

# Spatial variability of length-specific production in shell, somatic tissue and sexual products of *Macoma balthica* in the Lower St. Lawrence Estuary. I. Small and meso scale variability\*

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**ABSTRACT:** A field study was conducted on clams *Macoma balthica* (L.) in 6 adjacent bays along the south shore of the Lower St. Lawrence Estuary. Data collected at 12 stations from the upper and lower levels of the tidal zone showed that the length-specific energy budgets of shell, somatic tissue and sexual products were very variable between stations during the 1986 growing season. In each bay, the standard length-specific (5, 10 and 15 mm) energy budget values were greater at the lower level stations than at the upper level stations except in one bay where the reverse was true. Tidal level effects on individual growth were far stronger than both density and sediment effects. Intra-population variations in shell, somatic tissue and gamete production due to the tidal level effect were more important than the inter-bay variations due to local density and/or sediment effects. The significant relationships between tidal level and length-specific energy budget of each body component allowed us to construct a 3-dimensional model showing the seasonal length-specific production in shell, flesh and sexual products at each tidal level of a tidal flat. From these models, it appears that in each bay, the seasonal (May to November) production in shell, somatic tissue and sexual products was mostly attributable to a small number of individuals living in the lower part of the tidal flat.

## INTRODUCTION

Tidal flats are transitional between terrestrial and marine ecosystems. The periodicity of tides induces very different immersion times for upper and lower parts of tidal flats. Thus, animal populations living in this environment are submitted to a wide range of environmental conditions within a small distance, to which they must be well adapted. The adaptability of an organism can be estimated by measuring the allocation of assimilated energy to growth and reproduction (Barbault & Blandin 1980), as growth rate and repro-

ductive output represent the integrated response of physiological activities within the organism (MacDonald & Thompson 1985).

The influence of environmental conditions on population energy balance and production is an important feature of several studies on marine bivalves (Bayne & Newell 1983). The approach often used has been to compare the energy flow between animals collected in different environmental conditions, including various tidal levels (Dame 1976, Griffiths 1981), various water depths (Kautsky 1982, Rodhouse et al. 1984, MacDonald & Thompson 1985) and latitudinally separated areas (Barber & Blake 1983, Beukema & Meehan 1985). Nevertheless, a complete 3-dimensional model showing the relationships between length-specific energy budget and a measured gradient of environmental conditions has never been attempted.

\* This publication is dedicated to the memory of my friend Dr. Estelle Laberge, lost at sea during a scientific cruise in December 1990 (M.H.)

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In clams *Macoma balthica* (L.), most studies have considered shell and/or soft tissue growth (Beukema et al. 1977, Beukema & Meehan 1985, Thompson & Nichols 1988, Bonsdorff & Wenne 1989) but reproductive output was rarely taken into account. In previous studies, Vincent et al. (1987) and Harvey & Vincent (1989, 1990) showed that the immersion time was a factor of primary importance for the growth and reproduction of *M. balthica* in the Lower St. Lawrence Estuary (LSLE), Canada. A field study conducted in 19 stations on a transect perpendicular to the coast showed that annual shell growth increased with immersion time (Vincent et al. 1987). Further, Harvey & Vincent (1989), in a 2 yr field study conducted at 2 tidal levels, showed that gamete production for the whole population was largely derived from individuals at the lower level. Harvey & Vincent (1990) showed that the zone of highest growth rate of both shell and soft tissue shifted from the upper tidal level during spring to the lower tidal level during summer. This resulted in individuals at the lower level being longer and heavier than those at the upper level by the end of the growing season. Until now, a complete annual length-specific energy budget including shell, somatic tissue and gamete production has not been evaluated. Furthermore, because studies were conducted on only one tidal-flat population, allowing only the study of intra-population variability, they do not permit us to generalize the results for other populations located on a small or large spatial scale in the LSLE.

The objective of this study was to compare the intra- and inter-population variability of energy allocation between shell, somatic tissue and sexual products, in the upper and lower part of adjacent bays along the south shore of the LSLE.

## MATERIALS AND METHODS

**Study sites and data collection.** This study was carried out in the intertidal zone of 6 adjacent bays located within a 15 km line along the south shore of the LSLE in a region where the maximal amplitude of tide is 4.8 m (Fig. 1). In each bay, 2 stations were located respectively in the upper and lower parts of the tidal flat. Tidal levels at each site were determined by the difference in height between the site and a reference point placed simultaneously in all bays at high tide. Zero value was attributed to the lowest site, which was located at 0.5 m above the lower-low water level, while others were adjusted with respect to the level of that site.

It was not possible to place the stations at the same tidal level in all bays because of the differing topography of each bay. All stations were located between 0.5 and 2.8 m above the lower-low water level. The periods of immersion at those levels were 90 and 42% respectively. The upper level stations were located between 1.5 and 2.8 m and the lower level stations between 0.5 and 1.2 m. The smallest and largest differences between upper and lower levels stations in any one bay were at l'Anse à Mercier (0.6 m) and l'Anse à l'Original (1.8 m) respectively.

As observed by Harvey & Vincent (1989, 1990), the reproductive and growth cycles of *Macoma balthica* do not coincide in the LSLE. Shell and somatic tissue growth occurred at the same time during spring and summer of the considered year (mid-May to the end of August). However, sexual products development occurred in part during summer and early fall (July to September) of one year and in part in early spring (March and April) of the following year, just before spawning which occurs in May and June. On the basis

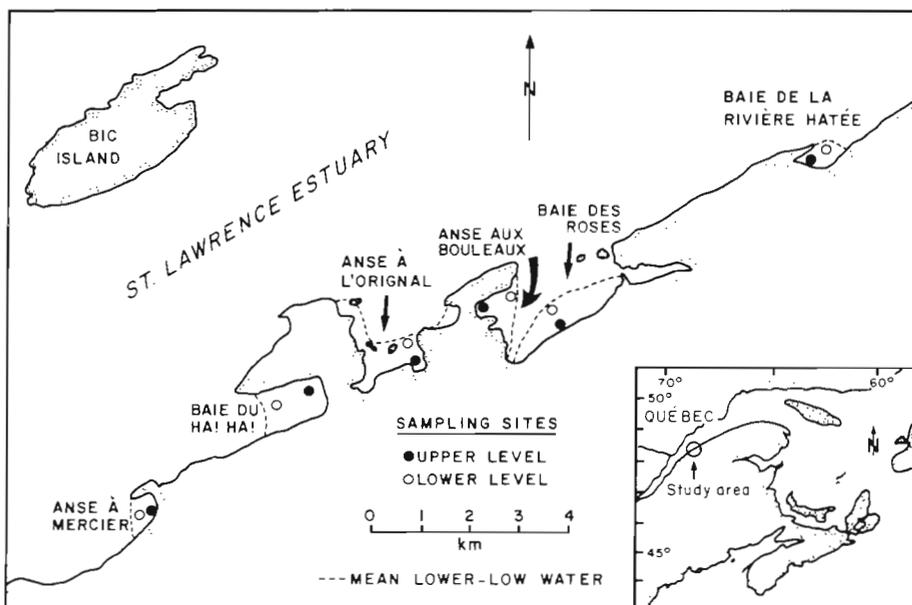


Fig. 1. Location of sampling sites along the south shore of the Lower St. Lawrence Estuary

of these results, and in order to compare the energy allocation between each body component produced simultaneously during a given period, samples were collected twice in 1986: at the beginning of May before shell and somatic growth and in November at the end of the growing season and at the end of the first period of gonadal maturation. At each station, 3 randomly selected 20 × 20 cm sediment samples were collected. Each sample was sieved through a 1 mm mesh. Specimens were removed manually, stored alive for 24 h in seawater at 5°C, counted and frozen.

In the laboratory, 20 individuals were randomly selected from each 20 × 20 cm sampling unit. In all sampling units, size-range of individuals were representative of the size-frequency distribution observed by Harvey & Vincent (1990) at Baie des Roses. The following values were determined for each individual: in May, total shell length (TSL) and somatic tissue dry weight (STDW); in November, TSL, last year mark length (YML), STDW and sexual products dry weight (SPDW). TSL in May 1986 and YML in November 1986 are equivalent values since both represent the length at the start of the 1986 shell growing season. TSL and YML were measured on the longest axis of the shell under a stereomicroscope (60×) equipped with a micrometer (accuracy: ± 0.1 mm). To estimate STDW in May, the soft parts were removed from the shells and placed under a stereomicroscope in a 32% ammonium formate solution. Sexual products present at this period were separated from the somatic tissue by microdissection. Somatic tissue was then placed onto preweighed 45 mm Whatman GF/C glass-fiber filters, dried for 24 h in an oven at 60°C and weighed on a Mettler balance (accuracy: ± 0.001 mg). We did not consider sexual products weight at this sampling date because an important part of them were built up during the preceding year. For the November samples, we used the same microdissection procedure to separate somatic tissue and sexual-products, but in this case both somatic tissue and sexual products were separately dried and weighed. On the basis of the observations made by Harvey & Vincent (1989) at both upper and lower level stations of Baie des Roses, we considered that gonads were completely empty during the preceding spawning period (May–June) at all stations. Since gonadal development occurs in 2 phases (summer and early-fall of one year and early-spring of the next spring), and somatic tissue may lose weight during winter (Harvey & Vincent 1990), both sexual products and somatic tissue weight obtained in November represent only a part of the total annual production for these. This data is nevertheless interesting because these somatic and gonadal components were built up during the same period of time during which annual production of shell takes place, permitting us to compare the energy allo-

cation between each body component within a given period. Hereafter we will use the term seasonal production to designate shell, somatic tissue and sexual products productions measured in this study (May to November), although shell seasonal production represents, in fact, annual production because shell material, of course, cannot be lost during winter.

Sediments were collected in November for the determination of organic matter content and grain size structure. Analyses of sediments for all samples were performed following a protocol based on the granulometric methods of Rivière (1977).

**Data analysis.** In May, mean STDW was compared among sampling units and stations using a 2-level nested ANCOVA on STDW with sampling units and stations as factors and TSL as covariate, after logarithmic transformation of variables. In November, mean TSL, STDW and SPDW were compared among sampling units and stations in the same way using YML as covariate. Thereafter, the 3 sampling units within each station were regrouped.

In the following equations, all variables with subscript 1 refer to the May samples and those with subscript 2 refer to the November samples. In May, using the 60 randomly selected individuals from each station, values for  $\log(\text{STDW}_1)$  and  $\log(\text{TSL}_1)$  were fitted to the allometric equation:

$$\log(\text{STDW}_1) = \log(a_1) + b_1 \log(\text{TSL}_1) \quad (1)$$

where  $\log(a_1)$  and  $b_1$  = respectively intercept and slope. In November, values for TSL, YML,  $\log(\text{STDW})$ ,  $\log(\text{SPDW})$  and  $\log(\text{YML})$  were also fitted to the allometric equations:

$$\log(\text{STDW}_2) = \log(a_2) + b_2 \log(\text{YML}_2) \quad (2)$$

$$\log(\text{SPDW}_2) = \log(c_2) + d_2 \log(\text{YML}_2) \quad (3)$$

$$\text{TSL}_2 = e_2 + f_2 \text{YML}_2 \quad (4)$$

where  $\log(a_2)$ ,  $\log(c_2)$  and  $e_2$  = intercepts; and  $b_2$ ,  $d_2$ , and  $f_2$  = slopes.

In order to compare the seasonal production in shell, somatic tissue and sexual products and the energy allocation pattern at different tidal levels and in different populations, we constructed 2-dimensional (2-D) models representing shell length increment (SLI), somatic tissue dry weight increment (STDWI) and sexual products dry weight increment (SPDWI) at each station between May and November as functions of the total shell length at the start of the growing season ( $\text{TSL}_1$  or  $\text{YML}_2$ ).

SLI represents the difference in shell length between the beginning (May) and the end (November) of the growing season and is estimated from shell measurements made on individuals sampled in November:

$$\begin{aligned} \text{SLI} &= \text{TSL}_2 - \text{YML}_2 = (e_2 + f_2 \text{YML}_2) - \text{YML}_2 \\ &= e_2 + (f_2 - 1) \text{YML}_2 \end{aligned} \quad (5)$$

STDWI represents the difference in somatic tissue weight between spring and fall for an individual having the same total shell length at the beginning of the growing season ( $\text{TSL}_1$ ). It is estimated directly from Eqs. (1) and (2):

$$\text{STDWI} = \text{STDW}_2 - \text{STDW}_1 = (a_2 \text{TSL}_1^{b_2}) - (a_1 \text{TSL}_1^{b_1}) \quad (6)$$

SPDWI represents a part of the 1986 sexual products production from July to November. Assuming that all sexually mature individuals had spawned in May–June (Harvey & Vincent 1989), sexual products increment would be equal to  $\text{SPDW}_2$  and can be estimated directly from Eq. (3):

$$\text{SPDWI} = \text{SPDW}_2 = c_2 \text{YML}_2^{d_2} \quad (7)$$

Eqs. (5), (6) and (7) were calculated for all YML from individuals sampled in November at each sampling site and the results were used in the models.

In order to compare the energy allocation between different size classes, SLI, STDWI and SPDWI were estimated for standard-length individuals with YML's of 5, 10 and 15 mm. A principal component analysis from the correlation matrix was used as a method of ordination for these estimates. In order to study the effect of environmental parameters on SLI, STDWI and SPDWI, we introduced tidal level, density, grain size structure and organic matter as independent variables in stepwise multiple regression models, with these estimates as dependent variables.

In order to compare energy allocation between stations, SLI, STDWI and SPDWI were first estimated for standard-length individuals of 10 mm, which correspond to the mean shell length over all stations. Thereafter, these estimates and tidal levels were fitted to allometric equations after log transformation of variables and SLI, STDWI and SPDWI residuals had been computed for each station. These residuals represent the deviation between the observed values (SLI, STDWI, SPDWI) and the values predicted by the regression model. Residuals were correlated among themselves in order to establish if SLI, STDWI and SPDWI varied in the same way at all stations.

Two-dimensional models representing somatic tissue, sexual products and shell production at each station were extended to 3-dimensional (3-D) models by introducing tidal level (TL) as a second independent variable in Eqs. (5), (6) and (7). First, for each station and each equation (5, 6, 7),  $\log_{(10)}$  of intercept and slope were separately introduced as dependent variables in 2 distinct linear regressions with  $\log_{(10)}$  of TL as an independent variable. Thereafter, we substituted intercept and slope of Eqs. (5), (6) and (7) by (i) their estimate in

function of TL if the regression was significant, or (ii) the mean of their values at each station if the regression was not significant.

## RESULTS

At l'Anse à l'Original, Baie des Roses and l'Anse aux Bouleaux, upper and lower stations presented the same variations in grain size structure, with more sand at the lower level stations and more silt at the upper level stations (Table 1). At Baie de la Rivière Hatée and Anse à Mercier, both upper and lower level stations had similar grain size structure with little silt. At Baie du Ha! Ha!, percentage of sand was greater at the upper level station than at the lower level station which was characterized by a high percentage of gravel (Table 1).

In all bays, the number of *Macoma balthica* was at all dates greater at the upper level stations than at the lower level stations, except at Baie du Ha! Ha! and Anse aux Bouleaux where the situation was reversed (Fig. 2). In the fall, after the time of new recruit settlement, population density increased at only 2 stations: Baie des Roses upper level and Baie du Ha! Ha! lower level.

### Energy allocation modelling

There were significant relationships between STDW and TSL in May and between STDW, SPDW and TSL versus YML in November at all stations (Tables 2 and

Table 1. Sediment parameters at each station

Sampling site	Gravel (%)	Sand (%)	Silt (%)	Organic matter
Original				
Upper	7.0	77.7	13.7	1.6
Lower	0.0	97.6	1.1	1.3
Roses				
Upper	9.6	59.8	28.6	2.0
Lower	0.2	97.0	1.4	1.4
Bouleaux				
Upper	3.5	19.2	72.0	5.3
Lower	0.0	96.7	2.1	1.2
Hatée				
Upper	12.4	83.7	2.6	1.3
Lower	1.4	93.7	3.5	1.4
Ha! Ha!				
Upper	0.5	77.5	21.0	1.0
Lower	27.0	58.6	11.8	2.6
Mercier				
Upper	12.3	81.3	4.5	1.9
Lower	12.5	80.1	5.4	2.0

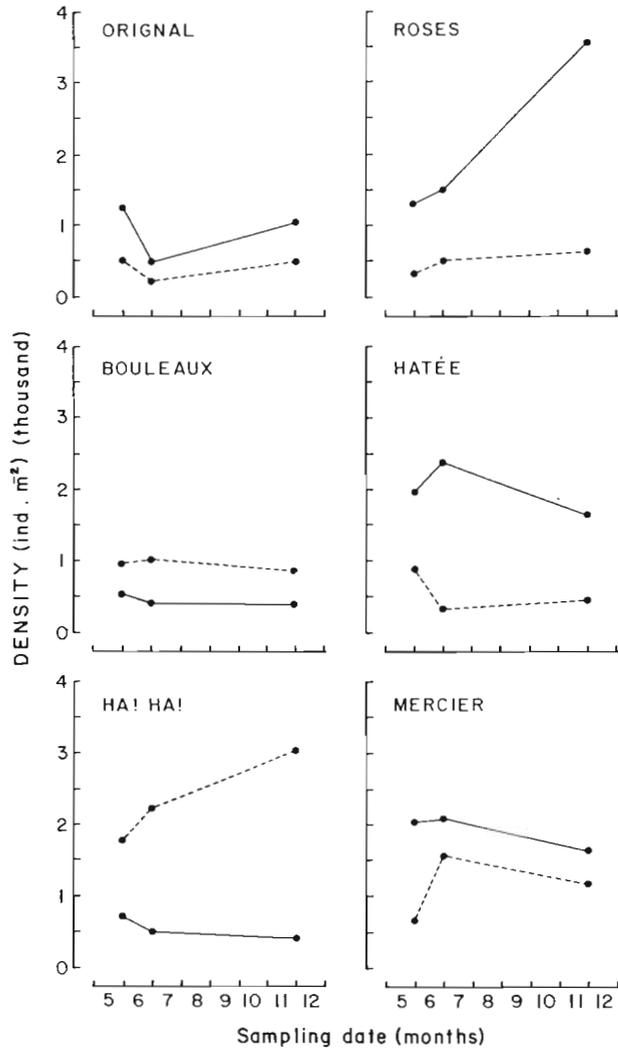


Fig. 2. *Macoma balthica*. Temporal variations of density (ind.  $m^{-2} \pm SE$ ) at each sampling site. Standard error (SE) bars are smaller than the diameter of a point. (—) Upper level, (----) lower level

3). Furthermore, there were significant effects of stations and samples within stations on STDW in May and on STDW, SPDW and TSL in November (Table 4). The higher p values obtained for the within-station effect compared to the inter-station effect showed the latter to be dominant. It should be noted that the inter-station effect included shore level and site effects. Results of ANCOVA's carried out separately at each station showed that such small-scale heterogeneity, due to the within-station effect, was not observable at all stations and for all body components ( $0 \leq F \leq 1566.19$ ,  $0.997 \leq p < 0.001$ ). Therefore, data from samples at each station were pooled in order to describe the seasonal length-specific energy budget at each station, recognizing that this procedure would increase the variance in growth estimates for a given station. The intercept and slope given by these regressions (Tables 2 and 3)

Table 2. *Macoma balthica*. Intercept (a) and slope (b) of linear regressions between somatic tissue dry weight (STDW) versus total shell length (TSL) in May or year mark length (YML) in November for each station. All variables were transformed to  $\log_{(10)}$  prior to analysis. All regressions were significant at  $p < 0.001$

Date (1986)	Bay	Level	a	b	r
May	Mercier	Upper	-1.94	2.79	0.97
		Lower	-2.01	2.80	0.97
	Ha! Ha!	Upper	-1.80	2.55	0.97
		Lower	-1.86	2.54	0.96
	Original	Upper	-1.69	2.36	0.93
		Lower	-2.02	2.70	0.98
	Roses	Upper	-1.81	2.58	0.98
		Lower	-1.88	2.63	0.99
	Bouleaux	Upper	-1.74	2.50	0.90
		Lower	-1.99	2.82	0.99
	Hatée	Upper	-1.81	2.55	0.98
		Lower	-2.01	2.78	0.99
November	Mercier	Upper	-0.76	1.62	0.96
		Lower	-1.19	2.04	0.97
	Ha! Ha!	Upper	-0.91	1.86	0.98
		Lower	-1.12	1.88	0.91
	Original	Upper	-0.81	1.56	0.89
		Lower	-0.82	1.68	0.95
	Roses	Upper	-1.01	1.63	0.95
		Lower	-1.23	2.06	0.96
	Bouleaux	Upper	-0.77	1.54	0.99
		Lower	-0.92	1.87	0.96
	Hatée	Upper	-1.05	1.81	0.97
		Lower	-1.07	2.09	0.93

were fitted into Eqs. (5), (6) and (7) on individuals sampled in November to obtain, for each station, 2-D models showing SLI, STDWI and SPDWI against the length at the start of the growing season (initial length) (Fig. 3).

By thus viewing simultaneously the seasonal production of shell, somatic tissue and sexual products for each size class at all stations, it is possible to compare energy allocation at different shell lengths. There were negative linear relationships between SLI and initial length at all stations except at Baie de la Rivière Hatée (lower level), where the relationship was positive (Fig. 3); at some stations, larger individuals did not show any SLI. In general, the slopes of the relationships were greater at the lower level for all stations, except at Baie du Ha! Ha! where the reverse was observed. Although the slope varied within upper and lower levels in all bays, variations were greater between stations from the lower level than between stations from the upper level (Fig. 3). SPDWI increased exponentially with initial length at all stations and, as previously discussed for SLI, values for a given initial length were greater at lower level stations than at upper level stations except

Table 3. *Macoma balthica*. Intercept (*a*) and slope (*b*) of linear regressions between year mark length (YML) (independent variable) versus sexual products dry weight (SPDW) and total shell length (TSL) (dependent variables) for each station. YML and SPDW were transformed to  $\log_{(10)}$  prior to analysis

Variable	Bay	Level	<i>a</i>	<i>b</i>	<i>r</i>	<i>p</i>	
SPDW	Mercier	Upper	-1.49	1.35	0.49	0.001	
		Lower	-1.95	1.95	0.73	<0.001	
	Ha! Ha!	Upper	-2.23	2.45	0.92	<0.001	
		Lower	-2.65	2.40	0.58	<0.001	
	Orignal	Upper	-1.68	1.41	0.42	0.009	
		Lower	-2.92	2.96	0.78	0.002	
	Roses	Upper	-2.20	1.69	0.79	0.001	
		Lower	-3.22	3.22	0.83	<0.001	
	Bouleaux	Upper	-1.70	1.46	0.49	0.001	
		Lower	-2.64	2.80	0.88	<0.001	
	Hatée	Upper	-2.35	1.85	0.58	<0.001	
		Lower	-3.12	3.41	0.88	<0.001	
	TSL	Mercier	Upper	3.12	0.78	0.99	<0.001
			Lower	2.33	0.88	0.98	<0.001
Ha! Ha!		Upper	2.24	0.92	0.99	<0.001	
		Lower	2.53	0.79	0.97	<0.001	
Orignal		Upper	2.34	0.81	0.97	<0.001	
		Lower	2.27	0.86	0.98	<0.001	
Roses		Upper	2.06	0.80	0.98	<0.001	
		Lower	2.31	0.87	0.97	<0.001	
Bouleaux		Upper	2.87	0.78	0.99	<0.001	
		Lower	2.31	0.90	0.98	<0.001	
Hatée		Upper	2.07	0.86	0.99	<0.001	
		Lower	1.42	1.04	0.97	<0.001	

Table 4. *Macoma balthica*. Summary of 2-level nested ANCOVA of somatic tissue dry weight (STDW), sexual products dry weight (SPDW) and total shell length (TSL), with samples and stations as factors and year mark length (YML) as covariate (SS: sum of squares; df: degrees of freedom; MS: mean square)

Date	Variable	Source of variation	SS	df	MS	<i>F</i>	<i>p</i>
May	STDW	Stations	1.29	11	0.12	8.6	<0.001
		Samples w/in station	0.33	24	0.01	1.7	0.027
		Samples (error)	5.06	616	0.01		
November	STDW	Stations	3.94	11	0.36	13.1	<0.001
		Samples w/in station	0.63	24	0.03	1.8	0.011
		Samples (error)	8.62	592	0.01		
	SPDW	Stations	15.00	11	1.36	9.5	<0.001
		Samples w/in station	3.58	24	0.15	2.1	0.002
		Samples (error)	28.50	399	0.07		
	TSL	Stations	54.27	11	8.20	8.2	<0.001
		Samples w/in station	14.35	24	0.60	2.3	<0.001
		Samples (error)	154.63	592	0.26		

at Baie du Ha! Ha! (Fig. 3). Relationships between STDW and initial length indicate that STDW increased in the smaller size classes and decreased in the larger size classes at all stations except at Baie de la Rivière Hatée lower level. Some negative values were recorded for larger individuals at some stations, indicating a somatic tissue weight loss during the 1986 growing season. Except at Baie du Ha! Ha!, values for a

given initial length were also greater at lower level stations than at upper level stations in all bays (Fig. 3).

Results obtained at Baie du Ha! Ha! are interesting and will be discussed in more detail below. Nevertheless, because they represent a complete inversion compared to results obtained in the other bays, which considerably complicates the interpretation of the results, both upper and lower level stations from Baie

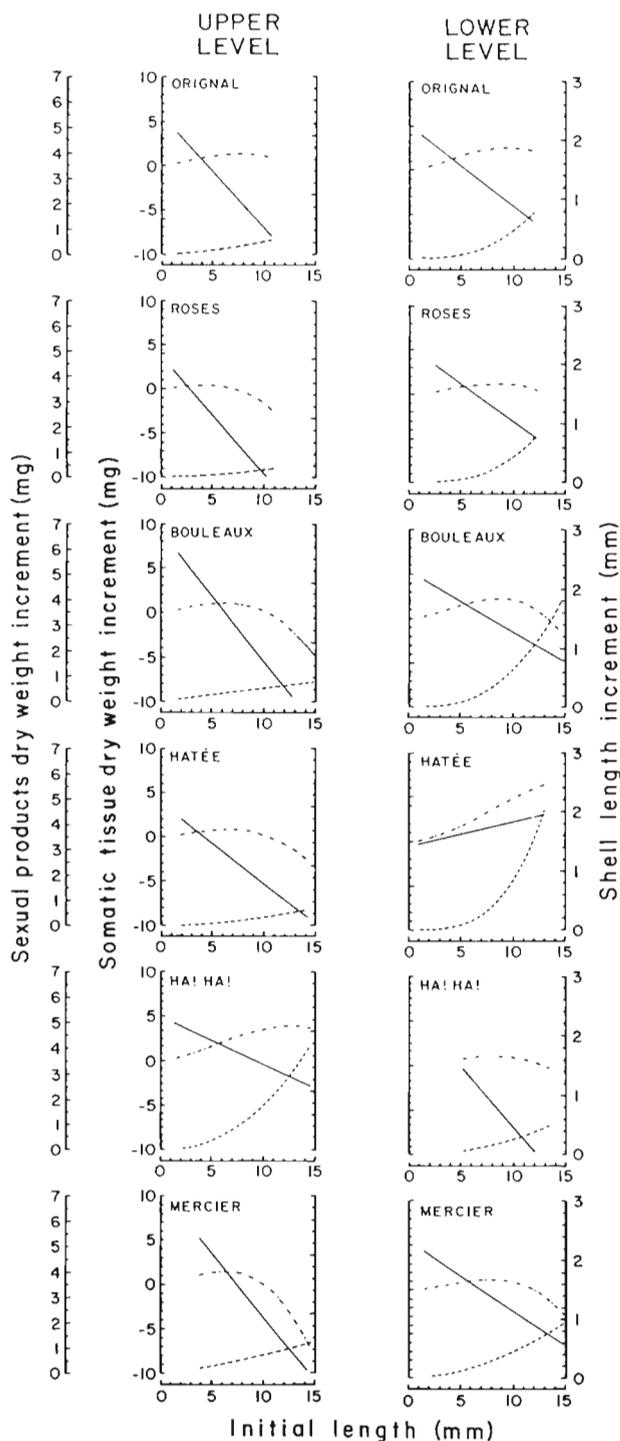


Fig. 3. *Macoma balthica*. Seasonal production of sexual products (— · — · — ·), somatic tissue (— · — · — ·) and shell (—) against length at the start of the growing season (initial length) for the 1986 growing season at each sampling site

du Ha! Ha! were excluded from all further analyses.

Principal component analysis on SLI, STDWI and SPDWI, as calculated for standard length individuals of 5, 10 and 15 mm, showed that all variables, except

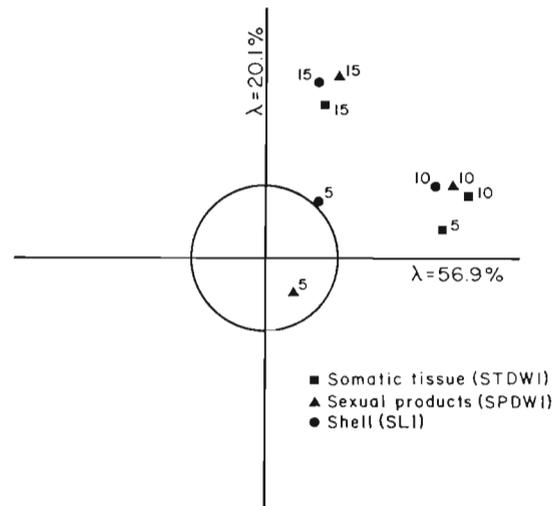


Fig. 4. *Macoma balthica*. Vectors extremities of the principal component analysis on the standard length estimated values of shell length increment (SLI), somatic tissue dry weight increment (STDWI) and sexual products dry weight increment (SPDWI) and equilibrium circle of descriptors. Numbers refer to standard lengths (5, 10, 15 mm). Baie du Ha! Ha!, upper and lower level stations, were not considered

SPDWI(5), were located in the same quadrant (Fig. 4). Although 2 groups, representing individuals of 10 and 15 mm, were apparent, relationships between SLI and STDWI were significant in individuals of 5 and 10 mm ( $0.56 \leq r \leq 0.81$ ,  $p < 0.05$ ) and in individuals of 10 and 15 mm ( $0.55 \leq r \leq 0.90$ ,  $p < 0.05$ ) but not significant in individuals of 5 and 15 mm ( $0.05 \leq r \leq 0.52$ ,  $p > 0.005$ ). SPDWI was also correlated with other variables for individuals of 10 and 15 mm ( $0.60 \leq r \leq 0.91$ ,  $p < 0.05$ ) but not for individuals of 5 mm ( $-0.05 \leq r \leq 0.27$ ,  $p > 0.05$ ).

The number of environmental parameters having a significant effect on SLI, STDWI and SPDWI increased with the initial length of the individual. No environmental parameter had a significant effect on the smaller size class individuals whereas 1, 2 or 3 parameters could be having a significant effect in the larger size class individuals (Table 5). Environmental parameters explained between 50 and 96 % of the SLI, STDWI and SPDWI variance between stations in the larger size classes. In both 10 and 15 mm size class individuals, tidal level was the first parameter introduced in the SLI and SPDWI stepwise multiple regression models, but density effect was predominant on STDWI in both size classes. Sediment effect was observed only in the largest size class (Table 5).

There were significant relationships between tidal level and SLI, STDWI and SPDWI as estimated for individuals of 10 mm (log-transformed data) (Fig. 5). Furthermore, there were significant relationships between the residual values of STDWI and SLI ( $r = 0.69$ ;  $p = 0.029$ ) but no significant relationships in the

Table 5. *Macoma balthica*. Significant results of stepwise multiple regressions used to explain the inter-population variability of size-adjusted (5, 10, 15 mm) shell length increment (SLI), somatic tissue dry weight increment (STDWI) and sexual products dry weight increment (SPDWI) in relation to environmental parameters. Baie du Ha! Ha!, upper and lower level stations, were not considered. df: degrees of freedom

Dependent variable	Independent variable	r	R <sup>2</sup>	df	F	p
SLI(5)	No variable					
STDWI(5)	No variable					
SPDWI(5)	No variable					
SLI(10)	Tidal level	0.86	0.74	8	22.87	0.001
STDWI(10)	Density	0.71	0.50	8	8.19	0.021
SPDWI(10)	Tidal level	0.81	0.66	8	15.12	0.005
SLI(15)	Tidal level	0.91	0.83	8	33.85	0.001
STDWI(15)	Density	0.78	0.61	8	10.57	0.014
	Organic matter	0.83	0.69	8	15.06	0.005
SPDWI(15)	Tidal level	0.80	0.64	8	12.17	0.010
	Gravel	0.95	0.90	8	27.43	0.001
	Sand	0.98	0.96	8	48.64	<0.001

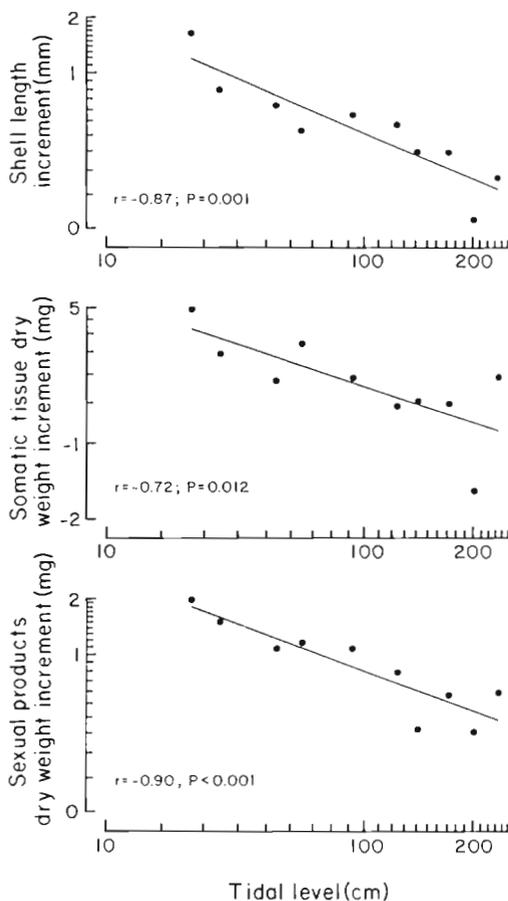


Fig. 5. *Macoma balthica*. Relationships between tidal level and standard length (10 mm) estimated values of sexual products dry weight increment, somatic tissue dry weight increment and shell length increment. Baie du Ha! Ha!, upper and lower level stations, were not considered

Table 6. *Macoma balthica*. Intercepts (*a*) and slopes (*b*) of linear regressions between tidal level and intercepts (variables =  $a_1, a_2, c_2, e_2$ ) from Eqs. (5) to (7) and between tidal level and slopes (variables =  $b_1, b_2, d_2, f_2$ ) from Eqs. (5) to (7). All variables were transformed to  $\log_{10}$  prior to analysis

Equation	Variable	<i>a</i>	<i>b</i>	r	p
(6)	$a_1$	-2.44	0.29	0.82	0.001
	$b_1$	0.53	-0.07	-0.89	0.003
(6)	$a_2$	-1.28	0.16	0.36	0.303
	$b_2$	0.45	-0.11	-0.76	0.011
(7)	$c_2$	-4.30	1.05	0.62	0.054
	$d_2$	1.00	-0.37	-0.77	0.009
(5)	$e_2$	0.14	0.12	0.47	0.173
	$f_2$	0.09	-0.08	-0.83	0.003

regressions using residual values of SPDWI (STDWI vs SPDWI:  $r = 0.60$ ,  $p = 0.068$ ; SLI vs SPDWI:  $r = 0.46$ ,  $p = 0.179$ ). If we exclude residual values obtained at Baie de la rivière Hatée (upper level) because sexual production was lower than expected on the basis of tidal level, relationships between residual SPDWI and the other residuals become highly significant (STDWI vs SPDWI:  $r = 0.89$ ,  $p = 0.001$ ; SLI vs SPDWI:  $r = 0.78$ ,  $p = 0.013$ ). Thus, except at Baie de la Rivière Hatée (upper level), where sexual products production was lower, SLI, STDWI and SPDWI varied in the same way at all stations. Therefore, we can assume that there were no differences in energy allocation between stations.

There were significant relationships between log-transformed tidal level and log-transformed slope values of STDWI, SPDWI and SLI, as obtained from Eqs. (5), (6) and (7) (Table 6). Log-transformed intercept values obtained from these equations and log-transformed tidal level values were also correlated in the second part of Eq. (6) and in Eq. (7) but not correlated in

the first part of Eq. (6) and in Eq. (5) (Table 6). Thus, in order to construct a 3-D model representing SLI, STDWI and SPDWI against initial length and tidal level, we substituted slopes used in Eqs. (5), (6) and (7) by their estimate in function of TL in all equations. Intercepts were substituted as follows: by their estimate in function of TL in the second part of Eq. (6) and in Eq. (7) and by the mean values in the first part of Eq. (6) and in Eq. (5).

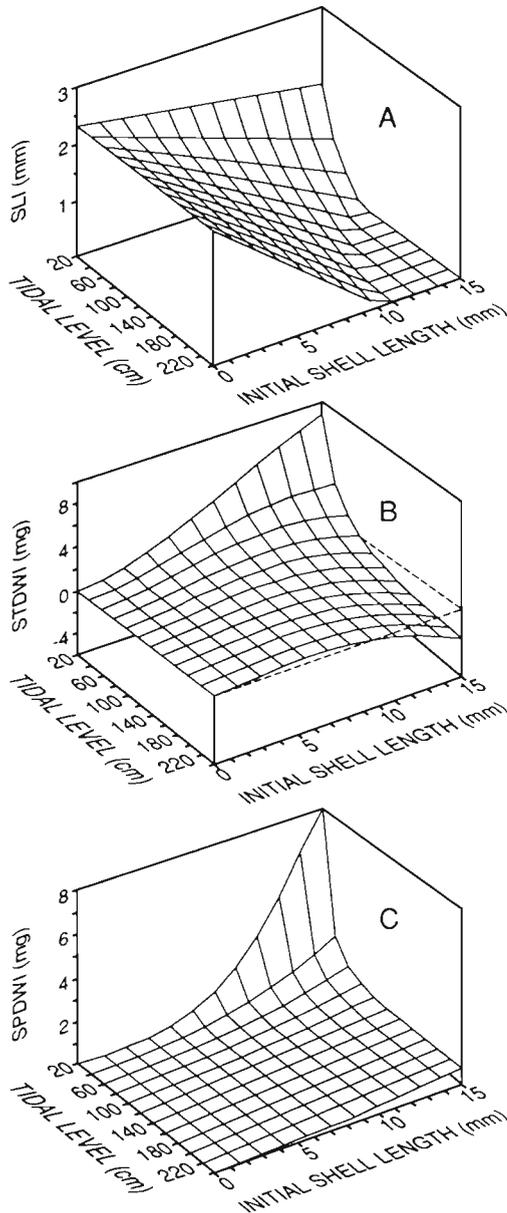


Fig. 6. *Macoma balthica*. Three-dimensional models showing relationships between initial shell length, tidal level and seasonal production in (A) shell, (B) somatic tissue and (C) sexual products in the study area. Baie du Ha! Ha!, upper and lower level stations, were not considered (SLI = shell length increment; STDWI = somatic tissue dry weight increment; SPDWI = sexual products dry weight increment)

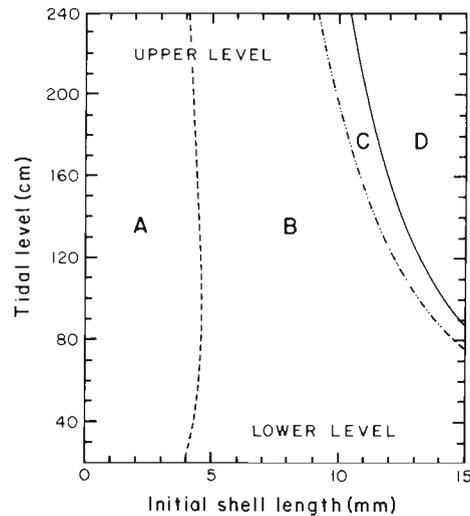


Fig. 7. *Macoma balthica*. Relationships between tidal levels and size at sexual maturity (---- SPDWI = 0), size of no somatic tissue dry weight increment (--- STDWI = 0) and size of no shell length increment (— SLI = 0) (A = no reproduction, shell and somatic tissue growth; B = reproduction, somatic tissue and shell growth; C = reproduction, shell growth no somatic tissue growth; D = reproduction, no shell and somatic tissue growth)

Relationships between initial length and SLI, STDWI or SPDWI in the 3-D models (Fig. 6) are of the same type as the ones described in the 2-D models (Fig. 3). As suggested previously by these latter models, larger individuals living in the upper half of the tidal flat showed low sexual production, no shell length increment and a somatic tissue weight loss during the 1986 growing season (Fig. 6). Furthermore, consistent with the observation that SLI, STDWI and SPDWI values for a given initial length were greater at lower level stations than at upper level stations in all bays, relationships between tidal level and SLI, STDWI or SPDWI became obvious in the 3-D models (Fig. 6). These relationships were exponential, indicating a logarithmic scale for the increase in the tidal level effect with shell length (Fig. 6).

3-D models can be easily compared in substituting zero values for SLI, STDWI and SPDWI in equations giving these models, in order to obtain the relationships between tidal level and size at no shell length increment (SLI = 0), size at no somatic tissue weight increment (STDWI = 0) and size at sexual maturity (SPDWI = 0) (Fig. 7). The no somatic tissue weight increment and no shell length increment curves are very close to each other. There was no tidal level effect on size at sexual maturity, but a significant effect, increasing with tidal level, on size of no somatic tissue weight increment and size of no shell length increment. In the lower part of the tidal flat (between 0 and 80 cm), all individuals greater than 5 mm showed shell, somatic tissue and gonadal production, whereas in the middle and upper

parts of the tidal flat, larger individuals showed low reproduction, no shell length increment and somatic tissue weight loss (Fig. 7).

## DISCUSSION

Analysis of clam growth within stations showed no homogeneity in growth rate of any body component among samples (Table 4). This heterogeneity in growing conditions within stations suggests that in a small area, at a given tidal elevation, some biotic factors such as intra- or inter-specific competition for space and/or food or abiotic factors such as grain size structure or local current flow can influence growing conditions. Nevertheless, the higher *p* values obtained for within-station effects compared to inter-station effects (Table 4) showed the latter to be dominant.

The seasonal length-specific energy budget of *Macoma balthica* at all stations shows that the relative importance of various body components changes as the clam grows older (Fig. 3). Shell growth decreased from the smaller to the larger individuals, except at one station where the reverse was true. Somatic growth increased in relation to shell length up to a certain length, before declining in larger individuals. Gamete production continued to increase in relation to shell length throughout the life of the individual. This type of energy budget appears to be the norm in marine bivalve species and has been observed on other species by many researchers (Bayne & Worrall 1980, Vahl 1981, Thompson 1984, MacDonald & Thompson 1986). Lammens (1967) and Beukema et al. (1977) also observed a decreasing shell length increment in relation to the size of the individual in *M. balthica*, which they termed 'catching-up phenomenon'.

Inter-station variation in absolute value of shell, somatic tissue and gamete production was high (Fig. 3). In 5 of the 6 bays sampled, length-specific seasonal production in shell, somatic tissue and sexual products was greater in the lower part of the tidal flat than in the upper part. This result, already observed by Vincent et al. (1987), Vincent et al. (1989) and Harvey & Vincent (1990), can therefore be considered as representative of this region of the LSLE. Nevertheless, higher length-specific seasonal production of all body components observed in the upper part of the tidal flat at Baie du Ha! Ha! showed that the direction of this gradient can be completely reversed. Thus, on a mesoscale, the inter-population variability, which can be high, showed that it is hard to propose a regional model of variation from results concerning only one population; even for a tidal flat where the effect of tidal level and of its related factors (temperature and food) are generally considered as dominant (Green 1973, Beukema et al. 1977,

Bachelet 1980, Vincent et al. 1987, Harvey & Vincent 1990). Although a simple explanation for this observation may not exist, the particular topography of this bay with a long tidal flat (2 km) and a very gentle slope suggests that its hydrodynamics is different from those of other bays. This assumption is supported by the grain size structure observed in this bay (higher gravel percentage at the lower level station). Furthermore, the higher density observed at the lower level station compared to the upper one may also explain in part this inversion, but more extensive studies would be necessary for a better understanding.

The positive relationship between individual size classes and the number of environmental parameters having a significant effect on SLI, STDWI and SPDWI is interesting (Table 5). In younger individuals, short-term exposure did not reveal any effect of the environment on growth rate of any body component. In older individuals, long-term exposure demonstrated the cumulative effects of many environmental parameters on all body components. This has already been observed for shell growth of *Macoma balthica* (Vincent et al. 1987) and *Mya arenaria* (Roseberry et al. 1991).

Many studies have been conducted to compare shell and soft tissue growth in different populations of *Macoma balthica* (Beukema et al. 1977, Beukema & Desprez 1986, Thompson & Nichols 1988, Bonsdorff & Wenne 1989) and other marine bivalves (Bayne et al. 1983, MacDonald & Thompson 1985, Bricelj et al. 1987). In general, faster shell growth and more pronounced somatic growth have been recorded for populations growing under more favourable conditions of food and temperature. In our study, food and temperature may also explain the observed difference in growth between stations, although within the limits set by the tidal level effect. The spatio-temporal variations in food and temperature induced by immersion time on a tidal flat and their effect on shell and soft tissue growth of *M. balthica* have been discussed in detail by Harvey & Vincent (1989, 1990). Our present results again show that the effect of tidal level on shell and gamete production was far stronger than both density and sediment effects. Peterson & Black (1987) observed the same predominant effect of immersion time, as opposed to density, on individual growth of *Anomalocardia squamosus*, *Circe lenticularis* and *Callista impar* in Western Australia.

Density effect on somatic tissue production was stronger than both tidal level and sediment effects (Table 5). In experimental and descriptive field studies on *Macoma balthica* at Anse à L'Original, Vincent et al. (1989) showed a strong density effect on shell growth increasing with tidal level. Olafsson (1986) showed that the growth of *M. balthica* was density dependent in muddy sand sediments, but no such effect could be

demonstrated for clams in sandy sediments. It is difficult to explain why somatic tissue production was mostly density dependent whereas shell and gamete productions were mostly tidal level dependent. Nevertheless, the highly significant relationships between length-specific STDWI (10 mm) and tidal level (Fig. 5) indicate that somatic tissue growth was also dependent on tidal level.

The significant relationships between STDWI, SLI and SPDWI residual values obtained from the regressions between tidal level and SLI, STDWI or SPDWI (Fig. 5) imply that there were no differences in energy allocation between stations when tidal level effect was excluded. Except for some local density and sediment effects, shell, somatic tissue and gamete productions did not vary significantly between stations. On a meso scale (15 km), these results are not surprising, as all individuals are under the same climatic, salinity and food regime. In this area, intra-population variations in shell, somatic tissue and gamete productions due to tidal level effect, as observed in Harvey & Vincent (1989, 1990) and in the present study, are more important than the inter-bay variations due to local density and/or sediment.

The empirical 3-D models illustrate well the relationship between shell, somatic tissue and gamete productions versus shell length at the start of the growing season and tidal levels (Fig. 6). Within the limits of the models, values of shell, somatic tissue and gamete production are very similar to those obtained in the 2-D models (Fig. 3) which were constructed from field data. Shell, somatic tissue and sexual products growth curves obtained at both the highest and lowest stations in the 2-D models, respectively Orignal upper and Hatée lower, are comparable to the curves obtained in the 3-D models at both upper and lower tidal level limits. Therefore, these latter models appear as valuable tools for interpreting results at the population scale.

The exponential relationships between growth curves and tidal level imply a logarithmic scale, suggesting a multiplicative effect of tidal level on shell, somatic tissue and gonadal growth. This exponential effect was first observed in the 2-D SLI model where variations between slopes were greater between stations from the lower level than between stations from the upper level.

Several studies have already shown a tidal level effect on the growth rates of *Macoma balthica* (Green 1973, Beukema et al. 1977, Bachelet 1980, Vincent et al. 1987) and other bivalve species (Griffiths 1981, Peterson & Black 1987). In the present study, the tidal level effect is in an offshore-onshore direction, except at Baie du Ha! Ha!, but it may be reversed in other climatic regions (Green 1973, Bachelet 1980). Harvey &

Vincent (1989) observed that most of the gonadal production is contributed by individuals living at the lower level of the tidal flat. The present study extends this observation to seasonal shell and somatic tissue production. Thus, in each bay, the seasonal production of shell, somatic tissue and sexual products of the population was mostly attributable to a small number of individuals living at the lower tidal level.

As suggested by MacDonald & Thompson (1986), a distinction must be made between conditions which favour the individual and those which favour the population. Immersion time is the single most important factor determining individual production. In terms of populations however, topography, density and energy budget of individuals at each level will influence total production in a given bay. Thus, because of the variability in tidal elevation of the upper level stations in each bay, the upper level stations of one bay may be equivalent to the middle level station in another bay. Individuals at the upper level of the former bay could then contribute to production in shell, somatic tissue and sexual products as much as those at the middle level of the latter bay. Also, the greater density observed at the upper level stations, except at Baie du Ha! Ha! and Rivière Hatée, means that a greater number of individuals contribute to the total production of a given bay. However, the negative somatic tissue energy budget and the absence of shell length increment and weak reproductive output observed in larger individuals from the upper part of each bay (Fig. 6) contribute to decrease total production. Consequently, one cannot predict the total production of a bay without considering all these factors. For example, at Baie des Roses, where the upper station was 117 cm above the lower station, the biomass of sexual products was respectively 3.5 and 6 times greater at the lower level than at the upper level in 1985 and 1986 (Harvey & Vincent 1989).

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