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Bay-scale patterns in the distribution, aggregation and spatial variability of larvae of benthic invertebrates

Rémi M. Daigle[1,*], Anna Metaxas[1], Brad deYoung[2]

[1]Department of Oceanography, Dalhousie University, Halifax, Nova Scotia B3H 4R2, Canada
[2]Department of Physics and Physical Oceanography, Memorial University, St. John's, Newfoundland A1B 3X9, Canada

ABSTRACT: This study aimed to investigate mechanisms of pattern formation in the larval distributions of benthic invertebrates by relating the spatial and temporal variability in the larval distributions to that of physical and biological variables, such as temperature, salinity, fluorescence and current velocity. Larvae were sampled at 11 sites on Aug 7–8 and 11–12, 2008 and at 16 sites on Aug 2–4, 2009, with a 200 µm plankton ring net (0.75 m diameter) towed for 5 min at 3 m and 12 m depth (in and below the mixed layer, respectively) in St. George's Bay, Nova Scotia, Canada. In 2009, density, temperature, salinity, and fluorescence were measured with a conductivity-temperature-density (CTD) cast at each station, and currents were quantified with an acoustic Doppler current profiler (ADCP) moored at 5 locations throughout the bay. In 2008, we only measured temperature. Gastropod, bivalve and, to a lesser extent, bryozoan larvae had very similar spatial distributions, but the distribution of decapod larvae followed a different pattern. These findings suggest that taxonomic groups that have functionally (i.e. swimming ability) similar larvae (e.g. bivalves and gastropods) also show similar dispersion properties (distribution and spatial variability), while the opposite is true for groups with functionally dissimilar larvae (e.g. bivalves and decapods). We also found that larval distributions of all taxa were significantly aggregated, although the degree of aggregation varied among taxa. Using an aggregation-diffusion model, we demonstrated that horizontal swimming was not an effective means of forming aggregations even at modest levels of diffusion. We hypothesize that patterns in observed horizontal distribution at this scale (<40 km) are determined during the larval phase, and that the primary mechanism for pattern formation is larval interaction with physical oceanographic structures (e.g. stratification and tidal currents).

KEY WORDS: Larval distribution · Larval aggregation · Aggregation-diffusion model · Larval dispersal · Larval ecology · Long residence times

INTRODUCTION

Larval dispersal is a key factor regulating the persistence of populations of marine benthic invertebrates and population dynamics of adults (Levin 2006, Cowen & Sponaugle 2009). Adult populations can be affected by spatio-temporal variations in the supply of settling larvae (Gaines & Roughgarden 1985, Underwood & Fairweather 1989). In turn, larval supply of settling larvae depends on a host of factors such as reproductive output, larval transport, larval behaviour, rates of mortality, and settlement behaviours in response to various cues (Rumrill 1990, Grosberg & Levitan 1992, Shanks & Brink 2005, Fuchs et al. 2007, DiBacco et al. 2011). Larvae of different species are often associated with water masses with markedly different temperature and/or salinity (Jillett 1976, Shanks et al. 2002). Spatial patterns in larval distributions are affected by biological processes (e.g. mortality) and by interaction with physical fea-

*Corresponding author: rm954459@dal.ca

tures (e.g. fronts) in the water column (Pineda 1991, Grosberg & Levitan 1992, Morgan 1995, DiBacco et al. 2011, Thompson et al. 2012, Daigle 2013). Spatially disjunct populations are connected both demographically and genetically by this interdependence of larval and adult stages (Levin 2006, Cowen & Sponaugle 2009).

It is well established that the vertical distribution of larvae will affect their dispersal distance and direction (North et al. 2008, Tapia et al. 2010, Lloyd et al. 2012a,b). Larvae can alter their vertical distribution by sinking, floating or swimming in response to cues such as light, tidal cycle, temperature, salinity, and food availability (Tremblay & Sinclair 1990, Kingsford et al. 2002, Sameoto & Metaxas 2008, Daigle & Metaxas 2011). Larvae that occupy different layers of the water column are exposed to different current patterns and have different resulting dispersal trajectories.

Different mechanisms for cross shelf larval migration have been documented, such as tidal stream transport (DiBacco et al. 2001, Forward et al. 2003), and the upwelling-relaxation paradigm (Wing et al. 1995, Miller & Emlet 1997). In selective tidal stream transport, larvae exploit the vertical shear in current velocity by vertically migrating over a tidal cycle. For example, larvae that are in the surface layer during flood tide and migrate to the bottom layer (with lower current velocities) during ebb tide will experience net transport towards the mouth of an estuary (Forward & Tankersley 2001). Along the western margins of continents where major upwelling occurs, larvae can exploit cross-shelf currents to disperse offshore during upwelling periods and return to a coastal habitat to settle during a period of relaxation (Wing et al. 1995, Miller & Emlet 1997). There are also mechanisms that occur at smaller scales and can affect larval transport and aggregation, such as internal tidal bores (Pineda 1991), or frontal systems and Langmuir cells (Omori & Hamner 1982). These mechanisms operate by aggregating larvae in up- or down-welling areas, since larvae can float, sink or swim in response to vertical current velocities. However, all these behaviours appear to be specific to species or developmental stage, and can also vary among populations (Forward et al. 2003, Shanks & Brink 2005, Tapia et al. 2010).

Horizontal swimming is not generally considered an important factor regulating larval transport or patch formation since invertebrate larvae are relatively poor swimmers (Chia et al. 1984). However, it is feasible that orientated swimming may assist shoreward transport for the stronger swimmers, such as crab megalopae (Shanks 1995). Despite poor larval swimming ability, horizontal larval aggregations, or patches, are commonly observed (Olson & Olson 1989, Folt & Burns 1999). These patches can form because of spatially heterogeneous mortality due to predation, lack of food availability, or other environmental variables, such as low salinity or extreme temperatures (Rumrill 1990). Patches can also form due to the interaction between vertical swimming and physical features of the water column (internal tidal bores, vertical currents, etc).

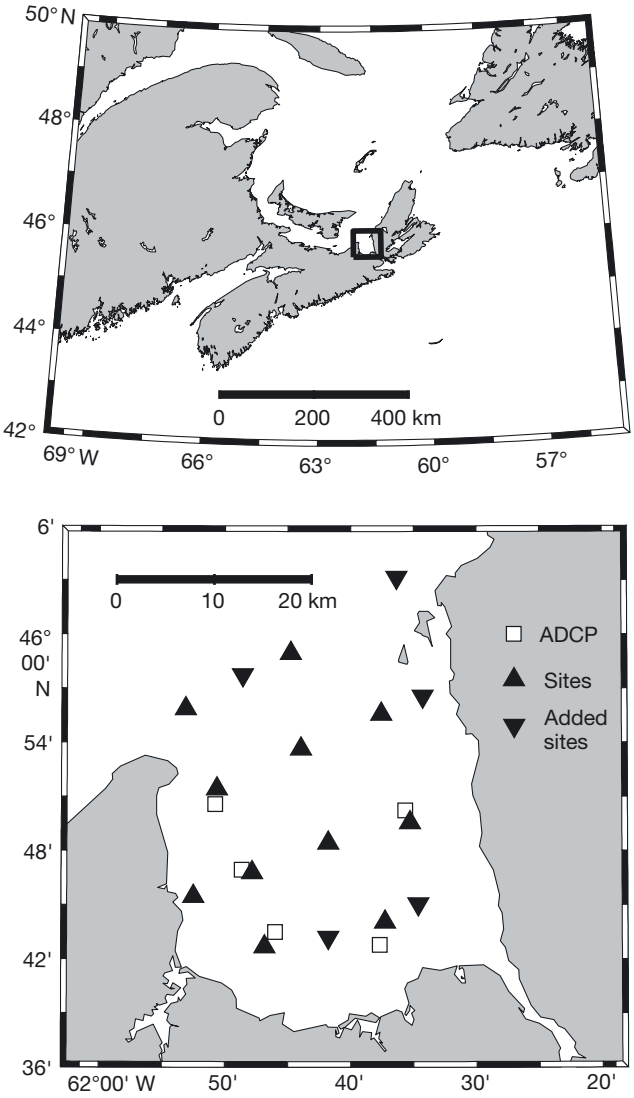

Fig. 1. Regional map showing the location of study site (St. George's Bay, Nova Scotia) and bay-scale map showing the location of the Acoustic Doppler Current Profiler (ADCP) moorings deployed in July and August 2009, as well as the larval sampling locations for 2008 and 2009. In 2008, larvae were collected from 11 sites, while 5 additional sites were sampled in 2009 for a total of 16 sites

By comparing patterns of larval distribution and the physical properties of the water column (temperature, salinity, fluorescence, current velocities), we can identify potentially important larval transport mechanisms. We conducted this study in a bay with no strong oceanographic features (e.g. estuarine plumes, upwelling events, or markedly different water masses; see detailed description in 'Results') to identify mechanisms that affect larval dispersal that are not dependent on these strong features. Such mechanisms have the potential to be more broadly applicable in coastal embayments throughout the world. We also constructed an aggregation-diffusion model to explore the potential role of horizontal swimming in the formation of larval aggregations.

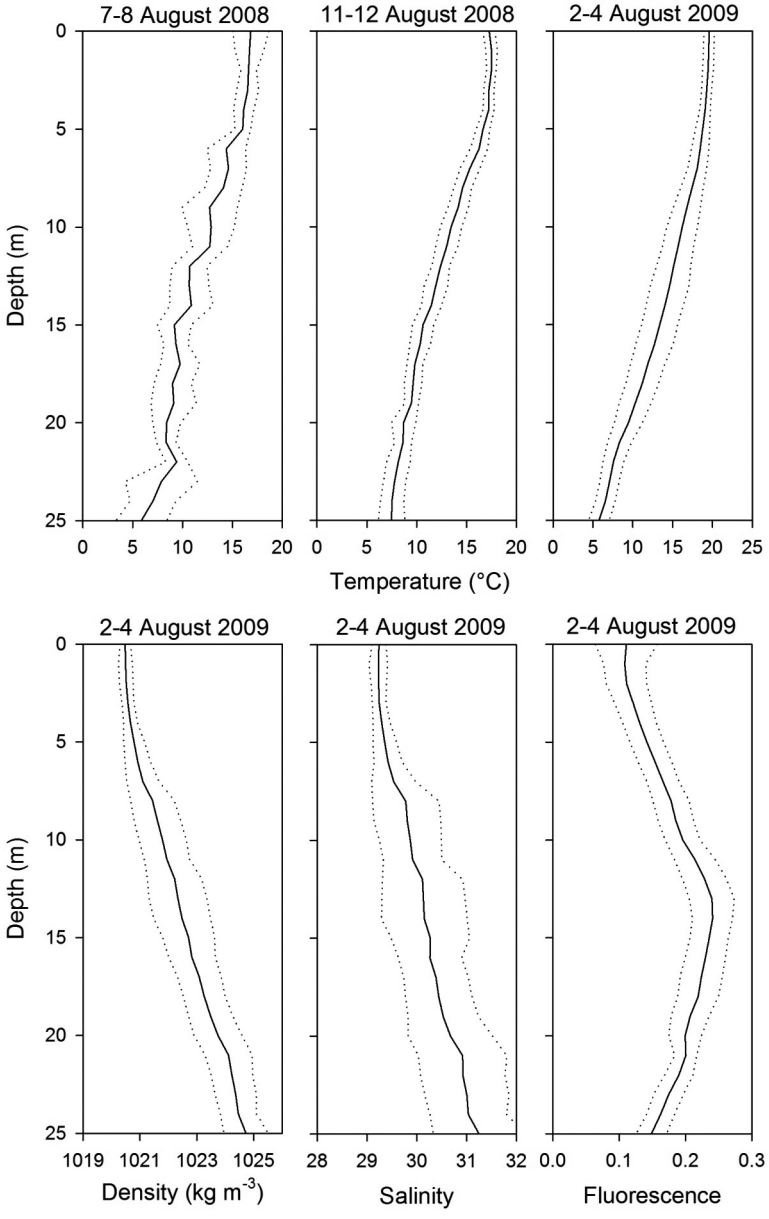

Fig. 2. Average vertical profiles of temperature for all sampling periods, and density, salinity and fluorescence from 2 to 4 August 2009 in St. George's Bay, Nova Scotia, Canada (±1 SD, n = 32 for 2009, n = 22 for 11 and 12 August 2008 and n = 4 to 22 for 7 and 8 August 2008). In 2009, temperature, salinity and fluorescence were measured with a conductivity-temperature-density (CTD) profiler. In 2008, temperature was measured with a Vemco Minilog Temperature-Depth Recorder

MATERIALS AND METHODS

Field sampling

The study site was located at St. George's Bay, Nova Scotia, Canada (Fig. 1), a bay without strong oceanographic features and with a flushing time on the order of a month (Petrie & Drinkwater 1978). The depth at the sampling locations ranged from 18 to 36 m. The water column in St. George's Bay in August 2008 and 2009 was stratified, and the surface mixed layer extended to 5–10 m depth below which there was a gradient of increasing salinity, decreasing temperature, and increasing density extending to the seafloor (Fig. 2).

In 2009, temperature, conductivity, pressure and fluorescence were measured with a conductivity-temperature-density (CTD) profiler immediately before and after larval sampling at each station. Data from the 2 down-casts were averaged into 1 m bins. Since we did not detect any large site-specific differences in salinity, temperature or density, data from all sites were averaged over the entire bay (Fig. 2). At 3 m, differences across sites were less than 1.5°C, 0.4 relative salinity, 0.5 kg m^{-3} and 0.08 relative fluorescence and at 12 m, differences were less than 4°C, 1.2 relative salinity, 2 kg m^{-3} and 0.09 relative fluorescence. No conductivity-temperature-density (CTD) data are available for 2008 because of instrument failure. However, some data was provided by a Vemco Minilog Temperature-Depth Recorder (TDR) attached to the net during plankton tows on 7 and 8 August 2008, and TDR casts to 30 m depth were completed on 11 and 12 August 2008.

To measure circulation patterns throughout the bay, five 600 kHz Teledyne RDI Workhorse Sentinel Acoustic Doppler Cur-

Table 1. Location of sampling sites and specific sampling dates within each sampling period: 7 and 8 August 2008 (2008A), 11 and 12 August, 2008 (2008B), and 2 to 4 August 2009

Longitude (°W)	Latitude (°N)	2008A	2008B	2009
61.8751	45.7578	7&8 Aug	11 Aug	3&4 Aug
61.7974	45.7799	7 Aug	12 Aug	3 Aug
61.6965	45.8072	7 Aug	12 Aug	3 Aug
61.5881	45.8261	7 Aug	12 Aug	3 Aug
61.6214	45.7343	7 Aug	12 Aug	4 Aug
61.7807	45.7115	7 Aug	12 Aug	4 Aug
61.8440	45.8573	8 Aug	11 Aug	2 Aug
61.8852	45.9312	8 Aug	11 Aug	2 Aug
61.7461	45.9825	8 Aug	11 Aug	2 Aug
61.6260	45.9263	8 Aug	11 Aug	3 Aug
61.7325	45.8942	8 Aug	11 Aug	2 Aug
61.6964	45.7199			4 Aug
61.5772	45.7508			4 Aug
61.5710	45.9424			3 Aug
61.6058	46.0522			2 Aug
61.8096	45.9624			2 Aug

rent Profilers (ADCP) were deployed on the seafloor, sampling the full water column in 1 m depth bins every 20 min from 11 Jul to 22 Aug 2009 (Fig. 1). The ADCP in the south-east corner of the bay malfunctioned and only recorded data from 11 to 14 Jul 2009. For each profile, only the horizontal velocities were included in the bin centered at 3 m (2.5 to 3.5 m) and 12 m (11.5 to 12.5 m) for calculation of mean current velocities.

Larval abundance was sampled at 11 sites on 7–8 and 11–12 August 2008 and at 16 sites on August 2–4, 2009 (Table 1), with a 200 µm plankton ring net (0.75 m diameter) towed for 5 min at both 3 m and 12 m depth. These depths were designed to sample (1) the surface mixed layer and (2) within the pycnocline, at or near the fluorescence maximum. The net was towed at ~1.7 m s^{-1} and the volume of filtered water was quantified using a General Oceanics flow meter. Using a net of this mesh size may underestimate abundance of small larvae (<200 µm). However, it is a necessary compromise in this multi-species study to allow capture of a wide range of larval types at sufficient numbers (e.g. very abundant but small gastropods to larger but rare decapods). All plankton samples were preserved in 95% ethanol and larvae were identified and enumerated under a Nikon SMZ 1500, as described in Lloyd et al. (2012b). Samples were split into subsamples using a Folsom plankton splitter. For n = 8, samples were split to 1/64 of the original volume and all subsamples were processed. Based on those samples, we determined that at least 20 ind. of each species were required to obtain an estimate of abundance that was within 5% of the true sample abundance. The remainder of the samples were split to between 1/128 and 1/1 to ensure that ≥20 ind. of the most abundant species (*Margarites* spp., *Astyris lunata*, *Mytilus* spp., *Electra pilosa* and *Cancer irroratus*) were enumerated. In addition to these 5 species that met the above criteria, we used some less abundant species in some data analyses (see below); however, the validity of the results should not be affected because there was no bias in the estimated abundances and there was often spatial and/or temporal replication.

Data analyses

The logarithm (base 10) of larval abundance (no. m^{-3} for each station by depth combination) was used for all statistical tests because it improved the normality of count data (Zar 1999). For some analyses, species were combined into 4 taxonomic groups (bryozoans, gastropods, bivalves and decapods) to allow taxonomic generalizations of the results. We used 2-way ANOVA to examine the effects of depth (fixed factor; 2 levels) and sampling period (random factor; 3 levels) on the larval abundance of each species, and also of each taxonomic group, using different sites as replicates. In cases where the p-value for the interaction term was ≥0.250, we pooled the mean squares and degrees of freedom from the interaction with those of the error term, and used the pooled error term to calculate a new *F*-statistic for depth (Underwood 1997). We also used non-metric multidimensional scaling (nMDS) plots on Bray-Curtis similarities to visualize (1) the similarity in distribution of sites among species for each depth (combined for all sampling periods) and (2) the similarity of species assemblages among sampling sites (combined for all sampling periods). Species with more than 1/3 null abundance were not used in the nMDS analysis. To test hypotheses related to the nMDS analyses, we used permutational multivariate analysis of variance with distance matrices (PERMANOVA) as part of the 'vegan' package in R (Oksanen et al. 2012).

We examined the relationships among larval abundances of the most abundant species and of the 4 taxonomic groups within a sampling period, as well as among abundances at different sampling periods using Pearson's correlations. The former analysis was performed on (1) the entire data set to identify overall patterns (n = 79) and on (2) each of the first 2 sampling periods (7–8 and 10–11 August 2008) sepa-

rately to compare the relative significance of cross-group relationships within a sampling period and among sampling periods, with similar statistical power (n = 22). Using the 2009 data, we also examined the relationship between the physical variables of the water column (temperature, salinity and fluorescence) and larval abundance using Pearson's correlations. For these analyses, we used only the 2 most abundant species from each taxonomic group (except bryozoans for which we used 1 species) because the estimates for the less abundant species were highly variable and less accurate. We calculated the index of dispersion (I_D) for each taxonomic group given by:

$$I_D = \frac{\sigma}{\mu} \quad (1)$$

where μ is the mean of larval abundance, σ is its variance, and I_D follows a χ^2 distribution with $n-1$ degrees of freedom (Cox & Lewis 1966). We also calculated Morisita's index of dispersion (I_M) given by:

$$I_M = \frac{n\sum_i x_i^2 - x_i}{n\bar{x}^2 - n\bar{x}} \quad (2)$$

where x_i is the larval abundance at site i, and n is the number of sites. We calculated the statistic:

$$I_M\left(\sum_i x_i - 1\right) + n - \sum_i x_i \quad (3)$$

which follows a χ^2 distribution with $n-1$ degrees of freedom test for departures from randomness (Morisita 1959).

Table 2. Summary statistics of larval abundance (ind. m^{-3}), during plankton sampling in St. George's Bay, Nova Scotia, Canada, in August 2008 at 11 sites, and August 2009 at 16 sites. Proportional species composition for each group is also shown

(a) Basic statistics	Mean	Median	Minimum	Maximum
Bryozoans	14.1	10.8	0.01	54.7
Bivalves	32.5	10.7	0.05	436
Gastropods	44.0	20.9	0.06	709
Decapods	2.38	1.27	0.00	13.1

(b) Composition Species	%
Bryozoans	
Electra pilosa	99.2
Membranipora membranacea	0.80
Bivalves	
Mytilus spp.	61.9
Modiolus modiolus	3.40
Anomia simplex	8.00
Other	26.7
Gastropods	
Margarites spp.	39.4
Astyris lunata	31.5
Diaphana minuta	8.20
Crepidula spp.	11.6
Arrhoges occidentalis	1.80
Bittiolum alternatum	3.90
Other	3.60
Decapods	
Cancer irroratus	71.5
Crangon septemspinosa	24.1
Neopanopeus sayi	0.50
Carcinus maenas	3.90

Aggregation-diffusion model

We developed a 1-dimensional horizontal individual-based aggregation-diffusion model to examine the effect of the interaction between diffusion and aggregative horizontal swimming on the larval distribution as detected by a sampling design comparable to the one we used in St. George's Bay (see the Supplement at www.int-res.com/articles/suppl/m503p139_supp/). All simulations were initiated with a 40 km 1-dimensional transect with reflective boundaries, representing the width of the bay. The transect was randomly seeded with 3.3×10^4 to 7.78×10^5 individual simulated larvae (SL) to approximate the mean larval densities of 4 taxonomic groups in St. George's Bay (Table 2). Aggregative swimming behaviour was simulated by SL swimming horizontally towards the nearest 'point of attraction'. These stationary points in space could represent any hypothetical point to which a larva may swim towards (e.g. food patch, ideal settling location, etc). This simulation was not intended to represent a specific scenario, but was designed to assess the feasibility of aggregation formation through horizontal swimming. We placed points of attraction every 3 km, to reflect an estimated larval patch size in St. George's Bay (Daigle 2013). The horizontal position (x_t) of each larva at time t after a time interval (Δt) was given by:

$$x_t = x_{t-1} + (u_t + d_t) \times \Delta t \quad (4)$$

where u_t is the larval swimming speed, set to 0.75 mm s^{-1} for bryozoans, 1.35 mm s^{-1} for bivalves, 1.3 mm s^{-1} for gastropods, and 13 mm s^{-1} for decapods (reflecting mid-range values from the literature; Ryland 1977, Chia et al. 1984, Shanks 1995, Young 1995). We varied the diffusion index (D) from 0 to 50 m^2 s^{-1}, by adding random movement (d_t) based on a normal distribution with a null mean and a standard deviation (SD) given by:

$$SD = \sqrt{q_i D \Delta t} \quad (5)$$

where q_i is a numerical constant that depends on dimensionality (in this case $q_i = 2$) and Δt is the time interval (Δt = 1 h) (Einstein 1956). To ensure that aggregations were given sufficient time to form, we chose to run the simulation for 30 d which reflects realistic average planktonic larval durations for these species. I_M and I_D were calculated based on larval abundance on Day 30, which was sampled with 11 randomly-located, 500 m long simulated tows along the transect (reflecting the empirical sampling design).

RESULTS

Physical characteristics of St. George's Bay

St. George's Bay is an open coastal embayment, ~45 × 45 km, that is generally shallow, with a mean depth of ~20 m and a maximum depth of 35 to 40 m. There is little freshwater runoff into the Bay, and the primary forcing of the circulation is from the tides and wind, both local and from the neighbouring Gulf of St. Lawrence. The tidal currents in the Bay are generally weak mixed diurnal to semidiurnal, with a tidal range of about 1.5 m (Canadian Hydrographic Service; www.charts.gc.ca/twl-mne/index-eng.asp). The dominant tidal constituent, the semi-diurnal M_2 velocity, has an amplitude near the mouth of ~0.10 m s^{-1}. Other tidal constituents are much smaller.

Peak surface currents observed during the summer approach 0.30 m s^{-1} at the surface (Lesperance et al. 2011a), and are somewhat lower near the seafloor. In 2009, mean current velocity at the 5 stations where we deployed ADCPs was <0.05 m s^{-1} (SD: 0.05 to 0.10 m s^{-1}). Petrie & Drinkwater (1978) suggested a clear clockwise circulation, with similar current amplitudes to those we observed. However, our observations in 2009 (Lesperance et al. 2011a) and in 2010 (Lesperance et al. 2011b) did not reveal such a clear, persistent circulation pattern (Fig. 3). For summer, the mean circulation is primarily a result of the persistent winds, forcing locally within the Bay and in the Gulf of St. Lawrence.

In 2009, mean (±SD, n = 241 to 3100) vertical current speed at specific sites ranged from 0.07 ± 2.3 mm s^{-1} to 0.83 ± 5.0 mm s^{-1}. Horizontal current speed ranged from 0.002 ± 0.081 m s^{-1} to 0.038 ± 0.068 m s^{-1} at 3 m, and from 0.006 ± 0.081 m s^{-1} to 0.071 (±0.084) m s^{-1} at 12 m (Fig. 3). The highest mean velocities were recorded by the ADCP in the south-east corner of the Bay, and only represent a few days of data because it malfunctioned. Mean current velocities in either N-S or E-W directions at all sites were generally half the magnitude of a single standard deviation.

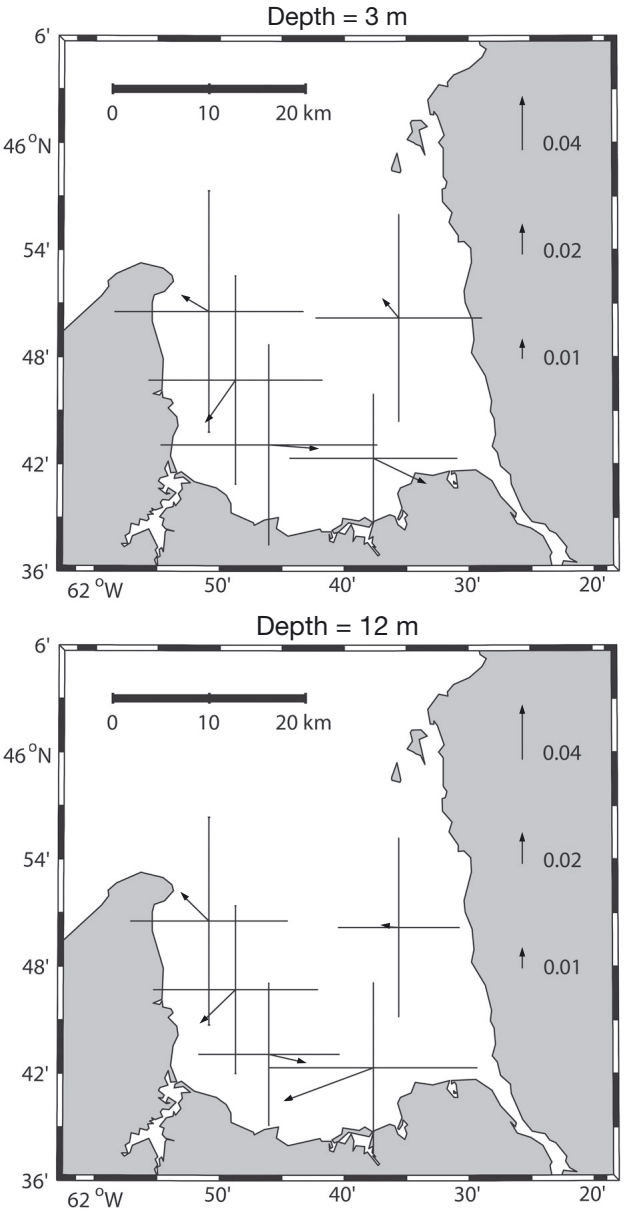

Fig. 3. Mean current velocities (m s^{-1}) at 5 ADCP moorings from 11 July to 22 August 2009 at 3 and 12 m. Error bars indicate one standard deviation (n = 3081, 3085, 3088, 241, 3100, respectively, counter-clockwise from N-E) in both the N-S and E-W directions

The residence time in the Bay is surprisingly long given the scale of the Bay. Petrie & Drinkwater (1978) estimated time scales for tidal exchange of 15 d and for the mean circulation of 40 d. Using a numerical model of the circulation (Saucier & Chassé 2000), we

estimated an e-folding residence time for water in the Bay between 10 and 15 d (B. deYoung, unpubl. data).

There is relatively weak horizontal spatial structure in the density field, and essentially no geostrophic circulation given the weak lateral stratification. The surface mixed-layer in summer is formed by solar heating and wind-forcing and deepens over the summer period, with very weak gradients in the top 10 m. However, there is a strong, often nearly linear, gradient in temperature, salinity, and density from the base of the surface mixed-layer (10 m) to at least 25 m depth (Fig. 2). The temperature, salinity, and density gradually changes from 17°C, 29.8 and 1021.6 kg m^{-3}, respectively, at 10 m to 6°C, 32, and 1024.7 kg m^{-3} at 25 m. Consequently, there is a strong density gradient and a clear boundary between the well-mixed surface waters (0 to 10 m) and the stratified near-bottom water (Fig. 2), from 10 to at least 25 m below the surface. The fluorescence maximum was at ~13 m. While only temperature profiles were available in 2008, the temperature profiles from all 3 sampling periods (Fig. 2) are very similar (except for the higher variability on 7 and 8 August due to lower sample size), lending support to the consistency of the observed patterns.

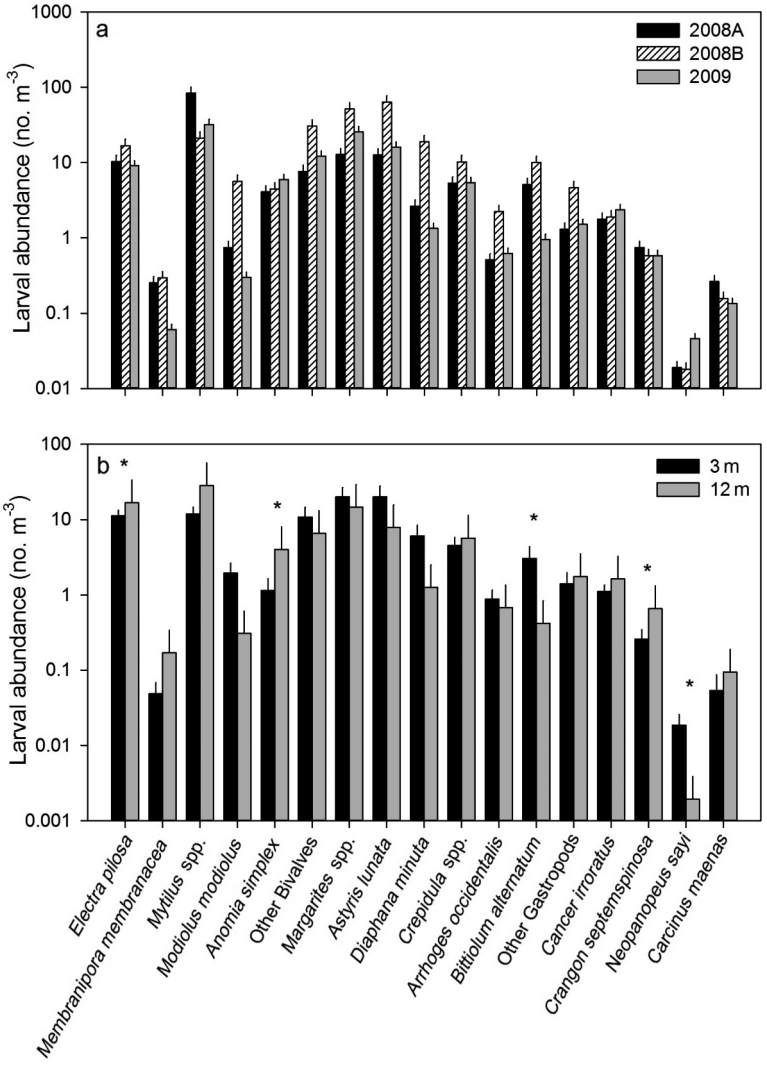

Fig. 4. Average larval abundance of species in St. George's Bay, Nova Scotia, Canada, at different (a) sampling dates and (b) depths. Larvae were sampled at 3 and 12 m depth with a 200 µm plankton ring net (0.75 m diameter) on 7 and 8 August 2008 (2008A), 11 and 12 August 2008 (2008B), and 2 to 4 August 2009. Error bars indicate standard errors (n = 79) and asterisks indicate significant differences ($p < 0.05$) as detected by ANOVA (see Table 3 for details)

Patterns in larval abundance

Each taxonomic group consisted mostly of a few species (Table 2). The bryozoans consisted almost entirely of *Electra pilosa*, whereas the bivalves were mostly *Mytilus* spp. The gastropods consisted of *Margarites* spp. and *Astyris lunata*, and the decapods were mostly *Cancer irroratus*. For each species, there was little variability in abundance among sampling periods at the bay scale (Fig. 4, Table 3). Only the larval abundance of *E. pilosa*, *Anomia simplex*, *Bittiolum alternatum, Crangon septemspinosa* and *Neopanopeus sayi* varied significantly with depth (Fig. 4, Table 3). Additionally, there was a significant interaction between period and depth for *Modiolus modiolus, Margarites* spp. and *Diaphana minuta*, indicating that their depth distribution varied over time. When combined into taxonomic groups (Fig. 5), larval abundance did not vary with sampling period and only bryozoan abundance varied significantly with depth (Table 4). In contrast, the ordination of species based on sites (i.e. horizontal distribution) revealed that several gastropod and bivalve species were clustered in the center of the plot, while the bryozans, all decapods and a few gastropod and bivalve species were on the periphery (Fig. 6). These results suggest that the horizontal distributions vary with species and this may be the result of vertical gradients (e.g. *A. simplex, B. alternatum, C. septemspinosa*) or not (e.g. *C. irroratus, M. modiolus*). PERMANOVA

Table 3. Results of ANOVAs examining the random effect of sampling period (P) and fixed effect of depth (D) on the logarithm (base 10) of larval abundance by species. Asterisks indicate significant differences (*p < 0.05; **p < 0.01; ***p < 0.001). **Bold** values indicate where the sums of squares and df from error term have been pooled with those of P × D (when p ≥ 0.250 for P × D), and *F* and p values for D (df = 1,75) have been recalculated. Depth preference type (B = 'bottom', S = 'shallow', ND = 'no difference') for the PERMANOVA in Table 5 is indicated for each species included in the analysis. Type X species were not included because their abundance was >1/3 null (more than a third of the sample counts were zero)

Taxon	Type	P (df = 2,73)		D (df = 1,2)		P × D (df = 2,73)	
		F	p	*F*	p	*F*	p
Bryozoans							
Electra pilosa	B	0.902	0.526	**8.953**	**0.004****	1.411	0.250
Membranipora membranacea	X	2.318	0.301	4.455	0.167	2.230	0.115
Bivalves							
Mytilus spp.	ND	0.175	0.851	1.027	0.416	1.898	0.157
Modiolus modiolus	ND	2.032	0.330	5.512	0.142	3.671	0.030*
Anomia simplex	B	1.969	0.337	**11.397**	**0.001****	1.333	0.270
Other bivalves	ND	0.734	0.577	0.328	0.624	1.616	0.206
Gastropods							
Margarites spp.	ND	1.100	0.476	0.071	0.815	3.841	0.026*
Astyris lunata	ND	0.545	0.647	**2.144**	**0.147**	0.797	0.455
Diaphana minuta	ND	3.417	0.226	2.881	0.231	3.520	0.035*
Crepidula spp.	ND	1.885	0.347	**1.895**	**0.173**	0.471	0.626
Arrhoges occidentalis	ND	2.828	0.261	**0.015**	**0.901**	1.303	0.278
Bittiolum alternatum	S	1.236	0.447	**15.199**	**<0.001*****	1.302	0.278
Other gastropods	ND	0.811	0.552	2.255	0.270	1.897	0.157
Decapods							
Cancer irroratus	ND	5.245	0.160	**0.685**	**0.41**	0.362	0.698
Crangon septemspinosa	B	5.759	0.148	**13.554**	**<0.001*****	0.560	0.574
Neopanopeus sayi	X	20.261	0.047*	**5.034**	**0.028***	0.012	0.988
Carcinus maenas	ND	0.083	0.923	0.368	0.605	3.082	0.052

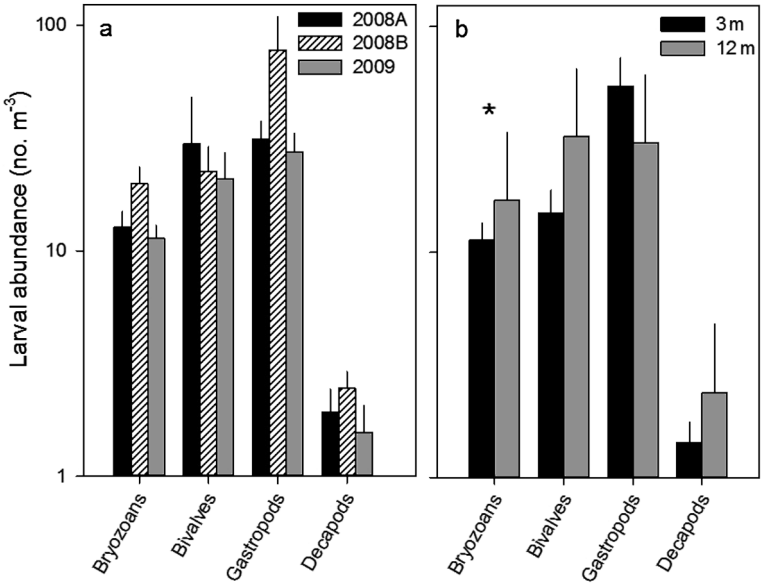

Fig. 5. Average larval abundance of taxonomic groups in St. George's Bay, Nova Scotia, Canada, at different (a) sampling dates and (b) depths. Larvae were sampled at 3 and 12 m depth with a 200 µm plankton ring net (0.75 m diameter) on 7 and 8 August 2008 (2008A), 11 and 12 August 2008 (2008B), and 2 to 4 August 2009. Error bars indicate standard errors (n = 79) and asterisk indicates significant difference (p < 0.05) as detected by ANOVA (see Table 3 for details)

revealed that depth preference had a significant effect on the similarity in distribution among species (Table 5). Depth preference type was determined by the significance (or not) and the direction of the skew in the depth distribution, illustrated in Fig. 4 and Table 3. The relationship between species assemblages and depth is unclear as there was no clear distinction of clustering by depth or sampling period in the nMDS plot (Fig. 7). However, the PERMANOVA revealed that both depth and sampling period had a significant effect on the species assemblage (Table 5).

Larval distribution of all taxonomic groups showed significant departures from randomness (Table 6), i.e. exhibiting aggregation. For gastropods and bivalves, I_D was more than an order of magnitude higher, and the overall I_M was more than double that of bryozoans and decapods. Therefore, the distributions of gastropods and bivalves consistently

Table 4. Results of ANOVAs examining the random effect of sampling period (P) and fixed effect of depth (D) on the logarithm (base 10) of larval abundance by taxonomic group (error df = 73). Asterisk indicates significant difference ($p < 0.01$). **Bold** values indicate where the sums of squares and df from error term have been pooled with those of P × D (when $p \geq 0.250$ for P × D), and *F* and p values for D (df = 1, 75) have been recalculated

Taxon	P (df = 2, 73)		D (df = 1, 2)		P × D (df = 2, 73)	
	F	p	*F*	p	*F*	p
Bryozoans	0.938	0.516	**9.0251**	**0.004****	1.396	0.254
Bivalves	0.232	0.812	0.362	0.608	1.171	0.188
Gastropods	0.288	0.776	0.079	0.805	2.573	0.083
Decapods	16.711	0.057	**3.403**	**0.069**	0.169	0.844

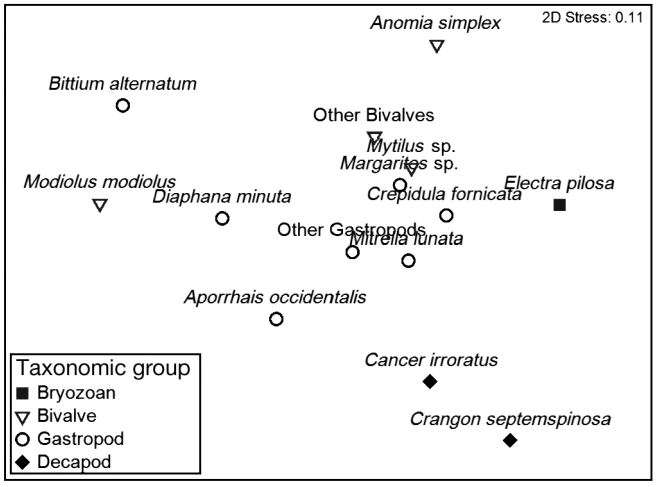

Fig. 6. Ordination from nonmetric multidimensional scaling of the species based on the similarity in larval abundance at each site, sampling period, and depth. Sites and sampling periods were used as replicates

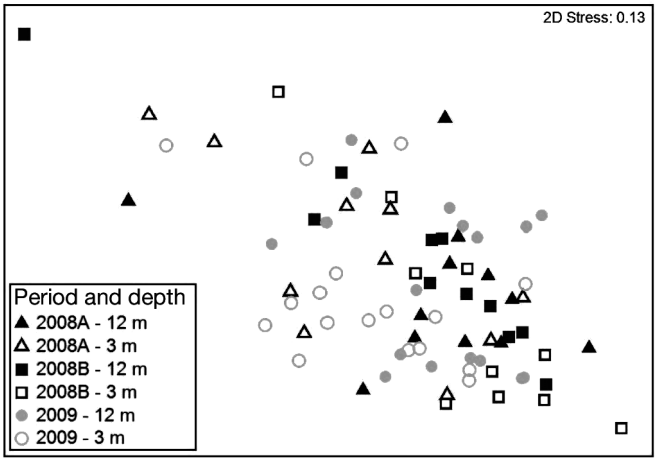

Fig. 7. Ordination from nonmetric multidimensional scaling of the sites by depth combinations based on the similarity in abundance of larval assemblages. Species were used as replicates

showed the highest degree of aggregation. This trend was fairly consistent over time and depth as there were only 2 instances where decapod distributions were more aggregated than that of gastropods (7 and 8 August 2008 at 3 m and 2 to 4 August 2009 at 12 m), and only 2 instances where decapod distributions were more aggregated than that of bivalves (7 and 8 August 2008 and 2 to 4 August 2009 at 3 m). The I_M for decapods was highly variable and ranged from 1.54 (Table 6), corresponding to a random distribution, to 3.65 (Table 6), which is higher than that of gastropods at that time and depth. Conversely, the I_M for bryozoans at all depths and times was consistently close to 1 (Table 6), but still high enough to depart from randomness.

Geographically, there was no consistent pattern of larval abundance over time. For 7 and 8 August 2008, there was a fairly even distribution of larvae of all taxonomic groups throughout the bay except

Table 5. Results of PERMANOVAs examining (a) the effect of depth and species, taxonomic group, and depth preference ('bottom', 'shallow', or 'no difference'; see Fig. 4 and Table 3) on the similarity in larval abundance of species (Fig. 6); and (b) the effect of depth and sampling period on the similarity in abundance of larval assemblages at sites (Fig. 7). Asterisks indicate significant differences (*$p < 0.05$; **$p < 0.01$). In (a) sites and sampling periods are used as replicates, and in (b) species are used as replicates

(a) Similarity of species	df	*F*	R^2	p
By species:				
Species	13	3.341	0.383	0.001**
Depth	1	0.942	0.008	0.312
Species × Depth	13	1.004	0.115	0.184
By taxonomic group:				
Taxon	3	3.633	0.120	0.001**
Depth	1	0.753	0.008	0.471
Taxon × Depth	3	0.998	0.033	0.302
By depth preference:				
Type	2	1.854	0.043	0.036*
Depth	1	0.709	0.008	0.513
Type × Depth	2	1.487	0.035	0.111
(b) Similarity of sites	df	*F*	R^2	p
Depth	1	5.109	0.060	0.002**
Period	2	2.119	0.050	0.016*
Depth × Period	1	1.861	0.044	0.290

Table 6. Index of dispersion (σ/μ) and Morisita's Index (I_M) for larval abundance (ind. m^{-3}) of each taxonomic group, during plankton sampling in St. George's Bay, Nova Scotia, Canada, on 7 and 8 August 2008 (2008A) and on 11 and 12 August 2008 (2008B) at 11 sites, and on 2 to 4 August 2009 at 16 sites. Morisita's index was calculated for the overall distribution, and for distributions for each depth and sampling period. All aggregative dispersal indices were significant at $p < 0.001$

	Bryozoans		Bivalves		Gastropods		Decapods	
Index of dispersion								
	σ/μ	p	σ/μ	p	σ/μ	p	σ/μ	p
Overall	11.02	<0.001	126.07	<0.001	164.43	<0.001	3.46	<0.001*
Morisita's Index								
	I_M	p	I_M	p	I_M	p	I_M	p
Overall	1.77	<0.001	6.22	<0.001	4.83	<0.001	2.78	<0.001*
3 m								
2008A	1.73	<0.001	2.34	<0.001	2.23	<0.001	3.59	<0.001*
2008B	1.83	<0.001	3.06	<0.001	3.13	<0.001	1.54	<0.001*
2009	1.90	<0.001	3.06	<0.001	2.42	<0.001	3.14	<0.001*
12 m								
2008A	1.37	<0.001	5.83	<0.001	1.48	<0.001	1.79	<0.001*
2008B	1.48	<0.001	1.71	<0.001	2.02	<0.001	1.74	<0.001*
2009	1.32	<0.001	4.09	<0.001	2.37	<0.001	3.65	<0.001*

at the northernmost site and near the southeast corner of the bay which had higher and lower abundances, respectively (Fig. 8a). For 11 and 12 August 2008, sites in the southern half of the bay generally had higher larval abundance than sites in the northern half across all taxa (Fig. 8b). For 2 to 4 August 2009, sites along the eastern and southern shores of the bay generally had higher abundance of bryozoans, bivalves and gastropods. Decapods were more abundant in the northwest corner of the bay (Fig. 8c).

Larval abundance (combined for both depths) was correlated for most pairs of taxonomic groups both when sampling period were combined, and within each sampling period. When considering the entire data set, the highest correlation was between the larval abundances of gastropods and bivalves (Table 7a), and the only non-significant correlation was between decapods and bivalves. When considering the specific sampling dates, the highest correlation was also between the larval abundances of gastropods and bivalves (Table 7b). On 11 and 12 August 2008, correlations among all pairs were significant, while 4 of 6 pairs were significantly correlated on 7 and 8 August. In general, the correlations among the larval abundance of decapods and other taxa were relatively weak, and most often occurred with bryozoans. A similar pattern was observed in the correlation of pairs of species (Table 8). The abundances of gastropod and bivalve species were highly correlated with one another, whereas decapod species were not significantly correlated with species of either bivalves or gastropods. Additionally, significant correlations were recorded among species within the same taxonomic group. However, when comparing site-specific abundances from 7 and 8 August to those from 11 and 12 August 2008, there were no significant correlations for any pair of taxa or species (Table 8c). This suggests that the spatial relationship among taxonomic groups at any one time is stronger than the temporal relationship within a single taxonomic group.

Overall, fluorescence and salinity showed the highest correlations with larval abundance (Table 9). Fluorescence was significantly positively correlated with both gastropods species and *Mytilus* spp. at 3 m, and with *Crangon septemspinosa* at 12 m. Fluorescence was positively correlated with 6 of 7 species at 3 m and all species at 12 m (although not all cases were significant). At 3 m, salinity was significantly negatively correlated with both bivalve species and significantly positively correlated with *Cancer irroratus*. Overall, salinity was negatively correlated with 5 of 7 species at 3 m and positively correlated with all species at 12 m. Temperature was only significantly negatively correlated with *C. irroratus* at 3 m, but was positively correlated with 4 of 7 species at 3 m and negatively correlated with all species at 12 m.

The aggregation-diffusion model showed that horizontal swimming does not reproduce the level of aggregation observed in the field when larvae were

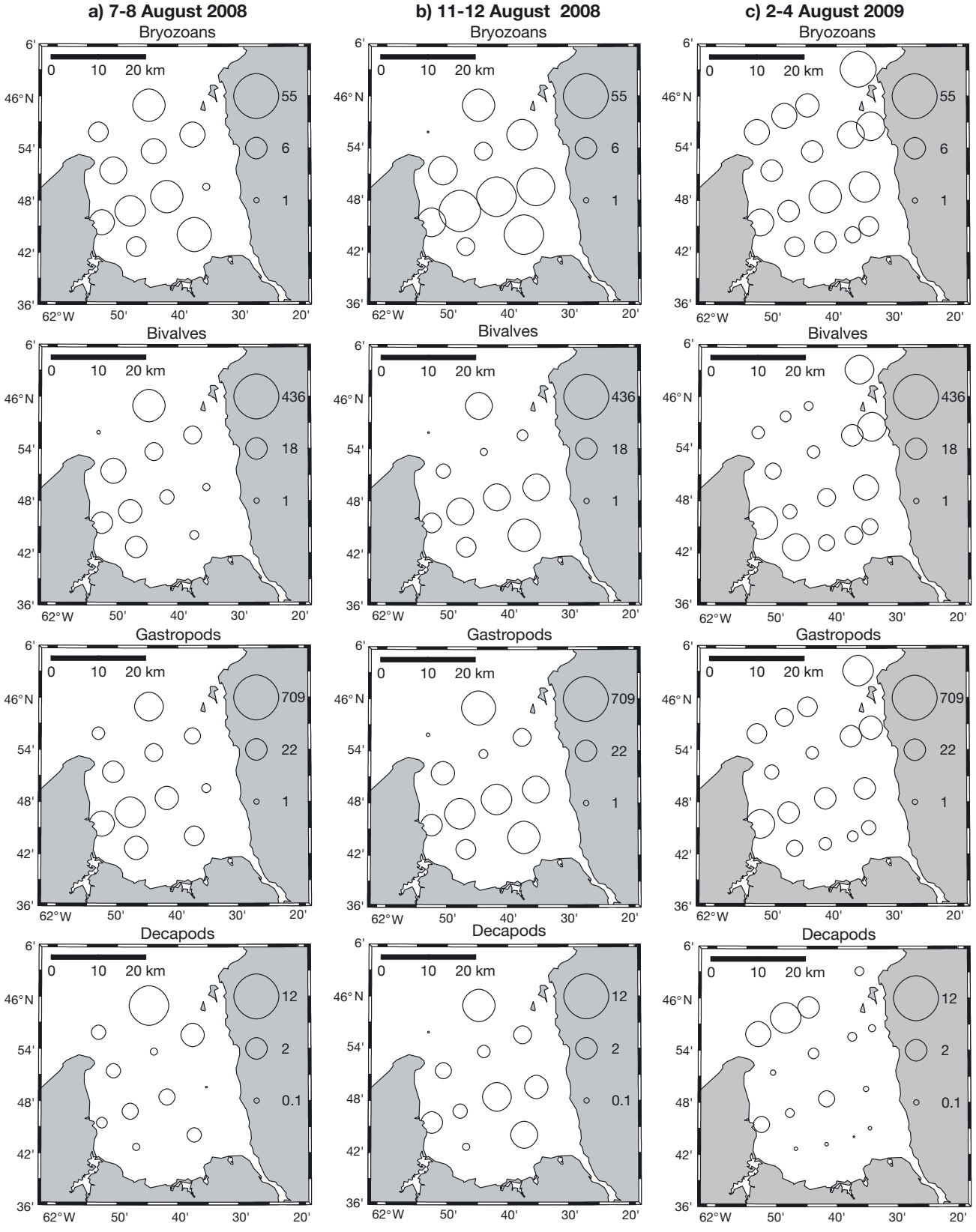

Fig. 8. Larval abundance (no. m^{-3}; averaged across depth) of taxonomic groups in St. George's Bay, Nova Scotia, Canada, at 11 different sampling sites. Larvae were sampled with a 200 µm plankton ring net (0.75 m diameter) on (a) August 7 and 8, 2008, (b) August 11 and 12, 2008, and (c) August 2 to 4, 2009. The size of the bubble is proportional to abundance

Table 7. Pearson correlation examining the relationship in logarithm (base 10) abundance (all sampling depths combined) for pairs of taxa—bryozoans (Bz), bivalves (Bv), gastropods (Gp) and decapods (Dp)—calculated for (a) all 3 sampling dates combined (n = 79), (b) specific sampling dates (n = 22), and (c) within and among taxa at different sampling dates (rows represent abundances from 7 and 8 August 2008 while the columns represent that from 11 and 12 August 2008; n = 22). In (a) and (b) the upper half of the matrix indicates the correlation coefficients for larval abundance while the lower half indicates the p-value. In (c) the number in brackets is the p-value. Statistically significant correlations are indicated in **bold** ($p < 0.05$)

	Bz	Bv	Gp	Dp
(a) All dates				
Bz	1	**0.532**	**0.708**	**0.584**
Bv	**<0.001**	1	**0.739**	0.163
Gp	**<0.001**	**<0.001**	1	**0.437**
Dp	**<0.001**	0.152	**<0.001**	1
(b) Specific sampling dates				
7 and 8 August 2008				
Bz	1	0.414	**0.584**	**0.655**
Bv	0.050	1	**0.683**	0.290
Gp	**0.003**	**<0.001**	1	**0.438**
Dp	**0.001**	0.180	**0.037**	1
11 and 12 August 2008				
Bz	1	**0.771**	**0.763**	**0.710**
Bv	**<0.001**	1	**0.902**	**0.646**
Gp	**<0.001**	**<0.001**	1	**0.564**
Dp	**<0.001**	**0.001**	**0.006**	1
2 to 4 August 2009				
Bz	1	**0.421**	**0.734**	**0.406**
Bv	**0.013**	1	**0.675**	−0.234
Gp	**<0.001**	**<0.001**	1	0.303
Dp	**0.017**	0.183	0.082	1
(c) 7 and 8 August vs. 11 and 12 August 2008				
Bz	0.319 (0.148)	0.194 (0.388)	0.143 (0.525)	0.410 (0.058)
Bv	0.344 (0.117)	0.115 (0.612)	0.114 (0.615)	0.287 (0.196)
Gp	0.330 (0.134)	0.222 (0.321)	0.223 (0.318)	0.250 (0.262)
Dp	0.125 (0.578)	0.061 (0.788)	0.181 (0.420)	0.395 (0.069)

exposed to diffusion (Fig. 9). Only at a diffusion index of 0 $m^2 s^{-1}$ were the I_M and I_D for bryozoans, bivalves and gastropods comparable to that from the field observations (Table 6). For the decapods, the I_M and I_D were similar to the values obtained from the field observations for diffusion indices 8 to 9 $m^2 s^{-1}$. Any evidence (I_M >1.1) of aggregations was removed for diffusion indices >2 $m^2 s^{-1}$ for bryozoans, >3 $m^2 s^{-1}$ for bivalves and gastropods, and >30 $m^2 s^{-1}$ for decapods.

DISCUSSION

At the bay scale, mean larval abundance of all 17 species and 4 taxonomic groups did not change significantly over the 3 sampling periods, but abundance was highly variable among individual sites over time. However, our sampling was limited to the first 2 wk in Aug 2008 and 2009 to maximize larval abundance of most species, and would not have captured seasonal effects. In the same region, Lloyd et al. (2012a,b) found that the vertical distributions of invertebrate larvae vary with depth. We found that 3 species (*Electra pilosa*, *Anomia simplex*, and *Crangon septemspinosa*) were significantly more abundant at 12 m, while *Bittiolum alternatum* and *Neopanopeus sayi* were significantly more abundant at 3 m. Lloyd et al. (2012b) also found that *B. alternatum* was more abundant above the thermocline in St. George's Bay over shorter time scales. The highest concentrations of bryozoans occurred at 18 m, and showed a positive relationship with fluorescence (Lloyd et al. 2012a). In contrast, bryozoan abundance in St. Margarets Bay (also in Nova Scotia) was higher at 4 m than at 12 m (Saunders & Metaxas 2010). However, the salinity and temperature at 4 m depth in St. Margarets Bay was more similar to that at 12 m in St. George's Bay. This pattern suggests that bryozoan larvae may prefer ~15°C and salinity of ~30. *A. simplex* was most abundant at 12 m in our study, which is in the thermocline, and were also found to be concentrated around the thermocline off Tuckerton, New Jersey, USA (Ma et al. 2006). We observed no significant difference in vertical distributions for bivalve larvae, but other studies with more rigorous sampling of depth distributions have found that they are most abundant below the thermocline (Lloyd et al. 2012a). Similarly, we found higher abundance of *C. septemspinosa* at the deepest sampling point (12 m); in Chesapeake Bay, USA, larvae of *C. septemspinosa* were found to be most abundant in the lower water column with higher salinities (Wehrtmann 1994).

Overall, the variability in larval abundance between depths was in most cases smaller than the spatial variability in larval abundance among sites. The similarity in species distributions appears to be affected by the vertical distribution of those larval populations with a vertical skew indicated by the fact that species with the largest differences in depth distribution were at the periphery of the nMDS plot, and depth preference type ('shallow', 'bottom' or 'no difference') had a significant effect on the similarity of species assemblages. However, *Cancer irroratus* and

Table 8. Pearson correlation examining the relationship in logarithm (base 10) abundance (all sampling depths combined) for pairs of taxa—*Electra pilosa* (Bz1), *Mytilus* spp. (Bv1), other bivalves (Bv2), *Margarites* spp. (Gp1), *Astyris lunata* (Gp2), *Cancer irroratus* (Dp1), *Crangon septemspinosa* (Dp2)—calculated for (a) all 3 sampling dates combined (n = 79), (b) specific sampling dates (n = 22) and (c) within and among taxa at different sampling dates (rows represent abundances from 7 and 8 August 2008, while the columns represent that from 11 and 12 August 2008; n = 22). In (a) and (b) the upper half of the matrix indicates the correlation coefficients for larval abundance for while the lower half indicates the Bonferroni-corrected p-values. In (c) the number in brackets is the p-value. Statistically significant correlations are indicated in **bold** ($p < 0.05$)

	Bz1	Bv1	Bv2	Gp1	Gp2	Dp1	Dp2
(a) All dates							
Bz1	1	**0.547**	**0.393**	**0.583**	**0.548**	**0.529**	**0.442**
Bv1	**<0.001**	1	**0.831**	**0.776**	**0.397**	0.124	0.302
Bv2	**<0.001**	**<0.001**	1	**0.696**	**0.471**	−0.056	0.121
Gp1	**<0.001**	**<0.001**	**<0.001**	1	**0.560**	**0.241**	**0.288**
Gp2	**<0.001**	**<0.001**	**<0.001**	**<0.001**	1	**0.367**	0.301
Dp1	**<0.001**	0.278	0.625	**0.033**	0.001	1	**0.574**
Dp2	**<0.001**	0.007	0.288	**0.010**	0.007	**<0.001**	1
(b) Specific sampling dates							
7 and 8 August 2008							
Bz1	1	**0.424**	0.297	**0.431**	0.381	**0.547**	**0.671**
Bv1	**0.044**	1	**0.792**	**0.842**	0.018	0.203	**0.595**
Bv2	0.169	**<0.001**	1	**0.849**	0.316	−0.018	0.309
Gp1	**0.040**	**<0.001**	**<0.001**	1	0.395	0.218	**0.495**
Gp2	0.073	0.935	0.142	0.062	1	0.227	0.250
Dp1	**0.007**	0.354	0.935	0.319	0.299	1	**0.666**
Dp2	**<0.001**	**0.003**	0.151	**0.016**	0.25	**0.001**	1
11 and 12 August 2008							
Bz1	1	**0.764**	**0.640**	**0.660**	**0.678**	**0.675**	0.349
Bv1	**<0.001**	1	**0.854**	**0.815**	**0.784**	**0.572**	**0.473**
Bv2	**0.001**	**<0.001**	1	**0.874**	**0.859**	**0.440**	0.393
Gp1	**0.001**	**<0.001**	**<0.001**	1	**0.858**	**0.451**	0.262
Gp2	**0.001**	**<0.001**	**<0.001**	**<0.001**	1	**0.504**	0.300
Dp1	**0.001**	**0.005**	**0.040**	**0.035**	**0.017**	1	0.278
Dp2	0.111	**0.026**	0.070	0.238	0.176	0.210	1
2 to 4 August 2009							
Bz1	1	**0.473**	0.331	**0.591**	**0.525**	0.366	0.277
Bv1	**0.005**	1	**0.888**	**0.840**	**0.407**	−0.245	−0.084
Bv2	0.056	**<0.001**	1	**0.712**	0.328	−0.314	−0.073
Gp1	**<0.001**	**<0.001**	**<0.001**	1	0.317	−0.050	−0.001
Gp2	**0.001**	**0.017**	0.058	0.068	1	0.330	0.310
Dp1	0.033	0.162	0.071	0.779	0.057	1	**0.6535**
Dp2	0.113	0.635	0.681	0.995	0.074	**<0.001**	1
(c) 7 and 8 August vs. 11 and 12 August 2008							
Bz1	0.32	0.212	0.098	0.004	0.199	0.332	0.322
	(0.147)	(0.344)	(0.664)	(0.986)	(0.375)	(0.131)	(0.144)
Bv1	0.336	0.142	−0.085	−0.038	0.043	0.272	−0.042
	(0.126)	(0.529)	(0.706)	(0.865)	(0.85)	(0.221)	(0.852)
Bv2	0.219	0.05	−0.168	−0.061	−0.012	−0.025	−0.033
	(0.328)	(0.826)	(0.456)	(0.787)	(0.957)	(0.914)	(0.886)
Gp1	0.352	0.21	0.003	0.1	0.158	0.164	0.101
	(0.109)	(0.349)	(0.988)	(0.657)	(0.484)	(0.466)	(0.654)
Gp2	0.197	0.278	0.103	0.214	0.138	0.023	0.329
	(0.381)	(0.211)	(0.649)	(0.339)	(0.541)	(0.919)	(0.135)
Dp1	0.068	−0.023	0.031	0.174	0.212	0.349	0.136
	(0.765)	(0.921)	(0.892)	(0.44)	(0.344)	(0.111)	(0.546)
Dp2	0.24	0.175	−0.046	−0.001	0.083	0.391	0.132
	(0.283)	(0.437)	(0.84)	(0.995)	(0.715)	(0.072)	(0.558)

Table 9. Pearson correlation coefficients examining the relationship between physical variables of the water column and the logarithm (base 10) of abundance of *Electra pilosa* (Bz1), *Mytilus* spp. (Bv1), other bivalves (Bv2), *Margarites* spp. (Gp1), *Astyris lunata* (Gp2), *Cancer irroratus* (Dp1), *Crangon septemspinosa* (Dp2) from 2 to 4 August 2009 for sampling depths of (a) 3 m (n = 16) and (b) 12 m (n = 15). The number in brackets is the p-value. **Bold** indicates statistically significant correlations ($p < 0.05$)

	Temperature (°C)	Salinity	Fluorescence
(a) 3 m			
Bz1	−0.111 (0.682)	−0.226 (0.400)	0.201 (0.455)
Bv1	0.355 (0.177)	**−0.601 (0.014)**	**0.579 (0.019)**
Bv2	0.172 (0.524)	**−0.509 (0.044)**	0.456 (0.076)
Gp1	0.050 (0.853)	−0.248 (0.355)	**0.531 (0.034)**
Gp2	0.354 (0.178)	−0.174 (0.520)	**0.678 (0.004)**
Dp1	**−0.547 (0.028)**	**0.557 (0.025)**	−0.111 (0.683)
Dp2	−0.073 (0.787)	0.221 (0.410)	0.447 (0.082)
(b) 12 m			
Bz1	−0.299 (0.278)	0.476 (0.073)	0.249 (0.371)
Bv1	−0.210 (0.453)	0.490 (0.064)	0.185 (0.510)
Bv2	−0.105 (0.710)	0.303 (0.273)	0.153 (0.586)
Gp1	−0.263 (0.344)	0.392 (0.149)	0.250 (0.370)
Gp2	−0.268 (0.335)	0.481 (0.069)	0.305 (0.269)
Dp1	−0.370 (0.175)	0.110 (0.696)	0.466 (0.080)
Dp2	−0.420 (0.119)	0.089 (0.753)	**0.561 (0.030)**

Modiolus modiolus had no detected vertical skew in larval population, and were also located at the periphery of the nMDS plot.

The distributions of all taxonomic groups were found to be significantly aggregated horizontally, based on both indices used (I_D and I_M). Generally, larval bivalves and gastropods, with intermediate swimming abilities compared to the other groups, showed the strongest aggregation, whereas larval bryozoans, which are the weakest swimmers, were the least aggregated. The magnitude of aggregation for decapod distributions was highly variable. While I_M is density independent (Hurlbert 1990), we suggest that this apparent variability in aggregation is related to the low abundance of decapods — which could affect our ability to accurately estimate abundance. In fish, smaller larvae showed weaker aggregation than larger ones, clearly indicating that swimming ability can be important and suggesting the importance of increasing influence of viscosity for smaller larvae (Stanley et al. 2012). Conversely, the swimming of large larvae is mostly dominated by inertial forces and they showed a higher degree of aggregation in the same study. However, the swimming of invertebrate larvae is mostly dominated by viscous forces because of their small size (Chia et al. 1984). It is likely that vertical swimming interacts with physical features of the water column to result in the formation of aggregations (Queiroga & Blanton 2005, DiBacco et al. 2011). While our study does not identify a mechanism for the formation of aggregations (e.g. aggregations caused by larvae swimming upwards in a downwelling current), it does appear that the degree of aggregation is related to swimming ability.

A well-defined mean circulation pattern, as determined by current velocity, was lacking at the study site. There was no evidence of a persistent clockwise gyre, as suggested by Petrie & Drinkwater (1978), but the relatively low mean (±SD) current velocities (0.001 ± 0.073 to 0.071 ± 0.084 m s^{-1}) are indicative of long residence times (~10 to 15 d). The bay is a semi-enclosed system that will retain larvae longer than would occur in regions of the open ocean. There is no major upwelling/downwelling or estuarine circulation; therefore, the upwelling-relaxation (Wing et al. 1995, Miller & Emlet 1997) and tidal-stream transport (DiBacco et al. 2001, Forward et al. 2003) paradigms do not apply in this system.

The aggregation diffusion model illustrated that horizontal swimming of invertebrate larvae (0.0008 to 0.013 m s^{-1}) is not an effective means of forming aggregations even at modest levels of diffusion. The horizontal current speed (0.002 ± 0.081 m s^{-1} to 0.071 ± 0.084 m s^{-1}) can be similar, but is often greater than larval swimming speeds (0.0008 to 0.013 m s^{-1}). While the mean currents are not strong (0.05 m s^{-1}), the semi-diurnal tidal velocity is 0.1 m s^{-1} and the peak observed currents approach 0.3 m s^{-1}. Over a period of 2 d these observations indicate spatial length scales of 10 km for the mean current, 20 km for the tidal current and 60 km for the strong episodic current. The relevant diffusive length scale is given by $\sqrt{K_v t}$ where K_v is the horizontal diffusivity and t is time. If $K_v = 100$ m^2 s^{-1}, then for a period of 2 d, the diffusive length scale is ~6 km. However, diffusion is acting to disperse organisms, while the advective forcing may lead to spatial re-distribution or aggregation. Even though the larval swimming speeds are similar to the mean horizontal current velocities, the variability (both as detected by the ADCP and at the diffusion time/length scale of the larvae) likely overwhelms the larval ability to form patterns by swimming horizontally. Interestingly, the level at which aggregations were no longer detectable was directly proportional to larval swimming ability. For example, bryozoans which swim at 0.75 mm s^{-1} did not form noticeable aggregations beyond diffusion indices of 2 m^2 s^{-1} (SD = 120 m h^{-1} or 33 mm s^{-1}), while decapods (which swim at 13 mm s^{-1}) did not form notice-

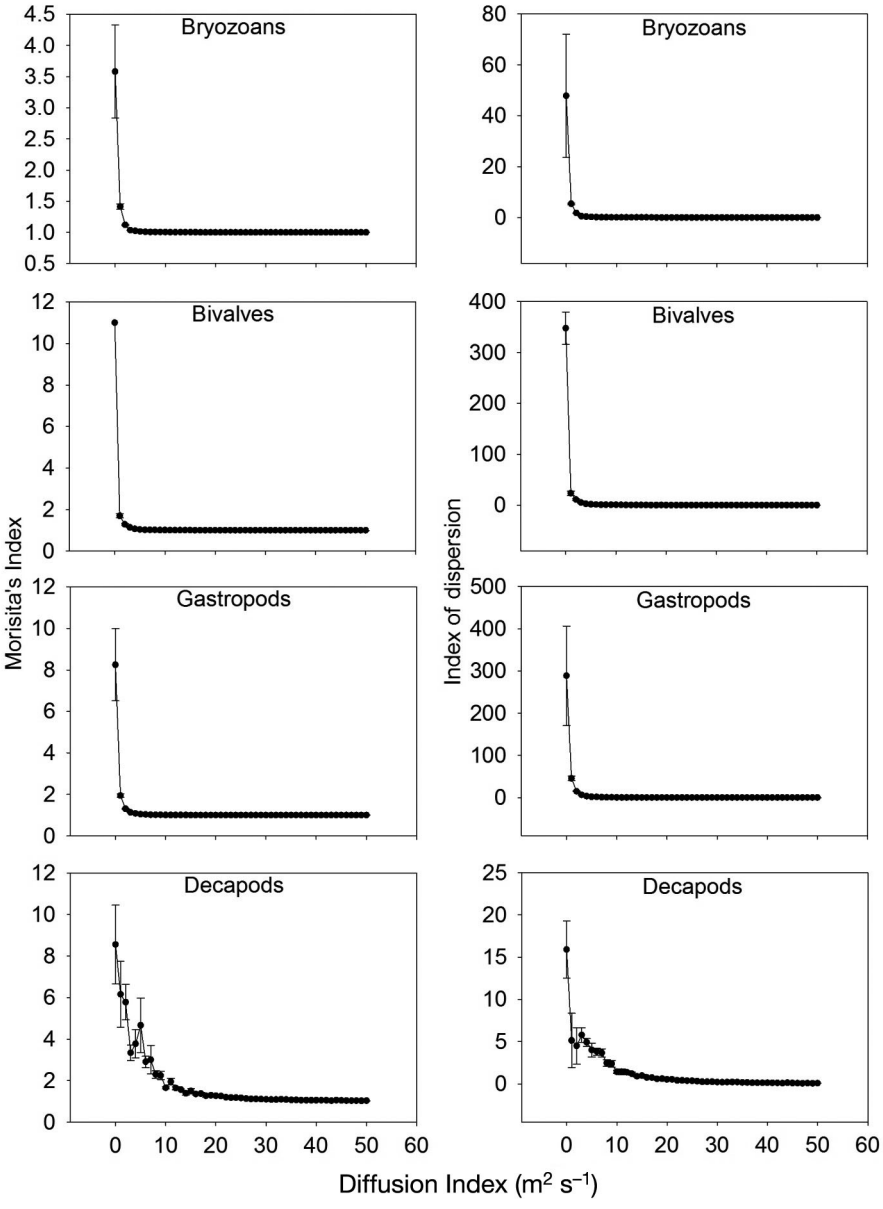

Fig. 9. Relationship between mean Morisita's Index or index of dispersion (±1 SE, n = 5) and the diffusion index for 4 taxonomic groups. Morisita's Index and the index of dispersion were calculated from 11 simulated 500 m net tows at randomly selected sites along a modelled 1-dimensional 40 km larval distribution

able aggregations beyond 30 m^2 s^{-1} (SD = 436 m h^{-1} or 129 mm s^{-1}). Also, representative levels of aggregations were achieved in a realistic time scale (30 d), but only at very low levels of diffusion.

The role of swimming varies greatly between the vertical and the horizontal dimensions. Vertical currents (mm s^{-1}) are generally much smaller than horizontal ones (cm s^{-1}). While we observed horizontal currents >5 cm s^{-1}, we rarely observed vertical current speeds >1 mm s^{-1}. Larval swimming speed, which is typically greater than 5 to 10 mm s^{-1} for decapods, is fast enough to overcome the vertical current speed and allow larvae to move from the seafloor to the surface in <1 h. The relatively greater impact of swimming in the vertical than in the horizontal dimension is a result of the short spatial scales (10s of meters) and the greater speed of swimming relative to that of the current.

We observed that larval horizontal spatial distribution is similar among taxonomic groups and that these spatial patterns change over time. Spatial patterns in larval distributions are affected by larval supply, survival and mortality (e.g. predation increases mortality, while food availability increases survival) (Grosberg & Levitan 1992, Morgan 1995), as well as by interaction with physical features in the water column. These include the spatial patterns in mean or tidal currents, internal waves, downwelling fronts, the presence of different water masses or the scale of spatially coherent physical forcing (Pineda 1991, DiBacco et al. 2011, Thompson et al. 2012, Daigle 2013). It is unlikely that the similarity in spatial distributions of taxonomic groups in this study were caused by predation, since the most abundant predators in St. George's Bay, scyphozoans (*Cyanea capillata*) and planktivorous fish, were found to differentially select for or against particular species or broader taxonomic groups of meroplanktonic prey (Short et al. 2012). For example, *C. capillata* was found to select against gastropods and for brachyurans; therefore, this predator would deplete the brachyuran population while having a relatively smaller effect on gastropod population. Spatial distributions of different taxonomic groups would diverge through selective feeding, rather than become more similar if all larvae were preyed upon equally. Food availability should not be playing a role in determining the horizontal patterns in distribution in this

study since the vertical fluorescence gradient was twice that of the horizontal dimension. For example, throughout the entire bay, fluorescence measurements ranged from 0.08 to 0.17 at 3 m, while at a single site at different depths, the range was from 0.08 to 0.31. The vertical distribution of a broad range of planktotrophic larval species (bryozoans, carideans and some gastropods) is positively related to fluorescence (Lloyd et al. 2012a,b), suggesting that they aggregate where there is high food availability. However, this does not appear to be the case in this study since the abundance of some species were negatively correlated with fluorescence. Lastly, if the location of the larval source was the dominant driver of observed patterns, one would expect to see that (1) different taxonomic groups might have different regions of high abundance and (2) larval distributions would be stable over a timescale of days since the benthic adult source population is effectively sessile. Therefore, it is unlikely that larval source affects the observed spatial distributions of larvae over the time scale of days to a week. Consequently, we propose that events occurring after the gamete/larval release, such as dispersal by currents, determined the observed horizontal patterns. Additionally, we suggest that dispersal by currents may have been more important than mortality due to predators, food availability or environmental variables (salinity, temperature, etc) in determining the observed horizontal patterns.

The degree of similarity in spatial distribution among taxonomic groups or species within a sampling date suggests that bay-scale patterns of larval abundance are related to some extent to swimming ability. Gastropods and bivalves have almost identical swimming speeds, while decapods have much higher swimming speeds than the other groups. The distribution of gastropods and bivalves were most strongly correlated, whereas that of decapods was generally weakly correlated with that of other groups. Unexpectedly, decapods were significantly correlated with bryozoans, but this pattern did not appear to be temporally consistent for a particular species of decapod, suggesting that the relationship between decapods and bryozoans may be spurious. This overall pattern was also observed at small-scales (<10 km) in St. George's Bay (Daigle 2013), suggesting that swimming ability is critical to the formation of spatial patterns in larvae distribution at scales from 0.5 up to at least 40 km (the extent of this study).

We have shown with the aggregation-diffusion model that larval horizontal swimming of larvae does not lead to aggregations of appropriate strength under even modest diffusion. Yet, we have also shown that distribution patterns are related to swimming ability. We propose that the horizontal spatial patterns in larval distributions in St. George's Bay are driven mainly by the interaction of swimming with physical features in the water column. Physical processes that create or enhance aggregations include interaction with internal waves and tidal bores (Shanks 1983, Pineda 1991), larvae swimming upwards in a downwelling flow (DiBacco et al. 2011), resulting from filamentation and eddy-eddy interactions (Harrison et al. 2013), at fronts through flow-induced circulation (Epstein & Beardsley 2001), or at the pycnocline where there is a strong density-gradient (Dekshenieks et al. 2001). In all of these aggregation-forming mechanisms, larvae swim against the vertical current and maintain their vertical position, thereby accumulating in the upwelling or downwelling current. If larvae are able to maintain position in downwelling or upwelling flow, larvae accumulate in these areas like flotsam accumulating in windrows due to Langmuir circulation (Langmuir 1938), through differential surface-layer mixing (Cromwell & Reid 1955) or through other circulation patterns, such as in estuaries or eddies that lead to horizontal or vertical convergence (Owen 1981). However, any larval patchiness generated by Langmuir circulation would be on the order of 100 to 300 m, while the observed spatial scale of larval patches in St. Georges Bay in August 2009 was ~3 km (Daigle 2013). Additionally, the length of the net tows (~500 m) would not resolve patchiness at such a fine scale. Mesoscale eddies (10 to 100 km) are too large to be responsible for the aggregations we observed, but the related twisting and folding of water masses can produce patterns at scales relevant to the observations (Lévy et al. 2012, Harrison et al. 2013). Submesoscale fronts (1 to 10 km) also occur at a relevant scale, but they only last a few days.

We can estimate the feasibility of larval aggregations forming at scales of a few kilometres in just a few days, by assuming that the median abundance is equal to the non-aggregated background level of larval abundance. The maximum observed larval abundance was 5, 41, 34 and 13 times more aggregated than the background abundance for bryozoans, bivalves, gastropods and decapods, respectively. If during an event of vertical flux, such as a tidal front associated with internal tidal dynamics or a local topographically-induced current associated with a wind-forced event, all larvae are transported to a particular depth by swimming, fully developed

aggregations would form within a tidal period (12 h). For example, for bivalves, where the maximum abundance was 41 times higher than the background, there must be a vertical flux of 41 m^3 every 1 m^3 over 12 h. This would require vertical transport of 0.78 mm s^{-1} (41 m per 12 h converted to mm s^{-1}: 41 m × 1000 mm m^{-1} per [12 h × 3600 s h^{-1}]). At the other extreme, bryozoans would require vertical transport of 0.12 mm s^{-1} (5 m × 1000 mm m^{-1} per [12 h × 3600 s h^{-1}]) over the same time period. Alternatively, fully developed aggregations could develop in under 2 h given a vertical transport of 0.78 mm s^{-1}. This range of vertical current speed is within the range that we measured with the ADCP (0.07 ± 2.3 to 0.83 ± 5.0 mm s^{-1}).

Since the interactions between swimming and current velocity occur at fairly small scales (<3 km), we believe that the most effective method of measuring larval dispersal will occur at these small scales, most often along the vertical axis (i.e. over depth). We propose that large scale meroplankton surveys can be a useful tool to study patterns in biogeography, but not the most effective method to measure larval dispersal. Instead, both smaller scale field studies and laboratory experiments could be useful to evaluate behavioural (i.e. swimming) interactions among physical features in the water column on the vertical axis.

Data archive. Data related to this publication is available in an open access repository at www.datadryad.org. Title: Data from: Bay-scale patterns in the distribution, aggregation and spatial variability of larvae of benthic invertebrates. Data identifier: doi:10.5061/dryad.fh505

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