

Variation in recruitment: differentiating the roles of primary and secondary settlement of blue mussels *Mytilus* spp.

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ABSTRACT: Recruitment has often been cited as a key factor regulating population abundance and community structure in benthic marine ecosystems, where the life cycle of many species includes a dispersive planktonic phase. Still, the patterns and causes of temporal heterogeneity in the recruitment process, from daily to annual scales, are poorly understood for most taxa. We conducted weekly (2008) and biweekly (i.e. every 2 wk; 2008–2009) assessments of settlement of the marine mussels *Mytilus* spp. in the St. Lawrence maritime estuary, and differentiated between primary (metamorphosis) and secondary (post-metamorphosis movements) settlers. At a biweekly temporal resolution, recruitment in 2008 occurred over a 2 mo period with a single peak in August. A more complex pattern of recruitment involving multiple peaks of primary and secondary settlement was, however, revealed at a weekly resolution. In 2009 the biweekly settlement rates were an order of magnitude lower, with again only a single peak. In both years, secondary settlement was observed throughout most of the season and contributed as much or more (50–81 %) than primary settlement for several peaks. Based on prodissoconch II size and estimated larval growth rates, the mean planktonic larval duration was estimated to be 38 d, but may have ranged from 27 to 67 d depending on the actual growth rate. The importance of secondary settlement increased over time and was a major contributor to local recruitment dynamics. Variation in primary and secondary settlement as well as inter-annual variations could strongly affect estimates of recruitment rates, local dynamics and the spatial scales of connectivity among coastal populations, and thus our understanding of local population regulation and metapopulation dynamics.

KEY WORDS: Recruitment · Primary settlement · Secondary settlement · *Mytilus* spp. · Prodissoconch II · Boreal

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INTRODUCTION

Temporal and spatial variation in the availability of planktonic larvae is recognized as a strong ecological driver of population dynamics in a wide range of marine systems (Roughgarden et al. 1988, Caley et al. 1996, Kinlan & Gaines 2003). Larval supply is particularly important for sessile and sedentary benthic invertebrates as dispersal after settlement is either lim-

ited or non-existent. Larval supply is controlled by many biotic (e.g. behavior, settlement cues, survival rates) and abiotic (e.g. waves, currents, topography) factors and, depending on the scale of observation, these factors influence larval dispersal and settlement differently and generate variability in settlement (Woodin 1986, Cowen & Sponaugle 2009, Pineda et al. 2010). For bivalves—important ecosystem engineers in many communities (Gutierrez et al. 2003)—the

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supply of settlers can result from 2 disparate processes that operate over contrasting spatial scales: (1) primary settlement at the end of the larval phase, i.e. metamorphosis and initial attachment to a substratum, and (2) secondary settlement (post-metamorphosis). This latter process can involve post-settlement movements (drifting or crawling) presumably to select a more suitable substratum or microhabitat (Bayne 1964, Sigurdsson et al. 1976, Buchanan & Babcock 1997, Newell et al. 2010), sometimes far from the initial location of settlement (Shanks & Shearman 2011). Such movement can also result simply from dislodgment by water motion (Martel 1993). Regardless, it is only once a sessile organism is definitively established in an area that it can be considered a recruit (Rodríguez et al. 1993).

Although secondary settlement through juvenile drifting appears to be a widespread dispersal phenomenon in bivalves (Lane et al. 1985, Baker & Mann 1997, Bownes & McQuaid 2009), it is often ignored (e.g. Leonard et al. 1998, Connolly et al. 2001, Pelc et al. 2009), and in spite of its potential to contribute substantially to observed recruitment, the relative importance of secondary settlement is rarely well documented (e.g. Martel & Chia 1991, Martel 1993). Distinguishing the relative contribution of these 2 processes is, however, crucial for assessing the role of larval supply in determining the population dynamics of benthic species.

Because dispersal scales depend on the type of settlement, important differences can occur when assessing connectivity of populations, i.e. metapopulation dynamics (Kinlan & Gaines 2003). The spatial scale over which primary settlement will operate will depend in a large part on the duration of the dispersal phase prior to settlement (Shanks & Shearman 2011). For example, the dispersal event leading to the primary settlement (planktonic larval duration [PLD]) is generally thought to last for approximately 4 wk for *Mytilus* spp. (Thorarinsdottir 1996), leading to dispersal distances on the order of 10s to 100s of kilometers (Kinlan & Gaines 2003, Becker et al. 2007, Smith et al. 2009). This contrasts with the much shorter secondary dispersal events that operate on the order of 10s to 100s of meters (Lane et al. 1985, Gunther 1992, Cáceres-Martínez & Figueras 1998), and in spite of the possible repetitiveness of such secondary dispersal events, the total distance covered should be orders of magnitude smaller than for primary settlers (Lane et al. 1985). Thus the distinction between primary and secondary settlers can provide more precise information on the dispersal of settlers (i.e. regional versus local). Demographically speaking,

this will allow better estimates of settlement patterns for the different phases of dispersal rather than total recruitment, which normally combines all sizes of settlers and therefore primary and secondary phases of dispersal. The latter approach can result in overestimates of primary settlement, and thus the degree of connectivity of populations in time and space. The distinction between types of settlers will determine the importance of each dispersal process within observed peaks of settlement, and target main periods affecting connectivity patterns. Failing to distinguish between primary and secondary settlers will therefore bias measurements of dispersal, resulting in inaccurate estimates of the timing, magnitude, and duration of major dispersal events.

Many studies have shown that timing in reproduction and larval settlement of bivalves varies between regions, primarily because of differences in climate and hydrodynamic regime (Ramírez & Cáceres-Martínez 1999, Jenkins et al. 2000, Philippart et al. 2003, Broitman et al. 2008, Porri et al. 2008). Dispersal during the planktonic larval stage depends largely on the PLD, which is principally influenced by environmental factors such as temperature and planktonic food availability (Sprung 1984, Widdows 1991). Moreover, in boreal and subarctic regions, reproduction occurs over a shorter period during the warm season than in temperate regions (Thorarinsdottir & Gunnarsson 2003, Frantzen 2007). The timing of reproduction can thus influence planktonic larval development.

Although the PLD is generally difficult to estimate, the end of the planktonic larval stage in bivalves is marked by a change in shell morphology and composition after metamorphosis, creating a distinct visual demarcation between the prodissoconch II (PII, or larval shell) and the dissoconch (D, or benthic shell) (Martel et al. 1999, Zardus & Martel 2002). The PII thus provides valuable information about the larval phase history, especially the size at metamorphosis (i.e. at the time of primary settlement). If larval growth rate is known or can be estimated, we suggest that the size at metamorphosis can then be used to determine the PLD (Martel et al. 1995). In systems where variations in plankton and temperature are relatively small over the spatial and temporal scales of the planktonic larval phase, PII shell morphometry can then be an efficient tool for estimating PLD at the level of individuals.

In this study, we documented spatial and temporal patterns of primary and secondary settlement by assessing the variation in blue mussel (*Mytilus* spp.) recruitment in a boreal ecosystem, the St. Lawrence

maritime estuary. A previous study (Smith et al. 2009) documented substantial spatial along-shore variations in seasonal mussel recruitment in this region. However, short-term variations in this process and the relative importance of secondary settlement remain unexplored. Using size and larval shell characteristics, we estimated the primary and secondary settlement over the summer and thus obtained information about their relative contributions to recruitment patterns. We also used PII measurements to obtain information on size at metamorphosis as well to estimate the PLD of settlers. Our study provides valuable insights into dispersal scales among larvae (i.e. PII size variability and PLD estimates), recruitment rates and metapopulation connectivity (i.e. distinction between primary and secondary settlement) in *Mytilus* spp. in a boreal estuary.

MATERIALS AND METHODS

Study area

Settlement and recruitment of *Mytilus* spp. were examined during the spring and summer of 2008 and 2009 on the southern shore of the St. Lawrence maritime estuary (Québec, Canada) at 3 intertidal sites (Pointe-Mitis, 48° 40' N, 68° 02' W; Saint-Ulric, 48° 46' N, 67° 44' W; and Sainte-Félicité, 48° 54' N, 67° 17' W; Fig. 1) near the city of Matane on the Gaspé Peninsula. (NB although the terms 'settler/settlement' and 'recruit/recruitment' are used some-

what interchangeably in the literature, we try here to use the former terms for short-term observations where we are trying to infer settlement and the latter terms for longer-term demographic phenomena.) The study sites consist primarily of rocky shores (benches and boulders fields) that experience semi-diurnal tides ranging up to 4 m. The intertidal communities were largely dominated by *Mytilus* spp. (20 to 60 % cover) in the mid and low zones. As seen elsewhere in the maritime regions of Canada (Toro et al. 2004, Moreau et al. 2005), these populations are mixtures of *M. trossulus*, *M. edulis*, and their hybrids (J. Turgeon, unpubl. data), and individuals cannot be readily distinguished morphologically. We thus considered this complex as a whole because environmental conditions are comparable among sites (Ouellet et al. 2011), and similar larval growth rates have been observed within this complex for temperatures typical of this region (Rayssac et al. 2010). The Gaspé Current, the dominant current in this area, runs downstream (west to east) along the shore towards the Gulf of St. Lawrence (Sheng 2001). Temperature and wind data for the region were obtained from an oceanographic buoy (IML-4) located 40 km upstream from Pointe-Mitis and 18 km offshore of Rimouski (48°40.000 N, 68°35.000 W; Fisheries and Oceans Canada, Oceanographic Data Management System [ODMS]; available at <http://slgo.ca/app-sgdo/en/accueil.html>). Salinity was not analyzed in this study because it was spatiotemporally homogeneous (24.5 ± 1.7 psu in 2008 and 25.8 ± 1.6 psu in 2009 [mean \pm SD]; ODMS data).

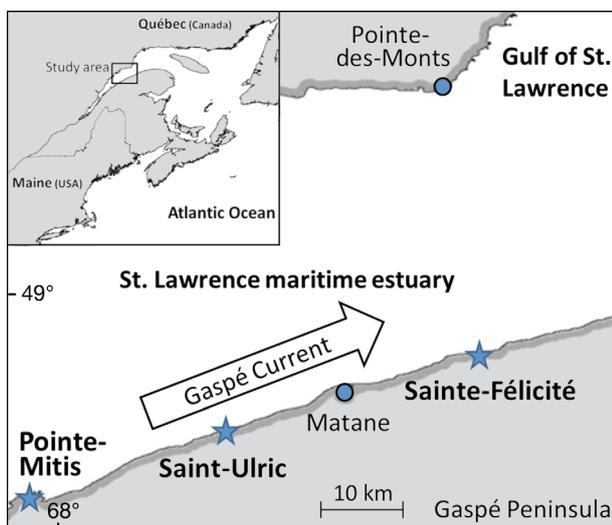


Fig. 1. *Mytilus* spp. Study sites (stars) where mussel settlement was studied along the St. Lawrence maritime estuary, Québec, Canada. Arrow: eastward net flow of the Gaspé Current

Settlement experiments

Plastic multifilament nylon scouring pads (S.O.S. Tuffy) were used to collect mussel settlers (Menge 1992, Pulfrich 1996, Ramirez & Cáceres-Martínez 1999) as larval mussels generally first attach to filamentous material (e.g. byssus threads of established mussels and filamentous algae; Yang et al. 2007). Collectors were anchored to bedrock with screws and wall anchors in the low mid-intertidal zone (the presence of the red alga *Porphyra* sp. was used as the tidal level indicator among sites). After collection, pads were preserved in 70 % ethanol until laboratory processing. To extract settlers, a high-pressure jet of fresh water was used to detach them from the pad into a 150 μ m mesh sieve that separated mussel settlers from smaller particles and organisms. Settlers were then identified and counted under a stereomicroscope (Olympus SZX 12). When >200 ind. were

observed in a sample, samples were split using a Folsom splitter. Samples mainly contained mussels, but other taxa (e.g. bivalve settlers of *Mya* sp., *Macoma* sp., *Hiatella* sp., and the periwinkles *Littorina* spp.) were also collected. No apparent saturation of the collectors was observed.

For all experiments, 8 collectors were set out at the same tidal level at each site and replaced every 7 or 14 d from the end of June to mid-September, depending on the time scale of interest. Experiments were conducted at 3 different combinations of spatio-temporal scales (Table 1): (Expt 1) biweekly (i.e. every 2 wk) at all 3 sites (Fig. 1) in 2008 to compare spatial variation in the temporal pattern of recruitment; (Expt 2) weekly at one site (Pointe-Mitis) in 2008 to examine how temporal resolution of sampling affects patterns of recruitment (relative to the biweekly sampling at this site); and (Expt 3) biweekly at one site (Pointe-Mitis) in 2009 to examine interannual differences in the patterns of recruitment (relative to the 2008 sampling of this site). In parallel, 8 collectors were anchored for the whole summer (from mid-July to late-September) at all 3 study sites in 2008.

Size frequency and distinction of primary and secondary settlers

Variation of the size frequency of settlers throughout the summer was investigated using subsamples from the collections at Pointe-Mitis (Expts 2 and 3). At least 3 collectors from each date (late June to late September) were processed when sufficient numbers of settlers were present (11 sampling dates in 2008 [weekly] and 6 in 2009 [biweekly]). Because large settlers prefer natural substrates (Roughgarden et al. 1988, Porri et al. 2008), we measured shell length of all individuals in collectors that were

<2000 μm (except when abundant, when 100 were haphazardly selected) with a range of 71 to 518 settlers per sampling date. We restricted the maximum shell length because larger settlers prefer attaching to hard natural substrata rather than filamentous substrata (Hunt & Scheibling 1996, Alfaro 2006). Individuals were measured using a stereomicroscope (Olympus SZX 12) with a PixeLink digital camera and the software iSolution. We measured the maximum length (anterior–posterior dimension) of the shells using a wet preparation (70% ethanol). Shells were carefully oriented to assure that they were in the ocular plane to avoid underestimation of their length.

To distinguish primary settlers from secondary settlers, we estimated a conservative size threshold (i.e. biased towards underestimating the abundance of secondary settlers compared with primary settlers) as a function of the size at metamorphosis and the potential growth on collectors after settlement. This threshold was estimated by using the maximum size at metamorphosis observed (370 μm) based on PII shell length and the maximum *in situ* post-settlement growth rate of mussels in this region (15 $\mu\text{m d}^{-1}$; N.L.C. unpubl. data) multiplied by the maximum number of days that settlers could have been in the collectors. This average growth rate corresponded to the slope of a linear regression using successive measurements of the size of settlers sampled from the same cohort in Pointe-Mitis during summer 2008. This calculation led to estimates of threshold sizes of 475 and 580 μm for collector deployments of 7 (Expt 2) or 14 d (Expt 3), respectively. The proportion of primary and secondary settlers in the subsample was then multiplied by the total settler count to estimate their total numbers in each sample.

To explore the influence of the physical environment on levels of primary and secondary settlement, we examined rates of settlement as a function

of average wind speed and temperature during the preceding week, as calculated from measurements taken by the nearby oceanographic buoy (see above). Wind speed is a proxy for wave action along this relatively sheltered coastline where no oceanic swell occurs (L.E.J. unpubl. data). Data for both 2008 (weekly and biweekly) and 2009 (biweekly only) were analyzed separately for primary and secondary settlers.

Table 1. *Mytilus* spp. Study sites where the settlement experiments were conducted along the St. Lawrence maritime estuary, Québec, Canada. Replacement frequency, number of sample periods, number of collectors (in parentheses) and deployment period are indicated for each experiment. Dates are d/mo/yr; biweekly: every 2 wk

Expt	Locality	Year	Collector replacement	No. of sample periods (collectors)	Deployment period	
					Start	End
1	Pointe-Mitis	2008	Biweekly	6 (8)	27/06/2008	21/09/2008
	Saint-Ulric	2008	Biweekly	6 (8)	27/06/2008	21/09/2008
	Ste-Félicité	2008	Biweekly	6 (8)	27/06/2008	21/09/2008
2	Pointe-Mitis	2008	Weekly	11 (8)	07/07/2008	21/09/2008
3	Pointe-Mitis	2009	Biweekly	7 (8)	21/06/2009	30/09/2009

Prodissoconch II analysis and age at settlement

We examined the PII region of the larval shell to determine the size of individual settlers at the time of settlement and metamorphosis. Since larval shell length changes linearly with time (Sprung 1984, Pechenik et al. 1990, Galley et al. 2010, Rayssac et al. 2010), we could thus estimate a range of the period of PLD based on the maximum and minimum planktonic growth rates observed in laboratory experiments at similar water temperatures (Bayne et al. 1975, Beaumont & Budd 1982, Sprung 1984, Pechenik et al. 1990, Beaumont et al. 2004, Hayhurst & Rawson 2009, Rayssac et al. 2010). Sixteen individuals (when available) <475 μm in total length were randomly chosen from each of 4 collectors used for the weekly samples in Expt 2 (the size criterion was applied to avoid including secondary settlers; see above). Maximum PII length was measured using a stereomicroscope (Olympus SZX 12, 90×1.2) equipped with a digital camera (6.6 megapixels, software: iSolution). To assess the age of primary settlers in 2009, the same method was used, but because it was a biweekly experiment only individuals <580 μm in total length were randomly chosen. For both years, we examined the relationship between PII size and average water temperature during the 38 d period before collection.

Statistical analysis

For the biweekly settlement analysis in 2008, a 2-way mixed model ANOVA was used with date (fixed) and site (random) as factors to determine whether differences in total recruitment (without distinguishing between primary and secondary settlers) occurred between sampling periods. Date was considered independent because collectors were replaced each time. A one-way ANOVA was used for the weekly recruitment analysis in 2008 and the biweekly recruitment analysis in 2009, and a parametric post hoc test was then used after ANOVA analysis to compare settling rates among dates or sites ($\alpha = 0.05$). Log-transformed data were used in these analyses to respect ANOVA assumptions. The size frequency of settlers was analyzed by using the percentage in each size class (from 250 to 2000 μm , in 50 μm classes, except for the last class, which ranged from 900 to 2000 μm) for each date in 2008 and 2009. Distributions were then compared among sampling dates chronologically using Kolmogorov-Smirnov tests on pairs of sequential dates and *F*-tests to compare variances. PII shell size analysis

on individuals (log-transformed PII shell length) related to period of settlement was conducted using a one-way ANOVA and a post hoc Tukey's test. Linear regressions were used to examine the relationship between primary and secondary settlers and the average wind speed of the preceding week (weekly [2008] and biweekly [2008, 2009] at Pointe-Mitis and biweekly [2008] at the other sites). Linear regressions were also used to test for a relationship between average water temperature (during 35 d before settlement) and average PII size of primary settlers in 2008 and 2009. For the PII analysis of biweekly settlers in 2009, we used a non-parametric test (Kruskal-Wallis test) and then a post hoc multiple comparison test because of strong non-normality of the data. R software version 2.13 (R development core team, www.r-project.org) was used for all statistical analyses.

RESULTS

Temporal variability in total settlement

In 2008, overall settlement rate of *Mytilus* spp. (all settlers) in Expt 1 (Fig. 2A–C) showed significant differences between biweekly periods ($p < 0.001$, ANOVA), with no or low mussel settlement in early/mid-July at the 3 sites (group d, Tukey's test), followed by a small, but significant, increase in late July (group c), August (group b) and a major peak in late August (group a). Subsequently, little settlement was observed in September (group b). This pattern was generally consistent among the 3 sites, although settlement was twice as high at Saint-Ulric (group a, Tukey's test among sites) relative to the other sites (group b, among sites), and the August peak began earlier at Sainte-Félicité. In 2009 (Pointe-Mitis only), settlement was an order of magnitude lower and generally occurred earlier in the summer (Fig. 2D; Expt 3). As in 2008, almost no settlement was observed in early July (group e, Tukey's test), but distinct settlement peaks were observed in both mid-July (group a) and mid-August (group ab), the latter corresponding approximately with the single peak observed in 2008.

The higher-resolution data from weekly sampling in 2008 (Expt 2, one site) revealed a more complex pattern of settlement relative to the single peak observed in biweekly sampling (Expt 1, 3 sites; see above). First, there was a minor but significant peak in settlement in early July (Fig. 3). Second, the August peak was composed of 2 significantly distinct peaks. In terms of total rates of settlement, the com-

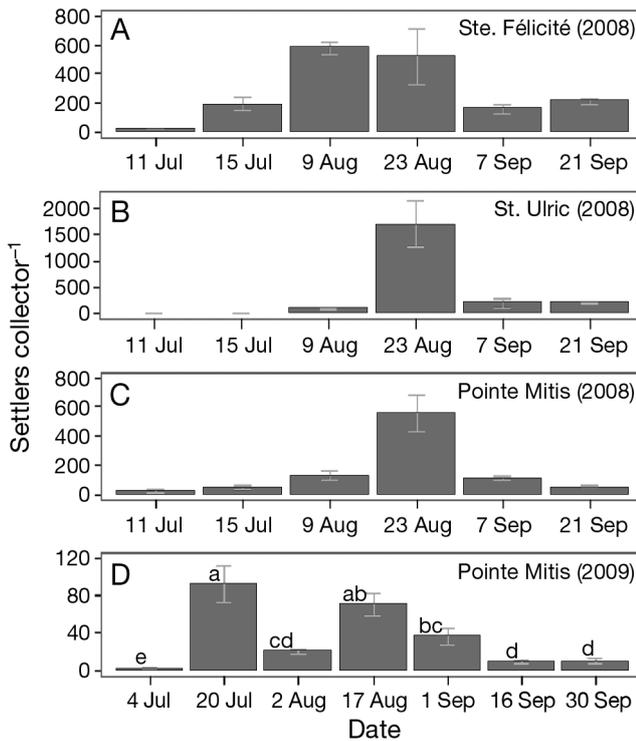


Fig. 2. *Mytilus* spp. Mean (\pm SE) number of settlers in collectors replaced biweekly (i.e. every 2 wk) from late June to late September on the south shore of the St. Lawrence maritime estuary, Québec, Canada, at Sainte-Félicité (A), Saint-Ulric (B) and Pointe-Mitis (C) in 2008 (Expt 1), and at Pointe-Mitis in 2009 (Expt 3, D). For 2009, periods with the same letter above the bar were not significantly different. Statistical results for 2008 are not shown here but are described in 'Results'. Note differences in y-axes scales

parison of samples collected at Pointe-Mitis showed that total settlement per collector location (i.e. the sum of all settlers collected at a specific location throughout the 3 mo experimental period) was strikingly similar regardless of the duration of deployment: 864 ± 179 and 907 ± 204 settlers location⁻¹ (mean \pm SD; n = 8) for the weekly and biweekly experiments, respectively. However, these numbers were significantly lower than those from collectors deployed for the entire 3 mo period (1750 ± 378 recruits location⁻¹; n = 8). Cumulative totals for biweekly collector locations at the other 2 sites (2233 ± 557 and 1679 ± 337 settlers location⁻¹ at Saint-Ulric and Sainte-Félicité, respectively) were much closer to the number of settlers observed in the 3 mo collectors (2699 ± 439 and 1549 ± 445 recruits location⁻¹, respectively).

Primary versus secondary settlement

In 2008, mean shell length of settlers collected weekly at Pointe-Mitis varied from $325 \pm 35 \mu\text{m}$ (mean \pm SD, n = 297) in early July to $608 \pm 199 \mu\text{m}$ (n = 82) in mid-September (Fig. 4). Two main periods with small settlers were seen, one in mid-July and another in mid-August, with average sizes $<440 \mu\text{m}$. After each of those periods, there was generally a gradual increase in the average size of settlers between each sampling date ($p < 0.05$, except between 1 and 8 September and between 15 and 21 September, Kolmogorov-Smirnov test). Using a $475 \mu\text{m}$ threshold, the percentage of secondary settlers was always $\geq 10\%$ (except for the first sampling period) and exceeded 50% for 4 different periods. Percentages were generally low (0–29%) during periods of high settlement, with the exception of the 4 August peak, when one of the highest percentage of secondary settlers (73%) was observed. In 2008, secondary settlement measured weekly at Pointe-Mitis was positively correlated with the average wind speed of the preceding week (Fig. 5; adjusted $R^2 = 0.72$, $p < 0.001$; n = 11, linear regression analysis) whereas primary settlement was not (adjusted $R^2 = -0.06$, $p = 0.52$; n = 11, linear regression analysis). Neither primary nor secondary settlement was correlated with wind speed for biweekly collections at any of the 3 sites. Mean daily average wind speed was $5.2 \pm 2.0 \text{ km h}^{-1}$ (mean \pm SD) from 1 June to 30 September in 2008.

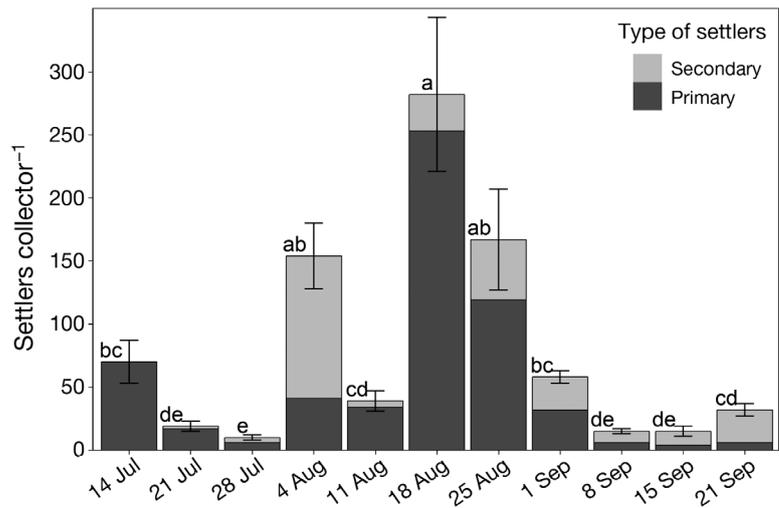


Fig. 3. *Mytilus* spp. Mean (\pm SE) number of settlers in collectors replaced weekly from early July to mid-September 2008 at Pointe-Mitis (Expt 2). Primary settlement (dark grey) and secondary settlement (light grey) were differentiated by an analysis of shell sizes, using $475 \mu\text{m}$ as a threshold size to distinguish primary from secondary settlers. Periods with common letters (above bars) are not significantly different

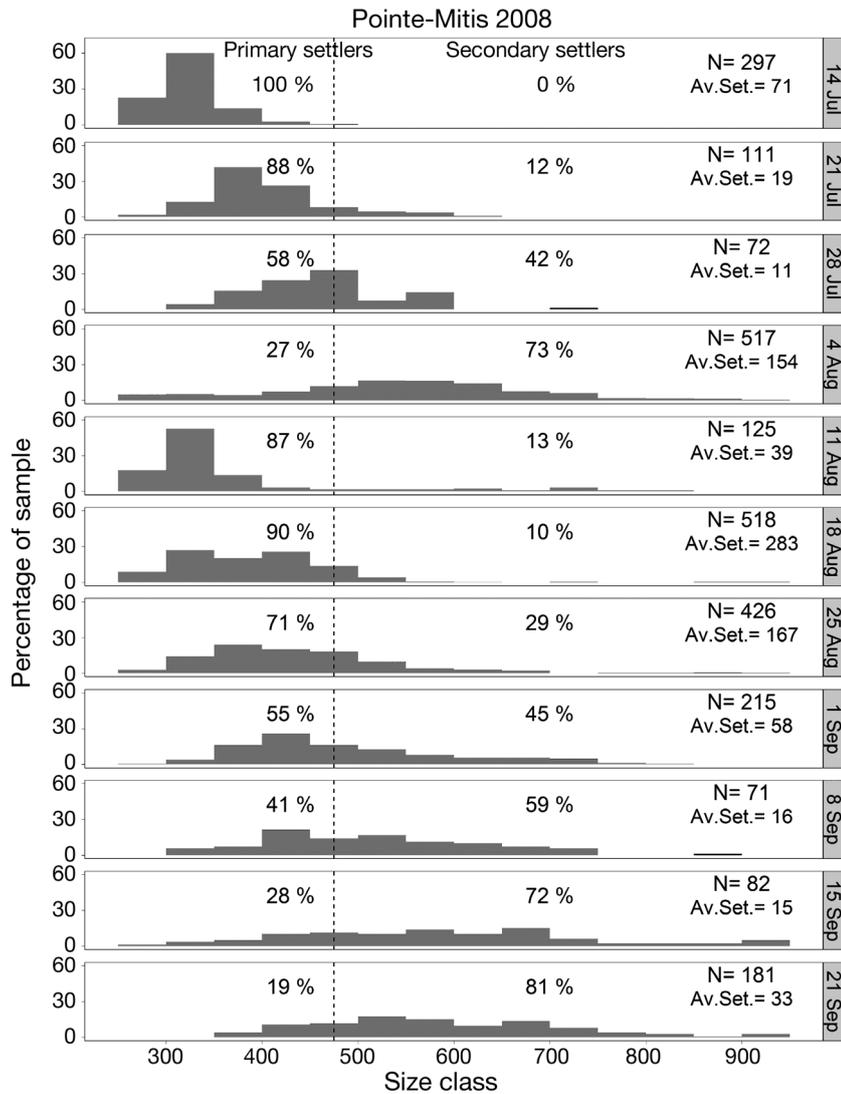


Fig. 4. *Mytilus* spp. Temporal change in size–frequency distribution (250–2000 µm, the last size class ranges from 900 to 2000 µm) of settlers collected weekly at Pointe-Mitis, Québec, Canada, during summer 2008 (Expt 2). Vertical dashed line: threshold (475 µm total shell length) distinguishing primary and secondary settlers. N: total number of ind. measured; Av.Set.: average number of mussel settlers per collector occurring during each period

In 2009, the mean (\pm SD) settler size ranged from 352 ± 46 µm in mid-July ($n = 299$) to 903 ± 281 µm in late-September ($n = 53$), and we observed a continuous increase in the average size and in the variation in shell length throughout the summer (Fig. 6; $p < 0.001$, Kolmogorov-Smirnov test), except between 16 and 21 September, when no significant difference was observed. The size of settlers became more heterogeneous as the season progressed, with a range of 250–550 µm in July and 300 to >900 µm in September ($p < 0.001$, F -test). Corresponding with this shift to larger sizes, our estimate of the proportion of sec-

ondary settlers also increased over the summer (from 0% of secondary settlers in July to 91% at the end of September). Once again the earliest peak in settlement (20 July) was exclusively primary settlers whereas the later peak (17 August) had a substantial portion (50%) of secondary settlers. Overall, in spite of the reduced settlement in 2009, a similar evolution of the settlement pattern was seen in both years, with an increase in the average size and a larger number of secondary settlers in the weeks following events of primary settlement. Neither primary nor secondary settlement was correlated with the preceding wind conditions for the biweekly collections at Pointe-Mitis in 2009. Mean daily average wind speed in 2009 (5.4 ± 1.7 km h⁻¹, mean \pm SD) was very similar to that of 2008 for the same time period (see above).

Prodissoconch II analysis

For primary settlers collected weekly at Pointe-Mitis in 2008, mean (\pm SD) PII size ranged from 284 ± 16 µm (4 August, $n = 51$) to 319 ± 28 µm (25 August, $n = 71$), with individual values varying from 242 to 384 µm (Fig. 7). Using values of planktonic larval growth rates ranging from 3 to 8 µm d⁻¹ (= water temperature from 6 to 15°C; see above) and an initial prodissoconch I shell ('D-shell') length of ≈ 110 µm after 3 d of post-fertilization development (Bayne et al. 1975, Sprung 1984, Pechenik et al. 1990, Beaumont et al. 2004, Hayhurst & Rawson 2009,

Rayssac et al. 2010), we estimated PLD to be 38 d on average with a growth rate of 5.5 µm d⁻¹ (range: 27 to 67 d for growth rates of 8 and 3 µm d⁻¹, respectively, for a 302 µm settler, the overall average size in 2008). In 2008, for the first 6 wk, mean PII length did not vary significantly ($p > 0.05$, group d, Tukey's test), but by late August (25 August and 1 September) PII size was significantly larger than previously observed ($p < 0.001$, ANOVA; group a, Tukey's test). A progressive return to smaller PII size (median around 295–300 µm) occurred at the end of the season. Depending on the value of the larval growth rate

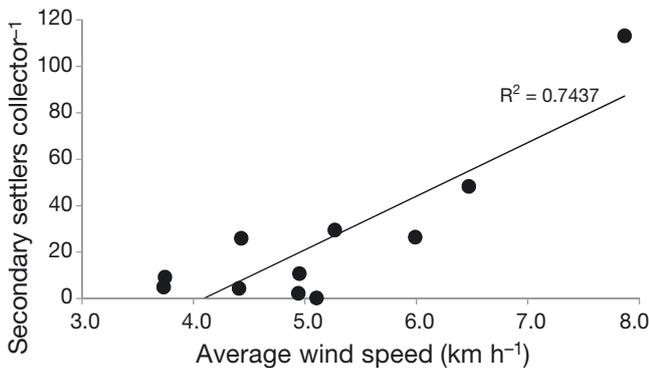


Fig. 5. *Mytilus* spp. Average number of weekly secondary settlers as a function of the mean wind speed during the week prior to replacement of collectors in summer 2008 at Pointe-Mitis, Québec, Canada. The significant linear regression and R^2 values are also shown

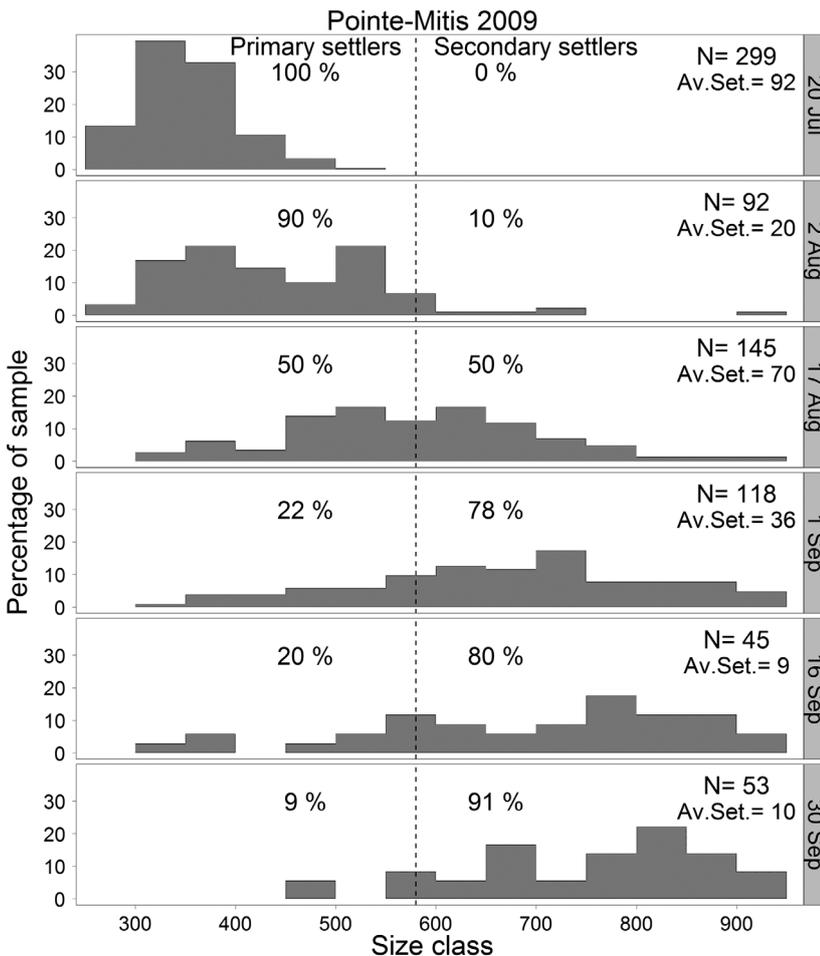


Fig. 6. *Mytilus* spp. Temporal change in size–frequency distribution (250–2000 μm , the largest size class ranges from 900 to 2000 μm) of settlers collected biweekly at Pointe-Mitis, Québec, Canada, during summer 2009 (Expt 3). Vertical dashed line: threshold (580 μm total shell length) distinguishing primary and secondary settlers. N: total no. of ind. measured; Av.Set.: average no. of mussel settlers per collector occurring during each period

used, the maximum variation between different weeks in the estimated larval period was 4.4 to 12 d. PII length and water temperature prior to settlement were not correlated in 2008.

In 2009 a similar pattern in PII size was detected in the biweekly samples collected at Pointe-Mitis, and PII shell lengths were significantly different (data not shown, $p \leq 0.02$, Kruskal-Wallis test) among certain periods. PII size generally increased throughout the summer from 20 July ($290 \pm 12 \mu\text{m}$, $n = 50$) to 1 September ($308 \pm 24 \mu\text{m}$, $n = 22$; $p < 0.05$, Kruskal-Wallis post hoc test), but was followed by a small decrease in September. In 2009 the mean PII shell length was $296 \pm 20 \mu\text{m}$ ($n = 162$), corresponding to a mean PLD of 37 d (range: 26 to 65 d) when based on a growth rate of $5.5 \mu\text{m d}^{-1}$. We estimated that the maximum differences in PLD among sampling periods ranged from 2.5 to 7.0 d. However, the increase in PII shell lengths occurred earlier in 2009 than in 2008 (as did overall settlement; see above). As in 2008, PII length and water temperature prior to settlement were not correlated in 2009.

DISCUSSION

Except for a few earlier studies (Bayne 1964, Garcia et al. 2003, Bownes & McQuaid 2009, Newell et al. 2010), most previous studies of bivalve recruitment (e.g. Porri et al. 2006, Lagos et al. 2007, Smith et al. 2009) have not distinguished between primary and secondary settlers and thus have tended to overestimate levels of larval supply by including secondary settlers already *in situ* at the site. In the present study we measured settlement with the most common methods currently used, but then refined estimates by distinguishing between the 2 types of settlers depending on their size. Important differences were found, allowing us to distinguish among different scenarios of settlement over time. Neither a scenario of settlement as a relatively continuous process during the summer, nor a simple peak of primary settlement was observed. Rather, when a distinction

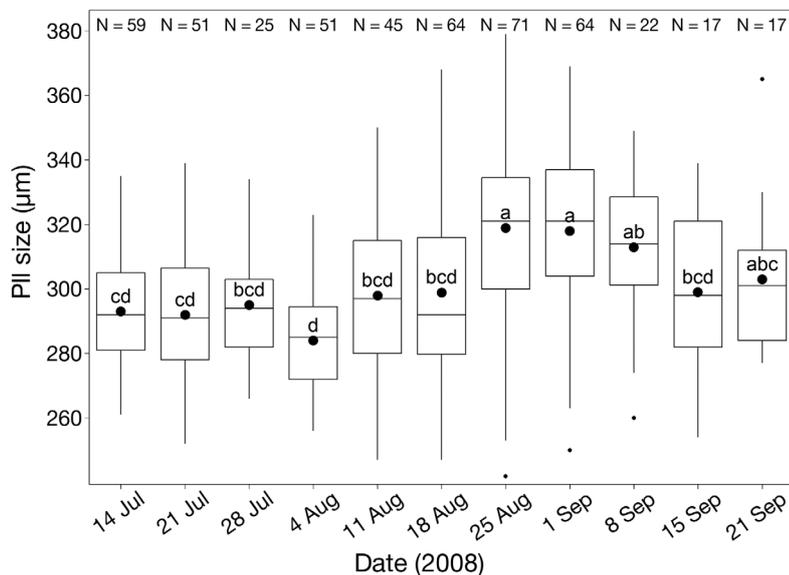


Fig. 7. *Mytilus* spp. Mean size (large filled circle) and box-and-whisker diagram (central line: median; box: lower and upper quartiles; whiskers: smallest and largest observations; small circles: over-dispersed observations) of prodissoconch II (PII) shell length of weekly settlers at Pointe-Mitis (Expt 2) during summer 2008. Individuals were considered to be primary settlers if their total length was $<475 \mu\text{m}$. Letters represent significantly different groups. N: number of settlers measured

was made between the types of settlers (and thus the scale of dispersal), limited periods of large-scale dispersal (i.e. primary settlement) were observed followed by an increasing importance of secondary dispersal, especially within the first weeks after settlement and metamorphosis. Substantial variability in timing and magnitude of settlement between the 2 years was also observed, suggesting that long-term variability in connectivity also needs to be considered when examining population dynamics, especially at a metapopulation level (Le Corre et al. 2012). Finally, the duration of the planktonic larval phase appeared remarkably constant between the 2 years. Moreover, the observed sizes at settlement and metamorphosis during the summer were comparable to those from other boreal/subarctic studies (e.g. Kautsky 1982, Rodhouse et al. 1984).

Temporal settlement patterns

Studies in other boreal environments (Baltic Sea, northern Norway, Iceland, and Ireland) have usually revealed a single main event of spawning/settlement during the warm season (Kautsky 1982, Rodhouse et al. 1984, Thorarinsdottir 1996, Garcia et al. 2003, Thorarinsdottir & Gunnarsson 2003, Frantzen 2007),

although a partial (i.e. smaller) spawning event can occur earlier during late spring (Rodhouse et al. 1984, Garcia et al. 2003, Frantzen 2007). Our settlement data, taken at a much higher resolution, showed that more complex patterns can occur. At a biweekly resolution, the typical pattern of one main recruitment event was observed in 2008 and occurred at all our sites with only small spatial differences in the magnitude and timing of recruitment. Low variability in recruitment at this spatial scale (30 km) along a relatively homogeneous shoreline is consistent with previous results reported from the same region (Smith et al. 2009). In contrast, the low recruitment in 2009 revealed the high temporal variability between years and could explain corresponding inter-annual variability in the scale and strength of population connectivity (Le Corre et al. 2012).

The higher resolution provided by weekly sampling showed that recruitment can be more complex, e.g. 3 peaks in 2008. Discrimination of primary settlers

from secondary settlers revealed that only 2 of the peaks were due mainly to primary settlement, the first in mid-July and a second, higher peak in mid-August. Those events may be the consequence of 2 separate spawning events, asynchronous spawning at 2 different places, or possibly biological differences between the 2 species that occur in the estuary (*Mytilus edulis* and *M. trossulus*). These results demonstrate the importance of proper temporal resolution for documenting key properties of recruitment patterns. For example, the bimodal settlement pattern observed in 2008 was only documented by our weekly sampling and was missed entirely by our biweekly sampling scheme.

Primary versus secondary settlement

Primary settlement occurred over the whole sampling period, but our analysis revealed a clear modal or bimodal distribution through that period. Secondary settlers were present throughout the summer and were relatively abundant at certain times during the season. However, secondary settlement was likely to have been underestimated because: (1) a few large settlers ($>2000 \mu\text{m}$) were excluded from the sampling, (2) large settlers are known to prefer natural

substrata rather than artificial substrata (Roughgarden et al. 1988, Porri et al. 2008), and (3) the threshold size used to discriminate between primary and secondary settlement was intentionally biased towards overestimating primary settlement (i.e. maximum PII size, maximal period for growth, and maximal post-settlement growth rates were used to determine the threshold size). Secondary settlement may also be occurring throughout the year, as seen in some subarctic areas (Garcia et al. 2003), but ice cover during winter prevented us from sampling throughout the year in the St. Lawrence Estuary. After the 2 main settlement events of 2008, we observed a distinct increase in the size/age of settlers over time with individuals settling on the collectors through post-larval dispersal (Hunt & Scheibling 1998, Garcia et al. 2003). Our results thus demonstrate the high mobility of settlers, even weeks after first settlement, and support the idea that the transition between the planktonic and benthic phase is not as abrupt as generally thought (Lane et al. 1985, Newell et al. 2010). Despite important inter-annual variability in settlement peaks, the temporal sequence of primary and secondary settlement was consistent between years, with increasing secondary settlement occurring over time, likely due to the increasing pool of post-settlement individuals as primary settlement occurred and settlers accumulated.

Secondary dispersal and settlement can be the result of either active or passive processes. After settlement, the post-metamorphic stage can detach itself from the original substratum, drift or crawl on the substratum, and then reattach to an alternative substratum; thus active behavior by the organism itself can contribute to the occurrence of secondary settlers observed in collectors (Bayne 1964, Cáceres-Martínez et al. 1994, Hunt & Scheibling 1998). Alternatively, dislodgment by water motion is a more passive means of secondary dispersal, one that may even be undesirable for the organism (Cáceres-Martínez et al. 1994). Discriminating between these 2 possibilities is difficult, but the recruitment peak in 2008 that was dominated by secondary settlers (4 August) coincided with a storm in early August. Moreover, weekly secondary settlement in 2008 was positively correlated with regional wind speeds, a proxy for wave action in this system. Thus, in *Mytilus* spp., secondary settlement appears to be primarily a passive process controlled by water motion (i.e. wave action), as observed elsewhere (Martel 1993, Newell et al. 2010). In these studies, where primary settlement was distinguished from secondary settlement, rarely has each settler type been thoroughly teased out and

their relative importance quantified through time. Newell et al. (2010) examined settlement of *Mytilus edulis* on eelgrass blades in tidal channels in Maine and reported a strong temporal component in the relative proportion of primary settlers (predominance early in the season) versus secondary settlers (predominance late in the season). Moreover, in a study on the bivalve *Dreissena polymorpha*, Martel (1993) distinguished between primary and secondary settlement and found that the secondary settlers (drifting juveniles) represent a high proportion of settlers. In that study, an average 46% of all individuals collected had arrived as drifting post-metamorphic stages, and, as in this study, peak periods of secondary settlement coincided with periods of high winds and associated high wave action.

Although water motion may redistribute settlers within a site, we did not observe any evidence of a net loss of settlers from collectors over time. The comparison of weekly versus biweekly recruitment showed that the cumulative numbers of recruits for any particular location were the same, i.e. there was no net loss over time from the collectors that were deployed for a longer period. This result contrasts with studies of algal and invertebrate recruitment, which have shown that post-settlement losses are high (e.g. Widdows 1991, Gosselin & Qian 1997, Lamote & Johnson 2008), but is similar to other studies on mussels (Hunt & Scheibling 1998, Bownes & McQuaid 2009). In our study, recruitment to collectors deployed over the entire season was consistent with these shorter-term results, as it was equivalent or greater than the cumulative totals for collectors deployed for 2 wk periods, indicating low post-settlement mortality and importance of initial colonization in determining spatial distribution of mussels (Hunt & Scheibling 1998). Indeed, the much higher recruitment in collectors deployed for the entire season at 2 sites suggests that some type of substratum 'conditioning' (e.g. loss of chemical from the plastic, development of a biofilm; Dobretsov 1999, Bao et al. 2007, von der Meden et al. 2010, Shimeta et al. 2012) or possibly enhanced settlement was occurring in response to the presence of conspecifics (e.g. Chase & Bailey 1996, von der Meden et al. 2010).

Dispersal distances are very different between the 2 types of settlement, with primary settlers dispersing on a much larger scale than secondary settlers (Gunter 1992). When assessing connectivity among populations, the focus should be on primary settlers to determine large-scale dispersal and precise timing of the phenomenon. In contrast, secondary settlement is a more diffusive process with less impact on large-

scale connectivity, which may occur for a few weeks and remain largely local because drifting periods are much shorter than the planktonic larval phase. Our results indicate that large-scale dispersal via primary settlement occurred mainly after 1 (2009) or 2 (2008) short spawning periods. Secondary dispersal in the following weeks then allowed further localized spreading of these more isolated events of large-scale dispersal. However, if only overall recruitment had been measured, with no distinction between primary and secondary settlement, then we may have erroneously concluded that settlement (and thus connectivity) was a more temporally diffuse process, occurring across the entire season.

Prodissoconch II analysis

The average PII shell length (or size at settlement and metamorphosis) of primary settlers (242 to 384 μm) was similar to what has been reported for *Mytilus* spp. elsewhere *in situ* (Seed 1976, Sprung 1984, Hendriks et al. 2005, Bownes & McQuaid 2009), and similar to what has been observed in one laboratory study in Germany (Sprung 1984), but slightly larger than in another in the Netherlands (Hendriks et al. 2005). The average temperature is approximately 10°C along the southern shore of the St. Lawrence maritime estuary where this study was conducted, which should produce slower larval development and thus a longer larval phase duration and greater size at metamorphosis than in more temperate climate zones (Bayne 1965, Beaumont & Budd 1982, Hodgson & Bourne 1988, Widdows 1991). In the St. Lawrence estuary, we estimated that mussel larvae spent an average of 38 d (range: 27 to 67 d) in the water column before attaching to the substratum, longer than most estimates of PLD in temperate regions (Seed 1976, Widdows 1991, Lutz & Kennish 1992) but similar to estimates from subarctic areas (Kautsky 1982, Thorarinsdottir 1996, Garcia et al. 2003, Thorarinsdottir & Gunnarsson 2003). Longer PLD increases planktonic mortality but is necessary to achieve adequate development, as size and health of the settlers at metamorphosis play a major role in juvenile growth. Recruitment success varies with individuals and cohorts (Gosselin & Qian 1997, Pechenik et al. 1998), and one potential source of variability is variation in larval condition, or quality, at metamorphosis (Phillips 2002). The larger primary settlers of late August may thus have had a better potential for survival. Further experimental studies (Phillips 2002) on settlement size and success across the season need to be pursued.

The consistent size at settlement and metamorphosis (i.e. PII) during the first half of the season suggests that there is either steady, low-level reproduction occurring regionally or different sub-populations that are asynchronously reproducing, but their larvae are then well distributed within the system. In 2008, the peak of small settlers observed on 18 August strongly suggests a single large and widespread spawning event occurring in early July, as seen elsewhere (Duinker et al. 2008). Indeed, increases in shell size at settlement (PII) in the subsequent weeks would then correspond to a simple delay in settlement (i.e. longer PLD), generating the larger individuals observed in late August 2008 (some individuals up to 370 μm). Greater PII values during August 2008 were not caused by higher water temperatures since there is a reverse correlation between PII size and water temperature (Bayne 1965, Hodgson & Bourne 1988, Schejter et al. 2010), but were rather due to longer PLD of those larvae prior to settlement and metamorphosis. The smaller PII shell length of settlers in September is suggestive of a minor, secondary spawning event in weeks prior (Duinker et al. 2008). Late-September settlers could also be secondary settlers that had slow post-settlement growth and thus were still counted as primary settlers based on our estimated size threshold (this size threshold was, however, quite conservative, i.e. largest PII size combined with maximal possible period of growth). More perplexing are the smaller early pulses of settlers (early July in 2008 weekly data, and mid-July in 2009) that demonstrate that minor spawning events consistently occur in these populations early in the season.

The planktonic larval phase is known to be influenced by several interacting biological and physical parameters operating at various scales (Cowen & Sponaugle 2009). Larval growth and development of *Mytilus* larvae is known to be largely influenced by water temperature (Widdows 1991). Seasonal and annual variability of water temperature and food availability might have a considerable impact on larval development rates and, therefore, PLD and PII shell length (Widdows 1991, Fotel et al. 1999). These sources of variation were not, however, a focus of our study, and we accounted for them by using a range of growth rates and PLD estimates. The variations of PII shell length observed within a single period (e.g. weekly collections) also suggest different origins of larvae within a recruitment event. This variation could be explained by the same combination of mechanisms: different spawning times (varying PLD) and/or different spawning locations. For the latter, different hydrological regimes encountered during

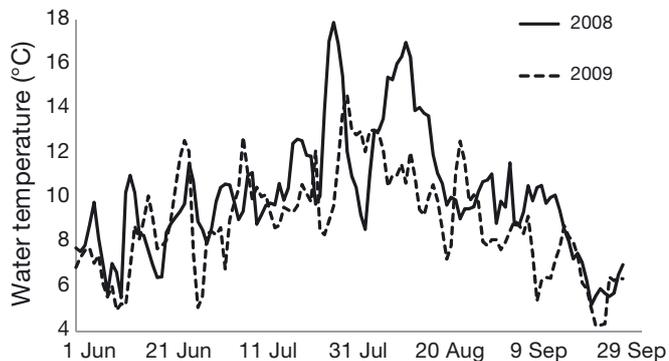


Fig. 8. *Mytilus* spp. Time series of average daily water temperature (°C) observed from 1 June to 30 September in 2008 (line) and 2009 (dashed line) measured at the Fisheries and Oceans Canada oceanographic buoy (IML-4), located 40 km upstream from Pointe-Mitis at 48° 40' N, 68° 35' W

the larval phase can generate variability in both PLD and size at metamorphosis due either to longer pathways taken by larvae (i.e. time) or to different environmental conditions encountered en route (i.e. growth). However, despite lower water temperatures in 2009 (Fig. 8; $10.1 \pm 2.7^\circ\text{C}$ in 2008 vs. $8.9 \pm 2.3^\circ\text{C}$ in 2009; mean \pm SD of average daily temperature from 1 June to 30 September), no major variations in PII size were noticed between years. The seasonal variability in size at settlement and metamorphosis, coupled with different timing of settlement peaks, suggests that there are important variations in the dispersal patterns of *Mytilus* in the St. Lawrence Estuary, and thus high variability in connectivity within the region (Le Corre et al. 2012).

CONCLUSIONS

We have demonstrated the importance of distinguishing between primary and secondary settlement when assessing the scale and timing of dispersal. Using only primary settlement data, we have shown that large-scale dispersal of *Mytilus* spp. prior to primary settlement occurs for a limited period of time in the St. Lawrence maritime estuary, usually in mid-July and mid-August. However, secondary dispersal and settlement is not as limited and can take place throughout the whole summer, and therefore better knowledge of this latter process is necessary to understand local population dynamics. The large within-season and inter-annual variability in the timing and magnitude of primary settlement demonstrates, however, that the larger-scale metapopulation dynamics are also highly variable and may be driven by exceptional years of high settlement.

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