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Thriving and declining: climate variability shaping life-history and population persistence of *Mesodesma donacium* in the Humboldt Upwelling System

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ABSTRACT: Large-scale environmental patterns in the Humboldt Current System (HCS) show major changes during strong El Niño episodes, leading to the mass mortality of dominant species in coastal ecosystems. Here we explore how these changes affect the life-history traits of the surf clam *Mesodesma donacium*. Growth and mortality rates under normal temperature and salinity were compared to those under anomalous (El Niño) higher temperature and reduced salinity. Moreover, the reproductive spatial–temporal patterns along the distribution range were studied, and their relationship to large-scale environmental variability was assessed. *M. donacium* is highly sensitive to temperature changes, supporting the hypothesis of temperature as the key factor leading to mass mortality events of this clam in northern populations. In contrast, this species, particularly juveniles, was remarkably tolerant to low salinity, which may be related to submarine groundwater discharge in Hornitos, northern Chile. The enhanced osmotic tolerance by juveniles may represent an adaptation of early life stages allowing settlement in vacant areas at outlets of estuarine areas. The strong seasonality in freshwater input and in upwelling strength seems to be linked to the spatial and temporal patterns in the reproductive cycle. Owing to its origin and thermal sensitivity, the expansion and dominance of *M. donacium* from the Pliocene/Pleistocene transition until the present seem closely linked to the establishment and development of the cold HCS. Therefore, the recurrence of warming events (particularly El Niño since at least the Holocene) has submitted this cold-water species to a continuous local extinction–recolonization process.

KEY WORDS: El Niño · Fresh water input · Geographic distribution · Reproductive cycle · Sandy beach ecology · Submarine groundwater discharge · Macroecology

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INTRODUCTION

The surf clam *Mesodesma donacium* (Lamarck, 1818) is an important species from both an economical and ecological perspective. It is one of the most important species for Chilean and Peruvian benthic fisheries in the Humboldt Current System (HCS), an ecosystem ranking among the most productive marine systems worldwide (Tarifeño 1980, Defeo et al. 1993, McLachlan et al. 1996, Thiel et al. 2007). *M. donacium* often exhibits high densities and extremely high annual production (up to 2900 g shell-free dry mass m^{-2}), thus representing >95% of the shallow soft-bottom community (Arntz et al. 1987). This filter-feeding clam inhabits the swash zone of exposed, high-energy intermediate and dissipative sandy beaches, often located near river mouths, where it typically burrows down to a depth around 10 cm, though it can sometimes reach

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25 cm when disturbed (Tarifeño 1980, Jaramillo et al. 1994). In Chile, adult clams are primarily confined to the subtidal, at water depths ranging between 3 and 15 m, while the vast majority of juveniles occur mainly in the intertidal zone, often in the outlets of estuarine areas (Tarifeño 1980, Jaramillo et al. 1994, Riascos et al. 2008a), although an inverse depth pattern between juvenile and adult clams has been described for Peruvian populations (Arntz et al. 1987). The reproductive cycle of *M. donacium* has been found to be influenced by local variability in water temperature and food availability (Tarifeño 1980, McLachlan et al. 1996). The long meroplanktonic larval stage (30 to 45 d) allows plenty of time for the phytoplanktophagous larvae to find suitable unoccupied sediments in which to settle (Tarifeño 1980).

Environmental conditions in the HCS are broadly characterized by nutrient-rich, cool waters, showing limited seasonal temperature variability compared to that in other coastal ecosystems at similar latitudes (e.g. Arntz et al. 1987, Camus 2001, Thiel et al. 2007). The influence of the year-round upwelling of cold subsurface water causes an atypical weak north–south temperature gradient and extends the influence of cold environmental conditions northward (Menzies 1962, Camus 2001). As a consequence, many species in the HCS exhibit broad distributional ranges and are adapted to fairly constant low water temperatures in this area (Santelices 1980, Brattström & Johanssen 1983, Urban 1994). However, during strong El Niño events (the warm phase of the El Niño–Southern Oscillation) warmer, nutrient-poor, less-saline waters are transported into the nearshore zone by coastal Kelvin waves, triggering several physical changes in the water column (Arntz et al. 2006). These changes result in mass mortalities of *Mesodesma donacium* and leave an impoverished sandy beach community mainly consisting of small opportunistic organisms (Arntz et al. 1987). Originally distributed from Peru (Sechura, 5° 10′ S) to southern Chile (Chiloe, 43° 20′ S) (Tarifeño 1980), *M. donacium* was set back south to 14° S (southern Peru) after the severe El Niño in 1982-83 (Arntz et al. 1987) and further south after the El Niño in 1997-98, which wiped out large populations in Arica (18° 20′ S) and Coquimbo (29° 55′ S) (Thiel et al. 2007), leaving only some minor, scattered populations in between.

The shallow-water fauna in the HCS is closely adapted to sea surface temperature. This distinctive feature defines large-scale biogeographical patterns in this region (Castilla 1979, Camus 2001). Therefore, thermal anomalies are expected to explain changes in performance and distribution of marine bivalves during El Niño (Urban 1994). On the other hand, reduced salinity seems particularly important to understand *Mesodesma donacium* responses to El Niño, given the strong increases in freshwater input to the coastal zone during these events (e.g. Waylen & Caviedes 1990). However, the lack of experimental work addressing factor-specific effects precludes convincing explanations for the numerous changes that have been described (Arntz et al. 2006, Thatje et al. 2008). Establishing links between the life-history traits of *M. donacium* and large-scale environmental settings during non-El Niño conditions is a crucial step in assessing the responses to El Niño and subsequent recovery. Reproduction and recruitment are key processes controlling long-term variability and persistence of marine bivalve populations (Bricelj et al. 1987, Lima et al. 2000, Beukema & Dekker 2007). Based on both, observational and experimental data sources, this paper aims to: (1) determine the effects of higher temperature and reduced salinity, expected under El Niño conditions, on growth and mortality of *M. donacium*; (2) describe the latitudinal patterns of reproductive activity and assess the link with large-scale environmental variability; and (3) analyse consequences for the long-term development and persistence of this species in Chile and Peru.

MATERIALS AND METHODS

Effects of temperature and salinity on growth and mortality. Specimens of *Mesodesma donacium* (n = 135) were collected in February 2006 from Hornitos, northern Chile (22° 54′ S; Fig. 1), which is currently the northernmost population of this species. Juvenile clams were collected in the intertidal, whereas adults were collected in the shallow subtidal (i.e. up to 5 m). After sampling, clams were immediately transported to the laboratory and acclimated for 25 d at ambient temperature (17.4°C) and salinity (~35 psu) in a 12 h day: 12 h night cycle before being transferred to experimental conditions. Clams were fed ad libitum with a mixed diet (1:1) of micro-algae (*Chaetoceros calcitrans* and *Isochrysis galbana*). Low mortality (9 clams) was observed during this period.

After acclimation, clams were incubated for 3 h in slightly aerated filtered seawater containing 50 mg l^{-1} calcein (Sigma, CAS 1461-15-0). This procedure was used to incorporate a fluorescent band in shells of *Mesodesma donacium* in order to determine short-term growth increments after the treatment (for details see Riascos et al. 2007). After calcein marking, individuals were divided into 2 groups based on anterior–posterior shell length (mm): juveniles: (6.0 to 29.9 mm; average = 13.5 mm) and adults (52.7 to 72.4 mm; average = 62.6 mm). Clams from each group were randomly assigned to a 3×2 factor experimental design: 3 salinities (10 ± 1, 20 ± 1 and 35 ± 1 psu) and 2 temperatures

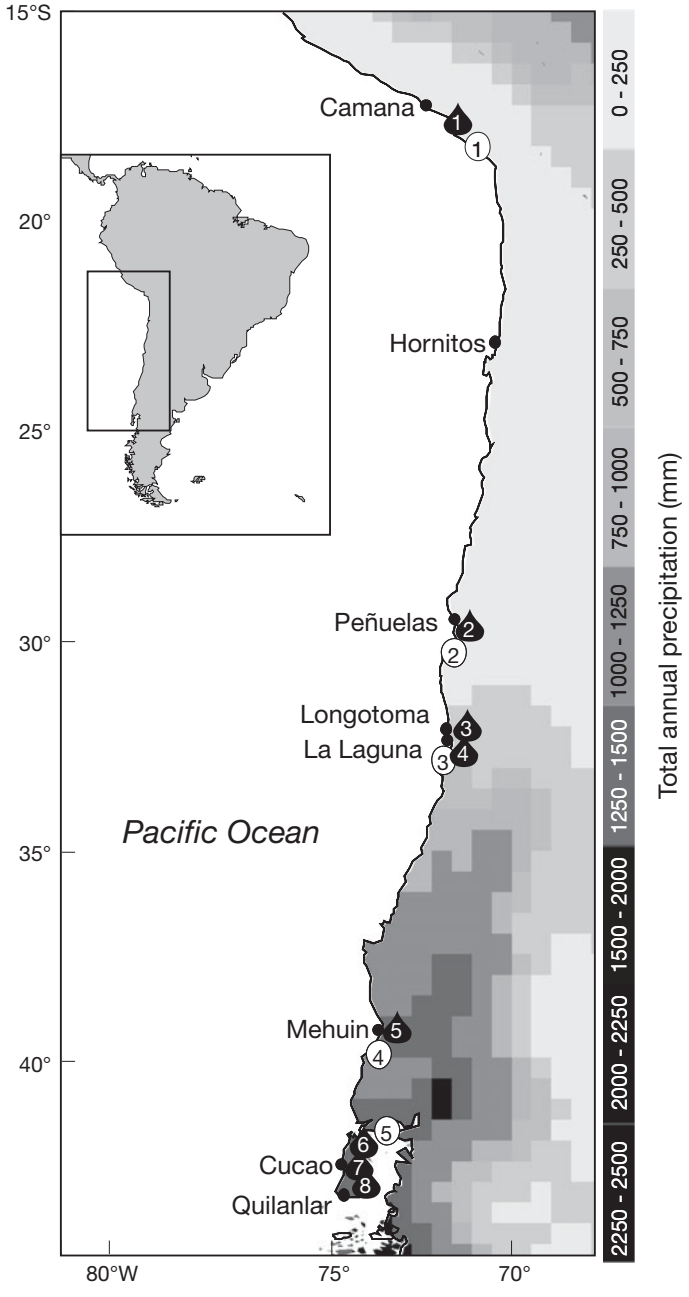

Fig. 1. Total annual precipitation (modified from Legates & Willmott 1990) in the study area, geographic location of sandy beaches (black dots) considered in the analysis of the reproductive cycle of *Mesodesma donacium* and location of stations for sea surface temperature (circles — 1: Ilo; 2: Coquimbo; 3: Valparaíso; 4: Corral; 5: Puerto Montt) and precipitation (drop symbols — 1: Mollendo; 2: La Serena; 3: Petorca; 4: La Ligua; 5: Toltén; 6: Tres Cruces; 7: Piruquina; 8: Castro). Data sources as indicated in Table 2

(17.4 ± 0.5°C, the historical annual average, hereafter called 'the normal temperature' and 24.2 ± 0.5°C, the maximum temperature registered during El Niño 1982-83, hereafter called 'the El Niño temperature'; data from CENDHOC 2008). Each combination was run with 3 replicates and 7 clams replicate^{-1}. Clams were conditioned over 2 wk to high temperature and low salinities by gradually increasing temperature and/or reducing salinity. They were fed as stated before and held in experimental conditions for 1 mo in 35 l tanks (1/3 sterilised sand) in temperature-controlled rooms and a 12 h day:12 h night cycle. Seawater was filtered (0.1 µm), continuously aerated and exchanged daily. Twice a day, sand was aerated, dead clams were counted and removed, and shells were kept for further analysis. After 43 d, the remaining individuals were sacrificed and shell length was measured to the nearest 0.1 mm. All shells were cleaned, oven-dried at 65°C for 24 h and processed according to Riascos et al. (2007), to determine the micro-growth increment (calcein mark to shell edge) to the nearest 1 µm under a fluorescence microscope using blue light (460 to 490 nm) and the individual growth rate (µm d^{-1}).

To evaluate the effect of temperature and salinity on growth rate, the general linear model (GLM) procedure in JMP 7.0.1 (SAS Institute Inc.) was used to apply a 2-way analysis of covariance (ANCOVA) model for juveniles and adults, separately. The model treated salinity and temperature as fixed effects and shell length as the covariate and used the full interaction (separate slopes) model approach. Therefore, the interactions between the covariate and the main effects were included as additional effects. In order to assess the effect of temperature and salinity on mortality of juvenile and adult clams, the time (in days) elapsed between the beginning of the experiment and the death of each clam was estimated and modelled using a 2-way ANCOVA model under the GLM procedure. Salinity and temperature were treated as fixed effects, and shell length was used as covariate.

In a preliminary stage, the 'aquarium' effect was included in the models to assess the significance of the between-aquaria variability using the difference in the residual sum of squares of the fitted model with and without this effect, resulting in non-significance in all cases. Prior to analysis, mortality data were square-root transformed in order to meet assumptions of the ANCOVA model. Tukey's honestly significant difference test was used for post hoc comparisons of least-squared means between effect levels.

Gametogenic cycle and its relationship with environmental variability. We integrated information on the gametogenic cycle of *Mesodesma donacium* scattered in local sources (Table 1) and published them in the open-access library PANGAEA (Publishing Network for Geoscientific & Environmental Data). These data sets refer to 8 sandy beaches and include our own data from a 2 yr study in Hornitos (northern Chile). Thus, our study covers the entire current distribution range of *M. donacium* (Camaná, 16° 36' S, to Quilanlar,

42° 23′ S; Fig. 1). With the exception of the 11 mo study by Rubilar et al. (2008) (Table 1), only data sets based on standard histological gonad examinations, taken at monthly intervals for at least 1 yr were included. Two studies performed during strong El Niño/La Niña years were excluded, because they included short-term and scattered samplings that did not provide sufficient and reliable evidence on deviations in reproductive patterns under normal conditions. In each study, tissue samples were previously fixed either in aqueous Bouin's fixative or in formaldehyde-acetic-alcohol and stained thereafter with haematoxylin-eosin or Arteta trichromic stain. Individuals were classified into 4 or 5 gametogenic stages (Table 1). However, 2 consecutive, distinct stages were consistently distinguished in each study for both males and females. In the 'active' or ripe stage, which represents the period of gamete maturation, the acini are large and crowded, with complete walls and are full of free germ cells. Abundant mature sperm form dense masses in the follicles, and oocytes are large and numerous, with ovoid to spherical shape, typically showing a prominent nucleolus. The early germ line in this stage is occasionally represented by a few oogones and previtellogenic oocytes of small size. In contrast, in the 'spawning' or spent stage, representing the period of gamete release, the acini are small, with a rough basal membrane and only a few residual free germ cells, often in a stage of degeneration. In order to determine the transition from the final stages of gametogenesis to the spawned state, significant reductions in the proportions of active stages coinciding with a significant increase in the proportion of spawning states between months were evaluated using the McNemar test for dependent samples (Zar 1999) and interpreted as indicative of spawning events.

Overall, original studies did not include environmental data or they were based on snapshot measurements. Long-term monthly mean data on sea surface temperature (SST; °C), river inflow ($m^3 s^{-1}$) and coastal precipitation (mm) were obtained from the nearest hydrological or meteorological governmental stations in Chile and Peru (Table 2, Fig. 1). Moreover, the long-term (1981 to 2008) monthly mean upwelling index ($m^3 s^{-1}$ per 100 m of coastline) was computed for each location (1° of nominal resolution) using the Live

Table 1. *Mesodesma donacium*. Details of data sets included in the analysis of the gametogenic cycle, including geographical location, corresponding sampling periods, monthly sample size (N) and number of gonad stages (GS) used to characterize the cycle. All studies were based on standard histological techniques

Location	Latitude	Sampling period	N	GS	Source
Camaná	16° 36′ S	Mar 1973 to Feb 1974	65	4	Salgado & Ishiyama (2008)
Hornitos	22° 54′ S	May 2005 to Apr 2007	18–30	4	Riascos et al. (2008c)
Peñuelas	29° 50′ S	Jun 1994 to Jul 1995	20–30	5	Jerez et al. (2008)
Longotoma	32° 22′ S	Jun 1994 to Jul 1995	20–30	5	Jerez et al. (2008)
La Laguna	32° 37′ S	Aug 1969 to Nov 1970	50	5	Tarifeño (2008)
Mehuin	39° 26′ S	Jul 1989 to Jun 1991	30	4	Filun (2008)
Cucao	42° 35′ S	Sep 2000 to Aug 2001	16–89	5	Rubilar et al. (2008)
Quilanlar	43° 23′ S	Oct 2000 to Aug 2001	27–64	5	Rubilar et al. (2008)

Table 2. Station names and sources of environmental data used to assess the environmental influence on the reproductive cycle of *Mesodesma donacium* at several locations along the Peruvian–Chilean coast. The base period (in parentheses) used to calculate long-term monthly means is given if available. SST: sea surface temperature; n.a.: not available

Study site	SST station (yr)	River inflow station (yr)	Precipitation station (yr)
Camaná	Ilo[a] (1995–2007)	Camaná[c] (1973–1974)	Mollendo[e] (1888–1900)
Hornitos	Hornitos[f] (2005–2007)	–	–
Peñuelas	Coquimbo[b] (1982–2006)	Elqui[d] (2000–2005)	La Serena[e] (1869–1982)
Longotoma	Valparaíso[b] (1982–2006)	Petorca[d] (2001–2007)	Petorca[e] (1931–1960)
La Ligua[d] (1979–2002)	La Ligua[e] (1931–1960)		
La Laguna	Valparaíso[b] (1982–2006)	Petorca[d] (2001–2007)	Petorca[e] (1931–1960)
La Ligua[d] (1979–2002)	La Ligua[e] (1931–1960)		
Mehuin	Corral[b] (1982–2006)	Cruces[d] (1969–2001)	Toltén[e] (1931–1965)
Cucao	Puerto Montt[b] (1982–2006)	Deñal (n.a.)	Tres Cruces[e] (1931–1960)
Quilanlar	Puerto Montt[b] (1982–2006)	Quilanlar (n.a.)	Castro[e] (1930–1962)

[a]IMARPE (2008) (Peru), [b]CENDHOC (2008) (Chile), [c]INRENA (1994), [d]DGA (2008) (Chile), [e]Vörösmarty et al. (1998), [f]Present study

Access Server (Pacific Fisheries Environmental Laboratories, NOAA; available from http://las.pfeg.noaa.gov). The index was calculated at 1° offshore to avoid potential effects of extreme coastal topography on the calculations. For Hornitos, our own data on SST and salinity were registered. An Onset StowAway logger was installed on a floating structure located in front of the beach to register SST at hourly intervals and salinity every 15 min during monthly samplings using a multiparameter datasonde (Yellow Springs Instrument Company, Model 6600).

A multivariate approach of linking environmental variability patterns to biotic patterns developed by Clarke & Ainsworth (1993) was adapted to assess the temporal influence of SST and precipitation, river flow, or salinity on gametogenic stage composition. A Bray-Curtis similarity matrix was calculated for each locality using untransformed gonad stage percentages between months. The original classification of gonad stages of the corresponding study (Table 1) was used to calculate Bray-Curtis matrices. Environmental variables were normalised ($X_n = X - X/S$) to account for scale differences and enable comparisons, and between-month Euclidean distance matrices were calculated for each locality.

To determine whether the monthly pattern of gonad stage composition may be explained by monthly changes in environmental factors, the BIO-ENV analysis of the PRIMER V6.1.6 software package (Clarke & Gorley 2006) was used. This is a non-parametric permutation procedure calculating the Spearman rank correlation (ρ) between Bray-Curtis similarity matrices and Euclidean distance matrices. A global permutation test of the significance of ρ was calculated under the null hypothesis that there is no relationship between the 2 matrices. The BIO-ENV procedure defined single or suites of environmental variables that best 'explain' the variability of gonad stage composition.

RESULTS

Effects of temperature and salinity on growth and mortality

Growth rate of juvenile *Mesodesma donacium* varied between temperatures, but not between salinity levels (Table 3). Growth rate at El Niño temperature decreased to approximately one-half that at normal temperature (Fig. 2). Only the temperature term showed a significant interaction with the covariant, reflecting stronger effects on smaller clams. The growth rate of adult clams varied between temperatures and between salinity levels (Table 3). Multiple comparisons showed that, at El Niño temperature, growth rate was significantly lower at 10 psu than at 35 psu (Tukey's test, $p < 0.05$). In contrast, at normal temperature, no significant differences in growth rate were observed between salinity levels (Fig. 2).

Table 3. *Mesodesma donacium*. Results of the analyses of covariance testing the effects of temperature and salinity on growth rate of juvenile and adult clams. SL: shell length; boldface print: significant at $p < 0.05$

Source	df	SS	*F* ratio	Prob > *F*
Juveniles				
Temperature (A)	1	44.204	279.418	**<0.001**
Salinity (B)	2	1.079	3.0132	0.061
SL (covariant)	1	23.014	145.477	**<0.001**
SL × A	1	5.915	37.389	**<0.001**
SL × B	2	0.197	0.623	0.541
A × B	2	0.175	0.554	0.578
Error	25	6.960		
Adults				
Temperature (A)	1	9.817	136.132	**<0.001**
Salinity (B)	2	0.848	5.885	**0.004**
SL (covariant)	1	2.099	29.107	**<0.001**
SL × A	1	0.287	3.985	0.051
SL × B	2	0.092	0.641	0.530
A × B	2	0.390	2.704	0.075
Error	64	18.076		

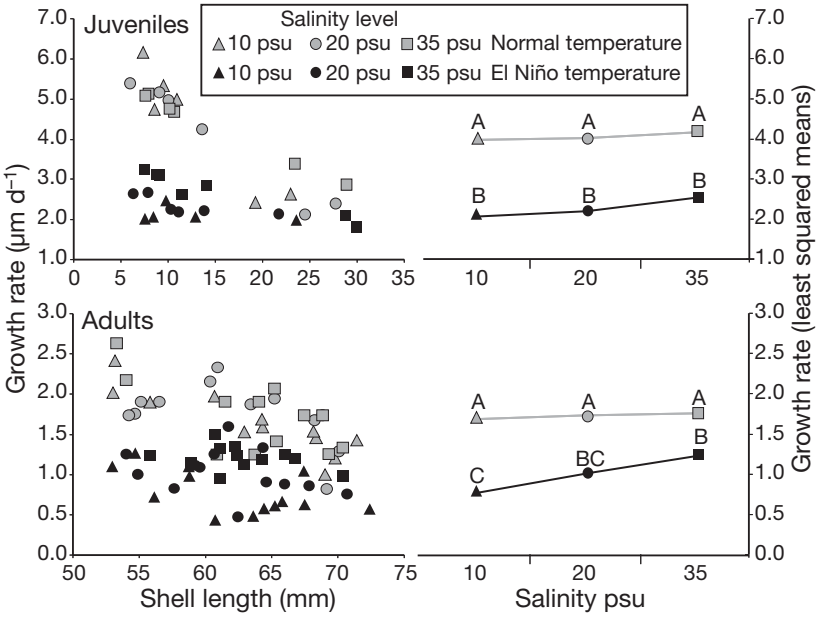

Fig. 2. *Mesodesma donacium*. Growth rate against initial shell length of juvenile and adult clams submitted to different experimental temperatures and salinities and comparisons of least-squared means of each treatment. Levels not sharing the same letter are significantly different (Tukey's test, $p < 0.05$)

Overall, mortality was higher at El Niño temperature at all salinity levels, reaching 50% after 23 d. In contrast, mortality was generally low at normal temperature. It was <20% at 35 and 20 psu and <50% at 10 psu (Fig. 3). The ANCOVA model revealed that juvenile clams died significantly faster at El Niño temperature, but no differences were observed between salinity levels (Fig. 4, Table 4). Non-significant interaction was observed between the main effects, and shell length was not significant as a covariant (Table 4). Therefore, the interaction between the main effects and the covariant was excluded from the model. In contrast, mortality of adults was significantly affected by both temperature and salinity, with

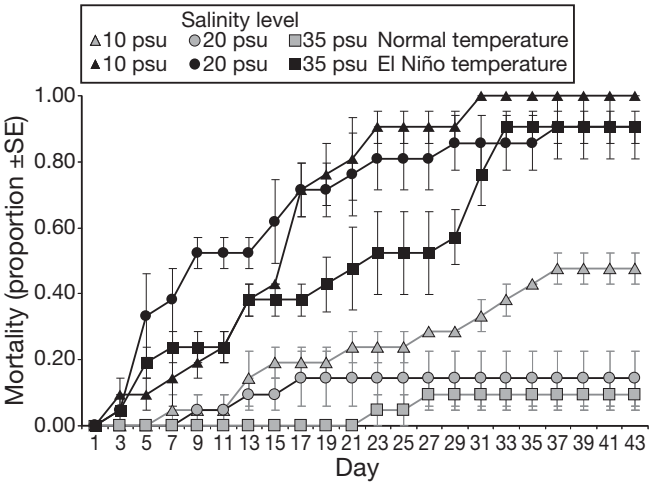

Fig. 3. *Mesodesma donacium*. Mortality of clams submitted to different experimental temperatures (normal and El Niño) and salinities (10, 20 and 35 psu) throughout a 45 d experiment

Table 4. *Mesodesma donacium*. Results of the analyses of covariance testing the effects of temperature and salinity on mortality (days elapsed until dead) of juvenile and adult clams. SL: shell length; boldface print: significant at $p < 0.05$

Source	df	SS	*F* ratio	Prob > *F*
Juveniles				
Temperature (A)	1	20.058	26.648	**<0.001**
Salinity (B)	2	0.067	0.0446	0.956
SL (covariant)	1	0.008	0.011	0.915
A × B	2	0.133	0.088	0.915
Error	29	6.960		
Adults				
Temperature (A)	1	83.935	64.854	**<0.001**
Salinity (B)	2	20.792	8.033	**<0.001**
SL (covariant)	1	0.051	0.0395	0.843
A × B	2	9.922	3.833	**0.026**
Error	64	18.076		

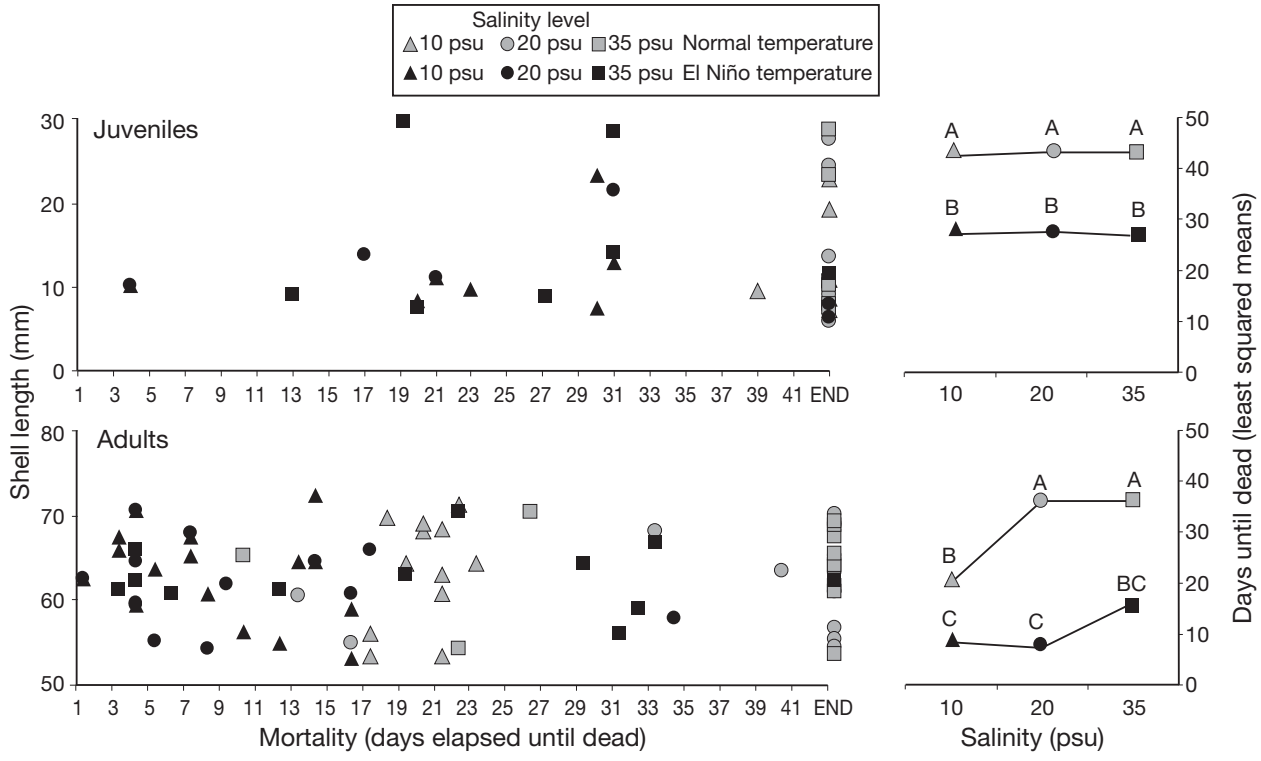

Fig. 4. *Mesodesma donacium*. Mortality against initial shell length of juvenile and adult clams submitted to different experimental temperatures and salinities and comparisons of least-squared means of each treatment. END: individuals surviving until the 43rd day, i.e. the end of the experiment. Levels not sharing the same letter are significantly different (Tukey's test, $p < 0.05$)

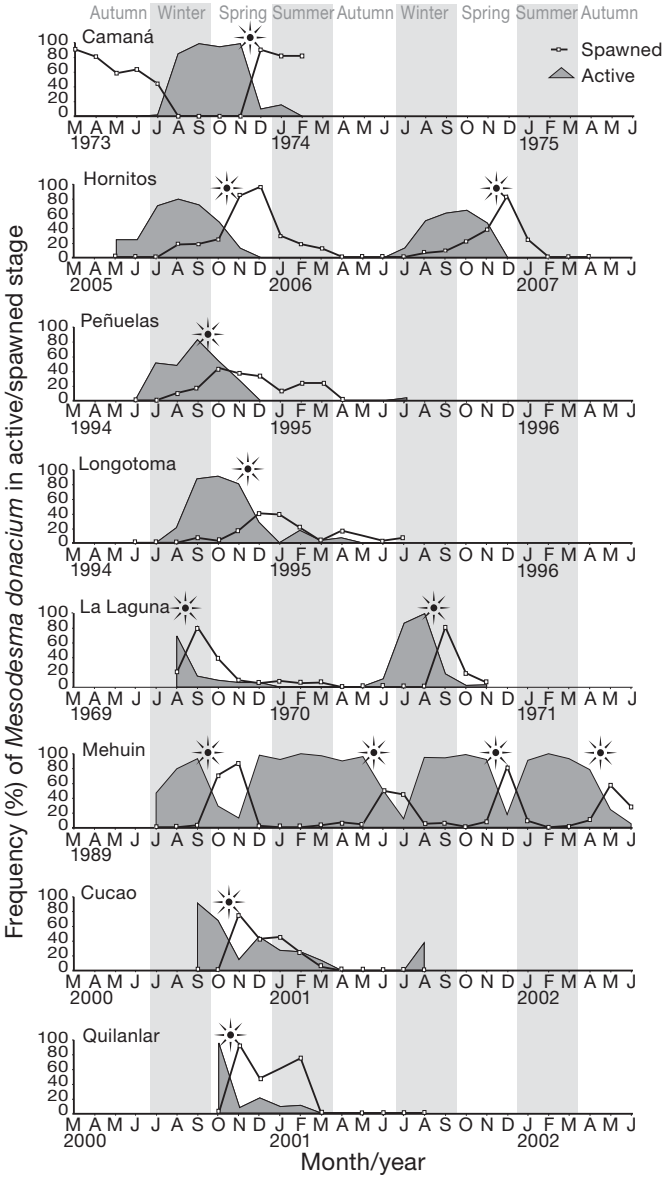

Fig. 5. *Mesodesma donacium.* Spatial and temporal patterns of reproductive activity, based on histological examination of gonad tissue. Transition between active and spawned gonad state (stars) based on significant drops in the active stage frequency coinciding with a significant increase in the spawning state frequency between months (see 'Materials and methods')

a significant interaction between the main effects. Mortality was higher under El Niño conditions, showing an additional increase at low salinities (10 and 20 psu). Under normal temperature conditions, adult clams died faster only at the lowest salinity, whereas no differences were observed between 20 and 35 psu (Fig. 4).

Influence of environmental variability on the gametogenic cycle

Reproductive activity of *Mesodesma donacium* along the distribution range showed a consistent temporal pattern with few departures (Fig. 5). The breeding season generally started in winter (seasons hereafter referring to austral) and extended into spring. Overall, a single spawning event was observed throughout the year, starting in late winter or spring and extending into summer. In contrast, gonad activity was continuous, and spawning events were biannual (spring and autumn) at Mehuin (39° S), thereby showing a departure from the above-mentioned pattern.

BIO-ENV analyses (Table 5) showed a significant correlation between the gonad stage composition and environmental factors analysed: the Spearman rank correlation ρ was significant for 6 out of 7 study sites, the exception being Peñuelas. Environmental variables showing significant correlations with the gametogenic cycle were plotted in Fig. 6. Stronger correlations were obtained for northern beaches. Generally, the upwelling index was significantly correlated with gonad development only at northern beaches (Camaná and Hornitos). The transition between the breeding period and the spawning season coincided with the season of stronger upwelling. In contrast, precipitation and river inflow were mainly correlated with reproductive stages at central and southern places; in this case the breeding–spawning transition occurred shortly after the seasonal precipitation/river inflow maximum. Temperature was involved in significant global correlations only at Mehuin.

Table 5. *Mesodesma donacium*. Results of BIO-ENV analyses testing the relationship between gonad stage composition and environmental changes. Significant ($p < 0.05$) Spearman rank correlation coefficients (ρ) are shown in boldface print and the corresponding selection of the best 'explanatory' variable(s) is given

Location	ρ	p	Selection of variable(s)
Camaná	**0.727**	<0.01	Upwelling index, precipitation (Mollendo)
Hornitos	**0.525**	0.01	Upwelling index
Peñuelas	0.245	0.10	–
Longotoma	**0.585**	0.01	River inflow (Petorca)
La Laguna	**0.649**	<0.01	River inflow (Ligua), precipitation (Ligua)
Mehuin	**0.387**	0.01	River inflow (Cruces), precipitation (Toltén)
Cucao	**0.340**	0.04	Precipitation (Tres Cruces)
Quilanlar	**0.341**	0.03	Precipitation (Castro)

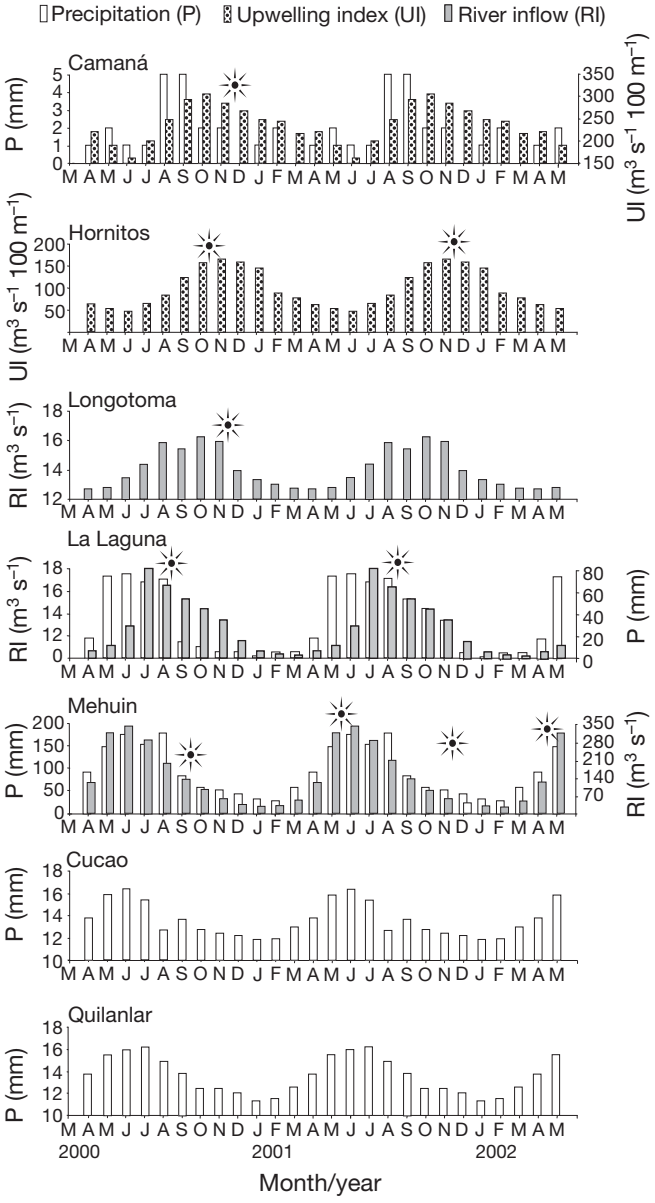

Fig. 6. Long-term variability of environmental factors showing significant correlations with the reproductive cycle of *Mesodesma donacium* in the study area. Transition between active and spawned gonad state of *M. donacium* (star symbols) at the corresponding location are indicated. Environmental data sources as indicated in Table 2

DISCUSSION

Influence of temperature and salinity on growth and mortality

The observed short-term effects of increased temperature on the growth and mortality of juvenile and adult *Mesodesma donacium* from Hornitos give strong experimental support to the hypothesis that the anomalous higher temperature during El Niño is the main factor explaining the mortality of this clam. However, the actual effects of anomalous temperature on *M. donacium* along its distribution range depend on a number of interacting factors including the strength, extent and spatial features of El Niño, the effects of associated physical changes, the dynamics of parasitic interactions under environmental stress (Riascos et al. 2008a) and the potential for behavioural thermoregulation (e.g. migration to deeper waters; Arntz et al. 1987) and increased parasitic interactions. Fig. 7a shows that the magnitude of thermal changes during El Niño depends on the geographic location, being weaker toward higher latitudes. As El Niño thermal anomalies are propagated southward by coastal Kelvin waves, their magnitude commonly declines towards higher latitudes, producing a latitudinal impact gradient (Camus 2008). It is not possible to define a threshold for the thermal tolerance of *M. donacium* across its geographic range based solely on our results. However, it is reasonable to expect that during strong El Niños the thermal tolerance and the potential of behavioural thermoregulation of populations north of Hornitos would be surpassed, given the stronger thermal changes in northern beaches, which may last for several months. A local adaptation of clams from northern beaches to higher temperature does not seem feasible, because there is not a strong latitudinal gradient of temperature along the HCS under normal conditions (Fig. 7a). Moreover, northern beaches have to be recolonized after strong El Niño episodes from southern populations, likely adapted to slightly cooler waters. Considering the populations south of Hornitos, even assuming that the weaker thermal changes would not produce mortality, they may still produce sublethal stress for several months on the northern and central Chilean coast. This stress, along with the stress produced by associated changes in salinity (i.e. lower salinity further reduces growth and increases mortality at El Niño temperatures; Figs. 3 & 4) and other abiotic factors (e.g. food availability, sediment load and wave action among others) during strong El Niño events may ultimately lead to mass mortality events. In fact, these events have only been reported between ~12 and ~30° S, coinciding with the latitudinal range where thermal anomalies during El Niño are more clear (Fig. 7a).

In contrast to its sensitivity to high temperature, *Mesodesma donacium* was less vulnerable to reduced salinity, with a higher tolerance for juvenile clams. The ability of *M. donacium* to cope with such a wide salinity range resembles that of euryhaline species; an intriguing result in view of the lack of coastal precipitation and river discharge in Hornitos, located off the Atacama Desert of northern Chile, one of the most arid zones in the world. Nevertheless, salinity in Hornitos showed relatively high variability (Fig. 8). Mean salin-

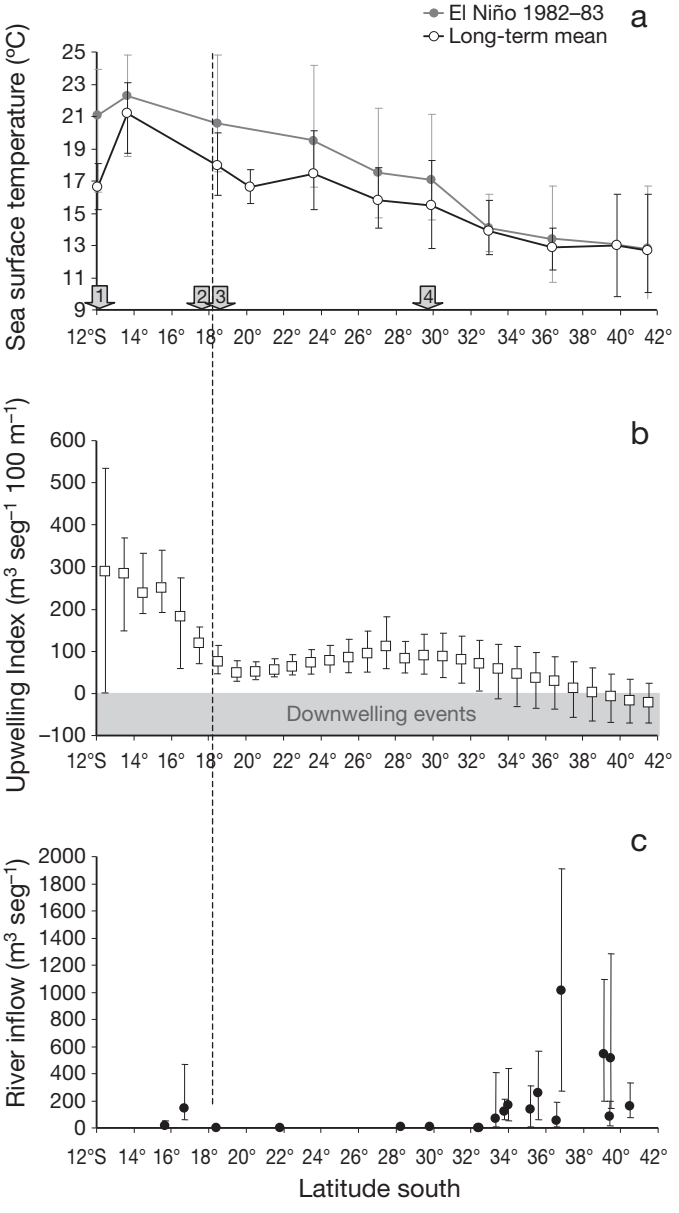

Fig. 7. Long-term annual mean and mean seasonal variability ('error bars': upper/lower bar represents the highest/lowest long-term monthly mean) of environmentals factors among latitudes (centesimal units) in the Humboldt Current System of Chile and Peru. (a) Long-term (Peru: 1956 to 1982; Chile: 1982 to 2006) annual mean sea surface temperature (SST) and mean seasonal oscillations compared with SST during El Niño 1982-83. Numbered arrows show locations of mass mortality events of *Mesodesma donacium* reported in literature in connection with El Niño (1: Arntz et al. 1987; 2: Quiroz & Barriga 1998; 3: Jerez et al. 1999; 4: Aburto & Stotz 2003). (b) Long-term (1981 to 2008) annual mean upwelling index and mean seasonal oscillations. (c) Long-term (variable number of years in record) annual mean river inflow and mean seasonal oscillations. Vertical dotted line: Peruvian–Chilean political border. Data sources: SST: IMARPE (2008) (Peru) and CENDHOC (2008) (Chile); upwelling index: Pacific Fisheries Environmental Laboratories, NOAA; river inflow: INRENA (1994) (Peru), DGA (2008) (Chile) and Vörösmarty et al. (1998)

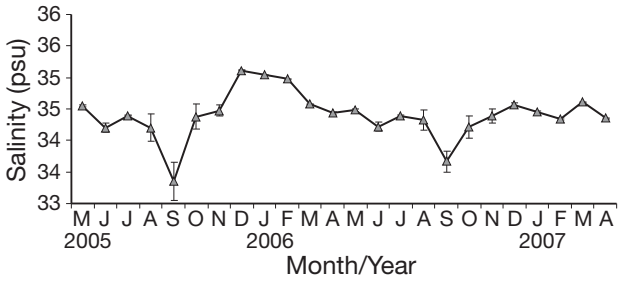

Fig. 8. Temporal variability of salinity at Hornitos, northern Chile, between May 2005 and April 2007

ity in September significantly differed from that during the rest of the year (Student's *t*-test = –3.628; $p < 0.01$). These drops in salinity coincided with the occurrence of submarine seepage through holes (~25 cm diameter) distributed along a narrow belt of about 500 m parallel to the coast line in the shallow subtidal (1.5 to 2.5 m depth). These holes were observed interspersed among the adult clam belt, but never in the intertidal. Water collected from several holes revealed low salinity (average = 19.5 psu; SD = 11.3; n = 12). The features of the groundwater flow at Hornitos most likely correspond to submarine groundwater discharge (SGWD; sensu Church 1996), which occurs where an unconfined aquifer is hydraulically connected with the sea through permeable bottom sediments and where its (head) water level is above sea level (Johannes 1980). Although unconfined aquifers are common along the Chilean–Peruvian desert coast (e.g. Rojas et al. 1995, Squeo et al. 2006), this is the first observation of recent SGWD on the western coast of South America. On sandy shores, SGWD may affect both the intertidal and subtidal, leading to strong salinity changes, particularly at the upper tidal levels during low tides (Johannes 1980, McLachlan & McGwynne 1986). It is difficult to confirm whether the osmotic tolerance of *M. donacium* is related to the SGWD observed in Hornitos. Our salinity measurements may not accurately reflect the magnitude and temporal variability of this flux of freshwater, the measurement of which is inherently difficult (Burnett et al. 2001, Gallardo & Marui 2006). The high osmotic tolerance may, instead, represent a more general adaptation of this species to a significant influence of freshwater discharge along its geographic distribution.

Reproductive cycle

Given the frequent correlation between seasonal temperature change and seasonal reproductive activity of marine animals, temperature was long assumed to be a causative factor for reproductive rhythms in the

marine realm (Giese & Pearse 1974). However, the existence of seasonal reproductive rhythms in places with slight seasonal temperature fluctuations led to the recognition that other seasonal factors may fluctuate more dramatically and may be more important for synchronizing reproduction (Pearse & Lockhart 2004). The reproductive cycle of *Mesodesma donacium* along its geographic range showed clear seasonality, with a low correlation with seasonal changes in temperature. The persistent northward flow of the cold Humboldt Current causes slight seasonality in the temperature of the HCS, typically a few degrees (Fig. 7a); this change is smaller than that of other marine systems at comparable latitudes (Arntz et al. 1987), and it appears unlikely that this slight fluctuation may act to synchronize reproduction. In contrast, strong effects of temperature on the intraannual variation of reproduction of several shallow-water bivalves, including the surf clam *M. mactroides*, have been reported for the mid-temperate Atlantic beaches of South America, where the temperature seasonality is high (e.g. Defeo et al. 1992, Morsan & Kroeck 2005, Fiori & Defeo 2006, Hermann et al. 2009). In fact, between-ocean differences in thermal patterns have been suggested to explain differences in the biogeographic patterns of populations of the Pan-American species *Excirolana brasiliensis* (Cardoso & Defeo 2004).

According to our analyses, the reproductive cycle is mostly correlated to the upwelling index, river inflow and precipitation, which all display strong seasonal and geographical patterns. Upwelling strength and river inflow vary by several orders of magnitude between seasons (Fig. 7b,c). This enormous variability, particularly of river inflow, can be expected to have a strong local influence on the nutrient input and phytoplankton production and, thus, to influence the reproductive cycles of bivalves (e.g. Riascos 2006, Riascos et al. 2008b). Our results show a link between increased upwelling strength and river inflow (i.e. food availability) and the season of gamete maturation of *Mesodesma donacium*. However, 2 factors may obscure the results of our analyses: (1) the potentially confounding effect of interannual differences on reproductive activities among the populations analysed here and (2) the offshore calculation of the upwelling index may not accurately reflect the nearshore nutrient availability, where upwelling is often influenced by beach geomorphology (Thiel et al. 2007).

Macroscale variations in upwelling strength, river inflow (Fig. 7b,c) and precipitation (Fig. 1) along the HCS seem to better explain the observed shift between the upwelling-influenced reproductive cycle of northern beaches and the river-influenced reproductive cycle of central and southern beaches. Upwelling strength decreases with latitude, while river inflow and precipitation increase with latitude. The lack of a significant correlation between environmental factors and the reproductive cycle at Peñuelas (29° 50′ S) may be related to its location near a 'transitional zone' between 30 and 33° S, where upwelling is weaker and the frequency of both downwelling events and river inflow increases. On the other hand, the observed continuous gonad activity and biannual pattern of spawning events at Mehuin (39° 26′ S) could be explained by the stream flow regime of large rivers influencing the coastal zone up to 75 km offshore (Dávila et al. 2002). River runoff is an integral response to precipitation patterns, snow melt, delayed groundwater discharge and human water use throughout the river basins. Rivers in this region have a mixed pluvial–nival regime, with one peak flow due to winter precipitation and a second peak flow in summer due to snowmelt at higher altitudes (Dávila et al. 2002, Houston 2006).

Latitudinal variations in river inflow, upwelling strength and the higher osmotic tolerance of juvenile clams observed in our experiments may explain conflicting evidence regarding the spatial segregation between juvenile and adult *Mesodesma donacium*. According to Tarifeño (1980) and Jaramillo et al. (1994), juvenile clams settle near river mouths at both La Ligua (~32° S) and Mehuin (~39° S), showing an alongshore spatial segregation from adults, which seems a common pattern among sandy beach clams (see Donn 1987). The enhanced ability of juveniles to cope with low salinities may represent an early physiological trait allowing larvae to settle in vacant areas by active or passive processes (e.g. Mann et al. 1991, Shanks & Brink 2005) and thereby to reduce strong intraspecific and interspecific competition for food and habitat quality (Tarifeño 1980, Dugan et al. 2004) and increasing recruitment success. However, contradictory evidence regarding spatial segregation related to salinity has been reported by Ortiz & Stotz (1996). They pointed out that abundances of juveniles were lower near small river inlets in Coquimbo (~29° S). This might be related to the fact that river runoff is minor and intermittent throughout the year in Coquimbo Bay, whereas that at La Ligua and Mehuin is perennial and more abundant. Therefore, if some relationship does exist between a salinity gradient and alongshore distribution of different sizes, it would be hard to detect in Coquimbo. Moreover, as larvae are commonly transported onshore during downwelling and offshore during upwelling (Shanks & Brink 2005), the prevalence of downwelling currents throughout the year in southern Chile would favour larval retention and, thereby, increase interspecific interactions.

However, establishing a link between differential osmotic tolerance and spatial size segregation in the field related to salinity remains speculative because:

(1) the results of our experiment are limited to a single population involving a few animals, (2) observations regarding the spatial distribution of *Mesodesma donacium* are mostly circumstantial and do not take into account its inherently dynamic nature, and (3) appropriate quantitative models are needed to study spatial patterns on sandy beaches (see Defeo & Rueda 2002, Schoeman & Richardson 2002). Clearly, more experimental and field work on the environmental factors affecting early life stages is needed to conciliate this evidence, as it may shed light on the recruitment process, one of the key factors regulating the population dynamics of sandy beach clams (Lima et al. 2000).

Implications for population persistence

Our findings depict how macroscale spatial patterns and seasonal variability in temperature, river inflow and upwelling strength in the HCS may affect growth, mortality and the reproductive cycle of *Mesodesma donacium*. However, these findings may be useful in interpreting how long-term environmental variability in the HCS has affected population persistence.

Earlier fossil records of *Mesodesma donacium* have been found in late Pliocene deposits at Horcón and Quebrada Blanca, central Chile (Herm 1969), and at Tablazos, northern Peru (DeVries 1986). A well-recognized mass extinction, presumably caused by the development of the oxygen minimum zone after the establishment of the HCS during the mid-to late Miocene (McRoberts & Newton 1995, Ibaraki 1997, Tsuchi 1997, Rivadeneira & Marquet 2007), took probably place during the Pliocene/Pleistocene transition (Herm 1969, DeVries 2001, Rivadeneira & Marquet 2007). Coinciding with this mass extinction, several species with sub-Antarctic affinity, which were formerly scarce during the Pliocene, became dominant in their corresponding biotope in the Pleistocene (Herm 1969, DeVries 1986). In general, the development of the HCS involved both the northward advance of sub-Antarctic biota and the northward retraction of a former tropical/subtropical biota, with consequences that still persist (Brattström & Johanssen 1983, Camus 2001). Therefore, the expansion and dominance of *M. donacium*, a species with a presumably Antarctic origin (von Ihering 1907, Marins & Levy 1999), seem closely linked to the expansion of cold-water conditions through the Humboldt Current. Given its sensitivity to high temperature, the recurrent warming effect of El Niño, at least since the Holocene (Ortlieb et al. 2000), has caused a recurrent southward retraction of *M. donacium* populations as demonstrated by changes in diversity and abundance of species in kitchen middens found along the Peruvian coast (Quilter & Stocker 1983, Sandweiss 1996). A progressive southern retraction of *M. donacium*, along with several sub-Antarctic species, may also be foreseeable under the scenario of an increasing frequency of El Niño events, which has been discussed in connection with ongoing global warming (Timmermann et al. 1999).

Overall, the ecological, biogeographical and evolutionary consequences derived from the recurrent local extinction–recolonization dynamics undergone by species that are heavily affected by El Niño are not understood (Thiel et al. 2007). While we focus here on the ecological implications of these dynamics, further studies on the latitudinal patterns of life-history traits of *Mesodesma donacium* and their environmental drivers may be crucial for a broader understanding of the biogeographical and evolutionary consequences.

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