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Reproductive cycle and gonad development of the Northern Argentinean *Mesodesma mactroides* (Bivalvia: Mesodesmatidae)

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Abstract The reproductive cycle and gonad development of the yellow clam *Mesodesma mactroides* was studied over a period of 24 months (January 2005–December 2006) at the Argentinean sandy beach Santa Teresita. Histological examination of gonadal tissue revealed that sex ratios did not significantly deviate from the proportion of 1:1 and no case of hermaphroditism was found. The reproductive cycle of *M. mactroides* followed an annual cyclicity, which was significantly correlated to monthly mean sea surface temperatures (SST). Oocytes showed highest abundance in winter, indicating a process of gonadal development and sexual maturation. The mean oocyte size decreased significantly during spring. Modal oocyte sizes decreased significantly during winter and late spring of each year, suggesting spawning events. The condition index was not useful in describing the annual reproductive cycle of *M. mactroides*. Ash-free, shell-free dry mass was chosen to detect the condition of the specimens, and this significantly correlated with monthly mean SST and the gametogenic cycle. Annual recruitment patterns during summer–autumn indicated a 3-month-long planktonic phase of *M. mactroides*. The reproduction cycle and gonad development of

M. mactroides showed only weak differences between data from the present study and those collected 40 years ago.

Keywords Yellow clam · Histology · Condition index · Ash-free, shell-free dry mass · Oocyte size and abundance

Introduction

The yellow clam *Mesodesma mactroides*¹ Reeve,² 1854 (Bivalvia: Mesodesmatidae), locally called ‘almeja amarilla’, was historically the most common bivalve in its geographic distribution (Parodiz 1942; Stuardo 1964; Defeo 1989). However, recently, its abundance has significantly decreased (Lima et al. 2000; Bergonci and Thomé 2008; Herrmann 2009). The suspension-feeder currently inhabits intertidal Atlantic sandy beaches from tropical (23°S Ilha Grande, Rio de Janeiro State, Brazil) to temperate regions (40°S Isla del Jabalí, Province of Buenos Aires, Argentina; Rios 1994; Fiori and Morsán 2004). Thus, its distributional range covers about 1,800 km of South Brazilian sandy beaches, 22 km in Uruguay, and 375 km in Argentina, where it represents the only *Mesodesma* species occurring throughout the mediolitoral (Olivier et al. 1971). On the beaches of northern Argentina,

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¹ *M. mactroides* reference specimens were deposited in the collections of the ‘Museum für Naturkunde der Humboldt-Universität zu Berlin’ and the ‘Museo Argentino de Ciencias Naturales—Bernardino Rivadavia’ under the reference numbers ZMB/Moll.104643 and MACN-In37513, respectively.

² In previous studies, Deshayes 1854 was cited falsely as the author who first described *M. mactroides*. However, this description was not published by Deshayes but by his colleague Reeve; thus, the corresponding author of *M. mactroides* is Reeve (see Reeve 1854; Deshayes 1855).

it is found together with the sympatric and dominant surf clam *Donax hanleyanus* (Olivier et al. 1971; Penchaszadeh and Olivier 1975; Herrmann 2009). During the 1940s and 1950s, *M. mactroides* was an important economic resource for Argentina, with a maximum exploitation rate of 1,079 tonnes in 1953. As a consequence of overfishing, the clam fishery was closed in 1956 (Coscarón 1959). Argentinean *M. mactroides* populations never recuperated and in the 1990s and recently populations were further depleted by mass mortality events. Although red tides and high heavy metal concentrations were given as possible reasons for the massive decimation, the actual cause was never found (Odebrecht et al. 1995; Fiori and Cazzaniga 1999; Thompson and Sánchez de Bock 2007). Various authors have suggested illegal extractions and the impact of tourist activities as probable main factors for the failure of stock recovery (Bastida et al. 1991; Bastida et al. 1996; Herrmann 2009).

Aspects of population dynamics for *M. mactroides* such as recruitment, growth, production, and mortality are very well studied for the Argentinean (Bastida et al. 1996; Fiori and Cazzaniga 2002; Fiori et al. 2004; Fiori and Morsán 2004; Fiori and Defeo 2006; Herrmann 2009), the Uruguayan (Defeo et al. 1986, 1988, 1991, 1992; Defeo 1989; Brazeiro and Defeo 1999; Lima et al. 2000), and the Brazilian coasts (Narchi 1981; Gil and Thomé 2000; Bergonci and Thomé 2008). However, with the exception of Christiansen (1971), we know of no further studies dealing with the reproductive cycle of this species.

The present study aims to describe the reproductive cycle and gonad development of the yellow clam population of the northern Argentinean sandy beach Santa Teresita in comparison with the above-mentioned study, which was carried out 40 years ago.

Materials and methods

Study area

The present study was carried out at the three south Atlantic sandy beaches Santa Teresita (36°32'S, 56°41'W), Mar de las Pampas (37°19'S, 57°00'W), and Faro Querandí (37°29'S, 57°07'W; Fig. 1), whereby we want to highlight that *M. mactroides* was only abundant at the first mentioned location during the entire sampling period. Therefore, the reproductive cycle and gonad development of the intertidal yellow clam was studied during alternate spring tides only from the sandy beach Santa Teresita. According to McLachlan's (1980) rating scale for exposure and Short and Wright's (1983) classifications of beach types, Santa Teresita can be characterised as sheltered and dissipative (for detailed parameters see: Herrmann 2009).

This is an open ocean beach receiving continuous wave action and is subject to semidiurnal tides, with a maximum tide range of 1.6 m; spring tides average 1.7 m and mean neap tides 0.2 m. The sea surface temperature (SST) varies between 11°C in winter and 23°C in summer. The study site is composed of good-moderate fine sand, with a mean particle diameter of 2.26 phi (Herrmann 2009). The sandy beach of Santa Teresita is affected by a freshwater seepage and a southward current that brings water masses from the 290 km long and up to 220 km wide estuary of the Río de la Plata and is thus characterized by a mean salinity of 31. This beach is well drained and oxygenated.

Sampling and histological examination

Samples of *M. mactroides* were collected monthly between January 2005 and December 2006 at a series of stations (4 m intervals). The stations were positioned along three transects separated by 20 m intervals and located perpendicular to the shoreline from the spring tide high water mark to the neap tide low water mark. At each station, three replicated sand samples were excavated to 35 cm depth using a 0.16 m² steel corer, and thereafter sieved individually on a 1 mm mesh. For biomass determinations as well as for calculations of the condition index (CI), a total of 720 sampled specimens were preserved in 70% ethanol and subsequently analysed in the laboratory, as described in the following paragraph. For histological examinations, again, a total of 720 individuals were sampled and gonads, covering the full range of sizes of specimens under gametogenic activity (2–64 mm anterior-posterior shell length [apSL]), were selected for histological analysis. The apSL of clams was measured in situ to the nearest 0.01 mm with a digital vernier calliper (Mitutoyo, model 500–161). For histological processing, intact clams with cut through adductor muscles were fixed in Bouin's solution for two hrs, afterwards transferred into a 70% ethanol solution and later processed in the laboratory using standard methods (Romeis 1989), including embedding in paraffin, sectioning at 5 µm and staining with hematoxylin-eosin. Photographical analyses were carried out with a Zeiss Axio Imager Z1 light microscope equipped with a Sound Vision digital camera using the imaging software AxioVision 4.4 (2008). Abundance (mm⁻²) and size of oocytes (mean diameter obtained from measurements of 30 oocytes per specimen) were determined from histological slides, except for the period of January to February 2005 and January 2006, where clams showed only the gonad stage 0 (sexual rest stage with apSL < 10 mm). Gonads of *M. mactroides* were classified into five developmental stages following Christiansen (1971), but combining the early active with the late active stage and the early ripe with the ripe stage (Fig. 2,

Fig. 1 Map of the study sites Santa Teresita (S), Mar de las Pampas (M) and Faro Querandí (F). *M. mactroides* was only abundant at the first mentioned location during the entire sampling period (black ladled). Filled circle indicates the southern-most distribution limit of *M. mactroides* at Isla del Jabalí. Dotted areas present northern and southern sandy beaches of the Province of Buenos Aires where major *M. mactroides* populations existed in 1959 (Coscarón)

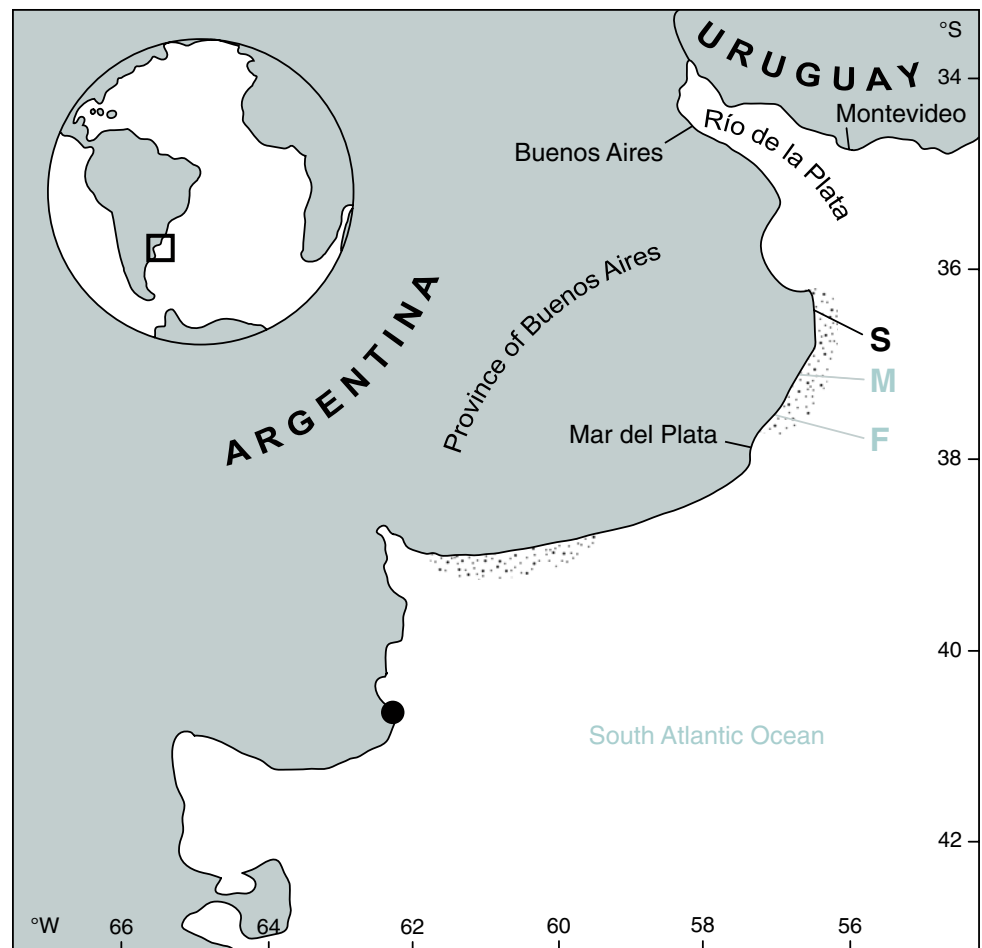


Table 1). Individuals without germ cells were categorized in the sexual rest stage. Using chi-square (χ^2) analysis, the sex ratio of *M. mactroides* was calculated according to the presence of oocytes and sperms. As clams were in a resting stage between January and March of both years, the respective sex ratio could not be determined. The SST was measured daily at 13:00 pm using a digital thermometer to a precision of 0.1°C. Data of length-frequency distributions of *M. mactroides* and their consequent cohort analyses were taken from Herrmann (2009).

Condition index, biomass and recruitment

The CI of preserved *M. mactroides* was calculated to trace seasonal variation in the visceral mass. After blotting on filter paper, the total wet mass was recorded immediately to the nearest 0.1 mg. After this, valves, mantle, siphons, retractor and adductor muscles were removed. The wet mass of the resulting standard compact unit consisting of the visceral mass and foot was recorded. The CI was calculated according to the equation of de Villiers (1975), namely $CI = 100 M_v / (M_t - M_v)$, where M_v is the wet visceral mass (including the foot) and M_t is the total wet mass.

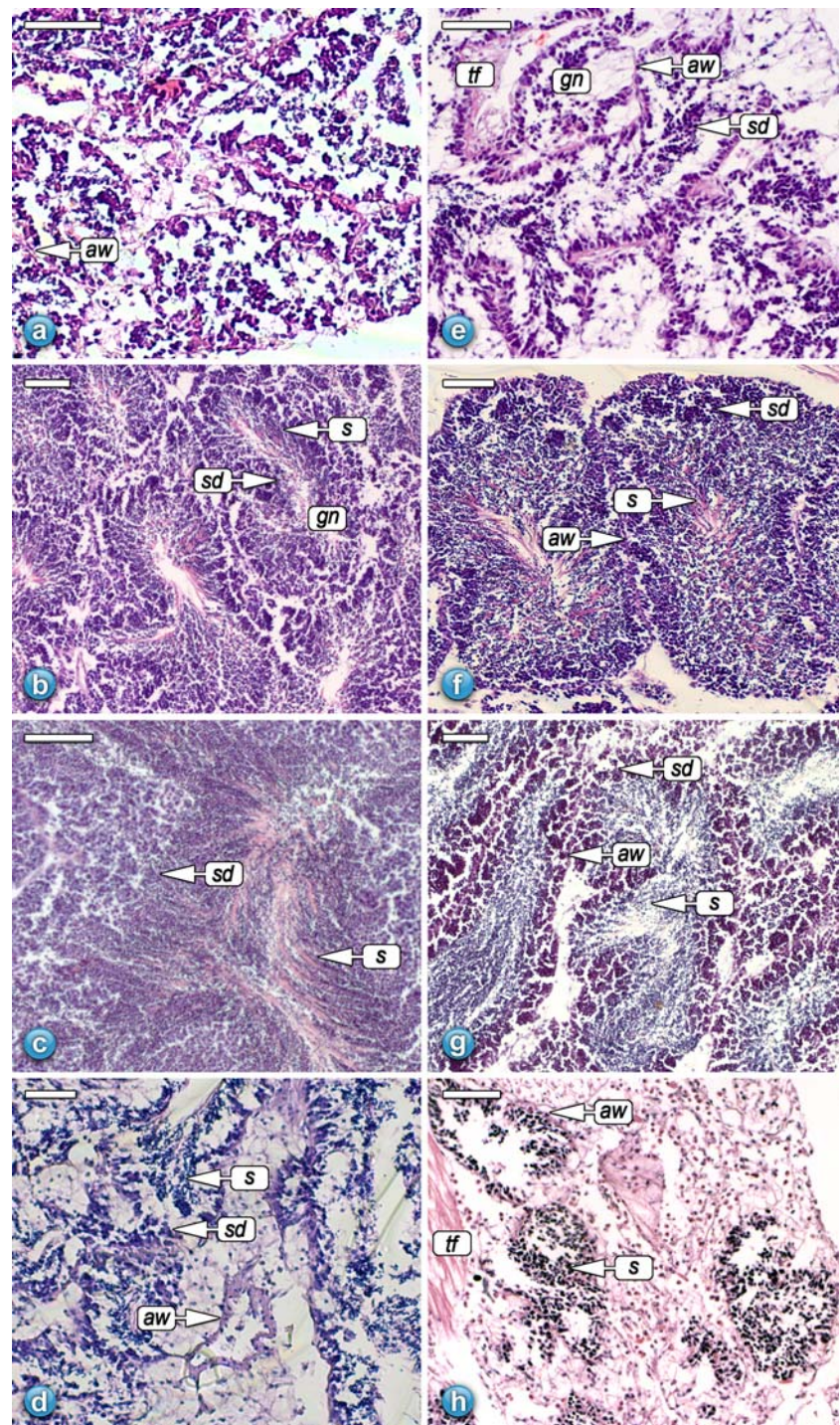
As shown below, the CI was not the best proxy to evaluate the condition of the individuals, since the gonad-foot unit could not be separated very accurately. Therefore, ash-free, shell-free dry mass (AFDM) of preserved yellow clams was recorded throughout the sampling time as an estimator of specimens' condition, whereby the conversion factor of 0.186 was empirically determined according to Brey et al. (1988).

Recruits, here defined as clams ranging from 2 to 6 mm apSL, were sampled and measured as described in the previous chapter.

Statistical analysis

Sex ratios (male:female) of yellow clams were calculated according to the presence of oocytes and spermatozoa using χ^2 analysis. The influence of SST on the gametogenic cycle, as well as its correlation with CI and AFDM were statistically analyzed by Spearman's rank order correlation. Furthermore, to evaluate the null hypothesis of no difference in the gametogenic cycle throughout the year, one-way analysis of variance (ANOVA) was performed with subsequent Tukey HSD post hoc test when differences

Fig. 2 Microphotography (colour pictures of full size: Herrmann et al. 2008) of male gonad stages of *M. mactroides*: **a** early active stage, **b** late active stage, **c** early ripe stage, **d, e** ripe stage, **f** partially spawned stage, **g** spent stage, **h** recovery stage (*aw* alveolar wall, *gn* goias, *s* sperm, *sd* spermatids, *tf* transverse fibre, scale bars are 100 μ m)



were found, using months or seasons as factor and proportion of ripe and spawning individuals as dependent variable. Temporal differences of oocyte abundance were tested by one-way ANOVA. All statistical analyses were carried out using the statistical package SPSS version 17.0 (SPSS 2008). Differences were considered significant at a level of $\alpha = 5\%$ (Zar 1999).

Results

Gonad development

Histological examinations of the gonads from the 24 month sampling series demonstrated that the reproductive cycle of *M. mactroides* has a distinct seasonality.

Table 1 Explanation of the gametogenic scale and the use of descriptive terms (primer column: present study; second column: after Christiansen 1971), utilized in scoring histological analysis of gonad tissue to assess the gametogenic stages of *M. mactroides*

Gonad stages		Brief description of gonad		*Photo
Present study	After Christiansen (1971)			
Sexual rest	0	Sexual rest	A total absence of gametes, making it impossible to distinguish between sexes, empty follicles are observed	
Active	I	Early active stage	Follicles few and small, sex distinguishable, protogonia and gonia in mitosis	a
	II	Late active stage	Follicle size increases, spermatogonia and spermatocytes in males, oogonia and previtellogenic oocytes in females	b
Ripe	III	Early ripe stage	Follicle size increases and occupies the entire tissue, germinal cells in all phases of gametogenesis	c
	IV	Ripe stage	Polygonal follicles almost full of ripe gametes, spermatozoa occupy most of follicle, free ripe polygonal oocytes in the lumen	d and e
Spawning	V	Partially spawned stage	Gonoducts with mature gametes in emission. Spermatozoa lose radial disposition. Free ripe rounded oocytes in the lumen and empty spaces	f
	VI	Spent stage	Follicles small and practically empty, residual gametes degrading	g
Cytolysed	VII	Recovery stage	Gonadal follicles at this stage are empty, except for residual gametes, amoebocytes are present within the follicles, close to the walls and in the centre	h

The individual stages of male and female yellow clam gonads are imaged at Figs. 2 and 3, respectively (*Photo)

The sex ratio did not deviate significantly from the proportion of 1:1 ($\chi^2 = 1.711$, $df = 1$, $p > 0.05$) during the study period. About 42% ($N = 302$) of the individuals were identified as females, 38% ($N = 274$) as males, and 20% ($N = 144$) were in a sexual rest stage, which occurs mainly in summer. No case of hermaphroditism was found. Male (Fig. 2a, b) and female (Fig. 3a, b) gonads were active from austral autumn–spring with maximum values in winter and in the ripe stage (male: Fig. 2c–e, female: Fig. 3c–e) during the same period (Fig. 4a, b). Spawning of males (Fig. 2f, g) took place mainly in winter–spring (from July to November 2005 and from August to December 2006; Fig. 4a). Females spawned (Fig. 3f, g) between October and November (2005) and June, and November and December (2006) (Fig. 4b). Male gonads were cytolysed (Fig. 2h) during winter and spring (Fig. 4a), whereas cytolysed stages of females (Fig. 3h) were present between autumn and winter (in June, July) and in late spring (November to December 2005 and December 2006; Fig. 4b).

Reproduction cycle

The examination of histological sections confirmed a seasonal gonadal development in *M. mactroides*. SST (Fig. 5a) was significantly correlated twice with the gametogenic cycle (gonad stages ripe and spawning, Fig. 5b); between February and March of both years (Spearman's rank order correlation, $r_s = -0.833$, $p < 0.05$,

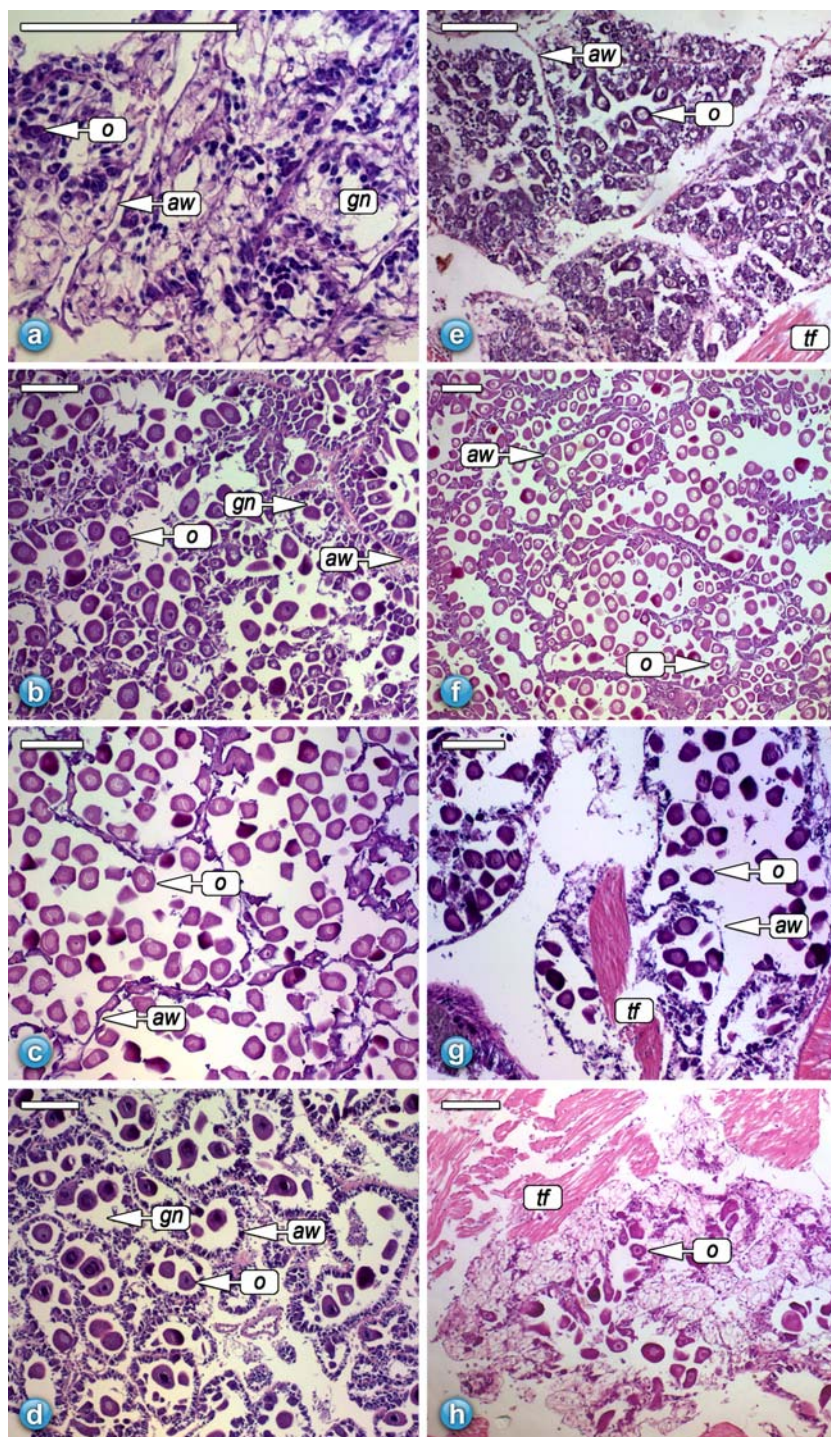
$N = 8$) and between July and October of both years (Spearman's rank order correlation, $r_s = 0.850$, $p < 0.05$, $N = 8$). Furthermore, the relative proportion of ripe and spawning individuals was significantly different between months ($F_{11,12} = 7.623$, $p < 0.05$) and seasons ($F_{3,20} = 7.305$, $p < 0.05$), whereas the proportion of ripe and spawning female individuals was significantly higher in spring and autumn (Tukey HSD post hoc test; Fig. 5b).

In both years, yellow clam oocytes showed highest abundance in winter with a maximum in September (one-way ANOVA, August to October vs. remaining year, $F_{1,15} = 6.594$, $p < 0.05$; Fig. 5c), indicating a seasonal process of gonadal development and sexual maturation. Minimum oocyte abundance was observed in autumn–winter and in late spring of both years (one-way ANOVA, May to July and December vs. rest of the year, $F_{1,15} = 4.847$, $p < 0.05$; Fig. 5c), where most of the clams were in the cytolysed stage (Fig. 4).

Mean oocyte size decreased significantly in spring of both years (one-way ANOVA, October–December vs. April–September, $F_{1,15} = 4.692$, $p < 0.05$) (Table 2).

Unimodal histograms of monthly oocyte size classes ranged from 5 μm in November–December to 60 μm in August–September (Fig. 6). Modal oocyte sizes decreased significantly twice each year in winter and late spring, suggesting two spawning events (one-way ANOVA testing August and December vs. the other months, $F_{1,12} = 35.368$, $p < 0.05$; see dotted arrows in Fig. 6).

Fig. 3 Microphotography (colour pictures of full size: Herrmann et al. 2008) of female gonad stages of *M. mactroides*: **a** early active stage, **b** late active stage, **c** early ripe stage, **d, e** ripe stage, **f** partially spawned stage, **g** spent stage, **h** recovery stage (*aw* alveolar wall, *gn* goias, *o* oocyte, *tf* transverse fibre, *scale bars* are 100 μ m)



Condition index, biomass, and recruitment

Although the annual reproductive cycle of *M. mactroides* did not significantly correlate with the CI (Spearman's rank order correlation, $p > 0.05$), specimens showing periods of ripeness and spawning demonstrated an increasing trend of CI in autumn–winter, and specimens showing periods of

cytolyzed and active stages demonstrated a decreasing trend of CI in spring–summer of both years, respectively (Fig. 5b, d).

The seasonal variation of the yellow clams' biomass (AFDM) was significantly correlated with SST during winter and spring (July–December) of both years (Spearman's rank correlation, $r_s = 0.789$, $p < 0.05$, $N = 12$), an

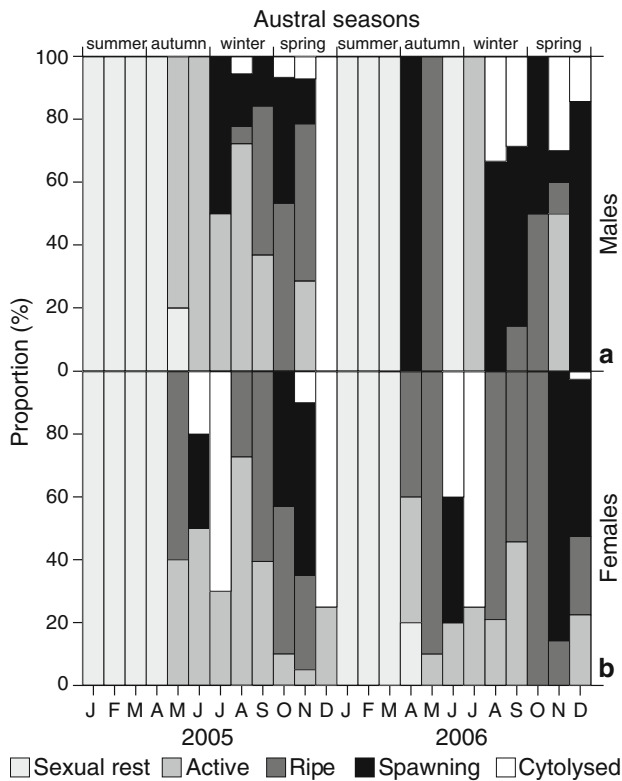


Fig. 4 Proportion of distinct gonad stages in mature male (a) and female (b) *M. mactroides*, sampled at Santa Teresita

increase of AFDM occurred alongside higher SST (Fig. 5a, e). Values of AFDM were also significantly correlated with mature gonad stages (ripe and spawning) during winter and spring (July–November) of 2005 and 2006 (Spearman’s rank correlation, $r_s = 0.721$, $p < 0.05$, $N = 10$). The AFDM increased concurrently with the maturation of the gonad (Fig. 5c, e). In the second year, higher values of AFDM indicated growth and gonad development in the same cohort analyzed already in the previous year.

Recruits of the yellow clam settled on the Santa Teresita sandy beach in both years during summer and autumn (in 2005: January–July; in 2006: February–May; Fig. 5f). Thus, the settling period of recruits is again significantly correlated with SST: abundance of recruits increased significantly during summer–autumn in both years (Spearman’s rank order correlation, $r_s = 0.421$, $p < 0.05$, $N = 24$; Fig. 5a, f).

Discussion

Gonadal development

The reproductive strategy of *M. mactroides* from Santa Teresita (present study) is summarized in Table 3 and

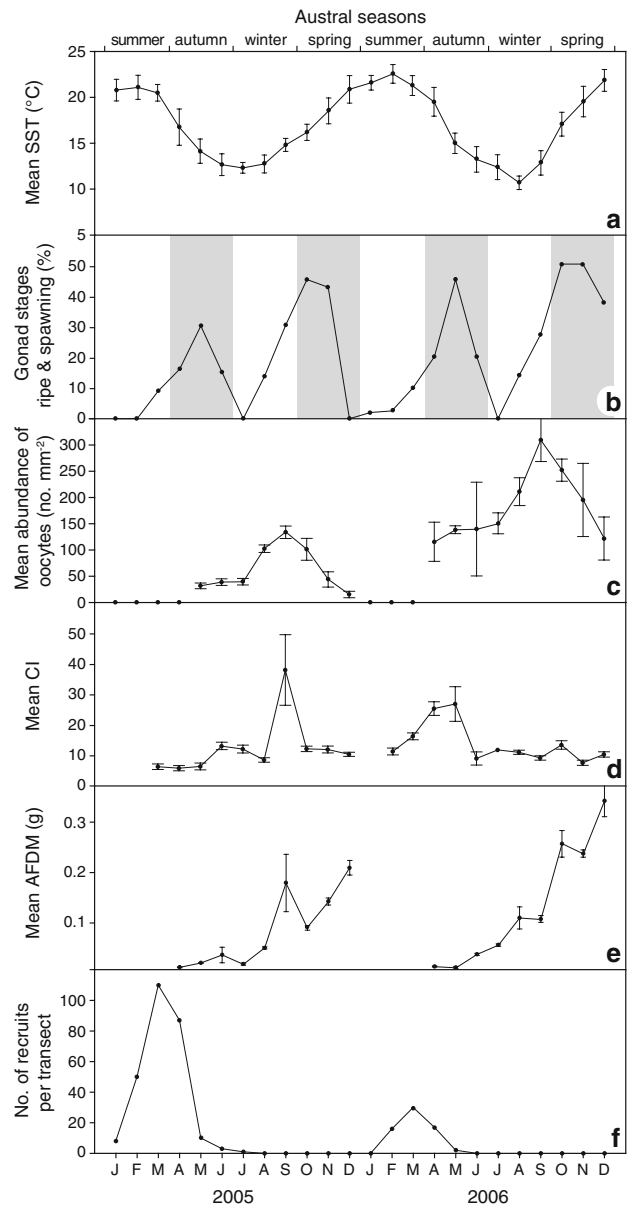


Fig. 5 *M. mactroides* at Santa Teresita: **a** mean SST measured daily at Santa Teresita, **b** percentage of gonad stages ripe and spawning, **c** mean abundance of oocytes (no. mm⁻²), **d** mean condition index (CI), **e** mean biomass (AFDM) (g) and **f** number of recruits (2–6 mm apSL) recorded per monthly transect. Grey areas indicate seasons where Carreto et al. (1995) observed chlorophyll *a* maxima with main peaks during spring and secondary peaks during autumn in the Buenos Aires shelf region. Error bars standard deviation. Data sets of graphics are published in Herrmann et al. (2008)

compared with the 40-year-old historical data obtained from a *Mesodesma*-population approximately 100 km south of the Santa Teresita population (Mar Azul, Christiansen 1971). Table 3 shows a clear difference between the gonad stages during summer. Whereas Christiansen (1971) found nearly all developmental stages all year round, in the

Table 2 *M. mactroides*. Monthly SST (°C), values of oocyte size (μm), mean oocyte size (\bar{x}), number of females (f), number of measured oocytes (o), and stages of oocyte development (according to Table 1)

Year	Month	SST (°C)	Oocyte size (μm)	$\bar{x} \pm SD$ (μm)	f	o	Stage of development
2005	Jan	21	–	–	–	–	Sexual rest
	Feb	21	–	–	–	–	Sexual rest
	Mar	20	–	–	–	–	Sexual rest
	Apr	17	–	–	–	–	Sexual rest
	May	14	29–30	29.00 ± 1.06	3	60	Ripe
	Jun	13	23–49	27.83 ± 1.19	3	30	Active
	Jul	12	12–43	36.80 ± 1.03	3	90	Cytolysed
	Aug	13	10–53	26.85 ± 0.55	17	289	Active
	Sep	15	15–48	32.43 ± 1.36	11	316	Active and spawning
	Oct	16	18–45	31.30 ± 1.27	6	208	Ripe
	Nov	19	8–58	30.95 ± 2.16	10	273	Spawning
	Dec	21	8–47	16.01 ± 1.56	3	25	Cytolysed
2006	Jan	22	–	–	–	–	Sexual rest
	Feb	23	–	–	–	–	Sexual rest
	Mar	21	–	–	–	–	Sexual rest
	Apr	20	16–44	33.17 ± 4.27	3	54	Active and ripe
	May	15	23–45	34.66 ± 0.90	3	28	Ripe
	Jun	13	13–43	33.16 ± 2.08	3	90	Spawning and cytolysed
	Jul	12	13–45	36.01 ± 2.02	3	60	Cytolysed
	Aug	11	10–53	25.70 ± 2.71	10	286	Ripe
	Sep	13	10–55	30.53 ± 2.80	10	325	Ripe
	Oct	17	13–59	33.61 ± 0.87	13	454	Ripe
	Nov	20	8–45	24.21 ± 2.95	5	208	Spawning
	Dec	22	13–51	32.37 ± 2.43	7	195	Spawning

present study, the active, ripe, spawning, and cytolysed stages were only recorded from autumn to spring and the sexual rest stage occurred only in summer. The existence of a sexual rest period has also been described for other bivalves (*Donax serra*: Laudien et al. 2001; *Ensis siliqua* and *E. arcuatus*: Darriba et al. 2004, 2005). The absence of active gonad stages in both summers studied is attributed to a single cohort with a small shell length (mean apSL of 8 mm in summer seasons: Herrmann 2009) and to the consequent immaturity (sexual rest stage) of *M. mactroides* during this period. In contrast to the recent population structure of the yellow clam, Olivier and Penchaszadeh (1971) found three cohorts where individuals of commercial size (>60 mm, Coscarón 1959) were found throughout the year. However, comparison of data from areas with different beach morphodynamics (Santa Teresita: dissipative and sheltered; Mar Azul: exposed and intermediate) is difficult; Delgado and Defeo (2007) found differential behavior patterns in the reproductive strategy of *D. hanleyanus* when comparing reflective and dissipative beaches.

Reproduction cycle

The present investigation of *M. mactroides* gonads suggests two reproductive events per year; the first one in winter and the second one in spring. Christiansen (1971) also recorded two spawning events for the same species at the same beach; however, these occurred later in the season (spring and early summer). For the congener *M. donacium*, two spawning events were also observed by Filun Villablanca (1992) in northern Chile where reproductive events occurred in spring–summer and autumn. However, Peredo et al. (1986) observed only one spawning period for *M. donacium* from the southern Chilean coast. These differences may be attributed to distinct environmental conditions such as SST, salinity, and food availability (Sastry 1970; de Villiers 1975; Peredo et al. 1986; Penchaszadeh et al. 2000; Kraeuter and Castagna 2001; Laudien et al. 2001). Seasonal changes in SST trigger gametogenesis, and further to this, short-term temperature changes may stimulate spawning (Ansell 1961; Seed 1976). The present results show that changes in SST are

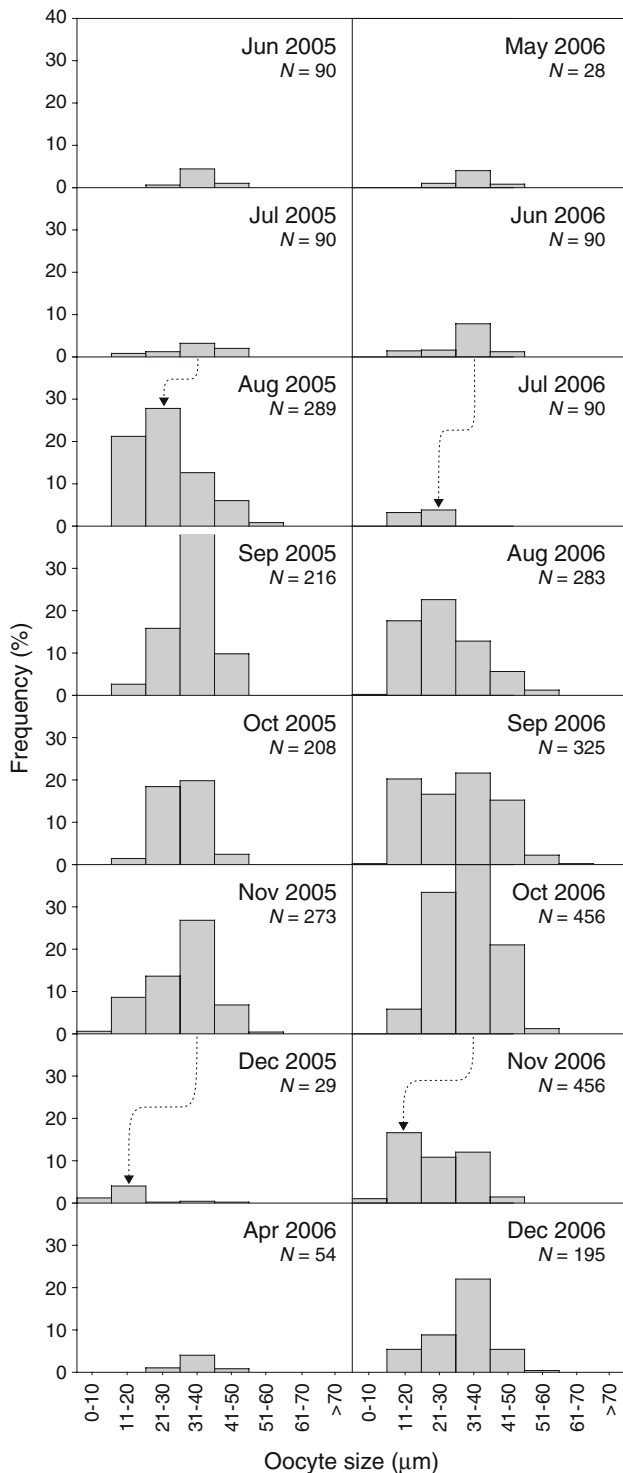


Fig. 6 Monthly oocyte size-frequency distribution of *M. macroides* collected at Santa Teresita. The abrupt decreases of oocyte modal sizes in August/December 2005 and in July/December 2006 indicate two spawning events per year (dotted arrows). *N* number of oocytes

significantly correlated with gonad development. Low mean temperatures coincided with maximum oocyte size and gamete initiation (late Fall–winter). Increases in SST

Table 3 Reproductive strategy of *M. macroides* comparing data from present study with data four decades ago (Christiansen 1971)

	Gonad stages	Summer	Autumn	Winter	Spring
Present study	Active		×	×	×
	Ripe		×	×	×
	Spawning		×	×	×
	Cytolysed		×	×	×
Christiansen (1971)	Active	×	×	×	×
	Ripe	×	×	×	×
	Spawning	×	×	×	×
	Cytolysed	×	×		×

throughout winter periods of both years matched well with the growth of gametes (mean oocyte size: 5 µm in July to 41 µm in September 2005 and 4 µm in July to 48 µm in September 2006) and an increase in the number of individuals in ripe and spawning stages (Fig. 5a, b). Maximum gamete ripeness and size observed in winter (July–August) was related to seasonal minimum SST. Noticeable decreases in oocyte sizes (Fig. 6), abundance, and the increased number of spawned and spent individuals was associated with rapid increases in SST during spring (Fig. 5a). Multiple stages of gonad conditions were also observed in late spring (November). However, several authors (e.g. Sastry 1968; Giese 1974; Sastry 1979) have mentioned that the reproductive cycle of suspension feeders is not only influenced by physical parameters such as SST, but also by changes in phytoplankton biomass and species compositions. The increase of chlorophyll *a* concentrations in the Buenos Aires shelf region observed during winter and summer by Carreto et al. (1995) with a main peak in spring and a secondary peak in autumn, correspond considerably with the dominance of *M. macroides* in ripe and spawning stages (Fig. 5b). This suggests that phytoplankton may also have a direct impact on the reproductive cycle of *M. macroides*.

Monthly oocyte size-frequency distribution histograms (Fig. 6) have proved to be a useful method for studying the gonad development of the yellow clam, as they have also been for several bivalves from previous studies (e.g. *Donax hanleyanus*: Penchaszadeh and Olivier 1975; *Atrina seminauda*: Soria et al. 2002; *Tawera gayi*: Morriconi et al. 2007). Unimodal histograms showed smaller size classes of oocytes (>15 µm) in winter and spring, corresponding to a weak spawning event during June–August and a second stronger one during October–December of each year. The increase of oocyte diameters (15 µm in July to 40 µm in September) corresponds to gonad activity. The modal of oocyte sizes ranged between 15 and 45 µm with lower values in winter (August 2005, July 2006) and spring

(December–November 2005) due to gamete releases. The unimodality of the histograms (Fig. 6) explains the absence of successive periods of maturing oocytes.

Condition index, biomass, and recruitment

The CI is a useful tool to describe the reproductive cycle of marine bivalves with easily separable gonads (e.g. *Mytilus edulis*: Petersen et al. 2004; *Hyotissa hyotis*: Duprat-Bertazzi and García-Domínguez 2005; *Mercenaria mercenaria*: Hofmann et al. 2006). This index generally indicates the gonadal mass changes throughout the year (Grant and Tyler 1983) with highest values when gonads are mature. The CI proved to indicate the gametogenic cycle even in bivalves with a gonad not easily separable from the foot such as *Donax trunculus* (Gaspar et al. 1999), *D. serra* (Laudien et al. 2001), and *M. donacium* (Riascos et al. 2008). However, for *M. mactroides*, the CI was not useful as it did not significantly correlate with the gametogenic cycle (cf. Fig. 5b, d). Although CI decreased in spring 2005 marking the main spawning period, in winter to Fall 2005, the values of CI were still low despite the gonads being mature and a high percentage of clams being ripe. A decrease in the CI as a result of spawning activity in 2006 was not identified. Thus, the CI is not useful to describe the spawning of the yellow clam. As a consequence of the prolonged spawning period of the population, all reproductive stages were present between May and December (Fig. 4). However, seasonal variation of the AFDM was positively correlated with SST as well as with the gametogenic cycle (Fig. 5a, c, e).

When assuming that the collected recruits originated from the studied adult population, the results indicate a meroplanktonic phase of approximately 3 months. Recruits appeared in the intertidal zone of Santa Teresita in summer–autumn of both years (from January to July 2005 and from February to May 2006), where the latter occurrence is apparently the result of the spawning event between November and December 2005 (Figs. 4, 5f, 6). After weak gamete release periods in July–August 2005 and June–July 2006 (Fig. 6), recruits were not present in the sampling area (Fig. 5f). However, the absence of recruits does not necessarily indicate a lack of spawning activity (Caddy and Defeo 2003) as environmental conditions, which strongly influence recruitment of marine invertebrates (e.g. hydrodynamic processes: Roughgarden et al. 1988; food limitation: Olson and Olson 1989; predators: Sale 1990), may not have been favourable for successful recruitment at the ‘parent beach’. In contrast, four decades ago, Christiansen (1971) observed recruits during spring (November and December) as well as the recruitment event in summer (March). This may be due to changes in the population structure of *M. mactroides* during the last four

decades; while Olivier and Penchaszadeh (1971) monitored three cohorts between 1968 and 1969, Herrmann (2009) detected only one cohort during 2005–2006.

In conclusion, only weak differences in the reproduction cycle and gonad development of *M. mactroides* between the present study and those of Christiansen (1971) were found. This could be due to the fact that recently just one cohort at one sandy beach was found (Herrmann 2009) and the beaches were dissimilar.

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