BIODIVERSITY RESEARCH

Elevated seasonal temperatures eliminate thermal barriers of reproduction of a dominant invasive species: A community state change for northern communities?

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Abstract

Aim: Couple field and modelling studies to evaluate the effects of rising water temperature on reproduction of a dominant marine species and how temperature induced changes in a species' phenology may affect fouling communities that occur along a temperature gradient.

Location: North western Atlantic.

Methods: We examined the interaction between maximum and seasonal elevations in seawater temperature and reproductive phenology of a global invader to forecast the effect of climate warming on traits associated with the spread and establishment (i.e., growth and reproduction) of an invasive species. We then coupled these data with a study of early succession along a temperature gradient to forecast invasion success in species assemblages across a range of latitudes.

Results: Elevated seasonal temperature will lead to greater asexual reproduction and to multi-annual sexual reproduction in areas that currently have bi-annual or annual reproduction. The output from our model combined with our field studies of early succession in communities suggest that in colder environments, communities may be more affected by climate-induced shifts in reproductive phenology as they have more free space at the beginning of the growing season and fewer competitively superior species.

Main conclusions: Predicted elevated water temperature will eliminate the thermal barriers that limit reproductive success of a cosmopolitan invasive species. Increased reproduction combined with limited biological resistance in regions with cooler water temperatures may lead to a community state change.

KEYWORDS
biogeography, climate warming, invasion dynamics, invasive species, reproductive phenology, seasonality, species composition

1 | INTRODUCTION

The coastal waters of the northeastern United States, Arctic and northern Pacific oceans are warming much faster than previously predicted,

(IPCC, 2014; Mills et al., 2013). This has given rise to greater human-mediated activities such as exploitation of natural resources and increased shipping activities that are important pathways for the dispersal of introduced species (Miller and Ruiz 2014). Elevated ambient annual temperature patterns, coupled with more human-mediated species introductions, has the potential to induce dramatic changes in northern

benthic communities. Warming water temperatures are thought to enhance growth of invasive species, a critical element for their success (Sorte, Williams, & Zerebecki, 2010; Stachowicz, Terwin, Whitlatch, & Osman, 2002). A second element is the existing native community and its resistance to would be invaders. Other elements of success involve the species phenology and include survival, growth and reproduction in the invaded habitat, which is driven by the physiological tolerance of a species in its novel environment and their ability to acquire food and space.

Phenology, the seasonal determination of life cycle events, is a key driver of species distribution because it defines the season and duration of growth and reproduction (Schwartz, 2003). In many plants and animals, having a phenology that matches life history stages with seasonal resource availability is essential for individual reproductive success and survival (Rosenzweig et al., 2008; Schwartz, 2003). Recent findings have identified phenology as one, and perhaps the most important, trait shaping species distribution (Chuine, 2010; Post & Inouye, 2008). One of the challenges in climate change research is to determine how it will influence the persistence of individual species, populations and communities. Empirical studies have focused on growth and reproduction of species exposed to constant temperatures (Cockrell & Sorte, 2013; Grey, 2011). Models have used "envelope" or "habitat" algorithms to predict the distribution of species to changes in climate (e.g., Berry, Dawson, Harrison, & Pearson, 2002; Herborg, Jerde, Lodge, Ruiz, & MacIsaac, 2007; Pearson, Dawson, Berry, & Harrison, 2002; de Rivera, Steves, Fofonoff, Hines, & Ruiz, 2011). Few studies incorporate seasonal temperatures to forecast their establishment and growth. Seasonal temperatures are an important component for species in which reproduction (e.g., time to propagule release, asexual or sexual) is highly correlated with temperature. Incorporating time to propagule release captures the interaction between ambient temperature and propagule development time prior to release, a factor that controls the phenological appearance of species in a community. This is particularly apparent in temperate assemblages whose cyclical fluctuations in species composition result from environmentally driven seasonal reproduction of their dominant species (Dijkstra & Harris, 2009; Dijkstra, Westerman, & Harris, 2011; Reinhardt, Whitlatch, & Osman, 2013; Stachowicz et al., 2002).

In this study, we investigate the effects of elevated seasonal temperature patterns (changes in both maximum water temperatures and growing season duration) on the reproduction of a dominant marine introduced colonial ascidian species, *Botrylloides violaceus*. *B. violaceus* is a dominant member of subtidal assemblages in the Gulf of Maine (GOM) and out-competes other space occupying species (Grosberg, 1981; Wethey & Walters, 1986). It occurs from Cape Cod, MA to Eastport, ME (Dijkstra, Harris, & Westerman, 2007a; Miller & Etter, 2011). Its colonies are made up of genetically identical zooids connected by an internal vascular system. Like all colonial ascidians, it has two types of reproduction: asexual reproduction (a process known as blastogenesis), and sexual reproduction. Asexual reproduction occurs through synchronous cycles of colony-wide budding and complete zooid replacement, while sexual reproduction occurs via release of sperm by the zooids followed by internal fertilization and brooding

of the developing oocyte (Millar, 1971). We modelled the effects of current and predicted seasonal temperature patterns on growth and reproduction using annual temperature data from three different sites in the GOM and evaluated the model using field studies at three sites that span a latitudinal gradient. We predicted growth and reproduction of the species using long-term changes in water temperature collected from several sites in the GOM. Our model allows us to account for the effect of continuous fluctuations in temperature (i.e., seasonal temperature patterns) on metabolic processes in ectothermic animals. This provides a more biologically accurate estimate of the effect of predicted temperature changes on reproduction than models that use constant temperatures.

We then examined the effect of estimated climate-induced shifts in reproduction on early succession in communities that span a temperature gradient. In the GOM, the biological resistance of communities to invasions will likely depend upon latitude as the assemblages of species and the amount of free space, strong determinants for the successful establishment of invasions, that make up fouling communities are not equal across latitudes (Pederson et al., 2005; Wells et al., 2014). Northern GOM benthic communities have lower numbers of introduced species compared to more southern GOM communities (Dijkstra, Sherman, & Harris, 2007b; Pederson et al., 2005; Wells et al., 2014). This may stem from environmental resistance to invasion due to cold-water seasonal temperatures or the ability of the communities to resist invasion. Rapid ocean warming in the GOM, a region that experiences widely varying latitude and seasonal water temperature, may break down the physiological thermal barriers that preclude the successful establishment of self-sustaining (i.e., reproductive) populations.

2 | METHODS

2.1 | Climate change effects on asexual and sexual reproduction

2.1.1 | Water temperature patterns

To establish long-term temperature trends on reproduction and growth of *B. violaceus*, we plotted annual temperatures using surface temperature data obtained from the NOAA buoys in Boston Harbour (Massachusetts [MA], 42°21′18″N 71°3′1″W), Coastal Marine Laboratory (New Hampshire [NH], 43°4′20.45″N, 70°42′40.41″W), Portland (Maine [ME], 43°39′22″N 70°14′46″W) and in Eastport (ME, 44°54′22.47″N, 66°59′2.49″W) for all years possible from 1982–2014.

We also collected water temperature at our field sites (Salem, MA, 42°31′16.88″N, 70°52′55.06″W; Damariscotta, ME, 43° 56.0′N, 69° 34.8′ W; and Eastport, ME, 44°54′22.47″N, 66°59′2.49″W; Figure 1) using HOBO temperature data loggers, and a GoMOOS buoy for temperatures in Eastport, ME. The Eastport buoy is located inshore ~100 m from our study site. These temperature data were collected in 2006 and used, in addition to 10 years' worth of data from our long-term temperature sites, to validate the use of the Gaussian curve as an estimate of seasonal ambient temperature patterns in the GOM.
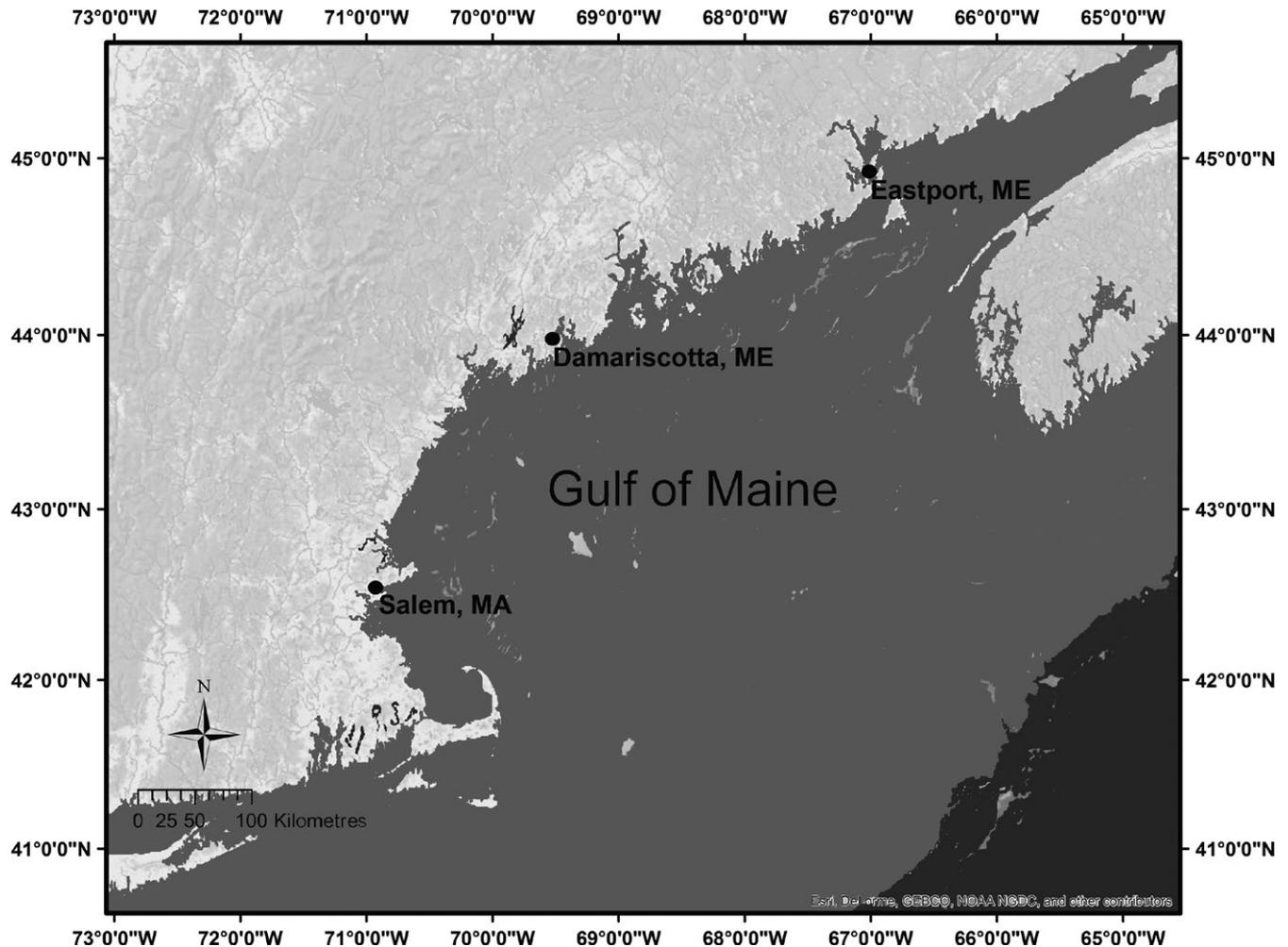
FIGURE 1 Field sampling sites of *Botrylloides violaceus* growth, temperature and early succession species assemblage in 2006

2.1.2 | Field study

Three 100 cm² Plexiglas® panels (low sample size was due to space limitations) were attached to bricks and deployed horizontally one metre below the water surface off of floating docks in Salem, MA, and Damariscotta, ME (Figure 1), from 03-June-2005 to 31-January-2006. *Botrylloides violaceus* was allowed to settle and grow as a monoculture by removing all other recruits. This procedure allowed us to observe seasonal cycles in percent cover under different field conditions by *B. violaceus* unconstrained by interspecific spatial competition. Panels were photographed bi-weekly after all organisms other than *B. violaceus* were removed, using a Nikon Coolpix 995, 950, or a Canon Rebel 2000.

Percent cover was calculated using a point count analysis of images viewed in iPhoto®. Percent cover data were arcsine transformed and space occupancy patterns used as a proxy for growth and compared among treatment and sites using one-way ANOVA of transformed data.

2.2 | Modelling methods for reproduction

To examine the relationship between ambient and predicted seasonal temperature patterns and growth (described here as an increase in number of zooids per colony) and reproduction (asexual and sexual reproductive cycles), we expanded upon our previous model describing the relationship between temperature, asexual and sexual reproductive cycles in *B. violaceus* (Westerman, Whitlatch, Dijkstra, & Harris, 2009). The difference between the model described below and our previous model of botryllid ascidian asexual and sexual reproduction is the use of a Gaussian function to approximate fluctuating seasonal temperature patterns. We used a Gaussian function as an estimate of annual temperature as temperature patterns at our study sites displayed a Gaussian distribution, and are well fit by a Gaussian function with a correlation of r^2 = .72 (Salem, MA), .78 (Damariscotta, ME) and .66 (Eastport, ME) (Figure 2). Temperature patterns at our long-term temperature sites (Boston Harbour, MA, Portsmouth, NH, Portland, ME, and Eastport, ME) are also well fit by a Gaussian function (representative years: Boston Harbour, 2006, 2009, r^2 = .93; Portsmouth, 1985, 2001, 2014, r^2 = .79, 0.86 and .91 respectively; Portland 1985, 1988, 2013, r^2 = .80, .89 and .87; and Eastport, 2011 and 2012, r^2 = .91 and .95). Using this equation eliminates the assumption of discrete reproduction (i.e., reproductive dormancy during the winter months) and decreases the sampling interval used to estimate growth rates. Laboratory studies using individual *B. violaceus* collected from
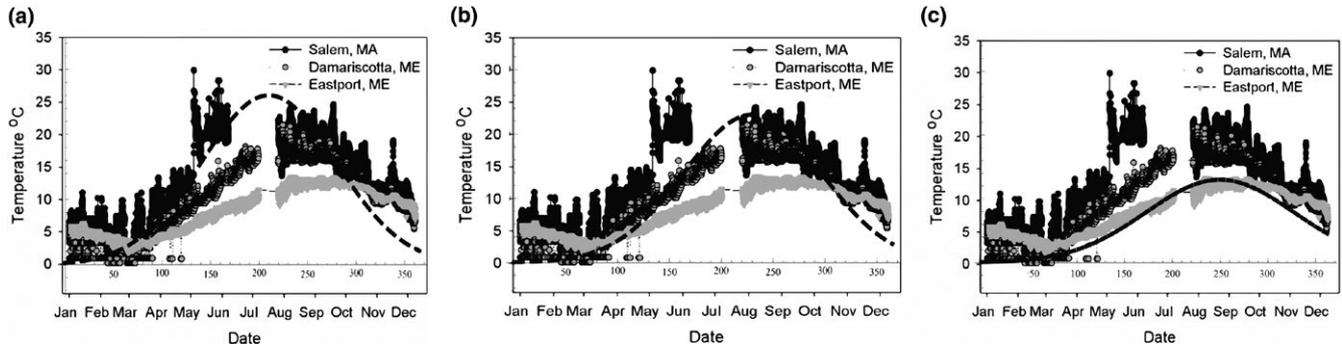
FIGURE 2 Gaussian curves plotted on top of actual 2006 temperature curves at three sites in the Gulf of Maine (GOM). (a) Salem, MA. Thick dashed black line: Gaussian curve with slope (a) = 12,000, maximum t_{max} = 27. (b) Damariscotta, ME. Thick dashed grey line: Gaussian curve with a = 10,400, t_{max} = 23. (c) Eastport, ME. Thin close-set dashed black line: Gaussian curve with a = 9,600, t_{max} = 13. Numerical x-axis corresponds to day (x) for the Gaussian curves

several sites within the GOM show a positive growth response to temperature (J. A. Dijkstra, unpub. data), suggesting our model applies to GOM populations.

2.2.1 | Modelled temperature on asexual reproduction

Asexual reproduction (colony growth measured in terms of the numbers of zooids [A] in *B. violaceus*) is dependent on the number of buds each zooid produces (z), and the number of blastogenic cycles (regular asexual reproductive cycles of colony-wide complete zooid replacement and zooid addition [B]) a colony has each year (Saito, Mukai, & Watanabe, 1981). During blastogenesis in botryllid ascidians, adult zooids are reabsorbed into the colony, and replaced by developing buds (reviewed in Rinkevich, 2002). Colonies only grow when adult zooids produce multiple buds (asexual growth). Asexual growth is predominantly cyclical and iterative and occurs at the end of a blastogenic cycle, when all the budding zooids in the colony reach maturity. Laboratory studies have demonstrated that in western North Atlantic populations of botryllid ascidians, blastogenic cycling (L; length in days of one asexual reproductive cycle) are positively correlated with ambient water temperature (°C, T) and fits the equation:

$$[L(T) = (s/T) - i, \tag{1}$$

where s (empirically based, inferred duration of blastogenic cycle if ambient temperature is ~1°C [Grosberg, 1982]) and i (intercept) are constants, and for *B. violaceus*, s = 185.99, and i = 2.1876, Equation 1] (Grosberg, 1982; Westerman, Dijkstra, & Harris, 2009). As the number of blastogenic cycles (B) a colony has a year = 365/L, and (L) is a function of temperature, (A) is a function of (z) and (B):

$$A = 1 + z^B, \tag{2}$$

where 1 is the oozoid, or first zooid, and

$$B = \frac{365\,\text{days}}{L}. \tag{3}$$

Seasonal temperature patterns were approximated using the Gaussian curve equation which allowed us to vary the maximum temperature, the slope of the temperature curve, and the input value at

which the maximum temperature occurs. These three variables correspond to maximum average daily temperature (°C, t_{max}), breeding season duration (slope of the curve) (α), and day of t_{max} (d). We held (d) constant at d = 220, as it approximates the day of maximum temperature during the year for our sites in the GOM (Figure 2). Temperature on any given day (x) during the year was therefore represented by the equation:

$$T(x) = t_{max}\, e^{\frac{-(x-d)^2}{\alpha}}\ (0 < x < 365). \tag{4}$$

Manipulating (t_{max}) and (α) allowed us to find curves that closely matched the actual annual temperature patterns at our three sites in the GOM (Figure 2).

Equation 4 provides us an estimate of daily average temperature as it changes through the year. As the duration of blastogenic cycling is dependent on daily average temperature, we substituted Equation 3 into Equation (1) for blastogenic cycles (modified from Westerman, Whitlatch et al., 2009) to give the proportion of a blastogenic cycle that occurs on a given day with a given daily average temperature. A summation of 0 < x < 365 outcomes results in an estimate of number of blastogenic cycles (L) in a year for a given (t_{max}) and a given (α) (slope of spring warming/fall cooling).

$$L(x) = \frac{1}{i} + \frac{s}{T(x)}\ (0 < x < 365). \tag{5}$$

Using Equation 5, we estimated L at 2°C intervals from 10°C < (t_{max}) < 32°C, and at four different breeding season duration estimates (α = 8,000, 9,600, 10,400, 12,000; 8,000 indicates the smallest slope gradient which corresponds to ambient 2006 temperature patterns at Eastport, ME, and 12,000 indicates the largest slope gradient, which corresponds to forecasted elevated temperature patterns and elongated breeding seasons), to investigate how changes in temperature and breeding season duration may influence colony asexual reproduction. To account for slight variation in seasonal temperature patterns within each range, we sampled the 200 closest seasonal temperature patterns on either side of each of the four sample temperature curves (i.e., 7,800–8,200). We then used linear regression to estimate the relationship between annual maximum daily temperature and number of blastogenic cycles, giving us an estimate of the

relationship between seasonal temperature and annual asexual reproductive cycles.

2.2.2 | Modelled temperature on sexual reproductive cycles

We have revised the equation presented in Westerman et al. (2009) for estimating annual number of sexual reproductive cycles to incorporate ambient and predicted seasonal temperature patterns, and have made the model more general, so it could be modified and used to calculate the brooding period duration of other botryllid ascidians. The number of annual sexual reproductive cycles (R) for a botryllid ascidian is dependent on the number of days the average water temperature is above the critical reproductive temperature for the species (C) and the duration of the brooding period (D). D is a species-specific number of blastogenic cycles (B) (Saito et al., 1981), and for *B. violaceus* $D = 7B$ (Saito et al., 1981). Therefore, for *B. violaceus*, number of annual reproductive cycles is influenced by average water temperature and duration of reproductive season.

$$R = \frac{C}{7B}. \tag{6}$$

Note that the denominator could be modified to represent the brooding period of different colonial Botryllid species. For example, the brooding period of *Botryllus schlosseri* is 1 blastogenic cycle; therefore, the equation would read $R = C/B$ for *B. schlosseri*. However, critical reproductive temperatures are not known for all populations of *B. violaceus*, or for any cosmopolitan ascidian species, thus in this model, we assume that ascidians do not exhibit annual, temperature-induced reproductive diapause. R is therefore simplified to:

$$R = L/7. \tag{7}$$

L is blastogenic cycles per year, as described in Equation 5. Using this model we estimated the effect of changes in maximum water temperature and duration of summer water temperatures on the number of annual sexual reproductive cycles for *B. violaceus*, and compared these estimated results with data recovered from our three sites in the GOM.

2.2.3 | Species assemblage

To examine the effect of climate-induced shifts in reproduction of *B. violaceus* on species assemblages that span a thermal gradient, we deployed 100 cm^2 Plexiglas panels ($n = 3$, low replication was due to space limitations) in Salem, MA, Damariscotta, ME and Eastport, ME (Figure 1). Panels were deployed ~0.5 m below the surface off floating docks from the week of 15-June-2006, to the first week of 10-September-2006. Panels were deployed during the summer months, the peak period for reproduction and growth of many temperate, benthic organisms (Dijkstra, Sherman, Harris, 2007b; Stachowicz, Whitlatch, & Osman, 1999). During this period, entire assemblages were allowed to develop on the panels. Panels were photographed at

the end of the 3 months. Individuals were identified to species (See Appendix S1). Abundance of species and open space were recorded as percent cover.

To detect differences in early succession species composition among sites, a Bray–Curtis similarity matrix was constructed using arcsine transformed percent cover data (Clarke & Warwick, 2001). Non-Metric Multidimensional ordination (nMDS) and a one-way Analysis of Similarities (ANOSIM) were used to detect differences in pioneer assemblages among sites. NMDS is a method that preserves species-specific formation and is sensitive in detecting changes in species assemblages (Clarke & Ainsworth, 1993). ANOSIM is a non-parametric permutation test that applies the same (rank) similarity matrix used for nMDS ordination (after Clarke & Warwick, 2001). Contributions of each species to the average similarity within site faunal composition were calculated using SIMilarities PERcentages (SIMPER). The average contribution of a single species (e.g., species A) was calculated by taking the average percent cover of species A, over all panels within a site, and comparing it to contributions of all other within site species (Clarke & Ainsworth, 1993). Higher space occupancy by a single species on individual panels within a site has a greater contribution within site faunal composition. Community analyses and graphs were generated using Primer 6.0 (Primer-E).

3 | RESULTS

3.1 | Climate change effects on asexual and sexual reproductions

3.1.1 | Temperature across sites

Warmer seasonal temperatures corresponded with latitude, with higher temperatures observed in Salem, MA than in Eastport, ME (Figure 2). Seasonal temperatures have risen at all sites, with observed site-specific variations in annual maximums and minimums (Figure 3). There is a more pronounced increase in seasonal temperatures in Eastport, ME and Portsmouth, NH, than at Boston, MA. This may be due to the quantity of data we have for Portsmouth relative to Boston, or a combination of site-specific attributes, such as the latitude of Eastport, ME relative to the rest of our sites.

All of our sites in the GOM now have an extended growing and breeding seasons with over 250 days exceeding 4°C and 150 days exceeding 10°C (Figure 4), proposed critical temperatures for survival, growth and reproduction for many marine species (Portner, 2002).

3.1.2 | Field study

In 2006, *B. violaceus* had two local maxima (August and November) of percent cover at our southernmost site, Salem, MA and a single local maximum (August) at our mid-latitudinal site, Damariscotta, ME. Initial settlement and growth began in Salem 1 month earlier than in Damariscotta and continued 1 month longer (Figure 5).
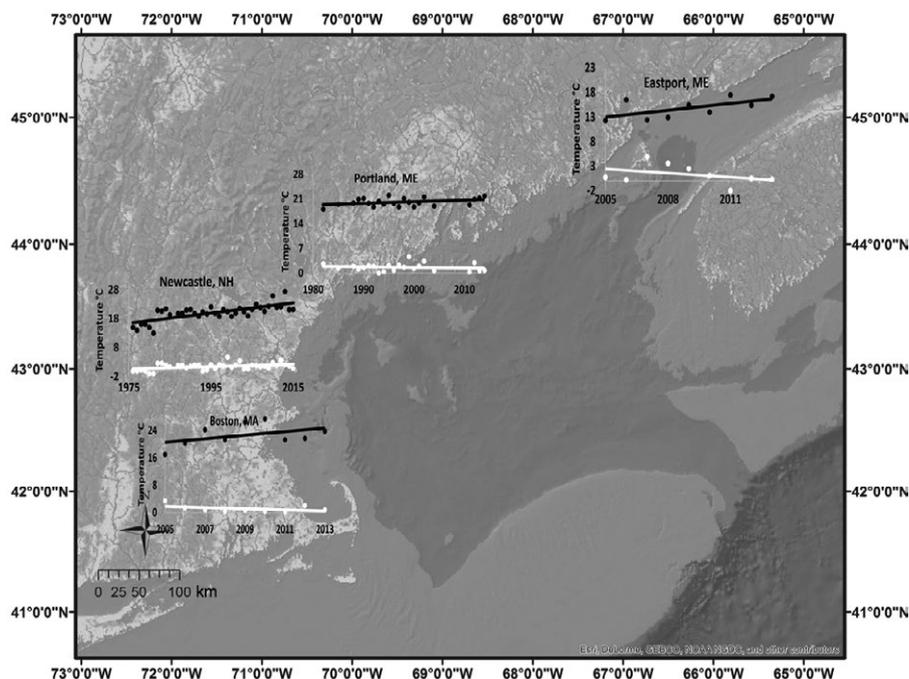
FIGURE 3 Slopes of maximum (orange; upper slope) and minimum (blue; lower slope) temperatures from Boston (Massachusetts) to Eastport (Maine). Maximum temperatures have steadily risen at all sites in the Gulf of Maine (GOM). Minimum temperatures slightly decline in Eastport, remained constant in Portland (Maine) and Boston and slightly increase in Portsmouth (New Hampshire). [Colour figure can be viewed at wileyonlinelibrary.com]
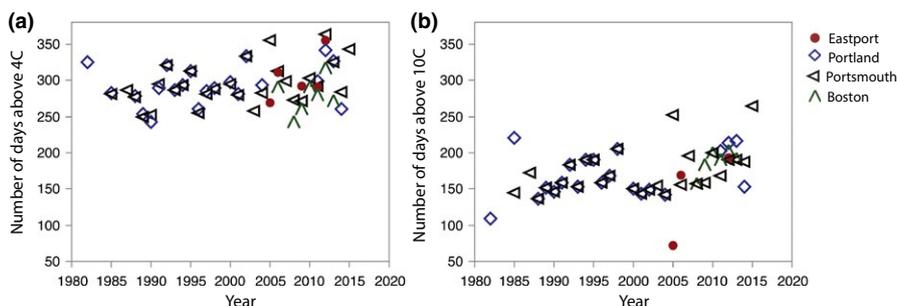
FIGURE 4 Breeding season duration in coastal waters of the Gulf of Maine (GOM) 1983–2015. Number of days above 4°C (a) and 10°C (b) per year for Boston MA, Portsmouth NH, Portland ME, and Eastport ME. Data spanning 1983–2013, though variable years for each site. While the amount of increase in breeding season over the last 30 years is site specific, there is a general trend in increased number of days above both 4 and 10°C for all sites. [Colour figure can be viewed at wileyonlinelibrary.com]

3.2 | Modelling methods for reproduction

3.2.1 | Modelled temperature on asexual reproduction

Using a range of maximum temperatures that correspond to the range of maximum temperatures that have been observed over the last 30 years in the GOM, and then extending to the predicted 2°C increase above current temperatures, our model predicts that both greater maximum temperature and elevated seasonal temperatures will result in more asexual reproductive cycles (Figure 6a, See Appendix S2). In all instances other than when zooids were replacing themselves ($z = 1$), colony size increased logarithmically with maximum ambient temperature, regardless of the speed of spring warming or number of new asexual buds produced by each zooid ($z > 1$) (Log fit of colony

growth and maximum annual temperature with different α: $\alpha = 8,000$; slope = 0.8884; $\alpha = 9,600$; slope = 0.968; $\alpha = 10,400$; slope = 1.005; $\alpha = 12,000$; slope = 1.072) (Figure 7). Elevated seasonal temperatures did not have as strong of an effect on asexual reproduction compared to the effect of maximum temperature but did still result in increased annual colony growth (linear fit of asexual cycles and maximum annual temperature: slope = 1.418, Figure 6a; linear fit of asexual cycles and duration of growing season: slope = 0.0001, See Appendix S2).

3.2.2 | Modelled temperature on sexual reproductive cycles

Our model estimated three sexual reproductive cycles in Salem, MA and two in Damariscotta, ME. The model slightly overestimated the number of reproductive cycles with ambient water temperatures in
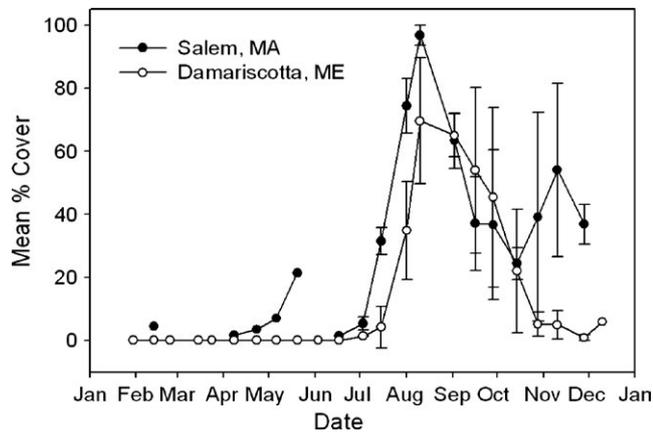
FIGURE 5 Percent cover of *Botrylloides violaceus* in Salem, MA (black circles) and Damariscotta, ME (open circles). Two peaks of percent cover are observed in Salem, while only one peak is observed in Damariscotta.

Salem, MA and Damariscotta, ME as our observed *in situ* reproductive patterns revealed two sexual reproductions in Salem, MA and one in Damariscotta, ME. This is inferred from our peak field percent cover analysis. Colonies of *B. violaceus* undergo periods of growth, followed by larval release and senescence of the parent colony, similar to that observed in *B. schlosseri* (Grosberg, 1988; Yund & Stires, 2002). The precipitous decline in percent cover on the panels indicate the colonies underwent senescence after larval release. The consistent slight overestimate of number of reproductive cycles can be subtracted from model outputs to give a more accurate estimate of expected number of reproductive cycles. Using our forecasted values of maximum temperatures, our model predicted an increase in the number of sexual reproductive cycles (generations) at each site (linear fit of annual sexual reproductive cycles on maximum ambient temperature: slope = 0.203) (Figure 6b). Similarly, our model predicted that

elevated seasonal temperatures would lead to greater sexual reproduction across sites.

3.3 | Species assemblage

Early successional species composition among sites was significantly different in both composition and dominance (Figure 8a; ANOSIM: $R = 1.0$, $p < .004$). According to a one-way SIMPER analysis, two encrusting ectoprocts (the gelatinous *Alcyonidium gelatinosum*, the hard surfaced *Cryptosula pallasiana*) and one vine-like species (the cnidarian, *Obelia* spp.) characterized the fouling assemblage of our northernmost site: Eastport, ME (See Appendix S1, Figure 8a). These two encrusting ectoprocts were replaced by two encrusting colonial ascidians (*Botrylloides violaceus* and *Didemnum vexillum*), the solitary, soft-bodied ascidian (*Molgula* spp.) , and the vine-like cnidarian (Obelia spp.) in spatial dominance ranking at our midlatitude site in the GOM, Damariscotta, ME. These three ascidian species joined the vine-like cnidarian (*Obelia* spp.) as the top space occupiers. At our southernmost site in Salem, MA, two encrusting colonial ascidians (*B. violaceus* and *Diplosoma listerianum*), a solitary, soft-bodied ascidian (*Ascidiella aspersa*), and an arborescent ectoproct (*Bugula* spp.) dominated the early succession assemblage. There was a significant main effect of site on open space ($F_{2,9} = 22.4$, MS = 3.89, $p = .0003$, Figure 8b) with open space significantly greater in Eastport, ME (30%) than in Salem, MA (5%) or Damariscotta, ME (18%) (Tukey–Kramer set to .05 significance).

4 | DISCUSSION

Our study indicates that predicted rise in sea surface temperatures facilitates population growth of *Botrylloides violaceus* in northern GOM fouling communities where historical seasonal temperatures were prohibitively low for *B. violaceus* reproduction and growth. Specifically,
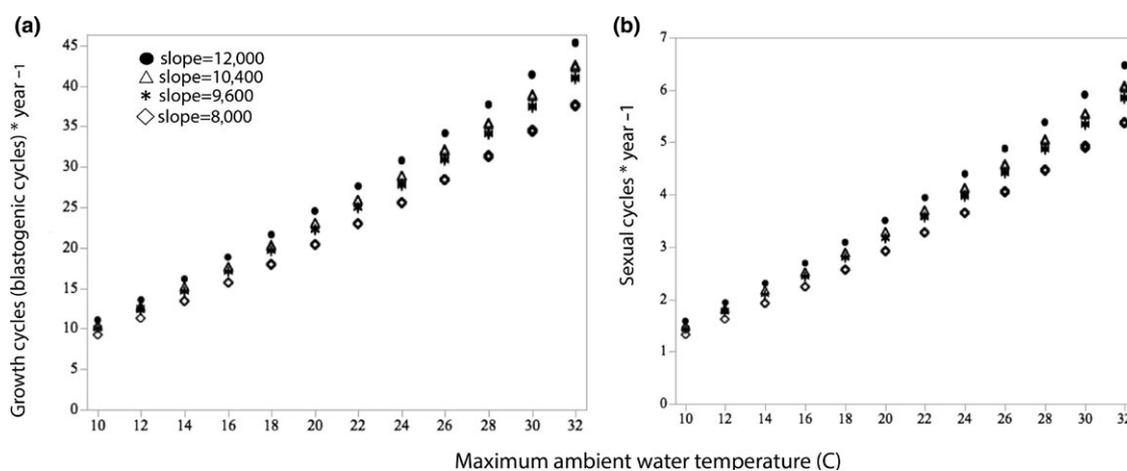
FIGURE 6 Number of asexual and sexual generations per year increases with both elevated maximum and seasonal water temperature. (a) Annual number of growth cycles (asexual reproductive cycles) is positively correlated with maximum ambient water temperature. (b) Annual number of sexual generations, which is a function of number of growth cycles for *Botrylloides violaceus*, exhibits a similar pattern of positive correlation with elevated maximum and seasonal water temperatures. ambient water temperature. Slight variation in slope (breeding season duration variation of ± 100) had a small effect on number of asexual and sexual generations per year, again making the 200 different estimated numbers of asexual and sexual reproductive cycles corresponding to each maximum temperature difficult to distinguish.

FIGURE 7 Annual colony growth increases logarithmically with rising maximum ambient water temperatures. Estimated effect of temperature on annual colony growth potential, in terms of final colony zooid count at the end of a year for a colony that started from one newly settled zooid at the beginning of the year and grew without spatial limitation for 365 days, when the estimated temperature curve has a slope of (a) 8,000 ± 100, (b) 9,600 ± 100, (c) 10,400 ± 100, and (d) 12,000 ± 100. Z = average number of buds produced per zooid. Slight variation in slope (breeding season duration variation of ± 100) had a small effect on colony growth, making the 200 data points corresponding to each maximum temperature difficult to distinguish
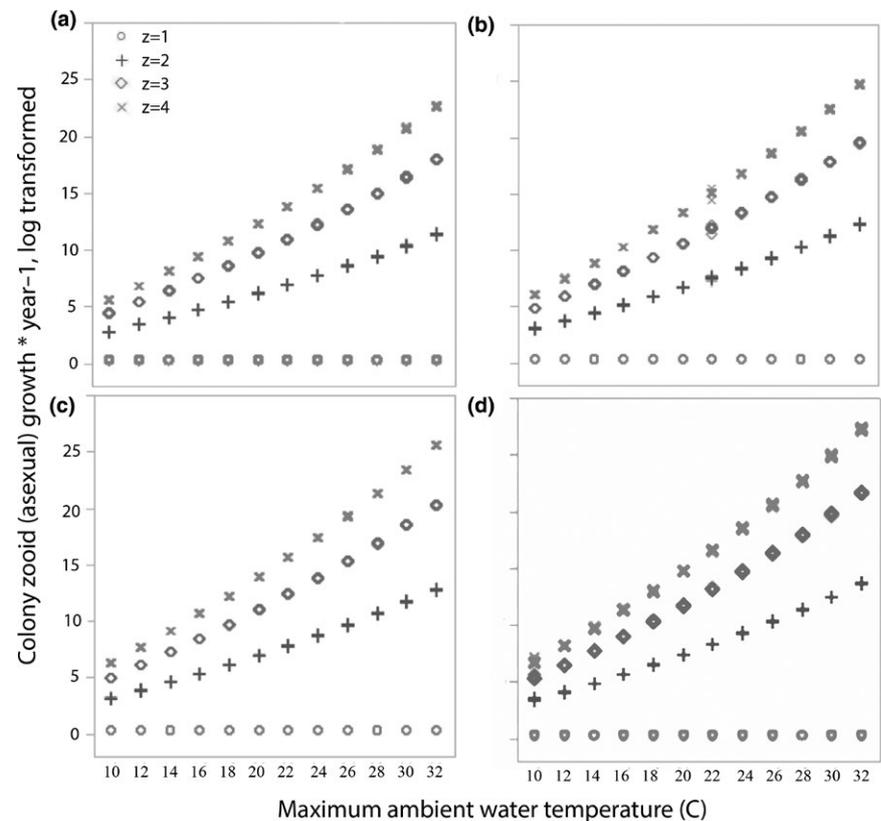
elevated maximum and seasonal temperatures will lead to greater annual sexual reproduction by accelerating the duration of asexual reproduction and oocyte development time. The observed population dynamics of *B. violaceus* in the GOM articulate these findings. *B. violaceus* can physiologically persist in areas with low water temperature (Dijkstra et al., 2007); however, population growth will not occur unless temperatures remain elevated long enough for reproduction to occur (e.g., Saito et al., 1981; Westerman et al., 2009). Reproduction in *B. violaceus* is complicated; colonies undergo a number of asexual cycles before sexually reproducing. When we took this association with predicted maximum and elevated seasonal temperature into account, we predicted an increase in both growth and in the number of annual reproductive cycles, particularly at the most northern site (Eastport, ME). A continuous growth model similar to that used in our study to estimate ascidian colony growth may become increasingly more biologically accurate than models which suggest many months of dormancy.

While critical maximum temperatures (temperatures high enough to prevent reproduction) can occur for benthic invasive species (Brunetti, 1976), it is unlikely water temperatures at our northern sites (Damariscotta, ME and Eastport, ME) will reach maximum critical temperatures for *B. violaceus*. This species grows and reproduces in waters with much higher average temperatures and ranges than predicted for this region (e.g., Bullard, Whitlatch, & Osman, 2004; Westerman et al., 2009). Our model suggests that a 3°C increase in maximum temperature, which is well within the range of predicted temperatures for the 21st century (IPCC, 2014; Knutti & Sedláček, 2013), will result in an additional sexual generation at all of our sites, irrespective of changes in growing season duration. An additional

increase in elevated seasonal temperatures will further enhance the number of sexual generations *B. violaceus* may have a year. This is exemplified in our field studies in which there was a single peak, followed by a sharp decline in percent cover per reproductive season for *B. violaceus* in Damariscotta, ME. The sharp decline in percent cover is indicative of larval release from the parent colony as the colony senesces after reproduction (Dijkstra & Harris, 2009; Grosberg, 1982, 1988). This suggests that the growing season at this site is only long enough to produce one cohort of reproductive colonies. The occurrence of two peaks, followed by a sharp decline in percent cover in Salem, MA, suggests that two cohorts were able to reach reproductive maturity and complete their life-cycle during the growing season at this site. While other factors such as constant reproduction, competition or predation may affect peak percent cover (Osman & Whitlatch, 1998; Simkanin, Dower, Filip, Jamieson, & Therriault, 2013), previous studies have shown strong seasonal recruitment and abundance peaks of botryllid ascidians (e.g., Grosberg, 1988; Sams & Keough, 2012; Yund & Stires, 2002). This change in *B. violaceus* phenology will enhance its presence in species assemblages throughout the GOM, and may have a particularly dramatic effect on *B. violaceus* abundance at northern latitudes.

As a case example, under 2006 ambient temperatures at our northernmost site (Eastport, ME), *B. violaceus* sexually reproduces biannually. But the recently observed (and forecasted) elevation in water temperatures facilitates annual sexual reproduction. These results differ from the modelled results of Cockrell and Sorte (2013). The discrepancy between these two studies may be due to our inclusion of brooding period duration in our set of model parameters and Cockrell
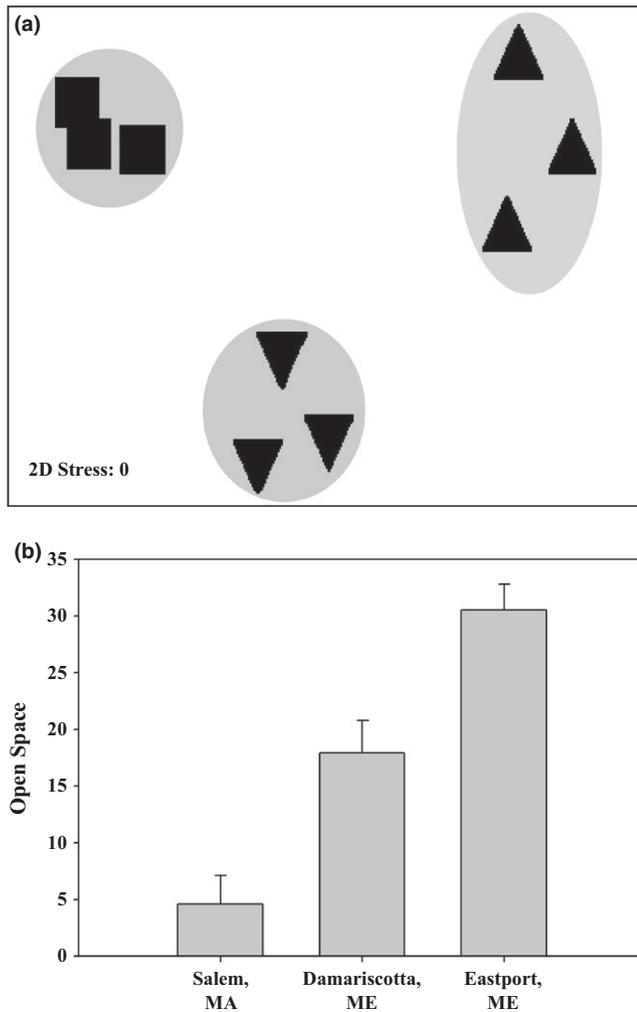
FIGURE 8 (a) Two-dimensional non-metric multidimensional ordination representing species composition of early succession (~4 months, June to September 2006) species assemblages. Each point represents average percent cover of individual species observed on panels collected from Salem, MA, Damariscotta, ME and Eastport, ME. Significant differences in species assemblages were detected among sites (analysis of similarities (ANOSIM) $R = 1.0$, $p < .004$). (b) Percent available bare space ($\pm SE$) observed in early succession (~4 months) species assemblages at the three sites.

and Sorte's (2013) use of *B. schlosseri*'s age and size at sexual maturity to model population structure of *B. violaceus*. The seven asexual cycle brooding period of *B. violaceus* exceeds the duration of the adult life stage period observed in the mesocosm study used to determine the parameters for Cockrell and Sorte (2013) model. The incongruity between our study and Cockrell and Sorte (2013) highlights the effect brooding period (i.e., larval development and generation time) may have on the ability of organisms to respond to changes in temperature. As variation in the response of species to climate change is great, incorporating species-specific response in reproductive phenology to climate warming is critical (Chen, Hill, Ohlemuller, Roy, & Thomas, 2011). This is particularly important for species that have the capacity to spatially dominate substrates and may produce a community state change through growth and build-up of local populations.

Colonial ascidians are ideal models to examine the relationship between ocean warming and phenology, as they do not mass spawn, have reduced or less complex juvenile periods, and have a relatively stable food source that is independent of nutrient levels in coastal waters. Thus, their development rate is likely to respond to any changes in temperature. In contrast, species that have prohibitive spawning cues, complex life cycles and temporally patchy food sources may not be able to respond similarly to rising water temperatures. For example, corals that use lunar cycles to coordinate mass spawning (Babcock, Wills, & Simpson, 1994) may be unlikely to alter reproductive phenology in response to temperature because their reproductive cues are not associated with temperature. Other examples include species with feeding pelagic juveniles such as urchins. They may be too dependent on temporally isolated larval food sources to increase reproduction in response to warmer waters or extended breeding seasons. As such, it is likely that phenological responses to elevated seasonal temperatures are likely species, and perhaps biome, specific.

Site-specific population growth of *B. violaceus* at elevated seasonal temperatures will depend on many factors such as predation, intra-specific and inter-specific competition, and post-settlement mortality (Freestone, Osman, Ruiz, & Torchin, 2011; Grey, 2011; Osman & Whitlatch, 1995; Simkanin et al., 2013). Warmer water temperatures may increase the metabolism of invertebrate competitors and predators (Portner, 2002). This may lead to more intense competition for resources and rates of predation on *B. violaceus*. However, the relationship between temperature, growth and reproduction of potential cold-water northern temperate species is unclear as warmer waters may restrict their growth and reproductive output which may limit their competitive ability and abundance (Mah & Hansson, 2011; McMahon & Russell-Hunter, 1977; Moore, Thompson, & Hawkins, 2011). Further, previous studies in California and the Gulf of Maine indicate that at elevated water temperature tunicates, including *B. violaceus*, are dominant species (Dijkstra et al., 2011; Sorte, Williams, & Zerebecki, 2010). Ocean acidification may also affect population growth of invertebrate species. Recent studies suggest that declining pH favours dominance by soft-bodied species such as ascidians, suggesting that ocean acidification may have a positive influence on their populations (Dijkstra et al., 2011; Peck et al., 2015; Wootton, Plifster, & Forester, 2008). Free space, another important component for the growth of *B. violaceus* (Lord 2016), is also greater at Eastport, ME than the southern sites in early succession assemblages. The presence of adult individuals may also affect the success of *B. violaceus*. However, field and laboratory studies suggest that settlement and establishment of *B. violaceus* are not restricted by the presence of adult heterospecifics, and that *B. violaceus* is a superior competitor for space (Blum et al., 2007; Dijkstra et al., 2007b; Gittenberger & Moons, 2011; Wethey & Walters, 1986). Further, ascidians have the capacity to form large colonies through fusion of juveniles (Smith, Stefaniak, Saito, Gemmill, & Fidler, 2012; Westerman et al., 2009). As such, an increase in water temperature is expected to favour local population growth of *B. violaceus*. Given that it is a highly competitive species for space and resources, greater seasonal temperatures will likely facilitate its dominance in northern temperate subtidal species assemblages.

5 | CONCLUSIONS

Our study suggests that elevated seasonal and maximum ocean temperatures will eliminate the thermal barriers that limit the reproductive success of *B. violaceus*. Rising annual temperatures will accelerate its reproduction in areas where water temperatures were previously too cold to promote population growth, thereby increasing its abundance in assemblages where it is currently not a dominant member. While many factors have the potential to alter species composition, the limited biological resistance in northern communities combined with temperature dependent increases in annual *B. violaceus* reproductive output may lead to a novel community state (*sensu* Osman, Munguia, Whitlatch, Zajac, & Hamilton, 2010), in northern GOM assemblages. This change may take the form of the northern assemblage resembling that of more southern GOM fouling assemblages in which ascidians are the dominant members (Dijkstra & Harris, 2009).

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SUPPORTING INFORMATION

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