ECOTROPICA 16: 125–139, 2010

QUANTITATIVE EVALUATION OF GAMETOGENESIS IN THE MANGROVE MUSSEL *MYTELLA GUYANENSIS*

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Abstract. The mangrove mussel *Mytella guyanensis* is a species of both ecological and economic importance. Little information is available concerning its reproductive cycle in Brazil. Given the fact that it is exploited as a food source, and is also an important indicator of ecosystem health, such information may be useful for culture and management. Gametogenesis in *M. guyanensis* was investigated using histological methods between January 2004 and January 2005 at a site in the Caeté mangrove estuary, Bragança, northern Brazil. All animals sampled were mature and varied between pre-spawning, spawning, and recovery stages. Variation in reproductive activity was similar in both visceral mass and mantle tissue. Male and female cycles were highly synchronous and gametogenesis in both sexes was continuous throughout the year. A number of small peaks in activity were observed, particularly during the dry season when larger oocyte diameter, higher spermatozoa production, and an increase in spawning activity were recorded. The pattern of reproductive activity is consistent with other studies of tropical bivalves, and the ability of *Mytella* to use a variety of seasonally abundant food sources may explain the relatively constant gametogenetic activity observed.

Resumo. O mexilhão do mangue *Mytella guyanensis* é uma espécie com importância tanto ecológica quanto econômica. Pouca informação é disponível sobre seu ciclo reprodutivo no Brasil. Dado o fato que é explorado como fonte de alimento e é um indicador importante da saúde do ecossistema, tais informações podem ser importantes para seu cultivo e manejo. Gametogênese em *M. guyanensis* foi investigado usando métodos histológicos, entre janeiro de 2004 e janeiro de 2005 em um sítio no manguezal do estuário do Caeté, Bragança, Norte do Brasil. Todos os animais amostrados foram maduros e variaram entre os estágios pré-desova, desova e recuperação. Variação em atividade reprodutiva foi semelhante tanto na massa visceral quanto no tecido do manto. Os ciclos do macho e fêmea foram altamente síncronos e atividade gametogenética em ambos os sexos foi contínua ao longo do ano. Um número de pequenos picos em atividade foram observados, especialmente durante a estação seca quando maior diâmetro do oócito, maior produção de espermatozóides e um aumento na proporção de indivíduos desovando foram registrados. O padrão de atividade é consistente com outros estudos de bivalves tropicais e a habilidade de *Mytella* aproveitar diversos fontes de alimento, sazonalmente abundantes, poderia explicar o nível relativamente constante de atividade gametogenética observada.

Key words: *Amazonia*, *Brazil*, *Mytilidae reproduction*, *seasonality*, *tropical estuary*.

INTRODUCTION

The mangrove mussel *Mytella guyanensis* (Lamarck, 1819) is widely distributed along the coast of Brazil (Klappenbach 1965, Rios 1994), where it is of both economic and ecological importance (Nishida & Leonel 1995, Mora & Alpízar 1998, Pereira *et al*. 2003, Nishida *et al*. 2006, Pereira *et al*. 2007). *M. guyanensis* has been used as an environmental indicator of both heavy metal (Lacerda *et al*. 1983, Silva *et al*. 2006) and organic pollution (Torres *et al*. 2002) in mangrove habitat.

Mytella guyanensis is found buried in a vertical position with the posterior region projecting slightly above the sediment surface (Klappenbach 1965, Bacon 1975, Cruz & Vilalobos 1993a), anchored by a dense nest of byssus threads (Bacon 1975, Cazabon 1996). They especially tend to occur in the firm muddy sediment, often associated with green and brown algae (Sibaja 1986), around the aerial roots of the black mangrove *Avicennia germinans* L. (Bacon

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1975), but may also be found in coarser substrates (Sibaja 1986). Mean densities vary between 1 and over 200 mussels m^{-2} (Bacon 1975, Nishida & Leonel 1995, Pereira *et al*. 2003, Beasley *et al*. 2005, Pereira *et al*. 2007).

Mytella guyanensis is generally dioecious with a sex ratio of 1:1 (Cruz & Villalobos 1993a, Carpes-Paternoster 2003). Young mussels begin to mature and spawn when between 18 and 22 mm in length (Cruz & Villalobos 1993a). Year-round gametogenesis occurs in *M. guyanensis*, but distinct peaks in activity have been recorded at certain times of the year in Brazil (Carpes-Paternoster 2003) and in Costa Rica (Sibaja 1986, Cruz & Villalobos 1993a). Similar variation in larval settlement has been observed by Sibaja (1988).

As with other marine bivalves, mussels have a great capacity to transform phytoplanktonic primary production into biomass (Dame 1996) and are considered an excellent food source (Marques 1998, Furlan *et al*. 2007). Natural beds of *Mytella guyanensis* are harvested by hand, both in northeastern (Nishida *et al*. 2006) and southeastern (Pereira *et al*. 2003, Pereira *et al*. 2007) Brazil, where the market size is around 40 mm (Pereira *et al*. 2003). *M. guyanensis* accounts for 60% of the net production of non-cultivated bivalves along the Brazilian coast (Ostini & Poli 1990) and is thus an important natural resource. Although not cultivated in Brazil, *M. guyanensis* has been successfully grown on floating rafts in Costa Rica (Mora & Alpízar 1998) using locally collected seed.

As the management (Narchi 1976, Fernandes & Castro 1982) and culture (Marques 1987, Sibaja 1988, Rajagopal *et al*. 1998) of mussels depend on knowledge of the breeding season and larval settlement period, information on the timing of reproduction is important. Furthermore, there is a lack of seasonal data on reproduction of this species in Brazil, with only one other study available, dealing with the southern end of its range in Brazil (Carpes-Paternoster 2003). The present study aims to quantify seasonal variation in the reproductive activity of *Mytella guyanensis* from the Caeté mangrove estuary, Pará state, at the northern end of its range in Brazil.

METHODS

The Caeté mangrove estuary is located along the northeastern coast of the State of Pará, northern Brazil, and details of the geomorphology, social structure, economy, and ecology of the region have been reviewed elsewhere (Wolff *et al*. 2000, Lara 2003, Saint-Paul 2006). The study area and sampling in the field is described in Gomes *et al*. (2009). Salinity, expressed in the Practical Salinity Scale, was measured at the mussel bed on each sampling occasion using an optical refractometer. Length (mm) of all individuals was measured along the anterior-posterior axis of the shell. Reproductive tissue from the visceral mass and mantle was removed and processed using standard histological techniques as described in Gomes *et al*. (2009).

A quantitative analysis of gametogenesis was carried out based on Haggerty *et al*. (1995), which involves determining the mean number of gametes per follicle (see Rodríguez-Jaramillo *et al*. 2008 for a computer-based analysis). For females, the mean number of oocytes in the visceral mass was determined from counts using a total magnification of 100X, in 30 randomly selected follicles. Using a microscope reticule, the mean diameter (µm) along the longest axis was determined from a sample of 30 individual oocytes per section. In the case of female mantle tissue, 10 follicles were examined per section. Ten randomly chosen acini were examined in each male section using a total magnification of 400X. Counts of cells were made along a transect along the longest axis of the follicle, from which the mean number of mature (spermatozoa) and immature cells per acini were determined. In male mantle tissue, five acini were examined per section. Percentage coverage of reproductive tissue (gonad area) was visually determined in sections of visceral mass and mantle tissue of male and female mussels.

Five consecutive developmental stages were identified by Nascimento (1968a) for the closely related *Mytella falcata* (*M. charruana* (d´Orbigny, 1842)): I (Immature), II (Maturing), III (Pre-spawning), IV (Total or partial spawning) and V (Recovery). A monthly Gonad Index (GI) was calculated for *M. guyanensis*, using the stages described above, by multiplying the number of individuals in each stage by the numerical value of the stage (III-V, there were no individuals at stages I and II) and dividing the sum of this product by the total number of individuals in the monthly sample.

A t-test with Welch correction for unequal variances (Zar 1999) was used to check for a difference in mean length between male and female mussels. The effect of tissue type and month of the year on mean values of immature cells and spermatozoa in males, oocyte numbers and diameter in females, and gonad area from the visceral mass and mantle tissue

TABLE 1. Summary of ANOVA of numbers of immature cells and spermatozoa per acinus and gonad area (%) in visceral mass and mantle tissue of male *Mytella guyanensis* at the Furo do Meio tidal channel bed, between January 2004 and January 2005.

Source of variation	d.f.	Immature cells		Spermatozoa		Gonad area	
		Mean Square	F	Mean Square	F	Mean Square	F
Tissue (T)	1	49.68	2.19 n.s.	81.47	0.34 n.s.	0.0446	2.97 n.s.
Month (M)	12	62.25	2.74 **	852.34	3.55 ***	0.0211	1.40 n.s.
Interaction (TXM)	12	11.40	0.50 n.s.	107.96	0.45 n.s.	0.0127	0.84 n.s.
Residuals	114	22.70		240.33		0.0150	

Tukey HSD ($p < 0.05$ unless otherwise stated). Immature cells: January 2004 > February, April. Spermatozoa: October > April, May; December > February ($p = 0.053$), April, May; January 2005 > April ($p = 0.06$), May.

of both sexes was evaluated using two-way analysis of variance (ANOVA). Diagnostic plots of residuals were used to verify the assumptions of normality and homogeneity of variances, which were met in all analyses. Where a group difference occurred, Tukey's Honestly Significant Difference (HSD) test was used to determine the significance of pairwise monthly differences. Pearson's correlation coefficient (r) was used to correlate gametogenesis (numbers of immature male cells, spermatozoa and oocyte numbers, oocyte diameter, and gonad area in both sexes) in the visceral mass with gametogenesis in the mantle tissue. Correlation analysis was also used to determine the relationship between salinity and gametogenesis. All data were analyzed and graphed using the R statistical software (Ihaka & Gentleman 1996, R-project 2010).

RESULTS

Mussel length varied between 23.4 mm and 67.7 mm. There was no significant difference in mean (± s.d.) length between male (48.2 ± 7.4 mm) and female (47.5 ± 10.5 mm) mussels ($t = 0.425$, d.f. = 136.9, n.s.).

Quantitative evaluation of gametogenesis. There was no significant variation in the mean number of immature male cells and spermatozoa per acinus and gonad area (%) between visceral mass and mantle tissue (Table 1, Fig. 1a, b, c) and for all three variables, no significant interaction was detected between tissue type and month of the year (Table 1). However, there was a highly significant difference in numbers of immature cells between months (Table 1, Fig. 1a) where values in January 2004 were greater than

TABLE 2. Summary of ANOVA of numbers of oocytes per follicle and oocyte diameter (µm) and gonad area (%) in visceral mass and mantle tissue of female *Mytella guyanensis* at the Furo do Meio tidal channel bed, between January 2004 and January 2005.

Source of variation	d.f.	Oocytes		Oocyte diameter		Gonad area	
		Mean Square	F	Mean Square	F	Mean Square	F
Tissue (T)	1	25.89	1.62 n.s.	36.81	0.77 n.s.	0.1426	12.19 ***
Month (M)	12	43.19	2.70 **	190.09	3.99 ***	0.0374	3.20 ***
Interaction (TXM)	12	9.99	0.62 n.s.	14.27	0.30 n.s.	0.0278	2.38 ***
Residuals	116	15.95		47.64		0.0117	

Tukey HSD ($p < 0.05$ unless otherwise stated). Oocyte numbers: March > July ($p = 0.072$); November > January 2004 ($p = 0.075$), February and July. Oocyte diameter: January 2004 > February, April, July ($p < 0.001$), August ($p < 0.001$) and October; March > July ($p = 0.055$) and August; June > July ($p = 0.079$) and August ($p = 0.05$). Gonad area: September > January 2004 ($p < 0.01$), February ($p < 0.001$), April ($p < 0.01$) and July.

FIG. 1a

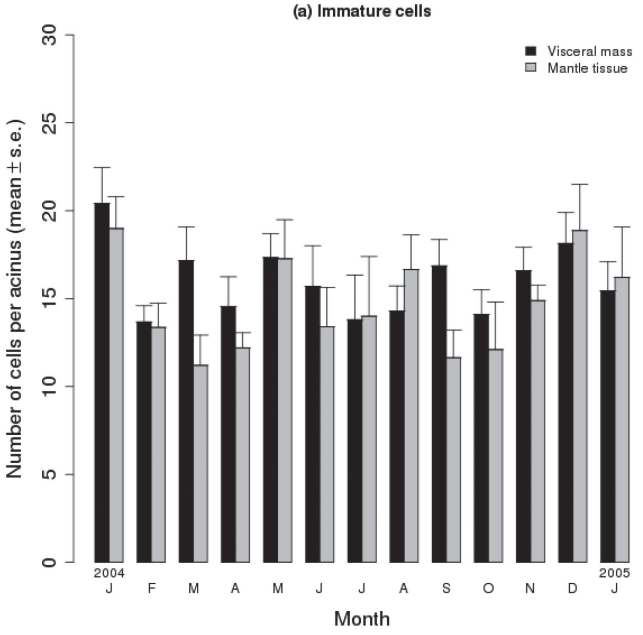
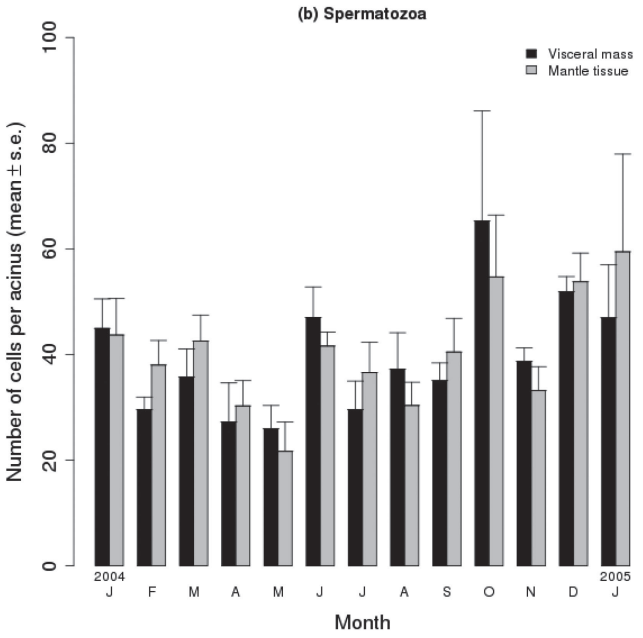

(a) Immature cells
Visceral mass
Mantle tissue
Number of cells per acinus (mean ± s.e.)
0
5
10
15
20
25
30
2004
J
F
M
A
M
J
J
A
S
O
N
D
2005
J
Month

FIG 1b


(b) Spermatozoa
Visceral mass
Mantle tissue
Number of cells per acinus (mean ± s.e.)
0
20
40
60
80
100
2004
J
F
M
A
M
J
J
A
S
O
N
D
2005
J
Month

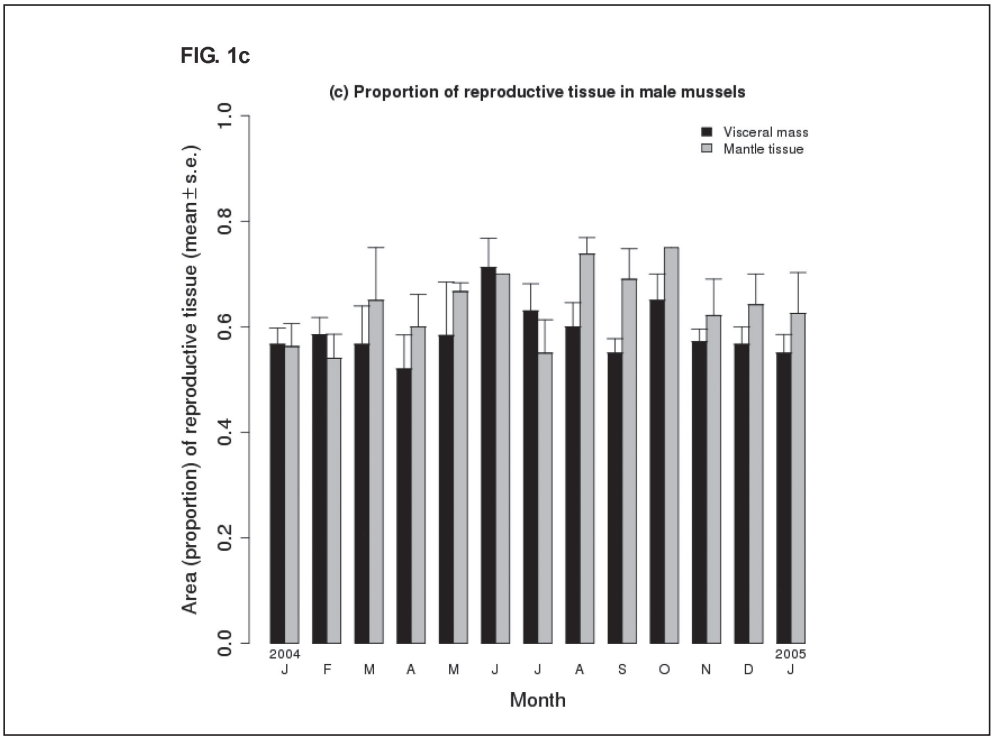


FIG. 1. Mean numbers of (a) immature cells and (b) spermatozoa per acinus, and (c) gonad area (%) in visceral mass and mantle tissue of *Mytella guyanensis* from the study area at the Furo do Meio tidal channel bed, between January 2004 and January 2005.

those in February and April (Table 1). Means ranged from 13.7 to 20.4 in the visceral mass and from 11.2 to 18.9 in mantle tissue. The mean number of spermatozoa per acinus was higher in October, December, and January 2005 in the dry season, in comparison with February, April, and May in the wet season (Fig. 1b, Table 1). Means ranged from 25.9 to 65.3 in the visceral mass and from 21.7 to 59.4 in mantle tissue. No differences in gonad area of male mussels were found between months of the year (Fig. 1c, Table 1).

No differences in mean numbers of oocytes per follicle and oocyte diameter were found between visceral mass and mantle tissue (Table 2, Fig. 2ab). There was, however, significant monthly variation in oocyte numbers and diameter (Table 2), though interaction between tissue type and month of the year was not significant. Oocyte numbers were highest in March and November and were greater than those in January 2004, February, and July (Table 2, Fig. 2a), with means ranging from 8.8 to 17.8 in the visceral mass and from 8.7 to 17.6 in mantle tissue. Individual observations of oocyte diameter ranged from a minimum of 12 to a maximum of 62 µm. Mean values ranged from 27.8 to 41.4 µm in the visceral mass and from 26 to 41.7 µm in mantle tissue. Oocyte diameter was greatest in January 2004, least in July and August, and relatively low in February, April, and October (Table 2, Fig. 2b). Values thus tended to oscillate between minima and maxima every 2-3 months (Fig. 2b). Gonad area in female mussels varied significantly between tissue types and among months of the year (Table 2). However, significant interaction between tissue type and month can be seen as greater mean values in the visceral mass during the wet season and relatively similar mean values in both tissue types in the dry season (Fig. 2c). Among months of the year, the mean in September was greater than those in January 2004, February, April, and July (Fig. 2c).

FIG. 2a

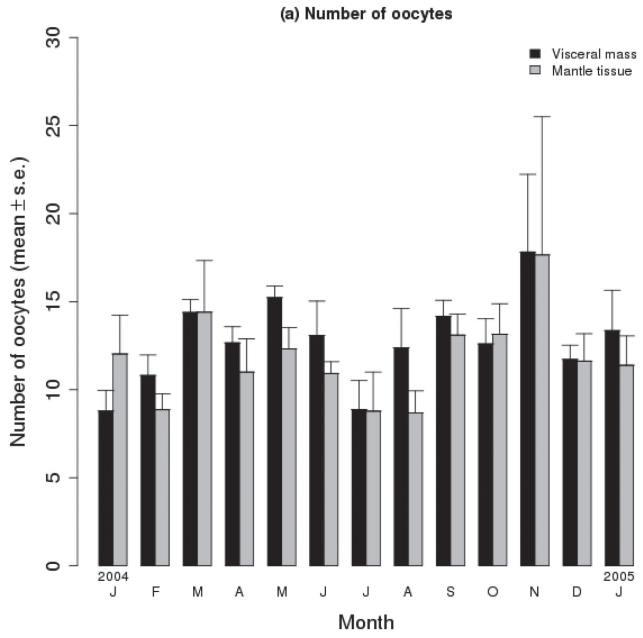
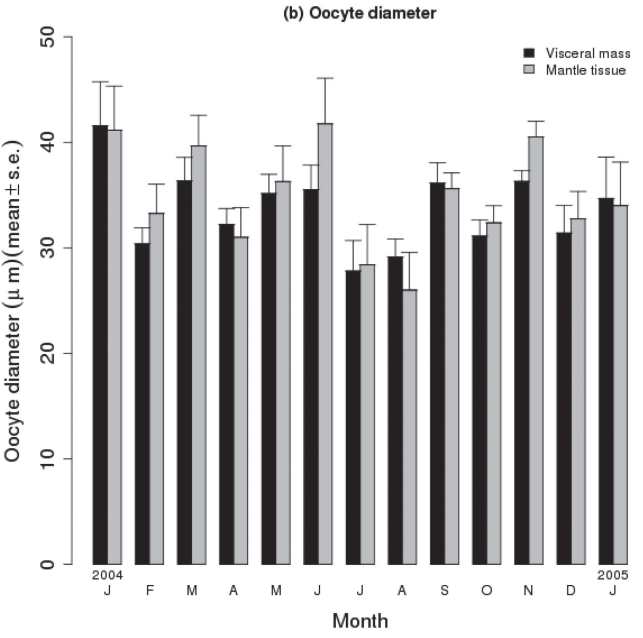

(a) Number of oocytes
Visceral mass
Mantle tissue
Number of oocytes (mean ± s.e.)
0
5
10
15
20
25
30
2004
J
F
M
A
M
J
J
A
S
O
N
D
2005
J
Month

FIG. 2b


(b) Oocyte diameter
Visceral mass
Mantle tissue
Oocyte diameter (μ m)(mean ± s.e.)
0
10
20
30
40
50
2004
J
F
M
A
M
J
J
A
S
O
N
D
2005
J
Month

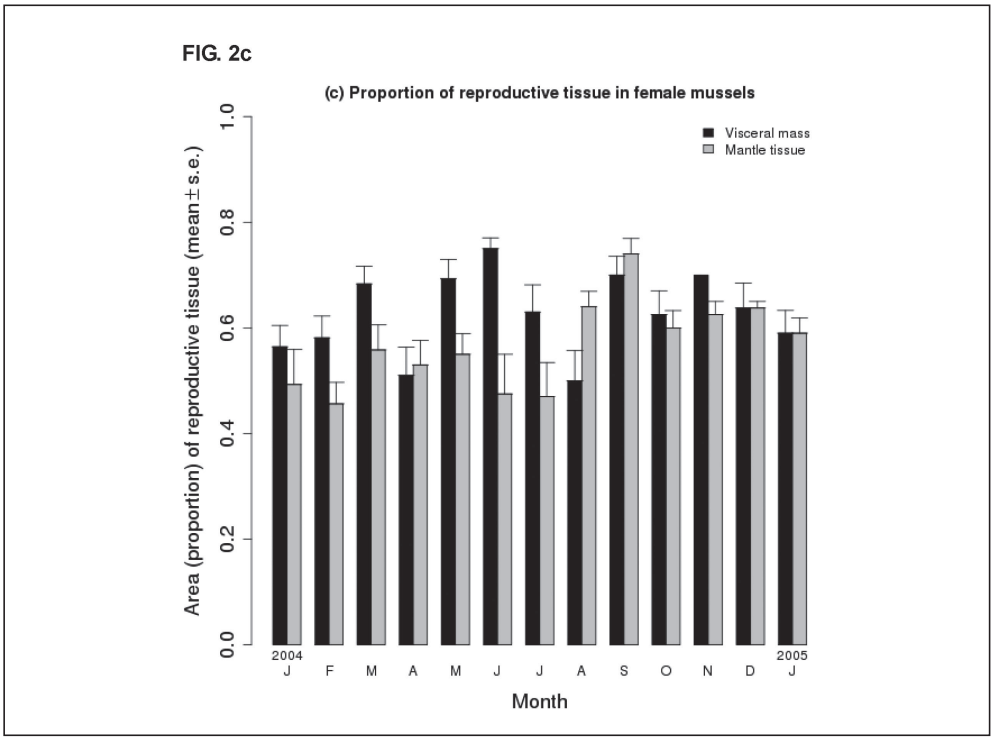


FIG. 2. Mean values of (a) oocyte numbers, (b) oocyte diameter (µm) and (c) gonad area (%) in visceral mass and mantle tissue of *Mytella guyanensis* from the study area at the Furo do Meio tidal channel bed, between January 2004 and January 2005.

Declines in oocyte numbers and oocyte diameter as well as in gonad area, that may indicate spawning, occurred between January 2004 and February, March and April, June and July/August, and between November and December. General trends in female mussel data indicate greatest activity in the middle of the wet (March) and dry (November) seasons with least activity in July and August, the transition period between both seasons.

Gametogenesis in the visceral mass was significantly correlated with gametogenesis in the mantle tissue (numbers of immature male cells: $r = 0.497$, d.f. = 68, $p < 0.001$, spermatozoa: $r = 0.544$, d.f. = 68, $p < 0.001$, male gonad area: $r = 0.377$, d.f. = 68, $p < 0.01$ and oocytes: $r = 0.634$, d.f. = 69, $p < 0.001$, and oocyte diameter: $r = 0.382$, d.f. = 69, $p < 0.01$). In female mussels, gonad area in the visceral mass was not significantly correlated with gonad area in mantle tissue ($r = 0.199$, d.f. = 69, $p = 0.09$).

Seasonal variation in reproductive stages and Gonad Index. Evidence from visceral mass tissue indicated that only a small proportion of males spawned in January and October 2004 (Fig. 3a) and GI values also indicated spawning (stage IV) in those months (Fig. 4a). However, individuals in recovery phase are relatively numerous throughout most of the year and this is also evident from the high GI values. Mantle tissue sections show that males were spawning continuously throughout the year, especially between May and October, and in January (Fig. 3b). GI values were close to 4 in January, June to September, November and December (Fig. 4b). Thus in males, spawning appears to predominate during months with lower rainfall and higher salinity.

Spawning in females occurs throughout the year in both types of tissue. In visceral mass tissue, spawning predominated in February, July, and December (Fig. 3c). GI values were close to 4 in visceral mass

FIG 3a

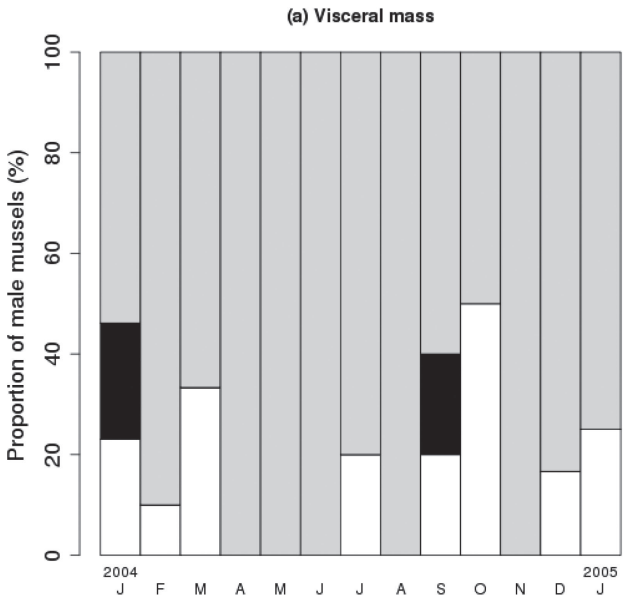


FIG. 3b

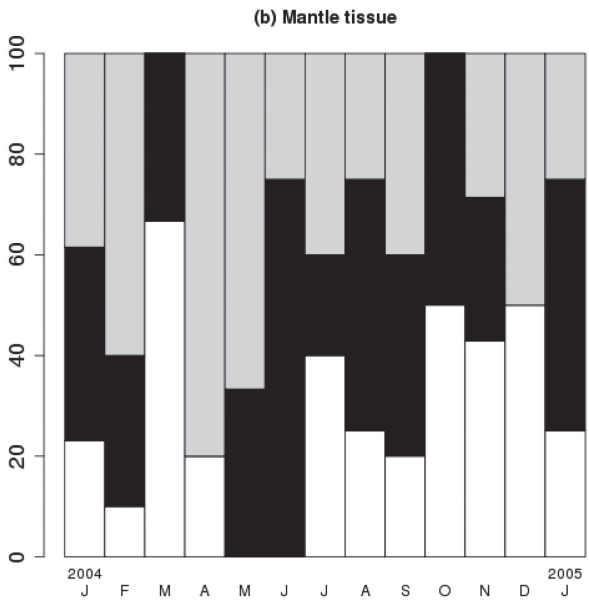


FIG. 3. Seasonal variation in the proportion of mussels of each sex in the pre-spawning (white), spawning (black), and recovery (gray) stages of the reproductive cycle of *Mytella guyanensis*, from the study area at the

FIG. 3c

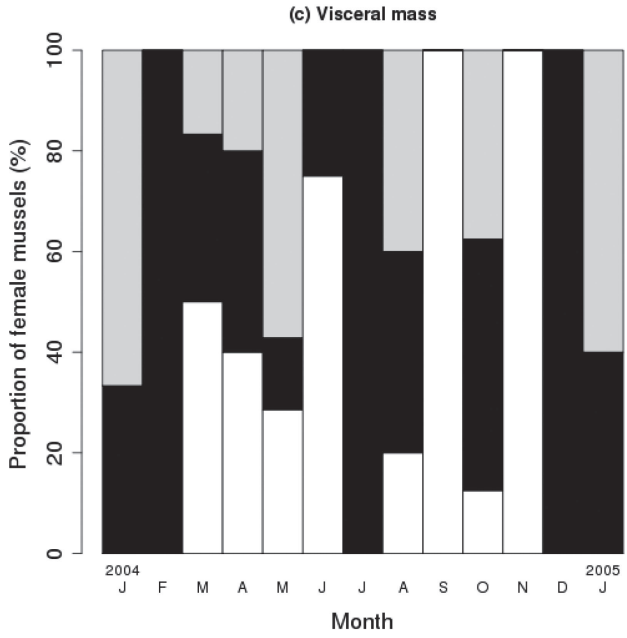
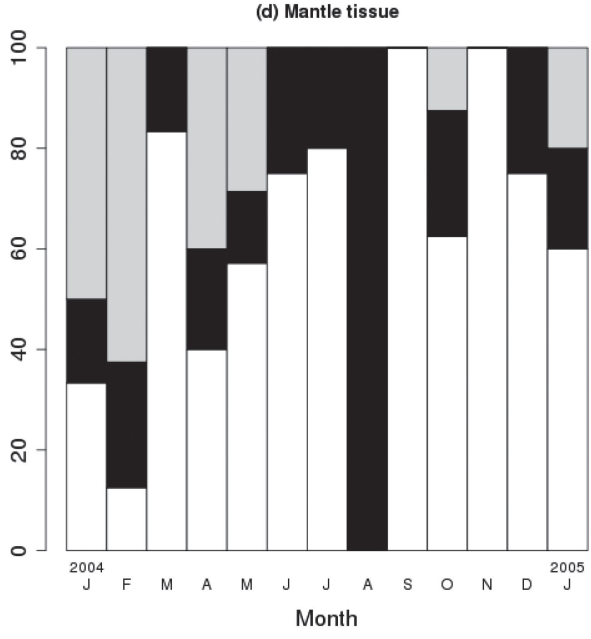


FIG. 3d



Furo do Meio tidal channel bed, between January 2004 and January 2005. (a, b) Male and (c, d) female mussels identified from visceral mass and mantle tissue sections respectively.

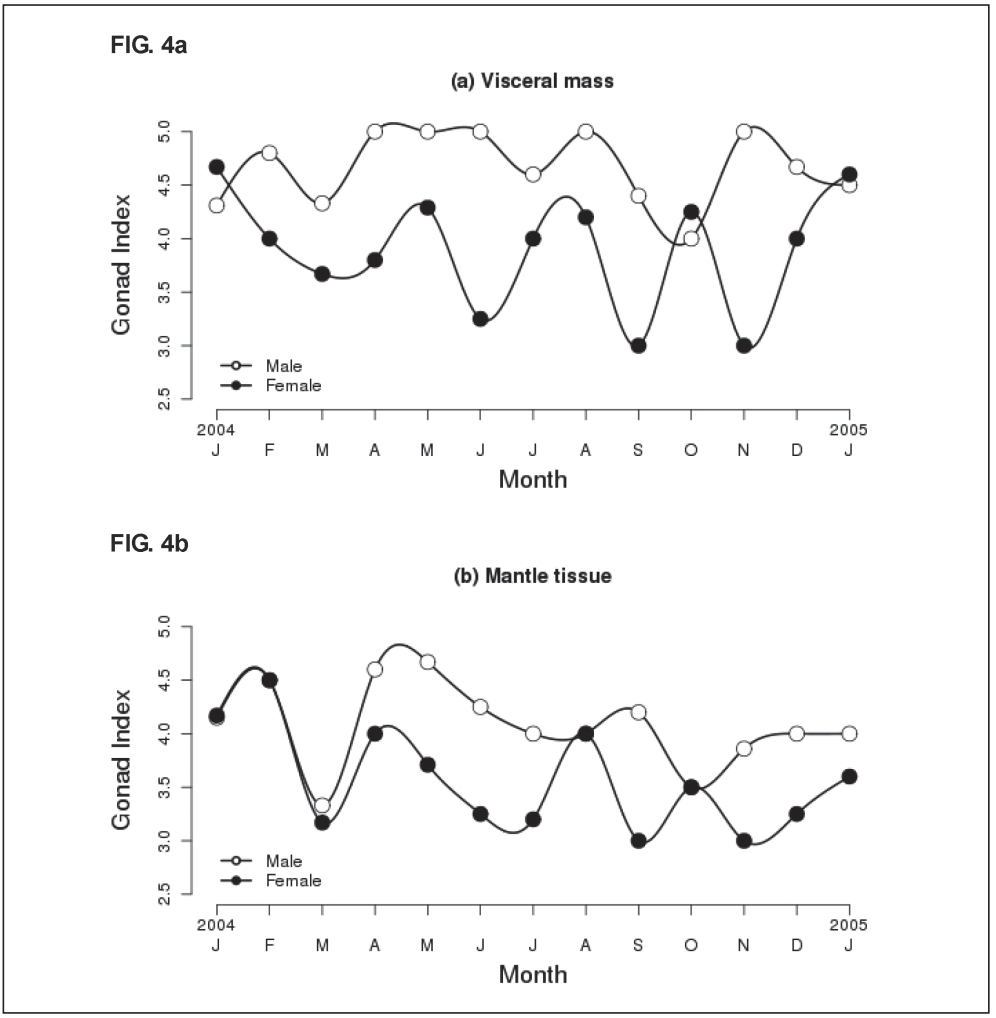


FIG. 4. Gonad Index values for male (open circles) and female (closed circles) mussels using (a) visceral mass and (b) mantle tissue sections of *Mytella guyanensis*, from the study area at the Furo do Meio tidal channel bed, between January 2004 and January 2005.

tissue during the same periods (Fig. 4a). Mantle tissue sections showed predominance of spawning individuals in August (Fig. 3d) and GI values were close to 4 in January, April, and August (Fig. 4b). Similar to male mussels, spawning in females also appears to predominate in the dry season.

There was close correspondence between GI values of males and females in the same tissue type (Fig. 4ab). However, there was less variation in GI values in males in both tissue types indicating relatively stable proportions of individuals in each reproductive stage from month to month. In contrast, in female mussels, GI values fluctuated widely from month to month (Fig. 4). This was especially evident in both tissues between June and December, when values varied between 3 and 4, indicating alternating predominance of pre-spawning and spawning females in the population. GI values were usually lower in mantle tissue than in visceral mass tissue, especially in male mussels (Fig. 4).

Relationship between salinity and reproductive activity. Salinity varied between 10 in March, during the wet season, and 45 in December, close to the end of the dry season (Fig. 5). A large number of dead mussels were found in May and such mortality may be linked to the accumulation of rainfall resulting in pools of hyposaline water. The only significant correlation was between salinity and the mean number of spermatozoa ($r = 0.646$, n = 11, $p < 0.05$). Although reproductive activity in *Mytella guyanensis* from northern Brazil is relatively constant throughout the year, increased oocyte diameter, spermatozoa production and, spawning activity in both males and females appear to be associated with the drier months of the year.

DISCUSSION

As mussels are dioecious, the sex ratio does not usually depart from 1:1, and usually the sexes cannot be differentiated by external appearance (Gosling 2003). As reported earlier (Gomes *et al*. 2009), the sex ratio of *Mytella guyanensis* was not significantly different from 1:1 and a single hermaphrodite was found among the 150 individuals examined during the present study. No sexual dimorphism of the shell has been reported for *M. guyanensis* (Sibaja 1986). Thus, *M. guyanensis* from northern Brazil appears to be typical with respect to these mytilid features. The overall sex ratios of *Mytella falcata* at Lagoa Mundaú, northeastern Brazil (Nascimento 1968b), and in a southern Brazilian population (Carpes-Paternoster 2003), were also 1:1. The proportion of hermaphrodites (1/480) in the latter study did not differ significantly from that of the present study ($\chi^2 = 0.002$, d.f. = 1, p = 0.97). The sex ratio of *M. guyanensis* from the Gulf of Nicoya, Costa Rica was consistently strongly skewed in favor of females (Sibaja 1986), however subsequent studies in the same area showed a 1:1 sex ratio in *M. guyanensis* (Cruz & Villalobos 1993a).

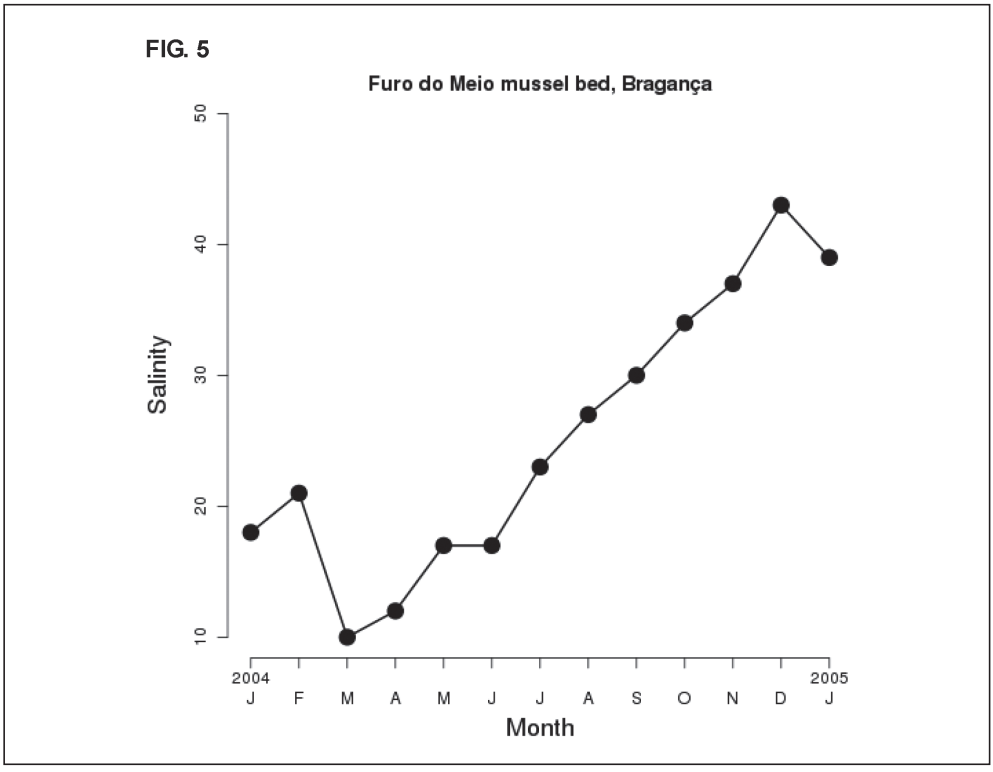


FIG. 5. Observed measurements of pore-water salinity (expressed in the Practical Salinity Scale) from the *Mytella guyanensis* mussel bed at the Furo do Meio tidal channel, between January 2004 and January 2005.

Mytella guyanensis can reach a maximum size of between 65.0 and 86.2 mm in Brazil (Carpes-Paternoster 2003, Gomes 2003, Pereira *et al*. 2003) and between 67.8 and 84.3 mm in Costa Rica and Trinidad (Bacon 1975, Sibaja 1986, Sibaja & Villalobos 1986). An average growth rate of 3.76 to 6.23 mm per month in the first 12 months of life in their natural intertidal habitat was recorded by Sibaja & Vilalobos (1986). In culture, the growth rate of *M. guyanensis* is 5.77 mm per month (Mora & Alpízar 1998). Mussels smaller than 20 mm were not examined in the present study but individuals as small as 23-24 mm in size were sexually mature. Similarly, size at first maturity was between 18 and 22 mm (Cruz & Villalobos 1993a) and 20 to 25 mm (Sibaja 1986) in *M. guyanensis* from Costa Rica. The size range of mussels examined in the present study was high and may include several cohorts with individuals in different stages of sexual maturity, accounting for some of the observed variation in gametogenesis. Visceral mass and mantle tissue were similar in terms of reproductive activity in this species. For regular histological monitoring, the use of mantle tissue is recommended as it is simpler to dissect and process, with none of the contamination from the digestive system that is found in the visceral mass.

Reproductive activity in mussels from non-tropical zones is usually related to changes in temperature (Gray *et al*. 1997, Myrand *et al*. 2000, Gosling 2003). However, mangrove air temperature does not vary significantly in tropical northern Brazil (Nordhaus *et al*. 2006), and *Mytella guyanensis* is not exposed to strong variation in air temperature at low tide because of the shade from the mangrove canopy. Reproduction in mussels from temperate zones is highly synchronous and there is an accumulation of ripe gametes in the gonad, usually preceded by the storage of nutrients in specialized cells (Mathieu & Lubet 1993). In contrast, the co-existence of individuals in different reproductive states along with constant shedding of gametes appears typical of tropical and sub-tropical bivalve populations (Lunetta & Grotta 1982, Cárdenas & Aranda 2000, Arrieche *et al*. 2002), including *Mytella guyanensis* (Cruz & Vilalobos 1993a, b) and *Geukensia demissa* (Dillwyn, 1817) introduced to Venezuela (Báez *et al*. 2005). However, despite year-long continuous gametogenesis in *M. guyanensis* from Costa Rica, significant reductions in lipids and proteins were observed during spawning, probably indicating their use in gamete production, especially oocytes (Cruz & Villalobos 1993b). Thus, peaks in reproductive activity may also occur in populations of tropical mussels.

Mean oocyte diameter in *M. edulis* varied between 42 and 57 µm during the summer reproductive period in the St. Lawrence estuary, Canada, where sharp declines in mean diameter were associated with spawning (Myrand *et al*. 2000). In contrast, declines in mean oocyte diameter of *Mytella guyanensis* occurred at intervals throughout the entire year corresponding to spawning events (Gonad Index of 4).

In a subtropical mangrove in southern Brazil, gametogenesis and spawning in *Mytella guyanensis* were continuous in males but were rather more punctuated in females and there was clearly less reproductive activity during the winter months (Carpes-Paternoster 2003). Sibaja (1986) and Cruz & Villalobos (1993a, b) also found continuous breeding in *M. guyanensis* in Costa Rica, although a peak in spawning occurred during the end of the dry season (April-May) in the former and from August to November (wet season) and February to April (dry season) in the latter two studies. Thus, there appears to be evidence from these and the present study that *M. guyanensis* is a continuously breeding mussel but with some seasonality in spawning activity. Similarly, the related *Mytella strigata* (*M. charruana*) from two lagoon sites along the central Pacific coast of Mexico showed constant gametogenesis throughout the year (Cárdenas & Aranda 2000) and with a single well-defined spawning period during the warmer and wetter period (July-October).

Spermatozoa production in *Mytella guyanensis* was associated with higher salinity values in the dry season. Forty percent of the population of the introduced ribbed mussel *Geukensia demissa* from Lake Maracaibo, Venezuela spawned at the beginning of the rainy season and 69% at the beginning of the dry season (Báez *et al*. 2005), presumably responding to the intermediate values in salinity characteristic of these transitional periods. Although relatively constant throughout the year, greater gametogenetic activity in *M. guyanensis* appears to be associated with the end of the dry season when higher salinity values prevail. Although capable of surviving wide variation in salinity (Leonel & Silva 1988), reproductive processes may be influenced by changes in osmotic regulatory processes caused by such variation (Lunetta & Grotta 1982).

Other factors may also be important in influencing reproductive activity; an apicomplexan para-

site is known to infect *Mytella guyanensis* (Azevedo & Matos 1999, Padovan *et al*. 2003). However, the seasonality of the rate of infection and any effects on mussel mortality or reproductive activity are not yet known.

Reproductive activity in mussels has been linked to food availability (Lunetta & Grotta 1982, Mathieu & Lubet 1993). Increased chlorophyll *a* concentration as a result of upwelling was found to be the primary factor responsible for variation in gonad growth in the bivalve *Lima scabra* (*Ctenoides scabra* (Born, 1778)) from Zúlia, Venezuela and spawning in this species was associated with the decrease in temperature that occurs at the onset of upwelling (Lodeiros & Himmelman 1999). A similar situation has been described for the mytilid *Perna perna* from Sucre, Venezuela (Arrieche *et al*. 2002). Where tidal immersion time is lower, and thus there is less time for feeding, sexual maturity is delayed (Franz 1996) and reproductive output is reduced (Borrero 1987) in populations of the ribbed mussel *Geukensia demissa*.

Changes in phytoplankton food sources, which occur as a result of variation in nutrient and light availability due to seasonal riverine discharge (Santos *et al*. 2008), may influence reproductive activity in *Mytella guyanensis* from northern Brazil. However, wide seasonal variation in stomach contents has been found in *M. falcata* (Eskinazi-Leça 1969). A switch from phytoplankton, abundant in the dry season (Santos *et al*. 2008), to benthic diatoms (Eskinazi-Leça 1969) in the wet season, could explain why gametogenesis is relatively constant in this species in northern Brazil.

Although *M. guyanensis* is not cultivated in Brazil it has potential as a target species for aquaculture since it is larger and heavier than *Mytella falcata* (Pereira *et al*. 2003). Experiments with the latter species in northern Brazil showed that market size can be attained in 4-5 months (pers. obs.) and similar performance might be expected from *M. guyanensis*. The fact that gametogenesis in *M. guyanensis* from northern Brazil is relatively constant means that seed is available throughout the year for attempts to cultivate this species. In Costa Rica, peaks in the settlement of seed for aquaculture coincided with previously reported periods of sexual maturity and spawning in *M. guyanensis* (Mora & Alpízar 1998).

ACKNOWLEDGMENTS

CPG and SMOP were supported by scholarships from the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq). We also thank the Secretaria Executiva de Ciência, Tecnologia e Meio Ambiente, Pará State and Banco da Amazônia, S. A. for financial support. This study was carried out as part of the Mangrove Dynamics and Management (MADAM) Project, a joint German-Brazilian cooperative scientific program.

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