Recurrent, thermally-induced shifts in species distribution range in the Humboldt current upwelling system

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ABSTRACT

El Niño-Southern Oscillation (ENSO) is a global climate variablility, which fundamentally influences environmental patterns of the Humboldt Current System (HCS) off Chile and Peru. The surf clams *Donax obesulus* and *Mesodesma donacium* are dominant and highly productive bivalves of exposed sandy beaches of the HCS. Existing knowledge indicates that El Niño (EN, warm phase of ENSO) and La Niña (LN, cold phase of ENSO) affect populations of both species in a different way, although understanding of the mechanisms underlying these effects is still lacking. The aim of this study was to test hypotheses attempting to explain field observations on the effect of strong EN or LN events by using controlled experimental conditions. Growth and mortality rates of both species were registered during a four-week experiment under EN temperature conditions, normal temperature conditions and LN temperature conditions. While *D. obesulus* exhibited reduced growth and higher mortality under LN conditions, *M. donacium* showed reduced growth and higher mortality under EN conditions. The results clearly indicate different temperature tolerance windows for each species, possibly reflecting the evolutionary origins of the Donacidae and Mesodesmatidae in regions with contrasting temperature regimes. These results provide experimental support for previous hypotheses suggesting that thermal tolerance is the driving factor behind observed changes in the species distributions of *D. obesulus* and *M. donacium* during the extreme phases of ENSO.

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1. Introduction

The Humboldt Current System (HCS) is among the most productive marine ecosystems in the world. Strong, coastal upwelling driven by trade winds brings deep, nutrient-rich water into the euphotic layer, fueling vast primary production. Unlike other coastal ecosystems at similar latitudes, the HCS exhibits cool, stable temperature conditions throughout the year. According to Thiel et al. (2007, Fig. 1), three biogeographical units can be distinguished within the HCS: (i) the first northern unit dominated by subtropical and temperate biota and extending from northern Peru to northern Chile (4−6°S to 30−36°S); (ii) the second southern unit dominated by a subantarctic and temperate biota extending from the Chilean archipelago to the Magellan Province (41−43°S to 54°S); and (iii) in between, a transitional unit characterized by strong numerical reductions in subantarctic and subtropical species at its northern and southern borders

respectively (30−36°S to 41−43°S). These biogeographical units are subject to continual fundamental changes caused by the El Niño-Southern Oscillation (ENSO), the strongest signal in the interannual variation of the ocean−atmosphere system (Wang et al., 1999). During El Niño (EN, the warm phase of ENSO) and La Niña (LN, the cold phase of ENSO) events, multiple and contrasting abiotic changes trigger strong biotic changes, including alternations in species composition, abundance and biomass (e.g. Tarazona et al., 1985; Arntz and Fahrbach 1991; Castilla and Camus, 1992; Riascos, 2006; Thatje et al., 2008). Taking into account the normally stable thermal regime of the HCS and the strong thermal anomalies associated to the extremes of ENSO, temperature has been proposed as a key factor driving changes at the population and community level, and thereby influencing community structure and the latitudinal distributions of marine benthic organisms within this system (e.g. Soto, 1985; Tomicic, 1985; Arntz and Fahrbach 1991; Díaz and Ortlieb, 1993; Urban, 1994; Laudien et al., 2007). Unfortunately, cause-and-effect explanations of the described changes during extremes of ENSO are hampered by the lack of experimental and physiological evidence (Arntz et al., 2006; Thatje et al., 2008).

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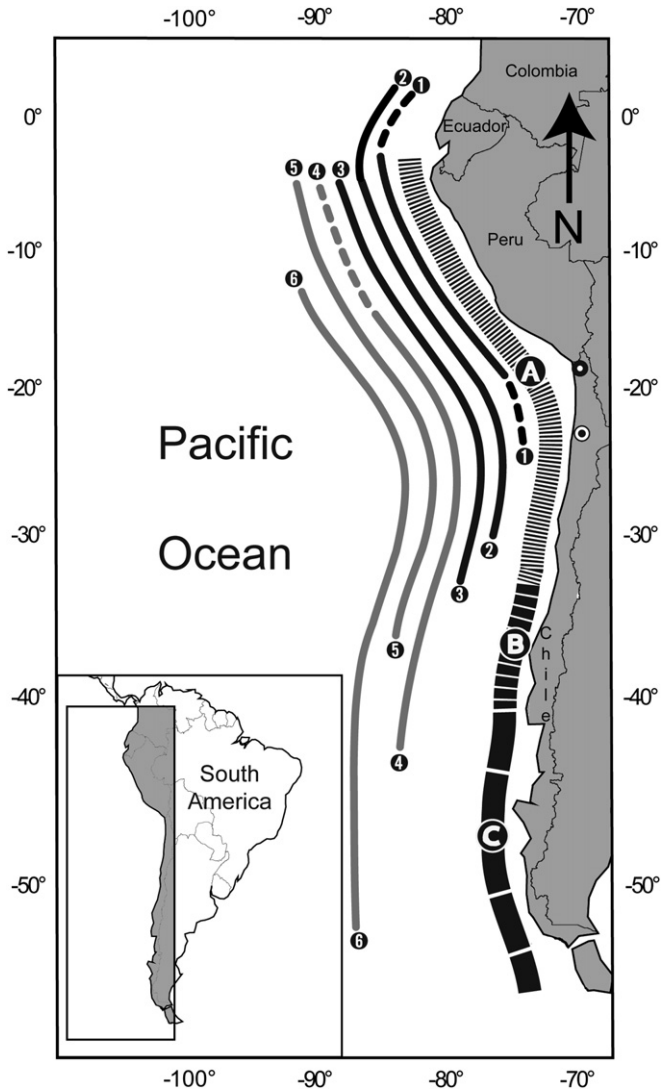
Fig. 1. Biogeographical units of the Humboldt Current System after Thiel et al. (2007): A: The Peruvian province, B: The transition zone and C: The Magellanic province. Sample location of *Donax obesulus* ⊙ in Arica; Chinchorro beach and *Mesodesma donacium* ⊚ in Antofagasta; Hornitos beach. Lines in black indicate species with tropical origin: ❶ Black and black dashed lines indicate historic distribution of *D. obesulus* after Coan (1983). Black line indicates current distribution after an ample sampling. ❷ Distribution of *Argopecten purpuratus* and ❸ *Thais chocolata* after Guzmán and Viana (1998a). Lines in grey indicate species with tropical origin: ❹ Grey and grey dashed lines indicate historic distribution of *M. donacium* after Tarifeño (1980). Grey line indicates current distribution after an ample sampling. ❺ Distribution of *Semimytilus algosus* after Olsson (1961). ❻ Distribution of *Aulacomya ater* after Guzmán and Viana (1998a). For further details see Table 3.

Donax obesulus Reeve, 1854 and *Mesodesma donacium* Lamarck, 1818 are two common surf clams of reflective and dissipative sandy beaches. Whereas *D. obesulus* is restricted to the intertidal zone, *M. donacium* inhabits both, the intertidal (juveniles) and the shallow subtidal (adults) (Riascos et al., 2008). Both species show high abundance along their distribution range in the HCS (Carstensen, 2010; Arntz et al., 1987). These species occupy the same niche and have similar ecological roles (Tarazona et al., 1986; Beu, 2006). Therefore, strong competitive interactions may be expected, such as reported between *Donax hanleyanus* and *Mesodesma mactroides* at the Atlantic coast of South America (Defeo and de Alava 1995; Herrmann et al., 2009). As poikilothermic organisms, their temperature is directly dictated by the temperature of the

surroundings. A small increase of the 'normal operating temperature range' of an organism can reduce scope for growth and reproduction (Pörtner et al., 2005, Pörtner and Knust, 2007; Wang and Overgaard, 2007).

Within their distributional range both species are affected differently by extreme phases of ENSO (Soto, 1985; Arntz et al., 1987, 1988, Arntz and Fahrbach, 1991; Díaz and Ortlieb, 1993; Thiel et al., 2007). Historically, *D. obesulus* (synonyms: *D. marincovichi* and *D. peruvianus*; Carstensen et al., 2009) was distributed from the Ecuadorian coast (0°26′S) to the North of Chile (23°05′S) (Coan, 1983; Fig. 1) and temporarily expands its distribution range southward during strong EN episodes (Tomicic, 1985). In contrast, the historic distribution of *M. donacium* spans from Chiloé, southern Chile (16°36′S) to Sechura, northern Peru (42°23′S) (Tarifeño, 1980; Fig. 1). During EN, the species suffers mass mortalities in the northern part of its geographical range (Tomicic, 1985; Arntz et al., 1987; Guzmán et al., 1998b).

Generally, the distributional ranges of species are determined by different and interacting contributory factors, including environmental conditions, species interactions and population demographics (Sagarin et al., 2006). Apart from purely descriptive accounts, some evidences suggest that distribution shifts may not be entirely explained by corresponding shifts in temperature. First, it is not clear whether sympatric *D. obesulus* and *M. donacium* develop competitive interactions (Arntz et al., 1987). Second, *M. donacium* reveals a remarkably poor ability to recover its former distribution following EN events in spite of several cycles of warm and cold (Arntz et al., 2006). Third, parasitic interactions and, interspecific interactions generally have been shown to play a role in mortality events and species distribution (Dugan et al., 2004; Riascos et al., 2008). In this context, determining the physiological responses of particular species to temperature would provide a mechanistic understanding of the observed changes and discriminate this factors from others contributing to changes in distribution.

Therefore, this study aimed to (i) evaluate experimentally the effect of temperatures typically observed during EN and LN events on growth and mortality of the two surf clams, and (ii) compare these results with the observed changes in distribution. Therefore, bivalves were collected from the current southernmost extent of the *D. obesulus* disributional range of, and from the northernmost point in the *M. donacium* disributional range, both within the area impacted by the cold and warm episodes of ENSO, and used in a series of *in vitro*-experiments.

2. Material and methods

2.1. Distribution and sampling site

Given that EN and LN have caused changes in the historical distributional range of both study species, an ample sampling and a compilation of historical data were performed to determine the current southern distribution limit of *D. obesulus* (Carstensen, 2010), and the current northern distribution limit of *M. donacium* along the Peruvian and Chilean coast (Riascos, 2008). The southernmost population of *D. obesulus* was located at Chinchorro beach (Northern Chile, Arica, 18°27′53.8′ S; 70°18′24.3′W; Fig. 1). The northernmost population comprising the full range of size classes of *M. donacium* was found at Hornitos beach (Antofagasta, 22°54.99′S; 70°17.42′W; Fig. 1). Specimens of both species were collected in February 2007 (*D. obesulus*, n = 104; *M. donacium*, n = 122) and transported to the laboratory. To minimize stress, clams were transported within 12 h of collection and transferred immediately to laboratory conditions at the Marine Laboratory of the University of Antofagasta.

2.2. In vitro-experiment

During the first two weeks after collecting, the bivalves were acclimatized in the laboratory at the temperatures corresponding to local conditions at the collection sites (*D. obesulus*: 17.8 °C; *M. donacium*: 17.4 °C). Low mortality (<5%) was observed during the acclimatization period. The sampling sites for each species lies approximately 800 km apart, hence the slight difference in temperature. Considering this, experimental temperatures were set to mimic normal temperature conditions (NTC), El Niño typical temperature conditions (ENTC) and La Niña typical temperature conditions (LNTC) at each sampling site (Fig. 1). Temperatures were defined according to the analysis of a long-term (1980–2006) sea surface temperature (SST) data archived in the database of the Servicio Hidrográfico y Oceanográfico de la Armada de Chile (available from http://www.shoa.cl). For *D. obesulus*, NTC was defined as the long-term annual mean SST (17.8 °C), ENTC reflected the highest monthly mean SST registered during EN 1982–1983 (24.6 °C), and LNTC mimicked the lowest monthly mean SST during LN 1990 (14.9 °C) at the Arica station (18°28′S, 70°19′). Similarly, for *M. donacium* NTC was set to 17.4 °C, ENTC was 24.2 °C, and LNTC was 14.5 °C.

After acclimatization, the shell length (maximal anterior–posterior shell length; SL) of each specimen was measured to the nearest 0.01 mm with a vernier caliper and the specimen was tagged with a consecutive code to ensure individual identification. Thereafter, clams were incubated for 3 h in moderately aerated, filtered seawater containing 50 mg l^{-1} Calcein (Sigma, CAS 1461-15-0) to incorporate a non-deleterious fluorescent mark in the shell, that would allow the measurement of short-term (i.e. daily) growth increments (Riascos et al., 2007). Thereafter, clams were randomly assigned to a single factor (temperature), three-level (NTC, ENTC, LNTC) experimental design, with three replicate aquaria per level and 12 individuals of *D. obesulus* and 16 individuals of *M. donacium* per replicate.

Specimens were maintained under experimental conditions in closed circulation systems for 31 days (March 2007) in a 12:12 h day–night cycle. Aquaria were filled with filtered (1 μm) seawater and sufficient sand for clams to be able to retract completely (∼13 cm depth). Experimental temperature was maintained within a 0.3 °C fluctuation range, using a computer-controlled system. Sand was aerated and ∼15% of the water was replaced daily to minimize water pollution by accumulation of nutrients (NH_4^+, NO_2^-, NO_3^-) from excreted waste. Animals were fed daily with a mixture (50:50) of *Isochrysis galbana* (T-ISO) and *Chaetoceros calcitrans* (∼40.000 cells ml^{-1}) ad libitum. Dead animals (open shell, foot and siphons extended) were removed on a daily basis and shells were cleaned and stored for further analysis.

At the end of the experiment, all animals were sacrificed, soft parts were removed and shells oven-dried at 65 °C for 24 h. A section through the right valve of each clam was obtained by cutting across the longest growth axis and the section embedded in epoxy-resin. In order to clearly identify the Calcein mark included in the shell, the surface of the resulting section was polished using a speed grinder–polisher (Buehler, Alpha, 2 Speed Grinder–Polisher) with grinding paper (200 μm–5 μm) and a polycrystalline diamond suspension (1 μm–0.05 μm). Microgrowth was measured (to the nearest μm) from the Calcein mark to the shell edge, by analyzing digital fluorescence micrographs (blue light, 460–490 nm). The daily growth rate (μm day^{-1}) was calculated for each specimen. Mortality of each species was calculated from the daily percentage of surviving clams throughout the experimental period (31 days). A dosage–mortality approach (Urban, 1994) was used to determine the point at which 50% of the experimental population had died (LT_{50}). This parameter was obtained by plotting the relationship between time and mortality, and extrapolating the time corresponding to 50% mortality.

2.3. Statistical analysis

To evaluate the effect of temperature on growth rate (μm day^{-1}), the general linear model (GLM) procedure in JMP 7.0.1 (SAS Institute Inc.) was used to apply a one-way analysis of covariance (ANCOVA) model. The model treated temperature as a fixed effect, growth rate as the response variable and shell length as the covariate under the full interaction (separate slopes) model approach. Therefore, the interactions between the covariate and the main effects were included as additional effects. In order to deal with variation within replicates and between replicates, a nested design was used (aquaria within temperature), thus including an additional effect in the model. Tukey's honestly significant difference test was used for post-hoc comparisons of least squared means between effect levels.

To analyse mortality, the slope of a linear regression of the relationship between mortality (proportions of dead clams) and time (days) was calculated for each replicate, following the approach of Menge et al. (2007). Mortality data were square root-transformed, thus obtaining good fits ($r^2 \geq 0.762$) of all relationships to the linear model. The slope of the regression could thus be taken as an appropriate measure of mortality. An analysis of variance (ANOVA), using temperature as a three-level-treatment and the slope of the regression as the response variable was used to test for effects of temperature on mortality of each species. Significant differences for between-levels were tested by the Tukey post-hoc-Test. Previously, the Shapiro–Wilk test and Barlett's test were used to assess normality and homogeneity of variances to meet ANOVA and ANCOVA assumptions respectively.

3. Results

3.1. Growth rate

Growth rate of *D. obesulus* was significantly dependent on shell size, with larger clams showing lower growth rates, and revealing significant differences between temperatures (Table 1, Fig. 2). Growth was fastest under NTC, followed by ENTC and slowest at LNTC. There was no significant interaction between temperature and shell size, and within aquaria variability was not significant. Post-hoc comparisons showed significant differences between NTC and LNTC and between ENTC and LNTC (Tukey test; $p < 0.01$; $p = 0.012$ respectively), but no differences between NTC and ENTC (Tukey test: $p = 0.497$).

Table 1
Results of ANCOVA performed on *Donax obesulus* and *Mesodesma donacium* growth rate, with temperature as the main factor and shell size as the covariant. Significant probability values are highlighted in bold.

Source of variation	DF	Sum of Squares	F-ratio	Prob > F
Donax obesulus				
Temperature (T)	2	8.865	9.215	**<0.001**
Shell size (SL)	1	5.627	11.698	**0.001**
T × SL	2	2.234	2.993	0.104
Aquaria [T]	6	3.751	4.215	0.061
Error	84	40.405		
Mesodesma donacium				
Temperature (T)	2	16.591	7.936	**<0.001**
Shell size (SL)	1	11.317	10.827	**0.001**
T × SL	2	20.425	9.770	**<0.001**
Aquaria [T]	6	1.799	0.2869	0.941
Error	74	77.346		
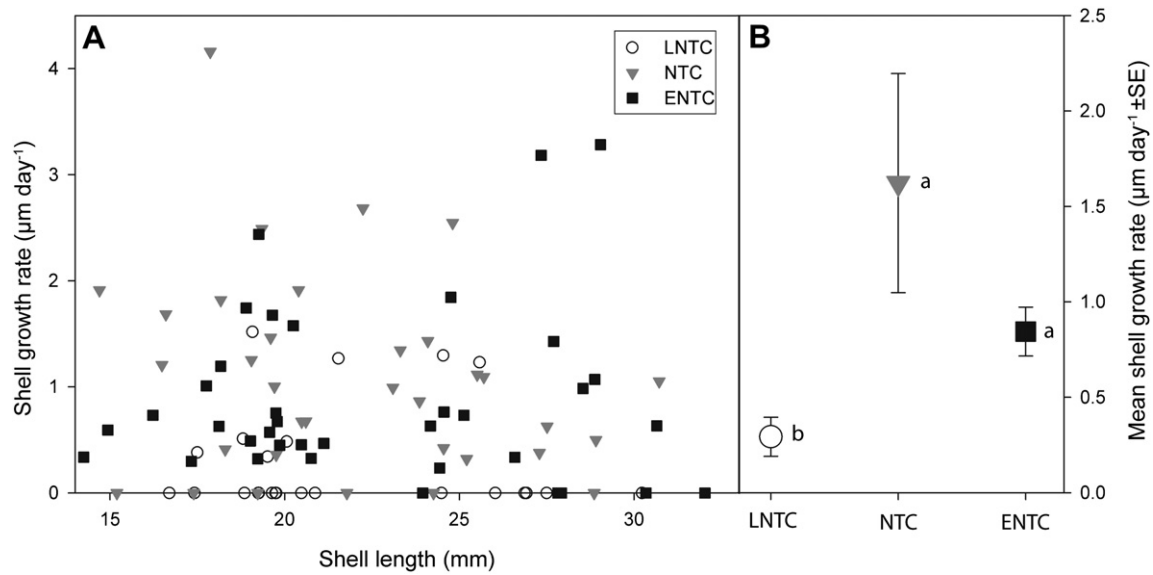
Fig. 2. (A): Shell growth rate (μm day^{-1}) of *Donax obesulus* under three different experimental temperature conditions: normal (NTC), La Niña (LNTC) and El Niño (ENTC). (B): comparison of mean shell growth rates (±Standard Error) for each temperature condition. Levels not sharing the same letters are significantly different (Tukey's test, $p < 0.05$).

The growth rate of *M. donacium* was inversely correlated to shell size and showed significant differences between temperature regimes (Table 1, Fig. 3). A significant interaction between temperature and shell size was detected (Table 1), indicating that differences between temperatures were less clear among larger clams. Multiple *a posteriori* comparisons showed that growth rate of *M. donacium* differed significantly between NTC and LNTC and between NTC and ENTC (Tukey test; $p = 0.021$; $p < 0.01$, respectively), but did not differ between LNTC and ENTC (Tukey's HSD test: $p > 0.864$).

3.2. Mortality

Mortality of *D. obesulus* revealed significant differences between experimental temperatures (Table 2), being higher and earlier at LNTC (Fig. 4). Post-hoc comparisons showed significant differences between NTC and LNTC and between ENTC and LNTC (Tukey test; $p < 0.01$, $p = 0.02$, respectively) but no significant differences between NTC and ENTC (Tukey test; $p = 0.87$). This species showed high sensitivity to LNTC, with high mortality after 48 h of exposure and 100% mortality after three weeks. In contrast, under NTC and ENTC, a few dead specimens were observed after four days, rising slightly until day 18. Mortality did not exceed 15% at the end of the experiment.

M. donacium was comparatively more resistant to changing temperatures than *D. obesulus* (Fig. 4). Our analysis revealed significant differences in mortality rates of *M. donacium* between experimental temperatures (Table 2). Tukey tests showed significant differences between LNTC and ENTC ($p < 0.01$) and between NTC and ENTC ($p < 0.01$). In contrast, no differences were found between LNTC and NTC (Tukey test; $p = 0.91$) as all clams survived until the end of the experiment (Fig. 4). Under ENTC *M. donacium*
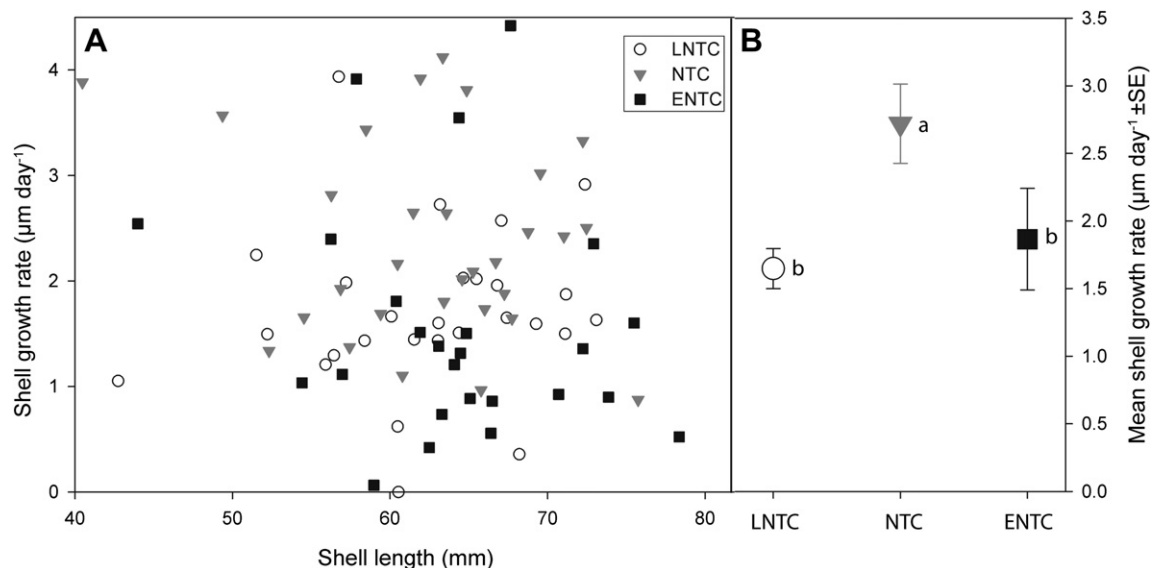
Fig. 3. (A): Shell growth rate (μm day^{-1}) of *Mesodesma donacium* under three different experimental temperature conditions: normal (NTC), La Niña (LNTC) and El Niño (ENTC). (B): comparison of mean shell growth rates (±Standard Error) for each temperature condition. Levels not sharing the same letters are significantly different (Tukey's test, $p < 0.05$).

Table 2
Results of ANOVA performed to test differences of mortality of *Donax obesulus* and *Mesodesma donacium* among three temperatures. Significant probability values are highlighted in bold.

Source of variation	DF	Sum of squares	F-ratio	Prob > F
Donax obesulus				
Temperature	2	0.0002	7.3095	**0.0246**
Error	6	0.0001		
Mesodesma donacium				
Temperature	2	0.0014	42.0577	**<0.001**
Error	6	0.0001		

showed a slight increase in mortality after the tenth day with a constant trend until day 17, thereafter increasing to 67% until the end of the experiment (Fig. 4).

As indicated by the LT_{50} values, *D. obesulus* responded much faster to temperature changes compared to *M. donacium*. The former species reached LT_{50} under LNTC after eight days, whereas LT_{50} of *M. donacium* under ENTC was reached at day 27 of the experiment (Fig. 4). No other level of the treatment resulted in 50% of mortality during the experimental period.

4. Discussion

Temperature has been considered the most significant abiotic factor controlling growth, reproduction, nutrition and other physiological processes in marine bivalves, (Laudien et al., 2001; Heilmayer et al., 2004; Miyaji et al., 2007; Riascos et al., 2009). SST in the costal HCS shows little seasonal variability and similar conditions over a broad range of latitudes. Therefore marine species are sensitive to anomalous thermal changes (Urban, 1994; Camus, 2001; Riascos et al., 2009). This study showed a high, contrasting sensitivity to short-term anomalous temperatures, with sublethal and lethal effects in both species. While *D. obesulus* was sensitive to LNTC, and tolerant to ENTC, *M. donacium* was sensitive to both ENTC and LNTC.

In general, the present results support the hypothesis that temperature is an important factor causing regime shifts during EN. In the period before and during EN 1982–1983 Arntz et al. (1987) followed recently-recruited cohorts of *D. obesulus* off southern Lima ($\sim 12°$S). This species showed significantly reduced growth when SST peaked in February and March 1983, but was able to survive this strong warming event (Arntz and Fahrbach, 1991). In contrast, *M. donacium* populations exhibited mass mortality when

SST peaked. Interestingly, in that studies, specimens of *M. donacium* were seen to open their shells a few days before they died, coinciding with observations made under laboratory conditions in the current study. Accordingly, the local extinction of *M. donacium* described above and the survival of *D. obesulus* after strong EN was observed repeatedly elsewhere off Peru and northern Chile (Tomicic, 1985; Arntz et al., 1987; Carbajal et al., 1995; Aburto and Stotz, 2003; Quiroz et al., 2006; Thiel et al., 2007; Riascos et al., 2009). A southward extension of the geographic distribution of *D. obesulus* has been reported following EN warming, enabling this species to temporarily reach as far south as $\sim 23°$S (Tomicic, 1985; Carbajal et al., 1995), about 800 km south of its current southern distribution limit.

Despite the fact that the present results reflect responses to extreme values of a single factor and that they are spatially limited to one end of the current species distribution boundaries they may provide insights into the mechanism underlying observed changes related to EN events. However, for most EN/LN episodes, SST anomalies may be far less extreme, and species may also be affected by other factors which may either reduce or increase any potential negative temperature effects, depending on the physical characteristics of the locality. On the other hand, this study provides insights into the responses of *D. obesulus* and *M. donacium* to LN, which have been only marginally addressed in previous studies. One striking aspect of the results is that although the two clams showed opposite responses to ENTC, they both seem to be sensitive to LNTC, showing slower growth in comparison with NTC. This is probably the reason why (i) *D. obesulus* has been unable to establish viable populations within southern areas colonized during EN (Tomicic, 1985), and (ii) remnants of *M. donacium* populations are not able to rapidly recolonize northern beaches during LN (Arntz et al., 1987, 2006), as would be expected under a contrasting response pattern. Despite the fact that *D. obesulus* and *M. donacium* are sympatrically distributed along large parts of the coastal HCS, their biogeography reflects different environmental affinities, which may explain their contrasting responses to the extremes of ENSO cycle. The family Donacidae primarily inhabits warm areas, with most of the living species (>75%) restricted to the tropics (Ansell, 1983). *D. obesulus* most likely represents a species of tropical affinity with adaptations to cooler waters. It is thus able to survive during strong EN and to expand temporarily southwards, but hampered in its ability to establish viable populations in those areas under LN conditions. In contrast, recent species of the family Mesodesmatidae generally inhabit cold and temperate waters (Marins and Levy, 1999; Beu, 2006). Therefore, the distribution and population stability of *M. donacium* seem closely linked to the interannual thermal variability associated to ENSO in the HCS (Riascos et al., 2009).

Shallow-water molluscs display significant changes in abundance associated to ENSO (e.g. Arntz and Fahrbach, 1991; Arntz et al., 2006; Thiel et al., 2007). Table 3 shows changes in abundance reported for several shallow-water molluscs distributed along the HCS (Fig. 1). Clearly, all these species show a strong nexus between their tropical/temperate origin and their changing abundance during EN (Fig. 1). Although studies exhibiting changes in abundance associated with LN appear to be almost non-existent, the present results suggest that such changes may also be dependent on biogeographical affinity. On the other hand, distributional ranges are similar for all species of tropical origin. These molluscs (Table 1) inhabit exclusively the first biogeographical unit (Thiel et al., 2007), reflecting the distributional range of *D. obesulus* (Thiel et al., 2007; Fig. 1 and Table 1). Conversely, all temperate species inhabit mainly the area of the second and third biogeographical unit (Thiel et al., 2007; Fig. 1 and Table 1), as in the case of *M. donacium*.
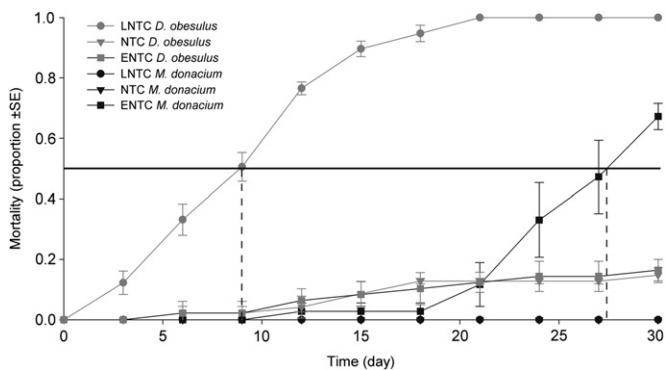
Fig. 4. Mortality of *Donax obesulus* and *Mesodesma donacium* under three different experimental temperature conditions: normal (NTC), La Niña (LNTC) and El Niño (ENTC). Vertical dashed lines indicate LT_{50} values for *M. donacium* (right) and *D. obesulus* (left).

Table 3
Effects of El Niño events on population abundance (decrease (↓); increase (↑) of shallow-water molluscs of the Peruvian and Chilean coast (Arntz and Tarazona, 1990).

Species (affect EN)	Origin	Distribution	References
❶ *Donax obesulus* (↑)	tropical	0°26′S to 23°05′S	Olsson (1961); Coan (1983)
❷ *Argopecten purpuratus* (↑)	tropical	0°55′S to 29°57′S	Wolff (1987); Guzmán et al. (1998b)
❸ *Thais chocolata* (↑)	tropical	05°04′S to 33°02′S	Keen (1971); Guzmán et al. (1998b)
❹ *Mesodesma donacium* (↓)	subantarctic	16°36′S to 42°23′S	von Ihering (1907); Tarifeño (1980)
❺ *Semimytilus algosus* (↓)	temperate	03°34′S to 36°54′S	Olsson (1961); Caro and Castilla (2004)
❻ *Aulacomya ater* (↓)	temperate	12°03′S to 52°46′S	Jaramillo and Navarro (1995); Guzmán et al. (1998b)

The responses to changing temperature regimes depicted here may also operate at larger temporal scales. Inter-decadal shifts in the biological regimes of pelagic ecosystems corresponding to shifts in fundamental physical properties of the HCS are now being recognized (e.g. Bakun and Broad, 2003; Chavez et al., 2003; Montecinos et al., 2003; Ayón and Swartzman, 2008). Although no attempt has been made to evaluate potential effects in coastal populations of the HCS, a strong effect seems feasible (Southward et al., 1995). Moreover, the hypothesized increase in the frequency of ENSO under a scenario of ongoing global warming (Timmermann et al., 1999) may significantly affect current distribution and abundance patterns of coastal species in the HCS.

Even though our results support the hypothesis of a strong link between temperature tolerance, anomalous temperature and distribution shifts of *D. obesulus* and *M. donacium*, we cannot expect those shifts to be explained solely in terms of this relationship. There are several further biotic and abiotic processes that have to be taken into account for a proper understanding of the biological responses of these species to ENSO. A whole array of abiotic factors is modified during ENSO, notably salinity, wave action, sediment load, upwelling strength and hence nutrient and food availability, which act simultaneously to produce an integrated effect on these species (e.g. Arntz et al., 2006) that may be difficult to address in experimental studies.

Interspecific interactions play an important role in defining population processes and community structure in sandy beach ecosystems (see review by Defeo and McLachlan, 2005). These interactions may be significantly modified under strong environmental stress and may modulate the responses of species to the extremes of ENSO. These interactions may be implicated in the poor ability of *M. donacium* to recover its former abundance and distribution and in the inability of *D. obesulus* to thrive at southern beaches in the wake of EN events. However, it is not clear whether competition occurs between these clams: After the mass mortality of *M. donacium* in Peru during EN 1982–1983, *D. obesulus* and the mole crab *Emerita analoga* never reached the density formerly attained by *M. donacium*; instead, an impoverished community consisting mainly of small opportunistic polychaetes became established, leading Arntz et al. (1987) to suggest that no competition exists between these commonly dominant species. On the other hand, the parasitic association between *M. donacium* and the spionid *Polydora bioccipitalis* may also play a role in the process of recovery of abundance and distribution range after strong warming events (Riascos et al., 2008).

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