

Environmental stress and parasitism as drivers of population dynamics of *Mesodesma donacium* at its northern biogeographic range

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Mesodesma donacium is a commercially important bivalve in Chile and Peru. During strong *El Niño* events, populations at the northern end of its geographic distribution are wiped out, so to understand its threshold responses to biotic and abiotic factors, the population dynamics of one of the northernmost population remnants was analysed between 2005 and 2007. Strong interannual differences were found in abundance, body mass, growth rate, somatic production, and the prevalence of the parasite *Polydora biocccipitalis*. A Spearman rank correlation analysis showed that changes in beach slope, seemingly linked to repeated storm surges, negatively affected the clam's abundance and seemingly also affected growth, mortality, body mass somatic production, and parasite prevalence. Infestation by *P. biocccipitalis* was restricted to adult clams. Juvenile clams suffered high mortality because they inhabit the intertidal zone, where wave action is strong. Larger clams also showed high mortality, which seemed best explained by a synergistic effect of parasite load and environmental stress. This parasite-climate-driven mortality of larger clams had a strong impact on somatic production and implied a dramatic loss of fecundity (82%), which may significantly affect the ability of the species to recover its former abundance and distribution.

Keywords: environmental effects, parasites, population dynamics, sandy beaches, South America, species distribution.

Introduction

The surf clam *Mesodesma donacium* ranks among the most important species for Chilean and Peruvian artisanal fisheries (Defeo *et al.*, 1993; McLachlan *et al.*, 1996; Thiel *et al.*, 2007), with annual landings of up to ~11 000 t in Chile and ~4000 t in Peru. The species also plays an ecologically important role in shallow soft-bottom ecosystems. It is frequently a dominant species on Peruvian beaches, exhibiting high abundance and extremely high somatic production (Arntz *et al.*, 1987), although it can be outcompeted by other species on Chilean beaches (Contreras *et al.*, 2000; Jaramillo *et al.*, 2001).

The species has an extensive geographic distribution, from Chiloé (43°20'S) in southern Chile to Sechura (5°10'S) in northern Peru, hence inhabiting temperate, subtropical, and tropical beaches of the Humboldt Current System (HCS). Although large surf clams of the Mesodesmatidae are commonly restricted to temperate or subtropical beaches, *M. donacium* is the only species reaching tropical sandy beaches, which are commonly dominated by smaller species of *Donax* (McLachlan *et al.*, 1996; Herrmann, 2009). From a biogeographical perspective, the HCS includes three units: the warm-temperate biota of the Peruvian province, the cold-temperate biota of the Magellanic province, and a transition zone in between (Brattström and Johanssen, 1983; Camus,

2001). The northward expansion and hence wide distribution of many Subantarctic species through this transition zone has been likely facilitated by the northward transport of cool waters of Subantarctic origin by the Humboldt Current (Menziés, 1962; Castillo, 1968; Alveal *et al.*, 1973; Santelices, 1980; Riascos *et al.*, 2009), which extends cool conditions north, more than along other coasts at comparable latitudes (Viviani, 1979; Camus, 2001).

However, environmental conditions in the HCS are strongly modified by *El Niño*–Southern Oscillation (ENSO) phenomena, the strongest signal in the interannual variation in the ocean–atmosphere system (Wang *et al.*, 1999). During *El Niño*, the warm phase of ENSO, the arrival and poleward propagation of coastal Kelvin waves along the Peruvian and Chilean coasts leads to strong abiotic changes, including an anomalous increase in sea surface temperature (SST) and a drastic deepening of the pycnocline and nutricline, reducing the efficiency of the upwelling process (Barber and Chavez, 1983; Arntz *et al.*, 2006). These changes have dramatic and widespread biological effects, operating at different spatial scales and levels of organization levels (Arntz and Fahrback, 1996; Arntz *et al.*, 2006; Thiel *et al.*, 2007; Thatje *et al.*, 2008).

The mass mortality of *M. donacium* represents the most conspicuous and long-lasting impact of strong *El Niño* events on

sandy beach communities of the HCS. After the severe *El Niño* of 1982/1983, the distribution of *M. donacium* was pushed back south to 14°S, and even farther south after the *El Niño* of 1997/98, leaving only a few decimated populations consisting of juveniles in southern Peru and northern Chile (Arntz et al., 1987; Quiroz and Barriga, 1998; Aburto and Stotz, 2003; Thiel et al., 2007). After more than 25 years, the species has not yet recovered its former distribution, although the subdominants *Donax marincovichii* and *Emerita analoga*, which both survived the *El Niño*, did not attain densities comparable with those previously observed for *M. donacium*. Long-term population fluctuations seem typical of sandy beach species with planktonic larvae structured as metapopulations, owing to environmental disturbances and stochasticity in reproduction and recruitment (Defeo and McLachlan, 2005). Examining the responses of reproduction and recruitment to environmental variability in marginal populations may give insights into the ability of the species to recover its former distribution.

Experimental and field data suggest that the upper thermal tolerance of *M. donacium* and the increased prevalence and intensity of infestation of the spionid parasite *Polydora biocephalis* under warmer conditions might explain the observed mass mortality events in northern areas, where thermal anomalies are much stronger (Riascos et al., 2008, 2009). However, the factors underlying the reduced ability of *M. donacium* to recover its former distribution and dominance remain obscure.

As the species range is supposed to be determined by an alignment of different interacting factors, notably environmental conditions, species interactions, and population demographics (Sagarin et al., 2006), a detailed analysis of these factors at the boundary of the species range is crucial to assessing the responses of *M. donacium* to recurrent warming events and the process leading to subsequent recovery. Therefore, this work aims to (i) analyse the population dynamics of *M. donacium* near its northern boundary, (ii) determine the biotic and abiotic factors affecting the observed population processes during a period of contrasting environmental stress, and (iii) analyse the implications of these processes for the recovery of former abundance and distribution.

Material and methods

Study site and environmental parameters

A small population of *M. donacium*, distributed along ~400 m of coastline and not exploited commercially owing to the closure of the fishery, was sampled from May 2005 to April 2007 in Hornitos (22°54'S 70°17'W; Figure 1), northern Chile. The population represents one of the northernmost remnants after populations were decimated during the severe *El Niño* events of 1982/1983 and 1997/1998. Hornitos is located at the northern entrance of Mejillones Bay, which is influenced by upwelling shadows during spring and summer, creating an area of high temperature and larval retention within the upwelling system (Marin et al., 2003; Figure 1).

Environmental parameters in Hornitos were measured *in situ* and also derived from other sources to assess drivers of biological change. SST (°C) was measured hourly during the study period with an Onset StowAway temperature logger installed on a float located ~100 m seawards. Salinity and chlorophyll *a* (Chl *a*) concentration (mg l⁻¹) were registered every 15 min during the sampling day using a multiparameter data sonde (Yellow Springs Instrument Company, model 6600). Sediment samples were

taken at each tidal level within the across-shore distribution of *M. donacium*. We estimated the median particle size (50% point of a cumulative frequency curve of grain size diameter) using the dry-sieving method (Bale and Kenny, 2005). Wave height and period were estimated using graduated poles against the horizon and a stopwatch at the time of sampling. Beach slope (cm m⁻¹) was determined monthly by Emery's profiling technique (Emery, 1961), and the dimensionless Dean's parameter (Ω ; Short, 1996) was calculated from

$$\Omega = \frac{Hb}{W_s \times T}, \quad (1)$$

where Hb is the breaker height (m), W_s the sandfall velocity (m s⁻¹), and T the wave period (s). Tables from Gibbs et al. (1971) were used to estimate sandfall velocities based on particle size.

The monthly mean upwelling index (m³ s⁻¹ 100 m⁻¹ of coast) was computed using a 1° nominal resolution for the area included between 22°30'–23°30'S and 72°30'–73°30'W, using the Live Access Server of the Pacific Fisheries Environmental Laboratories–NOAA (available from <http://las.pfeg.noaa.gov>).

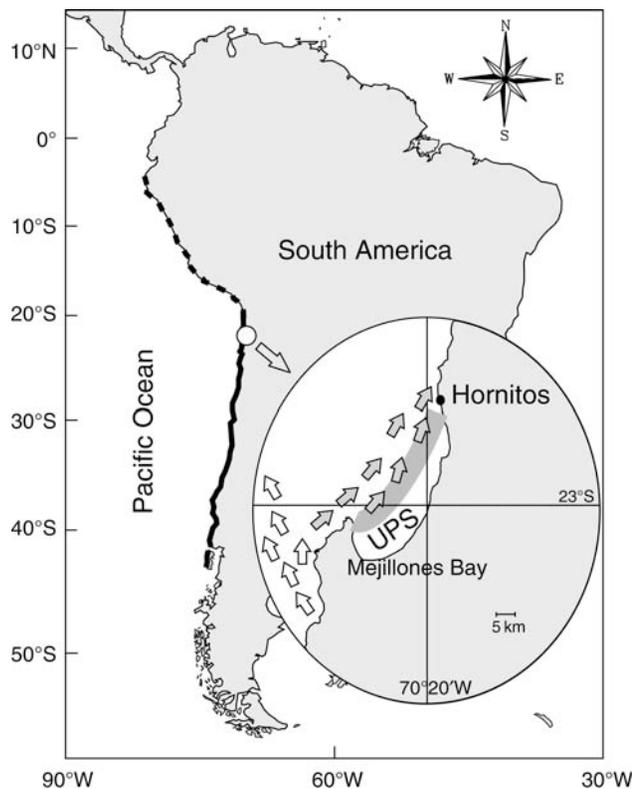


Figure 1. Geographic range of *M. donacium* along the west coast of South America. Continuous line, current range of distribution; dashed line, former extent of northward distribution before strong *El Niño* episodes. Inset: location of the study site and scheme of the typical distribution of offshore (white arrows) and alongshore (grey arrows) cold-water filaments during spring–summer upwelling, which generates a thermal front (grey line) and the upwelling shadow (UPS) inside the bay. There is a reverse circulation pattern in the absence of upwelling caused by decreased windspeed. Scheme redrawn from Marin et al. (2003).

The index was calculated 1° offshore to avoid the potential effects of extreme coastal topography of the zone on the calculations. A dependent *t*-test was used to evaluate between-year differences (pooled data for each year) in environmental parameters.

Sampling strategy

A species-driven sampling strategy (*sensu* Defeo and Rueda, 2002) was used to collect monthly samples along a transect perpendicular to the shore during spring tides. Three replicate samples 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 at two consecutive depthlines (generally ~4–5 m water depth). When samples yielded clams, replicates were extended to 5–10 at each tidal level, depending on tidal conditions. A sheet-metal box (0.16 m², 0.35 m deep) was used for the intertidal, and a diver-operated push boxcorer (0.02 m², 0.25 m deep) for the subtidal, and sediment was sieved through a 0.5-mm mesh.

Abundance, prevalence of infestation, and environmental triggers

The clams collected were measured (anterior–posterior shell length) to the nearest 0.5 mm, and the prevalence of the parasite *P. biocipitalis* was calculated as the percentage of infested clams in monthly samples (Martin and Britayev, 1998). Monthly abundance (ind. m⁻²) was also determined from these quantitative samplings. The correlation between environmental variables and the abundance of *M. donacium* and the prevalence of its parasite was evaluated with a Spearman rank correlation analysis.

Length–mass relationship and fecundity

The annual length–mass relationship was determined for two periods (May 2005–April 2006 and May 2006–April 2007) by selecting 50 clams covering the whole size range from monthly samples. All remaining clams were released on the beach. In the laboratory, soft parts were removed and dried at 70°C to constant mass, and the shell-free dry mass was determined. Ash-free dry mass (AFDM) was obtained by ignition at 550°C for 6 h, and the constants *a* and *b* of the length–mass relationship, where SL is shell length, were estimated using the power function

$$AFDM = aSL^b. \tag{2}$$

An ANCOVA model was used to compare the length–mass relationship between years. The model used year as the main factor, mass as the response variable, and length as a covariate regressor. Data were first log-transformed to fulfil ANCOVA assumptions.

The fecundity of *M. donacium* among shell classes was estimated as the number of oocytes per female clam. For this, we used the parameters of the exponential model explaining the relationship between the fecundity of *M. donacium* and its shell size provided by Rubilar *et al.* (2001), and the size at first maturity and sex ratio (56.3 mm SL and 1:1, respectively) reported by Salgado and Ishiyama (1979). Finally, the mean annual abundance of mature clams was used to estimate the relative fecundity (oocytes m⁻²) among shell classes for each year.

Individual growth

Monthly length frequency distribution data from each year were fitted to the von Bertalanffy Growth Function (VBGF; von

Bertalanffy, 1938):

$$L_t = L_\infty(1 - e^{-K(t-t_0)}), \tag{3}$$

where *L_t* is the length at age *t*, *L_∞* the asymptotic length (mm), *K* the curvature parameter (year⁻¹), *t* the age (years), and *t₀* the age at zero length. A three-step procedure was followed: (i) 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); (ii) the resulting mean lengths and standard deviations representing population cohorts were linked using FISAT II software to produce size-increment datapairs; and (iii) these data were fitted to the VBGF using the method developed by Fabens (1965), which rearranges the VBGF to size-increment datapairs:

$$L_2 = L_1 + (L_\infty - L_1)(1 - e^{-K(t_2-t_1)}), \tag{4}$$

where *L₁* is the length at the start and *L₂* the length at the end of the time interval *t₂ - t₁*. The parameter *t₀* cannot be estimated with this method. However, assuming this parameter to be zero, growth curves can be plotted against relative ages (years - *t₀*). Equation (4) was fitted using an iterative, least-square, non-linear regression routine using the quasi-Newton algorithm to estimate standard errors for the parameters. An analysis of the residual sum of squares (Chen *et al.*, 1992) was performed to evaluate intra-annual differences between the fitted VBGF for each year.

Mortality

Total mortality *Z* (year⁻¹) was calculated for each year (May 2005–April 2006 and May 2006–April 2007) by the single negative exponential model

$$N_t = N_0e^{-Zt}, \tag{5}$$

where *t* is the time and *N₀* 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:

$$\frac{N_i}{\Delta t_i} = N'_0e^{-Zt_i}, \tag{6}$$

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

$$\log_e\left(\frac{N_i}{\Delta t_i}\right) = a + bt_i; \quad Z = -b. \tag{7}$$

An ANCOVA was employed to compare the slope (*Z*) of the relationship between $\log(N_i/\Delta t_i)$ and *t_i* between years. The model used year as the mean effect, $\log(N_i/\Delta t_i)$ as the response variable, and the relative age (*t_i*) as the covariate regressor. Data were previously checked to meet all ANCOVA assumptions.

Productivity

The mass-specific growth rate method (Crisp, 1984) was used to calculate total somatic production *P* (g AFDM m⁻² year⁻¹) for

each year using abundance, pooled length frequency data, VBGF parameters, and the length–mass relationship [Equation (2)]:

$$P = \sum N_i M_i G_i, \tag{8}$$

where N_i is the mean annual abundance in length class i , M_i the mean body mass in length class i , and G_i the mass-specific growth rate:

$$G_i = bK \left[\left(\frac{L_\infty}{L_i} \right) - 1 \right], \tag{9}$$

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

$$B = \sum N_i M_i. \tag{10}$$

Finally, annual productivity was calculated as the ratio between P and \bar{B} [Equations (8) and (10)].

Results

The abundance of *M. donacium* and the prevalence of its parasite showed strong intra- and interannual variability (Figure 2). Generally, they were high during the first year and significantly lower in the second ($t = 4.724, p < 0.001$; $t = 4.109, p = 0.001$, respectively). During the first year, these parameters showed a seasonal, inverse pattern, with lesser abundance and higher prevalence in spring (referring to austral seasons). This seasonal pattern was indistinguishable in the second year.

Overall, all oceanographic parameters evaluated here fluctuated seasonally (Figure 3), and no significant differences were observed between years (SST: $t = 0.449, p = 0.662$; salinity: $t = 1.659, p = 0.125$; Chl *a*: $t = 1.203, p = 0.254$; upwelling index: $t = 0.867, p = 0.404$). As for beach parameters (Figure 3c), peak values were observed in March/April for Dean’s parameter, an indication

of the beach’s morphodynamic state, with no interannual differences ($t = 1.203, p = 0.254$). In contrast, significant between-year differences were found in beach slope ($t = -3.594, p = 0.004$), with a steeper slope during the second sampling season, particularly after September 2007, coinciding with the period of lower clam abundance and lower prevalence of the parasite.

According to the Spearman rank correlation analysis (Table 1), beach slope was the only environmental parameter showing significant negative correlations with abundance of *M. donacium* and the prevalence of its parasite. As shown before, these three parameters also showed significant interannual differences.

The length–mass relationship pooled for each year was exponential [Figure 4, with parameters of the power function, Equation (2)]. The soft body mass of clams with similar shell size was significantly higher during the first year compared with the second year (Table 2). The abundance of mature clams (Figure 5a) was much higher during the first year. During the second sampling season, larger mature clams mainly disappeared, and only smaller mature clams were found (Figure 5a). These differences were obviously reflected in strong differences in the estimated relative fecundity among shell classes (Figure 5b). In 2005/2006, fecundity for the whole population amounted to $\sim 125.4 \times 10^6$ oocytes m^{-2} , whereas in the next year, it reached 22.5×10^6 . Therefore, the decrease in the abundance of larger mature clams in the population represented a reduction of 82% of total fecundity.

The estimated values of the curvature parameter and the asymptotic length in the growth model [Equation (3)] were higher for 2005/2006. Therefore, the analysis of residual sum of squares indicated that the growth of *M. donacium* was significantly faster in 2005/2006 than in 2006/2007 ($F = 5.413, p = 0.004$). Results obtained for total mortality (Table 3) are consistent with those of growth; the ANCOVA analysis demonstrated that mortality was significantly higher during the second year (Table 2). Larger clams in the first sampling season were mostly parasitized (Figure 6), and their abundance dropped strongly after August in the second sampling season, coinciding with strong increments in beach slope (Figure 3). Therefore, the increased mortality in the second

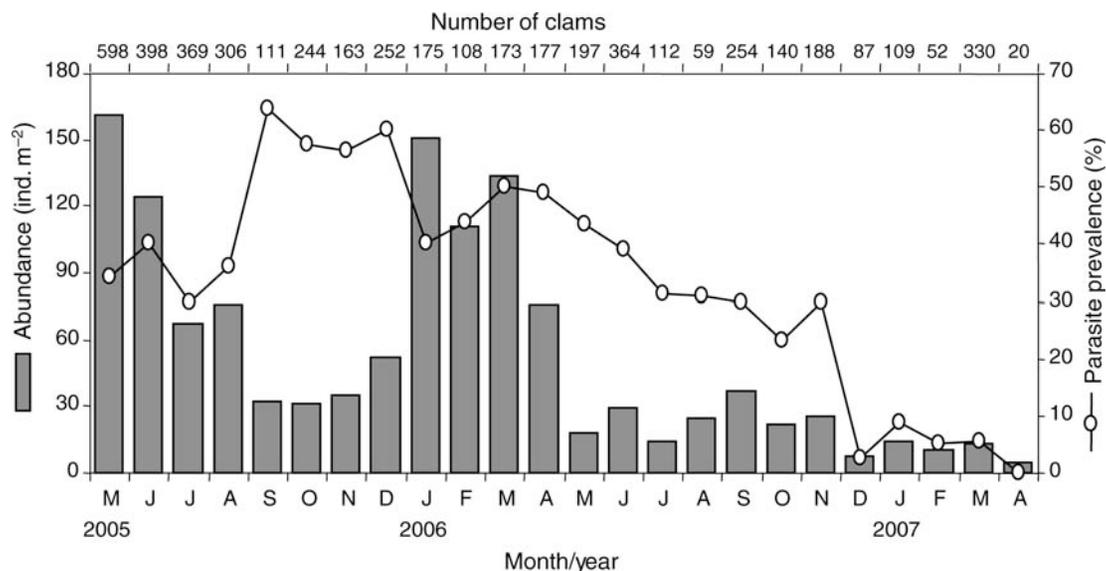


Figure 2. Monthly variability in the abundance of *M. donacium* and the prevalence of its parasite (*P. biocipitalis*).

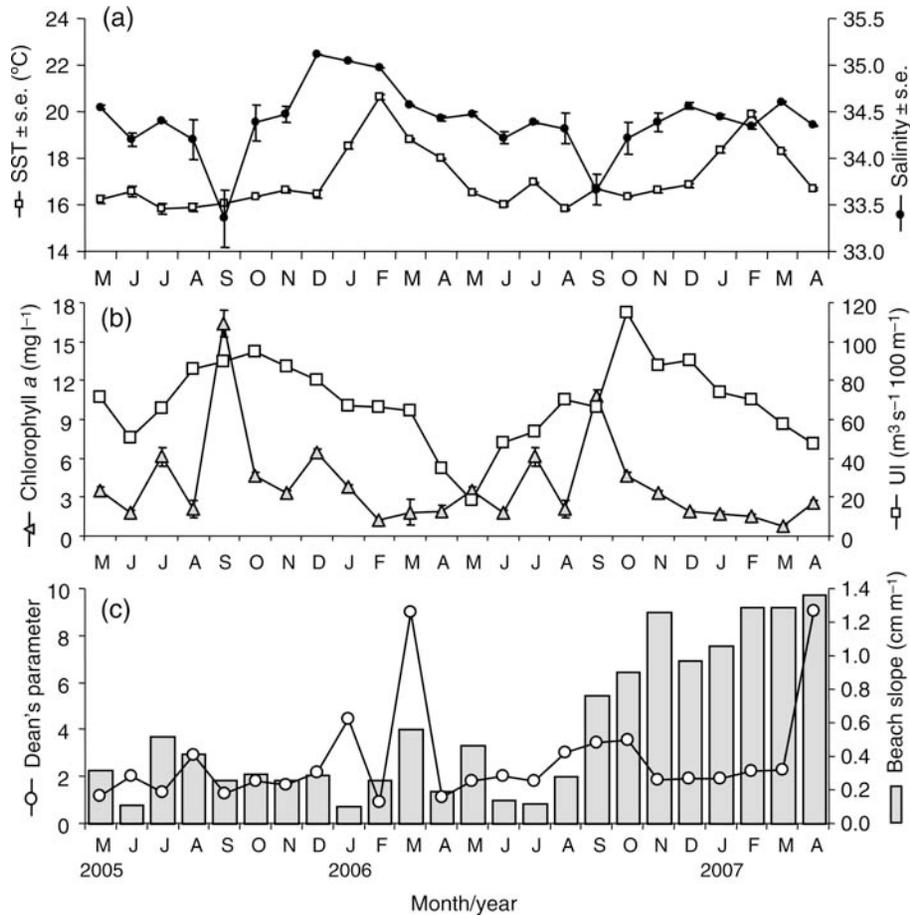


Figure 3. Monthly variability in environmental parameters at Hornitos (northern Chile). (a) SST and salinity; (b) chlorophyll *a* concentration and upwelling index (UI); (c) Dean's parameter and beach slope.

Table 1. Results of the Spearman rank correlation analysis between abundance of *M. donacium*, the prevalence of infestation by *P. bioquipitalis*, and environmental parameters in the study area.

Parameter	Abundance	Prevalence	SST	Salinity	Chl <i>a</i>	UI	Bs
Prevalence	0.6224						
SST	-0.1174	-0.1607					
Salinity	0.1530	0.1397	0.4872				
Chl <i>a</i>	0.1593	0.2961	-0.4756	-0.1994			
UI	-0.0444	0.0370	-0.2444	-0.1157	0.2943		
Bs	-0.5760	-0.6942	0.1766	0.0017	0.2020	0.1791	
Ω	-0.1835	-0.3795	0.1074	-0.1461	-0.0823	-0.0304	0.3512

SST, sea surface temperature; Chl *a*, chlorophyll *a*; UI, upwelling index; Bs, beach slope; Ω, Dean's parameter. *n* = 24; significant relationships (*p* < 0.05) shown emboldened.

year seemed to be related to the mortality of this parasitized component of the population. The abundance of juveniles was higher from May to August 2005 and again from January to March 2006, suggesting that the seasonal pattern of abundance in 2005/2006 was driven by changes in the abundance of juveniles. The second peak of abundance of juveniles in the first year (Figure 6) seems to have been related to summer recruitment in the first sampling season, which was not observed in the second year.

Somatic production was five times higher during the first year than during the second (Table 3). Although small clams (SL < 12 mm) were more abundant during the first year, somatic production was higher among medium-size and large clams

(Figure 7). The abundance of the whole population decreased strongly during the second year, particularly among smaller and larger sizes (SL < 12; SL > 74; Figure 7). As a consequence, mostly medium-size clams were responsible for the somatic production in the second period. Therefore, mean annual biomass decreased by a factor of seven during the second year. In contrast, the *P/B* ratios were fairly similar for both years (Table 3).

Discussion

The population dynamics of *M. donacium* in Hornitos was characterized by strong interannual differences in nearly all the demographic parameters evaluated. During the first year,

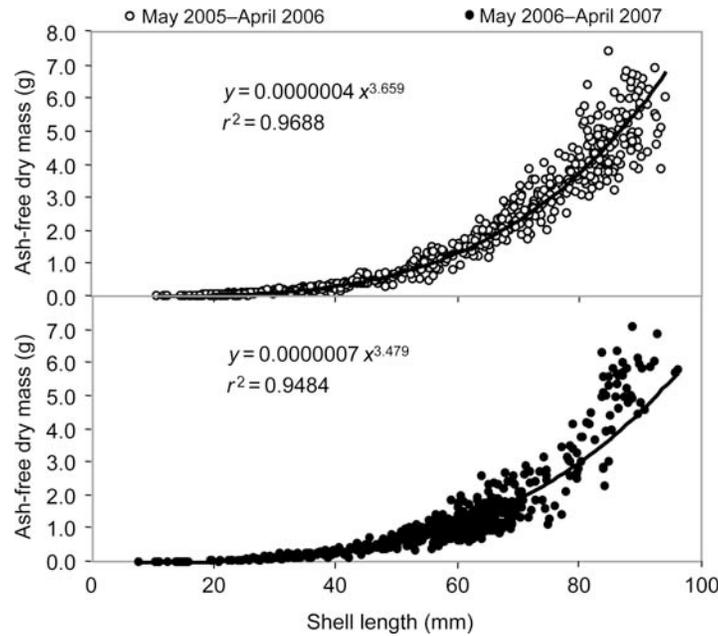


Figure 4. Relationship between soft body mass and shell size of *M. donacium* in two sampling seasons. The parameters a and b of the power function [Equation (2)] describing the relationship and the coefficient of determination are given.

the abundance of *M. donacium* and the prevalence of its parasite were higher and showed a seasonal pattern. This seasonality seemingly resulted from the dynamics of the reproductive cycle, recruitment episodes, and the infestation ability of the parasite, which in turn seemed to be affected by environmental seasonality. In a conceptual model based on a study by Riascos *et al.* (2009), spawning takes place episodically in spring each year in Hornitos, coinciding with seasonally strengthening upwelling (Figure 8a). As the meroplanktonic larval stage lasts for 30–45 d (Tarifeño, 1980), a recruitment episode is expected in summer. This recruitment pulse would explain the temporally increased total abundance in summer 2006 (Figure 2) and the increased abundance of juveniles in the same season (Figure 7). Intra- and interspecies interactions promote high rates of mortality among small recruits (Tarifeño, 1980), which would explain the rapid drops in abundance.

After the energetically demanding process of gametogenesis of bivalves, spawning implies a loss of body mass and general weakening, as well as the start of the recovery process (Pipe, 1987). Therefore, a relationship between poor body condition (spawning) and the infestation ability of polydorids has been hypothesized (Handley, 1998; Riascos *et al.*, 2008). This could be the underlying mechanism for the observed increase in parasite prevalence coinciding with spawning events.

In contrast, the above-mentioned seasonality in abundance of *M. donacium* and prevalence of *P. biocipitalis* was not observed in 2006/2007 (Figure 2). No changes were observed in the timing of the spawning events in 2007 (Figure 8b). Therefore, a recruitment failure seems to explain the lack of the summer peak in abundance of juveniles and total abundance better, which in addition seems to be the main, but certainly not the only, reason for the clear interannual differences in abundance. The continuous reduction in prevalence of *P. biocipitalis* between 2006 and 2007 (Figure 2) most likely is attributable to a selective pattern of mortality, as discussed below.

Table 2. Results of ANCOVA of the relationship between shell length and mass and the mortality of *M. donacium*.

Source	d.f.	Sum of squares	F-ratio	Probability
Length–mass relationship				
Year	1	0.930	46.780	<0.0001
Length	1	550.836	27 703.840	<<0.0001
Error	1 117	22.209	0.020	
Total	1 119	573.052		
Mortality				
Year	1	6.121	12.560	0.0006
Relative age	1	179.970	369.279	<0.0001
Error	111	54.096	0.487	
Total	113	281.341		

Our analysis suggested that beach slope was the only environmental parameter showing a significant relationship with clam abundance and the prevalence of *P. biocipitalis* (Table 1). However, they should not be taken as cause-and-effect relationships. Instead, they may reflect the fact that beach morphodynamics are closely associated to community structure and distribution (Jaramillo *et al.*, 1998). In our case, changes in beach slope should be taken as a proxy of changes in beach conditions. Strong changes in the beach environment associated with storm surges and barometric tides have detrimental effects on intertidal organisms (Brown, 1983; Defeo, 2003). Normally, interannual differences in beach environments in Hornitos are small (Contreras *et al.*, 2000). However, we found strong interannual changes in beach slope, likely connected to interannual differences in mortality (Table 3) and sublethal effects for survivors, consisting of reduced growth, mass-at-size, relative fecundity, and somatic production (Figures 4, 5, and 7; Table 3). The effects of a harsh beach environment seem to vary among size classes, because this species exhibits a clear across-shore pattern of size segregation, with juvenile clams mainly inhabiting the

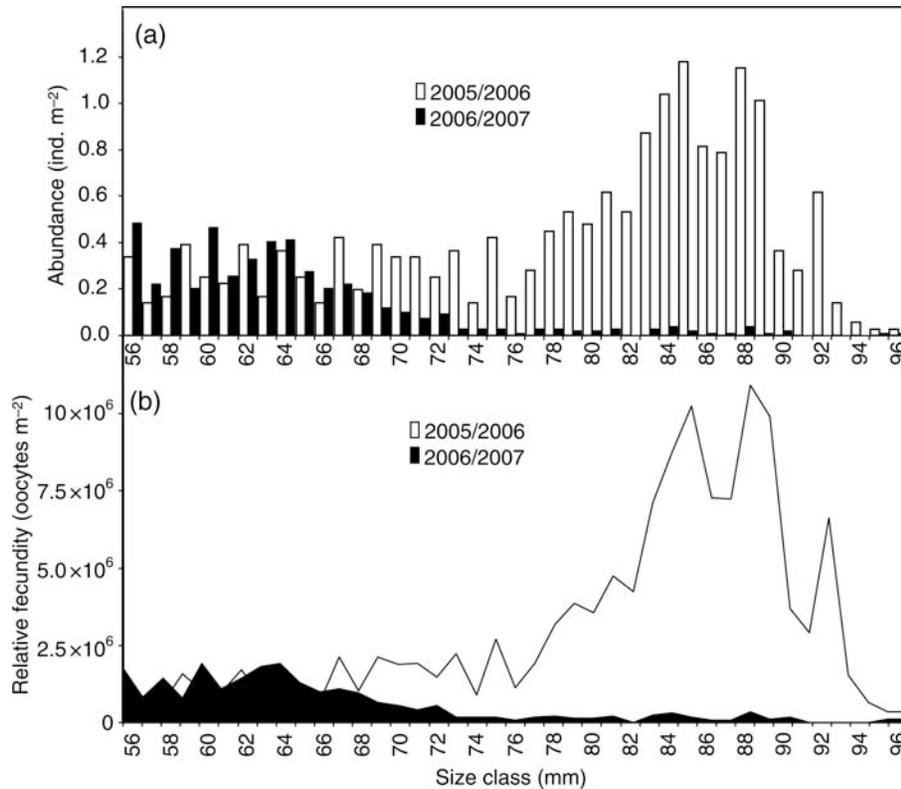


Figure 5. (a) Abundance of shell size classes of sexually mature *M. donacium* in 2 years at Hornitos, northern Chile. (b) Comparison of relative fecundity among shell classes between 2 years at Hornitos, northern Chile. Only clams >56 mm, the size at first maturity (Salgado and Ishiyama, 1979), are included.

intertidal area that receives stronger wave action, and adults being restricted to the shallow subtidal (Tarifeño, 1980; Jaramillo *et al.*, 1994; Riascos *et al.*, 2008). As a result, juvenile clams are more exposed to harsh conditions than other components of the population, and a size-dependent mortality pattern would be expected, as observed in other species displaying differential zonation patterns (Defeo *et al.*, 2001). The size frequency distribution (Figure 6) depicts this mortality pattern: juveniles observed during the first year almost disappeared during the second. This was confirmed by observations of large numbers of stranded juveniles during the second year. Harsher beach conditions after September 2007 might also have hampered the summer recruitment pulse expected in 2007 (Figure 8b). However, clam recruitment is a highly variable process, which depends on a series of stochastic and/or deterministic factors (Lima *et al.*, 2000; Ripley and Caswell, 2006) that cannot be ruled out as explaining this missing pulse.

Adult clams (SL > 70 mm) also suffered greater mortality than medium-size clams during the second year (Figure 6). Several pieces of evidence suggest that increased mortality among larger clams was driven by parasitic effects acting synergistically with environmental stress. First, experimental evidence shows that the infestation of *M. donacium* by *P. biocipitalis* is restricted to adult clams and affects their digging ability, growth rate, and body condition, which lowers their resistance to environmental stress (Riascos *et al.*, 2008). Second, stranded clams observed after high swell during monthly sampling consisted chiefly of juvenile and large infested clams (JMR, pers. obs.). Third, the

Table 3. Estimation of population dynamics parameters of *M. donacium* from Hornitos (northern Chile) between May 2005 and April 2007.

Parameter	2005/2006 estimate (± s.e.)	2006/2007 estimate (± s.e.)
Mean annual abundance (ind. m ⁻¹)	86.339 (± 6.056)	17.389 (± 0.441)
Prevalence of <i>P. biocipitalis</i> (%)	46.709 (± 3.181)	20.824 (± 4.466)
Curvature parameter <i>K</i> (year ⁻¹)	0.496 (± 0.089)	0.301 (± 0.055)
Asymptotic length <i>L</i> _∞ (mm)	93.093 (± 7.694)	89.527 (± 7.121)
Total mortality <i>Z</i> (year ⁻¹)	0.556; <i>r</i> ² = 0.685	0.703; <i>r</i> ² = 0.703
Annual somatic production <i>P</i> (AFDM, g m ⁻²)	28.208	5.657
Annual mean biomass \bar{B} (AFDM, g m ⁻²)	70.315	9.861
Productivity (<i>P</i> / \bar{B} ratio)	0.401	0.574

few surviving adult clams towards the end of 2007 were almost exclusively non-infested clams, explaining the steady decrease in prevalence of *P. biocipitalis* throughout the second year (Figures 2 and 6). Parasitism has been identified as a process with the potential to drive key processes at the population and

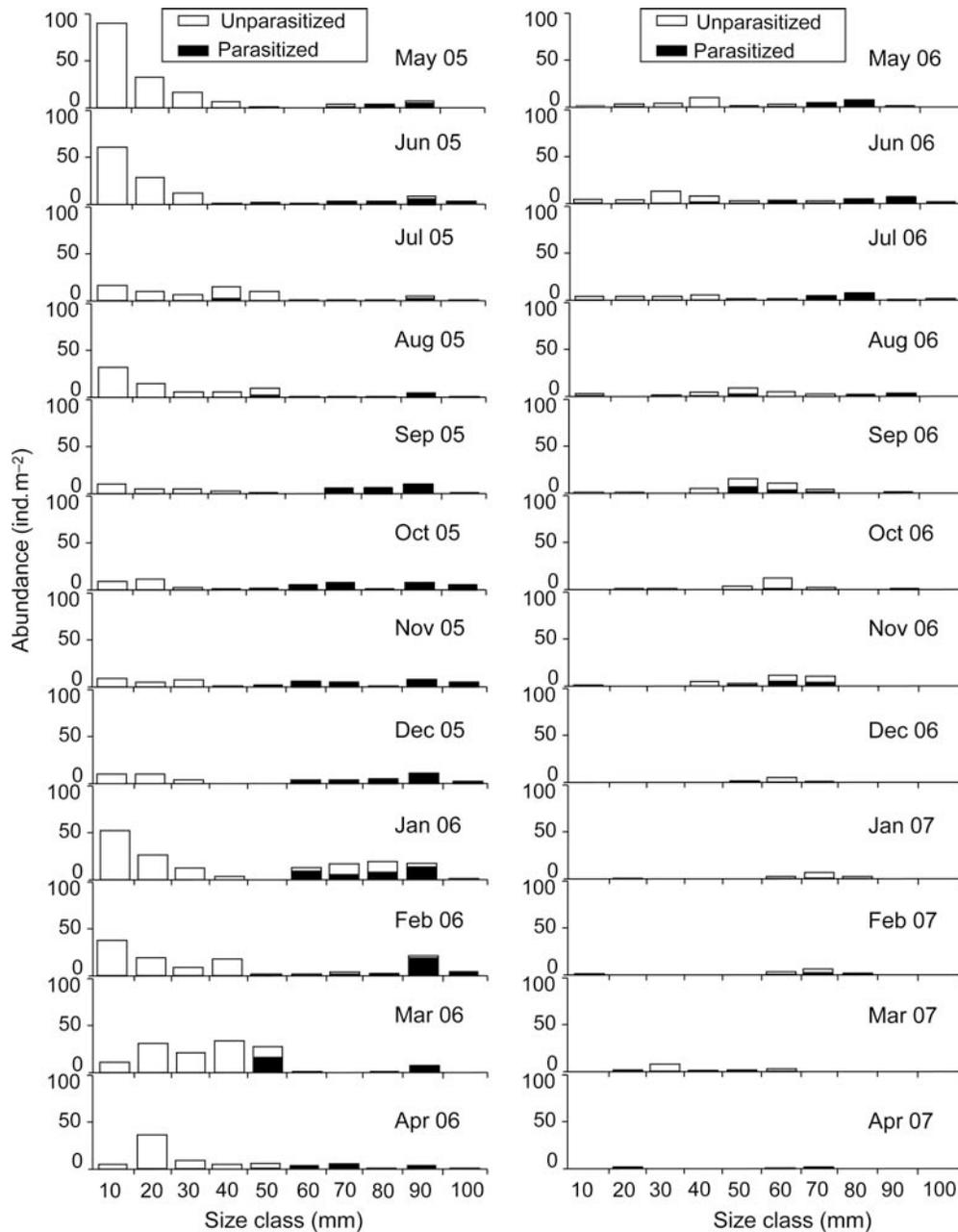


Figure 6. Monthly changes in abundance among size classes of *M. donacium* parasitized and unparasitized by *P. biocipitalis*.

community level (Defeo and McLachlan, 2005). Our findings suggest mechanisms by which parasitism can drive selective mortality patterns of this clam, but further studies are needed to test the validity of this hypothesis.

Mortality among juvenile clams was higher than among adults. However, the consequences of adult mortality seem to have been more significant in terms of population energy flow and could also have affected the ability of this clam species to regain its former northern distribution and abundance. Medium-size and large clams yielded the major part of population somatic production (Figure 7). Smaller clams (SL < 20 mm) yielded a comparable somatic production in both years, whereas larger clams (SL > 20 mm) yielded more somatic production in the first

year, implying that the decrease in abundance of larger clams in the second year caused a greater loss of somatic production in the whole population.

The decrease in abundance of larger clams also had a strong impact on the population's fecundity (Figure 6b). It represented a loss of fecundity of 82% during the second year. As fewer reproductive adults remained during the second year, a weak spawning pulse would have been expected if this is a self-recruiting population. Therefore, pre- and/or post-settlement processes may be responsible for the observed recruitment failure during the second sampling season.

This loss of fecundity of course represents a substantial reduction in the capacity for larval self-replenishment of the

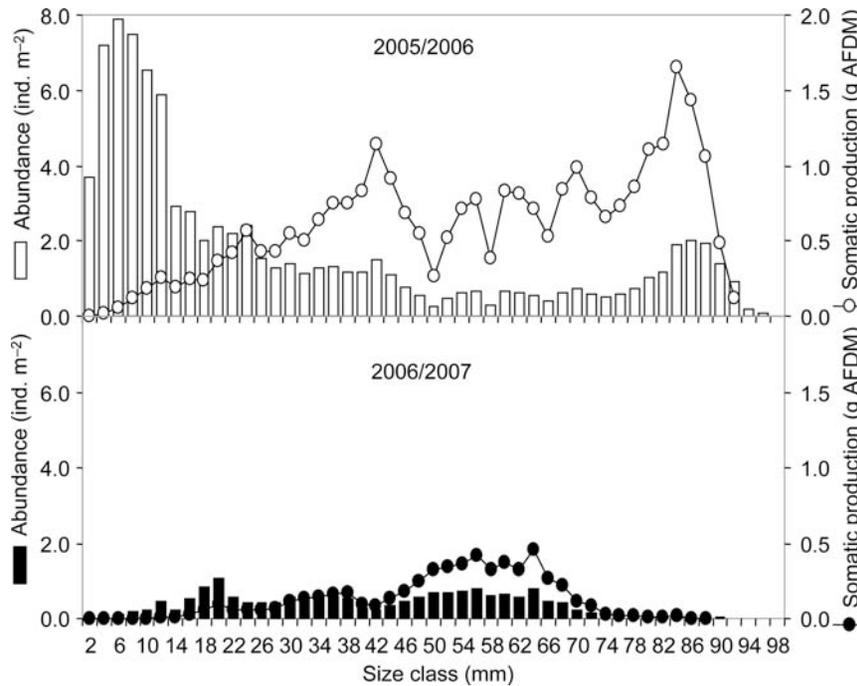


Figure 7. Mean annual abundance and somatic production of *M. donacium* among length classes in two different sampling seasons. Length intervals are 2 mm.

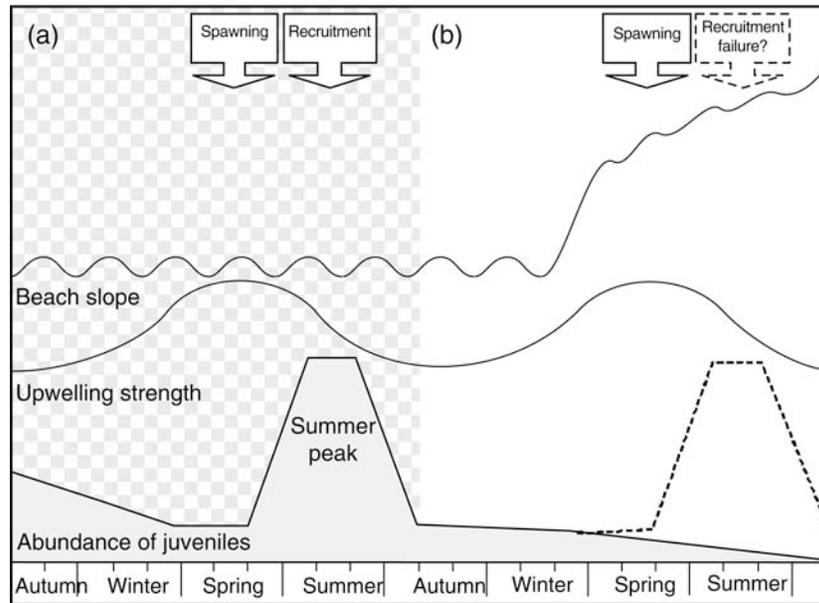


Figure 8. Conceptual model of the timing of spawning and recruitment of *M. donacium*, and their interaction with key environmental factors during two sampling seasons. (a) Season 2005/2006; (b) season 2006/2007. The onset of spawning events and the triggering effect of upwelling strength variability is deduced according to [Riascos et al. \(2009\)](#), and the duration of larval stage is taken from [Tarifeño \(1980\)](#).

species. More importantly, given that (i) the Hornitos population is located near the northern edge of the current geographic distribution, (ii) large populations making significant contributions to fisheries are located ~800 km south (Coquimbo, central Chile; [Thiel et al., 2007](#)), and (iii) sandy beach clams are commonly structured as metapopulations ([Defeo, 1996](#); [Defeo and](#)

[McLachlan, 2005](#)), this population and other small, marginal populations are crucial for population connectivity with former large populations in central and southern Peru. Although long-term data are more definitive, a good representation of different size classes in a population suggests frequent successful annual recruitments and is indicative of source populations ([Defeo and](#)

McLachlan, 2005). The seasonal increase in total abundance of *M. donacium* (Figure 2), coupled with the abundance of juveniles during the first sampling season and the presence of all size classes (Figure 7), suggests frequent, successful recruitments. Moreover, the prevalent circulation pattern of the upwelling system off Mejillones Bay may act as an efficient retention zone for planktonic organisms (Figure 1; Marin et al., 2003), enhancing the capacity of this population to self-replenish. However, the combined effect of parasitism and environmental stress may affect the balance of local rates of birth and death, and hence determine whether the population acts as a sink or source population capable of seeding northern beaches. As the prevalence of infestation of *M. donacium* by *P. biocipitalis* likely increases towards lower latitudes and could be enhanced by environmental stress (Riascos et al., 2008), future field and experimental research needs to focus on the direct impact of this parasite on individual gamete production under normal and anomalous environmental conditions.

To conclude, the results of this study strongly suggest that storm events have significant effects on local population dynamics of *M. donacium*. These events are normally uncommon in northern Chile, but seemingly increase during *El Niño* episodes (Thiel et al., 2007). Therefore, the question arises whether the storm events observed here were linked to the weak *El Niño* of 2006/2007 (McPhaden, 2008). Unfortunately, long time-series would be needed to assess this potential relationship reliably.

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