

Changes in the intertidal community structure after a mass mortality event in sandy beaches of Argentina

José R. Dadon

Departamento de Ecología, Genética y Evolución, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, (1428) Buenos Aires, Argentina, e-mail: dadon@ege.fcen.uba.ar

Keywords: Surf clams, *Mesodesma mactroides*, *Donax hanleyanus*, sandy beaches, benthos, Argentina, species interactions

Abstract

After a massive mortality of the dominant species (the clam *Mesodesma mactroides*) occurred in 1995, changes in the intertidal community in sandy beaches of Argentina were monitored. Eight sampling stations were established in a 40 km open stretch and samples were taken every October each year up to 2001. Biomass, density, size frequency distribution and mean growth rates for the most abundant species were analyzed. During the mortality event, only the benthic stages of *M. mactroides* were affected, their total mean biomass diminishing from 1,399 g to 2 g per running meter beach. Post-mortality recruitment was normal and the growth rates for the youngest cohorts were similar to those previously reported. After a two years' lag, the wedge clam *Donax hanleyanus* replaced *M. mactroides* as the dominant species, increasing from 6.0 g/m up to 24.3 g/m. However, dominance replacement did not restore the productivity of the intertidal macrobenthic assemblage and, despite the increment of *D. hanleyanus* stocks, the community total biomass remained < 1% of the pre-mortality levels. Since 1998 on, *M. mactroides* and *D. hanleyanus* showed several peaks in abundance. Disturbance, mainly due to non-regulated fisheries, has been delaying the community recovery. Taking into account the interactions among species and human activities, the present individual resource-based management should be replaced by an integrated system-based management program including both conservation and tourism requirements.

Contents

Introduction	27
Materials and Methods	29
Study area	29
Sampling procedure	29
Data analysis	30
Results	32
Control data (October 1994-March 1995)	30
Effects of the mass mortality event in the study area	31
Post-mortality data (1996-2001)	32
Discussion	32

Pre-mortality structure of the macrobenthic intertidal biota	32
Changes in the community structure after the mass mortality	35
Management implications	36
Acknowledgements	38
References	38

Introduction

The macrobenthic intertidal communities of north-eastern sandy beaches of Argentina show a low number of species and a high biomass, being the surf clam *Mesodesma mactroides* ('yellow clam') the dominant species. The geographical range of this suspension feeder extends from Brazil to Argentina. In this country, it inhabits the Buenos Aires Province northern (170 km) and southern (205 km) sandy shores, avoiding the central area (250 km) between them.

In spring 1995, a mass mortality affected almost all populations of *M. mactroides* of Argentina. The mortality was transmitted southward in a pulse that began in late October and that reached the southern extreme in less than one month. The coastline was covered with yellow clams that suffered a lethargic state, were unable to burrow, and finally, died. Population loss was extremely high. For example, in a 20 km southern resort (Monte Hermoso: 38°59'S; 61°41'W), almost all clams died in about 10 days (11-20 November) and 428 ton (fresh weight with shells) were lost (Fiori and Cazzaniga, 1999).

Though unexpected, this event had been preceded by two previous mass mortality events, affecting the whole geographic range of the species. Between February and March 25, 1993, the yellow clam had been virtually eliminated along 350 km of the southern

Brazilian coast (30 to 33°S) (Odebrecht *et al.*, 1995). In December 11, 1994, similar phenomena had been registered both in a 12 km beach near Hermenegildo (southern Brazil) and in Barra del Chuy (a 22 km beach in northern Uruguay); this time, the estimated losses were about 9 tons (Méndez, 1995). As a result of these serial events, the status of the species changed from being the most important economical resource of the intertidal fauna of the Southwestern Atlantic sandy beaches, to almost extinct ("critically endangered", according with the IUCN 1994 criteria; Fiori and Cazzaniga, 1999).

The causes of these mortalities were discussed by several authors. It is not clear whether any relationship could be found with the 1991-1995 El Niño disappearing - reappearing event. Odebrecht *et al.* (1995) observed that the 1993 mortality occurred simultaneously with the passage of a cold atmospheric front and a bloom of dinoflagellates in the surf zone. They proposed a harmful algal bloom (HAB) as the cause for the mortality observed in Brazil. However, Méndez (1995) did not find evidences of a HAB during the 1994 mortality. Mouse bioassays indicated that diarrhetic but not paralytic shellfish toxins were present at that moment. Water temperature and salinity were normal for the season. Other bivalves seemed to be affected too in uruguayan shores, and since diatoms, dinoflagellates and silicoflagellates were very abundant at that moment, she suggested that the clam siphons could be physically blocked due to the bloom.

During the 1995 mortality, strong southern (polar) winds in 10-11 November contributed to drive the superficial oceanic water to the coast of Buenos Aires Province; however, the mortality pulse had begun two weeks before in the northern extreme. Consequently, meteorological phenomena would not have had a direct incidence. Fiori and Cazzaniga (1999) found no detectable symptoms of diseases. They performed specific analyses for heavy metal contamination, phytotoxins, abnormal phytoplankton composition, and protozoan tissue-parasites; all of them rendering negative. Bastida *et al.* (1996) proposed that a specific viral disease might have been the most probable cause of this event.

The 1995 clam mortality turned out a unique opportunity to perform a before *versus* after mortality comparison in order to study the effects of the dominant species removal under natural, non-controlled

conditions. Testing hypotheses in sandy beaches is very complex due to the inherent difficulties in the experimental manipulation of the mobile infauna in a mobile substrate, and to the three-dimensional structure of the habitat (Branch, 1984; Wilson, 1991). The assessment of the effects of unpredictable natural events like this are, at best, *ad hoc* and only mensurative studies can be performed (Schoeman *et al.*, 2000). This report deals with the changes registered in the macrobenthic intertidal community of the northeastern (36°18'S-36°52'S) beaches of Buenos Aires Province after the mortality of the dominant species. The spatial scale of the analysis was much larger than in any standard manipulative study about species exclusion, the environmental factors were not manipulated and no interference was added. The community changes were studied applying comparable data obtained throughout eight years. Consequently, the results are expected to be realistic and they allow to draw some conclusions in reference to the stability of this type of community.

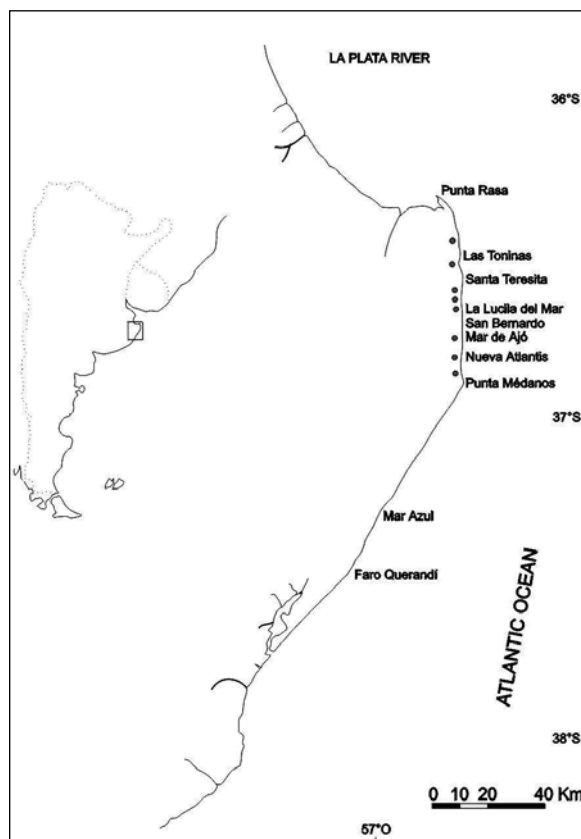


Fig. 1. Study area. The shaded circles indicate the sampling stations.

The present study was originally initiated to investigate variations in density, biomass and recruitment of the two species which were responsible for at least 95% of the community biomass. Thus, additional information on other, less important species was not analysed in great detail here. Noteworthy, this is the first record for the Southwestern Atlantic that provides data on a surf clam status both immediately before and after a mass mortality episode.

Materials and methods

Study area

The study area is located in the northernmost marine coast of Argentina, comprising 5 km south of Punta Rasa (36°18'S, 56°46'W) to 5 km north of Punta Médanos (36°52'S, 56°40'W) (Fig. 1). The stretch is 40-km long, continuous, open, exposed, with no river discharges and geomorphologically homogeneous. The climate is temperate. The mean air temperature is 14.6°C; the annual minimum is -5°C and the annual maximum is 35°C. The sea surface temperatures are 15.5°C (mean), 5°C (annual minimum) and 25.5°C (annual maximum). The net along shore drift is northward (Mazzoni and Spalletti, 1978). The tidal regime is microtidal, semidiurnal with diurnal inequalities. The beach is wide (30-80 m), intermediate to dissipative (*sensu* Wright and Short, 1984; Brown and McLachlan, 1990; Masselink and Short, 1993). Sediments are made up by 97% of fine to medium (0.20-0.26 mm grain size) sand. The beach slope varies from 1° to 2.5°.

Several resorts are located in this sector (Fig. 1). The most urbanized ones are La Lucila del Mar – San Bernardo – Mar de Ajó complex (a continuous urban area originated by the coalescence of three urban centers) and Santa Teresita. *Pinus maritimus*, *Acacia melanoxylon*, *Ulex europaeus*, *Tamarix gallica*, *Eucalyptus* spp. and other shrubs are usually planted for dune fixation, as a precursor-to-urbanization stage. Consequently, non-forested, forested and urban patches alternate with each other along the dune field (Dadon, 1999).

Sampling procedure

Mesodesma mactroides inhabits the subtidal level in winter and migrates to the intertidal zone in early

spring (Coscarón, 1959; Olivier *et al.*, 1971). *Donax hanleyanus* inhabits the intertidal zone and does not migrate seasonally. Both species can be easily sampled in the intertidal zone in October. At that moment, populations are composed mainly of large individuals, and recruitment is still low (Olivier *et al.*, *op. cit.*; Penchaszadeh and Olivier, 1975). In addition, since the tourism season extends from late December to March - April, human disturbance in that month is acceptably low.

In the studied area, the mass mortality occurred along the last week of October 1995, as it was reported by local inhabitants (personal communications) and by some regional newspapers (i. e., Anon., 1995a). Intensive checks were performed between November 6-10 to evaluate the mortality situation. Since stations 2 to 5 used to be the most productive sectors of the area (Dadon *et al.*, 2001), transects were sampled at those stations and extensive, meticulous small-scale searches were carried out along that stretch to assess the immediate effects on the community.

After the mortality, samples were collected once a year in October for 1996-2001 at eight fixed sampling stations (Fig. 1), according to a systematic design. Sampling quadrats (50 × 50 × 50 cm) were spaced 1 m on transects perpendicular to the shoreline, to cover the beach from the base of the dunes down to the low tide level (beach width: 30-100 m, depending to the station). At each sampling station, one to three transects were sampled. The sediment was sieved through a 2-mm mesh and the animals were handpicked and determined. The shell maximum length was measured with a caliper (minimum interval: 1 mm) and the specimens were immediately restored to the sediments.

The only available data obtained immediately before the mass mortality for the entire region located to the south of the La Plata river were provided by a long-term monitoring program performed by the University of Buenos Aires at Stations 2, 6, 7 and 8. The samples were taken in October 1994, January and March 1995, proximate enough to characterize the pre-mortality status for the study area. The data were obtained with the same sampling methodology described above.

Taking into account the pre- and post-mortality analysis, in total 9,482 specimens were determined and measured.

Data analysis

All transects were considered for density and biomass estimations. Density and biomass were referred per running metre beach (ind./m and g/m, respectively).

The biomass of *M. mactroides* and *D. hanleyanus* were estimated using the following functions:

M. mactroides: $W = 0.0174 d^{2.7061}$ (Castaños, 1995)

D. hanleyanus: $W = 0.0189 d^{2.71}$ (J. M. Cruses, unpublished data)

where W is the dry mass of a non-purged individual (mg), and d is the maximum shell length (mm).

The one-way (fixed effects) ANOVA was used for comparisons between years (Sokal and Rohlf, 1995). Normality and homogeneity of variances assumptions were studied with the Lilliefors test, the Shapiro-Wilk's W test (normality) and Bartlett's Chi-square test (homogeneity of variances) with the software STATISTICA (Anon. b, 1995); in all cases, assumptions were not rejected ($\alpha = 0.05$) when using the transformation $x = \log(x+1)$.

Results

Control data (October 1994 - March 1995)

During the pre-mortality period, *Mesodesma mactroides* was the most abundant species. The mean density peaked on January (Fig. 2); the highest density (9474 ind./m) recorded at Station 2. Despite January density maxima, biomass was higher in

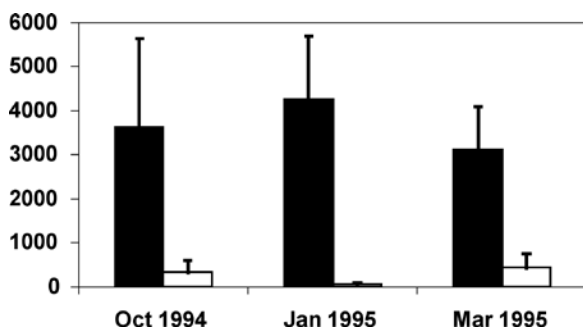


Fig. 2. Mean density (ind./m) of the surf clams *Mesodesma mactroides* (black) and *Donax hanleyanus* (white) during 1994-1995. Standard error is shown.

October (Fig. 3), ranging from 275 to 3600 g/m (mean value: 1399 g/m). Noticeably, most of the specimens were medium (20-40 mm) and large (>40 mm) at that moment, while recruits were scarce (Fig. 4). The mean biomass remained constant in January and it decayed in March due to the loss of large animals during summer.

The size frequency distribution was always polymodal, several cohorts co-occurring through October to March (Fig. 4). The youngest cohort fell in the 30-38 mm interval in October, and in the 41-48 mm interval in March. The mean length increment of this cohort was $2.60 \text{ mm.month}^{-1}$. During the same period, another cohort ranging in the 45-57 mm interval, incremented to the 56-60 mm one, outcoming in a mean length growth of $1.30 \text{ mm.month}^{-1}$. The oldest cohorts showed no clear separation among them.

Recruitment took place in January and March (Fig. 4), showing an heterogeneous spatial pattern. Marked differences were observed among sampling stations, recruits density varying from 138 to 3888 ind./m. Despite these numerical differences, at the end of the summer recruits boomed while large specimens declined.

Donax hanleyanus showed great variability among stations and dates, values varying between 0 and 1158 ind./m (Fig. 2). Biomass was very variable among stations and resulted far lower than that of *M. mactroides*. The general trend was dropping from spring to summer (Fig. 3). The apparent number recovery in March (Fig. 2) corresponded to late estival recruitment (Fig. 4), but it did not replace the lost biomass during summer (Fig. 3).

The following cohorts occurred in the three sampling periods, namely: the 8-17 mm and 21-24 mm

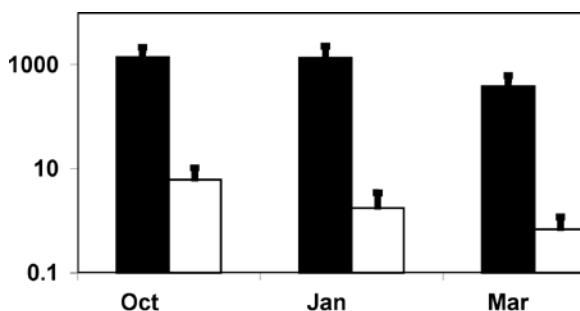


Fig. 3. Mean dry biomass (g/m) of the surf clams *Mesodesma mactroides* (black) and *Donax hanleyanus* (white) during 1994-1995. Standard error is shown.

Table 1. Comparison between pre- and post-mortality mean values. In bold, significant differences (alpha = 0.05).

Mean values	October 1994	November 1995	Lilliefors normality test p		Shapiro normality test p		Bartlett homogeneity test p	ANOVA F	ANOVA p-level
			Oct-94	Nov-95	Oct-94	Nov-95			
<i>M. mactroides</i>									
Recruits density (ind./m)	161	144	> 0.20	> 0.20	< 0.288	--	0.148	0.766	0.431
Non-recruits density (ind./m)	3467	9	> 0.20	> 0.20	< 0.999	--	0.563	22.488	0.009
Total biomass (g/m)	1398.96	2.28	> 0.20	> 0.20	< 0.955	--	0.901	38.093	0.003
<i>D. hanleyanus</i>									
Recruits density (ind./m)	291	309	> 0.20	> 0.20	< 0.753	--	0.519	0.436	0.545
Non-recruits density (ind./m)	42	6	< 0.20	> 0.20	< 0.140	--	0.744	0.180	0.693
Total biomass (g/m)	6.06	5.17	> 0.20	> 0.20	< 0.870	--	0.877	0.030	0.871

intervals in October; the 13-19 mm in January; and the 2-8 mm in March (Fig. 4). The progress of the October cohort could be traced in, with an estimated growth rate of 2.81 mm.month⁻¹.

The recruits were only present in March, density ranging from 0 to 1,430 ind./m (mean: 380 ind./m). Even when the density of recruits was always lower for *D. hanleyanus* than for *M. mactroides*, the ratio recruits/non recruits was higher for the former (oscillating from 7 to 14) than for the latter (0.05-2.8).

Small crustaceans were widespread, mainly the isopod *Excirrolana armata* (= *Cirolana argentina*; V. Ribetti and D. Roccatagliata, pers. comm.). The gastropods *Olivancillaria auricularia* and *Buccina-nops duartei* frequently appeared with a very patchy distribution, the diameter of the patches being less than 10 m. An annelid, identified as *Hemipodus olivieri* by D. Nahabedian, was also common. Isolated individuals of the anomuran decapod *Emerita brasiliensis* were only occasionally found.

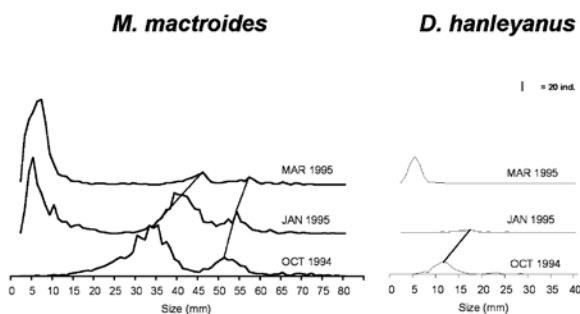


Fig. 4. Length frequency distribution of *Mesodesma mactroides* and *Donax hanleyanus* in 1994 - 1995, before the mass mortality event.

Effects of the mass mortality event in the study area

The intensive checks performed immediately after the mortality event (see Materials and Methods) showed that no remnants of dead *M. mactroides* persisted on the beaches after a week, due to tidal drift and sea birds picking. The surviving yellow clams were scarce. The maximum density of medium and large specimens had fallen from 9,000 ind./m (October 1994) to 18 ind./m. The mean density barely accounted for the 4% of the premortality population. The total biomass also declined abruptly. The mean biomass was hardly 0.16% of the former values (Table 1).

Despite of the sudden extinction of the medium and large animals, recruitment was registered in November 1995. The recruits density showed no significant differences with the observed values with the ones obtained for late October 1994 (Table 1).

Similar analyses were performed for *Donax hanleyanus*. Total biomass, recruit density and non-recruit density were compared between October 1994 and November 1995. They did not show significant differences (Table 1). In addition, no evidence was found that any other mollusk, crustacean, annelid or fish had been affected.

Post-mortality data (1996 - 2001)

Noticeable changes were observed in the structure of the intertidal communities in the post-mortality years. After a decay to 50% in 1996, the frequency of the yellow clam oscillated between 50% and >90% during 1997-2001. The mean density varied between 3 to 140 ind./m (Fig. 5). The mean biomass

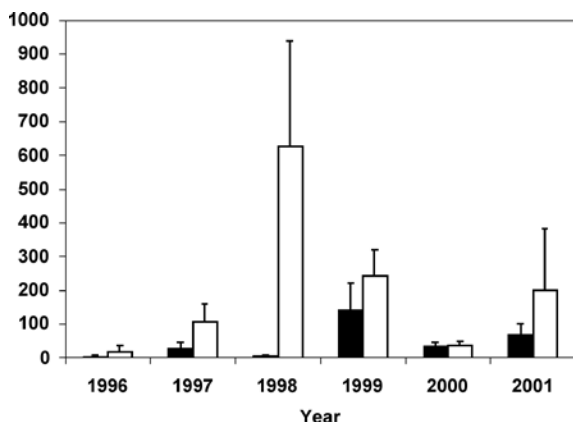


Fig. 5. Mean density (ind./m) of *Mesodesma mactroides* (black) and *Donax hanleyanus* (white) every October (1996-2001). The vertical scale is different from Figure 2. Standard error is shown.

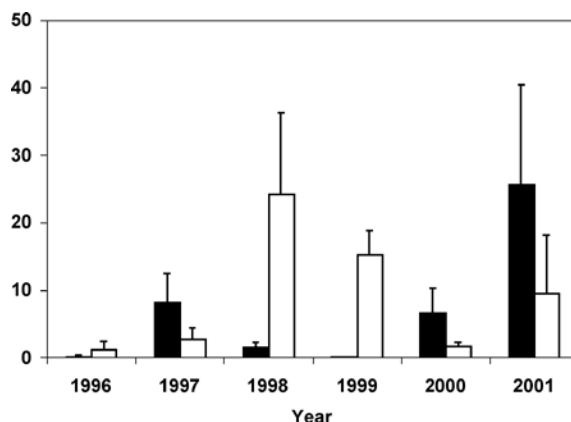


Fig. 6. Mean dry biomass (g/m) of *Mesodesma mactroides* (black) and *Donax hanleyanus* (white) every October (1996-2001). The vertical scale is different from Figure 3. Standard error is shown.

showed less variability, ranging between < 0.1 and 25 g/m (Fig. 6), with a tendency to increase due to the growing numbers of larger specimens in the beds.

The size frequency distribution remained similar among years. Most of the individuals ($> 91\%$) were medium and large; recruits seldom appeared and when so, always in very low density (aprox. 10 ind./m) (Fig. 7). The large specimens were present in 25-50% of the transects, usually in the northern stations (Stations 1-3). An exceptional event was observed in 1999, when the whole population consisted of recruits (Fig. 7), their density peaking (up to 590 ind./m) in Stations 1 to 6. This recruitment accounts for the peak registered in 1999.

The abundance pattern of *D. hanleyanus* gradually changed during 1996-2001. The frequency of this species rose to 75-90%, resulting from 1997 on, in the most abundant stocks recorded for the study area. The average density reached a maximum of 625 ind./m (Fig. 5). High numbers of recruits (up to 2300 ind./m) were found in some stations (Stations 3-6). The mean biomass peaked to 24.3 g/m in 1998 and proceeded to fluctuate (Fig. 6).

Two post-mortality mean biomass maxima were registered in 1998 and 2001 (Fig. 6). The first one corresponded almost exclusively to *Donax*, while the second accounted both for the yellow clam (75%) and the wedge clam (25%).

Discussion

Pre-mortality structure of the macrobenthic intertidal biota

Pre-mortality records in literature of sandy beaches of Argentina (Coscarón, 1959; Olivier *et al.*, 1971; Penchaszadeh and Olivier, 1975; Bastida *et al.*, 1991), documented that intertidal species diversity was low, being *M. mactroides* the dominant species in most of the undisturbed stretches. The yellow clam was highly frequent (97.82%), accounting for the 73.86% of the intertidal macro-infauna numbers (Olivier *et al.*, 1971). Large ($> 5 \text{ km}$) continuous beds covered beaches during the warm season (Coscarón, 1959) and they were an important touristic attraction.

Donax hanleyanus and *Emerita brasiliensis* migrated from Uruguay in the 20th century (Olivier *et al.*, 1971; Penchaszadeh and Olivier, 1975). *E. brasiliensis* was (and it is at present, see Results) a rare species, but *D. hanleyanus* settled quickly and successfully in northeastern beaches of Argentina. The wedge clam was frequent (61% of the samples according to Olivier *et al.*, 1971) and its density was variable, recruits reaching local peaks with $10,000 \text{ ind./m}^2$ (Penchaszadeh and Olivier, 1975). The predators *Olivancillaria auricularia*, *O. uretai* and *Buccinanops duartei* were common (Coscarón, 1959; Olivier *et al.*, 1971) but, according with their trophic

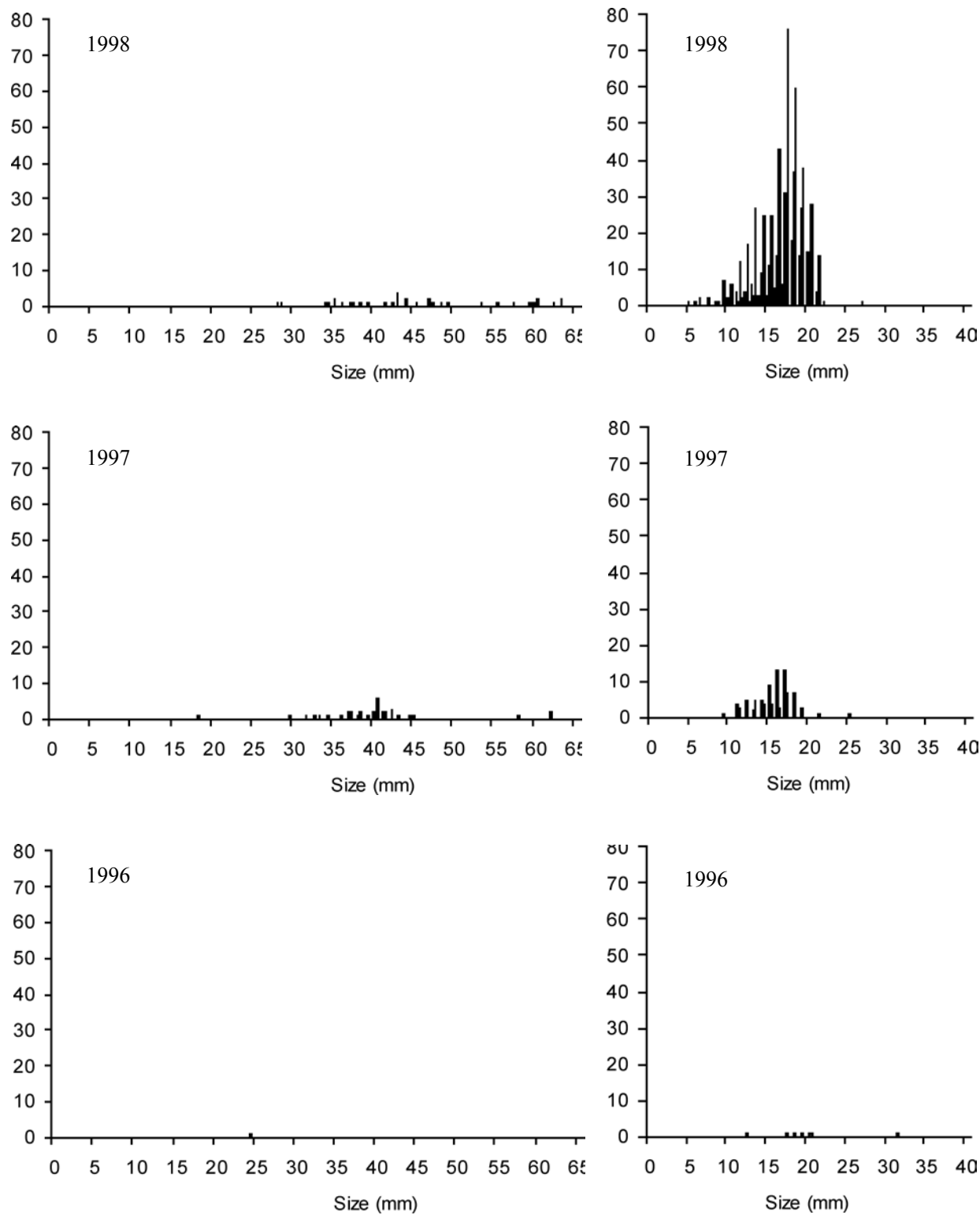


Fig. 7. Size (mm) frequency distributions of *Mesodesma mactroides* and *Donax hanleyanus* every October (1998-1996).

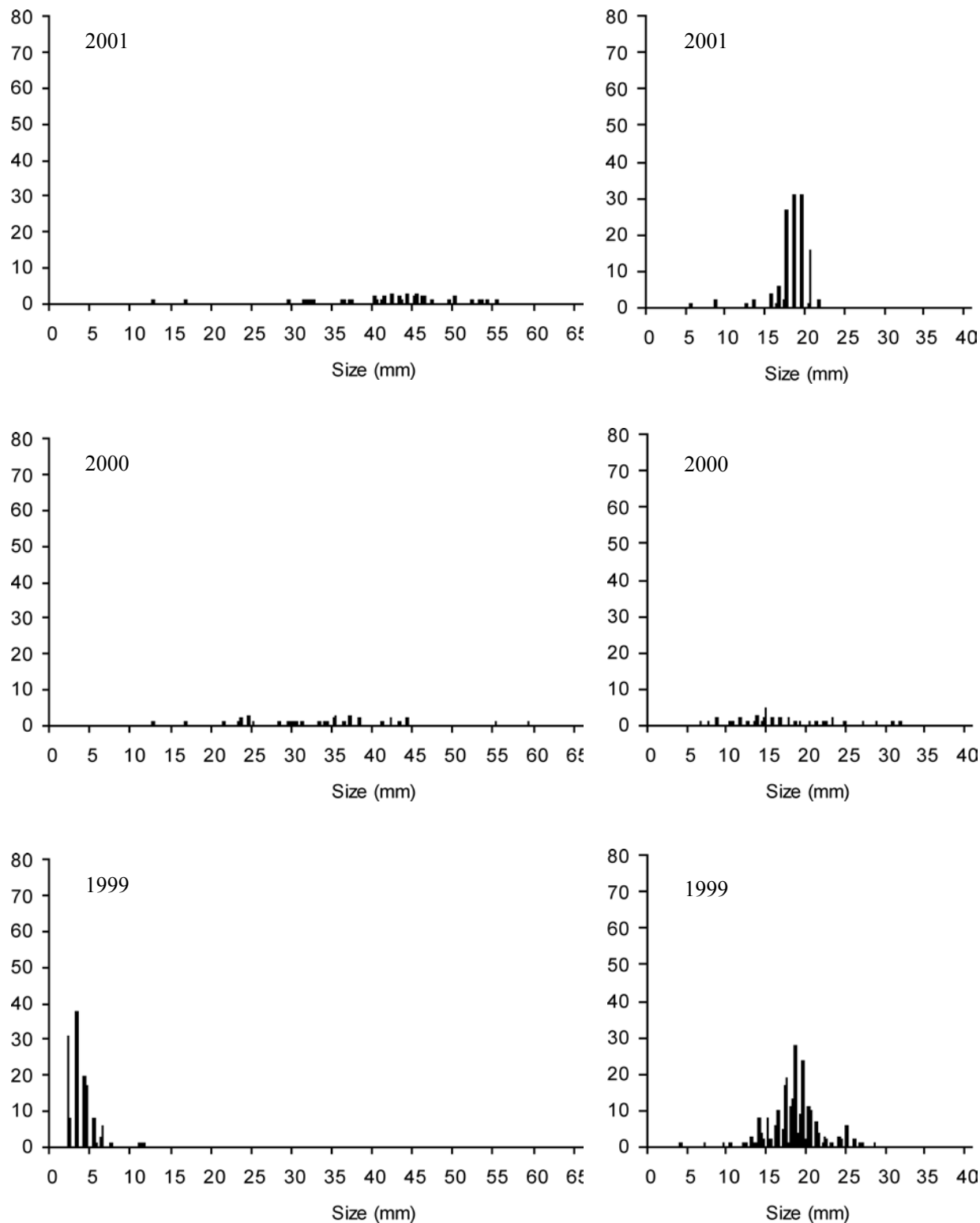


Fig. 7 (contnd.) Size (mm) frequency distributions of *Mesodesma mactroides* and *Donax hanleyanus* every October (2001-1999).

position, they were not abundant (relative density <0.01%; Olivier *et al.*, *op. cit.*).

Our 1994 and 1995 data showed that, under the pre-mortality conditions, the community structure was identical to the previously reported, including the relative frequency and the abundance of macrobenthic species. *M. mactroides* appeared with a frequency close to 99%, and no differences could be detected in the population size distribution when confronting with the data from Olivier *et al.* (1971). The growth rates estimated for the youngest cohort (0.08 mm.day⁻¹) was similar to those informed by Olivier *et al.* (*op. cit.*) for September – October for Mar Azul beach (0.09 mm.day⁻¹). Yet the following cohort grew with a faster rate (0.04 mm.day⁻¹ vs 0.02 mm.day⁻¹).

D. hanleyanus abundance turned out variable and its size frequency distribution resembled those reported by Penchaszadeh and Olivier (1975) for Mar Azul. The estimated growth fell within the expected values, according to literature (0.061 vs 0.056 mm.day⁻¹; *op. cit.*).

Mortality events were recurrent at the intertidal environment of Argentine beaches, usually restricted to the small (local) scale. They were the product of changes in the sedimentary balance after one or even two successive strong storms (Coscarón, 1959; Olivier *et al.*, 1971; Lasta and Zampatti, 1980; Isla *et al.*, 2001). Local mortalities may possibly play an important role in the community dynamics, since the clearance of some areas allows new settling and promotes populations' rejuvenescence. The impact of human activities are likely to provoke similar consequences. Some stretches showed symptoms of human disturbance (i. e., recreative fisheries, heavy trampling in urban resorts) coinciding with local extinctions of *M. mactroides*, particularly in the southern sector (Bastida *et al.*, 1991; Dadon, 1999; Dadon *et al.*, 2001). However, the influence of natural and human disturbance was limited and the regional intertidal macrobenthic assemblage structure had remained without major changes during the last 30 years, up to the 1995 mortality event.

Changes in the community structure after the mass mortality

Mortality broke out in the sampling area in October 1995 and progressed southward in a few days. The

mean density of the beds plunged to 0.2% of the former levels. The reproduction period of the yellow clam is very short (no longer than 20 days) and gamete evacuation occurs normally in September–October (Olivier *et al.*, 1971). The recruitment was normal during summer 1995 and so was the growth of the offspring born that year. Thus, only the benthic stages of *Mesodesma mactroides* must have been affected by the mortality, dying after or during the reproduction period. Meanwhile, *Donax hanleyanus* was not affected (see Effects of the mass mortality event in the study area) and evidence of macrobenthos, fish or mammal mortalities, harmful algae blooms or other related phenomena were not found nor reported in the literature.

The analysis of the size frequency distributions showed that, since 1996 on, the new successive cohorts of the yellow clam grew normally. Even when scarce, large individuals reaching the first maturity stage (42.12–44.25 mm; Olivier *et al.*, 1971) were found every October (see Postmortality data). Most of them vanished in early summer, but many undoubtedly survived long enough to leave a new offspring. In fact, in late summer almost the entire population (> 99%) was composed by recruits (own unpublished data).

The decay of the dominant species was followed by changes in the community structure. After a two-years' lag, *D. hanleyanus* boosted as never before. In summer 1998–1999, the increase of the wedge clam became very evident in all the northeastern beaches, even for the casual observer (own unpublished data). Compared to former values, the mean density and the mean biomass increased to 187% and 430%, respectively. At the same time, changes in the population structure were noticeable (Fig. 5).

Such a boom of the wedge clam after the crash of the yellow clam suggests some kind of interaction between both bivalves. Several authors pointed out that biological interactions might play an important role in the establishment and maintenance of the community structure in sandy beaches. For example, competitive interactions between two intertidal haustoriid amphipods (*Acanthohaustorius millsii* and *Haustorius canadensis*) may account for the changing seasonal zonation patterns of these species (Crocker and Hattfield, 1980). Grain size preferences of the isopods *Excirolana natalensis*, *Pontogeloides latipes* and *Eurydice kensleyi* indicated that their across-shore distribution is governed by biological inter-

actions (Nel, 2001). McLachlan and Jaramillo (1995) reviewed data on at least two species overlapping niches, and they proposed that the co-occurrence of two bivalves (a larger, less mobile species and a smaller, tidally migrating species) may reflect the evolutionary consequences of past competition and available niches. However, they conclude, “there seems little evidence to indicate competitive interactions as being important” (p. 324). McLachlan *et al.* (1996) pointed out that “although competitive interactions have not been demonstrated in exposed sandy beaches, the presence of substantial numbers and biomass of large filter feeders may be expected to affect other species on the beach”. At the same time, some authors assumed that competition in sediments would not be strong because the space is three-dimensional, organisms are mobile, and predation is effective in keeping numbers below the carrying capacity (Peterson, 1979; McLachlan and Jaramillo, 1995; McLachlan *et al.*, 1996). Consequently, even if the competitive interactions were frequent, it would be very difficult to demonstrate their existence.

Interaction between *Mesodesma* and *Donax* had been suggested since early studies. Olivier *et al.* (1971) argued that the trophic niches of the *M. mactroides* and *D. hanleyanus* overlapped and consequently, “a limitation of the food availability may occur for the yellow clam” in a near future (*op. cit.*, p. 22). On Peruvian beaches, Penchaszadeh (1971) and Tarazona *et al.* (1985) found that *Donax peruvianus* and/or *Emerita analoga* formed dominant populations when *Mesodesma donacium* was absent or in low numbers. Arntz *et al.* (1987) described changes in the community structure of Santa Maria beach (Perú) during the exceptionally strong El Niño (EN) event of 1982–83. During normal times, the very dense *M. donacium* populations left few gaps for other macrobenthos, but as a consequence of EN, the populations collapsed. Before EN, *D. peruvianus* showed few year-to-year differences in the population parameters but its density increased coincidentally with the collapse of *M. donacium* and it became the first dominant. The authors concluded that, despite the similar appearance and way of life, *M. donacium* and *D. peruvianus* never seriously competed for the resources at Santa Maria beach. On the contrary, de Alava (1993) and Defeo and de Alava (1995) observed that two density peaks of *D. hanleyanus* coincided with the lowest catches of the exploited *M. mac-*

troides in Barra del Chuy (Uruguay). They suggested that there would be “a dissimilar response to human disturbance, and hence a possible competitive dominance of *M. mactroides* in the colonization of the released space after harvesting”. This mechanism might explain the community changes observed on the northeastern beaches of Argentina after the collapse of the yellow clam.

According to the background and the results obtained between 1996 and 2001, we are able to set a retrospective analysis of the historical data of Argentina. The presence of *D. hanleyanus* had not been mentioned in surveys previous to the sixties (i.e. Coscarón, 1959), though it had been found in fossil layers of the Quaternary (Ihering, 1907; Camacho, 1966). The first registers of living specimens dates from 1962 (Castellano and Fernández, 1965). Olivier *et al.* (1971) documented their quick expansion during the 1960's. At that time, they were concerned that such expansion might generate a decrease in the available food resources for *M. mactroides*, at that moment a protected species due to its overexploitation during the 1950's.

However, the expansion mechanism for *D. hanleyanus* seems to have been different. The wedge clam would have raised concomitant with the overexploitation and disappearance of *M. mactroides*. Human activities and uses (commercial and recreational fisheries, beaches urbanization, sand mining; Dadon *et al.*, 2001) would have originated gaps likely to be colonized by the wedge clam. In fact, the most productive beds of *M. mactroides* during the 1960's (on the coastline south of Punta Médanos; Olivier *et al.*, 1971), were exploited up to their extinction some decades ago. Even when occasionally found on that area, due to transport by coastal drift, recruits of *M. mactroides* did not repopulate the south of Punta Médanos. Moreover, *D. hanleyanus* became the dominant species on that stretch, its abundance being higher than on beaches where it was sympatric with *M. mactroides* (Dadon *et al.*, 2001). Therefore, it is reasonable to assume that overexploitation and human disturbance might have been the main factor for the expansion of *D. hanleyanus* in Argentina.

Management implications

Surf clams are the main touristic and commercial resource of the intertidal zone of the northeastern

sandy beaches of Argentina. Even when other mollusks like *Olivancillaria* and *Buccinanops* are also collected, they occur in low density and the extraction is only opportunistic.

Since 1996, all ontogenetic stages of the yellow clam have been under total protection by law, in order to contribute to the restoration of the beds. Despite this protection, 70% of the large specimens usually disappear from October to December (Dadon *et al.*, 2002), partly due to animal predation, but mostly by furtive extraction.

As mentioned above, evidences indicate that decrease in living stocks of *M. mactroides* favours the expansion of *D. hanleyanus*. Up to now, *D. hanleyanus* did not reach the beaches south of Mar del Plata (38°03'S - 57°33'W), where *M. mactroides* used to be dominant before 1995 (Fiori and Cazzaniga, 1999). However, it would be possible for the wedge clam to extend its geographical range southward, taking advantage of the present drop of the yellow clam, providing the environmental conditions (water quality, temperature, salinity, currents, swash climate,

etc.) were favorable. Since fossils of the wedge clam were recorded for that area (Ihering, 1907; Camacho, 1966), it might be possible for this species to regain its ancient geographic range.

There are, however, factors operating on the opposite direction. The successive changes in the intertidal communities occurred since 1995 have not remained undetected by casual observers. In 1999, *D. hanleyanus* increment became so obvious that its extraction, which up to that moment had only been occasional, turned out into massive exploitation every summer. In fact, the drops in the abundance trend of *D. hanleyanus* after 1999 were consequence of harvesting pressure. Typically, the tourists use to fill up 5 or 8 liter containers with wedge clams (personal observations). At the same time, a commercial fishery has been established and the wedge clam is offered as frozen product in supermarkets (Fig. 8). In contrast to the yellow clam case, the activities of these fisheries have never been regulated.

Human activity may delay or even prevent the restoration of the shallow-water communities of



Fig. 8. Packs of frozen wedge clams (*Donax hanleyanus*) in supermarkets of Buenos Aires city (Argentina).

Argentinian sandy beaches. Our results showed that the yellow clam grew and reproduced normally after 1995. The increment of biomass was related to changes in population structure, i.e., increments in the density of large specimens rather than recruits. Thus, the resource conservation goals should focus on the reproductive specimens more than on the recruitment.

Even when the wedge clam increased its numbers, it did not produce an important recovery in the intertidal community biomass as a whole, since the total surf mollusks biomass never reached the pre-mortality levels. In fact, during the *Donax* peaks, joint biomass barely reached 1.8% of the pre-mortality values.

Human activities are probably one of the main factors interfering with the recovery of the bivalves beds. According with the results previously described, the present legal normative would not warrant the recovery of the community productivity. Regulations should be applied to protect the intertidal system as a whole, instead of protecting each resource individually. Since the yellow clam is considered an emblematic species for local inhabitants and tourists, a conservation plan focused on that resource but preserving the associate assemblage should be conceived with social consensus. If not, the present situation might drift from a system that provides easily accessible protein and that has recreative and commercial value, to a completely unproductive one. As a final recommendation, and taking into account the existence of complex interrelationships among species and human activities, the present individual resources-based management should be replaced by an integrated system-based management including both conservation and tourism requirements.

Acknowledgement

To Drs Wolf E. Arntz, Felicita Scapini and Anton McLachlan for their critical revision of the manuscript and valuable suggestions; to Graciela Chiappini, Mabel Salinas and Adrián Marozzi, for their technical assistance during sampling; to Marina Díaz and Brenda Doti for figures.

References

Alava A de. 1993. Interdependencias ecológicas entre dos bivalvos simpátricos en una playa arenosa de la costa atlántica uruguaya. Mérida: CINVESTAV-IPN. (MSc Thesis).

- Anonimous 1995a.** No a los moluscos bivalvos. *Sucesos de la Costa*, año 8, N° 143 (11/5/1995).
- Anonimous 1995b.** *STATISTICA for Windows*. Tulsa: StatSoft, Inc.
- Arntz WE, Brey T, Tarazona J, Robles A. 1987.** Changes in the structure of a shallow sandy-beach community in Perú during an El Niño event. In: Payne AIL, Guillard JA, Brink KH, eds. *The Benguela and Comparable Ecosystems S. Afr. J. mar Sci.* **5**: 645-658.
- Bastida RA, Roux A, Bremec C, Gerpe M, Sorensen M. 1991.** Estructura poblacional de la almeja amarilla (*Mesodesma mactroides*) durante el verano de 1989, en la provincia de Buenos Aires, Argentina. *Frente Marítimo* **9 A**: 83-92.
- Brown AC, McLachlan A. 1990.** *Ecology of Sandy Shores*. Amsterdam: Elsevier.
- Camacho HH. 1966.** *Paleontografía bonaerense. III. Invertebrados*. La Plata: Comisión de Investigaciones Científicas de la Provincia de Buenos Aires.
- Castaños C. 1995.** Estudio de los factores que determinan la distribución del recurso natural Almeja Amarilla (*Mesodesma mactroides* Desh. 1856). Informe Consejo de Investigaciones Científicas (Provincia de Buenos Aires, Argentina). 29 pp. (unpublished).
- Castellanos ZA de, Fernández D. 1965.** Sobre la presencia de *Donax hanleyanus* en la costa Argentina. *Neotropica* **11(35)**: 58.
- Coscarón S. 1959.** La “almeja amarilla” (*Mesodesma (T.) mactroides* Deshayes) de la costa de la Provincia de Buenos Aires. *AGRO Publ. Téc.* **1(3)**: 1-66.
- Crocker RA, Hatfield EB. 1980.** Space partitioning and interactions in an intertidal sand-burrowing amphipod guild. *Mar. Biol.* **61**: 79-88.
- Dadon JR. 1999.** Gestión de sistemas con baja biodiversidad: Las playas arenosas del Noreste de la Provincia de Buenos Aires. In: Matteucci SD, Solbrig OT, Morello J, Halfpeter G, eds. *Biodiversidad y uso de la tierra. Conceptos y ejemplos de Latinoamérica*. Buenos Aires: EUDEBA, 529-548.
- Dadon JR, Castaños C, Pérez García R, Chiappini MTG, Cruces JM. 2001.** Efectos a largo plazo de las pesquerías de almeja amarilla (*Mesodesma mactroides*) y berberecho (*Donax hanleyanus*), y de la urbanización sobre las comunidades intermareales. In: Alveal K, Antesana T, eds. *Sustentabilidad de la Biodiversidad*. Concepción: University of Concepción, 703-715.
- Dadon, JR, Chiappini GTM and Rodríguez MC. 2002.** Evaluación del Estado de la Almeja Amarilla (*Mesodesma mactroides*) en el Partido de La Costa durante el año 2001. *Tecn. Rep. Univ. Buenos Aires - Municipio de La Costa*. 18 pp.
- Defeo O, Alava A de. 1995.** Effects of human activities on long-term trends in sandy beach populations: the wedge clam *Donax hanleyanus* in Uruguay. *Mar. Ecol. Progr. Ser.* **123**: 73-82.
- Fiori SM, Cazzaniga NJ. 1999.** Mass mortality of the yellow clam, *Mesodesma mactroides* (Bivalvia: Mactracea) in Monte Hermoso beach, Argentina. *Biol. Conserv.* **89**: 305-309.
- Ihering H von. 1907.** Les mollusques fossiles de Tertiaire et du Cretacé Supérieur de l'Argentine. *Anuar. Mus. Nac. Buenos Aires, ser. 2*.

- Mazzoni MM, Spalletti LA. 1978.** Evaluación de los procesos de transporte de arenas litorales bonaerenses a través de análisis texturales y mineralógicos. *Acta Oceanogr. Argent.* **2**: 51-67.
- Masselink G, Short AD. 1993.** The effects of tide range on beach morphodynamics and morphology: a conceptual model. *J. Coast. Res.* **9**(3): 785-800.
- McLachlan A, Jaramillo E. 1995.** Zonation on sandy beaches. *Oceanography and Marine Biology: an Annual Review* (Ansell AD, Gibson RN and Barnes M, eds.) **33**: 305-335, UCL Press.
- McLachlan A, Dugan JE, Defeo O, Ansell AD, Hubbard DM, Jaramillo E, Penchaszadeh P. 1996.** Beach clam fisheries. *Oceanogr. Mar. Biol. ann. rev.* **34**: 163-232.
- Méndez S. 1995.** Bivalve mortality on southwest Atlantic shores. *Harmfull Algae News* **10-11**: 12.
- Nel R. 2001.** Factors affecting faunal communities on sandy beaches: A new insight. In: Beaches – What future? An integrated approach to the ecology and evolution of beaches and sand dunes. In: *Workshop Sandy beaches: What Future?* Abstract Volume. Firenze: Dipartimento di Biologia Animale e Genetica “Leo Pardi”, Università di Firenze – Centro di Studio per la Faunistica ed Ecologia Tropicali del CNR – European Commission: 59-60.
- Odebrecht C, Roig L, García VT, Abreu PC. 1995.** Shellfish mortality and a red tide in southern Brazil. In: Lassus P, ed. *Harmfull Marine Algal Blooms*, New York: Springer-Verlag, 213-218.
- Olivier SR, Capezzani DAA, Carreto JL, Christiansen HE, Moreno VJ, Aizpun de Moreno JE, Penchaszadeh PE. 1971.** Estructura de la comunidad, dinámica de la población y biología de la almeja amarilla (*Mesodesma mactroides* Desh. 1854) en Mar Azul (Pdo. de Gral Madariaga, Bs. As., Argentina). *Inf. Técn. Proy. Des. Pesq. FAO* **27**: 1-90.
- Penchaszadeh PE. 1971.** Observaciones cuantitativas preliminares en playas arenosas de la costa central del Perú con especial referencia a las poblaciones de muy-muy (*Emerita analoga*) (Crustacea, Anomura, Hippidae). *Doc. Inf. Ofic. Cienc. UNESCO Am. Lat., Montevideo* **6**: 1-16.
- Penchaszadeh PE, Olivier SR. 1975.** Ecología de una población de “berberecho” (*Donax hanleyanus*) en Villa Gesell, Argentina. *Malacologia* **15**(1): 133-146.
- Peterson CH. 1979.** Predation, competitive exclusion and diversity in the soft-sediment benthic communities of estuaries and lagoons. In: Livingston RJ, ed. *Ecological processes in coastal and marine systems*. New York: Plenum, 233-264.
- Schoeman DS, McLachlan A, Dugan JE. 2000.** Lessons from a disturbance experiment in the intertidal zone of an exposed sandy beach. *Estuar. Coast. Shelf Sc.* **50** (6): 869-884.
- Sokal RR, Rohlf FJ. 1995.** *Biometry: the principles and practice of statistics in biological research*. New York: Freeman WH and Co.
- Tarazona J, Arntz WE, Canahuire E, Ayala Z, Robles A. 1985.** Modificaciones producidas durante “El Niño” en la infauna bentónica de áreas someras del ecosistema de afloramiento peruano. In: Arntz WE, Landa A, Tarazona J, eds. “*El Niño*”, su Impacto en la Fauna Marina. Boln. Inst. Mar. Perú – Callao, Spec. Issue (Proceedings of the Ninth Latin American Congress of Zoology, Arequipa, Perú, October 1983): 55-63.
- Wilson WH. 1991.** Competition and predation in marine soft-sediment communities. *Ann. Rev. Ecol. Systematics* **21**: 221-241.
- Wright LD, Short AD. 1984.** Morphodynamics variability of surf zones and beaches: a synthesis. *Mar. Geol.* **96**: 93-118.

Received: 5 September 2002

Accepted: 2 May 2005

