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INFLUENCES OF PHYSICAL AND BIOLOGICAL VARIABLES ON SOFTSHELL CLAM (*MYA ARENARIA* LINNEAUS 1758) BURIAL

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ABSTRACT Stock enhancement of the infaunal bivalve, *Mya arenaria,* is becoming an increasingly important strategy for fisheries managers and the clamming industry in eastern Canada and the New England states. There is also a growing interest towards softshell clam culture. A fast burial after the seeding should decrease (1) passive dispersion by currents and waves; (2) exposure to extreme changes in temperature; and (3) predation by crabs, flatfishes, birds, and similar. Thus, a fast burial could reduce losses shortly after seeding and possibly benefit later harvests. However, little is known about factors acting on burial. This study provides clam growers in our area with general guidelines to better manage their seeding operations. Five factors possibly influencing the burial rate were examined in the present study: clam size, seeding density, emersion period prior to seeding, substratum softening prior to seeding, and seasonal period. Most experiments were performed in field conditions on sandy beaches in Iles-de-la-Madeleine, (southern Gulf of St. Lawrence). Only clam size and seasonal period showed significant effects. Clam size (15–40 mm SL) was inversely related to burial rate. Clams buried faster in late August when water temperature reached 23°C and then slowed down steadily as temperature dropped to 7°C in early October. An increase in clam density from 100–350 clams (25–30 mm SL) · m^{-2} had no negative effects on burial rate as well as emersion periods up to 4 h prior to seeding. Softening of the sandy substratum had no positive effects on burial rate.

KEY WORDS: *Mya arenaria*, burial, seeding

INTRODUCTION

In North America clam culture targets mainly hard shell clams, *Mercenaria mercenaria* (Linnaeus 1758), on the East coast (Malouf & Siddall 1985, Petrovits 1985, Buckner 1988, Kraus 1988), and Manila clams, *Tapes philippinarum* (Adams & Reeve 1850), on the West coast (Chevarie & Myrand 2005). The softshell clam (*Mya arenaria*) culture began only recently (DFO 2002, Buttner et al. 2004, Chevarie & Myrand 2006). Enhancement of softshell clam-flats is performed in New England using wild or hatchery-reared seed but only anecdotal information is available (Beal 2005, Calderon et al. 2005, Beal 2006b). Although some experiments have been carried out with this species (e.g., Beal 1993, Beal et al. 1995, Parker et al. 1998, Beal et al. 1999, Beal & Kraus 2002, Beal 2006a, Beal 2006b) much remains unknown about softshell clam culture/enhancement.

One important aspect in clam culture/enhancement is seeding because any problem encountered during this phase could impact production. When seeded, individual clams are spread directly on the sediment and must bury by themselves. A fast burial should have a positive impact on seeding success by reducing (1) passive dispersion by currents and waves; (2) exposure to extreme changes in temperature; and (3) predation by rock crabs, flatfishes, birds, etc (Emerson et al. 1990, Zaklan & Ydenberg 1997, Strasser et al. 1999, Tallqvist 2001). Inversely, a slow burial may increases losses shortly after seeding.

Burial involves muscular movements (Trueman 1968, Pérès 1976). It requires energy, which to our knowledge has not been quantified yet. Therefore burial could possibly be affected by factors influencing the energy balance of the clam, including its general condition. For example, a clam under stress must invest larger quantities of energy to maintain its internal equilibrium (Hoffmann & Parsons 1991) and thus will possibly have less energy to invest for its burial. That could possibly slow down burial. Indeed, burial rate is considered as a valuable indicator of stress level in clams (Chicharo et al. 2003).

Hatchery-reared clams are seeded at a size <15 mm of shell length (SL) (see Beal's experiments). Such small clams usually bury within 10 min (Emerson et al. 1990, Beal & Vencile 2001). Thus, burial rate should not be a major concern when using small healthy clams as seed supply. However clam seed for enhancement/culture often comes from wild populations and its size range is usually 15–45 mm SL (Calderon et al. 2005, Beal 2006b, Chevarie & Myrand 2006). These larger clams need more time to rebury and in some instances complete burial can require up to 72 h (Lise Chevarie, pers. obs).

Few ecological studies have been reported on the burial of infaunal bivalves, including *M. arenaria*, and most of them investigated on burial depth rather than burial rate. Water temperature, clam size, and type of substratum are known to influence the burial rate of softshell clams (Baptist 1955, Pfitzenmeyer & Drobeck 1967, Emerson et al. 1990, Newell 1991, Zaklan & Ydenberg 1997, Lardies et al. 2001). Burial has been reported to slow down at temperatures below 8.8°C and above 21°C (Pfitzenmeyer & Drobeck 1967, Newell 1991) and to be fastest at ~18°C in muddy-sandy substrates (Newell 1991). The influence of clam size was studied with small (<25 mm) and large (36–70 mm) clams (Baptist 1955, Pfitzenmeyer &

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Drobeck 1967). Small softshell clams usually bury more rapidly than larger ones (Baptist 1955, Pfitzenmeyer & Drobeck 1967, Zaklan & Ydenberg 1997, Tallqvist 2001). Burial rate is higher in fine- to medium-sand substratum with a granulometry <0.5 mm (Pfitzenmeyer & Drobeck 1967, Lardies et al. 2001) as found at the clam culture lease in Iles-de-la-Madeleine (Chevarie & Myrand 2006).

The main objective of this study is to examine various biological and environmental factors possibly acting on clam burial rates. The effect of clam size, emersion period prior to seeding, substrate softening prior to seeding, seeding density, and seasonal period were all examined simulating culture conditions in Iles-de-la-Madeleine (southern Gulf of St. Lawrence). Although size is known to be inversely correlated to burial rates, this relation was examined specifically for the local stock and the size range (15–40 mm) currently used for seeding. It has been suggested that substratum softening before seeding could ease and accelerate burial (Thomas Landry, DFO-Moncton and Leon Lanteigne, SEnPAq Consultants, Tracadie-Sheila, N.B.; pers. comm.). Beal (2006b) also asked about the interest of roughening surface to enhance burial rate of clams. This hypothesis is tested in the present study. Clams are held out of water for some time during their transfer to the seeding area and during the seeding operations *per se*, particularly when seeding is done at a large scale (L. Chevarie, pers. obs.). However, the effect of the duration of the emersion period prior to seeding has not yet been examined even if emersion leads to stress (Newell 1991, Chicharo et al. 2003) and metabolic depression (anaerobic metabolism). To date, the possible effect of clam density has not been studied although it could play a role because of the possible physical contacts between the individuals at the time of seeding. Finally, little is known on the seasonal variability of the burial rate. Several parameters that could influence burial (temperature, salinity, food, general condition, reproductive cycle, etc.) interact together under field conditions. The seasonal pattern of burial rate was thus studied in relationship with these parameters.

MATERIALS AND METHODS

Experimental clams were gathered from the intertidal flat providing seed supply to the local commercial grower in the southwestern area of the Havre-aux-Basques lagoon in Iles-de-la-Madeleine (47°26′19″N, 61°47′34″W), Gulf of St. Lawrence (Fig. 1). Clams were excavated with a hydraulic device (pressurized water from a 4 hp pump) similar to the type used for commercial clam culture (Chevarie et al. 2003). To recover from possible stress caused by the harvest (Chicharo et al. 2003) and transfer operations, clams were kept in a flow-through tank supplied with ambient seawater pumped from Havre-aux-Maisons lagoon for at least 24 h before experiments.

All experiments were conducted under field conditions except the "seasonal period" experiment, which was performed in flow-through tanks to minimize possible confounding effects caused by variations in some environmental conditions like wind and tidal level at the time of measurements.

All experiments (except the clam size experiment) were performed with 25–30 mm SL clams, which belong to the most abundant size-class in the natural population (Bourque et al. 2006) and, thus, are most likely to be used for seeding. Each clam was used only once.

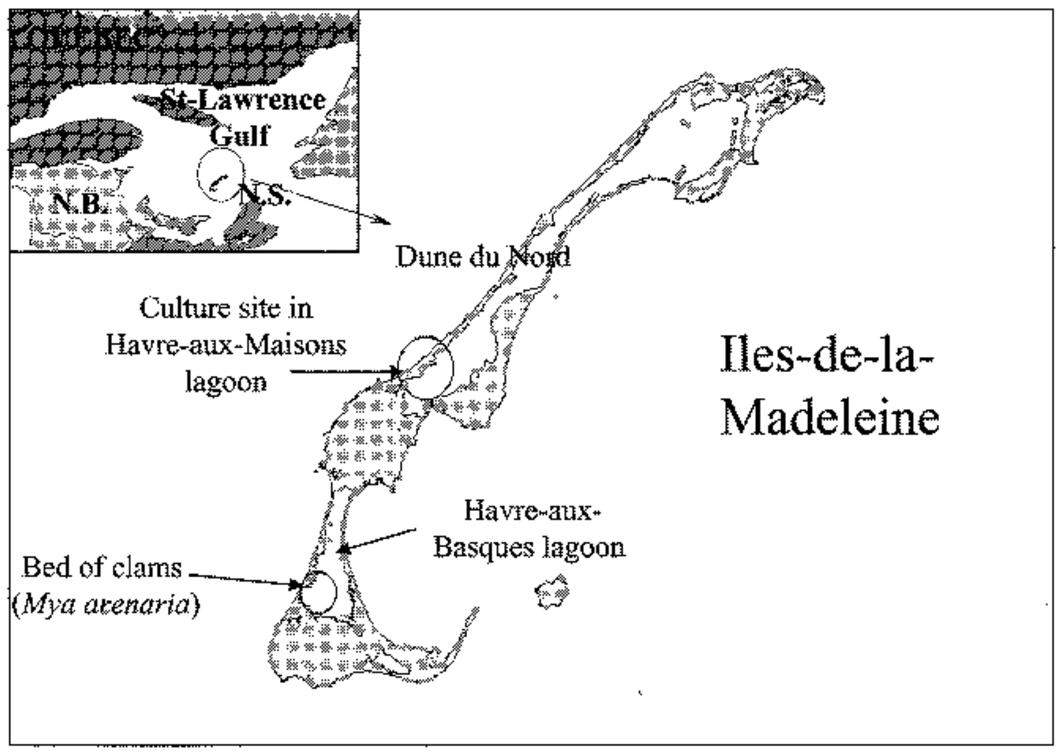

Figure 1. Localization of the Havre-aux-Basques lagoon (natural bed) and the clam culture lease in the Havre-aux-Maisons lagoon (seeding site) in Iles-de-la-Madeleine (southern Gulf of St. Lawrence; 47°26′19″ N, 61°47′34″ W).

Experiments Under Field Conditions

Experiments on clam size, density, emersion period, and substratum softening were conducted in shallow water (<30 cm) at the commercial clam lease in the Havre-aux-Maisons lagoon. The basic experimental set-up was as follows unless otherwise stated.

Clams were placed individually in enclosures made with PVC tubes (10-cm diameter) introduced vertically into the sediments. The top 2 cm of the tubes was kept out of the sediments as a barrier against possible passive dispersion of clams caused by currents. Tubes were not covered with nets (Beal & Kraus 2002) because the presence of the experimenter precluded predation.

Each treatment included 20 replicate clams for a total of 60 or 80 experimental individuals (3 or 4 treatments per experiment). Tubes with individual clams were arrayed in 4 rows × 15 or 20 columns. The tubes were spaced from each other by ~4 cm. To ease observations, a 50-cm wide corridor was arranged after every five columns to allow for the experimenter's passage. This set-up minimized heterogeneity in environmental conditions of a given replicate (substratum, currents, tidal height, temperature). Clams from each treatment were randomly distributed within the array.

Individual clams were not closer than 14 cm from each other at the beginning of the observations (each placed in the middle of a 10-cm tube and two successive cylinders being separated by ~4 cm). Thus, the burial behavior of a given clam should not impact its neighbors. Indeed no spatial patterns were observed in burial rate within a given replicate thus suggesting independent responses of the clams.

The diameter of the tubes was large enough to minimize any possible change in water flow caused by the physical set-up. The experiments were done in calm weather conditions. Water flow was weak because the maximal tidal amplitude is only about 50 cm in this area (V. Koutitonsky, ISMER, pers. comm.). No obvious changes in water circulation were observed within the cylinders. If there were some changes, they were of a limited extent and comparable for each clam.

Burial level was measured for individual clams through time and provided information on burial rate. The buried portion of a given individual (0, 1/4, 1/3, 2/4, 2/3, 4/4) was evaluated every 15 min for the first 2 h and, thereafter, every 30 min for a total duration of 3 h. There were no clam losses during the observations and the buried proportion of the clams throughout a given period of observation always showed a positive progression.

Clam Size Experiment

This experiment was performed in 9 replicates between July 23 to 25, 2002. Burial level was recorded for clams from three size classes: 15–20, 25–30, and 35–40 mm. These classes span the size range of clam seed used at a commercial scale in Iles-de-la-Madeleine (Chevarie et al. 2003).

Emersion Period Experiment

This experiment was performed in 9 replicates between June 7 to 9, 2002 to get environmental conditions close to those observed during the recommended period for seeding, spring and early summer (Beal 2005).

Burial level was measured after various periods of emersion in the morning (no emersion, 1 h, 2 h, and 4 h). The longest emersion period was limited to half a day (from 7h–11h or 4 h), which is plausible for a large-scale commercial operation. During emersion, clams were kept in a single layer in "pearl-nets" under the combined desiccating effect of the sun and the wind. Clams were not covered with wet clothes or paper towels during emersion to mimic the local commercial seeding operations. Such exposure probably adds some stress on clams and thus may amplify the negative effects of emersion.

Obviously, the emersion conditions could not be tightly controlled under natural conditions but all emersion treatments in a given replicate were applied under the same conditions. Also, consecutive experimental days provided comparable weather conditions.

Substratum Softening Experiment

This experiment was performed in 9 replicates between August 26–28, 2002. Burial rate was recorded according to the time spent between substratum softening and seeding. Four treatments were compared: no softening, 1 day, 5–7 days, and 13–15 days after softening. The substratum was softened with a hydraulic device as used for commercial harvesting. This machine directs a pressurized water-jet (Honda pump 4 hp) towards the sediments through 10 nozzles equally spaced along a 1 m horizontal bar. The water jets fluidize and stir up sediments down to a 10-cm depth (Chevarie & Myrand 2006).

The clams exposed to the various treatments could not be laid down randomly as in the previous experiments because the substratum could not be softened on areas as small as the size of the tubes (individual clams). Therefore, the treatments rather than the individuals were distributed randomly on the experimental site. Large areas of substratum were softened on three occasions at 1-wk intervals to provide the 3 softening treatments. An adjacent area was left undisturbed to provide a control.

The observations were done the day after the last softening operation to compare the four treatments simultaneously. Caution was taken to avoid new disturbance of sediments when planting the tubes. Further, the diameter of the tubes was large enough to avoid disturbance of sediments at their center (i.e., where were placed the experimental clams). For each replicate, the 20 clams of a given treatment were arrayed in 4 rows × 5 columns on a randomly selected area submitted to the chosen treatment.

Density Experiment

This experiment was carried out between September 9 and 10, 2002 with 6 replicates. Water temperature (13°C) was lower than during the other experiments performed in the summer. Three densities were examined: low (100 clams · m^{-2}), medium (225 clams · m^{-2}), and high (350 clams · m^{-2}). These densities are within the range of those used in seeding experiments (Chevarie et al. 2003).

No tubes could be used in this experiment. About 80 clams were used for each replicate of a given density. Of these, 20 clams were marked (numbered) individually on both valves with a brite-mark pen and placed on an area corresponding to the desired density. Metal frames were used to demarcate the needed area for each experimental density with the 20 marked clams: 400 cm^2 for the low, 81 cm^2 for the medium, and 32 cm^2 for the high clam density. The frames were then removed. For each treatment 60 unmarked clams were dispersed all around the experimental (marked) individuals at a similar density to avoid any bias caused by an edge effect. Burial rate was followed for the 20 marked clams.

Experiment (Seasonal Period) in Flow-through Tanks

The seasonal pattern of burial rate was measured in flow-through tanks with 9 replicates every three weeks between May 28 and October 23, 2002. Experimental tanks were located in a wet laboratory on the dock of the Havre-aux-Maisons lagoon. Each tank measured 1.9 m L × 1.1 m W × 0.6 m H. The bottom was covered with 10-cm layer of sand taken from the clam culture lease and sifted through an 800-µm mesh-sieve. Each tank was supplied with sand-filtered seawater pumped from the lagoon at a flow rate of 3 L · min^{-1}. Inflow water was distributed over the width of the tank through perforated tubings.

Before each experiment, sand was raked to remove organisms, which could have settled and to minimize any compaction effect over time. Each tank received 20 clams placed in the center of individual tubes arrayed in 4 rows × 5 columns. In contrast to the experiments under field conditions, the tubes did not extend above the substratum because the weak water circulation could not disperse clams. Tubes (10-cm diameter) were separated from each other by ~4 cm. The experimental clams were no closer than 55 cm from the inflow and 45 cm from the outflow. Burial was measured as previously (every 15 min for the first 2 h and, thereafter, every 30 min) but over a 4-h period.

Environmental and Biological Parameters

Environmental parameters were measured weekly at the tidal flat where experimental clams were collected (Havre-aux-Basques lagoon) to identify possible links with the seasonal variation in burial rate. Temperature and salinity were measured with a YSI field thermosalinometer. Water from the surface was also sampled for total particulate matter (TPM) and

organic content (POM) according to Myrand and Gaudreault (1995). These measurements were made on triplicate samples of 2 L of water.

Further, 25–30 mm clams were collected weekly to examine variation in tissue mass and condition index. Twenty-five clams were sampled from the flat, except for the weeks when the "seasonal period" experiment was performed. For these weeks, clams were collected from among those used for burial measurements in tanks (also taken from the flat). Three clams were randomly sampled from each replicate after burial rate measurements for a total of 27 clams (3 clams × 9 replicates). Clams were kept frozen until analysis of their total dry tissue mass (65°C to 70°C during 72 h). Because of the restricted range of the clam size (weekly mean: 26.9–28.7 mm) it was not necessary to use a tissue mass: shell mass ratio to get a reliable condition index measurement (Bonardelli & Himmelman 1995). Thus, the temporal changes in tissue dry mass provided information on the variation of clams general condition and, indirectly, on their reproductive cycle.

Statistical Analyses

For each experiment, the change of the burial level (buried portion) through time was tested using ANOVAs with repeated measurements. When a significant difference was found, new ANOVAs with repeated measurements were carried out to compare pairs of treatments. This procedure allowed us to identify where the observed differences occurred. A sequential Bonferroni correction was applied to the multiple comparisons to keep an overall $\alpha = 0.05$ (Rice 1989).

A stepwise forward regression analysis was carried out with the data from the "seasonal period" experiment. The buried level reached after 4 h in the tanks was selected as an index of the burial rate and used as the dependent variable, whereas the environmental data and dry tissue mass values were used as explanatory variables. The data fulfilled the conditions of normality (Kolmogorov-Smirnov test) and homogeneity of the variances (Levine test). The nonsignificant ($P > 0.05$) explanatory variables according to the stepwise regression were discarded from the model.

RESULTS

Size Class

Burial rate of the three size classes differed significantly ($F_{(2,24)} = 37.85$; $P < 0.0001$) and differed from each other (all $F_{(1,16)} > 15.35$ and $P < 0.001$) with an inverse relationship between size and burial level (Fig. 2). For example, an average burial of 50% of the shell was obtained after ~15 min for the small clams (15–20 mm) but only after 30–45 min for the average clams (25–30 mm) and >60 min for the larger ones (35–40 mm). Burial rate followed an asymptotic curve over time with a fast initial burial that slowed down with time. The difference between sizes tended to decrease with time. The mean burial level reached a maximum of 94% for the small clams after the 3-h observation period in late July.

Duration of the Emersion Period Prior to Seeding

An emersion period up to 4 h before seeding had no negative effects on the burial rate of the 25–30 mm SL clams because

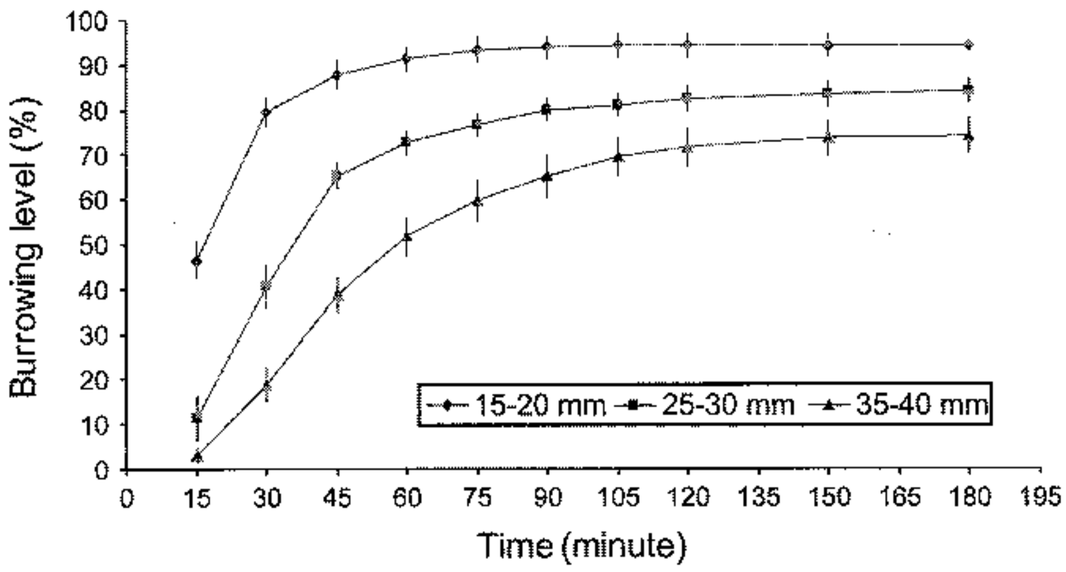

Figure 2. Burrowing level (mean proportion buried length of shell ± s.e.) of the softshell clams (*Mya arenaria*) relative to their size (15–20, 25–30, and 35–40 mm). The observations were made over 3-h periods under field conditions in Iles-de-la-Madeleine, $n = 9$ (July 23 to 25, 2002).

there were no significant differences among the various treatments ($F_{(3,32)} = 0.43$; $P = 0.74$), which included a control in continuous immersion. Burial level over time followed again an asymptotic curve and average burial level was about 80% after 3 h for all the treatments in early June (Fig. 3).

Substratum Softening Before Seeding

Substratum softening with a small hydraulic rake had no positive effect on the burial rate of 25–30 mm SL clams because no significant differences were observed between the treatments ($F_{(3,32)} = 0.07$; $P = 0.97$), which included a control (no substratum softening). Once again burial level followed an asymptotic curve through time and after 3 h and the average burial level was a little more than 80% for all treatments in late August (Fig. 4).

Seeding Density

Increase in experimental density from 100–350 clams (25–30 mm SL) · m^{-2} did not impact burial rate ($F_{(2,15)} = 0.05$; $P = 0.96$). The maximum burial level reached after the 3-h period was a little less than 50% of the shell for the three densities (Fig. 5). However, this experiment took place in September 2002 when water temperature was lower than during the other experiments performed during summer.

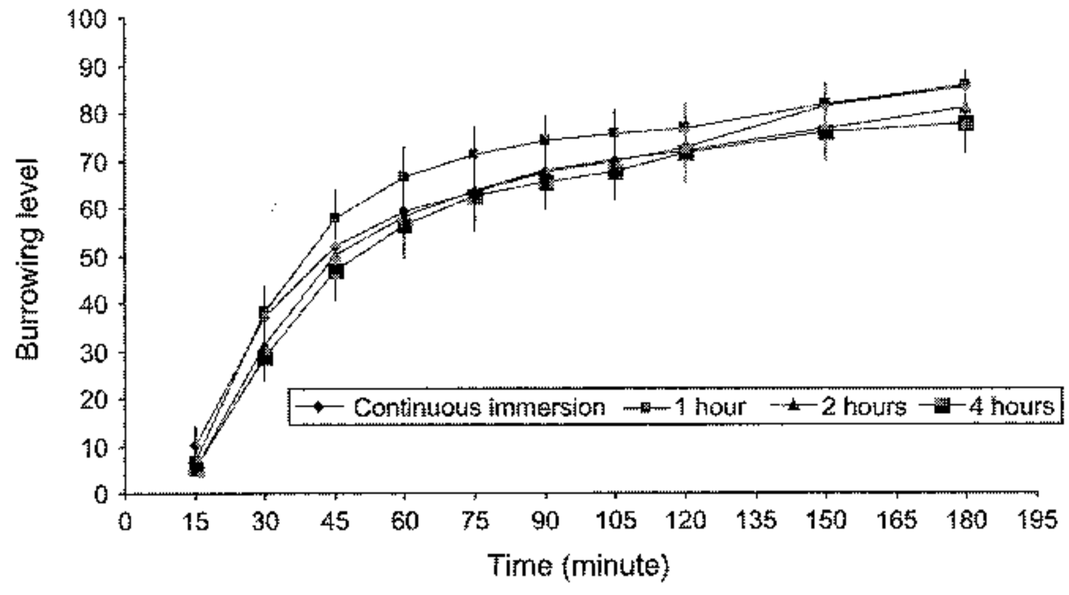

Figure 3. Burrowing level (mean proportion buried length of shell ± s.e.) of 25–30 mm softshell clams (*Mya arenaria*) relative to the duration of emersion prior seeding (continuous immersion, 1-h, 2-h, and 4-h emersion). The observations were made over 3-h periods under field conditions in Iles-de-la-Madeleine, $n = 9$ (June, 7 to 9 2002).

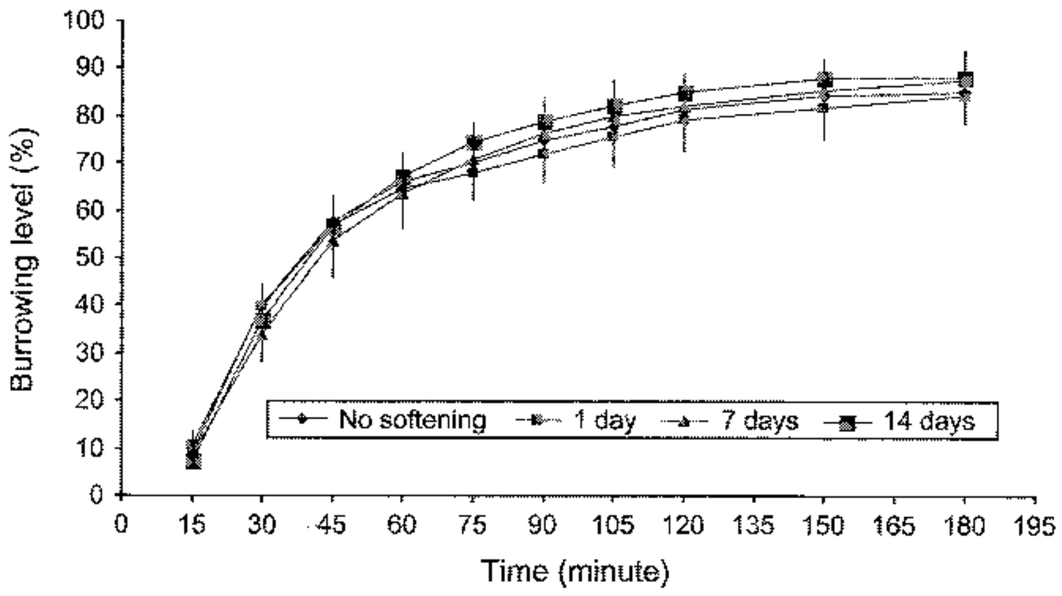

Figure 4. Burrowing level (mean proportion buried length of shell ± s.e.) of 25–30 mm softshell clams (*Mya arenaria*) relative to the period of time after softening with a small hydraulic rake (no softening, 1 day, 7 days, and 14 days after softening). The observations were made over 3-h periods under field conditions in Iles-de-la-Madeleine, $n = 9$ (August 26–28, 2002).

Seasonal Period

Burial rate varied with season ($F_{(7,64)} = 29.85$; $P < 0.0001$; Fig. 6). A subsequent series of ANOVAs with repeated measurements were then performed on paired dates to locate the differences. Burial rate was significantly faster on August 20–22, 2002 compared with all other periods (all $F_{(1,16)} > 9.71$ and $P < 0.0001$), except from May 28–30, 2002. Burial rate was also significantly slower on October 21 to 23, 2002 compared with all other periods (all $F_{(1,16)} > 50.29$ and $P < 0.0001$). Four hours after seeding, the mean burial level varied between 15% and 84% according to the date.

Seasonal Variation of Environmental and Biological Parameters Versus Burial

As expected, environmental and biological parameters varied greatly between May and October 2002 in the Havre-aux-Basques lagoon where the experimental clams were collected. None of these parameters alone could explain the observed fluctuations in the clam burial level reached 4 h after seeding (Fig. 7a). Salinity was relatively stable (27‰ to 31‰) throughout the investigated season except for lower values of 23‰ during two weeks: one in May before the onset of the observations and the other in mid June (Fig. 7b). Water temperature fluctuated in early summer but increased quickly from 11°C to 23°C by early July (Fig. 7c). Maximum temperatures of 20°C to 23°C were measured during two months (early July to early September) and then dropped steadily. Large variations in burial level reached 4 h after seeding were observed despite the relative stability of water temperature in July to August. Concentrations of total particulate matter (1.36–12.96 mg · L^{-1}) and of particulate organic matter (0.61–6.88 mg · L^{-1}) varied throughout season with the highest values (4.17 and 2.34 mg · L^{-1}, respectively) in fall when burial levels 4 h after seeding were low (Fig. 7d). General condition of the clams, expressed by their mean dry tissue mass, fluctuated during the season but showed a steady decline between mid June (0.186 g) and late July (0.115 g) before recovering in late July/early August (Fig. 7c). This 38% decrease in tissue mass between mid-June and late July suggests a decline in general condition and/or some reproductive activity of the 25–30 mm clams.

The combined effects of the environmental and biological parameters (temperature, salinity, particulate organic matter, and dry mass of the clam tissues) on the burial level 4 h after seeding were evaluated with a stepwise forward regression using only the values measured during the weeks corresponding to the observation periods of burial rate. Only two variables were significantly related to burial level 4 h after seeding and were thus kept in the model:

$$BL = -56.92 + 2.57\ T + 497.00\ DW$$

$$(F_{(2,69)} = 37.63;\ P < 0.0001;\ R^2 = 0.52)$$

where BL = burial level 4 h after seeding, T = temperature and DW = dry tissue mass of clams. Together, water temperature and dry tissue mass of clams explained 52% of the observed seasonal variability of the burial level reached 4 h after seeding. Not surprisingly, salinity had little influence given its relative stability throughout the season.

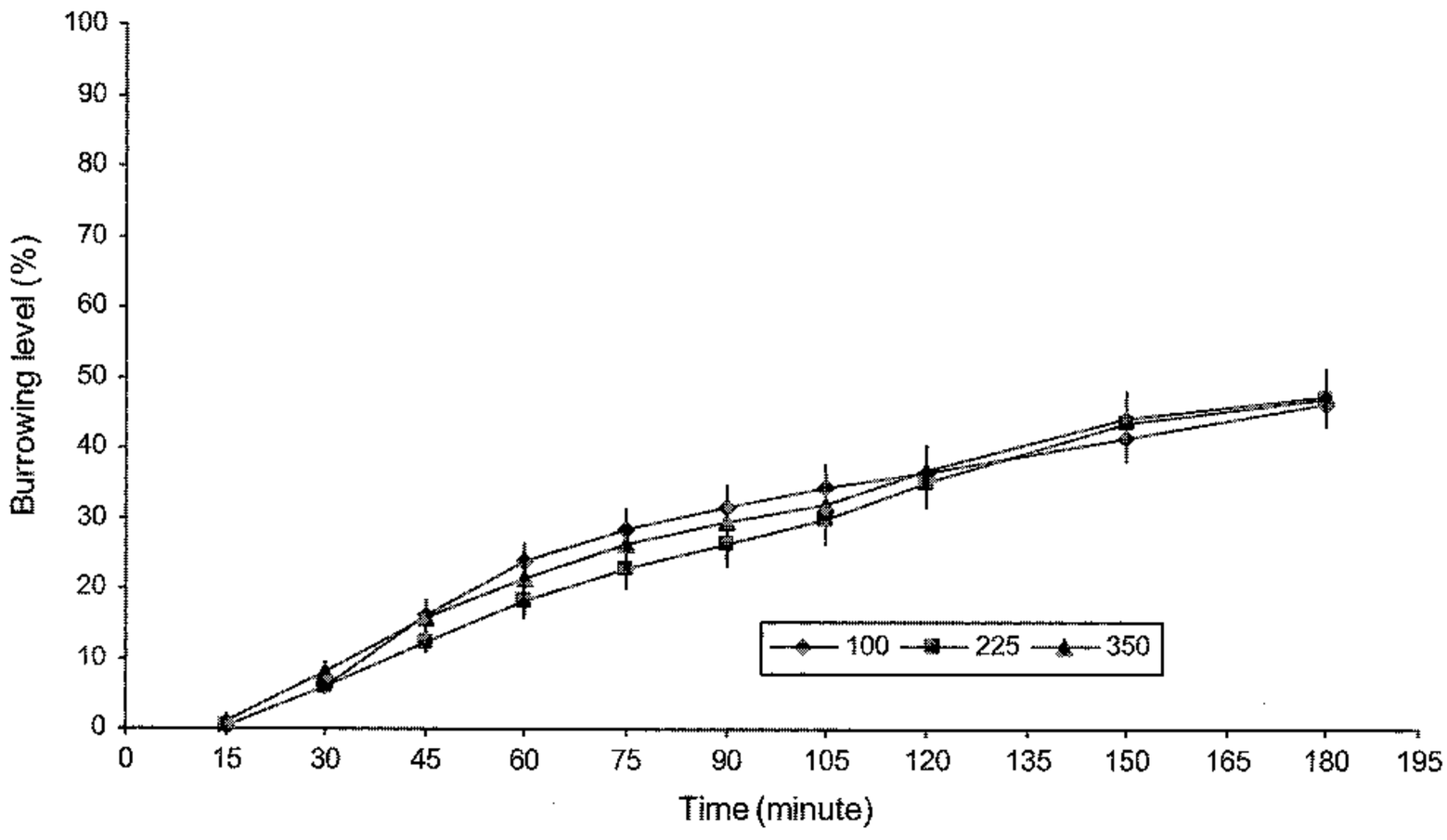

Figure 5. Burrowing level (mean proportion buried length of shell ± s.e.) of 25–30 mm softshell clams (*Mya arenaria*) relative to three densities (100, 225, and 350 clams · m^{-2}). The observations were made over 3-h periods under field conditions in Iles-de-la-Madeleine, $n = 6$ (September 9–10, 2002).

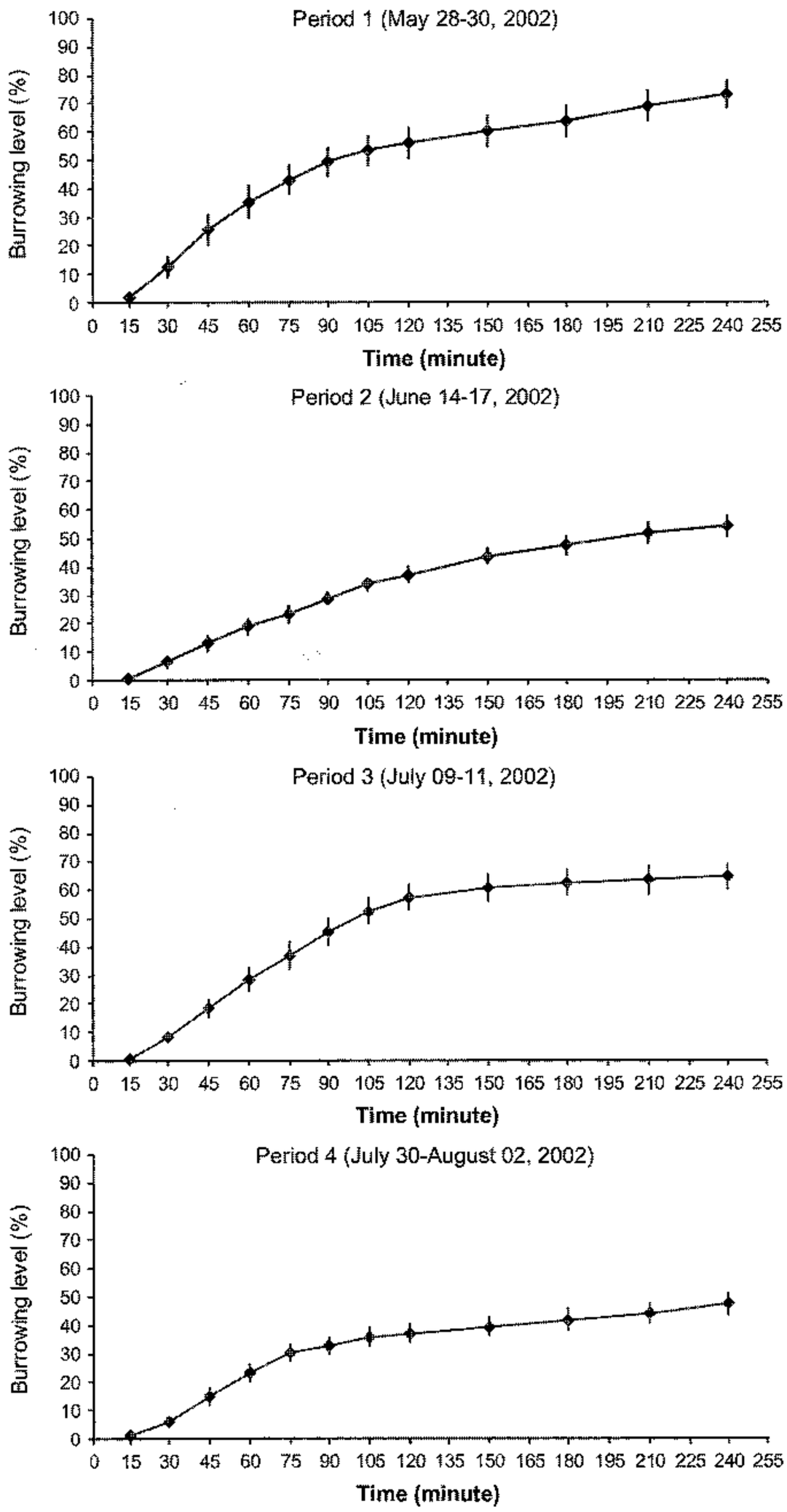

Figure 6. Burrowing level (mean proportion buried length of shell ± s.e.) of 25–30 mm softshell clams (*Mya arenaria*) between late May and late October 2002. The observations were made over 4-h periods in flow-through tanks in Iles-de-la-Madeleine, $n = 9$.

DISCUSSION

Of the biotic and abiotic factors examined, only clam size and seasonal period significantly influenced burial rate of softshell clams. However, it is important to follow clam burial repeatedly over a certain period of time to draw reliable conclusions. Burial rate followed an asymptotic curve overtime for all field trials except for the "density" study, which was made in the fall when water temperature was cooler. Baptist (1955) and Pfitzenmeyer and Drobeck (1967) also documented such asymptotic curves to describe how clams buried overtime. An initial period of fast burial is followed by a marked slowing down, which may allow the slower clams to catch-up, at least partly, with the faster ones as supported by results obtained during the "clam size" experiment.

Small clams are more prone to predation (Beal 1993, Zaklan & Ydenberg 1997, Beal & Vencile 2001) and dispersion by currents (Baptist 1955) than larger clams. However, they can escape most benthic predators and dispersion by burrowing rapidly after seeding. In the present study, burial rate was negatively correlated with clam size. Emerson et al. (1990) reported that 2–5 mm clams bury completely in <5 min whereas 60–80 mm individuals need 10–22 h. Other studies (Baptist 1955, Pfitzenmeyer & Drobeck 1967, Zaklan & Ydenberg 1997) also showed inverse relationships between size and burial rate. Beal and Vencile (2001) reported that hatchery-reared 12-mm

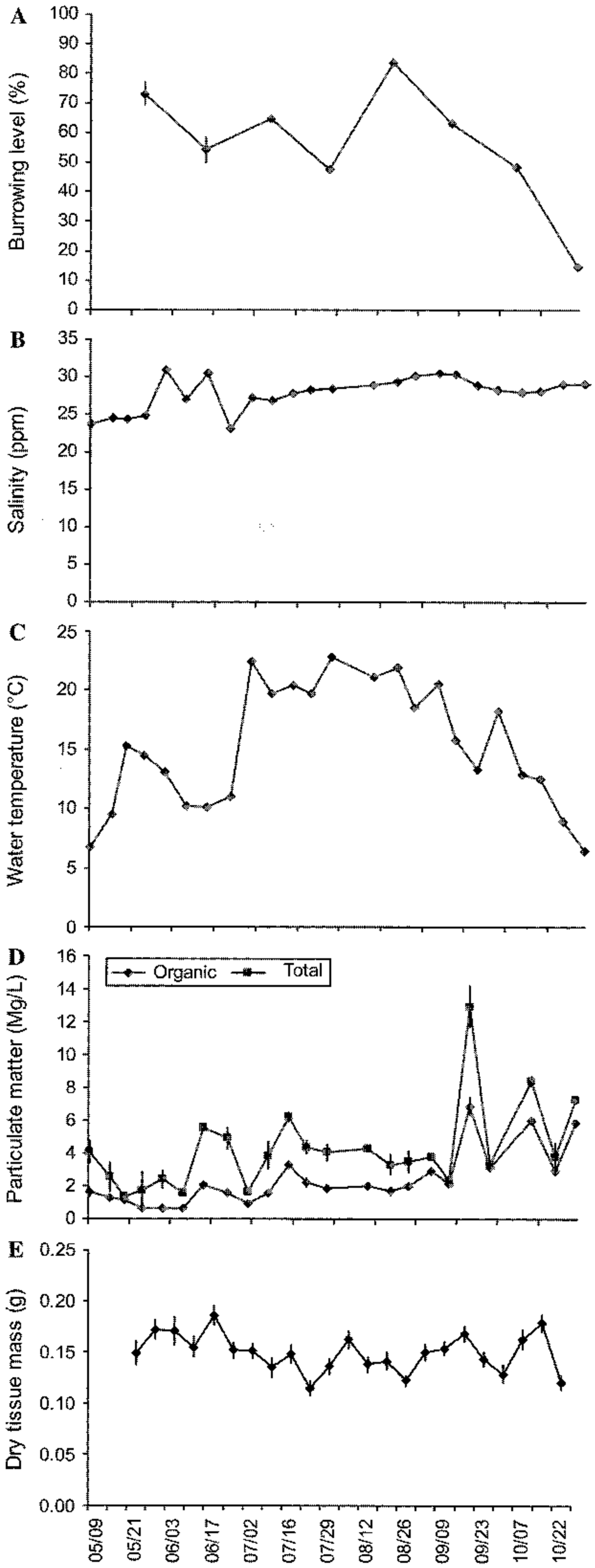

Figure 7. (A) Seasonal variation of the burrowing level (mean proportion buried length of shell ± s.e.) of 25–30 mm softshell clams (*Mya arenaria*) reached 4 h after seeding. Temporal variation of environmental and biological parameters (means ± s.e.) measured at the harvesting site of the experimental clams (Havre-aux-Basques lagoon): (B) salinity, (C) temperature, (D) total and organic particulate matter, and (E) dry tissue mass of 25–30 mm clams.

clams usually bury in <10 min in May, and that most individuals are no longer visible within 5 min after seeding.

The burial process was not slowed by increasing seeding densities of 25–30 mm SL individuals from 100–350 m^{-2}. Clam growth may be diminished at high densities reflecting strong intraspecific competition (Krauter & Castagna 1989, Jensen 1993, Beal et al. 1995, Rask 1999). As density increases the likelihood that clams will have physical contacts with their neighbors also increases. These contacts could produce physical obstacles or create stress, which would slow down or even prevent burial. Thus, a high density might be expected to lead to a slow burial rate. In the present study, no physical interactions were observed between the individuals, even at the highest density (350 clams · m^{-2}). This was probably because the surface of a 27.5 mm clam (median size of the experimental clams) laying down on the substratum is ~465 mm^2 (shell length × height; unpublished data), so that only 16% of the experimental area was covered by clams at this relatively high density for seeding. Thus, it would probably be necessary to seed at much higher densities to bring about enough physical contact to impact burial rate negatively.

Substratum softening before seeding using a small hydraulic rake did not accelerate clam burial. It was suggested that clams could sink more easily and thus more rapidly into soft sediments resulting from artificial substratum softening. In the present study, clams seeded on sediments that had been softened 1, 7, or 14 days earlier did not bury faster than those seeded on untreated surfaces. This is in agreement with Trueman et al. (1966) who reported that sandy sediment returns to its initial compaction within 24 h of disturbance. We also observed a fast recompaction of the disturbed sandy sediment during this study. The ineffectiveness of substratum softening on burial could simply be related to the sediment granulometry of the experimental surfaces, which are characterized by medium-sized sand with 0.25–0.50 mm particles (Chevarie & Myrand 2006). This soft substratum is also preferred by clams over coarser sediments (Pfitzenmeyer & Drobeck 1967, Lardies et al. 2001).

An emersion lasting up to 4 h under the morning sun of June had no negative effects on softshell clam burial rate. At a commercial scale, it is difficult to keep clams constantly immersed prior to seeding because tens of thousands of individuals must be handled at a time. There could be several hours between clam retrieval from the holding structures in which they had been stored and their subsequent seeding. This period can easily be stretched over a period of about 4 h. The local clam grower usually keeps the retrieved clams in perforated trays on a floating platform until they are seeded. Doing so, the clams to be seeded are kept out of the water and are directly exposed to the sun during a relatively long period. When air-exposed, clams are subjected to a certain level of desiccation and warming caused by the sun (Jacques 1983). Further, the clams shift from an acrobic to an anaerobic metabolism during emersion and thus reduce sharply their energy expenditure to meet just their vital needs (Shick & Widdows 1981, Newell 1991). At the time of reimmersion, the waste products accumulated during the anaerobic metabolism are expelled through a burst of pumping activity called overshooting (Newell 1991). It is possible that these changes caused by emersion may diminish clam capacity for a fast burial at the time of seeding (reimmersion). In the present study, emersion

periods varying between 1 and 4 h caused no slowdown in burial rate compared with clams kept under constant immersion. This finding is important in terms of logistical aspects for seeding at a commercial scale.

The burial rate varied by season with á maximum in mid August (August 20–22, 2002) and a dramatic slowdown thereafter. Like many other activities, burial capacity should vary throughout the year because several environmental factors (water temperature, salinity, food quantity, and quality, and similar) and clam biological factors (general condition, reproductive cycle, etc.) interact together to influence clam physiology (Matthiessen 1960, Zaklan & Ydenberg 1997, Lardies et al. 2001). Further, burial depth of bivalves varies with season (Zwarts & Wanink 1989, Goeij & Luttikhuizen 1998, Lardies et al. 2001, Goeij & Honkoop, 2003). Taken separately, none of the environmental and biological paramcters examined in the present study could explain the observed variability in burial rates.

Water temperature was a major factor influencing seasonal burial rates (burial level reached 4 h after seeding). Interestingly, the fastest rate was observed during the period of peak temperatures (~23°C). However, a variable burial rate was observed during this period including a relatively slow burial in late July to early August. Nevertheless, fast burial was observed at high temperatures (20°C to 23°C), which is in contrast with results from Chesapeake Bay clams whose burial rate was faster at 18°C and slowed down at temperatures >21°C (Newell 1991). Clearly, burial slowed down in the fall (September to October 2002) probably because of the rapid cooling of water temperatures. Newell (1991) reported that clams bury slowly at 8°C, a temperature we measured in early October 2002. Fall is an unsuitable period for seeding in Iles-de-la-Madeleine because burial rate is slowing down at a time when weather conditions are becoming more difficult (winds, storms, etc.). As a result, clams are burrowing slowly coincidentally with weather conditions leading to a possible increase in losses through dispersion by waves and currents.

The other major factor positively influencing seasonal burial rate was clam dry tissue mass. The relationship between these two factors is plausible as a reduction in the tissue dry mass can be related to a decline in general condition or to spawning (Lucas & Beninger 1985, Crosby & Gale 1990). The observed reduction in dry tissue mass between mid June and late July 2002 may suggest spawning despite the relatively small size of the clams (25–30 mm). Clams of this size can reproduce even if fecundity is limited (Brousseau 1978, Roseberry et al. 1991). Further, clams in Iles-de-la-Madeleine usually spawn during this period in the lagoons (unpublished data). Whether related to spawning or to a decrease in general condition, the decrease in dry tissue mass starting in mid June 2002 and leading to the low values observed in late July 2002 seems associated with slow burial measured on July 30 to August 2, 2002. These observations are derived from only one season (May to October 2002) and thus, cannot be extrapolated directly. However, the present results provide useful general indications for planning the seeding activities.

Not surprisingly salinity had no influence on burial rate as a result of its relative stability. In any case, softshell clams have a great tolerance to variations in salinity (Matthiessen 1960, Newell 1991). The quantity of food, estimated from the particulate organic matter concentration, only had a limited influence. It should be noted that the highest seston concentrations were obtained in autumn at a time when burial rate decreased.

This study made possible to better define the most favorable burial conditions at seeding. Thus, a general guideline could be proposed to clam growers, at least in Iles-de-la-Madeleine and nearby areas:

- Burial rate decreases as size increases
- Seeding densities up to 350 clams (25–30 mm) · m ^{2} have no negative impact on the burial rate
- It is not necessary to soften the substratum before seeding to increase the burial rate of clams, at least for medium-sand
- In early summer clams can sustain emersion periods up to 4 h without negative side effect on the burial rate
- Water temperature reaching 20°C to 23°C does not decrease burial rates
- A substantial decrease in clam condition, probably associated to spawning, seems to have a negative impact on burial rates
- Seeding in fall (starting in September with a temperature around 6°C to 10°C) is not recommended because of the important slow down of burial rate associated with weather conditions increasing the possibilities of dispersion by currents and waves

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