

Analysis of the potential geographic range of the Pacific oyster *Crassostrea gigas* (Thunberg, 1793) based on surface seawater temperature satellite data and climate charts: the coast of South America as a study case

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Abstract Ecological niche modeling based on surface seawater (SST) and atmospheric (AT) temperature records was used to predict the potential range of distribution of *Crassostrea gigas*, focusing on the South American coast as a study case. In its native range, the species maintains self-sustaining populations at thermal regimes with mean SST ranging from 14.0° to 28.9°C for the warmest month and from –1.9° to 19.8°C for the coldest month of the year. Settlement is also constrained to mean AT varying between 15° and 31°C for the warmest month and between –23° and 14°C for the coldest month of the year. Latitudinal limits for the species' distribution in South America predicted by the analysis of AT regimes were Valdivia-Chiloe Island (39.8°–42.0°S, Chile) and Pisco (13.4°S,

Peru) on the Pacific coast, and San Julian port (49.3°S) (Argentina) and Garopaba-Rio Grande (28.0°–32.0°S, Brazil) on the Atlantic coast. Geographical limits of distribution predicted by analysis of SST regimes were Chiloe Island (42.0°S, Chile) and Mancora (4.1°S, Peru) on the Pacific coast, and Puerto Deseado ria (47.7°S, Argentina) and Paranaguá (25.7°S, Brazil) on the Atlantic coast. Therefore, SST regimes would expand the potential range on the Pacific coast equatorward relative to AT.

Keywords Ecological niche modeling · Non-indigenous species · Temperature range · Ecological risk · Oyster introduction

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Introduction

The Pacific cupped oyster *Crassostrea gigas* is a widely introduced species, which has established naturalized populations in many countries where introduced for aquaculture (Chew 1990; Ruesink et al. 2005). Even though its ecological impacts on native species and major ecosystem functions are widely recognized (Shatkin et al. 1997; Molnar et al. 2008), and notwithstanding that prevention of its introduction should be considered the most effective strategy to protect native communities (Leung et al. 2002), pressure generated by the expansion of aquaculture activities worldwide has not only caused

new unintended and deliberate inoculations but also resulted in the extension of invaded geographical ranges of distribution (Andrews 1980; Naylor et al. 2001).

The introduction of non-indigenous species (NIS) is of particular concern in South America, where they constitute approximately 70% of aquaculture production (FAO 2008a). During the last quarter century, *C. gigas* was introduced to several South American countries, including Chile (VI, V and X Regions, 30°, 32° and 42°S), Peru (Guaynumá Bay, 9°S), Ecuador (Caraquez Bay, 2°S) along the Pacific coast, and Argentina (Anegada Bay, 40°S) and Brazil (states of Bahia, 13°S; Rio de Janeiro, 21°S; São Paulo, 25°S, and Santa Catarina, 27°S) on the Atlantic coast (CPPS 1998; Möller et al. 2001; Orensanz et al. 2002; Ruesink et al. 2005; Melo et al. 2009). For Chile, Peru and Ecuador there is no published information on the establishment of wild populations, even when some of these countries are reporting high commercial production (FAO 2008b; Sernapesca 2007). In Argentina, the species was placed in Anegada Bay (40°S) in 1982, but aquaculture was soon abandoned; 10 years later, a wild population was discovered (Orensanz et al. 2002; Escapa et al. 2004; Borges 2006). Since then, it has spread both north (Tres Bonetes Hill, 40°S) and south (Punta Bermeja, 41°S) (Borges 2006; personal observations by the authors), affecting the geomorphology of coastal areas with high recreational value. In Brazil, the presence of 27 populations in Santa Catarina State (27°S) has just been confirmed (Melo et al. 2009).

Frequently stated arguments in support of marine NIS translocations for aquaculture into new coastal areas rest on the assumption that thermal conditions of the selected sites will inhibit gonad maturation, avoiding the uncontrolled settlement of naturalized populations (Mann et al. 1991; Shatkin et al. 1997). For *C. gigas* in particular, seawater temperature is a likely abiotic control on establishment because the lower threshold for gamete release is approximately 16°C and diseases appear problematic above 30°C (Ruiz et al. 1992; Shatkin et al. 1997). Atmospheric temperature could have an additional effect on intertidal oysters, particularly via heat stress or freezing, resulting in juvenile or adult mortality (Evans and Langdon 2006; Zhang et al. 2006). Unfortunately, studies on the ability of NIS to establish in sites of new aquaculture projects often

fail to take into consideration long-term environmental variability or trends (Diederich et al. 2005). Methodological approaches to predict the success of NIS introductions include: (1) comparative historical analysis of past introductions (Sol et al. 2008); (2) examination of physical means or agents by which species are transported (vector science) (Carlton and Ruiz 2002; Mineur et al. 2007); (3) ecological niche modeling (Herborg et al. 2007), and (4) development of risk assessments using complex conceptual models (Colnar and Landis 2007). Ecological niche modeling is based on the determination of the environmental burdens conditioning the presence of a species within its native range and their extrapolation to invaded regions (Peterson 2003), being perhaps the most appropriate method to predict large ranges of latitudinal distribution of NIS.

In the particular case of South America no projections of the potential for a geographic expansion of *C. gigas* are available for the administration sectors to implement decision rules allowing or denying introductions to new locations. Taking this into consideration, the objective of the present work is to evaluate the thermal limits of distribution of the species around the world and based on them, to project the potential invaded range of *C. gigas*, particularly along the coasts of South America. In our analysis, we assume that only seawater and atmospheric temperatures experienced by native and naturalized populations of *C. gigas* are suitable for establishment.

Methods

A search was conducted to gather information on the geographic distribution of *C. gigas*, including its native range, the areas where the species was introduced and established naturalized populations, and the localities where it was introduced but did not succeed in establishing. Data was obtained from the literature and from consultation with experts (Table 1). Considering this information, SST regimes were analyzed for the period 1997–2006 at selected geographic points based on estimations (single 4 × 4 km grid cells closest to the point of interest, including no land) available in public access databases (AVHRR Pathfinder 5, NOAA-NASA). SST was estimated for each location and any given month of the year by least-square non-linear regression of the function

Table 1 List of references and experts consulted to determine the present distribution of *Crassostrea gigas* in its native range and other regions where the species has been introduced

Location and country	References and experts	Experts affiliation
Belgium	Ruesink et al. 2005	
Isefjord, Denmark	Wang et al. 2007	
Norway	Nehring 2006	
	Wrangle et al. 2009	
Sweden	Wrangle et al. 2009	
Puerto Rico	Ruesink et al. 2005 Chew 1990 FAO/FIGIS 2009	
Iceland	Nehring 2006	
Greenland	Nehring 2006	
Namibia	Robinson et al. 2005 Jennifer Ruesink	University of Washington, USA
Witsand, South Africa	Robinson et al. 2005	
Anegada Bay, Argentina	Orensan et al. 2002 Borges 2006	National Patagonian Center, Argentina
Seychelles	Authors of this paper Ruesink et al. 2005 FAO/FIGIS 2009	
Los Angeles, USA	Cohen et al. 2005	
Alaska, USA	Graham Gillespie	Pacific Biological Station, Fisheries & Ocean, Canada
British Columbia, Canada	Graham Gillespie	Pacific Biological Station Fisheries & Ocean, Canada
De-Kastri Bay, Russia	Scarlato 1981 Sirenko et al. 1988 Kolpakov 2006 Konstantin Lutaenko Nina Grigoryeva Yuri Yakovlev	A.V. Zhirmunsky Institute of Marine Biology, Far East Branch of Russian Academy of Sciences, Russia
Cape Mariya, Russia	Yuri Yakovlev	A.V. Zhirmunsky Institute of Marine Biology, Far East Branch of Russian Academy of Sciences, Russia
Petropavlovsk, Russia	Kolpakov 2006	
Guam	Ruesink et al. 2005	
Hawaii	Coles et al. 1999	
Hong Kong, China	Yutaka Honda Wayne O'Connor Higo et al. 1999	Mie University, Japan Port Stephens Fisheries Institute, Australia
New Zealand	Ruesink et al. 2005 Chew 1990 FAO/FIGIS 2009	
Vietnam	Wayne O'Connor O'Connor 2005	Port Stephens Fisheries Institute, Australia
Peru	Percy A. Gallegos Carlos Paredes	San Marcos Mayor National University, Peru

Table 1 continued

Location and country	References and experts	Experts affiliation
Chile	Möller et al. 2001 Patricia Möller	CEA, Chile
Ecuador	Mare Cornejo	CENAIM-ESPOL Foundation, Ecuador
Western Australia	Wayne O'Connor	Port Stephens Fisheries Institute, Australia
New South Wales, Australia	Wayne O'Connor	Port Stephens Fisheries Institute, Australia
Tahiti	Ruesink et al. 2005 Bourne 1979	
Antarctica	NRC 2004	

$$\text{SST}(t) = T_0 + T_1 \cos[w(t - t_0)],$$

to the corresponding SST series, where T_0 is the annual mean temperature, T_1 is the amplitude of the seasonal cycle, $w = 2\pi/12$ month, t is the time in months counted from 1 January and t_0 is the phase that coincides with the month of the year in which temperature is maximum (T_0 , T_1 and t_0 are parameters to be estimated). These functions use the whole SST time series, providing reliable estimations for monthly mean SST when some data are missing from the satellite registers (due to cloud or ice cover). Based on them, the predicted temperatures during the warmest and coldest months of the year were calculated for each location. At sites where the sea surface is covered by ice during part of the year (no data on the SST satellite registers), estimated functions deviated from SST data. Therefore, months presenting SST close to the freezing point (-1.9°C for 35-psu-seawater) were excluded when fitting the functions. For these locations, seawater temperature during the coldest month of the year was considered as that of the freezing point. Except for the localities placed between the tropics and close to the polar circles, where SST year amplitudes are approximately 3°C or less, coefficients of determination (R^2) of the function adjustments ranged between 0.70 and 0.97. Also, considering that *C. gigas* is an intertidal organism in direct contact with air during variable periods of the day, mean monthly atmospheric temperatures (AT) for the warmest and coldest months of the year were obtained for each location from Climate Charts Qwikcast (<http://qwikcast.weatherbase.com/>) and (<http://climexp.knmi.nl/>) databases. Since these provide averaged monthly mean AT for all the years on record, and reported values are based on continuous thermometer

registers, fitting functions like those used to estimate SST regimes was neither possible nor necessary. Scatterplots for the relationships of predicted SST of the warmest month on that of the coldest month were drawn based on 10-year averaged data for each location. Similarly, the relationship of mean AT of the warmest month on that of the coldest month was based on at least 10-year average data series. Based on their analysis, thermal ranges suitable for the species to establish populations were determined. Finally, the potential geographic range of distribution of naturalized populations of *C. gigas* in South America was estimated by comparing 10-year temperature records (both SST and AT) at several locations along the Atlantic and Pacific coasts with the thermal burdens limiting the establishment of the species elsewhere.

Results

The native range of distribution of *C. gigas* extends from Cape Mariya (Russia) to Hong Kong (China) (Fig. 1; Table 1). There, wild populations of the species are present in locations with predicted SST between 14.0° and 28.6°C for the warmest month of the year, and between -1.9° and 19.8°C for the coldest month (Fig. 1). Within this range mean AT varies between 15° and 31°C for the warmest month and between -23°C and 14°C for the coldest month of the year (Fig. 1). These extreme temperatures delimit the thermal conditions at the areas where the species has established naturalized populations out of its native range (Fig. 1), except for some inlets off Vancouver Island (Canada), where SST of the warmest month averages 13.5°C (Fig. 1).

On the Pacific coast of South America, the geographic range with SST suitable for *C. gigas* to establish extends from Mancora (Peru, 4.10°S) to Chiloé Island (Chile, 42.13°S) (4,210-km wide on a straight line) (Figs. 2, 3). On the Atlantic coast, this range spans from Paranaguá (Brazil, 25.69°S) to Puerto Deseado (Argentina, 47.75°) (2,885-km wide) (Figs. 2, 3). With respect to AT, the potential geographic range extends from Pisco (Peru, 13.45°S) to a locality between Valdivia (Chile, 39.82°S) and Chiloe Island (42.13°S) on the Pacific coast (approximately 3,000-km wide), and from Rio Grande (Brazil, 32.01°S) to San Julián Port (Argentina, 49.30°S) (2,330-km wide) on the Atlantic coast (Figs. 2, 3). Equatorward of the predicted northern limits set by SST and AT, winter temperatures do not drop sufficiently to fall below the maximum tolerated by the oysters (Figs. 2, 3). Poleward of the southern limit, summer temperatures do not become sufficiently high to exceed the minimum apparently required for establishment (Figs. 2, 3).

Discussion

In recent decades, *C. gigas* has been introduced to coastal waters of all continents but Antarctica (NRC 2004). Even though the distribution of the species around the world has been documented by several authors (FAO/FIGIS 2009; Ruesink et al. 2005), there are no projections on the geographical range the species could occupy in the future.

The Pacific cupped oyster is such a commercially appreciated species that it has been introduced as a substitute for overexploited native bivalves to protect local economies (Shatkin et al. 1997). This is the case of the Valdivia estuary in Chile (CPPS 1998; Möller et al. 2001), Ancash Bay in Perú (Gallegos, Personal Communication), and the Entrada and Ayanque bays and coast of the El Oro Province in Ecuador (Cornejo, Personal Communication) (Fig. 3). This viewpoint is particularly concerning because, although culturing the species may benefit a sector of the economy, it would negatively affect many activities at the local and regional scales, such as tourism, fishing (angling and seining) and marine industrial activities (e.g., fouling on heat exchangers), and may expose intertidal systems to threats such as the modification of the geomorphology (e.g., reduction of the transverse

section of coastal channels and covering of limestone terraces), the transmission of diseases (viral and bacterial), and negative interactions with native benthic species (Shatkin et al. 1997; Orensanz et al. 2002; Rajagopal et al. 2005; McKinsey et al. 2007). Particularly for the coast of Chile it has been stated that *C. gigas* will not establish self-sustaining populations due to the unsuitability of the local temperature ranges (CPPS 1998). In Argentina, based on the same assumption, hatchery produced spat (CRIAR Program, IBMyP Almirante Storni) were planted on the coasts of Patagonia (Caleta Olivia, San Julián port and Rio Gallegos) (Orensanz et al. 2002) (Fig. 3). Our analysis shows that in both regions the species may establish wild populations (Fig. 3).

Since *C. gigas* is a predominantly intertidal species, and considering that: (1) SST in intertidal environments tends to be modified by AT, and (2) oysters are in direct contact with the atmosphere during part of the tidal cycle, we incorporated AT in our analysis. According to the results of our analysis, latitudinal limits imposed by this variable at the southern and northern extremes of distribution of *C. gigas* on the Atlantic coast of South America are approximately the same as those set by SST. In contrast, on the Pacific coast AT constrains the distribution of the species to a much narrower latitudinal range than SST (Fig. 3). Along the Atlantic coast off South America, where shallow continental slope and wind stress generate a thermally-homogeneous well-mixed seawater upper layer, a higher similarity between SST and AT is observed in comparison to the Pacific coast (Greenland 2005). There, a more abrupt depth change in the continental slope, along with prevailing wind direction and the presence of the cold water Humboldt Current, allows the upwelling of cold water from bottom layers, resulting in a decoupling between SST and AT (Greenland 2005). As an outcome, SST at a given latitude is lower on the Pacific coast of South America than on the Atlantic coast, resulting in an extension of the northern boundary of the range of potential distribution of *C. gigas* on the Pacific coast, as predicted by our analysis of SST regimes (Figs. 2, 3). On the other hand, although potential ranges of distribution of the species set by AT are similar in extension on both coasts, the Pacific coast distribution is displaced northward compared to the Atlantic. This difference is due to the presence of permanent anticyclonic atmospheric gyres driving warm tropical air

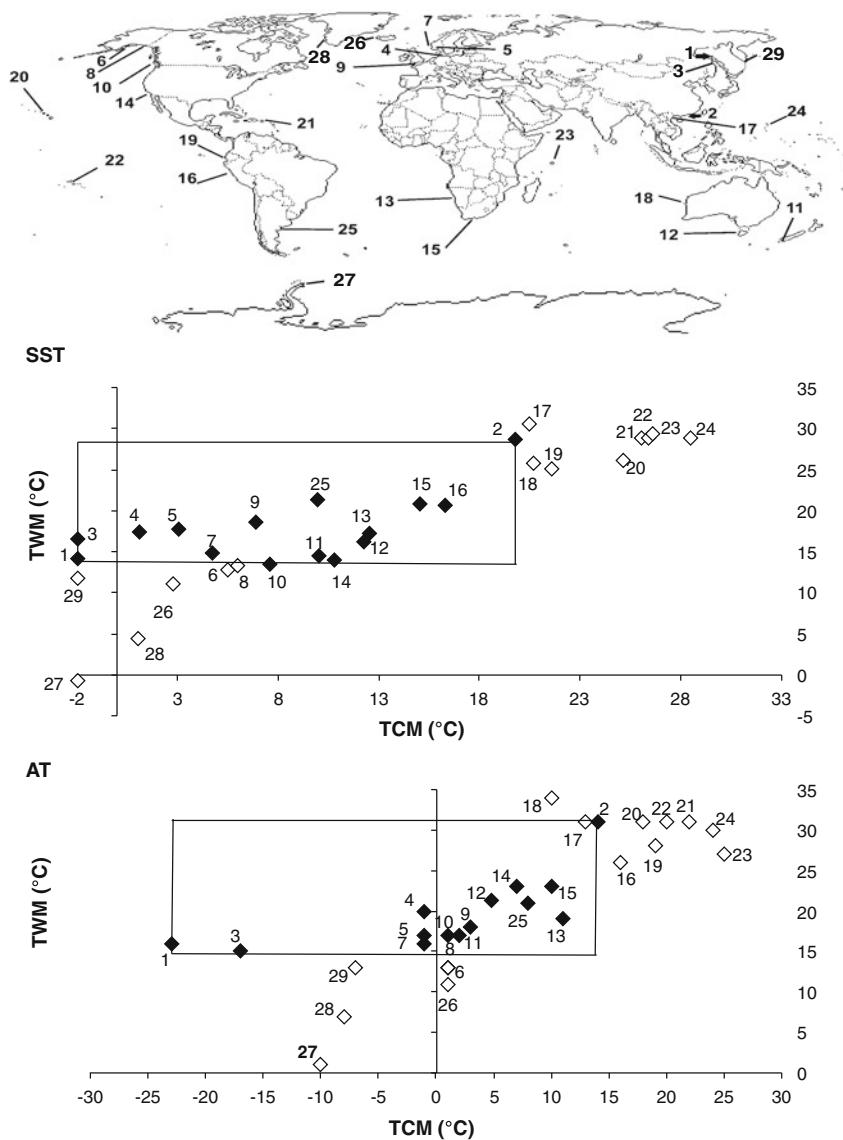


Fig. 1 Scatterplot of predicted temperatures of the coldest month (TCM) on predicted temperatures of the warmest month (TWM) at locations with confirmed presence of naturalized populations of *Crassostrea gigas* (black diamonds), and confirmed absence (empty diamonds). *Upper*: World map showing geographical positions of localities for which SST and AT regimes were analyzed; *Middle*: Surface seawater temperature (SST) estimations based AVHRR Pathfinder 5, NOAA-NASA database; *Lower*: Atmospheric temperature (AT) estimations based on Qwikcast and Climate Charts databases. 1. Cape Mariya (Sakhalin Island—Russia); 2. Hong Kong (China); 3. De-Kastri Bay (Russia); 4. Isefjord (Denmark); 5. Kragerø Port (Norway); 6. Coffman Cove (Southern Alaska, USA); 7. Fedje (Norway); 8. Dundas Island (British Columbia, Canada); 9. Le Havre (France); 10. Vancouver Island

(Canada); 11. Ruapuke Island (New Zealand); 12. Western Tasmania (Australia); 13. Walvis Bay (Namibia); 14. Los Angeles (California, USA); 15. Witsand (South Africa); 16. Gauynamá Bay (Perú); 17. Cat Ba (Vietnam); 18. Bernier Island (Western Australia); 19. Caraquez Bay (Ecuador); 20. Honolulu (Hawaii); 21. Puerto Rico; 22. Tahiti (French Polynesia); 23. Seychelles Islands; 24. Guam; 25. Anegada Bay (Argentina); 26. Iceland; 27. Esperanza Base (Antarctic Peninsula); 28. Nuuk (Greenland); 29. Petropavlovsk (Russia). *Rectangle* in the middle and lower graphs enclose temperature regimes at locations suitable for the establishment of wild populations of the Pacific cupped oyster. *Black arrows* in the upper graph indicate the latitudinal limits of the native range of distribution of *C. gigas*

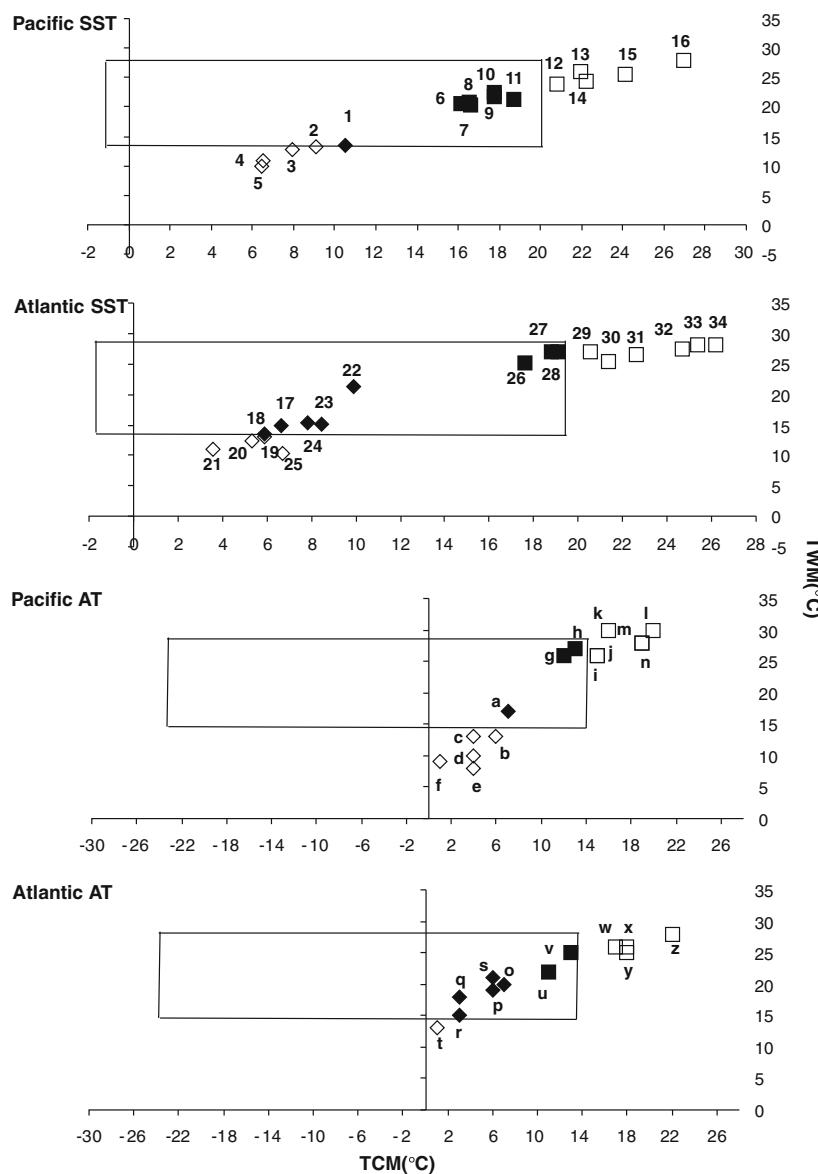


Fig. 2 Scatterplots of predicted temperatures of the coldest month (TCM) on predicted temperatures of the warmest month (TWM), showing the thermal regimes at different localities along the coast of South America, and comparison with the thermal thresholds (rectangle) constraining the presence of wild populations of *Crassostrea gigas*. Squares and diamonds respectively represent locations at the northern and southern boundaries of the potential range of distribution of the species. Full and empty symbols respectively represent localities with thermal regimes within or outside the thermal thresholds suitable for settlement of naturalized populations of the Pacific cupped oyster. SST Pacific: 1. Chiloe Island; 2. Isquilac Island; 3. Campana Island; 4. Contreras Island; 5. London Island; 6. Callao; 7. Chilcayo; 8. Trujillo; 9. Sechura; 10. Paita; 11. Talara; 12. Mancora; 13. Pongalillo Port; 14. Santa Elena; 15. Manta; 16. Esmeraldas. SST Atlantic: 17. Comodoro Rivadavia Port; 18. Puerto Deseado Ria; 19. Laura Bay; 20. San Julián Port; 21. Río Gallegos Ria; 22. San Blas Bay; 23. Bustamante Bay; 24. Cape Blanco; 25. Mazaredo Port; 26. Garopaba; 27. Florianopolis Island; 28. Paranaguá; 29. Guarujá; 30. Rio de Janeiro; 31. Aracruz; 32. Texeira de Freitas; 33. Salvador; 34. Maceió. AT Pacific: a. Valdivia; b. Chiloe Island; c. Isquilac Island; d. Campana Island; e. Contreras Island; f. Hoste Island; g. Ilo; h. Pisco; i. Lima; j. Paita; k. Talará; l. Mancora; m. Pongalillo Port; n. Santa Elena. AT Atlantic: o. Puerto Madryn; p. Comodoro Rivadavia Port; q. Puerto Deseado Ria; r. San Julián Port; s. San Blas Bay; t. Río Gallegos Ria; u. Chui; v. Rio Grande; w. Florianopolis Island; x. Paranaguá; y. Guarujá; z. Rio de Janeiro

Manta; 16. Esmeraldas. SST Atlantic: 17. Comodoro Rivadavia Port; 18. Puerto Deseado Ria; 19. Laura Bay; 20. San Julián Port; 21. Río Gallegos Ria; 22. San Blas Bay; 23. Bustamante Bay; 24. Cape Blanco; 25. Mazaredo Port; 26. Garopaba; 27. Florianopolis Island; 28. Paranaguá; 29. Guarujá; 30. Rio de Janeiro; 31. Aracruz; 32. Texeira de Freitas; 33. Salvador; 34. Maceió. AT Pacific: a. Valdivia; b. Chiloe Island; c. Isquilac Island; d. Campana Island; e. Contreras Island; f. Hoste Island; g. Ilo; h. Pisco; i. Lima; j. Paita; k. Talará; l. Mancora; m. Pongalillo Port; n. Santa Elena. AT Atlantic: o. Puerto Madryn; p. Comodoro Rivadavia Port; q. Puerto Deseado Ria; r. San Julián Port; s. San Blas Bay; t. Río Gallegos Ria; u. Chui; v. Rio Grande; w. Florianopolis Island; x. Paranaguá; y. Guarujá; z. Rio de Janeiro

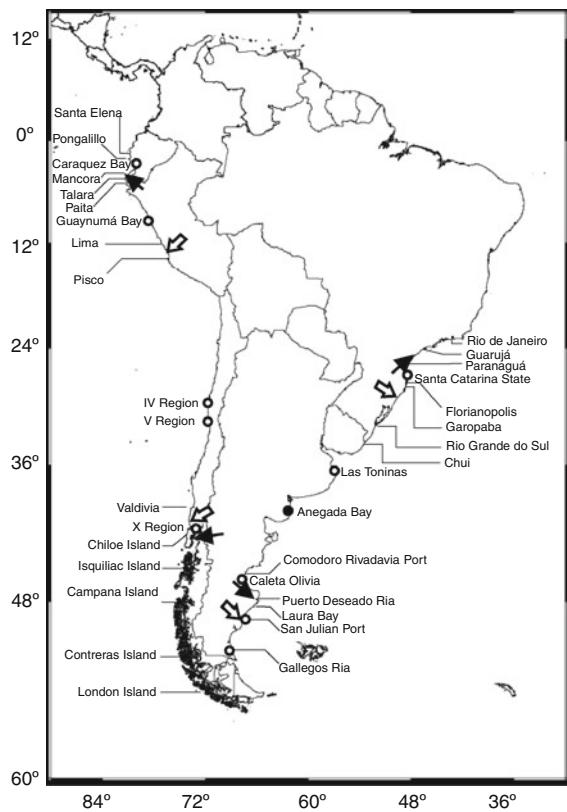


Fig. 3 Map of South America showing several coastal locations for which regimes of surface seawater temperature (SST) and atmospheric temperature (AT) were analyzed. Black arrows indicate the latitudinal limits of distribution of *Crassostrea gigas* set by SST; empty arrows show latitudinal limits imposed by AT; empty dots indicate localities where *C. gigas* has been introduced for aquaculture but no information is available on the settlement of naturalized populations; black dots show areas where naturalized populations of *C. gigas* have established

masses to the south along the Atlantic coast off South America and cold sub-Antarctic air masses to the north along the Pacific coast (Prohaska 1976). In regards to the direct effect of AT on *C. gigas*, recent experimental work has demonstrated that exposure to air temperatures due to the immersion/emersion cycles typical from intertidal environments causes stress in oysters (Zhang et al. 2006; Song et al. 2007). Furthermore, these experiments have shown that stress is higher in exposures to high air temperatures (Zhang et al. 2006).

Reviewing the literature allowed us to observe a geographic expansion of *C. gigas* in several regions where it was introduced (Robinson et al. 2005; Ruesink et al. 2005; Wang et al. 2007). On the coasts

of Vancouver Island and Pacific Canada, *C. gigas* has established naturalized populations up to 50.41°N, showing irregular settlement of postlarvae in several inlets at the margins of its current distribution depending on the summer temperatures attained in different years (Gillespie, Personal Communication). However, since Meyers et al. (1990) documented the attainment of maturity in specimens of *C. gigas* at a grow-out station located in southern Alaska (56.0°N, 132.8°W) during a warm summer season, the potential for a sporadic settlement of the species in that region should not be completely discarded. In Tomales Bay (California, USA), summer temperatures of approximately 25°C produce the activation of an herpesvirus, generating high seed mortality (Burge et al. 2007). Although it has been demonstrated that *C. gigas* can resist temperatures up to 35°C (FAO/FIGIS 2009; Wang et al. 2007), our analysis indicates that wild populations will not prosper in localities with mean seawater temperatures of the warmest month higher than 29.0°C. This finding is in agreement with the results reported by LeGall and Raillard (1988), who pointed out that juveniles of *C. gigas* attain a sub-lethal level, reflected in the lack of biochemical reserves and almost null growth, when acclimated at 30°C. On the Atlantic and Baltic coasts of northern Europe, the introduction of *C. gigas* was authorized after considering that low seawater temperatures would not allow the establishment of naturalized populations; however, high seawater temperatures in the warmest months of some years resulted in successful reproduction, and allowed it to establish in the Wadden Sea, at the margins of the Skagerrak and on the Atlantic coast off southern Norway (Diederich et al. 2005; Wang et al. 2007; Schmidt et al. 2008; Wrangé et al. 2009). On the coast of South Africa *C. gigas* is cultured from Alexander Bay to Kowie where it has set wild populations from Breed to Knysna (Robinson et al. 2005). Also, the species is cultured in Walvis Bay, Namibia (Robinson et al. 2005) where mean monthly seawater temperatures of the coldest and warmest months would allow wild populations to prosper. However, no evidence of spatfall settlement has been found yet in the region despite careful inspection of rocky outcrops and anthropogenic substrates (Ruesink, Personal Communication). In Southern Australia, the Pacific cupped oyster has established in New South Wales, Victoria and Tasmania (Chew 1990;

Ruesink et al. 2005). Though its presence has been reported for Western Australia (Ruesink et al. 2005), the seawater temperature regime at this region is out of the thermal thresholds found in our analysis. This contradiction led us to review the literature, and the presence of *C. gigas* in Western Australia is erroneous and based on a misinterpretation of the results reported by Thompson (Thomson 1952, 1959). Furthermore, after consultation with experts (O'Connor, Personal Communication) we confirmed that the species is not present in that region. In North Vietnam, where only the AT regime is suitable for the establishment of the species, no records are available on the presence of naturalized populations although it has been cultured since 2005 (O'Connor 2005; O'Connor, Personal Communication).

Intra-specific genetic adaptation to particular thermal conditions is a common phenomenon among marine organisms distributed along wide geographic ranges (Lucassen et al. 2006; Pernet et al. 2008). The adaptation acquired by *C. gigas* throughout evolution along its native range of distribution has generated a source of races adapted to colonize a variety of thermal niches (Andrews 1980; Shatkin et al. 1997). Therefore, import of *C. gigas* seed could pose a particularly high risk of establishment if it involved lines that were thermally pre-adapted to the recipient location (Andrews 1980; Diederich et al. 2005; Wang et al. 2007). Furthermore, ongoing breeding programs to obtain thermally resistant strains of *C. gigas* (e.g., MOREST project, IFREMER) (Delaporte et al. 2007) are likely to enhance the invasive capability of the species at the extremes of the potential ranges of distribution worldwide.

Since 16°C is recognized as a lower thermal limit for spawning in *C. gigas* (Mann et al. 1991; Ruiz et al. 1992), mean SST of the warmest month of the year seems too low at some locations where the species has established and even within the native. On one hand, SST satellite data used in our analysis reflect thermal regimes at near-coastal locations that could differ to some extent from that experienced by oysters at their growing areas, especially in estuaries and tidal flats. On the other hand, it must be taken into account that thermal boundaries used in this work are based on mean monthly temperatures averaged over several years, and that in warm-summer years individuals may experience temperatures higher than the average,

suitable for spawning, larval survival and settlement, as reported by Diederich et al. (2005).

Classic models to predict the potential range of distribution of *C. gigas* are based on the experimental examination of physiological limits imposed by seawater temperature for growth, reproduction and survival (Shatkin et al. 1997; CPPS 1998). In contrast, ecological niche modeling applications incorporate a combination of environmental variables in the analysis (Herborg et al. 2007; Therriault and Herborg 2008). The objective of the present work was to develop a simple model to obtain a first general prediction of the potential range of geographical distribution of *C. gigas* on the coast of South America. Although more complex models can incorporate statistical combinations of predictor variables (Elith et al. 2006), we did not determine whether SST, AT or a combination gives the best prediction. Until a better estimation is obtained, we recommend adoption of a precautionary approach by considering that the Pacific cupped oyster is capable of establishing naturalized populations within the broadest range predicted. Several other environmental variables should be incorporated in our analysis in the future to address further modification of the potential geographic occupation, including wave exposure (Ekebom et al. 2002), substrate type, geomorphology, tidal regime and salinity (Herborg et al. 2007). In the meantime, the method presented here provides a simple tool to assess the risk of deliberate introduction of *C. gigas* to any given locality, by simple inspection of its thermal regime and comparison with the boundaries we report.

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