



Effects of fishing, market price, and climate on two South American clam species

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ABSTRACT: Coastal shellfish are being threatened by several drivers acting at multiple temporal and spatial scales, including fishing, climate, and globalization of markets. We evaluated large-scale and long-term combined effects of fishing, climate, and economic variables on 2 congeneric clams that inhabit sandy beaches of the Pacific (*Mesodesma donacium*) and the Atlantic (*M. mactroides*) in South America. Bioeconomic and climatic variables, such as coastal sea surface temperature anomalies (SSTA) and broad-scale climatic indices (Pacific Decadal Oscillation and Atlantic Multidecadal Oscillation), were related to variations in clam populations in a differential way according to latitude and oceanographic features. For *M. donacium*, the nature and sign of the relationships between landings and explanatory predictors markedly differed between bioclimatic units. El Niño Southern Oscillation events negatively affected landings in Peru and northern Chile, whereas landings increased in southern Chile and showed a positive correlation with increasing SSTA, suggesting a positive effect at the southernmost edge of the species distribution. Long-term trends in the abundance of *M. mactroides* were related to fishing intensity and SSTA. As anticipated by basic economic theory, deficit of supply relative to demand, exacerbated by very low harvesting costs, pushed the price up and has driven these clam species to levels close to extinction (anthropogenic Allee effect). The lack of response of the stocks to long-term closures suggests that these systems exceeded critical thresholds (tipping points). Information on early warnings of tipping points is needed to help manage coastal shellfisheries that are increasingly threatened by long-lasting and large-scale stressors.

KEY WORDS: Intertidal clams · Sandy beaches · Climate variability · Fisheries bioeconomics

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INTRODUCTION

Many small-scale shellfisheries in the world are data-poor and have critical socioeconomic connotations worldwide (Caddy & Defeo 2003, McClanahan et al. 2009). In Latin America, these fisheries are based on high-value species and represent sources of food for subsistence and employment, generating important direct incomes to fisher communities and, in

some cases, export earnings (Castilla & Defeo 2001). However, shellfisheries sustainability has been difficult to achieve. Nowadays, many shellfish populations in Latin America are overexploited or depleted (Carranza et al. 2009a, b). In addition to local drivers affecting shellfish condition, global change drivers have exacerbated stock depletion rates, particularly (Defeo & Castilla 2005, 2012, Beck et al. 2011, Perry et al. 2011): (1) increasing prices for shellfish highly em-

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bedded in global markets, and (2) climate variability, such as temperature rise. Thus, the resilience of these social-ecological systems can be degraded by several drivers acting simultaneously (Ling et al. 2009, Miller et al. 2010). However, the integration of biophysical and socioeconomic information in long-term fisheries modeling has been more complex than previously thought (Cury et al. 2008).

Climatic processes have drastic effects in the functioning of marine biological systems at a wide range of temporal and spatial scales (e.g. Bakun 1996, Rouyer et al. 2008). Ocean climate variables, such as shifting currents and temperature changes, alter feeding, growth, and migratory patterns of marine fauna (Miller et al. 2010). In South America, these scenarios are related to interannual (e.g. El Niño Southern Oscillation [ENSO]) and multidecadal (e.g. Pacific Decadal Oscillation [PDO] and Atlantic Multidecadal Oscillation [AMO]) environmental variability associated with broad-scale oceanic climatic variations, which influence currents and water mass properties. This atmospheric-oceanic multiscale variability affects ecosystems, including their fishery resources (Chavez et al. 2003, Montecino & Lange 2009).

The effects of climate change may be profoundly felt in the macrofauna present in sandy beaches, a largely forgotten ecosystem despite its coverage of >70% of the open coasts of the world (Defeo et al. 2009). The position at the land-sea margin renders sandy beaches highly vulnerable to climate change, being at risk of significant habitat loss and ecological impacts from warming and erosion caused by sea-level rise and increased storms (Dugan et al. 2010). These cumulative effects are also exacerbated by the extraction of easily accessible and high-value resources inhabiting intertidal sandy shores, notably clams (McLachlan et al. 1996). Although these fisheries are generally of small scale, fishing impacts can be significant and can be amplified or reinforced by: (1) continuous erosion of beaches that reduced clam habitats (Beentjes et al. 2006), and (2) mass mortalities (Fiori et al. 2004, Riascos et al. 2009).

Sandy beach clams of the genus *Mesodesma* are a valuable resource along the Atlantic and Pacific coasts of South America (Defeo 2003). Humans have been harvesting these marine invertebrates for a long time (Rivadeneira et al. 2010). In the Pacific, the surf clam *M. donacium* (macha) is one of the most important shellfishes exploited in Chile and Peru, even though it is also a data-poor fishery where effective fishing-effort estimates are rarely available. In the Atlantic, the yellow clam *M. mactroides* is commercially exploited in sandy beaches of Brazil, Uruguay, and

Argentina (Herrmann et al. 2011). The genus *Mesodesma* has an Antarctic origin and can be associated with cold water systems, both in the Pacific and Atlantic. This genus invaded South American coasts in the late Pliocene or possibly in the early Pleistocene, during a major migration of mollusks from Antarctica, following 2 cold currents: Malvinas on the east coast and the Humboldt Current System (HCS) on the west coast (von Ihering 1907). This migration was probably triggered by decreasing temperatures at the end of the Tertiary and early Quaternary periods. According to von Ihering (1907), the dispersion of *M. mactroides* on the Patagonian coast occurred during the Pleistocene and has only recently encompassed the Brazilian littoral, delayed by the strong zoogeographic barrier represented by the Rio de la Plata (Marins & Levy 1999). These filter-feeding clams inhabit the intertidal and shallow subtidal zones of exposed, high-energy dissipative sandy beaches, where they typically burrow to a depth ~30 cm (McLachlan et al. 1996).

Mass mortalities decimated populations of both *Mesodesma* species along their entire geographic ranges during the last 30 yr. These mass mortalities have been attributed to a number of factors, namely positive sea temperature anomalies, harmful algal blooms, environmental stress, parasitism, and storms (Odebrecht et al. 1995, Fiori et al. 2004, Riascos et al. 2009, 2011, Carstensen et al. 2010). In the case of *M. mactroides*, it has been suggested that the effect of these mortalities may swamp management measures (Defeo 2003). However, large-scale and long-term records that could be used to evaluate the relative importance of climate and fishing in these sandy beach species are lacking. In the present paper, we evaluate the relative explanatory power of fishing and climate variability in explaining long-term fishery and abundance trends in *M. donacium* and *M. mactroides* clams. We focused on 3 key issues that rule the discussions in fisheries nowadays (Defeo & Castilla 2012): (1) the role of climate in fisheries landings, (2) the effects of fishing, and (3) market prices as drivers in the fate of stocks.

MATERIALS AND METHODS

Study area and ecological settings

Mesodesma donacium

The surf clam *Mesodesma donacium* (Lamarck, 1818) is one of the most important bivalves harvested

in Pacific sandy beaches of South America. The species is distributed from Sechura Bay, Peru (5°S ; Álamo & Valdivieso 1997) to southern Chile ($\sim 42^{\circ}\text{S}$; Tarifeño 1980) (Fig. 1). *M. donacium* often exhibits high densities and extremely high annual production, representing $>95\%$ of the biomass in the shallow soft-bottom community (Arntz et al. 1987). The across-shore distribution of *M. donacium* is patchy and adult clams are primarily confined to the surf zone, while the vast majority of juveniles occur in the swash zone (Tarifeño 1980, Jaramillo et al. 1994). In Chile, surf clams constitute a sequential fishery (sensu Seijo et al. 1998), with 2 groups of artisanal fishers spatially segregated: (1) fishers who manually collect clams from the intertidal and shallow subtidal beach fringes during low tides, and (2) 'hookah' divers that use small deckless boats with air compressors to extract clams located at the surf zone. In Peru, the macha is extracted both manually in the intertidal by digging with shovels and dredges in the shallow subtidal (Ibárcena et al. 2005).

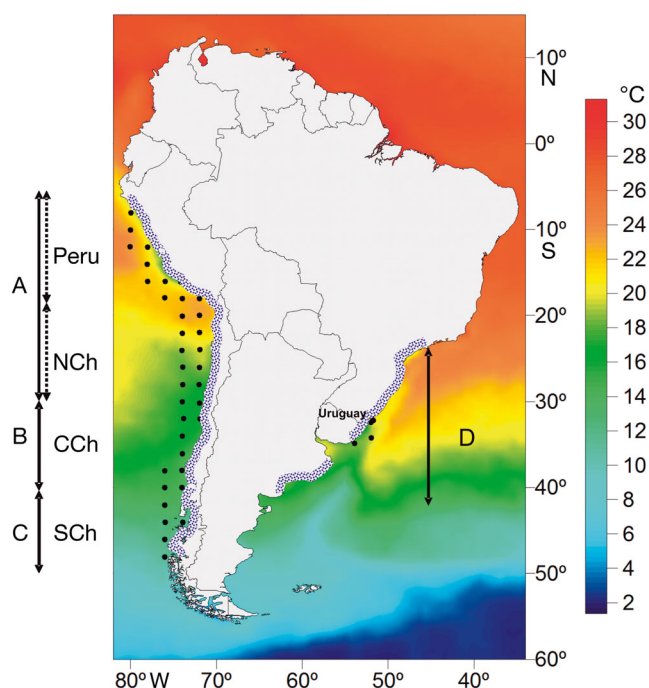


Fig. 1. Geographic distribution of the genus *Mesodesma* along the coasts of South America (purple stipple), highlighting the bioclimatic units: (A) subtropical-temperate, including 2 sub-units, Peru and Northern Chile (NCh); (B) transitional (Central Chile: CCh); (C) subantarctic (Southern Chile: SCh); and (D) the Warm-Temperate Southwestern Atlantic province. •: locations where sea surface temperature anomalies derived from Reynolds et al. (2002) were obtained. The satellite image is an annual composite (1996) of sea surface temperature (color scale in $^{\circ}\text{C}$) derived from the Moderate-Resolution Imaging Spectroradiometer (MODIS-Aqua)

Environmental conditions in the HCS are broadly characterized by nutrient-rich, cool waters, showing slight seasonal temperature variability compared to those found in other coastal ecosystems at similar latitudes (Camus 2001, Thiel et al. 2007). The influence of the continuous upwelling of cold subsurface waters, mainly at northern Chile and Peru, and seasonal upwelling in southern-central Chile (Thiel et al. 2007), causes an atypical weak north-south temperature gradient and extends the influence of cold environmental conditions northward (Camus 2001). Therefore, many species in the HCS exhibit broad distributional ranges and are adapted to moderately constant low water temperatures (Riascos et al. 2009).

According to Thiel et al. (2007), 3 bioclimatic units can be distinguished within the HCS (Fig. 1): (1) a northern unit, dominated by subtropical and temperate biota, extending from Peru to Northern-Central Chile (4°S to 30°S) (where NCh is Northern Chile); (2) a transitional unit (Central Chile or CCh: 30°S to 40°S), characterized by strong numerical reductions in subantarctic and subtropical species; and (3) a southern unit (Southern Chile or SCh: 40°S to 50°S), dominated by subantarctic and temperate biota, extending from the Chilean archipelago to the Magellan Province.

Mesodesma mactroides

The yellow clam *Mesodesma mactroides* Reeve, 1854, is found in sandy shores of the Warm-Temperate Southwestern Atlantic (WTSa) province of South America (Spalding et al. 2007), from Brazil (24°S) to Argentina (41°S) (Fiori & Defeo 2006; our Fig. 1). This fast-growing, short-lived species (<4 yr) is artisanally exploited (shovels and hand-picking) in the intertidal of sandy beaches from Brazil, Uruguay, and Argentina (Defeo 2003).

The WTSa is characterized by a marked seasonality, with predominance of Subantarctic Water during the cold period (austral winter-spring) and Tropical Water and Subtropical Shelf Water in the warm period (summer-autumn) (Lima et al. 1996, Piola et al. 2000, Ortega & Martínez 2007). The area located over the shelf (27°S to 35°S) is controlled by winter intrusions of Subantarctic Water along with Rio de la Plata and Patos-Mirim discharges, and has large annual sea surface temperature (SST) ranges (7 to 10°C) and an extremely high secular trend toward warming (1.2 to 1.6°C per 100 yr), especially in the proximity of estuaries (Zavialov et al. 1999). In austral winter, the

occurrence of a thermal front separates warm tropical water associated with the Brazil Current and cold Subantarctic Water flowing northward on the shelf with an admixture of coastal freshwater discharges. In summer, shelf break coastal upwellings have been registered along the coast (Podestá 1990), particularly around Cabo Frio (22°S) and Ilha de Sao Sebastiao (24°S), at the northernmost limit of the yellow clam distribution. These upwellings pump up oxygen and nutrient-rich South Atlantic Central Water to the euphotic zones in the inner continental shelf, and weaken considerably during the austral winter (Piola et al. 2000). The southernmost distribution limit of the yellow clam is characterized by a major influence of oceanic cold waters (Guerrero et al. 2010).

Data analysis

SST anomalies (SSTA) for the Pacific and Atlantic coastal regions were estimated by the monthly-average gridded 0.5° latitude by 0.5° longitude recorded by Reynolds et al. (2002). The annual mean SSTA was also determined by biogeographic unit (Fig. 1). Since the northern bioclimatic unit in the Pacific was divided into NCh and Peru (see 'Study area and ecological settings'), the same methodology was applied to estimate mean SSTA for each sub-unit. Long-term biological information for the yellow clam in the Atlantic was available only for the eastern coast of Uruguay, and thus SSTA were estimated for this specific area.

Two broad-scale climate indices were used to represent large-scale processes that may influence clam abundance: the AMO and PDO. PDO and AMO time series were taken from www.esrl.noaa.gov/psd/data/climateindices/list/. Standardized PDO values are derived from monthly SSTA in the North Pacific Ocean, poleward of 20°N. In order to estimate PDO values, monthly mean global SSTA are removed to separate this effect from any 'global warming' signal that may be present in the data (Zhang et al. 1997). The AMO is a climate pattern of long-duration changes in the SST of the North Atlantic Ocean, with identifiable characteristics, specific regional effects, and often oscillatory behavior, which has its principal expression in the SST field (Enfield et al. 2001). As such, the AMO presents cool and warm phases that may last for 20 to 40 yr at a time. A cumulative sum (annual mean values) of the AMO and PDO indices was used to detect sustained shifts in climate, marked by changes in slope of the cumulative sum plot (Fiedler 2002).

Long-term *Mesodesma donacium* landings from Chile (1966 to 2009) and Peru (1970 to 2009) were discriminated by bioclimatic unit. To this end, annual landings (clam catch that is put ashore) from 16 regions in Peru and 12 regions in Chile were assigned to the corresponding unit (no information on fishing effort is available). Peruvian landings were obtained from official sources (e.g. Ministerio de Pesquería del Perú, Ministerio de la Producción de Perú). For Chile, official landings were obtained from the Servicio Nacional de Pesca (SERNAP), and exportation volumes (tons or t) and economic revenues (US\$) were obtained from the Servicio Nacional de Aduanas (Chile). Unit export prices were obtained by the ratio between economic revenues and exportation volumes. Given the marked temporal differences in the development of fishery phases (sensu Castilla & Defeo 2001) and also in SSTA trends (see 'Results') between NCh and Peru (subtropical-temperate bioclimatic unit), data from these 2 sub-units were analyzed separately.

Concerning the yellow clam *Mesodesma macroides*, a long-term analysis was carried out only for Uruguay. The lack of statistical coverage in Brazil and Argentina precluded a more comprehensive analysis throughout this species' distribution range. In Uruguay, the yellow clam fishery is developed only along a 22 km sandy beach fringe located between La Coronilla and Barra del Chuy (Defeo 2003). Yellow clam abundance, estimated as the number of individuals per strip transect (ind.m⁻¹), were obtained from seasonal surveys carried out during 27 consecutive years (1982 to 2008), according to a systematic design developed to quantify the stock (see Defeo 1996 for details). All clams retained in each sample were measured (maximum valve length) and counted, covering the full range of individual sizes (1 to 76 mm). Annual abundance estimates were obtained by averaging seasonal estimates, which were provided for the whole population and also for the harvestable stock (individuals >50 mm; Defeo 1996). Concerning fishery-dependent statistics, daily information on catch, effective fishing effort (hours), and unit price paid by middlemen to fishers (the product is sold only in the local market) was collected on a per-fisher basis (Defeo 1996).

Generalized additive models (GAM; Hastie & Tibshirani 1990) were used to assess the relationship between landings (surf clam: Peru and Chile) or abundance (yellow clam: Uruguay) and predictor variables: SSTA and unit price were used in the

former, whereas SSTA and effective fishing effort were used in the latter. Taking into account the relatively short time period when the yellow clam fishery was active (see 'Results'), unit price was not considered for modeling purposes. In both cases, time of fishery development (in years) was also included as an independent variable in order to explore long-term trends in partial residuals. Partial residuals remove the effects of all the other variables from the dependent variable and therefore can be used to model the effects against predictors (Xiang 2001). A moving average of landings with a period of 3 yr was performed to model macha landings in the Pacific. All models were estimated using the functions GAM (model building) and mgcv (estimation of smoothing parameters) included in R statistical software (R Development Core Team 2008). Smoothing parameters and degrees of freedom of the functions were estimated using the generalized cross-validation, and penalized cubic regression splines were used as smooth terms (Wood 2006). Different models were evaluated by the significant difference of residual deviance using the *F*-test. The final model was selected according to the level of deviance explained and Akaike's information criterion (AIC). Non-significant terms ($p > 0.05$) were dropped from the model. Additional analyses were performed involving only landings (*Mesodesma donacium* in Chile) or abundance (*M. mactroides* in Uruguay) with price and fishing effort, respectively. The residuals of these models (i.e. the variance not explained by unit price or fishing effort) were modeled against SSTA to test if this climatic variable could account for the variance not explained by the model mentioned before.

RESULTS

Multidecadal basin scale

Mesodesma donacium

The cumulative sum of the PDO showed a marked shift in the ocean-climate regime from a cold to a warm phase in 1977 (Fig. 2A). *Mesodesma donacium* landings in Peru and NCh linearly increased with PDO ($r^2 = 0.28$, $p < 0.05$ and $r^2 = 0.24$, $p < 0.001$, respectively), being low during the cold phase and increasing during the warm phase (Fig. 2B,C). By contrast, landings from CCh and SCh showed no significant correlations with PDO.

Mesodesma mactroides

The cumulative sum of the AMO showed a regime shift between 1994 and 1995 (Fig. 3A). This climatic index was positively correlated with SSTA recorded for the study zone ($r^2 = 0.39$, $p < 0.005$), displaying the best fit with a lag of 4 yr between them (i.e. $SST_{(t+4)}$ vs. $AMO_{(t)}$) (Fig. 3B). Yellow clam abundance was inversely correlated with AMO variations, displaying the best fit with a lag of 4 yr (i.e. $abundance_{(t+4)}$ vs. $AMO_{(t)}$; $r^2 = 0.19$, $p < 0.05$), meaning higher abundance during the cold period and lower during the warm one (Fig. 3C).

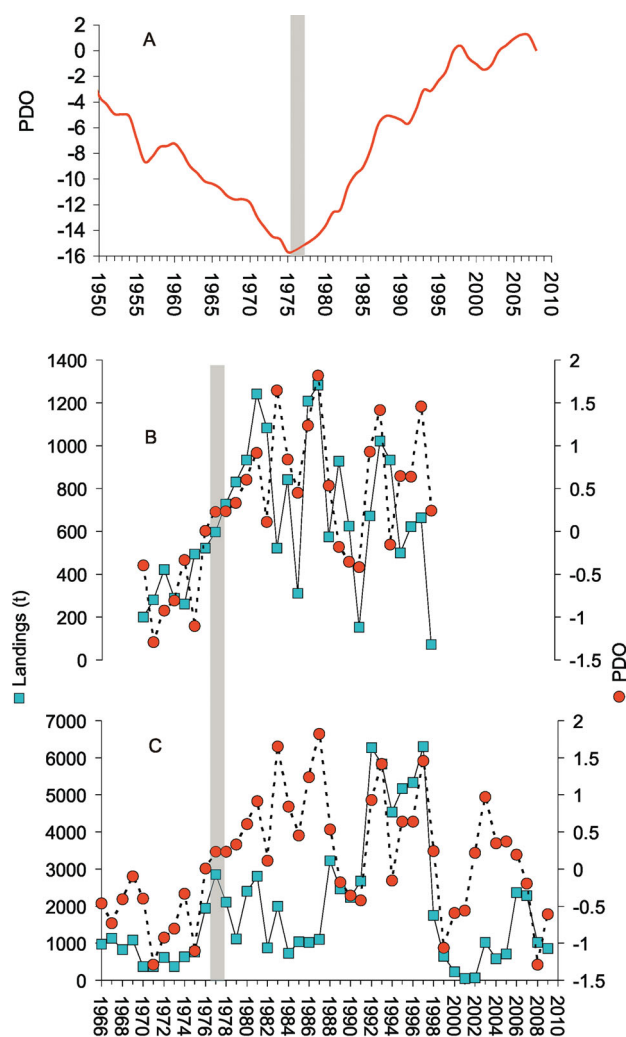


Fig. 2. *Mesodesma donacium*. (A) Cumulative sum of the Pacific Decadal Oscillation (PDO) index; and long-term variations in landings (■) and in the PDO (●) for (B) Peru and (C) Northern Chile. Shaded bar: climate shift in 1977, according to Fiedler (2002) and Chavez et al. (2003). Note the different scales on the x-axes in (A) and (B,C), and in the left-hand y-axes in (B,C)

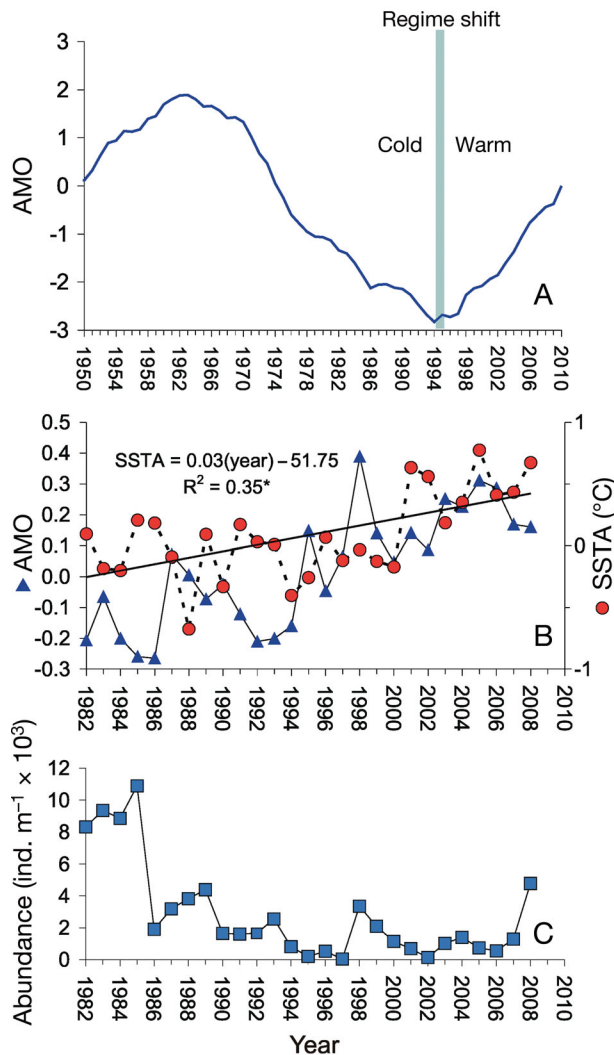


Fig. 3. (A) Cumulative sum of Atlantic Multidecadal Oscillation (AMO) from 1950 to 2008; (B) annual variations in sea surface temperature anomalies (SSTA, ●) and AMO (▲) for the period 1982 to 2008; (C) long-term variations in abundance of *Mesodesma mactroides*, from sampling surveys conducted between 1982 and 2008. The regression equation in (B) corresponds to the models fitted between SSTA and time (years) (* $p < 0.001$). Shaded bar in (A): shift in the ocean-climate regime from a cold to a warm period between 1994 and 1995 (see Goldenberg et al. 2001 for details on this shift)

Interannual coastal scale

Mesodesma donacium

The *Mesodesma donacium* fishery in Peru showed an initial phase characterized by landings ranging between 200 t in 1970 to 521 t in 1976. The expansion phase occurred between 1977 and 1980, when catches reached ca. 4000 t, during the period preceding the strongest ENSO event, which occurred in 1982–83. This event caused mass mortalities, and no

live surf clams were found in shallow waters south of Lima. After another strong warm ENSO event (1997–98), the fishery was closed (1999). This management decision is still in place in Peru (Fig. 4).

The macha fishery in Chile showed an initial fishery phase between 1966 and 1982, characterized by landings ranging between 1000 and 6000 t (Fig. 4). The expansion phase extended approximately between 1983 and 1989 (Fig. 4), as a response to a strong trend toward diversification in the exportation of many Chilean shellfish products. Landings peaked in 1989, reaching ~18 000 t, and drastically declined thereafter (1990 to 2006) down to <4000 t. The reduction in the exported volume from 2329 t (1989) to 1641 t (1992) was compensated by a higher exportation price, reaching the highest export earnings in 1988 (US \$ 9 381 000). Long-term variations in macha unit prices from Chile significantly increased through time, particularly between 1986 and 1988 and from 2002 to 2008 (Fig. 4).

All bioclimatic units showed oscillations in SSTA through time associated with cold and warm periods. With the exception of Peru, SSTA significantly increased through time (Fig. 5), with the highest temperatures observed during the strong ENSO events of 1982–83 and 1997–98 (shaded areas in Fig. 5). Landings in Peru drastically decreased from 4000 t in 1978 to 500 t in 1983 (Fig. 6A). Between 1984 and 1997, landings were ~800 t, and drastically dropped from 700 to 70 t during the 1997–98 ENSO event. Since 1999, the fishery has been closed.

Concerning NCh, the fishery showed a development phase between the 1960s and the mid-1970s, followed by an expansion phase that was interrupted in 1983 (ENSO). The fishery was recovered during the 1990s, reaching the highest historical value in 1997 (6000 t), and dramatically declined 1 yr later (<2000 t), until reaching the lowest value in 2001 (45 t, see Fig. 5B). Concerning CCh, landings showed 2 peaks: the first was observed in the early 1970s, concurrently with a period of negative SSTA, whereas the second occurred in 1986 (7500 t), thereafter decreasing until reaching the lowest values after the 1997–98 ENSO (Fig. 5C). In SCh, landings also showed 2 major peaks (Fig. 5D): the main one in 1988–89 and the second one in 1998, during the ENSO event. A strong increase in landings occurred just after the ENSO of 1982–83, and was followed by an exponential drop during the 1990s (from 9000 to <500 t between 1993 and 1997). Landings increased 8-fold during the 1997–98 ENSO event (4000 t), but this pulse was followed by an exponential decrease, reaching <2000 t yr⁻¹ at the end of the period.

GAM results are shown in Table 1. SSTA was a significant predictor of long-term variations in Peruvian landings (Table 1). Partial residuals showed a linear decrease through time and a nonlinear relationship with SSTA. In the latter, landings were highest at SSTA values close to -1°C , and dramatically declined with positive SSTA values (Fig. 6A). The decline in partial residuals through time suggests that the effect of SSTA alone was insufficient to change the observed trend in landings (Fig. S1A in the supplement at www.int-res.com/articles/suppl/m469p071_supp.pdf). In NCh, unit price was a significant nonlinear predictor of long-term variations in landings (Fig. 6B), but partial residuals showed a similar trend through time to that observed in raw data, particularly from 1976 onwards, when market statistics began, suggesting that the effect of market price was not the only explanatory variable of landing fluctuations (Table 1; Fig. S1B in the supplement).

For CCh, GAM results showed that price and SSTA were the best significant predictors ($p < 0.01$) of macha landings, as evidenced by the consistent increase in r^2 and explained deviance, concurrently with a decrease in AIC (Table 1). Partial residuals followed a nonlinear decreasing relationship with unit price and a negative linear relationship with SSTA (Fig. 7A; Fig. S2A in the supplement). No statistical differences in residual deviance were observed ($p(F)$

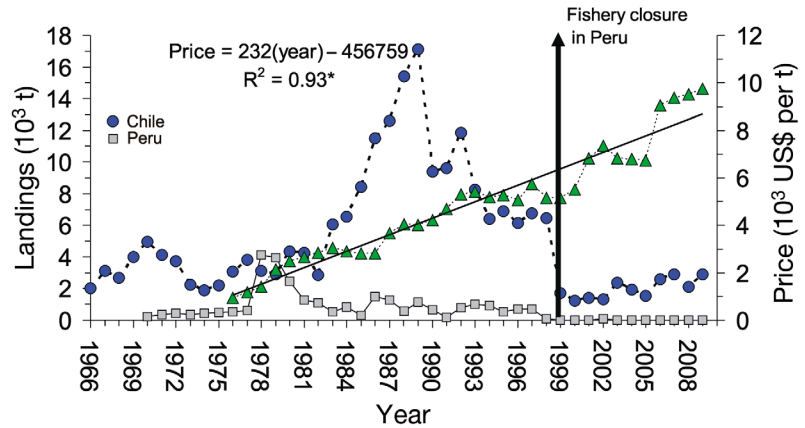


Fig. 4. *Mesodesma donacium*. Long-term trends in landings for Chile (●) and Peru (■), and in unit prices for the Chilean fishery (▲). The regression equation corresponds to the linear model fitted between unit price and time (year) (* $p < 0.001$)

= 0.18) between the model with price (GAM CCh²) and the one with SSTA (GAM CCh³) (Table 1), meaning that both variables have the same importance as predictors of long-term trends. However, the shape of the curve of partial residuals through time did not differ from the one observed with raw data, indicating that market price and SSTA cannot explain entirely the observed trends. The effect of market price is noticeable in partial residuals of the model: removing the effect of market price determined a change in the relationship between landings and SSTA (Fig. S3 in the supplement).

Concerning SCh, unit price and SSTA were also the best significant predictors ($p < 0.01$) of long-term macha landings. Partial residuals showed a nonlinear negative relationship with unit price and, in contrast with the other bioclimatic units, a positive linear relationship with SSTA (Figs. 7B, S2B). The model that included only unit price (GAM SCh²) explained a higher percentage of deviance, and had a lower AIC and lower residual deviance ($p(F) < 0.001$) than the model that only included SSTA (GAM SCh³) (Table 1). Partial residuals showed a similar trend through time to that observed in raw data, indicating that the effect of market price and SSTA cannot explain entirely the observed trend in landings. Further analyses performed by modeling macha landings versus price (only for Chile, for which price information is available) showed that this relationship was significant for all 3

Table 1. *Mesodesma donacium* and *M. mactroides*. Generalized additive model selection, (GAM) for *M. donacium* landings and *M. mactroides* abundance. Non-significant terms ($p > 0.05$) were dropped from the model. Superscripts in the GAM column denote different models for the same region. The best model for each region and species is in **bold**. edf: estimated degrees of freedom; adj.: adjusted; DE: deviance explained; AIC: Akaike information criterion; s: spline smoother; Lan: landings; AB: abundance; f: fishing effort; SSTA: sea surface temperature anomalies; CCh: Central Chile; NCh: Northern Chile; SCh: Southern Chile; Uy: Uruguay

GAM	Terms	edf	Adj. r^2	DE (%)	AIC
Peru	Lan ~ s(Year) + s(SSTA)	3.70	0.36	44.7	463
NCh	Lan ~ s(Year) + s(Price)	8.98	0.91	94.0	494
CCh¹	Lan ~ s(Year) + s(Price) + s(SSTA)	9.01	0.94	95.8	486
CCh ²	Lan ~ s(Year) + s(Price)	8.06	0.92	94.1	495
CCh ³	Lan ~ s(Year) + s(SSTA)	9.34	0.92	94.7	494
SCh¹	Lan ~ (Year) + (Price) + s(SSTA)	11.27	0.82	88.8	537
SCh ²	Lan ~ (Year) + (Price)	10.27	0.77	84.8	545
SCh ³	Lan ~ (Year) + (SSTA)	1.85	0.19	24.2	580
Uy¹	AB ~ s(Year) + s(f) + s(SSTA)	9.01	0.94	96.0	410
Uy ²	AB ~ s(Year) + s(f)	4.57	0.88	90.4	424

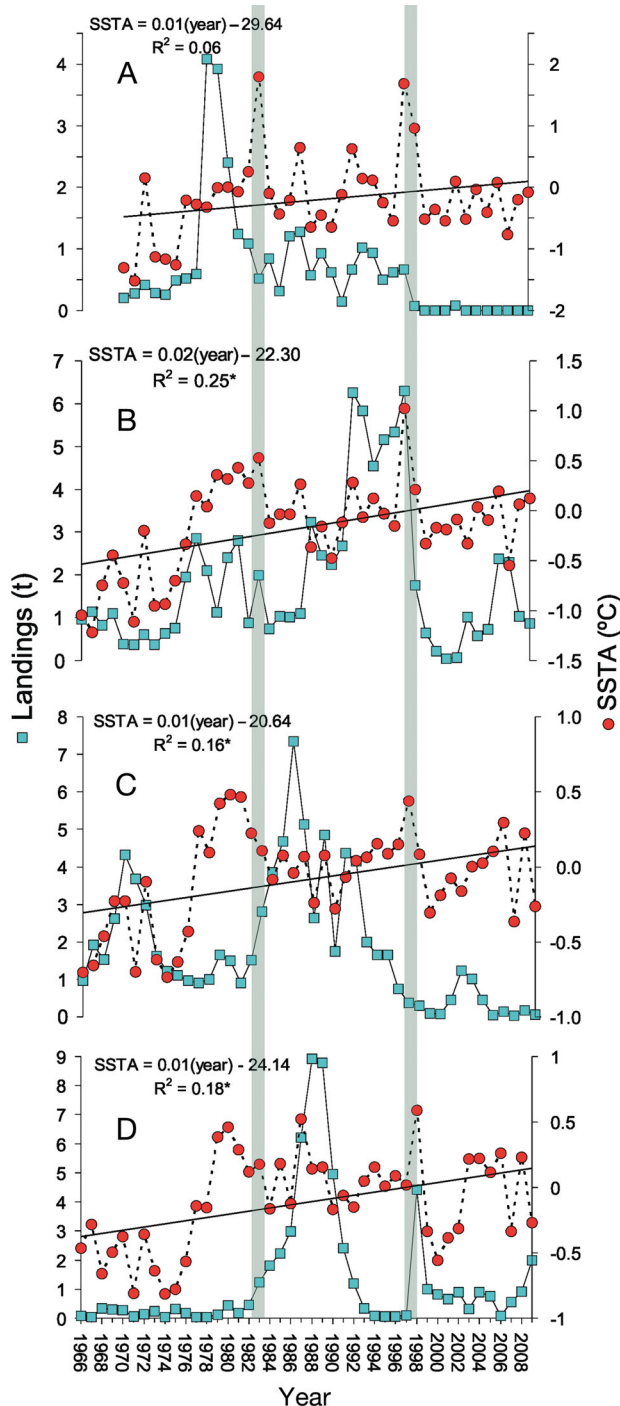


Fig. 5. *Mesodesma donacium*. Annual landings (■) and regional annual mean sea surface temperature anomalies (SSTA) (●) for (A) Peru, (B) Northern Chile, (C) Central Chile, and (D) Southern Chile. Shaded bars: strong El Niño Southern Oscillation (ENSO) events of 1982–83 and 1997–98, which matched with the highest SSTA and a decrease in landings in Peru and Northern Chile. The regression equations correspond to the models fitted between SSTA and time (year) (* $p < 0.001$). Note the different scales for both the right- and left-hand y-axes

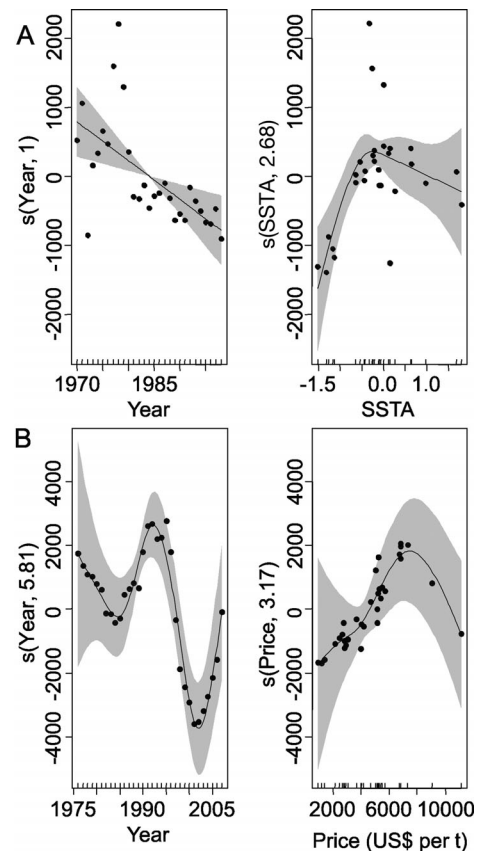


Fig. 6. *Mesodesma donacium*. Estimated generalized additive model (GAM) terms showing the partial residuals (solid lines) of annual landings after fitting against (A) time (year) and sea surface temperature anomalies (SSTA) in Peru; and (B) time (year) and price in Northern Chile. Shaded area: ± 2 SE above and below the estimated smooth curve. Numbers on each y-axis are the estimated degrees of freedom of the plotted terms (partial residuals of landings)

Chilean regions (Table S1 in the supplement). The relationship between model residuals and SSTA was not significant for NCh and SCh, whereas a negative relationship ($r^2 = 0.16$, $p < 0.05$) was found for CCh (Fig. S4A in the supplement).

Mesodesma mactroides

The long-term analysis of the artisanal yellow clam fishery in Uruguay showed a initial phase during early 1980s, followed by an overexploitation phase and the closure of the fishery in 1987 (Fig. 8A). An increase in unit price was observed through time, even at low landing and abundance levels (Fig. 8A). The best unit price-catch relationship followed a function of the form ($r^2 = 0.78$; $p < 0.001$): $\text{Price} = 19.33 \times \text{Catch}^{-0.63}$. The percentage of the harvestable

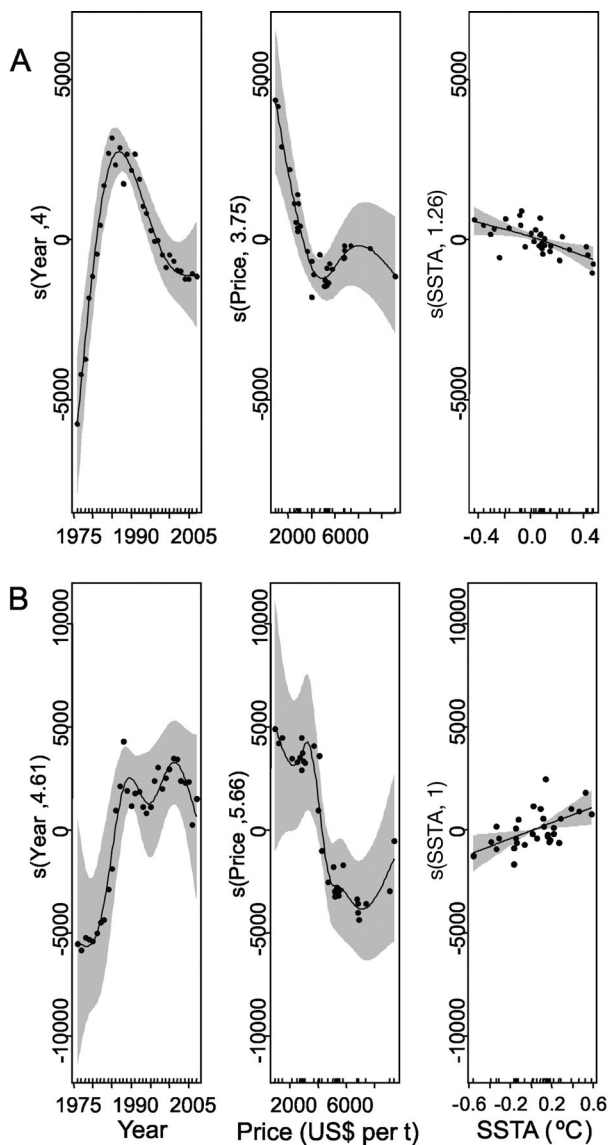


Fig. 7. *Mesodesma donacium*. Estimated generalized additive model (GAM) terms showing the partial residuals of annual landings (solid lines) after fitting against time (years), price, and sea surface temperature anomalies (SSTA) for (A) Central Chile and (B) Southern Chile. Shaded areas: ± 2 SE above and below the estimated smooth curve. Numbers on each y-axis are the estimated degrees of freedom of the plotted terms (partial residuals of landings). Note the different scales

(adult abundance) significantly increased between 1989 and 1994, just after the fishery closure (1987 to 1989). However, the occurrence of several mass mortality events that began in late 1993 determined a new fishery closure until 2008, without showing evidence of stock recovery throughout this period, particularly in the case of the adult (harvestable) stock (Fig. 8B).

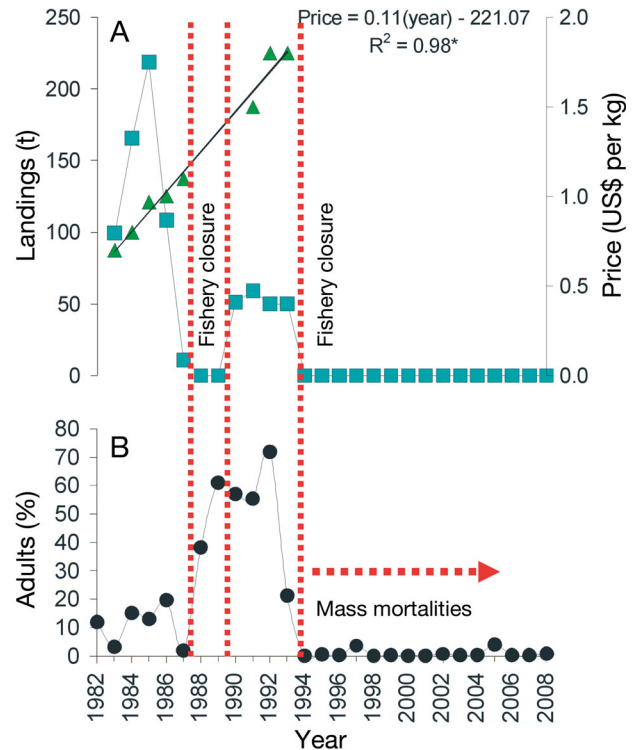


Fig. 8. *Mesodesma mactroides*. Long-term variations in: (A) landings (■) and unit price (▲); and (B) the harvestable stock, as denoted by the percentage of adults (●). The regression equation in (A) corresponds to the linear model fitted between unit price and time (year) ($*p < 0.001$). The red arrow highlights the beginning of mass mortalities since 1993–94 (see Fiori et al. 2004 for details on mass mortalities)

Fishing effort exerted in the previous year and SSTA were the best predictors of yellow clam abundance (Fig. 9, Fig. S5 in the supplement, Table 1). Partial residuals showed a positive relationship with fishing effort and 2 contrasting trends with SSTA: a positive nonlinear relationship with negative SSTA and a negative one with positive SSTA. Partial residuals through time showed the same pattern as for abundance, indicating that the effect of fishing effort and SSTA are insufficient to explain temporal variations in yellow clam abundance. The relationship between abundance and fishing effort was statistically significant (Table S1 in the supplement). The residuals of the model were negatively correlated with SSTA ($r^2 = 0.19$; $p < 0.05$) (Fig. S4B in the supplement).

DISCUSSION

This paper gives evidence of long-term and large-scale effects of fishery bioeconomic factors and climate variability in intertidal sandy beach clams. The

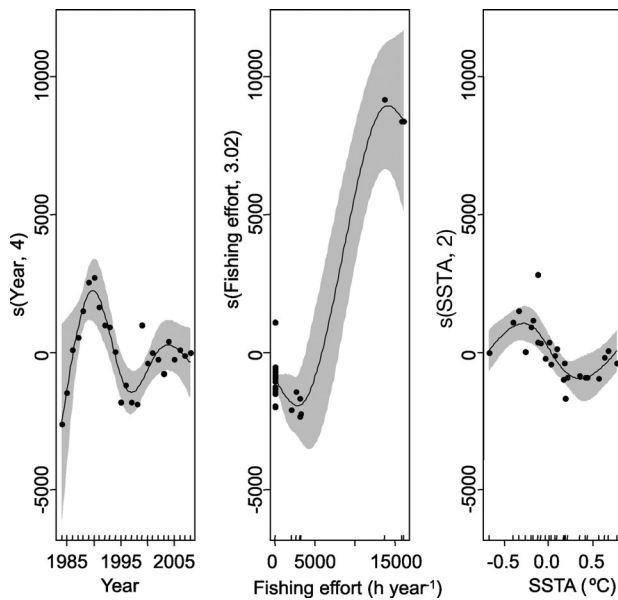


Fig. 9. *Mesodesma mactroides*. Estimated generalized additive model (GAM) terms showing the partial residuals (solid lines) of abundance after fitting against time (year), fishing effort exerted in the previous year, and sea surface temperature anomalies (SSTA). Shaded areas: ± 2 SE above and below the estimate of the smooth curve. Numbers on each y-axis are the estimated degrees of freedom of the plotted term (partial residuals of abundance)

effect of these variables on *Mesodesma donacium* and *M. mactroides* clam fisheries was complex and varied in a differential way according to latitude and the intrinsic characteristics of the oceanographic systems. In this setting, the nature and sign of the relationship between Pacific macha landings and explanatory predictors varied by bioclimatic unit. Indeed, Peruvian landings were negatively correlated with SSTA and appeared to be dramatically affected by ENSO events (particularly 1997–98). By contrast, landings in SCh were positively and significantly correlated with SSTA, suggesting that species abundance could respond positively to slight increases in temperature at its southernmost distribution range. Our findings reinforce the notion that systems can respond in different ways to changes in drivers such as exploitation pressure or temperature rise (Scheffer et al. 2009). Even though our modeling approach was useful to assess the effects of market price, fishing effort, and climate on long-term trends in landings or abundance of sandy beach clams, it is not suitable for predictive purposes. In this vein, modeling catastrophic events (mass mortalities) needs another approach that is far beyond the scope of the present paper.

The dramatic drop in landings at the northernmost edge of the *Mesodesma donacium* range (Peru) and in NCh, observed during or close to strong ENSO events, supports the notion that ENSO constitutes an important natural threat for the macha in the northernmost bioclimatic unit. ENSO is the major intra-decadal and large-scale climate-driven forcing factor in the Chilean–Peruvian coastal upwelling system (Baumgartner & Ortlieb 2002, Chavez et al. 2003, Montecino & Lange 2009), causing dramatic changes in faunal assemblages (e.g. Barber & Chavez 1983, Castilla & Camus 1992, Chavez et al. 1999, Tarazona & Arntz 2001), and affecting the domestic economy of Chile and Peru (Thatje & Heilmayer 2008), including artisanal fisheries (see Castilla & Camus 1992). In addition, the fast boom-and-bust cycle of the fishery in Peru aggravated the situation, suggesting that cumulative impacts of climate and fishing could have prompted the fishery collapse.

The inverse relationship between landings and temperature should be seen as a threshold where other processes took place. The increase in SSTA through time and the occurrence of ENSO events might have challenged *Mesodesma donacium* by distancing populations from optimal environmental conditions, operating directly through physiological processes (metabolism or reproduction) or indirectly through related changes in ecosystem structure (Stenseth et al. 2002). In this vein, mass *M. donacium* mortalities that occurred during strong warm ENSO events have been mainly associated with rising temperatures and increasing susceptibility to parasitism and diseases under anomalous environmental conditions (Arntz et al. 1987, Ibarcena et al. 2005, Riascos et al. 2009, 2011). These mass mortalities, which mainly occurred at the northernmost bioclimatic unit, generated drastic changes in the ecosystem and in the macrofaunal community structure, including increasing densities of subordinate competitors, such as the clam *Donax obesulus* (Arntz et al. 1987, Carstensen et al. 2010).

Mesodesma donacium landings in SCh increased under positive SSTA and during ENSO events, showing an opposite pattern to that observed for the northernmost edge. These trends suggest positive effects of increasing temperatures on clam abundance or fishery activity in this bioclimatic unit, which could be explained by 3 non-mutually exclusive hypotheses: (1) an increase in temperature in an actually cold system, together with a southward weakening of ENSO environmental effects and an improvement in climatic conditions; (2) a 'mining-shellfish exploitation strategy' behavior (sensu Defeo

& Castilla 2005), where fishers and divers sequentially move into less-exploited clam beds (i.e. from NCh to SCh); and (3) the existence of a genetic structure along geographic distribution of the species, with 2 groups of haplotypes and a contact zone between 32° and 34° S (CCh), which could explain different responses to climate variability (Peralta 2008). Populations at the edges of a species range could have particular adaptations to extreme conditions, but climate changes make them even more vulnerable to fishing activity. From a management and conservation point of view, this means that special protection should be placed on these populations, where the first adverse environmental impacts are expected to occur (e.g. Peru and NCh). As the rate of change may overwhelm the ability of a species to adapt, a policy of 'managed retreat' (Brander 2010) should be needed. Indeed, a main implication of these trends is that efforts to reduce the risk of unwanted state shifts should address the gradual changes that affect resilience (Scheffer et al. 2001).

Long-term abundance fluctuations in the Atlantic yellow clam clearly showed that environmental effects, reflected by a systematic increase in SSTA, in addition to uncontrolled fishing at the beginning of the study period, have swamped management measures. Indeed, the fishery closure implemented between 1987 and 1989 allowed a fast and strong recovery of the harvestable (adult) stock (Defeo 1996, 1998; our Fig. 8). The fishery was reopened from December 1989 onwards, under a co-management scheme and a precautionary approach that included several management regulations (Defeo 1998). During the co-management phase, harvestable stock abundance increased and catch per unit effort (CPUE) was much higher than in preclosure years (see our Fig. 8B; Castilla & Defeo 2001). However, the occurrence of mass mortalities registered from 1994 onwards decimated the stock, which has not fully recovered since then (see our Fig. 8B; Defeo 2003). A similar situation was observed in Brazil and Argentina (Fiori & Defeo 2006, Herrmann et al. 2011). These mass mortalities sequentially occurred in a north-south direction from 1993 (southern Brazil) to 2002 (Isla del Jabali, Argentina), mainly between late spring and early summer, when these cold-water clams are more sensitive to diseases (Fiori et al. 2004). It is hypothesized that the systematic increase in SSTA, associated with a southward migration of a critical warm isotherm, has exacerbated the negative influence of oceanic warm waters (L. Ortega et al. unpubl.). Concurrently with the systematic increase in SSTA, long-term increasing effects of diseases and

deformities (e.g. foot and gills) have been observed in this clam (Fiori et al. 2004, E. Delgado et al. unpubl.).

Regional warming could also have triggered drastic long-term changes in Atlantic sandy beach communities: mass mortalities of yellow clam promoted an exponential increase of warm-favoring species, such as the wedge clam *Donax hanleyanus* and the mole crab *Emerita brasiliensis*, which are subordinate competitors for space and food in this suspension-feeding guild (Defeo 2003). This shift that occurred in the ecosystem after surpassing a critical threshold or tipping point has been observed in sandy beach ecosystems from southern Brazil, Uruguay (Defeo 2003), and Argentina (Dadón 2005, Herrmann et al. 2009, Thompson & Sánchez De Bock 2009).

We found a significant effect of broad-scale climate variations on both clam fisheries. Tropical SSTA variations are in phase with AMO, which adds support to the evidence that AMO influences South American climate (Seager et al. 2010). In the Uruguayan coast, the positive correlation between SSTA and the AMO suggests that the latter could also affect circulation patterns. In fact, the observed shift from a cold to a warm phase after 1994, the sustained rise in temperature in the SW Atlantic, the southward range shift of tropical species (Segura et al. 2009, Izzo et al. 2010), and the mass mortalities observed since 1993 reinforce the hypothesis of changing of circulation patterns. These effects have been mainly documented in the northern Atlantic (Beaugrand 2004, Gröger & Fogarty 2011), whereas catch fluctuations in the southern Atlantic have been associated with unidentified low-frequency oceanographic anomalies and overfishing (e.g. Brazilian sardine; Matsuura 1996).

In the HCS, biological and non-biological components, ecosystem processes, and fisheries are known to be affected by multidecadal scale variations. In fact, air and ocean temperatures, atmospheric carbon dioxide, landings of pelagic fish, and the productivity of coastal and open ocean ecosystems have varied over periods of about 25 to 50 yr (Montecino & Lange 2009). In the mid-1970s, the Pacific changed from a cold to a warm regime (see Fig. 2A). A shift back to a cold regime occurred in mid to late 1990s (our Fig. 2B,C; Chavez et al. 2003). These basin-scale climate shifts might have influenced NCh and Peru *Mesodesma donacium* landings, with a positive response during the warm phase and a decline during the cold phase, concurrently with the 1997–98 ENSO. The prevailing hypothesis is that the PDO is caused by a 'reddening' (oceanic or other slow components of the climate system outside the domain of

study) of ENSO events, combined with stochastic atmospheric forcing, which goes against the idea that PDO may regulate decadal climate variability (Newman et al. 2003, Pavia 2009, Shakun & Shaman 2009). Consequently, the PDO could be seen as a consequence of past accumulated ENSO events that produce mild ENSO-like conditions in southern tropical Pacific coastal zones (i.e. deeper thermocline, positive SSTA, higher sea level). In contrast, high-frequency climate variations like ENSO, especially strong events, had dramatic negative effects on *M. donacium* at the northern Pacific bioclimatic units.

Unit price significantly increased through time in both *Mesodesma* clam fisheries. The steady increase in prices at low landing levels accelerated changes in resource use motivated by profit, suggesting that this variable constitutes a key economic driver that could lead to stock depletion. The growing demand associated with high export prices in *M. donacium* triggered an increase in fishing effort, which in turn affected stock sustainability. This response to market forcing was clearly shown in NCh, where landings dropped after reaching a certain unit export price, probably masking the relationship with SSTA. A similar pattern was observed in the artisanal Peruvian bay scallop *Argopecten purpuratus* fishery (Badjeck et al. 2009). In Peru, the negative effects of ENSO (1982–83) on *M. donacium* were exacerbated by a high fishing intensity (1980 to 1981) and a sustained increase in global market demand (i.e. the southern Peru production of macha was exported to Chile; Ibarcena et al. 2005). In addition, the opening of *M. donacium* foreign markets (i.e. Spain) towards the selection of clam sizes lower than the legal marketable size has been observed (Defeo et al. 1993). Thus, overexploitation trends were aggravated by globalization of markets. The increase of prices even at low landing and abundance levels, observed in both Pacific and Atlantic *Mesodesma* fisheries, resemble the anthropogenic Allee effect, in which exploitation rates increase with decreasing population size or density (Courchamp et al. 2006, Berec et al. 2007). This phenomenon is particularly noticeable in coastal stocks artisanally harvested, such as the intertidal clams analyzed here, because price values of the exploited species largely exceed the negligible exploitation costs in easily and readily accessible fishing grounds (Defeo & Castilla 2012). This highlights the need to consolidate institutional management responses, supported by integrative science, as a means to develop solid governance fishery systems to promote resilience under uncertainty (Thatje et al. 2008, Miller et al. 2010, Gutiérrez et al. 2011, Perry et al. 2011).

In summary, a complex combination of intensive exploitation, bioeconomic factors, and climate variability explained large-scale and long-term trends in landings and abundance of sandy beach clams. These factors acting together may accelerate the decline in the clams' abundance, leading them to population levels close to extinction. The lack of response of the stocks to drastic management measures (i.e. long-term closures) suggests that these complex social-ecological systems have exceeded critical thresholds (tipping points), shifting abruptly from one state to another through a catastrophic bifurcation that propels the system through a phase of directional change towards a contrasting state (Scheffer et al. 2009). Early warnings of climate tipping points (Lenton et al. 2008, Scheffer et al. 2009, Lenton 2011) could provide information to help manage sandy beach ecosystems that are increasingly threatened by long-lasting and large-scale stressors (Defeo & McLachlan 2005, Schlacher et al. 2007, Defeo et al. 2009).

Acknowledgements. This paper is part of the PhD thesis of L.O. We thank the 'Benthic Ecology Group' of UNDECIMAR for field and laboratory assistance. Financial support was provided by The Pew Charitable Trust to O.D., DINARA (Food and Agriculture Organization (FAO) and Global Environmental Facility (GEF) projects), Agencia Nacional de Investigación e Innovación (ANII), and Programa de Desarrollo de las Ciencias Básicas (PEDECIBA). J.C.C. acknowledges financial support from, Ministerio de Economía, Fomento y Turismo, Chile. C. H. Peterson and 2 anonymous referees provided useful comments that improved the manuscript.

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*Submitted: February 13, 2012; Accepted: August 21, 2012
Proofs received from author(s): November 9, 2012*