High recruitment of the introduced bryozoan *Membranipora membranacea* is associated with kelp bed defoliation in Nova Scotia, Canada

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ABSTRACT: For many organisms, the magnitude of recruitment of settlers into the juvenile population is a key life-history parameter, which has pronounced effects on population dynamics. However, for benthic colonial organisms, abundance may also be highly influenced by availability of space, growth rate, senescence, and mortality. On the southern shore of Nova Scotia, Canada, outbreaks of the introduced epiphytic bryozoan *Membranipora membranacea* on kelps have occurred periodically since 1992. We monitored the abundance, size distribution, and percent cover of *M. membranacea* colonies on blades of the kelp *Saccharina longicruris* at 2 sites in St. Margarets Bay, Nova Scotia, from July 2005 to November 2006. Following a warm winter, juvenile and adult colonies occurred earlier and were an order of magnitude more abundant in 2006 compared to 2005. The percent cover of *M. membranacea* on kelp was higher in 2006 compared to 2005 in summer and early autumn, but there was no difference between both years in late autumn. Colonies were larger in summer 2006 than in 2005, but were smaller in late autumn in 2006, suggesting that large colonies had been lost due to kelp blade breakage. By November 2006, there was a 70 % decrease in the canopy cover of kelp on the benthos, despite a similar frequency and magnitude of storms compared to the previous year. We propose that outbreaks of *M. membranacea* in the northwest Atlantic are the result of periods of early and high settlement and recruitment. By causing kelp defoliation, these outbreaks can have a pronounced ecological effect on kelp beds.

KEY WORDS: Recruitment · Population dynamics · Introduced species · Benthic colonial organisms · Kelp beds · *Membranipora membranacea*

INTRODUCTION

For species with intermittent, ephemeral populations, the processes regulating population dynamics are complex and often poorly understood (Harvell et al. 1999). For many species, the process of recruitment, defined here as the movement of settlers into the juvenile population, is a key determinant of the size of the adult population (Caley et al. 1996). However, variations in recruitment do not always affect the abundance of the adult population directly. For example, if factors such as food or substratum availability are limiting, or if predation increases disproportionately at high population abundances, then high recruitment may not result in high adult abundance; rather, these density-dependent negative feedbacks can cause populations to increase when small and to decrease when large (Turchin 1999, Hixon et al. 2002). A population is regulated when it persists over many generations, is bounded above zero and below a finite size, and has a tendency to increase when small and to decrease when large (Murdoch 1994, Turchin 1999). If variations in the abundance of the adult population track variations in the abundance of settlers and juveniles, then we may conclude that recruitment regulates the adult population (Caley et al. 1996). However, if the adult population remains relatively stable despite variations in the juvenile population, other factors (such as resource limitation) likely control the population (Caley et al. 1996). For benthic colonial species, where abundance

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may be quantified either as the number or expanse of colonies (surface area, volume, or percent cover on the substratum), the role of recruitment in regulating the population is less clear. For example, high percent cover of a colonial organism may be obtained either by a small number of large colonies or a large number of small colonies. Furthermore, colonial organisms can shrink or senesce, causing a decrease in percent cover (Harvell et al. 1990).

The epiphytic colonial bryozoan *Membranipora membranacea* was first observed in the Gulf of Maine in 1987 (Lambert et al. 1992), where it was presumably introduced via ballast water from European populations (Schwaninger 1999). It was first observed on the southern shore of Nova Scotia in 1992 (Scheibling et al. 1999), and it has since established populations along the coast of Nova Scotia, New Brunswick (M. Saunders pers. obs.), and Newfoundland (C. McKenzie pers. comm.). Larvae (cyphonautes) of *M. membranacea* settle preferentially on the proximal (meristematic) ends of blades of laminarian algae (kelp) (Seed 1976) and then bud asexually to form encrusting colonies. In Nova Scotia, *M. membranacea* larvae begin to settle between May and July and reach peak settlement in September or October (Saunders & Metaxas 2007). In St. Margarets Bay, Nova Scotia, the abundance of *M. membranacea* settlers was significantly related to growing degree-day (GDD), an index of thermal history, and was an order of magnitude higher after a significantly warmer winter (Saunders & Metaxas 2007).

Presence of *Membranipora membranacea* colonies on kelp reduces the survival of the host (Levin et al. 2002) and greatly exacerbates the natural seasonal cycle of kelp bed decline in autumn. Colonies can cause kelp blades to become brittle (Dixon et al. 1981) and to break during periods of intense wave action (qualitatively described in Lambert et al. 1992, Scheibling et al. 1999), although the specific structural changes in the kelp tissue responsible for breakage have not been identified. Defoliation (partial or complete removal of kelp blades) results in decreased benthic canopy cover of kelps, but blades can regenerate the following spring if the basal meristem remains intact (Johnson & Mann 1988). Complete removal of kelp blades leaves only stipes and holdfasts, which cannot regenerate and subsequently rot (described in Scheibling et al. 1999), resulting in decreased abundance of individual kelps. By defoliating kelp beds, *M. membranacea* facilitates the introduction and establishment of monospecific stands of the green algae *Codium fragile* ssp. *fragile* (Levin et al. 2002, Scheibling et al. 1999, Scheibling & Gagnon 2006).

Within the introduced range, the abundance of *Membranipora membranacea* has typically been measured as percent cover on algae (e.g. Berman et al. 1992,

Lambert et al. 1992, Harris & Mathieson 1998, but see Saier & Chapman 2004). However, percent cover of colonial organisms could be influenced either by variations in settlement and recruitment or by variations in colony growth and survival. In the northwest Atlantic, the role of recruitment of *M. membranacea* in determining the abundance of the adult population is unknown, and in Nova Scotia, the role of *M. membranacea* outbreaks in kelp defoliation has been qualitatively described (Scheibling et al. 1999, Chapman et al. 2002), but not quantified. Furthermore, extratropical storms periodically impact the region during the late summer and autumn, when *M. membranacea* is most abundant, and it is unknown whether losses of kelp attributed to *M. membranacea* can alternatively be explained by abnormally large wave events.

In previous studies, we observed that settlement of *Membranipora membranacea* larvae on the numerically dominant kelp *Saccharina longicruris* (formerly *Laminaria longicruris*, Lane et al. 2006) at 2 sites in St. Margarets Bay, Nova Scotia, occurred earlier and was an order of magnitude higher in 2006 than in 2005 (Saunders & Metaxas 2007). We hypothesize that, in years of earlier and higher *M. membranacea* settlement and recruitment, we will also observe higher percent cover of the bryozoan on kelp, earlier seasonal occurrence of large colonies, and increased loss of kelp in autumn. In the present study, we examine the abundance of 'juvenile' (2 to 5 zooid rows) and 'adult' (>5 zooid rows) colonies of *M. membranacea* on *S. longicruris*, at the same 2 sites in St. Margarets Bay, from July 2005 to November 2006. Our objectives are to compare spatial (m to km) and temporal (wk to yr) patterns in: (1) the abundance of juvenile and adult colonies (no. colonies m^{-2} kelp); (2) the percent cover of *M. membranacea* on kelp; (3) size-frequency distributions of *M. membranacea*; and (4) the abundance (ind. m^{-2}) and canopy cover (%) of the host kelp substratum. Because changes in kelp cover and abundance could alternatively be attributed to the occurrence of unusually intense storms, we also examine the frequency and magnitude of large wave events (indicated by significant wave height) in autumn of each year.

MATERIALS AND METHODS

Study area. We sampled 2 sites on the southern shore of Nova Scotia, Canada (Fig. 1), both characterized by granitic substratum with extensive kelp beds. Lodge (L) (44° 33′ 3″ N, 64° 1′ 9″ W) is on the western shore of St. Margarets Bay and has a moderately steeply sloping substratum dominated by granite outcroppings, large boulders, and cobbles. Paddy's Head (PH) (44° 31′ 6″ N, 63° 57′ 2″ W) is on the eastern shore
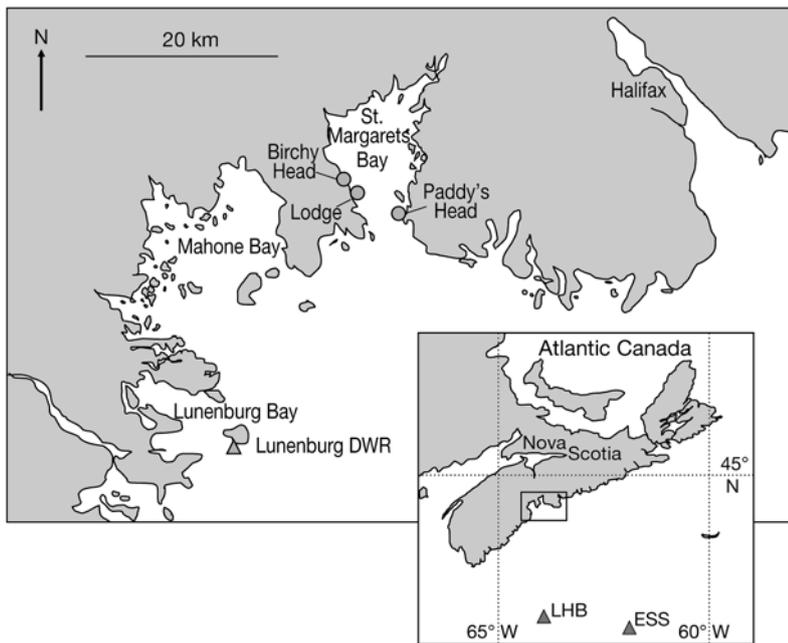
Fig. 1. Study area on the southern shore of Nova Scotia, Canada, with the 2 sampling sites in St. Margarets Bay, Lodge and Paddy's Head. Additional data were obtained from Birchy Head to extend the length of the temperature time series. Significant wave height data were obtained from the directional wave rider buoy (DWR) located at the mouth of Lunenburg Bay and from the East Scotia Slope (ESS) and La Have Bank (LHB) buoys located offshore

did not grow, indicating that the length of time between collection and processing did not affect results. The calcium carbonate zooecia of deceased zooids remained present on the kelp, so any mortality that may have occurred in the lab did not affect our measures of abundance.

Quantification of *Membranipora membranacea* colonies. Juvenile colonies were defined as any colony with 2 to 5 rows of zooids from the ancestrula to the outer edge of the colony. Based on laboratory growth experiments at temperatures of 10 to 14°C, juvenile colonies in this size range were ~2 to 3 wk old (M. Saunders unpubl. data) and unlikely to have been reproductive. Adult colonies were defined as any colony with >5 rows of zooids. Although we did not assess reproductive status, all colonies within the adult size range could have potentially been capable of reproduction if crowded by conspecifics or grazed upon (Harvell & Grosberg 1988). Populations of *M. membranacea* in Nova Scotia are strongly seasonal, with few colonies surviving the winter. As a result, most adult colonies would have settled 3 wk to 8 mo before sampling.

Membranipora membranacea colonies were enumerated on each kelp blade, using 15× magnification and LED lighting when necessary. In September 2005, when the number of colonies on each blade increased markedly, and for the remainder of the study period (except for September 2006), a randomly chosen half of 1 side of each kelp blade was subsampled. In September 2006, colonies were subsampled within twelve 25 cm^2 square sections of each blade. The blade was subdivided lengthwise into 6 equidistantly spaced strata, and 2 square sections were haphazardly selected at each stratum, 1 each from the edge and from the centre of the blade. Colonies were enumerated if >50% was within the sampled area. This method of subsampling likely underestimated the abundance of larger (>20 mm) colonies, but since these constituted a small fraction of the total, it would not have significantly affected our total estimate of the abundance of adult colonies. To obtain the number of *M. membranacea* colonies m^{-2} kelp, the number of colonies (juveniles and adults) on each blade was divided by the surface area of the blade.

Surface area of kelp blades. To measure the surface area of the kelp blades, one side of each blade was photographed using an HP Photosmart 435 3.1MP digital camera, and the image was analyzed using SPSS SigmaScan Pro Image Analysis 5.0. Because

near the mouth of St. Margarets Bay and is more exposed to the predominant swells than Lodge. Sampling was conducted at the site's outer wall, where the substratum is granite bedrock that slopes steeply towards a sandy bottom at ~18 m depth. Both sites were permanently marked along a transect perpendicular to shore at 4, 8, and 12 m depth relative to chart datum.

Sample collection. Blades of the kelp *Saccharina longicruris* were sampled approximately weekly from 1 July to 4 August 2005 and in September 2005, and approximately monthly from October 2005 to November 2006. On each sampling date, approximately 10 blades were haphazardly collected from each depth at each site. The length of kelp blades ranged from 13 to 362 cm (91 ± 33 cm, mean ± SD, n = 1240), but most blades were selected to be between 80 and 150 cm long. The width of blades ranged from 6 to 86 cm (23 ± 8 cm). Both sites were usually sampled on the same date, but if this was not possible due to weather or logistical difficulties, the second site was sampled within 2 to 8 d of the first. Kelp blades were kept in plastic tubs without seawater until arrival at Dalhousie University's Aquatron facility (3 to 6 h after collection), where they were kept in aquaria with running ambient seawater until processing was completed (1 to 8 d). While in the aquaria, small colonies (settlers and juveniles)

the blades of *Saccharina longicruris* are extensively crenulated, we measured the ratio of photographed surface area to flattened surface (obtained by cutting the blade into small pieces) for 9 kelps from each depth, at each site, in November 2005. The average ratio of surface area for flattened and crenulated blades was calculated for each depth at each site, and these values were used to correct the kelp surface area values for all other sampling dates. Although this ratio most likely varies seasonally, variations in the 'correction' of kelp area are far smaller than the seasonal changes in abundance of the bryozoan, thus not affecting the overall patterns.

Percent cover of *Membranipora membranacea* on kelp. The surface area of *M. membranacea* on each kelp blade was obtained for summer (August), early autumn (September), and late autumn (November) of both 2005 and 2006, by tracing all the colonies on one side of the blade onto clear plexiglass and then photographing and measuring the tracings with image analysis as above. Percent cover of *M. membranacea* on kelp was calculated by dividing the surface area of bryozoan cover by the surface area of the kelp blade and multiplying by 100.

Size-frequency distributions of bryozoan colonies. The maximum diameter ('length') of each colony was measured in August and November 2005 and 2006 using a clear plastic ruler (accuracy 1 mm). For colonies <3 mm, the maximum number of zooid rows was counted (measured from the ancestrula to the outer edge of the colony; incomplete zooids were counted as '0.5'), and the length of the colony was calculated using the equations:

Summer (measured in July 2005):
$$L = 0.43e^{0.40Z}, \; n = 363, \; R^2 = 0.90 \tag{1}$$

Autumn/winter (measured in November 2005):
$$L = 0.59e^{0.28Z}, \; n = 89, \; R^2 = 0.93 \tag{2}$$

where L is the length in mm, and Z is the number of zooid rows.

Quantification of the kelp population. The population of the host kelp *Saccharina longicruris* was measured by: (1) calculating the canopy cover (%) of kelp on the benthos from digital images and (2) enumerating kelps in quadrats along transects. To minimize the impact of our previous collections on the measured canopy cover of kelp, photos were obtained and quadrats were enumerated in an area adjacent to the region from which kelps were collected for *Membranipora membranacea* samples.

The canopy cover (%) of *Saccharina longicruris* on the benthos during autumn was calculated using digital images (from Lodge only) on each of 2 sampling dates in 2005 and 2006 (11 October 2005, 17 November 2005, 9 October 2006, and 19 November 2006). Images

were taken from 1.5 m above and perpendicular to the benthos at 4 and 8 m depth. Data from 12 m depth were not available due to low-light conditions. In 2005, frames were grabbed randomly using iMovie from 30 m long video transects conducted with a Sony TR101 digital camera in an Amphibico housing. In 2006, still images were taken haphazardly along transects of approximately 30 m length with a Canon S50 digital camera in a Canon DC300 housing. To obtain canopy cover (%) of kelp projected on the substratum, the area in each digital image occupied by kelp was measured using SigmaScan Pro software, divided by the surface area of the photo, and multiplied by 100.

Abundance of all established *Saccharina longicruris* individuals (>20 cm) was measured in mid-June of 2005 and 2007 (before and after the study period, respectively). The number of kelps within randomly placed 0.25 m² quadrats was determined along 30 m transects at each of 3 depths (4, 8, and 12 m) at both study sites (Paddy's Head and Lodge).

Wave measurements. To evaluate the potential effect of storm-induced wave action on the canopy cover of kelp, we compared the frequency and intensity of storms occurring in autumn (from 1 September to 30 November) between 2005 and 2006. Hourly measures of nearshore significant wave height (H_s) were obtained from the Centre for Marine Environmental Prediction directional waverider (DWR) buoy (www.cmep-av.ocean.dal.ca), located at the mouth of Lunenburg Bay, ca. 30 km SW from the mouth of St. Margarets Bay (Fig. 1). To extend the length of the wave data series, additional data were obtained from offshore buoys (East Scotia Slope [ESS] and La Have Bank [LHB]) operated by the Environment Canada Marine Environmental Data Service (www.meds-sdmm.dfo-mpo.gc.ca). The locations of all 3 buoys are more wave exposed than either of the study sites, but the wave data were used to compare relative temporal patterns between years, rather than spatial patterns in H_s. Because wave events in the region are caused by large-scale, wind-driven, meteorological events, the temporal patterns in H_s would have been relatively similar between Lodge and Paddy's Head.

Temperature measurements. Temperature was measured at 10 min intervals from 1 July 2005 to 30 June 2007 using HOBO® Pendant Data Loggers (Onset Computer Corporation) (accuracy ± 0.47°C). The loggers were attached to the permanent site markers at 4, 8, and 12 m depth at both sites. To extend the length of the temperature series, additional data, obtained using Onset HOBO® StowAway TidbiT loggers (accuracy ± 0.2°C) at 30 min intervals from 1 January 2005 to 1 July 2005 at 8 m depth at Birchy Head (Fig. 1), were included. The temperature data series were smoothed using a 7 d moving average.

Statistical analyses. To examine the overall patterns in the abundance of juvenile and adult *Membranipora membranacea* colonies between years, raw data were pooled across depths for each site, and the effects of year (2005 and 2006) and site (Lodge and Paddy's Head) were examined using 2-way ANOVA for each size class (juveniles and adults). Because the measured peak in abundance occurred earlier in 2006 than in 2005, comparisons were made between dates of highest measured abundance in each year (juveniles: September 2006 with November 2005 for both sites; adults: November 2005 with November 2006 for Lodge, November 2005 with September 2006 for Paddy's Head).

The effects of depth (4, 8, and 12 m) and site (Lodge and Paddy's Head) on the abundance of colonies (juveniles and adults) were examined using 2-way ANOVA for each of 4 different sampling dates during the periods of peak abundance (September and November in both 2005 and 2006) (Table 1). Post hoc multiple comparisons were done with Tukey's tests.

The effect of year (2005 and 2006) on the percent cover of *Membranipora membranacea* growing on kelp was examined for August, September, and November at each site (Paddy's Head and Lodge) using Student's *t*-test for unequal variances.

Temporal effects of date (October and November in 2005 and 2006) on patterns in canopy cover of the kelp *Saccharina longicruris* on the benthos were examined for each depth using ANOVA. The effects of year (2005 and 2007) on the abundance of *Saccharina longicruris* (ind. 0.25 m^{-2}) were examined using Student's *t*-test for unequal variances for each depth (4, 8, and 12 m) at both sites (Paddy's Head and Lodge).

For all analyses, site was treated as a fixed factor, because both sites were selected specifically based on location (opposite sides near the mouth of St. Margarets Bay), bathymetry, substratum, and algal compo-

sition. Depth was treated as a fixed factor because the depths were selected specifically to span the depth range (shallow, intermediate, and deep) over which kelp is commonly found in the region. Year was treated as a fixed factor because in one year (2005), larval settlement of *Membranipora membranacea* was low, and in the other (2006), larval settlement was high (Saunders & Metaxas 2007). Date was a fixed factor because each date corresponded to either mid- (October) or late-autumn (November).

When necessary, abundances (no. of *Membranipora membranacea* juvenile and adult colonies m^{-2} kelp and of kelp m^{-2} benthos) were log(x+1)-transformed to meet assumptions of normality as detected by the Shapiro-Wilk test and homogeneity of variances as detected by Levene's test. Cover data (% *M. membranacea* on kelp and % *Saccharina longicruris* on the seafloor) were arcsine square-root transformed. Instances where the assumption of homogeneity of variance could not be met through data transformations are indicated (Fig. 6, Tables 2 & 3). In some cases, data could not be transformed to meet the assumption of normality; however, ANOVA is robust to deviations from normality (Underwood 1997).

Length-frequency distributions of *Membranipora membranacea* colonies were compared between years for each month (August and November) using Pearson χ^2 tests. To standardize the number of observations on each date, counts (C) within each bin (5 mm bins for August, 10 mm bins for November) were divided by the number of observations on each respective sampling date. The standardized counts (C_s) were then log($100 \times C_s + 1$) × 100 transformed to even the influence of the relatively rare large colonies with that of the more abundant small ones.

To examine whether unusually large waves could have been responsible for observed decreases in kelp canopy cover, we examined the frequency and intensity of wave events during the intervals when canopy cover on the benthos was measured at Lodge (11 October to 17 November 2005 and 9 October to 19 November 2006). Because data from the inshore buoy (Lunenburg) were incomplete for both years, analyses of significant wave height (H_s) were conducted for data from the offshore buoy at ESS. Missing values in 2006 were replaced with values from the LHB buoy, corrected using:

$$H_{s(ESS)} = 0.832\, H_{s(LHB)} + 0.013 \qquad (3)$$

where H_s is the significant wave height at ESS and LHB, respectively (n = 1020, R^2 = 0.80, p < 0.001). This relationship was obtained by linear regression of concurrently available data from ESS against data from LHB in 2006. To identify the periods of most energetic waves, we calculated the H_s delineating the top 10th

Table 1. *Membranipora membranacea*. Dates and sample sizes included in 2-way ANOVA examining: (1) spatial effects (site and depth) and (2) spatial (site) and temporal (date) effects on the abundance of juvenile and adult colonies. n: number of *Saccharina longicruris* blades collected from each depth (4, 8, and 12 m). L: Lodge; PH: Paddy's Head

| Sampling date | Site | n | | |
		4 m	8 m	12 m
20 Sep 2005	L	10	10	10
22 Sep 2005	PH	10	10	10
29 Nov 2005	L	9	10	10
29 Nov 2005	PH	10	9	10
9 Sep 2006	L	8	8	8
14 Sep 2006	PH	8	8	8
19 Nov 2006	L	10	10	9
13 Nov 2006	PH	10	8	7

percentile of the distribution of wave heights for all waves measured at ESS from 1 September to 30 November in 2005 and 2006. A 'large wave event' occurred when H_s was in the top 10th percentile. The duration of each event was the number of consecutive hours over which the H_s remained in the 10th percentile. For the periods of 11 October to 17 November 2005 and 9 October to 19 November 2006, the effect of year (2005 and 2006) was examined on: (1) the average H_s of all waves; (2) the average H_s of all large wave events; and (3) the duration (h) of each large wave event, using the Mann-Whitney U-test. Statistical analyses were conducted using JMP IN 5.1 and SPSS 13.0.

RESULTS

Interannual differences in the abundance of *Membranipora membranacea*

Juvenile colonies. The onset and peak of abundance of juvenile colonies was 1 to 2 mo earlier in 2006 compared to 2005 (Fig. 2A). Maximum abundance was observed in November in 2005 and in September in 2006. At the peak of the season in each year (November 2005 and September 2006), juvenile colonies were significantly more abundant in 2006 than in 2005 (Table 2). There was no difference in the abundance of juvenile colonies between sites.

Adult colonies. There was a similar seasonal shift in the abundance of adult colonies between 2005 and 2006 (Fig. 2B). At the peak of the season (November 2005, September and November 2006 for PH and L, respectively), adult colonies were significantly more abundant in 2006 compared to 2005 for both sites, and there was no difference between sites for either year (Table 2).

Bathymetric patterns in the abundance of *Membranipora membranacea*

Juvenile colonies. In general, abundance of juvenile colonies was greatest at 12 m and lowest at 4 m, although patterns differed slightly among dates and between the 2 sites (Fig. 3A & B). In autumn of both 2005 and 2006, the abundance of juvenile *Membranipora membranacea* colonies varied between sites and/or among depths for all dates tested, except November 2006 (Fig. 3A,B, Table 3). Abundance of juvenile colonies differed between sites at particular depths,
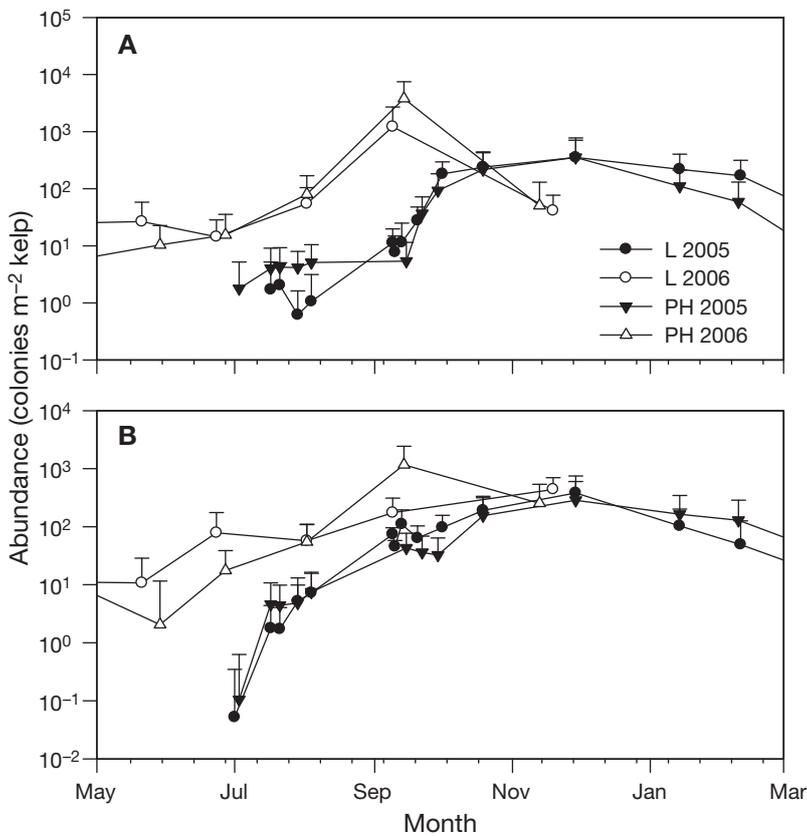

Fig. 2. *Membranipora membranacea* on *Saccharina longicruris*. Abundance (mean + SD, n = 24 to 43) of (A) juvenile colonies and (B) adult colonies on kelp measured at 2 sites in St. Margarets Bay, Nova Scotia (PH: Paddy's Head, L: Lodge), from 1 July 2005 to 10 February 2006 ('2005') and from 21 May to 19 November 2006 ('2006'). Data are pooled across 4, 8, and 12 m depths

Table 2. *Membranipora membranacea*. Results of 2-way ANOVA examining the effects of year and site (pooled across depths) on the abundance of juvenile and adult colonies in St. Margarets Bay, Nova Scotia. Dates of peak abundance for each site used are indicated below for both life-history stages. Multiple comparisons were conducted with Tukey's test. Significant (p < 0.05) effects are highlighted in **bold**

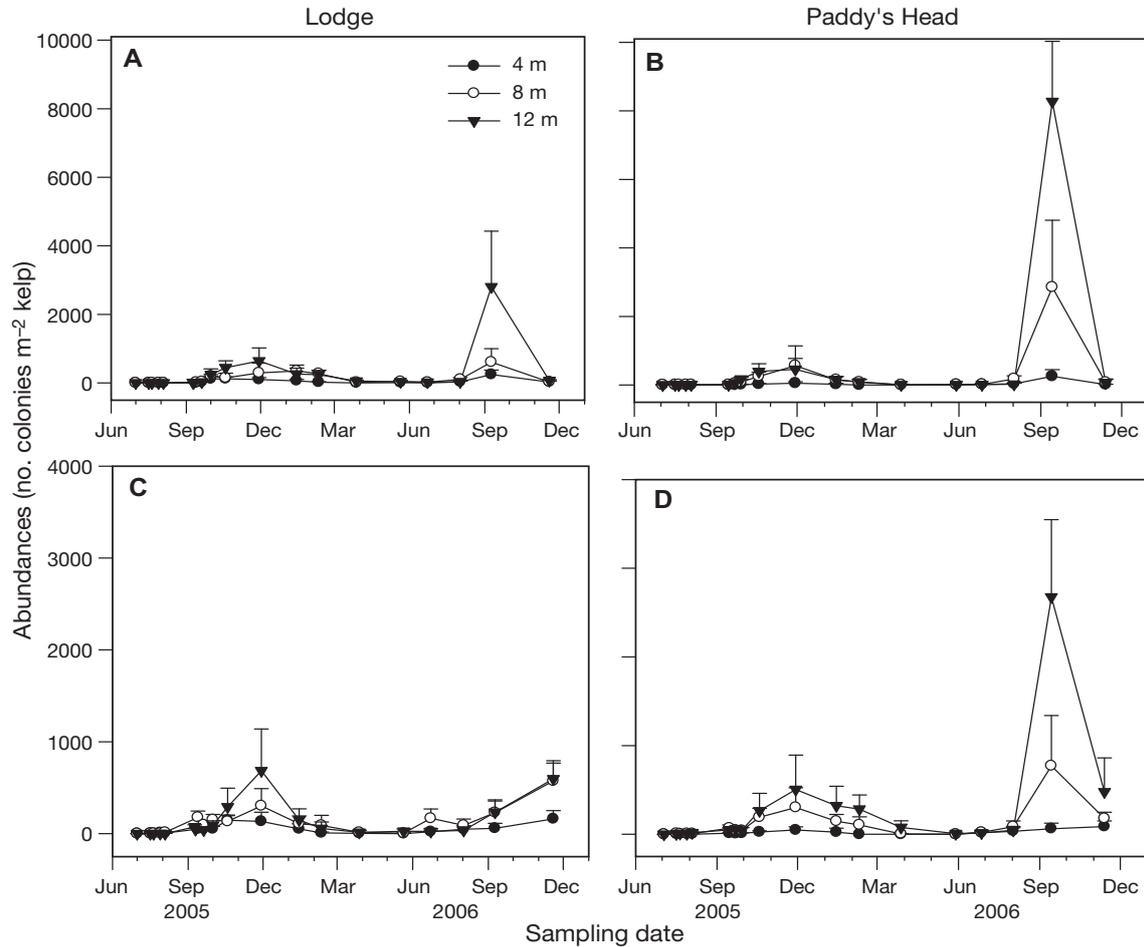| Factor	MS	$F_{(df)}$	p
Juveniles Nov 2005, Sep 2006 (both sites)			
Site	0.078	$0.13_{(1,102)}$	0.71
Year	6.59	$11.7_{(1,102)}$	**<0.001**
Site × Year	0.62	$1.10_{(1,102)}$	0.29
Error	0.56		
Tukey's HSD	2005 < 2006		
Adults Nov 2005 (L & PH); Sep 2006 (PH); Nov 2006 (L)			
Site	0.50	$1.23_{(1,107)}$	0.27
Year	1.90	$4.70_{(1,107)}$	**0.032**
Site × Year	0.34	$0.84_{(1,107)}$	0.36
Error	0.40		
Tukey's HSD	2005 < 2006[a]		
[a]Assumption of homogeneity of variances was not met			

Fig 3. *Membranipora membranacea* on *Saccharina longicruris*. Abundance (mean + SD, n = 7 to 15) of (A,B) juvenile colonies and (C,D) adult colonies on kelp, measured at 3 depths at Lodge and Paddy's Head in St. Margarets Bay, Nova Scotia, from 1 July 2005 to 19 November 2006

but the patterns were not consistent among dates. For example, in September 2005, they were more abundant at Lodge than at Paddy's Head at 4 m, whereas in September 2006, they were more abundant at Paddy's Head than at Lodge at 8 and 12 m.

Adult colonies. Abundance of adult colonies was also generally highest at 12 m and varied between sites and among depths for all dates tested (Fig. 3C,D, Table 3). Abundance was lower at 4 m than at 12 m for all dates at Paddy's Head, and on most dates at Lodge. Abundance was greater at Lodge than at Paddy's Head at 4 m on 3 of the 4 sampling dates while there were no consistent patterns between sites at 8 or 12 m depth.

Percent cover of *Membranipora membranacea* on kelp

The percent cover of *Membranipora membranacea* colonies on the kelp *Saccharina longicruris* was

greater in 2006 than in 2005 in summer (August) and early autumn (September) at both sites (Fig. 4). There was no difference between both years in late autumn (November) at either site.

Length-frequency distributions of *Membranipora membranacea* colonies

Length-frequency distributions were right-skewed and dominated by the smallest colonies (Fig. 5). In summer (August) and autumn (November), the length distributions differed between 2006 and 2005 (August: $\chi^2_{23} = 220$, p < 0.001; November: $\chi^2_{30} = 136$, p < 0.001). In summer, there were more larger colonies present in 2006 than in 2005, whereas the opposite trend was observed for late autumn. In both years, the length distribution varied between August and November and, overall, more large colonies were present later in the season.

Table 3. *Membranipora membranacea.* Results of 2-way ANOVA examining the effects of depth and site on the abundance of juvenile and adult colonies on the kelp *Saccharina longicruris,* measured in September and November in 2005 and 2006. Significant effects (p < 0.05) are indicated in **bold**

		Juveniles			Adults	
Effect	MS	$F_{(df)}$	p	MS	$F_{(df)}$	p
Sep 2005						
Site	4.23	$21.8_{(1,54)}$	<0.001	5.98	$39.6_{(1,54)}$	<0.001
Depth	0.35	$1.79_{(2,54)}$	0.18	0.60	$3.99_{(2,54)}$	0.024
Depth × Site	2.55	$13.1_{(2,54)}$	**<0.001**	2.23	$14.8_{(2,54)}$	**<0.001**
Error	0.19			0.15		
Tukey's HSD	(4) L > PH; (8, 12) L = PH			(4) L > PH; (8, 12) L = PH[a]		
	(L) 4 = 8 = 12; (PH) 4 < 8 = 12			(L) 4 = 8 = 12; (PH) 4 < 8 = 12		
Nov 2005						
Site	0.17	$0.31_{(1,52)}$	0.58	0.81	$5.45_{(1,52)}$	**0.023**
Depth	3.05	$5.66_{(2,52)}$	**0.006**	1.37	$9.24_{(2,52)}$	**<0.001**
Depth × Site	1.04	$1.93_{(2,52)}$	0.15	0.13	$0.89_{(2,52)}$	0.42
Error	0.54			0.15		
Tukey's HSD	4 = 8 < 12[a]			L > PH[a]		
				4 = 8, 8 = 12, 4 < 12		
Sep 2006						
Site	<0.001	$0.10_{(1,42)}$	0.75	<0.001	$<0.001_{(1,42)}$	0.998
Depth	2.23	$32.9_{(2,42)}$	<0.001	2.30	$7.42_{(2,42)}$	0.002
Depth × Site	0.55	$8.12_{(2,42)}$	**0.001**	1.16	$3.83_{(2,42)}$	**0.030**
Error	0.07			0.31		
Tukey's HSD	(4) L = PH; (8, 12) L < PH			(4, 8) L = PH; (12) L < PH		
	(L, PH) 4 < 8 < 12			(L, PH) 4 < 8 = 12[a]		
Nov 2006						
Site	1658	$0.52_{(1,48)}$	0.47	0.43	$9.22_{(1,48)}$	0.004
Depth	4955	$1.55_{(2,48)}$	0.22	1.18	$25.4_{(2,48)}$	<0.001
Depth × Site	5545	$1.74_{(2,48)}$	0.19	0.34	$7.37_{(2,48)}$	**0.002**
Error	3193			0.05		
Tukey's HSD				(4, 8) L > PH; (8,12) L = PH		
				(L) 4 < 8 = 12; (PH) 4 < 8 = 12		

[a]Assumption of homogeneity of variances was not met

Interannual differences in the kelp population

Canopy cover of kelp on the benthos. For both measured depths (4 and 8 m), canopy cover of *Saccharina longicruris* on the benthos at Lodge was not significantly different between October 2005, November 2005, and October 2006 (Fig. 6). However, at both depths, there was a significant decrease in canopy cover of kelp by 19 November 2006.

Abundance of kelp. *Saccharina longicruris* was significantly more abundant in June 2005 than in June 2007 at each location (depth within site), except at 12 m at Paddy's Head, where no difference was detected (Fig. 7).

Environmental conditions

Significant wave height. Waves at the inshore buoy at Lunenburg were generally smaller than at the offshore buoys. At the offshore buoy, for both seasons combined, the H_s that delineated the top 10th percentile of wave heights measured from 1 September to 30 November in both 2005 and 2006 was 3.52 m (Fig. 8). During the sampling period, the maximum wave height was greater in 2005 (7.64 m) than in 2006 (7.38 m).
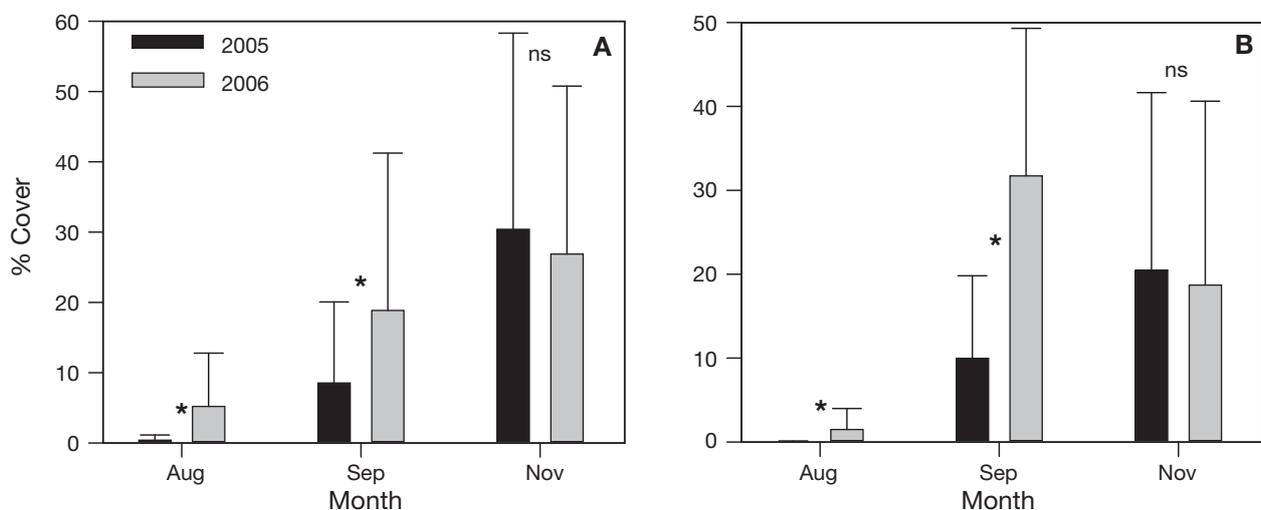

Fig. 4. *Membranipora membranacea* on *Saccharina longicruris.* Percent cover of *M. membranacea* on kelp (mean + SD, n = 24 to 33), measured at (A) Lodge, (B) Paddy's Head, in August, September and November in 2005 and 2006. *Significant effects of year as detected by Student's *t*-test for unequal variances (Lodge: Aug: $t_{(33.2)} = -4.71$, p < 0.001; Sep: $t_{(38.3)} = -2.58$, p = 0.014; Nov: $t_{(53.7)} = 0.645$, p = 0.52; Paddy's Head: Aug: $t_{(30.9)} = -4.85$, p < 0.001; Sep: $t_{(46.6)} = -5.67$, p < 0.001; Nov: $t_{(54.9)}=0.09$, p = 0.92). ns: not significant
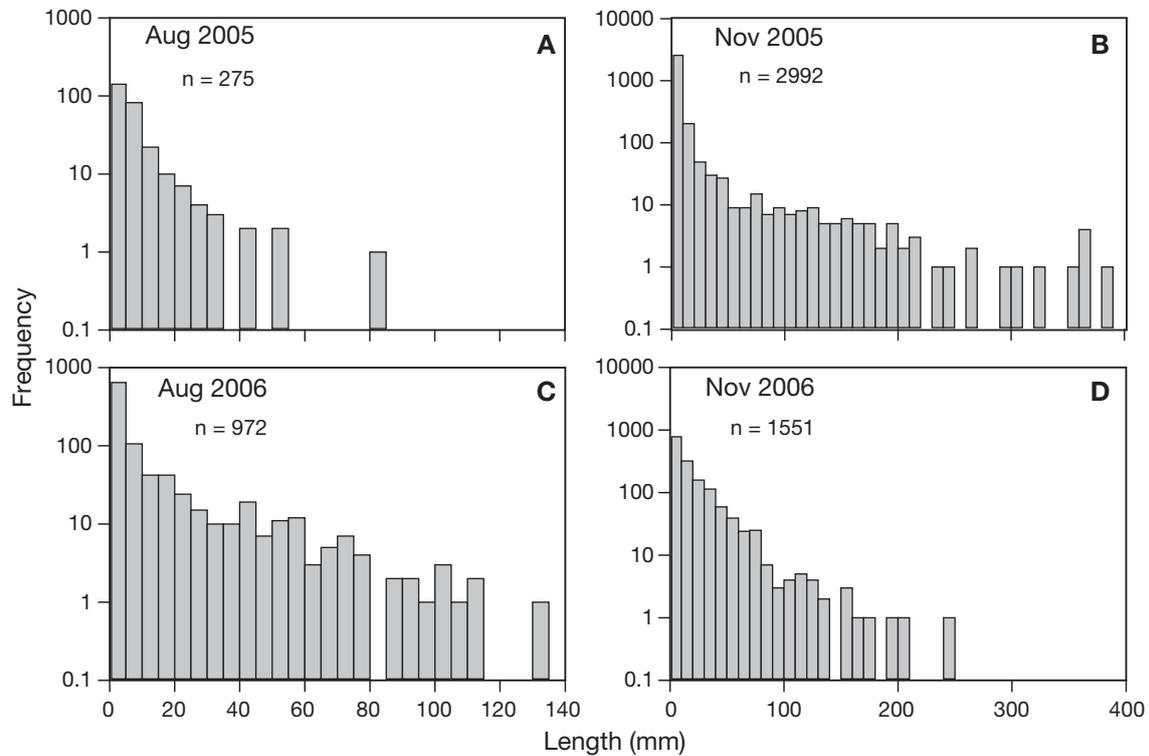
Fig. 5. *Membranipora membranacea* on *Saccharina longicruris.* Length-frequency distributions of colonies on kelp blades (pooled across sites and depths) sampled in St. Margarets Bay, Nova Scotia, in (A) August 2005, (B) November 2005, (C) August 2006; (D) November 2006. Data are in 5 mm bins for August and in 10 mm bins for November

Average significant wave height was also greater during the sampling period in 2005 (2.49 ± 1.25 m, mean ± SD, n = 879) than in 2006 (1.99 ± 1.20 m, n = 942) ($U = 3.0 \times 10^5$, p < 0.001). However, the H_s of the top 10th percentile of waves (≥3.52 m) was 0.3 m larger during the sampling period in 2006 (4.82 ± 0.93 m, n = 99) than in 2005 (4.53 ± 0.92 m, n = 164) ($U = 6490$, p = 0.006). Within the sampling period, the average duration of large wave events was not significantly different between years (2005: 11.6 h, n = 22; 2006: 12.4 h, n = 12; $U = 95.5$, p = 0.185), and the longest large wave event occurred in 2005 (84 h compared to 26 h in 2006). Large wave events were more frequent in 2005 than in 2006 (22 and 12, respectively).

Temperature. Temperature was strongly seasonal (Fig. 9), with the warmest weekly temperatures (18°C) observed in September and the coldest temperatures (0 to 2°C) observed in January, February, and March in both years. The water was significantly colder in winter 2005 than in winter 2006 (Saunders & Metaxas 2007). The water column was periodically stratified between 4 and 12 m from May until October, with a temperature difference of up to 8°C. Large fluctuations in temperature (due to wind-driven processes) were observed in summer and early autumn of both years.

DISCUSSION

Earlier and increased settlement of *Membranipora membranacea* in 2006 (Saunders & Metaxas 2007) resulted in correspondingly earlier and higher recruitment and abundance of adult colonies compared to the previous year. This seasonal shift allowed the presence of very large (>100 mm) colonies, and a high percent *M. membranacea* cover on kelp, to occur earlier in the season. In 2006, the canopy cover of the host kelp *Saccharina longicruris* had declined by 70% by late autumn compared to both earlier in the autumn and to the previous year. Similarly large decreases in canopy cover of kelp during this period were also observed at other sites within 50 km of St. Margarets Bay (M. Saunders pers. obs., R. E. Scheibling pers. comm.). No significant decreases in kelp canopy cover were observed in autumn 2005, when abundances of *M. membranacea* settlers, recruits, and adults were an order of magnitude lower than in 2006. The distribution of colony lengths included larger colonies in late autumn 2005 compared to 2006, suggesting that, in the second year, kelp blades with the largest colonies had broken off. The loss of kelp was also indicated by a decrease in the abundance of individual kelps between June 2005 and June 2007, suggesting that kelp blades broke off below the meristem and that the mature
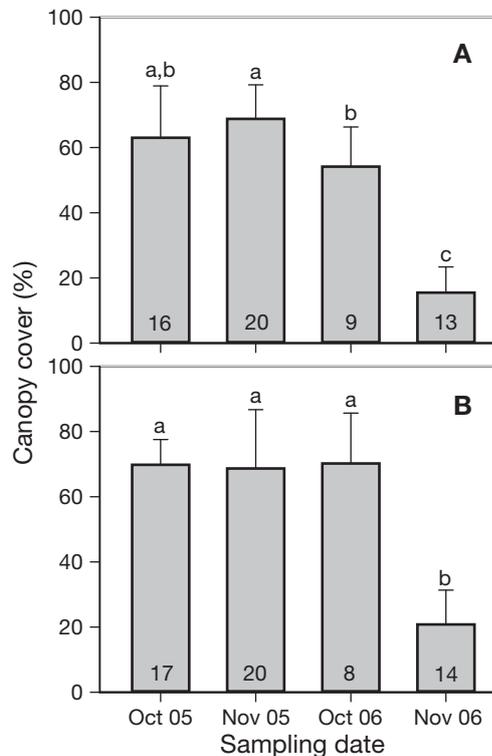
Fig. 6. *Saccharina longicruris*. Canopy cover (%) of kelp on the seafloor (mean + SD, n indicated in bars), measured at 2 depths, (A) 4 m and (B) 8 m at Lodge, St. Margarets Bay, Nova Scotia, in October and November 2005 and 2006. Results of ANOVA on the effect of date on canopy cover of kelp at each depth: 4 m: $F_{(3, 54)} = 54.8$, p < 0.001; 8 m: $F_{(3, 55)} = 38.1$, p < 0.001. Different letters (a,b,c) on top of bars indicate significant differences as detected by Tukey's post hoc tests. Data at 8 m did not satisfy the assumption of homogeneity of variances

Fig. 7. *Saccharina longicruris*. Abundance (ind. 0.25 m^{-2}) (mean + SD, n indicated in bars), measured at 2 sites in St. Margarets Bay, Nova Scotia: (A) Lodge and (B) Paddy's Head in June 2005 and 2007, at each of 3 depths (4, 8, and 12 m). *Significant effects of year at each depth within each site as detected by Student's *t*-test for unequal variances (Lodge 4 m: $t_{(24.0)} = 3.66$, p = 0.001, Lodge 8 m: $t_{(27.7)} = 3.29$, p = 0.003, Lodge 12 m: $t_{(17.6)} = 3.12$, p = 0.006; Paddy's Head 4 m: $t_{(24.2)} = 2.74$, p = 0.011, Paddy's Head 8 m: $t_{(28.1)} = 2.07$, p = 0.048, Paddy's Head 12 m: $t_{(12.7)} = 1.78$, p = 0.099. ns: not significant

kelp bed had not recovered by the following summer. We propose that damaging outbreaks of *M. membranacea* in the northwest Atlantic are caused by earlier and increased settlement and recruitment, which permit colonies to achieve larger sizes and to have higher cover on kelps by the time autumn storms impact the region.

During the period of kelp defoliation in autumn 2006, the maximum and average significant wave heights (H$_s$), and the frequency and duration of large wave events, were not greater than during the sampling interval in the previous year. However, the average H$_s$ of the top 10th percentile of waves was 0.3 m larger during this interval in 2006 than in 2005. We consider this difference alone unlikely to have been responsible for such significant reductions in the kelp canopy. Instead, we suggest that the large population of *Membranipora membranacea*, combined with relatively typical fall storms, was responsible for the pronounced reduction in kelp cover.

In general, physical damage to kelp tissue reduces the magnitude of force required to break blades (Duggins et al. 2001), increasing susceptibility to fragmen-
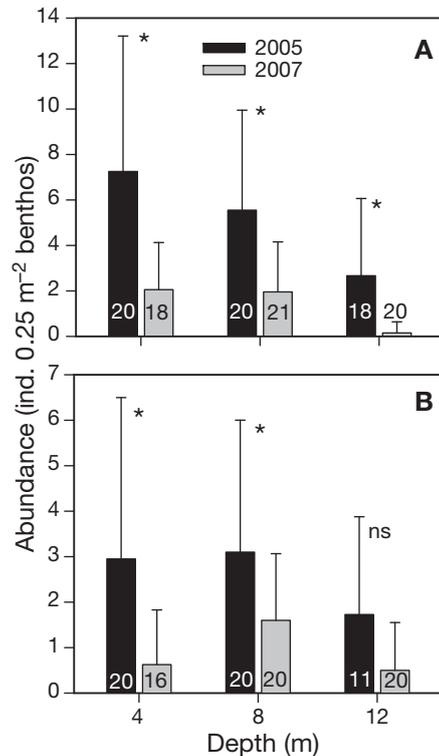
tation by waves. Epiphytic bryozoans can negatively impact their host substratum by a number of mechanisms, including reduced rates of growth (Levin et al. 2002), nutrient uptake (Hurd et al. 2000), and photosynthesis (Cancino et al. 1987). At our study sites, kelp tissue underneath older, larger *Membranipora membranacea* colonies often appeared degraded and, in some cases, had completely senesced, suggesting that the presence of colonies had damaged it. The relationship between *M. membranacea* percent cover, wave force, and kelp breakage remains to be quantified.

In Nova Scotia, the only organisms other than *Membranipora membranacea* capable of significantly decreasing kelp canopy cover are the sea urchin *Strongylocentrotus droebachiensis* and the snail *Lacuna vincta*. Urchins can destructively graze large areas of kelp, leaving behind barrens of rock and coralline algae (Scheibling et al. 1999); however, urchins were extremely rare at both of our study sites. In contrast, snails were occasionally highly abundant at both sites, but they graze only 0.05% of the biomass of the mar-
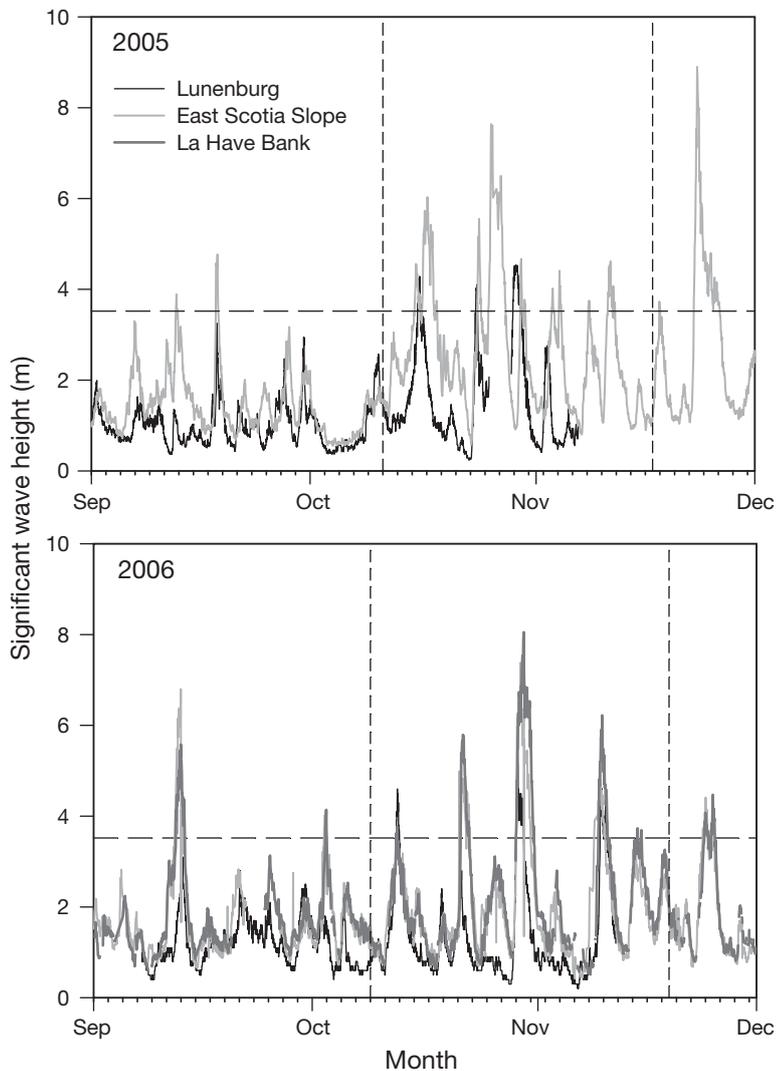
Fig. 8. Significant wave height measured hourly from 1 September to 30 November in 2005 and 2006. Data were obtained from 3 buoys located at the mouth of Lunenburg Bay (inshore, nearest to the study sites), East Scotia Slope (ESS) (offshore), and La Have Bank (offshore). Data from La Have Bank were unavailable for 2005. H_s of the top 10th percentile of waves measured at ESS (>3.52 m) are located above the horizontal long-dashed line. Comparisons of significant wave height, duration of wave events, and frequency of wave events were made for the dates indicated between the vertical-dashed lines for each year, corresponding to the dates when the canopy cover of kelp on the benthos was measured at Lodge

et al. 2002, Scheibling & Gagnon 2006). It is unclear how removal of kelp and replacement by other algal species may affect future bryozoan settlement and recruitment. However, we and others (Harris & Mathieson 1998) have observed *Membranipora membranacea* colonies on a number of other host algal species, albeit in relatively low abundances. If facilitating the removal and exclusion of its preferred substratum during years of high abundance results in decreased bryozoan abundance in the following year, then the population is probably self-limiting. On evolutionary time scales, there will likely be pressure on both *M. membranacea* and its algal substratum to minimize damage to the host, and thus mortality to both (Hepburn & Hurd 2005). This process may in part explain why destructive outbreaks of *M. membranacea* are not typically reported within the native range in the eastern Atlantic. Alternatively, a lack of predators or competitors in the introduced range may allow newly recruited colonies to achieve large sizes, which subsequently results in increased kelp breakage.

In general, harmful outbreaks of newly introduced species may occur because there is a lack, or a mismatch in the timing (Werner et al. 2006), of competitors (Byers 2000), parasites (Torchin et al. 2001), or predators (Wolfe 2002). Within the native range of *Membranipora membranacea* on the west coast of North America, populations are strongly regulated through grazing by specialist nudibranchs (Harvell 1985, Yoshioka 1982) and fish (Bernstein & Jung 1979). In Nova Scotia in contrast, we have not observed any considerable grazing on *M. membranacea* by fish or by the generalist nudibranch *Onchidoris muricata*, which grazes preferentially on the native bryozoan *Electra pilosa* (Pratt & Grason 2007), suggesting that predation is not a significant source of colony mortality. Instead, the primary limiting factor for established *M. membranacea* colonies in Nova Scotia is likely the space available on kelp blades (Yoshioka 1982), which decreases with increasing colony abundance. For example, in late autumn, the same percent cover of bryozoa on kelp was achieved in both years, despite colonies being smaller at that time in the second year.

Underlying the pronounced seasonal and interannual patterns in size and abundance of *Membranipora membranacea* colonies are spatial patterns across
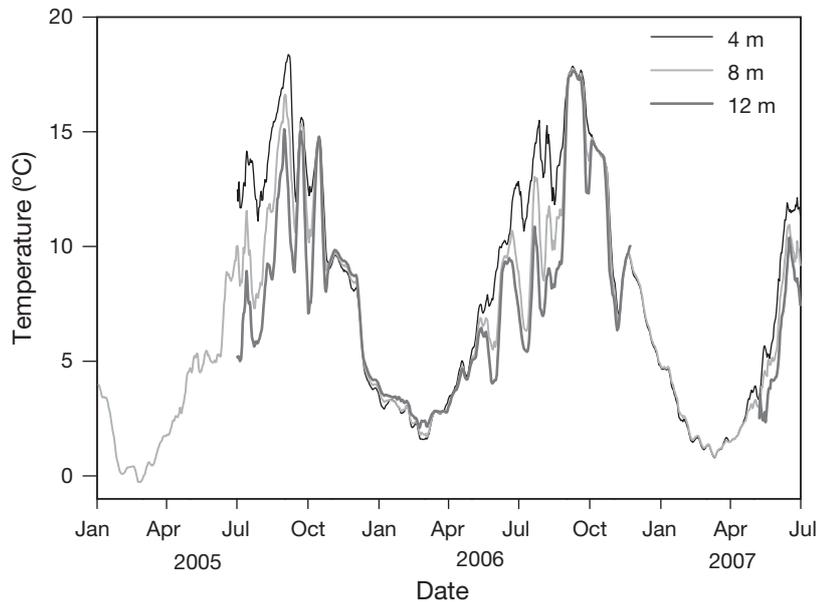
gins of kelp blades without causing kelp mortality (Johnson & Mann 1986). Consequently, it is unlikely that the observed decline in kelp abundance was the result of grazing.

Following kelp defoliation, and in the absence of grazers, kelps can recruit the following spring (Scheibling et al. 1999) and restore the kelp canopy in 1.5 to 4 yr (Johnson & Mann 1988). Since the early 1990s, however, the introduced alga *Codium fragile* ssp. *fragile* has colonized some of the areas left vacant by bryozoan defoliation and sea urchin mass mortalities (Levin

Fig. 9. Seawater temperature (°C), smoothed with a 7 d moving average, measured in St. Margarets Bay, Nova Scotia, from 1 January to 1 July 2005 at Birchy Head (8 m depth) and from 1 July 2005 to 30 June 2007 at Lodge (4, 8, and 12 m depth). Data for 12 m are unavailable from 20 November 2006 to 10 May 2007

and early autumn, but not in the late autumn, in the second year of the study. Because of earlier recruitment in 2006, colonies were larger in summer than in the previous year. By encrusting the kelp blades with large colonies earlier in the season in 2006, *M. membranacea* led to the defoliation of kelp in autumn, despite relatively typical fall storms. Because of defoliation of kelp blades in autumn 2006, colonies were smaller by late autumn than in the previous year. By promoting defoliation of the host during years of high recruitment, *M. membranacea* will likely have lower recruitment in following seasons, unless kelp beds reestablish quickly or larvae settle on alternative algal hosts.

depths. In the present study, colony abundance generally increased with depth, as was previously observed for settlers (Saunders & Metaxas 2007). During the growing season, when *M. membranacea* juvenile colonies are increasing in abundance in Nova Scotia, the water is strongly thermally stratified (Fig. 9), a condition which may lead to the depth patterns observed. For example, in Southern California, when the water was warm and stratified, larvae were more abundant below the thermocline (Yoshioka 1973), and colonies on kelp were more abundant at depth than near the surface (Bernstein & Jung 1979). In the present study, colonies were less abundant, but larger (M. Saunders unpubl. data) at shallower depths in summer, probably because of faster growth in warmer water (Menon 1972). The growth rate of bryozoans is also influenced by food availability (O'Dea & Okamura 1999), which is potentially greater in shallower water. For example, water velocity is typically greater in shallower water than in deeper water, and increased water velocity can enhance food supply and growth rates of filter-feeding organisms (Lenihan et al. 1996). However, increased wave energy in shallower water also leads to greater potential for algal breakage (Thomsen & Wernberg 2005) and thus colony loss, particularly for heavily encrusted blades.

In summary, we have shown that, for the introduced bryozoan *Membranipora membranacea* in Nova Scotia, earlier and increased recruitment led to a higher percent cover of the bryozoan on kelp in the summer

LITERATURE CITED

Berman J, Harris L, Lambert W, Buttrick M, Dufresne M (1992) Recent invasions of the Gulf of Maine: three contrasting ecological histories. Conserv Biol 6:435–441

Bernstein BB, Jung N (1979) Selective pressures and coevolution in a kelp canopy community in southern California. Ecol Monogr 49:335–355

Byers JE (2000) Competition between two estuarine snails: implications for invasions of exotic species. Ecology 81: 1225–1239

Caley MJ, Carr MH, Hixon MA, Hughes TP, Jones GP, Menge BA (1996) Recruitment and the local dynamics of open marine populations. Annu Rev Ecol Syst 27:477–500

Cancino JM, Muñoz J, Muñoz M, Orellana MC (1987) Effects of the bryozoan *Membranipora tuberculata* (Bosc.) on the photosynthesis and growth of *Gelidium rex* Santelices and Abbott. J Exp Mar Biol Ecol 113:105–112

Chapman AS, Scheibling RE, Chapman ARO (2002) Species introductions and changes in the marine vegetation of Atlantic Canada. In: Claudi R, Nantel P, Muckle-Jeffs E (eds) Alien invaders in Canada's waters, wetlands, and forests. Natural Resources Canada, Canadian Forest Service, Science Branch, Ottawa, p 133–148

Dixon J, Schroeter SC, Kastendiek J (1981) Effects of the encrusting bryozoan, *Membranipora membranacea*, on the loss of blades and fronds by the giant kelp, *Macrocystis pyrifera* (Laminariales). J Phycol 17:341–345

Duggins D, Eckman JE, Siddon CE, Klinger T (2001) Interactive roles of mesograzers and current flow in survival of kelps. Mar Ecol Prog Ser 223:143–155

Harris LG, Mathieson A (1998) Patterns of range expansion, niche shift and predator acquisition in *Codium fragile* ssp. *tomentosoides* and *Membranipora membranacea* in the Gulf of Maine. Proc Nat Conf Bioinvasions, New Hampshire Sea Grant, Cambridge, NH, p 46–56

Harvell CD, Grosberg RK (1988) The timing of sexual maturity in clonal animals. Ecology 69:1855–1864

Harvell CD, Caswell H, Simpson P (1990) Density effects in a colonial monoculture: experimental studies with a marine bryozoan (*Membranipora membranacea* L.). Oecologia 82:227–237

Harvell CD, Kim K, Burkholder JM, Colwell RR and others (1999) Emerging marine diseases—climate links and anthropogenic factors. Science 285:1505–1510

Harvell CD (1985) Partial predation, inducible defense and the population biology of a marine bryozoan. PhD dissertation, University of Washington, Seattle, WA

Hepburn CD, Hurd CL (2005) Conditional mutualism between the giant kelp *Macrocystis pyrifera* and colonial epifauna. Mar Ecol Prog Ser 302:37–48

Hixon MA, Pacala SW, Sandin SA (2002) Population regulation: historical context and contemporary challenges of open vs. closed systems. Ecology 83:1490–1508

Hurd CL, Durante KM, Harrison PJ (2000) Influence of bryozoan colonization on the physiology of the kelp *Macrocystis integrifolia* (Laminariales, Phaeophyta) from nitrogen-rich and -poor sites in Barkley Sound, British Columbia. Phycologia 39:435–440

Johnson CR, Mann KH (1986) The importance of plant defence abilities to the structure of subtidal seaweed communities: the kelp *Laminaria longicruris de la Pylaie* survives grazing by the snail *Lacuna vincta* (Montagu) at high population densities. J Exp Mar Biol Ecol 97:231–267

Johnson CR, Mann KH (1988) Diversity, patterns of adaptation, and stability of Nova Scotian kelp beds. Ecol Monogr 58:129–154

Lambert WJ, Levin PS, Berman J (1992) Changes in the structure of a New England (USA) kelp bed: the effects of an introduced species? Mar Ecol Prog Ser 88:303–307

Lane CE, Mayes C, Druehl LD, Saunders GW (2006) A multigene molecular investigation of the kelp (Laminariales, Phaeophyceae) supports substantial taxonomic re-organization. J Phycol 42:493–512

Lenihan HS, Peterson CH, Allen JM (1996) Does flow speed also have a direct effect on growth of active suspension-feeders: an experimental test on oysters. Limnol Oceanogr 41:1359–1366

Levin PS, Coyer JA, Petrik R, Good TP (2002) Community-wide effects of nonindigenous species on temperate rocky reefs. Ecology 83:3182–3193

Menon NR (1972) Heat tolerance, growth and regeneration in three North Sea bryozoans exposed to different constant temperatures. Mar Biol 15:1–11

Murdoch WW (1994) Population regulation in theory and practice. Ecology 75:271–287

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

Pratt MC, Grason EW (2007) Invasive species as a new food source: does a nudibranch predator prefer eating an invasive bryozoan? Biol Invasions 9:645–655

Saier B, Chapman AS (2004) Crusts of the alien bryozoan *Membranipora membranacea* can negatively impact spore output from native kelps (*Laminaria longicruris*). Bot Mar 47:265–271

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

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

Scheibling RE, Hennigar AW, Balch T (1999) Destructive grazing, epiphytism, and disease: the dynamics of sea urchin–kelp interactions in Nova Scotia. Can J Fish Aquat Sci 56:2300–2314

Schwaninger HR (1999) Population structure of the widely dispersing marine bryozoan *Membranipora membranacea* (Cheilostomata): implications for population history, biogeography, and taxonomy. Mar Biol 135:411–423

Seed R (1976) Observations on the ecology of *Membranipora* (Bryozoa) and a major predator *Doridella Steinbergae* (Nudibranchiata) along the fronds of *Laminaria saccharina* at Friday Harbor, Washington. J Exp Mar Biol Ecol 24:1–17

Thomsen MS, Wernberg T (2005) Miniview: what affects the forces required to break or dislodge macroalgae? Eur J Phycol 40:139–148

Torchin ME, Lafferty KD, Kuris AM (2001) Release from parasites as natural enemies: increased performance of a globally introduced marine crab. Biol Invasions 3:333–345

Turchin P (1999) Population regulation: a synthetic view. Oikos 84:153–159

Underwood AJ (1997) Experiments in Ecology. Cambridge University Press, Cambridge

Werner SM, Albers MA, Cryderman T, Diminic D and others (2006) Is the outbreak status of *Thrips calcaratus* Uzel in North America due to altered host relationships? For Ecol Manag 225: 200–206

Wolfe LM (2002) Why alien invaders succeed: support for the escape-from-enemy hypothesis. Am Nat 160:705–711

Yoshioka PM (1973) The population dynamics and ecology of the encrusting ectoproct *Membranipora serrilamella*. PhD dissertation, Scripps Institute of Oceanography, University of California, San Diego, CA

Yoshioka PM (1982) Role of planktonic and benthic factors in the population dynamics of the bryozoan *Membranipora membranacea.* Ecology 63:457–468