Veliger Size at Metamorphosis and Temporal Variability in Prodissoconch II Morphometry in the Blue Mussel (*Mytilus edulis*): Potential Impact on Recruitment

VELIGER SIZE AT METAMORPHOSIS AND TEMPORAL VARIABILITY IN PRODISSOCONCH II MORPHOMETRY IN THE BLUE MUSSEL (*MYTILUS EDULIS*): POTENTIAL IMPACT ON RECRUITMENT

ANDRÉ L. MARTEL,[1,]* RÉJEAN TREMBLAY,[2] NICOLAS TOUPOINT,[2] FRÉDÉRIC OLIVIER[2,3] AND BRUNO MYRAND[4]

[1]*Zoology Section (Malacology), Research and Collections, Canadian Museum of Nature, PO Box 3443, Station D, Ottawa, Ontario K1P 6P4, Canada;* [2]*Institut des Sciences de la Mer-ISMER, Université du Québec à Rimouski, 310 Allée des Ursulines, Rimouski, Québec G5L 3A1, Canada;* [3]*UMR BOREA 7208 CNRS/MNHN/UPMC/IRD, Muséum National d'Histoire Naturelle, Bâtiment des Arthropodes, CP53, 61 Rue Buffon, 75231 Paris Cedex 5, France;* [4]*MERINOV, Centre d'Innovation de l'Aquaculture et des Pêches du Québec, Cap-aux-Meules, Québec G4T 1B3, Canada*

ABSTRACT Examination of the larval shell (prodissoconch) of molluscs with planktotrophic development can provide valuable information on their planktonic and early benthic life. We examined temporal variability of abundance and size among 11,994 veligers of the blue mussel (*Mytilus edulis*) in a coastal lagoon during settling periods between 1995 and 2009. Size and date at metamorphosis during the recruitment season were determined for 1,925 postlarvae (shell length, 255–900 μm) with prodissoconch II (PII) measurements. Emphasizing the recurrence of metamorphosis delay in the field, our study reveals a net increase in mean size at metamorphosis through time, with means for PII size ranging from 255–288 μm early in summer (after peak spawning events) to 400–422 μm (PII) during late July to early September. By estimating the "true" settlement date using the amount of dissoconch secreted after metamorphosis, such time-series analyses appropriately recapitulated the temporal pattern of mean pediveliger (competent larvae) size in the plankton. Our results demonstrate that greater settlement success rates were related to small size at metamorphosis—in particular, less than 320 μm. Seasonal increase in mean PII size occurring during the latter part of the settling period may be explained by competent veligers remaining adrift and delayed metamorphosis as a result of the lack of favorable encounters with a suitable substrate or the absence of specific trophic signals, or cues, required for stimulating settlement, thus forcing larvae to continue planktonic growth. The difference between the smallest and largest means for PII size corresponds to 122 μm of larval shell growth, or 47.8%, potentially representing a 322% difference in larval body mass at settlement.

KEY WORDS: blue mussel, veligers, prodissoconch II, delayed metamorphosis, larval settlement, recruitment, *Mytilus edulis*

INTRODUCTION

The life cycle of many marine benthic molluscs, including bivalves such as mussels, involves the production of a free-swimming planktotrophic larval stage during which the veliger larva goes through an obligate period of development in the plankton (Thorson 1950). During its planktonic development, the veliger larva feeds, grows, and disperses via water currents for a prolonged period of time, usually from 1 to many weeks (McEdward 1995, Bhaud 2000). Near the end of its planktonic period, the advanced veliger, or pediveliger, is said to become competent—that is, physiologically capable of settling and metamorphosing onto a substrate (Pechenik & Heyman 1987, Hadfield et al. 2001). After settlement, the metamorphic processes transform the planktonic pediveliger into a postlarval benthic mollusc (Lutz & Kennish 1992, Zardus & Martel 2002, Bishop et al. 2006, Pechenik 2006). For many species of benthic marine invertebrates, including molluscs, factors affecting duration of the planktonic larval life, as well as variability in size at settlement and metamorphosis, are not well understood. Yet, these are key life history traits important to research and to advances in evolution, ecology, conservation, as well as aquaculture of marine invertebrate species.

Molluscs offer a unique advantage in field studies on larval biology and ecology of marine benthic invertebrates because the molluscan shell, especially that of well-preserved early juvenile (or postlarval) stages, contains a preserved skeletal record of the growth and developmental history of the animal (Jablonski & Lutz 1980). In nearly all other groups of marine invertebrates, larval structures degenerate after the young animal has metamorphosed, making it impossible to measure precisely variables such as larval size at the time of metamorphosis. In the case of bivalves with planktotrophic larval development, the information preserved in the shell includes the size of the first larval shell secreted (prodissoconch I [PI]), representing the early veliger, or D-shape stage (which also correlates with egg size) (Chanley & Andrews 1971, Casse et al. 1998, Martel et al. 2000, Zardus & Martel 2002), and the maximum size the veliger larva reached before metamorphosis (prodissoconch II [PII]). The PII shell thus represents the size of the bivalve at metamorphosis at the onset of its benthic life (Martel et al. 1995, Martel et al. 2001), thus providing valuable *post facto* information on the larval ecology and early benthic ecology of the animal.

Although previous studies on benthic molluscs with planktotrophic larval development have shown that the size of veligers at competence (pediveligers) displays wide variation (Bayne 1965, Coon et al. 1990, Pechenik 1990, Lesoway & Page 2008, Toupoint et al. 2012b), how the size at metamorphosis varies in space or time remains largely unexplored (Phillips & Gaines 2002). To address this question, we conducted the

current study on the blue mussel, *Mytilus edulis*, in a coastal lagoon located in Îles-de-la-Madeleine (Canada's Atlantic coast). A key element for the popularity of mussel aquaculture relates to the natural supply for seed (or spat) production; larvae are abundantly available in coastal plankton and settle massively on artificial collectors for grow-out operations. However, mussel spat abundance varies annually in the main collection site of Îles-de-la-Madeleine, as demonstrated by Bourque and Myrand (2007). In this study, we examined whether annual variability of settlement rates observed during spat collection is linked to delayed metamorphosis (inferred from PII size). We test the hypothesis that modulation in delayed metamorphosis, reflected by large PII size, relates to the annual variability of settlement rates observed during mussel culture by spat collection. To this end, we developed two objectives: to determine the extent to which average PII shell length varies monthly within a given year, as well as annually, and to determine how variability of PII size relates to settlement success.

METHODS

Site Characteristics

This study was carried out in the Bassin du Havre Aubert (BHA), at the southern tip of the Îles-de-la-Madeleine (47°13'35.6'' N, 61°52'44.8'' W), central Gulf of St. Lawrence, Québec (Fig. 1) during the mussels' recruitment seasons of 1995, 1996, 1997, 1998, 1999, and 2009. This 3-km^2 semienclosed lagoon is described in Toupoint et al. (2012b) and is used by local mussel growers as a spat collecting site (Myrand et al. 2002). Daily temperature was measured at the mussel collector level (ca. 2 m below the surface) by two Hobo thermographs (Onset, Pocasset, MA). Salinity in BHA, because of scant freshwater runoff, was not measured because of its stability (28–31) (Myrand et al. 2000). Previous genetic studies have shown that Îles-de-la-Madeleine lagoons are dominated (>98%) by *Mytilus edulis* (Tremblay et al. 1998, Myrand et al. 2009).

Collection and Measurements of Veligers

Veligers were collected using a Rule submersible bilge pump (model R14; 15.5 A; maximum Output, 228 L/min) powered with a deep-cycle 12-V marine battery, which does not cause physical damage to veligers (Martel et al. 1994). Larval concentration (individuals per liter) was assessed from seawater (1,000 L) sampled 0.5–2 m below the surface and immediately sieved on 390 µm, then 53 µm Nitex filters. Three separate plankton samples were taken in the central area of BHA every 2–5 days, between early May and mid September. For each sample, the material retained on the 53-µm Nitex was transferred to an 800-mL glass jar, in which the water volume was adjusted to 500 mL with 53 µm filtered seawater. The samples were held on ice (maximum, 6 hours) until identification and counting (Aucoin et al. 2004) using an upright Olympus BX41 compound microscope on 5 subsamples of 1 mL. Absence of dissoconch was used to determine nonmetamorphosed veliger stage. For each sample, 30–90 veligers were taken randomly, and their size (longest anteroposterior dimension) was determined using a calibrated eyepiece micrometer or the software Image-Pro v.5.0.
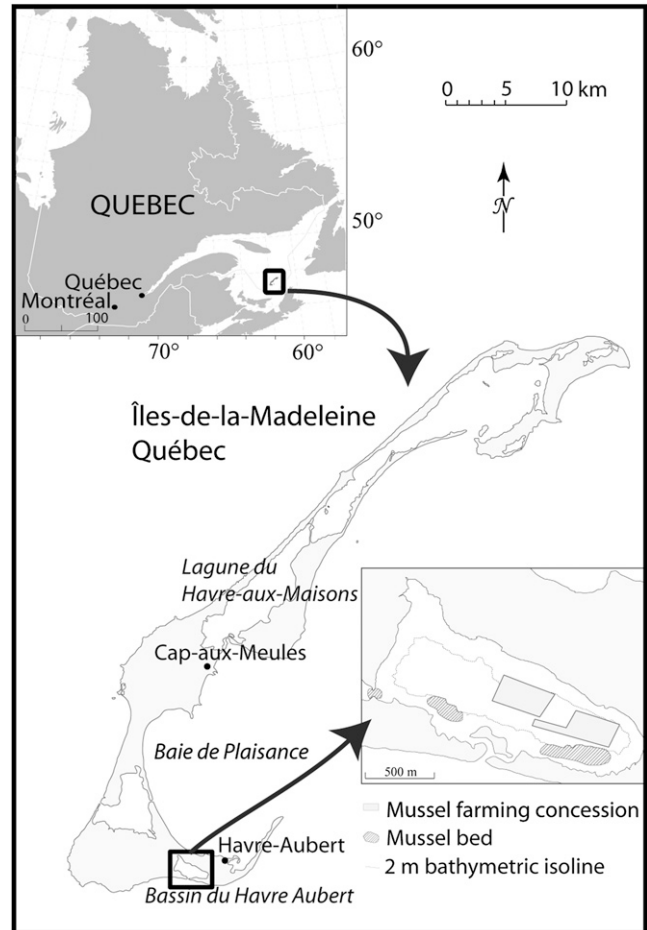

Figure 1. Map of Îles-de-la-Madeleine (Gulf of St. Lawrence, Quebec, Canada) showing the study site of Bassin du Havre-Aubert (BHA).

Collection of Postlarvae

Recently settled postlarval stages of *Mytilus edulis* were sampled from collector ropes deployed between 2 mussel farm areas (concessions) in BHA (Fig. 1). Collectors were similar to those used by mussel growers and consisted of polypropylene, 1.27 cm in diameter and 1.33 m in length, suspended vertically from longlines 0.5 m below the surface (Mallet & Myrand 1995). In this study, collectors were immersed for 1 wk from May/June to late September for measuring settlement rates. The number (sample size) of replicate collectors was as follows: for 1995, 24; 1996, 18; 1997, 18; 1998, 6; 1999, 5; and 2009, 9. For each collector (replicate), settled postlarvae were counted on a 20-cm section of rope cut off from the collector and examined under a stereomicroscope (10× magnification; MZ75, Leica Microsystems SA) to assess the settlement rate (individuals per meter per day). Settlers were preserved in 800-mL glass jars containing 500 mL 70% ethanol until PII analysis. The PII region remained very clear, and postlarval organs such as gill buds or filaments, foot, eyespot, and the digestive gland remained intact even after years of preservation.

Prodissoconch II Measurements

In *Mytilus*, the larval shell region PII (secreted before metamorphosis) is pale or reddish, contrasting with the rest of

the shell. The dissoconch, secreted after metamorphosis, is darker in color. A clear demarcation formed by a comarginal growth line occurs at the boundary between PII and dissoconch, indicating the end of larval life. Postlarval mussels were placed in holding glass Petri dishes and oriented using a modified version of the method described in Martel et al. (1995, 2001). A small ridge of dark Plasticine (ca. 3 mm wide, 20 mm long, 2 mm thick) was prepared on the bottom of a 5-cm glass Petri dish for postlarval measurement. A narrow groove was then made with a scalpel in the middle of the ridge, and 3 mm of ethanol 70% was added to the dish as to cover the Plasticine. Postlarvae were placed side by side, inside or just outside the Plasticine groove, for the examination of PII (the longest distance across the anteroposterior axis, ending at the PII-dissoconch boundary). Another type of observation dish was also used and involved using crushed silicon carbide grains (Tech-Met Canada) of 120–240 μm placed as a small mound in the center of the dish. Postlarvae could be placed and oriented in any fashion among grains.

Measurements of PII and total length of postlarvae were made using an Olympus SZH stereomicroscope (15–128× with 2× plan objective; measured at 128×) equipped with a drawing attachment and projecting images onto a Jandel/SigmaScan digitizer. Measurements were made and stored using SigmaScan (v.3.9). Error estimates (SD expressed as the percent of the mean, or coefficient of variation) using the digitizer setup were ~0.7–1.2% (Martel et al. 1995). Some measurements were made with an Olympus SZX12 (8.4–108× with 1.2× plan apo objective; measured at 108×) equipped with a PixeLink 6.6Mpx digital camera and iSolutions. The coefficient of variation obtained with replicate measurements was typically less than 1%. A total of 30–50 individual postlarvae were involved for each date when mean PII size was determined.

Data and Statistical Analysis

Comparisons of frequency distributions of PII size during the settlement period (3-wk blocks, all years combined) was evaluated using Kolmogorov–Smirnov tests with Statgraphics Plus 4.1. Analyses of variance among means of PII size were made using Kruskal–Wallis tests (because of nonnormality of data or heteroskedasticity of variances) followed by Steel-Dwass multiple comparisons using R software (v.2.15.2). Comparison of temporal patterns of PII size (i.e., size at metamorphosis) in recently settled postlarvae and pediveliger size in the plankton (pediveliger: those ≥210 μm, with a well-defined foot [Lutz & Kennish 1992]) was done using the date postlarvae were retrieved from collectors (deployment: 1 wk) and the estimated date of metamorphosis of postlarvae using a "dissoconch correction." The dissoconch correction involved determining the size of the dissoconch (or juvenile shell) of individual postlarvae by subtracting mean PII size from the total shell of the postlarva. The number of days it took the dissoconch to grow to that size after metamorphosis was then calculated using a postmetamorphic growth rate of 25 μm/day; this mean value was obtained during *in situ* growth experiments on postlarval *Mytilus trossulus* along the west coast of Vancouver Island (Martel, unpubl. data) and is similar to values obtained by Satuito et al. (1994) (22 μm/day) and by Bownes and McQuaid (2009) (up to 29 μm/day for postlarvae <1 mm) in *Mytilus galloprovincialis*. An estimated date of metamorphosis

for a given collector sample was "retrocalculated" by subtracting the estimated number of days of dissoconch growth from the actual sampling date of collectors. Correlations between PII size and pediveliger size through time were made using plankton samples collected close to the corrected date of metamorphosis. The correlation between pediveliger size and PII size was tested with the Kendall's rank correlation method (Sokal & Rohlf 1995) using BIOMstat (v.3.3; Exeter Software, E. Setauket, NY) and the statistical tables of Rohlf and Sokal (1995).

RESULTS

Seasonal Increase in Size at Metamorphosis: PII Size Analysis

Temporal variations in size of veligers (all stages) in the plankton in BHA as well as in size at metamorphosis (PII) are shown in Figure 2. From mid May to mid October, there was a distinct seasonal shift of PII size as settling periods progressed. The median (pooled data for all 6 y) for PII size was 270–280 μm during early June whereas it was 320–360 μm at the end of the settling period during late July to September. By early to mid August, large size at metamorphosis (PII) predominated; more than 30% of postlarvae had PII larger than 360 μm (Fig. 2). For the 6 combined years of data, the size distribution of PII shifted toward larger PII size for the 4 3-wk group intervals between June 1 and August 31 (Kolmogorov–Smirnov tests between adjacent 3-wk intervals: June 1–21 and June 22–July15, D = 0.3449, $n_1 = 158$, $n_2 = 488$, $P < 0.001$; June 22–July 15 and July 16–August 7, D = 0.4166, $n_1 = 488$, $n_2 = 559$, $P < 0.001$; July 16–August 7 and August 8–August 31, D = 0.3529, $n_1 = 559$, $n_2 = 466$, $P < 0.001$). Moreover, analysis of PII size–frequency distributions revealed a nearly 3-fold increase in the range of PII sizes from 1–21 June (240 < PII < 300 μm; range = 60 μm) to August 8–31 (250 < PII < 420 μm; range = 170 μm). In addition to the overall body size difference, differences in morphometry of anatomic organs occurred between small and large settlers, including size of eyespot, foot, adductor muscles, and gill bud or filaments (Fig. 3A). The increasing size at metamorphosis in *Mytilus edulis* during the settling period in BHA was also confirmed by the common presence of large planktonic veligers during late July to August, with some measuring 350–400+ μm (Fig. 2). In contrast with early June to August, there was no significant shift or change in size distribution of PII for settlers collected from August 8 to September 21 (Kolmogorov–Smirnov test, D = 0.1003, $n_1 = 466$, $n_2 = 227$, $P > 0.05$; Fig. 2).

When individual means of PII size were examined for each of the 3 y with complete water temperature and larval data sets (1995, 1996, and 2009), the distinct pattern of seasonal variation in PII size observed previously with pooled size–frequency distributions (Fig. 2) also emerged. In all 3 y, the PII mean size increased significantly between the start and the end of the settling period (Figs. 4E, 5E, and 6E; Kruskal–Wallis tests: 1995, chi-square = 161.2, df =8, $P < 0.001$; 1996, chi-square = 239.7, $df = 12$, $P < 0.001$; 2009, chi-square = 146.7, $df =8$, $P < 0.001$). For the 3 y, the PII means were low at the beginning of the settling period in mid to late June (282–288 μm), but reached high values later in the season (e.g., August), with means of 346–377 μm. During 1996, mean size at metamorphosis increased from a low 255 μm on July 22 to a record-high PII mean of 377 μm on August 19 (i.e., a 122-μm [42%] increase in mean size at metamorphosis during a 1-mo period (Fig. 5E).
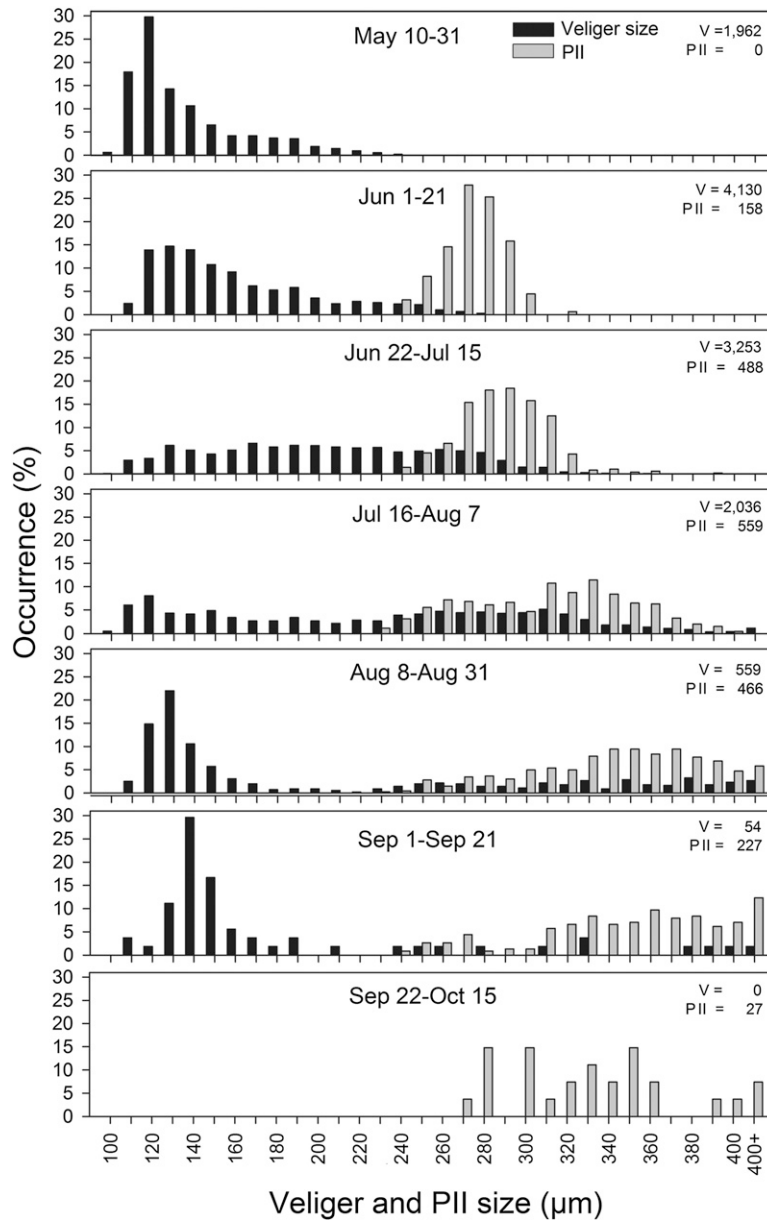
Figure 2. Size–frequency distributions of *Mytilus edulis* veligers and prodissoconch II (PII) of postlarvae collected in Bassin du Havre Aubert (BHA), Îles-de-la-Madeleine, from May to September 1995, 1996, 1997, 1998, 1999, and 2009. Veligers (all stages) were collected near the surface using a plankton pump; early postlarvae (spat; for PII analysis) were collected from collector ropes in BHA. The 7 histogram panels show the veliger and PII size data according to 3-wk periods, from early May to mid October. The panels involve pooled data for the 6 nonconsecutive studied years and include a total of 11,994 veligers and 1,925 PII measurements.

The period during which mean size at metamorphosis (PII size) increased rapidly and exceeded 300 μm (start of delay of metamorphosis) was different among years (Figs. 4E, 5E, and 6E). Prodissoconch II values greater than 300 μm occurred at the end of July or beginning of August during 1995 and 1996. In contrast, in 2009, a year of much reduced larval settlement rates (Figs. 4C, 5C, and 6C), evidence of delayed metamorphosis occurred earlier in the season, in early July (Fig. 6E).

Veliger Abundance, Settlement Rate, and Seasonal Temperature

Similar trends emerged for seasonal temperature regime, veliger abundance, and settlement rate for 1995, 1996, and 2009

(Figs. 4A–C, 5A–C, and 6A–C). In the BHA lagoon, mean water temperature was about 10–12°C at the time the first veligers occurred in the plankton during late May/early June, reached 17–19°C by mid July, and peaked at 20–22°C during August. Main episodes of veliger abundance (all stages combined) occurred from late May to early July, with minor or low periods of larval abundance during the rest of the summer, when the temperature exceeded 15°C in the lagoon (Figs. 4A, B; 5A, B; and 6A, B). The first and primary peak of veliger settlement occurred approximately 3–4 wk after the peak of veliger abundance for each of the 3 y (Figs. 4C, 5C, and 6C). An extended period of low settlement rate occurred for the rest of the summer in 1996 (Fig. 5C), whereas secondary peaks of settlement occurred during late July/
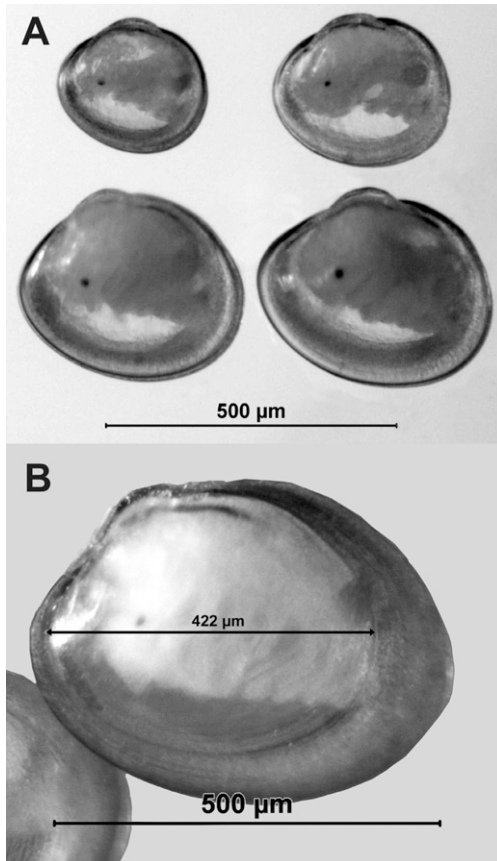
Figure 3. (A) Pictures depicting 4 recently settled mussels retrieved from collector ropes in June/early July (upper row) and in August 2009 (lower row) in Bassin du Havre Aubert. The 4 individuals had no dissoconch secreted yet (only prodissoconch I and II present) and reveal the wide size range of competent veligers (capable of settling and metamorphosis) present in the water column during the settling period. (B) Postlarva (presence of dissoconch) from the same collector sample that displays a large PII size, indicative of a large veliger size (in this case, 422 μm) at the time of metamorphosis.

August in both 1995 and 2009, representing approximately 25% of the primary peak (Figs. 4C and 6C).

Overall, primary (and first) peaks of larval settlement observed early during the settling period (late June to early July; Figs. 4C, 5C, and 6C) coincided with smaller PII sizes, with mean values of 282–313 μm (Fig. 2) and relatively small variances within samples (Figs. 4E, 5E, and 6E). In contrast, settlement in mid to late summer (e.g., late July/August, and until early September) coincided with a high proportion of large veligers at metamorphosis (large PII), with means of 321–377 μm displaying much greater variances within samples. The temporal patterns of settlement rates were similar among years, but magnitude showed important annual differences (Figs. 4C, 5C, and 6C). During 1995 and 1996, the maximum settlement rate in 1 wk was measured at more 600 individuals/ m/day, and the most important rates (>200 individuals/m/day) were observed when the mean PII size was less than 300 μm. Conversely, less than 100 individuals/m/day represented the maximal settlement rate measured in 2009, which was, at the commercial level, characterized by a very low success of spat collection for all mussel farms using this lagoon.

Pediveliger Size, PII Size, and the Dissoconch Correction

Overall, temporal variation in veliger size and PII size followed similar trends, with the PII pattern delayed by approximately 1–2 wk. As shown by the timing of the first and second peaks for veliger size and PII size, a similar trend, including the 1–2-wk delay between the 2 parameters, was particularly obvious in 1995 (Fig. 4D, E) and rather more complex during 1996 and 2009 (Figs. 5D, E and 6D, E).

When mean PII size was plotted through time (Fig. 7), a temporal correction was brought to the date postlarvae were retrieved from collectors by estimating the number of days they had grown since metamorphosis (i.e., days of postlarval growth before sampling date). For 1995, 1996, and 2009, mean size of the dissoconch portion of postlarvae gathered from rope collectors ranged from 13–436 μm, with estimated days (age) since metamorphosis ranging from about 1–17 days (Table 1). Considering the weekly deployment of collectors, the latter values would imply postmetamorphic drifting (Lane et al. 1985, Martel & Chia 1991). For all 3 y tested, Kendall's rank correlation tests revealed a significant concordance between the temporal pattern of PII and pediveliger size in BHA when plotted as a function of the estimated date of metamorphosis (Fig. 7), with *P* values < 0.01 in 1995 and 1996 (τ = 0.7222 and 0.8001, respectively) or *P* < 0.05 in 2009 (τ = 0.6671).

DISCUSSION

Prodissoconch II and Recruitment Success

For several years, we observed a similar and important seasonal variability in size at metamorphosis (PII) of blue mussels. The beginning of the recruitment season was characterized by the presence of small PII size, with means ranging from 255–288 μm. Such mean sizes at metamorphosis are less than those reported by LeCorre et al. (2013) for *Mytilus* spp. (*edulis–trossulus* hybrids) at the beginning of and during peak recruitment season along the Gaspé Peninsula in the St. Lawrence maritime estuary (means, 285–300 μm). In BHA, however, in the weeks that followed the main recruitment peak on collectors, we observed mean PII sizes reaching values as high as 377 μm, with some individuals displaying a PII of 422 μm. The combination of these 2 behaviors or strategies occurring during the same recruitment season could maximize the success of the new generation, as discussed later.

The results support our primary working hypothesis during good years of settlement when lower mussel settlement rates were related to delayed metamorphosis reflected by large PII size. Specifically, the most important peaks of larval settlement (between 200 individuals/m/day and 600 individuals/m/day) observed early during the settling period of 1995 and 1996 coincided with smaller PII size (<300 μm). In addition, metamorphosis delays more than 300 μm were related to settlement rates less than 100 individuals/m/day, which occurred each year from midsummer until autumn. In comparison with 1995 and 1996, peak settlement during the 2009 season was much lower (mean, <90 individuals/m/day) and metamorphosis delays more than 300 μm occurred earlier (early July), suggesting less favorable planktonic conditions for mussel veligers.

The blue mussel *Mytilus edulis*, at this site of Iles-de-la-Madeleine, is thus characterized by the ability to lengthen its larval duration period, which could lead to differential survival and fitness patterns.
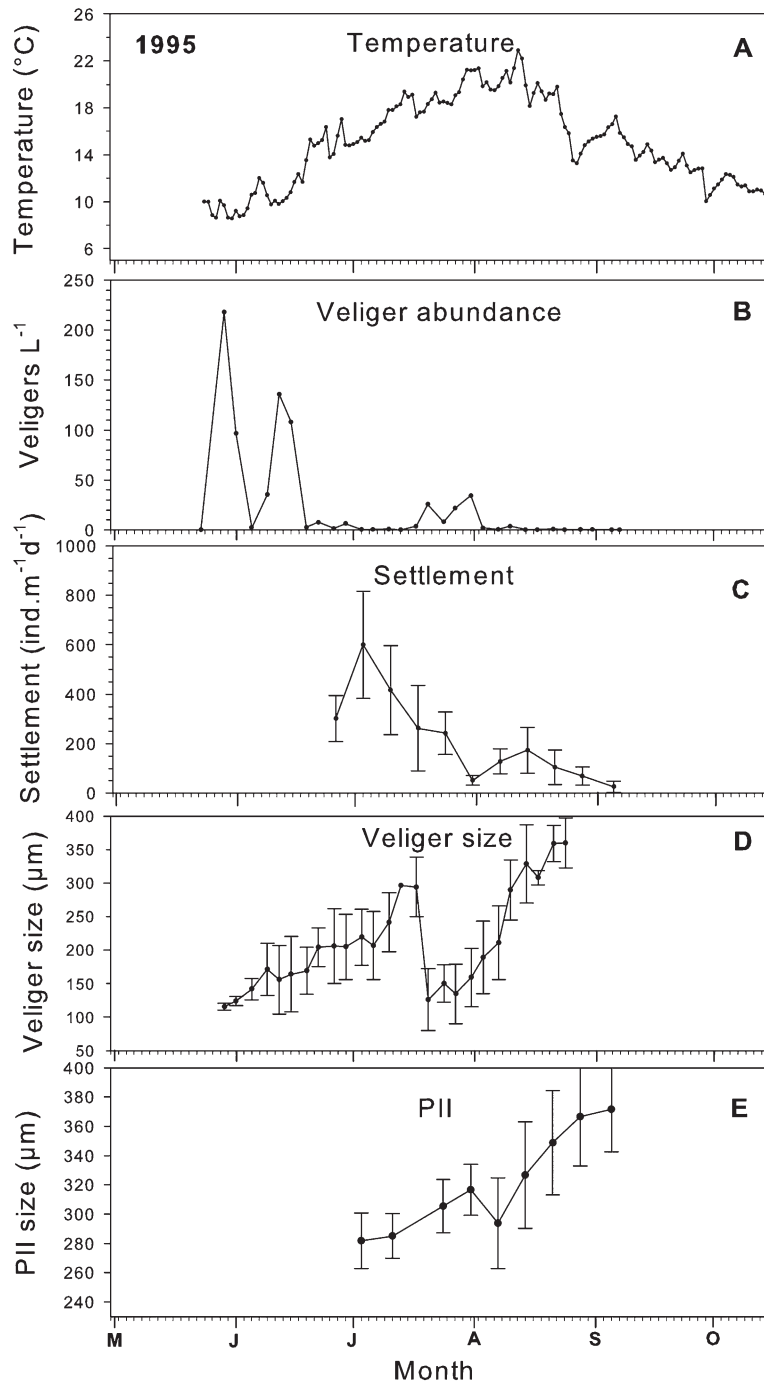
Figure 4. Observed temporal patterns (1995) of planktonic (veliger abundance and size) and benthic (settlement rates, prodissoconch II size) variables in *Mytilus edulis* **of Bassin du Havre Aubert (BHA), Îles-de-la-Madeleine, from May to October 1995. Each tick along *x*-axis represents 2 days. (A) Daily seawater temperatures taken 2 m below the surface near the middle of BHA. (B) Abundance of veligers (all sizes) in BHA. Each dot represents the mean of 3 replicate plankton samples. (C) Settlement rates on polypropylene nylon rope collectors. Each dot represents the mean ($\pm$ SD) of 24 collector replicates. (D) Size of veligers (all sizes) in the plankton of BHA. Each dot represents the mean size ($\pm$ SD) of 30–90 replicates. (E) Prodissoconch II (PII) size of postlarvae measured from recently settled individuals gathered from rope collectors in BHA. Each dot represents the mean ($\pm$ SD) of 30 PII replicates. Below each bar, samples with the same letters are not significantly different (Steel-Dwass, alpha level = 0.05).**

Possible Factors Explaining Observed Metamorphosis Delay

The duration of the planktonic period has a direct effect on the size veligers reach at the end of their planktonic life and their size at metamorphosis. Laboratory studies have shown that under similar food supply and seawater temperature conditions, the longer the veligers keep swimming and feeding in the water column, the larger they grow, and the larger their size at settlement (Pechenik et al. 1990). Moreover, in many marine molluscs with planktotrophic development, the pediveliger has
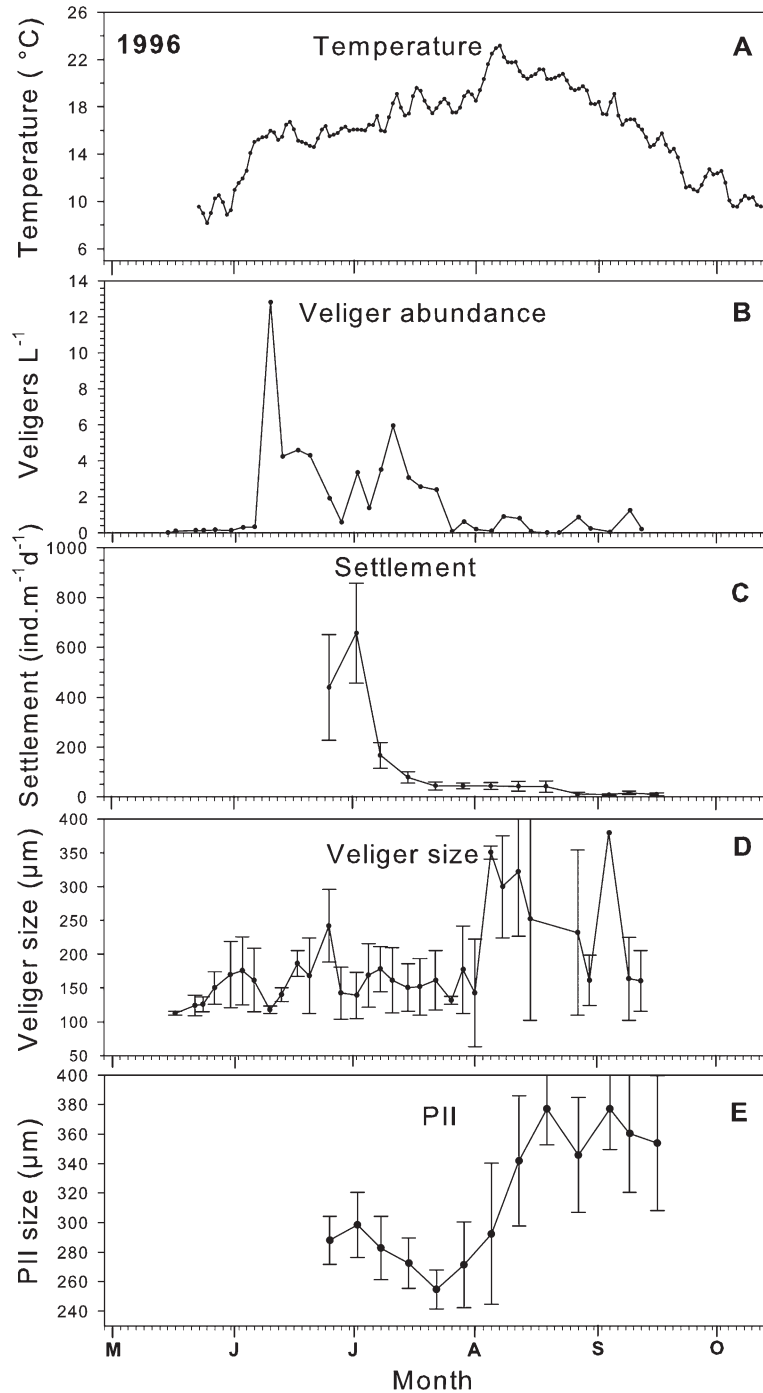
Figure 5. Observed temporal patterns (1996) of planktonic (veliger abundance and size) and benthic (settlement rates, prodissoconch II size) variables in *Mytilus edulis* of Bassin du Havre Aubert (BHA), Îles-de-la-Madeleine, from May to October of 1996. Each tick along *x*-axis represents 2 days. (A) Daily seawater temperatures taken 2 m below the surface near the middle of BHA. (B) Abundance of veligers (all sizes) in BHA. Each dot represents the mean of 3 replicate plankton samples. (C) Settlement rates on polypropylene nylon rope collectors. Each dot represents the mean ($\pm$ SD) of 18 collector replicates. (D) Mean size of veligers (all sizes) in the plankton of BHA. Each dot represents the mean size ($\pm$ SD) of 30–90 replicates. (E) Prodissoconch II size of postlarvae measured from recently settled individuals gathered from rope collectors in BHA. Each dot represents the mean ($\pm$ SD) of 30 PII replicates. Below each bar, samples with the same letters are not significantly different (Steel-Dwass, alpha level = 0.05).

been shown to be capable of extending the duration of its planktonic life significantly, thus delaying metamorphosis. Such a delay has been well documented in the laboratory culture of larval bivalves and gastropods (Bayne 1965, Coon et al. 1990, Pechenik 1990, Pechenik et al. 1990, Pechenik et al.

1993, Lesoway & Page 2008). The most accepted hypothesis explaining the phenomenon of delay of metamorphosis in molluscan larvae, including in *Mytilus* mussels, is that it occurs when the pediveliger does not come in contact with a suitable substrate, thus resulting in the pediveliger continuing, at least
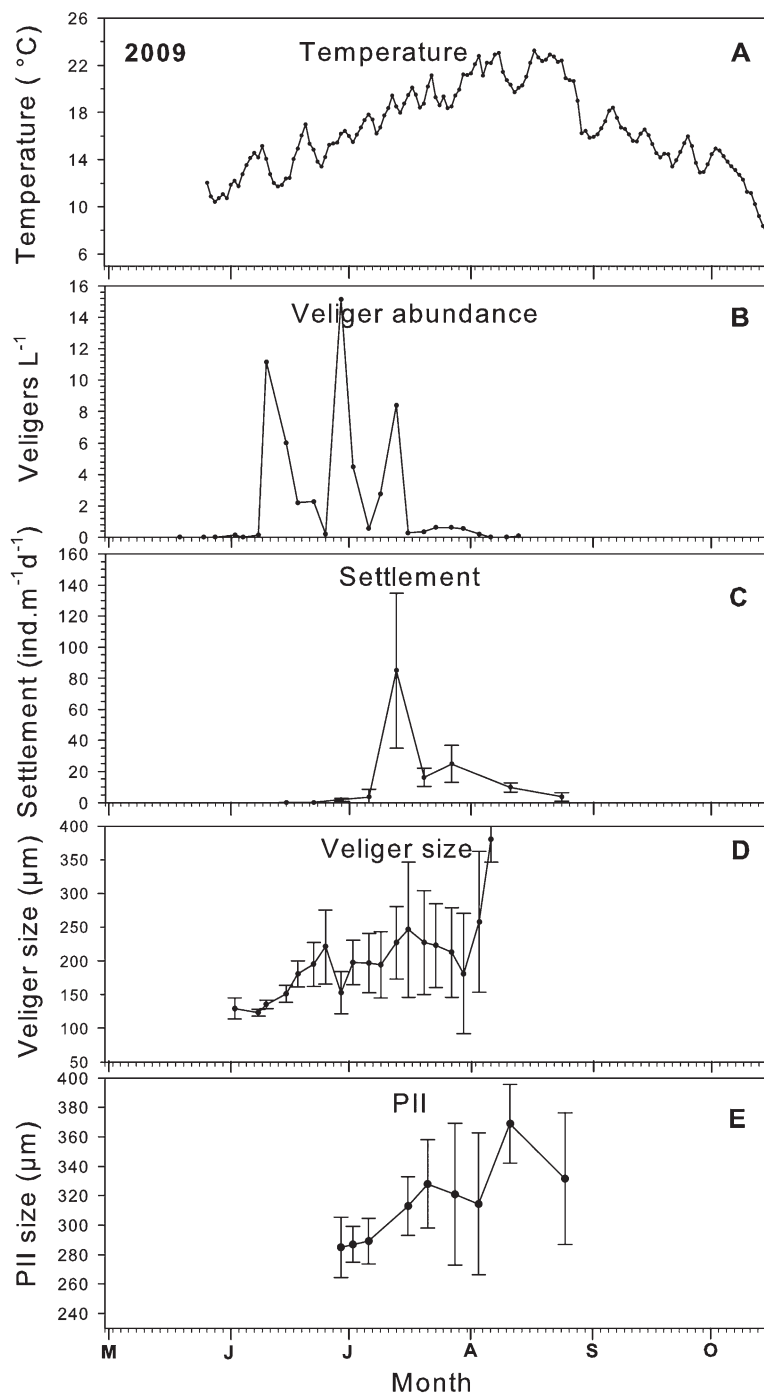
Figure 6. Observed temporal patterns (2009) of planktonic (veliger abundance and size) and benthic (settlement rates, prodissoconch II size) variables in *Mytilus edulis* of Bassin du Havre Aubert (BHA), Îles-de-la-Madeleine, from May to October 2009. Each tick along *x*-axis represents 2 days. (A) Daily seawater temperatures taken 2 m below the surface near the middle of BHA. (B) Abundance of veligers (all sizes) in BHA. Each dot represents the mean of 3 replicate plankton samples. (C) Settlement rates on polypropylene nylon rope collectors. Each dot represents the mean ($\pm$SD) of 9 collector replicates. (D) Mean size of veligers (all sizes) in the plankton of BHA. Each dot represents the mean size ($\pm$SD) of 30–90 replicates. (E) Mean prodissoconch II size of postlarvae measured from recently settled individuals gathered from rope collectors in BHA. Each dot represents the mean ($\pm$SD) of 24–56 PII replicates. Below each bar, samples with common letters are not significantly different (Steel-Dwass, alpha level = 0.05).

for some time, its growth in the plankton (Bayne 1965, Bayne 1976, Pechenik et al. 1990, Bishop et al. 2006). In some species, competent veligers have been shown to delay metamorphosis for periods as long as, or even longer than, the entire precompetent larval period itself. When delaying, pediveligers can settle repeatedly onto substratum and be resuspended in the water column, where they continue to swim and feed. Veligers of *Mytilus edulis* are capable of delaying settlement and metamorphosis significantly, so that the total larval period could be more than 50 days in the laboratory (Pechenik et al. 1990).
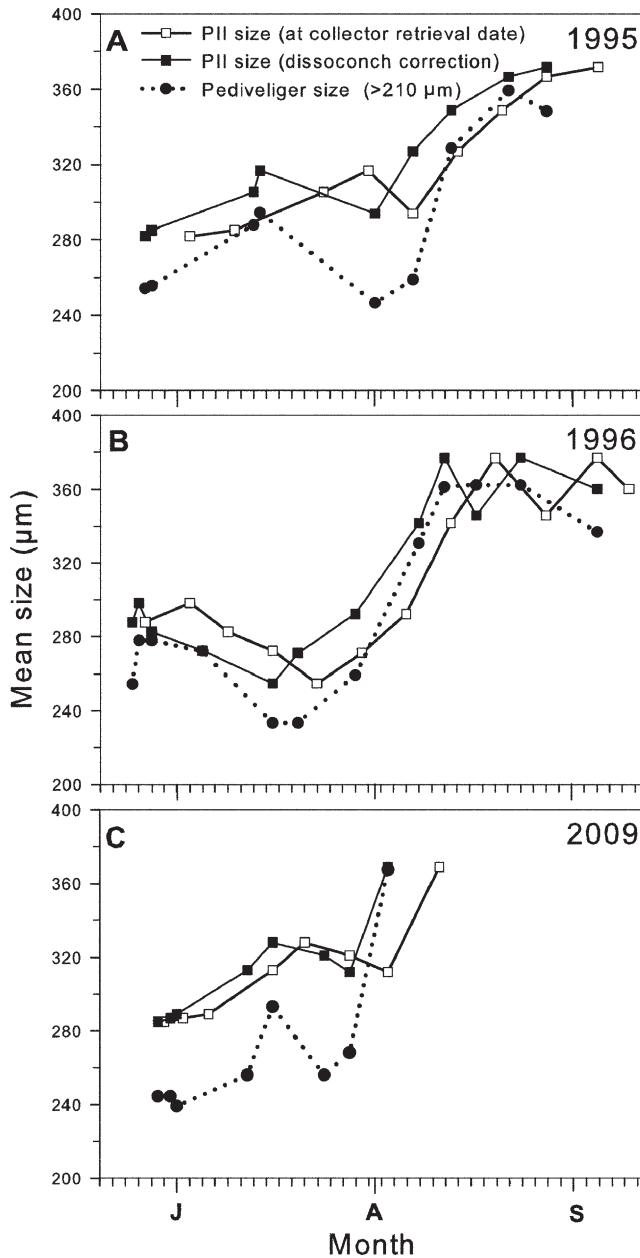
Figure 7. (A–C) Comparison of temporal patterns of *Mytilus edulis* prodissoconch II size (size at metamorphosis) in recently settled postlarvae and pediveliger size (≥210 μm) in the plankton at Bassin du Havre Aubert (BHA), during 1995 (A), 1996 (B), and 2009 (C). For each graph, the continuous line with open squares represents the mean PII value as a function of the day postlarvae were retrieved from collectors. The continuous line with solid squares represents the mean PII size as a function of the estimated date of settlement–metamorphosis of individuals in that sample, calculated using a "dissoconch correction" (see Methods and Table 1). The dotted line with solid circles represents the mean size of pediveligers (veligers, ≥210 μm) present in the plankton at or nearest the estimated date of settlement (Table 1).

Bayne (1965) showed that in the absence of a suitable substrate, *M. edulis* veligers can delay settlement and metamorphosis for up to 46 days. Moreover, Pulfrich (1996) indicated that winter settlement of *M. edulis* veligers on collectors as well as natural substrates in the Wadden Sea provides evidence for their ability

for extensive delay of metamorphosis (see also Beaumont and Budd [1982]).

Environmental factors are known to affect the size of veligers at the end of their planktonic life and, accordingly, the size of postlarvae at the beginning of their benthic life. Factors such as water depth where planktotrophic veligers spend at least part of their developmental period have been linked to variability in PII size at settlement (Robertson 1994, Martel et al. 2001). However, water depth is likely not a significant factor in the shallow environment at BHA and in the usual habitat of *Mytilus edulis* inhabiting the intertidal and the shallow subtidal environment. On the other hand, food supply during the planktonic phase, as well as seawater temperature (Pechenik et al. 1990, Emlet & Sadro 2006), are among the most important environmental factors affecting the size of veligers at the end of their planktonic life. Experimental studies conducted in the laboratory have shown that both quality and quantity of the planktonic food used by invertebrate larvae can influence their growth significantly (Basch & Pearse 1996, McEdward & Qian 2001, Phillips 2002, Reitzel et al. 2005). Mussel larvae are omnivorous, feeding mainly on bacteria, cyanobacteria, phytoplankton, and heterotrophic protists (Raby et al. 1997). The metamorphic process requires high energy expenditure and especially high-quality reserves accumulated during the larval phase; such reserves determine both metamorphic success and early juvenile performance (Holland 1978, Phillips 2002, Pernet et al. 2004, Pechenik 2006). Studies on food (seston) used by mussels larvae in BHA in 2008 demonstrated that temporal and spatial seston quality, estimated by fatty acids profiles and quantity, showed no sign of deficiency even if pediveliger size at settlement varied between 260 μm to more than 360 μm (Toupoint et al. 2012b). The presence of large pediveligers at the end of recruitment season was explained by metamorphosis delay related to the absence of settlement cues. Toupoint et al. (2012a, 2012b) suggested that abundance of picoplankton enriched in polyunsaturated fatty acids acts as a trophic settlement trigger for mussel larvae. Thus, it is possible that the large PII observed each year in this small coastal lagoon could be related to the absence of a specific trophic signal required for stimulating settlement, thus forcing mussel larvae to continue growing into the water column. Absence of a trophic settlement trigger could explain the low settlement success observed in 2009 and the relative absence of settlement at sizes smaller than under 300 μm that year. We suggest that triggers were present later in summer 2009 and required veligers to delay their metamorphosis until they reached more than 300 μm. A longer period of time in plankton would increase mortality and decrease settlement success.

Water temperature is another primary environmental factor tested in the laboratory and shown to influence significantly the size of marine molluscan larvae during settlement. A strong inverse relationship between seawater temperature and maximum size at larval settlement has been shown in various marine bivalve species, including mussels (Bayne 1965, Manoj Nair & Appukuttan 2003), oysters (Flores-Vergara et al. 2004, Ben Kheder et al. 2010), scallops (Cragg 2006), and clams (Lutz & Jablonski 1978). Thus, lower or decreasing seawater temperatures leads to an increase in both larval duration and size at settlement (i.e., larger PII size). On the other hand, our results from BHA show that temperature variations could not explain

TABLE 1.

Estimation of the date of settlement of postlarval *Mytilus edulis* sampled from collectors in BHA using a "dissoconch correction," which involves using the mean dissoconch size of the postlarvae sampled.

Year	Collector retrieval date	Retrieval day (Julian)	TL			PII			Dissoconch (µm)	Days since settlement	Estimated date of settlement	Estimated day of settlement (Julian)	Size of pediveligers at date of settlement (µm)
			µm	SD	n	µm	SD	n					
1995	Jul 3	184	450.7	41.3	30	281.9	18.9	30	168.9	7	Jun 26	177	254.1
	Jul 10	191	615.6	224.4	30	285.0	15.4	30	330.6	13	Jun 27	178	255.4
	Jul 24	205	577.2	51.3	30	305.3	18.1	30	271.9	11	Jul 13	194	287.9
	Jul 31	212	752.5	76.6	30	316.6	17.3	30	435.9	17	Jul 14	195	294.4
	Aug 7	219	444.5	96.7	30	293.9	31.0	30	150.6	6	Aug 1	213	246.3
	Aug 14	226	505.8	58.5	30	326.8	36.4	30	179.0	7	Aug 7	219	258.8
	Aug 21	233	537.5	87.6	30	348.7	35.6	30	188.8	8	Aug 13	225	328.5
	Aug 28	240	518.4	64.8	30	366.6	33.9	30	151.7	6	Aug 22	234	359.2
	Sep 5	248	569.8	84.8	30	371.5	29.1	30	198.3	8	Aug 28	240	348.2
1996	Jun 25	177	327.8	18.4	30	288.0	16.3	30	39.8	2	Jun 23	175	254.3
	Jul 2	184	493.6	49.9	30	298.5	22.0	30	195.1	8	Jun 24	176	278.1
	Jul 8	190	593.2	64.9	30	282.7	21.5	30	310.5	12	Jun 26	178	278.1
	Jul 15	197	535.5	112.0	30	272.5	17.2	30	262.9	11	Jul 4	186	272.2
	Jul 22	204	426.7	48.7	30	254.7	13.3	30	172.0	7	Jul 15	197	233.3
	Jul 29	211	527.2	103.2	30	271.4	28.9	30	255.9	10	Jul 19	201	233.6
	Aug 5	218	503.5	76.1	30	292.3	47.7	30	211.2	8	Jul 28	210	259.2
	Aug 12	225	470.7	60.9	30	341.6	44.1	30	129.0	5	Aug 7	220	330.7
	Aug 19	232	587.0	24.3	30	376.9	24.4	30	210.1	8	Aug 11	224	361.3
	Aug 27	240	615.8	39.0	30	345.8	39.0	30	270.0	11	Aug 16	229	362.4
	Sep 4	248	674.9	50.4	30	376.9	27.5	30	297.9	12	Aug 23	236	362.4
	Sep 9	253	479.7	100.5	30	360.2	39.9	30	119.5	5	Sep 4	248	336.8
2009	Jun 29	180	297.7	22.4	52	284.8	20.4	52	12.9	1	Jun 28	179	244.4
	Jul 2	183	344.2	44.1	24	287.0	12.3	24	57.2	2	Jun 30	181	244.4
	Jul 6	187	402.5	79.4	54	289.1	15.5	54	113.4	5	Jul 1	182	239.1
	Jul 16	197	409.2	56.8	56	313.0	20.0	56	96.3	4	Jul 12	193	255.9
	Jul 21	202	446.3	78.0	42	327.9	29.9	42	118.4	5	Jul 16	197	293.1
	Jul 28	209	430.1	79.6	39	320.9	48.1	39	109.2	4	Jul 24	205	255.9
	Aug 3	215	465.7	94.6	40	311.9	45.6	40	153.8	6	Jul 28	209	268.1
	Aug 11	223	573.9	89.7	39	368.9	26.7	39	204.9	8	Aug 3	215	367.4

Values of the mean of total length (TL), prodissoconch II size (PII), and dissoconch size (dissoconch = TL – PII) are shown. Mean size of the dissoconch portion of postlarvae and a postmetamorphic growth rate of 25 µm/day (see Methods) were then used to estimate the number of days since larval metamorphosis had occurred to estimate the date of settlement (including in Julian day format). The mean size of pediveligers (veligers, ≥210 µm) from plankton samples collected the same or close to (±3 days) the day to that of the estimated (corrected) date of metamorphosis is also shown.

larger veliger sizes at settlement in mid or late summer; PII sizes more than 350 µm occurred when seawater temperature reached the maximum value of 23°C. Whether seasonal variability in food quality (ref. trophic signal or cue required for triggering settlement) can mask or neutralize the effect of increasing temperature in mid or late summer remains unanswered.

Delayed Metamorphosis and Cost/Benefits to Offspring

Shorter larval duration (associated with small size at settlement) is assumed to decrease larval mortality potential, whereas longer larval duration (settling at larger sizes) may decrease probability of early benthic juvenile mortality (larger juveniles). Indeed, previous studies have shown that, in general, larvae that remain in the plankton for shorter periods reach smaller total size (in the case of bivalves, smaller PII) before settling and may be subject to lower overall larval mortality because of decreased exposure to predation during planktonic life (Morgan 1995, Pechenik & Levine 2007, Pedersen et al. 2008, Hayhurst &

Rawson 2009). In general, metamorphosis during the planktonic larval stage is considered to be the critical phase in terms of mortality in the life cycle of Bivalvia (Pechenik 1999, Pedersen et al. 2008). The mortality cost for species with a planktonic larval stage has been estimated to be 5–8 times greater than for species with direct development (Rumrill 1990). However, after planktonic larvae settle and metamorphose, these small individuals may be subjected to a wider range of sources of early benthic mortality, such as siltation, reduced feeding opportunity, and predation by microscopic predatory species (Phillips 2002, Gosselin & Rehak 2007). High postlarval mortality is very common for marine invertebrates and could be as high as 90% (Gosselin & Qian 1997). Interannual variations in the adult population of most benthic invertebrates do not appear to be related to variability in larval supply, but rather to postsettlement processes (Olafsson et al. 1994, Olivier & Retière 1998). Predation on mussel settlers on artificial collectors suspended on longlines is limited by the new predator recruits settling at the same time as the mussels (Mallet &

Myrand 1995). Thus, on these specific collectors, high settlement success of postlarvae may relate to high recruitment levels. This is indicated by the higher spat collection levels obtained by mussel farmers in 1995 and 1996 (high settlement success of settlers <300 μm) compared with low spat collection levels in 2009 (low settlement success of settlers <300 μm).

Larger mussel settlers observed after delayed metamorphosis (large PII size) could show greater survival in natural collection sites where predators are more abundant and diverse. The difference between the smallest and largest (up to 422 μm) means for PII size represents 122 μm of additional larval shell growth, or 47.8%, assuming that the veliger body mass follows the usual cubic progression in relation to shell length. The difference in PII size could then represent a 322% increase in larval body mass at metamorphosis. In marine benthic invertebrates, the size of the first postlarval or juvenile stage is recognized as a key life history parameter constituting a biological attribute of significance in the ecology, ethology, and evolutionary biology of the species (Moran 1999, Del Rio Portilla & Beaumont 2000, McEdward & Qian 2001, Phillips 2002, Emlet & Sadro 2006, Gosselin & Rehak 2007). Individuals with a longer planktonic phase increase their potential planktonic mortality, but their greater body mass and size at settlement could increase their overall fitness, including feeding efficiency and additional protection against small benthic predators.

Estimating Delay of Metamorphosis

As shown in the current study, delay of metamorphosis can be inferred and measured when examining time series of the PII size of young postlarval or early juvenile specimens. Rayssac et al. (2010) conducted laboratory culture of *Mytilus edulis* larvae kept at 17–25°C and originating from Îles-de-la-Madeleine, and estimated that larval growth was about 8.4 μm/day. Using this value, we can estimate, using the observed means for PII size, that each summer a significant number of veligers typically delay their metamorphosis in natural conditions for about 10–15 days (22 days if we use the smallest and the largest PII values observed: 236 μm and 422 μm). Toupoint et al. (2012a, 2012b) suggested that the absence of a trophic cue could lead to metamorphosis delay, thus explaining the large veliger (>350 μm) they observed. From an ecological perspective, this delay may increase the dispersal potential (Bayne 1965, Roberts & Lapworth 2001). The large variability of PII size and the delay of metamorphosis are well known from laboratory studies but, to our knowledge, this is the first time that delayed metamorphosis of 15 days or more is reported for *M. edulis* in the natural environment, and for several years. Our study was, however, not designed to assess potential contrasting survival rates and recruitment success of long-delay settlers versus small or no-delay settlers.

Moreover, we propose that the PII size parameter could be used to estimate the date of metamorphosis of young postlarvae with a known growth rate. For example, if we adopt a mean daily growth of 25 μm/day (see data analysis section in Methods), we can then estimate the time of settlement and the mean size of competent veligers at the date of metamorphosis for each sampling period. Although in this study we used a mean daily growth value originating from postlarval mussels raised at a location different from BHA, the 25-μm/day value

used is comparable with that published in other *Mytilus* studies in temperate climates and may apply overall to the BHA postlarval mussels. For future research on *Mytilus* settlement, our study emphasizes the necessity of gathering accurate *in situ* daily growth rate data obtained near the site where larval collectors are deployed. When such data are obtained, the use of a dissoconch correction to calculate the date of metamorphosis can allow the reconstruction of the size–distribution patterns of pediveligers in the plankton during the settling period.

CONCLUSIONS

Our study reveals a net increase in mean size at metamorphosis among *Mytilus edulis* veligers through the settling period in BAH, with means of PII size ranging from 255–288 μm early in summer (after peak spawning events) and reaching sizes as large as 400–422 μm during late July to early September. Greater settlement success rates are related to small size at metamorphosis—in particular, less than 300 μm. We propose that the seasonal increase in mean PII size during the latter part of the settling period may be explained by competent veligers remaining adrift and delaying metamorphosis, leading to the observed occurrence of high numbers of veligers with 350–400+-μm shell length. This delayed metamorphosis may be the result of a lack of encounter with a suitable substrate or an absence of a specific trophic signal or cue required for stimulating settlement, forcing larvae to continue planktonic growth (refer to studies by Toupoint et al. [2012a, 2012b] conducted in the same basin). A difference of 122 μm between the smallest and largest means of PII size was observed, corresponding to 47.8% of additional larval shell growth and potentially representing a 322% difference in larval body mass at settlement. Biological information provided by PII analysis is of interest to larval biologists and ecologists, as well as those involved in mussel culture. Further research should be conducted on the functional anatomy, behavior, physiological condition, and survival/fitness among settlers of different size ranges to evaluate more fully the costs or benefit of settling, and metamorphosis at extreme sizes. The increase of seasonal PII in wild settlers needs to be tested in other environments as well as in other molluscs.

LITERATURE CITED

Aucoin, F., S. Doiron & M. Nadeau. 2004. Guide d'échantillonnage et d'identification des larves d'espèces à intérêt maricole. Guide/publication G005. Quebec: MAPAQ. 73 pp.

Basch, L. V. & J. S. Pearse. 1996. Consequences of larval feeding environment for settlement and metamorphosis of a temperate echinoderm. *Oceanol. Acta* 19:273–285.

Bayne, B. L. 1965. Growth and the delay of metamorphosis of the larvae of *Mytilus edulis* (L.). *Ophelia* 2:1–47.

Bayne, B. L. 1976. The biology of mussel larvae. In: B. L. Bayne, editor. Marine mussels: their ecology and physiology. London: Cambridge University Press. pp. 81–120.

Beaumont, A. R. & M. D. Budd. 1982. Delayed growth of mussel (*Mytilus edulis*) and scallop (*Pecten maximus*) veligers at low temperatures. *Mar. Biol.* 71:97–100.

Ben Kheder, R., J. Moal & R. Robert. 2010. Impact of temperature on larval development and evolution of physiological indices in *Crassostrea gigas*. *Aquaculture* 309:286–289.

Bhaud, M. 2000. Two contradictory elements determine invertebrate recruitment: dispersion of larvae and spatial restrictions on adults. *Oceanol. Acta* 2000:409–422.

Bishop, C. D., M. J. Huggett, A. Heyland, J. Hodin & B. P. Brandhorst. 2006. Interspecific variation in metamorphic competence in marine invertebrates: the significance for comparative investigations into the timing of metamorphosis. *Integr. Comp. Biol.* 46:662–682.

Bourque, F. & B. Myrand. 2007. Essais de stratégies pour contrer l'effet négatif des algues sur la collecte de moules au Bassin du Havre Aubert. MAPAQ, DIT. Rapport de R-D no. 157. 13 pp.

Bownes, S. J. & C. D. McQuaid. 2009. Mechanisms of habitat segregation between an invasive and an indigenous mussel: settlement, post-settlement mortality and recruitment. *Mar. Biol.* 156:991–1006.

Casse, N., N. Devauchelle & M. Le Pennec. 1998. Embryonic shell formation in the scallop *Pecten maximus* (Linnaeus). *Veliger* 41:133–141.

Chanley, P. & J. D. Andrews. 1971. Aids for identification of bivalve larvae of Virginia. *Malacologia* 11:45–119.

Coon, S. L., W. K. Fitt & D. B. Bonar. 1990. Competence and delay of metamorphosis in the Pacific oyster *Crassostrea gigas*. *Mar. Biol.* 106:379–387.

Cragg, S. M. 2006. Development, physiology, behaviour and ecology of scallop larvae. In: S. E. Shumway & G. L. Parsons, editors. Scallops: biology, ecology and aquaculture. Developments in aquaculture and fisheries science, book 35. Amsterdam: Elsevier. pp. 45–122.

Del Rio Portilla, M. A. & A. R. Beaumont. 2000. Larval growth, juvenile size and heterozygosity in laboratory reared mussels, *Mytilus edulis*. *J. Exp. Mar. Biol. Ecol.* 254:1–17.

Emlet, R. B. & S. Sadro. 2006. Linking stages of life history: how larval quality translates into juvenile performance for an intertidal barnacle (*Balanus glandula*). *Integr. Comp. Biol.* 46:334–346.

Flores-Vergara, C., B. Cordero-Esquivel, A. N. Ceron-Ortiz & B. O. Arredondo-Vega. 2004. Combined effects of temperature and diet on growth and biochemical composition of the Pacific oyster *Crassostrea gigas* (Thunberg) spat. *Aquacult. Res.* 35:1131–1140.

Gosselin, L. A. & P.- Y. Qian. 1997. Juvenile mortality in benthic marine invertebrates. *Mar. Ecol. Prog. Ser.* 146:265–282.

Gosselin, L. A. & R. Rehak. 2007. Initial juvenile size and environmental severity: influence of predation and wave exposure on hatching size in *Nucella ostrina*. *Mar. Ecol. Prog. Ser.* 339:143–155.

Hadfield, M. G., E. J. Carpizo-Ituarte, K. del Carmen & B. T. Nedved. 2001. Metamorphic competence, a major adaptive convergence in marine invertebrate larvae. *Am. Zool.* 41:1123–1131.

Hayhurst, S. & P. D. Rawson. 2009. Species-specific variation in larval survival and patterns of distribution for the blue mussels *Mytilus edulis* and *Mytilus trossulus* in the Gulf of Maine. *J. Mollusc. Stud.* 75:215–222.

Holland, D. L. 1978. Lipid reserves and energy metabolism in the larvae of benthic marine invertebrates. In: D. C. Malin & J. R. Sargent, editors. Biochemical and biophysical perspectives in marine biology. London: Academic Press. pp. 85–123.

Jablonski, D. & R. A. Lutz. 1980. Molluscan larval shell morphology (ecological and paleontological applications). In: D. C. Rhoads & R. A. Lutz, editors. Skeletal growth of aquatic organisms. New York: Plenum Press. pp. 323–377.

Lane, D. J. W., A. R. Beaumont & J. R. Hunter. 1985. Byssus drifting and the drifting threads of the young postlarval mussel *Mytilus edulis*. *Mar. Biol.* 84:301–308.

LeCorre, N., A. L. Martel, F. Guichard & L. E. Johnson. 2013. Variation in recruitment: differentiating the roles of primary and secondary settlement of blue mussels, *Mytilus* spp. *Mar. Ecol. Prog. Ser.* 481:133–146.

Lesoway, M. P. & L. R. Page. 2008. Growth and differentiation during delayed metamorphosis of feeding gastropod larvae: signatures of ancestry and innovation. *Mar. Biol.* 153:723–734.

Lutz, R. A. & D. Jablonski. 1978. Larval bivalve shell morphometry: a new paleoclimatic tool? *Science* 202:51–53.

Lutz, R. A. & M. J. Kennish. 1992. Ecology and morphology of larval and early postlarval mussels. In: E. Gosling, editor. The mussel *Mytilus*: ecology, physiology, genetics and culture. Vol. 25. Amsterdam: Elsevier. pp. 53–86.

Mallet, A. & B. Myrand. 1995. The culture of the blue mussel in Atlantic Canada. In: A. D. Boghen, editor. Cold-water aquaculture in Atlantic Canada, 2nd edition. Moncton, Quebec: Canadian Institute for Research on Regional Development. pp. 255–296.

Manoj Nair, R. & K. K. Appukuttan. 2003. Effect of temperature on the development, growth, survival and settlement of green mussel *Perna viridis* (Linnaeus, 1758). *Aquacult. Res.* 34:1037–1045.

Martel, A. L., L. M. Auffrey, C. Robles & B. M. Honda. 2000. Identification of settling and early post-larval stages of mussels (*Mytilus* spp.) from the Pacific coast of North America, using prodissoconch morphology and genomic DNA. *Mar. Biol.* 137:811–818.

Martel, A. L., B. S. Baldwin, R. M. Dermott & R. A. Lutz. 2001. Species and epilimnion/hypolimnion-related differences in size at larval settlement and metamorphosis in *Dreissena* (Bivalvia). *Limnol. Oceanogr.* 46:707–713.

Martel, A. L. & F. S. Chia. 1991. Drifting and dispersal of small bivalves and gastropods with direct development. *J. Exp. Mar. Biol. Ecol.* 150:131–147.

Martel, A. L., T. M. Hynes & J. Buckland-Nicks. 1995. Prodissoconch morphology, planktonic shell growth, and size at metamorphosis in *Dreissena polymorpha*. *Can. J. Zool.* 73:1835–1844.

Martel, A. L., A. F. Mathieu, C. S. Findlay, S. J. Nepszy & J. H. Leach. 1994. Daily settlement rates of the zebra mussel, *Dreissena polymorpha*, on an artificial substrate correlate with veliger abundance. *Can. J. Fish. Aquat. Sci.* 51:856–861.

McEdward, L. R., editor. 1995. Ecology of marine invertebrate larvae. Boca Raton, FL: CRC Press. 480 pp.

McEdward, L. R. & P.- Y. Qian. 2001. Effects of the duration and timing of starvation during larval life on the metamorphosis and

initial juvenile size of the polychaete *Hydroides elegans* (Haswell). *J. Exp. Mar. Biol. Ecol.* 261:185–197.

Moran, A. L. 1999. Size and performance of juvenile marine invertebrates: potential contrasts between intertidal and subtidal benthic habitats. *Am. Zool.* 39:304–312.

Morgan, S. 1995. Life and death in the plankton: larval mortality and adaptation. In: L. McEdward, editor. Ecology of marine invertebrate larvae. Boca Raton, FL: CRC Press. pp. 279–322.

Myrand, B., H. Guderley & J. H. Himmelman. 2000. Reproduction and summer mortality of blue mussels *Mytilus edulis* in the Magdalen Islands, southern Gulf of St. Lawrence. *Mar. Ecol. Prog. Ser.* 197:193–207.

Myrand, B., R. Tremblay & J.- M. Sévigny. 2002. Selection against blue mussels (*Mytilus edulis* L.) homozygotes under various stressful conditions. *J. Hered.* 93:238–248.

Myrand, B., R. Tremblay & J.- M. Sévigny. 2009. Impact of suspension culture using mesh sleeves on genetic characteristics of *Mytilus edulis* L. in Canada. *Aquaculture* 291:147–153.

Olafsson, E. B., C. H. Peterson & W. G. Ambrose. 1994. Does recruitment limitation structure populations and communities of macroinvertebrates in marine soft sediments? The relative significance of presettlement and postsettlement processes. *Oceanogr. Mar. Biol. Annu. Rev.* 32:65–109.

Olivier, F. & C. Retière. 1998. The role of physical–biological coupling in the benthic boundary layer under megatidal conditions: the case of the dominant species of the *Abra alba* community in the eastern Baie de Seine (English Channel). *Estuaries* 21:571–584.

Pechenik, J. A. 1990. Delayed metamorphosis by larvae of benthic marine invertebrates: does it occur? Is there a price to pay? *Ophelia* 32:63–94.

Pechenik, J. A. 1999. On the advantages and disadvantages of larval stages in benthic marine invertebrate life cycles. *Mar. Ecol. Prog. Ser.* 177:269–297.

Pechenik, J. A. 2006. Larval experience and latent effects: metamorphosis is not a new beginning. *Integr. Comp. Biol.* 46:323–333.

Pechenik, J. A., L. S. Eyster, J. Widdows & B. L. Bayne. 1990. The influence of food concentration and temperature on growth and morphological differentiation of blue mussel *Mytilus edulis* L. larvae. *J. Exp. Mar. Biol. Ecol.* 136:47–64.

Pechenik, J. A. & W. D. Heyman. 1987. Using KCl to determine size at competence for larvae the marine gastropod *Crepidula fornicata* (L.). *J. Exp. Mar. Biol. Ecol.* 112:27–38.

Pechenik, J. A. & S. H. Levine. 2007. Estimates of planktonic larval mortality using the marine gastropods *Crepidula fornicata* and *C. plana*. *Mar. Ecol. Prog. Ser.* 344:107–118.

Pechenik, J. A., D. Rittschof & A. R. Schmidt. 1993. Influence of delayed metamorphosis on survival and growth of juvenile barnacles *Balanus amphitrite*. *Mar. Biol.* 115:287–294.

Pedersen, T. M., J. L. S. Hansen, A. B. Josefson & B. W. Hansen. 2008. Mortality through ontogeny of soft-bottom marine invertebrates with planktonic larvae. *J. Mar. Syst.* 73:185–207.

Pernet, F., R. Tremblay, C. Langdon & E. Bourget. 2004. Effect of additions of dietary triacylglycerol microspheres on growth, survival, and settlement of mussel (*Mytilus* sp.) larvae. *Mar. Biol.* 144:693–703.

Phillips, N. E. 2002. Effects of nutrition-mediated larval condition on juvenile performance in a marine mussel. *Ecology* 83:2562–2574.

Phillips, N. E. & S. D. Gaines. 2002. Spatial and temporal variability in size at settlement of intertidal mytilid mussels from around Pt. Conception, California. *Invertebr. Reprod. Dev.* 41:171–177.

Pulfrich, A. 1996. Attachment and settlement of post-larval mussels (*Mytilus edulis* L.) in the Schleswig-Holstein Wadden Sea. *J. Sea Res.* 36:239–250.

Raby, D., M. Mingelbier, J. J. Dodson, B. Klein, Y. Lagadeuc & L. Legendre. 1997. Food-particle size and selection by bivalve larvae in a temperate embayment. *Mar. Biol.* 127:665–672.

Rayssac, N., F. Pernet, O. Lacasse & R. Tremblay. 2010. Temperature effect on survival, growth, and triacylglycerol content during the early ontogeny of *Mytilus edulis* and *M. trossulus*. *Mar. Ecol. Prog. Ser.* 417:183–191.

Reitzel, A. M., C. M. Miles, A. Heyland, J. D. Cowart & L. R. McEdward. 2005. The contribution of the facultative feeding period to echinoid larval development and size at metamorphosis: a comparative approach. *J. Exp. Mar. Biol. Ecol.* 317:189–201.

Roberts, R. D. & C. Lapworth. 2001. Effect of delayed metamorphosis on larval competence, and post-larval survival and growth, in the abalone *Haliotis iris* Gmelin. *J. Exp. Mar. Biol. Ecol.* 258:1–13.

Robertson, R. 1994. Protoconch size variation along depth gradients in a planktotropic *Epitonium*. *Nautilus* 107:107–112.

Rohlf, F. J. & R. R. Sokal. 1995. Statistical tables, 3rd edition. New York: Freeman. 199 pp.

Rumrill, S. S. 1990. Natural mortality of marine invertebrate larvae. *Ophelia* 32:163–198.

Satuito, C. G., K. Natoyama, M. Yamazaki & N. Fusetani. 1994. Larval development of the mussel *Mytilus edulis galloprovincialis* cultured under laboratory conditions. *Fish. Sci.* 60:58–65.

Sokal, R. R. & F. J. Rohlf. 1995. Biometry: the principles and practice of statistics in biological research, 3rd edition. New York: Freeman. 887 pp.

Thorson, G. 1950. Reproductive and larval ecology of marine bottom invertebrates. *Biol. Rev. Camb. Philos. Soc.* 25:1–45.

Toupoint, N., V. Mohit, I. Linossier, N. Bourgougnon, B. Myrand, F. Olivier, C. Lovejoy & R. Tremblay. 2012a. Effect of the biofilm age on *Mytilus edulis* settlement. *Biofouling* 29:985–1001.

Toupoint, N., L. Solomon-Gilmore, F. Bourque, B. Myrand, F. Pernet, F. Olivier & R. Tremblay. 2012b. Match/mismatch between the *Mytilus edulis* larval supply and seston quality: effect on recruitment. *Ecology* 93:1922–1934.

Tremblay, R., B. Myrand & J.- M. Sevigny. 1998. Genetic characterization of wild and suspension-cultured blue mussels (*Mytilus edulis* Linneaus, 1758) in the Magdalen Islands (southern Gulf of St. Lawrence, Canada). *J. Shellfish Res.* 17:1191–1202.

Zardus, J. D. & A. L. Martel. 2002. Phylum Mollusca: Bivalvia. In: C. M. Young., M. A. Sewell & M. E. Rice, editors. Atlas of marine invertebrate larvae. San Diego, CA: Academic Press. pp. 290–325.