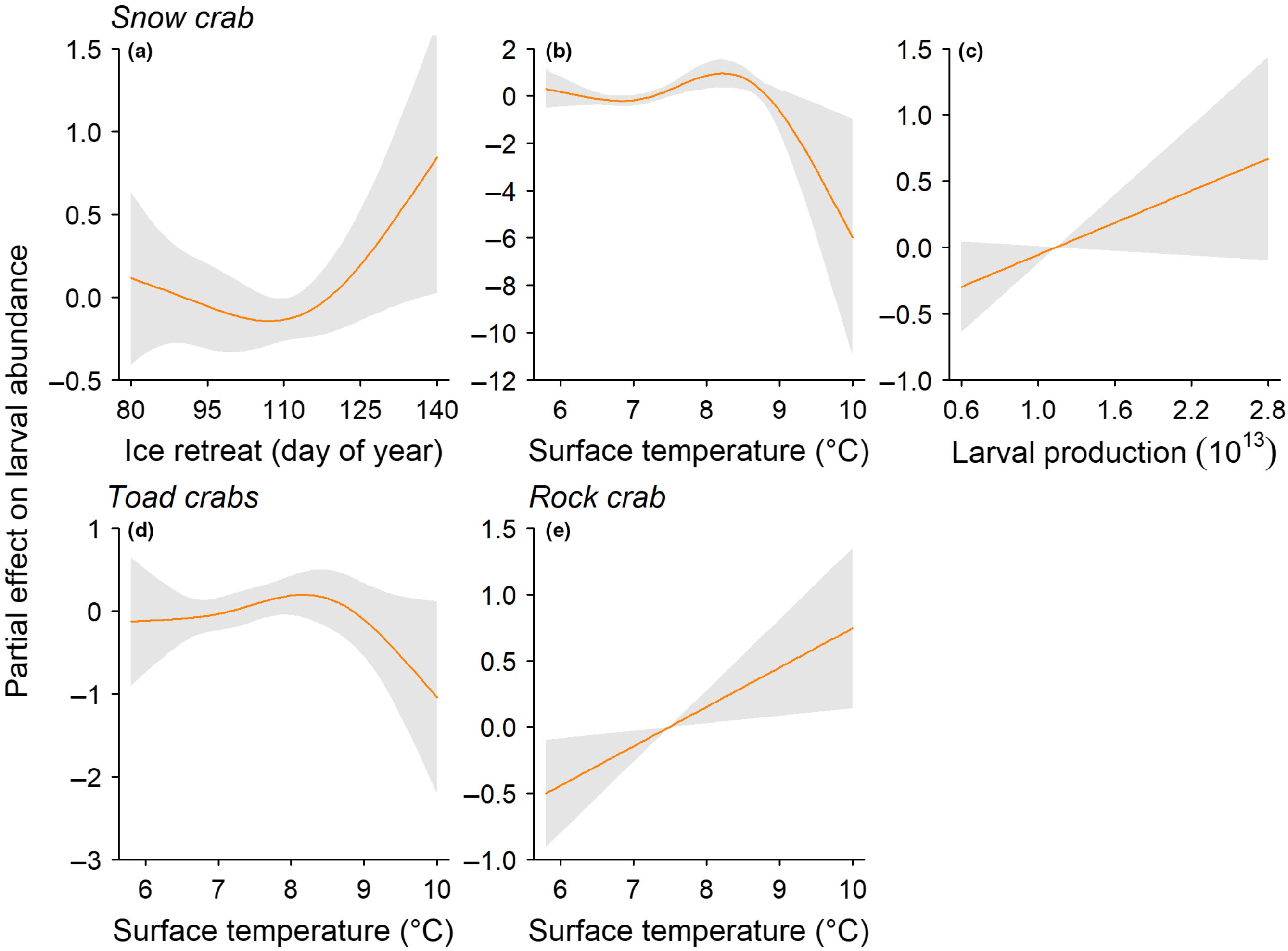

FIGURE 7 Generalized additive model results showing the partial effects of the timing of ice retreat, surface water temperature and larval production index on the larval abundance index of snow crab (a-c), and of surface water temperature on larval abundance indices of toad crabs (d) and rock crab (e). Fitted lines (solid line) and 95% confidence intervals (grey shaded areas) are shown [Colour figure can be viewed at wileyonlinelibrary.com]

The process by which snow crab (and toad crabs) could adjust hatch time to spring bloom is uncertain. Larval hatching in snow crab appears to be under endogenous (embryo) control (Kuhn, Graham, & Choi, 2011), but the cue for hatching remains elusive. Starr et al. (1994) provided some evidence that sinking, senescent phytoplankton cues larval release for snow crab in the GSL, potentially allowing for direct/

phased coupling between the two events. However, Kuhn et al. (2011) refuted this possibility for snow crab on the Scotian Shelf (Figure 1) and suggested, instead, that hatching may be cued by hydrostatic pressure or faster currents associated with spring high tides (also see Stevens, 2003), or triggered by internal embryo pressure or biochemical signals linked to development. Spring tides are not a good candidate cue for matching hatch time to spring bloom, because their occurrence is not correlated to time of spring bloom (or ice retreat). Notwithstanding the need to further explore the hypothesis of a direct phytoplankton cue for larval release, one possibility consistent with an internal trigger for larval release is that spawning time has evolved according to regional (basin-scale) long-term average bottom temperatures to make hatch and bloom times coincide, as seems to be the case for the northern shrimp *Pandalus borealis* (Koeller et al., 2009). Indeed, development rate in later-stage embryos of snow crab is directly related to incubation temperature, such that embryos mature and become competent for hatching sooner in warmer than in colder water (Moriyasu & Lanteigne, 1998; Webb et al., 2007). In our study, CIL temperature during late egg incubation was negatively correlated with both timing of ice retreat and the larval phenology indices of snow crab and toad crabs, suggesting that these two taxa may also have adapted their spawning times to bottom temperatures in order to match hatching with optimal food supply for larvae. Although there is some evidence of adjustment to the timing of the bloom, we cannot say with our data how effective this adjustment is at tracking the change in phenology of the bloom.

The negative trend between surface water temperature and the larval phenology index of snow crab and toad crabs found in our study (Table 2, Figure 6) very likely reflects temperature-induced changes in the duration of their larval stages (O'Connor et al., 2007). Warmer temperatures increase metabolic and growth rates, which can lead to shorter stage durations (Fisher, 2006), as demonstrated in snow crab (Ouellet & Sainte-Marie, 2018; Yamamoto et al., 2014) and toad crabs (Anger, 1983, 1984). Based on a mean warming of surface temperature of ~1.4°C in our study area over the period 1991–2012 and the larval development regressions from Ouellet and Sainte-Marie (2018), the durations of snow crab zoea I and zoea II stages are expected to have decreased from ~43 to 35 days and from ~44 to 36 days, respectively, for an overall average decline of ~16 days. Thus, more recently, a greater proportion of larvae hatching around mid-May, the known period of peak larval release in the GSL during the 1990s (Conan et al., 1996; Sainte-Marie, 1993), would be expected to reach the zoea II stage by the time of our June surveys. Also, the presence of megalopae only in the plankton samples from 2006 to 2012 further supports the idea that snow crab and toad crab larvae have recently been developing faster due to higher temperatures.

4.2 | Abundance

The larval abundance of snow crab fluctuated periodically over the study period with peaks recurring approximately every 8 years (Figure 4). This 8-year period is the same as the cycle length previously reported for snow crab in the northwest GSL (Émond et al., 2015; Sainte-Marie et al., 1996) and is similar to the 7-year cycle reported for the eastern Bering Sea (Ernst et al., 2012). Moreover, our analysis provides evidence for the existence of synchrony among snow crab populations in the GSL. Peaks in larval abundance in our study (1983–1984, 1992–1994, 2000–2002 and 2007–2008) were fully coherent with the peaks in the abundance of age 0^+ snow crabs in Baie Sainte-Marguerite (Figure 1) in the northwest GSL (1993, 2001 and 2008; Émond et al., 2015), suggesting basin-scale (GSL) synchrony in larval supply. This result is consistent with findings from Puebla et al. (2008), showing that snow crab within Atlantic Canada from southern Labrador to Nova Scotia had no significant genetic spatial structure, and it indicates high connectivity among populations through larval dispersal. The synchronicity between snow crab larval abundance measured in the southern GSL and inferred in the northern GSL could also be reinforced by a Moran effect, that is due to spatially correlated extrinsic effects such as weather, food availability or predation intensity (Liebhold, Koenig, & Bjørnstad, 2004). Indeed, Colton, Wilberg, Coles, and Miller (2014) suggested that the synchrony between the blue crab (*Callinectes sapidus*) populations along the U.S. east coast resulted from a combination of both larval dispersal and a Moran effect due to the position of the north wall of the Gulf Stream or winter temperature. In this study, surface temperature may be in part responsible for the synchrony between the northern and southern GSL as it is an important driver of snow crab larval abundance or recruitment in both areas (Émond et al., 2015).

The warming trend observed in the study area since the early 1990s (Figure 5) appears to have been at least partly responsible for the observed decline in the larval abundance of snow crab from 1992 to 2006 (Figure 3). Surface temperature >8.5°C had a negative influence on the larval abundance of snow crab (Figure 7). Warmer surface waters may have been physiologically unfavourable for larvae, resulting in poorer larval growth and survival (Émond et al., 2015; Yamamoto et al., 2014). Timing of ice retreat, used as a proxy for the magnitude of the spring bloom, was also selected in the best model explaining variations in the abundance index of snow crab larvae (although not statistically significant at $p < .05$, Table 3). Sea ice extent may have an indirect effect on larval survival by affecting the magnitude of the spring bloom (Szuwalski & Punt, 2013). Ouellet et al. (2011) found that larval survival of northern shrimp was higher during years when the phytoplankton bloom attained higher concentrations of chlorophyll a. In our study, however, snow crab larval abundance was higher when ice retreat was late and bloom magnitude was relatively low (Figure 7). Although late ice retreat results in a bloom of lower intensity, it could be associated with better food quality for crabs. Sommer and Lengfellner (2008) found that higher temperatures (e.g. due to early ice retreats) reduced food quality for copepod zooplankton by shifting the distribution of phytoplankton size towards smaller individuals. The relationship between the abundance of snow crab larvae and the magnitude of the spring bloom showed that abundance was also high at higher levels of bloom magnitude (Figure 7). A high-magnitude bloom may increase food availability and thus still result in good larval survival even if food quality is reduced.

The larval production index, based on the abundance of mature female snow crabs in the study area, was also selected as best explaining the variability in snow crab larval abundance (although not statistically significant at $p < .05$, Table 3). The positive relationship between snow crab larval production and pelagic larval abundance found in this study (Figure 7) is consistent with a previous short-term study linking larval abundance to adult female abundance (Incze et al., 1987) and with a long-term study linking larval production to abundance of the age 0^+ benthic stage (Émond et al., 2015). Larval production in the study area was high during the period 1988–1995, but remained moderately low afterwards, which was consistent with the decrease in larval abundance observed during the second half of the study period (Figures 3 and 5). The larval production index, that is the female spawning biomass, of snow crab displayed a declining trend over the study period that was more apparent than the one seen in the larval abundance index. One possibility for this decline is that the CIL warming sustained since the mid-1990s in the southern GSL may have been particularly disadvantageous to the early benthic stages of snow crab and have, at a lag, reduced subsequent adult female abundance. These early stages are the most stenothermic of all life history stages, with a thermal preferendum in the range of 0–2°C (Dionne et al., 2003). In the eastern Bering Sea, population recruitment success of snow crab was found to differ between warm and cold years due to differences in the size of suitable habitat for larval settlement and the survival of early benthic stages (Parada et al., 2010, 2007). In the southern GSL, the extent of suitable snow crab thermal habitat decreased over the study period and is expected to continue to shrink if climate warming increases (Chassé et al., 2015). Continued warming due to climate change may, therefore, have further detrimental effects on cold-water species such as snow crab as conditions become more and more unfavourable to larval survival and size of suitable settlement habitat decreases.

The warming trend observed in the study area appears to have been favourable to rock crab larvae and moderately unfavourable to toad crab larvae, which are less stenothermic and appear to have a slightly higher thermal optimum than snow crab larvae. The demographic response of local or regional populations of marine species to an increase (or decrease) in temperature depends on the difference between the local/regional ambient temperature and the optimum/preferendum of the species (Pörtner, 2010). Therefore, species that are at the northern limit of their distribution may increase in abundance, while species that are at the southern limit of their distribution may decrease in abundance as they get close to or above their limit of thermal tolerance (Rijnsdorp, Peck, Engelhard, Möllmann, & Pinnegar, 2009). The positive effect of water temperature on abundance of rock crab larvae is consistent with experimental studies showing highest survival rates of larvae at warmer temperatures for rock crab (Johns, 1981; Sastry, 1977) than for snow crab and toad crabs (Anger, 1983, 1984; Ouellet & Sainte-Marie, 2018).

In summary, this study provided evidence that snow crab and toad crab larvae exhibited a shift towards earlier phenology during the period 1982–2012 in the southern GSL in response to climate warming. This change likely resulted from both a shift in the timing of hatch and accelerated larval development. The warming trend appears to have been unfavourable to snow crab, which is the most cold-specialized and stenothermic of the crab taxa examined in this study. On the other hand, the warming trend appears to have been beneficial for rock crab. As cold-water species decline, species that have an increased capability to tolerate higher temperatures, such as rock crab, may become more common. Though we found a significant shift in the larval phenology of snow crab and toad crabs, the methodologies used in this study did not allow us to determine which of advancing larval release and faster larval development was most important to the phenological change. Distinguishing the relative role of these two processes would allow us to better understand and predict the impacts of climate change on snow crab and toad crab abundance.

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

AUTHOR CONTRIBUTIONS

All authors conceived the study. KE made substantial contributions to acquisition of data, analysis and interpretation of data. KE drafted the manuscript with input and revisions from BSM and JB.

ETHICAL APPROVAL

The authors confirm that the manuscript has been submitted solely to this journal and is not published, in press, or submitted elsewhere, and that all the research meets the ethical guidelines, including adherence to the legal requirements of the study country.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request with permission of Fisheries and Ocean Canada.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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