Population dynamics of the Argentinean surf clams *Donax hanleyanus* and *Mesodesma mactroides* from open-Atlantic beaches off Argentina

Populationsdynamik der Argentinischen Brandungsmuscheln *Donax hanleyanus* und *Mesodesma mactroides* offener Atlantikstrände vor Argentinien

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Dedicated to my family

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1 Summary

1.1 English Version

The surf clams *Mesodesma mactroides* Reeve, 1854 and *Donax hanleyanus* Philippi, 1847 are the two dominating species in macrobenthic communities of sandy beaches off northern Argentina, with the latter now surpassing *M. mactroides* populations in abundance and biomass. Before stock decimation caused by exploitation (during the 1940s and 1950s) and mass mortality events (1995, 1999 and 2007) *M. mactroides* was the prominent primary consumer in the intertidal ecosystem and an important economic resource in Argentina. Since *D. hanleyanus* was not commercially fished and not affected by mass mortality events, it took over as the dominant species, but did never reach the former abundance of *M. mactroides*. Currently abundance and biomass of both surf clams are a multiple smaller than those of forty years ago, indicating the conservation status of *D. hanleyanus* and *M. mactroides* as endangered. Therefore the aim of this study is to analyse the population dynamics (population structure, growth and reproductive biology) of *D. hanleyanus* and *M. mactroides*, and to compare the results with historical data in order to detect possible differences within surf clam populations forty years ago and at present.

Monthly quantitative sampling was carried out between December 2004 and December 2006 in the intertidal zone of Santa Teresita, Mar de las Pampas and Faro Querandí. All three sandy beaches display different exposures with contrasting morphodynamics and can be classified as sheltered-dissipative, exposed-intermediate and exposed-reflective, respectively. While *D. hanleyanus* inhabits all three beaches, *M. mactroides* was almost exclusively present at Santa Teresita. Whereas the latter is an endemic species to Argentina, living specimens of *D. hanleyanus* were first reported on Argentinean beaches in 1960, although fossils have been found from the Querandinense period in the early Holocene. Live individuals of *D. hanleyanus* measured between 3 and 40 mm and those of *M. mactroides* showed an anterior-posterior shell length (*apSL*) between 2 and 64 mm. Both surf clams were found associated with very few species and low abundance of other macrozoobenthic fauna. The gastropod *Olivancillaria vesica auricularia* was recorded as a

potential predator of both surf clam species especially in Santa Teresita. At Faro Querandí the American oystercatcher *Haematopus ostralegus* was observed feeding on *D. hanleyanus*.

Mean abundance of *M. mactroides* was recorded as 110 ind. m^{-2} and those of *D. hanleyanus* as 50 to 267 ind. m^{-2}. The abundance of the latter was linked to sand grain size. Highest abundance was recorded at the reflective beach Faro Querandí, which is characterised by coarse sediment. The decrease of *D. hanleyanus* in summer periods appears to be principally related to human activities.

The intertidal biomass of the surf clam populations ranged between 0.04 and 1.32 g shell-free ash-free dry mass (*AFDM*) $m^{-2}yr^{-1}$ (*D. hanleyanus*) and 0.06 to 0.07 g *AFDM* $m^{-2}yr^{-1}$ (*M. mactroides*). The individual production of *D. hanleyanus* revealed the highest value at 30 mm *apSL* (0.16 g *AFDM* $m^{-2} yr^{-1}$), with an individual production of *M. mactroides* of 0.35 g *AFDM* $m^{-2}yr^{-1}$ at 47 mm *apSL*. Annual production for *D. hanleyanus* ranged between 0.08 and 0.99 g *AFDM* $m^{-2}yr^{-1}$ and for *M. mactroides* between 0.12 and 0.19 g *AFDM* $m^{-2} yr^{-1}$, resulting in an annual renewal rate ($P/\bar{B}$) of 0.82-2.16 and 1.84-2.93, respectively. A review of the renewal rate of several *Donax* species revealed that the renewal rate increased with decreasing latitude from temperate to tropical regions.

Growth estimations based on length-frequency distributions (*LFD*s) confirmed that both surf clams are fast growing species (*D. hanleyanus*: $L_\infty = 44$ mm, $K = 0.46$-0.47 yr^{-1}; *M. mactroides*: $L_\infty = 71$ mm, $K = 0.47$ yr^{-1}), and both have a potential for aquaculture. Seasonally oscillating growth with slowest growth rates in austral autumn (*WP* = 0.45 ~ mid-May) were revealed for *D. hanleyanus* (*C* = 0.8) and weak seasonality with slowest growth rates occurring in austral winter (*WP* = 0.7 ~ mid-August) for *M. mactroides* (*C* = 0.1). Compared with growth studies from the 1970s, a slower growth of *D. hanleyanus* was estimated, but a higher maximum length was recorded. *M. mactroides* now grow faster but maximum length is lower. Life span of *D. hanleyanus* was calculated as 4.96-5.18 yrs, and that of *M. mactroides* was estimated at 6.19 yrs. Overall growth performance (*OGP*) indices of *D. hanleyanus* (*OGP* = 4.54-4.60) and *M. mactroides* (*OGP* = 5.23-5.24) resulting from estimated growth parameters showed values comparable with those of other temperate surf clams. The study showed that *OGP* is inversely correlated with the latitudinal distribution of Argentinean, Uruguayan and Peruvian *Mesodesma* populations.

For growth estimates of both surf clams tagging-recapture experiments using the *in situ* fluorescent marking (*IFM*) method and subsequent size-increment analyses were a useful alternative to conventional *LFD* analyses. The fluorescence marker 'calcein' produced clear marks in shells of *D. hanleyanus* and *M. mactroides*, emitting a bright green fluorescence band under blue light, which was readily distinguished from naturally occurring autofluorescence, even in low concentrations and short immersion times. Thus calcein is suitable as growth marker of short-term, high-resolution growth studies for both surf clams. Daily growth rates of *D. hanleyanus* ranged between 8 and 72 µm d^{-1} and those of *M. mactroides* between 1 and 70 µm d^{-1}. The relationship between final umbo-shell margin length ($umSL_2$) and daily growth rates was best described by exponential functions.

The reproductive biology of *M. mactroides* was studied at Santa Teresita, and of *D. hanleyanus* at all three study sites. The gametogenic cycle of the latter correlated significantly with sea surface temperature (*SST*), relative spermatozoon abundance (*RSA*), condition index (*CI*), *AFDM* and mean size and abundance of oocytes for all three populations. In line the annual reproductive cycle of *M. mactroides* also correlated with *SST*. Oocytes of *M. mactroides* showed highest abundance in winter, indicating a process of gonadal development and sexual maturation. Mean oocyte size decreased significantly in winter and late spring, suggesting spawning events. Annual recruitment patterns in summer-autumn indicate a three-months-long planktonic phase of *M. mactroides*. The habitat harshness hypothesis was tested, comparing population responses of *D. hanleyanus* with contrasting habitat morphodynamics. The reproductive phase was more extended in the reflective beach and males and females from the dissipative and intermediate beach were smaller and had lower biomass at maturity. Recruits were more abundant at the dissipative beach, where the recruitment period was also more extended. Spawning events took place twice each year at the dissipative (early spring and spring-summer) and the intermediate beach (winter and summer), whereas continuous gamete releases were noted at the reflective beach. Size and biomass at first maturity were lower at the dissipative beach.

In conclusion, although the commercial fishery of *M. mactroides* is closed since more than 50 years and extractions are still forbidden and *D. hanleyanus* is not used as a natural living resource yet, the strong decline of surf clam abundance and biomass within the last four decades implies that populations of the Argentinean *D. hanleyanus* and *M. mactroides* are in unstable conditions, due certainly to the increasing anthropogenic impact.

Future work should integrate sand grain size analyses and mass tourism data (human trampling) in studies of population dynamics of intertidal species, since the abundance of surf clams is principally related to these factors. Furthermore phytoplankton data such as biomass and species composition should be incorporated, as increasing chlorophyll *a* concentrations trigger the maturation of both surf clams. In order to answer the question where the surf clams migrate to during summer months, sampling in the lower sublittoral is recommended.

1.2 Deutsche Version

Die Brandungsmuscheln *Donax hanleyanus* Philippi, 1847 und *Mesodesma mactroides* Reeve, 1854 dominieren die Sandstrand-Makrobenthosgemeinschaften Nordargentiniens, wobei Abundanz und Biomasse von *D. hanleyanus* die von *M. mactroides* gegenwärtig übersteigt. Vor der durch Überfischung (während der 40er and 50er Jahre) and Massensterben (1995, 1999 und 2007) hervorgerufenen Bestandsdezimierung war *M. mactroides* der bedeutendste Primärkonsument im Ökosystem der Gezeitenzonen und eine ökonomisch wichtige Ressource in Argentinien. Da *D. hanleyanus* nicht kommerziell befischt wurde und auch nicht von Massensterben beeinträchtigt wurde, dominiert sie seitdem, erreichte jedoch nie die ehemaligen Abundanzen der *M. mactroides*-Populationen. Gegenwärtig sind die Bestände von *D. hanleyanus* und *M. mactroides* als gefährdet einzustufen, da Abundanzen und Biomassen beider Brandungsmuscheln um ein Vielfaches kleiner sind als noch vor vierzig Jahren. Ziel dieser Arbeit ist es daher, die Populationsdynamik (Populationsstruktur, Wachstum und Reproduktionsbiologie) von *D. hanleyanus* und *M. mactroides* zu analysieren und diese mit historischen Daten zu vergleichen, um mögliche Unterschiede zwischen Populationen vor vierzig Jahren und in der Gegenwart aufzudecken.

Monatlich wurden zwischen Dezember 2004 und Dezember 2006 Proben in der Gezeitenzone der Strände von Santa Teresita, Mar de las Pampas und Faro Querandí genommen. Die drei Sandstrände sind verschieden exponiert, durch eine unterschiedliche Morphodynamik geprägt und werden daher entsprechend als „geschützt-dissipativ“, „exponiert-intermediär“ und „exponiert-reflektierend“ klassifiziert. Während *D. hanleyanus* alle drei Strände besiedelt, kam *M. mactroides* fast ausschließlich in Santa Teresita vor. Letztere ist in Argentinien eine endemische Art. Von lebenden *D. hanleyanus* wurde erstmalig 1960 berichtet, obwohl Fossilien aus der „Querandinense-Periode“ im frühen Holozän bekannt sind. Die beprobten lebenden *D. hanleyanus* hatten eine „anterior-posterior“ Schalenlänge (*apSL*) von 3 bis 40 mm, *M. mactroides* von 2 bis 64 mm. Beide Brandungsmuscheln sind mit sehr wenig anderer Makrozoobenthosfauna assoziiert. Während der Gastropode *Olivancillaria vesica auricularia* speziell in Santa Teresita als potentieller Räuber beider

Muschelarten angesehen werden kann, frisst der Amerikanische Austernfischer *Haematopus ostralegus* in Faro Querandí auf jeden Fall *D. hanleyanus*.

M. mactroides erreichte mittlere Abundanzen von 110 Tieren pro Quadratmeter, während für *D. hanleyanus* Abundanzen zwischen 50 und 267 Tieren pro Quadratmeter gefunden wurden. Die Werte dieser Art sind an die Sandkorngröße gekoppelt. Höchste Abundanzen wurden daher am reflektierenden, durch grobes Sediment charakterisierten Strand Faro Querandí gefunden. Grund für den Rückgang von *D. hanleyanus* während der Sommermonate scheint hauptsächlich der Einfluss des Menschen zu sein.

Die Gezeitenbiomasse beider Brandungsmuscheln variiert zwischen 0,04 g und 1,32 g schalenfreier aschefreier Trockenmasse (*AFDM*) m^{-2}Jahr^{-1} für *D. hanleyanus* und zwischen 0,06 g und 0,07 g *AFDM* m^{-2}Jahr^{-1} für *M. mactroides*. Die individuelle Produktion von *D. hanleyanus* ist bei einer Schalenlänge (*apSL*) von 30 mm (0,16 g *AFDM* m^{-2}Jahr^{-1}) am größten, bei *M. mactroides* wurde ein maximaler Produktionswert von 0,35 g *AFDM* m^{-2} Jahr^{-1} bei einer Schalenlänge von 47 mm (*apSL*) erreicht. Die jährliche Produktion von *D. hanleyanus* schwankt zwischen 0,08 und 0,99 g *AFDM* m^{-2} Jahr^{-1} und die von *M. mactroides* zwischen 0,12 und 0,19 g *AFDM* m^{-2}Jahr^{-1}, wobei beide jeweils eine jährliche Erneuerungsrate ($P/\bar{B}$) von 0,82 bis 2,16 beziehungsweise von 1,84 bis 2,93 aufweisen. Ein Vergleich der $P/\bar{B}$-Raten verschiedener *Donax*-Arten zeigte, dass diese von gemäßigten zu tropischen Breiten steigen.

Wachstumsabschätzungen, die auf Längenhäufigkeitsverteilungen (*LFD*s) basieren, bestätigen, dass beide Brandungsmuscheln schnellwachsende Arten sind (*D. hanleyanus* $L_\infty = 44$ mm, $K = 0{,}46\text{-}0{,}47$ Jahr^{-1}; *M. mactroides*: $L_\infty = 71$ mm, $K = 0{,}47$ Jahr^{-1}) und deshalb potentiell für die Aquakultur geeignet wären. Saisonal wächst *D. hanleyanus* im australen Herbst (*WP* = 0,45 ~ Mitte-Mai) langsamer (*C* = 0,8), wohingegen *M. mactroides* (*C* = 0,1) nur sehr geringe jahreszeitliche Wachstumsschwanken im australen Winter (WP = 0,7 ~ Mitte-August) aufweist. Im Vergleich zu Wachstumsstudien von 1970 wächst *D. hanleyanus* langsamer, erreicht jedoch eine höhere Maximalgröße. Im Gegensatz dazu wächst *M. mactroides* gegenwärtig schneller, erreicht jedoch eine kleinere maximale Schalenlänge. *D. hanleyanus* hat rechnerisch eine Lebensdauer von 4,96 bis 5,18 Jahren und *M. mactroides* von 6,19 Jahren. Der

Gesamtwachstums-Performance-Index (*OGP*) von *D. hanleyanus* (*OGP* = 4,54-4,60) und *M. mactroides* (*OGP* = 5.23-5.24) zeigte mit denen anderer Brandungsmuscheln gemäßigter Breiten vergleichbare Werte. Diese Studie ergab, dass *OGP*-Daten negativ mit der Breitengradverteilung von *M. mactroides* aus Argentinien, Uruguay und Peru korrelieren.

Mit beiden Brandungsmuscheln durchgeführte Markierungs-Wiederfang-Experimente, nach *in situ* Fluoreszenz-Markierung (*IFM*) und anschließender Größenzuwachs-Analyse, haben sich als gute Alternative zur konventionellen *LFD*-Methode erwiesen. Der Fluoreszenzfarbstoff Calcein produziert eine in den Schalen von *D. hanleyanus* und von *M. mactroides* klar erkennbare Marke. Dabei wird selbst noch bei geringen Calcein-Konzentrationen und kurzen Immersionszeiten hellgrüne Fluoreszenz von blauem Licht emittiert, die sich eindeutig von der Autofluoreszenz der Schale unterscheidet. Daher ist Calcein als Wachstumsmarker für kurzzeitige, hochauflösende Wachstumsanalysen beider Brandungsmuscheln geeignet. Tägliche Wachstumsraten variieren zwischen 1 und 72 µm Tag^{-1}. Die Beziehung zwischen Umbo-Schalenrandlänge ($umSL_2$) und täglicher Wachstumsrate wird am besten mit einer exponentiellen Funktion beschrieben.

Die Reproduktionsbiologie von *M. mactroides* wurde in Santa Teresita, die von *D. hanleyanus* an den drei Stränden untersucht. In allen drei Populationen korreliert der Gametenzyklus von *D. hanleyanus* signifikant mit der Meeresoberflächentemperatur (*SST),* mit der relativen Spermatozoon-Abundanz (*RSA*), dem Konditionsindex (*CI*), mit *AFDM* und der mittleren Oozytengröße und -abundanz. Ebenso korreliert auch der Reproduktionszyklus von *M. mactroides* mit der *SST*. *M. mactroides*-Oozyten sind im Winter am häufigsten, was auf die Gonaden- und sexuelle Reifeentwicklung hindeutet. Mittelwerte von Oozytengrößen zeigen im Winter und späten Frühling einen deutlichen Abfall, vermutlich aufgrund von Laichereignissen. Rekrutierungsereignisse im Sommer-Herbst deuten auf eine dreimonatige Larvenphase von *M. mactroides* hin.

Der Vergleich von *D. hanleyanus*-Populationen von Stränden mit unterschiedlichen morphodynamischen Eigenschaften erlaubte die „Habitat-Harshness-Hypotese“ (HHH) zu testen. Am reflektierenden Strand war die Reproduktionsphase länger, am dissipativen und intermediären Strand waren männliche und weibliche Muscheln kleiner und wiesen geringere Biomassen auf. Junge Muscheln waren am dissipativen Strand mit ausgedehnterer Rekrutierungszeit häufiger. Laichereignisse wurden zweimal pro Jahr (früher Frühling und Frühling-Sommer) am dissipativen und intermediären Strand (Winter und Sommer) beobachtet, wohingegen Gameten am reflektierenden Strand kontinuierlich abgegeben wurden. Bei Eintritt der ersten Geschlechtsreife waren Größe und Biomasse am dissipativen Strand geringer.

Zusammenfassend lässt sich feststellen, dass der starke Brandungsmuschel-Rückgang (Abundanz und Biomasse) der letzen vier Jahrzehnte nicht aufgehalten werden konnte, obwohl *M. mactroides* seit mehr als 50 Jahren nicht mehr kommerziell befischt wird und die Extraktion dieser Art immer noch verboten ist, und obwohl *D. hanleyanus* nicht als natürliche Ressource genutzt wird. Die instabile Situation von *D. hanleyanus*- und *M. mactroides*-Populationen hat mit hoher Wahrscheinlichkeit mit dem wachsenden anthropogenen Einfluss zu tun.

Da die Abundanz von Brandungsmuscheln hauptsächlich von der Sandkorngröße und vom Massentourismus bestimmt wird, sollten künftige Forschungsarbeiten beide Faktoren in Untersuchungen der Populationsdynamik von Gezeitenarten aufnehmen. Des Weiteren sollten Biomasse und Artzusammensetzung des Phytoplanktons bekannt sein, da die Reife beider Brandungsmuscheln von der Chlorophyll *a*-Konzentration beeinflusst wird. Um die Frage beantworten zu können, wohin die Brandungsmuscheln in den Sommermonaten wandern, wird eine zusätzliche Probennahme im Sublitoral empfohlen.

1.3 Versión Español

Las almejas *Mesodesma mactroides* Reeve, 1854 y *Donax hanleyanus* Philippi, 1847 son especies dominantes en comunidades macrobentónicas de las playas arenosas en el norte de Argentina, donde actualmente predomina *D. hanleyanus* en abundancia y biomasa. Antes de la gran reducción poblacional causada por la pesquería (durante las décadas de los 1940 y 1950) y por eventos de mortalidad masiva (1995, 1999 y 2007), *M. mactroides* era una especie prominente en el intermareal, actuando como consumidor primario, y un recurso económico muy importante en Argentina. Dado que *D. hanleyanus* no era objeto de las pesquerías y no fue afectada por eventos de mortalidad masiva pasó a ser la especie dominante, aunque nunca alcanzó la abundancia inicial de *M. mactroides*. Actualmente, la abundancia y biomasa de estas especies son significativamente más bajas que las de cuarenta años atrás, provocando la designación de estas especies bajo el estatus de conservación “amenazado”. En consecuencia, este estudio tiene como objetivo analizar la dinámica poblacional, (estructura poblacional, crecimiento y biología reproductiva) de *D. hanleyanus* y *M. mactroides* y comparar los resultados con datos históricos para detectar posibles diferencias entre poblaciones de cuarenta años atrás y en el presente.

Se realizaron muestreos cuantitativos mensuales entre diciembre de 2004 y diciembre de 2006 en la zona intermareal en playas de Santa Teresita, Mar de las Pampas y Faro Querandí. Las tres playas arenosas muestran diferentes grados de exposición, con tipos morfodinámicos distintos. Estos pueden clasificarse como protegidos-disipativos, expuestos-intermedios y expuestos-reflectivos, respectivamente. Mientras *D. hanleyanus* habita en las tres playas mencionadas, *M. mactroides* habita casi exclusivamente en Santa Teresita. En contraste con *M. mactroides*, que es una especie endémica de Argentina, individuos vivos *D. hanleyanus* se reportaron por primera vez en playas argentinas en 1960, aunque se han encontrado fósiles del periodo Querandinense en el Holoceno temprano. Individuos vivos de *D. hanleyanus* midieron entre 3 y 20 mm y los de *M. mactroides* entre 2 y 64 mm de longitud anterior-posterior de la concha (*apSL*). Ambas almejas se encontraban asociadas con muy pocas especies, con baja abundancia, en la comunidad macrozoobentónica. Se registró el gasterópodo *Olivancillaria vesica auricularia* como predador potencial de las dos especies estudiadas, especialmente en Santa Teresita. En Faro Querandí se observó al "ostrero" *Haematopus ostralegus* alimentándose de *D. hanleyanus*.

La abundancia media de *M. mactroides* fue de 110 ind. m^{-2}, y la de *D. hanleyanus* de 50 a 267 ind. m^{-2}, la abundancia de esta última se encontró relacionada con el tamaño de grano de la arena. La mayor abundancia se registró en la playa reflectiva de Faro Querandí, que se caracteriza por sedimentos gruesos. La reducción de *D. hanleyanus* en verano parece estar relacionada, principalmente, con actividades humanas.

La biomasa de las dos almejas en la zona intermareal fluctuó entre 0,04 y 1,32 g de peso seco libre de concha y ceniza (*AFDM*) m^{-2}año^{-1} (*D. hanleyanus*) y entre 0,06 y 0,07 g *AFDM* m^{-2}año^{-1} (*M. mactroides*). La máxima producción individual de *D. hanleyanus* se encontró en individuos de 30 mm *apSL* (0,16 g *AFDM* m^{-2}año^{-1}), mientras que la máxima producción individual de *M. mactroides* fue 0,35 g *AFDM* m^{-2}año^{-1} a 47 mm *apSL*. La producción anual de *D. hanleyanus* fluctuó entre 0,08 y 0,99 g *AFDM* m^{-2}año^{-1} y la de *M. mactroides* entre 0,12 y 0,19 g *AFDM* m^{-2}año^{-1}, resultando en una tasa de renovación anual ($P/\bar{B}$) de 0,82-2,16 y 1,84-2,93, respectivamente. Una revisión de la tasa de renovación de varias especies de *Donax* mostró que ésta aumenta con la reducción de la latitud, desde regiones templadas hacia regiones tropicales.

El crecimiento, estimado a partir de distribuciones de frecuencias de longitudes (*LFDs*), mostró que ambas especies crecen rápidamente (*D. hanleyanus*: L_∞ = 44 mm, K = 0,46-0,47 año^{-1}; *M. mactroides*: L_∞ = 71 mm, K = 0,47 año^{-1}) y ambas tienen potencia para la acuacultura. En *D. hanleyanus* el crecimiento mostró estacionalidad (C = 0,8), la tasa más baja de crecimiento ocurrió en el otoño austral (WP = 0,45 ~ mediados de mayo). En contraste, *M. mactroides* mostró una estacionalidad débil; la tasa más baja ocurrió en el invierno austral (WP = 0,7 ~ mediados de agosto). En comparación con estudios en la década de los 1970s, el crecimiento estimado de *D. hanleyanus* fue más lento, aunque se registró una mayor longitud máxima. Actualmente, *M. mactroides* crece más rápido, aunque la longitud máxima es menor. La esperanza de vida de *D. hanleyanus* fue 4,96 – 5,18 años y la de *M. mactroides* fue 6,19 años. En general, el índice de eficiencia del crecimiento (*OGP*) de *D. hanleyanus* (*OGP* = 4,54-4,60) y *M. mactroides* (*OGP* = 5,23-5,24) calculado a partir de los parámetros de crecimiento estimados en este estudio, mostró valores comparables con los de otras almejas de regiones templadas. Este estudio indica que el *OGP* está inversamente correlacionado con la latitud en poblaciones de *Mesodesma* en Argentina, Uruguay y Perú.

El método de estimación del crecimiento por marcaje fluorescente *in situ* (*IFM*) y el análisis posterior de incrementos de tallas resultó ser una alternativa útil a los análisis convencionales de distribuciones de frecuencias de longitudes (*LFD*). La calceina, como marcador fluorescente produjo marcas claras en conchas de *D. hanleyanus* y *M. donacium,* emitiendo una banda verde brillante fluorescente bajo luz azul, la cual se puede distinguir claramente de la autofluorescencia natural, aún en bajas concentraciones y después de periodos de inmersión cortos. Entonces, la calceina es un marcador de crecimiento adecuado en estudios de corta duración y de alta resolución para el caso de estas almejas. La tasa diaria de crecimiento de *D. hanleyanus* fluctuó entre 8 y 72 µm d^{-1} y la de *M. mactroides* entre 1 y 70 µm d^{-1} y la relación entre la longitud final umbo-margen ($umSL_2$) y las tasas de crecimiento diario se ajustaron a un modelo exponencial.

La biología reproductiva de *M. mactroides* se estudió en Santa Teresita, y la de *D. hanleyanus* en los tres sitios de estudio. El ciclo gametogénico de esta última mostró una correlación significativa con la temperatura superficial del mar (*SST*), la abundancia relativa de espermatozoos (*RSA*), el índice de condición (*CI*), *AFDM* y la talla media y abundancia de oocitos en las tres poblaciones. Similarmente, se encontró una correlación significativa entre el ciclo reproductivo anual de *M. mactroides* y la *SST*. La mayor abundancia de oocitos de *M. mactroides* fue mayor en invierno, indicando un proceso de desarrollo gonadal y maduración sexual. La talla media de los oocitos disminuyó significativamente en invierno y finales de primavera sugiriendo eventos de desove. Los patrones anuales de reclutamiento en verano-otoño indicaron una fase de vida planctónica de tres meses para *M. mactroides*. Se evaluó la hipótesis de rigurosidad del hábitat, comparando las respuestas poblacionales de *D. hanleyanus* en hábitats con morfodinámicas distintas. La fase reproductiva tuvo mayor duración en la playa reflectiva, y los machos y hembras de las playas disipativas e intermedias fueron más pequeños y tuvieron una menor biomasa en edad de madurez sexual. Los reclutas fueron más abundantes en la playa disipativa, donde el periodo de reclutamiento también fue más largo. Se detectaron dos eventos de desove al año en la playa disipativa (al inicio de primavera y entre primavera y verano) y en las intermedias (invierno y verano), mientras que en la playa reflectiva se observó una evacuación continua de gametos. La talla y biomasa en edad de madurez fueron inferiores en la playa disipativa.

En conclusión, aunque la pesquería comercial de *M. mactroides* está vedada hace más de 50 años y las extracciones artesanales aún están prohibidas y *D. hanleyanus* no es usado como recurso pesquero aún, la fuerte reducción de la abundancia y biomasa de estas almejas en las cuatro últimas décadas implican que las poblaciones de *D. hanleyanus* y *M. mactrodes* en Argentina se encuentran en una condición inestable, debido muy probablemente al incremento del impacto antropogénico.

Futuros trabajos deberían integrar análisis granulométricos y datos sobre el turismo masivo (human trampling) en estudios de dinámica poblacional de especies intermareales, dado que la abundancia de estas almejas se relaciona principalmente con estos factores. Además, se deberían incorporar datos sobre la biomasa y composición de especies del fitoplancton, ya que el incremento de la concentración de clorofila *a* gatilla la maduración de ambas especies. Para responder la pregunta de donde migran estas almejas durante los meses de verano, es recomendable realizar muestreos también en el sublitoral.

2 Introduction

2.1 Sandy Beach Ecosystems

The world's open coastlines are dominated by almost 70 % of sandy beaches (Bascom 1964; McLachlan and Brown 2006), at which 39 % of the global human population are living (within 100 km from the coast, CIESIN 2000). Exposed sandy beaches are one of the most dynamic environments, where sediment is being constantly moved by waves, winds, and tides (McLachlan and Brown 2006). Previous investigations have demonstrated the influence of biological parameters (e.g. Defeo *et al.* 1992b; Defeo and de Alava 1995; Defeo 1996b), as well as humans (e.g. Defeo 1998; Brazeiro and Defeo 1999), on the dynamics of populations and communities. However, physical parameters, mainly wave energy and particle size, are suggested as the main factors controlling the responses of the macrofaunal populations and communities (McLachlan *et al.* 1995a; McLachlan *et al.* 1996a). Short and Wright (1983) developed a classification system of beach types (dissipative, intermediate and reflective) and McLachlan (1980) a rating scale for beach exposure (very sheltered, sheltered, exposed and very exposed). Both rating systems were used for a variety of previous studies investigating sandy beaches with contrasting morphodynamics (e.g. Souza and Gianuca 1995; Calliari *et al.* 1996; Gómez and Defeo 1999; Ricciardi and Bourget 1999; Jaramillo *et al.* 2000; Nel *et al.* 2001; Veloso and Cardoso 2001; de la Huz *et al.* 2002; Defeo and Martínez 2003; Laudien *et al.* 2003a; Brazeiro 2005; Celentano and Defeo 2006; Delgado and Defeo 2007b; Schlacher and Thompson 2008) and applied in the present work to characterises the study sites (see part 'Material and Methods', page 28).

Due to the ability to absorb wave energy, sandy beaches are one of the most debitable types of dynamic coastlines. The wave energy is used in driving surf-zone water movement, which transports sand offshore during storms and moves it back onshore during calms. Sandy beaches are greatly influenced by the transport of sand not only driven by waves but also by wind in the backshore and dunes. Most of the global sandy beaches are naturally backed by dunes (before the human influence, e.g. constructions in coastal dunes) and interact with them by supplying or receiving immense volumes of sand. Thus, sandy beaches are extremely dynamic environments where both mass of sand and water, are always on the move (Komar 1998; Short 1999). Furthermore, the sandy beach ecosystem is characterized by sediment grains, which define the pore space between sediment particles. This so-called interstitial system is important as a habitat for organisms and for the filtration of seawater. The interstitial environment of sandy beaches is mainly controlled by the factors grain size, sorting, shape, packing, porosity, pore size and permeability (McLachlan and Turner 1994).

The intertidal of sandy beaches is normally devoid of macroflora so that the microflora and detritus attain an important significance as a food resource for specimens living in this type of environment. The sandy beach flora is usually composed of benthic microalgae and surf-zone phytoplankton, both of which are regularly dominated by diatoms. Although surf clams are commonly the main primary consumers in soft bottom communities, and can contribute up to 95 % of the total biomass (McLachlan *et al.* 1981; Arntz and Fahrbach 1991; Ieno and Bastida 1998), sandy beaches are inhabited by most phyla of invertebrates as interstitial forms or as members of the macrofauna, or both.

2.2 The Wedge Clam

2.2.1 Distribution

The intertidal wedge clam *Donax hanleyanus*[1] Philippi, 1847 (Bivalvia: Donacidae) (Fig. 2), also known under the Spanish synonym ‘berberecho’, is common in the intertidal along the South American Atlantic coast from tropical (17°S Caravelas, Brazil) to temperate regions (37°S Punta Mogotes in Mar del Plata, Province of Buenos Aires, Fig. 5b) (Penchaszadeh and Olivier 1975; Narchi 1978; Cardoso and Veloso 2003). The eurytopic and superficially burrowing (mainly 3-5 cm deep) *D. hanleyanus* is capable of inhabiting beaches of all morphodynamic types (*sensu* Short and Wright 1983), from steep, reflective beaches with coarse sands (Veloso *et al.* 1997) to flat, dissipative

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[1] *D. hanleyanus* reference specimens were deposited in the collection of the ‘Museum für Naturkunde der Humboldt-Universität zu Berlin’ under the reference number ZMB/Moll.104642.

beaches with fine sands (Penchaszadeh and Olivier 1975; Defeo and de Alava 1995). In the Argentinean sublittoral the wedge clam represents the only *Donax* species; it co-occurs negatively correlated with the yellow clam *M. mactroides* (Olivier *et al.* 1971; Penchaszadeh and Olivier 1975). Negative correlations between the abundance of *D. hanleyanus* and co-occurring filter feeders *M. mactroides* and *E. brasiliensis*, respectively, were also observed at Uruguayan (Defeo and de Alava 1995) and Brazilian sandy beaches (Cardoso and Veloso 2003).

As is characteristic of donacids, this bivalve has adapted to life in exposed swash zones characterized by a fair amount of wave action aerating the sediment. This keeps organic detritus in suspension and allows for tidal migration (Mori 1938; Ansell and Trevallion 1969; Penchaszadeh and Olivier 1975; Narchi 1978; Ansell 1983). Vertical distribution patterns of temperate *D. hanleyanus* appear to be different from other tropical and subtropical *Donax* species. Whereas for example *D. incarnatus* from India (Ansell and Trevallion 1969) and *D. trunculus* from Algeria (Mouëza 1972) keep their position relative to the swash zone during tides, *D. hanleyanus* shows an intensive migration to the upper intertidal during high tides (Penchaszadeh and Olivier 1975).

The variability in physical factors is unrelated to temporal abundance fluctuations of the wedge clam but not to its geographical distribution. Penchaszadeh and Olivier (1975) determined that the constitution of sediments is one of the principle factors affecting the distribution of *D. hanleyanus*. It is remarkable that fossil findings in South America indicate that *D. hanleyanus* was a very common species during the Querandinense period of the early Holocene (von Ihering 1907; Camacho 1966; Martinez and del Río 2005), but living specimens of *D. hanleyanus* were reported not earlier than 1960 from the Argentinean coast (de Castellanos and Fernández 1965; Penchaszadeh and Olivier 1975), from Brazil in 1949 (Lange de Morretes 1949) and from Uruguay in 1951 (Barattini 1951). It is expected that planktonic larvae of *D. hanleyanus* had to cut across the Río de la Plata with favourable ocean currents and to settle on sandy beaches south of this estuary (de Castellanos and Fernández 1965; Penchaszadeh and Olivier 1975).

2.2.2 Biology and Ecological Role

D. hanleyanus is bisexual, the sex ratio does not differ from 1:1 (Penchaszadeh and Olivier 1975; Gil and Thomé 2004a; Delgado and Defeo 2007b). In common with other intertidal suspension feeding invertebrates *D. hanleyanus* plays an important role in the food web by linking benthic and planktonic ecosystems (Wade 1967a; McLachlan *et al.* 1981; McLachlan and Lewin 1981; McDermott 1983; DeLancey 1989; Heymans and McLachlan 1996; Soares *et al.* 1997). The wedge clam is the main primary consumer and is in turn subject to predators such as the gastropods *Olivancillaria vesica auricularia* and *Buccinanops duartei* (Marcus and Marcus 1959; Gianuca 1985; Rocha-Barreira de Almeida 2002), demersal fish such as the black drum (*Pogonias cromis*, 'corvina negra'), the white croaker (*Micropogonias furnieri*, 'corvina rubia'), the jewsharp drummer (*Menticirrhus martinicensis*, 'corvina de perita' or 'burriqueta') and seabirds such as the American oystercatcher *Haematopus ostralegus* (Olivier *et al.* 1971; Penchaszadeh and Olivier 1975; Cousseau and Perrotta 2000).

2.2.3 Population Dynamics

D. hanleyanus has two spawning periods (August-September and January-February) with two corresponding periods of recruitment (October-November and February-March) (Penchaszadeh and Olivier 1975). Furthermore, the authors reported that wedge clams are sexually differentiated at the age of two (males) and four months (females) and no period of complete gonadal inactivity was found. Population dynamic aspects of *D. hanleyanus* vary somehow between populations within its distribution area (Penchaszadeh and Olivier 1975; Defeo 1996; Cardoso and Veloso 2003). Wedge clams grew faster in Argentina ($K = 1.18$ yr^{-1}) in the 1970s than presently in Uruguay ($K = 0.80$ yr^{-1}) and Brazil ($K = 0.80$ yr^{-1}) and reach the smallest maximum length in the northern limits of their distribution (33.5 mm; 30.0 mm and 26.4 mm, respectively). Previous investigations demonstrated that the growth of *D. hanleyanus* is subject to moderate seasonality ($C = 0.8$) with slowest growth rates between March and May ($WP = 0.25$-0.4). The longevity of this species was estimated for the Brazilian populations to be 1.5 yrs (Cardoso and Veloso 2003) and for the Argentinean one 3 yrs (Penchaszadeh and Olivier 1975) with a mortality ranging between 1.55 and 1.70.

2.2.4 Fishery

Fig. 1: Shell free *D. hanleyanus* (**a**) and *M mactroides* (**b**) offered by a supermarket in Buenos Aires (Argentina) for approximate 9 € (34.90 Argentinean Pesos) and 10 € (39.90 Argentinean Pesos) per kilo, respectively, even though extractions are forbidden, as indicated by large prohibition signs at tourist destinations at the coast of Buenos Aires (**c**).

Although globally several *Donax* clams such as *D. denticulatus* and *D. striatus* in the Caribbean, *D. trunculus* in Europe, *D. serra* in Africa, *D. cuneatus* and *D. faba* in Asia, and *D. deltoides* in Australia are targeted by commercial and artisanal fisheries (McLachlan *et al.* 1996b), *D. hanleyanus* is not commercially exploited yet in Argentina, but is used as bait for the recreational fishery. The wedge clam is edible and tasty (Veloso *et al.* 1953; Penchaszadeh and Olivier 1975) and offered occasionally in grocery stores (Fig. 1a). However, this species is generally not used as a food resource in Argentina, very probably due to the relatively cheap and very high quality beef.

2.2.5 Systematic Classification

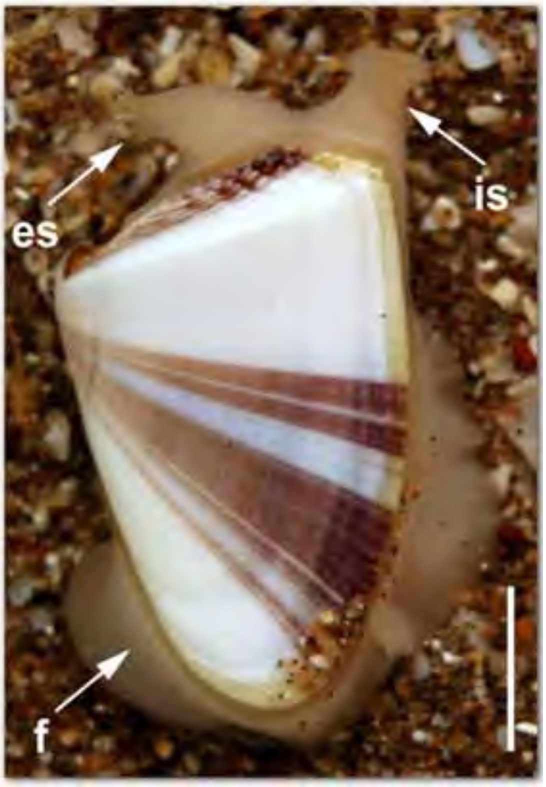

Fig. 2: Argentinean wedge clam *D. hanleyanus* (*apSL* = 35 mm) collected at Faro Querandí, *arrows*: exhalant siphon (**es**), inhalant siphon (**is**) and foot (**f**), *scale bar*: 10 mm.

Table 1: Taxonomic hierarchy of the wedge clam *D. hanleyanus*.

Taxonomic hierarchy	
Species	*Donax hanleyanus* Philippi, 1847
Genus	*Donax* Linnaeus, 1758
Family	DONACIDAE Fleming, 1828
Super Family	TELLINOIDEA Blainville, 1814
Order	VENEROIDA H. Adams and A. Adams, 1856
Subclass	HETERODONTA Neumayr, 1884
Class	BIVALVIA Linnaeus, 1758
Phylum	MOLLUSCA Linnaeus, 1758
Kingdom	ANIMALIA Linnaeus, 1758

On a global basis, the family Donacidae (super family Tellinoidea) form by far the most diverse group, inhabiting highly dynamic sandy beach ecosystems, integrating the genera *Egeria*, *Iphigenia* and *Donax*, with the latter group being composed of 64 species (Pearse *et al.* 1942; Ansell 1983; Brown and McLachlan 1990; Wilson 1999). In some cases, the latter dominate the macrozoobenthic communities in number and biomass (> 95 %: McLachlan *et al.* 1981; Arntz and Fahrbach 1991; Ieno and Bastida 1998). Most well-known *Donax* species are included in the geographical distribution map (Fig. 5b).

2.3 The Yellow Clam

2.3.1 Distribution

The yellow clam *Mesodesma mactroides*[2] Reeve[3], 1854 (Bivalvia: Mesodesmatidae) (Fig. 3), also known under the Spanish synonym 'almeja amarilla', is distributed along the warm-temperate Atlantic coast of South America, from Ilha Grande (23°S, Rio de Janeiro State, Brazil) to Isla del Jabalí[4] (40°S, Province of Buenos Aires, Argentina, Fig. 5b) (Olivier and Penchaszadeh 1968b; 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. The native yellow clam is the only *Mesodesma* species that is distributed in the intertidal of north Argentina (Parodiz 1942; Stuardo 1964), where it co-occurs with the sympatric wedge clam *D. hanleyanus* (Olivier *et al.* 1971; Penchaszadeh and Olivier 1975). *M. mactroides* populations are primarily abundant in the intertidal zone of dissipative beaches (*sensu* Short and Wright 1983), which are characterized by gentle slope, fine sand and heavy wave action (Olivier *et al.* 1971; Defeo 1985; Defeo *et al.* 1986). A decreasing trend of yellow clam abundances was observed by Defeo *et al.* (1986) near estuarine zones or freshwater discharges and on sheltered beaches (Defeo *et al.* 1992b). Furthermore, a reduction of the stock is provoked by freshwater inflows, coarser and poorly sorted sands and the dominance of erosional processes (McLachlan *et al.* 1996b). Intertidal and vertical *M. mactroides* distributions diverge seasonally (Coscarón 1959; Olivier *et al.* 1971). Whereas in winter specimens are mainly found 30-40 cm deep in the sediment and below the swash zone, in summer this species populates the beach close to the sediment surface and above the swash zone. No clear distributional pattern can

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[2] *M. mactroides* reference specimens were deposited in the collection of the 'Museum für Naturkunde der Humboldt-Universität zu Berlin' under the reference number ZMB/Moll.104643.

[3] In previous studies Deshayes 1854 was cited spuriously 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 1854 (see Reeve 1854; Deshayes 1855).

[4] Seven single adult specimens were found in February 1970 at the sandy beach of Las Grutas (Fig. 5a), south of Isla del Jabalí (Olivier and Penchaszadeh 1971a).

be observed in spring and autumn. Furthermore, *SST* and correlated factors (e.g. chlorophyll *a* concentration, gonadal development) appear to be important in determining the intertidal distribution and depth stratification of *M. mactroides* adults (Coscarón 1959; Olivier *et al.* 1971). Recruits are mainly abundant in the upper intertidal (Defeo 1985; Defeo *et al.* 1986; Bergonci and Thomé 2008). The zonation within the population indicates that distinct ontogenetic stages of *M. mactroides* selectively populate their desired microhabitat (Coscarón 1959; Olivier *et al.* 1971).

2.3.2 Biology and Ecological Role

M. mactroides populations at Argentinean (Christiansen 1971) and Uruguayan sandy beaches (Defeo 1985) demonstrated a 1:1 sex ratio and two spawning periods per year: one between October and December and another from February to April. Spawning events occur when *SST* is close to 20°C, which indicates that the gonadal development is triggered by *SST*. The mean size at first maturity was determined as 43 mm (1986). Recruits appear in the intertidal zone from January to May in Uruguay (Masello and Defeo 1986) and from November to December and in March at the Argentinean coast (Christiansen 1971). *M. mactroides* is described as a suspension feeder (Coscarón 1959; Olivier *et al.* 1971; Narchi 1981; Gianuca 1983; Defeo 1985), but laboratory and field observations demonstrated that it also has a deposit feeding mechanism (Defeo and Scarabino 1990). *M. mactroides* has the same predators as *D. hanleyanus* (see 2.2.2).

2.3.3 Population Dynamics

Recruitment events of *M. mactroides* appear to be ‘stock-dependent’. Whereas populations of a moderately low abundance with medium sized specimens generated maximum recruitment, populations of highly abundant adult specimens produced extremely low recruitment, probably caused by filtering larvae out of the water by the adult stock (Defeo 1993). *M. mactroides* is also a fast-growing species (K = 0.3-0.9 yr^{-1}; Capezzani *et al.* 1971; Defeo *et al.* 1992a; Defeo *et al.* 1992c; Fiori and Morsán 2004). At Uruguayan beaches maximum length is 75-100 mm (Defeo *et al.* 1992a; Defeo *et al.* 1992c) and off Argentina 80-85 mm (Carcelles 1939; Capezzani *et al.* 1971). Strong seasonal variation in the growth rate was found for an Uruguayan population (C = 1.0: Defeo *et al.* 1992c), whereas the Argentinean populations demonstrated low (C = 0.45: Fiori and Morsán 2004) or no seasonality (Capezzani *et al.* 1971). The longevity and morality of *M. mactroides* is controversially discussed. Whereas for Argentinean *M. mactroides* Olivier *et al.* (1971) estimated a maximum age of ~ 8 yrs and a relatively low mortality ($Z = 0.85\ \mathrm{yr}^{-1}$), Defeo *et al.* (1988a) suggested a life span of ~ 3.5 yrs with a mortality ranging between 2.26 and 2.91 for Uruguayan *M. mactroides* populations.

2.3.4 Fishery

In Argentina *M. mactroides* was an important economic resource during the 1940s and 1950s. However, after a maximum exploitation of 1,079 tons the yellow clam stock crashed and the commercial fishery had to be closed in 1956 (Coscarón 1959; Olivier and Penchaszadeh 1968a). To date, even with the fishery closed, the stock has diminished due to illegal extraction (Fig. 1b) (Bastida *et al.* 1991; Bastida *et al.* 1996; Mabragaña 1997). Information on the fishery of *M. mactroides* in Brazil is scarce. However, here yellow clams are consumed and used as bait (Gianuca 1983). In Uruguay, *M. mactroides* constitutes an important artisanal fishery. Yellow clams are collected by hand-gathering techniques and marketed either as bait or for human consumption, mainly during the tourist season (McLachlan *et al.* 1996b).

2.3.5 Systematic Classification

Fig. 3: Yellow clam *M mactroides* (*apSL* = 55 mm) collected at Santa Teresita, *arrows*: exhalant siphon (**es**), inhalant siphon (**is**) and foot (**f**), *scale bar*: 10 mm.

Table 2: Taxonomic hierarchy of the yellow clam *M. mactroides*.

Taxonomic hierarchy	
Species	*Mesodesma mactroides* Reeve, 1854
Genus	*Mesodesma* Deshayes, 1832
Family	MESODESMATIDAE Gray, 1839
Super Family	MACTROIDEA Lamarck, 1809
Order	VENEROIDA H. Adams and A. Adams, 1856
Subclass	HETERODONTA Neumayr, 1884
Class	BIVALVIA Linnaeus, 1758
Phylum	MOLLUSCA Linnaeus, 1758
Kingdom	ANIMALIA Linnaeus, 1758

The family Mesodesmatidae (super family Mactroidea) comprises the genera *Atactodea*, *Donacilla*, *Mesodesma*, *Monterosatus* and *Paphies*. The few species within these genera inhabit coastal sandy beaches from the intertidal to shallow water. Besides *M. mactroides*, the Chilean and Peruvian *M. donacium* (e.g. Arntz *et al.* 1987; Seijo *et al.* 2004; Riascos *et al.* 2008) and the New Zealand species *Paphies ventricosa* (Rapson 1954; Cassie 1955; Redfearn 1974; Stace 1991) and *P. subtriangulata* (Greenway 1981; Redfearn 1987; Haddon 1988; McLachlan *et al.* 1996b) are important for the ecosystem and for recreational or commercial fisheries. In addition to *M. mactroides* from the present study (Fig. 3, Table 2), only of a small number of *Mesodesma* species biological information is available. The most well-known ones are marked in the geographical distribution map (Fig. 5b).

2.4 Aims

The aim of this study was to investigate the population dynamics of the Argentinean surf clams *D. hanleyanus* and *M. mactroides* from open-Atlantic beaches off Argentina. In this frame a combination of five subjects was studied by investigating the corresponding objectives as illustrated in Fig. 4.

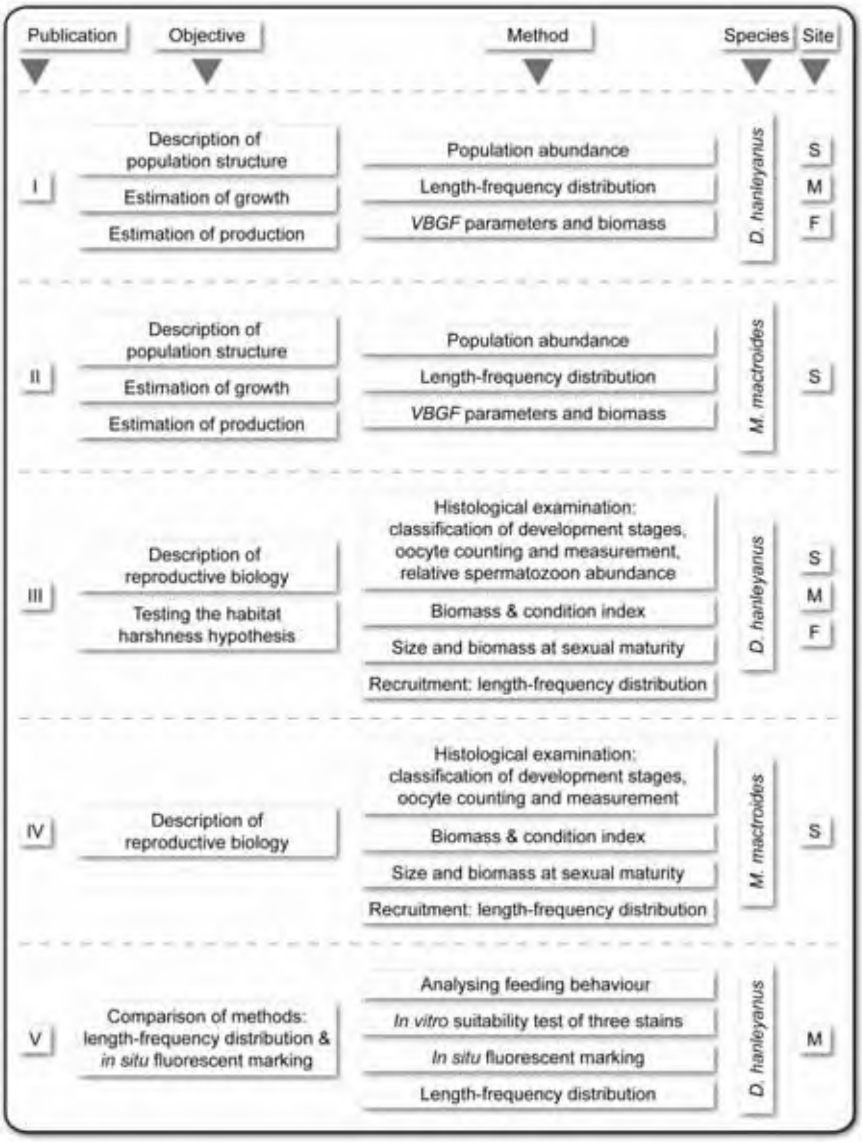

Fig. 4: Summary of methods used during this study for achieving a specific objective studied from the two Argentinean surf clams *D. hanleyanus* and *M. mactroides* inhabiting different study sites (**S**: Santa Teresita, **M**: Mar de las Pampas and **F**: Faro Querandí). Respectively publication numbers are given.

3 Materials and Methods

3.1 Study Sites

Argentina has a 6,816 km long coast line[5] (Diez 2008) populated by above average numbers of humans (45.1 %, measured by the world population living in coastal areas, CIESIN 2000). The population dynamics of both surf clams were studied during alternate spring tides at (i) the beach Santa Teresita (36°32'S, 56°41'W), which is heavily influenced by mass tourism during the summer season (> 1,000 tourists 100 m^{-1} coastline), (ii) the beach Mar de las Pampas (37°19'S, 57°00'W), which is marginally influenced by humans (< 10 tourists 100 m^{-1} coastline), and (iii) the beach Faro Querandí (37°29'S, 57°07'W), which is unaffected by humans (< 0.01 angler 100 m^{-1} coastline) and naturally protected (pers. observ., Fig. 5b, Fig. 6). All three open ocean beaches are located on the 1,949 km long, mainly sandy, coast of the Province of Buenos Aires (Diez 2008) and are linked to each other with a north-south shoreline orientation, which is stable on a long term basis (Marcomini and López 1993). According to McLachlan`s (1980) scale for rating exposure and Short and Wright's (1983) classifications of beach types, Santa Teresita is sheltered/dissipative, Mar de las Pampas exposed/intermediate, and Faro Querandí exposed/reflective (Fig. 6), composed of fine, medium and coarse sands with a mean particle diameter of 0.21 mm, 0.37 mm and 0.48 mm, respectively ('Publication I', page 79). All three beaches are, however, exposed to continuous wave action and subject to semidiurnal tides with a maximum tidal range of 1.6 m (springs tide mean 1.7 m, neaps 0.2 m). They all are affected by freshwater seepage due to the Brazil Current bringing water masses of the large-scale Río de la Plata estuary (Guerrero *et al.* 1997; Acha *et al.* 2008; Möller Jr *et al.* 2008). The salinity ranges between 31 and 34. The mean *SST* (± SE) varies between 11 ± 0.14°C in winter and 23 ± 0.21°C in summer. A full characterization of all beaches is summarised in Table 3.

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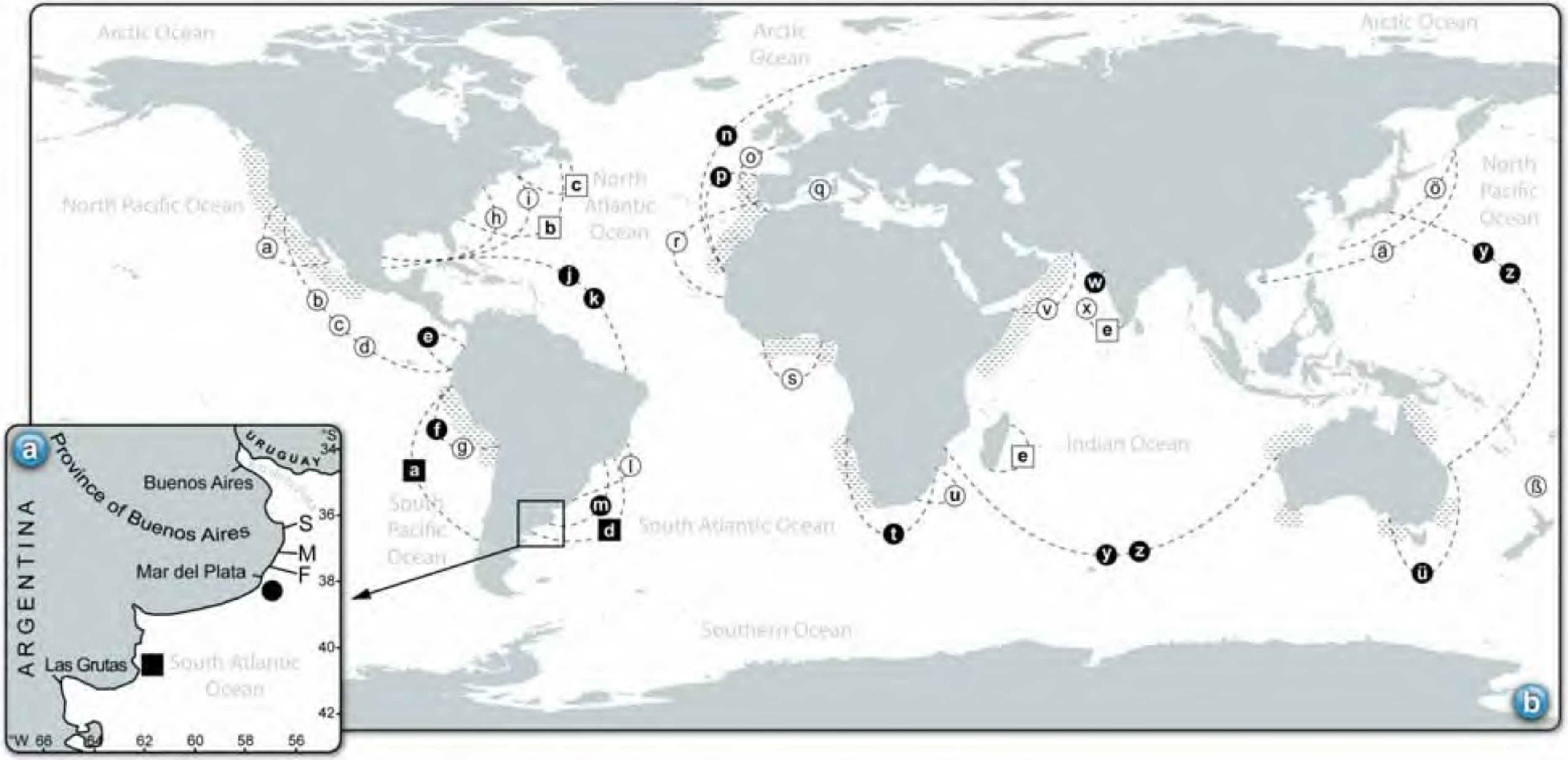
[5] Previous investigations of the Argentinean Navy and the Argentinean Military Geographical Institute measured the coast of Argentina erroneously with 4,725 km and 5,087 km, respectively, but recently advanced high-resolution measurements demonstrated that it is 2,000 km longer (Diez 2008).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Buenos Aires
URUGUAY
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ARGENTINA
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Arctic Ocean
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Fig. 5a: Map of the three study sites Santa Teresita (**S**), Mar de las Pampas (**M**) and Faro Querandí (**F**) at the Argentinean Atlantic coast, indicating respectively the southernmost distribution of *D. hanleyanus* at Punta Mogotes, south of Mar del Plata (●) and of *M. mactroides* at Isla del Jabalí (■). **Fig. 5b:** Geographical distribution of thirty selected donacids and five mesodesmatids of which scientific publications are available. From this, population dynamic data were found published of twelve *Donax* and two *Mesodesma* species (marked black with white letters, for sources see Table 5 and Table 6, respectively), used in this study for comparisons of growth parameters. Major coastal upwelling regions of the World Oceans are figured as dotted fields (modified from Mittelstaedt 1986). **Donacidae** (○,●): **a**: *D. gouldii* (Hoffman *et al.* 2006), **b**: *D. carinatus* (Paredes and Cardoso 2001), **c**: *D. panamensis* (Garcés B. 1993; d' Croz *et al.* 1994), **d**: *D. punctatostriatus* (Coan 1983; Cartron *et al.* 2005), **e**: *D. dentifer* (Palacios *et al.* 1983; Riascos 2006), **f**: *D. marincovichi*[6] (Huaraz and Ishiyama 1980; Mamani 1985; Arntz *et al.* 1987; Vakily 1992; Carbajal *et al.* 1995; Paredes and Cardoso 2001), **g**: *D. obesulus*[6] (Carbajal *et al.* 1995; Paredes and Cardoso 2001), **h**: *D. fossor* (Jacobson 1955; Chanley 1969a; Dougherty and Russell 2005), **i**: *D. variabilis* (Loesch 1957; Turner and Belding 1957; Chanley 1969b; a; Mikkelsen 1981; Leber 1982; Schneider 1982; Wolcott and Wolcott 1984; Mikkelsen 1985; Estes and Adamkewicz 1991; Bonsdorff and Nelson 1992; Nelson *et al.* 1993; Ellers 1995a; b; Adamkewicz and Harasewych 1996; Wilson 1999; Jones *et al.* 2004; Jones *et al.* 2005; Quitmyer *et al.* 2005), **j**: *D. denticulatus* (Wade 1967b; Wade 1968; Wade 1969; Trueman 1971; Farache 1980; Sastre 1984; Vélez *et al.* 1985; García *et al.* 2003; Marcano *et al.* 2003; Miloslavich *et al.* 2004), **k**: *D. striatus* (Wade 1967a; Farache 1980; Rajkumar *et al.* 1992; Matos *et al.* 1995; Rocha-Barreira de Almeida *et al.* 2002; Delgado *et al.* 2003), **l**: *D. gemmula* (Paes 1991; Passos and Domaneschi 2004), **m: *D. hanleyanus*** (Deshayes 1855; von Ihering 1907; Veloso *et al.* 1953; de Castellanos and Fernández 1965; Bertullo *et al.* 1967; Penchaszadeh and Olivier 1975; Narchi 1978; Méndez 1992; Defeo and de Alava 1995; Gil and Thomé 1998; 2000a; c; 2001a; c; b; Luzzatto and Penchaszadeh 2001; Marcomini *et al.* 2002; Cardoso and Veloso 2003; Gil and Thomé 2004b; a; Dadon 2005; Herrmann *et al.* 2006; Delgado and Defeo 2007b; Herrmann *et al.* 2008b; López *et al.* 2008; das Neves *et al.* 2008; Herrmann *et al.* under review-c; Herrmann *et al.* under review-d; Herrmann *et al.* under review-e), **n**: *D. vittatus* (Ansell 1972; Ansell and Sivadas 1973; Frenkiel and Mouëza 1979; Ansell *et al.* 1980a; Ansell and Lagardère 1980; Guillou and Le Moal 1980; Guillou 1982; Salas-Casanova 1987; Vakily 1992; Ansell 1994; Ansell *et al.* 1998; Ansell *et al.* 1999), **o**: *D. variegatus* (Ansell and Lagardère 1980; Hayward and Ryland 1990), **p**: *D. trunculus* (Ansell *et al.* 1980a; Ansell *et al.* 1980b; Ansell and Lagardère 1980; Guillou and Le Moal 1980; Bodoy 1982; Guillou 1982; Bayed and Guillou 1985; Mazé and Laborda 1988; Neuberger-Cywiak *et al.* 1990; Guillou and Bayed 1991; Sousa and Oliveira 1994; Ramon *et al.* 1995; Plohl and Cornudella 1996; Ruiz-Azcona *et al.* 1996; Plohl and Cornudella 1997; Voliani

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[6] Newest investigations resulted in that *D. marincovichi* and *D. obesulus* are one single species. At present the species name is not yet specified (pers. com. Daniel Carstensen, AWI-Bremerhaven, Germany).

et al. 1997; Bayed 1998; Tirado and Salas 1998; Fishelson *et al.* 1999; Gaspar *et al.* 1999; Lagbouri and Moukrim 1999; Ramon *et al.* 1999; Gaspar *et al.* 2002; de la Huz *et al.* 2002; Martínez *et al.* 2002; Zeichen *et al.* 2002; Petrović and Plohl 2005), **q**: *D. semistriatus* (Ansell *et al.* 1980a; Neuberger-Cywiak *et al.* 1990; Tirado and Salas 1999), **r**: *D. venustus* (Guillou and Bayed 1991; Tirado and Salas 1999), **s**: *D. oweni* (Longhurst 1957; Gofas *et al.* no date), **t**: *D. serra* (de Villiers 1975a; b; McLachlan and Hanekom 1979; Ansell 1981; Hodgson 1982; Donn 1986; Donn *et al.* 1986; Birkett and Cook 1987; Donn 1987; Maasdorp 1987; Salie 1987; Brown *et al.* 1989; Matthews *et al.* 1989; Cockcroft 1990; Donn 1990a; b; Donn and Els 1990; Schoeman 1994; Stenton-Dozey and Brown 1994a; b; c; Farquhar 1995; Lastra and McLachlan 1996; Soares *et al.* 1996; Soares *et al.* 1997; McLachlan 1998; Soares *et al.* 1998; Dugan and McLachlan 1999; Schoeman *et al.* 2000; Laudien *et al.* 2001; Laudien *et al.* 2002; Schoeman and Richardson 2002; Laudien *et al.* 2003a; Laudien *et al.* 2003b), **u**: *D. sordidus* (McLachlan 1979; Ansell 1981; Cockcroft 1990; McLachlan 1998), **v**: *D. townsendi*, **w**: *D. incarnatus* (Ansell *et al.* 1972; Nair *et al.* 1978; Mohan *et al.* 1986; Thippeswamy and Joseph 1991; Mathew and Menon 1992; Thippeswamy and Joseph 1992; Mathew and Menon 1993; 2004), **x**: *D. spiculum* (Ansell *et al.* 1972), **y**: *D. cuneatus* (Nayar 1955; Talikhedkar *et al.* 1976; Inouye 2000), **z**: *D. faba* (Alagarswami 1966; Hughes 1966; Smith 1975; Ansell 1985; Din and Abu 1992; Eshky and Ba-Akdhah 1992; Eshky 1998; Ong and Din 2001), **ä**: *D. kiusiuensis* (Yashiki 2002), **ö**: *D. semigranosus* (Mori 1938), **ü**: *D. deltoides* (King 1976; 1985; Saenger and Keyte 1990; Haynes *et al.* 1995; James and Fairweather 1995; Haynes *et al.* 1997; Murray-Jones and Ayre 1997; Murray-Jones and Steffe 2000; Ferguson and Mayfield 2006), **ß**: *D. pallidus*. **Mesodesmatidae** (□,■): **a**: *M. donacium* (Cepeda 1980; Rozbaczylo *et al.* 1980; Peredo *et al.* 1986; Arntz *et al.* 1987; Jaramillo *et al.* 1994; Pérez E. and Chávez V. 2004; Carré *et al.* 2005; Riascos *et al.* 2006a; Riascos *et al.* 2006b; Riascos *et al.* 2008), **b**: *M. arctatum* (Davis 1966; Allen 1975; Giguere and Lamoureux 1978; Merrill *et al.* 1978; Brêthes *et al.* 1986), **c**: *M. deauratum* (Hutcheson and Stewart 1994), **d:** ***M. mactroides*** (Coscarón 1959; Rapoport 1960; Olivier *et al.* 1971; Narchi 1981; Bastida *et al.* 1991; Bastida *et al.* 1996; Defeo 1996; Brazeiro and Defeo 1999; Fiori and Cazzaniga 1999; Lima *et al.* 2000; Fiori *et al.* 2004a; Fiori and Morsán 2004; Fiori *et al.* 2004b; Fiori and Defeo 2006; Thompson and Sánchez de Bock 2007; Bergonci and Thomé 2008; Herrmann *et al.* 2008a; Herrmann *et al.* under review-a; Herrmann *et al.* under review-b), **e**: *M. glabratum* (Maugé 1976; Bhargava *et al.* 1977; 1979; 1986; Rajan and Rajapandian 1988).

Fig. 6: Study sites Santa Teresita (**a**, **d** and **g**), Mar de las Pampas (**b**, **e** and **h**) and Faro Querandí (**c**, **f** and **i**) in summer (**a**, **b** and **c**) and autumn-spring (**d**, **e** and **f**) with contrasting beach morphodynamics (**g**, **h** and **i**) (modified from McLachlan and Brown 2006) and corresponding physical parameters (**P.**): (**Ω**) Dean's parameter, (H_b) wave height (m), (T) wave period (s), (M_s) mean slope of tidal, (M_z) mean grain size (mm) and (W) sand fall velocity (m s^{-1}). Sizes of letters indicate respective trends: large letters stand for high values of physical parameters and small ones for low values. *Arrows* in **c** indicate four wheel drive vehicles of some few recreational anglers at Faro Querandí during summer.

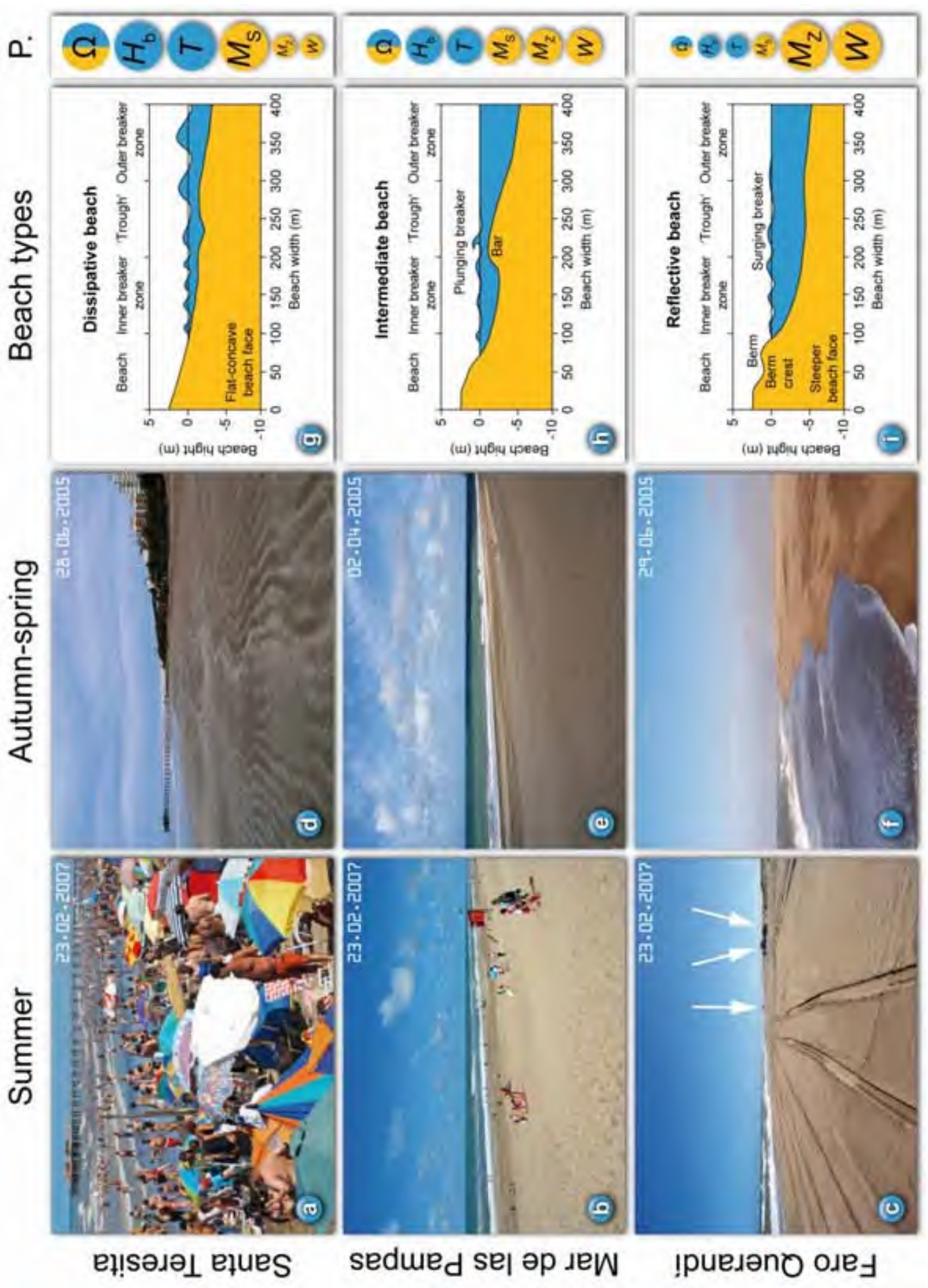
Summer
Autumn-spring
Beach types
P.
Santa Teresita
Mar de las Pampas
Faro Querandí
a
23·02·2007
b
23·02·2007
c
23·02·2007
d
28·06·2005
e
02·04·2005
f
29·06·2005
g
Dissipative beach
Beach
Inner breaker zone
'Trough'
Outer breaker zone
Flat-concave beach face
h
Intermediate beach
Beach
Inner breaker zone
'Trough'
Outer breaker zone
Plunging breaker
Bar
i
Reflective beach
Beach
Inner breaker zone
'Trough'
Outer breaker zone
Berm
Berm crest
Steeper beach face
Surging breaker
Beach hight (m)
5
0
-5
-10
Beach width (m)
0
50
100
150
200
250
300
350
400
Ω
H_b
T
M_S
M_z
W

Table 3: Characterization of physical and biological attributes of the three studied localities.

Beach features	**Santa Teresita**	**Mar de las Pampas**	**Faro Querandí**
Latitude	36°32'S	37°19'S	37°29'S
Longitude	56°41'W	57°00'W	57°07'W
Beach width (m)	< 80	< 70	< 100
Intertidal zone width (m)	< 70	< 60	< 60
Tidal range (m)	1.8	1.7	1.7
Mean grain size (phi/mm) ^{A}	2.26/0.21	1.43/0.37	1.05/0.48
Median grain size (phi) ^{A}	2.28	1.39	0.99
Sorting ^{A,B,C}	Good (0.36)	Moderate (0.68)	Moderate (0.51)
Skewness ^{A,B}	-0.11	+0.07	-0.11
Textural group ^{E}	Fine	Medium	Coarse
Mean slope of intertidal (%)	1/43	1/16	1/14
Exposure ^{D}	Sheltered	Exposed	Exposed
Morphodyn. type ^{E}	Dissipative	Intermediate	Reflective
Dean parameter (Ω) ^{F*}	1.92-2.53	1.50-1.86	3.28-3.93
D. hanleyanus belt (m)	30	12	10
Macrofauna richness (species)	5	3	3

Used methods after: ^{A} Flemming and Thum (1978) and after Flemming and Ziegler (1995), ^{B} Inman (1952), ^{C} McLachlan and Brown (2006), ^{D} McLachlan (1980), ^{E} Short and Wright (1983), ^{F} Dean (1973). * Calculated for specific seasonal *SST* from 9°C to 25°C.

3.2 Population Structure

3.2.1 Sampling and Laboratory Procedures

Quantitative sampling of both surf clams was carried out at monthly intervals (Santa Teresita and Mar de las Pampas: December 2004 to December 2006; Faro Querandí: March 2005 to December 2006) from a series of stations (4 m intervals). The latter were located 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 (40 x 40 cm) were excavated to 35 cm depth using a 0.16 m^2 steel corer, and thereafter sieved individually on a 1 mm mesh. The associated macrozoobenthic fauna was preserved in 70 % ethanol immediately after sampling. In the laboratory, organisms were identified to species level under a binocular microscope using classification literature for polychaetes (Orensanz 1974; Elías 2002) and isopods (Bastida and Torti 1973). For biomass analysis monthly subsamples of 35 randomly taken specimens from each of the three locations were stored in 70 % ethanol. Thereafter soft tissues were weighed to estimate shell-free wet mass (*SFWM*) after blotting on filter paper. Subsequently, samples were dried to a constant mass at 70°C, reweighed to determine shell-free dry mass (*SFDM*) and finally ignited in a muffle furnace at 550°C for 5 h in order to estimate *AFDM*.

3.2.2 Data Analyses

For the study of surf clam biomass and production, the relationships between length and biomass were estimated by regression analyses, total annual production (*P*) was calculated using mass-specific growth rates and annual biomass ($\bar{B}$) and annual renewal rates ($P/\bar{B}$) were evaluated. Methods are described in detail in 'Publication I' (page 79) and 'Publication II' (page 109), for *D. hanleyanus* and *M. mactroides* respectively.

3.2.3 Statistics

Spatial and temporal differences of surf clams abundance (one-way ANOVA) and the influences of *SST* and anthropogenic factors (Spearman`s rank order correlation) were analyzed using the statistical package SPSS version 16.0.1 (SPSS 2007). Differences were considered significant at a level of $\alpha = 5$ % (Zar 1999). The relationship between monthly mean abundance and mean grain size was analyzed through non-metric multi-dimensional scaling (nMDS), using square root transformed data and calculated Bray-Curtis similarities (PRIMER 2007) (e.g. Rumohr and Karakassis 1999; Jaramillo *et al.* 2001; Sousa *et al.* 2008). Correlation analysis was used to assess the relationships between renewal rate ($P/\bar{B}$ ratios) and latitude of surf clams compared with those of several *Donax* and *Mesodesma* species from other areas. The relation between the population abundance of *D. hanleyanus* and *M. mactroides* was estimated by linear regression analysis.

3.3 Growth Estimation

3.3.1 Sampling and Laboratory Procedures

Monthly sampling was carried out following a systematic design as in chapter 3.2.1 described. Maximum *apSL* (Fig. 7) of collected surf clams was measured to the nearest 0.1 mm with a digital vernier calliper (Mitutoyo, model 500-161U) to obtain monthly length-frequency distributions (*LFD*s). Growth rates of both surf clams were not only estimated from the indirect *LFD* analyses, but additionally from direct analyses of individual growth increments recorded after recapture following *in situ* fluorescent marking (*IFM*). In order to facilitate recapture stained surf clams were reared *in situ* in four replicated experimental cages (Fig. 8a, b) in the exposed intertidal zone of Mar de las Pampas. During a period of seven weeks, weekly samples were taken by carefully sieving the sand through the cage mesh to avoid damage (Fig. 8c) before shells of *D. hanleyanus* and *M. mactroides* were processed as illustrated in Fig. 7 in order to calculate the absolute growth rate of both clam species as specified in ‘Publication V’ (page 179).

Fig. 7: Shells of *D. hanleyanus* (**a**-**c**) and *M. mactroides* (**d**-**f**) indicating *apSL*, initial shell length between umbo and shell margin ($umSL_1$), **CL**: crossed-lamellar layer, **PM**: pallial myostracum, **CCL**: complex crossed-lamellar structure, **u**: umbo, **sm**: shell margin, **so**: shell outside, and **si**: shell inside. Transverse shell sections of longest growth axis observed with a transmitted-light microscope (**b**) and a fluorescent microscope (**e**) with final shell length between umbo and shell margin ($umSL_2$) after experimental time. Image ‘**c**’ and ‘**f**’ are details of ‘**b**’ and ‘**e**’ (square and rectangle, respectively), showing growth increment after *in situ* rearing period observed with a scanning electronic microscope (SEM) (**c**) and a fluorescent microscope (**f**). *Green Arrows* (➔) in ‘**c**’, ‘**e**’ and ‘**f**’ indicate fluorescent growth marks.

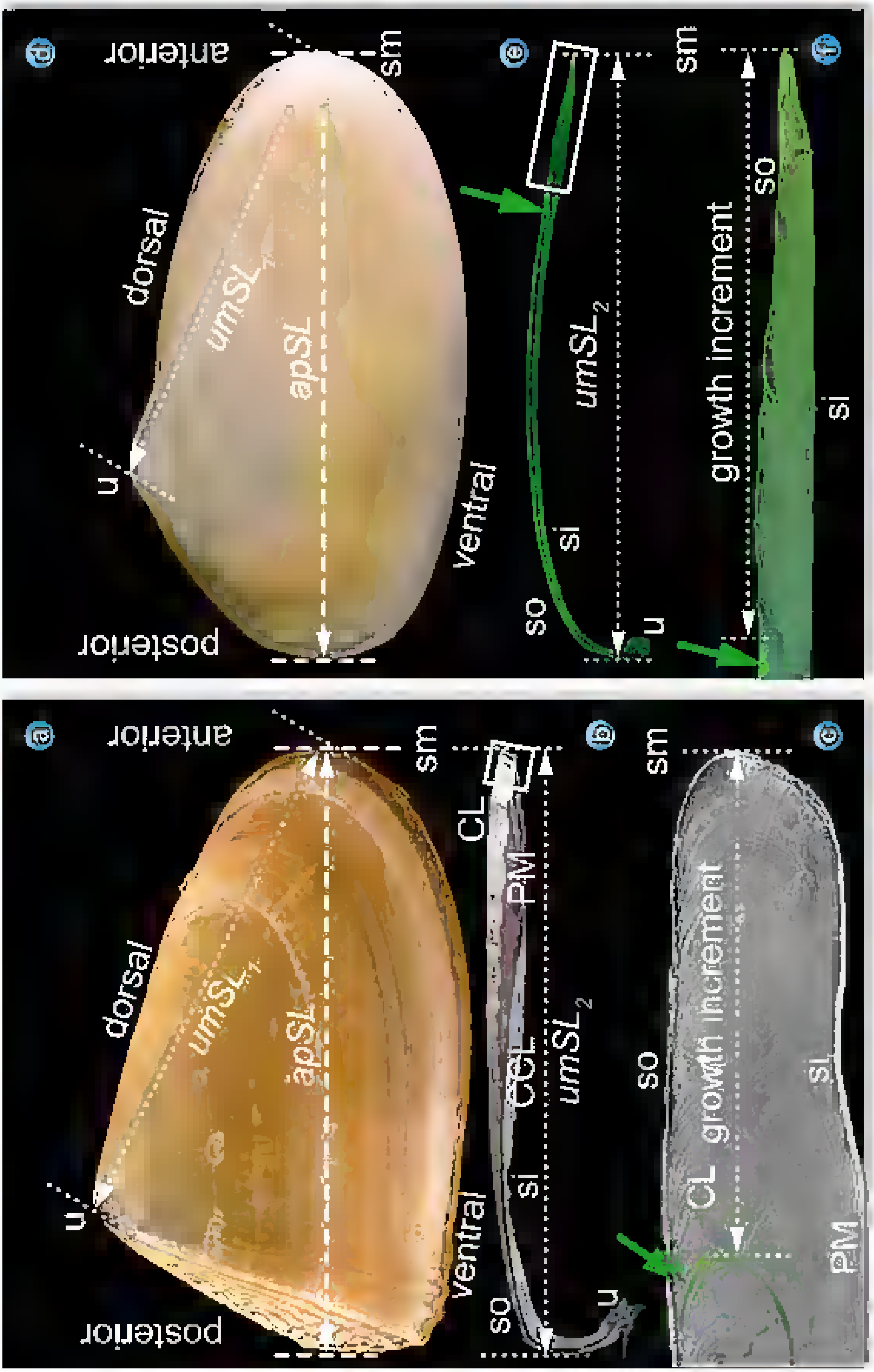
a
anterior
sm
dorsal
$umSL_1$
apSL
u
ventral
posterior
b
sm
CL
PM
CCL
$umSL_2$
si
so
u
c
sm
growth increment
so
si
CL
PM
d
anterior
sm
dorsal
$umSL_2$
apSL
u
ventral
posterior
e
sm
$umSL_2$
si
so
u
f
growth increment
so
si

Fig. 8: Cage (40 x 40 x 40 cm) bonded with 1 mm mesh (**a**) installed in the intertidal zone (**b**) and during weekly sampling (**c**).

3.3.2 Data Analyses

In order to study growth, growth performance and life span of both surf clam species von Bertalanffy growth functions (*VBGF*s) were fitted to *LFD* data (accordingly to von Bertalanffy 1938) using the electronic length-frequency analysis 'ELEFAN I' routine of the FiSAT II program package (Gayanilo Jr. *et al.* 2005). The overall growth performance index (*OGP*) and the theoretical life span ($t_{\max}$) were estimated, as described in 'Publication I' (page 79) and 'Publication II' (page 109), respectively. Furthermore growth of *D. hanleyanus* and *M. mactroides* was estimated via the *IFM* method. *VBGFs* were fitted to size-increment data (*SID*) following Appeldoorn (1987) described in detail in 'Publication V' (page 179). Comparative growth analyses between the *IFM* and *LFD* method were carried out interpreting the latter as size-at-age data (*SAD*) and fitting general von Bertalanffy growth functions (*gVBGF*s) to *SAD* and *SID* using the computation worksheet of Brey (2001), applying Microsoft Excel's SOLVER routine. Details are provided in 'Publication V' (page 179). Additionally, transverse sections of *D. hanleyanus* and *M. mactroides* shells were monitored using a SEM (Philips XL 30) at the Natural History Museum of Buenos Aires (MACN). Samples were treated using the critical point dehydration method, followed by palladium (60 %) - gold (40 %) coating.

3.3.3 Statistics

Chi-square (χ^2) analyses were applied to determine if significant differences on mortality rates occurred by using stains to mark surf clams during *in vitro* suitability tests and *in situ* growth experiments. The relation between $umSL_2$ and daily growth rate was estimated by exponential regression analysis. Effects of $umSL_2$ and exposure time on growth rate were analysed by utilising a one-way ANCOVA (growth rate as dependent variable, days of exposure as fixed factors and initial length as covariate). Differences of growth rates within the three ontogenetic groups 'recruits', 'juveniles' and 'adults' were analysed by a one-way ANOVA with a Scheffé-procedure post hoc test. *LFD* analyses and tagging-recapture experiments using the *IFM* method and subsequent size-increment analyses, used to estimate growth of both surf clams, were compared by an ANOVA of the residuals of the *gVBGF*s.

3.4 Reproduction

3.4.1 Sampling and Laboratory Procedures

Following the systematic approach as in chapter 3.2.1 specified, a total of 35 wedge clams was collected monthly from all three beaches and a total of 30 yellow clams was collected monthly from Santa Teresita, covering the full range of *apSL*s, respectively. Surf clams with severed adductor muscles were fixed in Bouin's solution for two hours, then transferred into 70 % ethanol and later processed in the laboratory. For histological examinations gonadal tissue of *D. hanleyanus* and *M. mactroides* (Fig. 9, respectively) was prepared and processed using standard histological methods i.e. embedding in paraffin, sectioning at 5 µm and staining with hematoxylin-eosin (following Howard *et al.* 2004). Gonads were examined using a Zeiss Axio Imager Z1 light microscope and designated to one of five developmental stages (sexual rest, pre-active, active, spawning and cytolysed). Images of each sample were captured using a Sound Vision digital camera and processed using the imaging software AxioVision version 4.4 (2008). For all developmental stages except sexual rest, the mean oocyte diameter was determined by measuring 30 oocytes per specimen. Furthermore, the abundance of oocytes in each sectioned female gonad was examined by counting oocytes from one square millimetre surface area.

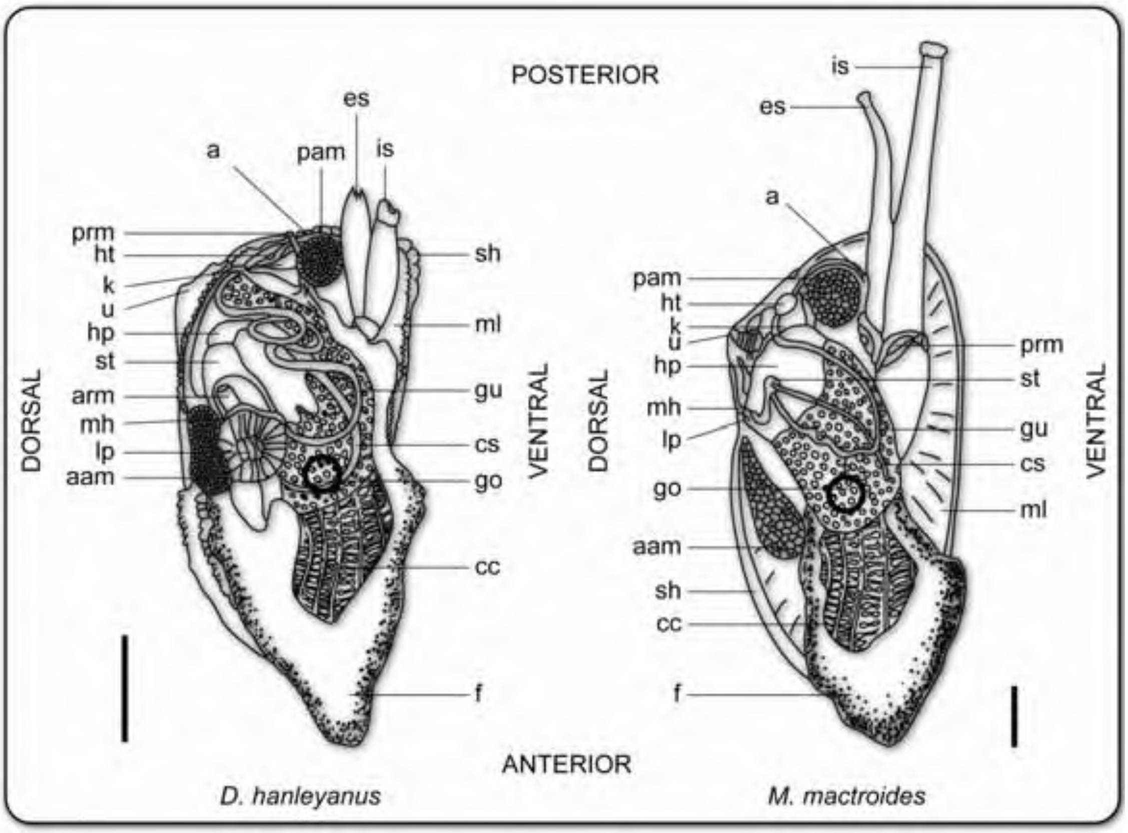

Fig. 9: Anatomy of *D. hanleyanus* (*left*) and *M. mactroides* (*right*) schematically represented: (**a**) anus, (**aam**) anterior adductor muscle, (**arm**) anterior retractor muscle, (**cc**) central cavity with longitudinal and transverse fascicles, (**cs**) crystalline style, (**es**) exhalant siphon, (**f**) foot, (**go**) gonad, (**gu**) gut, (**hp**) hepatopancreas, (**ht**) heart, (**is**) inhalant siphon, (**k**) kidney, (**lp**) labial palp, (**mh**) mouth, (**ml**) mantle, (**pam**) posterior adductor muscle, (**prm**) posterior retractor muscle, (**sh**) shell, (**st**) stomach and (**u**) umbo. *Circles*: locations of the tissue sample used for histological examination. *Scale bars*: 10 mm.

3.4.2 Data Analyses

The reproductive biology of *D. hanleyanus* and *M. mactroides* was examined histologically and the gonads of both surf clams classified into five development stages. The index *CI* was calculated, the size and biomass at sexual maturity estimated, and recruitment events recorded. Furthermore, *RSA* was implemented to simplify the classification of gonadal tissue. Methods are described in detail in 'Publication III' (page 131) and 'Publication IV' (page 159), respectively.

3.4.3 Statistics

Sex ratios (male:female) of surf clams were calculated according to the presence of oocytes and spermatozoa using chi-square (χ^2) analysis. The influence of *SST* on the gametogenic cycle, as well as its relationship with *RSA*, *CI*, *AFDM*, abundance and size of oocytes within the population inhabiting each of the three beaches were statistically analyzed by Spearman's rank order correlation. Spatial and temporal differences in the gametogenic cycle and oocyte abundance as well as mean and modal sizes of oocytes were tested by one-way analysis of variance (ANOVA). For all beaches the three ontogenetic groups 'recruits' (< 11 mm), 'juveniles' (11-22 mm, the size class where sex can be differentiated for the first time) and 'adults' (> 22 mm, size where individuals were 100 % mature) of *D. hanleyanus* were tested for differences by two-way ANOVA using the factors 'beach' and 'ontogenetic group'. Based on the Durbin-Watson coefficient, residuals of the logistic functions of size and biomass at sexual maturity were tested for autocorrelation. The closer the coefficient to value '2' (within the range of 0 and 4) the less significant the autocorrelation (SigmaStat 2004). To compare results of size and biomass at 50 % population maturity, as estimated for both sexes and for each of the three beaches, analyses of the residual sum of squares (ARSS) were performed (Chen *et al.* 1992).

4 Summary of Results

4.1 Population Structure

4.1.1 *Donax hanleyanus*

The smallest recorded *D. hanleyanus* measured 3-4 mm and the largest 35-40 mm. Annual abundance (mean ± SE) was 78 ± 42 ind. m^{-2} (2005) and 40 ± 15 ind. m^{-2} (2006) at Santa Teresita, 55 ± 23 ind. m^{-2} (2005) and 50 ± 12 ind. m^{-2} (2006) at Mar de las Pampas and 84 ± 22 ind. m^{-2} (2005) and 267 ± 77 ind. m^{-2} (2006) at Faro Querandí. Maximal absolute abundance was recorded in spring (2,475 ind. m^{-2} at Santa Teresita in December 2004, 531 ind. m^{-2} at Mar de las Pampas in December 2004 and 950 ind. m^{-2} at Faro Querandí in November 2006). At Santa Teresita *LFD* showed cohorts, which were tracked up to ten months reaching approximately 20 mm *apSL* before the cohort disappeared and new recruits were recorded (Fig. 10). In March 2006 a new cohort at Santa Teresita and two additional cohorts at Mar de las Pampas were detected and could be followed until the end of the study in December 2006 (Fig. 11). Adult individuals co-occurring in two (February 2005 until March 2006) and three cohorts (April 2006 to October 2006) were found at Faro Querandí (Fig. 12).

D. hanleyanus was found living with the sympatric *M. mactroides*. The abundance of the latter significantly negatively correlated with the absence of *D. hanleyanus* at Santa Teresita. The intertidal biomass ranged between 0.04 and 1.32 g *AFDM* $m^{-2}yr^{-1}$. Individual production revealed the highest value at 30 mm length (0.16 g *AFDM* $m^{-2}yr^{-1}$) and annual production was 0.08 to 0.99 g *AFDM* $m^{-2}yr^{-1}$, resulting in renewal rates ($P/\bar{B}$) from 0.82 to 2.16. The $P/\bar{B}$ ratios increased with decreasing latitude from temperate to tropical regions.

Spatial differences in abundance were significantly related to sand texture as confirmed by non-metrical multidimensional scaling, but not to *SST*. However, the decrease in *D. hanleyanus* abundance appears to be principally related to human activities. Population structure results of *D. hanleyanus* are provided more specifically in ‘Publication I’ (page 79).

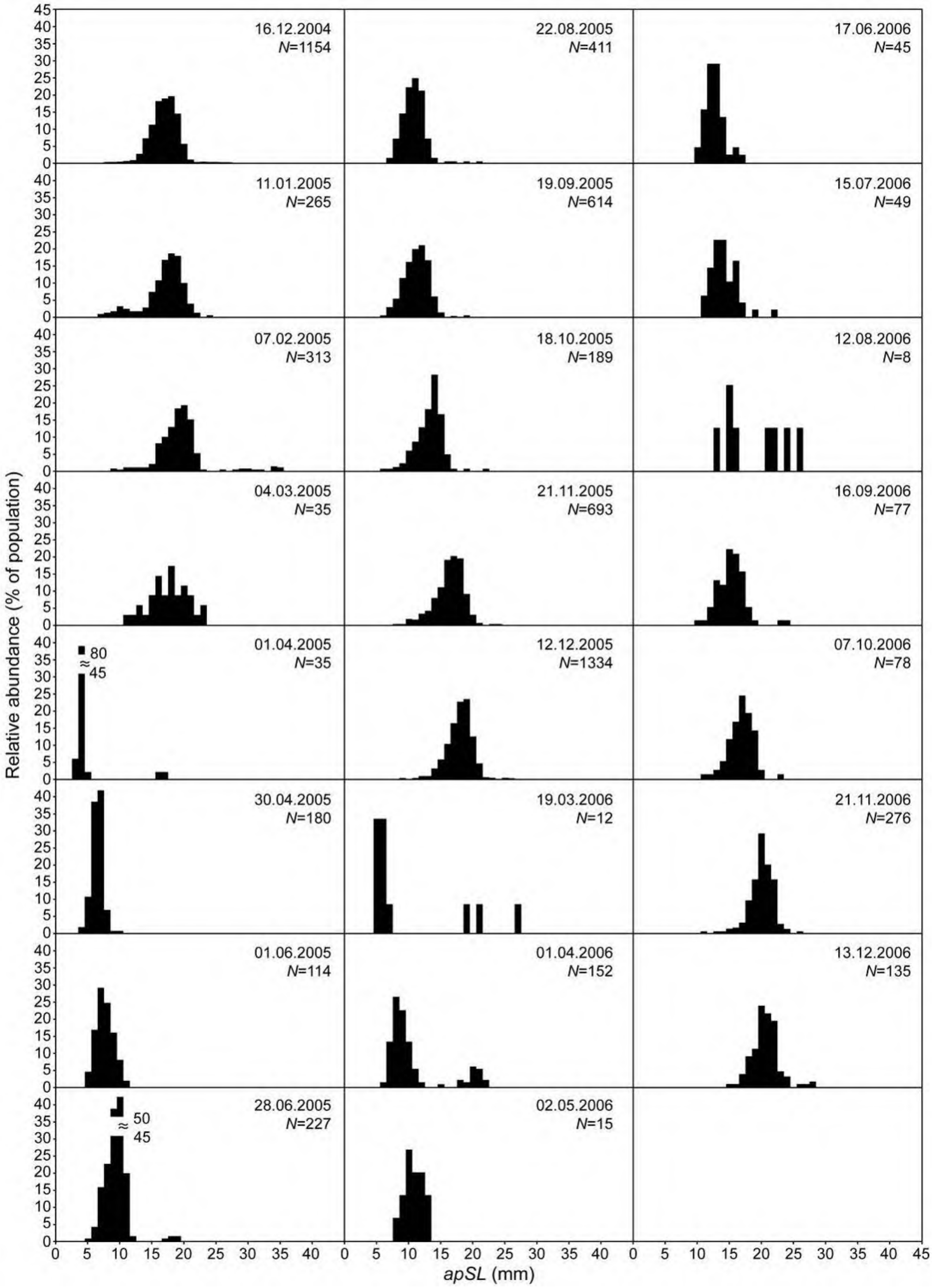

Fig. 10: Monthly *LFDs* of *D. hanleyanus* collected between December 2004 and December 2006 at Santa Teresita.

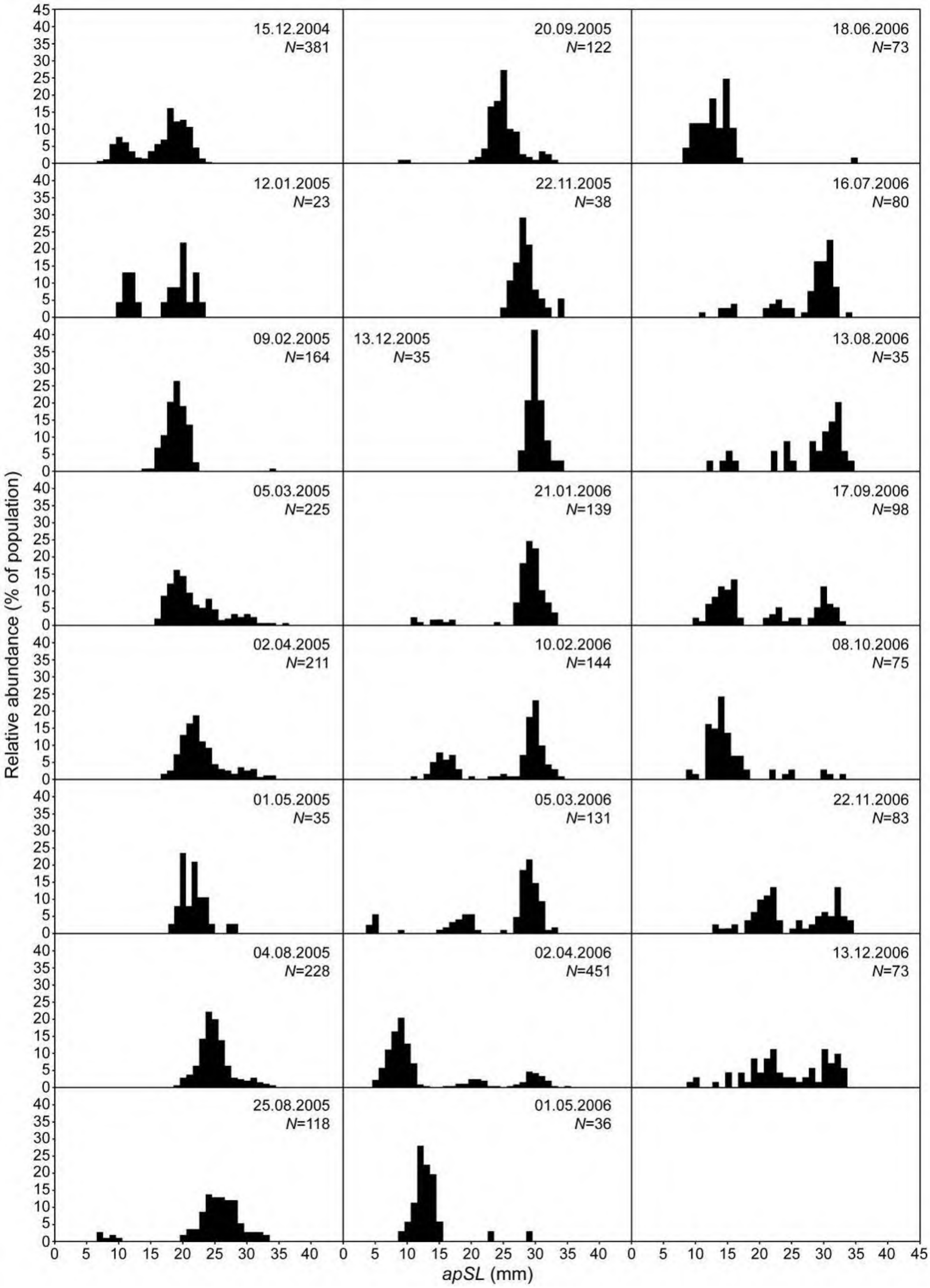

Fig. 11: Monthly *LFD*s of *D. hanleyanus* collected between December 2004 and December 2006 at Mar de las Pampas.

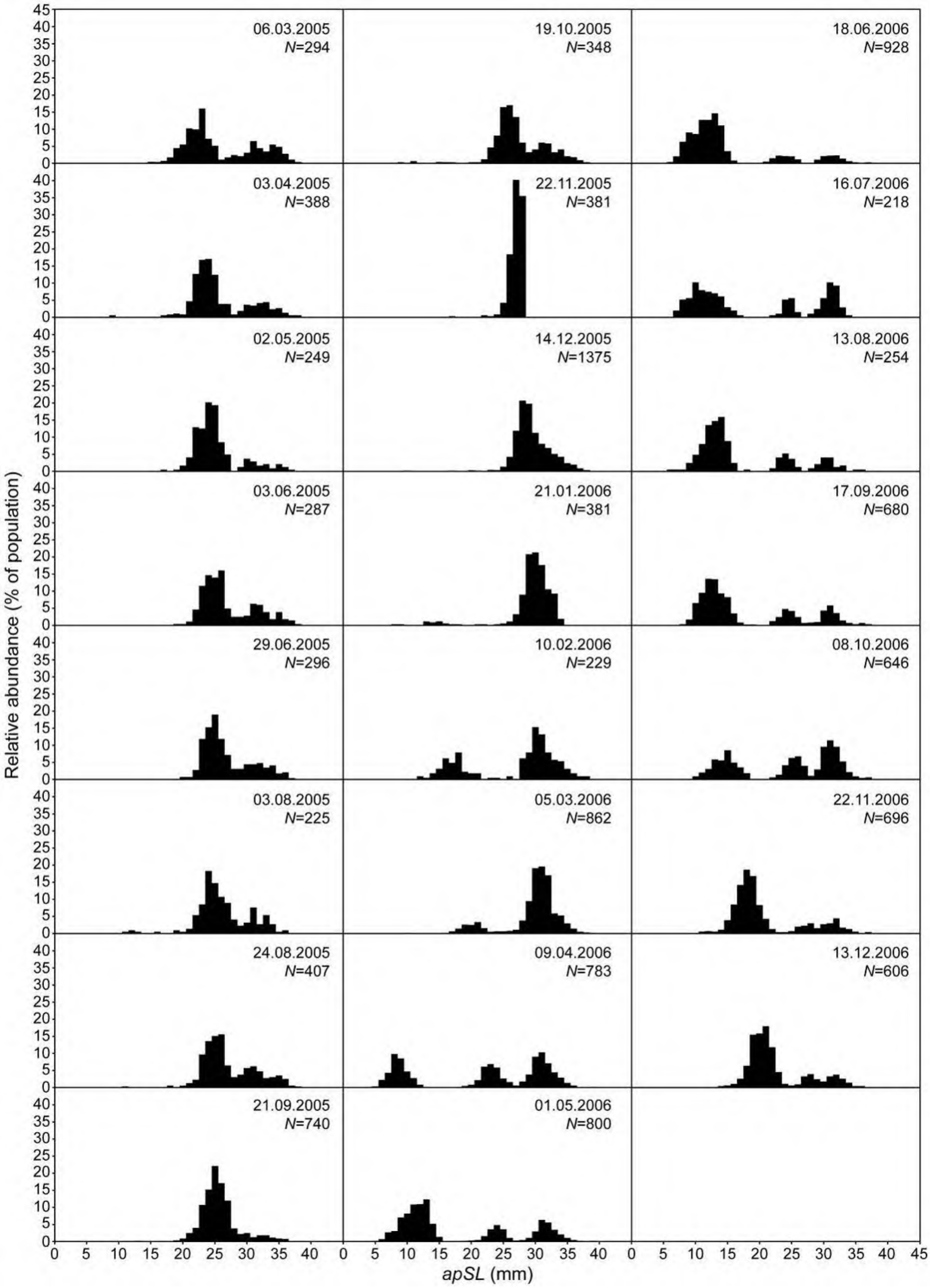

Fig. 12: Monthly *LFD*s of *D. hanleyanus* collected between March 2005 and December 2006 at Faro Querandí.

4.1.2 *Mesodesma mactroides*

South of Santa Teresita no *M. mactroides* population was discovered during the entire sampling period, thus population parameters and production were estimated for one site only. Maximum abundance was recorded in May 2005, with 110 ± 25 ind. m^{-2} (mean ± SE) and absolute abundance peaked at 543 ind. m^{-2} (size-class 2-4 mm) in April 2005. In both years, a single new cohort was observed during February. New cohorts were tracked for up to eleven months reaching an *apSL*s of 27 mm in 2005 and approximately 35 mm in 2006 before disappearing probably to the subtidal. Cohorts never reached the 'commercial size' of 60 mm (Coscarón 1959) (Fig. 13). The intertidal biomass of *M. mactroides* ranged between 0.06 and 0.07 g *AFDM* m^{-2} yr^{-1}. Individual production increased to a maximum *apSL* value at 47 mm (0.35 g *AFDM* m^{-2} yr^{-1}) and annual production ranged between 0.12 and 0.19 g *AFDM* m^{-2} yr^{-1}, resulting in renewal rates ($P/\bar{B}$) between 1.84 and 2.93. *M. mactroides* abundance was significantly negatively correlated with the abundance of *D. hanleyanus*. The population structure of *M. mactroides* is described in detail in 'Publication II' (page 109).

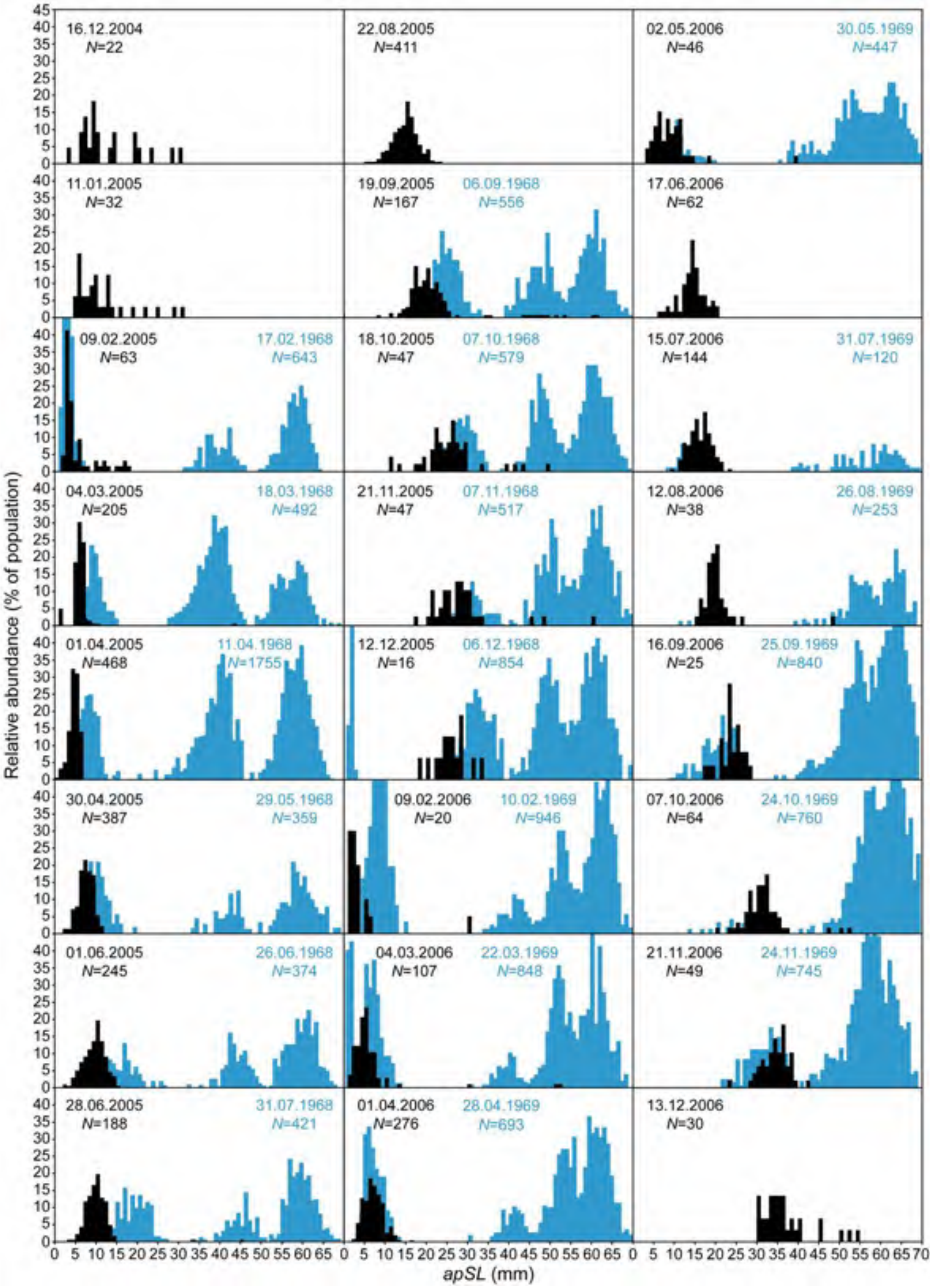

Fig. 13: Monthly *LFD*s of *M. mactroides* collected between December 2004 and December 2006 at Santa Teresita (black histograms) compared with historical data from Olivier *et al.* (1971) sampled between 1968 and 1969 at Mar Azul (blue histograms).

4.1.3 Associated Fauna

Both studied surf clams were found associated with only four macrozoobenthic species (Table 4):

Table 4: Macrozoobenthic fauna associated with the surf clams at Santa Teresita (**S**), Mar de las Pampas (**M**) and Faro Querandí (**F**) specifying the corresponding feeding mode (**fm**): suspension feeder (**s**), carnivore (**c**) and detritivore (**d**).

Species	Class	S	M	F	fm	References[7]
Donax hanleyanus	Bivalvia	●	●	●	s	ZMB/Moll.104642
Mesodesma mactroides	Bivalvia	●	●		s	ZMB/Moll.104643
Olivancillaria vesica auricularia	Gastropoda	●			c	ZMB/Moll.107176
Hemipodus olivieri	Polychaeta			●	c	ZMB/Vermes.11243
Excirolana armata	Isopoda	●	●	●	d	ZMB/Crust.27673
Serolis bonaerensis	Isopoda	●			d	ZMB/Crust.27672

At Santa Teresita *O. vesica auricularia* feeds on both surf clams, which show escape behaviour when the snail approaches them, even without direct contact. *H. olivieri* co-occurs with *D. hanleyanus* populations infrequently at Faro Querandí, however no predation was observed. There was no significant correlation between the surf clam population abundance and the presence of the associated *S. bonaerensis* and *E. armata*. Furthermore, *H. ostralegus* (Fig. 14a) was observed feeding on *D. hanleyanus* at Faro Querandí (Fig. 14b). Abundances of 3 ± 0.31 ind. km^{-1} (mean ± SE) with a maximum of 5 ind. km^{-1} in March 2006 were registered.

Fig. 14: *H. ostralegus* seeking *D. hanleyanus* as food resource (**a**), leftover *D. hanleyanus* shells - pecked from oystercatchers (**b**), both at the intertidal zone of Faro Querandí.

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[7] Reference specimens were deposited in the collection of the 'Museum für Naturkunde der Humboldt-Universität zu Berlin' under reference numbers respectively.

4.2 Growth Estimation

4.2.1 *Donax hanleyanus*

The maximum sized valve of 44 mm was found at Faro Querandí used as a fixed L_∞ value to calculate a seasonal *VBGF* from *LFD*s with the growth constants $K = 0.47$ (*OGP* = 4.60) at Mar de las Pampas and $K = 0.48$ (*OGP* = 4.61) at Faro Querandí. Estimates of growth indicated moderate seasonal oscillations ($C = 0.8$), with slowest growth rates occurring in austral autumn (*WP* = 0.45 ~ mid-May). Due to the lack of larger size classes at Santa Teresita a reliable *VBGF* (Gayanilo Jr. *et al.* 2005) could not be calculated. The computed theoretical life span (t_{max}) ranged between 4.96 yrs (Mar de las Pampas) and 5.18 yrs (Faro Querandí). Growth rates of *D. hanleyanus* were also estimated from size increments obtained from an *in situ* experiment and fluorescence marked specimens, whereby growth was measured from sectioned shells (Fig. 15) described in 'Publication V' (page 179). Maximum growth increments were found in juvenile wedge clams (e.g. $umSL_2$ = 7.31 mm + 1.86 mm in 45 days, Fig. 16). Individual daily growth rate ranged between 8 µm d^{-1} and 72 µm d^{-1}. The relationship between $umSL_2$ and daily growth

Fig. 15: *D. hanleyanus* ($umSL_2$ = 12.88 mm). Transverse shell section after 14 days experimental time, observed through a fluorescent microscope showing a growth increment of 233 µm (*curly bracket*) and autofluorescence; **so**: shell outside, **si**: shell inside, **u**: umbo, *arrow*: calcein mark, *scale bar*: 1 mm.

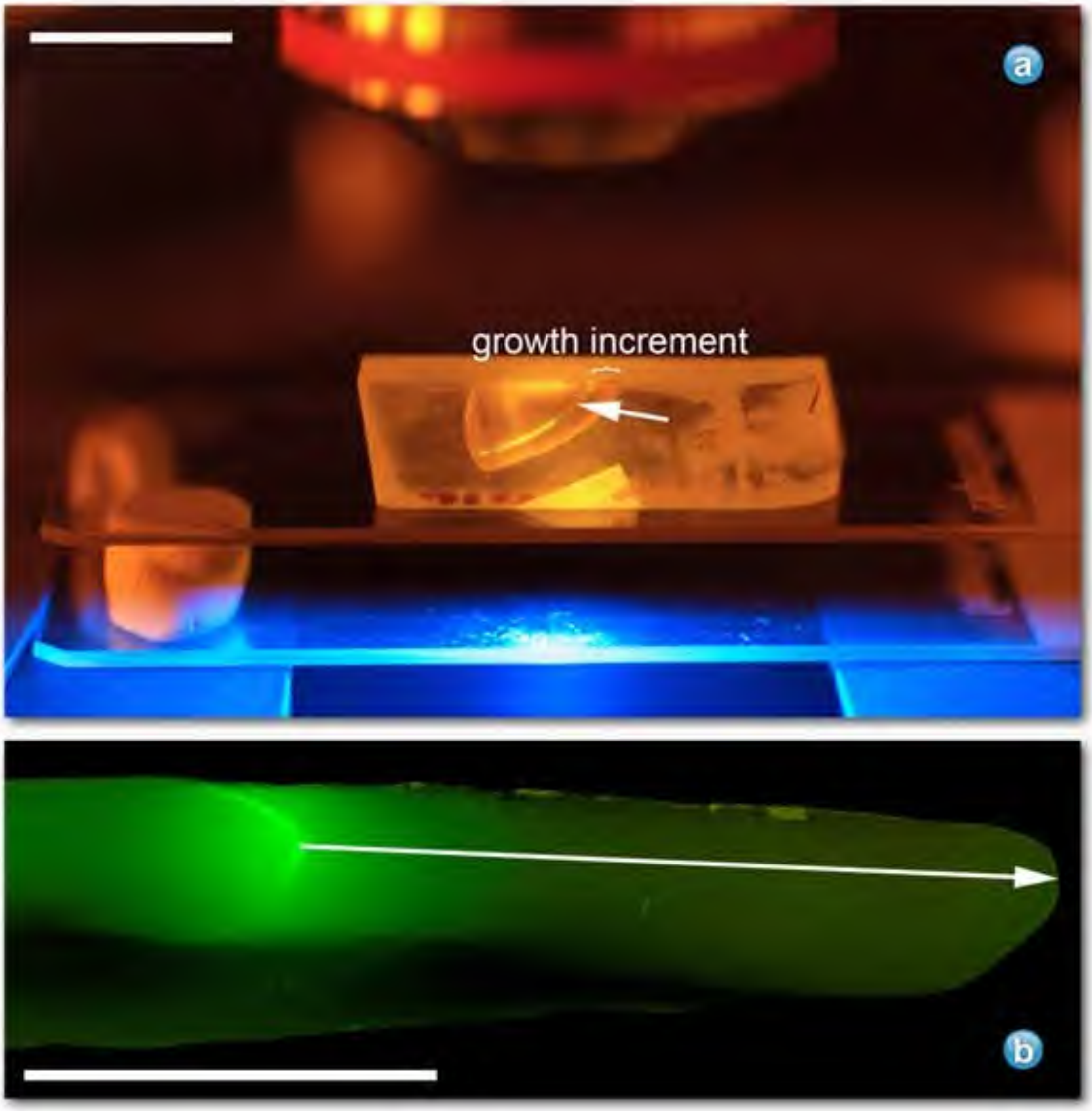

Fig. 16: Epoxicure resin block section of *D. hanleyanus* ($umSL_2$ = 7.31 mm) under a fluorescent microscope equipped with blue light, sampled after 45 days experimental time, *curly brace* indicates growth increment, *arrow* indicates incorporated calcein mark, both visible with naked eye (**a**). Resulting thin section indicates a growth increment of 1.86 mm, *arrow* shows the direction of growth (**b**). *Scale bars*: (**a**) 10 mm, (**b**) 1 mm.

was best described by an exponential function ($y = 144.76 \cdot e^{-0.201x}$, $r^2 = 0.91$, $N = 113$), which indicates that growth decreases exponentially with age (Fig. 17). Both, $umSL_2$ ($F_{1,96} = 191.249$, $p < 0.05$) and exposure time ($F_{5,96} = 17.415$, $p < 0.05$) had significant effects on growth rate (one-way ANCOVA: growth rate as dependent variable, days of exposure as fixed factors and initial length as covariate). A seasonal *VBGF* was fitted to *SID*, originated from the *IFM*, using the maximum sized valve (*umSL* = 37 mm [analogical to *apSL* = 44 mm]) found at Faro Querandí as a fixed value of L_∞ to calculate the growth constant $K = 0.41\ y^{-1}$ ($r^2 = 0.69$).

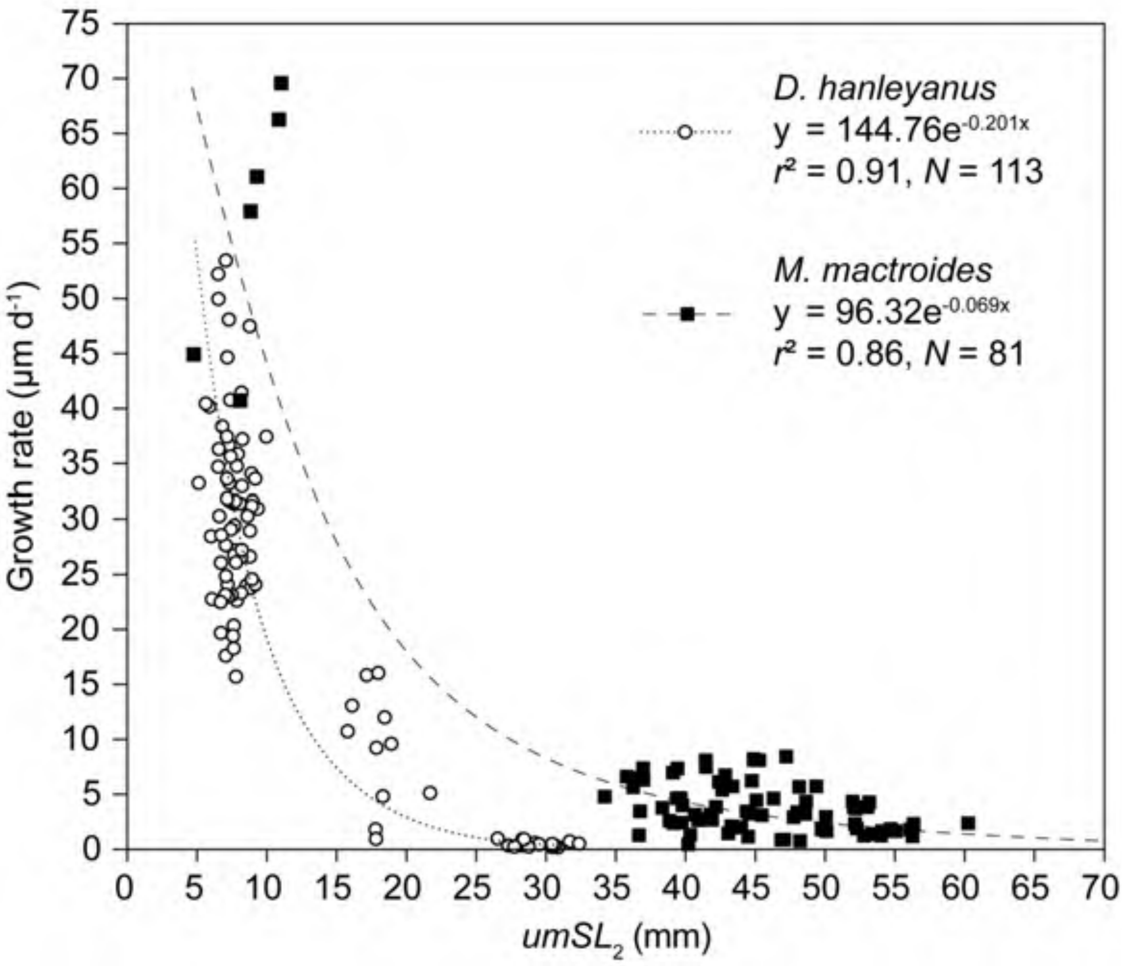

Fig. 17: *D. hanleyanus* (○) and *M. mactroides* (■). Relationship between $umSL_2$ (mm) and daily growth rate (mm d^{-1}).

4.2.2 *Mesodesma mactroides*

A seasonal *VBGF* with an asymptotic length (L_∞) of 71 mm and a growth constant K of 0.47 yr^{-1} was established from *LFD*s of the *M. mactroides* population at Santa Teresita. The corresponding *OGP* index (5.23) is compared in Fig. 27 and Table 6 with those of *M. mactroides* growth parameters, calculated from different areas, as well as with data of *M. donacium* from Peru. The constant $C = 0.10$ indicates weak seasonal variation in the growth of yellow clams, with lowest growth rates occurring in winter ($WP = 0.7$ ~ mid-August). The calculated life span (t_{max}) of *M. mactroides* amounts to 6.19 yrs and the instantaneous mortality rate (Z) is 0.83 yr^{-1}. Results of the growth analysis carried out by the indirect *LFD* method are detailed in 'Publication II' (page 109). Growth rates of *M. mactroides* were estimated realizing an *in situ* experiment that utilised the direct *IFM* method whereby growth was measured from sectioned shells (Fig. 18) as described for *D. hanleyanus* in 'Publication V' (page 179). Maximum growth increments were found in juvenile yellow clams (e.g. $umSL_2 = 9.93$ mm + 1.83 mm in 45 days, Fig. 18). Individual daily growth rate ranged between 1 µm d^{-1} and 70 µm d^{-1}. The relationship between $umSL_2$ and daily growth rate of yellow clams was best described by

Fig. 18: *M. mactroides* ($umSL_2 = 9.93$ mm). Transverse shell section of after 45 days experimental time, observed through a fluorescent microscope showing a growth increment of 1.83 mm (*curly bracket*) and autofluorescence of the shell; **so**: shell outside, **si**: shell inside, **u**: umbo, *arrow*: calcein mark, *scale bar*: 1 mm.

an exponential function ($y = 96.32 \cdot e^{-0.069x}$, $r^2 = 0.86$, $N = 81$), which indicates that growth decreases exponentially with age (Fig. 17). A seasonal *VBGF* was fitted to *SID*, originated from *IFM* to calculate the growth parameters $L_\infty = 71$ mm and $K = 0.48$ y^{-1}.

4.2.3 Comparison of Growth Estimation Methods

The suitability of tagging-recapture experiments using the *IFM* method and subsequent size-increment analyses was assessed *versus LFD*s analyses. Results of the two methods were compared by plotting the residuals *versus* the estimated *apSL*, reflecting a very good fit for both, *D. hanleyanus* ($r^2 = 0.998$, Fig. 19a) and *M. mactroides* ($r^2 = 0.992$, Fig. 19b). Analyses of variance of the residuals of the *gVBGF*s showed no significant difference between the two methods for *D. hanleyanus* (ANOVA, $F_{1,64} = 2.153$, $p > 0.05$) and for *M. mactroides* (ANOVA, $F_{1,98} = 0.019$, $p > 0.05$). The comparative growth analysis between *LFG* and *IFM* of *D. hanleyanus* is described in detail in 'Publication V' (pages 179).

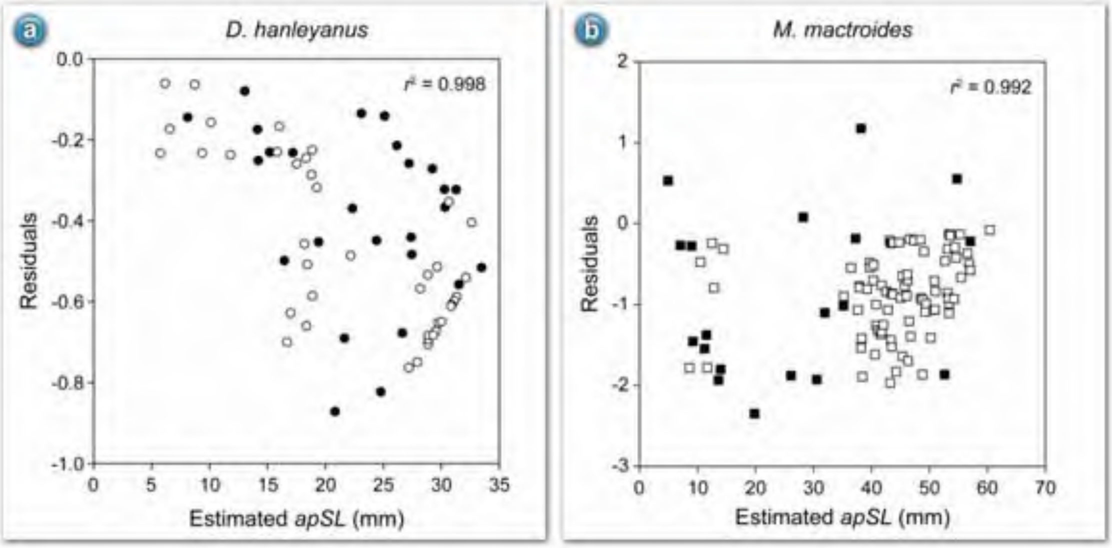

Fig. 19: Residuals of estimated shell lengths (*apSL*) of (●,■) *SAD* (converted from *LFD*) and of (○,☐) *SID* (from *IFM*), showing no significant difference between the two growth estimation methods for *D. hanleyanus* (**a**) and *M. mactroides* (**b**).

4.3 Reproduction

4.3.1 *Donax hanleyanus*

In order to compare the current reproductive biology of *D. hanleyanus* (Bivalvia: Donacidae) with that of forty years ago (Penchaszadeh and Olivier 1975), sampling over a period of 25 months from all three beaches with contrasting morphodynamics (dissipative, intermediate and reflective) was carried out. Histological examinations of gonad tissue demonstrated that sex ratios did not significantly deviate from 1:1 at the intermediate (Mar de las Pampas) and reflective beaches (Faro Querandí), but there was a greater proportion of females at the dissipative beach (Santa Teresita) in December 2004, January 2005 and April 2006. No case of hermaphroditism was found. Furthermore, histological analysis revealed that the reproductive cycles of both male and female *D. hanleyanus* (Fig. 20) undergo a distinct seasonality at all three beaches. The reproductive phase was extended in the reflective beach. Males and females from the dissipative and intermediate beaches were significantly smaller and had a lower biomass at maturity than those from the reflective beach. Recruits were significantly more abundant and the recruitment period was significantly extended at the dissipative beach. Spawning events took place twice each year at the dissipative (early spring and spring-summer) and the intermediate beach (winter and summer), whereas continuous gamete releases were noted at the reflective beach. Size and biomass at first maturity were lower at the dissipative beach, whereas monthly mean abundance of *D. hanleyanus* was higher at the reflective beach. The gametogenic cycle correlated significantly with *SST*, *RSA*, *CI*, *AFDM* and mean size and abundance of oocytes for all three populations. The results of the *D. hanleyanus* reproductive biology are reported in detail in ‘Publication III’ (page 131).

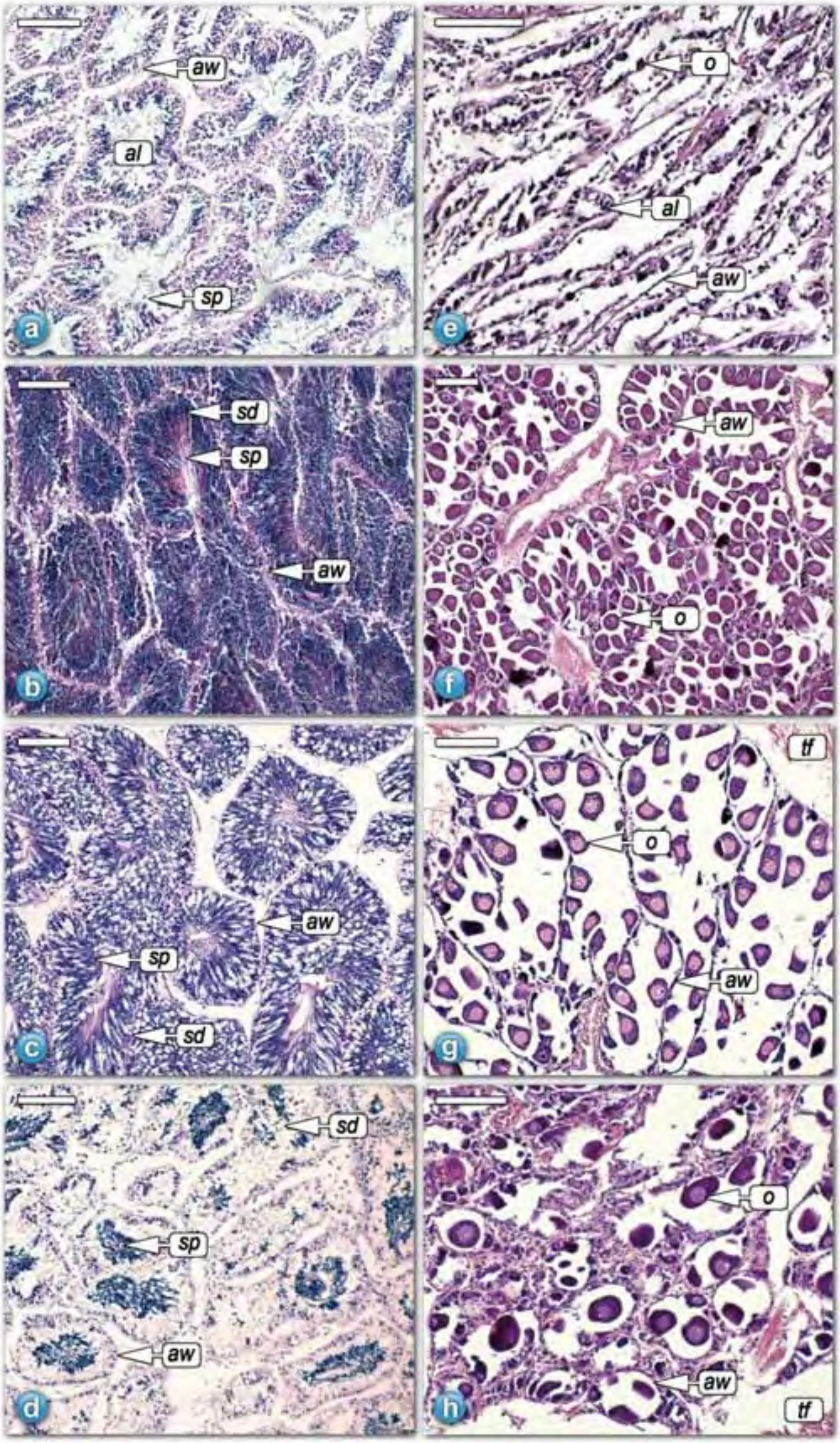

Fig. 20: Microphotography of male (**a-d**) and female (**e-h**) gonad stages of *D. hanleyanus*: (**a, e**) pre-active, (**b, f**) active, (**c, g**) spawning, (**d, h**) cytolysed (***aw***: alveolar wall, ***al***: alveolus, ***o***: oocyte, ***sp***: sperms, ***sd***: spermatids, ***tf***: transverse fibre, *scale bars* are 100 µm).

4.3.2 *Mesodesma mactroides*

Histological examination of *M. mactroides* 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 was significantly correlated to monthly mean *SST*. Male (Fig. 21) and female (Fig. 22) gonads were active and ripe from austral autumn to spring showing a maximal percentage of gonad stages in winter. Spawning of males took place mainly in winter-spring (from July to November 2005 and from August to December 2006). Females spawned in late autumn (June 2005, 2006) and in spring (October-November 2005, November-December 2006). Male gonads appeared cytolysed during winter and spring, whereas cytolysed female gonads were present between autumn and winter (in June, July both years) and in late spring (November-December 2005, December 2006). Oocytes showed highest abundance in winter, indicating gonadal development and sexual maturation. The mean oocyte size decreased significantly in spring. Modal oocyte sizes decreased significantly in winter and late spring of each year, suggesting spawning events. The *CI* was not useful in describing the annual reproductive cycle of *M. mactroides*. *AFDM* was chosen to indicate the condition of the specimens, and this significantly correlated with monthly mean *SST* and the gametogenic cycle. Annual recruitment patterns were significantly correlated with *SST*. The settling period of recruits in summer-autumn indicated a three-month-long planktonic phase. Details of the *M. mactroides* reproductive cycle are reported in 'Publication IV' (page 159).

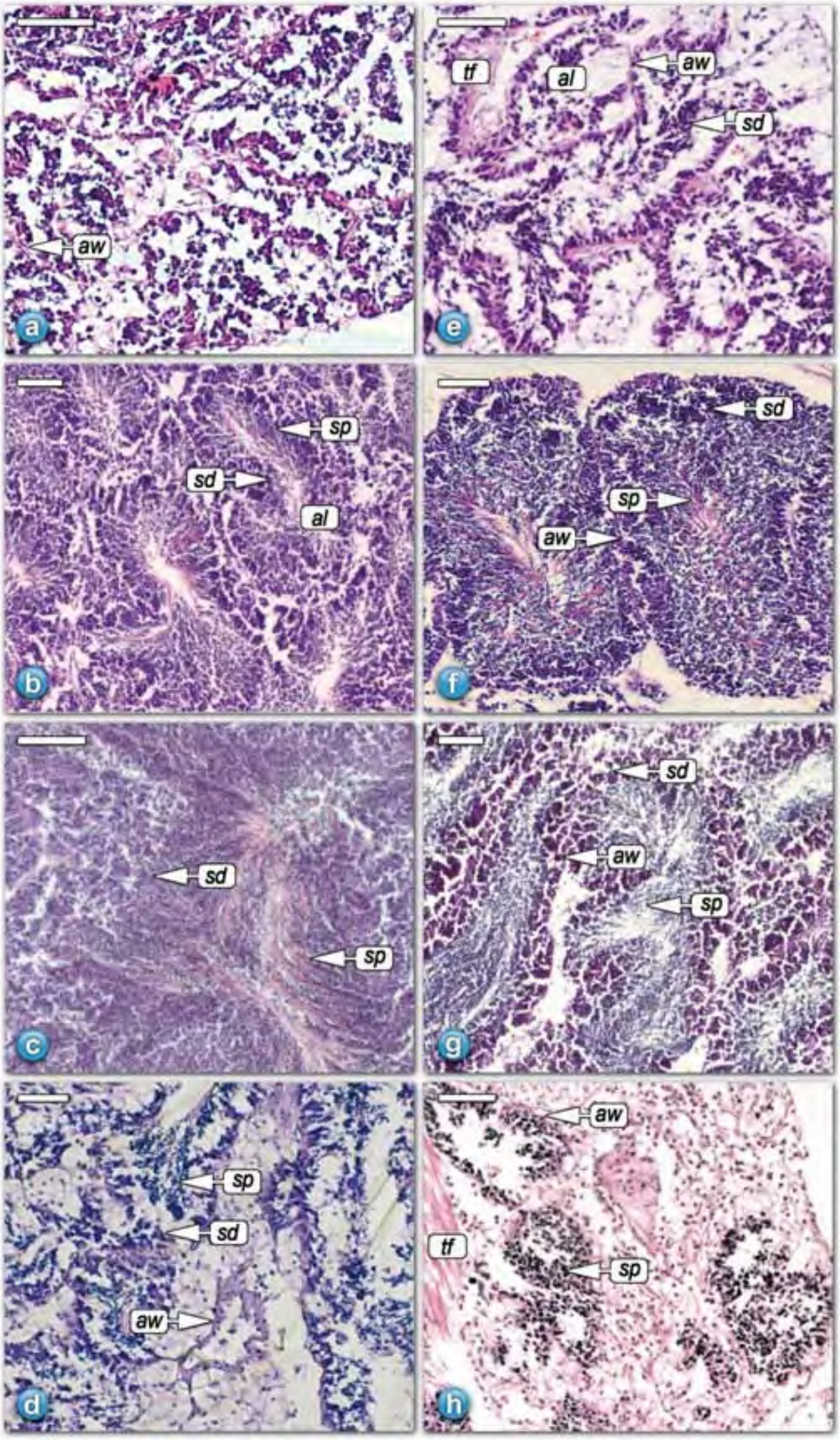

Fig. 21: Microphotography of male gonad stages of *M. mactroides*: (**a**) early active stage, (**b**) late active stage, (**c**) early ripe stage, (**d**, **e**) ripe stage, (**f**) partially spawned stage, (**g**) spent stage, (**h**) recovery stage (***aw***: alveolar wall, ***al***: alveolus, ***sp***: sperms, ***sd***: spermatids, ***tf***: transverse fibre, *scale bars* are 100 µm).

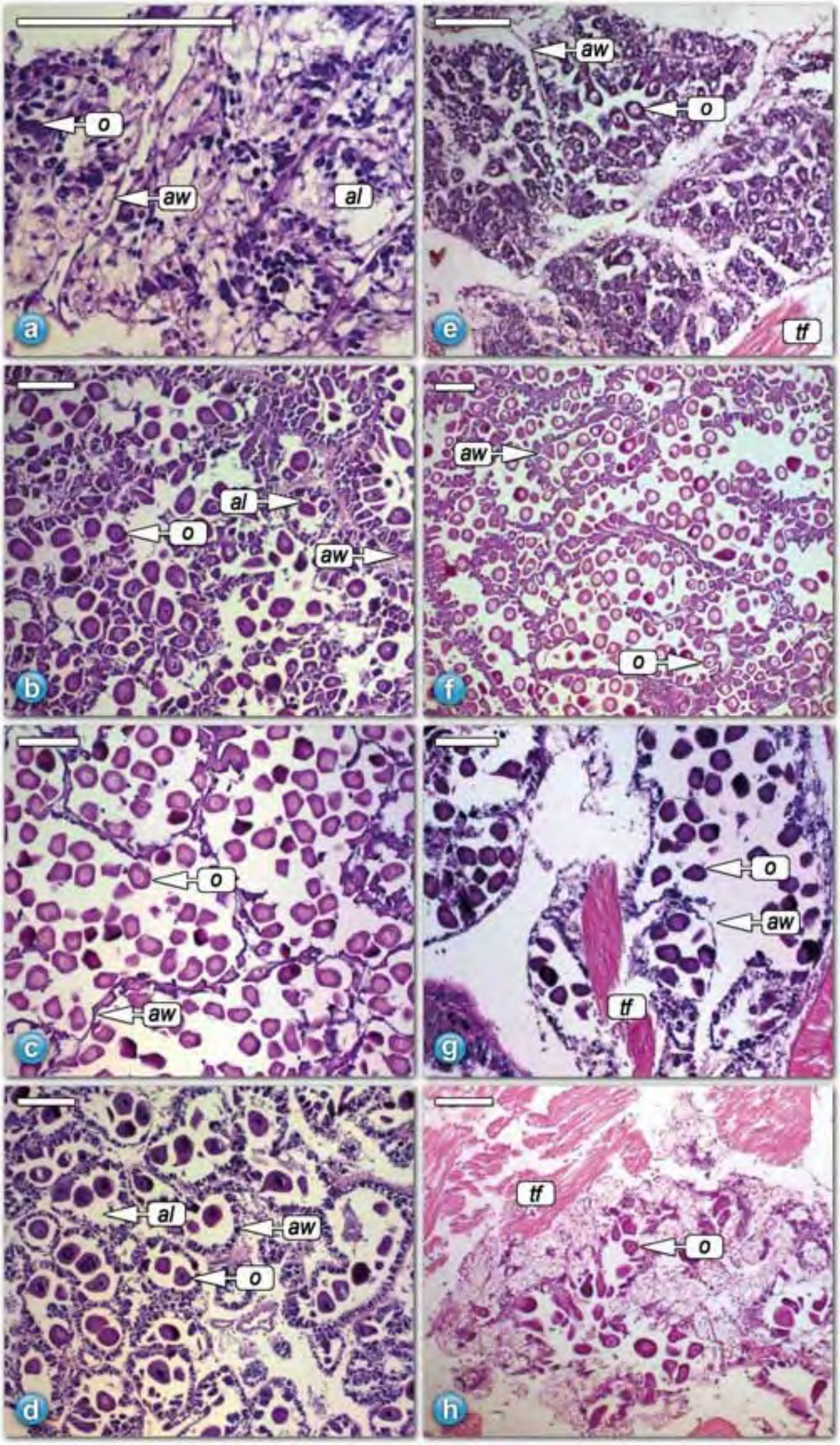

Fig. 22: Microphotography of female gonad stages of *M. mactroides*: (**a**) early active stage, (**b**) late active stage, (**c**) early ripe stage, (**d**, **e**) ripe stage, (**f**) partially spawned stage, (**g**) spent stage, (**h**) recovery stage (***aw***: alveolar wall, ***al***: alveolus, ***o***: oocyte, ***tf***: transverse fibre, *scale bars* are 100 µm).

5 General Discussion and Conclusions

5.1 Population Structure

The present study confirms all aspects of previous conclusions (Olivier *et al.* 1971; Penchaszadeh and Olivier 1975), which stated that that the variability in physical factors is unrelated to temporal abundance fluctuations of the Argentinean surf clams. The *SST* was not correlated with the abundance of the surf clams at all three sampling sites, but differences in the surf clam abundance may be correlated to the mean grain size and with it to the compactness of the sand: the more compacted the sand, the more difficult for adult clams to burrow and consequently they can be washed away. This hypothesis is supported by Trueman (1971) stating that *Donax* is only secure against the drag of the waves when the shell is oriented with the current and at least two thirds of the shell are buried. In accordance, Alexander *et al.* (1993), McLachlan *et al.* (1995b) and Nel *et al.* (2001) also described substrate-sensitivity of *Donax* species, although the clams are able to penetrate into sediments with a wide spectrum of grain sizes.

5.1.1 Species Interactions

The sympatric and once dominant yellow clam *M. mactroides* is known to co-occur with *D. hanleyanus* populations since the seventies (Olivier *et al.* 1971; Penchaszadeh and Olivier 1975). The balance between these two species appears to have been disturbed following overfishing (Coscarón 1959; Olivier and Penchaszadeh 1968a) and mass mortality events affecting *M. mactroides* populations in March 1993 (red tide incidence: Odebrecht *et al.* 1995), November 1995 (undiscovered event: Fiori and Cazzaniga 1999) and September 2004 (probably caused by high heavy metal concentrations: Thompson and Sánchez de Bock 2007). *D. hanleyanus*, which was not object of the commercial fishery and not affected by the mass mortality events, took over immediately as the dominant species, but failed to reach the former abundance of *M. mactroides*. Similar changes in the structure of Peruvian shallow sandy beach communities have been ascribed to EN. Arntz *et al.* (1987) observed that

D. marincovichi (formerly *D. peruvianus*) prevailed over *M. donacium* immediately after EN but, like Argentinean *D. hanleyanus,* never matched the abundance of the previously dominant *M. donacium*.

D. hanleyanus and *M. mactroides* are scarcely associated macrozoobenthic fauna. Although *Emerita* spp. is a very common species associated with South American *Donax* and *Mesodesma* communities in Venezuela (Penchaszadeh 1983), Brazil (Veloso and Cardoso 1999), Peru (Arntz *et al.* 1987), Chile (Jaramillo *et al.* 1993; Jaramillo *et al.* 1994), Uruguay (e.g. Lercari and Defeo 1999; Defeo and Cardoso 2004; Delgado and Defeo 2006) and Argentina (Olivier *et al.* 1971; Penchaszadeh and Olivier 1975), anomuran mole crabs did not occur at the studied beaches. However, two predators of the surf clams were detected: known as *Donax* and *Mesodesma* predator from Brazilian beaches (Marcus and Marcus 1959; Gianuca 1985; Rocha-Barreira de Almeida 2002), *O. vesica auricularia* also feeds on the Argentinean surf clams *D. hanleyanus* and *M. mactroides*, and the oystercatcher *H. ostralegus* was observed feeding on *D. hanleyanus*. Similar predator-prey relationships between seabirds and surf clams were observed at Chilean beaches where *H. ostralegus pitanay* feeds on *Mesodesma donacium* (Googall *et al.* 1951).

5.1.2 Human Impacts

Worldwide, most of the sandy beach ecosystems are not only characterized by physical parameters, they also are impacted by a variety of anthropogenic factors, which can affect the population structure of intertidal invertebrates. Pollution, recreational activity, urbanization, change of the landscape, modification of geological processes, and global climate change affect beaches (Godfrey and Godfrey 1980; Wolcott and Wolcott 1984; Castilla 1993; Defeo and de Alava 1995; Marcomini and López 1997; Stephenson 1999; Nordstrom 2000; Brown and McLachlan 2002; Williams *et al.* 2004; McLachlan and Brown 2006; Moss and McPhee 2006; Marcomini *et al.* 2007; Schlacher *et al.* 2007). Because sandy beaches are the prime sites for human recreation, they underpin many coastal economies around the world (Klein *et al.* 2004); more people use sandy beaches than any other type of seashore. Up to one million tourists (Secretaría de Turismo, Mar del Tuyú) visit the coast of the Buenos Aires region during each holiday season and disturb the intertidal zone (Fig. 6). At Santa Teresita the number of visiting tourists (> 1000 tourists 100 m^{-1} coastline, pers. observ.) was significantly correlated with the decrease of the *D. hanleyanus* population during the summer months of both years (Spearman`s rank order correlation, $r_s = -0.829$, $p < 0.05$, $N = 6$). At Mar de las Pampas (< 10 tourists 100 $m^{-1}$ coastline, pers. observ.) this correlation was not found (Spearman`s rank order correlation, $r_s = -0.371$, $p > 0.05$, $N = 6$), and at Faro Querandí no tourist effect was apparent (< 0.01 angler 100 m^{-1} coastline, pers. observ.). Chandrasekara and Frid (1996) reported that human trampling changed the saltmarsh benthic fauna of the English coast. Van der Merwe and van der Merwe (1991) found a negative effect on two intertidal *Donax* species off South Africa and Schlacher and Thompson (2008) described a modification of the physical environment of two Australian sandy beaches, both caused by off-road driving. In a Dutch intertidal mudflat, trampling affected the abundance and population dynamics of the clam *Macoma balthica* and the cockle *Cerastoderma edule* (Rossi *et al.* 2007). The authors assume that trampling directly kills or buries specimens, provoking asphyxia. On Argentinean shores it is evident that human activities and urbanization affect the presence and abundance of surf clams in coastal areas (Marcomini *et al.* 2002). Bastida *et al.* (1996) assumed that human activities are probably one of the main factors interfering with the recovery of bivalve populations. The abrupt decrease of *D. hanleyanus* during summer especially at Santa Teresita (‘Publication I’, page 79) is significantly related to mass tourism. Therefore it may be argued that anthropogenic impact is one of the main causes of strong reductions in *D. hanleyanus* abundance at Santa Teresita. Further research should therefore focus on human activities as an important abundance oppressing factor.

5.2 Growth Estimation

5.2.1 *Donax hanleyanus*

The von Bertalanffy growth constant *K* varied insignificantly between 0.47 yr^{-1} (Mar de las Pampas) and 0.48 yr^{-1} (Faro Querandí). During the first two years of life differences in growth parameters become obvious by comparing the present values (Table 5, values 1-3) with those of Penchaszadeh and Olivier (1975) (Table 5, values 4). Forty years ago populations of *D. hanleyanus* grew faster within the first two years ($K = 1.18$) compared to the wedge clams presently studied ($K = 0.48$), but reached a smaller maximal length (33.5 mm *versus* 44.0 mm, Fig. 23). This difference in growth may be caused by relaxed competition with the co-occurring *M. mactroides* population (Fig. 24). Other studies have also demonstrated abundance-dependant growth for various bivalves (Broom 1982; Peterson 1982; Peterson and Black 1987; Peterson and Black 1988; Peterson and Beal 1989; Jensen 1993; Defeo and de Alava 1995; Weinberg 1998; Talman and Keough 2001).

Non-linear growth functions such as the *VBGF* are difficult to compare, and several authors (e.g., Pauly 1979; Munro and Pauly 1983; Moreau *et al.* 1986; Laudien *et al.* 2003a; Herrmann *et al.* under review-d) have demonstrated the suitability of composite indices of *OGP* for inter- and intraspecific comparisons for various clam species. *OGP* data compiled from numerous *Donax* studies (Table 5) confirmed the hypothesis of Laudien *et al.* (2003a) that

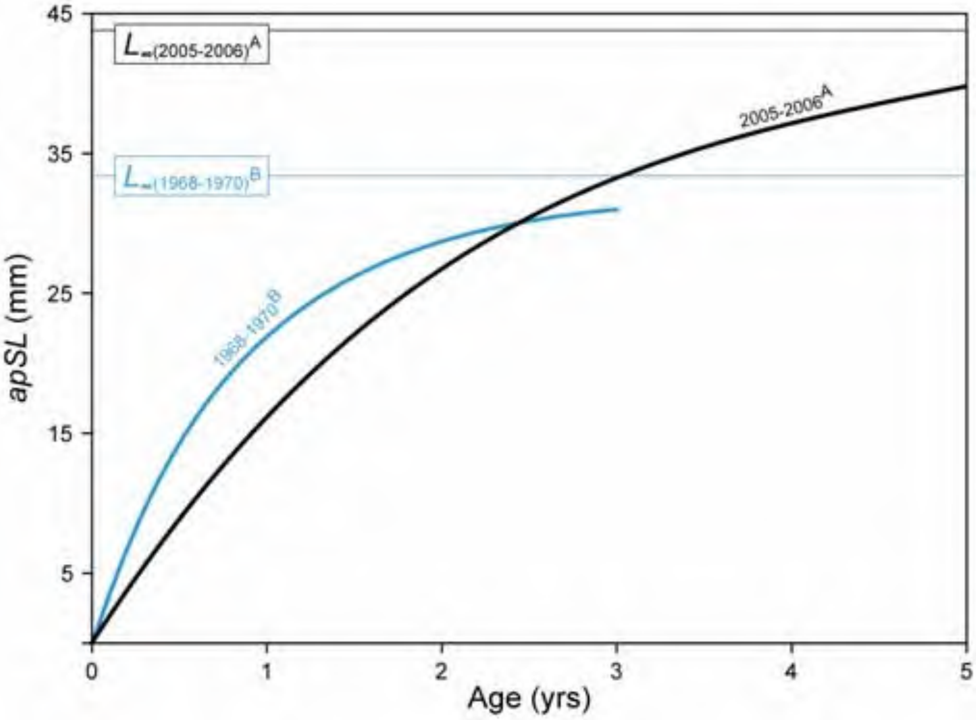

Fig. 23: *VBGF*s of *D. hanleyanus* with the parameters $L_\infty = 44$ mm and $K = 0.47$ yr^{-1} at Mar de las Pampas during 2005-2006 (**A**: present study) in comparison with estimated growth parameters $L_\infty = 33.5$ mm and $K = 1.18$ yr^{-1} at Villa Gesell during 1968-1970 (**B**: Penchaszadeh and Olivier 1975).

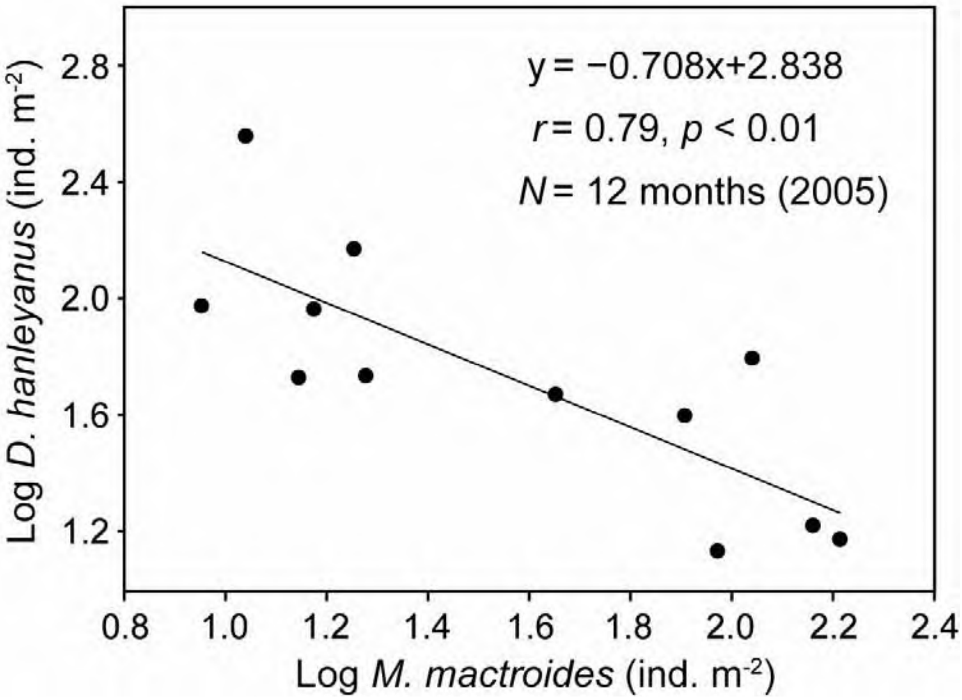

Fig. 24: *D. hanleyanus* - *M. mactroides* linear correlation of abundance (Log ind. m^{-2}) in 2005 at Santa Teresita. Data set published in Herrmann *et al.* (2008b).

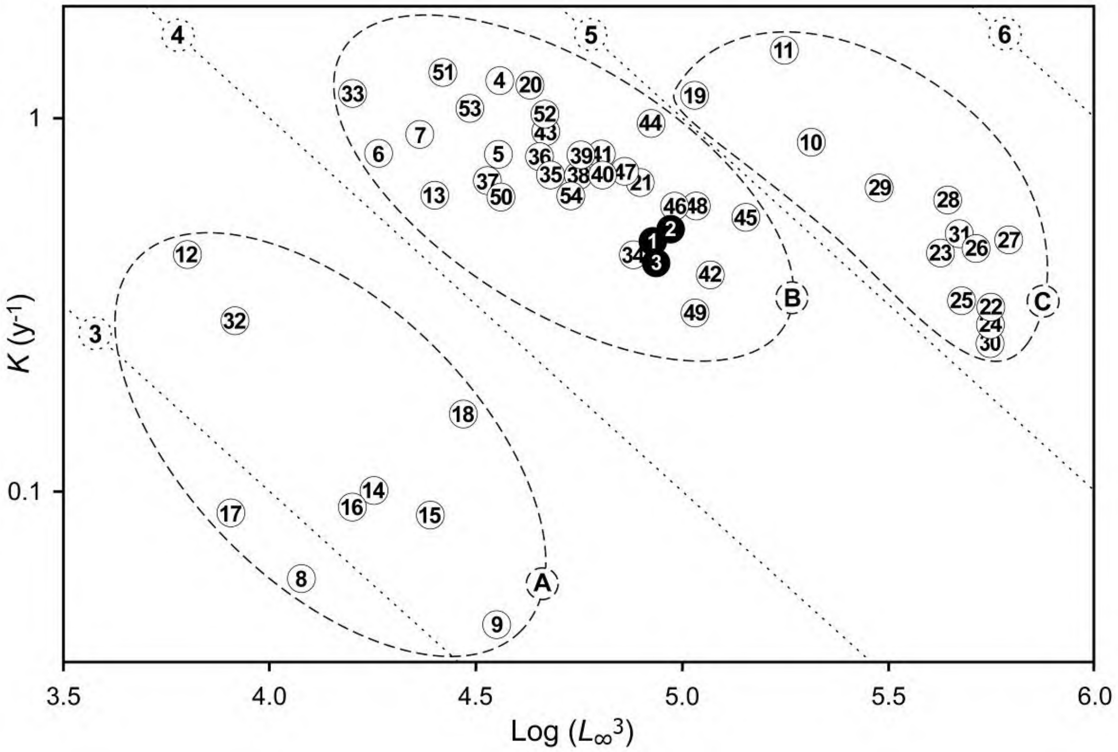

Fig. 25: The auximetric grid compares *OGP* of the Argentinean *D. hanleyanus* from present study (●) with several *Donax* species from different areas (○). Donacids are grouped by the plot (dashed lines) in tropical-subtropical (**A**), temperate (**B**) and upwelling species (**C**). Diagonal dotted lines indicate equal values of *OGP* (numbers in circles). For keys and data sources see Table 5; for the distribution of plotted *Donax* species see Fig. 5.

OGP is habitat-specific (Fig. 25); species populating tropical-subtropical regions show lowest *OGP* (2.84-3.68, group A), temperate species have intermittent *OGP* (4.17-4.91, group B), while species of upwelling areas show the highest *OGP* (5.06-5.65, group C). Even the effect of climate anomalies (Arntz *et al.* 1987) may be detected with the help of the auximetric grid, as indicated by the upwelling surf clam *D. marincovichi* sampled in Peru during normal upwelling years (Table 5, Fig. 25, no. 19) in comparison to the population sampled during (Table 5, Fig. 25, no. 20) and shortly after an El Niño (EN) event 1982-83 (Table 5, Fig. 25, no. 21). Furthermore, *OGP* of the tropical *D. dentifer* (Riascos and Urban 2002) sampled during the EN event 1997-98 (Table 5, Fig. 25, no. 13) clustered with the temperate species (Fig. 25, B), indicate the abnormality during the climate anomaly. As shown for *D. striatus* (Table 5, Fig. 31, no. 33; Rocha-Barreira de Almeida *et al.* 2002) the methods for growth estimates based on *LFD* analyses may not be useful for tropical species with several recruitments throughout the year (Sparre and Venema 1998). A tagging-recapture experiment using for instance *IFM* is recommended.

Table 5: The *VBGF* parameters *K* (yr^{-1}) and L_∞ (mm) of *D. hanleyanus* from the present study (**1-3**) are compared with data of previous investigations (**4-7**) of the same species and with data of several other *Donax* species from different climate areas (Ca). Variations in *OGP* are given for tropical-subtropical (A), temperate (B) and upwelling (C) species. Code numbers (No.) are equivalent to Fig. 25. For the distribution of *Donax* species see Fig. 5.

No.	Species	Country	Area	Fig. 5	Lat.	Long.	Ca	*K*	L_∞	*OGP*	Source
1	*D. hanleyanus*[2]	Argentina	Mar de las Pampas	m	37°19'S	57°00'W	B	0.47	44.00	4.6	Present study (*LFD* method)
2	*D. hanleyanus*[2]	Argentina	Faro Querandí	m	37°29'S	57°07'W	B	0.48	44.00	4.61	Present study (*LFD* method)
3	*D. hanleyanus*[6]	Argentina	Mar de las Pampas	m	37°19'S	57°00'W	B	0.41	44.00	4.54	Present study (*IFM* method)
4	*D. hanleyanus*[2]	Argentina	Villa Gesell	m	37°16'S	56°59'W	B	1.18	33.50	4.65	Penchaszadeh and Olivier (1975)
5	*D. hanleyanus*[2]	Uruguay	Barra del Chuz	m	33°40'S	53°29'W	B	0.80	33.00	4.46	Defeo (1996)
6	*D. hanleyanus*[2]	Brazil	Marambaia	m	23°03'S	43°34'W	B	0.80	26.40	4.17	Cardoso and Veloso (2003)
7	*D. hanleyanus*[2]	Brazil	Marambaia	m	23°03'S	43°34'W	B	0.90	28.50	4.32	Cardoso and Veloso (2003)
8	*D. cuneatus*[2]	India	Palk Bay	y	9°17'N	79°05'E	A	0.06	22.87	2.84	Nayar (1955)
9	*D. cuneatus*[2,5]	India	Miriya Bay, Ratnagiri	y	17°N	53°E	A	0.04	33.02	3.19	Talikhedkar *et al.* (1976)
10	*D. deltoides*[2]	Australia	Goolwa	ü	-	-	C	0.86	59.00	5.25	King (1985)
11	*D. deltoides*[2]	Australia	New South Wales	ü	36°S	151°E	C	1.59	56.00	5.45	Saenger and Keyte (1990)
12	*D. denticulatus*[2]	Venezuela	Araya Península	j	10°38'N	64°16'W	A	0.43	18.50	3.43	Vélez *et al.* (1985)
13	*D. dentifer*[2]	Colombia	Bahía Málaga	e	4°05'N	77°16'W	A	0.62	29.30	4.19	Riascos and Urban (2002)
14	*D. faba*[1,5]	India	Gulf of Mannar	z	-	-	A	0.10	26.15	3.25	Alagarswami (1966)
15	*D. incarnatus*[2,5]	India	Shertallai	w	9°42'N	76°20'E	A	0.09	29.04	3.33	Ansell *et al.* (1972)
16	*D. incarnatus*[2,5]	India	Cochin	w	10°00'N	76°12'E	A	0.09	25.13	3.16	Ansell *et al.* (1972)
17	*D. incarnatus*[2,5]	India	Goa	w	15°22'N	73°52'E	A	0.09	20.06	2.85	Nair *et al.* (1978)
18	*D. incarnatus*[2]	India	Panambur	w	12°27'N	74°48'E	A	0.16	30.94	3.68	Thippeswamy and Joseph (1991)
19	*D. marincovichi*[2]	Peru	Santa Maria del Mar	f	12°20'S	76°50'W	C	1.00	46.00	4.99	Arntz *et al.* (1987) → *before EN*
20	*D. marincovichi*[2]	Peru	Santa Maria del Mar	f	12°20'S	76°50'W	C	1.17	35.00	4.70	Arntz *et al.* (1987) → *during EN*
21	*D. marincovichi*[2]	Peru	Santa Maria del Mar	f	12°20'S	76°50'W	C	0.70	42.00	4.71	Arntz *et al.* (1987) → *after EN*
22	*D. serra*[2]	South Africa	Elands Bay	t	32°19'S	18°21'E	C	0.28	82.00	5.19	de Villiers (1975a)
23	*D. serra*[2]	South Africa	Elands Bay	t	32°19'S	18°21'E	C	0.43	75.00	5.26	de Villiers (1975a)
24	*D. serra*[2]	South Africa	Melkbosstrand	t	33°42'S	18°26'E	C	0.28	82.00	5.18	de Villiers (1975a)
25	*D. serra*[2]	South Africa	Melkbosstrand	t	33°42'S	18°26'E	C	0.32	78.00	5.19	de Villiers (1975a)
26	*D. serra*[2]	South Africa	Elands Bay	t	32°19'S	18°21'E	C	0.46	79.00	5.36	Laudien *et al.* (2003a)
27	*D. serra*[2]	South Africa	Koeberg	t	33°40'S	18°25'E	C	0.47	85.00	5.46	Laudien *et al.* (2003a)
28	*D. serra*[2]	South Africa	St Francis Bay	t	33°59'S	25°20'E	C	0.60	76.00	5.42	Laudien *et al.* (2003a)

Table 5: *(continued)*

No.	Species	Country	Area	Fig. 5	Lat.	Long.	Ca	*K*	L_∞	*OGP*	Source
28	*D. serra* [2]	South Africa	St Francis Bay	t	33°59'S	25°20'E	C	0.60	76.00	5.42	Laudien *et al.* (2003a)
29	*D. serra* [2]	South Africa	St Francis Bay	t	33°57'S	25°04'E	C	0.65	67.00	5.29	Laudien *et al.* (2003a)
30	*D. serra* [2]	South Africa	Langestrand	t	22°47'S	14°33'E	C	0.27	82.00	5.18	Laudien *et al.* (2003a)
31	*D. serra* [2]	South Africa	Paaltjies	t	22°59'S	14°24'E	C	0.47	78.00	5.32	Laudien *et al.* (2003a)
32	*D. striatus* [2]	Venezuela	Tucucas, Txori	k	-	-	A	0.29	20.20	3.37	Farache (1980)
33	*D. striatus* [2]	Brazil	Futuro Beach	k	03°42'S	38°27'W	A	1.16	25.10	4.26	Rocha-Barreira de Almeida *et al.* (2002)
34	*D. trunculus* [2,4]	France	Vertbois	p	45°50'N	1°20'W	B	0.45	43.48	4.57	Ansell and Lagardère (1980)
35	*D. trunculus* [2,4]	France	Vertbois	p	45°50'N	1°20'W	B	0.70	36.33	4.53	Ansell and Lagardère (1980)
36	*D. trunculus* [2,4]	France	Vertbois	p	45°50'N	1°20'W	B	0.79	35.55	4.55	Ansell and Lagardère (1980)
37	*D. trunculus* [2,4]	France	Vertbois	p	45°50'N	1°20'W	B	0.68	32.25	4.36	Ansell and Lagardère (1980)
38	*D. trunculus* [2,4]	France	Vertbois	p	45°50'N	1°20'W	B	0.70	38.22	4.59	Ansell and Lagardère (1980)
39	*D. trunculus* [2,4]	France	St. Trojan	p	45°50'N	1°20'W	B	0.72	38.41	4.61	Ansell and Lagardère (1980)
40	*D. trunculus* [2,4]	France	St. Trojan	p	45°50'N	1°20'W	B	0.74	39.78	4.67	Ansell and Lagardère (1980)
41	*D. trunculus* [2,4]	France	St. Trojan	p	45°50'N	1°20'W	B	0.77	39.70	4.68	Ansell and Lagardère (1980)
42	*D. trunculus* [2]	France	Bay of Douarnenez	p	48°05'N	4°18'W	B	0.38	48.90	4.65	Guillou and Le Moal (1980)
43	*D. trunculus* [2]	France	Camarque	p	43°27'N	4°26'W	B	0.96	35.99	4.65	Bodoy (1982)
44	*D. trunculus* [2]	Spain	Atlantic	p	-	-	B	0.97	43.80	4.91	Fernández *et al.* (1984)
45	*D. trunculus* [2]	Spain	Atlantic, El Barquero	p	-	-	B	0.55	52.84	4.91	Mazé and Laborda (1988)
46	*D. trunculus* [2]	Spain	Mediterano, Callera	p	-	-	B	0.58	46.00	4.75	Ramon *et al.* (1995)
47	*D. trunculus* [3]	Spain	Mediterano, Callera	p	-	-	B	0.71	41.80	4.71	Ramon *et al.* (1995)
48	*D. trunculus* [2]	Portugal	Faro	p	36°57'N	7°53'W	B	0.58	47.30	4.79	Gaspar *et al.* (1999)
49	*D. trunculus* [2]	Italy	Apulia	p	41°55'N	15°26'E	B	0.30	47.56	4.51	Zeichen *et al.* (2002)
50	*D. vittatus* [2]	France	St. Trojan	n	45°50'N	1°20'W	B	0.61	33.15	4.35	Ansell and Lagardère (1980)
51	*D. vittatus* [2]	France	St. Trojan	n	45°50'N	1°20'W	B	1.32	29.76	4.54	Ansell and Lagardère (1980)
52	*D. vittatus* [2]	France	St. Trojan	n	45°50'N	1°20'W	B	1.01	35.90	4.67	Ansell and Lagardère (1980)
53	*D. vittatus* [2]	France	Vertbois	n	45°50'N	1°20'W	B	1.06	31.28	4.51	Ansell and Lagardère (1980)
54	*D. vittatus* [2,4]	France	Bay of Douarnenez	n	48°05'N	4°18'W	B	0.68	38.00	4.57	Guillou and Le Moal (1980)

[1] Maximum length, [2] age estimated from *LFD*s, [3] age estimated from hyaline growth rings, [4] age estimated from external growth rings, [5] values calculated on monthly basis from raw data reported by the authors and [6] age estimated from *IFM*.

5.2.2 *Mesodesma mactroides*

The *VBGF* with the best fit confirms that *M. mactroides* is a fast-growing species ($K = 0.47$; Table 6, no. 1-2), in line with estimates from previous studies of Argentinean and Uruguayan populations ($K = 0.3$-0.9; Table 6, no. 3-14). However, changes in growth parameters are evident by comparing recent values (Table 6, no. 1-2) with those of Capezzani *et al.* (1971) (Table 6, no. 3). Yellow clams showed a lower growth constant ($K = 0.28$ *versus* 0.47) in 1968-1970, indicating that the growth within the first five years of life was slower four decades ago, but that maximum length was larger than at present (Fig. 26, $L_{\infty(1968\text{-}70)} = 84$ mm; $L_{\infty(2005\text{-}06)} = 71$ mm). Several studies have estimated maximum shell lengths of *M. mactroides* between 84 mm (in Argentina: Olivier *et al.* 1971) and 100 mm (in Uruguay: Defeo *et al.* 1992a). This difference may be attributed to competition with the dominant *D. hanleyanus* population (Fig. 24), but also due to different methods applied (*LFD*s, external growth rings or size at age data - analysed with ELEFAN I, Shepherd's length composition analysis, SLCA or CAST: Stamatopoulus and Caddy 1989) (cf. Table 6, no. 1-13). While Defeo *et al.* (1992c) observed strong seasonal variation ($C = 1.0$) in growth rates for a *M. mactroides* population from Uruguay, the variation documented by Fiori and Morsán (2004) was low ($C = 0.45$), and Olivier *et al.* (1971) recorded no seasonal growth variation for this species from the Argentinean coast. The present study also estimated only very weak seasonality ($C = 0.1$).

In line with *Donax*, the application of the *OGP* index has proven to be a useful tool to compare non-linear *VBGF*s of several *Mesodesma* populations. *OGP* values for *M. mactroides* from the present study, ranging from 5.23 to 5.24 (Table 6, Fig. 27, no. 1-2) are conform with values of 5.22 and 5.30 calculated from data sets of Olivier *et al.* (1971) and Fiori and Morsán (2004), respectively from Argentinean populations of the same species. It can be assumed that *SST* and food availability are key factors affecting growth as well as aspects of population dynamics such as production, reproduction, recruitment and mortality. The relatively high values of *OGP*s from Uruguay (Table 6, Fig. 27, no. 11-14) and Peru (before and during an EN event, Table 6, Fig. 27, no. 15-16), suggest a negative correlation with latitude, which is discussed further in

'Publication II' (page 109). This trend provides support to the latitudinal gradient hypothesis of marine invertebrates (Defeo and Cardoso 2002), which predicts a positive correlation between body size and latitude: populations from subtropical beaches exhibit higher growth and mortality rates and shorter life spans than those of temperate beaches. However, the latitudinal difference in *OGP* would be better understood if growth studies on several populations could be linked to quantitative and qualitative phytoplankton data. Results compiled from several studies of two different *Mesodesma* species confirmed again the habitat-specific *OGP* hypothesis (Laudien *et al.* (2003a) (Fig. 27): *OGP* is lowest (5.22-5.81, group A) for *M. mactroides* populating temperate regions, and highest (6.33, group B) for *M. donacium* of an upwelling area. Again climate anomalies may be detected, indicating a lower *OGP* for the upwelling surf clam *M. donacium* sampled in Peru during and shortly after EN 1982-1983 (Fig. 27, no. 15-16) compared to data from normal upwelling years (Fig. 27, no. 14) (Arntz *et al.* 1987).

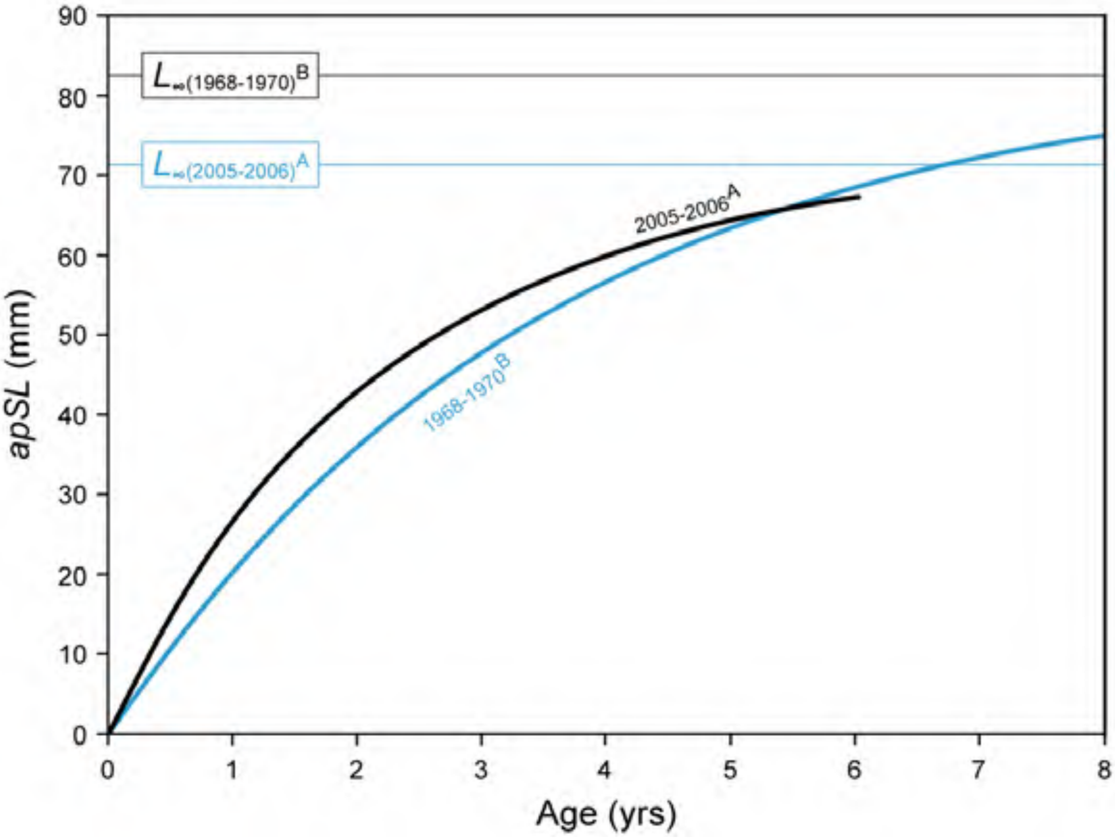

Fig. 26: *VBGF*s of *M. mactroides* with the parameters L_∞ = 71 mm and *K* = 0.47 yr^{-1} from Santa Teresita (**A**: present study) in comparison to estimated growth parameters L_∞ = 84 mm and *K* = 0.28 yr^{-1} from Mar Azul during 1968-1970 (**B**: Capezzani *et al.* 1971).

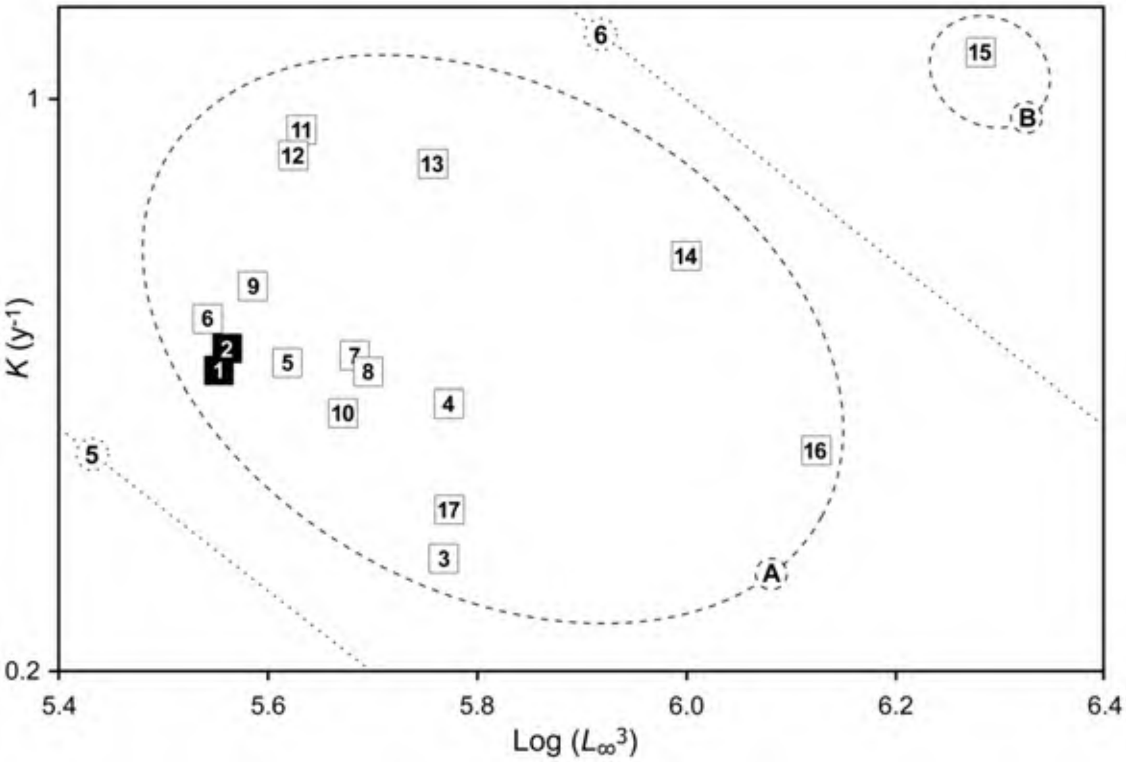

Fig. 27: Auximetric grid comparing *OGP* of the Argentinean *M. mactroides* from the present study (■) with several *Mesodesma* species from different areas (□) showing temperate (**A**) and upwelling species (**B**). Diagonal dotted lines indicate equal values of *OGP* (numbers in circles). For keys and data sources see Table 6; for the distribution of plotted *Mesodesma* species see Fig. 5.

Table 6: The *VBGF* parameters *K* (yr^{-1}) and L_∞ (mm) of *M. mactroides* from the present study (**1** and **2**) are compared with data of previous investigations (**3-14**) of the same species and with data of *M. donacium* (**15-17**) from different climate areas (Ca). Variations in *OGP* are given for temperate (A) and upwelling (B) species. Code numbers (No.) are equivalent to Fig. 27. The distribution of listed *Mesodesma* species is shown in Fig. 5.

No.	Species	Country	Area	Fig. 5	Lat.	Long.	Ca	*K*	L_∞	*OGP*	Source
1	*M. mactroides* [1,5]	Argentina	Santa Teresita	d	36°32'S	56°41'W	A	0.47	71.00	5.23	Present study (*LFD* method)
2	*M. mactroides* [4,5]	Argentina	Santa Teresita	d	36°32'S	56°41'W	A	0.48	71.00	5.24	Present study (*IFM* method)
3	*M. mactroides* [3]	Argentina	Faro Querandí	d	37°29'S	57°07'W	A	0.28	83.76	5.22	Capezzani *et al.* (1971)
4	*M. mactroides* [1,5]	Argentina	Costa Chica	d	36°31'S	56°41'W	A	0.43	84.00	5.41	Luzzatto (2007)
5	*M. mactroides* [2,5]	Argentina	Monte Hermoso	d	38°59'S	61°15'W	A	0.48	74.66	5.30	Fiori and Morsán (2004)
6	*M. mactroides* [3,5]	Argentina	Monte Hermoso	d	38°59'S	61°15'W	A	0.54	70.42	5.28	Fiori and Morsán (2004)
7	*M. mactroides* [1,5]	Argentina	Isla del Jabalí	d	40°33'S	62°14'W	A	0.49	78.42	5.37	Fiori and Morsán (2004)
8	*M. mactroides* [1,5]	Argentina	Isla del Jabalí	d	40°33'S	62°14'W	A	0.47	79.13	5.37	Fiori and Morsán (2004)
9	*M. mactroides* [2,5]	Argentina	Isla del Jabalí	d	40°33'S	62°14'W	A	0.59	72.77	5.36	Fiori and Morsán (2004)
10	*M. mactroides* [3,5]	Argentina	Isla del Jabalí	d	40°33'S	62°14'W	A	0.42	77.73	5.30	Fiori and Morsán (2004)
11	*M. mactroides* [3,7]	Uruguay	Coronilla-Barra del Chuy	d	33°39'S	53°28'W	A	0.90	75.47	5.59	Defeo *et al.* (1992c)
12	*M. mactroides* [1,5]	Uruguay	Coronilla-Barra del Chuy	d	33°39'S	53°28'W	A	0.84	75.00	5.55	Defeo *et al.* (1992c)
13	*M. mactroides* [1,5]	Uruguay	Coronilla-Barra del Chuy	d	33°39'S	53°28'W	A	0.82	83.00	5.67	Defeo *et al.* (1992a)
14	*M. mactroides* [1,6]	Uruguay	Coronilla-Barra del Chuy	d	33°39'S	53°28'W	A	0.64	100.00	5.81	Defeo *et al.* (1992a)
15	*M. donacium* [1,5]	Peru	Mar Santa Maria del Mar	a	12°20'S	76°50'W	B	1.13	124.00	6.33	Arntz *et al.* (1987) → *before EN*
16	*M. donacium* [1,5]	Peru	Mar Santa Maria del Mar	a	12°20'S	76°50'W	B	0.38	110.00	5.70	Arntz *et al.* (1987) → *during EN*
17	*M. donacium* [1,5]	Peru	Mar Santa Maria del Mar	a	12°20'S	76°50'W	B	0.32	84.00	5.28	Arntz *et al.* (1987) → *after EN*

[1] age estimated from *LFD*s, [2] age estimated from external growth rings, [3] age estimated from size at age data, [4] age estimated from *IFM*, [5] values obtained by the application of ELEFAN, [6] values obtained by the application of SLCA, [7] values obtained by the application of CAST.

5.2.3 Comparison of Growth Estimation Methods

Short time *in situ* growth experiments with *D. hanleyanus* and *M. mactroides* showed that the fluorescent stain calcein can be recommended as a non-lethal marker for surf clams. Both methods used, the analysis of size increments derived after an experimental time following *IFM* and the analysis of *LFD*, are equally appropriate to estimate growth of both surf clams as indicated by the residuals derived from both methods. Residuals were of similar magnitude and distribution. However, each method has its own limitations. In comparison the direct method has the following advantages: daily growth can be determined, necessary numbers of specimens are relatively low, costs for fieldwork are lower and less sampling time is needed to obtain data. On the other hand the *LFD* analysis may reveal seasonality, less laboratory work is required, no expensive equipment is needed and fieldwork requires less manpower. In conclusion, growth of temperate bivalves such as *D. hanleyanus* and *M. mactroides* can be estimated well by carrying out a relatively short-time tagging-recapture experiment, however it is recommended to use both, the *IFM* and the *LFD* method to determine growth of tropical bivalves, which have several recruitments throughout the year (Sparre and Venema 1998).

5.3 Reproduction

5.3.1 *Donax hanleyanus*

Results of the wedge clam's reproductive biology, obtained from three beaches over 25 months, demonstrate that at population level *D. hanleyanus* respond systematically to beach morphodynamics in a manner contrary to that predicted by the habitat harshness hypothesis (HHH: Defeo *et al.* 2001; 2003) (Fig. 28).

The HHH, combining the 'autoecological hypothesis' (AH) (Noy-Meir 1979) and the 'swash exclusion hypothesis' (SEH) (McArdle and McLachlan 1991; 1992) (for details see 'Publication IV', page 159), predicts that (i) at the community level, reflective beaches will exhibit lower species richness, diversity and abundance while (ii) at the population level, they will be characterised by lower abundance, growth, fecundity, reproductive output and higher mortality rates. However, other recent investigations suggest that populations co-occurring in sandy beaches with a range of contrasting morphodynamics do not conform consistently to these predictions.

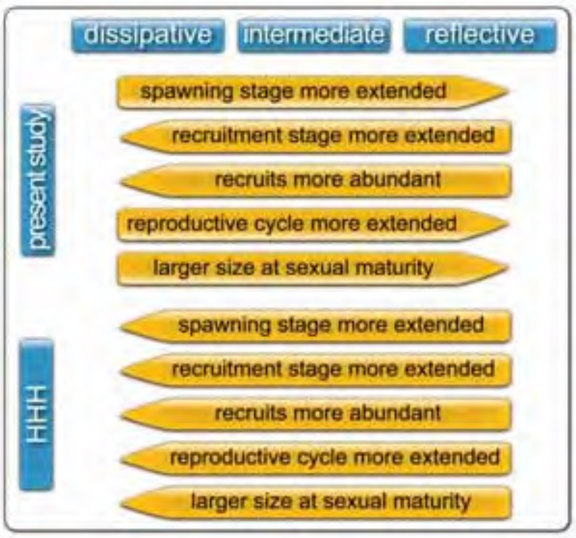

Fig. 28: The reproductive biology of *D. hanleyanus*, reflecting beach morphodynamics of a dissipative (Santa Teresita), intermediate (Mar de las Pampas) and reflective beach (Faro Querandí) compared to predictions of the HHH.

The population at Santa Teresita (dissipative beach) exhibited a greater abundance of recruits and an extended recruitment period, but spawning specimens were greatly outnumbered by those in the sexual rest stage. Spawning events were registered twice each year at Santa Teresita (early spring and spring-summer) and Mar de las Pampas (intermediate beach) (winter and summer), whereas continuous gamete release was noted at Faro Querandí (reflective beach). Maturity was first observed with approximately 9 mm *apSL* and 0.02 g *SFWM* in single *D. hanleyanus* individuals. About 50 % of the population attained maturity at 15 mm *apSL* and 0.15 g *SFWM*, and 100 % were mature at a size of 23-27 mm *apSL* and 0.4-

0.9 g *SFWM*. Size and biomass at first maturity were lower at the dissipative beach, whereas the monthly mean abundance of *D. hanleyanus* was higher at the reflective beach. Furthermore, the current study demonstrated that the ‘hypothesis of habitat safety (HHS)’, originally postulated by Defeo and Gómez (2005) for supralittoral species, may be extended to intertidal species. The combination of narrow swashes and steep slopes make reflective beaches a safer and more stable environment for supralittoral and intertidal species such as *D. hanleyanus*. Details of the wedge clam’s reproductive biology are presented in ‘Publication III’ (page 131).

5.3.2 *Mesodesma mactroides*

Presently, the reproductive biology of *M. mactroides* shows a clear difference in the composition of gonad stages during summer, compared with a forty years old investigation, obtained from a *Mesodesma* population approximately 100 km south of the Santa Teresita population (Mar Azul, Christiansen 1971). Whereas the later author found nearly all developmental stages all year round, the present study recorded active, ripe, spawning and cytolysed stages only from autumn to spring, and the sexual rest stage occurred only in summer. The absence of these gonad stages in both summers is attributed to a single cohort with small shell length (Fig. 13, mean *apSL*s of 8 mm in summer seasons, ‘Publication II’, page 109) and to the consequent immaturity (sexual rest stage). In contrast to the recent population structure Olivier and Penchaszadeh (1971b) found three cohorts and individuals of commercial size (> 60 mm, Coscarón 1959) were found throughout the year (Fig. 13, blue histograms). However, comparisons of histological data from areas with different beach morphodynamics such as Santa Teresita (dissipative/sheltered) and Mar Azul (exposed/intermediate) are possible only to some extent, since different behavioural patterns in the reproductive strategy of *D. hanleyanus* populations were found, comparing a reflective and a dissipative beach (‘Publication III’, page 131). The present investigation of *M. mactroides* gonads suggests two reproductive events per year; the first one in winter and the second one in spring, which is in line with observations of Christiansen (1971). Seasonal changes in *SST* trigger gametogenesis, while short-term temperature changes may stimulate spawning (Ansell 1961; Seed 1976). The present results demonstrate that *SST* is significantly correlated with gonad development. Low mean temperatures coincided with maximum oocyte size and gamete initiation (late autumn-winter). Increases in *SST* 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 ripe and spawning individuals. Maximum gamete ripeness and size was observed in winter (July-August) and reflected seasonal minimum *SST*. Noticeable decreases in oocyte sizes, oocyte abundance and the increased number of ripe and spawned individuals was associated with rapid increases in *SST* during spring (Fig. 29a-c). Furthermore, seasonal variation of the *AFDM* was positively correlated with *SST* as well as with the gametogenic cycle (Fig. 29a, d). 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 composition. Thus, 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 ripe and spawning *M. mactroides* (Fig. 29b). This suggests that phytoplankton may also have a direct impact on the reproductive cycle of *M. mactroides*. When assuming that the collected recruits originated from the studied adult population, it can be assumed that *M. mactroides* has a meroplanktonic phase of approximately three 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 (Fig. 29e). After weak gamete release periods in July-August 2005 and June-July 2006, recruits were not present in the sampling area. In contrast, four decades ago Christiansen (1971) observed recruits during spring (November and December) as well as an 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 (1971b) monitored three cohorts between 1968 and 1969, the present study detected only one cohort during

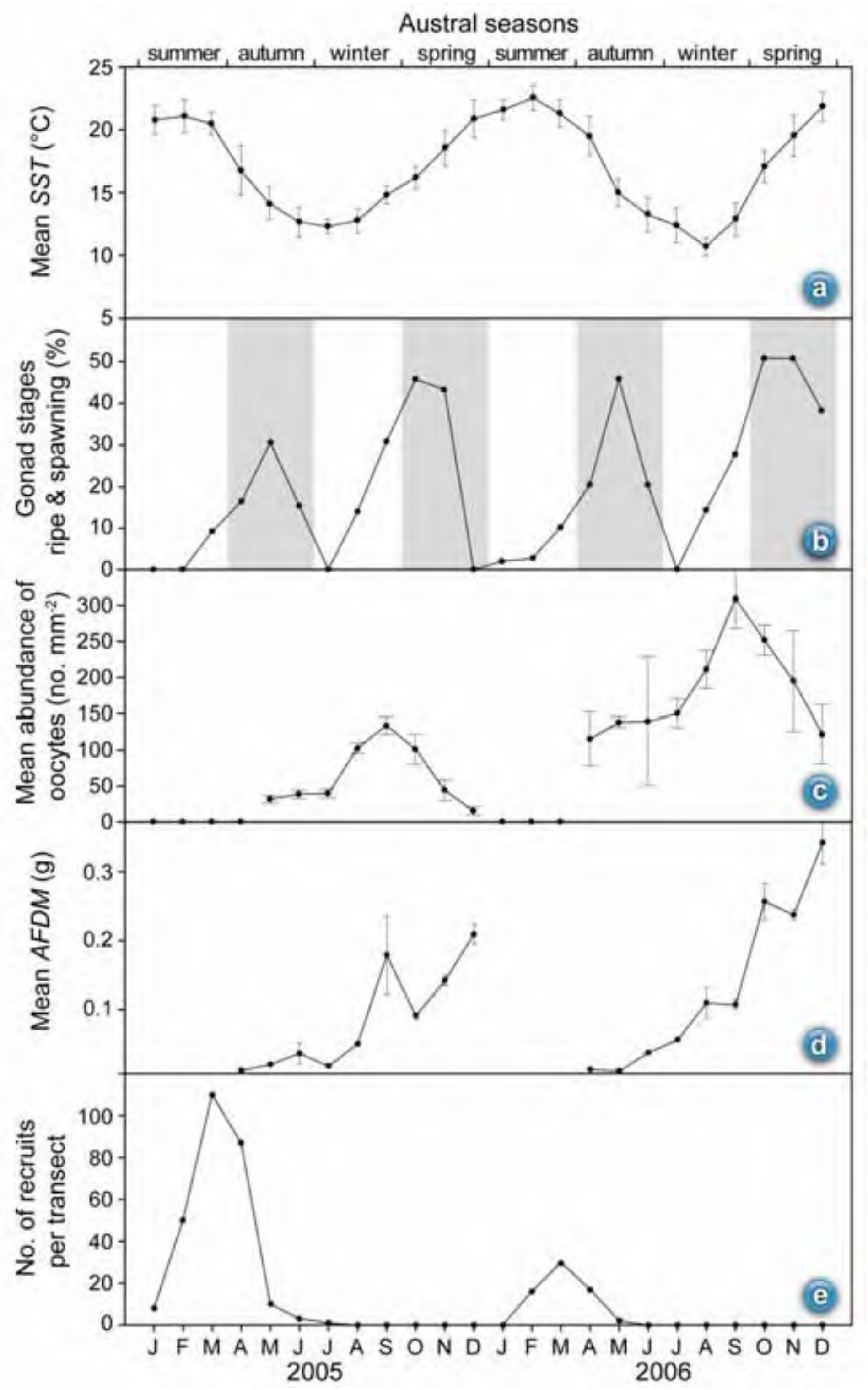

Fig. 29: *M. mactroides* at Santa Teresita: (**a**) mean *SST* (°C) measured daily at Santa Teresita, (**b**) percentage of gonad stages ripe and spawning, (**c**) mean abundance of oocytes (no. mm^{-2}), (**d**) mean biomass (*AFDM*) (g) and (**e**) number of recruits (2-6 mm) recorded per monthly transect. *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 deviations (SD). Data sets of plots are published in Herrmann *et al.* (2008a).

2005-2006 (Fig. 13, blue histograms). Unimodal oocyte size-frequency distribution histograms (‘Publication IV’, page 159) 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 explains the absence of successive periods of maturing oocytes.

6 Publications

The five publications[8] included in this doctoral thesis are listed below and my contribution to each investigation is given in detail:

Publication I

Marko Herrmann, Jürgen Laudien, Pablo E. Penchaszadeh, Sönke Fischer, Wolf E. Arntz (1st revision under review). Population structure, growth and production of the wedge clam *Donax hanleyanus* (Bivalvia: Donacidae) from northern Argentinean beaches. Estuarine, Coastal and Shelf Science.

I developed the scientific idea with the second author and collected monthly samples by measuring 21,405 *D. hanleyanus* on three different sandy beaches during 25 months. Besides, I did the analysis of data as well as the statistical analysis. The fourth author calculated the growth parameters. The manuscript was written by myself and improved in cooperation with the co-authors.

Publication II

Marko Herrmann, José E. F. Alfaya, Jürgen Laudien, Pablo Penchaszadeh, Wolf E. Arntz (under review). Population structure, growth and production of the yellow clam *Mesodesma mactroides* (Bivalvia: Mesodesmatidae) from a high-energy, temperate beach in northern Argentina. Helgoland Marine Research.

I developed the scientific idea and collected monthly samples by measuring 3,015 *M. mactroides* on three different sandy beaches during 25 months assisted by the second author. I did as well the analysis of data as well as the statistical analysis. The manuscript was written by myself and improved in cooperation with the co-authors.

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[8] For reasons of space in this doctoral thesis the reference lists respectively of the five publications have been left out but the literature of all papers has been summarised under 'References' (page 7.5).

Publication III

Marko Herrmann, Pablo E. Penchaszadeh, Wolf E. Arntz, Jürgen Laudien (under review). Testing the habitat harshness hypothesis: Reproductive biology of the wedge clam *Donax hanleyanus* (Bivalvia: Donacidae) at three Argentinean sandy beaches with contrasting morphodynamics. Marine Biology.

I developed the scientific idea with the last author and collected 2,520 *D. hanleyanus* by monthly sampling on three different sandy beaches during 25 months. Of all samples I prepared histological micro sections. Besides, I did the analysis of data, after counting 15,450 oocytes and measuring 17,779 of them as well as the statistical analysis. The manuscript was written by myself and improved by the co-authors.

Publication IV

Marko Herrmann, José E. F. Alfaya, Mauro L. Lepore, Pablo E. Penchaszadeh, Jürgen Laudien (under review). The reproductive cycle and gonad development of the Northern Argentinean *Mesodesma mactroides* (Bivalvia: Mesodesmatidae). Helgoland Marine Research.

I developed the scientific idea and collected 720 *M. mactroides* by monthly sampling on three different sandy beaches during 25 months assisted by the second author. I did the statistical analysis and together with the second author data were analysed by preparing histological micro sections of all samples. The manuscript was written jointly with the second author. The paper was improved by all co-authors.

Publication V

Marko Herrmann, Wolf E. Arntz, Pablo E. Penchaszadeh, Jürgen Laudien (under review). Growth estimations of the Argentinean wedge clam *Donax hanleyanus*: A comparison between length-frequency distribution and size-increment analysis. Journal of Experimental Marine Biology and Ecology.

I developed the scientific idea with the last author. I realised *in vitro* and *in situ* feeding and growth experiments, analysed all data and did the statistical analysis. The manuscript was written by myself and improved by the co-authors.

6.1 Publication I

Population structure, growth and production of the wedge clam *Donax hanleyanus* (Bivalvia: Donacidae) from northern Argentinean beaches.

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Estuarine, Coastal and Shelf Science, manuscript number: ECSS-D-08-00016R1, 1st revision *under review*

Keywords wedge clam, population dynamics, growth performance indices, grain size analysis, human impact

Abstract *Donax hanleyanus* (Bivalvia: Donacidae) dominates fine to coarse sandy beach communities of the northern Argentinean Atlantic coast. The population biology of this intertidal wedge clam was studied by determining population structure, growth and production at the three locations Santa Teresita, Mar de las Pampas (both from December 2005 to December 2006) and Faro Querandí (from March 2005 to December 2006). Von Bertalanffy growth functions were established from length-frequency distributions using an asymptotic length (L_∞) of 44 mm and the growth constants (K) of 0.46 and 0.47 yr^{-1} respectively of Mar de las Pampas and Faro Querandí. Compared with growth studies four decades ago, *D. hanleyanus* today is growing more slowly, but is reaching a higher maximum length. Longevity is estimated to be approximately five years. The present study confirms that the overall growth performance index (*OGP*) is habitat-specific, grouping Donacidae into tropical-subtropical, temperate and upwelling species. The intertidal biomass of *D. hanleyanus* ranged between 0.04 and 1.32 g *AFDM* m^{-2} yr^{-1}. Individual production revealed the highest value at 30 mm length (0.16 g *AFDM* $m^{-2}yr^{-1}$) and annual production ranged between 0.08 and 0.99 g *AFDM* $m^{-2}yr^{-1}$, resulting in renewal rate values ($P/\bar{B}$) between 0.82 and 2.16. The $P/\bar{B}$ ratios of *D. hanleyanus* populations increased with decreasing latitude from temperate to tropical regions. *D. hanleyanus* was found living with the sympatric yellow clam *Mesodesma mactroides*, whereby the abundance of the latter significantly negatively correlated with the absence of *D. hanleyanus* at Santa Teresita. Spatial differences in abundance are significantly related to sand texture as confirmed by non-metrical multidimensional scaling, but not to *SST*. However, the decrease of *D. hanleyanus* appears to be principally related to human activities.

Introduction

Exposed sandy beaches are some of the most dynamic environments in the world. Their invertebrate populations and communities are usually considered to be regulated mainly by beach morphodynamics depending on physical parameters such as wave energy, wind velocity, tide forces and sand grain size. On a worldwide basis, Donacidae (super family Tellinacea) form by far the most diverse group inhabiting such highly dynamic environments integrating the genera *Egeria*, *Iphigenia* and *Donax*, with the latter group being composed of 64 species (Pearse *et al.* 1942; Ansell 1983; Brown and McLachlan 1990; Wilson 1999). In some cases, they dominate the macrozoobenthic communities in number and biomass, which is also the case for the studied *Donax* populations (> 95 %: McLachlan *et al.* 1981; Arntz and Fahrbach 1991; Ieno and Bastida 1998).

Donax hanleyanus Philippi, 1847, also known as the wedge clam and in Argentina as ‘berberecho’, can be found along the South American Atlantic coast from tropical (17°S Caravelas, Brazil) to temperate regions (37°S Punta Mogotes in Mar del Plata, province of Buenos Aires) (Penchaszadeh and Olivier 1975; Narchi 1978; Cardoso and Veloso 2003). This intertidal suspension-feeder represents the only *Donax* species occurring throughout the Argentinean intertidal (Penchaszadeh and Olivier 1975). As is characteristic of donacids, this bivalve has adapted to live in exposed swash zones characterized by a fair amount of wave action aerating the sediment. This keeps organic detritus in suspension and allows for tidal migration (Mori 1938; Ansell and Trevallion 1969; Penchaszadeh and Olivier 1975; Narchi 1978; Ansell 1983). Although fossils of *D. hanleyanus* have been recorded in South America since the

Querandinense period of marine transgression in the early Holocene (von Ihering 1907), live specimens of *D. hanleyanus* were reported from the Argentinean coast not earlier than 1960 (Penchaszadeh and Olivier 1975), from Brazil in 1949 (Lange de Morretes) and from Uruguay in 1951 (Barattini). Planktonic larvae of *D. hanleyanus* have been shown to cut across the Río de la Plata with favourable ocean currents and settled on sandy beaches south of this estuary (Penchaszadeh and Olivier 1975).

Although several *Donax* clams are targeted by artisanal fisheries (McLachlan *et al.* 1996b) and *D. hanleyanus* is edible (Veloso *et al.* 1953; Penchaszadeh and Olivier 1975), this species is not commercially exploited in Argentina. However, like most donacids *D. hanleyanus* plays an important role in the food web by linking benthic with planktonic ecosystems (Wade 1967a; McLachlan *et al.* 1981; McLachlan and Lewin 1981; McDermott 1983; DeLancey 1989; Heymans and McLachlan 1996; Soares *et al.* 1997). This wedge clam is the main primary consumer in soft bottom communities is in turn subject to predation by a wide variety of invertebrates, fish, birds and mammals (Penchaszadeh and Olivier 1975; Peterson *et al.* 2000; Salas *et al.* 2001). Only a few studies on *D. hanleyanus* from Argentinean shores are published dealing with ecological aspects (Penchaszadeh and Olivier 1975), beach morphodynamics and their influence on wedge clam's abundance (Marcomini *et al.* 2002), anthropogenic influences (Dadon *et al.* 2001) and siphon regeneration (Luzzatto and Penchaszadeh 2001); however, none of the studies investigated the population dynamics.

Therefore the aim of this study is (i) to analyse the population structure of *D. hanleyanus*, (ii) to estimate its growth and production parameters, (iii) to compare these results with values of other *Donax* species, (iv) to examine the possible influences of sand grain size and sea surface temperature on abundance, (v) to discuss the effect of mass tourism, and (vi) to reveal the relationship between *M. mactroides* and *D. hanleyanus* abundances.

Material and Methods

Study Area

The population structure of the intertidal wedge clam *D. hanleyanus* was studied during alternate spring tides at (i) the beach Santa Teresita (36°32'S, 56°41'W), which is heavily influenced by mass tourism during the summer season (> 1000 tourists 100 m^{-1} coastline, pers. observ. and local tourist office 'Secretaría de Turismo, Mar del Tuyú', Argentina), (ii) the beach Mar de las Pampas (37°19'S, 57°00'W), which is marginally influenced by humans (< 10 tourists 100 m^{-1} coastline, pers. observ.), and (iii) the beach Faro Querandí, which is unaffected by humans (< 0.01 angler 100 m^{-1} coastline, pers. observ.) and naturally protected (37°29'S, 57°07'W). All three open ocean beaches are located in the Province of Buenos Aires, Argentina (Fig. 1A) and flow continuously into one another with a north-south shoreline orientation, which is stable on a long term basis (Marcomini and López 1993).

Abiotic Factors and Anthropogenic Impacts

Accordingly to McLachlan`s (1980) scale for rating exposure and Short and Wright's (1983) classifications of beach types, Santa Teresita is sheltered and dissipative, Mar de las Pampas exposed and intermediate, and Faro Querandí exposed and reflective. The three sampling sites receive continuous wave action and are subject to semidiurnal tides, with a maximum tidal range of 1.6 m; a spring tide average of 1.7 m and a neap tide mean of 0.2 m. The sea surface temperature (*SST*) varies between 11 ± 0.14°C (mean ± SE) in winter and 23 ± 0.21°C (mean ± SE) in summer (Fig. 2). The study sites are composed of fine (Santa Teresita), medium (Mar de las Pampas) and coarse sands (Faro Querandí), with a mean particle diameter of 2.26 phi, 1.43 phi and 1.05 phi, respectively (Table 1). All three beaches are affected by freshwater seepage as confirmed by satellite images and a southward current bringing water masses from the 290 km long and up to 220 km wide estuary of the Río de la Plata. Mean salinity ranges between 31 and 34. All three beaches are well drained and oxygenated.

Settling velocities of sediments were estimated in order to characterize the physical attributes of the *Donax* belt. Particle size analyses form the studied areas were carried out by sampling sediments with a plastic corer of 3.5 cm diameter to a depth of 10 cm. Sand samples were washed with freshwater overnight to remove salt and then dried at 70°C. Subsequently, any shell fragments were extracted and the remaining part of the samples was analysed using a MacroGranometer™ settling tube (e.g. Flemming and Thum 1978; Flemming and Ziegler 1995) and the SedVar™ V6.2p software package (Brezina 1997), which is part of the system. The data processing software makes use of the more versatile equation of Brezina (1979) rather than that of Gibbs *et al.* (1971), which is applicable to smooth glass spheres only to calculate settling velocities. All textural parameters presented in this study were calculated using the percentile statistics of Inman (1952), while sediments were classified according to the Wentworth scale (1922).

Wave height was estimated by measuring the height of breaking waves ($N = 10$) with graduated poles against the horizon, and adding the result to the height difference between the location of the observer and the lowest point at which the backwash met the next incoming swash bore. The wave period was measured as the time interval between breakers ($N = 50$). The morphodynamic state of each studied site was described by the Dean parameter (Ω) (Dean 1973):

$$\Omega = H_b \frac{100}{WT} , \tag{1}$$

which is based on mean wave height H_b (m) divided by wave period T (s) and sand fall velocity W (m s^{-1}). The slope of the beach face was measured by the height difference (Emery 1961) between the drift and the water line. The swash period was estimated according to McArdle and McLachlan (1991). Salinity (Optech portable refractometer, model RSM) as well as the *SST* were measured monthly *in situ* at the three sample locations. For additional detailed information the *SST* was measured daily at Santa Teresita between October 2005 and December 2006 and was supplemented with data of the Argentinean Marine Institute (CEADO: Centro Argentino de Datos Oceanográficos, Servicio de Hidrografía Naval, Buenos Aires, Argentina), which operates a permanent weather station at this beach.

Data of tourists visiting the coast of Buenos Aires was provided by the local tourist office (Secretaría de Turismo, Mar del Tuyú, Argentina).

Sampling and Laboratory Procedures

Quantitative sampling of *D. hanleyanus* was carried out at monthly intervals (Santa Teresita and Mar de las Pampas: December 2004 to December 2006; Faro Querandí: March 2005 to December 2006) from a series of stations (4 m intervals). The latter were located along three transects separated by 20 m intervals and located perpendicular to the shoreline from the spring tide high water mark to the spring tide low water mark. At each station, three replicated sand samples (40 x 40 cm) were excavated to 35 cm depth using a 0.16 m^2 steel corer, and thereafter sieved individually on a 1 mm mesh. Maximum anterior-posterior shell length (*apSL*) of the retained wedge clams was measured to the nearest 0.1 mm with a digital vernier calliper (Mitutoyo, model 500-161U) to obtain monthly length-frequency distributions. For biomass analysis monthly subsamples of 35 randomly taken specimens from each of the three locations were stored in 70 % ethanol. Thereafter soft tissues were removed to estimate shell-free wet mass (*SFWM*) by weighing after blotting on filter paper. Subsequently, samples were dried to a constant mass at 70°C, weighed again to determine shell-free dry mass (*SFDM*) and finally ignited in a muffle furnace at 550°C for 5 h in order to estimate shell-free ash-free dry mass (*AFDM*).

Growth, Growth Performance and Life Span

A series of 25 month length-frequency distributions provided the basic information for growth estimates. A von Bertalanffy growth function (*VBGF*) (von Bertalanffy 1938) was fitted to the data using the electronic length-frequency analysis ‘ELEFAN I’ routine of the FiSAT II program package (Gayanilo Jr. *et al.* 2005). Due to the pronounced seasonal changes in temperature (Fig. 2a) the modified version of the *VBGF* was used, which incorporates seasonal oscillation in growth:

$$L_t = L_\infty \left[1 - e^{\left[-K(t-t_0)+\left(\frac{KC}{2\pi}\right)\sin 2\pi(t-t_s)-\left(\frac{KC}{2\pi}\right)\sin 2\pi(t_0-t_s)\right]}\right] , \quad (2)$$

where L_t is the *apSL* (mm) at time *t*, L_∞ the asymptotic maximum *apSL* (mm), *K* (yr^{-1}) is the curvature parameter, *C* is a constant, which defines the degree of seasonal oscillation (ranging from 0, which defines continuous non-oscillating growth, to 1, when growth comes to a complete halt at the 'winter point' [*WP*]), t_0 is the theoretical age at zero length and t_s is the initial point of oscillation in relation to $t = 0$ and the *WP*. The different subroutines of ELEFAN (*K*-scan, response surface analysis) were used to identify the *VBGF* that best fits the monthly size-frequency data, using the R_n value as a criterion of fit.

Due to the absence of adult individuals at Santa Teresita it was not possible to apply a *VBGF* (Gayanilo Jr. *et al.* 2005). Thus the monthly length-frequency distributions of Santa Teresita were converting to size-at-age data (*SAD*) and thereafter fitting to a general von Bertalanffy growth function (*gVBGF*) (Gulland and Holt 1959) applying Microsoft Excel's SOLVER routine (Brey 2001). Differences in growth among sites were checked by variance analysis of the residuals of the *gVBGF*.

To compare growth performance the growth index phi prime (ϕ') was used:

$$\phi' = 2\log_{10}(L_\infty) + \log_{10} K . \quad (3)$$

This criterion was chosen because the negative correlation between *K* and L_∞ invalidates direct comparisons between individual parameters (Pauly and Munro 1984). Finally the overall growth performance index:

$$OGP = \log(K[L_\infty]^3) , \quad (4)$$

which represents growth rate at the point of inflexion of the size-growth curve (Pauly 1979), was calculated to compare growth of *D. hanleyanus* with other *Donax* species.

The theoretical life span t_{max} (equal to relative age, because the larval period of this species is unknown, $t = 0$) of *D. hanleyanus* was estimated by the inverse von Bertalanffy growth equation (Taylor 1958):

$$t_{max} = \frac{[\ln L_{95\%} - \ln(L_\infty - L_{95\%})]}{K} , \quad (5)$$

where $L_{95\%}$ represents 95 % of the maximum shell length recorded during field sampling.

Biomass and Production

To compare biomass of *D. hanleyanus* with values of other *Donax* species, all published values were converted to *AFDM* (according to Brey *et al.* 1988), based on the empirically determined conversion factor of 0.186 (*SFWM* to *AFDM* for preserved *D. hanleyanus*). Parameters of the relationship between length and biomass of *D. hanleyanus* were estimated by regression analysis

$$M = aL^b \,, \tag{6}$$

where *M* is the *AFDM* (g), *L* is the *apSL* (mm) of the size class, and *a* and *b* are constants. *AFDM* was determined for 400 specimens covering all size classes between December 2004 and December 2006.

Total annual production was calculated for *D. hanleyanus* belts at Santa Teresita, Mar de las Pampas (January-December 2005 and January-December 2006) and Faro Querandí (March-December 2005 and January-December 2006) by the mass specific growth rate method (Crisp 1984; Brey 2001). The latter requires information from size-mass relationships and the size-frequency distribution obtained from all pooled samples and the *VBGF*:

$$P = \sum N_i M_i G_i \ (\mathrm{g}\ AFDM\ \mathrm{m}^{-2}\mathrm{yr}^{-1}) \,, \tag{7}$$

where N_i is the average number of animals (number per m^2) and M_i is the mean individual *AFDM* in length class *i*, and G_i is the mass-specific growth rate:

$$G_i = bK\left[\left(\frac{L_\infty}{L_i}\right) - 1\right] \ (\mathrm{yr}^{-1}) \,, \tag{8}$$

where *b* is the exponent of the size-mass relation, *K*, L_∞ are *VBGF* parameters and L_i is the mean size in class *i*.

Mean annual biomass was estimated by:

$$\bar{B} = \sum N_i M_i \ (\mathrm{g}\ AFDM\ \mathrm{m}^{-2}) \tag{9}$$

and annual renewal rates ($P/\overline{B}$ ratios) of the *D. hanleyanus* populations were calculated from annual total production *P* and annual mean biomass $\overline{B}$.

Statistical Analysis

Spatial and temporal differences of the population abundance (one-way ANOVA) as well the influence of *SST* and anthropogenic factors on the population abundance (Spearman`s rank order correlation) were analysed using the statistical package SPSS version 16.0.1 (SPSS 2007). Differences were considered significant at a level of *A* = 5 % (Zar 1999). The relationship between monthly mean abundance and mean grain size was analyzed through a non-metric multi-dimensional scaling (nMDS), using square root transformed data and calculated Bray-Curtis similarities (PRIMER 2007) as used by several authors (e.g. Rumohr and Karakassis 1999; Jaramillo *et al.* 2001; Sousa *et al.* 2008). Correlation analysis was used to assess the relationships between renewal rate ($P/\overline{B}$ ratios) and latitude of *D. hanleyanus* compared with those of several *Donax* species from other areas. The relation of between the population abundance of *D. hanleyanus* and *M. mactroides* was estimated by linear regression analysis. Mean *OGP*s of the three species groups ‘tropical-subtropical’, ‘temperate’ and ‘upwelling’ were tested for differences using a one-way ANOVA with Bonferroni-Dunn post-hoc test.

Results

Abiotic Factors and Anthropogenic Impacts

Results of grain size and sand fall velocity analyses, as well as the associated parameters are summarized in Table 1. The nMDS analysis, based on monthly mean abundance data, identified two main areas of distinct granulometry: mean grain size 1.43 and 2.26 phi (at Mar de las Pampas and Santa Teresita, respectively, Fig. 3A), and mean grain size 1.05 phi (at Faro Querandí, Fig. 3B). The present stress factor of 0.08 indicates an excellent representation with no prospect of misinterpretation (Clarke and Warwick 2001).

Mean annual *SST* was 17.6 ± 0.17°C (mean ± SE), with lowest temperatures of 9.8°C and 9.1°C in austral winter (June 2005 and July 2006, respectively), and highest values of 24.8°C and 24.5°C in austral summer (December 2005 and February 2006, respectively) (Fig. 2a). *SST* was not correlated with the abundance of *D. hanleyanus* at all three sampling sites (Spearman`s rank order correlation: Santa Teresita $r_s = -0.013$, $p > 0.05$, $N = 25$; Mar de las Pampas $r_s = 0.122$, $p > 0.05$, $N = 25$; Faro Querandí $r_s = 0.077$, $p > 0.05$, $N = 22$). However, at Santa Teresita the number of visiting tourists (> 1000 tourists 100 m^{-1} coastline, pers. observ. and local tourist office 'Secretaría de Turismo, Mar del Tuyú', Argentina) was significantly correlated with the decrease of the wedge clam population during the summer months of both years (Spearman`s rank order correlation, $r_s = -0.829$, $p < 0.05$, $N = 6$). At Mar de las Pampas (< 10 tourists 100 $m^{-1}$ coastline, pers. observ.) this correlation was not found (Spearman`s rank order correlation, $r_s = -0.371$, $p > 0.05$, $N = 6$), and at Faro Querandí no tourist effect was apparent (< 0.01 angler 100 m^{-1} coastline, pers. observ.).

Population Structure

During the study period of 25 months, 21,405 *D. hanleyanus* were collected and measured: in the first year at Santa Teresita 4,230 ind., at Mar de las Pampas 1,545 ind. (December 2004-November 2005) and at Faro Querandí 3,911 ind. (March 2005-November 2005). During the second year 2,183 ind. were measured at Santa Teresita, 1,452 ind. at Mar de las Pampas and 8,524 ind. at Faro Querandí (December 2005-December 2006). The smallest recorded individual had an *apSL* of 3 mm at Santa Teresita and 4 mm at both Mar de las Pampas and Faro Querandí. The largest individual measured 35 mm, 36 mm and 40 mm respectively.

Annual *D. hanleyanus* abundance (mean ± SE, respectively) was 78 ± 42 ind. m^{-2} (2005) and 40 ± 15 ind. m^{-2} (2006) at Santa Teresita, 55 ± 23 ind. m^{-2} (2005) and 50 ± 12 ind. m^{-2} (2006) at Mar de las Pampas and 84 ± 22 ind. m^{-2} (2005) and 267 ± 77 ind. m^{-2} (2006) at Faro Querandí. Maximal abundance was recorded in spring (2,475 ind. m^{-2} at Santa Teresita in

December 2004, 531 ind. m^{-2} at Mar de las Pampas in December 2004 and 950 ind. m^{-2} at Faro Querandí in November 2006).

In 2005 population abundance was not significantly higher than in 2006 at Santa Teresita and Mar de las Pampas (ANOVA, $F_{1,22} = 2.427$, $p > 0.05$; $F_{1,22} = 2.209$, $p > 0.05$, respectively), but it was significantly lower in 2005 compared to 2006 at Faro Querandí (ANOVA, $F_{1,22} = 11.891$, $p < 0.05$). In all three beaches, population abundance differed significantly between months (Santa Teresita: $F_{11,13} = 1.171$, $p > 0.05$; Mar de las Pampas: $F_{11,13} = 0.681$, $p > 0.05$; Faro Querandí: $F_{11,10} = 0.542$, $p > 0.05$; ANOVA respectively). Monthly mean abundance was significantly higher in the reflective beach, Faro Querandí (ANOVA with Scheffé-procedure post hoc test, $F_{2,69} = 14.675$, $p < 0.05$). The highest abundance of *D. hanleyanus* was recorded mainly in spring (at Santa Teresita 361 ± 149 ind. m^{-2} in December 2004 and 95 ± 27 ind. m^{-2} in December 2006, at Mar de las Pampas 125 ± 32 ind. m^{-2} in December 2004 and 111 ± 71 ind. m^{-2} in September 2005 and at Faro Querandí 190 ± 45 ind. m^{-2} in November 2005 and 667 ± 205 ind. m^{-2} in November 2006, [mean ± SE, respectively]) (Fig. 2S, M, F). During the present study we did not find any migration evidence of *D. hanleyanus* although the abundance may vary drastically at a given location (Fig. 2). Additional random sampling south and east of transects did not reveal higher abundance compared to the monthly stations. Further random sampling in the highly dynamic wave breaking zone, taken with a diver-operated corer (Rumohr and Arntz 1982), confirmed that clams did not migrate into the swash zone.

The length-frequency distribution of *D. hanleyanus* of Santa Teresita, Mar de las Pampas and Faro Querandí showed distinct cohorts. One single new cohort was observed during both years (April 2005 and March 2006) at Santa Teresita. Cohorts were tracked up to ten months reaching approximately 20 mm *apSL* before the cohort disappeared and new recruits were recorded (Fig. 4S). In March 2006 a new cohort was detected along with two additional cohorts At Mar de las Pampas and could be followed until the end of the study in December 2006 (Fig. 4M). Adult individuals co-occurring in two (February 2005 until March 2006) and three cohorts (April 2006 to October 2006) were found at Faro Querandí (Fig. 4F).

Growth and Life Span

The maximum sized valve of 44 mm was found at Faro Querandí. This length was used as a fixed L_∞ value to calculate a seasonal *VBGF* with a growth constant $K = 0.47$ yr^{-1} at Mar de las Pampas and $K = 0.48$ yr^{-1} at Faro Querandí (Fig. 4M, F). Estimates of growth indicated moderate seasonal oscillations ($C = 0.8$), with slowest growth rates occurring in austral autumn ($WP = 0.45$ ~ mid-May). At Santa Teresita adult individuals were not abundant which prevented to reliable calculation of a *VBGF* with FiSAT (Gayanilo Jr. *et al.* 2005). Thus monthly length-frequency distributions of Santa Teresita were converted to size-at-age data (*SAD*) and fitted to a *gVBGF*. Variance Analysis of the residuals ($p > 0.05$) revealed that growth parameters of Santa Teresita deviated strongly from those of populations inhabiting the beaches of Mar de las Pampas and Faro Querandí. Due to the lack of larger size classes and the resulting methodological bias we decided to only compare growth parameters from the two latter populations.

The calculated life span ($t_{\max}$) was 4.96 yrs (Mar de las Pampas) and 5.18 yrs (Faro Querandí) (Table 2).

Biomass and Production

The observed relationship between length and calculated *AFDM* of *D. hanleyanus* $M_{(AFDM)} = (4.27 \cdot 10^{-6}) \cdot L_{(mm)}^{3.19}$ ($N = 2{,}233$, $r^2 = 0.98$) was used for production estimates.

Within the *Donax* belt these abundance values represent an average annual biomass $\overline{B}$ of 0.21 g *AFDM* m^{-2} yr^{-1} (2005) and 0.04 g *AFDM* m^{-2} yr^{-1} (2006) at Santa Teresita, of 0.17 g *AFDM* m^{-2} yr^{-1} (both, 2005 and 2006) at Mar de las Pampas and of 1.32 g *AFDM* m^{-2} yr^{-1} (2005) and 0.96 g *AFDM* m^{-2} yr^{-1} (2006) at Faro Querandí (Fig. 5b-g). Individual production increased to its highest value at 30 mm length (0.16 g *AFDM* m^{-2} yr^{-1}) and decreased thereafter (Fig. 5a). The distribution of total annual production *P* and the abundance among the size classes are illustrated in Fig. 5b-g. Annual production ranged between 0.08 and 0.99 g *AFDM* m^{-2} yr^{-1}, depending on beach and year, and $P/\overline{B}$ ratios were between 0.82 and 2.16.

Discussion

Abiotic factors

A clear spatial pattern of *D. hanleyanus* inhabiting dissipative to reflective beaches was revealed from monthly mean abundance data. Mean grain size of sediments is dependent on currents, the mean slope, the exposure and thus the morphodynamic type of the beach (McLachlan and Brown 2006). Therefore mean grain size integrates over the latter parameters and is therefore a suitable factor to be analysed for physical effects on beach organisms. The nMDS analysis distinguishing two main sites (Fig. 3), A: the first area (Santa Teresita and Mar de las Pampas) is characterised by a fine to medium textural group and smaller grain size (210-370 µm, dissipative to intermediate beach morphology), and B: a second one (Faro Querandí, reflective beach morphology) by larger grain size (480 µm) and a coarse textural group (Table 1). Thus, differences in the abundance of *D. hanleyanus* (Fig. 2) may be related to the compactness of the sand: the more compacted the sand, the more difficult for adult clams to burrow and consequently they can be wash away. This hypothesis is supported by Trueman (1971) stating that *Donax* is only secure against the drag of the waves when the shell is oriented with the current and at least two thirds of the shell are buried. In conformity with our work, Penchaszadeh and Olivier (1975) already stated in the 1970is that sediments characteristics are principle factors for the distribution of *D. hanleyanus*. In accordance, Alexander *et al.* (1993), McLachlan *et al.* (1995b) and Nel *et al.* (2001) also described substrate-sensitivity of *Donax* species, although the clams are able to penetrate into sediments with a wide spectrum of grain sizes. In addition Guillou and Bayed (1991) observed higher abundance of *D. trunculus* in sediments with larger mean grain sizes (from 190 to 230 µm) and minimum abundance in sediments with smaller mean grain size (≤ 160 µm).

Anthropogenic Impacts

Sandy beaches such as Santa Teresita are prime sites for human recreation: especially during the holiday season, short intense anthropogenic disturbances can affect organisms at several biological scales, ranging from biogeochemistry and physiology up to the community level. Chandrasekara and Frid (1996) reported that human trampling changes the saltmarsh benthic fauna of the English coast. Schlacher and Thompson (2008) described a modification of the physical environment of two Australian sandy beaches and van der Merwe and van der Merwe (1991) found a negative effect on two intertidal *Donax* species in South Africa, both caused by off-road driving. In a Dutch intertidal mudflat, trampling affected the abundance and population dynamics of the clam *Macoma balthica* and the cockle *Cerastoderma edule* (Rossi *et al.* 2007). The authors assume that footsteps directly kill or bury specimens, provoking asphyxia. On Argentinean shores it is evident that human activities and urbanization in coastal areas affect the presence and abundance of *D. hanleyanus* (Marcomini *et al.* 2002). Some authors (Bastida *et al.* 1996; Dadon 2005) assume that human activities are probably one of the main factors interfering with the recovery of bivalve populations. The abrupt decrease of the *D. hanleyanus* population during summer especially at Santa Teresita (*Arrows* in Fig. 2S) is significantly related to mass tourism. Up to one million tourists (Secretaría de Turismo, Mar del Tuyú, Argentina) visit the coast of Buenos Aires during each holiday season (Fig. 2b) and disturb the intertidal zone by intensive trampling. Therefore we argue that anthropogenic impact is one of the main causes of strong reductions in *D. hanleyanus* abundance at Santa Teresita. Further research should therefore focus on human activities as an important abundance oppressing factor.

Growth

The von Bertalanffy growth constant *K* varied insignificantly between 0.47 yr^{-1} (Mar de las Pampas) and 0.48 yr^{-1} (Faro Querandí). During the first two years of life differences of growth parameters become obvious by comparing the present values (Table 3, values m1, m2) with those of Penchaszadeh and Olivier (1975) (Table 3, value m3). Forty years ago populations of *D. hanleyanus* grew faster within the first two years ($K = 1.18\ yr^{-1}$) compared to the wedge clams presently studied ($K = 0.48\ yr^{-1}$), but reached a smaller maximal length (33.5 mm) (presently 44.0 mm). This difference in growth may be caused by a relaxed competition with the co-occurring *M. mactroides* population, which of late is more exactly entered (Table 3, Fig. 8). Thus, growth of *D. hanleyanus* is apparently depending on this competition. Other studies have also demonstrated abundance-dependent growth for various bivalves (Broom 1982; Peterson 1982; Peterson and Black 1987; Peterson and Black 1988; Peterson and Beal 1989; Jensen 1993; Defeo and de Alava 1995; Weinberg 1998; Talman and Keough 2001).

Non-linear growth functions, such as the *VBGF*, are difficult to compare, whereas several authors (e.g. Pauly 1979; Munro and Pauly 1983; Moreau *et al.* 1986) demonstrated the suitability of the *OGP* index for inter- and intraspecific comparisons. The *OGP* of the studied *D. hanleyanus* (4.60 at Mar de las Pampas and 4.61 at Faro Querandí) conforms well with values calculated from data sets of the same species from the Brazilian (4.17 and 4.32: Cardoso and Veloso 2003), Uruguayan (4.46: Defeo 1996) and Argentinean coast (4.65: Penchaszadeh and Olivier 1975). *OGP* values (Fig. 6) from Uruguay (m4) and Brazil (m5-m6) are conspicuously lower than those from Argentina (m1-m3), which may be caused by the lower mean *SST*. This trend provides support to the latitudinal gradient hypothesis (*LGH*) postulated by Defeo and Cardoso (2002), which predicts a positive correlation between body size of species and latitude. Thus, subtropical beaches exhibit higher growth and mortality rates and shorter life spans than temperate beaches. However, the *LGH* cannot be generalized for invertebrates since there are different, sometimes opposing, results for different taxa (cf. Schilder 1956; Jones and Simons 1983; Henmi 1993; Barnes and Arnold 2001; Hausdorf 2003; Clarke *et al.* 2004). The present data compilation from several studies confirmed the hypothesis of Laudien *et al.* (2003a) that the *OGP* is habitat-specific (Fig. 6): species populating tropical-subtropical regions show the lowest *OGP* (2.84-3.68, group A), temperate species have intermittent *OGP* (4.17-4.91, group B), while species of upwelling areas show the highest *OGP* (5.06-5.65, group C). Mean *OGP*s of the three groups were significantly different ($F_{2,58} = 45.655$, $p < 0.05$). Even the effect of climate anomalies may be detected with the help of the auximetric grid, as indicated by the upwelling surf clam *D. marincovichi* sampled in Peru during and shortly after an El Niño event 1982-1983 (Fig. 6, values f2, f3) in comparison to the population sampled during normal upwelling years (Fig. 6, value f1) (Arntz *et al.* 1987).

A few *OGP* values calculated from tropical-subtropical regions deflect from the model of the auximetric grid (Fig. 6), namely the growth performance of *D. dentifer* (e1: Riascos and Urban 2002) and *D. striatus* (k2: Rocha-Barreira de Almeida *et al.* 2002), classifying these species as temperate. Reason for this might be, that sampling of *D. dentifer* were carried out during the 'El Niño 1997-1998' phenomenon and used method to estimate growth of *D. striatus* was not the suitable one, as Sparre and Venema (1995) state that growth estimates, based only on length-frequency data, may not always be useful for tropical species with several recruitment events along the year.

Life Span

Most *Donax* species have a relatively short life span of 1-2 yrs (McLachlan 1979; Ansell 1983). While Penchaszadeh and Olivier (1975) estimated a longevity of *D. hanleyanus* from the Argentinean coast of three years with a maximal length of 33 mm, the recent study indicates an even longer life span of approximately five years (maximal length of 44 mm) for the same species and region. In contrast to our estimation, Cardoso and Veloso (2003) noted for Brazilian *D. hanleyanus* only 1.5 yrs as the maximal life period. Similarly shorter maximal life spans were reported for various *Donax* species from temperate areas, such as *D. vittatus* (3.5 yrs) from the French coast (Ansell and Lagardère 1980) or *D. deltoides* (3.5 yrs) from South Australia (for data source see at Laudien *et al.* 2003a). The recent value is however in accordance with *D. trunculus* from France (6 yrs, Guillou and Le Moal 1980; Guillou 1982) and *D. serra* (> 5 yrs, de Villiers 1975a) from South Africa. Lower values of longevity were reported for tropical-subtropical *Donax* species, *D. faba* and *D. cuneatus* from India probably does not reach 3 yrs (McLachlan *et al.* 1996b) and *D. striatus* (McLachlan *et al.* 1996b) and *D. denticulatus* (Vélez *et al.* 1985) from Venezuela have a life span of only approximately 1.5 yrs. The analysis suggests a longer life span of temperate *Donax* species compared to tropical-subtropical *Donax* species (climate areas of *Donax* species are compared in Table 3 and Fig. 6).

Biomass and Production

The intertidal biomass of the *D. hanleyanus* population ranged between 0.04 and 1.32 g *AFDM* m^{-2} yr^{-1} (Fig. 5). These values are in accordance with biomass data of *Donax* species from other temperate and tropical-subtropical areas (Ansell *et al.* 1978; Warwick *et al.* 1978; McLachlan 1979; McLachlan and van der Horst 1979; Wilson 1999). However, values are in contrast to biomasses from upwelling systems (Laudien *et al.* 2003a), which can be three magnitudes higher than the present values (Table 4). Four decades ago *D. hanleyanus* reached a biomass of 7.5 g *AFDM* $m^{-2}yr^{-1}$(calculated from Penchaszadeh and Olivier 1975), which is approximately seven times higher compared to recent values.

Annual intertidal production of *D. hanleyanus* ranged between 0.08 and 0.99 g *AFDM* $m^{-2}yr^{-1}$ (Table 4, Fig. 5) and is therefore within the span (0.79-3.67 g *AFDM* $m^{-2}yr^{-1}$) observed by Cardoso and Veloso (2003), but lower than that recorded by Gianuca (1985) (13.56 g *AFDM* $m^{-2}yr^{-1}$). By comparing production, biomass and renewal rate among different *Donax* species from several geographical regions (Table 4, Fig. 7), it is evident that the renewal rates ($P/\overline{B}$) increase from temperate to tropical regions, which was also observed for several other donacids (Ansell *et al.* 1978; Kaletiam and Hockey 1991; Cardoso and Veloso 2003).

Clam Interaction

Presently *D. hanleyanus* numerically dominates the community at Santa Teresita. The sympatric yellow clam *M. mactroides* is known to co-occur with *D. hanleyanus* populations since the seventies (Olivier *et al.* 1971; Penchaszadeh and Olivier 1975). However, *M. mactroides* was only abundant at Santa Teresita (mean annual abundance of 47 ± 13 ind. m^{-2} in 2005 and 29 ± 3 ind. m^{-2} in 2006, [mean ± SE; respectively]); in Mar de las Pampas and in Faro Querandí no more than single individuals were found during the whole sampling period (Herrmann *et al.* under review-a). In contrast, Olivier *et al.* (1971) found a mean abundance of 538 ind. m^{-2} in a sampling section including Santa Teresita and 629 ind. m^{-2} in a sampling section including Mar de las

Pampas and Faro Querandí in 1968-1970. A significant negative correlation between abundances of these two suspension-feeders (Fig. 8) suggests that abundance peaks of *D. hanleyanus* are related with population crashes of *M. mactroides*. Penchaszadeh and Olivier (1975), Dadon (2005) as well as Defeo and de Alava (1995) observed similar inverse correlations between abundances of *D. hanleyanus* and *M. mactroides* from Argentinean and Uruguayan beaches. In agreement, surf clam populations from the Peruvian Pacific coast revealed the same relations; *D. marincovichi* increased coincidentally with the collapse of *M. donacium* (Penchaszadeh 1971; Tarazona *et al.* 1985; Arntz *et al.* 1987). Defeo and de Alava (1995) hypothesized that interspecific competition may be the cause and Olivier *et al.* (1971) provided evidence by describing overlapping trophic niches of the two clams.

Conclusion

In conclusion, lowest abundance of *D. hanleyanus* was observed at intermediate to dissipative beaches (Mar de las Pampas and Santa Teresita) composed of finer sediment. The present results confirm that the abundance of *D. hanleyanus* is influenced by sand grain size. Highest abundance was recorded at the reflective beach Faro Querandí characterized by coarse sediment. Decrease in *D. hanleyanus* abundance during the holiday season at Santa Teresita was significantly related to human trampling (mass tourism). *D. hanleyanus* abundance was negatively correlated with *M. mactroides* abundance, but was not significantly influenced by *SST*. In comparison with a forty years old data set, growth of *D. hanleyanus* is now slower, but specimens reach a larger maximal length and have a longer life span. The *OGP* index of *D. hanleyanus* conforms well with values calculated from several *Donax* species of other areas. Thus, as expected, the Argentinean wedge clam *D. hanleyanus* is classified into the temperate group of Donacidae on an auximetric grid. Presently the intertidal biomass of *D. hanleyanus* is seven times lower compared with data from the 70ies. Thus, without a sustainable management the conservation status of *D. hanleyanus* is endangered.

Appendix

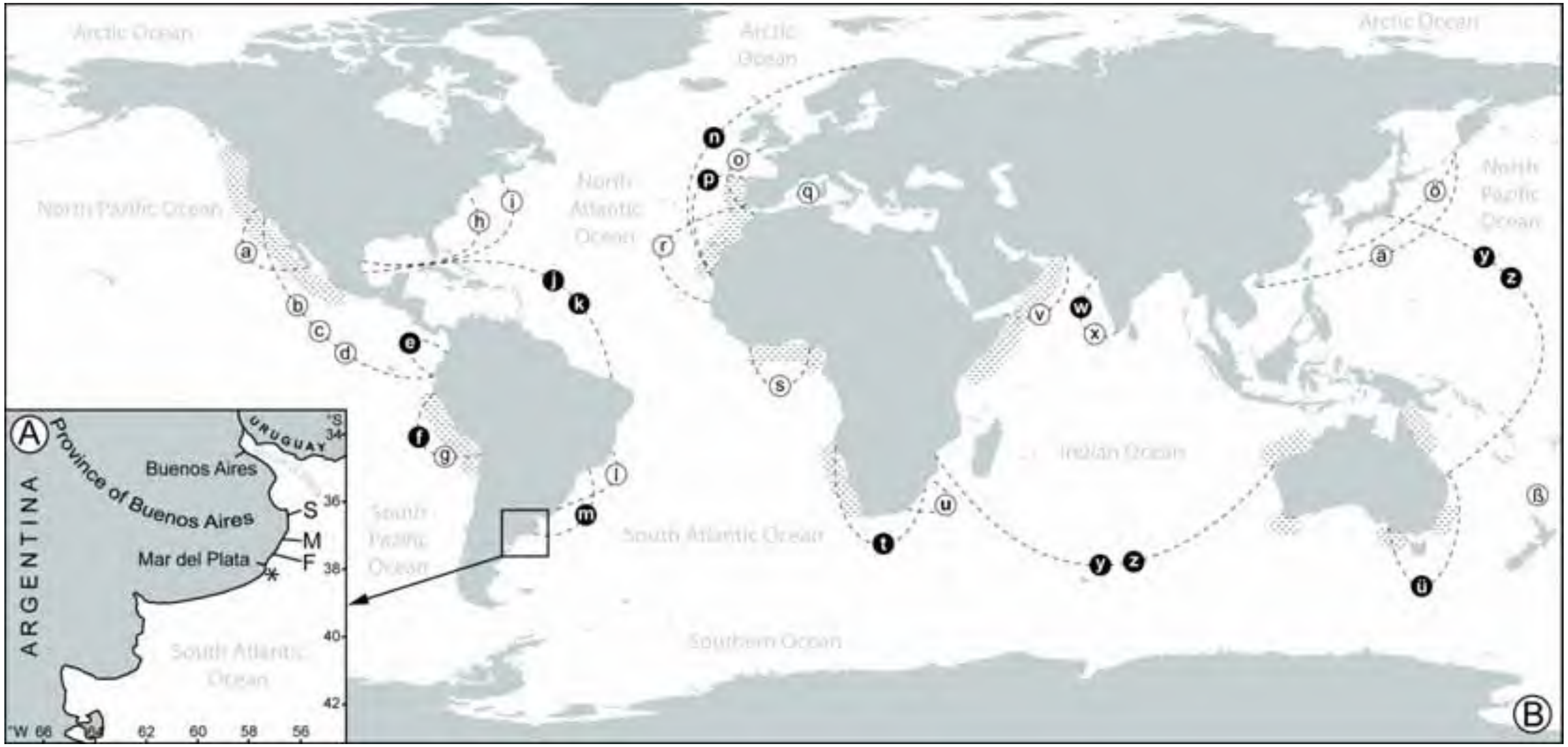


Fig. 1A: Map of the three study sites at the Argentinean Atlantic coast: Santa Teresita (**S**), Mar de las Pampas (**M**) and Faro Querandí (**F**). * Indicate the southern most distribution of *D. hanleyanus* at Punta Mogotes, south of Mar del Plata. **Fig. 1B:** Geographical distribution of 30 selected donacids with known scientific information, of which 12 *Donax* species are marked with black dots (for data sources of white letters, see Table 3) used for growth in this study. Major coastal upwelling areas are dotted. Map modified and extended after Laudien (2002): a: *D. gouldii*, b: *D. carinatus*, c: *D. panamensis*, d: *D. punctatostriatus*, e: *D. dentifer*, f: *D. marincovichi*, g: *D. obesulus*, h: *D. fossor*, i: *D. variabilis*, j: *D. denticulatus*, k: *D. striatus*, l: *D. gemmula*, m: *D. hanleyanus*, n: *D. vittatus*, o: *D. variegatus*, p: *D. trunculus*, q: *D. semistriatus*, r: *D. venustus*, s: *D. oweni*, t: *D. serra*, u: *D. sordidus*, v: *D. townsendi*, w: *D. incarnatus*, x: *D. spiculum*, y: *D. cuneatus*, z: *D. faba*, ä: *D. kiusiuensis*, ö: *D. semigranosus*, ü: *D. deltoides*, ß: *D. pallidus*.

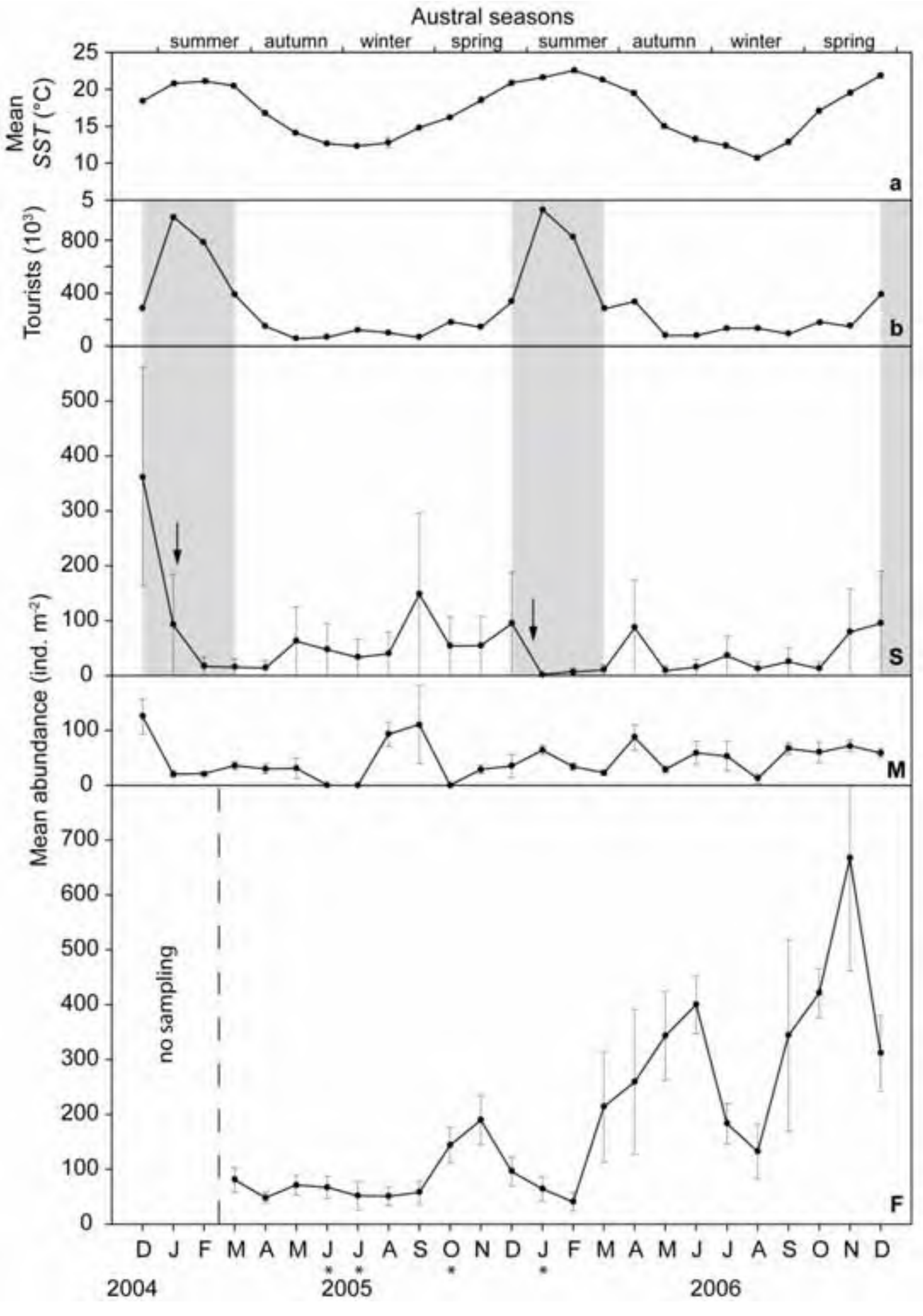


Fig. 2: Monthly mean abundance of *D. hanleyanus* at Santa Teresita (**S**), Mar de las Pampas (**M**) (from December 2004 to December 2006, respectively) and at Faro Querandí (**F**) (from March 2005 to December 2006) in relationship to monthly mean *SST* (**a**) and visiting tourists at the coast of the Province Buenos Aires (**b**). * *D. hanleyanus* was not abundant in June, July and October 2005 at Mar de las Pampas, and also not in January 2006 at Santa Teresita. *Error bars*: standard error (SE). *Grey areas*: high tourist season. *Arrows*: indicate significantly decreases of the *Donax* population during high tourist season. Datasets are published in Herrmann *et al.* (2008b).

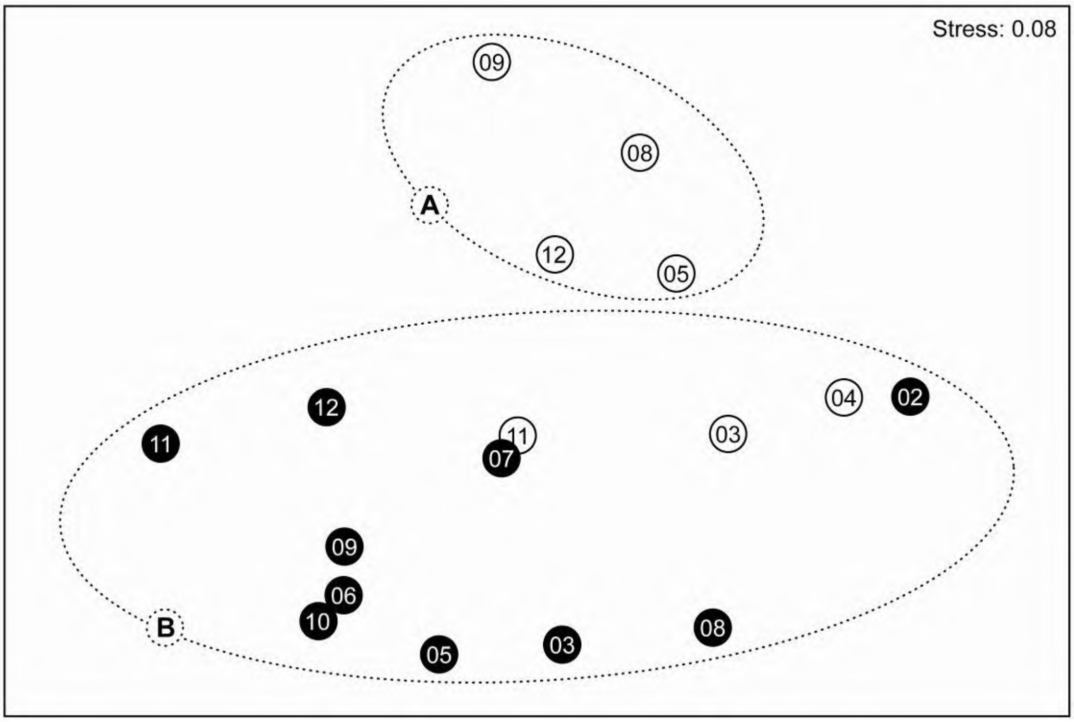


Fig. 3: Resulting from square root transformed data and calculated Bray-Curtis similarity of 78 % (PRIMER 2007) the nMDS diagram identifies two main areas of distinct granulometry, which is based on monthly mean abundance data (months in circles) in 2005 (○) and in 2006 (●): **A:** mean grain size 1.43-2.26 phi (Mar de las Pampas and Santa Teresita, respectively), **B:** mean grain size 1.05 phi (Faro Querandí).

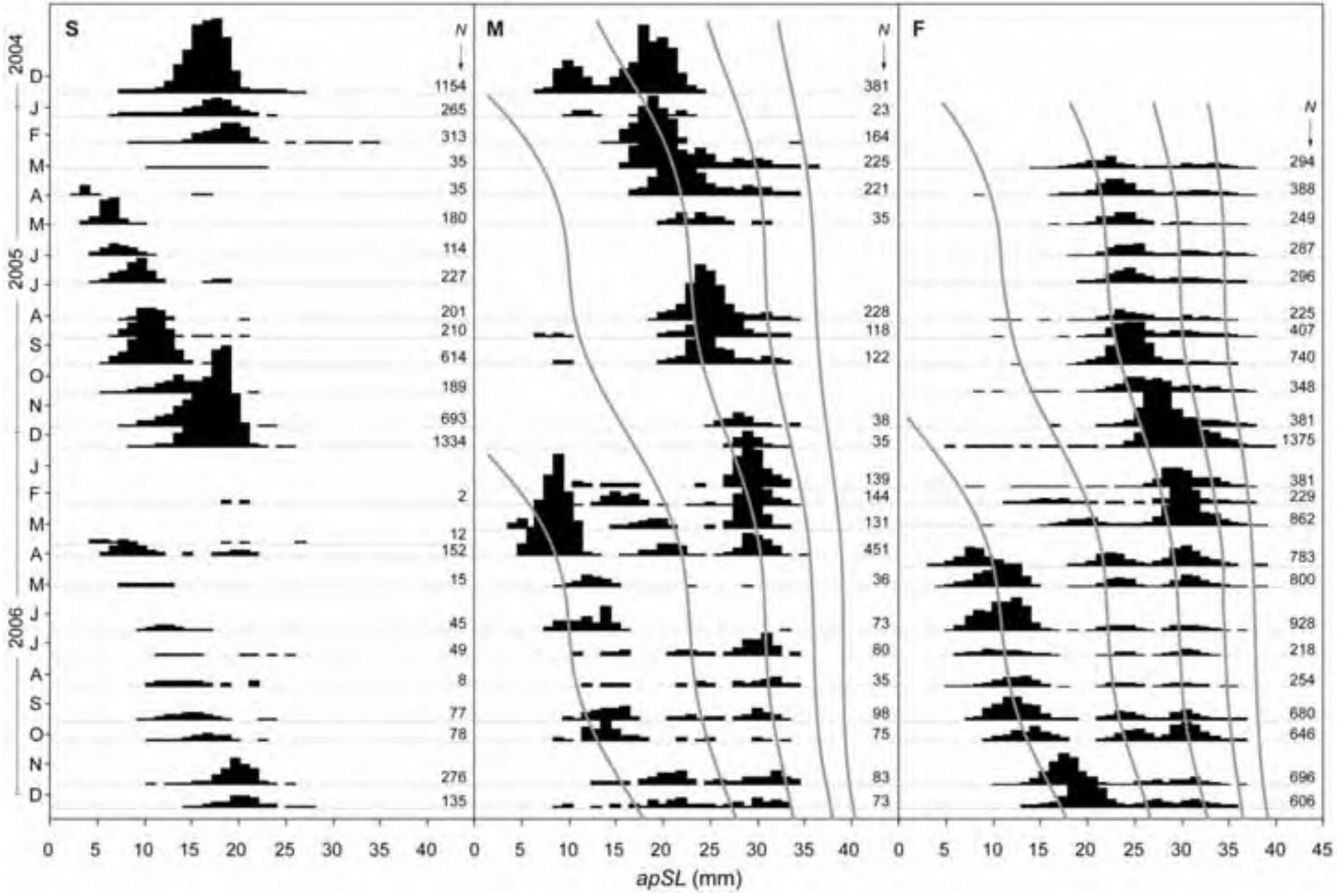


Fig. 4: Growth curves (*grey lines*) of *D. hanleyanus* estimated with the FiSAT program from monthly length-frequency data (*black histograms*) for the periods of December 2004 to December 2006 (**M**: Mar de las Pampas) and of March 2005 to December 2006 (**F**: Faro Querandí). Electronic length-frequency analysis was not applicable at Santa Teresita (**S**) because of the absence of adult individuals. Shaded parts of the histograms indicate peaks in each sample. Datasets are published in Herrmann *et al.* (2008b).

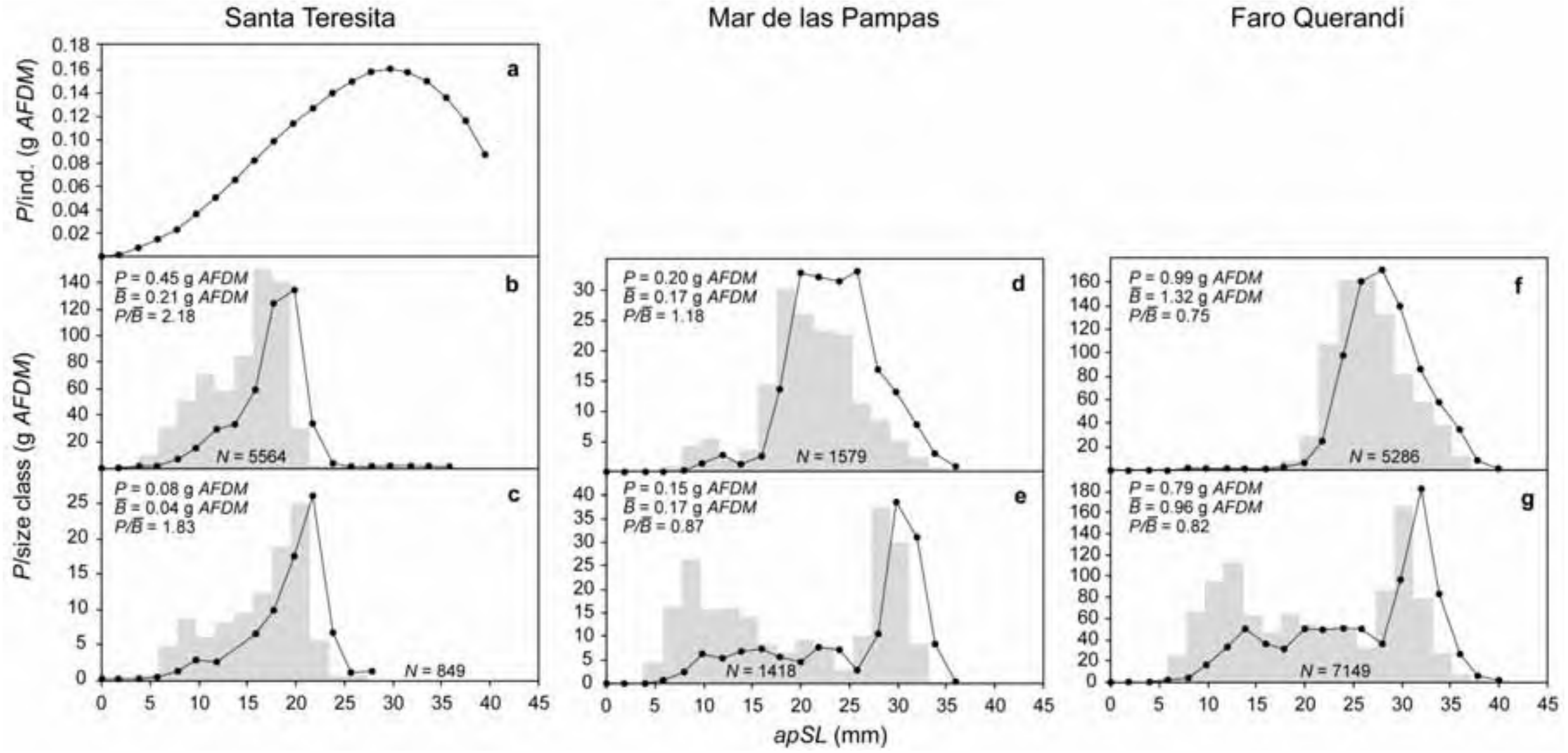
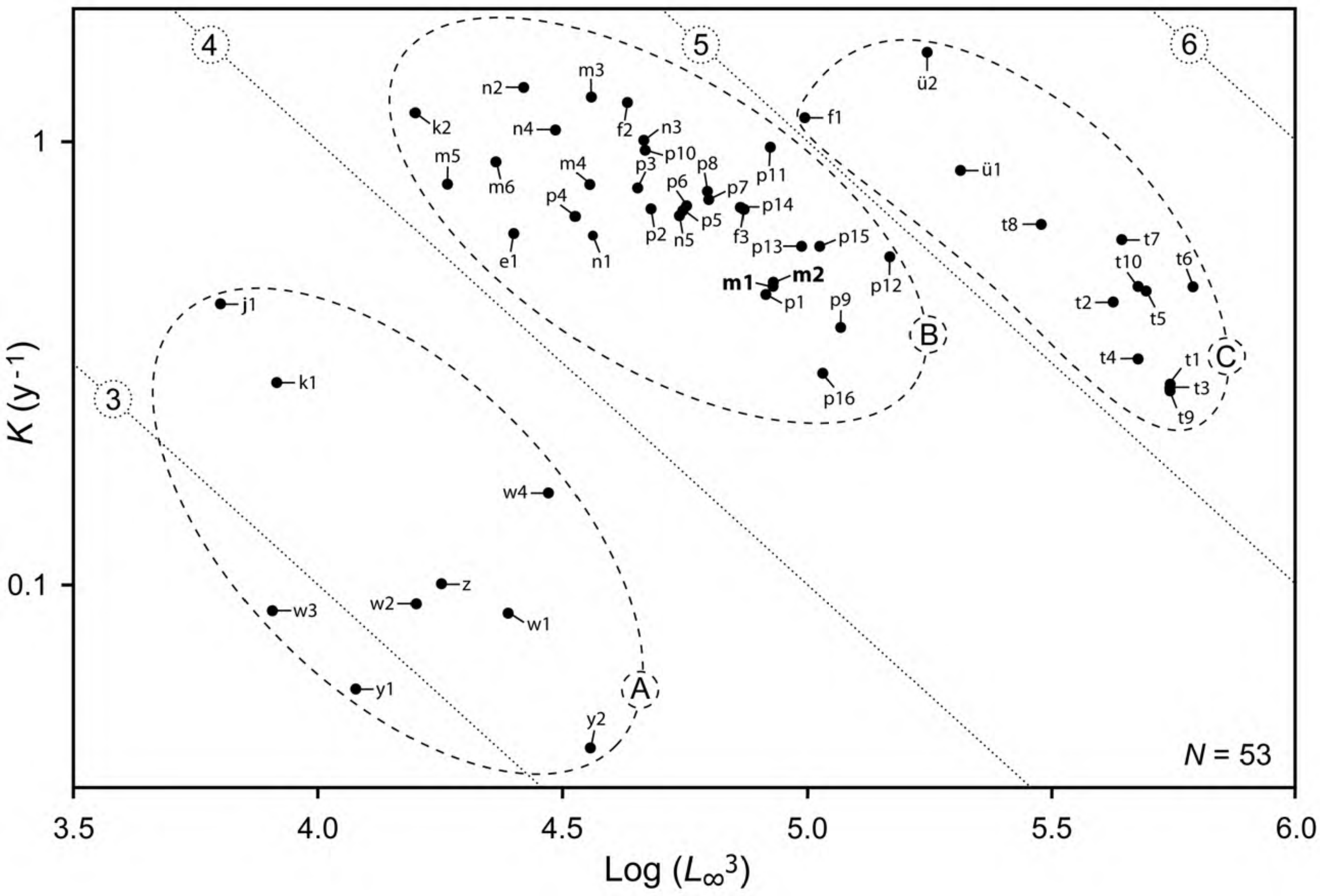


Fig. 5: Distribution of annual somatic individual (**a**) and population production at Santa Teresita for 2005 (**b**) and 2006 (**c**), at Mar de las Pampas for 2005 (**d**) and 2006 (**e**) and at Faro Querandí for 2005 (**f**) and 2006 (**g**). Additionally the mean abundance (grey area = 100 %) for the different length classes of *D. hanleyanus* is provided. Datasets are published in Herrmann *et al.* (2008b).


K (y-1)
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0.1
Log (L∞3)
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4.0
4.5
5.0
5.5
6.0
3
4
5
6
A
B
C
N = 53
j1
k1
w3
w2
z
w1
w4
y1
y2
k2
n2
m3
m5
m6
n4
f2
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p12
p16
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ü1
t8
t7
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t1
t3
t9

Fig. 6: Auximetric grid (extended and corrected from Laudien *et al.* 2003a) comparing *OGP* of the Argentinean *D. hanleyanus* (**m1** and **m2**) with several Donacidae from other areas. Plot indicates three groups (dashed lines): tropical-subtropical (**A**), temperate (**B**) and upwelling species (**C**). Diagonal dotted lines indicate equal values of *OGP* (numbers in circles). For keys and data sources see Table 3; for the distribution of the plotted *Donax* species see Fig. 1B. Stitches at data points in the grid are not representing any value; they only serve as help for labelling. Dataset is published in Herrmann *et al.* (2008b).

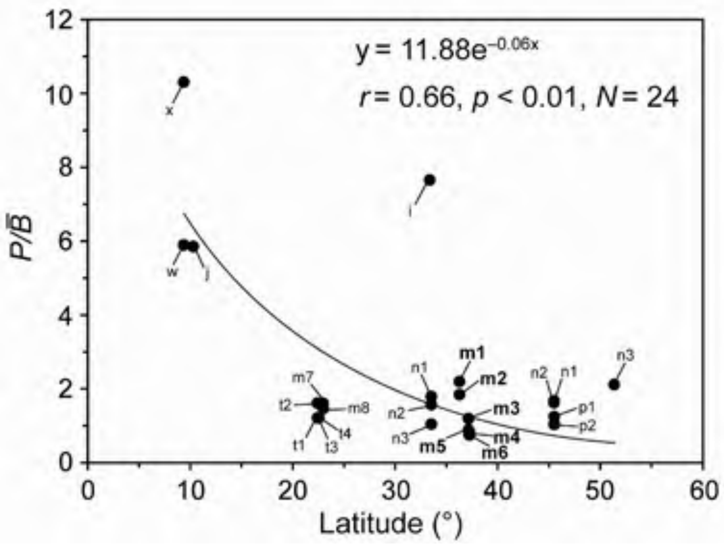

Fig. 7: Relationship between the renewal rate ($P/\bar{B}$ ratios) and latitude of *D. hanleyanus* from the present study (**m1-m6**) in comparison with several *Donax* species. For keys and data sources see Table 4. For the distribution of the mapped *Donax* species see Fig. 1B. Dataset is published in Herrmann *et al.* (2008b).

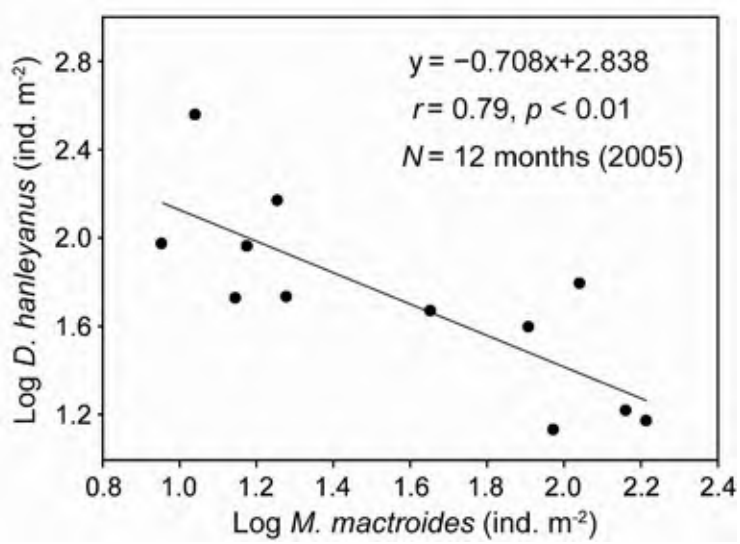

Fig. 8: *D. hanleyanus* - *M. mactroides* linear correlation of the abundance (Log ind. m^{-2}) in 2005 at Santa Teresita. Dataset is published in Herrmann *et al.* (2008b).

Table 1: Characterization of physical and biological attributes of the three studied localities at north Argentinean Atlantic coast.

Beach features	**Santa Teresita**	**Mar de las Pampas**	**Faro Querandí**
Latitude	36°32'S	37°19'S	37°29'S
Longitude	56°41'W	57°00'W	57°07'W
Beach width (m)	< 80	< 70	< 100
Intertidal zone width (m)	< 70	< 60	< 60
Tidal range (m)	1.8	1.7	1.7
Mean grain size (phi/mm) ^{A}	2.26/0.21	1.43/0.37	1.05/0.48
Median grain size (phi) ^{A}	2.28	1.39	0.99
Sorting ^{A,B,C}	Good (0.36)	Moderate (0.68)	Moderate (0.51)
Skewness ^{A,B}	-0.11	+0.07	-0.11
Textural group ^{E}	Fine	Medium	Coarse
Mean slope of intertidal (%)	1/43	1/16	1/14
Exposure ^{D}	Sheltered	Exposed	Exposed
Morphodyn. type ^{E}	Dissipative	Intermediate	Reflective
Dean parameter (Ω) ^{F*}	5.76-7.60	1.08-1.34	0.26-0.31
D. hanleyanus belt (m)	30	12	10
Macrofauna richness (species)	5	3	3

^{A} after Flemming and Thum (1978) and after Flemming and Ziegler (1995), ^{B} after Inman (1952), ^{C} after McLachlan and Brown (2006), ^{D} after McLachlan (1980), ^{E} after Short and Wright (1983), ^{F} after Dean (1973), * calculated for specific seasonal *SST* from 9°C to 25°C.

Table 2: *D. hanleyanus* von Bertalanffy growth parameters: L_∞ = asymptotic length (mm), K = curvature parameter (yr^{-1}), C = constant for the amplitude of seasonal oscillation of growth, WP = point of lowest growth rate (yr), R_n = goodness-of-fit index, $L_{95\%}$ = length (mm) representing 95 % of maximum shell length that was used to estimate $t_{\max}$ = life span (yrs), ϕ' = standard growth index (according to Pauly and Munro 1984).

Localities	L_∞	K	C	WP	R_n	$L_{95\%}$	$t_{\max}$	ϕ'
Mar de las Pampas	44	0.47	0.80	0.45	0.202	40.11	4.96	2.96
Faro Querandí	44	0.48	0.80	0.45	0.350	40.62	5.18	2.97

Table 3: *D. hanleyanus* (**m1**, **m2**) in comparison with several other *Donax* species and their variation in growth performance using the von Bertalanffy growth parameter *K* (yr^{-1}) and L_∞ (mm) as well as the standard growth index $\phi'\phi'$ and the *OGP*. Climate areas (Ca) are: tropical-subtropical (A), temperate (B) and upwelling (C) species. Code letters (*L.*) are equivalent to Fig. 1B. Datasets are published in Herrmann *et al.* (2008b).

L.	Species	Country	Area	Lat.	Long.	Ca	*K*	L_∞	ϕ'	*OGP*	Source
m1	*D. hanleyanus*[2]	Argentina	Mar de las Pampas	37°19'S	57°00'W	B	0.47	44.00	2.96	4.60	Present study
m2	*D. hanleyanus*[2]	Argentina	Faro Querandí	37°29'S	57°07'W	B	0.48	44.00	2.97	4.61	Present study
m3	*D. hanleyanus*[2]	Argentina	Villa Gesell	37°16'S	56°59'W	B	1.18	33.50	3.12	4.65	Penchaszadeh and Olivier (1975)
m4	*D. hanleyanus*[2]	Uruguay	Barra del Chuz	33°40'S	53°29'W	B	0.80	33.00	2.94	4.46	Defeo (1996)
m5	*D. hanleyanus*[2]	Brazil	Marambaia	23°03'S	43°34'W	B	0.80	26.40	2.75	4.17	Cardoso and Veloso (2003)
m6	*D. hanleyanus*[2]	Brazil	Marambaia	23°03'S	43°34'W	B	0.90	28.50	2.86	4.32	Cardoso and Veloso (2003)
j1	*D. denticulatus*[2]	Venezuela	Araya Península	10°38'N	64°16'W	A	0.43	18.50	2.17	3.43	Vélez *et al.* (1985)
e1	*D. dentifer*[2]	Colombia	Bahía Málaga	4°05'N	77°16'W	A	0.62	29.30	2.73	4.19	Riascos and Urban (2002)
y1	*D. cuneatus*[2]	India	Palk Bay	9°17'N	79°05'E	A	0.06	22.87	1.48	2.84	Nayar (1955)
y2	*D. cuneatus*[2,5]	India	Miriya Bay	17°N	53°E	A	0.04	33.02	1.67	3.19	Talikhedkar *et al.* (1976)
z	*D. faba*[1,5]	India	Gulf of Mannar	-	-	A	0.10	26.15	1.84	3.25	Alagarswami (1966)
k1	*D. striatus*[2]	Venezuela	Tucucas, Txori	-	-	A	0.29	20.20	2.07	3.37	McLachlan *et al.* (1996b)
k2	*D. striatus*[2]	Brazil	Futuro Beach	03°42'S	38°27'W	A	1.16	25.10	2.86	4.26	Rocha-Barreira de Almeida *et al.* (2002)
w1	*D. incarnatus*[2,5]	India	Shertallai	9°42'N	76°20'E	A	0.09	29.04	1.86	3.33	Ansell *et al.* (1972)
w2	*D. incarnatus*[2,5]	India	Cochin	10°00'N	76°12'E	A	0.09	25.13	1.76	3.16	Ansell *et al.* (1972)
w3	*D. incarnatus*[2,5]	India	Goa	15°22'N	73°52'E	A	0.09	20.06	1.55	2.85	Nair *et al.* (1978)
w4	*D. incarnatus*[2]	India	Panambur	12°27'N	74°48'E	A	0.16	30.94	2.19	3.68	Thippeswamy and Joseph (1991)
f1	*D. marincovichi*[2]	Peru	Santa Maria del Mar	12°20'S	76°50'W	C	1.00	46.00	3.33	4.99	Arntz *et al.* (1987) → *before El Niño*
f2	*D. marincovichi*[2]	Peru	Santa Maria del Mar	12°20'S	76°50'W	C	1.17	35.00	3.16	4.70	Arntz *et al.* (1987) → *during El Niño*
f3	*D. marincovichi*[2]	Peru	Santa Maria del Mar	12°20'S	76°50'W	C	0.70	42.00	3.09	4.71	Arntz *et al.* (1987) → *after El Niño*
n1	*D. vittatus*[2]	France	St. Trojan	45°50'N	1°20'W	B	0.61	33.15	2.83	4.35	Ansell and Lagardère (1980)
n2	*D. vittatus*[2]	France	St. Trojan	45°50'N	1°20'W	B	1.32	29.76	3.07	4.54	Ansell and Lagardère (1980)
n3	*D. vittatus*[2]	France	St. Trojan	45°50'N	1°20'W	B	1.01	35.90	3.11	4.67	Ansell and Lagardère (1980)
n4	*D. vittatus*[2]	France	Vertbois	45°50'N	1°20'W	B	1.06	31.28	3.02	4.51	Ansell and Lagardère (1980)
n5	*D. vittatus*[2,4]	France	Bay of Douarnenez	48°05'N	4°18'W	B	0.68	38.00	2.99	4.57	Guillou and Le Moal (1980)
p1	*D. trunculus*[2,4]	France	Vertbois	45°50'N	1°20'W	B	0.45	43.48	2.93	4.57	Ansell and Lagardère (1980)

Table 3: *(continued)*

L.	Species	Country	Area	Lat.	Long.	Ca	*K*	L_∞	ϕ'	*OGP*	Source
p2	*D. trunculus* ^{2,4}	France	Vertbois	45°50'N	1°20'W	B	0.70	36.33	2.97	4.53	Ansell and Lagardère (1980)
p3	*D. trunculus* ^{2,4}	France	Vertbois	45°50'N	1°20'W	B	0.79	35.55	3.00	4.55	Ansell and Lagardère (1980)
p4	*D. trunculus* ^{2,4}	France	Vertbois	45°50'N	1°20'W	B	0.68	32.25	2.85	4.36	Ansell and Lagardère (1980)
p5	*D. trunculus* ^{2,4}	France	Vertbois	45°50'N	1°20'W	B	0.70	38.22	3.01	4.59	Ansell and Lagardère (1980)
p6	*D. trunculus* ^{2,4}	France	St. Trojan	45°50'N	1°20'W	B	0.72	38.41	3.02	4.61	Ansell and Lagardère (1980)
p7	*D. trunculus* ^{2,4}	France	St. Trojan	45°50'N	1°20'W	B	0.74	39.78	3.07	4.67	Ansell and Lagardère (1980)
p8	*D. trunculus* ^{2,4}	France	St. Trojan	45°50'N	1°20'W	B	0.77	39.70	3.09	4.68	Ansell and Lagardère (1980)
p9	*D. trunculus* ^{2}	France	Bay of Douarnenez	48°05'N	4°18'W	B	0.38	48.90	2.96	4.65	Guillou and Le Moal (1980)
p10	*D. trunculus* ^{2}	France	Camarque	43°27'N	4°26'W	B	0.96	35.99	3.09	4.65	Bodoy (1982)
p11	*D. trunculus* ^{2}	Spain	Atlantic	-	-	B	0.97	43.80	3.27	4.91	Fernández *et al.* (1984)
p12	*D. trunculus* ^{2}	Spain	Atlantic, El Barquero	-	-	B	0.55	52.84	3.19	4.91	Mazé and Laborda (1988)
p13	*D. trunculus* ^{2}	Spain	Mediterano, Callera	-	-	B	0.58	46.00	3.09	4.75	Ramon *et al.* (1995)
p14	*D. trunculus* ^{3}	Spain	Mediterano, Callera	-	-	B	0.71	41.80	3.09	4.71	Ramon *et al.* (1995)
p15	*D. trunculus* ^{2}	Portugal	Faro	36°57'N	7°53'W	B	0.58	47.30	3.11	4.79	Gaspar *et al.* (1999)
p16	*D. trunculus* ^{2}	Italy	Apulia	41°55'N	15°26'E	B	0.30	47.56	2.83	4.51	Zeichen *et al.* (2002)
ü1	*D. deltoides* ^{2}	Australia	Goolwa	-	-	C	0.86	59.00	3.48	5.25	King (1985)
ü2	*D. deltoides* ^{2}	Australia	New South Wales	36°S	151°E	C	1.59	56.00	3.70	5.45	Laudien *et al.* (2003a)
t1	*D. serra* ^{2}	South Africa	Elands Bay	32°19'S	18°21'E	C	0.28	82.00	3.28	5.19	de Villiers (1975a)
t2	*D. serra* ^{2}	South Africa	Elands Bay	32°19'S	18°21'E	C	0.43	75.00	3.39	5.26	de Villiers (1975a)
t3	*D. serra* ^{2}	South Africa	Melkbosstrand	33°42'S	18°26'E	C	0.28	82.00	3.27	5.18	de Villiers (1975a)
t4	*D. serra* ^{2}	South Africa	Melkbosstrand	33°42'S	18°26'E	C	0.32	78.00	3.29	5.19	de Villiers (1975a)
t5	*D. serra* ^{2}	South Africa	Elands Bay	32°19'S	18°21'E	C	0.46	79.00	3.46	5.36	Laudien *et al.* (2003a)
t6	*D. serra* ^{2}	South Africa	Koeberg	33°40'S	18°25'E	C	0.47	85.00	3.53	5.46	Laudien *et al.* (2003a)
t7	*D. serra* ^{2}	South Africa	St Francis Bay	33°59'S	25°20'E	C	0.60	76.00	3.54	5.42	Laudien *et al.* (2003a)
t8	*D. serra* ^{2}	South Africa	St Francis Bay	33°57'S	25°04'E	C	0.65	67.00	3.47	5.29	Laudien *et al.* (2003a)
t9	*D. serra* ^{2}	South Africa	Langestrand	22°47'S	14°33'E	C	0.27	82.00	3.27	5.18	Laudien *et al.* (2003a)
t10	*D. serra* ^{2}	South Africa	Paaltjies	22°59'S	14°24'E	C	0.47	78.00	3.46	5.32	Laudien *et al.* (2003a)

[1] Maximum length, [2] age estimated from length-frequency distributions, [3] age estimated from hyaline growth rings, [4] age estimated from external growth rings, [5] values calculated on monthly basis from raw data reported by the authors.

Table 4: Secondary production (*P*, g *AFDM* m^{-2}yr^{-1}), biomass ($\bar{B}$, g *AFDM* m^{-2}) and renewal rate (*P/*$\bar{B}$) of *D. hanleyanus* at Santa Teresita (**m1**, **m2**), Mar del las Pampas (**m3**, **m4**) and Faro Querandí (**m5**, **m6**) between 2005 and 2006 in comparison with several *Donax* species from different geographical regions. Table modified from (Cardoso and Veloso 2003). Code letters (*L.*) are equivalent to Fig. 1B and were used for visualizing the relationship between the production-to-biomass (*P/*$\bar{B}$) ratio and latitude in Fig. 7. Datasets are published in Herrmann *et al.* (2008b).

L.	**Species**	***P***	$\bar{B}$	***P/***$\bar{B}$	**Lat.**	**Long.**	**Source**
m1	*D. hanleyanus*	0.45	0.21	2.18	36°32'S	56°41'W	Present study (Santa Teresita 2005)
m2	*D. hanleyanus*	0.08	0.04	1.83	36°32'S	56°41'W	Present study (Santa Teresita 2006)
m3	*D. hanleyanus*	0.20	0.17	1.18	37°19'S	57°00'W	Present study (Mar de las Pampas 2005)
m4	*D. hanleyanus*	0.15	0.17	0.87	37°19'S	57°00'W	Present study (Mar de las Pampas 2006)
m5	*D. hanleyanus*	0.99	1.32	0.75	37°29'S	57°07'W	Present study (Faro Querandí 2005)
m6	*D. hanleyanus*	0.79	0.96	0.82	37°29'S	57°07'W	Present study (Faro Querandí 2006)
m7	*D. hanleyanus*	0.76	0.48	1.59	23°03'S	43°34'W	Cardoso and Veloso (2003)
m8	*D. hanleyanus*	3.67	2.53	1.45	23°03'S	43°34'W	Cardoso and Veloso (2003)
t1	*D. serra*	356.60	288.80	1.20	22°47'S	14°33'E	Laudien *et al.* (2003a)
t2	*D. serra*	273.20	171.90	1.60	22°47'S	14°33'E	Laudien *et al.* (2003a)
t3	*D. serra*	637.30	545.90	1.20	22°59'S	14°24'E	Laudien *et al.* (2003a)
t4	*D. serra*	166.90	141.20	1.20	22°59'S	14°24'E	Laudien *et al.* (2003a)
u1	*D. sordidus* ^{A}	0.38	0.21	1.78	33°57'S	25°40'E	McLachlan and van der Horst (1979)
u2	*D. sordidus* ^{A}	0.15	0.10	1.56	33°57'S	25°40'E	McLachlan (1979)
u3	*D. sordidus* ^{A}	0.13	0.12	1.03	33°57'S	25°40'E	McLachlan (1979)
i	*D. variabilis* ^{A}	1.96	0.26	7.64	33°41'S	78°53'W	Wilson (1999)
j	*D. denticulatus* ^{A,B}	31.39	-	5.84	10°38'N	64°16'W	Vélez *et al.* (1985)
p1	*D. trunculus* ^{A}	18.98	15.42	1.23	45°50'N	1°20'W	Ansell and Lagardère (1980)
p2	*D. trunculus* ^{A}	39.99	39.35	1.02	45°50'N	1°20'W	Ansell and Lagardère (1980)
n1	*D. vittatus* ^{A}	12.33	7.66	1.61	45°50'N	1°20'W	Ansell and Lagardère (1980)
n2	*D. vittatus* ^{A}	17.33	10.43	1.66	45°50'N	1°20'W	Ansell and Lagardère (1980)
n3	*D. vittatus* ^{A}	0.60	0.29	2.10	51°41'N	4°28'W	Warwick *et al.* (1978)
w	*D. incarnatus* ^{A}	1.08	0.18	5.88	9°42'N	76°20'E	Ansell *et al.* (1978)
x	*D. spiculum* ^{A}	0.87	0.08	10.29	9°42'N	76°20'E	Ansell *et al.* (1978)

^{A} Transformed values (g *AFDM* m^{-2} yr^{-1}) by Ricciardi and Bourget (1998), ^{B} maximum daily value (0.016 g *AFDM* d^{-1} x 365 days).

References

(see page 206)

6.2 Publication II

Population structure, growth and production of the yellow clam *Mesodesma mactroides* (Bivalvia: Mesodesmatidae) from a high-energy, temperate beach in northern Argentina.

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Abstract The yellow clam *Mesodesma mactroides* (Bivalvia: Mesodesmatidae) was once an important commercial resource on the Atlantic coast of northern Argentina. A study of the population inhabiting the intertidal zone of a fine sandy beach at Santa Teresita from December 2004 to December 2006 yielded information on the species' population biology, including demographic structure, growth and production. A von Bertalanffy growth function with an asymptotic length (L_∞) of 71 mm and a growth constant (K) of 0.47 yr^{-1} was established from length-frequency distributions. The results were compared with those of growth studies conducted on *M. mactroides* forty years ago, showing that present growth rates are faster now, but that the maximum length attained has decreased. The longevity of the species is estimated at approximately six years. The present study confirmed that the overall growth performance index (*OGP)* is habitat-specific, and can be used to group *M. mactroides* and *M. donacium* from different areas into temperate and upwelling species. Furthermore, *OGP* is inversely correlated with the latitudinal distribution of *Mesodesma* populations. At Santa Teresita, the intertidal biomass ranged between 0.06 and 0.07 g *AFDM* $m^{-2}yr^{-1}$. Individual production was observed to be highest at 47 mm length (0.35 g *AFDM* m^{-2} yr^{-1}) and annual production ranged between 0.12 and 0.19 g *AFDM* m^{-2} yr^{-1}, resulting in renewal rate ($P/\bar{B}$) values between 1.84 and 2.93.

M. mactroides was found associated with very low species diversity and small numbers of individuals of other macrozoobenthic fauna. The abundance of *M. mactroides* showed a significant negative correlation with the abundance of *Donax hanleyanus*. The gastropod *Olivancillaria vesica auricularia* was identified as a potential predator of *M. mactroides*.

Introduction

The yellow clam *Mesodesma mactroides* Reeve, 1854 (Bivalvia: Mesodesmatidae), also known as 'almeja amarilla' in Argentina and Uruguay, is a peculiar species (Parodiz 1942; Stuardo 1964). As one of the most common bivalves of South America (Defeo 1989) it inhabits intertidal Atlantic sandy beaches from tropical (23°S Ilha Grande, Rio de Janeiro State, Brazil) to temperate latitudes (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 South Brazilian sandy beaches, 22 km in Uruguay, and 375 km in Argentina. A suspension-feeder, the yellow clam is the only *Mesodesma* species occurring throughout the Argentinean intertidal (Olivier *et al.* 1971). It co-occurs in the north of Argentina with the sympatric and numerically dominant surf clam *Donax hanleyanus* (Herrmann *et al.* under review-d). During the 1940s and 1950s, *M. mactroides* was an important economic resource in Argentina. A maximum exploitation of 1,079 tonnes was reached in 1953, but the fishery was closed in 1956 following a stock crash (Coscarón 1959) from which the population never recovered. Abundances were decimated further by subsequent mass mortality events in March 1993 due to a red tide incident (Odebrecht *et al.* 1995), in the 1990s due to an unknown cause (Fiori and Cazzaniga 1999) and most recently as a likely result of heavy metal pollution (Thompson and Sánchez de Bock 2007). Illegal extractions and the impact of tourism may also be contributing factors in the failure of the species to make a recovery (Bastida *et al.* 1991). Although there are a number of recent studies on populations of *M. mactroides* from Uruguay (e.g., Defeo *et al.* 1986; Defeo *et al.* 1988b; Defeo 1989; Defeo *et al.* 1991; Defeo *et al.* 1992c; Brazeiro and Defeo 1999; Lima *et al.* 2000), the last Argentinean study is forty years old (Olivier *et al.* 1971). The aim of this study is to estimate contemporary population parameters and production and to make comparisons with data from the historical study. Additionally, the present study aims to examine the possible influence of physical and biological factors on the yellow clam growth and to compare observed population parameters with those of other members of the genus from elsewhere.

Material and Methods

Study Area

The population structure of the intertidal yellow clam, *M. mactroides* was studied at three sandy beaches located in the Province of Buenos Aires, Argentina (Fig. 1): Site i) Santa Teresita (36°32'S, 56°41'W) is an anthropogenically influenced beach, especially affected by mass tourism during the summer season, while at Site ii) Mar de las Pampas (37°19'S, 57°00'W), anthropogenic impacts are less apparent. Site iii) Faro Querandí (37°29'S, 57°07'W), is naturally sheltered and apparently unaffected by human interference.

Environmental Parameters

Accordingly to McLachlan`s (1980) scale for rating exposure and the beach type classifications of Short and Wright (1983), Santa Teresita is sheltered and dissipative, Mar de las Pampas exposed and intermediate, and Faro Querandí exposed and reflective.

All three are open ocean beaches subject to continuous wave action and semidiurnal tides, with a maximum tidal range of 1.6 m. Spring tides average 1.7 m and mean neap tides are 0.2 m. Sea surface temperature (*SST*) varies between 11°C in winter and 23°C in summer (Fig. 2). The study sites are composed of good moderate fine (Santa Teresita), medium (Mar de las Pampas) and coarse sands (Faro Querandí). All three beaches are affected by freshwater seepage due to the southward current bringing water masses from the extensive estuary of the Río de la Plata (290 km long and up to 220 km wide according to satellite images). Mean salinity ranges between 31 and 34. All three beaches are well drained and oxygenated. A full physical and biological characterization of all beaches is detailed in Herrmann *et al.* (under review-d).

Sampling and Laboratory Procedures

Quantitative sampling of *M. mactroides* was carried out at monthly intervals (Santa Teresita and Mar de las Pampas: from December 2004 to December 2006; Faro Querandí: from March 2005 to December 2006) using a series of stations located at 4 m intervals along a transect running perpendicular to the shoreline from the spring tide high water mark to the spring tide low water mark. At each station, three replicate sand samples (40×40 cm) were excavated to 35 cm depth using a stirring corer, and sieved individually on a 1 mm mesh. To obtain monthly length-frequency distributions, the maximum *apSL* of yellow clams retained on the mesh was measured to the nearest 0.1 mm using a digital vernier calliper (Mitutoyo, model 500-161U). For biomass analysis, monthly sub samples of 35 specimens were collected and stored in 70 % ethanol. To estimate shell-free wet mass (*SFWM*), soft tissues were removed and weighed after blotting on filter paper in the laboratory. Samples were subsequently dried to constant mass at 70°C, weighed again to determine shell-free dry mass (*SFDM*) and ignited in a muffle furnace at 550°C for 5 h in order to estimate shell-free ash-free dry mass (*AFDM*).

Physical attributes of the study areas including *SST*, salinity, wave height, wave period, sediment grain size and the consequent sand fall velocity as well as the Dean parameter (Ω) (Dean 1973) were ascertained in a parallel study (Herrmann *et al.* under review-d).

Growth, Growth Performance, Life Span and Mortality

A series of 25 length-frequency distributions provided the basic information for growth estimates. A von Bertalanffy growth function (*VBGF*) (von Bertalanffy 1938) was fitted to the data using the electronic length-frequency analysis 'ELEFAN I' routine of the FiSAT II program package (Gayanilo Jr. *et al.* 2005):

$$L_t = L_\infty \left[1 - e^{\left[-K(t-t_0)+\left(\frac{KC}{2\pi}\right)\sin 2\pi(t-t_s)-\left(\frac{KC}{2\pi}\right)\sin 2\pi(t_0-t_s)\right]}\right], \qquad (1)$$

where L_t is the *apSL* (mm) at time t, L_∞ the asymptotic maximum *apSL* (mm), K (yr^{-1}) is the curvature parameter, C is a constant defining the degree of seasonal oscillation (ranging from 0 indicating continuous non-oscillating growth, to 1 when growth comes to a complete halt at the 'winter point' (*WP*)), t_0 is the theoretical age at zero length (yr) and t_s is the initial point of oscillation in relation to $t = 0$ and the *WP*. The different subroutines of ELEFAN I (*K*-scanning) were used to identify the *VBGF* that best fitted the monthly size-frequency data, using the R_n value as a criterion of fit.

To measure growth performance, the growth index phi prime (ϕ') defined as:

$$\phi' = 2\log_{10}(L_\infty) + \log_{10} K, \qquad (2)$$

was used. This criterion was chosen because the negative correlation between K and L_∞ invalidates comparisons based on individual parameters (Pauly and Munro 1984). Finally the overall growth performance index

$$OGP = \log(K[L_\infty]^3), \qquad (3)$$

which represents growth rate at the point of inflexion of the size-growth curve (Pauly 1979), was calculated to compare growth of *M. mactroides* with other surf clam species.

The theoretical life span ($t_{\max}$) was estimated by an inverse of the von Bertalanffy growth equation, considering maximum shell length as 95% of the asymptotic length (Taylor 1958):

$$t_{max} = \frac{[\ln L_{95\%} - \ln(L_\infty - L_{95\%})]}{K}, \qquad (4)$$

where $L_{95\%}$ represents 95% of the maximum shell length recorded during field sampling.

Total mortality (Z) was calculated from length-converted catch curves (Pauly 1995) yielded by the ELEFAN II routine of the FiSAT program (Gayanilo Jr. *et al.* 2005). Z was estimated by:

$$\ln(N) = g - Z \cdot t, \qquad (5)$$

where N is the number of individuals, g the regression intercept, Z (yr^{-1}) is the unbiased mortality estimate, and t is the estimated age (yr) for each cohort (Pauly 1995).

Biomass and Production

To compare biomass of *M. mactroides* with values for other species, all published values retrieved were converted to *AFDM* (according to Brey *et al.* 1988), whereby a conversion factor of 0.186 (*SFWM* to *AFDM* for ethanol [70 %] preserved *M. mactroides*) was empirically determined. Parameters of the relationship between length and biomass of *M. mactroides* were estimated by regression analysis

$$M = aL^b, \tag{6}$$

where M is the *AFDM* (g), L is the *apSL* (mm) of the size class (mm), and a and b are constants. *AFDM* was determined for 400 specimens of all size classes sampled between December 2004 and December 2006.

Total annual productivity was calculated for the *M. mactroides* belt at Santa Teresita (January-December 2005 and January-December 2006) using the mass specific growth rate method (Crisp 1984; Brey 2001) from size-mass relationships, the size-frequency distribution obtained from all pooled samples and the *VBGF*:

$$P = \sum N_i M_i G_i \ (\mathrm{g}\ AFDM\ \mathrm{m}^{-2}\mathrm{yr}^{-1}), \tag{7}$$

where N_i and M_i are the average abundance of animals (number m^{-2}) and mean individual *AFDM* in length class i, respectively, and G_i is the mass-specific growth rate:

$$G_i = bK\left[\left(\frac{L_\infty}{L_i}\right) - 1\right] \ (\mathrm{yr}^{-1}), \tag{8}$$

where b is the exponent of the size-mass relation, K, L_∞ are *VBGF* parameters and L_i is the mean size in class i.

Mean annual biomass was estimated as

$$\bar{B} = \sum N_i M_i \ (\mathrm{g}\ AFDM\ \mathrm{m}^{-2}), \tag{9}$$

and annual renewal rates ($P/\bar{B}$ ratios) of the *M. mactroides* population were calculated from annual total production *P* and mean annual biomass $\bar{B}$.

Statistical Analysis

Spatial and temporal differences in the population abundance of *M. mactroides* (one-way ANOVA), the influence of *SST* (Spearman`s rank order correlation) and mean *OGP* (one-way ANOVA) were analysed statistically using the software package SPSS version 16.0.1 (2007). Differences were considered significant at a level of $A = 5$ % (Zar 1999).

Results

No *M. mactroides* populations were discovered south of Santa Teresita during the sampling period. Only a few individuals were recorded at Mar de las Pampas (August 2005: 31 ind. m^{-2}) and Faro Querandí (August 2005: 19 ind. m^{-2}; March, April and October 2005: 6 ind. m^{-2} and February 2006: 6 ind. m^{-2}) meaning that population parameters and production could not be estimated for these two areas.

Population Structure

There was no significant difference in abundance of *M. mactroides* between the two sampling years 2005 and 2006 (ANOVA, $F_{1,21} = 3.913$, $p > 0.05$) and no significant difference between respective months (ANOVA, $F_{10,12} = 1.625$, $p > 0.05$) (Fig. 2). Greatest abundance was recorded in May 2005, with 110 ± 25 ind. m^{-2} (mean ± SE) and absolute abundance peaked at 543 ind. m^{-2} (size-class 2-4 mm) in April 2005. Even though the relationship between abundance of *M. mactroides* and *SST* over the entire sampling period was not considered specifically (Spearman`s rank order correlation, $r_s = -0.291$, $p > 0.05$, $N = 24$), it appears that abundance was significantly correlated with *SST* in both years, explicitly during the astral winter from May to November (see gray areas in Fig. 2) (Spearman`s rank order correlation, $r_s = -0.625$, $p < 0.05$, $N = 14$). Distinct cohorts were apparent in the length-frequency distributions obtained (Fig. 3). In both years, a single new cohort was observed during February. New cohorts were tracked for up to eleven months in which they reached *apSL*s *of* 27 mm in 2005 and approximately 35 mm in 2006 before disappearing, after which new recruits appeared. The cohort studied at Santa Teresita never reached the 'commercial size' of 60 mm (Coscarón 1959); indeed only three individuals with *apSL* of > 60 mm were recorded in the entirety of the study period.

Growth, Longevity and Mortality

During the 25 month study period 3,015 *M. mactroides* were collected and measured at Santa Teresita; 2,142 ind. in the first year and 873 ind. in the second year. The smallest recorded individual (*apSL* 2 mm) was found in winter (September 2005) and the largest specimen (*apSL* 64 mm) was found in summer (February 2005). The estimated *VBGF* of the *M. mactroides* population at Santa Teresita with the growth parameter $K = 0.47$ (yr^{-1}) and $L_\infty = 71$ mm (*apSL*) are shown in Fig. 4. The corresponding ϕ' index (3.37) and *OGP* (5.23) are compared in Table 1 with those of *Mesodesma* growth parameters, calculated from different areas. Parameter $C = 0.10$ indicated weak seasonal variation in growth, with lowest growth rates occurring in winter ($WP = 0.7$ ~ mid-August). The calculated life span (t_{max}) of *M. mactroides* was 6.19 yrs and the instantaneous mortality rate (Z) was 0.83 yr^{-1} (Table 1).

Biomass and Production

The observed relationship between length and calculated *AFDM* of *M. mactroides* $M_{(AFDM)} = (9.44 \cdot 10^{-6}) \cdot L_{(mm)}^{2.83}$ ($N = 606$, $r^2 = 0.98$) was used for production estimates.

Annual abundance of *M. mactroides* was 48 ± 13 ind. m^{-2} (mean ± SE) in 2005 and 29 ± 3 ind. m^{-2} (mean ± SE) in 2006. Within the *Mesodesma* belt these abundance values represent an average annual biomass $\bar{B}$ of 0.07 g *AFDM* m^{-2} yr^{-1} (2005) and 0.06 g *AFDM* m^{-2} yr^{-1} (2006) (Fig. 5b-c). Individual production increased to its highest value at 47 mm length (0.35 g *AFDM* m^{-2} yr^{-1}) and decreased thereafter (Fig. 5a). The distribution of total annual production *P* and abundance among the size classes are illustrated in Fig. 5b-c. Annual production ranged between 0.12 and 0.19 g *AFDM* m^{-2} yr^{-1}, and $P/\overline{B}$ ratios were between 1.84 and 2.93.

Discussion

Growth and Growth Performance

The data presented here confirm that *M. mactroides* is a fast-growing species ($K = 0.47$; $\phi' = 3.4$), and fall in line with estimates from previous studies of Argentinean and Uruguayan populations ($K = 0.3$-0.9; $\phi' = 3.3$-3.8; Table 2). However, changes in growth parameters are evident when the recent values (Table 2, no. 1) are compared with those of Olivier *et al.* (1971) (Table 2, no. 9). In 1968-70 *M. mactroides* showed a lower growth constant ($K = 0.28$ *versus* 0.47), indicating that yellow clam growth within the first five years of life was slower four decades ago, but that eventual maximum length was greater than at present ($L_{t(1968\text{-}70)} = 84$ mm; $L_{t(2005\text{-}06)} = 71$ mm). Several studies have estimated maximum shell length for *M. mactroides* at between 84 mm (in Argentina: Olivier *et al.* 1971) and 100 mm (in Uruguay: Defeo *et al.* 1992a). This difference may be attributed to competition with the dominant *D. hanleyanus* population (Herrmann *et al.* under review-d) but also to the different methods applied (length-frequency distributions, external growth rings or size at age data - analysed with ELEFAN I, Shepherd's length composition analysis, SLCA or CAST: Stamatopoulus and Caddy 1989) (cf. Table 2, no. 1-13).

While Defeo *et al.* (1992c) observed strong seasonal variation ($C = 1.0$) in growth rates for a *M. mactroides* population in Uruguay, the variation documented by Fiori and Morsán (2004) was low ($C = 0.45$), and Olivier *et al.* (1971) recorded non-seasonal variations for this species from the Argentinean coast. In support of these latter findings, the present study estimated $C = 0.1$.

Non-linear growth functions such as the *VBGF* are difficult to compare, and several authors (e.g., Pauly 1979; Munro and Pauly 1983; Moreau *et al.* 1986; Laudien *et al.* 2003a; Herrmann *et al.* under review-d) have demonstrated the suitability of composite indices of overall growth performance (*OGP*) for inter- and intraspecific comparisons for various clam species. *OGP* is proportional to the maximum rate of body mass increase during a lifetime, i.e. mass increase at the inflexion point of the *VBGF*. Few values of maximum body mass can be found in the literature and maximal mass is proportional to L_∞. The *OGP* value of 5.23 (Table 2, no. 1) obtained for *M. mactroides* in the current study conforms with the values of 5.22 (Olivier *et al.* 1971) and 5.30 (Fiori and Morsán 2004) calculated from data sets of previous studies on Argentinean populations of the same species and also with the value of 5.28 for a population of *M. donacium* from the Peruvian sampled after an El Niño (EN) event (Arntz *et al.* 1987). It can be assumed that *SST* and food availability are key factors affecting growth and aspects of population dynamics such as production, reproduction, recruitment and mortality. The relatively high values of *OGP* from Uruguay (Fig. 6, no. 10-13) and Peru (before and during an EN event, Fig. 6, no. 14-15), suggest a negative correlation with latitude (Fig. 7: $y = 6.77-0.04x$, $r = 0.94$, $p < 0.05$, $N = 12$). This trend provides support to the latitudinal gradient hypothesis of marine invertebrates (Defeo and Cardoso 2002), which predicts a positive correlation between body size and latitude: populations from subtropical beaches exhibited higher growth and mortality rates and shorter life spans than those of temperate beaches. However, this observation would be better understood if growth studies on several populations could be linked to quantitative and qualitative data regarding phytoplankton. Results compiled from several studies of two different *Mesodesma* species confirmed the hypothesis of Laudien *et al.* (2003a) that *OGP* is habitat-specific (Fig. 6). *OGP* is lowest (5.22-5.81, group A) for *M mactroides* populating temperate regions, and highest (6.33, group B) for *M. donacium* of an upwelling area. Mean *OGP*s of the two groups were significantly different (ANOVA, $F_{1,14} = 21.716$, $p < 0.05$). Climate anomalies may be detected with the help of the auximetric grid, as indicated by the lower *OGP* for the upwelling surf clam *M. donacium* sampled in Peru during and shortly after EN (1982-1983, Fig. 6, no. 15-16) compared to data from normal upwelling years (Fig. 6, no. 14) (Arntz *et al.* 1987).

Life Span and Mortality

There is some controversy concerning longevity estimates for *M. mactroides*. Olivier *et al.* (1971) estimated a maximum age of ~ 8 yrs for the Argentinean yellow clam population, using length-frequency analysis. In contrast, Defeo *et al.* (1988a) suggested a life span of ~ 3.5 yrs for Uruguayan *Mesodesma* populations, derived by the interpretation of shell growth rings. Length-frequency analysis of the current data set yields a life span of ~ 6 yrs, an intermediate estimate within the range of the aforementioned extremes.

The present study revealed an instantaneous mortality rate (*Z*) for *M. mactroides* of 0.83 yr^{-1} closely matches that obtained four decades ago (0.85 yr^{-1}) by Olivier *et al.* (1971). In contrast, Defeo *et al.* (1992c) recorded much greater mortality for the same species from Uruguay, with estimates ranging between 2.26 and 2.91 yr^{-1}. Arntz *et al.* (1987) also found higher mortality rates ($Z = 2.5$ yr^{-1}) for the closely related *M. donacium* inhabiting Peruvian sandy beaches. Thus we hypothesise that the life span of *Mesodesma* species increases and mortality decreases from subtropical to temperate regions, as with other marine invertebrates such as the surf clam *D. hanleyanus* (Cardoso and Veloso 2003) and the isopods *Excirolana brasiliensis* (Cardoso and Defeo 2004) and *Excirolana armata* (cf. de Alava and Defeo 1991; Souza 1998). The lower mortality rates recorded for *M. mactroides* from Argentina may be related to lower predation rates by the gastropod *Olivancillaria vesica auricularia*, which was observed preying on surf clams during sampling, and of other carnivores, such as the gastropod *Buccinanops duartei* and demersal fish such as the black drum (*Pogonias cromis*, corvina negra), the white croaker (*Micropogonias furnieri*, corvina rubia) and the jewsharp drummer (*Menticirrhus martinicensis*, corvina de perita or burriqueta). In Uruguay and Chile the higher mortality rates in *Mesodesma* populations coexisting with 155 ± 36 ind. m^{-2} (mean ± SE) *Emerita brasiliensis* (calculated from Delgado and Defeo 2007a) and 29,704 ind. m^{-1} *E. analoga* (Contreras *et al.* 2003), may be evidence for possible competition between surf clams and suspension-feeding mole crabs. This suggestion is supported by the lower mortality rates of *M. mactroides* in the present study where *Emerita* species are scarce and *D. hanleyanus* abundances were low, at just 60 ± 12ind. m^{-2} (mean ± SE) (Herrmann *et al.* under review-d).

Biomass and Production

Annual intertidal biomass of the *M. mactroides* population at Santa Teresita ranged between 0.06 and 0.07 g *AFDM* m^{-2} yr^{-1} and production varied between 0.12 and 0.19 g *AFDM* $m^{-2}yr^{-1}$. Unfortunately comparable information on the species from elsewhere is very scarce. To the best of our knowledge, no study of this kind has been carried out in Brazil. Defeo (1985) estimated a biomass of 133 g *AFDM* m^{-2} (converted from *SFWM* values published) for the Uruguayan *M. mactroides* population, while four decades ago the biomass of Argentinean *M. mactroides* was estimated at 323 g *AFDM* m^{-2} (Olivier *et al.* 1971, calculated from published *SFWM* data). Thus, the once-prominent role of this primary consumer in the ecosystem appears to be reduced. The individuals observed during the present study were small compared to the records of Olivier *et al.* (1971), in which individuals of commercial size (> 60 mm) were found throughout the year. The reason may be a change in environmental conditions, which has impacted directly on food supply. Biomass data ranging from 141 to 546 g *AFDM* m^{-2} yr^{-1} for the similar-sized surf clam *D. serra*, which occupies a similar ecological position in the Benguela upwelling system (Laudien *et al.* 2003a) lead us to hypothesise that environmental conditions off Argentina may have been more favourable with regard to major primary production four decades ago. Indeed, changes in the environmental conditions of the Argentinean coast are implicated in a study of historically *SST*s (Bava *et al.* 1999). The authors reported that EN 1992 evoked negative *SST* anomalies throughout the south western Atlantic. However, a detailed understanding of the collapse of the Argentinean *M. mactroides* population would require analysis of further historical climate and phytoplankton data.

Ecological Aspects

The carnivorous gastropod *Olivancillaria vesica auricularia*, a known predator of surf clams in Brazilian sandy beaches (Marcus and Marcus 1959; Gianuca 1985; Rocha-Barreira de Almeida 2002), also attacks *M. mactroides* and *D. hanleyanus* at Santa Teresita (V. S. Teso, pers. communication). Predator-prey relationship tests revealed escape behaviour in both clams, when approached by the snail. Surf clams sought refuge even without direct contact, excavating themselves within 10 seconds in order to escape with the next wave (M. Herrmann, unpublished data).

From previous investigations (e.g., Olivier *et al.* 1971; Penchaszadeh and Olivier 1975; Bastida *et al.* 1991) it is well-known that intertidal sandy beach communities of northern Argentina were inhabited by large co-existing populations of the surf clams *M. mactroides* and *D. hanleyanus*. However, the significant negative correlation between the abundances of *D. hanleyanus* (data taken from Herrmann *et al.* under review-d) and *M. mactroides* (Fig. 8) at Santa Teresita in 2005 suggests that the timing of abundance peaks of *D. hanleyanus* may be related to periods of low *M. mactroides* abundance. Penchaszadeh and Olivier (1975), Dadon (2005) and Defeo and de Alava (1995) observed similar inverse correlations between *D. hanleyanus* and *M. mactroides* abundance on Argentinean and Uruguayan beaches. Furthermore, surf clam populations from the Peruvian Pacific coast also showed the same relationship, and abundances of *Emerita analoga* and *D. marincovichi* (formerly *D. peruvianus*) increased coincidentally with the collapse of *M. donacium* populations (Penchaszadeh 1971; Tarazona *et al.* 1985; Arntz *et al.* 1987). Defeo and de Alava (1995) hypothesized that interspecific competition for space and food might explain the relationship between *D. hanleyanus* and *M. mactroides*. Olivier *et al.* (1971) supported this by describing overlapping trophic niches of the two species and predicted that limited food availability might soon impact on *M. mactroides*. However, results in the present study suggest that the two surf clam species do not compete for resources at Santa Teresita. The fact that abundances of *D. hanleyanus* and *M. mactroides* populations were previously much higher than at present (Olivier *et al.* 1971; Penchaszadeh and Olivier 1975) makes food availability an even less likely limiting factor in the current scenario.

This said, the balance between these two species appears to have been disturbed following mass mortality events affecting *M. mactroides* in March 1993 (Odebrecht *et al.* 1995), November 1995 (Fiori and Cazzaniga 1999) and September 2004 (Thompson and Sánchez de Bock 2007) (Fig. 9). *D. hanleyanus*, which was not affected by the mass mortality events, took over immediately as the dominant species, but failed to reach the former abundance of *M. mactroides*. Similar changes in the structure of Peruvian shallow sandy beach communities have been ascribed to EN. Arntz *et al.* (1987) observed that *D. marincovichi* (formerly *D. peruvianus*) prevailed over *M. donacium* immediately after EN but, like Argentinean *D. hanleyanus,* never matched the abundance of the previously dominant *M. donacium*.

Environmental Aspects

Another hypothesis explaining the recent dominance of *D. hanleyanus* over *M. mactroides* is a change in granulometry. Penchaszadeh and Olivier (1975) reported that sediment characteristics are principle factors in the distribution of surf clams. Olivier *et al.* (1971) also described substratum-sensitivity in *M. mactroides*, although the clams are able to penetrate into sediments with a wide spectrum of grain sizes. The present study found *M. mactroides* almost exclusively at the fine sand locality Santa Teresita where mean grain size was 0.21 mm (results from granulometric analysis are given in Herrmann *et al.* under review-d). The lack of yellow clams at the other sites Mar de las Pampas (medium sand, mean grain size 0.37 mm) and Faro Querandí (coarse sand, mean grain size 0.48 mm) precludes further conclusions regarding grain size from this study.

The present study found no evidence for along-shore migration in *M. mactroides,* although abundances are seen to vary considerably a given location. Additional random sampling south and east of the transect did not reveal greater abundances than those recorded at the monthly stations. Further random sampling with a dive corer (Rumohr and Arntz 1982) in the highly dynamic wave breaking zone, confirmed that unlike Peruvian *Donax* populations *D. hanleyanus* did not extend into the surf zone.

Appendix

Fig. 1: Map of the three study sites at the Argentinean Atlantic coast: Santa Teresita (**S**), Mar de las Pampas (**M**) and Faro Querandí (**F**). ● indicates the southernmost distribution of *M. mactroides* at Isla del Jabalí. Dotted areas indicate northern and southern sandy beaches of the Province of Buenos Aires where major *M. mactroides* populations existed in 1953-1956 (Coscarón 1959).

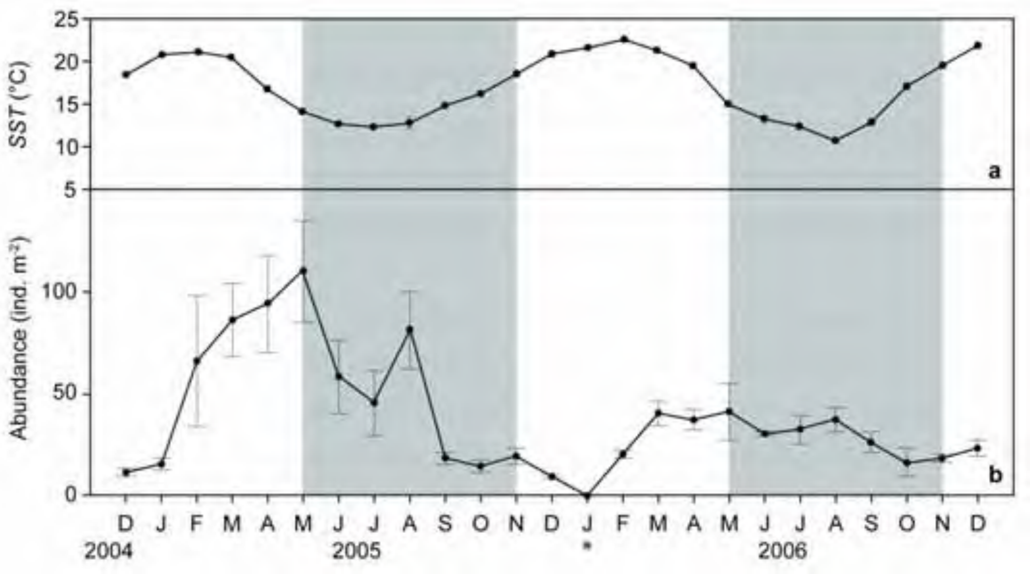

Fig. 2: Population abundance of *M. mactroides* from December 2004 to December 2006 at Santa Teresita (**b**) in relation to monthly mean *SSTs* (**a**). * *M. mactroides* was not abundant during sampling in January 2006. *Error bars*: standard error (SE). *Grey areas*: austral autumn-winter season.

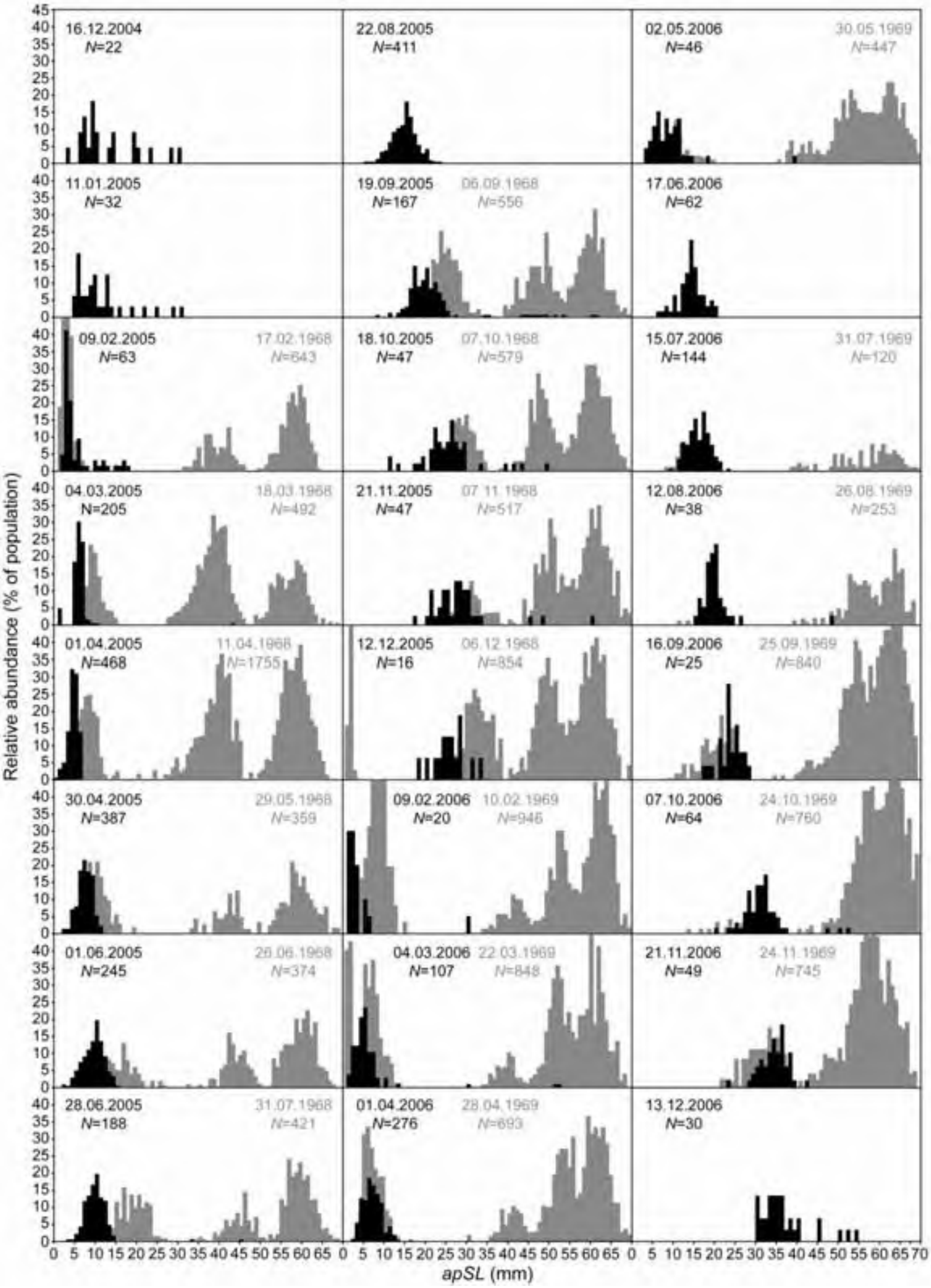

Fig. 3: Monthly length-frequency distribution of *M. mactroides* collected between December 2004 and December 2006 at Santa Teresita (*black histograms*) compared with historical data from Olivier *et al.* (1971) sampled between 1968 and 1969 at Mar Azul (*grey histograms*).

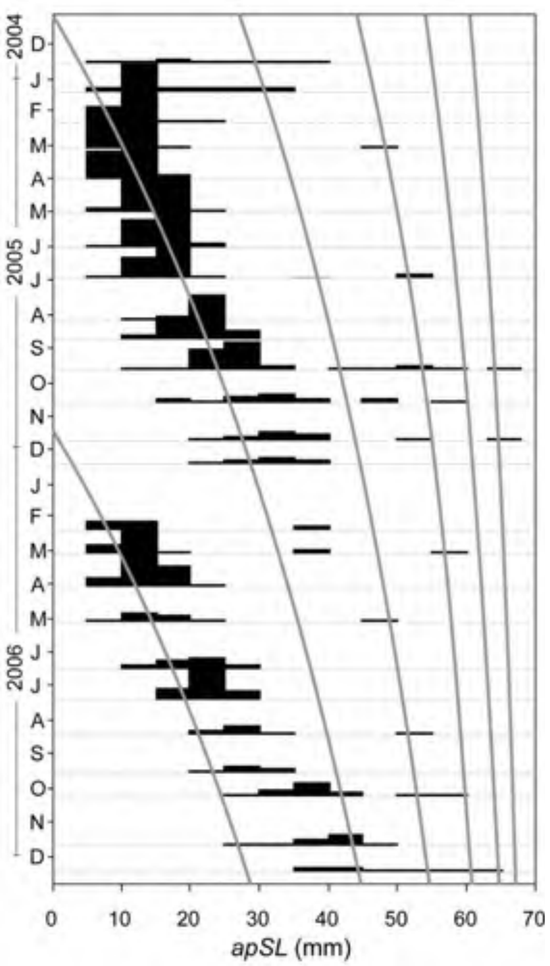

Fig. 4: The *VBGF* (*grey lines*) of *M. mactroides* was estimated with the FiSAT program from monthly length-frequency data (*black histograms*) for the period December 2004 to December 2006.

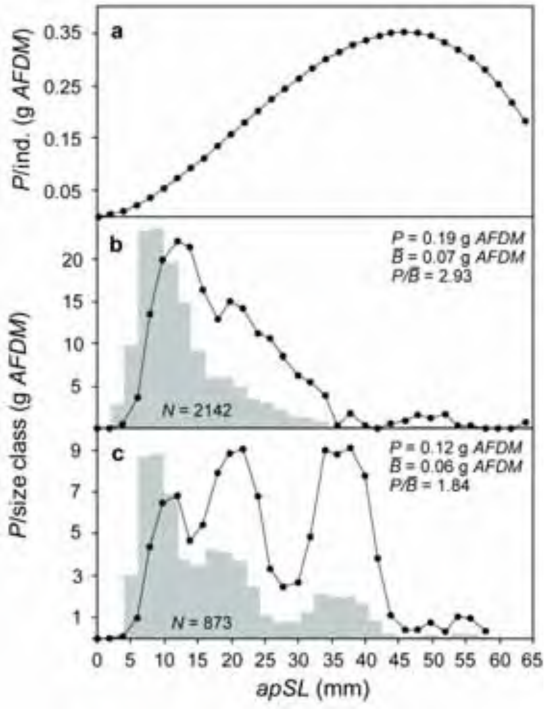

Fig. 5: Distribution of annual somatic individual (**a**) and population production at Santa Teresita for 2005 (**b**) and 2006 (**c**). Mean abundance (*grey area* = 100%) for the different length classes of *M. mactroides* is also given.

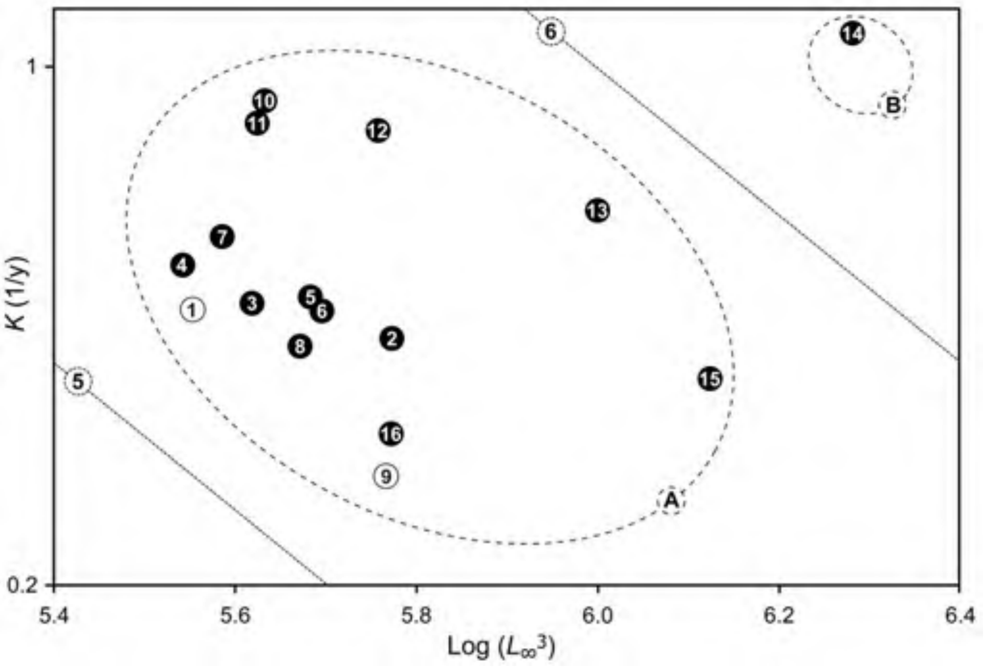

Fig. 6: Auximetric grid comparing the *OGP* of the Argentinean *M. mactroides* from the present study (①) and from Olivier *et al.* (1971) (⑨) with several *Mesodesma* populations from different areas (●). Plot indicates two groups: temperate (A) and upwelling species (B). Dotted diagonal lines indicate equal values of *OGP* (numbers in dotted circles). For keys and data sources see Table 2.

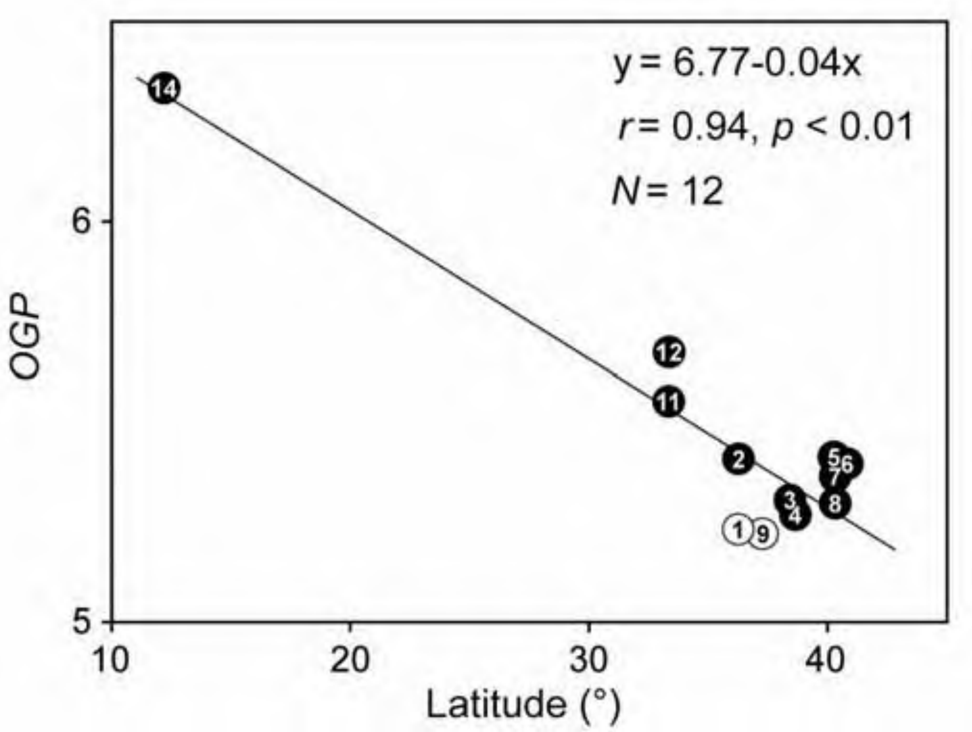

Fig. 7: *OGP* estimated from length-frequency data and obtained from ELEFAN by several populations of *M. mactroides* (1-12) and *M. donacium* (14) located at different latitudes. Comparing values (see Table 2) from this study (①) and from Olivier *et al.* (1971) (⑨).

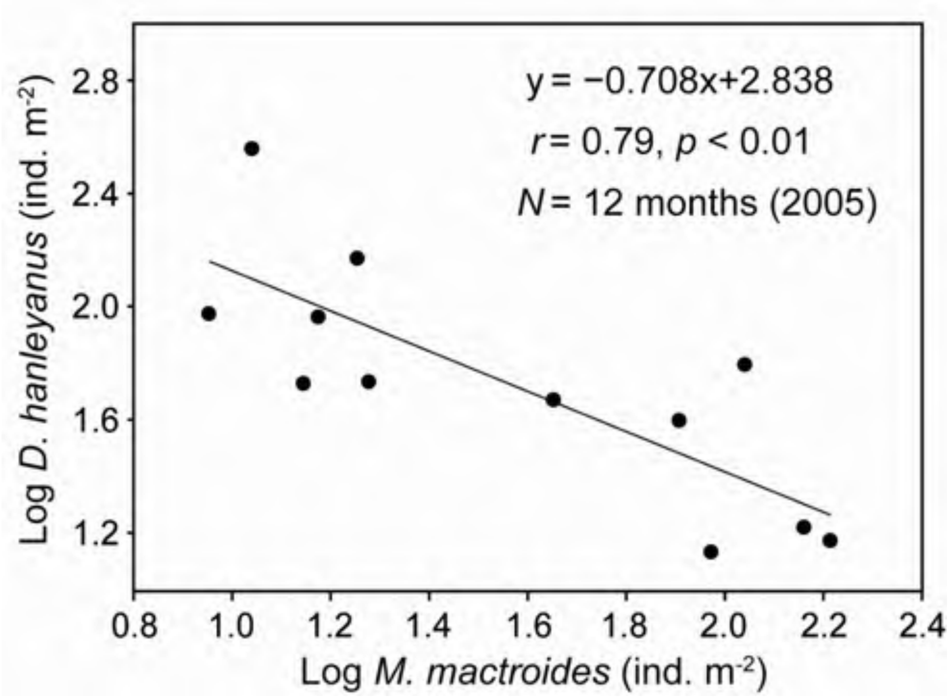

Fig. 8: *M. mactroides* - *D. hanleyanus* linear correlation of abundances (Log ind. m^{-2}) from 2005 at Santa Teresita.

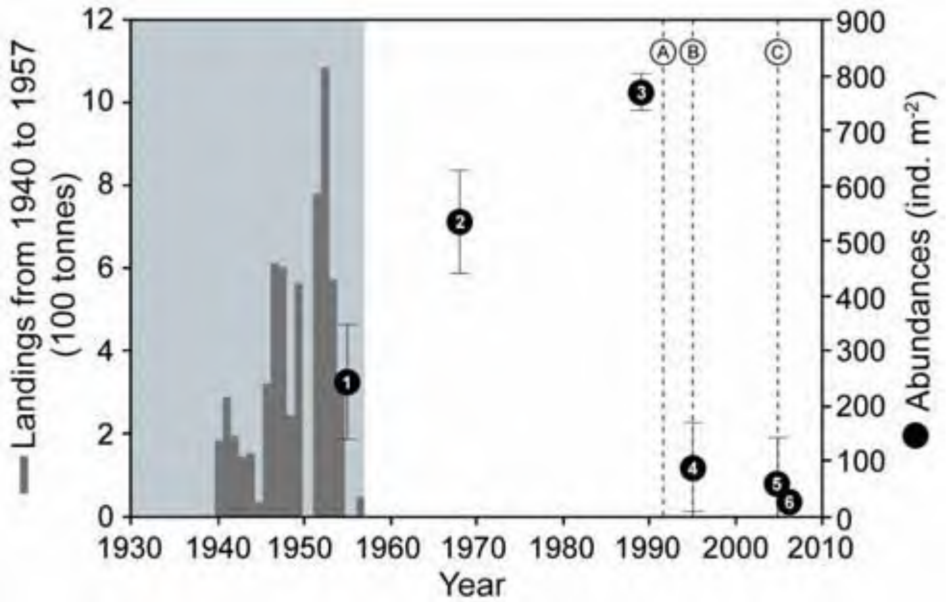

Fig. 9: Population trends in the Argentinean surf clam *M. mactroides*: mean abundances from the present study (**5**: 2005; **6**:2006) compared with historical records (**1**: Coscarón 1959; **2**: Olivier *et al.* 1971; **3**: Bastida *et al.* 1991; **4**: Mabragaña 1997) and landing data (histogram: Coscarón 1959). Ⓐ indicates mass mortality of *M. mactroides* in South America (in March 1993: Odebrecht *et al.* 1995), Ⓑ and Ⓒ unexplained mass mortality events in Argentina (in November 1995: Fiori and Cazzaniga 1999; in September 2004: Thompson and Sánchez de Bock 2007, respectively). Grey area shows the period when *M. mactroides* was commercially fished, the white area is the period when the clam fishery was closed.

Table 1: *M. mactroides* from present study (**1**) in comparison with studies on two South American mesodesmatids and their variation in growth performance with the von Bertalanffy growth parameter K (yr^{-1}) and L_∞ (mm) as well as the standard growth index ϕ' and the *OGP*. Climate areas (Ca): temperate (A) and upwelling (B) species. Code numbers (No.) are equivalent to Fig. 7.

No.	Species	Country	Area	Lat.	Long.	Ca	K	L_∞	ϕ'	*OGP*	Source
1	*M. mactroides* ^{1,4}	Argentina	Santa Teresita	36°32'S	56°41'W	A	0.47	71.00	3.37	5.23	Present study
2	*M. mactroides* ^{1,4}	Argentina	Costa Chica	36°31'S	56°41'W	A	0.43	84.00	3.48	5.41	Luzzatto (2007)
3	*M. mactroides* ^{2,4}	Argentina	Monte Hermoso	38°59'S	61°15'W	A	0.48	74.66	3.43	5.30	Fiori and Morsán (2004)
4	*M. mactroides* ^{3,4}	Argentina	Monte Hermoso	38°59'S	61°15'W	A	0.54	70.42	3.43	5.28	Fiori and Morsán (2004)
5	*M. mactroides* ^{1,4}	Argentina	Isla del Jabalí	40°33'S	62°14'W	A	0.49	78.42	3.48	5.37	Fiori and Morsán (2004)
6	*M. mactroides* ^{1,4}	Argentina	Isla del Jabalí	40°33'S	62°14'W	A	0.47	79.13	3.47	5.37	Fiori and Morsán (2004)
7	*M. mactroides* ^{2,4}	Argentina	Isla del Jabalí	40°33'S	62°14'W	A	0.59	72.77	3.49	5.36	Fiori and Morsán (2004)
8	*M. mactroides* ^{3,4}	Argentina	Isla del Jabalí	40°33'S	62°14'W	A	0.42	77.73	3.40	5.30	Fiori and Morsán (2004)
9	*M. mactroides* ^{3}	Argentina	Faro Querandí	37°29'S	57°07'W	A	0.28	83.76	3.29	5.22	Olivier *et al.* (1971)
10	*M. mactroides* ^{3,F}	Uruguay	La Coronilla-Barra del Chuy	33°39'S	53°28'W	A	0.90	75.47	3.71	5.59	Defeo *et al.* (1992a)
11	*M. mactroides* ^{1,4}	Uruguay	La Coronilla-Barra del Chuy	33°39'S	53°28'W	A	0.84	75.00	3.67	5.55	Defeo *et al.* (1992a)
12	*M. mactroides* ^{1,4}	Uruguay	La Coronilla-Barra del Chuy	33°39'S	53°28'W	A	0.82	83.00	3.75	5.67	Defeo *et al.* (1992c)
13	*M. mactroides* ^{1,E}	Uruguay	La Coronilla-Barra del Chuy	33°39'S	53°28'W	A	0.64	100.00	3.81	5.81	Defeo *et al.* (1992c)
14	*M. donacium* ^{A,4}	Peru	Santa Maria del Mar	12°20'S	76°50'W	B	1.13	124.00	4.24	6.33	Arntz *et al.* (1987) → *before EN*
15	*M. donacium* ^{A,4}	Peru	Santa Maria del Mar	12°20'S	76°50'W	B	0.38	110.00	3.66	5.70	Arntz *et al.* (1987) → *during EN*
16	*M. donacium* ^{A,4}	Peru	Santa Maria del Mar	12°20'S	76°50'W	B	0.32	84.00	3.35	5.28	Arntz *et al.* (1987) → *after EN*

[1] Age estimated from length-frequency distributions, [2] age estimated from external growth rings, [3] age estimated from size at age data, [4] values obtained by the application of ELEFAN, [5] values obtained by the application of SLCA, [6] values obtained by the application of CAST.

Table 2: *M. mactroides* von Bertalanffy growth parameters: L_∞ = asymptotic length (mm), K = curvature parameter (yr^{-1}), C = constant for the amplitude of seasonal oscillation of growth, WP = point of lowest growth rate (yr^{-1}), R_n = goodness-of-fit index, $L_{95\%}$ = length representing 95% of maximum shell length (mm) that was used to estimate life span ($t_{\max}$) (yr^{-1}), ϕ' = standard growth index, the *OGP* and Z = mortality rate (yr^{-1}).

Locality	L_∞	K	C	WP	R_n	ϕ'	OGP	$L_{95\%}$	$t_{\max}$	Z
Santa Teresita	71	0.47	0.10	0.70	0.411	3.37	5.23	67.22	6.19	0.83

References

(see page 206)

6.3 Publication III

Testing the habitat harshness hypothesis: Reproductive biology of the wedge clam *Donax hanleyanus* (Bivalvia: Donacidae) at three Argentinean sandy beaches with contrasting morphodynamics.

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Keywords surf clams, sandy beach ecology, condition index, relative spermatozoon abundance, size and biomass at first maturity, size and abundance of oocytes, (HHH), hypothesis of habitat safety (HHS)

Abstract In order to test the habitat harshness hypothesis (HHH) the reproductive biology of *Donax hanleyanus* (Bivalvia: Donacidae) was studied histologically, comparing populations from three beaches with contrasting morphodynamics (dissipative, intermediate and reflective) over 25 months. The reproductive phase of *D. hanleyanus* was extended in the reflective beach compared to the other two. Males and females from the dissipative and intermediate beaches were significantly smaller and had lower biomass at maturity than those at the reflective beach. Recruits were significantly more abundant and the recruitment period was extended significantly at the dissipative beach. Spawning events took place twice each year at the dissipative (early spring and spring-summer) and the intermediate beach (winter and summer), whereas continuous gamete releases were noted at the reflective beach. Size and biomass at first maturity were lower at the dissipative beach, whereas monthly mean abundance of *D. hanleyanus* was higher at the reflective beach. The gametogenic cycle correlated significantly with sea surface temperature, relative spermatozoon abundance, condition index, shell-free ash-free dry mass and mean size and abundance of oocytes for all three populations. In conclusion, at the population level, many of the reproductive responses of the Argentinean *D. hanleyanus* to physical variables were opposite to those predicted by the HHH including; greater abundance, extended reproductive cycle, extended period with spawning individuals and larger size and higher biomass at first maturity at the reflective beach. In summary, the current study demonstrated that the hypothesis of habitat safety (HHS), originally proposed for supralittoral species, may be extended to intertidal species; a combination of narrow swashes and steep slopes makes reflective beaches a safer and more stable environment for intertidal species such as *D. hanleyanus*.

Introduction

Macrobenthic communities populating exposed sandy beaches demonstrate clear increases in ecological diversity, species richness, abundance and biomass from reflective to dissipative beach morphotypes (e.g. McLachlan 1990; Ricciardi and Bourget 1999; Defeo *et al.* 2003). In physically controlled environments such as sandy beaches, communities are structured by constituent species responding independently to the physical environment rather than by biological interactions, giving strong support to the ‘autoecological hypothesis’ (AH) (Noy-Meir 1979). In agreement with this hypothesis, but restricted to the intertidal of sandy beaches, the ‘swash exclusion hypothesis’ (SEH) (McArdle and McLachlan 1991; 1992) predicts a consistent increase in species richness, abundance and biomass from reflective to dissipative beaches. Furthermore, previous studies have shown that organisms in harsh reflective beaches need to invest more energy in maintenance processes than in growth and reproduction (Gómez and Defeo 1999; Defeo *et al.* 2001). Defeo *et al.* (2001; 2003) combined the community level AH and SEH, to postulate the ‘habitat harshness hypothesis’ (HHH). The HHH predicts that (i) at the community level, reflective beaches will exhibit lower species richness, diversity and abundance while (ii) at the population level, they will be characterised by lower abundance, growth, fecundity, reproductive output and higher mortality rates. However, other recent investigations suggest that populations co-occurring in sandy beaches with a range of contrasting morphodynamics do not conform consistently to these predictions. Veloso and

Cardoso (2001) demonstrated no significant changes in abundance of macrobenthic communities between intermediate and reflective beaches. At the population level Defeo *et al.* (1997) recorded that the isopod *Excirolana braziliensis* exhibited higher abundance at a reflective beach than at a dissipative one, a finding that was confirmed by Defeo and Martínez (2003). In further contrast to the predictions of the HHH, the amphipod *Pseudorchestoidea brasiliensis* presented greater abundance, egg production potential and recruitment levels and lower natural mortality at a reflective beach (Gómez and Defeo 1999). Following a two year study of seven Uruguayan sandy beaches with contrasting morphodynamics, the same authors recently demonstrated that the amphipod *Atlantorchestoidea brasiliensis* (Defeo and Gómez 2005) shows clear population responses to physical variables in direct opposition to those predicted by the HHH, including an increase in abundance and individual size from dissipative to reflective beaches. Furthermore, abundances of the decapod *Emerita brasiliensis* did not vary between dissipative and reflective beaches and at the latter beach type displayed higher male growth rates as well as lower natural mortality (Defeo *et al.* 2001). In summary, these studies suggest that beach morphodynamics might not be the primary factor affecting abundance, population dynamics and life history traits of macrobenthic species. However, the HHH has not been tested comprehensively with respect to reproductive biology. The only investigation dealing with this subject to date was a 13 month study in which 150 Uruguayan wedge clams from two different beach morphotypes were examined. The results in that instance appeared to confirm the HHH (Delgado and Defeo 2007b).

The wedge clam *Donax hanleyanus* Philippi, 1847 (Bivalvia: Donacidae) is a numerically dominant intertidal warm-temperate species in South American sandy beaches and is distributed from tropical (17°S Caravelas, Brazil) to temperate regions (37°S Punta Mogotes in Mar del Plata, province of Buenos Aires) (de Castellanos and Fernández 1965; Penchaszadeh and Olivier 1975; Narchi 1978; Cardoso and Veloso 2003). Wedge clams inhabit a range of Argentinean intertidals (Marcomini *et al.* 2002; Herrmann *et al.* under review-d) providing an opportunity to assess responses to contrasting morphodynamic regimes. The present study tests the HHH at the population level, comparing the reproductive biology of *D. hanleyanus* from three Argentinean sandy beach habitats, one dissipative, one intermediate and one reflective. Following predictions of the HHH (Defeo *et al.* 2001; 2003), we sought to determine whether *D. hanleyanus* at the dissipative beach do indeed exhibit greater abundance of recruits, larger size at first sexual maturity, larger maximum individual size and mass and extended periods of reproduction, recruitment and spawning.

2 Material and Methods

2.1 Study Area

The reproductive biology of the wedge clam *D. hanleyanus* was studied at three Argentinean sandy beaches with contrasting morphodynamics at the southernmost extent of the species' distribution. Accordingly to McLachlan`s (1980) scale for rating exposure and Short and Wright's (1983) classifications of beach types, Santa Teresita (36°32'S, 56°41'W) is sheltered and dissipative, Mar de las Pampas (37°19'S, 57°00'W) exposed and intermediate, and Faro Querandí (37°29'S, 57°07'W) exposed and reflective. The study sites are composed of fine (Santa Teresita), medium (Mar de las Pampas) and coarse sands (Faro Querandí), with a mean particle diameter of 0.21 mm, 0.37 mm and 0.48 mm, respectively. The three sampling sites are subject to continuous wave action, generated by semidiurnal tides, with a maximum tidal range of 1.6 m; a spring tide average of 1.7 m and a neap tide mean of 0.2 m. The sea surface temperature (*SST*) varies between 11 ± 0.14°C (mean ± SE) in winter and 23 ± 0.21°C (mean ± SE) in summer. All three beaches are affected by freshwater seepage due to the southward Brazil Current bringing water masses from the extensive estuary of the Río de la Plata (290 km long and up to 220 km wide according to satellite images). Mean salinity ranges between 31 and 34. All three beaches are well drained and oxygenated. A full physical and biological characterization of both beaches is given in Herrmann *et al.* (under review-d).

2.2 Sampling and Histological Examination

Following the systematic approach detailed by Herrmann *et al.* (under review-d), a total of 22,519 *D. hanleyanus* were collected from the three study beaches named above between December 2004 to December 2006. Quantitative sampling of wedge clams was carried out at monthly intervals (Santa Teresita and Mar de las Pampas: December 2004 to December 2006; Faro Querandí: March 2005 to December 2006) at a series of survey stations set at 4 m intervals along three transects. The transects ran perpendicular to the shoreline between the spring tide high water mark and the spring tide low water mark and were separated by 20 m intervals. At each station, three replicate sand samples (40 x 40 cm) were excavated to 35 cm depth using a 0.16 m^2 steel corer, and sieved individually on a 1 mm mesh. Specimens of *D. hanleyanus* were measured to the nearest 0.1 mm with a digital vernier calliper (Mitutoyo, model 500-161U) and returned alive to their habitat. For biomass determinations as well as for calculations of the condition index (*CI*) a total of 2,205 specimens were preserved in 70 % ethanol and subsequently analysed in the laboratory. For histological examinations a total of 35 wedge clams, covering the full range of anterior-posterior shell lengths (*apSL*) (Santa Teresita: 5 to 28 mm, Mar de las Pampas: 9 to 38 mm and Faro Querandí: 9 to 39 mm), was collected monthly from the three beaches (N_{total} = 2,275 specimens). Wedge clams with severed adductor muscles were fixed in Bouin's solution for two hours, then transferred into 70 % ethanol and later processed in the laboratory using standard histological methods i.e. embedding in paraffin, sectioning at 5 µm and staining with hematoxylin-eosin (following Howard *et al.* 2004). Gonads were examined using a Zeiss Axio Imager Z1 light microscope and designated to one of five developmental stages (sexual rest, pre-active, active, spawning and cytolysed; Fig. 1, Table 1). Images of each sample were captured using a Sound Vision digital camera and processed using the imaging software AxioVision version 4.4 (2008). For all developmental stages except sexual rest, the mean oocyte diameter was determined by measuring 30 oocytes per specimen (N_{total} = 17,286 oocytes measured). Furthermore, the abundance of oocytes in each sectioned female gonad was examined by counting oocytes from one square millimetre surface area (N_{total} = 15,450 oocytes counted). *SST* was measured daily (at 13 pm) at Santa Teresita using a digital thermometer with a precision of 0.1°C. Since monthly *SST*s taken at Mar de las Pampas and Faro Querandí did not vary from those of Santa Teresita (one-way ANOVA, $F_{2,69} = 0.089$, $p > 0.05$), for logistic reasons daily *SST*s from the latter could be applied for all three beaches.

2.3 Data Analysis

2.3.1 Estimation of Relative Spermatozoon Abundance

Relative spermatozoon abundance (*RSA*) is a measure of male gonad activity. *RSA* values were used to simplify the classification of male gonadal tissue and to analyse seasonal variations in the gametogenic cycle. *RSA* is calculated as:

$$SRA = \frac{1}{\text{grey value} \cdot 10^9} \tag{1}$$

where the grey value per mm^2 was measured from greyscale digital images of histological sections using the digital imaging software package Adobe Photoshop version CS3 Extended (2008). The grey value is equal to the brightness of pixels in a digital image, commonly expressed in integers ranging from 0 (black) to 255 (white) on an 8-bit digital signal.

2.3.2 Condition Index, Biomass and Recruitment

Condition Index (*CI*) was calculated to detect seasonal variations in the mass of the visceral mass of *D. hanleyanus*. The total shell-free, wet mass (*SFWM*) of each ethanol-preserved clam was recorded to the nearest 0.1 mg immediately after dabbing off on blotting paper. Mantle, siphons, retractor and adductor muscles were then removed, and the *SFWM* of the resulting standard compact unit comprising the visceral mass and foot was recorded. Following the equation of de Villiers (1975b), *CI* was calculated as:

$$CI = \frac{100\, M_v}{(M_t - M_v)} \tag{2}$$

where M_v is the wet ethanol-preserved visceral mass (including the foot) and M_t is the total ethanol-preserved *SFWM*. Additionally the shell-free ash-free dry mass (*AFDM*) was estimated as an indicator of the wedge clam condition, using the conversion factor of 0.186 provided by Brey *et al.* (1988).

Wedge clams were measured monthly at each beach (data taken from Herrmann *et al.* under review-d) and a pooled two year length-frequency distribution was plotted for each of the three populations ('population' in this paper refers to all specimens of *D. hanleyanus* inhabiting the geographic location without any implication of reproductive connection). On the basis of the histological results, these length-frequency distributions represented three discrete ontogenetic stages: (1) recruits (< 11 mm), (2) juveniles (11-22 mm, the size class where sex can be differentiated for the first time) and (3) adults (> 22 mm, size where individuals were 100 % mature).

2.3.3 Size and Biomass at Sexual Maturity

Size at which 100 % of the population is mature was estimated from the proportion of mature females and males respectively at different size classes, using the logistic equation of McGullagh and Nelder (1997):

$$B_{apSL} = \frac{a}{1 + e^{\left[\frac{-(x-x0)}{b}\right]}} \tag{3}$$

where B_{apSL} is the proportion of females and males respectively with mature gonads in each size class (*apSL*), and *a*, *b* and *x0* are parameters. The biomass at which 100 % of the population is mature was estimated using to the same formula, whereby B_{SFWM} is the proportion of females and males respectively with mature gonads in each biomass class (*SFWM*).

Mature wedge clams were allocated to the development stages 'active' and 'spawning', while immature individuals were deemed to be in the sexual rest stage. Equation (3) was fitted by non-linear least squares, using the quasi-Newton algorithm of the software package SigmaPlot version 11 (2008) to estimate the standard error of parameters. Size at 50 % population maturity ($apSL_{50\%}$) was estimated as:

$$apSL_{50\%} = -b * \ln\left(\frac{a}{50} - 1\right) + x0 \tag{4}$$

and the biomass at which 50 % of the population is mature ($SFWM_{50\%}$) was estimated accordingly.

2.3.4 Statistical Analysis

Sex ratios (male:female) of *D. hanleyanus* were calculated according to the presence of oocytes and spermatozoa using chi-square (χ^2) analysis. The influence of *SST* on the gametogenic cycle, as well as its relationship with *RSA*, *CI*, *AFDM*, abundance and size of oocytes within the population inhabiting each of the sampled beaches were statistically analyzed by Spearman's rank order correlation. Spatial and temporal differences in the gametogenic cycle and oocyte abundance as well as mean and modal sizes of oocytes were tested by one-way analysis of variance (ANOVA). For all beaches the three ontogenetic groups were tested for differences by two-way ANOVA using the factors 'beach' and 'ontogenetic group'. Based on the Durbin-Watson coefficient, residuals of the logistic functions of size and biomass at sexual maturity were tested for autocorrelation. The closer the coefficient to value '2' (within the range of 0 and 4) the less significant the autocorrelation (SigmaStat 2004). To compare results of size and biomass at 50 % population maturity, as estimated for both sexes and for each of the three beaches, analyses of the residual sum squares (ARSS) were performed (Chen *et al.* 1992). All statistical analyses were carried out using the statistical package SPSS version 16.0.1 (2007). Differences were considered significant at the level of $A = 5$ % (Zar 1999). Results of the statistical comparisons of the three wedge clam populations are summarised in Table 2.

3 Results

3.1 Gametogenic Cycle

Histological examinations of gonadal tissue from a 25 month sampling series demonstrated that sex ratios did not significantly deviate from 1:1 at the intermediate and reflective beaches (Table 2a), but there was a greater proportion of females at the dissipative beach in December 2004 ($\chi^2 = 8.758$, $df = 1$, $p < 0.05$), January 2005 ($\chi^2 = 11.765$, $df = 1$, $p < 0.05$) and April 2006 ($\chi^2 = 4.571$, $df = 1$, $p < 0.05$). No case of hermaphroditism was found. Furthermore, histological analysis revealed that the reproductive cycle of both male and female *D. hanleyanus* undergoes a distinct seasonality at all three beaches (Table 2b): males (Fig. 1b) and females (Fig. 1f). Sexual activity was detectable mainly during spring and summer (Fig. 2, Table 2t) at all three beaches. At the dissipative beach, the spawning period of wedge clams was restricted mainly to spring and summer, while gamete release continued all year round in the intermediate (except in July, August 2005 and July, December 2006) and reflective beach (except July, August 2005 and August, November, December 2006) populations respectively (Fig. 2). In both years of the study, cytolysed specimens dominated the population in autumn and winter at all three beaches (Fig. 2, Table 2u). Wedge clams of indistinguishable sex were found at the reflective and intermediate beaches during all months except during summer, while a high proportion of individuals in the sexual rest stage appeared at the dissipative site in early autumn 2005 and in late summer 2006 (Fig. 2, Table 2v).

The gametogenic cycle (active and spawning) of *D. hanleyanus* was correlated significantly with *SST* (Fig. 3a, c, Table 2c). In both years, the size of oocytes (Table 2f, Table 3) and their abundance (Fig. 3d, Table 2g) was correlated significantly with the gametogenic cycle (Fig. 3c) at all three beaches. Furthermore, both parameters correlated significantly with *SST* at the dissipative and reflective beaches (Table 2j, k). At all three beaches, wedge clam oocytes showed increased abundance in spring (Fig. 3d, Table 2m), whereas oocyte abundance decreased in autumn-winter (Fig. 3d, Table 2n), when most specimens were in the cytolysed stage (Fig. 1d, h).

Analyses of monthly oocyte size classes showed a unimodal distribution, with size ranges from 2 µm to 70 µm (Fig. 4), a situation which did not vary significantly between beaches (ANOVA, $F_{2,54} = 0.194$, $p > 0.05$). At the dissipative beach the modal oocyte size decreased twice each year, in early spring (September) and in spring-summer (December). A twice annual decrease was also recorded at the intermediate beach each year, in winter (August) and in summer (twice in February, once in December 2006) while at the reflective site decreases were observed during all seasons (autumn: April 2005 and March 2006; winter: June and July 2006; spring: September 2005; and summer: January 2006) (Table 2l), suggesting two spawning events at the dissipative and intermediate beaches and more continuous gamete releases at the reflective beach (Fig. 4).

3.2 Relative Spermatozoon Abundance

RSA correlated significantly with the gametogenic cycle (active and spawning gonad stages) of *D. hanleyanus* at all three beaches (Fig. 3b, Table 2q), whereby wedge clam *RSA* showed significant increases at the dissipative and intermediate beaches in spring and at the reflective beach in spring-summer (Fig. 3b, Table 2r). At all three beaches *RSA* decreased significantly in autumn-winter (Fig. 3b, Table 2s).

3.3 Condition Index, Biomass and Recruitment

At all three study beaches, the annual reproductive cycle of *D. hanleyanus* correlated significantly with *CI* (Table 2d). *CI* was correlated significantly with *SST* at both the dissipative and the reflective beach (Table 2h). Seasonal variations in wedge clam biomass (*AFDM*) within the respective beach populations correlated significantly with *SST* (Table 2i) and with mature gonad stages (ripe and spawning) at all three beaches (Table 2e) but did not vary between beaches (ANOVA, $F_{2,59} = 0.425$, $p > 0.05$). Recruits of *D. hanleyanus* were found in all seasons at all three beaches during both sampling years (except at the dissipative beach in January 2006 and at the intermediate beach in June, July and October 2005). However, the peak of settlement was recorded at the intermediate beach in summer 2005 and in summer-autumn 2006 (Fig. 3, [IIg], Table 2p), at the reflective beach in autumn 2005 and autumn-winter 2006 (Fig. 3, [IIIg], Table 2p), and at the dissipative beach for extended periods during autumn-winter 2005 and summer-autumn 2006 (Fig. 3, [Ig], Table 2p). Despite this apparent seasonality, the settlement period of recruits was not significantly correlated with *SST* (Table 2o). The length-frequency distributions covering two years revealed that the intermediate and reflective beaches were populated by considerably larger wedge clams than the dissipative site ($F_{2,21836} = 63.618$, $p < 0.05$). The mean *apSL* of juveniles found at the dissipative beach was significantly higher than that of both other populations, but adult *apSL* was considerably smaller ($F_{2,21836}$ = 11,302.263, $p < 0.05$). The analysis of the population structure indicated that at the dissipative beach, recruits represented 22.8 % of the population and adults accounted for only 1.5 %, whereas the reflective beach population comprised a mere 10.5 % recruits and 65 % adult wedge clams (Fig. 5).

3.4 Size and Biomass at Sexual Maturity

Single individuals of *D. hanleyanus* matured smaller (*apSL*) and lighter (*SFWM*) at the dissipative beach (males: 8.61 mm, 0.02 g; females: 9.35 mm, 0.04 g) than at the intermediate (males: 12.72 mm, 0.10 g; females: 13.21 mm, 0.12 g) or reflective (males: 22.92 mm, 0.55 g; females 22.44 mm, 0.39 g) beaches. At all three study locations, the relationship between size and biomass at 50 % population maturity was explained convincingly ($p < 0.05$) by the non-linear regression given as Eq. 4 for both males and females (Fig. 6, Table 4). At the dissipative beach, wedge clams were 100 % mature on reaching an *apSL* of approximately 23 mm (both sexes) and an *SFWM* of 0.4 g. Females at the intermediate beach reached up to 20 mm *apSL* and 0.9 g *SFWM* before attaining 100 % maturity, while for males *apSL* and *SFWM* at 100 % maturity were even higher, at 27 mm and 0.5 g respectively. In contrast, at the reflective beach wedge clams were largest and heaviest (approximately 30 mm *apSL* and 1.8 g *SFWM*, both sexes) when reaching 100 % maturity (Fig. 6, Table 4). The logistic function of male wedge clam *apSL* was significantly steeper at the dissipative (ARSS $F_{2,21}$ = 324.631, $p < 0.05$) and intermediate beaches (ARSS $F_{2,23}$ = 418.321, $p < 0.05$), indicating that 50 % population maturity was reached at a significantly larger size ($apSL_{50\%}$) at the reflective beach (Fig. 6a, Table 4). A similar pattern was found in female specimens, where the slope of the logistic function was also significantly steeper at the dissipative (ARSS $F_{2,20}$ = 658.950, $p < 0.05$) and intermediate beach (ARSS $F_{2,23}$ = 973.554, $p < 0.05$), resulting in significantly larger female clams in a 50 % mature population ($apSL_{50\%}$) at the reflective beach (Fig. 6b, Table 4). Size and biomass (both sexes) at 50 % population maturity ($SFWM_{50\%}$) were significantly higher at the reflective beach (Fig. 6c, d), leading to significantly steeper logistic *SFWM* function at the dissipative (ARSS: males $F_{2,50}$ = 253.423, $p < 0.05$, females $F_{2,53}$ = 579.924,

$p < 0.05$) and intermediate beaches (ARSS: males $F_{2,152} = 481.643$, $p < 0.05$, females $F_{2,125} = 761.464$, $p < 0.05$) (Table 4).

4 Discussion

4.1 Comparison of Reproductive Biology on Morphodynamically Distinct Beach Types

Histological analyses from the 25 month sampling series revealed differences in the reproductive biology of *D. hanleyanus* populating three morphodynamically distinct beaches. However, in contrast to the 13 month data set of Delgado and Defeo (2007b), which documented the reproductive cycle of Uruguayan *D. hanleyanus* from two sandy beaches and supported the HHH, the present study does not confirm all predictions of this hypothesis for the reproductive cycle of the Argentinean species.

4.1.1 Consistency with Predictions of the HHH

In accordance with the HHH, the settlement period of *D. hanleyanus* recruits was extended and recruits were more abundant at the dissipative beach compared to either the intermediate or reflective beach. Although there have been several previous studies on the reproduction biology of *Donax* species (Argentinean D. hanleyanus: Penchaszadeh and Olivier 1975; Peruvian D. marincovichi: Huaraz and Ishiyama 1980; Portuguese D. trunculus: Gaspar *et al.* 1999; Spanish D. semistriatus and D. venustus: Tirado and Salas 1999; Brazilian D. hanleyanus: Gil and Thomé 2004a), data on recruitment at beaches with different morphodynamics are scarce and inconsistent. The present results are in keeping with those of Delgado and Defeo's (2007b) conclusions regarding recruitment from the Uruguayan *D. hanleyanus* population, in that both abundance of recruits and recruitment period are greater at a dissipative beach. The results of the current study suggest a shorter recruitment season for *D. hanleyanus* in reflective beach populations and therein coincide with a prediction of the HHH. However, recruits of *Donax* do not always show the same pattern. For instance, Laudien *et al.* (2001) observed a longer period of recruitment in Namibian *D. serra* at a reflective beach than a dissipative one, a find that directly contradicts the predictions of the HHH.

4.1.2 Contrasts to predictions of the HHH

The ‘spawning’ stage of wedge clams was restricted in the dissipative beach population than in those from the beaches exhibiting intermediate and reflective morphodynamics. Furthermore, the proportion of specimens in the sexual rest stage varied from beach to beach. While at the reflective and intermediate beach gonads of indistinguishable sex appeared in low percentages from autumn to spring, large numbers of specimens in the sexual rest stage were only found twice (early autumn 2005 and late summer 2006) at the dissipative beach. Comparable size classes were present at all three beaches at the same time (Herrmann *et al.* under review-d). Additionally, *RSA* was lower at the dissipative and intermediate beaches than at the reflective one.

Further evidence for an extended reproductive cycle at the reflective beach, contrary to the predictions of the HHH, was derived from monthly oocyte size-frequency distributions. Modal oocyte values indicate two spawning events per year at the dissipative and intermediate beaches and continuous gamete releases at the reflective beach.

Size and biomass at first maturity of both sexes were lower at the dissipative beach, suggesting an abrupt transition from sexual rest to reproductive activity at this site.

Monthly mean abundance of *D. hanleyanus* was significantly higher at the reflective beach (ANOVA, $F_{2,69} = 14.675$, $p < 0.05$), compared to the dissipative and intermediate locations (Herrmann *et al.* under review-d), which is also counter to the predictions of the HHH. Consequently, the present study supports the results of previous investigators documenting increases in abundance of isopods (*E. braziliensis*: Defeo *et al.* 1997; Defeo and Martínez 2003), amphipods (*P. brasiliensis*: Gómez and Defeo 1999; *A. brasiliensis*: Defeo and Gómez 2005) and decapods (*E. brasiliensis*: Defeo *et al.* 2001) at Uruguayan reflective beaches.

4.2 Comparison of the Reproductive Biology among the Three Beaches

4.2.1 Gametogenic cycle

The histological examination of *D. hanleyanus* gonads suggests several reproductive events per year (Fig. 2), with an underlying seasonality, confirmed by a significant correlation with *SST* at all three beaches. Gonad classifications revealed two annual spawning events at the dissipative beach (spring and summer) and the intermediate beach (spring and summer-autumn) and a continuous gamete release over the year at the reflective beach (Table 5A). These are in line with results from Delgado and Defeo (2007b) and Gil and Thomé (2004a), who observed two spawning events at dissipative beaches and continuous spawning at reflective sites in Uruguay and Brazil respectively. However, spawning events can be determined more exactly by oocyte measurements (e.g. Penchaszadeh and Olivier 1975; Sarkis *et al.* 2006; Morriconi *et al.* 2007). Modal values of the oocyte size-frequency distributions (Fig. 4) indicate two spawning events at the dissipative beach (September and December), and three each at the intermediate beach (February, August and December) and the reflective beach (January, April-July and September), with a more extended period at the latter (Table 5B). Similarly, four decades ago Penchaszadeh and Olivier (1975) detected two spawning events (January-February and August-September) of *D. hanleyanus* by measuring oocyte sizes at Villa Gesell, 10 km north of the intermediate beach Mar de las Pampas. In agreement with previous investigations on the reproductive biology of *D. hanleyanus* (Penchaszadeh and Olivier 1975; Gil and Thomé 2004a; Delgado and Defeo 2007b), the present study confirms that there is no period of complete gonadal inactivity in this species. The same is true in the Peruvian *D. marincovichi* (Huaraz and Ishiyama 1980) and the Namibian *D. serra* (Laudien *et al.* 2001), but not in the Portuguese *D. trunculus* (Gaspar *et al.* 1999) and the Spanish *D. venustus* and *D. semistriatus* (Tirado and Salas 1999). The discrepancy may be caused by the significant differences in seasonal ranges in *SST* range routinely experienced by different species (Urban and Campos 1994; Sasaki *et al.* 1997; Laudien *et al.* 2001).

However, *SST* is not the only parameter influencing the reproduction cycle of suspension feeders (Sastry 1968; Giese 1974; Sastry 1979). Changes in phytoplankton biomass and species composition are also key factors. Thus, 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, corresponds convincingly with the dominance of ripe and spawning stages of *D. hanleyanus* (Fig. 3). This suggests that phytoplankton abundance may also have a direct impact on the reproductive cycle of *D. hanleyanus*.

4.2.2 Relative Spermatozoon Abundance

As documented in 3.2 and discussed in 4.1.2 above, *RSA* was lower at the dissipative and intermediate beach (spring), than at the reflective one (spring-summer). The measurement of spermatozoon abundance turned out to be a good reflection of male gonadal tissue condition and thus a useful indicator in the investigation of seasonal variations in the gametogenic cycle between beaches with contrasting morphodynamics. This method negates the need for time-consuming microscopical examination of gonads to assign samples to different developmental stages. *RSA* may be used to analyse the relationships between abiotic and biotic parameters and the gametogenic cycle. Furthermore, *RSA* may be calibrated species-specifically; counting spermatids per surface area allows estimations of absolute spermatozoon abundance.

4.2.3 Condition Index, Biomass and Recruitment

CI and *AFDM* are useful tools in describing the reproductive biology of *D. hanleyanus*. Both indicate gonadal mass changes throughout the year, with highest values when gonads are in the mature stage. The results presented here are in line with studies of other surf clams, where the *CI* was also successfully used to describe changes in the gametogenic cycle (D. trunculus: Gaspar *et al.* 1999; D. serra: Laudien *et al.* 2001; Mesodesma donacium: Riascos *et al.* 2008). Recruitment pattern and abrupt changes in oocyte size appear to indicate a meroplanktonic phase of approximately three months, assuming that collected recruits originated from the studied adult population. Recruitment patterns observed in the present study provide clear evidence that juvenile wedge clams occur only sporadically and recruitment varies between years, agreeing with the findings of other studies (e.g. Arntz *et al.* 1987; Laudien *et al.* 2001). It should be noted that the absence of recruits does not necessarily indicate a lack of spawning activity (Caddy and Defeo 2003). Environmental conditions may strongly influence recruitment of marine invertebrates (e.g. hydrodynamic processes: Roughgarden *et al.* 1988; food limitation: Olson and Olson 1989; predators: Sale 1990), and unfavourable conditions may lead to failure of recruitment at the parent beach.

4.2.4 Size and Biomass at Sexual Maturity

Single individuals of *D. hanleyanus* in the present study matured with an average shell length of 9 mm (and 0.02 g *SFWM*) and reached gonadal maturity $apSL_{50\%}$ at 16 mm (and 0.15 g $SFWM_{50\%}$). The present results coincide well with estimates of forty years ago (15 mm: Penchaszadeh and Olivier 1975), and with data from the Uruguayan *D. hanleyanus* population (minimal length with gonad development 10 mm, gonad maturity 12 mm: Delgado and Defeo 2007b).

4.3 Conclusion

In conclusion, the results of the present study obtained from three beaches over 25 months demonstrate that at the population level *D. hanleyanus* respond systematically to beach morphodynamics in a manner opposite to that predicted by the HHH. The population at the dissipative beach exhibited a greater abundance of recruits and an extended recruitment period, but spawning specimens were greatly outnumbered by those in sexual rest stages. Spawning events were registered twice each year at the dissipative (early spring and spring-summer) and intermediate beaches (winter and summer), whereas continuous gamete release was noted at the reflective beach. Maturity was first observed in single *D. hanleyanus* individuals with approximately 9 mm *apSL* and 0.02 g *SFWM*. 50 % of the population attained maturity at 15 mm *apSL* and 0.15 g *SFWM*, and 100 % were mature at a size of 23-27 mm *apSL* and 0.4-0.9 g *SFWM*. Size at first maturity and biomass at first maturity were lower at the dissipative beach, whereas monthly mean abundance of *D. hanleyanus* was higher at the reflective beach. Finally, the current study demonstrated that the ‘hypothesis of habitat safety (HHS)’, originally postulated by Defeo and Gómez

(2005) for supralittoral species, may be extended to intertidal species; the combination of narrow swashes and steep slopes make reflective beaches a safer and more stable environment for supralittoral and intertidal species such as *D. hanleyanus*.

Appendix

Table 1: Qualitative descriptions of histological preparations of *D. hanleyanus* gonad used to assess gametogenic stages. Individual stages of male and female wedge clam gonads are shown in Fig. 1.

Stage	Definition	Brief description of gonad	Fig. 1
0	Sexual rest	Follicles few and small, sex indistinguishable, protogonia and gonia in mitosis.	-
I	Pre-active	Reproductive material is scant and intersected by transverse muscular fascicle cells, alveoli appear loosely arranged, phagocytes are common.	a, e
II	Active	Germ cells are in various stages of development and fill the alveoli, which are large with complete and closed walls.	b, f
III	Spawning	Clear loss of gametes, reproductive material varies in quantity but it is fairly abundant, alveolar pattern is disturbed, walls are broken and alveoli appear flattened.	c, g
IV	Cytolysed	Reproductive material is completely degenerated; alveoli are very small and wide apart, massive numbers of phagocytic cells.	d, h

Table 2: Results of statistical analysis of the gametogenic cycle of *D. hanleyanus* in relation to abiotic and biotic factors at the three beaches.

	Parameter	Statistic results at following beaches:		
		Santa Teresita (dissipative)	**Mar de las Pampas (intermediate)**	**Faro Querandí (reflective)**
a	Sex ratio (females:males) [1]	*For values see text*	$\chi^2 = 0.718$, $df = 1$, $\boldsymbol{p > 0.397}$	$\chi^2 = 1.029$, $df = 1$, $\boldsymbol{p = 0.310}$
b	Gametogenic cycle *vs.* time course [2]	$F_{11,9} = 5.644$, $\boldsymbol{p = 0.007}$	$F_{11,10} = 15.595$, $\boldsymbol{p = 0.000}$	$F_{11,10} = 8.861$, $\boldsymbol{p = 0.001}$
c	Gametogenic cycle *vs.* SST [3]	$r_s = 0.726$, $\boldsymbol{p = 0.000}$, $N = 21$	$r_s = 0.787$, $\boldsymbol{p = 0.000}$, $N = 22$	$r_s = 0.799$, $\boldsymbol{p = 0.000}$, $N = 22$
d	Gametogenic cycle *vs.* CI [3]	$r_s = -0.556$, $\boldsymbol{p = 0.025}$, $N = 16$	$r_s = 0.480$, $\boldsymbol{p = 0.024}$, $N = 22$	$r_s = 0.575$, $\boldsymbol{p = 0.005}$, $N = 22$
e	Gametogenic cycle *vs.* $AFDM$ [3]	$r_s = 0.557$, $\boldsymbol{p = 0.016}$, $N = 18$	$r_s = 0.669$, $\boldsymbol{p = 0.001}$, $N = 22$	$r_s = 0.445$, $\boldsymbol{p = 0.043}$, $N = 21$
f	Gametogenic cycle *vs.* mean size of oocytes [3]	$r_s = 0.721$, $\boldsymbol{p = 0.004}$, $N = 14$	$r_s = 0.501$, $\boldsymbol{p = 0.021}$, $N = 21$	$r_s = 0.443$, $\boldsymbol{p = 0.039}$, $N = 22$
g	Gametogenic cycle *vs.* abundance of oocytes [3]	$r_s = 0.708$, $\boldsymbol{p = 0.000}$, $N = 21$	$r_s = 0.779$, $\boldsymbol{p = 0.000}$, $N = 22$	$r_s = 0.639$, $\boldsymbol{p = 0.001}$, $N = 22$
h	CI *vs.* SST [3]	$r_s = 0.507$, $\boldsymbol{p = 0.032}$, $N = 18$	$r_s = 0.337$, $p = 0.125$, $N = 22$	$r_s = 0.673$, $\boldsymbol{p = 0.001}$, $N = 22$
i	$AFDM$ *vs.* SST [3]	$r_s = 0.574$, $\boldsymbol{p = 0.016}$, $N = 17$	$r_s = 0.600$, $\boldsymbol{p = 0.003}$, $N = 22$	$r_s = 0.581$, $\boldsymbol{p = 0.005}$, $N = 22$
j	Oocyte mean size *vs.* SST [3]	$r_s = 0.741$, $\boldsymbol{p = 0.002}$, $N = 14$	$r_s = 0.334$, $p = 0.139$, $N = 21$	$r_s = 0.448$, $\boldsymbol{p = 0.037}$, $N = 22$
k	Abundance of oocytes *vs.* SST [3]	$r_s = 0.504$, $\boldsymbol{p = 0.020}$, $N = 21$	$r_s = 0.743$, $\boldsymbol{p = 0.000}$, $N = 22$	$r_s = 0.701$, $\boldsymbol{p = 0.000}$, $N = 22$
l	Oocyte modal size *vs.* seasons (spawning) [2]	$F_{1,12} = 10.154$, $\boldsymbol{p = 0.008}$	$F_{1,19} = 4.777$, $\boldsymbol{p = 0.042}$	$F_{1,12} = 5.680$, $\boldsymbol{p = 0.027}$
m	Oocyte abundance increases *vs.* seasons [2]	$F_{1,19} = 10.864$, $\boldsymbol{p = 0.004}$	$F_{1,20} = 6.214$, $\boldsymbol{p = 0.022}$	$F_{1,20} = 5.609$, $\boldsymbol{p = 0.028}$
n	Oocyte abundance decreases *vs.* seasons [2]	$F_{1,19} = 10.142$, $\boldsymbol{p = 0.005}$	$F_{1,20} = 9.346$, $\boldsymbol{p = 0.006}$	$F_{1,20} = 14.107$, $\boldsymbol{p = 0.001}$
o	Settling period of recruits *vs.* SST [3]	$r_s = -0.327$, $p = 0.119$, $N = 24$	$r_s = -0.123$, $p = 0.584$, $N = 22$	$r_s = -0.356$, $p = 0.104$, $N = 22$
p	Appearances of recruits	$F_{1,22} = 224.266$, $\boldsymbol{p = 0.000}$	$F_{1,20} = 16.064$, $\boldsymbol{p = 0.001}$	$F_{1,20} = 25.997$, $\boldsymbol{p = 0.000}$
q	Gametogenic cycle *vs.* RSA [3]	$r_s = 0.804$, $\boldsymbol{p = 0.000}$, $N = 21$	$r_s = 0.856$, $\boldsymbol{p = 0.000}$, $N = 22$	$r_s = 0.822$, $\boldsymbol{p = 0.000}$, $N = 22$
r	RSA increases *vs.* seasons [2]	$F_{1,19} = 6.889$, $\boldsymbol{p = 0.017}$	$F_{1,20} = 11.661$, $\boldsymbol{p = 0.003}$	$F_{1,20} = 35.507$, $\boldsymbol{p = 0.000}$
s	RSA decreases *vs.* seasons [2]	$F_{1,19} = 15.366$, $\boldsymbol{p = 0.001}$	$F_{1,20} = 30.139$, $\boldsymbol{p = 0.000}$	$F_{1,20} = 55.621$, $\boldsymbol{p = 0.000}$
t	Gonad in active and spawning stage [2]	$F_{1,40} = 33.454$, $\boldsymbol{p = 0.000}$	$F_{1,42} = 8.032$, $\boldsymbol{p = 0.007}$	$F_{1,42} = 17.539$, $\boldsymbol{p = 0.000}$
u	Gonad in cytolysed stage [2]	$F_{1,19} = 17.898$, $\boldsymbol{p = 0.000}$	$F_{1,20} = 4.542$, $\boldsymbol{p = 0.046}$	$F_{1,20} = 9.767$, $\boldsymbol{p = 0.005}$
v	Gonad in sexual rest stage [2]	$F_{1,19} = 46.143$, $\boldsymbol{p = 0.000}$	$F_{1,20} = 5.301$, $\boldsymbol{p = 0.032}$	$F_{1,20} = 4.484$, $\boldsymbol{p = 0.047}$

[1] Chi square (χ^2) test, [2] one-way ANOVA, [3] Spearman`s rank order correlation, **Bold** = significantly correlated.

Table 3: *D. hanleyanus*. Monthly *SST* (°C), mean oocyte size (µm) ($\bar{x}$ ± standard deviation SD in µm), number of females per month (N_f) and number of measured oocytes (N_o) from individuals inhabiting one of the three sampling localities Santa Teresita, Mar de las Pampas and Faro Querandí.

Year	Month	*SST* (°C)	Santa Teresita (dissipative)			Mar de las Pampas (intermediate)			Faro Querandí (reflective)		
			$\bar{x}$ ± SD (µm)	N_o	N_f	$\bar{x}$ ± SD (µm)	N_o	N_f	$\bar{x}$ ± SD (µm)	N_o	N_f
2004	Dec	18.42	35.52 (9.53)	177	25	39.10 (11.23)	141	17	no sampling		
2005	Jan	20.79	37.52 (8.45)	176	27	40.14 (10.67)	187	19			
	Feb	21.08	41.79 (10.15)	185	16	35.53 (10.09)	106	13			
	Mar	20.49	39.78 (9.45)	237	21	40.96 (10.07)	233	12	38.09 (10.05)	116	14
	Apr	16.75	-	-	-	36.97 (10.58)	117	13	30.49 (11.19)	61	16
	May	14.14	-	-	-	39.41 (9.40)	102	15	32.55 (10.43)	53	21
	Jun	12.67	-	-	-	-	-	-	39.34 (12.69)	38	19
	Jul	12.31	-	-	-	-	-	-	37.51 (12.13)	53	16
	Aug	12.74	-	-	-	35.65 (11.89)	122	35	33.97 (11.12)	71	41
	Sep	14.84	7.62 (2.41)	73	8	29.36 (11.08)	65	12	23.01 (11.42)	49	14
	Oct	16.18	28.14 (9.85)	454	16	-	-	-	29.52 (9.89)	591	20
	Nov	18.53	38.24 (4.64)	570	20	36.22 (5.83)	510	17	40.14 (5.60)	514	18
	Dec	20.87	35.32 (5.66)	540	18	36.88 (5.99)	612	20	40.09 (4.46)	660	22
2006	Jan	21.59	-	-	-	38.10 (5.04)	540	18	36.34 (4.59)	390	13
	Feb	22.55	-	-	-	34.84 (7.14)	360	12	37.61 (5.33)	330	11
	Mar	21.29	-	-	-	30.78 (8.19)	540	18	26.54 (8.21)	359	12
	Apr	19.51	34.89 (5.74)	90	3	29.70 (12.07)	390	13	32.78 (9.89)	390	13
	May	14.99	-	-	-	-	-	-	30.91 (10.87)	457	17
	Jun	13.24	-	-	-	32.56 (9.62)	30	1	29.98 (11.53)	556	20
	Jul	12.40	28.49 (12.61)	66	1	31.03 (11.89)	554	19	21.16 (12.40)	460	14
	Aug	10.69	-	-	-	18.91 (12.44)	480	16	14.79 (8.29)	237	9
	Sep	12.86	9.29 (4.22)	208	12	12.90 (7.65)	347	13	12.90 (7.80)	460	17
	Oct	17.07	21.56 (9.28)	410	15	15.52 (5.62)	162	9	20.73 (9.27)	180	6
	Nov	19.54	38.64 (5.06)	420	14	34.11 (8.36)	480	16	37.45 (4.27)	540	18
	Dec	21.84	36.28 (4.14)	17		35.26 (8.10)	570	19	39.66 (7.68)	450	16

Table 4: Parameters (*a*, *b* and *x0*) estimated values and associated statistics relating to size (*apSL*) and biomass (*SFWM*) at sexual maturity function (Ep. 3) and size of 50 % population maturity ($apSL_{50\%}$) and biomass of 50 % population maturity ($SFWM_{50\%}$), respectively (Eq. 4). Values are mean ± SE, mean size at first maturity in mm (*apSL*) and biomass at first maturity in g (*SFWM*), Durbin-Watson statistic (*DW*), * $p < 0.05$.

	Males						**Females**					
	Santa Teresita		Mar de las Pampas		Faro Querandí		Santa Teresita		Mar las Pampas		Faro Querandí	
	SFWM	*apSL*	*SFWM*	*apSL*	*SFWM*	*apSL*	*SFWM*	*apSL*	*SFWM*	*apSL*	*SFWM*	*apSL*
a	101.62 (1.39)*	102.96 (3.32)*	97.94 (0.73)*	97.66 (1.92)*	98.84 (0.75)*	101.03 (2.45)*	100.63 (1.04)*	100.61 (2.09)*	99.12 (0.66)*	99.41 (1.23)*	98.62 (0.80)*	101.74 (2.52)*
b	0.05 (0.01)*	1.95 (0.27)*	0.03 (0.01)*	1.93 (0.24)*	0.12 (0.01)*	1.14 (0.20)*	0.04 (0.00)*	1.49 (0.16)*	0.08 (0.01)*	0.72 (0.09)*	0.11 (0.01)*	1.61 (0.23)*
x0	0.15 (0.01)*	15.81 (0.32)*	0.19 (0.01)*	17.57 (0.27)*	0.92 (0.01)*	24.40 (0.23)*	0.15 (0.00)*	15.77 (0.19)*	0.24 (0.01)*	16.37 (0.11)*	0.89 (0.01)*	23.54 (0.27)*
50%	0.15	15.69	0.19	17.66	0.92	24.38	0.15	15.75	0.25	16.38	0.89	23.49
r^2	0.91	0.97	0.89	0.97	0.89	0.97	0.96	0.99	0.92	0.99	0.90	0.97
DW	1.62	1.64	1.99	2.49	1.84	2.32	1.73	2.11	1.99	2.39	2.18	2.43

Table 5: Annual reproductive events of *D. hanleyanus* from Argentinean (AR), Uruguayan (UY) and Brazilian (BR) beaches of different morphodynamic types (M.): dissipative (D), intermediate (I) and reflective (R). **A**: spawning events [grey] indicated by classifying gonad tissue into different gametogenic stages, **B**: spawning events [grey] derived from oocyte measurements.

	J	F	M	A	M	J	J	A	S	O	N	D	Beach	M.	Source
A	▨	▨	▨							▨	▨	▨	Santa Teresita (AR)	D	present study
	▨	▨	▨	▨	▨					▨	▨	▨	Mar de las Pampas (AR)	I	present study
	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	Faro Querandí (AR)	R	present study
	▨	▨	▨								▨	▨	Arachania (UY)	R	Delgado and Defeo (2007b)
	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	Barra del Chuy (UY)	D	Delgado and Defeo (2007b)
	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	Arroio Teixeira (BR)	D	Gil and Thomé (2004a)
B									▨			▨	Santa Teresita (AR)	D	present study
		▨						▨				▨	Mar de las Pampas (AR)	I	present study
	▨			▨	▨	▨	▨		▨				Faro Querandí (AR)	R	present study
	▨	▨						▨	▨				Villa Gesell (AR)	I	Penchaszadeh and Olivier (1975)

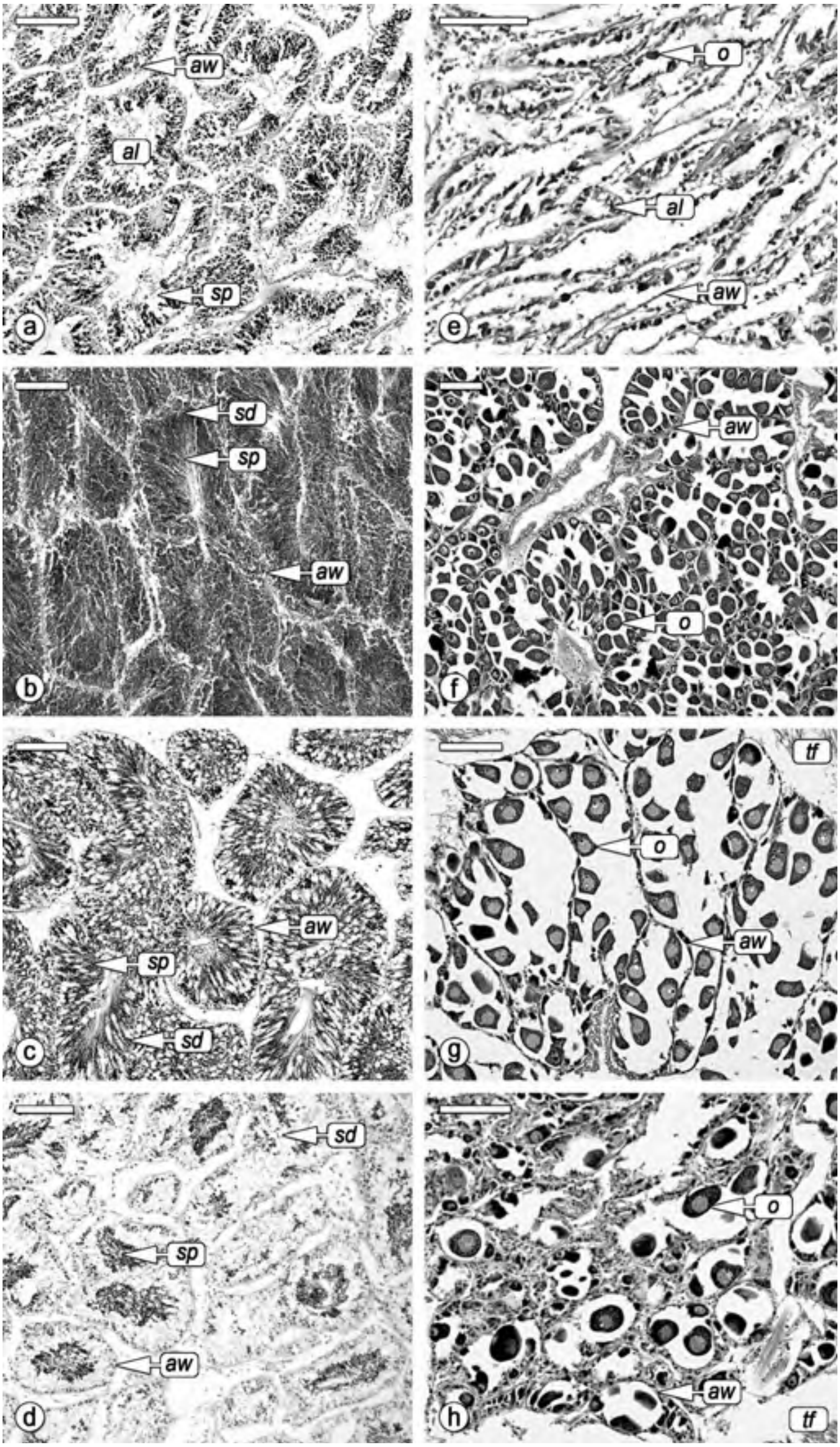

Fig. 1: Microphotography of male (**a-d**) and female (**e-h**) gonad stages of *D. hanleyanus*: (**a, e**) pre-active, (**b, f**) active, (**c, g**) spawning, (**d, h**) cytolysed (***aw***: alveolar wall, ***al***: alveolus, ***sp***: sperms, ***sd***: spermatids, ***tf***: transverse fibre, *scale bars* are 100 µm).

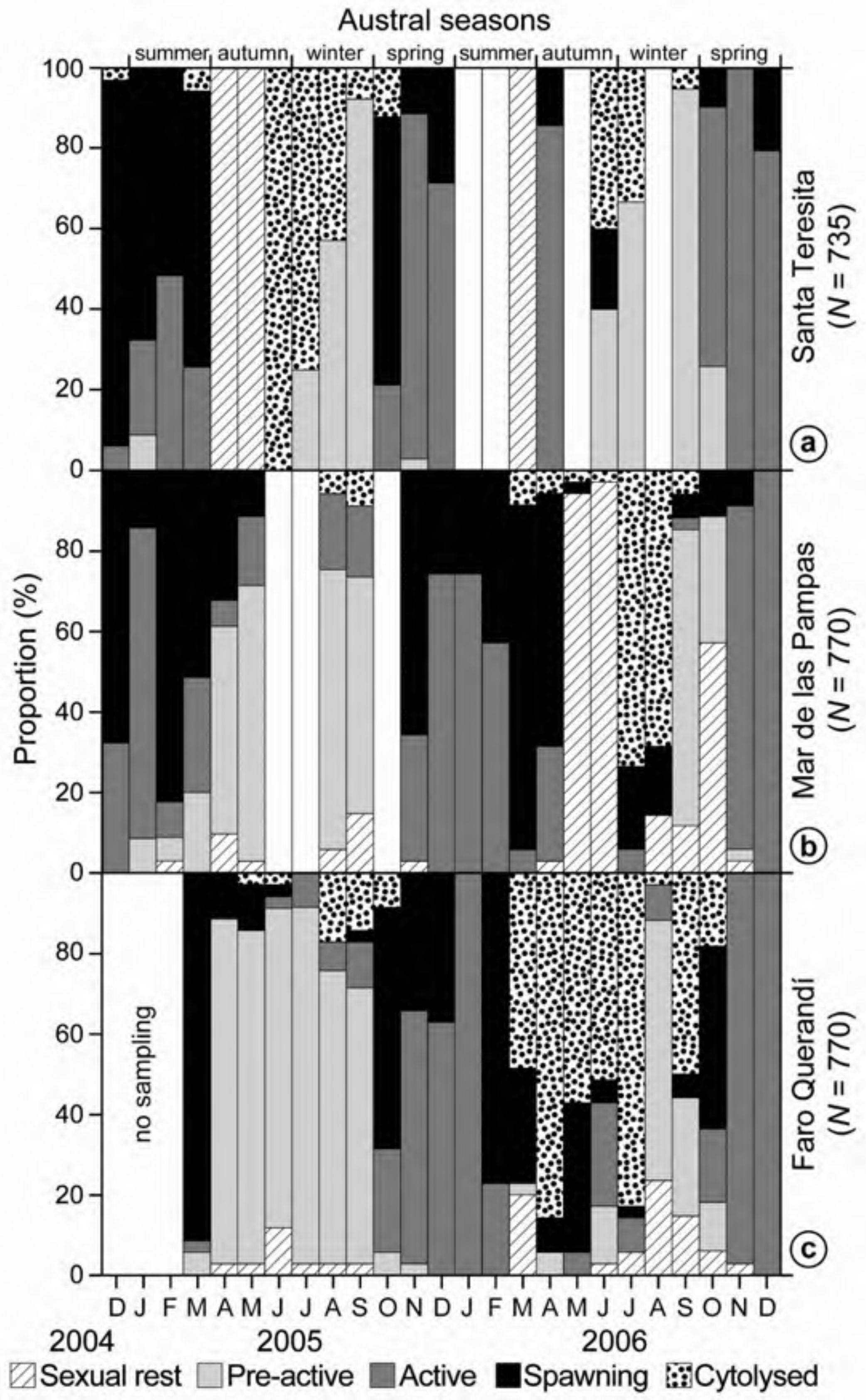

Fig. 2: Gametogenic cycle of *D. hanleyanus* indicating proportions of distinct gonad stages of individuals sampled at (**a**) the dissipative, (**b**) intermediate and (**c**) reflective beach. White bars: no individuals were found. *N* = numbers of analysed clams per beach.

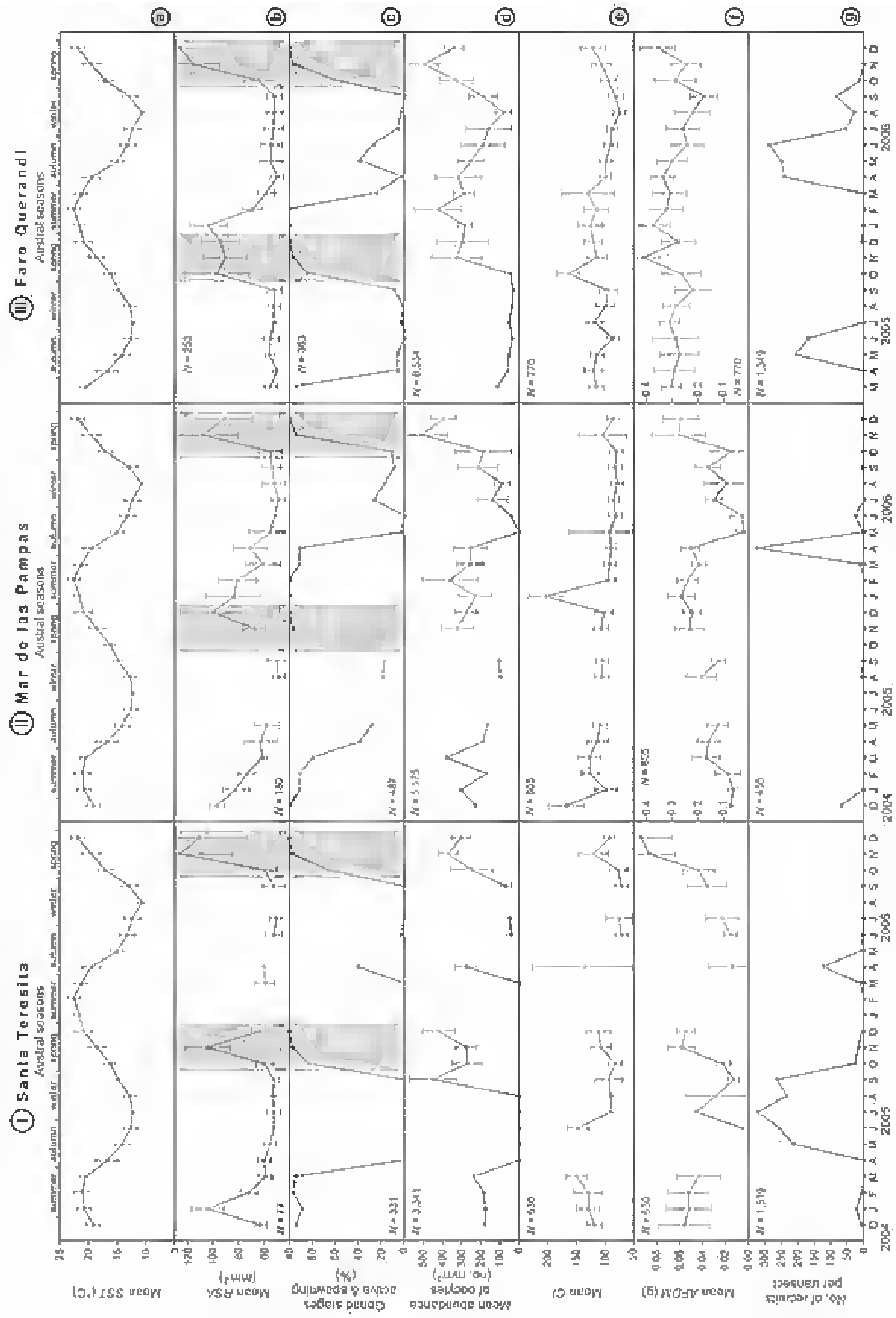

Fig. 3: Gametogenic cycle of *D. hanleyanus* in relation to abiotic and biotic factors at (**I**) the dissipative, (**II**) intermediate and (**III**) reflective beach: (**a**) mean *SST* (°C), (**b**) mean *RSA* (mm^{-2}), (**c**) percentage of gonad stages 'ripe' and 'spawning', (**d**) mean abundance of oocytes (numbers mm^{-2}), (**e**) mean *CI*, (**f**) mean *AFDM* (g) and (**g**) numbers of recruits (< 11 mm) per transect. *Grey bars*: indicate seasons where Carreto *et al.* (1995) observed chlorophyll *a* maxima in the Buenos Aires shelf region. *Error bars*: standard deviation (SD). Note different scale at *Y*-axis in graphic **IIf** and **IIIf**.

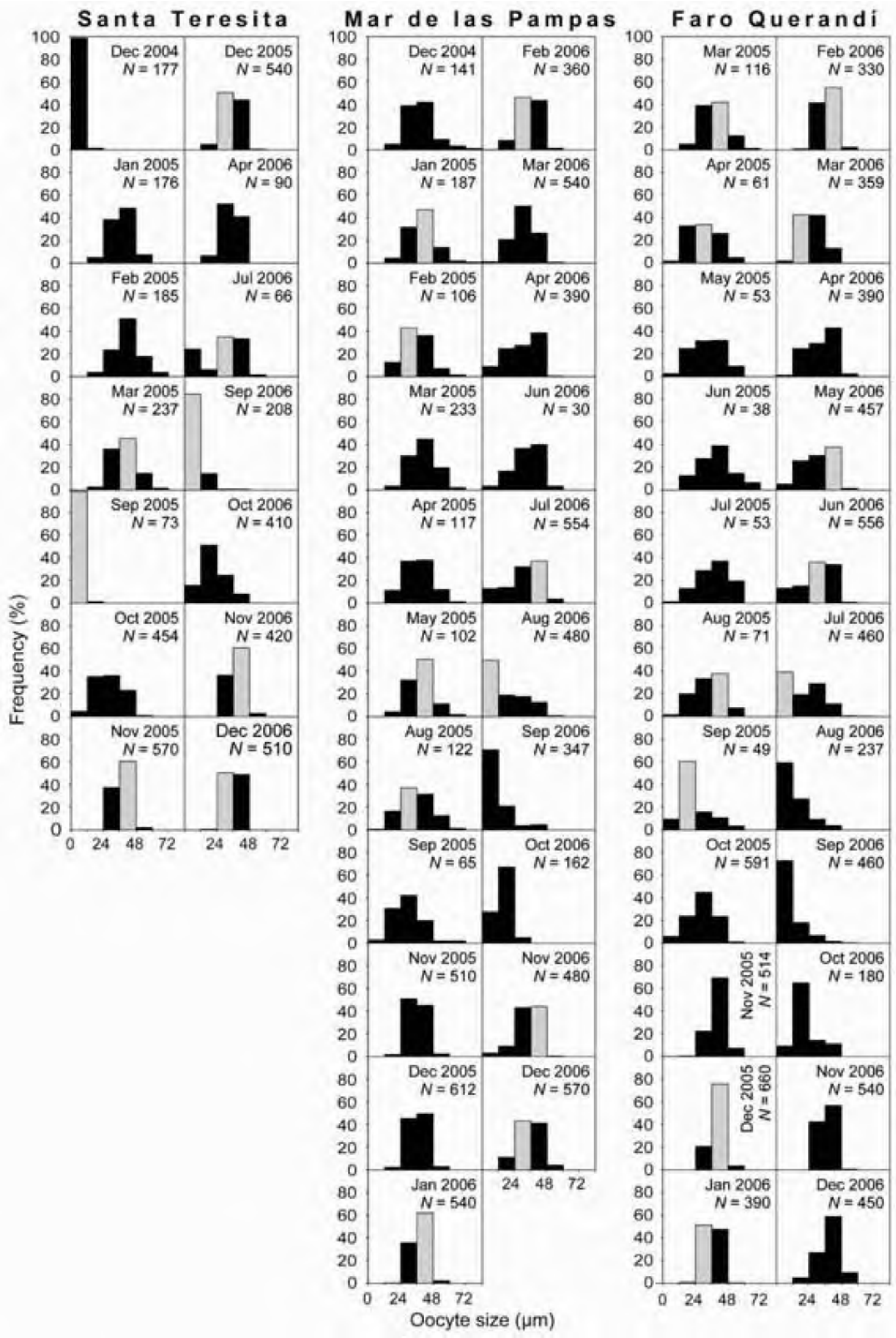

Fig. 4: Monthly oocyte size-frequency distribution of *D. hanleyanus*. Grey bars show modal values indicating the record prior to and after a sudden reduction of oocyte sizes. *N* = numbers of measured oocytes per month.

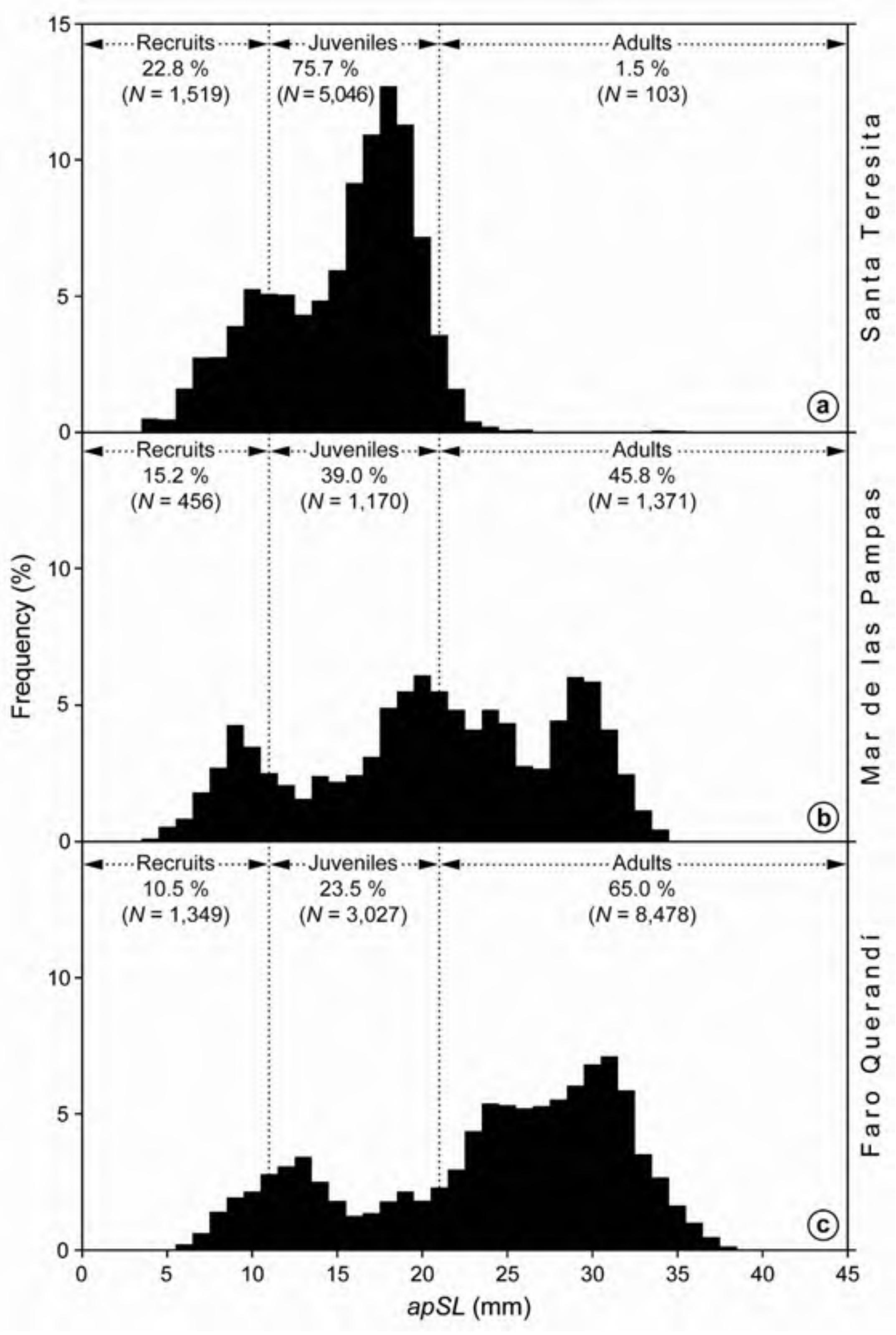

Fig. 5: Length-frequency distribution (pooled from 25 monthly samples) of *D. hanleyanus* at (**a**) the dissipative, (**b**) intermediate und (**c**) reflective beach, classified into three ontogenetic groups: recruits (< 11 mm), juveniles (11-22 mm), and adults (> 22 mm). Note the different scale at the *Y*-axis.

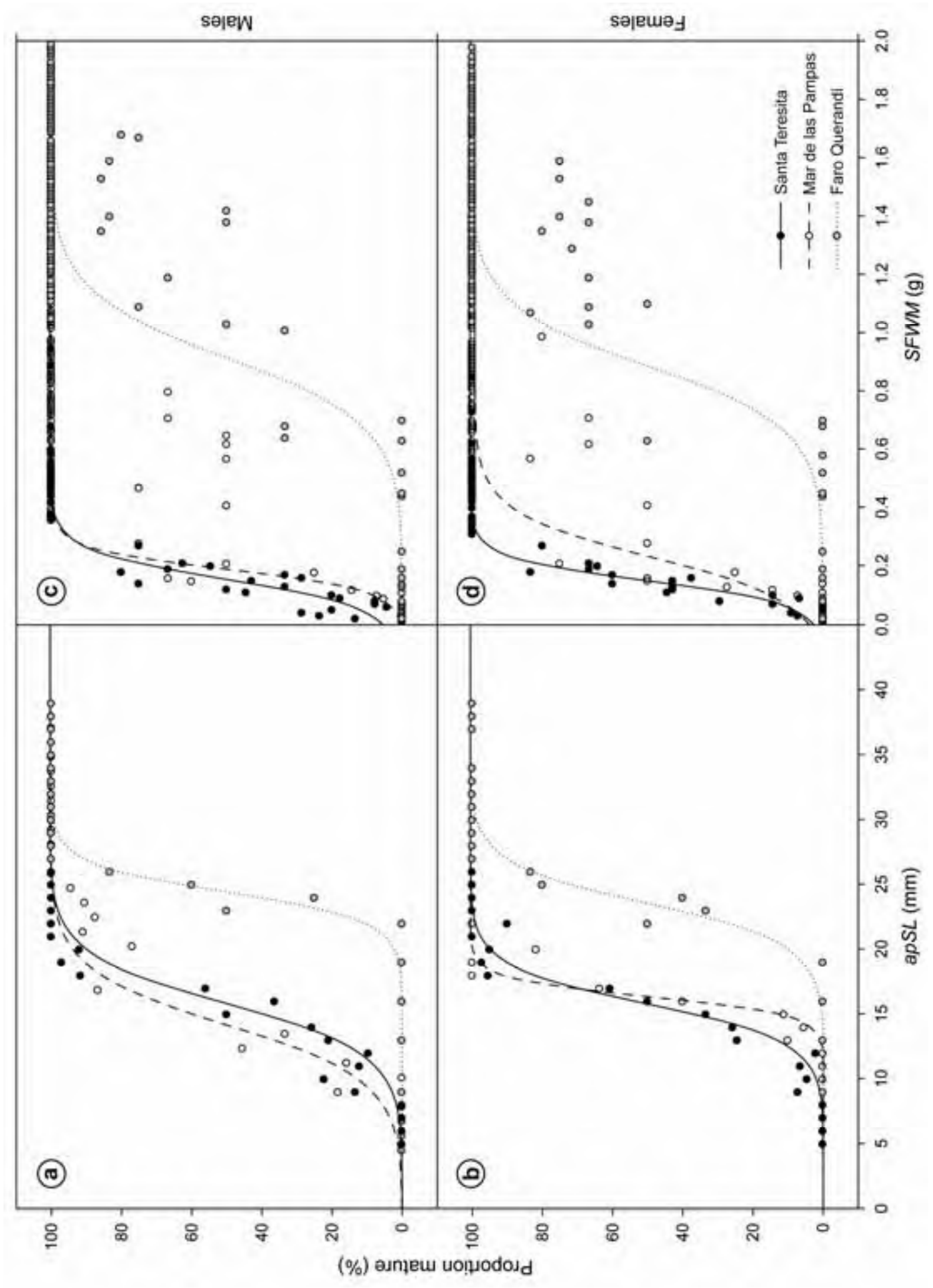

Fig. 6: Logistic function (Eq. 3) indicating size (*apSL*) and biomass (*SFWM*) at sexual maturity in male and female *D. hanleyanus*, fitted by non-linear regression, showing sex-specific differences. Statistical results are provided in Table 4.

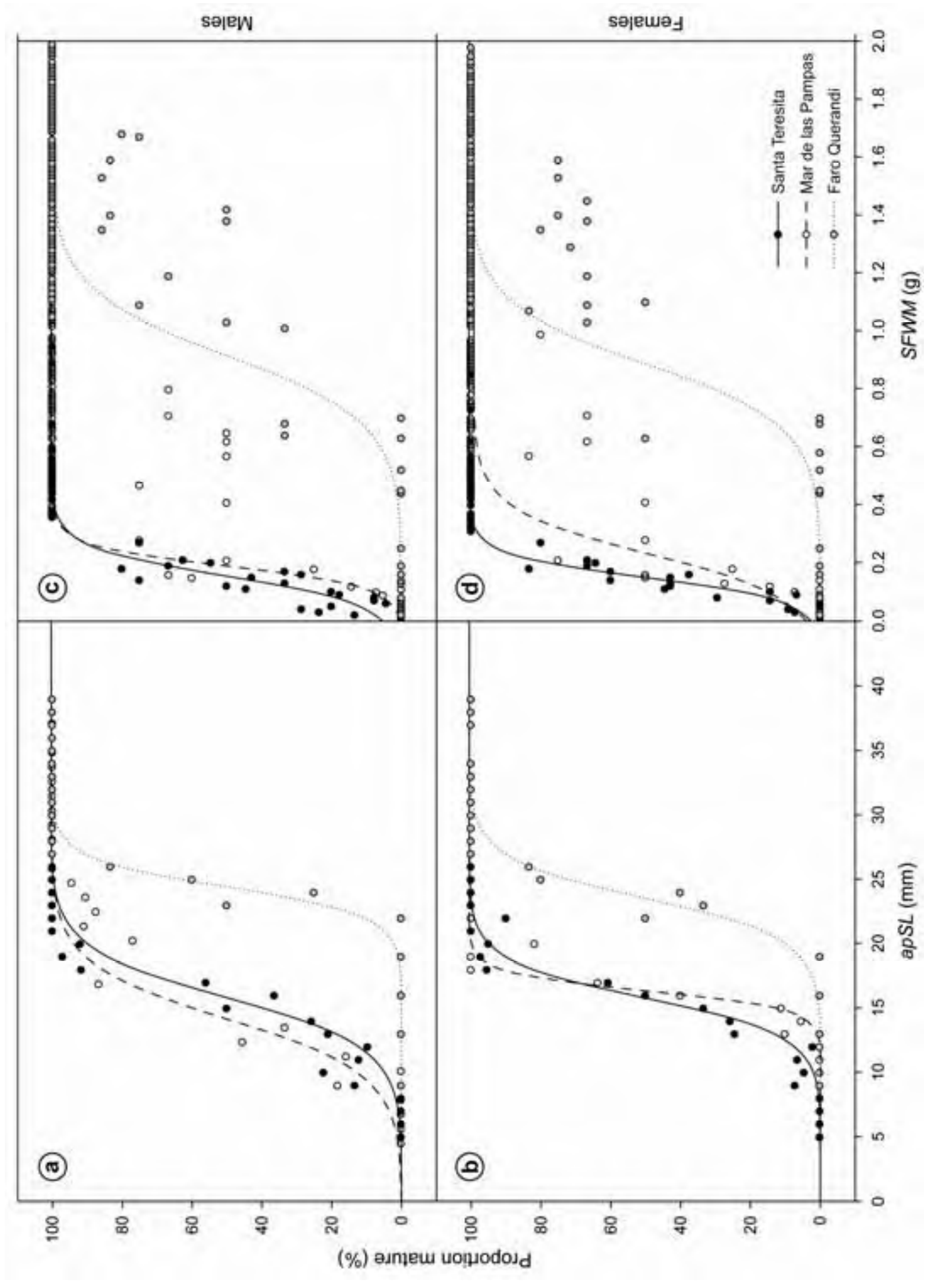

Fig. 6: Logistic function (Eq. 3) indicating size (*apSL*) and biomass (*SFWM*) at sexual maturity in male and female *D. hanleyanus*, fitted by non-linear regression, showing sex-specific differences. Statistical results are provided in Table 4.

References

(see page 206)

6.4 Publication IV

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

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Keywords yellow clam, sandy beach ecology, condition index, biomass, size and abundance of oocytes

Abstract The present work analyses why populations of the yellow clam *Mesodesma mactroides* (Bivalvia: Mesodesmatidae), which was once an important economic resource for Argentina, never recovered after intensive stock decimation caused by exploitation and mass mortality events. The reproductive cycle and gonad development of *M. mactroides* was studied over a period of 24 months at Santa Teresita, an Argentinean sandy beach. Histological examination of the 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 cyclicality, which was significantly correlated to monthly mean sea surface temperatures. Oocytes showed highest abundance in winter, indicating a process of gonadal development and sexual maturation. The mean oocyte size decreased significantly in the spring. Modal oocyte sizes decreased significantly in the 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*. The shell-free ash-free dry mass was chosen to detect the condition of the specimens, and this significantly correlated with monthly mean sea surface temperatures and the gametogenic cycle. Annual recruitment patterns in summer-autumn indicated a three-month-long planktonic phase of *M. mactroides*. Discussed changes in the population dynamics of the last four decades implies that *M. mactroides* is at risk of extinction in Argentina.

1 Introduction

The yellow clam *Mesodesma mactroides* Reeve, 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 *et al.* under review-a). It 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). The biogeographical range of the suspension-feeding yellow clam covers hundreds of kilometres of sandy beaches in Brazil, 22 km in Uruguay, and it also covers 375 km in Argentina, where it represents the only *Mesodesma* species occurring throughout the intertidal (Olivier *et al.* 1971). On the beaches of northern Argentina it is found together with the sympatric and dominant surf clam *Donax hanleyanus* (Herrmann *et al.* under review-d). During the 1940s and 1950s *M. mactroides* was an important economic resource for Argentina, with a maximum exploitation rate of 1,079 tons in 1953. As a consequence of overfishing, the clam fishery was closed in 1956 (Coscarón 1959). Argentinean *M. mactroides* populations never recuperated and populations were further depleted by mass mortality events in both the nineties and recently, caused by red tides (Odebrecht *et al.* 1995), by an unknown reason (Fiori and Cazzaniga 1999) and probably by high heavy metal concentrations (Thompson and Sánchez de Bock 2007). Various authors (e.g. Bastida *et al.* 1991; Herrmann *et al.* under review-d) have suggested illegal extractions and the impact of tourist activities as probable main factors for the failure of stock recovery.

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.* 2004a; Fiori and

Morsán 2004; Fiori and Defeo 2006; Herrmann *et al.* under review-a), the Uruguayan (Defeo *et al.* 1986; Defeo *et al.* 1988b; Defeo 1989; Defeo *et al.* 1991; Defeo *et al.* 1992c; Brazeiro and Defeo 1999; Lima *et al.* 2000) and the Brazilian coasts (Narchi 1981; Gil and Thomé 2000b; 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 forty years ago. This work will also discuss why populations of *M. mactroides* never recovered after intensive stock decimation caused by exploitation and mass mortality events.

2 Material and Methods

2.1 Study Area

The present study was carried out at the 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 *M. mactroides* was only abundant at the first mentioned location during the whole sampling period. The population structure of the intertidal yellow clam *M. mactroides* was studied during alternate spring tides from the anthropogenically influenced sandy beach Santa Teresita, which is especially affected by mass tourism during the summer season. Accordingly 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 (10, mean slope 1/43) (for detailed parameters see: Herrmann *et al.* under review-d). 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 *et al.* under review-a). The sandy beach of Santa Teresita is affected by a freshwater seepage and a southward current which 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.

2.2 Sampling and Histological Examination

Monthly sampling was carried out from January 2005 to December 2006 following the systematic design described in Herrmann *et al.* (under review-a). For biomass determinations as well as for calculations of the condition index (*CI*) a total of 30 *M. mactroides* was preserved in 70 % ethanol and afterwards measured to the nearest 0.1 mm with a digital vernier calliper (Mitutoyo, model 500-161U) in the laboratory. For histological examinations a total of 30 yellow clams, covering the full range of anterior-posterior shell length (*apSL*) available, was fixed in Bouin's solution with sectioned adductor muscles for two hours, transferred into a 70 % ethanol solution, and later processed in the laboratory. Histological microsections were prepared using standard methods (Howard *et al.* 2004) including embedding in paraffin, sectioning at 5 µm and staining with hematoxylin-eosin. Photographical analyses were carried out using a Zeiss Axio Imager Z1 light microscope equipped with a Sound Vision digital camera and 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 during the period of January-February 2005 and January 2006, where clams showed only the gonad stage 0 (sexual rest stage with anterior-posterior shell length < 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 and 3, Table 1). Individuals without germ cells were categorized to be 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 sperm. 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.

2.3 Condition Index, Biomass and Recruitment

A condition index (*CI*) of *M. mactroides* was calculated to trace seasonal variation in the visceral mass. After blotting on filter paper, total shell-free ethanol preserved wet mass (*SFWM*) was recorded immediately to the nearest 0.1 mg. After this, mantle, siphons, retractor and adductor muscles were removed. The *SFWM* 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 (1975b), 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 *SFWM*.

As shown below, the *CI* was not the best proxy by which to evaluate the condition of the individuals, since the gonad-foot unit was not able to be separated very accurately. Therefore shell-free ash-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 according to Brey *et al.* (1988) was empirically determined.

Recruit (individuals 2-6 mm) counts and anterior-posterior shell length measurements of *M. mactroides* were made monthly (Herrmann *et al.* under review-a).

2.4 Statistical Analysis

All statistical analyses were carried out using the statistical package SPSS version 16.0.1 (2007). Differences were considered significant at a level of $\alpha = 5$ % (Zar 1999).

3 Results

3.1 Gonad Development

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 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 to 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) in late autumn (June 2005, 2006) and in spring (October-November 2005, November-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-December 2005 and December 2006) (Fig. 4b).

3.2 Reproduction Cycle

Histological examinations of the gonads from a 24 months sampling series demonstrated that the reproductive cycle of *M. mactroides* has a distinct seasonality (one-way ANOVA, $F_{11,12} = 7.623$, $p < 0.05$) (Fig. 5b). *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, $r_s = 0.850$, $p < 0.05$, $N = 8$).

In both years, yellow clam oocytes showed highest abundance in winter with a maximum in September (one-way ANOVA, August-October *versus* 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-July and December *versus* 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 *versus* 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 *versus* the other months, $F_{1,12} = 35.368$, $p < 0.05$) (see dotted *Arrows* in Fig. 6).

3.3 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 cytolysed 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, $r_s = 0.789$, $p < 0.05$, $N = 12$), in that an 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).

4 Discussion

4.1 Gonadal Development

The reproductive strategy of *M. mactroides* from Santa Teresita (present study) is summarized in Table 3 and compared with the forty 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 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 these gonad stages in both summers studied is attributed to a single cohort with small shell length (mean anterior-posterior shell length of 8 mm in summer seasons: Herrmann *et al.* under review-a) 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 (1971b) 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) are difficult; Delgado and Defeo (2007b) found differential behavior patterns in the reproductive strategy of *D. hanleyanus* when comparing a reflective and a dissipative beach.

4.2 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 1975b; 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 significantly correlated with gonad development. Low mean temperatures coincided with maximum oocyte size and gamete initiation (late fall-winter). Increases in *SST* 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 composition. 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. mactroides* in ripe and spawning stages (Fig. 5b). This suggests that phytoplankton may also have a direct impact on the reproductive cycle of *M. mactroides*.

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 seminuda: 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.

4.3 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 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), *Donax serra* (Laudien *et al.* 2001) and *M. donacium* (Riascos *et al.* 2006c). 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-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 three 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 (Fig. 4, Fig. 5f, Fig. 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 (1971b) monitored three cohorts between 1968 and 1969, Herrmann *et al.* (under review-a) 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 that of Christiansen (1971) were found. In contrast, important differences in the population dynamics were reported by Herrmann *et al.* (under review-a) and less than ten times lower mean abundance. This strong change within the last four decades implies that the Argentinean yellow clam *M. mactroides* is still in an unstable condition.

Appendix

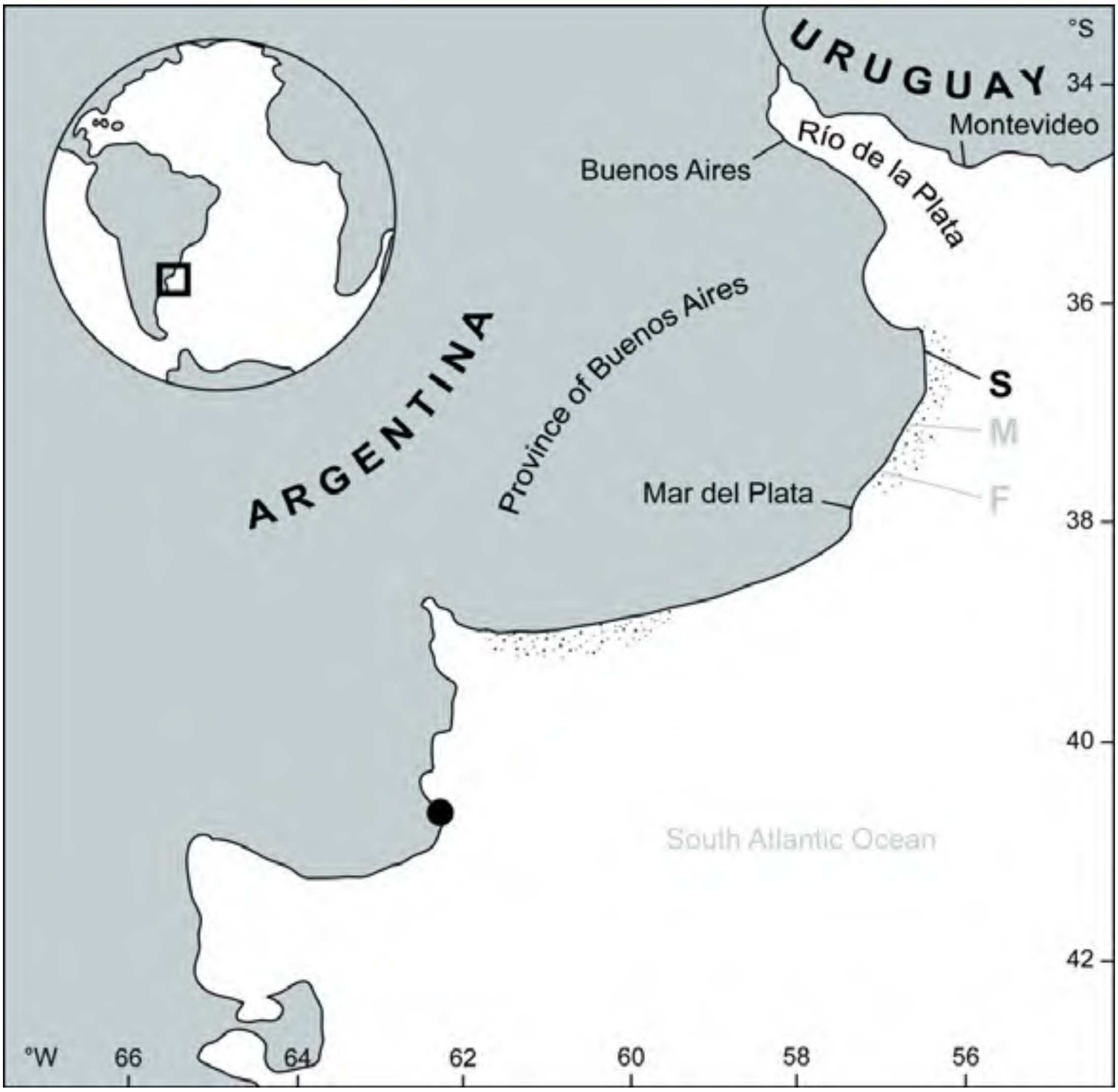

Fig. 1: Map of the study site Santa Teresita (**S**), Mar de las Pampas (**M**) and Faro Querandí (**F**), where *M. mactroides* was only abundant at the first mentioned location during the entire sampling period (black ladled). ● Indicates the southern most distribution of *M. mactroides* at Isla del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

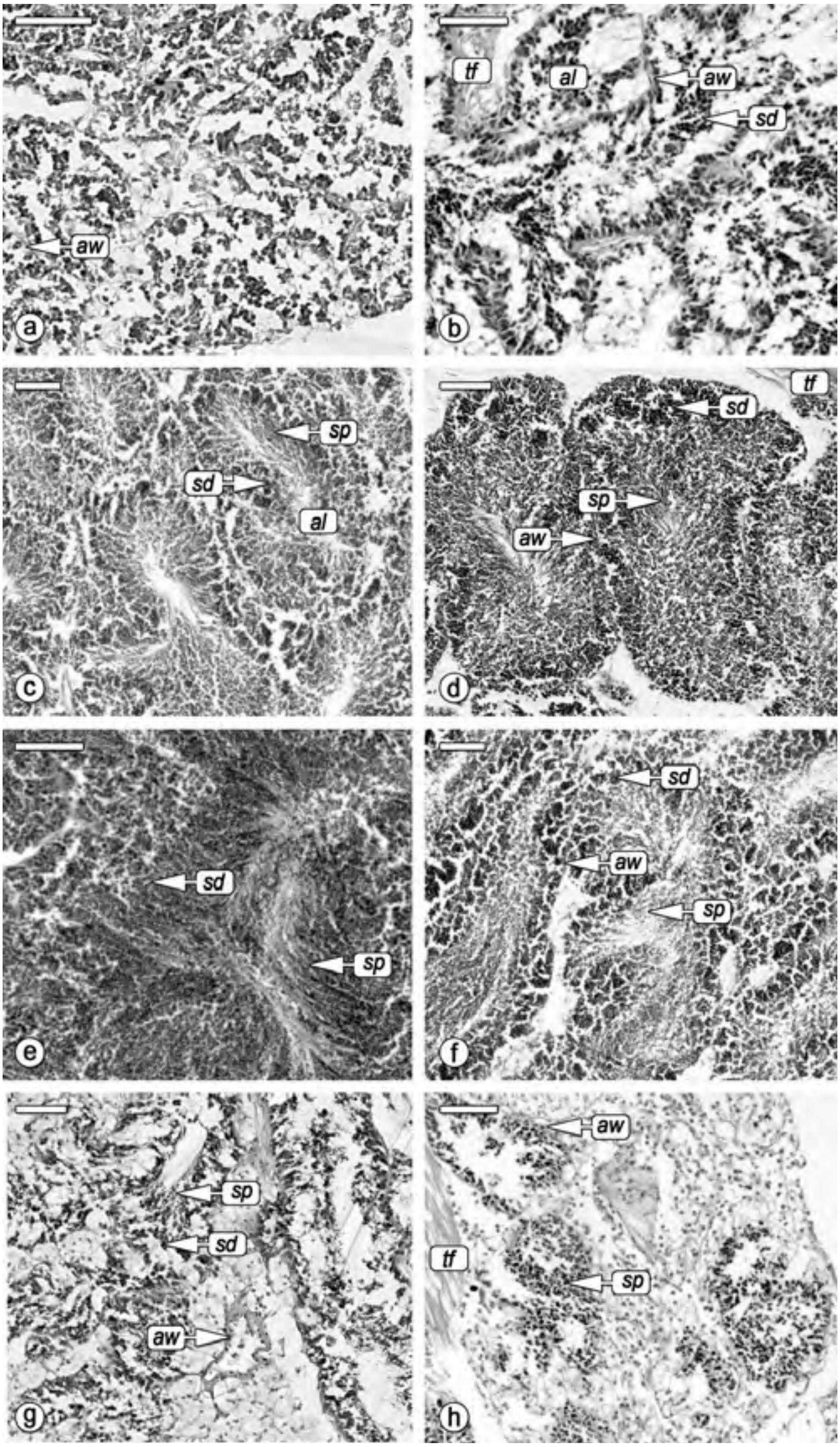

Fig. 2: Microphotography (colour pictures of full size: Herrmann *et al.* 2008a) of male gonad stages of *M. mactroides*: (**a**) early active stage, (**b**) late active stage, (**c**) early ripe stage, (**d, e**) ripe stage, (**f**) partially spawned stage, (**g**) spent stage, (**h**) recovery stage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

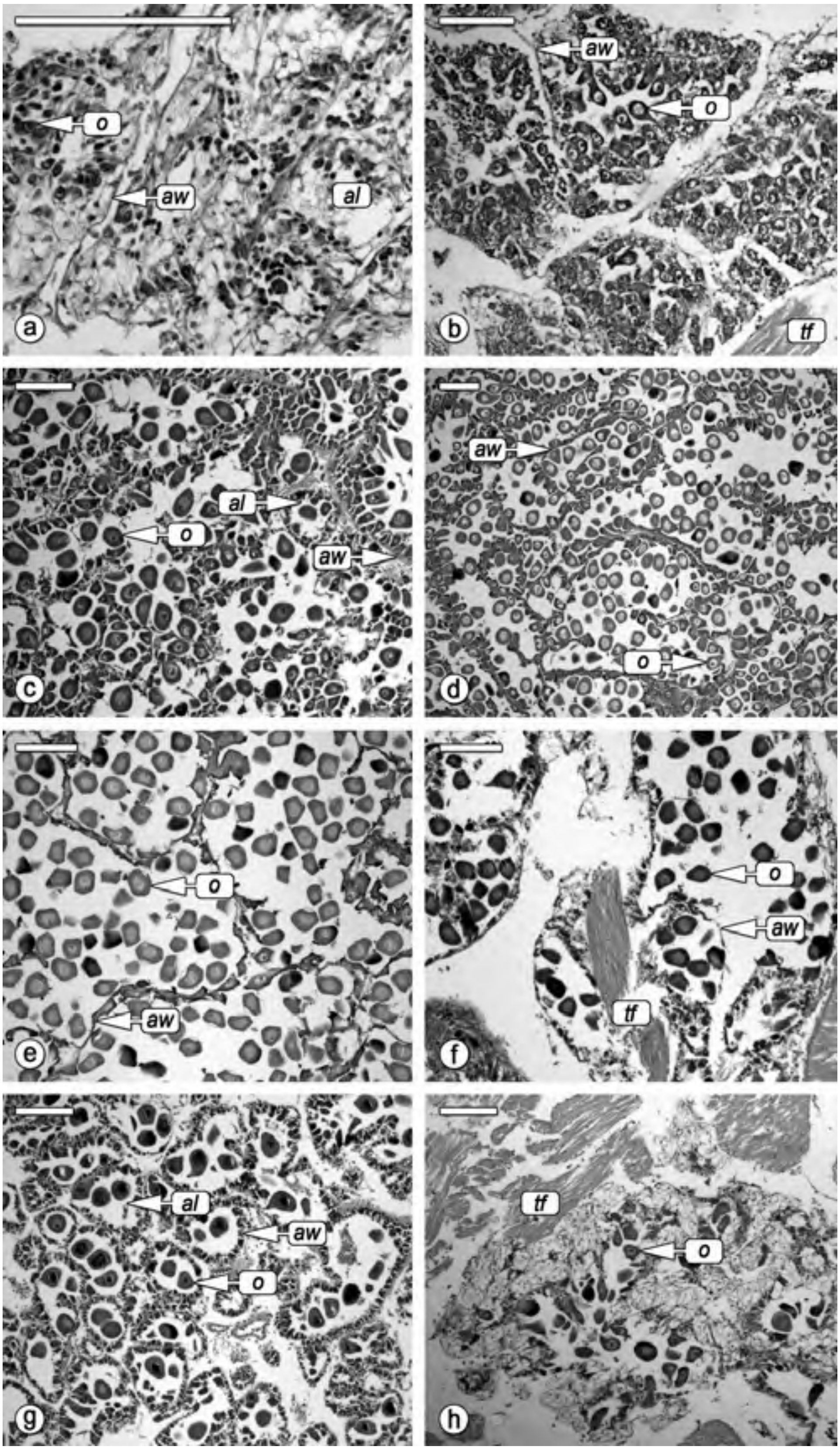

Fig. 3: Microphotography (colour pictures of full size: Herrmann *et al.* 2008a) of female gonad stages of *M. mactroides*: (**a**) early active stage, (**b**) late active stage, (**c**) early ripe stage, (**d, e**) ripe stage, (**f**) partially spawned stage, (**g**) spent stage, (**h**) recovery stage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

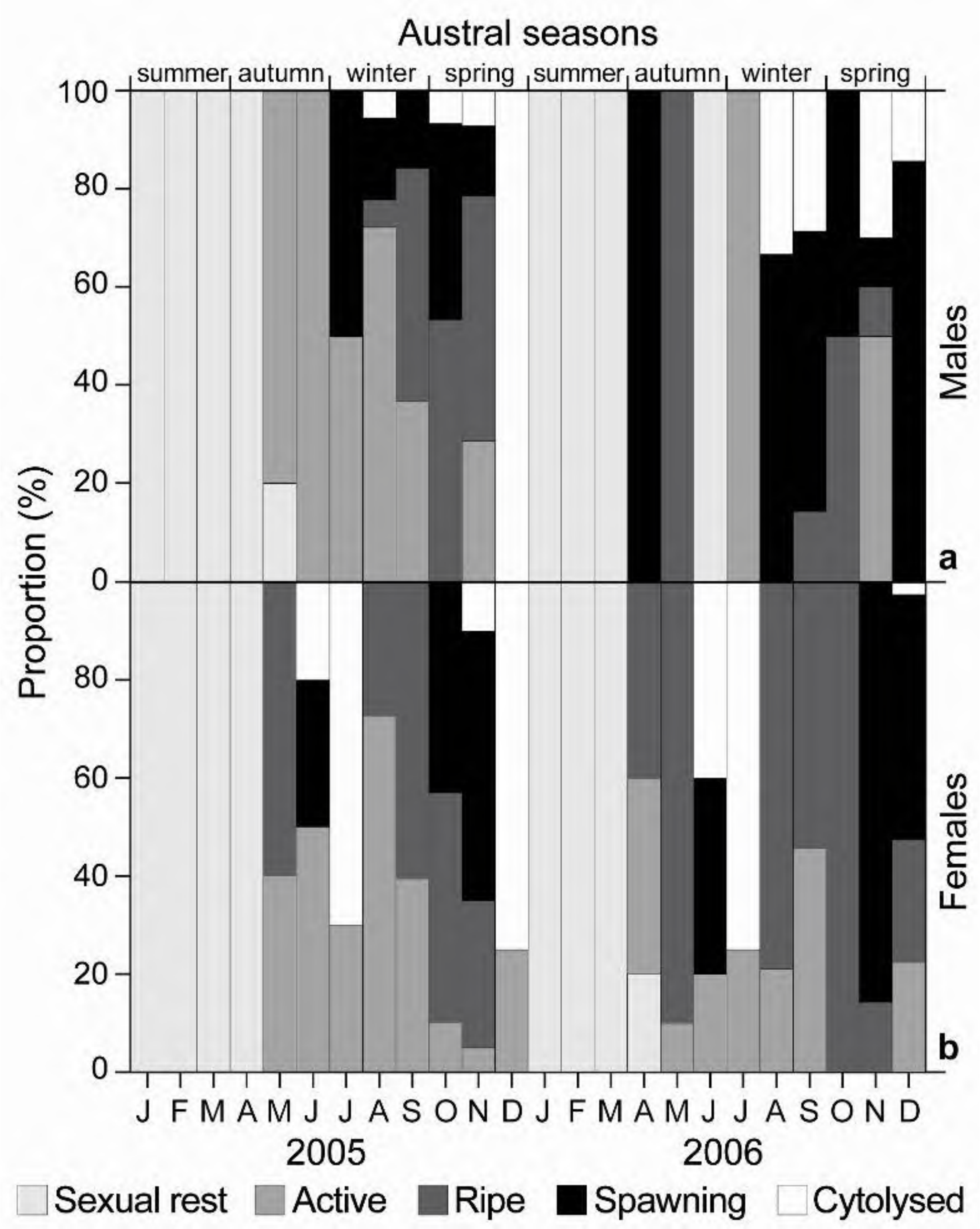

Fig. 4: Proportion of distinct gonad stages in mature male (**a**) and female (**b**) *M. mactroides*, sampled at Santa Teresita.

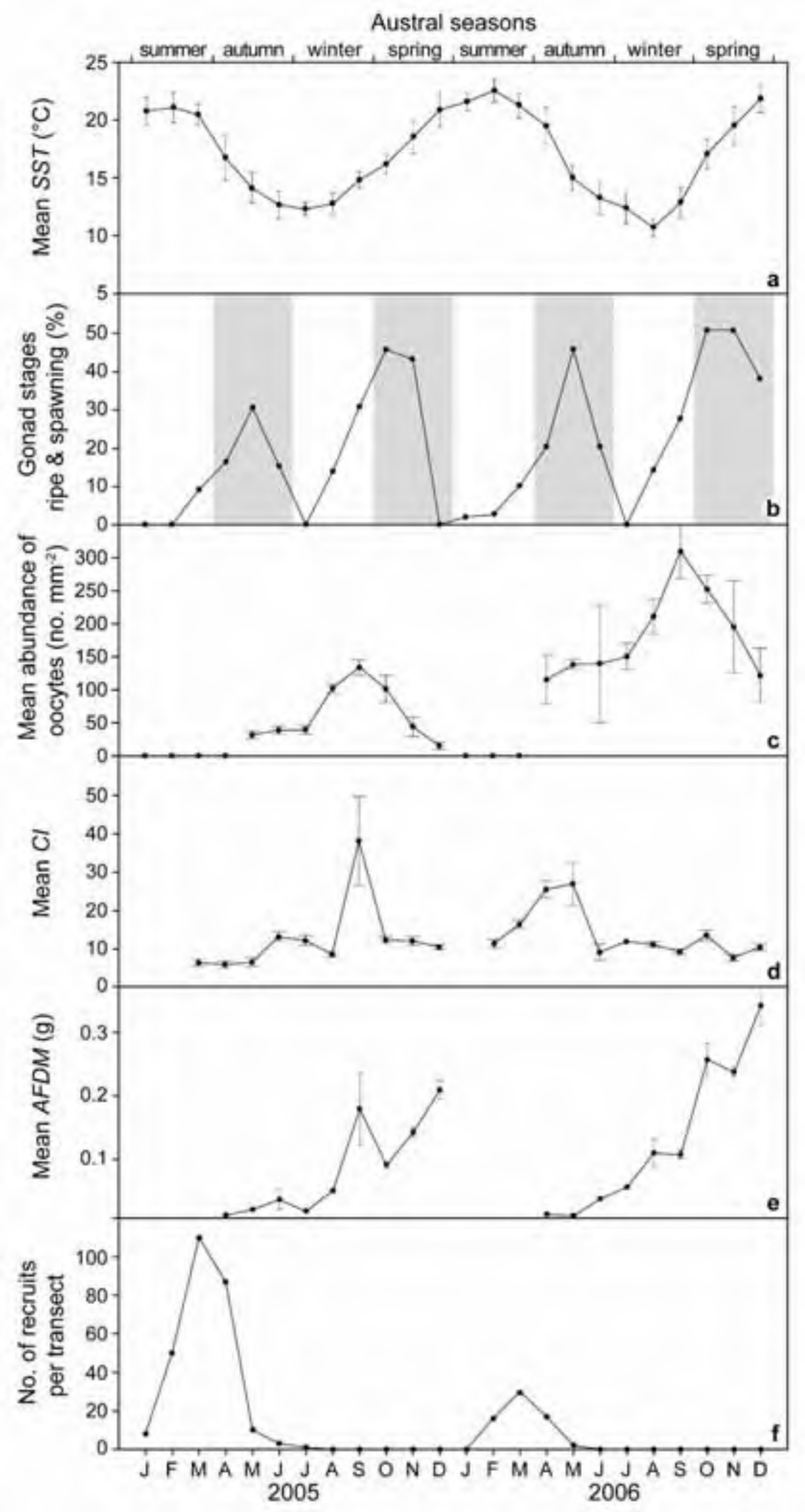

Fig. 5: *M. mactroides* at Santa Teresita: (**a**) mean *SST* (°C) measured daily at Santa Teresita, (**b**) percentage of gonad stages ripe and spawning, (**c**) mean abundance of oocytes (no. mm^{-2}), (**d**) mean condition index (*CI*), (**e**) mean biomass (*AFDM*) (g) and (**f**) number of recruits (2-6 mm) 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 deviations (SD). Data set of graphics are published in Herrmann *et al.* (2008a)

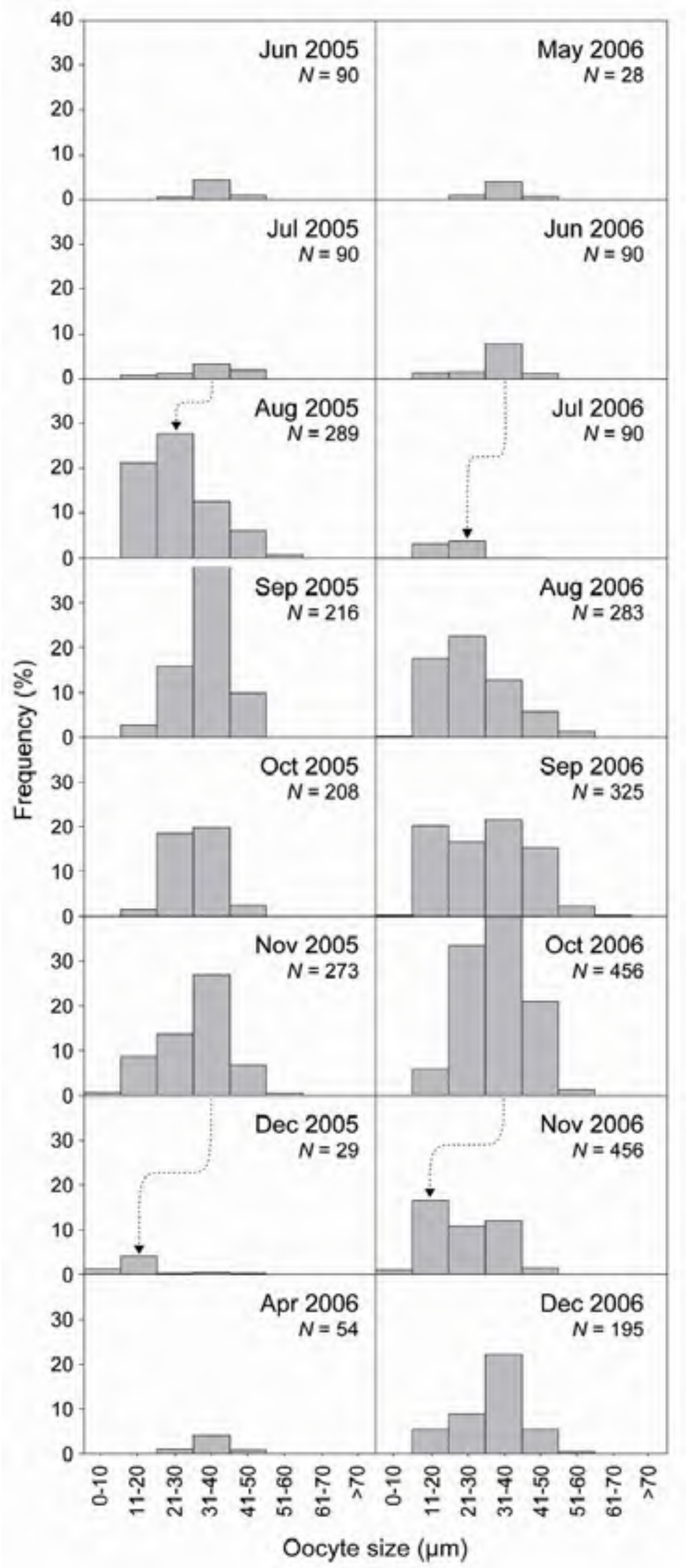

Fig. 6: Monthly oocyte size-frequency distribution of *M. mactroides* collected at Santa Teresita. The abrupt decreases of oocyte modal sizes in August/December 2005 and in July/December 2006 indicate two spawning events per year (dotted *Arrows*). *N* = number of measured oocytes per month.

Table 1: Explanation of the gametogenic scale and the use of descriptive terms (primer column: present study; second column: after Christiansen 1971), utilised in scoring histological analysis of gonad tissue to assess the gametogenic stages of *M. mactroides*. The individual stages of male and female yellow clam gonads are imaged at Fig. 2 and Fig. 3, respectively (*Photo).

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 & 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

Table 2: *M. mactroides*. Monthly *SST* (°C), range of oocyte size (µm), mean oocyte size ($\bar{x}$) with standard deviation (SD), number of females (N_f), number of measured oocytes (N_o) and stages of oocyte development (according to Table 1).

Year	Month	*SST* (°C)	Oocyte size (µm)	$\bar{x}$ ± SD (µm)	N_f	N_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 & 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 & ripe
	May	15	23-45	34.66 ± 0.90	3	28	Ripe
	Jun	13	13-43	33.16 ± 2.08	3	90	Spawning & 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

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

	Gonad stages	summer	autumn	winter	spring
Present study	Active		X	X	X
	Ripe		X	X	X
	Spawning		X	X	X
	Cytolysed		X	X	X
Christiansen (1971)	Active	X	X	X	X
	Ripe	X	X	X	X
	Spawning	X	X	X	X
	Cytolysed	X	X		X

References

(see page 206)

6.5 Publication V

Growth estimations of the Argentinean wedge clam *Donax hanleyanus*: A comparison between length-frequency distribution and size-increment analysis.

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Keywords in vitro *suitability of stains,* in situ *fluorescent marking, calcein, daily growth rate, length-frequency distribution, comparison of methods*

Abstract Growth rates of the Argentinean wedge clam *Donax hanleyanus* were estimated comparing two different methods at the intertidal of the exposed sandy beach Mar de las Pampas: (i) results of a relatively shortly (45 days) tagging-recapture experiment using the *in situ* fluorescent marking (*IFM*) method and subsequent size-increment analyses were compared with results from (ii) length-frequency distributions (*LFD*) analysis originating from a time consuming 25 month quantitative sampling. Residuals, derived from *IFM* method and *LFD* analysis, were of similar magnitude and distribution, indicating that both methods are equally appropriate to estimate growth of *D. hanleyanus*. Comparing overall growth performance indices (*OGP*s) of several *Donax* species from different climate areas it resulted that growth of temperate bivalves can be estimated well by carrying out a relatively short-time tagging-recapture experiment using *IFM* but it is recommended to use both, the *IFM* as well as the *LFD* method to determine growth of tropical bivalves. Furthermore, an *in vitro* suitability test of the three stains strontium chloride hexahydrate, alizarin red and calcein resulted that the latter is useful as non-lethal growth marker for *D. hanleyanus*, emitting a bright green fluorescence band

under blue light. Additionally, pre-experiments of the feeding behaviour of *D. hanleyanus* under controlled conditions resulted that the wedge clam feeds preferably on *Isochrysis galbana*.

1 Introduction

The growth rate of an organism provides basic ecological data and is one of the prime parameters to describe the respective population dynamics. In fisheries, growth rates linked with recruitment data, are used to estimate the sustainable stock yield (Jennings *et al.* 2001; Hilborn and Walter 2003; King 2007). Growth rates of commercially and artisanally extracted bivalves have been well studied (e.g. McLachlan *et al.* 1996b), via various methods such as (i) analysis of size-increments following mark-recapture experiments using tags (Heald 1978; Riascos and Urban 2002), filed notches (Ropes and Merrill 1970; Richardson 1989; Richardson *et al.* 1990; McQuaid and Lindsay 2000; Laudien *et al.* 2003a) labelling paint (Seed 1969; Beal *et al.* 1999; Cummings and Thrush 2004; Kesler *et al.* 2007), and fluorescent stains (Hidu and Hanks 1968; Richardson *et al.* 1979; Parsons *et al.* 1993; Rowley and Mackinnon 1995; Kaehler and McQuaid 1999; Sato-Okoshi and Okoshi 2002; Heilmayer *et al.* 2005; Riascos *et al.* 2006a; Miyaji *et al.* 2007), (ii) length-frequency distribution (*LFD*) analysis (e.g. Nayar 1955; Alagarswami 1966; Talikhedkar *et al.* 1976; Arntz *et al.* 1987; Gaspar *et al.* 1999; Rocha-Barreira de Almeida *et al.* 2002), (iii) shell growth ring analysis (e.g. Capezzani *et al.* 1971; Ansell and Lagardère 1980; Guillou and Le Moal 1980; Sasaki 1981; Richardson 1989; Ramon *et al.* 1995; Fiori and Morsán 2004; Morsán and Orensanz 2004), (iv) analysis of stable isotopes (Jones *et al.* 1983; Brey and Mackensen 1997; Heilmayer *et al.* 2003; Carré *et al.* 2005; Jones *et al.* 2005; Schöne *et al.* 2005) and (v) analysis of the autofluorescent age pigment lipofuscin (Lomovasky *et al.* 2002). Estimations of growth and longevity resulting from differing methods are however, often contradictory (e.g. *Mesodesma mactroides*: Capezzani *et al.* 1971 calculated a life span of ~ 8 yrs ; whereas Defeo *et al.* 1988a suggest ~ 3.5 yrs). Current methods for growth and age determination of bivalves all have specific limitations. *LFD* analyses require well-defined age cohorts and normally large sample sizes, invasive tagging-recapture methods promote physical disturbance and contingently uncharacteristic growth rates, whereas quantification of shell growth rings are affected by surface erosion and disturbance events (for revisions of growth methods see Griffiths and Griffiths 1987; Richardson 2001).

To overcome these limitations, a series of previous studies tested the suitability of several chemicals as shell growth markers in different marine invertebrates. Within the diversity of markers (Nakahara 1961; Hidu and Hanks 1968; Monaghan 1993; Pricker and R. 1993; Day *et al.* 1995; Peck *et al.* 1996), calcein has proven to be a suitable marker for bivalves, in order to investigate growth increments after marking (Kaehler and McQuaid 1999; Fujikura *et al.* 2003; Heilmayer *et al.* 2005; Riascos *et al.* 2006a; Riascos *et al.* 2008; present study). The polyanionic calcein is a fluorescent compound that binds with calcium carbonate in biomineralised growing structures of organisms such as shells and which fluoresces lime-green when viewed under blue light (Wilson *et al.* 1987).

However, to the best of our knowledge, comparisons of growth rate estimations of marine invertebrates, resulting from tagging-recapture experiments using the *in situ* fluorescent marking method (*IFM*), and from the conventional *LFD* method, have not been previously made. By now, such comparisons between a direct and indirect method, respectively, were delicate inasmuch as investigations originated from different areas and analysed distinct species from disparate periods. The present study bridges this gab by a comparative growth rate analysis of the Argentinean wedge clam *Donax hanleyanus* Philippi, 1847 (Bivalvia: Donacidae). Data were collected from the same exposed sandy beach.

This study aims to determine *in situ* daily growth rates of *D. hanleyanus* based on an *IFM* enclosure experiment. Growth parameters of the von Bertalanffy growth function (*VBGF*) will be estimated and results be compared with growth parameters estimated from *LFD*, comparing the residuals and applying an overall growth performance index (*OGP*). The later allows an intra- and interspecific comparison of growth parameters with other *Donax* populations from different geographical locations. Finally, the suitability of tagging-recapture experiment using the *in situ* fluorescent marking method will be assessed *versus* the method of length-frequency analysis.

2 Material and methods

2.1 *In vitro* suitability test of three stains

2.1.1 Sampling and maintenance

In March 2005, 210 specimens of *D. hanleyanus*, covering the full range of anterior-posterior shell lengths (*apSL*: 21-32 mm) available during that month, were collected intertidal by excavating them with hands at the exposed sandy beach Mar de las Pampas (Province of Buenos Aires, Argentina: S37°19', W57°01'). The *apSL* of all specimens was measured to the nearest 0.1 mm with a digital vernier calliper (Mitutoyo, model 500-161U). Specimens were maintained in the hatchery of the Instituto de Biología, Marina y Pesquera, 'Alte Storni' in three 350 l conical tanks equipped with a rounded latern net (each with 70 specimens) containing filtered (using cartridge filters: [I] ECPP-010.7, 10 µm; [II] ECPP-005.7, 5 µm; [III] ECPP-001.7, 1 µm) and aerated circulating seawater under controlled conditions (salinity 34, water temperature 12-14°C) at least for two weeks, before experiments were carried out. The analysis of the feeding behaviour of *D. hanleyanus* on the microalgae *Isochrysis galbana*, *Chaetoceros gracilis*, *Tetraselmis suecica* and a microalgae mix in proportion 1:1 (*I. galbana*, *C. gracilis*) had shown that wedge clams preferably feed on *I. galbana* (own unpublished data). Each tank of specimens were fed daily with 38 l of *I. galbana* (600 cell l^{-1}, determined using a Neubauer counting camber 0.1 mm deep and a surface of 0.0025 mm^2 area).

2.1.2 Staining experiment

In order to test the suitability of three stains to mark shells of *D. hanleyanus*, the stains alizarin red (Sigma, CAS 130-22-3), calcein (Sigma, CAS 1461-15-0) and strontium chloride hexahydrate ([strontium chloride], Sigma, CAS 10025-70-4) were tested at different concentrations and immersion periods (Table 1), which for alizarin red and calcein were chosen based on previous studies (Day *et al.* 1995; Kaehler and McQuaid 1999; Moran 2000; Riascos *et al.* 2006a). Following Fujikura *et al.* (2003) and Riascos *et al.* (2006a) strontium chloride concentrations were used for the staining experiment 30, 120 and 360 times the strontium concentration of natural seawater of the South Atlantic Ocean (8.8 mg l^{-1} on average: Mackenzie 1964; Angino *et al.* 1966; de Villiers 1999). For each treatment 15 wedge clams, which were conditioned before for two weeks, covering the full range of *apSL* available. The staining process was standardised as follows: (i) specimens were placed in 2 l aquaria with aerated circulating seawater containing the respective stain; (ii) each aquarium was placed into the dark to prevent light degradations of the fluorescent chemicals during the immersion period; and (iii) after immersion, wedge clams were restored in the above mentioned 350 l conical tanks and reared in the hatchery for 20 days to allow growth. Dead animals were registered daily and extracted from the tanks.

2.1.3 Shell preparation and detection of growth marks

After the 20 days rearing period, test clams were scarified and the empty shells cleaned and dried at room temperature for 48 hrs. For the detection of incorporated marks, produced during the immersion in the respective stain solution, shells were embedded in Epoxicure resin (Distraltec LY 554 and HL 554) and transverse shell sections produced across the longest growth axis (Fig. 1). A Buehler diamond saw (model Isomet) was used for sectioning. Thereafter, cuts were successively polished on glass slides with different grades of Buehler silicium carbide powder (125-68-30-12-5 µm), and finally with 1 µm Buehler aluminium oxide suspension. Alizarin red and calcein marks were detected and photographed using the digital image processing software AxioVision release 4.6.3 (2008) with a fluorescence microscope (Zeiss Axio Imager Z1) under blue (450 to 490 nm) and red light (330 to 385 nm). In order to detect strontium chloride marks, shell sections were analysed under a Philips 515 scanning electron microscope (SEM) equipped with an EDAX 9100 X-ray microprobe system, whereby the electron beam was irradiated at an accelerating voltage of 15 kV and a lifetime of around 150 s.

2.2 Size-increment analysis

2.2.1 Growth marker

From the *in vitro* tests with alizarin red, calcein and strontium chloride it was evident, that marking with calcein does not affect survival or growth. Calcein produces a clearly detectable fluorescent band. Thus, all clams used during the *in situ* experiment were exclusively stained with calcein.

2.2.2 Sampling, staining and *in situ* growth experiment

In order to study the growth of *D. hanleyanus* derived from the *IFM*, 240 specimens, covering the entire size range available (*apSL*: 5-32 mm), were collected at Mar de las Pampas in March 2006. The *apSL* of all specimens was measured as described. In order to analyse growth differences due to differing *apSL*, wedge clams were divided into three ontogenetic stages, based on histological analyses (Herrmann *et al.* under review-e): (A) recruits (< 11 mm), (B) juveniles (11-22 mm) and (C) adults (> 22 mm). The water temperature was set to resemble the ambient temperature of 20°C. 180 specimens were stained with calcein (50 mg l^{-1} for 3 hrs) as described above. Additionally, a non-treated control group of 60 specimens, randomly assigned, was maintained in similar a tank. After immersion, test and control clams were reared *in situ* in four replicated experimental cages (Fig. 2A) in the exposed intertidal zone of Mar de las Pampas. Cubic cages consisted of round steel bars with a diameter of 1.5 cm and a side length of 40 cm, bonded with a 1 mm nylon mesh, to allow sediment (mean grain size = 0.37 mm: Marcomini *et al.* 2002; Herrmann *et al.* under review-d) and microalgae (< 50 µm: Coscarón 1959) to pass through. A plastic zip on the top of the cage simplified sampling. The experimental set up was installed within the *Donax*-belt approximately 35 cm deep in the sediment and with minimal interspaces of 10 m. Each cage was secured via an underground rope fixed to an anchor, buried in the sublittoral zone. To protect the experiment it was guarded over the whole experimental time. During a period of seven weeks, every seventh day samples were taken by carefully sieving the sand through the cage mesh to avoid damage (Fig. 2C). Dead animals, noted as washed-out on the sediment surface, were registered daily and extracted from the experimental cages.

2.2.3 Shell preparation and detection of absolute growth rate

In order to calculate the absolute growth rate of *D. hanleyanus*, shells of test clams were prepared and analysed as described in 2.1.3. Absolute growth rate was measured as shell growth along time:

$$absolute\ growth\ rate = \frac{SL_2 - SL_1}{t_2 - t_1} = \frac{\Delta SL}{\Delta t} \qquad (1)$$

where $umSL_1$ is the initial shell length (mm) between umbo and shell margin before staining (t_1) and $umSL_2$ the final shell length (mm) between umbo and shell margin at the end of the experimental period (t_2) (Fig. 1).

2.3 Length-frequency distribution analysis

2.3.1 Sampling and data collection

Quantitative samples of *D. hanleyanus* were collected from the same beach (Mar de las Pampas) from a series of stations (4 m intervals) at monthly intervals between December 2004 and December 2006. Sample stations were located along three transects separated by 20 m intervals and located perpendicular to the shoreline from the spring tide high water mark to the spring tide low water mark. At each station, three replicated sand samples (40 x 40 cm) were excavated to 35 cm depth using a 0.16 m^2 steel corer. Thereafter, samples were sieved individually over a 1 mm mesh and *apSL* of the retained wedge clams was determined as described above to obtain monthly *LFD*s.

2.4 Comparison of methods

In order to compare growth estimates of both methods used in this study, *LFD* data were interpreted as size-at-age data (*SAD*). The *IFM* data set consisting of *umSL* values was converted to *apSL* data by the linear regression equation *umSL* = 0.8381 • *apSL* + 0.0037 ($N = 280$, $r^2 = 0.99$). General von Bertalanffy growth functions (*gVBGF*s) were fitted to size-increment data (*SID*) resulting from *IFM* method and to *SAD* resulting from *LFD* analysis using the computation worksheet of Brey (2001), applying Microsoft Excel's SOLVER routine:

$$L_t = L_\infty\left[1 - e^{-K(t-t_0)}\right]^D \tag{2}$$

where L_t is the *apSL* (mm) at time *t*, L_∞ the mean asymptotic *apSL* (mm), *K* the growth constant (yr^{-1}), *D* determines the shape of the curve (inflection point if $D > 1$), and t_0 is the age when *apSL* equals zero. Both methods were compared by analysing the variance of the residuals of the *gVBGF*s.

Additionally, calculated overall growth performance (*OGP*) indices were useful to compare the *VBGF*s, since several authors (e.g. Pauly 1979; Munro and Pauly 1983; Moreau *et al.* 1986; Laudien *et al.* 2003a; Defeo and Cardoso 2004) demonstrated the suitability of composite indices for *OGP* for inter- and intraspecific comparisons. *OGP* is proportional to the maximum rate of body mass increase during lifetime, i.e. the mass increase at the inflexion point of the *VBGF*, since few values of maximum body mass can be found in the literature and maximal mass is proportional to L_∞. In this context, the *OGP* of *D. hanleyanus* derived from both methods used in this study was calculated as:

$$OGP = \log(K[L_\infty]^3) \tag{3}$$

and compared with results from several Donacidae at different localities.

2.5 Statistical analysis

All statistical analysis were carried out using the statistical package SPSS version 16.0.1 (2007). Differences were considered significant at a level of $\alpha = 5\,\%$ (Zar 1999). Chi-square (χ^2) analyses were applied to determine if significant differences on mortality rates occurred by using stains to mark surf clams during *in vitro* suitability tests and *in situ* growth experiments. The relation between $umSL_2$ and daily growth rate was estimated by exponential regression analysis. Effects of $umSL_2$ and exposure time on growth rate were analysed by utilising a one-way ANCOVA (growth rate as dependent variable, days of exposure as fixed factors and initial length as covariate). Differences of growth rates within the three ontogenetic groups ‘recruits’, ‘juveniles’ and ‘adults’ were analysed by a one-way ANOVA with a Scheffé-procedure post hoc test. *LFD* analyses and tagging-recapture experiments using the *IFM* method and subsequent size-increment analyses, used to estimate growth of both surf clams, were compared by an ANOVA of the residuals of the *gVBGF*s.

3 Results

3.1 *In vitro* suitability test of three stains

Results of the *in vitro* suitability test of the three stains are summarised in Table 1. For *D. hanleyanus* alizarin red staining was less successful (Table 1A) as marking with calcein (Table 1B). The latter produced clearly visible fluorescent growth bands, easily distinguishable from the natural autofluorescence, at all concentrations and immersion periods (Table 1B). Strontium chloride was not detectable (Table 1). The numbers of dead wedge clams for each treatment are also listed in Table 1. After staining mortality was relatively low (9 %) and did not statistically differ between treatments including the control group (χ^2 = 3.000, *df* = 2, *p* > 0.05).

3.2 Size-increment analysis

The described cages proved to be suitable for the *IFM* enclosure experiment in the exposed intertidal zone of Mar de las Pampas. All cages resisted the wave exposure during the entire experimental period. Visually, no difference was determined in the turbidity of water out- and inside the cages, no filter residue was recognisable on the mesh and no clogging of the mesh by sediment was registered, which indicates natural feeding conditions for the test specimens. Additionally, there was no distinguishable difference of grain size out- and inside of the cages, and no tidal current scouring was detectable indicating optimal near-natural conditions for the stained wedge clams and control specimens.

Calcein marks were conspicuous in 86 % ($N = 155$) of the specimens from which growth increments were found and measured in 73 % ($N = 113$). Over the 45 days of the experiment mortality was relatively low and ranged between 4 % ($N = 9$) and 6 % ($N = 14$) for the stained specimens and 5 % ($N = 11$) for the control clams. Thus, calcein marking did not affect survivorship of *D. hanleyanus* ($\chi^2 = 0.384$, $df = 3$, $p = 0.943$) and therefore calcein is a useful non-lethal marker for field experiments.

As expected, maximum growth increments were found in juvenile *D. hanleyanus* (e.g. $umSL_2 = 7.31$ mm + 1.86 mm in 45 days) (Fig. 3). Individual daily growth rate ranged between 8 µm d^{-1} and 72 µm d^{-1}. The relationship between $umSL_2$ and daily growth rate was best described by an exponential function (Fig. 4). Both, $umSL_2$ ($F_{1,96} = 191.249$, $p < 0.001$) and exposure time ($F_{5,96} = 17.415$, $p < 0.001$) had significant effects on growth rate (one-way ANCOVA: growth rate as dependent variable, days of exposure as fixed factors and initial length as covariate). Growth decreased exponentially from recruits to adults ($y = 144.76 \cdot e^{-0.201x}$, $r^2 = 0.91$, $N = 113$): daily growth rates of recruits were significantly higher (Fig. 4, group A: 32.43 ± 11.21 µm d^{-1} [mean ± SD]) compared to juveniles (Fig. 4, group B: 8.93 ± 5.24 µm d^{-1} [mean ± SD]) and adults (Fig. 4, group C: 0.41 ± 0.24 µm d^{-1} [mean ± SD]) (one-way ANOVA with a Scheffé-procedure post hoc test, $F_{2,110} = 97.983$, $p < 0.001$).

A *gVBGF* was fitted to *SID*, originated from *IFM*, using the maximum length (*umSL* = 37 mm [analogical to *apSL* = 44 mm]) found at Mar de las Pampas as a fixed value of L_∞ to calculate the growth constant $K = 0.41$ y^{-1} ($r^2 = 0.69$).

3.3 Length-frequency distribution analysis

In order to analyse length-frequency distributions of *D. hanleyanus*, 2,997 specimens were collected from Mar de las Pampas (first year $N = 1{,}545$ ind., second year $N = 1{,}452$ ind.) during the 25 months. The smallest live wedge clam recorded had an *apSL* of 4 mm and the largest measured 36 mm (*apSL*). The growth constant $K = 0.47$ yr^{-1} ($R_n = 0.202$) was computed by fitting a *gVBGF* to this data set, using the maximum length (*apSL* = 44 mm) found at Mar de las Pampas as a fixed value of L_∞.

3.4 Comparison of methods

The two methods used in this study were compared by residual analyses. Plotting residuals *versus* the estimated shell lengths showed a very good fit ($r^2 = 0.99$) (Fig. 5). The analysis of variance of the residuals of the *gVBGF*s showed no significant difference between the two methods (ANOVA, $F_{1,64} = 2.153$, $p > 0.05$).

Computed *OGP* values of *D. hanleyanus*, resulting from *IFM* (*OGP* = 4.45) and *LFD* (*OGP* = 4.60), were plotted close to each other within the auximetric grid (Fig. 6, no. 16 and no. 17, respectively).

4 Discussion

Marks incorporated in *D. hanleyanus* shells demonstrated qualitative differences, depending on the stain type, concentration and immersion time. The fluorescence marker ‘calcein’ emitted a bright green fluorescence band under blue light, which was readily distinguished from naturally occurring autofluorescence, even in low concentrations and short immersion times. Alizarin red showed imprecise faint growth bands, however, only at higher concentrations and longer immersion periods. Strontium chloride did not produce any detectable growth mark, although high concentrations and long immersion periods were used. The present results agree with previous observations that calcein produces clear marks in molluscs under controlled conditions, which enables short-term, high-resolution growth studies (e.g. *Haliotis rubra*: Day *et al.* 1995; *Perna perna*: Kaehler and McQuaid 1999; *Adamussium colbecki*: Heilmayer *et al.* 2005; *Concholepas concholepas* and *Mesodesma donacium*: Riascos *et al.* 2006a).

Early growth studies using fluorochromes demonstrated that adversely affected test organisms had substantial mortality (Nakahara 1961; Schmitt 1984; Monaghan 1993; Pricker and R. 1993; Day *et al.* 1995). A variety of fluorochromes were tested and showed that calcein exhibits little toxicity (Wilson *et al.* 1987; Hales Jr and Hurley 1991; Monaghan 1993; Day *et al.* 1995; Rowley and Mackinnon 1995). In accordance with recent studies (Moran

2000; Riascos *et al.* 2006a) the present study revealed that calcein marking did not affect survivorship of *D. hanleyanus* during the *in vitro* and the *in situ* experiments, however performed under relatively low concentrations and immersion periods. This supports that calcein can be recommended as a non-lethal marker for *D. hanleyanus*.

The distinct and narrow fluorescent band incorporated into the growing shell edge at the time of calcein exposure was successfully used as a datum point in growth measurements. Fluorescent marks were readily detected in stored samples at least two years after the experiment without visible degradation of the growth marks. The potential for using calcein as a growth-marker in long-term growth studies is therefore great (see also Rowley and Mackinnon 1995; Kaehler and McQuaid 1999; Moran 2000; Riascos *et al.* 2006a).

The *in situ* experiment showed that specimens of *D. hanleyanus* grew between 0.41 µm d^{-1} and 32.43 µm d^{-1} whereby the daily growth rate was correlated to the $umSL_2$ as described by an exponential function, depending on individuals' size classes (Fig. 4A, B, C; respectively). Apparently, recruits use the major part of energy for growth until specimens reach the size at first maturity of approximately 11 mm *apSL* (Fig. 4, dotted line) (Herrmann *et al.* under review-e).

The residuals derived from *IFM* and *LFD* were of similar magnitude and distribution, indicating that both methods are equally appropriate to estimate growth of *D. hanleyanus*. Growth of wedge clams calculated from the 45 days *in situ* experiment (*IFM*) in March-April conforms well to shell growth of the 25 months observation (*LFD*). Furthermore, *OGP* values of the Argentinean *D. hanleyanus* resulting from *IFM* (4.45, Fig. 6, no. 16) and *LFD* (4.60, Fig. 6, no. 17) show small distances to values calculated from data sets of the same species from the Argentinean (4.65, Fig. 6, no. 12: Penchaszadeh and Olivier 1975), Uruguayan (4.46, Fig. 6, no. 13: Defeo 1996) and Brazilian coast (4.17 and 4.32, Fig. 6, no. 14 and 15, respectively: Cardoso and Veloso 2003). Therefore it can be concluded that alternatively to *LFD* analyses, tagging-recapture experiments using the *IFM* method and subsequent size-increment analysis are appropriate to estimate growth of the Argentinean wedge clam *D. hanleyanus*.

Moreover, the auximetric grid (Fig. 6), comparing *OGP*s of several donacids, indicates that tagging-recapture experiments using the *IFM* method and subsequent size-increment analyses are required to estimate growth of tropical *Donax* species. In this way, *OGP*s of *D. dentifer* (4: Riascos and Urban 2002) and *D. striatus* (Fig. 6, no. 11, Rocha-Barreira de Almeida *et al.* 2002) demonstrate a relatively large distance to other tropical donacids such as *D. cuneatus* (Fig. 6, no. 1 and 2), *D. denticulatus* (Fig. 6, no. 3), *D. faba* (Fig. 6, no. 5), *D. incarnatus* (Fig. 6, no. 6-9) and *D. striatus* (Fig. 6, no. 10) and in contrast much lower distance to the temperate donacids *D. hanleyanus* (Fig. 6, no. 12-17), to *D. trunculus* (Fig. 6, no. 18-33) and to *D. vittatus* (Fig. 6, no. 34-38). Since tropical species exhibit continuous spawning events or recruit over a longer period, compared to temperate donacids, *LFD* analysis only may not be useful for tropical species to estimate growth (Sparre and Venema 1998). On this account tagging-recapture experiments coupled for example with the *IFM* method are recommended to estimate adequate the growth of tropical species.

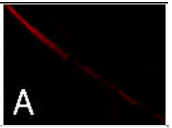
However, both, the *IFM* and the *LFD* method, have advantages and disadvantages, which are summarised in Table 2. A great pro of the *IFM* is accuracy, allowing daily growth rate measurements of *D. hanleyanus;* furthermore a relatively low number of specimens is needed in comparison to the *LFD* analyses. The *IFM* can thus also be used for scattered populations difficult to sample enough specimens for clear cohort detection. On the other hand the *LFD* analysis allows detection of seasonal growth (Appeldoorn 1987) and specimens can live on after data collection. Although the present study showed similar growth parameters calculated from *LFD* and *IFM*, the latter method may not always detect growth of adults accurately, due to the slow growth rate and the short experimental time period. Therefore the *IFM* must be applied over an adequate period, dependent on the growth rate of the species. On the other hand, long study periods necessary for the *LFD* analysis are vulnerable to bias caused by alongshore migration of cohorts, which may not be clearly followed. Although several surf clam species seem to favour river mouths for settlement and successively migrate alongshore (Tarifeño 1980; Donn 1987; Jaramillo *et al.* 1994; Lastra and McLachlan 1996), such an ontogenetic alongshore migration was not recorded during the present study as there are no rivers or dry riverbeds located in the sampling site. Furthermore, the histograms did not display certain size classes unexpectedly (dis)appearing. In addition, carrying out only short-time experiments may lead to an underestimation of L_∞ due to a possible lack of large adult specimens. Here *LFD* analyses are more precise due to the longer sampling period. Furthermore, strong wave exposure can destroy an entire *in situ* experiment, but collection for the *LFD* analysis may be postponed.

5 Conclusions

Both methods are suitable to estimate growth of the Argentinean wedge clam *D. hanleyanus*, whereby each has its own limitations (Table 2). For the fluorescent marking *in situ* method approximately one and a half months were used to accomplish the experiment and another three months for preparation and analyzing all samples. To realize this method a budget of approximate 2,700 € was necessary (fluorescent microscope equipped with a digital camera not included). At the present study the *LFD* method was much more time-consuming and expensive, a 25 month sampling consumed approximately 5,600 €. In conclusion, for the *IFM* method more man power was used in the field compared to the second method where monthly sampling was comparatively easy. Growth of temperate bivalves can be estimated well by carrying out a relatively short-time tagging-recapture experiment using *IFM* but it is recommended to use both, the *IFM* as well as the *LFD* method to determine growth of tropical bivalves.

Appendix

Table 1: Photomicrographs of shell sections (**A**: alizarin red, 10 mg l^{-1},6 h, magnification 1000x; **B**: calcein, 50 mg l^{-1}, 3 h, magnification 400x) after staining with three different fluorescent stains, concentrations, immersion periods, results on quality of marks and mortality for treated Argentinean wedge clam *D. hanleyanus* under controlled conditions.

Stain	**Concentration ($mg\ l^{-1}$)**	**Immersion period (h)**	**Mortality (*N*)**	**Quality of mark**	**Incorporated mark**
Alizarin red	10	3	0	No mark	
Alizarin red	10	6	1	Faint mark	
Alizarin red	50	3	2	Faint mark	
Alizarin red	50	6	1	Faint mark	
Calcein	50	3	1	Clear mark	
Calcein	50	6	2	Clear mark	
Calcein	100	3	1	Clear mark	
Calcein	100	6	2	Clear mark	
Strontium chloride ^{I}	264	3	2	No mark	No mark visible
Strontium chloride ^{I}	264	6	1	No mark	
Strontium chloride ^{II}	1,056	3	1	No mark	
Strontium chloride ^{II}	1,056	6	2	No mark	
Strontium chloride ^{III}	3,168	24	3	No mark	
Control group	-	-	2	-	

30 (**I**), 120 (**II**) and 360 (**III**) times, respectively, the concentration of strontium in Atlantic seawater (8.8 mg l^{-1} on average: Mackenzie 1964; Angino *et al.* 1966; de Villiers 1999).

Table 2: Attributes of the *IFM* and *LFD* analysis.

	Category	*IFM*	*LFD*
Scientific aspects	Determination of daily growth	yes	no
	Direct growth estimation	yes	no
	Numbers of studied specimens necessary	low	high
	Humans effecting sampling	yes	no
Economic aspects	Costs	lower	higher
	Sampling time	less	more
	Laboratory work	more	less
	Expensive equipment necessary	yes	no
	Man power	more	less

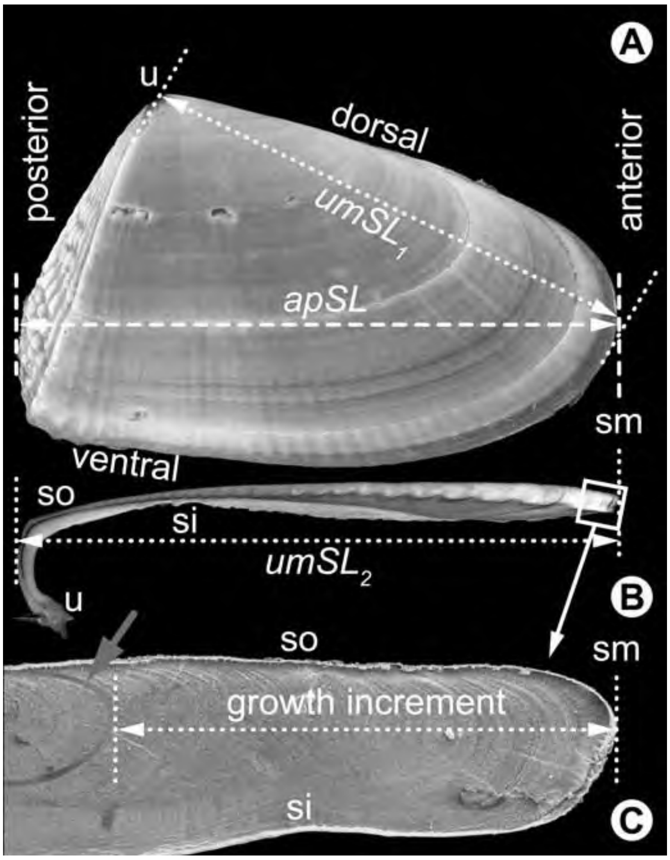


Fig. 1: Shell of *D. hanleyanus* (**A**) and transverse shell sections of longest growth axis observed with a transmitted-light microscope (**B**) and a scanning electronic microscope (SEM) (**C**) indicating anterior-posterior shell length (*apSL*), initial shell length between umbo and shell margin (*umSL*$_1$), final shell length between umbo and shell margin (*umSL*$_2$) and growth increment after experimental time, respectively. Square in image 'B' is detailed in image 'C'. *Grey arrow* indicate fluorescent growth mark, **u**: umbo, **sm**: shell margin, **so**: shell outside and **si**: shell inside.

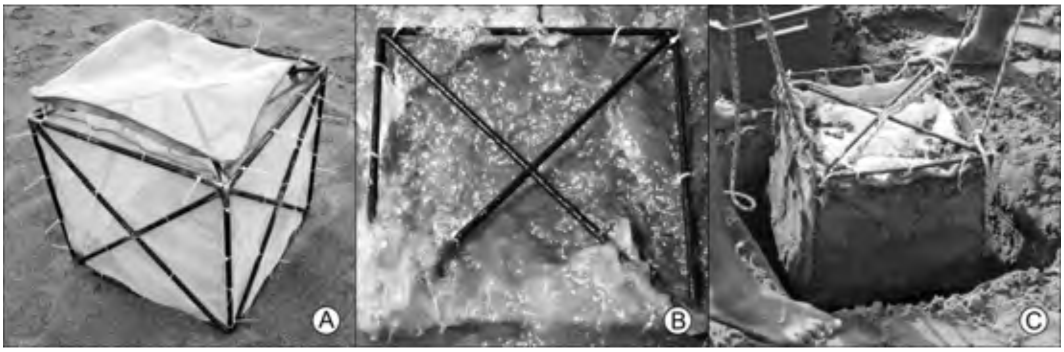


Fig. 2: Cage (40 x 40 x 40 cm) with 1 mm mesh bonded (**A**) installed during the *in situ* experiment (**B**) and during a weekly sampling (**C**).

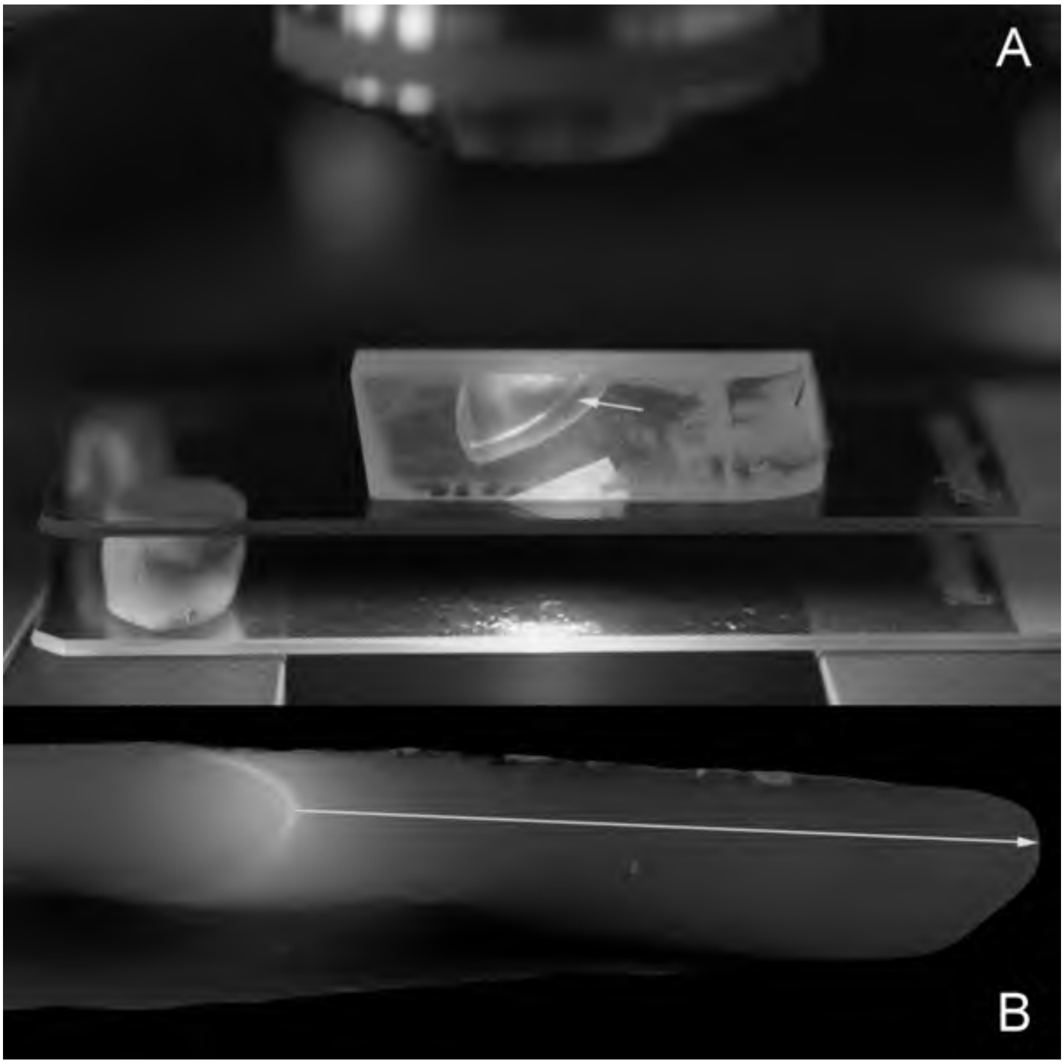


Fig. 3: *D. hanleyanus* (*umSL*$_2$ = 7.31 mm) under a fluorescent microscope equipped with blue light, sampled and embedded in Epoxicure resin after 45 days experimental time (**A**). Thin section (**B**) along the major growth axis indicates a growth increment of 1.48 mm and the direction of growth (*arrow*).

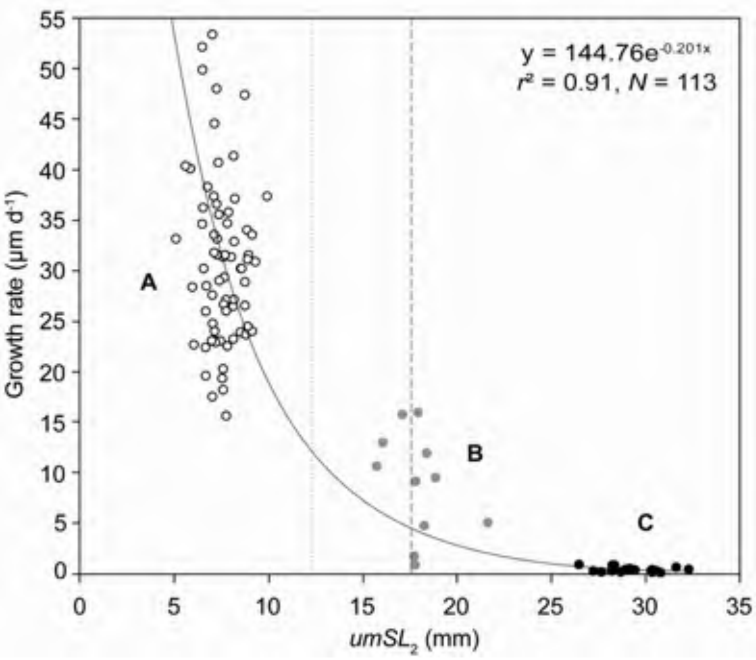


Fig. 4: *D. hanleyanus*. Relationship between *umSL*$_2$ (mm) and growth rate (µm d^{-1}) within the three groups, defined following Herrmann *et al.* (under review-e): ○ recruits (**A**: < 11 mm *iapSL*), ● juveniles (**B**: 11-22 mm *iapSL*) and ● adults (**C**: >22 mm *iapSL*). Dotted line indicate size at first maturity (13 mm) and dashed line indicate size of 50 % population maturity (17 mm) (Herrmann *et al.* under review-e).

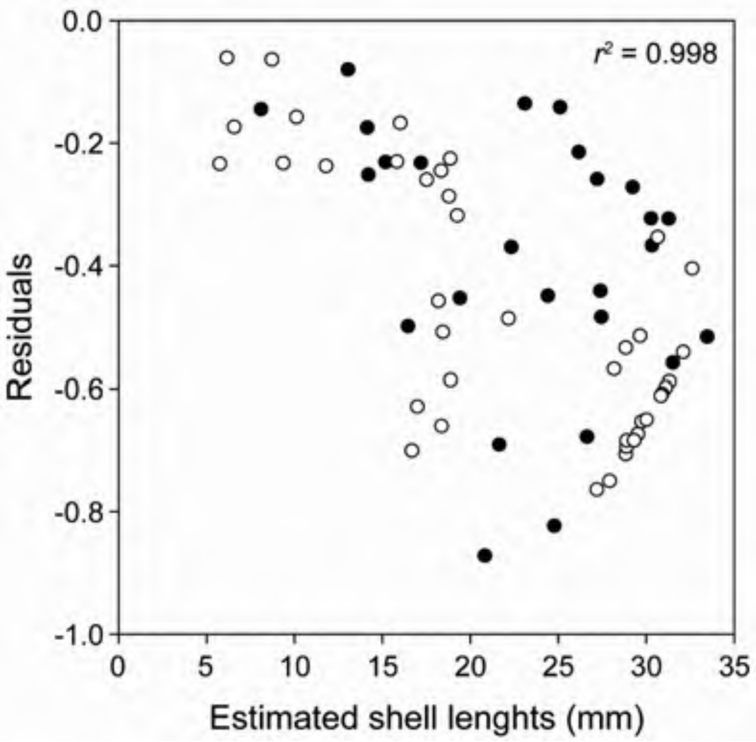


Fig. 5: *D. hanleyanus.* Residuals of estimated shell lengths of (●) *SAD* converted from *LFD* and of (○) *SID* from *IFM*, showing no significant difference (ANOVA, $F_{1,64}$ = 2.153, $p > 0.05$).

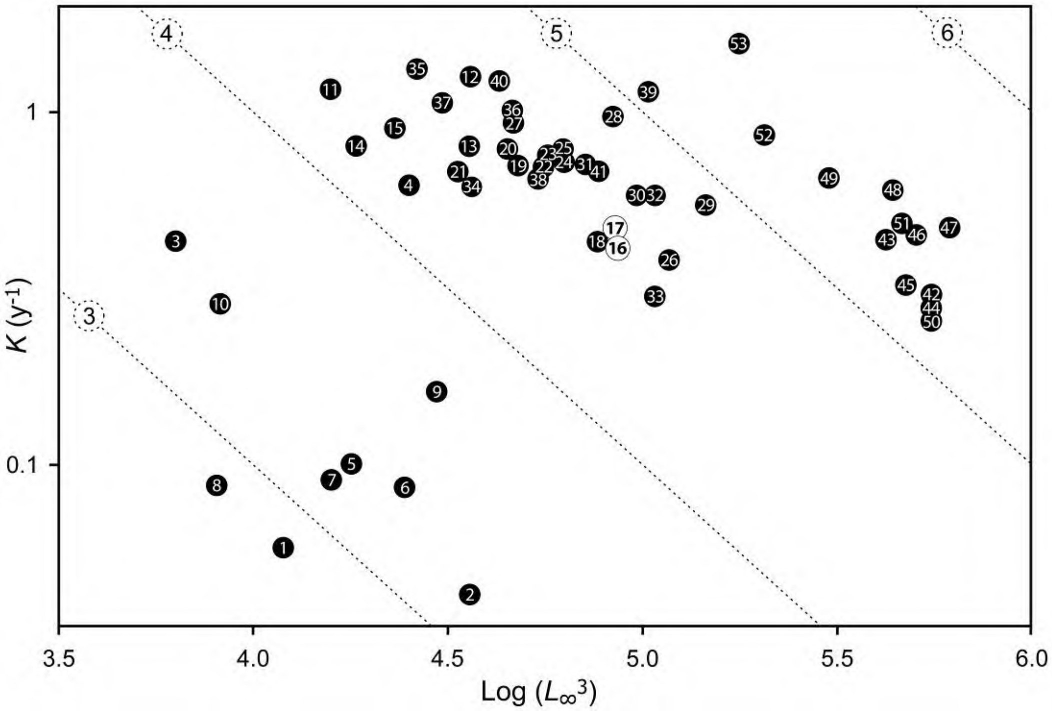


Fig. 6: Auximetric grid comparing *OGP* (Eq. 3) of several Donacidae (●) with Argentinean *D. hanleyanus* from the present study (○). Diagonal lines indicate equal values of P (numbers in dotted circles). Data sources: *D. cuneatus* (1: Nayar 1955; 2: Talikhedkar *et al.* 1976), *D. denticulatus* (3: Vélez *et al.* 1985), *D. dentifer* (4: Riascos and Urban 2002), *D. faba* (5: Alagarswami 1966), *D. incarnatus* (6, 7: Ansell *et al.* 1972; 8: Nair *et al.* 1978; 9: Thippeswamy and Joseph 1991), *D. striatus* (10: McLachlan *et al.* 1996b; 11: Rocha-Barreira de Almeida *et al.* 2002), ***D. hanleyanus*** (12: Penchaszadeh and Olivier 1975; 13: Defeo 1996; 14, 15: Cardoso and Veloso 2003; **16**: present study estimated from *IFM*; **17**: present study estimated from *LFD*), *D. trunculus* (18-25: Ansell and Lagardère 1980; 26: Guillou and Le Moal 1980; 27: Bodoy 1982; 28: Fernández *et al.* 1984; 29: Mazé and Laborda 1988; 30, 31: Ramon *et al.* 1995; 32: Gaspar *et al.* 1999; 33: Zeichen *et al.* 2002), *D. vittatus* (34-37: Ansell and Lagardère 1980; 38: Guillou and Le Moal 1980), *D. marincovichi* (39 before, 40 during and 41 after El Niño: Arntz *et al.* 1987), *D. serra* (42-45: de Villiers 1975a; 46-51: Laudien *et al.* 2003a), *D. deltoides* (52: King 1985; 53: Laudien *et al.* 2003a).

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(see page 206)

7 Appendix

7.1 Conference Presentations

Herrmann, M., Penchaszadeh, P. E., Arntz, W. E., Laudien, J. (2008). Testing the habitat harshness hypothesis: The reproductive biology of the wedge clam *Donax hanleyanus* (Bivalvia: Donacidae) from three Argentinean sandy beaches with contrasting morphodynamic. VII Latin American Congress of Malacology – CLAMA 2008, The Faculty of Sciences of the Universidad Austral de Chile and Latin American Malacology Association, Valdivia, 03.-07.11.2008.

Lepore, M. *L*., Penchaszadeh, P. E., **Herrmann, M.** (2008). Estudio del crecimiento de la almeja amarilla argentina *Mesodesma mactroides* por marcación fluorescente *in situ* y comparación con el método de distribución de frecuencia de tallas. VII Latin American Congress of Malacology – CLAMA 2008, The Faculty of Sciences of the Universidad Austral de Chile and Latin American Malacology Association, Valdivia, 03.-07.11.2008.

Herrmann, M., Alfaya, J. E. F., Lepore, M. *L*. (2007). Dinámica de poblaciones de bivalvos en playas arenosas de la Provincia de Buenos Aires, La Reunión Ciencia, Tecnología y Sociedad III (CTS III), Montevideo, Uruguay, 20.-22.06.2007.

Alfaya, J. E. F., **Herrmann, M.**, Penchaszadeh, P. E. (2007). Desarrollo gonadico invernal y desove primaveral, de la almeja amarilla *Mesodesma mactroides* (Bivalvia: Mesodesmatidae) en las playas de Santa Teresita, XX Encontro Brasileiro de Malacologia (EBRAM), Rio de Janeiro, 05.-10.08.2007.

Carstensen, D., **Herrmann, M.**, Laudien, J. (2007). Similitud morfológica de espermatozoides de *Donax marincovichi* y *Donax obesulus* (Bivalvia: Donacidae), XX EBRAM, Rio de Janeiro, Brasil, 05 a 10 de agosto de 2007.

Herrmann, M., Laudien, J., Arntz, W. E., Penchaszadeh, P. E. (2007). Growth estimats of the Argen-tinean surf clam *Donax hanleyanus* (Bivalvia: Donacidae) derived from fluorescent marking, XII CO-LACMAR, XII Congreso Latinoamericano de Ciencias del Mar, Florianópolis, SC, Brasil, April 2007.

Herrmann, M., Laudien, J., Arntz, W. E., Penchaszadeh, P. E. (2007). Population structure of *Donax hanleyanus* (Bivalvia: Donacidae) on two sandy beaches on the Argentinean coast, XX Encontro Bra-sileiro de Malacologia (EBRAM), Rio de Janeiro, 05.-10.08.2007.

Lepore, M. *L*., **Herrmann, M.**, Penchaszadeh, P. E. (2007). Estimación del crecimiento de la almeja amarilla *Mesodesma mactroides* (Bivalvia: Mesodesmatidae) por marcación fluorescente, XX Encontro Brasileiro de Malacologia (EBRAM), Rio de Janeiro, 05.-10.08.2007.

Alfaya, J. E. F., **Herrmann, M.**, Giménez, J. (2006). Population structure and reproduction of the yellow clam *Mesodesma mactroides* on the sandy beach of Santa Teresita (Argentina): Changes in the last 35 years?, VI Jornadas Nacionales de Ciencias del Mar, Puerto Madryn, Argentina, 4 al 8 de diciembre de 2006.

Carstensen, D., **Herrmann, M.**, Laudien, J., Schiel, S., Arntz, W., Leese, F., Held, C. (2006). Genetic variability of Chilean and Peruvian surf clams (*Donax marincovichi* and *Donax obesulus*), International Congress on Bivalvia, July 22-27, 2006, Universitat Autònoma de Barcelona.

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7.2 Supervision of Diploma Theses

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Alfaya, J.E.F. (2007). Estructura poblacional y reproducción de la almeja amarilla *Mesodesma mactroides* en la playa de Santa Teresita. Cambios en 35 años. Diploma thesis, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires: 59 p.

Lepore, M.*L.* (2008). Crecimiento de la almeja amarilla *Mesodesma mactroides* (Bivalvia: Mesodesmatidae) estimado por marcación fluorescente. Diploma thesis, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires: 71 p.

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7.4 List of Selected Abbreviations

Abbreviation	Explanation (unit in parentheses)
a	Anus
α	Level of significance (= 5 %)
A	Tropical-subtropical species
aam	Anterior adductor muscle
$AFDM$	Shell-free ash-free dry mass (g)
AH	Autoecological hypothesis
al	Alveolus
ANCOVA	Analysis of covariance
ANOVA	Analysis of variance
$apSL$	Anterior-posterior shell length (mm)
$apSL_{50\%}$	Size at 50 % population maturity (mm)
arm	Anterior retractor muscle
ARSS	Analyses of the residual sum squares
aw	Alveolar wall
B	Temperate species
$\bar{B}$	Biomass (g $AFDM$)
B_{apSL}	Size at which 100 % of the population is mature (mm)
B_{SFWM}	Biomass at which 100 % of the population is mature (g)
c	Carnivore
C	Upwelling species
C	Constant, which defines the degree of seasonal oscillation
Ca	Climate areas
χ^2	Chi-square analysis
cc	Central cavity with longitudinal and transverse fascicles
CCL	Complex crossed-lamellar structure
CI	Condition index
CL	Crossed-lamellar layer
cs	Crystalline style
d	Detrivore
DM	Dry mass (g)
ELEFAN	Electronic length-frequency analysis
EN	El Niño
es	Exhalant siphon
f	Foot
F	Faro Querandí
fm	Feeding mode
G_i	Mass-specific growth rate
go	Gonad

gu	Gut
gVBGF	General von Bertalanffy growth function
H_b	Mean wave height (m)
hp	Hepatopancreas
HHH	Habitat harshness hypothesis
HHS	Hypothesis of habitat safety
ht	Heart
IFM	*In situ* fluorescent marking
ind.	Individuals
is	Inhalant siphon
k	Kidney
K	Growth constant of *VBGF* (yr^{-1})
$L_{95\%}$	Represents 95 % of the maximum shell length (mm)
L_∞	Asymptotic shell length (mm)
LFD	Length-frequency distributions
LGH	Latitudinal gradient hypothesis
lp	Labial palp
L_t	Length at age t (mm)
$L_{t(1968-70)}$	Length at age t from historical study (mm)
$L_{t(2005-06)}$	Length at age t from present study (mm)
M	Mar de las Pampas
M	*AFDM* (g)
mh	Mouth
ml	Mantle
M_s	Mean slope of tidal
M_t	Total wet mass (g)
M_v	Wet mass of visceral mass (g)
M_z	Mean grain size (mm)
N	Number of individuals
nMDS	Non-metric multi-dimensional scaling
o	Oocyte
OGP	Overall growth performance
Ω	Dean's parameter
ϕ'	Growth index phi prime
p	The probability of obtaining a value of the test statistic at least as extreme as the one that was actually observed, given that the null hypothesis is true
P	Production (g *AFDM*)
$P/\bar{B}$	Annual renewal rate
pam	Posterior adductor muscle
PM	Pallial myostracum
prm	Posterior retractor muscle
R_n	Criterion of fit of the *VBGF*
r_s	Spearman`s rank order correlation
RSA	Relative spermatozoon abundance

s	Suspension feeder
S	Santa Teresita
SAD	Size-at-age data
sd	Spermatids
SD	Standard deviation
SE	Standard error
SEH	Swash exclusion hypothesis
SFDM	Shell-free dry mass (g)
SFWM	Shell-free wet mass (g)
$SFWM_{50\%}$	Biomass at which 50 % of the population is mature (g)
sh	Shell
si	Shell inside
SID	Size-increment data
sm	Side of shell margin
so	Shell outside
sp	Sperms
su	Shell umbo side
SST	Sea surface temperature (°C)
st	Stomach
t	Age (yr)
T	Wave period (s)
t_0	Age at zero length (yr^{-1})
tf	Transverse fibre
t_{max}	Theoretical life span (yr^{-1})
u	Umbo
umSL	Shell length between umbo and shell margin (mm)
$umSL_1$	Initial shell length between umbo and shell margin (mm)
$umSL_2$	Final shell length between umbo and shell margin (mm)
VBGF	Von Bertalanffy growth function
W	Sand fall velocity ($m\ s^{-1}$)
WM	Wet mass (g)
WP	Winter point
Z	Total instantaneous mortality rate

7.5 References

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