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Temperature explains settlement patterns of the introduced bryozoan *Membranipora membranacea* in Nova Scotia, Canada

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ABSTRACT: Settlement is a critical life-history stage for benthic invertebrates with a planktonic larval form, and is important for understanding mechanisms of larval supply and population dynamics. We examined spatial (metre to kilometre scales) and temporal (weekly to yearly scales) patterns in abundance of settlers of the introduced bryozoan *Membranipora membranacea* on the numerically dominant kelp *Saccharina longicruris*, at 2 sites in St. Margarets Bay, Nova Scotia, Canada. Relationships between patterns in settlement and indices of the temperature regime, such as average weekly temperature, temperature fluctuations, water column stratification and thermal history (growing degree-day) were determined using multiple linear regressions. Although settler abundance varied interannually, it was highest in early autumn, and was generally higher at depth (12 and 8 m) than in the shallows (4 m). Abundance was an order of magnitude greater after a significantly warmer winter. Growing degree-day accounted for up to 81 % of the variability in settler abundance, whereas average temperature, temperature fluctuations and stratification were less important. The strong positive relationship between thermal history and settlement of this ecologically important species suggests that abundance of established introduced marine species may increase with the increased temperatures predicted to result from climate change.

KEY WORDS: Larval settlement · Temperature · Thermal history · Stratification · Bathymetric patterns · Benthic invertebrates · Introduced species · Climate change

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INTRODUCTION

The importance of larval supply in regulating populations of meroplanktonic benthic invertebrates is widely acknowledged for many species (e.g. Caley et al. 1996). Consequently, settlement, defined here as the movement of larvae from the plankton to the benthos and subsequent metamorphosis, is one of the key processes in the life history of benthic invertebrates. Moreover, an analysis of settlement patterns can lend insight into the mechanisms of larval transport to the adult benthic habitat, a process that is extremely challenging to measure in the water column (Pineda 2000).

Species with a dispersive larval phase have a great probability of being introduced to non-native ecosystems because of their ability to be transported in

ballast water (Carlton 1989). Moreover, species with a rapid means of dispersal (for example a larval phase) are considered more likely to be successful invaders (Ricciardi & Rasmussen 1998). However, observed range expansion via larval dispersal is often less than would be predicted solely by physical circulation models (Grosholz 1996). For example, in Australia, the yearly range expansion of the European green crab *Carcinus maenas* is only a few kilometres per year, despite a long (up to 50 d) planktonic period (Thresher et al. 2003). Clearly, the processes that regulate dispersal, settlement and recruitment into the adult population can affect the success of non-native species in their new environments.

The encrusting epiphytic colonial bryozoan *Membranipora membranacea* has recently been introduced

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to the kelp beds of the rocky subtidal in Nova Scotia, Canada. It was first observed in Atlantic North America, off New Hampshire and southern Maine, in 1987, where it became the dominant epiphyte on kelps within 2 yr (Berman et al. 1992). It was first observed in Nova Scotia, in Mahone Bay and St. Margarets Bay, in 1992 (Scheibling et al. 1999). Genetic studies indicate that Atlantic North American populations are closely related to those in Europe (Schwaninger 1999), and they were probably introduced from that source in ballast water.

The planktotrophic larvae of *Membranipora membranacea* (cyphonautes) remain in the water column for approximately 4 wk (Yoshioka 1973). They settle preferentially on the proximal (meristematic) ends of laminarian algae (Seed & O'Connor 1981), where they metamorphose into a feeding stage, and then asexually bud new zooids to form a colony. The presence of *M. membranacea* colonies can have pronounced negative effects on the growth and survival of its algal substrates. Heavy encrustations of the bryozoan increase the brittleness of kelp blades (Dixon et al. 1981), leading to defoliation during periods of intense wave action (Lambert et al. 1992, Scheibling et al. 1999).

The population dynamics of *Membranipora membranacea* in Nova Scotia, or elsewhere along the eastern coast of North America, are poorly understood. In the Gulf of Maine, colonies grow and reproduce in summer and senesce in autumn (Ellison & Harvell 1989). In Nova Scotia, outbreaks of *M. membranacea* occur in autumn, particularly during years with warmer than average sea surface temperature (R. E. Scheibling unpubl. data). The resultant defoliation (Scheibling et al. 1999) has facilitated the establishment of the introduced green alga *Codium fragile* ssp. *tomentosoides* (Chapman et al. 2002, Levin et al. 2002). This shift in ecosystem structure may potentially have pronounced implications for commercial fisheries of sea urchins and lobster, which rely on kelp beds for food and habitat (Chapman et al. 2002). The role of warmer water in effecting earlier or greater settlement, more successful recruitment, or faster colony growth of *M. membranacea* is unknown. In fact, no detailed observations exist on the spatial and temporal patterns in larval settlement of *M. membranacea* in Nova Scotia, or elsewhere along the Atlantic coast of North America. Such measures of larval supply can provide information on the factors responsible for initiation of outbreaks of harmful species, such as *M. membranacea*.

In Nova Scotia, water temperatures may fall below 0°C in winter, and can be periodically as high as 20°C in summer. Temperature has a direct effect on the metabolic rate of ectothermic organisms, with warmer temperatures generally associated with shorter devel-

opment times and increased growth rates (Atkinson 1994). Importantly, both the current temperature and the thermal history experienced by ectothermic organisms in the past will regulate many life-history characteristics, such as growth, development and reproduction (Trudgill et al. 2005). Across depths, temperature may be homogeneous (well-mixed) or heterogeneous (stratified), and these conditions may have profound implications for distributions of larvae. For example, larvae may vary in abundance across a thermocline, or be restricted to a particular water layer. Temporal fluctuations in temperature can signal changing water masses during oceanographic processes, such as tidal movements, or upwelling and downwelling. In California, associations between temperature and upwelling processes, and abundance and transport of *Membranipora membranacea* larvae have been suggested (Yoshioka 1982).

The present study had 3 objectives: (1) to document spatial (metre to kilometre scales) and temporal (weekly to yearly scales) patterns in abundance of settlers of the introduced bryozoan *Membranipora membranacea* on the numerically dominant kelp *Saccharina longicurvis* (formerly *Laminaria longicurvis*, Lane et al. 2006) in Nova Scotia; (2) to examine relationships between patterns in settlement and indices of the temperature regime, including average weekly temperature, temperature fluctuations, water column stratification and thermal history (growing degree-day); and (3) to examine the effect of winter temperature on abundance of settlers. Determining the effect of temperature regime on settlement of *M. membranacea* will improve our understanding of its population dynamics, facilitate comparison of native and introduced populations, and enable prediction of climate change effects on this introduced species.

MATERIALS AND METHODS

Study area. We sampled 2 sites on the southern shore of Nova Scotia, Canada (Fig. 1), which have a granitic substratum with extensive kelp beds. The Lodge (44° 33' 3" N, 64° 01' 9" W) is located on the eastern shore of St. Margarets Bay and faces east-north-east. The substratum is dominated by large boulders and cobbles, with granite outcroppings, and the bottom slope is moderately steep. At depths < 8 m, the kelp bed is largely dominated by *Saccharina longicurvis*, whereas between 8 and 14 m it consists of mixed stands of *S. longicurvis* and *Agarum clathratum*. Paddy's Head (44° 31' 6" N, 63° 57' 2" W) is located on the western shore near the mouth of St. Margarets Bay, and faces northwest. We sampled at the site's outer wall, where the substratum is granite bedrock that

slopes steeply towards a sandy bottom at ~18 m depth. At depths <8 m, the kelp bed consists mostly of *S. longicurvis* with fewer *Laminaria digitata*, and between 8 and 18 m it is dominated by *A. clathratum*, with fewer *S. longicurvis* and *L. digitata*. At each site, permanent markers were affixed to the substratum at 4, 8 and 12 m depths relative to Chart Datum along a transect perpendicular to shore.

Because of a well-established pattern in kelp morphology with wave exposure (Gerard & Mann 1979), we used it to infer relative water motion between sites. In high wave exposure regions, the blades of *Saccharina longicurvis* are long, narrow, thick and strap-like, with fluted edges. In contrast, when growing in low-energy environments, blades are wider and thinner, and have extensively crenulated edges. Based upon observations of kelp morphologies and supported by observations of the aspect and exposure of the shorelines to the direction of predominant swells (SW), we determined that both sites are moderately exposed, but that Lodge is considerably more sheltered than Paddy's Head.

The mean current direction along the coast of Nova Scotia is from the northeast towards the southwest, and the mean circulation in St. Margarets Bay is counter-clockwise (Heath 1973). Mean flushing time through the bay is approximately 5 to 10 d in the upper 5 to 10 m, and 10 to 30 d in the deeper layer. In summer, the water column is strongly stratified throughout the bay, and large fluctuations in temperature attributed to wind-driven coastal upwelling are observed in late summer and early autumn (Heath 1973, Petrie et al. 1987). The tides in the region are semidiurnal, with a mean range of 1.49 m and a maximum range of 2.04 m (Canadian Tide and Current Tables 1988).

Temperature measurements. HOBO Pendant Data Loggers (Onset Computer Corporation) (accuracy \pm 0.47°C) were used to measure temperature at 10 min intervals throughout the study period, from 1 July 2005 to 14 September 2006. The loggers were affixed to the permanent site markers near the benthos at 4, 8 and 12 m depths, at both sites. To extend the length of the temperature time series, temperature measures collected at 30 min intervals using Onset HOBO StowAway Tidbit loggers (accuracy \pm 0.2°C), from 1 January 2005 to 1 July 2005, at 8 m depth at Birchy Head, were also included in the analyses. Birchy Head is located ~2 km from Lodge towards the head of the bay, along the adjacent shore (Fig. 1), with similar substratum and bottom cover of algae. Wave exposure, currents and proximity to freshwater sources, and therefore mixing processes, are more similar between the 2 above-mentioned sites than compared to Paddy's Head. Temperature data are presented as daily averages.

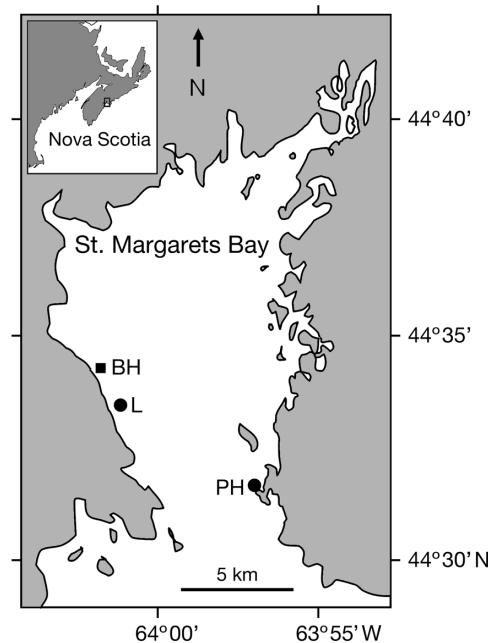


Fig. 1. Study area on the southern shore of Nova Scotia, Canada, indicating the 2 sampling sites (●), Lodge (L) and Paddy's Head (PH). Additional data were obtained from Birchy Head (BH, ■), to extend the length of the temperature time series

Temperature indices. For ectothermic organisms, physiological time is often tightly coupled to thermal history (Trudgill et al. 2005). Integrated indices of thermal history (e.g. growing degree-day, GDD) have been successfully used to explain variability in many biological processes, including timing of egg hatch, germination of crops and weeds, and development of insect species (Trudgill et al. 2005). GDD is calculated by sequentially adding daily average temperatures that are above a threshold temperature for the biological process of interest. Because the threshold temperature for growth and reproduction of *Membranipora membranacea* in Nova Scotia is unknown, we set the threshold value to -1.8°C , the freezing point of seawater. GDD was calculated by (1) standardising daily average temperature to positive values by adding 1.8°C to each daily temperature, and (2) sequentially adding standardised daily temperature, starting at the beginning of January. This starting date was selected because temperatures between the 2 years sampled were similar until mid-January, when they began to diverge. By calculating GDD from January onwards, we accounted for all of the interannual difference in winter temperature. Moreover, in Nova Scotia, the coldest months are January, February and March, and thus January can generally be considered the onset of the thermal season.

To further describe the temperature regime during the settlement of *Membranipora membranacea*, indices of weekly temperature (T), stratification (ΔT) and temperature fluctuations (T') were calculated. Based upon laboratory growth rates of new settlers (M. Saunders unpubl. data), at the temperatures during the sampling period ($10.9 \pm 3.4^\circ\text{C}$, mean \pm SD), on any 1 sampling date, settlers could have been present on kelp for 7 ± 3 d (range: 0 to 15 d). Thus, to best describe temperature regime during settlement, the temperature indices were integrated over the week prior to sampling settlers. Consequently, our analysis is specific to time lags of up to 1 wk. T was calculated by averaging daily temperature over the week prior to sampling settlers, for each date, at each depth, at each site. ΔT , an index of stratification in the top 12 m of the water column, was calculated by subtracting the mean daily temperature at 12 m from the mean daily temperature at 4 m, and then averaging the daily differences over the week prior to sampling settlers, for each date, at each site. T' were obtained by calculating the absolute change in temperature between consecutive days, and averaging the daily changes over the week prior to sampling settlers, for each date, at each depth, at each site.

Sample collection. Blades of *Saccharina longicruris* were sampled approximately weekly from 1 July to 4 August 2005 and in September 2005, and approximately monthly from October 2005 through September 2006. On each sampling date, 7 to 15 blades were haphazardly collected from each depth, at each site. Since settlers are microscopic and clear in colour, during collection using SCUBA no investigator bias was introduced. The length of kelp blades ranged from 35 to 362 cm (108 ± 37 cm, mean \pm SD, $n = 993$), and the width ranged from 10 to 49 cm (23 ± 7 cm). On most occasions, we sampled both sites on the same date. If this was not possible because of time and/or weather limitations, the second site was sampled within 1 to 8 d of the first. Kelps were collected in mesh bags and transported in plastic tubs without seawater to the laboratory, where they were placed in aquaria with running ambient seawater in Dalhousie University's Aquatron facility. The total length of time out of water was 3 to 6 h. Plants were held in aquaria until processing was completed (1 to 8 d). New settlers did not grow while in aquaria (M. Saunders unpubl. data), indicating that the length of time in aquaria prior to processing did not affect results.

Quantification of settlers. The number and size of settlers of *Membranipora membranacea* were counted on each kelp blade using $15\times$ magnification and LED lighting. Settlers were defined as any colony with <2 zooid rows (up to and including ancestrula with 1 incompletely formed zooid, generally 0.5 to 0.9 mm diameter). From laboratory growth experiments (M. Saunders unpubl.

data), we estimated these to be 0 to 3 d old at 14°C , 0 to 5 d old at 10°C and 0 to 15 d old at 6°C .

When the number of settlers on each plant increased markedly in September 2005, and for the remainder of the study period, we subsampled 1 randomly chosen quarter of the kelp blade. In September 2006, we subsampled settlers within twelve 25 cm^2 square sections of each blade. The blade was subdivided into 6 equidistantly spaced strata along its length. At each stratum, 2 square sections were haphazardly selected, 1 from the edge and 1 from the centre of the blade. For all sampling dates, the number of settlers on each blade was divided by the surface area of the blade to obtain the number of settlers m^{-2} kelp.

To obtain surface area of the kelp blade, the length and width of each blade were recorded, and 1 side of the blade was photographed against a white background using an HP Photosmart 435 3.1MP digital camera. The surface area of the kelp was measured using SPSS Sigma Scan Pro Image Analysis 5.0. Since the blades of *Saccharina longicruris* are extensively crenulated, the ratio of photographed surface area to flattened surface area was measured for 9 kelps from each depth, at each site, in November 2005. Each intact kelp blade was photographed, and then cut into small (25 to 100 cm^2) flat pieces, and the flattened pieces were then photographed. The images were digitally analysed, and the surface areas of the flattened kelps were divided by the intact surface areas. The average ratio of surface area for flat to intact blades (crenulations) was calculated for each location, and this relationship was used to correct kelp surface area for all other sampling dates.

Statistical analyses. For the periods of maximum settlement (29 September 2005 to 19 October 2005, and 2 August 2006 to 14 September 2006) differences in abundance of settlers between sites (fixed factor, 2 levels) and among depths (fixed factor, 3 levels) were examined using 2-way ANOVA. Site was a fixed factor because the 2 sites were selected specifically for their bathymetry (substrata that slope relatively steeply) and locations (opposite sides near the mouth of St. Margarets Bay). When sites were not sampled on the same date (e.g. Lodge on 20 October 2005 and Paddy's Head on 22 October 2005; Table 1) the 2 closest dates were used. Significant differences between means were examined with Tukey's HSD post hoc tests. The data were $\log(x + 1)$ -transformed to remove heterogeneity of variance as detected by Levene's test. The transformations were successful except for September 2006 ($\alpha = 0.05$), when the lowest mean (Paddy's Head, 4 m) had much higher variance compared to the other depth-by-site combinations.

Relationships between abundance of settlers and indices of the temperature regime preceding settle-

Table 1. Dates included in 1-way ANOVA examining spatial effects (depth and site) on the abundance of *Membranipora membranacea* settlers at depths of 4, 8 and 12 m. Numbers of *Laminaria longicurvis* blades that were collected from each depth, at each site, on each date are indicated (n). L: Lodge; PH: Paddy's Head

Date	Site	Date sampled	n (4, 8, 12 m)
Sep 2005	PH	29 Sep 2005	9, 10, 10
	L	1 Oct 2005	9, 8, 7
Oct 2005	L	19 Oct 2005	10, 10, 10
	PH	19 Oct 2005	10, 9, 9
Aug 2006	L	2 Aug 2006	10, 9, 10
	PH	2 Aug 2006	10, 10, 10
Sep 2006	L	9 Sep 2006	8, 8, 8
	PH	14 Sep 2006	8, 8, 8

ment were explored using stepwise multiple linear regressions. The relationships between abundance of settlers and GDD, T , ΔT and T' were examined (1) for all data pooled across sites and depths, (2) for each depth pooled across sites and (3) for each site pooled across depths. We did not examine relationships for specific depths within sites as our aim was to identify the broadest scale on which statistically significant relationships between abundance of settlers and temperature regime could be generated and patterns generalised. We only used data during periods of increasing abundance of settlers (summer and early autumn).

The independent effect of GDD on abundance of settlers [$\log(x + 1)$ -transformed] was examined using linear regression, for data from both years combined, and for each year (2005 and 2006) separately. Analysis of covariance (ANCOVA) was used to examine the difference in magnitude of slopes between years (fixed factor, 2 levels) with GDD as a covariate. Year was treated as a fixed factor because of thermal history, as Year 1 was colder than Year 2.

For all regression analyses, settler data were $\log(x + 1)$ -transformed to meet assumptions of normality (Shapiro-Wilk test), homogeneity of variances (examination of predicted vs. residual values) and, for the multiple regressions, multicollinearity (examination of tolerance and variance inflation values). The data met assumptions of independence (Durbin-Watson test). All tests were considered significant at $\alpha = 0.05$.

RESULTS

Temperature patterns

Bathymetric patterns in temperature were strongly seasonal, with the most pronounced changes occurring at 4 m (Fig. 2). During the sampling period, the water

was warmest in early September 2005 (19.3°C at Lodge, 4 m, and 18.0°C at Paddy's Head, 4 m) and coldest in late February and early March 2006 (1.2°C at 4 m at both sites). Interannual differences were compared at 8 m, using the combined data sets from Birsby Head (1 January to 30 June 2005) and Lodge (1 July to 31 August 2005) for 2005, and the data set from Lodge (1 January 2006 to 31 August 2006) for 2006 (Fig. 3A). The minimum daily average winter temperature was colder in 2005 than in 2006 (-0.69°C on 26 February 2005, 1.43°C on 4 March 2006; Fig. 3A). Moreover, the average winter water temperature (January, February and March) was significantly warmer in 2006 than in 2005 (2.71 ± 0.56 and $1.21 \pm 1.34^{\circ}\text{C}$, respectively; mean \pm SD, $n = 90$, 1-tailed t -test, $p < 0.0001$). Because of the warmer winter temperatures in 2006, GDD in the spring (April to June) was advanced by 4 to 5 wk compared to 2005 (Fig. 3B).

The water column was strongly stratified from July to mid-September 2005 and from mid-May until

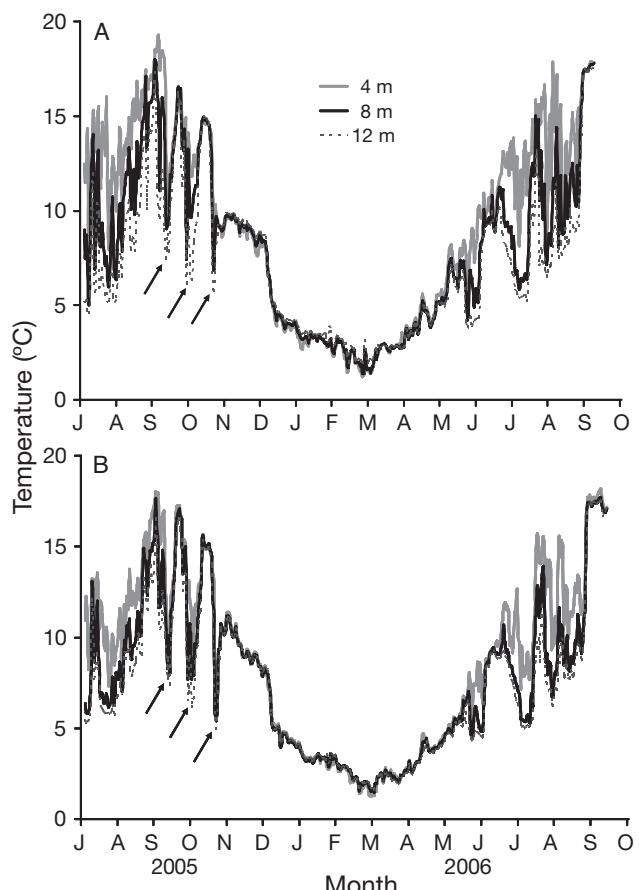


Fig. 2. Mean daily temperature ($^{\circ}\text{C}$) at 3 depths, at (A) Lodge and (B) Paddy's Head within St. Margarets Bay, Nova Scotia, Canada, measured over 15 mo in 2005 and 2006. Three upwelling events in September and October 2005 are indicated with arrows

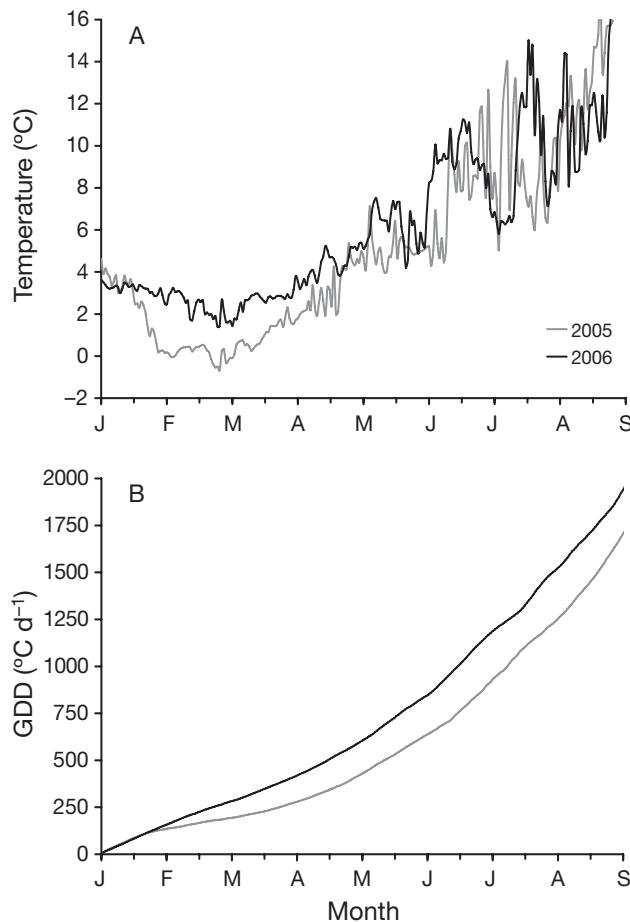


Fig. 3. Interannual differences in the winter temperature regime, measured at 8 m depth at Birchy Head (1 January to 30 June 2005) and Lodge (1 July to 31 August 2005, 1 January to 31 August 2006) presented as (A) daily temperature and (B) growing degree-day (GDD)

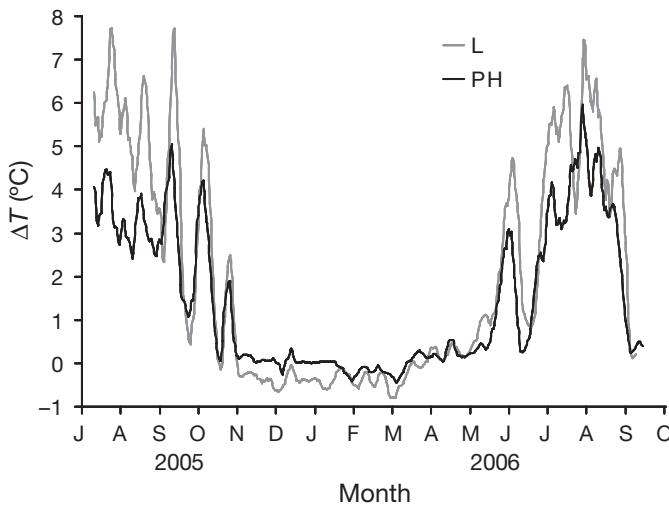


Fig. 4. Daily stratification (ΔT) at each of 2 sites (Lodge [L], Paddy's Head [PH]) within St. Margarets Bay, Nova Scotia, measured over 15 mo in 2005 and 2006

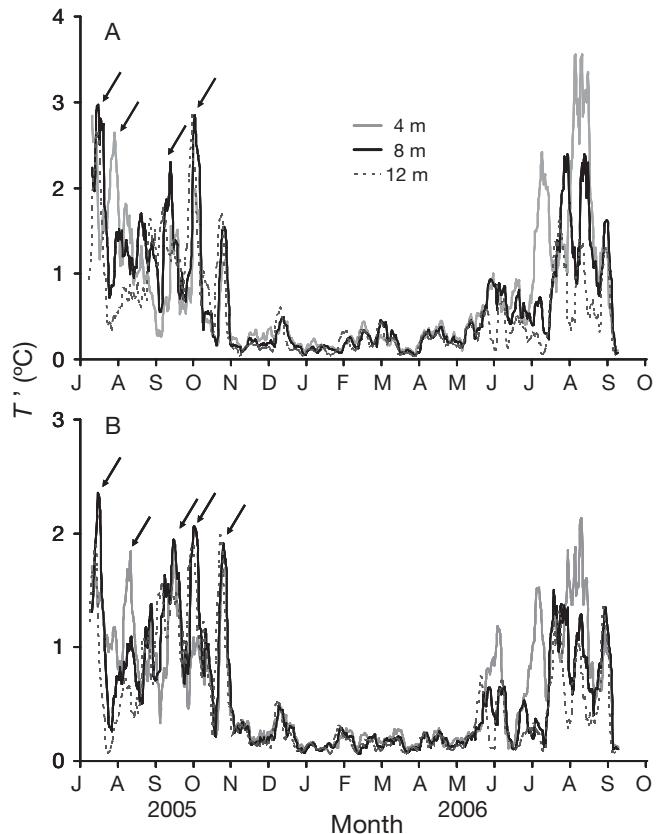


Fig. 5. Daily temperature fluctuations (T') at 3 depths, at (A) Lodge and (B) Paddy's Head within St. Margarets Bay, Nova Scotia, measured over 15 mo in 2005 and 2006. Large fluctuations in temperature in July, August, September and October 2005 are indicated with arrows

August 2006. Maximum values of ΔT of 8°C (Lodge) and 6°C (Paddy's Head) were observed in July and September 2005, and in July 2006, respectively (Figs. 2 & 4). Stratification periodically broke down due to upwelling in September and October 2005 (Fig. 2), and the water column was well mixed from the end of October 2005 to mid-May 2006 (Figs. 2 & 4).

Large fluctuations in temperature were observed during periods of stratification in July to October 2005 and May to August 2006 (Figs. 2 & 5). At both sites, 3 pronounced decreases in water temperature were observed in September and October 2005 (Fig. 2). These decreases in temperature occurred throughout the water column, and were consistent with wind-driven upwelling, as has been described for this region (Heath 1973, Petrie et al. 1987). Seasonal and bathymetric patterns in temperature fluctuations were similar between sites (Figs. 2 & 5), and cross-correlation of the temperature time series from 12 m at the 2 sites demonstrated that pronounced changes in temperature at Lodge lagged behind those at Paddy's Head by 8 to 24 h. This is probably because Lodge is located

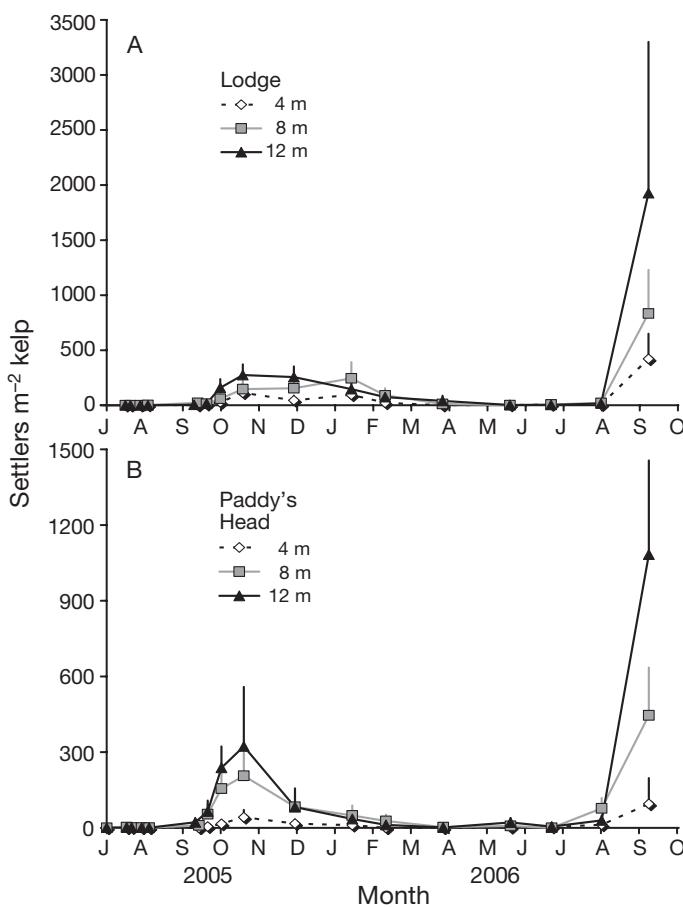


Fig. 6. *Membranipora membranacea* settlers on *Laminaria longicurvis*. Abundance (mean + SD, n = 7 to 15) at 3 depths, at (A) Lodge and (B) Paddy's Head within St. Margarets Bay, Nova Scotia, from 1 July 2005 to 14 September 2006

further towards the mouth of the bay, so cross-shelf directional motions in the water column (e.g. up- and down-welling) reach Lodge slightly later than Paddy's Head.

Settler patterns

The abundance of settlers was strongly seasonal (Fig. 6). In 2005, the first new settlers were observed at both sites in early July, and were present in low abundance (0 to 2.7 ± 4.3 ind. m^{-2} kelp, mean \pm SD) through July and August. The abundance of settlers increased in September, peaked on 19 October 2005 (Paddy's Head, 12 m: 323 ± 235 ind. m^{-2} kelp, n = 9; Lodge, 12 m: 275 ± 97 ind. m^{-2} kelp, n = 10) and

declined until April. In 2006, the lowest abundances were observed from March to May (0 to 2.6 ± 4.8 ind. m^{-2} kelp). Abundance increased from May through to September 2006 at both sites. The highest abundances for the study period were observed in September 2006, at 12 m depth at both sites (Paddy's Head, 12 m: 1083 ± 372 ind. m^{-2} kelp, n = 8; Lodge, 12 m: 1926 ± 1373 ind. m^{-2} kelp, n = 8).

Temporal settlement patterns were similar between sites in summer and early autumn, but differed in late autumn and winter (Fig. 6). At Paddy's Head, settler abundance decreased after 19 October 2005, whereas, at Lodge, abundance remained high until January 2006 and subsequently declined. Water temperatures from December to April were $<5^\circ\text{C}$ (Fig. 2); it is not known whether settlers develop into colonies at those temperatures, and, if so, at what rate. It is possible that settlers observed in winter had settled many weeks or months previously.

There was considerable inter-annual variability in the timing of occurrence and in the abundance of settlers (Fig. 7). Overall, the settlement season was advanced in 2006 compared to 2005. Seasonal increases in settlers were first observed in July in 2005, and in May in 2006. Pronounced increases in the abundance of settlers were first observed in September in 2005, and in August in 2006 (Figs. 6 & 7). Furthermore, abundance in September 2006 was 2 orders of magnitude greater than in September 2005, and 1 order of magnitude greater than during the peak of settlement (19 October) in 2005 (Figs. 6 & 7).

The bathymetric patterns in abundance of settlers were similar for the 4 dates tested (Fig. 6, Table 2). In August 2006, at both sites, abundance of settlers was

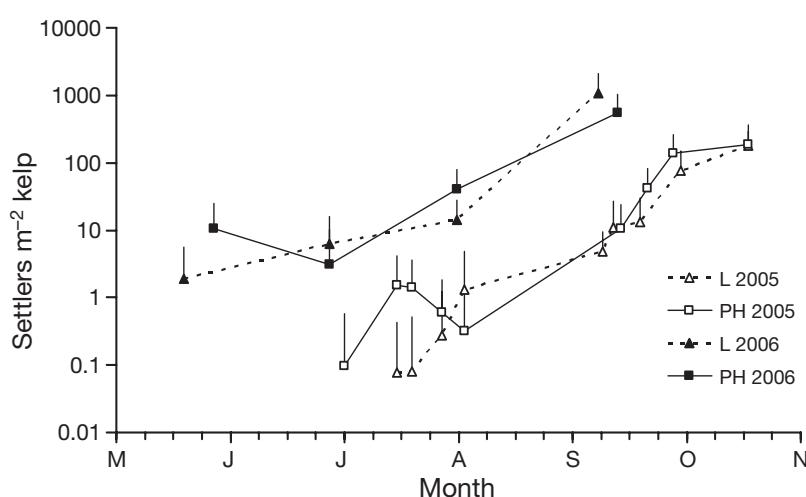


Fig. 7. *Membranipora membranacea* settlers on individual *Laminaria longicurvis* blades. Abundance (mean + SD, n = 24 to 43) at Lodge (L) and Paddy's Head (PH) in St. Margarets Bay, Nova Scotia, pooled across 3 depths, from 1 July to 19 October 2005 and from 21 May to 14 September 2006

Table 2. ANOVA on the effects of depth and site on the abundance of settlers of *Membranipora membranacea* done for the dates of maximum settlement in 2005 (September and October) and 2006 (August and September). L: Lodge; PH: Paddy's Head

Effect	MS	F _(df)	p	Tukey's HSD
Sep 2005				
Site	0.16	0.97 _(1, 47)	0.33	4, 8, 12 m: PH = L
Depth	5.97	36.3 _(2, 47)	<0.0001	L: 4 m = 8 m = 12 m
Depth × Site	0.56	3.43 _(2, 47)	0.04	PH: 4 m < 8 m = 12 m
Error	0.16			
Oct 2005				
Site	1.29	0.08 _(1, 57)	0.78	4, 8, 12 m: PH = L
Depth	19.6	11.6 _(2, 57)	<0.0001	L: 4 m = 8 m = 12 m
Depth × Site	3.12	4.16 _(2, 57)	0.02	PH: 4 m < 8 m = 12 m
Error	0.68			
Aug 2006				
Site	2.24	8.83 _(1, 53)	0.005	L < PH
Depth	3.50	13.8 _(2, 53)	<0.0001	4 m < 8 m = 12 m
Depth × Site	0.08	0.32 _(2, 53)	0.72	
Error	0.16			
Sep 2006				
Site	3.07	15.4 _(1, 42)	0.0003	4 m: PH < L
Depth	4.82	24.3 _(2, 42)	<0.0001	8, 12 m: PH = L
Depth × Site	1.01	5.07 _(2, 42)	0.01	PH: 4 m < 8 m = 12 m
Error	0.20			L: 4 m = 8 m = 12 m

lower at 4 than at 8 and 12 m. For the other 3 dates, abundance was lower at 4 than at 8 and 12 m at Paddy's Head, but did not vary significantly across depths at Lodge. Comparison between sites showed that abundance of settlers was similar between the 2 sites for all dates and depths, except for August 2006 (when abundance was greater at Paddy's Head than at Lodge) and September 2006 (when abundance was greater at Lodge than at Paddy's Head, but only at 4 m).

Relationships between temperature and settlement

We obtained consistently strong relationships between abundance of settlers and the temperature regime (Table 3). GDD was always included in the stepwise multiple linear regressions, whereas T was only included at 12 m, and the effects of ΔT and T' were inconsistent. For all significant relationships, settlers were positively related to GDD and T , and negatively related to ΔT and T' . When data from both sites and all depths were combined, GDD and ΔT explained 65% of the variance in settler abundance (Table 3). At Lodge, GDD and ΔT explained 76% of the variance in abundance, whereas at Paddy's Head, GDD explained 54% of the

variance in abundance. At 8 m, GDD explained 69% of the variance in abundance, whereas at 12 m, GDD and T' explained 63% of the variance in abundance.

Because GDD was the variable most consistently included in the multiple regressions explaining settler abundance, and because settler abundance was an order of magnitude higher in 2006 than in 2005, we examined the direct relationship between GDD and settlers, for both years and for each year independently, using simple linear regressions. When data from both years were included in the analysis, GDD explained 62% of the variance in settler abundance ($F_{(1, 76)} = 128$, $p < 0.001$). When the years were considered separately, GDD explained 76 to 81% (2005: $F_{(1, 52)} = 226$, $p < 0.001$, $r^2 = 0.81$; 2006: $F_{(1, 22)} = 72.8$, $p < 0.001$, $r^2 = 0.76$) of the variance in settler abundance (Fig. 8). The slopes of the regressions did not vary between years ($t_{(1, 75)} = -0.78$, $p > 0.05$), although the elevation was greater in 2006 than in 2005 (ANCOVA, $F_{(1, 75)} = 75.5$, $p < 0.001$).

DISCUSSION

GDD, a measure of thermal history, explained up to 81% of the variability in the abundance of settlers of the introduced bryozoan *Membranipora membranacea* in St. Margarets Bay, Nova Scotia. The strong relationship between GDD and the abundance of *M. membranacea* settlers suggests that predicted increases in temperature attributable to anthropogenically induced climate change (IPCC 2001) may cause increases in abundance of this introduced species. GDD has been used to model climate change effects in many agricultural and forestry systems (e.g. De Melo-Abreu et al. 2004), but it has been used infrequently for studies of marine systems (Neuheimer & Taggart 2007). The rela-

Table 3. Results of multiple linear regression analyses exploring relationships between the abundance of settlers of *Membranipora membranacea* [$\log(x + 1)$ -transformed] and indices of temperature regime for different site and depth combinations. See 'Materials and methods' for calculations for growing degree-day (GDD), weekly temperature (T), stratification (ΔT), and temperature fluctuations (T'). $p < 0.001$ for all tests

Location	Eq. for $\log(\text{settlers} + 1)$	r^2	$F_{(df)}$
All locations (all data)	= 0.001GDD – 0.121 ΔT – 0.336	0.653	67.8 _(2, 69)
Lodge (all depths)	= 0.001GDD – 0.141 ΔT – 0.282	0.762	57.0 _(2, 33)
Paddy's Head (all depths)	= 0.001GDD – 0.901	0.538	41.8 _(1, 34)
4 m (both sites)	= 0.001GDD – 0.462 T' – 0.004	0.630	20.6 _(2, 21)
8 m (both sites)	= 0.001GDD – 1.202	0.686	51.2 _(1, 22)
12 m (both sites)	= 0.001GDD + 0.125 T – 1.301	0.697	27.5 _(2, 21)

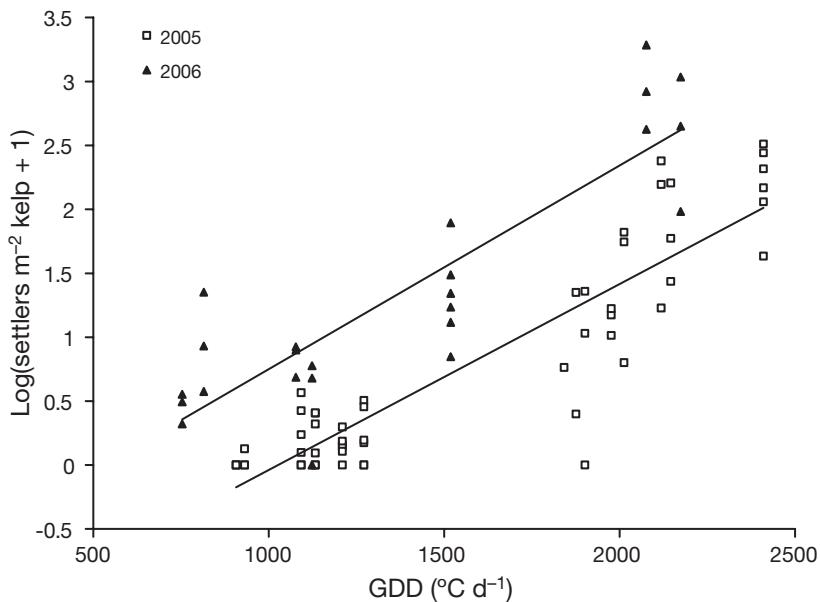


Fig. 8. *Membranipora membranacea*. Relationships between the abundance of settlers and growing degree-day (GDD) from 1 July to 19 October 2005 and from 21 May to 14 September 2006, for all depths and both sites, combined, in 2005 ($R^2 = 0.81$) and 2006 ($R^2 = 0.76$)

tionship between increased temperatures associated with climate change and species invasions has also not been as thoroughly addressed in marine as in terrestrial systems (Carlton 2000, Stachowicz et al. 2002). In one of few studies, invasive tunicates settled earlier in the season than native tunicates during years with warmer winters in New England (Stachowicz et al. 2002). In the Wadden Sea, recruitment of invasive oysters was higher in years with above-average summer sea surface temperature (Diederich et al. 2005). The importance of changes in extreme temperatures (such as winter or summer temperatures) for invertebrate population dynamics is well known for insects (Sinclair et al. 2003). For example, increased temperatures can result in increased insect (many of which are introduced or pest species) populations (e.g. Battisti et al. 2006). Our results suggest that populations of marine bryozoans, like many other invertebrates, are sensitive to changes in winter temperature. For an invasive species such as *M. membranacea*, which suffers little predation or competition in its introduced habitat (Berman et al. 1992), warmer winter temperatures may result in dramatic increases in population size.

Within each year, abundance of settlers increased exponentially from onset until the peak of settlement. Because GDD is related approximately linearly to time, it is possible that the observed relationship between abundance of settlers and GDD reflects this increase over the growing season. However, by standardising settlement rate to GDD rather than to time, we can

generalise comparisons between years, as well as among regions with different thermal regimes (e.g. northern vs. southern hemisphere; sub-polar vs. temperate environment). The effect of thermal history on settlement was consistent between years, as indicated by the lack of a difference in slopes between years. However, the elevation of the regression was higher for 2006 than for 2005. If GDD alone was responsible for explaining the variability in abundance of settlers, then the elevations of the regressions would not differ significantly between years. We suggest that warmer winter temperatures allow a greater number of adult colonies to overwinter, bud new growth, become reproductive, and provide larvae for the next season. Early season settlers can then grow into reproductively active adults, and produce larvae later in the same season. We propose that it is this increase in adult colonies and consequent

increase in settlers that is reflected in increased elevation. In winter 2006, many of the observed overwintering colonies continued to grow, as indicated by a 'milky fringe' at the edge of the colony (Lutaud 1961). Furthermore, settlers were observed on all sampling dates throughout the winter of 2006. In contrast, in the winter of 2005, colonies were fragmented and covered in algae and detritus, and regenerated growth (Menon 1972) was not observed until June 2005. The absence of new juveniles or adults in the spring of 2005 (M. Saunders unpubl. data) suggests that settlement was not occurring at that time.

There was a weak, negative relationship between stratification and abundance of settlers at Lodge, but not at Paddy's Head, perhaps because of greater surface mixing due to waves at the more exposed location. While other studies (Yoshioka 1973, Bernstein & Jung 1979, Scrope-Howe & Jones 1986) have attributed seasonal bathymetric patterns in larvae or settlers to stratification, our results were equivocal. We observed lower settlement at 4 m than at 8 and 12 m, both in the presence and in the absence of stratification. Significant differences in settler abundance across depths were observed on 19 October 2005 and in early September 2006, when the water column had been well-mixed for over 1 wk. Although stratification probably has an effect on bathymetric patterns of settler abundance, variables other than temperature can also influence larval abundance in the water column. Many other abiotic (light, salinity, density structure) and

biotic (predators, prey) variables that vary across bathymetric gradients can also influence zooplankton distributions (Scrope-Howe & Jones 1986).

Fluctuations in temperature were less important than stratification in explaining abundance of settlers. Peak abundances in both years occurred when water temperatures had been stable ($T' < 0.7^{\circ}\text{C}$) for periods >1 wk. However, early (May 2006) and late (September 2005) seasonal increases in the abundance of settlers occurred when water temperature was fluctuating widely due to wind-driven upwelling. It is possible that changes in abundance of settlers coincided with sharp changes in temperature caused by cross-shelf directional movements in the water column (e.g. upwelling or downwelling). Such mechanisms of larval transport have been previously suggested. In California, cyphonautes were more abundant on the shoreward, colder side of fronts than on the warmer, offshore side (Pineda 1999). Conversely, Yoshioka (1973) hypothesised that upwelling of cold, nutrient-rich, larval-deficient deep water, pushed larval-rich surface water offshore, resulting in a decrease in larval abundance and settlement. On the east coast of North America, the effect of oceanographic features on larval supply of *Membranipora membranacea* has not been investigated, although the importance of wind- and buoyancy-driven flow for larval transport of other invertebrates and fish is recognised (Epifanio & Garvine 2001).

The strong relationship between the temperature regime and the abundance of settlers may not necessarily be causative, because a number of factors can co-vary with temperature. For example, increased temperatures may be a result of decreased exchange between the bay and the open ocean, resulting in increased larval retention, and thus increased local settlement. Similarly, abundance of phytoplankton is related to temperature, and may have affected growth rate of adult colonies (O'Dea & Okamura 1999) and resulted in increased larval production. Abundance of *Membranipora membranacea* in Nova Scotia has fluctuated widely since its introduction in the early 1990s (R. E. Scheibling unpubl. data), suggesting that increases in abundance in 2006 were not simply due to expansion of this introduced population.

The seasonal patterns in the abundance of settlers of *Membranipora membranacea* in Nova Scotia differ from those of larval supply (larvae or settlers) reported for other regions. In Lough Hyne, Ireland, highest abundances were observed in May and August (Greenwood et al. 2001). On the Isle of Man, cyphonautes occurred in plankton samples from February to November, and settlers were abundant from June to August (Eggleson 1972). In Southern California, larval and new settler abundance on the kelp *Macrocystis*

pyrifera peaked in late winter and was lowest in late summer (Bernstein & Jung 1979, Yoshioka 1982). At Friday Harbor, Washington, settlement occurred from May until September (Harvell et al. 1990). Between 45 and 55°N, there appears to be a trend towards later seasonal settlement in locations with colder winter temperatures (e.g. spring and summer in Washington and Ireland and autumn in Nova Scotia). Across latitudinal scales, larvae and settlers occur in spring, summer, or early autumn in northern regions (e.g. Washington and Ireland) and in winter in southern regions (Southern California). Similar latitudinal trends in seasonality have been observed for other species, including molluscs and annelids (Lewis 1986), and may be attributed to shorter growing seasons in northern regions, compared to summer heat stress in southern regions (Lewis 1986).

We have documented spatial and temporal patterns in settler abundance of the introduced bryozoan *Membranipora membranacea* in Nova Scotia, and demonstrated that GDD, a measure of thermal history, explains most of the variance in settler abundance. Settlement is considered a critical stage in the life history of benthic invertebrates, and has important consequences in population dynamics. For an introduced invertebrate, such as *M. membranacea*, increases in settlement may have important ecological effects. At Friday Harbor, *M. membranacea* larvae that settled earlier in the season lived longer (Harvell et al. 1990). Furthermore, growth rate is positively related to temperature (Lutaud 1961, Menon 1972) and size, so warm temperatures may allow colonies to reach larger sizes. Our results suggest a possible synergism between increased temperatures caused by climate change and introduced invasive marine species. This may have a considerable effect on kelp beds in Atlantic North America, where colonies can reach sufficient sizes to defoliate kelp beds during fall storms (Scheibling et al. 1999). To further understand the mechanisms regulating settlement and, thus, the population dynamics of this species, the relationship between large-scale oceanographic events and larval supply of *M. membranacea* in its native and introduced regions clearly merits further investigation.

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