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Population dynamics of the invasive bryozoan *Membranipora membranacea* along a 450-km latitudinal range in the subarctic northwestern Atlantic

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Abstract Thermal environment is often regarded as a key determinant of distribution limits in marine invertebrates and hence may represent one of the most important barriers to invasion by non-indigenous species. For the first time in the subarctic northwestern Atlantic, we investigated variation in the timing and magnitude of settlement, recruitment, and colony cover of the recently (early 2000s) introduced bryozoan *Membranipora membranacea* on the kelp *Saccharina longicruris* and how this variation relates to changes in sea temperature (thermal histories) across eight sites spanning a 450-km latitudinal range between southwestern Newfoundland and southeastern Labrador, Canada. We show that (1) up to 61 % of the variation in settlement, recruitment, and colony cover was explained by sea temperature alone, with highest and lowest abundances at warmest and coldest sites, respectively; (2) between-site differences in rates of sea cooling explained 85 % of the variation in settler abundance; (3) varying the temporal window over which data were aggregated increased the explanatory power of sea temperature to as much as 98 % for settlement and recruitment, and 86 % for colony cover; (4) exposure to waves and surface area of colonies improved relationships between sea temperature and settlement and recruitment by up to 11 %; and (5) recruit abundance was a strong predictor of colony cover, explaining as much as 89 % of the variation. Consistently low abundances of settlers and recruits at the northern tip of Newfoundland and southern tip of Labrador suggest that *M. membranacea* is nearing its northern distribution limit in the northwestern Atlantic. Our findings extend knowledge of population dynamics of *M. membranacea* in the northwestern Atlantic, while highlighting the complexity of the interactions between physical and biological factors and processes that affect population dynamics in invertebrates with planktonic larvae in predominantly cold marine habitats.

Introduction

Settlement, which is the process whereby a competent larva searches for a suitable substratum, attaches to it, and metamorphoses into its pre-juvenile benthic form, as well as recruitment, which is the transition from a recently settled larva to the benthic juvenile stage (Keough and Downes 1982; Rodriguez et al. 1993; Jenkins et al. 2009), are key processes regulating populations in a number of marine benthic invertebrates with planktonic larvae (Minchinton and Scheibling 1991; Connolly and Roughgarden 1999; Jenkins et al. 2009). Vertical and horizontal transport of these larvae by wave and current energy may result in larvae being supplied from distant pools, which can create open populations in which settlement and recruitment are, to various extent, decoupled from local larval production (Roughgarden et al. 1988; Caley et al. 1996; Sundelöf et al. 2010). In general, variation in settler and recruit abundances is largely determined by microhabitat availability, predation, and competition at small spatial scales (10–100 km) and by larval supply at larger scales (10–100 km) (Paine 1974; Keough and Downes 1982; Pineda 1991; Morgan and Fisher 2010).

Sea temperature affects growth, reproduction, and survival in marine invertebrates (Chen and Chen 1993; Matsuda et al. 2002; Thiyagarajan et al. 2003), which

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ultimately determines species' northern and southern distribution limits (Zacherl et al. 2003; Zippay and Hofmann 2010). High physiological stress and low settlement and recruitment near these limits generally result in smaller populations with larger and older individuals compared to mid-distribution populations (Kendall and Lewis 1986; Sorte and Hofmann 2004; Gilman 2006). Recruitment at a species distribution margin is often limited to years in which sea temperature and hydrodynamic conditions are favorable for settlement and post-settlement survival (Kendall and Lewis 1986; Zacherl et al. 2003; Fenberg and Rivadeneira 2011). Larval supply is greatly affected by water circulation and its interaction with temperature (Connolly and Roughgarden 1998; Gaylord and Gaines 2000; Connolly et al. 2001). In particular, coastal upwelling and downwelling, which cause marked changes in water temperature, as well as horizontal currents, can affect settlement and recruitment by altering larval supply and pre- and post-settlement survival (Connolly et al. 2001; McQuaid and Lindsay 2007; Saunders and Metaxas 2010). Such physical processes interact with biological traits, including fecundity and larval swimming behavior, which altogether determine settlement and recruitment success (Hughes et al. 2000; Shanks and Brink 2005; Morgan and Fisher 2010).

The bryozoan *Membranipora membranacea* (Linnaeus) (Lophophorate: Chelistomata) exhibits a life cycle alternating between a planktotrophic, cyphonautes larval stage, and a benthic, colonial adult stage (Ryland 1970). Cyphonautes larvae may spend up to 4 weeks in the water column before settling and metamorphosing into the first benthic stage called the ancestrula that gives rise to the first two zooids of any colony (Yoshioka 1982; Stricker 1988). Indigenous to the northeastern Pacific, *M. membranacea* is a common component of *Macrocystis pyrifera* (Linnaeus) C. Agardh kelp forests from California to British Columbia (Bernstein and Jung 1979; Yoshioka 1982; Schwaninger 2008). The species was introduced to the northwestern Atlantic in the Gulf of Maine in the mid-1980s where it rapidly invaded shallow subtidal kelp habitats (Berman et al. 1992; Lambert et al. 1992). Current distribution of *M. membranacea* in eastern Canada includes the Atlantic coast of Nova Scotia (Watanabe et al. 2009), south shore of Québec (Gendron et al. 2007), and the coast of Newfoundland and Labrador where it was discovered for the first time in the early 2000s (Robert Hooper, Memorial University of Newfoundland, personal communication). The timing and magnitude of settlement, recruitment, and colony growth vary within and between these regions. In California, larvae and recruits of *M. membranacea* are abundant in surface waters and on kelp during winter, though are virtually absent in July and August when sea temperature goes above 20 °C, whereas in Washington, colonies are most abundant between May and September (Menon 1972; Bernstein and Jung 1979;

Yoshioka 1982; Harvell et al. 1990). In Nova Scotia and the Gulf of Maine, larvae and recruits are generally abundant from May to October, when sea temperature ranges from 6 to 18 °C, whereas colony cover and density on the kelps *Laminaria digitata* (Hudson) J.V. Lamouroux and *Saccharina longicruris* (Bachelot de la Pylaie) Kuntze peak between August and February (Berman et al. 1992; Saunders and Metaxas 2007, 2008; Saunders and Metaxas 2009b).

Most of our understanding of population dynamics of *M. membranacea* in the northwestern Atlantic is based on a few studies in central Nova Scotia. These studies showed that settler abundance and colony cover on kelp (*S. longicruris*) are positively correlated with sea temperature, while settlers and recruits can occur earlier in spring and be more abundant after a milder winter (Saunders and Metaxas 2007, 2008; Scheibling and Gagnon 2009). Thermo-haline stratification during fall presumably affected the distribution of cyphonautes larvae, with possible onshore transport during wind-driven downwelling events (Saunders and Metaxas 2010). Overall, these pioneering studies conducted in a relatively small area (all study sites were located within a range <50 km) have helped elevate the importance of sea temperature in affecting local patterns of settlement, recruitment, and growth in *M. membranacea*.

The recent introduction of *M. membranacea* to Newfoundland and Labrador provided an opportunity to investigate relationships between temperature, settlement, recruitment, and colony cover over a large spatial domain encompassing cold, subarctic marine environments. Firstly, the west coast of Newfoundland stretches approximately 450 km along a north–south axis. Conceivably, sea temperature along this latitudinal range should vary in space and time, with an expected decrease from south to north. Secondly, cold water from the Arctic flows year round into the Gulf of St. Lawrence through the relatively narrow Strait of Belle Isle (18 km across at its narrowest point), which separates the northern tip of the island of Newfoundland and southeastern tip of Labrador. This channel could form a natural barrier to the northward dispersal of *M. membranacea*, and hence recruitment and settlement should differ between both sides of the straight, being higher on the Newfoundland than Labrador side. Thirdly, hydrodynamic conditions should vary along this coast, which may affect larval supply, settlement, and recruitment. Given the putative importance of sea temperature in regulating the abundance of *M. membranacea* in southeastern Canada, a corollary hypothesis is that its population dynamics in northern, colder environments of Newfoundland and Labrador differ due to preponderance of suboptimal (or lethal) thermal conditions.

In this study, we investigate the variation in the timing and magnitude of settlement, recruitment, and colony cover

of *M. membranacea* on the kelp *S. longicruris* and how this variation relates to changes in sea temperature (thermal histories) across eight sites spanning a 450-km latitudinal range between southwestern Newfoundland and southeastern Labrador. Specifically, we (1) test the overall hypothesis that settler and recruit abundances as well as colony cover are positively correlated with temperature, being generally higher and lower at warmer and colder sites, respectively, (2) examine how these relationships may change across biologically meaningful temporal windows over which settlement, recruitment, colony cover, and temperature data are aggregated, (3) investigate whether variation in settler and recruit abundances relates to exposure to waves and the surface area of colonies [which is commonly used as a proxy for fecundity in *M. membranacea*] on kelp, and (4) determine whether recruit abundance can be used to predict colony cover.

Materials and methods

Study sites

This study was conducted at eight sites spanning ~450 km between southwestern Newfoundland (47°34′N) and southeastern Labrador (51°43′N): (1) Port aux Basques [southernmost site], (2) Lark Harbour, (3) Norris Point [centermost site], (4) Daniel's Harbour, (5) Port au Choix, (6) Bird Cove, (7) Green Island Cove, and (8) Red Bay [northernmost site, located in Labrador] (Fig. 1). The shallow (0–20 m depth) rocky seabed in southwestern Newfoundland consists mainly of sedimentary (sites 1 and 3) and igneous (sites 2 and 4) boulders and bedrock outcrops. Sedimentary bedrock outcrops and ledges predominate north of 50°1′N (sites 5, 6, and 7) in Newfoundland, whereas granitic boulders and bedrock prevail in southeastern Labrador (site 8) (Colman-Sadd and Scott 1994). Kelp beds occurred at all sites within the 5–15 m depth range (chart datum), especially in sheltered and moderately exposed locations. The shallowest beds were generally dominated by the kelps *S. longicruris* and to a lesser extent *Alaria esculenta* (Linnaeus) Greville, *L. digitata*, and *Saccorhiza dermatodea* (Bachelot de la Pylaie) J.Agardh. These species were gradually replaced with increasing depth by the grazing-resistant and shade-tolerant kelp, *Agarum clathratum* (Dumortier) (Vadas 1968; South 1983; Gagnon et al. 2005). Exposure of kelp beds to wave action differed between sites ("Appendix," see below).

Collection of kelp blades

To investigate the spatial and temporal variation in the abundance of settlers and recruits as well as colony cover of

M. membranacea on kelp, blades of the kelp *S. longicruris* were collected by fish harvesters once every month from August to October 2008 at all sites (1–8). Although we originally aimed to obtain kelp in the third week of each month, rough seas at certain sites occasionally prevented collection, therefore resulting in kelp blades being collected within a period of 8–14 days in each month. Likewise, we could not obtain blades in August at sites 3 and 8 and September at sites 1 and 2 ("Appendix"). On each collection day, fish harvesters collected a minimum of eight kelp blades at a depth of approximately 6 m. Kelp blades were collected from decks of fishing vessels using a manually operated device we designed, which cut kelp individuals above the holdfast (leaving blades intact) and trapped them in a collector until brought to the surface. Most fish harvesters were not able to collect kelp blades after October due to increasingly rough seas or seasonal closure of fisheries. Therefore, we used SCUBA diving to haphazardly collect five–ten blades in late November at all but the southernmost (1) and northernmost (8) sites ("Appendix"). Upon collection, kelp blades were rolled within hermetic plastic bags, placed on ice within a sealed plastic cooler, and shipped using expedite courier (fish harvester collections) or transported directly (diver collections) to the Ocean Sciences Centre (OSC). Blades collected by fish harvesters arrived at the OSC within two (sites 1–7) to three (site 8) days from collection, whereas those collected by divers arrived within 1–7 days. Upon arrival at the OSC, the blades were placed in large (330 L) holding tanks supplied with cold (10.5 ± 2.6 °C [SD]) seawater pumped in from a depth of ~10 m in the adjacent embayment, Logy Bay. Approximately 90 % of the blades were analyzed (see below) within 2 days of receipt and the rest within 5 days.

Concurrent experiments examining the growth of *M. membranacea* colonies on kelp under various temperature regimes indicated that colony cover increased by no more than 2 % in 3 days at 10 °C (Caines and Gagnon unpublished data). Bryozoans can tolerate hypoxia by halting growth momentarily (Sagasti et al. 2001). Therefore, stress in and growth of recruits and colonies on blades shipped on ice under hypoxic conditions for up to 7 days and maintained in the tanks in relatively cold water for up to 5 days prior to analysis were most likely negligible and would have affected our measurements of recruitment and colony cover equally across the majority of the blades. The latter assumption was corroborated by our thorough inspection of a subset of recruits and colonies that had experienced some of the longest transportation and holding times, which indicated that deterioration of calcified structures occurred only on kelp blades that had begun to deteriorate. As an added precaution, only those blades that showed no sign of deterioration (e.g., large portions missing, production of mucilage, softening or discoloration of tissues) were

Fig. 1 Location of the eight study sites on the west coast of Newfoundland and southern tip of Labrador, Canada: *1* Port aux Basques, *2* Lark Harbour, *3* Norris Point, *4* Daniel's Harbour, *5* Port au Choix, *6* Bird Cove, *7* Green Island Cove, and *8* Red Bay
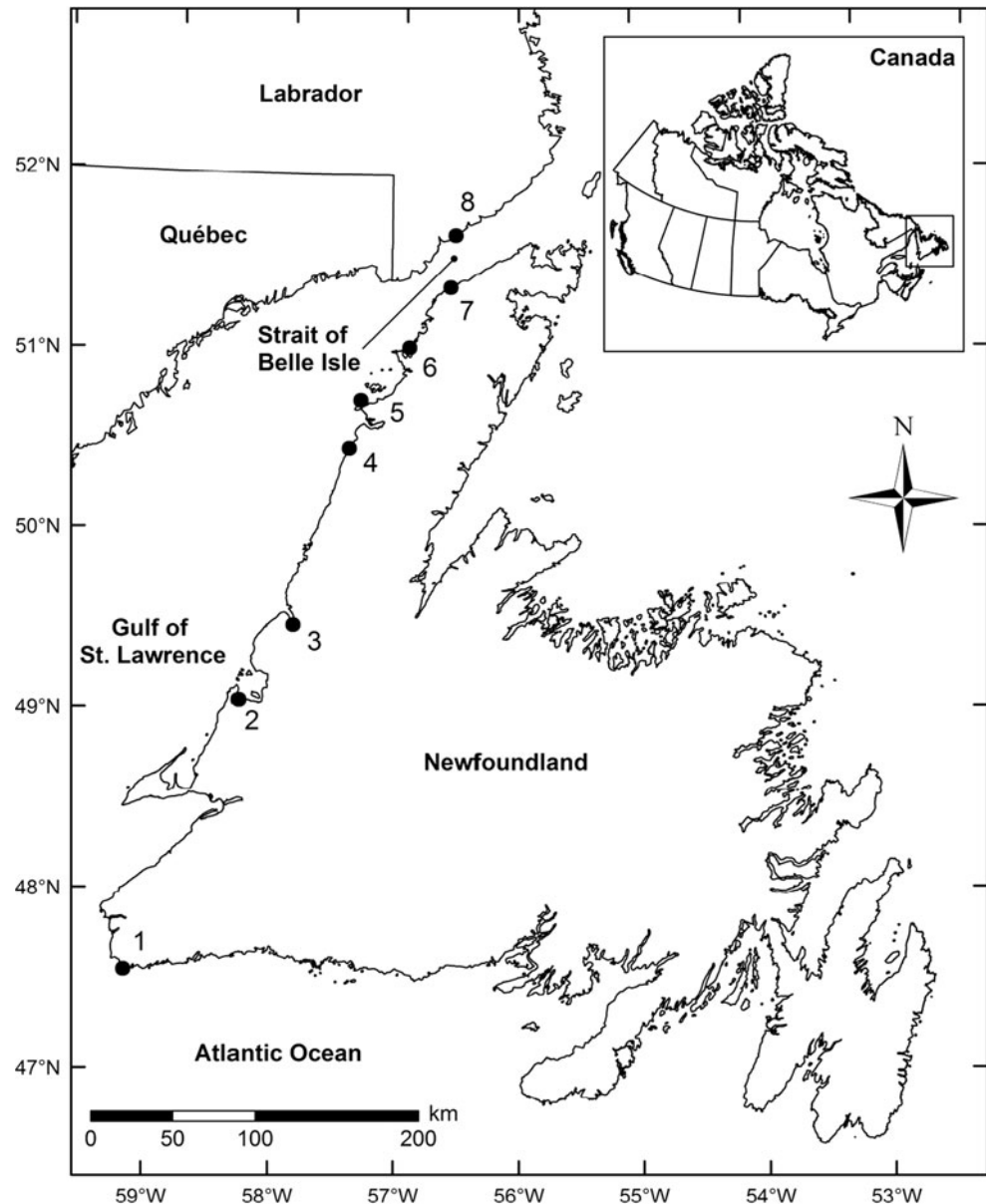
analyzed (see below). Accordingly, the number of blades analyzed for each site in each of August, September, October, and November, which corresponds to the sample size (n), ranged from five to ten ("Appendix").

Abundance of *M. membranacea* settlers and recruits on kelp

In this study, "settler" refers to a pre-ancestrula with larval shells or a fully metamorphosed ancestrula with first two calcified zooids (after Yoshioka 1986; Stricker 1988, 1989), whereas "recruit" refers to a fully developed ancestrula with at least one daughter zooid (three zooids in total) or any cluster of zooids with a diameter <5 mm. Clusters of 5 mm

typically have five or six rows of zooids and an estimated maximum age of 3 weeks when grown at temperatures between 10 and 14 °C (Saunders and Metaxas 2008). To obtain representative estimates of the abundance of settlers and recruits of *M. membranacea* on kelp, the blade of each kelp was divided into three contiguous portions along its length: (1) bottom [the lower or proximal third of the blade including the meristem], (2) center [the middle third of the blade], and (3) top [the upper or distal third of the blade]. Within each zone, we cut with a scalpel three square pieces of blade tissue of 16 cm^2 (for blades ≤80 cm in length) or 25 cm^2 (blades >80 cm) each: one in the center and the two others on the left and right margins of the blade. The vertical position of each piece in each zone was determined based on

the occurrence of colonies of *M. membranacea*: pieces were taken halfway through the length of each zone when the former contained no colony with a diameter >1 cm (pieces with larger colonies did not offer enough bare surface for settlers), else they were taken up or down the center until this criterion was met. Heavy infestation of kelp blades by *M. membranacea* in certain months at a few sites limited the sampling to less than nine pieces in 43 % of the blades. The density of settlers on one side (chosen randomly) of each piece of kelp was obtained by dividing the number of settlers (determined by visual count with a stereomicroscope set at 15× magnification) by the surface area of the piece. For each kelp blade, settler density was determined by averaging densities across all pieces (up to 9).

Cover of *M. membranacea* colonies on kelp

We use the term "colony" to refer to any cluster of *M. membranacea* with a diameter ≥5 mm and at least 6 rows of zooids. To investigate the spatial and temporal variation in the cover of *M. membranacea* colonies on kelp, a sheet of transparent acrylic was placed over each kelp blade (this was done prior to quantifying settler and recruit abundances to avoid damaging colonies). Contours of kelp blade and each colony were traced onto the sheet with markers. The sheet was then placed above a white countertop and photographed from above with a digital camera (Powershot A720; Canon). Surface areas of the kelp blade and each colony were determined by analyzing photographs with the image analysis software Sigma Scan Pro 5. Certain colonies extended within folds and corrugations of kelp blades, which resulted in partial marking of their margins on the sheet. To better estimate the true surface area of these colonies, we developed a blade corrugation index (BCI) for each site on each collection date. The blade was cut into pieces that were flattened on the white surface and photographed. We used the image analysis software ImageJ (v.1.43d) to calculate surface areas of the flattened pieces. Each blade was assigned a BCI value expressing the ratio of surface areas of flattened pieces to intact blade, therefore providing an estimate of the degree of corrugation. Accordingly, the degree of corrugation was minimal when BCI = 1 (i.e., a perfectly flat blade for which intact and flattened surfaces areas are equal) and increased with increasing BCI value. Visible portions of partially marked colonies of each blade were then multiplied by the corresponding mean BCI value for that particular site and collection date. Those few smaller colonies completely hidden within blade folds could not be measured reliably, and hence they were discarded from analyses. Although excluding such colonies underestimated the actual colony cover, the method was systematically applied to all blades, which provided consistent measurements across sites and months. Colony cover on each blade was obtained by dividing the total surface area of colonies (i.e., the sum of corrected surface areas of partly visible colonies and raw surface areas of fully visible colonies) by the total surface area of blade pieces multiplied by 100. Mean total surface area of colonies and colony cover at each site in each month was used in regression analyses (see below).

Collection and integration of temperature and wave exposure data

To test the hypothesis that spatial and temporal variation in settlement and recruitment of *M. membranacea* is correlated with sea temperature, while determining whether exposure to waves and the surface area of *M. membranacea* colonies on kelp affect settlement and recruitment (see below), we recorded sea temperature at each site with one temperature logger (HOBO Pendent, Onset Computer Corporation; ±0.5 °C precision). Each logger was attached to an eyebolt secured to the seabed with marine epoxy (Z-Spar) at a mean depth of 4.7 ± 1.2 (SD) m (chart datum) ("Appendix"). Loggers were installed where we aimed to obtain kelp blades on a dedicated trip to the west coast of Newfoundland in early June 2008. However, most fish harvesters had to patrol larger areas than we anticipated, which resulted in inevitable changes in the locations of kelp collection (we could not revisit the sites until fall). As a result, loggers were located within 4 km of kelp collection sites except at site 8 where the logger was approximately 22 km away due to an unforeseen change, between August and September, in fish harvester and associated kelp collection site. Given that most sites were located on open coasts and the fair distance (at least 40 km) that separated adjacent sites, we assumed that temperature regimes over 4 km were relatively constant and representative of temperatures at kelp collection sites. Site 8 was located on the north side of the Strait of Belle Isle, which covers a large body of water where sea temperature is relatively low and constant throughout the year (Han et al. 1999; this study), and hence unlikely to vary within 22 km. Therefore, this site was included in the analyses despite the greater distance between the logger and collection site than at the other sites. Temperature was recorded every hour from June 13 to November 24 at sites 1–7, and from July 10 to November 24 at site 8. All loggers were retrieved by December 1. The mean daily temperature for each site was calculated from hourly recordings (Fig. 2).

Studies in eastern Canada used integrated indices of thermal history to relate sea temperature to settlement and cover of *M. membranacea* colonies on kelp (Saunders and Metaxas 2007; Scheibling and Gagnon 2009). In these studies, thermal histories were constructed by adding mean daily sea temperature over a given period of time. We used

Fig. 2 Change in mean daily sea temperature at each study site (ordered *horizontally* from *south* to *north*) from June to November 2008 at sites 1–7 and July to November 2008 at site 8. Values are mean (±SE) temperature calculated over the entire dataset. Note the sudden fluctuations in temperature in August at all sites and in September at all but sites 2 and 3 (see "Appendix" and Fig. 1 for location of sites)
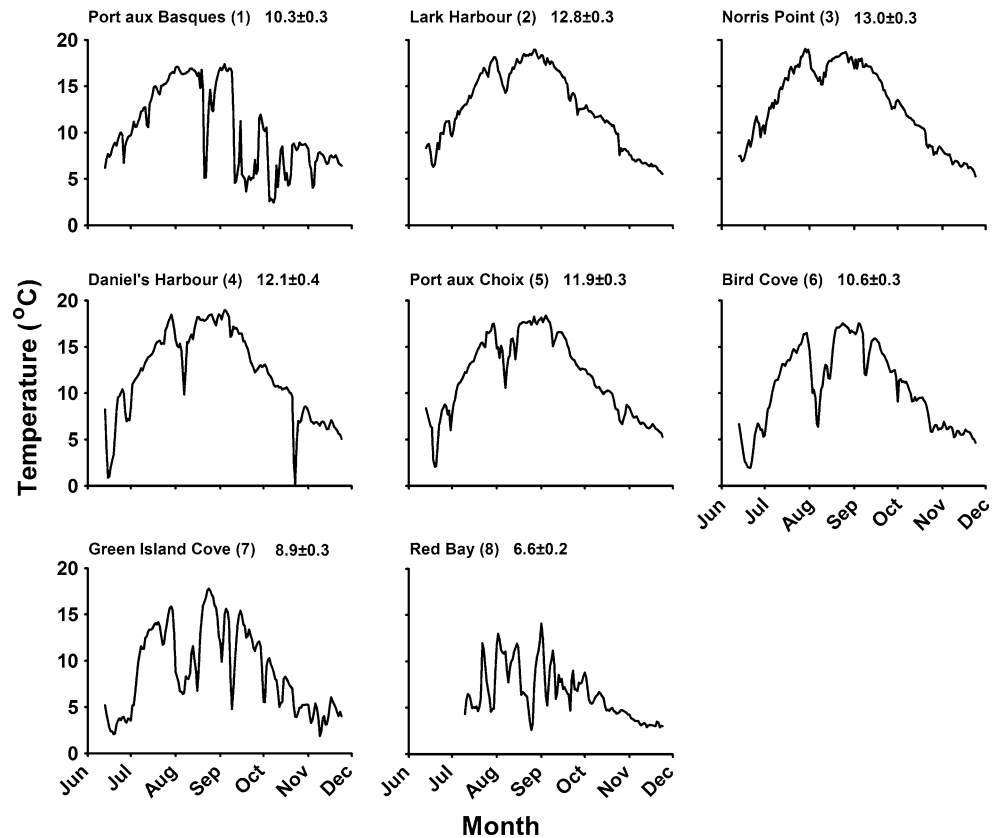
a similar approach by constructing thermal integrals, TI_N, where N is the number of days over which mean daily sea temperature was summed: 14, 21, 28, and 76 days preceding every kelp collection from September to November (period during which we observed highest settlement values). The longest period of time with temperature data available for all months simultaneously was 76 days (~10 weeks), which, conceivably, was long enough to encompass the entire larval period as well as part or all of the growth and reproduction in most colonies. It has been suggested that the larval period in *M. membranacea* typically lasts 2–4 weeks (Yoshioka 1982). However, the larval period in marine invertebrates is highly variable and is dependent on temperature, salinity, and food conditions (Hoegh-Guldberg and Pearse 1995; Thiyagarajan et al. 2003). Therefore, TI_{14}, TI_{21}, and TI_{28} were used to determine whether thermal indices representative of part or all of the larval stage duration could better predict variation in settlement than TI_{76} (see below).

Inspection of raw temperature data indicated that sharp decreases in temperature occurred over the course of approximately 3 weeks following seasonal peaks at sites 2–6 (Fig. 2) and that these declines appeared to correspond with higher settlement values. To examine the relationship between decreases in sea temperature and settlement of *M. membranacea* on kelp (see below), we created another thermal integral for sites 2–6, TI_{Diff}, which was the sum of

the differences in mean daily sea temperature from day to day ([day 2 − day 1] + [day 3 − day2] + [day 4 − day 3] + ⋯ + [day 21 − day 20]) over the 21 days (3 weeks) preceding each kelp collection from August to November. Accordingly, TI_{Diff} was negative or positive when there was a net decrease or increase in sea temperature, respectively.

We used the Baardseth index (Baardseth 1970) to estimate the relative degree of exposure to waves of each kelp collection site. The center of a transparent circular disk divided into 36 sectors of 10° was placed over a satellite image (Google Earth 1:50 000) of each site. The number of sectors encompassing sea surface only (no landmass) within a radius of 7.5 km from the center of the disk (collection site) was counted. Accordingly, the degree of exposure to waves ranged from 0 (minimum exposure) to 36 (maximum exposure). These data were used to examine the extent to which the wave environment explained the variation in settlement and recruitment (see below).

Statistical analysis

To investigate the spatial (between-site) variation in settler and recruit abundances as well as colony cover, we analyzed data from all sites using three one-way ANOVAs (one for each of settlement, recruitment, and colony cover) with the factor site (random factor with 8 levels: sites 1–8). No transformation corrected the lack of homoscedasticity

in the data in the three analyses, and hence the ANOVAs were also run with the rank-transformed data. Because analyses on both raw and ranked transformed data gave similar results, we presented the results from analyses of the rank-transformed data as suggested by Conover (1980).

Simple linear regression analysis (Sokal and Rohlf 1995) was used to examine the relationships between mean abundances of *M. membranacea* settlers and recruits on kelp and sea temperature (thermal integrals) from September to November (period during which we observed peak settlement values) across all sites (1–8). We performed four separate analyses, one for each of the four thermal integrals (TI_N, calculated over 14, 21, 28, and 76 days prior to each collection day) to determine which thermal integral, if any, best explained the variation in the abundance of settlers. Thermal integral TI_{76} emerged as the strongest predictor of settler density (see "Results"). Therefore, TI_{76} was also used to examine the relationships between recruit abundance and sea temperature, while determining if relationships between settler and recruit abundances and temperature varied among September, October, and November. Multiple linear regression analysis (Sokal and Rohlf 1995) was used to examine the combined contribution of temperature (TI_{76}), exposure to waves (Exp), and the surface area (SA) of *M. membranacea* colonies to variation in the abundance of settlers on kelp from September to November across all sites (1–8). Lastly, we used a second-order polynomial regression analysis to determine the relationship between the abundance of settlers on kelp and the sum of the differences in daily sea temperature between consecutive days over the 21 days preceding kelp collection (TI_{Diff}) from sites 2–6.

Multiple linear regression analysis was used to investigate the combined contribution of temperature (TI_{76}) and wave exposure (Exp) to variation in the abundance of recruits from September to November across all sites (1–8). Subsequent inspection of the data suggested that recruit abundance and Exp were linked by a nonlinear relationship (which was not the case for the abundance of settlers in the analysis explained above). Accordingly, a quadratic regression was used to characterize the relationship between recruit abundance and Exp from September to November across all sites (1–8).

Simple linear regression analysis was used to examine the relationships between colony cover and temperature (TI_{76}) and between colony cover and recruit abundance across all sites from September to November, in September, and in October and November pooled. Data in October and November were pooled since >98 % of the colonies in each of these 2 months were small (mean ≤ 1.7 cm^2), and hence the relationship between recruit abundance and colony cover was unlikely to change between months (see "Results"). In all regressions, settlement and recruitment

data were log $(x + 1)$ transformed, whereas colony cover data were arcsine $(\sqrt{x})$ transformed to obtain homoscedasticity and normality of the residuals.

In all analyses, normality was verified using Shapiro–Wilk's statistic and homogeneity of variance by using Levene tests and examining the graphical distribution of the residuals (Snedecor and Cochran 1989). To detect the differences among levels within a factor, we used Tukey–Kramer multiple comparison tests (comparisons based on least-square means) (Sokal and Rohlf 1995). A significance level of 0.05 was used for all statistical tests. All analyses were conducted with JMP 7.0 and Minitab 16.

Results

Variation in settlement, recruitment, and colony cover of *M. membranacea* on kelp

Analysis of the data pooled over August, September, October, and November indicated that the abundance of *M. membranacea* settlers and recruits on the kelp *S. longicruris* varied among the eight study sites (Table 1). Specifically, mean settler and recruit abundances peaked at mid-latitudes (site 3), were intermediate at sites 2, 4, 5, and 6, and lowest at the southernmost and northernmost sites (1, 7, and 8) (Fig. 3). The general decrease in settler abundance with increasing latitude from site 3 to site 8 was accompanied by a gradual decline in mean sea temperature, from a maximum of 17.6 °C in August at site 3 to a minimum of 3.3 °C in November at site 8 (Fig. 3). The major drop

Table 1 Summary of one-way ANOVAs (applied to rank-transformed data) showing the effect of Site (eight study sites: 1, 2, 3, 4, 5, 6, 7, and 8) on the abundance of settlers and recruits as well as colony cover of *M. membranacea* on kelp (*S. longicruris*) (see "Appendix" and Fig. 1 for location of sites and dates of kelp collection in each month)

Source of variation	df	MS	F	p
Settlers				
Site	7	53,012.3	22.0	<0.001
Error	217	2,410.2		
Corrected total	224			
Recruits				
Site	7	58,329.4	27.2	<0.001
Error	217	2,141.8		
Corrected total	224			
Colony cover				
Site	7	70,527.9	38.6	<0.001
Error	212	1,827.6		
Corrected total	219			

Fig. 3 Change in mean (±SE) sea temperature (a), abundance of settlers (b) and recruits (c), and colony cover (d) of *M. membranacea* on kelp (*S. longicruris*) across all study sites (1–8) in August, September, October, and November. Each temperature data point in (a) is the average of mean daily sea temperature within each month at each site (*n* = 31 [Aug], 30 [Sep], 31 [Oct], and 24 [Nov]) or across the 4 months at each site (*n* = 116 [Overall]). Values at the *top* in (b), (c), and (d) are the mean abundance or cover (SE not shown for clarity) for the 4 months at each site. Values not sharing the same *letters* are different (LS Means, *p* < 0.05; *n* = 5 to 10 kelp blades) (see "Appendix" and Fig. 1 for location of sites and dates of kelp collection as well as sample sizes in each month)
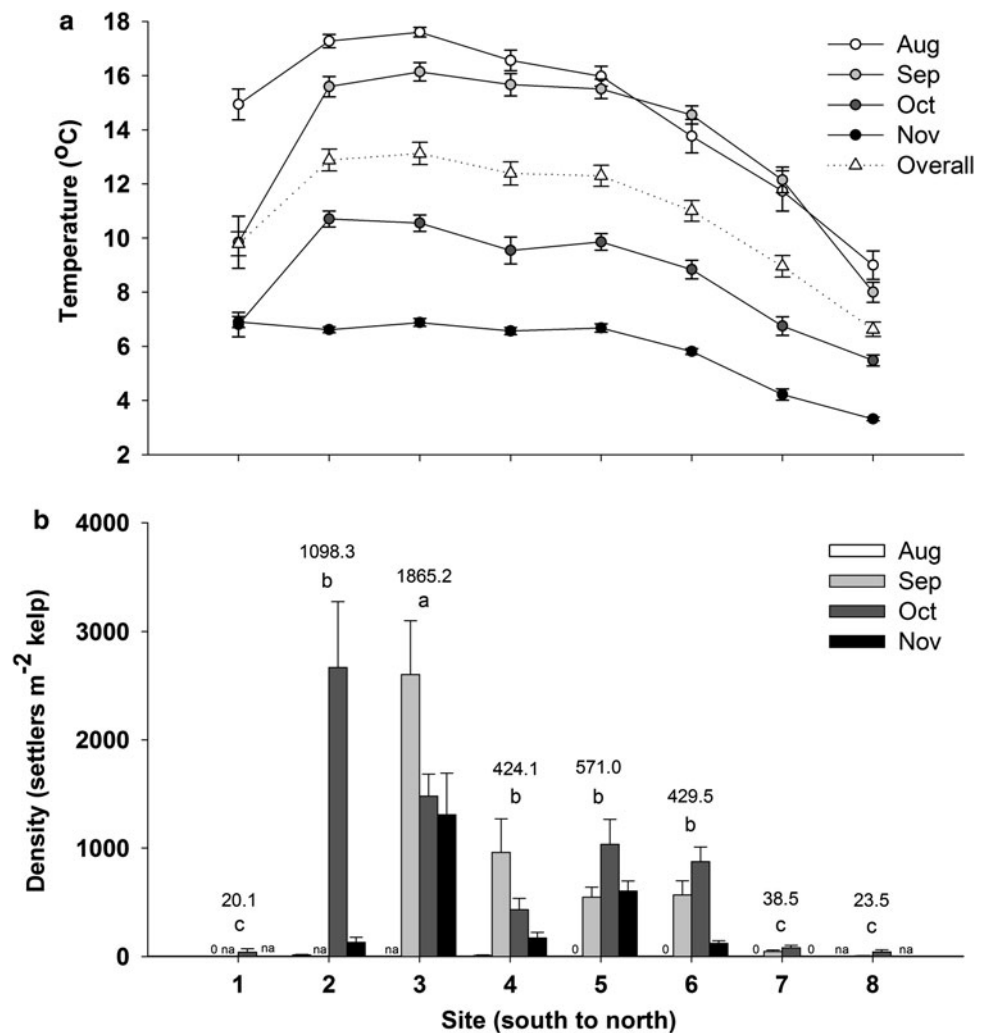
(98 %) in recruit abundance in October from site 3 to site 4 was accompanied by a decrease of only 1.1 °C between sites. Daily sea temperature at site 1 varied substantially throughout the study (especially between August and November, Fig. 2) though was similar, on average, to that at sites 7 and 8 in September and October (Fig. 3). Settlement and recruitment patterns at sites 7 and 8 closely resembled those at site 1, with consistently low values (a maximum of 81.2 ± 21.2 settlers m^{-2} at site 7 and 42.5 ± 15.5 recruits m^{-2} at site 1 in October) (Fig. 3).

Analysis of the data pooled over August, September, October, and November also indicated that colony cover on kelp varied among sites (Table 1; Fig. 3). Changes in colony cover generally followed the same trends as for settler and recruit abundances, with highest cover values in the center (sites 3 and 4) of the latitudinal range and a gradual decline southwards and northwards (Fig. 3). Surprisingly, colony cover was highest (up to 46.1 ± 9.6 %) in November at site 4 even though recruitment there was among the

lowest of all sites (Fig. 3). Once again, changes in colony cover from site to site coincided relatively well with changes in mean sea temperature, with lowest cover values at the coldest sites (e.g., <5 % cover in any month at sites 7 and 8) (Fig. 3).

Contribution of temperature, exposure to waves, and surface area of *M. membranacea* colonies to variation in settler abundance

As shown by simple linear regression analyses, temperature alone was positively correlated with variation in settler abundance from September to November across all sites (1–8) regardless of the number of days over which temperature data were aggregated (TI$_N$) (Table 2). Nevertheless, the longest thermal integral, TI$_{76}$, emerged as the strongest predictor with 60.9 % of the variation in settler abundance explained (Table 2). The predictive capability of TI$_{76}$, in each month taken individually, increased by at least

Fig. 3 continued
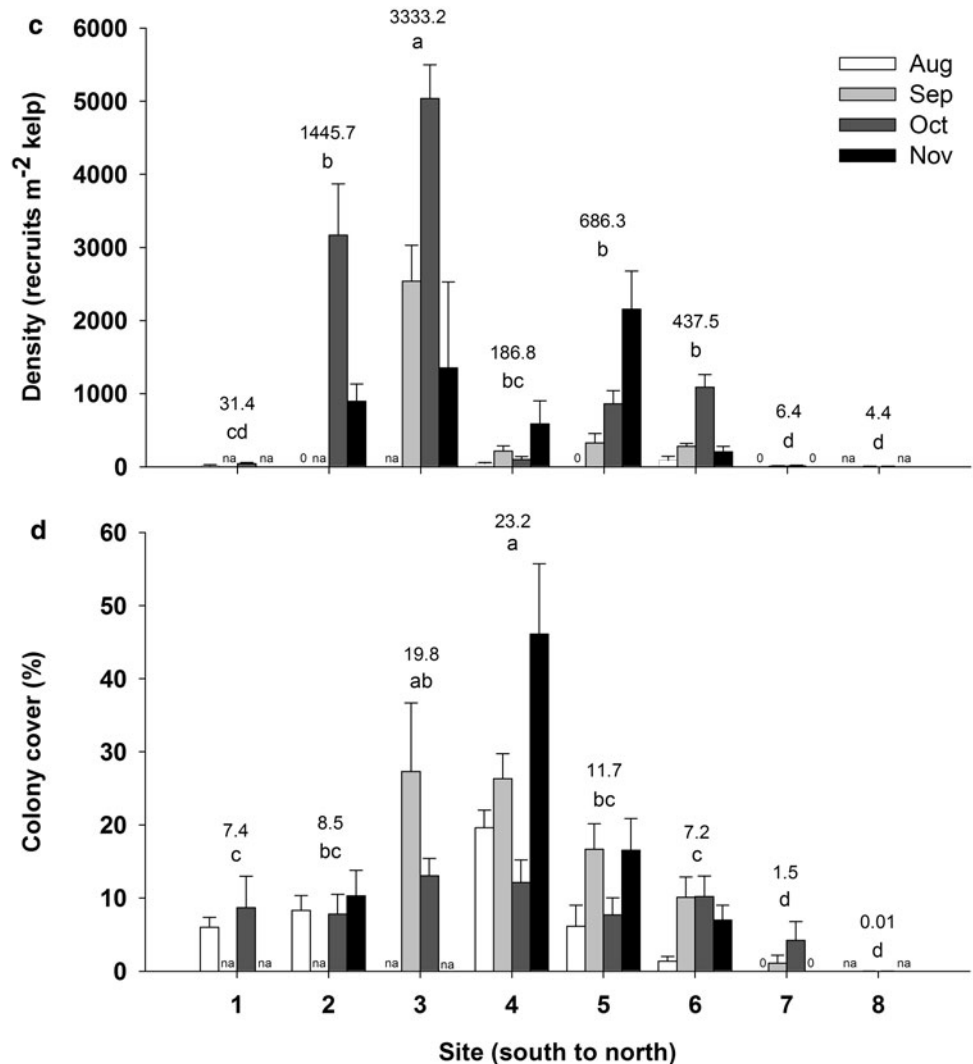
20.2 %, peaking at 97.1 % in November (Table 2). The second-order polynomial regression analysis of the August to November data for sites 2–6 showed a strong relationship ($r^2 = 0.846$) between settler abundance and the magnitude of changes in sea temperature over the 21 days preceding kelp collection (TI_{Diff}) (Fig. 4). Specifically, settlement increased with increasing rates of cooling. Indices of exposure to waves (Exp) ranged from 0 (minimum) at site 8, to 15 (intermediate) at site 7 ("Appendix"). As shown by multiple regression analysis, 71.9 % of the variation in settler abundance from September to November across all sites (1–8) was explained by TI_{76}, Exp, and the surface area (SA) of colonies, which altogether increased the predictive capability of the model with TI_{76} alone by 11 % (Table 2). Overall, these results indicate that temperature was the dominant predictor of spatial and temporal variation in the abundance of *M. membranacea* settlers on kelp between the southwestern tip of Newfoundland and southeastern tip of Labrador.

Relationships between temperature, exposure to waves, and *M. membranacea* recruit abundance and colony cover on kelp

Simple linear regression analyses showed that temperature (TI_{76}) alone was positively correlated with variation in both recruit abundance and colony cover from September to November across all sites (1–8) (Table 3). In fact, 31.5 % of the variation in recruit abundance during this period was explained by temperature, which increased by at least 42 % when analyzing months singly (Table 3). Multiple linear regression analysis showed that sea temperature and exposure to waves (Exp) together explained 37.6 % of the variation in recruit abundance from September to November (Table 3). Yet, further regression analysis indicated that recruit abundance and Exp were linked by a quadratic relationship that explained 46.8 % of the variation in the data (Fig. 5). Accordingly, recruit abundance peaked at Exp values between 6 and 8, and

Table 2 Results of simple and multiple linear regression analyses examining the relationships between the abundance of settlers of *M. membranacea* on kelp (*S. longicruris*), sea temperature (TI_N), expo- sure to waves (Exp), and the surface area (SA) of colonies across all sites (1–8) over different sampling periods (see "Materials and methods" for calculations of TI_N, Exp, and SA)

Sampling month(s)	Explanatory variable(s)	Equation for log (settlers m^{-2} kelp + 1)	r^2	$F_{(df)}$	p
Sep–Nov	TI_{14}	$2.69 + 0.020\ TI_{14}$	0.310	$8.1_{(1,18)}$	0.011
Sep–Nov	TI_{21}	$2.46 + 0.014\ TI_{21}$	0.362	$10.2_{(1,18)}$	0.005
Sep–Nov	TI_{28}	$2.51 + 0.010\ TI_{28}$	0.321	$8.5_{(1,18)}$	0.009
Sep–Nov	TI_{76}	$-1.00 + 0.007\ TI_{76}$	0.609	$28.1_{(1,18)}$	<0.001
Sep	TI_{76}	$-3.76 + 0.009\ TI_{76}$	0.944	$67.7_{(1,4)}$	0.001
Oct	TI_{76}	$-1.27 + 0.007\ TI_{76}$	0.811	$25.8_{(1,6)}$	0.002
Nov	TI_{76}	$-16.60 + 0.030\ TI_{76}$	0.971	$132.4_{(1,4)}$	<0.001
Sep–Nov[a]	TI_{76}, Exp, SA	$-0.52 + 0.006\ TI_{76} - 0.012\ Exp + 0.004\ SA$	0.719	$12.8_{(3,15)}$	<0.001

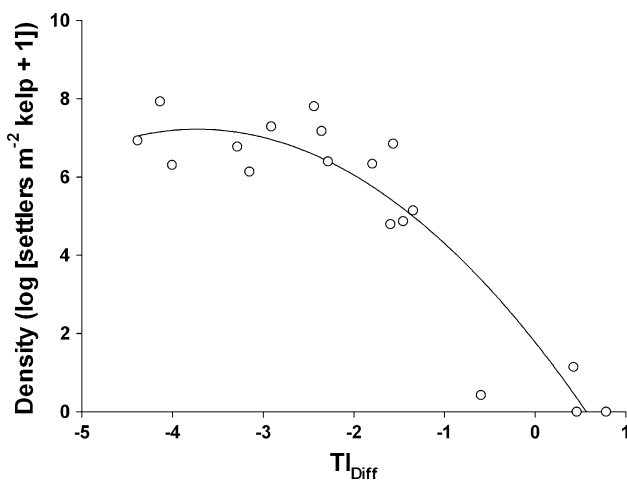[a] No estimate of SA available for site 3 in November

Fig. 4 Relationship between the abundance of settlers of *M. membranacea* on kelp (*S. longicruris*) and the sum of the differences in daily sea temperature (TI_{Diff}) between consecutive days over the 21 days preceding kelp collection at sites 2–6 in August, September, October, and November. The line is the second-order polynomial fit to these data ($r^2 = 0.846$, $p < 0.001$, $n = 18$). *Negative* and *positive* TI values denote decreasing and increasing temperatures, respectively (see "Materials and methods" for calculation of TI_{Diff})

decreased gradually with decreasing and increasing Exp values outside this range (Fig. 5).

Temperature (TI_{76}) alone explained 24.9 % of the variation in colony cover from September to November across all sites (1–8) (Table 3). Inspection of monthly size-frequency distributions from August to November indicated that >98 % of all colonies were small (mean ≤1.7 cm^2) in October and November (Fig. 6), and hence that the majority of them most likely grew from new recruits. This pattern along with our observations that these small colonies represented 42 % (October) and 49 % (November) of total colony surface area, suggested a positive relationship between recruitment and colony cover. Accordingly, recruit abundance explained 56.3 % of the variation in colony cover

from September to November across all sites (1–8) (Table 3) and 89.1 % of it in September only. Interestingly, the explanatory power of sea temperature and recruit abundance on colony cover was comparable in September (85.7 vs. 89.1 %), though differed markedly in October and November (41.2 % in favor of recruit abundance) (Table 3). Overall, these results indicate that sea temperature and recruit abundance were both strong predictors of *M. membranacea* colony cover on kelp, though their relative importance varied over time, with recruit abundance being more critical than sea temperature in the late fall.

Discussion

We investigated the variation in the timing and magnitude of settlement, recruitment, and colony cover of the invasive bryozoan *M. membranacea* on the kelp *S. longicruris* and how this variation relates to thermal histories at eight sites spanning a latitudinal range of 450 km between southwestern Newfoundland and southeastern Labrador. We found differences in settler and recruit abundances of up to three orders of magnitude between sites, with peak abundances at mid-latitudes (site 3), where mean sea temperature from August to November was highest (on average 13.1 °C), and lowest abundances at the two geographic extremities (sites 1 and 8), where temperature was among the lowest (9.8 and 6.6 °C, respectively). Temperature explained up to 61 % of the variation in settler and recruit abundances from September to November, while recruit abundance explained 56 % of the variation in colony cover. These patterns strongly support our general hypothesis that the abundance of settlers and recruits along the west coast of Newfoundland are positively correlated with temperature. However, the dramatic decline in settlement and recruitment from sites 3 to 4 despite the relatively short distance (85 km) and small difference in mean sea

Table 3 Results of simple and multiple linear regression analyses examining the relationships between the abundance of recruits of *M. membranacea* on kelp (*S. longicruris*), sea temperature (TI_{76}), colony cover on kelp, and exposure to waves (Exp) across all study sites (1–8) over different sampling periods (see "Materials and methods" for calculations of TI_{76} and Exp)

| Response variable (sampling month[s])	Explanatory variable(s)	Equation for log (recruits m^{-2} kelp + 1) or arcsine($\sqrt{\text{cover}}$)	r^2	$F_{(df)}$	p
Recruits (Sep–Nov)	TI_{76}	$0.04 + 0.006\ TI_{76}$	0.315	$8.3_{(1,18)}$	0.010
Recruits (Sep)	TI_{76}	$-4.2 + 0.009\ TI_{76}$	0.812	$17.3_{(1,4)}$	0.014
Recruits (Oct)	TI_{76}	$-3.8 + 0.010\ TI_{76}$	0.735	$16.6_{(1,6)}$	0.007
Recruits (Nov)	TI_{76}	$-21.8 + 0.039\ TI_{76}$	0.976	$163.4_{(1,4)}$	<0.001
Recruits (Sep–Nov)	TI_{76}, Exp	$0.75 + 0.0060\ TI_{76} - 0.11\ \text{Exp}$	0.376	$5.1_{(2,17)}$	0.018
Cover (Sep–Nov)	TI_{76}	$-0.052 + 0.0004\ TI_{76}$	0.249	$5.6_{(1,17)}$	0.030
Cover (Sep)	TI_{76}	$-0.60 + 0.0009\ TI_{76}$	0.857	$24.0_{(1,4)}$	0.008
Cover (Oct and Nov)	TI_{76}	$0.13 + 0.0002\ TI_{76}$	0.072	$0.9_{(1,11)}$	0.374
Cover (Sep–Nov)	Recruits	$0.016 + 0.062\ \text{Recruits}$	0.563	$21.7_{(1,17)}$	<0.001
Cover (Sep)	Recruits	$-0.11 + 0.098\ \text{Recruits}$	0.891	$32.7_{(1,4)}$	0.005
Cover (Oct and Nov)	Recruits	$0.049 + 0.052\ \text{Recruits}$	0.484	$10.3_{(1,11)}$	0.008
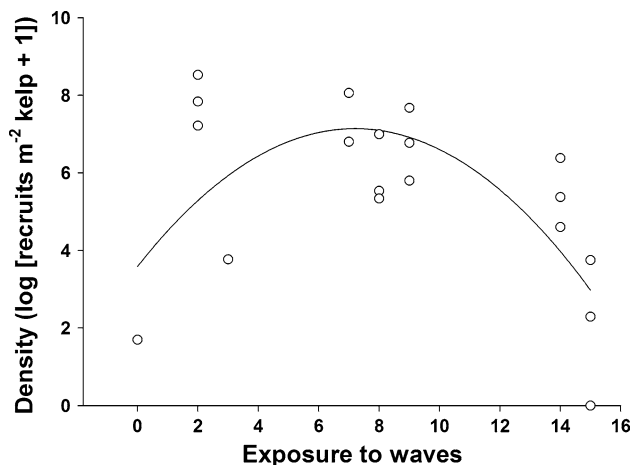
Fig. 5 Relationship between the abundance of recruits of *M. membranacea* on kelp (*S. longicruris*) and exposure to waves (Exp) across all study sites (1–8) in September, October, and November. The *line* is the quadratic fit to these data ($r^2 = 0.468$, $p = 0.005$, $n = 20$) (see "Materials and methods" for calculation of Exp)

temperature (1.1 °C) between these sites suggest that at site 4 the relationship with sea temperature was obscured by at least one other factor (see below).

September marked the start of major increases in settlement at the warmest sites (3–6), which suggests that cyphonautes larvae had recently achieved competency and began settling out of the water column. Saunders and Metaxas (2010) documented high abundances (up to ~117 larvae m^{-3}) of competent larvae of *M. membranacea* in the second half of September and early October 2007 in St. Margarets Bay (Nova Scotia) followed by a substantial decrease (~9 larvae m^{-3}) into mid-November. Settlement and recruitment were low in September and October at the two northernmost sites (7 and 8) and had ceased altogether

in November. Low sea temperature combined with relatively high exposure to waves (site 7 had the highest indices of wave exposure of all sites) likely caused low settlement and recruitment at these sites. Interestingly, abundances of settlers and recruits in October at the southernmost site (1) were similar to those at the two northernmost sites. Upwelling events are frequent at site 1 (Mouland 2006), which may help explain the low sea temperature in September and October while causing offshore transport of larvae, as suggested for *M. membranacea* in California and Nova Scotia (Yoshioka 1982; Saunders and Metaxas 2010).

Selective mortality during early phases of introduction of a species can promote the survival of individuals adapted to biotic and abiotic controls that differ from their native range (Gilchrist and Lee 2007; Lenz et al. 2011). Populations of *M. membranacea* in its native range, the northeastern Pacific, occur as far north as Kodiak (Alaska), where mean sea temperature typically ranges from only 3 to 12 °C annually (Barnes and Dick 2000; Schwaninger 2008). Mean sea temperature at our northernmost site during the warmest half of the year (June–November) barely surpassed 6 °C, which is only a few degrees above the lower limit (3 °C) in the Pacific and even lower winter averages of −1.7–2.0 °C in this portion of the Strait of Belle Isle (Han et al. 1999; Galbraith 2006). Accordingly, we propose that the low settlement and recruitment at our northernmost sites are an indication that *M. membranacea* gradually adapts to increasingly cold seawater as it invades shallow coastal habitats further north in the northwestern Atlantic.

Experimental studies show that colony growth in *M. membranacea* is positively correlated with temperature, at least within the range of 6–18 °C (Menon 1972; Saunders and Metaxas 2009a), which compares with temperature ranges in this study. Colony cover generally followed
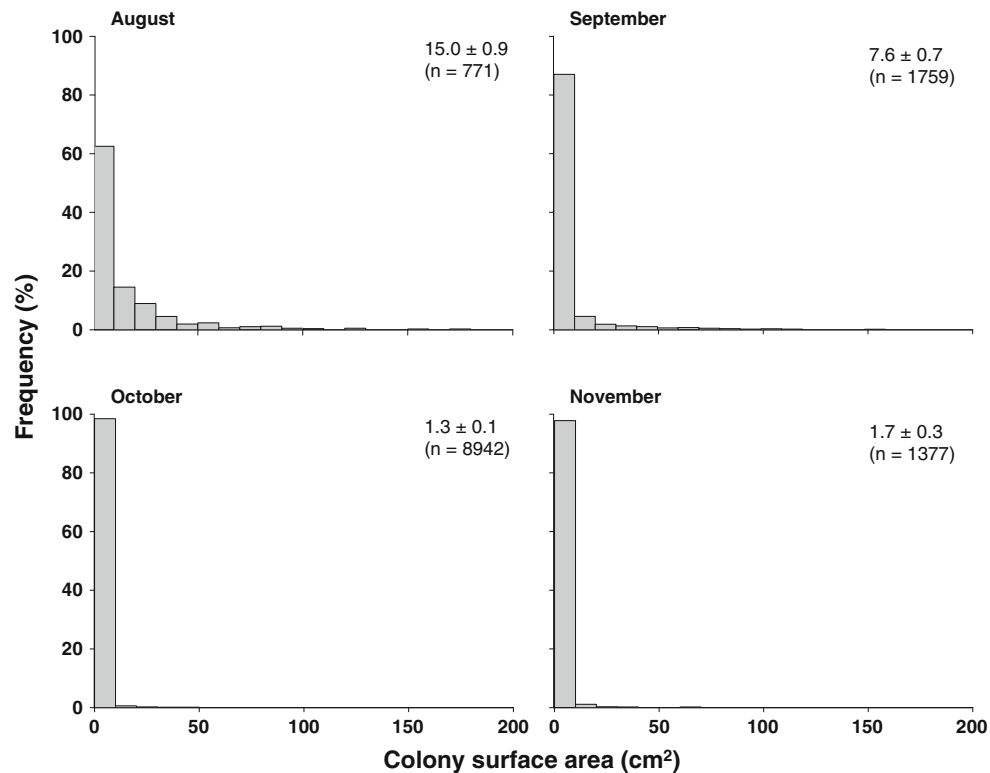
Fig. 6 Size-frequency distributions of colonies of *M. membranacea* on kelp (*S. longicruris*) across all study sites (1–8) in August, September, October, and November. Data are mean colony surface area ±SE (sample size is shown in *parentheses*)

temperature patterns, being highest at mid-latitudes and lowest at the two northernmost sites. The unexpectedly high cover at site 4, despite the low settlement and recruitment, was due to an artificial increase in cover values caused by the prevalence of small kelp individuals compared to the other sites (Caines and Gagnon, unpublished data). Overall, these results support our hypothesis that population dynamics of *M. membranacea* in northern, colder environments of Newfoundland and Labrador differ from warmer regions of the northwestern Atlantic due to the preponderance of suboptimal (or lethal) thermal conditions.

Settlement of *M. membranacea* on *S. longicruris* during two consecutive years (2005 and 2006) at two sites separated by ~7 km in Nova Scotia was positively correlated with sea temperature, with 62–81 % of the variation explained (Saunders and Metaxas 2007). In the present study, which was conducted over a much larger spatial domain encompassing cold temperate and subarctic environments, sea temperature alone explained 61 and 32 % of the variation in settler and recruit abundances, respectively. The predictive capability of TI_{76} (the sum of daily mean sea temperature over the 76 days preceding kelp collection) for settler abundance was higher than that of shorter thermal integrals (14, 21, and 28 days). These findings along with the contention that larval period in *M. membranacea* typically lasts up to ~4 weeks (Yoshioka 1982) suggest that

thermal histories encompassing growth of sexually mature colonies are important in predicting settlement. The stronger relationships between sea temperature, settlers, and recruits in November suggest that settlement and recruitment were influenced by interactive effects of temperature and some other factors in early fall (September and October), whereas thermal effects dominated in late fall (November), when temperature was lower and more similar across sites.

Settler abundance was strongly correlated ($r^2 = 0.846$) with the magnitude of changes in sea temperature (or rate of cooling, TI_{Diff}) over the 21 days preceding kelp collection. Sudden marked drops and subsequent rises in mean daily sea temperature occurred in late August or early September at all sites. Although sea temperature at each site was recorded at a single depth, such marked shifts in temperature were indicative of changes in the vertical structure of the water column, which could have enabled deeper larval populations to move into shallow water and settle on kelp. This suggestion is supported by pioneering observations in the Irish Sea and along the coast of California of cyphonautes larvae of *M. membranacea* congregating in deep (20–80 m) water during periods of vertical stratification, while exhibiting a shallower distribution when the water column becomes cooler and well mixed (Yoshioka 1982; Scrope-Howe and Jones 1986). In Nova Scotia,

settlement of cyphonautes larvae is highest during fall and presumably occurs during periods of downwelling (Saunders and Metaxas 2010). These and our findings suggest that vertical mixing triggers the migration of larvae to shallower water while downwelling events transport these larvae to subtidal kelp habitats. More research addressing the connections between temperature, larval transport, and ocean currents (e.g., vertical mixing, upwelling, and downwelling) is needed to better understand factors that trigger settlement in *M. membranacea*.

There are a few predators of *M. membranacea* in the northwestern Atlantic, including the snail *Astyris lunata* (Say) and nudibranchs *Onchidoris muricata* (Müller) and *Doridella obscura* (Verrill), but none has demonstrated the ability to control populations of this invader (Harris and Mathieson 2000; Harris and Dijkstra 2007; Pratt and Grason 2007). Our findings suggested that the physical environment had a stronger influence than biological interactions on settlement and recruitment of *M. membranacea*. For example, multiple regression analysis showed that 72 % of the variation in settler abundance was explained by TI_{76}, exposure to waves (Exp), and the surface area (SA) of colonies, which increased the predictive capability of the model with TI_{76} alone by 11 % (fecundity in bryozoans is proportional to colony surface area; Yoshioka 1973). The quadratic relationship between recruit abundance and Exp ($r^2 = 0.468$) suggested that both low and high exposure to waves can negatively affect larval supply, settlement, or post-settlement survival as seen in other invertebrate species (Pawlik and Butman 1993; Larsson and Jonsson 2006; McQuaid and Lindsay 2007). Other studies also suggest that physical factors, such as temperature, can largely determine invasion success by demonstrating positive relationships between milder winters, and settlement intensity and competitive ability in introduced species (Stachowicz et al. 2002; Saunders and Metaxas 2008).

Like recruitment, colony cover was only moderately related ($r^2 = 0.249$) to TI_{76} from September to November, though was largely explained ($r^2 = 0.857$) by TI_{76} in September. Interestingly, recruitment explained 41 % more of the variation in colony cover than temperature in October and November. Growth normally ceases at contacting margins of adjacent colonies of *M. membranacea* (Harvell et al. 1990). Presumably, infrequent crowding from June to September allowed colonies to grow under the dominant influence of temperature, which helps explain the strong relationship between colony cover and thermal history in September. The lesser influence of temperature on colony growth, and hence colony cover, in October and November could have been due to the large increases in recruits in these months, which monopolized space at the expense of fewer, smaller colonies. Relationships between recruitment and colony cover were generally strong regardless of the

temporal window over which we aggregated data. In California, sea temperature and the abundance of *M. membranacea* cyphonautes larvae in the water column explained 55 and 70 % of the variation in recruitment on kelp, respectively, and up to 79 % when analyzed together (Yoshioka 1982, 1986). Likewise, in Nova Scotia, temperature patterns explained 83 % of interannual variation in peak cover of *M. membranacea* on kelp (Scheibling and Gagnon 2009). The weaker relationships between recruitment, colony cover, and sea temperature we noted may be due to increased variability across the larger spatial domain over which we sampled *M. membranacea*. Differences in the way temperature data were aggregated in this and those studies prevented comparisons of the absolute effect of temperature on settlement, recruitment, and colony cover.

This study provides the first integrated analysis of spatial and temporal variation in the timing and magnitude of settlement, recruitment, and colony cover of the invasive bryozoan *M. membranacea* on kelp (*S. longicruris*) and how this variation relates to changes in sea temperature in the subarctic northwestern Atlantic. We showed that (1) up to 61 % of the variation in settlement, recruitment, and colony cover was explained by sea temperature alone, with highest and lowest abundances at warmest and coldest sites, respectively; (2) between-site differences in rates of sea cooling explained 85 % of the variation in settler abundance; (3) varying the temporal window over which data were aggregated increased the explanatory power of sea temperature to as much as 98 % for settlement and recruitment, and 86 % for colony cover; (4) exposure to waves and surface area of colonies improved the relationships between sea temperature and settlement and recruitment by up to 11 %; and (5) recruit abundance was a strong predictor of colony cover, explaining as much as 89 % of the variation. Consistently low abundances of settlers and recruits at the northern tip of Newfoundland and southern tip of Labrador suggest that *M. membranacea* is nearing its northern distribution limit in the northwestern Atlantic. This limit could be imposed by combined effects of low temperature and the likely natural dispersal barrier represented by the Labrador Current, which flows southward along the Labrador side of the Strait of Belle Isle (Gaylord and Gaines 2000; Zacherl et al. 2003; Han 2004). Extremely low settler and recruit abundances at the northernmost site may also reflect small, recently established populations that may grow and spread further north with time.

Working over multiple spatial and temporal scales enabled both generalization and refinement of patterns in Nova Scotia, the Gulf of Maine, and California. The highest mean colony cover in this study, 46 %, was lower than the >75 % peak cover values reported in years of heavy infestation (1993, 1997, and 1999) in central Nova Scotia (Scheibling and Gagnon 2009) and elsewhere in the

northwestern Atlantic and northeastern Pacific (Dixon et al. 1981; Berman et al. 1992; Lambert et al. 1992). Dramatic kelp defoliation following high covers of *M. membranacea* has occurred many times in these regions (Dixon et al. 1981; Lambert et al. 1992; Saunders and Metaxas 2008; Scheibling and Gagnon 2009). In the northwestern Atlantic, *M. membranacea* has facilitated the spread of another invasive species, the green alga *Codium fragile* ssp *fragile* (Suringar) Hariot, through the formation of gaps within kelp beds (Levin et al. 2002; Scheibling and Gagnon 2006; Kelly et al. 2011). We witnessed drops of approximately 40–60 % in kelp cover between September and November during our dives at some of our mid-latitude, warmest sites, and no decline at the more northerly, colder sites where colony cover was virtually null. These and our study suggest that kelp habitats in the middle of the west coast of Newfoundland are currently the most vulnerable to the introduction of *M. membranacea*.

It is expected that ocean warming will trigger range expansion in many marine invertebrates (Southward et al. 1995; Zacherl et al. 2003). Therefore, a corollary hypothesis is that kelp habitats at the southern and northern tips of Newfoundland and in Labrador will be increasingly at risk as sea temperature continues to rise and growth conditions become more favorable for *M. membranacea*. Our findings extend knowledge of population dynamics of *M. membranacea* in the northwestern Atlantic, while highlighting the complexity of the interactions between physical and biological factors and processes that affect population dynamics in invertebrates with planktonic larvae in predominantly cold marine habitats. Experimental research on effects of low water temperature on growth and survival of larvae, settlers, and colonies is required to improve our ability to predict changes in populations of *M. membranacea* and associated impacts on marine ecosystems in Newfoundland and Labrador.

Appendix

See Table 4.

Table 4 Geographic location (degrees-minutes-seconds) of each study site with corresponding dates of kelp collection (and associated sample size in parentheses), degree of exposure to waves (Exp), and depth of temperature logger (chart data) (See "Materials and methods" for calculation of Exp)

Study site (number)	Geographic location (N, W)	Kelp collection date (number of kelp blades collected [=n])				Degree of exposure to waves (Exp)[a]	Depth of temperature logger (m)
		August	September	October	November		
Port aux Basques (1)	47°34′43″ 59°05′28″	26 (10)	–	26 (10)	–	3	4.7
Lark Harbour (2)	49°06′25″ 58°21′23″	19 (10)	–	27 (10)	1 (5)[b]	7	4.8
Norris Point (3)	49°30′10″ 57°53′32″	–	17 (9)	14 (10)	25 (5)	2	6.7
Daniel's Harbour (4)	50°14′29″ 57°35′20″	19 (10)	9 (10)	14 (10)	29 (5)	14	4.5
Port au Choix (5)	50°43′56″ 57°18′44″	18 (8)	23 (10)	21 (10)	25 (5)	9	5.4
Bird Cove (6)	51°03′19″ 56°56′25″	19 (10)	14 (10)	13 (10)	26 (5)	8	5.2
Green Island Cove (7)	51°22′36″ 56°36′28″	18 (8)	15 (10)	14 (10)	26 (5)	15	2.2
Red Bay (8)	51°43′35″ 56°25′44″	–	23 (10)	13 (10)	–	0	3.5

[a] The higher the value, the greater the exposure to waves

[b] Kelp blades were collected on December 1 and analyzed as part of the November data (see "Materials and methods")

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