Experimental management of an exploited sandy beach bivalve population

Manejo experimental de un bivalvo explotado en playas arenosas

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ABSTRACT

Variation in physical factors is considered the primary organizational force regulating macrobenthic populations and communities of exposed sandy beaches. However, there has been no quantitative evaluation of the intensity of human predation on the macrofauna inhabiting these systems, and information on biological interactions is also lacking. In the present study I review the results of a long-term monitoring study on the yellow clam *Mesodesma mactroides* (Deshayes, 1854) (Bivalvia: Mesodesmatidae) of an Uruguayan exposed sandy beach, including the effect of a human exclusion experiment as a way to acquire knowledge about its population structure and dynamics. Experimental management was based on the closure of the fishery for 32 months, in which a great part of the artisanal fishery community and the coastal marine authorities were involved in control operations. The experiment was a useful approach to testing the effect of fishing disturbing or altering the yellow clam population: the wide range of fishing effort levels through time allowed the detection of some patterns and processes that until the closure were unknown, namely: (1) the stock recruitment-relationship showed overcompensation, *i.e.* the inhibition of recruitment at highest adult densities; (2) growth rates of the newly settled cohorts were inversely correlated with the corresponding average adult density; (3) post-settlement natural mortality was highest in the densest cohorts, and was also a function of fishing activity; (4) the amount of fishing effort exerted over *Mesodesma mactroides* explained variations in abundance of the sympatric population of the wedge clam *Donax hanleyanus* Philippi, 1845 (Bivalvia: Donacidae). It is concluded that experimental management is a powerful approach to identify factors governing the dynamics of exploited sandy beach populations, to acquire the basic biological knowledge needed to perform adequate management strategies and to quantify the effect of harvesting on other components of the macrofauna. It is also stressed that further research in sandy beach populations should include human activities as important factors affecting long-term trends.

Key words: *Mesodesma mactroides*, population dynamics, fishing, long-term.

RESUMEN

Las playas de arena expuestas constituyen ambientes marinos rigurosos, en los cuales variaciones en los factores físicos son considerados como reguladores de la abundancia de poblaciones y comunidades macrobentónicas. Sin embargo, no existe una evaluación cuantitativa de la intensidad del impacto humano (pesca) en la macrofauna que habita esos sistemas, y la información referida a interacciones biológicas es fragmentaria o inexistente. En este trabajo presento una revisión de los resultados sobre un estudio de largo plazo de la almeja amarilla *Mesodesma mactroides* (Deshayes, 1854) (Bivalvia: Mesodesmatidae) de la costa atlántica uruguaya, incluyendo el efecto de un experimento de exclusión humana (clausura de la pesquería) como una alternativa para adquirir conocimientos básicos sobre la dinámica de la población. El manejo experimental estuvo basado en la clausura de la pesquería por 32 meses, en los cuales la autoridad marítima y la comunidad pesquera artesanal participaron en el control de la medida. El experimento fue una poderosa herramienta para evaluar el efecto de la pesca como agente de disturbio de la población de almeja amarilla: los contrastantes niveles de esfuerzo pesquero (incluyendo la ausencia de explotación) permitieron la detección de algunos patrones y procesos que antes de la clausura de la pesquería no eran conocidos, tales como: (1) la relación stock-reclutamiento fue sobrecompensatoria, mostrando la inhibición del reclutamiento ante altas densidades de adultos; (2) las tasas de crecimiento de los individuos menores a un año estuvieron relacionadas en forma inversa con la densidad de adultos; (3) la mortalidad natural de los individuos menores a un año fue denso-dependiente de la potencia del reclutamiento, aumentando también con la actividad pesquera; (4) se encontró una correlación negativa altamente significativa entre la intensidad de pesca ejercida sobre *Mesodesma mactroides* y la abundancia del bivalvo simpátrico *Donax hanleyanus* Philippi, 1845. Se concluye que el manejo experimental es una herramienta poderosa para identificar los factores que gobiernan la dinámica de poblaciones explotadas de playas de arena. Se remarca la necesidad de que futuras investigaciones en el tópico incluyan al hombre como un factor clave en la explicación de las fluctuaciones poblacionales a largo plazo.

Palabras clave: *Mesodesma mactroides*, dinámica poblacional, pesca, largo plazo.

INTRODUCTION

Exposed sandy beaches are amongst the harshest marine environments on earth, in which variation in physical factors is considered the primary organizational force regulating macrobenthic populations and communities (McLachlan, 1988). Sandy beaches have been likened to "marine deserts" (McLachlan, 1983), in which distribution and abundance of fauna can be fully explained in terms of wave climate, sand particle size, and tide range (McLachlan et al., 1993). However, there has been no quantitative evaluation of the intensity of human predation on the macrofauna inhabiting these systems, as it has been demonstrated for rocky shores (see e.g., Castilla & Durán 1985; Oliva & Castilla 1986). In this context, experimental manipulation of populations in the field has been recommended as one of the most useful steps needed to understand population and community dynamics of exploited invertebrates (Jamieson & Caddy, 1986, Cobb & Caddy, 1989, Castilla, 1990, Defeo et al., 1993).

One the few examples is based on the yellow clam *Mesodesma mactroides* on the Atlantic coast of Uruguay. Here, this bivalve is exploited along 22 km of exposed sandy beach, where 50 to 150 fishers work, collecting clams by means of shovels. The total annual production varied from 62 tons in 1981 to a peak of 219 tons in 1985. Until 1983, the yellow clam fishery was open access, and after the peak in 1985, catch rates decreased rapidly (Defeo, 1987, 1989). Many unknowns concerning the biology, population dynamics and ecology of the yellow clam precluded the possibility of instigating scientifically based management practices. Nonetheless, an attempt to protect a part of the stock was made by prohibiting clam digging along the 22 km sandy beach for 32 months from April 1987 to November 1989. This was treated as a human exclusion experiment, directed to observe the response of the stock under a non-exploitation regime and to improve the knowledge of the population dynamics of the species. It is also important to point out that little is known about other components of the macroinfauna in this sandy beach. Among these, the wedge clam,

Donax hanleyanus, is of particular interest because it is also a potentially exploitable bivalve and it shares virtually the same habitat as the yellow clam.

The present paper presents an overview of the results of an eight-year study of the population structure of *Mesodesma mactroides*, including the effects of the human exclusion experiment. In addition, the effects of *Mesodesma mactroides* fishery on the temporal and spatial variability of the wedge clam are analyzed to determine impacts of harvesting on the macrofauna associated with the yellow clam.

MATERIAL AND METHODS

The study was conducted between 1983 and 1990 on 22 km of continuous sandy beach on the east coast of Uruguay, between Barra del Chuy (33° 40' S, 53° 29' W) and La Coronilla (33° 50' S, 53° 27' W). This is a dissipative, exposed beach with gentle seaward slopes and fine to very fine well-sorted sands (de Alava & Defeo, 1991). Although maximum tidal amplitude is less than 50 cm, onshore winds can cause dramatic and extensive modifications to the beach. This coast has the highest values in species richness and diversity in macrofauna among Uruguayan sandy beaches (Defeo et al., 1992a). The beach/surf community is biomass-dominated by the larger yellow clam, and the wedge clam is competitively subdominant (Defeo et al., 1992a).

Samples were obtained at least every three months. A permanent transect was set up at each of the 22 km of sandy beach sampled, perpendicular to the shore; sample stations were located every 4 m, from the base of the sand dunes, until two successive samples were recorded without clams. Each sample was taken with a cylinder of diameter 28.2 cm and 40 cm deep; some 200 sample stations were analized during each sample period. Each sample was sieved separately through a 0.5 mm mesh, and all individuals for both species retained in each quadrat were measured (maximum valve length) and counted. In the case of yellow clams, new recruits were defined as those individuals which were 1 to 10 mm length (Defeo, 1993),

and in the case of wedge clams this size class ranged from 1 to 5 mm (de Alava, 1993). Minimum lengths for adults were 43 mm in the yellow clam, and 15 mm in the wedge clam (Masello & Defeo, 1986; Penchaszadeh & Olivier, 1975). The stock-recruitment relationship in *Mesodesma mactroides* was modelled by employing the mean density estimates of parent stock from December to March and those of recruits generated from February to May; however, in 1989 peak numbers of recruits were recorded in August. Additional information for the year 1982 was obtained from Defeo (1985; unpublished). The full range of sizes for both species (1 to 76 mm for yellow clam and 1 to 33 mm for the wedge clam) was recorded for all sample periods. A total of more than 150,000 specimens of both species were measured over the entire study.

I analyzed the length frequency distributions of each of the eight *Mesodesma mactroides* cohorts (= year class in this work) 1983-1990 through their first year of life. For this end, a mean cohort length for each sample i was calculated. The mean length per transect (L_r) of the young-of-the-year was calculated by weighing each mean length (l) per quadrat i pertaining to transect r (l_{ir}) with respect to the observed density (ind • m^{-2}: d_{ir}):

$$L_r = \frac{\sum_i l_{ir} d_{ir}}{\sum_i d_{ir}}$$

Monthly progression of mean lengths was calculated for each cohort for each of the 22 transects; an overall mean length per month for the entire beach was calculated as a simple average of the mean lengths per transect and was used to represent the overall mean size of each cohort for each sample period. Finite average daily size increments (expressed in mm/day) for the young-of-the-year, were calculated from differences between mean cohort lengths between consecutive sampling dates, for which the number of clams in both samples was greater than 50. Seven years' data, from 1983 through 1989, were analized; the cohort recruited in

1990 was excluded because it was not possible to follow it over a complete yearly cycle. It must be clarified that both species have fast growth rates and a life span of about three years. The curvature parameter (K) of the von Bertalanffy growth equation varies from 0.6 to 0.9 • yr^{-1} for the yellow clam, with the growth index ϕ' varying from 3.67 to 3.75 (Defeo et al., 1992a, 1992b). In the case of *Donax hanleyanus*, K is close to 0.8 • yr^{-1}. The rapid growth rates of both species enabled an easy separation of recruits and adults. Further details on the biology, ecology and population dynamics of both species are given in Defeo (1993) and de Alava (1993).

Natural mortality (M) was estimated for the unexploited portion of the yellow clam population, *i.e.* from 1 to 50 mm, the latter being the minimum size commercially exploited, when the fishery was open (from 1983 to 1987) and from the entire population when the fishery was closed. Estimations of M were made by regressing the natural logarithm of the number of individuals per stripe transect (IST) against mean estimated age. For this end, weighed mean lengths were converted to age utilizing the growth parameters from the von Bertalanffy growth model estimated by Defeo (1990) and Defeo et al. (1992b).

IST estimates were done by averaging the q densities (ind • m^{-2}) recorded in the n quadrats sampled in transect r (q_{ir}) and multiplying by the corresponding width of the clam bed in each transect (w_r):

$$IST_r = \frac{\sum_i q_{ir}}{n_{ir}} \, w_r$$

IST is expressed as ind • m^{-1} and is employed in order to avoid problems of interpretation that occur as a result of using these averages after beach profiles have been impacted during either rough or calm conditions different from those which occurred during the sample period; these differences in environmental conditions can result in dramatic changes in distributions and densities of the sandy beach organisms (McLachlan, 1983).

The *Mesodesma mactroides* catch of each and every fisherman was checked daily by the coastal fisheries officer, and monthly catch data were available from 1983. In the same way, daily estimates of effective fishing effort (man-hours/day) and catches per fishermen were recorded from 1984 to 1987 and from 1990 onwards. Information was available in each of the four fishing grounds identified to perform a spatial analysis of the resource and the fishery (see Defeo, 1993 and de Alava, 1993 for details on the spatial analysis of both the yellow clam and the wedge clam and correlated fishery variables).

RESULTS

The human exclusion experiment was very useful in detecting some population patterns and processes that, until the closure of the fishery, were unknown. They can be summarized as follows:

The yellow clam Mesodesma mactroides

A great capacity of population recovery following human perturbation (fishing pressure) was observed from 1988 on, as a result of natural restocking of depleted areas (Fig. 1a). The adult population recovered to nearly twice its exploited level within a year of closure of the fishery (Fig. 1a). The average density of adults per sample period showed the lowest value in 1987, just before the fishery was closed (mean ± SE: 21 ± 3 ind • m^{-2}), and the highest in 1990 (232 ± 18 ind • m^{-2}). In 1985, when the adult population was at an intermediate level, just before it plummeted to its lowest, recruit density was highest (769 ± 96 ind • m^{-2}). The density of recruits was lowest in 1986 (118 ± 19 ind • m^{-2}), and reached also very low values in 1989 (151 ± 25 ind • m^{-2}), during the third year of the closure of the fishery (Fig. 1a).

The stock-recruitment curve (Fig. 1b), generated by plotting spawning stock densities against the resulting densities of recruits, was well described by the Ricker model (Ricker, 1975) of the form:

$$R = aSe^{(-bS)} + \varepsilon$$

where R is the density of recruits, S is the density of the spawning stock, a (nonlinear estimate = 16.91 ± 4.00) is the density-independent parameter related to the fecundity of the stock, b (0.012 ± 0.002) is the stock-dependent mortality parameter which describes how the numbers of recruits-per-spawner decrease with increasing adult abundance; and ε is the error term. Both the nonlinear and linearized versions of the model, as well as all their parameters, were highly significant at the 1% level (Defeo, 1993). The yellow clam population showed evidence of stock-dependent recruitment, that is, the lowest density of recruits occurred with the highest adult densities, at the beginning of the third year of the closed season (1989),
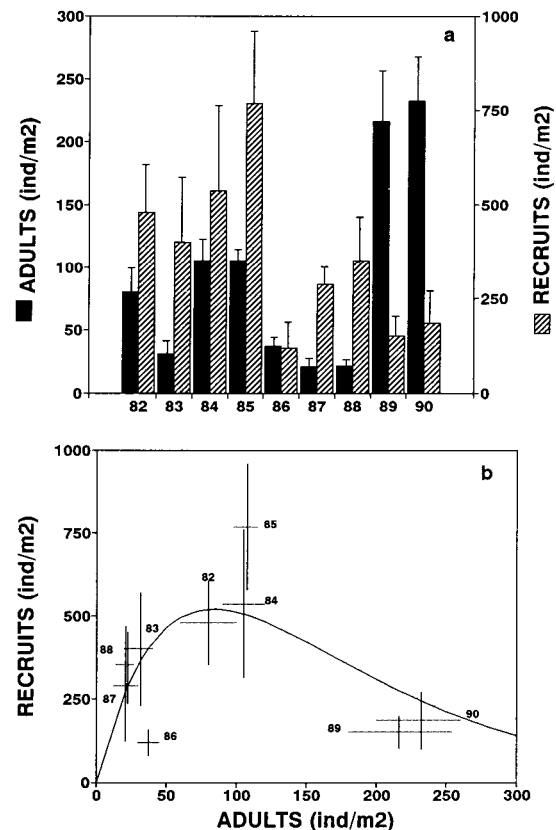

Fig. 1: M. mactroides. (a) Mean density ± 95% c.i. of recruits and spawning stock, from 1982 to 1990. (b) "Ricker recruitment curve" generated by mean density (± 95% c.i.) of recruits (vertical lines) and adults (horizontal lines).

M. mactroides. (a) Densidad media ± 95% i.c. de reclutas y stock desovante entre 1982 y 1990. (b) Curva de reclutamiento "tipo Ricker" generada en base a densidades medias (± 95% i.c.) de reclutas (líneas verticales) y adultos (líneas horizontales).

whereas maximum recruit densities occurred with moderately low and medium densities of adult stock (Fig. 1b).

At a "quadrat scale", highest densities of recruits were never coincident with highest densities of older clams. Maximum densities of recruits per sample core were observed during 1984 and 1985, when they reached between 4000 and 5000 ind • m^{-2}; during the same period, maximum adult densities were between 400 and 600 ind • m^{-2} but not in the same samples where the maximum recruit densities were recorded. These values of adult density, which correspond to the period of active fishery, were far below the maxima recorded after the fishery had been closed; in 1989 they reached 800-900 ind • m^{-2}. It is notable that when adult densities were at least 300 ind • m^{-2}, recruitment was almost absent in the same sample. The negative relation between recruit and adult densities for all years combined is shown in Fig. 2. An arbitrary line, which defines the upper limits of the relationship, represents maximum adult densities for varying levels of maximum recruitment; below the line, the lower values represent a wide range of suboptimal environmental conditions (Maller, 1990). The arbitrary limit, linear in this case, mainly reflected higher densities of recruits during the years 1984-1985, and those of adults inhibiting recruitment during the experiment, i.e. in 1989 (Fig. 2).

Growth rates of young-of-the-year were inversely correlated to average adult density per sample period: finite growth rates were negatively correlated (r = -0.81; p < 0.027) with the corresponding average adult density per year. Mean monthly lengths increased fastest in 1988, 1984 and 1983, while minimum average monthly growth rates were observed in 1989 (Fig. 3). The 1989 cohort virtually dissapeared by May 1990, and it was impossible to follow it during subsequent months.

The "constant *M*-axiom" (*sensu* Caddy, 1991) was rejected for the yellow clam population. This bivalve presented marked variability in *M* for the eight cohorts studied: the minimum value was obtained for the 1990 cohort (mean ± SE: 0.90 ± 0.50 • yr^{-1}), and the highest mortality for the densest 1985 cohort (3.17 ± 0.34 • yr^{-1}) (Fig. 4a). Depress-
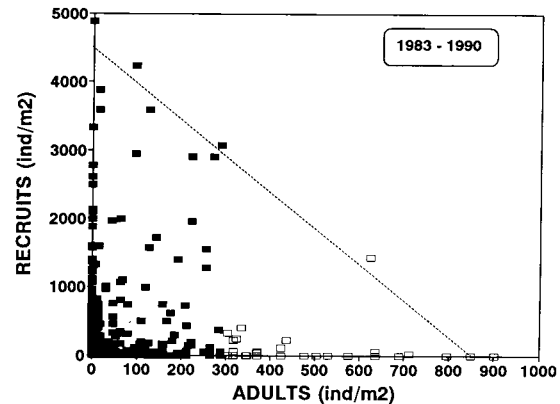

Fig. 2: Scatter diagram of recruit density plotted against adult density in each quadrat, for the months when recruitment peaked: see the difference between recruitment densities observed during (■) 1983-1988 under low adult densities, and (□) 1989-1990, as a result of the experiment. The dotted line defines the upper limits of the relationship between stock and recruitment, and represents maximum adult densities for varying levels of maximum recruitment (see text for details).

Diagrama de dispersión de densidades de reclutas y adultos estimadas para cada cuadrante para los meses en los cuales se observó el máximo reclutamiento (período 1983-1990): obsérvese la diferencia entre las densidades de reclutas observadas durante (■) 1983-1988 ante bajas densidades de adultos, y (□) 1989-1990, como resultado del experimento. La línea punteada define el límite superior de la relación entre stock y reclutamiento, y representa a las máximas densidades de adultos para niveles variables de máximo reclutamiento (ver texto para más detalles).
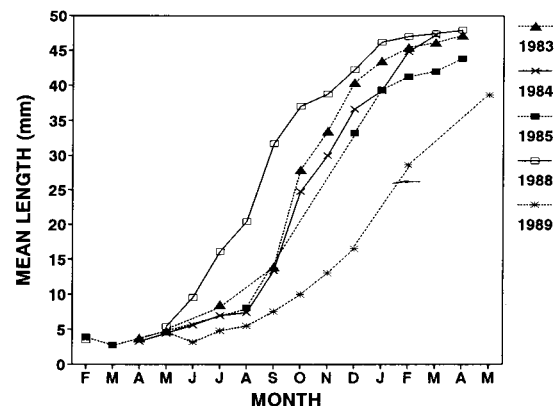

Fig. 3: *M. mactroides.* Monthly progression of mean lengths discriminated by cohort (1983, 1984, 1985, 1988 and 1989).

M. mactroides. Progresión mensual de longitudes medias discriminadas por cohorte (1983, 1984, 1985, 1988 y 1989).

ed growth and increased mortality in the 1985 cohort can be considered as a proximal effect of density-dependent starvation (Fig.

4b). Both figures were not statistically significant, but reflect a trend that must be confirmed in future work.

Temporal and spatial variations in natural mortality of the young-of-the-year were highest during years of heavy intensity of fishing. In fact, the highest M value for the 1985 cohort occurred when catches peaked, whereas the lowest M was obtained when the fishery was closed (*i.e.* for the 1989 cohort). As a result of these trends, M was positively correlated ($r = 0.77$; $p < 0.006$) with both the fishing effort (number of annual trips) and the amount of catches ($r = 0.74$; $p < 0.01$) observed per fishing ground (see Defeo, 1993 and de Alava, 1993 for details).
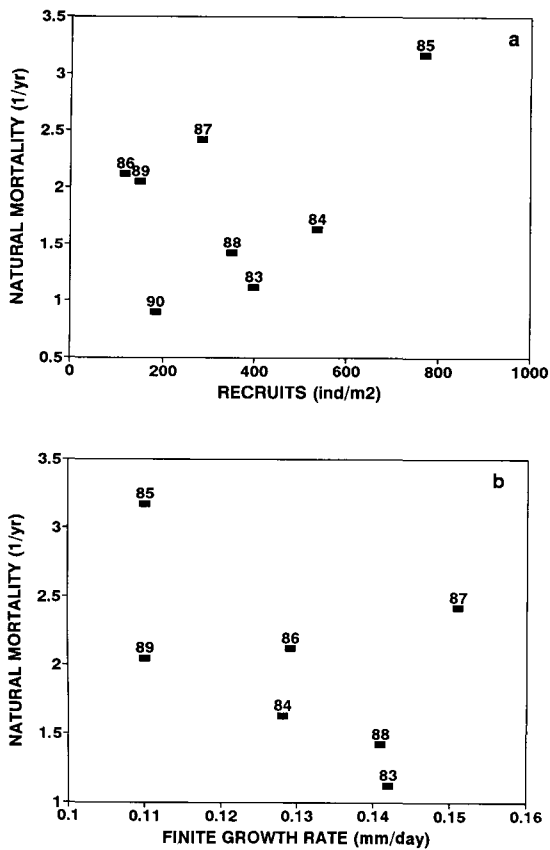

Fig. 4: Relationship between annual estimates of M for the young-of-the-year and: (a) the mean density of recruits during recruitment period; (b) finite growth rates.

Relación entre estimaciones anuales de M para individuos menores a un año con respecto a: (a) la densidad media de reclutas durante el período de reclutamiento: (b) tasas de crecimiento finitas.

The wedge clam Donax hanleyanus

The potential effects of *Mesodesma mactroides* harvesting on the sympatric and unharvested *Donax hanleyanus* population, were analyzed in both time and space over the same eight-year period during which the yellow clam was studied (see de Alava, 1993; Defeo & de Alava, 1995). The average annual density of *Donax hanleyanus* showed a clear increase over the study period, from 73 ± 14 in 1983 to 178 ± 15 ind • m^{-2} in 1990. During the three years immediately before the yellow clam fishery was closed, the lowest density values were recorded, with the lowest value at 19 ind • m^{-2} in 1984 (Fig. 5a). Immediately after the closure of the *Mesodesma mactroides* fishery at the beginning of 1987, the wedge clam population rose dramatically. The highest densities of *Donax hanleyanus* occurred in 1990, months after the reopening of the fishery, the peaks during the exploited period (1983, first three months of 1987) being negatively correlated with *Mesodesma mactroides* catches and fishing effort (see below).

When the study area was closed to yellow clam fishing, an immediate increase in recruitment of wedge clams resulted in a rapid increase in its population growth, with adult densities far above what had been recorded during yellow clam exploitation. There was a strong inverse relation between the mean density of wedge clam recruits and the catch of yellow clams ($r = -0.82$; $p < 0.01$) (Fig. 5b). This was best described by a monotonic decreasing exponential function of the form $R_y = 173e^{-0.021*Cy}$, where R_y is the recruitment density during recruitment time in year y and C_y is the observed *Mesodesma mactroides* catch (Defeo & de Alava, 1995). A similar inverse exponential relationship was found between mean annual density of juvenile plus adult wedge clams (A_y) and the total annual catch of yellow clams (C_y): $A_y = 107e^{-0.007*Cy}$; $r = -0.75$; $p < 0.03$) (Defeo & de Alava, 1995).

DISCUSSION

The long-term study of both yellow clam and wedge clam populations described herein

constitutes one of the first examples in the literature that illustrates the effects of human fishing activities on intertidal, sandy beach populations. The closing of the fishery, creating a de facto human exclusion experiment, showed the important consequences the exploitation activities can have from an ecological point of view. The experimental manipulation of the fishery led to important changes in the overall abundance of both harvested and unharvested bivalves, as well as in the kinds of processes regulating the

Fig. 5: (a) Annual mean density (± D.E.) of the whole population of Donax hanleyanus for the eight years of study. The closed season of Mesodesma mactroides fishery (April 1987 - November 1989), is highlighted. (b) Exponential decay function between recruitment density of Donax hanleyanus and Mesodesma mactroides catches, estimated during recruitment time.

(a) Densidad media anual (± D.E.) para la población de Donax hanleyanus durante los ocho años de estudio. Se remarca el período abril 1987 - noviembre 1989, durante el cual la pesquería de Mesodesma mactroides fue clausurada. (b) Función exponencial decreciente entre el reclutamiento de Donax hanleyanus y la captura de Mesodesma mactroides durante el período de reclutamiento.

dynamics of these exposed sandy beach populations.

Temporal analysis of the yellow clam resource, under regimes of exploitation and non-exploitation, confirmed the existence of density-dependent processes affecting recruitment, growth and natural mortality. A significant overcompensatory relationship between spawning stock and recruitment density was modelled for the first time in an exposed sandy beach population, with two unequivocal trends: 1) high adult densities resulted in extremely low rates of recruitment; 2) moderately low and medium densities of spawning stock resulted in maximum recruitment (see also Defeo, this volume).

The response of the yellow clam population in reaching high density, possibly an upper threshold in the absence of fishing pressure, highlighted the importance of density-dependent factors on mortality and growth. Good growth years for young-of-the-year coincided with years of low adult density, indicating density-dependence. Good growth years were also good recruitment years, but only when adult densities were below 90-110 ind/m^2, which is proposed as a threshold for the overcompensatory mechanism to occur. The strength of a newly settled cohort was inhibited not only by an overcompensatory mechanism in the SRR, but also by density-dependence in growth rate. Depression of recruitment and growth rates under conditions of high adult density showed repercussions in subsequent recruitment events produced by these affected cohorts. For example, the 1985 and 1989 cohorts produced relatively small densities of recruits, and in the case of the latter, delayed recruitment.

The actual density dependent mechanisms affecting growth in M. mactroides are unknown. The majority of the investigations dealing with suspension feeders have attributed this phenomenon to intraspecific competition for either food and/or space (Peterson, 1982; Hall, 1983; Fréchette & Bourget, 1985; Orensanz, 1986; Peterson & Black, 1987; 1988; Peterson & Beal, 1989), but the evidence is only fragmentary. The marked differences in growth rates for dense, newly settled cohorts in the presence of the highest adult densities, suggests that con-
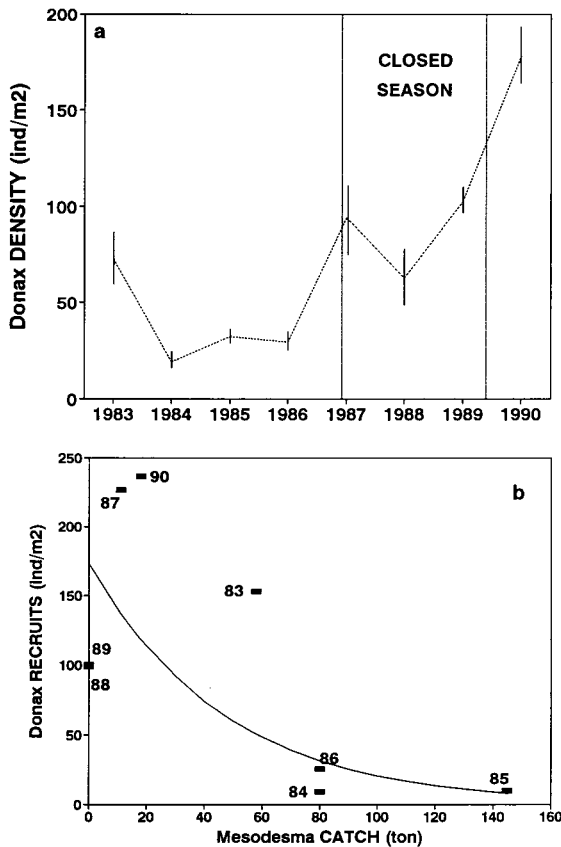
ditions of resource depletion and density-dependent growth are met preferably when dense beds of adults occur, limiting food availability for recruits (Orensanz, 1986).

Estimated M varied between cohorts of yellow clams, and was correlated with biotic and abiotic factors (Defeo, 1993). Mortality of the young-of-the-year was highest in the densest cohorts, coincidently those with the lowest growth rates, intermediate adult densities and in conditions of intense fishing activity (*e.g.* cohort 1985). Depressed growth and increased mortality in the 1985 cohort, which also produced maximum recruitment at intermediate stock levels, can be considered as a proximate effect of density-dependent starvation. Inter-annual variations in M-at-age, in this case the young-of-the-year, has not been previously documented in the literature on sandy beach populations.

Mortality of young-of-the-year was also correlated with intense fishing activity. The strong positive relationship between M and annual catch, or fishing intensity, suggests the effects of physical stress and incidental mortality due to handgathering techniques. Suffocation (Peterson, 1985; Peterson & Black, 1988), perturbation of sediment texture, prolonged exposure to air following harvest, and the hindering of filtering activities by clogging of the ctenidia and palps, might be causes of incidental mortality resulting from harvesting activities. A decrease in the bearing capacity of reworked sediment may also pose particular problems for suspension feeders, such as the yellow clam, because they may lose contact with their food supply in the overlying water, or be exposed to desiccation. These kinds of disturbances may be anthropogenic, but they could also be caused by natural disturbances such as the perturbation of the sea bed through high winds and wave action (Probert, 1984).

Temporal fluctuations in the abundance of the sympatric bivalve *Donax hanleyanus* could also be explained by differences in harvesting activities, with consequent incidental mortality or damage, as well as physical stress produced by sediment disturbance, which could make the substratum unsuitable for settlement. The significant correlations between wedge clam abundance and fishing effort are a first step in identifying potential effects of harvesting and perturbation of sediment structure and effects on long-term patterns of recruitment in sandy beach populations (see also Defeo & de Alava, 1995). Because these conclusions are based on correlations, true cause and effect relationshipss need to be tested by direct quantification of incidental damage and the effects of substrate perturbation.

From a management point of view, three years of exclusion of humans, the top predator, resulted in a rapid recovery of the yellow clam population to levels above those recorded during exploitation, but this was accompanied by a dramatic reduction in *Mesodesma mactroides* recruitment, demonstrating that a relatively long closed season (three years is nearly the entire life span of the species) could have negative consequences for the resource and the fishery. Adequate levels of exploitation will prevent monopoly of resources by adults, and will allow an increase in settlement/recruitment of the population, which will tend to maximize the benefits derived from the yellow clam fishery.

As in species inhabiting rocky intertidal shores, in which the long term effects of intensive fishing pressure have been well documented (Castilla & Durán, 1985, Oliva & Castilla, 1986), the present study shows that humans may play a critical role in determining the magnitude of fluctuations of sandy beach populations, not only for species subjected to exploitation but also for other species within the community. Hence, research on sandy beach populations should include human activities as key factors in regulating long-term fluctuations.

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