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HISTORICAL LANDINGS AND MANAGEMENT OPTIONS FOR THE GENUS *MESODESMA* IN COASTS OF SOUTH AMERICA

DESEMBARQUES HISTORICOS Y OPCIONES DE MANEJO PARA EL GENERO MESODESMA EN COSTAS SUDAMERICANAS

Omar Defeo[1], Anita de Alava[1], Violeta Valdivieso[2] y Juan Carlos Castilla[3]

ABSTRACT

This work compiles and updates information on the development of surf clams' fisheries of the genus *Mesodesma* in the coasts of South America. Landings, prices and exportation values (when available), are analyzed for those countries where the species are present: Brazil, Argentine, Uruguay, Peru and Chile. A marked increase in catches during the 80's was observed in Chile, Peru and Uruguay. Argentine maintains a closed season imposed since 1958, while the lack of available data preclude us to analyze the evolution of the Brazilian fishery. A lack of regulatory measures, the prevailing open access-system established in four of the five countries analyzed and the marked increase in demand for the product by domestic and foreign markets, suggest a serious risk of over-exploitation of the *Mesodesma* resource. A dissimilar state of ecological and fishery knowledge observed in the mentioned countries aggravates the above situation. Implications derived from different management scenarios are discussed. Finally, future lines of research that ought to be developed in the region are proposed.

Key words: Mesodesma, small-scale artisanal fisheries, landings, management, South America; spatial population dynamics

RESUMEN

Este trabajo recopila y actualiza información sobre el desarrollo de las pesquerías de bivalvos del género *Mesodesma* en América del Sur. El análisis considera la evolución histórica de los volúmenes de desembarque y fluctuaciones de precios y exportaciones en los países donde ocurren especies pertenecientes al género: Brasil, Argentina, Uruguay, Perú y Chile. En los tres últimos se observó un marcado incremento en las capturas a partir de la década del 80. Por su parte, Argentina aún mantiene la veda impuesta en 1958, mientras que la carencia de datos impidió conocer la evolución de las capturas en Brasil. La ausencia de medidas de regulación, el prevaleciente régimen de libre acceso en cinco de los seis países analizados, y el incremento en la demanda del producto por parte de los mercados interno y externo, aumentan la probabilidad de que se suscite una sobreexplotación del recurso. Esta situación se ve agravada si se considera el precario y desactualizado estado de su conocimiento. Se discuten las distintas implicancias de los principales mecanismos tendientes a su manejo, y se proponen futuras líneas de investigación que deberían ser desarrolladas.

Palabras claves: Mesodesma, pesquerías artesanales, desembarques, manejo, Sudamérica, dinámica espacial de poblaciones.

[1]*División Biología Pesquera, Instituto Nacional de Pesca. Constituyente 1497, Casilla 1612. Montevideo, Uruguay.*
[2]*Mari-Export. Pucusana, Las Ninfas, Perú.*
[3]*Estación Costera de Investigaciones Marinas, Las Cruces. Facultad de Ciencias Biológicas. P. Universidad Católica de Chile, Casilla 114-D, Santiago, Chile.*

INTRODUCTION

During the last two decades there has been a strong trend toward diversification in the exploitation and exportation of small-scale shellfisheries in South America. Moreover, local consumption of shellfish products, which has been always important in Chile and Peru, increased in Uruguay, Brazil and Argentine. Both factors reflected in the size of shellfish catches, and in some cases they have led to the over-exploitation of stocks (Bustamante & Castilla, 1987; Defeo, 1989, 1991).

Within the South American bivalves landings, the small-scale fisheries of the surf clams *Mesodesma mactroides* and *Mesodesma donacium* play an important socio-economic role. The genus *Mesodesma*, which in South America includes *M. donacium* and *M. mactroides*, is distributed in exposed, dissipative beaches (*sensu* McLachlan, 1980a; b), exclusively along the Pacific and Atlantic coasts of South America (Fig. 1). The "macha" *M. donacium* is found in the Pacific, from Sechura, Peru (5°S) to Chiloe Island, Chile (43°S) (Tarifeño, 1980), and the "almeja amarilla" *M. mactroides* is found in the Atlantic, from Sao Paulo State, Brazil (24°S) to the south of the Buenos Aires Province, Argentine (41°S) (Olivier *et al.*, 1971).

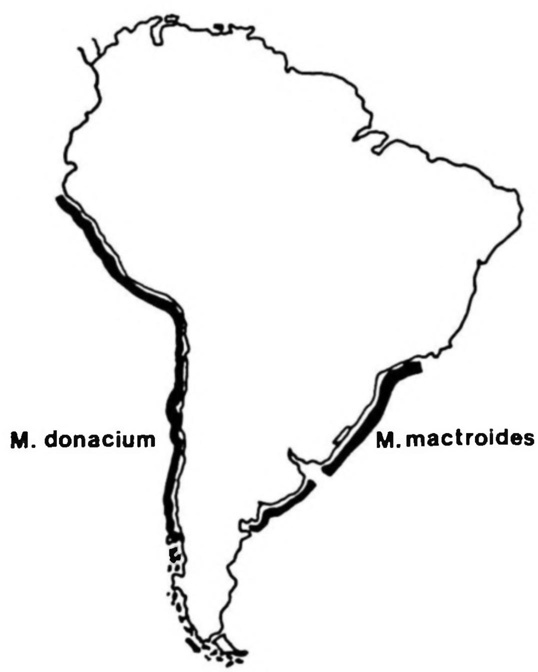

Figure 1. Geographical distribution of *M. mactroides* and *M. donacium* in Atlantic and Pacific coasts of South America.

This paper compiles and updates data on the development of *Mesodesma* small-scale fisheries in South America, discusses possible measures to regulate the fisheries and suggests future research topics to be undertaken to improve the management strategies for both species.

DESCRIPTION OF THE FISHERY

Harvesting techniques

M. mactroides is one of the main malacological resources of the Atlantic coast of South America. In this region, the clams are collected from the intertidal zone of sandy beaches by hand or by means of simple implements such as shovels; thereafter they are transported in bags and kept in nearby storehouses. They are marketed either for bait or for human consumption, in which case the clams are cleaned in tanks filled with sea water. In Uruguay, some attempts have been made to export canned clam meat, but the lack of processing technology and infrastructure have precluded successes; therefore, the whole production goes to the domestic Uruguayan market.

In the Pacific, the fishing of *M. donacium* has became extremely important in Peru and Chile. In the later, clams are collected manually in sandy beaches during low tides. Moreover, subtidal clams are readily extracted manually by free and semi-autonomous (hookah) divers operating from artisanal wooden boats (Bustamante & Castilla, 1987). Even though in Chile a great component of the catches reaches local markets, an increasing trend to export clam meat has been observed during the last decade (Bustamante & Castilla, 1987). Peruvian fishermen also target on intertidal and subtidal clam populations. Arntz *et al.* (1987) described the collecting procedures and techniques used by Peruvian clam fishermen. In Peru, a sizeable part of *M. donacium* production is also utilized by small-scale fishermen and their families for local consumption (Arntz *et al.*, 1987), but increasing landings could promote commercial exploitation, either for local or foreign markets.

Landings and fishing effort by country

Argentine

In this country, *M. mactroides* is found along hundreds of kilometers of sandy beaches, mainly along the Buenos Aires Province (Olivier & Penchaszadeh, 1968a, 1968b; Olivier *et al.*, 1971). Its exploitation has been carried out since the 40's, coinciding with the development of the canned industry. Landings peaked in 1953 to 1,078 tons due to the use of tractors, instead of manual collection, which markedly increased the fishing power (Olivier & Penchaszadeh, 1968b). This fact led to a resource over-exploitation and total closure of the fishery from 1958 onwards. Studies directed to open the fishery are still in progress, but up to now, to the best of our knowledge, the fishery continues closed and alternative management considerations have not been taken.

Brazil

Up to the present we do not have information about the existence of a time series of *M. mactroides* catch and effort statistics in Brazil. The available studies have focussed mainly on ecological aspects of the species. Hence, we can consider the Brazilian *Mesodesma* fishery as an open-access system along hundreds of kilometers of sandy beaches (*i.e.*, between Barra do Chui - border with Uruguay- and Río de Janeiro). Gianuca (1983) pointed out that the yellow clam almost disappears at the end of each summer season around every important seaside resort, where it is usually consumed as food and utilized as bait. Furthermore, he observed a rapid rate of repopulation (Gianuca, 1982), attributable to a high growth rate and enough space to allow for successful settlement (Defeo, 1992).

Uruguay

In Uruguay, from a landing point of view, the yellow clam *M. mactroides* is the second most important malacological resource, after the blue mussel *Mytilus edulis platensis.* About 50-150 fishermen work in the yellow clam fishery, which occurs in 22 km of exposed sandy beach localized between Barra del Chuy (33°40'S, 53°20'W) and La Coronilla (33°50'S, 53°27'W). The number of fishermen fluctuates greatly according to the demand for clams, availability of alternative employment in adjacent urban centers and the allowable number of fishermen estimated by the Instituto Nacional de Pesca (INAPE). The price paid from middlemen to fishermen in the beach fluctuates between 0.5 and 1 US$ per kg, while the market value for consumers is around 5 US$ per kg (including valves).

Up to 1983, the Uruguayan yellow clam fishery operated under an "open-access" policy, being monthly catch data and a directory of active fishermen the only records kept by INAPE. The general features of this small-scale fishery have been studied from 1983, in response to the large increase in catch observed from 1981 onwards (Fig. 2). This increase was triggered by a lack of alternative employment in the northeast of the country, and by enhanced demand for clams, mainly during summer months (Defeo, 1987; Defeo *et al.*, 1986).

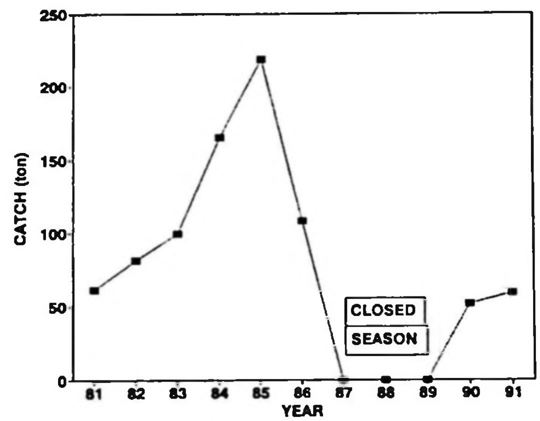

Figure 2. ***M. mactroides.*** **Uruguayan time series of catches between 1981 and 1991.**

The marked increase of yellow clam catches during the above period, coupled with a massive juvenile mortality due to climatic factors, translated into an important decline in the catch per unit of effort, which determined a temporal closure of the fishery between 1987 and 1989. A rapid recovery of the stock was observed from December 1988 on, as a result of the successful recruitment and natural restocking of depleted areas (Defeo, 1992). The above was reflected in the catch per unit effort achieved by the fishermen when the fishery was reopened in December 1989 (Fig. 3).

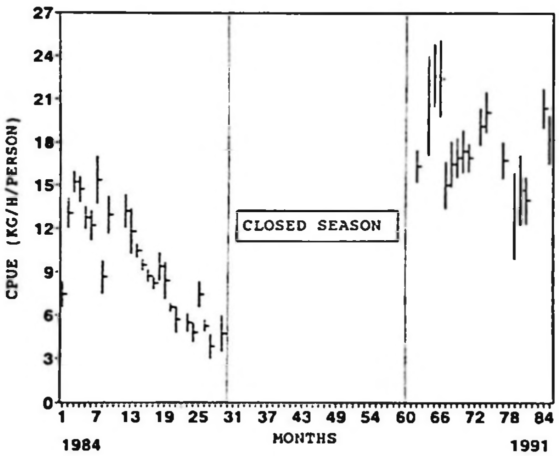

Figure 3. *M. mactroides*. Monthly mean values of catch/effort data (±1 SE) in Uruguay, between November 1984 (month 1) and December 1991 (month 86).

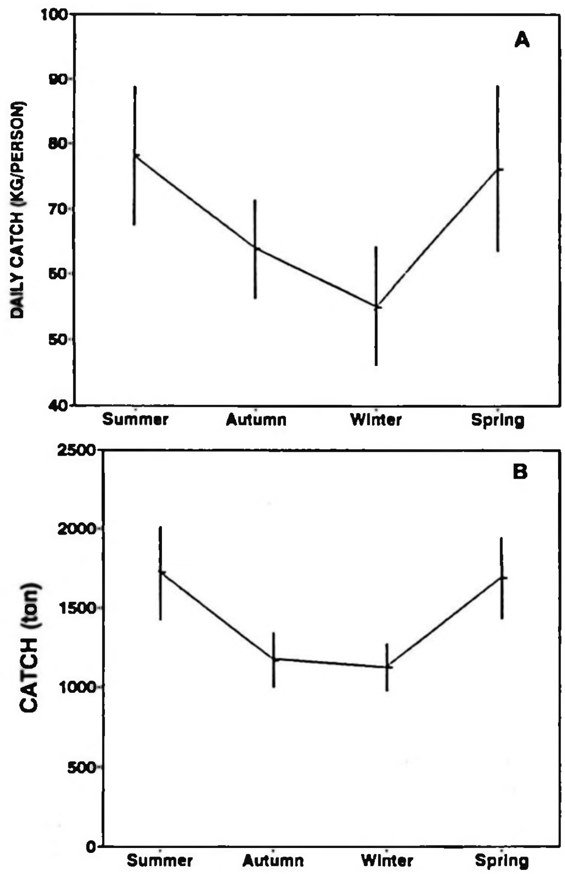

Figure 4. (A) Average daily catch per fishermen (± SD) in *M. mactroides* fishery of Uruguay; and (B) Chilean landings of *M. donacium*, discriminated by season (± SD).

The Uruguayan yellow clam fishery shows strong seasonal fluctuations. In fact, catch increases during spring and summer (Fig. 4a), as a result of higher demand for human consumption in the local market. A low demand and reduced availability of the resource due to subtidal migration explain the reduced catches in autumn and winter months (Defeo *et al.*, 1986).

Chile

The Chilean littoral extends for over 4,000 km of arid, semi-arid, mediterranean and cold coasts (Castilla *et al.* 1993) from 18°S to 56°S. It is unknown how many sandy beaches along this littoral contain resources such as *M. donacium*, and moreover how many artisanal fishermen are engaged (totally or partially dedicated) in this fishery. The statistical information available (Servicio Nacional de Pesca, SERNAP) deals only with landings. Hence, Fig. 5 shows the historical series of "macha" landings from 1965 to 1991. The marked increase from 1983 onwards was a response to a strong trend toward diversification in the exportation of many Chilean shellfish products (see Bustamante & Castilla, 1987). Landings peaked in 1989, reaching ca 18,000 tons, and declined thereafter (1990-1991) down to 9,000 tons, probably due to over-exploitation and/or fluctuations in market demand. Indeed, a trend of the foreign market (i.e. Spanish market)towards the selection of clam sizes lower than the legal marketable size, has been observed (Potocnjack, pers. com.).

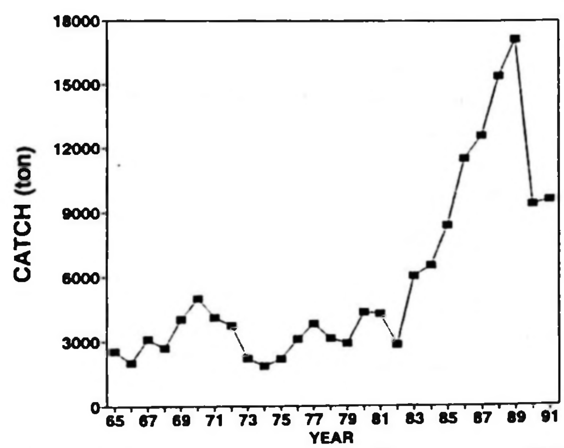

Figure 5. *M. donacium*. Chilean landings between 1965 and 1991.

Fig. 6 shows the Chilean *M. donacium* exported volumes and exportation values from1984 to 1992. A marked increase from 1986 on was observed. While total landings increased from 2,843 tons in 1982 to 17,122 tons in 1989 (Fig. 5), exportation values increased from ca. 1.0 to 9.3 million US$ between 1984 and 1989: both variables increased by a factor of six in seven years, and were significant correlated ($r=0.97$; $p<0.01$). Nonetheless, the reduction in the exported volume from 2,329 tons (1989) to 1,641 tons (1992) was compensated by a higher exportation value (from US$ 9.4 millions to US$ 8.7 millions respectively). In fact, export earnings were the highest in 1992. As can be deduced the external market demands seem to play a critical role in the Chilean small scale fishery of *Mesodesma*.

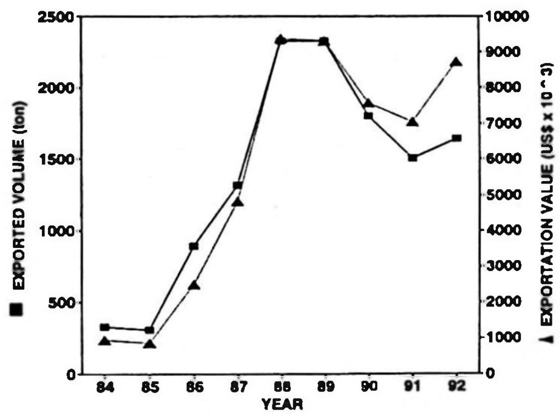

Figure 6. *M. donacium*. Chilean exported volume (■) and export earnings (▲), between 1984 and 1992.

In order to determine how landings fluctuated along the Chilean coast, the country was divided from North to South into four zones: Far Northern Zone, Near Northern Zone, Central Zone and Southern Zone. This responds to both major geographical reasons and somehow administrative ones, since the Servicio Nacional de Pesca de Chile in many instances separates the Chilean artisanal landings approximately into those zones. The spatial analysis of *M. donacium* landings revealed similar catches in the northern zones and a strong increase in volumes landed in Central and Southern zones from 1981 on (Fig. 7). However, a drastic decline in landings was observed in the latter during 1990 and 1991; the underlying causes being unknown: the Southern Zone of Chile has an elevated number of shellfish industries, the artisanal shellfishermen groups are numerous, and fishing technology is readily available. Hence, the drastic reduction in *M. donacium* landings most probably reflects a trend towards over-exploitation.

As in Uruguay, the Chilean fishery shows strong seasonal fluctuations. Catch increases in spring and summer (Fig. 4b), possibly as a result of higher demand for the product from the local market, and greater accessibility of the resource due to climatic factors.

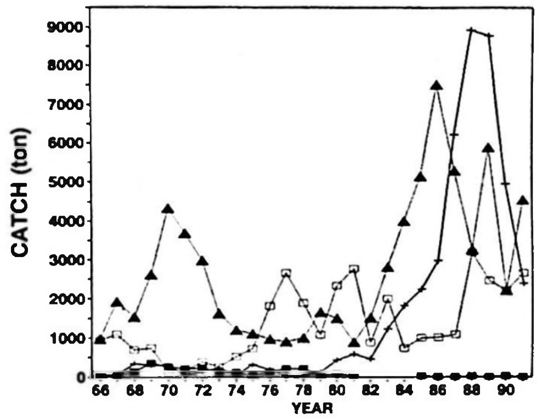

Figure 7. *M. donacium*. Regional distribution of Chilean landings between 1966 and 1991. (■) Far Northern Zone (Regions I, II); (□) Near Northern Zone (Regions III, IV); (▲) Central Zone (Regions V to IX); and (+) Southern Zone (Region X).

Peru

Fig. 8 shows the evolution of landings of the macha *M. donacium* in Peru. They steady increased from 1964 (36 tons) to 1977 (597 tons), reaching an impressive peak between 1978 and 1979, when catches were multiplied by a factor of seven (*ca.* 4,000 tons). This happened during the period preceding "El Niño" (EN) event of 1982-1983. The decline from 1980 to 1985 might be caused by a combined effect of resource over-exploitation (1980-1981) and negative effects of EN (1982-1983) on *M. donacium* populations (Castilla & Camus, 1992). Arntz *et al.* (1987) pointed out that from March 1983 on, no live surf clams were found in shallow waters south of Lima, and reported no recovery up to 1986. Landings from 1986 to 1989 showed a recovery of the resource, although never reaching the landing levels of 1978-1979.

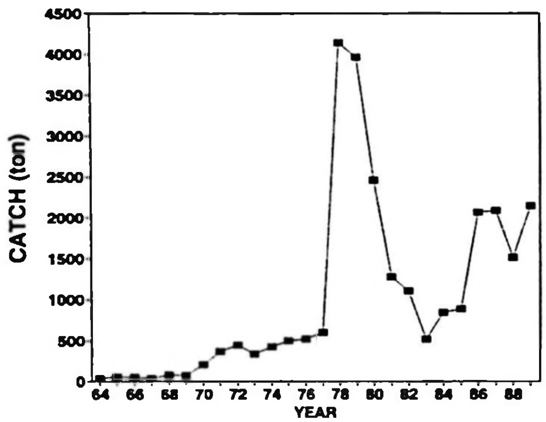

Figure 8. *M. donacium*. Peruvian landings between 1964 and 1989.

PRESENT STATE OF KNOWLEDGE

Tables 1a and 1b summarize the scientific research undertaken on both species, evidencing that more research, particularly in topics related to population biology and fisheries, is needed. In fact, there are numerous gaps of knowledge in the case of *M. donacium* of Chile and Peru. It must be pointed out that this species is by far the most valuable one of the two hereby discussed; therefore, it seems to us that there is an urgent need to complete the above mentioned gaps of knowledge.

MANAGEMENT CONSIDERATIONS

The relative success of different management strategies tending to achieve an adequate assessment of the yellow clam *M. mactroides* of Uruguayan coasts is fully discussed in Defeo (1989). He demonstrated that the implemetation of overall catch quotas resulted in a complete failure, because they were reached in a very short time due to stockpile of yellow clams during days preceding the opening of the season. This, in turn, led to a deterioration in the quality of the product. This observation was also noticed by Geaghan & Castilla (1986) for the fishery of the gastropod *Concholepas concholepas* in Chilean coasts.

Defeo (1987, 1989) also suggested several tools for the rational management of the Uruguayan yellow clam, namely: a minimum

Table 1a. *M. mactroides*. Current state of its scientific knowledge in Argentine, Brazil and Uruguay. The reference list does not include technical reports or abstracts.

SUBJECT	ARGENTINE	BRAZIL	URUGUAY
Population dynamics	Cabrera (1960) Olivier et al. (1971)		Defeo (1985b;1992) Defeo et al. (1988a; 1988b) (1992a; 1992b)
Reproductive biology	Olivier et al. (1971)		Masello (1987) Masello & Defeo (1986)
Feeding behaviour	Castellanos (1948) Coscaron (1959)	Narchi (1981)	Defeo & Scarabino (1990)
Zonation patterns	Olivier et al. (1971)	Gianuca (1983)	Defeo (1985a; 1992) Defeo et al. (1986)
Stock estimates	Olivier & Penchaszadeh (1968a)		Defeo et al. (1988b)
Fisheries management	Olivier & Penchaszadeh (1968b		Defeo (1987; 1989; 1992) Defeo et al. (1991)

TABLE 1b. *M. donacium*. Current state of its scientific knowledge in Chile and Peru. Neither technical reports nor abstracts are included in the reference list.

SUBJECT	CHILE	PERU
Population dynamics	Tarifeño (1980)	Arntz et al. (1987)
Reproductive biology	Tarifeño (1980) Peredo et al. (1987)	Salgado & Ishiyama (1979)
Feeding behaviour	Tarifeño (1980)	
Zonation patterns	Tarifeño (1980) Sánchez et al. (1982)	
Stock estimates	Tarifeño et al. (1990)	
Fisheries management		

profitable catch volume per fisherman, differential fishing quotas per season, and optimum rotation of areas. In this sense, taking into account habitat heterogeneity of the beach (which explains spatial variations in resource abundance and fishing effort allocation) from 1984 the 22 km fishing ground was divided in four sections of similar size, with boundaries set at right angles to the coastal line (Defeo *et al.*, 1986, 1991). The spatial management scheme upon an optimum rotation of areas was successfully applied, under the heterogeneous conditions above described (Defeo, 1989). Finally, a minimum legal clam size (5 cm) for commercial harvest, considering length/age at first maturity (Masello & Defeo, 1986), was also used as a regulatory measure (Defeo, 1987).

Olivier & Penchaszadeh (1968a, 1968b) proposed regulatory measures to manage *M. mactroides* in Argentinean coasts. They suggested a closed season for some fishing zones with diminishing standing stocks. The use of tractors for fishing caused a marked increment in fishing mortality, discard of broken individuals, and hence a collapse of the fishery. A spatial management scheme and a minimum legal size limit were also suggested. Due to the absence of an adequate regulatory policy, these measures had relative success.

The experience accumulated out of the yellow clam fisheries in Argentine and Uruguay shows that there is no need to improve the manual or shovel harvesting technology (Defeo, 1987). The continuation of these practices would contribute to the conservation of the species and would benefit artisanal fishermen by providing permanent employment. This is an important factor to bear in mind in view of the scarce labor opportunities in coastal zones in these developing countries. The introduction of more sophisticated harvesting technologies could cause an increment in fishing power and a collapse of the fishery.

Another reason to restrict the use of sophisticated harvesting technologies is the occurrence of physical stress produced by sediment disturbance during harvesting activities. Indeed, Defeo (1992) demonstrated a close relationship between natural mortality rates of the young-of-the-year and annual catch or fishing intensity, considered as a clear indication of incidental natural mortality due to hand-gathering techniques. Suffocation, perturbation of sediment texture, prolonged air exposure following harvest and limitation of filtering activities by clogging of the ctenidia and palps, might be involved in incidental mortality (Defeo, 1992).

In Brazil, there are no regulatory measures for the fishery, so it can be defined as an open-access fishery (*sensu* Gordon, 1954), as there is apparently unrestricted access to the resource. In the long-run, this situation will conduct to an open-access bioeconomic equilibrium, *i.e.* the dissipation of the economic rent derived from the fishery, where total sustainable revenues equal total costs (Clark, 1985; Anderson, 1986).

In the case of *M. donacium* in Chile, a minimum legal size (7 cm) is the only fishery regulatory mechanism actually implemented throughout the country. Nonetheless, a preliminary policy has been established in some beaches of Central Chile (V Region), regulating fishing effort through a system of 15 days closure and 15 days opening of the fishery. A rotational scheme of fishing grounds has failed so far, mostly because of the lack of clear policies and organization of artisanal fishermen associations. The new Chilean Fishing Law (1991) contains important tools which will enable in the near future the implementation of adaptive fishing schemes (Walters, 1986, Hilborn & Walters, 1992; see Castilla, in press). The lack of alternative management measures can lead to resource over-exploitation, even more if we consider that the marked increment of catches has not been complemented with an integrated analysis of the whole species distribution, neither incorporating interactions between biological and socio-economic factors.

The situation of the surf clam fishery of Peru is similar to that of Brazil. No regulatory mechanisms have been established, so it can be considered as an open-access fishery. Taking into account the occurrence of large-scale environmental fluctuations such as EN events, which generates massive mortalities and recruitment failures (Arntz *et al.*, 1987), regulatory measures and investigations focussed on the monitoring of spatial and temporal fluctuations in the magnitude of recruitment are urgently needed.

SOME GUIDELINES FOR FUTURE RESEARCH

A number of future research efforts ought to be carried out to provide the scientific basis to manage the fisheries of *Mesodesma* in South America. The following topics deserve special consideration:

Sampling strategies for data acquisition of the stock and the fishery.

Given the high and scale-dependent spatial variability in the alongshore distribution by size/age of *Mesodesma* populations, as in their growth and mortality parameters (Tarifeño, 1980; Defeo *et al.*, 1986; Arntz *et al.*, 1987; Defeo, 1992), we find little advantageous to use the traditional random sampling. A better approach, commonly used for benthic populations, is to employ a systematic sampling. This strategy will allow the use of contouring methods, such as geostatistics and autocorrelation techniques, to evaluate the stock and to describe spatial variations in population distribution and environmental variables (Hall, 1983; Conan 1985; McArdle & Blackwell, 1989; Rossi *et al.*, 1992). Up to present, these methods are increasingly used in soft-bottom population studies. On the other hand, an echo-acoustic method for assessing clam populations (*M. donacium* and *Tagelus dombei*) has been recently described by Tarifeño *et al.* (1990).

Systematic sampling involves the following confident elements (Hancock & Urquhart, 1965): (1) it does not match spatially periodic sources of variability; (2) it avoids visual bias in the selection of stations; (3) further, the likelihood that samples taken at different times come from an identical position is low. Advantages of systematic sampling for benthic populations have also been highlighted by Conan (1984) and McArdle & Blackwell (1989).

On the same vein, since the allocation of fishing effort usually follows quite closely spatio-temporal variations in resource abundance, time series of fishing effort and catches should be obtained discriminately by homogeneous areas (Caddy, 1975; Conan, 1984; Conan & Maynard, 1983). This will require a precise location of the areas used, which should be easy to identify both by fishermen and researchers (Defeo, 1991; Defeo *et al.*, 1991).

The desagregated analysis of *Mesodesma's* stocks, the surrounding environment and the fishery, will be a useful tool for: (1) the assessment of spatial dynamics of catch and fishing effort; (2) the detection of changes in length or age composition of the catch; (3) monitoring changes in stock abundance and its composition by size/age, as well as in population dynamics parameters and environmental variables. From the above, an integrated approach could be built to develop a comprehensive management scheme of the fishery (see below).

Physical-biological coupling, and the definition of relevant scales of analysis.

Physical and biological factors should be considered as the proximal agents generating the spatio-temporal patterns of *Mesodesma* populations (Olivier *et al.*, 1971; Tarifeño, 1980; Defeo *et al.*, 1986; Arntz *et al.*, 1987). In this sense, it has been emphasized that the importance of biotic factors to structure populations in a harshly environment (exposed sandy beaches) must not be neglected, as stated by Defeo (1992).

Moreover, as population patterns and processes in invertebrates are scale-dependent (Orensanz, 1986; Butman, 1987; Thrush, 1991; Defeo, 1992), the recognition of a physical-biological coupling in different scales according to specific research questions, will show an alternative approach concerning the study of population regulation and dynamics of *Mesodesma*.

Assessment of recruitment variability.

The ability to predict the magnitude of recruitment from a given level of spawning stock is an essential issue in benthic resources management (Hancock, 1973; Botsford, 1986; Caddy, 1986, 1989a, 1989b; Caputi & Brown, 1986; Fogarty, 1989). It has been recognized that recruitment magnitude in organisms with pelagic larval phase is related not only to the parental stock, but to fluctuations in environmental variables as well (*e.g.*, Holm, 1990; Phillips & Brown, 1989; Possingham & Roughgarden, 1990; Roughgarden *et al.*, 1985; Penn *et al.*, 1989). Even though a clear overcompensation mechanism was demonstrated for the yellow clam *M. mactroides* of Uruguayan coasts (Defeo, 1992), it will be desirable to evaluate the incidence of environmental variables and to include the relevant ones in recruitment models. The two stage procedure with "exploratory correlations" between environmental variables and recruitment estimates (Tang, 1985) may provide better forecasts of recruitment.

The determination of a stock-recruitment relationship, incorporating adult and recruitment variability through time, will be a useful tool to elaborate and discuss "risk-averse" management strategies that minimize the probability of stock depletion, prevent recruitment overfishing, and forecast a threshold level of spawning stock density in order to improve the chances of a sustainable level of recruitment (Hilborn & Walters, 1992).

The wide range of fishing effort levels that would be achieved by adaptive management experiments (*sensu* Hilborn & Walters, 1992) will provide a range of variability in the spawning stock size, which in turn will allow to determine the exact shape of the recruitment curve even with a short time data series (Defeo, 1992).

The dispersive abilities of planktonic larvae of *Mesodesma* stocks in the sea are unknown. Research efforts should be directed to study planktonic stages, their swimming ability, and the role of near-shore hydrodynamics ("surf zone environment") in settlement/ recruitment processes. It will also be necessary to conduct, if possible, laboratory experiments directed to demonstrate mechanisms of overcompensation, such as the passive filtering of planktonic larvae by established adults (see Defeo, 1992). Studies of the planktonic component of *Mesodesma's* life cycle are particularly important to determine the spatial scales at which the population dynamics is to be considered an open process (*sensu* Hughes, 1990).

The concept of "supply-side ecology", *i.e.* that the dynamics of adult populations is more related to the arrival rates of larvae than to post-settlement processes (Lewin, 1987; Roughgarden *et al.*, 1988; Underwood & Fairweather, 1989), has shown to be successful when applied to terrestrial and rocky intertidal populations, but needs to be explored in exposed sandy beaches. It would be also important to include physical-oceanographic information related to larval dispersal.

Growth and mortality.

Growth rates of *Mesodesma* clam vary markedly in space and time, mainly due to density-dependent processes and environmental factors (Tarifeño, 1980; Defeo, 1992; Defeo *et al.*, 1992a, 1992b). Thus, spatio-temporal differences are crucial to model population dynamics of these stocks, and to determine environmental and biotic control factors.

Natural and fishing mortality rates also vary between cohorts and are correlated with biotic and abiotic factors and fishing pressure. Mortality of the young-of-the-year is usually highest in the densest cohorts, coinciding with lowest growth rates, intermediate adult density, intense fishing activity and environmental harshness (Defeo, 1992). The effect of physical stress produced by sediment disturbance and incidental damage during harvest activities, must be evaluated as a source of incidental natural mortality and population fluctuations. Fishing pressure behaves as a source of disturbance, but it also acts as a way of releasing space, thus enabling the recolonization of disturbed patches. Thus, it will be important to determine those harvesting levels within which the magnitude of natural mortality could diminish, promoting successful recruitment and attenuating the intensity of intraspecific competition.

Modelling and management.

The modern approach to fisheries management is to characterize and predict population processes through mathematical models, which, since the 50's, have been designed for finfish populations (Schaefer, 1954; Beverton & Holt, 1957). These models consider the stock as a closed, self-sustaining unit of population with uniform distribution over the whole area, so that the effect of fishing effort (also assumed to be uniformly distributed) is absorbed by the whole stock through recruitment and/or redistribution of organisms (Ricker, 1975). Hence, fluctuations in stock size may be reflected by the size of catches.

In sessile and sedentary organisms the above assumptions are rarely valid (Hancock, 1979): the patchy distribution of populations (Elliott, 1977) and their scarce, or null, mobility are important restrictions for the application of traditional finfish models. For instance, mollusks cannot redistribute themselves quickly over a fishing ground, and cannot fill gaps in patches resulting from a sequential depletion pattern produced by the heterogeneous allocation of fishing effort (Hancock, 1979; Caddy, 1975; Orensanz *et al.*, 1991). Moreover, their population dynamics are extremely dependent on local environmental conditions and the more intense biological interactions regulate demographic variations in such a way as to make predictions weaker than for pelagic fishes (Conan, 1984). Consequently, invertebrate fisheries should use different strategies for their management. Two complementary approaches seem to be appropriate to analyze and model *Mesodesma* stocks (Defeo, 1992):

a) To relax the assumption of spatial homogeneity in resource distribution (see above). Extensive fishing grounds with variable environmental conditions, thus heterogeneous in their patterns of abundance, growth, mortality, and allocation of fishing effort, can be divided into smaller areas that should be considered as independent units (Caddy, 1975, 1989b; Sluczanowski, 1984, 1986). Hence, for a stock showing a continuous geographic range of population characteristics, a useful approach is to consider it as composed by several discrete subpopulations which can be studied independently and the predictions integrated afterwards. A spatial management upon an optimum rotation of fishing areas could be useful to manage these shellfisheries (Caddy, 1975; Hall, 1983; Defeo *et al.*, 1986, 1991). The functional unit stock concept (*sensu* Caddy, 1989b: p. 668) must be considered an appropriate framework for population modelling, identifying different subsets of the population capable of being treated independently from the rest of the species distribution. This assumption becomes necessary to perform any stock-recruitment analysis and also for management purposes.

b) To develop a comprehensive approach for managing these shellfish stocks, integrating characteristics such as: effects of different environmental regimes on spatial population structure, spatial heterogeneity of fishing effort, biological interactions, and implications of economic factors and human attitudes (behaviour of resource managers and users: Boutillier *et al.*, 1988; Charles, 1989). In view of the uncertainty involved in estimations of the above factors, it is advisable to consider and use stochastic models instead of deterministic ones (Sissenwine, 1984a, 1984b; Seijo, 1986; Fogarty, 1989). Multiple-objective optimization functions should be incorporated to optimize management strategies that fulfill pre-existing resource managers preferences (Díaz de León & Seijo, 1992; Seijo *et al.*, 1992).

Stock enhancement.

Taking into account that, under the present knowledge, these species cannot be cultivated, and considering their increasing demand, it becomes necessary to initiate restocking experiments -either by "sowing" or colonization (*sensu* Castilla, 1988)- in order to increase the actually limited standing stocks. Two of the three strategies fully discussed in Castilla (1988), are proposed for increasing *Mesodesma* stocks: (a) restocking through management of natural areas, and (b) restocking through direct seeding of juveniles or adults. Alternatively, the spatial management scheme would complement the first strategy with regard to the spatial variation in the magnitude of recruitment, so as to protect those areas with high probability of successful recolonization (Caddy, 1989b; Defeo, 1992). An analysis of restocking of shellfish species is found in Castilla (1988, 1990, in press) and Oliva & Castilla (1990).

Allocation of property rights.

Allocation of exclusive property rights to fishermen appears to be the soundest management strategy in small-scale artisanal fisheries (Defeo, 1987, 1989; Castilla, 1990, in press; Seijo & Fuentes, 1989). Legal measures to allocate temporal property rights to fishery communities or to individual fisherman, in the form of coastal reserves, marine concessions or individual catch quotas, should be alternative mechanisms to avoid "the tragedy of the commons" (*sensu* Hardin, 1973; see also Smith & Berkes, 1991; Castilla, in press).

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