

**Thriving and declining: Population
dynamics of the macha (*Mesodesma
donacium*, Bivalvia, Mesodesmatidae)
along a latitudinal gradient of the
Humboldt Current Upwelling System**

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Tumaco – Colombia (1973)

*A mi cálida manada de nacimiento, a quien debo todo lo
bueno que pueda haber en mi.*

*A Ibonita, por estar en los altos y los bajos, por su níveo
amor, por su alma incontenible de guerrero, por el calor de
hogar.*

Al mar, por teñir de azul mi destino para siempre

A mi país, que es imposible no amar

*A mis fantasmas, que me susurran utopías y me inspiran a
seguirlas*

*A mi perro negro, última voz, que encuentro fiel en las
esquinas, que me muestra los dientes cuando pierdo el rumbo*

*A la vida, por el privilegio de seguir vagando, de seguir
siendo, en esencia, lo que siempre quise ser: un recolector de
bichos, proclive a la utopía*

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Abstract

The mass mortality of the highly dominant and abundant bivalve *Mesodesma donacium* along Peruvian sandy beaches represents one of the most conspicuous cases of impacts of strong El Niño events (EN) in nearshore ecosystems, causing considerable shifts in the whole community. More than 25 years after EN-related mass mortalities began, the northern geographic distribution of this commercially important clam is still confined to northern Chile, illustrating its low ability to regain the former distribution. The present work uses a combination of ecophysiological experiments, field work and a literature data compilation. These data were used to assess (i) the significance of the biotic interactions with the spionid polychaete *Polydora biocipitalis* in terms of the population persistence of *M. donacium*; (ii) the response of *M. donacium* to main abiotic changes expected during EN; (iii) the demographic processes of *M. donacium* at the current northern range boundary and (iv) the geographical trends in population dynamics of this species and the environmental factors driving them. Features of the association between *P. biocipitalis* and *M. donacium* confirm that the polychaete is a parasite causing deleterious effects on the clam's performance. Evidence of the infestation in fossil shells of *M. donacium* from fossiliferous deposits of central and northern Chile strongly suggests a long-term association, at least since the Middle Pleistocene, between these species. Even during weak environmental stress events, this parasite can cause the mortality of adult clams, which represents a loss of overall fecundity amounting to over 90% that may delay or prevent northward recolonization. *M. donacium* was highly sensitive to high temperature, suggesting that the northward distribution is limited by high sea surface temperature. In contrast, it was remarkably tolerant to low salinity, particularly juveniles, which may be related to the selection of river mouths as suitable areas for recruitment. Strong freshwater-input seasonality best explained the patterns in the reproductive cycle of this clam. Owing to the limited upper thermal tolerance, the long-term expansion and dominance of *M. donacium* from the Pliocene/Pleistocene transition until present seems closely linked to the establishment and development of the cold Humboldt Current Upwelling System (HCUS). Consistent patterns of increasing abundance, growth performance, mortality and productivity of *M. donacium* with decreasing latitude

seem mainly related to large-scale differences in primary productivity associated to upwelling centres and river input in the HCUS. Tropical and subtropical sandy beaches in the HCUS are highly productive but unpredictable environments for *M. donacium*. Hence, populations developed there are ephemeral and act as sink populations, whereas those in central and southern Chile act as sources and should, therefore, be given priority in management and conservation strategies.

Zusammenfassung

Massensterben der dominanten und häufigen Muschelart *Mesodesma donacium* an den Sandstränden Perus führen als einer der augenfälligsten Effekte starker El Niño-Ereignisse (EN) zu Verschiebungen in der Artengemeinschaft in den küstennahen Ökosystemen. Über 25 Jahre nach dem Beginn der von EN ausgelösten Massensterben ist die nördliche Verbreitungsgrenze dieser kommerziell wichtigen Art bisher nicht über Nordchile hinausgekommen. Dies zeigt die geringe Fähigkeit der Art, ihr ursprüngliches Verbreitungsgebiet wieder zu besiedeln. Die vorliegende Arbeit basiert auf einer Kombination von ökophysiologischen Versuchen, Feldforschung sowie einer Literaturrecherche. Mittels der Ergebnisse wurden eingeschätzt (i) die Bedeutung des Auftretens des spioniden Polychaeten *Polydora biocciptalis* auf den Populationsbestand von *M. donacium*; (ii) die Reaktion von *M. donacium* auf die wichtigsten abiotischen Veränderungen während EN; (iii) die Populationsdynamik von *M. donacium* an ihrer nördlichen Verbreitungsgrenze und (iv) die geographischen Veränderungen in der Populationsdynamik und die zugrunde liegenden Umwelteinflüsse. Eigenschaften der Beziehung von *P. biocciptalis* und *M. donacium* bestätigen, dass der Polychaet ein Parasit ist, der sich schädlich auf die Leistungsfähigkeit der Muschel auswirkt. Funde befallener fossiler *M. Donacium*-Schalen aus Ablagerungsstätten in Zentral- und Nordchile deuten auf eine mindestens seit dem mittleren Pleistozän bestehende Assoziierung dieser beiden Arten hin. Selbst unter leichtem Umweltstress kann dieser Parasit zur Sterblichkeit ausgewachsener Muscheln führen. Dies führt zu einem Fekunditätseinbruch von über 90%, der eine nördliche Wiederbesiedlung verzögert oder verhindert. *M. donacium* reagiert sensibel auf hohe Temperaturen, was daraufhin deutet, dass die nördliche Verbreitung durch hohe Temperaturen des Oberflächenwassers begrenzt wird. Im Gegensatz hierzu zeigte sich *M. donacium*, insbesondere Jungtiere, erstaunlich tolerant gegenüber niedrigen Salzgehalten, was sich in der Wahl von Flussmündungen als Ansiedlungsgebiete widerspiegeln mag. Starke Saisonalität im Süßwassereinfluss lieferte die beste Erklärung für Muster im Fortpflanzungszyklus. Aufgrund der geringen Temperaturtoleranz nach oben scheint die Langzeit-Verbreitung und Dominanz von *M. donacium* seit dem Übergang vom Pliozän zum Pleistozän bis zum heutigen Tag an das Entstehen

und die Entwicklung des kalten Humboldtstrom-Auftriebssystems gebunden zu sein. Beständige Muster wie Häufigkeitszunahme, gesteigertes Wachstum, höhere Sterblichkeit und Produktivität von *M. donacium* mit abnehmender Breite scheinen hauptsächlich mit großskaligen Unterschieden der Primärproduktion in Auftriebszentren und Süßwassereinfluss zusammenzuhängen. Tropische und subtropische Sandstrände im Humboldtstrom-Auftriebsgebiet sind äußerst produktiv, aber sie bieten unvorhersagbare Umweltbedingungen für *M. donacium*. Populationen in solchen Gebieten entwickeln sich primär aufgrund von Larvenfällen und sind wenig beständig. Die Gebiete Zentral- und Südchiles hingegen repräsentieren beständige Laichgebiete, denen daher übergeordnete Bedeutung in Bezug auf Strategie, Schutz und Management zukommen sollte.

Resumen

La mortalidad masiva del bivalvo *Mesodesma donacium* en playas arenosas del Perú, donde es usualmente muy abundante y dominante, constituye uno de los casos mas notables sobre impacto de eventos El Niño (EN) en ecosistemas costeros, con consecuencias importantes para toda la comunidad. Después de más de 25 años desde los primeros registros de mortalidades masivas de este bivalvo atribuibles a EN, la distribución geográfica norte de esta almeja con alto valor comercial se encuentra aún retraída en el norte de Chile, ilustrando la baja capacidad de esta especie para recuperar su antigua distribución geográfica. En este trabajo se combinan datos de experimentos ecofisiológicos, trabajos de campo y una recopilación de datos de la literatura científica. Estos datos se usaron para evaluar (i) la relevancia de las interacciones bióticas con el poliqueto *Polydora biocipitalis* en términos de la persistencia poblacional de *M. donacium*; (ii) la respuesta de *M. donacium* frente a los cambios físicos esperados durante eventos EN; (iii) los procesos demográficos de *M. donacium* en el límite norte de distribución geográfica y (iv) las tendencias latitudinales de la dinámica poblacional de esta especie y los factores que las modulan. Las características de la asociación entre *P. biocipitalis* y *M. donacium* confirman que se trata de una relación parasítica que causa efectos deletéreos en la almeja. La evidencia de infestación encontrada en conchas fósiles de *M. donacium* en depósitos fosilíferos del centro y norte de Chile sugiere claramente que la asociación entre estas especies es antigua, y data al menos desde el Pleistoceno Medio. Aún durante eventos de estrés ambiental moderado, el parásito puede causar la mortalidad de almejas adultas, lo que representa una pérdida de fecundidad de más de 90%, que puede retrasar o impedir la recolonización de esta especie hacia el norte. *M. donacium* es muy sensible a la temperatura alta, lo que sugiere que su distribución norte esta limitada por la temperatura superficial del mar. En contraste esta especie, especialmente los juveniles, fue marcadamente tolerante a bajas salinidades, lo que podría estar relacionado con la selección de zonas cercanas a los ríos como áreas adecuadas para el reclutamiento. El ciclo reproductivo de esta especie se relacionó principalmente con la fuerte estacionalidad de flujos de agua dulce. Debido a la limitada tolerancia de esta especie a las altas temperaturas, la expansión y dominancia de esta especie

desde la transición Plioceno/Pleistoceno hasta el presente, parece estar ligada al establecimiento y desarrollo ulterior del Sistema de Afloramiento de la Corriente de Humboldt (SACH). Los patrones latitudinales de incremento de la abundancia, eficiencia del crecimiento, mortalidad y productividad de *M. donacium* hacia el ecuador parecen estar relacionados, principalmente, con diferencias de gran escala en la productividad primaria asociada a focos de afloramiento y descargas riverinas en el SACH. Las playas tropicales y subtropicales en el SACH representan ambientes altamente productivos pero impredecibles para *M. donacium*. Por tanto, las poblaciones desarrolladas ahí son efímeras y actúan como poblaciones sumidero, mientras aquellas en el centro y sur de Chile actúan como fuente y deberían, por lo tanto, priorizarse en las estrategias de manejo y conservación destinadas a esta especie.

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List of selected abbreviations and acronyms

Abbreviation/Acronym	Description (unit)-
AFDM	Ash-free dry mass (g)
ANCOVA	Analysis of covariance
ANOVA	Analysis of variance
<i>b</i>	Mass coefficient
\bar{B}	Biomass (g AFDM)
BCI	Body condition Index (g)
CENSOR	Climate variability and El Niño-Southern Oscillation: implications for natural coastal resources and management
Chl <i>a</i>	Chlorophyll <i>a</i> concentration (mg l ⁻¹)
DM	Dry mass (g)
Dt	Digging time (s)
DO	Dissolved oxygen (mg l ⁻¹)
EN	El Niño
ENSO	El Niño-Southern Oscillation
GSI	Gonado-somatic Index
Gr	Growth rate (µm day ⁻¹)
HCUS	Humboldt Current Upwelling System
K	Curvature parameter of VBGF (year ⁻¹)
L _∞	Asymptotic shell length (mm)
LN	La Niña
M	Natural mortality rate
MSGRM	Mass specific growth rate method
N	Number of individuals
OGP	Overall growth performance
P	Production (g AFDM m ⁻²)
P/\bar{B}	Productivity (year ⁻¹) = production: biomass ratio
PI	Prevalence of infestation (%)
SD	Standard deviation
SE	Standard error
SFDM	Shell-free dry mass (g)
SL	Anterior-posterior shell length axis (mm)
Tb	Thickness of blister walls (µm)

SST	Sea surface temperature (° C)
SGD	Submarine groundwater discharge
VBGF	von Bertalanffy growth function
ϕ'	Growth index phi prime

1 INTRODUCTION

1.1 The Humboldt Current Upwelling System

In terms of fish production, the Humboldt Current Upwelling System (HCUS) is the most productive of the Eastern Boundary Current Systems, and one of the most productive marine ecosystems on earth. It extends along the west coast of South America from southern Chile (~42°S) up to Ecuador and the Galapagos Islands near the equator (e.g. Montecino et al. 2006; Fig. 1-1). The oceanography of the HCUS is characterised by a predominant northward flow of surface waters from the subantarctic region and by strong upwelling of cool nutrient-rich subsurface waters of equatorial origin (Thiel et al. 2007). The injection of nutrients into the euphotic zone through upwelling events results in extremely high primary production, which fuels zooplankton and fish production over extensive areas (e.g. Daneri et al. 2000, Thiel et al. 2007).

The spatial distribution of nutrients in the HCUS shows high variability, associated with upwelling pulses and mixing. Elevated concentrations occur inshore and usually decrease in offshore direction (Escribano et al. 2003, Marín et al. 2003). The Peruvian and Chilean regions differ in their upwelling characteristics. Off Peru, the stronger winds and the smaller Coriolis term combine to create strong offshore Ekman transport and thus stronger upwelling of subsurface countercurrent waters, which creates intense upwelling core regions (Bakun 1996). Off Chile, subantarctic waters of the equatorward flowing coastal current are upwelled due to less intense Ekman transport (Wolff et al. 2003). Four zones are recognized by stronger upwelling, most likely due to topographic enhancement by headlands: Antofagasta (23°S), Coquimbo (30°S), Valparaíso (33°S) and Concepción (37°S) (Figueroa and Moffat 2000, Mesías et al. 2003).

The hydrological regime is another important factor influencing the biogeochemistry of the water column. Overall, the northern side of the HCUS is a rather arid coastal zone with a few relevant fluvial inputs into the ocean, particularly along the Atacama Desert. At the central and southern Chilean coast, however, terrestrial inputs (freshwater, nutrients and sediments) may play an important role on fluxes of trace metals, nutrients and particulate matter (Thiel et al. 2007). Off southern-central Chile (36–40°S), coastal stratification imposed by freshwater runoff becomes important even during summer upwelling conditions

(Atkinson et al. 2002). This input has the potential to affect meso-scale oceanographic processes, with important consequences on the dynamics of nearshore ecosystems (Dávila et al. 2002, Navarrete et al. 2004, Sobarzo et al. 2007).

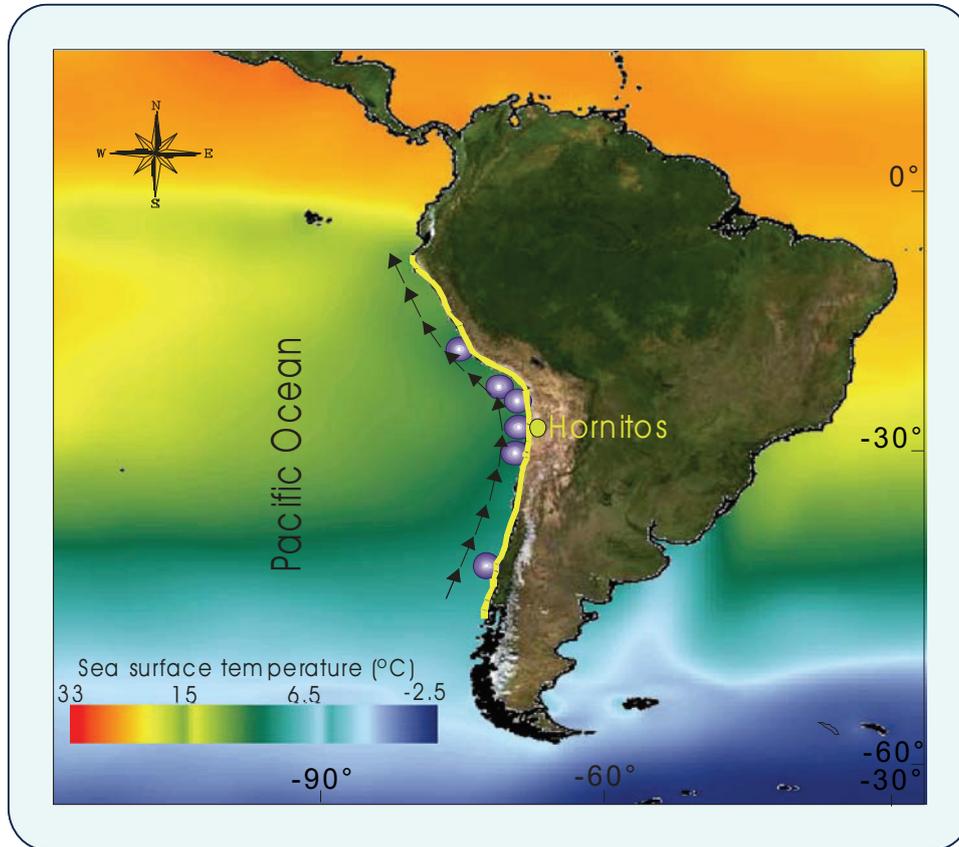


Fig. 1.1 Distribution of sea surface temperature (summer 2001) in the Eastern Pacific Ocean (adapted from World Ocean Atlas 2001; <http://www.lme.noaa.gov/Portal>) showing the cooling effect of the northward Humboldt Current (arrows) on the western coast of South America. Main upwelling centres along the Chilean and Peruvian coast are represented by blue circles (after Bakun 1996, Thiel et al. 2007). Yellow line shows the geographic distribution of *Mesodesma donacium* and the yellow circle indicates the location of the main field sampling station at Hornitos beach (northern Chile).

Owing to the predominant northward flow of the Humboldt Current, cool conditions are extended northward, more than in other continents at comparable latitudes (Camus 2001). According to Viviani (1979), sea surface temperature is 10°C lower at the northern edge of the HCUS, than it could be expected at similar latitudes. The origin and installation of the cold HCUS during the mid to late Miocene and subsequent fluctuations in the Quaternary (Villagrán 1995, Ibaraki 1997, Tsuchi 1997, 2002) largely defined a biogeographic transition zone between warm-temperate biota (Peruvian Province) and cold-temperate biota (Magellanic Province) (see Brattström and Johansen 1983, Camus 2001 for

reviews). This biogeographic unit is characterised by strong numerical reduction of subtropical and subantarctic species towards its southern and northern borders, respectively. However, several species occurring throughout this transition zone have a subantarctic affinity and a wide distribution in Chile and Peru (Menzies 1962, Castillo 1968, Alveal et al. 1973, Santelices 1980), probably facilitated by cool water masses transported by the HC towards the north, which is also considered to be the main reason why the area lacks a definite biogeographic character (Thiel et al. 2007).

Sandy beaches are a common coastal habitat of the western coast of South America (Jaramillo 1994, Jaramillo et al. 2001). They are characteristics of exposed shorelines, sheltered bays and coastal islands. Overall, macrobenthic infaunal communities of intertidal and shallow water in these sandy beaches are characterized by a low number of species, some of which are highly dominant and develop high biomasses (Arntz et al. 1987, Jaramillo et al. 2001). Species richness and biomass is, however, influenced by beach morphodynamics and bottom-up processes, increasing toward dissipative beaches, which are located near areas of persistent upwelling (Jaramillo et al 2001). The shoreline along the HCUS has a clear north-south orientation, where sandy beaches are the most representative habitats (Jaramillo et al. 2001), and strong environmental gradients affect their biota. However, little is known about the latitudinal factors driving the population dynamics of invertebrates of sandy beaches (Thiel et al. 2007). This knowledge is important for sound management of commercially important resources, as their exploitation should take into account the natural latitudinal variability in population dynamics and productivity.

Summary

- The HCUS is one of the most productive marine ecosystems on earth, and is characterized by a predominant northward flow of surface waters from the subantarctic region and by strong upwelling of cool nutrient-rich subsurface waters.
- Sandy shores are among the most common coastal habitats in the HCUS
- The features of the HCUS define the current biogeographic character of the associated biota.

1.2 El Niño-Southern Oscillation and the Pacific Decadal Oscillation: consequences for coastal ecosystems

Coastal ecosystems of the HCUS are under the influence of the El Niño-Southern Oscillation (ENSO), the strongest signal in the interannual variation of the ocean-atmosphere system (Wang et al. 1999). Oceanic ENSO signals originate as eastward-propagating equatorial Kelvin waves in the western Pacific, which intrude on the continental margin of South America and are converted into poleward coastal Kelvin waves, triggering warm El Niño (EN) events (Arntz et al. 2006). Moreover, the poleward propagation of Kelvin waves leads to a gradual decline in the magnitude of EN impacts towards higher latitudes (Thiel 2007, Camus 2008). Depending on the strength of EN, this process may lead to a drastic deepening of the pycno- and nutricline along the Peruvian-Chilean coast, extending the warm surface water layer to considerable depths and making upwelling, which is then derived from the low-nutrient warm water sphere, inefficient (Barber and Chavez 1983). Concomitant abiotic changes during EN include strong increases in surface temperature, increased sea level, greater wave action, and increased penetration of UV radiation. During most of these events, several regions of the western Andean slope experience positive precipitation anomalies and river inflow may increase dramatically, notably in central Chile and northern Peru, modifying salinity and transporting sediments and terrestrial vegetation into nearshore coastal waters (Vuille et al. 2000, Montecinos et al. 2000, Miranda 2001, Houston 2006). Such alterations can trigger a complex chain of biological effects, which may involve several levels of biological organisation at different spatial scales, during and between EN (Thiel et al. 2007).

The two severe EN events of 1982-83 and 1997-98 allowed the identification of dramatic and widespread biological effects in the HCUS, such as bathymetric or latitudinal migrations, invasion by warm-water species, behavioural alterations, reproductive and recruitment failures, increasing abundance of some species, and population decrease due to mass mortality of other species (Soto 1985, Tomicic 1985, Arntz 1986, Tarazona et al. 1988a, b, Camus 1990, Castilla and Camus 1992, Sielfeld et al. 2002, Vega et al. 2005, Arntz et al. 2006, Castilla et al. 2005, Vásquez et al. 2006, Ashton et al. 2008). There is, however, a lack of physiological and experimental work to arrive at

cause-and-effect explanations for the numerous changes that have been described (Arntz et al. 2006).

ENSO has been a crucial factor in the global climate for at least the past 130,000 yr (Cane 2005), showing continuous, although variable, activity during the last 12,000 yr (Moy et al. 2002). This suggests that coastal communities in the HCUS have continuously been shaped by impacts of EN events (Camus 1990, 2001). Therefore, EN has submitted several species and sometimes entire communities (e.g. kelp forest) to a recurrent extinction-recolonization dynamic whose ecological, biogeographical and evolutionary consequences are not yet fully understood (Thiel et al. 2007).

Only recently consciousness has developed including decadal oscillations, in particular the Pacific Decadal Oscillation, as an important factor influencing life in the sea (Arntz et al. 2006, Arntz and Laudien, 2006). Although increasing evidence exist on the effects of these oscillations in the pelagic ecosystem (e.g. Schwartzlose et al 1999, Peterson and Schwing 2003, Alheit and Niquen 2004) no attempt has been made to analyse the relationship between long-term fluctuations of coastal resources and decadal climate oscillations.

Summary

- Coastal ecosystems of the HCUS are severely affected by climate interannual and possibly interdecadal variability. Abiotic changes during EN trigger a series of responses at different spatial scales and levels of biological organisation.
- The recurrence of EN has submitted species and even entire communities to a continuous extinction-recolonization process, whose consequences and mechanisms are poorly understood.

1.3 The family Mesodesmatidae

The family Mesodesmatidae is represented by a few genera and species of marine bivalves. These organisms inhabit sandy beaches of temperate and subtropical systems, where they usually are the dominant organisms (Marins and Levy 1999, McLachlan et al. 1996). The genera *Phapies* and *Mesodesma* includes the largest, most abundant and commercially exploited mesodesmatids

(McLachlan et al. 1996, Beu 2006). *Paphies* is restricted to New Zealand, where its recent members are among the most abundant and familiar of shallow-water bivalves on sand beaches and near the mouths of estuaries (Beu 2006). The genus *Mesodesma* is represented by four species distributed in North and South America. The Arctic wedge clams, *M. deauratum* (Turton 1822) and *M. arctatum* (Conrad, 1831) are found on the western North Atlantic coast. Although there is apparently little distributional overlap, the habitats of the two species are essentially alike – coarse, sandy bars and banks at the mouths of rivers, streams and tidal inlets (Davis, 1967). In South America, *M. donacium* belongs to the Chile–Peru Malacological Zoogeographic Province (Tarifeño 1980), while *M. mactroides* is distributed on the eastern coast of South America. Although *M. mactroides* is one of the best studied species among beach clams and its commercial fishery is closed since more than 50 years (McLachlan et al. 1996, Fiori and Defeo 2006, Hermann 2008), the strong decline of abundance and biomass associated to overexploitation and mass mortality events has led to consider it at risk, probably with a critically endangered status (Fiori and Cazzaniga 1999, Hermann 2008).

Summary

- Species within Mesodesmatidae are numerically dominant marine bivalves typically inhabiting temperate and subtropical sandy beaches.
- Two species, *M. mactroides* and *M. donacium*, are distributed along the eastern and western coast of South America, respectively.

1.4 *Mesodesma donacium*

1.4.1 Distribution and life history – The surf clam *Mesodesma donacium* (Lamarck 1818, Fig. 1.2) is an endemic species of the Chilean and Peruvian coast, where it is known under the common name “macha”. This species is distributed from the Island of Chiloé (Southern Chile, at ~43°S) to Sechura (Peru, at ~5°S) (Alamo and Valdivieso 1987) and inhabits the low intertidal and the swash zone up to 15-20 m of exposed, semiexposed or sheltered beaches frequently receiving freshwater flow from rivers and/or freshwater streams, either seasonally or perennially (Tarifeño 1980, Jaramillo et al. 1994, Riascos et al. 2008a, Riascos et al. submitted). River inflow often displays a strong seasonal

signal that represents a major forcing function for coastal ecosystems and defines their productivity at local scales (Kjerfve et al. 2001). Despite that, no attempt has been made to determine the effects of river inflow on the ecology of *M. donacium*. Alongshore, *M. donacium* often shows a discontinuous distribution, with separated patches of similar shell sizes. Patches of juvenile clams are often found near the outlet of rivers and estuaries (Tarifeño 1980, Jaramillo et al. 1994, but see Ortiz and Stotz 1996).

The across-shore distribution shows a well defined size-related pattern at Chilean beaches, with recruits and juveniles primarily occurring in the low intertidal and adults being confined to the shallow subtidal (Tarifeño 1980, Jaramillo et al. 1994, Ortiz and Stotz 1996, Riascos 2008a). However, an opposite trend was found by Arntz et al. (1987) for populations from Santa María del Mar, Peru.



Fig. 1.2 *Mesodesma donacium* (Lamarck 1818).
Photo: Tom Ashton

Local changes in temperature and food availability have been suggested to explain latitudinal differences in the timing of gametogenesis and spawning periods of *M. donacium* along the Chilean coast (Tarifeño 1980, Peredo et al. 1987, McLachlan et al. 1996), but an appropriate assessment of the general trends across the geographic range of this species is still lacking. *M. donacium* is a large, fast-growing species (maximum shell length: 124 mm; average growth performance: 3.74), with northern populations

showing faster growth rates (McLachlan et al. 1996). Likewise, northern populations of *M. donacium* often exhibit high abundances and extremely rich annual somatic production, which may reach 2,900 g shell-free dry mass·m⁻² and

contribute to more than 95% of the shallow soft-bottom community (Arntz et al. 1987). In contrast, abundances and dominance reported from central-southern Chilean beaches are lower (see Tarifeño 1980, Jaramillo et al. 1994). Considering these differences, strong patterns in life history traits of this species along the geographic range are likely.

Summary

- *M. donacium* is distributed from northern Peru to southern Chile and inhabits the intertidal and shallow subtidal of sandy beaches.
- Several life history traits of *M. donacium* show differences between Peruvian and Chilean sandy beaches.

1.4.2 Interspecific interactions – Several relationships of predation, commensalism and parasitism have been described for *M. donacium* (Fig. 1.3). Sea birds heavily prey on small (<30 mm shell length) surf clams living in the intertidal, which are dislodged from the sediments by wave action. Fish occurring in sandy habitats also prey on *M. donacium* (Tarifeño 1980). Parasitism can be a potentially important process influencing demographic patterns and distribution of sandy beach macrofauna (Defeo and McLachlan 2005). Parasites may play a role in explaining massive natural mortality events of the yellow clam *M. mactroides* along thousands of kilometres of sandy beaches in Brazil, Uruguay and Argentina (Cremonte and Figueras 2004, Fiori et al. 2004), thus providing an alternative explanation to the widely held notion that mass mortalities in beach macrofauna are due to toxins from harmful algal blooms (McLachlan et al. 1996b). Although a significant parasitic interaction can not be ruled out, the reported prevalence of plerocercoids of the cestod *Rhodobotrium mesodesmatium* is low in *M. donacium* (Tarifeño 1980, Riascos 2008a). In contrast, the spionid *Polydora biocipitalis* shows a latitudinal pattern of increasing prevalence toward lower latitudes (Riascos et al. 2008a). There are at least two reasons to further investigate the association between *M. donacium* and *P. biocipitalis*. First, spionid worms of the genus *Polydora* and related genera have been labelled as pests on cultured and wild commercially important molluscs throughout the world (Lleonart et al. 2003, Simon et al. 2006). Second, a recent study included *P. biocipitalis* within a group of non-indigenous species

(NIS, *sensu* Carlton 1996) invading Chilean waters (Moreno et al. 2006) thus rising concerns about the threat for *M. donacium* and other native mollusc species (Moreno et al. 2006).

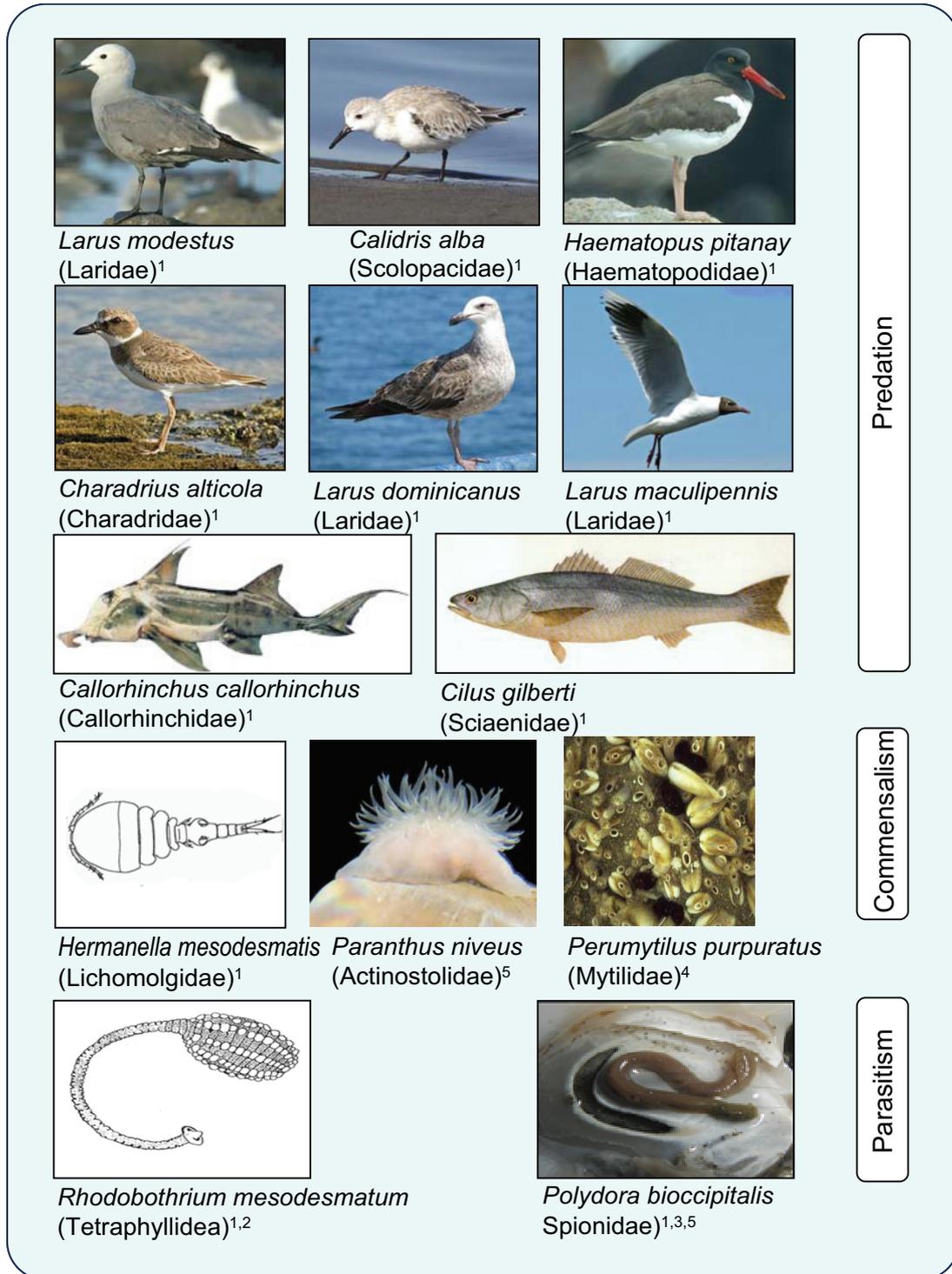


Fig. 1.3 Fauna associated to *Mesodesma donacium* according to Tafireño (1980)¹; Carvajal and Mellado (2007)²; Moreno et al. (2006)³; Villegas et al. 2006⁴; this study⁵.

Summary

- Among a variety of species maintaining a biological relationship (predation, commensalism, parasitism) with *M. donacium*, the spionid polychaete *P. biocciptalis* has the potential to influence demographic processes of this clam.

1.4.3 Impacts of El Niño on *Mesodesma donacium* – The mass mortality of *M. donacium* populations after EN events constitutes one of the most conspicuous cases of severe, long lasting and widespread effects of sudden temperature increase events on marine invertebrates, causing considerable shifts in the whole sandy beach community (Arntz et al. 1987, Clarke 1993). Originally distributed from Sechura (5°10'S), Peru to Chiloé (43°20'S), southern Chile, this surf clam was set back southward to 14°S after the severe EN 1982-83 (Tarifeño 1980, Arntz et al. 1987). Few years later, EN 1997-98 wiped out surf clam populations in Moquegua (17°40'S), Tacna (18°09'S), Arica (18°20'S) and Coquimbo (29°55'S) within a few days (Quiroz and Barriga 1998, Aburto and Stotz 2003, Thiel et al. 2007). The beds in Coquimbo were washed into the bay by a river flood due to heavy rainfall (Miranda 2001). In the Coquimbo area, the only beds left were in Tongoy Bay, which were exploited according to –what was considered then– a very conservative strategy. However, despite dynamic (and apparently conservative) management, these beds also disappeared (Aburto and Stotz 2003). While mass mortality events seem to be related to EN-increased temperatures, mass mortality events in central Chile, where thermal anomalies are much lower, suggest that other factors may also play a role (Miranda 2001). Unfortunately, the general lack of physiological and experimental work represents a gap to arrive at cause-and-effect explanations for the numerous changes observed during EN events (Arntz et al. 2006).

The low ability of *M. donacium* to recover its former dominance and productivity is remarkable. After more than 20 years, only an impoverished community consisting mainly of small opportunistic polychaetes persists in beaches formerly dominated by *M. donacium*. Moreover, the subdominant surf clam *Donax marincovichii* and mole crab *Emerita analoga*, which both survived EN, never attained the role of *M. donacium* (Arntz et al. 1987). Assessment of the

demographic processes at the species range boundaries is critical to understand the threshold responses to environmental change and predict the future distributions (Lawton 2000, Gaston 2003, Hampe 2004). Although a small population of juvenile individuals of *M. donacium* remained in southern Peru (Ilo ~17°S) the northernmost population showing a representation of all length classes is located at Hornitos (northern Chile, Fig. 1.1) and represents the current range boundary. Therefore, a detailed study of the population dynamics of this population is needed to gain insights into the responses of this species to biotic and abiotic factors limiting the northward recolonization after strong EN events.

Summary

- Strong EN events caused mass mortalities of *M. donacium* and the poleward retraction of the northern geographic distribution. This species shows a remarkably low ability to recolonize its former distribution.

1.4.4 Fisheries – Owing to its abundance and accessibility, *M. donacium* has been used as food source at least since the Terminal Pleistocene (Sandweiss et al. 1998). Today, this clam is still one of the most important species in small-scale benthic fisheries in the HCUS (Tarifeño 1980, Defeo et al. 1993, McLachlan et al. 1996, Thiel et al. 2007). The surf clam is primarily harvested by artisanal fishers operating from the beach and entering the surf zone during low tides (Fig. 1.4). They collect the clams by twisting their feet and using their body weight to excavate the sand until clams emerge at the sediment surface to be picked up.

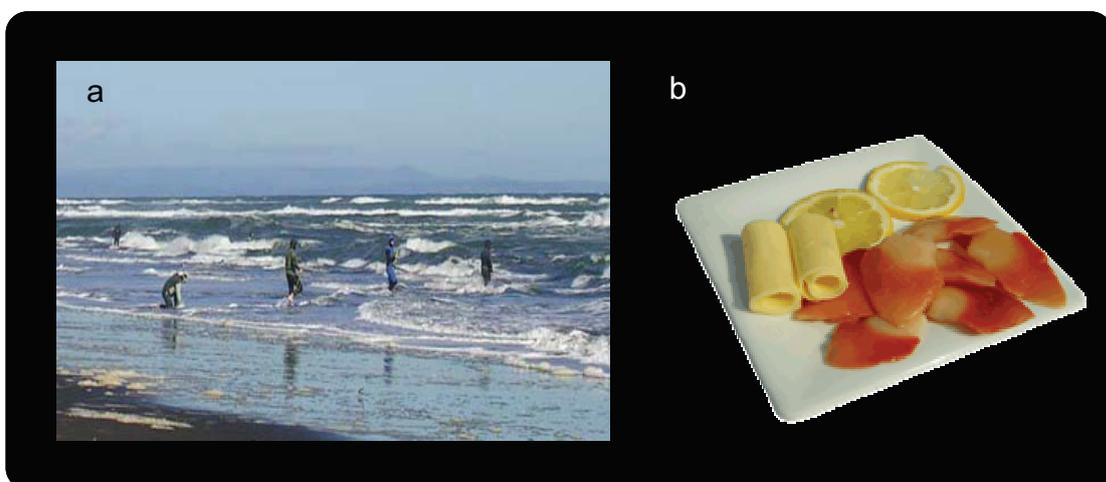


Fig. 1.4 a Artisanal fishermen collecting *M. donacium* during low tide; b typical dish offered in Chilean restaurants.

In general, the fluctuations of landings in Chile and Peru (Fig. 1.5) show the classical signs of a “boom and bust” fishery: after the discovery of the stock, the fishery developed and subsequently overexploitation took place until the stock collapsed (Thiel et al. 2007). Moreover, they reflect the natural variability of the environment of the HCUS, notably EN events as described above.

Differences in management strategies of *M. donacium* between Chile and Peru likely reflect the “volatile” nature of this resource in Peru, where the fishery can be considered an open access system. Landings in Peru showed a steady increase from 1964 to 1977, reaching an impressive peak in 1978 and 1979. Certainly the strong decline between 1979 and 1985 and 1997 and 1999 was mainly due to EN impacts, but over-exploitation also played an important role (Castilla and Camus 1992). The combination of these factors explains the decreasing trend of landings two years before EN 1982-83 in Peru and may also explain the main fluctuations of landings in Chile (Thiel et al. 2007). However, the latter has established a system of territorial user rights for fisheries, called Areas de “Manejo y Explotación de Recursos Bentónicos” (AMERB or Management and Exploitation Areas for Benthic Resources MEABR). Legally established in 1997, this management tool grants exclusive fishing rights over a defined coastal area to legally established organisations of local fishermen.

The establishment of AMERB’s has recently highlighted the natural variability of the environment of the HCUS. Global-scale phenomena, which produce an outburst of some resources and disappearance of others, together with more localised processes of upwelling and current systems, generate a complex, spatially and temporally changing mosaic of conditions (Thiel et al. 2007).

Summary

- The fluctuations of landings of *M. donacium* in Chile and Peru reflect the classical signs of a badly regulated fishery and the natural variability of the environment. The depletion of several populations has encouraged recent management strategies in Chile.

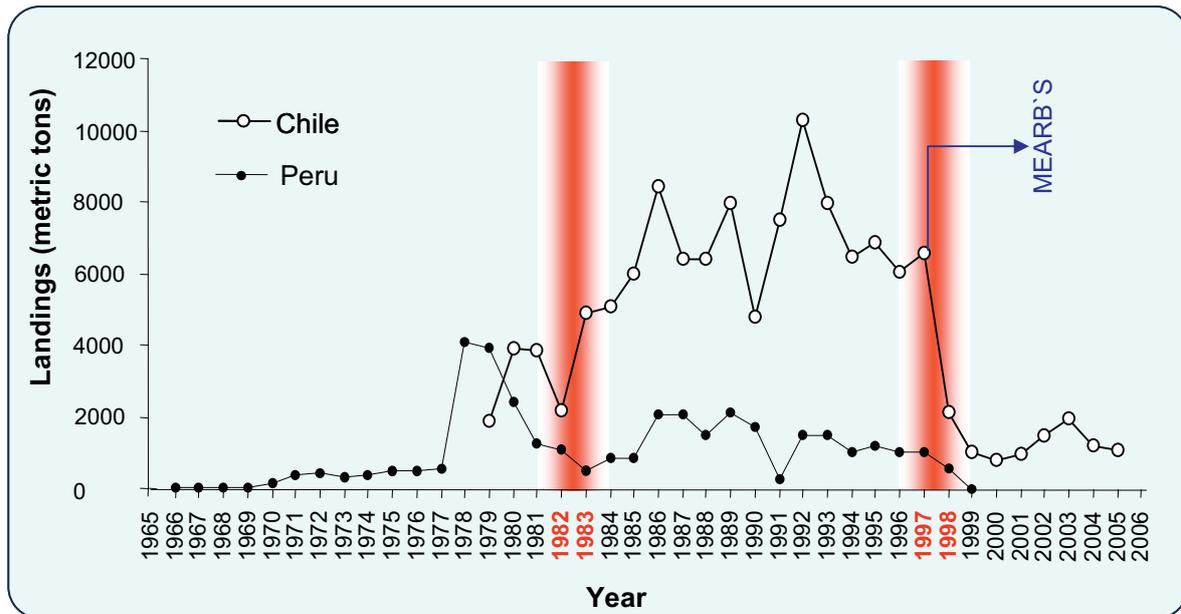


Fig. 1.5 Peruvian and Chilean landings of *Mesodesma donacium* according to fishery statistics of IMARPE (www.imarpe.gob.pe) and SERNAPESCA (www.sernapesca.cl). The two last severe El Niño events are indicated with red bars, as well as the establishment of MEARB's (management and exploitation areas for benthic resources) in Chile.

2 AIMS OF THIS STUDY

This study aims to understand the major environmental and biological factors driving latitudinal trends of *M. donacium* population dynamics along its geographic range. Because of the inherently large spatial scale involved, this study used a combination of 1) compiled field data covering the relevant spatial scale; 2) laboratory work to evaluate specific hypotheses and validate methodological tools and 3) field work to fill specific gaps and address specific questions. “Grey literature” is still one of the most important sources of knowledge about natural science research and management of natural resource systems in Latin American countries (Thatje et al. 2007). Hence, a comprehensive assessment of the information dispersed in several universities, research centres and governmental offices was performed, and relevant data sets were archived in the open-access library PANGAEA (Publishing Network for Geoscientific & Environmental Data). This thesis comprises a collection of publications addressing five objectives involving specific hypotheses where appropriate:

- (i) To develop a reliable methodological tool enabling accurate measurements of short-term growth of *M. donacium* (Publication I).
- (ii) To study the features of the association between *M. donacium* and the spionid *P. biocipitalis* at Hornitos (Northern Chile). Hypothesis: The infestation by *P. biocipitalis* can negatively affect the performance of *M. donacium* populations (Publication II).
- (iii) To determine whether the association between *M. donacium* and *P. biocipitalis* is the result of a recent introduction of *P. biocipitalis* to the Chilean-Peruvian coast or if this association rather represents a long-term association. Hypothesis: the changes in *M. donacium* shell morphology produced by the infestation represent a distinctive feature of the association, which can be tracked back in the fossil record (Publication III).
- (iv) To determine the effects of increased temperature and reduced salinity, typically observed during EN, on growth rate and mortality of *M. donacium*. Hypothesis: Anomalous temperature and salinity have distinct, measurable effects on *M. donacium* growth and mortality (Publication IV).
- (v) To establish the spatial and temporal patterns of the reproductive cycle of

M. donacium and determine their relationship with temperature and salinity.

Hypothesis: The patterns of the reproductive cycle of *M. donacium* are related to either temperature or salinity changes (Publication IV).

- (vi) To analyse demographic processes of *M. donacium* at the current northern range boundary and determine the geographical trends in population dynamics. Hypotheses: demographic changes of *M. donacium* towards the northern range boundary reflect the threshold tolerance to biotic and abiotic factors. Large-scale patterns in abundance, growth, mortality and productivity are linked to the spatial variability of specific environmental factors (Publication V).

3 MATERIALS AND METHODS

In the following chapter, I will briefly describe the data sources and principal methods used in this study. Detailed methods can be found in the corresponding publications.

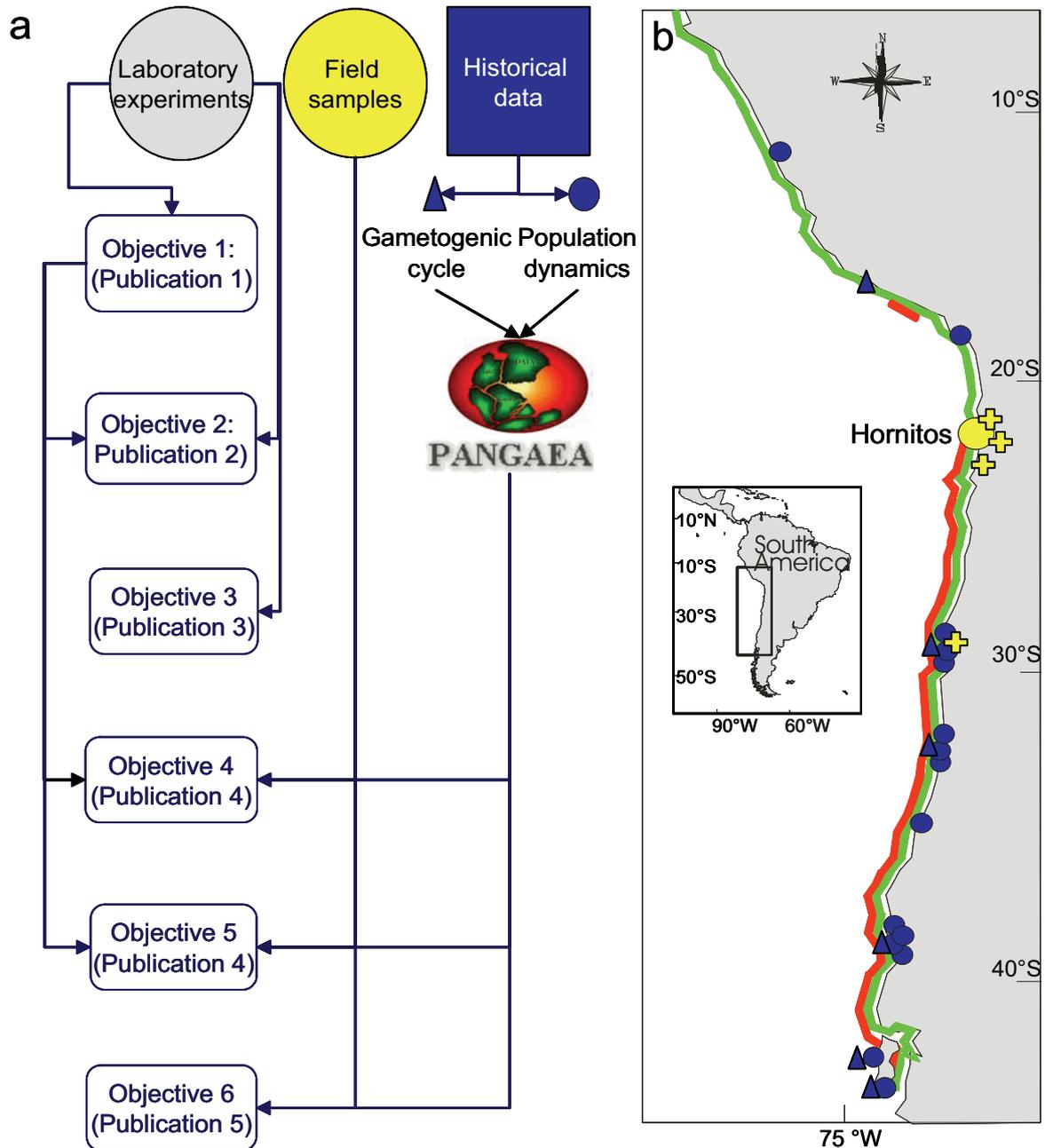


Fig. 3.1a Flow chart showing the data sources used in this study to achieve specific objectives. **b** The combined field (yellow) and historical data (blue symbols) covered most of the former geographical distribution of *Mesodesma donacium* (green line). Field work was focussed in the northern limit of the current geographic distribution (red line). The yellow circle corresponds to the main field station (Hornitos, northern Chile); yellow crosses represent fossiliferous deposits in northern-central Chile (Publication 3).

3.1 Sampling site and sampling

Sampling of *M. donacium* was conducted from May 2005 to April 2007 at Hornitos (22°54.998'S; 70°17.416'W; Fig. 3.1), a sandy beach at the northern side of Mejillones Bay, Antofagasta, northern Chile. This population represents one of the northernmost remnants after populations were decimated during the severe EN 1982-83 and 1997-98 events and the only one showing a relatively even composition of length classes. The population is distributed along ~400 m sandy beach and not exploited commercially owing to the small size of the bed and its low abundance. A species-driven sampling strategy (*sensu* Defeo and Rueda 2002) was used to collect monthly samples along a transect perpendicular to the shoreline during spring tides. Samples (three replicates, spaced 5 m apart) were taken along a transect from the spring tide high water mark towards the shallow subtidal at 4 m intervals until no clams were found in two consecutive depth lines. When samples yielded clams, replicates were extended to five or ten, depending on tidal conditions. A sheet-metal box (0.16 m², 0.35 m deep; e.g. Laudien et al. 2003) was used for the intertidal and a diver-operated push box-corer (0.02 m², 0.20 m deep; Rumohr and Arntz 1982) for the subtidal sampling. Clams retained after sieving through a 0.5 mm mesh were measured (SL, anterior-posterior shell length) to the nearest 0.5 mm. To characterize the sampling site, the following parameters were measured: sea surface temperature (SST; °C), registered in hourly intervals during the whole study period with an Onset StowAway temperature logger installed on a float located ~100 m seaward. Salinity and Chlorophyll *a* concentration (Chl *a*; mg l⁻¹) were registered every 15 minutes during monthly samplings using a multiparameter data sonde (Yellow Springs Instrument Company, model 6600). The beach slope (Bs, cm m⁻¹) was determined by Emery's profiling technique (Emery 1961). Monthly changes in the Oceanic Niño Index (ONI; 3-month running mean of SST anomalies in the El Niño 3.4 region) reported by the NOAA/Climate Prediction Center, USA, were used to characterize the ENSO status during this study.

3.2 Testing chemical stains for labelling *M. donacium* shells

Specimens of *M. donacium* were collected at Hornitos (Fig.3.1) and immediately transported to the laboratory. Specimens were maintained in a 1,000 l-tank with circulating seawater. The standard length (SL) of all specimens was measured to

the nearest millimetre below. Clams were acclimated and fed *ad libitum* with a mixture of three microalgae cultures during one month before the experiment started. Three stains (strontium chloride, calcein, and alizarin red) were used at two different concentrations (strontium chloride: 225 and 900 mg l⁻¹; calcein and alizarine red: 50 and 100 mg l⁻¹) and two immersion periods (strontium chloride: 17 and 24 h; calcein and alizarine red: 3 and 6 h). Thirteen animals covering the whole size range available were randomly assigned for each treatment. For staining, animals were placed in 4 l aquaria with aerated sea water containing the respective treatment. After immersion, clams were reared in the laboratory during 20 days to allow growth. A control group was treated in exactly the same way without adding staining dye to the water. Dead animals were registered daily during the experiments. Growth rate ($Gr = SL \text{ increment} \cdot \text{day}^{-1}$) and body condition index ($BCI = [\text{dry mass}/SL] \cdot 100$) were calculated at the end of the rearing period. After the rearing period, animals were sacrificed and the shells were cleaned and dried. Transverse shell sections were cut, embedded in resin and polished for detecting growth marks. Scanning electron microscopy and fluorescence microscopy were used to detect strontium chloride-induced marks and calcein/alizarin-induced marks, respectively.

A log-linear analysis on a cross tabulation table (4*2*2) was performed to test effects of the different treatments on mortality (Zar 1984). An analysis of covariance (ANCOVA) was used to compare growth rates between treatments, with marker, concentration and time exposition as factors and SL as the covariate. Correspondingly, an ANCOVA was performed to compare BCI between treatments using the same factors and the covariate. Data were linearized to fulfil ANCOVA assumptions. The Tukey honest significant difference test for unequal sample sizes was used for multiple comparisons (Zar 1984).

3.3 The infestation of *M. donacium* by *Polydora biocipitalis*

From monthly samples taken at Hornitos, the prevalence of infestation (PI; % of infested clams) was estimated to model the relationship between the infestation by *P. biocipitalis* and the size of *M. donacium* by using non-linear, least squared methods. Moreover, the temporal variability of the infestation was studied by measuring the thickness of blisters (Tb) formed by the clams when they become infested by the polychaete. Blister wall sections were embedded in resin,

grounded, polished and the T_b measured to the nearest $1\ \mu\text{m}$ under a reflective light microscope. A one-way analysis of variance (ANOVA) was used to test for differences in mean T_b between months. The correlation between temperature and T_b or PI was determined using Spearman's rank correlations.

The body condition index (BCI), the gonado-somatic index (GSI, see Laudien et al. 2001), the growth rate (Gr) and the burrowing ability of *M. donacium* were used as performance measures to test the effects of the infestation by *P. biocipitalis*. Both BCI and GSI were estimated from field samples, which were classified into four levels of increasing infestation by *P. biocipitalis* (Level 0 to Level III). Adult infested and not infested clams ($N = 40$) were selected to study the effect of the infestation on the Gr and the burrowing ability of the clam under laboratory conditions. After 25 days-acclimation period, clams were stained in calcein ($50\ \text{mg l}^{-1}$; 3 h) to incorporate a mark in the shell matrix and allow short-term growth measurements. Subsequently, they were maintained in a 1,000 l flow-through-tank with sand (25 cm depth) for 45 days. Every five days, all clams were removed from the sand and subsequently released on the sand surface. Individual digging time (Dt; min) was registered as the time period from release until the clam was completely buried in the sand. At the end of the experiment, all animals were sacrificed and classified according to the above mentioned infestation levels. Shells were dried and cut along the axis of maximum growth; the resulting sections were embedded in resin and polished to detect calcein labels. Growth increments starting from the fluorescent mark were measured to the nearest $1\ \mu\text{m}$ under a fluorescence microscope using blue light (460 to 490 nm) (Riascos et al. 2007). One-way ANCOVA's were performed to compare the effect of infestation level on log-transformed data of BCI and GSI, using SL as the covariate. Growth rate and Dt between clams of different infestation levels were compared by one-way ANOVA. The Shapiro-Wilk test and Bartlett's test were used to check ANOVA and ANCOVA assumptions. Tukey honest significant difference tests were used for multiple comparisons, when significant differences were detected.

3.4 Evidence of infestation of fossil shells of *M. donacium*

Fossil shell valves of *M. donacium* ($N = 183$) were collected in fossiliferous coastal deposits at Michilla ($22^{\circ}43'S$; $70^{\circ}16'W$), Chacaya ($22^{\circ}57'S$; $70^{\circ}18'W$)

and Las Lozas (23°28`S; 70°28`W), north of Antofagasta and at Los Porotitos (29°48`S; 71°17`W), near La Serena (Fig. 3.1). These deposits correspond to well preserved sequences of sediments associated with marine terraces formed during high seastands of the last interglacial periods (Marine Isotopic Stages). The age of each fossiliferous deposit was determined by using a combination of geochronological and geomorphological approaches (Radtke 1989; Leonard and Wehmiller 1991, 1992; Ortlieb et al. 1995, 1996). Recent *M. donacium* shells (N = 665) collected at Hornitos were also analysed for comparisons. For both, fossil and recent shells, the SL was measured to the nearest 0.5 mm and the location, presence and internal features of blisters were registered. Fossil and recent shells analysed in this work are deposited at the IRD-Universidad de Antofagasta Paleontological Collection (Antofagasta, Chile). A variance ratio test (Zar 1999) was used to test for differences between SL variance of blistered fossil and recent shells. The Shapiro-Wilk test was used to assess normality of each data set, needed to meet the assumptions of this test.

3.5 Effects of temperature and salinity change on *M. donacium*

3.5.1 Growth and mortality

A laboratory experiment was performed to test the effect of anomalous (EN) higher temperature and lower salinity on the Gr and mortality of *M. donacium*. Specimens (N = 135) collected at Hornitos were acclimated for 25 days at ambient temperature (17.4°C) and salinity (~35). After acclimation, clams were stained in calcein (50 mg l⁻¹; 3h), divided into juveniles (SL ≤ 50 mm) and adults (SL > 50 mm) and randomly assigned to a 3*2 factor experimental design: three salinities (10 ± 1, 20 ± 1 and 35 ± 1) and two temperatures (17.4 ± 0.5°C, the historical annual average and 24.2 ± 0.5°C the maximum registered during EN 1982-83; CENDHOC). Each combination was run with three replicates and seven clams per replicate. Animals were held in experimental conditions during one month. Twice a day, sand was aerated, dead clams were counted, removed and shells were kept for further analysis. After the experiment, all the shells were cut and processed as described above to detect calcein labels and shell length increments were measured to the nearest 1 µm under a fluorescence microscope.

The parameter K of the relationship between Gr and SL (Gulland and Holt 1959) was used as a measure of growth for each replicate under each set of temperature - salinity condition and analysed using two-way, fixed effects ANOVA for juveniles and adults, with salinity and temperature as factors. Differences of the slope of the regression between mortality and time in each replicate were analysed using two-way ANOVA for juveniles and adults, with salinity and temperature as factors. Data were $\log(X + 1)$ transformed to meet the assumptions of normality and independence of error terms. Homogeneity of variances was checked using Cochran's C -tests.

3.5.2 The gametogenic cycle

A subsample of 50 clams was selected from the field samples from Hornitos. These clams were fixed in aqueous Bruin's fixative and processed later on following standard histological procedures. After dehydration, tissues were embedded in paraplast wax, sectioned at 3-7 μm and stained with hematoxylin-eosin. Based on the morphological development of the germ lines in the acinus of the gonads, individuals were classified into four gametogenic stages (inactive, active, spawned and recovering). Similar studies containing reliable information on the gametogenic cycle of this species were carefully analysed and the corresponding data sets were archived in the open-access library PANGAEA and used for latitudinal comparisons. The resulting data sets stem from eight sandy beaches covering the entire current distribution range of *M. donacium* (Fig. 3.1). The two consecutive gonad stages - active and spawned - were objectively distinguished in each study for both males and females and their frequencies were used herein to describe the spatial-temporal variability of the gametogenic cycle. Monthly-averaged data on SST, river inflow ($\text{m}^3 \text{seg}^{-1}$) and coastal precipitation (mm) were obtained from open-access hydrological and meteorological databases of Chile and Peru.

A multivariate approach of linking environmental variability patterns to biotic patterns developed by Clarke and Ainsworth (1993) was adapted to assess the 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. Environmental variables were normalised to account for scale differences and enable

comparisons, and between-months Euclidean distance matrices were calculated for each locality. To determine whether the monthly pattern of gonad stage composition may be related to monthly changes in environmental factors, the BIO-ENV analysis of the PRIMER v6.1.6 software package (Clarke and Gorley 2006) was used. This procedure defined single or suites of environmental variables that best “explain” the variability of gonad stage compositions.

3.6 Population dynamics of *M. donacium* at Hornitos

3.6.1 Abundance, length-mass relationship and individual growth

Monthly abundance (ind m⁻²) and mean annual abundance were determined from monthly field samples. A subsample (N = 50) covering the whole size range was selected to determine the parameters of the length-mass relationship (Mass = a SL^b). The ash-free dry mass (AFDM; g) was used as estimator of body mass change and was obtained by ignition of dry soft tissues at 550°C for 6 h. The monthly length frequency distribution data were fitted to the von Bertalanffy Growth Function (VBGF) to determine individual growth. The curvature parameter K (yr⁻¹) and the asymptotic length L_∞ of this model were used to estimate the growth performance index phi prime ($\Phi' = 2 \log L_{\infty} + \log K$) and enable growth comparisons.

3.6.2 Mortality and productivity

Total mortality Z (year⁻¹) was estimated using the single negative exponential model ($Nt = N_0e^{-Zt}$; where t is the time and N₀ is the number of individuals at t = 0) and the length converted catch curve (Pauly 1983). The mass specific growth rate method (Crisp 1984) was used to calculate total annual somatic production P (g AFDM m⁻² year⁻¹) using the abundance estimation, the pooled length–frequency data, the VBGF parameters and the length–mass relationship. The annual mean biomass \bar{B} (g AFDM m⁻²) of the population was estimated from the abundance data and the length-mass relationship. Finally, the productivity was calculated as the P/ \bar{B} ratio and was used for further comparisons.

3.7 Demographic data compilation and modelling of biogeographic patterns

Information on demographic parameters of *M. donacium* from a wide range of sources corresponding to 16 sandy beaches (Fig. 3.1) between Santa María del

Mar (Peru, 12°04' S) and Quilánlar (Southern Chile, 42°23' S) were compiled, thus covering almost the entire species distribution range. These data, including the corresponding details on methods and sampling design, were archived in the open-access library PANGAEA. Biogeographical patterns were defined using latitude as independent variable and population parameters (mean annual abundance, growth performance, mortality and productivity) as dependent variables. The relationship between biotic and abiotic variables was modelled by linear and non-linear fitting procedures, selecting the model with the best goodness of fit. To assess trend changes related to EN, the parameter “*b*” (slope) of the EN and non-EN regressions was compared using *t*-Student tests (Zar, 1999). A common regression line/curve was calculated when no statistical differences were found.

4 RESULTS AND PUBLICATIONS

4.1 Overview

Calcein produced clearly visible fluorescent growth bands in shells of *M. donacium* at all concentrations and exposure times. Alizarin red markings were successful to a lesser extent: distinct fluorescent bands were only detectable after 6 h immersion and at higher concentration (100 mg l⁻¹). Strontium chloride did not produce marks. A new attempt with a higher concentration and immersion time (2880 mg l⁻¹ for 24 h) was necessary to produce clear bright bands. Growth of *M. donacium* was too slow in adult clams (~0.002 µm day⁻¹) to form measurable shell material after the marginal bright bands. Consequently, growth comparisons between treatments were not possible. No statistical differences in BCI of *M. donacium* were found between stains (F = 0.16, p > 0.1). Mortality was generally low and was independent from treatments ($\chi^2 = 0.985$, df = 10, p = 0.999). Therefore, no lethal or sublethal (body condition) effects were observed for any of the used stains, even at higher concentrations and immersion times, but calcein was the best option in terms of staining success. The relationship between PI and clam size was best fitted to a logistic model (Fig. 4.1). The smallest infested clam had 34 mm SL, coinciding with the range of length at first maturity. PI clearly increased after 55 mm SL, coinciding with the appearance of a gap in shell closure in medium-size clams (Fig. 4.1). The parameter β of the logistic model was close to 1, indicating that almost all old clams were infested.

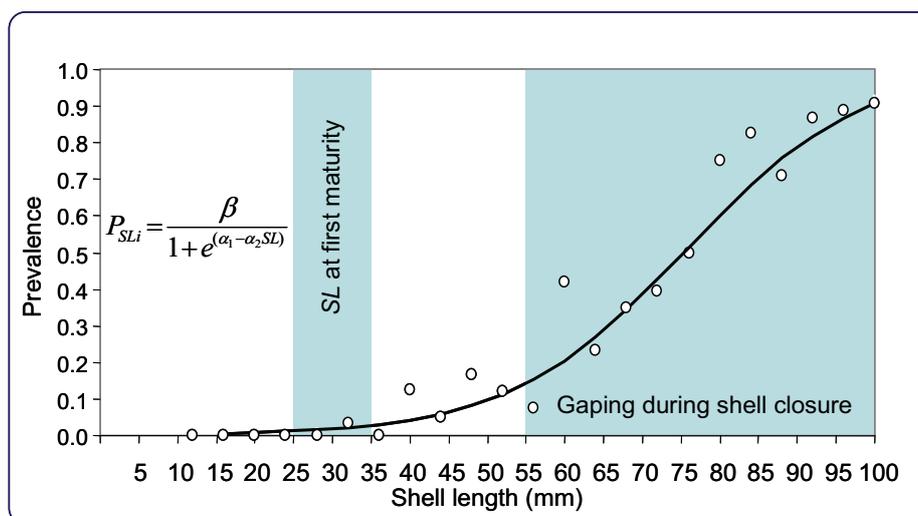


Fig. 4.1 Logistic function of the relationship between the shell length of *Mesodesma donacium* and the prevalence of *Polydora biocpipitalis*; range of shell length at first maturity (Jerez et al. 2007a, b) and range of shell gaping are indicated.

Mean thickness of blisters differed between months ($F = 2.388$; $p < 0.01$), showing a bimodal pattern with higher values in September 2005 and March 2006 (Fig. 4.2). The opposite trend was observed for the prevalence of infestation, which tends to increase when mean thickness of blisters decreases. Therefore, the infestation was inferred to occur mainly during October-December and April.

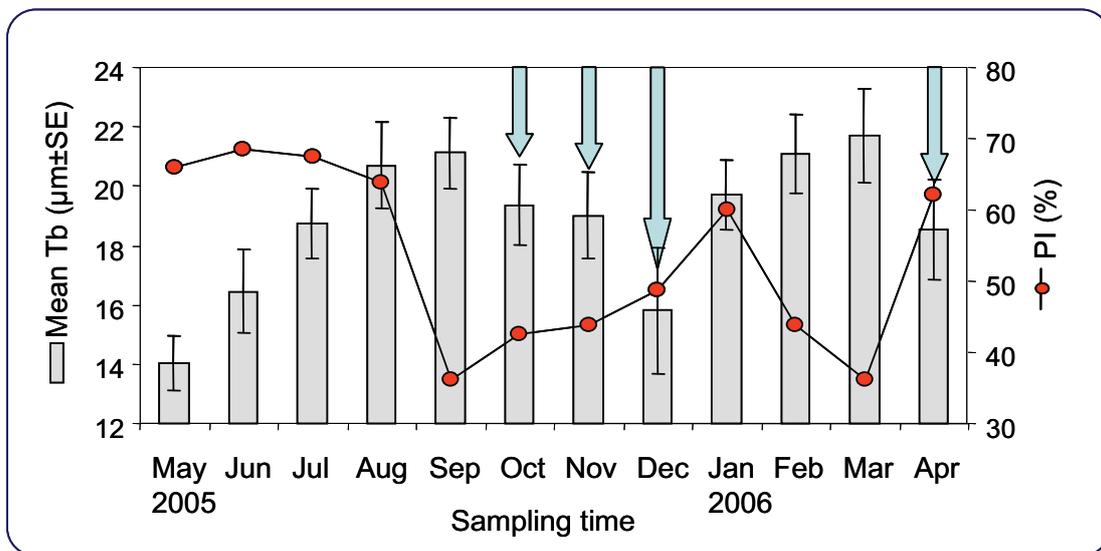


Fig. 4.2 Changes in mean thickness of blister walls (Tb) from shells of *M. donacium* and prevalence infestation by *P. biocpipitalis* (PI). Decreases in mean thickness and increases in prevalence were considered as evidence of new infestations (arrows).

Mean GSI between clams with distinct infestation levels was not significantly different ($F = 0.322$; $p = 0.89$). In contrast, mean BCI significantly differed between clams with distinct infestation levels ($F = 8.606$; $p < 0.01$). Multiple comparisons showed that mean BCI of level 0, level I and level II clams did not differ from each other (Tukey's test: $p > 0.05$), but were significantly higher (Tukey's test: $p < 0.01$) than those of heavily infested clams (level III, Fig. 4.3a).

Both, mean digging time and mean growth rate of *M. donacium* differed between infestation levels ($F = 3.21$; $p = 0.034$, $F = 6.14$; $p < 0.01$, respectively) (Fig. 4.3b). Multiple comparisons revealed that the first three levels did not differ (Tukey's test: $p > 0.05$), neither in digging time, nor in growth rate, whereas clams

infested at level III differed (Tukey's test: $p < 0.01$) from the other levels in both parameters.

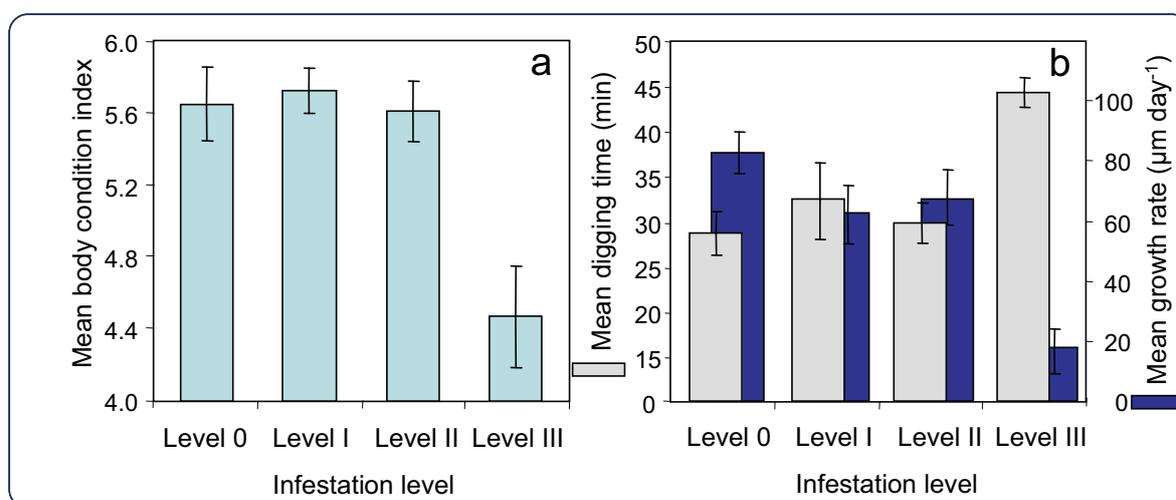


Fig. 4.3 **a** Body condition index (mean \pm SE) of *M. donacium* at different levels of infestation by *P. bioceppitalis*; **b** Growth rate ($\mu\text{m day}^{-1}$; mean \pm SE) and burrowing time (min; mean \pm SE) of *M. donacium* at different levels of infestation by *P. bioceppitalis* reared during 45 days in the laboratory.

The age of fossil *M. donacium* shells from coastal deposits varied from 6,725 years (i.e. the Holocene) at Michilla to 330,000 years (the Middle Pleistocene) at Chacaya, Las Lozas (northern Chile) and Los Porotitos (central Chile). The shell blistering pattern formed as a reaction of the mollusc to the infestation was identical in both fossil and recent shells. Blisters were exclusively located near the posterior shell margin, surrounding the posterior adductor muscle insertion and the paleal sinus. Moreover, blisters were formed in a progressive series of up to eight blisters in larger clams. Earlier (smaller) blisters were consistently located toward the dorsal margin, while blisters formed later (larger) were located toward the ventral margin (Publication 3). Overall, the infestation of fossil and recent shells was restricted to larger shells (SL > 32.0 mm). Fossil blistered shells ranged between 43.7 mm and 105.6 mm SL, whereas recent shells ranged from 34.0 mm to 96.0 mm SL. The variance ratio test showed no differences in SL variance between blistered fossil and recent shells ($F_{25, 192} = 1.69$; $p < 0.05$).

Growth rates of juvenile and adult *M. donacium* were significantly lower at high temperature but were generally not affected by salinity changes. Indeed, juveniles showed a higher growth rate at lower salinity (Publication 4). Similar results were observed for mortality: juvenile and adult mortality was significantly

affected by increased temperature. At normal temperature, clams were generally tolerant to salinity changes, particularly juveniles (Publication 4).

Reproductive activity of *M. donacium* along the distribution range was characterized by a breeding season generally starting in winter and extending into spring and a single spawning season between late winter or spring and summer. Main departures of the general pattern occurred at Mehuín (39°S), where an uninterrupted gonad activity and two annual spawning events (spring and autumn; black and white arrows, respectively) were observed. Populations in Camaná, Cuafo and Quilanlar showed similar departures, consisting of slightly extended breeding and spawning seasons.

Seasonal SST variability in the study area was small, ranging from 2.3°C in Camaná to 6.9°C in Mehuín. Coastal precipitation was almost nonexistent in northern populations; scarce in semi-arid central Chile (Peñuelas to La Laguna) and abundant in Mehuín, Cuafo and Quilanlar. Precipitation displayed a strong seasonal signal; it typically varied by a factor of 4 - 8 in most places and by a factor of 75 in central Chile. Except for Camaná, river flow was rather scarce in the northern and central areas of the geographic range and abundant in Mehuín. River discharge varied seasonally from nearly a factor of 2 in the Elqui river (~30°S, near Peñuelas) up to a factor of 52 in the Ligua river (~32°S). Lower and higher SST consistently occurred in summer and winter (respectively) through the geographic range of *M. donacium*. Higher (autumn/winter) and lower (spring/summer) precipitation were also consistent, except for Camaná. In contrast, timing of higher/lower river discharge changed through the geographic range without showing a clear trend. In Hornitos salinity varied from 33.3 in winter to 35.1 in spring. Lower salinity in September coincided with the occurrence of submarine seepage through holes distributed along a narrow belt parallel to the coast line in the shallow subtidal (1.5 to 2.5 m depth).

BIO-ENV analyses showed a significant correlation between gonad stage composition and environmental factors analysed in six out of seven study sites (Publication 4). SST was one of the selected variables involved in significant global correlations only at Camaná and Mehuín. In contrast, salinity, river inflow and precipitation were involved in all the significant correlations. Indeed, one of these variables was selected as single “explanatory” variable in gonad stage composition for the populations of Longotoma, Cuafo and Quilanlar.

A weak EN event occurred between August 2006 and January 2007 confirmed by the ONI for the El Niño 3.4 Region (NOAA/CPC). However, this event was not reflected in higher SST at Hornitos. Indeed, between October 2006 and April 2007 SST showed lower values compared to the historical (1980–2006) SST off Antofagasta, located 60 km south of Hornitos. Abundance of *M. donacium* showed strong intra- and interannual variations, and was significantly correlated only with the beach slope (Spearman $R = -0.626$; $p < 0.001$). Strong differences were observed in most of the population parameters estimated for both years at Hornitos (Publication 5). Interannual changes in abundance and somatic production (Fig. 4.4) were mainly due to a strong reduction in recruits (SL = ~2 – 25 mm) and adults (SL = ~75 – 95 mm), while abundance and somatic production of medium sized clams remained relatively unchanged.

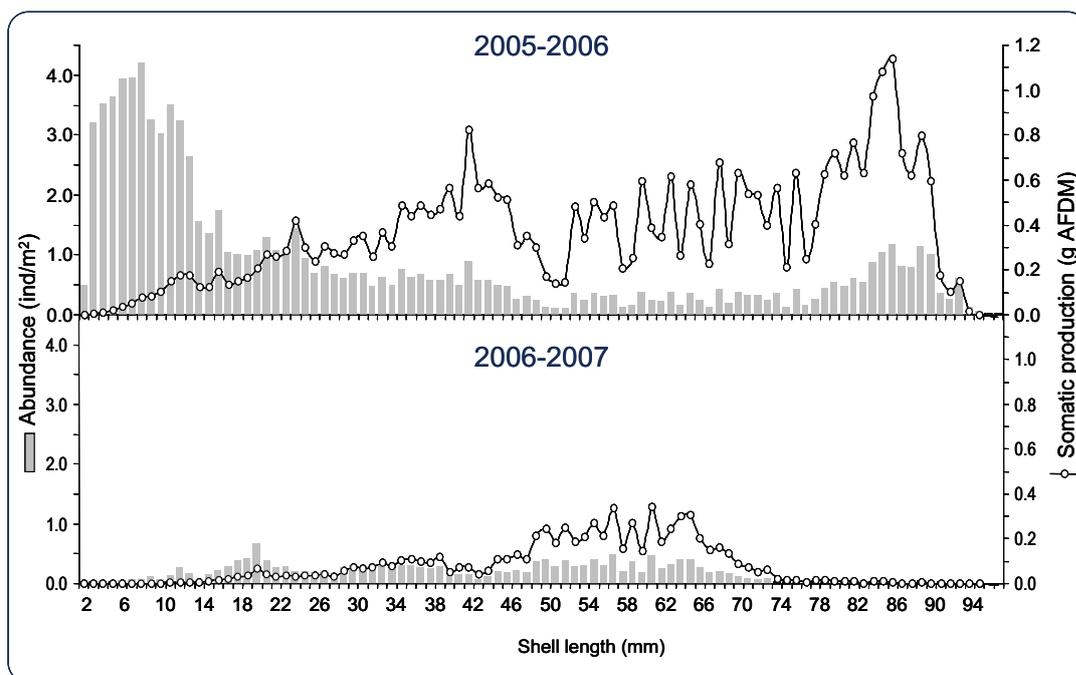


Fig. 4.4. Mean abundance and annual somatic production of *M. donacium* in 1-mm length classes during the periods May 2005 - April 2006 and May 2006 - April 2007.

All the assessed population features of *M. donacium* showed statistically significant latitudinal patterns. Abundances were lower in southern populations and were significantly increasing towards the northernmost limit of the geographical distribution (Fig. 4.5a). This pattern was best described by a power regression model. The slope of the observed trend showed significant differences with the trend observed during EN events ($t_{10} = 1.875$; $p = 0.045$). Abundances

were strongly reduced in northern populations, while central populations remained almost unaffected. Similarly, growth performance of *M. donacium* increased linearly with decreasing latitude (Fig. 4.5b), and a significant trend shift ($t_{10} = 2.009$; $p = 0.036$) is observed during EN years. Mortality of *M. donacium* decreased with increasing latitude, the pattern being best fitted to an exponential model (Fig. 4.5c). No significant differences were found between the slope of EN and non-EN regressions ($t_5 = 1.533$; $p = 0.186$), therefore, a common regression was fitted for all estimations. Productivity of *M. donacium* also decreased exponentially with increasing latitude (Fig. 4.5d) and again no significant differences were found between the slope of EN and non-EN regressions ($t_5 = 1.055$; $p = 0.253$) allowing a common regression to be fitted.

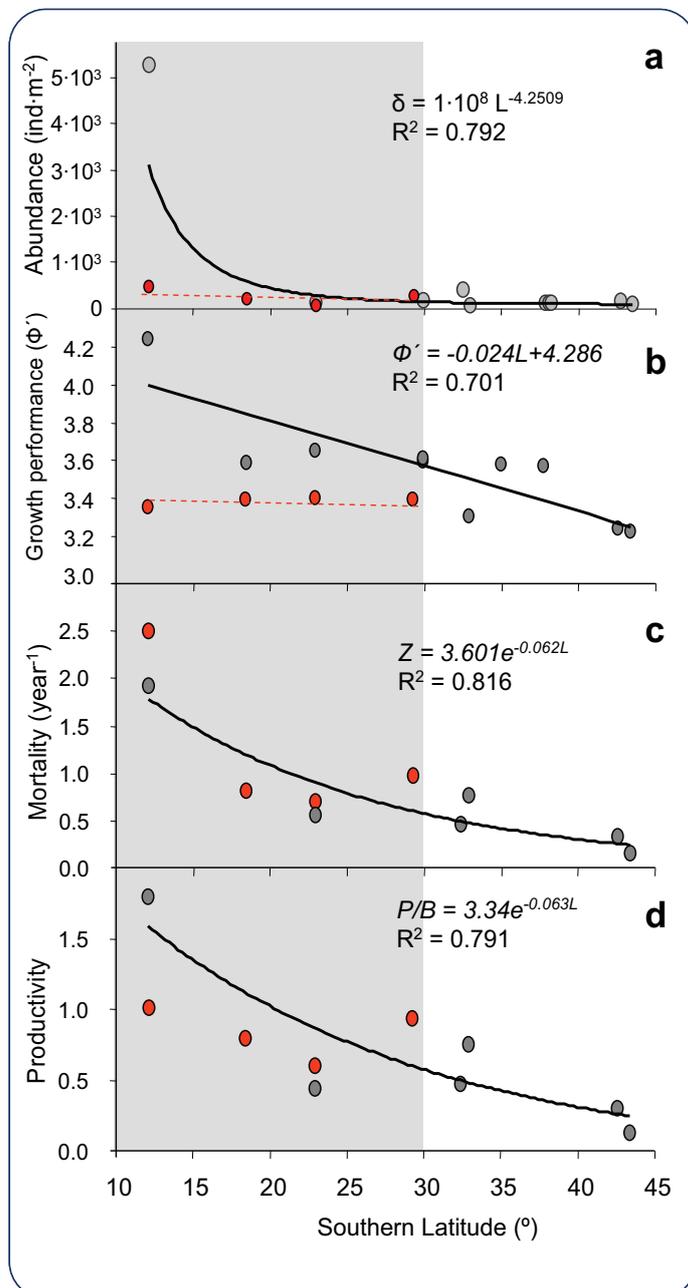


Fig 4.5 Relationship between latitude (centesimal units) and **a**: abundance; **b**: growth performance; **c**: mortality and **d** productivity of *M. donacium*. Red dots correspond to estimations of population parameters during El Niño events. Grey area corresponds to the latitudinal range where mass mortality events have been reported (Arntz et al. 1987, Quiroz and Barriga 1998, Aburto and Stotz 2003, Thiel et al. 2007)

4.1 Publications

The publications included in this work are listed below and my contribution thereof is given in detail.

Publication 1: Riascos JM, Guzmán N, Laudien J, Heilmayer O, Oliva M (2007) Suitability of three stains to mark shells of *Concholepas concholepas* (Gastropoda) and *Mesodesma donacium* (Bivalvia). *Journal of Shellfish Research* 26: 1-7

I developed the scientific idea with the third and fourth authors and performed the laboratory work with help of the second author. I did the statistical analysis. The manuscript was mainly written by me and improved in cooperation with the co-authors.

Publication 2: Riascos JM, Heilmayer O, Oliva ME, Laudien J, Arntz WE (2008) Infestation of the surf clam *Mesodesma donacium* by the spionid polychaete *Polydora biocipitalis*, *Journal of Sea Research* 59: 217–227

I developed the scientific concept of this paper, performed the sampling and the statistical analysis. The manuscript was mainly written by me and improved in cooperation with all authors.

Publication 3: Riascos JM, Guzmán N, Laudien J, Oliva ME, Heilmayer O, Ortlieb L (2008) A long-term association between *Mesodesma donacium* and the boring polychaete *Polydora biocipitalis* on the Chilean coast. *Diseases of Aquatic Organisms* (in press)

I developed the concept of this paper. The analysis of fossil material was carried out with the second author, and paleontological aspects were discussed with the second and last authors. The manuscript was mainly written by me and improved in cooperation with all authors.

Publication 4: Riascos JM, Carstensen D, Laudien J, Arntz WE, Oliva ME, Güntner A, Heilmayer O (2008) Thriving and declining: climate variability shaping life-history and population stability of *Mesodesma donacium* in the Humboldt Upwelling System. Marine Ecology Progress Series (in press)

I developed the scientific idea of this paper. The experimental design of the laboratory experiments was developed with the second and last authors. I carried out the practical work and the statistical analysis. The manuscript was mainly written by me and improved in cooperation with all authors, particularly with the last author.

Publication 5: Riascos JM, Heilmayer O, Oliva ME, Laudien J. (2008) Latitudinal trends in population dynamics of *Mesodesma donacium* modulated by El Niño. Journal of Marine Systems (submitted)

The initial concept of this study was worked out in cooperation with the last author. I expanded the scope, performed the field work, the literature compilation and the statistical analysis. The manuscript was mainly written by me and improved in cooperation with all authors.

Further articles published during the study period covering related subjects

Riascos JM, Heilmayer O, Laudien J (2008) Population dynamics of the tropical bivalve *Cardita affinis* from Málaga Bay, Colombian Pacific related to La Niña 1999–2000. Helgoland Marine Research 62:73-71

I developed the scientific idea of this paper and carried out the practical work, the statistical analysis and the first draft of the manuscript, which was improved in cooperation with all authors.

Ashton T, Riascos JM, Pacheco A (2008). First record of *Cymatium keenae* Beu, 1970 (Mollusca: Ranellidae) from Antofagasta Bay, northern Chile, in connection with El Niño events. Helgoland Marine Research 62 (Suppl): S107-S110

All the authors contributed equally to this paper.

4.2.1 PUBLICATION 1

Journal of Shellfish Research, Vol. 26, No. 1, 1–7, 2007.

SUITABILITY OF THREE STAINS TO MARK SHELLS OF *CONCHOLEPAS CONCHOLEPAS* (GASTROPODA) AND *MESODESMA DONACIUM* (BIVALVIA)

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ABSTRACT Different stains are used to internally mark calcified structures of mollusc shells in growth experiments. Because of interspecific variations in marking success, an assessment of suitability for each species is necessary. The potential of calcein, alizarin red, and strontium chloride hexahydrate (strontium chloride) was investigated for the Chilean abalone *Concholepas concholepas* and the surf clam *Mesodesma donacium*, two molluscs of commercial importance in Chile. Wild specimens from Northern Chile were marked using different concentrations and immersion periods of the three stains. Animals were reared for 20 days to allow growth, mortality, body condition index (BCI), and growth rate was measured to assess the effects of the treatments. To detect marks, individuals were culled and shell sections analyzed using scanning electron microscopy for strontium chloride and fluorescence microscopy for calcein and alizarin red, respectively. Strontium chloride produced narrow bright bands only at concentrations of 2,880 mg·l⁻¹ and 24 h exposure. Calcein markings produced fluorescent bands detectable in all treatments (50 and 100 mg·l⁻¹, 3 and 6 h) whereas alizarin red only yielded irregular bands with 50–100 mg·l⁻¹ and 6 h exposure. Our results show that growth rates of *C. concholepas* are significantly affected by the stains factor: Strontium chloride showed the lowest growth rates whereas that of alizarin red and calcein was similar to the control group. High concentrations of strontium chloride negatively affected ($P < 0.05$) the body condition of the gastropod. Although no statistical differences were found, BCI of *M. donacium* followed the same trend as observed for *C. concholepas*. In conclusion, calcein was the best growth marker for both species because it produced bright, long-lasting bands even at low concentrations and immersion times without detectable lethal or sublethal effects.

KEY WORDS: alizarin red, calcein, Chilean abalone, growth rate, strontium chloride, surf clam

INTRODUCTION

Growth rate is one of the basic parameters to describe population dynamics. In fisheries growth as well as recruitment is used to estimate the sustainable stock yield, (Hilborn & Walters 1992, Vakily 1992, King 1995). The Chilean abalone, *Concholepas concholepas* (Bruguière, 1789), and the surf clam *Mesodesma donacium* (Lamarck, 1818) rank among the most important commercial species for Chilean and Peruvian shellfisheries (Bustamante & Castilla 1987, Rabí & Marabí 1997, Rubilar et al. 2001). Accordingly their growth rates have been analyzed using various methods, including length-frequency analysis, tagging-recapture experiments, and the interpretation of shell growth rings (Tobella 1975, Acuña & Stuardo 1979, Gallardo 1979, Castilla & Jerez 1986, Arntz et al. 1987, Stotz & Pérez 1992, Jerez et al. 1999). Estimations are, however, often contradictory (Wolff 1989), because current methods for growth and age determination of molluscs all have specific limitations. Length-frequency analyses require well-defined age cohorts and large sample sizes, invasive tagging-recapture methods promote physical disturbance and contingently uncharacteristic growth rates, whereas quantification of growth rings or internal growth marks are affected by surface erosion and disturbance events (Kaehler & McQuaid 1999, for revisions of growth methods see Griffiths & Griffiths 1987, Richardson 2001).

To overcome the shortcomings of current methods for growth and age estimations, a number of staining methods as

shell growth markers have been tested in a variety of marine animals. The organisms exposed to stains successfully incorporated the chemical into growing calcified structures in the form of an internal growth mark that could subsequently be used to estimate growth from time of exposure (e.g., Hernaman et al. 2000, Leips et al. 2001, Bashey 2004, Bernhard et al. 2004, Marschal et al. 2004, Heilmayer et al. 2005). Thus, this method provides a temporal frame for age validation of increment periodicity (Hales & Hurley 1991, Oliveira 1996) and enables the analysis of environmental controls on short-term growth rates (Schöne et al. 2003).

The toxicity of some chemicals, even at low concentrations represents one serious potential drawback of these rapid marking methods (Bumgardner & King 1996, Gelsleichter et al. 1997). Consequently, a diversity of markers is needed to overcome species-specific variation in marking success (Bashey 2004). Suitable markers must be: (1) reliable and easy to detect in shell preparations; (2) not alter the viability of marked individuals; and (3) be retained for an appropriate period of time. Within the diversity of markers, calcein, alizarin red and strontium chloride have been proven to be suitable for molluscs (Day et al. 1995, Kaehler & McQuaid 1999, Moran 2000, Fujikura et al. 2003, Heilmayer et al. 2005). The aim of the current study is to test the potential of these growth markers for further studies concerning the environmental control on shell growth rates of the Chilean abalone *C. concholepas* and the surf clam *M. donacium*. The suitability of the marks produced at different concentrations and immersion periods and their effects on growth, body condition and survivorship are assessed.

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MATERIALS AND METHODS

Sampling Sites and Maintenance

In March 2005, 277 specimens of *C. concholepas* (anterior-posterior shell length, *SL*: 33.5–56.7 mm) were collected in southern San Jorge Bay (Antofagasta, Chile; 23°42.297' S; 70°25.482' W). Additionally 203 specimens of *M. donacium* (*SL*: 14.4–88.7 mm) were collected in Hornitos (22°54.998' S; 70°17.416' W), a sandy beach at the northern side of Mejillones Bay, Antofagasta. Specimens were maintained in 1,000 l-tanks with circulating seawater. The *SL* of all specimens was measured to the nearest millimeter using a vernier caliper. Sand collected from the study site was used to allow *M. donacium* to borrow. Water temperature of the rearing tanks was monitored every 30 min with a temperature data logger (StowAway Tidbit, ONSET). Because seawater temperature in the laboratory was slightly higher (1°C to 2°C) compared with the sampling sites, molluscs were acclimated for one month before the experiment started. During the maintenance period the carnivore *C. concholepas* was fed with the mussel *Perumytilus purpuratus* (8 kg per week and 277 specimens), whereas *M. donacium* was fed daily with a mixture of three micro algae in proportion 1:1:1 (*Isochrysis galbana*, *Chaetoceros gracilis* and *Pavlova lutheri*; 3×10^6 cell/L and 203 specimens). After the initial handling the first two days no mortality was observed during the acclimation time.

Staining Experiment

Three stains (calcein – Sigma, CAS 1461–15–0; strontium chloride hexahydrate [strontium chloride] – Sigma, CAS 10025–70–4, and alizarin red S – Sigma, CAS130–22–3) were used at different concentrations and immersion periods (Table 1). Concentrations and immersion periods were chosen in accordance with previous studies (Day et al. 1995, Kaehler &

McQuaid 1999, Moran 2000, Fujikura et al. 2003). Thirteen animals covering the whole size range available were randomly assigned for each treatment. The staining process was standardized as followed: (1) animals were placed in 41 aquaria with aerated sea water containing the respective stain; (2) each aquarium was placed in the dark to prevent light degradation of the fluorescent chemicals during the immersion period; and (3) after immersion, molluscs were reared in the laboratory during 20 days to allow growth of the organisms. A control group was treated in exactly the same way without adding staining dye to the water.

Detection of Growth Marks

After the 20-day rearing period all animals were sacrificed. Empty shells were cleaned and oven-dried at 60°C for 24 h. A transverse shell section was cut across the longest growth axis. For the detection of incorporated marks produced by the immersion in strontium chloride, the transverse sections were embedded using Epoxicure resin (Buehler) before successively polishing on glass slides with 125–68–30–12 and 5- μ m SiC powder, and finally 1- μ m Al₂O₃ suspension (Brot). Finally, the embedded shell sections were gold-coated. The detection of Sr-enriched marks was performed using a scanning electron microscope (SEM) JEOL (JSM-6360LX). Once the Sr-marks were recognized as bright bands, strontium concentrations in those bands and outside the bands (background) were determined by an energy dispersive X-ray spectrometer (EDS) coupled to the SEM. The electron beam was irradiated at an accelerating voltage of 15 kV and a lifetime of around 150 s.

For detection of calcein and alizarin red marks, thin sections were prepared by successive polishing of transverse shell sections glued to a thin glass plate, as described earlier. Marks were detected under a fluorescence microscope (Olympus BX51) using blue (460–490 nm) and red (330–385 nm) light, respectively.

TABLE 1.

Stains, concentrations, immersion periods and results on quality of marks and mortality for treated Chilean abalone *Concholepas concholepas* and surf clams *Mesodesma donacium*.

Stain Concentration (mg·l ⁻¹)	Immersion Period (h)	Quality of Mark		Mortality (n)		
		<i>M. donacium</i>	<i>C. concholepas</i>	<i>M. donacium</i>	<i>C. concholepas</i>	
Strontium chloride						
Low: 225*	17	No mark	No mark	1	0	
	24	No mark	No mark	3	0	
	High: 900†	17	No mark	Faint mark	0	0
		24	No mark	Faint mark	2	0
Alizarin red						
Low: 50	3	Faint mark	Faint mark	2	0	
	6	Faint mark	Clear mark	2	0	
	High: 100	3	Faint mark	Clear mark	3	1
		6	Clear mark	Clear mark	1	0
Calcein						
Low: 50	3	Clear mark	Clear mark	1	1	
	6	Clear mark	Clear mark	2	2	
	High: 100	3	Clear mark	Clear mark	3	0
		6	Clear mark	Clear mark	4	0
Control						
—	—	—	—	1	1	

*, †: 30, 120 times, respectively, the concentration of strontium in coastal sea-water in Antofagasta (7.5 mg/l on average; J. Román personal communication).

SUITABILITY OF THREE STAINS TO MARK MOLLUSC SHELL

3

Viability: Mortality, Growth, and Body Condition Index

Dead animals were registered daily and extracted from the tanks. Growth and *BCI* were calculated at the end of the rearing period.

Absolute growth rate was measured as shell growth along time:

$$\text{absolute growth rate} = \frac{SL_2 - SL_1}{t_2 - t_1} = \frac{\Delta SL}{\Delta t}$$

where, SL_1 is the shell length before staining (t_1) and SL_2 the shell length at the end of the rearing period (t_2). Because *M. donacium* growth was too slow to be detected reliable with a caliper, the shell length increase was determined on sectioned shells with a micrometer installed in a light microscope by measuring the distance (μm) between the staining mark and the growth tip. For growth comparisons we used the linear relationship between growth rate and \overline{SL} (Gulland & Holt 1959):

$$\frac{\Delta SL}{\Delta t} = a + b \times \overline{SL}_{(t)}$$

where \overline{SL} is the mean shell length between SL_1 and SL_2 , a the intercept and $-b$ the slope of regression, corresponding to K (the curvature parameter of the von Bertalanffy growth model).

For body condition comparisons, the *BCI* was estimated as:

$$BCI = \frac{DM}{SL} \times 100$$

where, *DM* is the soft tissue mass (g) dried at 65°C for 48 h and *SL* the shell length (mm).

Statistical Analysis

A log-linear analysis on a cross tabulation table ($4 \times 2 \times 2$) was performed to test effects of the different treatments on mortality (Zar 1984). An analysis of covariance (ANCOVA) was used to compare growth rates between treatments, with marker, concentration and time exposition as factors and *SL* as the covariate. Correspondingly, an ANCOVA was performed to compare *BCI* between treatments using the same factors and the covariate. Data were linearized to fulfill ANCOVA assumptions. Tukey honest significant difference (HSD) test for unequal sample sizes was used for multiple comparisons (Zar 1984). An isolated or “hanging” control group design was chosen to analyze the control treatment for analysis of covariance. All analyses were performed using the software STATISTICA for windows (StatSoft inc 1998).

RESULTS

Quality of Marks

Results of the staining experiments are summarized in Table 1. Calcein produced clearly visible fluorescent growth bands in shells of both species at all concentrations and exposure times (e.g., Fig. 1a, d). Alizarin red markings were successful in a lesser extent: In *C. concholepas* a clear mark can be detected at concentrations of 50 $\text{mg}\cdot\text{l}^{-1}$ after 6 h immersion and at 100 $\text{mg}\cdot\text{l}^{-1}$

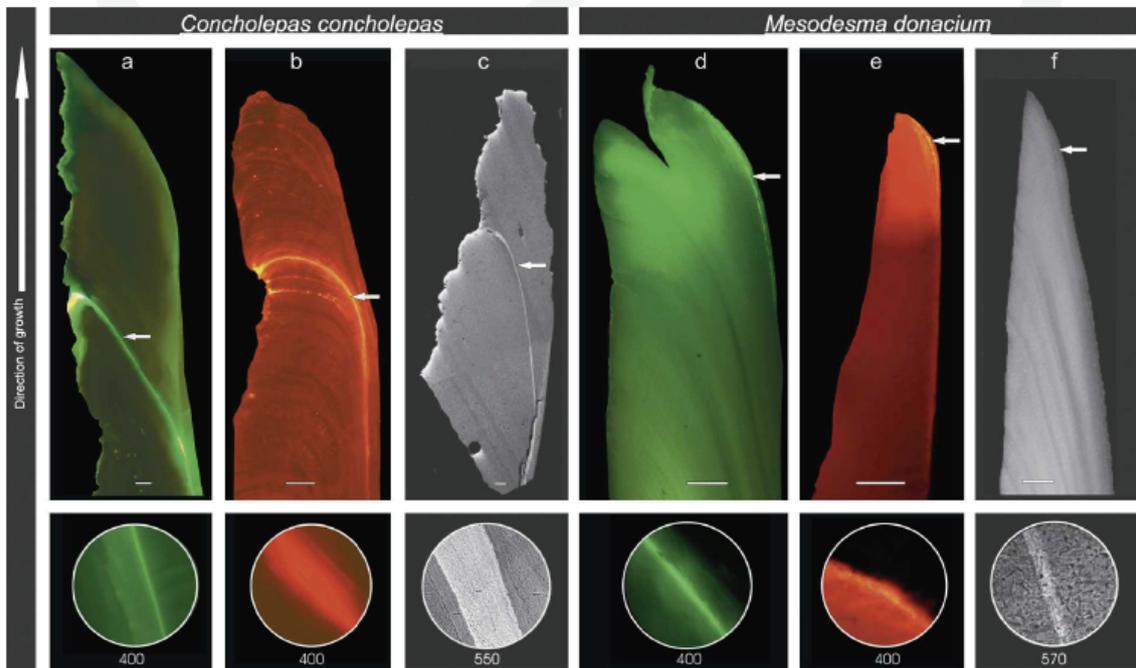


Figure 1. Photomicrographs of shell sections (*Concholepas concholepas*: a, b, c; *Mesodesma donacium*: d, e, f) after staining. The left side of each shell section corresponds to the outside part of the shell, whereas the right side corresponds to the mantle cavity side. Arrows indicate the place where the bright band below was magnified. Calcein treatment (a, d): 100 $\text{mg}\cdot\text{l}^{-1}$, 6 h; Alizarin red treatment (b, e): 100 $\text{mg}\cdot\text{l}^{-1}$, 6 h; Strontium chloride (c, f): 2880 $\text{mg}\cdot\text{l}^{-1}$, 6 h. Scalebars: 20 μm .

after 3 h and 6 h immersion (e.g., Fig. 1b). In *M. donacium* alizarine red produced distinct fluorescent bands only after 6 h immersion and at higher concentration (e.g., Fig. 1e).

Strontium chloride markings showed poor results to produce detectable bands (Table 1). Only faint marks were observed after staining at $900 \text{ mg}\cdot\text{l}^{-1}$ for 24 h immersion in shells of *C. concholepas*, whereas no marks were observed for *M. donacium*. The concentrations used here were based on the study of Fujikura et al. (2003) (30 and 120 times the strontium concentration of natural seawater). However, because it is important to know the concentration needed to produce visible marks an additional staining was performed ($2880 \text{ mg}\cdot\text{l}^{-1}$ for 24 h). This treatment produced clear bright bands in *C. concholepas* and *M. donacium* (e.g., Fig. 1c, f). Energy-dispersive X-ray spectrometry confirmed that bright shell bands in animals treated with strontium chloride at $2880 \text{ mg}\cdot\text{l}^{-1}$ for 24 h correspond to enhanced levels of strontium. The background strontium concentration was close to the detection limit (below $2 \text{ counts}\cdot\text{s}^{-1}$), whereas the strontium concentration in the bands was notably higher (Fig. 2), indicating that strontium was accumulated because of the staining process during shell formation. The boundary between strontium-enriched and nonenriched areas appeared more distinct compared with fluorescent and nonfluorescent areas. No differences in stability of marks were observed between the stains; all the marks were readily detected in stored samples at least seven months after the experiment.

On the other hand, interspecific differences in staining success were observed. Shells of *C. concholepas* showed wider and clearer bright bands than shells of *M. donacium*, particularly for strontium chloride and alizarin red markings (Fig. 1, Table 1). Moreover, because bright bands in shells of *M. donacium* were close to the shell margin, they were often difficult to identify.

Effects of Staining on Viability

Analysis of covariance showed differences in growth rates of *C. concholepas* between markers ($F_{3,108} = 4.1651$, $P = 0.018$) whereas no differences were found for concentrations, immersion periods or interactions among these factors. The HSD test, however, did not reveal the individual differences between markers because the P value was too close to the critical value and *post hoc* test are more conservative. Based on these results, mean growth rates of the studied length classes were plotted for each marker (Fig. 3). Animals tagged with strontium chloride showed a lower mean growth rate in almost all length classes, whereas faster mean growth rates were observed in specimens marked with calcein, alizarin, and nontreated individuals. Growth of *M. donacium* was slow (around $0.002 \mu\text{m}\cdot\text{day}^{-1}$) and only small specimens formed bright bands, allowing measures of growth increments. Moreover, some treatments failed to produce a detectable mark on the shells (Table 1). Consequently, comparisons of short-term growth between treatments of this species were not possible.

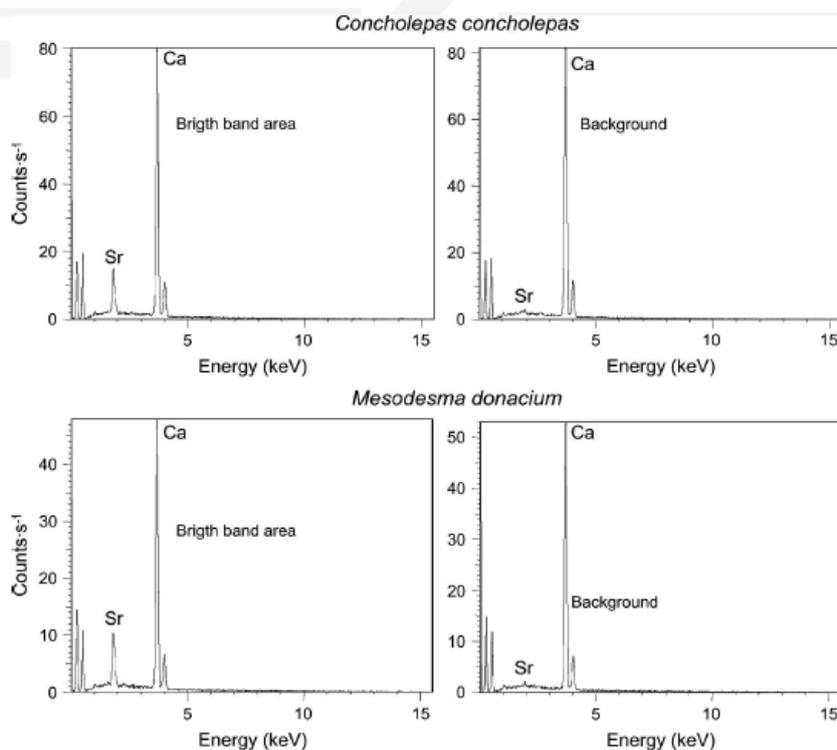


Figure 2. Strontium concentrations detected by energy dispersive X-ray of bright bands and background areas in shell sections of *Concholepas concholepas* and *Mesodesma donacium* stained with strontium chloride ($2880 \text{ mg}\cdot\text{l}^{-1}$, 6 h).

SUITABILITY OF THREE STAINS TO MARK MOLLUSC SHELL

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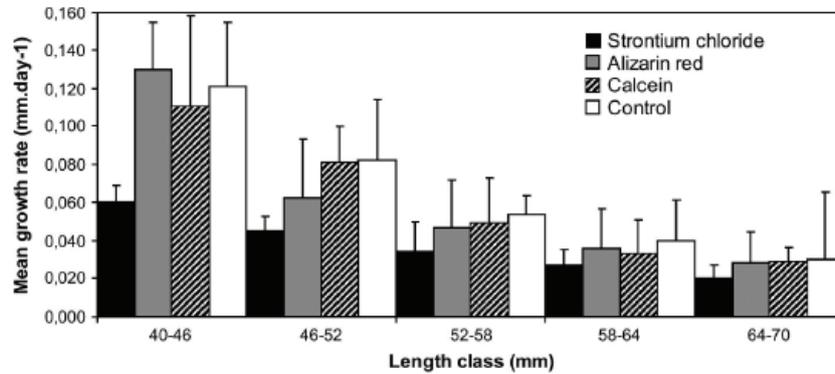


Figure 3. Comparison of growth rates ($\text{mm}\cdot\text{day}^{-1}$) of *C. concholepas* stained with strontium chloride, calcein and alizarin red among length classes. Standard deviations are included.

Analysis of covariance showed significant different of *BCI* between concentrations of stains for *C. concholepas* ($F_{3,29} = 8.208$, $P = 0.007$); the HSD test for multiple comparisons showed that observed differences in *BCI* are explained by low and high concentrations of strontium chloride. No significant differences in *BCI* between factors were found for *M. donacium*. Mean *BCI* corresponding to the high and low concentrations of strontium chloride and each stain and control for *C. concholepas* and *M. donacium* are shown in Table 2. Although no statistical differences in *BCI* of *M. donacium* were found between stains ($F = 0.106$, $P > 0.1$) mean *BCI* agrees well with the observed pattern of mean growth rates between treatments in *C. concholepas* (Fig. 3): animals marked with strontium chloride showed the lowest mean *BCI*, those marked with alizarin red and calcein showed intermediate values and non-marked animals showed the highest mean *BCI*.

The number of dead animals for each treatment and the control are summarized in Table 1. For both species mortality was relatively low, only four individuals (2.36%) of *C. concholepas* and 24 (14.20%) of *M. donacium* died after staining whereas only one individual of each species from the control group did not survive. The number of dead animals was independent from treatments for *C. concholepas* ($\chi^2 = 0.120$, $df = 10$, $P = 0.99$) and *M. donacium* ($\chi^2 = 0.985$, $df = 10$, $P = 0.999$).

TABLE 2.

Comparison of mean *BCI* between concentrations and stains for *Concholepas concholepas* and *Mesodesma donacium*.

	Mean <i>BCI</i>	
	<i>M. donacium</i>	<i>C. concholepas</i>
Low concentration (strontium chloride)	1.951	10.268
High concentration (strontium chloride)	1.647	6.282
Strontium chloride	1.773	8.428
Alizarin red	2.039	8.732
Calcein	2.083	8.835
Control	1.977	10.748

DISCUSSION

Quality of Marks

The incorporated marks in shells of *C. concholepas* and *M. donacium* showed a different quality, depending on (1) the stain type, concentration and immersion time and (2) interspecific differences in growth rate. Calcein produced clearly visible fluorescent bands in shells of both species, even at low concentrations and immersion times, whereas alizarin red often showed imprecise bands only at higher concentrations and immersion periods (Fig. 1, Table 1). Strontium chloride produced clear and narrow bright bands; however, it needed a high concentration (around 30 times that of calcein) and a long immersion time, thus making this staining method expensive and time-consuming for this species. Our results agree with several studies showing that calcein produces clear marks, which enables short-term, high-resolution growth studies (e.g., Rowley & Mackinnon 1995, Day et al. 1995, Kaehler & McQuaid 1999, Hernaman et al. 2000, Heilmayer et al. 2005, Thébault et al. 2005).

In general better marks were observed in *C. concholepas* than in *M. donacium* (Fig. 1, Table 1). This agrees with Day et al. (1995) who showed that the success of staining depends on the growth rate of each species because the transfer of ions or the stain through the mantle epithelium is quicker in rapidly growing organisms. As can be seen in Figure 1 *C. concholepas* grew faster than *M. donacium*. Hence, the observed differences in staining success can be attributed to these differences in growth rate. Additionally, as the rate of shell accretion decreases throughout the life span of many organisms, an age-dependent effect on the success of staining can be expected (Day et al. 1995, Thébault et al. 2005), which explains the higher staining success in small individuals compared with large ones.

Viability of Individuals After Staining

Assessing the suitability of a stain for short-term growth studies includes that marked individuals have unaltered viability after treatment. Traditionally mortality rate was the only parameter used to evaluate the effects of staining (e.g., Monaghan 1993, Brooks et al. 1994, Day et al. 1995, Bumguardner & King 1996, Gelsleichter et al. 1997, Kaehler & McQuaid 1999, Fujikura

et al. 2003, Bernhard et al. 2004). However, parameters evaluating sublethal effects on treated animals (activity rates, filtration rates, body condition, and growth rate) have been rarely addressed (Moran 2000, Leips et al. 2001, Frenkel et al. 2002, Bashey 2004, Thébault et al. 2005). According to our results, none of the treatments affect the mortality of the stained animals, but showed significant effects on growth rate and body condition index.

Variations in growth rates of molluscs are controlled by environmental factors and physiological constraints (Wilbur & Owen 1964, Schöne et al. 2003). The underlying goal of a study looking for a suitable growth marker is the accurate measurement of growth after the mark produced by the stain and the identification of the environmental and/or physiological controls. Consequently, identifying the effects of staining on growth rate should be an obvious requirement.

Figure 3 shows the effect of the stains on the growth rate of *C. concholepas*: Animals immersed in strontium chloride showed the lowest mean growth rate along all length classes, whereas those immersed in alizarin red and calcein showed similar values to the nonmarked control individuals (Fig. 3). Calcein and alizarin red remain between the most commonly tested stains for growth studies; despite the fact that calcein seems to affect the survival of juvenile fishes (Brooks et al. 1994, Bumgardner & King 1996, Gelsleichter et al. 1997) several studies demonstrate no effects of these stains on growth in a variety of animals (Rowley & Mackinnon 1995, Moran 2000, Leips et al. 2001, Frenkel et al. 2002, Bashey 2004). Effects of strontium chloride, in contrast, have been scarcely tested. Fujikura et al. (2003) did not show conclusively results on growth effects because they did not include any control treatment and they used only three individuals in each treatment. Peck et al. (1996) found no significant differences on growth of treated and control individuals of the patellid gastropod *Nacella concinna* reared in seawater enriched with strontium (between 20–80 times the natural concentrations of strontium in seawater). However, because the shell material secreted during the experiments always contained less strontium than expected from the levels used in treatments, they concluded that *N. concinna* discriminate against strontium during shell deposition, which seems a common feature of gastropods and bivalves (Dodd 1967). A physiological mechanism, and therefore an energy investment would be needed to discriminate against strontium in a strontium-enriched environment. Because higher concentrations of strontium were used in our

experiments, consequences of this energy investment on growth rate could be expected.

The body condition index of *C. concholepas* differed between high and low concentrations of strontium chloride (Table 2), which could be related to the mechanism stated before. No significant effects of the treatments on *BCI* of *M. donacium* were detected; this may be because of the fact that the specimens closed the valves and stopped filtering water several times during the experiment. Consequently, the success of staining was lower for *M. donacium*. It is nonetheless interesting that the mean *BCI* for each stain follows a similar trend in both species (Table 2) and this resembles the trend observed for the effects on growth of *C. concholepas*, in which strontium chloride showed stronger departures from the control (Fig. 3). Because these results could hardly be obtained by chance, they may be interpreted as an approximation of the effects of the stains on *M. donacium*.

In conclusion and taking into account the results on quality of marks and effects of the stains, calcein is recommended as shell growth marker for both species for the following reasons: (1) it produces bright, long-lasting fluorescent bands with an appropriated magnification level for observation, even when the animals are stained at low concentrations (2) non detectable lethal or sublethal effects were found for this stain, (3) simpler methods are required for detection of marks (i.e., light microscopy) thus enabling the analysis of large numbers of samples, and (4) short immersion time is required for staining, which enables the tagging of the animals in the field thus reducing the manipulation effects.

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4.2.2 PUBLICATION 2*



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Infestation of the surf clam *Mesodesma donacium* by the spionid polychaete *Polydora biocipitalis*

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Abstract

The surf clam *Mesodesma donacium* is an economically important species for Chilean and Peruvian shellfisheries. This clam is often infested by *Polydora biocipitalis*, a species belonging to the Spionidae, the most common parasitic polychaete group. To study this association, clams were sampled monthly over a one-year period in northern Chile. Collected clams covered the entire available size range and were classified into four infestation levels in order to study: (1) the relationship between prevalence of infestation (*PI*) and host size, (2) the temporal pattern of infestation events related to seasonal temperature changes, and (3) the relationship between infestation, body condition index (*BCI*) and gonado-somatic index (*GSI*). Additionally, growth rate and digging ability of clams with different infestation levels was studied. A logistic regression model best explained the relationship between *PI* and host size, with the smallest infested clam being 34 mm long and *PI* increasing steeply thereafter. Ontogenetic shifts in the habitat of the clam and ontogenetic changes, mainly in shell morphology, seem to explain the sigmoid pattern. Periods of increased shell blistering after infestation by *P. biocipitalis* showed a similar seasonal pattern with *GSI* and *BCI* of non-infested clams, suggesting either an association between infestation ability and low condition of the clam or common environmental triggers for those factors. Heavily infested clams showed a significant lower *BCI*, growth rate and digging ability; however, given its low number, they are unlikely to be significant in terms of the local population survival. However, the infestation could play a key role in explaining mass mortality of northern populations during El Niño events, given the latitudinal differences in *PI* and the fact that infestation ability could be enhanced by increased temperature and facilitated in stressed clams.

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Keywords: Surf clam; Boring polychaetes; Blister worms; El Niño; Northern Chile

1. Introduction

Spionid worms of the genus *Polydora* have a worldwide distribution (Lauckner, 1983). These so-called “blister worms” are a matter of considerable concern, as they inhabit the shells of many commercially important bivalves (see Wargo and Ford, 1993 and references therein), often causing substantial mortalities (Lauckner, 1983). While the highest number of polychaete species

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considered as parasites belong to the family Spionidae (38%; Martin and Britayev, 1998), an extensive ongoing debate exists on their parasite status, mainly due to (1) concurrent controversy in defining parasitism (e.g. Zelmer, 1998; Rohde, 2005), (2) their consideration as parasitic organisms from an anthropogenic rather than ecological point of view (Martin and Britayev, 1998) and (3) the low level of knowledge on the biology of the species involved in the association (Martin and Britayev, 1998). Beyond this debate, the study of ecological interactions between *Polydora* and their commercially important hosts is crucial in a scenario of rising global demand for good-quality seafood and the need for improved knowledge to assist in more efficient marine resource management.

The surf clam *Mesodesma donacium* has been exploited as a human food source along the South American Pacific coast since the arrival of early settlers (Sandweiss et al., 1998). It still plays an important socio-economic role for small-scale fisheries in Chile and Peru due to its extremely high biomass (Arntz et al., 1987; Defeo et al., 1993; McLachlan et al., 1996). This filter-feeder clam is distributed from Bahía Sechura (Peru, 5°S) to Isla de Chiloé (Chile, 43°S) and inhabits the swash zone of exposed high-energy intermediate and dissipative sandy beaches, where it typically burrows down to a depth around 10 cm, though can sometimes reach 25 cm, when disturbed (Tarifeño, 1980). Adult clams are primarily confined to the surf zone, while the vast majority of juveniles occurs in the swash zone (Tarifeño, 1980). The reproductive strategy of *M. donacium* changes along its geographical range according to local variability in environmental factors such as water temperature and food availability (Tarifeño, 1980; McLachlan et al., 1996). In northern/central Chile first maturity occurs at 30–40 mm shell length, with the clam reaching a maximum shell length of around 90 mm corresponding to a life span of eight years (Jerez et al., 2007a,b).

Mesodesma donacium populations are regularly devastated during El Niño events. As a consequence of El Niño 1982–1983, most populations disappeared from Peruvian beaches and withdrew seven degrees of latitude south from the previous geographic distribution (Arntz et al., 1987). Although those mortalities are most likely related to increased temperatures, several studies suggest that parasite associations may play a role in mass mortalities of clams inhabiting sandy beaches (Fiori and Cazzaniga, 1999; Ramón et al., 1999; Fiori et al., 2004). The effects of spionids on their hosts are variable and have been shown to depend on differences in the severity of infestation, host size and species involved in the association (Loosanof and Enge, 1943;

Leonart et al., 2003). Furthermore, infestations are responsive to environmental conditions, notably temperature and tidal elevation (Dorsett, 1961; Handley and Bergquist, 1997), and the health of the host (Newell and Barber, 1988; Wargo and Ford, 1993).

The spionid polychaete *Polydora biocippitalis* has been reported as the only polychaete infesting *M. donacium* (Blake, 1983; Moreno et al., 2006) that produces a specific shell blistering around the siphon area. Shell blisters (commonly referred to as “mud-blisters”) result from secretions of conchiolin and successive calcite layers that the clam produces as a mechanism to isolate the worm (Kent, 1979; Lauckner, 1983). These blisters often only appear after the mollusc reaches a certain size (Davis, 1967; Ambariyanto and Seed, 1991). Although it is difficult to evaluate the expenditure of metabolic energy linked to this extraordinary secretion of protective layers (and thus, to determine to what extent the performance of the host clam might be affected), the mollusc may suffer a certain degree of distress (Kent, 1979). Despite the observed prevalence and potential effects of the infestation of *M. donacium* by *P. biocippitalis*, information on the ecology of this association is completely lacking. Therefore, this study aims to analyze (1) the relationship between the prevalence of infestation (*PI*) by *P. biocippitalis* and the size range of *M. donacium*, (2) the temporal pattern of the infestation in relation to seasonal temperature changes and (3) the relationship between distinct infestation levels and performance of the clam (i.e. body condition index, gonado-somatic index, growth rate, and burrowing ability).

2. Materials and methods

2.1. Sampling and classification of infestation

Monthly samples of *M. donacium* were taken along a transect at the sandy beach “Hornitos” (22°54.99’S; 70°17.42’W), northern Chile between May 2005 and April 2006. The transect, perpendicular to the coastal line, included both the intertidal and the upper subtidal zone down to 1.5 m water depth covering the across-shore distribution of the *M. donacium* population. Along the transect, every 4 m three replicated sediment samples (each 0.16 m² and 0.30 m deep) were taken using a push-corer. After sieving through a 0.5 mm mesh clams were counted and the anterior-posterior shell length (*SL*) was measured to the nearest 0.5 mm. Two sub-samples were selected for further analysis, while remaining bivalves were released after measurements; (A) 50 clams covering the whole size range available (i.e. 5 mm to 100 mm *SL*)

and (B) 30 adult clams (i.e. 70 to 100 mm *SL*). Sea surface temperature was registered every 10 min during sampling using an YSI sensor.

Clams of the two sub-samples were opened and classified into increasing infestation levels as follows: level 0: non-infested clams; level I: clams with inhabited shell blisters (i.e. living *P. biocipitalis*) in just one valve or clams with abandoned shell blisters (one or both valves); level II: clams with inhabited shell blisters in both valves; and level III: clams with inhabited shell blisters in both valves and abandoned shell blisters in one or both valves.

2.2. Patterns of infestation: prevalence of infestation and host size

Prevalence of infestation (*PI*, percentage of infested clams in monthly samples, *sensu* Martin and Britayev, 1998) was estimated (1) to study the relationship between infestation by *P. biocipitalis* and *SL* of *M. donacium* and (2) to estimate the *SL* at 50% *PI*. A preliminary assessment suggested that *PI* could be affected by the ontogenetic formation of an anterior gap between the valves (i.e. in the siphon area) when clams are growing, hence we measured the dorsal-ventral length or “shell height” at which gaping begins to occur and calculated its corresponding *SL* from linear regression analysis.

2.3. Patterns of infestation: temporal variability

The infestation by *P. biocipitalis* on *M. donacium* is always represented by blisters formed only around the siphon area. When polydorids reach the inner side of the mantle cavity, the bivalve hosts immediately start secreting consecutive shell layers to isolate the worm, thus forming blisters (Kent, 1979; Lauckner, 1983). Therefore, the thickness of blisters can be used to estimate the time since the worm reached the mantle cavity of the host. This estimation was used in conjunction with monthly changes in *PI* to assess temporal patterns of the infestation. To determine the thickness of blisters, small shell blister sections were cut with a scalpel from the introversive blister wall of the clam’s shells. Blister wall samples were embedded in Epoxycure resin, ground on glass slides, with 125, 68, 30, 12 and 5 μm SiC powder, and polished with 1 μm Al_2O_3 suspension, to obtain smooth perpendicular cut surfaces. To estimate mean thickness of blister sections (*Tb*), polished sections were measured to the nearest 1 μm under a reflective light microscope. A one-way analysis of variance (ANOVA) was used to test for differences in mean *Tb* between

months. The Shapiro-Wilk test and the Bartlett’s test were used to assess normality and homoscedasticity of variances, respectively, to meet ANOVA assumptions. The correlation between temperature and *Tb* or *PI* was determined using Spearman’s rank non-parametric correlation coefficients.

2.4. Infestation and host performance

We studied body condition index (*BCI*), growth rate and burrowing ability as performance measures (*sensu* Kingsolver and Huey, 2003) of *M. donacium* in relation to infestation. Sub-sample A was used to estimate mean *BCI* as:

$$BCI = \frac{DM}{SL} \times 100 \quad (1)$$

Soft tissue dry mass (*DM*; in g) was determined to the nearest 0.1 mg after oven-drying at 65 °C until constant mass was recorded, and *SL* was measured to the nearest 0.1 mm.

Subsample B (30 adult clams) was used to track changes in gonad condition. Soft tissue wet mass (*WM*; in g) was registered individually to the nearest 0.1 mg. Thereafter, mantle, gills, siphons, and the retractor and adductor muscles were removed. Wet mass of the resulting standard compact unit (*WM_s*; in g), consisting of visceral mass, gonad and pedal muscle was recorded (see Laudien et al., 2001). The monthly mean gonadosomatic index (*GSI*) was calculated as:

$$GSI = \frac{100 \times WM_s}{WM - WM_s} \quad (2)$$

Between September and November 2005, a laboratory experiment was performed to study the relationship between infestation, growth rate and digging ability of *M. donacium*. Adult clams (*SL* > 80 mm) showing distinct external signs of infestation (*N* = 20) or no infestation at all (*N* = 20) were selected. To reduce age-related effects on growth rate, specimens with similar *SL* were selected (average = 87.5 ± 3.4 mm) and acclimatized for 25 days before experiments started. Sand collected from the study site allowed clams to burrow in 1,000 l flow-through-tanks. Animals were fed daily with a mixture of three microalgae at a ratio of 1:1:1 (*Isochrysis galbana*, *Chaetoceros gracilis* and *Pavlova lutheri*; ca. 3×10^6 living cells Γ^{-1}). No mortality was observed during the acclimation period.

Subsequently, all clams were individually numbered (external code fixed with cyanoacrylate glue) and immersed for three hours in a four-litre aquarium filled with aerated seawater containing 50 mg Γ^{-1} calcein (Sigma,

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CAS 1461-15-0). This procedure has proven to be effective to incorporate a fluorescent band in shells of *M. donacium* with no sublethal effects, thus allowing the measurement of short-term growth increments following the treatment (Riascos et al., 2007). Thereafter, specimens were allowed to grow in a 1,000 l flow-through-tank with sand (25 cm depth) for 45 days. Clams were fed daily with the above-mentioned mixture of microalgae. Every five days, all clams were removed from the sand and subsequently released on the sand surface. Individual digging time (Dt ; min) was registered as the time period from release until the clam was completely buried in the sand. This procedure was assumed to induce minimal stress, as animals are used to being washed out by waves in their natural environment.

At the end of the experiment, all animals were sacrificed and classified according to the above mentioned infestation levels. Shells were cleaned and oven-

dried at 65 °C until constant mass was achieved (24 h). The right valve of each specimen was cut along the axis of maximum growth, using a low-speed diamond-saw. To measure growth increments, the resulting cross-sectioned valves were embedded and polished as described above for blister wall sections. Growth increments starting from the fluorescent mark were measured to the nearest 1 μm under a fluorescence microscope using blue (460 to 490 nm) light (for a more detailed description see Riascos et al., 2007). Three clams in which calcein failed to produce a clear mark were excluded from the analysis.

One-way analyses of covariance (ANCOVA) were performed to compare the effect of infestation level on log-transformed data of BCI and GSI , using SL as the covariate. Growth rate ($\mu\text{m day}^{-1}$) and Dt (min) between clams of different infestation levels were compared by one-way ANOVA. The Shapiro-Wilk test and

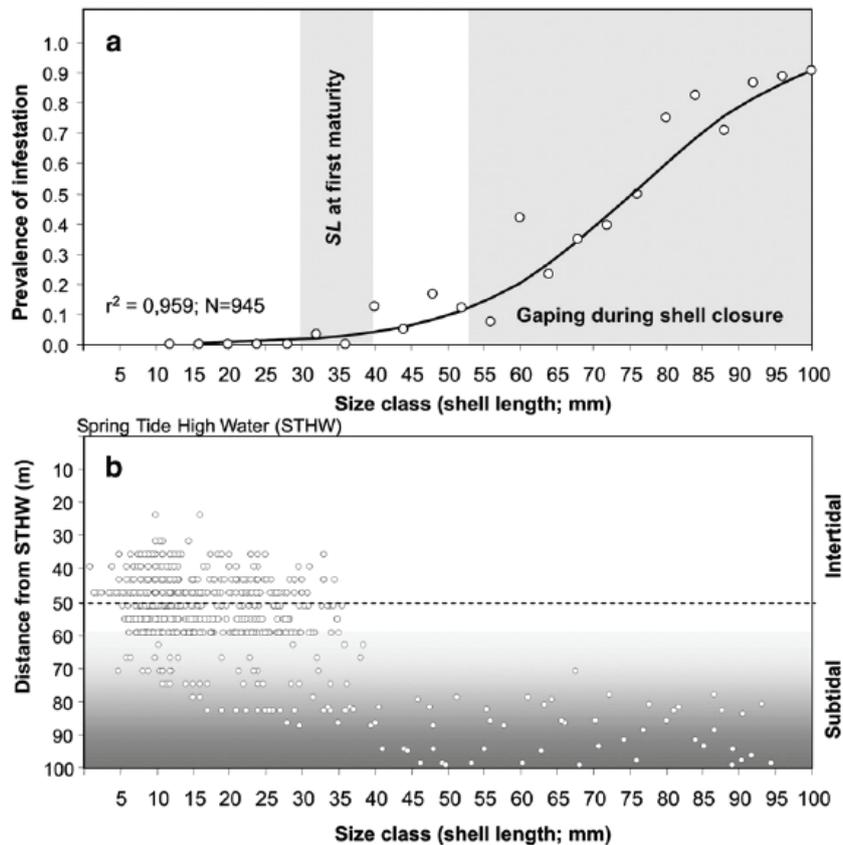


Fig. 1. (a) Logistic function (Eq. (3)) of the relationship between the shell length of *Mesodesma donacium* and the prevalence of infestation of *Polydora biocipitalis*; range of shell length (SL) at first maturity (Jerez et al., 2007a,b) and range of shell gaping are indicated. (b) Spatial distribution of clams ($N=1739$) at different shell lengths along a gradient of tidal elevation from the spring tide high water (STHW). Intra-annual changes of the fluctuation of the intertidal and subtidal zone are indicated, as it depends on several physical factors.

the Bartlett's test were used to test normality and homoscedasticity of variances, respectively, as required to meet ANOVA and ANCOVA assumptions. Tukey honest significant difference tests (HSD) for unequal sample sizes were used for multiple comparisons, when significant differences were detected.

3. Results

3.1. Relationship between *PI* and host size

The relationship between *PI* and clam size was best explained ($r^2=0.96$) by a logistic function with three parameters (Fig. 1a):

$$P_{SLi} = \frac{\beta}{1 + e^{(\alpha_1 - \alpha_2 SL)}} \quad (3)$$

where P_{SLi} is the *PI* in each size class. The function was fitted with the Levenberg-Marquardt algorithm by non-linear least squares to estimate the standard error (SE) of the parameters: $\beta=1.013$ (SE=0.100; $p<0.01$), $\alpha_1=6.518$ (SE=0.900; $p<0.01$), and $\alpha_2=0.088$ (SE=0.014; $p<0.01$). *SL* at 50% of *PI* was estimated as $\alpha_1/\alpha_2=73.6$ mm, and chosen as an unbiased estimation of the

lowest size to be included in comparisons of *BCI* and *GSI* between infestation levels. The smallest infested clam was 34 mm long, thereafter the *PI* steeply increased. Parameter β was close to 1, indicating that almost all old clams were infested (Fig. 1a). Total *PI*, estimated from pooled monthly samples (N=945), was 47.2%. About 60.9% of the infested clams corresponded to infestation level I; 31.4% to level II and 7.6% to level III.

Valve gaping started at 26.9 mm (SE=1.4; N=294) shell height. This corresponds to 53.1 mm *SL* (shell height = $0.485 \times SL^{1.014}$; $R^2=0.99$; N=683). Juveniles of *M. donacium* inhabited mainly the intertidal whereas adults inhabited the subtidal (Fig. 1).

3.2. Temporal pattern of infestation

In total, 583 blisters were sampled to estimate monthly mean thickness, which proved to differ between months (ANOVA: $F_{11, 571}=2.388$; $p<0.01$), showing a bimodal pattern. Peaks were observed in September 2005 (21.12 μm ; SE=1.20) and March 2006 (21.69 μm ; SE=1.59), whereas the lowest values were found in May 2005 (14.35 μm ; SE=0.92) and December 2005 (15.81 μm ; SE=2.12) (Fig. 2a). The opposite trend was

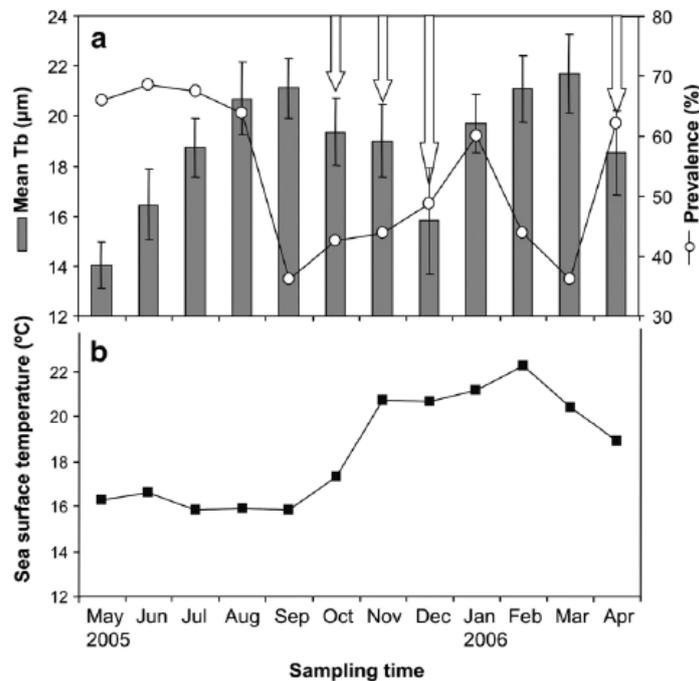


Fig. 2. (a) Changes in mean thickness of blister walls (Tb; μm) from shells of *Mesodesma donacium* and prevalence of infestation (*PI*) by *Polydora biocipitalis*. Decreases in mean Tb and increases in *PI* were considered as evidence of new infestation events (arrows). (b) Sea surface temperature off Hornitos, northern Chile.

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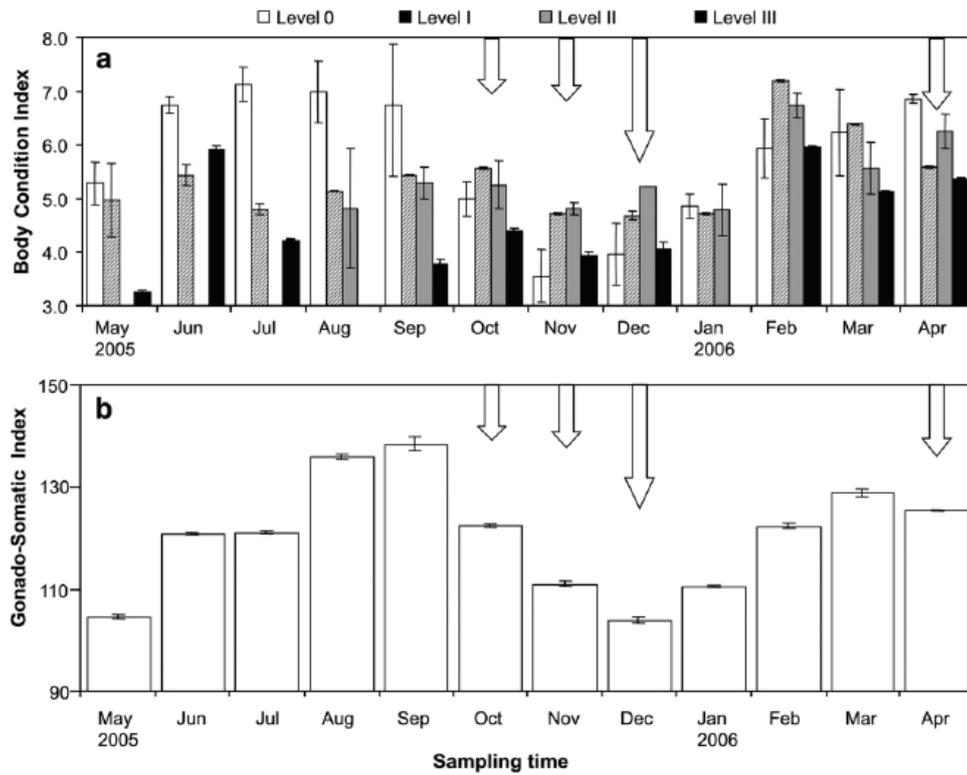


Fig. 3. (a) Mean monthly body condition index (\pm SE) of *Mesodesma donacium* at different levels of infestation by *Polydora biocipitalis*; bars are missing when no clams occur at a given infestation level. (b) Monthly mean gonado-somatic index (\pm SE) of infested and non-infested clams; arrows indicate infestation events; only clams larger than 73.6 mm (shell length at 50% of infestation) were included.

observed for the *PI*, which tends to increase when mean *Tb* decreases (October to December 2005 and April 2006). No significant correlations were observed both between mean *Tb* and *PI* and mean sea surface temperature (SPEARMAN=0.22; $p>0.05$ and SPEARMAN=0.42; $p>0.05$, respectively) of the study area (Fig. 2b).

3.3. Infestation and host performance

Mean *BCI* significantly differed between clams with distinct infestation levels (ANCOVA: $F_{3,175}=8.606$; $p<0.01$). In contrast, mean *GSI* between clams with distinct infestation levels was not significantly different (ANCOVA: $F_{3,356}=0.322$; $p=0.89$). Therefore, monthly mean *GSI* of infested and not infested clams were pooled (Fig. 3b). Multiple *a posteriori* comparisons showed that mean *BCI* of level 0, level I and level II clams did not differ significantly from each other (Turkey's HSD test: $p>0.05$), but were significantly higher (Turkey's HSD

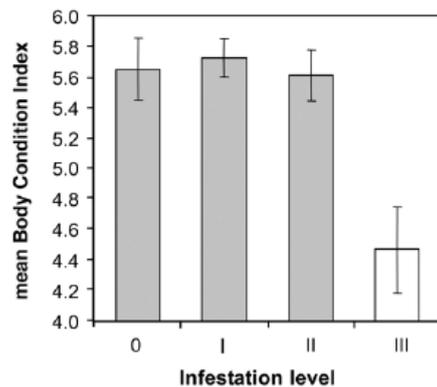


Fig. 4. Mean body condition index (mean \pm SE) of *Mesodesma donacium* at different levels of infestation by *Polydora biocipitalis*. Only clams larger than 73.6 mm (shell length at 50% of infestation) were included in the analysis. The number of clams classified in each level is indicated. Different colours (grey and white) denote groups showing statistical differences after multiple comparisons.

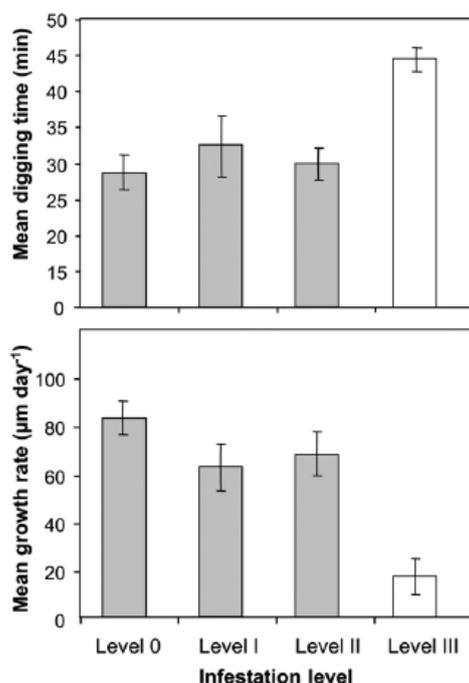


Fig. 5. Mean growth rate ($\mu\text{m day}^{-1}$; mean \pm SE) and burrowing time (min; mean \pm SE) of 40 individual *Mesodesma donacium* at different levels of infestation by *Polydora bioocipitalis* reared during 45 days in the laboratory. Different colour group (grey and white) denote groups showing statistical differences after multiple comparisons.

test: $p < 0.01$) than those of heavily infested clams (level III, Fig. 4).

Both, mean digging time (Dt) and mean growth rate of *M. donacium* differed between infestation levels (ANOVA: $F_{3, 33} = 3.21$; $p = 0.034$, $F_{3, 33} = 6.14$; $p < 0.01$, respectively) (Fig. 5). Multiple comparisons revealed that the first three levels did not differ (Turkey's HSD test: $p > 0.05$), neither in Dt , nor in growth rate, whereas clams infested at level III differed (Turkey's HSD test: $p < 0.01$) from the other levels in both parameters.

4. Discussion

4.1. Patterns of infestation

The PI of *M. donacium* by *P. bioocipitalis* showed a size-specific pattern, with juvenile clams smaller than 34 mm SL being non-infested and the largest clams showing the highest PI . The fitted logistic model not only explained the lack of infestation in juveniles, but also the rapid increase of PI in clams between 55 mm and 85 mm SL (Fig. 1a).

An ontogenetic shift from the intertidal to the (shallow) subtidal reported for *M. donacium* (Tarifeño, 1980; Jaramillo et al., 1994) was also observed during our study: juvenile clams mainly inhabit the intertidal area, while adults are restricted to the subtidal (Fig. 1b). Handley and Bergquist (1997) found that the ability of several spionids to infest oysters is affected by intertidal exposure. Therefore, this shift of habitat may partially explain the lack of infestation observed in juvenile clams, as the periodic air exposure and warm temperatures of the intertidal might prevent the settlement and thus infestation of *P. bioocipitalis*. This, however, does not explain completely the observed pattern, since some juveniles do occur in the subtidal (Fig. 1b). An alternative explanation arises from the hypothesis that infestation is limited below a certain host size (Davis, 1967; Ciocco, 1990; Ambariyanto and Seed, 1991; Rozbaczylo and Cañete, 1993), which depends on the requirement of space by the epibiont. We frequently observed *P. bioocipitalis* externally settling (without boring signs) near the siphon area of non-infested small clams (30.2–37.8 mm SL ; $N = 93$) in the subtidal. While *P. bioocipitalis* is able to settle on juvenile clams, the infestation cannot be performed easily on juveniles but only on the larger ones inhabiting the subtidal. Therefore, this observation cannot be assumed as support for the host-size limit hypothesis.

The onset and increase of infestation by *P. bioocipitalis* (Fig. 1a) appears to be related to ontogenetic changes in the host. The onset of first maturity of *M. donacium*, which was registered for clams between 30 and 40 mm SL in northern Chile (Jerez et al., 2007a,b), may increase the susceptibility to infestation. Reproductive condition has been shown to be a major factor affecting filtration and respiration rates of bivalves (e.g. Iglesias and Navarro, 1991; Smaal et al., 1997; Heilmayer et al., 2004). The elevated water flow rate in turn may facilitate the entrance of juvenile worms or larval stages into the mantle cavity, thus explaining the onset of the infestation in this size class (Fig. 1a). Additionally, clams start developing a gap between valves at 53 mm SL , which leaves space at the siphon area and may allow *P. bioocipitalis* to enter, even when the valves are "closed". This increased susceptibility can further foster an increasing prevalence in adult clams. It has been commonly observed that PI increases when host susceptibility increases (Anderson and Crombie, 1985), i.e., Kavanagh (1941) observed differences of infestation due to distinct shell gapping of the oysters *Crassostrea gigas* and *C. virginica* infested by *P. websteri*.

Tidal level and the localization of clams may also be a factor determining recruitment, infestation ability and distribution of *P. bioocipitalis* along the depth gradient,

as intertidal may represent a harsh environment for this polychaete. In fact, intertidal exposure levels were correlated with *P. websteri* recruitment on oysters Handley and Bergquist (1997).

The *P. biocipitalis* seasonal pattern of infestation was characterized by two periods of simultaneous drop in mean *Tb* and increasing *PI*. Although the infestation process may be initiated earlier by the settlement of juvenile worms on small sized clams, this pattern proves that the infestation episodes are completed when the worm reaches the mantle cavity, as indicated by the onset of the clams reaction to form new blisters. Both environmental and host related factors can underlie temporal host finding patterns in marine parasitic associations (Bush et al., 2001). Sea surface temperature can influence developmental stages, as well as distribution, selectivity of *Polydora* and intensity of infestations (Davis, 1967; Blake, 1969). However, the expected correlation between seasonal changes of this parameter and *Tb* or *PI* was non distinguishable in our study.

Increased infestation of *Polydora* spp. has often been related with decreased host condition (e.g. Kent, 1979; Ambariyanto and Seed, 1991; Simon et al., 2006). Thus, an influence of poor clam condition on the infestation ability was hypothesized (Handley, 1998). However, this hypothesis remains to be tested, as contrasting results concerning the relationship between infestation and condition have been reported (see Schleyer, 1991). On the other hand, our results demonstrate that periods of increased blistering may coincide with periods of decreased *GSI* and *BCI* of uninfested clams (Fig. 3). Therefore, the observed pattern may result just from the same environmental factor(s) influencing body condition of the clam, as well as the infestation ability of *P. biocipitalis*.

4.2. Infestation and host performance

Effects of *Polydora* spp. infestations on bivalve hosts have been related to negative effects, including poor body condition (e.g. Kent, 1979; Ambariyanto and Seed, 1991; Wargo and Ford, 1993; Handley, 1998), enhanced mortality (e.g. Korringa, 1952; Wisely et al., 1979; Lleonart et al., 2003) and low marketability due to flesh condition or shell damage (Handley, 1995; Tinoco-Orta and Cáceres-Martínez, 2003). In contrast, other studies reported commensalistic associations (e.g. Medcof, 1946; Stephen, 1978; Handley and Bergquist, 1997) and even symbiosis (Schleyer, 1991). These contrasting conclusions may either be due to the existence of indeed different types of associations or to the researchers' perception in relation with differences in the severity of infestation, in the boring activity of the polydorid or in

the relative size of the polychaete and the host species, among other possibilities. Loss of condition and general weakening is expected in heavily blistered bivalves, as they have to expend energy making the blisters, they lose internal shell volume, and the blisters may interfere with the feeding currents within the mantle cavity (Korringa, 1951; Lauckner, 1983). Although our results indicate a negative relationship between *P. biocipitalis* infestation and *BCI*, growth rate and burrowing ability of *M. donacium* as well as the restriction of this negative influence to adult clams, this does not necessarily imply a cause-effect relationship. Further experiments are thus necessary to confirm these initial observations.

The primary energy reserve stored by marine bivalves is glycogen (Barber et al., 1988), mainly in the gonad, mantle and adductor muscle. As glycogen is used up during gametogenesis, the gametogenic cycle is influenced strongly by the bivalve's condition (Perdue and Erickson, 1984; Masson and Nell, 1995). Although differences in mean *BCI* between heavily infested and non-infested clams were observed, the expected differences in *GSI* were not detected. On the one hand, this can be related to an enhancement of reproductive effort (the proportion of an individual's total energy intake devoted to reproduction) as a stress response (e.g. Bayne and Widdows, 1978; Hirshfield, 1980; Thompson, 1983). On the other hand, gonad-area-based indices proved to be not powerful enough to detect *BCI* losses (Handley, 1998), which seems the more likely explanation in the present case. Hence, the use of physiological condition indices (see Newell and Barber, 1988) may be a more appropriate method to detect the polydorid impacts on bivalve hosts.

It is worth mentioning that the observed changes of *BCI*, growth rate and burrowing ability could have been masked by the presence of the tapeworm *Rhodobothrium mesodesmatum*, which has been reported as a parasite of *M. donacium* (Carvajal et al., 1982). However, the low *PI* of this parasite reported in southern Chile (Tarifeño, 1980) is confirmed by our study (only six out of 445 individuals were infested) so that the possibility of a concurrent effect can be discarded.

Commensalism has been defined as an association in which an organism uses food supplied in the internal or external environment of a host without affecting the host in any way. In contrast, when the association negatively affects the host it implies parasitism (Rohde, 2005). Given the relationship between infestation level and clam performance and the fact that *P. biocipitalis* may even compete with its host for food (Ambariyanto and Seed, 1991), we suggest a parasitic relationship between *P. biocipitalis* and *M. donacium*. The classical parasitic association often implies a trophic relationship between

the parasite and its host and a degree of coevolution (Zelmer, 1998). However, indirect trophic relationships (stealing food when the host is feeding) have been also assumed as parasitism even for polydorids (e.g. Radashevsky 1993, Martin 1996, Martin and Britayev, 1998). This seems more likely to be the case of *P. biocipitalis*. In fact, the worms are always concentrated around the siphons of the host and produce a unique blistering pattern not observed elsewhere within polydorids (Olivares, 2006), which suggest a certain degree of coevolution between species.

4.3. Implications for *Mesodesma donacium* populations

Long-term population shifts of *M. donacium* remain one of the most conspicuous impacts of El Niño events along Peruvian sandy beaches (Arntz et al., 2006). May the infestation by *P. biocipitalis* play an additional role in those shifts? Under the spatial and temporal frame of our study, the percentage of heavily infested clams in the entire population was low and therefore the infestation is unlikely to be significant in terms of local population survival. However, at a large geographical scale, several reasons support the possible relevance of the infestation by *P. biocipitalis* in understanding the population shifts of *M. donacium* during El Niño. First, a south-north gradient of increasing *PI* of *P. biocipitalis* seems to exist, which ranges from non present at 42°S (Sato-Okoshi and Takatsuka, 2001), to “occasional” at 33°S (Tarifeño, 1980), 16.7% at 30°S (Olivares, 2006), 47.26% at 23°S (present study) and seems to be even higher at 12°S in southern Lima, Peru, as inferred from washed up blistered valves (Riascos, personal observations). Second, *Polydora* spp. infestations are enhanced in environmentally stressed bivalves (Jeffries, 1972; Newell and Barber, 1988), which in turn may facilitate the infestation by other parasites (Wargo and Ford, 1993). Third, anomalous water temperature may influence not only the abundance of *Polydora* spp. but also the intensity of their invasiveness (Davis, 1967): increased temperatures result in faster embryonic growth, earlier release from capsules into the plankton and induction of asexual reproduction (Blake, 1969; Dorsett, 1961; Tinoco-Orta and Cáceres-Martínez, 2003).

The observed differences of *PI* (higher when northern) appear to be related to the different water temperatures along the distribution range of the clam (higher in the at North, Bernard, 1983). Therefore, under non-El Niño conditions, the stress level induced by *P. biocipitalis* is expected to be higher in northern *M. donacium* populations. During strong El Niño events, the substantial warming of coastal waters affects several

ecological and physiological processes, which alter the performance of individual organisms, the dynamics of populations, the species distribution and the community structure (e.g. Riascos, 2006; Laudien et al., 2007; Ashton et al., 2007). Warmer conditions could rapidly raise the local prevalence and intensity of *P. biocipitalis* in stressed clams. Given the observed gradient of *PI*, northern populations are more likely driven to collapse during El Niño, as in fact observed (Arntz et al., 1987). Temperature-mediated changes in parasite abundance and transmission have been recognized as an important process in a global warming scenario (Poulin, 2006; Oliva et al., 2007). Future research should therefore focus on infestation mechanisms and reproductive strategies of *P. biocipitalis*. Particularly, an ongoing study will try to assess the effects of temperature on the infestation ability and the reproductive strategy of this worm.

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4.2.3 PUBLICATION 3***A long-term association between *Mesodesma donacium* and the boring polychaete *Polydora biocipitalis* on the Chilean coast**

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ABSTRACT - *Polydora* and related genera are common pests for mollusks. Establishing differences between native and recent invaders provide the basis for understanding their impact, with implications for resource management. *P. biocipitalis*, has been reported as a recently introduced species at the Chilean-Peruvian coast, raising concerns about its threat on native bivalve species. In contrast, studies on the infestation of *P. biocipitalis* on the surf clam *Mesodesma donacium*, one of the most important species for shellfisheries, suggest a long lasting, parasitic relationship. This study analyses infested (i.e. blistered) fossil shells of *M. donacium* deposited during the Holocene and Middle Pleistocene and critically reviews evidences supporting recent introduction of *P. biocipitalis*. The blistering pattern of fossil and recent shells can be considered species-specific for the infestation of *M. donacium* by *P. biocipitalis*. No evidence was actually found on vectors, introduction pathways or range distribution to support the status of *P. biocipitalis* as an introduced species. On the contrary, our findings point to a long-term association, at least for several hundred thousand years, between *M. donacium* and *P. biocipitalis*.

KEY WORDS: *Blister worm · fossil polychaetes · non indigenous species · mollusk parasites*

* This is the authors version of a work submitted to Diseases of Aquatic Organisms

INTRODUCTION

Spionid worms of the genus *Polydora* and related genera, commonly termed polydorids, have a worldwide distribution (Lauckner 1983; Ruellet 2004). First described in the late 1800s, their ability to bore calcareous substrates has labelled polydorids as pests on cultured and wild commercially important molluscs throughout the world (Handley 1995; Leonart et al. 2003; Simon et al. 2006). International shipping activities and aquaculture are well-recognized means to disperse species outward from their native regions (Castilla et al. 2005; Naylor et al. 2001). The current development of aquaculture in Chile includes several introduced species (e.g. salmon, abalone, oyster) harbouring pathogens (Buschmann et al. 1996). Evidence exists of the introduction of Spionid worms (Radashevsky and Olivares 2005). This is strengthened by a recent study showing that six polydorids species are marine non-indigenous species (NIS, sensu Carlton 1996) invading Chilean waters (Moreno et al. 2006). The accelerating invasion of marine systems by NIS has become a subject of environmental concern, because they act as stressors, affecting native species, community structure and function as well as ecosystems (D'Antonio and Vitousek 1992; Orensanz et al. 2002; Robinson and Griffiths 2004).

Polydora biocipitalis (Blake and Woodwick 1971) has been included in the group of polydorid NIS, rising concern about the threat for native and commercial mollusc species (Moreno et al. 2006). The surf clam *Mesodesma donacium* (Lamarck 1818), one of the most important species for artisanal fisheries of Chile and Peru (McLachlan et al. 1996; Thiel et al. 2007), is commonly infested by *P. biocipitalis* (Blake 1983; Riascos et al. 2008a). Recent analyses of the ecology of the association between *P. biocipitalis* and *M. donacium* defy the classification of this polydorid as a NIS and suggest a long lasting coexistence between the two species: Infestation by this worm increases during periods of poor condition of *M. donacium* and affects its growth rate, body condition and activity patterns, which suggests a parasitic relationship (Riascos et al. 2008a). On the other hand, the reproductive strategy of *P. biocipitalis* seems to be closely related to the life history traits of *M. donacium* (Olivares, unpublished).

Defining the characteristics of the association of polydorids and commercially important hosts is crucial in a scenario of rising global demand for

good-quality seafood, the rapid expansion of invasive species and the need for improved management of marine living resources. In this context, this study aims to i) report trace fossils in *M. donacium* shells in several fossiliferous deposits from Chile; ii) comparatively analyse the blistering pattern of fossil and recent shells of *M. donacium* as evidence for the long-term existence of the *P. bioccpitalis* - *M. donacium* association and iii) review evidences defining the status of *P. bioccpitalis* as native or non-indigenous species.

MATERIALS AND METHODS

Fossil shell valves of *M. donacium* (N = 183) were collected in fossiliferous coastal deposits at Michilla (22°43'S; 70°16'W), Chacaya (22°57'S; 70°18'W) and Las Lozas (23°28'S; 70°28'W), north of Antofagasta and at Los Porotitos (29°48'S; 71°17'W), near La Serena (Fig. 1).

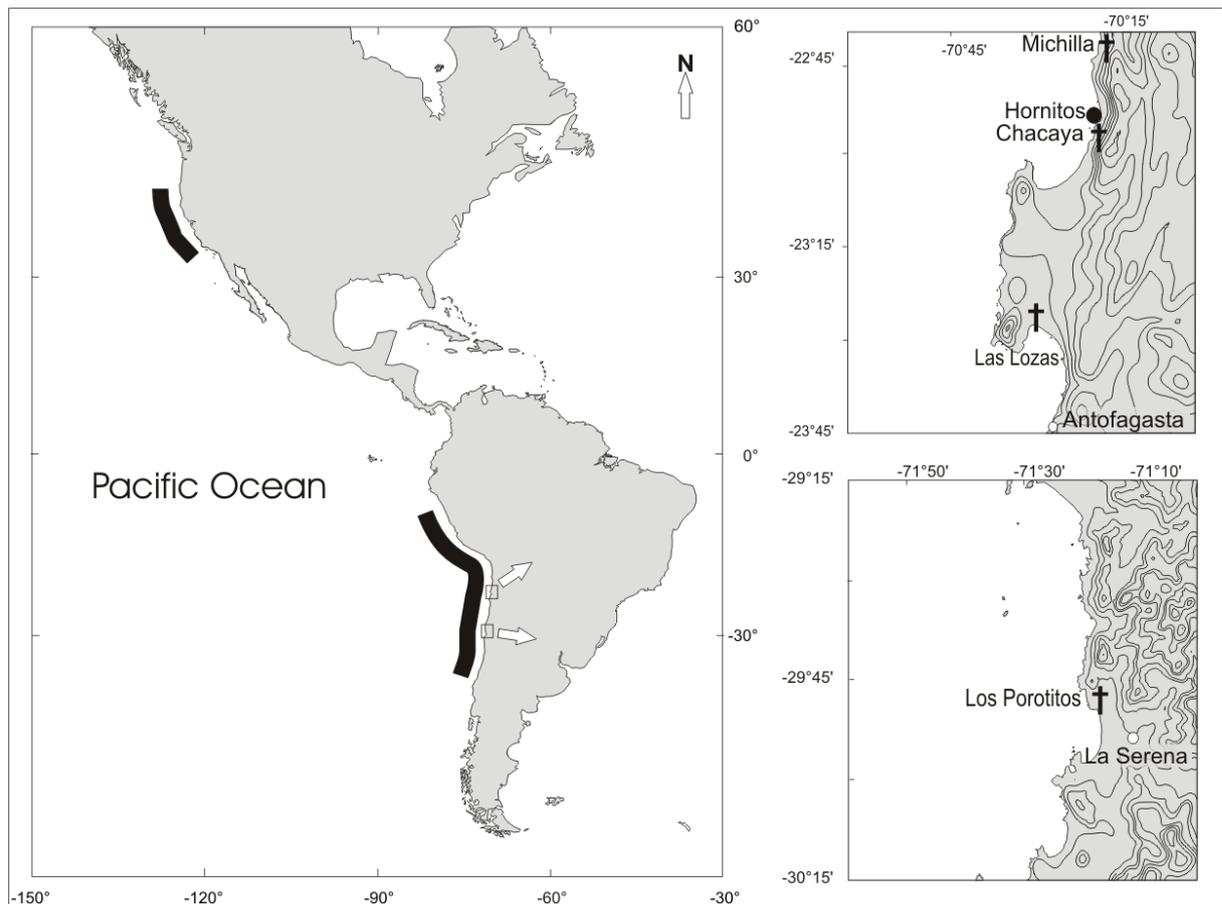


Fig. 1 Geographic distribution of *Polydora bioccpitalis* (black line) and collection places of fossil (†) and recent (●) *Mesodesma donacium*.

These deposits correspond to well preserved sequences of sediments associated with marine terraces formed during high seastands of the last interglacial periods (Marine Isotopic Stages). The age of each fossiliferous deposit was determined by using a combination of geochronological and geomorphological approaches (Radtke 1989; Leonard and Wehmiller 1991, 1992; Ortlieb et al. 1995, 1996; summarized in Table 1).

Table 1 Locality and geochronological methods used to assign ages to each fossiliferous deposit. Method references: 1 = Leonard and Wehmiller (1991); 2 = Ortlieb et al. (1995); 3 = Radtke (1989); 4 = Ortlieb et al. (1996); 5 = Leonard and Wehmiller (1992).

Locality	Geochronological method (reference)	Age
Michilla	¹⁴ C dating (1)	6,725 ± 95 yBP
	Th/U dating (2)	6,990 ± 80 yBP
Chacaya	Aminostratigraphy (3)	Marine Isotopic Stage 5
	Th/U dating and morphostratigraphy (4)	~120,000 y
Las Lozas	Th/U dating and Electron Spin Resonance (3)	Marine Isotopic Stage 9
	Aminostratigraphy and morphostratigraphy (4)	~330,000 y
Los Porotitos	Th/U dating and Electron Spin Resonance (3)	Marine Isotopic Stage 9
	Aminostratigraphy (5)	~330,000 y

For comparisons, recent *M. donacium* shells (N = 665) collected during a study performed at Hornitos (22°54.99'S; 70°17.42'W; Fig 1) between May 2005 and April 2006 were also analysed. For both, fossil and recent shells, the anterior-posterior shell length (SL) was measured to the nearest 0.5 mm and the location and presence of blisters was registered. Blisters were exposed by fracturing the walls with a scalpel and hammer to describe internal features. Fossil and recent shells analysed here are deposited at the IRD-Universidad de Antofagasta Paleontological Collection (Antofagasta, Chile) and selected specimens were deposited at the Museo Nacional de Historia Natural de Chile. A variance ratio test (Zar 1999) was used to test for differences between SL variance of blistered fossil and recent shells. The Shapiro-Wilk test was used to assess normality of each data set, as needed to meet the assumptions of this test.

RESULTS

Ages of fossil *M. donacium* shells from coastal deposits varied from the Holocene (Michilla) to the Middle Pleistocene (Chacaya, Las Lozas, Los Porotitos) (Table 1). The polydorid infestation of *M. donacium* was exclusively evidenced in the formation of mud-blisters (sensu Blake and Evans 1973) in the inner shell surface, with no signals of burrows on the exterior shell surface, as commonly

observed for most polydorid infestations. The blistering pattern of both fossil and recent shells was identical and rather specific: blisters were exclusively located near the posterior shell margin, surrounding the posterior adductor muscle insertion and the paleal sinus (Fig. 2a, 2b). Moreover, blisters were formed in a progressive large series (Fig. 2c) of up to eight blisters in larger clams. Earlier (smaller) blisters were consistently located toward the dorsal margin, while blisters formed later (larger) were located toward the ventral margin (Fig. 2c). Blisters are generally pear-shaped, with the narrow end communicating with the outside at the posterior shell margin.

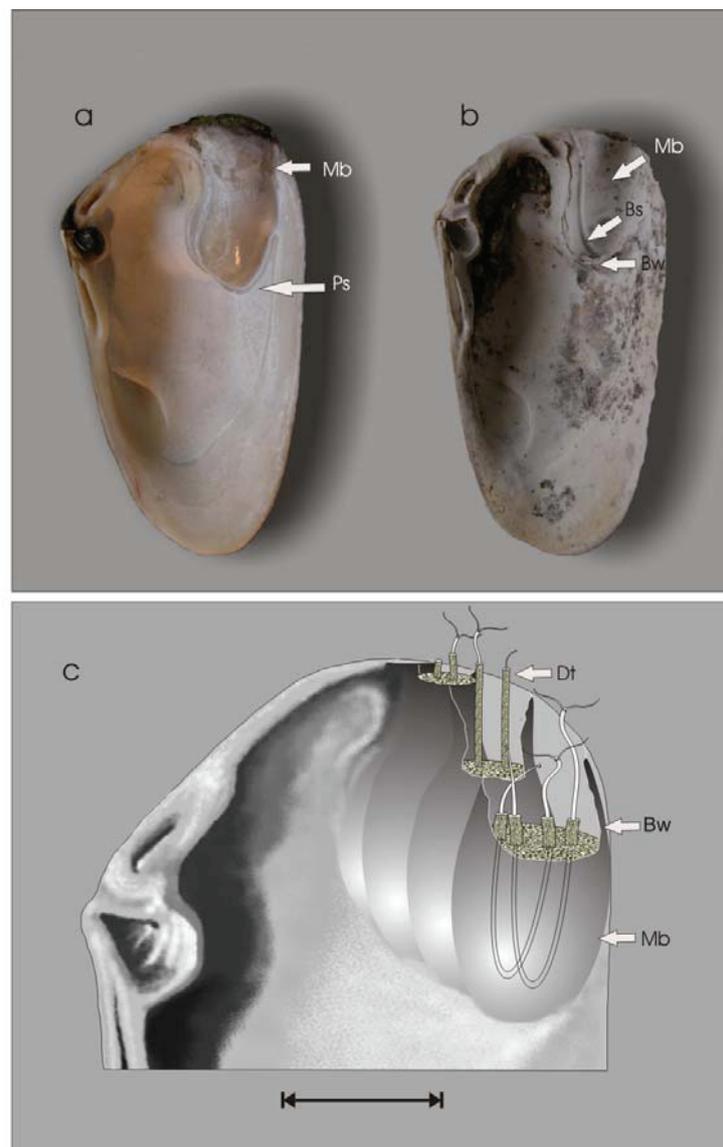


Fig. 2 Shell blistering pattern of (a) recent *Mesodesma donacium* collected from Hornitos, Northern Chile and (b) *Mesodesma donacium* valve from Middle Pleistocene deposits in Los Porotitos, Central Chile; (c) line drawing of the internal features of the blistering produced by the infestation of *Polydora biocippitalis* in shells of *Mesodesma donacium*. Mb: mud-blister; Dt: detrital tube; Bw: blister wall; Ps: paleal sinus; Bs: blister scar. Scale bar: 2 cm.

Blisters in recent shells were filled with detrital material deposited by the polychaete, which builds a U-shaped detrital tube inside the blister. Tube openings communicate with the outside of the shell (Fig. 2c) allowing the worm to feed near the inhalant and exhalant siphon currents. The continuous back and forth movement of the worm along the detrital tubes commonly produces a scar in the internal blister wall, revealing the position of the U-shaped detrital tubes inside the blister. No traces of internal detrital tubes were recorded in fossil blisters, but U-shaped scars were well evident, and comparable to those of recent shells (Fig. 2a, b) allowing estimations of worm lengths ($\sim 32 - 38$ mm), and diameter ($\sim 0.8 - 1.0$ mm), which coincided well with measurements of living *P. biocipitalis* (Fig. 2b).

Overall, the infestation (i.e. recordable blisters) of fossil and recent shells was restricted to larger shells (SL > 32.0 mm) as shown by the size-blister distribution (Fig. 3). Fossil blistered shells ranged between 43.7 mm and 105.6 mm, whereas recent shells ranged from 34.0 mm to 96.0 mm. The variance ratio test showed no differences in SL variance between blistered fossil and recent shells ($F_{25, 192} = 1.69$; $p < 0.05$).

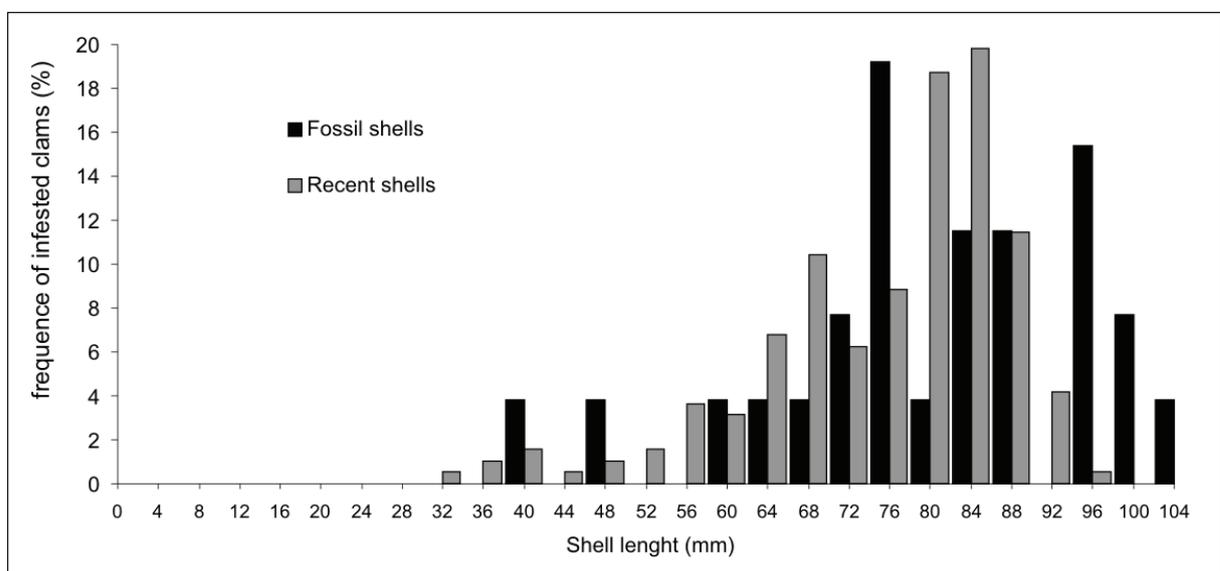


Fig. 3 Frequency distribution of maximum anterior-posterior shell lengths of blistered fossil and recent shells of *Mesodesma donacium*.

DISCUSSION

Studies on the relationship between the boring activity of polydorid species and their habitat have demonstrated that burrowing patterns are species-specific (Sato-Okoshi and Okoshi 1997; Sato-Okoshi and Takasuka 2001). Three main types of polydorid burrows in bivalve shells have been well described by Blake and Evans (1973): (i) Surface fouling, which occurs when the worms settle on a surface building a detrital burrow, but do not penetrate, (ii) U-shaped burrows that penetrate the structure of the shell; the basic pattern typical of *Polydora* shell infestations, and (iii) mud blisters, which result when the worms reach the inner surface of the shell, either by crawling between the mantle and the inner shell surface or by shell penetration, and the host secretes new shell layers to isolate the worm. Concurrently, the worms fill the newly formed space with loose mud, and then compact it leaving U-shaped detrital tubes that communicate with the exterior. Although surface fouling by *P. biocipitalis* has been observed on juvenile *M. donacium*, during preliminary infestation stages (Riascos et al. 2008a) direct shell excavation by the polychaete was never observed. Evidence of the infestation in fossil and recent shells consisted exclusively in a rather specific and serial blistering pattern (Fig 2).

Single mud-blisters in bivalve shells infested by polydorids have been extensively reported (see revisions by Blake and Evans 1972; Lauckner 1983; Martin and Britayev 1998 and references therein). However, the shell blistering observed in *M. donacium* infested by *P. biocipitalis* present distinctive structural features not previously reported and can therefore be considered species-specific. First, a series of blisters is formed in response to the infestation. Second, blisters are consistent in form and location, allowing the worm(s) to feed near the currents generated by inhalant and exhalant siphons. Third, although worms of the genus *Polydora* are known for their ability to bore (Blake 1969b, 1980; Blake and Evans 1973), blisters *M. donacium* shells are formed without evidence of boring activity. In addition, no differences were found in the SL range between blistered (i.e. infested) fossil and recent shells (Fig. 3). The shell range, in which the infestation takes place is a rather distinctive feature of the association between the two species, as the infestation of juvenile *M. donacium* depends on ontogenetic changes in shell morphology that increases the susceptibility to

infestation (Riascos et al. 2008a). It is often difficult to assign taxonomic identity to species producing trace fossils, as evidence of life activities rather than soft tissues are being considered (Cameron 1969). However, the singularity of the described shell blistering, the similarity of the blister characteristics in fossil and recent shells and the fact that *P. biocipitalis* is the only known polychaete associated with *M. donacium* (Blake 1983; Moreno et al. 2006; Riascos et al. 2008a), strongly suggest that blisters were produced due to *P. biocipitalis* infestations in both, fossil and recent shells.

In a review on boring spionid polychaetes, Moreno et al. (2006) reported nine species, with six species (including *P. biocipitalis*) being classified as NIS, based on the criteria outlined by Oresanz et al. (2002) and Castilla et al. (2005). For *P. biocipitalis*, Moreno et al. (2006) did not find direct evidence on vectors and introduction pathways into the Chilean-Peruvian coast. They based its inclusion as NIS on the apparently notorious, biogeographically incongruous range distribution and its recent record outside their “native or historic” range of distribution, i.e. California (USA) and the North Atlantic (Europe: France, United Kingdom, Ireland, North Sea) and its introduced range as the South Pacific (Chile, Australia, New Zealand). However, an analysis of the given references in Moreno et al. (2006, Table 2 therein) and an own extensive literature research reveals a different distribution range of *P. biocipitalis* restricted to the eastern coast of North and South America (Fig. 1).

P. biocipitalis was first described by Blake and Woodwick (1971) in Malibu Beach (34°02'N) and Santa Barbara (34°24'N), California (USA) as a commensal of *Pagurus hirsutiusculus* hermit crabs inhabiting gastropod shells (*Murex gemma*, *Ocenebra poulsoni*, *Polinices reclusianus* and *Olivella biplicata*). Since then, all additional records of *P. biocipitalis* refer to the Chilean - Peruvian coast. Rozbaczyllo et al. (1980) reported *P. biocipitalis* inhabiting living shells of *M. donacium* from Playa Morrillos (30°09'S). Latter, Blake (1983) reported it from mud-blisters of *M. donacium* from Playa Aguila (20°54'S), 100 km south of Iquique. Additionally, Moreno et al. (2006) recorded *P. biocipitalis* from a specimen of the clam *Mulinia edulis*, collected in Playa Santo Domingo (33°38'S), south of the port of San Antonio. Finally, Riascos et al. (2008a) showed a latitudinal gradient of increasing prevalence of *P. biocipitalis* infesting *M. donacium* from southern Chile (42°S) to central Peru (12°S). It is worth noting

that *P. biocipitalis* does not infest *Crepidula fecunda*, *Crepidula* sp. and *Fissurella nigra* as inferred by Moreno et al. (2006, Table 1) from the studies of Sato-Okoshi and Takatsuka (2001) and Bertrán et al. (2005). According to these authors, the mentioned gastropods are only infested by *P. rickettsi*, *Dipolidora huelma* and *D. giardii*.

Although discontinuous (Fig. 1), the observed geographic range distribution of *P. biocipitalis* cannot be considered incongruous. At least three spionid species (*P. cirrosa*, *P. rickettsi*, and *Boccardia tricuspa*) present a similar distribution pattern in the western South and North America (Blake 1983; Ruellet 2004). This may well reflect the fact that while the northern and southern (California 42 species and southern coast of South America 19 species) spionid fauna have been relatively well sampled and described, the coastal tropical regions of Latin America have been neglected (2-6 species) (Ruellet 2004, Fig. 38 therein). Interestingly, Kern et al. (1974) reported fossil spionid tubes in gastropod shells occupied by hermit crabs found in the Pliocene and Pleistocene strata of California and Baja California similar to those constructed by *Polydora commensalis* and *P. biocipitalis*. This, and the trace fossils described here from Middle Pleistocene deposits suggest that *P. biocipitalis* has been present at both ends of the distributional range for a long time.

In conclusion, our findings strongly suggest a long-term association, at least since the Middle Pleistocene, between *M. donacium* and *P. biocipitalis* and indicate that this spionid worm was not introduced by man to the Chilean-Peruvian coast.

ACKNOWLEDGEMENTS

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4.2.4 PUBLICATION 4***Thriving and declining: climate variability shaping life-history and population stability of *Mesodesma donacium* in the Humboldt Current Upwelling System**

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ABSTRACT - Large-scale environmental patterns in the Humboldt Current System (HCS) deeply change during strong El Niño episodes, leading to the mass mortality of dominant species in coastal ecosystems. Here we explore how temperature and salinity change affect 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 temperature and salinity variability was assessed. *M. donacium* is highly sensitive to temperature changes, suggesting that the northward distribution is limited by high sea surface temperature. In contrast, this clam, particularly juveniles, was remarkably tolerant to low salinity, which may allow the spat to select river mouths as suitable areas for recruitment. Strong freshwater-input seasonality was found to best explain general patterns in the reproductive cycle and some local departures. Reported for the first time for the HCS, submarine groundwater discharge may act as stepping stone areas in the Atacama Desert coast, with a similar effect as river discharge in *M. donacium* populations. Owing to its narrow thermal tolerance, the expansion and dominance of *M. donacium* from the Pliocene/Pleistocene transition until present seems 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 extinction-recolonization process, in which thermal and osmotic tolerances play a key role.

KEY WORDS: El Niño, fresh water input, geographic distribution, reproductive cycle, sandy beach ecology, submarine groundwater discharge.

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INTRODUCTION

The surf clam *Mesodesma donacium* (Lamarck 1818) is an important species from both an economical and ecological perspective. It has been one of the most important species for Chilean and Peruvian “marisco” 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 more than 95% of the shallow soft-bottom community (Arntz et al. 1987). However, this species is severely affected during El Niño (EN), the warm phase of the El Niño–Southern Oscillation (ENSO), which (among other characteristics) brings warmer, nutrient-poor, less saline waters into the nearshore zone. These changes result in mass mortalities of *M. donacium* and leave an impoverished sandy beach community consisting mainly 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 southward up to 14° S after the severe EN 1982-83, (Arntz et al. 1987) and further south after EN 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 close dependence on surface temperature is a distinctive feature of shallow water fauna in the HCS, which defines large-scale biogeographical patterns (Castilla 1979, Camus 2001). Therefore, this dependence is expected to explain changes in performance and distribution of marine bivalves during EN (Urban 1994). On the other hand, reduced salinity seems particularly important to understand *M. donacium* responses to EN, given the strong increases of freshwater input during these events (e.g. Waylen & Caviedes 1990) and the location of *M. donacium* near river mouths (Jaramillo et al. 1994, Fig. 1). 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).

Establishing links between life-history traits of *M. donacium* and large-scale environmental settings during non-EN conditions is a crucial step to assess responses to EN and subsequent recovery. Key processes controlling long-term

variability and persistence of marine bivalve populations are reproduction and recruitment (e.g. 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, on growth and mortality of *M. donacium*; (2) describe the latitudinal patterns of reproductive activity and assess the link with large-scale variability patterns of temperature and salinity, 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 ($22^{\circ} 54' S$, Fig. 1). After sampling, clams were immediately transported to the laboratory and acclimated for 25 days at ambient temperature ($17.4^{\circ} C$) and salinity (~ 35) in a 12:12 h day-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 three hours 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 *M. 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 two groups based on anterior-posterior shell length (SL, mm): juveniles: $SL \leq 50 \text{ mm}$ and adults: $SL > 50 \text{ mm}$ (McLachlan et al. 1996) and randomly assigned to a 3 x 2 factor experimental design: three salinities (10 ± 1 , 20 ± 1 and 35 ± 1) and two temperatures ($17.4 \pm 0.5^{\circ} C$, the historical annual average and $24.2 \pm 0.5^{\circ} C$, the maximum registered during EN 1982-83; CENDHOC). Each combination was run with three replicates and seven clams per replicate. Clams were conditioned over two weeks to high temperature and low salinities by gradually increasing temperature and/or reducing salinity. Animals were fed as stated before and held in experimental conditions during one month in 35 l-tanks (1/3 sterilised sand) in temperature-controlled rooms and a 12:12 h day-night cycle. Seawater was filtered ($0.1 \mu\text{m}$), continuously aerated and exchanged daily. Twice a day, sand

was aerated, dead clams were counted, removed and shells were kept for further analysis.

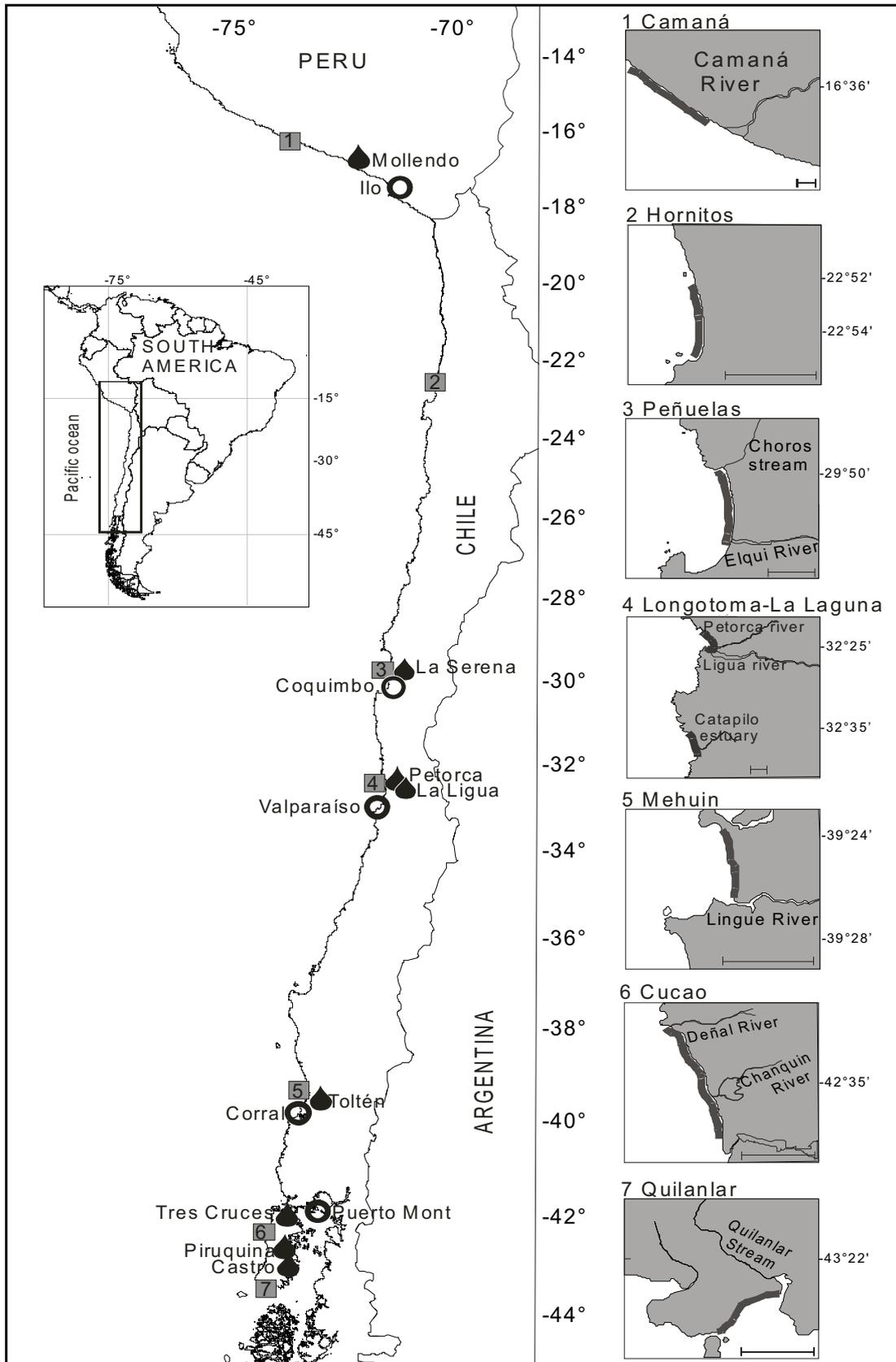


Figure 1. Geographic location of sandy beaches (numbered squares) considered in the analysis of the reproductive cycle of *Mesodesma donacium* and location of stations for sea surface temperature (circles;) and precipitation data (drop symbol) along the Chilean-Peruvian shoreline. Data sources: CENDHOC (Chile). Scale bars: 5 km.

At the end of the experiment, the remaining animals were sacrificed and SL 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 total growth increment (calcein mark to shell edge). Shell length increments were measured to the nearest 1 µm under a fluorescence microscope using blue light (460 to 490 nm). To analyse growth data the linear relationship between growth and SL was used (Gulland & Holt 1959): $SLI/t = a + b*SL$, where SLI is the shell length increment (µm), t is time (days) between marking and death of each individual and a and b are parameters. From this relationship the curvature parameter K was calculated ($K = -b$; Gulland & Holt 1959). K was used as the measure of growth rate for each replicate under each set of temperature - salinity condition and analysed using two-way, fixed effects analysis of variance (ANOVA) for juveniles and adults, with salinity and temperature as factors. Similarly, we calculated the slope of a linear regression between the proportions of dead clams *versus* time for each replicate under each set of conditions. The slope of the regression was used as measure of mortality rate and analysed using two-way ANOVA for juveniles and adults, with salinity and temperature as factors. Data were log ($X + 1$) transformed to meet the assumptions of normality and independence of error terms. Homogeneity of variances was checked using Cochran's C-tests. ANOVA analyses were performed using the statistical packages JMP 7.0.1.

Gametogenic cycle and its relationship with temperature and salinity

We integrated information on the gametogenic cycle of *Mesodesma donacium* scattered in local sources (Table 1) and published it in the open-access library PANGAEA (Publishing Network for Geoscientific & Environmental Data).

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 characterise the cycle. All studies were based on standard histological techniques.

Location	Reference	Latitude	Sampling period	N	GS
Camaná	Salgado & Ishiyama 2008	16° 36' S	03-1973 to 02-1974	65	4
Hornitos	Riascos et al. 2008b	22° 54' S	05-2005 to 04-2007	18-30	4
Peñuelas	Jerez et al. 2008a	29° 50' S	06-1994 to 07-1995	20-30	5

Longotoma	Jerez et al. 2008a	32° 22' S	06-1994 to 07-1995	20-30	5
La Laguna	Tarifeño 2008a	32° 37' S	08-1969 to 11-1970	50	5
Mehuín	Filun 2008	39° 26' S	07-1989 to 06-1991	30	4
Cucao	Rubilar et al. 2008	42° 35' S	09-2000 to 08-2001	16-89	5
Quilanlar	Rubilar et al. 2008	43° 23' S	10-2000 to 08-2001	27-64	5

These data sets stem from eight sandy beaches and include our own data from a two-year 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 months-study by Rubilar et al. (2008) (Table 1) only data sets based on standard histological gonad examinations, taken at monthly intervals for at least one year were included. We excluded studies performed during El Niño/La Niña years, as these events are expected to affect temporal patterns (e.g. Riascos 2006, Riascos et al. 2008c). Although individuals were classified into slightly distinct gametogenic stages in each study (Table 1), two consecutive stages - active and spawned - were objectively distinguished in each study for both males and females and were used herein to describe the spatial-temporal variability of the gametogenic cycle. Monthly frequencies (%) of individuals at active and spawned stage were plotted for each locality to describe the spatial-temporal variability of the breeding and spawning seasons. For descriptive purposes, frequencies higher than 25 % of active stages, with corresponding lower frequencies of spawned stages were judged as indicators of breeding seasons, while the opposite was judged as indicative of spawning seasons.

Table 2. Station source of regional data bases for monthly mean sea surface temperature (SST), river inflow and precipitation in each study site. In parentheses, number of years used to calculate monthly-averaged historical values. SP = denotes that data were available for the same sampling period indicated in Table 1 for the corresponding locality.

Study site	SST (period)	River inflow (period)	Precipitation (period)
Camaná	Ilo ¹ (SP)	Camaná ³ (SP)	Mollendo ⁵ (13)
Hornitos	This study	--	--
Peñuelas	Coquimbo ² (SP)	Elqui ⁴ (6)	La Serena ⁵ (63)
Longotoma	Valparaíso ² (SP)	Petorca ⁴ (7) La Ligua ⁴ (24)	Petorca ⁵ (31) La Ligua ⁵ (31)
La Laguna	Valparaíso ² (SP)	Petorca ⁴ (7) La Ligua ⁴ (24)	Petorca ⁵ (31) La Ligua ⁵ (31)
Mehuín	Corral ² (SP)	Cruces ⁴ (32)	Toltén ⁵ (38)
Cucao	Puerto Mont ² (SP)	Not available	Tres Cruces ⁵ (31) Piriquina ⁵ (26)

Quilanlar	Puerto Mont ² (SP)	Not available	Castro ⁵ (34) Piruquina ⁵ (26)
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¹IMARPE (Peru); ²CENDHOC (Chile); ³INRENA 1994; ⁴DGA (Chile); ⁵Vörösmarty et al. 1998

Overall, original studies did not include data on sea surface temperature (SST) or salinity. Monthly-averaged data on SST, river inflow ($\text{m}^3\text{seg}^{-1}$) and coastal precipitation (mm) were obtained from the nearest hydrological and meteorological governmental stations of Chile and Peru (Table 2, Fig. 1). For Hornitos, 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 ($^{\circ}\text{C}$) at hourly intervals and salinity every 15 minutes during monthly samplings using a multiparameter data sonde (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 ($X = X - \bar{X} / SD$) to account for scale differences and enable comparisons, and between-months 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 two matrices. The BIO-ENV procedure defined single or suites of environmental variables that best “explain” the variability of gonad stage compositions.

RESULTS

Effects of temperature and salinity on growth and mortality

Growth rate of juvenile *Mesodesma donacium* varied between temperatures ($F_{1,12} = 17.328$, $P < 0.01$) but did not vary with salinity levels (ANOVA: $F_{2,12} = 7.629$, $P = 0.236$). The interaction term of temperature \times salinity was not significant ($F_{2,12} = 0.484$, $P = 0.627$). Growth rate was highest at 10 salinity and 17.5 °C and lowest at 35 salinity and 24.2 °C, while the remaining combinations of factors were grouped in a medium-level growth rate, as revealed by multiple comparisons (Fig. 2). Growth rate of adults was generally low (Fig. 2) and varied significantly only with temperature (ANOVA: $F_{1,12} = 7.384$, $P < 0.05$) while the effect of salinity and the interaction between factors were not significant ($F_{2,12} = 0.048$, $P = 0.952$, and $F_{2,12} = 0.081$, $P = 0.922$; respectively).

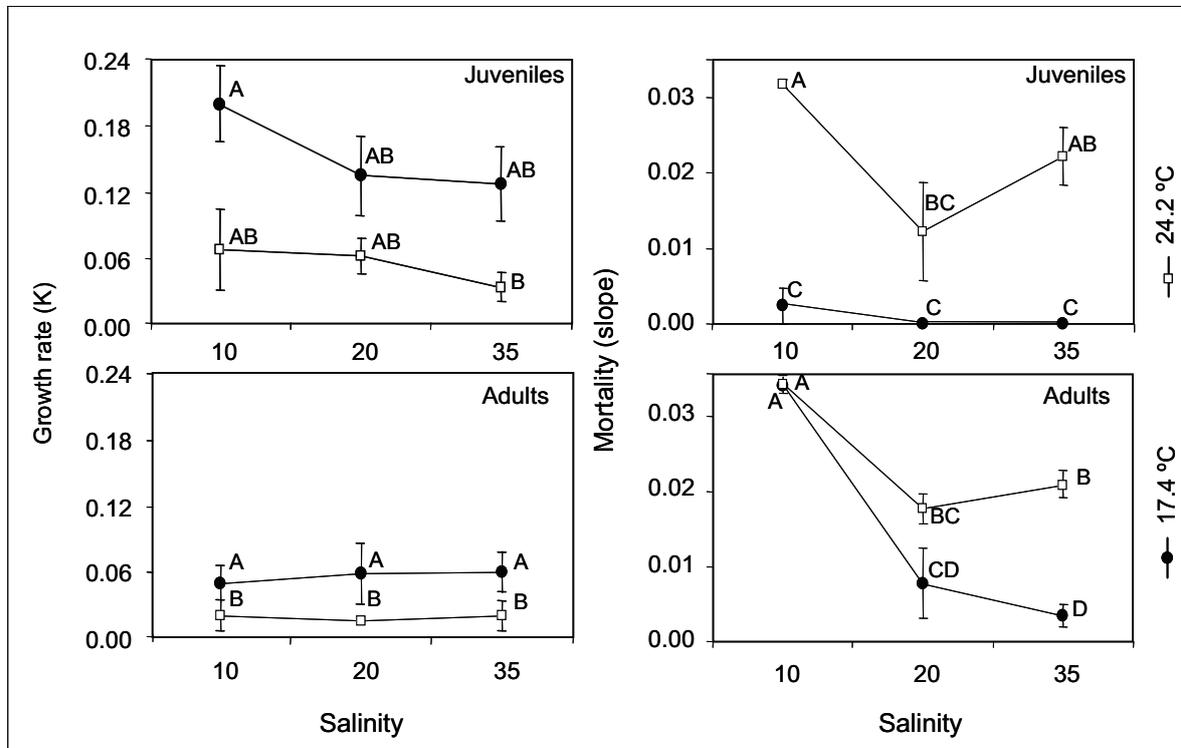


Figure 2. *Mesodesma donacium*. Mortality and growth rate (mean \pm SE) of juveniles and adults. Levels not sharing the same letter are significantly different (Tukey test, $P < 0.05$). (dots = low temperature treatment, 17.4°C; open squares = high temperature treatment, 24.2°C)

Mortality rate of juvenile clams was significantly affected by both, temperature and salinity (ANOVA: $F_{1,12} = 65.272$, $P < 0.001$ and $F_{2,12} = 5.779$, $P < 0.05$; respectively) with non-significant interaction effect ($F_{2,12} = 3.531$, $P = 0.062$). Multiple comparisons showed that overall mortality rates were higher at high temperature (Fig. 2). Mortality rate did not differ between salinity levels at

normal temperature ($P > 0.05$) but differed ($P < 0.05$) at high temperature (Fig. 2). For adult clams, mortality rate significantly differed between temperatures (ANOVA: $F_{1,12} = 23.344$, $P < 0.001$) and between salinity levels ($F_{2,12} = 58.058$, $P < 0.001$). Between temperature levels adult mortality rates were context dependent (significant temperature \times salinity interaction: $F_{2,12} = 5.779$, $P = 0.017$): in normal and moderately low salinity levels, mortality rate was significantly lower at 17.4 °C, but it was higher at the lowest salinity, independent of temperature (Fig. 2).

Influence of temperature and salinity on the gametogenic cycle

Reproductive activity of *Mesodesma donacium* along the distribution range showed a consistent temporal pattern with few departures (Fig. 3). The breeding season generally started in winter (seasons hereafter referring to austral) and extended into spring. A single spawning season (black arrows, Fig. 3) started in late winter or spring and extended into summer. Main departures of the general pattern occurred at Mehuín (39° S), where an uninterrupted gonad activity and two annual spawning events (spring and autumn; black and white arrows, respectively; Fig. 3) were observed. Populations in Camaná, Cucao and Quilanlar showed similar departures, consisting of slightly extended breeding and spawning seasons.

The variability of environmental factors at each locality is shown in Figure 4. Seasonal SST variability was small, ranging from 2.3 °C in Camaná to 6.9 °C in Mehuín. Coastal precipitation was almost nonexistent in northern populations; scarce in semi-arid central Chile (Peñuelas to La Laguna) and abundant in Mehuín, Cucao and Quilanlar. Precipitation displayed a strong seasonal signal; it typically varied by a factor of 4 - 8 in most places and by a factor of 75 in central Chile. Except for Camaná, river flow was rather scarce in the northern and central areas of the geographic range and abundant in Mehuín. No data on river flow were available for Cucao and Quilanlar. River discharge varied seasonally, from nearly a factor of 2 in Elqui river (~30° S, near Peñuelas) up to a factor of 52 in Ligua river (~32° S).

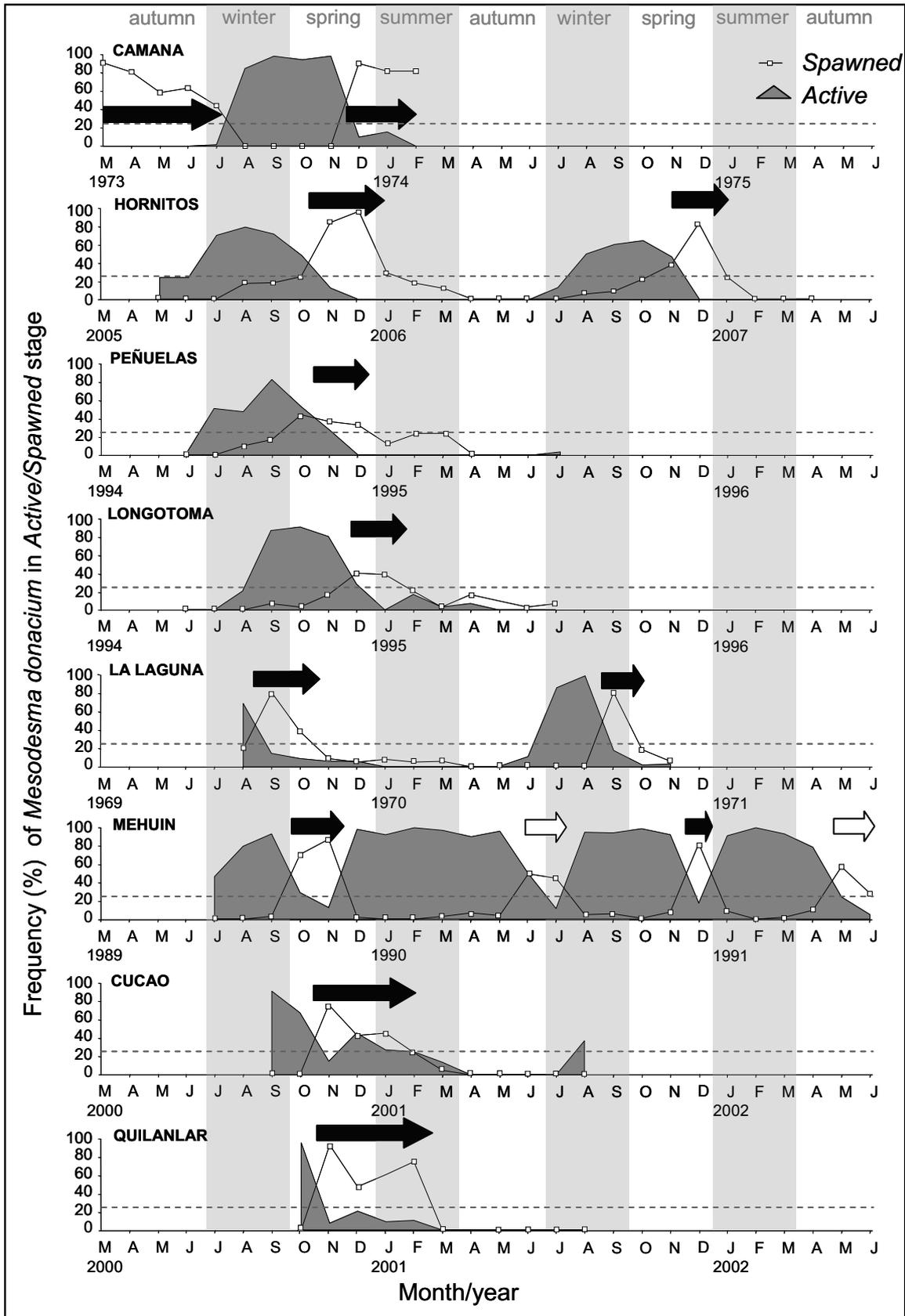


Figure 3. *Mesodesma donacium*. Spatial and temporal patterns of reproductive activity, based on histological examination of gonad tissue. Timing of spawning events is indicated by black arrows (spring-starting spawning season) or white arrows (autumn-starting spawning season). Dotted line denotes the 25% frequency limit to define breeding and spawning events.

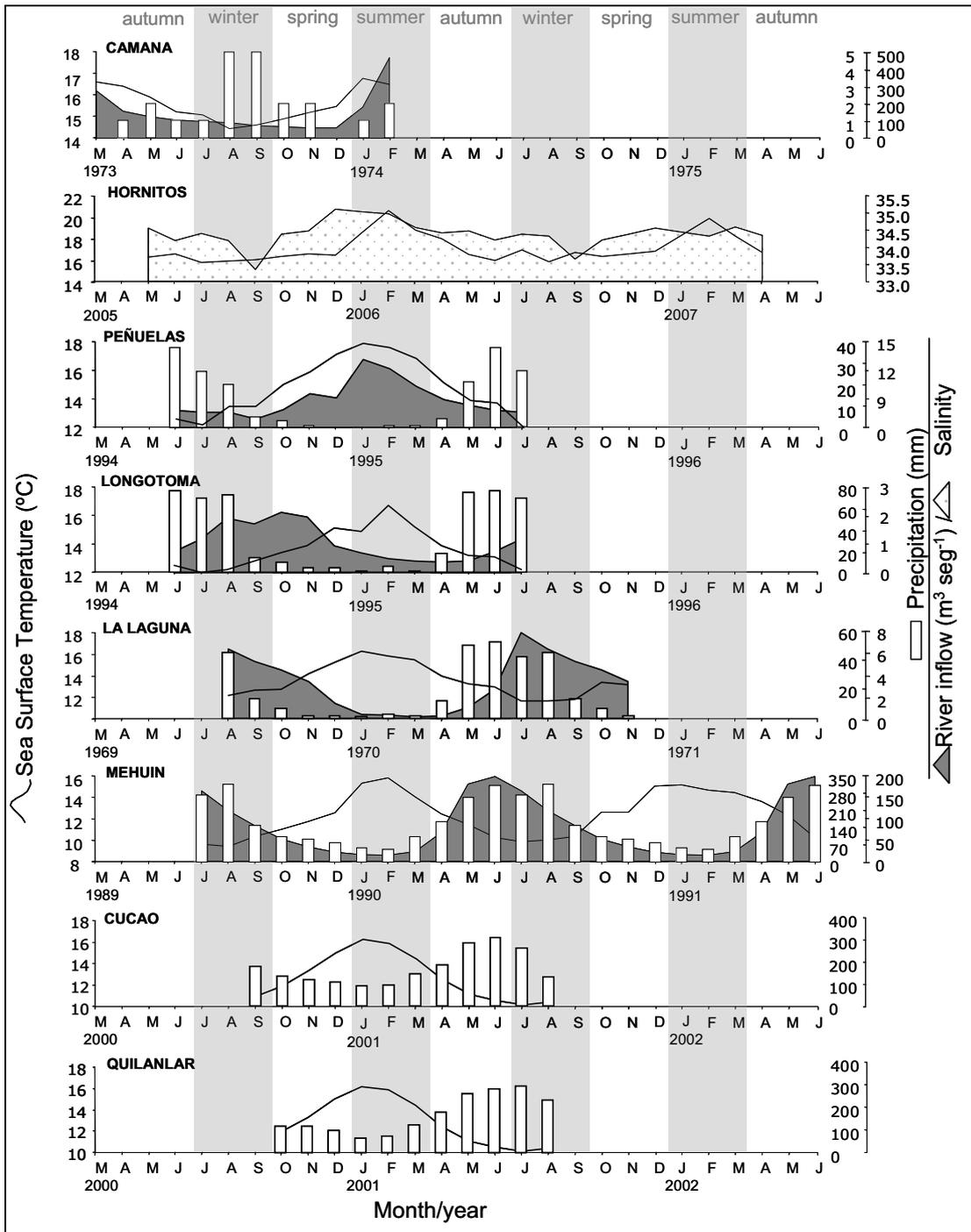


Figure 4. Spatial and temporal variability of sea surface temperature (solid line); river inflow (grey areas), coastal precipitation (bars) and salinity (dotted areas) in the study area. Data sources and as indicated in Table 2.

Lower and higher SST consistently occurred in summer and winter (respectively) through the geographic range. Higher (autumn/winter) and lower (spring/summer) precipitation were also consistent, except for Camaná. In contrast, higher/lower timing of river discharge changed through the geographic range without showing a clear trend. Neither river inflow nor precipitation was observed in Hornitos.

Here, salinity varied from 33.3 in winter to 35.1 in spring. Lower salinity in September coincided with the occurrence of submarine seepage through holes (~25 cm diameter) distributed along a narrow belt parallel to the coast line in the shallow subtidal (1.5 to 2.5 m depth). Water collected from several holes revealed low salinity (Average = 19.5; SD = 11.3; $n = 12$)

BIO-ENV analyses (Table 3) showed a significant correlation between gonad stage composition and environmental factors analysed: Spearman rank correlation ρ was significant in six out of seven study sites, the exception being Peñuelas. SST was one of the selected variables involved in significant global correlations only at Camaná and Mehuín. In contrast, salinity (at Hornitos) and river inflow or precipitation were involved in all the significant correlations. Indeed, one of these variables was selected as single “explanatory” variable in gonad stage composition for the populations of Longotoma, Cucao and Quilanlar.

Table 3. *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 printed in bold face and the corresponding selection of the best “explanatory” variable(s) is given. SST: sea surface temperature, Prec: precipitation, RI: river inflow

Location	ρ (probability)	Selection of variable(s)
Camaná	0.512 ($P = 0.01$)	SST-Camaná, Prec.
Hornitos	0.254 ($P = 0.03$)	Salinity, SST
Peñuelas	0.245 ($P = 0.10$)	--
Longotoma	0.585 ($P = 0.01$)	RI-Petorca
La Laguna	0.649 ($P < 0.01$)	RI-Ligua, Prec-Ligua
Mehuín	0.381 ($P = 0.01$)	RI-Cruces, Prec-Toltén, SST-Corrales
Cucao	0.342 ($P = 0.04$)	Prec-Tres Cruces
Quilanlar	0.339 ($P = 0.03$)	Prec-Castro

DISCUSION

Influence of temperature and salinity

Growth and mortality - The coastal upwelling system off Peru and Chile is broadly characterised by nutrient-rich, cool-waters, showing low seasonal temperature variability compared to other coastal ecosystems at similar latitudes (e.g. Arntz et al. 1987, Camus 2001, Thiel et al. 2007). As a consequence, many species exhibit broad distributional ranges and are adapted to a fairly constant low water temperature in this area (Brattström & Johanssen 1983, Santelices

1980, Urban 1994). This general feature is reflected in the low seasonal SST variability observed at Hornitos (15.8 °C in winter to 20.6 °C in summer, Fig. 3). Therefore, the higher experimental temperature was expected to significantly affect growth and mortality of *Mesodesma donacium*. While studying the thermal tolerance of ten bivalve species off Chile and Peru, Urban (1994) found that the upper lethal temperature varied between 24.8 and 27.9 °C for bivalves from Dichato Bay (Chile, 36° S) and between 27 and 31 °C for bivalves from Independence Bay (Peru, 14° S). He predicted that most of those species would only be affected by strong EN events. Accordingly, some of those species were locally affected during EN 1982-83 (Arntz & Fahrbach 1996). In contrast, *M. donacium* underwent mass mortalities, which constitutes one of the most conspicuous cases of severe, long lasting and widespread effects of EN on marine invertebrates (Arntz et al. 2006). This and our results strongly suggest that *M. donacium* lives near its upper thermal tolerance. Hence, temperature may have the potential to control the limits of distribution over different temporal scales as discussed below.

In contrast, *M. donacium* seems less vulnerable to reduced salinity: nearly no mortality was observed among salinity levels at normal temperature. Indeed, juvenile clams grew faster at lowest salinity (Fig. 2). The response of juveniles to reduced salinity was less clear under anomalous high temperature. They grew faster at low salinity (10 – 20), but mortality rate at the lowest salinity was also higher. No obvious explanations can be offered for this result, but field data suggest that *M. donacium* reacts to anomalous higher temperature with an atypical growth before dying (Arntz et al. 1987). Overall, adult clams were also able to cope with reduced salinity under both, normal and high temperature, but only within the salinity range between 20 and 35 (Fig. 2).

The ability of *M. donacium* (particularly juveniles) to cope with such a wide salinity range resembles that of euryhaline species; an intriguing result in view of the low salinity variability registered at Hornitos, and the lack of coastal precipitation and river discharge in the Atacama Desert of Northern Chile, one of the most arid zones in the world. Does this osmotic tolerance mirror a high salinity variability range caused by groundwater flow, not fully recorded in our salinity measurements at Hornitos?

Features of groundwater flow at Hornitos correspond to submarine groundwater discharge (SGD, *sensu* Church 1996), which occurs anywhere that an unconfined aquifer is connected hydraulically with the sea through permeable bottom sediments and its head is above sea level (Johannes 1980). Although unconfined aquifers are common in the Chilean-Peruvian desert coast (e.g. Rojas et al. 1995, Squeo 2006), this is the first study reporting on recent SGD on the western coast of South America. SGD may locally be substantial, however this flux of freshwater is often ignored as its impact is small at regional scales and its measurement is inherently very difficult (Burnett et al. 2001, Gallardo & Marui 2006). In sandy shores, SGD may affect both the intertidal and subtidal, leading to strong salinity changes particularly at upper tidal levels during low tides (Johannes 1980, McLachlan & McGwynne 1986). As different hydrologic and oceanographic techniques should be used to accurately determine this flow, the measurements can not be expected to accurately reflect the impact of freshwater on *M. donacium* beds.

Reproductive cycle - Overall, our results show that salinity or related variables, rather than temperature, better explain the temporal pattern of the gametogenic cycle of *Mesodesma donacium* (Table 3). SST showed a rather low seasonal variability (Fig. 4). This seasonality is small compared to other marine systems and resembles that of the Arctic realm (Giese & Pearse 1974, Arntz et al. 1987). Although slight seasonal temperature fluctuation may act to synchronize reproduction, this appears unlikely. Rather, other seasonal factors that fluctuate more dramatically can be expected to affect reproductive rhythms in these areas (Pearse & Lockhart 2004). Likewise, the strong seasonal fluctuations observed in river inflow and coastal precipitation (Fig. 4) seem more important to affect *M. donacium* reproduction, as confirmed by BIO-ENV analysis.

Deviations from the general temporal pattern of the reproductive cycle of *M. donacium* (Fig. 3) may be explained by spatial-temporal differences in river inflow in the study area. SST and precipitation consistently showed the highest/lowest values in summer and the lowest/highest in winter, respectively along latitude (Fig. 4). In contrast, river runoff seasonality showed a more complex north-south pattern as it is an integral response to precipitation patterns, snow melt, delayed groundwater discharge and human water use throughout the

river basins. In general, the seasonal stream flow regime varies with latitude; while the few rivers crossing the coastal Atacama Desert (southern Peru-northern Chile) tend to have the stream flow maximum in summer due to rainfall in the Andes, rivers in the semi-arid central Chile have a winter-centred pluvial regime and those in the southern part of the study area 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 altitude (Dávila et al. 2002, Houston, 2006). The extended breeding and spawning seasons observed in Camaná, Cucao, Quilánlar and specially in Mehuín seems to be linked to the locally increased fresh-water input (monthly $>100 \text{ m}^3 \text{ seg}^{-1}$ river inflow or $> 100 \text{ mm}$ precipitation; Fig 4). At 39° S , the combined inflow of several large rivers (e.g. Cruces, Toltén, Valdivia), which ranges between ~ 650 and $\sim 2200 \text{ m}^3 \text{ seg}^{-1} \text{ month}^{-1}$, and the coastal precipitation give rise to a biannual pattern in salinity (Dávila et al. 2002). This may explain the observed continuous breeding season and the biannual spawning pattern in the reproduction of *M. donacium* at Mehuín ($39^\circ 26' \text{ S}$).

Freshwater input should not be assumed as the “ultimate or proximate cause” (*sensu* Giese & Pearse 1974) of reproduction rhythms. Instead, freshwater input may interact with other factors, notably photoperiod, organic matter and phytoplankton production, given the relationship between freshwater input and nutrient and sediment load. SGD may locally influence marine geochemical budgets as river runoff does (Johannes 1980). Therefore, if *M. donacium* benefits from nutrient load, as our data suggest, SGD may play a critical “stepping stone” role for population connectivity along the coast of the hyperarid Atacama desert.

Recruitment - Juvenile *Mesodesma donacium* showed a higher osmotic stress tolerance than adults (Fig. 2). According to Tarifeño (1980) and Jaramillo et al. (1994), juvenile clams settle in river mouths, showing an alongshore spatial segregation with adults at Mehuín and La Ligua. The enhanced ability of juveniles to cope with low salinities may represent a physiological trait allowing juveniles to select suitable areas for settlement and recruitment thus reducing intraspecific competition for food. 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) although low abundances were also found close to dry river inlets in Guanaqueros and Tongoy bay (~30° S). Unfortunately observations regarding the spatial distribution of *M. donacium* are mostly circumstantial and do not take into account its inherently dynamic nature. Clearly, more scientific attention is needed to conciliate this evidence, as it may shed light on the recruitment process, one of the key factors regulating the population dynamics. Moreover, this may help to understand the low ability of the northernmost *M. donacium* populations to recover after EN events, given the scarcity of rivers along the Atacama Desert coast and the disturbances associated to increased sediment loads during EN.

Implications for population persistence

Fluctuations of SST, river inflow and precipitation depicted in Figure 4 largely mirror the north-south trends of temperature and salinity along the HCS of Chile and Peru. First, 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). Second, unlike temperature, freshwater input displays a strong latitudinal gradient. It is minimal and scattered along the coastal Atacama Desert and substantially increases toward central-southern Chile (Thiel et al. 2007). As a result, freshwater input influences highly localized coastal processes in the north and regional processes over the continental shelf toward the south (Dávila et al. 2002, Sobarzo et al. 2007, Thiel et al. 2007). Our findings depict how temperature and salinity affect life-history traits of *Mesodesma donacium* in this environmental scenario. However, they may also provide insights into the mechanisms regulating population persistence.

Fossil records of *M. donacium* first appear in late Pliocene deposits at Horcón and Quebrada Blanca, central Chile (Herm 1969) and at Tablazos, northern Peru (DeVries 1986), although recent dating by $^{87}\text{Sr}/^{86}\text{Sr}$ isotopes (Le Roux et al. 2006) suggests that central Chile's account corresponds to late Miocene to early Pliocene. A well recognized mass extinction event took place, probably during the Pliocene/Pleistocene transition, which may have affected ~66% of all species along the Pacific coast of South America (Herm 1969, DeVries 2001, Rivadeneira & Market 2007). Although there is no direct

palaeoceanographic evidence, the development of the oxygen minimum zone linked to the high productivity of the HCS established during the mid to late Miocene (Ibaraki 1997, Tsuchi 1997, but see Camus 2001) may be the cause of the mass extinction (McRoberts & Newton 1995, Rivadeneira & Market 2007). The north-flowing cold Humboldt Current, was also linked to the establishment of the arid climate of western South America (Hartley & Chong 2002) and thus to the establishment of the latitudinal freshwater input gradient. The development of the HCS involved both the northward advance of Subantarctic biota and the northward retraction of a former tropical/subtropical biota, with consequences that persist until the present (Brattström & Johanssen 1983, Camus 2001). Coinciding with the Pliocene/Pleistocene mass extinction, *M. donacium* (and other species with Subantarctic affinity) formerly scarce during the Pliocene became dominant in their corresponding biotope in the Pleistocene (Herm 1969, Devries 1986). Therefore, the expansion and dominance of *M. donacium*, a species with a presumably Antarctic origin (see von Ihering 1907, Marins & Levy 1999) and a narrow thermal tolerance, seems closely linked to the expansion of cold water conditions through the Humboldt Current. The recurrent warming effect of EN at least since the Holocene (Ortlieb et al. 2000) has caused a recurrent retraction of northernmost *M. donacium* populations (Quilter & Stocker 1983, Arntz et al. 1987). Given the observed influence of freshwater input on reproduction and the potential implications on recruitment of *M. donacium*, the ability of northern populations to recover could be constrained by the scarcity of freshwater input sources along the Atacama Desert coast.

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

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4.2.5 PUBLICATION 5***Latitudinal trends in population dynamics of *Mesodesma donacium* modulated by El Niño****J. M. Riascos^{1, 2, 1}, O. Heilmayer³, M. E. Oliva¹, J. Laudien²**

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ABSTRACT. The surf clam *Mesodesma donacium* (Lamarck 1818) is a commercially important species in Chilean and Peruvian sandy beaches. During strong El Niño (EN) events, the warm phase of El Niño-Southern Oscillation, populations on the northern side of the species geographic distribution are rapidly wiped out, and the recovery process may take decades. To understand the threshold responses to biotic and abiotic factors, the population dynamics of *M. donacium* at Hornitos (northern Chile), the current northern range boundary, was analysed between May 2005 and April 2007. Moreover, the geographical trends in abundance, growth performance, mortality and productivity and their shifts during EN years were studied. Population dynamics in Hornitos were characterised by a size-specific mortality and a strong reduction of abundance, growth performance and somatic production during the second year of study. This was seemingly related to the combined effect of biotic interactions and the significant increase of strong swell, probably related to the weak EN 2006-2007 event. Abundance, growth performance, mortality and productivity showed significant spatial patterns. All these parameters strongly decrease with increasing latitude. The observed trends do not fit classical assumptions that species are most abundant in the centre of their range and decline in abundance toward the range edges. The strong spatial pattern in coastal upwelling strength and its associated primary productivity seems responsible for the observed patterns and would explain the shifts of these patterns during EN events.

KEY WORDS: El Niño, latitudinal patterns, geographic distribution, population dynamics, sandy beach ecology.

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INTRODUCTION

The surf clam *Mesodesma donacium* (Lamarck 1818) ranks among the most important species for the Chilean and Peruvian artisanal fisheries (Defeo et al. 1993, McLachlan et al. 1996). This fishery can be considered as a 'boom-and-bust' fishery, where emerging natural stocks are quickly depleted and fishermen move to other regions, which led Chilean authorities to the establishment of a system of territorial user rights, called MEABR (Management and Exploitation Areas for Benthic Resources) to regulate its exploitation (Thiel et al. 2008). *M. donacium* plays an ecologically important role in shallow soft-bottom ecosystems; especially in Peruvian sandy shores, where it exhibits high abundances, extremely high annual somatic production and dominance i.e. often representing more than 95% of the whole shallow soft-bottom community (Arntz et al. 1987).

The predominant northward flow of surface waters of subantarctic origin in the HCS results in a northward extension of cool conditions (e.g. Camus 2001, Viviani 1979). This transport of cool waters probably facilitated the northward expansion and hence wide distribution of many subantarctic species through this zone (e.g., Menzies 1962, Castillo 1968, Alveal et al. 1973, Santelices 1980). This is the case of *M. donacium*, whose distribution spans from Chiloé (43° 20' S) to Sechura (5° 10' S) thus inhabiting temperate, subtropical and tropical beaches (Tarifeño 1980). While in general, large sandy beach clams are found on temperate beaches, *M. donacium* is the only one reaching also tropical and subtropical sandy beaches, which are usually dominated by smaller Donacid clams (McLachlan et al. 1996).

Environmental conditions of the cool HCS are strongly modified during El Niño events (EN), the warm phase of the El Niño-Southern Oscillation (ENSO), leading to different biotic responses at several organization levels, including strong changes in species distributions (e.g. Arntz & Fahrbach 1996, Escribano et al. 2004). Strong EN events cause *M. donacium* mass mortalities, which implies a change from a highly productive "*Mesodesma* community" to an impoverished community consisting mainly of small polychaetes (Arntz et al. 1987). After the severe EN 1982-83 the distribution of *M. donacium* was set back southward to 14° S and further south after EN 1997-98, leaving only a few decimated populations in southern Peru and northern Chile (Arntz et al. 1987, Quiroz &

Barriga 1998, Thiel et al. 2007).

Changes in species abundance and distributional range coinciding with climate change have been increasingly documented in recent years, especially in coastal invertebrates (e.g. Helmuth et al. 2006, Lima et al. 2007). A better understanding of spatial-temporal population dynamics across species ranges is urgently needed to address timely questions on resource management and species responses to these changes. Understanding demographic processes during both EN and non-EN conditions are a crucial step to assess responses of *M. donacium* to these recurrent warming events and the process leading to subsequent recovery. To face this challenge, a detailed assessment of populations at its northern range boundary is crucial to understand the threshold responses to environmental change.

Given the ecological and economical importance of this species, it is important to integrate the existing – although sparse and scattered in local sources – information to address large-scale population patterns. Thus, this work aims to (i) analyse the population dynamics of *M. donacium* at its current northern range boundary to understand the threshold responses to environmental warming (ii) determine the geographical trends in abundance, growth performance, mortality and productivity and shifts during EN years to identify potential causes and mechanisms. To address these issues, data from 16 sandy beaches distributed along the Chilean and Peruvian coast were gathered and assessed.

MATERIAL AND METHODS

Sampling site and sampling

In order to assess the population dynamics at the northern range boundary, a *M. donacium* population was sampled from May 2005 to April 2007 in Hornitos (Northern Chile (22° 54' S, Fig. 1)). This population represents one of the northernmost remnants after populations were decimated during the severe EN 1982-83 and 1997-98 events and the only one showing a relatively even composition of length classes. The population is distributed along ~400 m and not exploited commercially owing to the small size of the bed and its low abundance. Only few, local fishermen (<6) were occasionally observed during the first five months of this study.

A species-driven sampling strategy (*sensu* Defeo & Rueda 2002) was used to collect monthly samples along a transect perpendicular to the shoreline during spring tides. Samples (three replicates, spaced 5 m apart) were taken along a transect from the spring tide high water mark towards the shallow subtidal at 4 m intervals until no clams were found in two consecutive depth lines. When samples yielded clams, replicates were extended to five to ten, depending on tidal conditions. A sheet-metal box (0.16 m², 0.35 m deep; e.g. Laudien et al. 2003) was used for the intertidal and a diving-operated push box-corer (0.02 m², 0.20 m deep; Rumohr & Arntz 1982) for the subtidal sampling. Clams retained after sieving through a 0.5 mm mesh were measured (SL, anterior-posterior shell length) to the nearest 0.5 mm. A Spearman-rank correlation analysis was used to check the correlation between environmental parameters and monthly changes in abundance of *M. donacium*.

To characterise the sampling site the following parameters were measured: sea surface temperature (SST; °C), registered in hourly intervals with an Onset StowAway temperature logger installed on a float located ~100 m seaward from the beach during the entire sampling period. Salinity, dissolved oxygen (DO, mg l⁻¹) and Chlorophyll *a* concentration (Chl *a*; mg l⁻¹) were registered every 15 minutes during monthly samplings using a multiparameter data sonde (Yellow Springs Instrument Company, model 6600). The beach slope (Bs, cm m⁻¹) was determined by Emery's profiling technique (Emery 1961). Monthly changes in the Oceanic Niño Index (ONI; 3-month running mean of SST anomalies in the Niño 3.4 region) were downloaded from the database of NOAA/Climate Prediction Center, USA.

Abundance and length-mass relationship

Monthly abundance (δ ; ind m⁻²) and mean annual $\bar{\delta}$ were determined from monthly samples. The length-mass relationship was determined from monthly samples using 50 individuals covering the whole size range. Soft parts were removed and dried at 70° C to constant mass and shell-free dry mass (SFDM) was determined. Ash-free dry mass (AFDM) was obtained by ignition at 550° C for 6 h. The constants “*a*” and “*b*” of the length-mass relationship were estimated using the power function:

$$AFDM = aSL^b \quad (1)$$

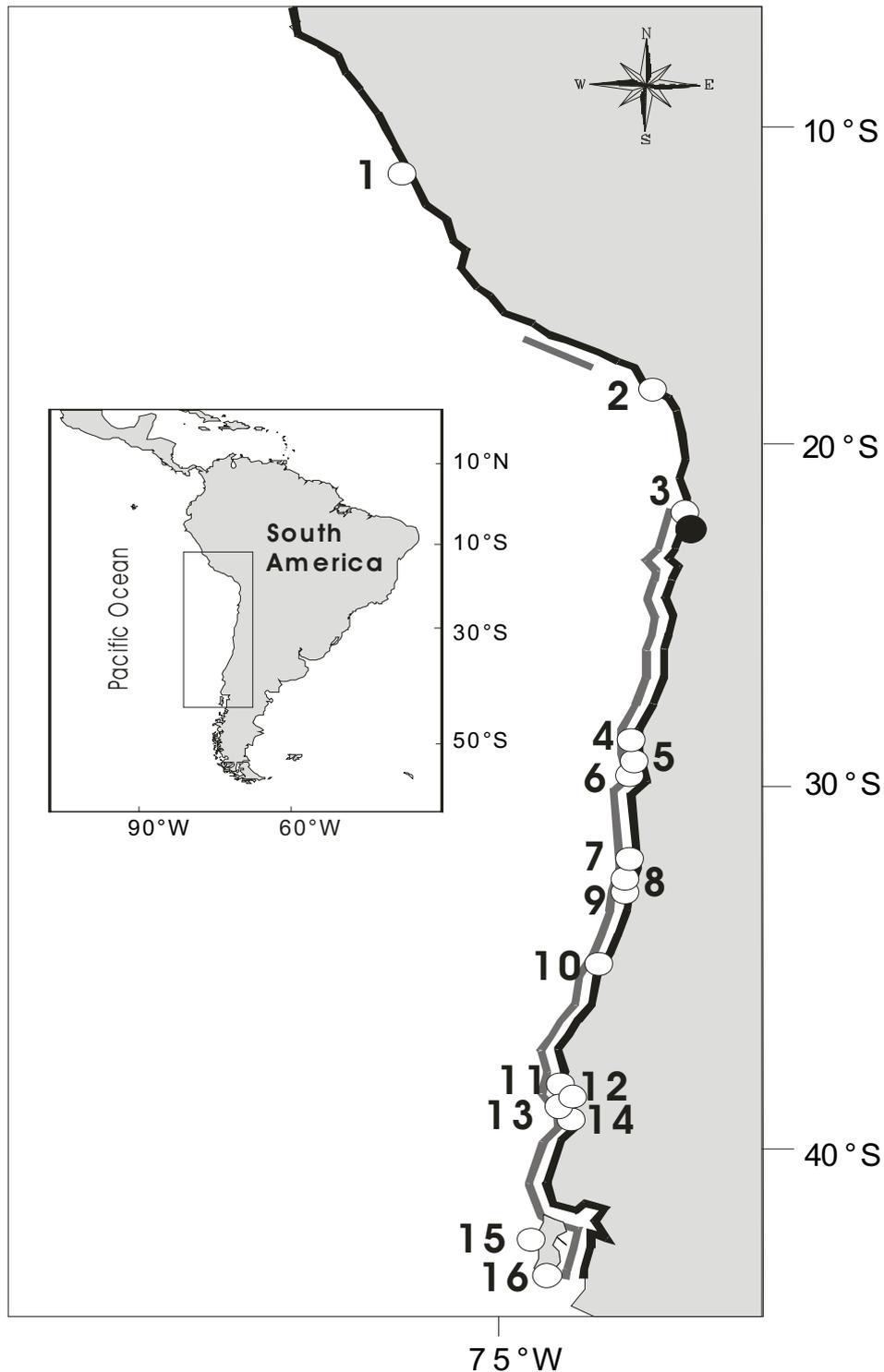


Figure 1. Geographic range of *Mesodesma donacium*, along sandy beaches off South America before (black thick line) and after (grey thick line) mass mortalities during El Niño events and location of Peruvian (1) and Chilean (2-16) sandy beaches (open circles) analysed in this study. 1: Santa María del Mar; 2: Las Machas; 3: Hornitos; 4: Los Choros; 5: Peñuelas; 6: Coquimbo; 7: Longotoma; 8: La Ligua; 9: Ritoque; 10: Putú; 11: Punta Morguilla; 12: Quidico; 13: Playa Chica; 14: Cura; 15: Cucao; 16: Quilanlar.

Filled circle shows the location of Antofagasta, where the historical SST data were measured

Table 1. Geographic location and sampling periods of studies reporting on demographic parameters of *M. donacium*. Studies carried out under the influence of El Niño (EN) events are indicated.

Code	Location	Latitude	Sampling period	EN	Reference
1	Santa María del Mar	12° 04' S	12-1980 to 09-1982	X	Arntz et al. 1987
2	Las Machas	18° 26' S	12-1997 to 04-1998	X	Jerez et al. 2008b
2	Las Machas	18° 26' S	12-1996 to 10-1997		Pérez 2008
3	Hornitos	22° 54' S	05-2005 to 04-2007	X	This study
4	Los Choros	29° 16' S	01-1998 to 01-1999	X	Jerez et al. 2008b
5	Peñuelas	29° 50' S	06-1993 to 07-1994		Ariz et al. 2008
5	Peñuelas	29° 50' S	08-1994 to 08-1995		Jerez et al. 2008c
6	Coquimbo	29° 53' S	12-1996 to 10-1997		Pérez 2008
7	Longotoma	32° 22' S	08-1994 to 08-1995		Jerez et al. 2008c
8	La Ligua	32° 24' S	08-1969 to 11-1970		Tarifeño 2008b
9	Ritoque	32° 52' S	06-1993 to 07-1994		Ariz et al. 2008
9	Ritoque	32° 52' S	08-1994 to 08-1995		Jerez et al. 2008c
10	Putú	34° 59' S	12-1996 to 10-1997		Pérez 2008
11	Punta Morguilla	37° 44' S	08-2005		Hernández et al. 2008
12	Quidico	37° 44' S	12-1996 to 10-1997		Pérez 2008
13	Playa Chica	37° 59' S	09-2005 to 11-2005		Hernández et al. 2008
14	Cura	38° 08' S	10-2005 to 11-2005		Hernández et al. 2008
15	Cucao	42° 35' S	09-2000 to 08-2001		Rubilar et al. 2008a
16	Quilanlar	43° 23' S	10-2000 to 08-2001		Rubilar et al. 2008a

Individual growth

Length frequency distribution data were fitted to a von Bertalanffy growth function (VBGF), following a three-step procedure: (1) the Bhattacharya method and a separation index > 2 was used as criterion to separate contiguous normal components of monthly length frequency distributions grouped by 4 mm (Gayanilo and Pauly, 1997). (2) The resulting mean lengths and standard deviation series representing population cohorts were linked using the Fisat II software to produce size-increment data pairs. (3) The data were fitted to a seasonal VBGF using the method developed by Appeldoorn (1987), which rearranges the VBGF to size increment data pairs:

$$L_2 = L_\infty \left\{ 1 - \left(1 - L_1 / L_\infty \right) e^{-K[(t_2 - t_1) - C \sin(2\pi(t_1 - t_s)) / 2\pi + C \sin(2\pi(t_2 - t_s)) / 2\pi]} \right\} \quad (2)$$

where K is the curvature parameter (yr^{-1}), L_∞ is the asymptotic length (mm), C is the amplitude of the growth oscillation (yr^{-1}), t_s the starting point of oscillation C , L_1 is the length at the beginning and L_2 the length at the end of the time interval $t_2 - t_1$. Equation 2 was fitted using an iterative, least-square, non-linear regression routine using the quasi-Newton algorithm to estimate standard errors for the parameters. Finally, the growth performance index phi prime ($\Phi' = 2 \log L_\infty + \log K$; Brey 2001) was calculated to allow for growth comparisons.

Mortality

Total mortality Z (year^{-1}) was calculated by the single negative exponential model:

$$N_t = N_0 e^{-Zt}, \quad (3)$$

where t is the time and N_0 is the number of individuals at $t = 0$, and the length converted catch curve (Pauly 1983). The lengths of pooled length–frequency samples were converted into ages using the parameters of the VBGF:

$$N_i / \Delta t_i = N_0 e^{-Zt_i} \quad (4)$$

where N_i is the number of individuals in length class i , Δt_i is the time required to grow through this size class and t_i is the age of the middle length class i . For each year mortality was calculated separately by linear regression analysis:

$$\log_e(N_i / \Delta t_i) = a + bt_i; \quad Z = -b \quad (5)$$

Productivity

The mass specific growth rate method (Crisp 1984) was used to calculate total annual somatic production P (g AFDM $\text{m}^{-2} \text{year}^{-1}$) using δ , the pooled length–frequency data, the VBGF parameters and the length–mass relationship (Eq. 1):

$$P = \sum \delta_i Mi Gi \quad (6)$$

where δ_i is the mean abundance in length class i , Mi the mean body mass in length class i and Gi , the mass-specific growth rate:

$$Gi = bK[(L_\infty / Li) - 1] \quad (7)$$

where b is the exponent of the length–mass relationship (Eq. 1), K and L_∞ are parameters of the VBGF and Li is the mean length in length class i . The annual mean biomass \bar{B} (g AFDM m^{-2}) of the population was estimated as:

$$B = \sum Ni Mi \quad (8)$$

Finally, productivity was calculated as the ratio between P and \bar{B} (Eq. 6 and 8).

Data compilation and modelling of biogeographic patterns

Information on demographic parameters of *M. donacium* from a wide range of sources (Table 1) corresponding to 16 sandy beaches (Table 1, Fig. 1) between Santa María del Mar (Peru, 12° 04' S) and Quilanlar (Southern Chile, 42° 23' S) were compiled, thus covering almost the entire species distribution range. These data, including the corresponding details on methods and sampling design, were archived in the open-access library PANGAEA (Publishing Network for Geoscientific & Environmental Data [www.pangaea.de]). For the present analysis, only estimations of growth parameters derived from studies with monthly samples taken over at least 1 yr were included. When more than one-year data were available, annual estimations were taken as independent entries. Biogeographical patterns were defined using latitude (centesimal units) as independent variable and population parameters (mean annual abundance, growth performance, mortality and productivity) as dependent variable. The relationship between biotic and abiotic variables was modelled by linear and non-linear fitting procedures, selecting the model with the best goodness of fit. To assess trend changes related to EN, the parameter “ b ” (slope) of the EN and non-EN regressions were compared using t -Student tests (Zar, 1999). A common regression line/curve was calculated when no statistical differences were found.

RESULTS

Population dynamics of *M. donacium* at Hornitos

A weak EN episode occurred between August 2006 and January 2007 confirmed by the ONI for the El Niño 3.4 Region (NOAA/CPC; Fig. 2). However, this event was not reflected in higher SST at Hornitos. Indeed, between October 2006 and April 2007 SST showed lower values compared to the historical (1980-2006) SST off Antofagasta, located 60 km south of Hornitos (Fig. 2). Abundance of *M. donacium* showed strong intra- and interannual variations, which were significantly correlated with the beach slope (Table 2). Strong differences were observed in most of the population parameters estimated for both years at Hornitos (Table 3).

Table 2. Results of the Spearman-rank correlation analysis between abundance of *Mesodesma donacium* and environmental parameters (sea surface temperature SST, salinity, Oceanic Niño Index ONI, Chlorophyll *a*, beach slope) of Hornitos, northern Chile. N = 24; Significant relationship ($P < 0.05$) highlighted in bold.

Parameters	Spearman R	t test	p-level
Abundance & SST	-0.117	-0.555	0.584
Abundance & Salinity	0.153	0.726	0.475
Abundance & ONI	-0.338	-1.686	0.106
Abundance & Chl <i>a</i>	0.159	0.757	0.457
Abundance & Beach slope	-0.626	-3.766	0.001

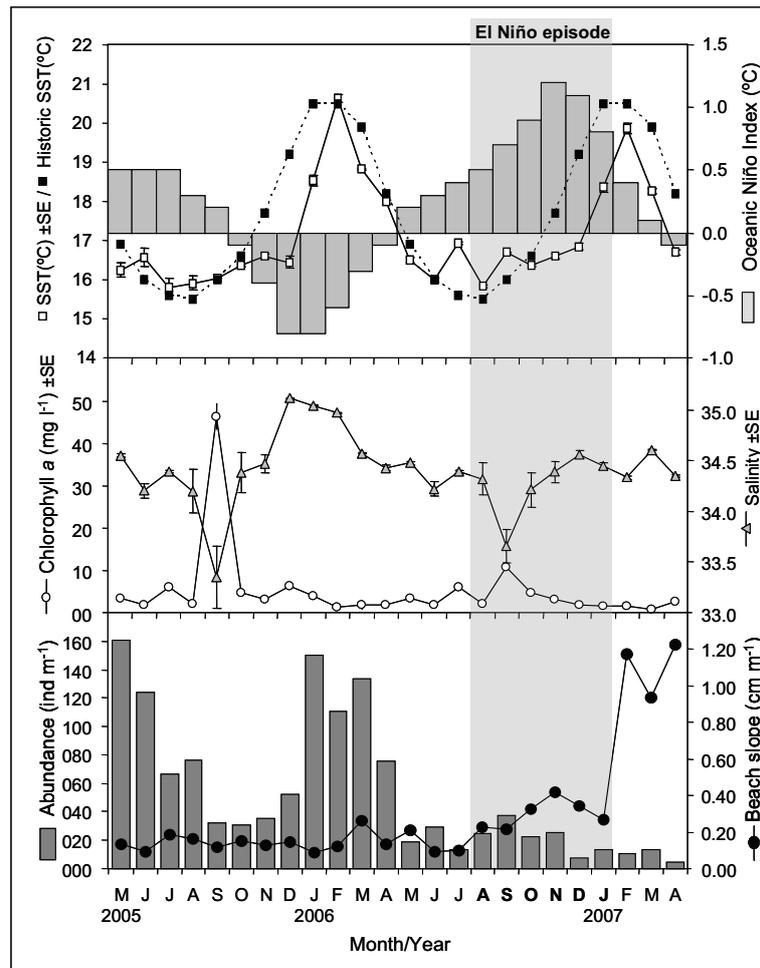


Figure 2. Monthly variability of environmental parameters (sea surface temperature SST, Oceanic Niño Index, Chlorophyll *a*, salinity, beach slope) and abundance of *Mesodesma donacium* off Hornitos (northern Chile) between May 2005 and April 2007. Historic sea surface temperature of the period 1980-2000 for Antofagasta (CENDHOC-Chile). Designation of El Niño episode (grey background area; August 2006 to January 2007) is based on a threshold of $+0.5^{\circ}\text{C}$ for the Oceanic Niño Index (see methods) during at least 5 consecutive months. Data available from www.cpc.noaa.gov/products

Mean annual abundance was five fold higher during the first year. Likewise, growth performance and mortality were moderately higher for the first year of study. Mean annual somatic production and biomass were three, respectively, ten

times higher during the first year in comparison to the second year (EN), productivity was rather similar between years. Interannual changes in abundance and somatic production (Figure 3) were mainly due to a strong reduction in recruits (SL = ~2 – 25 mm) and adults (SL = ~75 – 95 mm), while abundance and somatic production of medium sized clams remained relatively unchanged.

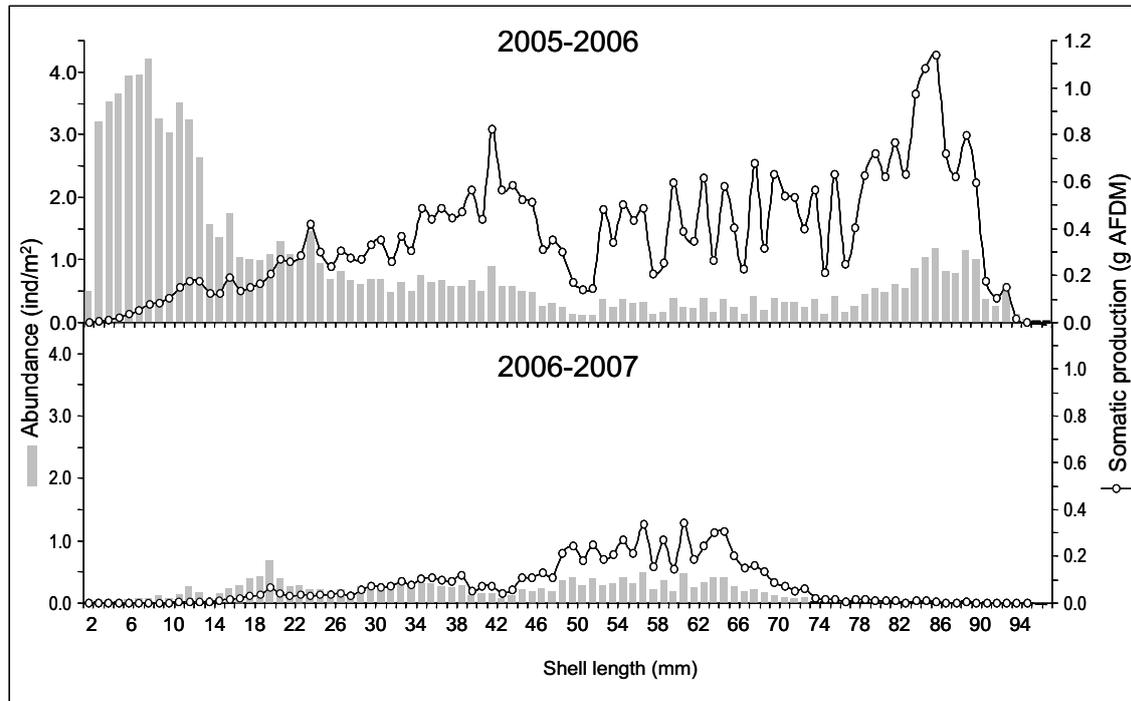


Figure 3. Mean abundance and annual somatic production of *Mesodesma donacium* in 1-mm length classes during May 2005-April 2006 and May 2006-April 2007.

Latitudinal patterns

All assessed population features of *M. donacium* showed statistically significant latitudinal patterns (Table 3).

Table 3. Estimation of population dynamic parameters of *Mesodesma donacium* from Hornitos (Northern Chile) between May 2005 and April 2007.

Parameter	2005-2006	2006-2007
	Estimation (\pm SE)	Estimation (\pm SE)
Mean annual abundance (δ ; ind m ⁻²)	86.339 (\pm 6.056)	17.389 (\pm .441)
Curvature parameter (K ; y ⁻¹)	0.506 (\pm 0.075)	0.307 (\pm 0.056)
Asymptotic length (L_{∞} ; mm)	94.279 (\pm 6.539)	90.469 (\pm 10.287)
Amplitude (C ; yr ⁻¹)	0.123 (\pm 0.051)	0.134 (\pm 0.052)
Starting point of oscillation (t_s)	0.961 (\pm 0.091)	0.814 (\pm 0.124)
Growth performance (Φ')	3.653	3.401
Total mortality (Z ; y ⁻¹)	0.556	0.712
Annual somatic production (P ; AFDM g m ⁻²)	34.934	12.109
Annual mean biomass (\bar{B} ; AFDM g m ⁻²)	78.912	7.325
Productivity (P/\bar{B} ratio)	0.443	0.605

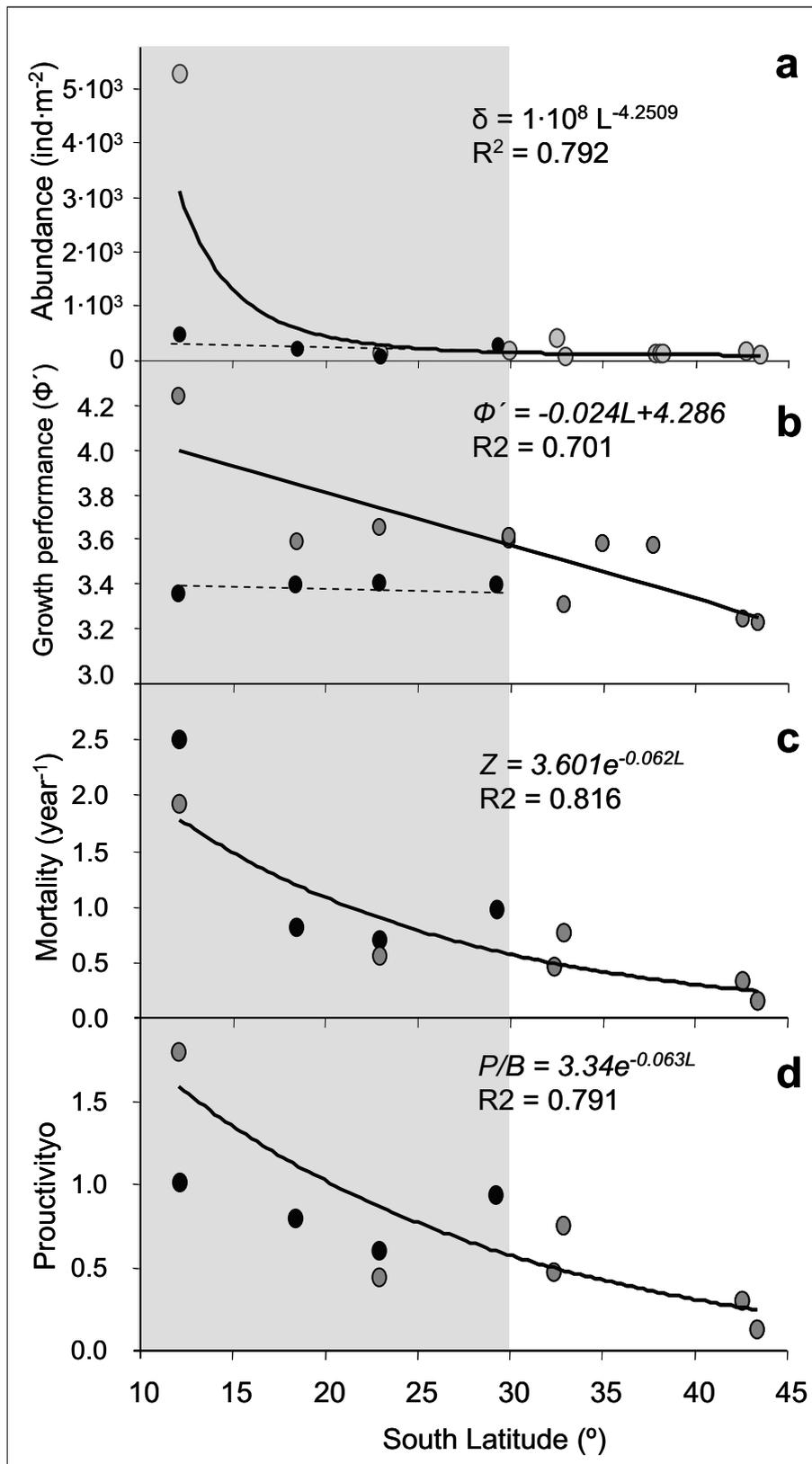


Figure 4. Relationship between latitude (centesimal units) and (a): abundance; (b): growth performance; (c): mortality and (d) productivity ratio. Statistical results of model fitting and sample size are given in Table 2. Black dots correspond to estimations of population parameters during El Niño events. Grey area corresponds to the latitudinal range where mass mortality events have been reported in the literature (Arntz et al. 1987, Quiroz & Barriga 1998, Aburto & Stotz 2003, Thiel et al. 2007)

Abundances were higher in northern populations and were significantly decreasing towards the southernmost limit of the geographical distribution (Fig 4a). This pattern was best described by a power regression model. The slope of the observed trend showed significant differences with the trend observed during EN events ($t_{10} = 1.875$; $P = 0.045$). Abundances were strongly reduced in northern populations while central populations remained almost unaffected. Similarly, growth performance of *M. donacium* decreases linearly with increasing latitude (Fig 4b), and a significant trend shift ($t_{10} = 2.009$; $P = 0.036$) was observed during EN years. Mortality of *M. donacium* decreased with increasing latitude, the pattern being best fitted to an exponential model (Fig 4c, Table 3). No significant differences were found between the slope of EN and non-EN regressions ($t_5 = 1.533$; $P = 0.186$), therefore, a common regression was fitted for all estimations. Productivity of *M. donacium* also decreased exponentially with increasing latitude (Fig 4d, Table 3) and again no significant differences were found between the slope of EN and non-EN regressions ($t_5 = 1.055$; $P = 0.253$) allowing a common regression to be fitted.

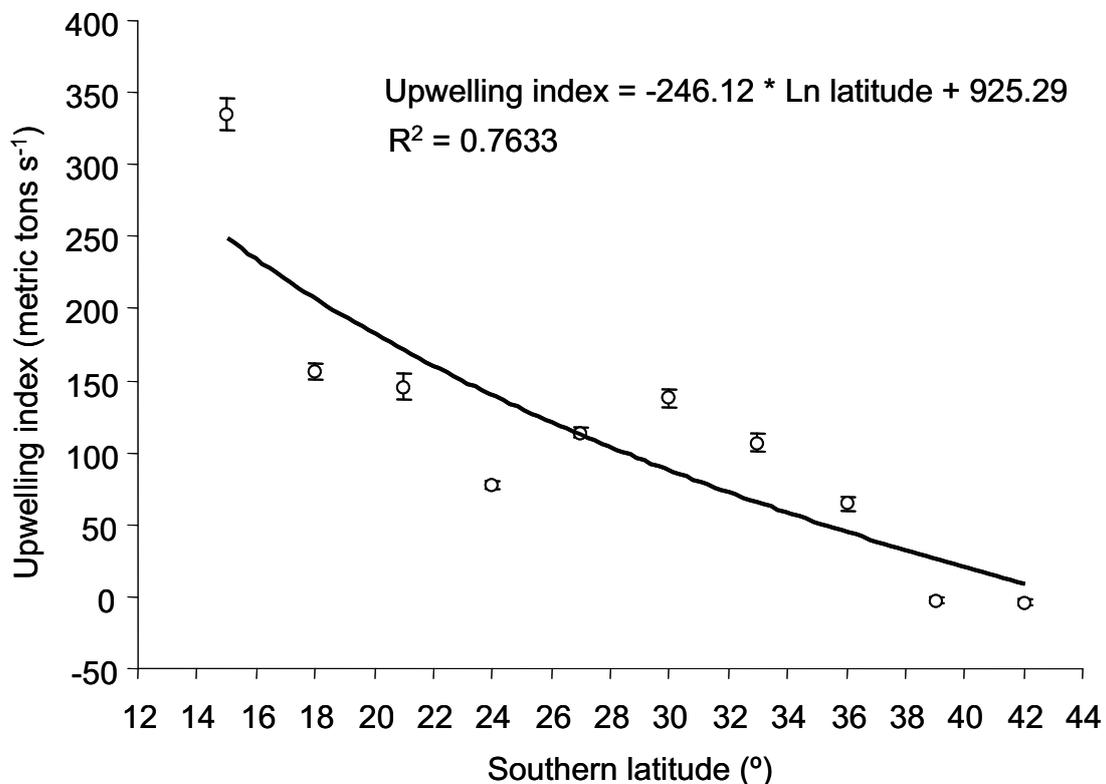


Figure 5. Monthly-averaged Upwelling Index of the Humboldt Current System at 10 locations from 15° S to 42° S (period: 1981-2001) as reported by NOAA/Pacific Fisheries Environmental Laboratory. Data available from <http://www.pfeg.noaa.gov>

Table 4. Results of linear and non-linear regression analyses and associated statistics between population parameters of *Mesodesma donacium* and latitude (L, centesimal units). δ : abundance; Φ' : growth performance index; Z: total mortality; P/\bar{B} : Productivity. Significant relationships ($P < 0.05$) are highlighted in bold.

Parameter	Model	a (\pm SE)	b (\pm SE)	R ²	N	P
δ	$\delta = aL^b$	$4 \times 10^9 (\pm 3.1 \times 10^{10})$	-5.55 (± 1.471)	0.792	11	0.003
Φ'	$\Phi' = a - bL$	4.286 (± 0.176)	0.024 (± 0.005)	0.701	10	0.002
Z	$Z = ae^{bL}$	5.372 (± 1.650)	-0.078 (± 0.019)	0.816	10	0.011
P/\bar{B}	$P/\bar{B} = ae^{bL}$	2.247 (± 0.744)	-0.047 (± 0.016)	0.587	10	0.016

DISCUSSION

Population dynamics of *Mesodesma donacium* at Hornitos

A weak EN episode occurred at the end of the study period (August 2006–January 2007). Positive SST anomalies are a major feature of EN events in the Humboldt Upwelling System (e.g. Urban 1994, Arntz et al. 2006). However, SST at Hornitos did not show consistent departures from historical records. Likewise, no interannual differences were observed in salinity and Chl *a*. Abiotic changes caused by EN in nearshore habitats mainly depend on the strength of the event (Arntz et al. 2006), hence EN 2006/2007 was probably not strong enough to induce detectable changes in those parameters.

In contrast, strong interannual differences in beach slope were observed at Hornitos, with steeper slopes during the second year (Fig. 2). This was the only environmental parameter recorded, which showed a significant correlation with the general drawback in population abundance at Hornitos. Strong changes in beach slope were related to repeated storms, which caused high swells and considerable damage in several northern Chilean locations during and after the EN episode. This increased strength and frequency of storms probably caused the negative effects observed in growth performance, mortality, somatic production and the strong reduction in abundance during the second year, as suggested by the observation of recently dead individuals, mainly small juveniles and adults, found at Hornitos. EN 2006/07 may be linked to the repeated storms causing the changes in beach slope, as suggested by the weak correlation between the ONI and beach slope (Spearman $R = 0.384$; $p = 0.063$). This relationship has been reported elsewhere: the number and strength of high swell events impacting California's coast display an important interannual variability,

which correlates well with EN events (Seymour 1996, Storlazzi & Griggs 2000). Long-term data series off northern Chile are required to assess this relationship.

Towards the end of the present study period at Hornitos, the population consisted mainly of medium-size clams, whereas recruits and adults were almost lacking, implying an age-related mortality pattern (Fig. 3). This pattern may result from abiotic and biotic factors affecting selectively different population size-classes. *M. donacium* shows a clear across-shore spatial segregation pattern, with recruits and juveniles inhabiting mainly the intertidal, while adult clams are restricted to the shallow subtidal (Tarifeño 1980, Jaramillo et al. 1994, Riascos et al. 2008a). As a consequence, stronger swell during the EN year mainly affected juvenile clams. On the other hand, *M. donacium* is commonly infested by the parasitic polychaete *Polydora biocipitalis* (Blake 1983, Moreno et al. 2006). Riascos et al. (2008a) showed that at high infestation levels – which were only observed in older clams – the infestation may affect body condition, growth and burrowing time. Thus, older, heavily infested clams are expected to be much more sensitive to environmental stress, even in the subtidal. This prediction was confirmed by the fact that recently dead clams observed during samplings in the second year of this study were infested in the vast majority. In conclusion, populations of *M. donacium* at the northern range boundary seem highly vulnerable to interspecific interactions and environmental stressors possibly related to weak EN events.

Latitudinal patterns

Brown's (1984) principle is a classical, widespread concept in biogeography, which predicts that species are most abundant in the centre of their range and decline in abundance toward the range edges (Brown 1984, Curnutt et al. 1996, Sagarin et al. 2006). However, this relies on two assumptions: (1) individuals are best matched to environmental conditions near the range centre; and (2) local population density reflects individual success. Therefore, higher growth and productivity and lower mortality should be expected at the range centre.

In contrast, the observed latitudinal trends in population dynamics features of *M. donacium* (Fig. 3) are in line with recent evidence showing that large-scale demographic patterns of coastal invertebrates often do not match Brown's principle (e.g. Sagarin & Gaines 2002, Gilman 2005, Sagarin et al. 2006). The

present results indicate that abundance and individual success (in terms of growth performance and productivity) are highest at the northern distributional limit (Fig. 4), precisely at the site, where adverse environmental conditions recurrently lead to strong decreases in growth performance and ultimately to mass mortality events. As mortality is a density-dependent demographic process (e.g. Rumrill 1990, Lambers et al. 2002), the higher mortality observed towards lower latitudes does not necessarily reflect a reduction of individual success in northern populations. Given the typical “boom-and-bust” fishery of this clam (Thiel et al. 2007) denser populations support much more fishing effort, which potentially biases mortality estimations.

Which are the environmental and/or biological factors driving the observed biogeographical trends in population dynamics of *M. donacium*? Given that temperature commonly varies with latitude, range boundaries and large-scale demographic patterns of coastal invertebrates are often related to temperature gradients (e.g. Gaston 2003, Cardoso & Defeo 2004, Defeo & McLachlan 2005). For the present study site, temperature alone is unlikely to influence the observed patterns due to the persistent northward flow of the Humboldt Current transporting cool subantarctic water masses along the Chilean and Peruvian coast (e.g. Camus 2001, Arntz et al. 2006, Thiel et al. 2007). As a result, sea surface temperature varies little (i.e. mean annual SST = 15.79 °C at Ilo [Peru, 17° 39 S] and 12.7 °C at Puerto Mont [Southern Chile, 41° 29 S]) and does not show a clear latitudinal pattern (Riascos, unpublished). In contrast, coastal upwelling, the characteristic oceanographic process in the HCS, shows clear spatial-temporal patterns and has been identified as a factor linked to large spatial changes in productivity and biomass in Chilean sandy beaches (Jaramillo et al. 2001).

Although upwelling centres are interspersed by stretches of coastline with sporadic and less intense upwelling (Thiel et al. 2007), on a larger scale upwelling strength substantially increases with latitude (Fig. 5). Moreover, upwelling changes from being mostly continuous (aseasonal) at lower latitudes to a more seasonal pattern in southern-central Chile (Thiel et al. 2007). Therefore, although in a long term (decadal, interdecadal) scale northern shallow sandy bottoms of the HCS may represent a recurrently changing environment related to ENSO, in shorter spatial scales (years) they represent more stable and highly

productive environments. Thus, the increased upwelling strength in low latitude areas and the narrow thermal window of this species (Riascos et al. unpublished) may explain the higher abundance, growth performance and productivity of northern *M. donacium* populations and the mass mortality events that those populations experience during strong EN events.

ACKNOWLEDGEMENTS

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5 General discussion

A detailed discussion of the specific topics covered in this work was provided in the publications of the previous chapter. The following chapter will provide an integrative discussion of the main results of this study.

5.1 Chemical labelling as a tool for *M. donacium* growth studies

The incorporation of chemical labels in calcifying structures is being used recently in studies aiming to understand growth cycles and the use of shells as high resolution archives of the many different environmental factors that may influence physiology and shell growth (e.g. Thébault et al. 2007, Lazareth et al. 2007, Thébault et al. 2007). As the use of this tool relies on the assumption that the stain does not significantly affect the growth rate, a species-specific validation of this tool is needed. In line with studies comparing several chemicals, calcein was the best stain to mark shells of *M. donacium* with non detectable toxic effects (Publication 1). The calcein labelling proved useful in accurately assessing short term growth responses of *M. donacium* exposed to different infestation levels of *P. biocipitalis* (Publication 2) and to different salinity and temperature regimes (Publication 4). However, the potential of this method goes beyond these applications and will be particularly useful to study the environmental drivers of growth rates in field conditions using sclerochronological approaches. The short immersion time and low concentration required to successfully staining *M. donacium* shells (Publication 1) allowed to carry out a preliminary *in situ* mark-recapture experiment in Hornitos. In this study, 650 clams were marked and five clams were recaptured after 1 to 4 months, a recapture rate normal for clams living in highly dynamic sandy beach environments (e.g. Dugan and McLachlan 1999, Laudien et al. 2003). These specimens can be used as high-resolution archives of skeletal growth and its relation with environmental variability at Hornitos in the last few years. Although sclerochronological methods have been used already to assess the potential of *M. donacium* for paleoceanographic SST reconstructions (Carré et al. 2005), these reconstructions were based on the assumption of fortnight cycles of biomineralization. Mark-and-recovery experiments are the only way to assign exact calendar dates to portions of the shell and thus to validate assumptions about cycles of biomineralization in this

kind of studies (Schöne et al. 2003). Figure 5.1 depicts the potential of calcein labelling to introduce artificial marks allowing age validations of growth increment periodicity.

Conclusion:

Calcein labelling is a non-deleterious, practical and accurate tool for short term growth estimations of *M. donacium*. The validation of this method allows for further applications in sclerochronological studies.

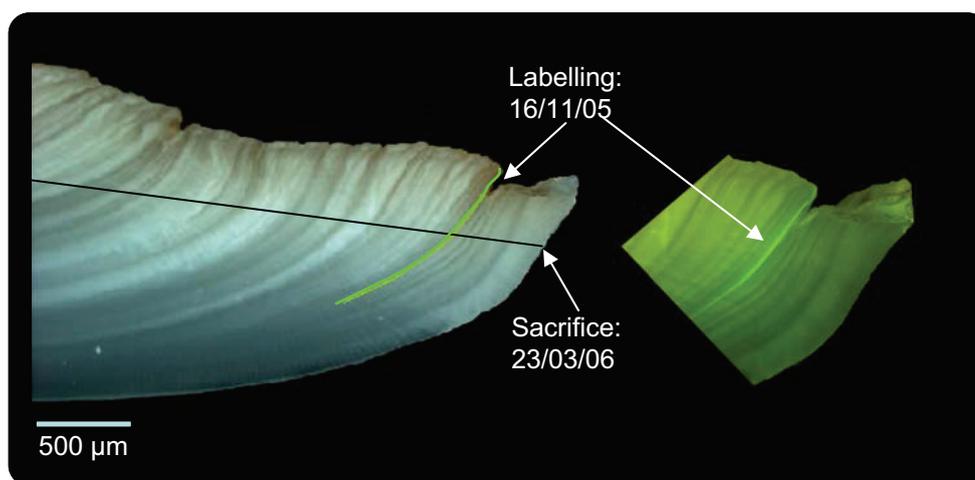


Fig. 5.1 Calcein labelling (fluorescent green line) of a *M. donacium* shell enabling assignment of exact calendar dates to shell portions for the interpretation of growth increment cycles.

5.2 Biotic interactions affecting *M. donacium* through space and time

5.2.1 Impact of the infestation at Hornitos, northern Chile – The prevalence of the infestation by *P. biocipitalis* on *M. donacium* follows a size-specific pattern in which larger clams show almost 100% prevalence (Fig. 4.1). The infestation increases mainly during spring and autumn and affects body condition, growth rate and burrowing ability of the large, heavily infested clams (Fig. 4.2-4.3). Given that Chilean *M. donacium* perform an ontogenetic habitat shift from the intertidal to the subtidal (Tarifeño 1980, Jaramillo et al. 1994, Publication 2), it can be assumed that the infestation is restricted to animals inhabiting the subtidal. Thus, under normal environmental conditions the infestation only produces sublethal effects in adult clams inhabiting the subtidal zone. Based on these patterns, it was predicted that these effects may be biologically significant in terms of survival under adverse environmental change, given that stress lowers resistance rendering heavily infested clams more prone to mortality (Publication 2). This

prediction was confirmed by recent field data from Hornitos (Fig 4.4, Publication 5): large clams, which were heavily infested by *P. biocipitalis* died, coinciding with a significant increase in wave action during EN 2006-2007. In contrast, the few adult survivors were exclusively non-infested clams.

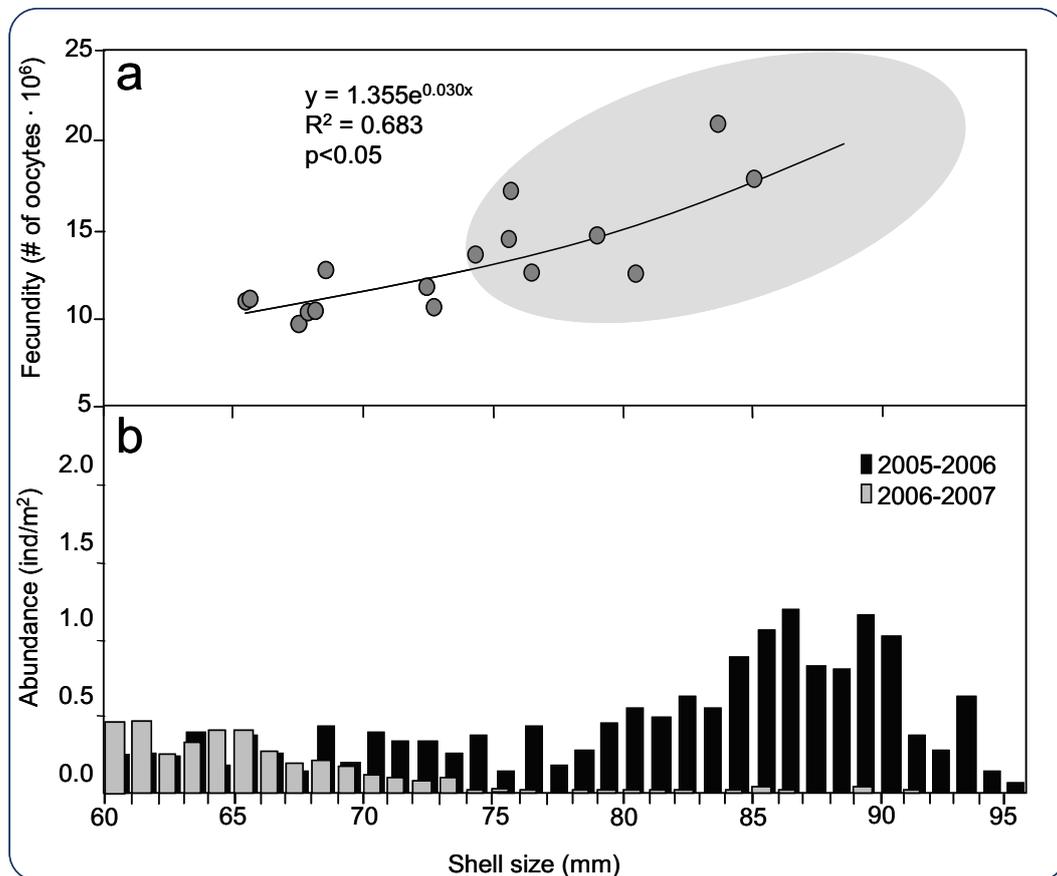


Fig. 5.2a Relationship between fecundity and shell size of *M. donacium* (after Rubilar et al. 2001); **b** abundance of shell sizes of *M. donacium* during two years of sampling at Hornitos, northern Chile. Grey ellipse represents the lost fecundity during the second year due to mortality of larger specimens (>76 mm).

Rubilar et al. (2001) found that the relationship between fecundity and shell size of *M. donacium* in southern Chile can be best described by an exponential function (Fig. 5.2a). Although fecundity may vary with latitude and/or other environmental factors, the relationship between fecundity and shells size is expected to be the same. Therefore, from the observed abundance of shell sizes (Fig. 5.2b), the average fecundity during 2005-2006 corresponds to $7.672 \cdot 10^6$ oocytes·m⁻² whereas during 2006-2007 it only corresponded to $0.544 \cdot 10^6$ oocytes·m⁻². This implies that mortality of larger clams caused a loss of overall fecundity amounting 92.9%.

Conclusion:

The parasite *P. biocipitalis* induces a background stress level on *M. donacium*, which, even under slightly adverse environmental conditions, causes a selective mortality with consequences on lower fecundity and probably recruitment. These effects may delay or prevent the northward recolonization after strong EN.

5.2.2 Role of the infestation in mortality events – The prevalence of infestation shows a south-north gradient along the geographic distributional range of *M. donacium*. Prevalence varies from zero or no infestation at 42°S (Sato-Okoshi and Takasuka 2001); “occasional” at 33°S (Tarifeño 1980); 16.7 % at 30°S (Olivares 2006) to 47.26 % at Hornitos (23°S, this study). Although prevalence might not be calculated in unpaired shells found at 12°S in shell mounds at southern Lima, 91% of them were infested, suggesting that prevalence is higher than that of Hornitos (personal observation). This pattern may be the result of large-scale differences in SST and host’s abundance. Even when SST does not show a strong latitudinal gradient, it is higher toward lower latitudes (see Publication 4) and abundance of *M. donacium* shows a strong latitudinal pattern of increasing abundance towards lower latitude (see Publication 5). SST has been shown to influence the abundance of polydorids and the intensity of their infestations as increased SST results in faster embryonic growth, earlier release from capsules into the plankton and induction of asexual reproduction (Davis 1967, Blake 1969a, Dorset 1961, Tinoco-Orta and Cáceres-Martínez 2003). In contrast, spionids are generally affected by cool La Niña episodes in the northern Chilean coast (Quiroga et al. 1999).

Conclusion:

Three factors may act synergistically to drive northern populations to collapse during EN events: i) “background stress” or sublethal effects induced by the infestation of *M. donacium* by *P. biocipitalis*, which enhances the vulnerability of clams to thermal stress; ii) SST anomalies, which affect the performance of *M. donacium* and enhance the infestation ability of *P. biocipitalis*, and iii) the high abundance of *M. donacium*, which further foster the infestation ability of the latter.

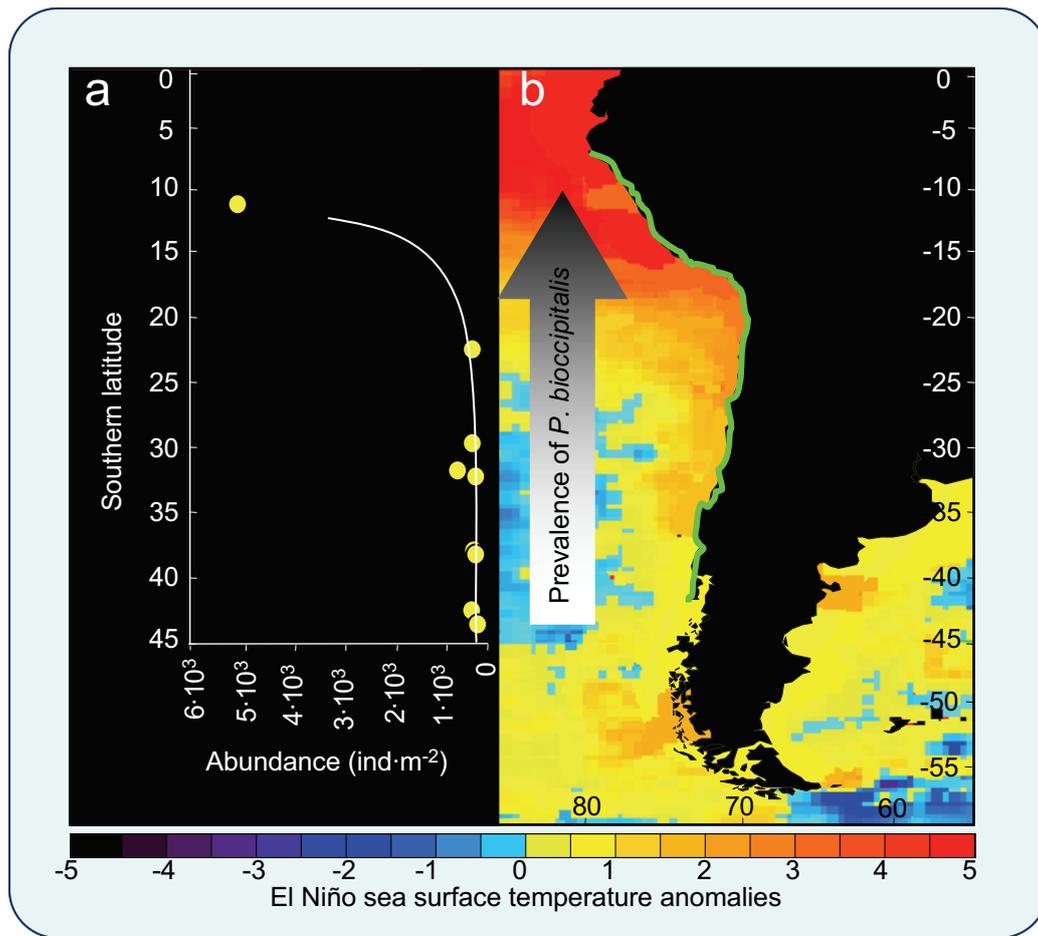


Fig. 5.3 a Abundance variability of *M. donacium* along latitude; b sea surface temperature anomalies (July 12th 1997) in western South America at spatial resolution 0.5 degree (adapted from NOAA/NEDSIS, available from <http://www.pmel.noaa.gov>). The grey arrow represents the increasing gradient of prevalence of the infestation of *M. donacium* by *P. biocipitalis*. The green line shows the geographic distribution of *M. donacium*.

5.2.3 Implications for the persistence of the *M. donacium* stock – Despite a recent review on Chilean boring spionid polychaetes reporting *P. biocipitalis* as a non-indigenous species (Moreno et al. 2006), three lines of evidence indicate that this spionid has been associated to *M. donacium* since at least the Middle Pleistocene (~330 thousand years, Publication 3), thus having implications for the long-term persistence of its host.

First, the infestation produces a species-specific blistering pattern in shells of *M. donacium*, whose structural features are identical among recent and fossil shells deposited in marine terraces from central and northern Chile (Publication 3). Second, two independent studies on the association between *P. biocipitalis* and *M. donacium* suggest a certain degree of co-evolution of the species life history traits, which are characteristic of parasitic relationships: Infestation by this

worm increases during periods of poor condition of *M. donacium* (Riascos et al. 2008a) and the reproductive strategy of *P. biocipitalis* is closely adapted to the habitat and behaviour of its host (Olivares 2006). Third, there is no evidence on vectors and introduction pathways into the Chilean-Peruvian coast. In addition, although the geographic distribution of *P. biocipitalis* is discontinuous along the western coast of the Americas, it cannot be considered incongruous and it rather reflects a common distribution pattern among spionids. Finally, while no reliable estimations of the paleo-prevalences were possible from the fossil shells, they seem similar to the prevalences observed nowadays in central and northern Chile and the size range of infested recent and fossil shells is nearly the same.

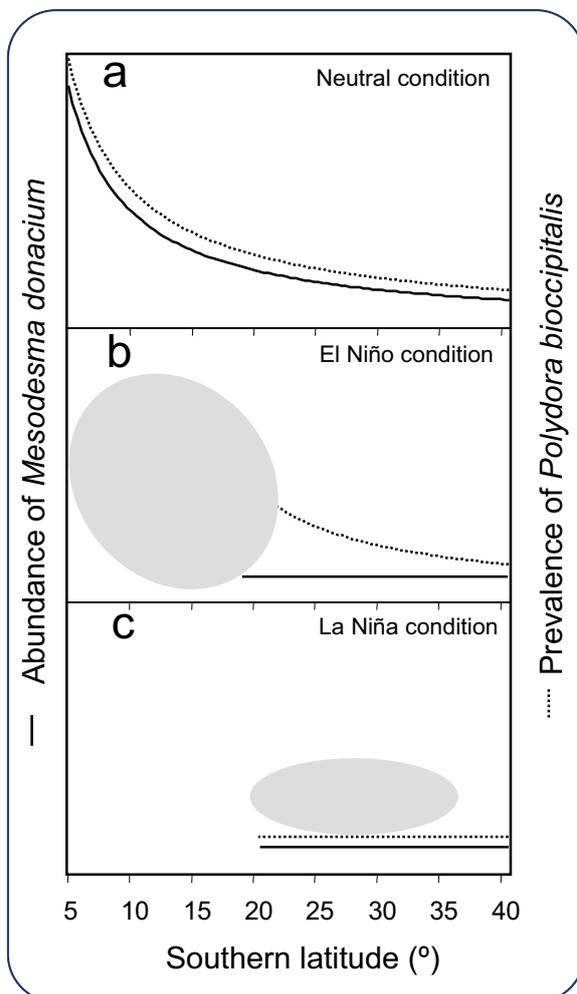


Fig. 5.4 Hypothetical model of the dynamics of the parasitic association between *M. donacium* and *P. biocipitalis* during a: neutral conditions; b: El Niño; c: La Niña. Grey areas represent the spatial scale where main effects take place.

The long-term co-existence of these species in the Chilean and Peruvian coast implies that the dynamics of this parasitic association have been affected by EN and LN since ENSO became a major influence on the western coast of South America in the Holocene (Ortlieb et al. 2000, Maldonado and Villagrán 2002). From the findings on the spatial patterns in the prevalence of infestation by *P. biocipitalis*, the abundance of *M. donacium*, and the possible effects of SST anomalies for the two species, an hypothetical model of the dynamics of the association is shown in Fig. 5.4: Under neutral conditions, both, abundance of *M. donacium* and the prevalence of *P. biocipitalis* increase northwards (Fig. 5.4a). During EN, anomalous higher SST, the clam's high abundance developed in neutral conditions and the increased

infestation ability of the polychaete lead to mass mortality events of both species at northern beaches (Fig. 5.4b). However, some populations surviving EN may suffer increased infestation, which may be subsequently reduced by anomalous low SST during LN (Fig. 5.4c). Of course, the described dynamics would largely depend on the strength and frequency of occurrence of EN-LN events and further studies will be needed to validate or improve this hypothetical model.

Conclusion:

Given the contrasting thermal sensibility of *P. biocipitalis* and *M. donacium*, the host-parasite interaction dynamics seem to be modulated by the EN-LN cycle

5.3 Main abiotic factors affecting *M. donacium* through space and time

The results of this study show that physical properties of the HCUS influence population features of *M. donacium* at different temporal and spatial scales. Major historical events on the western coast of South America seem relevant to explain the modern distribution and dominance of *M. donacium*.

5.3.1 Sea surface temperature – Temperature affects everything that an organism does (Clarke 2003). As such, it is one of the most important environmental factors controlling the latitudinal distribution of marine benthic organisms (e.g. Defeo and Cardoso 2002, Cardoso and Defeo 2004). Despite its being at a low latitude, the HCUS is a cold-temperate ecosystem showing little latitudinal and seasonal SST variability because of the persistent cooling effect of upwelled water from below the thermocline (Rosenberg et al. 1983). As a consequence, seasonal SST variability seems not to play a determinant ecological role in coastal communities and populations (Urban 1994, Thiel et al. 2007), which seems also to be true for *M. donacium*. For instance, SST variability did not play the typical triggering role in the reproductive cycle of *M. donacium* (Publication 4). This is in line with findings on reproductive patterns of several marine invertebrates (e.g. *Perumytilus purpuratus*, *Nothochthamalus scabrosus*, *Chiton granosus*) from the HCUS, which rather seem related to primary productivity associated to upwelling centres (see Thiel et al. 2007 and references therein).

In contrast, SST interannual variability associated to EN has shown dramatic effects on *M. donacium* populations. This study confirms the low tolerance of this clam to increased temperature: 2.6°C above the normal summer SST in Hornitos significantly reduced growth and increased mortality. As SST anomalies associated to EN gradually increase towards lower latitudes (Arntz et al. 2006, Thiel et al. 2007, Camus 2008) mass mortality events of *M. donacium* observed in Peru and northern Chile can be chiefly explained by its low thermal tolerance.

The low upper thermal tolerance of *M. donacium* seems linked to its presumably southern origin. According to von Ihering (1907), the *Mesodesma* stock arrived to South America in either the middle or late Pliocene during a massive migration of Antarctic molluscan species. Under the influence of the cold Humboldt and Malvinas oceanic currents, this stock migrated northwards and subsequently underwent speciation (*M. donacium* and *M. mactroides*). Recent work on Antarctic mollusc fossil records does not provide support for Ihering's hypothesis (see Stilwell and Zinsmeister 1992). However, a southern origin of this genus seems plausible since it occurs with a number of other 'southern' taxa (e.g. *Concholepas*, *Xanthochorus*, *Priene*, *Crassilabrum*) in late Pliocene deposits from northern Peru (DeVries, personal communication). On the other hand, several dispersive processes in the Southern Ocean oceanic circulation may offer alternative explanations for the presence of southern taxa at the Chilean coast (Castilla and Guiñez 2000).

As a consequence of a Pliocene/Pleistocene mass extinction, *M. donacium* and other species with subantarctic affinity formerly scarce during the Pliocene became dominant in their corresponding biotope in the Pleistocene (Herm 1969, DeVries 1986, Rivadeneira and Market 2007). Although there is no direct paleoceanographic evidence, the development of the oxygen minimum zone, linked to the high productivity of the HCUS established during the mid to late Miocene (Ibaraki 1997, Tsuchi 1997, but see Camus 2001) seems to be related to the Pliocene/Pleistocene mass extinction (McRoberts and Newton 1995, Rivadeneira and Market 2007). This illustrates how long-term physical changes associated with the development of the cold HCUS may have influenced the northward expansion and the modern dominance of *M. donacium* along the western coast of South America.

Conclusion:

While the low seasonal variability of the SST seems not to play a determinant role in driving biological rhythms of *M. donacium*, at longer time scales SST variability strongly affects the population persistence and dominance.

5.3.2 Freshwater input – Although *M. donacium* inhabits open ocean beaches these beaches are usually watered by rivers, streams or estuaries. Freshwater

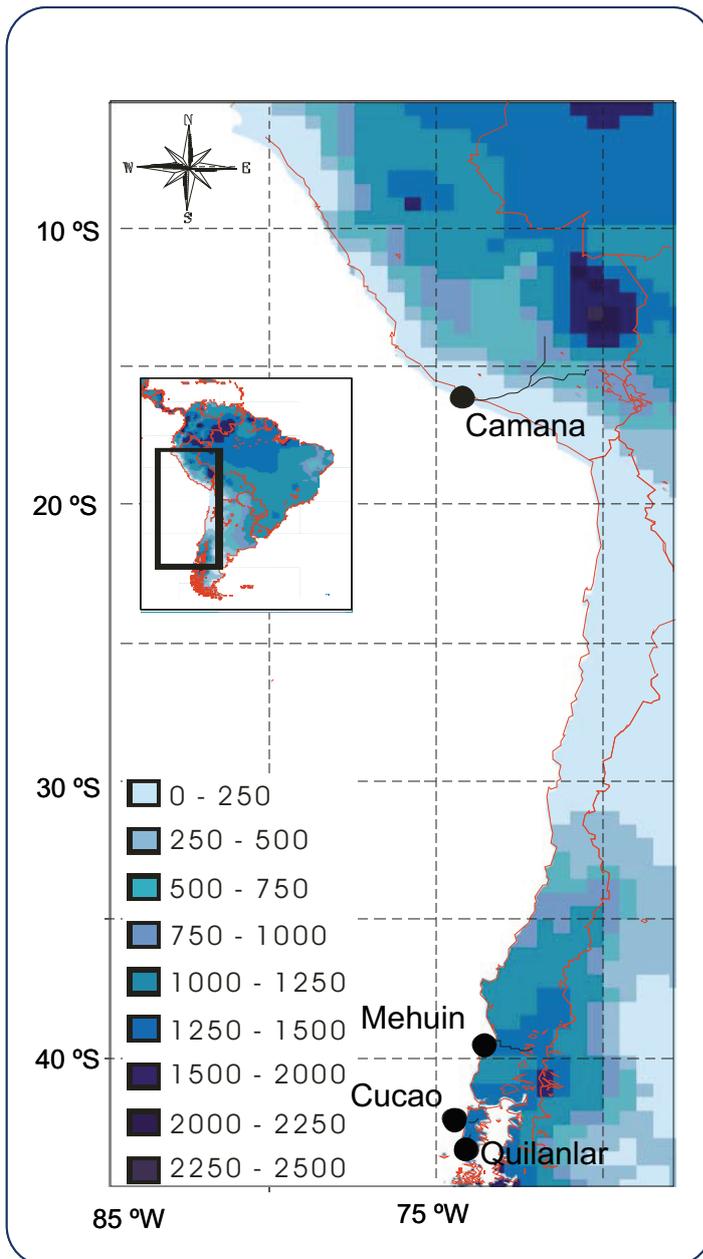


Fig. 5.5 Total annual precipitation (mm y⁻¹) in the Andean margin of Chile and Peru, with a spatial resolution of 30 min (adapted from Vörösmarty et al. 1998).

runoff brings about several physical and chemical changes that have profound effects on the character of coastal ecosystems (Kjerfve et al. 2001). It is also a major source of nutrients displaying a strong seasonal signal, which has the potential to influence biological processes of marine biota (e.g. Kjerfve et al. 2001, Medeiros et al. 2001, Riascos et al. 2006).

Freshwater input shows a well defined latitudinal gradient, mainly determined by large-scale hydrologic features along the Andean margin (Fig 5.5): in Peru and northern Chile, the coastal region is a narrow desert belt receiving almost no rain, although it is watered in the subsurface along river courses by runoff from melting snow of the high Andes. In contrast, the south-central Chilean coast receives

abundant precipitation, and a mountainous terrain provides large volumes of detritus through numerous short rivers. This seasonal and spatial variability in precipitation and river inflow showed significant correlations with the reproductive cycle of *M. donacium* along its geographic distribution, exemplifying the influence of primary productivity (i.e. food availability) in specific periods of the reproductive cycle (Publication 4). The cycle showed a general pattern consisting in a breeding season between (austral) winter and spring and a single spawning season between early spring and summer (Publication 4). Populations from Camaná, Mehuín, Cucao and Quilanlar showed departures from the general pattern: breeding and spawning seasons were longer at Camaná, Cucao and Quilanlar, whereas breeding was continuous and spawning biannual at Mehuín. Interestingly, those populations are located in areas receiving high precipitation rates, either directly (Mehuín, Cucao and Quilanlar) or through river basins from the high Andes (Camaná) (Fig. 5.5).

The influence of freshwater input on the reproductive cycle of *M. donacium* was particularly clear in Mehuín, at 39°26'S (Fig. 5.6). Nearshore salinity values calculated for 39°S latitude show a clear biannual-peak pattern, coinciding well and showing a significant correlation with the biannual spawning pattern (Publication 4). In contrast, SST showed the same pattern observed across latitude i.e. higher in summer and lower in winter. The observed pattern in nearshore salinity in Mehuín is related to the streamflow regime of rivers in southern Chile, which have a mixed pluvial-nival regime with one peak flow due to winter precipitation and another in summer due to snowmelt at higher altitude (Dávila et al 2002).

Located in the Atacama desert coast, Hornitos (~23°S) was the only sandy shore showing no river input. However, this beach is affected by submarine groundwater discharge in September, coinciding with the time when the frequency of mature and spawned clams starts to decrease and increase (respectively). Determining to what extent groundwater discharge at Hornitos is comparable with the relationship between freshwater input and the reproductive cycle is beyond the scope of this study, mainly because of the inherent difficulty of reliably measuring this water flux (Burnet et al. 2001). However, the significant increase of Chl *a* and the simultaneous reduction of salinity in September (Fig. 5.7) suggest that SGD may also influence primary productivity and hence the

reproductive cycle. This is in line with previous findings on the influence of SGD on local chemical budgets and biological process in the coastal ocean (Johannes 1980, Burnet et al. 2001).

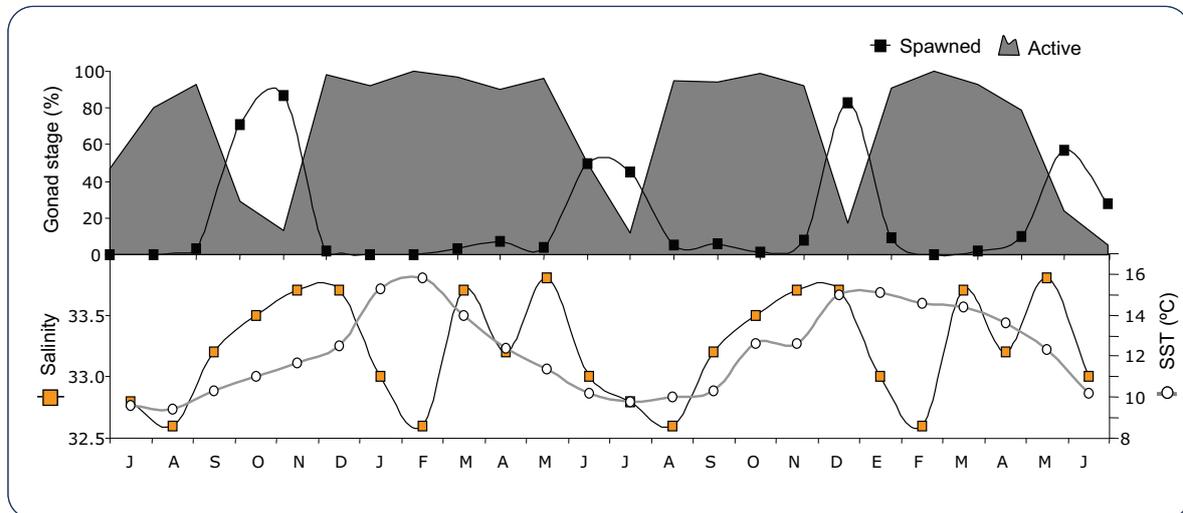


Fig. 5.6 a Frequency of active (mature) and spawned gonad stages of *M. donacium* in Mehuín (Rubilar et al. 2008); **b** Monthly mean salinity calculated for one degree interval of latitude (39°S; SHOA 1996) and historic (1985-2000) monthly mean SST in Corral station (39°52'S) (Data freely available from www.shoa.cl).

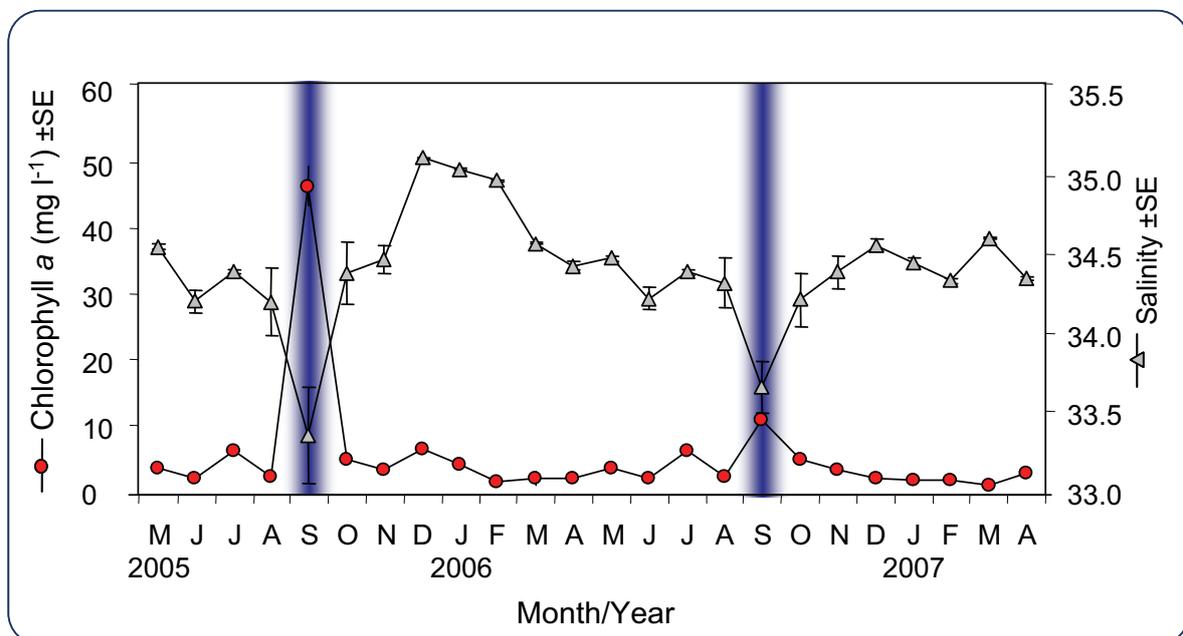


Fig. 5.7 Monthly Chlorophyll a concentrations and salinity at Hornitos, northern Chile. Blue bars indicate events of submarine groundwater seepage observed during samplings.

Finally, given the higher tolerance of juveniles to changing salinities (10-35) in comparison with adults (20-35), across shore differences in freshwater influence

may result in vacant areas near the river mouths suitable for spat and recruitment of juveniles. Spatial segregation between recruits and adults is a common feature of beach clams (McLachlan et al. 1996, Donn 1987); unfortunately, its ecological significance remains unknown. As recruitment has been identified as a crucial factor controlling population dynamics of *Mesodesma* species (Lima et al. 2000), testing contrasting evidence supporting/rejecting this hypothesis is critical and may also have consequences for resource managing (e.g. defining areas for conservation and restocking).

Conclusion:

Freshwater input to the coastal zone, and the associated fluxes, displays a strong seasonal signal, which may affect biological processes, particularly the reproductive cycle and perhaps the spatial variability in recruitment success.

5.3.3 Primary production – Upwelling of cool, nutrient-rich waters is the most important oceanographic process determining the huge productivity of the HCUS. Although upwelling frequency and intensity is affected by local factors such as width of the shelf, coastal topography and sources of upwelled waters, they mainly depend on large-scale climatic forcing and latitudinal/seasonal signals (Thomas et al. 2004). As a result, upwelling is stronger and mostly continuous in the northern HCUS and shifts to more seasonal and less intense towards higher latitudes (Thiel et al. 2007, Publication 5). Therefore, northern beaches represent more suitable environments for *M. donacium* populations, with a year-round, abundant food source allowing the development of dense, fast-growing and highly productive populations. In contrast, at the central-southern Chilean coast the upwelling-based primary production is lower and the food availability may principally depend on the local effect of freshwater input, which is stronger in those regions. This would explain the strong latitudinal patterns in abundance, growth performance, mortality and productivity of *M. donacium* along the HCUS (Fig. 4.5, Publication 5)

Overall, beach clams are found in areas of high primary production and tend to reach their highest population density and biomass in eutrophic conditions, often in proximity to river estuary systems, where increased organic matter content fuels higher population abundances (McLachlan et al. 1996,

Denadai et al. 2005). For *M. donacium*, southern temperate sandy beaches, whose primary production seems mainly determined by river inflow may represent its primary habitat, whereas subtropical sandy shores with upwelling-related higher primary production probably represent suitable but more recently available habitats. Not only the above-discussed link between the northward expansion of *M. donacium* and the development of the HCUS's productive conditions give support to this hypothesis. *Mesodesma* species are commonly restricted to high latitude sandy shores with strong influence of freshwater inflow (Davis 1967, McLachlan et al. 1996, Brunel et al. 1998). In fact, *M. donacium* is the only species within its genus reaching tropical beaches (5°S) usually dominated by *Donax* species (Herrmann 2008).

The productivity, predictability, and size of the environment determines whether populations grow or shrink, expand or contract geographically, spawn daughter populations or represent evolutionary dead ends, and whether they play crucial ecological roles or function merely as ancillary ornaments (Vermeij and Dietl 2006). In this broad sense, tropical and subtropical shores in the HCUS may represent large, highly productive but unpredictable environments for *M. donacium*, a species sensitive to high temperatures. Several studies show that the Peruvian and northern Chilean coast has been the scenario of long-term recurrent southward extension of tropical coastal species with concomitant retraction of cool water species during warming events (e.g. Guzmán et al. 2001, Castilla et al. 2005, Paredes et al. 2004). Therefore, *M. donacium* populations developed in tropical and subtropical shores are ephemeral, showing periods of high abundance and secondary production with periods of rapid declining and southward retraction. Given that prevailing currents in the HCUS encourage predominantly northward larval migration (Aiken et al. 2007), northward populations may mostly act as sink populations, which cannot be expected to be adapted to physical changes brought about by EN/LN because their phenotypes reflect the conditions under which the source (southern) populations evolved. In this context, small populations inhabiting beaches of the Atacama Desert coast (~17-29°S) may represent a transition between northern and southern populations whose productivity seems to mainly depend on coastal upwelling and river inflow, respectively. Since EN/LN anomalies are stronger at lower latitudes, these populations have the chance to survive strong events and are crucial for

northward recolonization after EN/LN cycles, depending on larval dispersal ability. Therefore, they should be given priority in management and conservation strategies, even though these populations only contribute a small fraction of Chilean landings according to statistics of the Fisheries National Service (SERNAPESCA-Chile).

Conclusions:

Primary productivity along the HCUS displays a strong spatial pattern, which may explain the geographic patterns in population dynamics and productivity of *M. donacium* in the HCUS. The strong interannual variability in primary production largely defines the functionality of populations as sources (southern ones) or sinks (northern ones).

5.4 Future research perspectives

Management of exploitable sandy beach resources must account for temporal and geographical variation in life history and population dynamics (McLachlan et al. 1996). My hope is that this work had shed light on the main factors driving the variation in *M. donacium* and this knowledge can be used to improve present and future management decisions. At least three reasons suggest that soundness of management decisions will determine the fate of this species: (1) landings of this species show a long-term decreasing pattern in Chile and Peru (Fig 1.5); (2) aquaculture of sandy beach clams seems not feasible yet for most of the species supporting commercial or recreational fisheries (McLachlan et al. 1996), and (3) the increasing demands on sea food in the global market will increase the pressure on natural stocks. Therefore, I will put forward some research needs that will further assist resource management and conservation strategies:

5.4.1 Settlement and recruitment process – Further research is needed to study the responses of larvae to low salinity and other environmental cues and determine if nearshore salinity changes act as an environmental cue for settlement near river mouths. Along-shore population structure should be studied in detail to reconcile contrasting evidence on spatial segregation among size classes. These studies should account for the dynamic, and spatially

autocorrelated nature of these patterns and consider the suitability of geostatistical approaches (Defeo and Rueda 2002). In addition, underlying explanations for spatial segregation and potential mechanisms associated with over-compensatory processes in the stock-recruitment relationship, such as passive filtering of larvae by adults, should be examined by field and laboratory studies. These studies would be relevant to define spatial management schemes accounting for spatial variation in the magnitude of recruitment and thus to protect those areas with high probabilities of successful settlement and recruitment. Moreover, these studies could be useful to improve the result of recent attempts of population restocking using juvenile clams.

5.4.2 Submarine groundwater discharge – While the occurrence of this phenomenon was an unforeseeable aspect in this study, both the ample osmotic tolerance of *M. donacium* and the variability in salinity and Chl *a* concentrations at Hornitos coinciding with seepage suggest that this flux may influence the ecology of this species. Existing data suggest that this phenomenon has been influencing the coastal zone since the Pleistocene, and may be common given the presence of large aquifers at the Atacama coastal Desert (Kriete et al. 2004, Nester et al. 2007). Therefore, future research should evaluate to what extent submarine groundwater discharge is ecologically significant for *M. donacium* populations and soft bottom communities in northern Chile and southern Peru.

5.4.3 Parasite load and temperature – Temperature-mediated changes in parasite abundance and transmission are being increasingly recognized as an important process in a global warming scenario (Poulin 2006, Oliva 2007). Laboratory studies should be used to test the influence of anomalous high/low temperature on the reproductive activity of *P. biocipitalis*. It should be specifically evaluated if higher temperature may trigger a shift to asexual reproduction of *P. biocipitalis* as a mechanism to rapidly increase the infestation level as evidence on other polychaete species suggests. Likewise, the impact of the cestod *Rhodobotrioum mesodesmatium* and its relationship with temperature change should be assessed.

5.4.4 Oxygen isotopic composition of *M. donacium* shells – Shell oxygen-isotopes ratios ($\delta^{18}\text{O}$) provide important clues to environmental conditions during

shell formation. The oxygen isotope composition of mollusc shells is controlled by both the $\delta^{18}\text{O}$ and the temperature of the ambient seawater in which the animals live. In turn, the $\delta^{18}\text{O}$ value of the seawater changes with the influx of freshwater of different $\delta^{18}\text{O}$ values or evaporation. As SST can be calculated from the fractionation relationship of $\delta^{18}\text{O}$ values of the shell aragonite (Grossman and Ku 1986), differences between SST derived from shell $\delta^{18}\text{O}$ values and *in situ* SST measurements can be used to estimate salinity changes (Schöne et al. 2003). Therefore, combined studies on oxygen isotopic composition of *M. donacium* shells and on microscopic variations of calcification rates through time (i.e. sclerochronology) can be used to further evaluate some of the hypotheses concerning the described macro-scale patterns of *M. donacium*: (1) the latitudinal gradient in the strength of freshwater input from rivers or SGD affecting this species (e.g. Schöne 2003, Schöne et al. 2003); (2) the temporal coupling between changes in $\delta^{18}\text{O}$ associated to freshwater fluxes and specific events of the reproductive cycle (e.g. Sato 1995); (3) the latitudinal pattern of growth performance and its relationship with primary production (e.g. Hall et al. 1974, Sato 1997).

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