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Implications of warming temperatures for population outbreaks of a nonindigenous species (*Membranipora membranacea*, Bryozoa) in rocky subtidal ecosystems

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Abstract

To quantify and explore the role of temperature on population outbreaks of a nonindigenous bryozoan (*Membranipora membranacea*) in kelp beds in the western North Atlantic (Nova Scotia, Canada), we constructed an individual-based model using field-derived estimates for temperature-dependent colony settlement and growth. Using temperature as the single input variable, the model successfully simulated the timing of onset of settlement, colony abundance, colony size, and coverage on kelps. We used the model to examine the relative effect on the population of varying temperature by −2°C to +2°C each day. The timing of onset of settlement varied by 18 d °C^{-1} with changes in temperature from January to August. Variations in temperature had nonlinear effects on the population, with an increase in daily temperature of 1°C and 2°C causing the cover of colonies on kelps to increase by factors of 9 and 62, respectively. Changes in winter and spring temperature had the most pronounced effects on the timing and abundance of colonies, while changes in summer temperature had the most pronounced effect on colony size and coverage on kelp blades. Outbreaks of this species will increase in frequency and intensity if temperatures warm as a result of climate change, causing defoliation of kelp beds and, thus, facilitating the invasion of other nonindigenous benthic species.

In marine environments, the incidence of diseases (Harvell et al. 2002), toxic organisms such as harmful algal blooms (Anderson 1997; Hayes et al. 2001), and nonindigenous species (Dukes and Mooney 1999; Carlton 2000) have increased in recent decades. Outbreaks, defined as a higher occurrence of disease than would typically be encountered within a particular region, are often related to environmental disturbances or change, such as periods of above-average temperature. Changes in extreme temperature (e.g., warmer summers or winters) are often as ecologically important to populations as changes in mean annual temperature (Sinclair et al. 2003; Bruno et al. 2007). For example, in terrestrial environments, warming winter temperatures have caused increased severity and frequency of outbreaks of the mountain pine beetle *Dendroctonus ponderosae* in the forests of western Canada and the United States (Logan and Powell 2001). In marine environments in the northeastern United States, the spread and increased incidence of Dermo disease (*Perkinsus marinus*), a pathogen of the oyster *Crassostrea virginica*, has been attributed to warming winter and summer temperatures (Ford and Smolowitz 2007). Similarly, on the Great Barrier Reef, incidence of white syndrome, an emergent disease (or group of diseases) in Pacific reef-building corals, is positively related to the frequency of warm sea-surface temperature anomalies (Bruno et al. 2007). Such cases have led to concerns that warming temperatures predicted by climate change will cause an increase in outbreaks of harmful organisms in a variety of environments. Identifying the mechanisms responsible for these outbreaks is necessary for predicting occurrence and for mitigating resultant damage.

In the rocky subtidal ecosystem of the Atlantic coast of North America, outbreaks of the nonindigenous bryozoan *Membranipora membranacea* have occurred periodically since it was first observed in the late 1980s and early 1990s (Berman et al. 1992; Lambert et al. 1992; Scheibling et al. 1999), after it was introduced from European populations (Schwaninger 1999). *M. membranacea* forms sheetlike colonies on laminarian algae (kelps), and in years of particularly high abundance it encrusts entire blades (Fig. 1), causing them to become fragile and to break off (Dixon et al. 1981) during periods of intense wave action in autumn. The consequence is the occurrence of extended defoliated regions of bladeless stipes, which subsequently rot (Scheibling et al. 1999; Fig. 1). In the western North Atlantic, outbreaks of *M. membranacea* in the Gulf of Maine, Maine, United States of America, and in Nova Scotia, Canada, resulted in periodic large-scale (10s–100s-km) losses of the kelp beds in the 1980s–2000s (Berman et al. 1992; Lambert et al. 1992; Saunders and Metaxas 2008). Following disturbance, kelps are capable of recruiting and reforming a mature canopy within 1–4 yr (Johnson and Mann 1988; Scheibling et al. 1999). However, recruitment of kelps is inhibited by the presence of another nonindigenous species, the green alga *Codium fragile* ssp. *fragile* (Levin et al. 2002; Scheibling and Gagnon 2006), which in some defoliated regions has replaced the indigenous flora and formed monospecific meadows. The removal of kelp and its subsequent replacement by *C. fragile* could have significant and broad-ranging effects on the rocky subtidal ecosystems of the western North Atlantic (Schmidt and Scheibling 2007), with coincident effects on economically important fisheries for lobsters and sea urchins (Chapman et al. 2002).

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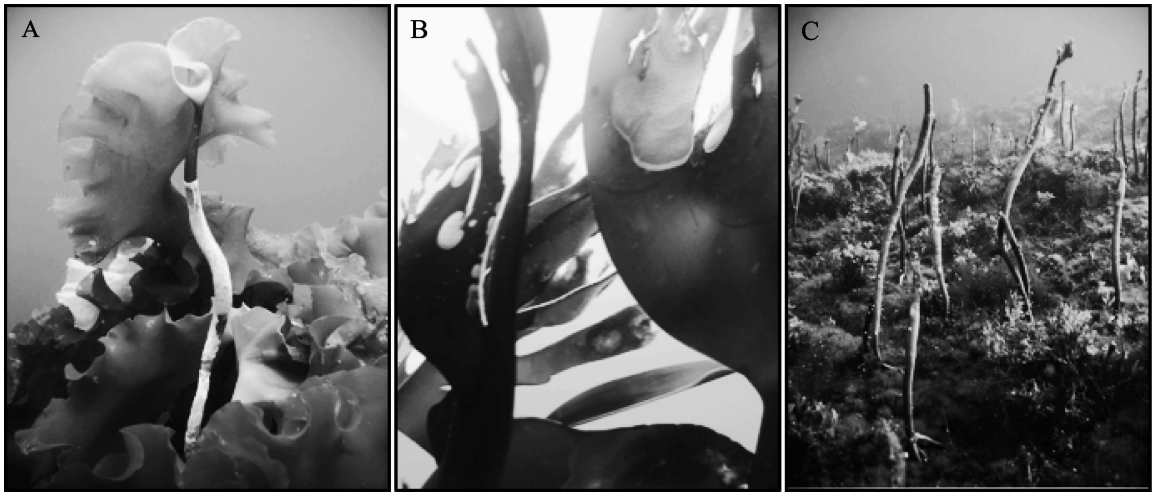

Fig. 1. Laminarian algae in kelp beds in the western North Atlantic (southern shore of Nova Scotia, Canada): (A) in luxurious condition preceding an outbreak of the nonindigenous bryozoan *Membranipora membranacea*, (B) encrusted by *M. membranacea* at the onset of an outbreak, and (C) defoliated following an outbreak of *M. membranacea* (A and C courtesy of R. E. Scheibling).

As for many ectothermic species, the timing of occurrence and abundance of populations of *M. membranacea* is linked to the thermal seasons. In winter, colonies cease growing and senesce, which, in combination with the period of high growth of the host kelp blades, results in bryozoan colonies being sloughed off the distal ends of kelps. By spring, the few remaining bryozoan colonies are located on the distal ends of kelps, on holdfasts or stipes, or on alternative substrates, such as rocks or other algae. Overwintered colonies are capable of new growth when the water warms (Lutaud 1961; Menon 1972), and these few colonies are most likely the source of the larvae that are released in late spring and summer. The planktotrophic larvae become competent to settle in $\sim$ 4 weeks (Yoshioka 1982). Settlement in Nova Scotia begins to occur between May and July, and increases exponentially until a maximum in September or October (Saunders and Metaxas 2007). During settlement, larvae metamorphose into an ancestrula (a pair of sessile filter-feeding zooids), which subsequently bud asexually to form sheet-like colonies (Fig. 1). Growth in species of temperate bryozoans occurs mainly during the period of increasing seasonal temperature (Ryland 1970), which in Nova Scotia occurs from March to September. Colony growth rates (linear increase in maximum dimension) increase with initial colony size and temperature, and range from 0.1 mm d^{-1} to 12 mm d^{-1} (Saunders and Metaxas 2009*a*). Colonies may become reproductive 40 d after settlement or earlier if they are crowded or grazed (Harvell and Helling 1993).

In the introduced range, the combination of a short reproductive cycle, fast growth rates (Pratt 2008; Saunders and Metaxas 2009*a*), the ability to reach large sizes, and the presence of only few competitors (Berman et al. 1992) or predators all likely contribute to the invasive success of *M. membranacea*. The specific causative factors involved in the interannual pattern of outbreaks are not entirely understood, making the prediction of such outbreaks unachievable. However, it is likely that physical factors play the most important role in regulating its population dynamics. Saunders and Metaxas (2007, 2008) suggested that an outbreak of *M. membranacea* in Nova Scotia in 2006 that caused 70% reduction of kelp cover was caused by earlier and more abundant settlement and recruitment, in turn the result of unusually warm water temperatures the preceding winter (Jan–Mar). However, because colony growth rate is also greatly dependent on temperature (Menon 1972; Saunders and Metaxas 2009*a*), it is possible that outbreaks are instead primarily caused, or at least exacerbated, by warmer temperatures during the growth period in summer and early autumn. This hypothesis is supported by Scheibling and Gagnon (2009), who report that percent cover of *M. membranacea* on kelp was significantly related to the thermal integral during the postsettlement period from August to October for a 10-yr data series.

Our objective was to identify the effect of the magnitude and timing of variations in temperature on the population dynamics of the introduced bryozoan *Membranipora membranacea* in the western North Atlantic. To do so, we created an individual-based model using temperature- and size-dependent colony growth rate and included settlement data as a function of the thermal integral (growing degree-day [GDD]). The relationships used to estimate various parameters in the model were based on our previously collected empirical data for this species. The model was validated using field estimates of the population from St. Margarets Bay, Nova Scotia, Canada. Using the model, we conducted numerical experiments to examine the effects of the magnitude and timing of temperature variation on population dynamics (timing of settlement, numerical abundance, colony size, and percent cover on kelp). Our results suggest that an increase in temperature as small as 1°C, which is well within the range predicted for the region by the end of the 21st century as a result of climate change (IPCC 2007), will cause earlier and more abundant occurrences of this nonindigenous species; the resultant outbreaks could have profound implications for the native ecosystem.

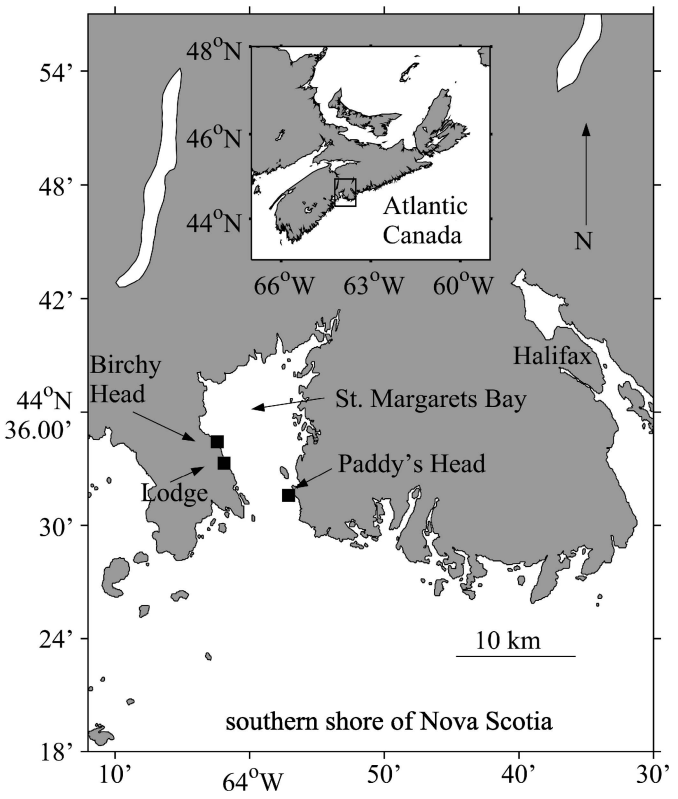

Fig. 2. Study sites located on the southern shore of Nova Scotia, Canada. Temperature data used to force the model and bryozoan population data used to validate the model were obtained from Lodge. The relationship between settlement and growing-degree day used to construct the model were obtained from Paddy's Head. To extend the length of the temperature time series for 2005, additional temperature data were obtained from Birchy Head.

Methods

Model parameterization—An individual-based model that calculates numerical abundance of *M. membranacea* colonies based on settlement and mortality, and size of colonies based on growth, was developed using Matlab 6.5 (The Mathworks). The model was forced at daily time-steps using temperature data (sampled at 10-min intervals and then averaged over 24 h to calculate daily temperature) from a depth of 8 m at Lodge (44°33′3″N, 64°01′9″W), on the western shore of St. Margarets Bay, Nova Scotia (Fig. 2), for January–August from 2005 to 2008 (Fig. 3). For each model run, the model was initiated on 01 January (calendar day 1, hereafter referred to as d1), and run until either d216 (04 Aug) or d240 (28 Aug), depending on the scenario (*see* below).

Colony abundance—At each time-step 't + 1' (day), colony abundance was calculated as

$$N_{t+1} = N_t + S_{t+1} - M_t \quad (1)$$

where N is the number of colonies (m^{-2} kelp), S is the number of new settlers (m^{-2} kelp), and M is the number of colonies (m^{-2} kelp) removed from the population due to mortality.

Colony settlement—The addition of new colonies into the population (settlement, S) was included as a function of the thermal integral, GDD (°C d), which was calculated as

$$\mathrm{GDD}_t = \sum_{1 \to t} T_t + 1.8 \quad (2)$$

where GDD is growing-degree day at time t (day), and T is average daily temperature (°C). In general, the thermal-integral is calculated by sequentially adding temperatures above a threshold value for the process of interest (Neuheimer and Taggart 2007), and because the threshold temperatures for *M. membranacea* growth and development in Nova Scotia are unknown, we selected the freezing point of seawater (−1.8°C) to standardize temperatures to positive values (Saunders and Metaxas 2007). For each year, the model was initiated with 0 colonies on d1, and new colonies of diameter 0.6 mm 'settled' into the population at each time 't' using

$$\log_{10}(S_t + 1) = \alpha_S + \beta_S \mathrm{GDD}_t \quad (3)$$

where S is the number of newly settled colonies (m^{-2} kelp, rounded to the nearest positive integer), GDD is the growing degree-day, and α_s and β_s are regression parameters. Based on empirical data collected in 2005–2006 from 8-m depth at Paddy's Head (44°31′6″N, 63°57′2″W), 7 km SE of Lodge on the eastern side of St. Margarets Bay (Fig. 2), the mean values for the parameters were: α_s = −0.974 colonies m^{-2}, and β_s = 0.00142 colonies m^{-2} °C^{-1} d^{-1} (linear regression: R^2 = 0.65, p = 0.001, calculated from data published in Saunders and Metaxas [2007]). For each set of simulations, we generated a normal distribution of α_s using a standard deviation of ± 5% of the mean value, and then randomly selected a value of α_s from this distribution to use for each individual model run. This variability corresponded to a range of dates for the onset of population growth of ~ 2 weeks (*see* Table 1), which, in turn, corresponded to the additive uncertainty in estimating the timing of onset of settlement in the field of the shortest sampling interval (~ 1 week) and the time that settlers may exist on kelp blades (~ 1 week; Saunders and Metaxas 2007). Variability in β_s was not included because the regression was obtained using data from 2 yr and, thus, the variability in β_s indicated the variability in the relationship among years, rather than the variability in the relationship among individual kelp blades in a single year; additionally, the slope of the relationship between settlement and GDD does not vary between years (Saunders and Metaxas 2007). We used 1 m^2 as the unit surface area to account for the total blade area of ~ 1 mature kelp (M. Saunders unpubl.). Because cover of overwintering colonies on kelp is typically < 0.1% (Saunders and Metaxas 2009*b*; unpubl.), the model was initiated each year with 0 colonies, and assumes that larvae are supplied from colonies overwintering on kelps outside the modeled area. The exponentially increasing function of settlement with GDD is valid only until the peak in settlement in September or October (GDD ≤

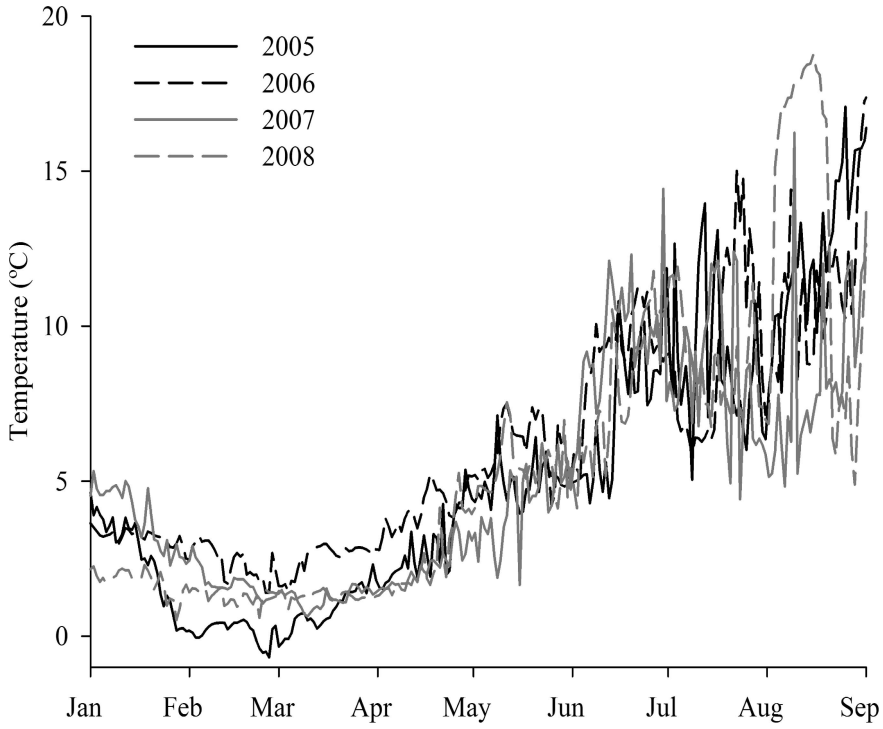

Fig. 3. Daily average temperature (°C) at 8-m depth on the western side of St. Margaret's Bay, Nova Scotia, from 01 January to 30 August 2005–2008. Temperature data were obtained using Pendant data loggers (Onset, accuracy ± 0.47°C) at 10-min intervals. The loggers were affixed to the benthos from 01 January to 01 July 2005 at Birchy Head (44°34′4″N, 64°02′2″W), and from 01 July 2005 to 30 August 2008 at Lodge (44°33′3″N, 64°01′9″W; *see* Saunders and Metaxas [2007] for site descriptions). Data were binned into daily averages.

2400°C d; Saunders and Metaxas 2007), which was within the range of input values used in the model.

Colony mortality—Colonies were removed from the population according to

$$M_t = \sum_{1 \to n_t} P(N_n) \quad (4)$$

where M is the number of colonies removed, and $P(N_n)$ is the probability that each colony n in population N will die each day. Each colony was assigned a constant and size-independent probability of mortality of 1.25% each day. This value was selected as an intermediate value based on the range of values for colony mortality (0–2.5% d^{-1}) estimated for *M. membranacea* on blades of the kelp *S. longicruris* at Lodge, Nova Scotia, in 2005–2009 (M. Saunders unpubl.). The functional relationship between colony mortality and temperature has not been quantified in Nova Scotia, or elsewhere. Therefore, we used the model to explore this relationship under different scenarios (*see Population response to variations in temperature under different rates of mortality*, below).

Colony size—The size of each colony n at $t + 1$ was calculated as

$$D_{t+1,n} = D_{t,n} + G_{t,n} \quad (5)$$

where D is the colony diameter (mm), and G the growth increment (mm) from t to $t + 1$. A linear relationship

Table 1. Day of year (DOY) of onset of population growth of *Membranipora membranacea*, and four indices of winter temperature (winter minimum [°C], winter maximum [°C], winter average [°C], growing degree-day [GDD] on calendar day 74 [d74; 15 Mar; °C d]) in 2005–2008. Modeled day of year (DOY) of onset of population growth depicts the day of first settlement (95th percentile of range of values obtained using the quantile method from 1000 model runs); observed DOY depicts the earliest day that new colonies (which in each year were slightly larger than new settlers) were observed.

	DOY of onset of population growth		Temperature index			
Year	Observed	Modeled	Minimum	Maximum	Average	GDD d74
2005	182	167–180	−0.69	4.62	1.21±1.34	223
2006	141	140–157	1.40	3.64	2.71±0.56	338
2007	147	158–170	0.64	5.32	2.27±1.31	319
2008	173	164–176	0.51	2.29	1.45±0.37	247

between growth rate, temperature, and size was obtained from field measures of individual *M. membranacea* colonies 0.5–128 mm (maximum dimension) in summer at 8.6–16.2°C (Saunders and Metaxas 2009*a*). Using this relationship, growth of each colony n at each time t was calculated as

$$\log_{10} G_{t,n} = \alpha_G + \beta_G \log_{10} D_{t,n} + \chi_G T_t \quad (6)$$

where G is the growth increment (mm), D is colony diameter (mm), T is temperature (°C), and α_G, β_G, and χ_G are regression parameters. We generated normal distributions of each of the regression parameters using their means and standard errors ($\alpha_G = -1.665 \pm 0.086$ mm; $\beta_G = 0.719 \pm 0.032$; $\chi_G = 0.072 \pm 0.008$ mm °C^{-1} [Saunders and Metaxas 2009*a*]). We then randomly selected values for each parameter from these distributions to generate a unique combination of growth parameters for each colony n, which remained constant for the duration of the 'lifespan' of that colony. To limit growth within the range of values observed in the field (0.01–12 mm d^{-1}; Saunders and Metaxas 2009*a*), G was capped at 12 mm for each day. This condition was used only rarely (for example, when a colony settled early in the year, had a combination of 'fast' growth parameters, and was modeled using an unusually warm temperature data-series [*see* 'Numerical experiments' below]) and in those instances resulted in a conservative estimate of size at age. We assumed that colonies grew continuously and did not shrink, and that space was not limiting (e.g., colonies did not grow into one another or run out of substrate). These assumptions are reasonable for the population up until the end of August, when colonies are uncrowded, but would not be met during autumn when colonies are densely aggregated and eventually begin to senesce and shrink (Harvell et al. 1990). Colonies were considered to be 'adults' when they reached a diameter > 2 mm (i.e., excluding new settlers and 'juvenile' colonies [Saunders and Metaxas 2008]).

Output—For each model run, five indices of the population dynamics of *M. membranacea* were calculated: (1) 'Timing,' the day of the year that colonies first settled into the population; (2) 'Total abundance,' the total number of colonies m^{-2}; (3) 'Adult abundance,' the number of colonies > 2 mm m^{-2}; (4) 'Size,' the diameter (mm) of the largest colony in the population; and (5) 'Cover,' the percentage of kelp covered by colonies. The model was run 1000 times for each year (2005–2008) and for each numerical experiment, and data for indices 2–5 are shown for either t = d216 or t = d240 (for comparisons with field observations or for one of the numerical experiments, respectively, *see* below).

A relationship between colony surface area and diameter was estimated from colonies ($n = 100$) measured on blades of the kelp *S. longicruris* collected from 8-m depth at Lodge in September 2009, and was used to calculate the surface area (mm^2) of each colony (A):

$$\log_{10} A_{t,n} = \alpha_x + \beta_x D_{t,n} \quad (7)$$

where D is the diameter (mm) of each colony n at time t, and α_x and β_x are regression parameters ($\alpha_x = -0.14$ [mm^2], $\beta_x = 1.88$ [mm]; linear regression: $R^2 = 0.99$, $p < 0.001$, $n = 100$). The percent cover of colonies on kelp C_t at time t was calculated using

$$C_t = \frac{\sum_{1 \to n} A_{t,n}}{K} \times 100 \quad (8)$$

where A is the surface area (mm^2) of each colony n at time t, and K is the total area of the kelp (mm^2). We assumed that the surface area of the host kelps did not change, likely a valid assumption for summer when growth and erosion rates from the basal and distal ends of the kelp blades, respectively, are similar (K. Krumhansl, Dalhousie University, unpubl.). Moreover, in summer, new *M. membranacea* colonies are not typically located at the distal ends of kelps where erosion is occurring. However, this assumption would not hold in autumn, when blade erosion exceeds growth and kelps undergo a process of seasonal decline. Therefore, the model was only run until August in all scenarios.

Model validation and sensitivity—The model was validated by comparing 'modeled' estimates of the five indices of the population dynamics to 'sampled' field estimates. For the sampled date of onset of population growth, the model was validated using the earliest day of the year that new colonies were observed in St. Margarets Bay (2005–2006: Saunders and Metaxas [2007]; 2007–2008: M. Saunders unpubl.). In all years, the diameter (mm) of the largest new colony (assumed to be the oldest) found on the earliest date was larger (0.7–9.7 mm) than settler size (< 0.6 mm). New colonies were easily distinguished from colonies from the previous year that had overwintered because they were round, did not contain brown bodies (Menon 1972), and were not fouled.

For the sampled estimates of colony abundance, size, and cover, colonies of *M. membranacea* on the kelp *Saccharina longicruris* were quantified at 8-m depth at Lodge, St. Margarets Bay, Nova Scotia, on 04 August 2005 and 02 August 2006 (sampling details are given in Saunders and Metaxas [2007, 2008]; 'total colonies' are the sum of settlers, juvenile and adult colonies). Therefore, comparisons between sampled and modeled estimates of abundance (total and adult colonies m^{-2} kelp), colony size (diameter, mm), and percent cover of colonies were made for d216 (04 Aug) in 2005 and 2006. We elected to use this single date for several reasons. First, early August is the first day of the year where data from the sampled population are available for the same date in both 2005 and 2006 (Saunders and Metaxas 2007, 2008). Data for earlier in the year were obtained in July in 2005 and for May and June in 2006 (Saunders and Metaxas 2007, 2008). Furthermore, earlier in the season, measuring very small and rare colonies on large kelp blades presented logistical difficulties and compromised accuracy. We did not use the model to simulate the population in autumn, because parameters for kelp growth and erosion are not currently available. We suggest, rather, that the modeled population in August integrates parameters for settlement, growth, and mortality from the previous months.

The data used to force and validate the model were obtained from 8-m depth at Lodge, which are independent from those data used to construct the model. The relationship between settlement and GDD was obtained from a different site (Paddy's Head), and is very similar to the one from Lodge. Therefore, data from the population at one site can be used to model the population at the other site. The data can be considered independent in the sense that colonies settle at one location, and once settled cannot move to other locations; thus, settlers at Paddy's Head are independent of colonies existing at later dates at Lodge. Growth data were obtained from a range of depths at various locations (Saunders and Metaxas 2009*a*) and, thus, represent a population-wide measure.

To examine the sensitivity of the model, each of the modeled parameters used in estimating settlement (α_s, β_s), mortality ($P[N_n]$), and growth (α_G, β_G, χ_G; Eqs. 3, 4, and 6, respectively) was varied by either 10% or −10%, while all other parameters were maintained as previously described and the model was run using the 2005 temperature data. For each scenario, the average values for the population dynamic indices (timing of settlement, adult abundance, total colony abundance, size, and cover), for 100 model runs was divided by the average values obtained using the standard model. In general, results were most sensitive to variations in the growth parameters; this variability was incorporated into the model by varying the growth rate of each individual colony (Eq. 6). Variability was included in each parameter of the model except for $P(N_n)$ and, thus, the effect of varying $P(N_n)$ was explored using the model (*see Population response to variations in temperature under different rates of mortality*, below).

Numerical experiments

Population response to variations in temperature: To quantify the effect of changes in temperature on the population dynamics of *M. membranacea*, for each of 1000 model runs, a randomly selected value between −2°C and +2°C (ΔT) was added to observed daily temperature for each consecutive day from d1 to d216 in 2005 (Magnitude of temperature-d216). ΔT was maintained at a constant value for each model run, and the indices of the population dynamics were determined on d216. The 2005 data series was used because the *M. membranacea* population was sampled extensively during that year (Saunders and Metaxas 2007, 2008). The seasonal trends in temperature for 2005 were typical for the region and not unusually warm (unlike winter 2006; Fig. 3); therefore, an increase in daily temperature of up to 2°C for this series was within the range of observed interannual variability, and the results of the simulations are realistic for warmer years within the contemporaneous climate regime. Furthermore, average increases of up to 2°C by the end of the 21st century are predicted for the western North Atlantic under the most conservative global climate models (IPCC 2007). To obtain mean values for specific incremental changes in temperature, population indices were also calculated for d216 for 1000 model runs for each scenario of −2, −1, 0 (Baseline-d216), +1, and +2°C added on each day (e.g., 1000 model runs with 2°C subtracted each day, 1000 runs with 1°C subtracted each day, etc.).

Population response to variations in temperature under different rates of mortality: To examine the effect of colony mortality rate on the population, we incorporated different scenarios for mortality in the numerical experiment *Population response to variations in temperature* (Magnitude of temperature-d216). Based on estimates from the field, colony mortality rate at temperatures < 8°C was 0%, and the highest rate (2.5%) was observed when water temperatures were the warmest (14°C; M. Saunders unpubl.). To explore the potential for temperature-dependent mortality to limit the *M. membranacea* population, we derived the probability of colony mortality from a linear relationship with temperature, with a probability of mortality of 0% at ≤ 8°C, and 2.5%, 5%, or 10% at 14°C. In this numerical experiment, we used five scenarios, each with a different probability of colony mortality: (1) 0% (constant); (2) 1.25% (constant, same as 'Magnitude of temperature-d216'); (3) 2.5% (temperature dependent); (4) 5% (temperature dependent); and (5) 10% (temperature dependent). For each population index (except day of onset of population growth, which did not vary with mortality rate) under each mortality scenario, data were $\log_{10}$-transformed and modeled using second- or third-order polynomial equations with 95% confidence intervals.

Population response to the timing of a warm month: To examine the effect of the seasonality of warming temperatures on the *M. membranacea* population, the temperature of the 2005 data series was raised by 2°C each day for 30 consecutive d to simulate a month with a positive temperature anomaly. For each of 1000 model runs, the first of the 30 d on which temperature was raised (day of onset of 'warm month') was randomly selected between d1 (01 Jan) and d210 (29 Jul; Random warm month-d240), and the model was run until d240 (28 Aug), when the indices of the population were calculated. To quantify specific seasonal effects, the population indices were also calculated from 1000 model runs for each of four scenarios: (1) +2°C on d1–d31 (Winter warm month-d240); (2) +2°C on d120–d150 (Spring warm month-d240); (3) +2°C on d210–d240 (Summer warm month-d240); and (4) no increase in temperature (Baseline-d240). The indices of the population on d240 calculated for the random, winter, spring, and summer scenarios were standardized by dividing by the Baseline-d240 population. In these scenarios, variability in α_s, the intercept of the settlement vs. GDD relationship, was not included, because it obscured differences in population indices attributable to the warm month. This was because the effect of a warm month changed the timing of onset of settlement by only up to 6 d, which was less than the variability in the timing of onset of settlement when variability was included in α_s.

Statistical analyses—The timing of onset of population growth of ectothermic organisms is frequently linked to temperature the preceding winter. To examine this process in *M. membranacea*, for each year, the day of onset of population growth in the modeled and sampled populations was compared to indices of temperature from the preceding winter. For each year, minimum and maximum

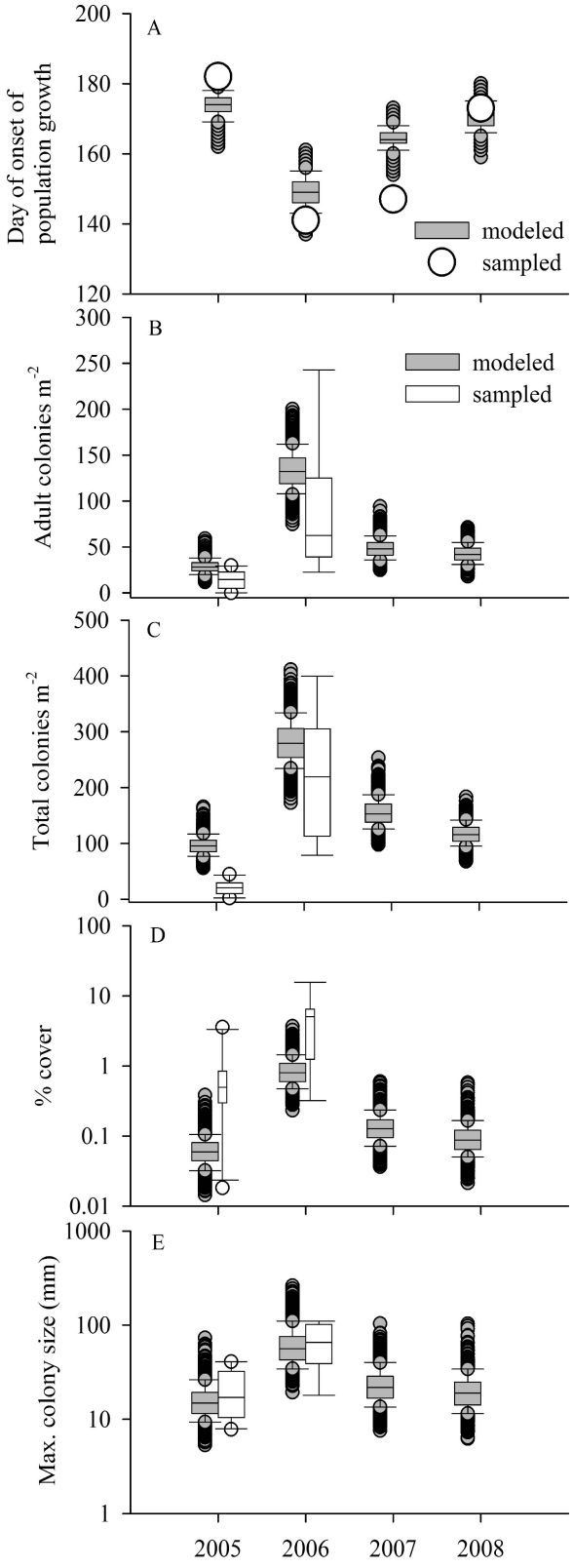

Fig. 4. Sampled (n = 9–10) and modeled (n = 1000) estimates of population characteristics for *M. membranacea* at 8 m at Lodge, St. Margarets Bay, Nova Scotia, in 2005–2008: (A) timing of onset of population growth (day of year), (B) total colony abundance (m^{-2}), (C) adult colony abundance (m^{-2}), (D) maximum colony size (mm), and (E) percent cover on kelp. In each instance, the line within the box marks the median, the boundaries of the box indicate the 25th and 75th percentile, the error bars indicate the 90th and 10th percentiles, and circles indicate outliers. Sampled values were not available for 2007 and 2008. Modeled values for 2005 provide the 'Baseline-d216' estimate for the numerical experiment on the effect of variations in temperature. Data for B–E are population estimates for d216 (04 Aug).

temperature were defined as the warmest (n = 1) and coldest (n = 1) daily temperature observed from d1 to d90 (Jan–Mar), respectively. Average winter temperature was calculated as the mean of daily temperatures between d1 and d90 (Jan–Mar; n = 90). The effect of GDD on d74 (15 Mar) was examined because mid-March is typically the annual thermal minimum in Nova Scotia. We compared the effects of approach (sampled, modeled [mean DOY from 1000 model runs]) on the estimates of the date of onset settlement in each year (2005, 2006, 2007, 2008) using ANCOVA, with day of the year of onset of the population as the dependent variable, approach as a fixed factor, and winter temperature (separate models for each of 4 indices: minimum, maximum, average, and GDD on d74) as a covariate. Full models were run to test for an interaction between approach and temperature; because the interactions were not significant, a reduced model was run using only the main factors. Statistical analyses were conducted using SPSS 15.0.

Results

Model validation

Timing of settlement: Depending on year (2005–2008), the 95% confidence intervals for the modeled estimate of timing of onset of population growth overlapped, or fell within 11 d of the sampled date (Table 1; Fig. 4A). There was no effect of approach (sampled, modeled) on the relationship between timing of onset of population growth and winter temperature for any temperature scenario (Table 2). Timing of onset of population growth was explained by each of minimum winter temperature, average winter temperature, and GDD on d74 (15 Mar), but not by maximum winter temperature (Table 2), with earlier onset of population growth in years with warmer winters.

Colony abundance, size, and cover: In 2005 and 2006, the 95% confidence intervals for each index of the population (except for total colony abundance in 2005), overlapped between the modeled and sampled populations (Fig. 4). The sampled estimates of total colony abundance in 2005 may be lower than the modeled estimates due to difficulty in sampling small, rare, newly settled colonies early in the season, considering that the modeled and sampled estimates of adult colony abundance in 2005 overlap. Also, the temporal trends in the population characteristics were similar between the modeled and sampled populations in 2005 and 2006 (Fig. 4). The model predicted that total and adult colony abundance, maximum size, and percent cover of *M. membranacea* were all highest

Table 2. Results of ANCOVA examining the effect of approach (sampled, modeled) and winter temperature index as a covariate (winter minimum, winter maximum, winter average, growing degree-day [GDD] on 15 Mar [d74]) on the timing of onset of *Membranipora membranacea* population growth in 2005–2008. Bold values indicate significant effects. SS = sum of squares, MS = mean square.

Factor	SS	df	MS	*F*	*p*
Minimum temperature	1097	1	1097	12	**0.018**
Approach	28	1	28	0.3	0.60
Error	457	5	91	—	—
Adjusted R^2	0.60	—	—	—	—
Maximum temperature	35	1	35	0.12	0.75
Approach	28	1	28	0.09	0.77
Error	1518	5	304	—	—
Adjusted R^2	0.34	—	—	—	—
Average temperature	1370	1	1370	37	**0.002**
Approach	28	1	28	0.8	0.42
Error	184	5	37	—	—
Adjusted R^2	0.84	—	—	—	—
GDD d74 (15 Mar)	1342	1	1342	32	**0.002**
Approach	28	1	28	0.7	0.45
Error	212	5	42	—	—
Adjusted R^2	0.81	—	—	—	—

in 2006 compared to other years (Fig. 4). This corresponds to observations of an outbreak of *M. membranacea* in autumn 2006 that resulted in a 70% decrease in the canopy cover of kelp on the benthos (Saunders and Metaxas 2008). Furthermore, for all years, the modeled estimates of the relationship between percent cover and the number of colonies was within the 95% prediction intervals of the sampled estimates (Fig. 5). In sum, the model appears to simulate the indices of the *M. membranacea* population in early August.

Population response to variations in temperature—Cooling or warming the temperature series by up to 2°C on each consecutive day from January to August (Magnitude of temperature-d216) yielded pronounced differences in timing of settlement, and the abundance, size, and coverage of colonies on kelp at the beginning of August (Fig. 6). In general, warming temperatures caused settlement to occur earlier in the season, and colonies to be more abundant, larger, and to occupy greater area on kelps (Fig. 6). The day of first settlement advanced linearly as a function of variation in temperature (Fig. 6A) and the rate was described by the equation

$$D_s = 174 - 18\Delta T \tag{9}$$

where D_s is the day of onset of settlement, and ΔT is the change in daily temperature between d1 and d216 (adjusted $r^2 = 0.97$, $F_{1,997} = 3.0 \times 10^4$; $p < 0.001$). There were

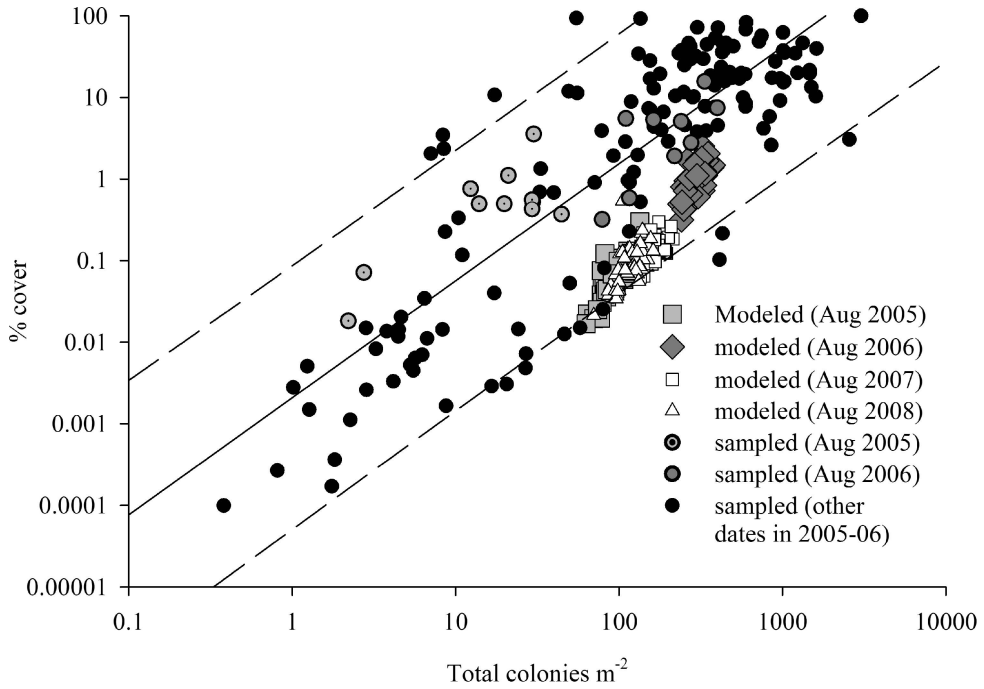

Fig. 5. Comparison of the relationship between the percent cover and the number of colonies (m^{-2}) from modeled and sampled estimates of the *M. membranacea* population. Sampled estimates were quantified on blades of the kelp *Saccharina longicruris* obtained at 8-m depth at Lodge, St. Margarets Bay, Nova Scotia, at weekly–monthly intervals from 01 July 2005 to 19 November 2006 (*see* Saunders and Metaxas [2007, 2008] for sampling details). The solid and dashed lines are regression (log[percent cover] = −2.68 + 1.43log[total colonies]; $p < 0.001$; adjusted $R^2 = 0.71$) and 95% prediction intervals around the sampled values, respectively.

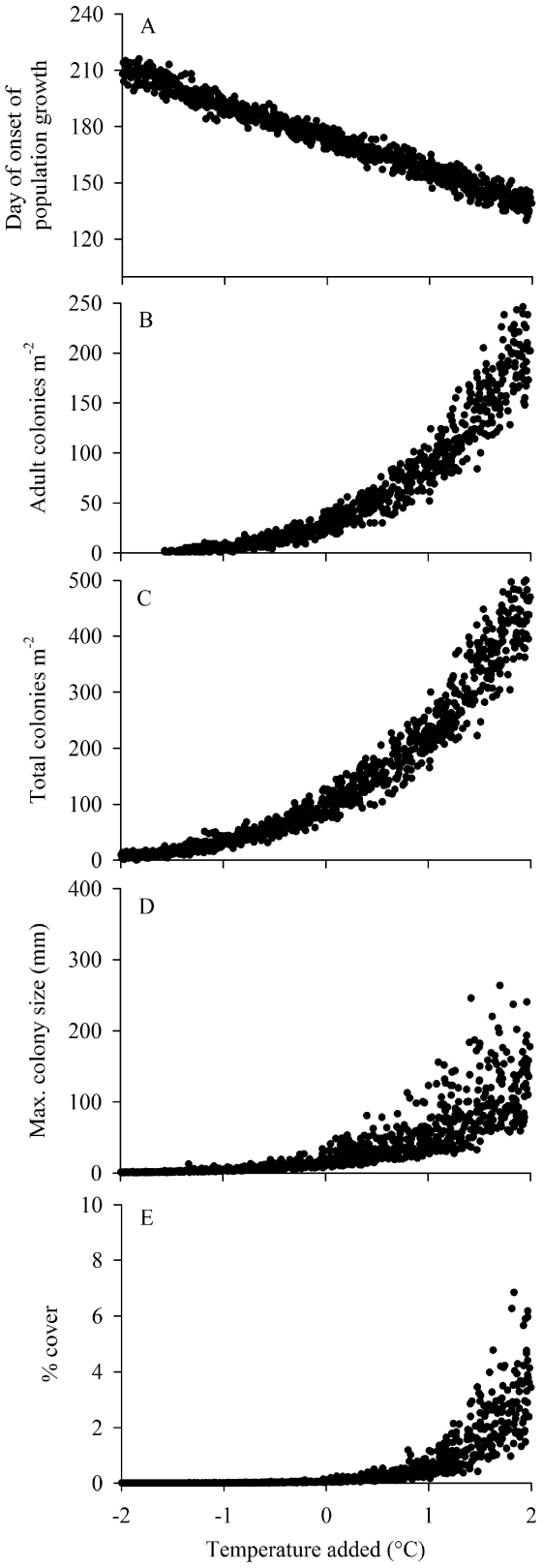

Fig. 6. Response of the modeled *M. membranacea* population to variations in temperature (Magnitude of temperature-d216): (A) timing of settlement (onset of population growth), (B) adult colony abundance, (C) total colony abundance, (C) maximum colony size, and (D) % cover on kelp. Each data point represents the population results from one model run simulated using the 2005 temperature series that had been varied by a constant value between −2°C and +2°C d^{-1} from d1 to d216 (01 Jan–04 Aug).

nonlinear relationships between ΔT and adult colony abundance, colony size, and cover on kelp (Fig. 6). A 1°C increase in temperature resulted in a doubling of the abundance of colonies; a tripling of the maximum colony size and of the abundance of adults; and an increase by a factor of nine in the cover on kelp (Table 3). A 2°C increase in temperature resulted in a five-fold increase in the abundance of colonies, a nine-fold increase in the maximum size, an eight-fold increase in the abundance of adult colonies, and 62-fold increase in the cover on kelp (Table 3). Conversely, decreases in daily temperature of 1–2°C resulted in the presence of few (3.9–33 m^{-2}), very small (max. size 0.8–4.1 mm) colonies with a minute (0.0002–0.006%) coverage on kelps (Table 3). A decrease in daily temperature of 2°C also resulted in the absence of adult colonies in the population (Table 3).

Population response to variations in temperature under different rates of mortality—For each index of the population (adult and total colony abundance, colony size, and cover), there were negligible differences among mortality scenarios when the temperature series was cooled (ΔT −2°–0°C; Fig. 7); however, when the temperature of the 2005 data series was warmed, the effects were noticeable. Unsurprisingly, abundance of adult and total colonies, colony size, and cover on kelp were all higher when probability of mortality was 0% than when mortality was included in the model. Results were very similar when probability of mortality was 1.25% (constant), 2.5% (temperature dependent), and 5% (temperature dependent). Pronounced decreases in each of the population indices (relative to those in 'Magnitude of temperature-d216', $P(N_n)$ = 1.25% [constant]) occurred when the probability of mortality was 10% (temperature dependent). The latter scenario also resulted in an asymptote of curves for colony abundance, size, and cover under warming conditions, which was not observed for the other scenarios.

Population response to the timing of a warm month—The effect of warming by 2°C each day for 1 month (30 consecutive d) on the timing of onset of settlement, total colony abundance, adult abundance, and cover of colonies on kelp depended on the timing of the temperature increase (Fig. 8 [Random warm month-d240]). Colonies settled up to 6 d earlier when warming occurred during winter and spring, but not when it occurred during summer (Table 4; Fig. 8A). The proportional (relative to the 'Baseline-d240' population) increase in the total number of colonies was lower when water temperatures warmed later in the season (Table 4; Fig. 8B). The proportional change in the abundance of adult colonies generally followed a similar trajectory, increasing the most (1.27×) as a result of warming in winter and spring, and the least (1.23×) as a

Table 3. Indices (mean ± SD from 1000 model runs) of the modeled *Membranipora membranacea* population on d216 as a result of consistent variations (°C d^{-1}) in the 2005 temperature series from d1 to d216. Also shown are values standardized to the 'Baseline-d216' scenario ($\Delta T = 0$°C). For example, an increase in daily temperature of 2°C resulted in an increase in the percent cover of *M. membranacea* on kelp by a factor of 62 relative to the results obtained from the unmanipulated temperature data series.

	Change in temperature (°C d^{-1})				
	−2	−1	0 (Baseline-d216)	1	2
Indices (mean±SD) of modeled population					
Timing of settlement (DOY)	212±3	191±3	174±3	157±4	139±4
Adult abundance (m^{-2})	0.00±0.00	5±3	29±7	87±15	216±31
Colony abundance (m^{-2})	3.9±3.3	33±8	97±16	225±31	482±61
Size (max. diameter, mm)	0.8±0.17	4.1±1.9	17±8	56±29	151±70
Cover (%)	0.0002±0.0002	0.006±0.003	0.07±0.04	0.6±0.3	4.2±1.9
Mean of values standardized to mean of baseline values					
Timing of settlement (DOY)	1.2	1.1	1	0.9	0.8
Adult abundance (m^{-2})	0	0.2	1	3	8
Colony abundance (m^{-2})	0.04	0.3	1	2	5
Size (max. diameter, mm)	0.05	0.2	1	3	9
Cover (%)	0.003	0.1	1	9	62

result of warming in summer (Table 4; Fig. 8B). A shift in this trajectory beginning on d203 (22 Jul) is the result of a large number of settlers transitioning into the > 2-mm size class because of fast growth. In turn, this accelerated growth was realized because of the additive effects of increasing temperature during the period when observed water temperature was already the highest (Fig. 3). While the maximum colony size was extremely variable and there was no linear trend with respect to the timing of warming (Fig. 8C), the greatest proportional increase (1.6×) was caused by warming in summer (Table 4). Percent cover on kelp also increased the most as a result of warming in summer (3×), and was equally affected (1.5×) by warming in winter and spring (Table 4; Fig. 8D).

Discussion

Effects of warming on outbreak dynamics—Changes in temperature associated with climate change are predicted, and have already started, to have pronounced effects on the distributions and abundances of the earth's biota (McCarty 2001; Walther et al. 2002; IPCC 2007). In general, introduced species have been predicted to benefit more from global change than native species (Dukes and Mooney 1999).

Our numerical experiments suggest that warmer winters and springs will result in colonies of the nonindigenous bryozoan *Membranipora membranacea* occurring earlier and in higher abundance in the western North Atlantic, and warmer temperatures during the growth period will result in colonies occupying a larger coverage on kelps. Given that warming during both the pre- and postonset of settlement period result in increased bryozoan abundance, the most pronounced outbreaks of *M. membranacea* should occur during years with temperatures that are warmer both in winter and summer. However, changes in temperature after the settlement period will have a relatively greater effect on coverage of bryozoan on kelp than changes before settlement and, therefore, warmer summers in particular will increase the probability of kelp bed defoliation. Field observations over a 10-yr period recorded a significant relationship between percent cover of *M. membranacea* on kelp in autumn and the thermal integral from August to October, but not from January to June (Scheibling and Gagnon 2009). It is possible that populations could be regulated by the occurrence of temperatures above deleterious levels. For example, in southern California, colonies of *M. membranacea* are least abundant in summer when mean monthly sea surface temperature exceeds 20°C (Bernstein and Jung 1979). However, it would take considerable warming for average monthly summer temperature to reach > 20°C in Nova Scotia, where it is currently ~ 15°C during the warmest period in August and September. Furthermore, the upper thermal threshold of *M. membranacea* is higher than temperatures are likely to reach in Nova Scotia. For colonies of *M. membranacea* obtained from North Sea and acclimated to temperatures of 6–18°C in the laboratory, colony mortality was 100% over 24 h at 25–27.5°C, with 0% mortality observed at 20°C (Menon 1972). The range of *M. membranacea* in low latitudes may be expected to recede as temperatures warm, as is generally predicted for a variety of species (Harley et al. 2006). In our model, decreasing temperature resulted in extremely low abundance, size, and cover of *M. membranacea* in August, suggesting that the population in Atlantic Canada is near the cold end of the thermal range.

Kelp beds have the ability to recover from typical levels and frequencies of disturbance (Dayton et al. 1999). For example, in Nova Scotia, kelp beds recruit and form closed canopies within 1–4 yr of disturbance (Johnson and Mann 1988). Following the first recorded severe outbreak of *M. membranacea* in 1993, kelps recovered fully and reformed the canopy at Little Duck Island, Nova Scotia, by the following year (Scheibling et al. 1999). However, increased frequency of disturbance likely diminishes a system's capacity to recover (Dayton et al. 1999). After successive bryozoan outbreaks in 1997 and 1999, the kelp canopy at Little Duck Island did not recover and was instead replaced

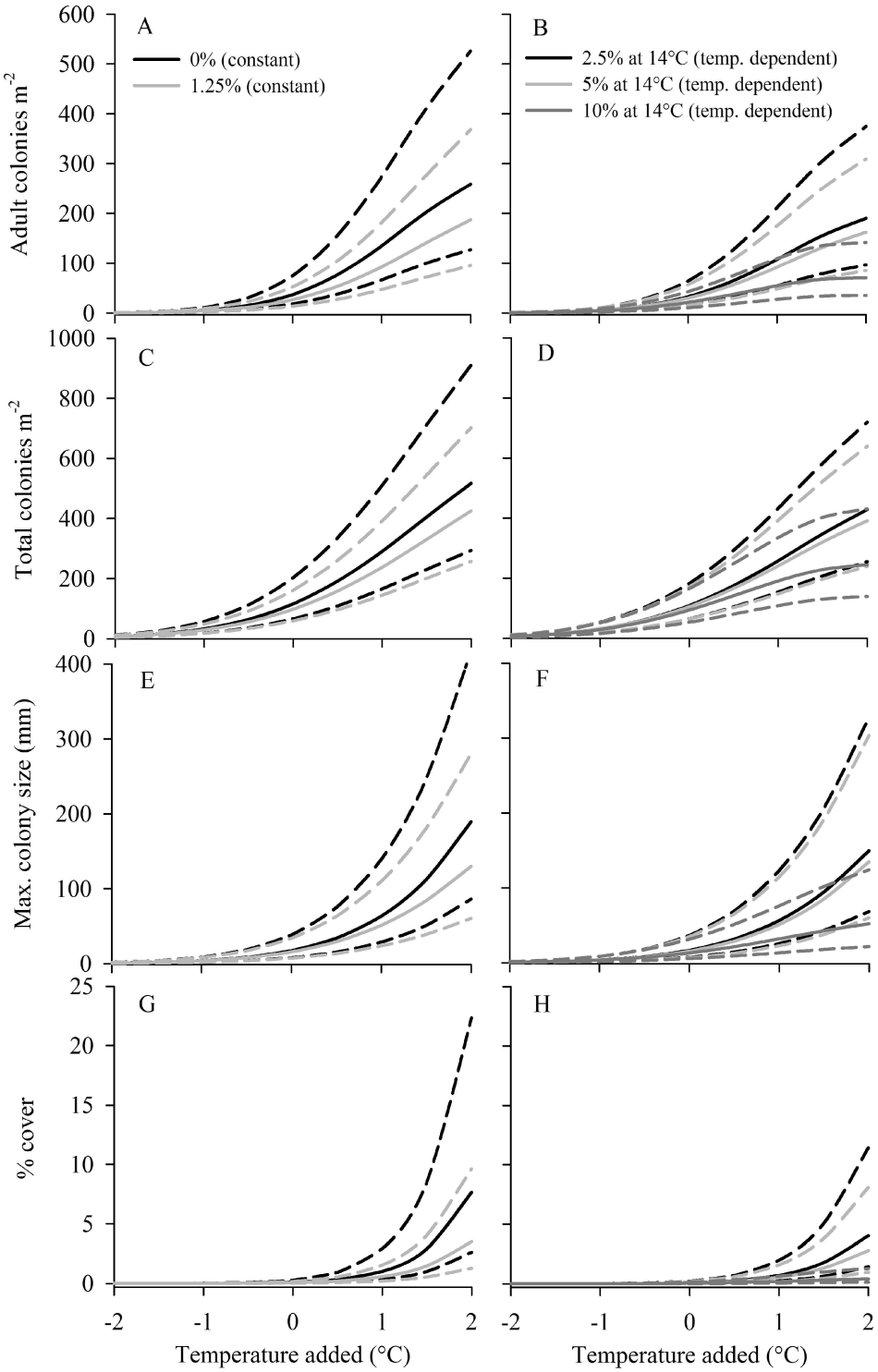

Fig. 7. Response of the modeled *M. membranacea* population on d216 (04 Aug) to variations in temperature under varying conditions for colony mortality rate: (A, B) adult colony abundance (m^{-2}), (C, D) total colony abundance (m^{-2}), (E, F) maximum colony size (mm), and (G, H) % cover on kelp. Solid lines represent polynomial regressions through the modeled data from 1000 model runs using a random value for temperature added for each run. Dashed lines indicate 95% confidence intervals. Simulations using a temperature-dependent varying rate of colony mortality (B, D, F, H) included 0% mortality up to 8°C, and a linearly increasing rate using the reported value (2.5%, 5%, or 10%) at 14°C.

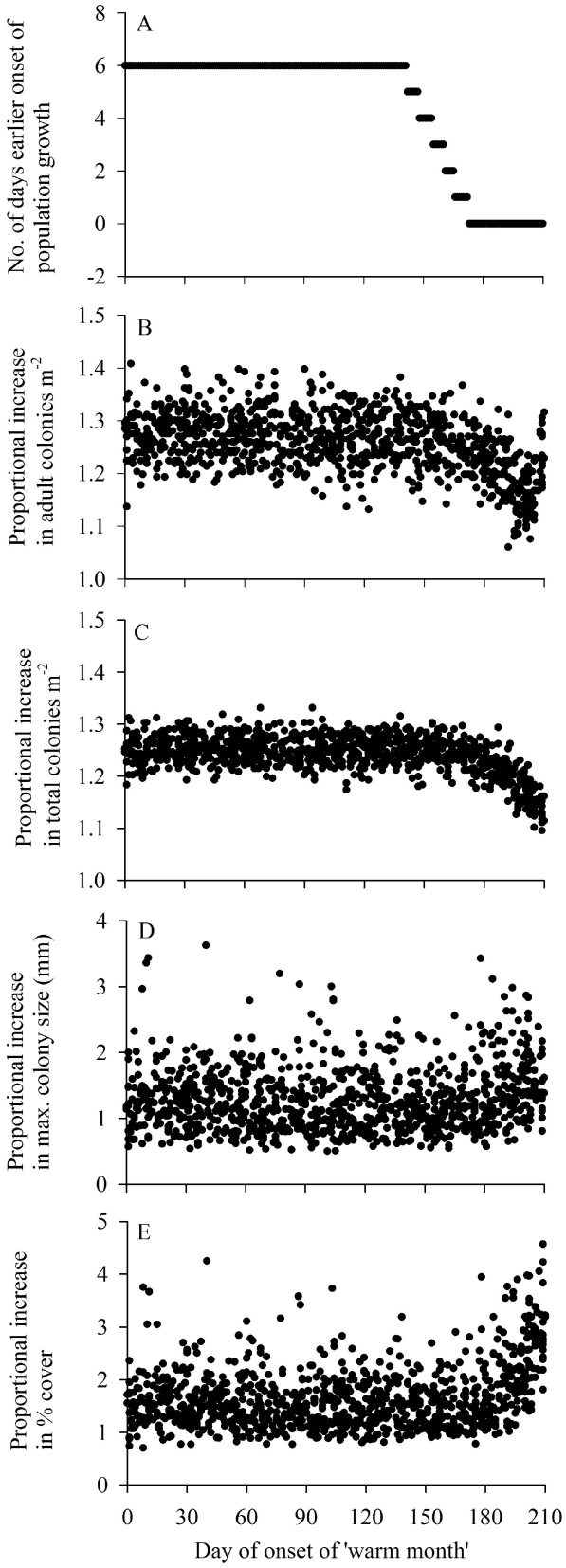

Fig. 8. Response of the modeled *M. membranacea* population on d240 (end of Aug) to a warm month (an increase in temperature of 2°C each day for 30 consecutive d) commencing on randomly selected dates between d1 and d210 (Random warm month-d240): (A) timing of settlement (onset of population growth), (B) adult colony abundance,; (C) total colony abundance, (D) maximum colony size, and (E) % cover on kelp. Values were standardized to the mean values obtained using 1000 model runs of the unmanipulated temperature series from 2005—they are presented as the proportional increase relative to Baseline-d240 (no temperature change) values.

by a meadow of *C. fragile*, which persisted for several years (Chapman et al. 2002). Kelps are cold-adapted species that occur in temperate and subarctic regions, and for *Saccharina longicruris*, the optimum and maximum temperature for survival are ~ 10°C and 23°C, respectively (Bolton and Lüning 1982). In the western North Atlantic, warming temperatures will likely favor more thermally tolerant algal species, such as *C. fragile*, over kelps (Harris and Tyrrell 2001). Thus, warming temperatures and the resultant increase in outbreaks of *M. membranacea* will likely have synergistic negative effects on kelp beds. Changes in the production rate of kelp beds will have important effects on associate nearshore communities that rely on its export in the form of detritus (Harley et al. 2006), which may or may not be compensated for by the production of other algae. While *M. membranacea* has been observed on other algal substrates in kelp beds, including *C. fragile* (M. Saunders pers. observation), it is unclear to what extent the invasive bryozoan is able to persist on alternative algal substrates in the absence of kelps. If successive severe outbreaks of *M. membranacea* result in loss of kelp beds, the epiphytic bryozoan may eventually only achieve low population abundance because of decreased availability of its preferred substrate.

We have demonstrated using both field and modeling approaches, that winter temperature determines the timing of onset of settlement of *M. membranacea* in spring, with an 18-d shift (Eq. 9) in the timing of the population predicted per 1°C change in daily temperature. Similar results have been observed for the timing of recruitment and maximum abundance of nonindigenous tunicates in New England, although timing of recruitment of native tunicates was not equally affected (Stachowicz et al. 2002). On a global scale, average surface warming of 0.7°C from 1906 to 2005 (IPCC 2007) has been associated with pronounced shifts in the phenology (timing of seasonal activities of organisms) and distributions of many organisms, including birds, plants, and insects (McCarty 2001; Walther et al. 2002), and plankton (Edwards and Richardson 2004; Hays et al. 2005). However, clearly, the phenological response to changing conditions varies among organisms. For example, meroplankton typically have a more pronounced response to changing temperature than holoplankton (Hays et al. 2005), and the timing of occurrence of zooplankton grazers has advanced less in response to warming than that of phytoplankton upon which they graze (Edwards and Richardson 2004; Winder and Schindler 2004). By decoupling relationships with other species, shifting the phenology of a particular organism can have significant effects on the associated

Table 4. Indices (mean ± SD from 1000 model runs for each scenario) of the modeled *Membranipora membranacea* population on d240 as a result of a 2°C increase in daily temperature in the 2005 temperature series over 30 d (warm month). The 'warm month' commenced on d1 (winter warm month-d240), d120 (spring warm month-d240), and d210 (summer warm month-d240). For the Baseline-d240 scenario the temperature series was not manipulated (no warming). Also shown are values standardized to the Baseline-d240 scenario. For example, warming in summer caused the percent cover of *M. membranacea* on kelp to increase by a factor of 3.04 relative to the results obtained from the unmanipulated temperature data series.

	Day of year of onset of 'warm month'			
	Baseline-d240 (0°C change)	d1 (winter)	d120 (spring)	d210 (summer)
Indices (mean±SD) of modeled population				
Timing of settlement (DOY)	174	168	168	174
Adult abundance (m^{-2})	195±8	247±9	248±9	240±9
Colony abundance (m^{-2})	317±7	397±8	397±8	359±7
Size (max. diameter, mm)	106±41	129±48	130±50	167±46
Cover (%)	2.4±0.7	3.6±1.1	3.7±1.1	7.2±1.7
Values standardized to baseline				
Timing of settlement (DOY)	1	0.97	0.97	1
Adult abundance (m^{-2})	1	1.27	1.27	1.23
Colony abundance (m^{-2})	1	1.25	1.25	1.13
Size (max. diameter, mm)	1	1.22	1.22	1.57
Cover (%)	1	1.52	1.54	3.04

ecosystem (Harley et al. 2006). Timing of key life-history events, such as spawning or germination, can have a significant effect on later portions of the life cycle. For example, in the western Wadden Sea, there was a significant effect of timing of spawning on the growth and development rates of larvae of the clam *Macoma balthica* (Bos et al. 2006). The timing of occurrence of populations also has implications for their interactions with the abiotic environment. For *M. membranacea*, advancing the season so that coverage on kelps occurs earlier will increase the likelihood that blades will be highly encrusted before the onset of autumn storms (Saunders and Metaxas 2008), leading to defoliation of kelp beds.

Although we focus on the implications of warming in this system, global circulation models cannot presently accurately predict the magnitude or direction of change in temperature at regional scales such as on the Scotian Shelf. However, on a larger spatial scale, the most conservative estimates suggest that sea surface temperature in the western North Atlantic will rise by 1.5–2°C by the end of the 21st century, and less conservative estimates suggest a rise of 3.5°C (IPCC 2007). Interestingly, in Nova Scotia, there has been an increase in spring GDD from 1992 to 1999 (Scheibling and Gagnon 2009), coinciding with the period of invasion and expansion of the *M. membranacea* population in Atlantic Canada. On a global scale, climate change will not only cause changes in water temperature, but also in ocean chemistry, circulation, the frequency and intensity of storms, ultraviolet radiation, salinity, productivity, and biological communities, which may have equally pronounced effects on the distributions and abundances of marine organisms (Hays et al. 2005; Harley et al. 2006). Although the interactive effects of these factors will need to be measured to predict the outcomes of climate change on marine biota (Harley et al. 2006), changes in temperature will have a relatively important role in determining the population outcomes of those species exhibiting thermally controlled outbreak dynamics.

Model success and limitations—Using a single input variable, temperature, our model successfully simulated the earlier settlement, larger colony size, and higher abundance of *M. membranacea* that were observed in St. Margarets Bay, Nova Scotia, in 2006 relative to 2005 (Saunders and Metaxas 2007, 2008). Although field estimates of the population were not available for 2007 and 2008, *M. membranacea* occurred on kelps in Nova Scotia during those years, but unusually severe outbreaks resulting in significant loss of kelp were not observed (M. Saunders, pers. observation).

Colony mortality rates of *M. membranacea* in the introduced range in the western North Atlantic have not been well-quantified, although our (unpubl.) data from summer and autumn 2005, 2006, and 2009, indicate mortality rates of ~ 0–2.5% d^{-1} on blades of *S. longicruris*. These rates are lower than those reported for the San Juan Archipelago, Washington, of up to 7% d^{-1} (derived from data in Harvell et al. [1990]), a reasonable pattern because *M. membranacea* is nonnative in Nova Scotia and, thus, likely has fewer predators ('Enemy release hypothesis' [Wolfe 2002]). Because colony mortality rates, or the functional relationship between colony mortality and temperature, have not been well-parameterized, we used the model to explore the effects of mortality on the population. Using a constant probability of colony mortality of 1.25%, or a probability of mortality that increased linearly with temperature from 0% at 8°C up to 2.5% or 5% at 14°C, had very little effect on the variation in population indices with temperature. However, when the mortality rate was increased to a level higher than is likely to occur (10% at 14°C), there were pronounced decreases in population size. In sum, the model results suggest that within a range of ecologically relevant levels for mortality, the results are not highly sensitive to the parameter for probability of mortality.

A potential limitation of our model is that every year the population was initiated with 0 colonies, and the entire

population in August was based on colonies that had settled from larvae from a regional source. The rare overwintered colonies observed in sampled populations likely contribute to the coverage on kelp in August, while not significantly influencing the number of colonies in 'typical' years. However, in certain years, for example following warmer winters, relatively larger quantities of colonies may survive (Saunders and Metaxas 2009*b*). By not including overwintered colonies, our model provides a conservative estimate of the abundance and coverage of colonies under warming scenarios.

Although we consider the simplicity of our model its greatest strength, it is very likely that parameters other than temperature, particularly food availability, also affect the population dynamics of *M. membranacea*. Bryozoans feed on phytoplankton and, thus, variations in phytoplankton concentration will directly affect the growth of colonies (O'Dea and Okamura 1999). In Nova Scotia, phytoplankton concentrations vary seasonally, with the highest abundance occurring during the spring bloom in March, and a smaller peak in abundance in October. The spring bloom occurs when water temperatures are too cold (typically -1.5–4°C; Greenan et al. 2004), for food availability to have a significant effect on colony growth (O'Dea and Okamura 1999; Saunders and Metaxas 2009*a*). Indeed during this time of the year the very few overwintering colonies present are senescent. Chlorophyll concentrations in late spring and summer (the period we have modeled) are low (usually $\sim$ 1 mg m^{-3}; Greenan et al. 2004) and may vary on short (hourly to weekly) time scales due to tidal and wind-driven processes (Côté and Platt 1983). We have incorporated variability in colony growth into the model based on in situ measurements of colony growth that were obtained at numerous site $\times$ depth combinations over several time periods in several years and, thus, encompass a range of phytoplankton concentrations encountered in the field (Saunders and Metaxas 2009*a*).

Our model uses temperature from January to August to predict abundance of *M. membranacea* during those times, and demonstrates that warmer temperatures in summer have a relatively greater effect on bryozoan coverage on kelps than warming earlier in the season. However, the highest abundance of *M. membranacea* occurs in autumn, and it is during autumn storms that defoliation events occur. Warming temperatures in September or October will likely cause similarly (or in fact even more pronounced) increases in bryozoan cover. To accurately represent the population dynamics of *M. membranacea* in autumn, information on colony shrinkage and mortality rates, as well as the parameters for peak and declining settlement and growth will be required. Furthermore, the population dynamics of kelps (growth and erosion, bryozoan- and wave-dependent breakage rates, and recruitment) will also need to be parameterized and incorporated in the model. Nonetheless, the strong agreement between the modeled and sampled estimates of *M. membranacea* timing of settlement and colony abundance in our study suggest that temperature is indeed the primary driver of population dynamics up until August at the onset of the autumn outbreak.

In summary, using an individual-based model based solely on temperature, we were able to simulate interannual patterns in the timing and abundance of the introduced bryozoan *Membranipora membranacea* in Atlantic Canada. We found a nonlinear relationship between variations in temperature and the measured abundance, size, and percentage cover of colonies. Temperature during the winter determined the timing of settlement the following spring and affected the abundance of bryozoan during summer. However, temperature during the growth period in summer had a relatively greater effect on the cover of colonies on kelp. We predict that variability in temperature during autumn will be similarly important to the population as variability during summer, although the population dynamics of densely crowded colonies, and of the host kelps, must also be considered. We expect outbreaks to occur when summer (and autumn) water temperatures are warmer, and the most pronounced outbreaks to occur during years where water is warmer from winter through summer and autumn. Given our results, we predict that if water temperatures in the coastal western North Atlantic warm by as little as 1°C, which is within the range predicted to occur with climate change, outbreaks of *M. membranacea* will increase in frequency and intensity. Due to the associated loss of kelp, and the potential for defoliated regions to become populated by other nonindigenous species, this could have significant implications for the rocky subtidal ecosystem.

Acknowledgments

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References

Anderson, D. M. 1997. Turning back the harmful red tide. Nature **388:** 513–514, doi:10.1038/41415

Berman, J., L. Harris, W. Lambert, M. Buttrick, and M. Dufresne. 1992. Recent invasions of the Gulf of Maine: Three contrasting ecological histories. Conserv. Biol. **6:** 435–441, doi:10.1046/j.1523-1739.1992.06030435.x

Bernstein, B. B., and N. Jung. 1979. Selective pressures and coevolution in a kelp canopy community in southern California. Ecol. Monogr. **49:** 335–355, doi:10.2307/1942488

Bolton, J. J., and K. Lüning. 1982. Optimal growth and maximal survival temperatures of Atlantic *Laminaria* species (Phaeophyta) in culture. Mar. Biol. **66:** 89–94, doi:10.1007/BF00397259

Bos, O. G., C. J. M. Philippart, G. C. Cadee, and J. van Der Meer. 2006. Recruitment variation in *Macoma balthica*: A laboratory examination of the match/mismatch hypothesis. Mar. Ecol. Prog. Ser. **320:** 207–214, doi:10.3354/meps320207

Bruno, J. F., and others. 2007. Thermal stress and coral cover as drivers of coral disease outbreaks. PLoS ONE **5:** e124, doi:10.1371/journal.pbio.0050124

Carlton, J. T. 2000. Global change and biological invasions in the oceans, p. 31–54. *In* H. A. Mooney and R. J. Hobbs [eds.], Invasive species in a changing world. Island Press.

Chapman, A. S., R. E. Scheibling, and A. R. O. Chapman. 2002. Species introductions and changes in the marine vegetation of Atlantic Canada, p. 133–148. *In* R. Claudi, P. Nantel and E. Muckle-Jeffs [eds.], Alien invaders in Canada's waters, wetlands, and forests. Natural Resources Canada, Canadian Forest Service, Science Branch, Ottawa.

Côté, B., and T. Platt. 1983. Day-to-day variations in the spring–summer photosynthetic parameters of coastal marine phytoplankton. Limnol. Oceanogr. **28:** 320–344, doi:10.4319/lo.1983.28.2.0320

Dayton, P. K., M. J. Tegner, P. B. Edwards, and K. L. Riser. 1999. Temporal and spatial scales of kelp demography: The role of oceanographic climate. Ecol. Monogr. **69:** 219–250, doi:10.1890/0012-9615(1999)069[0219:TASSOK]2.0.CO;2

Dixon, J., S. C. Schroeter, and J. Kastendiek. 1981. Effects of the encrusting bryozoan, *Membranipora membranacea*, on the loss of blades and fronds by the giant kelp, *Macrocystis pyrifera* (Laminariales). J. Phycol. **17:** 341–345, doi:10.1111/j.1529-8817.1981.tb03120.x

Dukes, J. S., and H. A. Mooney. 1999. Does global change increase the success of biological invaders? Trends Ecol. Evol. **14:** 135–139, doi:10.1016/S0169-5347(98)01554-7

Edwards, M., and A. J. Richardson. 2004. Impact of climate change on marine pelagic phenology and trophic mismatch. Nature **430:** 881–884, doi:10.1038/nature02808

Ford, S. E., and R. Smolowitz. 2007. Infection dynamics of an oyster parasite in its newly expanded range. Mar. Biol. **151:** 119–133, doi:10.1007/s00227-006-0454-6

Greenan, B. J. W., B. D. Petrie, W. G. Harrison, and N. S. Oakey. 2004. Are the spring and fall blooms on the Scotian Shelf related to short-term physical events? Cont. Shelf Res. **24:** 603–625, doi:10.1016/j.csr.2003.11.006

Harley, C. D. G., and others. 2006. The impacts of climate change in coastal marine systems. Ecol. Lett. **9:** 228–241, doi:10.1111/j.1461-0248.2005.00871.x

Harris, L. G., and M. C. Tyrrell. 2001. Changing community states in the Gulf of Maine: Synergism between invaders, overfishing and climate change. Biol. Invasions **3:** 9–21, doi:10.1023/A:1011487219735

Harvell, C. D., H. Caswell, and P. Simpson. 1990. Density effects in a colonial monoculture: Experimental studies with a marine bryozoan (*Membranipora membranacea* L.). Oecologia **82:** 227–237, doi:10.1007/BF00323539

———, and R. Helling. 1993. Experimental induction of localized reproduction in a marine bryozoan. Biol. Bull. **184:** 286–295, doi:10.2307/1542447

———, C. E. Mitchell, J. R. Ward, S. Altizer, A. P. Dobson, R. S. Ostfeld, and M. D. Samuel. 2002. Climate warming and disease risks for terrestrial and marine biota. Science **296:** 2158–2162, doi:10.1126/science.1063699

Hayes, M. L., J. Bonaventura, T. P. Mitchell, J. M. Prospero, E. A. Shinn, F. V. Dolah, and R. T. Barber. 2001. How are climate and marine biological outbreaks functionally linked? Hydrobiologia **460:** 213–220, doi:10.1023/A:1013121503937

Hays, G. C., A. J. Richardson, and C. Robinson. 2005. Climate change and marine plankton. Trends Ecol. Evol. **20:** 337–344, doi:10.1016/j.tree.2005.03.004

Intergovernmental Panel on Climate Change [IPCC]. 2007. Climate change 2007: Synthesis report. Contribution of working groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change, Geneva, Switzerland.

Johnson, C. R., and K. H. Mann. 1988. Diversity, patterns of adaptation, and stability of Nova Scotian kelp beds. Ecol. Monogr. **58:** 129–154, doi:10.2307/1942464

Lambert, W. J., P. S. Levin, and J. Berman. 1992. Changes in the structure of a New England (USA) kelp bed: The effects of an introduced species? Mar. Ecol. Prog. Ser. **88:** 303–307, doi:10.3354/meps088303

Levin, P. S., J. A. Coyer, R. Petrik, and T. P. Good. 2002. Community-wide effects of nonindigenous species on temperate rocky reefs. Ecology **83:** 3182–3193, doi:10.1890/0012-9658(2002)083[3182:CWEONS]2.0.CO;2

Logan, J. A., and J. A. Powell. 2001. Ghost forests, global warming, and the mountain pine beetle (Coleoptera: Scolytidae). Am. Entomol. **47:** 160–172.

Lutaud, G. 1961. Contribution to the study of budding and growth in colonies of the cheilostome bryozoan *Membranipora membranacea*. Ann. Soc. R. Zool. Belg. **91:** 157–199.

McCarty, J. P. 2001. Ecological consequences of recent climate change. Conserv. Biol. **15:** 320–331, doi:10.1046/j.1523-1739.2001.015002320.x

Menon, N. R. 1972. Heat tolerance, growth and regeneration in three North Sea bryozoans exposed to different constant temperatures. Mar. Biol. **15:** 1–11, doi:10.1007/BF00347433

Neuheimer, A. B., and C. T. Taggart. 2007. The growing degree-day and fish size-at-age: The overlooked metric. Can. J. Fish. Aquat. Sci. **64:** 375–385, doi:10.1139/F07-003

O'Dea, A., and B. Okamura. 1999. Influence of seasonal variation in temperature, salinity and food availability on module size and colony growth of the estuarine bryozoan *Conopeum seurati*. Mar. Biol. **135:** 581–588, doi:10.1007/s002270050659

Pratt, M. C. 2008. Living where the flow is right: How flow affects feeding in bryozoans. Integr. Compar. Biol. **48:** 808–822, doi:10.1093/icb/icn052

Ryland, J. S. 1970. Bryozoans. Hutchinson.

Saunders, M., and A. Metaxas. 2007. Temperature explains settlement patterns of the introduced bryozoan *Membranipora membranacea* in Nova Scotia, Canada. Mar. Ecol. Prog. Ser. **344:** 95–106, doi:10.3354/meps06924

———, and ———. 2008. High recruitment of the introduced bryozoan *Membranipora membranacea* is associated with kelp bed defoliation in Nova Scotia, Canada. Mar. Ecol. Prog. Ser. **369:** 139–151, doi:10.3354/meps07669

———, and ———. 2009*a*. Effects of temperature, size, and food on the growth of *Membranipora membranacea* in laboratory and field studies. Mar. Biol. **156:** 2267–2276, doi:10.1007/s00227-009-1254-6

———, and ———. 2009*b*. Population dynamics of a nonindigenous epiphytic bryozoan (*Membranipora membranacea*) in the western North Atlantic: Effects of kelp substrate. Aquat. Biol. **8:** 83–94, doi:10.3354/ab00208

Scheibling, R. E., and P. Gagnon. 2006. Competitive interactions between the invasive green alga *Codium fragile* ssp. *tomentosoides* and native canopy forming seaweeds in Nova Scotia (Canada). Mar. Ecol. Prog. Ser. **325:** 1–14, doi:10.3354/meps325001

———, and ———. 2009. Temperature-mediated outbreak dynamics of the invasive bryozoan *Membranipora membranacea* in Nova Scotian kelp beds. Mar. Ecol. Prog. Ser. **390:** 1–13, doi:10.3354/meps08207

———, A. W. Hennigar, and T. Balch. 1999. Destructive grazing, epiphytism, and disease: The dynamics of sea urchin–kelp interactions in Nova Scotia. Can. J. Fish. Aquat. Sci. **56:** 2300–2314, doi:10.1139/cjfas-56-12-2300

Schmidt, A. L., and R. E. Scheibling. 2007. Effects of native and invasive macroalgal canopies on composition and abundance of mobile benthic macrofauna and turf-forming algae. J. Exp. Mar. Biol. Ecol. **341:** 110–130, doi:10.1016/j.jembe.2006.10.003

Schwaninger, H. R. 1999. Population structure of the widely dispersing marine bryozoan *Membranipora membranacea* (Cheilostomata): Implications for population history, biogeography, and taxonomy. Mar. Biol. **135:** 411–423, doi:10.1007/s002270050642

Sinclair, B. J., P. Vernon, C. J. Klok, and S. L. Chown. 2003. Insects at low temperatures: An ecological perspective. Trends Ecol. Evol. **18:** 257–262, doi:10.1016/S0169-5347(03)00014-4

Stachowicz, J. J., J. R. Terwin, R. B. Whitlatch, and R. W. Osman. 2002. Linking climate change and biological invasions: Ocean warming facilitates nonindigenous species invasions. Proc. Natl. Acad. Sci. **99:** 15497–15500, doi:10.1073/pnas.242437499

Walther, G.-R., and others. 2002. Ecological responses to recent climate change. Nature **416:** 389–395, doi:10.1038/416389a

Winder, M., and D. E. Schindler. 2004. Climate change uncouples trophic interactions in an aquatic ecosystem. Ecology **85:** 2100–2106, doi:10.1890/04-0151

Wolfe, L. 2002. Why alien invaders succeed: Support for the escape-from-enemy hypothesis. Am. Nat. **160:** 705–711, doi:10.1086/343872

Yoshioka, P. M. 1982. Role of planktonic and benthic factors in the population dynamics of the bryozoan *Membranipora membranacea*. Ecology **63:** 457–468, doi:10.2307/1938963

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