Vol. 418: 131–145, 2010
doi: 10.3354/meps08842

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published November 18

Physical forcing of distributions of bryozoan cyphonautes larvae in a coastal embayment

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ABSTRACT: In shallow rocky subtidal ecosystems in the western North Atlantic, outbreaks of the nonindigenous encrusting epiphytic bryozoan *Membranipora membranacea* cause defoliation of laminarian algae, facilitating a phase transition from native kelp beds to meadows of invasive algae. We quantified spatial (m [depth] to km [sites]) and temporal (hourly to monthly) patterns in the abundance of larvae of *M. membranacea,* and a morphologically similar native species, *Electra pilosa*, in relation to physical structure (temperature, salinity, density) of the water column in St. Margarets Bay, Nova Scotia, Canada, on 8 dates from September to November 2007. During the study period, the water column ranged from strongly stratified to well mixed, and cross-shore movements of water masses (wind-driven upwelling and downwelling) were indicated by shoaling of the isoclines. When a strong pycnocline was located between the 2 sampled depths (4 and 12 m), larvae of both species were more abundant in the shallower, warmer, fresher layer. The linear relationship between strength of stratification and the relative abundance of larvae between depths was significant over 2 temporal (hourly, weekly) and 1 spatial (km) scale examined for *M. membranacea,* but not for *E. pilosa*. Highest abundance of larvae of both species in the warm fresh surface layer suggests onshore transport during wind-driven downwelling events. Dissimilar patterns in size-frequency distributions between the indigenous and nonindigenous bryozoan larvae suggest that species-specific characteristics of larvae of *M. membranacea* may be a contributing factor to its success as an invader in the western North Atlantic.

KEY WORDS: Nonindigenous invasive species · Larval abundance and dispersal · Physical oceanographic processes · Coastal embayment · Bryozoan · *Membranipora membranacea* · *Electra pilosa*

INTRODUCTION

The introduction and establishment of nonindigenous species in new environments is one of the greatest contemporary threats to marine ecosystems (Carlton 2000). In the western North Atlantic, a nonindigenous encrusting epiphytic bryozoan, *Membranipora membranacea,* undergoes significant population outbreaks in kelp beds (Lambert et al. 1992, Scheibling et al. 1999) during years with warmer than average temperatures (Saunders & Metaxas 2008, Scheibling & Gagnon 2009, Saunders et al. 2010). During these outbreaks, colonies of *M. membranacea* can encrust entire blades of kelps, causing them to become brittle and fragile, and to subsequently break (Dixon et al. 1981, Lambert et al. 1992). The resultant defoliation of kelps facilitates a phase transition from kelp beds to monospecific stands of the nonindigenous algae *Codium fragile* spp. *fragile* (Levin et al. 2002, Scheibling & Gagnon 2006), which may have significant implications for the community composition (Schmidt & Scheibling 2007) and productivity of rocky subtidal habitats. In these same habitats, an indigenous encrusting bryozoan, *Electra pilosa,* commonly forms small (mm to cm) star-shaped colonies on blades of kelps and turf algae, but these colonies are not typically detrimental to their hosts. Both species have relatively long-lived planktotrophic cyphonautes larvae

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(*M. membranacea* 4 to 8 wk, Yoshioka 1982; planktonic larval duration not known for *E. pilosa*, although assumed to be similar). Distributions and abundances of larvae of these 2 species have not been quantified in the western North Atlantic; therefore, the role of larval supply in the regulation of adult populations of the invasive and indigenous species is unknown.

The population dynamics of benthic meroplanktonic marine species are strongly influenced by mechanisms and dynamics of larval settlement and recruitment into the adult habitat (Caley et al. 1996), which in turn are greatly affected by physical oceanographic processes acting on larvae (Pineda et al. 2009). For example, high abundances of larvae or new settlers of a variety of species (e.g. barnacles, crabs, bivalves) have been associated with upwelling (Shanks et al. 2000, 2003, Shanks & Brink 2005), downwelling (Almeida & Queiroga 2003, Ma 2005), or periods of relaxation of upwelling winds (Roughgarden et al. 1991, Wing et al. 1995, Miller & Emlet 1997). Whether larvae are advected shoreward or seaward by upwelling or downwelling depends on their vertical position in the water column (Shanks & Brink 2005). Vertical position may, in turn, be affected by larval buoyancy or swimming behaviour in relation to density discontinuities caused by gradients in temperature and/or salinity (Metaxas 2001). For example, zooplankton may be restricted to a particular layer of a stratified water column (Olivar & Sabatés 1997, Gallager et al. 2004), and also may be more (Pineda & López 2002) or less (Valdés & Moral 1998) abundant during stratified than well-mixed conditions. Spatial, temporal, and ontogenetic patterns in larval abundance and distribution (e.g. Lamare & Barker 1999, Tapia & Pineda 2007) may allow inferences of transport processes, including the role of upwelling and downwelling events (e.g. Shanks et al. 2003, Ma 2005).

Cyphonautes larvae are relatively weak swimmers, using only cilia for directed movement, and are thus not likely to be able to regulate their horizontal position in relation to advective flows. However, modifications of swimming behaviour can potentially influence their vertical position in the water column. For example, cyphonautes are negatively geotactic, and under static conditions in the lab young larvae are found most commonly near the surface, whereas older larvae slowly sink (Silén & Jansson 1972). Furthermore, larvae of *Membranipora membranacea* appear to alter their swimming behaviour in the presence of a thermocline (Bernstein & Jung 1979). In the laboratory, disruption of swimming in warm water causes larvae of *M. membranacea* to sink, a behaviour that may explain higher occurrences of larvae and settlers below the thermocline under strongly stratified conditions in the field (Bernstein & Jung 1979, Yoshioka 1982).

Mechanisms of larval supply of benthic invertebrates can be quantified by using patterns of larval settlement, defined as the number of larvae adhering to the adult substrate per unit time, as a proxy (Pineda 2000, Pineda et al. 2009). In 2005 to 2006, we examined settlement patterns of *Membranipora membranacea* on blades of the kelp *Saccharina longicruris,* at 2 sites in St. Margarets Bay, Nova Scotia, Canada (Saunders & Metaxas 2007). This coastal embayment is considered near the epicenter of the *M. membranacea* invasion in Nova Scotia (Scheibling et al. 1999, Watanabe et al. 2010). Abundances of newly settled colonies were quantified at 3 depths spanning the depth distribution of the kelp beds (4, 8, 12 m) on weekly–monthly timescales over 15 mo (Saunders & Metaxas 2007). Newly settled colonies were first observed in summer, with peaks in settlement occurring in autumn in each year (Saunders & Metaxas 2007). Settlement was typically higher at 12 than at 4 m depth, suggesting that larvae were more abundant deeper in the water column (Saunders & Metaxas 2007). The period of highest settlement of *M. membranacea* occurred when the water column was warm and well mixed throughout the upper 12 m (Saunders & Metaxas 2007), suggesting that larvae may have been transported with shoreward moving warm surface water (downwelling). Similar measures of settlement of *Electra pilosa* have not been made; however, in Nova Scotia, this species generally settles in the same season (summer/fall) and at the same locations (on macroalgae) as *M. membranacea*. While settlement data may provide insights into larval supply mechanisms, they may not always directly reflect patterns of larval abundance in the water column (Pineda 2000, 2009, Rilov et al. 2008. Therefore, to understand larval transport in these 2 species of bryozoan, measurements of abundance and size distributions of larvae in the water column across space and time are necessary.

Our objective was to describe relative distributions and abundances of the 2 species of bryzoan (an introduced and a native) with similar morphologies (cyphonautes larvae with similar swimming abilities) and life histories (reproduction beginning in late spring, ~1 mo larval duration, and epiphytic colonial adults) in relation to variations in the stratification of the water column. Based on this overall objective, we made 3 predictions. First, larvae will be more abundant below the thermocline when the water column is stratified, based on observations of *Membranipora membranacea* from California, USA (Bernstein & Jung 1979, Yoshioka 1982). Furthermore, in Nova Scotia, when differences in the abundances of newly settled colonies among depths (4, 8, 12 m) occurred, abundance increased with depth, suggesting that larval supply may be higher at the deeper locations (Saunders & Metaxas 2007). Sec-

ond, if physical structure of the water column determines larval depth distributions, abundance will be bathymetrically homogeneous when the water column is well mixed. Third, highest total larval abundance will occur when the water column is warm and well mixed. This prediction is based on temporal observations of settlement in Nova Scotia over 2 seasons, where in each year the peak in settlement occurred when the water column was warm and well mixed (Saunders & Metaxas 2007). We also examined size-frequency distributions and the proportional abundance of competent larvae for each species, recognizing that the settlement data that we used to inform our predictions would be likely be more influenced by competent than precompetent larvae.

To address our overall objective and test our predictions, we quantified distributions of larvae of *Membranipora membranacea* and *Electra pilosa* in relation to the vertical structure of physical properties (temperature, salinity, density) of the water column in a coastal embayment. The physical structure (vertical dimension) of the water column varies temporally, and also to a lesser extent horizontally; therefore, we sampled over time and space to capture varying physical oceanographic settings and a range of strengths in vertical stratification.

MATERIALS AND METHODS

Study area. St. Margarets Bay is a small (8 × 16 km) coastal embayment located on the southern shore of Nova Scotia, Canada (Fig. 1). The centre of the bay is 40 to 70 m deep, with a 100 m deep depression located on the inward side of a shallow (25 m) sill at the mouth of the bay. A deeper (70 m) channel cuts through the sill on the west side of the mouth of bay. Mean horizontal circulation in the bay is anticlockwise, with water entering on the east side and exiting on the west side (Heath 1973). In summer, the bay has a 2-layered structure, with mean flushing time of 5 to 10 d in the upper layer, and 10 to 30 d in the lower layer (Heath

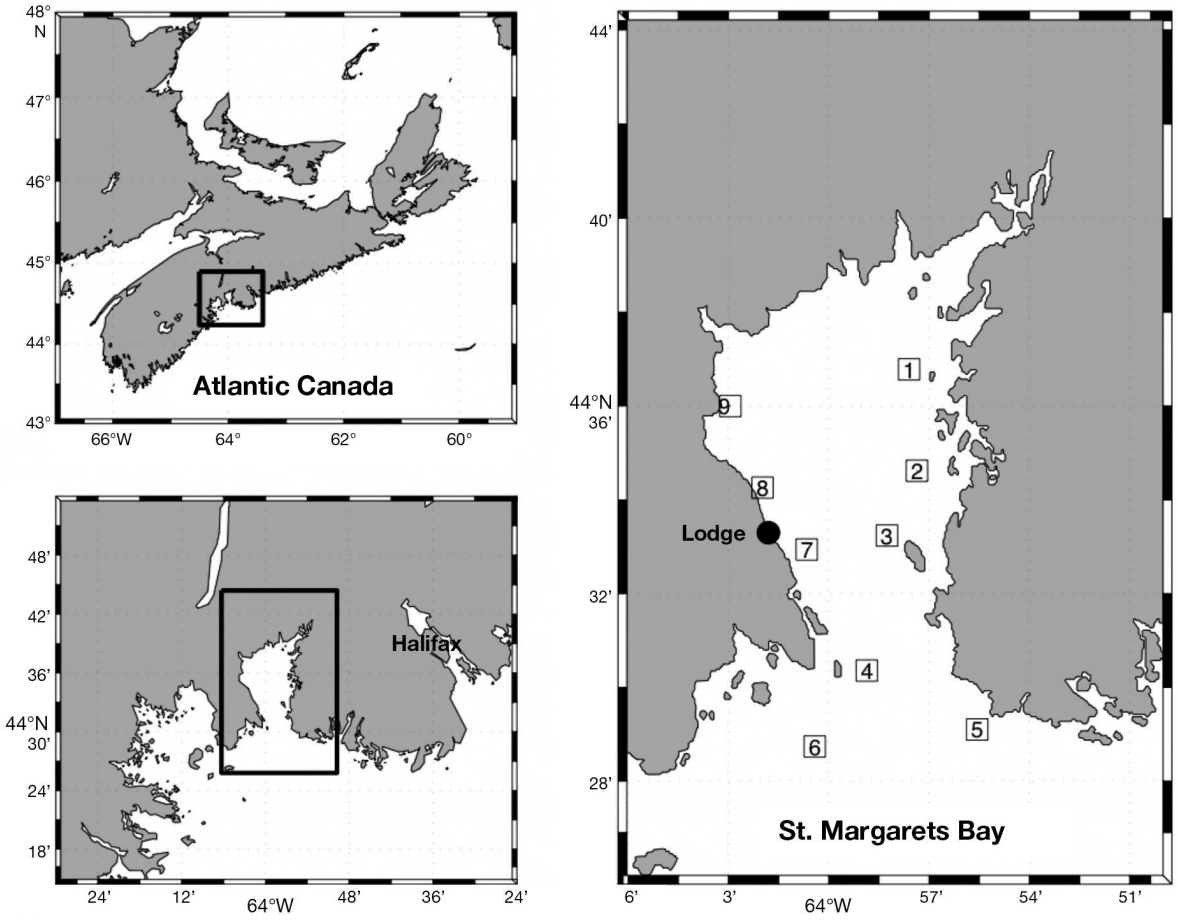

Fig. 1. Study site located on the southwestern shore of Nova Scotia, Canada. Nine stations (indicated with squares) in St. Margarets Bay were sampled on 8 dates from September to November 2007. Temperature during the study period was measured continuously at the benthos at 4, 8 and 12 m depth at Lodge (●)

1973). 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). Daily mean water temperature at 4 to 12 m depth measured on the bottom at Lodge (44° 33′ 3″ N, 64° 01′ 9″ W), on the west side of the bay (Fig. 1) ranged from –0.69°C (February) to 19.3°C (September) in 2005 (Saunders & Metaxas 2007). From late May to early October, the water column is strongly stratified between 4 and 12 m (weekly average difference in temperature, ΔT, between the 2 depths = 2 to 8°C), except during periods of pronounced mixing, upwelling or downwelling (Saunders & Metaxas 2007). There are a number of small rivers that empty into the bay; however, total discharge is small relative to tidal inflow (0.003 to 0.02%) (Denman 1977). The shoreline consists mainly of granitic cobbles, boulders, and bedrock, interspersed by sheltered areas of sand or mud. Kelp beds consisting primarily of *Saccharina longicruris, Laminaria digitata, Agarum clathatrum* and turf algae dominate the rocky benthos from 0 to 20 m depth, and provide settlement habitat for *Membranipora membranacea* and *Electra pilosa*.

Nine stations distributed inside and outside the bay, along both the east and west sides, were selected based on the relative proximity to the shoreline (0.5 to 2.5 km) (and thus to suitable substrata for larval settlement), and on depth (≥40 m) (Fig. 1). Sampling was conducted on 8 dates from September to November 2007, when larval abundances were predicted to be highest based on previous studies of settlement of *Membranipora membranacea* (Saunders & Metaxas 2007). Settlement of *Electra pilosa* in the region has not been quantified, although it occurs during the same period in similar habitats (M. Saunders pers. obs.). For logistical reasons it was not possible to sample every station on all sampling dates; the stations sampled on each date are shown in Table 1. In general, the time required to sample a station and to travel to the following station was 1 to 1.5 h. We did not conduct replicate tows at any one location because we wanted to maximize the spatial extent of our sampling. Therefore, when data are presented as averages, the source of variation is among tows conducted at the same depth on the same date. However, to estimate temporal variability in abundance at a single location, on 20 and 30 September, Stn 1 was sampled repeatedly each hour over several hours.

Larval sampling and processing. At each station on each date, horizontal net tows (1 per depth, except for on 20 and 30 September, see above) were conducted at each of 2 depths. The depths sampled were selected based on our previous studies of larval settlement of *Membranipora membranacea* in kelp beds (Saunders & Metaxas 2007), and were classed as 'deep,' ~12 m (11.8 ± 2 m, n = 48); and 'shallow,' ~4 m (4.5 ± 0.9 m, n = 48), (mean ± SD from all tows). Tows were conducted with a 75 cm diameter, 3:1 length:diameter, 200 µm mesh plankton net weighted with 11 kg, with a choke band and a 11.25 cm diameter cod end. On the first sampling date (6 September) less weight was used on the nets, and consequently the shallow and deep tows were slightly shallower (~3 and 7 m) than on subsequent dates. The net was quickly lowered in the open position, towed at depth for a nominal duration of 6.5 min (to ensure sampling ~100 m^{-3} seawater), closed at depth, and retrieved using a powered winch (Honda). Flow through the net was measured with a General Oceanics mechanical flow meter. A Vemco 8-bit Minilog Temperature Depth recorder (TDR) (temperature: resolution 0.2°C, accuracy ± 0.3°C; depth: resolution 0.2 m) was mounted to the mouth of the net and set to sample at 5 s intervals. Upon retrieval of the net, plankton were immediately preserved in ~70% EtOH and transferred to 95% EtOH for storage within 10 h. Plankton samples were serially divided using a Folsom plankton splitter (Wildlife Supply Company) and a subsample (1/8 to 1/512, depending on sample volume and relative abundance of bryozoan larvae) was sorted using a Bogorov counting chamber (Wildlife Supply Company) with a Nikon SMZ 1500 dissecting scope. Bryozoan larvae were identified to species and photographed using a Nikon E995 digital camera under 120× magnification. The length of each larva along the ciliated band was measured from photographs using Sigma Scan Pro

Table 1. *Membranipora membranacea* and *Electra pilosa*. Dates on which 9 stations located in St. Margarets Bay, Nova Scotia, Canada (shown in Fig. 1), were sampled for larvae of the bryozoans in relation to physical structure of the water column. On 20 and 30 September, Stn 1 was sampled repeatedly once each hour, 3 and 8 times, respectively

Date	Station									Notes
	1	2	3	4	5	6	7	8	9	
6 Sep	X	X	X							Inner Bay
9 Sep	X		X	X	X	X	X	X	X	Whole Bay
19 Sep			X	X	X	X	X			Outer Bay
20 Sep	X (3×)	X						X	X	Inner Bay
25 Sep	X		X	X			X	X	X	Inner Bay
30 Sep	X (8×)									Inner Bay
4 Oct	X		X		X	X				Transect
14 Nov	X		X	X		X	X	X	X	Whole Bay

image analysis software. For each species at each location (depths within sites) on each date, total larval abundance was calculated by standardizing larval counts to the volume sampled (larvae m^{-3}).

To compare ontogenetic patterns in distributions, we divided the data for each species into 'precompetent' and 'competent' size classes based on assumed relationships between size and age. For both species, precise estimates of size at competence are not available for the population in the western North Atlantic. However, values from the literature are available for other populations, which we adapted for our study. Larvae of *Membranipora membranacea* were nominally divided into <500 µm (precompetent) and ≥500 µm (competent) size classes based on the use of larvae of 400 to 550 µm in settlement studies in the San Juan Islands, WA, USA (Stricker 1989), and observations from our photos of larvae >~500 µm having the appropriate structures for settlement. Larvae of *Electra pilosa* reach smaller maximum sizes than *M. membranacea* (maximum length along the ciliary band of 550 compared to 800 µm, respectively). Larvae of *E. pilosa* were divided into <440 µm (precompetent) and ≥440 µm (competent) size classes based on information from European populations provided in Atkins (1955). For each species, at each depth, on each date, we calculated the percentage of all larvae that were greater than or equal to competent size. We also calculated size-frequency distributions for each species on each date (pooled across depths), with 10 µm bins for *E. pilosa*, and 20 µm bins for *M. membranacea*.

Characterization of physical properties of the water column. At each sampling station on each date, vertical profiles of conductivity, temperature and depth (CTD) of the water column to 20–35 m were obtained with a Seabird 25 Sealogger (8 Hz, accuracy 0.002°C, 0.0003 S m^{-1}, 0.6 m). For each CTD cast, seawater density (σ_t, kg m^{-3} – 1000) was calculated based on temperature (°C) and salinity using the 'swstate' function in Matlab 6.5 (The Mathworks Co.). Temperature, salinity, and density profiles were linearly interpolated between depths and resampled at 0.5 m intervals. Vertical density gradients for each station on each date were calculated as $\delta\sigma_t/\delta z$, where σ_t is density (kg m^{-3} – 1000), and z is depth (m), from the interpolated data. To compare density gradients among dates, the mean ± SD were calculated for all the stations sampled on each date (n = 3 to 8).

Throughout the study period, temperature was also recorded continuously at 10 min intervals using Onset Pendant data loggers (Onset Computer Corporation) (resolution 0.10°C, accuracy ± 0.47°C) attached to the benthos at 4, 8 and 12 m depth (relative to chart datum) at Lodge (44° 33′ 3″ N, 64° 01′ 9″ W) located on the western side of St. Margarets Bay (Fig. 1). The time-series of temperature data were smoothed using a 24 h moving average centered around noon to remove the high frequency (tidal and diurnal) variability, and linearly interpolated among depths.

Data analysis. To examine bathymetric patterns in larval distributions, the effect of depth (deep, shallow) on the abundance of each species on each date was examined with Student's *t*-tests for unequal variances, using individual stations as replicates (n = 3 to 8). Simple linear regression was used to examine the relationship between the strength of stratification and variations in larval abundance between depths. For each species, at each station, on each date, we calculated the difference in the abundance of larvae between depths (ΔL) as $\text{abundance}_{(4m)} - \text{abundance}_{(12m)}$. The depth of each tow was calculated based on the TDR data as the average depth from the time the net was deployed to the time the net closed. For each tow, density (σ_t, kg m^{-3} – 1000) at the average depth of the tow was obtained from the CTD data, and for each station on each date, the difference in density between the depths of the shallow and deep tows ($\Delta\rho$) was calculated as $\sigma_{t(4m)} - \sigma_{t(12m)}$. Linear regressions between ΔL and $\Delta\rho$ were conducted for data over 2 temporal and 1 spatial scales: (1) to examine the relationship between vertical patterns in larval abundance and stratification on broad (weeks to months) temporal scales, ΔL and $\Delta\rho$ were averaged across all samples for each date; (2) on 30 September, Stn 1 was sampled repeatedly each hour over 7 h (for a total of 8 samples), allowing an analysis over a finer temporal scale (hourly values used in the analysis); and (3) on 4 October, there was pronounced horizontal spatial variation in the depth of the thermo- and haloclines (among the 4 stations sampled), providing the opportunity to examine this relationship in the spatial dimension without the confounding effect of weekly–monthly variations in larval abundance (values from each individual station used in the analysis).

RESULTS

Bathymetric and temporal variation in abundance of larvae was 1 to 2 orders of magnitude throughout the study period, and patterns were similar between *Membranipora membranacea* and *Electra pilosa* (Fig. 2A). Abundance (averaged across all stations) was typically similar between depths, or higher in the shallow than in the deep tows (Fig. 2A). Differences in abundance between depths were consistent when larvae were sampled repeatedly at the same station at hourly intervals over 7 h (Fig. 3). The percentage of larvae that were competent varied between 0 and >90% depending on date, and were more similar between depths for

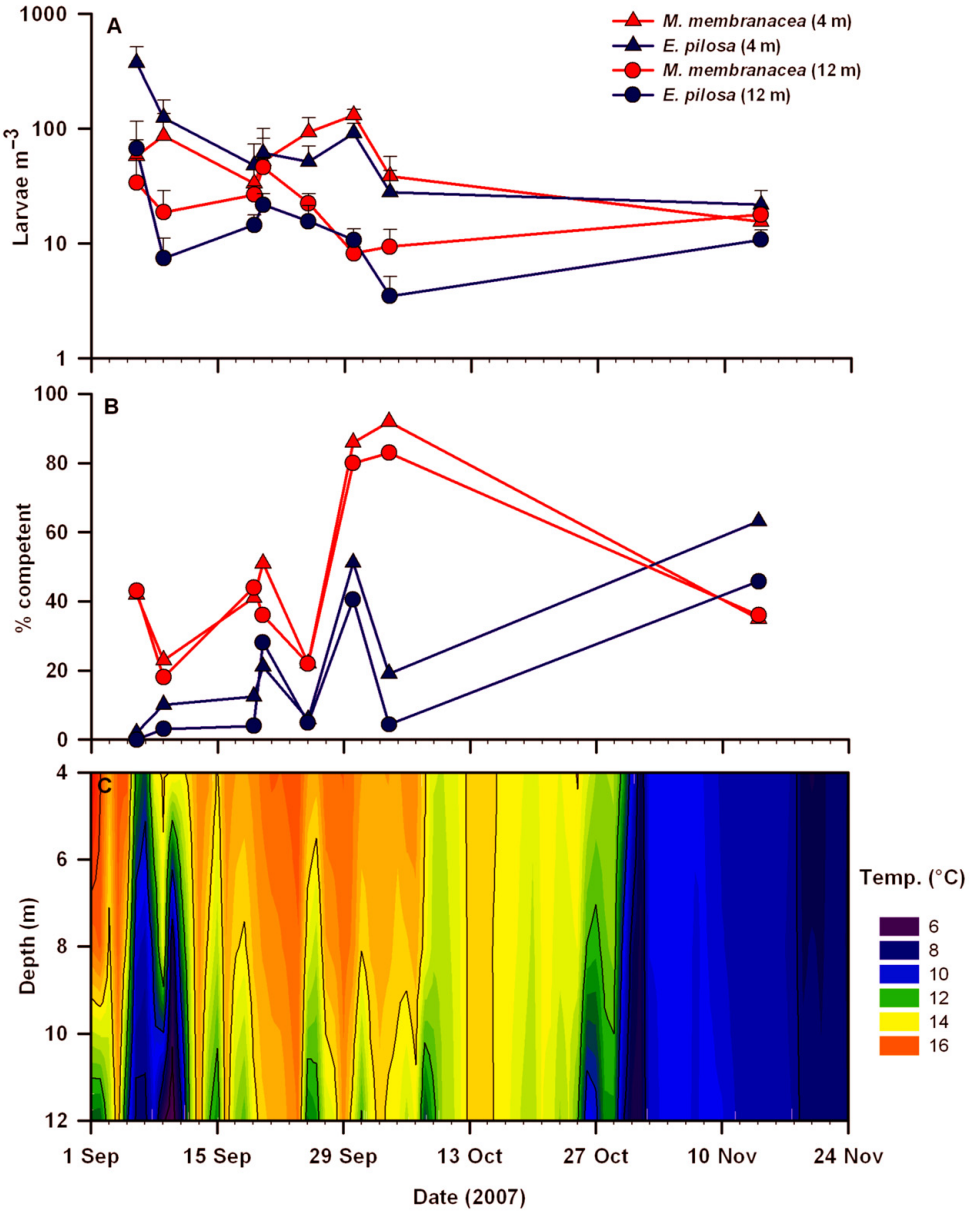

Fig. 2. *Membranipora membranacea* and *Electra pilosa*. (A) Temporal patterns in abundance of larvae of the bryozoans sampled at 2 depths (shallow = 4 m, deep = 12 m) at several stations (n = 3 to 8, mean + SE) in St. Margarets Bay, Nova Scotia, Canada, from September to November 2007. (B) Percentage of larvae of each species at each depth that were competent (based on size: *E. pilosa* >440 µm, *M. membranacea* >500 µm). (C) Thermal structure in the water column quantified using moored loggers at 4, 8, and 12 m depth at Lodge, on the western side of the bay, ranged from strongly stratified to well mixed

each species than between species (Fig. 2B). A peak in the percentage of competent larvae of *M. membranacea* occurred on 30 September to 4 October, and peaks in the percentage of competent larvae of *E. pilosa* occurred on 30 September and 14 November (Fig. 2B).

For both species, the size-frequency distributions show a transition of cohorts dominated primarily by smaller larvae in early September, to cohorts dominated by larger (competent) larvae on 30 September and 4 October (Fig. 4). However, although the size-frequency distributions of *Electra pilosa* were typically unimodal, those of *Membranipora membranacea* were broader and multipeaked, with more cohorts appearing in November (Fig. 4).

Water temperature (as measured at the Lodge) during the study period at 4 to 12 m ranged from 6 to 16°C, and the thermal structure ranged from strongly stratified between 4 and 12 m in September and October

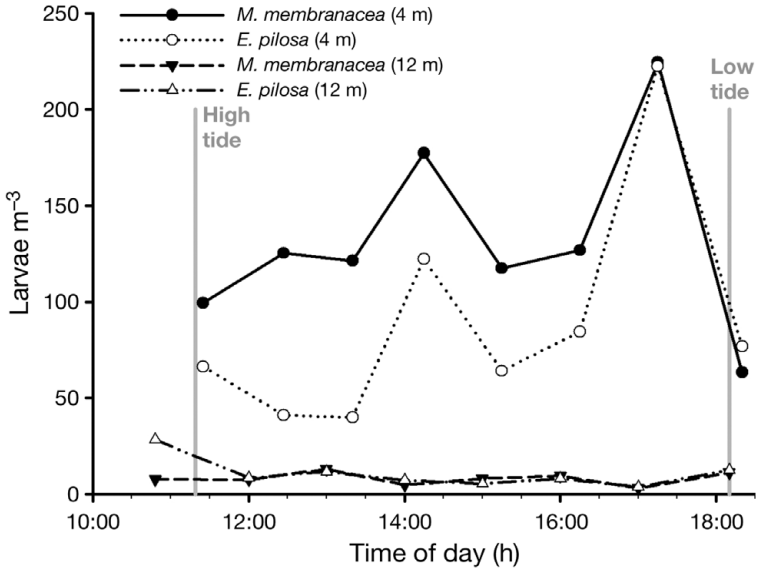

Fig. 3. *Membranipora membranacea* and *Electra pilosa*. Abundance of larvae of the bryozoans at 2 depths (shallow = 4 m, deep = 12 m) in St. Margarets Bay, Nova Scotia, Canada, sampled hourly during a falling tide on 30 September 2007

(except for on 19 to 20 September) to well mixed in November (Fig. 2C). Plankton were sampled during a range of physical conditions, including upwelling (6 and 9 September) and downwelling (19 and 20 September), as indicated by the shoaling of the isotherms (Fig. 2C).

To examine the relationship between abundance of larvae and variations in the water masses sampled on each date, we plotted expanding symbol representations of *Membranipora membranacea* larval abundance in relation to the temperature, salinity, and density of the water in which they were sampled (Fig. 5) (Physical data for *Electra pilosa* were the same since larvae were obtained from the same tows as for *M. membranacea*; for clarity, size of circles representing abundance of *E. pilosa* not shown). On 25 and 30 September, there was a clear separation between the water masses sampled in the deep and shallow tows, respectively (Fig. 5). Conversely, on 19 and 20 September, both the deep and shallow tows occurred in the warm, fresh layer. On 6 September, 9 September, and 4 October the deep and shallow tows were not as clearly confined to particular layers (Fig. 5). For example, on 6 and 9 September most of the shallow tows were in the cold, saline layer, and on 4 October most of the deep tows were in the warm, fresh layer (Fig. 5). By November, the water column was cooler (8 to 9°C), less saline (30.5 to 30.9), and well mixed (Fig. 2C), and the deep and shallow tows both sampled water with similar physical characteristics (Fig. 5). When data from the entire sampling period are combined, it is apparent that larvae were sampled from a relatively linear continuum of density from September to October (Fig. 5). Notably, larvae were found in all water parcels sampled, and although abundance was typically higher in the warmer less saline layer, they were not restricted to that layer.

Differences between depths in the abundance of larvae of each species occurred on some, but not all, dates (Table 2, Fig. 6). When there was a significant difference between depths, larvae were more abundant in the shallow tow for both species on 30 September (*Membranipora membranacea*: $t_{15} = 14.3$, $p < 0.001$; *Electra pilosa*: $t_{15} = 7.9$, $p < 0.001$), for *E. pilosa* on 9 September ($t_{14} = 3.5$, $p = 0.003$), and for *M. membranacea* on 25 September ($t_{10} = 3.4$, $p = 0.007$) (in all other cases $p > 0.05$, Table 2). On the dates when abundance of larvae varied significantly between depths, the depth of the pycnocline (indicated by the highest vertical density gradients) was located approximately between the depths of the tows (Fig. 6), and more larvae were present in the less dense, shallower water than in the denser deeper water. A similar trend was observed on 6 and 9 September, but it was not statistically significant. On these

Table 2. *Membranipora membranacea* and *Electra pilosa*. Results of Student's *t*-tests examining the effect of depth (deep = 12 m, shallow = 4 m) on abundance of larvae (m^{-3}) of the bryozoans sampled at 3 to 8 stations in St. Margarets Bay, Nova Scotia, Canada, from September to November 2007. In all cases where a significant effect was observed ($p < 0.05$, indicated in bold), larvae were more abundant in the shallow than the deep tow

Date	*t*	df	p
M. membranacea			
06 Sep	0.912	4	0.414
09 Sep	0.783	14	0.447
19 Sep	0.101	8	0.922
20 Sep	−0.679	10	0.512
25 Sep	3.374	10	**0.007**
30 Sep	14.267	15	**<0.001**
04 Oct	2.088	6	0.082
14 Nov	−0.895	12	0.389
E. pilosa			
06 Sep	2.009	4	0.115
09 Sep	3.542	14	**0.003**
19 Sep	1.537	8	0.163
20 Sep	0.692	10	0.504
25 Sep	2.122	10	0.06
30 Sep	7.859	15	**<0.001**
04 Oct	1.652	6	0.15
14 Nov	1.138	12	0.278

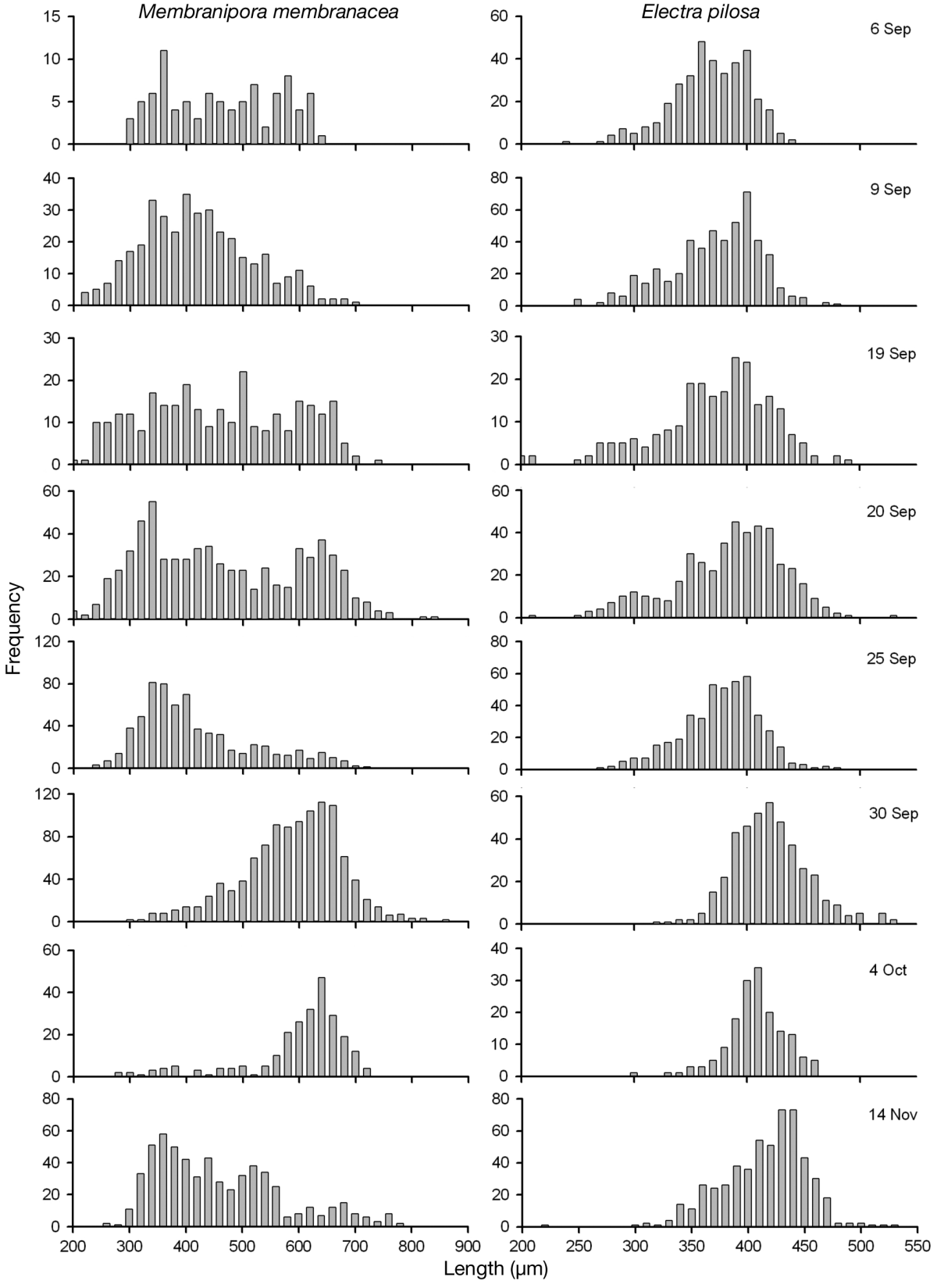

Fig. 4. *Membranipora membranacea* and *Electra pilosa*. Length-frequency distributions of larvae sampled at 2 depths at 3 to 8 stations (pooled) on 8 dates from September to November 2007 in St. Margarets Bay, Nova Scotia, Canada

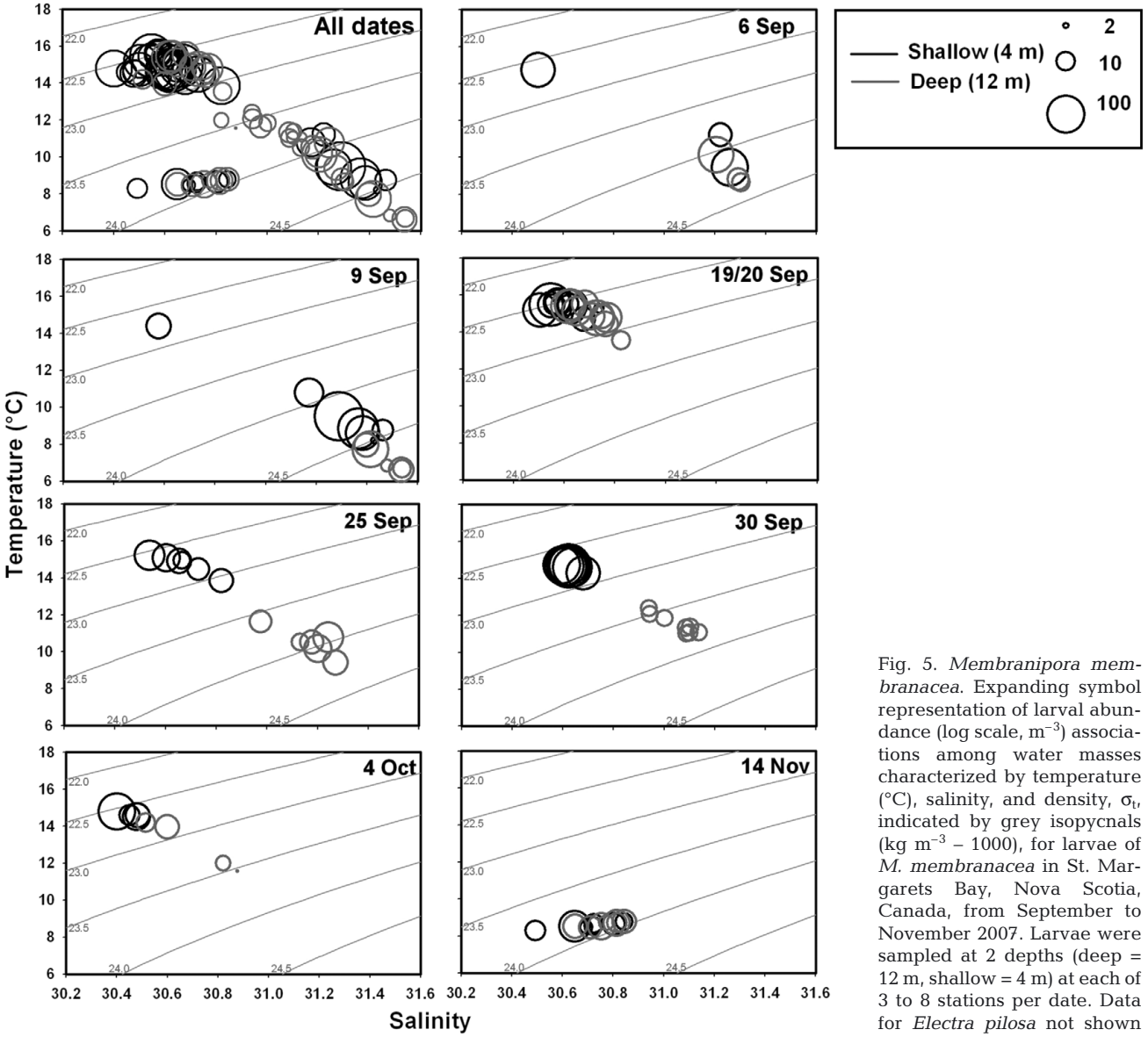

Fig. 5. *Membranipora membranacea*. Expanding symbol representation of larval abundance (log scale, m^{-3}) associations among water masses characterized by temperature (°C), salinity, and density, σ_t, indicated by grey isopycnals (kg m^{-3} – 1000), for larvae of *M. membranacea* in St. Margarets Bay, Nova Scotia, Canada, from September to November 2007. Larvae were sampled at 2 depths (deep = 12 m, shallow = 4 m) at each of 3 to 8 stations per date. Data for *Electra pilosa* not shown

2 dates, the shallow tows occurred near the depth of the pycnocline (Fig. 6), at some stations below, and at others above (Fig. 5). Consequently, the abundance of larvae in the shallow tows was highly variable, and low statistical power (because of small sample sizes) likely precluded the detection of a significant difference between depths. There was no difference in the abundance of larvae between depths for dates on which the water column was well mixed to below the depth of the deep tow (19 and 20 September, 14 November) (Fig. 6).

The linear relationship between the strength of stratification ($\Delta\rho$) and the magnitude of variation in abundance of larvae (ΔL) was significant for *Membranipora membranacea* over the 2 temporal (coarse and fine) scales and one spatial scale examined (Fig. 7) and was described by the equations:

Temporal (coarse):

$$\text{Log } \Delta L = -1.25(\Delta\rho) + 0.63;\ \text{Adj. } R^2 = 0.80,\ p = 0.004$$

Temporal (fine):

$$\text{Log } \Delta L = -0.94(\Delta\rho) + 1.16;\ \text{Adj. } R^2 = 0.72,\ p = 0.005$$

Spatial:

$$\text{Log } \Delta L = -2.30(\Delta\rho) - 0.44;\ \text{Adj. } R^2 = 0.87,\ p = 0.045$$

In all cases, stronger stratification between the deep and shallow tows was associated with a greater difference in the abundance of larvae between depths. Similar trends were observed for larvae of *Electra pilosa* (Fig. 7), although the relationships were not statistically significant (in all cases, $p > 0.05$).

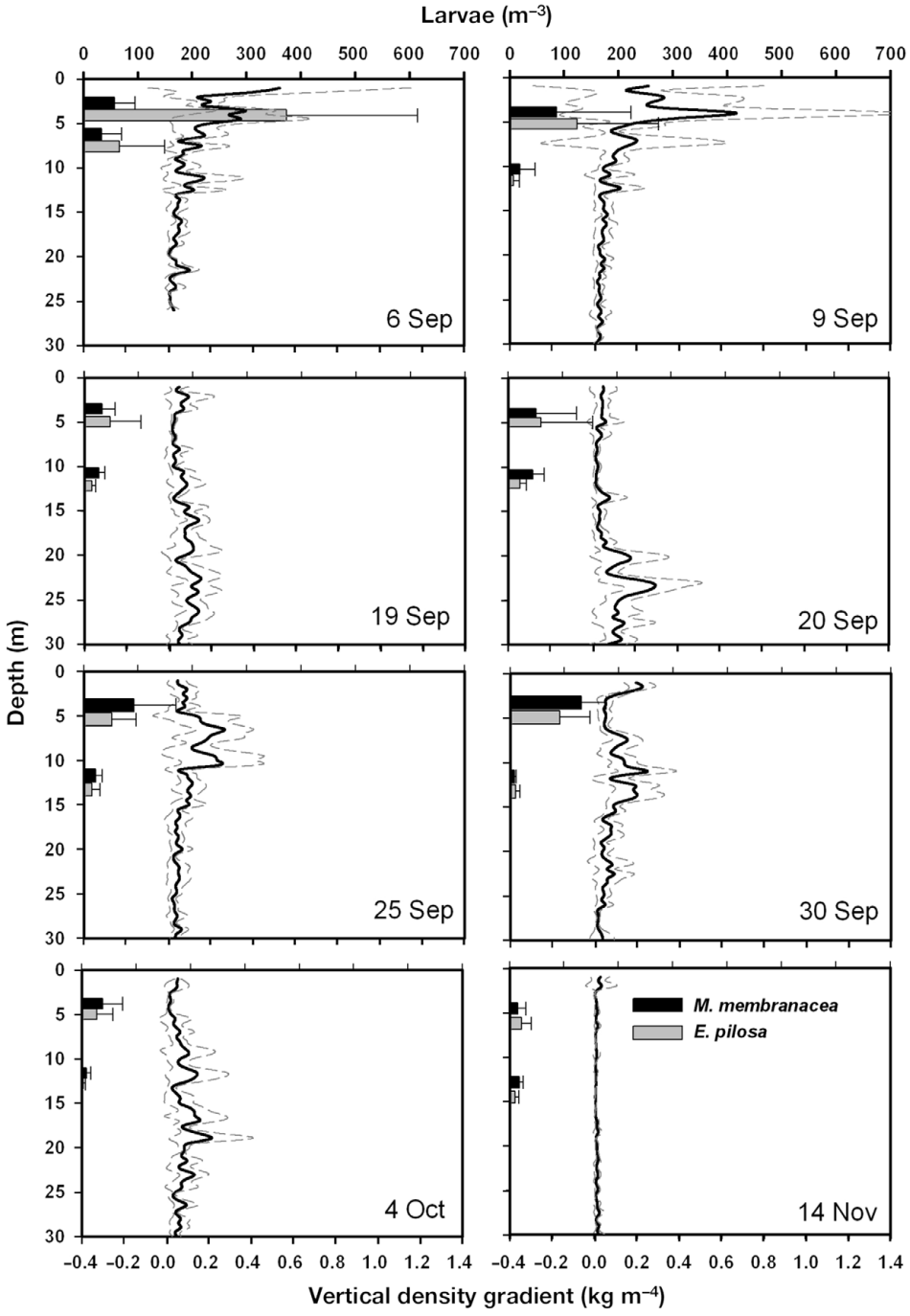

Fig. 6. *Membranipora membranacea* and *Electra pilosa*. Abundance of larvae at 2 depths sampled on each of 8 dates from September to November 2007 (bars = mean + SD, n = 3 to 8). The corresponding vertical density gradients ($\delta\rho/\delta z$, kg m^{-4}) in the water column were calculated from CTD casts (solid ± dashed lines indicate mean ± SD over the stations sampled on each date)

DISCUSSION

For 2 species of epiphytic bryozoa with planktotrophic, weakly swimming larvae, spatial and temporal patterns in distributions were strongly influenced by density gradients in the water column. Strength of stratification explained variations in the distributions of larvae of the invasive bryozoan *Membranipora membranacea* on several different scales, and the relationships were somewhat stronger over space (87% of variability explained) than time (72 to 80%). This linear relationship between differences in larval

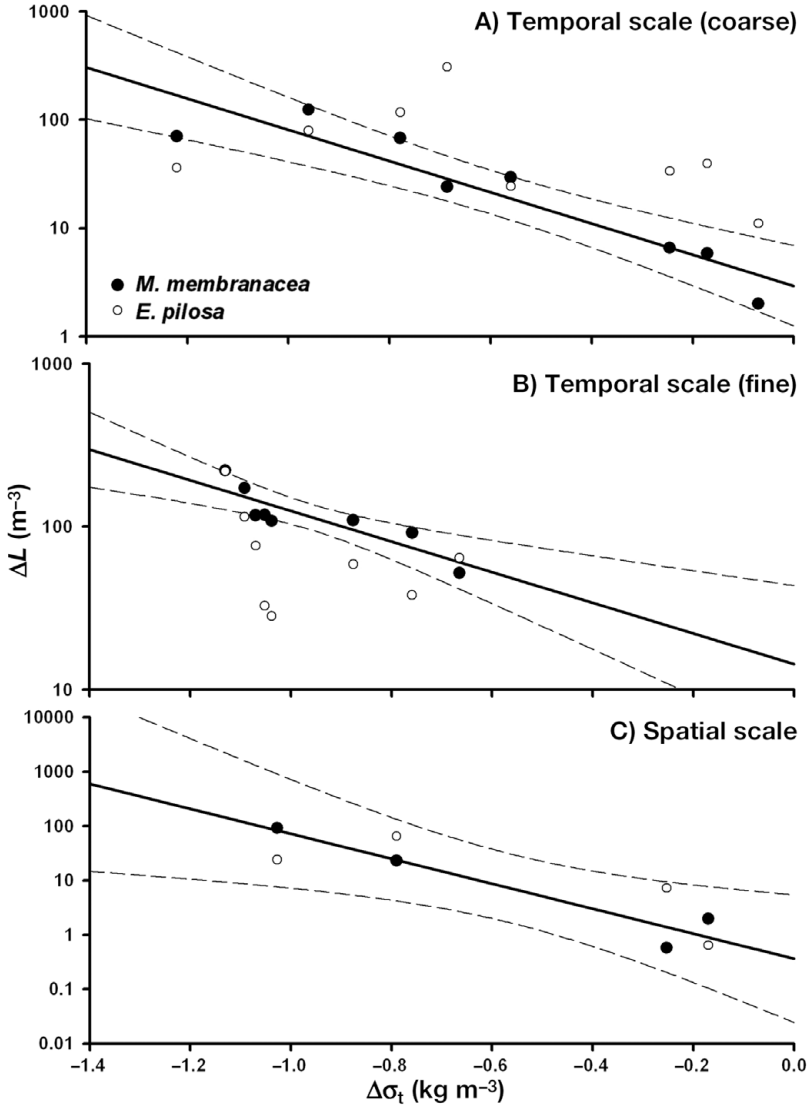

Fig. 7. *Membranipora membranacea* and *Electra pilosa*. Relationship of the difference in abundance of larvae between shallow (~4 m) and deep (~12 m) samples and the difference in seawater density (σ_t) between those 2 depths. Data points are (A) the average of n = 3 to 8 stations for 8 dates sampled from September to November 2007 (coarse temporal variability); (B) the values from samples collected hourly over 7 h at Stn 1 on 30 September 2007 (fine temporal variability); and (C) the values from each of 4 stations sampled on 4 October 2007 (spatial variability). For *M. membranacea* the relationship between the difference in larvae (ΔL) and density ($\Delta\rho$, calculated as $\rho_{4\ m} - \rho_{12\ m}$) between depths was significant, and solid and dashed lines indicate the regression mean and 95% prediction intervals, respectively. The relationship was not significant ($p > 0.05$) for *E. pilosa*, for any case

abundance of *M. membranacea* and stratification between depths was significant only when strong vertical gradients between the sampled depths existed, and while overall trends were similar for larvae of the native bryozoan *Electra pilosa*, they were not statistically significant.

Patterns in larval abundances will clearly be strongly influenced through time by biological factors, such as rates of spawning, growth, mortality, and settlement (e.g. Yoshioka 1982). Species-specific differences in the magnitude and timing of these factors may explain why, despite similar trends between the 2 species, the linear relationships were not significant for both species. Furthermore, the thermal range and optima for growth and development of larvae of the native species *Electra pilosa* may differ from those of the introduced species *Membranipora membranacea*, causing differences in the relationship between stratification and abundance; however, to our knowledge, these relationships have not been quantified. A larger proportion of larvae of *M. membranacea* were competent in September than of *E. pilosa*, suggesting that settlement and establishment of the invasive could occur earlier in the season than that of the native bryozoan. While the size-frequency distributions of *E. pilosa* were unimodal, those of *M. membranacea* typically had several peaks, suggesting numerous spawning events. This could be an advantageous strategy for an opportunistic species occupying an ephemeral habitat (kelp blades), and may partially explain the ecological success of *M. membranacea* over *E. pilosa* in the western North Atlantic.

Several factors could confound the relative distributions of larvae we observed in this study. Despite being weak swimmers, cyphonautes distributions may vary diurnally (Irigoien et al. 2004) or with lunar or tidal cycles (M. Lloyd, Dalhousie University, unpubl. data). However, we consistently sampled during daytime, and we found that for both species, relative patterns across depths were consistent over a 7 h period during the day, and over various dates with similar stratification throughout the fall. For logistical reasons, we could not sample multiple stations concurrently, as is typically the case with oceanographic sampling. Therefore, the time taken to transit between stations could be confounding in the patterns in larval distribution; however, the relevant physical conditions (water column stratification) usually vary over longer time periods (~weekly) than the temporal sampling scale within a sampling date (hourly).

Contrary to our prediction based on local studies of settlement (Saunders & Metaxas 2007), and studies of both settlement and larval distributions from the Pacific coast of North America (Bernstein & Jung 1979, Yoshioka 1982), when differences in the abundance of larvae occurred between depths, larvae were consistently more abundant in the shallower than deeper tows. When the water column was strongly stratified, there was a layer of warmer, less saline water overlying a deeper layer of colder, more saline water. On dates when the pycnocline was located between the depths of the deep and shallow tow, we found more larvae of both species in the warmer less saline layer than deeper. This regional difference may be a consequence of the cooler surface temperatures in summer in coastal Nova Scotia (up to 16 to 17°C in the present study) compared to southern California (22 to 24°C, Yoshioka 1982). Similarly relatively high abundances of cyphonautes near the surface have been reported for the west coast of Sweden (Silén & Jansson 1972), where water temperatures are similar to those in Nova Scotia. On dates when the less dense surface layer extended below the depth of the deep tow (e.g. 19 to 20 September), the cool saline layer extended above the depth of the shallow tow (e.g. 6 September), or mixing had occurred between the 2 water masses (e.g. 14 November), there was no difference in the abundance of larvae between depths.

Strength of stratification has been shown to influence the depth distribution and degree of aggregation of larvae of many taxa, including scallops (Tremblay & Sinclair 1990a,b, Gallager et al. 1996a), polychaetes (Thiébaut et al. 1992) and various bivalves (Raby et al. 1994). However, the precise location of larvae in relation to the pycnoline varies with species. For example, larvae of the scallop *Placopecten magellanicus* aggregated directly above the pycnocline in strongly stratified conditions in the field (Tremblay & Sinclair 1990a), but larvae of ophiuroids (Gallager et al. 1996b) and several species of bivalves (Raby et al. 1994) aggregated directly below the pycnocline. Laboratory studies have also shown larvae of a variety of species to accumulate at density discontinuities, such as echinoderms at haloclines (Sameoto & Metaxas 2008), and scallops at thermoclines (Gallager et al. 1996a). Regulation of position in relation to density discontinuities may be the result of modified swimming behaviour near the discontinuity, such as alternation between active swimming under certain conditions and passive sinking under others (Metaxas 2001).

Accumulation of passive particles at a density discontinuity may also occur, by a reduction in sinking speed in water of higher density and viscosity (MacIntyre et al. 1995). For example, in California, 87% of aggregations of marine snow in the upper 100 m of the water column were found at density discontinuities in the water column where N^2 (the Brunt Väisälä frequency) was higher than 1.25×10^{-4} s^{-2}, and 56% of peaks were found where N^2 exceeded 2.5×10^{-4} s^{-2} (MacIntyre et al. 1995). By multiplying the vertical density gradients ($\delta\rho/\delta z$) in this study by g/ρ, where ρ is density and g is the gravitational constant, we estimate that N^2 in St. Margarets Bay ranges from 10^{-5} to 10^{-3} s^{-2}, in many instances exceeding the values associated with particle aggregations in other studies (MacIntyre et al. 1995).

The vertical position of larvae in the water column will have pronounced effects on their dispersal distances. For example, in tidally dominated estuarine areas, positioning in the shallow, less saline water will favour transport out of the estuary, whereas positioning in the deeper more saline water will favour retention and return into the estuary (e.g. Knights et al. 2006). In St. Margarets Bay, retention time has been estimated as 5 to 10 d in the surface layer (10 m), and 10 to 30 d in the deeper layer (Heath 1973). The higher abundance of larvae in the shallower tows in stratified conditions suggests greater dispersal distances than those of larvae in the deeper layers. The residence time of the deeper layer is of the same order as the larval duration of *Membranipora membranacea*, suggesting that some of the larvae produced in the bay may be retained; however, residence times will vary greatly with atmospheric forcing (Heath 1973). Coastal embayments such as St. Margarets Bay, typically have recirculating currents, and consequently higher retention times than open coasts, promoting the retention of locally produced larvae (Largier 2003); consequently, they may provide ideal locations for the establishment of newly introduced species.

Variability in temperature affects the growth and development rates of larvae (O'Connor et al. 2007). Larval development rates for many species increase with temperature, leading to shorter pelagic larval durations, decreased risk of larval mortality (Neverman & Wurtsbaugh 1994), and shorter dispersal distances (Metaxas & Saunders 2009). This suggests that retention within embayments could be higher for these coastally produced larvae in years with higher temperatures. Indeed, outbreaks *Membranipora membranacea* in kelp beds have been linked to periods of warmer water temperatures (Saunders & Metaxas 2008, Scheibling & Gagnon 2009).

The larvae of both species were found in the warmer, fresher surface layer and thus may be transported offshore (and possibly out of the bay) during wind-driven upwelling, due to the offshore movement of the surface layer under such conditions. A similar mechanism has been inferred in California, where larvae and new settlers of *Membranipora membranacea* were less abundant during upwelling than otherwise, suggesting that larvae had been displaced offshore (Yoshioka 1982). In contrast, if there is an offshore pool of compe-

tent larvae present in the warm surface water, they may be advected shoreward (and into embayments) during downwelling. Consequently, supply of competent larvae to the adult habitat (kelps at the shoreline) would be most pronounced during downwelling events, which at the shore are indicated by the downward movement of the isopycnals and decreased stratification. Using published data on settlement of *M. membranacea* in St. Margarets Bay from 2005 to 2006 (Saunders & Metaxas 2007), we found a negative relationship between abundance of settlers and thermal stratification, with highest settlement occurring when the water column structure was uniform between 4 and 12 m (Fig. 8). This relationship supports the hypothesis that downwelling is implicated in shoreward transport of larvae, as has been observed for other species (Roughgarden et al. 1991, Shanks & Brink 2005). Alternatively, the uniform structure of the water column between 4 and 12 m could be caused by mixing of the deep and shallow layers. Larvae were sampled from a relatively linear continuum of density from September to October, suggesting periodic mixing of the warm, fresh and cold, saline layers during this time. Furthermore, uniform vertical temperature distributions on 14 November suggest overturning (vertical convection) of the water column by this date.

Settlement patterns, from which we informed our sampling design in this study, should theoretically be more strongly influenced by the abundance of competent than precompetent, larvae. It does not appear that ontogenetic variations in distribution and abundance affect vertical patterns in larval distribution, since for each species, similar proportions of precompetent and competent larvae were observed at both depths. However, the proportion of competent larvae did vary between species, and over time. In particular, 80 to 90% of larvae of *Membranipora membranacea* were competent at the end of September and beginning of October, compared to <50% during other time periods. This could lead to a peak in settlement, which would not necessarily be reflected by an overall peak in larval abundance. Simultaneous measures of larval supply and settlement at fine temporal scales (d) at the shoreline are necessary to link the two (Pineda et al. 2009). Importantly, the processes of delivery of larvae from the pelagic to benthic habitats may be regulated or modified on very fine (m to 10s m) spatial scales in the surf zone close to the shore and the patterns of larval abundance may be, at best, only weakly related to patterns of settlement (Rilov et al. 2008, Dudas et al. 2009). For example, Rilov et al. (2008) found no relationship between the abundance of larvae of mussels 100s of m from shore and of settlement in the intertidal, suggesting that fine scale processes at the shore regulated larval settlement. Mechanisms that could decouple the 2 processes may include behavioural modifications in response to cues (Kingsford et al. 2002), such as chemical (Raimondi 1988, Koehl et al. 2007) or auditory (Radford et al. 2007, 2008) signals emitted from the settlement habitat. For example, the cyphonautes larvae of *M. membranacea* (and presumably *Electra pilosa*) are induced to transition to the benthic habitat and settle by a chemical cue released by macroalgae (Seed & O'Connor 1981, Stricker 1989).

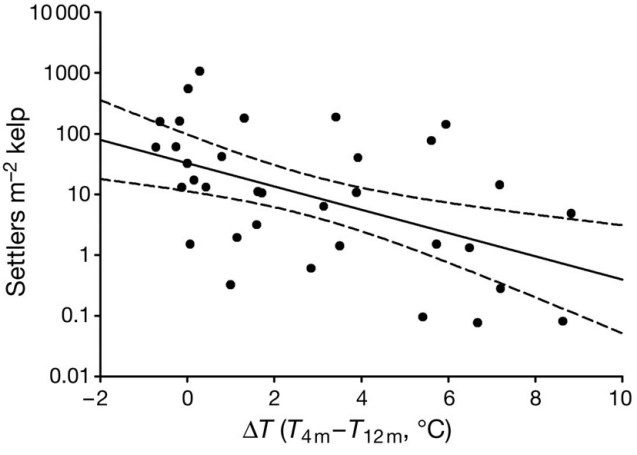

Fig. 8. *Membranipora membranacea*. Relationship between the abundance of newly settled colonies of the bryozoan and thermal stratification (temperature at 4 m – temperature at 12 m, °C), sampled at weekly-monthly intervals from July 2005 to September 2006. Data are average values for the number of newly settled colonies on n = ~30 kelps *Saccharina longicruris* obtained from 4, 8 and 12 m depth (pooled) on each date at each of 2 sites located in St. Margarets Bay, Nova Scotia, Canada (data published in a different form in Saunders & Metaxas 2007). For each date, ΔT was averaged over 7 d to correspond to the maximum duration over which settlers occur on kelps. Solid line was calculated based on least squares regression, log(settlers) = 1.52 – 0.20ΔT, p = 0.002, Adj. R^2 = 0.26; dashed lines are 95% confidence intervals

The larvae of both the native species *Electra pilosa* and the invasive species *Membranipora membranacea* responded similarly to changes in stratification, although the response was slightly more pronounced for *M. membranacea*. Similar distributions and abundances of the 2 species during this sampling period suggest that higher abundances of larvae of *M. membranacea*, or differences in transport processes between the 2 species, are not responsible for the invasive success of *M. membranacea* in the western North Atlantic. Rather, it more likely that continuous or repeated spawning events, fast colony growth rates, and the ability to reach large sizes all contribute to the success of *M. membranacea* (Scheibling & Gagnon 2009, Saunders et al. 2010). However, while overall patterns of distribution and abundance of larvae of the 2 species were similar, the earlier occurrence of high proportions of competent larvae, and the presence of multiple cohorts, may contribute to the success of *M. membranacea* in

ephemeral habitats, such as the blades of kelps. Long-term studies of larval distributions and settlement of both species over longer periods are recommended to fully identify the role of larval dispersal in regulating the population dynamics of these 2 species.

CONCLUSIONS

We made several predictions regarding the distributions of larvae of 2 species of bryozoan in relation to physical features of the water column. First, vertical larval distributions were predicted to be affected by the strength of stratification, and in a strongly stratified water column larvae to be located below the pycnocline. While there was a strong relationship between the strength of stratification and the vertical distributions of larvae, abundance was in fact greater above the density discontinuity, in the surface mixed layer. A linear relationship between strength of stratification and depth distributions was significant for *Membranipora membranacea* over temporal scales of hours and weeks, and spatial scales of kms, but did not hold for *Electra pilosa*. Second, larvae were predicted to be uniformly abundant between depths when the water column was well mixed, and this prediction was supported. Lastly, highest total abundance of larvae was predicted to occur when the water column was warm and well mixed; however, this was not the case for either species. The high concentrations of larvae in the surface mixed layer suggest larval transport towards the adult habitat at the shore during wind-driven downwelling, which agrees with observations of high settlement under non-stratified conditions.

Acknowledgements. We thank N. Kelly, S. Watanabe, J.-S. Lauzon-Guay, B. Scheibling, J. Lindley, and A. Yorke for assistance in the field; M. Merrimen, A. Hay, C. Taggart, W. Judge and D. Shillinger for providing and assisting with equipment; and J. Short, A. Logan, K. Dinning and A. Roy for assistance in the laboratory. Comments from Drs. R. E. Scheibling, J. Sheng, and C. Taggart helped improve the manuscript. The work was funded by a grant from the Canadian Aquatic Invasive Species Network (CAISN) to A.M. and R. E. Scheibling, and by a National Sciences and Engineering Research Council (NSERC) Discovery Grant to A.M. M.I.S. was supported by fellowships from NSERC, the Killam Trusts, and the Faculty of Graduate Studies at Dalhousie University.

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Editorial responsibility: Richard Osman, Edgewater, Maryland, USA

Submitted: January 16, 2010; Accepted: September 23, 2010
Proofs received from author(s): November 12, 2010