

Research Article

Ocean temperature does not limit the establishment and rate of secondary spread of an ecologically significant invasive bryozoan in the northwest Atlantic

Danielle Denley^{1*}, Anna Metaxas¹ and Nathalie Simard²

¹Department of Oceanography, Dalhousie University, 1355 Oxford Street, PO BOX 15000, Halifax, Nova Scotia, Canada, B3H 1X5

²Maurice Lamontagne Institute, 850 Route de la Mer, PO BOX 1000, Mont-Joli, Quebec, Canada, G5H 3Z4

Author e-mails: danielle.denley@dal.ca (DD), metaxas@dal.ca (AM), nathalie.simard@dfo-mpo.gc.ca (NS)

*Corresponding author

Citation: Denley D, Metaxas A, Simard N (2019) Ocean temperature does not limit the establishment and rate of secondary spread of an ecologically significant invasive bryozoan in the northwest Atlantic. *Aquatic Invasions* 14(4): 594–614, <https://doi.org/10.3391/ai.2019.14.4.03>

Received: 14 February 2019

Accepted: 28 May 2019

Published: 16 July 2019

Handling editor: Tammy Robinson

Thematic editor: Charles W. Martin

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Abstract

A mechanistic understanding of the factors that influence establishment and secondary spread of introduced species is critical for predicting the spatial extent and magnitude of negative impacts of species invasions. In the northwest Atlantic, an ecologically significant invasive bryozoan (*Membranipora membranacea*) has expanded its range northwards over the last 30 years. Warm ocean temperature has been linked to population outbreaks of *M. membranacea* within its established invasive range in southwestern Nova Scotia; however, rates of spread and the physical and biological factors affecting establishment of founding populations have not been explicitly quantified. Here, we use unique baseline data on presence/absence and abundance of this bryozoan near its current northern range limit to quantify rates of spread and identify factors influencing its establishment in three regions in the Gulf of St. Lawrence. Except for one potential incident of human-facilitated long-distance dispersal, the rate of spread of *M. membranacea* in the northwest Atlantic was comparable to that of other invasive marine invertebrates. Contrary to our predictions based on long-established populations in Nova Scotia, the abundance of *M. membranacea* was not strongly related to regional differences in ocean temperature at its northern range limit. Our results suggest that colder temperatures are not limiting the northward spread of this bryozoan in the northwest Atlantic. Instead, relationships between temperature and abundance of *M. membranacea* in the Gulf of St. Lawrence may be moderated by a lack of available kelp substrate. Our findings, therefore, have important implications regarding the potential for *M. membranacea* to impact vulnerable Arctic ecosystems where laminarian kelps are widespread.

Key words: climate change, kelp, invasive marine invertebrate, range expansion

Introduction

Invasive species pose one of the greatest threats to marine biodiversity, tantamount to increasing ocean temperature due to climate change (Costello et al. 2010). There is evidence to suggest that the frequency of biological invasions has increased in recent decades and may continue to increase in the future (Seebens et al. 2017). Numerous regulatory frameworks have been developed to address the growing threat of marine invasions (Hewitt et al. 2009). For marine and freshwater environments,

the limited feasibility of controlling and managing introduced species once they become established has made the prevention of further species introductions a primary management priority (e.g. CBD 2000; European Commission 2014). Consequently, much of the research aimed at directing applied management approaches focuses on identifying vectors of introduction and predicting potential future invaders (Ojaveer et al. 2015).

A mechanistic understanding of the factors affecting establishment and rates of secondary spread at the boundaries of an invasive range can be useful in predicting the geographic limit, and consequently the spatial extent of impact, of an invasion when prevention efforts fail. Anticipating the rate and extent of secondary spread may allow for preemptive mitigation of impacts of invasive species at local to regional scales within the predicted invaded range. For example, information on the future spatial extent of invasive species can be incorporated into site selection criteria for marine protected areas to either avoid or target sites based on their vulnerability to invasive species (Giakoumi et al. 2016). However, accurate rates of secondary spread are not always available due to uncertainty in the timing of first establishment of founding populations outside of the epicenter of introduction (e.g. De Blauwe and Faasse 2001; Bishop et al. 2013, 2015; Loxton et al. 2017).

Membranipora membranacea (Linnaeus, 1767) is a cosmopolitan and highly invasive epiphytic bryozoan that has the capacity to dramatically alter invaded ecosystems (Lambert et al. 1992; Saunders and Metaxas 2008; Krumhansl et al. 2014; Filbee-Dexter et al. 2016; O'Brien and Scheibling 2018). The bryozoan occurs in both warm and cold temperate waters in the Pacific (North and South America, Japan, Australia and New Zealand) and eastern Atlantic (Europe and South Africa) oceans (Schwaninger 2008). The only range expansion exhibited by *M. membranacea* in historic time was the anthropogenic introduction of the bryozoan to the Gulf of Maine in the northwest Atlantic in 1987 (Berman et al. 1992; Schwaninger 2008). In its invasive range, *M. membranacea* heavily encrusts kelp blades, weakening the underlying tissue and resulting in increased rates of blade breakage, erosion and overall loss of kelp biomass (Lambert et al. 1992; Krumhansl and Scheibling 2011; Krumhansl et al. 2011). Loss of kelp biomass resulting from outbreaks of *M. membranacea* can be so substantial that kelp beds are unable to fully recover by the following year (Saunders and Metaxas 2008), and recurrent bryozoan outbreaks can have profound wide-spread and potentially long-term effects on kelp bed ecosystems (Filbee-Dexter et al. 2016; O'Brien and Scheibling 2018). *Membranipora membranacea* undergoes an annual lifecycle during which the timing and magnitude of recruitment early in the season and colony growth later in the season are both strongly positively related to ocean temperature within its invasive range (Saunders and Metaxas 2007; Saunders and Metaxas 2009a). Consequently, outbreaks of *M. membranacea* and resulting loss of kelp have been linked to both the

magnitude and seasonal timing of ocean warming events (Saunders and Metaxas 2008; Scheibling and Gagnon 2009).

The northwest Atlantic has been identified as an ocean warming hotspot, where ocean temperatures are increasing at rates faster than 90% of the rest of the world's oceans (Hobday and Pecl 2014). This is of particular concern given the proximity of the northwest Atlantic to the Canadian Arctic and the potential for rapidly changing regional climatic conditions to facilitate species introductions into vulnerable polar ecosystems (e.g. Tavares and DeMelo 2004; Reid et al. 2007). Predictive models show that population growth of *M. membranacea* in the northwest Atlantic will accelerate in the near-term in response to projected increases in ocean temperature (Denley et al. 2019). However, the magnitude of accelerated population growth will also depend on kelp species community composition of invaded kelp beds (Denley et al. 2019) which varies regionally within the northwest Atlantic. Nova Scotia is dominated by mixed-species kelp beds composed of *Saccharina latissima* ((Linnaeus) CE Lane, C Mayes, Druehl and GW Saunders, 2006), *Laminaria digitata* ((Hudson) J.V. Lamouroux, 1813) and *Agarum clathratum* (Dumortier, 1822) (Saunders and Metaxas 2009b). The northern Gulf is characterized by extensive urchin barrens with patchily distributed macroalgae, predominantly *Alaria esculenta* ((Linnaeus) Greville, 1830), *Desmarestia viridis* ((Bory) ME Ramírez and AF Peters, 1993) and *Agarum clathratum* (Dumont et al. 2004; Bégin et al. 2004; Merzouk and Johnson 2011). Based on qualitative descriptions from the few studies available these species are often but not exclusively found in mono-specific stands. The Magdalen Islands are surrounded by sand with macroalgae limited to intermittent patches of hard substrate (C. McKindsey, *pers. comm.*). The effects of temperature and kelp substrate availability on the rate of spread of *M. membranacea* in the northwest Atlantic are not known. Thus, our ability to predict how this ecologically significant invasive species will impact Arctic ecosystems under projected increases in ocean temperature and shifts in the distribution of cold-temperate macroalgae (Muller et al. 2009) remains limited.

Membranipora membranacea produces long-lived (~ 4-week larval duration, Yoshioka 1973; Temkin 1994) planktotrophic larvae, enabling widespread natural dispersal; it is also a fouling species that can colonize artificial substrates, providing opportunity for human mediated long-distance dispersal. *Membranipora membranacea* was initially introduced to the east coast of North America in the Gulf of Maine in 1987 (Berman et al. 1992) and was first observed off the southwestern shore of Nova Scotia in 1992 (Scheibling et al. 1999). Over the last 30 years, *M. membranacea* has expanded its range to include the entire Atlantic coast of Nova Scotia (Watanabe et al. 2010) and west coast of Newfoundland (Caines and Gagnon 2012). Spread of the bryozoan in the northwest Atlantic occurred rapidly; in many cases, by the time local-scale occurrence of *M. membranacea* was

quantified, it was already widespread within the greater region (e.g. Newfoundland, Caines and Gagnon 2012; Nova Scotia, Watanabe et al. 2010; Sephton et al. 2014, 2015; New Brunswick, Sephton et al. 2017). The lack of baseline zero abundance data for many regions of the northwest Atlantic precludes our ability to accurately determine the timing of introduction and consequently the rate and mechanism (natural versus anthropogenic) of spread of *M. membranacea*. However, ongoing aquatic invasive species (AIS) monitoring initiated in the Gulf of St. Lawrence in 2006, and therefore prior to the introduction of *M. membranacea*, captures the initial establishment and subsequent annual abundances of *M. membranacea* in three regions of the northwest Atlantic: the Gaspé Peninsula, the Magdalen Islands, and the northern coast of the Gulf of St. Lawrence.

In this study, we take advantage of unique baseline data on the early stages of establishment of *M. membranacea* in the Gulf of St. Lawrence to examine factors influencing the abundance and rate of spread of this ecologically significant invasive bryozoan at its current northern range limit in the northwest Atlantic. Based on (1) well documented relationships between ocean temperature and abundance of introduced sessile marine invertebrates (Stachowicz et al. 2002; Sorte and Stachowicz 2011; Lord 2017); and (2) previously quantified relationships linking warmer seawater temperature to increased abundance of *M. membranacea* for well-established invasive populations in southwestern Nova Scotia (Saunders and Metaxas 2007; Scheibling and Gagnon 2009), we hypothesize that the abundance and rate of spread of *M. membranacea* in the Gulf of St. Lawrence will be driven primarily by regional differences in ocean temperature.

Materials and methods

Data collection

We obtained data on presence/absence and abundance of *Membranipora membranacea* on collectors deployed in the Magdalen Islands (IM), Gaspé Peninsula (GA), and the northern coast of the St. Lawrence (CN) through Maurice Lamontagne Institute (Fisheries and Oceans Canada) collected as part of their Aquatic Invasive Species (AIS) monitoring program from 2006 to 2016 (Supplementary material Figures S1–S11). Collectors consisted of three 10 cm × 10 cm plates made from polyvinyl chloride (PVC), horizontally suspended at 20 cm intervals along a weighted rope line (Figure 1). The line was weighted to hang vertically in the water column with the top plate approximately 1 m below the surface. Beginning in 2008, a 23 cm inverted plastic flowerpot saucer with three 100 mm petri dishes attached to the underside was suspended on the float line above the first plate (Figure 1). Four collectors were deployed at each site in spring (May/June) of each year, two of which were retrieved in August (early season collectors) and replaced by two new collectors (late season collectors),

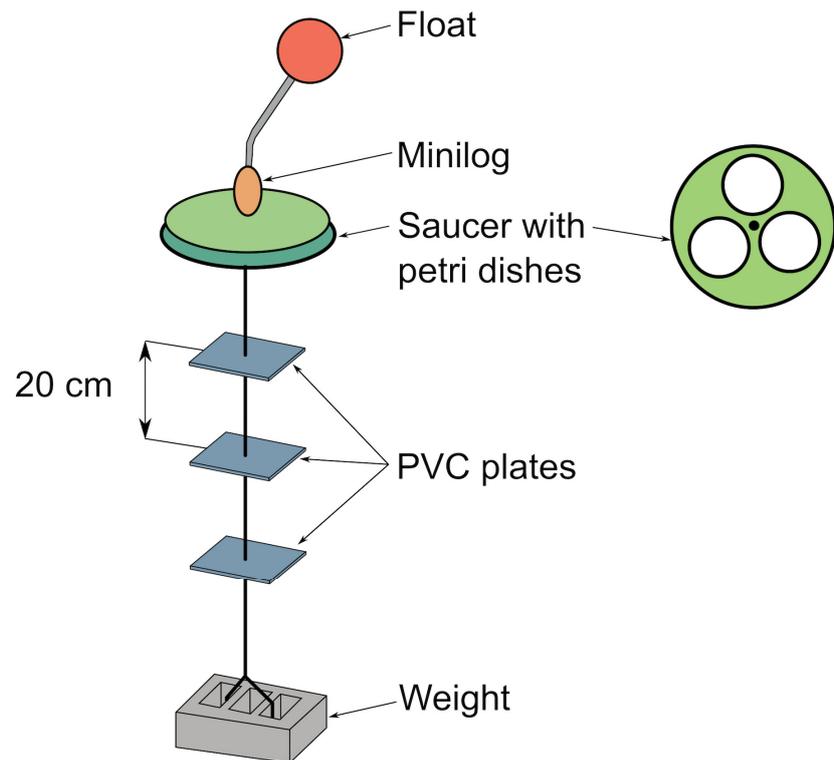


Figure 1. Diagram of AIS monitoring collectors deployed by the Department of Fisheries and Oceans Canada, Maurice Lamontagne Institute as part of their Aquatic Invasive Species (AIS) monitoring program from 2006 to 2016.

which, along with the remaining two deployed for the full seasonal cycle of *M. membranacea* (full season collectors), were retrieved in fall (October/November). This design resulted in six collectors at each monitoring site per year to capture seasonal dynamics (early: May/June to August, late: August to October/November, and full: May/June to October/November) in the occurrence and abundance of *M. membranacea* over the course of its annual lifecycle. Abundance of *M. membranacea* on each plate (or petri dish after 2008) within a collector was visually estimated as categorical percent cover (categories 0 to 5; 0: absence of *M. membranacea*, 1: $\leq 25\%$, 2: 26–50%, 3: 51–75%, 4: 76–99%, 5: 100% cover).

Seawater temperature was also recorded at 15 to 30 minute intervals at ~ 1 m below the surface at each monitoring site over the deployment duration (May/June to October/November) using HOBO pendant data loggers attached to full season collectors. In addition, we acquired annual daily average (3 day averages for days when SST was not available) sea surface temperature (SST) for each site from 2006 to 2012 from the Maurice Lamontagne Institute SST database using a 5 km search radius.

Data analysis

Rate of spread of *M. membranacea*

We determined the rate of spread of *M. membranacea* from its known invasive range in 2000 (~ 100 km linear distance from Halifax Harbour to

Liverpool, Watanabe et al. 2010) along the coast of Nova Scotia and within the Gulf of St. Lawrence (GSL) based on video and dive surveys off the Atlantic coast of Nova Scotia in 2007 (Watanabe et al. 2010) and on the initial establishment of *M. membranacea* on AIS monitoring collectors at each site in GSL (Table S1, Figures S1–S11), respectively. Secondary spread is typically defined as an increase in the range of an invasive species following its initial invasion (O’Loughlin and Green 2017), and therefore could be used to describe the spread of *M. membranacea* in both Nova Scotia and GSL. However, to differentiate between rates of spread in Nova Scotia and GSL for the purpose of this study, we refer to the spread of *M. membranacea* along the Atlantic coast of Nova Scotia as initial spread. We refer to the spread of the bryozoan in GSL following its initial introduction to the Gaspé Peninsula in 2008 as secondary spread. Because *M. membranacea* has an annual lifecycle, we considered colonizing populations to be viable after two years since first record. Thus, we defined establishment as the occurrence of *M. membranacea* on one or more collectors at a given site for at least two consecutive years. If this condition was met, we then considered the first year during which *M. membranacea* was detected as the time of initial establishment. In some cases, for sites located in close proximity (e.g. within the same bay), collectors at both sites were considered in combination in determining establishment of *M. membranacea* at relevant local scales (Table S1). Although *M. membranacea* was not detected on AIS monitoring collectors deployed off the Gaspé Peninsula until 2008, the bryozoan was observed on cultivated kelp (*Saccharina latissima*) transferred to the ocean on 4 floating longlines in Baie de Paspébiac, approximately 60 km from the nearest monitoring site, in May 2006 (Gendron et al. 2007) and April 2007 (Gendron and Tamigneaux 2008). Therefore, in addition to determining the rate of spread of *M. membranacea* in GSL using standardized monitoring techniques, we also quantified rate of spread based on the initial detection of the bryozoan at kelp aquaculture sites in 2006.

Spatial and temporal patterns in abundance of *M. membranacea*

Because of low abundance and consequently large variance among plates, we examined abundance (% cover) of *M. membranacea* at the level of the individual collector by averaging median categorical percent cover values (0: 0, 1: 12.5, 2: 38, 3: 63, 4: 87.5, 5: 100) across all plates and petri dishes within a collector and thus over the entire depth range covered by the collectors. Given the limited range in depth covered by the collectors (~ 1 m) we do not expect significant depth-related variation in bryozoan abundance among plates within the sample collector. Thus, relating potential differences in abundance of *M. membranacea* to depth below the surface is outside of the scope of the current study.

We examined the effects of region (3 levels: IM, GA, CN) and sampling year (7 levels: 2009, 2010, 2011, 2012, 2013, 2014, 2015, 2016) on the abundance (percent cover) of *M. membranacea* using linear mixed effects models with separate intercepts for the random effect of season. Region and year were considered to be fixed effects because regions were chosen to represent different thermal regimes within the GSL and years were chosen to include only those during which *M. membranacea* was determined to be established in GSL (2009–2016). Season was considered a random effect because the exact dates when collectors were deployed and recovered for each season varied among years and sites and only approximately corresponded to the seasonal timing of events in the annual lifecycle of *M. membranacea*, which can vary regionally and inter-annually (Saunders and Metaxas 2007, 2008, 2009b; Caines and Gagnon 2012). Heterogeneity of variance resulted from a high number of collectors with zero percent cover of *M. membranacea* and could not be alleviated by transformation of abundance data. Accordingly, we also examined the main effects of region and year on the abundance of *M. membranacea* using zero-inflated negative binomial models (Zuur et al. 2009). We modelled the probability of measuring a false zero (π_i) for the binomial distribution in terms of the random effect of season, since zero abundance of *M. membranacea* may reflect monitoring that occurred prior to the seasonal onset of settlement by bryozoan larvae in the spring, or after the seasonal occurrence of peak settlement by bryozoan larvae in the fall (Denley et al. 2014; Saunders and Metaxas 2008).

Spatial and temporal patterns in regional ocean temperature and the effect of temperature on abundance of *M. membranacea*

Using a combination of daily averaged *in situ* ocean temperature (~ 1 m depth, June to November only, 2006–2016) and satellite SST data (year-round, 2006–2012) we calculated three temperature indices: 1) annual summer peak (average seawater temperature from 1 July to 31 August) and winter trough (average seawater temperature from 1 February to 31 March) for all regions (IM, GA, CN) from 2006 to 2012; 2) thermal regime (growing degree-day (GDD), °D, after Saunders and Metaxas 2007) calculated by sequentially adding standardized daily average temperatures from 1 January of each year for years and regions for which complete annual temperature data were available (GA and CN only, 2006–2012); and 3) time-integrated thermal integral (TI, °D, after Scheibling and Gagnon 2009) calculated by sequentially adding standardized daily average temperatures over the 3 month warm period prior to peak bryozoan abundance on late season collectors (TI_w, 1 July through 30 September, all regions, 2008–2016) and over the 5 month cool period (TI_c, 1 January through 31 May, GA and CN only, 2008–2012). Satellite SST data were not

consistently available for the Magdalen Islands precluding our ability to calculate GDD and TI_C for this region.

We assessed changes in temperature over the period 2006–2012 for each region using simple linear regression of annual summer peak and winter trough temperature. We evaluated interannual and regional differences in thermal regime (GDD) using two-way ANOVA of the effects of region (fixed factor, 2 levels: GA, CN) and year (fixed factor, 7 levels: 2006, 2007, 2008, 2009, 2010, 2011, 2012) on GDD ($^{\circ}D$). We considered year to be a fixed factor because years were chosen to include all years for which complete annual temperature (SST) data were available during the period (2006–2016) when AIS monitoring data were collected. We examined the effect of interannual and regional variation in ocean temperature on the abundance of *M. membranacea* pooled across all regions (when data were available) using simple linear regression between early (early season collectors) and peak (late season collectors) abundance and thermal integrals TI_C and TI_W , respectively. We also examined the effect of interannual variation in thermal regime (GDD) pooled across regions (GA and CN) on abundance of *M. membranacea* on late season collectors using simple linear regression. Because late season collectors from different sites within each region were retrieved on different dates, we used GDD in mid-October (October 15) of each year from 2006–2012 for our analysis.

Results

Rate of spread of Membranipora membranacea

The range of *M. membranacea* expanded by approximately 1740 km from southwestern Nova Scotia to the north coast of the St. Lawrence in 11 years (2000 to 2011) (Figure 2). The rate of spread of *M. membranacea* ranged from 73.42 km yr⁻¹ along the Atlantic coast of Nova Scotia to ~ 130 km yr⁻¹ in the Gulf of St. Lawrence (GSL) (Figure 3, Table S2). *Membranipora membranacea* exhibited bi-phasic range expansion (Shigesada et al. 1995), characterized by low initial slope of range size over time (initial expansion) followed by a steeper linear slope (secondary expansion), and lastly a saturation phase (Figure 3). The rate of spread of *M. membranacea* in the GSL based on standardized AIS monitoring collectors alone (130.8 km yr⁻¹) was comparable to the rate of spread that included the observations of the bryozoan on cultivated kelp in Baie de Paspébiac in 2006 and 2007 (132.6 km yr⁻¹, Figure 3, Table S2).

Spatial and temporal patterns in abundance of M. membranacea

There was a significant interaction between region and sampling year on the abundance of *M. membranacea*, and this result was consistent after accounting for zero-inflated data (Tables 1 and 2). Among regions, the abundance of *M. membranacea* was greater in the Magdalen Islands (IM) than

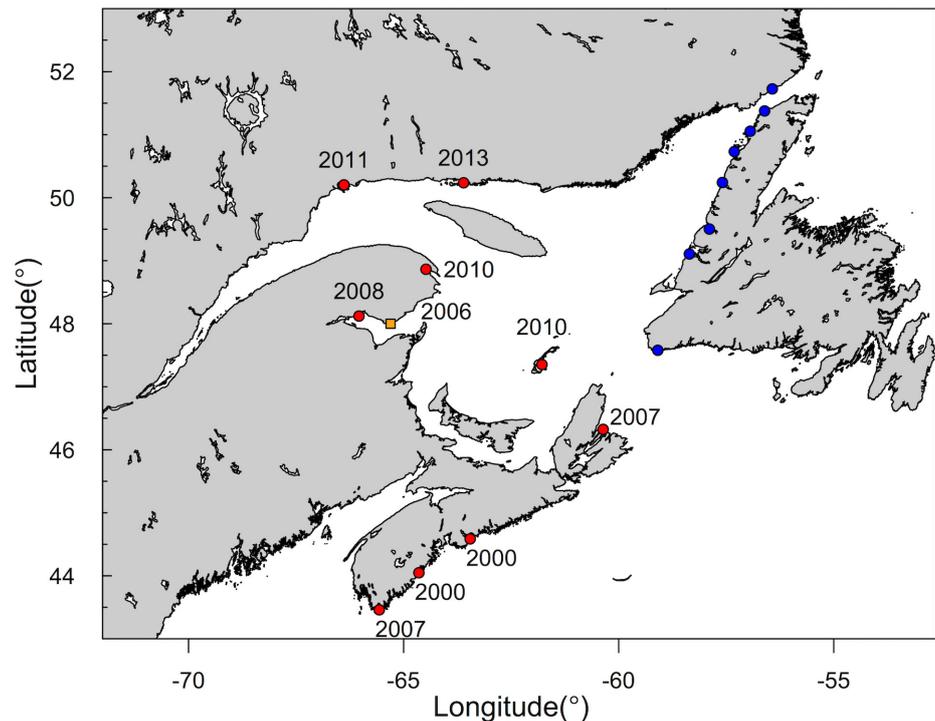


Figure 2. The rate of spread of *M. membranacea* in Nova Scotia and the Gulf of St. Lawrence (red dots). Dates indicate the known range of *M. membranacea* observed on natural substrates during video/dive surveys (2000, 2007, Tables S1 and S2) and the year of initial establishment of *M. membranacea* detected by AIS monitoring collectors (2008–2013, Tables S1 and S2). Orange square indicates location of *M. membranipora* observed on cultured kelp (Gendron et al. 2007; Gendron and Tamigneaux 2008), see Methods. Blue dots indicate the range of *M. membranacea* in southwestern Newfoundland and southeastern Labrador in 2008 (data from Caines and Gagnon 2012), see Discussion section.

on the northern coast of the St. Lawrence (CN) or the Gaspé Peninsula (GA) in 2011, greater in CN than IM and GA in 2013, and greater in GA than IM and CN in 2014 and 2015; in 2016, abundance was greater in GA than CN only (Figure 4, Table 1). The random effect of season was also significant, with highest abundance of *M. membranacea* on late season collectors (Figure 4, Table 1).

Spatial and temporal patterns in regional ocean temperature and the effect of temperature on abundance of M. membranacea

Winter trough (February to March) ocean temperature warmed significantly from 2006 to 2012 in all regions, however, r^2 values were low (0.011–0.037, Figure 5). Rates of warming over winter ranged from 0.026 °C yr^{-1} (CN) to 0.045 °C yr^{-1} (IM) and were intermediate for GA (0.031 °C yr^{-1}) (Figure 5). CN was the only region that experienced concurrent warming of summer peak ocean temperature (July to August) of 0.054 °C yr^{-1} (Figure 5). There were consistent significant regional differences in GDD between GA and CN, with GDD for CN being lower than GA for all years from 2006 to 2012 (Figure 6, Table 3). However, there was no relationship between annual GDD and peak abundance of *M. membranacea* on late season collectors for either GA or CN over the same time period (Figure 7). Peak abundance of

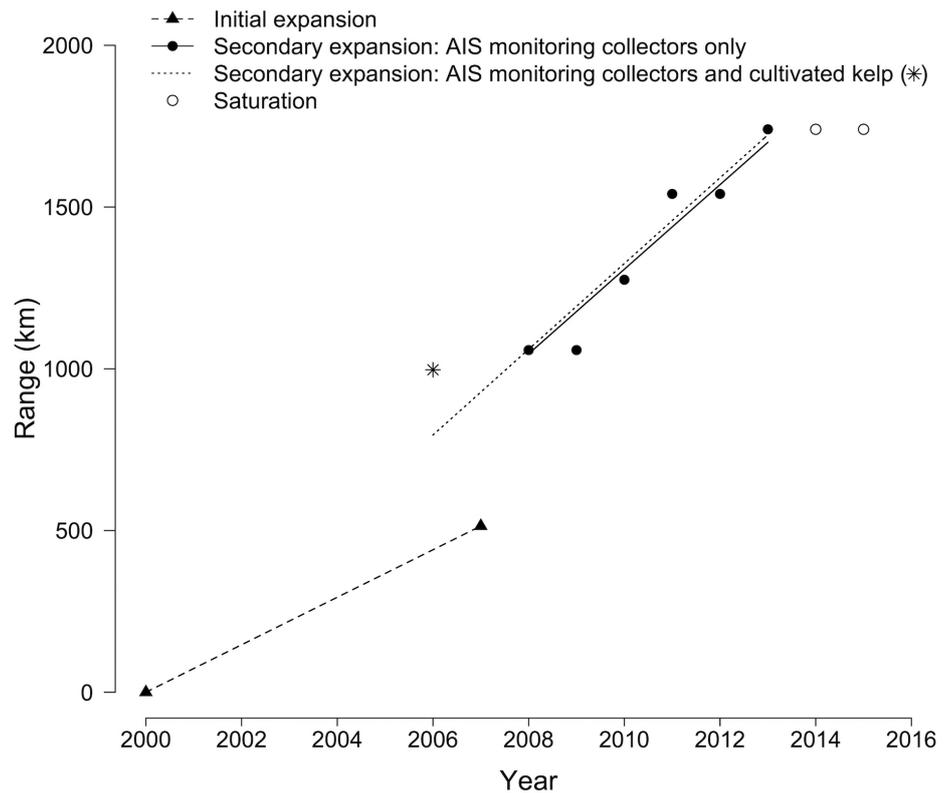


Figure 3. Range size over time for *M. membranacea* in Nova Scotia (closed triangles and dashed line, initial expansion) and the Gulf of St. Lawrence (closed circles and solid line, secondary expansion based on AIS monitoring collectors only; dotted line, secondary expansion based on AIS monitoring collectors and including the observations of *M. membranacea* on cultivated kelp in Baie de Paspébiac in 2006 and 2007 (star); open circles, “saturation” phase) following its establishment in southwestern Nova Scotia in 2000. The range of *M. membranacea* was observed on natural substrates during video/dive surveys (2000, 2007), on AIS monitoring collectors (2008–2016), and on cultivated kelp in 2006 (Gendron et al. 2007) and 2007 (Gendron and Tamigneaux 2008). Regression equations: initial expansion = 73.42 km yr^{-1} ; secondary expansion (AIS collectors only) = 130.8 km yr^{-1} , $r^2 = 0.997$; secondary expansion (including cultivated kelp) = 132.6 km yr^{-1} , $r^2 = 0.99$; overall (excluding the saturation phase) = $121.50 \text{ km yr}^{-1}$, $r^2 = 0.987$.

M. membranacea was significantly linearly related to the thermal integral over the preceding 3 month warm period (TI_w) across all regions but there was no relationship between early abundance of *M. membranacea* and the thermal integral over the preceding 5 month cool period (TI_c) pooled across GA and CN (Figure 8).

Discussion

The rate of spread of *Membranipora membranacea* in Nova Scotia (73.42 km yr^{-1}) is comparable to natural rates of spread for other invasive marine invertebrates with planktonic larvae (12 to 115 km yr^{-1} , Grosholz 1996), and to *M. membranacea* in other regions (20 km yr^{-1} , Gulf of Maine, Lambert et al. 1992 in Grosholz 1996). Secondary expansion of *M. membranacea* within the Gulf of St. Lawrence occurred more rapidly ($\sim 130 \text{ km yr}^{-1}$) but was still within the observed range of non human-mediated secondary rates of spread for invasive marine species (16 to 235 km yr^{-1} , mean of $70.9 \pm 19.6 \text{ km yr}^{-1}$, Appendix S1 of Sorte et al. 2010). Therefore, with the rapid

Table 1. Results of linear mixed effects models examining the fixed effects of region (3 levels: IM, GA, CN) and sampling year (7 levels: 2009, 2010, 2011, 2012, 2013, 2014, 2015, 2016), and random effect of season (early: May/June to August; late: August to October/November; full: May/June to October/November) on abundance (mean % cover \pm SD among collectors) of *M. membranacea*. Significant *p*-values shown in bold at $\alpha = 0.05$

	χ^2 (df)	<i>p</i>	Tukey's HSD
<i>Fixed effects</i>			
Region	14.4(2)	0.123	2009: GA = IM = CN 2010: GA = IM = CN 2011: CN = GA < IM 2012: GA = IM = CN 2013: GA = IM < CN 2014: CN = IM < GA 2015: CN = IM < GA 2016: IM = GA, IM = CN, CN < GA
Sampling year	61.7(7)	0.0001	GA: 2009 = 2010 = 2011 = 2013 < 2014 2009 < 2012 = 2014 = 2015 = 2016 IM: 2009 ^d = < 2012 < 2011 = 2013 2009 ^d = 2010 = 2014 = 2015 = 2016 < 2011 = 2013 2010 = 2012 = 2014 = 2015 = 2016 < 2011 = 2013 CN: 2009 ^d = 2010 ^d = 2012 = 2014 = 2015 = 2016 < 2013 2009 ^d = 2010 ^d = 2011 = 2012 = 2014 = 2015 = 2016 2011 = 2013
Region x sampling year	83.1(14)	<0.0001	
<i>Random effects</i>			
Season	23.8(1)	<0.0001	Early = Full < Late

^dYears with zero abundance

Table 2. Results of model selection using zero-inflated negative binomial models (ZINB) of the effects of region (fixed effect, 3 levels: IM, GA, CN), sampling year (fixed effect, 7 levels: 2009, 2010, 2011, 2012, 2013, 2014, 2015, 2016), and season (random effect, early: May/June to August; late: August to October/November; full: May/June to October/November) on abundance (mean % cover \pm SD among collectors) of *M. membranacea*. ZINB was chosen over zero-inflated Poisson (ZIP) to account for overdispersion in the count data. The mean (μ_i) for the count data and the probability (π_i) for the binomial distribution (probability of false zero) are modelled in terms of the fixed (region, year) and random (season) variables, respectively. See Methods for details. Significant *p*-values shown in bold at $\alpha = 0.05$

Dropped term	df	AIC	Likelihood ratio test
None	28	2703	
Region x sampling year from μ_i	14	2715	$\chi^2 = 40.5$ (df = 14, <i>p</i> = 0.0002)
Region from μ_i	12	2716	$\chi^2 = 4.32$ (df = 2, <i>p</i> = 0.115)
Sampling year from μ_i	7	2745	$\chi^2 = 43.8$ (df = 7, <i>p</i> < 0.0001)
Season from π_i	26	2725	$\chi^2 = 26.6$ (df = 2, <i>p</i> < 0.0001)

spread into colder waters, it appears that cold temperatures do not seem to be inhibiting natural northward spread of *M. membranacea*, at least over the thermal range examined in this study (annual range in daily-averaged SST for the northern coast: -1.8 °C to 18.4 °C).

The northwest spread of *M. membranacea* to the Gaspé Peninsula between 2006 (cultivated kelp) and 2008 (AIS monitoring collectors) is in the opposite direction of the predominant ocean circulation in the region which is from the northeast to the southwest shelf (El-Sabh 1976). Thus, the introduction of *M. membranacea* to the Gaspé was likely the result of human-mediated long-distance dispersal. Two possible anthropogenic vectors that may have facilitated the introduction and establishment of the

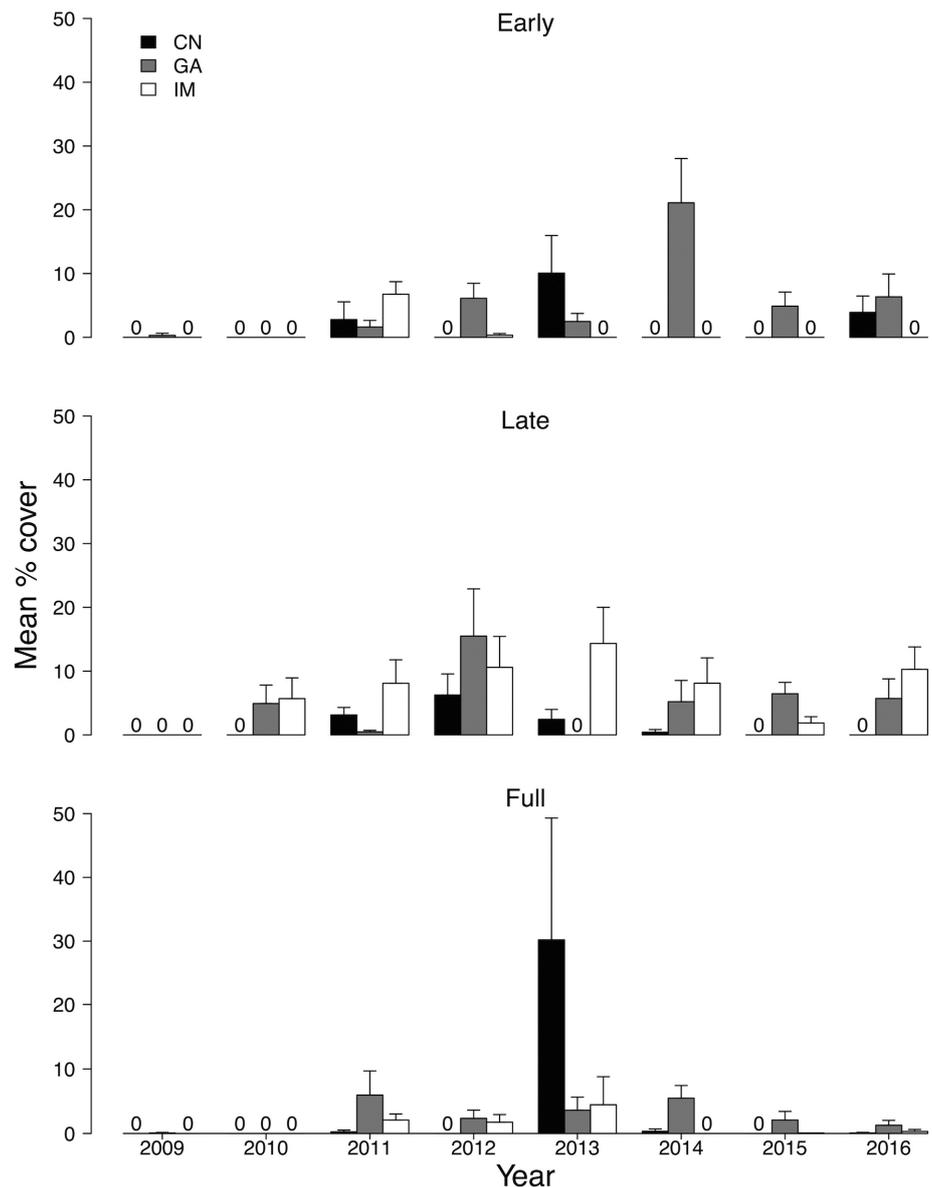


Figure 4. Abundance (% cover, mean \pm SD among collectors, $n = 4\text{--}33$) of *M. membranacea* on AIS monitoring collectors in 3 regions, Magdalen Islands (IM), Gaspé Peninsula (GA), and north coast of the St. Lawrence (CN) and over 3 seasons, early (May/June–August), late (August–October/November), full (May/June–October/November) from 2009 to 2016.

bryozoan into this region are recreational boating and kelp aquaculture, respectively. Recreational boating is a major vector contributing to the spread of invasive marine species through hull fouling (Ashton et al. 2006; Clarke Murray et al. 2011). The Magdalen Shallows ecoregion, which includes the southern Gaspé Peninsula, receives the second greatest number of transient boats in Atlantic Canada (after the Scotian Shelf ecoregion) (Pelletier-Rousseau et al. 2019), and Baie des Chaleurs has a relatively high density of small craft harbours, marinas and yacht clubs (Gagnon 1997) suggestive of high recreational vessel traffic. Additionally, kelp aquaculture practices may increase the probability of establishment and rate of spread of *M. membranacea* by providing additional natural substrate for recruitment and colony growth (e.g. Forde et al. 2016). *Membranipora*

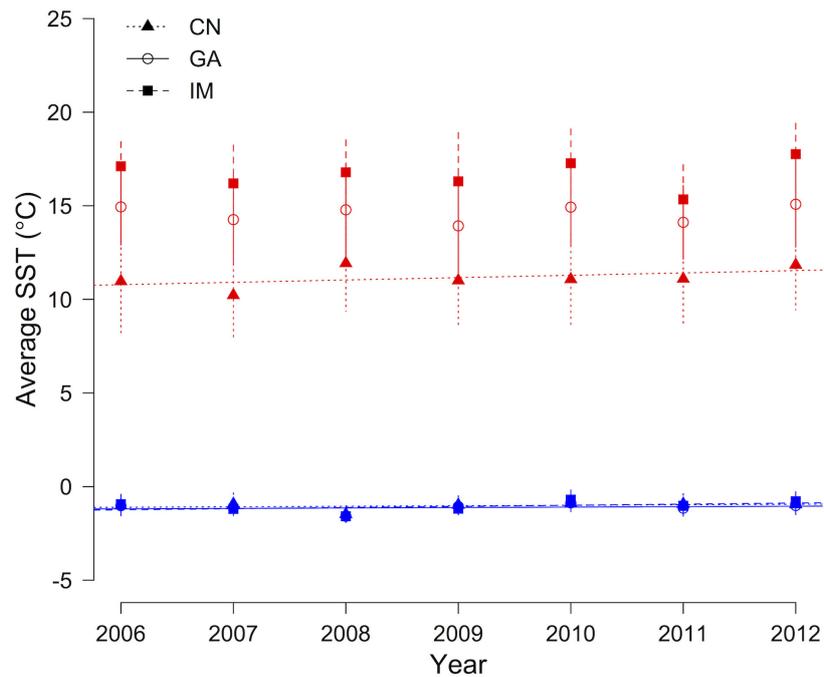


Figure 5. Average daily sea surface temperature (SST) pooled across AIS monitoring stations (mean \pm SD) in 3 regions, Magdalen Islands (IM, $n = 16$), Gaspé Peninsula (GA, $n = 24-25$), and north coast of the St. Lawrence (CN, $n = 16$) during the annual summer peak (red: July to August) and the winter trough (blue: February to March) from 2006 to 2012. Regression equations: GA: $T_{\text{trough}} = 0.031Y - 1.22$, $r^2 = 0.020$, $p < 0.0001$; IM: $T_{\text{trough}} = 0.045Y - 1.28$, $r^2 = 0.037$, $p < 0.0001$; CN: $T_{\text{trough}} = 0.026Y - 1.15$, $r^2 = 0.011$, $p < 0.0001$, $T_{\text{peak}} = 0.054Y + 10.9$, $r^2 = 0.002$, $p = 0.0001$. No significant trend in annual summer peak SST for GA or IM.

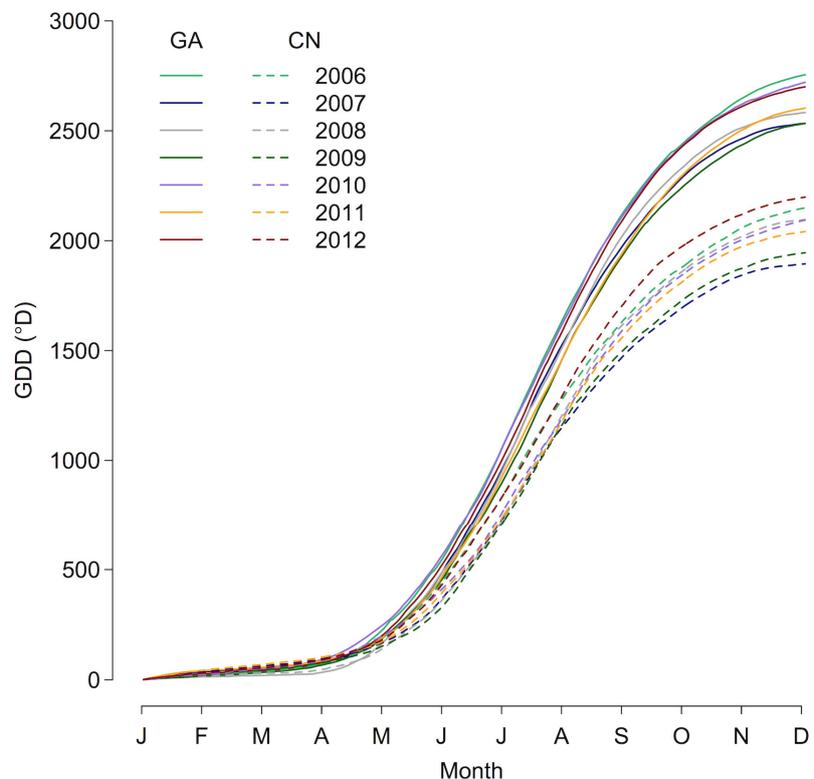


Figure 6. Interannual and regional differences in GDD for AIS monitoring stations on the Gaspé Peninsula (GA) and the north coast of the St. Lawrence (CN) from 2006 to 2012. GDD is calculated based on daily average sea surface temperature pooled across AIS monitoring stations in each region (GA, $n = 24-25$; CN, $n = 16$). GDD is significantly lower for CN than GA for all years (Table 3).

Table 3. Two-way ANOVA examining the effects of region (fixed factor, 2 levels: GA, CN) and year (fixed factor, 7 levels: 2006, 2007, 2008, 2009, 2010, 2011, 2012) on GDD (°D)

Factor	MS	$F_{(df)}$	p	Tukey's HSD
Region	6.7×10^7	82.8 ₍₁₎	< 0.0001	CN < GA
Year	1.2×10^6	1.50 ₍₆₎	0.176	
Region x year	1.5×10^5	0.188 ₍₆₎	0.980	
Error	8.1×10^5			

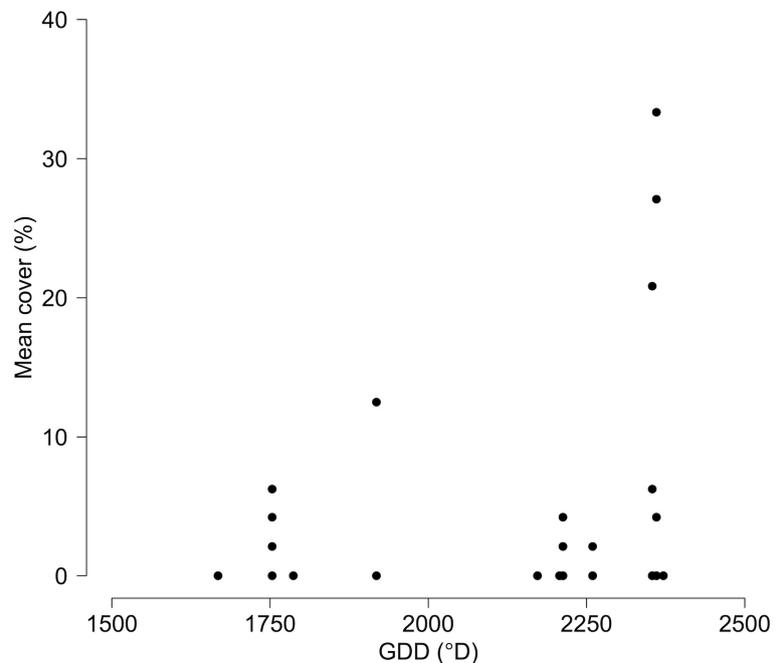


Figure 7. Relationship between abundance of *M. membranacea* on late season collectors (mean % cover pooled across collectors deployed from August to October/November, $n = 4-26$) and GDD on October 15 of each year pooled across AIS monitoring stations in two regions, Gaspé Peninsula ($n = 16-22$) and north coast of the St. Lawrence ($n = 4-6$), from 2006 to 2012. Regression equation: Abundance = $0.010GDD - 17.5$, $p = 0.121$, $r^2 = 0.012$.

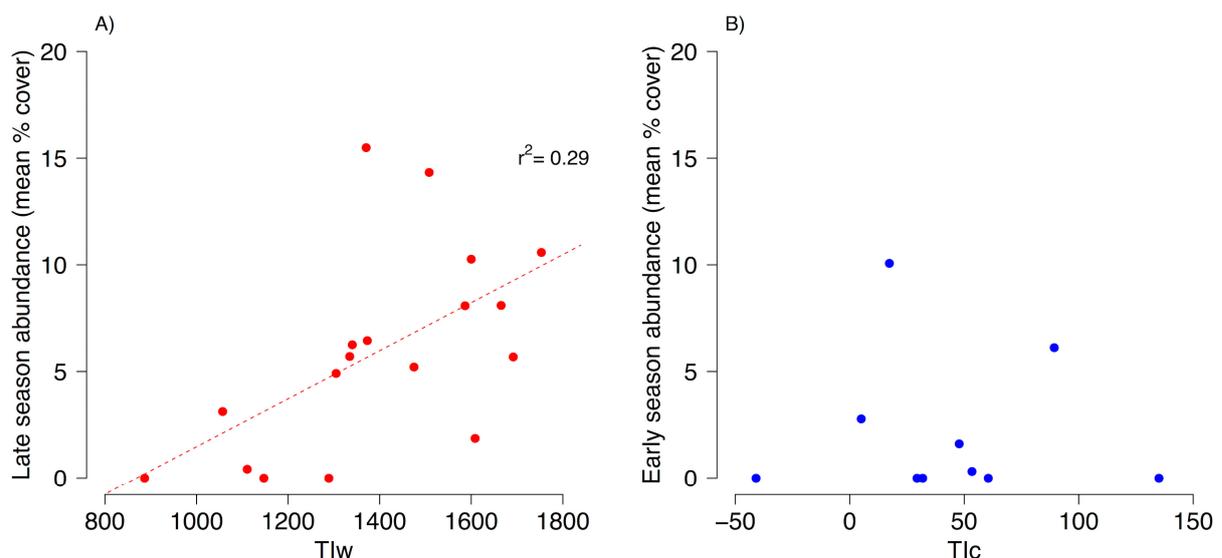


Figure 8. Relationships between abundance of *M. membranacea* (mean % cover pooled across collectors, $n = 4-33$) and thermal integrals (TI, °D). A) Peak abundance (late season collectors) in relation to the previous 3-month warm period (TI_w, July through September, 2008 to 2016) pooled across all regions (Magdalen Islands: IM, Gaspé Peninsula: GA, north coast of the St. Lawrence: CN), regression equation: abundance = $0.011TI_w - 9.79$, $r^2 = 0.29$, $p = 0.013$. B) Early abundance (early season collectors) in relation to the 5-month cool period (TI_c, January through May, 2008–2012) pooled across GA and CN only. Satellite SST data were not consistently available for IM precluding our ability to calculate TI_c for this region.

membranacea has been observed in 2017 and 2018 (data not shown) on kelp at an aquaculture site that was established on the north coast in Baie de Sept-Îles in 2014 (following the initial detection of the bryozoan on AIS monitoring collectors deployed in the same bay in 2011, this study). An experimental kelp aquaculture site was also established in the Magdalen Islands in 2014 and *M. membranacea* was observed on cultured kelp at this site in 2015 (data not shown). However, as for the northern coast, observations of the bryozoan on cultured kelp in the Magdalen Islands occurred after the initial introduction of *M. membranacea* to the region in 2010 (this study).

The stable range size observed from 2013 to 2015 is suggestive of a saturation phase in the spread of *M. membranacea* along the northern coast of the St. Lawrence. Saturation phases in invasion biology are typically characterized by geographic limits to the available space for expansion (Shigesada and Kawasaki 1997); however, lags in invasive species range expansion can also occur in response to a variety of physical (e.g. lack of suitable substrata for recruitment, Bohn et al. 2015) and biological (e.g. predation pressure, Forrest et al. 2013) dispersal barriers. The specific mechanisms responsible for the lack of range expansion by *M. membranacea* between 2014 and 2015 are unknown. *Membranipora membranacea* was observed on monitoring plates at Port-Cartier in 2016, approximately 40 km southwest of the nearest established population in 2015 (Figure S11). However, 2016 was the first year AIS monitoring was conducted at Port-Cartier making it impossible to determine whether the occurrence of *M. membranacea* at this location represents further range expansion or a continuation of the saturation phase. The bryozoan was not detected on collectors deployed at Port-Cartier in 2017 and 2018 (data not shown).

Differences in abundance of *M. membranacea* were inconsistent among recently (~ 2008) invaded regions in the northwest Atlantic and did not reflect significant regional differences in thermal regime. For example, peak abundance of *M. membranacea* was not significantly related to growing degree-day for two regions with consistently warmer (Gaspé Peninsula) and colder (north coast of the St. Lawrence) ocean temperatures. In comparison, intermediate values of growing degree-day relative to the Gaspé and north coast in southwestern Nova Scotia are strongly related to the abundance of settlers of *M. membranacea* (explaining up to 81% of the variability in settler abundance, Saunders and Metaxas 2007) and consequently the percent cover of colonies on kelp (Saunders and Metaxas 2008). At broader scales that included all three regions in the Gulf of St. Lawrence, peak abundance of *M. membranacea* was positively related to the thermal integral over the previous three-month warm period; however, this relationship was weak and no relationship was observed between early abundance and the thermal integral over winter. Our results suggest that significant warming trends in seawater temperature over winter observed

across all regions during the initial introduction and establishment of *M. membranacea* are not driving range expansion of this invasive species within the Gulf of St. Lawrence.

Increased abundance on late season collectors in the Gulf of St. Lawrence suggests similar seasonal timing of the annual lifecycle of *M. membranacea* to that of longer established populations in Nova Scotia (Saunders and Metaxas 2008, 2009b; Denley et al. 2014). However, in Nova Scotia, annual population outbreaks of *M. membranacea* have been linked to warm ocean temperatures through strong positive relationships between temperature and recruitment (Saunders and Metaxas 2007, 2008) and colony growth (Saunders and Metaxas 2009a). Consequently, the thermal integral over the previous three-month warm period explained 83% of the observed interannual variability in peak cover of *M. membranacea* on kelp for recently established (1992 to 1994 and 1997 to 1999) invasive populations in southwestern Nova Scotia (Scheibling and Gagnon 2009), compared to only 29% of the variability in peak bryozoan cover for recently established populations in the Gulf of St. Lawrence (this study).

We cannot explicitly quantify the role of natural kelp substrate relative to artificial collectors in contributing to the observed differences in the population dynamics of *M. membranacea* in its early stages of establishment in Nova Scotia compared to the Gulf of St. Lawrence. Assemblages of sessile marine invertebrates can differ on natural compared to artificial substrates (Bulleri 2005); in particular, the relative abundance of invasive species compared to native species can be greater on artificial substrates (Tyrrell and Byers 2007; Dafforn et al. 2009). However, in southwestern Nova Scotia concurrent sampling of *M. membranacea* on artificial settlement plates and adjacent (within 5 m) kelp beds yielded no significant difference in the number of colonies between substrate types (Table S3), suggesting that for *M. membranacea* abundance on artificial collectors reasonably approximates natural abundance in the local environment.

Population models show that population growth of *M. membranacea* in response to increasing ocean temperature is greater for mixed-species kelp beds than for mono-specific stands of the same total kelp abundance (Denley et al. 2019). Reduced rates of bryozoan population growth for mono-specific compared to mixed species kelp beds under the same projected increases in ocean temperature suggest that the availability and species composition of kelp beds can modulate direct effects of temperature on the abundance of *M. membranacea*. In Nova Scotia, mixed-species kelp beds showed 75–100% cover along most of the Atlantic coast in 2007 (Watanabe et al. 2010). In contrast, the northern Gulf and Magdalen Islands are characterized by patchily distributed macroalgae (Dumont et al. 2004; Bégin et al. 2004; Merzouk and Johnson 2011; C. McKindsey, *pers. comm.*). The thermal response of populations of *M. membranacea* in the Gulf of St. Lawrence may therefore be moderated due

to lack of available algal substrate. For example, in 2008 *M. membranacea* was already established along the entire west coast of Newfoundland and into southeastern Labrador, where mixed kelp beds are similar to those of Nova Scotia (Caines and Gagnon 2012, Figure 1). In Newfoundland, temperature explained 61% of the variation in settlement, recruitment, and colony cover on kelp (*Saccharina latissima*) among 8 sites with mixed kelp beds despite subarctic ocean temperatures (monthly averaged temperature from August to November ranged from ~ 4 °C to 17 °C) (Caines and Gagnon 2012).

In combination, rates of spread and regional abundances of *M. membranacea* suggest that colder temperature does not inhibit establishment of invasive populations at its current northern range limit within the northwest Atlantic. This is consistent with the native range of *M. membranacea* on the west coast of North America, which extends to Kodiak Alaska where sea surface temperatures range from 1.7 to 12.7 °C (Dick and Ross 1986; Schwaninger 2008). Although colder ocean temperature may not directly inhibit the spread of *M. membranacea*, it could affect the frequency and magnitude of destructive population outbreaks when kelp substrate is not limiting. This could explain the strong relationships between temperature and abundance of *M. membranacea* resulting in temperature-mediated population outbreaks in Nova Scotia (Saunders and Metaxas 2007, 2008; Scheibling and Gagnon 2009; Saunders et al. 2010). For example, despite similar occurrence of mixed kelp beds, peak percent cover of *M. membranacea* on kelp is lower in Newfoundland (~ 30%, Caines and Gagnon 2012) than in southwestern Nova Scotia (~ 80%, Scheibling and Gagnon 2009; Saunders and Metaxas 2009b; Denley et al. 2014) where daily averaged temperature from August to November ranges from ~ 7 °C to 20 °C at 4 m depth (Saunders and Metaxas 2007). However, comparatively lower peak cover of *M. membranacea* in Newfoundland was still associated with 40–60% declines in kelp cover, evidence that this invasive bryozoan can facilitate substantial loss of kelp even in subarctic cold-water environments (Caines and Gagnon 2012).

Declines in the latitudinal extent of sea ice and increases in seawater temperature predicted for the northwest Atlantic (Loder and van der Baaren 2013) are likely to favour the northward spread of *M. membranacea* by increasing the number and frequency of anthropogenic transport vectors, as well as the extent of suitable habitat for establishment of *M. membranacea* (Goldsmith et al. 2018). We propose that available algal substrate may be more important than temperature in limiting the spread and abundance of *M. membranacea* at its current invasive northern range limit. Given that laminarian kelps are widespread in the northeastern Canadian Arctic (Filbee-Dexter and Scheibling 2014 and references therein), our findings have important implications with respect to the probability of spread and the resulting ecological impacts of *M. membranacea* in vulnerable Arctic ecosystems.

Acknowledgements

We would like to thank Isabelle Bérubé, Sophie Boudreau and Selma Pereira for assistance in the field, Michèle Pelletier-Rousseau for data compilation, Joel Chassé for providing access to temperature data, and two anonymous reviewers for providing comments on an earlier version of this manuscript. This research was funded by a the AIS monitoring program of Fisheries and Oceans Canada and a Natural Sciences and Engineering Research Council (NSERC) Discovery grant to AM.

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Supplementary material

The following supplementary material is available for this article:

Table S1. Location of sites surveyed and year of the known range (Nova Scotia) or first detection (Gulf of St. Lawrence) of *Membranipora membranacea* shown in Figure 2.

Table S2. Observed rates of spread of *Membranipora membranacea* (km yr⁻¹) from its initial established range (~100 km) in southwestern Nova Scotia (Watanabe et al. 2010) to the Gulf of St. Lawrence.

Table S3. ANOVA on the effect of natural (kelp) versus artificial (PVC plates) substrate on the abundance (colonies per m² substrate) of *Membranipora membranacea* during 3 seasonal sampling times (fall: November 2012, spring: June 2013, summer: August–September 2013) at two sites (The Lodge, Sandy Cove) in southwestern Nova Scotia.

Figure S1. Location of Maurice Lamontagne Institute (Fisheries and Oceans Canada) Aquatic Invasive Species (AIS) monitoring stations in the Magdalen Islands (IM), Gaspé Peninsula (GA), and the northern coast of the St. Lawrence (CN) in 2006.

Figure S2. Location of Maurice Lamontagne Institute (Fisheries and Oceans Canada) Aquatic Invasive Species (AIS) monitoring stations in the Magdalen Islands (IM), Gaspé Peninsula (GA), and the northern coast of the St. Lawrence (CN) in 2007.

Figure S3. Location of Maurice Lamontagne Institute (Fisheries and Oceans Canada) Aquatic Invasive Species (AIS) monitoring stations in the Magdalen Islands (IM), Gaspé Peninsula (GA), and the northern coast of the St. Lawrence (CN) in 2008.

Figure S4. Location of Maurice Lamontagne Institute (Fisheries and Oceans Canada) Aquatic Invasive Species (AIS) monitoring stations in the Magdalen Islands (IM), Gaspé Peninsula (GA), and the northern coast of the St. Lawrence (CN) in 2009.

Figure S5. Location of Maurice Lamontagne Institute (Fisheries and Oceans Canada) Aquatic Invasive Species (AIS) monitoring stations in the Magdalen Islands (IM), Gaspé Peninsula (GA), and the northern coast of the St. Lawrence (CN) in 2010.

Figure S6. Location of Maurice Lamontagne Institute (Fisheries and Oceans Canada) Aquatic Invasive Species (AIS) monitoring stations in the Magdalen Islands (IM), Gaspé Peninsula (GA), and the northern coast of the St. Lawrence (CN) in 2011.

Figure S7. Location of Maurice Lamontagne Institute (Fisheries and Oceans Canada) Aquatic Invasive Species (AIS) monitoring stations in the Magdalen Islands (IM), Gaspé Peninsula (GA), and the northern coast of the St. Lawrence (CN) in 2012.

Figure S8. Location of Maurice Lamontagne Institute (Fisheries and Oceans Canada) Aquatic Invasive Species (AIS) monitoring stations in the Magdalen Islands (IM), Gaspé Peninsula (GA), and the northern coast of the St. Lawrence (CN) in 2013.

Figure S9. Location of Maurice Lamontagne Institute (Fisheries and Oceans Canada) Aquatic Invasive Species (AIS) monitoring stations in the Magdalen Islands (IM), Gaspé Peninsula (GA), and the northern coast of the St. Lawrence (CN) in 2014.

Figure S10. Location of Maurice Lamontagne Institute (Fisheries and Oceans Canada) Aquatic Invasive Species (AIS) monitoring stations in the Magdalen Islands (IM), Gaspé Peninsula (GA), and the northern coast of the St. Lawrence (CN) in 2015.

Figure S11. Location of Maurice Lamontagne Institute (Fisheries and Oceans Canada) Aquatic Invasive Species (AIS) monitoring stations in the Magdalen Islands (IM), Gaspé Peninsula (GA), and the northern coast of the St. Lawrence (CN) in 2016.

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