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GLOBAL CHANGE ECOLOGY – ORIGINAL RESEARCH

Community composition influences the population growth and ecological impact of invasive species in response to climate change

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Abstract
Predicting long-term impacts of introduced species is challenging, since stressors related to global change can influence species–community interactions by affecting both demographic rates of invasive species and the structure of the invaded ecosystems. Invasive species can alter ecosystem structure over time, further complicating interactions between invasive species and invaded communities in response to additional stressors. Few studies have considered how cumulative impacts of species invasion and global change on the structure of invaded ecosystems may influence persistence and population growth of introduced species. Here, we present an empirically based population model for an invasive epiphytic bryozoan that can dramatically alter the structure of its invaded kelp bed ecosystems. We use this model to predict the response of invasive species to climate change and associated changes in the invaded community. Population growth of the bryozoan increased under near-future projections of increasing ocean temperature; however, the magnitude of population growth depended on the community composition of invaded kelp beds. Our results suggest that, in some cases, indirect effects of climate change mediated through changes to the structure of the invaded habitat can modulate direct effects of climate change on invasive species, with consequences for their long-term ecological impact. Our findings have important implications for management of invasive species, as modifying invaded habitats at local to regional scales may be more logistically feasible than addressing stressors related to global climate change.

Keywords Population dynamics · Population model · Kelp beds · Bryozoan · Temperature

Introduction

Predicting which species have a high probability of becoming invasive and which ecosystems are most vulnerable to invasion has been a long-time goal of invasion science (Pimm 1989; Carlton 1996; Kolar and Lodge 2001). However, although some generalizations relating patterns of invasion success to characteristics of introduced species and recipient regions have emerged (Kolar and Lodge 2001; Dick et al. 2017), our ability to predict the success of individual invaders and the resulting consequences for invaded ecosystems remains limited (Williamson 1996; Hulme et al. 2013). This limitation is compounded by the occurrence of concurrent anthropogenic stressors related to global change, which further complicate general patterns of species invasions (Strayer 2012). However, our limited capacity to predict which species will invade where has led to an increased recognition of the specific role of species–community interactions in determining invasion success, including feedbacks between invaders and invaded habitats (Vitousek 1990; Lodge 1993a, b; Ricciardi et al. 2013). For example, model simulations have shown that equilibrium abundance of invasive species varies non-linearly with the availability of suitable habitat within the invaded landscape (Barlow and Kean 2004). These model outcomes suggest that small changes in the amount of suitable habitat may substantially

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impact the abundance, and consequently the invasiveness, of introduced species.

Invasive species themselves can also impact ecosystem structure, increasing or decreasing the resilience of the ecosystem to invasion (MacDougall and Turkington 2005; Simberloff 2011). This is particularly true for invasive ecosystem engineers, the capacity of which to alter ecosystems directly can result in cascading effects for resident species (Crooks 2002). However, invasion dynamics involving ecosystem engineers are complex, and model simulations predict that overexploitation of native habitat by an invasive engineer can lead to population collapse of the invader when its intrinsic rate of population increase is high (Gonzalez et al. 2008). Therefore, stressors related to global change can theoretically influence invasion success through both direct effects on the demography of invaders and indirect effects on the structure of invaded ecosystems (Occhipinti-Ambrogi 2007; Hellmann et al. 2008; Rahel and Olden 2008). However, few studies consider impacts of species invasions and habitat modification simultaneously (1.2% of studies on species invasions published between 2002 and 2007, Didham et al. 2007), and empirical data that explicitly test model predictions are lacking (but see Kean and Barlow 2000).

Climate change and invasive species are major contributors to global change (Vitousek et al. 1997), and rank among the greatest threats to rocky reef ecosystems (Halpern et al. 2007). In general, effects of climate change are expected to favour invasive species over native species, enhancing the impact of species invasions on ecosystems globally (Dukes and Mooney 1999; Hellmann et al. 2008). However, the responses of marine biological invasions to global climate change are highly variable (Carlton 2000). Climatically driven changes in ocean temperature and physicochemical conditions can enhance or depress new invasions by altering dispersal mechanisms and competitive interactions at local scales (Occhipinti-Ambrogi 2007). Consequently, in marine epiphytic communities, increasing ocean temperature can facilitate local shifts to dominance by some, but not all introduced species (Stachowicz et al. 2002; Sorte et al. 2010, Cockrell and Sorte 2013).

In an ocean-warming hotspot in the northwest Atlantic, rising sea temperature in combination with population outbreaks of an invasive epiphytic species has been proposed as the main drivers of a dramatic ecosystem shift from highly productive kelp beds to less productive communities dominated by turf algae (Krumhansl et al. 2014; Filbee-Dexter et al. 2016; O'Brien 2018). Along the central coast of Nova Scotia, mean sea temperature exceeded the upper limit for optimal growth of the kelps *S. latissima* and *L. digitata* for 50–100 days each year from 2004 to 2014 (Filbee-Dexter et al. 2016). Ocean temperature is positively related to both growth of the invasive bryozoan *Membranipora membranacea* (Saunders and Metaxas 2009a) and the timing of the onset of recruitment of colonies on kelp (Saunders and Metaxas 2007). Consequently, warm ocean temperatures have been linked to both a decline in kelp growth (Filbee-Dexter et al. 2016) and to population outbreaks of *M. membranacea* in this region (Saunders and Metaxas 2007; Scheibling and Gagnon 2009). In addition, encrustation by *M. membranacea* further reduces growth and survival of kelp (Levin et al. 2002) and weakens kelp tissue (Krumhansl et al. 2011) resulting in substantial loss of kelp following bryozoan outbreaks (Saunders and Metaxas 2008). If ocean temperatures continue to increase, indirect effects on kelp beds resulting from enhanced epiphytism by *M. membranacea* may lead to even greater loss of kelp and, importantly, inhibition of kelp bed recovery, than predicted based on direct effects of temperature alone on kelp (Saunders et al. 2010). Differential impacts of both increased temperature and the invasive epiphyte on different kelp species (Saunders and Metaxas 2008, 2009b; Simonson et al. 2015) may confer a new competitive advantage to the competitive inferior kelp *Agarum clathratum* and alter the community composition of regional kelp beds (e.g. Gulf of Maine, Harris and Tyrrell 2001). Thus, *M. membranacea* can be considered an invasive ecosystem engineer that interacts with and modifies its invaded habitat.

In this study, we use the unique dynamics between the invasive bryozoan and its algal hosts in the northwest Atlantic as a model system to test predictions of the response of invasive populations to climate change and associated changes in the invaded communities. To achieve this, we incorporate relationships between temperature, kelp substrate, and demographic rates previously quantified for *M. membranacea* (Saunders and Metaxas 2009a; Denley and Metaxas 2016, 2017a, b) into a matrix population model for this bryozoan in its invaded habitat. We use the model to predict the persistence and intensity of outbreaks of this invasive species in the region over the next 20 years in response to near-future projections of increasing ocean temperature and potential changes in the community composition of kelp beds. We expect that warming ocean temperature will lead to increased abundance (Saunders et al. 2010) and consequently enhanced ecological impacts of *M. membranacea* in Nova Scotia. However, we hypothesize that effects of temperature on bryozoan abundance will vary spatially in relation to the total abundance and species composition of the algal hosts, and temporally in response to projected changes in available kelp substrate. Our study is unique in that it incorporates both direct effects of climate change on an invasive species and the cumulative impacts of climate change and species invasion on the invaded ecosystems into predictive models of population growth of introduced species.

Methods

Model construction

We used a stage-based matrix model (Lefkovitch 1965) to explore the population dynamics of *M. membranacea* on each of the three numerically dominant kelp species (*Saccharina latissima*, *Laminaria digitata*, and *Agarum clathratum*) in its invaded habitat in the northwest Atlantic. The model is of the form:

$$n^{k+1} = \mathbf{A}n^{k}, \quad (1)$$

where n^k is a vector of the abundance of individuals (per m^2 kelp) in each stage of the population at time index k, $k+1 = k+\Delta k$ with time step Δk, and $\mathbf{A}$ is a population projection matrix (specific to each kelp substrate). We chose 1 m^2 kelp as our model domain because it represents a standard unit of substrate for *M. membranacea* and allows for direct comparisons to be made among kelp species. Five stage classes were defined based on colony size (< 1 cm diameter, 1–3 cm diameter, 3–6 cm diameter, 6–8 cm diameter, > 8 cm diameter). Size classes were selected to correspond with approximately 2-week growth intervals (Saunders and Metaxas 2009a) based on the water temperature at the time of initial field sampling in June 2012. The elements of $\mathbf{A}$ represent: (1) familiar demographic processes of unitary organisms: growth, sexual reproduction, and mortality; and (2) a demographic process unique to colonial organisms: partial mortality of individual zooids (colony shrinkage/senescence) (Online Resource 1: Model construction).

We generated model parameters and variables used to calculate transition probabilities based on empirically derived relationships between demographic rates (colony growth, whole-colony mortality, colony senescence, potential colony fecundity) and intrinsic (colony size) and environmental (temperature, kelp substrate) factors measured at The Lodge (44°33′3″N, 64°01′9″W) on the western shore of St. Margarets Bay, Nova Scotia (Table 1, Online Resource 2: Model parameterization).

The model evolves at bi-weekly time steps, representing the minimal time required for colonies in size class i to grow to size class $i+1$, from 01 January to 31 December of each year. The first size class consists entirely of new recruits, with 100% of colonies in this size class either growing into a larger size class or experiencing mortality due to senescence during each time step. For the first year for which the model is run, the model is initiated on 11 March with an initial population vector based on empirical data of the number of colonies on each of the three kelp substrates in November–December at three sites on the southwestern shore of Nova Scotia (The Lodge, Paddy's Head and Sandy Cove) in 2005, 2006 (Saunders and Metaxas 2009b) and 2012 (Online Resource 1: Table S1). For each kelp substrate, the number of colonies per m^2 kelp was recorded in 2005 and 2006, and the number and size category of colonies per m^2 kelp in 2012. We calculated the average number of colonies per m^2 kelp in November–December across all years,

Table 1 Summary of model equations used to generate parameters included in a matrix population model for *Membranipora membranacea* in Nova Scotia

Parameter	Measurement	Location	Duration	Dependent on	Equation (and source)
G	Rate of colony growth (mm day^{-1})	TL FHL Lun	Aug 2005, Aug–Sep 2006 May 2006 Jul–Aug 2007	Colony size (D) Temperature (T)	$\log_{10}(GR) = \alpha^c + \beta^c \times \log_{10}(D) + \chi^c(T)$ (Saunders and Metaxas 2009a) Online Resource 2, Eq. 3, Fig. S1
S	Rate of colony shrinkage (cm^2 day^{-1})	TL	25 Jul–7 Oct 2014	Colony size (A)	$SR = \delta^c(A) - \gamma^c$ (Denley and Metaxas 2016) Online Resource 2, Eq. 4
P	Rate of whole colony mortality (μ, $\%day^{-1}$)	TL	2012: Jun, Aug, Sep, Nov 2013: Mar, Jun, Aug	Colony size Kelp substrate	Mean and standard deviation of μ^b (Denley and Metaxas 2016) Online Resource 2, Fig. S2
F	Fecundity (f, oocytes $colony^{-1}$)	TL	2012: Jun, Aug, Sep, Nov 2013: Mar, Jun, Aug 2014: May, Jun, Jul, Aug, Sep, Oct, Nov 2015: Mar, Apr, May, Jun, Jul, Aug, Sep, Oct, Nov	Colony size Kelp substrate	Mean and standard deviation of f^a (Denley and Metaxas 2017a) Online Resource 2, Fig. S3

Locations are: The Lodge, NS (TL), Friday Harbor Laboratories, WA (FHL), and Lunenburg Bay, NS (44°20′ 18″N, 64°15′00″W) (Lun). $\alpha = -1.665 \pm 0.086$, $\beta = 0.719 \pm 0.032$, $\chi = 0.072 \pm 0.008$; $\delta = 0.064 \pm 0.018$ day^{-1}, $\gamma = -2.07 \pm 1.43$ cm^2 day^{-1}

[a]Normal

[b]log-Normal

[c]Multivariate Normal

as well as the size distribution of colonies for 2012. We used the relative proportion of colonies in each size class in November–December 2012 to partition the average number of colonies per m^2 kelp among the five size classes. To estimate the initial population vector on 11 March, we multiplied the number of colonies per m^2 kelp in each size class for each kelp substrate by an over-winter survival probability of 0.005 or 0.5%. We calculated the proportion of colonies surviving over winter (P_{OW}) from 30 December to 11 March (70 days) as

$$P_{\mathrm{OW}} = e^{-\mu t}, \quad (2)$$

where μ is the instantaneous rate of mortality (0.075%day^{-1}, Denley and Metaxas 2016) and t is the time in days (70 days). Each successive year is initiated on 01 January with a population vector equal to the final population vector on 31 December of the previous year.

Model projections

Because the data used to construct the model were obtained from The Lodge, we forced the model using independent data from two other sites, Paddy's Head (44°31′6″N, 63°57′2″W) and Sandy Cove (44°27′6″N, 63°42′4″W) (for a detailed description all three sites see Saunders and Metaxas 2009b). There is no evidence that temperature- or kelp substrate-dependent demographic rates (mortality, fecundity) vary among sites (Denley and Metaxas 2016, 2017a); therefore, data from the population at The Lodge can be used to model the populations at the other two sites. However, the temperature regimes do vary slightly among sites, and the mixed kelp beds are characterized by different absolute and relative abundance of kelps (Denley and Metaxas 2016, 2017a). Site-specific temperature was used to force the model by incorporating depth-averaged daily average temperatures (Paddy's Head: 4, 8, 12 m; Sandy Cove: 4, 8 m) for each year into the equation for colony growth rate (Online Resource 2: Eq. 3). To apply our model to mixed species kelp beds that differ in absolute abundance and relative species composition of kelp, kelp abundances at each site were estimated from field sampling conducted approximately every 6 weeks from June 2012 to August 2013 (Denley and Metaxas 2016). For each month at each site, we generated normal distributions of kelp abundance using the mean and standard deviation of the surface area of each kelp species per m^2 seabed pooled across depths and years (except for cases when abundance was more accurately described by a log-normal distribution: *L. digitata* at Paddy's Head in August and at The Lodge in June; *A. clathratum* at Sandy Cove in August and at The Lodge in June, August, and September) (Online Resource 2, Figure S6). We then randomly sampled abundance for each month from these distributions, and used linear interpolation to generate kelp abundances for each time index k. We restricted the maximum abundance of kelp to within the range observed in the field for each kelp species (D. Denley unpubl data, *S. latissima*: 2.4 m^2 per m^2 seabed, *L. digitata*: 1.2 m^2 per m^2 seabed, *A. clathratum*: 0.67 m^2 per m^2 seabed). Site-specific kelp abundances were used to convert model output (colonies per m^2 kelp) into colonies per m^2 seabed by multiplying the abundance of colonies (per m^2 kelp) at each point in time with the corresponding surface area of each kelp species (m^2) per m^2 seabed.

Although *M. membranacea* occurs predominantly on kelps, it is also found on alternative algal substrates, primarily *Fucus* spp. (Yorke and Metaxas 2012). *Fucus* occurs in shallow waters (<4 m depth) and is spatially separated from mixed kelp beds; however, colonies on *Fucus* may provide an additional supply of allochthonous propagules to adjacent mixed kelp beds. To incorporate the larval contribution of colonies on *Fucus* at each site, we estimated monthly larval supply (number of oocytes) from colonies on *F. evanescens* as potential colony fecundity (oocytes $colony^{-1}$) for each size class of colony multiplied with the number of colonies of each size class per m^2 seabed on *F. evanescens*. Fecundity estimates were based on approximately monthly sampling of colonies on *F. evanescens* at The Lodge and Sandy Cove from 2012 to 2015 and at Paddy's Head from 2012 to 2013 (Denley and Metaxas 2017a, Online Resource 2, Figure S7). Size frequency of colonies was measured at each site approximately monthly from June 2012 to August 2013 (Denley unpubl data). We added the monthly larval supply from colonies within a 3 m^2 patch *F. evanescens* (offset by +2 time-steps) multiplied with the corresponding monthly larval mortality to F_{total} for each bi-weekly time step (see Online Resource 2, Model parameterization: Colony fecundity). We chose 3 m^2 as the area occupied by *F. evanescens* in our model based on the area of *F. evanescens* beds sampled at each site (2–5.5 m^2).

To reduce any artifacts of initialization, we allowed the model to spin up under consistent annual temperature conditions until the *M. membranacea* population reached a dynamical steady state (approximately 5 years, Online Resource 2 Figure S8) prior to all model validation and model projections.

Response of *M. membranacea* to projected increases in ocean temperature

We initiated the model on 11 March 2016 using daily averaged temperatures from that year (Online Resource 2, Figure S9). We allowed the model to spin up under 2016 temperature conditions for 5 years and then ran the model consecutively for 19 years (from 2017 to 2035) under three scenarios of projected increases in ocean temperature by the year 2035: + 0.5 °C, + 1 °C, and + 3 °C (Kirtman et al.

2013). The reliability of regional climate change projections for the northwest Atlantic remains uncertain (Loder et al. 2015). Therefore, we selected increasing ocean temperature scenarios to encompass the globally averaged near-term changes in ocean temperature projected under the range of Representative Concentrations Pathways (RCP2.6–RCP8.5) for emissions scenarios considered by the Intergovernmental Panel on Climate Change in their Fifth Assessment Report (Kirtman et al. 2013). For each temperature scenario, we divided the projected increase in ocean temperature by the year 2035 by the number of years between 2016 and 2035 (e.g. 2035–2016 = 19 years; 0.5 °C ÷ 19 years = 0.026 °C year^{-1}) and added the resulting value to each daily averaged temperature used to parameterize colony growth (G_i, Online Resource 2: Model parameterization) for each consecutive year the model was run. This resulted in a cumulative increase in daily averaged ocean temperature of + 0.5 °C, + 1 °C, or + 3 °C by 2035. Kelp abundances for each year were generated as described previously, and bi-weekly relative abundances of each kelp species were re-calculated for each consecutive year to reflect interannual variation in kelp bed community composition. We determined the mean of the annual maximum numbers of colonies of *M. membranacea* per m^2 seabed (indicative of the annual impact of *M. membranacea* on its kelp host which is greatest during peak colony abundance) and 95% bootstrap percentile intervals from 1 January 2017 to 31 December 2035 for 1000 iterations (Caswell 2001). Using this same mean, we calculated the stochastic population growth rates and corresponding 95% quantiles for each site and temperature scenario after Caswell (2001).

Response of *M. membranacea* to changes in the community composition of kelp beds

We ran the model for each species of kelp separately to compare seasonal population dynamics of *M. membranacea* (colonies per m^2 seabed) among mono-specific stands of each of the three kelp species. We chose to run the model for mono-specific stands rather than mixed kelp beds with various relative abundances of each kelp species because shifts in the relative abundance of kelp species within kelp beds are difficult to predict and will likely vary spatially in response to local conditions. Thus, we used the model to predict near-future responses of *M. membranacea* to extreme changes in the species composition of kelp beds. We initiated the mono-specific model on 11 March 2012 using the same starting vector of *M. membranacea* abundance for each kelp species as for mixed kelp beds and allowed the model to spin up for 5 years under 2012 temperature conditions before running the model consecutively from 1 January 2012 to 31 December 2013. For the mono-specific model, total kelp abundance (m^2 kelp per m^2 seabed) was the same as for mixed kelp beds. This assumption allows us to isolate the effect of kelp species on the population dynamics of *M. membranacea* rather than confounding effects of available kelp species with effects of total available substrate. In addition, oocytes produced by colonies on each substrate entered the first size class on that same substrate according to Eq. 6 (Online Resource 2), where F_{total} is now the total number of oocytes produced by colonies of all size classes on a specific substrate and R is the proportion of the total number of settlers occurring per m^2 kelp summed across all three kelp species.

Response of *M. membranacea* to the combined effects of projected increases in ocean temperature and community composition of kelp beds

To examine the combined impact of projected increases in ocean temperature and changes in kelp bed community composition on *M. membranacea* in the northwest Atlantic, we ran the model for mono-specific stands of *S. latissima*, *A. clathratum* and *L. digitata,* while increasing daily averaged temperatures annually from 1 January 2017 to 31 December 2035 for each temperature scenario. We initiated the model on 11 March 2016 using the same starting vector of *M. membranacea* abundance for each kelp species as for mixed kelp beds and allowed the model to spin up under 2016 temperature conditions for 5 years before running the model consecutively for an additional 19 years (from 2017 to 2035). Direct effects of increasing ocean temperature on kelp substrate are not included in our model; however, projecting the population dynamics of *M. membranacea* under mono-specific kelp bed conditions can provide insight into the response of the population to climate driven changes in kelp bed community composition under the most extreme scenario, local extirpation of all but one kelp species.

For mono-specific stands of each kelp species, we determined the mean annual maximum number of colonies of *M. membranacea* per m^2 seabed under each projected increase in ocean temperature from 2017 to 2035 for 1000 iterations. We calculated the stochastic population growth rates and corresponding 95% quantiles for all combinations of kelp species and temperature scenario after Caswell (2001).

Results

Model validation

For all three sites, 95th percentiles for modeled populations overlapped with 95% confidence intervals for sampled populations for each of two population indices, total number of colonies per m^2 seabed and total surface area of colonies (cm^2) per m^2 seabed, during both early and peak

seasonal abundance of *M. membranacea* (Fig. 1, Online Resource 2: Model validation). On average, differences between model estimates and corresponding field data (MAE) were within the range of standard deviations observed in the field except for the total number of colonies per m^2 seabed during peak seasonal abundance at The Lodge (Table 2). Model estimates agreed most strongly with corresponding field data for Paddy's Head (lowest MAE); however, the model consistently underestimated the *M. membranacea* population at both Paddy's Head and Sandy Cove (negative values of ME, Table 2).

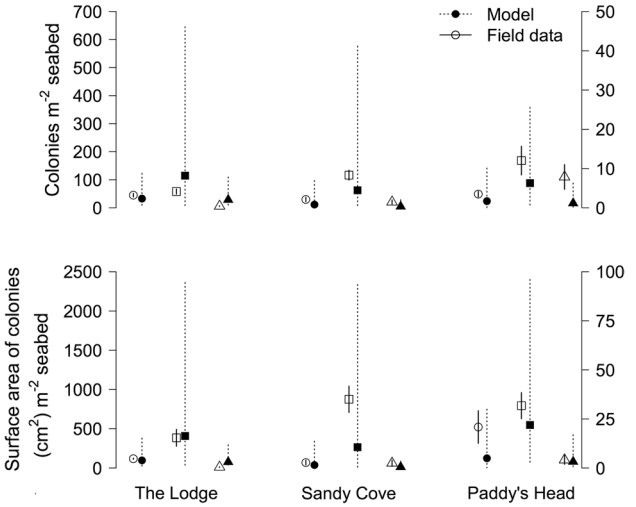

Fig. 1 Model validation. Modeled estimates (mean ± 95% percentile intervals of 1000 model runs) and field data (mean ± 95% confidence intervals) of two population indices: the number of colonies per m^2 seabed (top panels) and the surface area of colonies (cm^2) per m^2 seabed (bottom panels) during the early (July–August 2012: circles, July–August 2013: triangles) and peak (September–October 2012: squares) stages of the seasonal occurrence of *Membranipora membranacea* at 3 sites on the southwestern shore of Nova Scotia: The Lodge (source of data used in constructing the model), Paddy's Head and Sandy Cove (sites used for validating the model). Data for The Lodge and Sandy Cove are with respect to the left *y* axis, data for Paddy's Head are with respect to the right *y* axis

Model projections

For mixed kelp beds at both Sandy Cove and Paddy's Head, stochastic population growth rate and variability in population growth rate of *M. membranacea* increased with increasing ocean temperature (Table 3, Fig. 2); however, abundance was consistently greater at Sandy Cove than Paddy's Head (Fig. 2).

The abundance and seasonal dynamics of *M. membranacea* differed among mono-specific stands of the three kelp species, and these differences were consistent among sites (Fig. 3). Most notably, peak colony abundance was greater for mono-specific stands of *L. digitata* than the other two species, and peak colony abundance was comparatively low for mono-specific stands of *S. latissima* (Fig. 3). Additionally, colony abundance increased earlier in the season for mono-specific stands of *S. latissima* and *L. digitata* than *A. clathratum* (Fig. 3).

Table 2 Model validation

	Colonies per m^2 seabed			Surface area (cm^2) per m^2 seabed		
	MAE	ME	SD	MAE	ME	SD
The Lodge			5.2–38.6			6.69–442
Early 2012	28.53	− 12.27		79.36	− 21.09	
Peak 2012	91.95	56.68		386.0	19.35	
Early 2013	23.27	22.72		66.72	65.75	
Sandy cove			10.5–155			12.7–1323
Early 2012	31.31	− 18.30		80.63	− 31.36	
Peak 2012	128.5	− 54.41		878.7	− 602.65	
Early 2013	18.98	− 15.60		62.36	− 48.44	
Paddy's Head			2.08–17.8			3.99–48.8
Early 2012	3.17	− 1.79		19.02	− 16.32	
Peak 2012	9.28	− 5.76		23.89	− 9.89	
Early 2013	7.18	− 6.65		4.26	− 0.775	

Mean absolute error (MAE) and mean error (ME) of modeled estimates (1000 iterations) compared to corresponding field data (1000 random samples from the mean and 95% confidence intervals, Fig. 1) of two population indices: the number of colonies per m^2 seabed and the surface area of colonies (cm^2) per m^2 seabed during the early (July–August 2012, July–August 2013) and peak (September–October 2012) stages of the seasonal occurrence of *Membranipora membranacea* at 3 sites on the southwestern shore of Nova Scotia: The Lodge (source of data used in constructing the model), Paddy's Head and Sandy Cove (sites used for validating the model). Also shown is the range of standard deviation (SD) for each population index observed in the field

Table 3 Stochastic population growth rate ($\log\lambda_s$, $year^{-1}$ and 95% quantiles) for *Membranipora membranacea* in the northwest Atlantic in response to projected increases in ocean temperature

Site	Projected temperature (°C)	$\log\lambda_s$ (lower : upper 95% quantiles)
Paddy's head	+ 0.5	0.002 (− 0.120:0.116)
	+ 1.0	0.017 (− 0.106:0.124)
	+ 3.0	0.128 (− 0.056:0.309)
Sandy cove	+ 0.5	− 0.025 (− 0.259:0.107)
	+ 1.0	0.004 (− 0.245:0.148)
	+ 3.0	0.182 (− 0.176:0.399)

Stochastic population growth rates are calculated after Caswell (2001) based on model projections (means of 1000 iterations) of the annual maximum number of colonies of *M. membranacea* per m^2 seabed for mixed kelp beds at Paddy's Head and Sandy Cove under projected increases in ocean temperature for the northwest Atlantic of + 0.5 °C, + 1 °C, and + 3 °C by the year 2035 (Fig. 2)

$\log\lambda_s > 0$ indicates exponential population growth, $\log\lambda_s = 0$ indicates population stability, $\log\lambda_s < 0$ indicates exponential population decline

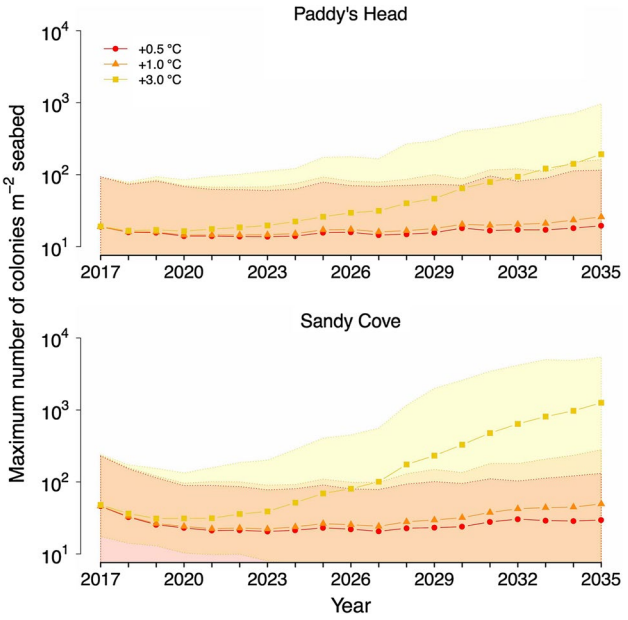

Fig. 2 Response of *Membranipora membranacea* to temperature alone. Model projections of the annual maximum number of colonies of *M. membranacea* per m^2 seabed for mixed kelp beds at Paddy's Head and Sandy Cove under projected increases in ocean temperature for the northwest Atlantic of +0.5 °C, +1 °C, and +3 °C by the year 2035. The model was initiated using temperature data from 2016 and daily average temperatures were increased annually from 2017 to 2035 by 0.026 °C, 0.053 °C, and 0.158 °C respectively. Points are the means of 1000 iterations, shaded areas indicate the 95% percentile intervals

Differences in the abundance of *M. membranacea* among kelp substrates were reflected in the response of the bryozoan population to the combination of increases in ocean temperature and changes in the community composition of

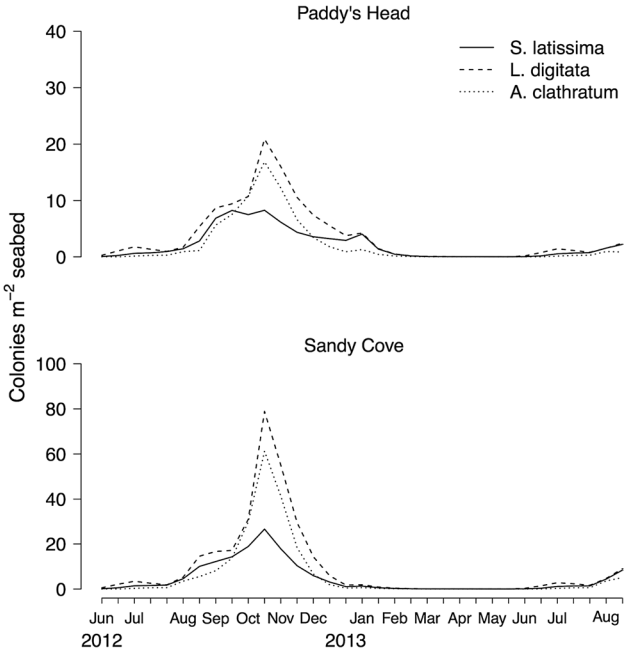

Fig. 3 Response of *Membranipora membranacea* to the composition of kelp beds alone. Model projections (means of 1000 iterations) of the seasonal dynamics of the population of *M. membranacea* (colonies per m^2 seabed) from June 2012 to August 2013 (for comparison with model validation for mixed kelp beds from June 2012 to August 2013, Online Resource 2: Figure S10) at 2 sites on the southwestern shore of Nova Scotia: Paddy's Head and Sandy Cove (sites used for validating the model) for mono-specific stands of *Saccharina latissima*, *Laminaria digitata*, and *Agarum clathratum*. Tickmarks on the x-axis correspond to bi-weekly time indices. The model was initiated on 11 March 2012, resulting in 2 time indices in each of Jun, Aug, Sep Oct, and Nov, and 3 time indices in Jul and Dec (see Methods: Model construction for details)

kelp beds. Stochastic population growth rate of *M. membranacea* increased with increasing ocean temperature for mono-specific stands of all three kelp species, although bryozoan abundance was consistently greater for mono-specific stands of *L. digitata* and *A. clathratum* than for mono-specific stands of *S. latissima* (Table 4, Fig. 4). However, the population growth rate of *M. membranacea* in response to projected increases in ocean temperature was lower for mono-specific stands of all kelp species compared to mixed kelp beds at Paddy's Head under all temperature projection scenarios, except for *A. clathratum* under the + 0.5 °C temperature scenario (compare Table 3 and Table 4). At Sandy Cove, the population growth rate of *M. membranacea* was lower for mono-specific stands of all kelp species than for mixed kelp beds under the + 3.0 °C temperature scenario (compare Table 3 and Table 4). Consequently, the maximum number of colonies per m^2 seabed under the temperature projection scenario of + 3.0 °C by the year 2035 was an order of magnitude lower for mono-specific stands than for mixed kelp beds at both sites (compare Fig. 2 and Fig. 4).

Table 4 Stochastic population growth rate ($\log\lambda_s$, $year^{-1}$ and 95% quantiles) for *Membranipora membranacea* in the northwest Atlantic in response to projected increases in ocean temperature

Site	Projected temperature (°C)	$\log\lambda_s$ (lower:upper 95% quantiles)
Paddy's head		
S. latissima	+ 0.5	− 0.008 (− 0.167:0.123)
L. digitata		− 0.005 (− 0.079:0.065)
A. clathratum		0.007 (− 0.025:0.039)
S. latissima	+ 1.0	− 0.010 (− 0.117:0.083)
L. digitata		− 0.011 (− 0.087:0.055)
A. clathratum		0.013 (− 0.020:0.049)
S. latissima	+ 3.0	0.061 (− 0.120:0.294)
L. digitata		0.072 (− 0.093:0.250)
A. clathratum		0.070 (0.007:0.147)
Sandy cove		
S. latissima	+ 0.5	0.000 (− 0.235:0.215)
L. digitata		0.002 (− 0.137:0.082)
A. clathratum		− 0.008 (− 0.033:0.035)
S. latissima	+ 1.0	0.008 (− 0.345:0.297)
L. digitata		0.004 (− 0.145:0.125)
A. clathratum		0.006 (− 0.031:0.038)
S. latissima	+ 3.0	0.123 (− 0.166:0.509)
L. digitata		0.100 (− 0.045:0.238)
A. clathratum		0.075 (− 0.010:0.162)

Stochastic population growth rates are calculated after Caswell (2001) based on model projections (means of 1000 iterations) of the annual maximum number of colonies of *M. membranacea* per m^2 seabed for mono-specific stands of *Saccharina latissima, Laminaria digitata,* and *Agarum clathratum* at Paddy's Head and Sandy Cove under projected increases in ocean temperature for the northwest Atlantic of + 0.5 °C, + 1 °C, and +3 °C by the year 2035 (Fig. 4)

$\log\lambda_s > 0$ indicates exponential population growth, $\log\lambda_s = 0$ indicates population stability, $\log\lambda_s < 0$ indicates exponential population decline

Discussion

Our study supports previous studies linking range expansion and increased abundance of non-native marine epiphytes to warming seawater temperature at local and regional scales (Stachowicz et al. 2002; Sorte et al. 2010; Sorte and Stachowicz 2011; Rius et al. 2014). Projected increases in ocean temperature were predicted to enhance population growth of the invasive *M. membranacea*, increasing the probability of persistence and the ecological impacts of this species in the northwest Atlantic. The prediction was consistent across two sites (Paddy's Head and Sandy Cove) that differ in both total abundance and species composition of available kelp substrate. Increased temperature due to climate change may increase or decrease the impact of non-native species depending on their thermal optima (Iacarella et al. 2015) and the seasonal timing of the temperature increase (Mech et al. 2018). Annually averaged projected increases in ocean temperature for the northwest Atlantic are within the range at which colony growth rate of *M. membranacea* was enhanced in the field (5.7–16.2 °C, Saunders and Metaxas 2009a). Maximum daily average temperature under the most extreme warming scenario (+ 3 °C) in our region is 22 °C, but colony growth of *M. membranacea* is not retarded at this temperature (Yoshioka 1973).

Growth of the population of *M. membranacea* was sensitive to variations in whole-colony mortality rate driven by loss of kelp substrate (Online Resource 2: Sensitivity analysis). Erosion is the primary mechanism of loss of kelp tissue in Nova Scotia, and rates of erosion are predicted to increase by ~ 4% over the next 20 years in response to increases in ocean temperature of 0.022 °C $year^{-1}$ (Krumhansl et al. 2014), which approximately corresponds to our + 0.5 °C temperature scenario (+ 0.026 °C $year^{-1}$). Enhanced mortality rates related to temperature-induced loss of kelp tissue may lessen the effect of increasing ocean temperature on population growth of *M. membranacea*. Although kelp dynamics (growth, erosion, mortality, dislodgement) are not directly included in our population model, coupling our model with existing models of kelp substrate dynamics (e.g., Krumhansl et al. 2014) could be used to more explicitly examine the effects of changing climate conditions (temperature, significant wave height) on the interaction between the invasive bryozoan and its host kelp.

Interestingly, the magnitude of the direct effect of climate change on *M. membranacea* depended on the community composition of kelp beds regardless of total kelp abundance. Removal of any two of the three predominant kelp species had a moderating effect on bryozoan population growth in response to increasing temperature, suggesting that indirect effects of climate change mediated through changes to the structure of the invaded ecosystem may interact antagonistically with direct effects of climate change on the bryozoan's demography. Reduced rates of population growth in response to mono-specific stands of equivalent total kelp abundance suggests that persistence of invasive populations of *M. membranacea* may be maintained through differences in the timing and magnitude of demographic rates (fecundity and mortality) among kelp substrates. In mixed kelp bed habitats, variation in the timing of the onset and seasonal peak in fecundity of colonies on different kelp substrates (Denley and Metaxas 2017a, Online Resource 2: Figure S3) ensures a near continuous larval supply, while differences in seasonal rates of colony mortality among different kelp substrates (Online Resource 2: Figure S2) act to maintain a year-round population of mature colonies.

Substantial loss of kelp has been observed in our region over the past ~ 30 years, corresponding to an increase in the average sea temperature at 2–6 m of 1.58 °C (Filbee-Dexter et al. 2016). Total kelp abundance is expected to continue to decline in response to projected increases in

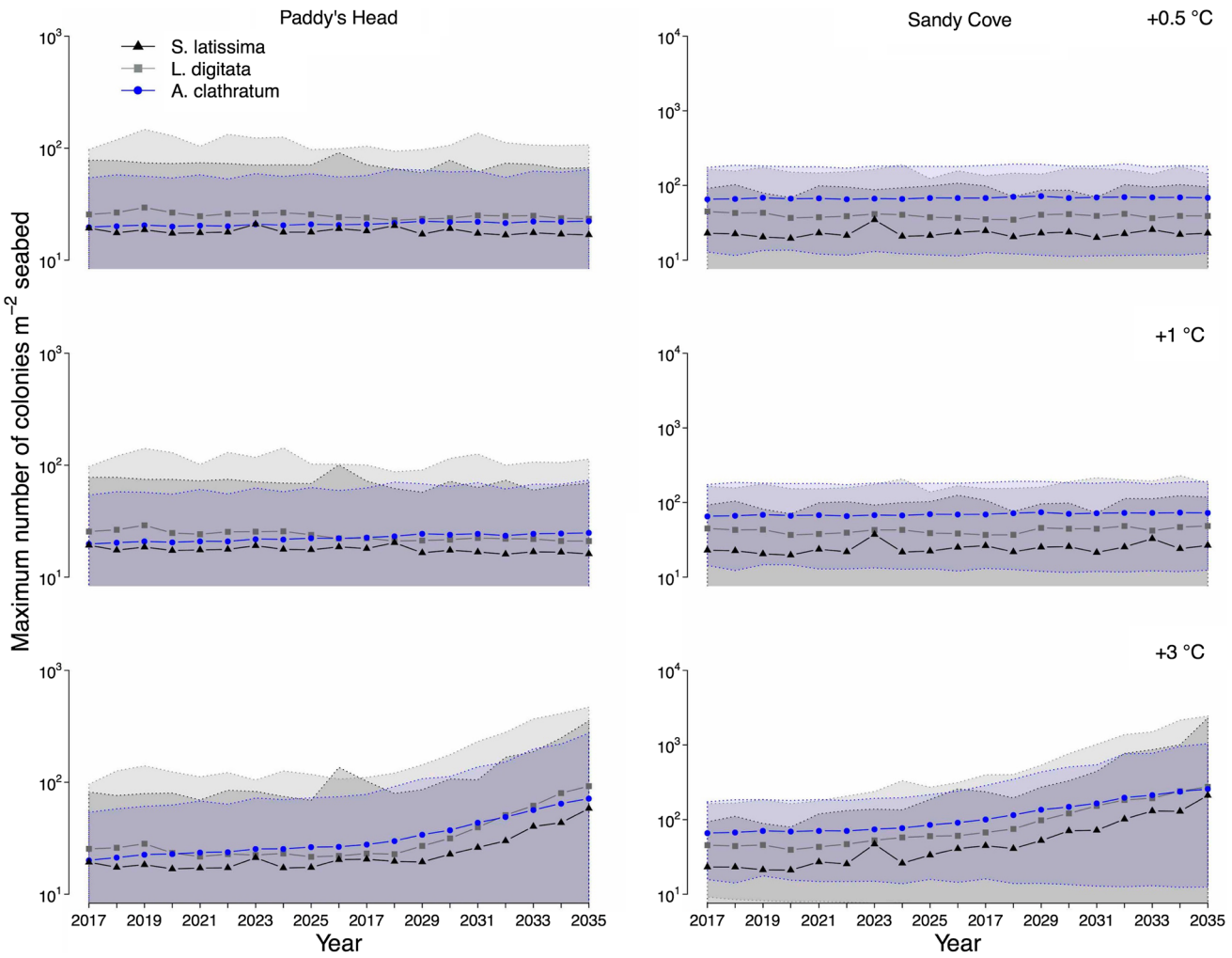

Fig. 4 Response of *Membranipora membranacea* to the combination of temperature and composition of kelp beds. Model projections of the annual maximum number of colonies of *M. membranacea* per m^2 seabed for mono-specific stands of *Saccharina latissima*, *Laminaria digitata*, and *Agarum clathratum* at Paddy's Head and Sandy Cove under projected increases in ocean temperature for the northwest Atlantic of + 0.5 °C, + 1 °C, and + 3 °C by the year 2035. The model was initiated using temperature data from 2016 and daily average temperatures were increased annually from 2017 to 2035 by 0.026 °C, 0.053 °C, and 0.158 °C, respectively. Points are the means of 1000 iterations and shaded areas indicate the 95% percentile intervals

ocean temperature that exceed historical observations; however, rates of decline are likely to differ among the three kelp species. In laboratory experiments, *A. clathratum* exhibited limited tissue damage at increased temperature treatments (14–21 °C), and was less susceptible to temperature-induced tissue loss than *S. latissima* or *L. digitata* (Simonson et al. 2015). However, *S. latissima*, and to a lesser extent *A. clathratum*, are more susceptible than *L. digitata* to defoliation following temperature-induced bryozoan outbreaks (Saunders and Metaxas 2009b). Consequently, near-future kelp bed ecosystems may be characterized by reduced overall abundance of kelp and increased relative abundance and depth distribution of *A. clathratum* or *L. digitata*, resembling mono-specific stands of these species in our model.

The capacity of *M. membranacea* to enhance the susceptibility of its host kelp to negative impacts of increasing temperature suggests that under future warming conditions, seasonal abundance of *M. membranacea* in its invaded habitat may be driven by differences in thermal optima for colony growth and growth and survival of kelp species. Mismatches in thermal performance optima in host–parasite systems can lead to reduced abundance or local extirpation of obligate parasites under similar projected increases in ocean temperature to those examined in our study (Gehman et al. 2018). Anticipated negative impacts of increasing temperature on kelp, modeled as local extirpation resulting in mono-specific kelp beds, reduced the overall abundance of *M. membranacea* in our study. However, the bryozoan population continued to increase in response to climate-warming scenarios

that included extreme indirect effects (local extirpation of two of the three kelp species) mediated through effects of climate change on its primary host. Under this scenario, population growth was maintained through near continuous larval supply due to the ability of *M. membranacea* to colonize substrate other than its primary host (*Fucus evanescens* in this case), underscoring the role of alternative substrate in contributing to the persistence of *M. membranacea* in its invaded habitat.

Native geographic range size, degree of phenotypic plasticity, and ability to use multiple habitat types have all been positively associated with invasion success, implying that invasive species tend to be habitat generalists (Rejmánek 1995; Rosecchi et al. 2001; Blackburn et al. 2009). Our results support this theory, suggesting that *M. membranacea* is a generalist introduced species that persists by taking advantage of a diverse range of resources, in this case algal substrates. At broad scales (≥ 1 km^2), habitat heterogeneity can be positively related to invasive species richness (Fridley et al. 2007) due to reduced strength of competitive interspecific interactions with increasing resource availability (Byers and Noonburg 2003). In fact, homogenous habitats can act as a dispersal barrier for non-native species that are more abundant in mixed substrata habitat types (Bohn et al. 2015).

Propagule supply has emerged as one of the few general predictors for successful establishment, persistence, and impact of invasive species (Kolar and Lodge 2001; Drake et al. 2005; Ricciardi et al. 2011, 2013). Our local scale model corresponds reasonably with empirical values. However, our assumption of a closed system may be responsible for the model underestimating the *M. membranacea* population at two of our three study sites (Paddy's Head and Sandy Cove), particularly if these sites are sinks for additional external sources of larvae that have not been accounted for in our model. Our model incorporates the importance of allochthonous propagule supply in contributing to the persistence of invasive species in response to changes in the invaded habitat through the contribution of larvae from an alternative substrate, the alga *F. evanescens*, which is external to mixed kelp beds. Similarly, for invasive terrestrial plants, propagule supply from seedbanks can rescue small or disturbed populations from extinction, allowing invasive populations to persist or even increase in size following eradication efforts (Drayton and Primack 1999). For invasive marine epiphytes in particular, anthropogenic structures can act as external sources of propagule supply, facilitating persistence in adjacent natural habitats (Lambert 2003; Dafforn et al. 2009; Forrest et al. 2013; Simons et al. 2016).

Our study provides evidence for the role of interactions between introduced species and recipient communities in determining invasiveness under climate change scenarios. Under near-future climate conditions, habitat modification through the combined impacts of climate change and epiphytism by the invasive bryozoan modulated the effect of increasing temperature on the abundance of *M. membranacea*, and consequently its impact on kelp bed ecosystems. Our results suggest that limiting additional propagule reservoirs in the form of jetties, buoys, aquaculture or other manmade structures could help to reduce population growth of *M. membranacea* under near-future climate conditions. This finding has important implications for management of species invasions, since modification of invaded habitats at local to regional scales may be a more rapid and logistically feasible response to mitigate impacts of introduced species than addressing effects of global climate change.

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Author contribution statement DD collected and analysed field data, developed the study design and matrix population model, analysed model output, and wrote the manuscript. AM supervised the study design and analysis and edited the manuscript, KF supervised the development of the matrix population model and analysis of model output and edited the manuscript.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable national and institutional guidelines for the care and use of animals were followed in accordance with the recommendations of the Canadian Council on Animal Care and the policies of Dalhousie University.

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